



History Dependence of Insect Circadian Rhythms 【Review article】

經歷依變的昆蟲日週律動【綜合論述】

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Received: 2005/11/08 Accepted: 2006/03/13 Available online: 2006/06/01

Abstract

Circadian rhythms are endogenous, ~24-h oscillations governing various behavioral and physiological functions. The rhythm synchronizes to and is profoundly affected by light cycles. In free-running conditions under constant darkness, some parameters of the rhythm such as the free-running period and waveform show long-lasting changes caused by lighting conditions given before transfer to constant darkness. The change in the free-running period is called the after-effects and is thought to contribute to stable entrainment to the light cycle. Photoperiodic modulation of the waveform also contributes to appropriate synchronization to seasonally changing photoperiods. Considerable similarity of the waveform modulation to photoperiodic responses implies its involvement in the photoperiodic time measurement mechanism. The mechanism for these history-dependent changes has yet to be elucidated.

摘要

日週律動是由內在大約24小時震盪器，來掌握著不同行為及生理功能。它的規律性是受外界光週期的影響，而且與之同步。在全暗自由律動的條件下，有些規律性的參數，例如自由律動週期與波動形式，顯示在進入全暗環境之前的光週期有長效性的作用，對自由律動週期的影響，稱為後續效應，被認為是對光週期的穩定導引作用。而光週期對波動形式的調控，也是對季節性改變的光週期，做出適當的同步現象。波動形式的調控，呈現相當高的相似性，隱含著對光週期時間量測機制的參與。這類經歷依變的機制仍待研究。

Key words: circadian rhythm, photoperiod, after-effects, circadian waveform, history dependence

關鍵詞: 日週律動、光週期、後續效應、日週波動形式、經歷依變性

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History Dependence of Insect Circadian Rhythms

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ABSTRACT

Circadian rhythms are endogenous, ~24-h oscillations governing various behavioral and physiological functions. The rhythm synchronizes to and is profoundly affected by light cycles. In free-running conditions under constant darkness, some parameters of the rhythm such as the free-running period and waveform show long-lasting changes caused by lighting conditions given before transfer to constant darkness. The change in the free-running period is called the after-effects and is thought to contribute to stable entrainment to the light cycle. Photoperiodic modulation of the waveform also contributes to appropriate synchronization to seasonally changing photoperiods. Considerable similarity of the waveform modulation to photoperiodic responses implies its involvement in the photoperiodic time measurement mechanism. The mechanism for these history-dependent changes has yet to be elucidated.

Key words: circadian rhythm, photoperiod, after-effects, circadian waveform, history dependence

Introduction

Circadian rhythms exhibit ~24-h rhythmicity that is driven by an endogenous mechanism called the circadian system and which manifests in various behavioral and physiological functions of insects, including locomotor activity and sensitivity of compound eyes (Saunders, 2002). The circadian system consists of three major components, a circadian clock that generates the rhythmicity, photoreceptors necessary for photic entrainment, and driven systems which transduce the

temporal information from the clock to various overt physiological rhythms (Eskin, 1979). The most important role of the circadian clock is to set the physiological events of insects to occur at an appropriate time of day. Synchronization to the environmental cycle is a prerequisite for this role. The most powerful environmental synchronizer (zeitgeber) is the light-dark cycle. The light resets, in a phase dependent manner, the phase of the clock, the natural period of which slightly differs from 24 h. It usually phase-delays the

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clock when given during the early subjective night and advances it during the late subjective night, while it has almost no effect when given during the subjective day (Johnson, 1990).

The daily light cycle is not constant but changes with seasons, especially in the temperate zone. Insects show activity rhythms well adapted to seasonally changing daily cycles. For example, some mosquitoes show bimodal activity with peaks before sunset and after sunrise, changing their phase relationship to the light-dark cycle dependent on the photoperiod, but the rhythm basically remains a crepuscular type (Chiba and Tomioka, 1992). To accomplish this kind of fine-tuning of the waveform to a seasonally changing photoperiod, the circadian rhythm is known to change its properties. Studies have been performed using various lighting conditions to investigate the underlying mechanism in vertebrate species (Aschoff, 1981), revealing that preceding lighting conditions have profound effects on the free-running period in the ensuing constant conditions. Such history-dependent changes in the free-running period are referred to as the after-effects. Similarly, the circadian waveform, such as the durations of the subjective night and day, is also affected by the lighting regimen (Pittendrigh, 1974). Photoperiodic modulation of the circadian waveform is now under investigation at the molecular level by examining temporal expression profiles of so-called clock genes under different photoperiodic conditions (Johnston, 2005). However, only physiological explanations are available for the after-effects (Page *et al.*, 2001).

In insects, there are plenty of studies available on the effects of photoperiod on physiology such as nymphal development, diapause, or seasonal form formation (Beck, 1980; Saunders, 2002), while knowledge of photoperiodic effects on the circadian rhythm is rather limited. In

this short paper, we review the photoperiodic modulation of insect circadian rhythms and its mechanisms and consider its functional roles.

After-effects

The free-running periods of circadian rhythms often show history-dependent changes. Long-lasting changes in the period of free-running rhythms can often be observed after transfer to constant darkness (DD) from pretreatment with specific lighting conditions such as constant light (LL), or light/dark (LD) with various periods. These long-lasting changes in the free-running period are termed after-effects. In the cricket, *Teleogryllus commodus*, exposure to continuous red light resulted in lengthening of the free-running period which gradually shortened during the next 3 weeks in DD (Sokolove, 1975). After-effects were also observed when insects were exposed to non-24-h cycles. The cockroach, *Leucophaea maderae*, showed significantly longer free-running periods when exposed to LD 8:18 than those exposed to LD 8:14. Induction of the after-effects required more than 1 week of entrainment. After induction by 2 weeks of entrainment, the after-effects persisted in DD for over 40 days, decaying very slowly (Page *et al.*, 2001).

The after-effects were observed even after exposure to 24-h LD cycles but with different photoperiods. In the cricket, *Gryllus bimaculatus*, adults exposed to either LD 16:8 or LD 20:4 for 10 cycles showed a significantly shorter free-running period than those kept in LD 12:12 or LD 4:20 (Koga *et al.*, 2005). Another example of the after-effects of photoperiods was reported for the blow fly, *Calliphora vicina* (Kenny and Saunders, 1991). When newly emerged flies were entrained to LD 4:20 for several days before transfer to DD, the flies initially showed a short free-running period which then abruptly lengthened to longer than 24 h.

A change in the free-running period can often be observed after a single perturbation of free-running rhythms in constant darkness by a light pulse. Single light pulses cause phase shifts in a phase-dependent manner: generally phase delays are induced during the early subjective night and phase advances during the late subjective night. No clear correlation was seen between the direction of phase shifts and the change in the free-running period in *G. bimaculatus* (Okada *et al.*, 1991).

Temperature induces no after-effects

Temperature is a strong zeitgeber for synchronizing the rhythm, and non-24-h temperature cycles also entrain the circadian rhythm. Page *et al.* (2001) examined the effects of entrainment of temperature cycles with an amplitude of 10°C (Warm at 30°C and Cool at 20°C) in the cockroach, *L. maderae*. The cockroaches were entrained to either a 23- or a 25-h cycle for 2 weeks and then transferred to either a 22.5- or a 26-h cycle, respectively, for additional 2 weeks. In the ensuing constant temperature, there were no differences in the free-running periods between the T22.5 and T26 animals. The fact indicates that entrainment to a temperature cycle does not cause after-effects. In addition, the temperature pulse did shift the phase but had no effect on after-effects; in other words, it induced no apparent change in the free-running period. The authors thus suggested that light may be unique in its ability to induce after-effects of entrainment.

Waveform modulation

Environmental lighting conditions affect not only the free-running period but also the circadian waveform such as the duration of the subjective night and day. It was shown in the cricket, *G. bimaculatus*, that the ratio of duration of the active phase and that of the resting phase (α/ρ -ratio) in the free-running

condition was highly dependent on photoperiods of 24-h LD in which they had been raised (Tomioka and Chiba, 1989a; Koga *et al.*, 2005). The duration of the active phase was longer when exposed to LDs with shorter photoperiods. Figure 1 exemplifies the modulatory effects of photoperiod on the α/ρ -ratio. The average α/ρ -ratios were 0.63 and 1.29 when crickets experienced 10 cycles of LD 20:4 and LD 4:20, respectively. The magnitude of the change was dependent on the number of cycles to which the cricket was exposed. Even a single exposure to LD 20:4 of crickets that had been raised in LD 12:12 induced a slight but significant reduction in the α/ρ -ratio. The reduction reached a maximum when exposed to 10 cycles. The change occurred at least partly at the circadian pacemaker, since the waveform of the electrical activity rhythm in the optic lobe showed changes dependent on the photoperiod (Tomioka and Chiba, 1989b; Koga *et al.*, 2005). However, it was also shown that the modulation and maintenance of the waveform required mutual interaction between the 2 optic lobe circadian pacemakers (Koga *et al.*, 2005).

The waveform change does not exactly parallel the change in the free-running period. The free-running period changed at nearly a maximal degree even after a single exposure to LD 20:4, and no further change was observed when the cycles of exposure were increased (Koga *et al.*, 2005). The instantaneous change in the period is not surprising, given that single light pulse treatment often induces both phase shifts and changes in the free-running period of rhythms in constant darkness (Okada *et al.*, 1991). This fact suggests that modulation of the waveform occurs through a pathway different from that for the change in the free-running period.

Effects of temperature entrainment on the circadian waveform have not been studied yet. Since it is known that

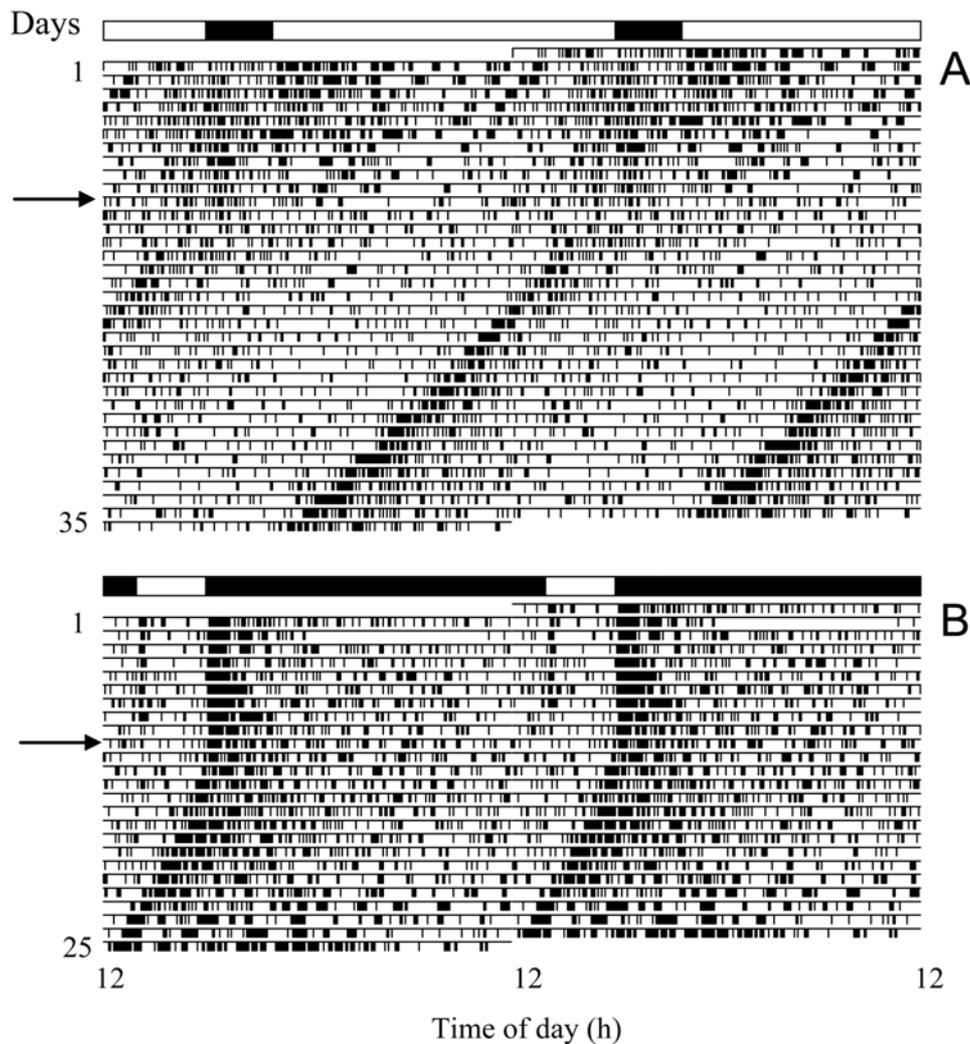


Fig. 1. Photoperiodic modulation of circadian locomotor rhythms in adult male crickets, *Gryllus bimaculatus*. The crickets that had been kept in LD 12:12 were exposed to either LD 20:4 (A) or LD 4:20 (B) for 10 cycles, then transferred to DD. Both the free-running period and the active phase were shorter in LD 20:4 crickets. White and black bars indicate light and dark, respectively. Arrows indicate the day of transfer to DD.

temperature substantially modulates the circadian locomotor rhythm (Brady, 1981), temperature might have some effect on the waveform.

Effects of photoperiod during post-embryonic development

In the cockroach, *L. maderae*, lighting

conditions during post-embryonic development were found to have major effects on the free-running period of adults. Animals raised in LD 11:11 or LD 13:13 exhibited either shorter or longer free-running periods than those raised in LD 12:12 (Page and Block, 1980). The effects of light were reported to be almost

permanent in this case and greater than those experienced as an adult (Page *et al.*, 2001). Thus light during development probably causes some permanent change in the circadian system in addition to ordinary after-effects.

Similarly, a photoperiod of 24-h LD during larval development also affected the free-running period in the fruit fly, *Drosophila melanogaster*. The flies showed clear free-running rhythms even when they were reared in LL or DD, suggesting that the circadian clock can be assembled during development with no external cyclical photic information. The free-running period was significantly longer in flies reared in LD 12:12 or LD 8:16 and shorter in those reared in LL, LD 20:4, or LD 16:8 than those reared in DD (Tomioka *et al.*, 1997). These facts suggest that the photoperiod influences the developing circadian clock by altering its period.

The history-dependent changes in circadian rhythms are often associated with a change in the shape of the phase response curve (PRC). When PRCs were measured for 6-h light pulses for cockroaches (*L. maderae*) raised in LD 11:11 (T22), LD 12:12 (T24), and LD 13:13 (T26), the delay portion of the PRC was significantly reduced in T22 animals compared to T24 animals, while the advance portion was reduced in T26 animals (Page and Barrett, 1989). The relationship between the free-running period and the shape of the PRC was discussed in detail by Pittendrigh and Daan (1976). Based on their data for nocturnal rodents, they pointed out that animals with shorter free-running periods typically exhibited larger delay and smaller advance regions of the PRC than did animals with longer free-running periods. They hypothesized that this relationship between the free-running period and the shape of the PRC was functionally adaptive for establishing a stable phase relationship between activity

rhythms and the light cycle. However, this hypothesis is not applicable to the case of the cockroach since animals with a shorter free-running period (T22) showed a reduction in the delay region while animals with a longer free-running period (T26) exhibited a reduction in the advance region (Page and Barrett, 1989). The functional significance of the changes still remains to be explained.

Mechanism of after-effects and changes in the waveform

The mechanism inducing after-effects has yet to be elucidated. One explanation based on results for mammalian systems is that entrainment sets the phase relationships between weakly coupled oscillators and that the period of the system is determined by the resultant phase relationship (Pittendrigh and Daan, 1976; Daan and Berde, 1978). However, Page *et al.* (2001) stressed that, especially in the cockroach, *L. maderae*, this explanation seemed unlikely. This statement was based on the fact that temperature pulses that induced large phase shifts had no effects on the free-running period. They also suggested that the after-effects were induced by a specific mechanism associated with the photic entrainment, because no apparent after-effects were observed following entrainment to temperature cycles. They speculated that after-effects were a consequence of a stable change in a parameter of the circadian system which was caused by repetitive exposure to light cycles (Page *et al.*, 2001).

The effect of light on the circadian system has been explained at the molecular level in *Drosophila* (Stanewsky, 2002; Hardin, 2004). The oscillatory system is composed of two interlocked autoregulatory feedback loops (Fig. 2). One includes a feedback loop for *period* (*per*) and *timeless* (*tim*): transcription of the two genes is stimulated by the transcription factors, CLOCK (CLK) and

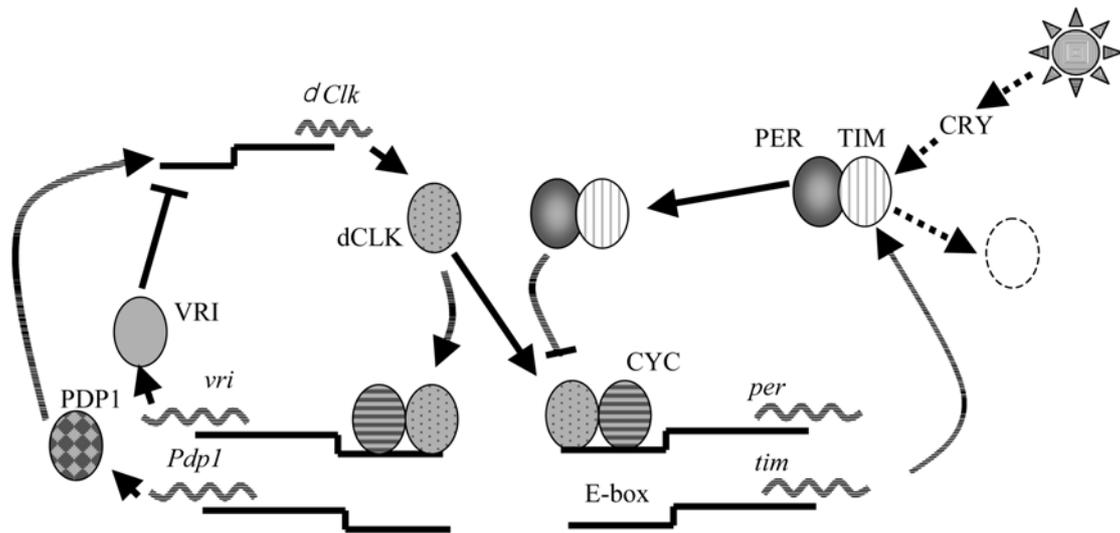


Fig. 2. Schematic diagram of *Drosophila* clockwork. dCLK/CYC heterodimers bind to E-box of *per* and *tim* to activate their transcription late in the day, and their product proteins, PER and TIM, accumulate during the night. PER/TIM heterodimers enter the nucleus late in the night to suppress their own transcription through inactivation of dCLK/CYC. Decreased levels of PER and TIM allow dCLK/CYC to activate transcription of *per* and *tim* to begin another cycle of the loop. dCLK/CYC heterodimers also activate *vri* and *Pdp1*. VRI immediately accumulates in the nucleus and inhibits *dClk* transcription. Subsequently, PDP1 accumulates in the nucleus and promotes *dClk* transcription. Accumulated dCLK binds to CYC, and dCLK/CYC heterodimers initiate another cycle of *vri* and *Pdp1* transcription. Light input occurs through CRY, which resets the clock by promoting TIM degradation. For explanations see text.

CYCLE (CYC), and activated during the late day to early night. Translated proteins, PER and TIM, increase during the night and form heterodimers which are translocated into the nucleus and inhibit their own transcription through inactivation of CLK and CYC. This inhibition results in a decrease of the proteins during the day that results in activation of transcription of *per* and *tim*, starting the next cycle. CLK is regulated by another loop including *vri* and *Pdp1* which increase during the day. It has been shown that light resets the loop by decreasing TIM protein levels through CRYPTOCHROME, a photoreceptive flavoprotein. However, this light-dependent degradation of TIM occurs only acutely. There is thus no explanation for the

long-lasting after-effects at the molecular level.

There have been some reports demonstrating that the expression patterns of some clock genes change with photoperiod. In *Drosophila*, short days induced earlier *per* mRNA accumulation via increased alternative splicing at the 3' end of the *per* gene's transcript (Majercak *et al.*, 1999). In the head of the linden bug, *Pyrrhocoris apterus*, there is only a weak diurnal rhythm in both *per* and *Clock (Clk)* mRNA under diapause-preventing long days and no rhythm under diapause-promoting short days. The pattern persisted in the first day of DD and LL, indicating that these were not direct responses to light. The level of *per* mRNA was about tenfold and that of

Clk mRNA about twofold higher under short days than under long days (Syrova *et al.*, 2003). In the flesh fly, *Sarcophaga crassipalpis*, photoperiod also influenced the expression patterns of *per* and *tim* mRNA (Goto and Denlinger, 2002). The peak of *per* mRNA expression shifted in association with onset of the scotophase, while *tim* mRNA expression showed less-pronounced shifts. The amplitude of *tim* mRNA was severely dampened during long days, but no apparent change was observed in that of *per* mRNA. At present, a common explanation of photoperiodic regulation of the clock genes for these species is not available, but the photoperiod-dependent changes in gene expression patterns might play some role in determining photoperiodic responses such as circadian waveform modulation and diapause.

Photoperiodic modulation of clock gene expression has also been reported for mammalian systems. The waveforms of the photoinducible genes, *Per1* and *Per2*, together with their protein products, are dependent on photoperiod (Nuesslein-Hildesheim *et al.*, 2000; Sumova *et al.*, 2003), and the waveform persists in DD. Two alternative models have been postulated for an explanation. Both assume two oscillatory components tracking dawn and dusk, respectively, to show that the gene expression profile is dependent upon the photoperiod (Fig. 3A). One model hypothesizes that distinct groups of core clock genes are associated with either morning or evening phases of the daily light cycle (Daan *et al.*, 2001). The other suggests that different neuronal populations track dawn and dusk (Johnston, 2005). Recent physiological and molecular data support the latter (Jagota *et al.*, 2000; Hazlerigg *et al.*, 2005). Many insects also show bimodal rhythmicity with peaks at dawn and dusk. In *Drosophila*, the two peaks were recently revealed to be controlled by different sets of clock neurons (Grima *et al.*, 2004; Stoleru *et al.*,

2004). These facts prompted us to consider the above two models in future studies.

Another possible explanation is that the photoperiod-dependent changes in clock gene expression might occur within a single clock (Fig. 3B). A single clock tissue is also composed of many clock neurons like the mammalian suprachiasmatic nucleus (SCN). Gene expressions in constituent cells in a single SCN are not in phase but are dispersed within a considerable range, and the gross pattern of the tissue is a sum of the cells (Yamaguchi *et al.*, 2003; Ohta *et al.*, 2005). Our results revealed that photoperiodic modulation can occur and be maintained in a single optic lobe in the cricket, *G. bimaculatus* (Koga *et al.*, 2005). The facts are consistent with this explanation. However, it is still unknown whether there is any relationship between the photoperiodic modulation of gene expression and after-effects of the free-running period. This issue should be addressed in future studies.

Significance of history dependency

A possible functional significance of after-effects may be related to the stability of the entrainment to environmental light cycles. There are some factors that may affect the entrainment of the rhythm. One is fluctuations in the environmental entraining signals: even during the daytime the light intensity changes with weather. The other is day-to-day spontaneous variations in the free-running period. Page *et al.* (2001) hypothesized that in the face of these factors, the accuracy of entrainment is substantially enhanced when the daily light pulse not only corrects the phase, but also adjusts the angular velocity of the circadian system.

The history-dependent modulation of the circadian waveform may have several functional roles. Changes in the circadian waveform in response to photoperiod seem to play an important role in tuning

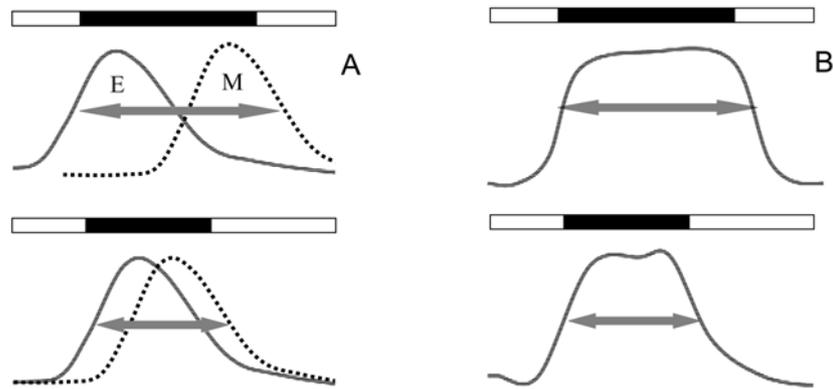


Fig. 3. Two hypothetical models of the photoperiodic modulation of circadian waveforms. (A) The evening (E) and morning (M) oscillations track dusk and dawn, respectively, to show a photoperiodic modulation in clock gene expression. (B) A single oscillation changes its waveform. See text for details. White and black bars represent light and dark, respectively. Gray arrows indicate the duration of gross subjective night.

an insect's behavior to seasonally changing day length. In the case of the nocturnal cricket, *G. bimaculatus*, changing the subjective night length in response to environmental light cycles not only fits its activity during the night phase but also allows it to accurately anticipate daily changes in environmental lighting condition even in occasional dark environments such as in a burrow or on cloudy days (Mrugata *et al.*, 2000).

Another possible role of the photoperiodic modulation of the circadian waveform may be a part of the photoperiodic time measurement mechanism. Involvement of the circadian system in photoperiodic time measurement has been hypothesized for many years. Most hypothetical models, including the external and internal coincidence models, are only concerned with the phase of the circadian clock but not with the waveform (Saunders, 2002). Given that photoperiodic modulation of the circadian rhythm is thought to be a part of the photoperiodic time measurement in the avian pineal gland and in mammalian SCN for seasonal adaptation (Sumova *et al.*, 1995;

Brandstatter *et al.*, 2000; Mrugata *et al.*, 2000), the possible involvement of waveform modulation in insect photoperiodic time measurement is worth testing in future studies.

Acknowledgments

This work was supported in part by grants from the Japanese Ministry of Education, Science, Technology, Sports and Culture, and the Japan Society for Promotion of Science, and by an Excellent Research Project Grant (ERPG) of Okayama University.

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Received: November 8, 2005

Accepted: March 13, 2006

經歷依變的昆蟲日週律動

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摘 要

日週律動是由內在大約 24 小時震盪器，來掌握著不同行爲及生理功能。它的規律性是受外界光週期的影響，而且與之同步。在全暗自由律動的條件下，有些規律性的參數，例如自由律動週期與波動形式，顯示在進入全暗環境之前的光週期有長效性的作用，對自由律動週期的影響，稱爲後續效應，被認爲是對光週期的穩定導引作用。而光週期對波動形式的調控，也是對季節性改變的光週期，做出適當的同步現象。波動形式的調控，呈現相當高的相似性，隱含著對光週期時間量測機制的參與。這類經歷依變的機制仍待研究。

關鍵詞：日週律動、光週期、後續效應、日週波動形式、經歷依變性。