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INTERACTION BETWEEN ABDOMINAL GANGLIA DURING THE PERFORMANCE OF HORMONALLY TRIGGERED BEHAVIOURAL PROGRAMMES IN MOTHS

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SUMMARY

1. The isolated chain of four abdominal ganglia of *Hyalophora cecropia* has previously been shown to respond to the eclosion hormone by generating a pre-eclosion motor programme followed by the eclosion programme.

2. Abdominal nervous systems reduced at any two ganglia could still generate both programmes.

3. Selective addition of hormone to individual ganglia of the intact abdominal CNS resulted in the coordinated performance of both programmes by the entire CNS.

4. In the eclosion programme, burst frequency was little influenced by which ganglion was exposed to hormone but in many cases the eclosion waves were initiated by the neurones in the treated ganglion rather than at the normal site in the terminal ganglion.

5. When ganglia were removed from hormone-treated preparations during eclosion, the remainder of the chain showed a transient disruption in the bursting frequency but the frequency often eventually returned to pre-cut levels. Removal of anterior ganglia had no effect on the patterning of posterior bursts but removal of posterior ganglia resulted in a permanent reduction in the length of eclosion bursts in anterior ganglia.

6. It was concluded that the information for both the pre-eclosion and eclosion programmes is patterned into each ganglion of the abdominal chain. For the pre-eclosion behaviour, the endogenous programme becomes progressively longer in more posterior ganglia and each ganglion appears to have mutually exciting interactions with the other ganglia in the chain. In the intact animal the most anterior ganglion appears to drive the behaviour. By contrast, the eclosion behaviour also has segmental burst generators but they appear very similar in their properties. Each burst generator has an excitatory input on to the next anterior ganglion and inhibitory influences on posterior ganglia. Normally, the most posterior ganglion serves as driver for the eclosion behaviour.

INTRODUCTION

In the giant silkmoths, a peptide hormone, the eclosion hormone, triggers a stereotyped behavioural sequence which enables the moth to escape from the pupal cuticle and cocoon (Truman & Riddiford, 1970; Truman, 1971). The sequence begins with a

series of abdominal movements: firstly, pre-eclosion behaviour lasting about 60 min and then eclosion behaviour lasting about 10 min (Truman, 1978). The underlying pattern of central nerve impulses has been characterized by recording from the dorsal nerves (the first pair of lateral nerves) of the abdominal ganglia (Truman & Sokolove, 1972; Truman, 1978) and can be triggered by the direct action of the eclosion hormone on the isolated abdominal cord (Truman, 1978). The present paper examines the relationship of the various abdominal ganglia in the generation of the pre-eclosion and eclosion behaviours.

METHODS AND MATERIALS

Hyalophora cecropia were wild-collected animals purchased as pupae from dealers, or progeny from wild stock reared on leaves or an artificial diet (Riddiford, 1968). Pre-emergence (pharate) moths which had completed resorption of moulting fluid were sensitive to the eclosion hormone and they were selected as described by Truman (1978).

The initial connective transection experiments were performed on the de-afferented nervous system in isolated abdomens (Truman & Sokolove, 1972). Later experiments were done with the isolated chain of abdominal ganglia, bathed in a modified Weevers' saline (Weevers, 1966) and supplied with air through cannulated tracheal trunks (Truman, 1978). Motor activity was monitored through the segmental dorsal nerves and data were recorded on magnetic tape and integrated as previously described (Truman, 1978). For each preparation the taped data were analyzed and the patterning of each motor burst examined. Most bursts could be readily classified as either rotational or eclosion bursts using the criteria listed below. These determinations were the basis for the schematic representations of the motor responses from the cords.

To apply hormone to individual ganglia, one or two silicone grease (Dow Corning) partitions were laid transversely across the connectives. In the early experiments, after a recording session amaranth dye was added to the chamber containing the hormone to check for leakage through the grease. In later experiments 20000 cpm of [^{3}H]inulin was supplied to the appropriate compartment at the time of hormone addition. Preparations that showed any signs of leakage were discarded. No attempt was made to examine the possibility of transport of hormone down the connectives within the CNS.

Extracts with eclosion hormone activity were obtained by homogenizing the corpora cardiaca from pharate *Manduca sexta* in a small volume of saline. Extract was added to the preparations in an amount that would give a final concentration of approximately two corpora cardiaca pairs per ml.

RESULTS

1. *Transaction of the abdominal connectives before hormone exposure*

The pre-eclosion motor programme consists of two parts of equal duration: the active and the quiet periods. The active period is composed of frequent motor bursts that show 'rotational' patterning; during a burst, ipsilateral roots along the chain of ganglia show synchronous volleys of motor firing and the volleys alternate between

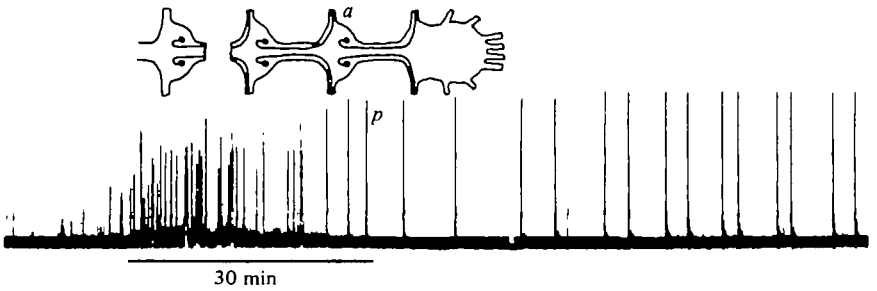

Fig. 1. Integrated record of the spontaneous motor activity evoked by addition of hormone to an abdominal CNS whose connectives had been cut behind A_3. *a*, Location of recording electrode; *p*. first eclosion burst. Record begins 50 min after addition of hormone.

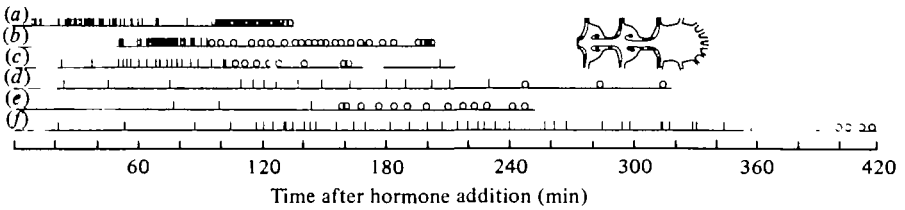

Fig. 2. Schematic representation of the dorsal nerve motor activity evoked by addition of eclosion hormone to abdominal systems consisting of $A_4+A_5+A_6$. Circles are eclosion bursts; vertical lines represent bursts having a rotational patterning. The end of the horizontal base line marks the termination of recording.

right and left roots. The following quiet period is characterized by a marked decline in the frequency of rotational bursts. The pre-eclosion programme lasts 60 min in intact animals but it may be lengthened to several hours in isolated abdominal cords (Truman, 1978). The motor programme for eclosion behaviour involves repetitive 'eclosion bursts', which begin in the most posterior ganglion and move anteriorly, with bilateral roots of a given ganglion bursting synchronously. This programme generates the anteriorly directed peristaltic waves that extract the moth from its pupal cuticle. These movements are normally terminated when the moth sheds the cuticle but in isolated abdominal cords the eclosion bursts may continue for a number of hours.

The abdominal nervous system of *H. cecropia* consists of a chain of three segmental ganglia (A_3, A_4 and A_5) and a compound terminal ganglion (A_6). To determine to what extent the nervous system could be reduced and still produce the proper motor programme, preparations were subdivided by transection of the connectives at various levels, hormone added, and the motor output of the fragments recorded. It is important to note that in moths 80–90% of the motor neurones whose axons are in the dorsal nerve which supplies a particular segment have their cell bodies and dendritic branches in the next anterior ganglion (Taylor & Truman, 1974). Consequently, the cutting of the connectives at a particular level abolishes most of the motor activity that can be recorded in the next posterior dorsal nerve.

In early experiments the connectives between A_3 and A_4 were severed. Attempts at long-term monitoring of the activity of A_3 motor neurones by recording from the connectives met with little success. Consequently, only data from the posterior

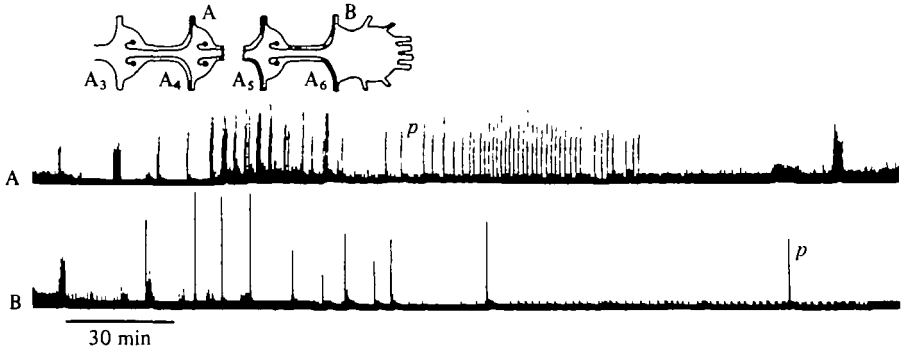

Fig. 3. Simultaneous integrated records of the spontaneous motor activity from two dorsal nerves after exposure of the abdominal nervous system to the eclosion hormone. The connectives had been transected behind A_4 prior to hormone addition. Traces A and B recorded from from positions A and B on inset, respectively; *p*, first eclosion burst recorded in each root. Records start 25 min after addition of each hormone.

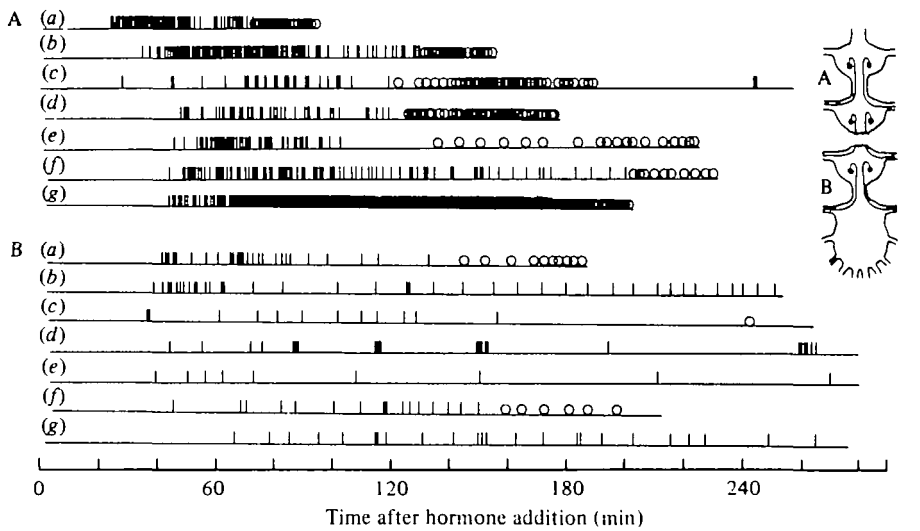

Fig. 4. Schematic representation of dorsal nerve motor activity evoked by addition of eclosion hormone to abdominal nervous systems whose connectives had been transected behind A_4. A, Records from A_3+A_4; B, records from A_5+A_6, as shown on inset. The same lower case letters are given to pairs of ganglia from the same individual. Symbols as in Fig. 2.

set of three ganglia ($A_4+A_5+A_6$) are presented (Figs. 1, 2). Upon exposure to hormone, two of the preparations (Fig. 2*a*, *f*) showed a complete pre-eclosion programme, consisting of both active and quiet phases, and then eclosion. Three more responded with the active phase of the pre-eclosion programme (Fig. 1, 2*b–d*) but this was followed immediately by eclosion rather than by a quiet period. In the last preparation (Fig. 2*e*) eclosion bursts started about 160 min after addition of hormone but they were not preceded by an organized pre-eclosion behaviour. These data show that the intact chain of four ganglia is not required for the generation of both programmes, but the disruption of the chain may have some minor influences on the organization of the pre-eclosion sequence.

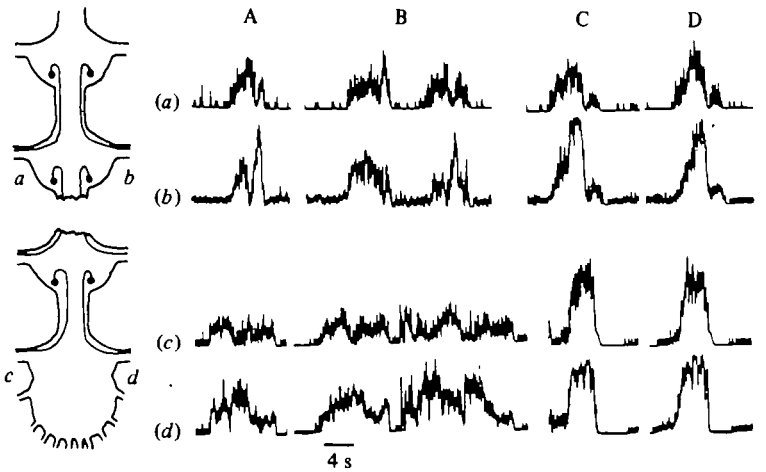

Fig. 5. Examples of integrated motor bursts recorded from pairs of ganglia A_3+A_4 and A_5+A_6 after exposure to the eclosion hormone. (A, B) bursts during the active phase of the pre-eclosion behaviour (C, D) bursts during the eclosion behavior. Lower case letters show the positions of recording electrodes.

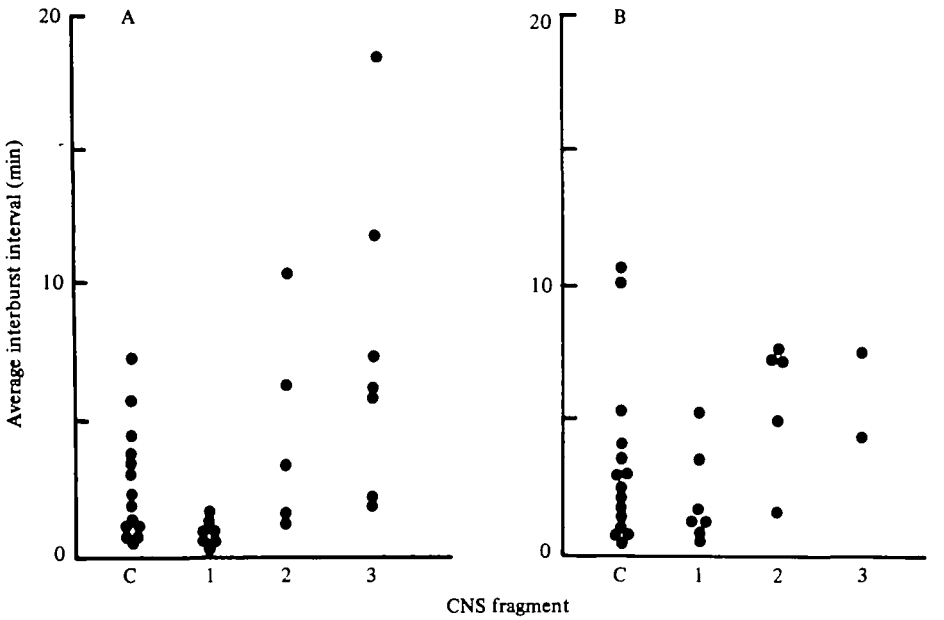

Fig. 6. The average interburst intervals seen in various hormone-treated, CNS fragments during (A) the active phase of the pre-eclosion behaviour and (B) the eclosion behaviour. (C) The intact, isolated abdominal CNS (from Truman, 1978); 1, A_3+A_4; 2, $A_4+A_5+A_6$; 3, A_5+A_6. Each dot represents a single preparation.

In seven deafferented nervous systems, the connectives between A_4 and A_5 were transected and the motor activity of the resulting pairs of ganglia were monitored through the dorsal nerves of A_4 and A_6 respectively. Addition of eclosion hormone evoked bursting in all seven of the A_3+A_4 pairs that were tested (Figs. 3A, 4A). Bursts appeared within 25–60 min and showed a distinct rotational patterning. In six of the

seven preparations (Fig, 4A, *a–f*) the rotational bursts continued at a high frequency for 30–40 min and then the burst frequency markedly declined into a period of relative quiet. In the seventh case (Fig. 4A, *g*) the quiet period was absent. All of the A_3+A_4 pairs also showed the eclosion programme. The sequential patterning of the eclosion bursts could not be determined because most of the motor axons in the A_3 dorsal nerve had necessarily been severed while making the preparation, but the eclosion patterning could be recognized as brief, bilaterally symmetrical bursts (Fig. 5). Thus, the anterior two abdominal ganglia can generate both the pre-eclosion and eclosion programmes in response to hormone exposure.

Figs. 3B, 4B show the result of exposure of the posterior pair of ganglia (A_5+A_6) to the eclosion hormone. In all cases the preparations responded with rotational bursts but the bursting frequency was always lower than that displayed by the anterior pair from the same animal. The division of the pre-eclosion programme into an active and a quiet period was seen in two preparations (Figs. 4B, *a*, *c*) while the quiet period was clearly absent in a third (Fig. 4B, *f*). Experiments with the remaining four preparations were terminated before the end of the pre-eclosion period, after about 4 h. Since later experiments showed that the pre-eclosion programme can last for over 6 h, it is possible that the above four preparations would have shown a quiet period and eclosion had the experiments been prolonged. However, the observation that some of the A_5+A_6 pieces did show a complete pre-eclosion programme followed by eclosion indicates that the posterior ganglia also contain the neural information for both programmes.

The results presented above show that the neural information for the pre-eclosion and eclosion behaviours is repeated at least twice in the chain of abdominal ganglia. In the case of the pre-eclosion programme, the A_3+A_4 pairs consistently generated patterns with short active periods and closely spaced rotational bursts (Fig. 6A). The variability in interburst intervals among these pairs was less than that observed in the intact isolated CNS preparations (Truman, 1978). In posterior sets of ganglia, the average interburst intervals were more variable and greatly lengthened. In the case of the eclosion programme, the frequency of bursting seemed less dependent on the part of the CNS that was used (Fig. 6B). The anterior pair of ganglia tended to show shorter interburst intervals than did the posterior pairs, but in all cases the values were within the range observed for the intact abdominal CNS.

2. *Addition of hormone to selected ganglia of the intact abdominal CNS*

(*a*) *Temporal organization of the pre-eclosion and eclosion programmes*

In initial experiments, hormone was added to pairs of ganglia in the intact chain, as described in Materials and Methods. As seen in Fig. 7A, exposure of only A_3+A_4 of the intact CNS to hormone resulted in the triggering of the active phase of the pre-eclosion programme in 5 of 6 cases. In 4 of the preparations this was followed by a quiet period and eclosion. When hormone was added to A_5 and A_6 the pre-eclosion active periods tended to show long interburst intervals and a quiet period was evident in most of the preparations (Fig. 7B). Only 2 of the 5 preparations showed eclosion

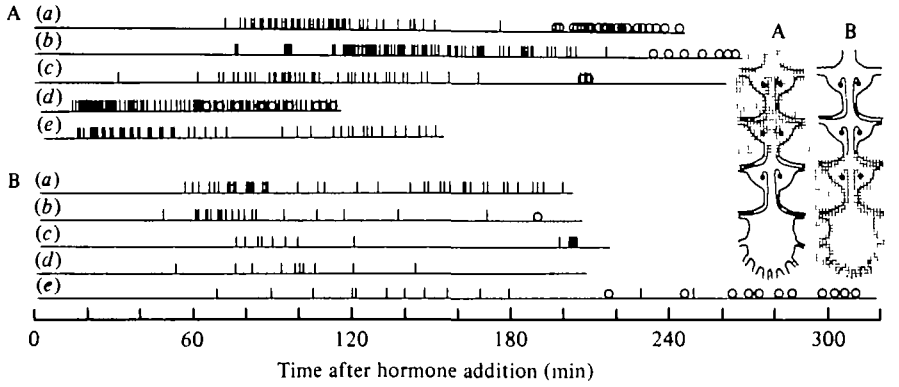

Fig. 7. Schematic representation of the dorsal nerve motor activity evoked by the addition of hormone to various ganglia of the intact abdominal CNS. (A) To A_3+A_4; (B) to A_5+A_6. Symbols as in Fig. 2.

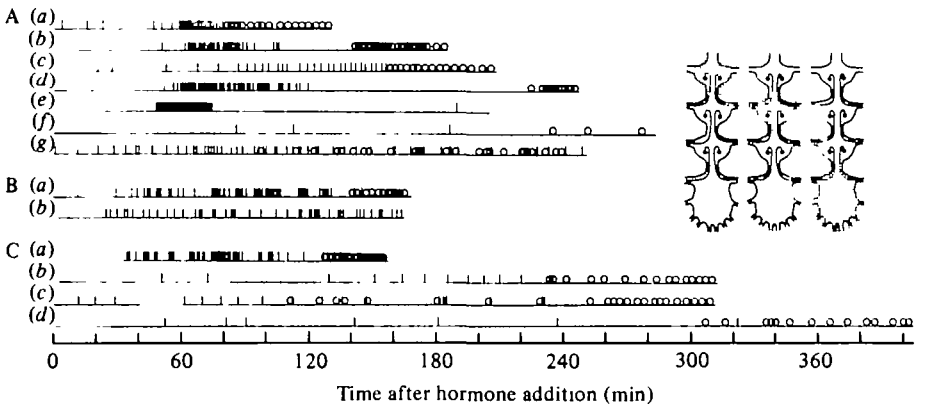

Fig. 8. Schematic representation of the dorsal nerve motor activity evoked by addition of hormone to various ganglia of the intact abdominal CNS (A) to A_3, (B) to A_4, (C) toA_6. Symbols as in Fig. 2.

bursts but in some cases (e.g. Fig. 7B, *d*) the recording period may not have been long enough to allow the eclosion programme to appear.

In further experiments hormone was added to individual ganglia of the intact chain. In nine preparations only A_3 was exposed to hormone. Of these, seven showed a motor response to the treatment and are represented in Fig. 8A. Six of the 7 generated a pre-eclosion active phase which was followed by a quiet period in 2 instances (Fig. 8A, *b*, *d*); a third case (8A, *e*) is uncertain because no eclosion was subsequently seen. In 3 other preparations, eclosion bursts were seen immediately after the end of the active period (Fig. 8A, *a*, *c*, *g*). In the seventh nervous system eclosion began about 220 min after addition of hormone without a preceding pre-eclosion programme (Fig. 8A, *f*).

The rotational bursts of the active period were generated in 2 of 4 nervous systems after A_4 was supplied with hormone (Fig. 8B). In both cases, however, a clear quiet period was not evident and only one CNS showed eclosion. Exposure of A_5 was not

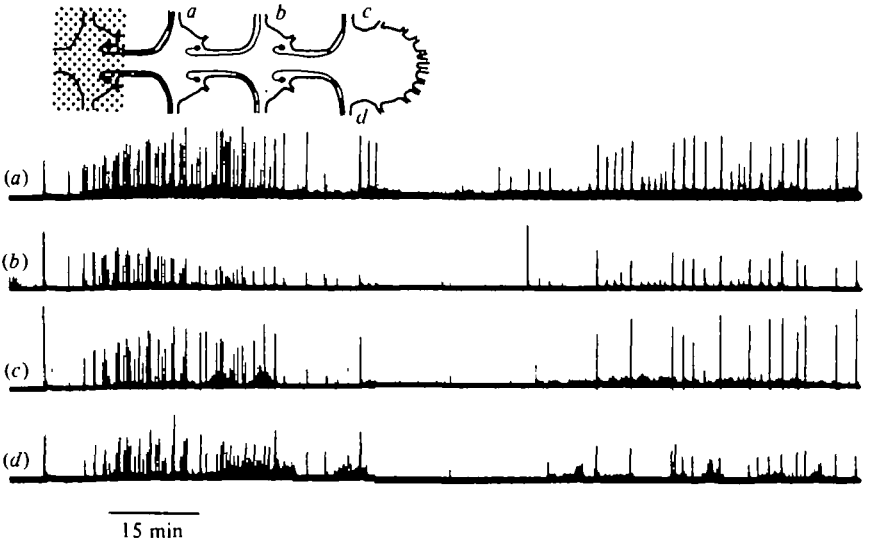

Fig. 9. Integrated records of spontaneous motor activity from various dorsal nerves of an intact abdominal CNS after addition of hormone to A_3 (stippled ganglion in inset). Letters refer to location of recording electrodes. Record starts 45 min after addition of hormone.

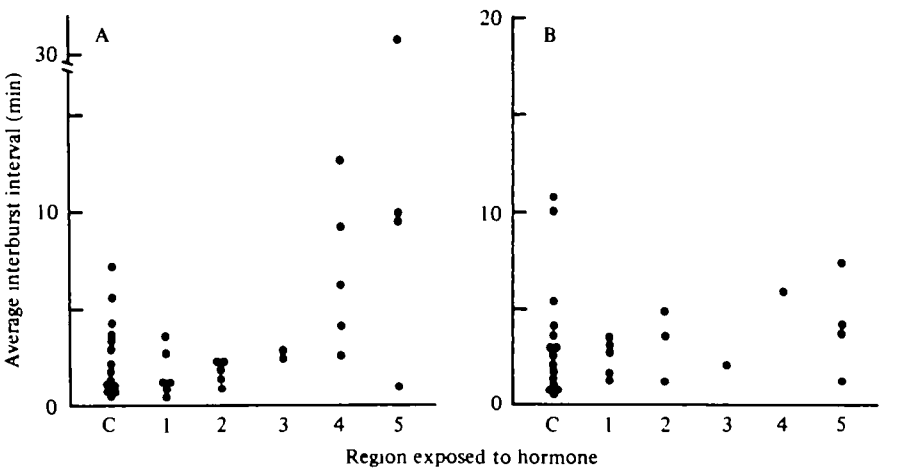

Fig. 10. The average interburst intervals seen in intact abdominal CNS preparations after the exposure of selected ganglia to hormone. (A) Active phase of pre-eclosion behaviour; (B) the eclosion behaviour. (C) the entire CNS exposed (from Truman, 1978); 1, A_2; 2, A_3+A_4; 3, A_4; 4, A_5+A_6; 5, A_6.

attempted but hormone was applied to A_6 in 6 preparations. Four of these responded with the generation of the pre-eclosion and eclosion programmes (Fig. 8C). Two of the 4 showed distinct quiet periods (Fig. 8C, *a*, *d*) while one omitted the quiet period entirely (Fig. 8C, *b*). The other (Fig. 8C, *c*) was interesting in that eclosion bursts were interspersed through what appeared to be the late part of the active period and the quiet period of the pre-eclosion programme.

In the above experiments exposure of an individual ganglion to hormone resulted in the play-out of the motor programmes from the entire abdominal CNS including regions not exposed to the hormone. This is shown for ganglion A_3 in Fig. 9.

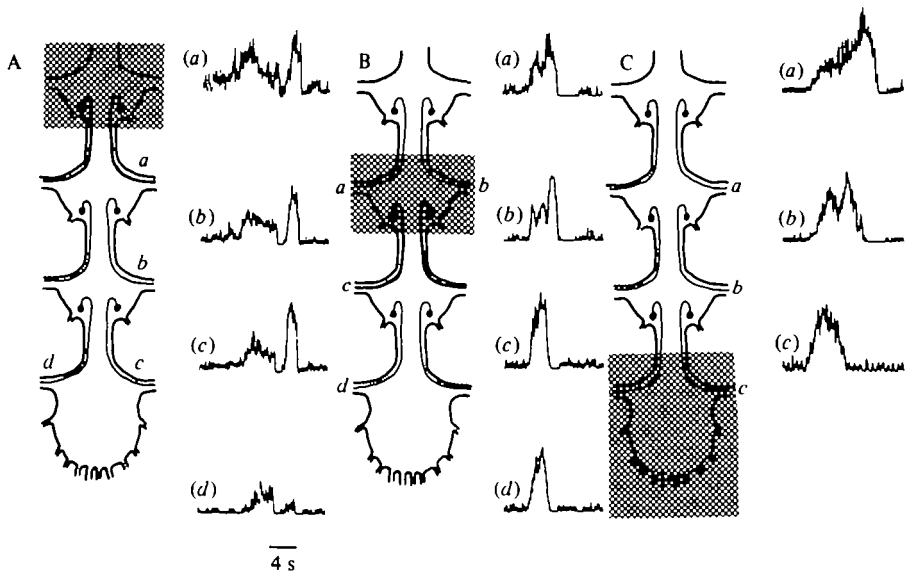

Fig. 11. Integrated records of the typical eclosion bursts seen after exposure of individual ganglia of the intact chain to hormone. (A) Exposure of A_3. (B) of A_4, (C) of A_6. Drawing to the left of each record shows treated ganglion (cross-hatched) and location of recording electrodes.

As with the connective transection data, the above experiments indicate that the frequency of occurrence of rotational bursts during the pre-eclosion behaviour varies according to the ganglion which is exposed to the hormone. From Fig. 10A, it is clear that addition of hormone to the anterior ganglia resulted in responses that consistently showed short interbursts intervals. The average values obtained from these preparations were similar to those seen when the entire abdominal CNS was exposed to hormone. When posterior ganglia were treated, the resultant pre-eclosion programme showed longer interburst intervals and a longer overall duration. In contrast to the pre-eclosion programme, the frequency of eclosion bursts was little influenced by which part of the nervous system was exposed to hormone (Fig. 10B).

(*b*) *Structure of motor bursts*

The patterning of the pre-eclosion rotational bursts showed extreme variation, but similar variation is also seen when the entire nerve cord is exposed to hormone (Truman, 1978). In most cases the motor output from unexposed ganglia faithfully mimicked that from the exposed part of the CNS irrespective of whether the hormone was added to anterior or posterior ganglia in the chain.

In contrast, the eclosion bursts often showed variations in patterning which were a function of the particular ganglion that was exposed to hormone. When only A_6 or A_5+A_6 were treated with hormone, the subsequent eclosion bursts always showed a normal patterning with the eclosion wave starting in A_6 and proceeding anteriorly (Fig. 11C).

After treatment of only A_4, the initial eclosion bursts began in the A_5 dorsal nerve (which contains the axons of the A_4 motor neurones) and then progressed anteriorly in the normal fashion (Fig. 11B). The A_6 roots burst in synchrony with those of A_5

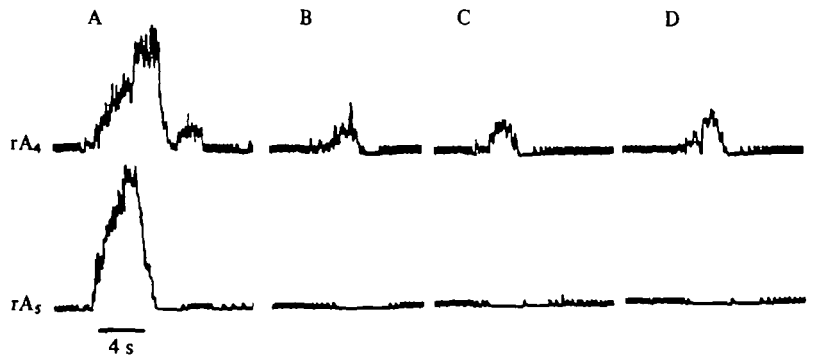

Fig. 12. Integrated eclosion bursts from isolated CNS preparation in which the posterior roots frequently failed to fire during attempted eclosion bursts by the anterior ganglia. (A) Normally patterned eclosion bursts; (B)–(D) examples in which posterior root shows only inhibition of tonic motor activity. rA_4 and rA_5 are the right dorsal nerves from A_4 and A_5 respectively.

rather than before them. Eclosion bursts of similar patterning were also seen after addition of hormone to A_3+A_4. It should be noted that some of the above nervous systems also showed normally patterned eclosion bursts. These usually appeared well into the programme after a series of aberrant bursts.

Exposure of A_3 to hormone resulted in three types of eclosion bursts. In one type, illustrated in Fig. 11A, the dorsal roots from A_4, A_5 and A_6 burst in synchrony. This was followed by a brief period of inhibition and then a short intense burst. The latter burst was presumed to be an exaggerated version of the post-inhibitory rebound that is often seen after normal eclosion bursts. In a second type of burst, which was less frequently observed, the burst from the neurones of A_3 was not accompanied by motor activity from the posterior ganglia. In these cases the burst in A_3 was reduced and the posterior roots showed a distinct inhibition of tonic activity (Fig. 12). The third type of burst that was seen had the normal eclosion patterning. These last bursts typically showed up late in the eclosion period.

Thus, in many cases, the treatment of a single ganglion with the hormone resulted in the treated ganglion serving as the initiator of the eclosion wave. The wave then progressed normally through anterior unexposed ganglia but posterior ganglia either burst in synchrony with the initiating ganglion or failed to burst at all.

3. *Transection of connectives during the eclosion programme*

The necessity of particular ganglia after the initiation of the eclosion programme was also examined. As seen in Fig. 13A, the ablation of A_3 essentially abolished the motor output through the dorsal nerve of A_4 because the A_3 motor axons were severed in the process. However, the intensity and duration of eclosion bursts in more posterior roots was unaffected. By contrast, removal of A_6 caused an immediate shortening of burst duration in the anterior ganglia although the phase relationships of the anterior roots remained unaffected (Fig. 13B). Removal of A_5 further reduced the duration of subsequent anterior bursts. Thus, during the eclosion programme there are strong excitatory influences between ganglia that extend anteriorly.

The immediate effects of ganglion removal on the frequency of bursting were

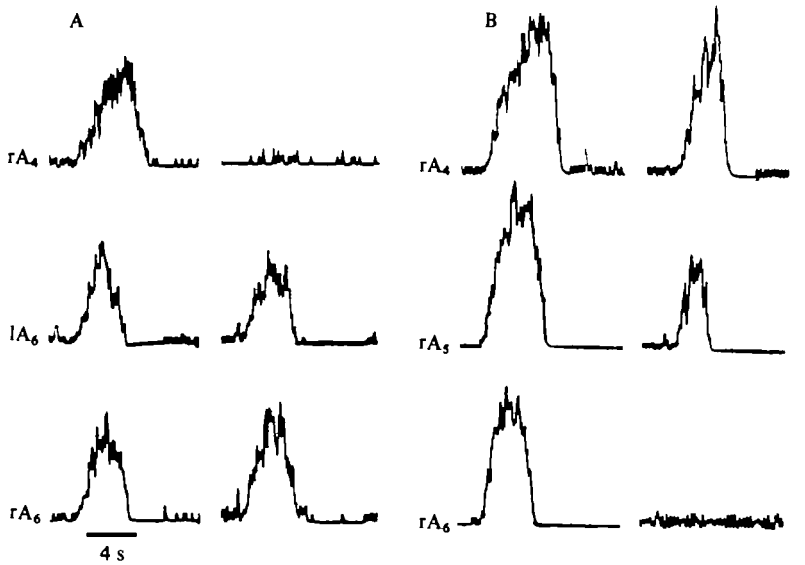

Fig. 13. Examples of integrated eclosion bursts before and after the removal of: (A) the most anterior (A_3) ganglion of the chain; (B) the most posterior (A_6) ganglion. Designation of motor roots as in Fig. 12.

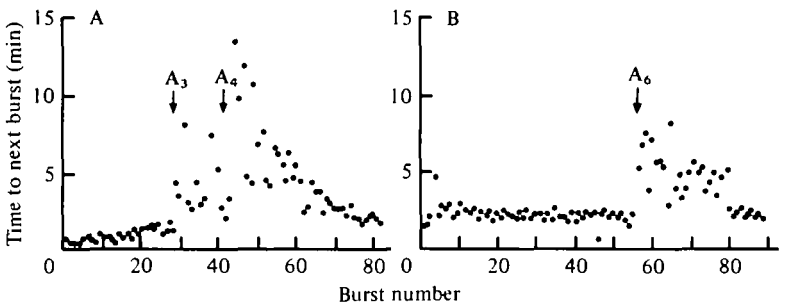

Fig. 14. The effect of the removal of various ganglia during the eclosion behaviour on the interval between successive bursts. (A) Removal of A_3 and then A_4; (B) removal of A_6.

inconsistent. Typically, removal was followed by a drop in frequency or the cessation of bursting but transient increases in frequency were also seen. But as shown in Fig. 14, after a time the frequency tended to return to the level that was seen before the transection. This return was observed after ablation of either A_3 or A_6.

DISCUSSION

One of the major problems in the study of the hormonal control of behaviour is the relationship of the hormone target cells to the circuitry that mediates that behaviour. Target cells have been shown to be separate from the mediational circuitry in the rat brain, in studies of the effect of oestrogen on lordosis behaviour (Pfaff *et al.* 1974, Modianos & Pfaff, 1976) and on the stimulaton of drinking by angiotensin II (Epstein, 1976). In insects, such a separation is likely in the hormonal release of copulatory behaviour in male cockroaches (Milburn & Roeder, 1962). However, for some be-

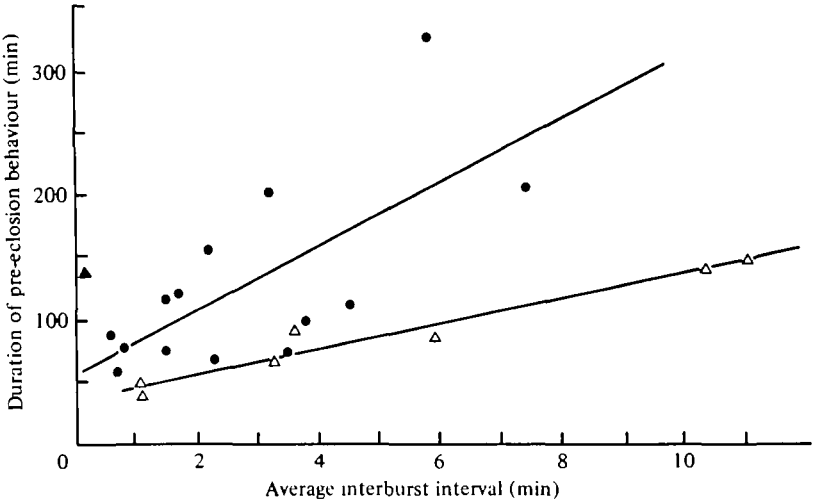

Fig. 15. Relationship of the interburst interval during the active period to the over-all duration of the pre-eclosion behaviour. Circles: intact isolated CNS preparations (from Truman, 1978); triangles: treated preparations which lacked a quiet period (see text). Lines are the least-squares plot through the two groups of data. The filled triangle (preparation in Fig. 2A, *g*) was not used in the computation.

haviour, part of the mediational circuitry can be a target for the hormone. For example, the motor neurones involved in androgen-dependent song production in the male zebra finch appear to be targets for androgens (Arnold, Nottebohm & Pfaff, 1976).

In the present study the relationship of the hormone-sensitive elements to the meditational circuitry is complex. The observation that the exposure of a single ganglion will release the pre-eclosion and eclosion programmes from the entire abdominal CNS implies that all of the mediational circuitry need not be exposed to the hormone for the programmes to be generated. It also follows that each ganglion tested in this fashion, and probably A_5 also, contain target elements for the hormone.

The connective transection experiments show that the abdominal nervous system can be reduced to as few as two ganglia and still generate both behavioural programmes in correct sequential fashion. Recording from an isolated ganglion was complicated by the anatomical arrangement of the motor neurones so it is not known whether a single ganglion can do likewise. A second important observation is that any pair of ganglia can respond but that the quality of response varies with the ganglia that are selected. In the case of the pre-eclosion programme, exposure of any set of abdominal ganglia to hormone resulted in the onset of rotational bursts after an appropriate latency, but the frequency of bursting was much lower when sets of posterior ganglia were exposed as compared to the anterior set (Fig. 6A). Similarly when hormone was added to selected ganglia of the intact abdominal CNS, the exposure of anterior ganglia resulted in the highest frequency of bursting (Fig. 10A). The presence of a quiet phase in the programmes generated by both the A_3+A_4 and the A_5+A_6 fragments showed that the information for this part of the pre-eclosion behaviour is also repeated at least twice in the abdominal CNS. However, a substantial percentage of the preparations did not show a quiet phase so it seems that some degree of interaction may occur between the segmental programmes to reinforce this part of the behaviour.

The absence of a quiet period in some of the above preparations could occur in two ways. The quiet period could be omitted entirely, halving the duration of the pre-eclosion behaviour. Alternatively, the active period could be extended to cover the entire pre-eclosion behaviour and consequently the duration of the behaviour would remain unchanged. To determine which was occurring, the duration of the pre-eclosion programme was plotted against the average interburst interval during the active period, and compared with the relationship in untreated preparations (cf. Truman, 1978). For seven of the eight preparations that had not shown a quiet period, this comparison indicated a length of the pre-eclosion behaviour that was about one-half of that expected from control preparations (Fig. 15). Thus, it appears that in these cases only the active phase of the pre-eclosion behaviour was read-out and that it was then followed immediately by eclosion. However, the data from the eighth preparation (shown in Fig. 2A, *g*) did not fit this relationship so other factors may also be involved in the disappearance of a quiet period.

The segmental organization for eclosion differs from that discussed above for the pre-eclosion programme. Of particular interest were the results of adding hormone to specific ganglia. In these cases the ganglion that was exposed to the hormone often served as the site of initiation of the eclosion wave. It appears that the eclosion burst generator and the hormone sensitive components to activate it are repeated in each ganglion in the chain. When the nervous system is uniformly exposed to hormone, then A_6 (the most posterior ganglion) undoubtedly serves as the driver of the pattern. It is of interest that during the eclosion programme in isolated abdomens, the initial eclosion waves may occasionally show segments contracting out of order (unpublished observations). Similarly, the first eclosion bursts shown by an isolated CNS sometimes show improper phase relationships between ganglia (Truman, 1978). These observations are consistent with the hypothesis that each ganglion has an independent eclosion generator and that an intermediate ganglion may serve as a driver if the A_6 generator is not yet fully activated.

Another feature of the patterning of eclosion bursts is that the duration of the burst becomes progressively longer in more anterior ganglia (e.g. Fig. 13). This increase in burst duration is not an endogenous property of the segmental burst generators because removal of a posterior ganglion causes an immediate reduction in the burst duration in all anterior ganglia. Thus, the various segmental burst generators appear to be approximately equivalent and the increase in duration of the motor burst is a product of additional excitatory input from more posteror ganglia. Thus, in respect to its segmental organization, the eclosion programme is similar to other multisegmental motor programmes in which each segmental ganglion has essentially equivalent oscillators which are connected together to give a coordinated motor output (Ikeda & Wiersma, 1964; Miller, 1974; Stein, 1978; Stent *et al.* 1978).

From the data presented above a model can be presented (Fig. 16) for the minimal segmental organization of the pre-eclosion and eclosion programmes. In the case of the pre-eclosion behaviour, each ganglion apparently contains a burst generator but the frequency and overall duration of these varies between ganglia. The burst generators appear to be mutually coupled to one another so that when one has been activated by the addition of hormone, it can drive other burst generators in both anterior and posterior ganglia. In the normal situation of the entire CNS being exposed

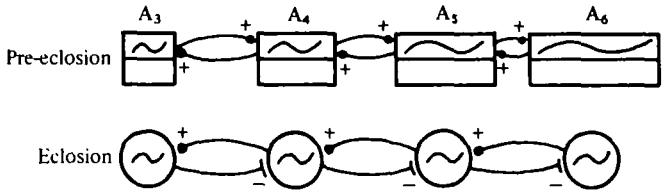

Fig. 16. Model for the minimal segmental (A_3, A_4, A_5 and A_6) interactions of the burst timers that generate the pre-eclosion and eclosion behaviours. The divided boxes represent the active and quiet phases of the pre-eclosion behaviour.

to hormone, A_3 probably serves as the pacemaker for the network. In the case of the eclosion behaviour, burst generators are also present in each ganglion but they appear similar to each other in their properties. The interaction between segments is polarized in that each burst generator appears to have excitatory input to the next anterior ganglion and inhibitory input onto posterior ganglia. In the intact animal, it appears that A_6 serves as the driver for the eclosion programme. Thus, these two hormonally released motor programmes show segmental organizations that are distinct from one another and are normally driven from opposite ends of the abdominal CNS.

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