

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

II. THE REFRACTORY PERIOD

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The effect of temperature on the refractory period in nerve fibres is of the same magnitude as its effect on the duration of the action potential (Tasaki, 1949) or as the effect of temperature on the duration of the falling phase of the spike (Adrian, 1921). Temperature coefficients (Q_{10}) as high as 4 have been calculated for the refractory period in single fibres of the frog by Schoepfle & Erlanger (1941). According to Tasaki (1949), the Q_{10} value of the absolute refractory period is about 3.5 for a single node in the myelinated fibres of the frog, when determined for the temperature interval 13.7-19° C.

Eccles, Granit & Young (1933) found similar refractory periods for the median and the lateral giant fibres of the earthworm. Bullock (1945) gives 2-4 msec. as the duration of the absolute refractory period in the giant fibres of the earthworm at 20° C. The relative refractory period is longer. The giant fibres respond to each stimulus, if these are repeated at a frequency not higher than 200-250 per sec. Arshavski, Berkinblit, Kovalev & Chailachyan (1964) placed the nerve cord of the earthworm in a temperature gradient, where the temperature of the cord decreased from room temperature to 8-10° C. in the direction of the travelling impulses. If the nerve cord was stimulated at frequencies from 15 to 50 per sec., the giant fibres soon failed to respond to each stimulus. This was especially prominent in the coldest region of the nerve cord. Both an increase of the refractory period caused by cold and fatigue contribute to this phenomenon.

As the conduction velocity and the duration of the rising and, especially, of the falling phase of action potential show compensatory temperature acclimation in the giant fibres of the earthworm (Lagerspetz & Talo, 1967), the effects of temperature acclimation of the refractory period and on its thermal characteristics were chosen for further study.

MATERIALS AND METHODS

The animals were mature earthworms of the species *Lumbricus terrestris* L. They were collected and stored as described previously (Lagerspetz & Talo, 1967). Some of the animals used for the determinations of the refractory period were acclimated to 23° C. for 10-14 days. In measurements of the absolute refractory period the same equipment was used for the production of identical stimulus pairs and for display and recording as in the study referred to above.

Some experiments were made in order to estimate the maximal stimulus frequency at which the giant fibres still respond to each individual stimulus. In these measurements, a Mingograph 24 B two-channel jet recorder was used with Grass P 511 R preamplifiers. The warm-acclimated animals used for these experiments were kept for 5-13 days at 23° C.

RESULTS

The results of the measurements of the absolute refractory period are presented in Table 1. The refractory period in the giant fibres of animals acclimated to 23° C. is somewhat longer than that of those acclimated to 13° C. The differences between the means are only significant for the median fibre at about 6° C. and 13° C. The absolute refractory period is of approximately the same duration in the median as in the lateral fibres, as already stated by Eccles, Granit & Young (1933).

Table 1. *Effect of temperature acclimation on the duration of the absolute refractory period in the giant fibres at different temperatures*

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

AT (°C.)	ET (°C.)		Absolute refractory period (msec.)					
			Median giant fibre			Lateral giant fibres		
	Variation	Mean	Variation	Mean	<i>n</i>	Variation	Mean	<i>n</i>
13	4.6-6.8	6.0	4.3-8.1	6.50†	5	5.3-8.2	6.70	6
23	5.5-7.2	6.2	6.2-19.6	12.04†	8	5.65-14.0	9.28	10
13	11.7-13.5	12.8	2.5-3.6	3.09‡	8	1.5-3.9	2.96	8
23	12.2-13.8	13.1	2.7-4.3	3.72‡	12	2.2-5.3	3.50	11
13	22.1-24.2	22.7	1.0-1.7	1.24	6	1.10-2.15	1.53	6
23	22.4-23.3	23.1	1.15-2.0	1.47	12	1.00-2.80	1.50	11

† Difference between the mean values significant at the level $P < 0.05$.

‡ Difference between the mean values significant at the level $P < 0.01$.

Table 2. *Effect of temperature acclimation on the temperature coefficient of the absolute refractory period*

AT (°C.)	ET interval (°C.)	Temperature coefficient Q_{10}					
		Median giant fibre			Lateral giant fibres		
		Variation	Mean	<i>n</i>	Variation	Mean	<i>n</i>
13	6.0-12.8	1.49-3.63	3.25	5	6.92-1.88	4.15	6
23	6.2-13.1	2.18-12.85	7.84	9	3.22-9.46	6.59	10
13	12.8-22.7	2.79-3.43	3.21	3	1.32-3.91	2.68	3
23	13.1-23.1	1.91-3.34	2.56	12	1.32-3.50	2.34	12

Table 3. *Effect of temperature acclimation on the maximum response frequency of the giant fibres*

AT (°C.)	ET mean (°C.)	Mean maximum response frequency (1/sec.)	<i>n</i>	$P <$
13	5.3	68.5	7	0.01
23	5.7	38.3	6	

The mean temperature coefficient of the refractory period (Table 2) for the temperature interval 6–13° C. is significantly higher in the median fibre of the warm-acclimated animals than in that of the cold-acclimated earthworms ($P < 0.02$).

The determinations of the maximal response frequency of the giant fibres were performed only at an experimental temperature of about 5.5° C. The results of these measurements are presented in Table 3. In spite of the small number of experiments the differences between the means of the cold-acclimated and warm-acclimated groups are statistically significant.

DISCUSSION

The Q_{10} values for the refractory period are rather high, especially for the temperature interval 6–13° C. in the earthworms acclimated to 23° C. The refractory period seems to be the most temperature-dependent variable of those studied in the giant fibres of the earthworm (Lagerspetz & Talo, 1967).

On the basis of determinations of the maximum frequency at which the giant fibres can transmit impulses, the minimum interval between impulses in a train can be calculated. At 5.5° C. this value averaged 14.6 msec. for the giant fibres of animals acclimated to 13° C. and 26.1 msec. for those acclimated to 23° C. The corresponding absolute refractory periods averaged 6.50 and 12.04 msec., respectively. The ratio between the minimum impulse interval and the absolute refractory period was thus 2.24 for cold-acclimated and 2.17 for warm-acclimated animals. This ratio does not seem to be affected by temperature acclimation. In *Carcinus* nerve fibres, Hodgkin (1938) found this ratio to be about 2 at 20° C., and the same value holds for mammalian fibres with an absolute refractory period of about 0.5 msec. (Gasser & Grundfest, 1936). It is of interest to see that both the absolute refractory period and the maximum response frequency show temperature acclimation. The ratio of these parameters, on the other hand, remains unchanged.

Evidence for temperature acclimation of the functional parameters of the giant fibres of the earthworm has been presented in this study and in a previous paper (Lagerspetz & Talo, 1967). It is difficult to say whether this phenomenon plays any important role in compensation for behavioural and gross physiological changes connected with a change in ambient temperature. In natural conditions temperature acclimation is usually connected with seasonal acclimatization. In earthworms Kao & Grundfest (1957, p. 556) were unable to find any seasonal differences in the functional characteristics of the giant fibres. Their measurements were, however, performed at 19–24° C., and according to the present results (see also Lagerspetz & Talo, 1967) differences between the cold-acclimated and warm-acclimated animals were obvious at low temperatures only, although the difference in the acclimation temperatures was as large as 10° C. The situation may be different in animals of another species and from other climatic conditions (Pampapathi Rao, 1967). On the other hand, acclimation of synaptic transmission on the central level may possibly contribute to the compensation of physiological effects of temperature changes in functions which are controlled by the nervous system.

SUMMARY

1. The temperature dependence of the absolute refractory period and of the maximum response frequency 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 absolute refractory period in the median giant fibre was statistically significant at 6° and 13° C. The temperature coefficient (Q_{10}) was significantly lower in cold-acclimated animals.
3. Compensatory acclimation of the maximum response frequency was significant at 6° C. The ratio between the minimum impulse interval and the absolute refractory period was about 2.2. It was unaltered by temperature acclimation.

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