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Histamine-like immunoreactivity in the visual system and brain of *Drosophila melanogaster*

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Summary. In this study, immunohistochemistry on cryostat sections is used to demonstrate anti-histamine immunoreactivity in the *Drosophila* brain. The results support earlier findings that histamine is probably a transmitter of insect photoreceptors. It is further shown that, in *Drosophila*, all imaginal photoreceptors including receptor type R7 are anti-histamine immunoreactive, whereas the larval photoreceptors do not seem to contain histamine. In addition to the photoreceptors, fibres in the antennal nerve and approximately 12 neurons in each brain hemisphere show strong histamine-like immunoreactivity. These cells arborize extensively in large parts of the central brain.

Key words: Photoreceptor cells – Nervous system, central – Visual system – Histamine – Transmitter – Immunohistochemistry – *Drosophila melanogaster* (Insecta)

Histamine has been shown to be a neuroactive substance both in vertebrates and invertebrates. In insects, histamine accumulates in photoreceptors. This has been demonstrated immunocytochemically in several insect species (Nässel et al. 1988; Pirvola et al. 1988; Schlemermeyer et al. 1989). In addition, there is convincing evidence from physiological and pharmacological studies that histamine is a synaptic transmitter in these cells (Elias and Evans 1983, 1984; Hardie 1987, 1988, 1989; Simmons and Hardie 1988; Sarthy 1989). These studies do not show, however, whether this is true for the complete set of photoreceptor cells in the ommatidia (R1–R8). It has been suggested that receptor type R7 might use a different transmitter (Datum et al. 1986; Nässel et al. 1988). Whereas there are numerous studies on the visual system, histamine-like immunoreactive neurons in the insect central nervous system have only been investigated in *Blaberus* (Pirvola et al. 1988), in *Manduca* (Homberg and Hildebrand 1991), and in the thoracal ganglia of *Calliphora* and *Drosophila* (Nässel et al. 1990).

In the present study, we describe the distribution of anti-histamine reactive elements in the brain of *Drosophila melanogaster*. Our main focus was on the analysis of photoreceptor R7 and the larval photoreceptors. In addition, we examined immunoreactive elements in the central brain of *Drosophila*.

For a comprehensive anatomical description of *Drosophila* retina and optic lobes, we refer the reader to the work of Cagan and Ready (1989) and Fischbach and Dittrich (1989), respectively. We have relied largely on the work of Power (1943) on *Drosophila*, and Strausfeld (1976) on larger flies, for the description of the central brain.

Materials and methods

The *Drosophila* strains used in this study were wildtype Berlin K and the mutant sevenless (sev^{LY3}, 1–33.2).

Immunocytochemical staining was carried out on 10-µm-thick cryostat sections. The histological procedures are described in detail in Buchner et al. (1986). Briefly, *Drosophila* heads were dissected in ice-cold 4% carbodiimide (1-ethyl-3(3-dimethylaminopropyl)carbodiimide, Sigma) in phosphate buffer (0.15 M, pH 7.4), fixed for 2.5 h in the same fixative, and left in 25% sucrose in phosphate-buffered saline overnight before sectioning. The primary antibody used was a polyclonal serum raised in rabbit against synthetic histamine coupled to succinylated keyhole limpet hemocyanin with carbodiimide (Incstar, Stillwater, Minn., USA). We used the peroxidase-anti-peroxidase (PAP) technique (Dako Corp. Santa Barbara, Calif., USA) with diaminobenzidine (DAB) as chromogen.

Preabsorption of the serum with histamine coupled to human serum albumin abolished any immunohistochemical staining, whereas the uncoupled components had no effect.

To obtain retinal lesions, a Historange microtome (LKB) equipped with a razor blade mounted onto a modified loudspeaker was used. Anesthetized flies were glued onto the object holder and the swinging blade inserted into the retina under microscopic control. Up to 7 days later, the lesioned flies were used for immunocytochemistry.

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Results

The photoreceptor cells

The visual system of *Drosophila* shows heavy histamine-like staining of retinal photoreceptor terminals in the lamina (R1–6) and medulla (R7, R8) (Fig. 1). In the retina, the fenestrated layer is stained in most preparations, whereas the cell bodies of the receptors are hardly labelled at all. The lamina monopolar cells seem to be free of label, although there is some staining in this area possibly attributable to photoreceptor axons penetrating the lamina cell body layer. In the medulla only the terminals of the long visual fibres are stained. Terminal endings can easily be recognized in the individual medulla columns, although R7 and R8 in a given column cannot be distinguished. The stained structures show a characteristic morphology with thickenings in the most distal layer of the medulla neuropile, a slight thickening at about 30%–40% medullar depth, and a button-shaped terminal structure at about 50% depth, just distal to the serpentine layer. The relative medullar depth is measured from distal to proximal, with the distal surface of the neuropile being 0%, the proximal border being 100%. The morphology and the medullar depth of the terminals is in agreement with the combined morphology of R7 and R8 in Golgi preparations (Fischbach and Dittrich 1989).

In order to demonstrate the individual morphology of R7 and R8 cells, we made lesions in the eyes of wild-type flies as shown in Fig. 2. Thus, we were able to obtain, in the same eye, ommatidia with intact receptor cells, ommatidia where only the distal receptor cells R1–R7 are damaged, and an adjacent area where all receptor cells R1–R8 are damaged. The damaged cells degenerate rapidly (Griffiths and Boschek 1976); after 2 days, no trace of anti-histamine immunoreactivity remains. The resulting pattern of degeneration can be analysed in the lamina and the medulla, and allows a comparison of the three lesion patterns in a single histological section (Fig. 3). In the lamina, a zone of label-free cartridges indicates the projection area of degenerated R1–R6 cells. In the medulla, unlabelled columns correspond to ommatidia with damaged cells R1–R8. In most of the remaining columns, the intact long retinal fibres are stained in the same way as those in the contralateral medulla innervated from the intact contralateral eye. In addition, there are some columns with input from retinal ommatidia where only R8 has survived. The terminals of these fibres end at a depth of 40% and lack the terminal knob-like structure so characteristic of R7. The profiles labelled there correspond in their morphology and projection depth with the R8 as seen in Golgi preparations (Fischbach and Dittrich 1989). This demonstrates that both cells R7 and R8 are stained in the wildtype.

We could further confirm this result when staining sections of the mutant *sevenless (sev)*. In this mutant, the receptor cell R7 does not differentiate in the retina and never grows an axon towards the optic lobes (Tomlinson and Ready 1986). Instead, the long retinal fibres projecting into the medulla originate exclusively from

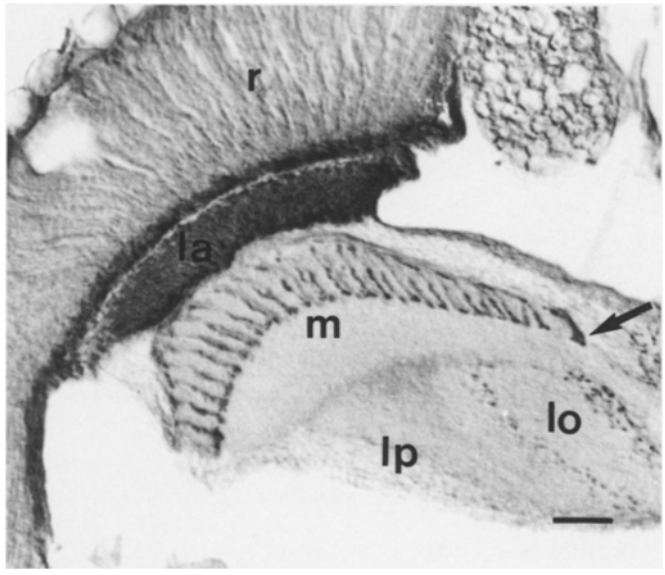

Fig. 1. Wild type retina and optic lobe. Horizontal section, stained with anti-histamine serum. Anterior is to the top, medial to the right. There is only weak labelling in the retina (*r*), whereas the photoreceptor terminals in the lamina (*la*) and the medulla (*m*) are clearly stained. Some staining is also present in the fenestrated layer between the retina and lamina. Terminals originating from cells in the posterior fenestrated layer are stained (*arrow*) in front of the medulla neuropile. *lo* Lobula; *lp* lobula plate. *Scale bar:* 20 μm

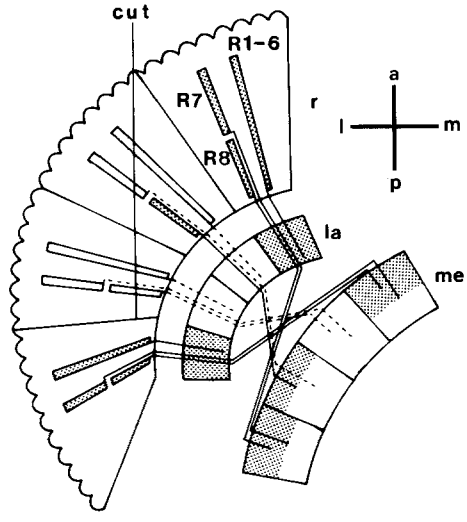

Fig. 2. Schematic drawing to illustrate the retinal lesion and the resulting degeneration pattern in the lamina and the medulla. *a* Anterior; *cut* retinal lesion; *l* lateral; *la* lamina; *m* medial; *me* medulla; *p* posterior; *r* retina; *R1–6*, *R7*, *R8* photoreceptor cells 1–8. *Solid lines* and *shaded areas* indicate intact fibres and terminals, respectively; *broken lines* indicate degenerated projections

R8 cells, as judged by developmental and histological criteria (Campos-Ortega et al. 1979). The anti-histamine staining demonstrates that, in *sevenless*, the terminal knob-like structure is much smaller. Usually, the labelled terminals end at a depth of about 40%. Only occasionally do terminals of R8 fibres grow further and end at a depth close to the normal depth of R7 cells. However,

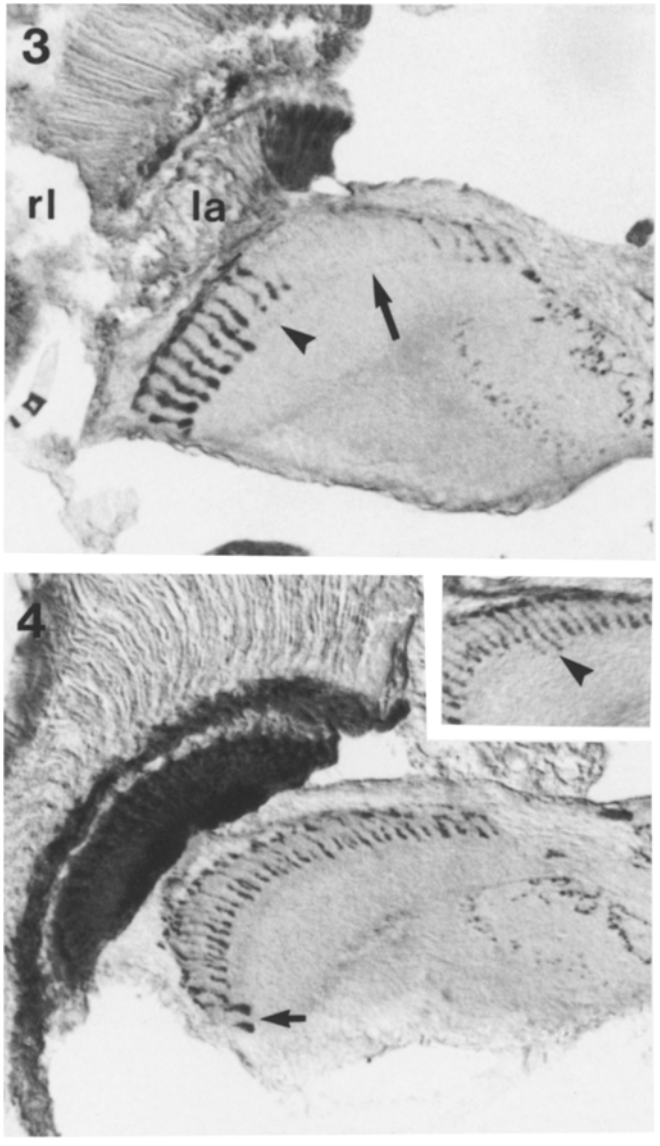

Fig. 3. Wildtype retina and optic lobe after lesioning of the retina (*rl*). Horizontal section. In the lamina (*la*), only terminals in the most anterior part are stained, indicating the presence of surviving receptor cells R1–6 in the corresponding part of the retina. The posterior part of the lamina is (in this sectioning plane) free of labelling because of the lesion in the retina. The terminals of R7 and R8 are intact in the posterior medulla, but are absent in the central medulla (*arrow*). Several columns with only the terminals of surviving R8 receptors (*arrowhead*) lie at the border between these two areas. In the most anterior medulla, some terminals are stained indicating that there are intact ommatidia in the posterior retina not shown in this sectioning plane. Same magnification as in Fig. 1

Fig. 4. Staining in the mutant sevenless. Horizontal section. Most medullar terminals are shorter compared with the wildtype and lack the terminal knob-like structure. The *inset* shows two terminals (*arrowhead*) that reach to a deeper medullar layer, typical for R7 terminals in the wildtype. These terminals do not show the wildtype R7 morphology. The *arrow* indicates terminals in the posterior dorsal medulla, illustrating the specialized morphology of marginal R8 cells. Same magnification as in Fig. 1

these R8 endings never develop the terminal knob typical of wildtype R7 endings (Fig. 4).

In the most posterior columns of the dorsal medulla, the long retinal fibres show a different morphology. There, the R8 terminals end deeper, close to normal R7 (Fig. 4). They are also thicker than normal R8 terminals. As in larger flies (Nässel et al. 1988), this morphology is also present in the wildtype, but because of the stained R7 endings, it is not as conspicuous as in the mutant.

We found heavy staining in the ocellar ganglion as reported for other diptera (Nässel et al. 1988). This indicates that the terminals of ocellar photoreceptors are also stained.

In addition to the retinal photoreceptors, a fibre bundle is stained in the optic lobes; these fibres terminate anterior to the medulla near the emerging posterior optic tract (Fig. 1). A corresponding bundle shows histamine-like immunoreactivity in *Musca* and *Calliphora* (Nässel et al. 1988). The fibres originate from a cell group near the fenestrated layer at the posterior border of the retina (Hofbauer and Buchner 1989). The function of these cells is still unknown.

After finding that probably all photoreceptor cells in the adult *Drosophila* are anti-histamine immunoreactive, we wondered whether this is also true for the larval photoreceptors. The *Drosophila* larva possesses a group of light sensitive cells lateral to the mouthhooks. These cells project to the brain via Bolwig's nerve, which enters the larval brain hemisphere through the optic stalk (Bolwig 1946; Steller et al. 1987). We stained cryostat sections of larval brains at the end of the third larval instar. Although we found stained neurons in the central hemispheres and in the thoracic and abdominal ganglia (data not shown), there was no staining of the Bolwig nerve or its terminals in the larval brain.

Anti-histamine reactive cells in the brain

Prominently stained large cell bodies lie just anterior and ventral to the optic peduncle, which connects the lobula with the central brain. More stained cell bodies are found in front of the lobula, anterior to the medulla neuropile, in the lateral dorsal cell body layer between the optic lobes and central brain, and in the dorsal cortex of the protocerebrum near the calyces. About 12 cells are stained in each hemisphere.

Despite the small number of stained cell bodies, heavily stained arborizations are found throughout large parts of the brain. The areas most densely labelled are the ventral lateral parts of the protocerebrum near the lobula, the area along the great cerebral commissures, and distinctive parts within the posterior and superior protocerebrum. The ventral lateral protocerebrum is densely innervated by large arborizations that are contiguous to fibres and terminal in the medial protocerebrum above the oesophagus, along the great cerebral commissures, and ventral and posterior to the fan-shaped body (Figs. 5, 6). Some fibres connect the ventral

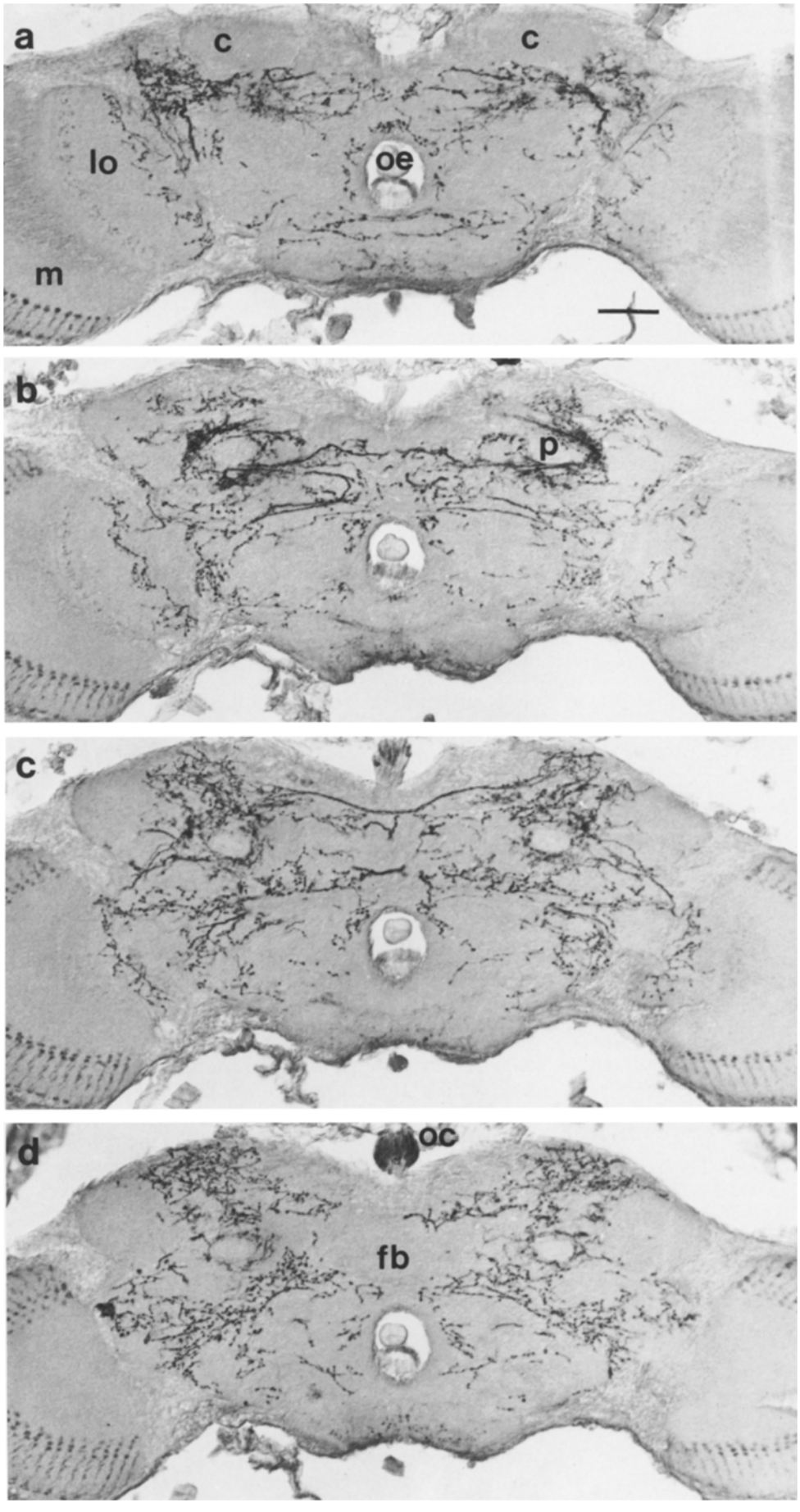

Fig. 5a–d. Transverse sections from a series of the wildtype central brain posterior to the fan-shaped body. The section in **a** is the most posterior. Immunoreactive elements are concentrated in the protocerebrum around the pedunculi (*p*), and in parts of the superior protocerebrum. The calyces (*c*), the pedunculi, and the fan-shaped body (*fb*) are free of labelling. Stained tangential elements are visible in the lobula (*lo*). In the sections in **c** and **d** photoreceptor terminals are stained in the ocellar ganglion (*oc*). *m* Medulla; *oe* oesophagus. *Scale bar:* 30 μm

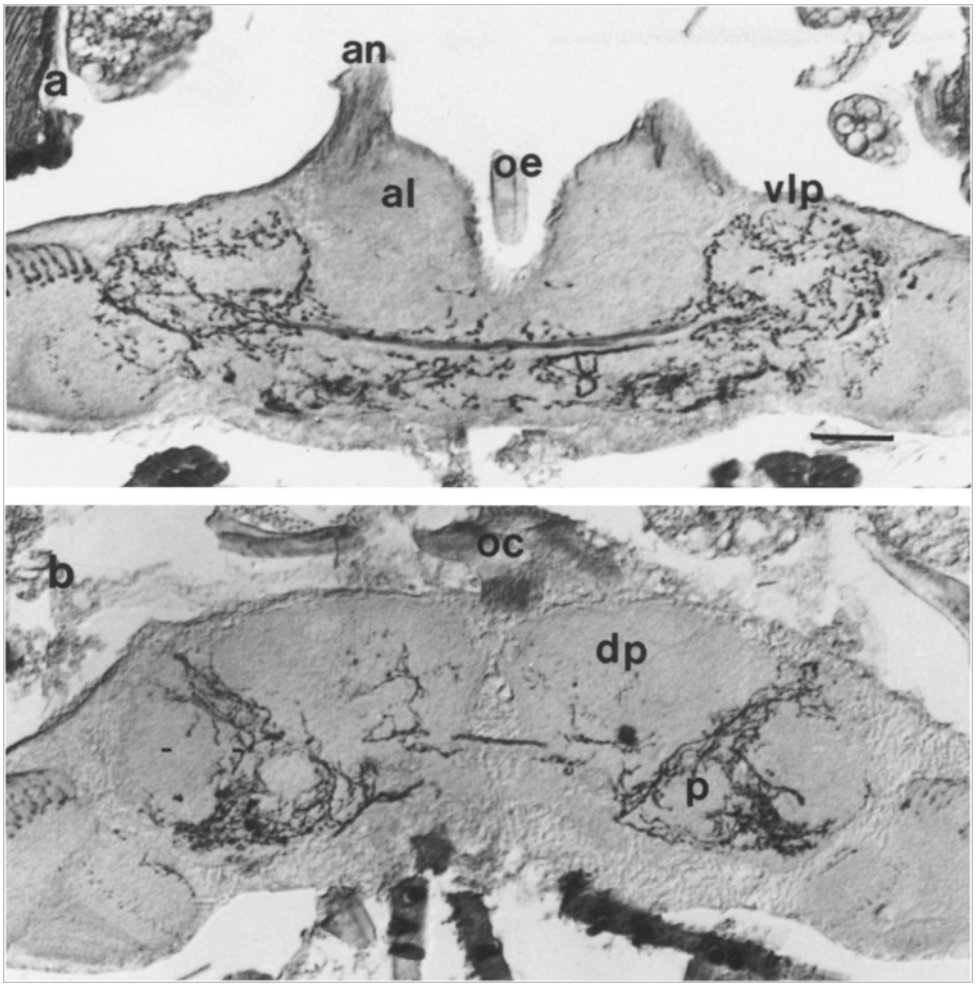

Fig. 6a, b. Oblique horizontal sections of the wildtype protocerebrum. The section in **a** is just dorsal to the oesophagus. The dense arborizations in the ventral lateral protocerebrum (*vlp*) and their interhemispheric connections dorsal to the oesophagus are shown. The antennal lobes (*al*) are free of labelling. The section in **b** is more dorsal and presents a sectioning plane perpendicular to the peduncles of the mushroom bodies (*p*). Densely innervated areas and areas free of labelling are demonstrated in the dorsal protocerebrum (*dp*). *an* Antennal nerve; *oc* ocellar ganglion; *oe* oesophagus. *Scale bar*: 50 μm

lateral protocerebrum of both hemispheres. Prominent fibres originating from the area near the optic peduncle run dorsally and end near the pedunculi of the mushroom bodies just ventral to the calyces. There, a very dense network of fibres and endings is formed in the neuropile surrounding the pedunculi, and between the pedunculi and the lateral protocerebrum. The pedunculi themselves are never invaded by stained fibres. Again, these areas have interhemispheric connections (Fig. 5b–d). Adjacent to these arborizations, there is a dense network of stained fibres in the most dorsal and lateral area of the superior protocerebrum. Still more fibres originate from the area near the optic peduncle and project caudally, forming a network in the posterior protocerebrum near and around the oesophagus.

Immunoreactive elements send arborizations into two layers of the lobula. Clearly stained terminals can be seen in the most medial layer and in a more lateral layer facing the lobula plate. The terminals in the lateral layer are finer and more faintly stained (Fig. 7). In both cases, the arborizations seem to belong to large tangential elements with an extended arborization originating only from one or a few cells. These cells show a similar, although not identical, morphology to some of the Golgi-stained lobula tangential cells described by Fischbach and Dittrich (1989).

Other parts of the brain contain fewer histamine-like immunoreactive structures and in several areas stained terminals are conspicuously absent. These are: the proximal medulla, the lobula plate, the antennal glomeruli, the ellipsoid body, the fan-shaped body, the noduli, as well as the mushroom body lobes, pedunculi, and calyces. Furthermore, regions of the anterior and the dorsal lateral protocerebrum exhibit no or only a few immunoreactive fibres.

In addition to the described immunoreactive neurons in the brain, a system of stained fibres and terminals originates from cells outside the brain. The fibres that enter the brain via the antennal nerve bypass the antennal glomeruli, and project to the suboesophageal ganglion. There, the projections from both antennal nerves meet in an area crossing the midline (Fig. 7).

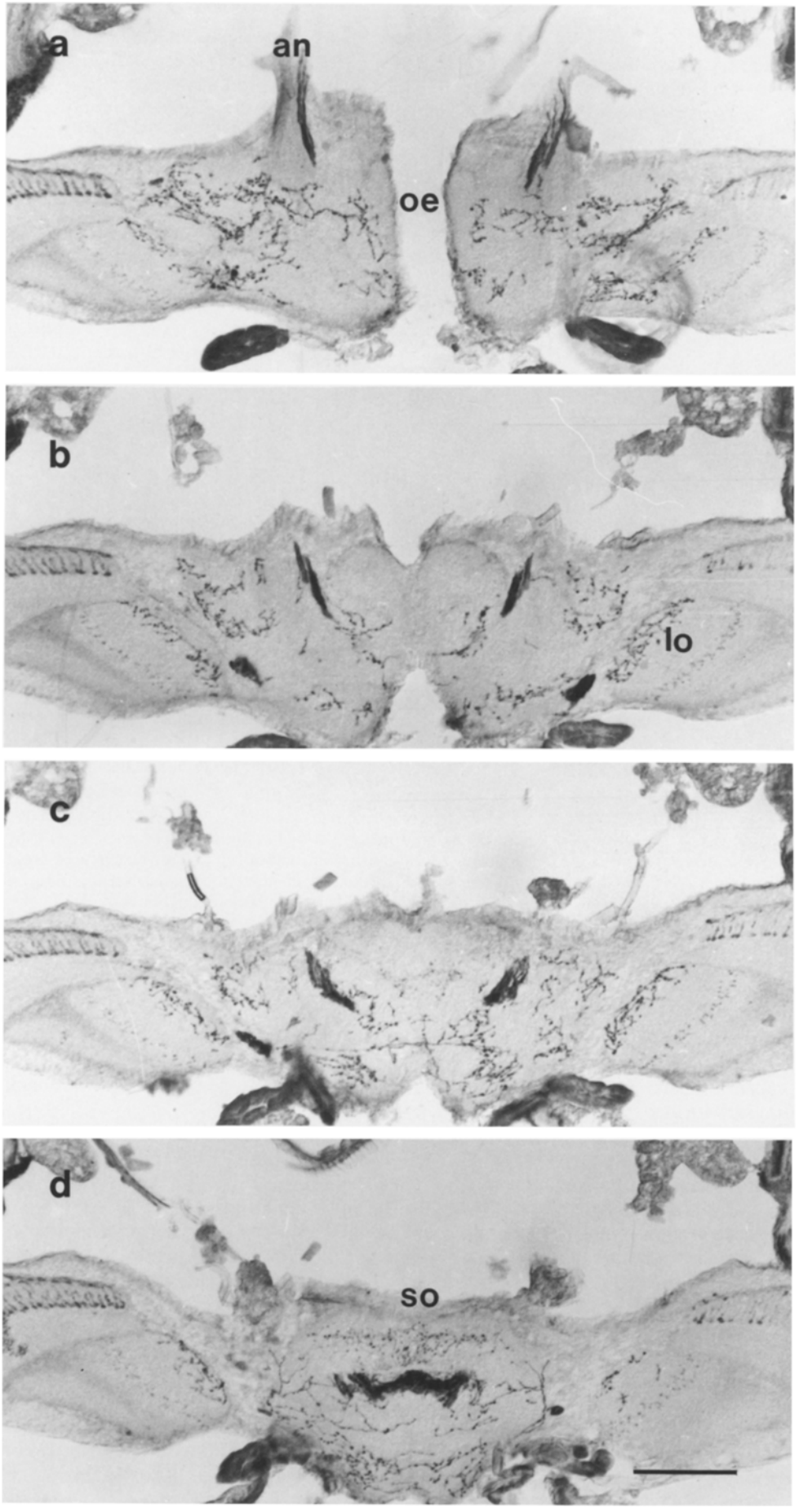

Fig. 7a–d. A series of horizontal sections ventral to the oesophagus (*oe*). Wildtype.
a The most dorsal section. The series shows incoming fibres from the antennal nerves (*an*), which bypass the antennal glomeruli and terminate in the suboesophageal ganglion (*so*). *lo* Lobula.
Scale bar: 50 μm

Discussion

Our study demonstrates the histamine-like immunoreactivity in photoreceptor cells and in neurons of the central brain of *Drosophila*. We confirm the reactivity of the photoreceptors R1–6 and R8, and of the ocellar receptors as observed in larger flies (Nässel et al. 1988). Furthermore, we show that there is no difference in the immunoreactivity of R7 and R8. Only the larval photoreceptors seem to be non-reactive. In addition, we describe the distribution and arborization pattern of neurons that lie outside the optic lobes and that exhibit histamine-like immunoreactivity.

Quantitative experiments show that most of the histamine in the insect head is concentrated in the retina (Elias and Evans 1983; Sarthy 1989). In contrast, we find only a little histamine-like reactivity in the retina, but heavy staining in the retinal terminals. The reason for this could be that during sectioning all retina cells are damaged and that histamine is washed out during the histological procedures.

Increasing evidence from physiological, pharmacological, and immunohistochemical experiments in several insect species indicates that histamine functions as a neurotransmitter of adult photoreceptors (Elias and Evans 1983; Hardie 1987, 1988, 1989; Simmons and Hardie 1988; Nässel et al. 1988; Schlemermeyer et al. 1989; Sarthy 1989). In larger diptera, it has been proposed that not all photoreceptors contain histamine, but that the receptor type R7 might use γ-amino-butyric acid (GABA) as transmitter (Datum et al. 1986; Nässel et al. 1988). R7 cells of *Drosophila*, however, did not show immunoreactivity related to GABA or its synthetic enzyme (Buchner et al. 1988). Our experiments, using the mutant *sevenless* and wildtype flies with experimental lesions in the retina, demonstrate that R7 is also antihistamine immunoreactive and that, in this respect, it does not differ from the other receptor types. Interestingly, the larval photoreceptors seem to use a different transmitter.

Retinal terminals in the columns of the posterior dorsal medulla exhibit a special morphology. They belong to specialized central receptor cells of ommatidia at the dorsal and anterior margin of the eye. These ommatidia exhibit a specialized morphology (Wada 1974), and their R7 and R8 cells express the rhodopsin gene Rh3, which in other areas of the retina is expressed exclusively in a subpopulation of R7 cells (Fortini and Rubin 1990). In larger flies, the morphology and projection of these receptors have been studied extensively (Wunderer and Smola 1982a, b; Strausfeld and Wunderer 1985; Nässel et al. 1988). These data and physiological experiments (Hardie 1984) suggest that they are specialized receptors for polarized light. Behavioural experiments demonstrate that *Drosophila* is able to use polarized light for orientation. It is doubtful, however, whether this ability can exclusively be attributed to the central receptors of the marginal ommatidia of the anterior retina (Wolf et al. 1980).

Histamine-immunoreactive neurons other than photoreceptors have been analysed immunohistochemically in *Blaberus* (Pirvola et al. 1988), in the thoracic ganglia of *Calliphora* and *Drosophila* (Nässel et al. 1990), and in *Manduca* (Homberg and Hildebrand 1991). In these studies, typically large-field elements are stained, indicating that they might have a modulatory function. In the thoracic ganglia, stained cells have been identified as neurosecretory cells (Nässel et al. 1990). The comparision of immunoreactive elements in the central brain of *Blaberus* and *Manduca* with our results in *Drosophila* demonstrate a common staining pattern. In all these species, dense arborizations in the ventral lateral protocerebrum and connections from there to the ipsilateral and contralateral central protocerebrum are stained. The pedunculi of the mushroom bodies are surrounded, but never invaded, by a dense network of immunoreactive arborizations. Apart from these corresponding patterns, however, there are also distinct differences in the staining of immunoreactive repetitive cells in the lamina and medulla of the optic lobes, and of stained elements in the calyces, the central complex, and the antennal lobes. All these structures are free of labelling in *Drosophila*. In contrast, there are no immunoreactive fibres in the antennal nerve in *Blaberus* and *Manduca*, whereas this nerve undoubtedly contains stained fibres in *Drosophila*. These fibres are probably part of an antennal projection to the suboesophageal ganglion, a projection previously demonstrated by Stocker and Lawrence (1981) using the cobalt filling technique.

Such differences might be attributable to the different sensitivities of the methods and antisera used. There are, however, arguments against this. The labelled structures in our preparations are strongly stained, and in the antennal nerve, we find labelling where there is none in the other species. Thus, the staining patterns indicate true differences between the species, rather than method-related effects.

Because of the strong labelling and the clear staining of few neurons, it might be possible to define homologous elements in different insect species. Furthermore, the cloning of the rat gene for the histamine-synthesizing enzyme histidine decarboxylase (Joseph et al. 1990) might lead to the isolation of the corresponding *Drosophila* gene, thus opening up the evolutionary and neurogenetic analysis of histaminergic neurons.

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References

Bolwig N (1945/46) Senses and sense organs of the anterior end of the house fly larvae. Vidensk Medd Dan Naturhist Foren Khobenhavn 109:81–217

Buchner E, Buchner S, Crawford G, Mason WT, Salvaterra PM, Sattelle DB (1986) Choline acetyltransferase-like immunoreactivity in the brain of *Drosophila melanogaster*. Cell Tissue Res 246:57–62

Buchner E, Bader R, Buchner S, Cox J, Emson PC, Flory E, Heizmann CW, Hemm S, Hofbauer A, Oertel WH (1988) Cell-specific immuno-probes for the brain of normal and mutant *Drosophila melanogaster*. I. Wildtype visual system. Cell Tissue Res 253:357–370

Cagan RL, Ready DF (1989) The emergence of order in the *Drosophila* pupal retina. Dev Biol 136:346–362

Campos-Ortega JA, Jürgens G, Hofbauer A (1979) Cell clones and pattern formation: studies on sevenless, a mutant of *Drosophila melanogaster*. Roux Arch 186:27–50

Datum KH, Weiler R, Zettler F (1986) Immunocytochemical demonstration of gamma-aminobutyric acid and glutamic acid decarboxylase in R7 photoreceptors and C2 centrifugal fibres in the blowfly visual system. J Comp Physiol [A] 159:241–249

Elias MS, Evans PD (1983) Histamine in the insect nervous system: distribution, synthesis and metabolism. J Neurochem 41:562–568

Elias MS, Evans PD (1984) Autoradiographic localization of ^{3}H-histamine accumulation by the visual system of the locust. Cell Tissue Res 238:105–112

Fischbach K-F, Dittrich A (1989) The optic lobe of *Drosophila melanogaster*. Part I. A Golgi analysis of wild-type structure. Cell Tissue Res 258:441–475

Fortini ME, Rubin GM (1990) Analysis of *cis*-acting requirements of the Rh3 and Rh4 genes reveals a bipartite organization to rhodopsin promotors in *Drosophila melanogaster*. Genes Dev 4:444–463

Griffiths GW, Boschek CB (1976) Rapid degeneration of visual fibres following retinal lesions in the dipteran compound eye. Neurosci Lett 3:253–258

Hardie RC (1984) Properties of photoreceptors R7 and R8 in dorsal marginal ommatidia in the compound eyes of *Musca* and *Calliphora*. J Comp Physiol [A] 154:157–165

Hardie RC (1987) Is histamine a neurotransmitter in insect photoreceptors? J Comp Physiol [A] 161:201–213

Hardie RC (1988) Effects of antagonists on putative histamine receptors in the first visual neuropile of the housefly (*Musca domestica*). J Exp Biol 138:221–241

Hardie RC (1989) A histamine-activated chloride channel involved in neurotransmission at a photoreceptor synapse. Nature 339:704–706

Hofbauer A, Buchner E (1989) Does *Drosophila* have seven eyes? Naturwissenschaften 76:335–336

Homberg U, Hildebrand JG (1991) Histamine-immunoreactive neurons in the midbrain and suboesophageal ganglion of the sphinx moth *Manduca sexta*. J Comp Neurol 307:647–657

Joseph DR, Sullivan PM, Wang Y-M, Kozak C, Fenstermacher DA, Behrendsen ME, Zahnow CA (1990) Characterization and expression of the complementary DNA encoding rat histidine decarboxylase. Proc Natl Acad Sci USA 87:733–737

Nässel DR, Holmquist MH, Hardie RC, Hakanson R, Sundler F (1988) Histamine-like immunoreactivity in photoreceptors of the compound eyes and ocelli of the flies *Calliphora erythrocephala* and *Musca domestica*. Cell Tissue Res 253:639–646

Nässel DR, Pirvola U, Panula P (1990) Histamine-like immunoreactive neurons innervating putative neurohaemal areas and central neuropile in the thoraco-abdominal ganglia of the flies *Drosophila* and *Calliphora*. J Comp Neurol 197:525–536

Pirvola U, Tuomisto L, Yamatodani A, Panula P (1988) Distribution of histamine in the cockroach brain and visual system: an immunocytochemical and biochemical study. J Comp Neurol 276:514–526

Power ME (1943) The brain of *Drosophila melanogaster*. J Morphol 72:517–559

Sarthy PV (1989) Histamine: a neurotransmitter candidate for photoreceptors in *Drosophila melanogaster*. Invest Ophthalmol Visual Sci 30 S:290

Schlemermeyer E, Schütte M, Ammermüller J (1989) Immunocytochemical and electrophysiological evidence that locust ocellar photoreceptors contain and release histamine. Neurosci Lett 99:73–78

Simmons PJ, Hardie RC (1988) Evidence that histamine is a neurotransmitter of photoreceptors in the locust ocellus. J Exp Biol 138:205–219

Steller H, Fischbach K-F, Rubin GM (1987) Disconnected: a locus required for neuronal pathway formation in the visual system of *Drosophila*. Cell 50:1139–1153

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

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

Strausfeld HJ, Wunderer H (1985) Optic lobe projections of marginal ommatidia in *Calliphora erythrocephala* specialized for detecting polarized light. Cell Tissue Res 242:163–178

Tomlinson A, Ready D (1986) Sevenless: a cell specific homeotic mutation of the *Drosophila* eye. Science 231:400–402

Wada S (1974) Spezielle randzonale Ommatidien der Fliegen (Diptera: Brachycera): Architektur und Verteilung in den Komplexaugen. Z Morphol Tiere 77:87–125

Wolf R, Gebhardt B, Gademann R, Heisenberg M (1980) Polarization sensitivity of course control in *Drosophila melanogaster*. J Comp Physiol 139:177–191

Wunderer H, Smola U (1982a) Fine structure of ommatidia at the dorsal eye margin of *Calliphora erythrocephala* Meigen (Diptera: Calliphoridae): an eye region specialized for the detection of polarized light. Int J Insect Morphol Embryol 11:25–38

Wunderer H, Smola U (1982b) Morphological differentiation of the central visual cells R7/R8 in various regions of blowfly eye. Tissue Cell 14:341–358