Zeitschrift für Zellforschung 62, 701—716 (1964)

Massachusetts Eye and Ear Infirmary, Boston, Mass., and Yale University, School of Medicine, New Haven, Conn.

ORGANIZATION OF THE SENSORY HAIRS IN THE GRAVITY RECEPTORS IN UTRICULE AND SACCULE OF THE SQUIRREL MONKEY*

By

HEINRICH H. SPOENDLIN

With 10 Figures in the Text

(Received December 10, 1963)

The existence of two types of sensory hairs in the vestibular sensory epithelia has been reported by HELD (1926) and by KOLMER (1927). Using the electron-microscope, WERSÄLL (1956) and others have more clearly demonstrated these stereocilia and kinocilia. The basal body of a kinocilium has also been described in the cochlear hair cells of guinea pigs by FLOCK *et al.* (1962) as well as ENGSTRÖM *et al.* (1962). A morphological polarization of the sensory hairs in the cristae and the lateral line organ of fish seems to be in direct relation to the function of these sensory epithelia (LÖWENSTEIN and WERSÄLL, 1959).

The ultrastructure of the sensory cells in the maculae is basically the same as in the cristae. However, information on the organization of the cilia in the maculae is not complete.

Material and methods

Squirrel monkeys and guinea pigs were used for this investigation. In the anaesthesized animal, the vestibulum of one ear was widely opened and the maculae were exposed without damaging the blood supply. An excess of cold buffered osmic acid was then poured into the vestibulum, the maculae carefully removed and placed in cold osmic acid for further fixation. After dehydration and embedding in Epon 812, thin vertical and horizontal sections were obtained on an LKB Ultratome with a diamond knife. The sections were stained in uranyl acetate and studied in an RCA EMU 3G electron microscope.

Some thick sections (1—2 μ) were made for observation under the phase contrast light microscope, mainly to reconstruct the surface of an entire macula.

Results

The surface of the sensory epithelia of the macula utriculi and sacculi consists of the top of the hair cells of type I and type II as well as supporting cells. At the surface, all three types of cells have specific cilia. Each sensory cell carries many stereocilia and one kinocilium whereas the supporting cells have only one kinocilium and a great number of microvilli (Fig. 1). There is no significant difference between the cilia of the macula sacculi and the macula utriculi.

* This work was supported by NASA Research Grant NsC 268—62 to the Harvard University Medical School at the Dept. of Otolaryngology, Massachusetts Eye and Ear Infirmary, Boston, Mass. and by U.S.P.H.S. National Institute of Neurological Diseases and Blindness, Grant nos. B 3447 and B. 3779.

In horizontal sections close to the cell-surface we found from 60 to 105 stereocilia per sensory cell. More distant from the cell the number becomes progressively smaller until finally only very few stereocilia penetrate the otolithic membrane together with the kinocilium. The shortest of the stereocilia are 1 μ and the longest at least 12 μ long (Fig. 2). In our preparations we found no distinct lower limit of the otolithic membrane. The fibrillar appearance of this membrane may be a preparation artefact. The density of the fibrillar texture is the highest in the upper parts of the membrane, gradually decreasing towards the surface of the sensory epithelium. Only the longer hairs reach the denser region of the otolithic membrane.

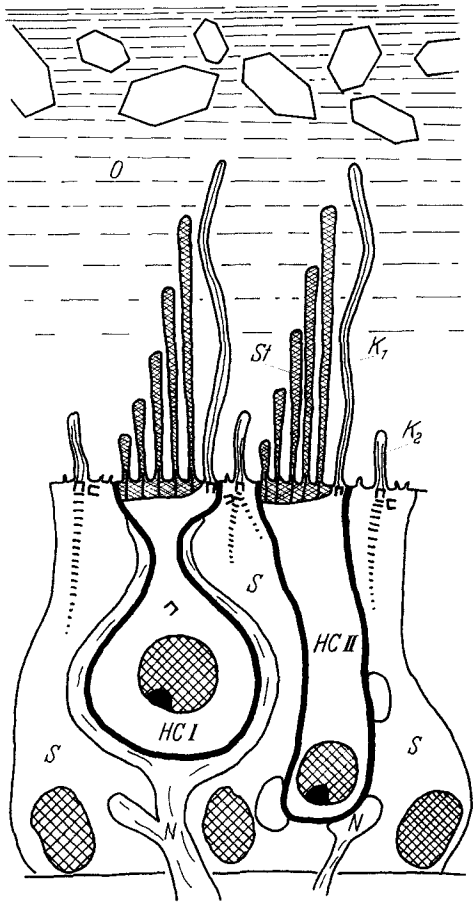


Fig. 1. Schematic drawing of 2 sensory cells (*HC I* and *HC II*) of the macula with the typical arrangement of stereocilia (*St*) and kinocilia (K_1) and their relation to the otolithic membrane (*O*). Each supporting (*S*) cell has one short kinocilium (K_2) with a striated rootlet

As demonstrated by RETZIUS (1884) and later by ENGSTRÖM *et al.* (1962), the longest of the stereocilia are always adjacent to the kinocilium. From this point, they gradually become shorter towards the other side of the cell surface (Fig. 2). Their clublike shape with a flattened end is best demonstrated in short cilia. The diameter varies from 0.04 μ at the base to 0.2 μ at the top (Fig. 3a). The stereocilia usually appear as straight rods and seem to have a relatively high rigidity as compared with kinocilia which are bent in most preparations (Fig. 3a). The weakest point of the stereocilia seems to be their thin neck part, where in some instances they are bent as well, probably due to mechanical stress during the tissue preparation (Fig. 4a) (cp. ENGSTRÖM *et al.*, 1962; WERSÄLL, 1956).

Our findings on the ultrastructure of the stereocilia correspond essentially with those of ENGSTRÖM *et al.* (1962). The dense rootlets of the hairs usually extend downward through the entire cuticular plante and upward for only a short distance into the neck of the cilia (Fig. 3a and 4a). The proper substance of the cilium has a fairly uniform extremely fine longitudinal wispy texture. The outer delimitation of the hair itself consists of two different membranes separated by a lighter zone which is about 70 Å thick (Fig. 3a). The outer membrane is a

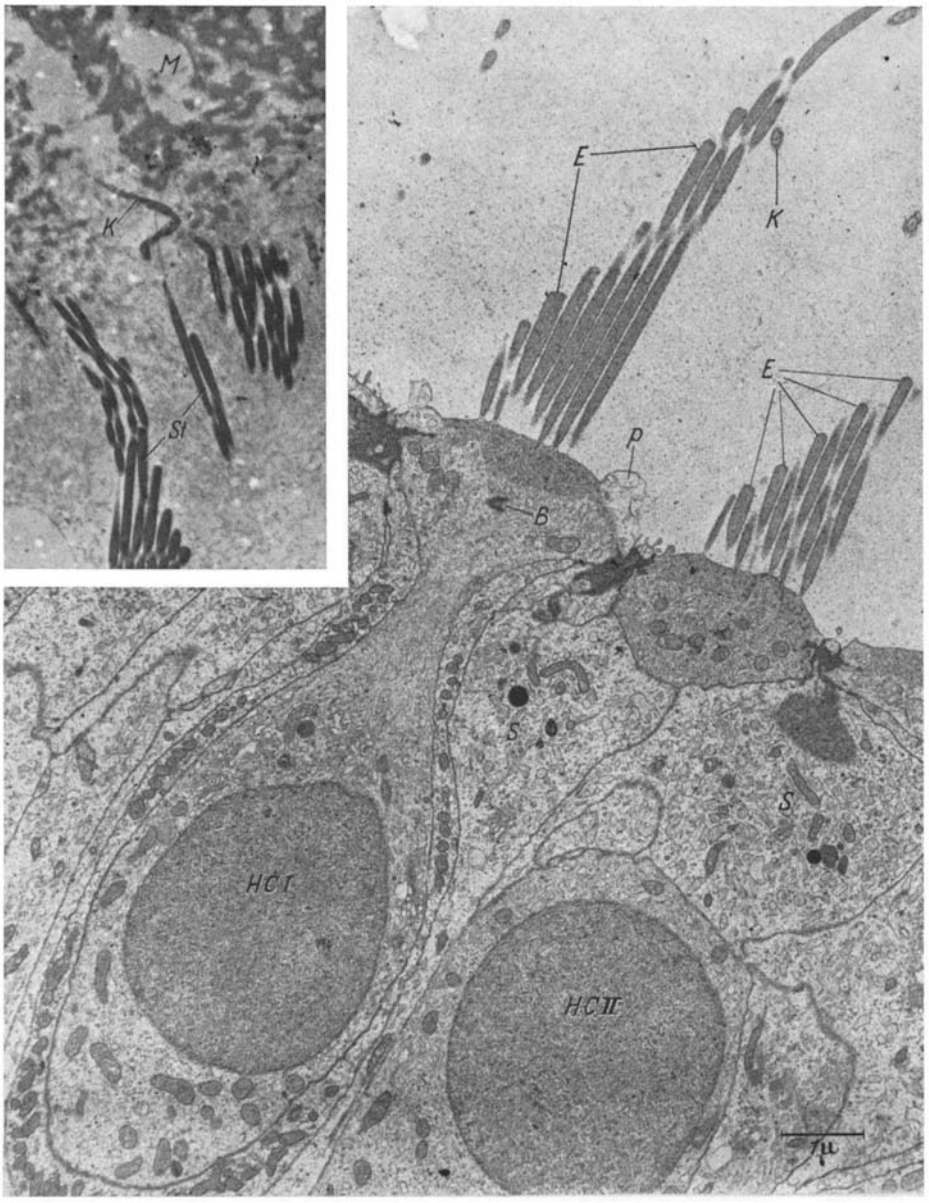
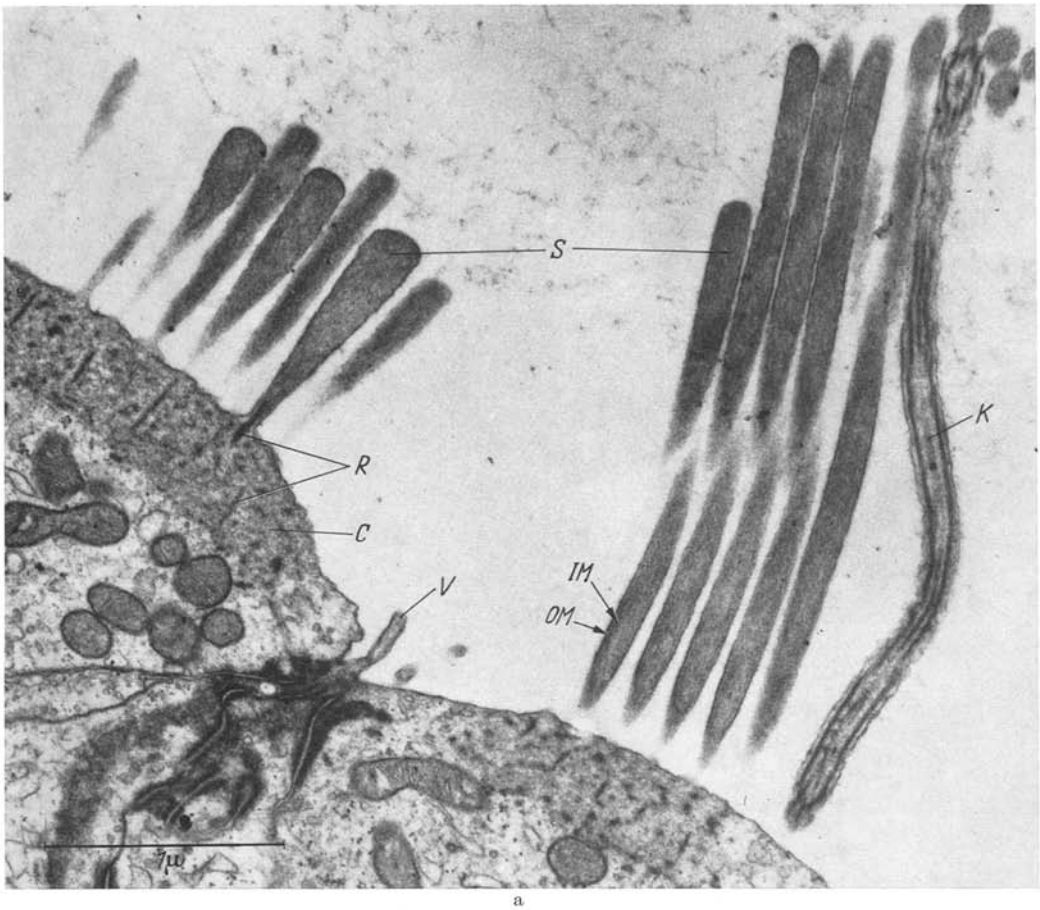
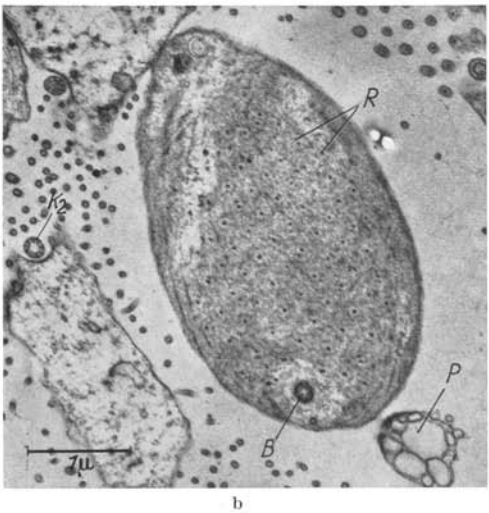


Fig. 2. Haircell type I (*HC I*) and type II (*HC II*) surrounded by supporting cells (*S*). The stereocilia present a stepwise increase in lengths from one side of the hair cell surface to the other. Their ends are flat and are therefore easily recognized (*E*). The longest stereocilia are always adjacent to the kinocilium (*K*). There usually are protuberances (*P*) at the cuticula free surface of hair cells type I. Sometimes an accessory basal body (*B*) can be found somewhere in the cytoplasm of the sensory cells. Inset: Relation of the upper part of the hair bundles to the otolithic membrane (*M*), which appears as a fibrillar substance with decreasing density towards the surface of the sensory epithelium. The kinocilia (*K*) usually penetrate the deepest into the otolithic membrane. Bundles of stereocilia (*St*)

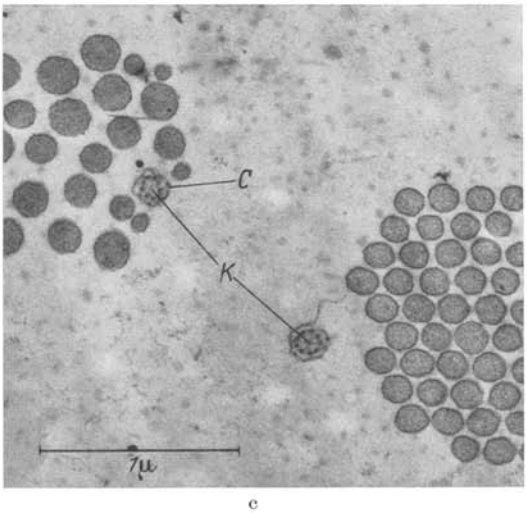
continuation of the plasma membrane of the sensory cell and consists of two separated layers in the sense of the unit membrane of Robertson (Fig. 4b).



a



b



c

Fig. 3a. Apical part of two sensory cells with rigid clublike shaped stereocilia (*S*) and one longitudinally sectioned kinocilium (*K*), which is more flexible. The rootlets (*R*) of the stereocilia extend from the narrow neck part of the hair into the cuticular plate (*C*). The outer limits of the stereocilia are characterized by an outer membrane of about 60 Å (*OM*), which is a continuation of the cell plasma membrane, and a very fine inner membrane of 20 Å (*IM*), which is continuous with the rootlet. Between the sensory cells is a small extension of a supporting cell with a microvillus (*V*)

Near the base, the stereocilia show a regular geometrical arrangement with the basic pattern of an equilateral triangle (Fig. 3b). This geometrical arrangement exists only close to the cell surface and disappears with increasing distance.

The spatial relationship between kinocilia and stereocilia has a very definite and typical pattern. The kinocilium always originates from a basal body which sits in a round cuticula-free zone on the small side of the ovalshaped cell surface (Fig. 3b). In one single horizontal section which covers an area of about 80 cells, the kinocilia of most sensory cells appear on the same side of the cell surface. They are polarized in the same direction with a variation of $\pm 20^0$ (Fig. 5). There are, however, always a variable number of cells with different polarization (Fig. 5a, 3c). This is illustrated by their relative numbers in some sections:

		Section		
		I	II	III
direction of polarization	anterior	1	1	14
	lateral	6	15	3
	posterior	35	2	1
	medial	3	0	1

Each column represents the number of sensory cells in one section which have been countet and sampled according tho the direction of polarziation of their kinocilia. Each section shows a different major direction of polarization.

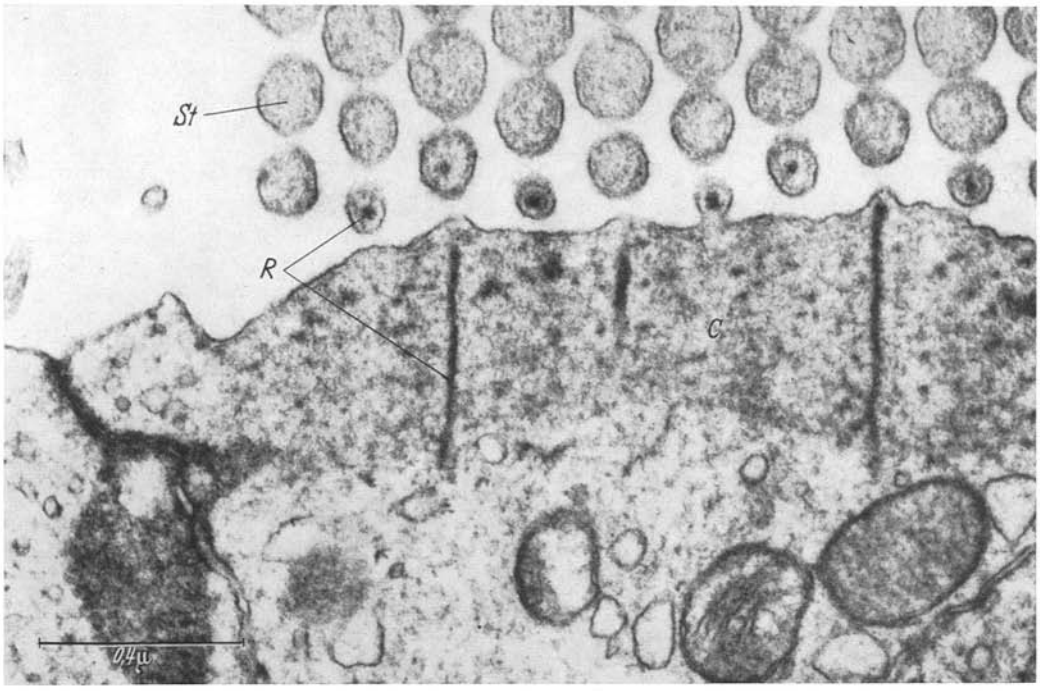
In addition, the general direction of polarization varies in different areas of the macula. In relatively thick (1 μ), but larger sections for phase contrast microscopy, the kinocilia and their basal bodies can still be recognized (Fig. 5b). In order to analyse the spatial relationship of the cilia of the entire macula, a macula is embedded and divided into several blocks of suitable size for sectioning. It is possible to keep each block in the same spatial orientation as the entire macula. If the cutting surface of each block — and therefore the sections — have the shape of an irregular quadrangel, we are able to orient the final sections according to the spatial orientation of the tissue in the animal.

In this way it is possible to reconstruct the spatial arrangement of the cilia of an entire macula. We found the general direction of kinociliar polarization different for each part of the macula (Fig. 10). In some instances, two opposite or distinctly different general directions of polarization were represented in one single section.

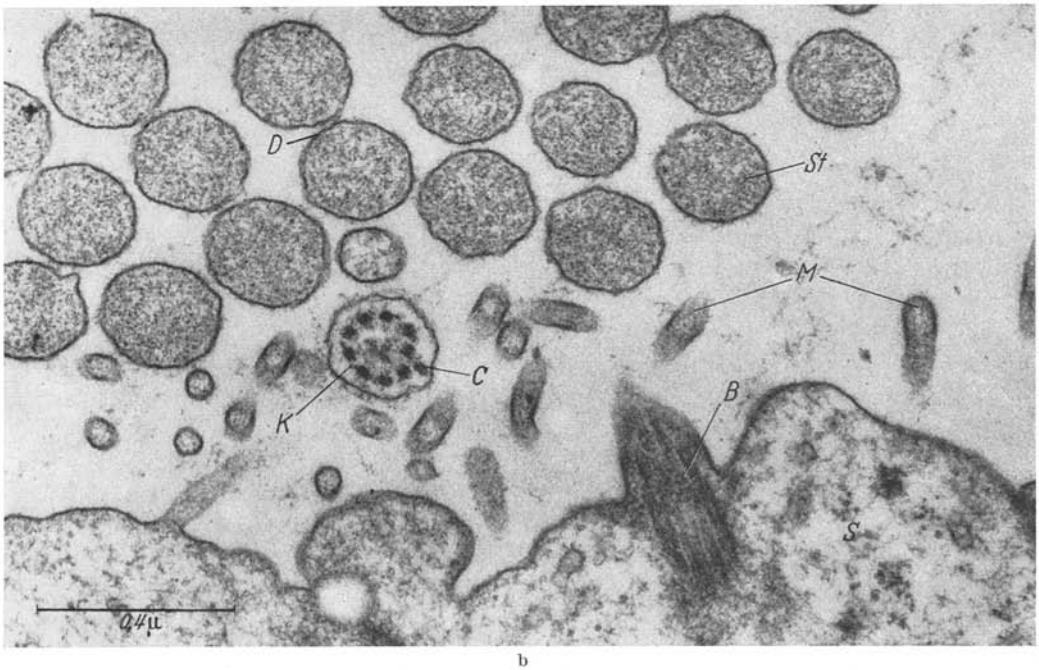
We have not yet been able to demonstrate a simple regular pattern of kinociliar polarization. However, it appears that groups of several hundred cells are polarized in the same direction and that there are many such groups with different polarization within one macula (Fig. 10).

Fig. 3b. Horizontal section through the cuticula of a sensory cell, with the geometrically arranged rootlets (R) of the stereocilia and the basal body (B) of the kinocilium on one side of the cell surface in a cuticula free zone. Each supporting cell has one kinocilium (K_s) among many microvilli. A vacuolar protuberance of the sensory cell surface is seen at (P)

Fig. 3c. Horizontal section through hair bundles slightly above the cell surface. In this instance the polarization of the kinocilia (K) is in opposite direction. In addition to the typical pattern of the kinocilium with 9 peripheral and two central filaments, there are some dense corpuscles (C) near the outer membrane of the cilium



a



b

Fig. 4a. Apical part of a sensory cell with longitudinally sectioned rootlets (*R*) of stereocilia (*St*), which usually extend through the entire cuticular plate (*C*). There is a questionable fine transverse striation in those rootlets. The stereocilia appear in cross section because they are bent just above the surface of the cuticula

Fig. 4b. Stereocilia (*St*) and one kinocilium (*K*) of a sensory cell in cross section. The typical pattern of a kinocilium with 9 peripheral and 2 central filaments and one additional peripheral corpuscle is clearly visible. The basal body (*B*) of a supporting cell (*S*) appears in an oblique section. The double layers of the cell membrane (unit membrane) can be seen at the cell membrane of the cell surface as well as on the microvilli (*M*) and a little less clearly on the stereocilia (*D*)

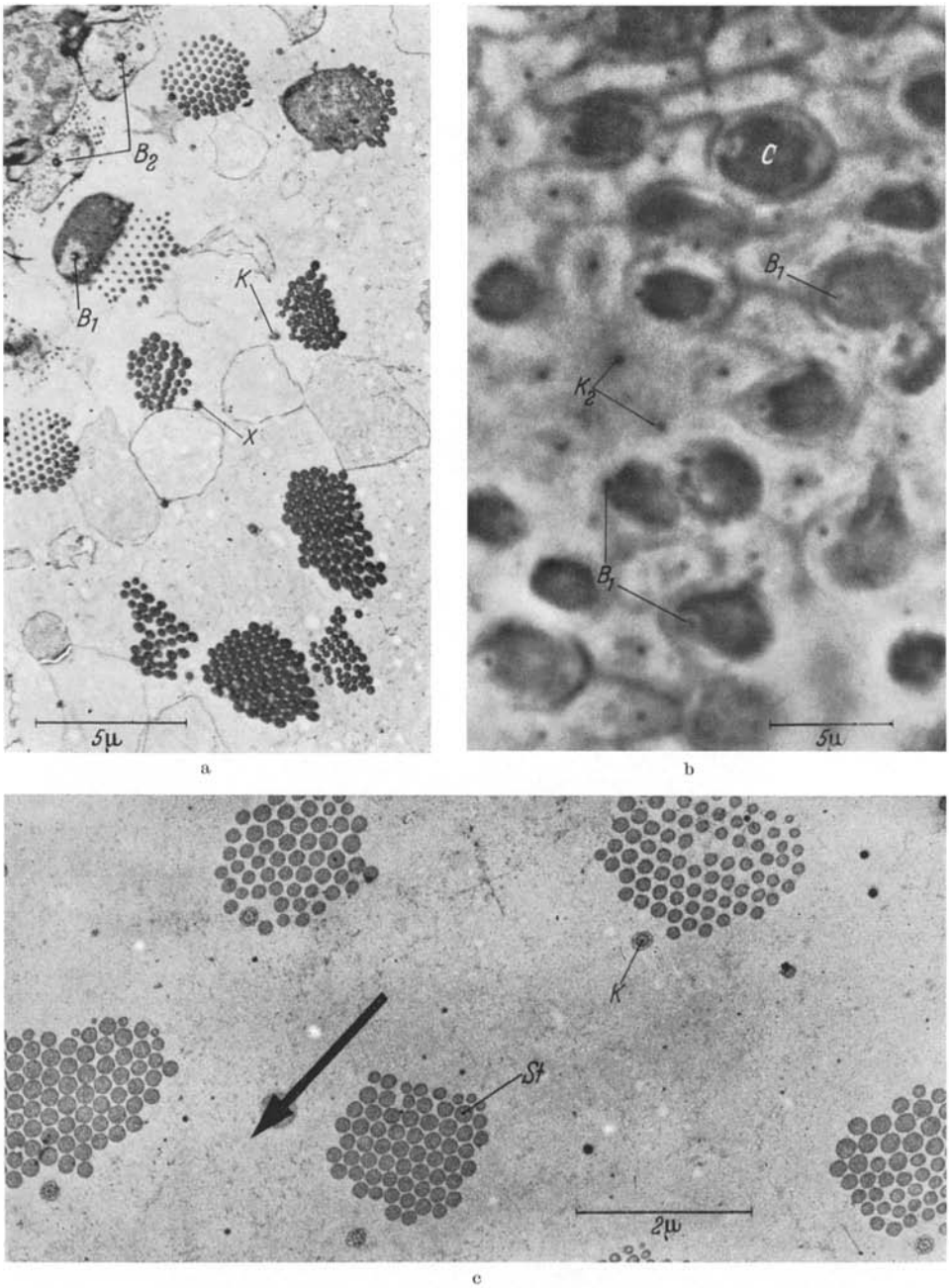
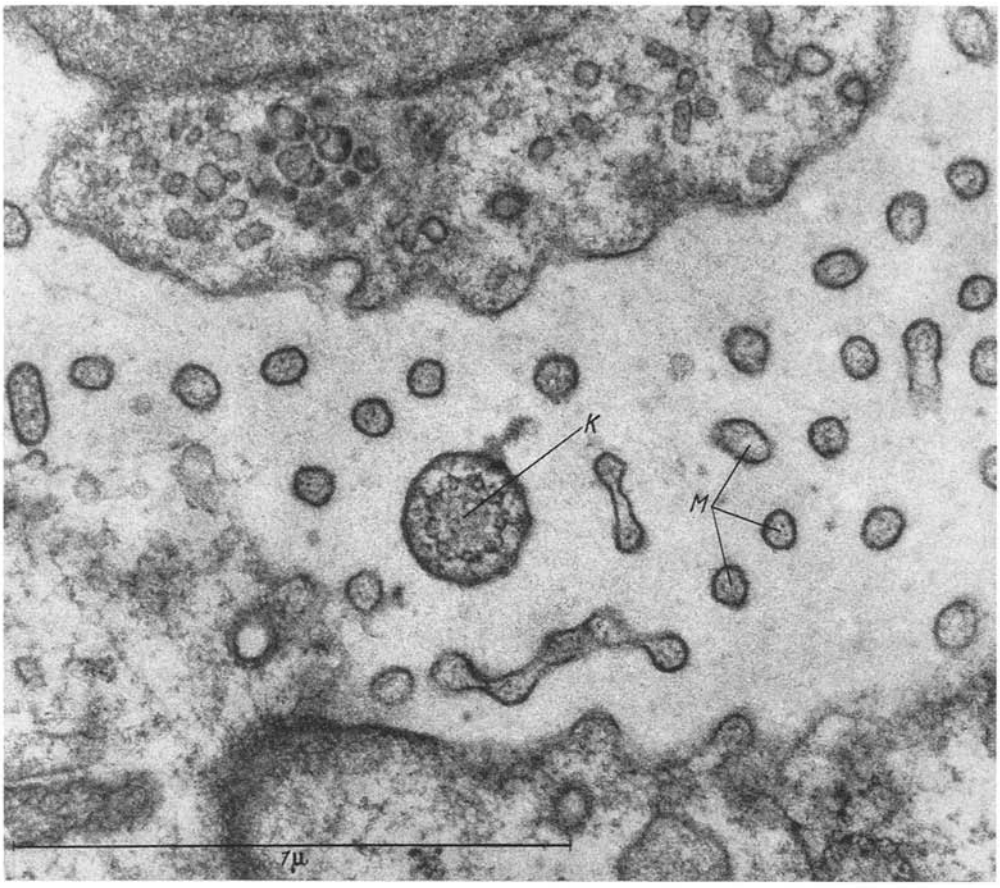


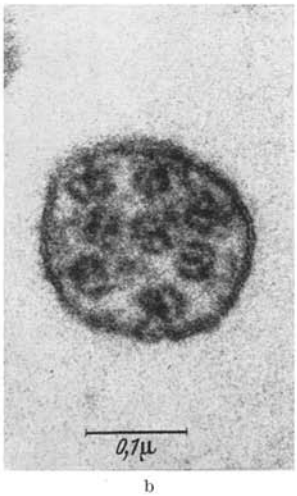
Fig. 5a. Horizontal section through the surface or slightly above the surface of the sensory epithelium of a macula. The kinocilia (K) or the basal bodies of the sensory cells (B_1) are polarized more or less in the same direction. Some kinocilia, however, do not follow the rule and are polarized in a different direction (X). Each supporting cell has its kinocilium with a basal body (B_2)

Fig. 5b. Thick section through the surface of the sensory epithelium observed with phase contrast light microscope. The cuticular area (C) of the sensory cells and the basal bodies of the kinocilia (B_1) are clearly visible. Each supporting cell shows a dark spot, which represents its kinocilium (K_2) or the basal bodies

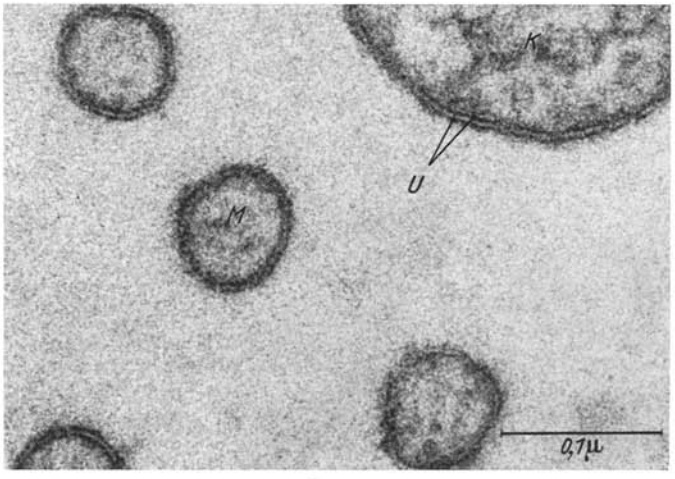
Fig. 5c. Horizontal section through sensory hair bundles close to the surface of the sensory epithelium. The main direction of polarization of the kinocilia (K) in relation to the stereocilia (St) is indicated by a large arrow



a



b



c

Fig. 6a. Horizontal section through the surface of a supporting cell. The tubular filaments in the kinocilium (*K*) are connected to a ring near the base of the kinocilium. The kinocilium and the microvilli (*M*) show the double membrane pattern of the unit membrane

Fig. 6b. Cross section through a kinocilium of a supporting cell a little further away from the cell surface. The double tubular filaments run without a specific order through the kinocilium and they are reduced in number

Fig. 6c. High magnification detail from Fig. 5a, which shows clearly the two dense layers, about 20 Å thick, separated by a lighter zone of about 30 Å. This pattern of a "unit membrane" (*U*) is present in kinocilia (*K*) and on the microvilli (*M*) as well as on the stereocilia

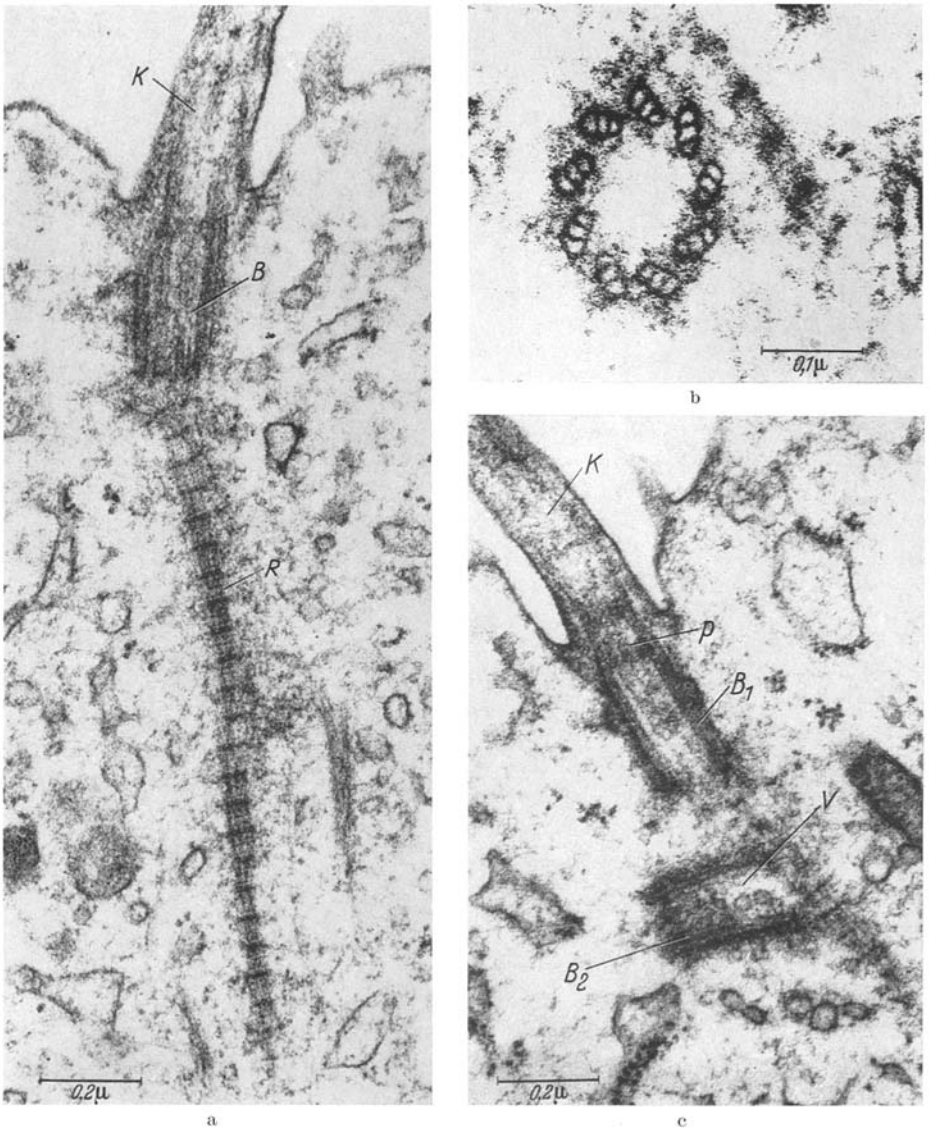


Fig. 7a. Basal body (B) and rootlet (R) of a kinocilium (K) in a supporting cell. The rootlet seems to be loosely attached to the bottom of the basal body. There is a clear transverse double periodicity in the rootlet. The large bands are about 100 Å thick and at a distance of approx. 500 Å from each other. The smaller striations between are approx. 50 Å thick

Fig. 7b. Cross section through a basal body in high magnification. The typical pattern of nine triple tubular filaments in a spiral arrangement corresponds exactly to the structure of a centriole. Those triple tubular filaments are the continuation of the peripheral filament in the kinocilium. The basal bodies of the kinocilia of supporting and sensory cells have the same appearance

Fig. 7c. Section through a basal body with an associated centriole in relation to a kinocilium (K) of a supporting cell. The kinocilia in the supporting cells usually have a basal body and an associated centriole, frequently in a perpendicular position to each other, which corresponds to the original position of the two centrioles in a diplosome. The basal body (B_1), which is perpendicular to the cell surface, is always in connection with the kinocilium, whereas the second one (B_2) lies more or less free in the cytoplasm. As in lower animals, there is a basal plate (P) between basal body and kinocilium. The lower end of the cylindrical basal body is open. Small vesicles (V) are frequently found inside the basal body

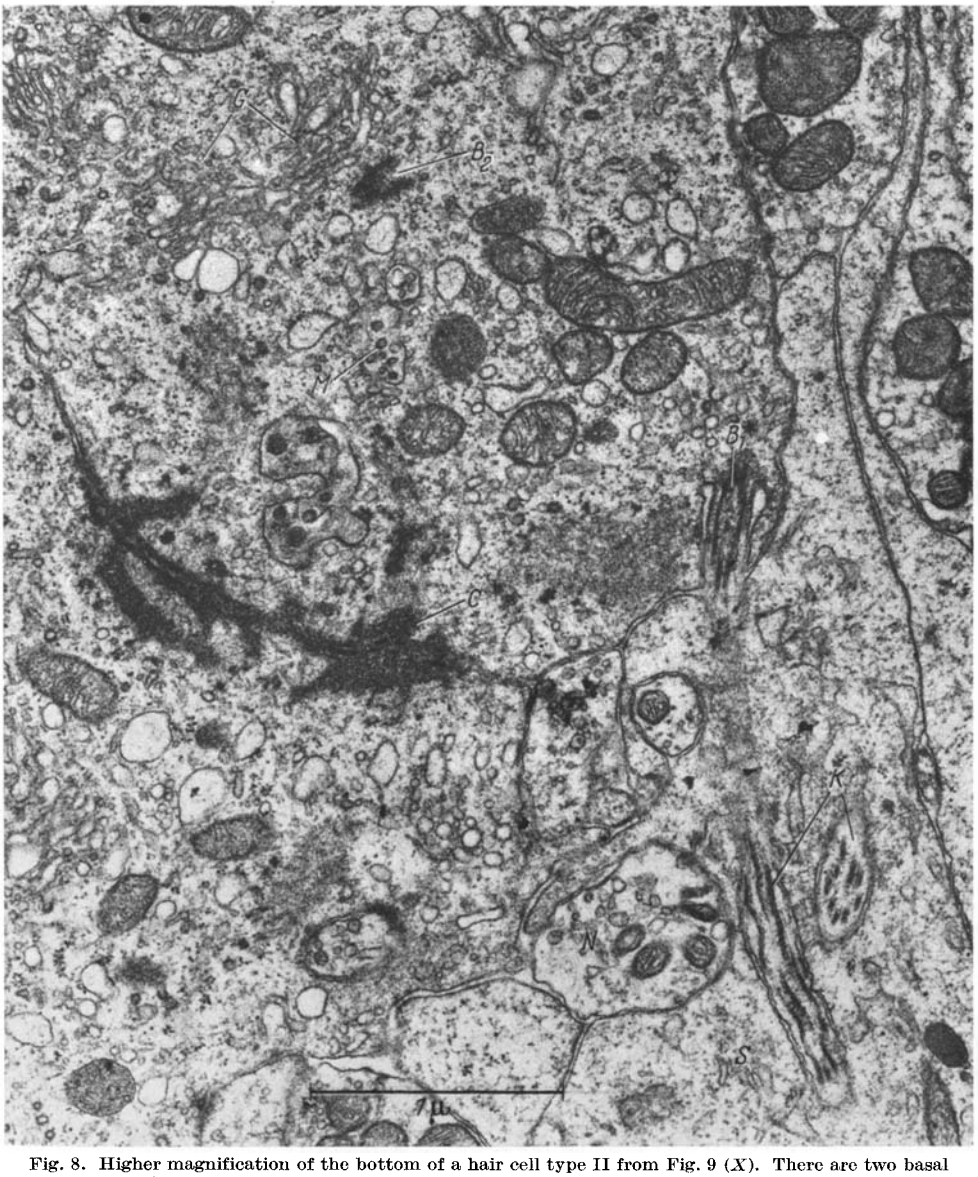


Fig. 8. Higher magnification of the bottom of a hair cell type II from Fig. 9 (*X*). There are two basal bodies (B_1 and B_2). A typical kinocilium (*K*) emerges from one basal body (B_1) and extends downward between supporting cells (*S*) and nerve fibres (*N*). A second kinocilium is seen in cross section right next to it. In addition to the kinocilia there is the beginning of differentiation of a cuticula (*C*). The great number of Golgi membranes (*G*) and related multivesicular bodies (*M*) is usual in the type II hair cells

The kinocilia of the vestibular sensory cells have the same basic structure as kinocilia elsewhere (Fig. 4b). They are the longest of all the cilia in the macula and penetrate into the otolithic membrane.

The outer limiting membrane of the kinocilium corresponds to the cell plasma membrane with the typical structure of a unit membrane (Fig. 6). In addition to the basic pattern of 9 peripheral doublets and two single central filaments, the kinocilia of the macular sensory cells frequently show excentric small corpus-

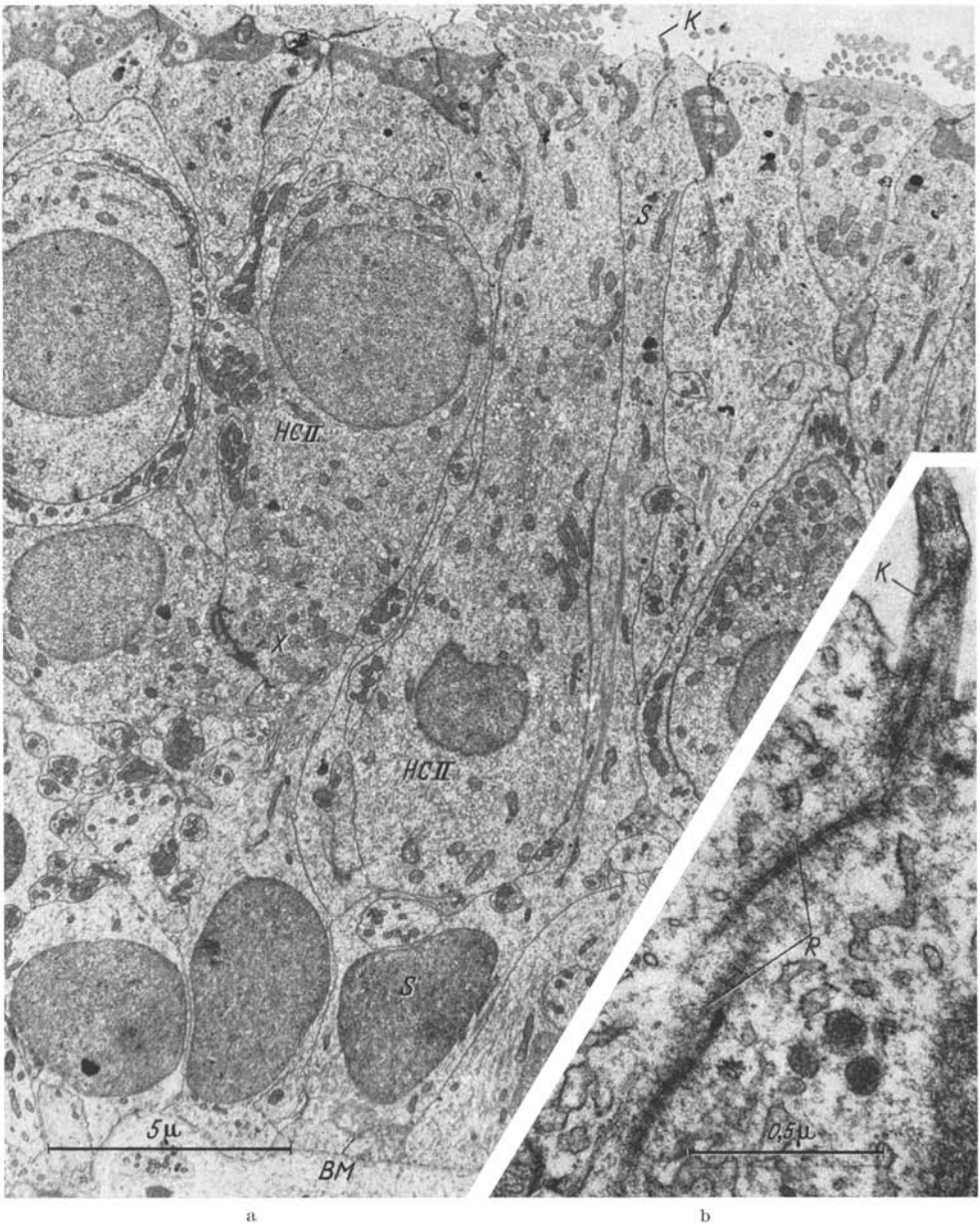


Fig. 9a. Survey picture of part of the sensory epithelium of a macula with 2 hair cells type II (*HC II*) and supporting cells, one of which (*S*) can be followed from the basement membrane (*BM*) up to the surface of the epithelium. At the top it carries a kinocilium with rootlets (*K*). (*X*) designates the area of a hair cell type II, which is reproduced at higher magnification in Fig. 8 and shows basal bodies and kinocilia at the bottom of the hair cell

Fig. 9b. Detail from the top of the supporting cell of Fig. 8a showing the kinocilium (*K*) with two striated rootlets (*R*)

cles, usually in close contact with the outer membrane of the cilium, but very irregular in number and orientation (Fig. 3c, 4b). Near the cell surface the peripheral filaments are joined together to form a ring. The filaments' intracellular

extensions form the cylindrical basal body. There the filaments assume a triple-tubular shape and appear in a spiral arrangement (Fig. 7b). At the upper end, the basal body is usually closed by the basal plate of the cilium whereas the lower end is open (Fig. 7c). A few small vesicles can often be distinguished inside the cylinder of the basal body.

On some occasions we have seen a typical kinocilium with its basal body originate at the bottom of the sensory cell and extend downward between supporting cells and nerve fibres (Fig. 8). In these cases, there exists a deep circumciliary invagination of the sensory cell's plasma membrane. Isolated centrioles, similar to basal bodies, can be found anywhere in the sensory cells (Fig. 2 and 8).

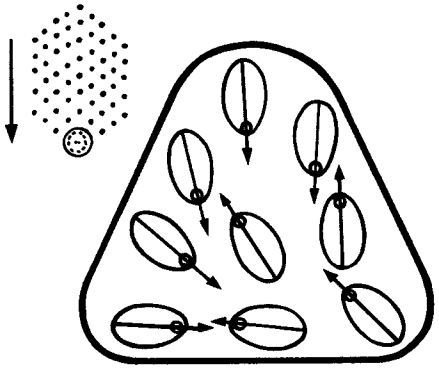


Fig. 10. Schematic drawing of a macula utriculi which has been reconstructed. The small figures with arrows indicate the main direction of polarization of the kinocilia in different areas of the macula. Each of those figures with arrows represents a group of several hundred sensory cells. At the upper left is a schematic picture of the arrangement of stereocilia (small plain dots) and the kinocilium (larger circle with dots) of one sensory cell

Each supporting cell has also one modified kinocilium more or less in the center of its surface (Fig. 5b and 9). Near the cell surface they show a $9 + 0$ pattern with missing central filaments (Fig. 6a). More distant from the cell surface, however, the peripheral filaments lose their regular annular arrangement and lie without a special order within the kinocilium (Fig. 6b). At the same time their number decreases.

The basal body reveals the same structure as it does in the sensory cells. There is, however, usually an associated centriole of the same dimensions and structure close to the basal body proper but without direct connection to it (Fig. 7c). In relation to the basal bodies in the supporting cells there are typical roots as long as 2 μ (Fig. 7a). Usually more than one root extends from the basal body in different directions. Those rootlets present a distinct periodicity in two phases in the form of transverse striations as well as a faint longitudinal texture (Fig. 7a). No special concentration of mitochondria or other cytoplasmic organelles around those rootlets are observed.

Besides the kinocilium with its related structures, many microvilli cover the surface of the supporting cells. They appear as simple cytoplasmic protrusions of the cell surrounded by a unit membrane (Fig. 6a, 6c).

Discussion

Attempts have recently been made to relate the structural features and spatial arrangement of the sensory hairs in the inner-ear sensory epithelia to the mode of excitation of the sensory cell (LÖWENSTEIN and WERTSÄLL, 1959; FLOCK *et al.*, 1962).

The bending of the stereocilia has been regarded as an important event in the hair cell excitation (DAVIS 1960). Their apparent stiffness makes it, however, more

likely that they transmit as pure mechanical levers the shearing motion between otolithic membrane and sensory cells as proposed by ENGSTRÖM *et al.* (1962) and SPOENDLIN (1960). However, the relatively high flexibility of the thin neck of the stereocilia (which is also evident in ENGSTRÖM's experiments on unfixed tissues) might also have functional significance, possibly in an attenuation of strong stimuli.

The stereocilia consist mainly of a dense proper substance without any cytoplasmic organelles on which the energy production or other metabolic activities rely. There is no true activity of dehydrogenases present in the stereocilia. We may therefore assume that only small amounts of energy-consuming processes take place within the stereocilia.

The regular geometrical arrangement of the stereocilia on top of the sensory cells gives them maximal mechanical properties for the transmission of shearing forces between sensory epithelium and otolithic membrane. The gradually increasing length of the stereocilia from one side of the sensory cell surface to the other might have functional significance as mentioned by ENGSTRÖM *et al.* (1962). Only the larger stereocilia are in permanent contact with the otolithic membrane. With increasing displacement of the membrane and inclination of the stereocilia under stimulation, more and more shorter cilia will be caught by the membrane and deviated.

The kinocilium represents an elementary structure and is found with basically the same ultrastructure in most animals. Its primary role seems to consist of motility as is expressed in its name. In certain situations, however, it may have quite a different functional significance.

Kinocilia have been demonstrated in the central nervous system (DAHL, 1963) as well as in the adeno-hypophysis (BARNES, 1961) where motility is very unlikely. They also are present in many types of sensory cells such as the rod cells of the retina where they differentiate further in an important part of the sensory cell (SJÖSTRAND, 1953; LASANSKY and DE ROBERTIS, 1960). The presence of kinocilia in a modified form in other sensory systems, such as the olfactory epithelium or sensory organelles in primitive unicellular animals (WOLKEN, 1956), certainly suggests their active role in some sensory systems.

As outlined by FAWCETT (1961), the mobile cilia retain the 9 + 2 pattern, whereas the cilia, with a probably different function, such as sensory, usually lose the central filaments and show a 9 + 0 pattern.

The functional significance of the kinocilia in the vestibular sensory cells is not yet fully understood. Here they remain in their original typical shape with a 9 + 2 pattern and only minimal further differentiation in the form of occasional additional marginal corpuscles.

It has become evident in recent years that the basal bodies of kinocilia in lower animals have an almost identical structure with the centriole of the cell (GIBBONS and GRIMSTONE, 1960). The basal bodies of cilia in higher animals are usually more or less modified. However, in the supporting cells and sensory cells of the maculae in squirrel monkeys, the basal bodies retain their original elementary structure very closely resembling a centriole. It is generally accepted that the basal body of a kinocilium is a homologue to the centriole (HENNEGUY, 1897, and LENHOSSÉK, 1898) and that it can be derived from a centriole (SOTELO, TRUJILLO CENOZ, 1958).

In the sensory epithelium of the maculae, a centriole can be situated in the lower part of the cell and the kinocilium can differentiate at the base of the sensory cell instead of at the top, as is usual (Fig. 8). In connection with a kinocilium at the base of the cell, there is also evidence for differentiation of a cuticular plate in this area of the cell. This illustrates that the centrioles, one of which will later become the basal body of the kinocilium, are in relation to the differentiation of certain cytoplasmic structures of the cell. The centriole is considered as the morphogenic center of the kinocilium (FAWCETT, 1961). The exceptional basal position of the centriole causes the differentiation of a kinocilium in this unusual direction. This can probably be considered as a slight disorganization of the cell-development resulting in mild malformation.

The perpendicular position of the basal body and the associated centriole of the supporting cells (Fig. 7c) corresponds to the typical position of the distal and proximal centriole of a diplosome as is found, for example, in spermatids (FAWCETT, 1961; GALL, 1961). The basal bodies and associated centrioles therefore retain not only the structure of the centrioles, but also their perpendicular orientation as in the original diplosome. This certainly illustrates again the homologeous nature of basal bodies and centrioles.

It is rather unusual to find well developped rootlets on kinocilia in adult mammals (Fig. 7a), (FAWCETT, 1961). Similar but much smaller rootlets have been reported from DAHL (1963) in granular cells of the cerebral cortex in rats and in the neural epithelium of a rabbit-foetus (TENNYSON, PAPPAS, 1962). In invertebrates, they are frequently observed and are considered as anchoring structures to stabilize the basal body of a motile kinocilium (FAWCETT, 1961). However, motility has never been demonstrated in the kinocilia of the vestibular sensory epithelia. The fact that squirrel monkeys are phylogenetically old animals may help to explain the presence of those rootlets which have the same structural characteristics as those observed in lower animals.

The great importance of the centriole in the organization of the cell and the concepts that basal bodies of kinocilia and centrioles are homologeous structures, certainly justifies the assumption that a basal body in the sensory epithelia in the inner ear still represents a very important center of the cell. This may be related to a functional polarization of the cell. ENGSTRÖM *et al.* (1962) consider the basal body as "the essential excitable structure" in the sensory cell. However, the fact that the same type of basal bodies are present also in the supporting cells and that they are more or less unmodified centrioles, makes this assumption somewhat questionable. In this original form basal bodies appear to be fairly unspecific structures. ENGSTRÖM *et al.* (1962) arrived at their concept on the basis of isolated "basal bodies" which they found in cochlear hair cells in guinea pigs. The mere presence of a basal body in a sensory cell, however, does not seem to be enough evidence for the assumption that it is essential for the receptor action as such. When a kinocilium-basal body complex is present in other sensory systems, it usually is modified to a certain extent (SJÖSTRAND, 1953; WOLKEN, 1956; CHAPMAN and TILNEY, 1959; ROUILLER *et al.*, 1956).

The interesting observation of a "basal body" in each cochlear hair cell in guinea pigs by FLOCK *et al.* (1962) and ENGSTRÖM *et al.* (1962) must be confirmed in other animals before conclusions on their functional significance are possible.

There is certainly evidence that the position of the kinocilium in the hair cell is related to a functional polarization of the cell. This has been shown by LÖWENSTEIN and WERSÄLL (1959) in the cristae of different animals and by FLOCK *et al.* (1962) in the lateral line organ of fish. According to these authors, an increase in the rate of discharge in the afferent nerve fibres occurs by displacement of the cupula in the direction of the kinociliar pole of the cell, whereas a cupular displacement in the opposite direction causes a decrease of nervous discharge. The polarization of the kinocilia in the maculae utriculi and sacculi appears to be more complex than has been found in the cristae by these authors. Reconstructions of the maculae reveal groups of several hundred sensory cells, each group with a different general direction of polarization (Fig. 10). All directions of polarization are represented among the cell groups of one macula. A preponderance of polarization in one direction can, however, not be excluded.

The results of BOS *et al.* (1963) in their experiments on positional nystagmus after unilateral labyrinthectomy in rabbits could indeed suggest that there is a preponderance of polarization in one direction.

If this anatomical polarization does correspond to a functional polarization, we must assume that the groups of uniformly polarized sensory cells represent functionel units. A linear acceleration in one direction would have a different effect on each of these functional units. The strongest effect could be expected on the group of sensory cells whose direction of polarization corresponds best with the direction of the linear acceleration, such as the gravitational force. Such assumptions on the receptor mechanism of the maculae, however, have to correspond finally with the results of functional studies.

Summary

The structural organization of the sensory hairs of the gravity receptors is mainly characterized by the presence of one kinocilium and 40—110 stereocilia on each sensory cell. The spatial arrangement of the kinocilia in relation to the stereocilia presents a polarization, similar to that in the sensory epithelia of the cristae. This polarization, however, is not uniform in the maculae. The direction of polarization varies between groups of several hundred sensory cells. Within one group the sensory cells are all polarized in the same main direction and these groups are considered as functional units.

The apparent stiffness and low metabolic activity of the stereocilia suggest their mechanical transmitter function between the otolithic membrane and the sensory cells.

The presence of modified kinocilia and basal bodies in other sensory systems raises the question of their significance in sensory receptors. Their unmodified structure in the maculae, however, where the basal bodies are almost identical with centrioles, and the presence of one kinocilium with a basal body and an associated centriole in the supporting cells as well, illustrate their unspecific nature. The centrioles, which later probably become basal bodies, are in close relation to the differentiation of apical cytoplasmic structures such as the kinocilium and the cuticula. This is demonstrated by the appearance of those structures at the bottom of the sensory cell, when the centrioles are situated in this part of the cell.

References

BARNES, BARBARA S.: Ciliated secretory cells in pars distalis of the hypophysis. J. Ultrastruct. Res. **5**, 453—467 (1961).

BOS, J. H., L. B. W. JONGKEES, and A. J. PHILIPSSZOON: On the action of linear accelerations upon the otoliths. Acta oto-laryng. (Stockh.) **56**, 477—489 (1963).

CHAPMAN, G. B., and L. G. TILNEY: Cnidocils in nematocysts. J. biophys. biochem. Cytol. **5**, 69—78 (1959).

DAHL, H. A.: Fine structure of cilia in rat cerebral cortex. Z. Zellforsch. **60**, 369—386 (1963).

DAVIS, H.: Neural mechanisms of auditory and vestibular systems. Eds.: G. L. RASMUSSEN and W. F. WINDLE, p. 21. Springfield, Ill. 1960.

ENGSTRÖM, H., H. ADES, and J. HAWKINS: Structur and function of the sensory hairs of the inner ear. J. acoust. Soc. Amer. **34**, 1356—1363 (1962).

FAWCETT, D. W.: Cilia and flagella, vol. 2, p. 217—297. New York: Academic Press 1961.

FLOCK, A., and J. WERSÄLL: A study of the orientation of the sensory hairs of the receptor cells in the lateral line organ of fish, with special reference to the function of the receptors. J. Cell Biol. **15**, 19—32 (1962).

GALL, J. G.: Centriole replication. J. biophys. biochem. Cytol. **10**, 163—193 (1961).

GIBBONS, I. R., and A. V. GRIMSTONE: On flagellar structure in certain flagellates. J. biophys. biochem. Cytol. **7**, 697—716 (1960).

HELD, H.: Die Cochlea der Säuger und der Vögel. A. BETHE: Handbuch der normalen und pathologischen Physiologie, Bd. 11, S. 467—541. Berlin: Springer 1926.

HENNEGUY, L. R.: Sur les rapports des ciles vibratiles avec les centrosomes. Arch. Anat. micr. **1**, 481—495 (1897).

JONGKEES, L. B. W., J. P. M., and A. J. PHILIPSSZOON: Clinical nystagmography. Pract. oto-rhino-laryng. (Basel) **24**, 65—93 (1962).

KOLMER, W.: Das Gehörorgan. In: Handbuch der mikroskopischen Anatomie des Menschen, Bd. III/1, S. 250—456. Berlin: Springer 1927.

LASANSKY, A., and E. DE ROBERTIS: Submicroscopic analysis of the genetic dystrophy of visual cells in C3H mice. J. biophys. biochem. Cytol. **7**, 679—684 (1960).

LENHOSSÉK, M. v.: Über Flimmerzellen. Verh. anat. Ges. **12**, 106—128 (1898).

LÖWENSTEIN, O., and J. WERSÄLL: A functional interpretation of the electron-microscopic structure of the sensory hairs in the cristae of the Elasmobranch Raja clavata in terms of directional sensitivity. Nature (Lond.) **184**, 1807—1808 (1959).

RETZIUS, M. G.: Morphologisch-histologische Studien. Das Gehörorgan der Wirbeltiere. II. Stockholm 1884.

ROBERTSON, J. D.: The ultrastructure of cell membranes and their derivatives. Symp. Biochem. Soc. **16**, 3—43 (1959).

ROTH, L. E.: Ciliary coordination in the protozoa. Exp. Cell Res., Suppl. **5**, 573—585 (1958).

ROUILLER, CH., E. FAURÉ-FREMIET, et M. GAUCHERY: Origine ciliaire des fibrilles scléroprotéiques pédonculaires chez les ciliés péritriches. Exp. Cell Res. **11**, 527—541 (1956).

SJÖSTRAND, P. S.: The ultrastructure of the inner segments of the retinal rods of the guinea pig eye as revealed by electron-microscopy. J. cell. comp. Physiol. **42**, 45—70 (1953).

SOTELO, J. R., and O. TRUJILLO-CENÒZ: Electron-microscopic study on the development of ciliary components of the neural epithelium of the chick embryo. Z. Zellforsch. **49**, 1—12 (1958).

SPOENDLIN, H.: Submikroskopische Strukturen im Cortischen Organ der Katze. Acta oto-laryng. (Stockh.) **52**, 111—130 (1960).

TENNYSON, V. M., and G. D. PAPPAS: An electron-microscopic study of ependymal cells of the fetal, early postnatal and adult rabbits. Z. Zellforsch. **56**, 595—618 (1962).

WERSÄLL, J.: Studies on the structure and innervation of the sensory epithelium of the cristae ampullares in the guinea pig. Acta oto-laryng. (Stockh.), Suppl. **126** (1956).

WOLKEN, J. J.: A molecular morphology of Euglena gracilis var. bacillaris. J. Protozool. **3**, 211—225 (1956).

Oberarzt Dr. H. SPOENDLIN,
Otorhinolaryngologische Klinik und Poliklinik der Univ., Kantonsspital Zürich (Schweiz),
Rämistr. 100