

TEMPERATURE ACCLIMATION
OF THE FUNCTIONAL PARAMETERS OF THE GIANT
NERVE FIBRES IN *LUMBRICUS TERRESTRIS* L.

I. CONDUCTION VELOCITY AND THE DURATION OF THE
RISING AND FALLING PHASE OF ACTION POTENTIAL

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Temperature acclimation in poikilotherms has been the subject of several recent reviews and symposia. Many of the acclimation phenomena occurring at the organismal or organ level have been shown to be accompanied by corresponding compensatory cellular changes. However, only in a few instances has thermal acclimation also been demonstrated to occur in isolated surviving tissues of animals (Precht & Christophersen, 1965; Lagerspetz & Dubitscher, 1966; Schlieper, 1966). In these cases of acclimation the mechanism of acclimation thus operates on the cellular or tissue level.

Not much is known about the mechanisms of temperature acclimations. It seems reasonable to assume that the primary phenomenon in temperature acclimation is confined to the system controlling the activity in question; in most cases this is the nervous system. Evidence for neural mediation of the temperature acclimation of the oxygen consumption of eel muscles has been presented by Prosser, Precht & Jankowsky (1965).

If the mechanisms of temperature acclimation ultimately lay in the compensatory actions of nervous control systems, the nervous functions should also show a high degree of acclimation. Temperature acclimation has been shown to occur in certain nervous functions (conduction, reflex activity, conditioning) in fish (Roots & Prosser, 1962; Prosser & Farhi, 1965). In the experiments of Kerkut & Taylor (1958, p. 262) isolated ganglia of cockroaches kept for four weeks at 22° C showed a maximum of spontaneous activity at that temperature, while those from animals kept at 31° C. exhibited highest activity at about 31° C.

There are also some results concerning the temperature acclimation of the peripheral nerves. The data of Engelhardt (1951) show that temperature acclimation probably occurs in nervus ischiadicus of the frog in animals kept at 5-10° C. or at 15-20° C. The acclimation effect is clear below 10° C. and above 25° C. (Engelhardt, 1951, Abb. 1, p. 126). Chatfield, Lyman & Irving (1953) found temperature acclimation in the cold-resistance of conduction in the peroneal nerve in the leg of herring gull. However, no differences were found by Grainger & Goldspink (1964) at 20° C. in the characteristics of nerve-muscle preparations from frogs acclimated to 10° C. or 22° C., or in the motor performance of these frogs at 18° C. Pampapathi Rao & Saroja (Pampapathi Rao, 1967, p. 105) found that the conduction velocity in the giant fibres of the

tropical earthworm *Lampito mauritii* at 28° C. was about 4 times higher in animals acclimated to 20° C. than in those acclimated to 35° C. The cholinesterase activity and the acetylcholine content were also higher in the nerve cords of animals acclimated to the lower temperature.

In order to elucidate the mechanisms of temperature acclimation it would be of importance to know whether the functions of single nerve fibres of poikilotherms exhibit temperature acclimation. If it can be shown that single fibres of poikilotherms compensate for temperature changes, many of the acclimation phenomena of the functions controlled by the nervous system probably could be explained as an outcome of acclimation of the nervous control. Measurements of the parameters should be made at several different experimental temperatures since much information is certainly lost if acclimated animals are compared at one intermediate temperature only. For technical reasons, the septate giant axons of earthworms were selected as most suitable material for this type of study.

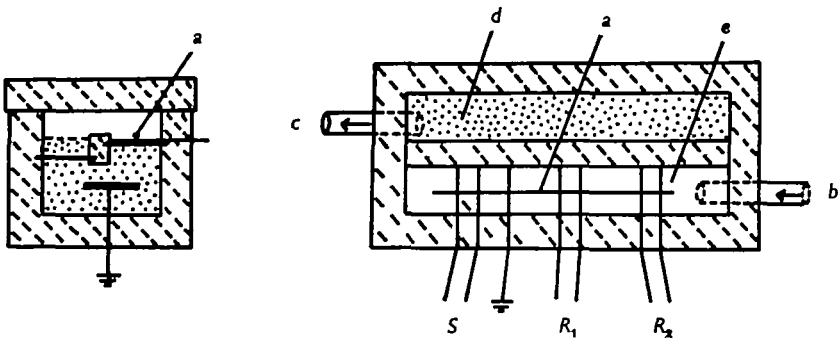


Fig. 1. The nerve chamber used in experiments. Vertical section to left, horizontal section to right. *S*, Stimulation electrodes; *R*₁ and *R*₂, recording electrodes. *a*, Nerve cord; *b*, water inlet for temperature control; *c*, water outlet; *d*, water for the control of the humidity in the chamber; *e*, glass plate.

MATERIAL AND METHODS

Mature earthworms of the species *Lumbricus terrestris* L. were collected from two parks in the city of Turku. The earthworms were stored at 13° C. in plastic boxes of a capacity of 60 l. in leaf mould. For acclimation to higher temperature the animals were kept for 7–14 days at 23° C. in otherwise similar conditions.

The nerve cord of non-narcotized animals (Laverack, 1961) was dissected out caudal from the 15th segment. The cord was placed for at least 5 min. in physiological saline (Rushton, 1945; see also Kao & Grundfest, 1957) which was kept at the acclimation temperature. In these conditions the giant fibres were found to be functional at least for 7 hr. at room temperature.

The nerve cord was then placed in a moist nerve-chamber (Fig. 1) on fixed electrodes. The experimental temperature was controlled by water flowing from a thermo-controlled bath or from an ice-bath through the lower part of the chamber. This was grounded by a large metal plate in order to avoid electrical disturbances caused by the water-pumps and the thermostat. The temperature was measured by a thin (0.8 mm). thermocouple from a strip of moist filter-paper close to the nerve cord. The lower limit of the experimental temperature with the present set-up was about 4.5° C. The

giant fibre function usually ceased at 31–35° C. The temperature could be changed at a rate of 10° C./min. or less. The measurements were made after 2–4 min. had elapsed from the equilibration of temperature.

For stimulation a Grass S4 stimulator was used with a stimulus-isolation unit. Frequencies of 5 Hz or less were generally used, and the duration of the stimulus was usually 0.5 msec. A Tektronix 502A two-channel oscilloscope was employed for display and recording. For photography a robot camera was available.

The conduction velocity was determined according to the method presented by Whitfield (1964, p. 79). The time-base unit of the oscilloscope was used for time calibration.

The duration of the rising and falling phase of action potential was determined graphically from the monopolar extracellular recordings. For monopolar recording the nerve cord was crushed between the distal pair of electrodes. An attempt was made to reduce the inaccuracy of the graphical method (Hodgkin & Katz, 1949a, p. 41) by using an expanded time-scale in the recording.

The Q_{10} values were calculated separately for each animal and each temperature interval.

Table 1. *Effects of temperature acclimation on conduction velocity of the impulse in giant fibres at different temperatures*

(AT, Acclimation temperature; ET, experimental temperature; *n*, number of experiments.)

AT (°C.)	ET (°C.)		Conduction velocity (m./sec.)					
	Variation range	Mean	Median giant fibre			Lateral giant fibres		
			Variation	Mean	<i>n</i>	Variation	Mean	<i>n</i>
13	4.8–8.6	5.9	3.7–10.0	6.33†	12	1.95–6.67	3.62†	22
23	5.4–7.5	6.5	1.95–6.67	3.71†	16	1.00–4.55	2.40†	24
13	12.3–16.0	13.2	7.15–16.00	10.00	16	4.65–8.34	6.22	22
23	12.3–15.0	13.3	5.55–14.82	8.41	21	3.15–9.10	5.42	28
13	21.3–23.8	22.4	11.76–28.60	16.15	14	6.00–14.30	9.40	19
23	22.0–24.4	23.5	8.70–21.50	15.24	24	5.00–14.30	9.26	33
13	27.2–29.5	28.9	15.40–23.54	20.11	8	7.40–13.80	10.49	13
23	27.5–29.2	28.3	15.40–21.75	18.43	6	7.40–11.40	9.29	9
13	30.0–33.4	31.8	14.30–25.00	20.10	4	8.70–15.40	11.94	10
23	30.0–33.1	31.9	16.70–22.80	19.43	6	5.88–18.20	10.98	7

† Difference between the mean values significant at the level $P < 0.001$.

RESULTS

(a) Conduction velocity

The results are presented in Table 1 and Fig. 2. In all cases the mean conduction velocity is higher in animals acclimated to 13° C. than in those acclimated to 23° C. However, the difference between the mean conduction rates is significant only at the lowest temperatures studied (about 6° C.; $P < 0.001$ for both the median and the lateral fibres). A slight compensatory temperature acclimation of conduction velocity can thus be demonstrated.

The mean Q_{10} values of the conduction velocity (Table 2) are at all temperatures lower for the cold-acclimated animals. In this case also, the only significant difference

is that for the lowest temperature interval, i.e. for 5.6–13.3° C. in the lateral fibres ($P < 0.001$). For all higher temperature intervals the Q_{10} values for the lateral fibres are again somewhat lower than the Q_{10} values for the median fibre.

At temperatures above 30° C. the conduction velocity sometimes decreased either in the median or in the lateral fibres, although an increase in the velocity was still observed in fibres of the other type. Bullock (1945) found an increase in the time of latency in the giant fibres just before the cessation of conduction.

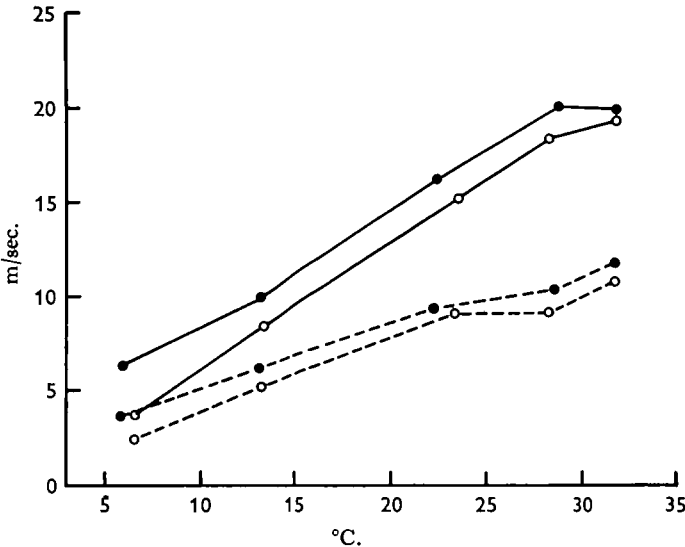


Fig. 2. Conduction velocity at different experimental temperatures. Solid circles, animals acclimated to 13° C.; open circles, animals acclimated to 23° C. Solid lines, median fibre; broken lines, lateral fibres.

Table 2. *Effect of temperature acclimation on the temperature coefficient of conduction velocity*

AT (°C.)	ET range (°C.)	Temperature coefficient Q_{10}					
		Median giant fibre			Lateral giant fibres		
		Variation	Mean	n	Variation	Mean	n
13	5.6–13.2	1.18–3.78	2.31	14	1.21–3.27	2.02	18
23	6.6–13.3	1.65–4.27	3.12	9	1.55–5.62	3.05	16
13	13.2–22.5	1.28–2.71	1.70	12	1.28–1.59	1.46	15
23	13.3–23.3	1.05–2.45	1.91	20	1.13–2.29	1.70	22
13	22.5–28.9	1.11–2.01	1.36	6	1.09–2.05	1.45	8
23	23.3–28.3	1.41–1.91	1.67	5	1.25–2.88	1.72	4

(b) *Duration of the phases of the action potential*

The results are presented in Tables 3 and 4 as well as in Figs. 3 and 4. The duration of both the rise and the fall of the action potential is generally somewhat higher in the giant fibres of warm-acclimated animals than in those of the cold-acclimated group. The differences between the mean values are significant at about 6° and 13° C., except for the rising phase of the spike in the lateral fibres at 13° C. Figs. 3 and 4 show

Table 3. Effect of temperature acclimation on duration of the rising and falling phases of action potential in the median giant fibre at different temperatures

AT (°C.)	ET (°C.)	Rising phase (msec.)				Falling phase (msec.)			
		Variation	Mean	n	P <	Variation	Mean	n	P <
13	5.9	0.6-1.4	0.94	15	} 0.001	2.8-6.0	4.48	12	} 0.001
23	6.5	0.9-2.5	1.80	13		4.8-10.0	7.04	13	
13	13.2	0.2-0.7	0.50	21	} 0.05	1.0-2.8	1.80	20	} 0.001
23	13.3	0.3-1.2	0.68	21		1.6-4.3	2.72	19	
13	22.4	0.13-0.6	0.28	14	} —	0.3-1.0	0.63	14	} —
23	23.5	0.15-0.6	0.33	25		0.5-1.2	0.92	25	
13	28.9	0.13-0.3	0.17	11	} —	0.3-0.8	0.45	11	} —
23	28.3	0.15-0.3	0.21	5		0.5-1.2	0.75	6	
13	31.8	0.10-0.3	0.16	8	} —	0.2-0.6	0.38	8	} —
23	31.9	0.15-0.3	0.24	6		0.4-0.9	0.58	6	

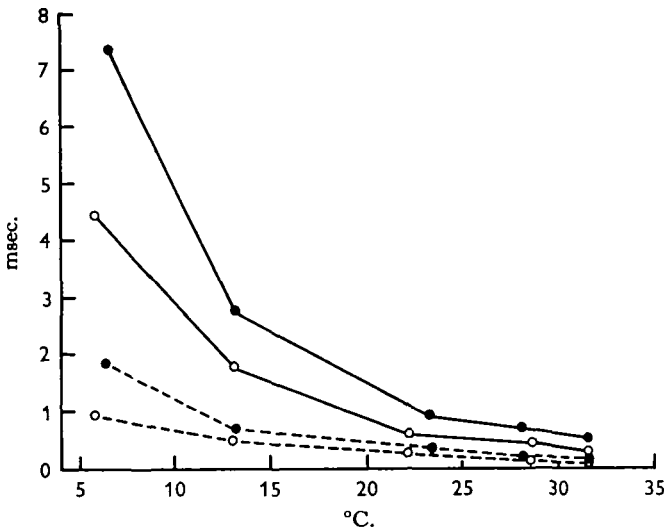


Fig. 3. Duration of the rising and falling phases of action potential in the median giant fibre at different experimental temperatures. Solid circles, animals acclimated to 23° C.; open circles, animals acclimated to 13° C. Solid lines, falling phase; broken lines, rising phase.

that the temperature acclimation of these parameters is efficient. In general, the duration of the rise is shorter and that of the fall longer in the median than in the lateral giant fibres.

The Q_{10} values are presented in Tables 5 and 6. The mean Q_{10} values are considerably higher at the lowest temperature interval (6-13° C.) in the animals acclimated to 23° C. However, only the difference in the rising phase of the spike in the lateral fibres is statistically significant ($P < 0.001$). The Q_{10} values for the cold-acclimated group exhibit less variation between the temperature intervals studied. It is also of interest that, according to the present observations, the Q_{10} values for the rising and falling phases of the action potential are not very different.

Table 4. *Effect of temperature acclimation on duration of the rising and falling phases of action potential in the lateral giant fibres at different temperatures*

AT (°C.)	ET (°C.)	Rising phase msec.				Falling phase (msec.)			
		Variation	Mean	n	P <	Variation	Mean	n	P <
13	5.9	0.4-1.5	1.11	19	} 0.001	1.6-6.0	3.87	18	} 0.001
23	6.5	1.0-5.0	2.37	23		3.8-10.0	6.13	23	
13	13.2	0.4-1.3	0.64	21	} —	0.7-2.2	1.50	19	} 0.001
23	13.3	0.3-1.3	0.77	27		1.8-4.5	2.48	25	
13	22.4	0.25-0.6	0.34	16	} —	0.4-1.7	0.73	16	} —
23	23.5	0.20-0.7	0.37	33		0.6-1.4	1.17	29	
13	28.9	0.2-0.4	0.27	13	} —	0.3-1.0	0.50	12	} —
23	28.3	0.2-0.6	0.31	10		0.4-1.3	0.72	10	
13	31.8	0.15-0.5	0.30	12	} —	0.3-0.8	0.45	12	} —
23	31.9	0.20-0.5	0.30	8		0.4-0.7	0.65	7	

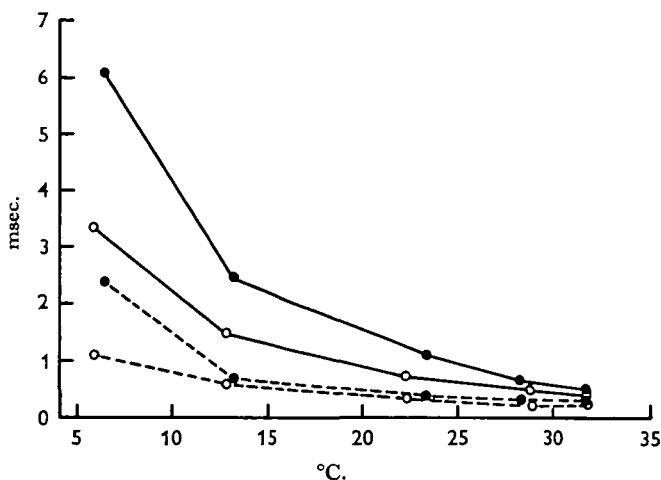


Fig. 4. Duration of the rising and falling phase of action potential in the lateral giant fibres at different experimental temperatures. Explanation as in Fig. 3.

Table 5. *Effect of temperature acclimation on the temperature coefficients of the duration of the rising and falling phases of action potential in the median giant fibre*

AT (°C.)	ET interval (°C.)	Temperature coefficient Q_{10}					
		Rising phase			Falling phase		
		Variation	Mean	n	Variation	Mean	n
13	5.6-13.2	1.50-5.32	2.85	14	2.06-4.51	3.00	11
23	6.6-13.3	1.21-8.67	3.90	11	2.25-5.76	4.04	12
13	13.2-22.5	1.25-6.55	2.45	13	1.53-5.43	3.25	12
23	13.3-23.3	1.14-3.21	2.25	21	1.60-5.45	2.83	20
13	22.5-28.9	1.28-4.46	2.40	8	1.91-6.90	3.27	8
23	23.3-28.3	1.53-2.26	1.78	4	1.15-3.44	2.05	4

Table 6. Effect of temperature acclimation on the temperature coefficients of the duration of the rising and falling phases of the action potential in the lateral giant fibres

		Temperature coefficient Q_{10}					
		Rising phase			Falling phase		
AT (°C.)	ET interval (°C.)	Variation	Mean	<i>n</i>	Variation	Mean	<i>n</i>
13	5.6-13.2	1.41-4.39	2.81	17	1.21-9.23	4.00	15
23	6.6-13.3	2.38-6.27	4.39	18	2.37-6.67	4.34	17
13	13.2-22.5	1.13-2.53	1.72	13	1.37-3.69	2.72	14
23	13.3-23.3	1.00-3.26	1.97	21	1.63-3.84	2.83	19
13	22.5-28.9	1.37-2.92	1.94	6	1.14-2.27	1.84	9
23	23.3-28.3	1.26-1.58	1.43	5	1.29-2.48	1.88	4

Table 7. Determinations of conduction velocity in giant fibres

Reference	Temperature (°C.)	Conduction velocity (m/sec.)	
		Median fibre	Lateral fibres
Eccles, Granit & Young (1933)	10-12	17-25	7-12
Turner (1955) (means)	22.3	18.8	9.6
Turner (1955) (means)	8.2	10.8	5.7
Kao & Grundfest (1957)	19-24	11.2-27.8	5.5-10.0
Goldman (1963)	17-21	16.4-24.8	—

DISCUSSION

The results of the earlier determinations of conduction velocity in the giant fibres of the earthworm are summarized in Table 7. Eccles, Granit & Young (1933) determined the conduction velocity *in situ*, the other authors using isolated nerve cords.

The mean Q_{10} values calculated by Turner (1955) for the temperature interval between 8.2° and 22.3° C. are 1.52 for the median and 1.48 for the lateral fibres. The present results are in general agreement with the previous ones and extend them to other temperature ranges.

The Q_{10} values calculated by Engelhardt (1951) for the conduction velocity in the nervus ischiadicus of the frog are also close to the present values. The Q_{10} value found by Engelhardt in frogs kept at 15-20° C. for the temperature interval 12-22° C. was 2, and the corresponding value for the earthworms kept at 23° C. for the interval 13-23° C. is in the present study 1.91. In frogs which had been stored for 8 days at 5-10° C. Englehardt (1951) found the Q_{10} value for the interval 6-16° C. to be 2.3. The present value for the cold-acclimated giant fibres of the earthworm for the interval 6-13° C. is 2.31.

Bullock (1951) observed that 2-5 successive impulses facilitate the giant fibre and thus induce a rise of 10-20% in the conduction velocity for the subsequent impulses. This phenomenon lasts for about 100-200 msec. When a stimulus frequency of 5 Hz or less is used, as in the present study, the effects of this phenomenon can probably be avoided.

The mean Q_{10} values for conduction velocity observed in the present experiments are greater than 2 only for the temperature interval 6-13° C. Only for 6° C. are the mean conduction velocities in the giant fibres of the cold-acclimated and warm-

acclimated animals significantly different, although a slight difference exists over the whole temperature range studied. This is an instance of the general rule that the temperature acclimation effect and the Q_{10} values are positively correlated.

Bullock (1945) determined the duration of the action potential in the giant fibres of the earthworm by extracellular recordings. The duration was 0.5–1.5 msec. By intracellular recordings at 20° C., Kao & Grundfest (1957) found a mean duration of 0.3 msec. for the rise of the spike and somewhat more than 1 msec. for the whole spike. Veprintsev (1962) observed durations of 0.3–0.4 msec. for the rise and 1.2–1.8 msec. for the fall of the action potential at 18° C. These results were obtained by intracellular recordings. Simultaneous extracellular recordings gave a corresponding result (Veprintsev, 1962). The present results are in agreement with the results of these earlier determinations.

Temperature has been usually found to affect the falling phase more than the rising phase of the action potential. Hodgkin & Katz (1949*b*) calculated Q_{10} values of 2.7, 2.07 and 1.54 for the rise of the spike in giant axons of the squid *Loligo forbesi* for the temperature intervals of 5–10°, 10–20° and 20–30° C., respectively. The corresponding Q_{10} values for the fall of the spike were 5.3, 3.3 and 2.06. Similar values have been obtained for the single nerve fibres in frogs whether the recording was made from an area of several nodes (Schoepfle & Erlanger, 1941; Arshavski, 1958), or from a single node of Ranvier (Tasaki & Fujita, 1948). Antonov (1961) found that the duration of the fall of the spike in the giant fibres of the earthworm increased about three times for each 10° C. between the temperatures of 30° and 7° C. It is not clear whether this result was only based on the two animals, the values for which are presented in the graph in Antonov's paper (p. 320).

The durations of the falling phase measured from the graph of Antonov (1961) are definitely shorter than those found in this study. This difference may be due to the fact that, in Antonov's experiments, the nerve cord was immersed in the saline during recordings, while in the present experiments it was kept in a moist chamber. Crescitelli (1957) has shown that lifting of the nerve into air for recording affects diffusion of ions and might thus influence the form of action potential. Although this phenomenon scarcely affects the comparisons between cold-acclimated and warm-acclimated groups, which is the subject of this paper, attention must be given for this technical detail when comparing the absolute values obtained by different authors.

According to the present experiments, the Q_{10} values for the duration of the rising phase do not deviate much from those calculated for the falling phase of the spike. This might depend on the experimental conditions, or be a phenomenon peculiar for the giant fibres of the earthworm. These structures differ from the other nerve fibres studied not only in this respect but also in their possessing definite segmentally arranged septa, which function as ephapses or synapses.

When the nerve function is impaired by monoiodoacetate there is an increase in the delay at septa in the giant fibres of the earthworm (Antonov, 1964). The Q_{10} values for this increase in the delay are very high, about 8. Antonov (1964) concludes that the ephaptic function of the septa is limited to optimal conditions only.

Hama (1959) found vesicles, similar to presynaptic ones, on both sides of the septa. Coggeshall (1965), however, found no such vesicles in *Lumbricus terrestris*. In addition, Coggeshall observed that the cell membranes are very close to each other in the middle

region of the septum. The distance between the membranes was only 50 Å, although this distance in synapses generally is about 120 Å. Bennett, Nakajima & Pappas (1967) conclude that in cases where electrotonic transmission can be observed the cell membranes are always very close to each other. These electron-microscopical studies are thus in agreement with the concept that transmission in giant fibre septa is ephaptic in nature, at least in optimal conditions.

As can be seen from Figs. 3 and 4, the durations of the rising and falling phases of the action potential show efficient temperature acclimation at low temperatures. This is again connected with the higher Q_{10} values at the lower temperature intervals. The duration of the falling phase exhibits the most complete temperature acclimation; the duration of this phase in the lateral giant fibres of animals acclimated to 13° C. at that temperature is equal to the duration at 20.5° C. in the lateral fibres of animals acclimated to 23° C.

SUMMARY

1. Temperature dependence of the conduction velocity and the duration of the rising and falling phase of action potential was studied in the median and lateral giant fibres of the nerve cord of earthworms acclimated to 13° or 23° C.

2. Compensatory acclimation of the conduction velocity was found at all temperatures studied from 6° to 32° C. However, the effect was statistically significant only at 6° C.

3. The temperature coefficient (Q_{10}) of the conduction velocity was lower at all temperatures for the cold-acclimated animals. The difference was significant only for the temperature interval from 6° to 13° C.

4. The compensatory acclimation of the duration of the rising and falling phases of the spike was statistically significant at 6° and 13° C. The corresponding Q_{10} values were lower for the cold-acclimated animals.

5. The duration of the falling phase of the action potential showed the most efficient compensatory acclimation of the parameters studied.

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