

THE MECHANISM OF THE PUPAL GIN TRAP

I. SEGMENTAL GRADIENTS AND THE CONNEXIONS OF THE TRIGGERING SENSILLA

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INTRODUCTION

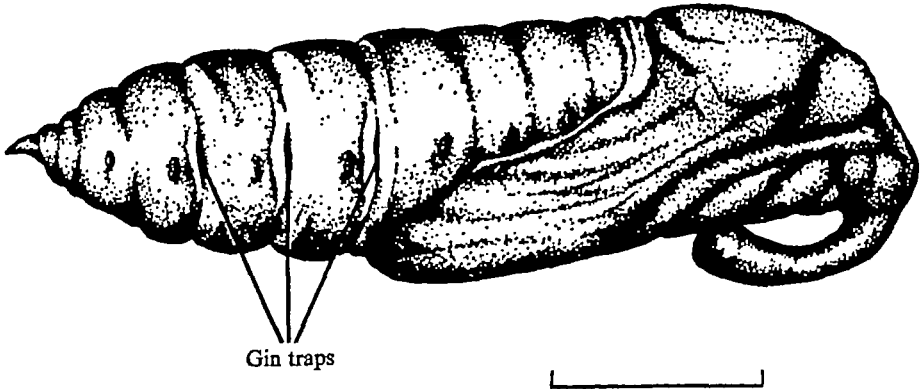
The reiterated cycles of growth and moulting in insects provide convenient material for the study of differentiation in the nervous system, for changes in form are accompanied by the acquisition of new or modified patterns of behaviour appropriate to the emerging instar. Stereotyped motor programmes such as song and flight are relatively independent of peripheral inputs and it may be possible to infer a sequence of developing connexions between central neurones from the performance of the uncompleted network (Bentley, 1973; Bentley & Hoy, 1970).

Events within the central nervous system are accompanied by the growth of new sensory structures and adjustments to the central connexions of existing ones. As in the case of amphibian metamorphosis, these changes provide an opportunity to explore the way in which specific central connexions are formed by different classes of peripheral neurones (Miner, 1956; Jacobson & Baker, 1968; 1969). In the amphibia, however, the approach is made more difficult by the central position of the afferent cell body. Theories which propose the rearrangement of central terminals in response to the peripheral 'sign' of grafted larval skin, and others which suggest that grafts are re-innervated by neurones uniquely appropriate to the grafted skin, are equally plausible (Gaze, 1970). Insect material does not suffer from this ambiguity because of the peripheral position of the sensory neurones, and in many ways the epidermal sensilla are ideal for such an investigation for a great deal is already known about the origin and differentiation of these cells (Stern, 1968; Wigglesworth, 1940, 1953).

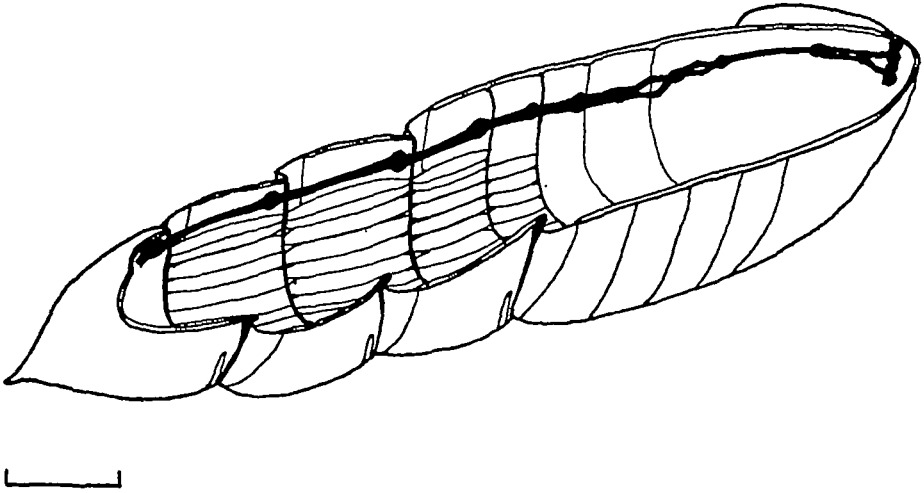
The aim of the present papers is to define a simple case of neuronal differentiation where the techniques already used in the investigation of pattern formation in the insect epidermis might be applied to the mechanisms which regulate the central connexions of the epidermal sensilla. The system concerned is known as the gin trap, and its function depends on a discrimination between similar sensilla at different positions in the same segment.

Pupal gin traps were first described by Hinton (1946, 1955). They occur in several different orders of insects and they commonly consist of dorsally or laterally placed jaws at the margins of the jointed abdominal segments. The jaws are opened and closed by contractions of the abdominal muscles and form simple traps capable of crushing mites and small insects. In *Sphinx ligustri*, the privet hawk moth (Text-fig. 1)

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Text-fig. 1. Diapausing pupa of *Sphinx ligustri* showing the position of the laterally placed gin traps. Scale: 1 cm.



Text-fig. 2. The pupa dissected for experiment. Scale: 5 mm.

the pupa is equipped with six gin traps in the form of pits, one on either side of each of the three jointed abdominal segments.

The trap closes when a group of sensilla arranged within it are disturbed. An efficient trap closes only when objects move within it, and in the case of the gin trap the closure reflex is not usually elicited by disturbing the sensilla which lie outside it. The intention here is to show that this discrimination, on which the function of the trap depends, is a consequence of the selective connexion of the sensilla within the trap with a central closure mechanism.

METHODS

An experimental preparation

Pupae obtained locally or from commercial sources were maintained in diapause at 20–25 °C. Animals chosen for experiment were dissected from the dorsal surface. An incision was made along the mid-dorsal line from the prothorax to the last abdominal segment. The two sides of the animal were then pinned out, ventral side down, on a wax block. The gut, a solid rod in the diapausing pupa, was removed

Together with some of the fat body and attached tracheae. This operation revealed the central nervous system, and one half of the preparation was removed by means of a longitudinal cut to one side of the chain of ganglia. The remaining half, its connexions with the central nervous system still intact, now appeared as in Text-fig. 2. It was pinned out by the head and tail to a wax block through which a rectangular hole had been cut to admit air to the spiracles and stimulus probes to the downward-facing gin traps. All connexions between the ganglia and their peripheral trunks were severed and the muscles in each segment were cut transversely to prevent spontaneous movements. The muscles lying over the traps were removed and the fat body and tracheae were carefully dissected away to reveal the nerve supply to the epidermal sensilla. At the beginning of each experiment the haemolymph was flushed out of the dissected preparation and replaced with a lepidopteran saline (Weevers, 1966*a*). During the course of the experiment the saline was periodically flushed out and replaced.

Recording and stimulation

To record impulses in the afferent bundles, the nerves were lifted onto single tungsten hook electrodes, insulated to the hook with an epoxy resin, and raised into a layer of liquid paraffin mixed with petroleum jelly. An indifferent electrode was immersed in the saline and the two were connected via a differential amplifier to an oscilloscope for display and photography.

For sinusoidal and step displacements of the hairs, a fine glass micropipette was attached to an arm mounted on a loudspeaker driven either by the output of a Levell oscillator, or by a battery connected via a switch and potentiometer which allowed the amplitude of the displacement to be varied when the switch was closed. A second stimulating probe mounted on a loudspeaker was inserted at right angles to the first for experiments involving the simultaneous stimulation of two sensilla. The output from the oscillator (which was a faithful record of the stimulus at frequencies from 1.5 to 40 Hz) was monitored simultaneously with the spikes in the afferent bundle and superimposed on this record for photography. The glass probes were attached to the tips of the hairs with a drop of Eastman 910 glue to ensure an adequate coupling between the two.

RESULTS

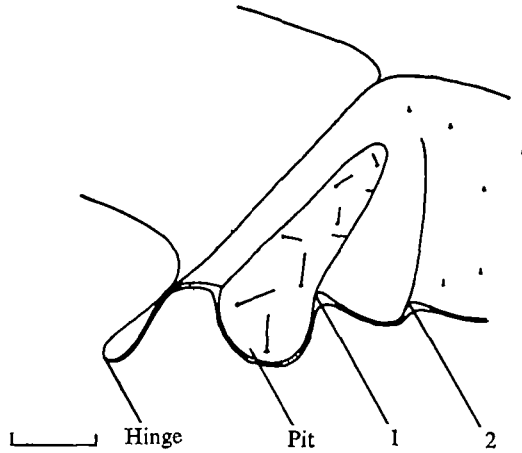
A. The trap and its receptors

The structure of the trap

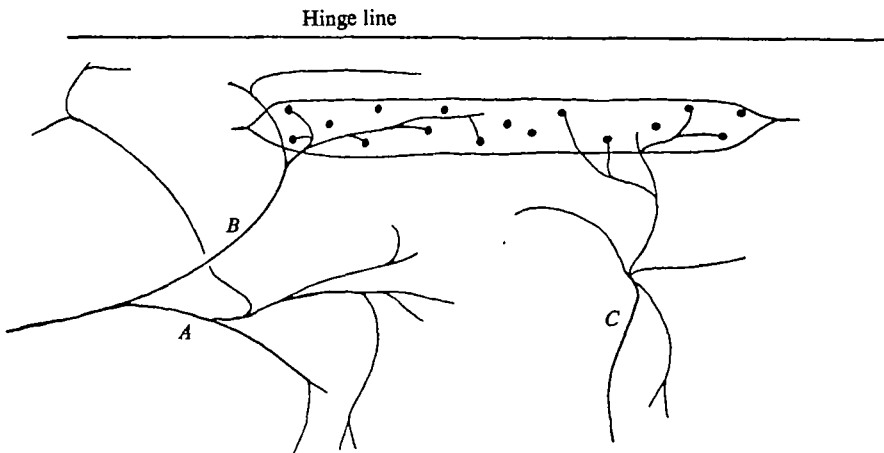
Each trap consists of a dorso-ventrally elongated pit which lies close to the anterior hinge line and the insertion of the longitudinal muscles (Text-fig. 3). The posterior edge of the pit is jagged and forms a jaw; behind it the cuticle is thrown into a ridge which forms a secondary jaw. Inserted on the curved walls of the pit there are 20-30 small hairs, irregularly arranged but oriented so that their shafts project into the interior of the pit, which they obstruct. A disturbance of these hairs triggers the closure of the trap by a reflex contraction of the muscles in the next anterior segment (Bate, 1973*a*).

The innervation of the trap

Text-fig. 4 is a diagram of the undersurface of a trap taken from a preparation stained with methylene blue. In fifteen such preparations the terminal branches of



Text-fig. 3. A diagram showing the relation between the hinge and the gin trap. 1 and 2: jaw and secondary jaw. Scale: 0.5 mm.



Text-fig. 4. A diagram of the innervation in the region of a gin trap as revealed by methylene blue. *A*, *B* and *C* are branches of the second segmental nerve.

the nerves were variable, whereas the main branches, labelled *A*, *B* and *C* were consistent from one animal to the next. These branches link the receptors in the trap and the surrounding epidermis with the second segmental nerve of the ganglion in the same segment. Branch *A* usually has no connexion with the trap, although rarely it has connexions with one or two sensilla in the trap. Nerve *B* is mainly linked with the trap although it sends a minor branch to the hinge as well, and nerve *C* ramifies widely inside and outside the trap.

Receptors inside and outside the trap

Cross-sections of the trap show that there are a few campaniform organs embedded in the cuticle between the trap and the hinge. In flat, cleared preparations these receptors are visible with their long axes oriented parallel to the hinge line and to the corrugations which encircle the cuticle at this point. A background discharge is



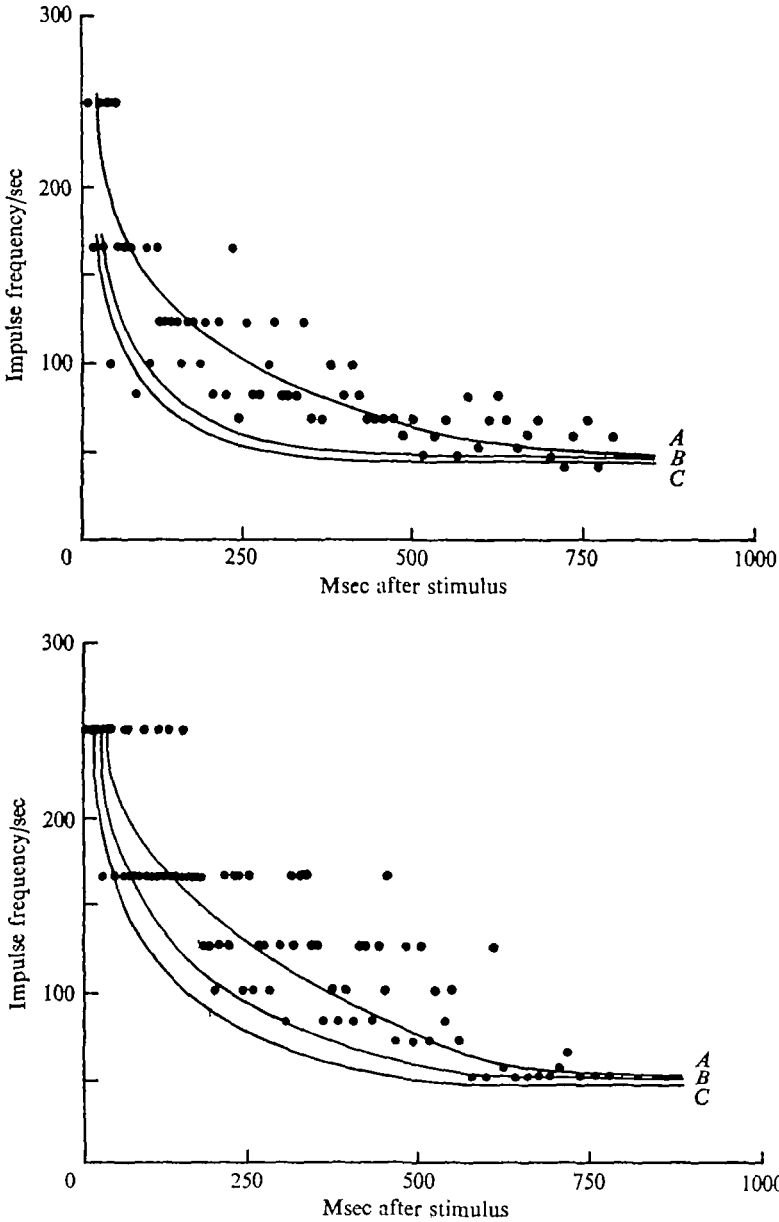
Text-fig. 5. (a) Discharge recorded from nerve B as a fine brush is moved in the corresponding gin trap (arrows). Several fibres are simultaneously active against a background discharge from receptors in the hinge. (b) Train of impulses in nerve B in response to a step displacement ($30\ \mu\text{m}$) of a single hair inside the trap. Onset and completion of stimulus arrowed. Time bar: 500 msec.

recorded from the afferent bundles which is at a high frequency when the hinge is fully extended, and the firing rate increases when the preparation is compressed dorso-ventrally. Both disturbances are likely to cause an increase in the compressive shear forces acting along the long axis of sensilla oriented in parallel with the hinge line. Pringle (1938*b*) proposed such an increase in compressive shear forces as a requirement for the excitation of campaniform endings, and these sensilla are therefore tentatively identified with the source of the background discharge. It is likely, positioned as they are in series with the longitudinal muscles, that they provide the insect with information about muscle tension, as opposed to the length-sensitive stretch receptors which lie in parallel with these muscles (Weevers, 1966*b*).

The hairs inside and outside the trap are typical trichoid sensilla (Plate 1). When an object such as a paint brush is moved within the trap, bursts of activity can be recorded in bundle B against a background discharge from the receptors in the hinge. Single hairs inside and outside the trap respond to a step displacement with a transient high-frequency burst which declines to a tonic level at a rate proportional to the amplitude of the stimulus (Text-figs. 5 and 6).

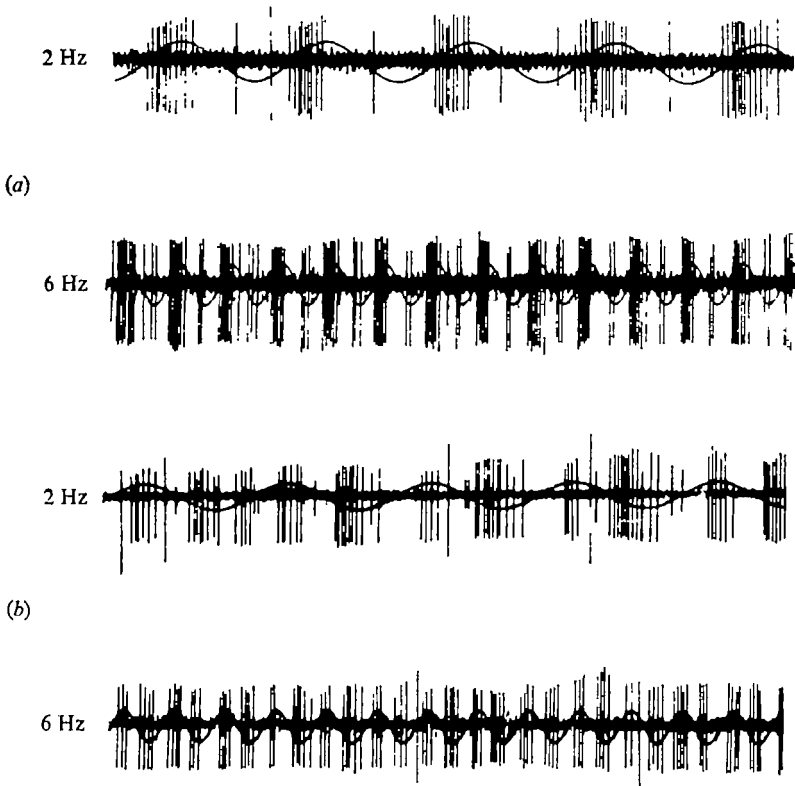
The sensilla inside and outside the trap respond to a sinusoidal stimulus about the resting position with two bursts of impulses per cycle. In contrast, Pringle & Wilson (1952) working with femoral spines in *Periplaneta* elicited continuous responses by applying a bias tension to the receptor which never allowed the sinusoidally varying stimulus to fall below threshold.

Inevitably, the receptor was seldom at its resting position mid-way between the two peaks of displacement, and the bias is most apparent with low-frequency stimuli (Text-fig. 7). At the lowest frequency the receptor may fire in one direction only, but as the frequency of the oscillation is raised spikes occur during the opposite half of the cycle. The amplitude is constant so that in common with other similar sensilla (Pringle & Wilson, 1952; Runion & Usherwood, 1968) the endings have a threshold frequency for firing at a particular amplitude of displacement. With increasing

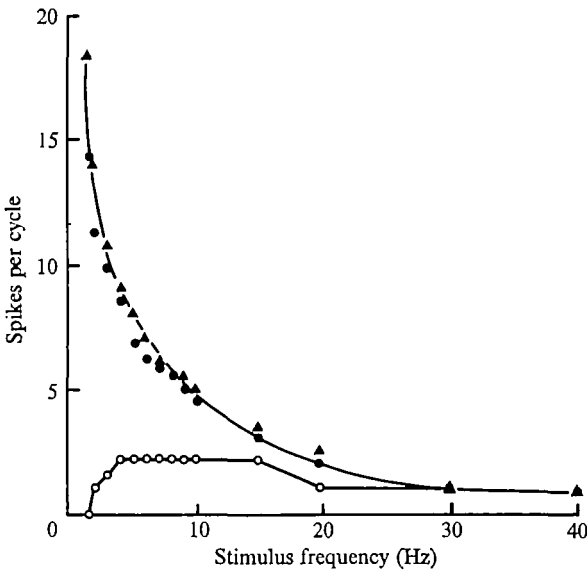


Text-fig. 6. Two graphs showing the decline in the frequency of impulses recorded after step displacements of single sensilla inside (above) and outside the trap (below). Amplitude of stimulus: *A*: 30 μm, *B*: 20 μm, *C*: 15 μm. In each case the points are drawn for stimulus *A*.

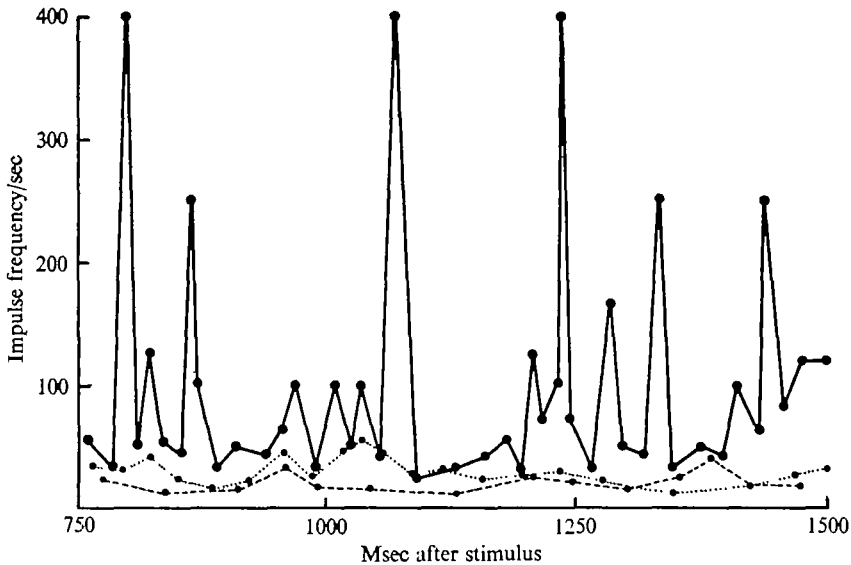
frequency the number of spikes per cycle declines (Text-fig. 8) although there is an initial rise against the bias of the stimulus as the threshold for the small-amplitude excitation is exceeded. The phase lead of the response to the oscillating stimulus, which is characteristic of velocity-sensitive endings, is retarded as the cycle time is reduced because of the constant delay caused by transmission from the receptor to the electrode.



Text-fig. 7. The response of a single sensillum (a) inside and (b) outside the trap to a sinusoidal stimulus at the indicated frequencies.



Text-fig. 8. The relation between the frequency of sinusoidal stimulation and the number of spikes per cycle. Closed circles: sensillum inside the trap, with the bias of the stimulus. Open circles: inside the trap against the bias. Triangles: outside the trap, with the bias.



Text-fig. 9. The frequency of the tonic discharge from the axons of two sensilla displaced singly (dashed and dotted lines) and together (solid line). When both sensilla are displaced, the beats in the tonic frequency indicate that more than one fibre is simultaneously active.

There is no characteristic difference in the responses recorded from the receptors inside and outside the trap. Both have properties which are characteristic of velocity-sensitive and displacement-sensitive endings. A discrimination between them must therefore depend on a consistent difference in the destination of their axons within the central nervous system.

B. Axonal fusion

I examined the receptors in the trap for evidence of axonal fusion to form a smaller number of trap-specific afferent fibres. There have been few electrophysiological analyses of axonal fusion, and various criteria have been adopted to diagnose the activity of a single fibre. Pringle (1938*a*) proposed a convergence ratio of 2-3:1 on the slender evidence of methylene-blue staining of afferent fibres issuing from the campaniform sensilla in the joints of the maxillary palp of *Periplaneta*, but this he supported by an electrophysiological demonstration that a single fibre was active when a group of sensilla was disturbed. Rowell (1961) proposed that fibres from sensilla on the sternal spine of the locust fused before the site of impulse initiation to form in effect a single sensillum with a punctate receptive field. Chapman & Nicholls (1969) made an exhaustive study of the tibial spines in *Blaberus craniifer*, distinguishing between one, or more than one, axon firing simultaneously by the shape of the pulses and their interaction at the recording electrode, rather than by the frequency characteristics used by Pringle. They found no evidence of fusion in any combination of each of the 18 spines.

The criterion which I used was different. Where a group of receptors is linked with a single afferent fibre, the rate at which the common fibre fires is the rate of the receptor discharging at the highest frequency in the innervated group (Pringle, 1938*a*). In such a case a simultaneous stimulus to two receptors causes a discharge

In the afferent bundle at a frequency no higher than the highest frequency of the receptor pair. Where the receptors have separate axons on the other hand, the recorded frequency in the afferent bundle is greater than when either is stimulated separately. Unless the discharges are at the same frequency or some multiple, they drift in and out of phase, so that the combined frequency shows characteristic beats. In this way the activity of one, or more than one, simultaneously active fibre can be distinguished.

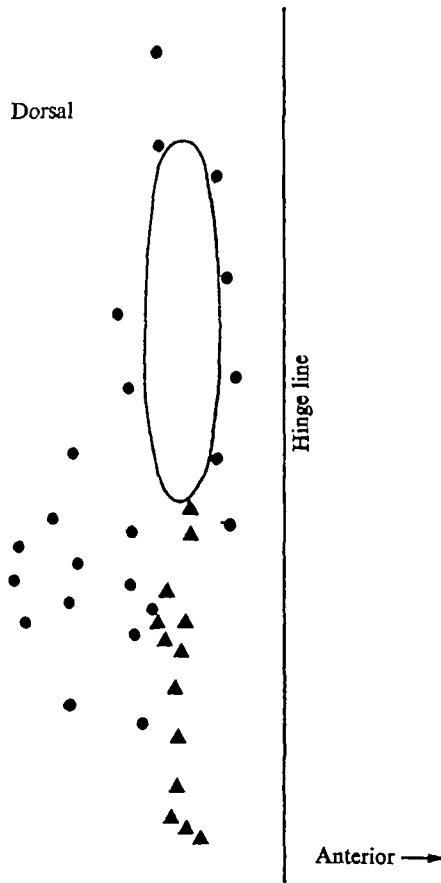
In three separate preparations records were taken (on the central side of the junction of *A* and *B*) from all pairs of sensilla accessible to two stimulating probes at right angles to each other, both within the trap and outside it. Each sensillum was stimulated singly and then the two were stimulated together. In many cases the amplitude of the spikes was sufficiently different for the two members of a pair to be distinguished at once, but in other cases it was necessary to compare the recordings from the individual sensillum and from the combined sensilla and to look for beats (Text-fig. 9). In every case it was possible to separate the activity of two fibres on one or other of these criteria when two sensilla were disturbed, showing that each epidermal sensillum has a separate axon leaving the region of the gin trap.

C. The criterion which identifies the triggering sensilla

The hairs which are scattered over the pupal abdomen, inside and outside the gin traps, are derived from the persistent sensilla of the previous larval instar, like those studied by Krumins (1952) in *Galleria*. At that earlier stage the sensilla and their central connexions are functionally uniform (Bate, 1972). In the pupa, however, the working of the gin trap shows that the hairs are of two kinds – those which will trigger the closure of the trap, and those which will not. Clearly the abdominal hair sensilla are divided into two classes by a differentiative process which occurs at pupation.

The results of the experiments so far described show that the triggering sensilla must be distinguished by their connexions within the central nervous system and not by a characteristic property of the peripheral endings. Whether or not they make new connexions at pupation or retain existing, but modified, junctions with higher-order neurones (Bate, 1973*b*), the differentiative change is restricted to a small proportion of the available larval sensilla. The hairs which are selected for this connexion must already possess a distinctive property which identifies them among the other similar hairs in the segment. So far it has been assumed that this property is a consequence of the position of the hairs within the margins of the developing gin trap. The actual criterion for selection is of interest because it reveals the rules on which the classification depends.

The freshly emerged pupa is exceedingly sensitive to mechanical stimuli; the disturbance of a single hair is sufficient to elicit the closure movement during the first few hours after the larval skin is shed. At this stage (unlike later stages when closure is triggered only by the simultaneous disturbance of several hairs) each receptor connected with the closure system can be separately identified and mapped at the surface. The common property which distinguishes these sensilla from others in the segment can be defined. In order to obtain sufficient numbers of pupating larvae, the experiments were performed on a non-diapausing sphingid, the tobacco hornworm, *Manduca sexta*, which is equipped with gin traps like those of *Sphinx ligustri*.



Text-fig. 10. A map of the hairs in the region of the gin trap of a freshly emerged pupa. Circles: hairs which do not elicit closure when disturbed. Triangles: hairs which elicit closure when disturbed. All the hairs which are within the margin of the gin trap are in this second category, and are not shown.

Hairs which would trigger the closure reflex were mapped at the surface of the abdominal segments less than one hour after the pupal moult. The hairs were moved with a fine Polythene probe mounted on a micromanipulator, and the position of each hair was marked on a grid. Text-fig. 10 is a map of the segment in the region of the gin trap, and it is typical of the results of many experiments. As expected, all of the hairs within the gin trap trigger the closure movement, whereas most of the hairs outside do not. The discrimination is incomplete, however, for closure movements can be elicited by disturbing the hairs which persist in a column of epidermis which is ventral to the trap itself. Persistent hairs are occasionally found dorsal to the trap, and some of these also trigger closure. The triggering and non-triggering hairs lie close together, but there is a sharp distinction between them, and hairs which fail to elicit closure when stimulated singly also fail when they are stimulated in groups. The distribution of the two classes is consistent; the boundaries between them are in the antero-posterior axis, never in the dorso-ventral. Clearly, connexion with the

Closure mechanism is not confined to the hairs within the trap but includes other hairs which are at a similar level in the antero-posterior axis. The common, distinctive property of the triggering sensilla is their position in this axis.

DISCUSSION

Provided that the distribution of the receptive endings is coded within the central nervous system, insects can derive considerable information from a strategic arrangement of sensory hairs. The wind-sensitive hairs on the face of the locust are a case in point. In recent papers Camhi (1969*a, b*) has proposed an integrative model for the central endings of these cells which is based on their connexions with higher-order cells signalling relative wind, wind direction, changes in wind angle and wind acceleration. The sensilla with which any direction-sensitive unit is connected all have a very similar orientation, and since the summed activity of several is necessary to fire the higher-order cell, its directionality is greater than any of the individual receptors with which it is linked. Similarly oriented sensilla lie together in groups on the head so that directional information is coded by the selective connexion of interneurons with receptors from a particular region. It is not clear how such a surface distribution is translated into an equivalent pattern of central terminals, but an integrative mechanism such as Camhi proposes depends on a property related to the position of the sensilla which regulates their connexions within the central nervous system.

In a similar way the differentiation of epidermal cells in a regionally differentiated integument depends on their relative position in the segment, though the differentiation is expressed in the synthesis of a patch of cuticle rather than the oriented growth of an axon. Experiments on the spatial pattern of cuticle synthesis and the orientation of polarized structures in the insect segment suggest that positional information is generated by a gradient established between the segment margins. In a series of experiments with *Galleria* pupae, Stumpf (1968) showed that the epidermal cells of the abdomen refer to information about their level in the antero-posterior axis and suggested that the response of competent cells depends on an interaction with a postulated gradient of positional information repeated in each of the segments. Her results are in agreement with the work of Piepho (1955), Locke (1959), and Lawrence (1966, 1970, 1971) demonstrating the existence of graded differences between epidermal cells in the antero-posterior axis by the manipulation of anisotropic structures such as hairs, scales and ripples.

The extension and reinforcement of the theory of segmental gradients as a source of positional information and polarity in the insect epidermis (Lawrence, Crick & Munro, 1972) are of great interest to neurobiologists. The theory provides a basis for assessing the class to which peripheral neurones are assigned, according to their position, which is independent of the evidence of their central connexions. The differences between neurones in such a gradient are continuous rather than discrete (Bate & Lawrence, 1973) and the axon of each cell may have a range of possible destinations. Its final choice would depend not only on the available terminals but on a competitive interaction with the axons of neighbouring cells.

In the case of the gin trap, connexion with the central closure mechanism may be

confined to those afferent neurones whose cell bodies lie within certain values of a segmental gradient. By a consistent error (departure from expectation) the pupa shows that it does not discriminate between receptors inside or outside the trap but between receptors at different points on the antero-posterior axis. Information about position in this axis is generated by a segmental gradient; the triggering sensilla are distinguished by their position in this gradient.

Whether the central terminals of the sensilla are indeed identified by this graded information, or whether they undergo a differentiation at pupation which is specific to their position at the surface, is another question, to be considered in a subsequent paper (Bate, 1973*b*).

SUMMARY

1. Pupae of the privet hawk moth *Sphinx ligustri* are equipped with defensive devices known as gin traps.
2. The function of the traps depends on a discrimination between receptors inside and outside their margins. The traps close when the sensilla within them are disturbed.
3. There is no consistent difference in the response of the trichoid sensilla inside and outside the traps. Discriminations between them must depend on a difference in their central connexions.
4. There is no fusion of the afferent axons from individual receptors in the region of the gin trap.
5. Maps of the triggering and non-triggering receptors show that the pupa does not discriminate between receptors inside and outside the trap, but between receptors at different points on the antero-posterior axis.
6. The distinctive feature of the triggering receptors may be their position in a segmental antero-posterior gradient.

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EXPLANATION OF PLATE

A section through the posterior half of a gin trap, showing the jagged margin of the pit, which forms a jaw, and beside it a single mechanoreceptive hair. Scale: 50 μ m.