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THE EFFECT OF ELECTROTONUS ON THE EXCITABILITY OF NERVE

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THE decrease in threshold of nerve excitation due to catelectrotonus, which with strong electrotonus may become an increase in threshold, and the increase in threshold with anelectrotonus are well established. Less, however, is known of the effect of electrotonus on the time-factor of excitation. Cardot [1914] and Cardot & Laugier [1914*a*; see also Laugier, 1921] found that the intensity-duration curve is raised or lowered parallel to itself by electrotonus. This involves a change in chronaxie. On the other hand Kodera [1928] found that the threshold intensities for different durations are all multiplied by a certain factor in electrotonus. This means that chronaxie is not affected by electrotonus. Bouman [1931] found a change in chronaxie by electrotonus which could easily be removed by a small alternating current. Complete intensity-duration curves were not determined in his experiments. Little moreover is known about the influence of various ions on electrotonus. These points are considered in this paper, while the last part of it deals with the influence of inter-electrode distance on the effects of electrotonus.

METHOD

All experiments are performed on sciatic nerves of Hungarian *Rana esculenta*. The electrical circuit is essentially that used by Hill [1936*b*] for determining the time-factor *k* of excitation. The nerve was stimulated by repetitive condenser discharges at a frequency of 20 per sec. The nerve impulse was detected by its action current, which was integrated by a sensitive galvanometer (Kipp Zd). Semimaximal response was always taken in order to give constant results and avoid double intensity-duration curves [Hill, 1936*b*, p. 449]. Stimulating and action current electrodes were calomel half cells with sharp-edged wooden electrodes.

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The discharge time of the stimulating circuit is determined by a resistance R_1 of 1000 ohms together with the capacity C of the stimulating condenser. A resistance R_2 of 200,000 ohms is connected in series with the nerve, so that changes in nerve resistance could have no significant influence on the discharge time of the condenser. A calibrated slide-wire potentiometer is also connected in series with the nerve for the adjustment of the polarizing current. The total resistance of this instrument (Pye, Cambridge) is 30 ohms, so that changes in the setting of the contact did not appreciably change the resistance of the nerve circuit. The 200,000 ohms also make the polarizing current approximately independent of nerve resistance. The voltage of the polarizing battery was measured before and after each experiment and the intensity of the polarizing current adjusted by the potentiometer.

All nerves were soaked in oxygenated Ringer's solution before starting any experiment. For those experiments requiring soaking times of 10 hours and more the major part of the soaking was done in a refrigerator without bubbling oxygen. The nerve was removed from the refrigerator 2–3 hours before the actual experiments and placed in a freshly oxygenated solution at room temperature.

The experiments require considerable care in order to obtain constant results. Fortunately Hill's theoretical equation [Hill, 1936*b*] provides a check on the results obtained. A few experiments had to be discarded because they did not fit this equation.

The actual experiments were performed in the following way. A certain discharge time RC was taken. First the threshold was determined without electrotonus. Then catelectrotonus was switched on and after a few seconds the threshold was determined again. Then electrotonus was removed and after a short interval the threshold was determined again. Next, anelectrotonus was introduced and another determination of the threshold was made. Finally, after switching off the electrotonus the threshold was determined again. This procedure was repeated for different condenser settings and in most experiments also for constant current pulses of long enough duration to give the rheobase. Occasionally the entire experiment was repeated for different strengths of polarizing currents. In most experiments, however, it was thought advisable not to perform too many series of experiments on the same nerve muscle preparation, if constant and reliable results were to be obtained.

The constancy of the results was easily checked, as the threshold without electrotonus should be the same before and after each series of determinations. The threshold without electrotonus determined between catelectrotonus and anelectrotonus was usually slightly higher than normal, due to the after-effect of catelectrotonus. The successive application however of catelectrotonus and anelectrotonus appears to give hardly any after-effect at all. At the end of each group of experiments with a certain strength of electrotonus the threshold was again determined with the same stimulus as at the beginning, to make sure that no appreciable change in threshold had taken place. All data had to fit Hill's equation for condenser discharges. From this the factor k was determined.

Results

Part I. *The influence of electrotonus on the intensity-duration (E–RC) curve*

Provided that the precautions mentioned above are taken, reliable results are obtained. Cardot & Laugier's statement that electrotonus simply shifts the intensity-duration curve up and down could not be confirmed. It is obvious from Table I that the difference between the

Table I. Thresholds (volts) for stimuli of long and short duration, with and without electrotonus

Exp. no.	Polarizing current μA.	Without electrotonus		Catelectrotonus		Anelectrotonus	
		Long	Short	Long	Short	Long	Short
1	0·5	1·06	7·4	0·9	6·55	—	—
2	1	1·33	10·0	0·96	8·9	1·91	13·3
3	2	1·46	22·6	0·92	15·6	2·73	34·6
4	5	1·44	15·2	0·68	8·7	4·46	33
5	1	1·36	25·4	1·04	21	1·89	32·4
6	2	1·16	20·4	0·62	13·6	2·34	31·9
7	5	2·51	16·4	1·26	9·5	7·2	36
8	1	1·62	31·2	1·24	26·2	2·30	36
9	2	1·28	21·4	0·92	18·2	2·13	25

thresholds for long and short duration is not independent of electrotonus as it would be if their conclusions were correct.

It was impossible also to confirm Kodera's statement that the ordinates of the intensity-duration curve with electrotonus bear a constant ratio to those without electrotonus, involving no change in time-factor of nerve excitation. On the contrary a clear change in the time-factor k was always found. Table II gives the time-factor k calculated from the E–RC curves for the same experiments as are given in Table I. It is found that the factor k is increased in catelectrotonus and decreased in anelectrotonus. In determinations of the U–V curve [Hill, 1936*a*] by short test shocks it is found that the curve does not return to its original level as a result of electrotonus. The amount of this deviation

TABLE II. The effect of electrotonus on the time-factor k of normal nerve

Exp. no.	Polarizing current μA.	Factor k: msec. Normal	Catelectrotonus	Anelectrotonus
1	0·5	0·28	0·50	—
2	1	0·48	0·63	0·35
3	2	0·29	0·34	0·16
4	5	0·31	0·45	0·19
5	1	0·30	0·40	0·40
6	2	0·25	0·35	0·17
7	5	0·39	0·44	0·33
8	1	0·21	0·44	0·13
9	2	0·71	1·00	0·39

is obviously the result of two counteracting effects: firstly, the reduction in threshold due to catelectrotonus and secondly, the increase in k (and therefore a relative increase in threshold for short stimuli) in catelectrotonus.

Part II. *The influence of different ions on the effects of electrotonus*

The double effect of electrotonus on threshold and time-factor offered an opportunity to study the effect of different ions. The intensity-duration curve can be taken with and without electrotonus at the same time. This avoids the comparison of results obtained on the same preparation before and after intoxication, and therefore eliminates any experimental uncertainties, allowing also for long soaking times if the condition of the nerve after prolonged soaking permits reliable data to be obtained.

The effect of potassium ions. After preliminary soaking in normal Ringer's solution the nerves were soaked in a solution containing excess potassium (ten times normal in most experiments). An electrotonus experiment was then performed in the usual way. A soaking time of 2 hours was found to be necessary, longer soaking times did not change the results.

Table III gives the changes in threshold with electrotonus in a nerve which has been treated with excess potassium. The results confirm those of Chweitzer [1935] so far as catelectrotonus is concerned: catelectrotonus instead of lowering the threshold, as it does in normal nerve, raises it in the potassium-soaked nerve. According to Chweitzer the effect of anelectrotonus is not reversed after the potassium treatment. In some of my experiments the effect of anelectrotonus also was reversed. The effect, however, of anelectrotonus is not as constant as that of catelectrotonus, and for no obvious reason the reversal in anelectrotonus does not always take place.

TABLE III. The effect of electrotonus on the threshold for long-lasting currents in a nerve soaked in Ringer's solution containing excess potassium

Exp. no.	Polarizing current μA.	Threshold: volts Normal	Catelectrotonus	Anelectrotonus
1	1	4·5	5·0	4·4
2	0·5	4·7	4·9	4·4
3	5	1·5	1·8	1·8
4	5	1·7	2·0	—
5	5	1·3	1·6	1·5
6	5	1·4	1·9	—

As the soaking in ten times normal potassium reverses the effect of catelectrotonus, it is obvious that there must be some concentration which just abolishes the effect of catelectrotonus. This has a certain importance, since electrotonus provides a disturbing factor in the determination of the U–V curve [Hill, 1936*a*]. As a method, however, for routine application this offers certain difficulties. For different nerves the required concentration varies somewhat and there is no way of determining in advance the concentration necessary for any particular

TABLE IV. Change in threshold (volts) with catelectrotonus, as percentage of the threshold without electrotonus, the effect of soaking in potassium-rich Ringer's solution on this percentage and the reversibility of this effect

Exp. no.	Polarizing current μA.	Before potassium	After potassium	After potassium followed by normal Ringer's solution
1	2	-16	2	-28
	5	-26	-2·6	-42
	10	-52	1·9	-45
2	1	-18	-1·4	-10
	2	-18	2·8	-22
	5	-18	11	-30
	10	-27	38	-30
3	1	-18	-1·3	-16
	2	-27	4·5	-24
	5	-44	31	-33
	10	-51	62	-37
4	1	-10	0	-14
	2	-22	0	-25
	5	-35	0·5	-39
	10	-42	4·4	-47
5	1	-15	0	-19
	2	-29	-1·2	-33
	5	-49	-1·2	-50
	10	-57	7·8	-54
6	1	-28	6	-11
	2	-29	9	-30
	5	-47	32	-36
	10	-52	125	-27

In all Tables the sign - means a fall in threshold.

nerve. The complete abolition of the effect of electrotonus on the threshold, at least for a current of not more than a few microamperes (which is of the order of magnitude for threshold of excitation), can be more easily obtained by reducing the soaking time in a potassium solution of constant concentration (ten times normal). The experiments of Table IV (with the exception of the last experiment) show the effect of soaking for 1 hour in Ringer's solution containing ten times normal potassium. The catelectrotonus effect in the experiments with fairly weak currents is almost entirely abolished. The experiments in Table IV were undertaken to test whether the effect of potassium is reversible. The fifth column gives the percentage of threshold change with electrotonus after the nerve has been soaked again in normal Ringer's solution for the same time as it had been soaked in potassium-rich solution before. The potassium effect is reversible. The last experiment was made with both soaking times 2 hours instead of 1 hour (potassium concentration ten times normal). In this experiment also the effect is found to be reversible.

In Table V are given some determinations of the factor k (calculated from the intensity-duration curve) in nerves soaked for 2 hours in Ringer's solution containing ten times normal potassium. The effect of

TABLE V. The effect of electrotonus on the time-factor k of excitation in nerves soaked for 2 hours in Ringer's solution containing ten times the normal amount of potassium

Exp. no.	Polarizing current μA.	k: msec. Normal		
		Normal	Catelectrotonus	Anelectrotonus
1	5	0·45	1·1	0·32
2	5	0·48	0·59	0·33
3	5	0·80	1·07	0·54
4	1	0·50	0·55	0·46
5	5	0·35	0·44	—
6	5	0·35	0·50	—
7	5	0·30	0·48	—

catelectrotonus is the same as in normal nerve, giving an increase in factor k. As in the threshold determinations the effects of anelectrotonus in the potassium-treated nerves are less reliable than the effects of catelectrotonus. Those experiments, however, which give results that fit Hill's equation [1936*b*] show the same decrease in k as in normal nerve.

Treatment therefore of the nerve with Ringer's solution containing excess potassium reverses the effect of electrotonus on the threshold determined with long-lasting currents, while it does not affect the influence of electrotonus on the time-factor k. This supports Hill's assumption [Hill, 1936*a*] that electrotonus is a separate phenomenon from excitation.

The effect of calcium ions. Table VI gives the effect, on the threshold for long-lasting currents, of soaking the nerve in Ringer's solution containing ten times the normal concentration of calcium. The effect is the same as in normal nerves.

TABLE VI. The effect of electrotonus on the threshold for long-lasting currents in nerves which have been treated with excess calcium for relatively short times

Exp. no.	Polarizing current μA.	Soaking time hours	Threshold: volts Normal	Catelectrotonus	Anelectrotonus
1	2	3	1·64	1·49	2·05
2	2	3½	3·88	2·90	5·02
3	5	5	2·95	1·26	3·28
4	2	6	3·8	2·7	5·0
5	2	7½	4·1	3·0	5·4
6	2	8	4·8	3·6	6·2
7	5	9½	2·4	2·0	3·1

Table VII gives the effect of soaking in Ringer's solution containing ten times normal calcium on the time-factor k. The results seem to indicate that the effect of electrotonus on k is either much diminished, or abolished or even reversed. Experiments therefore were carried out

TABLE VII. The effect of electrotonus on the time-factor k of excitation in nerves treated with excess calcium for relatively short times

Exp. no.	Polarizing current μA.	Soaking time hours	k: msec. Normal	Catelectrotonus	Anelectrotonus
1	2	3	0·48	0·33	0·29
2	2	3½	0·18	0·25	0·18
3	5	5	0·53	0·51	—
4	2	6	0·21	0·20	0·17
5	2	7½	0·21	0·21	0·20
6	2	8	0·25	0·28	0·22

with very much longer soaking times. The soaking was undertaken in a refrigerator in order to reduce the metabolism and depreciation with time. The nerves were removed from the refrigerator 2–3 hours before the actual experiments, and put in a fresh solution of the same concentration at room temperature.

Table VIII gives the effect of this treatment on the threshold for long-lasting currents. The influence of electrotonus on the threshold for long-lasting currents is the same as in normal nerve. Table IX, however, which gives the effect of prolonged calcium treatment on k, tells a different story. After this treatment catelectrotonus gives a decrease in k instead of an increase as in normal nerve. The influence of anelectrotonus is again less clear-cut than that of catelectrotonus. Those experiments which gave reliable results showed either an increase or a decrease

TABLE VIII. The effect of electrotonus on the threshold for long-lasting currents, in nerves treated with excess calcium for relatively long times

Exp. no.	Polarizing current μA.	Soaking time hours	Threshold: volts Normal	Catelectrotonus	Anelectrotonus
1	5	12½	1·58	1·43	—
2	5	14	2·42	1·73	4·0
3	5	15	2·38	1·60	3·98
4	5	15	2·52	1·88	3·35
5	5	15	3·6	2·68	4·72
6	5	16	2·7	2·02	3·92
7	5	17	2·24	1·79	3·16
8	5	17	2·35	1·76	3·6
9	5	19	2·48	2·13	—

TABLE IX. The effect of electrotonus on the time-factor k of excitation in nerves treated with excess calcium for relatively long times

Exp. no.	Polarizing current μA.	Soaking time hours	k: msec. Normal	Catelectrotonus	Anelectrotonus
1	5	12½	0·70	0·41	—
2	5	14	0·60	0·34	0·58
3	5	15	0·48	0·34	—
4	5	15	0·47	0·32	0·47
5	5	15	0·48	0·43	0·62
6	5	16	0·43	0·32	0·48
7	5	17	0·51	0·35	0·45
8	5	17	0·45	0·32	0·52
9	5	19	0·63	0·42	0·80

in k instead of the regular decrease as in normal nerves. We conclude, therefore, that prolonged calcium treatment does not alter the effect of electrotonus on the threshold for long-lasting currents, but reverses the effect of catelectrotonus on k.

The effect of cæsium ions. The results of the experiments with nerves soaked for a certain time in Ringer's solution containing cæsium chloride are given in a somewhat different form, to show the effect more clearly, in Tables X and XI. In Table X is given the effect of anelectrotonus, in Table XI that of catelectrotonus. The molar concentration of cæsium chloride was ten times that of potassium chloride in normal Ringer's solution.

TABLE X. The effect of anelectrotonus on the threshold and time-constant k of nerves treated with cæsium ions. Polarizing current 2μA.

Exp. no.	Threshold for long-lasting currents: volts Normal	Anelectrotonus	k: msec. Normal	Anelectrotonus
1	1·0	1·9	0·53	0·37
2	1·1	2·3	0·76	0·26
3	1·0	2·4	0·39	0·29
4	0·8	2·1	0·23	0·20

TABLE XI. The effect of catelectrotonus on the threshold and time-constant k of nerves treated with cæsium ions

Exp. no.	Polarizing current μA.	Threshold for long-lasting current: volts		k: msec.	
		Normal	Electrotonus	Normal	Electrotonus
1	2	1·14	1·16	0·53	0·54
2	2	0·56	0·56	0·85	0·85
3	5	0·45	0·44	0·85	0·85
4	5	0·62	0·61	0·83	0·83
5	5	0·63	0·63	0·33	0·33
6	5	0·58	0·57	0·72	0·72
7	5	0·58	0·57	0·72	0·72
8	5	0·79	0·78	0·59	0·59

In Table X the effect of anelectrotonus is very much the same as in normal nerves. The effect, however, of catelectrotonus is quite different (Table XI). Cæsium abolishes altogether the effect of catelectrotonus both on the threshold for long-lasting currents and on the time-factor k. In fact the intensity-duration curves with and without catelectrotonus are identical within the limits of error of the determinations.

The effects of lithium and rubidium ions. Tables XII and XIII give the effect of electrotonus on nerves soaked for 2 hours in Ringer's solution

TABLE XII. The effect of electrotonus on the threshold for long-lasting currents in nerves treated with lithium or rubidium ions

Exp. no.	Polarizing current μA.	Threshold: volts		
		Normal	Catelectrotonus	Anelectrotonus
Lithium:				
1	2	1·2	0·7	2·3
2	2	1·8	0·9	3·1
3	5	1·3	0·6	4·5
4	5	1·7	0·7	4·5
Rubidium:				
5	2	1·1	1·0	1·8
6	2	1·2	1·2	1·8

TABLE XIII. The effect of electrotonus on the time-factor k of excitation in nerves treated with lithium or rubidium ions

Exp. n	Polarizing current μA.	k: msec.		
		Normal	Catelectrotonus	Anelectrotonus
Lithium:				
1	2	0·60	0·80	0·34
2	2	0·45	1·00	0·30
3	5	0·48	1·00	0·19
4	5	0·41	0·62	0·20
Rubidium:				
5	2	1·4	2·0	—
6	2	0·74	0·95	0·62

containing excess of either lithium or rubidium ions. The molar concentration chosen was ten times that of potassium in normal Ringer's solution. The effect of electrotonus on the lithium-soaked nerve is the same as on normal nerve. The quality of the nerves treated with rubidium soon becomes very poor and therefore only a couple of experiments were performed.

Part III. *The effect of inter-electrode distance on electrotonus*

The effect of inter-electrode distance in nerve excitation is well known. With decreasing distance the threshold for long-lasting currents increases [Rushton, 1927, 1932, 1934], and the time-factor k decreases [Cardot & Laugier, 1914*b*; Bouckaert & Katz, 1935; Hill, 1936*b*]. The influence therefore of inter-electrode distance on the effect of electrotonus was investigated. The electrical circuit was as described above. A special form of wooden electrode was used which allowed very short inter-electrode distances to be used. Table XIV shows the change in threshold

TABLE XIV. The influence of inter-electrode distance on the change ($\pm$) of threshold produced by electrotonus (an. and cat.). Change of threshold expressed as percentage of threshold without electrotonus. All data are averages from six experiments

Polarizing current μA.	Short distance Dist. mm.	Catelec.	Anelec.	Medium distance Dist. mm.	Catelec.	Anelec.	Long distance Dist. mm.	Catelec.	Anelec.
½	1¼	−3	3	14	−13	14	25	−14	14
1		−4	4		−23	26		−19	29
2		−5	5		−24	47		−27	56
5		−10	10		−46	130		−44	150
10		−21	27		−58	160		−58	210
20		−36	49		−63	170		−56	220
50		−51	85		−29	300		−2	300
100		−65	85		−31	490		—	—

with electrotonus as a percentage of the threshold without electrotonus. It is seen that with short inter-electrode distance the effect of electrotonus is considerably reduced.

Rushton [1934] has shown that the increase in threshold with decreased inter-electrode distance can be explained by the difference in current distribution in the nerve with different inter-electrode distances. It was therefore investigated whether this same difference in current distribution may be responsible for the effect of inter-electrode distance on electrotonus. The experiments were performed as follows. The threshold was determined for short and long inter-electrode distance and the polarizing current was made proportional to this threshold. A comparison of columns B and C of Table XV shows that for *equivalent*

TABLE XV. The effect of inter-electrode distance on catelectrotonus if the polarizing current is made proportional to the rheobase for each inter-electrode distance

Exp. no.	Electrode distance mm. Short	Long	Polarizing current for short inter-electrode distance: μA.	A	B	C	C′
1	1	12	21	4·8	−42	−41	−90
			100		−90	−90	+23
2	1	12	21	4·8	−45	−41	−90
			100		−93	−90	−63
3	½	12	13·1	7·6	−30	−28	−83
			100		−83	−83	+42
4	1	12	16·2	6·2	−41	−39	−75
			100		−90	−75	+33
5	½	20	14·7	6·8	−15	−15	−50
			100		−50	−50	−29
6	½	20	16	6·3	−20	−18	−54
			100		−55	−54	−78

Col. A gives the ratio of the threshold for short and long inter-electrode distance.

Cols. B and C give the percentage change in threshold effected by electrotonus (− indicating decrease, + indicating increase), B for short and C for long inter-electrode distance, for polarizing currents in the same ratio as the respective thresholds.

Col. C′ gives (for comparison) the percentage reduction in threshold for long inter-electrode distance when the polarizing current is the same as for short distance (C).

polarizing currents (i.e. proportional to the respective thresholds) the percentage effect of catelectrotonus on the threshold is exactly the same for long as for short inter-electrode distance. For *equal* polarizing currents, however (compare columns B and C′), the percentage effect of catelectrotonus may be quite different in the two cases. If therefore the strength of the current producing electrotonus is made proportional to the threshold, the influence of inter-electrode distance on the effect of electrotonus on the threshold disappears completely.

It seems probable then that the effect of inter-electrode distance on electrotonus is due to the same current distribution in nerve as is responsible for the effect of inter-electrode distance on the threshold. This conclusion is a natural one if excitation is produced by current crossing a membrane and if electrotonus affects the state of that membrane.

In the experiments given in Table XIV electrotonus and excitation were applied to the nerve through the same set of electrodes. It was found that inter-electrode distance has a marked influence on the effect of electrotonus. The question remained to be investigated whether or not a constant electrotonus has any influence on the effect of inter-electrode distance on excitability. The electric circuit for the electrotonus was separated from the excitation circuit. One electrode of the electrotonus circuit was common with the cathode of the stimulating circuit. The inter-electrode distance of the stimulating electrodes was variable, the cathode remaining in a constant position. The electrodes for the electrotonus were fixed, one of them being the same as the cathode of the stimulating current. The inter-electrode distance of the electrotonus electrodes was larger than the long inter-electrode distance of the stimulating electrodes. The results (averages of five experiments) are given in Table XVI. The difference in threshold with short and long inter-electrode distance expressed in percentage of the threshold for long inter-electrode distance is given. It is seen that a strong constant electrotonus gives a decrease of the effect of inter-electrode distance on excitability. The influence is stronger in catelectrotonus than in anelectrotonus.

TABLE XVI. The influence of electrotonus on the effect of inter-electrode distance on the threshold for long-lasting currents. The difference in threshold with inter-electrode distance is expressed as percentage of the threshold for long inter-electrode distance. The values given are averaged from five separate experiments

Electrode distances: mm.			Polarizing current	Percentage change		
Short	Long	Electrotonus	μA.	Normal	Catelectrotonus	Anelectrotonus
1	13	19	1	260	250	250
			10	260	240	210
			20	260	230	190
			40	260	170	170
			70	230	100	180
			100	190	50	170

The results described in Table XIV therefore are due to two influences, first the effect of inter-electrode distance on electrotonus and second to the influence of a constant electrotonus on the effect of inter-electrode distance on excitability.

SUMMARY

Catelectrotonus increases the time-factor k of nerve excitation, anelectrotonus reduces it.

Soaking in excess of potassium reverses the influence of catelectrotonus on the threshold for long-lasting currents. This effect is reversible. Potassium treatment leaves the effect of electrotonus on the time-factor k unaltered.

Prolonged treatment (about 15 hours) with excess of calcium leaves the effect of electrotonus on the threshold for long-lasting currents unaltered. The effect of catelectrotonus on the time-factor is reversed, while the effect of anelectrotonus is rather variable.

Cæsium ions abolish the effect of catelectrotonus both on the threshold for long-lasting currents and on the time-factor k, leaving the effect of anelectrotonus unaltered.

Lithium ions do not change the effect of electrotonus either on the threshold for long-lasting currents or on the time-factor k. Rubidium ions damage the nerve so much that reliable results could not be obtained.

Decrease of inter-electrode distance diminishes the effect of electrotonus on the threshold for long-lasting currents. If, however, the polarizing current is made proportional to the rheobase for each inter-electrode distance, this effect disappears. A strong electrotonus with constant inter-electrode distance diminishes the effect of inter-electrode distance on the threshold for long-lasting currents.

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