assimilated was derived from the atmosphere.

The results of the balance data agree with these findings. The net absorption of lead was 25 μg/day. Mean urinary excretion of lead was 38 μg/day and loss of lead from hair, nails, and sweat was approximately 4 μg/day. Thus, total lead output exceeded dietary intake by 17 μg/day, which presumably came from the atmosphere. This value is in general agreement with that derived from the analysis of the isotopic blood data. This is also consistent with a value of about 16 μg/day calculated from the measured indoor concentrations of aerosol lead (about 2 $\mu g/m^3$) and reported values for absorption rates of inhaled lead (*7*). The subject smoked eight cigarettes per day of a brand which contained 0.9 μg per cigarette, about one-fourth the amount in the average American brand. From previous reports (*8*) we estimate that this subject absorbed about 1 μg/day from tobacco; the remainder of the absorbed aerosol component is presumed to come from the exhaust of leaded gasoline (*9*).

When the subject ingested the low-lead diet without supplemental lead, the absorption rate of dietary lead did not change. The lead excreted daily in the urine and the blood lead concentration each decreased in proportion to the change in the total amount of lead assimilated (Fig. 2), and the ratio (λ_{10}) of lead excreted daily in the urine to blood lead remained constant. When the subject was fed an uncontrolled hospital diet and smoked cigarettes at will (days 160 to 220), the lead concentration in the blood, urine, and feces increased to approximately the values before the study (Fig. 2). Thus, over this small range in exposure, no homeostatic mechanisms for maintaining lead concentrations in the blood were seen.

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References and Notes

1. R. Kehoe, *Roy. Inst. Pub. Health Hyg. J.* **24**, 1 (1961).
2. J. Hursh and T. Mercer, *J. Appl. Physiol.* **28**, 268 (1970).
3. M. Rabinowitz and G. Wetherill, *Environ. Sci. Technol.* **6**, 705 (1972).
4. J. Kopple and J. Coburn, *Medicine*, in press.
5. D. Barltrop and A. Smith, *Experientia* **27**, 92 (1971).
6. H. Schroeder and I. Tipton, *Arch. Environ. Health* **17**, 965 (1968).
7. K. Nozaki, *Ind. Health* **4**, 118 (1966).
8. D. Szadkowski, H. Schultze, K. Schaller, G. Lehnert, *Arch. Hyg. Bakteriol.* **153**, 1 (1969).
9. T. Chow and M. Johnstone, *Science* **147**, 502 (1965).
10. We thank D. Mulcare, R. Adachi, H. Dennin, J. Lee, and the nursing staff of the metabolic unit of Wadsworth Hospital Center for technical assistance; and the volunteer for his efforts and cooperation. Supported in part by NSF grant GI-38339. J.D.K. is a clinical investigator for the Veterans Administration.

12 June 1973

Temperature Sensitive Programming of the Silkmoth Flight Clock: A Mechanism for Adapting to the Seasons

Abstract. *When males of the silkmoth* Antheraea pernyi *were exposed to 12°C during adult development and then tested for flight activity at 25°C, the time of the onset of the activity was advanced to the early part of the night. This change in the time of activity was stable and persisted through the life of the moth. Females showed a corresponding shift in the time of sex pheromone release when they were treated in the same fashion.*

The behavior of the wild silkmoths is a striking example of temporal coordination between the sexes (*1*). These insects have developed an elaborate system of chemical communication which brings the partners together from distances of over a mile. During a specific portion of the day or of the night the female assumes a "calling" posture and releases pheromone. This behavior coincides with the time of male flight activity (*2*), and the coincidence of female pheromone release with male flight activity increases the probability that a male will encounter the odor plume from a female and that attraction and copulation will occur. We here report that the time of flight activity is not rigidly programmed, but it varies in a way that is related to the temperature of the environment during the development of the moth. This temperature sensitivity presumably allows the species to adjust its activity to anticipate seasonal fluctuations in daily temperature patterns.

Chilled pupae of the oak silkmoth, *Antheraea pernyi*, were exposed to a photoperiod consisting of 16 hours light and 8 hours dark (LD 16 : 8) at 25°C to terminate diapause. When adult development began 3 to 4 days later, groups of animals were exposed for various times to a LD 16 : 8 cycle at 12°C. The remainder of development occurred at 25°C. Shortly before emergence the moths were placed in activity-monitoring devices (*3*) with a photoperiod of LD 16 : 8 at 25°C.

The environmental temperature during the development of adult moths had a marked effect on the subsequent time of flight of male moths. Male *A. pernyi* exposed to temperatures of 25°C throughout development had a single peak of intense flight activity (Fig. 1). Flight began an average of 5.3 hours after lights off and ended abruptly with lights on. Males that were exposed to temperatures of 12°C during development and which were subsequently tested at 25°C began flying 1.3 hours after lights off. Their activity was very dispersed and there was intermittent flight through most of the night. Flight often ceased prior to lights on. This shift in the onset of activity was relatively stable: through the 7- to 10-day life-span of the adult there was only a slight drift in the time of flight initiation.

In an attempt to define a stage in development which was important in the determination of the timing of flight activity, the 20 days of adult development were arbitrarily divided into three equal portions (*4*) and groups of *A. pernyi* were exposed to all combinations of temperatures of 25°C and 12°C during these three time periods. No single developmental period was solely responsible for the resetting of the clock (Table 1). None of these treatments resulted in as prominent a shift in the time of the initiation of flight activity as that observed when the moths were exposed to temperatures of 12°C throughout development.

When the moths were exposed to the lower temperature during two of the developmental periods, the responses were more pronounced. Exposure to 12°C during the last two-thirds of development was almost as effective as exposure to 12°C throughout development. The temperature experienced through day 7 of development was

Table 1. The effect of developmental temperature on the subsequent time of flight activity of male *Antheraea pernyi* moths.

Group	Moths (No.)	Temperature during development (°C)			Time of flight onset* (hours)	Change in time of onset† (hours)
		First third	Second third	Last third		
1	10	25	25	25	5.3 ± 1.1	
2	5	12	25	25	4.5 ± 0.9	− 0.8
3	9	25	12	25	3.4 ± 0.9	− 1.9
4	5	25	25	12	2.8 ± 0.6	− 2.5
5	9	12	12	25	2.6 ± 0.8	− 2.7
6	9	12	25	12	2.9 ± 0.9	− 2.4
7	8	25	12	12	1.9 ± 0.6	− 3.4
8	10	12	12	12	1.3 ± 0.6	− 4.0

* Data from second, third, and fourth days after emergence for each moth are included; measured as hours after lights off in a LD 16 : 8 photoperiod at 25°C (mean ± standard deviation). † Relative to 25°C controls.

of minimal consequence. The results of these temperature pulse experiments show that there is a broad developmental period during which the flight clock can be influenced by temperature. A short exposure to low temperatures has little impact, but prolonged exposure over a number of days results in a progressive advance in the time of flight activity.

The effect of developmental temperature on the phase of the flight rhythm is not due to transient perturbations caused by the temperature shift from 12° to 25°C. When *A. pernyi* males are subjected to a 6-hour shift in the photoperiod cycle, the new steady-state rhythm is characteristically attained within one cycle. One would similarly expect that transient effects of a temperature shift would likewise subside within one or two cycles. Moreover, in the 12°C group individuals were returned to 25°C at the beginning, middle, and end of the 16-hour photophase. The time of transfer (and, thus, of the temperature step) had no effect on the subsequent time of flight beyond a transient effect seen on the first day after the switch.

The response of *A. pernyi* males to constant darkness is variable, but, under these conditions, some individuals show a free-running rhythm of flight activity during their life-span (*5*). Thus, this behavior is controlled by an endogenous circadian clock. The effects of temperature on circadian rhythms are well documented (*6*). This is the first report that environmental temperature during development can alter the phase of a rhythm and that this change will continue long after the temperature stimulus is removed. The mechanism with which the change in phase occurs is unknown. One possible hypothesis is that the change in phase is an indirect result of a permanent alteration in the free-running period of the activity clock. There are a number of examples of temperature influencing the period of a free-running rhythm (*6*). However, in most cases low temperatures have a slight lengthening effect on the period (*6*). Under photoperiod conditions this lengthening would then produce a delay in the entrained rhythm (*7*)—exactly the opposite result from that reported here. It therefore appears more likely that the temperature acts directly either by changing the coupling between the circadian clock and flight behavior or by triggering flight activity at a different time in the circadian cycle.

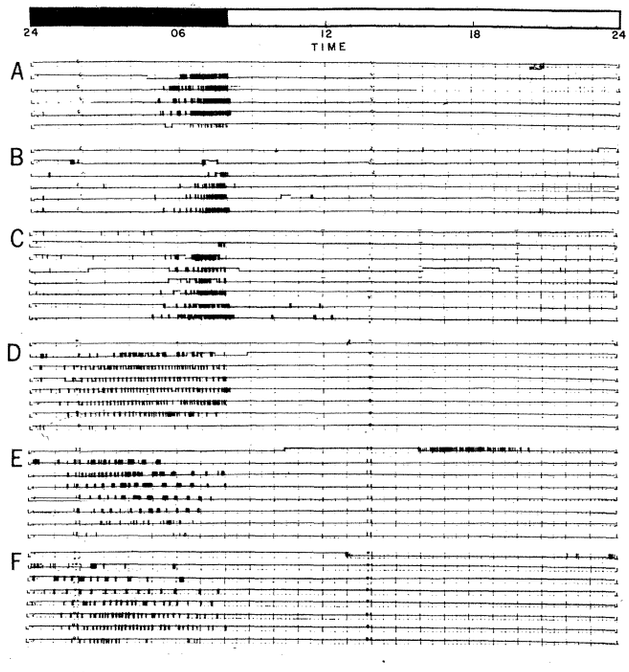

Fig. 1. Event recorder records of the activity of six male *Antheraea pernyi* moths which were exposed to a LD 16 : 8 photoperiod regimen at 25°C. Each moth lived for approximately 1 week after emergence. (A to C) Individuals that had experienced 25°C throughout development; (D to F) individuals that had experienced 12°C throughout development.

The dependence of flight time on developmental temperature apparently allows *A. pernyi* males to better adjust to seasonal changes in temperature. In another, large, wild silkmoth, *Hyalophora cecropia*, the metabolic energy necessary for flight increases by 50 percent when the ambient temperature is lowered from 25° to 18°C (*8*). Since the adult moth has a limited energy store, the lower temperature reduces the amount of time that the animal can spend in flight (*8*). These restrictions undoubtedly also hold for *A. pernyi*. Individuals that emerge in the late spring from overwintering pupae would, therefore, have a much reduced flight capacity if activity were delayed until 6 hours after dusk [the coldest part of the night (*9*)]. However, the cool spring temperatures during development would act to advance the onset of flight to shortly after dusk—a warmer and thus energetically more favorable part of the night. Males would then be allowed more flight time and, consequently, would have a greater chance of finding a female before the night temperatures became too restrictive.

This interpretation seems reasonable because low temperature treatments had no significant effect on the time of flight of the female. Females reared at 25°C began flight activity at 0.2 ± 0.2 hours after lights off (32 days of activity from eight moths), whereas females reared at 12°C started activity at 0.3 ± 0.2 hours after lights off (32 days of activity from eight moths). This result was expected because female *A. pernyi* normally fly during the warm time of dusk. However, the cool developmental temperatures did alter the time of pheromone release. Under continuous exposure to 25°C calling behavior begins approximately 6 hours after lights off (*2*, *10*). When females de-

veloped at 12°C, the onset of calling behavior was advanced to 1.9 ± 0.9 hours after lights off (21 days of data from six females) (*11*). Pheromone release in the female is shifted so that it coincides with the flight time of similarly treated males. Thus, temporal coordination between the sexes is preserved because both partners respond in a complementary fashion to changing environmental temperatures.

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References and Notes

1. E. O. Wilson and W. K. Bossert, *Recent Prog. Horm. Res.* **14**, 673 (1963).
2. J. W. Truman, L. P. Lounibos, L. M. Riddiford, in preparation.
3. The activity-monitoring device consisted of a screen cage (~ 12-cm cube) which was mounted on the end of a 30-cm strip of thin spring steel. The end of the strip which was opposite to the cage was fastened to a support. The other end was attached to a wire contact that extended beyond the cage. When the cage moved, due to the activity of the moth inside, this wire touched an external fixed contact and thus completed a circuit which included an event recorder pen. The apparatus was set so that it recorded the gross movements due to flight but not the smaller movements involved in preflight warm-up. The activity patterns obtained from various species of moths were consistent with the field observations of the mating times of these species [P. Rau and N. L. Rau, *Trans. Acad. Sci. St. Louis* **26**, 82 (1929)].
4. The periods of adult development were days 1 through 7, days 8 through 13, and days 14 through 20. These stages were defined by changes in the developing animal which could be seen through the pupal cuticle. Day 1 of development was characterized by the retraction of the wing epidermis from the overlying pupal cuticle, day 8 by the appearance of brown pigmentation in the developing compound eye, and day 14 by the pale coloration of the facial scales. The time table of development was modified from C. M. Williams and P. L. Adkisson, *Biol. Bull.* **127**, 511 (1964).
5. J. W. Truman, unpublished data.
6. B. M. Sweeney and J. W. Hastings, *Cold Spring Harbor Symp. Quant. Biol.* **25**, 87 (1960).
7. J. Aschoff, in *Circadian Clocks*, J. Aschoff, Ed. (North-Holland, Amsterdam, 1965), p. 262.
8. J. L. Hanegan and J. E. Heath, *J. Exp. Biol.* **53**, 611 (1970).
9. R. Geiger, *The Climate Near the Ground* (Engl. transl.) (Harvard Univ. Press, Cambridge, Mass., 1961), p. 611.
10. L. M. Riddiford, in *Experimental Analysis of Insect Behavior*, L. Barton-Browne, Ed. (Springer-Verlag, Berlin, in press).
11. ———, personal communication. The female moths were illuminated with a dim red light during the scotophase of the photoperiod. Each animal was then checked for "calling" at approximately 1-hour intervals throughout the night.
12. This research was conducted at the Concord Field Station of Harvard University. I thank Prof. L. M. Riddiford, L. P. Lounibos, and an anonymous reviewer for helpful suggestions and for a critical reading of the manuscript. Supported by NSF grant GB-35540.
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23 July 1973; revised 29 August 1973

Human Visual Ecology and Orientation Anisotropies in Acuity

Abstract. *The visual environment of Cree Indians from the east coast of James Bay, Quebec, is different from that of city-raised Euro-Canadians. So also are their corresponding orientation anisotropies in visual acuity. A Euro-Canadian sample exhibited the usual higher resolution for vertically and horizontally oriented gratings as compared with oblique orientations, while a Cree Indian sample did not. The most parsimonious explanation of these acuity differences is that orientation-specific detectors in humans are tuned by the early visual environment.*

Human visual acuity varies with stimulus orientation, being highest for lines oriented horizontally and vertically and poorest for lines oriented 45° to the left and right of vertical (*1, 2*). Furthermore, this orientation anisotropy is not produced by asymmetries in the dioptrics of the eye (*3*), and the neural origin of this effect is proximal to the origin of the electroretinogram (*2*).

Selective early visual experience of cats alters not only the perceptual but also the physiological responses of the visual system (*4*). Kittens raised in a visual environment consisting solely of vertical or horizontal stripes are functionally blind to orthogonally oriented contours, and no neurons in their visual cortices appear to be tuned to this orientation. That similar effects result from partial visual deprivation in humans has been suggested by studies (*5*) demonstrating that certain astigmatic subjects, after perfect optical correction, still exhibit a marked impairment in the resolution of contours in the plane of their astigmatism.

We present evidence here that the orientation anisotropy in visual acuity might also be the result of differential early visual experience. A sample of Euro-Canadians raised in a "carpentered" (*6*) environment, with its preponderance of vertical and horizontal contours, showed the usual anisotropic acuity pattern, while a Cree Indian sample raised in a traditional setting that presents a more heterogeneous array of contour orientations did not exhibit this effect.

The Euro-Canadian sample consisted of 20 university students (10 male and 10 female) from Kingston, Ontario. All subjects in this group were raised in and around typical North American houses and buildings, which provide a visual environment with a marked predominance of vertical and horizontal contours. The Cree sample consisted of 16 people (10 male and 6 female) from Wemindji, a small Indian village on the east coast of James Bay in northwest Quebec (79° longitude, 53° latitude). These subjects had all been raised in traditional housing, which alternated between a summer cook tent or *meechwop* (Fig. 1) and a winter lodge or *matoocan* (*7*). These structures, both internally and externally, present contours in virtually all orientations. Similarly, the taiga, consisting of coniferous trees, presents contours in many orientations. There are many horizontal and vertical contours in this environment (horizon, tree trunks, and so forth), but they do not predominate as they do in the carpentered environment. Cross-cultural data indicate that the spatial-perceptual abilities of both groups are high and comparable (*8*), and that both the Cree and English languages are rich in orientation-specific terms.

To measure orientation anisotropies in visual acuity, we constructed an apparatus that permitted a grating pattern to be rotated to various orientations. This device was constructed of Plexiglas and consisted of a white disk 10.5 cm in diameter surrounded by a black annulus 15.5 cm in outside diameter. The central disk was covered with a clear plastic sheet on which was printed a grid of black stripes 0.15 mm wide, with a spatial frequency of 15.75 line/cm (Letratone LT 70). A bolt mechanism with appropriately positioned holes permitted the experimenter to rotate and lock the grating pattern into either the horizontal, vertical, or left or right oblique orientations. The apparatus, mounted on a black wooden stand, was kept perpendicular to the surface of the table on which it was placed. To eliminate the need for verbal responses, we constructed a simple response indicator, which consisted of a white disk 10 cm in diameter with a black pointer mounted in the center and the four stimulus orientations marked at the circumference.

Subjects were seated in turn at one end of a 3.7-m table and instructed in their mother tongue how to respond to the stimuli. They were told to turn the