

Выводы. Помимо легочных рецепторов растяжения, иннервируемых волокнами группы А, существуют легочные рецепторы, иннервируемые волокнами группы С, оказывающие постоянное тоническое влияние на дыхательный центр. Некоторые химические вещества (вератрин, фенилдигуанид) увеличивают активность этих рецепторов. Такое же действие на них оказывают воспаление и отек

легких. Это следует учесть в анализе дыхательных хемо- и патологических рефлексов.

S. I. FRANKSTEIN and Z. N. SERGEEVA

*Institute of Normal and Pathological Physiology,
Academy of Medical Sciences, Moscow (USSR),
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Effect of Light and Dark Pulses on the Emergence Rhythm of *Drosophila pseudoobscura*

On the basis of studies on the petal movement of *Kalanchoe* flowers¹, it was suggested that light periods induce an optimal rhythm if the 'off-rhythm' (rhythm which is initiated by the transition from light to darkness) falls together with the 'on-rhythm' (rhythm which is initiated by the transition from darkness to light) in such a way that an off-maximum occurs at the same time as an on-maximum. This is schematically diagrammed in Figure 1. The superposition of an on- and off-rhythm would explain the fact that at certain day-lengths and/or night-lengths the petal movement reaches high amplitudes. It could further be a basis of time measurement in photoperiodism.

We tested this hypothesis in the case of the emergence rhythm of *Drosophila pseudoobscura*. *D. pseudoobscura* has the advantage of being well studied in regard to its emergence rhythm², and in contrast to *Kalanchoe* can be kept under continuous darkness (DD) during the whole development. At the time of emergence the cultures are exposed to single steps (LL-DD, DD-LL), which already results in a rhythmic pattern of emergence, or to single pulses (light period pulse LP, dark period pulse DP).

Since a pulse contains both a light-on as well as a light-off signal, the question arises whether the observed results of pulse experiments are explainable in terms of the results of single step experiments.

A stock of *D. pseudoobscura* was kindly supplied by C. S. PITTEDRIGH and reared in the usual way. At 20°C under LL or DD conditions the flies start to emerge after about 3 weeks and continue to emerge in a random fashion. If, however, the DD-cultures are transferred to LL (300 lux fluorescence tube light), a periodic emergence is induced and peaks occur at 1, 20, 50, 75, and 100 h after transfer until the rhythm fades away and again emergence becomes random (Figure 2). A periodic emergence is also achieved if LL-cultures are transferred to DD. In this case peaks occur 12, 39, 64, 89, and 111 h after transfer. Synchronization is sharper and longer maintained (Figure 2 below).

If both steps are combined in a single DP- or LP-pulse, the emergence distribution depends on the length of the pulse and the kind of pulse. Examples are given for 12 and 18 h DP and LP (Figure 3). Further results are shown in Figure 4, in which the DP was varied from 1 h up to 33 h and the LP from 3 h up to 39 h. Only the emergence distribution between 50 and 75 h after the start of the DP and between 40 and 65 h after the start

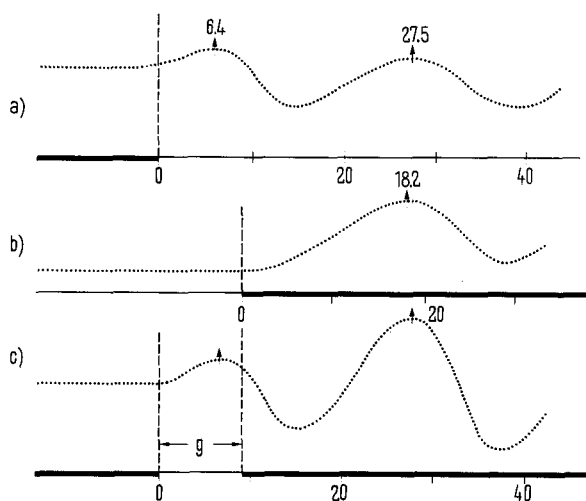


Fig. 1. Superposition of an on- and off-rhythm in the petal movement of *Kalanchoe blossfeldiana*. (a) Initiation of an on-rhythm by a single dark-light step; (b) initiation of an off-rhythm by a single light-dark step; (c) superposition of an on- and off-rhythm by a dark-light step followed by a light-dark step 9 h later. In this case the first maximum of the off-rhythm falls together with the second maximum of the on-rhythm (27.5-18.2 \approx 9 h).

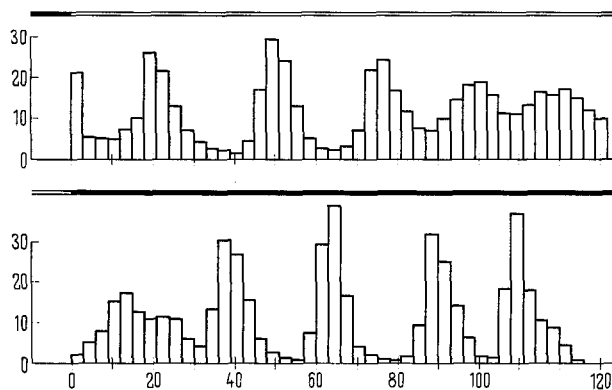


Fig. 2. Emergence rhythm in *Drosophila pseudoobscura* after transfer from continuous darkness to continuous light (above) and after transfer from continuous light to continuous darkness (below). Transfer at zero h. Abscissa: h after transfer. Ordinate: % of emerged flies (100% = sum of all flies between 2 minima).

¹ W. ENGELMANN, *Planta* 55, 496 (1960).

² C. S. PITTEDRIGH, *Cold Spring Harb. Symp. quant. Biol.* 25, 159 (1960).

of the LP are shown, since earlier and later peaks are less pronounced. Arrows indicate the calculated median of the emergence distribution, and bars indicate the percentage of flies emerged per time interval. The position of on- and off-peaks of single steps are shown as broken lines parallel to the start and end of the pulses. Also shown are the variances of the distributions. They are significantly different from the variance of the off-distribution at the 1% level, if they do not lie between the vertical broken lines (F-test).

We conclude from these results that the observed emergence distribution of pulse experiments are indeed explainable as superpositions of an on- and off-rhythm, which is initiated by the transition from darkness to light and from light to darkness. The peaks of the pulse synchronizations lie between or at the lines representing the position of on- and off-peaks (Figure 4), switching from 'delay' to 'advance', if the interval between an on- and off-peak becomes too large (compare 21 h-DP and 27 h-DP and -LP in Figure 4). If 1 peak lies in the middle of 2 others, 2 peaks appear or the rhythm disappears completely (24 h-DP and -LP in Figure 4). The variance as a measure for the synchronization of emergence demonstrates this even better. At pulse lengths, where on- and off-peaks fall together (e.g. 9 and 36 h-DP, Figure 4) the variance is low (high synchronization of emergence). At pulse lengths where on- and off-peaks fall between each other (e.g. 24 h-DP and -LP, Figure 4), the variance of the emergence distribution is high (weak synchronization). In intermediate cases the variance is not significantly different from the variance of single step emergence distributions (Figure 4, variances plotted against pulse length).

TAKIMOTO and HAMNER⁴ came to similar conclusions in the case of the photoperiodic flower response of the

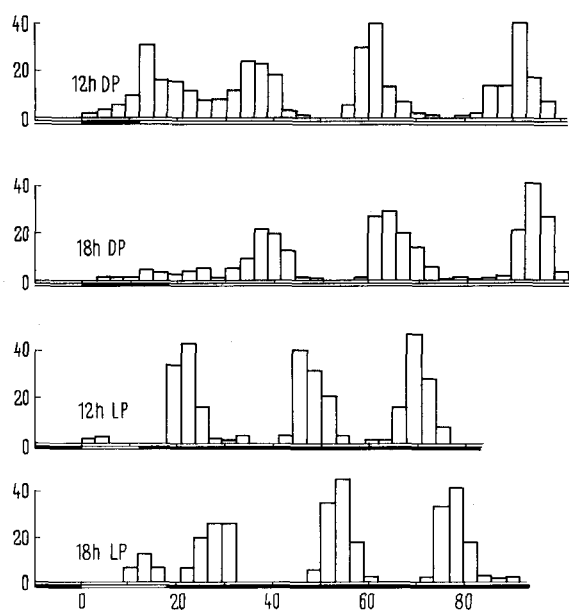


Fig. 3. Examples of emergence rhythms exhibited by a single 12 h-DP, 18 h-DP, 12 h-LP, and 18 h-LP. At 0 h start of DP or LP. Otherwise as in Figure 2.

³ The data for the calculation of the variance of short light periods (5 min) are from H. W. HONEGGER, unpublished.

⁴ A. TAKIMOTO and K. C. HAMNER, *Plant Physiol.* 40, 852 (1965).

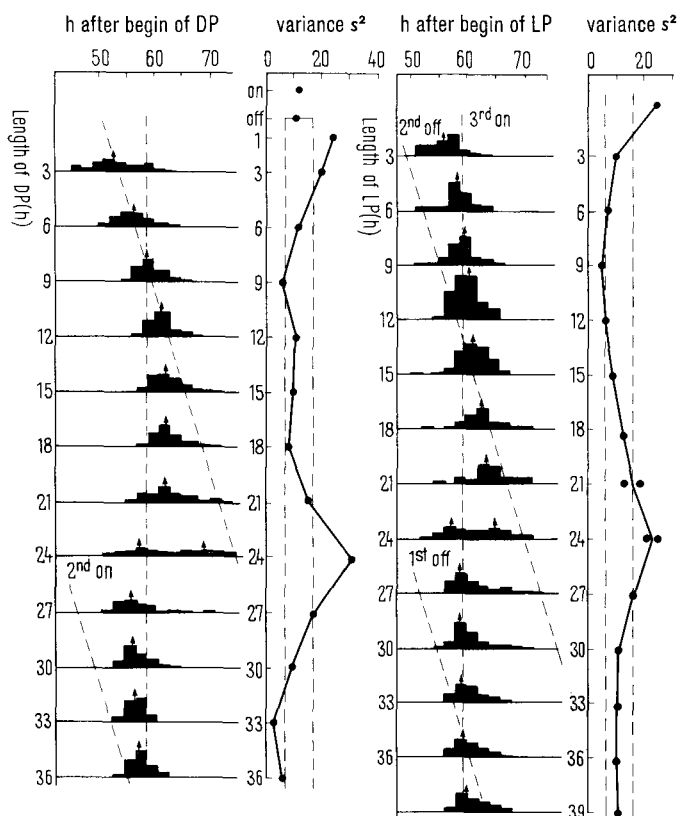


Fig. 4. Emergence rhythm between 45 and 75 h after start of DP's of various lengths (left) and LP of various lengths (right). Black bars = % of emerged flies. Arrows = position of the calculated median. Broken lines = position of the medians of single on- or off-emergence peaks, parallel to the transition. Also shown are the variances $s^2 = \sum (x - \bar{x})^2 / n - 1$ as a measure for the synchronization of the emergence distribution. All points outside of the vertical broken lines are significantly different at the 1% level from the variance of the off-emergence distribution. Also shown is the variance of emergence of a very short LP³. The broken vertical line in the left figure is the position of the 3rd off-maximum, the inclined one that of the 3rd on.

short day plant *Pharbitis nil*. The onset of light as well as the onset of darkness induce rhythmic sensitivities to red light. Only the on-rhythm shows in addition to this a rhythmic sensitivity to the length of the dark period, leading to a step-wise increase in flowering with variable dark period lengths. They conclude, therefore, that on- and off-rhythms are physiologically different. In our department investigations are under progress to characterize the on- and off-rhythms of *D. pseudoobscura* and to find out whether the two rhythms are qualitatively different⁵.

The validity of the on- and off-rhythm concept is further stressed by experiments on *Drosophila* emergence, in which more complicated programmes such as repeated cycles of pulses are given. Even in this case the experimental results are in fairly good agreement with the predictions of superimposed on- and off-rhythms⁶. Another point which is under investigation and will be published elsewhere should be mentioned: short light periods (2.5 min) still contain the information of both the on- and off-signal⁷. An important paper by WEVER⁸ will be discussed in respect to this work and to similar experiments on the petal movement of *Kalanchoe* in another place.⁹

Zusammenfassung. Bei *Drosophila pseudoobscura* synchronisiert ein einmaliger Übergang von Dauerdunkel zu Dauerlicht und von Dauerlicht zu Dauerdunkel das Schlüpfen der Fliegen aus dem Puparium (Figur 2). Die Ergebnisse von Licht-Puls- und Dunkel-Puls-Experimenten lassen sich als Überlagerung solcher einfachen Stufeneffekte erklären.

W. ENGELMANN

Botanisches Institut der Universität, 74 Tübingen (Germany), March 28, 1966.

⁵ M. K. CHANDRASHEKAR, unpublished.

⁶ D. HENGST, unpublished.

⁷ H. W. HONEGGER, unpublished.

⁸ R. WEVER, Z. vergl. Physiol. 57, 1 (1965).

⁹ This work was supported by the Deutsche Forschungsgemeinschaft.

Electrolyte Content of the Cerebral Cortex in Developing Rats after Prenatal X-Radiation¹

Prenatal X-radiation alters the functional development of the central nervous system (CNS) as shown by enhanced appearance of the maximal seizure pattern², by abnormal electrocorticograms and encephalograms^{3,4}, increased susceptibility to spontaneous⁵ and audiogenic⁶ seizures. These effects of prenatal X-radiation may reflect anatomical, neurochemical, and physiological changes during CNS development.

In view of the role of the ionic environment in the development of CNS activity, the present study was designed to investigate electrolyte content in the cerebral cortex of rats irradiated in utero.

At 14 days of gestation, pregnant rats were exposed to a single dose of 100 r whole body X-radiation at a rate of 19 r/min. A 180 kV 15 mA X-ray machine was used. The filters were 0.5 mm Cu and 1.0 mm Al. The animals were placed in individual open-ended lucite cylinders rotated on a movable table 59 cm from the X-ray source. A Victoreen R-meter was used for dose calibrations. As controls, pregnant rats sham-irradiated at 14 days of gestation were used.

Litters of 6 rats were used. 2 rats from each litter were sacrificed by decapitation at 9, 23, and 44 days after birth. Samples of cerebral cortex from 8 controls and 8 irradiated animals were used for determinations of Na, K, and Cl content. Cerebral cortex samples were dried at 105°C to constant weight, and water content was calculated from the difference in wet and dry weights. The dried tissue was ground, extracted in 1 N HNO₃ for 48 h at 56°C, and Na and K contents were determined with a Li internal standard flame photometer. Cl was measured by the electrometric titration method of COTLOVE et al.⁷. To determine significance of differences between control and irradiated rats, the *t* test for non-paired data was applied⁸.

Water content decreased with age in both controls and irradiated animals; differences were not observed be-

tween the 2 experimental groups at any age period studied (Figure).

In control animals, K progressively increased and Na and Cl contents progressively decreased with age. This is in agreement with other studies by VERNADAKIS and WOODBURY⁹. In irradiated animals, K content remained generally constant with age, except at 9 days where it was significantly higher than in controls. Na and Cl contents progressively decreased with age. At days 23 and 44 these ions were significantly lower in the irradiated than those in appropriate controls, whereas at 9 days significant differences were not observed.

The changes induced by prenatal X-radiation on electrolyte content cannot be attributed to water changes between control and irradiated animals, but rather reflect changes in cellular brain compartments. BRIZZEE and JACOBS¹⁰ have shown that the glial index (number of glia divided by number of neurons) increases with age. VERNADAKIS and WOODBURY¹¹ have reported that during

¹ This work was supported by contract AT(11-1)-34, Project 82, from the U.S. Atomic Energy Commission.

² J. J. CURRY, G. J. MALETTA, and A. VERNADAKIS, Physiologist Wash. 8, 145 (1965).

³ J. T. EAYRS, In *Regional Neurochemistry* (Ed., S. S. KETY and J. ELKES; Pergamon Press, New York 1961), p. 423.

⁴ M. BERRY, B. G. CLENDENNIN, and J. T. EAYRS, Electroenceph. clin. Neurophysiol. 75, 91 (1963).

⁵ M. R. SIKOV, J. S. MEYER, C. F. RESTA, and J. E. LOFSTROM, Radiat. Res. 12, 472 (1960).

⁶ J. WERBOFF, J. DEN BROEDER, J. HAVLENA, and M. R. SIKOV, Expl. Neurol. 4, 189 (1961).

⁷ E. H. COTLOVE, H. V. TRANHAM, and R. L. BOWMAN, J. Lab. clin. Med. 57, 461 (1958).

⁸ R. A. FISHER, *Statistical Methods for Research Workers* (Hafner, New York 1950).

⁹ A. VERNADAKIS and D. M. WOODBURY, Am. J. Physiol. 203, 748 (1962).

¹⁰ K. R. BRIZZEE and L. A. JACOBS, Growth 23, 337 (1959).

¹¹ A. VERNADAKIS and D. M. WOODBURY, Arch. Neurol. 12, 284 (1965).