Projection patterns of different types of antennal sensilla in the antennal glomeruli of *Drosophila melanogaster**

R.F. Stocker[1,2], R.N. Singh[1], M. Schorderet[2], and O. Siddiqi[1]

[1] Molecular Biology Unit, Tata Institute of Fundamental Research, Bombay, India;
[2] Institute of Zoology, University of Fribourg, Pérolles, Fribourg, Switzerland

Summary. Cobalt fills from small, defined regions of the antenna in *D. melanogaster* show that the three types of sensilla on the third segment, the flagellum, and a fourth sensillum located in the arista, project into the glomeruli of the antennal lobe. We have identified 19 glomeruli in each lobe, according to their location, shape, and size. At least ten of these represent major projection areas of flagellar or aristal sensilla. The large majority of glomeruli is innervated from both antennae, but a small group of five receive exclusively ipsilateral input. A particular sensory fiber appears to terminate only in one specific glomerulus, either in the ipsilateral or in both lobes. Fills from flagellar regions bearing a single type of sensillum, yield a specific pattern of glomeruli containing stained terminals. Aristal projections remain strictly ipsilateral, whereas those from the other sensilla consist of an ipsilateral and a bilateral component. When filling from different points in an area bearing one type of sensillum, similar projections are produced, suggesting that projection patterns observed reflect predominantly the type of sensillum rather than its location on the flagellum. Accordingly, individual glomeruli might represent functional units, each receiving antennal input in a characteristic combination.

Key words: Antennal sensilla – Central projections – Antennal glomeruli – Orthograde cobalt diffusion – *Drosophila melanogaster*

In insects, olfactory projections are much less well understood than visual connections. This results, to a large extent, from the fact that in the olfactory system sensory neurons and their target interneurons are less regularly ar-

ranged and farther apart than in the visual system, which obscures their connections. The olfactory receptors in dipterans are located on the third antennal segment, the flagellum (Barrows 1907; Kaib 1974). The sensilla on this segment which might be composed of receptors of different modalities, project via the antennal nerve predominantly into the antennal lobe (Power 1946; Strausfeld 1976; Stocker and Lawrence 1981), a center identified as the primary olfactory association area in other insects (Yamada 1971; Boeckh et al. 1977; Waldow 1977; Matsumoto and Hildebrand 1981). The antennal lobe of flies is not overtly structured as the visual ganglia, but as in other insects anatomical subunits, to so-called glomeruli, have been recognized (Power 1946; Strausfeld 1976; Gundersen and Larsen 1978). However, no attempt has so far been made to identify the glomeruli, such as in hymenopterans (Masson and Strambi 1977) or cockroaches (Chambille et al. 1980; Chambille and Rospars 1981; Prillinger 1981).

Several groups have recently obtained interesting results on olfactory mechanisms in *D. melanogaster* by analyzing behavior, sensory physiology, and genetics (Kikuchi 1973; Fuyama 1976, 1978; Rodrigues and Siddiqi 1978; Rodrigues 1980; Venard and Pichon 1981; Borst and Heisenberg 1982). In order to provide a neuroanatomical basis for these studies we describe here the central projections of three different morphological types of sensilla on the antennal flagellum of *D. melanogaster* by the use of a refined technique of orthograde filling with cobalt chloride. In particular, we try to answer whether the projections of a particular sensillum are established according to its type or according to its location on the flagellum. *Drosophila* is a particularly favorable object for such a task since its antenna is characterized by several regions which contain only one type of sensillum (Mindek 1968). This is in contrast to many other insects such as *Oncopeltus* (Harbach and Larsen 1976), *Periplaneta* (Schaller 1978), *Manduca* (Sanes and Hildebrand 1976), *Apis* (von Frisch 1965), and even *Calliphora* (Kaib 1974), where two or more types of sensilla occur side by side on the antennal flagellum.

We present evidence to show that (i) 19 glomeruli in each antennal lobe may be individually identified, and that (ii) there exist specific patterns of connections between different types of sensilla and certain groups of glomeruli. These data, we hope, will provide the necessary anatomical basis for understanding olfactory integration, and serve as a background for examining sensory projections in olfactory mutants.

Materials and methods

Three- to five-day-old females of the strains Canton-S or Sevelen of *D. melanogaster* were used; no neuroanatomical differences between the two strains have been observed. Sensory projections of selected antennal regions were examined by orthograde diffusion of cobalt chloride. Modelling clay was used to fix the flies on a microscope slide and to immobilize their antennae. A fine-drawn glass microcapillary whose trip was broken off was attached with another piece of plasticine on the same slide and filled with a solution of $CoCl_2$. In most series 6% aqueous solutions were used, although a 2% solution in 70% ethanol worked equally well. With the broken tip a small region of the third antennal segment was slightly lesioned

under the dissecting microscope, and then the capillary was firmly pressed against the lesioned site. In other experiments no damage was done to the antenna, but the entire third segment was introduced into a capillary of appropriate tip diameter. When alcoholic solutions were used in such fills, the proximal part of the antenna was covered with petroleum jelly to prevent dispersion of the cobalt chloride over the whole antenna.

After 3 h of cobalt diffusion the flies were decapitated, and the heads were opened dorsally and ventrally to facilitate infiltration of fixing and embedding media. Precipitation (with ammonium sulfide), fixation (with Bouin-Duboscq fluid), silver intensification (Timm's method) and embedding (in Epon) followed the schedules described by Bacon and Altman (1977), Strausfeld and Hausen (1977) and Stocker and Lawrence (1981). A critical evaluation of the cobalt diffusion technique and its limitations has been given by Stocker and Lawrence (1981). Fifteen-μm serial sections were cut in horizontal and transverse directions with a rotary or sledge microtome with steel knives. Light microscopic examination was greatly facilitated by the use of a combination of polarizing filters inserted into the binocular microscope, giving a three-dimensional impression of the neuronal pathways within the section (K. Fischbach, personal communication).

Results

The surface of the third antennal segment, the flagellum, of *D. melanogaster* bears three basic types of sensilla, *s. trichodea*, *s. coeloconica*, and *s. basiconica*, which are arranged in a characteristic pattern (Mindek 1968) (Fig. 1). In certain areas only one type is present, whereas in others two or three types occur side by side. The maps of sensilla on the anterior and posterior sides of the flagellum are roughly mirror-symmetric except for a group of six to ten isolated *s. coeloconica* present on the posterior side facing the head capsule.
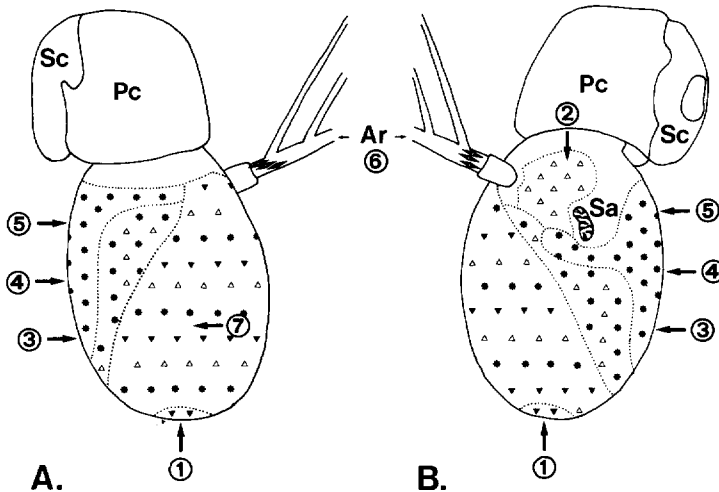

Fig. 1 A, B. Diagram of left antenna of *D. melanogaster* indicating approximate distribution of three types of sensilla (*s. trichodea* ▼; *s. coeloconica* ▵; *s. basiconica* *) on the flagellum, and location of a fourth type of sensillum (*rhombs*) in the arista (*Ar*). *Arrows* indicate sites lesioned with glass micropipettes before filling with cobalt chloride. Numbers refer to Fig. 15. **A** Anterior side of antenna in rest position. **B** Posterior side facing head capsule when antenna is in rest position. *Sa* sacculus, *Sc* scape, *Pc* pedicel
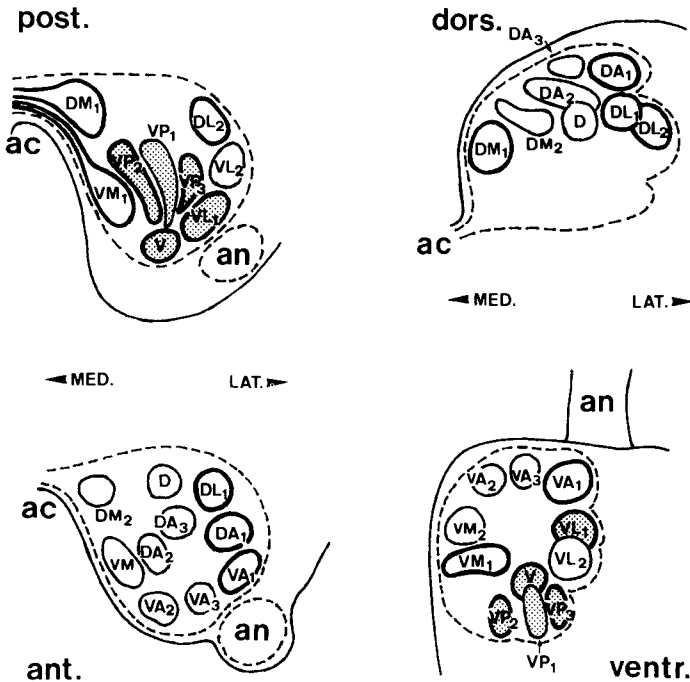
Fig. 2. Diagrams of right antennal lobes in *D. melanogaster* showing relative position, shape, and size of 19 glomeruli identified in cobalt fills performed on the antennal flagellum or the arista. The 10 glomeruli heavily outlined appear to represent major antennal projection areas. The 5 stippled glomeruli receive exclusively ipsilateral input; the remaining receive bilateral projections; *post., ant.* transverse view of posterior and anterior levels; *dors., ventr.* horizontal view of dorsal and ventral levels. The terminology roughly indicates relative positions of glomeruli within the lobe (*V* ventral; *D* dorsal; *A* anterior; *P* posterior; *L* lateral; *M* medial); *ac* antennal commissure, *an* antennal nerve, *lat.* lateral, *med.* medial

By careful examination of more than 400 cobalt preparations we have been able to identify 19 glomeruli in each antennal lobe according to their location, shape, and size (Fig. 2). Conventional methods such as trichromic staining, reduced silver or Golgi preparations, failed to delineate individual glomeruli unequivocally, although these methods yielded excellent results in other insects (Masson and Strambi 1977; Hildebrand et al. 1979; Chambille et al. 1980). The glomeruli described here are restricted to the periphery of the antennal lobe, a majority of them occupying the anterior surface. We have identified only those glomeruli which receive sensory projections from the flagellum; others not related to this antennal region might be present. The nomenclature designates approximately the location of individual glomeruli within the lobe (for details, see Fig. 2).

In order to analyze the connections between the antennal sensilla and their first order targets in the antennal lobes, we have concentrated first on sensory projections of regions occupied by one type of sensillum (Fig. 1). In the following sections the main projection patterns of these cobalt fills will be briefly described. Five of the glomeruli, situated ventrally and close

to the entrance of the antennal nerve, i.e., V, VP_1, VP_2, VP_3 and VL_1, receive exclusively ipsilateral input (Figs. 2, 5, 10, 13–15); the remaining are innervated bilaterally resulting in a precise mirror-symmetric pattern when filling is done from one antenna (Figs. 3, 7, 9, 11, 12, 15). Many preparations in which one or two axons are visualized demonstrate that an individual fiber produces terminal branches only in a particular glomerulus, occupying corresponding positions in both lobes (in five of the glomeruli, as mentioned earlier, only ipsilateral projections are present). Ipsi- and contralateral branches of bilateral projections bifurcate within or close to the ipsilateral glomerulus. The almost invariable occurrence of fibers extending via the antennal commissure into contralateral glomeruli (Fig. 15) shows that whenever an axon has taken up cobalt, the staining reaction appears along its entire length.

When filling is done from the tip of the flagellum, a region almost exclusively occupied by *s. trichodea,* sensory terminals appear mainly in the two glomeruli VA_1 and DA_1 situated in the anterolateral corner of the antennal lobe, and to a lesser extent in VL_1 (Figs. 3–6, 15, 16). Fibers that go into the contralateral DA_1 and VA_1 pass to the antennal commissure via the anterior edge of the lobe. The group of isolated *s. coeloconica* on the posterior side of the flagellum yields a very different projection pattern which is almost exclusively restricted to VL_1, VM_1 and DL_2 (Figs. 7–9, 15, 16). Fibers reach VM_1 via the ventromedian edge of the lobe, and DL_2 via its lateral border.

A large area of the flagellum bears only *s. basiconica* (Fig. 1). By filling from several points on a proximodistal axis within this region we wanted to ask whether the projection pattern associated with a certain type of sensillum also reflects its location on the flagellum. The three localized *basiconica* fills differ from the projections of *s. trichodea* or *s. coeloconica,* but only slightly between themselves (Figs. 10–12, 15, 15). The glomeruli invariably affected are V, VM_1 and DM_1, whereas the proportion of stained VM_2, VA_2, D and/or DL_1 varies among the three filling types. Fibers extend into DM_1, VM_1 and VA_2 via the anteromedian edge of the lobe, and into D and DL_1 via its lateral border. Despite the quantitative variations mentioned, the similarity in the overall pattern produced by distal, middle, and proximal fills suggests to us that the location of *s. basiconica* in the region that we have examined hardly affects the projection pattern.

The projections of the sensillum situated within the arista, the pinnate appendix of the flagellum (Fig. 1), has been reported elsewhere (Stocker and Lawrence 1981; Stocker, in preparation), but shall be mentioned here briefly for completeness. The six, presumably mechanosensory axons originating from this sensillum terminate exclusively in VP_2 and VP_3 of the ipsilateral lobe, glomeruli which are bypassed by the axons from other flagellar sensilla (Figs. 13–16).

Since intact sensilla on the mouthparts may take up cobalt solution under certain conditions (Stocker and Schorderet 1981), we tried to fill antennal projections in the same way. When aqueous or ethanolic cobalt solutions were applied to the intact flagellum, stained projections were obtained in
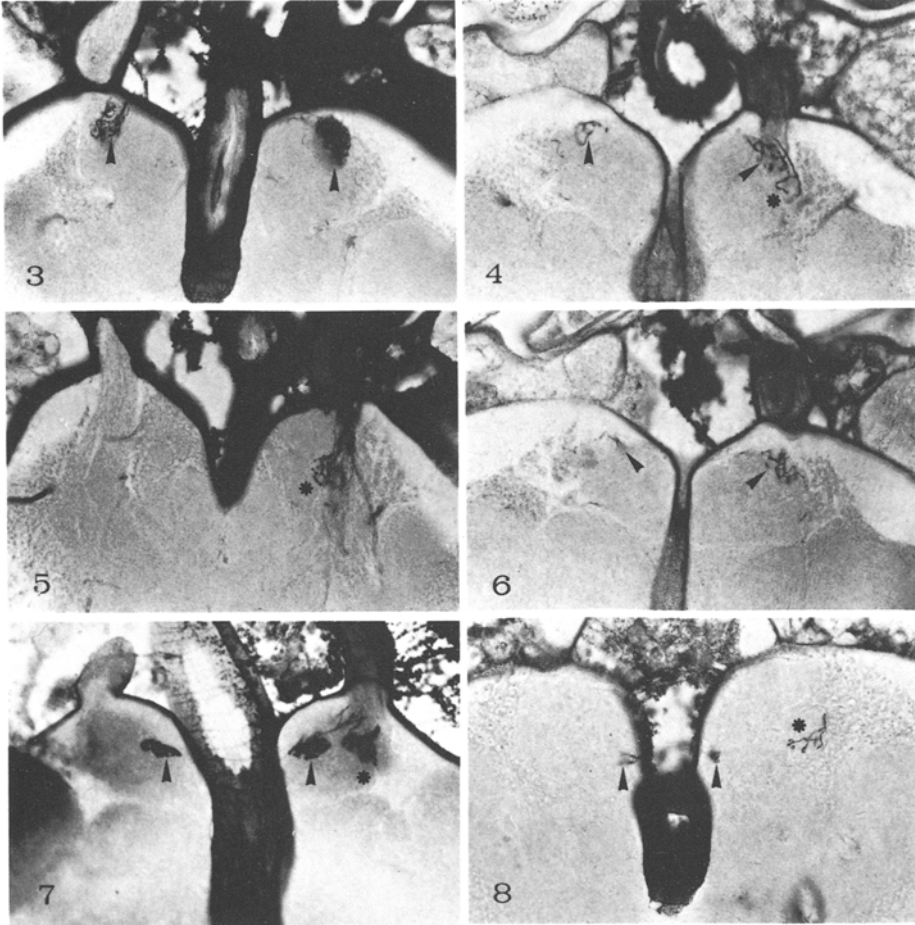
Figs. 3–14. Micrographs of 15-μm horizontal sections through antennal lobes after cobalt filling from flagellum or arista. Injured antenna on right side. Anterior on top. ×216

Figs. 3–6. Fills from tip, a region almost exclusively occupied by *s. trichodea*. **Fig. 3.** Stained terminals in both ipsi- and contralateral glomeruli VA_1 (*arrows*). **Fig. 4.** In addition to VA_1 (*arrows*), branching of single axon in ipsilateral VL_1 (*). **Fig. 5.** Axons projecting into ipsilateral VL_1(*). **Fig. 6.** In dorsal lobe region both DA are affected (*arrows*); on contralateral side most terminals are contained within an adjacent section

Figs. 7–9. Fills from posterior *s. coeloconica* region. **Figs. 7, 8.** Projections occupying both VM_1 (*arrows*) and ipsilateral VL_1 (*). **Fig. 9.** In dorsal region terminals are present in both DL_2 (*arrows*)

about one third of the conventional fills. The patterns visualized are most reminiscent of the *coeloconica* pattern, although in the aqueous series the DL_2 component is missing (Fig. 15). Specific filling of *s. coeloconica* by this method seems plausible because of the presence of a terminal pore or pores on their shaft (Aiyar and Singh, unpublished, Link and Stocker,
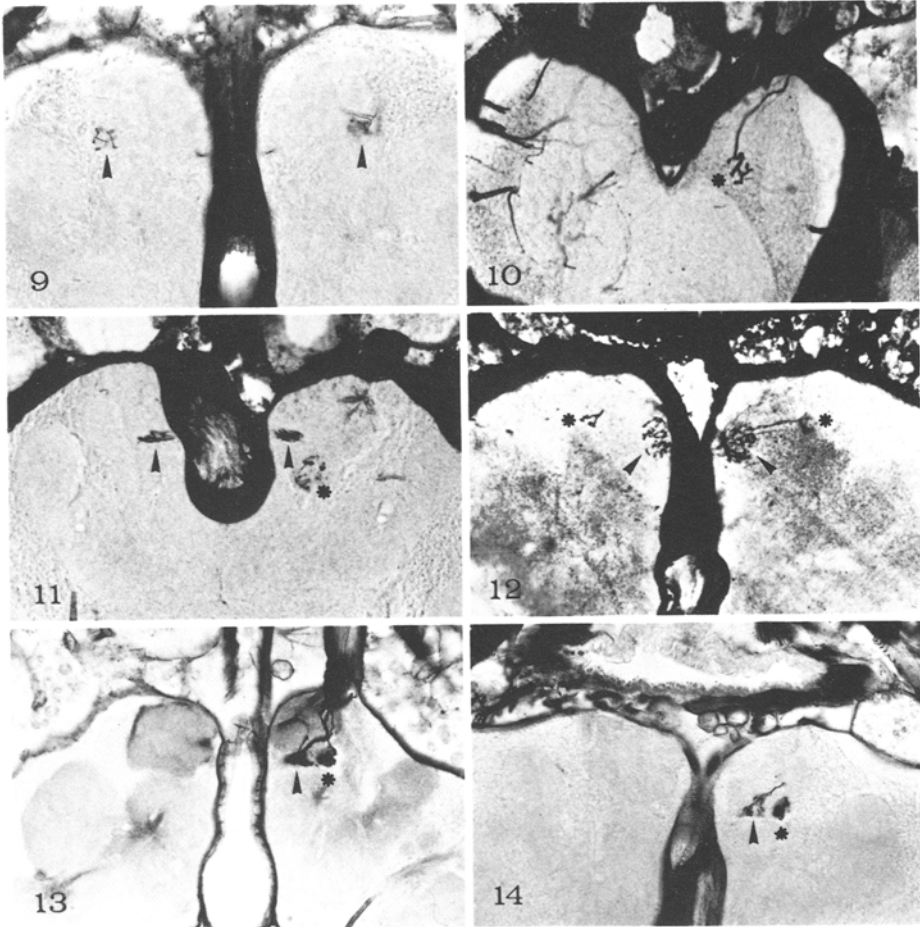
Figs. 10–12. Fills from middle part of *s. basiconica* region. **Fig. 10.** Single axon branching in ipsilateral V (*). **Fig. 11.** Terminal branches occupying V (*) and both VM_1 (*arrows*). **Fig. 12.** In dorsal lobe part, terminals in DM_1 (*arrows*) and DL_1 (**)

Figs. 13, 14. Fills from arista show terminals in ipsilateral VP_2 (*arrows*) and VP_3 (**) (for details, cf. Stocker and Lawrence 1981)

unpublished). If this interpretation is correct, these fills of the intact flagellum would further support our notion of type-specific rather than location-specific projection.

In a final series of experiments the region on the anterior side of the flagellum bearing all three types of sensilla was filled (Fig. 1). The pattern of glomeruli affected corresponds to a combination of the projections from *s. trichodea, s. coeloconica,* and *s. basiconica,* i.e., there are maxima in V, VL_1, VM_1, VA_1, DL_2, DM_1 and DA_1 (Fig. 15). This result is consistent with our interpretation of type-specific projections.
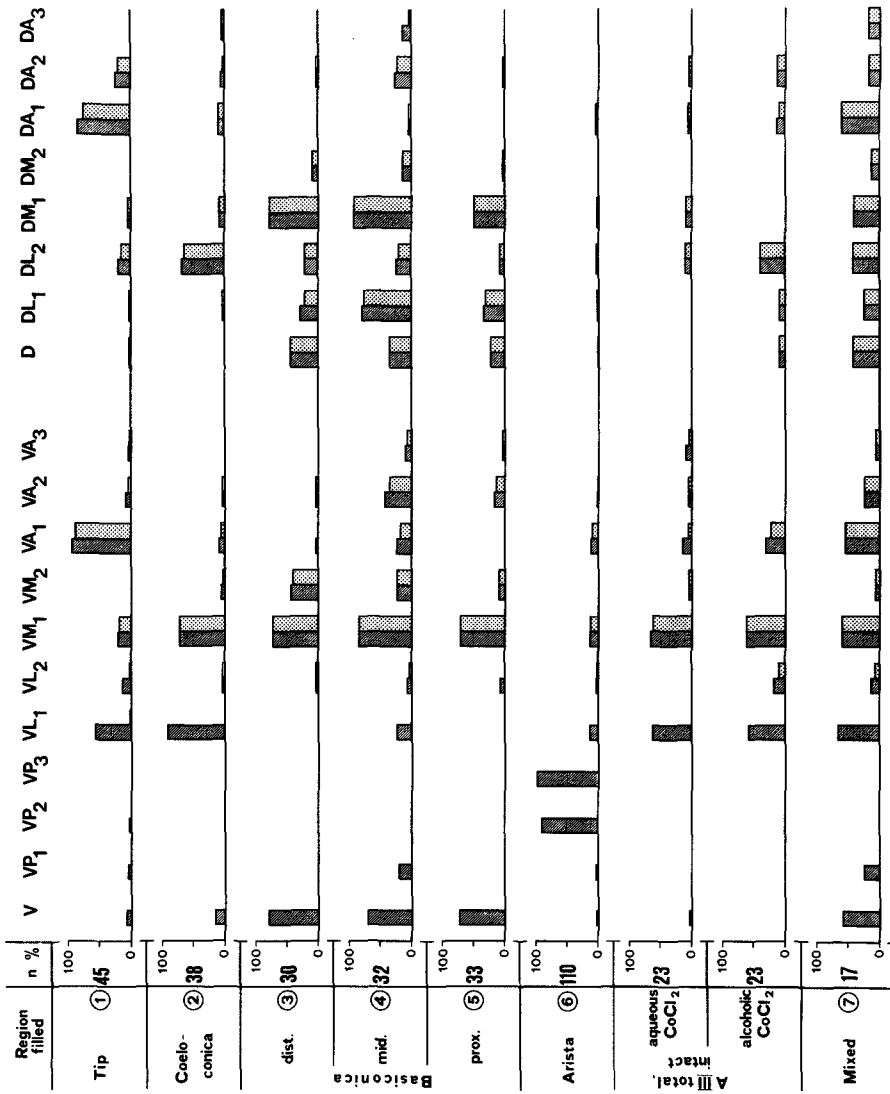
Fig. 15. Diagram summarizing percentages of flies in each type of experiment (numbers correspond to those in Fig. 1) exhibiting cobalt filled terminals in identified glomeruli. Hatched columns: ipsilateral projections, stippled columns: contralateral projections. Note that 5 ventrally located glomeruli V, VP_1, VP_2, VP_3 and VL_1 receive only ipsilateral input. Fills from tip- ($= trichodea$), *coeloconica-*, *basiconica-*; and mixed regions made after lesioning of appropriate sites with glass micropipette; aristal projections (cf. Stocker and Lawrence 1981) filled by cutting arista at its base; for filling through intact cuticle, the whole flagellum was introduced into pipette of appropriate tip diameter; n number of successful fills
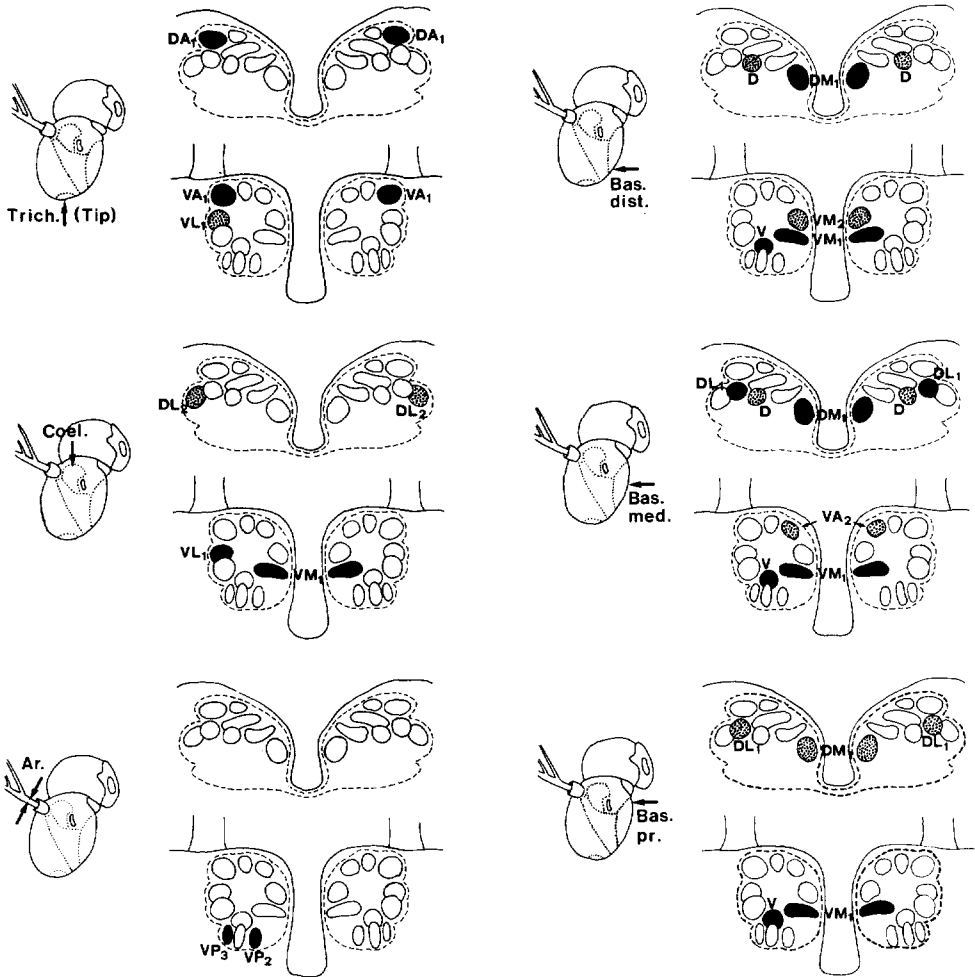
Fig. 16. Diagrams showing main projection patterns of 6 major antennal regions (*arrows*). The two horizontal views of antennal lobes to right of each type of filling represent dorsal (*upper*) and ventral (*lower*) halves. Ipsilateral to injured antenna is on left. *Black:* glomeruli affected in 70–100% of positive fills; *stippled:* affected in 30–69%; *white:* affected in 0–29%

Discussion

The main findings of this study are the following: (i) We have identified 19 glomeruli in each antennal lobe, at least ten of which represent major projection areas of flagellar sensilla. (ii) Five glomeruli, situated close to the entrance of the antennal nerve, receive only ipsilateral input; the rest receive bilateral input. (iii) A particular sensory fiber terminates in a specific glomerulus, either in one lobe or in both, in case of a bilateral projection. (iv) Cobalt filling from identified types of sensilla on the flagellum results in consistent and specific patterns of glomerular staining. (v) Data from

experiments in *s. basiconica* suggest that the projection patterns observed reflect the type of sensillum rather than its location on the flagellum.

When the results are analyzed quantitatively, it becomes evident that the glomeruli affected in a particular type of filling do not receive terminals to the same extent: some exhibit projections in the majority of cases, others in no more than 20–40% of the fills, or even more rarely. For example, in the fillings from the proximal *basiconica* region, V, DL_1 and VM_2 represent the first, second, and third group of glomeruli, respectively (Fig. 15). We interpret the first group as being "strongly" connected via sensory fibers with the lesioned site on the antenna. The significance of the second group is less obvious: apart from reflecting true variability, these projections could belong to sensory neurons refractory to the cobalt diffusion procedure, or they merely represent artifactually filled axons that are not related to the lesioned site. The latter is the most likely explanation of the third group of glomeruli. In view of these uncertainties, the conclusions drawn in this study will be, almost exclusively, based on the "strong" connections.

In contrast to cockroaches (Boeckh et al. 1970), bees (Pareto 1972; Suzuki 1975) or moths (Camazine and Hildebrand 1979), the sensory antennal projection in dipterans is to a larger extent bilateral (Boeckh et al. 1970; Strausfeld 1976). Our results show that in *Drosophila,* the projections of *s. trichodea, s. coeloconica,* and *s. basiconica* consist of an ipsilateral and a bilateral component. Bilateral projections are not composed of separate ipsilateral and contralateral fibers, but any axon projecting to the contralateral lobe is also branching in the corresponding ipsilateral glomerulus. Therefore, since the same information is reaching the two glomeruli, the bilaterally innervated glomeruli may not be able to discriminate between ipsi- and contralateral input. Laterality seems to be perceived only in the small group of unilaterally innervated glomeruli. The latter projections are likely to be involved in osmotropotaxis, an olfactory behavior recently demonstrated in *Drosophila* (Borst and Heisenberg 1982). In contrast to the sensilla on the flagellar surface, the one in the arista projects exclusively into the ipsilateral lobe. This unique arrangement of aristal axons might be related to their unique function among flagellar sensilla: in terms of fine structure, aristal sensilla appear to be the only receptors for stretch in the distal part of the antenna (Stocker and Lawrence 1981; Stocker 1982).

Although individual neurons in each of the four types of antennal sensilla studied are ultrastructurally uniform (Stocker and Lawrence 1981; Stocker 1982; Aiyar and Singh, unpublished, Link and Stocker, unpublished), their axons may project into different glomeruli. In flagellar sensilla this is most likely due to functional specialization of individual neurons in a particular sensillum (Kaib 1974). However, in the mechanosensory aristal sensillum functional specialization of single neurons is difficult to understand.

The most striking observation in this study is the association of the flagellar regions bearing a single type of sensillum with a consistent and specific pattern of glomerular projection (Figs. 15, 16). This could imply two different mechanisms of wiring which, however, need not be mutually

exclusive: a particular pattern might be correlated with the *type* of sensillum or with its *location* on the flagellum. Cobalt filling of three different proximo-distal sites in the *s. basiconica* region, designed to decide between the two alternatives, yielded three fairly similar projection patterns. This observation supports *functional* rather than *spatial* representation of this flagellar region in the antennal lobe. Although other types of sensilla could not be tested in this rigorous manner, the data obtained by filling intact sensilla or by filling from the mixed region are in accord with this interpretation. It is therefore suggested that individual glomeruli are functionally specialized, each receiving a characteristic combination of antennal input. Support for this interpretation comes also from other insects (cf. Masson and Strambi 1977; Chambille et al. 1980; Matsumoto and Hildebrand 1981; Prillinger 1981). Thus, contrary to the visual system, in the olfactory association center a spatial representation of the periphery appears to be less pronounced. However, directional information about the smell flow from the positioning of sensilla cannot be excluded, although there need not be a topographic representation of olfactory input. For the present, nothing is known about possible functional specialization of individual glomeruli. However, recent advances in the physiology of individual flagellar sensilla, and the possibility of mapping stimulus induced activity in central pathways might eventually allow to uncover such properties.

References

Bacon JP, Altman JS (1977) A silver intensification method for cobalt-filled neurones in whole-mount preparations. Brain Res 138:359–363

Barrows WM (1907) The reactions of the pomace fly, *Drosophila ampelophila* Loew, to odorous substances. J Exp Zool 4:515–537

Boeckh J, Sandri C, Akert K (1970) Sensorische Eingänge und synaptische Verbindungen im Zentralnervensystem von Insekten. Z Zellforsch 103:429–446

Boeckh J, Boeckh V, Kühn A (1977) Further data on the topography and physiology of central olfactory neurons in insects. In: Le Magnen J, MacLeod P (eds) Olfaction and taste, vol 6., London, Washington, D C Information retrieval, pp 315–321

Borst A, Heisenberg M (1982) Osmotropotaxis in *Drosophila melanogaster*. J Comp Physiol 147:479–484

Camazine SM, Hildebrand JG (1979) Central projections of antennal sensory neurons in mature and developing *Manduca sexta*. Neurosci abstr 5, abstr 492

Chambille I, Rospars JP (1981) Deutocerebron de la blatte *Blaberus craniifer* Burm. (Dictyoptera: Blaberidae): Etude qualitative et identification morphologique des glomérules. Int J Insect Morphol Embryol 10:141–165

Chambille I, Masson C, Rospars JP (1980) The deutocerebrum of the cockroach *Blaberus craniifer* Burm. Spatial organization of the sensory glomeruli. J Neurobiol 11:135–157

Frisch K, von (1965) Tanzsprache und Orientierung der Bienen. Berlin Heidelberg New York, Springer

Fuyama Y (1976) Behavior genetics of olfactory responses in *Drosophila*. I. Olfactometry and strain differences in *Drosophila melanogaster*. Behav Genet 6:407–420

Fuyama Y (1978) Behavior genetics of olfactory responses in *Drosophila*. II. An odorant specific variant in a natural population of *Drosophila melanogaster*. Behav Genet 8:399–414

Gundersen RW, Larsen JR (1978) Postembryonic development of the lateral protocerebral lobes, corpora pedunculata, deutocerebrum and tritocerebrum of *Phormia regina* Meigen (Diptera: Calliphoridae). Int J Insect Morphol Embryol 7:467–477

Harbach RE, Larsen JR (1976) Ultrastructure of sensilla on the distal antennal segment of

adult *Oncopeltus fasciatus* (Dallas) (Hemiptera: Lygaeidae). Int J Insect Morphol Embryol 5:23–33

Hildebrand JG, Hall LM, Osmond BC (1979) Distribution of binding sites for ^{125}I-labeled α-bungarotoxin in normal and deafferented antennal lobes of *Manduca sexta*. Proc Natl Acad Sci USA 76:499–503

Kaib M (1974) Die Fleisch- und Blumenduftrezeptoren auf der Antenne der Schmeissfliege *Calliphora vicina*. J Comp Physiol 95:105–121

Kikuchi T (1973) Genetic alteration of olfactory functions in *Drosophila melanogaster*. Jap J Genet 48:105–118

Masson C, Strambi C (1977) Sensory antennal organization in an ant and a wasp. J Neurobiol 8:537–548

Matsumoto SG, Hildebrand JG (1981) Olfactory mechanisms in the moth *Manduca sexta:* response characteristics and morphology of central neurons in the antennal lobes. Proc R Soc Lond B 213:249–277

Mindek G (1968) Proliferations- und Transdeterminationsleistungen der weiblichen Genital-Imaginalscheiben von *Drosophila melanogaster* nach Kultur in vivo. W Roux Arch Entw Mech Org 161:249–280

Pareto A (1972) Die zentrale Verteilung der Fühlerafferenz bei Arbeiterinnen der Honigbiene, *Apis mellifera* L. Z Zellforsch 131:109–140

Power ME (1946) The antennal centers and their connections with the brain of *Drosophila melanogaster*. J Comp Neurol 85:485–509

Prillinger L (1981) Postembryonic development of the antennal lobes in *Periplaneta americana* L. Cell Tissue Res 215:563–575

Rodrigues V (1980) Olfactory behavior of *Drosophila melanogaster*. In: Siddiqi O, Babu P, Hall LM, Hall JC (eds) Development and neurobiology of *Drosophila*. New York, Plenum Press, pp 361–371

Rodrigues V, Siddiqi O (1978) Genetic analysis of chemosensory pathway. Proc Indian Acad Sci 87B:147–160

Sanes JR, Hildebrand JG (1976) Structure and development of antennae in a moth, *Manduca sexta*. Dev Biol 51:282–299

Schaller D (1978) Antennal sensory system of *Periplaneta americana* L. Cell Tissue Res 191:121–139

Stocker RF (1982) Genetically displaced sensory neurons in the head of *Drosophila* project via different pathways into the same specific brain regions. Dev Biol 94:31–40

Stocker RF Spatial relationships in an insect nerve between identified sensory axons of the same origin and destination (in preparation)

Stocker RF, Lawrence PA (1981) Sensory projections from normal and homoeotically transformed antennae in *Drosophila*. Dev Biol 82:224–237

Stocker RF, Schorderet M (1981) Cobalt filling of sensory projections from internal and external mouthparts in *Drosophila*. Cell Tissue Res 216:513–523

Strausfeld NJ (1976) Atlas of an insect brain. Berlin Heidelberg New York , Springer

Strausfeld NJ, Hausen K (1977) The resolution of neuronal assemblies after cobalt injection into neuropil. Proc R Soc Lond B 199:463–476

Suzuki H (1975) Antennal movements induced by odour and central projection of the antennal neurones in the honey-bee. J Insect Physiol 21:831–847

Venard R, Pichon Y (1981) Etude électro-antennographique de la réponse périphérique de l'antenne de *Drosophila melanogaster* à des stimulations odorantes. C R Acad Sci Paris, Sér III 293:839–842

Waldow U (1977) CNS units in cockroach (*Periplaneta americana*): specificity of response to pheromones and other odor stimuli. J Comp Physiol 116:1–17

Yamada M (1971) A search for odour encoding in the olfactory lobe. J Physiol Lond 214:127–143