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ANALYSIS OF THE ELECTROPHYSIOLOGICAL RESPONSES OF THE TROCHANTERAL HAIR RECEPTORS OF THE COCKROACH

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INTRODUCTION

In arthropods much of the body surface bears innervated hairs or bristles which have the general histological structure described by Snodgrass (1935) as sensilla trichoidea, and it is generally assumed from their positions that they are either mechanoreceptors or chemoreceptors. A number of studies have shown that trichosensilla of similar histological structure respond to very different sensory modalities and that to some extent the receptor response spectrum is determined partly by the structure of the hair and partly by the characteristics of the innervating neurone (Dethier, 1963).

Unfortunately there has been very little quantitative work on the stimulus-response characteristics of insect mechanoreceptors comparable to that carried out by Werner & Mountcastle (1965) on the mammalian Iggo's corpuscle, and much of what has been done appears to be of a rather cursory nature. Most workers have concentrated upon insect chemoreceptors and proprioceptors of other arthropod classes (Laverack, 1963, 1966; Mellon, 1963; Wyse, 1965; Sanjeeva-Reddy, 1971). The most thoroughly analysed insect mechanoreceptors to date appear to be the campaniform organs which underlie the bases of the large articulated spines of the cockroach legs, which are distorted when the spine bases bear upon them and function as phasic force transducers (Chapman & Smith, 1963; Chapman, 1965; Pringle & Wilson, 1952; and Crowe, 1967). However, these are quite distinct from the receptors of the trichosensillum type, although often erroneously classified as such.

As yet no workers appear to have attempted to determine the aspects of receptor responses that are physiologically significant to the animal, a task which could prove to be formidable since we have no intuitive knowledge of the sensory environment the insect dwells in. When Werner & Mountcastle (1965) attempted to do this for a mammalian touch receptor they had the assistance of a considerable body of psychophysical theory on sensory discrimination from which to select models that could be tested using the neurophysiological data. As a result of this lack of theory many of the characteristics of the receptor responses that have been analyzed by various workers may in fact be of little or no consequence to the animal, but may, however, provide extremely valuable information about the actual transduction mechanisms involved.

Both adult and juvenile cockroaches of the species *Periplaneta americana* of both

sexes possess prominent hair sensilla on the ventral surface of the proximal segment of all legs, which project perpendicularly downwards from the plane of the animal's body when the animal is at rest. In this position they would appear to have a possible role as detectors of surface vibrations or irregularities as the animal is moving about or they may function as contact chemoreceptors. This study was undertaken to determine the response characteristics of these receptors, with a view to both establishing their function and determining the nature of the receptor mechanisms involved.

MATERIALS AND METHODS

Adult cockroaches of the species *P. americana* were used for all studies.

The animals were lightly anaesthetized with CO_2 and a leg was cut off at the junction of the coxa and the thorax using fine scissors. The tibia was also cut off at its junction with the femur to reduce the size of the preparation and to reduce interference from possible stimulation of the distal segments. This truncated leg was mounted with wax on a cork platform at the centre of a calibrated turntable in such a manner that the trochanteral hair of interest lay at its centre. This permitted the preparation to be rotated with respect to the mechanical stimulator.

A silver-silver chloride indifferent electrode was inserted into the cut end of the coxa which was then covered with petroleum jelly to reduce evaporation. The recording electrode was inserted through a fine puncture made in the trochanter, just proximal to the hair receptor. The recording electrode consisted of a length of 25 μm diameter gold wire which proved to be the most satisfactory material for the purpose, since its almost complete lack of rigidity simplified electrode placement. For recording from the isolated leg preparation the placement of the recording electrode was not critical since there was little spontaneous activity in the leg nerves. Good records (action potential amplitudes > 200 μV) were obtained with electrode placement within 0·5 mm of the hair. For the free-walking preparation placement was far more critical, as will be discussed later.

The electrodes were connected via shielded wire to a capacity-coupled FET input pre-amplifier, which in turn was connected to a filter amplifier with a total gain of 10000 and a pass band of 330–10000 Hz.

In order to characterize the responses of the preparation to mechanical stimuli, a ramp mechanical stimulus, in which the velocity and amount of displacement could be independently varied, was used. Such a stimulus permits the separation of the dynamic and static components of the receptor response (Crowe, 1967). Due to the upper-frequency response limitations of the transducer, the range of ramp rates used was restricted to the range 1·0–10 mm/second.

The electromechanical transducer consisted of a miniature loudspeaker from which the metal surround and cone had been removed, leaving only the armature coil and suspension intact. A disc of thin mica perforated on the periphery was glued across the centre of the coil and in the centre of this disc was glued a 1 in long tapered 26-gauge tungsten needle which was used as the coupling rod.

The frequency response of this transducer was essentially flat from 0 to 75 cps, after which it peaked (3 × the amplitude at 25 cps) at 175 cps and declined rapidly until at 250 cps the response was less than 25% of that at 25 cps. Within this

frequency range there was little lateral oscillation of the tip of the coupling needle.

Within the displacement range ±0·5 mm the transducer displacement, as measured using a microscope with a calibrated eyepiece micrometer, was a linear function of driving voltage.

To permit tight mechanical coupling between the hair and the transducer, the hair tip was glued to the coupling needle with Tacki-wax using a fine electrically heated needle. If this was done rapidly enough, no damage to the hair could be observed or detected in the recordings. The use of the wax made it possible to rapidly disconnect and reconnect the hair for changing the direction of stimulation.

Sinusoidal signals were obtained from a gated function generator which generated either bursts of sinusoidal oscillation (1–25 cycles per burst) or a continuous signal.

Stimuli were presented at 5-second intervals to permit full recovery of the preparation following stimulation.

Impulses from the preparation, after shaping with a window discriminator, were recorded on a conventional monaural cassette tape recorder, the impulses being recorded at saturation level and a simultaneous voice commentary being recorded at a low level on the same track. On replay the impulses and voice could be readily separated using the window discriminator.

Between stimuli the amplifier output was muted to prevent spontaneous nerve activity in the preparation from triggering the analysis circuits. For all records the first two impulses preceding the response were the synchronizing and trigger pulse respectively, derived from the timing circuitry.

ANALYSIS SYSTEMS

Instantaneous rate analysis

To determine the relationship between the initial rate of receptor discharge and stimulus velocity, the recorded receptor response was fed into an instantaneous rate meter. This generated on a pulse-by-pulse basis an output voltage which was a linear function of the instantaneous frequency of the preceding pulse pair. The linearity of the rate-meter was better than 2% from 70 to 750 pps.

The rate-meter output voltage was fed into an averaging computer (CAT 400) and the averaged responses to each group of 10 identical stimuli were plotted out using an X–Y recorder. Since the impulses displayed considerable temporal coherence with the stimuli (fig. 3) little temporal resolution was lost as a result of the averaging procedure.

Cumulative count analysis

Since from initial observations the number of impulses per stimulus appeared to be the most meaningful measure of the receptor response, the recorded responses were processed by averaging the accumulated counts per stimulus for 10 stimulus presentations. This was repeated for each stimulus parameter.

The shaped impulses from the discriminator were used to drive a staircase generator (Spencer, 1972) and the resulting staircase voltage output was fed into the CAT 400 as described above. The staircase generator was re-set to zero between each sweep.

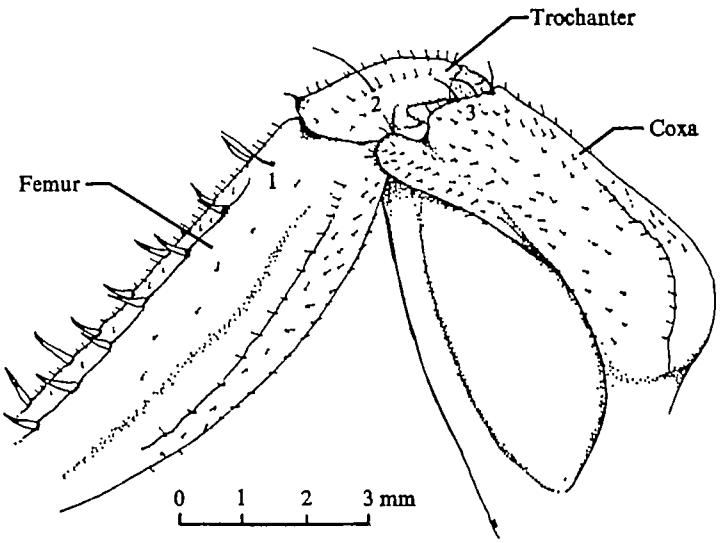

Fig. 1. Ventral view of the proximal part of the right third thoracic leg, showing the position and relative sizes of the trochanteral (2) and femoral (1) tactile hairs involved in the study. The coxal (3) hairs were not investigated. Most of the smaller cuticular hairs did not appear to generate a neural response to mechanical stimulation. Legs on both sides of the animal showed essentially the same distribution of the major sensilla, although supernumerary hairs appeared in some animals. The large spines on the anterior margin of the femur are similar to those studied by Chapman (1963, 1965) and Crowe (1967).

The resultant plot contains instantanous rate information (Fig. 3) given by the slope of the curve, as well as the total number of impulses per response.

Free-walking preparation

The technique used was essentially that described by Hoyle (Hoyle, 1964). Great care was exercised when placing the recording electrode to optimize its position to give maximum receptor spike amplitude, since activity in the nearby nerve 5 obscured receptor responses if their amplitude was less than 300 μV.

Chemical stimulation

Since the position of the hairs on the animal would make them possible contact or surface chemoceptors, this possibility was checked by applying various chemical solutions (e.g. glucose, saline, 0·01 M-HCl, protein hydrolysate) to the tip of the hair preparation described initially, using either a fine sable-hair brush dipped in the fluid, or a capillary tube filled with the test substances. Since no responses were evoked to any substance, the experiment was not pursued.

RESULTS

One sensillum occurs prominently on the trochanter and one on the upper femur (Fig. 1), while on the coxal-trochanteral joint three or four somewhat smaller sensilla fringe the margin of the socket. These last sensilla are not as prominent and do not project out in the manner of the trochanteral and femoral hairs, and were not considered in this study. The position and distribution of the sensilla varied little

from animal to animal and from one to another of the six legs. However, some animals possessed supernumerary hairs near the distal margin of the trochanter and on the femur.

The sensilla exhibit the basic structure of trichosensilla as described by Snodgrass (1935), Dethier (1963) and others. It consists of a long, hollow straight or slightly curved seta, about 1–2 mm long, which tapers from 11 μm at the base to 2 μm at the tip. The base of the seta is inserted into an annular ring of thin cuticle, which is surrounded by a raised thickened cuticular annulus.

Although not directly observed, the sensory axon from the receptor joins the large mixed nerve, nerve 5 (Nijenhuis & Dresden, 1955), which runs the length of the leg and enters the posterior margin of the thoracic ganglion of each segment.

RESPONSE TO SINUSOIDAL MECHANICAL STIMULATION

The threshold for stimulation varied somewhat with different preparations and with the rate of displacement, but in general appeared to be about 0·004 mm (4 μm) as determined from the responses to ramp stimuli.

At stimulus amplitudes just above threshold the receptor would fire coherently once with each cycle of stimulation for frequencies up to and exceeding 300 cps (Fig. 2). However, it was not feasible to measure the absolute changes in effective stimulus amplitude with increasing frequency because of the cut-off frequency of the transducer. Since the transducer output displacement falls rapidly with increasing frequency beyond 170 cps, it is probable that the threshold at high frequencies may well be lower than for frequencies of 100 cps or less. Similar behaviour has been reported by Runion & Usherwood (1968) for the tarsal hair receptor of the locust, and by Pringle & Wilson (1951).

For sinusoidal stimuli above threshold amplitude the receptor produces multiple bursts of spikes for each stimulus cycle. The receptor then rapidly adapts within the period of two or three stimulus cycles and the response remains constant at one spike per cycle (Fig. 2).

Responses to stimuli bordering the threshold value remain coherent with the stimulus, but do not necessarily occur at the onset of stimulation. This behaviour is probably due to the summation of the subthreshold receptor potential resulting from the stimulus, and internal 'noise' in the receptor itself. Where the sum exceeds threshold, spikes occur.

More than 70% of the sensillae responded synchronously to frequencies well in excess of 100 cps in contrast with the behaviour of the locust tarsal hair sensilla described by Runion and Usherwood (1968), which did not respond synchronously to sinusoidal stimuli with frequencies greater than 100 cps.

One receptor (Fig. 2*h*, *i*, *j*) exhibited synchronous afterdischarges to bursts of sinusoidal stimulation at frequencies in excess of 200 cps. At 100 cps the stimulus was above threshold for this preparation, and in the response illustrated the receptor was firing twice per stimulus cycle. At the end of the stimulus burst the receptor continued firing at the stimulus frequency for one or two more spikes. At higher frequencies the number of afterdischarge spikes increased to 6 at 300 cps. While the spikes retained coherence with the signal at 300 cps, the afterdischarge firing declined

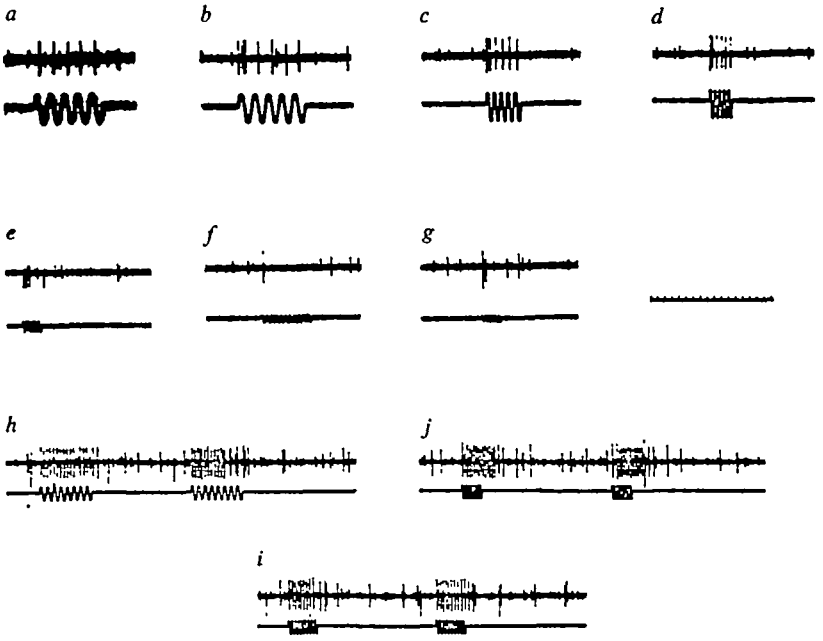

Fig. 2. Responses of the trochanteral hair sensillum to bursts of sinusodial mechanical stimulation. Note that in general the receptor fires once for each cycle of stimulation and shows a burst of impulses at the start of each stimulus which then rapidly adapts. *a* and *b*, 25 cps (±0·01 mm); *c*, 59 cps (±0·01 mm); *d*, 75 cps (±0·01 mm); *e*, 100 cps (±0·004 mm); *f*, threshold response at 75 cps, stimulus amplitude ×0·0025 mm. The time of occurrence of the response within each stimulus burst tended to be erratic but synchronous, a response characteristic of threshold responses. *g*, threshold response at 100 cps (±0·002 mm); *h*, *i*, and *j*, afterdischarges following sinusoidal stimulation at high frequencies (*h*, 100 cps; *i*, 200 cps; *j*, 300 cps). The amplitude at 100 cps (±0·013 mm) was about twice threshold for this preparation. Note that the receptor responds synchronously at all frequencies, the response at 100 cps showing doubling of the number of spikes. Despite the constancy of the stimulus drive amplitude (lower line of each trace), the amplitude of the actual mechanical stimulus declines with increasing frequency because of the limited frequency response of the transducer (see text). As a result of this the stimulus amplitude at 100 cps, ±0·013 mm, declines by about 2/3 at 200 cps, and to about 1/8 at 300 cps. Note that at all frequencies, and especially at 300 cps, there is a prolonged afterdischarge which maintains synchrony with the original stimulus (see text).

in frequency in steps that were submultiples of the stimulus frequency. This response of the hair receptor may possibly have been due to 'ringing' of the stimulator or its mountings at this frequency, but since the mass of the transducer armature assembly was both small (about 5 g) and well damped, and as its support was a massive magnetic base stand, this was unlikely.

Those receptors responding to stimulation at frequencies in excess of 100 cps also showed low rates of adaptation to repetitive sinusoidal stimuli. To characterize the degree of adaptation shown by the receptor, it was subjected to a continuous sinusoidal mechanical stimulus, above threshold for the preparation (0·04 mm) for 30 s, and the responses were recorded on moving film. From the film record a plot was made of the number of pulses per 10 cycle epoch against time. Receptor adaptation developed only after the first second and progressed slowly until by 4 seconds the

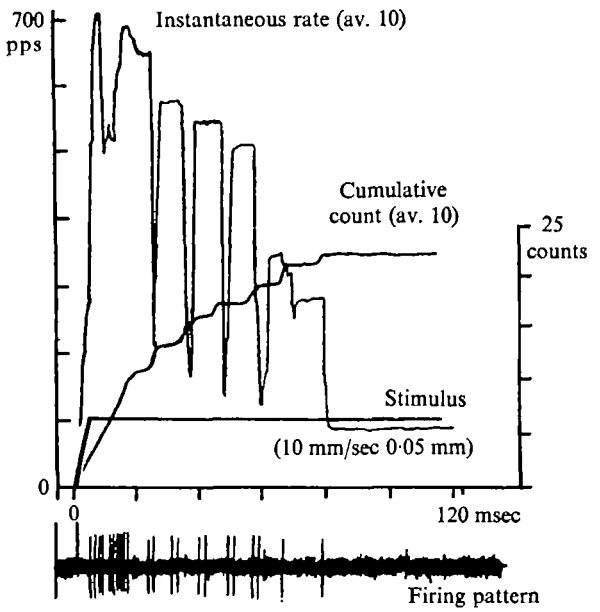

Fig. 3. Comparison between the stimulus, receptor firing pattern and the outputs of the data-analysis methods. It can be seen that the response duration (at these stimulus parameters) greatly exceeds the duration of the dynamic part of the stimulus. In this preparation the receptor is exhibiting patterned firing, a response not uncommon at this stimulus velocity. The temporal distortion inherent in the instantaneous rate-meter response is clearly evident, and is due to the fact that the rate-meter output lags by one pulse interval. In addition, the rate-meter output conveys no information about the total number of pulses.

While the cumulative count record obscures the response patterning it can be seen that it does permit both the measurement of the average firing rate from the slope of the curve as well as the number of pulses per response. Both the instantaneous rate and the cumulative count records are averages of 10 consecutive stimulations of the receptor carried out at 2·5-second intervals. (Retouched, composite illustration.)

receptor was firing in response to about 50% of the stimuli. Increasing the stimulus displacement to $\pm 0{\cdot}06$ mm restored the response to its original 1:1 relationship, showing that the drop in response was due to adaptation and not to fatigue.

RESPONSES TO RAMP STIMULATION

In all, 45 trochanteral hair-sensilla preparations were tried, and of these 30 yielded satisfactory records in that the preparations did not suffer from excessive background activity and maintained a consistent level of responsiveness for at least one complete series of stimulus presentations.

All the trochanteral hair sensilla investigated exhibited an increase in initial firing rate with increasing stimulus displacement velocity (i.e. ramp slope), provided the displacement was adequate. The duration of the receptor response, however, generally outlasted the stimulus, probably due to the time constant of the generator region. As can be seen from Fig. 4, the increase in firing rate would appear to reach a plateau rapidly at a maximum firing rate of 600–750 pps. However, before this plateau frequency is reached, the initial firing frequency appears to be a linear function of

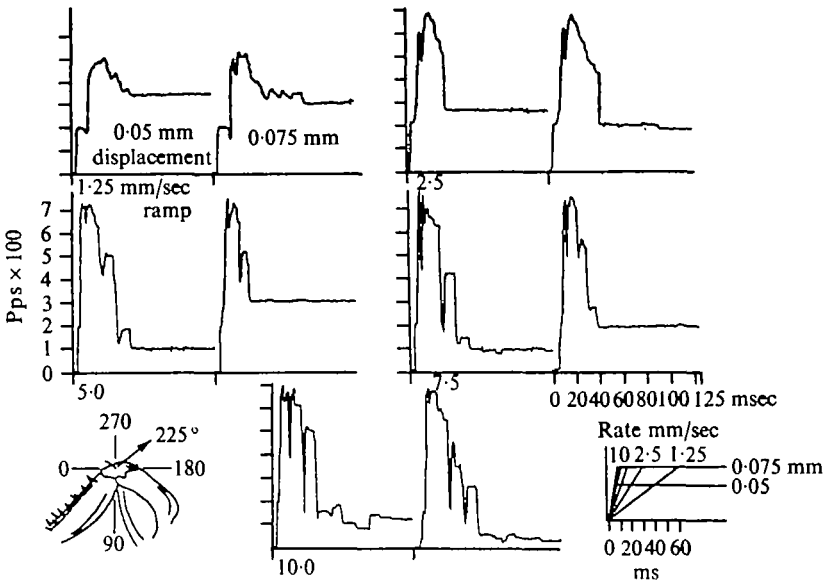

Fig. 4. Averaged instantaneous firing rates for a trochanteral hair (C2) for different stimulus velocities and displacements. Each histogram is the average of 10 responses, and the stimulus orientation is 225° to the axis of the trochanter (see left-hand side inset diagram).

It can be seen that the initial firing rate rapidly reaches maximum (750 pps) with increasing ramp velocity. The curves on the right-hand side can be used to determine stimulus ramp duration for various velocities and displacements. It might also be noted that after the response is over the rate-meter output remains at the voltage corresponding to the final firing frequency.

There are two histograms for each stimulus velocity, the right-hand and left-hand histogram of each pair are for displacements of 0·05 and 0·075 mm, respectively.

The time base (0–125 msec) and impulse frequency calibration scales apply to all the histograms. The lower right-hand scale gives the duration of the stimulus ramp for each velocity and displacement.

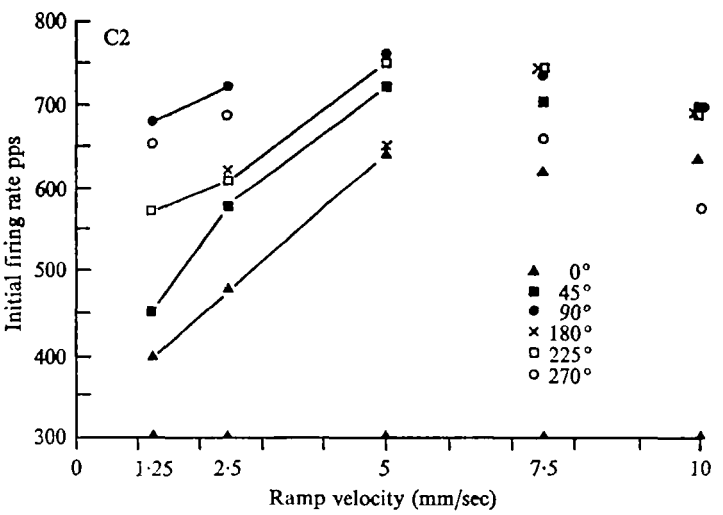

Fig. 5. Average initial firing rate of a trochanteral hair sensillum (pps) versus ramp velocity plotted for various stimulus angles, all displacement values for each velocity being pooled. Each point represents the average of from 20 to 70 individual responses. Note that there appears to be a linear increase of firing rate with increasing velocity until at about 5 mm/sec the response saturates. Some directional sensitivity is evident.

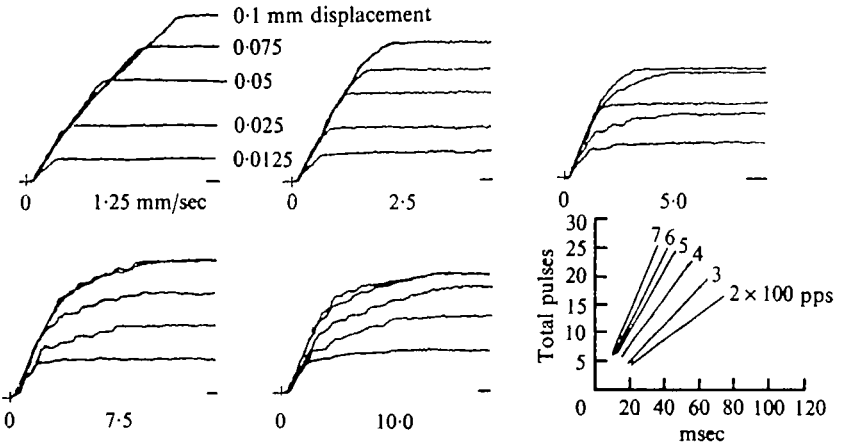

Fig. 6. Averaged cumulative counts for responses of a trochanteral hair sensillum to ramp mechanical stimuli of varying amplitude and velocity. Same preparation and conditions as in Fig. 4. Each family of curves represents the complete responses to varying displacement at a constant velocity and each curve represents the average of 10 responses. In each set of curves the order of displacement amplitude (from top to bottom) remains the same as that given in the top left-hand set. The vertical and horizontal axis calibration scales for all curves are given in the lower right-hand plot; the slope of the six lines is proportional to the instantaneous impulse frequency and can be used to determine the receptor firing rate. It can be seen that with increasing stimulus velocity, the receptor response shows 'saturation', as evidenced by the compression of the curves.

stimulus velocity (Fig. 5). In other words, the firing frequency F is proportional to the derivative of the stimulus velocity.

$$F = K_1 \frac{dS}{dt}.$$

At stimulus displacement velocities in excess of that at which the firing frequency peaks (about 5 mm/s), the firing rate declines somewhat, possibly due to receptor fatigue (Harvey & Matthews, 1961).

Some directional sensitivity in this response is evident both for the receptor illustrated in Fig. 5 and for others investigated, but this directionality does not appear to follow any consistent pattern, and probably reflects underlying structural asymmetries in the sensilla.

Despite the increase in initial firing rate for a given displacement, increasing the stimulus velocity results in a decrease in the total number of impulses generated per response. Presumably this is due to the reduction in the stimulus duration and hence the duration of the underlying generator potential. This is clearly evident in the responses illustrated in Fig. 6, which shows the averaged cumulative counts generated in response to a series of ramp mechanical stimuli of varying amplitudes and velocities. Despite the increasing degree of compression of the responses to large stimulus displacements with increasing stimulus relocity the receptor appears to obey the same non-linear relationship between displacement and response. This will be discussed more fully later.

One prominent characteristic of the receptor's response to identical stimuli is its extreme regularity, as can be judged from the patterning evident in the instantaneous rate histograms, despite the fact that these represent the average of 10 responses. Such

regularity would appear to be due to the existence of an underlying rhythmic mechanism set into action by the non-rhythmic receptor potential as suggested by Schwartzkopff (1964). Further evidence for this rhythmicity could be deduced from the occurrence of patterning of responses often seen when a receptor is given ramp stimuli having high velocities and large displacements, the patterning manifesting itself as regular and repeatable gaps in the pulse train. It must be noted that this patterning persisted despite the use of different methods of mounting the electromechanical transducer.

STIMULUS DISPLACEMENT

The amplitude of the displacement stimulus has no effect on firing rate *per se* but only on the number of impulses generated per response (Figs. 4 and 5). The possibility that the receptor encodes displacement by the number of impulses per burst was tested by recording the accumulated number of impulses per stimulus over a range of stimulus parameters in the manner described in the methods section. Families of curves, such as those illustrated in Fig. 5, were obtained from averaging the responses to 10 sequential, identical stimuli for each series of displacements at a given ramp velocity (i.e. one set of curves). It is evident from inspection that there exists a distinct relationship between displacement and the number of impulses generated. Plotting the receptor response data on log-log coordinates revealed a straight line relationship indicating that this receptor obeyed a stimulus-response relationship of the form.

$$R^* = KS_t^n \tag{1}$$

where R^* is the observed response expressed as the number of impulses, K is a constant which differs with different animals, stimulus velocities and direction, S_t is the stimulus intensity measured as a displacement of the tactile hair and n is the slope of the straight line fitted to the log-log plot.

To permit the determination of the stimulus-response relationship in the face of the observed spread of response values (Fig. 7*a*) all the results were normalized by setting the responses (R^*) from a stimulus velocity series as a percentage of the response ($R^*_{\max}$) to the maximum displacement stimulus of the series ($S_{t\max}$).

The normalized response R

$$= \frac{R^*}{R^*_{\max}} \frac{100}{1}. \tag{2}$$

Normalization affects the constant k, but not n. Its effect can be appreciated from Fig. 7*b*. The data are now clustered around a single curve. Since it is not within the scope of this study to determine in great detail the variations of individual receptor responses *vis à vis* the generalized responses of a population of receptors, the information lost as a result of normalization is not important.

To determine the statistical validity of the power function as a description of the stimulus-response relationship of the hairs, an exponential regression analysis was performed on the normalized data. The equation fitted was of the form:

$$R = a.e^{nx} \tag{3}$$

where R is the normalized response, $x = \log_e 1000\, S_t$ (where S_t is the initial stimulus), and a $= (100)^{1-n}$.

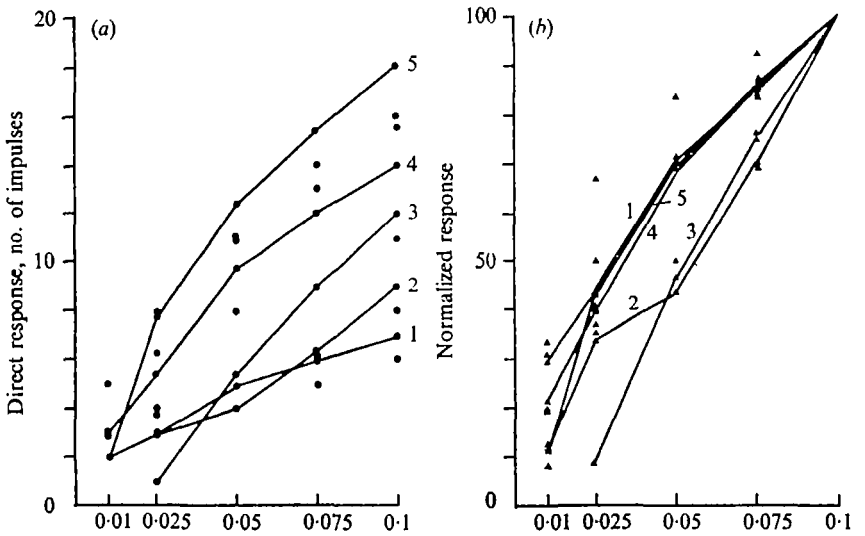

Fig. 7. Diagram illustrating the nature of the unprocessed receptor responses (*a*), as well as the effect of the normalizing procedure on the raw data (*b*). The responses have been chosen at random from the experimental data to illustrate the effects of the normalizing procedure and the range of R^*, the numbers of impulses per response, generated by the receptors. The same five receptors have been connected by lines in both plots. Note that normalizing process permits comparison of the basic response function in otherwise disparate results.

This formula was obtained as follows:

$$R^*_{\max} = K(S_{t\,\max})^n. \tag{4}$$

From (2) and (4),

$$R = \frac{100}{1}\left(\frac{S_t}{S_{t\,\max}}\right)^n.$$

Since

$$\frac{S_t}{S_{t\,\max}}\,\frac{100}{1} = 1000S_t,$$

$$R = (100)^{1-n}.(1000\,S_t)^n.$$

Taking logarithms of both sides of (1) we have:

$$\log R = \log a + n \log 1000\, S_t.$$

Thus n is the slope of the straight line log-log plot of R against S_t.

It was considered more suitable to fit the regression equation in the exponential rather than the linear form because of the nature of the error terms. The error terms of the observations about the exponential regression line appear to be additive and approximately normally distributed. Log transformations of normally distributed error terms will be highly skewed and not normally distributed.

The regression-analysis programme was run both on the responses of individual animals to different stimulation directions and on the pooled data of 82 sets of hair responses from 12 animals.

In the pooled data n can be interpreted as a weighted average of the values of n from the individual stimulus response sets.

Table 1

Analysis	r^2	a	n	Estimate of n from a	No. obs.
B 10 45°	0·968	2·192	0·824	0·830	15
B 10 135°	0·863	7·071	0·585	0·575	20
B 10 225°	0·956	7·103	0·577	0·574	20
B 10 270°	0·979	10·480	0·487	0·490	20
B 10 315°	0·974	4·697	0·667	0·664	15
C 2 90°	0·902	19·710	0·355	0·353	25
C 2 225°	0·929	6·553	0·597	0·592	30
C 6	0·939	6·685	0·594	0·587	42
C 7	0·891	19·690	0·382	0·353	42
Pooled	0·889	5·682	0·625	0·623	410

The values for the coefficient of determination r^2, a, n, and the second independent estimate of n obtained from a, for all the regressions performed, are listed in Table 1. In all cases the proportions of the total error explained by the regression r^2 was above 0·85 with a sample size of 15 or more. The use of the F test in this non-linear regression may not be strictly admissible; however, if the F values are calculated, in all cases r^2 is significantly different from zero, that is, the regressions are significant at least at the 5% ($P = 0{\cdot}05$) level.

It is interesting to note that the independent estimate of the exponent n, that obtained from a, is in close agreement with the value found for n directly. This increases the confidence one may place in the validity of the regression, i.e., that the stimulus-response relationship of the receptors studied indeed obeys a power function.

If we define sensitivity as a proportionate change in response R^* for a small proportionate change in stimulus S_t, the exponent n determined from the regression analysis using normalized data is equal to the sensitivity.

That is:

$$\text{Sensitivity} = \frac{dR^*/R^*}{dS_t/S_t} = n = \frac{dR/R}{dS/S},$$

where S is the stimulus S_t expressed as a percentage of maximum stimulus ($S_{t\ \max}$).

Thus for a given animal the response to an increase in absolute stimulus magnitude varies with the magnitude of the stimulus. However, the percentage change in response for a percentage change in stimulus is constant as demonstrated above. Also, only by use of the index of percentage change, n, can we compare receptors and it is not therefore practicable to define sensitivity in absolute terms of the number of impulses/mm displacement.

From Table 1 sensitivities for the sensilla investigated range from 0·355 to 0·824. The n for the pooled data, which represents the averaged sensitivity for the population, is 0·625. Some alterations in sensitivity with different stimulus directions are evident (Figs. 8, 9), but again, as for the effects on firing frequency, these changes do not appear to follow any consistent pattern.

While the majority of the measurements were carried out over the displacement range 0·01 to 0·1 mm, four preparations were tested at smaller displacements after modifications to the ramp generator. The results for these, as well as the regression

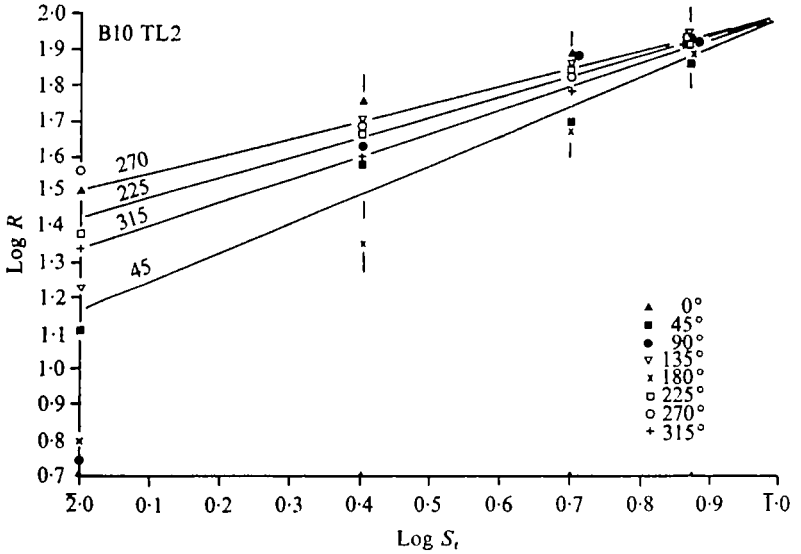

Fig. 8. Log-log plot of normalized responses of one trochanteral hair sensillum (left second thoracic leg), to ramp stimuli over the range 0·01 to 0·1 mm displacement; the responses are plotted for each stimulus angle. Each data point contains the pooled responses for each stimulus velocity and represents the average of the individual responses.

It can be seen there is some variation of sensitivity with direction (as estimated by the slope of the curve), but this does not seem to follow a consistent pattern. It can also be seen there is a straight line relationship between log S and log R for most of the responses, as shown by the fitted regression lines.

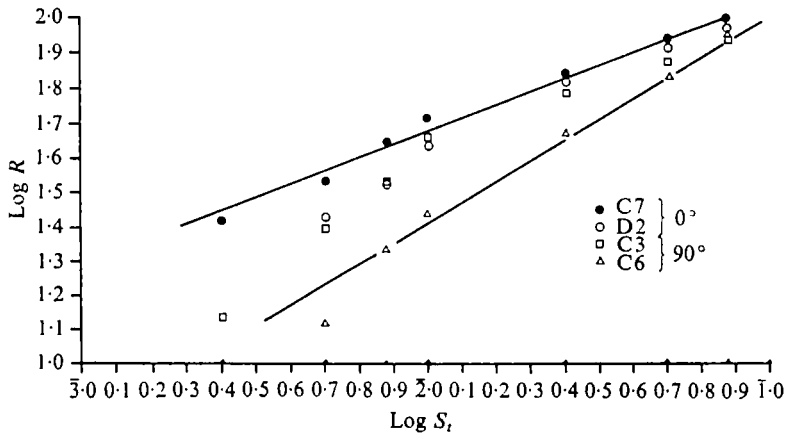

Fig. 9. Log-log plot of normalized response for the trochanteral hair sensilla of four different animals to a wide stimulus intensity range (0·0025 mm to 0·1 mm displacement). The values for different displacement velocities have been pooled so that each point represents from 20 to 60 individual responses.

Note that with the exception of C7 the actual responses deviate from a straight line fit at low stimulus intensities. C7 exhibits a lower sensitivity than the other sensilla, showing saturation of the response at displacements above 0·075 mm, but appears to have a lower displacement threshold. Both of the regression lines fitted have been calculated from the exponential regression analysis.

Fig. 10. Tonic responses of a secondary receptor to prolonged extreme mechanical displacement of a trochanteral hair sensillum (left third thoracic leg), the sensillum being bent until it was almost parallel with the surface of the cuticle. Note that the receptor fires in bursts of two or three spikes. (*a*) Response following displacement of the hair – the rapid firing at the start is due to the movement of the hair, and is probably from the phasic unit. (*b*) Discharge rate after 10 seconds of maintained deflexion. (*c*) Response of the phasic component to touching with a fine brush for comparison.

lines fitted from the regressions performed on two of the sets of results, are given in Fig. 9. It can be seen that the power function is approximated even with displacements as small as 2·5 μ.

TONIC DISPLACEMENT RECEPTORS

Several animals of those investigated exhibited evidence of tonic response to extreme sustained displacement of the hair sensilla. Unfortunately, a systematic investigation of all the preparations was not carried out so that it is impossible to state what proportions of the receptors showed this response. The effective stimulus appeared to be an extreme displacement of the hair so that it lay almost parallel to the surface of the cuticle. Fig. 10 illustrates such a response; the receptor can be seen to fire in pulse pairs at an initial rate of six bursts per second, declining to 4 per second after 10 s.

The amplitude of these action potentials appears to be the same as those produced by the phasic receptor, although there is no reason to presume that they are from the same receptor cell. No quantitative study of the nature of these responses was undertaken.

Hair receptors having multiple tactile responses do not seem to have been described from insects (Dethier, 1963) but have been described from scorpions (Sanjeeva-Reddy, 1971). Most often the hairs respond to two different sensory modalities, e.g. combined chemosensory and tactile receptors (Larsen, 1962).

FREE-WALKING PREPARATION

Unfortunately, despite many attempts to eliminate interference from the motor axons which run as part of nerve 5 through the trochanter, by various electrode placements in conjunction with a differential amplifier, it was not possible to record responses from the receptor when the animal was in active motion. When the limb was passively protracted as the animal moved forward, only then were any distinct receptor responses recorded.

Only when the animal was in the low position did scratching or jarring the substrate elicit any responses (Fig. 11), and only one spontaneous response that could be unequivocably assigned to the receptor was recorded (Fig. 11 *d*). This occurred when

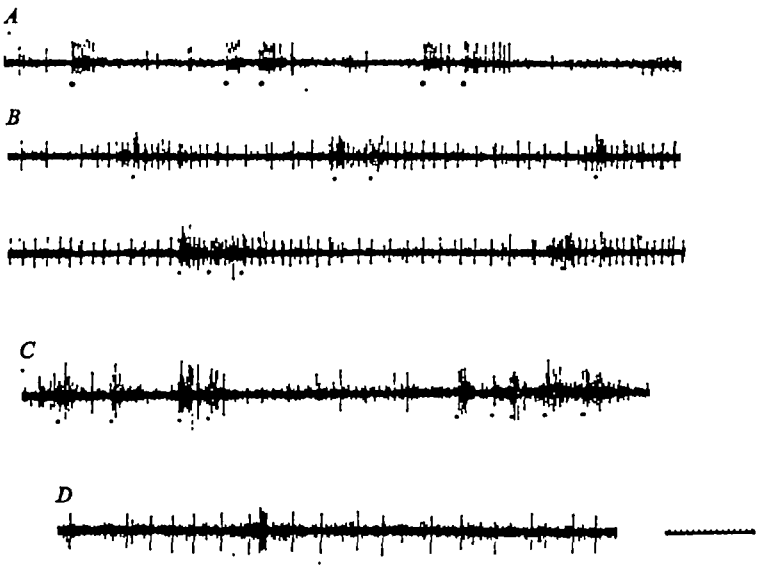

Fig. 11. Continuous film recording from unrestrained animal, the recording electrode in the trochanter of the second left thoracic leg in close proximity (*c* 200 μ) to the base of the trochanteral tactile hair. Pulse amplitude approximately 300 μV. Dots under the traces indicate the time of application of the stimuli.

A. Response to gently touching the sensillum with a fine camel-hair brush, the animal resting on the side of the constraining beaker. No overt behavioural response was elicited by this.

B. Response of the receptor to gently topping the bottom of the constraining beaker on the bench, the animal being in the low posture (see text). The increase in the discharge rate of the tonic unit, presumably a postural motor neurone, cannot be ascribed to the receptor stimulation but to the overall stimulation caused by the jarring.

C. Response to gently scraping the paper on which the animal was resting in a lowered position in which the trochanteral hairs appeared to be touching the paper. There were no observable behavioural responses to this.

D. Spontaneous response from the receptor, the leg being in protraction while the animal was walking on the paper disc in the beaker. This is one of the few spontaneous responses observed. Timing marks 10 msec apart.

the leg appeared to brush against some object on the substrate while the leg was being protracted.

While it was possible to continuously record the nervous activity in the leg on tape for protracted periods, it was never possible to be fully certain of the source of discharges which resembled those of the receptor, unless one was able to directly observe contact being made.

DISCUSSION

From the data presented it is difficult to come to any definite conclusion as to the role of these hair sensilla. The prominent position of the receptors on the ventral surface of the animals' limbs would make them ideal candidates for contact receptors, whether mechanical or chemosensory.

That they are not chemoreceptors appears to be the case from the lack of success attempts to stimulate them chemically.

Stimulation of the receptor in resting unanaesthetized animals produced no ov[illegible] responses, either in reflex leg-nerve activity, or in behavioural response. Sanjeeva Reddy (1971) has suggested that this is probably due to the considerable convergence of tactile sensory input to the insects CNS. As a result of this the minimum effective stimulus would require the simultaneous stimulation of a number of receptors. This requirement is in contrast to the response to chemosensory hair stimulation in many insects in which stimulation of one labellar hair is reported to release feeding behaviour (Dethier, 1963).

The resting cockroach often assumes a low posture in which the tips of the long sensory hairs are in contact with the substrate, in a manner that would suggest that they function as vibration receptors. However, Schneider (1950) (in Dethier, 1963) has demonstrated the existence of an exquisitely sensitive substrate-vibration detecting mechanism in the form of the subgenual organs in each leg. In the cockroach this organ can respond to displacement of 10^{-9} cm at 1500 cps. In the face of the existence of such an organ it is difficult to postulate the need for another. In addition, Florentine (1967, 1968) has described what he claims to be abdominal vibration receptors in the cockroach.

Although it was not possible to fully characterize the frequency response of the hair receptors, it is probable that they are capable of responding synchronously to frequencies well in excess of 300 cps, since the maximum receptor firing frequency ranged from 650–750 pps. If this is so, the hairs probably function simply as fast phasic tactile receptors when the animal is walking, even though it was not possible to demonstrate this unequivocably in this study in free-moving animals.

From the analysis of the responses to ramp stimuli the receptor encodes both rate of hair displacement and degree of displacement, the latter in accordance with a power-law relationship. However, since natural stimuli are seldom ramp stimuli, this degree of coding accuracy may be of no physiological significance to the animal, and as the response is a function of both stimulus and displacement, there is also a high degree of ambiguity in the receptor response. Schwartzkopff (1964) has pointed out that it is highly probable that the information from tactile receptors that is of importance to the insect is the time of contact and the anatomical position of the hair involved. Schwartzkopff contends that the intensity of the stimulus is not of first-order importance.

This contrasts with the situation in mammals in which the touch corpuscle (Iggo's corpuscle) (Werner and Mountcastle, 1965) encodes stimulus intensity, and there is little distortion of this coding in the thalamic relay neurones.

The analysis procedure used in this study, using a ramp mechanical stimulus, would appear to permit the separation of two components of the transduction process in the hair sensilla. For this, the receptor may be considered in terms of a simple compartmental model with an assumption of a uniform mechanism underlying the production of the generator potential for all sensilla in a population of animals. In other words, for an identical distortion of the receptor region there is developed an identical generator potential. Given this assumption it appears to be possible to ascribe variations in the observed responses to variations in the coupling between these compartments (Fig. 12).

From the results the value of n, the exponential term of the power function, would appear to reflect the degree of mechanical coupling between the stimulus and th[illegible]

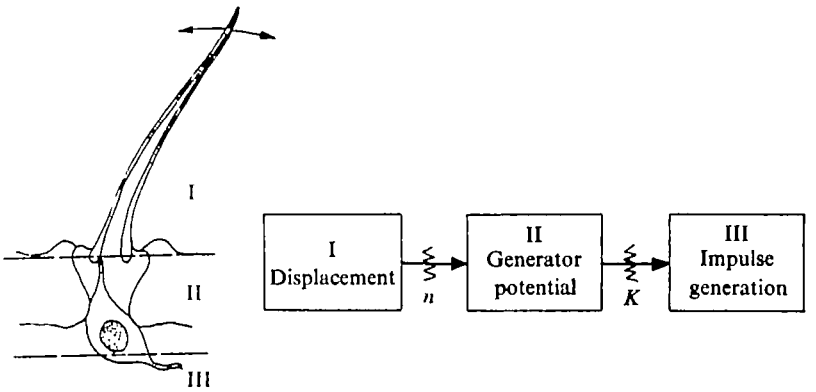

Fig. 12. Compartmental model of the hair sensilla. The zig-zag lines between the compartments represent the points of varying coupling efficiency corresponding to the terms n and K (see text).

generator region. This may be due to variations in shaft length, flexibility, compliance of the socket, etc. That this may be the case is reflected in the variations in n with the direction of the stimulus.

For different receptors given identical stimuli it is difficult to account for the spread of the observed response values, R^*, by the spread in n, the values for which are relatively constant for the receptors analyzed. It would appear that the spread in R^* reflects the spread in values of the constant K in equation (1), and that K is thus an index of the degree of coupling between the generator potential and the spike-initiating region. Regrettably, it was not possible in this study to perform the extensive statistical analyses which would be required to separate out the effects of n and K on the observed R to permit confirmation of this hypothesis, but it is hoped to be able to present this analysis in a subsequent communication.

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