EFFECT OF TEMPERATURE ON THE EXCITABILITY OF PIGEON MUSCLE

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(Received April 26, 1956. Presented by Active Member of the AMN SSSR D. N. Nasonov) *

In previous papers dealing with investigations of the effect of temperature on isolated frog and turtle nerves [2, 3], it was shown that the constants a and b in Gorveg's** formula [8] vary in opposite directions with temperature changes of 10° made in the temperature range from 5 to 30° C. On cooling, the rheobase of the tissue (constant b) is reduced, and the excitibility to stimuli of long duration increases; at the same time the threshhold of short-term excitability (constant a) increases, i.e. the excitability to short stimuli falls. As a result, the strength-duration curves of cooled and warmed nerves intersect, and the excitability to stimuli in the area where the curves intersect remains constant over a certain temperature range. (The nerves of winter frogs form an exception, and, unlike those of summer frogs, the strength-duration curves for the heated and cooled nerves do not intersect.)

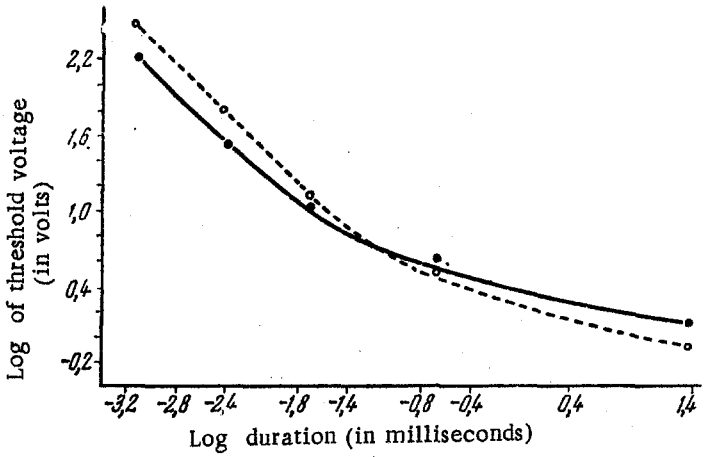

Fig. 1. Logarithmic curves of strength – duration for the m. flexor metacarpi radialis of the pigeon wing at 39°C (continuous line) and at 28.5°C (dotted line).

* Deceased.

** D. N. Nasonov and D. L. Rosental' [1] showed that the constants a and b of Gorveg's formula V= (a/t) + b can be used to describe tissue excitability if the index of t = I. The constant a determines the excitability to very short discharges. When t is very small, the value of a/t in the formula V = (a/t) + b becomes so large that the value of b can be neglected; then V = (a/t) or a = t • V. The constant b determines the sensitivity to stimuli of long duration, and is independent of the duration, because when t becomes very large, the value of a/t in the formula V = (a/t) + b becomes negligeable, and then V = b.

TABLE 1

Changes in the Excitability Constants for the m. flexor metacarpi radialis of the Pigeon Wing on Changing the Temperature from 39 to 29°C, and from 29 to 39°C (mean values from 7 experiments and standard deviations)

From 39 to 29°C				From 29 to 39°C			
a		b		a		b	
initial value (mv/msec)	after cooling (% of initial value)	initial value (volts)	after cooling (% of initial value)	initial value (mv/msec)	after heating (% of initial value)	initial value (volts)	after heating (% of initial value)
104,1	+48,7±13,5	1,03	−32,7±3,3	157	−35,0±5,3	0,86	+34,0±3,8

Key: a) threshold of short-term excitability; b) threshold of long-term excitability (rheobase).

TABLE 2

Variation in the Excitability Constants of the m. flexor metacarpi radialis of the Pigeon Wing on Changing the Temperature from 30 to 20°C and from 20 to 30°C (mean values of 7 experiments and standard deviations)

From 30 to 20°C				From 30 to 30°C			
a		b		a		b	
initial value (mv/msec)	after cooling (% of initial value)	initial value (volts)	after cooling (% of initial value)	initial value (mv/msec)	after heating (% of initial value)	initial value (volts)	after heating (% of initial value)
103,0	+212,0±88	0,91	−28,0±4,2	370,0	−58,0±10,2	0,73	+38,0±7,2

Key: symbols as in Table 1.

TABLE 3

Variation of the Excitability Constants of the m. flexor metacarpi radialis of the Pigeon Wing on Changing the Temperature from 20 to 10-8°C and from 10 to 20°C (mean values from 10 experiments and standard deviations)

From 20 to 10°C				From 10 to 20°C			
a		b		a		b	
initial value (mv/msec)	after cooling (% of initial value)	initial value (volts)	after cooling (% of initial value)	initial value (mv/msec)	after heating (% of initial value)	initial value (volts)	after heating (% of initial value)
385,0	+208,0±52	1,11	+51,0±17,6	1486,0	−64,0±6,2	1,86	−36,0±9,6

Key: symbols as in Table 1.

From this it may be concluded that the nerves of cold-blooded animals have the power to stabilize their excitability in face of temperature changes, and that this constancy is maintained over the range of stimuli of moderate length, a length which is approximately equal to that of physiological stimuli.

There are some differences between cold- and warm-blooded animals with respect to the dependence of the excitability of their nerves on temperature. The nerves of the former are able to regulate the excitability to voltages of a certain length over a wide range of temperatures [2, 3], while in the latter, the regulation of the excitability is effective only over a narrow temperature range – from 40 to 35°C [5].

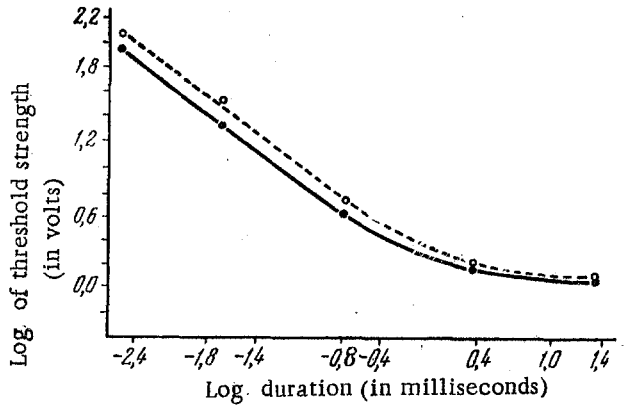

Fig. 2. Logarithmic curves of strength – duration for the m. flexor metacarpi radialis of the pigeon wing at 20°C (continuous line) and at 10°C (dotted line).

A study of the excitability of the muscles of warm-blooded animals (rats) at different temperatures [4] has shown that on cooling from 20 to 10°C, i.e. over a range of low temperatures, the excitability of the muscles both to short (a) and to long (b) stimuli is reduced, and that on heating to 20°C it increases. However, on cooling or heating at higher temperatures – from 20 to 30°C and from 30 to 40°C – the excitability of rat muscle changes in the same way as does the excitability of both nerve and muscle in cold-blooded animals [3, 5, 7], i.e. the constants a and b change in opposite directions. Cooling causes an increase in excitability to stimuli of long duration (reduction of constant b) and a reduction of excitability to short-acting stimuli (increase of constant a). On heating, the reverse effect obtains: the excitability to stimuli of long duration is reduced, while that to short stimuli is increased.

On account of these results we have undertaken a further set of experiments on the muscle of warm-blooded animals, but we have used another class – that of the birds – in order to discover whether the feature which we found previously – the dependence of the excitability of rat muscle on temperature, is also true for warm-blooded animals in general, or whether it is only a property of one particular species. The animals which we used for these experiments were pigeons.

METHOD

The muscle employed was the m. flexor metacarpi radialis, which was particularly useful for the task in hand. The muscles were isolated, bathed in Ringer's solution, and placed on electrodes separated by a distance of 1.5 cm in a chamber through which flowed vaseline oil whose temperature could be changed by 10°C in 3-5 minutes; the temperature could be kept constant to an accuracy of 1°C. Stimulation of the preparation was effected by condenser discharges of different durations. The effect of the stimulation was recorded by the contraction of the muscle. In some experiments the whole strength-duration curve of the muscle was plotted; in others, in order not to damage the preparation, the measurements were confined to the constant b – the rheobase measured in volts, and the constant a – the short-term excitability, where a was found, as had been proposed by D. N. Nasonov and D. L. Rozental' [1], by multiplying the potential in millivolts required to cause a muscular contraction by the corresponding duration in milliseconds (mV · msecs). The results were considered reliable if the difference between the mean values, expressed as a percentage, was greater than three times the root mean square error.

RESULTS

Altogether 3 sets of experiments were carried out over temperature ranges of 29-39°C, 20-30°C, and 20-10-8°C. There were 7 experiments in each of the first and second groups, since the change of excitability with temperature was very much the same for the two temperature ranges. In the third group, there were 10 experiments. On cooling the m. flexor metacarpi radialis from 39 to 29°C, the excitability to brief stimuli fell on average by 48.7% (the threshold value represented by the constant a increases), and the excitability to stimuli of long duration increased by 32.7% (the threshold corresponding to the constant b, or rheobase, decreases). Warming

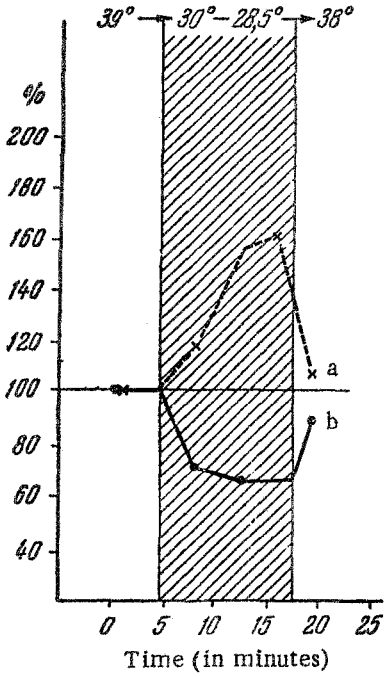

Fig. 3. Changes in the constant for short-term (a) and long-term (b) excitability of the m. flexor metacarpi radialis of the pigeon wing (in % of initial value) on cooling the muscle from 30 to 20-18°C and subsequently reheating to 30°C.

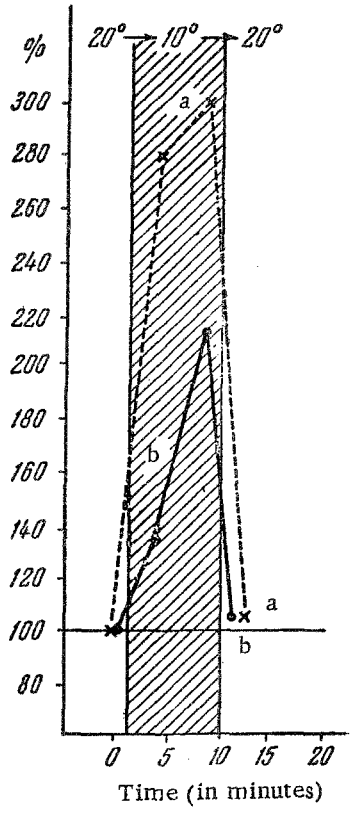

Fig. 4. Changes in the constant for short-term (a) and long-term (b) excitability of the m. flexor metacarpi radialis of the pigeon wing (in % of initial value) on cooling the muscle from 20 to 10°C and subsequently reheating to 20°C.

the muscle caused a reversal of this result: the excitability to brief stimuli increased by 35%, and that to long stimuli fell by 34% (Table 1).

A logarithmic plot of the strength-duration curve of one such experiment is shown in Fig. 1. Here the strength – duration curves taken at 39 and 29°C intersect at a value of 0.05 milliseconds. Fig. 2 shows changes in the constants a and b found during the same experiment, and here, the values obtained after heating or cooling are expressed as a percentage of their original values. It is clearly seen from the figure that on cooling, the two constants changed in opposite directions, and that on warming they almost returned to their initial values.

In the second set of experiments, a study was made of the excitability of the m. flexor metacarpi radialis on cooling from 30 to 20°C, and then reheating to 30°C. As can be seen from Table 2, on lowering the temperature from 30 to 20°C, the excitability changed in the same direction as was observed in the first set of experiments: on cooling, the rheobase was reduced by 28% (the excitability increased), while on heating, it increased by 38% (the excitability fell); at the same time, the excitability to brief stimuli was increased by 58% on heating to 30°C, and on cooling to 20°C it dropped sharply – on average by 212%. Here the standard deviation is very great, since the fall in the excitability in these experiments varies from 60 to 700%.

Thus, in the first and second sets of experiments, the excitability constants (a and b) of the pigeon muscle change in opposite directions, and are temperature-dependent both for long stimuli lasting from 0.20 to 24 milliseconds, as well as for short stimuli of from 0.02 to 0.008 milliseconds; the excitability to short stimuli (a) changes several times more than does the rheobase (b). However, in all experiments of the first two groups, there is a region in the strength-duration curves in which the curves of both the heated and cooled muscles intersect, i.e. for a certain intermediate duration of electrical stimulus, the excitability is either independent of the temperature or depends very little on it.

In the third set of experiments, we

tried to reduce the temperature of the muscle still further, lowering it from 20 to 10°C and sometimes as far as 8°C (on cooling below 8°C the muscle excitability failed), after which the temperature was returned to the initial value. It was found that on cooling, the excitability to brief stimuli falls, on average, by 208%, i. e. the same effect is observed to occur on changing temperature in the experiments described above. However, there is now the difference that the excitability to stimuli of long duration is also lowered by 51%. On heating, on the contrary, the excitability to short and to long stimuli is increased, so that both constants a and b are reduced. As can be seen from Table 3, the results of this set of experiments are statistically significant. Fig. 2 shows strength - duration curves from one of these experiments. The curves do not intersect, and any point on the curve falls in a region where the excitability is related to temperature; the relationship is different in the two cases – the excitability to short stimuli being greater than that to stimuli of long duration. Fig. 4 shows the changes in constants a and b from one of the experiments of this set, where the excitability of muscles to short and to long stimuli falls on cooling, and almost returns to its initial value on heating. The difference between the changes of the constants a and b in pigeon muscles on changing from one temperature range to another, can be very clearly seen by comparing Figs. 1 and 2 with Figs. 3 and 4. In the first case, i. e. on changing the temperature from 39 to 20°C, the constants a and b change in opposite directions; in the latter case, when the experiments are carried out in a low temperature region, from 20 to 10°C, both constants change in the same way.

The results we have described allow us to conclude that temperature changes in the temperature range from 20 to 40°C causes little change in excitability for stimuli of moderate length, but that for either long or short stimuli, the excitability changes in opposite directions. On changing the temperature from 20 to 10°C, the excitability of pigeon muscle to stimuli of any length falls on cooling and increases on heating. Similar results were obtained for both tonic and tetanic muscles of the rat [6]. Thus, no essential differences in the excitability reactions of muscles were found to differentiate homothermic from poikilothermic animals [5, 6, 8]. The only feature distinguishing the two groups of animals is the particular temperature range over which the strength-duration curves intersect, the intersection showing that there is a region over which the excitability to stimuli of moderate duration is constant. For muscles of warm-blooded animals, this temperature ranges from 40 to 20°C, while for the muscles of cold-blooded animals, it extends from 25 to 5°C. In other words, for warm-blooded animals in general, cell regulation of excitability in response to temperature change does occur, but over a different temperature range than for cold-blooded animals.

SUMMARY

The author studied the effect of cooling and warming of pigeon's m. flexor metacarpi radialis wing on its excitability to prolonged and short electric stimuli, and on the voltage-time curve. In cooling the muscle from 20° C to 10° and 8° C and its subsequent warming to 20° C there is no intersection of the voltage-time curves. Excitability to stimuli of any duration depends on temperature: it decreases with cooling and increases with warming of the muscle. Cooling of the muscle from 40° C to 30° C and from 30° C to 20° C increases the excitability to prolonged stimuli and decreases it to short ones. In warming (within the limits of the temperatures mentioned above) the excitability to prolonged stimuli is decreased and to short is increased.

The voltage-time curves cross in cooled and warmed muscles. Therefore, the excitability of the muscles to currents of certain medium duration (approximately corresponding to the duration of the physiological impulse), shows an insignificant change at various temperatures. Consequently, there is a cellular adjustment existing in the muscles of both warm- and cold-blooded animals, controlling the excitability of the muscles and protecting them from sharp changes at various temperatures.

LITERATURE CITED

[1] D. N. Nasonov and D. L. Rozental', Fiziol. zhurn. SSSR, 39, No. 4, 405 (1953).

[2] D. N. Nasonov and I. P. Suzdal'skaya, Fiziol. zhurn. SSSR, 42, No. 4, 415 (1956).

[3] D. N. Nasonov and I. P. Suzdal'skaya, Zhurn. Biofizika, volume 1, issue 4, 306 (1956).

[4] D. N. Nasonov and I. P. Suzdal'skaya, Fiziol. zhurn. SSSR, 44, No. 11, 1034-1039 (1958).

[5] I. P. Suzdal'skaya, Fiziol. zhurn. SSSR, 43, No. 1, 80 (1957).

[6] I. P. Suzdal'skaya, Fiziol. zhurn. SSSR, 43, No. 5, 449 (1957).

[7] I. P. Suzdal'skaya and M. B. Kiro, Byull. éksptl. biol. i med. volume 43, No. 5, 28-31 (1957).

[8] G. Hoorweg, Pflug. Arch. Bd. 52, 87 (1892).