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ELECTRICAL RESPONSES FROM DUALLY INNERVATED TACTILE RECEPTORS ON THE THORAX OF THE CRAYFISH

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INTRODUCTION

It has been recognized for more than 30 years that certain arthropod sensory systems offer unique advantages for the study of receptor-cell mechanisms. In many cases spatial isolation of the primary sensory neurons, not only from centrally located integrating centres but from one another as well, make these cells particularly susceptible to detailed electrophysiological study. An additional advantage accrues from the large size attained by some sensory neurons. It was this feature which originally directed attention to the multipolar neurons associated with abdominal stretch receptors in Crustacea, from which much detailed information has been gained concerning impulse generation and peripheral inhibitory mechanisms (for review see Eyzaguirre, 1961). Recently the bipolar sensory neurons associated with insect cuticular hairs have been extensively investigated. These structures are attractive because little difficulty is encountered in recording from single units; however, the small size of the neurons involved can present a serious technical problem to detailed investigations of electrical events preceding impulse initiation. Nonetheless, some information is available concerning impulse generation in these structures. In particular, the careful measurements made by Wolbarsht (1960) on insect mechanoreceptor hairs have disclosed a linear relationship between magnitude of receptor potential and impulse frequency in the bipolar sensory neurons associated with these structures. Wolbarsht has also presented evidence suggesting that the receptor potential is a consequence of an increase in the permeability of the dendritic membrane. It seemed evident that the sense cells associated with analogous crustacean receptors, by virtue of their greater size, might lend themselves more readily to electrophysiological analysis. Tactile receptive structures are found in respectable numbers on the appendages and body surfaces of most decapods. The present paper describes the response characteristics of tactile hair receptors on the thoracic carapace of the freshwater crayfish. A type of receptor is described which is innervated by two sensory neurons, both of which are sensitive to mechanical stimuli. In addition to the rather interesting comparative features presented by these receptors, the unique anatomical situation in which the cell bodies and axons of the sensory neurons are found provides a convenient approach to the detailed study of certain aspects of impulse generation. A preliminary account of this work has been published elsewhere (Mellon & Kennedy, 1962).

MATERIALS AND METHODS

Male and female individuals of the crayfish *Procambarus clarkii* Girard were used throughout the course of the present investigation; no apparent differences based on the sex of the animals were found in regard to the function or morphology of the receptors. All experiments were done at room temperature. In practice, sharp scissors were used to remove a portion of the carapace from one side of the animal, beginning with a cut just behind the cervical groove, and continuing dorsally and then posteriorly. The excised piece was then pinned out in van Harreveld's (1936) solution, receptor side down. Arranged in this manner, the exposed surface comprises the lateral wall of the gill chamber; it is covered with a thin transparent cuticle, from which projects a profusion of fine setae. In most preparations this cuticular covering may be carefully stripped off to expose the structures beneath. Embedded in the thin layer of hypodermis, situated between the exoskeleton and transparent inner cuticle, are the cell bodies and axons of sensory neurons. With appropriate lighting, bundles of sensory axons can be seen ramifying within the hypodermis from their point of divergence at the anterior margin of the carapace. For most recording purposes one of these bundles was teased away from the surrounding tissue and lifted onto a fine platinum electrode. The piece of carapace was then very carefully turned right side up for purposes of stimulation. Alternatively, a rectangular window can be made in the carapace of an intact animal. One of the sensory fibre bundles which run directly beneath the exoskeleton is then severed proximally and lifted up onto the recording electrode, as shown in Fig. 1*a*. A grounded indifferent electrode of platinum wire was placed in the bathing solution to complete the recording circuit. Impulses were led into a high-gain, capacity-coupled pre-amplifier for conventional oscilloscopic display and recording. In some instances the bundles of sensory axons were subdivided with fine steel forceps to ensure single unit recording. Unless otherwise stated, all experiments were performed with the receptors above the surface of the bathing medium.

RESULTS

The receptors studied were those which occur in shallow depressions or pits on the surface of the carapace, as illustrated in Fig. 1*b*. They are colourless, hair-like structures with lengths of 0·3–1·0 mm. Other tactile receptors also occur in this region, but these are found on the anterior slopes of raised tubercles, or in rows along the ventral and posterior margins. The pit receptors usually occur singly, but they are always accompanied by at least two apparently non-innervated hairs which can be identified by their reddish-brown pigmentation. The function of these 'companion' hairs is obscure; they do not respond to tactile stimuli.

The articulation of the pit receptors with the exoskeleton has some stiffness. Each receptor usually stands out from the carapace at some angle approximating ninety degrees; if a receptor is displaced with a small probe and then released, it will return to the normal position of its own accord. An exception to this occurs when just a film of water or Ringer's solution is present on the carapace; in such an instance the surface tension of the liquid may be sufficient to cause the receptor to lie flat against the exoskeleton. This does not occur if the carapace is dry, or if it is totally submerged.

The thoracic pit hairs are motion receptors; they respond to translational displacement with a burst of nerve impulses, the frequency of which depends on the speed of displacement. Although these receptors respond phasically, there is wide variation in the time course of the response to a given stimulus; complete adaptation to a single deflexion may occur within 50 msec., or it may take longer than 60 sec. This depends partly on the recent history of the unit under study, since the pit receptors also adapt to successively applied stimuli, as is the case with insect phasic mechanoreceptors (Wolbarsht & Dethier, 1958). In addition, the magnitude of response depends upon the degree of movement, the number of impulses and the time course of a burst increasing with more extensive deflexion. However, response differences

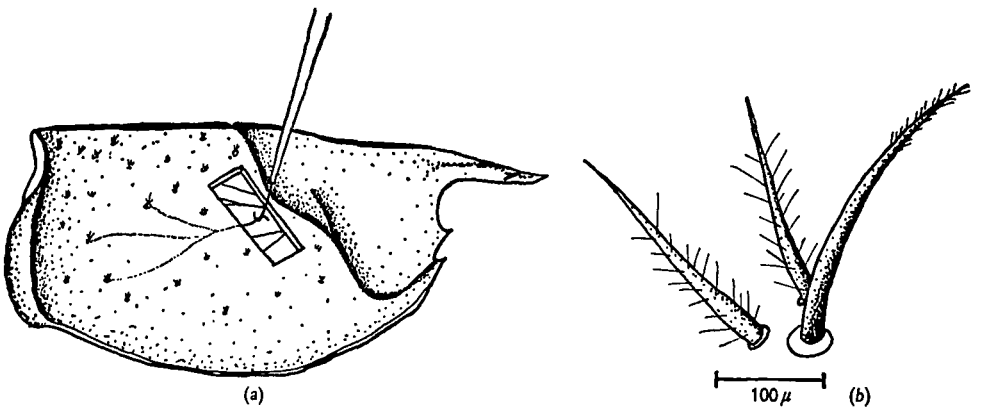

Fig. 1. (*a*) is a view of the right side of the cephalothorax. Through the window which has been made in the carapace several bundles of sensory nerve fibres can be seen running through the hypodermal layer. One of these has been severed and lifted up onto a recording lead. Finely stippled lines mark the course of its branches, each of which terminates at a sensory hair pit. (*b*) is a detailed illustration of a pit receptor. The sensory hair is the longest structure and is flanked by a pair of non-sensory 'companion' hairs

between receptors are often seen which cannot be eliminated by controlled conditions of stimulation. The possible explanation of such observations will be discussed below.

The most striking feature of the pit receptors is that they are dually innervated. Both of the sensory neurons supplying each receptor are sensitive to mechanical displacement, but if movement is specifically restricted to the direction parallel to the longitudinal axis of the animal, phasic responses are observed from only one cell at a time. Fig. 2 illustrates a typical case. A micropipette mounted on the arm of a signal magnet was slipped over the tip of a pit receptor, which was in its normal position. Contact with the pipette, which amplified small transient vibrations, occasioned a few sporadic impulses from one neuron. When the magnet was activated, moving the receptor in an anterior direction, a second neuron fired an impulse train, and upon release of the magnet the receptor returned to its previous position and a burst was evoked in the first neuron. While impulse size alone is an obvious criterion for establishing the separate identity of the two sensory cells in this preparation, in some receptors there is more extensive overlap of the sensory fields of the pair. The resultant simultaneous firing of both, with occasional electrical summations, offer rigorous proof that impulses of the two amplitudes arise in separate cells.

It is interesting to note that, even in two neurons which innervate the same receptor, the time course of adaptation to single identical stimuli differs very noticeably. An illustration of such a case may be seen in Fig. 3, which shows the response of the pair of neurons innervating another pit receptor. In the top record, at a point indicated by the arrow, the hair was deflected and maintained in a posterior direction by means of a small glass probe mounted on a micromanipulator. In the centre row, which is a continuation of the record above, the receptor was returned to its former position. Impulse discharge from the first neuron stopped abruptly, and a discharge of smaller spikes signalled the return motion. The bottom row records the responses to a subsequent

Fig. 2. Records from the pair of sensory cells innervating a pit receptor. Small spikes fire in response to movement in an anterior direction, large spikes in response to movement in a posterior direction. The lower trace monitors a 100 msec. rectangular pulse to the mechanical stimulator.

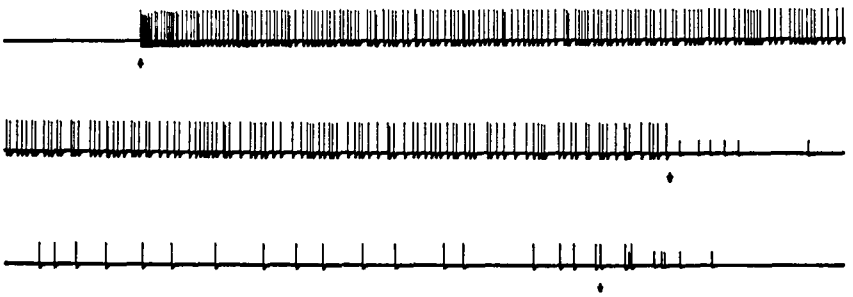

Fig. 3. Records from both sensory cells of a pit receptor. In the top row the arrow indicates approximate onset of motion in a posterior direction. The second row is a continuation of the top record. At the arrow the receptor was returned to its original position. In the bottom row the record was obtained 60 sec. after deflexion of the receptor in a posterior direction; note that the large spike has not adapted completely. Arrow indicates return motion.

identical stimulus sequence. The film was exposed 60 sec. after the onset of stimulation, and demonstrates the absence of complete adaptation even after that time interval.

In the majority of instances both of the sensory neurons which supply a pit receptor were extraordinarily sensitive to small vibrational stimuli which could not be eliminated from the experimental apparatus. The mechanical coupling of the hair shaft to the neurons, and the resultant stretch applied to the nerve terminals, may not be linear over the entire range of movement in any one direction. For example, one neuron will fire an impulse burst when the hair is moved in an anterior direction from the normal position; if the hair is maintained in this new position, the threshold of the active neuron for vibrational stimuli is a good deal lower than it was previously, and much lower than if the hair were maintained in a position posterior to normal. At the same time, the partner cell exhibits reciprocal behaviour, responding to stimuli only when the hair is displaced posteriorly. By correctly monitoring the input from a single pit receptor, therefore, the animal could theoretically determine the direction

of an applied stimulus, such as a current of water, with a good deal of accuracy. This may be readily appreciated from the records in Fig. 4, which are typical of the majority of receptors studied. In row *a*, when the tip of a pit receptor in normal position was contacted with a glass needle, both sensory neurons fired sporadically in response to transient vibrations transmitted through the recording apparatus. In row *b*, the receptor was rapidly moved posteriorly and maintained in a new position. This caused one neuron to respond during the motion with a phasic burst of activity, and thereafter it fired sporadically in response to vibrations. The threshold of the second neuron was raised above the level necessary for it to respond with equal intensity. In *c*, the receptor was moved anteriorly again, and reciprocal activity in the

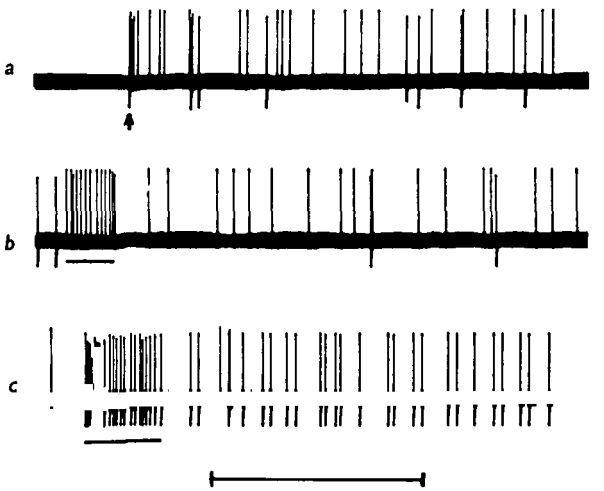

Fig. 4. Dual responses from the neurons of a pit receptor. In row *a*, at a point indicated by the arrow, a glass stylus was brought into contact with the receptor, thereby evoking sporadic activity in both sensory cells. In row *b* motion in one direction (the approximate duration of which is indicated by the horizontal bar at the start of the record) elicited a phasic burst of impulses in one cell. Thereafter that cell continued to fire in response to vibrational stimuli. In row *c* the receptor was moved in the opposite direction, and reciprocal activity can be seen in the second neuron. Time mark is 0·5 sec.

second neuron resulted. It is apparent that the pit receptors contain an inherent ambiguity, since it is patently impossible to determine whether, for example, the larger neuron in Fig. 3 simply adapts to a change of position very slowly, or whether it is responding to vibrational stimuli which cannot be detected by the experimenter. The distinction may not be of much importance to the animal, however, for it is evident that unambiguous information is provided by these receptors concerning the direction, magnitude, and termination of an applied stimulus.

The apparent differences in response characteristics between neurons have been studied. In the majority of over one hundred pit receptors observed, qualitatively similar response patterns were obtained from both neurons of a pair. Where differences do exist it is felt that these reflect variations in the coupling of the nerve endings with the cuticular structures, rather than differences in the membrane properties of the neurons involved. This conclusion was reached after experiments had been performed to test the response of cells to pulses of electric current. For that purpose, a pair of

platinum stimulating electrodes was placed on the carapace flanking the receptor to be studied. It is known (see below) that the dendritic processes of the sensory cells run for nearly 100 μ anterior to the receptor structure; the locus of strongest current density must therefore have been at or slightly distal to the cell body of the neuron. In other crustacean sensory cells spikes are initiated at a point up to $\frac{1}{2}$ mm. *proximal* to the cell body (Edwards & Ottoson, 1958). It is therefore clear that in the present experiments the stimulating current was largest in that region of the neuron normally sustaining only decrementally propagated receptor potentials, and it probably acted upon the spike-initiating zone much as does the normal receptor potential. In all experiments performed, both cells of a pair responded phasically to current pulses of

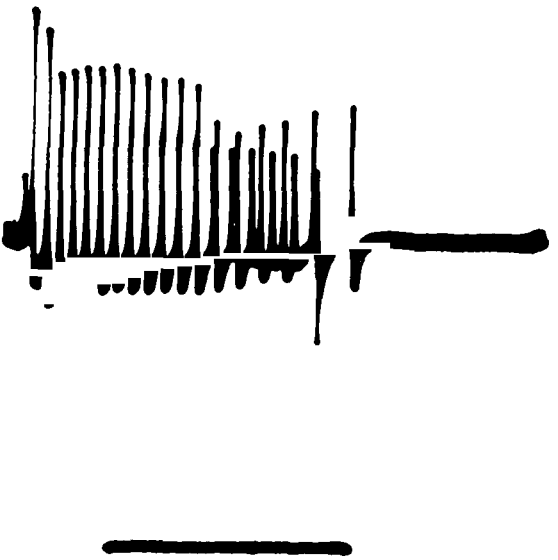

Fig. 5. Activity evoked in the neurons of a pit receptor by stimulation with electric current. Artifacts indicate onset and cessation of stimulus. Note that both cells fire in synchrony at first and come out of phase with one another in the latter half of the record. Time mark is 100 msec.

100 msec. duration; an initial high-frequency burst of impulses gradually decreased to zero with a time course which was proportional to the stimulus intensity. Even in those cases where qualitatively very different response patterns to tactile input were observed in two cells, their responses to suprathreshold electrical stimuli were remarkably similar. The record of Fig. 5 is typical. The initial frequencies of both neurons are almost identical, and only in the latter half of the record does the larger spike begin to lag behind the smaller.

The possibility of spontaneous activity in the pit receptors has also been considered. In the usual procedure the isolated piece of carapace was placed receptor side up in the tray containing the bathing solution. Enough solution was then aspirated off so that the area of exoskeleton under observation was well above the surface. Under these conditions, an electrode placed under one of the bundles of sensory fibres recorded an appreciable amount of arrhythmic activity from several cells. That such impulses are in fact responses to minute substrate-borne vibrations, and not to an inherent

autogenicity within the neurons, could be demonstrated simply by allowing the surface of the carapace to dry. As this happened, the fluid film covering the carapace and the receptors disappeared and the spontaneous activity gradually ceased. This was not due to a general deterioration of the preparation, for simply wetting the carapace caused the impulses to reappear with renewed vigour. Evidently the surface film constituted an efficient coupling device between the receptor hairs and substrate vibrations. An even more pronounced effect may be observed by bringing the tip of a receptor hair in contact with a glass needle mounted in a micromanipulator. Vibrations which are quite imperceptible to an observer are readily picked up by the sensory neurons. Row *a* in Fig. 4 illustrates this very clearly.

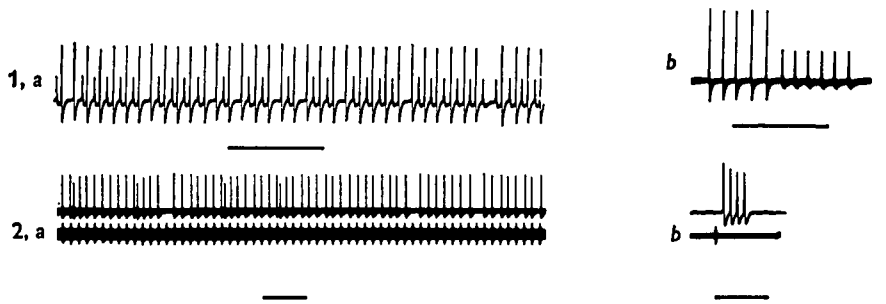

Fig. 6. In row 1, *a* trains of impulses from both cells innervating a pit receptor fire in response to their own spikes which have been amplified and transmitted to the preparation through the audio monitor. In row 1, *b*, the same cells fire selectively in response to movement in opposing directions. Row 2, *a* records the response of a single cell from another pit receptor to vibrational stimuli delivered through a glass stylus above the surface of the bathing solution. Lower trace monitors signals to the stylus. In 2, *b*, the cell fires a burst in response to a single deflexion of the stylus positioned close to the receptor beneath the surface of the solution. Time marks all indicate 100 msec.

The evident ability of the pit receptors to respond to low-intensity vibrational stimuli raised the question of the possible role of these structures in the underwater perception of vibrations, and experiments were performed to determine their ability to follow the frequency of repetitive mechanical stimuli. As a matter of convenience the first measurements were performed with the receptors out of the bathing solution. An electrically driven glass stylus was brought into contact with the receptor under study. Fig. 6, row 1 illustrates records characteristic of many receptors tested. After the stylus made contact with the receptor, the gain of the audio monitor was turned up. Occasional impulses were amplified and transmitted through the speaker back to the preparation. If the gain of the amplifier was high enough, the speaker output was sufficient to drive the receptor under study, and this feed-back loop evoked constant-frequency impulse trains at about 75/sec. in the neurons involved. In subsequent tests with other receptors which were driven by the stylus, no individual cells were found which supported a maintained response to a train of mechanical stimuli recurring with a frequency greater than 70/sec; thus around 75/sec. may represent a real mechanical limit for the pit receptors. In row 2 of Fig. 6 the response of one neuron from a receptor to stimuli occurring at 50/sec. is shown. Occasionally, as also happens with the receptor illustrated in row 1, impulses drop out of the train. This must be due to failure at the level of the nerve-receptor coupling, since the

sensory axons are capable of responding to electrical stimuli at frequencies of 200/sec.

When attempts were made to stimulate the pit receptors beneath the surface of the bathing medium, the frequency response dropped to less than 10/sec. It seems clear that the translational excursions of the receptors are effectively damped by the inertia of the solution, and, therefore, the possibility that the animals use them to detect underwater vibrations of even low frequencies appears remote. In 2*b* of Fig. 6, the same cell from which the record of 2*a* was taken is shown responding phasically to a single high-intensity mechanical pulse delivered from a glass stylus positioned near the receptor in the solution. Thus, there can be little doubt that the receptors do respond to gross movements of the fluid medium, as is the case for the peg-pit organs recently described for the lobster (Laverack, 1962).

After the above experiments with a pit receptor had been completed, vital staining procedures were often used to visualize the sensory neurons from which records had been obtained. All cells were stained in van Harreveld's solution to which rongalit and

Fig. 7. A pair of pit-receptor sensory neurons drawn to scale from a stained preparation. Note the increase in diameter of the sensory axons proximal to the cell bodies. The horizontal bar indicates 100 μ.

methylene blue had been added, as described by Pantin (1960). A pair of bipolar sensory neurons is associated with each receptor; Fig. 7 illustrates a pair of such cells which has been drawn to scale from a stained preparation. The cell bodies are plump, spindle-shaped elements 80–100 μ long and about 50 μ wide. They lie close to one another within the hypodermis, and each sends a single dendrite toward the base of the receptor, which is often 100 μ distal to the cell bodies. The proximal nerve processes, or axons, usually run together toward the central nervous sytem. They are of small diameter after they leave the cell bodies, the usual value approximating 4 μ. Within 0·5 mm. beyond the region of the axon hillock, however, both fibres abruptly increase their diameter four- to fivefold; the increase continues thereafter at a more gradual rate, and a total increase of tenfold has often occurred only 1 mm. proximal to the cell bodies. This means that the axons can attain diameters of up to 40 μ, which is a large figure even for central interneurons. Measured conduction velocities for five pit receptor sensory axons varied from 2·4 to 3·9 m./sec.

Just posterior to the cervical groove, all the sensory axons from the carapace converge to form a large trunk; this in turn joins with bundles of motor fibres innervating the scaphognathites, and the common nerve thus formed runs ventromedially to the suboesophageal ganglion. The fate of the sensory axons after they enter this ganglion has not been determined, although Wiersma (1958) has shown that some primary fibres from the pit receptors run straight through and are found in the circumoesophageal connectives.

Other neural elements also are present in the hypodermal layer. The great majority of these are much smaller sensory neurons which innervate the phasic tactile hairs

found on the exoskeletal tubercles and the marginal rows. In addition, large (*ca.* 100 μ) tripolar neurons have been observed. These cells are usually found at the junction of two tracts of sensory fibres, and they contribute a single process to each tract. The most plausible function for such cells is that they are multipolar sensory neurons which innervate more than one receptor; however, no unit yet recorded from was driven by more than a single receptor.

DISCUSSION

Only one paper (Laverack, 1962) has given more than passing mention to electrical responses from the neurons associated with the exoskeletal tactile receptors of crustaceans. The receptors which Laverack describes are phasic mechanoreceptors on the lobster claw, and are capable of determining the presence of water currents. The morphology of these organs differs in a great many respects from the pit receptors on the crayfish carapace, however, and there appear also to be evident divergences in the response characteristics of the neurons involved. In particular, Laverack states that from three to five sense cells innervate a single peg receptor; yet no indication is given that more than one of these responds to mechanical stimulation. All of the pit receptors so far examined on the crayfish thorax receive a dual nerve supply; each of the two neurons may respond when the receptor is moved, but a maximum phasic discharge is observed from only one of the pair in response to a given displacement along the animal's longitudinal axis. These structures are therefore admirably suited for detecting the flow of water along the animal in both directions, and may be instrumental in mediating orientation in response to current flow. While the pit receptors are most descriptively classed as phasic, they may also fire in a continuous, arrhythmic fashion in response to minute translational stimuli. Thus the turbulent flow of water along the surface of the carapace, no doubt enhanced by the numerous exoskeletal tubercles as well as by the pits themselves, would be expected to elicit sporadic activity in the sensory neurons. The central nervous system is thus supplied with a continuous input of information concerning the direction, and possibly the speed, of the mass flow of water over the body. Several investigators have reported activity in central interneurons of the crayfish in response to tactile stimuli applied to the tail and appendages (Wiersma, Ripley & Christensen, 1955; Kennedy & Preston, 1960).

The anatomical basis for the differential sensitivity of the pit receptors has not been investigated. In the statocyst receptors of the lobster (Cohen & Dijkgraaf, 1961) the dendrites of the neurons supplying the hairs are inserted on the inside of the hair shaft at a point distal to the articulation. Apparently the dendrite is under some tension, and moving the hair supplies the degree of stretch necessary to deform the neuron membrane and produce the receptor potential. In the crayfish preparation, vital staining techniques permit visualization of the sensory cell dendrites only for short distances beyond the cell bodies; thereafter, these processes turn deeper into the hypodermis where they are masked by the surrounding tissue. Occasionally, however, while records were being taken from a preparation, one of the active receptor hairs was broken off just distal to the articulation. When this happened a high-frequency discharge was evoked in the affected cells. Such activity gradually subsided and then ceased altogether within several seconds, and the neurons subsequently were inexcitable. This type of phenomenon has been observed for the bipolar neurons

associated with the contact chemosensory hairs of the blowfly when their dendrites were crushed or otherwise injured (Evans & Mellon, 1962), and it is therefore assumed that in the present case the dendrites invade the receptor shaft for a short distance above the basal articulation. If this interpretation is correct, a simple scheme may be proposed, as illustrated in Fig. 8, which will account for the dual sensitivity of these structures. The dendrites of the two sensory cells terminate on the inner wall of the receptor opposite to one another. Moving the receptor in one direction, as shown in Fig. 8, will apply stretch to one neuron and at the same time release some tension on the other cell, accounting for its increased threshold in this position. Electronmicroscopical evidence is needed to confirm this, however.

The apparent tonic activity of some pit receptors during maximal deflexion is similar to the behaviour of other primarily phasic mechanoreceptors. Loewenstein (1956) described tonic activity in cutaneous receptors of the frog when a maximal deformation applied to the skin was maintained. However, transient low-intensity

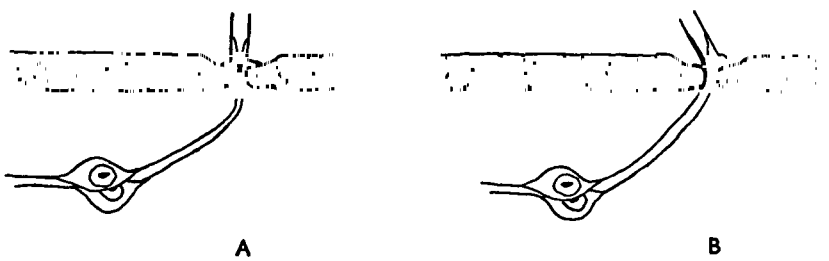

Fig. 8. Schematic representation of a possible mechanism to account for the directional sensitivity of the pair of neurons innervating a pit receptor. In A, the receptor is in 'normal' position and the tension applied to both dendrites is small. In B, the receptor is deflected, stretching the dendrite of one cell and producing slack in the other.

stimuli were effective in eliciting only phasic responses from the same receptors. He reasoned that 'non-elastic' elements in series and in parallel with the tactile endings are able to absorb transient deformations and also light maintained stretch applied to the skin. As the force responsible for deformation is increased, however, full expansion of the nerve ending occurs, resulting in a maintained depolarization for as long as the stimulus acts. It seems possible, therefore, that the rapid adaptation of some sensory neurons depends upon the mechanical properties of the transducing structure and may be unrelated to the electrical properties of the neuronal membrane. In the thoracic pit receptors, non-linear coupling of the dendrite to the receptor structure seems to offer the best explanation for the prolonged response of some cells to a maintained deflexion; in some positions the extreme sensitivity of the neurons to weak stimuli makes a period of absolute quiescence unlikely under natural conditions.

The site of impulse initiation in sensory neurons has aroused some interest in the past few years. In particular, this question has been successfully attacked in the Pacinian corpuscle (Loewenstein & Rathkamp, 1958), and in the crustacean stretch-receptor neurons (Edwards & Ottoson, 1958). The latter authors were able to establish that the site of impulse origin is proximal to the cell body of the neuron, and in fact may occur as much as 500μ from the axon hillock. The neurons associated with the crayfish pit receptors are of considerable interest in this connexion; as has been

described, the axons of these cells undergo a sudden and marked increase in diameter at a point several hundred microns from the cell body, and the question arises as to whether this point is the site of impulse origin. In his original observations of the stretch receptors Alexandrowicz (1951) described diameter increase in the sensory axons supplying those structures. It appeared to take place quite gradually, however, and no sudden enlargement is alluded to either by Edwards & Ottoson or by Florey & Florey (1955) in their investigations. An intriguing possibility is thus presented that, in the pit-receptor neurons, changes in the electrical characteristics of the membrane may be accompanied by visible morphological changes. Intracellular recording techniques are presently being employed to examine this question; the results will be reported in a subsequent paper.

SUMMARY

1. Electrophysiological recordings have been obtained from tactile receptors which occur in shallow pits on the crayfish carapace.

2. Controlled mechanical stimulation has established that each receptor is innervated by a pair of sensory neurons. One of these neurons responds when the receptor is moved anteriorly, and the partner cell responds to displacement in the opposite direction.

3. The receptors are sensitive to motion of the fluid medium in which they are immersed, and they may provide the animal with a means for determining the speed and direction of water currents.

4. Vital staining procedures have confirmed the presence of two bipolar sensory cells associated with each receptor. An abrupt increase in the diameter of the sensory axons occurs several hundred microns proximal to the cell bodies of the neurons, and it is suggested that this is the locus of spike initiation.

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