

FUNCTION OF THE SUPERNUMERARY
SENSE CELLS AND THE RELATIONSHIP BETWEEN
MODALITY OF ADEQUATE STIMULUS AND INNERVATION
PATTERN OF THE SCORPION HAIR SENSILLUM

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INTRODUCTION

There is much uncertainty as to the function of many of the sense cells associated with the hair sensilla in arthropods. The general consensus, at least for the hair sensilla of insects, is that the extra sense cells associated with a mechanoreceptive hair subserve 'some function other than mechanoreception' (Wolbarsht, 1960). In most cases, the tactile sensilla of the crustaceans have been found to be dually innervated, each sense cell being sensitive to displacement in opposite directions (Mellon, 1963; Laverack, 1964). The available literature indicates that the sensillum of the scorpion is associated with two differentially sensitive units, both of which discharge for displacement in any direction (Pompapathi Rao, 1964; Laverack, 1966; Babu & Sanjeeva-Reddy, 1967). But the anatomical studies of Venkateswara Rao (1963) have revealed the presence of four or five sense cells at the base of a B-type hair sensillum of the scorpion. Investigations of Pampapathi Rao (personal communication) showed that the 'B' type hairs are not sensitive to chemical stimuli. Laverack (1964) reported that the companion hairs of the lobster are occasionally innervated by as many as four neurones. What could be the function of these supernumerary sense cells associated with apparently purely mechanoreceptive hairs? According to Laverack (1964) one can only speculate as to the function of such supernumerary sense cells; they may be 'chemoreceptors, thermoreceptors, osmoreceptors or baroreceptors'. Detailed electrophysiological investigation of the stimulus-response relations of the hair sensillum of the scorpion has thrown much light upon this problem. The quantitative aspects and other details of the stimulus-response relations will be published in a subsequent paper. The present paper is concerned with the demonstration of the fact that there is no need to invoke the sensitivity of the 'extra' sense cells to any stimulus modality other than mechanical. Though the complete elucidation of the specific roles of different sensory units has not been accomplished, this work purports to show that all the sense cells discharge to the mechanical stimulus itself. The results are in conflict with the generally held notion that multiple innervation is characteristic of the chemoreceptive hairs as opposed to the mononeural innervation of the mechanoreceptive hairs (Prentiss, 1901; Bullock & Horridge, 1965). It will be shown that there is a need for thorough re-investigation of the stimulus-response relations and ultrastructure of the mechanoreceptive hairs of arthropods.

MATERIAL AND METHODS

The scorpion, *Heterometrus fulvipes*, was used. Details regarding the procurement and maintenance of the material, dissection procedure, the equipment used and manual stimulation of the hair were as described previously (Sanjeeva-Reddy & Pampapathi Rao, 1970).

Small-scale mechanical stimuli of uniform characteristics and of known frequencies were obtained with the help of a signal magnet. The stimulus assembly consisted of a miniature loudspeaker with a probe fixed to its diaphragm, Tektronix type 162 waveform generator, type 161 pulse generator and a power amplifier. The pulse generator was driven by the waveform generator. The output of the pulse generator was fed to the loudspeaker through the power amplifier. The output of the power amplifier was tapped and fed simultaneously as a stimulus signal to the second beam of the oscilloscope. The sweep of the oscilloscope was synchronized with the output of the pulse generator for making single-sweep recordings. The stimulator (loudspeaker) was mounted on a micro-manipulator (Narishige, Japan) so that fine controlled adjustments of the probe were possible and it could be properly positioned prior to stimulation. The position of the probe prior to and also during stimulation was checked under a binocular microscope (Carl Zeiss, Germany).

Impulses were led off from the centrally isolated nerves to the telson and fifth segment. Hairs represented in figs. 11 and 12 of Sanjeeva-Reddy (1969) were stimulated. Sufficient care was taken to see that the recorded discharges were due to the stimulation of a single hair but not due to the accidental stimulation of the adjacent receptors. When necessary the neighbouring hairs were either pulled off or cut to the base.

RESULTS

Adequate stimulation of a single hair results in the discharge of four or five units (Pl. 1, fig. 1A, B). Accurate determination of the number of units in these records is not possible because of overlapping and partial summation of the action potentials of the different sensory units. However, four units can be clearly distinguished. The sensory units are named as the large (L), intermediate (I) and small (S) units depending upon their amplitude. The stimulus-response relations of each of these units will be briefly dealt with below:

(i) '*L*' unit. This unit has the highest threshold and lowest latency (Pl. 1, fig. 1C). It fires only during the transient, dynamic component of the stimulus (Pl. 1, fig. 1D). Its discharge adapts very rapidly, i.e. phasic. The discharge frequency of this unit is dependent upon velocity of hair displacement (Sanjeeva-Reddy, 1969).

(ii) '*I*' unit. The stimulus threshold for this unit is slightly lower than that for the '*L*' unit (Pl. 1, fig. 1C). However, its threshold is highly labile as is evident from the fourth frame (Pl. 1, fig. 1C). Such lability of this unit was observed often and it will be dealt with at greater length in a subsequent paper. This unit responds to the sustained, static component of the stimulus (Pl. 1, fig. 1D). It is tonic in its discharge. The duration of its discharge is a function of the degree of displacement of the hair (Pl. 1, fig. 1E). In other words, this unit exhibits position sensitivity which means that the discharge characteristics depend upon position of the hair at the time of

stimulation. The discharge frequency of this unit also is dependent upon the stimulus velocity but not as sensitively as that of the 'L' unit. This unit participates in range fractionation (Pl. 1, fig. 1 F, G).

(iii) '*S*' unit. This unit is highly sensitive and has the lowest threshold (Pl. 1, fig. 1 C). Its discharge is predominantly confined to the dynamic phase of the stimulus (see the discharge during the return phase of the stimulus in Pl. 1, fig. 1 D). This unit fires only during the initial sector of the total displacement arc (Pl. 1, fig. 1 F), and fails to discharge when the hair is extensively displaced (Pl. 1, fig. 1 G). Thus the unit, together with the 'I' unit(s) introduces range fractionation in the sensitivity of the sense organ. If the stimulus is imparted when the hair is extensively displaced, the 'L' unit alone discharges while the other units remain silent (Pl. 1, Fig. 1 F, G). When the hair is subjected to repetitive stimulation, this 'S' unit alone responds synchronously even at 90/s whereas the other units become asynchronous at much lower frequencies. Cohen (1964) has suggested that range fractionation has been evolved to permit high resolution of a stimulus covering a wide energy range. The loss of its ability to discharge throughout the entire range of displacement is the price that the 'S' unit has paid so as to gain high sensitivity and to be able to respond to even very small-scale vibrations at high frequencies.

(iv) *Other units*. Apart from the 'S' and 'L' units, the 'I' category may contain more than one unit (Pl. 1, Fig. 1 A, B). The probable functional significance of these units and of multiple innervation in general will be dealt with in the discussion.

DISCUSSION

The impasse in explaining the function of the supernumerary sense cells has been overcome, at least, for the scorpion hair sensillum. One may wonder as to the necessity of four or five sense cells responding to the mechanical stimulus itself. What functional significance is attached to the discharge of each of these sensory units? The stimulus parameters that are represented by the 'L', 'I' and 'S' units are as follows.

All the units, especially the 'L' unit, can indicate the velocity of movement of the hair. The 'L' unit can also indicate the duration of the dynamic phase of stimulus. Its discharge means that the stimulus is of a relatively high amplitude. The discharge of the 'I' unit contains information about the position of the hair and the duration of the static component of the stimulus. The 'S' unit can signal the stimuli of relatively low magnitude, the sector of the displacement range and repetitive stimulation at high frequencies.

The stimulus parameters encoded in the discharge of other units are not so clear. The evidence from the experiments in progress indicates that they may be involved in directional sensitivity. Stimulus intensity can be more effectively discriminated if there are many sense cells with different stimulus thresholds than when a single sense cell responds to the entire range of stimulus intensity. The sound-sensitive abdominal receptor of the cockroach also contains three units with differential sensitivity (Florentine, 1967, 1968).

Multiple innervation, wherever met with, has always been found to have functional significance. Thus Roeder (1964) demonstrated the functional significance of the differentially sensitive sense cells associated with the ear of noctuid moths (Roeder

& Treat, 1961). Similarly Suga (1960) distinguished two auditory neurones which differ not only in the amplitude and time course of adaptation but also in the threshold to sound stimuli. Subsequent studies on the central organization of this tympanic system demonstrated the importance of these differences in the peripheral organization of the receptor system (Suga & Katsuki, 1961; Suga, 1963). Similarly it is possible that the different sensory units of the hair sensillum of the scorpion have highly specific central effects. The evidence to be presented in a subsequent paper will in fact demonstrate the differential central effects of the various sensory units.

Multiple innervation confers yet further functional versatility upon the sense organ. As is evident from the variations in impulse amplitude, the cell size of the different units is also likely to differ. The unpublished data of the author indicate that the units of the hair sensillum differ in conduction velocity. From the point of view of central interpretation of the frequency code, the arrival of impulses of the central receiving end, at various times (due to differences in conduction velocity) and through different channels, will have great integrative consequences. It is necessary to recall what Gasser (1943) has said about two decades back: 'Faster rate of conduction means that impulses in large fibers can initiate or facilitate effects which impulses in slower fibers go on to elaborate.' This multiple innervation of the hair sensillum may account for the relatively greater efficacy (in activating the central units) of the input from a single hair in the scorpion than that from the hairs of insects and crustaceans (Sanjeeva-Reddy & Pampapathi Rao, 1970).

The recent studies of Patton (1969) have shown that the statocyst hairs of decapods are innervated not by one receptor type as reported by Cohen (1955, 1960) but by three different receptor types. Is it likely that many such complexities underlying the organization of seemingly simple hair receptors have gone undetected? Wherever extra sense cells are found in association with seemingly purely mechanoreceptive hairs (Wolbarsht, 1960; Laverack, 1964) there is a need for thorough re-investigation of the stimulus-response relations. The extra sense cells may respond to the novel conditions—such as stimulation of the hair when it is in a displaced position (away from the morphological 'resting' position), or shifting the point of contact between the stimulating probe and the hair, or changing the character of the mechanical stimulus itself. Electronmicroscopic studies may reveal additional sense cells, as in the case of statocyst hairs of decapods (Schöne & Steinbrecht, 1968), whose function has yet to be demonstrated electrophysiologically. Evidently the time is ripe for a detailed study of the ultrastructure and electrophysiology of the mechanoreceptive hairs of a variety of arthropods.

Thus contrary to the generalization that multiple innervation is characteristic of chemoreceptors alone (Prentiss, 1901), a variety of sense organs, irrespective of the modality of adequate stimulus, do possess multiple innervation and such a situation greatly enhances the efficacy of these systems in resolving the stimulus parameters. The results permit a more positive assertion of the fact that mononeural innervation is not a 'must' for the mechanoreceptive hairs.

The validity of Prentiss's (1901) generalization has been already undermined when the discharges of purely mechanoreceptive hairs were found to contain two units (Mellon, 1963; Laverack, 1964). Further, multiple innervated hairs were found which are sensitive to chemical as well as mechanical stimuli (Dethier, 1955*a*; Hodgson &

Roeder, 1956; Wolbarsht & Dethier, 1958; Larsen, 1962). The A-type hairs of the scorpion also belong to the same category (Pampapathi Rao, 1964). Hence a definite correlation between innervation pattern and modality of the adequate stimulus is probably not warranted.

SUMMARY

1. Mechanical stimulation of a single hair results in the discharge of four or five sense cells thereby refuting the classical generalization that mononeural innervation is characteristic of the mechanoreceptive hairs.

2. By electrophysiological methods three functional units can be recognized: the 'L', 'I' and 'S' units. The 'L' unit conveys information about the duration and velocity of the dynamic phase; its discharge is phasic. The 'I' unit conveys information about the duration of the static phase and about the displacement of the hair; its discharge is tonic and the duration of discharge increases with extent of displacement. The 'S' unit is highly sensitive but responds only during the initial phase of displacement; if the hair is already extensively displaced the 'S' unit does not respond to further movement.

3. These findings indicate that all the functional units may be meaningfully concerned in encoding the parameters of a mechanical stimulus.

4. The widespread occurrence of multiple innervation of receptors, and its functional significance, is discussed; and a thorough re-investigation of stimulus-response relationships in the mechanoreceptive hairs of arthropods is advocated.

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EXPLANATION OF PLATE I

All the records read from left to right and were obtained from different preparations. The lower channel always displays the stimulus whereas the upper channel shows the sensory discharge. Except in A, in all other cases, hairs represented in Figure 12 (Sanjeeva-Reddy, 1969) were stimulated.

A, B. Discharges to the stimulation of 9th and 15th hairs respectively (see Sanjeeva-Reddy, 1969, figs. 11 & 12), to illustrate the multi-unit nature of the discharge from a single hair. The stimulus was given by the signal magnet. The hairs were in a slightly displaced position and the probe was in contact with the middle of the hair at the time of stimulation.

C. Oscillographs showing the differential sensitivity of the sensory units. The first frame is the control with no stimulus and hence no discharge. The stimulus strength was gradually increased from the threshold value of the 'S' unit (second frame) to the threshold values of the other units (third and fourth frames). The 25th hair was stimulated; the hair was in its 'resting' position.

D. Record showing the phasic and tonic nature of the discharges of 'L' and 'I' units respectively. The first hair was displaced manually in the cephalic direction. The spikes of the 'L' unit are not adequately reproduced. The limited discharge of the 'I' unit even after the hair was brought back to its normal position may be due to after-discharge.

E. Oscillograph showing the position sensitivity of the 'I' unit. The 21st hair was displaced manually in the cephalic direction in a stepwise manner. Notice the sharp contrast in the duration of discharge to displacement from the 'resting' position (first step) to displacement from a displaced position (third step). Apparently movement of the hair from a displaced position can fire the sensory neurone at its saturation frequency. The spontaneous discharge of about three units is evident in the record.

F, G. Records illustrating range fractionation in the sensitivity of the sense organ. The third hair was stimulated with signal magnet. In F the hair was in its 'resting' position whereas in G it was in a displaced position. Calibration time: 25 ms (A-C, F); 50 ms (G); 300 ms (D) and 600 ms (E). Voltage: 100 μ v (D, E); 200 μ v (A-C, F-G).

