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Photoperiodic modulation of insect circadian rhythms

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Circadian rhythms can be seen in a variety of physiological functions in insects. Light is a powerful zeitgeber not only synchronizing but also modulating the rhythm to adjust insect's temporal structure to seasonal changes in the environmental cycle. There are two general effects of the length of light phase within 24 hr light cycles on the circadian rhythms, i.e., the modulation of free-running period and the waveform. Since the photoperiodic modulation of the free-running period is induced even in the clock mutant flies, *per*^{S}, the free-running period is not fully determined genetically. In crickets, the ratio of activity (α) and rest phase (ρ) under the constant darkness (DD) is clearly dependent on the photoperiod under which they have been kept. When experienced the longer photoperiod it becomes smaller. The magnitude of change in α/ρ-ratio is dependent on the number of cycles they experienced. The neuronal activity of the optic lobe in DD shows the α/ρ-ratio changing with the preceding photoperiod. These data suggest that a single circadian pacemaker stores and maintains the photoperiodic information and that there is a system that accumulates the effects of single photoperiod to cause greater effects.

Key words: after-effects, circadian rhythm, circadian waveform, insect, photoperiodic modulation

INTRODUCTION

Most insects show daily rhythms in a variety of physiological functions such as locomotor activity, hormonal secretion and neural activity [9]. It is the general concept that the rhythm is generated by an endogenous mechanism called circadian system that consists of three major constituents, i.e. the circadian pacemaker or clock generating the 24 hr oscillation, the photoreceptor synchronizing the rhythm to the environmental light dark cycle, and the driven system that transforms the clock's temporal signal to various physiological functions [2]. Light is a powerful zeitgeber not only synchronizing but also modulating the rhythm to adjust the circadian rhythm to a seasonal change in environmental cycles [7]. The modulatory effects of light on the rhythm can be classified into the following two categories: i.e., modulation of free-running period, so-called after-effects, that persists for long period under constant darkness [6] and modulation of circadian waveform apparent in changes in duration of active phase [12]. One explanation for the photoperiodic modulation is that it is caused by a change in coupling state between the circadian oscillators constituting the circadian system. In this review, the mechanism and functional significance of the photoperiodic modulation are discussed.

PHOTOPERIODIC MODULATION OF FREE-RUNNING PERIODS

It has been reported for some insects that photoperiods affect the free-running period in the ensuing constant darkness (DD). The change in free-running period by the preceding environmental cycles is called after-effects. We raised wild type (*Canton-S*) flies of *Drosophila melanogaster* in various photoperiodic conditions from 4 h light and 20 h dark (LD4:20) to LD20:4 and measured the locomotor rhythms in DD. The free-running period of the flies changed dependent on the preceding photoperiodic conditions [13]. It was shorter when the photoperiod

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was 16 h or more than that after the experience of short photoperiodic conditions (Fig. 1). Similar after-effects were also observed in the clock mutant flies, *per*^{S}, which have a free-running period extremely shorter (19 h) than wild type flies. These data suggest that there is a common mechanism through which photoperiods cause the after-effects in wild type and *per*^{S} flies.

PHOTOPERIODIC MODULATION OF CIRCADIAN WAVEFORM

The circadian clock of insects often dramatically changes its waveform in response to the given light dark cycle. In the cricket, *Gryllus bimaculatus*, it has been shown that the duration of the subjective day phase becomes longer as the night length is increased during post-embryonic development [12]. Figure 2 exemplifies the waveform modulation by light cycles of LD20:4 and LD4:20. In LD20:4, the duration of subjective night measured as duration of the active phase (α) was much shorter compared with that of LD12:12. The shorter value continued for at least 20 days in the constant darkness. Further behavioral studies revealed that a similar modulation was induced by exposure to the light dark cycle as adults and that a minimal change was induced by a single exposure to the given cycle, but 10 cycles are required to cause a maximal change (M. Koga and K. Tomioka, in preparation).

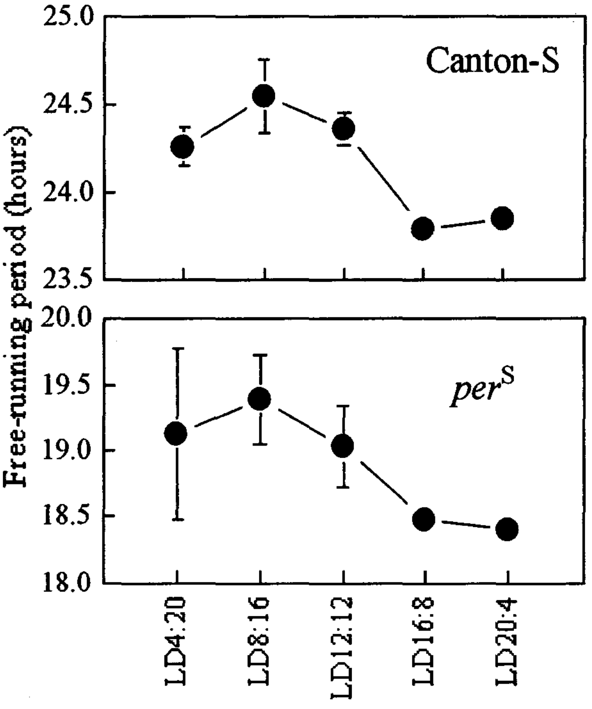

Fig.1 Free-running period in the fruit flies *Drosophila melanogaster* reared in various lighting conditions. Each point represents the mean of 8-26 animals. Vertical bars show SEM. In both wild-type (Canton-S) and *per*^{S} flies, free-running periods were shorter when exposed to photoperiod of 16 h or longer.

It has been suggested that the change in circadian waveform is caused by the change in coupling state between the component oscillators [8]. This idea has been supported also in crickets *Teleogryllus commodus* and fruit flies *Drosophila melanogaster* [3,15]. We have examined whether the photoperiodic modulation of the circadian waveform occurred at a single circadian oscillator. When the optic lobe was unilaterally removed just before the transfer to DD from LD12:12 or LD20:4, the α/ρ–ratio slightly changed from the values of animals with two optic lobes. The α/ρ–ratio differed significantly between the two groups, showing that the photoperiodic modulation of the waveform was maintained in an animal with a single optic lobe pacemaker. With electrophysiological experiments, we confirmed that the behavioral change reflected a change occurring at the circadian pacemaker level: the duration of subjective night, during which the neuronal activity of the optic lobe were highly active, became longer with the lengthening night phase of the light cycle in which the animal had been kept [11]. This fact also revealed that the effect of photoperiod was stored within the optic lobe even after isolated from the rest of the nervous system. It is thus likely that the optic lobe is the tissue in which the photoperiodic information is stored. However, we should await to conclude that a single circadian pacemaker itself is responsible for the photoperiodic modulation until more data to be accumulated, since the pacemaker itself is apparently composed of many oscillator cells [14] and the photoperiodic modulation might derive from the change in coupling sate among the oscillator cells.

Recent molecular studies of circadian clocks show that the oscillatory mechanism consists of rhythmical expression of several so-called clock genes, such as

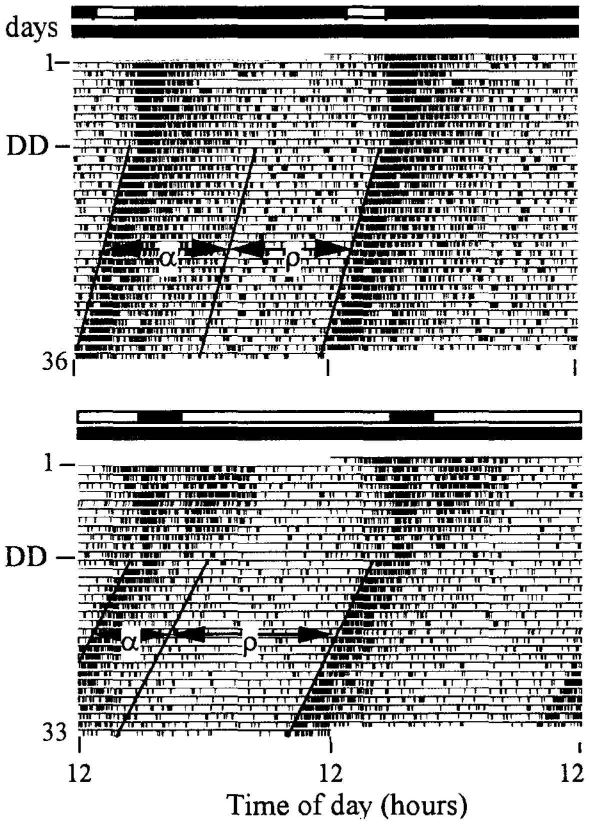

Fig.2 Photoperiodic modulation of circadian waveform in the cricket *Gryllus bimaculatus*. The crickets were exposed to either LD4:20 or LD20:4 for the first 10 days, then transferred to constant darkness (DD). The activity phase (α) became significantly shorter but the rest phase (ρ) became longer when exposed to short night conditions (LD20:4).

period, *timeless*, *clock* and *cycle* [1,16]. The photoperiodic modulation of the circadian waveform should be associated with the change of time-course of expression of these clock genes. Interestingly, it has been shown that in *Drosophila* at least the expression of *period* changes in response to photoperiod [4]. Future critical studies will reveal at molecular and cellular levels how the photoperiodic modulations of the waveform and free-running period are induced.

FUNCTIONAL SIGNIFICANCE OF THE PHOTOPERIODIC MODULATION

The photoperiodic modulation in circadian parameters may be important for the entrainment to seasonally changing photoperiodic conditions. Changes in the circadian waveform may adjust the physiological events such as locomotor activity to occur at an appropriate time of day. The change in free-running period may result in a change of the phase at which the light falls to cause the phase shifts of the rhythm. In addition, the photoperiod dependent change in phase shiftability to light [7] may also contribute for the seasonal adjustment for the entrainability.

The photoperiodic modulation in the circadian rhythm is thought to be a part of the photoperiodic time measurement in avian pineal organ and in the mammalian suprachiasmatic nuclei for seasonal adaptation [5,10]. It is still unclear, however, whether photoperiodic modulation of the circadian waveform is involved in the photoperiodic time measurement in insects. There are many cricket species that show clear photoperiodism in their developmental regulation or morphogenesis. It is quite challenging to examine the role of photoperiodic modulation of the waveform of the circadian pacemaker with those photoperiodic cricket species.

REFERENCES

1. Dunlap, J.C. (1999) Molecular bases for circadian biological clocks. *Cell* 96, 271-290.

2. Eskin, A.(1979) Identification and physiology of circadian pacemakers: Introduction. *Fed. Proc.* 38, 2570-2572.

3. Helfrich-Forster, C.(2000) Differential control of morning and evening components in the activity rhythm of *Drosophila melanogaster*--sex-specific differences suggest a different quality of activity. *J. Biol. Rhythms* 15, 135-154.

4. Majercak, J., D. Sidote, P.E. Hardin and I. Edery (1999) How a circadian clock adapts to seasonal decreases in temperature and day length. *Neuron*, 24, 219-230.

5. Mrugata, M., P. Zlomanczuk, A. Jagota and W.J. Schwartz(2000) Rhythmic multiunit neural activity in slices of hamster suprachiasmatic nucleus reflect prior photoperiod. *Amer. J. Physiol.*278, R987-R994.

6. Page, T.L., C. Mans and G. Griffeth (2001) History dependence of circadian pacemaker period in the

cockroach. *J. Insect Physiol.* 47, 1085-1093.

7. Pittendrigh, C.S.(1981) Circadian systems: Entrainment. In J. Aschoff (Ed.), Handbook of Behavioral Neurobiology, vol. 4 Biological Rhythms. Plenum Press, New York and London, pp. 95-124.

8. Pittendrigh, C.S. and S. Daan (1976) A functional analysis of a circadian pacemaker in nocturnal rodents. V. Pacemaker structure: a clock for all seasons. *J. Comp. Physiol.* 106, 333-355.

9. Saunders, D.S. (1982) Insect Clocks, 2nd edn. Pergamon Press, Oxford.

10. Sumova, A., Z.Travinickova, R. Peters, W.J. Schwartz and H. Illunerova (1995) The rat suprachiasmatic nucleus is a clock for all seasons. *Proc. Natl. Acad. Sci. U.S.A.* 92, 2319-2322.

11. Tomioka, K. and Y. Chiba (1989) Light cycle during post-embryonic development affects adult circadian parameters of the cricket (*Gryllus bimaculatus*) optic lobe pacemaker. *J. Insect Physiol.* 35, 273-276.

12. Tomioka, K. and Y. Chiba (1989) Photoperiod during post-embryonic development affects some parameters of adult circadian rhythm in the cricket, *Gryllus bimaculatus. Zool. Sci.* 6, 565-571.

13. Tomioka K., K. Uwozumi and N. Matsumoto (1997) Light cycles given during development affect freerunning period of circadian locomotor rhythm of *period* mutant in *Drosophila melanogaster. J. Insect Physiol.*43,297-305.

14. Welsh, D.K., D.E. Logothetis, M. Meister, and S.M. Reppert (1995) Individual neurons dissociated from rat suprachiasmatic nucleus express independently phased circadian firing rhythms. *Neuron* 14, 697-706.

15. Wiedenmann, G. and W. Loher (1984) Circadian control of singing in crickets: two different pacemakers for early-evening and before-dawn activity. *J. Insect Physiol.* 30, 145-151.

16. Williams, J.A. and A. Sehgal (2001) Molecular components of the circadian system in *Drosophila. Ann.Rev. Physiol.* 63, 729-755.