THE MECHANISM OF SENSORY TRANSDUCTION
IN A MECHANORECEPTOR

Functional Stages in Campaniform Sensilla During the Molting Cycle

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ABSTRACT

This paper describes the ultrastructural modifications that cockroach campaniform sensilla undergo at three major stages in the molting cycle and finds that the sensilla are physiologically functional at all developmental stages leading to ecdysis. Late stage animals on the verge of ecdysis have two completely separate cuticles. The campaniform sensillum sends a 220-μm extension of the sensory process through a hole in its cap in the new (inner) cuticle across a fluid-filled molting space to its functional insertion in the cap in the old (outer) cuticle. Mechanical stimulation of the old cap excites the sensillum. The ultrastructural geometry of late stage sensilla, coupled with the observation they are physiologically functional, supports the hypotheses (a) that sensory transduction occurs at the tip of the sensory process, and (b) that cap indentation causes the cap cuticle to pinch the tip of the sensory process, thereby stimulating the sensillum.

Receptor cells provide the sole informational point of contact between the environment and an animal’s nervous system. This interaction occurs through the process of sensory transduction, the generation of one energy form (electrical) in response to another (the stimulus). Although it is an extremely important biological process, the mechanism of sensory transduction in receptor cells is poorly understood. At the recent Neurosciences Research Program meeting devoted to sensory transduction, Dethier remarked, “We really don’t know a thing about transduction except in the visual system” (1). In his elegant study on Calliphora haltere campaniform sensilla, Smith (33) concluded, “neither the course of the transduction process nor the state of generation of receptor potentials is known in mechanoreceptors equipped with a ciliary derivative.”

We want to determine the role of cilia in sensory transduction. To that end, our objectives in this study are to observe the fine structure of campaniform sensilla at various stages during the molting cycle to determine the architectural changes undergone by sensilla in preparation for ecdysis, to determine the functional status of animals at different stages in the molting cycle, and to thereby gain insight into the way that modified cilia act as transducers in campaniform sensilla.

A working knowledge of the general morphol-
ogy of campaniform sensilla is prerequisite to understanding this paper. The fine structure of cockroach campaniform sensilla, described elsewhere in detail (20, 21), is summarized in Fig. 1. Each sensillum centers its function around a single large bipolar neuron. The axon travels to the central nervous system wherein its transmissions are integrated. The dendrite extends to the site of mechanical stimulation, a cap of modified exocuticle (21) at the surface of the exoskeleton. As the dendrite passes through a canal in the endocuticle, its diameter gradually decreases. The dendrite tip contains a basal body coextensive with a “9 + 0” connecting cilium that expands distally to form the sensory process, a membrane-limited cylinder packed with hundreds of parallel longitudinally oriented microtubules. The tip of the sensory process inserts directly into the cap. The sensory process, insulated by a “cuticular” sheath elaborated by the accessory supporting cell (ASC), passes through a channel in the cuticle lined by an enveloping cell (EC). The extracellular space that surrounds the sensory process is called the receptor lymph space (24).

Mechanical stimulation of the sensillum can be effected in one of two ways. In the laboratory, 100-200 Å indentation of the cap by a metal probe elicits a response (3, 35). In life, cuticular strains incurred during walking movements indent the cap and displace its attached sensory process. In both cases, indentation of the cap serves as the adequate stimulus (35).

During the molting cycle, the campaniform sensillum faces and solves morphological and physiological problems imposed by substantial architectural and biochemical alterations within the integument of which it is a part. During the intermolt period, the old cuticle is partially digested by molting fluid; a new cuticle is laid down by the epidermis. Before ec dysis, the insect has two distinct cuticles: an old cuticle, to be shed at the molt, and a new cuticle, the animal’s future exoskeleton (see Locke [16] for a detailed review). Several questions arise. What morphological changes occur in campaniform sensilla during the molting cycle? Do the sensilla remain functional when the animal has two cuticles? Some answers to these questions are available in the literature; the evidence, however, is scanty (see review by McIver [18], p. 391). The early light microscope studies of Wigglesworth (45) tell us that old and new caps of sensilla in pre-ecdysial Rhodnius are interconnected by a “terminal filament.” Recent electron microscope studies show that an extended sensory process connects old and new sites of stimulus reception in trichoid sensilla of Rhodnius (46) and in trichoid and campaniform sensilla of Gryllus (8, 31). In cockroach campaniform sensilla, an extension of the sensory process with its full complement of microtubules is shed with the skin at the molt (19). Little physiological evidence concerning the functional capacity of intermolt receptors is available. The most convincing studies are those of Walcott and Salpeter (44) with spider vibration receptors. In old and new cuticles of these animals, the receptor sites are interconnected by an extension of the sensory process; the receptors remain functional until ec dysis and experience little loss in sensitivity during the intermolt period.

We begin our study, then, with these facts in mind, and wish to obtain better insight into the mechanism of action of campaniform sensilla by undertaking a detailed morphological and physiological investigation of their development.

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MATERIALS AND METHODS

Microscopy

Two species of cockroach, Blattella germanica and Blaberus discoidalis, were used. Early, intermediate, and late stage nymphs were selected for study. Tibias containing campaniform sensilla of Pringle's (26) group 6 were removed under CO2 anesthesia, immersed in Karnovsky's fixative (10) at room temperature, rinsed briefly in 0.2 M cacodylate buffer, postfixed in buffered 2% OsO4, dehydrated in a graded acetone series, and embedded in Spurr's (36) low viscosity epoxy resin. Thick (0.5–1 μm) and thin (silver) sections, cut with an IVIC diamond knife in a Porter-Blum MT-2B ultramicrotome (DuPont Instruments, Sorvall Operations, Newtown, Conn.), were collected on Formvar-covered slot grids by the method of Rowley and Moran (29) and double-stained in uranyl acetate and full strength Reynolds' (27) lead citrate. Thin sections were studied at 60 kV in a Philips EM-300. Thick sections were examined and photographed at an accelerating voltage of 1,000 kV in the JEM-1000 HVEM at the Department of Molecular, Cellular, and Developmental Biology, University of Colorado, Boulder, Colo.

Physiology

Five individual cockroaches (B. discoidalis) were studied, one early stage, two intermediate stage, and two late stage nymphs. Suitable roaches were preselected by light microscope examination of sections of tarsi of 33 animals. Animals were anesthetized with CO2; legs were amputated at the coxa, sealed with Vaseline to prevent desiccation, and mounted by the femur upon a pair of insect pins that served as recording electrodes according to the method of Chapman (2). The recording electrodes were connected to a Tektronix 5A22N differential amplifier (Tektronix, Inc., Beaverton, Oreg.), displayed on a Tektronix R5103N oscilloscope, and monitored by loudspeaker. Individual group 6 campaniform sensilla were stimulated by a fine probe attached to a Prior micromanipulator (Stoelting Co., Chicago, Ill.). Legs from which extracellular records were obtained were examined in section by light microscopy to confirm the developmental stage of the animal relative to cuticle formation at the time of experimentation.

OBSERVATIONS

The animals used in this study exhibit three distinct patterns of integumentary architecture relative to their developmental progress through the molting cycle. We place the cockroach nymphs in three general categories: early, intermediate, and late “stages” of development. (For a detailed analysis of the temporal organization of events in the molt-intermolt cycle of cockroaches, see Kunkel [13].)

In the early stage, the molting cycle has just begun. Apolysis, the separation of epidermis from cuticle (9), has not occurred. In the intermediate stage, apolysis has recently occurred; deposition of new cuticle atop the epidermal cells has just begun. In the late stage, much of the old endocuticle has been digested by molting fluid, the new exocuticle has been established, the two cuticles are separated by a space filled with molting fluid, and the animal is ready to molt.

Microscopy

The Adult Integument: Although the two species of cockroach used differ in size, the pattern of integumentary and sensillar organization is constant. In adult B. germanica, for example, the completed tibial cuticle near group 6 measures 17 μm in thickness, whereas that of B. discoidalis is in excess of 100 μm thick. In both animals, the epidermis is a monolayer of cells. The epidermis around group 6, however, is thicker than elsewhere in the tibia, and houses bipolar neurons of campaniform sensilla and the adjacent subgenual organ.

The Early Stage: In the early stage, the epidermis is no longer a monolayer of cells. It has thickened by proliferative mitoses, indicating that the animal has completed the intermolt phase of the molting cycle and that the molting phase is underway (13). In Fig. 2, a survey electron micrograph of the early stage, the 20-μm thick epider-
Figure 2  TEM of an early stage B. germanica nymph's tibia. Field contains the caps of two campaniform sensilla (arrows). s, sensory process; A, accessory supporting cell; and cu, cuticle. Bar = 10 μm. × 2,040.

Figure 3  HVEM of 0.5-μm “thick” section through an intermediate stage B. germanica nymph. s, sensory process; m, molting space; arrow indicates new cuticulin deposit atop epidermal cells. Bar = 5 μm. × 4,150.
mis contains the tightly packed nuclei of epidermal cells that will spread out to underlie the new cuticle, designed to occupy an area 1.49 times greater than the old cuticle (13). Apolysis has not occurred, and the cuticle is intact. The campaniform sensilla (and, by inference, all cuticular mechano-receptors) have undergone several dramatic morphological changes. First, the sensory process of each bipolar neuron displays a considerable increase in length. Second, as elongation of the sensory process proceeds, the bipolar neuron is displaced within the epidermis and takes station many micrometers away from the cuticular cap of the sensillum. For example, the caps of two adjacent campaniform sensilla appear in Fig. 2. Although the section plane bypassed the bipolar nerve cell bodies, their sensory processes are clearly visible. One sensory process (arrow), surrounded at its base by an accessory supporting cell (20), is squeezed between epidermis and cuticle as it travels some 27 μm towards its cap. The elongated sensory process frequently follows a tortuous path. We have often seen it bent double and folded upon itself in the space immediately beneath the cap in intermediate stage cockroaches. This is of particular interest, for apolysis has traditionally been considered to be the morphological hallmark of the physiological onset of an instar (34, 46). In the early stage, however, we observed that elongation of the sensory process occurs before apolysis. Insects, it seems “tool up” for the intermolt phase by building a functional “extension cord” that will render their surfaces sensitive until ecdysis.

The Intermediate Stage: In intermediate stage cockroach nymphs, apolysis has occurred, and deposition of new cuticle is underway. Figure 3, a high voltage electron micrograph of a thick section through the integument of an intermediate stage cockroach, shows that the separation of epidermis from cuticle is far more pronounced beneath campaniform sensilla than elsewhere in the field of view. Enzymatic digestion of old cuticle has commenced. The epidermal cell's apical surfaces are covered with cuticulin, the outermost component of the epicuticle (14). Secretion and deposition of cuticle that comprises the caps of campaniform sensilla, however, proceeds at a faster rate, and/or begins earlier, than that of normal leg cuticle. Figs. 4 and 5 show that far more cuticle has been laid down atop the cap-forming cells than upon the epidermal cells nearby. In Fig. 4, the HVEM depicts a developing cap pierced by its sensory process. The same cap, cut in thin section and viewed at higher magnification, appears in Fig. 5. Here, a 25-μm thick layer of epicuticle that corresponds to layer L-1 of the mature cap (21) lies beneath the outer trilaminar cuticulin. The cytoplasm of the cap-forming cell, the accessory supporting cell of the mature sensillum (see Fig. 1), contains many microtubules laid down parallel to the cell's long axis. In addition to serving as cytoskeletons that maintain cell shape, these tubules may, as suggested by Locke (15), serve to guide dense and clear secretory vesicles emitted from the Golgi apparatus toward their site of ultimate discharge at the microvillate apical cell surface.

The Late Stage: In the late stage (Figs. 6-10) the cockroach is ready to molt. Much of the old cuticle has been digested by the molting fluid and resorbed; the new epicuticle has been deposited by the epidermis. Old and new cuticles are completely separated by a substantial molting space. The new cuticle has accordion-like pleats and folds that will flatten out after ecdysis when the animal swallows air and expands to its new full size. In Fig. 6, a survey electron micrograph of a late stage *B. germanica*, the new cuticle, 6–15 μm thick, is separated from the 8–15 μm thick old cuticle by a molting space traversed by the elongated sensory processes of trichoid and campaniform sensilla. The cuticular hairs of trichoid sensilla are well formed. The sensory process of a single campaniform sensillum is cut in longitudinal section as it passes through a tiny aperture in the new cap and travels some 80 μm to its functional insertion in the old cap. *B. discoidalis* is a much larger animal than *B. germanica*, and the elongation of its sensory processes is accordingly more dramatic. For example, the light microscope (Fig. 7) shows that the old and new caps of the same sensillum are separated by a linear distance of 220 μm, indicating that the sensory process, approx. 20 μm long in mature sensilla, has undergone a length increase of approx. 200 μm. An electron micrograph through the same campaniform sensillum appears in Fig. 8. Here the bipolar nerve cell body, measuring 15 μm across, tapers to form a dendrite that gives rise to the sensory process. (The plane of section bypassed the “9 + 0” connecting cilium at the dendrite tip that expands to form the sensory process.) This sensory process measures 15 μm long and 3.5 μm wide; it is encased within an electron-dense cuticular sheath closely applied against the cell membrane. The
Figure 4  HVEM of an intermediate-stage *B. germanica* nymph. The sensory process pierces the new developing cap (arrow) of a campaniform sensillum. *cu*, cuticle; and *M*, molting space. Bar = 5 µm. × 3,100.

Figure 5  TEM of a thin section through the cap shown in Fig. 5. The cuticle of the dome of the cap (c) is being laid down atop the accessory supporting cell (a). *s*, sensory process. Bar = 1 µm. × 19,650.
Figure 6 Survey TEM of a longitudinal section from the tibia of an advanced-stage *B. germanica*. New (arrowhead) and old (arrow) caps of one campaniform sensillum are interconnected by the extended sensory process (s) that crosses the fluid-filled molting space (M) separating old (upper) and new (lower) cuticles. Note developing trichoid sensilla (T). Bar = 20 μm. × 700.

Figure 7 Light micrograph of a similar field from the larger cockroach *B. discoidalis*. In the advanced stage, new (arrowhead) and old (arrow) caps, separated by a distance of 220 μm, are interconnected by a sensory process that has undergone a 10-fold increase in length. M, molting space; SO, subgenual organ. Bar = 30 μm. × 440.
sensory process contains a tubular body\(^1\) at its point of insertion into both old and new caps. Distal to the tubular body, the sensory process undergoes considerable attenuation as it passes completely through the new cap. Fig. 9 is a high magnification electron micrograph of a thin longitudinal section that captures the sensory process as it penetrates the new cap. The sensory process measures only 0.1 \(\mu m\) at its thinnest and contains the profiles of three microtubules. The cuticular sheath extends halfway through the 1.25-\(\mu m\) thickness of layer L-1 of the cap's dome, and then is replaced by material of lesser density. This material probably forms the plug that seals the cap when the extension of the sensory process breaks off at ec dysis. The cuticular sheath reappears as the sensory process exits the cap. The apparent disconnection of sheath from cap in Fig. 9 is arte- factual; the surface separation of epoxy from cuticle was induced by the heat of the beam.

In late stage cockroaches, the caps in the old cuticle are intact and do not appear altered by the molting fluid. In Fig. 10, the HVEM depicts the extension of the sensory process inserting into its cap in the old cuticle. Although the microtubules are seldom preserved in sensory processes of late stage animals, we know that they are present in life, as the tubes are always well preserved in fixed exuviae where the fixative can enter through the severed sensory process (19). The fact that microtubules in the extended sensory process of advanced stage animals are poorly preserved suggests that the "cuticular sheath"\(^2\) is an effective barrier to fixative diffusion. Since the cuticular sheath bars entry of low molecular-weight aldehydes, it probably serves to exclude the high molecular-weight enzymatic components of the molting fluid. We suggest that the cuticular sheath evolved as a diffusion barrier that protects the functional sensory process from enzymatic digestion by molting fluid. It is interesting to note that the occurrence of the cuticular sheath is restricted to receptors attached to the cuticles of animals that molt to grow, i.e., to Arthropods' cuticular mechanoreceptors (18) and chemoreceptors (32).

**Receptor Lymph Space Formation**

Two accessory cells are present in cockroach campaniform sensilla, the ASC and the EC, (37; see reference 20 for details). As diagrammed in Fig. 1, the ASC surrounds the proximal part of the sensory process and the dendrite itself. The EC wraps around the ASC and lines the channel in the cuticle through which the sensillum passes. In the late stage developing sensillum, both cells are enlarged and in contact with the underside of the new cap. The ASC is in contact with and underlies layer L-2 of the *dome* of the cap, whereas the EC underlies the cuticular collar and extreme lateral margins of the cap (Fig. 8). Since cells deposit cuticle upon their apical surfaces, we conclude that the accessory supporting cell secretes both L-1 and L-2 of the dome of the cap, whereas the enveloping cell elaborates the cuticular collar and lateral margins of the cap. After ec dysis, both cells retract, leaving behind a conspicuous fluid-filled space, the receptor lymph cavity (24), beneath the cap and around the sensory process.

It has been shown in several insect mechanoreceptors that the enveloping cell possesses an \(O_2\)-dependent ion transport system that actively pumps potassium ions into the receptor lymph space (11, 12, see Thurm [41] for review). The extracellular fluid in the receptor lymph space bathing the sensory process is positively charged relative to the hemolymph; the bipolar neuron is negatively charged relative to the hemolymph. Thurm proposes that the generator potential is established when the mechanical stimulus causes a local permeability change of the dendritic cell membrane to \(K^+\), causing \(K^+\) to flow from the receptor lymph space into the dendrite.

It is interesting to note that the tip of the sensory process in intermediate and advanced stage cockroach nymphs is *not* surrounded by a receptor lymph space, but rather by an extensive molting space between the two cuticles that is filled with molting fluid. If Thurm's ideas (40, 41) are correct, and the tip of the sensory process is indeed the transducer (see Discussion), one would predict the molting fluid to be rich in potassium ions and positively charged relative to the hemolymph and bipolar neurons of cuticular mechanoreceptors.

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\(^1\) The tubular body, a term coined by Thurm (38) and recently redefined (6), is a body of amorphous electron-dense material of unknown composition associated with microtubules in the sensory process tip. The dense material probably corresponds to the microtubule organizing centers (MTOC's) discussed by Pickett-Heaps (25).

\(^2\) The term "cuticular sheath" is an apparent misnomer; its substance bears no fine structural similarity to cuticle.

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Figure 8 TEM of the sensillum shown in Fig. 7. This thin section includes the bipolar nerve cell body (s), dendrite (D), sensory process (SP) and “new” cap. E, enveloping cell; A, accessory supporting cell; c, cuticular collar of cap. Bar = 10 μm. × 1,650.
Figure 9  High-magnification TEM of the center of the new cap shown in Fig. 7. The sensory process undergoes considerable attenuation as it passes through the channel in the cap. M, molting space. Bar = 0.5 μm. × 50,500.
Figure 10  TEM of the distal region of the extended sensory process as it functionally terminates in the old cap of an advanced-stage cockroach. M, molting space. Bar = 1 μm. × 13,125.
DISCUSSION

Since our objective is to learn more about sensory transduction in ciliated mechanoreceptors, we must ask: Does the present study tell us anything new about the course of the transduction process and the site of generation of receptor potentials?

The Site of Sensory Transduction

Previous studies indicate several probable transducer sites in campaniform sensilla: the body of the sensory process, the base of the cilium in the dendrite tip, and the distal tip of the sensory process. We will consider each of the possible transducer sites in order.

The Sensory Process: The presence of hundreds of parallel microtubules in the sensory process of cockroach campaniform sensilla led Moran et al. (20) to suggest the sensory process itself as the site of sensory transduction. Moran and Varela (22) observed that biochemical disassembly of sensory process microtubules by colchicine and vinblastine sulfate was accompanied by loss of receptor function, and said, “It is interesting to speculate that the 350-1,000 microtubules of the sensory process function as mechanochemical engines driven backwards by the force of the stimulus, creating conditions favorable to the formation of generator current.” They also suggested that microtubules, being polyelectrolytes, might release bound ions upon compression imparted by the mechanical stimulus. In addition, they discussed Satir’s notion (see below) that the microtubules might act as translation rods to convey the displacement received at the cap to a remote transducer site at the dendrite tip.

The Dendrite Tip: Satir’s (30) elegant sliding filament model for ciliary motility led him to suggest the following: “This model predicts information transfer over distances of tens of micrometers in ciliary-based systems. If operated so that displacement of filaments at the tip caused bending at the base, such a mechanism might be a feature of sensory transduction in certain systems, e.g., the campaniform sensillum.” A specialized structure, the ciliary necklace, exists at the base of motile cilia. Gilula and Satir (7) suggested that microtubule sliding, induced in cilia of mechanoreceptors by the mechanical stimulus, might “cause specific alterations in the particule patterns” in the membrane of the ciliary necklace, thereby altering ionic permeabilities conducive to the formation of generator current.

AT THE DISTAL TIP OF THE SENSORY PROCESS: Thurm (38) was the first investigator to observe microtubules and dense material (the “tubular body”) at the tip of the sensory process in both trichoid and campaniform sensilla. Thurm’s elegant studies indicate that compression of the tubular body is the adequate stimulus in honeybee hair-plate receptors, and concludes that the tubular body “might have a special function in the transducer process” (38, 39). Chevalier (4) concludes that the cuticular specializations in Drosophila haltere campaniform sensilla are designed to compress the “highly specialized distal process of the dendrite.” In his detailed study of campaniform sensilla in Calliphora halteres, Smith (33) observed an orderly arrangement of microtubules and filaments in the sensory process, and stated, “In the sensory tip of campaniform sensilla we find an array of microtubules and filaments that approaches the regularity of the myofibril, and it is not inconceivable that, in reverse order to the sequence of events in muscle, deformation of the array may induce ionic changes involved in the transduction process.” Working with cockroach campaniform sensilla, Spinola and Chapman (35) reported that recent biophysical investigations lead them to suggest that “the elaborate structure of the cap cuticle serves to amplify the tibial cuticular strain to squeeze the terminal of the dendritic sensory process.”

The present study strongly supports the hypothesis that the tip of the sensory process is the site of sensory transduction in campaniform sensilla. Microscope measurements show that the physiologically functional extension of the sensory process that traverses the molting space and interconnects old and new caps in advanced stage B. discoidalis is 220 μm long. Considerable slippage must occur between the folded, flexible new cuticle and the tanned old cuticle during normal locomotion. Chapman et al. (3) and Spinola and Chapman (35) have clearly shown that the adequate stimulus for Blaberus group 6 campaniform sensilla is a tiny indentation of the cap of 100–200 Å. Since the amplitude of the bending and twisting motions of the extended sensory process in walking advanced stage animals surely must greatly exceed 200 Å—and thus exceed the amplitude of movement conferred upon the sensory process by the adequate stimulus—models centered around the displacement of microtubules within the sensory process by the mechanical stimulus can be ruled out. Thus, we conclude that the transducer site is...
located at the tip of the sensory process. One question arises: If the sensory process tip is the transducer, then, in advanced stage animals, the generator current that arises at the outer cap must maintain sufficient strength to trigger action potentials after travelling the entire length of the extended sensory process. Given what we know about cable conduction, will this be the case?

We can answer this question by taking the value for the membrane length constant, \( \lambda \), as reported in cockroach axons (23). This value stands at approx. 1 mm. A generator potential of a magnitude \( E_g \) will, at a distance \( x \), reach a value \( E_x = E_g e^{-x/\lambda} \). Accordingly, for the case at hand (Blaberus discoidalis), a generator potential developed at the tip of the extended sensory process will maintain 78% of its value by the time it reaches the level of the cell body some 250 \( \mu \)m distant.

Not only does this show that transduction can occur at the tip, it suggests that transduction does occur at the tip of the sensory process, for, although it seems most unlikely that a mechanical stimulus of 200 Å can be carried undamped from the tip to the soma, a tip-generated electrical potential can travel the distance almost unchanged.

**The Mechanism of Sensory Transduction**

How does the sensory process tip function as a mechanoelectric transducer? Several interesting possible mechanisms have been put forward that involve microtubules, membranes, cross-bridges, and amorphous electron-dense material in various combinations. Smith (33) suggests that interactions between microtubules and filaments may effect ionic changes in haltere sensilla. Rice et al. (28), working with tsetse fly setiform sensilla, believe that the mechanical stimulus causes "the receptor membrane to be stretched against the neurotubular cytoskeleton" in the tip of the sensory process. In the cockroach campaniform sensilla, the tubular body contains microtubules surrounded by an apparently amorphous electron-dense matrix closely apposed against the cell membrane (20). The cell membrane fits tightly into a slot in the cap (21). The microtubules and dense material serve, it seems, to press the membrane of the sensory process tip tightly against the borders of the slot in the cap and maintain sufficient membrane tension so that indentation of the cap causes local deformation of the cell membrane. If so, can the adequate stimulus, a 200 Å indentation of the cap, deform the membrane alone sufficiently to effect transduction?

The tip of the sensory process is shaped like a flat paddle (21). Fig. 11 is a tracing of an electron micrograph of a longitudinal section taken at right angles to the minor axis of a cockroach campaniform sensillum's sensory process tip and cap. We agree with Thurm's idea that indentation of the cap during mechanical stimulation causes cuticle L-2 to be displaced horizontally and inward in the direction of the arrow, thus pinching the tip of the sensory process (see Thurm, reference 42, Fig. 13). If we assume that layer L-2 is anchored to the cuticular collar, pivots about point \( P \), and maintains its length \( C \) during stimulation, the geometry of the cap is such that a 200 Å vertical indentation of the dome of the cap will cause both "sides" of cuticle L-2 to be displaced inward through 650 Å, thereby pinching the membrane. The calculations obtained in Fig. 11 show that the cap acts as a mechanical amplifier that delivers a displacement to the tip of the sensory process some three times greater in amplitude than the adequate stimulus. Thus, our calculations approach the upper limit of Thurm's figures for Calliphora haltere campaniform sensilla, of which he says, "The adequate stimulus is probably represented by a monoaxial diminution of the tip diameter by 30-1,000 Å (0.5-15%) at the site of this tubular body" (Thurm, reference 42, p. 384). It is interesting to note that in the Pacinian corpuscle, a well-studied vertebrate mechanoreceptor, Loewenstein (17) calculates the strain sensitivity to be "10⁻⁵ cm (=1,000 Å) or better".

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FIGURE 11  This diagram, traced from an electron micrograph of a longitudinal section through the minor axis and sensory process of a *B. discoidalis* campaniform sensillum, shows how the cap can act as a mechanical amplifier of the stimulus. The adequate stimulus is a vertical cap indentation of 200 Å (3, 35). Assuming that layer L-2 does not undergo significant compression and moves about point P during stimulation, cap indentation will cause L-2 to move down 200 Å and swing inward in the direction of the arrows, pinching the tip of the sensory process. We can determine the amount the cap will be pinched by a simple geometric analysis of this tracing. In triangle abc, drawn in and below the tracing, the hypotenuse c interconnects pivot point P with the tip of the sensory process s. During cap indentation, c will be swinging into a new position, represented by dotted line c': a new triangle may be drawn, in which the 200 Å cap indentation has caused the vertical line to decrease in length y (y = 200 Å). Meanwhile, line a has increased by length x, and x represents the amount the sensory process tip has pinched in one side. Since triangles abc and (a + x) (b - y) c' have the same hypotenuse, we may, using actual dimensions, solve for x—the amount of pinching—as done at the right of the figure. Since x = A, and two sides are active in pinching the tip of the sensory process, the total monoaxial diminution in tip diameter is 650 Å, showing that the cap effects a threefold amplification of the stimulus.
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