

## CRITICAL INCREMENT FOR OPERCULAR BREATHING RHYTHM OF THE GOLDFISH.

BY W. J. CROZIER\* AND T. B. STIER.

*(From the Zoological Laboratory, Rutgers University, New Brunswick.)*

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### I.

The respiratory movements of fishes are about doubled in frequency when the temperature increases from 10° to 20°C. (*Cf.* Kanitz, 1915, 1923; Przißram, 1923.) The data for various species (due to Bethe, Baglioni, Babák, Kuiper, and others) show, however, considerable irregularity in the  $Q_{10}$  ratios for corresponding temperature intervals. This might be due to the occurrence of distinct controlling reactions in different parts of the temperature range, undetected unless numerous observations are made; or to the accidental effect of intrinsic variability in the frequency of movements; or to the existence of real differences in the critical increment for respiratory movements in different species or in the same species under different conditions.

To secure a basis for interpretation of the mechanism controlling respiratory rhythm more detailed observations are required. We have measured the frequency of opercular rhythm in the goldfish. This animal was chosen because measurements are available permitting estimation of the temperature characteristic for its gaseous exchanges.

The method of observation was similar to that already employed with the frog (Crozier and Stier, 1924-25). Each individual was confined in a flat-sided glass vessel immersed in a thermostat. The fish-container, partially filled with water, was closed by a sealed cover carrying a thermometer and tubes permitting air to be bubbled through the water. Air supplied in this way was first brought to thermostat temperature. The opercular breathing rhythm was watched

\* Research Associate, Carnegie Institution of Washington.

through a small opening in a yellow paper envelope surrounding the thermostat. By this procedure certain troublesome variations in breathing frequency, often associated with swimming movements, are greatly reduced. It was desired to obtain the critical increment in the absence of experimental interference with the animal and therefore we did not remove the eyes.

For some time before the commencement of the observations the fishes had been living in balanced aquaria at room temperature (not far from  $16^{\circ}$ ). These animals averaged 6 cm. in length, and withstood somewhat lower oxygen concentrations than found for larger goldfish by Gardner and King (1922). Comparative tests in which the

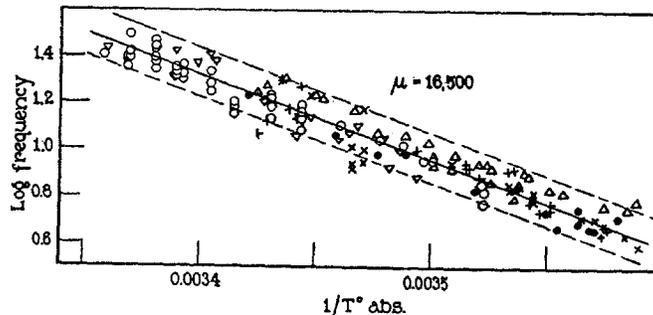


FIG. 1. The frequency (100 divided by time for 10 movements) of rhythmic opercular movements in six goldfish (different symbols) at different temperatures, when the pectoral fins are not obviously moving. The four most divergent points are single observations, the majority of the others, averages of four or more closely concordant readings. The critical increment is 16,500 calories. (The observations pertaining to one individual (black circles) are divided by 1.34.)

oxygen concentration was varied between 0.68 and 6.2 cc. per liter showed no significant effect of oxygen concentration upon breathing frequency, except that with high oxygenation the opercular movements may be quite in abeyance for considerable periods.

## II.

In the absence of visual stimulation periods of swimming activity tend to alternate with periods of quiescence. Three types of breathing frequency must be separated if a significant temperature characteristic is to be deduced. During active swimming the opercular

rhythm is irregular, and immediately after a period of vigorous movement the resting rhythm is accelerated. When the animal is quiet there is a corresponding greater frequency if the pectoral fins are in gentle movement. Reliable figures must therefore be obtained from

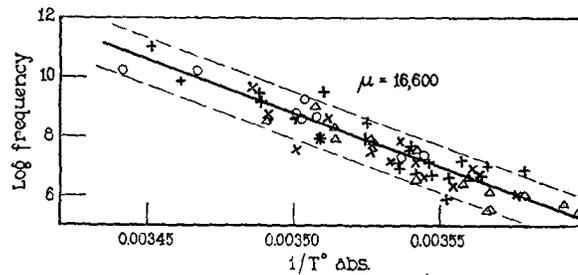


FIG. 2. Frequency of rhythmic opercular movements in four individuals starved 11 to 13 days. The readings with one animal (white circles) have been multiplied by 1.18. Other series of readings not plotted are fully consistent with these. The increment is the same as with non-starved animals (Fig. 1), and the latitude of variation at constant temperature is the same, but the mean frequency at any temperature is higher.

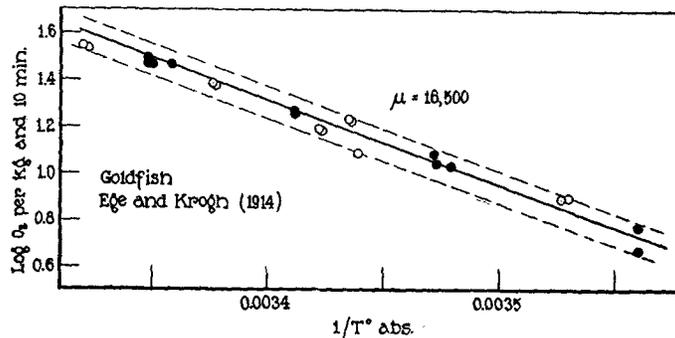


FIG. 3. The critical increment for velocity of oxygen consumption by goldfish is 16,500 calories. Data from Ege and Krogh (1914); white circles, narcotized with urethane.

quiet animals, with the pectorals at rest. It is not easy to secure large numbers of such readings above 15°C., although relatively easy to do so below that temperature.

Data from six experiments with different individuals are given in Fig. 1. These manifest the kinds of regularities already noted for

other phenomena controlled by temperature. The linear relationship between *log frequency of movements* and *reciprocal of absolute temperature* yields  $\mu = 16,500$  calories.

This magnitude of the critical increment also fits satisfactorily the observations obtained when the pectoral fins are moving (Fig. 4). The occurrence of rhythmic fin movements is accompanied by increased frequency of opercular movements. Starvation for several weeks produces alterations in the frequency of breathing movements, and somewhat increases the variability at constant temperature, but also without seriously affecting the thermal constant (Fig. 2). These facts serve to show that the temperature characteristic is indicative of some fundamental property of the respiratory center.

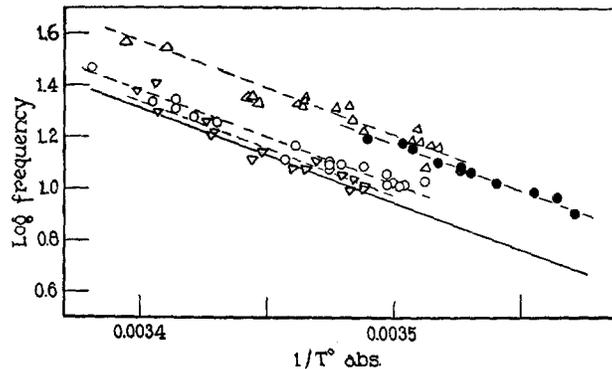


FIG. 4. The frequency of opercular movements in goldfish poised in mid water with pectoral fins moving rhythmically is higher at each temperature than in animals with motionless pectorals (Fig. 1); but the critical increment is unchanged. The solid line is drawn in the same position as in Fig. 1. The plotted points are averages. The amount of the frequency increase varies with the individual considered (different symbols).

### III.

The most significant series of measurements from which the temperature characteristic for metabolic oxidations in the goldfish may be estimated is that by Ege and Krogh (1914). The critical increment (Fig. 3) is 16,500 cal.<sup>1</sup> There is thus a quantitative corre-

<sup>1</sup>In a previous paper (Crozier, 1924-25, p. 200) this value was erroneously given as 16,100. The analyses by Gardner, King, and Powers (1922) provide

spondence between oxygen utilization and frequency of breathing movements. It is unlikely that the frequency of opercular movements determines the rate of total oxygen consumption. On the other hand, the critical increment for opercular rhythm serves provisionally to classify the controlling reaction among the respiratory oxidations which so frequently exhibit this increment (Crozier, 1924-25). From this standpoint the reaction respectively controlling opercular rhythm in the goldfish ( $\mu = 16,500$ ) and pharyngeal rhythm in the frog ( $\mu = 8,800$ ; Crozier and Stier, 1924-25, *b*) may perhaps be supposed to represent two distinct but possibly catenary reactions in the metabolism of cells composing the respiratory center.<sup>2</sup> The situation in these vertebrates would then be similar to that demonstrated among insects (Crozier and Stier, 1924-25, *a*). It might be predicted that, as with insects, under suitable experimental treatments the breathing rhythm of the goldfish and frog could be caused to exhibit new critical increments, such as characterize otherwise concealed reactions in the metabolism of the controlling nervous elements in the two forms. This prediction is being tested.

#### IV.

The nature of the variation in frequency of opercular movements, at constant temperature, requires brief consideration. The pertinent facts are these: the latitude of variation tends to be a well defined constant fraction of the mean frequency, at each temperature; the incidence of pectoral movements accelerates the opercular rhythm, but there is clear indication that the "central discharge" controlling the movements is thereby merely pitched at a new level,—for the critical increment is sensibly the same; a similar result is obtained under moderate starvation. It is possible to consider that these variations are similar in origin to the shift in frequency without change

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$\mu = 20,000$ , approximately, for velocity of  $O_2$  utilization and of  $CO_2$  output; it is not clear that the effects of movements are adequately excluded and the data show considerable irregularity, but the older measurements of Jolyet and Regnard (1887) are not wholly inconsistent with them.

<sup>2</sup>From a quite different standpoint this conclusion regarding the control of respiratory rhythm has been stated by Gesell (1923, 1924-25); *cf.* also McClendon (1917).

of increment which we have observed in the quiescent frog. A full theory of these effects awaits further testing, but it is believed that they permit the assumption of definite views regarding the mechanism of variability in certain kinds of central nervous processes. If it be supposed that the reactions controlling discharge from the respiratory center are specifically synaptic in locus, the effective mass of a governing catalyst might be varied according to the influx of nerve impulses from other parts of the central nervous system. Changes of this kind would abruptly alter the frequency of the observed activity, without changing its critical increment.

One method of testing this conception consists in determining the frequency and temperature characteristic for respiratory movements in amphibians after removal of the inhibitory control exercised by the forebrain. The results will be given in a following paper.

#### SUMMARY.

The temperature characteristic for opercular breathing rhythm in the quiescent goldfish is 16,500 calories. The reactions governing the frequency of breathing movements in vertebrates appear to be constituent links in the oxidative metabolism of the controlling cells.

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