[Reprinted from THE JOURNAL OF GENERAL PHYSIOLOGY, September 20, 1920, Vol. iii, No. 1, pp. 41–48.]

DYNAMICS OF NERVE CELLS.

I. THE TEMPERATURE COEFFICIENT OF THE NEUROGENIC RHYTHM OF THE HEART OF LIMULUS POLYPHEMUS.

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(Received for publication, June 1, 1920.)

The temperature coefficient of the rate of heart beat has been determined by many investigators on various animals both vertebrate and invertebrate.[1] In all it was found that the coefficient for 10°C. was approximately 2 in the intermediate ranges of temperature, greater at lower temperatures, and somewhat less at high temperatures.

In none of these determinations has it been possible, owing to the character of the hearts worked with, to determine whether the results were due to an effect of temperature on the coefficient of ganglionic activity, of muscular activity, or of both.

It has therefore seemed of importance to determine whether variations of temperature, affecting ganglion cells alone, would give temperature coefficients of the same order of magnitude as those obtained on the whole heart.

A suitable preparation for this purpose is the excised heart of *Limulus polyphemus*, the beats of which have been shown by Carlson to be purely neurogenic.[2] Carlson has also described methods by which the ganglion can be separated from the muscle and independently subjected to variations of temperature while the muscle records the beats.

[1] For a general review of the literature of this subject see Kanitz, A., Temperatur und Lebensvorgänge, Berlin, 1915. Loeb, J., The Organism as a whole, from a physicochemical viewpoint, New York, 1916. Snyder, C. D., *Am. J. Physiol.*, 1911, xxviii, 167.

[2] Carlson, A. J., *Am. J. Physiol.*, 1905–06, xv, 220; also *Ergebn. Physiol.*, 1909, viii, 427.

The ganglion of the heart of *Limulus polyphemus* occupies a median dorsal position on that organ; the nerve cells occupy a position over the posterior five or six segments of the heart and are connected with the anterior muscular segments by a median and two lateral nerves. This ganglion, which may be 10 or 15 cm. in length, can be dissected from the underlying tissue with ease and maintain functional connection with the muscle of the anterior segments.

In the experiments to be described a method was finally adopted in which a Dewar flask contained an immersion fluid, either sea water or *Limulus* blood serum. A system of glass tubes provided for renewal of the fluid at different temperatures which were recorded by a standard thermometer graduated to 0.1°C. Either the posterior segments of the whole heart, or the dissected ganglion, depended into the fluid through an opening in a paraffined cap. The two anterior segments were pinned to the cap, enclosed in a moist chamber, and kept at a constant temperature. The contractions of the anterior segments were graphically recorded and served as an index not only of the rate but of the effective strength of the impulses reaching the muscles. The study in its ramifications has extended to about 200 *Limulus* hearts.

Observations on the Whole Heart.

At Beaufort, N. C., the laboratory sea water was 27.7°C. and the average rate of 60 hearts was 23 beats per minute, while, at Woods Hole, the laboratory sea water was 20.1°C. and the average rate of 48 hearts was 11.6 per minute. A temperature coefficient of about 2.6 (Q_{10}) is obtained from these figures, calculating for the 10° interval. The individual hearts show wide variations in rate, and since the sea water of the two localities differs somewhat in concentration, this average coefficient for the whole heart can be considered only an approximation.

To illustrate the magnitude of the temperature coefficient of the whole heart for what may be considered a fairly normal range of temperature, ten experiments have been selected from our series—experiments in which it so happened that observations were made at exactly 15 and 25°C. The results are given in Table I. The experiments given in Table I show that the whole heart of *Limulus*, subjected to

15 and 25°C. respectively, has rates giving an average temperature coefficient (Q_{10}) equal to 2.23. This indicates that the rate is determined by the alteration of a chemical process. The coefficient is quite in conformity with that reported for other rhythmic biological processes for this range of temperature.

TABLE I.

Rate per min. at		Temperature coefficient. (Q_{10})
15°C.	25°C.	
6	15	2.5
6.1	12	1.9
9	23	2.4
7.5	14.2	1.8
8	19	2.3
8.5	17	2.0
5	12	2.4
6.8	13.5	2.0
7.2	20	2.7
7	16	2.3
Average...7.1	16.17	2.23

In order to obtain a more comprehensive conception of the variation in the temperature coefficient of the whole heart subjected to different temperatures, summaries of some experiments are given below. The first shows the effect of cooling the heart to −2°C. and then progressively warming in a single but typical experiment.

Temperature range.	Temperature coefficient. (Q_{10})	Temperature range.	Temperature coefficient. (Q_{10})
°C.		°C.	
8 to −2	3.7	25 to 15	2.8
10 " 0	3.3	28 " 18	2.5
13 " 3	3.2	30 " 20	2.2
15 " 5	3.1	33 " 23	1.9
18 " 8	3.2	35 " 25	1.7
20 " 10	3.0	38 " 28	1.5
23 " 13	2.9		

The progressive change from a large coefficient at low temperatures to the smaller values at high temperatures is not always as uniform as illustrated in this experiment, but the coefficients at very low temperatures are usually larger than those recorded above.

Extremes of temperature may alter the value of temperature coefficients subsequently determined. It seems best in view of this fact to show separately the effects of depression and of elevation of the temperature starting with the normal temperature of the sea water. Each series thus is based on observations only on one side of the normal temperature, *i.e.* between it and a single limiting temperature, and thus the secondary effects of excessive heat or cold are avoided. In Table II the results of ten experiments are given in each of which the posterior seven segments of the whole heart with its ganglion were subjected to temperature variations.

TABLE II.

Temperature range.	Temperature coefficient (Q_{10}).						Temperature range.	Temperature coefficient (Q_{10}).			
	Experiment 1.	Experiment 2.	Experiment 3.	Experiment 4.	Experiment 5.	Experiment 6.		Experiment 7.	Experiment 8.	Experiment 9.	Experiment 10.
°C.							°C.				
−2 to 8	6.0	4.6			7.6	7.2	20 to 30	2.3	2.5	1.8	
0 " 10	3.5	3.9	4.1	3.7	5.4	5.0	21 " 31	2.3	2.2		2.0
3 " 13		3.6		2.7			23 " 33		1.9	1.9	2.1
5 " 15	2.8	3.1	3.3	2.2	2.8	3.2	25 " 35	1.8	1.7		1.92
8 " 18		3.2		2.3	2.6		27 " 37				
10 " 20	2.5	2.8	3.0	2.0	2.66	3.0	28 " 38	1.6	1.5	1.7	1.67
11 " 21					2.5						

Observations on the Ganglion.

We may now compare the above results with those obtained by varying the temperature of the ganglion alone after dissecting it free from all adherent muscle tissue except the anterior segment. It would seem best for purposes of comparison with the results obtained above on the whole heart to observe the same precautions and to avoid the effects due to exposure of the ganglion to excessive heat or cold. The results tabulated in Tables III and IV are thus strictly comparable to those given in Table II since they show the simple effect of a progressive change in the temperature of the ganglion above or below the initial normal temperature of 20°C. In order to illus-

TABLE III.

Effects of Cooling the Heart Ganglion Alone.

Experiment.	Temperature.	Rate per min.	Coefficient for 10°C.	
			Temperature range.	(Q_{10})
	°C.		°C.	
1	20	17	20 to 10	2.2
	17	13	17 " 7	2.9
	15	11.7	15 " 5	2.9
	10	6.2	10 " 0	4.3
	7	4.4	7 " −2	4.5
	5	4	5 " −2	7.2
	0	1.4		
	−2	1		
2	20	8.6	20 to 10	1.9
	15	6.4	15 " 10	2.1
	10	4.4	15 " 5	2.1
	5	3	10 " 0	2.9
	0	1.5	5 " 0	4.0
3	20	16	20 to 10	2.5
	15	10.5	15 " 5	2.8
	10	6.2	10 " 0	3.5
	8	5	8 " −2	6.0
	5	3.7	5 " −2	8.9
	0	1.7		
	−2	0.8		
4	21.6	11.8	21.6 to 11.6	2.8
	16.5	7.0	16.5 " 6.5	3.3
	11.6	4.2	11.6 " 1.6	5.6
	6.5	2.3		
	1.6	0.74		
5	19.7	12.6	19.7 to 10	2.3
	16	9	16 " 6	2.1
	12	6.6	12 " 2	2.2
	10	5.4	10 " 0	2.4
	6	4.3		
	2	3		
	0	2.2		

trate the widest range of variation in experimental results, experiments on eight different animals were selected arbitrarily. As was expected the cardiac rate was slow when the ganglion was cooled and fast when it was warmed. In the lower ranges of temperature the temperature coefficient (Q_{10}) is well above 2 and at very low tempera-

TABLE IV.

Effects of Warming the Heart Ganglion Alone.

Experiment.	Temperature.	Rate per min.	Coefficient for 10°C.	
			Temperature range.	(Q_{10})
	°C.		°C.	
6	20	8	20 to 30	2.5
	22.5	12	22.5 " 32.5	2.1
	25	14	25 " 35	2.0
	28	20	28 " 38	1.6
	30	23		
	32.5	26		
	35	28		
	38	32		
7	20	12	25 to 30	2.2
	22	15	22 " 32	2.0
	25	17.5	25 " 35	1.9
	27	20	27 " 37	2.1
	30	27		
	32	31		
	35	33		
	37	35		
8	21	18.3	21 to 26	2.0
	26	26.8	21 " 31	1.8
	31	33	26 " 36	1.5
	36	40		

tures may be as large as 9. This places the process upon which the rate of the rhythmic ganglionic discharge depends unequivocally within the class of chemical reactions. The decrease in the coefficient at higher temperatures is the rule in both biological and chemical reactions and does not militate against this interpretation. The results in Tables III and IV are illustrated in Fig. 1.

If we now compare the results obtained on the whole heart with those obtained when the ganglion alone is subjected to changes of temperature we are struck with the fact that there is not a single feature of the temperature coefficients which will serve to differen-

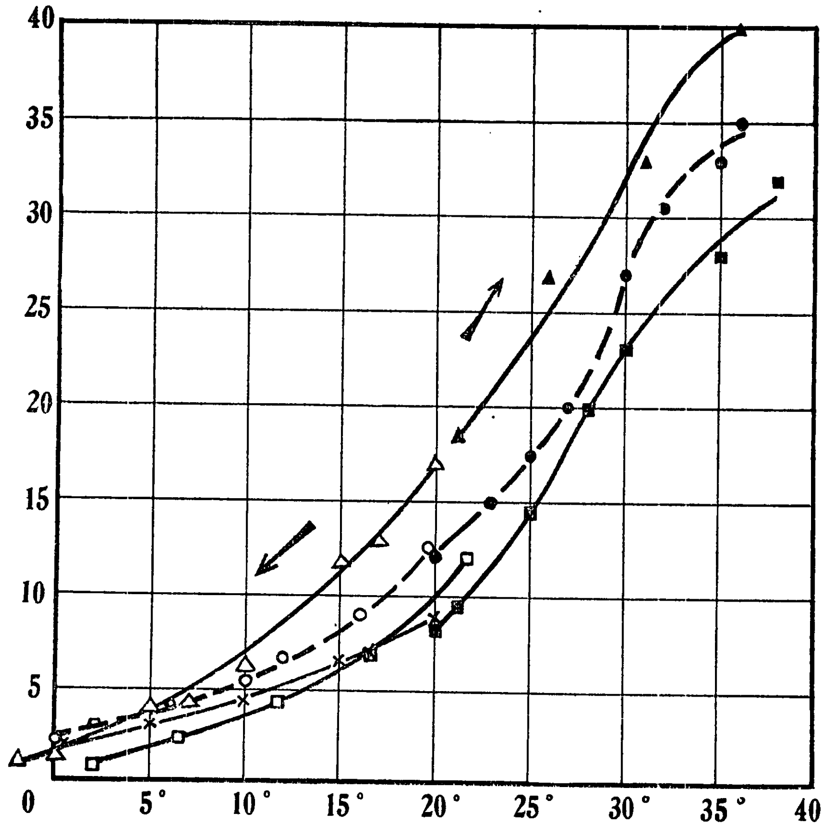

FIG. 1. Curves for the rates plotted against temperature. Data from Tables III and IV. △, ○, ×, and □ correspond to 1, 5, 2, and 4 respectively and show the effects of progressive cooling; ▲, ●, and ■ correspond to 8, 7, and 6 respectively.

tiate one from the other. The magnitude of the temperature coefficient and its variations are parallel in the two cases and we are justified in concluding that there is the same typical temperature coefficient for the rate of the heart beat of *Limulus* when the ganglion alone is subject to variations of temperature as when the whole heart is similarly treated. Furthermore chemical alteration in the ganglion determines the rate of heart beat.[3]

CONCLUSIONS.

In the case of the heart of *Limulus polyphemus* the same magnitude and variation of the temperature coefficient (Q_{10}) is obtained from the whole heart as from the ganglion alone. From the magnitude of the temperature coefficients and their variation with changes of temperature we may conclude that the rate of the heart beat is determined by alteration of chemical processes in the ganglion cells.

[3] The denervated heart muscle of *Limulus* was shown by Carlson to be without rhythmicity in its own blood or in sea water so that it is impossible to speak in connection with the tissue of a temperature coefficient which can have any bearing on the results communicated in this paper. The author has made this muscle rhythmic in M /2 NaCl and has been able to show that a rise of temperature of 10° may double the rate, but owing to the rapid incidence of toxic effects and to concomitant changes in rate, it is impossible to present reliable quantitative data at this time.