# ACTION CURRENTS OF SINGLE NERVE FIBERS AS MODIFIED BY TEMPERATURE CHANGES

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IN 1931 Gasser (1) carried out a very careful study on the effect of temperature changes upon the action potential of nerve. As Gasser himself states in his paper, comparison of the action potential forms at two different temperatures is subject to considerable possible error. This is mainly due to the different degree of temporal dispersion of the action potentials from different nerve fibers in a nerve trunk at different temperatures but this source of error can undoubtedly be obviated by the use of single fiber preparations for the experiments.

The method of "bridge-insulator," which we have adopted in the present study, seems to eliminate some of the possible sources of error in the ordinary technique of recording the action potential from a single nerve fiber using a slender nerve trunk. With the ordinary technique, the magnitude of the observed action potential is determined primarily by the resistance of the portion of the nerve between the two lead-off electrodes, and it may change from time to time as the fluid around the nerve vaporizes gradually. With a bridge-insulator, the potential is, on the contrary, essentially controlled by the shunting resistance connected between the lead-off electrodes. In the ordinary technique the observed action potential gives information on the activities of several nodes of Ranvier under the active electrode, while in the bridge-insulator method the node in the direct neighborhood of the bridge plays a predominant role in the production of the current observed.

It is the purpose of the present investigation to reexamine, with isolated single nerve fibers of the toad, Gasser's previous observations on the effects of temperature changes upon nerve activity. We are concerned in this paper with the changes in (i) the conduction time, (ii) the spike height, (iii) the spike duration and (iv) the strength-latency relation.

## METHOD

All the experiments described in this paper were performed on the single motor nerve fiber of the spring toad. The preparation, together with the bridge-insulator and the electrodes, was kept in a large metal chamber and the temperature was controlled by changing the temperature of the wall of the chamber. Care was taken to stir the air in the chamber and to minimize the gradient of temperature in the air. The moisture of the air was measured by means of a thermo-junction covered with cotton wool soaked in Ringer, and was controlled by introducing steam or dry air into the chamber.

The method used for action current observations was essentially that described by Tasaki and Takeuchi (4). In the first series of observations, in which the conduction time, spike height and spike duration were determined at varying temperature, fibers innervating the toe-flexor muscle were used, as a long conduction distance (about 100 mm.) was available in these preparations. The operation to isolate a single nerve fiber was carried out on

the nerve near its distal end where a small twig innervating the muscle branched off. The operated portion of the preparation was mounted on a "bridge insulator," and two lead-off electrodes (Zn-ZnSO₄-Ringer type) were immersed in the pools on both sides of the bridge-insulator(see Fig. 1, top left). The stimulation was effected by break shocks from an induction coil, the strength of the shocks being controlled by a resistance in the primary circuit. The secondary coil was insulated from the ground, and shocks of double the threshold strengths were applied to the nerve fiber near its proximal stump through a pair of platinum electrodes. Into the distal pool was introduced a 0.2 per cent cocaine-Ringer solution to make the lead "mononodal" (4).

In the second series of experiments, rectangular current pulses of 10 msec. in duration were used as stimuli. Both stimulation and recording were effected through one and the
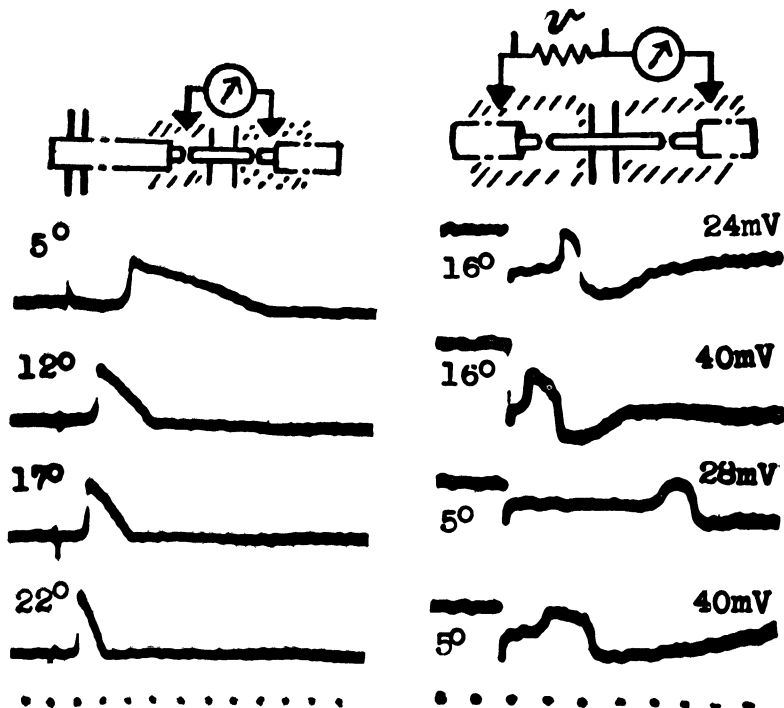


FIG. 1. Left column: Effect of temperature changes upon the "mononodal" action current of a single nerve fiber. Conduction distance in this case was about 30 mm. Right column: Effect of temperature changes upon the latent period in excitation of a single fiber by long rectangular current pulses. Strength of pulse and temperature at which the record was taken are given. Time msec.

same pair of non-polarizable electrodes dipped in the two pools of Ringer (see diagram in Fig. 1, right). As the action currents were recorded in these cases at the site of stimulation, there was no preference as to the kind of the preparation. Motor fibers innervating the gastrocnemius muscles were generally used.
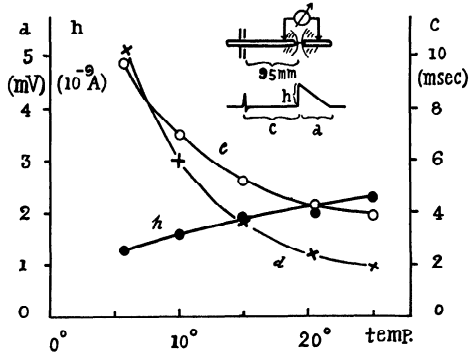
The range of temperature in which the observations were carried out was from 5° to 25°C. All the functions of the nerve fiber considered in this paper were affected by temperature changes in a perfectly reversible manner, and no progressive change was observed when the temperature in the nerve chamber was kept at a steady level.

## RESULTS

It was relatively easy to follow the temperature dependence of the conduction time, the spike height and the spike duration in single preparations.

In the example presented in Figure 2, all these three values were determined on one and the same preparation. In the example shown in Figure 3, where the logarithms of these quantities are plotted against the reciprocal of the absolute temperature, the height and duration of the spike were determined in a single preparation and the conduction time in another.



FIG. 2. Relation between temperature and conduction time (c), spike height (h) and spike duration (d). Data obtained from a single preparation.

Because of the long conduction distance employed, error arising from the latency at the stimulated locus (3) is considered negligible. The conduction rate varied considerably from preparation to preparation, but its temperature coefficient was found to be about the same in all cases. Between 5° and 20°C. it was regularly 1.8 in $Q_{10}$ value.

Of all the quantities examined, the spike duration showed the greatest temperature coefficient. In the range from 5° to 20°C., it had a value varying from 3 to 3.5 according to the preparation. Under these experimental condi-
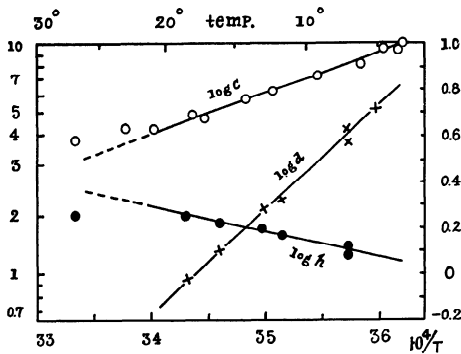


FIG. 3. Relation between the reciprocal of the absolute temperature and the logarithms of (c) the conduction time (in msec.), of (h) spike height (in $10^{-9}$A.) and of (d) spike duration (in msec.). In (c), the conduction distance was 82 mm.

tions, it was not feasible to determine the duration of the rising and falling phases of the action current separately, as the former value was too short to allow any accurate measurement.

It should be noticed that in our experiments the temperature coefficient of the spike height observed was extremely low. It was constantly about 1.3 for the temperature range between 5–20°C. For the same temperature

range, Gasser (1) has obtained coefficients mounting to over 100. As we shall see in a subsequent paper, the minimum quantity of electricity required for excitation (2) increases remarkably as the temperature falls off; it is doubled by a fall of about 13°. This rise of the threshold and a greater temporal dispersion at a lower temperature would probably account for the great temperature coefficient obtained by Gasser. At every temperature between 5° and 25°C., it was found that the relation between the voltage $v$ of a long rectangular pulse and the latency $t$ could be expressed by a hyperbola
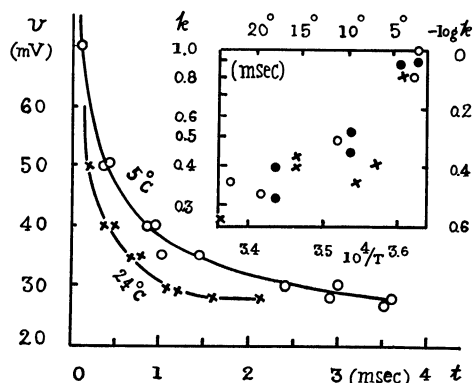


FIG. 4. The relation between the voltage $v$ of a long rectangular pulse and the interval $t$ from the make of the pulse to the beginning of a spike determined at two different temperatures. Inset: logarithms of the chronaxie for the latency ($k$) at varying temperatures.

$v = (k/t - 1)b$, where $b$ represents the rheobase and $k$ the chronaxie for the latency. The rheobase was not affected by temperature changes. It was the value of $k$ that changed markedly according to the temperature.

Data presented in Figure 4 show how the voltage-latency curve and the value of $k$ are affected by the temperature. Unfortunately, the latency could not be determined very accurately for high voltages, and consequently the determination of the temperature coefficient of chronaxie was not very satisfactory. In the inset of Figure 4, data from three different preparations were collected. If we assume in this case a linear relationship between log $k$ and the temperature, a coefficient of about 2 or slightly less is obtained for chronaxie.

In a previous paper (4) it has been shown that the internodal conduction time is determined by the latent period of a Ranvier node in excitation by the action current arising from the preceding node. Since the strength of the action current and the rheobase are not appreciably changed by the temperature, it is inferred that the temperature coefficient of the chronaxie $k$ should be approximately equal to that of the conduction time. And this is now shown to be actually the case.

## DISCUSSION

In all our experiments, the relations between the temperature and the logarithms of the above stated physiological quantities were expressed by

straight lines in the temperature range between 5 and 20°C. For the tempera-
ture above 20°C., the temperature coefficients showed a tendency to de-
crease. But, as a wide variation in the temperature is apt to bring about some
secondary effects harmful to the nerve fiber (such as evaporation or con-
densation of water), our observations above 20°C. were not very satisfactory.
In the range between 25 and 30°C., single nerve fiber-muscle preparations
lose their ability to respond to stimuli relatively quickly.

On several occasions we have examined the effect of temperature changes
upon the strength-latency relation for brief shocks. The duration of the
shock was about 0.03 msec. Records of action currents were taken at the
site of stimulation. At 5°C., the longest latent period observed was 1.3
msec. and the latent period for a shock of 110 per cent the threshold
strength was 0.5 msec. At 12°C., these values (*i.e.*, the longest latent period
for a threshold shock and the value for 110 per cent threshold) were 0.9 and
0.35 msec. At 20°C., they were 0.45 and 0.3 msec.

In connection with the theory of nerve excitation, one of us (I. T.) has
carried out a detailed observation on the effect of temperature changes upon
the excitability of the nerve fiber. We shall reserve a description of the results
for a subsequent paper.

## SUMMARY

The temperature coefficients of the conduction time, the spike height,
the spike duration and the chronaxie for the latency were determined on
isolated single nerve fibers of the toad in the range between 5° and 20°C.
They were found to be 1.8, 1.3, 3.5 and about 2 respectively.

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