

CRITICAL THERMAL INCREMENTS FOR RHYTHMIC RESPIRATORY MOVEMENTS OF INSECTS.

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I.

A survey of the critical thermal increments which could be deduced for rhythmic neuromuscular phenomena among arthropods led to the finding that in all but two instances, among those available, the critical increment or temperature characteristic was sensibly identical, namely 12,200 calories (Crozier, 1924-25, *a*; Crozier and Federighi, 1924-25, *b*, *c*). The empirically derived values of the quantity μ in the Arrhenius-Marcelin-Rice equation

$$K_2 = K_1 e^{\frac{\mu}{2} \left(\frac{1}{T_1} - \frac{1}{T_2} \right)}$$

were:

Velocity of progression, <i>Parajulus</i> * ¹	12,250
“ “ “ ants*.....	12,220
“ “ “ ants†.....	12,200 ±
Frequency of chirping, tree crickets*.....	12,200
“ “ flashing, fire-flies*.....	12,200
“ “ heart beat, <i>Limulus</i> *.....	12,000
“ “ “ “ <i>Ceriodaphnia</i> †.....	12,100
“ “ “ “ <i>Bombyx</i> larvæ§.....	12,200

The surprising degree of quantitative concordance evident in this list led to the assumption that not only do such rhythmic activities reflect the determination of the frequency of neuromuscular movements through the agency of chemical transformations, but that

¹ Values marked * were derived in a preceding paper (Crozier 1924-25, *a*); †, data from Shapley (1924); ‡, data from Robertson (1906); §, Crozier and Federighi (1924-25, *c*).

the *governing* chemical process must be of identical type in the several instances—at least in the sense that there is involved a common catalyst.² The conclusion is the more permissible because the activities compared may be taken to involve “central nervous discharge”³ as controlling element, and are thus truly homologous.

The rhythmic abdominal movements of respiration, however, in larvæ of *Libellula*, in *Dixippus*, and in other insects, fail to exhibit

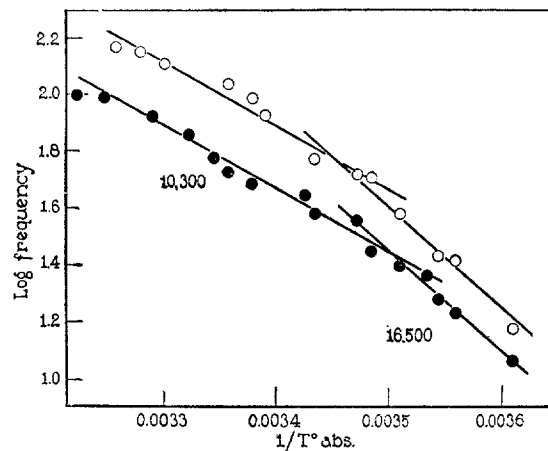


FIG. 1. Breathing rhythm of *Libellula* larvæ at various temperatures (data of Babák and Roček, 1909); black circles, well supplied with oxygen; white circles, under oxygen deficiency. Respiratory frequency is enhanced at low oxygen tensions, but within the limits of variation in the data, the temperature characteristics are unchanged. The increment assigned for the upper range of temperatures is probably too low, owing to the observations above 32°, at about which temperature there may occur destructive effects. There is a suggestion that the critical temperature, at which change of μ occurs, is shifted by oxygen deficiency.

the critical increment 12,200. The probable analytical utility of the method of critical increments makes it desirable to examine carefully the nature of these exceptional instances. The results of such examination, in part contained in the present paper, afford some interesting confirmations of the proposition that analysis

² The physicochemical foundation for this view is given in articles by F. O. Rice (1923, 1924).

³ Evidence that the increment 12,200 probably reflects activity of nerve centers and not of muscles was previously discussed (Crozier, 1924-25, a).

through temperature characteristics may ultimately permit the identification of reactions in living matter (Crozier, 1924, 1924-25, *a*, *b*; Crozier and Pilz, 1923-24). They also provide evidence for the validity of the conception of critical temperatures, at which control of a given activity may change from one fundamental reaction to another (Crozier, 1924-25, *a*; Crozier and Federighi, 1923-24, 1924-25, *b*).

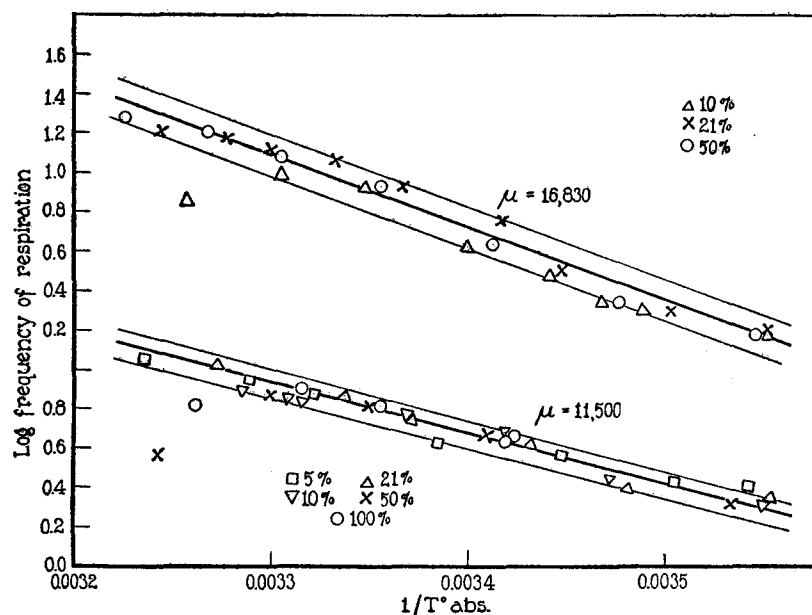


FIG. 2. Two sets of determinations of respiratory frequency in *Dixippus* (von Buddenbrock and von Rohr, 1922-23). Within the limits of variation inherent in the measurements, each set yields a definite but different value of the critical increment, which is consistently maintained in different concentrations of oxygen (percentage O_2 indicated by symbols). Above $32^\circ \pm C.$ destructive effects may enter, as shown by three points which depart widely from the rest.

As obtained from data published by Babák and Roček (1909) and by von Buddenbrock and von Rohr (1922-23) the critical increments for respiratory rhythm, in *Libellula* larvæ and in *Dixippus*, are 16,500 and 16,800 calories, respectively (Figs. 1 and 2). In the former case, at higher temperatures $\mu = 10,300 \pm$. A complication

enters when it is found that under certain circumstances, not easily ascertainable from the original accounts, the temperature characteristic for the rhythmic respiratory movements of *Dixippus* turns out to be $11,500 \pm$, not $16,500$ (Fig. 2). These two sets of measurements would perhaps not be conclusive by themselves, in view of the extent of variation, but it will be shown that they are consistent with new experimental results. The occurrence in some experiments of an increment holding for the total temperature range, which in other experiments pertains to only a portion of the temperature range, is especially interesting for two reasons. It has a very practical bearing upon the fitting of curves to portions of the data in cases exhibiting change of the governing process at a critical temperature (*cf.* Crozier, 1924-25, *a*, *b*); and in a theoretical way it is illuminating in relation to the notion of catenary or linked processes assumed to determine the velocities of vital activities.

II.

Increments of these two orders, 11,300 and 16,500, are found to occur characteristically in numerous sets of data upon oxygen consumption and carbon dioxide production as function of temperature (Crozier, 1924-25, *b*); additional increments occur in respiration experiments where inanition may be involved, or in which similar chemical disturbances of the complex respiratory mechanism maybe assumed. With the insects yielding increments 11,500 and 16,500 for frequency of respiratory movements it is demonstrable that the velocities of oxygen consumption and of carbon dioxide production also yield, under different circumstances, either the increment 11,500 or 16,200 calories (Fig. 3).

This kind of agreement is fairly strong evidence for the conclusion that the frequency of insect respiratory movements is controlled by the velocity of tissue respiration. It is not necessary to suppose, however, that the increments $11,300 \pm$ and $16,500 \pm$ correspond to the *only* two processes which may under any conditions be controlling ones in cell respiration. A certain number of cases are known, for example, involving gaseous exchange or activities which may be dependent thereon, in which there appear temperature characteristics approximately 8,000, 21,000, and 24,000 (Crozier, 1924-25, *b*:

Glaser, 1924-25). The mechanism of cell respiration, as thus far understood (*cf.* Meyerhof, 1924), comprises successive linked processes more numerous than are required to accommodate the several critical increments found associated with respiratory exchanges, if one wishes to assume that these have reference to diverse steps in the intermediary history of the respiratory substrate. These facts complicate the problem of deciding in what particular way the velocity of a given vital process (*i.e.* in morphogenesis) may be dependent upon the energy-yielding reactions.

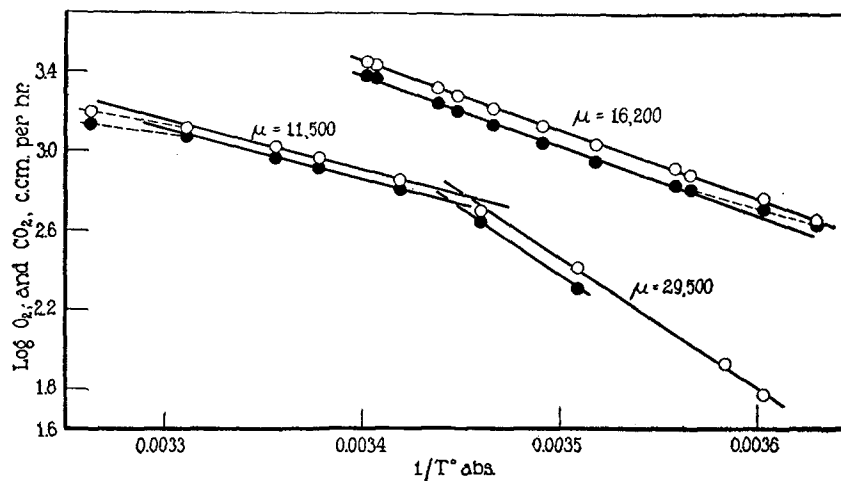


FIG. 3. Upper graphs, velocities of oxygen consumption (white circles) and of CO_2 production (black circles), lower graphs in *Dixippus*, corresponding data from an independent experiment (data of von Buddenbrock and von Rohr, 1922-23). The intersection occurs in the neighborhood of 17° . The deviations indicated by dashed lines may be real and significant.

That the difference between respiratory rhythms yielding respectively $\mu = 11,500 \pm$ and $\mu = 16,500 \pm$ is a real difference, and not an artifact of curve fitting, is shown by observations we have made with aquatic larvæ of the dragon fly *Anax*. Two illustrations are given in Figs. 4 and 5. We shall demonstrate presently that the nature of inherent variation in frequency of respiratory movements, at constant temperature, is such as to demand for treatment numerous observations at close temperature intervals. Within the tem-

perature limits used the effect of change in temperature is completely and very rapidly reversible.

In these experiments the animal is near the bottom of a tall beaker of water immersed in a large volume of water of which the tempera-

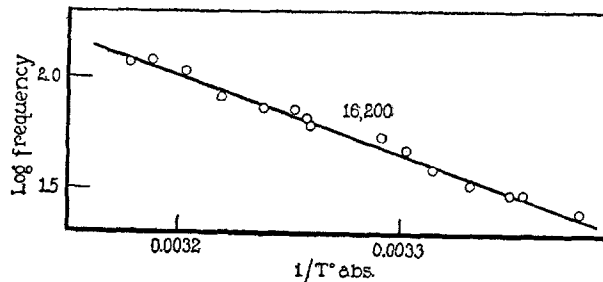


FIG. 4. Result of an experiment with *Anax* larva No. 3, in well aerated water. Each point is the mean of three to six closely concordant measurements. Within the temperature limits given the effects are rapidly and completely reversible.

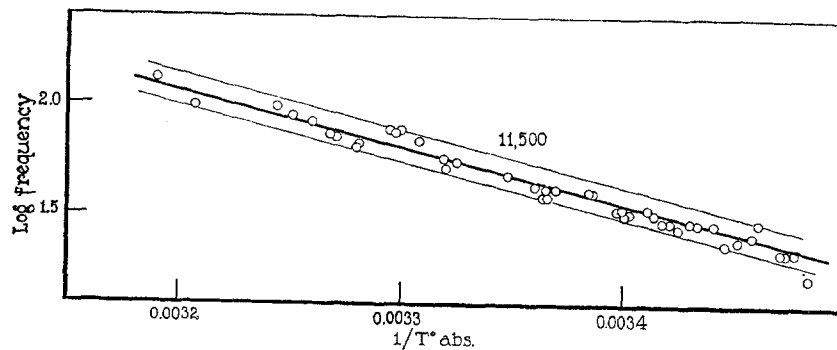


FIG. 5. Data from an experiment with *Anax* larva No. 5, of the same antecedents and history as No. 3 (Fig. 4), but with the animal in stale water (pH about 6.5). Each plotted point is the mean of three to six concordant readings. The extent of variation at each temperature tends to be a constant fraction of the associated mean frequency, so that, as in previous illustrations, the observations occupy a band of constant width. The right-hand terminal point is known to be doubtful.

ture is under control. A clamp may be adjusted upon the thorax of the larva in such a way as to hold the animal in vertical position with the posterior end upward; or the head of the larva may be inserted in a snugly fitting short rubber tube held vertically by a glass

rod. Confinement in this way for as much as 2 days does not affect the character of the rhythmic movements of the rectal respiratory pump. The rubber tube about the eyes eliminates effects due to optic stimulation. With a strong light placed to one side of the thermostat the frequency of the rectal pulsations may be timed very accurately, under a large reading lens, since the open respiratory chamber appears white against the surrounding dark green integument. The light from the lamp passes through an infra-red filter eliminating heat rays, and thus does not affect the temperature of the water or of the animal. We have counted the movements of the anal sclerites which close over the posterior aperture of the respiratory chamber. The figures demonstrate that if due attention be paid to the character of the intrinsic variations in speed of the activity being measured (Crozier and Federighi, 1924-25, *a, c*) one may derive values of the critical increments for biological phenomena which rival in precision those obtainable in simple chemical systems; in fact, there might be made out a very good case for the view that the values thus obtained in biological systems may be even more significant for purposes of analysis and identification.

III.

The evidence thus shows that the critical increment for respiratory rhythm of an insect may in one experiment be $11,500 \pm$, in another $16,500 \pm$. This difference is observed both in aquatic and in terrestrial forms. We have accordingly sought to determine if it is possible to so arrange the experimental conditions that the critical increment for such movements may be altered at will. In terms of the theory underlying these investigations this amounts to the deliberate selection of that particular process of an interrelated series which shall be the slow or controlling one.

It will be shown that it is possible to alter the critical increment for respiratory rhythm, and that the change from one controlling process to another is abrupt, so that one obtains (according to the conditions) one or another of several critical increments without intermediate gradations. The results also substantiate the interpretation previously proposed for cases in which two critical increments are found over different portions of a wide range of tempera-

tures. There is thus provided a definite standpoint from which one may attempt the control of vital processes, in a sense scarcely envisaged hitherto. In general, it may be sought to so alter environmental conditions as to differentially affect the catalytic mechanisms governing velocities of interlinked protoplasmic processes; or by the introduction of foreign materials into the organism one may seek to influence specific reactions. Reciprocally, there is available a possible means of chemically interpreting the mode of action of added catalytic or other agents.

It has been pointed out (Crozier, 1924-25, *a, b*) that certain substances, salts and adrenalin for example, may alter the velocity of a protoplasmic activity without changing the value of its temperature characteristic. This is taken to mean that the mechanism for production of the governing catalyst is so affected as to increase or to decrease its total velocity—*i.e.* the amount of catalyst is changed—but that the rate at which active molecules of catalyst are formed bears the same relation to the temperature as before the introduction of the salt or other substance. We now describe experiments in which it appears that of several interconnected processes concerned in the determination of the frequency of rhythmic movements in the grasshopper the respective velocities may be so affected by changed conditions that the normal or typical governing process is no longer in control.

The respiratory rhythm of grasshoppers, *Malanoplus femur-rubrum*, was measured under conditions which permitted a considerable degree of precision in estimations of the frequency of movements. Observations were made during October and November with freshly collected animals of both sexes, and with individuals kept for some days in terraria with growing grass. Each experiment consisted in timing the abdominal movements of one individual at short intervals over a considerable range of temperature. To accomplish this the animal was grasped with broad-tipped forceps on the wing covers, and so held at the center of a stoppered flask immersed in a large jar of water. With the legs removed from contact with a substratum spontaneous movements are reduced. The temperature of the water bath was controlled by addition of small quantities of water from a heated or cooled reservoir. The added water entered by way

of many fine openings in a coil of copper pipe. The temperature could be held constant in this way within 0.1°C . for periods of an hour, and yet rapidly changed. In the different experiments the average rate of heat change was 0.1° per 10 minute interval; this change was made in steps, the temperature being held constant during a measurement. The time required for ten respiratory movements was taken with a stop-watch, and the frequency calculated. A large reading lens, immersed in the thermostat, increased the ease of observation.

There may be distinguished in a practical way three types of respiratory movements in the grasshopper. (For accounts of the mechanism of the respiratory movements, *cf.* Packard (1898), Berlese (1909).) A gentle and very regular type of movement involves the rhythmic rise and fall of the floor of the abdomen. A less common type comprises the rather faint pulsatile activity of the two terminal abdominal segments. At high temperatures, or under oxygen deficiency, and occasionally as result of intrinsic individual circumstances, there occurs a very vigorous peristalsis of the whole abdominal wall. The frequency of this type of movement is less than that for the rise and fall of the ventral surface, but when it occurs continuously at ordinary temperatures its critical increment is the same. The peristaltic kind of movement begins at the anterior end of the abdomen and runs posteriorly; it seems connected with the tracheal circulation of air (Lee, 1924). Beginning at about 30°C ., and becoming clearer at temperatures above this, the shallow movements of the abdominal floor by gradations merge into the peristaltic type of breathing. The terminal type of pulsation is most clearly seen with female grasshoppers. Obviously, it is necessary to compare only rates of movements of one type; this has been carefully attended to.

Even with an individual breathing continuously by means of movements of one type, however, the rate of the movements is not constant, but fluctuates in a very definite manner. This is illustrated in Fig. 6. In seeking significant values of the temperature characteristics for such phenomena this type of variation makes it absolutely necessary to secure very numerous readings. The latitude of variation in frequency of rhythm is constant at constant tem-

perature, and as the temperature changes it remains a constant fraction of the mean frequency (unless the critical increment alters, in a new range of temperatures). At lower temperatures its absolute amount is small, and successive stop-watch readings of "time for ten pulsations" therefore agree very closely. At higher temperatures the latitude of variation is higher. This is the kind of organic variation

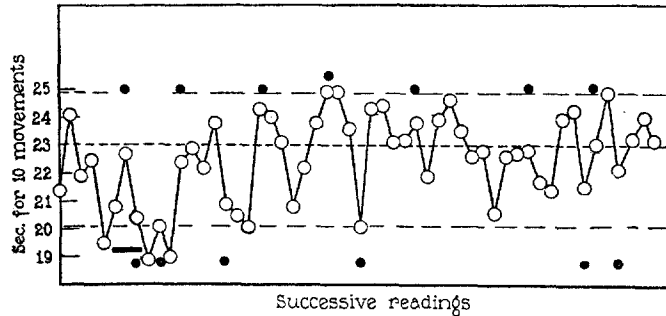


FIG. 6. The time required for ten respiratory movements, in successive groups of ten movements, at constant temperature 32.6° . By the use of two stop-watches no movements escaped enumeration. Since we are interested merely in the kinds of variation to be expected in successive determinations of "time for ten movements," the horizontal axis is divided into equal spaces. When treated from the standpoint of fluctuation in frequency as function of time, the periodic character of the complex tonus rhythms becomes even more apparent. The black horizontal bar indicates a period of defecation. Omitting the readings immediately following this event, it is obvious that, in spite of a very definite rhythmic fluctuation in rate, the extreme readings are confined within a band showing a constant maximal latitude of variation (broken lines). The distribution of the observations is slightly skewed, so that the line of modal frequency (central broken line) is nearer the limit of lower frequencies. It is of interest that the most rapid rates of breathing are coincident with gaping movements of the ovipositor (lower line of black dots), while the slowest rates are coincident with spontaneous movements of one or both anterior legs (upper line of black dots).

already recognized in cell division (*Arbacia* egg, Loeb and Chamberlain, 1915), in connection with the movements of *Oscillatoria*, and in the heart rhythm of silkworms (Crozier and Federighi, 1924-25, a.). It may be held to signify regulated fluctuation in the amount of substance (catalyst) which determines the velocity of the controlling process; or else, in more general terms, the result of dynamic balance between several processes implicated in the control of res-

piratory movements. Such fluctuation would be expected to result in a dynamical situation of the sort already assumed on the ground that different critical increments may be associated with a given kind of activity.

IV.

The first experiments were made with freshly collected normal grasshoppers. In order to reduce irregularities accompanying struggling movements due to optic stimulation by movements of

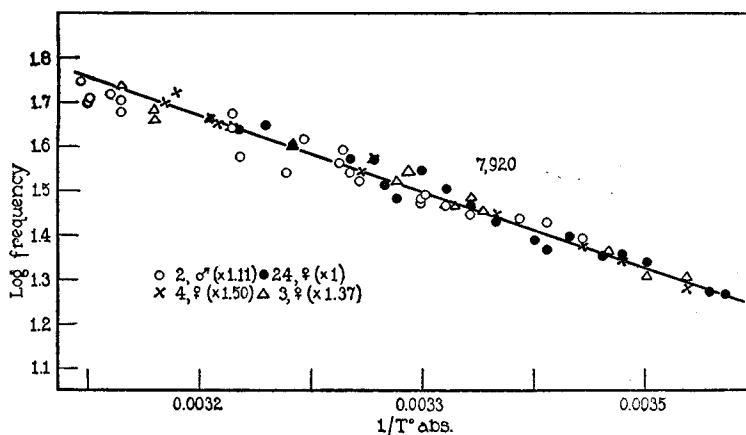


FIG. 7. The critical increment for quiet respiratory movements of normal grasshoppers, *Melanoplus femur-rubrum*, is 7,920 calories. When movements of the legs were evident, or bendings of the abdomen, the readings were discarded. The range of fluctuating variation is such as to make it desirable to combine observations obtained with numbers of different individuals. The data from each grasshopper are distinguished by a symbol. Every plotted point is the mean of a series of four to ten closely agreeing determinations at the particular temperature, with one animal. The rate of breathing movements differs with the individual, at constant temperature. The several series of determinations are brought together by multiplying each by a factor, which in the log plot moves the observations up or down on the vertical axis, but does not change the slope of the line fitting them. There is no constant difference in rate associated with sex. The observations with normal grasshoppers are somewhat more erratic than those with decapitated ones (*cf.* Fig. 8), and the range of variation is perceptibly greater at temperatures above 30°C. (due to greater frequency of spontaneous movements).

the observers, the animal was surrounded by a yellow paper cylinder in which a peep-hole had been cut opposite the abdomen. The

yellow paper admitted sufficient light to permit accurate timing. A small amount of water was present at the bottom of the chamber containing the insect.

With different individuals the determined points are found to be closely coincident (several series are plotted in Fig. 7). It is of especial interest that rhythmic respiratory movements do not appear below $15^{\circ}\pm C$. Whether the animal be warmed up from a lower temperature, or cooled down to below 15° , this temperature (14.5 – 16.0° in different instances) is a definite critical point. It will be shown later that this normal critical point may be experimentally shifted. But it adds one further instance to those previously enumerated (Crozier, 1924–25; *a* Crozier and Federighi, 1924–25, *b*, *c*) in which $15^{\circ}\pm$ appears as a critical region for the balance of interconnected processes in living matter.

Several additional critical temperatures were regularly encountered in these experiments. Restless leg movements, accompanied by deeper breathing movements, begin to occur sporadically at $30^{\circ}C$. Between 40° and 43° the rate of the breathing movements suddenly becomes increased, and if the observations are continued beyond this temperature the critical increment (40 – 49°) is found to be 45,000 to 50,000 calories—of a magnitude associated with processes of heat destruction and signifying structural breakdown in the controlling tissues. In decapitated animals also spontaneous kicking motions frequently become evident for the first time as the animal is brought to 30 – 31.5° , and again at 39 – 41° ; at the latter temperature sharp movements of the ovipositor, which may or may not accompany an act of defecation, tend to be exhibited.

The temperature characteristic obtained from the data in Fig. 7, and from other similar cases not plotted, is 7,920 calories. This value differs sharply from those previously cited for breathing rhythm in other insects. But turning to Bodine's (1921) measurements of CO_2 production at different temperatures by this particular species of grasshopper, we subsequently found that the CO_2 output increased very little between 0° and 15° , while at about 15° there begins a sharp increase in velocity of CO_2 excretion. From measurements at 15° , 25° , and 38° we find $\mu = 7,710 \pm 700$ calories. There is thus, again, a very striking agreement between respiratory movements on

the one hand, and on the other the velocity of respiratory processes, in their relation to temperature.⁴

We then used animals decapitated shortly before the beginning of an experiment. It is known that the head ganglia are not necessary for respiratory movements, but that the abdominal breathing motions are segmentally controlled (Ewing, 1904; Walling, 1906). The blood of *Orthoptera* coagulates readily, so that a seal is formed over the cut. Beheaded animals sometimes live almost as long (at least at this season) as do normal ones in a moist atmosphere but deprived of food (*i.e.* 3 to 6 days).³ For some typical instances the measurements are plotted in Fig. 8. The critical increment is

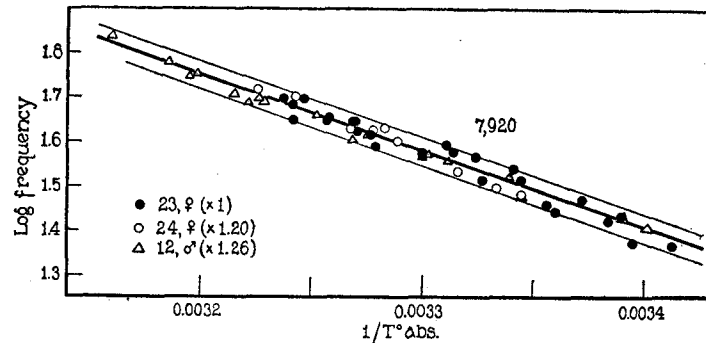


Fig. 8. Data similar to that represented in Fig. 7, but obtained with decapitated animals (experiments begun 1 to 4 hours after decapitation.) The rate of breathing movements is slightly accelerated after several hours subsequent to decapitation, but the critical increment is the same as with normal animals; $\mu = 7,920$. This is true regardless of sex, and is demonstrable in the records from single individuals studied before decapitation and after (*cf.* No. 24, which appears also in Fig. 7).

7,900, agreeing well with that secured in the case of the normal animals. The decapitated individuals are more satisfactory to work with because less subject to spontaneous brief irregularities, and because they did not require to be shielded from visual stimulation; this made it possible to mount a sheet of milk-glass behind the flask containing the grasshopper, so that, through the lens, very precise reckoning of pulsations became possible.

⁴Data from experiments by Batelli and Stern (1913), the interpretation of which may be doubtful because of the high temperatures involved, yield consistently the increment $8,000 \pm (30-40^\circ\text{C}.)$.

V.

If a grasshopper be decapitated and then kept for some hours in a moist atmosphere before being used for the experiment, the inner control of breathing frequency is found altered. The critical increment is then seen to be 16,200 or 11,200, not 7,900 (Fig. 9). Thus, processes characterized by these increments, previously masked, are revealed following decapitation; and it is especially significant

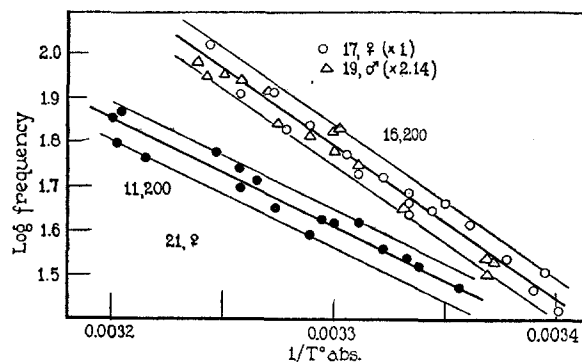
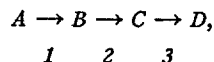


FIG. 9. Data from experiments with two individuals (Nos. 17 and 19) decapitated 15 hours before the beginning of the experiment. If exposed to temperatures above 36° the rate of breathing movements, on return to a lower temperature, is found permanently lowered. The processes involved in decreasing vitality lower the temperature at which thermal destructive effects are induced. In the region of reversible temperature effects, $\mu = 16,200$ to $16,600$ (in different experiments).

An experiment with Grasshopper 21, begun 19 hours subsequent to decapitation, shows $\mu = 11,200$.

that these particular thermal increments should be the ones to be evidenced. The (presumably central nervous) mechanism which controls the speed of breathing movements among insects might on this basis be pictured as comprising at least three steps,



in which the rate of formation of D determines the frequency of the movements. Under normal conditions Reaction 1, say, with Increment 7,900 would then be the slow process, in *Melanoplus*, though

concealed in the other insects studied; under the conditions of gradual exhaustion brought about in the decapitated animal Reaction 2, or again 3, with increments 16,500 and 11,500, would successively become the slow, determining, reactions. The latter ($\mu = 11,500$) is possibly an OH' catalysis, the former ($\mu = 16,500$) may be an iron-catalyzed cell oxidation (Crozier, 1924-25, *b*). It is not unreasonable to suppose that the progressive changes leading to death should, at the last, decrease the local OH' concentration to a point where its catalytic rôle would be in a limiting position. Since absence of food is known to lead to the death of uninjured *Melanoplus* within a relatively short time, these animals are particularly suitable for such experiments.

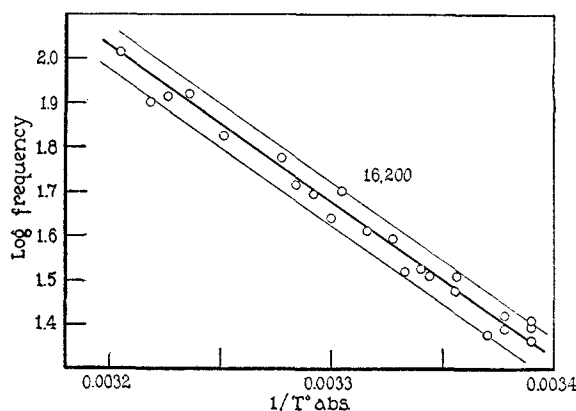


FIG. 10. Grasshopper 20, decapitated, had the two terminal abdominal segments amputated at the same time. The experiment began 1 hour later. The critical increment is 16,200 calories.

We are not rigidly committed, however, to this particular schematic outline. It may be that there are involved reactions not chemically linked but with different loci, spacially distinct. All one need be convinced of is, that several processes forming a catenary series necessary for respiratory rhythm have different temperature characteristics. To get some light upon this we have used (decapitated) animals from which the two posterior segments of the abdomen have been amputated. This was done under the impression that respiratory rhythms with increment other than 7,900 might originate in a different

portion of the ventral nerve chain. One such experiment is recorded in Fig. 10; the temperature characteristic is 16,200. The result of course does not solve the question proposed, but it shows that a freshly decapitated animal which has suffered additional injury may behave like an individual kept for some time following decapitation.

The real proof that consecutive processes with different thermal increments are concerned in the control of breathing rhythm is found in experiments yielding results of the kind illustrated in Fig. 11. The presence of two controlling processes, with gradual shift of the critical temperature, is unmistakable. It is noticeable, also, that

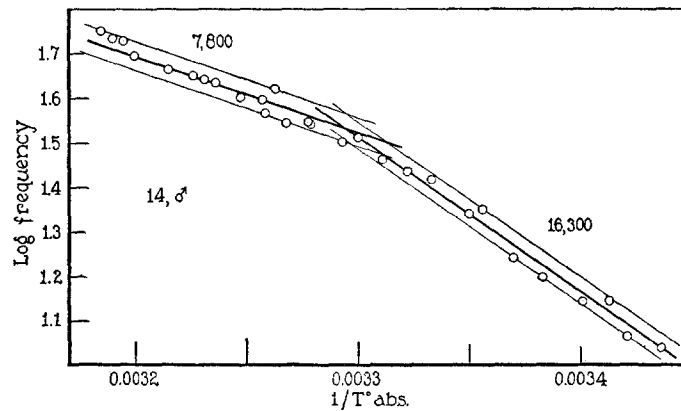


FIG. 11. Grasshopper 14, ♂, decapitated 5:45 p.m. Oct. 30; experiment begun 9:30 p.m. Below 30°C. the critical increment is 16,600; a rather sharp break in the graph is perceptible at 30°, the increment at temperatures above 30° being approximately 7,800. The three left-hand terminal points are less reliable than the others because of a tendency to exhibit kicking movements.

the lowest temperature for consistent rhythm is progressively advanced depending on the time since decapitation. There seems no fruitful way of understanding these results other than with the aid of the conception that the velocities of vital processes are determined by the velocities of dynamically linked systems of chemical transformations, differentially affected by conditions which lower vitality. The absolute magnitude of the pulsation rhythm shifts in a manner consistent with this view. As starvation progresses the frequency is at first increased (Figs. 9 and 10) then decreases.

This kind of interpretation is also consistent with the progressive shift of the minimum temperature for rhythmic breathing movements which is observed subsequent to decapitation. The normal *Melanoplus* initiates continuous rhythmic movements at 14–16.5°; this critical temperature obtains also with decapitated animals for about 4 hours; thereafter the critical temperature gradually moves upward—after 6 hours, 17–18°; after 15 hours, 19°; after 18 hours, 22.5°; after 19 hours, 25.0°. This applies to animals kept at room temperature; we have not yet studied the effect of temperature upon the process of exhaustion itself.

The mechanics of respiration in animals dependent upon a tracheal system are such as to suggest that oxygen supply is likely to be very commonly a limiting condition for respiration. The acidity of the hemolymph of some insects is also consistent with this view. It is not so surprising, then, to find that the frequency of respiratory movements seems to be controlled by the velocity of reactions which control cell respiration. Each of the three critical increments found for these movements, $11,300 \pm$ and $16,500 \pm$ in *Libellula*, *Dixippus*, *Anax*, *Melanoplus*, and 7,900 in *Melanoplus*, is represented among those associated with respiration in these insects and in a wide variety of other organisms (Crozier, 1924–25, *b*). That the temperature characteristics for respiratory rhythms differ from the one associated with other rhythmic neuromuscular activities of insects (movements of heart and of appendages) may signify merely that the respiratory movements are controlled by a different group of neurones, with metabolic processes adjusted in a slightly different way. Although the breathing movements are determined by abdominal ganglia, and progression movements (in ants) by thoracic ganglia, this is not the sort of distinction in view; because the contraction of the cardiac alary muscles of the *Bombyx* caterpillar, providing $\mu = 12,300$ as critical increment, are also mediated by abdominal segmental neurones. There is sufficient evidence, however, to suggest the existence of a definite group of neurones, metabolically distinct from those involved in progression movements for example, which form a kind of “respiratory center” (plurisegmental). We propose later to compare with this breathing rhythm of insects the temperature characteristic for respiration in vertebrates.

VI.

SUMMARY.

The rhythm of abdominal respiratory movements in various insects, aquatic and terrestrial, is shown to possess critical increments $11,500 \pm$ or $16,500 \pm$ calories (*Libellula*, *Dixippus*, *Anax*). These are characteristic of processes involved in respiration, and definitely differ from the increment 12,200 calories which is found in a number of instances of (non-respiratory) rhythmic neuromuscular activities of insects and other arthropods. With grasshoppers (*Melanoplus*), normal or freshly decapitated, the critical increment is 7,900, again a value encountered in connection with some phenomena of gaseous exchange and agreeing well with the value obtained for CO₂ output in *Melanoplus*. It is shown that by decapitation the temperature characteristic for abdominal rhythm, in *Melanoplus*, is changed to 16,500, then to 11,300—depending upon the time since decapitation; intermediate values do not appear. The frequency of the respiratory movements seems to be controlled by a metabolically distinct group of neurones. The bearing of these results upon the theory of functional analysis by means of temperature characteristics is discussed, and it is pointed out that a definite standpoint becomes available from which to attempt the specific control of vital processes.

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