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LOYOLA UNIVERSITY
SCHOOL OF MEDICINE .

now in

CHANGES OF ELECTRICAL RESISTANCE IN NERVE
DURING BLOCK BY COLD

A THESIS

SUBMITTED IN PARTIAL FULFILMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

DEPARTMENT OF PHYSIOLOGY

BY

IRVIN FRANKLIN HUMMON JR.

CHICAGO, ILL.

1934

A C K N O W L E D G E M E N T S

I wish to express to Professor T.E.Boyd my great appreciation for the direction and active cooperation which he has extended to me in the performance of this work.

I wish also to thank Professor H.N.Ets for his interest and suggestions offered throughout the year.

I N T R O D U C T I O N .

In 1932 Bahrman (1) reported a series of experiments investigating the relation of electrical resistance to physiological conductivity in frogs' nerves during block by cold. From his results he concluded that at, or immediately following, block by cold there was an abrupt change in slope of the temperature-resistance curve; that the resistance rose suddenly and rapidly to an extremely high value. He concluded from these experiments that this sudden increase in resistance was associated with the almost simultaneous loss of physiological conductivity of the nerve. His experimental conditions, as he describes them, were such as to always result in supercooling the nerve before blocking occurred and he reported his average blocking temperature to be -6.4 degrees centigrade. He also reported that the majority of the nerves which he blocked did not recover spontaneously on warming to room temperature. Recently Boyd and Ets (2) have reported that blocking of nerves by cold may occur under a variety of conditions. It may occur above or below zero centigrade without freezing or ice formation and such blocked nerves usually recover spontaneously on warming. Or it may occur with freezing and ice formation at just below zero centigrade or with varying degrees of supercooling down to as low as -10 degrees centigrade. Nerves blocked with freezing are less likely to recover spontaneously on warming

and the likelihood decreases markedly as the degree of super-cooling increases before blocking occurs. The type of block depends upon the previous treatment of the nerves, as nerves immersed in Ringer's solution containing from 4 to 10 times the usual amount of potassium usually block at higher temperatures, and also on the physical conditions existing in the experimental set-up.

It was our purpose to investigate the relation of electrical resistance to physiological conductivity of frogs' nerves during these various types of cold block and to attempt to find, in this way, whether the sudden change in slope of the temperature-resistance curve which Bahrman reported was associated with the blocking of the nerve or with some other phenomenon. We also supplemented this work with some resistance measurements on nerves blocked by heat.

M E T H O D .

The work was done during the winter months on nerves from the small green frog (*Rana Pipiens*) and also on nerves from the bull frog (*Rana Catesbiana*). Altogether measurements were made upon 68 preparations.

The usual gastrocnemius-sciatic muscle-nerve preparation was made with the nerve left as long as possible by cutting it at its spinal roots. It was then mounted directly in the moist chamber or treated and then mounted, with the paired preparation usually immersed in Ringer's solution and subsequently mounted as a control.

The moist chamber was made of paraffine, from a block with one side hollowed out to form a shallow receptacle into which the muscle-nerve preparation could be placed. This was then covered with a glass plate and the edges sealed with petroleum jelly. Filter paper saturated with water or Ringer's solution was placed in the bottom of the chamber to supply moisture. Preparations could be left in this chamber for several hours without showing any evidence of drying or of decreased irritability. Passing through the chamber was a tube, in some experiments glass and in others silver, through which the cooling agent flowed. This tube was so arranged that a length of several centimeters was exposed to the moist air of the chamber. This provided a means whereby ice could form some distance from the nerve, due to the temperature gradient, and could creep along the tube and envelop the nerve at a temperature slightly below zero. This technique enabled us to obtain cold blocks without supercooling. Whenever supercooling was desired this exposed length of tube was covered with rubber tubing so that the area exposed to the air was confined to that over which the nerve passed. On either side of the cooling tube were placed platinum electrodes which passed through the walls of the chamber through insulating glass bushings. The nerve was laid upon these electrodes and the interlying cooling tube and the segment of nerve between these electrodes was the part of the nerve whose resistance was

measured. The length of the measured segment varied in different experiments from .9 centimeters to 3.1 centimeters and the proportion of this segment subjected to local cooling varied from 20 to 100 per cent. Final figures for all experiments were reduced to a common unit of one centimeter of cooled or heated nerve. The free end of the nerve was laid upon a pair of stimulating electrodes connected to the secondary of a Harvard inductorium.

The temperature of the nerve was measured by means of a copper-constantan thermo-couple of small mass lying alongside the nerve on the cooling tube. The reference couple was kept at zero centigrade and the potential difference developed between the couples was measured by a null method by balancing it against a known potential difference supplied by working batteries through a Leeds and Northrup student type potentiometer. Complete set-up is given in the thesis of Dominic Baima (3). In some cases a Weston type 440 microammeter was used which could be made to read directly in degrees centigrade.

Cooling was obtained either by siphoning salt solution cooled to -13 to -16 degrees centigrade from a vacuum bottle through the cooling tube or by permitting expanding carbon dioxide gas to flow through the tube. The rate and degree of cooling could be controlled by varying the rate of flow of the cooling agent through the cooling tube. For heat block water at about 60 degrees centigrade replaced the salt solution.

It was our desire, if possible, to devise a method of measuring the resistance of the nerve without stimulating it with the measuring current. Attempts were made to use direct currents of extremely small magnitude, of the order of 10 to the minus tenth power amperes, but the polarization of the nerve even with these small currents made their use impossible. Several attempts were made to use alternating currents of various frequencies with vacuum tube voltmeters and with an impedance bridge built after one described by Stone (4). All of these required such large currents to operate them that stimulation of the nerve resulted at low frequencies and at higher frequencies it was thought that the heating effect due to the current passing through the nerve and the variation in capacity of the nerve with changing temperature would introduce uncontrollable complicating factors.

The method finally used consisted of a standard alternating current bridge, the resistance of the nerve being balanced by a variable resistance having a range of from 1,000 to 2,000,000 ohms, and the other two arms consisting of resistances of 100,000 ohms each. Alternating current to operate the bridge was supplied by an audiofrequency oscillator consisting of a triode(201A) with feed-back through an audio-frequency transformer having a frequency range of from 1000 to 2000 cycles per second. Using earphones as an indicating device the null point was quite good. In some cases a variable condenser of .0005 microfarads was placed in parallel

with the variable resistance to compensate for the capacity of the nerve which sharpened the end point appreciably. The bridge could be operated very satisfactorily with a current of sufficiently small magnitude that it did not stimulate the nerve and thus could be left on throughout each experiment. Occasional changes of frequency were resorted to to relieve the auditory fatigue of listening to one frequency for a long period of time.

A typical procedure was as follows: Paired muscle-nerve preparations were prepared and one of them mounted directly or treated and then mounted. The other one was usually put in Ringer's solution and subsequently mounted. The secondary of the inductorium was then adjusted for stimulation by break shock only and left so throughout each experiment. An initial resistance reading was made and the preparation left for several minutes until the resistance reading became constant. Then the cooling agent was allowed to flow through the cooling tube slowly and simultaneous temperature and resistance readings were made and recorded. The nerve was stimulated from time to time and was considered as conducting until no evidence of muscular response could be elicited. In the freezing type blocks the block usually was preceded by irregular twitching of the muscle and by evidence of warming as ice formation began, (Bühler] (5). Non-freezing blocks did not show these phenomena. After the nerve was blocked the rate

of flow of the cooling agent through the cooling tube was diminished and the temperature allowed to rise. Again simultaneous temperature and resistance readings were made and the nerve stimulated periodically to determine at what temperature the nerve would recover if at all. In some cases of non-freezing blocks and heat blocks the nerve was repeatedly blocked and allowed to recover several times. Each experiment took about one hour to run. A similar procedure was followed in studying heat block. Protocols of typical experiments follow:

T A B U L A T E D R E S U L T S .

1. Bull frog nerve supercooled.

Resistance in ohms	Temperature in degrees C.	
10,000	16.5	
12,000	10.0	
14,000	6.1	
16,000	2.5	
17,000	1.1	
18,000	0.0	
19,000	-3.0	
20,000	-4.0	
21,000	-4.5	
21,500	-5.4	
22,000	-6.1	
22,500	-6.6	
23,000	-7.1	
23,500	-7.8	
133,000	-8.8	Nerve blocked
120,000	-7.2	
100,000	-5.9	
70,000	-4.0	
23,000	-0.2	
17,000	5.5	
14,000	11.8	
13,000	15.1	Nerve did not recover

2. Green frog nerve, non-supercooled freezing block.

Resistance in ohm s	Temperature in degrees C	
40,000	26.3	
46,000	15.9	
60,000	6.5	
66,000	1.6	
70,000	0.0	
75,000	-1.0	
120,000	-1.9	Nerve blocked
127,000	-1.1	
106,000	00.0	
86,000	1.0	
80,000	1.5	Nerve recovered
75,000	2.2	
80,000	0.6	
92,000	0.2	Nerve blocked
105,000	0.0	
85,000	1.8	
80,000	1.9	Nerve recovered
78,000	1.3	
90,000	0.0	Nerve blocked
82,000	2.3	Nerve recovered
90,000	0.3	Nerve blocked
82,000	2.6	Nerve recovered

3. Green frog nerve, treated for one hour in Ringer's solution containing ten times the usual amount of potassium, showing a non-freezing block.

Resistance in ohms	Temperature in degrees C.
70,000	22.2
100,000	6.5
130,000	4.6
180,000	3.0
220,000	1.4
240,000	0.1 Nerve blocked
220,000	1.3 Nerve recovered
215,000	1.6
240,000	0.3 Nerve blocked
230,000	1.3 Nerve recovered
240,000	0.2 Nerve blocked
235,000	1.0 Nerve recovered
240,000	0.5 Nerve blocked
340,000	-2.8
580,000	-3.7 Water starting to freeze
1,100,000	-3.2
1,500,000	-3.7
1,000,000	-0.5
820,000	0.5 Water melting
500,000	0.9

4. Bull frog nerve, heat block.

Resistance in ohms	Temperature in degrees C.	
16,000	30.1	
14,600	34.0	
14,300	36.3	
13,600	38.5	
13,000	39.8	Nerve blocked
13,000	37.9	Nerve recovered
15,000	23.8	
14,500	33.5	
13,000	41.0	
12,900	42.5	Nerve blocked
14,000	27.3	Nerve recovered
13,300	39.0	
13,000	41.0	
12,300	43.0	Nerve blocked
12,200	41.0	Nerve recovered

D I S C U S S I O N .

The tabulated results, examples of which have been given, show a practically linear relationship between temperature and resistance of the nerve over a wide range, which relationship holds as long as the tissue fluids remain liquid. Subjecting thread or filter paper soaked with Ringer's solution to the same degree and kind of temperature variation resulted in comparable figures. Electrical conduction through a nerve is largely one of electrolytic conduction, by means of ionic movement through a fluid medium. Smith (6) gives tables for electrolytic conduction for various temperatures which also shows a linear relation. Thus one would expect to find this linear relation in nerves.

When we come to the point at which freezing and ice formation occurs then we are no longer dealing with a fluid medium but a crystalline medium through which ionic movement is practically impossible. The current then is probably being carried by electronic movement. The change of slope of the temperature-resistance curve is much more gradual in the non-supercooled blocks as the ice formation is slower and the loss of electrolytic conductivity less abrupt. In the supercooled block, however, the formation of ice takes place very rapidly throughout the whole cooled segment of nerve and the loss of electrolytic conductivity is very rapid. Thus it would appear that the electrical resistance of a nerve is a function of its physical state.

It is clear from our results that there is no consistent relationship between the physiological conductivity of a nerve and its electrical resistance as loss of physiological conductivity occurred both with heat, confirming the work of Bremer and Titeca, (7) and with non-freezing cold block without change in slope of the temperature-resistance curve. Even in the super-cooled blocks the nerve usually blocked just previous to the rise in resistance, which fact Bahrmann also mentions.

The values we obtained for resistance of nerves corresponds with those reported by Lullies (8) and by Krüger (9), namely of the order of 50,000 ohms per centimeter at 1,000 cycles for *Rana Pipiens* nerves at 20 degrees centigrade. For *Rana Catesbiana* nerves the value was of the order of 16,000 ohms under similar conditions.

The present concept of the method of propagation of the nervous impulse postulates a core conduction system, Hill (10), Gerard (11), Ebbecke (12). Each nerve fiber consists of a protoplasmic thread or axon surrounded by a dielectric sheath or membrane. In medullated nerves this is represented by the sheath while in non-medullated nerves the sheath is very thin, probably only a few molecules thick, and thus does not show in stained preparations. This sheath is permeable to potassium ions but not other ions and because of this selective permeability potassium is found in considerable concentration in the interior of the nerve and builds up a

potential difference between the interior of the nerve fiber and the outside of several millivolts. This potential difference can be detected ^{by} connecting to the interior of the nerve fiber with an electrode through an injured portion of the fiber and connecting the other electrode to the outside of the nerve fiber some distance from the injured portion. The nervous impulse is supposed to consist of a self-propagated wave of loss of impermeability of this membrane which allows this built up potential difference to progressively discharge itself along the nerve fiber. This progressive discharge gives rise to the action potential which accompanies the nervous impulse. This concept requires that there be a movement of ions through this membrane for the propagation of the nervous impulse and thus one would expect that anything which interferes with the free flow or movement of ions would interfere with the conduction of the nervous impulse. This we find to be true as blocking of the nerve always occurs with ice formation which in turn interferes with ionic movement. Gasser (13) reports decreased velocity with decreased temperature which also agrees with our findings of increased resistance to ionic movement as measured by the increase in electrical resistance. The explanation of the non-freezing and the heat block is, however, not so apparent.

In measuring the resistance of a nerve one is not dealing with a simple resistance but with a more or less

complicated circuit. Part of the measuring current, and perhaps a large part, is carried by the fluids on the outside of the nerve fiber. We tried to minimize this current as much as possible by covering the nerve with some nonconducting solution as isotonic glucose or nonconducting fluid as paraffine oil. Some of the current is taken up in the capacity of the sheath, and the remainder passes through the sheath and passes down the interior of the fiber. A study of the relation of these currents is given by Labes (14) and by Labes and Lullies (15). Our measurements do not separate these different current but represent the composite of them all.

S U M M A R Y .

We have conducted a series of experiments on frogs' nerves measuring the electrical resistance and its relation to physiological conductivity throughout a wide range of temperatures extending from above the point of heat block down to below the point of supercooled cold block. Cold blocks have been studied under different physical conditions and different treatment of nerves which have resulted in non-supercooled freezing blocks and in non-freezing blocks as well as in the freezing supercooled block.

C O N C L U S I O N S .

From our work we may conclude that:

1. The slope of the temperature-resistance curve is constant for temperatures at least as high as 45 degrees centigrade and down until ice formations occurs whereupon the slope becomes steeper.
2. Blocking of the nerve takes place with ice formation at whatever temperature this ice formation may occur.
3. Blocking without ice formation occurs without change in slope of the temperature-resistance curve.
4. The electrical resistance of a frogs nerve is a function of its physical state and not of its physiological state.

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