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Review article

The organization of the chemosensory system in *Drosophila melanogaster*: a rewiew

Reinhard F. Stocker

Institute of Zoology, University of Fribourg, Pérolles, CH-1700 Fribourg, Switzerland

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Abstract. This review surveys the organization of the olfactory and gustatory systems in the imago and in the larva of *Drosophila melanogaster*, both at the sensory and the central level. Olfactory epithelia of the adult are located primarily on the third antennal segment (funiculus) and on the maxillary palps. About 200 basiconic (BS), 150 trichoid (TS) and 60 coeloconic sensilla (CS) cover the surface of the funiculus, and an additional 60 BS are located on the maxillary palps. Males possess about 30% more TS but 20% fewer BS than females. All these sensilla are multineuronal; they may be purely olfactory or multimodal with an olfactory component. Antennal and maxillary afferents converge onto approximately 35 glomeruli within the antennal lobe. These projections obey precise rules: individual fibers are glomerulus-specific, and different types of sensilla are associated with particular subsets of glomeruli. Possible functions of antennal glomeruli are discussed. In contrast to olfactory sensilla, gustatory sensilla of the imago are located at many sites, including the labellum, the pharynx, the legs, the wing margin and the female genitalia. Each of these sensory sites has its own central target. Taste sensilla are usually composed of one mechano- and three chemosensory neurons. Individual chemosensory neurons within a sensillum respond to distinct subsets of molecules and project into different central target regions. The chemosensory system of the larva is much simpler and consists essentially of three major sensillar complexes on the cephalic lobe, the dorsal, terminal and ventral organs, and a series of pharyngeal sensilla.

Key words: Olfaction – Taste – Chemosensilla – Antennae – Chemosensory projections – Antennal lobe – Glomeruli – *Drosophila melanogaster* (Insecta)

Introduction

For most animals the chemical composition of the environment is one of the dominant cues for orientation in space. Volatile or dissolved molecules lead to food sources or oviposition sites, they warn of enemies or toxic conditions, and they represent a sophisticated means of interspecific communication. Classical and recent observations demonstrate that vertebrates and invertebrates share many aspects of the chemical senses. For example, a long known parallel is the compartmentalization of olfactory centers into glomeruli, or the types of neurons and connections in the antennal centers (Boeckh et al. 1990). Other remarkable similarities include the mechanisms of sensory reception and transduction (Lancet 1986; Anholt 1991; Stengl et al. 1992). The fact that insects perceive pheromones at extremely sensitive qualitative and quantitative levels (Schneider 1957) has led to their establishment as important model systems of olfactory research. Among the most widely used species in this field are moths (*Bombyx, Antheraea, Manduca*; Kaissling 1987; Homberg et al. 1989; Stengl et al. 1992) and cockroaches (*Periplaneta*; Boeckh et al. 1990). These relatively large insects allowed the application of electrophysiological and biochemical techniques, both at peripheral and central levels. In addition to olfactory research, insects have also been widely used to study the perception of taste, mainly in fly species (Dethier 1976).

An insect species, *Drosophila melanogaster*, has become one of the most important genetic model systems of multicellular organisms. The significance of the fruit fly has even increased during the last decade because of the establishment of powerful techniques of molecular genetics (Rubin 1988). The contribution of *Drosophila* to the genetic analysis of development has been convincingly demonstrated in the study of ommatidial differentiation (Banerjee and Zipursky 1990; Rubin 1991). The dual role of insects as model systems of chemosensory and genetic research makes *Drosophila* one of the most attractive experimental subjects for studying chemical senses, and in particular the genetic basis of their development and function. Furthermore, the organization of olfactory and gustatory systems in *Drosophila* is in many respects simpler than that of the other species mentioned.

The present review summarizes the structural organization of the adult and larval chemosensory system in *Drosophila* as a basis of genetic and molecular studies.

The essential question that will be addressed refers to the role of the different levels of the system in sensory reception and discrimination. In particular, the functional significance of individual antennal glomeruli will be discussed in the context of their inputs and outputs. A key feature in this discussion will be the often observed modality-specific segregation of chemosensory projections. Furthermore, I will compare the organization of the olfactory and gustatory systems and the surprisingly different structure of the larval and adult chemosensory systems. This paper will not focus on functional, behavioral, developmental, or genetic aspects of the system, which have been recently reviewed (Siddiqi 1987, 1991; Carlson 1991; Stocker et al. 1992). Earlier surveys on the organization of the *Drosophila* chemosensory system have been published by Hertweck (1931) and Miller (1950), and the chemosensory centers of flies have been reviewed by Strausfeld (1976). Excellent reviews of the antennal system in insects in general are those of Rospars (1988), Homberg et al. (1989), Boeckh et al. (1990), Masson and Mustaparta (1990) and Boeckh and Tolbert (1993).

The adult olfactory system

Antennal sensilla

Olfactory sensilla in *D. melanogaster* are restricted to the third antennal segment (funiculus) and the maxillary palps (Figs. 1, 2), but in both of these appendages they are intermingled with nonolfactory sensilla. Many of the ultrastructural characteristics of the funicular and maxillary sensilla are shared by those in *Musca*, *Phormia* (Dethier 1976), and the sheep head fly *Hydrotaea* (Been et al. 1988).

The majority of funicular sensilla occupy the surface of this segment (Figs. 2, 5), but many others line the wall of a pit (the sacculus) that is located proximally on its posterior side. An additional sensillum is contained within the pinnate appendage of the funiculus, the arista (cf. Fig. 5). Sensilla on the surface belong to three morphological types: club-shaped basiconic sensilla, spine-shaped trichoid sensilla, and small, cone-shaped coeloconic sensilla (Figs. 2, 3; Anders 1955; Mindek 1968; Hodgkin and Bryant 1978; Venkatesh and Singh 1984; Stocker et al. 1992).

Basiconic sensilla (BS). According to the terminology of Altner and Prillinger (1980), BS are of the single-walled, multiporous type (Fig. 3, Table 1). Numerous pores of about 30 nm diameter penetrate the wall of the shaft whose lumen is filled with multiple dendritic arborizations. The shafts are stainable with $AgNO_3$, which is apparently able to migrate through the pores. BS can be clearly assigned to a large or a small subtype (cf. Fig. 5). Large BS possess two or four neurons, whereas the small subtype appears to be equipped with two neurons only. BS have been identified by monoclonal antibodies (mab). Mab ca 51/2 recognizes sensory cell bodies and dendrites of BS (Fig. 4A; Störtkuhl et al. 1993). Two other mab bind to the region around the receptor lymph space of BS, whereas a third one labels the basal part of basiconic dendrites (Störtkuhl et al. 1994). Recently, several *lacZ*-expressing enhancer trap lines have been isolated whose staining patterns reflect the patterns of BS, TS, CS, or saccular sensilla (Pinto et al. 1992; Riesgo-Escovar et al. 1992). An example of a line (6865) that exhibits a funicular pattern similar to that of large BS is shown in Fig. 4C (Riesgo-Escovar et al. 1992).

BS have been clearly characterized as olfactory sensilla (Siddiqi 1983, 1987). Single unit responses have allowed one to distinguish at least eight classes of BS that differ in their response spectra to acetates, alcohols, ketones, aldehydes, or fatty acids. Responses to air were also observed, but so far no structural correlate of a mechano-, thermo-, or hygroreceptive neuron has been found. There is evidence that the different classes map to different sites on the funiculus (Siddiqi 1983, 1987). How these classes correlate with the multiple neurons per sensillum and with the diverse central projection patterns of BS (see below) is not known.

Strong alleles of the *lozenge* (*lz*) mutant lack antennal BS (Fig. 2; Stocker and Gendre 1988; Stocker et al. 1993). This has made possible the study of the behavioral significance of these sensilla. Courtship assays with mutant males suggest that antennal BS are neither crucial for the perception of attraction pheromones of virgin females, nor of inhibitory pheromones of mated females (Stocker and Gendre 1989). Locomotor and electroantennogram responses of flies stimulated with food odors indicate that antennal BS may be involved in the perception of short-chain alcohols and fatty acids (Venard and Stocker 1991).

Trichoid sensilla (TS). TS have been described as single-walled no-pore sensilla (Venkatesh and Singh 1984). However, other fine-structural evidence suggests that TS belong to the multiporous type, much like BS, though with pores of only 10 nm diameter (Link 1983; Fig. 3, Table 1). One to three unbranched dendrites, corresponding to the one to three sensory neurons present in TS, extend into the shaft. While physiological evidence is still lacking, the presence of fine pores and the absence of a large distal opening and of a flexible socket suggest that TS may be olfactory rather than gustatory or mechanosensory. Single-walled, multiporous insect sensilla have always been revealed to be olfactory (Altner and Prillinger 1980).

Coeloconic sensilla (CS). CS are of the double-walled, wall-pore type (Fig. 3, Table 1). Their surface is characterized by about ten longitudinal grooves. CS possess three neurons whose dendrites extend for some distance into the shaft. Sensilla of this type in the antennae of other insects often contain both olfactory and thermoreceptors (Altner and Prillinger 1980). CS are recognized by three mab, i.e., I24B5 (Fig. 4B; Störtkuhl et al. 1994). All three apparently bind to the area around the receptor lymph space.

Sensilla in the sacculus. The large entrance chamber of the three-chambered sacculus is lined by large and small,

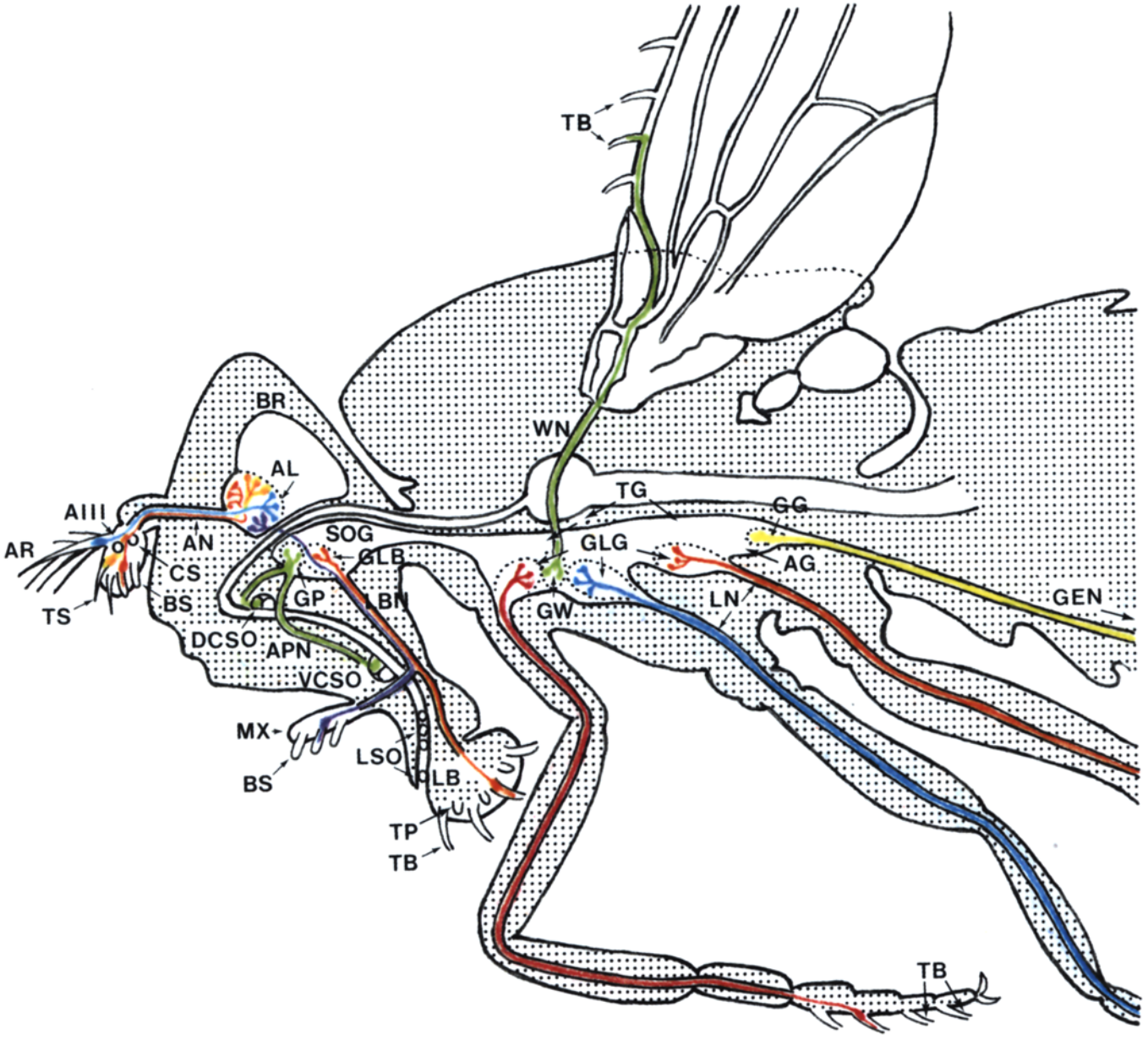
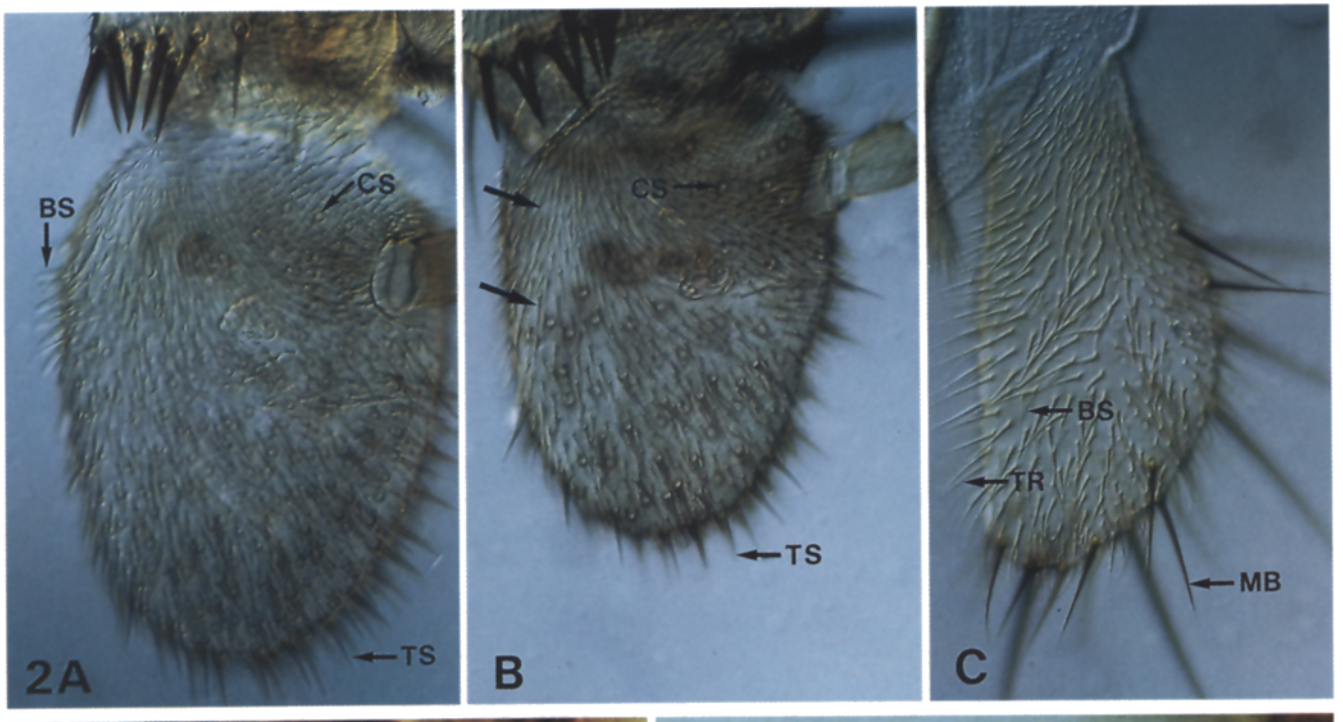


Fig. 1. Summary diagram of the known olfactory and gustatory sensilla in adult *D. melanogaster* and their primary central targets. *AIII* 3rd antennal segment (funiculus); *AG* abdominal ganglia; *AL* antennal lobe; *AN* antennal nerve; *APN* accessory pharyngeal nerve; *AR* arista; *BR* supraoesophageal ganglion (brain); *BS* basiconic sensillum; *CS* coeloconic sensillum; *DCSO* dorsal cibarial sense organ; *GEN* female genitalia; *GG* gustatory center of genitalia; *GLB* gustatory center of the labellum; *GLG* gustatory centers of the legs; *GP* gustatory center of the pharynx; *GW* gustatory center of the wing; *LB* labellum (labial palps); *LBN* labial nerve; *LN* leg nerves; *LSO* labral sense organ; *MX* maxillary palps; *SOG* suboesophageal ganglion; *TB* taste bristle; *TG* thoracic ganglia; *TP* taste peg; *TS* trichoid sensillum; *VCSO* ventral cibarial sense organ; *WN* wing nerve. Data are from Lienhard and Stocker (1987), Nayak and Singh (1985), Palka et al. (1979), Possidente and Murphey (1989), Shanbhag and Singh (1992a,b), Singh and Nayak (1985), Stocker and Schorderet (1981), Stocker et al. (1983, 1990), Taylor (1989)

grooved sensilla (GS1, GS2). BS-like sensilla are located in the smallest chamber, and blunt-tipped sensilla, in the middle chamber (Table 1; Itoh et al. 1991; Keller 1992). GS1 and GS2 are of the double-walled, wall-pore type and resemble CS (Fig. 3). The three mab that bind to CS (see above) also recognize GS1 and GS2 (Störtkuhl et al. 1994). Blunt-tipped sensilla bear no similarity to antennal surface sensilla. They are poreless and probably comprise thermo- and hygroreceptors (Altner et al. 1983b). The enhancer trap line 6865, which exhibits a pattern reminiscent of large BS, also stains saccular sensilla (Fig. 4C; Riesgo-Escovar et al. 1992).

The clustering of a subset of sensilla in a pit may indicate that they respond to slower changes of the olfactory environment than do those on the surface, due to reduced diffusion of molecules through the narrow opening of the sacculus.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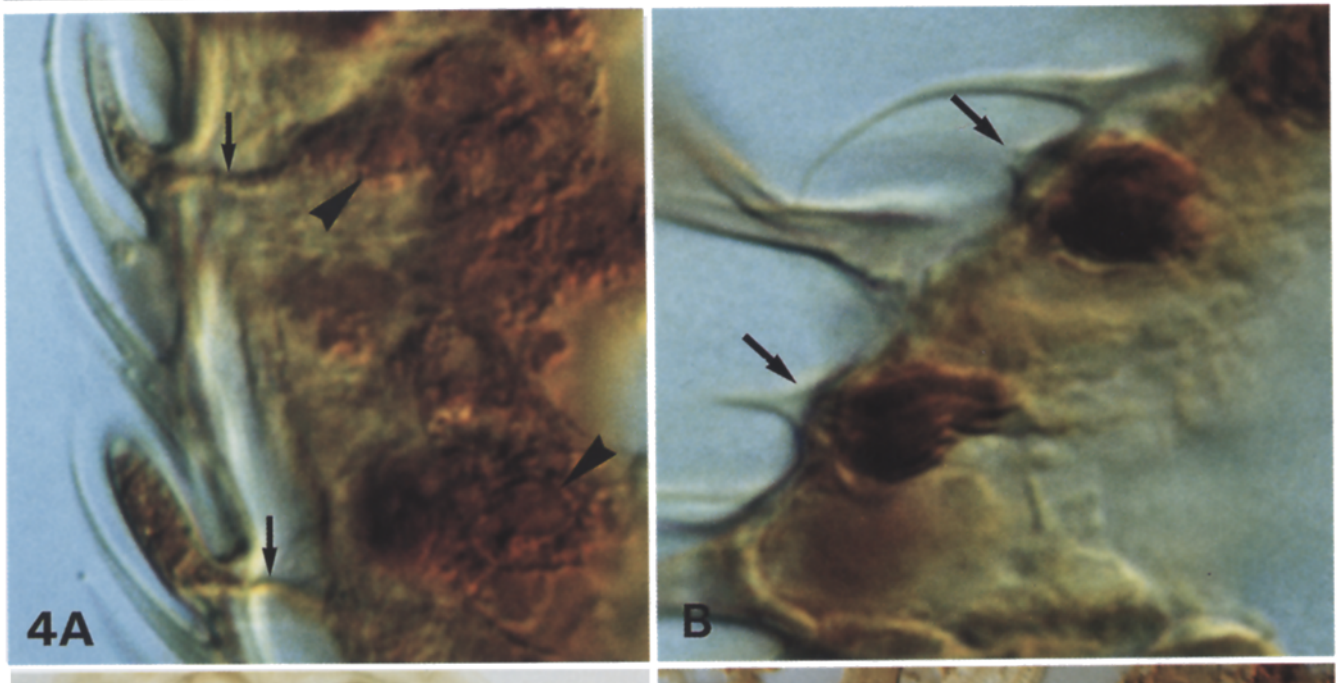
4A
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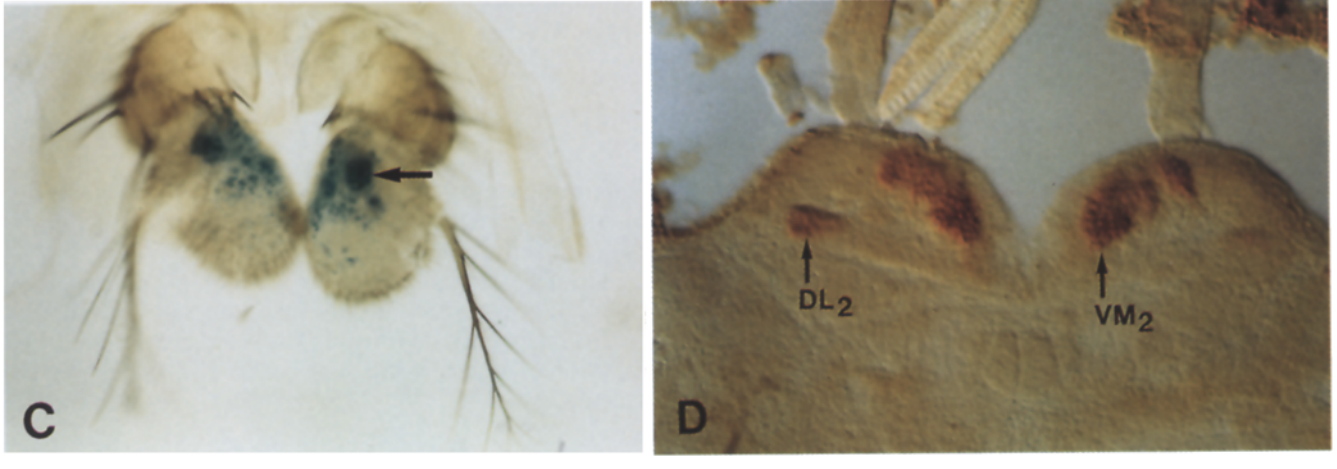
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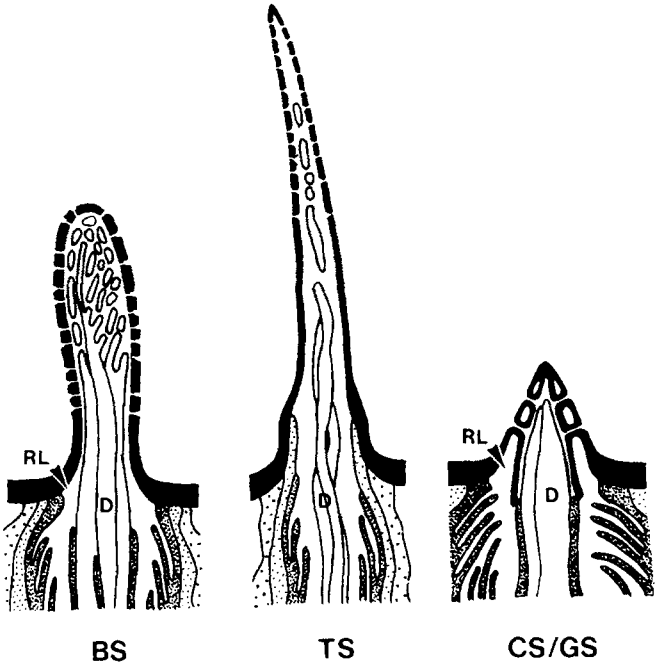


Fig. 3. The structure of olfactory sensilla as demonstrated by transmission electron microscopy (EM) (Link 1983; Venkatesh and Singh 1984). *BS* and probably also *TS* are single-walled and multiporous, while *CS* and *GS* (grooved sensilla of the sacculus) are of the double-walled, wall pore type. Dendrites (*D*) in *BS* arborize profusely. *RL* Outer receptor lymph space. Not drawn to scale

Aristal sensillum. The base of the arista contains an entirely different type of sensillum (Fig. 5), consisting of three units of two neurons each whose dendrites end freely in the aristal lumen (Foelix et al. 1989). One neuron of each unit has a highly lamellated dendritic tip with an array of small particles on the outside of its membrane. These characteristics are highly reminiscent of thermoreceptors on the antennae of other insects (Steinbrecht 1989). Although the role of the other three neurons remains unknown, the lack of a mechanical stimulus-transducing apparatus and the lack of pores in the aristal wall rule out a mechano- or a chemoreceptive function.

Fig. 2A–C. Olfactory sensilla of adult *D. melanogaster*. **A** and **B** show the posterior surface of the male funiculus in the wild-type (*Sevelen*) and in the *lozenge*^{3} mutant, respectively. *Large arrows* in **B** point to areas that lack BS. **C** Dorsal side of wild-type maxillary palp. *MB* Mechanosensory bristles; *TR* noninnervated trichomes. Other abbreviations as in Fig. 1. × 310

Fig. 4A–D. Staining patterns of selected monoclonal antibodies and enhancer trap lines in the funiculus and in the antennal lobe (Riesgo-Escovar et al. 1992; Störtkuhl et al. 1993). **A** mab ca 51/2 binds to the cell bodies (*arrowheads*) and dendrites (*arrows*) of basiconic neurons in the funiculus (micrograph shows section through pure BS region). × 2000. **B** mab I24B5 binds to antennal CS (*arrows*). × 2400. **C** Enhancer trap line 6865 shows pattern reminiscent of large BS pattern (cf. Fig. 5), and in addition strong but age-dependent staining in the sacculus (*arrow*). × 100. **D** Horizontal view of the antennal lobes showing staining of a subset of glomeruli by mab nc 10 (cf. Fig. 6). × 330. (**A**, **B** and **D** courtesy of K. Störtkuhl, A. Hofbauer, and V. Keller; **C** courtesy of J. Riesgo-Escovar and J. Carlson)

Pattern of funicular sensilla. The distribution of sensilla in different 'fields' of the funiculus has been described in detail (Mindek 1968; Stocker et al. 1983; Venkatesh and Singh 1984; Stocker and Gendre 1988). Most of the anterior and posterior surface of the funiculus is covered by a mixed population of TS, CS, and small BS (Fig. 5). The medial edge of the funiculus is occupied by a longitudinally extended dense cluster of large BS followed distally by a smaller cluster of small BS. In addition, a tightly clustered group of large BS spreads in a beltlike fashion distal to the sacculus (Fig. 5). BS units that are sensitive to acetates were found mainly among the large and small BS of these pure regions (Siddiqi 1983). Six to ten scattered CS lie basally on the posterior surface of the funiculus between the sacculus and the base of the arista. These CS vary also with respect to their location and are, therefore, not individually identifiable. Variation in the numbers of the other types of sensilla suggests that this is true for all funicular sensilla. The functional significance of the sensillar pattern on the funiculus remains unknown.

Sexual dimorphism of funicular sensilla. The three wild-type strains *Sevelen*, *Oregon-R* and *Canton-S*, are very similar with respect to the numbers and densities of the various sensilla. However, in each of them the antenna exhibits an obvious sexual dimorphism (Stocker and Gendre 1988; Stocker et al. 1993). Males not only have slightly reduced funiculi, but they possess about 30% more TS, and about 20% fewer large BS than females (Table 1). In *Oregon-R* and *Canton-S* males, there is also a significant decrease of small BS. The sex-specific changes in the sensillum pattern seem to be compensated at the level of afferent numbers. Based on axon counts at the base of the funiculus (Venkatesh and Singh 1984), subtractive fiber measurements in the antennal nerve after removal of the funiculus (Stocker 1979), and the numbers of the different types of sensilla and the numbers of neurons per sensillum (Stocker and Gendre 1988), the funiculus appears to give rise in both sexes to a total of 1100–1250 sensory axons.

Another kind of sexual dimorphism that is not related to a dimorphic sensillum pattern, but may reflect a difference in gene expression, is shown by an enhancer trap line that intensely stains the sacculus in the male but much less in the female (Riesgo-Escovar et al. 1992).

Maxillary sensilla

On the maxillary palps two categories of sensillum can be distinguished, mechanosensory bristles and sensilla of the BS type (Fig. 2, Table 1; Harris 1972; Hodgkin and Bryant 1978; Singh and Nayak 1985). Together they give rise to about 120 sensory axons per palp. The approximately 20 bristles are on the ventral side of the palp and have sometimes been called TS although they possess only a single neuron whose dendrite ends with a tubular body at the flexible socket. The BS-like sensilla cover the dorsal surface and the tip of the ventral surface of the maxillary palp (Singh and Nayak 1985). They share most

Table 1. Olfactory and gustatory sensilla of adult *D. melanogaster*. hygr., Hygrosensitive; mech. or M, mechanosensory; therm., thermosensory

	Shape	Type of sensillum[a]	Length of shaft	Dendritic profiles in shaft	Neuron number	No. of sensilla on each side[c]	Function	References[d]
Surface of funiculus								
Large basiconic	club	sw-mp	8–11 μm	multiple	2 or 4	m: ± 80 f: ±105	olfactory	1–6
Small basiconic	club	sw-mp	5–7 μm	multiple	2	m: ±120 f: ±140	olfactory?	2, 3, 5, 6
Trichoid	spine	sw-[b]	12–22 μm	1–3	1–3	m: ±150 f: ±120	olfactory?	2, 3, 5
Coeloconic	cone	dw-wp	3–4 μm	1–3	1–3	m: ± 65 f: ± 70	olf.-therm.?	2, 3, 5, 6
Sacculus								
Grooved 1	club	dw-wp	4 μm	1–?	2	≥22	olf.-therm.?	2,5–8
Grooved 2	cone	dw-wp	3 μm	1–?	?	≥10	olf.-therm.?	2,6–8
‚Basiconic'	spine	?	5 μm	?	?	≥ 7	olfactory?	2, 6, 8
Blunt tipped	cone	sw-np	2–4 μm	2	3	≥ 5	hygr.-therm.?	2,5–9
Maxillary palp								
Basiconic	club	sw-mp	8–10 μm	multiple	2	m: ±57 f: ±64	olfactory	10–13
Labellum								
Taste bristle	spine	sw-tp	20–40 μm	2–4	2–4+1 M	33–42	gust.-mech.	14–18
Taste peg	peg	sw-tp	3–4 μm	1	1+1 M	±30	gust.-mech.?	14
Pharynx								
Labral no. 7	hairless	ns-tp	–	–	8	1	gustatory?	15, 19
Labral no. 8, 9	hairless	ns-tp	–	–	1+1 M	1	gust.-mech.?	15, 19
Ventral cibarial	hairless	ns-tp	–	–	2–4	2–3	gustatory?	15, 19
Dorsal cibarial	hairless	ns-tp	–	–	3	2	gustatory?	15, 19
Leg								
Taste bristle, 1st leg	spine	sw-tp	12–45 μm	4	2–4+1 M	m: ±50 f: ±37	gust.-mech.	15, 20, 21
Taste, bristle, 2nd leg	spine	sw-tp	12–45 μm	4	2–4+1 M	±30	gust.-mech.	15, 20, 21
Taste bristle, 3rd leg	spine	sw-tp	12–45 μm	4	2–4+1 M	±31–32	gust.-mech.	15, 20, 21
Wing								
Taste bristle	spine	sw-tp	±50 μm	4	4+1 M	±40	gust.-mech.	22, 23
Female genitalia								
Trichoid	spine	?	≤5 μm	?	?	± 3	gustatory?	24
Thorn	thorn	?	10–20 μm	?	?	±10	gust.-mech.?	24

[a] Type of sensillum: dw, double-walled; mp, multiporous; np, no pores; ns, no shaft; sw, single-walled; tp, terminal pore; wp, wall pore

[b] mp according to (2), np according to (3)

[c] Numbers of sensilla on the funiculus, the maxillary palp and the forelegs are given independently for males (m) and females (f)

[d] References: (1) Siddiqi 1983, (2) Link 1983, (3) Venkatesh and Singh 1984, (4) Siddiqi 1987, (5) Stocker et al. 1992, (6) Störtkuhl et al. 1994, (7) Itoh et al. 1991, (8) Keller 1992, (9) Altner et al. 1983b (10) Singh and Nayak 1985, (11) Stocker and Gendre 1989, (12) Venard and Stocker 1991, (13) Ayer and Carlson 1992, (14) Falk et al. 1976, (15) Nayak and Singh 1983, (16) Rodrigues and Siddiqi 1978, (17) Fujishiro et al. 1984, (18) Arora et al. 1987, (19) Stocker and Schorderet 1981, (20) Possidente and Murphey 1989, (21) Shanbhag and Singh 1992b, (22) Palka et al. 1979, (23) Hannaford and Palka 1992, (24) Taylor 1989

of the characteristics of antennal BS (cf. Fig. 3), i.e., they are single-walled, multiporous, and stainable with $AgNO_3$, they possess multiple dendritic arborizations and are recognized by mab ca 51/2 (Störtkuhl et al. 1994). Maxillary BS are therefore additional candidates for olfactory sensilla. Yet, in contrast to antennal BS, *lozenge* mutations (even strong alleles) affect only a small proportion of maxillary BS, and this effect is restricted to a reduction in the length of the sensillum (Stocker et al. 1993). In contrast to antennal BS they apparently do not express enhancer trap line 6865 (Riesgo-Escovar et al. 1992).

Since BS are the only candidates for olfactory sensilla on these appendages, it is possible to study their role in smell detection by removing the palps. Palp-deprived males exhibit significantly more courtship activity towards mated females than intact males. This suggests that maxillary BS may be crucial for perceiving inhibitory female compounds (Stocker and Gendre 1989), e.g., the putative antiaphrodisiac *cis*-vaccenyl acetate (Ferveur et al. 1989). The locomotor responses of palp-deprived flies that are stimulated with food odors suggest that maxillary BS (like antennal BS) may be involved in the perception of short-chain alcohols and fatty acids and that the activity of maxillary BS may be under the (inhibitory) control of nonbasiconic antennal sensilla (Venard and Stocker 1991). Recently, 'electropalpograms' have proven that the palps respond to ethylacetate, propionic acid,

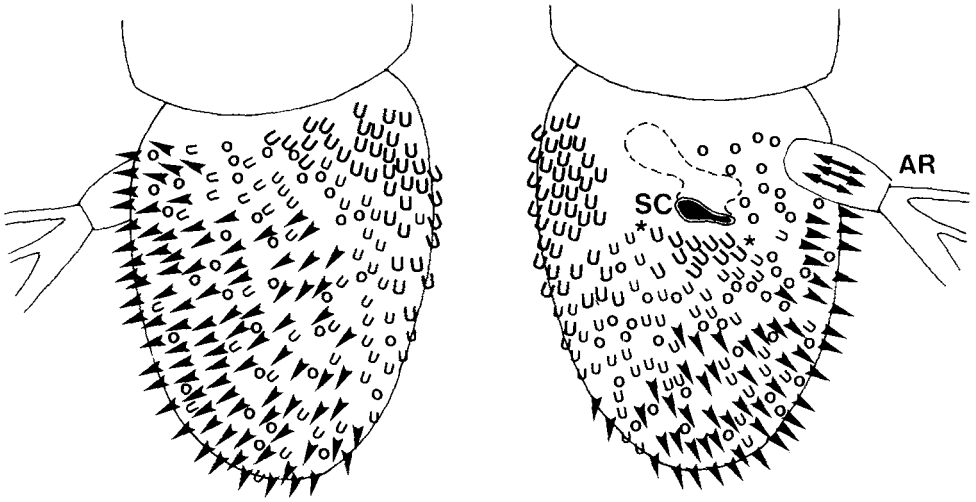


Fig. 5. Distribution of BS (**UUU**-uuu), TS (▼▼▼) and CS (ooo) on the anterior (*left*) and posterior (*right*) sides of the funiculus (cf. Fig. 2). Between the two *stars* is a beltlike cluster of BS distal to the sacculus. The aristal sense organ in the base of the arista (*AR*) is indicated by *double-headed arrows*. *SC* Sacculus

acetone, and butanol (Ayer and Carlson 1992). However, in contrast to antennae no measurable responses to water vapor and only weak responses to benzaldehyde were observed.

Peripheral pathways of antennal and maxillary afferents

The approximately 1200 afferents from the funiculus and the auditory Johnston's organ in the second antennal segment travel together in the antennal nerve (cf. Fig. 1). At their entrance into the brain they segregate. The latter extend straight into the antennal mechanosensory and motor center (AMMC; Power 1946; Strausfeld 1976; Rospars 1988; Homberg et al. 1989), whereas all the funiculus afferents (including those from the arista) turn dorsomedially and project into the antennal lobe, the primary olfactory association center (Strausfeld 1976; Stocker et al. 1983, 1990). The antennal lobe is also a target of afferents from the maxillary palps, most likely from BS (Singh and Nayak 1985; Stocker et al. 1990). These enter the brain via the labial nerve, travel through the suboesophageal ganglion (SOG), and arrive in the lobe from a ventroposterior direction (Fig. 1). The mechanosensory bristles on the palps appear to project into the SOG.

The glomerular organization of the antennal lobe

As in most insects, the antennal lobe is composed of anatomical subunits, the glomeruli, which are the sites of sensory terminals and of the dendritic arborizations of target interneurons (Power 1946; Rospars 1988; Homberg et al. 1989; Boeckh and Tolbert 1993). However, in contrast to most other insects the number of glomeruli is very low, i.e., about 35, many of which are directly identifiable (Fig. 6; Stocker et al. 1990; for a discussion of glomerulus numbers in different species, see Rospars 1988). The demarcation of glomeruli in *Drosophila* is less distinct than in moths, butterflies (Rospars 1983), or cockroaches (Chambille and Rospars 1981) perhaps because there is no elaborate glial sheath that separates neighboring glomeruli. Hence, it cannot be excluded that more than 35 glomeruli may exist. Identification of glomeruli was made according to three criteria, the background fluorescence in Lucifer yellow preparations, the projection pattern of individual afferent fibers, and the dendritic arborization of single relay interneurons (Stocker et al. 1990; see below). Applying the last two criteria, 14 'landmark' glomeruli are readily identifiable by their shape, size and location (Fig. 6: V, VA_1, VL_1, VL_2, VM_1, VM_4, VP_2, VP_3, DA_1, DL_1, DL_2, DM_1, DM_2, DP_1). The remaining, mostly smaller, glomeruli have been identified only in serial reconstructions of thin sections and by comparison with adjacent landmark glomeruli (Stocker et al. 1983, 1990; Pinto et al. 1988). The terminology used for individual glomeruli is based on their location within the lobe (see Fig. 6). The periphery of the lobe is occupied by 30 glomeruli, while 5 are located in its center. No obvious sexual dimorphism regarding the number, size or location of glomeruli has been observed (Stocker et al. 1990).

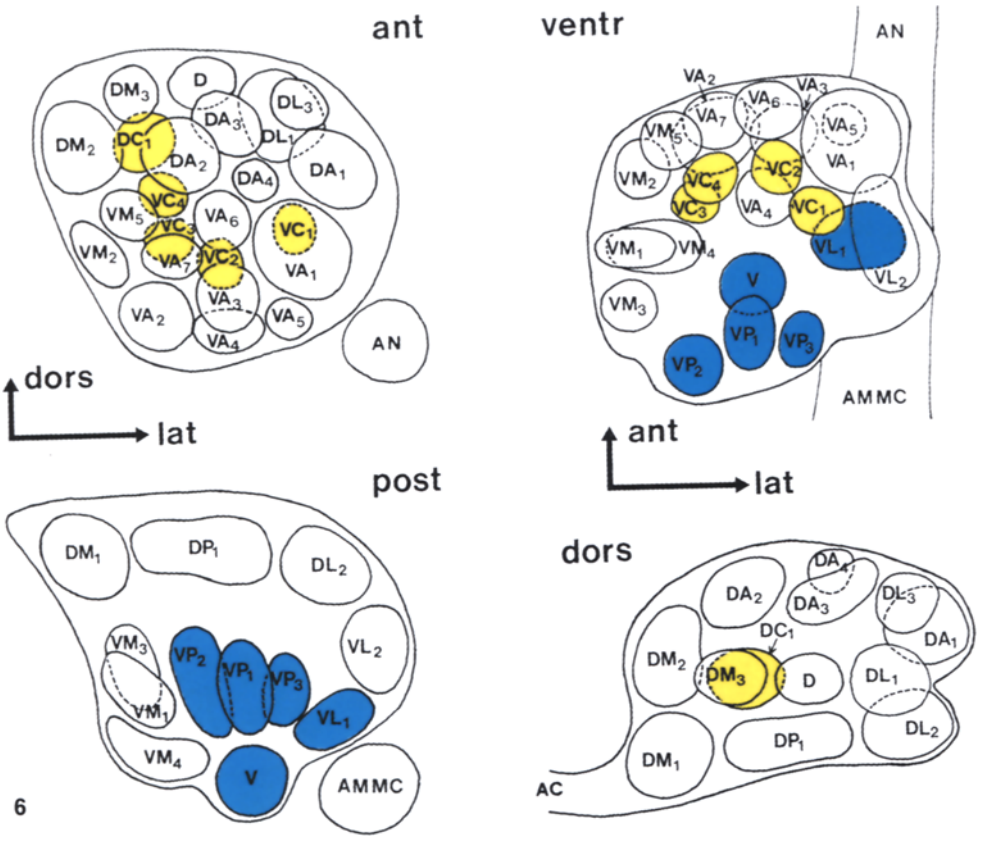
Rules of afferent projection patterns in the antennal lobe

Afferent projections in the antennal lobe have been analyzed mainly by orthograde filling of afferents with $CoCl_2$, horseradish peroxidase (HRP) or Lucifer yellow. The main features that emerged from these studies are the following (Figs. 7, 8; Stocker et al. 1983, 1990; Singh and Nayak 1985):

1. The antennal lobe is a target of all of the funicular, most of the maxillary and certain pharyngeal sensilla (Fig. 8).

2. Afferents from antennal BS, CS, and TS consist of unilaterally (Fig. 7A) and bilaterally projecting fibers (Fig. 7C), whereas fibers from the aristal sensillum project exclusively unilaterally (Fig. 7B). In contrast, maxillary afferents are always of the bilateral type (Fig. 7D).

3. Glomeruli V, VL_1, VP_1, VP_2, and VP_3 are exclusive targets of fibers from the ipsilateral antenna (Fig. 6), whereas the remaining 30 glomeruli receive bilateral



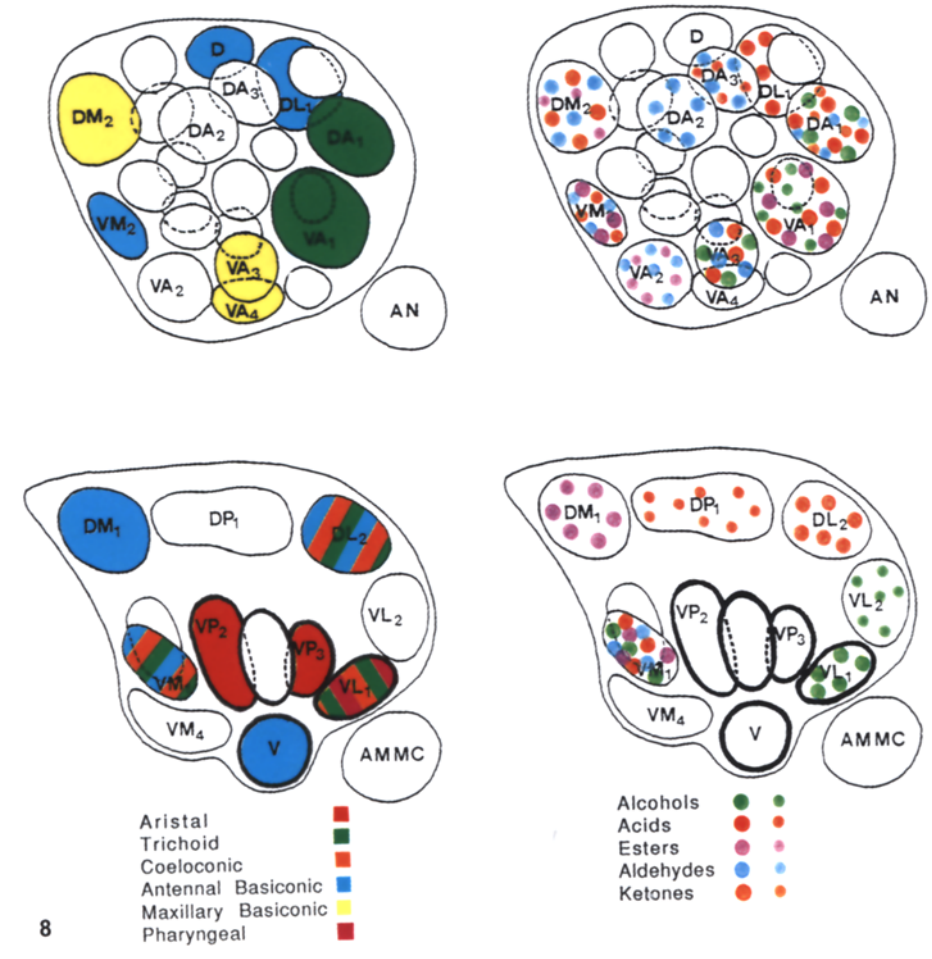


Fig. 6. Schematic representation of right antennal lobe in transverse (*left*) and horizontal view (*right*). The lobe has been divided in an anterior and posterior half or a ventral and dorsal half, respectively. The 35 glomeruli are termed according to their relative position. *A* Anterior; *D* dorsal; *L* lateral; *M* median; *P* posterior; *V* ventral. Glomeruli drawn in *blue* are exclusive targets of the ipsilateral antenna, whereas all the others are reached by afferents from both antennae or both maxillary palps. *Yellow* glomeruli reside in the center of the lobe. *AMMC* Antennal mechanosensory and motor center; *AN* antennal nerve (from Stocker et al. 1990, modified)

Fig. 8. Comparison of afferent projections (*left*; Stocker et al. 1983, 1990) and functional mapping data (*right*; Rodrigues 1988) in the antennal lobe. The right lobe is shown in transverse view. The five exclusively ipsilateral target glomeruli are heavily outlined. Dorsal is on top, lateral to the right. *Upper two diagrams* anterior half, *lower diagrams* posterior half. The density of symbols in the functional maps reflects the labeling intensity within the glomeruli after stimulation with particular odors

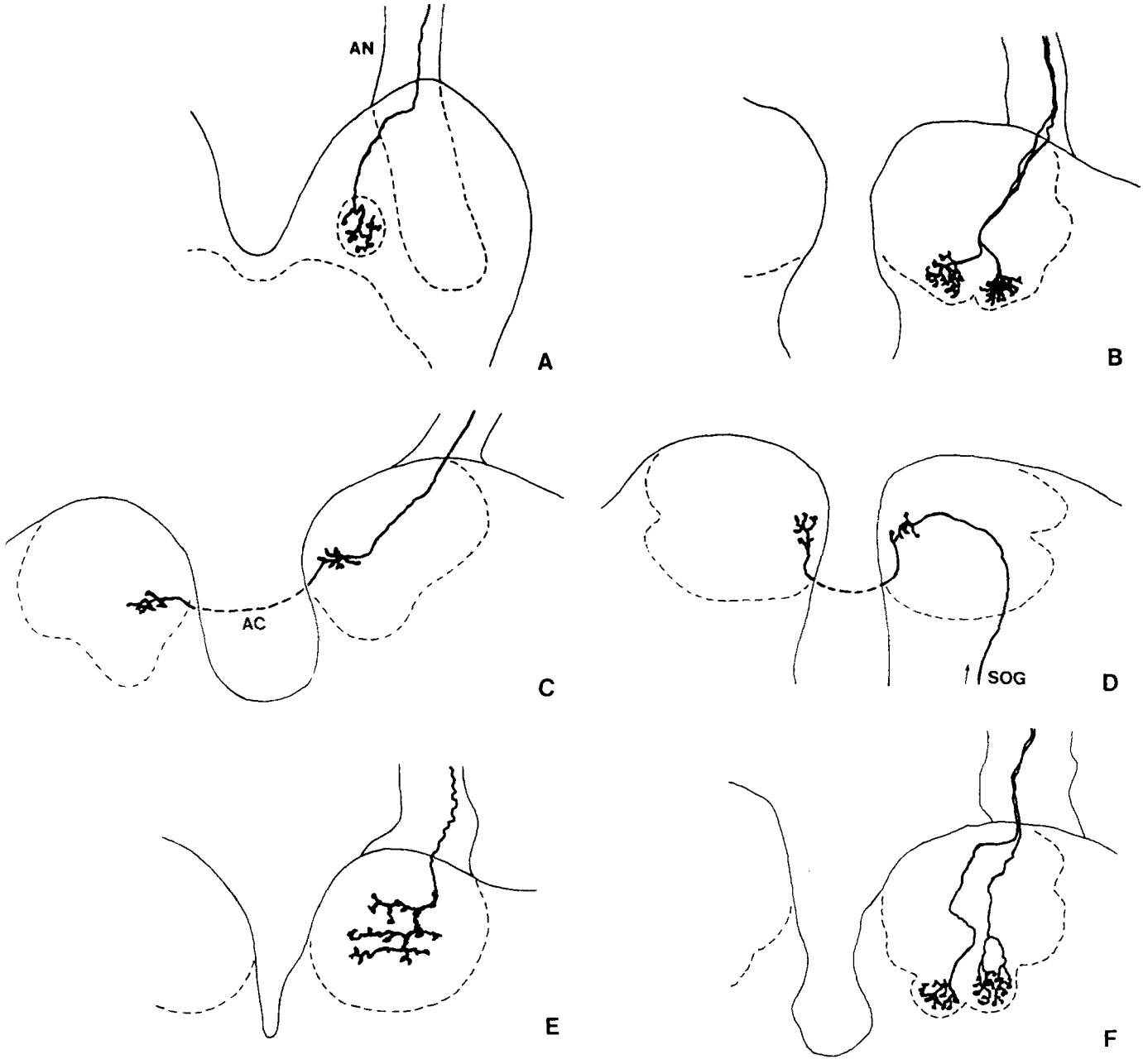


Fig. 7A–F. Camera lucida drawings of selected projections in the antennal lobe (horizontal views) showing the confined (glomerular) arborization of individual afferent terminals. **A** Unilateral projection from antennal BS in glomerulus V. **B** Unilateral projections from aristal sense organ in VP_2 (*left*) and VP_3 (*right*). **C** Bilateral projection of antennal BS in VM_1. **D** Bilateral projection of maxillary BS in VM_2 (**A–D** cf. Stocker et al. 1983, 1990). **E** Single afferent projection from the homoeotically transformed antenna of the *spineless-aristapedia* mutant spreads over several ventral glomeruli (cf. Stocker and Lawrence 1981) **F** Projections of duplicated arista in the *engrailed* mutant in VP_2 and VP_3 (cf. Lienhard and Stocker 1987). *AC* Antennal commissure; *AN* antennal nerve; *SOG* afferent arriving via SOG. × 375

fibers from both antennae or from both maxillary palps. The contralateral lobe is reached by collaterals passing through the antennal commissure (Fig. 7C, D). Deafferentation experiments suggest that roughly 200 of the 1200 funicular afferents are of the unilateral type, while the remaining 1000 are bilateral. Bilateral projections are a peculiarity of dipteran antennal systems (Boeckh et al. 1970).

4. Individual afferent fibers are invariably glomerulus-specific (Fig. 7A-D). In *Musca* at least four types of afferent arborizations in glomeruli have been described (Strausfeld 1976). If an antenna is replaced by an ectopic leg (e.g. in the homeotic mutant *spineless-aristapedia*), individual afferents no longer respect glomerular borders, irrespective of whether the central nervous system (CNS) is of mutant or wild-type genotype (Fig. 7E; Stocker and Lawrence 1981; R. Stocker, unpublished).

5. Irrespective of whether BS are located proximally or

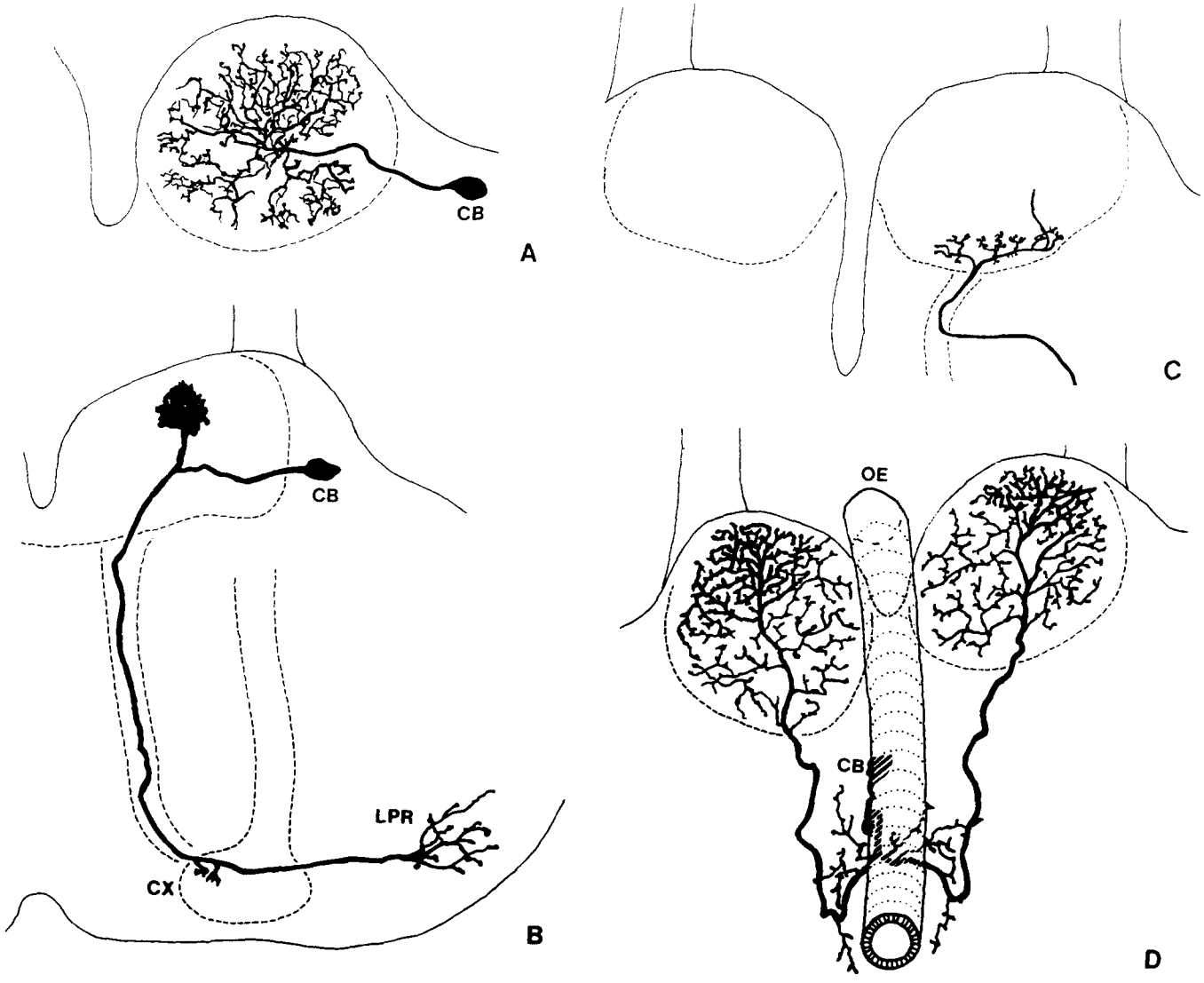


Fig. 9A–D. Camera lucida drawings of interneurons in the antennal lobe (horizontal views). **A** Local interneuron with lateral cell body (*CB*). **B** Uniglomerular relay interneuron connecting glomerulus VA_3 with the calyx (*CX*) and the lateral protocerebrum (*LPR*). **C** Multiglomerular relay interneuron arborizing in VP_2 and VP_3. **D** Giant symmetric interneuron with cell body in the midline of the SOG and extensive arborizations in both antennal lobes and in the posterior brain. *OE* Oesophagus. (**A** and **D** are from Stocker et al. 1990). × 375

distally within the pure BS region of the funiculus, their projection patterns are similar. This has led to the hypothesis that funicular projections are type-specific rather than topographic (Fig. 8; Stocker et al. 1983). However, since sensillar projections from the mixed region have not been studied, a role of topography cannot be excluded.

6. Two basic types of glomeruli can be distinguished, 'monosensillar' and 'polysensillar' glomeruli (Fig. 8). Well-documented examples of monosensillar glomeruli are VP_2 and VP_3, which appear to be reached by the six afferents from the aristal sensillum only (Fig. 7B). They are also the specific targets of duplicated aristal sensilla in the *engrailed* mutant (Fig. 7F; Lienhard and Stocker 1987). An attractive though untested idea is that either VP_2 or VP_3 may be the target of the three putative thermosensitive aristal fibers. Another putative monosensillar glomerulus is V, which is reached in orthograde fills exclusively by afferents from antennal BS and is missing in the *lz* mutant lacking these sensilla (Stocker and Gendre 1988). From other backfills there is evidence of additional candidate monosensillar glomeruli (Fig. 8).

7. Afferents from antennal and maxillary BS project into different glomeruli (Fig. 8). This may reflect their occurrence on different appendages or that antennal and maxillary BS are functionally distinct despite their identical morphology.

Interneurons of the antennal lobe

Like in other insects, two major types of interneurons may be distinguished by the Golgi technique in the antennal lobe of flies, local interneurons (LI) and relay or

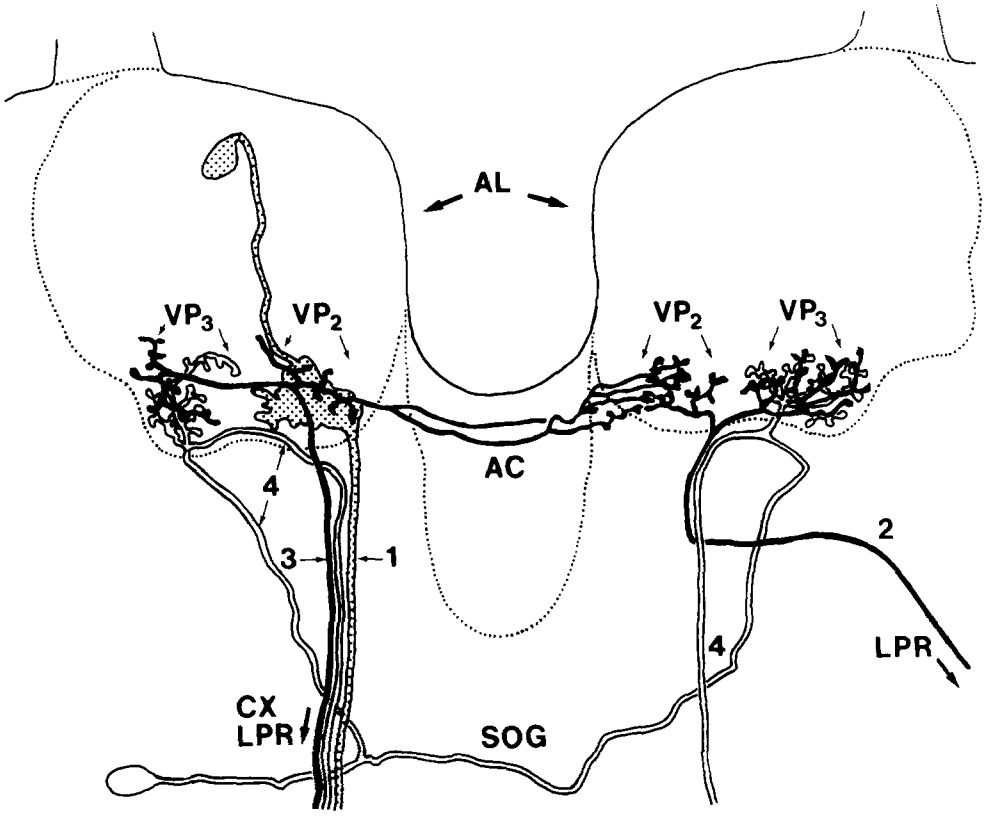


Fig. 10. Hypothetical specialized subsystem in the two aristal glomeruli VP_2 and VP_3 of the antennal lobe (*AL*). Four different types of RI that project into the calyx (*CX*) and lateral protocerebrum (*LPR*) (*1, 3, 4*) or only into the LPR (*2*) have been found to arborize exclusively within these glomeruli. Bilateral RI may send their collateral via the antennal commissure (*AC*) or via the SOG (according to Stocker et al. 1990). × 640

projection interneurons (RI; Strausfeld 1976; Stocker et al. 1990).

Local interneurons. LI branch in many (if not all) of the glomeruli of one antennal lobe and appear to connect glomeruli (Fig. 9A; Stocker et al. 1990). No data on the function or synaptic connectivity of LI are available in *Drosophila* although it has been postulated that they represent the substrate for concentration-invariant odor perception (Borst 1983). In cockroaches polysynaptic connections between the afferents and projection neurons have been shown to predominate with LI representing the intermediate elements (Malun 1991). In *Manduca* LI have been shown to be GABA-immunoreactive and to exert inhibitory control over RI, i.e., odor-induced suppression of LI may lead to spiking in normally quiescent RI (Boeckh and Tolbert 1993). Conversely, experimental activation of LI can lead to suppression of spikes in RI (Boeckh and Tolbert 1993; Christensen et al., submitted).

Relay interneurons. The most common type of RI in *Drosophila* or *Musca* (and in insects in general) is characterized by a dense arborization in a single glomerulus and a process that extends into the ipsilateral calyx of the mushroom bodies and into the lateral protocerebrum (LPR; Strausfeld 1976; Stocker et al. 1990) or exclusively into the LPR (Figs. 9B, 10). There is evidence that neurons of this type exist for most (and maybe all) of the known glomeruli. Golgi preparations suggest that one, or at most a few, of these RI occur per glomerulus. Recordings from similar neurons in locusts, cockroaches, and moths demonstrate that they represent output neurons of the lobe that respond to olfactory stimuli, or to a combination of olfactory, mechanical, and gustatory cues (Homberg et al. 1989; Kanzaki et al. 1989; Boeckh et al. 1990; Boeckh and Tolbert 1993).

Other RI spread their 'dendritic' arborization over more than one glomerulus (Figs. 9, 10; Stocker et al. 1990). Most of these elements project exclusively into the LPR. Multiglomerular RI have also been described in the moth (Kanzaki et al. 1989). A third type of RI with projections into higher brain centers are bilateral RI that connect the aristal glomeruli VP_2 or VP_3 of both antennal lobes with the calyx and LPR of either or both sides of the brain (Fig. 10; Stocker et al. 1990).

Among other types of antennal lobe interneurons, the giant bilateral neurons are the most conspicuous (Stocker et al. 1990). They are characterized by extensive mirror-symmetric arborizations in both antennal lobes, a pair of giant processes leading towards a second arborization region in the posterior brain, and a cell body located in the ventral midline of the SOG (Fig. 9D). The large diameter of their processes and the overlapping of the secondary branching region with arborizations of cervical giant interneurons known to be involved in the jump escape response (Tanouye and Wyman 1980) suggest that giant symmetric neurons may represent the neural substrate of the smell-driven jump reflex.

Molecular anatomy of the antennal lobe

The expression of transmitter-related genes in the brain has recently been reviewed in *Drosophila* (Restifo and

White 1990; Buchner 1991). Systemically administered [^{3}H]choline has been shown to become heavily accumulated in the antennal mechanosensory and motor center (AMMC), in the ipsilateral antennal lobe, in the tract carrying antennal RI into the calyx and in the SOG (Buchner and Rodrigues 1983). In the antennal lobe, a subset of glomeruli situated near the entrance of the afferents into the lobe was strongly labeled (Pinto et al. 1988). Applying a mab against *Drosophila* choline acetyltransferase or histochemically staining for acetylcholinesterase showed a much more widespread distribution in the brain (Buchner et al. 1986), a discrepancy discussed by Restifo and White (1990). Nevertheless, from these data and from physiological evidence in other insects (Restifo and White 1990), there is strong correlative evidence that antennal afferents in *Drosophila*, like in other insects, may be cholinergic.

Serotonin-immunoreactive processes were found in the antennal lobe and in the AMMC of blowflies (Nässel 1988). Those in the antennal lobe belong to two interneurons that appear to innervate all glomeruli in both lobes and possess a lateral cell body. They resemble but do not correspond to the giant symmetric neurons in *Drosophila* discussed above, which are not recognized by a polyclonal 5HT-antibody (K. Störtkuhl, unpublished). In *Drosophila* 5-HT-immunoreactive RI with arborizations in the antennal lobe and in the protocerebral bridge have been described (Hanesch et al. 1989).

In a search for biogenic amines that may act as classical neurotransmitters or as neuromodulators, no immunoreactivity against dopamine, tyrosine hydroxylase, and histamine was observed in the antennal lobe of *Calliphora*, *Phormia*, and *Drosophila* (Nässel and Elekes 1992; though dopamine was not tested in *Drosophila*). However, using a polyclonal antiserum against synthetic histamine, strong labeling occurred in antennal afferents of *Drosophila* projecting into the AMMC (Pollack and Hofbauer 1991). In *Calliphora* fibers in a subset of ventral and medial antennal glomeruli and many fibers in the antennal commissure (most likely antennal afferents) show immunoreactivity to a Met-8 enkephalin antiserum, suggesting that a subset of antennal afferents use Met-8-like peptidergic material as a neurotransmitter or modulator (Duve and Thorpe 1989).

Antibodies against GABA, a putative inhibitory transmitter in LI of moths (Hoskins et al. 1986; Waldrop et al. 1987; Boeckh and Tolbert 1993) and probably of other insects, have been applied in the antennal lobe of *Drosophila*, but so far with negative evidence (K.F. Störtkuhl, unpublished). Glutamate decarboxylase expression has been detected in the antennal lobes (Jackson et al. 1990) although its cellular localization remains unknown.

Monoclonal antibodies were found to bind to subsets of antennal glomeruli. One of them recognizes certain cells in the visual system, sensory neurons in the antenna, and 13 antennal glomeruli (Rane et al. 1987). The mab nc10 binds to antennal BS and GS and to a different set of about ten glomeruli, among which V, VM_2, DL_1, and DL_2 are well identifiable (Fig. 4D; Störtkuhl et al. 1994). All of them are important targets of antennal BS. The epitope recognized by these two mab is believed to reside on the sensory terminals.

Recently, the putative messenger molecule nitric oxide (NO) has been shown to be localized at high intensity in certain antennal lobe afferents and antennal glomeruli of the honey bee and of *Drosophila* (Müller 1993 and personal communication), suggesting a specific role of the NO-system in olfaction.

A model of the organization of the antennal lobe in Drosophila

The model of organization proposed here relies mainly on the anatomy of sensory projections and relay elements (Stocker et al. 1983, 1990), as well as on the activity mapping of glomeruli after olfactory stimulation (Rodrigues 1988). Because information on the synaptic connectivity and physiology of central neurons is largely lacking for *Drosophila*, other antennal model systems, in particular of moths and cockroaches, have been drawn upon (Homberg et al. 1989; Boeckh et al. 1990; Boeckh and Tolbert 1993). The five statements and hypotheses formulated below are based essentially on the glomerulus specificity of individual sensory fibers, the distinction between uni- and bilateral target glomeruli, and the association of particular glomeruli with particular types of sensillum (Fig. 8).

1. In terms of connectivity, the antennal lobe appears to be constructed of four types of glomeruli: monosensillar type-1 glomeruli, which are targets of specialized sensilla (VP_2 and VP_3: aristal sensillum); monosensillar type-2 glomeruli, receiving a wider spectrum of information from a single type of olfactory sensillum (V: antennal BS, VA_1: TS, DM_2: maxillary BS); polysensillar type-1 glomeruli, receiving olfactory input from different types of antennal sensilla (VM_1, DL_2: antennal BS, TS, CS), and polysensillar type-2 glomeruli, which are targets of antennal and nonantennal sensilla (Fig. 8). The last type of glomerulus may be multimodal (VL_1: TS, CS, pharyngeal sensilla). In Lepidoptera, a glomerulus resembling the monsensillar type 1 is represented by the target glomerulus of the CO_2-sensitive labial pit organ (Kent et al. 1986; Lee and Altner 1986) or the subunits of the macroglomerular complex, which receive very selective information about one pheromone component only (Hansson et al. 1992).

2. From these organizational criteria it may be speculated that individual glomeruli are functionally specialized, as has been proposed for other insect antennal systems (Rospars 1988; Homberg et al 1989). This idea is supported by data from [^{3}H]2-deoxyglucose mapping, which demonstrate that stimulation with different odors may excite specific subsets of glomeruli (Rodrigues 1988, Rodrigues and Pinto 1989). However, anatomical and functional data do not correspond in a simple way (Fig. 8). Some putative monosensillar glomeruli apparently respond to more than one chemical class of odorant (e.g., VA_1), whereas other glomeruli that are known polysensillar targets respond only to one type of chemical (e.g., VL_1). This suggests that certain olfactory neurons

may have broad perception spectra, as has been shown for antennal BS (Siddiqi 1983), and that, on the other hand, the same chemical may be perceived by different types of sensillum. A more straightforward correlation exists in the multisensillar glomerulus VM_1, which is activated by a wide range of substances, or in the monosensillar glomeruli DM_1 and DL_1, which appear to respond almost exclusively to acetates and organic acids, respectively (Rodrigues 1988). Another approach that may ultimately allow one to distinguish functional identities of glomeruli is chemical ablation of first larval instar neuroblasts. Flies treated in this way have severely reduced antennal lobes and show behavioral defects when stimulated with specific chemicals (DeBelle and Heisenberg 1993). However, it is not known whether the aberrant behavior is correlated with the loss of specific glomeruli.

3. Unilateral afferent projections may be important for supplying laterality information, which is the basis of behaviors like osmotropotaxis (Borst and Heisenberg 1982). Bilateral projections, on the other hand, may either increase the signal-to-noise ratio (by doubling the convergence ratio), or they may have an important laterality impact, depending on whether ipsi- and contralateral afferents establish identical connections or not. Functional mapping suggests that the latter may be the case (Rodrigues 1988; Rodrigues and Pinto 1989). Yet, it remains highly speculative why antennal BS, TS, and CS projections have both ipsi- and contralateral components, while maxillary projections are exclusively bilateral and aristal afferents are purely ipsilateral.

4. The antennal lobe is a center of topographic, multimodal, and numerical convergence (Fig. 8). It receives afferents from antennal, maxillary, and pharyngeal sensilla, it associates olfactory, gustatory, and probably thermal information, and it connects a considerable number of afferents with a smaller number of RI. Calculations suggest that each glomerulus receives no more than 10^2 sensory fibers, which is far less than the 10^3–10^4 afferents observed in cockroaches or moths (Boeckh et al. 1990). Similarly, the convergence ratio between antennal afferents and RI is only in the range of 30:1 (Stocker et al. 1990), in contrast to 500–1000:1 in ordinary glomeruli and 2000–4000:1 in the macroglomerular system of *Manduca* and *Periplaneta* (Boeckh and Ernst 1983; Boeckh et al. 1984; Homberg et al. 1988). While such an enormous convergence ratio certainly leads to successful detection of small amounts of odor (Boeckh and Ernst 1983), the low ratio in *Drosophila* argues for a relatively poor qualitative and quantitative resolution of odorants.

5. The presence of monosensillar type 1 (aristal) glomeruli and of several types of RI that arborize exclusively in them suggests that certain of the fibers leaving the lobe may form specific output channels that carry specialized information to higher brain centers (Fig. 10). Ignoring the significance of LI, the concept of functional specification of individual glomeruli could in these particular cases be pursued to the level of RI. As an intriguing parallel, certain RI of similar anatomy in moths and cockroaches have been shown to form a specific pathway for processing of pheromonal information (Homberg et al. 1989).

The adult gustatory system

In contrast to olfactory sensilla, contact chemoreceptors are located at many sites, i.e., the proboscis, the pharynx, the legs, wings, and female genitalia (Figs. 1, 11). Moreover, each of these sites is associated with its particular target area in the CNS. Gustatory sense organs have been extensively studied in flies, mainly because of their accessibility for recording (Dethier 1976; Siddiqi and Rodrigues 1980; Fujishiro et al. 1984; Arora et al. 1987; Ozaki 1988; Wieczorek and Wolff 1989; Morita 1992). In fact, the sugar receptor cells of blowflies have become one of the most thoroughly studied chemosensory cells. Moreover, the gustatory sense of flies has become famous for a simple reflex, the taste-driven proboscis extension response (Getting 1971; Dethier 1976).

Taste sensilla on the different appendages

Labellum. The labellum (labial palps) of *D. melanogaster* bears two major types of sensillum, taste bristles (TB) and taste pegs (TP; Fig. 11A, Table1). TB are single-walled, argyrophilic sensilla with a terminal pore and two to four chemosensory dendrites extending up to the tip (Fig. 12; Falk et al. 1976; Nayak and Singh 1983). TB possess two lumina, which are part of the electrical circuit involved in impulse initiation; one of them contains the dendrites, while the other is connected to the sensillum lymph space (Morita 1992). The different chemosensory neurons of individual sensilla are functionally distinct and respond to either sugar, salt, or water (Rodrigues and Siddiqi 1978; Fujishiro et al. 1984; Arora et al. 1987). In addition, a mechanosensory dendrite ends at the base of the shaft. No sexual dimorphism in the numbers of TB has been observed. Labellar TB are arranged in three rows (Fig. 11A) in a rather constant pattern that allows individual identification in most of them (though there is some variation in the numbers of neurons; Nayak and Singh 1983). *Phormia* and *Calliphora* have more TB, but they are structurally and functionally the same (Peters 1963; Wilczek 1967, Maes and Vedder 1978).

Between each two pseudotracheae of the labellum there is a row of four to seven TP (Fig. 11A; Table 1), each consisting of one or two BS-like sensilla, i.e., putative chemoreceptors, and an additional mechanoreceptor (Falk et al. 1976). These TP are missing or severely reduced in the mutant *echinus* (R. Stocker, unpublished). Solitary TP are associated also with the basis of each pseudotrachea.

Pharynx. Five groups of paired sensilla occur in the pharynx (Figs. 1, 11B–D, Table 1): the labral sense organ (LSO), the ventral and dorsal cibarial sense organs (VCSO and DCSO, respectively), a ventral and a dorsal row of 'fish-trap' bristles (VB and DB, respectively; Stocker and Schorderet 1981; Nayak and Singh 1983). The LSO consists of a heterogeneous group of nine identifiable sensilla in the pharynx directly behind the oral opening (Fig. 11B). Sensilla nos. 1–6 contain only one mechanosensory neuron, no. 7 contains eight chemosen-

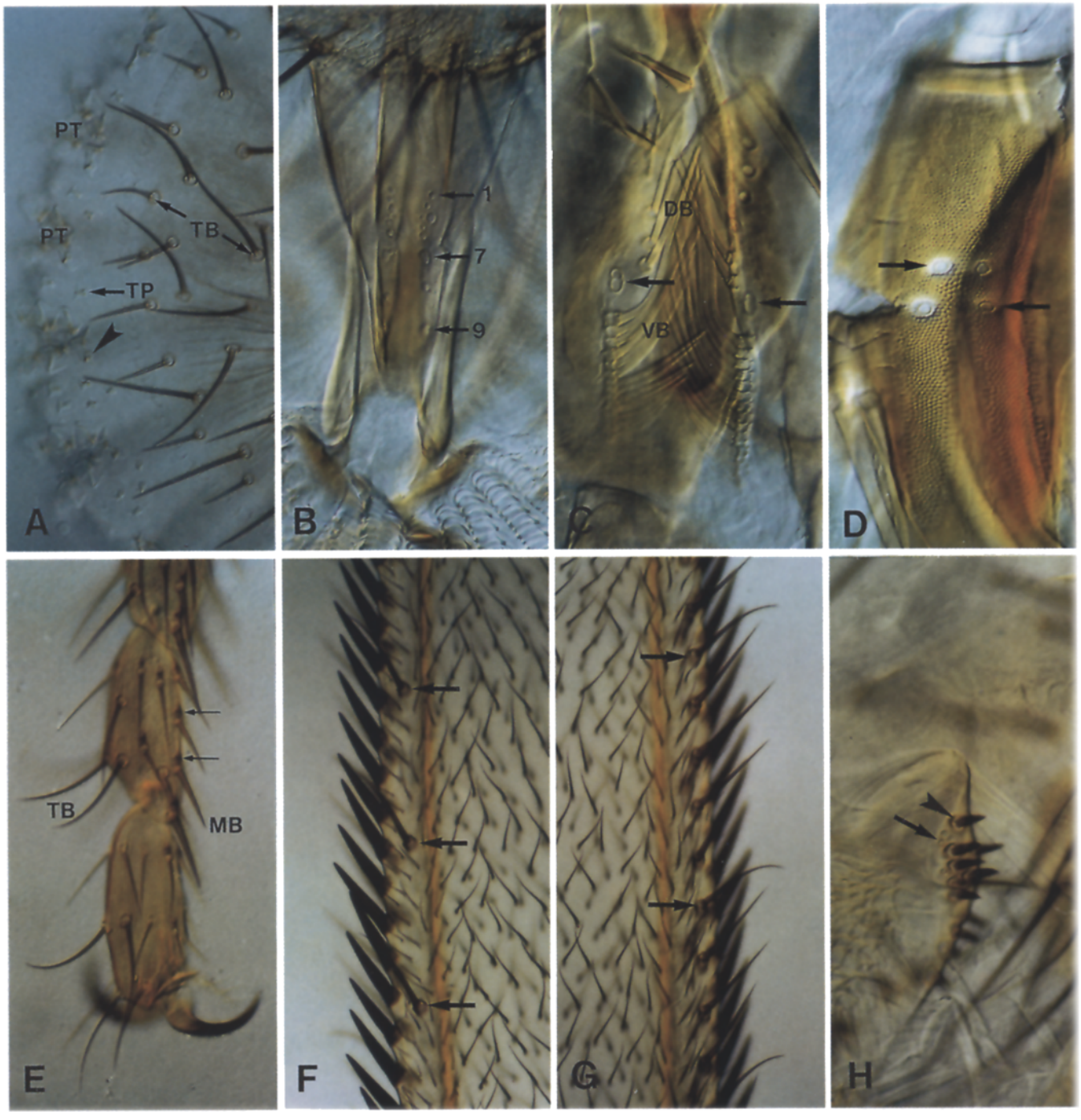


Fig. 11A–H. Gustatory sensilla of the adult. **A** The labellum is characterized by irregular rows of large and small taste bristles (*TB*), by irregular rows of taste pegs (*TP*) between each two pseudotracheae (*PT*) and by solitary TP at the base of each pseudotrachea (*arrowhead*). **B–D** Pharyngeal sensilla. **B** LSO nos. 1–9. **C** Dorsal and ventral fish-trap bristles (*DB/VB*) and VCSO (*arrows*). **D** DCSO (*arrows*). **E** Tip of male foreleg with straight mechanosensory bristles (*MB*), which are always accompanied by a bract (*small arrows*), and bent bractless *TB*. **F, G** Wing margin with isolated TB (*arrows*) in the dorsal 'triple row' (**F**) and TB (*arrows*) mixed with MB in the ventral triple row (**G**). **H** Left female vaginal plate with 'thorn bristles' (*arrowhead*) and 'trichoid hairs' (*arrow*). In **B–E** and **H** dorsal is on top. For comparison, see Fig. 1. × 310

sitive neurons (Fig. 12), and nos. 8 and 9 possess a mechano- and a chemosensitive neuron each (Nayak and Singh 1983). VCSO (Fig. 11C) and DCSO (Fig. 11D) each have two sensilla with two to four chemosensory neurons, while VB and DB are mononeuronal mechanosensory bristles (Nayak and Singh 1983).

Legs. The legs of flies are characterized by four types of sensillum, among which the mechanosensory bristles (associated with a cuticular bract near their socket) and the bractless taste bristles (TB) are the most numerous (*Phormia*: Grabowski and Dethier 1954; Hansen and Heumann 1971; Van der Wolk et al. 1984; Murphey et al.

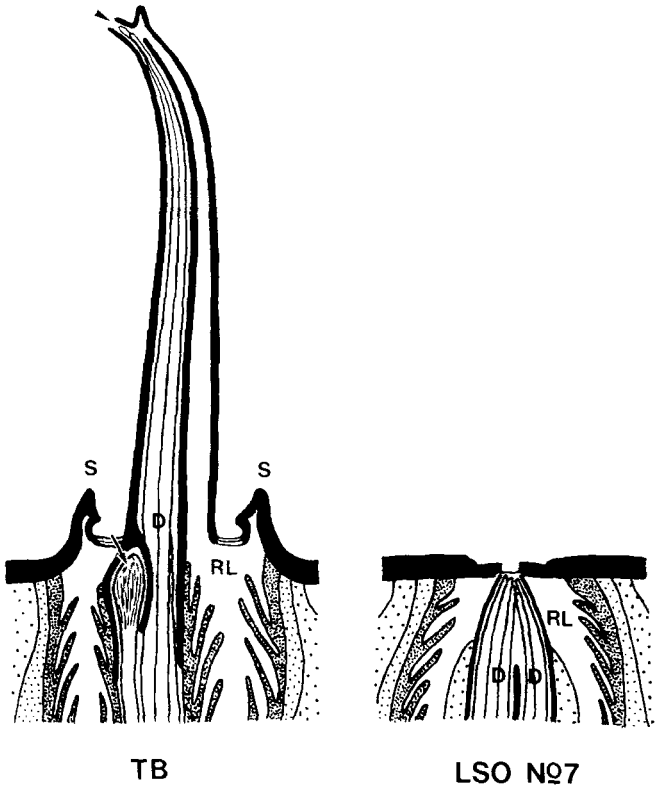


Fig. 12. The structure of gustatory sensilla as demonstrated by transmission EM. TB of the labellum, the legs and the wing margin are characterized by a terminal pore (*arrowhead*), two channels, three to four chemosensory dendrites (*D*) and one mechanosensory dendrite at the base of the shaft (*arrow*). The pharyngeal LSO no. 7 (and the DCSO/VCSO) is probably exclusively chemosensory. *RL* Outer receptor lymph space; *S* socket with flexible attachment of shaft (LSO according to Nayak and Singh 1983). Not drawn to scale

1989; *Drosophila*: Hannah-Alava 1958; Nayak and Singh 1983; Lienhard and Stocker 1987; Murphey et al. 1989; Shanbhag and Singh 1992b). The latter are structurally and functionally similar to the labellar TB, i.e., they are argyrophilic, possess a terminal pore and two lumina, and have usually four chemosensitive and a mechanosensitive neuron (Fig. 12, Table 1). Tarsal TB of flesh flies are responsive to sugar, salt, and water (Shiraishi and Tanabe 1974; Murphey et al. 1989) and it is well established that stimulation with sucrose elicits extension of the proboscis (Deak 1976; Stocker 1977). In *Drosophila* TB are found on tibiae and tarsi of all legs, with most on the first legs (Fig. 11E; Nayak and Singh 1983; Venard et al. 1989; Shanbhag and Singh 1992b). Strikingly, tarsi of male forelegs possess about one-third more TB than those of females (Nayak and Singh 1983; Possidente and Murphey 1989; Shanbhag and Singh 1992b), suggesting that male-specific tarsal TB may be involved in the detection of female cuticular pheromones (Robertson 1983; Venard et al. 1989).

Wings. Bristles sensitive to NaCl on the anterior wing margin have long been known in blowflies (Wolbarsht and Dethier 1958), and their importance in the control of feeding has been shown (Angioy et al. 1978). In *Drosophila* about 30 chemosensitive bristles are located at regular intervals on the dorsal surface of the costal vein and the radial 1 vein ('triple row'; Palka et al. 1979; Hartenstein and Posakony 1989; S. Hannaford, personal communication; Fig. 11F, Table 1). Moreover, on the ventral surface another 12 of them are interspersed with mechanosensory bristles (Fig. 11G). Like labellar TB these sensilla have a terminal pore, and they possess four apparently gustatory dendrites in their shaft and a mechanosensory dendrite that ends at the base of the bristle (Palka et al. 1979). Proboscis extension elicited by stimulation of these sensilla demonstrates that they are responsive to both sugar and salt as are labellar or tarsal TB (Hannaford and Palka 1992). It is conceivable that these sensilla are used for routine gustatory functions, for example in grooming behavior.

Genitalia. Bristlelike sensilla of varying shapes and sizes occur on most parts of male and female genitalia (Hodgkin and Bryant 1978; Laugé 1982; Taylor 1989). Based by their external aspect, most of them, and probably all in the male, have been interpreted to be mechanosensory. A chemosensory function has been surmised only for three pairs of microbristles (sensilla trichodea) on the female vaginal plate (Taylor 1989; Fig. 11H, Table 1). However, the short, blunt-tipped shape of a row of 10–15 thorn or spine bristles on the vaginal plate (Hodgkin and Bryant 1978) argues against their pure mechanosensory function. In support of this, the homologous vaginal plate of the sheep blowfly *Lucilia cuprina* bears ten 'trichoid' contact chemoreceptors and four multiporous, BS-like olfactory pegs (Merritt and Rice 1984; Merritt 1987). These chemosensors are believed to play a role during oviposition by sensing the immediate environment. The double-channeled trichoid sensilla of *Lucilia* contain several chemosensitive dendrites, some of which are responsive to salts (Rice 1977).

Projection patterns of taste sensilla

Labellar afferents. The approximately 195 afferents from the labellar TB and TP (Nayak and Singh 1983) reach the CNS via the labial nerve (together with those from the maxillary palps; see above) and terminate in the anterior, central neuropil of the SOG, the labellar gustatory association center of the head (Fig. 13; Stocker and Schorderet 1981). Two properties distinguish this center from the antennal lobe: the lack of obvious morphological boundaries and the absence of a glomerular organization comparable to that of the lobe. Although structural subdivisions exist in the SOG (Shanbhag and Singh 1992a), in contrast to the antennal lobe their borders are not recognized by the terminal arborizations of afferents.

Golgi studies have allowed the identification of seven classes of terminals of labellar fibers in distinct but partially overlapping regions (Nayak and Singh 1985). The seven classes have been interpreted as belonging to different types of chemosensory neurons in TB and TP (Nayak and Singh 1985). By applying the tracer HRP together with a specific stimulant to an identified TB, it has been

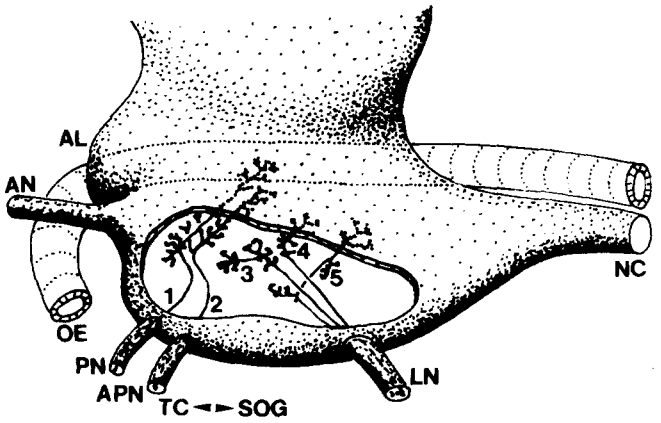


Fig. 13. Summary diagram of the gustatory centers in the tritocerebrum (*TC*) and in the SOG. The selected gustatory projections shown are from the DCSO (*1*), from the VCSO or LSO (*2*), from a labellar TB stimulated with an attractant (*3*), with a repellent (*4*) or with water (*5*). Projections 1 and 2 are according to Stocker and Schorderet (1981), 3–5 according to Shanbhag and Singh (1992a). All projections except fiber 3 have a contralateral branch (*stippled*). *AL* Antennal lobe; *AN* antennal nerve; *APN* accessory pharyngeal nerve; *LN* labial nerve; *NC* neck connective; *OE* oesophagus; *PN* pharyngeal nerve. Not drawn to scale

shown that each of the sensory neurons of the TB has a different projection pattern, corresponding to one of the seven classes (Shanbhag and Singh 1992a). Moreover, stimulating with the attractants 0.1 M sucrose or 0.1 M NaCl leads to staining of a different class of projection than with the repellent 0.1 M KCl or with HRP alone (Fig. 13). From this it was concluded that the neurons stimulated by these substances preferentially take up and transport the tracer (Shanbhag and Singh 1992a). Stimulus-specific labeling of sensory afferents has also been demonstrated in pheromone-sensitive TS of moths (Hansson et al. 1992).

In *Phormia regina* no anatomical segregation of axons by modality has been found (Yetman and Pollack 1986). However, it has been shown that putative mechanosensory axons from TB exhibit a topographic organization that may provide information for proboscis orientation during its extension (Edgecomb and Murdock 1992).

Pharyngeal afferents. The 6 axons from the DCSO travel in the pharyngeal nerve, whereas the approximately 18 afferents from the LSO, the 18–23 fibers from VB and DB and the 6 fibers from the VCSO reach the brain via the accessory pharyngeal nerve (Figs. 1, 13; Stocker and Schorderet 1981; Nayak and Singh 1983). $CoCl_2$ applied to intact pharyngeal sensilla appears to be taken up exclusively by the chemosensory neurons of LSO, VCSO, and DCSO. The afferents from these neurons terminate bilaterally with an overlapping pattern in the tritocerebral neuropil, which represents the pharyngeal gustatory association center (Fig. 13). It is located immediately anterior to the labellar center with which it slightly overlaps (Stocker and Schorderet 1981).

Candidate gustatory interneurons in the SOG and tritocerebrum. Several interneurons with arborizations in the labellar and pharyngeal taste centers have been described, both of the local and of the relay type (Nayak and Singh 1985). All of the putative gustatory RI observed have a process into the neck connective, and one of them is characterized by a secondary branching region in the calyces of the mushroom bodies. LI-like and RI-like interneurons that respond to labellar stimulation with sucrose, NaCl, and water have recently been described from *Sarcophaga* (Mitchell and Itagaki 1992).

Leg afferents. The sensory neurons of the legs project into their corresponding neuromere in the thoracico-abdominal ganglia (Fig. 1), whose anatomy has been studied in detail both in *Drosophila* (Power 1948; Singh 1992) and in *Phormia* (Merritt and Murphey 1992). Evidence from tracing studies suggests that the different types of leg afferents, i.e., from hair plate afferents, campaniform sensilla, chordotonal organs, and mechano- and chemosensitive bristles, show a great deal of segregation in the neuromere (Murphey et al. 1989; Possidente and Murphey 1989; Merritt and Murphey 1992). The terminals of TB appear to be located at the ventralmost level of the neuromere (Murphey et al. 1989). Recently it was shown in *Drosophila* that over-expression of the gene *poxn*, a putative transcriptional regulator that specifies the formation of poly-innervated (chemosensory) organs, leads to transformation of mechanosensory bristles into TB on the legs (Nottebohm et al. 1992). Intriguingly, the central projections of these sensilla are of the TB type as well (Nottebohm et al. 1992).

The projections of individual neurons within a particular TB segregate as well: a single fiber terminates at the anterior margin of the neuromere, whereas up to four fibers arborize more ventrally, at its periphery (Fig. 14; Lienhard and Stocker 1987; Possidente and Murphey 1989). In *Phormia*, the single axon is significantly thicker than the grouped axons and excitation from tactile stimulation travels at a higher conduction velocity than from gustatory stimulation (Murphey et al. 1989). This argues that the single large axon is mechanosensory, while the grouped smaller axons are gustatory (Murphey et al. 1989).

Backfilling of a tibial TB in midlegs of *Drosophila* with a mixture of HRP and a stimulant has been shown to stain two types of afferents, one dependent on and the other independent of the stimulus (Shanbhag and Singh 1992b). The independent afferents were suggested to be mechanosensory. Like in labellar TB, stimulus-dependent afferents were observed to arborize in different regions (cf. Shanbhag and Singh 1992a) depending on whether the attractants 0.1 M sucrose or 0.1 M NaCl or the repellents 0.1 M KCl or 0.5 M NaCl were used. In *Phormia*, however, little anatomical segregation between the different gustatory axons has been observed, suggesting that the modality segregation in gustation must be accomplished very locally or by higher order processing (Murphey et al. 1989).

In males of *Drosophila* some of the chemosensory axons of the forelegs cross the midline of the thoracico-abdominal ganglion and terminate in the contralateral leg neuromere, a pattern which may be part of the gustatory

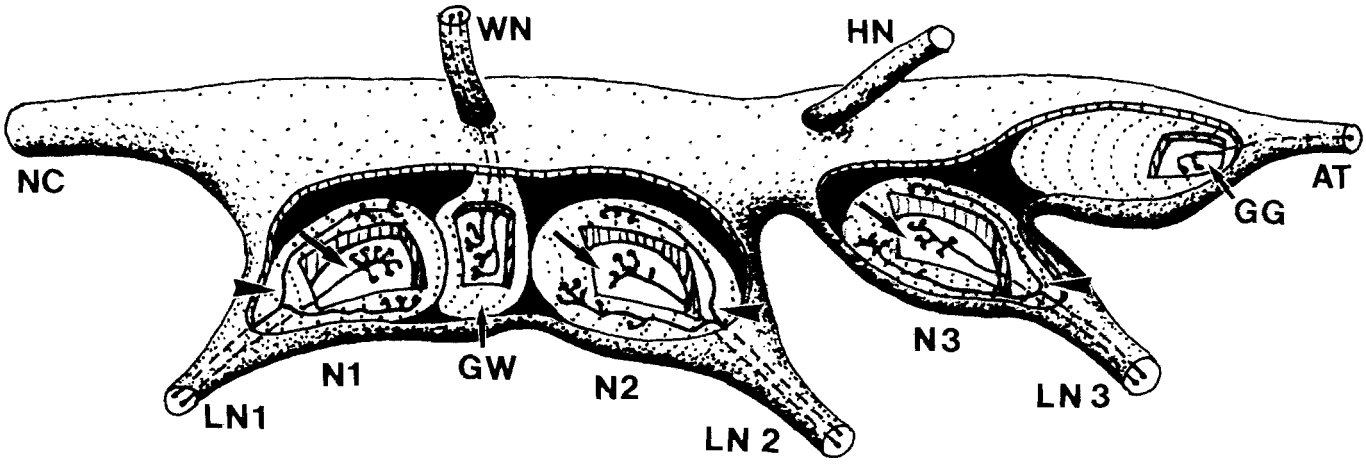


Fig. 14. Summary diagram of the gustatory centers in the thoracico-abdominal ganglion (Palka et al. 1979; Murphey et al. 1989; Taylor 1989; Merritt and Murphey 1992). In each leg neuromere (*N1-3*) the chemosensory (*arrows*) and mechanosensory (*arrowheads*) target areas of TB are shown. *AT* Abdominal nerve trunk; *GW* gustatory center of the wing ('ovoid'), *GG* gustatory center of the genitalia; *HN* haltere nerve; *LN1-3* nerves of the three legs; *NC* neck connective; *WN* wing nerve. Not drawn to scale

circuit underlying male courtship behavior (Possidente and Murphey 1989). Gynandromorphs demonstrate that the sex of the sensory neuron rather than the CNS controls this particular pattern (Possidente and Murphey 1989).

Some of the tarsal afferents from the three legs extend through the neck connective and terminate near or within the labellar taste center of the SOG (Lienhard and Stocker 1987). Similar fibers have been found in *Phormia* after dipping intact tarsi into a tracer solution (Edgecomb and Murdock 1992) or filling from individual TB (Murphey et al. 1989). Such fibers may represent the substrate of the leg-driven proboscis extension reflex.

Wing afferents. The afferents from wing chemosensilla are less well understood because so far no reliable fills of individual bristles are available. Yet, filling of the nerves on the wing blade at different locations allows one to define the projections to a certain extent. Selective filling from the marginal wing nerve leads to stained terminals exclusively in a neuropil, which is located ventrally between the first and second leg neuromeres and is called the accessory mesothoracic neuromere or 'ovoid' (Figs. 1, 14; Power 1948; Palka et al. 1979; Merritt and Murphey 1992; S. Hannaford, personal communication). It remains unclear, however, whether chemo- and mechanosensory afferents of the wing bristles segregate within this center.

Afferents from genitalia. Afferents of representative sensilla on the genitalia have been studied in the context of the sex-specific regulation of peripheral neurogenesis in *Drosophila* (Taylor 1989). Neurons of the thorn bristles of the vaginal plate (see above) have been shown to project ipsilaterally to the most posterior neuropil of the fused abdominal ganglion, a region which is also a target of mechanosensory genital bristles (Fig. 14).

The larval chemosensory system

Compared to the adult system the larval chemosensory system of *Drosophila* is very simple (Hertweck 1931; Kankel et al. 1980; Campos-Ortega and Hartenstein 1985). The three major chemosensory organs of fly larvae, the dorsal organ, the terminal organ and the ventral organ (Figs. 15, 16, Table 2), all situated on the cephalic lobe, have been studied in *Musca* by Bolwig (1946) and Chu-Wang and Axtell (1971, 1972a,b), and these observations have been essentially confirmed in *Drosophila* (Frederik and Denell 1982; Singh and Singh 1984). Since no recordings have been made from these sensilla, their putative functions can be inferred only by structural criteria. Yet, *Drosophila* larvae have been shown to respond to a variety of volatile substances including alcohols, acetates, aldehydes, ketones, and fatty acids (Monte et al. 1989; Ayyub et al. 1990; Cobb et al. 1992), as well as to gustatory stimuli like sugar, salt, and amino acids (Miyakawa 1982). The larval chemosensory system has been used for screens of chemosensory-specific P-element insertions, and a number of lines with specific expression in these sensilla have been isolated (Riesgo-Escovar et al. 1992; Pinto et al. 1992).

The dorsal (antennal) organ (DO). Due to their close proximity, the dorsal and terminal organs are known together as the antenno-maxillary complex. The DO (Fig. 16, Table 2) consists of seven different sensilla, the prominent 'dome' and six other receptors encircling the dome (Chu and Axtell 1971; Frederik and Denell 1982; Singh and Singh 1984). In the dome, 21 dendrites divide profusely and send their arborizations towards a common cuticular dome, which is perforated by numerous pore channels, properties that suggest an olfactory function for this sensillum. In fact the dome sensillum is usually presumed as the only site of olfaction in the larva. The six peripheral sensilla ('lateral pore receptor', 'contact chemoreceptor', 'unclassified receptor') have terminal pores, which

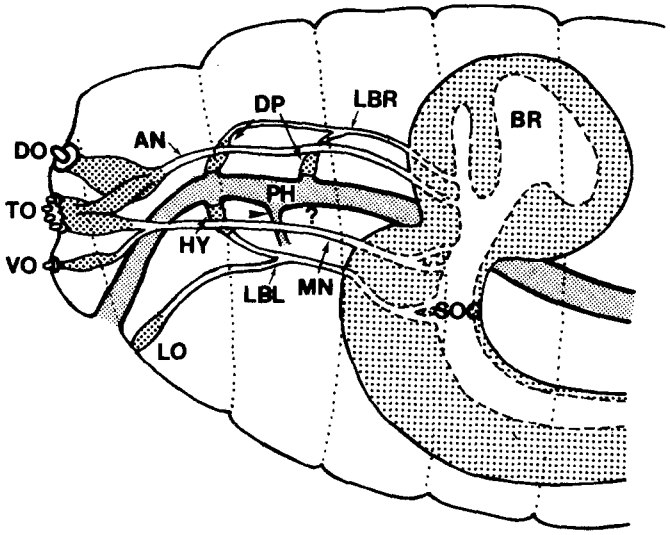


Fig. 15. Schematic representation of the known chemosensilla in the larva of *D. melanogaster*, sagittal view [after Campos-Ortega and Hartenstein (1985) and Schmidt-Ott et al. (1993), modified]. A gustatory function of dorsal pharyngeal sensilla (*DP*) is uncertain. The possible site of posteroventral pharyngeal sensilla is marked by ?. *AN* Larval antennal nerve; *BR* supra-oesophageal ganglion (brain); *DO* dorsal organ; *HY* anteroventral pharyngeal sensillum (hypophysis); *LBL* labial nerve; *LBR* labral nerve; *LO* labial organ; *MN* maxillary nerve; *PH* pharynx with salivary duct (*arrowhead*); *TO* terminal organ; *VO* ventral organ

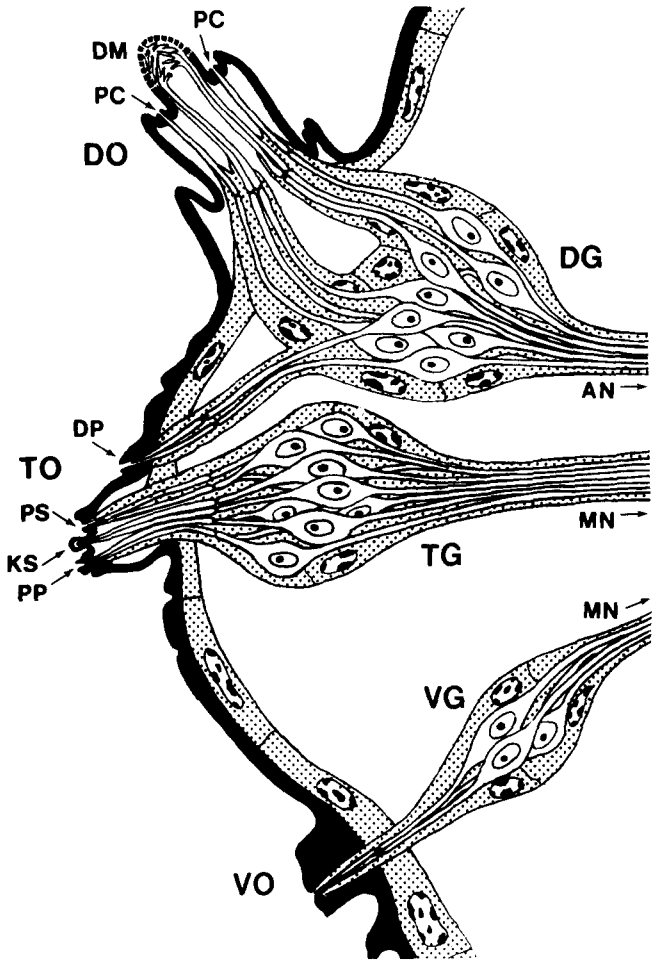


Fig. 16. The structure of the three major larval chemosensilla *DO*, *TO* and *VO* as demonstrated by transmission EM [according to Chu-Wang and Axtell (1972b) and Singh and Singh (1984), modified]. *AN* Larval antennal nerve; *DG* dorsal ganglion; *DM* dome; *DO* dorsal organ; *DP* dorsolateral papilla; *KS* knob sensillum; *MN* maxillary nerve; *PC* peripheral contact chemoreceptors; *PP* papilla; *PS* pit sensillum; *TG* terminal ganglion; *TO* terminal organ; *VG* ventral ganglion; *VO* ventral organ. Not drawn to scale

expose their one or two dendrites to the exterior, and are therefore interpreted as taste receptors (Fig. 16, Table 2; Chu and Axtell 1971). Some of the dendrites possess a tubular body, which suggests a combined taste and mechanoreceptive function. All perikarya of the 35–40 neurons and of the sheath cells are collected in a common 'dorsal ganglion' (Fig. 16).

The terminal (maxillary) organ (TO). The TO (Fig. 16, Table 2) is a complex of at least six different types of sensilla. They are arranged in two well-separated groups in *Musca*, the distal group and the dorsolateral group (Chu-Wang and Axtell 1972a), which lie within the same investing cuticular envelope in *Drosophila* (Frederik and Denell 1982). However, in both species the two groups appear to develop from different body segments and remain well separated below the cuticle (Frederik and Denell 1982; Singh and Singh 1984). Moreover, neurons of the dorsolateral group have their cell body in the ganglion of the dorsal organ, whereas the about 35 neuronal perikarya of the distal group are assembled in a 'terminal ganglion' (Fig. 16). In the distal group at the tip of the cephalic lobe, there are three 'papilla', five 'pit sensilla', two 'knob sensilla' and a 'spot sensillum' (Chu-Wang and Axtell 1972a; Singh and Singh 1984). The dorsolateral group consists of two papilla and a spot sensillum (Fig. 16, Table 2). Papilla, pit sensilla, and spot sensilla have each a terminal pore, and may therefore be contact chemoreceptors. The number of neurons varies from one to five. As in the DO, some neurons are assumed to serve a dual chemo- and mechanosensory function.

The ventral organ (VO). The VO anterior to the mouth opening (Fig. 16, Table 2) is a simple lobe consisting in *Drosophila* of five small pores (Singh and Singh 1984). Four of the pores are associated with a single neuron, and the fourth with four neurons. On fine structural criteria in *Musca* only the latter is thought to be a chemoreceptor (Chu-Wang and Axtell 1972b). All neurons are assembled in a 'ventral ganglion' whose nerve joins the axons from the terminal ganglion (Fig. 16).

Other external putative chemoreceptors. Additional candidate chemosensilla may be included in the 'labial organ' ventral to the mouth opening (Fig. 15), in the 'dorsal pits', and the 'knob in pit' sensillum on the cephalic segment (not shown in Fig. 15), in several types of sensory hairs on the thoracic segments, and on abdominal segments 1–7, as well as in sensory cones on the 8th and 9th abdominal segments (Kankel et al. 1980; Singh and Singh 1984). However, in none of these sensilla is the fine structure sufficiently known to allow any functional inference.

Table 2. Chemosensilla in the three major external sensory organs of larval flies (*D. melanogaster* and *Musca domestica*). mech. or M, mechanosensory; w. TB, dendrite with tubular body

	Shape	Type of sensillum[a]	Length of shaft (*Drosophila*)	Dendritic profiles in shaft	Neuron number	No. of sensilla per side	Function	References[b]
Dorsal organ								
'Dome'	dome	sw-mp	≤10 μm	multiple	21 (7×3)	1	olfactory?	1,2
'Lateral pore receptor'	hairless	ns-tp	–	2	2	1	gustatory?	1,2
'Contact chemoreceptor'	hairless	ns-tp	–	1–2	2	2	gustatory?	1,2
'Unclassified receptor'	hairless	ns-tp	–	1	1+1 M	2	gust.-mech.?	1,2
Terminal organ, distal group								
'Papilla'	papilla	sw-tp	≤1 μm	2 or 4	2 or 4+1 M	3	gust.-mech.?	1,3
'Pit sensillum' 1, 5	hairless	ns-tp	–	2 or 3	2 or 3+1 M	1	gust.-mech.?	1,3
'Pit sensillum' 2, 3, 4	hairless	ns-tp	–	2 or 5	2 or 5	1	gustatory?	1,3
'Spot sensillum'	hairless	ns-tp	–	1	1 (w. TB)	1	gust.-mech.?	1,3
Terminal organ, dorsolateral group								
'Papilla'	papilla	sw-tp	≤1 μm	2	2+1 M	1	gust.-mech.?	1,3
'Modified papilla'	papilla	sw-tp	≤1 μm	1	1 (w. TB)	1	gust.-mech.?	1,3
'Spot sensillum'	hairless	ns-tp	–	1	1 (w. TB)	1	gust.-mech.?	1,3
Ventral organ								
Sensillum V2	hairless	ns-tp	–	4 (*Musca*: 2)	4 (*Musca*: 2)	1	gustatory?	1,4

[a] The designations of sensilla are according to references 2–4: mp, multiporous, ns, no shaft; sw, single-walled; tp, terminal pore
[b] References: (1) Singh and Singh 1984, (2) Chu and Axtell 1971, (3) Chu-Wang and Axtell 1972a, (4) Chu-Wang and Axtell 1972b

Pharyngeal sensilla. Ten pairs of pharyngeal sensilla arranged in three groups have been identified (Singh and Singh 1984). In an anteroventral group, also called the hypophysis (Fig. 15; Hertweck 1931; Campos-Ortega and Hartenstein 1985) there is a single-pore compound sensillum with nine dendrites – a putative contact chemoreceptor. Posteroventrally, there exists another compound sensillum with six dendrites. Finally, six sensilla of unknown function are located in the dorsal wall of the pharynx.

Larval chemosensory afferents. The afferents from the DO and from the dorsolateral group of the TO are carried to the brain by the larval antennal nerve; the remaining fibers of the TO and all of the VO travel in the maxillary nerve (Fig. 15; Kankel et al. 1980; Campos-Ortega and Hartenstein 1985). Sensory fibers of the labial organ and the hypophysis reach the CNS via the labial nerve, and those of dorsal pharyngeal sensilla, via the labral nerve (Campos-Ortega and Hartenstein 1985). The adult antennal lobe develops from a larval precursor, a pair of small lobe-like structures at a location comparable to the adult lobe, which may represent the most important larval chemosensory center (Tissot 1992).

Conclusions

The adult olfactory system

The fundamental question addressed in this review is how the organization of the system relates to its function. What role do the different levels of the antennal system have in odor reception and discrimination? More precisely, what is the functional meaning of splitting the receptor level into different types of sensilla, each consisting of different neurons? Furthermore, what is the significance of individual glomeruli and what can we learn from comparing the inputs and outputs of the antennal lobe?

Although specific types of insect sensilla are not necessarily related to specific functions, a correlation between the structural and functional properties of insect sensilla has in fact been established (Altner et al. 1983a). Certain fine structural properties clearly act as filters that allow access of particular modalities but act as barriers to others. This is certainly the case for wall pores that serve as channels for odor molecules, for terminal pores that provide a pathway for diffusion of dissolved substances, or for structural components that allow mechanosensory transduction. BS, TS, and CS all possess wall pores, and may therefore all have an olfactory function. In support of this, the elimination of BS in the *lz* mutant shows that the molecules that stimulate BS (Siddiqi 1983, 1987) may be perceived by other antennal sensilla (Venard and Stocker 1991). Yet, quantitative differences in olfactory-driven behaviors suggest that particular sensilla are more sensitive for certain molecules than others (Venard and Stocker 1991). In moths this is well demonstrated by the fact that pheromones are perceived in TS whereas food odors are perceived by BS (Homberg et al. 1989).

Single unit recordings suggest that individual neurons in BS can respond to very different classes of molecules (Siddiqi 1983, 1987). However it is possible – though not proven experimentally – that the response spectra of dif-

ferent neurons in individual olfactory sensilla differ, like in taste bristles (Rodrigues and Siddiqi 1978; Fujishiro et al. 1984; Arora et al. 1987). Antennal and maxillary backfills show that projections of BS, TS, and CS and of the aristal sensillum consist each of several components that segregate in the antennal lobe (Stocker et al. 1983, 1990), implying that the different neurons of individual sensilla project into different glomeruli. This argument and the obvious association of particular types of sensilla with particular subsets of glomeruli strongly suggest that individual glomeruli receive qualitatively different information and support the hypothesis that glomeruli are functionally specialized. This is particularly clear for monosensillar glomeruli, and has been traced in the macroglomerular complex of moths even down to glomerular subcompartments (Hansson et al. 1992). However, the general principle may be valid for polysensillar glomeruli as well. Single unit recordings suggested also that BS with different response spectra map to different sites on the funiculus (Siddiqi 1983), but it is not known whether topography plays an important role in antennal projections. In summary, the sensory level has to be considered not as a pure receptive level but, due to the specific central projection patterns, as a first site of information processing as well.

What then is the associative function of glomeruli? The connectivity data extracted in *Drosophila* and in other insects suggest that glomeruli associated with very specialized sensilla, i.e., monosensillar type-1 glomeruli, may be specialized in their function as well. For example, the presence of a whole set of RI that arborize exclusively in the two aristal glomeruli suggests the presence of output channels that may carry rather specialized information. Thus, it is possible that in this type of glomerulus an association with other sensory inputs is more limited than in 'normal' glomeruli. Functional support of such an aristal subsystem is lacking, but there is evidence of a distinct pheromonal subsystem in moths and cockroaches (Homberg et al. 1989).

Regarding 'normal' glomeruli, the comparison of inputs and outputs of the lobe clearly demonstrates the principle of multiple convergence. Numerical convergence, i.e., the wiring of about 1200 funicular and 100 maxillary afferents onto probably less than 100 RI (Stocker et al. 1990) reflects one important function of glomeruli, the improvement of the signal-to-noise ratio. Qualitative and topographic convergence on the other hand, as shown by the projection of different types of sensilla from different sensory epithelia into the same target glomeruli, demonstrates that each receives a broad spectrum of sensory information, despite a certain preselection as mentioned above. A broad spectrum is suggested also just because many more biologically relevant molecules exist than glomeruli. The small number of output neurons strongly argues that a very selective extraction of relevant information must have occurred in the lobe. Glomeruli therefore may act by 'tailoring' the incoming information in diverse ways, certainly with the aid of local interneurons (see Homberg et al. 1989; Boeckh et al. 1990). Such associative processes include the generation of specific excitatory, inhibitory and temporal patterns, and the signals that are passed on by RI in an across-fiber pattern are in fact very different than the sensory inputs (Homberg et al. 1989; Boeckh et al. 1990).

The major targets of the outputs of the antennal lobe are the calyx of the mushroom bodies and the lateral protocerebrum (LPR). Behavioral testing of structural brain mutants in *Drosophila* with reduced mushroom bodies have suggested that the LPR is involved in olfactory discrimination, whereas the calyx may be the site of olfactory memory formation (Fischbach and Heisenberg 1984; Heisenberg et al. 1985; Heisenberg 1989; DeBelle and Heisenberg 1993; cf. also Davis and Dauwalder 1991; Han et al. 1992). Since certain RI project into both calyx and LPR while others exclusively terminate in the latter, these two functions might be separated to some extent already at the level of output neurons.

The adult gustatory system

Although the senses of smell and taste are functionally and phylogenetically closely related, the two subsystems are physically separated to a great extent in the adult nervous system. Another important issue is that apart from the BS on the maxillary palps (which may be a dipteran-specific transformation of taste sensilla; cf. Ayer and Carlson 1992), virtually all olfactory sensilla are concentrated on one appendage of the head, the antenna, whereas gustatory sensilla occur in many (and perhaps all) segments of the body posterior to the antennal segment. In close correlation to that, the CNS is equipped with only one center for smell, but with many taste centers. These properties may reflect the fact that the taste system is phylogenetically more primitive than the smell system. It suggests that the involvement of higher order centers in taste-driven behaviors may be less pronounced than in the olfactory sense.

Apart from these aspects, similar organizational principles apply to the olfactory and gustatory systems. In certain respects, the analysis is facilitated in the taste system because the different functions of individual neurons in single taste sensilla are known and their projections can be traced separately to a certain extent. On the other hand, the study of structure-function relationships at the central target level is more difficult, since glomeruluslike subcompartments are less evident than in the antennal lobe and because their borders seem to be penetrated regularly by afferent terminals. As in the antennal system, segregation of afferent projections is an important principle of organization. Modality-specific segregation of sensory projections in insects has been well demonstrated by Murphey and co-workers (Murphey et al. 1989; Merritt and Murphey 1992). In the taste system this is seen, for example, between pharyngeal and labellar afferents. Moreover, there is a modality-specific segregation of the targets of mixed chemo- and mechanosensory bristles, and there may be further segregation within each gustatory center between 'attractant' and 'repellent targets' (Shanbhag and Singh 1992a,b). Whether there is any topographic component in gustatory projections from a particular appendage remains unclear.

The larval chemosensory system

The larval chemosensory system of *Drosophila* differs from the adult system in its overall simplicity, in particular of the olfactory portion. This may be explained by the restricted need for long-range orientation of a crawling larva that usually lives directly on its food supply. Yet, it has to be cautioned that the simplicity may refer only to very general criteria, such as the number of sensilla or the apparent insignificance of the chemosensory centers. This seeming simplicity may not necessarily indicate poor functional capabilities, and it has in fact been shown that both the olfactory and gustatory performance of larvae is well-developed (Miyakawa 1982; Monte et al. 1989; Ayyub et al. 1990; Cobb et al. 1992). Moreover, unlike adult sensilla larval sense organs such as the DO or the TO consist of a complex array of different sensillar types. Still, it is probably safe to conclude that due to the smaller numbers of chemosensory neurons larvae are less sensitive than flies, and that in particular the smell system of the larva is very rudimentary compared to its adult counterpart.

Another striking peculiarity of the larval chemosensory system is its tight connection between the smell and the taste systems. This may reflect a phylogenetically more primitive state where the smell system has not yet become fully independent of the taste system.

Perspectives

The aim of this review was twofold: first, to provide a structural framework of the smell and taste systems of *D. melanogaster* for developmental and molecular studies of chemosensory gene function, and second, to stress the 'model' character of the chemosensory system of *Drosophila*. In favor of such a model is the relative simplicity of the system compared to other insects, e.g., regarding the number of glomeruli or the sensory equipment. Moreover, like the pheromone pathways of moths or cockroaches, specialized subsystems may exist in the fly olfactory system.

Limitations of *Drosophila* in the study of the chemosensory system have been mentioned several times in this review. It is obvious that the small size of this species seriously limits the use of electrophysiological and biochemical techniques. Consequently, the structure-function relationships in the fruit fly olfactory system largely rely on the olfactory systems of other insects, in particular *Manduca* and *Periplaneta* (cf. Boeckh and Tolbert 1993). However, a major advantage of choosing *Drosophila* compared to other species is the genetic argument (Siddiqi 1987, 1991; Carlson 1991). In contrast to other insects, the fruit fly offers a rich variety of molecular genetic approaches that allow one to dissect the organization and development of the chemosensory system in an unprecedented way. The use of monoclonal antibodies not only enables one to label specific subsets of the system and to characterize the corresponding antigens, but also to gain access to the underlying genes by screening expression libraries. Even more powerful, the lacZ-enhancer trap technology (O'Kane and Gehring 1987; Ghysen and O'Kane 1989) may reveal a wide variety of tissue- or cell-specifically labeled lines in the chemosensory system (cf. Pinto et al. 1992; Riesgo-Escovar et al. 1992) that will be extremely helpful for studying the development of the system. More importantly, it provides a means of identifying and possibly mutating chemosensory genes that are difficult to isolate through conventional mutational screens. A recent variant of the enhancer trap method, the GAL4-technique, offers yet other highly attractive possibilities of an experimental analysis of development, such as an ectopic expression of known genes or a specific ablation of GAL4-expressing cells by the expression of cell-autonomous toxin genes (Brand and Perrimon 1991; Technau 1992).

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