THE EXCITABILITY OF FROG MUSCLE WITH PARTICULAR REFERENCE TO ITS LATENT ADDITION

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Muscle substance appears to possess distinct advantages over nerve for the study of the dependence of the process of electrical excitation on various reagents such as drugs and inorganic salts for not only is there more known about the disposition of such substances in muscle, but further knowledge is probably much more easily obtainable. Unfortunately, however, Keith Lucas' assignment of the $\alpha$ excitability to the muscle substance has not been wholly acceptable and in particular, it has been questioned whether the $\alpha$ strength-duration curve is a "true" curve, in the sense of whether or not it is the simplest procurable. On the other hand, the direct stimulation of muscle with wire electrodes almost certainly may involve the nerve (if it does not always do so, as many believe) so its use probably yields more information about nerve than muscle.

Since Rushton's (1930) extensive work on the subject, there seems to be little doubt that the $\alpha$ curve is of the muscle, but a decision on the other matter as to whether it is the least distorted by extraneous factors is more difficult to make, and there is probably no very general agreement on this question.

One method of attacking the problem is to assume that a given mathematical form for the strength-duration curve, e.g. that derived from data on nerve, is the simplest and least distorted, so that it may be used as a criterion for the "trueness" of other curves. Lapicque (1931a) in fact, used his canonical equation (1926)\(^1\) to show that the $\alpha$ excitability is not of the usual class. This conclusion can only be tentative, however, even though the canon is adequate for one excit-

\(^1\) Lapicque (1926), p. 214.
ability, because the "trueness" of the canon itself is only an assumption. In any case, however, the canon has been shown to represent some muscle data (Colle and Delville, 1932) and not to represent some nerve data (Lapicque, 1926; Rushton, 1932; Colle and Delville, 1932). It appears, therefore, to be an adequate representation only of special cases of both excitabilities and no definite conclusion can be drawn from its application.

Another method, the one to be used chiefly here, is based on a general property of the excitatory state. There is agreement now, that the excitatory process is not cumulative only, but that it is also dissipative. The rate of the dissipative or subsidence process is measured in some way or other by the various time factors of excitation, the usual measures of excitability. On the other hand, this subsidence is the factor which determines latent addition. Thus, there must be a correspondence between the time factor of excitation and the interval for latent addition which is determined by the rate of subsidence of the excitatory state left by an inadequate stimulus. Therefore, a tissue of long chronaxie must have long latent addition intervals, and vice versa. And if for any reason, a tissue of short chronaxie yields a long pseudo chronaxie on account of the methods employed, the fault may be discovered by finding a short latent addition interval.

The purpose of the present paper is to discuss briefly the form of the $\alpha$ strength-duration curve and to show that the $\alpha$ latent addition times correspond in the same way to the low $\alpha$ excitability as do the latent addition times in the sciatic nerve to its high excitability.

The Strength-Duration Curve

It has been shown already (Blair 1932 a, b; 1935 a) that some strength-duration data of the $\alpha$ excitability by Lapicque (1931) and Benoit (1934) conform quite well to the equation,

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

in which $V$ is the strength of the stimulus, $R$ the rheobase, $t$ the duration of the stimulus, and $K$, $k$, and $\alpha$ are constants. The excitability

Lapicque (1926), pp. 91, 215.
of the tissue is measured in the usual way by $k$. These curves did not extend to very short durations, however, and with those that do it is necessary to use an additional term as required with nerve (Blair, 1937), i.e. it is necessary to use the equation,

$$\frac{V - R}{V} \times \frac{K + ka}{K} = e^{-at} + \frac{kae^{-at}}{K}$$

(2)

$a$, being a constant. This equation is the same as 1 except for the transient term in $e^{-at}$ which is negligible when $at$ attains a value of 4 or more as it usually does when the stimuli are longer than about 5 msec. A large number of data have been obtained, which can be used to test the validity of these equations.

**Apparatus and Method**

The apparatus for obtaining rectangular waves of direct current has been described previously (Blair, 1935b). In the present instance, the durations of the stimuli apart from the rheobase range from 1.12 to 4.5 msec. The threshold is obtained using the succession of stimuli whose frequency is given by the speed of rotation of the apparatus, which in this case is about 30 per minute. The 2 second interval is sufficiently long to avoid latent addition and the threshold is not influenced by repeated stimulation as is the case with some slow tissues (Lapicque, 1925; Bonnardel and Goudchaux, 1935).

The tissue, the sartorius muscle of *Rana pipiens*, is dissected the day before the experiment and is kept in Ringer's solution in the cold until about 2 hours before the measurements are made. It is then set up in Ringer's solution in one of two types of glass vessels, one of which is illustrated in Fig. 1, and allowed to stand in a water bath at the experimental temperature, about 22°C. With this procedure it is found that the preparations usually are quite stable for many hours, as far as the indications of the strength-duration curve are concerned.

Zinc electrodes are used in zinc sulfate solution separated from the experimental vessel by 15 cm. of agar made up in Ringer's fluid. A rather high potential, about 200 volts, is used in the main circuit to insure low resistance contacts. The current to the tissue is derived from a potentiometer arrangement. The minimal response of the muscle at a part distant from the place of stimulation is used as an index. It is difficult sometimes to get a response from the rheobase which is the same as for the stimuli of limited durations, but on the whole it is usually easy to satisfy the requirement that the same part of the muscle is excited by each stimulus throughout the curve. In determining the curves the tissue is considered to be stable if the rheobase and one other point have the same values within about 5 per cent initially and finally.

The vessel illustrated in Fig. 1 is of glass throughout. The rubber stoppers holding the electrodes are kept separated from the solution as indicated.
tube in which the distal end of the muscle is suspended is closed at the bottom so that the current flows only through the pelvic end, which almost fills the constricted part of the tube. With this arrangement the nerve is never excited.

Usually the right-hand electrode (Fig. 1) is connected to the anode of the battery. This is the current direction used by Rushton (1932b) who showed that excitation took place at the cathode in his arrangement. This point has not been studied but it is very probable that this also occurs here and that, therefore, the excitatory wave along the muscle is propagated through the anode when the stimulus is continuous. With the current in the other direction, cathode down, the strength-duration curve is not so easily determined.

![Fig. 1](image.png)

**Fig. 1.** Apparatus used for excitation. The muscle is suspended in Ringer's solution as shown. The electrodes at the top are Zn-ZnSO₄–agar in Ringer's solution.

The other type of vessel, which is the one most often used, differs only in that there is no inner tube surrounding the muscle. In this type, part of the current continues through the whole length of the muscle but the current density is so much higher at the constricted portion of the tube than it is lower down that the nerve seldom is excited. With the addition of certain electrolytes, however, in studying salt effects, the excitability of the nerve may become sufficiently high, relative to that of the muscle, that the Lucas type of curve is obtained.

**EXPERIMENTAL RESULTS**

Almost invariably the rheobase or a stronger stimulus, if maintained, evokes a repetitive response. Accommodation of the sort occurring
in nerve is absent therefore, and the recovery of excitability takes place while the current is flowing. As was remarked previously the minimal response to the rheobase is sometimes different from that obtained with other stimuli. Sometimes it is even at a different part of the muscle so that a greater than minimal stimulus must be used to elicit a response at the region which responds to minimal stimuli of shorter durations. Thus the rheobase, as has been remarked by others, e.g. Rushton (1930), Lapicque (1931a), and Benoit (1934), is not always a very satisfactory measurement. However, with the current directed downward (Fig. 1) it is quite stable and easily repeatable so that it usually appears in this case to be quite satisfactory. With the current reversed (cathode down, Fig. 1) all the measurements are inclined to be variable. Thus the current directions apparently most suitable are opposite in nerve and muscle.

In Fig. 2 are given typical strength-duration curves plotted with \( \log \frac{V}{V - R} \) as ordinates and the durations as abscissae, according to equation 1. It is found that the data are of two general types. The first type is illustrated in the lowest curve and the highest, which are linear throughout and which conform closely, therefore, to equation 1. The difference between them is only in the sign of the intercept on the ordinate which is negative in the highest. This type comprises only about 30 per cent of our data and it is not so common as we had been led to expect from data by Lapicque and Benoit (Blair, 1932a, b; 1935a). No numerical comparisons of the data of this type with the equation are given because a number of examples have been considered in the papers just mentioned.

The second type differs from the first in that the rheobase appears too small, as is evinced by a tendency of the points to fall below the line for the long durations. A pair of such curves is given numerically in Table II. It will be seen here that the voltages calculated according to equation 1 are systematically lower than the measured values for durations greater than about 40 msec. except for the rheobase which agrees because its measured value is taken as correct. In this type of curve in general the data can be fitted quite well to equation 1 if the rheobase is arbitrarily raised by about 5 per cent taking the rest of the curve as it is measured out to 0.1 second at least. The discrepancy can be laid, therefore, to the rheobase for the convenience of discussion.
and from this point of view some factor enters at long durations which lowers somewhat the threshold current. One suggestion which can be made in this regard is that prolonged currents in nerve do alter the parameters of the strength-duration curve (Nivet, 1934; Blair, 1936 c) and also the threshold amount of the local excitatory state; so the longer stimuli in this case may be bringing about these changes in

\[ \log \frac{V}{V-R} \]

![Graph](attachment:image.png)

**Fig. 2.** Typical strength-duration curves of the \( \alpha \) excitability plotted according to equation 1. Each curve has a separate ordinate scale.

sufficient amount to account for the discrepancy. Wire electrodes on slow muscle do not, however, show this effect (Blair, 1936 a), suggesting that the change of the parameters is associated with the diffuse current distribution of the fluid electrode system and not with the length of the time scale.

At the short-times end of the strength-duration curve, the same
effect is encountered as with nerve (Blair, 1937); i.e., equation 1 becomes inadequate and 2 must be used. This type is illustrated by the middle curve of Fig. 2. In this case, the points diverge downward from the line at about 10 msec. but usually the divergence begins at about 5 msec. Therefore, if equation 2 represents these curves it appears that $e^{-at}$ approaches 0 at about 5 msec. Taking $at = 5$ at this stage, $a = 1000$, which gives the order of magnitude of this constant in sartorius muscle. Since $k = 20$, approximately, in this tissue, $a = 50k$, approximately.

### TABLE I

**Colle's Strength-Duration Curve from the Frog's Heart**

The calculated voltages are derived from equation (2) and the given constants.

<table>
<thead>
<tr>
<th>Time (msec.)</th>
<th>$V_{obs.}$</th>
<th>$V_{calc.}$</th>
<th>$T = 5°C.$</th>
<th>$a = 4800$</th>
<th>$k = 59.1$</th>
<th>$\frac{K + ka}{K} = 1.04$</th>
</tr>
</thead>
<tbody>
<tr>
<td>230</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>95</td>
<td>1</td>
<td>1.03</td>
<td></td>
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</tr>
<tr>
<td>45</td>
<td>1.09</td>
<td>1.06</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>21</td>
<td>1.38</td>
<td>1.38</td>
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<td></td>
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<tr>
<td>10.5</td>
<td>2.06</td>
<td>2.06</td>
<td></td>
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<tr>
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<td>1.98</td>
<td>6.17</td>
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<td></td>
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<td>0.92</td>
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<td>10.7</td>
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<td></td>
</tr>
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<td>17.9</td>
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</tr>
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<td>0.195</td>
<td>28.6</td>
<td>28.6</td>
<td></td>
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</tr>
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</table>

* Experiment C, Colle (1933), p. 419.

Since our data do not extend to durations shorter than 4 msec. they are not well suited to testing equation 2. Data by Colle (1933) on the frog's heart appear to be very similar to $\alpha$ data, however. These extend to durations short enough that a large part of the curve diverges from equation 1. One example of these data was given previously (Blair, 1936 c), another set is given here in Table I. This as well as the previous example conforms fairly closely to equation 2. For the heart muscle, according to these data, $a$ is of the order of 7000, $k$ of 100, both factors being larger than in the sartorius muscle. Colle's data are not frequent enough for the middle durations to determine well the linear relation of Fig. 1. For this reason, only a few of his sets can be dealt with easily. With his data also, as with the $\alpha$ excit-
ability, the rheobase tends, sometimes, to be too low for equation 1 or 2. The nature of this transient effect, the term in $e^{-at}$ of equation 2, which is perhaps purely physical, has been discussed for nerve previously (Blair, 1937) so it will not be considered further here.

It seems possible to conclude from these data and those considered previously that equations 1 and 2 fit the data quite closely in only about one-third of the $\alpha$ curves, the remainder requiring some additional factor to account for a progressive lowering of the rheobase by about 5 per cent or so. Therefore, it is desirable to examine the indications of the data of latent addition before attempting to reach conclusions as to whether the $\alpha$ excitation is of the usual form or not.

**Latent Addition**

As was pointed out above, the fit of equation 1 or 2 to the data, while it provides a strong indication of the validity of the differential equation from which it is derived, is not so direct a test as a method in which the components of the excitatory process can be studied separately. Such a method is provided by a study of the latent addition, for according to the basis of equation 1 or 2 (Blair, 1932; 1936c), if the current is stopped before excitation has been accomplished, the excitatory state, $p$, will subside according to

$$\frac{dp}{dt} = -kp \quad (3)$$

i.e., at a rate proportional to its instantaneous magnitude if the factors giving rise to the term in $\alpha$ of equation 1 are neglected. During this phase, therefore, the subsidence factor alone is acting and it can be examined separately. This can be done by giving an inadequate stimulus followed after an interval by a test stimulus sufficient to bring about excitation. In the present case, for simplicity, two rectangular stimuli of equal durations are used, the only variables being the interval between them and their strengths which are, however, the same for both.

Letting the stimuli have strengths, $V$, and durations, $t$, it is easily seen on integrating in the usual way (Blair, 1932b) that at the end of the first stimulus,

$$p = \frac{KV}{k} (1 - e^{-at}) \quad (4)$$
$p$ then subsides according to equation 3 from this value to attain, after an interval, $t_2$, measured from the end of the first stimulus, a value,

$$p = \frac{KV}{k} e^{-k_0 t} (1 - e^{-k_1 t})$$

(5)

$k_0$ being used to allow for the $k_1$s of equations 1 and 3 being different. The second stimulus, to be adequate, must now, during a time, $t_1$, raise this value of $p$ to $k - \alpha V$ (using the negative sign only) (Blair, 1932b) so that again using equation 1 and substituting the rheobase, $R$, for $k_0$ there is obtained finally,

$$V - R = \frac{K + k_0}{K + k_0} e^{-k_0 t_1} - e^{-k_0 (e^{-k_1 t_1} - e^{-k_1 t_1})}$$

(6)

It will be observed that this applies only to the special case, as was pointed out above, in which the kinetics of the current transient on removing the stimulus are ignored. Actually, if this transient is contra-excitatory the process following the inadequate stimulus should be written

$$\frac{dp}{dt} = -\alpha V (a - k) e^{-at} - kp$$

(7)

and after performing the appropriate integrations as before there is finally obtained

$$V - R = \frac{K + k_0}{K + k_0} e^{-k_0 t_1} - e^{-k_0 (e^{-k_1 t_1} - e^{-k_1 t_1})}$$

(8)

which, however, is the same as 6 when $t_1$ is greater than about 4 msec. since the second member on the right disappears at this stage. It is implied therefore, in 6 that the transient is considered both for excitation and subsidence and that $t_1$ is sufficiently large to make $e^{-at}$ negligible. The experiments were done in such a way as to satisfy this requirement.

Equation 6 by itself contains three arbitrary constants, $K + k_0$, $k$, and $k_0$. Moreover, it is not easily applied because of its form. However, if a strength-duration curve is obtained at the same time, the
first two constants can be derived separately from equation 1. Then, since $V, R, t_1,$ and $t_2$ are measured, $k_2$ is the only arbitrary constant remaining. Its determination is considered in the next section.

**Apparatus and Method**

The data of latent addition are obtained by means of the following arrangement. On the same shaft, in addition to the disc used for direct current measurements are mounted two fiber discs 14 cm. in diameter and 1.3 in thickness. In the edge of each, through the whole thickness, is a brass segment 2 mm. wide. These segments are connected to each other and by means of a brush, to the same voltage supply and potentiometer as that used for the strength-duration measurements. The other contact from each segment is made by means of a steel bearing ball, 1 cm. in diameter, which is free to turn on lubricated carbon in a brass socket; a spring presses the ball against the edge of the disc. The discs are movable on the shaft so that they may be arranged with the brass segments separated by any desired distance along the circumference. The separation between the segments determines the interval between the stimuli, and the durations of the stimuli are fixed by the widths of the segments, since the balls make point contacts. The threshold for the two stimuli is determined by trial adjustment of the potentiometer while the discs are rotating continuously. As the time of rotation is 2 seconds, there should be no latent addition between successive pairs of stimuli and in fact a double response or none at all is obtained with intervals of 200 msec. or even less. The latent addition determinations are preceded and followed by the obtaining of a strength-duration curve. These curves provide an independent index of the stability of the tissue as well as the constants $\frac{K + k\alpha}{K}$ and $k$.

Equation 6 is applied by calculating the constant $e^{-k_2\alpha}$ using $k$ from the strength-duration curve and the measured duration of the stimulus, $t_1$. The factor, $e^{-k_2\alpha}$ can have values from 0 to 1 only, the respective limits being when the latent addition interval, $t_2$, is very long and zero. A graph of $\frac{V - R}{V}$ as ordinates and $e^{-k_2\alpha}$ as abscissae must therefore have an ordinate intercept $e^{-k_2\alpha}/\frac{K + k\alpha}{K}$ when $t_2$ is large, i.e. when $e^{-k_2\alpha} = 0$ and an ordinate $e^{-k_2\alpha}/\frac{K + k\alpha}{K}$ when $t_2 = 0$; i.e., when $e^{-k_2\alpha} = 1$. These ordinates are marked, therefore, on a graph at the point $e^{-k_2\alpha} = 0$ and 1, respectively, and are joined by a straight line. Now each experimental value of $\frac{V - R}{V}$ will give by means of the graph, a corresponding value of $e^{-k_2\alpha}$. From this $e^{-k_2\alpha}$ can be calculated and then $k_2$, because $t_2$ is measured. This procedure is followed for several data and the resulting values are used to obtain an average value for $k_2$, if there is one of the kind required by the hypothesis. The fit of equation 6 can then be tested by calculating $V$ for each interval and...
comparing it with the measured value. Or the calculated values of $e^{-kt}$ using the average $k_2$ can be plotted on the graph used previously as a graphic indication of the fit.

**TABLE II**

*Latent Addition Data (Lower Set) on the a Excitability Preceded and Followed by a Strength-Duration Curve (Upper Set)*

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<th>Duration</th>
<th>Initial</th>
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<td>450</td>
</tr>
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<td>112</td>
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</tr>
<tr>
<td>74.2</td>
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<td>1915</td>
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<td>1545</td>
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**EXPERIMENTAL RESULTS**

In Table II are given the data of a typical experiment which include an initial strength-duration curve, a set of latent addition measure-
ments, and a final strength-duration curve. The constants from each strength-duration curve are given. These are used separately to obtain the calculated voltages of the strength-duration curves, and their mean values are used in equation 6 for the latent addition calculations. In Fig. 3 (curve B) are plotted $\frac{V - R}{V}$ against $e^{-kt_2}$ for these data. These values of $e^{-kt_2}$ are calculated from a mean value of $k_2$ obtained previously from the same curve by the method given above. It will be seen that these data conform to equation 6 in fair approximation. In Table III are given three other examples of the latent addition data alone as measured and as calculated, using again the constants from strength-duration curves obtained at the same time. In Fig. 4 are given the curves of subsidence of the excitatory

\[ \text{Fig. 3. A method of plotting latent addition data according to equation 6 which predicts a linear relation. Curve B is for the data of Table II. Curves A and C are for sets A and C, respectively, of Table III.} \]
state for the data of Table II, curve A, and for sets B and C of Table III, curves B and C. These curves as drawn are the theoretical curves of subsidence using the mean value of $k_a$. The plotted points are the experimental values calculated from the measured voltages.

### TABLE III

**Typical Data for the Latent Addition of α Excitation**

The intervals are the intervals between the stimuli, $V$, whose durations are $t_1$. The calculated voltages are from equation (6) using the constants given.

<table>
<thead>
<tr>
<th>Interval</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
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<td></td>
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<td>$V_{calc}$</td>
<td>$V_{obs}$</td>
</tr>
<tr>
<td>[msec.]</td>
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<td>2110</td>
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<tr>
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<td>1520</td>
</tr>
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<td>236</td>
<td>237</td>
<td>1830</td>
</tr>
<tr>
<td>51.2</td>
<td>3190</td>
<td>3120</td>
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<td>63.9</td>
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<tr>
<td>68.2</td>
<td>3260</td>
<td>3280</td>
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</tr>
<tr>
<td>85</td>
<td>3270</td>
<td>3280</td>
<td>237</td>
</tr>
</tbody>
</table>

- $h_1 = 4.6$ msec.
- $k_1 = 16.0$
- $k_2 = 47.5$
- $K = 1.026$

- $t_1 = 8.8$ msec.
- $k_1 = 31.4$
- $k_2 = 81$
- $K = 1.533$

- $R = 325$
- $k_1 = 2.94$
- $K = 1.29$
- $R = 120$
- $k_2 = 2.57$
- $K = 1.533$

- $R = 680$
- $k_1 = 53$
- $K = 1.533$
- $k_2 = 2.46$
theoretical value greater than 3 and usually less than 2. All of our data are similar. It is concluded, therefore, from these results, that the subsidence of the excitatory state is exponential in close approximation.

Fig. 4. The subsidence of the $\alpha$ excitatory state. It is assumed for convenience that the first (inadequate) stimulus produces unit value of the excitatory state so the maximum ordinate is 1. Curve A represents the data of Table II. Curves B and C represent sets B and C, respectively, of Table III.

It will be observed, however, that $k_2$ is more than twice as great as $k$. That is, the subsidence is more than twice as fast when examined directly as it appears to be from the strength-duration curve. This result was quite unexpected and it was thought at first to be a feature of the $\alpha$ excitability only. Preliminary work on nerve gives, however, a similar result (Blair, 1936 c). There appear to be two alternative explana-
tions of this result; either that the mechanism postulated to give
equations 1 and 2 is quite wrong or that the excitatory state is dissi-
pated by factors in addition to those involved directly in the process
of excitation. It appears to be most probable at present that the
latter alternative is the correct one (Blair, 1936 c) but the matter is
open to question.

That the particular form of stimulus is not a factor in the determina-
tion of this ratio for single pulses in nerve, at least, is indicated by the
finding that the same value of $k$ is derived using either rectangular
pulses, condenser discharges, or linearly rising currents (Blair, 1935 b, c)
as stimuli.

The Refractory Period

The recent theoretical treatments of excitation (Rashevsky, 1933;
Monnier, 1934) relate the refractory period to the time constants of
excitation and accommodation. This point of view has received no
experimental justifications but there is perhaps some parallelism,
usually, between the length of the chronaxie and the refractory period.
This is not true of the $\alpha$ excitability, however. In this case prelimi-
nary measurements give the absolute phase as being of the order of
1 msec. at 20°C. which is somewhat shorter than most of the sciatic
nerve data. This is in agreement with the assumption which has
always been made by those using the muscle as an index while measur-
ing the refractory period of nerve, namely, that the refractory period
of the muscle must be as short or shorter to permit the method. As
the matter stands at present there does not seem to be sufficient evi-
dence of a connection between the strength-duration curve and the
refractory period to draw a conclusion with respect to the question
at issue.

CONCLUSIONS

Apart from this new problem which is raised by the dissimilarities
of the subsidence rates during and following the stimuli, it is apparent
that the $\alpha$ latent addition data are quite as appropriate as regards
their time scales to the $\alpha$ strength-duration curves with their small $k$
values, or large chronaxies as the latent addition data in nerve are
to the large $k$ values or short chronaxies encountered there. Thus it
can be concluded that the $\alpha$ process of excitation is essentially the same in its general nature as those occurring in other tissues and that there is no reason to believe that any information derived from its study will be any more or less distorted than that obtained elsewhere. It may be, in fact, that the $\alpha$ excitation process is the simplest because it does not involve any of the accommodation which occurs so frequently in other cases and which probably distorts somewhat the strength-duration curve.

**SUMMARY**

With a view to indicating that the $\alpha$ excitatory state in muscle is not of a special nature it is shown that the $\alpha$ strength-duration curves are of the same form as those determined for nerve and other tissues except that in about two-thirds of all cases the rheobase appears to be slightly too low. Also from experiments in latent addition it is found that the $\alpha$ excitatory state following an inadequate stimulus subsides exponentially at a rate which is related to the $\alpha$ excitability in the same way, approximately, as the subsidence rate in nerve is related to the nerve's excitability. In both tissues the subsidence as measured directly is 2–3 times as fast as it appears to be from the strength-duration curve. The $\alpha$ refractory period is at least as short as that of nerve so the $\alpha$ chronaxie is unusually long compared to the refractory period. There is no reason at present, however, to consider this as having any bearing on the problem at issue. It is concluded therefore, that the $\alpha$ excitability differs from others in the rates of its reactions rather than in its fundamental nature and that any conclusions about excitability drawn from its study will probably be valid quite generally.

I am indebted to Mr. W. B. Latchford for assistance in doing the experiments.

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