TEMPERATURE AND EXCITABILITY. BY KEITH LUCAS, *Fellow of Trinity College, Cambridge*, AND G. R. MINES, *Scholar of Sidney Sussex College, Cambridge.*

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OUR exact knowledge of the influence of temperature upon the excitability of muscle and nerve may be said to date from the work of Gotch and Macdonald[1]. For they first pointed out the physical error by which much previous work had been vitiated, namely the neglect of the fact that muscle and nerve are electrolytic conductors and that therefore their resistance rises as the temperature is lowered.

The conclusions to which Gotch and Macdonald came are well-known. They found that in nerve a fall of temperature increases the excitability towards currents of long duration, but decreases the excitability towards currents of short duration. In muscle a fall of temperature increases the excitability whatever the duration of the exciting current used.

These results suggest two problems towards the solution of which we have directed our experiments.

In the first place the different effect observed in nerve, according as the exciting current is long or short, raises the question whether there may not be two sorts of excitation, one provoked by long currents, the other by short currents. It was to this view that Gotch and Macdonald[2] leaned in discussing the results of their investigation. We have attempted to throw some light upon this question by determining at two different temperatures the excitability towards a large series of currents of graduated duration. In this way we have been able to draw curves relating the excitability to the current-duration at the two temperatures; and from these curves one can see how the change of excitability produced by a fall of temperature is related to the duration of the exciting current. It seemed probable that if there were two

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[1] Gotch and Macdonald. This *Journal*, xx. p. 247. 1896.

[2] *Loc. cit.* p. 297.

sorts of excitation set up, there would be some discontinuity in the relation between excitability and current-duration—some abrupt transition from one curve to another such as we know to accompany the passage from one excitable substance to another in the excitation of a mixed excitable tissue[1].

The second question with which we have dealt arises from the difference which Gotch and Macdonald observed between the behaviour of muscle and nerve towards currents of short duration. As we have already stated, a fall of temperature renders nerve less excitable and muscle more excitable when the exciting currents used are short. This might mean that the behaviour of muscle is fundamentally different from that of nerve, or the difference might be one of degree only. Towards the solution of this question we have made experiments in which the change of excitability resulting from a fall of temperature is measured for a large range of current-durations, our object being to see whether the curve relating excitability to current-duration rises more rapidly in the cool than in the warm muscle, or whether in muscle there is no sign at all of that phenomenon which leads in nerve to a reversal of the excitability-change.

At the time when our experiments were planned there was no experimental evidence bearing on the first of these questions; but during the present year M. and Mme Lapicque[2] have published some experiments in which they have dealt with it, using for excitation discharges from condensers of different capacities charged to different potentials. When we became aware of their results we had already arrived at a similar conclusion by the different method of excitation which we were using. We decided to publish our experiments because they were made with currents differing only in duration, and not also in rate of current-change as do the condenser discharges.

On the question of the difference between muscle and nerve the only evidence is that afforded by an experiment published by the same authors in 1903[3]: it shows the curves relating condenser capacity to potential of charge in muscle at two different temperatures approaching one another slightly as the capacity is decreased. This matter seemed to us to require further investigation.

Method. Gotch and Macdonald[4] in their experiments counteracted

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[1] Cf. Keith Lucas. This *Journal*, xxxv. p. 310. 1907.

[2] Lapicque, M. and Mme. *C. R. Soc. de Biol.* LXII. p. 37. 1907.

[3] Lapicque, M. and Mme. *Journ. de Physiol. et de Path. gén.* v. p. 1003.

[4] *Loc. cit.*

the change of resistance caused by change of temperature by introducing in the external circuit a resistance much higher than that of the tissue, so that changes in the conductivity of the latter produced a negligible effect on the current-strength. We were unable to adopt this method, because the introduction of a large external resistance would have necessitated the use of a very large battery in order to obtain a sufficient current-strength to stimulate the muscle when short durations were being tried. We therefore determined the actual resistance of the tissue at each temperature, and made allowance for the changes of resistance in calculating the current-strength used in each observation. The resistance was measured by Wheatstone's method with an alternating current which was rectified before being sent into the galvanometer. The current employed was so small as not to excite the tissue whose resistance was being measured.

The general method of experiment, whether made on nerve or on muscle, was the following. The tissue was excised and set up in fluid electrodes of the type previously described by one of us[1]. The electrodes were placed in a water-bath by which their temperature could be maintained for half an hour with a variation of less than 0·2° C. After the water-bath had been filled, an interval of 20 minutes was allowed to elapse for the electrodes and preparation to assume a uniform temperature. The resistance was then determined two or three times at intervals of a few minutes to make sure that the conditions were steady. As soon as consistent readings were obtained for the resistance, the determination of the liminal current-strength for various current-durations began. The current-durations to be used in the experiment were arbitrarily chosen, and obtained by means of the pendulum described elsewhere by one of us[2]. The relative current-strength required to excite with each current-duration was determined by a graduated potentiometer-wire. At the conclusion of a set of observations the water-bath enclosing the electrodes was emptied by means of a siphon and refilled with water at a different temperature. After an interval of 20 minutes the resistance was determined afresh, and a set of observations was taken at the new temperature. The original temperature was then restored, the resistance was measured again, and a third set of readings was taken. If the tissue continued in good condition these operations were repeated several times. At the conclusion of the whole experiment the current flowing through the tissue

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[1] Keith Lucas. This *Journal*, xxxiv. p. 375, Fig. 3. 1906.

[2] Keith Lucas. *Ibid.* xxxv. p. 314, Fig. 2. 1907.

was measured with a moving-coil instrument graduated in microampères, the resistance at the time being known and the potentiometer set at some particular value. From these data it was easy to calculate the strength of current employed in each individual observation. The observations were afterwards plotted on squared paper, the abscissæ representing the duration of the exciting current, the ordinates showing the liminal current-strength.

When the excitability of muscle was the subject of investigation the arrangement for maintaining the tissue at the desired temperature was very simple. In this case the muscle itself was stimulated and also served as the index of excitation. There was therefore no possibility of error due to change in conductivity: and the whole tissue could be subjected to the temperature change. The electrodes holding the muscle were therefore simply immersed in a large beaker of water, which was in turn enclosed in a tin vessel. The interval between the beaker and this vessel was packed with asbestos and cotton wool, spaces being left for the illumination and observation of the muscle through two holes in the outer vessel. The muscle (sartorius) was always so arranged in the electrodes that excitation was confined to the nerveless pelvic end.

In the experiments made on nerve the requirements were less easily fulfilled. The index of excitation was the contraction of the muscle in which the nerve terminated, and it is clear that if both muscle and nerve were exposed to changes of temperature, any observed alteration in the current required for excitation might be due either to a change in the excitability of the nerve itself or to a change in the excitability of the muscle towards the nervous impulse—in other words to an alteration in the conductivity from nerve to muscle[1].

We eliminated this source of error by the use of the apparatus shown in Fig. 1. The glass tubes *A* and *B* containing Ringer's solution were closed above by the porcelain candles *C* and *D* which passed through rubber stoppers. These candles were filled with zinc sulphate solution and held the zinc rods which complete the non-polarisable electrodes. The Ringer's solution in the tubes presented free surfaces at *E* and *F*, and the fluid was prevented from escaping by the stopper *G*. This stopper held in position the thread *H*, to which was fastened the small piece of vertebral column dissected out with the nerve. The piece of nerve traversing the air space *K* thus lay between the fluid electrodes. The nerve escaped from the lower electrode by the short tube *L*. The elec-

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[1] **Boycott** has shown that the conductivity of frog's *nerve* is not affected by changes of temperature. This *Journal*, XXVII. p. 488. 1902.

trodes were enclosed in the glass vessel *M*, which served as a water-bath. This was placed above a similar vessel *N*, and the two were separated by a sheet of asbestos, pierced in the centre to admit of the passage of the nerve. The lower vessel contained a small glass cup *P* filled with Ringer's solution, so placed that its brim was level with the edge of the vessel *N*. In this cup rested the muscle *Q*. By this arrangement the muscle was kept at a steady temperature in the lower water-bath throughout an experiment, while the temperature of the electrodes with the nerve contained in them was adjusted by changing the contents of the upper vesssel. The temperature of the lower water-bath was so

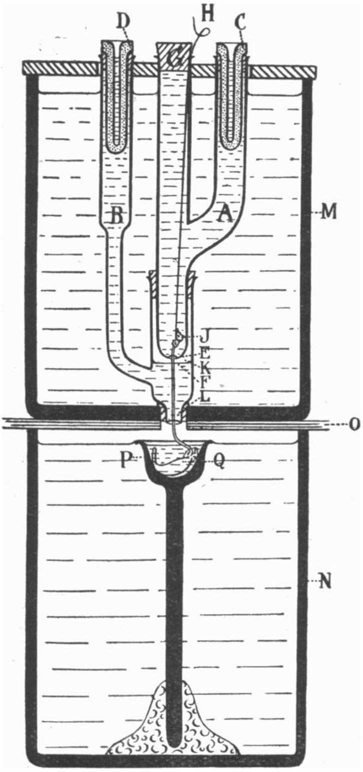

Fig. 1.

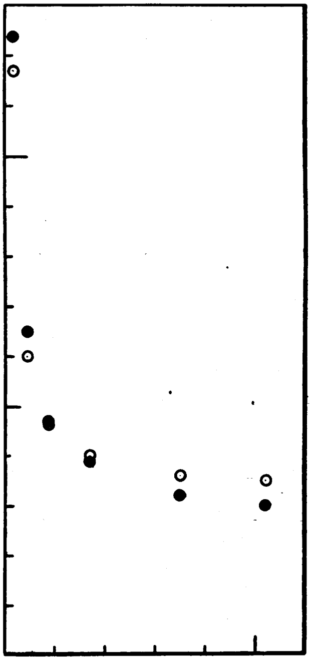

Fig. 2.

Fig. 1. Arrangement of electrodes and water-baths for experiments on nerve. For description see text.

Fig. 2. Exp. 1. Sciatic nerve of toad. Abscissæ measure current-duration; one division $= 0{\cdot}001$ sec. Ordinates measure current-strength; one division $= 1$ microampère. Observations made at the lower temperature are plotted as black discs, those made at the higher temperature as circles.

chosen as to lie midway between the two temperatures to which the nerve was to be subjected in the course of the experiment. This was found to be a very necessary precaution, for if the temperature of the two baths differed by more than about five degrees, the temperature gradient in the piece of nerve between the two vessels acted as a stimulus and caused twitching of the muscle.

Experiments made on nerve.

The sciatic-gastrocnemius preparation of the toad was used throughout these experiments. It was found impracticable to use extreme temperatures differing by more than 8° C. as the nerves showed themselves exceedingly sensitive to the establishment of a temperature-gradient along their length. The temperatures actually used were about 20° C. for the upper and 12° C. for the lower limit.

In Fig. 2 are plotted the results of a typical experiment (Exp. 1) showing the crossing of the excitability curves for the high and low temperatures. The curve for the high temperature is the mean of two sets of observations made before and after that at the low temperature. The full numerical data of the experiment are tabulated below. As Fig. 2 shows, the crossing of the two curves takes place in a smooth and regular manner, the distance between them changing continuously as the current-duration is changed. There is no evidence of discontinuity.

Exp. 1. Sciatic-gastrocnemius preparation of toad. Muscle kept at uniform temperature about 15·5° C. Excitation and change of temperature in nerve.

Liminal current-strength in microampères.

	A	B	C	
Duration of current in seconds	Temp. 19·9° C. Resist. 22650	Temp. 12·0° C. Resist. 26050	Temp. 19·0° C. Resist. 23700	Mean of A & C
0·0052	3·7	3·0	3·3	3·5
0·0035	3·7	3·2	3·5	3·6
0·0017	4·1	3·9	3·9	4·0
0·00087	4·5	4·7	4·7	4·6
0·00044	5·9	6·5	6·2	6·0
0·00017	11·4	12·4	12·2	11·7

All the experiments agreed in showing a continuous relation between the current-duration and the difference of excitability at the two temperatures. Also the curve for the low temperature always rose more rapidly than that for the high. But in some cases there was no actual crossing of the curves. In Exp. 2, for example, there is no crossing because for long current-durations the two curves are coincident.

Exp. 2. Sciatic-gastrocnemius preparation of toad. Muscle kept at uniform temperature about 15° C. Excitation and change of temperature in nerve.

Liminal current-strength in microampères.

	A	B	C	
Duration of current in seconds	Temp. 19·8° C. Resist. 15300	Temp. 12·0° C. Resist. 18100	Temp. 19·3° C. Resist. 16660	Mean of A & C
0·007	6·0	5·6	5·3	5·6
0·0052	6·1	5·8	5·5	5·8
0·0035	6·1	6·1	5·7	5·9
0·0017	6·3	7·6	6·8	6·5
0·00087	8·4	10·3	8·8	8·6
0·00044	12·2	15·7	12·8	12·5

In other experiments the curve for the low temperature would start so much below that for the high temperature that, though rising more steeply, it failed within the limits of the experiment to cross. The reason for these differences of behaviour lies no doubt in the progressive changes which are going on in the tissues. The observations at different temperatures are necessarily separated by a considerable interval of time, and during that time changes of the absolute excitability go on, which are not wholly eliminated by the method of comparing one set of observations with the mean of two sets taken before and after. However, for the present purpose we are concerned only with the continuity or discontinuity of the curves, not with their absolute values.

Experiments made on muscle.

It is a well-established fact that a muscle is more excitable towards currents of long duration when cool than when warm. The curve representing the excitability of the cooled muscle towards currents of different durations will lie, therefore, for long durations, below that for the warm muscle. If the behaviour of muscle resembles that of nerve we shall expect to find the curve for cool muscle rising more rapidly than the curve for warm muscle as the current-duration is diminished.

In searching for this phenomenon we may take any consecutive curves from the same muscle at different temperatures regardless of whether the absolute excitability of the muscle has altered in the interval between the two sets of observations from causes other than the change of temperature. Alteration in the absolute excitability will affect the level of the curve but it is clearly only the rate of its rise which is of importance for the present purpose.

The simplest way of comparing the rates of rise is to determine, at each of two temperatures, in what proportion the liminal current-strength must be increased for a given decrease in current-duration. We have used the two current-durations 0·024 sec. and 0·0035 sec. for this purpose. The current of 0·024 sec. belongs to that region of the current-duration current-strength curve in which the curve has become practically parallel to the abscissa; in other words it is a current of such duration as may be increased without much further decrease in the liminal current-strength. It may, therefore, be taken as a typical current of long duration. The current of 0·0035 sec. is one for which at about 10° C. the liminal current-strength has reached more than twice its minimum value. It is therefore for toad's muscle a short current. In the table below are shown the results of all our experiments in which current-durations as short as 0·0035 sec. were used. The third column of figures represents in the warm muscle the relative current-strength required to excite with a duration of 0·0035 sec. when that required to excite with a duration of 0·024 sec. is taken as unity: the last column represents the same for the cool muscle. Each horizontal line affords a comparison between the increase of current required for a warm and a cool muscle, the observations compared having been made consecutively on the same muscle. For example, in Exp. 4, observations *C* and *D*, one sees that at 17·2° C. the liminal current-strength must be increased in the ratio 1 : 2·1 for a decrease of current-duration from 0·024 sec. to 0·0035 sec., whereas at 9·0° C. the required increase is 1 : 3·4.

	Warm			Cold		
Exp.	Observ.	Temp.	Current-strength for 0·0035 sec. when that for 0·024 sec. = 1	Observ.	Temp.	Current-strength for 0·0035 sec. when that for 0·024 sec. = 1
3	A	16·5	2·5	B	8·8	3·6
	C	16·1	2·2	B	8·8	3·6
	C	16·1	2·2	D	8·2	2·6
4	C	17·2	2·1	D	9·0	3·4
	E	18·0	2·0	D	9·0	3·4
	E	18·0	2·0	F	8·9	5·0
	G	16·6	1·9	F	8·9	5·0
5	A	16·9	1·9	B	8·3	2·9
	C	16·9	2·9	B	8·3	2·9
6	A	17·9	3·6	B	8·0	3·9
7	A	17·2	3·6	B	8·0	4·0
	C	17·1	3·3	B	8·0	4·0
	C	17·1	3·3	D	7·0	3·1
	E	17·1	2·8	D	7·0	3·1

The table shows fourteen pairs of consecutive observations. In twelve of these the curve of the cool muscle is seen to rise considerably more steeply than that of the warm muscle. In one (5 *B*, *C*) there is no difference; in one the curve for warm muscle is slightly the more steep (7 *C*, *D*). It is clear therefore that the liminal current-strength usually increases more rapidly in the cool than in the warm muscle as the current-duration is decreased. And so far the behaviour of muscle resembles that of nerve.

The next question is whether the steeper rise of the curve for cool muscle leads to an approach or actually to a crossing of the curves for cool and warm muscle. We can settle this point only by the comparison of consecutive experiments made at different temperatures on the same tissue, under such conditions that we are sure that the tissue was undergoing no progressive change which could affect its absolute excitability. On this point we can be certain only if the two sets of observations made at like temperatures before and after a single set of observations at the changed temperature are found to agree sufficiently closely.

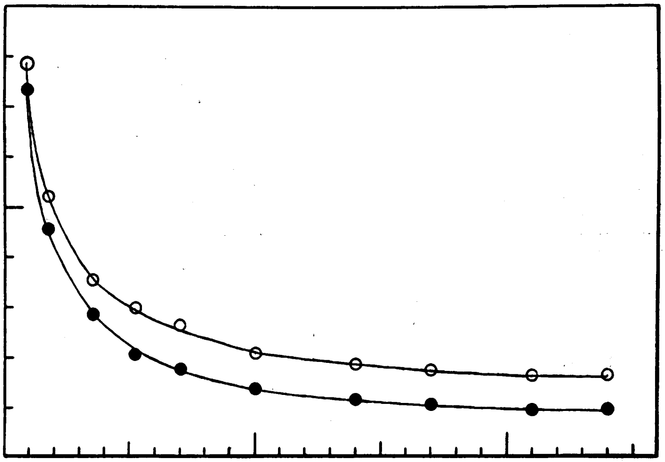

Fig. 3. Exp. 3. Sartorius muscle of toad. Abscissæ, one division = 0·001 sec. Ordinates, one division = 10 microampères. Observations made at the lower temperature are plotted as black discs, those made at the higher temperature as circles.

In most cases on plotting the mean of two sets of observations at like temperatures against the intermediate observations made under the changed temperature we found only an approach of the curves, not a crossing. An example of this sort is shown in Exp. 3, observations *B*, *C*, *D*, which is tabulated below and plotted in Fig. 3.

Exp. 3. Sartorius of toad, electrodes on extreme pelvic end.

Liminal current in microampères.

Duration of current in seconds	B	C	D	Mean of B & D Temp. 8·5° C.
	T. before exp. 8·7° C.	16·2	8·2	
	T. after exp. 8·9° C.	16·1	8·2	
	R. before exp. 14800 ohms	11900	14600	
	R. after exp. 14400 ohms	12100	14600	
0·024	8·7	16·1	10·0	9·43
0·021	8·7	16·1	10·0	9·43
0·017	9·6	17·2	10·9	10·3
0·014	10·5	18·3	12·3	11·4
0·010	11·8	20·5	15·5	13·7
0·007	16·4	26·3	18·2	17·3
0·0052	20·1	29·9	20·9	20·5
0·0035	31·0	35·5	26·4	28·7
0·0017	43·8	52·1	47·4	45·6
0·00087	68·4	78·8	78·5	73·5

But two of the five muscles used did show an actual crossing of the curves at the high and low temperatures. And in one of these muscles the crossing was found from five consecutive sets of observations. These five sets of observations are tabulated below (Exp. 4).

Exp. 4. Sartorius of toad. Cathode on extreme pelvic end.

Liminal current-strength in microampères.

Duration of current in seconds	C	D	E	F	G
	T. before exp. 17·3° C.	9·0	18·0	8·9	16·6
	T. after exp. 17·2° C.	9·1	18·0	9·0	16·6
	R. before exp. 11570 ohms.	14800	11600	14600	12500
	R. after exp. 12000 ohms.	14900	11900	14900	12600
0·024	41·8	26·1	38·7	19·2	26·1
0·021	41·8	28·1	39·3	21·2	26·7
0·017	42·5	29·1	40·0	23·2	27·3
0·014	44·4	34·2	40·6	25·3	27·9
0·010	46·9	39·2	43·1	27·8	29·1
0·007	58·3	52·3	52·0	35·4	33·2
0·0052	[81·2][1]	68·4	64·7	49·5	38·6
0·0035	88·8	87·5	78·6	96·0	49·3

If we take from these observations the mean of any two sets at like temperatures, and plot them against the intermediate set which was made at a different temperature, we find a crossing of the two curves. For example, the mean of *C* and *E* (17·2° and 18° C.) compared with *D* (9·0° C.) gives the following values, which are plotted in Fig. 4. Similar crossing will be found if the mean of *D* and *F* is compared with *E*, or the mean of *E* and *G* with *F*.

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[1] This is obviously an erroneous observation, as it fails to agree with the corresponding observation in *E*, and gives a single point lying outside the smooth curve of *C*.

	Liminal current-strength	
Duration of current in seconds	Mean of C & E (mean temp. 17·6° C.)	D 9·0° C.
0·024	40·3	26·1
0·021	40·5	28·1
0·017	41·2	29·1
0·014	42·5	34·2
0·010	45·0	39·2
0·007	55·1	52·3
0·0035	83·7	87·5

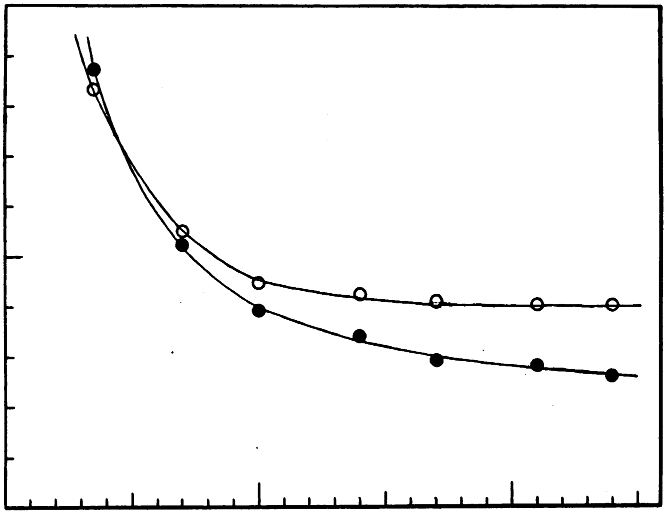

Fig. 4. Exp. 4. Sartorius muscle of toad. Values of abscissæ and ordinates as in Fig. 3.

The fact that Gotch and Macdonald did not find the reversal of the effect in muscle is in accordance with our experience that the large majority of sets of observations do not show it. The experiments described in this paper show that the increase of excitability towards currents of long duration caused by a given degree of cooling is much larger in muscle than in nerve[1]; so that one does not wonder at the greater frequence with which the reversal occurs in nerve. The difference between muscle and nerve appears then to be one of degree only.

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[1] The increase in excitability on cooling is greater in the tissue whose excitatory process is slower. Compare the observation of Grützner (mentioned by Zenneck, *Pflüger's Archiv.* LXXVI. p. 55), that the slow, sarcoplasmic fibres of the frog's sartorius, when tested by chemical stimuli, show a greater increase in excitability for a given fall of temperature than do the quick fibres.

SUMMARY AND CONCLUSIONS.

It was shown by Gotch and Macdonald that a nerve has its excitability increased by a fall of temperature when the exciting current is of long duration, and decreased when the current is of short duration. By employing a series of currents of graduated duration we have been able to investigate the curves relating excitability to current-duration at two different temperatures. We find that the difference of excitability between the warm and the cool nerve changes continuously as the current-duration is changed. The transition from an increased to a decreased excitability shows no break, such as would be demanded by the hypothesis that the reversal of the excitability-change is due to the production of two different sorts of excitation by the currents of different duration. This result obtained with battery-currents differing only in duration and strength confirms the result previously obtained by Lapicque with discharges from condensers of varying capacity.

In muscle Gotch and Macdonald did not find that the change of excitability brought about by alteration of temperature was reversed in direction when the duration of the exciting current was changed. Our experiments show that this does not imply any fundamental difference in the behaviour of muscle and nerve. We find that in cooled muscle the current-strength required for excitation increases with diminution of the current-duration more rapidly than in warm muscle. Whether this effect shall actually lead to a reversal of the excitability-change or not is only a matter of degree. The chief factor which prevents the reversal from taking place within the limits of ordinary experiments on muscle is the very large decrease of the liminal current-strength for long currents which is produced by a fall of temperature. This decrease appears to be much larger in muscle than in nerve. In spite of this the reversal does occasionally take place, as is shown by some experiments which we publish.

To sum this matter up we may make the following general statement, valid alike for nerve and for muscle. The cooler tissue requires less current-strength for its excitation when currents of long duration are used, but when short currents are used, this effect is masked either partially or completely by the greater increase of current-strength which the cooler tissue demands for a given decrease of current-duration.

The coupling of these two phenomena—a lower liminal current-strength for long currents and a more rapid increase of the liminal current-strength as the current-duration is decreased—is of particular interest. For it has been shown by one of us[1] that in the comparison of different excitable tissues belonging to a single animal the same phenomena are associated. In the sartorius muscle of the toad, for example, the muscle-fibres are excited by weaker currents than the nerve-fibres, provided that the exciting currents are of sufficiently long duration, and when the duration of the currents is decreased the nerve-fibres are excited by weaker currents than the muscle-fibres. In fact it is the coupling of these two phenomena which leads to a crossing of the curves relating current-duration to current-strength in the muscle-fibre and the nerve-fibre, and so effects a break in the current-strength and current-duration curve of a tissue containing both muscle-fibres and nerve-fibres.

When two tissues of one and the same animal are compared, it is the tissue whose excitatory process is slower which possesses the greater excitability towards long currents and the accompanying rapid increase of liminal current-strength with decrease of current-duration. For example, in the toad or frog it is in the muscle as opposed to the nerve that these phenomena appear; in the lobster it is in the nerve which evokes slow contractions as opposed to that which evokes rapid twitches. It is therefore significant that when one tissue is examined at different temperatures the same phenomena are found at the low temperature as opposed to the high. For the fall of temperature implies a slowing of the processes involved in excitation. The known conditions which lead to the simultaneous appearance of a lower liminal current-strength for long currents and a more rapid increase of the liminal current-strength with decrease of the current-duration may therefore be summed up simply as a slowing of the excitatory process.

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[1] Keith Lucas. This *Journal*, xxxv. p. 310. 1907.