not change for about 20 minutes after the addition of more thymine but it then doubled in the next 15 minutes. This result was obtained in four separate experiments. It is consistent with the hypothesis that the transcription event for the synthesis of this enzyme in the repressed state occurs at a particular time in the replication of the chromosome.

Our model would suppose that the entire bacterial genome is transcribed at least once in the course of its replication, as supported by evidence of McCarthy and Bolton (*14*), and that this event accounts for basal levels of inducible enzymes.

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6 April 1964

Mechanoreceptors in the Cuticle of the Honey Bee: Fine Structure and Stimulus Mechanism

Abstract. *The distal nerve process of hair plate sensilla and campaniform sensilla contains a special terminal structure in the form of a bundle of tubules herein designated the "tubular body." Physiological and morphological results indicate that compression at the site of this body probably acts as the stimulus at the cellular level. A ciliary structure separates an outer segment of the distal nerve process from the remaining distal fiber.*

Recent investigations show that the hair plates of insects function as position receptors in the joints and in this way can act as gravitation receptors (*1, 2*). An electrophysiological and microscopic study of the single receptor elements brought results which related to the mechanism of stimulation in the nerve endings (*3*). In the study reported here the morphological basis of the primary receptor processes was investigated by electron microscopy. The objects studied were the cervical hair plates of the honey bee (*2, 3*) and, for comparison, the campaniform sensilla of the head.

The sensilla of the hair plates and the campaniform sensilla each contain only one receptor cell of the bipolar type. The distal process of the cell enters through a canal in the cuticle and connects with the joint membrane in the hair plate sensillum, and with the cap membrane in the campaniform sensillum (Fig. 1). These cuticular structures probably consist of the rubber-like protein resilin (*4*), as indicated by their special staining properties, by their extraordinary deformability in the joint membrane, by their stress-birefringence, and by their digestability by pepsin. Both types of sensillum have a nearly bilaterally symmetrical form: the hairs in their resting position lean against an overhang of the cuticle at one side and can be freely pivoted only in the opposite direction; the campaniform sensilla have an elliptic form, when observed from above.

With the electron microscope (*5*) it is possible to distinguish in both types of sensilla an outer segment of the distal nerve process from the remaining distal fiber; the outer segment and the fiber are connected by a ciliary structure (Fig. 1). In each type of sensillum the outer segments are of roughly constant length (6 to 8.5 μ in the hair sensilla, 3.2 to 4.2 μ in the campaniform sensilla) independent of the thickness of the surrounding cuticle. Within the conical ending of the outer segment lies a prominent dense body (Figs. 2 and 3*A*) consisting of 50 to 100 tubules lying parallel to one

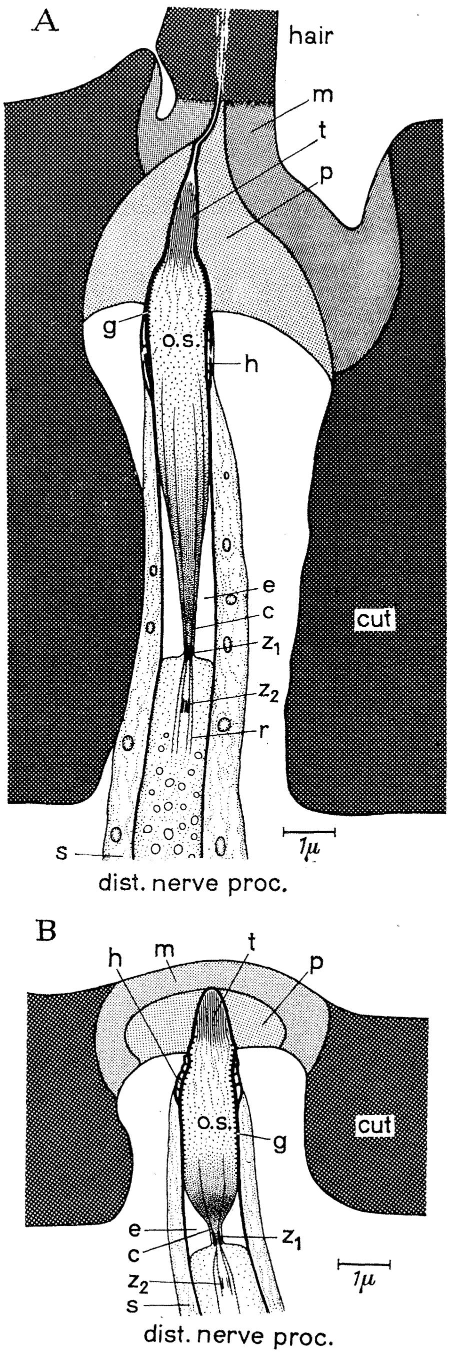

Fig. 1. Diagram of hair plate sensillum (*A*) and campaniform sensillum (*B*). Abbreviations: *c*, ciliary structure; *e*, extracellular space; *g*, granules; *h*, cuticular sheath; *m*, joint membrane (*A*), cap membrane (*B*); *o.s.*, outer segment; *p*, cap; *s*, Schwann cell; *r*, root fiber; *t*, tubular body; *cut*, cuticle; z_1, z_2, centrosome-like structures.

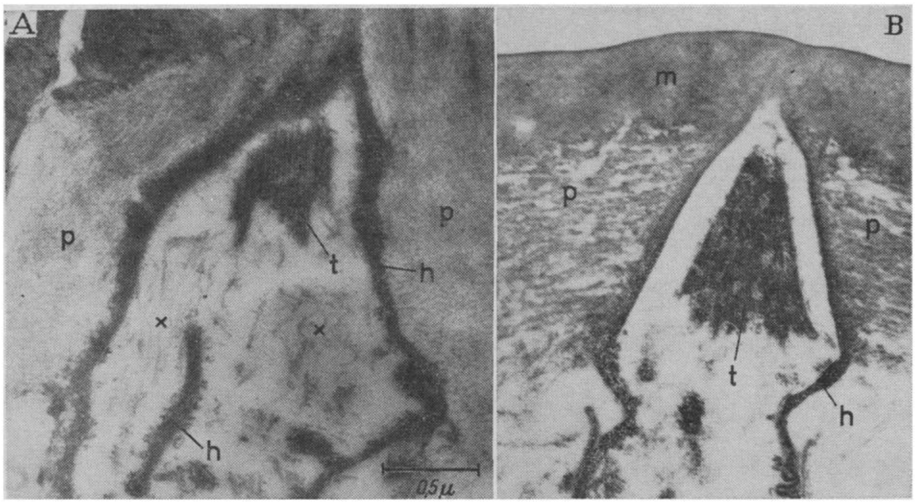

Fig. 2. The distal part of the outer segment of the hair plate sensillum (*A*) and the campaniform sensillum (*B*) with the tubular body (*t*) in longitudinal section. Note the free tubuli in *A* indicated by the crosses. At the infoldings of the cuticular sheath, *h*, the cell membrane is bordered with granules. For abbreviations see Fig. 1. The scale in *B* is the same as in *A*. Because of the extraordinary hardness of the dehydrated cuticle, sections thinner than 400 to 800 Å could not be made.

another in an electron dense material. The inner diameter of such a tubule is about 90 Å, and the wall about 30 Å thick; thus in size these tubules are very similar to those which form the filaments of the ciliary structure (Fig. 3). In the living cell this tubular body presumably fills up the end of the outer segment; however, with dehydration, the diameter of the tip becomes dilated by outer shrinkage, whereas the tubular body itself probably shrinks, resulting in greater distances between the membrane and the tubular body. The separate tubules leave the body at its proximal side and continue independently of each other in the cytoplasm toward the ciliary structure. However, it is not possible to follow them as far as this structure; continuity with the ciliary tubules remains doubtful. Only with the proximal reduction of the diameter of the outer segment are tubules visible again, where they form a ring consisting of about 18 pairs of tubules. Before the outer segment changes into the distal fiber the pairs become arranged in two concentric rings each consisting of nine double elements (Fig. 3*B*). Each pair in the inner ring is connected radially with one pair in the outer ring. The inner elements are connected with each other by a tubular membrane, as are the outer elements by the outer cell membrane. Within the ciliary structure the outer segment changes into the fiber-like distal nerve process; the diameter is abruptly enlarged to 1 μ, and the tubules are connected with a centrosome-like structure and thence to about nine root fibers, which show a cross striation of about 500 Å periodicity. These root fibers enclose a second parallel centrosome structure.

The outer segment contains few or no inclusions except the tubules described and thus differs remarkably from the fiber proximal to the ciliary structure, which contains an especially great number of irregular vesicles. In the region between the tubular body and the formation of the ciliary structure, however, the inner surface of the cell membrane of the outer segment is studded with granules of about 200 Å diameter, especially at the surface of the many infoldings of the membrane (Fig. 2*A*). These granules lie at rather regular distances from each other; in cross sections of the outer segment they are visible, lying side by side in rows of ten and more granules. Their chemical nature and their function are unknown.

The whole outer segment of the distal nerve process is enclosed within a relatively thick cuticular sheath. This sheath connects the outer segment with the joint membrane or the cap membrane of the sensilla. In the hair plate sensillum, but not in the campaniform sensillum, the sheath terminates in the form of a thin tube (inner diameter 200 Å) which changes into the wall of the hair. This point of fastening of the nerve process is always found in the plane of symmetry at the side of the overhang of the cuticle (*3*). In both types of sensillum there is a cap of spongy, fibrous material beneath the joint or cap membrane, which is continuous with this membrane. The ending of the outer segment, which encloses the tubular body, is embedded in this cap. The whole nerve process is enclosed by a Schwann cell beginning at the lower end of the cap. With the tapering of the nerve process to the ciliary structure an extracellular volume results between the nerve membrane and the Schwann cell.

Bending the hair has two effects on the nerve ending, as measured in vitro with 10-μ thick sections of the

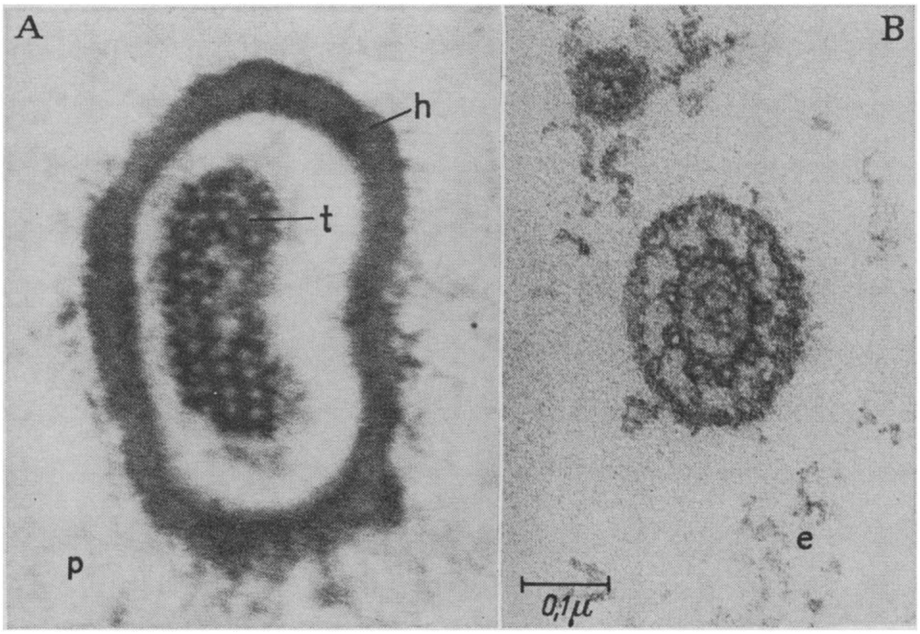

Fig. 3. Cross sections of the hair plate sensillum on the level of (*A*) tubular body and (*B*) the ciliary structure. Same scale in *A* as in *B*. For abbreviations see Fig. 1.

hair plate (*3*): its point of fastening at the joint membrane becomes elevated, and the joint membrane of one side is buckled into the hair base, compressing the cap and in this way shifting and compressing the nerve ending (Fig. 4). By means of push-pull experiments it was possible to apply these two distortions separately while recording their effect on the impulse activity of the cell (*3*). Pulling on a hair in its resting position had no measurable effects, pushing it in this position resulted in a weak excitation; pulling on a hair in its fully bent position abolished the high impulse frequency of the sense cell, although the length of the nerve ending could not be altered in this case; pushing the bent hair increased the high excitation further. An isolated compression of the cap without bending the hair was achieved by inserting a needle into the cuticle in the neighborhood of a sensillum; excitation of the sense cell increased with the thickness of the needle in the cuticle. In these cases only those distortions of the hair base which compressed the cap beneath the joint membrane were effective in stimulation. A compression directed transverse to the long axis of the nerve ending was most effective; it caused reactions covering the whole response range. In contrast, an elevation of the point of fastening of the nerve ending had no stimulus effect. These results indicate that a compression of a special part of the outer segment, which is located in the cap, is probably the normal stimulus event. A compression of this part, just measurable in the light microscope for maximal bending of the hair, is in the range of 0.1 μ.

The dynamic properties of the sensillum depend on the elastic and plastic properties of the joint membrane, cap, and cuticular sheath. Since cap and cuticular sheath react to staining and digestion with pepsin in the same manner as the joint membrane, it is reasonable to conclude that they are likewise composed of resilin. Resilin has no measurable plastic or flow properties (*4, 6*). A hair, released from a bent position after some hours, springs back precisely to its original resting position.

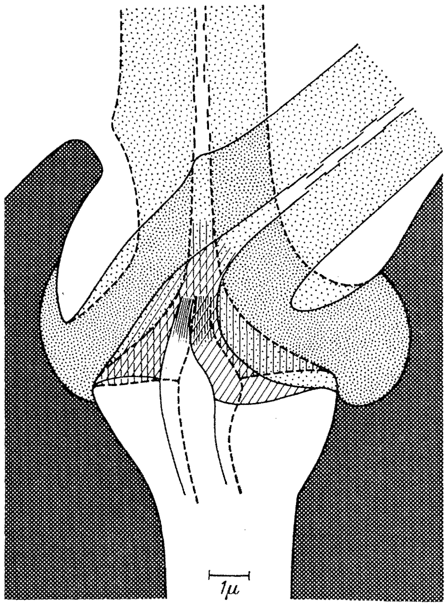

Fig. 4. The distortions of the hair base with bending of the hair; resting position with dashed lines, maximal bent position with full lines. From photomicrographs of a section in vitro.

The structures of the distal nerve processes are the same in the hair plate and in the campaniform sensilla; these types of sensilla are different in the structure of the supporting cuticular apparatus and in the connection of the outer segment to the cuticle; there are also quantitative differences in the formation of the outer segments. These results are in agreement with the concept that hair sensilla and campaniform sensilla are homologous sense organs (*7*). The mechanical distortions of the cuticular structures are different in the two types of sensillum, but these structures seem to function by transforming the different distortions of the cuticular parts into equal effects at the nerve endings. Campaniform sensilla respond to certain strains in the cuticle (*8, 9*) which are supposed to diminish the diameter of the sensillum. In this way a compression of the cap results, as in the hair sensilla; the structures for the subsequent processes of stimulus transmission are also the same. Other than in the hairplate sensilla it is probable that no shifting or bending of the nerve process takes place. One might, therefore, consider compression of the terminal region of the outer segment, which is enclosed in the cap, to be the primary stimulus effect in both the campaniform and the hairplate sensilla. In contrast to this, Pringle (*8*) based his hypothesis of the stimulatory mechanism of campaniform sensilla on the assumption that stretching the nerve ending acts as a stimulus at the nerve level. However, as already mentioned, in the similarly constructed hair sensilla stretching does not stimulate the receptor cell.

The principles of construction common to hair plate and campaniform receptors are similar to those of scolopidia sensilla reported in *Locusta* (*10*) and *Carcinus* (*11*). But in the hair plate and campaniform receptors the region of the stimulus action can be localized with more certainty. The tubular body is situated just in that part of the outer segment of the hair plate sensillum which is most compressed. This structure, therefore, might have a special function in the transducer process. In the scolopidia sensilla, structures corresponding morphologically to the tubular body are found—namely, in *Carcinus* (*11*), the numerous tubules which are of the same diameter as the tubules of the cilium, and, in *Locusta* (*10*), the elongated ciliary structure without central filaments. In contrast to these receptors, whose terminal regions are characterized by ciliary or tubular structures, there are a number of other mechano-receptors with sensitive regions structurally similar to an axon [Pacinian corpuscle (*12*); muscle spindle (*13*); stretch receptor (*14*)]. Their mechanical sensitivity is considered to be a specialization of the mechanical sensitivity of axons (see *15*). Perhaps receptors with ciliary structures have a different transducer mechanism, which may be a property of ciliary or related tubular structures—that is, the tubular body in the special case of the hair plate and campaniform receptors. But at present this remains an open question.

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