

drop in JHE activity prior to the O₂ peak (3 days after the previous peak) may contribute to the rise of the JH titer at that time, but changes in JHE activity can not explain the major drop in JH activity on the peak day of cycle. Regulation of JH biosynthesis is a more likely scenario, or possibly other degradative mechanisms involving epoxide hydase or microsomal oxidase are more important in metabolizing JH in this system.

Why O₂ is consumed in a cyclic fashion during diapause remains unresolved. Possibly periodic episodes of high metabolism are more economic than a sustained lower metabolic rate. That such an episodic event is regulated by a hormone is not unusual, but this appears to represent a novel role for JH, a hormone best known for its roles in regulating growth and reproduction.

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Temperature compensation in an ultradian rhythm of tyrosine aminotransferase activity in *Euglena gracilis* Klebs

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Summary. Tyrosine aminotransferase activity of *Euglena* oscillates with an ultradian period of approximately 4–5 h. The oscillation frequency in the time series was determined by cosine fitting. Experiments which were performed between 16 and 31.5 °C revealed temperature compensation.

Key words. *Euglena*; rhythm; temperature compensation; tyrosine aminotransferase; ultradian.

Temperature compensation denotes the ability of biological rhythms to re-adjust period length upon changes of temperature. Therefore, comparisons of the frequency of oscillation which are made at different steady state temperatures reveal Q₁₀ values close to 1. This phenomenon is usually regarded as a typical feature of circadian rhythms^{1,2}. However, this important property of biological oscillations has occasionally also been detected in infradian and ultradian periodicities^{2–5}. With regard to the ultradian cycles, there appear to exist two different classes², one of which is highly temperature-dependent, such as the leaf movement rhythm in *Desmodium gyrans*⁶, and another which is temperature-compensated. The few examples of the latter class which are known up to now have been documented most clearly in unicellular organisms². Almost all of these cycles exhibit periods in the range of 0.5 to 1 h. In this study, we demonstrate temperature compensation in a longer ultradian oscillation of about 4–5 h.

Material and methods. *Euglena gracilis* Klebs, strain Z (No. 1224-5/25) was grown autotrophically at 23 °C, in a light-dark cycle (LD 12:12), as described earlier⁷. Sta-

tionary cultures were transferred at CT ('circadian time') 23 h to the experimental temperature and were investigated, if not stated otherwise, in constant light (LL). Aliquots of 4 ml were removed after gently agitating the cultures. Cells were homogenized directly in the medium, using a KLN ultrasound generator 281/101, equipped with the sonatrod TU 157/1; samples were sonicated in an ice bath, applying 5 pulses of 10 s at intensity 7, with intermissions of 10 s. Activity of tyrosine aminotransferase (L-tyrosine:2-oxoglutarate aminotransferase; EC 2.6.1.5) was determined in the 18,000 × g supernatant by the method of Diamondstone⁸, at an incubation temperature of 32 °C. Protein as reference value was measured according to Lowry et al.⁹. In order to eliminate circadian trends¹⁰ from the time series, data were detrended by means of a moving average. Period length was computed by determining the best-fitting cosine, using a program for least square fitting run on an Atari 520+.

Results and discussion. In figure 1, three examples of ultradian rhythms in tyrosine aminotransferase activity are shown. The curves were obtained at different experimental temperatures covering a range of 13.5 °C. The

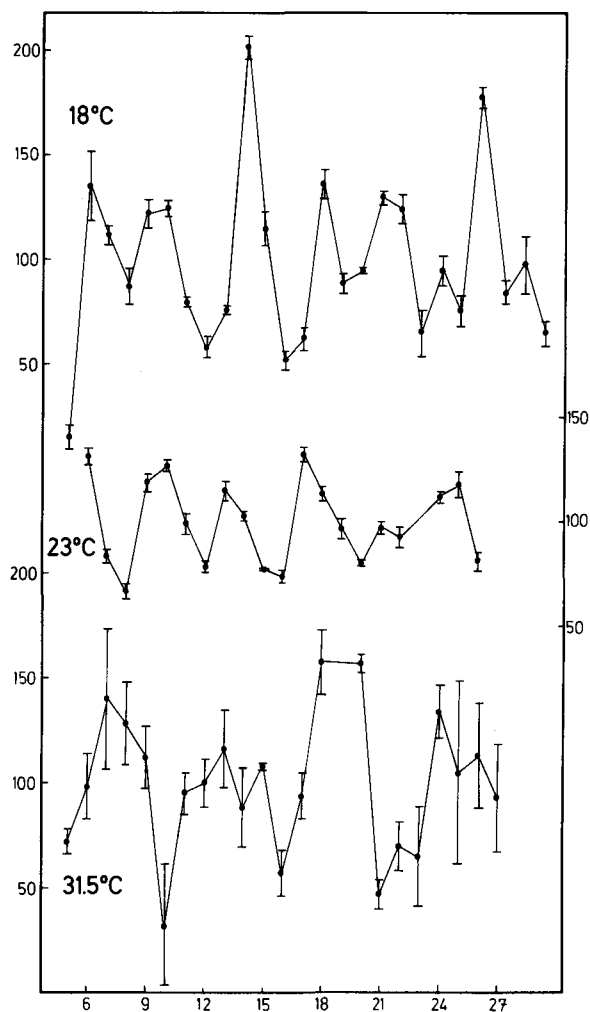


Figure 1. Ultradian rhythmicity of tyrosine aminotransferase activity at 3 different temperatures. Ordinates: enzyme activity (circadian trend removed; data expressed as percent of moving average); abscissa: hours in constant light; vertical lines: SEM.

ultradian fluctuations are statistically significant, with regard to both the standard errors (SEM) and an analysis of variance: an F-value was calculated on the basis of powers of regression for the fitted cycle and of residual error¹¹ (in all 3 experiments shown, a level of $p < 0.01$ was reached). Already from these curves, it becomes obvious that the ultradian rhythm is temperature-compensated.

This impression is supported by a plot of frequency vs temperature (fig. 2). The data spanning from 16 to 31.5°C show only minor variability and are obviously very different from the curve which would be expected at a Q_{10} of 2. On the contrary, especially at higher temperatures, there seems to exist a certain tendency to temperature overcompensation, i.e., a Q_{10} below 1, a phenomenon which has been observed also in some circadian rhythms^{1,2}.

Temperature compensation in the rhythm of tyrosine aminotransferase activity corresponds to findings by

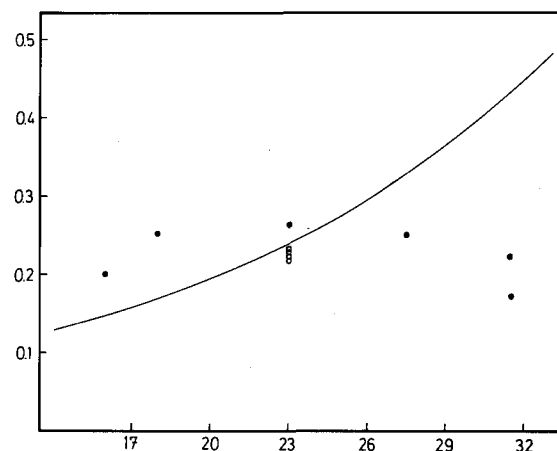


Figure 2. Temperature compensation as demonstrated by plotting the ultradian frequency vs temperature. Ordinate: frequency (h^{-1}); abscissa: °C. Full circles: data from constant light; open circles: data from a light/dark cycle of 12:12 h. The line represents calculations of data for a hypothetical non-compensated rhythmicity at a $Q_{10} = 2.0$.

Adams¹², who observed this phenomenon also in *Euglena*; however, in a rhythm of much higher frequency, namely, a cycle in motility of about 0.5 h. Again, the frequency of that oscillation turned out to be overcompensated¹³.

To the best of our knowledge, our data represent the second case in which a cellular rhythm of ca 4–5 h was shown to be temperature-compensated. The other example was found in tyrosine aminotransferase of *Tetrahymena*⁴. However, the situation in the ciliate is completely different insofar as in that organism ultradian and circadian rhythmicities of the enzyme represent alternatives between which the cells can switch, depending on nutritional conditions¹⁴. By contrast to this, the ultradian rhythm of tyrosine aminotransferase activity in *Euglena* occurs concomitantly with circadian oscillations of other cellular functions such as protein synthesis, cell shape, content of NAD^+ , and phototaxis^{10,11}.

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