

TEMPERATURE AND HEART RATE IN PTEROTRACHEA AND TIEDEMANNIA.

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I.

The attempt to give form and substance to various possibilities suggested by a study of thermal increments at present calls for an increase in the available data. It is necessary to analyze a greater array of biological processes in a greater variety of forms. Since the fauna at Naples affords abundant opportunities for investigations of this character, a number of organisms fairly common there were explored and, for the purposes in mind, the heart rates of the large heteropod *Pterotrachea coronata* and of the pteropod *Tiedemannia neapolitana* proved to be, in several respects, almost ideal. Aside from the great convenience of being completely transparent, both animals are very sensitive and permeable to heat, and their hearts are large enough to be seen clearly without a lens, under practically all circumstances. At intermediate temperatures pulsation in *Pterotrachea* in unit time is approximately twice as fast as in *Tiedemannia* where ten beats require slightly over 0.4 of a minute between 14° and 15°. Moreover, there are significant differences and resemblances between these two forms,—a fact which has acquired additional interest since Crozier and Stier (1924-25, *a*), have reported one

* The observations and experiments here recorded were made during the winter of 1924-25 while occupying the table supported at Naples by the American Association for the Advancement of Science. I take this opportunity to express my deep gratitude to both the Association and the Administration of the Stazione Zoologica. It is perhaps worth noting that under the leadership of Dr. R. Dohrn the conditions necessary for effective scientific work in the Naples laboratory are rapidly approaching the ideals of today.

temperature characteristic for the heart rate of *Limax* ($\mu = 16,300$), and another for *Anodonta* ($\mu = 11,200$). With these values at hand, it is now possible to compare and interpret the increments for two other molluscs widely different in systematic affinities, in mode of life, and in physical consistency.

II.

The observations on *Pterotrachea* were made after placing each animal in a separate aquarium, open to the air and containing about 1200 cc. of sea water. These vessels were stationed in a glass tank in which the level of the water was kept above that in the individual containers. To reach the upper ranges of temperature, definite amounts of water were removed from both the tanks and the aquaria and carefully replaced by equal quantities at higher temperatures. In this way both the levels and the differences of level were held sufficiently constant. The lower temperature limits were reached by allowing small flasks filled with ice, and corked, to float on the surface of the water in the containers, and by adding cold water or ice to the outer water jacket. In this case also, precautions were taken to maintain the original levels.

Final readings were begun at the lowest limits and on increasing the temperature 5 minutes were usually sufficient to establish the new equilibrium. In bringing this about, the uniform distribution of heat in the inner chambers was greatly facilitated by the gentle rhythm of the dorsal "fin" of the mollusc and moderate undulating movements on the part of the entire animal. *Pterotrachea* is almost never completely quiescent. The thermometers, like the animals, were always entirely submerged and after a given temperature had been maintained within $0.1-0.2^\circ$ for 5 minutes, the time required for ten complete cycles of the heart was determined with a stop-watch. In the earlier observations this process was repeated five times for each temperature, but later only three groups of ten beats each were counted. The results derived in this way from eight individuals and covering a range, collectively, from about $4-27^\circ$, are plotted in mass in Fig. 1 according to Crozier's method (1924-1925, *a*) and the familiar Arrhenius equation (1915).

It is at once apparent that individuals must differ decidedly in the actual rate of the heart beat at any given temperature; also, that within definite limits, both vertical and lateral on the plot, the observations may be represented by a straight line. The thermal increment that best describes the points between $1/T = 0.00340$ and $1/T = 0.00350$, is 11,200. Above and below these regions other conditions plainly hold.

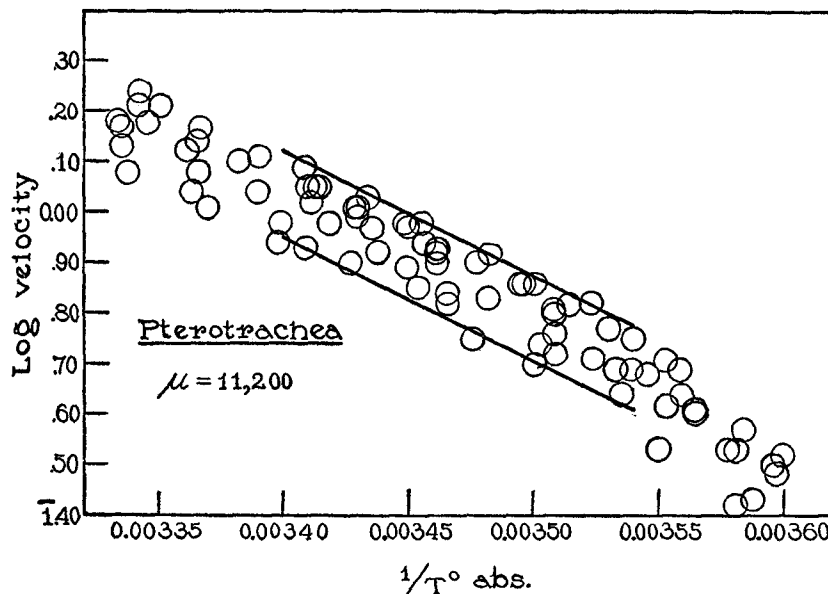


FIG. 1. Velocity of heart beat in *Pterotrachea coronata*; mass plot. Some of the points represent fifty beats but most of them, thirty. The slope is in accordance with the Arrhenius equation,

$$\ln \frac{K_1}{K_0} = \frac{\mu}{2} \left(\frac{1}{T_0} - \frac{1}{T_1} \right)$$

For intermediate temperatures, $\mu = 11,200$.

It is hoped that the presentation of all the data will avoid the criticism that might be levelled at selected cases. These, in view of certain difficulties reported by Rywosch (1905), would not be altogether adequate. Indeed this author considered the heart of *Pterotrachea* essentially lawless because at any given temperature the rate may be quite different in different individuals. Rywosch also notes that

sudden changes such as plunging an animal from 15° to 40.5° and returning it after 1 minute to 16.5° may stop the heart at once or dissociate auricular from ventricular rhythm. Such drastic methods of course produce results quite different from moderate physical violence or small but abrupt changes in temperature. Indeed, these alone are enough to induce some of the effects demonstrated by Rywosch; they may even initiate disharmonies of rhythm that become noticeable in the rate, or bring the heart to a standstill, not immediately, but at some quite different and totally innocent point on the temperature

TABLE I.
Pterotrachea Heart.

Animal.	μ (intermediate).
1	11,200
2	11,900 (twice).
3	11,100
4	11,000
5	11,000
6	11,500
7	10,800
8	11,100
Average.....	11,200

scale. Manipulative and experimental ineptitudes like these are perhaps useful in suggesting methods by which the heart might be controlled, but unfortunately they may also prove highly misleading.¹

From our general plot we should expect a reasonable uniformity among the increments deduced for separate individuals. This, as the list in Table I indicates, is true.

In selecting cases for individual presentation, it seemed best to choose the two that are farthest away from the average and the one that happens to exhibit the increment of 11,200. The data for these individuals are plotted in Fig. 2, and illustrate the precision with which

¹ Rywosch (*loc. cit.*, p. 361) writes: "Es lässt sich keine allgemeine Formel aufstellen in welchem Verhältniss etwa die Zunahme der Zahl der Pulse zur Erhöhung der Temperatur steht; ganz allgemein scheint es nur zu sein dass bei höheren Temperaturen auf einen Wärmegrad mehr Pulse kommen als bei niedrigeren."

the heart accelerates at intermediate temperatures. They also show, though not to greatest advantage, the terminal changes at extreme temperatures.

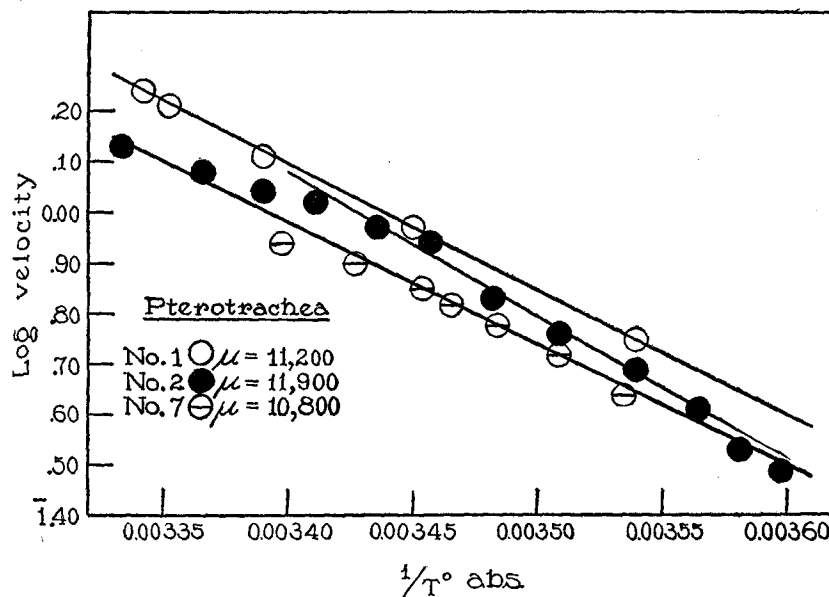


FIG. 2. *Pterotrachea*; heart rates of three animals, represented by different symbols. Of these individuals two give extreme values and one, 11,200. The increments are between 7,000 and 8,000 at high temperatures; and at low, in the neighborhood of 22,000. See Animals 1, 2, and 7, Tables I and III.

III.

Observations on the heart of *Tiedemannia* were made in exactly the same manner except that the aquaria, like the animals, were smaller. In the largest individuals moderate rhythmical movement of the "wings" facilitates the distribution of heat and does not obscure the view of the heart; in the smaller animals, however, it is often necessary to wait for periods of complete quiescence. In a general presentation of the data in a single plot, *Tiedemannia* in the middle ranges of these experiments exhibits an increment of 16,200.²

² Four out of eleven individuals exhibit an increment of $14,500 \pm$. The explanation cannot be found in manipulative irregularities committed in the course of experimentation. The points on which this increment is based could hardly demonstrate its reality with greater clearness. The matter will be discussed later.

These curves are in every way comparable with the results for *Pterotrachea*.

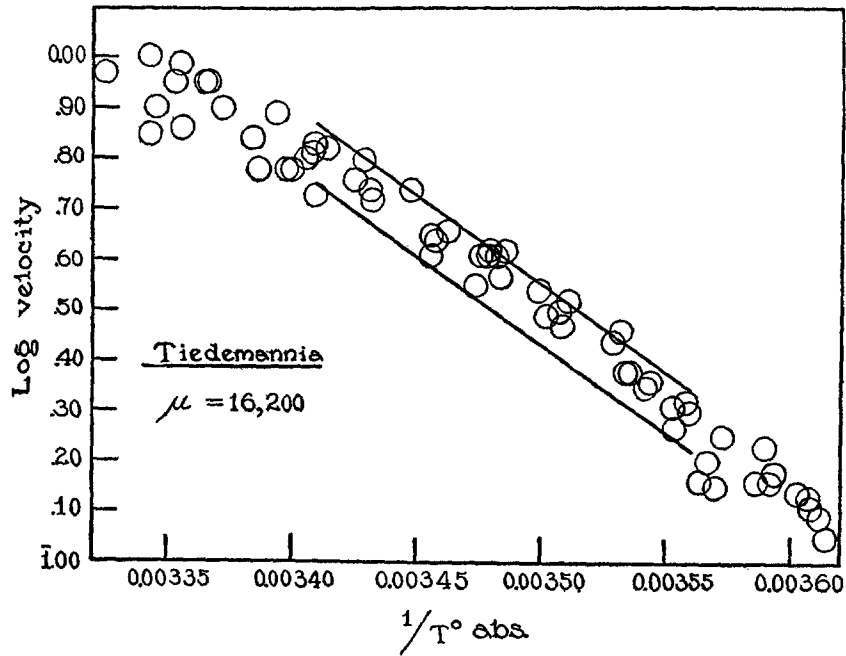


FIG. 3. *Tiedemannia neapolitana*; mass plot. At intermediate temperatures, $\mu = 16,200$.

TABLE II.
Tiedemannia Heart.

Animal.	μ (intermediate).
1	16,000
2	16,300
3	16,200
5	16,100
6	16,500
9	16,100
10	16,100
Average.....	16,200

IV.

Until further studies on the upper and lower limits of the temperature field are available, the results for these regions must be considered as essentially an orientation. Necessarily, observation in these distal ranges is greatly restricted. At both high and low temperatures certain individuals show no change of increment; whereas

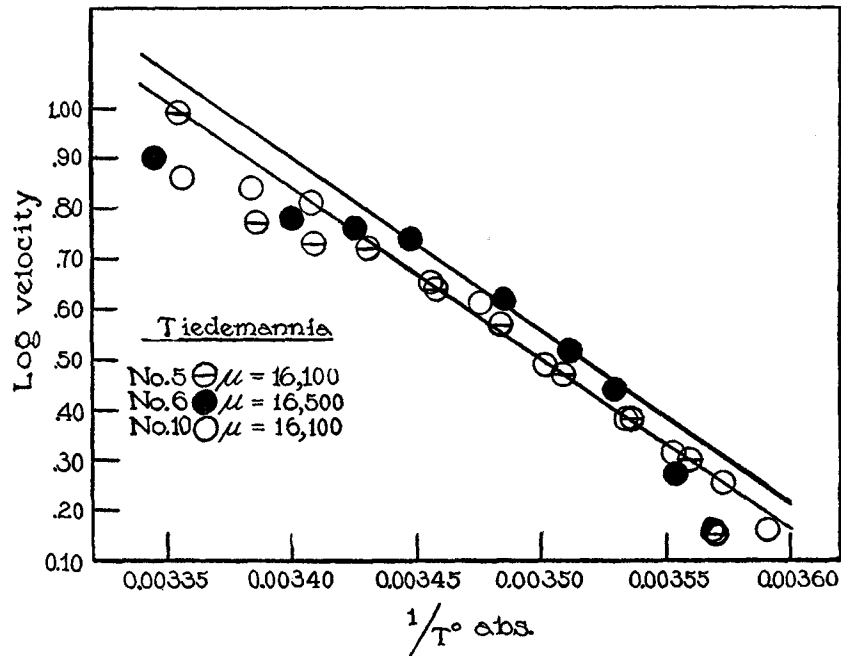


FIG. 4. *Tiedemannia*; heart rates of three individuals, see Animals 5, 6, and 10 Tables II and III. No. 5 illustrates the return to intermediate increment after an intermission at high temperatures.

in others, even with the exercise of great care, the heart beat becomes irregular, intermittent, or stops altogether. Near the upper limits, an intermission may be followed, significantly, by great and sudden variability. It is very difficult at times to be certain what the resulting points imply. Again, the onset of a shift in μ values appears to be influenced by the rate at which the temperature has been changed. Excluding the instances in which μ is either incalculable or unchanged,

it becomes relatively easy to rate the terminal increments as to their general order of magnitude with fair precision. As indicated in Table III, the values for μ at the extremes are sufficiently constant and different to suggest for *Pterotrachea* and *Tiedemannia* hearts the existence of apparently not less than two distinct terminal controls.

TABLE III.
Terminal Values for μ .

<i>Pterotrachea</i> No.	Temperatures.	
	High.	Low.
2	7,200	20,600
2	6,900	28,000
3	8,300	22,500
4	7,800	20,500
5	7,500	21,800
6	—	17,400
7	8,400	—
8	4,900	—
Average.....	7,300	22,000
<i>Tiedemannia</i> * No.		
1	7,000	—
3	9,200	20,100
4	5,900	21,700
5	7,000	—
6	7,200	27,800
7	8,900	20,900
8	7,400	26,400
9	7,200	—
10	5,900	—
Average.....	7,400	23,000

* This table includes the terminal data for the individuals with intermediate increments of $14,500 \pm$. These it will be observed are indistinguishable from those where the intermediate $\mu = 16,200 \pm$.

V.

There can be no doubt that the controlling mechanisms at high and low temperatures are different. The harmony between the comparable averages for *Pterotrachea* and *Tiedemannia* is astonishing

and very possibly not an accident. Yet within each list of high and low values, there are striking discrepancies. In the records, certain of these "increments" far above the average, and others as far below are attested by observations that can be interpreted, at present, in no other way. The precise meaning of these extreme variates and of certain intermediate irregularities remains problematical. Despite the remarkable agreements noted, certain temperatures, conceivably, may uncover in the heart rate one or more of a variety of processes which at other temperatures remain concealed. If this is a fact, then in certain states of equilibrium any one of these recessive reactions might be "exhumed" and fall momentarily into the position of control.

However, if we consider only the most frequent and closely concordant values, it seems safe to say that high temperatures disclose at least one controlling reaction whose characteristic lies between 7,000 and 8,000, while low temperatures uncover a second with its increment in the neighborhood of 22,000.

Are these or perhaps any of the other terminal values normal? From a purely physical standpoint this question is equivalent to asking whether a heart forced to disclose either both, or any, of the terminal increments, can return to the conditions that yield 11,200 or 16,200. Very likely if the animals were kept long enough at the extremes, the mechanism underlying the heart beat could be permanently altered. In these experiments the exposures were not sufficient to bring about such results. In every case a set of preliminary readings was taken at room temperature soon after the material had been brought into the laboratory. The animals were then cooled to the lower limit and when this was reached, usually after an hour, the first definitive observations were made. From this point on the temperature was increased step by step at regular intervals up to the maximum. In the intermediate zone, therefore, the performance of each individual occurred only after exposure to the lower thermal limit. The first reading at room temperature always coincides with the corresponding one made later on as part of the ascending series.

For the low values found at the upper limits, there are three checks. First, their general order of magnitude seems to rule out destructive effects such as irreversible coagulations or precipitations of proteins;

second, when the heart stops and after an intermission returns to rhythmical contraction with chambers properly synchronized, the results abruptly approach, or actually fall on the line characteristic for intermediate temperatures. This fact which at times makes the recognition of terminal increments difficult or impossible, is not without its compensations. Other possibilities granted, it suggests that during intermissions some essential material, exhausted, depleted, or "inactivated" by the great increase in heart rate, is restored to its original state or amount. Finally, in the case of *Pterotrachea* there is a special test. Individual 2 was run through the entire series of temperatures on 2 successive days. On January 26 in the range from 4–27°, the successive μ values were 20,600, 11,900, and 7,200; on January 27, from 4.6–26.8°, this animal gave respectively, 28,000, 11,900, and 6,900. Judging by their sense and absolute values and in view of the other considerations, these increments suggest no radical alterations in the underlying mechanism.

VI.

Within present limits of accuracy the intermediate increments of *Pterotrachea* and *Anodonta* on the one hand, and on the other of *Tiedemannia*, and *Limax* (Crozier and Stier), are identical. In sense and as averages the corresponding terminal characteristics for *Pterotrachea* and *Tiedemannia* are also the same. But homogeneity does not end with these indications. The fact that certain species exhibit increments of $16,000 \pm$ for rhythmic movements under circumstances which elicit $11,000 \pm$ from others, loses the qualities of an obstacle when we recall that in *Melanoplus* Crozier and Stier (1924–25, *b*) have experimentally changed the increment for abdominal rhythm from 16,500 to 11,300. For *Limax* the same authors (1924–25, *a*) find intermediate increments of 7,900 in December and 16,300 in March; while from Lang's results on *Helix*, they have deduced for the same temperatures μ values of 7,900 from data gathered in June, 11,300 from those of January, whereas February and March yielded 16,000. In all these instances the reaction in control at specific temperatures evidently differs as circumstances differ, yet the values at whatever temperature found, are always the same ones. What are the implications? Certainly in view of the taxonomic differ-

ences distinctive of the molluscs under consideration it would be hazardous to assume more than one catenary series of controlling reactions. Within the limits of viability, even this series, should further work lengthen it considerably, must be thought of as including at all times at least as many processes as there are trustworthy increments. Under certain conditions, most of which await precise definition, a particular region of the thermal scale may expose one reaction while under other circumstances the same temperatures may unearth quite another. Indeed, with the sole exception of artefacts or novelties introduced into the organism from without, a thermal field, biologically defined, can expose only normal constituents of the catenary system of control.

The logical consequences of this reasoning may appear ominous; and yet confusion and absurdity can be avoided even if thermal increments were to multiply equally for every biological process. After all, the total number of increments possible is probably restricted (Rice, 1923; Glaser, 1923; 1924–25, *b*). It is not difficult to imagine that circumstances might arise under which control could pass to chemical reactions which are not ordinarily in control. Our theory, at least, must be able to face the organism which discloses for all its measurable acts the same inventory of increments with differences only in serial order. In this somewhat academic event, analysis by means of temperature characteristics would be exhaustive because the series of catenary controls would contain as many items as there are types of reaction in the actual chemical system. If we could know where and how many times each type occurs, our diagnostic series and the actual system could be superimposed, point for point.³

³ The addition of every authentic increment is a step in the direction of the theoretical limit. For this reason the occurrence of two intermediate μ values in *Tiedemannia* seems important despite the absence of a convincing explanation. It is possible to assume differences in prelaboratory history, but whatever these may have been, the terminal increments remain unchanged. The lower value is not necessarily irreconcilable. Rare as it is, increments of this order associated with $11,000 \pm$ and $16,000 \pm$ have been reported in connection with respiratory processes and those that might be limited by the rates of gaseous exchange. Arrhenius (*loc. cit.*, p. 55) lists as a mean value for cell division in certain eggs, 14,100 and attaches to "respiration in plants," 14,800. According to Crozier (1924–25, *b*), Krogh's data on respiration in dogs under curare yield $\mu = 13,780$.

VII.

The low increments characteristic of high temperatures are well supported in the literature. Somewhere in the catenary chain underlying respiratory phenomena in general and phenomena controlled by respiration, is a reaction whose increment is between 7,000 and 8,000. In certain instances, such as translation in *Paramecium* (Glaser, 1924-25, *a*) and the heart rates of *Pterotrachea* and *Tiedemannia*, it requires a fairly high temperature to expose this reaction whereas in *Melanoplus*, as Crozier and Stier (1924-25, *b*) show, it may control in normal or decapitated individuals over the entire range. To these writers (*loc. cit.*) also, we owe an interesting suggestion. Between 15° and 38° Bodine's measurements on CO₂ production in *Melanoplus* yield $\mu = 7,710 \pm 700$, whereas the data of Batelli and Stern (Crozier and Stier), perhaps doubtful on account of the high temperatures employed (between 30° and 40°), yield an increment of $8,000 \pm$. Crozier and Stier plainly imply a relation between this value and the excretion of CO₂.

For the increment of $22,000 \pm$ at low temperatures, a provisional assignment is perhaps also possible. It is found frequently associated with $11,000 \pm$ and $16,000 \pm$ (Crozier, 1924-25, *b*). Under laboratory conditions the blood of *Panulirus* undergoes a rapid loss of

With the exception of cleavage, all these processes under different circumstances have also given $\mu = 16,000 \pm$ or $11,000 \pm$, or both. It is not impossible then that increments of $14,000 \pm$ are normally recessive in respiratory phenomena but for one reason or another, not apt to emerge.

The association of this value with curare is suggestive. *Tiedemannia*, as observed, moves its "wings" rhythmically. If the individual happens to be a small one it is often necessary to await those recurrent periods when the individual is completely quiescent. Just prior to such an interval the movements become slower and the excursions more prolonged—symptoms found during the rhythmical phase of reflexes approaching fatigue (Bayliss, 1924; p. 501). If we suppose that *Tiedemannia* comes to rest for the same or comparable reasons, an explanation for the value $14,500 \pm$ might be sought and perhaps found in the element common to the effects of curare and of certain fatigue substances, curare eliminating the final motor neurone by affecting a "receptive" material in the muscle and "fatigue" deleting the same neurone by blockade at the proximal synapse (*cf.* Bayliss, *loc. cit.*, p. 399 *et seq.*). Until the situation is clarified, however, we must withhold from the increment of $14,500 \pm$ the consideration given to the others.

glucose (Morgulis; *cf.* Crozier, 1924-25, *b*). In starving crayfish, Brunow's figures on the utilization of O_2 and the production of CO_2 yield $\mu = 22,000$ (Crozier, *loc. cit.*). It is easy to imagine that low temperatures might reduce, possibly reduce differentially, either the solubilities or the rates upon which a normal supply of glucose depends. If this is true, such temperatures would bring about changes in equilibrium closely comparable and perhaps identical with those characteristic of inanition. The temptation to attach 22,000 to hydrolytic reactions in which a substrate is prepared for oxidation is recognized by Crozier (*loc. cit.*).

VIII.

We can now attempt to picture the controlling mechanism for heart rate in molluscs, provisionally, as a catenary series of at least four reactions. Of these, the one with the smallest increment controls at high temperatures and the one with the largest value at low. Between these extremes control may fall to either of the remaining two, and these, as in *Melanoplus*, should be capable of being artificially substituted, one for the other.

Although we are not dealing exclusively with a muscle, it is perhaps not unreasonable to consider glycogen as a source of energy. Assuming an adequate original supply, O , a mechanism modelled on Meyerhof's (1924) conception of carbohydrate metabolism appears capable of accounting for the observed velocity controls. We can attach the increment of $22,000 \pm$, directly or *via* some catalyst, to a mobilization hydrolysis, $O \rightarrow A$. In a similar manner $11,000 \pm$ may be assigned to an "oxidation," $A \rightarrow B$, very likely catalyzed by OH' ; while $16,000 \pm$ may be taken to characterize a reaction $B \rightarrow E$ which liberates the energy and is catalyzed otherwise. The increment $7,000 \pm$ would then fall to the resynthesis $E \rightarrow O$ (lactic acid \rightarrow glycogen?), and on occasion also to any other pertinent reaction involving the production of CO_2 and important in maintaining the original source of supply.

While the interpretations on which this particular scheme is based should involve no irrevocable commitments, it has, nevertheless, certain advantages. For one thing, its form projects into the substrate the cyclical nature of rhythm, and, resting on the apparently

solid foundation laid by Meyerhof (*loc. cit.*) brings under one rubric phenomena superficially diverse. As a formulation we are obviously dealing merely with the harmonious enlargement of an idea suggested as applicable to linear translation in *Paramecium* (Glaser, 1924-25, a), where the thermal field so far has exposed only two values: 16,000 from 6-15° and 8,000 for the higher ranges. The interpretation of these values remains unchanged. As Crozier and his collaborators (1924-25) have shown, increments of 11,000 ± and 16,000 ± are characteristic of processes involving O₂ consumption and the produc-

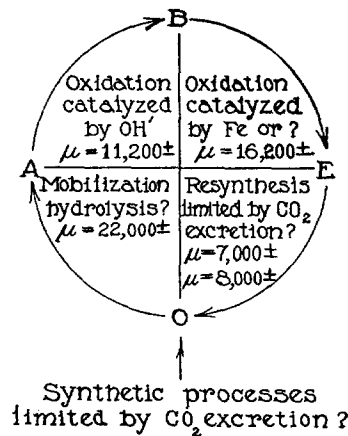


FIG. 5.

tion of CO₂. Of these values, the former is believed to reveal the activity of OH' (*cf.* Rice, 1923), although the reaction in which this intervention occurs may itself issue in oxidation (Oppenheimer, 1925, page 225); the second, 16,000 ± is perhaps definitely to be associated with a catalyzed oxidation. The assignment of 22,000 ± to a mobilization hydrolysis is admittedly the most speculative of all. On the other hand, for the lowest increment we can appeal to at least one other synthetic process. In the data of Miss Leitch (Crozier, 1924-25, b) μ below 15° is 8,170 for growth in the radicle of *Pisum*. If in the synthesis $E \rightarrow O$ the excretion of CO₂ should be a limiting factor, it is interesting to recall (Meyerhof) that the reaction which transforms lactic acid into glycogen also sets free six molecules of CO₂. Finally, the place assigned to the lowest increment makes it

conceptually easy to link the immediate cycle underlying the heart rate with the rest of the organism because the synthesis of *O* is not restricted to movements from *E*, but in the model may result, as it does in nature, from reactions spatially distinct yet with the same control.

SUMMARY.

1. For the heart rate in *Pterotrachea coronata*, intermediate temperatures disclose a thermal increment of $11,200 \pm$. This value is identical with the one reported by Crozier and Stier for the lamelli-branch, *Anodonta*. In the pteropod, *Tiedemannia neapolitana* the same temperatures typically reveal in the heart rate a μ value of $16,200 \pm$. This agrees quantitatively with 16,300 found by Crozier and Stier for the heart of the slug, *Limax maximus*.

2. At high temperatures the average value of μ for *Pterotrachea* is 7,300: for *Tiedemannia*, 7,400. The corresponding averages at the lower limits are 22,000 and 23,000.

3. The great variability found near the edges of the temperature field are explicable in two ways. During intermissions characteristic of high temperatures and occurring also at low, we can assume a restorative process; while at both the upper and lower limits we may, in addition, find that reactions assume control which under ordinary circumstances never do so. Special evidence indicates that the highest temperatures employed, 27°C., and the lowest, 4°C., caused no irreversible changes in mechanism.

4. The theoretical analysis of the experimental facts makes use of Meyerhof's conception of carbohydrate metabolism and projects the cyclical nature of rhythm into the substrate of control. Assuming as a source of energy an original supply of material *O*, the value of $22,000 \pm$ is assigned provisionally to a mobilization hydrolysis while $11,200 \pm$ and $16,000 \pm$ are attached to oxidative reactions influenced respectively by OH' and possibly Fe, or some other catalyst. The lowest value, $7,300 \pm$ is assumed to indicate a synthetic process (lactic acid \rightarrow glycogen?), possibly limited by CO_2 excretion. In the present state of our knowledge, this distribution and interpretation seems to account reasonably for the experimental facts, but until we know more about the neurogenic controls, is entitled to rank only as an hypothesis.

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