cochlear nucleus have been described; for example, the olivocochlear bundle, the intermediate acoustic stria, the dorsal acoustic stria, and the trapezoid body (*10*). The efferent fibers of both the olivocochlear bundle and intermediate acoustic stria originate in the superior olivary complex and terminate in the ventral cochlear nucleus (*10*), whereas the recurrent fibers of the dorsal acoustic stria and trapezoid body originate in the nuclei of the lateral lemniscus and terminate in the dorsal cochlear nucleus (*10*). The role of these brainstem systems in the development of cochlear nucleus response decrements is as yet not known, but, conceivably, could be an important one.

On the other hand, the acoustic nerve projects a terminal branch of each fiber to both dorsal and ventral cochlear nuclei and, in both nuclei, internuncial cells with intrinsic fiber connections relay the incoming stimulus through local polysynaptic circuits, a situation known to favor the development of response plasticity. In the isolated spinal cord, for example, response decrements of dorsal horn sensory neurons develop during repeated cutaneous stimulation; such habituation is readily observed in the absence of recurrent projections from higher levels and is a function of cells with polysynaptic, rather than monosynaptic, contacts with the primary afferent fibers (*16*). Thus, on the basis of current data, it would seem equally probable that intrinsic, rather than recurrent, circuits of the cochlear nuclei mediate the response decrements.

The continued decrement of the acoustic responses after strychnine blockade of postsynaptic inhibition is again similar to observations made during repeated somatosensory stimulation in the isolated spinal cord (*17*). Moreover, the low frequency of stimulation (once every 5 seconds) during which response decrements developed, and the time required for recovery (5 to 10 minutes), involve durations too long to reflect pre- or postsynaptic inhibition (*12*). Therefore, whereas a buildup of inhibition has been suggested as the source of cochlear nucleus response habituation (*5*), the unit response decrements described above seem best attributed to a progressive reduction of excitation either within intrinsic circuits or recurrent pathways to the cochlear nucleus. This conclusion is consonant with the synaptic depression hypothesis of habituation (*13, 17, 18*), which attributes decrements of neuronal response to decreased effectiveness of synaptic transmission through mechanisms such as transmitter depletion or diminished subsynaptic sensitivity.

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Silk Moth Eclosion: Hormonal Triggering of a Centrally Programmed Pattern of Behavior

Abstract. *The emergence of the adult cecropia silk moth from the pupal skin involves a stereotyped series of abdominal movements—the pre-eclosion behavior. This behavior, triggered by a neurosecretory hormone, consists of three phases that are characterized by the relative frequency and pattern of movements. Electrical recordings from a nerve cord with severed peripheral nerves demonstrate that the pre-eclosion behavior is prepatterned in the abdominal ganglia. In response to the hormone, the entire 1.25-hour behavioral program can be activated and "read off" in the absence of sensory feedback.*

In the giant silk moths, the control of adult emergence involves two separable neural components that are linked together by a neurosecretory hormone—the eclosion hormone (*1*, *2*). The first component is centered in the brain and involves an extraoptic photoreceptor, a biological clock, and a neuroendocrine output. The second component involves the neural circuitry that gives rise to the various behavior patterns in the adult emergence sequence and is independent of the brain. Of special interest is the first part of the emergence sequence—the pre-eclosion behavior. This behavior primarily involves abdominal movements and is performed by isolated abdomens after injection of homogenates containing the eclosion hormone (*2*). We report here that the pre-eclosion behavior arises from a centrally generated program of behavior that is activated and "read off" in response to a hormonal signal.

In the cecropia moth (*Hyalophora cecropia*), the pre-eclosion behavior is complex and consists of three distinct phases (Fig. 1) (*1*, *2*):

1) The behavior is initiated with a hyperactive period that lasts approximately 0.5 hour and involves abdominal rotations and various ventral "twitches."

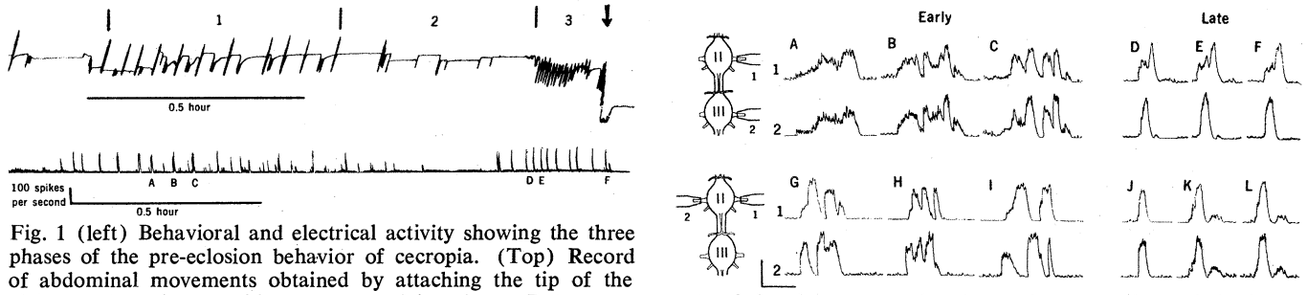

Fig. 1 (left) Behavioral and electrical activity showing the three phases of the pre-eclosion behavior of cecropia. (Top) Record of abdominal movements obtained by attaching the tip of the abdomen to a lever writing on a revolving drum. Rotary movements of the abdomen produced complete excursions of the lever. The downward deflections were produced by both ventrally directed twitches and peristaltic movements of the abdomen. (1) The first hyperactive period, (2) the quiescent period, and (3) the second hyperactive period. Arrow identifies the moment of adult emergence. (Bottom) Integrated efferent activity from the right nerve I of ganglion A_2 after addition of the eclosion hormone to a semi-isolated, deafferented abdominal nerve cord. Hormone was added to the preparation 40 minutes before the onset of the first burst. Letters refer to bursts presented in an expanded form in Fig. 2. Fig. 2 (right). Examples of integrated spontaneous bursts recorded from the semi-isolated, deafferented nerve cord after addition of the eclosion hormone. (Top) Electrodes placed sequentially on the right first roots of ganglia A_2 and A_3. (Bottom) Electrodes placed bilaterally on right and left first roots of A_2. Bursts A–C and G–I are of the rotational pattern typically observed during the first (early) hyperactive period. Bursts D–F and J–L are of the peristaltic pattern observed during the second (late) hyperactive period. Vertical line equals 100 spikes per second; horizontal line, 10 seconds.

2) The following quiescent phase also lasts about 0.5 hour. During this period the activity ranges from a reduced frequency of abdominal rotations to a complete cessation of movement.

3) The beginning of adult eclosion occurs with the onset of a second hyperactive phase. In this phase, movements consist primarily of peristaltic waves directed anteriorly. During the propagation of a wave, a given segment contracts bilaterally and then relaxes concomitantly with the contraction of the next anterior segment. These peristaltic movements assist the moth in shedding the pupal skin.

The major movements of the cecropia abdomen are accomplished by three paired bands of muscle (the dorsal, lateral, and ventral intersegmental muscles) that line the fourth through sixth abdominal segments (*3*). The abdominal nervous system consists of four ganglia. The first three (A_1 to A_3) are single ganglia, each of which is supplied with two paired and one unpaired nerve (Fig. 2). Nerve I innervates the three groups of intersegmental muscles (*4*). The fourth ganglion (A_4) is a compound one and supplies the intersegmental muscles of segment 6 as well as the minor musculature in the remaining posterior segments.

Electrical recordings were made from partially dissected, isolated abdomens from pharate cecropia moths (*5*). Each abdomen was severed from the thorax and thoroughly washed (*6*). It was then laid on its dorsal side, was pinned shut along the anterior margin, and was opened ventrally. The nerve cord was exposed by removing as much fat body as necessary. In deafferented preparations, peripheral nerves from ganglia A_1 to A_4 (*7*) were severed carefully so as not to damage the tracheal supply to the nerve cord.

We used standard suction-electrode techniques to record neural activity from both intact and deafferented preparations. Glass suction electrodes were applied either to the first roots on both sides of the same ganglion (usually ganglion A_2), or to the first roots on the same side of sequential ganglia (A_2 and A_3). Signals were differentially amplified and recorded on two tracks of a tape recorder (Ampex SP300) while being simultaneously monitored on an oscilloscope; tape records were then integrated (*8*). The resulting polygraph records thus gave the integrated nerve-spike activity of all efferent spikes (deafferented preparations) picked up by the two electrodes. During recordings on intact preparations, no attempt was made to distinguish between afferent (sensory) and efferent (motor) activity.

In control experiments additional cold Weevers solution was added to either deafferented or intact preparations. During the following 3 to 4 hours of recording, electrical activity consisted of a moderate level of spontaneous background activity. None of the three control preparations emitted more than three bursts during the entire recording period.

The addition of homogenates containing the eclosion hormone (*9*) to intact preparations was followed by a lag period of approximately 0.5 hour before the onset of the pre-eclosion behavior. During the first hyperactive period, the abdomen attempted rotary movements. The quiet phase followed, and then the second hyperactive period appeared, comprised of the peristaltic waves directed anteriorly, a characteristic of the beginning of eclosion. The electrical activity consisted of frequent bursts during the first phase, a quiet second phase, and then a second period of bursts.

The eclosion hormone elicited the same pattern of electrical activity in deafferented preparations as that seen in intact preparations. The three-part behavior pattern of the cecropia was clearly evident (Fig. 1), and the relative timing of the periods was comparable to that seen in intact animals.

Two major types of patterned electrical bursts were recorded from the deafferented nerve cords. The first type resembled that seen during rotary movements of the abdomen. These "rotational bursts" lasted up to 20 seconds and consisted of multiple volleys of firing. The typical interval between peak frequencies was 3 to 5 seconds. During a burst, a clear left to right alternation was evident (Fig. 2, G–I). The efferent activity from nerve I of ganglion A_2 was essentially identical with the activity from the corresponding ipsilateral root of A_3 (Fig. 2, A–C).

The second type of burst, the "peristaltic burst," showed a completely different pattern. In this type, the efferent outputs of the right and the left nerve I of A_2 were essentially identical (Fig. 2, J–L). In most cases each burst consisted of only one volley of firing (3 to 5 seconds in duration) followed by a small afterburst. Occasionally, certain preparations (Fig. 2, D and E) showed

bursts of multiple volleys, but here the last volley was always the largest. In nerve I of A_3 only single volley bursts were found. As with those in A_2, the bursts in A_3 characteristically ended abruptly and were followed by a small afterburst. It is important to note that the bursts in A_3 preceded the major volley in A_2 by 2 to 3 seconds (Fig. 2, D and E). This pattern serves to generate the peristaltic contractions that are observed in the intact animal.

The first hyperactive period that was provoked by application of hormone involved primarily rotational bursts. In the beginning, the bursts were relatively simple, consisting of one or two volleys. As the hyperactive period progressed, the complexity of the bursts increased, and those containing four or more volleys were not uncommon. The occurrence of rotational bursts continued into the quiet period. As in intact animals, activity during this second phase ranged from a decline in the frequency of bursts to a complete cessation of bursting. The appearance of the peristaltic pattern came with the onset of the third phase. Typically, this period was announced by a multivolley burst. Following this, the peristaltic bursts occurred at relatively constant intervals of 2 to 3 minutes. In occasional preparations, rotational bursts were mingled with those of the peristaltic type.

The response of deafferented preparations to the eclosion hormone clearly shows that the rotational and peristaltic movements arise from centrally generated motor patterns. Moreover, these patterns are parts of a central behavioral program that lasts approximately 1.5 hours and involves both the temporal arrangement of bursts and the progression from one burst type to the next. The information for repetitive oscillatory motor output (*10*) as well as rapid escape responses and postural changes (*11*) can be prepatterned in the nervous system. The pre-eclosion behavior differs from that in the above systems in that it involves a nonrepetitive sequence that lasts more than 1 hour and involves a number of distinct behavioral acts.

As with pheromones (*12*), the roles of hormones in behavior can be divided into two classes: "primers" and "releasers." Unlike pheromones, which are mainly releasers, hormones appear to serve typically a primer function; that is, the hormone alters the responsiveness of the nervous system so that a given set of stimuli evoke a new behavioral response. One such example in insects is the effect of juvenile hormone in promoting the maturation of adult reproductive behavior (*13*). A neurophysiological correlate of this type of primer function is seen in the action of various hormones on the level of spontaneous background activity in the insect central nervous system (*14, 15*). By contrast, the factor from the cockroach corpora cardiaca which causes a rhythmic bursting in the phallic nerve (*15*) serves as a releaser. The eclosion hormone serves a similar function in that it acts directly on the silk moth abdominal ganglia to release the appropriate prepatterned behavior.

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5. The term "pharate moth" refers to a moth prior to eclosion, that is, a moth which is still encased in the pupal cuticle [H. E. Hinton, *Nature* **157**, 552 (1946)]. For the present experiments it was important to have preparations that had not already been exposed to the eclosion hormone. To assure this, the moths emerging on a given day (as evidenced by the full resorption of the molting fluid) were decapitated just before the lights were turned on. [In the photoperiod (LD 17 : 7) to which the cecropia were exposed, the brain releases the eclosion hormone shortly after the lights are turned on.] For the remainder of the day, the abdomens were taken from the decapitated animals as needed.
6. A needle was inserted into the lumen and the abdomen was thoroughly washed out with 15 ml of cold Weevers solution [R. deG. Weevers, *J. Exp. Biol.* **44**, 163 (1966)]. During this procedure, we removed the gonads, gut, rectal sac, and as many of the Malpighian tubules as possible.
7. In the earlier preparations, the nerves to the genitalia from A_4 were left intact because of their intimate association with the trachea. The presence or absence of this innervation proved to be inconsequential.
8. Tape records of nerve activity were played back through a pair of window discriminators which were set to trigger on all spikes regardless of amplitude. The resulting trains of uniform pulses were then led to a pair of simple RC integrators (time constant, 0.1 second), and the integrated output of each data track was recorded on separate penwriter channels of a Grass polygraph.
9. The eclosion hormone was prepared from the brains and corpora cardiaca of two pharate moths. The organs were homogenized with 40 μl of Weevers solution in a ground-glass homogenizer. The entire homogenate was routinely added to the preparation at the onset of recording.
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Human Motor Cortex: Sensory Input Data from Single Neuron Recordings

Abstract. *Recordings were made from single neurons in the hand area of the human motor cortex while peripheral physiologic stimuli were applied. Such cells responded only to active and passive hand movements. Tactile and auditory (click) stimuli were ineffective. The majority of cells were activated only by movements of the contralateral hand, but a significant number (4 of 16) could be excited if a given movement was made by either hand. Of the cells responding to active movement, some showed an increased discharge before onset of the voluntary action. Such cells were excited by the same movement executed passively, a result that indicates sensory feedback from receptors activated by that movement.*

In a study of sensory input to the motor cortex (*1*), human subjects showed responses in the motor hand area which were evoked by electrical stimulation of the contralateral median nerve (MN). Stimulation of the ipsilateral MN and auditory (click) stimulation, both of which elicited responses in cat and squirrel monkey, were ineffective in man. Those observations suggested that the human motor cortex, compared with the homologous animal