Physiology of Insect Rhythms

IV. Role of the Brain in the Regulation of the Flight Rhythm of the Giant Silkmoths

James W. Truman*

The Biological Laboratories, Harvard University,
Cambridge, Massachusetts, USA

Summary. 1. Male giant silkmoths generally show 3 distinct peaks of flight activity each day: a brief burst of flight after lights-off (α_1), a longer bout of activity later in the night (α_2), and a lights-on response. The α_1 and α_2 activities are under circadian control, whereas the lights-on response occurs in response to an exogenous signal.

2. Surgical experiments showed that the brain was necessary for the expression of the flight rhythm. Moreover, an intact neural pathway from the brain to the thoracic motor centers was needed for overt rhythmicity.

3. Rhythmic flight activity continued after the removal of the optic lobes but not after excision of the cerebral lobes.

4. Extirpation of the compound eyes did not interfere with the entrainment of the α_1 and α_2 peaks, but it abolished the lights-on response. Ablation of the ocelli had no effect on any of the flight peaks. It was concluded that the flight clock(s) was entrained by an extraretinal photoreceptor.

5. Experiments involving covering the head with opaque wax indicated that the extraretinal receptor was in the head.

6. When the head was covered with opaque wax but the compound eyes were left exposed, the moths showed free-running activity even though they were in a photoperiod regimen. Consequently, the only pathway of photoperiod information to the locomotor clock is apparently via the extraretinal receptor.

7. It was concluded that adult activity was most likely controlled by centers in the cerebral lobe area of the brain. These presumably receive light directly and control activity via neural pathways to the thoracic ganglia.

Rhythmic influences pervade many aspects of the behavior and physiology of the giant silkmoths. Hatching (Riddiford and Johnson, 1971), the secretion of the prothoracicotropic hormone and ecdysone (Truman, 1972a), adult eclosion (Truman, 1972b), retinular pigment migration (Koyama, 1954), and adult flight activity (Truman, Lounibos and Riddiford, in preparation) occur in a rhythmical fashion and are controlled by internal circadian clocks. Of these rhythmic activities the best known is eclosion. The rhythm of adult emergence is controlled by a transplantable clock in the cerebral lobe area of the moth brain. This clock receives photoperiod information through an extraretinal receptor and directs the secretion of the "eclosion hormone" which in turn triggers the emergence behavior (Truman, 1972b, 1973a).

Outside of the silkmoths, most studies on the physiological aspects of insect rhythms have dealt with the control of locomotor activity (see Brady, 1974, for

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* Present address: Department of Zoology, University of Washington, Seattle, Washington 98195, USA.

a recent review). The best understood locomotor rhythm is that of the cockroach. With respect to the manner of photoreception, the location of the driving clock, and the means by which the overt rhythm is triggered, the cockroach locomotor rhythm differs markedly from the silkmoth eclosion rhythm. It was, therefore, of interest to examine the locomotor rhythm of silkmoths in order to establish whether the above differences were due to the phylogenetic positions of the respective insects or to the types of behavior under study.

Materials and Methods

1. Experimental Animals

Diapausing pupae of *Antheraea pernyi*, *Hyalophora cecropia*, and *Samia cynthia* were purchased from dealers and stored at 5° C. When needed, pupae were brought to 25° C and allowed to initiate adult development. Upon emergence, the moths were placed under their respective photoperiod conditions. The giant silkmoths do not feed or drink as adults and are relatively short lived. Individuals of *A. pernyi* survived for about one week; *H. cecropia* and *S. cynthia* moths usually lived for two weeks.

Flight activity was measured using the jiggle cages described in Truman (1973b). Data from the flight cages were recorded on Esterline Angus event recorders. With most experimental treatments some individuals died within the first day or had such a low level of locomotor activity that it was impossible to determine whether or not they were rhythmic. Records from these animals were not included in the Results.

2. Photoperiod Conditions

The present study was carried out in a subterranean bunker at the Concord Field Station of Harvard University. Bright light regimens (1000 lux at the level of the activity cage) were maintained in constant temperature rooms which were provided with fluorescent illumination programmed for daily photoperiod cycles.

Experiments designed to localize the photoreceptor for the activity clock involved covering parts of the head with black wax. A common difficulty with this type of experiment is that a reasonable fraction of incident light can penetrate uncovered parts of the cuticle and scatter through the tissues of the insect. This problem was circumvented by using dim light cycles. Illumination was provided by one 0.04 watt neon bulb inside each of a series of light-tight boxes. The bulbs emitted an orange light of an intensity of approximately 1 lux at the level of the activity cage. The boxes were placed in a constant temperature room at 25° C.

3. Operations and Painting Techniques

Most operations were performed on diapausing pupae according to described techniques (Williams, 1946, 1952; Truman, 1972b). The effect of each operation was then assessed by the performance of the resulting moths. Typically, regeneration of the severed nerves did not occur in these animals.

Moths that had had their ventral connectives cut did not expand their wings after emergence (Truman and Endo, 1974) and generally lived for only one or two days. Consequently, this operation was performed on adults. Each moth was anesthetized with CO_2 and positioned ventral side up with its head flexed back to expose the neck membrane. After an incision was made in the membrane, the nerve cord was grasped with forceps and transected behind the subesophageal ganglion with microscissors. A small amount of melted wax was placed over the wound site and the head was allowed to return to its normal position.

Excision of the compound eyes was also performed on anesthetized adults. The head was secured dorsal side up, and each eye was removed by means of a single cut just medial to the inner margin of the eye. The wound area was then checked for remaining fragments of ommatida. A few crystals of phenylthiourea (PTU) (Williams, 1952) were placed in the wound and the area covered with melted wax.

Until recently it was thought that the saturniid moths were without ocelli. However, Dickens and Eaton (1973) have reported that these insects have 2 rudimentary ocelli (ca. 10 μ in diameter) situated just posterior and medial of the antennal bases. These structures were removed by excision of a triangular piece of cuticle that extended posteriorly from between the antennal bases. Tissue adhering to the cuticle was also removed. The wound was treated with PTU and covered with wax.

Experiments involving the exclusion of light from various regions of the head relied on a black wax made from a mixture of charcoal powder and paraffin. In cases which required covering over the dorsal surface of the head, the antennae were first removed and then the entire area covered.

After the death of the moth, each head was placed in a concentrated KOH solution. This treatment digested away the soft tissue from the head area and left only the cuticle and the adhering wax. The heads were examined using transmitted light. This technique revealed imperfections in the wax covering, some of which would have been missed in an incident light examination.

Results

1. Patterns of Flight Activity of Intact Moths

A) Photoperiods Having Bright Light (1000 Lux)
during the Photophase

Male saturniid moths typically show 3 discrete peaks of flight activity within a 24-hour cycle (Truman, Lounibos and Riddiford, in preparation). These include a brief flight soon after lights-off (α_1 peak), a longer bout of activity which occurs during the night for the species considered here (α_2 peak), and a short flight burst immediately after lights-on. The α_1 and α_2 peaks persist in constant darkness (Truman, unpublished) and, thus, are under endogenous control. The lights-on activity is a response to an exogenous signal and appears to have no circadian basis.

The flight patterns of male *H. cecropia*, *S. cynthia*, and *A. pernyi* under L (1000 lux):D cycles are shown in Fig. 1. The α_1 peak of activity was small in *H. cecropia* and *S. cynthia*, and typically absent in *A. pernyi*. Similarly, only *H. cecropia* and *S. cynthia* regularly showed lights-on flight. The α_2 peak of flight was well developed in all three species.

A limited number of virgin *H. cecropia* and *S. cynthia* females were also used in this study. Females of these two species showed a brief period of flight activity that began shortly after lights-off. This flight peak in the females is presumably homologous to the α_1 peak of the males. Virgin females did not fly during the time of the α_2 peak of their respective males; instead they assumed the "calling" posture and released sex pheromone (Truman, Lounibos and Riddiford, in preparation). No lights-on response was observed.

B) Flight under Dim Light (1 Lux) Photoperiods

Only *H. cecropia* and *S. cynthia* were tested under L (1 lux):D conditions. Males of *S. cynthia* showed normal entrainment to the dim light regimen (Fig. 2C), and approximately one-half of them also gave a lights-on response. Most *S. cynthia* females entrained normally, but in a few individuals the α_1 peak tended to drift
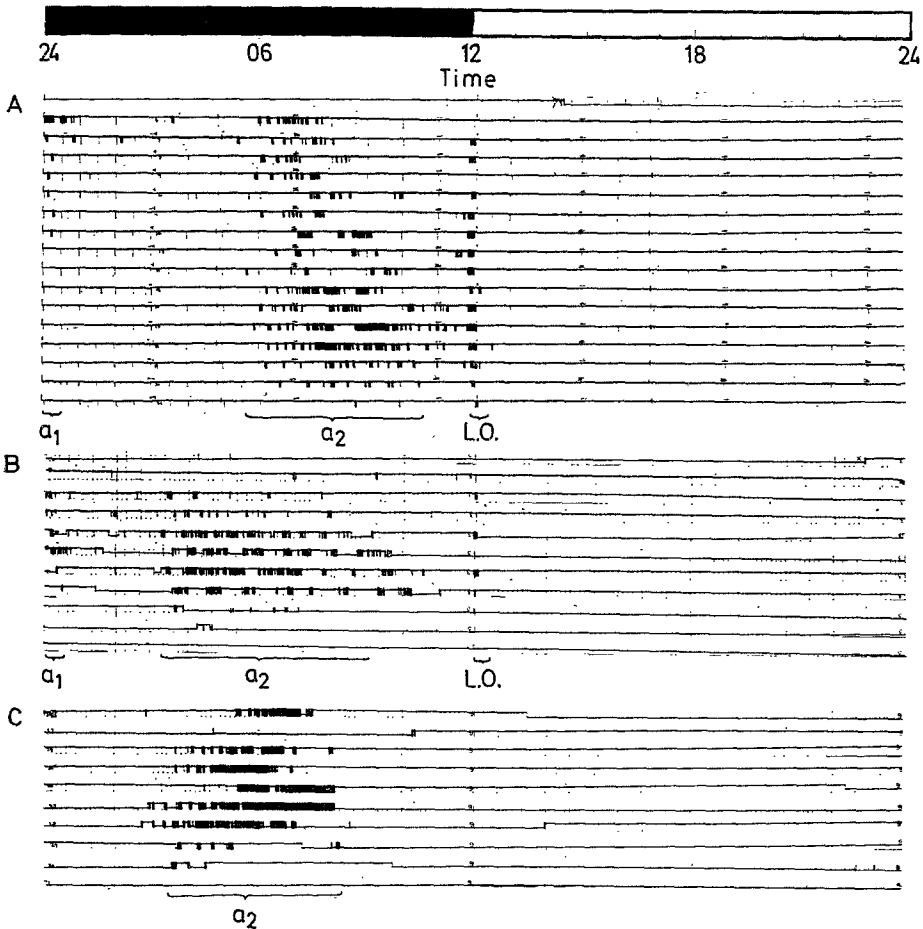
Fig. 1A—C. Records of the daily activity patterns of silkmoth males in a bright-light (1000 lux):dark regimen. (A) *H. cecropia*; (B) *S. cynthia*; (C) *A. pernyi*. The positions of the α_1, α_2, and lights-on peaks are indicated. The black bar indicates the duration of darkness

away from the lights-off signal (Fig. 2D), and in one moth activity was sporadically distributed throughout the cycle.

Male *H. cecropia* showed somewhat aberrant behavior in response to dim light photoperiods. The position of the α_2 peak was stable and many individuals showed a lights-on response. But the behavior of the α_1 peak was variable. In a few moths the α_1 peak remained at lights-off, but in others it gradually advanced into the day and assumed a new phase relative to the photoperiod (Fig. 2A). The α_1 peak also broadened and activity became dispersed. In still other males the α_1 peak shifted into the day but a new stable entrainment was not apparent and activity was sporadically distributed throughout the photophase. This dissociation of the α_1 and α_2 peaks under dim illumination indicates that they may be under separate control.
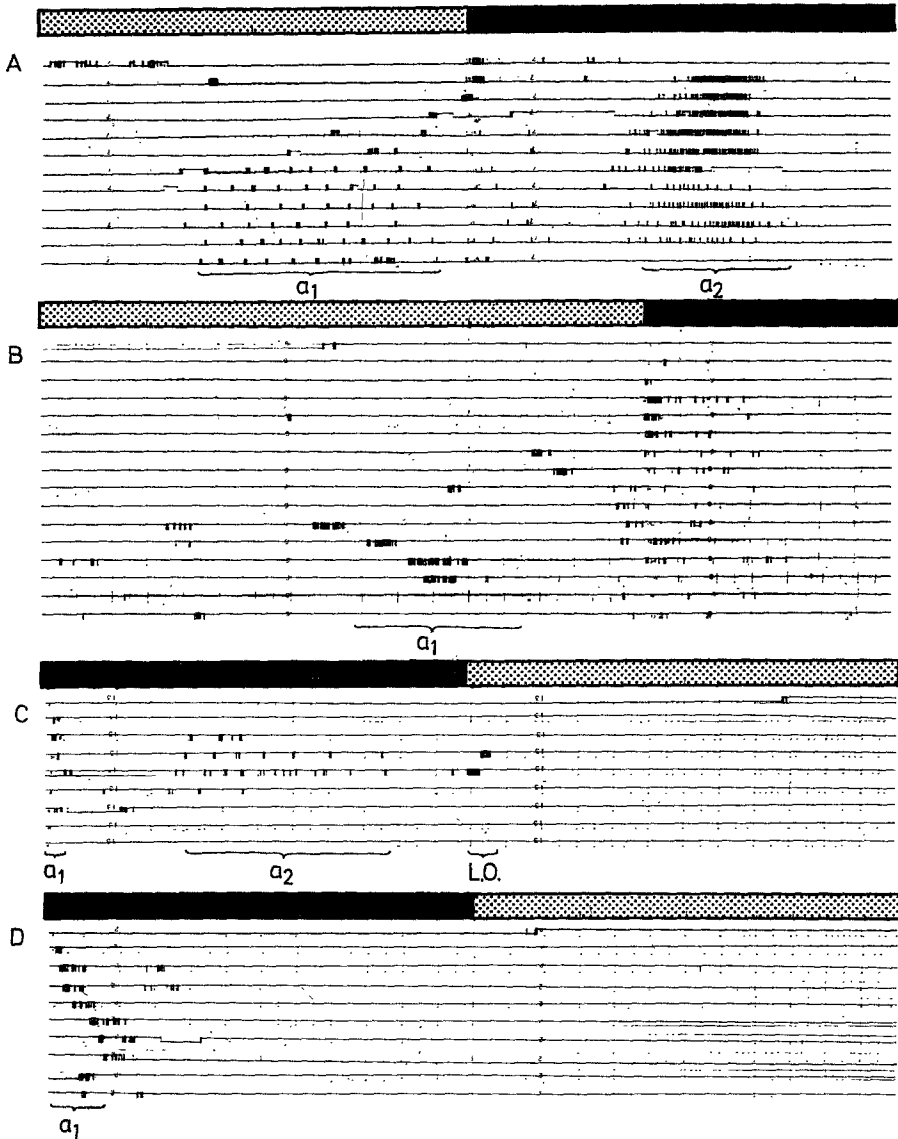
Fig. 2A—D. Records of the daily activity patterns of silkmoth adults in a dim light:dark regimen. (A) *H. cecropia* male; (B) *H. cecropia* female; (C) *S. cynthia* male; (D) *S. cynthia* female. The black portion of the bar indicates darkness; the stippled portion indicates 1 lux illumination

The behavior of the female *H. cecropia* was consistent with the contention that her major activity peak is homologous to the α_1 peak of the male. In some females activity was confined to lights-off, but most showed a spread of activity into the photophase (Fig. 2B), and a few individuals showed exclusively diurnal activity.

Table 1. The effects of various operations on the flight behavior of silkmoth males in a L(1000 lux): D regimen

Treatment	Species	Number	% showing activity			Level of activity[a]
			entrained	free-running	arrhyth-mic	
None	H. cecropia	20	100	0	0	—
	A. pernyi	16	100	0	0	—
Brain removed	H. cecropia	5	0	0	100	high
Brain transplanted to abdomen	H. cecropia	7	0	0	100	high
Circumesophageal connectives severed	H. cecropia	9	0	0	100	high
Subesophageal ganglion removed	A. pernyi	11	0	0	100[b]	low
Ventral nerve cord transected[c]	H. cecropia	6	0	0	100[b]	low
Brain bisected	A. pernyi	5	100	0	0	—
One-half of brain removed	A. pernyi	4	100	0	0	—
One cerebral lobe and both optic lobes removed	A. pernyi	6	100	0	0	—
	H. cecropia	3	100	0	0	—

[a] Refers only to activity of arrhythmic animals.
[b] Arrhythmia uncertain because of extreme low levels of locomotor activity.
[c] Sectioned immediately behind the subesophageal ganglion.

2. Effects of Surgery on the Moth Central Nervous System
A) Removal and Reimplantation of the Brain

The activity of 5 debrained H. cecropia males was monitored under L:D conditions (Table 1). None of the moths showed indications of either entrainment or free-running rhythmicity. The level of activity was high and locomotion was spread throughout the day and the night (Fig. 3A).

A brainless moth also shows unsynchronizable eclosion, but rhythmic control of this behavior can be reestablished by implanting a brain into the abdomen of the debrained animal (Truman and Riddiford, 1970; Truman 1972b). When similar "loose-brain" H. cecropia were tested for flight behavior, they showed the same lack of rhythmicity that characterized the debrained moth (Fig. 3B, Table 1).

B) Transection of the Neural Pathways between the Brain and Thoracic Motor Centers

Although the above experiments indicated that the brain was important for the daily flight patterns of the moth, they failed to indicate any hormonal involvement in this control. The prospect of a neural mediation of the flight rhythm was further examined by transecting the nerve cord at various levels between the brain and thoracic ganglia (Table 1). After transection of the circumesophageal
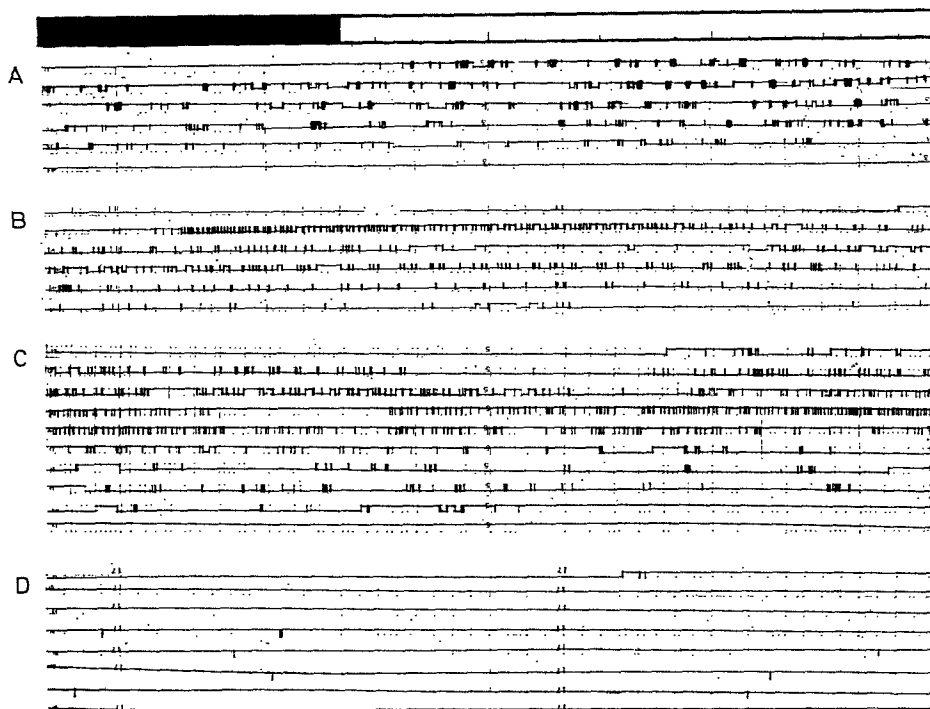
Fig. 3A—D. Examples of the effects of various operations on the daily activity patterns of male *H. cecropia* moths in 17L:7D photoperiod. (A) brain removed; (B) brain transplanted to abdomen; (C) circumesophageal connectives sectioned; (D) ventral nerve cord sectioned behind subesophageal ganglion

connectives, the moths acted similarly to debrained and loosebrained animals—they showed a high level of arrhythmic activity (Fig. 3C). Section of the nerve cord behind the subesophageal ganglion or removal of this ganglion resulted in a moth that was almost totally inactive (Fig. 3D). Because of the extremely low levels of spontaneous locomotion in these animals, one could not be sure whether or not they were rhythmic.

C) Surgery on the Silkmoth Brain

Various portions of the brain were removed from silkmoth pupae and the activity of the resulting moths was then monitored. As seen in Table 1, bisection of the brain through the midline did not interfere with entrainment of flight activity (Fig. 4A). Similarly, removal of one-half of the brain was without major effect (Fig. 4B).

In the cockroach, the clock controlling locomotor activity appears to be in the optic lobes (Nishiitsutsuji-Uwo and Pittendrigh, 1968b). In the silkmoth the eclosion clock resides in the cerebral lobes (Truman, 1972b). Therefore, it was of interest to determine which area of the brain was needed for the maintenance of the silkmoth locomotor rhythm. In a series of animals, one-half of the brain was
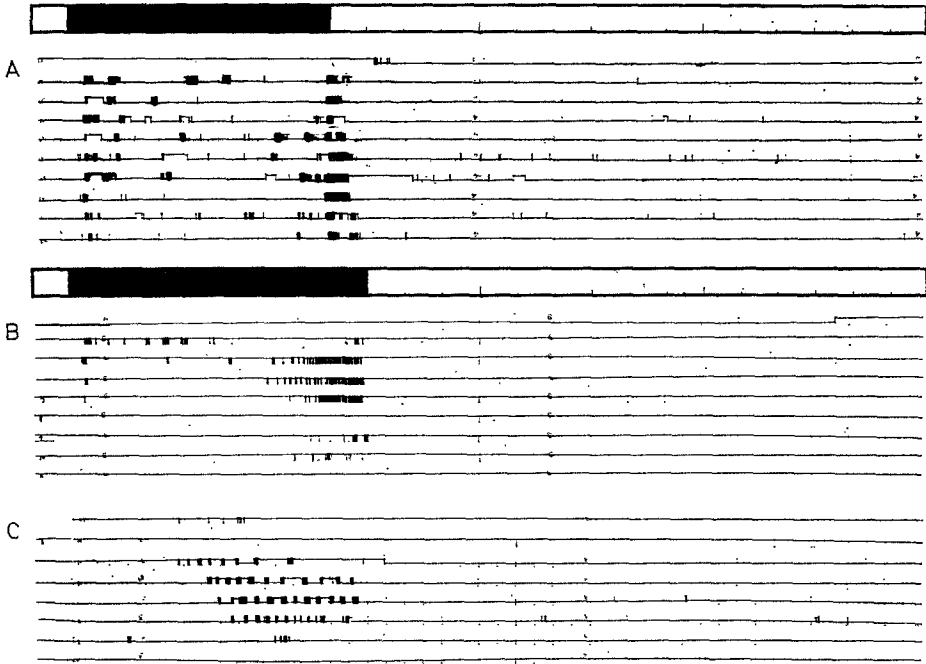
Fig. 4A—C. Examples of the effect of various operations on the silkmoth brain on the daily activity patterns of male silkmoths. (A) *H. cecropia* whose brain was bisected; (B) *H. cecropia* in which the left half of the brain was removed; (C) *A. pernyi* male which retains only a single cerebral lobe

removed and the optic lobe then excised from the intact half. These moths, which retained only one cerebral lobe, nevertheless showed entrainment to the L:D cycle (Fig. 4C). Thus, in the silkmoth the rhythmic center which controls locomotor activity most likely resides in the cerebral lobe area of the brain.

3. Effect of Removal of External Photoreceptors
A) Removal of the Compound Eyes

The compound eyes were excised from a series of *H. cecropia* males and the moths then placed in a 1000 lux photoperiod (Table 2). Of the 13 moths which survived the surgery, all entrained to the light-dark regimen. Typically they showed both the α_1 and α_2 peaks but no lights-on response. Moreover, the eyeless animals quickly reentrained after a 6 hour shift in the photoperiod regimen (Fig. 5A).

The above experiment showed that at intensities of 1000 lux the eyes are not necessary for the entrainment of the α_1 or α_2 peaks of the flight rhythm. To explore further the possible participation of the compound eyes in the flight rhythm, eyeless *H. cecropia* were placed in L(1 lux):D cycles (Table 2). In all instances the α_2 peak kept a relatively stable phase relationship to the entraining photoperiod, yet, as with intact moths, the behavior of the α_1 peak was variable.

Table 2. Effects of removal of external photoreceptors on the flight rhythm of silkmoths

Treatment	Species	Sex	Number	% showing activity			
				entrained	free-running	arrythmic	lights-on
None	H. cecropia[a]	♂	16	100	0	0	56
	S. cynthia[a]	♂	13	93	0	7	86
		♀	5	100	0	0	0
Compound eyes removed	H. cecropia[a]	♂	13	100	0	0	0
	H. cecropia[b]	♂	9	100	0	0	0
Ocelli removed	H. cecropia[a]	♂	4	100	0	0	—[c]
	S. cynthia[a]	♂	3	100	0	0	100
		♀	2	100	0	0	0
Compound eyes and ocelli removed	H. cecropia[a]	♂	8	100	0	0	—[c]
	S. cynthia[a]	♂	1	100	0	0	0
		♀	2	100	0	0	0

[a] Under L(1000 lux):D regimen.
[b] Under L(1 lux):D regimen.
[c] H. cecropia were exposed only to 17L:7D regimen under which conditions a lights-on response cannot be distinguished.

In some moths it remained at lights-off, but others the α_1 activity shifted into the photophase (Fig. 5D). Thus, even under dim illumination, the behavior of intact and of eyeless moths was very similar. The one difference was that none of the eyeless animals showed a lights-on response.

B) Removal of the Ocelli

In the cricket, Nowosielski and Patton (1963) claim that entrainment of the activity clock could occur either via the compound eyes or the ocelli. When both of these receptors were removed from silkmoth adults, the moths nevertheless showed good entrainment in a 1000 lux photoperiod (Table 2, Fig. 5C). As was seen in animals which lacked only their compound eyes, a lights-on peak was absent.

4. Effects of Covering over Parts of the Head with Opaque Wax
A) Covering the Entire Head

The above section points to the existence of an extraretinal photoreceptor that is involved in the entrainment of the flight rhythm. To determine if the head was the site of this receptor, the antennae were removed from 6 H. cecropia and the head of each moth was completely covered with black wax. Of the 5 individuals which gave reasonable activity, none entrained to the dim-light photoperiod and 4 showed distinct free running behavior (Table 3).

It was necessary to establish that the failure to entrain was due to the exclusion of light from the head and not to some other effect of the wax or to the removal of the antennae. Consequently, I removed the antennae and covered
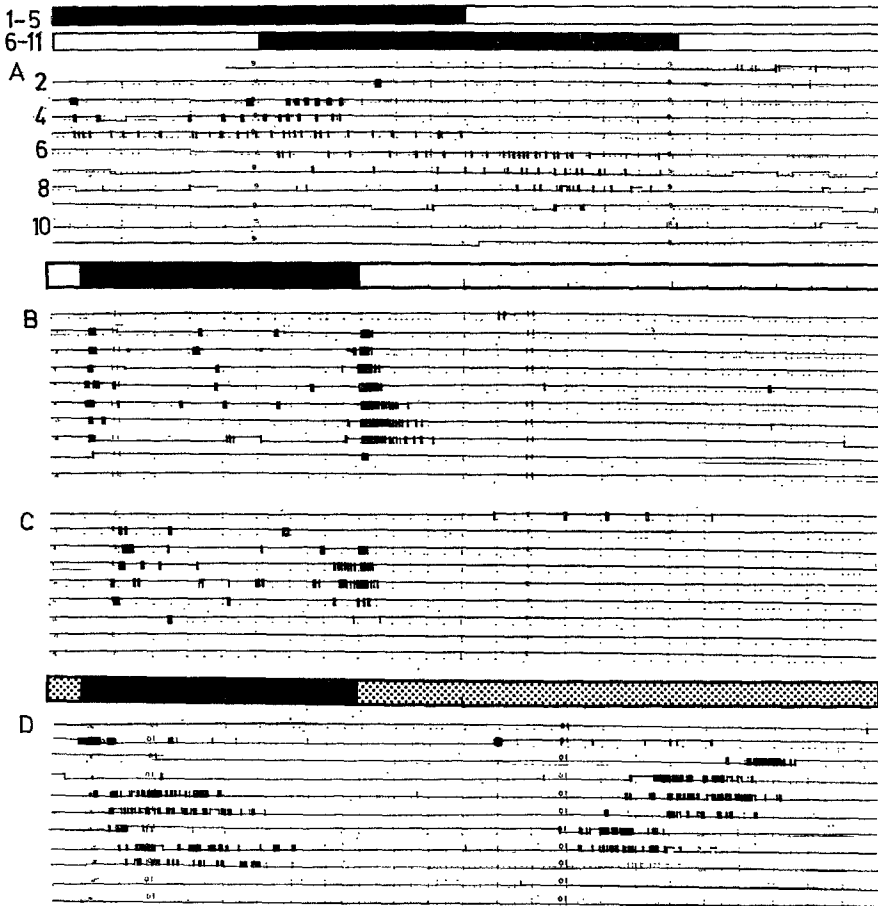
Fig. 5A—D. The effect of removal of external photoreceptors on the daily activity patterns of *H. cecropia* males. (A) compound eyes removed, a six hour delay in the photoperiod was given on day six; (B) ocelli removed; (C) both compound eyes and ocelli removed; (D) compound eyes removed and the moth placed in a dim-light regimen

the heads of 11 *H. cecropia* with clear wax. Seven had normal levels of activity and all entrained to the L:D cycle (Table 3).

B) Covering of External Photoreceptors

The effects of ablation of external photoreceptors were confirmed by covering the receptors with black wax. Moths that had their compound eyes covered typically entrained to the dim light regimen (Table 3), but approximately one-third of each group showed ambiguous activity patterns that have been classified as arrhythmic. It should be noted that no moth showed free-running activity under these conditions. Also, a lights-on response was absent.

When only the ocelli were covered, the males showed normal entrainment of the α_1 and α_2 peaks and the lights-on response (Table 3).

Table 3. Effects of covering various parts of the head with black wax on the flight behavior of silkmoths under L(1 lux):D regimen

Portion of head covered by black wax	Species	Sex	Number	% showing activity			
				Entrained	Free-running	arrhythmic	Lights-on
None	H. cecropia	♂	34	100	0	0	54
		♀	15	88	0	12	0
	S. cynthia	♂	17	94	0	6	53
		♀	11	81	0	18	0
Entire head	H. cecropia	♂	5	0	80	20	0
Head covered with clear wax	H. cecropia	♂	7	100	0	0	42
Compound eyes	H. cecropia	♂	3	66	0	33	0
	S. cynthia	♂	5	60	0	40	0
		♀	6	66	0	33	0
Ocelli	S. cynthia	♂	5	100	0	0	40
Entire head except compound eyes	H. cecropia	♂	23	30	22	48	5
	S. cynthia	♂	9	11	77	11	0
		♀	9	33	44	22	0

C) Covering of the Entire Head Except for the Compound Eyes

The above experiments confirmed that the compound eyes are not required for entrainment of the α_1 and α_2 activity peaks. However, they did not exclude the possibility that the eyes and the extraretinal receptor serve as redundant inputs to the clocks. To determine whether the eyes alone could suffice for entrainment of the activity rhythm, the entire head except for the compound eyes was covered with black wax. Under dim light photoperiods 41% of the moths showed a distinct free-running activity rhythm. In *H. cecropia* the free-running period was approximately 21 hours—similar to the value observed for intact moths in constant darkness (Truman, unpublished). Males of *S. cynthia* showed extremely long periods of about 35 hours (Fig. 6). Thus, in the silkmoths, shielding of the brain from light prevented entrainment even though the compound eyes were exposed to the photoperiod cycles.

As seen in Table 3, 11 moths showed signs of entrainment. The heads from 3 of these animals were lost, but the other heads were treated with KOH and checked for imperfections in the wax covering. Each head had small areas on the dorsal surface which were not covered by the black wax (Fig. 7). In most individuals the hole that resulted from the removal of the antenna was not properly covered. The area under the antennal sockets lacks the reflecting tracheal sacs which underlie most of the head cuticle. Consequently, a hole in this area would provide a relatively unobstructed pathway for light to reach the brain. The moths which showed free-running activity typically had either a complete covering over the head (except the compound eyes) or only small leaks on the ventral surface of the head.
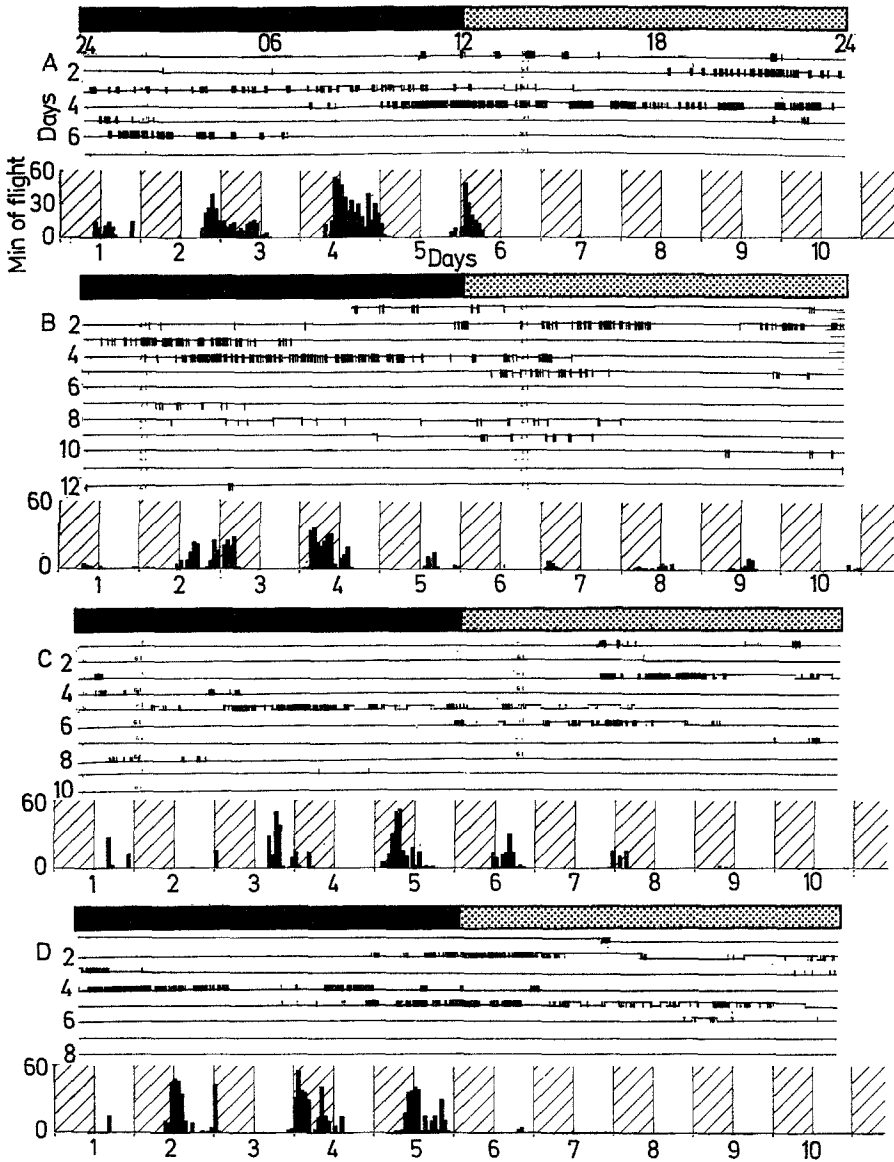
Fig. 6. Examples of the effect of covering over the entire head with black wax except for the compound eyes. The data for each individual are shown in the form of the event recorder records and of histograms. A to D represent four distinct *S. cynthia* males. The moths were exposed to 1 lux photoperiods

The possibility that the ocelli alone could entrain the activity rhythm could not be directly tested because of their close proximity to the antennal bases. Any effort to leave these minute structures exposed would also have afforded a pathway for light to the brain.
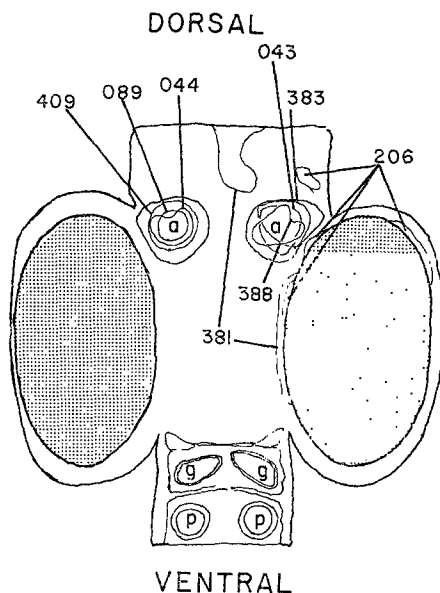
Fig. 7. A flattened view of the head capsule of a silkmoth adult. The numbered areas refer to locations of light leaks in the experimental moths that entrained to the dim-light:dark photoperiod. For further explanation see text. *a* antennal bases; *g* bases of galaea; *p* bases of palps

Discussion

1. Control of the Flight Rhythms in the Giant Silkmoths

Under constant dim illumination the activity rhythm of the tree shrew, *Tupaia*, splits into two components that initially free-run independently of one another (Hoffmann, 1971). A phenomenon which is superficially somewhat similar appears in the activity of *H. cecropia* males under dim light photoperiods. The fact that the α_1 peak can assume a new phase without markedly influencing the phase of the α_2 activity indicates that each may be under independent control. This independence could be accomplished by each being directed by a distinct circadian clock. Alternatively, the α_1 and α_2 activities could be controlled by separate driven components, both of which were coupled to the same driving clock (see Pittendrigh, Bruce and Kaus (1958) for a discussion of coupled circadian systems). The fact that the α_1 and α_2 peaks of the female direct different behaviors (flight and phero-mone release, respectively) suggests that separate clocks may be involved. How-ever, a convincing proof would be provided if the two peaks showed different free-running periods under constant conditions. This has not yet been observed in these silkmoths (Truman, unpublished).

The silkmoth activity clock(s) and the eclosion clock have some features in common. The response of the activity clocks to photoperiod cycles (Truman, in preparation) is consistent with the behavior of the eclosion clock under the same regimens (Truman, 1971, 1972b). Both the eclosion rhythm and the activity rhythms are entrained through extraretinal photoreceptors and both are appar-

ently controlled by rhythmic centers in the cerebral lobe area of the brain (Truman, 1972a). In these last two points the silkmoth rhythms are in contrast to the cockroach locomotor rhythm, which is controlled by a clock in the optic lobes and is entrained via the compound eyes (Nishiitsutsuji-Uwo and Pittendrigh, 1968a, b).

The eclosion and flight rhythms appear to differ in the mode of output from the clock. Eclosion behavior is hormonally triggered (Truman, 1973a). The fact that transection of the pathways between the brain and thoracic ganglia produces a moth that shows arrhythmic locomotion suggests that the flight rhythm may be mediated only through neural pathways. The relationship of the level of the cut to the amount of locomotor activity is similar to that originally reported for the mantis (Roeder, 1937). It is in accord with the idea that the locomotor patterns are driven by a center in the subesophageal ganglion and that this center is in turn controlled by inhibitory influences from the brain (Roeder, 1937). Presumably, this inhibitory influence of the brain is relaxed during the normal flight time of the moth. Indeed, Azaryan and Tyshchenko (1969) have recorded from the cricket brain high levels of electrical activity that were inversely correlated with locomotor activity.

Primarily on the basis of histological evidence, Hinks (1967) suggested a hormonal mediation of the flight rhythm of noctuid moths. The evidence presented in this paper indicates a neural control, but it should be emphasized that the evidence against hormonal involvement is not complete. I have not excluded the possibility of an activity hormone that acts back on controlling centers in the brain itself. Also, there is a possibility of some degree of hormonal modulation of a neurally driven flight rhythm. In the female silkmoth there is strong evidence that pheromone release behavior is hormonally controlled (Riddiford and William 1971; Riddiford, 1974). Therefore, in the female the output from the α_2 clock appears to be hormonal rather than neural.

2. Role of Photoreceptors in the Silkmoth Activity Rhythm

The role of photoreceptors in the entrainment of insect activity rhythms presents an extremely variable picture. In the orthopteriod groups, which have received most of the attention, external photoreceptors are involved in the synchronization of locomotor rhythms. In the cockroach (Nishiitsutsuji-Uwo and Pittendrigh, 1968a; Roberts, Skopik and Driskill, 1971) and the cricket (Nowosielski and Patton, 1963; Loher, 1972) external receptors are the sole route for photoperiod information to reach the brain. In the stridulatory rhythm of *Ephippiger*, both the eyes and an extraretinal photoreceptor apparently work in concert (Dumortier, 1972). The oviposition rhythm of the grasshopper *Chorthippus curtipennis* is also most likely entrained through retinal and extraretinal pathways (Loher and Chandrashekaran, 1970). The silkmoth deviates from the orthopteran pattern since retinal pathways appear to play no role in the entrainment of the flight rhythm. Although the precise location of this extraretinal receptor has not been determined, one would expect it to be in the cerebral lobe area of the brain as is the one for the eclosion rhythm (Truman, 1972b).

Aschoff (1960) has emphasized that the overall pattern of activity that an organism displays is a combination of endogenous and exogenous influences.
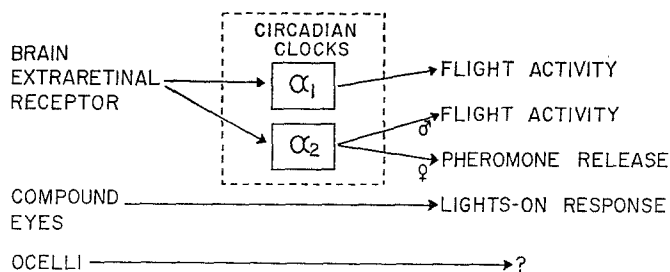
Fig. 8. A schematic representation of the roles of the various photoreceptors in the expression of the silkmoth activity rhythm

These two influences are evident in the pattern of silkmoth locomotion, but they are mediated through distinct photoreceptive pathways (Fig. 8). The brain photoreceptor apparently is the only receptor through which light can entrain the activity clocks. But at this time one cannot exclude the possibility that the external photoreceptors have a minor influence on either the phase or the duration of the activity peaks. The peak of flight activity that occurs immediately after lights-on is a response to an exogenous signal. This response is mediated through the compound eyes and not through the brain photoreceptor. Thus, in a manner similar to eclosion (Truman, 1972b), exogenous and endogenous factors, working through the compound eyes and brain photoreceptor respectively, combine to produce the overall pattern of locomotor activity.

References

Aschoff, J.: Exogenous and endogenous components in circadian rhythms. Cold Spr. Harb. Symp. quant. Biol. **25**, 11–28 (1960)

Azaryan, A. G., Tyshchenko, V. P.: Role of cerebral neurons in regulation of the circadian rhythm of behavior of the cricket *Gryllus domesticus* L. Dokl. Biol. Sci. **186**, 464–466 (1969)

Brady, J.: The physiology of insect circadian rhythms. Adv. Insect Physiol. **10**, 1–115 (1974)

Dickens, J. C., Eaton, J. L.: External ocelli in Lepidoptera previously considered to be anocellate. Nature (Lond.) **242**, 205–206 (1973)

Dumortier, B.: Photoreception in the circadian rhythm of stridulatory activity in *Ephippiger* (Ins., Orthoptera). Likely existence of two photoreceptive systems. J. Comp. Physiol. **77**, 80–112 (1972)

Hinks, C. F.: Relationship between serotonin and the circadian rhythm in some nocturnal moths. Nature (Lond.) **214**, 386–387 (1967)

Hoffmann, K.: Splitting of the circadian rhythm as a function of light intensity. In: Biochronometry (M. Menaker, ed.), p. 134–148. Washington: National Academy of Sciences Press 1971

Koyama, N.: Studies on the compound eye of the bombycid moths. J. Shinshu Univ. **4**, 97–144 (1954)

Loher, W.: Circadian control of stridulation in the cricket *Teleogryllus commodus* Walker. J. comp. Physiol. **79**, 173–190 (1972)

Loher, W., Chandrashekaran, M. K.: Circadian rhythmicity in the oviposition of the grasshopper *Chorthippus curtipennis*. J. Insect. Physiol. **16**, 1677–1688 (1970)

Nishiitsutsuji-Uwo, J., Pittendrigh, C. S.: Central nervous system control of circadian rhythmicity in the cockroach. II. The pathway of light signals that entrain the rhythm. Z. vergl. Physiol. **58**, 1–13 (1968a)

Nishiitsutsuji-Uwo, J., Pittendrigh, C. S.: Central nervous system control of circadian rhythmicity in the cockroach. III. The optic lobes, locus of the driving oscillation? Z. vergl. Physiol. **58**, 14–46 (1968b)

Nowosielski, J. W., Patton, R. L.: Studies on circadian rhythm of the house cricket, *Gryllus domesticus* L. J. Insect Physiol. **9**, 401–410 (1963)

Pittendrigh, C. S., Bruce, V. G., Kaus, P.: On the significance of transients in daily rhythms. Proc. nat. Acad. Sci. (Wash.) **44**, 965–973 (1958)

Roeder, K. D.: The control of tonus and locomotor activity in the praying mantis (*Mantis religiosa* L.). J. exp. Zool. **76**, 353–374 (1937)

Riddiford, L. M.: The role of hormones in the reproductive behavior of female wild silkmoths. In: Experimental analysis of insect behaviour (L. Barton Browne, ed.), p. 278–285. Berlin-Heidelberg-New York: Springer 1974

Riddiford, L. M., Johnson, L. K.: Synchronization of hatching of *Antheraea pernyi*. Proc. XIIIth Internatl. Congr. Entomol., vol. 1, 431 (1971)

Riddiford, L. M., Williams, C. M.: Role of the corpora cardiaca in the behavior of saturniid moths. I. Release of sex pheromone. Biol. Bull. **140**, 1–7 (1971)

Roberts, S. K., Skopik, S. D., Driskill, R. J.: Circadian rhythms in cockroaches: does brain hormone mediate the locomotor cycle? In: Biochronometry (M. Menaker, ed.), p. 505–516. Washington: National Academy of Sciences Press 1971

Truman, J. W.: Hour-glass behavior of the circadian clock controlling eclosion of the silkmoth *Antheraea pernyi*. Proc. nat. Acad. Sci. (Wash.) **68**, 595–599 (1971)

Truman, J. W.: Physiology if insect rhythms. I. Circadian organization of the endocrine events underlying the moulting cycle of larval tobacco hornworms. J. exp. Biol. **57**, 805–820 (1972a)

Truman, J. W.: Physiology of insect rhythms. II. The silkmoth brain as the location of the biological clock controlling eclosion. J. comp. Physiol. **81**, 99–114 (1972b)

Truman, J. W.: How moths "turn on": a study of the action of hormones on the nervous system. Amer. Scientist **61**, 700–706 (1973a)

Truman, J. W.: Temperature sensitive programming of the silkmoth flight clock: a mechanism for adapting to the seasons. Science **182**, 727–729 (1973b)

Truman, J. W., Endo, P. T.: Physiology of insect ecdysis. Neural and hormonal factors involved in wing spreading behaviour of moths. J. exp. Biol., in press (1974)

Truman, J. W., Riddiford, L. M.: Neuroendocrine control of ecdysis in silkmoths. Science **167**, 1624–1626 (1970)

Williams, C. M.: Physiology of insect diapause: the role of the brain in the production and termination of pupal dormancy in the giant silkmoth, *Platysamia cecropia*. Biol. Bull. **90**, 234–243 (1946)

Williams, C. M.: Physiology of insect diapause. IV. The brain and prothoracic glands as an endocrine system in the *Cecropia* silkworm. Biol. Bull. **103**, 120–138 (1952)

Dr. James W. Truman
Department of Zoology
University of Washington
Seattle, Washington 98195, USA