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THE MECHANISM OF THE PUPAL GIN TRAP

III. INTERNEURONES AND THE ORIGIN OF THE CLOSURE MECHANISM

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INTRODUCTION

The properties of the sensilla which trigger the closure of the gin trap are not different from the properties of these to which the pupa is relatively indifferent (Bate, 1973*a*). Nevertheless the efferent neurones involved in closure behave in a way which suggests that they respond to a trap-specific input (Bate, 1973*b*). Therefore there must be a consistent difference in the destination of the axons from the two classes of sensilla within the central nervous system, a difference which first becomes apparent at pupation. No functional discrimination can be made among the axons from similar sensilla until the first junction of those axons with second-order neurones. At this point distinctive properties may be revealed by the connexions which each axon makes and by the response of the cells with which they are linked. The behaviour of the interneurones which connect the triggering sensilla with the motor neurones concerned with closure is therefore of great interest. Part of this chain runs in the connective between the ganglion where the sensory fibres terminate and the anterior ganglion which encloses the synaptic regions of the efferent neurones (Bate, 1973*b*).

The neurones concerned are small, and their activity is extracted from background activity in the connective by averaging. The method depends on the integrative properties of the cells concerned, so that its usefulness is limited. The recorded neurones, which have a simple relation with the stimulus, are part of a larger population, with which the sensilla are connected, from which information could be obtained by using more refined methods and more complex stimuli: by taking account, for example, of sequences of events in space and time rather than the very simple input which is considered here. It is likely, however, that some of the integrative properties of these rather special cells are shared by other neurones in the connective.

METHODS

Some experiments were performed on the preparation described previously (Bate, 1973*a*) but in addition two modifications were made to retain both halves of the animal for experiment:

Modification 1: the pupa was pinned out as before, with the opposite half standing up at right angles to it (Fig. 1*a*).

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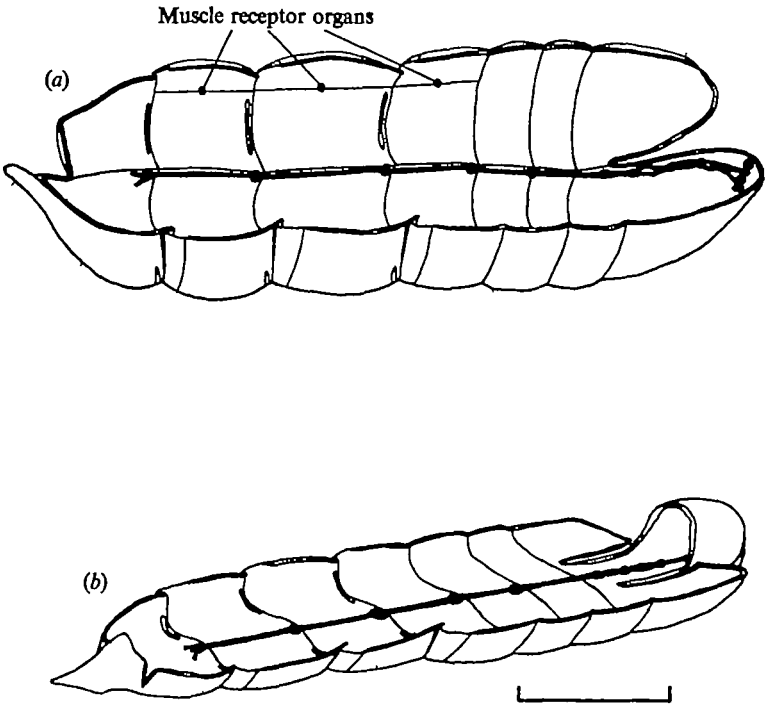

Fig. 1. Modifications to the original preparation (Bate, 1973*a*): (*a*) both halves are retained, one standing at right angles to the other to allow stimulation of the muscle receptor organs; (*b*) both halves are retained and laid flat for simultaneous stimulation of traps on opposite sides. Scale: 1 cm.

Modification 2: both sides of the pupa were pinned out flat, after partial separation from the head and tail (Fig. 1*b*).

The same techniques of stimulating and recording from nerve bundles were used as before (Bate, 1973*b*), but in some experiments an averaging technique was used to extract repetitive responses from background activity in the connective. Succeeding traces of the oscilloscope were triggered by the stimulus, superimposed and photographed. For some purposes the oscilloscope camera was rotated through 90° so that succeeding traces were recorded on film in sequence, one above the next.

Two linked pulse generators were used to deliver simultaneous outputs with independently variable voltage to separate stimulating electrodes.

RESULTS

The response recorded in the connective to a stimulus to nerve *B* (triggering sensilla; Bate, 1973*a*) follows 1:1 at a very constant latency (Fig. 2). It occurs only in the connective ipsilateral to the stimulated trap, and anterior to the ganglion in which the afferent fibres terminate. The recorded cell is therefore an interneurone which runs between the ganglia which enclose the terminals of the afferent and efferent neurones (Bate, 1973*b*).

The conduction velocity of the peak, calculated from the change in its latency when the recording electrode was moved along the connective, was 0·5 $msec^{-1}$. The afferent fibres conduct at a velocity of 0·6 $msec^{-1}$, and with these two values it is possible to

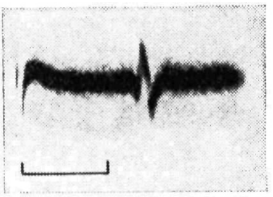

Fig. 2

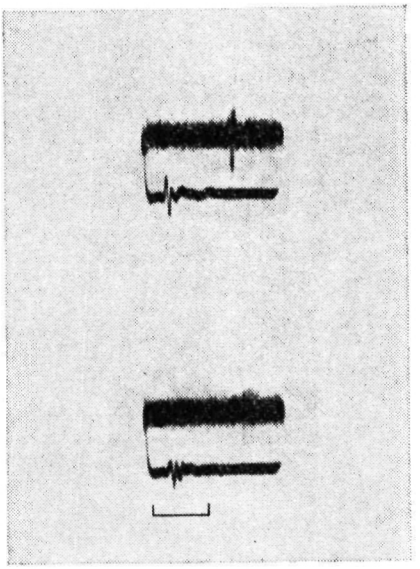

Fig. 3

Fig. 2. An interneurone recorded from the ipsilateral connective anterior to the ganglion where the stimulated afferents (nerve *B*, triggering sensilla) terminate. Stimulus to nerve *B*, 15 Hz; 25 traces triggered by the stimulus and superimposed. Time bar: 20 msec.

Fig. 3. Upper traces, as in figure 2; lower traces, compound action potential recorded from nerve *B*. The latency of the interneurone increases and becomes more variable as the amplitude of the stimulus to nerve *B* is reduced. Stimulus to nerve *B*, 15 Hz; 25 traces triggered by the stimulus and superimposed. Time bar 20 msec.

calculate the delay in the gangion where the afferent fibres terminate. In three separate experiments the values calculated in this way were 0·8 msec, 1·5 msec and 1·9 msec. These times suggest that the afferent fibres and the responding interneurone are separated by one, or possibly two junctions, using available estimates of synaptic delay (Boistel, 1968).

Inputs from the trap sensilla sum to fire the second-order cell, so that its latency varies with the amplitude of the stimulus to the afferent bundle (Fig. 3). Successive stimuli elicit responses of a constant amplitude, suggesting that a single interneurone is active.

Discriminations between individual afferent neurones must be completed before summation occurs. If the stimulating electrode is transferred from nerve *B* (triggering sensilla) to nerve *A* (non-triggering sensilla) in the same half-segment then it is no longer possible to record the 1 : 1 spike in the connective. This does not show that the neurone recorded when nerve *B* is stimulated is the only link between the trap sensilla and the efferent neurones, or that there are not similar cells connected with fibres from bundle *A*. A single inference is justified – the neurone responds to the combined input of a number of fibres in *B* and it does not respond in the same way to the summed activity of fibres in *A*. Therefore at this level, and in this neurone, there is a distinction between some of the fibres in *A* and some of the fibres in *B*.

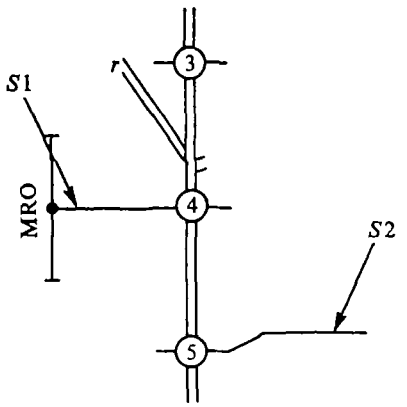

Fig. 4. Arrangement of stimulus and recording sites used in investigating inhibitory inputs driven by the MRO *S1*: mechanical or electrical stimulus to the MRO. *S2*: electrical stimulus to nerve *B*. *r*: recording site in the connective.

Inhibition by the contralateral muscle receptor organ

In addition to the excitatory input which the second-order cell receives from the trap sensilla, there is an inhibitory connexion which is driven by the output from the muscle receptor organ (MRO) contralateral to the muscles closing the trap. This receptor is stretched by the closure of the trap.

To investigate the role of this inhibitory input, the nerves from the trap in segment 5 were exposed on one side, while the contralateral half of the pupa, standing up at right angles (Fig. 1*a*), was cut free from the posterior end to the joint with segment 4. This free flap of cuticle was then attached to the arm of a micromanipulator so that it could be extended or relaxed about joint 4/5, so stretching and relaxing the MRO in segment 4 (Fig. 4).

At maximum stimulus amplitude to nerve *B* in segment 5 the interneuronal spike recorded in the connective was unaffected when the contralateral half of segment 4 was stretched. However, if the amplitude of the stimulus was reduced, so that the firing of the interneurone became more variable, and the MRO was stimulated by stretching segment 4, there was a transient (1–1·5 sec) inhibition of the interneurone. The method is imprecise, and the results of a more satisfactory experiment are shown in Fig. 5. Here an electrical stimulus was delivered to the afferent fibre of the MRO as a substitute for mechanical stretch (Weevers, 1966*b*). The electrical stimulus identifies the MRO positively as the source of the inhibition (a mechanical stretch probably excites many receptors besides the MRO). An input at 80 Hz from the afferent fibre of the MRO inhibited the spike in the connective, and the inhibition was maintained so long as the input continued. The difference in the time course of this effect and of the rapidly decaying inhibition caused by a mechanical stretch is a consequence of the adaptation of the MRO to a step displacement (Weevers, 1966*a*). The stretched MRO discharges transiently at frequencies as high as 120 Hz (Bate, 1972) which decline to a tonic level of 20–40 Hz at which the inhibitory input is no longer effective (Fig. 5*b*).

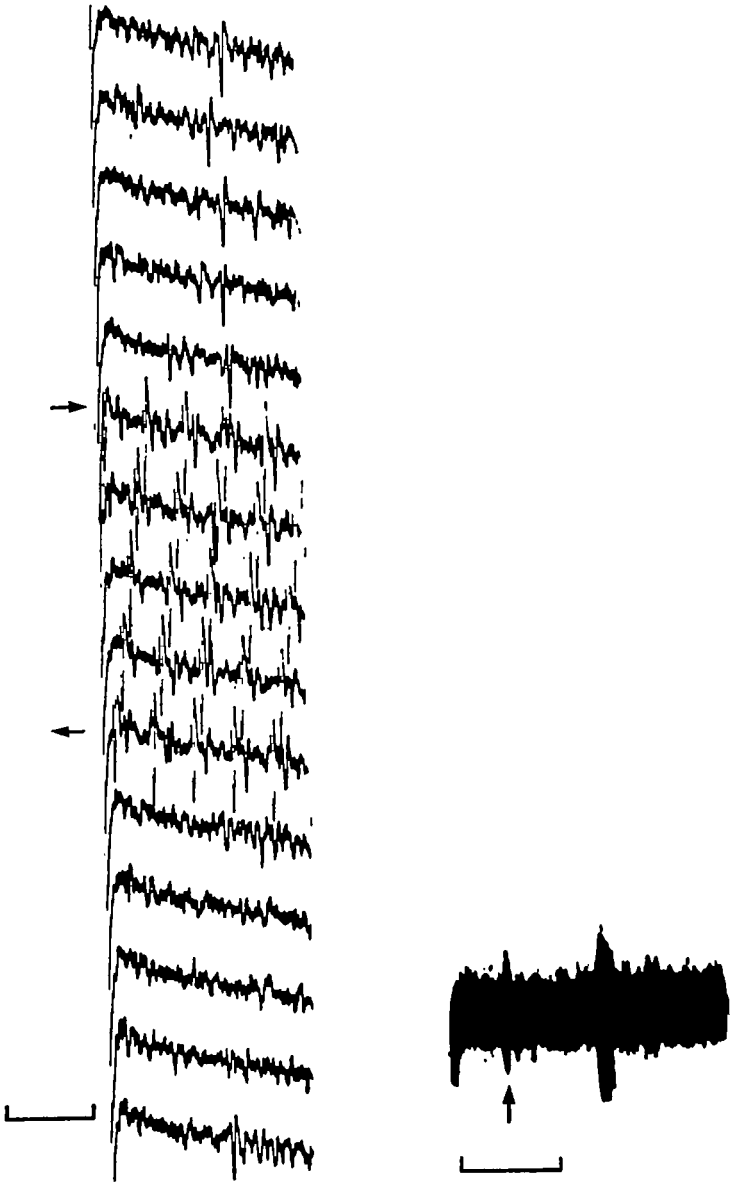

Fig. 5. Simultaneous stimulation of nerve *B* and the contralateral MRO in the adjacent anterior segment (see Fig. 4). (*a*) Succeeding traces triggered by the stimulus to nerve *B* (15 Hz) are displayed singly. The interneuronal spike is inhibited by a stimulus at 80 Hz to the MRO afferent fibre. During the stimulus (onset and completion arrowed) activity in the connective is obscured by an artefact and the ascending spike from the MRO afferent fibre. The inhibition persists during the first 4 traces after the removal of the stimulus. (*b*) As in (*a*) but succeeding traces are superimposed. A simultaneous stimulus to nerve *B* and the MRO at 20 Hz triggers the trace. The interneurone is not inhibited by input from the MRO at this frequency, and both it and the spike from the MRO afferent (arrowed) are recorded in the connective. Time bar (both): 20 msec.

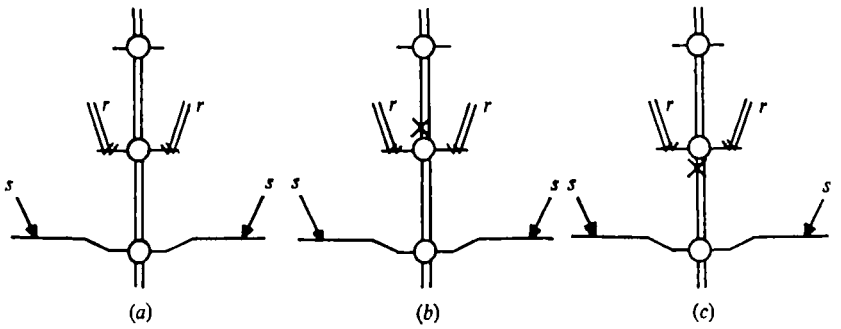

Fig. 6. The experimental arrangement used in studying inhibition. (*a*) Electrical stimuli are delivered to nerve *A* or *B* in the posterior segment (arrows) and recordings are made from ventral motor neurones in the anterior segment. (*b*), (*c*) As in (*a*) with the anterior or posterior connective cut on one side. An inhibitory effect persists after lesion (*b*) but disappears after lesion (*c*). *s*: stimulating electrode. *r*: recording electrode.

Interactions between opposite traps

When one trap is open, ready to respond, the trap on the opposite side of the segment is closed, so that in the intact animal it is impossible to stimulate traps on opposite sides of the same segment together. Yet this would be an interesting experiment, for it is plain that the movements which would be excited in this way would be in contradictory senses and might reveal a mechanism by which the nervous system copes with antagonistic inputs. Using the second modification of the preparation (Fig. 1*b*) it is possible to stimulate the nerves in the region of the traps on opposite sides of the same segment together while recording from the motor neurones in the segment next anterior. The stimulus is electrical, its amplitude is precisely variable and it is delivered simultaneously to the nerves on opposite sides.

When the nerves from the traps on opposite sides of the same segment are stimulated together (Fig. 6*a*), the motor neurones on only one side of the pupa respond (Fig. 7). The inhibitory relationship is consistent at different input frequencies so that the side which responds to a bilateral stimulus at 40 Hz also fires to one at 200 Hz. However, if the amplitude of the stimulus to the responding side is reduced, then the roles are reversed, and although both sets of motor neurones still fire when their respective traps are stimulated singly, it is the formerly inhibited member of the pair which now responds when they are stimulated together (Fig. 7*c*).

The effect of the bilateral stimulus on the response of the side which fires is interesting: at low frequencies the latency of the response is reduced when compared with the response to a simple stimulus to that side alone. As the stimulus frequency rises this co-operative effect disappears, and the side which fires to the bilateral high frequency stimulus responds with a longer latency and at a reduced firing rate (Fig. 7). At this point there is a reciprocal inhibitory relation between the two sides.

To localize the site of the inhibitory connexion, I cut the connective on one side above the ganglion in which the afferent fibres terminate (Fig. 6*b*), interrupting the excitatory connexions between afferent and motor neurones on that side (Bate, 1973*b*). The inhibitory relation between the two sides persisted after this operation (although it could only be demonstrated on the side which remained intact). After cutting th

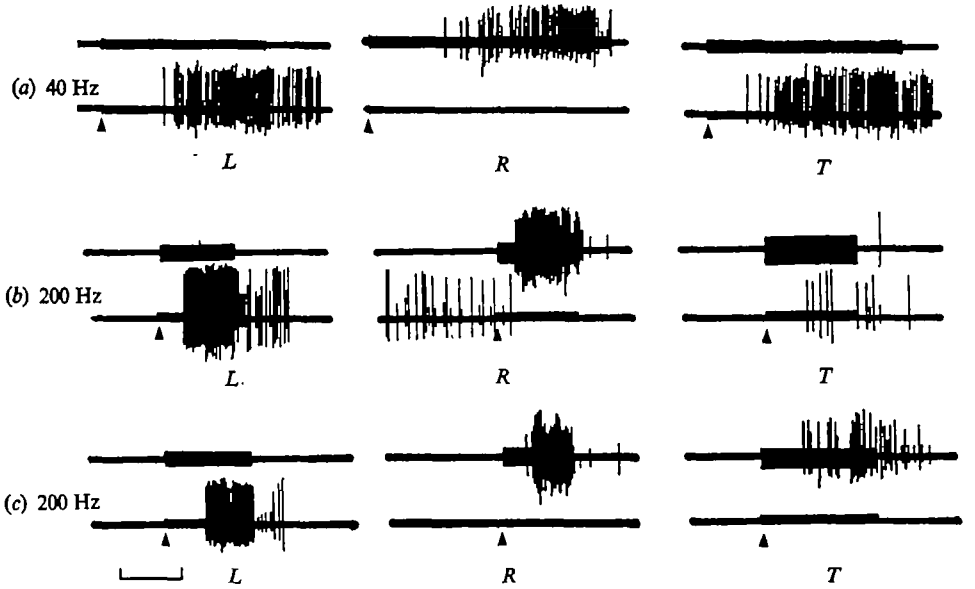

Fig. 7. The response of left (lower traces) and right (upper traces) ventral motor neurones to stimulation of nerve *B* on opposite sides of the adjacent segment at the indicated frequencies. *L*: stimulus to left-hand side. *R*: stimulus to right-hand side. *T*: both sides stimulated together. In (*b*) the left-hand side responds to the combined stimulus. In (*c*) the amplitude of the stimulus to the left-hand side is reduced, and the right-hand side now responds. Time bar: 500 msec. Stimuli arrowed.

connective on the same side below the ganglion in which the afferent fibres terminate (Fig. 6*c*) the inhibition between the two sides disappeared.

There is therefore an inhibitory connexion between neurones in the ganglion where the afferent fibres terminate. Although this does not exclude the possibility of additional inhibitory fibres running in the connective contralateral to the stimulated trap, it offers a simple explanation for the observed inhibition between the efferent neurones whose synaptic regions lie in the next anterior ganglion (Bate, 1973*b*).

Inhibition between second-order cells

The inhibitory interaction between simultaneously stimulated traps can be demonstrated in the interneurones which run in the connective between the terminals of the afferent neurones and the efferent neurones in the more anterior ganglion. Fig. 8 shows the result of an experiment in which both sides of the pupa were stimulated after one side of the connective had been disconnected above the ganglion in which the afferent fibres terminate (Fig. 6*b*). An interneuronal spike could be recorded as usual in response to the stimulus to nerve *B* on the intact side. When nerve *B* on the injured side was stimulated simultaneously, the spike disappeared. Before the connective was cut, the disconnected half was consistently the dominant half in the inhibitory relation between the efferent neurones.

As with excitatory inputs, the simultaneous demonstration of inhibition between interneurones in opposite halves of the connective and between motor neurones on opposite sides of the pupa does not show that these interneurones are the only link

Fig. 8. (*a*) Interneurone recorded from the connective as in Fig. 2, with the contralateral connective cut as in Fig. 6*b*. (*b*) As in (*a*) with a simultaneous stimulus to nerve *B* from the trap on the opposite side, which inhibits the interneurone in the intact half of the connective. Time bar: 20 msec.

between the trap sensilla and the motor neurones. The inhibitory relation may be common to many of the interneurones running in opposite halves of the connective and not confined to neurones with similar properties on opposite sides.

Insensitivity of the closure system to postural input

The pupal efferent neurones respond to a low-frequency stimulus to nerve *B* in the same way as they respond to a stimulus to the receptors outside the trap (Bate, 1973*b*). The efferents on one side fire together in a discharge characteristic of abdominal flexon. Flexion movements occur in either direction, depending on the posture of the abdomen, and not the source of the stimulus, so that when nerve *A* is stimulated, or nerve *B* is stimulated at low frequency, the response occurs on either side of the preparation and there is a corresponding inhibitory effect on the side opposite to that which is caused to respond (Fig. 9). By contrast, the trap closing response to a high-frequency stimulus to nerve *B* is consistently ipsilateral, and the inhibitory effect is always contralateral. The following experiment compares the sensitivity of the flexion and closure systems to postural input.

As before, recordings were taken from ventral motor neurones on both sides of the segment anterior to the chosen trap (Fig. 10). The nerves in bundle *B* leaving this trap were stimulated at frequencies from 40 to 200 Hz. In the intact preparation the responses were divided unequally between the efferent neurones on opposite sides (Fig. 11), the bias to the stimulated side increasing as the input frequency rose. When the afferent fibres of the ipsilateral MRO in the stimulated segment and the next anterior segment were cut, the proportion of responses on the contralateral side rose at low frequencies (Fig. 11*A*). In the converse experiment, when the afferent fibres of the contralateral MROs were cut, the initial bias to the stimulated side was reinforced (Fig. 11*B*) and the contralateral efferent neurones fired only once over the whole

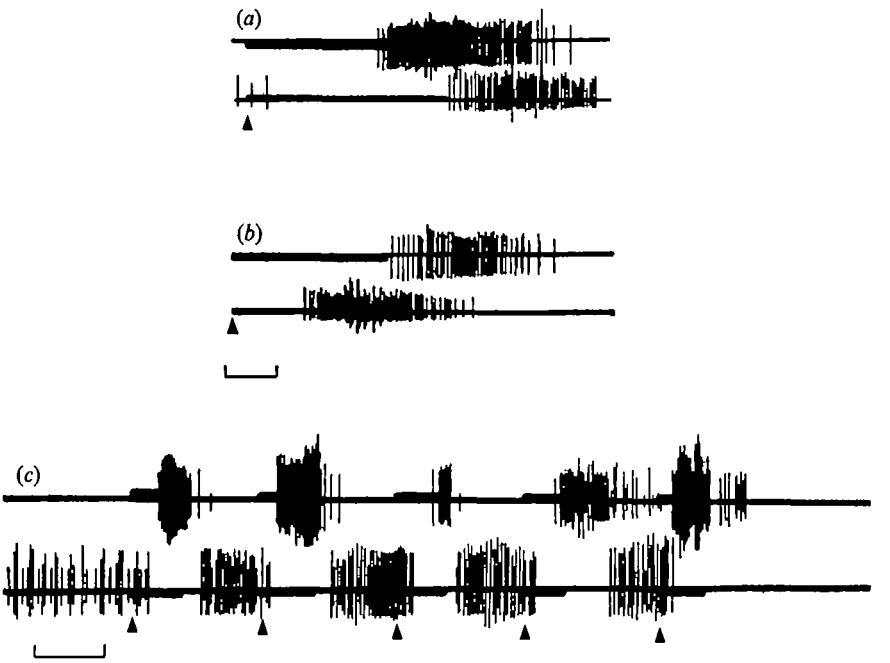

Fig. 9. (*a*) Response of ipsilateral ventral motor neurones (upper trace) to a stimulus to nerve *B* in the adjacent segment at 60 Hz. (*b*) As in (*a*) but the contralateral efferent neurones (lower trace) fire first. (*c*) Same preparation, stimulus frequency 200 Hz. The response is consistently ipsilateral, and contralateral efferent activity is inhibited. Time bar (both): 500 msec. Stimuli arrowed.

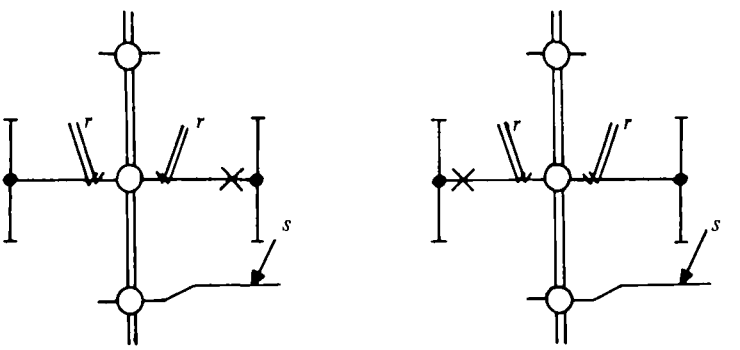

Fig. 10. The arrangement of stimulus (*s*) and recording (*r*) sites for the investigation of the postural sensitivity of the response to input to nerve *B* at different frequencies (see figure 11 and text). Left: ipsilateral MRO disconnected. Right: contralateral MRO disconnected.

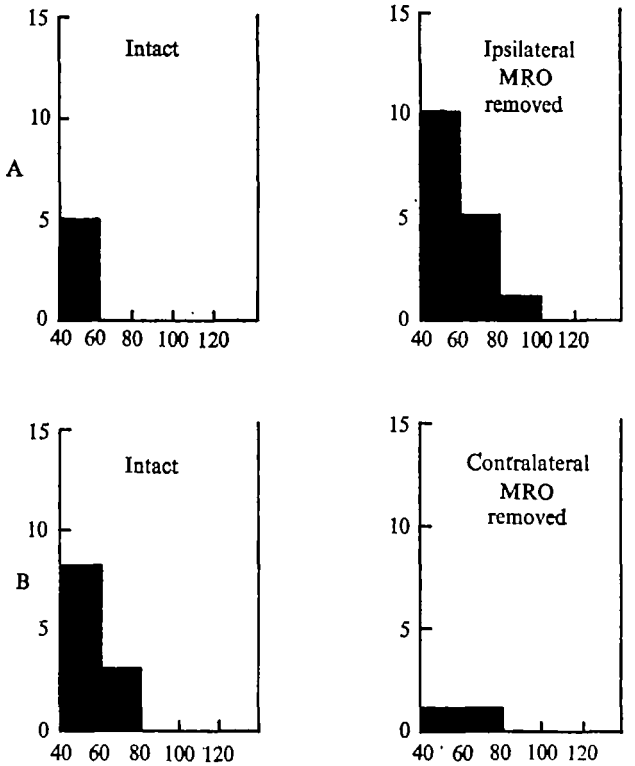

Fig. 11. Histograms of the number of responses in contralateral efferent neurones to a stimulus to nerve B in the adjacent segment, in the intact preparation and after disconnexion of the ipsilateral (A) or contralateral (B) muscle receptor organs. Ordinate: number of responses to 15 stimuli. When the contralateral efferent neurones fail to fire, the ipsilateral efferent neurones respond. Abscissa: stimulus frequency (Hz).

frequency range. The experiment confirms that at high input frequencies the output is insensitive to postural inputs – it is consistently ipsilateral. At low input frequencies the system is biased by inputs from the stretch receptors.

To summarize. There is an inhibitory relation between neurones on opposite sides of the pupa. This inhibition blocks or delays the activity of efferent neurones on the side opposite to that which is caused to respond. The inhibitory effects of a high-frequency stimulus to the trap sensilla complement the high-frequency discharge which closes the trap, that is the inhibitory effects are restricted to the efferents of a single segment and are independent of posture, so that the contralateral efferent neurones are invariably inhibited and there is no evidence of co-operation between inputs from opposite sides. By contrast, when the same receptors are stimulated at a low frequency the motor neurones of either side may fire, depending on additional postural inputs. In this case therefore the inhibition also may act on either side, with the result that at low frequencies the input from two stimulated traps combines to fire the efferents of the active side at a reduced latency.

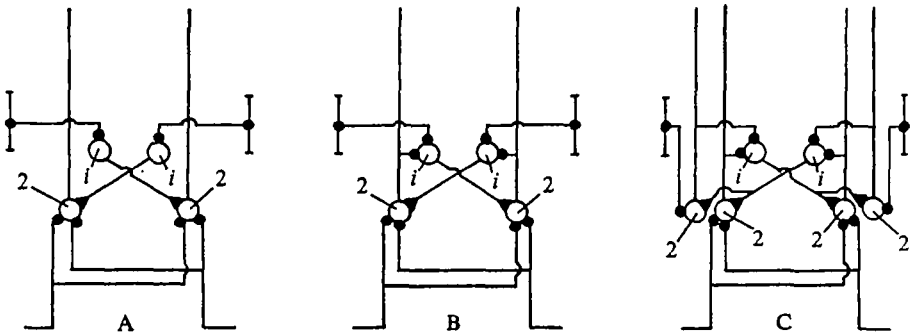

Fig. 12. Models of the arrangement of second-order neurones in the pupa. See text for details. *i*: inhibitory neurone. 2, second-order neurone. Filled triangles, inhibitory junctions. Filled circles, excitatory junctions.

A model of second-order pupal neurones

It is now possible to propose an arrangement of the second-order neurones which switches afferent to efferent connexions on the basis of abdominal posture and ignores the position of the stimulus – connexions which are characteristic of the receptors outside the trap, and at low input frequency of those inside the trap. The unique properties of the trap-closing system cannot be fitted to this scheme, because at high input frequencies the efferent neurones respond not according to posture but to the position and nature of the stimulus.

Afferent fibres from one side of the pupa are connected to second-order cells in both halves of the nervous system (Fig. 12A). Each second-order cell receives an inhibitory input driven by the tonic discharge of the contralateral stretch receptor. The tonic discharge frequency increases as the MRO is stretched, so that this connexion reduces the chance that a second-order cell will fire when the opposite side is stretched. Stimuli from both sides of the pupa tend to cause the cell on the side which is extended to fire, rather than those on the side which is flexed. Nonetheless, the mechanism is ambiguous, because the second-order cells of both sides could be fired simultaneously.

However, if each second-order cell is linked with its opposite number by an inhibitory collateral (Fig. 12B), the contrast between the two sides is enhanced by raising the threshold of the inactive cell. No matter what the source of the stimulus, the second-order cells of only one side fire, and the decision between them is made on the basis of posture.

The model makes direct use of experimental evidence, but it could be simplified, made less particular, and more consistent with arthropod neural economy. For example (Fig. 12C), there may be a single inhibitory input to each second-order cell, and the terminals of this inhibitory neurone need not be limited to a particular second-order cell, but to a group of such cells. If the MRO drives second-order cells in its own half of the connective only, and if these cells have the same inhibitory connexions with the other half as the cells in parallel with them, then the position-sensitive contrast-enhancement mechanism depends merely on the existence of an inhibitory connexion between the two sides and the unilateral connexion of the stretch receptors.

The value of models of this kind is not in their close relation to actual patterns of

connectivity, but in so far as they 'summarize a variety of findings with clarity and precision and at the same time suggest further experiments' (Miller, 1965). By assembling the available data about the central connexions of many sensilla the model emphasizes the unusual properties of the system to which the sensilla in the trap alone have access. The characteristics of that system will not conform to the model. As a summary, the model simplifies a discussion of the differential connexion of the trap sensilla and suggests ways in which the properties of the closure system might be derived. Like the more general model, these theories are open to further experimental analysis.

DISCUSSION

The clearest example of specific central inhibition in the insect nervous system is to be found in the auditory interneurones of grasshoppers. The inherent directionality of the tettigoniid and acridid ear is improved upon centrally by an inhibitory connexion between the tympanal nerves and the contralateral interneurones. The imbalance of the system derives from the ear itself, so that central inhibition enhances an initial bias which is peripheral and related to the stimulus. In the proposed model of the pupal second-order cells on the other hand, the inhibitory connexion enhances a central bias set by a peripheral input which is unrelated to the stimulus.

Suga & Katsuki (1961) suggested that in the tettigoniid *Gampsocleis* the contralateral inhibitory input is driven by the tympanal nerve rather than by the contralateral interneurone. McKay (1969) has confirmed that this is the arrangement in a second tettigoniid *Homorocoryphus*. In the model of the pupal mechanism the inhibitory link is postulated between interneurones and not between afferents and interneurones. This assumption is partially justified by the finding that at low stimulus frequencies inputs from opposite halves of the animal co-operate (Fig. 13 and above). This effect would be hard to understand if the afferent neurones were driving the inhibitory fibres unless the inhibition were temporarily in abeyance. But the inhibition is not in abeyance, for the efferent neurones on one side fail to fire at all. One-sided inhibition can be achieved with reciprocal connexions if the linkage occurs after the first-order to second-order junction.

The transient sensitivity of the recorded interneurone to the discharge of the contralateral MRO does not meet the requirements of the proposed model; nor does its apparently one-sided connexion with receptors from the ipsilateral trap. However, it is because of the commanding nature of the input from the ipsilateral trap sensilla that the cell is recorded at all. Its insensitivity to other inputs may be a consequence of its relay-like responsiveness to inputs from these sensilla. Neurones with characteristics like those proposed in the model would not behave in such a simple way because of their necessary sensitivity to inputs from other stimulus-unrelated sources such as the stretch receptors. They would not be recorded by the simple method used. Some of the properties of the recorded cell are similar to the anomalous behaviour of the trap-closing system itself. The closure system is relatively insensitive to posture and the observed inhibitory cross-connexion acts as a mechanism of selective attention to stimuli which evoke responses in mutually antagonistic classes of effectors.

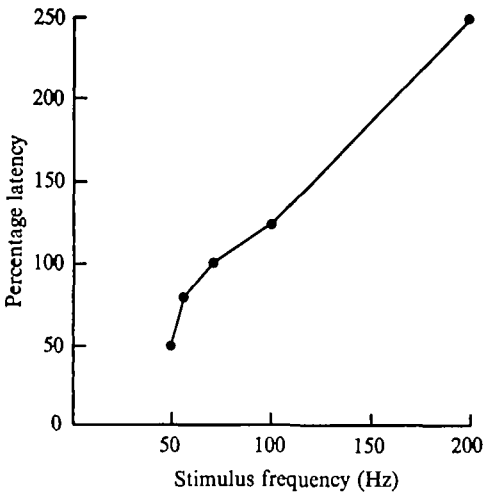

Fig. 13. The latency of the response in ventral motor neurones on one side of segment 4 to simultaneous stimuli to nerve *B* on both sides of segment 5, expressed as a percentage of the latency to an ipsilateral stimulus alone. A percentage greater than 100 indicates reciprocal inhibition.

The differentiation of the closure mechanism

If the mechanism of the gin trap were to rely on the selective connexion of the triggering hairs with a system of interneurones newly differentiated at pupation, a model of the closure mechanism could be constructed by attributing its anomalous properties to these new neurones. But these special properties appear only at high input frequencies. At low frequencies the trap sensilla reveal their connexions with a second system to which other receptors have access. This second system is also present in the preceding larval instar (Bate, 1972). The simplest comprehensive model of the closure mechanism includes this second connexion and depends not on the growth of new neurones, but on the modification of an existing but more generalized system. The model is limited by the properties of the neurones from which the mechanism is presumed to develop.

The proposed arrangement of pupal second-order cells depends on a balanced connexion between afferent fibres and interneurones on both sides of the nervous system. If the junctions of the afferent fibres and second-order cells in one half of this system change, so that the second-order cells are driven by the input from the afferent fibres, the balanced properties of the system are lost.

The model for the origin of the closure mechanism is as follows. Axons from the trap sensilla retain their connexions with a system of interneurones to which other sensilla have access (Fig. 14). The junctions of the triggering axons with the ipsilateral half of this general mechanism are uniquely modified so that at high input frequencies the ipsilateral interneurones are driven, irrespective of the tonic input from other receptors.

The response to a high-frequency stimulus to the triggering sensilla is therefore consistently ipsilateral, despite a persistent connexion with the opposite side, and the firing of the inhibitory collateral suppresses contralateral efferent activity. The junctions with contralateral interneurones remain insensitive to increases in the frequency

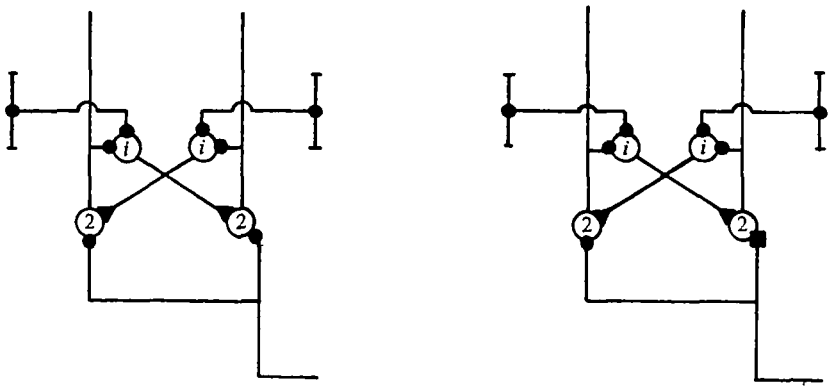

Fig. 14. A comparison between the model of second-order neurones already described (left) and a second model (right) with properties similar to those of the closure mechanism. The right-hand model is derived from that on the left by a change in the properties of the ipsilateral first-order to second-order junction indicated by the filled square. Other symbols as in Fig. 11. See text for details.

of the input, and at low stimulus frequencies the balanced properties of the system are restored.

The closure mechanism develops by an alteration of the ipsilateral first-order to second-order junction, which causes the level of the post-synaptic depolarization to rise sharply as the frequency of a train of afferent impulses is increased. The post-synaptic response at the contralateral junction, and at the first-order to second-order junctions of sensilla outside the trap, remains at a lower level over the whole frequency range. The suggested difference between these junctions which develops at pupation is similar to that described by Callec, Guillet, Pichon & Boistel (1971) in the post-synaptic response of cockroach giant fibres to input bursts from 'phasic' and 'tonic' receptors on the anal cercus.

A consequence of this theory is that the triggering sensilla are not necessarily identified within the central nervous system. A system with properties like those of the closure mechanism can develop from a change in the pre-synaptic terminals of receptors at a particular level in the antero-posterior axis, or possibly a segmental gradient (Bate, 1973*a*). On the other hand a differentiative change in a post-synaptic cell would depend on connexion of the terminals of triggering sensilla with particular second-order neurones, and the terminals would have to be identified according to the surface position of the receptors. Such a post-synaptic change might consist of selective differentiation of the post-synaptic membrane, or the complete differentiation of particular second-order neurones. If the change were selective, then triggering and non-triggering sensilla would be connected with the same second-order neurones, and the post-synaptic membrane would be a patchwork of differentiated and undifferentiated regions depending on the origin of the pre-synaptic terminals.

Further experiments are now planned to reduce the number of possible alternatives: to make a more comprehensive investigation of the interneurones with which the triggering and non-triggering sensilla are connected and to interfere selectively with the differentiation of the pre-synaptic fibres at pupation.

SUMMARY

1. The sensilla inside the gin trap are connected with an interneurone in the ipsilateral connective above the ganglion in which their axons terminate.

2. This cell is driven by the combined input of many fibres in the afferent bundle; it receives an inhibitory input driven by the contralateral muscle receptor organ and another driven by the contralateral trap sensilla.

3. There is an inhibitory relation between efferent activity on opposite sides of the nervous system.

4. A model is proposed which enhances contrast between the two halves of the nervous system by an inhibitory cross-connexion.

5. The closure mechanism of the gin trap does not fit this model but can be derived from it by a small change in the properties of the ipsilateral junction of triggering sensilla and second-order neurones.

6. A consequence of this theory is that the terminals of the triggering sensilla need not be identified within the central nervous system.

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