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# Relationship between Structure and Function of Antennal Chemo-, Hygro-, and Thermoreceptive Sensilla in *Periplaneta americana*

H. Altner*, H. Sass, I. Altner
Institut für Zoologie, Universität Regensburg, Regensburg, Federal Republic of Germany

**Summary.** On the antennae of *Periplaneta americana*, 25 chemo-, hygro- or thermosensitive sensilla were investigated electrophysiologically and, after marking, by transmission and scanning electron microscopy. A clear-cut relationship of functional types to structural types was observed. Two different stimulus conducting structures were observed: a) pore tubules which are found only in smooth, single-walled sensory pegs and b) secretion-filled canals which occur only in grooved double-walled sensilla. Temperature- and humidity-sensitive receptors occur only in double-walled sensilla with secretion material as the stimulus conducting system. Olfactory sensory cells were found in both types, however, those with a specific sensitivity for short-chain n-alcohols are restricted to single-walled pegs with pore tubules, while those which are most sensitive to short-chain n-acids and amines are found in double-walled sensilla, sometimes together with thermosensitive units. The stimulus conducting systems may control the access of odorous substances to the dendritic membranes and thus contribute to the discriminatory properties of the sensilla.

**Key words:** Chemoreception – Thermoreception – Hygroreception – Receptor cell structure – Insect sensilla.

## Introduction

To date, our understanding of the stimulus conducting structures in the olfactory-, hygro-, and thermosensitive organs of insects is inadequate. Although a number of descriptions of different forms of these structures has been made in recent years (Slifer et al., 1959; Ernst, 1969, 1972; Steinbrecht, 1969, 1973; Hawke and Farley, 1971a), little attempt has been made to correlate fine struc-

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*Send offprint requests to:* Prof. Dr. H. Altner, Universität Regensburg, Institut für Zoologie, Universitätsstr. 31, D-8400 Regensburg, Federal Republic of Germany

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ture and function. Slifer et al. (1959), Ernst (1969, 1972), Steinbrecht and Müller (1971) and Steinbrecht (1973) have reported pore tubuli as the most common stimulus conducting system and have described their development. In electron micrographs pore tubules show up as electron dense thread-like tubes with a light core. Their diameter stays close to 150 Å, their length varies. The supposition is that molecules of odorous substances diffuse one-dimensionally down their length to reach the membrane of the sensory cell (Kaissling, 1974). As a rule, pore tubuli occur in smooth-walled sensory hairs. In grooved hairs, on the other hand, cuticular canals separating the receptor lymph cavity from the outside world are plugged with an electron dense secretion. Hawke and Farley (1971b) were the first to find that the two systems differ in tracer permeability and susceptibility to solvents.

The question whether the differences between these two stimulus conducting systems, the pore tubules in smooth-walled hairs and the secretion-plugged canals in grooved hairs, are correlated with modality and specificity is of the utmost importance. Electrophysiological examination of the antennal sensilla in *Periplaneta americana* yields the following physiological types: 1) pentanol sensilla, characterized by the presence of a sensory cell with a specific sensitivity for pentanol: the pentanol cell; 2) hexanol sensilla, with a hexanol cell; 3) octanol sensilla, with an octanol cell; 4) alcohol-terpene sensilla, with a cell specifically sensitive to terpenes such as nerol; 5) butyric acid sensilla, with a butyric acid cell; 6) amine sensilla, with a cell typified by sensitivity to amines such as cyclo-hexylamine; 7) hexanoic acid-cold sensilla, with a hexanoic acid cell and a cold cell; and 8) cold-moist-dry sensilla, with one cold and two hygrosensitive cells, one for humid and one for dry air (Sass, 1976a, b; Loftus, 1976). By labeling single sensilla after recording, the sensillar types discriminated electrophysiologically could also be shown to exhibit different morphological properties.

## Material and Methods

### *A. Animals and Recording*

Experiments were performed on adult male *Periplaneta americana*, raised in our laboratory, and were limited to the region between the 50th and 90th segment of the antennae. Recordings were made only from the distal one-third of each segment. The frequency of the distinguishable sensillar types and the patterns in which they occur will be reported elsewhere. For the electrophysiological investigation the cockroaches were anesthetized with $CO_2$ and mounted on a specimen holder. For recording, standard techniques were applied (Boeckh, 1962). For stimulation techniques, see Sass (1976a, b).

### *B. Labeling and Electron Microscopic Procedures*

After recording, the position of the sensillum in the surrounding pattern of sensory bristles was sketched under a light microscope. A cactus needle was then inserted into a suitable position within the pattern as a label for subsequent examination. The operation left the recorded sensillum untouched. A total of 17 preparations of this kind with 21 recorded sensilla and 368 other sensilla in the surrounding were fixed (Dalton mixture), embedded (Durcupan AMC, Fluka, Buchs), and serially sectioned without lacuna (LKB Ultratome III, diamond knife, series length: 25–49 µm). Sensilla examined electrophysiologically were localized for further detailed study (Siemens Elmiskop 101). In 18 of the sensilla the crack in the cuticle from electrode insertion could be clearly identified.

In four other preparations labeled lengths of antenna were dried (Critical Point Apparatus II, Technics Inc., Alexandria, Virginia, USA), gold coated (Hummer II, Technics Inc., Alexandria, Virginia, USA) and examined under a scanning electron microscope (Cambridge Stereoscan S4-10).

## Results

### *A. Morphological Properties of Physiological Sensillar Types Established with the Transmission Electron Microscope*

Examination of the fine structure revealed an uneven distribution of the eight physiological types mentioned above (Sass, 1976b) among three morphological types: 1) smooth, single-walled sensory hairs with pore tubules, 2) grooved, double-walled pegs, and 3) atypical grooved hairs.

The first two morphological types can be further categorized. The pentanol, hexanol, octanol, and octanol-terpene sensilla were always single-walled, about 10 µm long with two sensory cells (Fig. 1). Other single-walled sensilla 20 µm in length containing four sensory cells were also present. As yet no substance has been found to stimulate them, although experiments indicate that they may respond to pheromones (Sass, in preparation). These sensilla comprise about 65% of all olfactory, hygro- and thermosensitive sensilla of the distal third of the antennal segments in the region between the 50th and 90th segment. The butyric acid cell was found in double-walled, grooved hairs together with two other sensory units which have not responded to any stimuli yet presented. These hairs had 16–19 grooves around their circumference. Both the amine and the hexanoic acid-cold units occurred in sensilla with four sensory cells (Figs. 2–4). These sensilla possessed 22–32 grooves. The cold-moist-dry sensillum was double-walled but atypical. (See Table 1 for a summary of the data.)

A comparison of the specific sensitivity of cells in smooth, single-walled sensilla with those of cells in grooved, double-walled sensilla yields information regarding the initial question: 1. Cells sensitive to alcohols (pentanol, hexanol, octanol, alcohol-terpene type) occurred exclusively in single-walled sensilla. 2. Cells with a marked sensitivity for fatty acids (butyric acid and hexanoic acid from the hexanoic acid-cold unit type) and also for amines were only found in double-walled hairs. These last three types are insensitive to n-alcohols ($C_1$ to $C_{10}$).

Temperature-sensitive units were also found only in grooved hairs, either in sensilla of the hexanoic acid-cold type (typical double-walled hairs with four sensory cells) or together with a hygrosensitive cell in a modified grooved hair containing either three or four sensory cells.

Attempts to determine the number of sensory cells in atypical double-walled hairs were not completely successful. In one such sensillum four cells could be distinguished clearly. Since the number of sensory cells in the other types

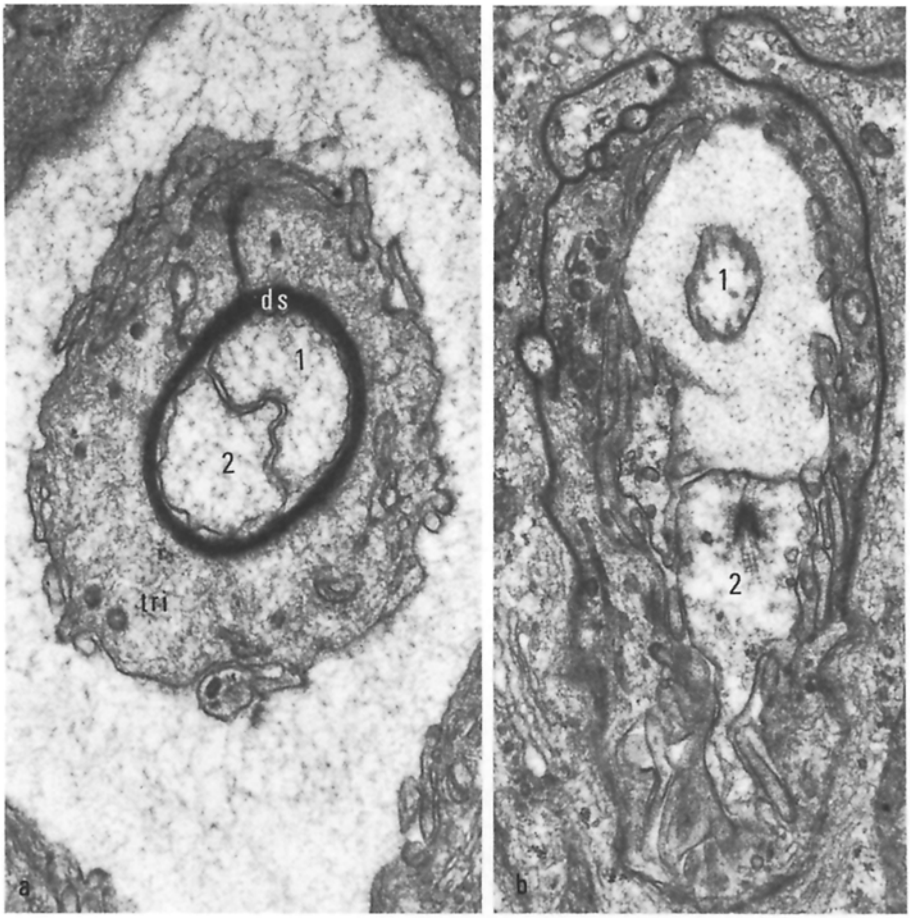
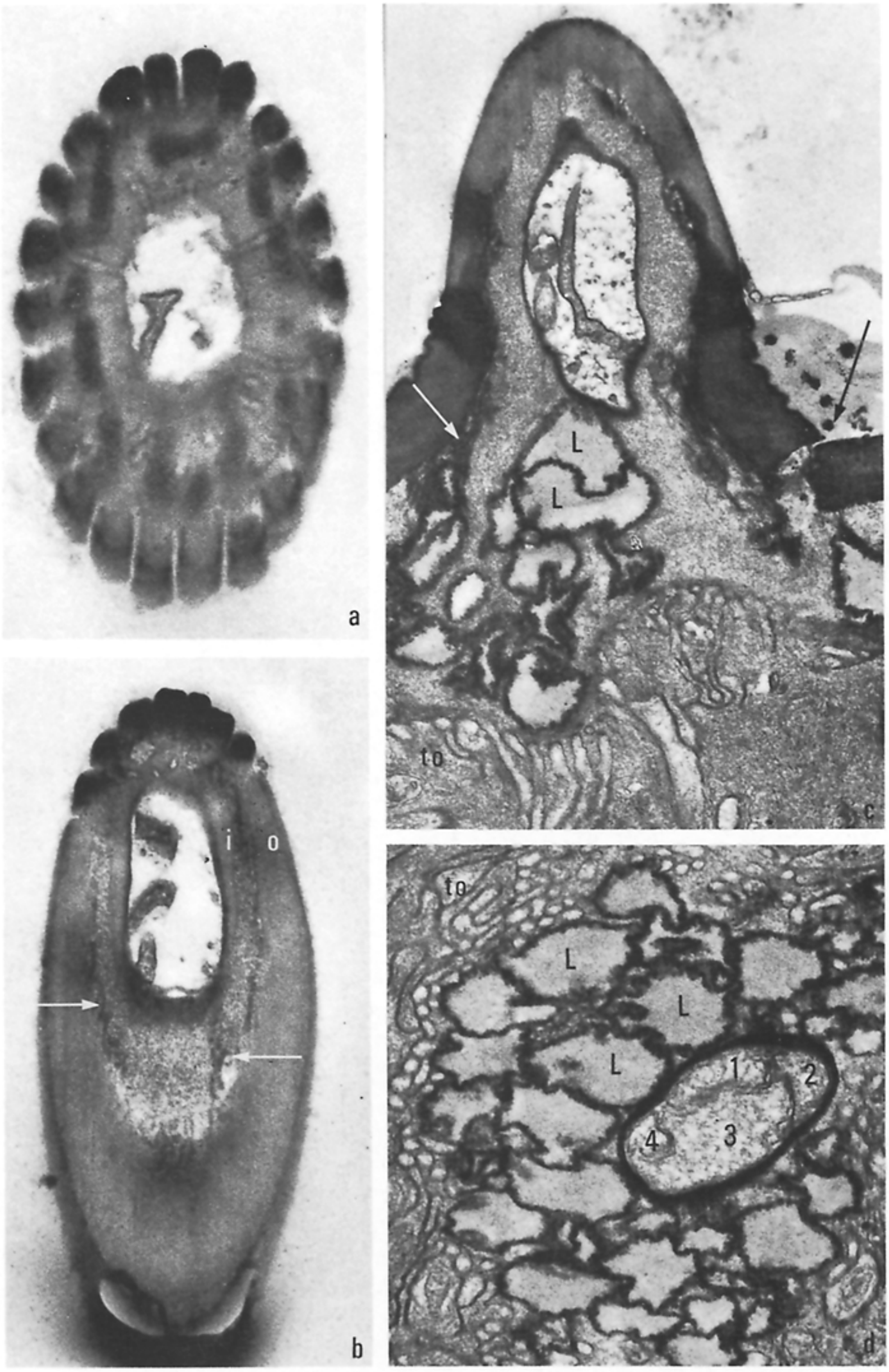


**Fig. 1a and b.** Two transverse sections through a labeled, smooth-walled sensillum in which a pentanol-cell was identified electrophysiologically. **a** Two dendritic outer segments (*1*, *2*), still unbranched at this level, are visible. They are surrounded by the cuticular sheath (*ds*) and a process of the trichogen cell (*tri*). **b** The same dendrites cut more proximally with the ciliary region of the outer segment (*1*) and apical portion of the inner segment (*2*) with basal body. (a) × 30,000, (b) × 25,000

**Fig. 2a–d.** Four transverse sections through a labeled, grooved, double-walled sensillum in which an amine-cell was identified electrophysiologically. Cuticular lesion caused by electrode insertion is seen in **c** (*dark arrow*). Four dendrites are visible within the cuticular sheath (*1–4*). The two concentric cuticular cylinders of the wall are seen in **b** (*i* inner wall, *o* outer wall). The receptor lymph cavity above the tormogen cell (*to*) contains granules (*L* in c, d) which consist presumably of lipids. Electron dense material which has separated from the granules and lies close to the outer wall of the sensillum is indicated by *white arrows* in **b** and **c**. (a) × 60,000, (b) × 30,000, (c) and (d) × 20,000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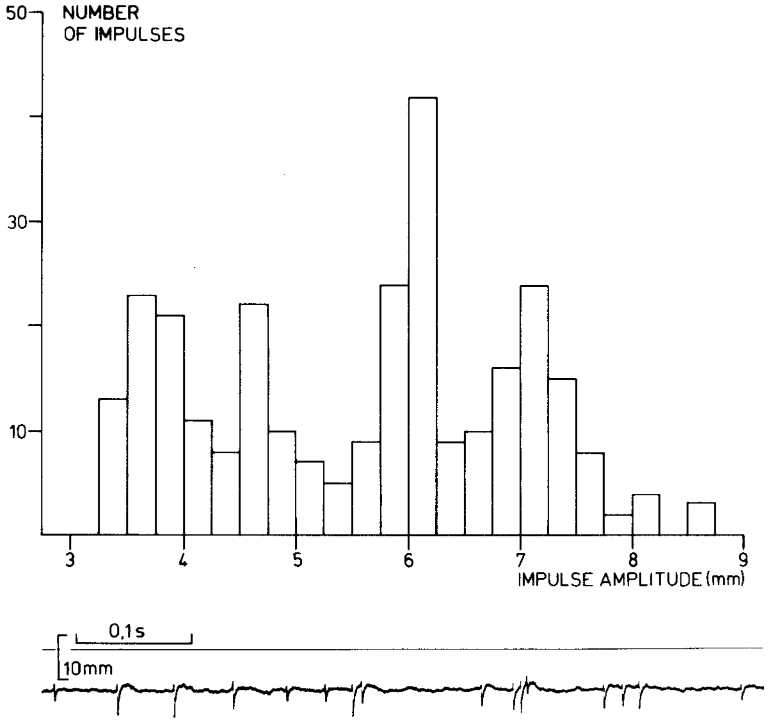

**Fig. 3.** Electrophysiological evidence for the existence of four sensory cells within a double-walled sensillum of the amine type. Above: Histogram of the amplitudes in mm from an 11-sec recording period (spontaneous activity) showing four peaks. Below: Section of recording from which the histogram was obtained

of sensilla did not vary, the number may be presumed to be constant here also.

Cold cells occurred in two different combinations: one with a moist and dry cell and the other with a hexanoic acid cell. This fact provokes the question of whether the reactions of the different cold cells can be distinguished on the basis of combination. In his current study of the dry cell on the antenna of *Periplaneta americana,* Loftus (1976) encountered cold units, the phasic and tonic responses of which hardly differ from those he described previously (1968, 1969, personal communication). Nevertheless, many cold cells of the 1968 study reached higher peak impulse frequencies than any of the current group and the peak frequencies of many units found currently are lower than those previously recorded. The significance of this difference, however, can be considered doubtful, for in all probability hexanoic acid-cold sensilla were included in the first study and in the second cold cells were by-products, sometimes so erratic that their low frequencies could be considered the result of insertion injury (Loftus, personal communication). Further investigation is required.

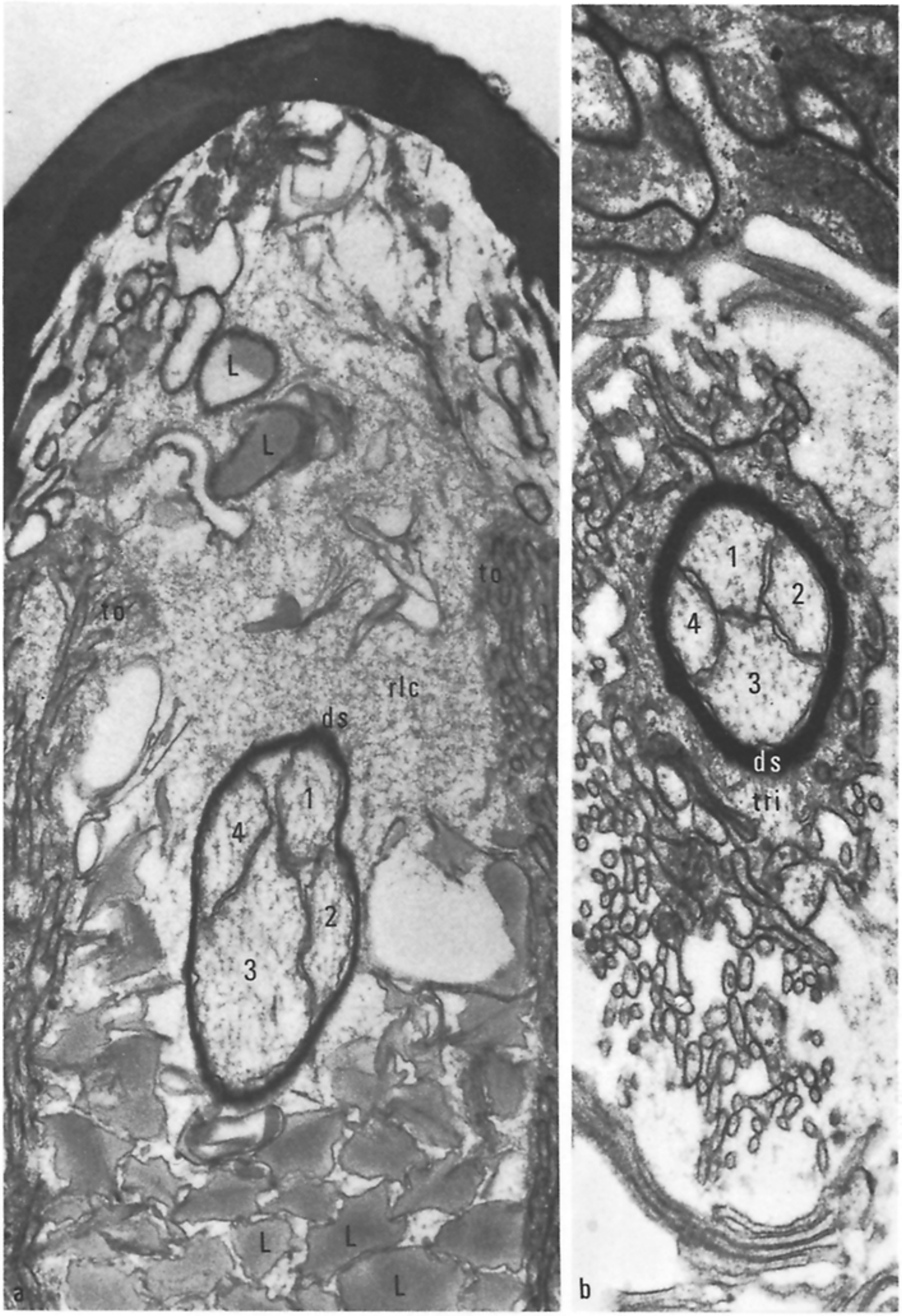

**Fig. 4a and b.** Two transverse sections through a labeled, grooved, double-walled sensillum of the hexanoic acid-cold type. Four outer dendritic segments (*1–4*) are visible. **a** The receptor lymph cavity (*rlc*) which is surrounded by microvilli of the tormogen cell (*to*) contains bodies (*L*) which consist presumably of lipids. **b** The same dendrites cut more proximally surrounded by the cuticular dendritic sheath (*ds*) and a process of the trichogen cell (*tri*). (a) × 20,000, (b) × 24,000

**Table 1.** Comparison of properties of 25 labeled chemo-, hygro- and thermosensitive sensilla on the antenna of *Periplaneta americana*. In addition to those described above, there are two other morphological types most probably olfactory: 1) smooth, single-walled pegs about 20 μm long with 4 sensory cells; 2) single-walled, sharp tipped hairs about 20 μm long, grooved at the base and with 2 sensory cells. Both have pore tubules in stimulus-conducting system

| Physiological type | Number of labeled sensilla investigated morphologically | Morphological properties | | | | | | Maximum sensitivity for | |
|---|---|---|---|---|---|---|---|---|---|
| | | Surface | | Stimulus conducting structures | Length | Other properties | Number of sensory cells | cell number | Substance |
| pentanol | 5 TEM<br>1 SEM | smooth | | single-walled peg with pores and pore tubules | about 10 μm | outer dendritic segments branched | 2 | 1<br>2 | pentanol<br>rotten meat |
| hexanol | 1 TEM | | | | | | 2 | 1<br>2 | hexanol<br>isoeugenol |
| octanol | 2 TEM<br>1 SEM | | | | | | 2 | 1<br>2 | octanol<br>? |
| alcohol-terpene | 1 TEM | | | | | | 2 | 1<br>2 | nerol, terpineol<br>? |
| butyric acid | 3 TEM | grooved | 16–19 grooves | double-walled peg with spoke canals filled with secretion | about 10 μm or less | outer dendritic segments unbranched | 3 | 1<br>2<br>3 | butyric acid<br>?<br>? |
| hexanoic acid – cold | 5 TEM<br>2 SEM | | 22–32 grooves | | | | 4 | 1<br>2<br>3<br>4 | fatty acids C 5–7<br>fruit, meat<br>cold |
| amine | 2 TEM | | 22–25 grooves | | | | 4 | 1<br>2<br>3<br>4 | cyclohexamine<br>fresh meat, fruit<br>rotten meat<br>? |
| cold-moist-dry | 2 TEM | grooved at tip | | atypical double-walled peg | | | 4? | 1<br>2<br>3<br>(4) | cold<br>moisture<br>dryness<br>(?) |

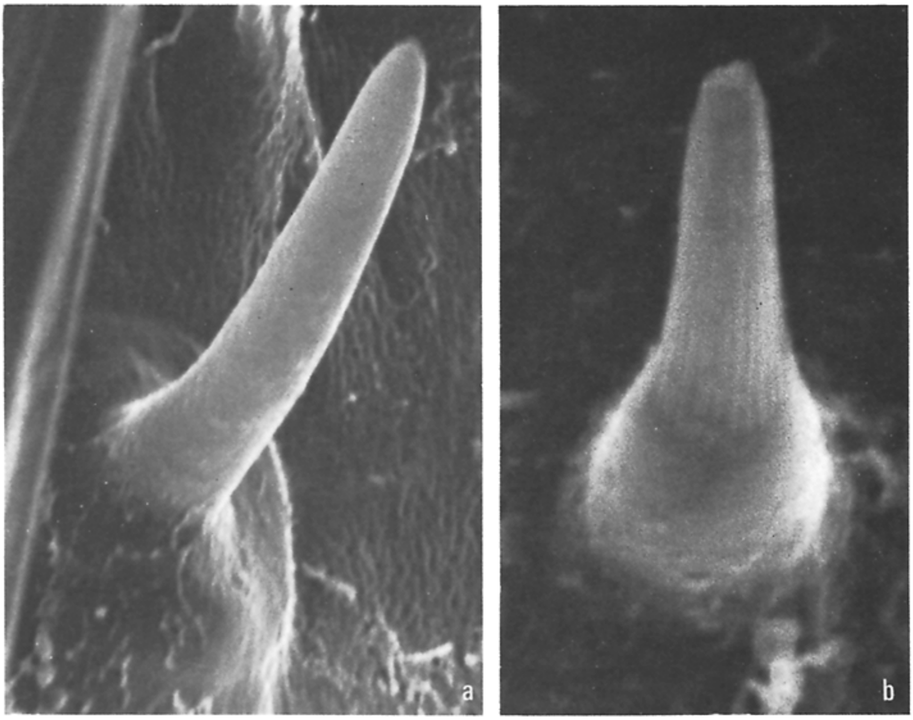

**Fig. 5. a** Smooth-walled sensillum of the pentanol type as shown by previous electrophysiological investigation. **b** Grooved hexanoic acid-cold type sensillum. The tip was broken off during preparation. (a) ×7,900, (b) ×12,000

### *B. Morphological Properties of Physiological Sensillar Types as Established with Scanning Electron Microscopy*

In four cases, sensilla, from which electrophysiological recordings had been made, were marked and examined under the scanning electron microscope. This procedure produced quick results but had the disadvantage of providing no information regarding internal structure (number of cells, stimulus conducting apparatus). The different types could be distinguished, however, by means of criteria established by transmission electron micrographs: presence of grooves and length.

The results confirm those from transmission electron microscopy and serial reconstructions. A pentanol and an octanol sensillum were both smooth-walled, and two hexanoic acid-cold sensilla were grooved (Fig. 5). Their outlines were also different. Grooved pegs had broader bases and pointed tips. The tips of the smooth-walled hairs were blunter and more rounded.

### *C. Comparison of Stimulus Conducting Systems in Smooth Single-Walled Sensilla and Grooved Double-Walled Hairs*

The smooth single-walled sensilla of *Periplaneta americana* were perforated by openings about 150 Å in diameter. The pores led into canals running through

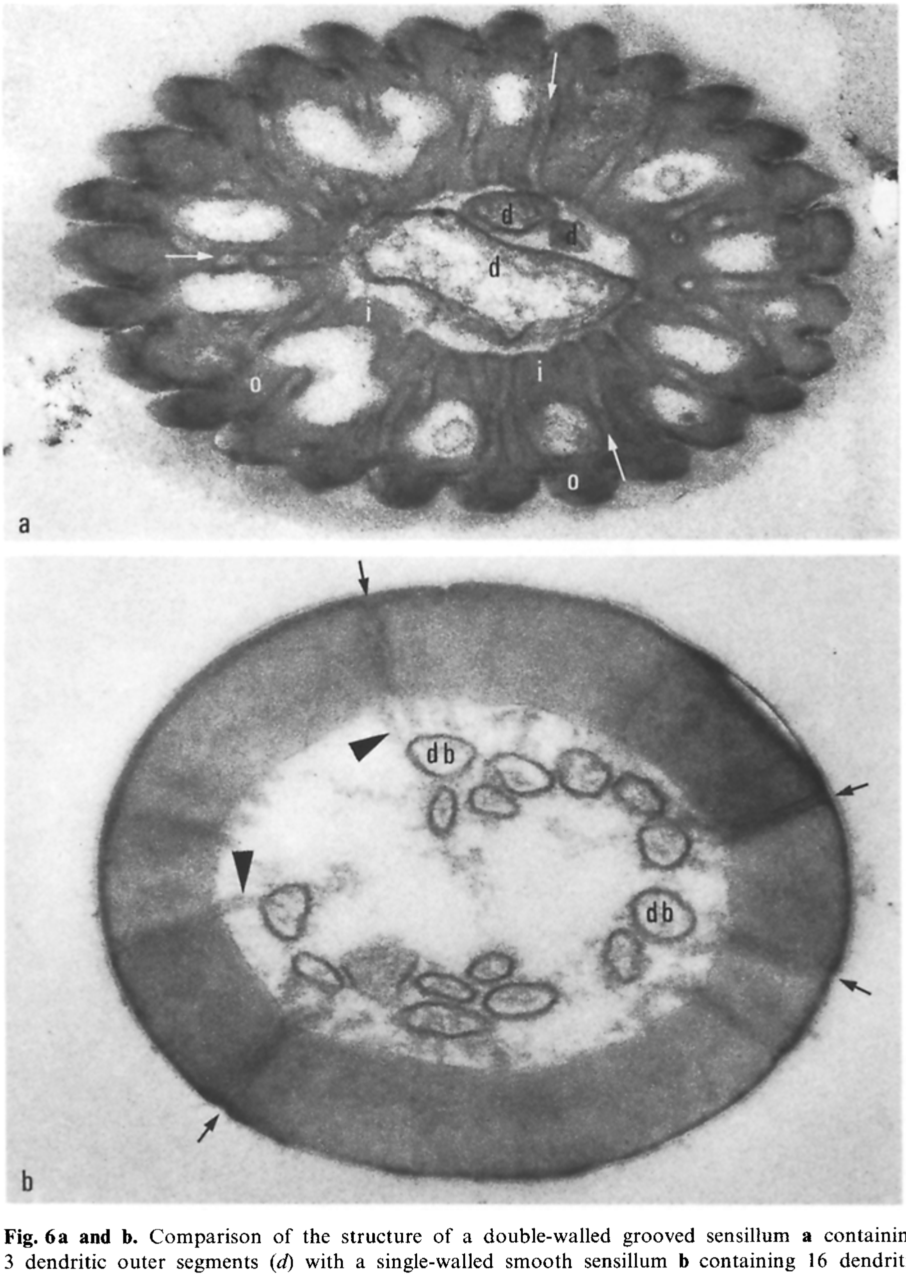

**Fig. 6a and b.** Comparison of the structure of a double-walled grooved sensillum **a** containing 3 dendritic outer segments (*d*) with a single-walled smooth sensillum **b** containing 16 dendritic branches (*db*). **a** Spoke canals are indicated by *arrows*. *o* outer wall, *i* inner wall. **b** Pores are indicated by *arrows*, pore tubules by *arrowheads*. (a) and (b) ×70,000

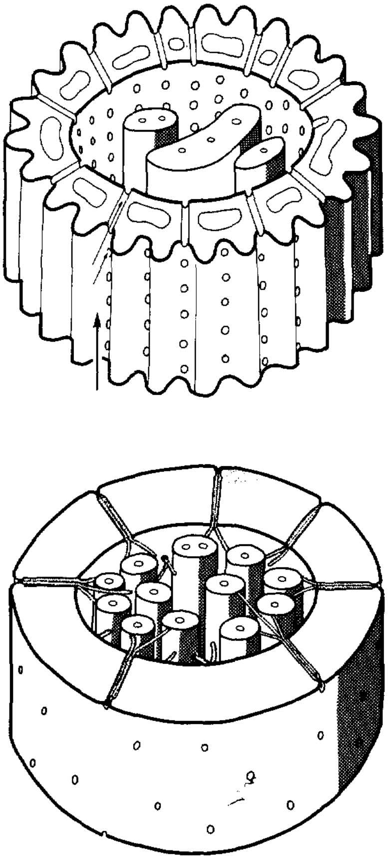

**Fig. 7.** Comparison of the structure of a double-walled grooved sensillum (above) with a single-walled smooth sensillum (below) showing the differences in the stimulus conducting systems

the cuticular wall which contain tightly packed pore tubules. From these base of the canals the tubules separated, extended a few hundred Å into the receptor lymph cavity (Figs. 6, 7) and terminated very often at the membrane of one of the dendrite branches running close to the bristle wall. However, many tubules ended without contacting a membrane.

Grooved hairs were double-walled. The dendritic sheath was connected to an inner cuticular cylinder in the lumen of which lie the unbranched outer segments of the dendrites. The outer wall was externally grooved and concentric with the inner wall. The two were connected by posts of cuticular material running the length of the sensillum and which gave the sensillum the cross-sectional appearance of two concentric circles joined by spokes (Figs. 6, 7). The bands were often perforated by a series of radial canals between 150 and 200 Å in diameter, the spoke canals. Stimuli could proceed along the spoke canals to reach the dendrites. The lumina between the spokes were continuous with the lymph cavity above the tormogen cell. The flaky, electron dense material which occurred in most cases within the lumen had, to all appearances, separated from the secretion granules which were located above the microvilli of the

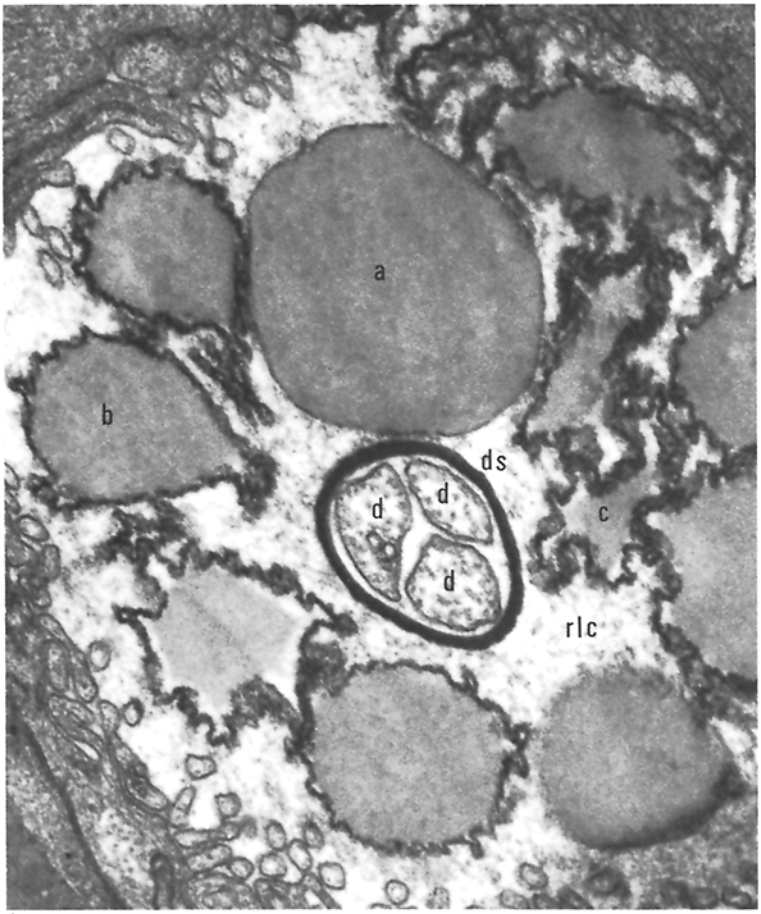

**Fig. 8.** Secretion material in the receptor lymph cavity (*rlc*) of a double-walled, grooved sensillum containing 3 sensory cells (*d* dendrites). The secretion granules (*a–c*) differ in shape and electron density of the surrounding surface. ×36,000

tormogen cell in all typical grooved hairs (Figs. 2, 4). Serial sections permit the conclusion that this material can be discharged through cuticular pores at the base of the sensillum into the grooves and flow up them toward the tip. Along this pathway, it could enter the spoke canals, the openings of which were at the base of the grooves. In this fashion the material could be shunted as a stimulus conducting medium between the outside world and the receptor lymph cavity. The granules within the receptor lymph cavity above the tormogen cell probably develop by confluence, since there were no recognizable precursor forms within the cell. They appeared like homogeneous lipid granules and, with the fixation used, were of medium electron density.

Their surface, however, differed from sensillum to sensillum. In one instance, it was simply a very thin, smooth, electron dense layer. In other cases the granules were star-shaped and had an electron dense coating frayed and folding outward and from which pieces appeared to tear away. Between these two extremes numerous transitions occurred (Fig. 8). It is noteworthy that the latter state was especially common in sensilla which had been recorded. This observation suggests that the sloughing off of electron dense material is enhanced by electrode penetration.

Atypical grooved hairs, the cold-moist-dry type, were also double-walled sensilla. The lymphatic space over the tormogen cell was extensive and almost completely filled with a secretion droplet, which could well be composed of lipids also. It was pear-shaped and measured 14–21 µm. Because of technical difficulties, there remains some uncertainty regarding the stimulus conducting system of this sensillum; presumably it is similar to that of typical grooved hairs. When the antenna was examined under transmitted light, the sensillum could be distinguished by virtue of the large, bright appearance of the region at its base.

## Discussion

### *A. Sources of Error*

*Localization of Sensilla.* The method of localization was greatly improved over an earlier study (Altner et al., 1973). Only those preparations were examined morphologically in which the position of the recorded sensillum could be clearly defined in relation both to an uncomplicated field of sensilla and to the position of the cactus marking needle. In 18 of the 21 marked sensilla complete serial sections also revealed the insertion lesion from the electrode. The insertion lesion did not always show up under the scanning electron microscope without subsequent enlargement, probably because the lesion was closed by hemolymph (see Davis, 1974; Yokohari et al., 1975). The fact that the different physiological types showed a clear relationship to the morphological types without exception is in itself an important result. A preliminary report (Altner et al., 1973) stated that thermo- and hygroreceptive units sometimes occurred in single-walled sensilla. We have been unable to reproduce this finding. The present exclusive choice of uncomplicated sensillar patterns coupled with improved marking leads us to the opinion that the antennal thermo- and hygroreceptors of *Periplaneta americana* are located exclusively in grooved, double-walled sensilla.

Odorous substances, dilution, stimulation. The treatment of Sass (1976) regarding the degree of purity of the odorous substances used, possible errors in dilution, and the limits of stimulus reproducability applies here since recordings were made under the same conditions.

### *B. The Relationship of Modality and of Specific Sensitivity to Different Stimulus Conducting Systems*

*a) Thermo- and Hygrosensitive Elements.* Two stimulus conducting systems can be distinguished in the antennal sensilla of *Periplaneta americana*: pore tubules and spoke canals coupled with secretion. The first are found only in smooth, single-walled bristles; the second exclusively in grooved double-walled hairs.

Present results indicate that the hygro- and thermosensitive units of Periplaneta all occur in grooved hairs. In general, one may suppose that the membrane characteristics of the dendrites are responsible for modal sensitivity. Nevertheless, the question remains whether the stimulus conducting system might also have properties which contribute to the specificity of the entire sensillum. In considering this possibility, however, one must bear in mind that sensilla of the hexanoic acid-cold type have not only a thermo-sensitive but also certainly one and probably even three chemosensitive cells. It is worth noting, however, that the majority of thermo- and hygro-sensitive units examined so far were located in grooved double-walled hairs. As was mentioned, the thermo-sensitive sensilla investigated here had the same electrophysiological characteristics as those described by Loftus (1968, 1976), and all were grooved. The scanning electron micrographs of Yokohari et al. (1975) showed a sensillum, the short apical grooves of which can be recognized, and therefore in all probability represents the moist-dry-cold sensillum as defined here.

Likewise, the hairs (sensilla coeloconica) of Locusta in which Waldow (1970) found thermo- and hygrosensitive cells are also double-walled. The same applies to the hygrosensitive unit which Bernard (1974) located in a "sensillum basiconicum" (type F2f) on the bug, Triatoma, in combination with three chemosensitive cells. From the observations of Slifer and Sekhon (1961) the cold and moisture receptors which Lacher (1964) recorded on the honeybee antenna should also be in grooved hairs. On the other hand, Davis and Sokolove (1975) recorded responses to thermal stimuli from a "coeloconic" sensillum of *Aedes aegypti* which, according to McIver (1973), is not grooved and is morphologically different from the sensilla of Locusta bearing the same name, even though it lacks pore tubuli and comparable structures. The hygrosensitive units of Aedes which were investigated by Kellog (1970), on the other hand, are located in grooved pegs, but according to Davis and Sokolove (1976) it is doubtful whether these cells are really specialized for the detection of water vapor, since their response to this stimulus is comparatively weak. In caterpillars, humidity receptors have been found in sensilla "basiconica" (Dethier and Schoonhoven, 1968), but too little is known regarding their structure to permit discussion here.

*b) Chemoreceptive Elements.* The results here do not only permit the conclusion that the thermo- and hygrosensitive units are to be found in connection with definite morphological sensillar types, they also show that units responding to short chained n-alcohols are located in smooth, single-walled sensilla with pore tubuli, whereas units sensitive to short chained n-acids and amines are found exclusively in double-walled hairs. If one is not disposed to view this situation as a coincidence, it would seem reasonable to consider the relationship as the result of adaptations leading to greater specificity of the sensillum. The stimulus conducting systems might differ in their affinity for various odorous substances; that is, they might have selective diffusion characteristics. The selectivity of the receptor molecules in the dendrite membranes of sensory cells might be complemented by previous filtering through the stimulus conducting system. Although olfactory cells occur in many sensilla which have evaded all attempts to classify them by chemically pure substances (see Table 1), this fact does not militate against our interpretation for the following reasons: 1)The chemoreceptive function of these cells is maintained when they are stimulated by natural mixtures of odors, and 2) in a sensillum with a cell responding, for example, to amines, to butyric and hexanoic acids but not to n-alcohols, neither do the other units of the sensillum react to n-alcohols, although one cannot state precisely which substances elicit a strong excitation in them. The corresponding situation applies to unclassified cells in sensilla with a unit reacting to short chained n-alcohols but not to fatty acids.

The question arises to what extent these results allow generalization. Unfortunately, very few papers provide data on both the graded sensitivity and fine structure of any definite sensillar type. Nevertheless, Boeckh (1974) mentioned in the case of Locusta that sensory cells in basiconic sensilla (i.e. the type with pore tubules) react only to alcohols and not to fatty acids. Cells sensitive to fatty acids were found in coeloconic sensilla (i.e. in grooved hairs). Kafka (1970) also found that olfactory cells in this type of sensillum were most sensitive to n-acids. Alcohols also elicited a response, but weaker. This finding fits our contention, for the stimulus conducting structures may well be selective not so much for a single substance but for groups of substances in varying degrees.

Our hypothesis is supported by the findings of Bernard (1974), Davis and Sokolove (1976), and, at least partly, by those of Kaib (1974). Bernard (1974) found cells in double-walled pegs on the antenna of Triatoma which respond to lactic, pyruvic, and butyric acids. Davis and Sokolove (1976) recorded responses to lactic acid from double-walled grooved hairs on the antenna of *Aedes aegypti* (A3-sensillum, cf. McIver, 1974). Kaib (1974) in Calliphora characterized a unit within a basiconic sensillum (pore tubules as stimulus conducting structures) as a hexanol type. Fatty acids ($C_4$–$C_6$) have little or no effect on this unit. The other unit which was observed within this sensillum reacts to terpenes. Kaib mentioned another sensillum, however, type A, which is double-walled and grooved. One unit within this sensillum responds moderately to alcohols ($C_5$, $C_6$) and mercaptans but not to fatty acids ($C_5$, $C_6$). Fresh and rotten meat, however, have a much stronger effect so that it is hard to classify the sensory cells within this sensillum by a pure odoriferous substance. There is uncertainty, however, to whether the basiconic sensilla of Necrophorus (Boeckh, 1962; Waldow, 1973) and the pore plates of Apis (Lacher, 1964) fit the framework of our hypothesis. Both forms of sensilla have pore tubuli and both react to fatty acids. Not every short chained n-fatty acid elicits a high impulse frequency, however. Propionic and butyric acids were rarely very effective in the case of Apis. In Necrophorus the reaction to $C_1$ to $C_3$ acids was inhibitory (Waldow, 1973). Nevertheless, the response to hexanoic acid was in both cases very pronounced (Boeckh, 1962; Lacher, 1964).

## *C. Characterization of Stimulus Conducting Structures and Classification of Sensilla*

To attempt a discussion of the properties of the stimulus conducting structures which could produce a prefiltration effect would go beyond current data. Our results indicate that the material filling the spoke canals of the grooved double-walled hairs is secreted by the tormogen cell and that it contains lipids. This agrees with the data of Hawke and Farley (1971b) who found in Arenivaga that the electron opaque material within the grooves and channels of the large grooved pegs can be extracted with acetone and chloroform. The comparison of the effects of various solvents in combination with tracer experiments leads these authors to suggest that there might be even different types of stimulus conducting systems which cannot be distinguished by electron microscopy without special pretreatment. This argument has to be considered seriously when comparing sensilla of similar appearance (see above).

Moreover, the specificity of the stimulus conducting system with respect to the sensitivity of the sensory cell membrane may vary, so that the correlations that we have found between morphology and physiology with sensilla in Periplaneta may not necessarily apply to sensilla in other species.

Furthermore, it should not be forgotten that even though the smooth, single-walled hairs with pore tubuli and grooved hairs with spoke canals filled with secretion form two categories which include a great number of sensillum forms; there are, nevertheless, sensory hairs in insects and even more in other arthropods which are outside these categories. Their stimulus conducting systems show similarities, but they are not the same (see, for example, Altner and Thies, 1972; Meinecke, 1975).

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