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HAIR CELL MECHANORECEPTION IN THE JELLYFISH *AGLANTHA DIGITALE*

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SUMMARY

1. The jellyfish *Aglantha digitale* is equipped with clusters of hair cells on the velum and on the tentacle bases. The cells have a central non-motile cilium surrounded by a collar of microvilli. The microvilli are graded in length, from long on one side to short on the other, giving the collar a marked polarity. The hair cells are set in specific orientations in all regions where they occur, as shown by this polarity.

2. Small mechanical displacements of the velum or tentacles in the vicinity of the hair cells evoke bursts of potentials which can be recorded extracellularly from the outer nerve ring. Intracellular recordings from the ring giant axon, which is implicated in escape locomotion, show patterns of facilitating EPSPs correlated with these potentials. Hair cell input may be important in feeding as well as in locomotory behaviour.

3. Three classes of hair cells were studied: those of the tentacle bases (T cells) and those of the velum (C cells and F cells). Direct stimulation of the tentacle bases shows that the T cells respond to slight mechanical displacements. To distinguish the functions of the C cells and F cells, which lie close together, a laser was used to ablate selectively one or other kind. It was found that the C cells respond to small mechanical displacements of the velum but no response could be assigned to the F cells.

INTRODUCTION

Aglantha digitale is a small, holoplanktonic hydrozoan medusa which shows an escape swimming response in addition to its normal 'slow' swimming behaviour. It is sensitive to touch, and escape swimming can be evoked by 'crushing or tugging one or more tentacles, by prodding the margin area or velum, by water currents directed against the margin, by shock waves in the sea water, and by a brief electrical pulse to

Key words: hair cell, mechanoreceptor, jellyfish, laser microsurgery.

the margin or a tentacle' (Roberts & Mackie, 1980). Groups of sensory cells, first described by Hertwig & Hertwig (1878) as *Tastkämme* (tactile combs) are distributed, along with isolated sensory cells, around the margin on the exumbrellar side of the velum near the outer nerve ring (Roberts & Mackie, 1980; Singla, 1983). These workers have suggested that the tactile combs are mechanoreceptor organs concerned with the escape swimming response. However, rubbing the margin in the vicinity of the combs is not particularly effective in evoking swimming, and Roberts & Mackie suggest that the escape response requires spatial summation of input from many receptors around the margin, as might occur following a variety of generalized disturbances in the surrounding water. No attempt has so far been made to record electrical signals associated with input from the sensory cells or to distinguish the functions of the ciliated cells comprising the tactile combs and the isolated sensory cells, but it seems likely that the two cell types are physiologically distinct because they differ histochemically: the isolated sensory cells show FMRFamide-like immunoreactivity, while the tactile comb cells do not (Mackie, Singla & Stell, 1985).

In this report, we show that the tactile comb cells (C cells) are mechanoreceptors associated with a characteristic type of impulse pattern recorded extracellularly from the ring nerve. Stimulation of the isolated sensory cells showing FMRFamide-like immunoreactivity (F cells) does not produce this kind of input, but stimulation of sensory cells on the tentacle bases (T cells) produces responses similar to those associated with the C cells.

MATERIALS AND METHODS

Specimens of *Aglantha digitale* were caught off the dock at the Friday Harbor Laboratories and kept in green, wide-mouthed bottles at 5 °C until ready for use. Material was fixed and processed for scanning electron microscopy using standard procedures, as described by Singla (1983).

For laser microsurgery, a Liconix Model 4050 helium–cadmium laser with a maximum output of 25 mW in the ultraviolet range (325 nm) was used in conjunction with a Zeiss research microscope equipped with an epi-illuminator and Nomarski differential interference contrast optics. A quartz camera lens (Ultra-achromatic Takumar 1:4·5/85, Asahi Optical Co.) was used to narrow and direct the 1 mm laser beam into the epi-illuminator. To allow the ultraviolet light beam to reach the preparation, an intermediate glass lens was removed from the epi-illuminator and quartz objectives (Zeiss Ultrafluar 10× and 32×) were employed. Though not ideal, these lenses are reasonably compatible with the standard Zeiss Nomarski system and, as the Wollaston prisms pass ultraviolet light, laser microsurgery can be carried out under excellent optical conditions and without adding a chromophore. The 32× Ultrafluar objective used had a phase ring, permitting viewing under phase contrast.

Specimens to be operated on with the laser were anaesthetized in a 1:4 mixture of isotonic magnesium chloride and sea water (giving 115 mmol l^{-1} Mg^{2+}) and pieces of the margin were removed and pinned out with cactus spines in shallow dishes with glass bottoms covered with a thin layer of Sylgard. As the laser spot was not visible,

the beam was first aligned using a pool of fluorescent dye on a glass slide to fix the position of the spot with reference to a point on an eyepiece graticule. The specimen to be operated on was transferred to the stage of the microscope. The structures to be ablated were located and brought under the laser spot position using the mechanical stage of the microscope, and could then be irradiated without any change in optical conditions. Using the 10× and 32× objectives the laser spot was about 10 μm and 3 μm in diameter, respectively. For ablation of individual sensory cells the smaller spot was better. Ablation took a few seconds and could be monitored visually. To destroy sensory cells functionally, it was not necessary to cause much visible damage; over-exposure to the beam could produce damage to tissues at focal levels above and below the focal point of the spot.

Extracellular recordings of nervous activity and extracellular stimulation were performed using polyethylene suction electrodes (approx. 50 μm internal tip diameter). Intracellular recordings were made with 3 mol l^{-1} KCl-filled glass pipettes with resistances of approx. 50 MΩ. For producing small, controlled mechanical displacements, a glass microelectrode was attached to a loudspeaker coil driven by a stimulator. Voltage settings on the stimulator were used as a measure of stimulus strength. The amount of movement produced at the probe tip at different voltages was not determined, and the possibility that single shocks produced oscillations at the tip cannot be excluded. However, when the tip was pressed against the animal's tissues, such oscillations would have been minimized. Signals were displayed on an oscilloscope or chart recorder.

RESULTS

Histology

The distribution of C cells as described by Hertwig & Hertwig (1878) in *Rhopalonema* and *Aglaura* and by Roberts & Mackie (1980) in *Aglantha* was confirmed. There are two tactile combs per tentacle, located symmetrically on the velum on either side of the tentacle base, but set at an angle to each other, pointing slightly outwards, away from the tentacle base (Figs 1B, 2A). Each comb consists of some 10–30 separate C cells, each with a single <30 μm long cilium (Fig. 2B) and a collar of microvilli (Fig. 2C). The cell bodies lie just below the sensory processes and send basal neurites to the nerve ring (Hertwig & Hertwig, 1878). The F cells, which also have microvillar collars but whose cilia are shorter (<15 μm long), occur singly or in small clusters between the comb pads (Fig. 2D). These cells almost certainly correspond to the population of FMRFamide-immunoreactive sensory cells decribed by Mackie *et al.* (1985). They also probably correspond to Singla's (1983) Type I sensory cells. Singla's Type II cells, which lack a collar of microvilli, could not be distinguished from ciliated epithelial cells in the preparations used in the present study. Roberts & Mackie (1980) did not describe F cells as such, but in their fig. 3 they show a few long cilia in positions where F cells would be expected to occur. In

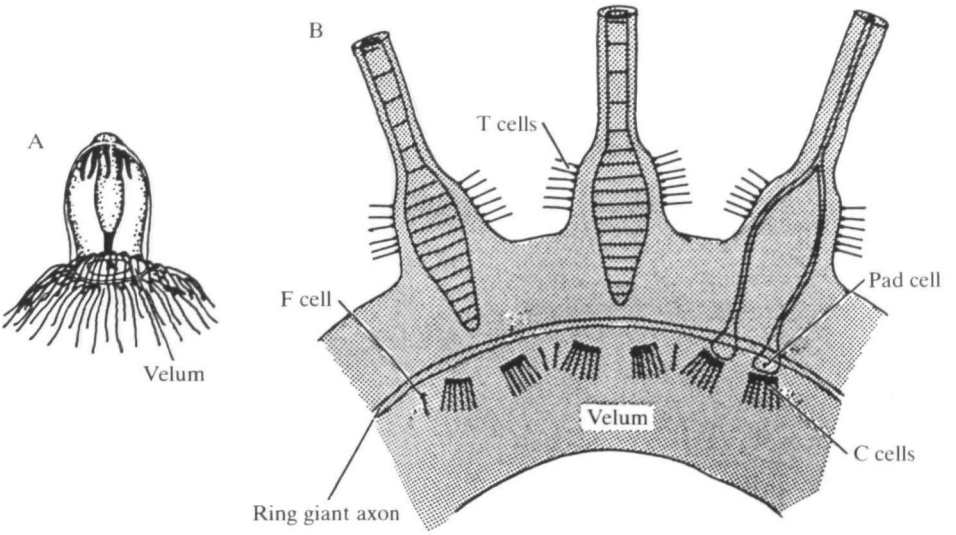
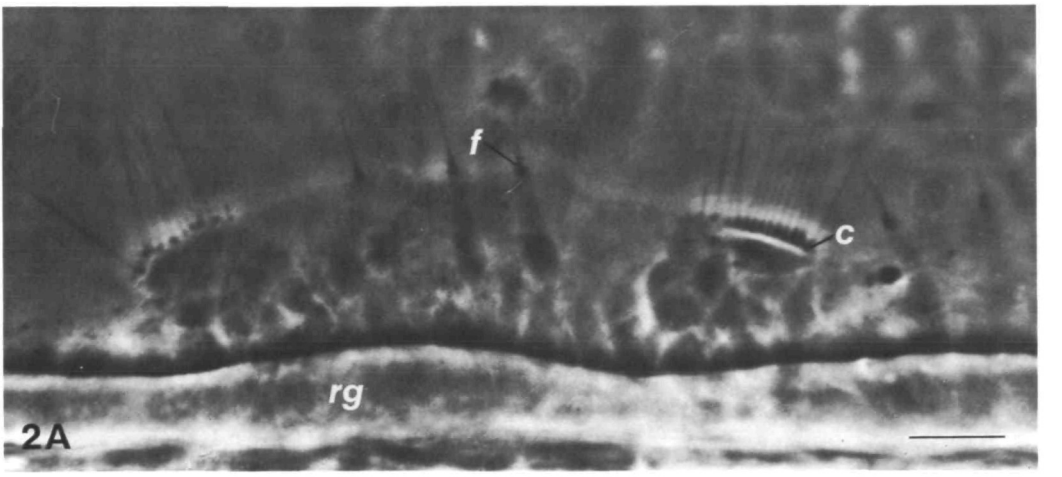


Fig. 1. (A) *Aglantha* from the side, tilted to show velum. Bell height in typical specimens is about 15 mm. (B) View from below of part of the margin, showing positions of sensory cells. The proportions have been altered to give prominence to the sensory components. The endodermal core of the tentacle on the right has been omitted, to show the course of the pad cell processes, which are believed to fuse on the aboral side to form the large 'axon' which runs along the tentacle.

view of the uncertainties in the previous literature dealing with these structures, we have included in Fig. 2 new illustrations of the F and C cells as presently defined and as they are seen using optical and scanning electron microscopy.

In both C and F cells the cilium is surrounded by a collar of microvilli graded in length with the longest situated furthest away from the tentacle base (Fig. 2C). Although there are many examples in the Cnidaria of sensory cells with a collar of microvilli surrounding a central cilium (reviewed by Peteya, 1975) we are not aware of any other case in which the microvilli are graded in length, giving the structure the distinct polarity seen here. As this polarity is a diagnostic characteristic of vertebrate hair cells it seems appropriate to use the term 'hair cell' for the C and F cells of *Aglantha*. Unlike vertebrate hair cells, however, these receptors are, as reported by the Hertwigs, primary sensory neurones.

Fig. 2. (A) A portion of the velum near the nerve ring showing tactile combs with C cells (*c*) and isolated F cells (*f*) adjacent to the ring giant axon (*rg*), as seen by phase contrast during microsurgery. Scale bar, 20 μm. (B) Tactile comb seen by Nomarski microscopy with C cells (*c*) and a pad cell process (*p*) crossing nerve ring (*nr*). Scale bar, 10 μm. (C) Scanning electron micrograph of C cell processes, in same orientation as in B. Arrowhead shows polarization of the microvillar collar towards the velum (*v*). Scale bar, 1 μm. (D) Scanning electron micrograph of F cells. Scale bar, 2 μm. (E) Tentacle base with four rows of T cells, some of which have lost their cilia. Arrowheads show polarity of collars. Scale bar, 2 μm.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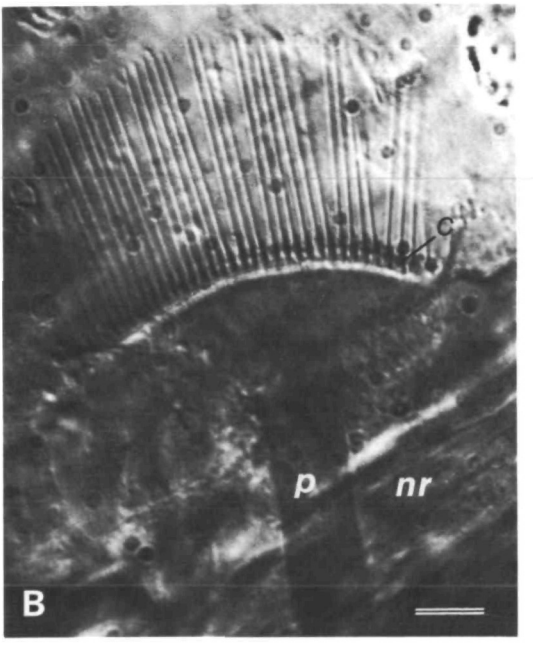
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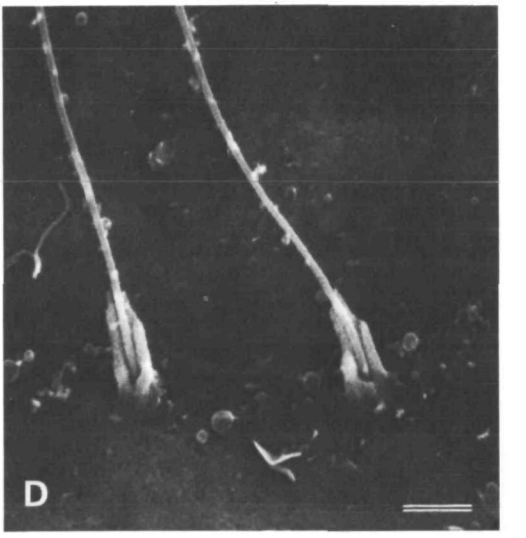
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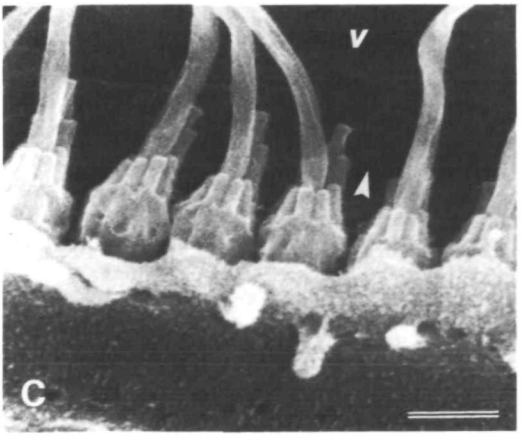
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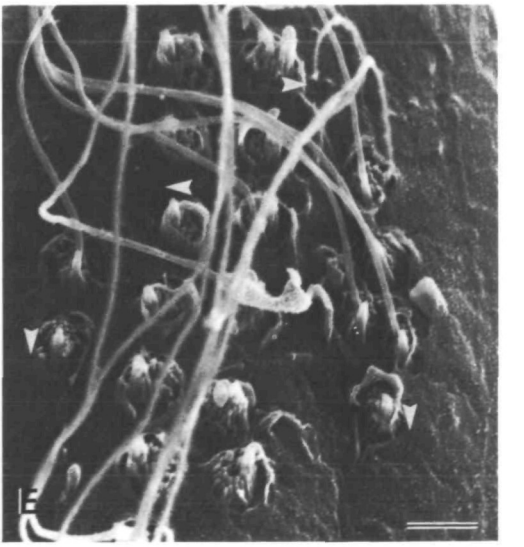
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Hair cells are found in at least two other locations: on the statocysts (Hertwig & Hertwig, 1878; Mackie, 1980; Singla, 1983) and on the tentacle bases (Hertwig & Hertwig, 1878). The latter (T cells) have more microvilli than the other hair cells. They are arranged in arrays on the lateral and lower sides of each tentacle, each array consisting of four rows of hair cells (two in immature tentacles). The polarity of the microvillous collars is the same in all the cells in any given row. In the lateral arrays, the collars of the cells in the top and bottom rows are polarized towards the base of the tentacle while those of the two middle rows are polarized orally and aborally, respectively (Figs 2E, 3).

Each tactile comb is associated with the cell body of an enormous epithelial 'pad cell' (Figs 1B, 2B) which sends out a long axon-like process that crosses the nerve ring and runs towards the tentacle base. There are two tactile combs per tentacle and one of these processes enters the tentacle base on each side. A preliminary examination by transmission electron microscopy (C. L. Singla, unpublished results) suggests that the processes pass around to the aboral side of the tentacle and fuse to become the large axon which runs along the tentacle (Roberts & Mackie, 1980). The physiological significance of the association between tactile combs and pad cells is still unclear.

Behaviour

We have confirmed that specimens of *Aglantha* respond, by swimming, to a variety of disturbances in the surrounding water. Specimens in a 5-l tank swam when the walls of the tank were tapped. However, swimming was not evoked when the coil-

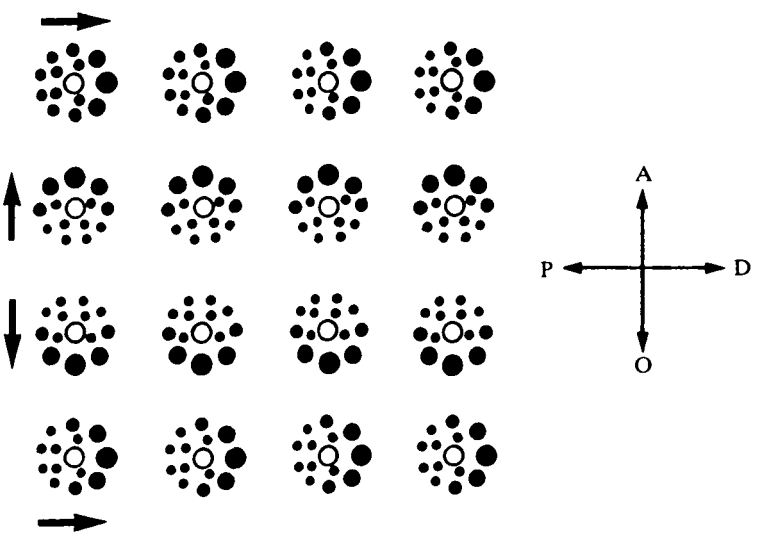

Fig. 3. Orientation of hair cells on tentacle base. The cells are arrayed in four parallel rows. In each cell, an open circle shows the cilium and closed circles show the microvilli surrounding it. The microvilli are graded in size with the longest (largest circles) lying at the ciliary pole. Polarities are indicated by arrows. Proximal–distal (P–D) and aboral–oral (A–O) axes are shown.

driven probe was caused to oscillate at frequencies up to 50 Hz a few millimetres from the animal in the water. Actual contact seemed necessary. A single 1 mm deflection of the probe sometimes induced swimming when the probe tip was placed against the side of the exumbrella. Small taps or prods applied to any part of the bell reverberated through the bell jelly and made the whole velum 'flicker' slightly, and it may be that these movements of the velum agitated the hair cells around the velar base. In quiescent animals in the natural condition, the tips of the C cell cilia lie close to the surface of the velum, and may actually touch it, though this is hard to judge from specimens mounted for microscopic observation.

Placing the probe directly against a tentacle base or delivering single strong electrical shocks to tentacles sometimes evoked escape swimming accompanied by rapid contraction of all the tentacles. Gentler stimulation produced a different response, a slow curling of the tentacles inwards in the immediate vicinity of the probe, which was usually accompanied by flexion of the manubrium towards the stimulated part of the margin. This 'pointing response', first described in *Eutonina* (*'Tiaropsis'*) *indicans* by Romanes (1877), is seen in many jellyfish, and occurs naturally when food is being transferred from the tentacles to the manubrium. In *Aglantha*, it was often accompanied by one or more slow swimming contractions.

Touching the statocysts so as to deflect them slightly (as would occur when the animal tilts) produced no visible behavioural change, although these structures are known to be necessary for vertical orientation of the animal during its slow swimming cycle (Mackie, 1980).

Physiology

Electrophysiological recordings from the ring nerves of whole specimens or portions of the marginal region pinned out in the recording dish showed that these preparations had an acute sensitivity to vibration. For example, a gentle tap on the table would elicit a burst of small potentials in extracellular recordings from the outer nerve ring. We have not succeeded in penetrating the neurones responsible for these events, but intracellular recordings from the ring giant axon, which can generate spikes setting off escape swimming (Roberts & Mackie, 1980), showed patterns of summing EPSPs apparently associated with the bursts recorded extracellularly (Fig. 4A). An exact, one-to-one correlation of extracellular spikes and EPSPs was not demonstrable, probably in part because the two electrodes could not be placed precisely in the same spot, and because the extracellular electrode might have picked up signals from only a proportion of the active units in its vicinity. A direct shock to the outer nerve ring excited several conduction systems including the ring giant, but by adjusting the shock strength and the position of the electrode tip it was sometimes possible to evoke bursts of small potentials similar to those elicited by vibration, without activating other systems (Fig. 4B). From such recordings we have calculated that the extracellularly recorded events were propagated at velocities in the range 37–45 $cm\,s^{-1}$. To the extent that they were individually discernible, the ring giant EPSPs showed temporal relationships with these propagated events consistent with the view that they were caused by them.

Using a probe mounted on a speaker coil it was possible to produce small bursts of potentials with stimuli of very low amplitude. In one set of experiments, the probe tip was placed on the velum close to a tactile comb so that displacement of the tip moved the velum in the oral direction. Displacements too small to be seen under the dissecting microscope, certainly less than 50 μm, were found to produce small bursts of potentials. Sensitivity declined as the tip was moved further away. In similar experiments, placing the probe tip on tentacle bases again produced responses to very small tip excursions. From these tests, we conclude that the C cells and the T cells were probably the mechanoreceptors responsible for the bursts of small potentials. Intracellular recordings from the ring giant show summation and facilitation of EPSPs following stimuli of graded strength applied close to individual tactile combs (Fig. 5A) and similar recordings have been made by stimulating T cell clusters. No such distinctive signals were recorded when the probe was applied to the statocysts.

It seems likely that the small potentials constituting these bursts are compound action potentials representing summed signals from variable numbers of C or T cells. With no change in stimulation parameters and using a near-threshold stimulus which should excite no more than one or a few combs, the bursts evoked by successive stimuli were found to vary markedly in the number, size and shape of the potentials and their time relationships (Fig. 5B), which suggests that we are dealing not with individual action potentials but with composite events. This would seem reasonable, given that there may be up to 30 C cells in a comb and at least twice that number of T cells on each tentacle base, and assuming that the cells do not all fire in response to each stimulus, but fire in different combinations at different times. The tactile combs lie close together and units in more than one comb might fire even when very small, local stimuli are used. This would contribute further to the variability of the latencies and wave forms observed. The potentials diminished in size (Fig. 5C) and number with distance from the site of stimulation, presumably because the processes carrying

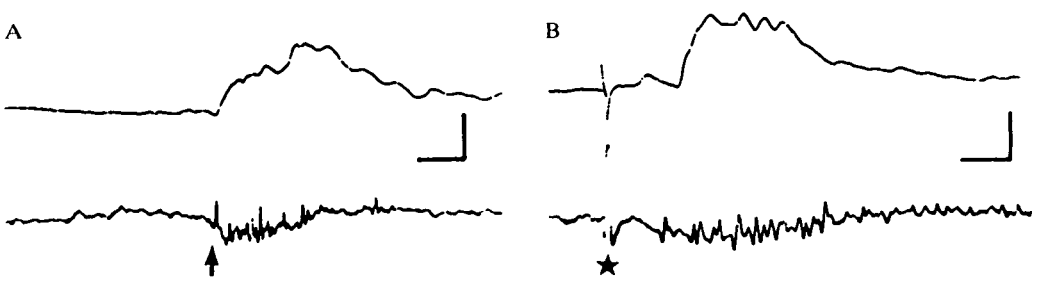

Fig. 4. Lower traces show bursts of potentials recorded extracellularly from the nerve ring following a tap on the table (arrow) in A and an electric shock (★) on the nerve ring in B. Upper traces show summing EPSPs recorded intracellularly from the ring giant axon during these bursts. In B, the intracellular electrode was closer than the extracellular electrode to the site of stimulation. Thus the first EPSP (upper trace) appears slightly ahead of the first extracellularly recorded event (lower trace). Scale bars, 20 ms and 10 ms (A and B, respectively); 10 mV (intracellular), 100 μV (extracellular).

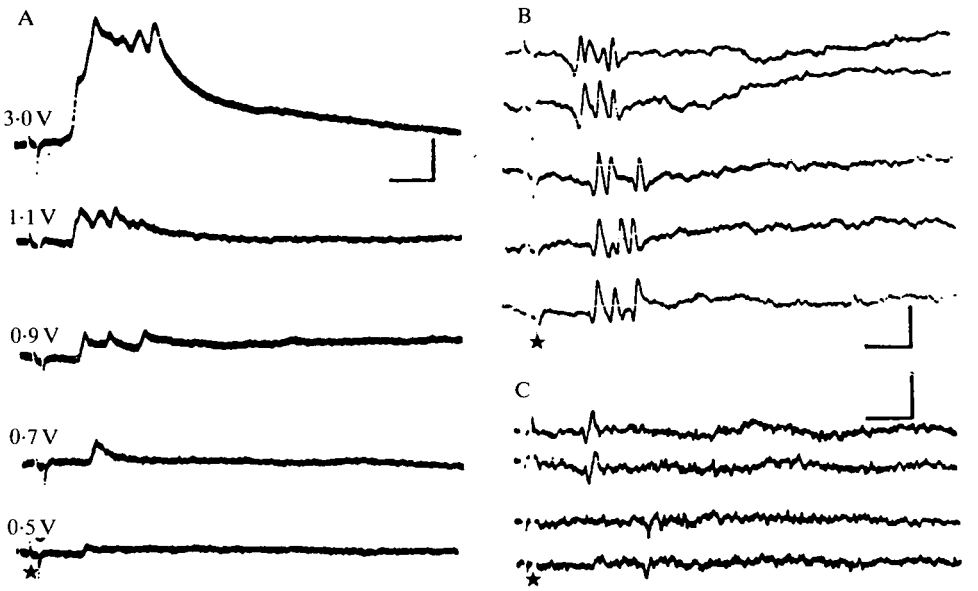

Fig. 5. (A) Intracellular records of EPSPs recorded from the ring giant axon following mechanical stimulation (★) of the velum near a tactile comb, using a probe mounted on the speaker coil. Voltage settings on the stimulator driving the coil are indicated at left. Scale bars, 5 ms, 5 mV. (B) Extracellular records of bursts produced by successive mechanical stimuli without change in stimulating or recording parameters. Scale bars, 5 ms, 100 μV. (C) Extracellular recordings of potentials from the outer nerve ring obtained by just-suprathreshold mechanical stimuli of velar receptors 2·6 mm (lower two traces) and 0·4 mm (upper pair) away from the recording electrode. Scale bars, 10 ms, 100 μV.

the input run for only limited distances around the nerve ring. A distance of about 4 mm from the stimulation site was the maximum for effective recording of responses.

The evidence presented above strongly implicates the C and T cells as mechanoreceptors responsible for the bursts of potentials recorded from the nerve ring, and we decided to test this possibility by selectively removing one or other receptor set. T cells were easily removed by cutting off the entire tentacle. After removal of the tentacles along a strip of margin, there was no change in the response obtained to near-threshold stimulation in the vicinity of the C cells, proving that C cells alone could produce the response. The converse operation, removing the C cells, was less easy because of their proximity to the nerve ring. There was the added difficulty that the F cells, which could have been contributing to the response, lie very close to the C cells. We therefore used a laser to ablate selectively the C cells and/or the F cells, after first removing the tentacles to abolish T cell input.

After removing all the F cells along a strip of the velum, there was no change in the threshold of stimulation required to produce a response (Fig. 6), indicating that F cells are not necessary for production of the normal response. When the C cells were all removed along a strip of margin, leaving the F cells intact, the stimulus threshold

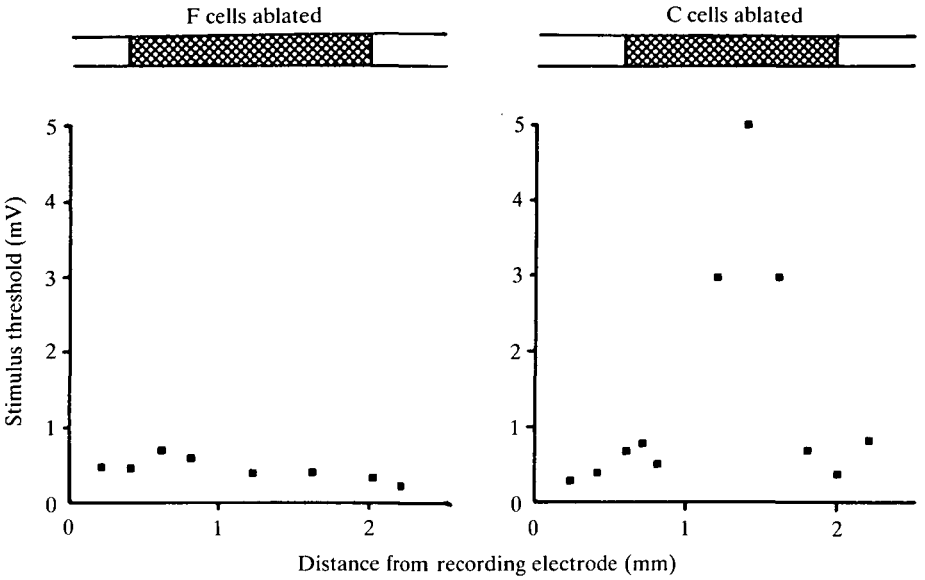

Fig. 6. Effect of ablation of F cells or C cells on responses to mechanical stimuli produced with a speaker-driven probe. The cells were ablated by laser microsurgery over a measured stretch of velum (shown cross-hatched above) lying at a known distance from the extracellular recording electrode, which was placed on the outer nerve ring at 0 mm. Points on the graphs represent stimulus intensity thresholds at various distances along the strip, starting in a region where the cells were intact, passing through the ablated region, and continuing into the intact region beyond. Threshold was defined as the lowest voltage setting applied to the probe capable of consistently evoking an extracellularly recordable response. Ablation of F cells had no significant effect on the sensitivity, but stimulus strength had to be greatly increased to produce a response in the region where the C cells had been ablated. The fact that a response could still be obtained in this region may be attributable to the stimulation of C cells in intact regions on either side of the ablated strip, as a result of movement transmitted passively through the intervening tissues. The further the probe moves into the C cell-free zone, the stronger the stimulus must be to produce any effect.

for producing the response was raised progressively as the probe moved along the strip, and returned to normal as the probe approached the other end of the strip. The fact that responses could still be obtained, albeit at higher thresholds, when stimulating in the C cell-free strip can probably be attributed to indirect stimulation of C cells in undamaged areas on either side of the strip by vibrations transmitted through the velar tissues from the point at which the probe was placed. It was concluded from these experiments that either the F cells do not respond to movements of the velum or their processes run for extremely short distances in the nerve ring. This last possibility was checked by placing the recording electrode close to F cells within the area from which C cells had been removed. No signals were recorded even when the stimulating probe and the recording electrode were both very close to F cells. It is also noteworthy that the processes of the F cells appear to

extend for considerable distances along the nerve ring in microscopic preparations of tissues treated with FITC-labelled anti-FMRFamide (G. O. Mackie, unpublished result). These observations suggest that the F cells are concerned with some sensory modality other than small movements of the velum. In another experiment, both C and F cells were removed. The resulting curve was similar to that obtained after removal of C cells alone. In a control experiment, the laser was used to make lesions along the line of the tactile combs but in areas where there were no sensory cells. In these preparations, there was no loss of sensitivity to mechanical stimulation. Removal of T cells was necessary in all these experiments because they are sensitive enough to pick up vibrations caused by larger-amplitude movements of the probe against the velum transmitted through the intervening tissues. Small-amplitude movements of the velum do not affect them, however.

DISCUSSION

The results reported here are significant first because they document one of the few cases where the electrophysiological correlates of stimulation of a cnidarian sensory receptor have been determined and second because they suggest that hair cells have evolved at least twice, once in vertebrates and once in cnidarians.

Cnidarians are known to be sensitive to chemical, tactile and photic stimuli, showing behavioural responses which, in some cases, have been correlated with changes in electrical patterns recorded from excitable tissues. In particular, some workers have recorded 'electroretinograms' from ocelli of hydromedusae (Weber, 1982*a*,*b*; Ohtsu, 1983*a*) and in a few cases intracellular recordings from medusan neurones have shown what are interpreted as the direct effects of light (e.g. Anderson & Mackie, 1977; Ohtsu, 1983*b*; Arkett & Spencer, 1986). However, in other areas of cnidarian sensory physiology we are not yet in a position to make even the most tentative correlations between specific receptor types and specific electrophysiological responses.

In the present study we describe electrophysiological responses evoked by mechanical stimulation of hair cells of one class (C cells) and abolished by laser ablation of the same cells, showing that these units are mechanoreceptors. At the same time, we have found that a second category of hair cells (F cells) appear unresponsive to this form of mechanical stimulation despite their morphological resemblance to C cells. While the goal of recording directly from these receptors has yet to be attained, these findings represent a step in the direction of discriminating functionally among different sorts of receptors, and provide us with a preparation which might be developed further for recording from individual receptor units. We have recorded intracellularly from the ring giant axon, showing that it receives input originating in the hair cells, although we cannot say for certain if the EPSPs recorded from the ring giant represent the direct input of hair cells, or whether intermediate elements are involved.

A considerable gap remains to be bridged between demonstration of mechanoreceptivity in the hair cells of immobilized preparations in the recording dish and the

determination of how this capability is used by the jellyfish in the natural environment. It seems clear, however, that the C and T hair cells provide excitatory input into the ring giant axon and so may affect the threshold of the escape swimming response or even provoke escape swimming. Local stimulation of small groups of hair cells as performed in our experiments did not evoke swimming but, in the case of more generalized stimulation, EPSPs due to hair cell and possibly other sensory input might be expected to sum, bringing the giant axon to spike threshold, as Roberts & Mackie (1980) suggested. It also seems likely that the hair cells are used in feeding behaviour, which involves localized tentacle flexions, manubrial pointing and in some cases slow (non-escape) swimming.

Vertebrate hair cells are frequently associated with sensitivity to vibrations, and it would therefore be interesting to experiment further with *Aglantha* to see if the receptors are tuned to particular frequencies. Preliminary experiments with the vibrating probe failed to evoke responses, possibly because larger amplitude stimuli or stimuli applied over a wider area are required. Responses to vibrating probes have been demonstrated in other gelatinous marine invertebrates, e.g. in ctenophores (Horridge, 1965) and chaetognaths (Horridge & Boulton, 1967; Feigenbaum & Reeve, 1977; Newbury, 1972), but the receptors mediating these responses bear no resemblance to hair cells.

Turning to the question of hair cell evolution, the distinguishing feature of vertebrate hair cells is the hair bundle, a group of fine villous processes (microvilli or stereocilia) projecting from the apical surface and graded in length from one side of the bundle to the other. This pattern is seen consistently in vertebrate hair cells 'throughout phylogenetic development from myxine to the mammalian labyrinth' (Wersäll & Bagger-Sjöbäck, 1974) but has not hitherto been reported in sensory cells outside the vertebrates. It has long been suspected that hair cells are directionally sensitive, and that the morphological polarization of the hair cell bundle is related to this functional directionality (e.g. Flock & Wersäll, 1962). It is now known that deflections of the hair bundle towards its long end evoke depolarizations, while deflections in the opposite direction produce hyperpolarizations (Hudspeth & Corey, 1977). Deflections at right angles to this axis produce no change in membrane potential (Shotwell, Jacobs & Hudspeth, 1981). A single true cilium is often present at the long end of the hair bundle, but it does not appear to be involved in mechanoelectrical transduction (Hudspeth & Jacobs, 1979). Hair cells are always mechanoreceptors, but they vary widely in the precise type of movement to which they respond, and this is frequently influenced by an accessory structure, such as the basilar membrane in the cochlea.

The hair cells of *Aglantha* are simple, having few microvilli compared with most vertebrates, and possessing a long, non-motile cilium with a 9+2 pattern of microtubules. The microvilli contain densely packed longitudinal filaments; judging from electron micrographs (Singla, 1983), these could be equivalent to the actin bundles seen in their vertebrate counterparts. The *Aglantha* hair cells show a marked gradation in hair length within the bundle, and the cilium is located at the long end, as in vertebrates. On the tentacle bases, the hair cells are set in rows with their hair

bundles oriented in specific directions in a manner recalling the patterns seen in vestibular end-organs (e.g. fig. 60 in Wersäll & Bagger-Sjöbäck, 1974). The velar tactile combs are likewise set in specific and invariable orientations. On morphological grounds alone it would be hard to avoid the conclusion that they function as mechanoreceptors with directional sensitivity. We have now provided physiological evidence that they are functional mechanoreceptors like their vertebrate counterparts, but we need to know more about their directional sensitivity and the precise modalities of movement to which they respond. Their location on the velum, which is a delicate membrane that oscillates when the animal is touched, is reminiscent of the relationship between the free-standing hair cells of the organ of Corti and the basilar membrane, although the two systems obviously differ in many respects.

The hair cells of *Aglantha* differ from those of vertebrates in many small ways, and in one major way, namely that they are primary sensory neurones with a basal neurite which runs into the outer nerve ring. Vertebrate hair cells are epithelial in origin and lack a basal process, although they make chemical synapses with afferent nerve terminals at their inner poles. It seems extremely likely that the *Aglantha* hair cells evolved independently, presumably from sensory cells of the type seen widely in the Cnidaria, with symmetrical microvillar collars. *Aglantha* and its immediate relatives (family Rhopalonematidae) are the only medusae known to have sensory cells with 'directional' collars, a feature which allows us to refer to them as hair cells. Unlike most hydromedusae, the rhopalonematids lack a sessile hydroid stage and are specialized as holoplanktonic animals, living in a densely populated mesopelagic zone along with many species of microcrustaceans, some of which they prey on, while others they avoid. They appear to be both more delicate and more acutely sensitive to stimulation than most medusae. A need for extreme sensitivity to mechanical stimuli of various sorts, often having a directional aspect, may have played a part in the evolution of hair cells in this group, as it presumably did in the ancestors of fishes.

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