THE EXCITATORY AND RECOVERY PROCESSES IN THE NERVE FIBRE AS MODIFIED BY TEMPERATURE CHANGES

by

ICHIJI TASAKI

Tokugawa Biological Institute, Mejiro, Toshima-ku and Medical Department, Keio University, Yotsuya, Tokyo (Japan)

In a preceding paper (TASAKI AND FUJITA, 1948), the results were reported of our investigation of the effect of temperature changes on the action current of a single myelinated nerve fibre. In the present paper, it is proposed to present data on the effect ot temperature on the excitatory process set up by electric stimuli and upon the process of recovery from a previous activity.

The excitability characteristics of the nerve fibre examined in this investigation are (1) the rheobase, (2) the minimal gradient or the constant of accommodation, (3) the minimum quantity of electricity required for excitation, (4) the time course of development of the excitatory state set up by a brief subthreshold shock, and (5) the recovery curve.

The effects of temperature on these quantities are a much discussed subject, and the present investigation is in a sense a re-examination, with isolated single nerve fibres, of previous experiments carried out by GOTCH AND MCDONALD (1896), SCHRIEVER (1932), ADRIAN (1914) and many others. But, since it has been revealed that the rules governing the process of electric excitation of an isolated single nerve fibre are somewhat different from those already known (TASAKI, 1942), it has been thought worth while to secure rigid experimental data showing how these quantities are affected by the change in temperature.

METHOD IN GENERAL

The material used was isolated single motor nerve fibres of the toad exclusively. The method of isolation and stimulation was the same as that adopted previously (TASAKI AND FUJITA, 1948). The single fibre preparation was mounted on a bridge-insulator and was introduced, together with the stimulating and lead-off electrodes, into a special nerve chamber of which the temperature was controlled by ice or by an electric hot plate supplied with direct current.

PROCEDURES AND RESULTS

1. *The effect of temperature upon the rheobase and the minimal gradient*

In this series of experiments, the arrangement shown in Fig. 1 was used. With the contact K_2 in the figure closed, opening of the contact K_1 initiated an exponentially rising stimulating voltage. The time constant of voltage rise was controlled by changing the capacity of the condenser C in the figure, and the final voltage was adjusted to threshold by means of a potential divider of 1 000 ohms. The stimulating current was interrupted by opening the second contact K_2 about 0.5 second after the onset of the stimulus. The pause between each trial (stimulation) was about 60 seconds. The time required for readjusting the temperature in the nerve chamber was about 10 minutes. And about 10 minutes after the temperature of the chamber had become steady at a new level, threshold determinations were begun. In this experiment, the response of the muscle was generally taken as index of nerve excitation.

In isolated single nerve fibres, as in the whole nerve trunk (SCHRIEVER, 1930; SOLANDT, 1936 and others), the relation between the time constant of voltage rise and the final voltage which barely excites is represented by a straight line. It should be added however that the deviation of the observed relation from a straight line is far less in the single nerve fibres than in the nerve trunks.

The data presented in Fig. 1, left, are an example of the results of the investigation. In this figure, the final voltage V is plotted as ordinate against the time constant of voltage rise rc as abscissa. The rheobase (LAPICQUE, 1909) is the threshold voltage for $rc = 0$, and the minimal gradient (LUCAS, 1907) is given by the slope of the straight line relating V and rc. HILL's time constant of accommodation (1936) is given by the rheobase into the reciprocal of LUCAS's minimal gradient.

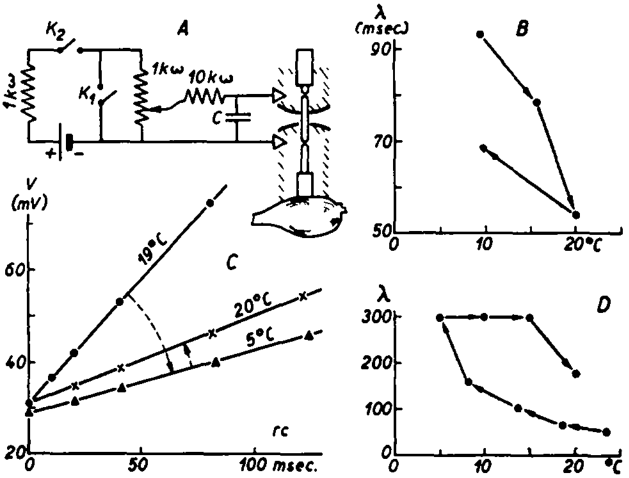

Fig. 1. A: Arrangement used to determine the threshold for exponentially rising voltages. B: Time constant of accommodation determined at four different temperatures. The arrows indicate the order of the measurement. C: The relation between the time constant of voltage rise rc and the threshold final voltage V in excitation by exponentially rising voltages at various temperature. D: Time constant of accommodation determined at eight different temperatures. The preparation is the same as that used in C, and three points are taken from the data of C.

According to the conclusion reached in our previous investigation (SAKAGUCHI AND TASAKI, 1943), the necessary and sufficient condition for a slowly rising voltage $V(t)$ to excite a nerve fibre is to make the stimulating voltage cross the rheobasic voltage b at a rate of rise greater than the minimal gradient m of the fibre, *i.e.*, at the moment when $V(t) = b, dV(t)/dt = \geq m$. It can be easily shown that, if this requirement is fulfilled by a set of exponentially rising voltages with varying constants of rise, the relation between the constant of voltage rise rc and the final threshold voltage V should be expressed by a straight line which intersects the voltage axis at a slope equal to the minimal gradient m. In excitation by these slowly rising voltages, action currents are set up soon after the stimulating voltages surpass the rheobase (see Appendix I).

The experimental result furnished in Fig. 1 indicates very clearly that the minimal gradient shows a tendency to be decreased by cold while the rheobase remains practically unaffected by temperature changes. It is further demonstrated that the minimal gradient is not a simple function of the temperature but it varies according to the history of the fibre. The data presented in Fig. 1, B and D, show how it depends upon the sequence of the measurement. In these figures the data are presented in terms of HILL's time constant.

Demonstration of hysteresis in the effect of temperature changes upon the minimal gradient of the nerve would probably not be very new, although COPPÉE (1940) did not seem to pay much attention to this phenomenon. SCHRIEVER has shown, in 1932, that his "Einschleichzeit" gradually changes when the nerve is subjected to constant, low temperature. His data clearly indicate that at a constant temperature the rheobase and the chronaxie of the nerve remain practically constant while the minimal gradient changes gradually as time elapses. He has further shown, in collaboration with CEBULLA (1938), that preparations taken from frogs which have been kept at low temperature show distinctly smaller minimal gradients than those taken from ordinary frogs.

It should be pointed out now that, among all the quantities characterizing the state of the nerve fibre so far examined, the minimal gradient is the only one that shows a pronounced hysteresis. It is in fact surprising that a nerve fibre is capable of retaining the effect of its previous environment.

Turning now to the effect of temperature changes upon the rheobase, all the previous investigations seem to indicate that it is significantly decreased by cold (GOTCH AND MCDONALD, 1896; WALLER, 1899; SCHRIEVER, 1932; SUZUKI, 1939 and many others). In the experiments on single nerve fibres, there seems also a slight tendency for it to be decreased by cold, but this tendency is too small to account for the results with nerve trunk.

In the experiments in which whole nerve trunks are used, the rheobase is considered to be strongly affected by the changes in the resistance and polarizability of the surrounding tissues and the body fluid. This effect of the shunt seems to become especially significant when the rheobase is measured in terms of the current, and not in voltages (SUZUKI, 1939). Thus the discrepancy between the present and previous results may probably be accounted for by some complication in the latter case resulting from the surrounding tissues.

2. *The minimum quantity of electricity required for excitation and the time course of the excitatory state*

In this series of experiments, the effect of a subthreshold current pulse, either a brief shock or a long rectangular pulse, was investigated by the shock test method at varying temperatures. The arrangement shown in Fig. 2, A, was generally used. Test and conditioning shocks of about 0.03 millisecond in duration were obtained with a HELMHOLTZ pendulum by the technique described by HOZAWA (1928); P and P′ in the figure indicate keys which close the circuit for such a brief period. When a long rectangular voltage pulse was to be employed as the conditioning stimulus, ordinary break contacts K_1 and K_2 of the pendulum were used instead of the "Punktkontakt" P′. The time intervals between the shocks were controlled by shifting the positions of the contacts of the pendulum. The strengths of the shocks were varied by means of potential dividers.

In the example of the experimental results furnished in Fig. 2, the direction of the conditioning shock was ascending with respect to the muscle and that of the test shock was descending. At 15° C (B in the figure), the threshold for the test shock (applied alone) was 0.34 volt. This resting threshold level was modified by a conditioning shock of 0.2 volt in strength and about 0.03 millisecond in duration as indicated by the circles connected with a continuous line. In this figure, the threshold for the test shock is plotted against the time interval from the onset of the conditioning shock to the beginning of the test shock. A constant voltage of 0.02 volt changed the resting threshold level as indicated by the triangles connected with a broken line.

When this preparation was cooled to 3° C (C in the figure), the resting threshold for the test shock increased to 0.74 volt, and this threshold level was modified by the conditioning stimuli as shown by the curves in the figure. The time course of the whole process is decidedly slower at the lower temperature than at the higher temperature.

Attention should be called in these experiments to the fact that the threshold level for the test shock is characteristically modified by the conditioning stimulus even when the test shock precedes the conditioning stimulus. An explanation of this experimental fact has been fully described in a previous paper (Tasaki, 1942). An outline of that explanation is as follows:

> The excitatory state set up in the nerve fibre by a brief subthreshold shock does not reach the maximum at the moment at which the shock terminates. This state rises first gradually and then quickly, and reaches a maximum about 0.3 millisecond after the termination of the brief shock (at room temperature). After this maximum is reached it finally begins to decay. As a result of this delayed maximum, the "excitability change" as revealed by the shock test method gives us the information on the state of the fibre about 0.3 millisecond after application of the test shock.
>
> The magnitude of the excitatory state increases proportionately with increasing shock strength. When many subthreshold shocks are applied to the nerve fibre in succession, the excitatory states set up by these individual shocks are superposed upon one another. As a consequence of this law of superposition, the excitatory state set up by a long rectangular voltage pulse is given by the intregration of the effects of all the voltage elements of which the continuous voltage can be regarded as composed (see Appendix II).

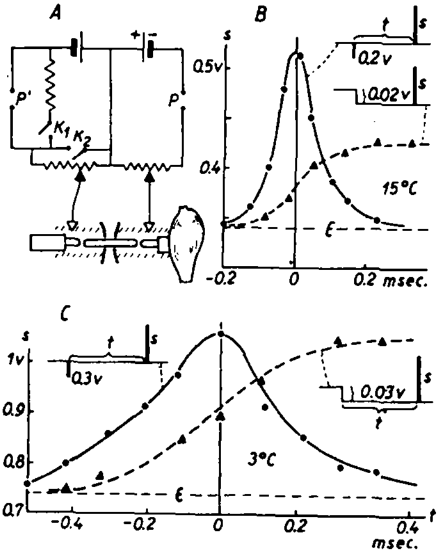

Fig. 2. A: Arrangement used to determine the variation in the threshold resulting from application of a brief subthreshold shock or a long rectangular current pulse. P's are Hozawa's "Punktkontakt", and K's break contacts of a Helmholtz pendulum. B: Curves showing the variation in the threshold caused by a brief shock and a long rectangular pulse determined at 15° C. The strengths of the conditioning stimuli are given in the figure. C: Similar experiment done at 3° C on the same preparation.

In the experimental result presented in Fig. 2, one may at once notice that, at every temperature, the gradient (or the first derivative) of the broken line gives a curve which closely resembles the continuous line. This fact is in accordance with the statement outlined above. It is also to be expected from the above statement that the broken line should be obtained by computing the area between the dotted line (representing the resting threshold level) and the continuous line (from $t = -\infty$ to an arbitrary value of t) and multiplying the area obtained by 0.1 (the ratio of the voltages in both cases). On actual computation by the graphical method, one finds that this requirement is fulfilled to a first approximation (cf. Appendix, equation 6).

The data presented in Fig. 3, left, indicate that, at every temperature, the magnitude of the change in the threshold for the test shock is proportional to the strength of the conditioning rectangular voltage pulse. Test shocks were in this case condenser discharges of time constant 0.02 millisecond and were applied 4 milliseconds after the onset of conditioning stimuli of varying strengths. The observed values lie on good straight lines, except in cases where the conditioning stimuli are near the rheobase.

In the above conception of treating the experimental data, two quantities serve to characterize the state of the nerve fibre: the minimum quantity of electricity required for excitation and a time constant which measures the period during which the excitatory state set up by a brief shock persists. Since it is not necessary here to know the absolute value of the quantity of electricity, one may represent it simply by the product of the strength of the threshold shock into its duration. As the time constant, one may adopt the area under the "latent addition curve" (the curve indicating the threshold variation set up by a brief shock) of which the height is taken as unity.

From the above relationship between the continuous and broken lines in Fig. 2, the total area under the latent addition curve can be obtained from the plateau level of the broken line, or, what is the same thing, from the slope of the straight line obtained in the experiment of Fig. 3, left. The slopes of these straight lines multiplied by the duration of the test shock gives the area (having a dimension of time) under the latent addition curve (see Appendix, equation 7).

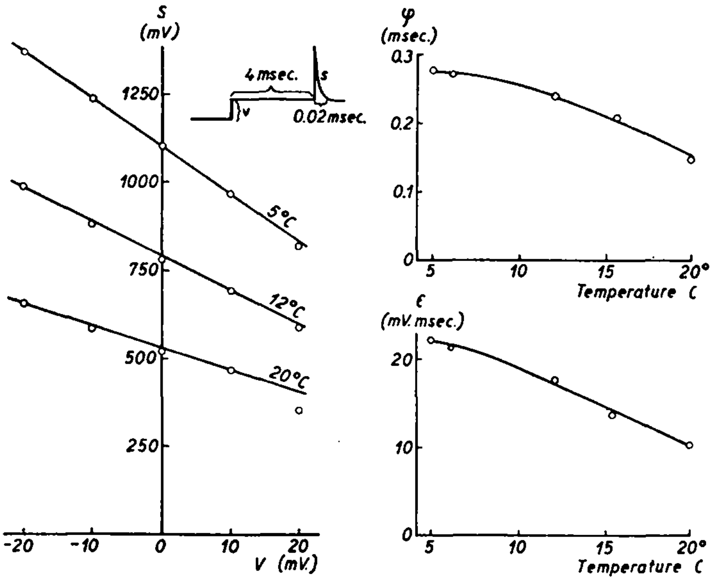

Fig. 3. Left: Relation between the strength of the (conditioning) rectangular voltage pulse v and the threshold for the (test) shock S determined at various temperatures. Right: The area under the latent addition curve, φ, and the minimum quantity of electricity required for excitation, ε, as functions of temperature. All the data in this figure are obtained for one preparation.

An example of the experimental results furnished in Fig. 3, right, shows how the minimum quantity for excitation (top) and the area under the latent addition curve (bottom) vary as the temperature. The changes in these quantities resulting from temperature changes are reversible, *i.e.*, there is no hysteresis. Both of them are increased by cold. The changes in the two quantities are parallel. Between 8 and 20° C the temperature coefficient was approximately 1.7. At low temperature there seems to be a slight decrease in the temperature coefficient, but it is possible that this is due to some error resulting from the inadequacy of the nerve chamber used in this experiment.

There is an extensive literature dealing with the effect of temperature changes upon the excitability, the chronaxie and the strength-duration relation of the nerve (GOTCH AND MCDONALD, 1896; LUCAS AND MINES, 1907; L. AND Mme LAPICQUE, 1907; GRANBERG AND HOLLANDER, 1927; DWORKIN AND FLORKIN, 1930; HOU, 1931; SCHRIEVER, 1932; BLAIR, 1935; SUZUKI, 1939, and others). In the present investigation, I made no direct measurement of the temperature coefficient for the strength-duration relation and the chronaxie. But, since WEISS' empirical formula holds good for the strength-duration relation in the single nerve fibre and consequently the chronaxie is given at every temperature by the minimum quantity divided by the rheobase, the effect of temperature upon the chronaxie is already evident from the experimental results stated above. As the rheobase is shown not to vary appreciably with temperature, the change in the minimum quantity indicates directly how the chronaxie is affected by temperature. The coefficient of about 1.7 given above seems to agree well with most of the previous results.

3. *The recovery curve*

When one sends two induction shocks into a nerve fibre through a pair of electrodes placed on the nerve trunk of a single nerve fibre preparation, one generally obtains a recovery curve such as shown in Fig. 4. In this figure, the reciprocal of the threshold for the second shock, as a percentage of the resting value, is plotted against the interval between these two shocks. Cold retards the process of recovery remarkably, as was first demonstrated by BRAMWELL AND LUCAS (1911).

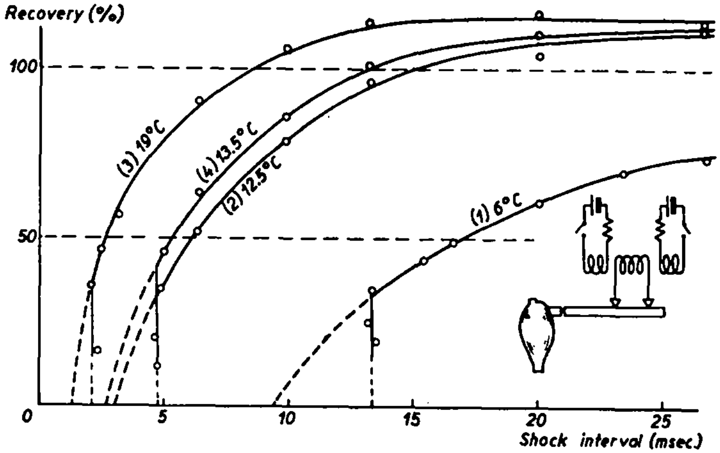

Fig. 4. The recovery curves of a nerve fibre determined at four different temperatures. The numerals in parentheses indicate the order of the determination. The broken lines are so drawn that the whole curves can be expressed roughly by continuous exponential functions.

In the experiment of Fig. 4, fluid electrodes of the type used by ADRIAN (1914) were employed. The preparation was placed in the nerve chamber, and the recovery curve was determined by taking as index the action current of the single nerve fibre. The strength of the first induction shock was fixed at double the resting threshold.

The recovery curve of a single nerve fibre thus obtained is discontinuous; the curves always become vertical at a certain time interval. This fact has often been noticed by ADRIAN (1914), who attributed it to some kind of decreasing conduction of the second impulse. In a previous paper (TASAKI AND TAKEUCHI, 1942) direct evidence has been

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presented indicating that this discontinuity is due to a decrease in the safety factor of transmission during the refractory period. In the early stage of the refractory period the threshold of individual nodes of RANVIER at the site of stimulation is so decreased that the reduced action current becomes ineffective in exciting the neighbouring node.

The discontinuity is thus a direct consequence of the electric transmission of the impulse, and the recovery curve without such discontinuity is due to some artefact resulting from the use of the propagated multifibre response as index.

Quantitative consideration leads us further to infer that the recovery of excitability at the interval where the recovery curve becomes discontinuous should be greater than about 20%. The safety factor in the resting fibre is about 5 (TASAKI AND TAKEUCHI, 1942); this means that, if the excitability of the node is decreased to 1/5th the normal value, transmission should be suspended even when the size of the electric response from the individual node remains normal. Since the size of the response, as is well known, decreases during the refractory period, it should be impossible for transmission to take place when the excitability is only 20% of normal. Although the problem of the duration of the testing current is considered to complicate the matter somewhat, all the experimental data hitherto obtained seem to verify this inference.

At the site of stimulation there is naturally no such discontinuity in the recovery curve, and the extension of the recovery curve indicated by the broken lines in Fig. 4 can actually be observed. It is therefore wise to distinguish the "absolutely refractory" period from the "non-conducting phase" in the relatively refractory period. The end of the non-conducting phase may by properly termed the "least interval" required for setting up two transmitted impulses in the nerve fibre.

Turning now to the temperature coefficient of the recovery process, the variation in the duration of the absolutely refractory period resulting from temperature changes is best discussed in connection with that in the spike duration. In the preceding paper, it was shown that the temperature coefficient of the spike duration is 3.5 for a change of 10°. If the duration of the absolutely refractory period has a temperature coefficient very different from that of the spike duration, the time interval between the end of the spike and the earliest return of excitability should vary according to the temperature. If, on the contrary, there is no difference in the temperature coefficients of the two processes, then the relative positions of the spike and the end of the absolutely refractory period should remain unaffected by a change of temperature.

Experiments carried out to test this point indicated that there is no detectable difference in the temperature coefficients. It was shown further that, as ADRIAN (1921) has pointed out, the end of the spike always coincides with the end of the absolutely refractory period, regardless of the temperature. Fig. 5 shows the method and an example of the results of the experiments.

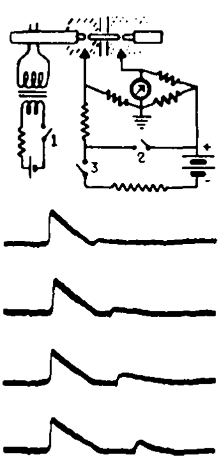

Fig. 5. Action currents of a nerve fibre evoked during the "non-conducting phase" in the relatively refractory period. The first spikes were induced by induction shocks, and the second subnormal spikes by rectangular pulses of 200 millivolts. The interval between the two stimuli was varied at a step of 1.5 millisecond. Temperature was between 8 and 7° C. Time marks below 1 millisecond apart.

A single motor nerve fibre, mounted on a bridge-insulator, was excited by an induction shock applied to the nerve trunk. As the portion of the fibre on the distal side of the bridge-insulator had been treated with a 0.2 % cocaine Ringer solution, the action current was completely "mononodal". The second stimulus, a reactangular current pulse, was applied to the operative region of the fibre. To suppress the displacement of the base line in the action current record by the stimulating current, the technique of the direct current Wheatstone bridge was used. The interval between the first (induction) shock and the second (rectangular) pulse was controlled with a HELMHOLTZ pendulum. The strength of the second pulse was about 6 times the rheobase.

As will be seen in the records, the size of the second response decreases continuously with decreasing shock interval. The relation between the size of the response and the interval between the stimuli indicates that the earliest return of excitability occurs immediately after the end of the spike. And this was true in all five experiments done at varying temperatures between 5 and 17° C. The interval from the end of the first spike to the earliest second spike (obtained by the extrapolation) was always less than about 15% of the total spike duration.

The effect of temperature changes on the time course of the whole recovery curve was investigated in only two cases. In the example illustrated in Fig. 4, the temperature coefficient for the 50% recovery was between 3.3 and 3.8. In the other case, in which determinations were made at 13°, 7° and 19° C, the coefficient was found to be about 4. Although the accuracy of these determinations is not very satisfactory, it seems safe to conclude that, confirming ADRIAN's previous finding, the recovery curve is affected by the temperature changes to the same extent as the spike duration.

All the findings described above are in general in good agreement with the results obtained by previous investigators. In 1914, ADRIAN found that the temperature coefficient of the recovery curve is the same whatever the specific percentage of recovery at which the comparison is made. AMBERSON (1930) made a thorough investigation on the temperature coefficient of "the least interval" for the double impulse. These authors, as well as GASSER (1931) who made use of a cathode ray oscillograph for the experiment, obtained a coefficient of approximately 3. In the results obtained by SCHOEPFLE AND ERLANGER (1941) on single nerve fibres, the coefficient varied as the temperature; at lower temperature, it seemed to approach about 4.

DISCUSSION

In a preceding paper, it was shown that, in single nerve fibres of the toad, the temperature coefficient for the conduction rate, the spike height and the spike duration are 1.8, 1.3 and 3.5, respectively. By cold, the process of conduction and of recovery are retarded and the spike height is slightly decreased. After the manuscript of our paper had been submitted for publication in this journal, the reprint of SCHOEPLE AND ERLANGER's paper (1941) became available, in which they reported the results of similar experiments on single nerve fibres. Their results are in general consistent with ours, except that in theirs cold increased the spike height instead of decreasing it. This discrepancy seems to be fully accounted for by change in the resistance of the inactive tissues which surround the fibre under observation in their preparation.

It has been shown by YAMAGIWA (1935) that the size of the action potential from a single nerve fibre is markedly augmented by an increase in the resistance of the surrounding fluid and tissue. The action potential of the nerve is determined by the resistance of the inter-electrodal portion of the nerve and the currents produced by individual

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nerve fibres. Thus an increase of the nerve action potential by cold seems to attest to a decreased conductivity of the interelectrodal portion of the nerve. Cold increases, as is well-known, the specific resistance of the electrolytic solution; but its effect upon the connective tissue sheath of the nerve is not known yet.

SCHOEPFLE AND ERLANGER investigated further the effect of cold upon the duration of the ascending and descending phases of the action potential. In their experiments, however, the inter-electrodal distance is long and several nodes of RANVIER are involved between the two lead electrodes. An action potential record obtained in such circumstances should arise by virtue of the currents flowing between these nodes, but a direct comparison of these results with our data is not very easy at present.

Nervous conduction is a process intrinsic to the nerve fibre, and therefore the conduction rate does not vary significantly according to the method of measuring it. There is a remarkable agreement among the data, old and new, on the effect of temperature on the conduction rate. The temperature coefficient obtained by LUCAS (1908) is just the same as that obtained by use of the single fibre technique. The duration of the refractory period seems to depend to some extent upon the experimental arrangement adopted, but still almost all investigators give approximately the same absolute values and the same temperature coefficient. The threshold and the chronaxie are influenced greatly by the method of measurement, and consequently the agreement among the data of different investigators is not very good.

APPENDIX

1. *The threshold for the exponentially rising voltage*

The time course of an exponentially rising voltage can be described by the formula

$$V(t) = V(1 - e^{-t/rc}),$$

where V stands for the final voltage and rc for the time constant of voltage rise. The time z at which the stimulating voltage crosses the rheobase b is given by the equation

$$b = V(1 - e^{-z/rc}). \tag{1}$$

The rate of voltage increase at this moment is given by

$$\left(\frac{dV(t)}{dt}\right)_{t=z} = \frac{V}{rc}\, e^{-z/rc}.$$

This rate must be greater than, or at least equal to, the minimal gradient m of the fiber in order that excitation can occur. Thus, for a threshold excitation,

$$V\,\frac{1}{rc}\, e^{-z/rc} = m. \tag{2}$$

Eliminating z from equations (1) and (2), we obtain the formula

$$V = mrc + b \tag{3}$$

which is fully verified by experiment.

2. *The excitability change for a rectangular current pulse*

We shall denote the "latent addition curve" (the continuous line in Fig. 2 B or C) by the equation

$$Q = \varepsilon + q \cdot \psi(t), \tag{4}$$

where q represents the quantity of electricity of the conditioning shock and Q the threshold (quantity) for the test shock. This curve extends over the negative side of the time axis as far as $t = -a$, owing to the delayed maximum of the excitatory state mentioned in the text.

When a series of conditioning shocks, of which the quantities are given by q_1, q_2, q_3, . . ., are applied to the nerve fibre in succession at times $t = 0.\ d_1, d_2, \ldots$, then the threshold for the test shock applied at time t is given, according to the law of superposition established by a previous experiment (TASAKI, 1942), by the equation

$$Q = \varepsilon + q_1 \cdot \psi(t) + q_2 \cdot \psi(t - d_1) + q_3 \cdot \psi(t - d_2) + \ldots \tag{5}$$

A continuous constant voltage v may be regarded as a succession of brief voltage pulses having a quantity vdx. Then the contribution to the threshold from the voltage pulse bounded by $t = x$ and $t = x + dx$ should be given, as in the preceding case, by $v \cdot dx \cdot \psi(t - x)$. As all the elements of pulse between the time zero (at which the voltage starts) and $t + a$ contribute to the variation of threshold at the time t, the value of Q at t is given by

$$Q = \varepsilon + v \int_0^{t+a} \psi(t - x)\,dx.$$

By the substitution $y = t - x$, we finally obtain the relation

$$Q = \varepsilon + v \int_{-a}^{t} \psi(y)\,dy. \tag{6}$$

The area under the latent addition curve is defined by

$$\varphi \equiv \int_{-\infty}^{\infty} \psi(y)\,dy = \int_{-a}^{\infty} \psi(y)\,dy.$$

For a sufficiently great value of t, equation (6) assumes the form

$$Q = \varepsilon + v\varphi. \tag{7}$$

This equation represents the linear relation between Q and v in the experimental results of Fig. 3, right. The ordinate S in Figs 2 and 3 corresponds to Q divided by the duration of the test shock.

SUMMARY

1. An exponentially rising current excites an isolated single nerve fibre when, and only when, it rises above and crosses the rheobase at a rate of rise greater than the minimal gradient of the fibre. The rheobase is not affected by changes in temperature. The minimal gradient shows a tendency to be increased by cold, but there is a marked hysteresis in the effect of temperature changes on the minimal gradient.

2. A brief subthreshold shock produces an excitatory state which first rises and then falls after the end of the shock. The time course of this process is retarded by cold. The minimum quantity of electricity needed to excite a single nerve fibre is increased by cold, its temperature coefficient being 1.7 for a change of 10° C.

3. At every temperature, the earliest return of excitability occurs immediately after the end of the spike. The process of recovery is affected by temperature changes to the same extent as the spike duration.

RÉSUMÉ

1. Un courant croissant exponentiellement excite une fibre nerveuse isolée lorsque, et seulement lorsque ce courant dépasse la rhéobase à une vitesse de croissance supérieure à celle du gradient minimum dans la fibre. La rhéobase n'est pas modifiée par les changements de température. Le gradient minimum montre une tendance à augmenter par le froid, mais il y a une hysteresis notable dans l'influence des changements de température sur le gradient minimum.

2. Un bref choc sous-liminaire produit un état d'excitation qui d'abord croît, puis diminue après la fin du choc. La durée de ce phénomène est retardée par le froid. La quantité minimum d'électricité requise pour exciter une seule fibre nerveuse est augmentée par le froid, le coefficient de température étant de 1.7 pour un changement de 10° C.

3. A chaque température, le début du retour de l'excitabilité a lieu immédiatement après la fin du "spike". Le processus de récupération est affecté par les changements de température de la même façon que la durée du "spike".

ZUSAMMENFASSUNG

1. Ein exponentiell wachsender Strom erregt einen isolierten einzelnen Nerv dann, und nur dann, wenn er die Rheobase übersteigt und mit einer Steigungsgeschwindigkeit kreuzt die grösser ist als das Mindestgefälle im Nervenstrang. Die Rheobase wird durch Temperaturänderungen nicht beeinflusst. Das Mindestgefälle zeigt die Tendenz, durch Kälte vergrössert zu werden, jedoch besteht eine beträchtliche Hysteresis in der Einwirkung von Temperaturänderungen auf das Mindestgefälle.

2. Ein kurzer unterschwelliger Schock bewirkt einen Erregungszustand welcher nach Ende des Schocks zuerst wächst und dann abnimmt. Der Zeitverlauf dieses Prozesses wird durch Kälte verlangsamt. Die zur Erregung eines vereinzelten Nervenstrangs benötigte Mindestmenge von Elektrizität wird durch Kälte vermehrt; der Temperaturkoeffizient beträgt 1.7 für eine Änderung von 10° C.

3. Bei jeder Temperatur findet die früheste Rückkehr der Erregbarkeit sofort nach dem Ende der "Spitze" statt. Der Erholungsprozess wird durch Temperaturänderungen in gleichem Ausmass beeinflusst als die "Spitzen"-Dauer.

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