ON TEMPERATURE CHARACTERISTICS FOR DIFFERENT PROCESSES IN THE SAME ORGANISM

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I

It is of interest for the theory of temperature characteristics of vital processes to test the assumption that in many cases the quantity \( \mu \) in the expression \( \ln K = \mu / RT \) may have a specific, local significance. One view in this connection has been expressed by Murray (1925-26) in a paper on the relation of temperature to the rate of contraction of embryonic heart muscle fragments of the chick in culture. He reported that he found no constancy in the values of the "temperature characteristics" (\( \mu \), in the Arrhenius equation; cf. Crozier, 1924) and no constancy in the "latitude of variation" (Crozier and Federighi, 1924-25; Crozier and Stier, 1926-27, a) over any portion of the temperature range.

As an explanation for the reported lack of constancy in the values of the temperature characteristics Murray proposed that "possibly the regularity of the temperature effect as empirically determined upon certain functions in vivo depends to a greater extent than is acknowledged upon the integrity of the organization and the interrelationships of the parts of the whole, and less upon one particular chemical reaction or catalyst" (Murray, 1925-26, p. 788). The inadequacy of this notion has been discussed by Crozier and Stier (1926-27, c).

The suggestion might be understood in either of two ways. The "organization"—factor might pertain simply to the heart or other structure immediately implicated in the observations; or it might be taken as a feature of the organism as a whole. The former effect must be granted at once as an obvious truism, in the sense that the structure of a heart, for example, permits control by a definite localized pace maker. The latter view can be tested by determining simul-
Simultaneously the temperature characteristics for two or more different activities in the same individual. Such experiments were made with *Asellus* (Crozier and Stier, 1926–27, b), determining synchronously the frequencies of heart beat and of respiratory movements in the same individual. It was found that the frequencies in these organs do not vary together, neither do they have the same temperature characteristic (cf. Fig. 7, Crozier and Stier, 1926–27, b). This holds also for the embryos of *Limulus*, the frequencies of gill movements yielding increments quite different from those obtained for the hearts (Crozier and Stier, unpublished).

The following experiments were made with more careful refinement of technique in order to test further the notion of whether the organism as a whole would determine one temperature characteristic for all its activities.

II

The cladoceran *Daphnia* was chosen because its respiratory movements and its heart beat are easily visible through the transparent carapace; and since Cladocera reproduce parthenogenetically, one obtains successive broods of individuals unusually uniform genetically and highly comparable in development. The *Daphnia* used for the greater part of these experiments (*Daphnia magna*) were at least second generation descendants produced parthenogenetically from one individual. The stocks for these experiments were furnished by Dr. L. A. Brown from his highly “purified” cultures. We wish to thank him for his kindness to us during these experiments.

A single animal was placed in a small glass trough through which a small stream of oxygenated culture fluid (cf. Banta, 1921, for ingredients) was allowed to flow. Each individual was placed in a glass tube of a bore sufficient to hold the animal without pressure; then by rotating each tube the heart and “gills” were both visible when the illumination was properly adjusted from below. Culture medium through which air had been bubbled for 10 hours was run into each tube in a small stream through a small-bore glass nozzle. Light was admitted through a window in the bottom of the water thermostat into which the glass container holding the preparations could be lowered. The observing microscope and an objective used as a water immersion lens passed through the cover of the vessel holding the animals, also a thermometer reading to 0.01°C. The temperature of the water bath was held constant to within ±0.01°C. A thermostat similar to the one described by Crozier and Stier (1926–27, c) was used for these experiments.
Time for ten to twenty movements of the heart and "gills" was taken simultaneously with stop-watches by two observers \(^1\) who could view the same preparation by aid of a divided ocular ("demonstration ocular").

III

The results of the experiments presented in Table I and Figs. 1 and 2 do not uphold Murray's contention of a control of the magnitude of temperature characteristics by the whole organism; the same value of \(\mu\) was not found for each of two processes tested simultaneously in the same organism. These differences of magnitudes of thermal increments for heart beat and respiratory movements respectively in *Daphnia* indicate that the frequencies of movements are controlled by different "governing reactions" (Crozier, 1924; 1925-26, a).

Not only do differences of temperature characteristic for these two processes exclude the possibility of the organism exerting some general kind of control, but there are differences in the behavior of the two organs pointing to an independence of direct control of one organ over the other. (1) Whenever "spontaneous movements" occur one can be sure to find some alteration in the frequency of gill movements, even as much as a temporary cessation; however, the heart beat usually continues with unchanged rhythm. (2) There are greater numbers of instances showing a "break" in the line relating frequency of respiratory movements to temperature than in the plots for heart beat. There are seven such instances for "gills" and only one for heart beat where \(\mu = 12,500\) above 11.1\(^\circ\)C. and 25,000 below. (3) The absolute frequencies of heart beat and "gill" movements differ by about 100 per cent.

Average critical temperatures (Crozier, 1925–26, b) for respiratory activity occurred at 3.4\(^\circ\), 5.0\(^\circ\), 11.2\(^\circ\), 13.0\(^\circ\), 14.4\(^\circ\), and 18.9\(^\circ\). For some reason as yet unknown, these values do not agree closely (except at 5.0\(^\circ\), 14.4\(^\circ\), and 18.9\(^\circ\)) with the modal values usually found for many biological processes (Crozier, 1925–26, b). Illustrations of other cases in which "atypical" values appear can be found in respiratory movements of decapitated grasshoppers (Crozier and Stier, 1924–25), and in the pulsations of "accessory hearts" in the amputated legs

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\(^1\) For assistance in these experiments we are indebted to Mr. T. Thornton Oxnard.
FIG. 1. All the graphs obtained from twelve experiments with *Daphnia* are given diagrammatically. The lines are based on six or more observations (each the average of at least ten stop-watch readings) spaced less than a degree apart. In cases where lines are based on fewer observations small crosses indicate the actual position of the observations in relation to the line.
of Notonecta (Crozier and Stier, 1926–27, b). In each of those cases progressive changes in the preparation are leading to death, so that

Fig. 2. Typical observations on frequency of heart beat and of respiratory movements made simultaneously by two observers at constant temperature, from two experiments with Daphnia over a wide range of temperature (cf. Fig. 1 for all other experiments). Open circles refer to "gill" movements, solid circles to heart beat. In each case there is a difference in the magnitudes of the temperature characteristics for heart beat and for gill movements. Another difference is found in the unbroken line relating frequency of heart beat to temperature, whereas for respiratory movements a "break" always occurs yielding two increments, one above the break and one below (cf. also Fig. 1). Two additional "breaks" occur above 21.9°C in the graph for Experiment 3. Above this temperature thermal "destruction" occurs and consequently the observations for both processes fall below the lines fitted to the data in the lower temperature range. For additional illustrations of this type of "break," consult Crozier, 1925–26, a.
abrupt change of $\mu$ comes about as a function of time, independently of change of temperature.

In *Daphnia* the critical thermal increment, 12,000 calories, appears only twice, and in each case it is obtained for frequency of heart pulsations, never for respiratory movements. This value has been frequently obtained for heart beat—rarely for respiratory movements (cf. Crozier, 1925–26, b).

### TABLE I

Significant temperature characteristics based on six or more observations spaced less than a degree apart yield average values of $\mu$:

<table>
<thead>
<tr>
<th>$\mu$ (calories)</th>
<th>Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>6,500</td>
<td>1 instance</td>
</tr>
<tr>
<td>8,680</td>
<td>4</td>
</tr>
<tr>
<td>11,080</td>
<td>3</td>
</tr>
<tr>
<td>14,900</td>
<td>2</td>
</tr>
<tr>
<td>16,550</td>
<td>2</td>
</tr>
<tr>
<td>20,940</td>
<td>1</td>
</tr>
<tr>
<td>32,430</td>
<td>3</td>
</tr>
</tbody>
</table>

For respiratory movements

<table>
<thead>
<tr>
<th>$\mu$ (calories)</th>
<th>Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>6,700</td>
<td>1</td>
</tr>
<tr>
<td>12,550</td>
<td>2</td>
</tr>
<tr>
<td>13,970</td>
<td>3</td>
</tr>
<tr>
<td>16,600</td>
<td>1</td>
</tr>
<tr>
<td>21,600</td>
<td>1</td>
</tr>
<tr>
<td>24,200</td>
<td>1</td>
</tr>
<tr>
<td>28,950</td>
<td>2</td>
</tr>
<tr>
<td>35,000</td>
<td>1</td>
</tr>
</tbody>
</table>

For heart beat

Sample experiments can be found in Fig. 2.

IV

We did not obtain the same temperature characteristic for each of the two processes measured simultaneously in the same organism. Furthermore, our observations on the behavior of the two processes with reference to “spontaneous” movements, absolute magnitudes of their frequencies, critical temperatures, and the distinct differences in the kinds of curves obtained, lead to the conclusion that the organism as a whole has no control over the determination of temperature characteristics for its separate activities. It is assumed that the initiation of pulsation arises in each organ in a few groups of cells,—pace makers; the inner metabolic states of these cell groups are thought to
be differently adjusted so that each organ might yield independently any one of the modal thermal increments represented in the series of linked chemical reactions governing the frequency of contraction (cf. Crozier, 1924–25).²

It is highly probable that there may be instances when the same temperature characteristic would be obtained simultaneously for several processes in the same individual organism. Distribution polygons of critical increments obtained from data on heart beat and rates of many other vital processes were found by Crozier (1925–26, a) to be superimposable—the same modal values of the temperature characteristic being obtained for heart beat and for all other vital processes.

What determines the change from one temperature characteristic to another for any physiological activity within the organism? Can the organism by virtue of its own organization control the change from one governing reaction to another in all of its different processes? The data we have reported uphold the view that the critical increment for each process is dependent upon the metabolic state of the elements governing its activity (e.g., the pace makers controlling the frequency of the heart beat); the temperature characteristic of a process is apparently independent of other processes in the same organism and is certainly not dependent upon a general "organization" factor.

**SUMMARY**

The temperature characteristics ($\mu$) for two activities (heart beat and respiratory movements) studied simultaneously in the same individual organism (*Daphnia magna*) were always found to differ in magnitude. The type of graph obtained when the frequency of these movements was plotted according to the Arrhenius equation was also distinctly different for each activity. The organism therefore does not determine a uniform magnitude of the temperature characteris-

² In a recent investigation (Wolf, 1932–33) of the relation of temperature to the pulsation frequency of the advisceral and abvisceral heart beats of *Ciona intestinalis* the same temperature characteristics and critical temperature were obtained for advisceral and abvisceral beats. The pulsation frequency of ad- and abvisceral heart beat was the same at any temperature in any one individual. These findings indicate that the general metabolic condition of the two ends of the heart (pace makers) is the same in any one individual.
tic for each of its activities; the values of \( \mu \) must therefore have, to this extent, a local, specific meaning.

CITATIONS