ON THE RATE OF VARIATION OF THE EXCITING CURRENT AS A FACTOR IN ELECTRIC EXCITATION. By KEITH LUCAS, *Fellow of Trinity College, Cambridge.*

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IN this paper I shall describe an attempt to obtain some exact knowledge of the relation existing between the rate of current-variation in an exciting current and the minimum current-strength required to produce an excitation. The problem is far from new. Du Bois Reymond[1] attempted something of the sort in 1862, but was baulked by the inadequacy of his apparatus. In the same year Bernstein[2] described an ingenious method of varying the rate of current-change; but he did not describe any results obtained. v. Fleischl[3] described his orthorheonom in 1877, and by its means showed that a given current-strength might cause an excitation if reached instantaneously, but be ineffective if reached slowly. Fuhr[4] used a method similar to that of v. Fleischl but concerned himself more with the time at which excitation began than with the current-strength required to excite at various current-gradients. v. Kries[5] improved v. Fleischl's method, making it capable of giving single linear current-variations with a considerable range of rapidity. He made many determinations of the current-strength required to excite at different current-gradients. From experiments made on the sciatic-gastrocnemius preparation of the frog he found that the liminal current-strength increased when the current-gradient was made less. But he failed to find a satisfactory agreement amongst the results obtained from preparations taken from different frogs. There was a wide variation in the increase of current-strength necessary for a

[1] Du Bois Reymond, *Gesam. Abhandlungen,* I. p. 198. *Abhl. d. k. Akad. d. Wiss. zu Berlin,* 1862. *Physikal. Abth.* p. 131.
[2] Bernstein, *Arch. f. Physiol.* p. 531. 1862.
[3] v. Fleischl, *Stzber. Wiener Akad.* LXXVI. III. Abth. p. 138. 1877.
[4] Fuhr, *Arch. f. d. ges. Physiol.* XXXIV. p. 510. 1884; and XXXVIII. p. 313. 1886.
[5] v. Kries, *Arch. f. Physiol.* p. 337. 1884.

given decrease of current-gradient, and, what was still more regrettable, the curve relating current-strength to current-gradient was of no constant form. v. Kries could find no reasonable explanation of the irregularity of his results. I shall have to refer to this question in a later part of this paper. Later some observations were made on the same lines by Schott[1]. He borrowed the apparatus used by v. Kries, and states that to excite the sciatic nerve of the toad the same current-strength was required whether the current-variation was instantaneous or occupied 0·1 sec. The most recent observations of which I am aware are those of Gildemeister[2]. He obtained from different frogs results which agreed quite well amongst themselves. The current-strength had to be increased if the current failed to reach its full value in 0·0003 sec. But the currents which he used were slowed by the use of variable self-induction in the circuit, so that they increased on an exponential curve. This method complicates the problem in an unnecessary way, for in any single observation the current-gradient is always varying, so that one cannot draw from his results any simple relation between the current-gradient and the current-strength.

Method. The method of obtaining linear current-variations used in my experiments differed fundamentally from the various methods used by other observers. I used in the battery circuit a large electrolytic resistance, whose value could be changed continuously at any required rate. The details of the apparatus are given below.

An ebonite trough 20 cm. high and 6·5 cm. wide was divided by vertical partitions into three chambers (Fig. 1, *A*, *B*, *C*). The two outer chambers contained amalgamated zinc plates (*D*, *E*), immersed in a saturated solution of zinc sulphate. The middle chamber contained a thin ebonite shutter *F*, which was freely movable in a vertical direction. The two partitions were pierced by a slot *G*, through which the current passed from one zinc plate to the other. As the shutter was raised or lowered it opened or closed the slot and so varied the resistance between the zinc plates.

The mechanism used for moving the shutter *F* is shown in Fig. 2. A light wooden arm *H*, 1 m. long, carried in a ball bearing at *J*, was attached at one end to the shutter *F*. On the opposite side of the bearing there were a dash-pot *K* filled with oil and surrounded by a large water-jacket, a scale-pan *M*, and a detent provided with two notches *N* and *O*. When the arm *H* was raised so that it rested in the

[1] Schott, *Arch. f. d. ges. Physiol.* XLVIII. p. 354. 1891; sp. p. 375.

[2] Gildemeister, *Arch. f. d. ges. Physiol.* CI. p. 203. 1901.

notch *N*, the slot in the trough was closed by the shutter *F*. When the
detent was drawn away, the weights in *M* drew the arm *H* downwards,
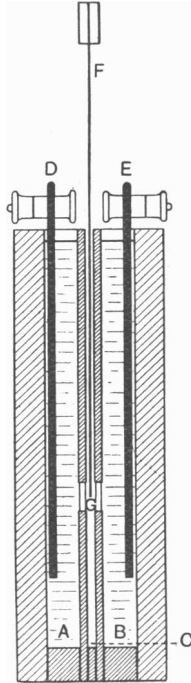

Fig. 1. Section of trough used for obtaining linear variations of current. For lettering
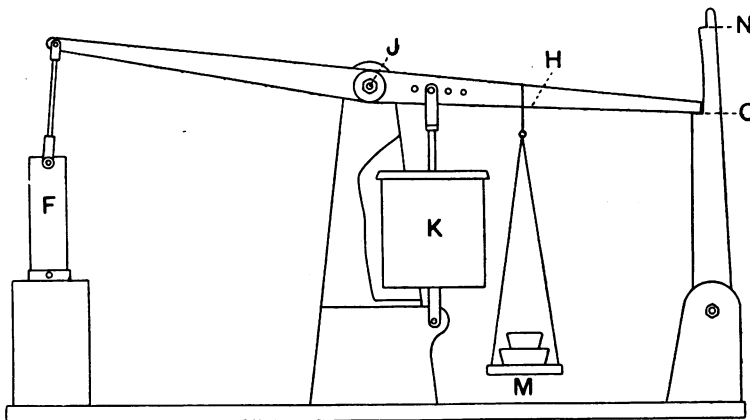see text.

Fig. 2. General view of apparatus used for obtaining linear variations of current.

and so raised the shutter *F*, until motion was arrested by the notch *O*. The velocity of the arm *H* was rendered uniform by the dash-pot *K*, which consisted of a cylinder filled with oil and containing a piston in which a leak was provided. The rate at which the shutter *F* was moved could be varied in any of the following ways:

1. By varying the load at *M*.

2. By varying the point of attachment of the dash-pot to the arm *H*.

3. By varying the leak in the piston of the dash-pot.

The second and third of these methods were used to adjust the range of velocities to suit any particular tissue upon which experiments were to be made. The first method alone was used for obtaining the actual velocities required during any single experiment. The velocity of the shutter *F* was recorded by means of a smoked paper drum upon which the arm *H* wrote directly. This drum is not shown in the figure. A fresh calibration of the velocities was made for each experiment, the water-bath which surrounded the dash-pot serving only to keep the viscosity of the oil constant for the time which one experiment occupied.

The shape of the slot *G* (Fig. 1) is a matter of the greatest importance. The current will vary inversely as the whole resistance in the circuit. If therefore the shutter moves with uniform velocity, and the slot is rectangular, so that equal areas are opened in equal times, then the current-variation will be linear only if the resistance between the zinc plates, with the slot fully open, is very large by comparison with any other resistance in the circuit. As a fact this condition is not realised. The circuit must contain the batteries and a potentiometer wire for varying the current sent into the nerve or muscle. The resistance of these two is about six ohms. That of the trough when fully open is about 15 ohms. In order then to yield a linear variation of current the slot must be opened more and more rapidly as its own resistance becomes a smaller proportion of that of the whole circuit. It is easy to calculate, for any relative values of the slot resistance and the remaining resistance, how the resistance of the slot is required to vary. The shape of the slot can then be made accordingly. I found it most convenient to calculate on the assumption that the resistance of the slot was equal to that of the remainder of the circuit, and then to add resistance to the circuit until this condition was realised.

Verification of the apparatus. To test whether the apparatus did actually yield linear current-variations under the conditions of experi-

ment it was necessary to record the current-change by means of a galvanometer whose period of oscillation should be much shorter than the duration of the current-changes used. Since I wished to use current-variations ranging in duration from 1·5 secs. to 0·03 sec., and reaching full values of from 10^{-6} to 10^{-4} ampère, the only instrument which would serve was the string galvanometer.

The instrument used was supplied by the Cambridge Scientific Instrument Company. I had it fitted with a "string" consisting of a silver wire of 20μ diameter. This relatively coarse wire executed an excursion of 13 mm. on the recording plate in 0·01 sec. when a current of 5×10^{-4} ampère was made instantaneously. It was therefore quick enough for testing the current-variation at all but the shortest durations.
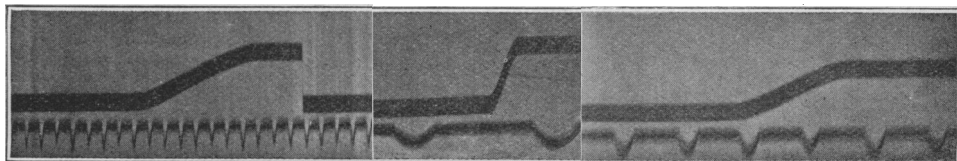

Fig. 3.   Fig. 4.   Fig. 5.

Fig. 3.   Record of current-variation. The current is turned on by the shutter-rheonom and broken by a key. Time-marker 0·2 sec. Current 5×10^{-4} ampère.

Fig. 4.   Rapid current-variation obtained with shutter-rheonom. Time-marker 0·2 sec. Current 5×10^{-4} ampère.

Fig. 5.   As Fig. 4; current reduced to 7×10^{-6} ampère.

Fig. 3 shows a record obtained under the conditions mentioned above, the slot in the ebonite trough being that actually used in the subsequent experiments on muscle and nerve. The current reached its full value in about 1·4 secs. Since the period of the string was less than a hundredth of this time, and since the deflections were proportional to the current-strength within less than 2 % over the range used, the actual deflection at any instant may be taken to represent fairly accurately the instantaneous value of the current. The record shows therefore that the current varied directly as the time, except for a small decrease in the rate of variation as the full value of the current was approached. This divergence is in the same direction as the small errors which arise from the damping of the string and from the slight decrease of deflection for a given increase of current as the string moves further from its mean position. So I did not attempt to straighten the curve out by any further alteration of the slot.

Fig. 4 is from an experiment made under conditions identical with those of Fig. 3, except that the slot was opened more rapidly. The current-variation occupied 0·04 sec. In this case the period of the string is only a quarter of the time of the current-variation, and there is consequently some distortion of the curve, especially noticeable as the string begins to move. In Fig. 5 the derived circuit from the potentiometer wire included not only the string galvanometer, as in the previous experiments, but also a toad's sartorius muscle and the usual non-polarisable fluid electrodes. The current was reduced to 7×10^{-6} ampère, about the minimal strength required for the excitation of muscle by an instantaneous increase of current. In order to yield deflection enough with this small current the string had to be slackened until its period fell to 0·03 sec. The duration of the current-variation was 0·3 sec. This record is included because it shows that the current-variation is practically linear under the actual conditions of experiment.

THE RELATION OF THE LIMINAL CURRENT-STRENGTH TO THE CURRENT-GRADIENT.

A. *The sciatic nerve of the toad.*

My first observations were made upon the toad, because toads are more resistant than frogs to the unhealthy conditions of laboratory life. The sciatic-gastrocnemius preparation was excised and placed in the fluid electrodes which I have described elsewhere[1]. The muscle lay in the Ringer's fluid of the upper electrode, and the nerve passed downwards across the air-space into the fluid of the lower electrode. The whole electrodes were as usual included in a large water-bath maintained at a temperature between 10° C. and 11·5° C. Descending currents were sent through the nerve, and the gastrocnemius was used as the index of excitation. Stimuli were not sent into the nerve more frequently than three a minute. An experiment consisted in determining the liminal current-strength first for an instantaneous increase of current, and then for a series of currents increasing in certain known times. The experiment was repeated after an interval of a few minutes, and if the two sets of observations failed to agree within 10 % the tissue was regarded as being in an unsteady state.

The first point which I noticed was that it was almost impossible to obtain the required agreement between two sets of observations made

[1] Cf. this *Journal*, xxxiv. p. 375, Fig. 3. 1906.

during the first half hour after the preparation had been excised. At
about one hour after excision the results became fairly steady, and
reliable observations could then be made at any time during the
succeeding six hours. I shall therefore begin by describing the results
obtained between the end of the first hour and the beginning of the
seventh, and shall afterwards consider what happens before the end of
the first hour.

Twelve experiments were made at various times between the end of
the first hour and the beginning of the seventh, the preparations being
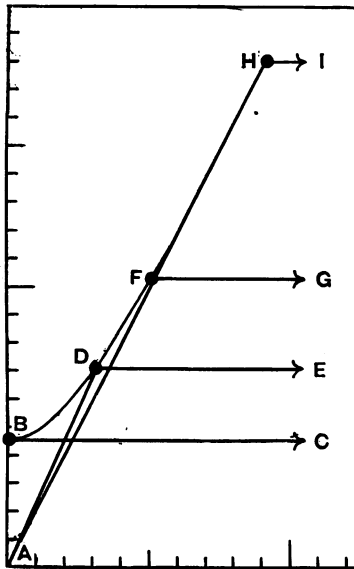taken from eight different toads. Fig. 6 (Exp. 1) is a typical example of

Fig. 6. Relation between the time in which the current reaches its full value and the
liminal current-strength. Sciatic nerve of toad. Abscissæ, 1 division=0·01 sec.
Ordinates, 1 division=1 microampère. For lettering see text.

the results obtained. In this figure abscissæ measure the time in which
the current reached its full value, and ordinates measure the current-
strength required to produce a minimal contraction. The point *B* marks
the current-strength required to excite when the current was turned
on instantaneously by means of a key. *D* marks the current-strength
required when the current reached its full value in 0·031 sec., *F* the
current-strength required when the current reached its full value in
0·051 sec., and so on. In other words, the current-variations required to
excite are represented by *ABC*, *ADE*, *AFG*, and *AHI*. It is clear at

once that there is a minimum current-gradient, represented by the line *AFH*, and that any gradient less steep than this will fail to provoke a twitch of the muscle, even though the current-strength finally reached be considerably increased. For example, if the current-strength ultimately reached be that represented by *H* instead of *F*, the current-gradient cannot be decreased, but must still follow the line *AFH*. The position of the point *D* indicates that as the current-gradient is decreased from *AB* to *AF* the liminal current-strength has to be increased gradually, somewhat as the curve joining the points *BDF* suggests.

All the twelve experiments made agreed in showing a minimal current-gradient similar to that of Fig. 6. Some showed the gradual increase of the liminal current-strength as the current-gradient was decreased from the instantaneous to the minimal, in others all the observations made fell upon the minimal gradient. Two examples are shown graphically in Fig. 7 (Exp. 2 *a*) and Fig. 8 (Exp. 3); in Fig. 7 the minimal gradient alone is seen, the times of current-increase chosen having been too long to illustrate the rest of the curve; in Fig. 8 the gradual approach to the minimal gradient is shown.
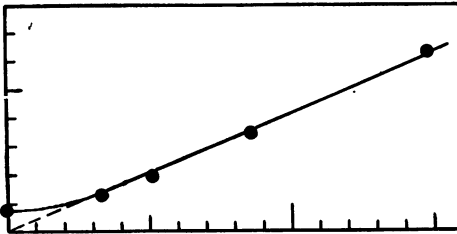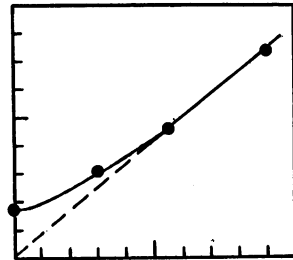

Fig. 7.   Fig. 8.

Fig. 7. As Fig. 6, showing four observations lying on the minimal current-gradient.
Fig. 8. As Fig. 6, illustrating the gradual approach to the minimal current-gradient.

The full numerical data of Exps. 1 to 3 are set out in Table A below. On comparing Exp. 1, which was made one hour and a half after excision, with Exp. 1 *a*, which was made on the same preparation at two and a half hours, we find a close agreement between the values found for the liminal current-strengths. The same agreement is even better illustrated in Exps. 2 and 2 *a*. It is clear that the preparations used were in a steady state. The remaining experiments are not shown in full detail, but the reduced results of all are given in Table A₁ below.

TABLE A. *Showing numerical values for experiments made on the sciatic nerve of the toad. (Experiments denoted by the same number, as* 1, 1 *a, were made on the same preparation.)*

Exp. 1. 1½ hours after excision. Temp. = 10·5° C.

Time of current-increase	Liminal current-strength (microampères)[1]			Relative current-strength
	1st obs.	2nd obs.	Mean	
Instantaneous	4·51	4·51	4·51	1
0·031 sec.	7·03	7·13	7·08	1·57
0·051 ,,	9·89	10·58	10·23	2·27
0·092 ,,	17·4	18·6	18·0	4·00

Exp. 1 *a*. Same preparation as Exp. 1. 2½ hours after excision. Temp. = 10·8° C.

Instantaneous	4·23	4·23	4·23	1
0·031 sec.	6·68	6·80	6·74	1·58
0·051 ,,	9·44	8·96	9·20	2·18
0·092 ,,	16·80	16·34	16·57	3·92

Exp. 2. Sciatic-gastrocnemius of toad. Experiment made 1¼ hours after excision. Temp. = 10·5° C.

Instantaneous	0·70	0·74	0·72	1
0·033 sec.	1·24	1·28	1·26	1·75
0·041 ,,	1·55	1·57	1·56	2·17
0·051 ,,	1·98	2·00	1·99	2·76
0·086 ,,	3·45	3·49	3·47	4·82

Exp. 2 *a*. Same preparation as Exp. 2. 2½ hours after excision. Temp. = 10·4° C.

Instantaneous	0·79	0·79	0·79	1
0·033 sec.	1·32	1·29	1·30	1·65
0·051 ,,	1·95	1·98	1·96	2·49
0·086 ,,	3·45	3·48	3·46	4·38
0·148 ,,	6·22	6·45	6·33	8·00

Exp. 3. 2 hours after excision. Temp. = 10·2° C.

Instantaneous	1·78	1·78	1·78	1
0·030 sec.	3·06	3·06	3·06	1·72
0·055 ,,	4·51	4·67	4·59	2·58
0·090 ,,	7·14	7·64	7·39	4·15

Now at first sight it appears that there is considerable divergence between the values of the minimal current-gradient obtained from experiments on different toads. For example, in Exp. 1 (Fig. 6) the minimal gradient is such that a current of 20 microampères is reached in 0·1 sec. In Exp. 2 (Fig. 7) on the other hand the current reached in 0·1 sec. is only 4 microampères. But this divergence disappears if we take as our unit in each experiment the current required to excite with instantaneous increase, and express the current-strength required for other times of increase in terms of this. We then find a close agreement between the two experiments.

[1] Microampère = 10^{-6} ampère.

	Exp. 1			Exp. 2	
Time	Relative current-strength		Time	Relative current-strength	
Inst.	1		Inst.	1	
0·031 sec.	1·57		0·033 sec.	1·65	
0·051 ,,	2·27		0·051 ,,	2·49	
0·092 ,,	4·00		0·086 ,,	4·38	

This is the method which v. Kries adopted for comparing the results obtained from different preparations. He used the term "Reizungs-divisor" to describe what I call the "relative current-strength." In Table A the right-hand column in every experiment gives the values of the relative current-strength, and on examining these columns one finds a close agreement between the values found for any particular time of current-increase. This means that if we take the liminal current-strength for an instantaneous increase of current as unity and express all other current-strengths used in terms of this unit, then the minimal current-gradient is nearly alike for all the preparations used. To make this point clear I have calculated for all the experiments made the relative current-strength which would be reached if the minimal current-gradient were followed for one second. The values found are tabulated below.

TABLE A_1. *Minimal current-gradients for sciatic nerve of toad between* 10° *C. and* 11·5° *C. The numbers represent the relative current-strength which would be reached in one second by a current increasing along the minimal gradient, the liminal current-strength for an instantaneous increase of current being taken as unity.*

Number of experiment	Time after excision	Relative current-strength reached in one second on minimal current-gradient
1	1½ hours	44
1 a	2½	43
2	1¼	55
2 a	2½	52
3	2	46
4	3	52
5 a	3	39
6	3	40
7	3	41
7 a	5	44
7 b	6½	50
8	1	51
	Mean	46

The values range from 39 to 55, with a mean of 46. It is interesting to note that they bear no constant relation to the time after

excision. As the time passes they may increase slightly as in Exp. 7, or decrease as in Exps. 1 and 2. Exp. 8 gives a value at 1 hour almost identical with that of Exp. 7 b at 6½ hours. One may conclude then that between the end of the first hour and the beginning of the seventh there is a definite minimal current-gradient, which changes very little; and this gradient is such as would arrive in one second at a current-strength about 40 or 50 times as great as the liminal current-strength for an instantaneous increase of current.

There remains the question, what occurs during the first hour after excision? As I have said, the results obtained during that period are not steady. But they agree in showing as a general rule a less steep minimal current-gradient than that obtained during the subsequent steady period. Take for example Exp. 5, which was made half an hour after excision upon the same preparation as Exp. 5 a already described.

Exp. 5. Sciatic-gastrocnemius of toad. Exp. ½ hour after excision. Temp.=10·4° C.

Time of current-increase	Liminal current-strength
Instantaneous	1·69 microampères.
0·03 sec.	2·24 ,,
0·05 ,,	2·82 ,,
0·09 ,,	3·85 ,,
0·16 ,,	5·38 ,,
0·27 ,,	8·03 ,,

This experiment is plotted in Fig. 9, and one sees that the minimal current-gradient is only just being approached at the slowest current-variation used. The relative current-strength reached in one second by a
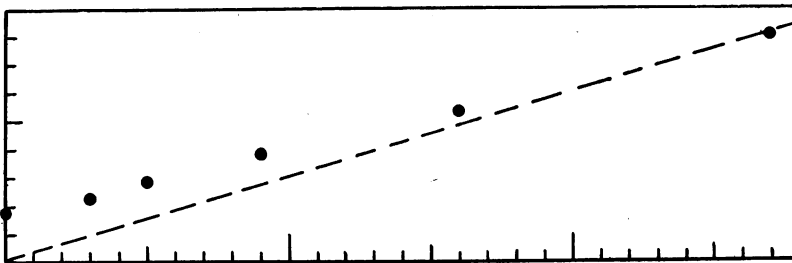

Fig. 9. Relation between time of current-increase and liminal current-strength from an experiment made half an hour after excision. Sciatic nerve of toad. The steady state has not yet been reached, and the minimal current-gradient is low. Abscissæ, 1 division=0·01 sec. Ordinates, 1 division=1 microampère.

current increasing along the minimal current-gradient would work out at something less than 18. The same preparation gave the value 39 at 3 hours (Exp. 5 a). It is clear that during the first hour after

excision the minimal gradient becomes more steep. But whether this change is the recovery of a normal state after the disturbance due to excision, or a transition from the normal state of life to a new steady state of survival, I am unable to say. This question demands for its solution experiments made without damage to the motor cells and trunk of the sciatic.

It may well be that this period of change was responsible for the irregular results which the experiments of v. Kries yielded. For experiments made at varying times during the first hour after excision would certainly show such discordance as he found.

As I have already stated, the experiments made by Schott[1] led him to conclude that to excite the sciatic nerve of the toad the same current-strength is required whether the current-increase is instantaneous or occupies 0·1 sec. My own experiments are in complete disagreement with this conclusion; for they show that a current increasing in 0·1 sec. would need to be on the average 4·6 times as great as one increasing instantaneously. Schott considers that the law for toad's nerve differs fundamentally from that for frog's nerve. With this I cannot agree, for, as I shall show in the next section, the curves relating current-strength to time of current-increase are of the same form in the frog and in the toad. The only difference which I am able to discover between preparations taken from the two animals lies in the fact that the minimal current-gradient is slightly steeper for the frog than for the toad.

B. *The sciatic nerve of the frog.*

The method of experiment for the frog was in every way identical with that already described for the toad. Seven experiments were made, and they all showed a definite minimal current-gradient. Two experiments showed the gradual increase of the liminal current-strength as the current-gradient was reduced from instantaneous to its minimal value. Exp. 9, which is plotted in Fig. 10, is an example of this.

＇The full numerical data for Exps. 9 to 11 are shown in Table B.

The experiments in Table B show that, as in the case of the toad, the absolute current-strengths for any time of current-increase vary considerably in different preparations. But the relative current-strengths agree closely enough. In the table below are given for the seven experiments made, the relative current-strengths which would be

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[1] Schott, *loc. cit.*

reached in one second by a current following the minimal current-gradient.

TABLE B. *Experiments made on the sciatic nerve of the frog.*

Exp. 9.   1 hour after excision.   Temp. = 10·0° C.

Time of current-increase	Liminal current-strength (microampères)			Relative current-strength
	1st obs.	2nd obs.	Mean	
Instantaneous	1·06	1·14	1·10	1
0·03 sec.	1·96	2·14	2·05	1·86
0·054 ,,	3·20	3·40	3·30	3·00
0·094 ,,	5·70	5·80	5·75	5·22

Exp. 9 a.   3¾ hours after excision.   Temp. = 10·5° C.

Instantaneous	1·35	1·37	1·36	1
0·030 sec.	2·94	2·85	2·89	2·13
0·054 ,,	5·03	5·03	5·03	3·70
0·092 ,,	9·10	9·18	9·14	6·72

Exp. 10.   4 hours after excision.   Temp. = 10·8° C.

Instantaneous	1·34	1·34	1·34	1
0·030 sec.	3·52	3·44	3·48	2·60
0·056 ,,	6·08	6·08	6·08	4·54

Exp. 11.   2½ hours after excision.   Temp. = 10·0° C.

Instantaneous	1·38	1·41	1·39	1
0·031 sec.	2·53	2·56	2·54	1·83
0·054 ,,	3·52	3·84	3·68	2·64
0·086 ,,	5·75	6·07	5·91	4·25

TABLE B₁.   *Minimal current-gradients for sciatic nerve of frog between* 10° C. *and* 11·5° C.

Number of experiment	Time after excision	Relative current-strength reached in one second on minimal current-gradient
9	1 hour	57
9 a	3¾ hours	72
10	4 ,,	81
11	2½ ,,	50
12	1¼ ,,	51
12 a	2½ ,,	67
13	2 ,,	60
		Mean 63

The values in this case vary between 50 and 81 with a mean of 63. The mean for the toad was 46.   The nerve of the frog has therefore a steeper minimal current-gradient than has the nerve of the toad.

C. *The sartorius muscle of the toad.*

v. Kries[1] states that the curarised muscle of the frog requires the same current-strength for its excitation whether the current reaches its full value instantaneously or in 0·125 sec.

I have found a similar result in the nerve-free pelvic end of the uncurarised sartorius of the toad. The muscle was set up in the fluid non-polarisable electrodes, with the anode and cathode both in the extreme 3 mm. of the pelvic end. The lower end of the muscle was attached to a thin glass rod, which passed vertically downwards through a hole in the U-tube which formed the lower electrode. The fluid could not escape by this hole, since the electrodes were made air-tight at every other point. The hole could therefore be made large enough to allow the glass rod to move up and down without sensible friction.
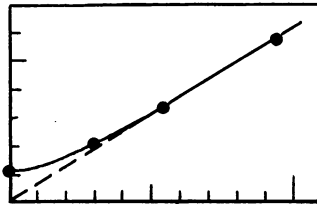

Fig. 10. Relation between time of current-increase and liminal current-strength in the sciatic nerve of the frog. Abscissæ, 1 division = 0·01 sec. Ordinates, 1 division = 1 microampère.

The lower end of the rod was attached to an optical lever, which indicated the contraction of the muscle with a magnification of twenty times. I found the current-strength required to produce a minimal contraction identical whether the current increased instantaneously or in any time up to 1·2 secs.

This result could probably have been foreseen. For we know that a muscle responds by a local cathodic contraction to a current passing at constant value; and the method used would indicate a local contraction or a conducted contraction without distinction. But we also know that when a current is sent through a muscle the occurrence of a contraction conducted over the muscle's length is associated with the initial and final periods of current-variation, not with the passage of the current at constant value. Therefore we should expect to find some definite relation between the current-gradient and the setting up of a conducted disturbance in the muscle. To investigate this relation we

[1] v. Kries, *loc. cit.* p. 358.

require a method which will indicate the occurrence of a conducted disturbance, but will take no notice of a local contraction.

For this purpose I excited as before in the extreme pelvic end of the muscle, and used an optical lever to indicate the thickening of the muscle at a point near its extreme tibial end. The arrangement of the apparatus is shown in Fig. 11. The upper electrode was formed by a tube *A*, filled with Ringer's fluid and closed above by the porous
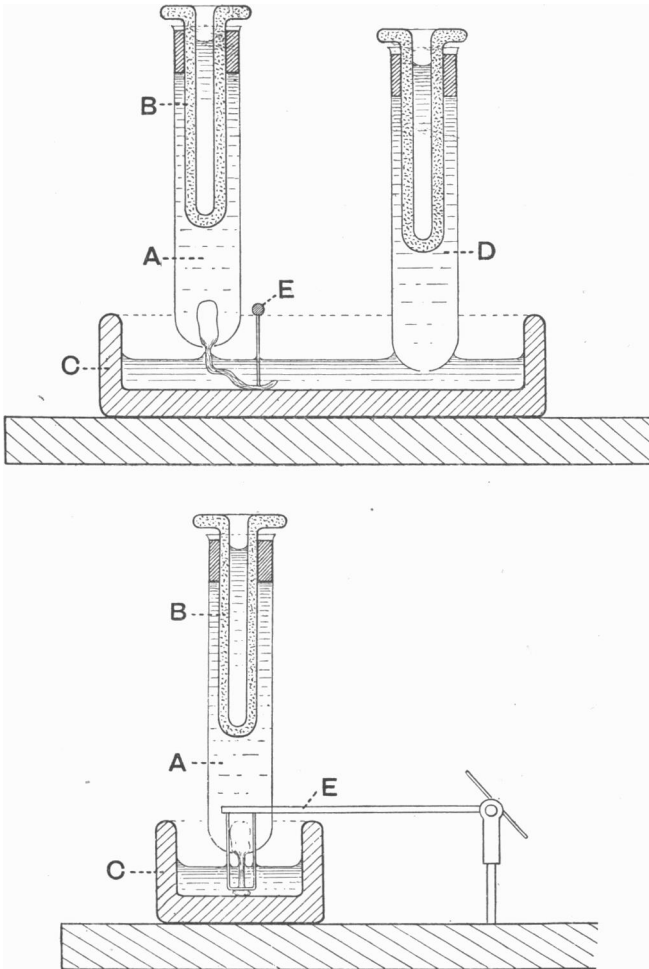

Fig. 11. Apparatus used for indicating the occurrence of a conducted excitation in the sartorius muscle. Two sections in planes at right angles. For description see text.

candle *B*, containing a saturated solution of zinc sulphate. From the
lower end of this tube the muscle passed into Ringer's solution
contained in the glass trough *C*. A second glass tube *D*, established
electric connection with the fluid in the trough. In effect the
electrodes were the fluid surfaces at the lower end of *A* and at the
point where the muscle entered the Ringer's fluid in *C*. The tibial
end of the muscle supported a platinum-pointed lever, *E*, which
carried a mirror on its axle and served to indicate the occurrence of
any contraction which might be caused by a conducted disturbance
travelling over the muscle from the seat of excitation.

It was apparent at once that with this arrangement the current-
strength had to be increased as the time of current-increase became
longer. To test the relation quantitatively, five experiments were
made at times varying between 1½ and 16 hours after excision. They
all showed the liminal current-strength increasing gradually with
decrease of the gradient until a minimal gradient was reached.
Fig. 12 (Exp. 14) and Fig. 13 (Exp. 17) are typical of the results
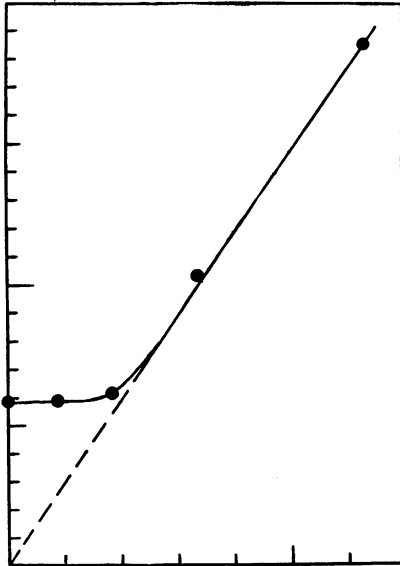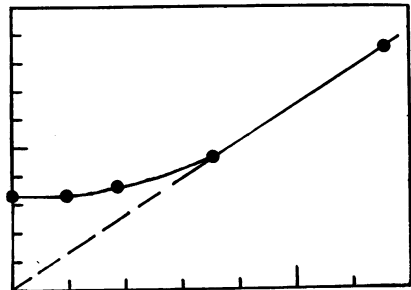

Fig. 12.   Fig. 13.

Fig. 12. Relation between time of current-increase and liminal current-strength in sartorius
    muscle of toad. Abscissæ, 1 division = 0·1 sec. Ordinates, 1 division = 10 micro-
    ampères.

Fig. 13. As Fig. 12, illustrating the gradual approach to the minimal current-gradient.

obtained. The full numerical values of the five experiments are given in Table C below.

TABLE C. *Experiments made on the sartorius muscle of the toad.*

EXP. 14. 1½ hours after excision. Temp. = 15·5° C.

Time of current-increase	Liminal current-strength (microampères)			Relative current-strength
	1st obs.	2nd obs.	Mean	
Instantaneous	57	60	58·5	1
0·089 sec.	57	60	58·5	1
0·184 ,,	60	63	61·5	1·05
0·337 ,,	105	106	103·5	1·77
0·63 ,,	184	185	184·5	3·16

EXP. 15. 1½ hours after excision. Temp. = 13·5° C.

Instantaneous	29·9	32·5	31·2	1
0·096 sec.	30·5	33·1	31·8	1·02
0·182 ,,	31·8	33·8	32·8	1·05
0·364 ,,	34·4	37·7	36·0	1·15
0·77 ,,	46·1	49·4	47·7	1·53
1·43 ,,	76·7	81·9	79·3	2·54

EXP. 15 a. 16 hours after excision. Temp. = 12·0° C.

Instantaneous	31·5	36·9	34·2	1
0·105 sec.	33·7	38·7	36·2	1·06
0·195 ,,	38·2	42·3	40·2	1·18
0·365 ,,	60·3	61·2	60·7	1·77

EXP. 16. 1½ hours after excision. Temp. = 14·0° C.

Instantaneous	57·7	60·3	59	1
0·105 sec.	57·7	61·2	59·4	1·01
0·195 ,,	69·6	74·8	72·2	1·22
0·365 ,,	136	163	149	2·51

EXP. 17. 5 hours after excision. Temp. = 15·0° C.

Instantaneous	33·6	33·6	33·6	1
0·096 sec.	33·6	33·6	33·6	1
0·185 ,,	37·2	36·0	36·6	1·09
0·354 ,,	49·2	44·4	46·8	1·39
0·655 ,,	87·7	84·0	85·8	2·55

The arrangement of these experiments rendered impossible the use of a water-bath enclosing the whole apparatus, so I had to be content with the temperature of the room. This varied, as Table C shows, between 12° and 15·5° C. In spite of this the minimal current-gradients found in the five experiments showed a tolerable uniformity. One only, Exp. 15, shows a large divergence from the rest.

TABLE C_1. *Minimal current-gradients for sartorius muscle of toad between* 12° *C. and* 15·5° *C.*

Number of experiment	Time after excision	Relative current-strength reached in one second on minimal current-gradient
14	1½ hours	5·1
15	1½ ,,	1·8
15 a	16 ,,	4·7
16	1½ ,,	6·7
17	5 ,,	3·8
		Mean 4·4

The mean value found is 4·4; that for toad's nerve was 46. The minimal current-gradient for toad's nerve is therefore about ten times as steep as that for toad's muscle. This difference seems to be due to a real difference between the tissues, and not in any considerable degree to the small temperature-difference between the two sets of observations. For amongst the experiments made on toad's muscle there is a considerable divergence of temperature, but there is no traceable relation between the temperature of each experiment and the value found for the minimal current-gradient, such as would lead us to suspect that the current-gradient had a very large temperature coefficient.

CURRENT-VARIATION AND THE THEORY OF ELECTRIC EXCITATION.

In recent years physiologists have become more fully aware of the part which the duration of the exciting current plays in the production of an excitation. In the nerves and muscles of many animals precise measurements have been made of the relation between the duration of the exciting current and the least current-strength which will suffice for excitation.

This new knowledge led at first to an unduly great reaction from the older view that current-variation alone determined the efficacy of an exciting current. Thus Weiss[1] formulated a law in which the excitation produced appeared as a function simply of the quantity of electricity brought into play. It seemed to me that any view of electric excitation which left current-variation wholly out of account must be incorrect, for the fact that slowly increasing currents needed to be stronger than rapidly increasing currents was well known. I sought therefore to find some means of reconciling the views, that on the one hand current-variation, and on the other hand current-duration at

[1] Weiss, *Arch. Ital. Biol.* xxv. p. 438.

constant value were the essential conditions for producing an excitation. In a paper published in 1907[1] I made use of a suggestion, put forward originally by Woodworth[2] in the course of a paper dealing with the excitation of smooth muscle, that the need of current-duration was in reality illusory, and depended upon the necessity of separating in time the opposed effects of make and break between which there would otherwise be interference.

This suggestion has not stood the test of closer examination. As Hoorweg[3] has pointed out, it fails to account for the fact that the relation between current-duration and liminal current-strength is the same for short-battery currents, in which the increase and decrease of current are both equally steep and constant, and for condenser-discharges, in which the decrease of current is of variable gradient always less steep than the increase.

It seems therefore that we must accept the view that the duration of a current is an essential condition of the efficacy as an exciting cause, in the sense that the actual passage of the current at constant value is contributing directly to the excitatory effect. But in basing upon this fact any theory as to the nature of the physical changes which constitute excitation we must not leave out of account the question of current-variation, whose importance is made clearer by the proof given in this paper of the very definite nature of the minimal current-gradient.

Now recent attempts to formulate a theory of excitation spring naturally from the idea to which Nernst[4] first gave expression, that since animal tissues are electrolytic conductors divided up by semipermeable membranes, electric currents passed through them will certainly produce polarisation across the membranes, and it is consequently worth while to enquire first of all whether the excitatory change may not consist in such a polarisation.

The knowledge that excitation demands a certain duration of current for its accomplishment at once inspires the hope that Nernst's suggestion may be put to the proof, and as Sutherland[5] has suggested, one is reminded by Weiss's law of Faraday's law of electrolysis. The most recent enquiries in this field are those of Lapicque[6]. The results

[1] This *Journal*, xxxv. p. 310. 1907.
[2] Woodworth, *Amer. Journ. Physiol.* iii. p. 33. 1899.
[3] Hoorweg, *Arch. f. d. ges. Physiol.* cxix. p. 39. 1907.
[4] Nernst, *Zeitschr. f. Electrochemie*, p. 665. 1904.
[5] Sutherland, *Arch. f. d. ges. Physiol.* cxv. p. 622.
[6] Lapicque, *Journ. de Physiol. et de Path. gén.*, p. 565, and p. 620. 1907; *C. R. de la Soc. de Biol.* lxiii. p. 37.

which he has obtained are of the highest interest. He shows that the well-known relation between the duration of an exciting current and its minimal current-strength can be reproduced with great fidelity from experiments made upon the polarisation across an artificial semipermeable membrane separating two electrolytes. In place of the current-strength required to produce an excitation in nerve or muscle he measures the current-strength required to produce at each current-duration a definite back E.M.F. of polarisation across his artificial membrane. The relation between current-strength and current-duration is identical in the two cases. The natural inference is that the effect which an exciting current has to produce is a definite degree of polarisation in the nerve or muscle. But if this were all, excitation would be independent of the rate of current-variation. Lapicque[1] admits the difficulty and ends with the words: "It is a defect, it is not an objection; one must recognise that these ineffective currents increase *very slowly* by comparison with the durations considered here; it is a question of times of a different order." In view of the more precise knowledge which we now possess we may enquire whether the existence of a minimal current-gradient for the excitation of nerve is any bar to the identification of the excitatory process with a simple polarisation.

We have seen that in muscle the production of a local cathodic contraction is independent of current-variation in the exciting current. For the production of a conducted disturbance on the other hand there is a definite minimal current-gradient. In the case of nerve also a certain rate of current-variation is essential if a conducted disturbance is to be provoked. The question of a local excitation of nerve could not be tested, since we have no criterion of excitation in a nerve except the effect produced when the excitation is conducted.

Now it is a question of the greatest importance for the theory of electric excitation whether the local cathodic contraction produced in muscle by an unvarying current involves the same excitatory process as that which is produced in the muscle when a conducted excitation is set up. If the two are identical, then it is clear that the conditions required for the mere production of the excitatory state might conceivably be shown to correspond completely with those necessary for the production of a simple polarisation, a definite current-gradient being necessary for neither. The need for a current-gradient would then appear as an additional requirement connected not with the

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[1] Lapicque, *Journ. de Physiol. et de Path. gén.* p. 635. 1907.

production of the excitatory state, but with its spread as a conducted disturbance to neighbouring parts of the tissue. It might be shown in fact that excitation meant merely the production of a certain concentration of ions, and that the change did not spread to neighbouring parts of the tissue unless the ions were moved at a certain rate.

But if the local cathodic contraction does not involve the ordinary excitatory change; if, as may well be, the current at constant value acts directly on the contractile mechanism, and so produces a contraction without calling the excitatory change into existence at all, then the need for a minimal current-gradient may be a more serious bar to the identification of the excitatory change with a polarisation. For in this case it would be necessary to suppose that the required concentration of ions could not be produced unless the current used were varying at a certain minimum rate. And a simple polarisation requires no such variation of current. Some additional factor would therefore have to be called in, such as would render the current less effective as the time of its passage increased.

I hope soon to publish some experiments dealing with this question.

The comparison which Lapicque draws between the conditions necessary for setting up a conducted disturbance in nerve and those necessary for producing a simple polarisation in his model, is of course perfectly legitimate, in spite of the fact that the nerve requires a current-variation and the polarisation does not. For the rates of current-variation in the currents used to determine the relation of current-duration to current-strength in the nerve are all extremely great, so great indeed as to lie in that region of current-gradients where current-variation may be changed considerably without involving any perceptible change in the liminal current-strength. That such a region exists for nerve we know from the experiments of Gildemeister[1]; the curves plotted in this paper show that it exists also for muscle.

In discussing in a former paper[2] the reason why in any excitable tissue the liminal current-strength began to increase when the current-duration was reduced beyond a certain fixed value, I came to the conclusion that such a duration was equal to the time occupied by the excitatory process in just reaching its full value. It is interesting to observe that on the assumption that excitation means polarisation the same would be true. For the current-strength would need to be increased only if the current-duration were not long enough to allow the necessary concentration of ions to be completed. The duration at which the liminal

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[1] *loc. cit.* [2] *loc. cit.* p. 319.

current-strength began to increase would therefore be that at which the polarisation effected by the minimal current just reached its full value.

SUMMARY.

A series of electric currents, increasing to their full values directly as the time but with different gradients, is sent into the sciatic nerve of the toad. It is found that as the current-gradient is decreased the current-strength required for excitation increases more and more rapidly, until a definite minimal gradient is reached. No gradient less steep than this will excite, even though the current-strength ultimately reached be as much as eight times as strong as the current-strength required to excite with an instantaneous increase of current

In toad's nerve between 10° C. and 11·5° C. the minimal gradient is such that a current increasing along it would reach in one second about 45 times the current-strength required for minimal excitation with a current increasing instantaneously.

In frog's nerve kept under like conditions the minimal gradient is steeper. It is such that in one second a current would be reached 60 times as great as that required for minimal excitation with a current increasing instantaneously.

These results are obtained by experimenting upon the tissues between one and seven hours after excision. During this period the value of the minimal gradient remains remarkably steady. During the first hour after excision the minimal gradient is unsteady.

Direct excitation of the toad's sartorius muscle shows that for the production of a local contraction the liminal current-strength is identical whether the exciting current increases instantaneously or in any time up to 1·2 sec. Experiments were not made with gradients less steep than this. If however the experiment is so arranged that only excitations conducted away from the seat of stimulation are recorded, the liminal current-strength increases with decrease of the current-gradient in a curve similar to that obtained from the experiments on nerve. The minimal current-gradient for the muscle is such that a current would reach in one second 4·4 times the value required to produce a minimal excitation with a current increasing instantaneously. The minimal gradient for nerve is therefore about ten times as steep as that for the muscle of the same animal.