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The optic lobe projection pattern of polarization-sensitive photoreceptor cells in *Drosophila melanogaster*

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Summary. Histological staining of wild-type and *sevenless* transgenic *Drosophila melanogaster* bearing *Rh3-lacZ* fusion genes permits the selective visualization of polarization-sensitive R7 and R8 photoreceptor cells located along the dorsal anterior eye margin. Diffusion of β-galactosidase throughout these cells reveals that they project long axons to the two most peripheral synaptic target rows of the dorsal posterior medulla, defining a specialized marginal zone of this optic lobe. Comparison of the staining patterns of marginal and nonmarginal *Rh3-lacZ*-expressing photoreceptor cells in the same histological preparations suggests that the marginal cells possess morphologically specialized axons and synaptic terminals. These findings are discussed with reference to the neuroanatomy of the corresponding dorsal marginal eye and optic lobe regions of the larger dipterans *Musca* and *Calliphora*, and in relation to the ability of *Drosophila* to orient to polarized light.

Key words: Photoreceptor cells – Dorsal margin – Polarized light detection – Optic lobes – Rh3 opsin gene – Transgenic flies – *Drosophila melanogaster* (Insecta)

The ability of certain insects to utilize the polarized light pattern of the sky for navigation was first demonstrated four decades ago by von Frisch (1949, 1951) for the bee *Apis mellifera*. Since then, behavioral experiments with bees and desert ants have shown that a small field of ommatidia along the dorsal margin of the hymenopteran compound eye is solely responsible for the detection of polarized light (Wehner 1982; Wehner and Strasser 1985; Fent 1986). These ommatidia are characterized by ultraviolet (UV)-sensitive photoreceptor cells with untwisted rhabdomeres, which have been found to be highly sensitive to the *e*-vector direction of light stimuli by direct electrophysiological recording (Labhart 1980, 1986). Moreover, within each ommatidium, the microvillar orientations of otherwise equivalent UV receptors are orthogonal to each other such that the resulting absorbance differences are an accurate measure of incident light *e*-vector direction and are unaffected by fluctuations in light wavelength or intensity (Brines and Gould 1982; Wehner 1989). Finally, the microvillar orientations of these specialized photoreceptors vary along the entire dorsal margin in close correspondence to the polarized light pattern of the sky (Wehner 1982, 1989). On the basis of these observations, it has been proposed that these dorsal marginal photoreceptors comprise a matched polarization filter, which permits the insect to orient itself with respect to the symmetrical array of sky *e*-vectors (Rossel and Wehner 1986; Wehner 1989). According to this "scanning" model, the insect rotates about its vertical body axis until a maximum overall response is obtained for all interneurons subserving the dorsal marginal region, at which point the insect's body is aligned with the solar meridian.

Morphological studies have revealed strikingly analogous dorsal marginal regions in the compound eyes of a number of other insect species, including lepidopterans (Meinecke 1981; Kolb 1986; Hämmerle and Kolb 1987), orthopterans (Burghause 1979; Egelhaaf and Dambach 1983), and dipterans (Wada 1971, 1974a). The properties of the specialized polarization-sensitive photoreceptor cells have been investigated in particular detail for the two dipteran species, *Musca domestica* and *Calliphora erythrocephala*. In these and other dipterans, the central photoreceptor cells R7 and R8 of the dorsal marginal ommatidia have features expected for polarized light analyzers (Hardie 1984; Wada 1974a, b; Wunderer and Smola 1982). Both cells contain the same UV-absorbing visual pigment, termed the 7p opsin, which is also present in ~30% of the nonmarginal R7 cell population. These cells also possess untwisted rhabdomeres and within each ommatidium, the R7 and R8 microvillar orientations are orthogonally arranged. Intracellular recordings from these cells have demonstrated up to 20-fold increases in sensitivity to light stimuli with *e*-vector directions parallel as opposed to perpendicular to the microvillar orientation (Hardie 1984). Injection of these cells with Lucifer yellow (Hardie 1984) and cobalt

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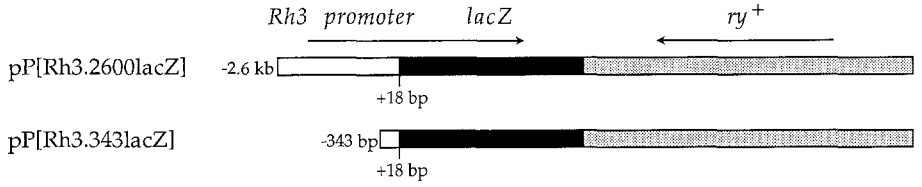


Fig. 1. *Rh3-lacZ* transcriptional fusion constructs used to produce transgenic *Drosophila* lines. Plasmid constructs pP[*Rh3.2600lacZ*] and pP[*Rh3.343lacZ*] contain *Rh3* promoter regions (*open rectangle*) extending 5′ to −2.6 kilobases (*kb*) and to −343 base pairs (*bp*), respectively, where +1 denotes the start of transcription. Both promoter segments extend 3′ to +18 bp of the 22-bp *Rh3* untranslated leader sequence and are fused to a 4.0-kb *E. coli lacZ* histological reporter gene (*solid rectangle*). The translational start region of this *lacZ* gene has been replaced with a eukaryotic start region from the *D. melanogaster Adh* gene (Mismer and Rubin 1987). These fusion genes are in the vector pDM30 (Mismer and Rubin 1987), which contains *rosy*$^+$ (*ry*$^+$; *shaded rectangle*) as the selectable marker for P element-mediated germline transformation. *Arrows* indicate the directions of transcription

(Strausfeld and Wunderer 1985) has revealed that they project unusually thick axons with exaggerated club-shaped terminals to the dorsal neuropil of the medulla, the second optic ganglion.

In this report, we describe the axonal projection pattern of these polarization-sensitive photoreceptor cells in the widely used experimental organism *Drosophila melanogaster*. Previous studies have shown that the *Drosophila* compound eye also possesses a specialized dorsal margin in which both central photoreceptor cells R7 and R8 contain a 7p-like opsin, Rh3 (Wada 1974a; Fortini and Rubin 1990). We have employed gene fusions of *Rh3* 5′ regulatory regions to the bacterial *lacZ* gene (encoding β-galactosidase) to create a sensitive histological marker for these cells and their axons. Serial sections through the compound eyes and optic lobes of transgenic flies bearing these *Rh3-lacZ* fusions has allowed us to reconstruct the complete axonal projection pattern of these specialized photoreceptor cells. A total of ~25 specialized R7/R8 pairs located along the extreme dorsal anterior eye margin extend axons through the optic chiasma to synaptic targets in the dorsal posterior neuropil of the medulla. Although these cells are present in only a single row of ommatidia, their synaptic terminals occupy the two most peripheral target rows of the corresponding medulla neuropil. Moreover, the axons and synaptic terminals of the dorsal marginal R7 and R8 cells generally exhibit more pronounced staining than those of nonmarginal R7 cells present in the same preparations, suggesting morphological specializations similiar to those of the equivalent axons in *Calliphora*. Our results indicate that the neuronal architecture of the dorsal eye margin and corresponding optic lobe regions specialized for the detection of polarized light is homologous between *Drosophila* and the larger dipterans *Musca* and *Calliphora*. Our data also emphasize the utility of histological marker gene fusions for the targeted visualization of functionally related neuronal assemblies, which is often not possible using more traditional dye injection techniques.

Materials and methods

Details concerning the construction of the *Rh3-lacZ* fusions pP[*Rh3.2600lacZ*] and pP[*Rh3.343lacZ*] and the production of transgenic *Drosophila* bearing these fusions are to be found in Fortini and Rubin (1990). Histochemical staining of 10- to 14-μm cryostat sections for β-galactosidase activity was performed as described by Mismer and Rubin (1987). Tissue sections were stained for 10–12 h at 37° C except for those shown in Fig. 2D and E, which were stained for 20 h at 37° C. The *sev*^{d2} allele used in this study was isolated by Banerjee et al. (1987).

Results

To label histologically the dorsal marginal photoreceptor cell axons in *Drosophila melanogaster,* we utilized the two *Rh3-lacZ* fusion gene constructs diagrammed in Fig. 1. Plasmid constructs pP[*Rh3.2600lacZ*] and pP[*Rh3.343lacZ*] contain 2.6 kilobases and 343 base pairs of *Rh3* 5′ promoter sequences, respectively. Previous analysis of the *Rh3* promoter has shown that both of these promoter fragments contain sufficient *cis*-acting regulatory sequences for proper quantitative and spatial expression of the *Rh3* gene (Fortini and Rubin 1990). Two transgenic fly lines were obtained for each construct using P element-mediated germline transformation. P[*Rh3.2600lacZ*]1 and 2 are insertions into the third chromosome; P[*Rh3.343lacZ*]1 and 2 are insertions into the X and third chromosomes, respectively. Within the retina, all four transgenic lines exhibit β-galactosidase activity in ~25 paired R7 and R8 cells along the dorsal anterior eye margin as well as ~30% of the nonmarginal R7 cells in the remainder of the eye (Fortini and Rubin 1990).

As seen in Fig. 2, diffusion of β-galactosidase throughout the cytoplasm of the photoreceptor cells allows their axonal projections and synaptic terminals in the optic lobes to be visualized histologically. In Fig. 2A, a horizontal section through the dorsal medulla of P[*Rh3.2600lacZ*]1 reveals two marginal R7 and two marginal R8 synaptic terminals at each edge of the medulla neuropil (circled terminals; at the topmost, anterior edge only one marginal R8 terminal is visible). The more central medulla regions contain the synaptic terminals of the nonmarginal *Rh3*-expressing R7 cells mentioned above, which are visible as small clusters of from one to three stained terminals that together form a discontinuous line of staining between the two marginal terminal locations. The discontinuity of this line reflects

the presence of unstained synaptic terminals corresponding to R7 cells that express *Rh4*, an alternative R7 opsin gene (Fortini and Rubin 1990). The marginal R8 terminals are located at a slightly more shallow level of the medulla than their paired marginal R7 terminals, which appear to be well-aligned with the stained synaptic terminals of nonmarginal *Rh3*-expressing R7 cells seen in the more central medulla neuropil.

The stained marginal R7 and R8 terminals in Fig. 2A define the two positions along the curved dorsal surface of the medulla neuropil that are intersected by this particular sectioning plane. Inspection of more dorsal sections shows that the marginal R7 and R8 terminals seen in Fig. 2A are cross sections of a continuous arc of such terminals occupying the two most peripheral R7 and R8 synaptic target rows of the dorsal medulla (cf. Fig. 3). The apex of this arc is clearly visible in Fig. 2B, which shows a horizontal section through the retina and medulla of P[*Rh3.2600lacZ*]2 at a more dorsal level than that of Fig. 2A. A single ommatidial row of dorsal marginal R8 cells in the retina and a number of their synaptic terminals in the dorsal medulla are stained in this section. Since *Drosophila* photoreceptor axons cross over each other in the horizontal plane at the first optic chiasma, the more anterior cells of the retina synapse in the more posterior regions of the medulla, and vice versa (cf. Fig. 2D). The location and extent of the dorsal medulla neuropil subserving these polarization-sensitive photoreceptor cells is seen perhaps most clearly in the tangential section of P[*Rh3.343lacZ*]2 shown in Fig. 2C. A dense arc of deeply stained synaptic terminals of the marginal photoreceptors is apparent along the dorsal posterior rim of the medulla neuropil. This preparation most likely represents a lengthwise cross section of the entire dorsal arc of marginal synaptic terminals. Faintly stained, irregularly spaced synaptic terminals seen elsewhere in this medulla are presumably those of nonmarginal *Rh3*-expressing R7 cells.

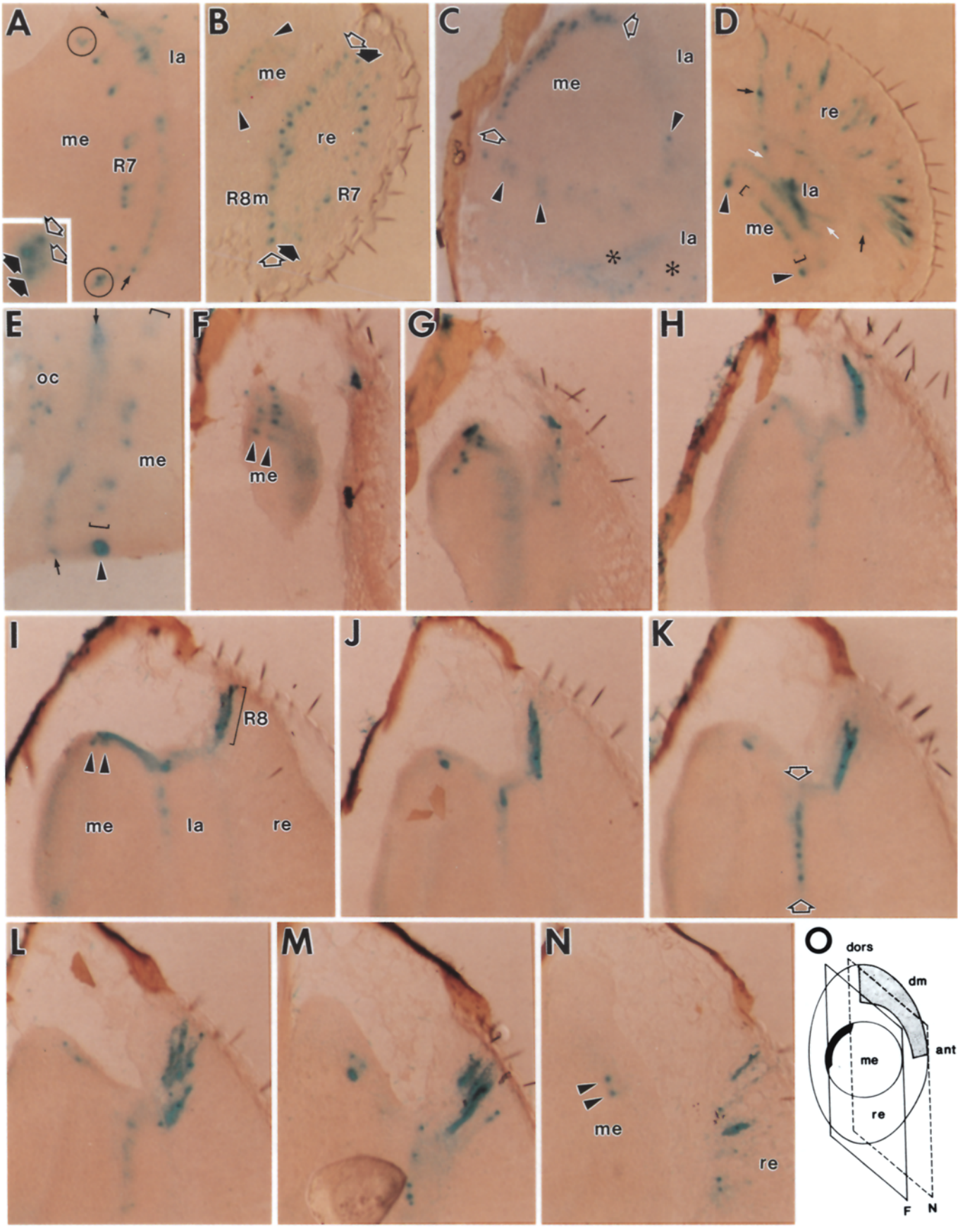
In almost all histological preparations of *Rh3-lacZ* transgenic head tissues, the synaptic terminals of the dorsal marginal central photoreceptors are more intensely stained than those of nonmarginal *Rh3*-expressing R7 cells (cf. Fig. 2B, C). This difference is most apparent in tissue sections that have been incubated for prolonged periods with the β-galactosidase staining solution. In Fig. 2D and E, well-stained horizontal sections through the compound eye and optic lobes of P[*Rh3.2600lacZ*]2 demonstrate that after emerging from the retina, heavily labeled axons of dorsal marginal central photoreceptor cells cross over each other at the optic chiasma and end with intensely stained terminals in the peripheral medulla neuropil. In contrast, axons and synaptic terminals of nonmarginal *Rh3*-expressing R7 cells display comparatively light staining in the same tissue sections.

To confirm that the stained synaptic terminals we observe in the dorsal medulla indeed correspond to specialized marginal photoreceptor cells, the *sevenless* (*sev*) mutation was used to eliminate R7 cells, which complicate the wild-type staining pattern. The *sevenless* mutation causes R7 cell precursors in the developing eye imaginal disc to incorrectly adopt a cone cell fate, resulting in the complete absence of R7 photoreceptors in the adult eye (Harris et al. 1976; Tomlinson and Ready 1986). The only stained synaptic terminals in *Rh3-lacZ* transgenic flies bearing the *sevenless* mutation should therefore correspond to specialized dorsal marginal R8 photoreceptor cells. A set of nine serial sections through dorsal head tissues of sev^{d2}; P[*Rh3.2600lacZ*]1 is presented in Fig. 2F–O. The eyes of genetically identical siblings were examined by antidromic illumination after optical neutralization of the cornea (Franceschini and Kirschfeld 1971a, b) to ensure that the sev^{d2} mutant phenotype is fully penetrant. No R7 cells were observed in any ommatidia, including those of the dorsal eye margin (data not shown). In the more posterior sections of sev^{d2}; P[*Rh3.2600lacZ*]1, two rows of marginal R8 synaptic terminals are seen ascending the steep posterior dorsal rim of the medulla (Fig. 2F–H; cf. Fig. 3). Vertically oriented R8 cell bodies also begin to display staining in these sections, marking the posterior limit of the dorsal marginal region in the retina. As the plane of sectioning proceeds more anteriorly, approximately two labeled R8 synaptic terminals of the dorsalmost medulla are observed in each section and the marginal R8 cells of the retina assume increasingly frontolateral visual axes (Fig. 2I–O; cf. Fig. 3). Additional dots of staining at the lamina-medulla interface represent axons of more anteriorly located marginal R8 cells bodies projecting through the sectioning plane to their synaptic targets in more posterior regions of the medulla (Fig. 2K; cf. Fig. 3).

Discussion

Histochemical analysis of *Rh3-lacZ* transgenic lines has allowed us to elucidate the neuronal architecture of the polarization-sensitive dorsal anterior eye margin in *Drosophila melanogaster* (Fig. 3). Within the retina, a single ommatidial row directly adjoining the head cuticle of the vertex and frons contains ~25 pairs of specialized R7 and R8 cells. This marginal region of the *Drosophila* eye is homologous to the corresponding areas of the *Musca* and *Calliphora* compound eyes, except that the specialized dorsal margin encompasses up to six ommatidial rows at its widest point in the larger dipterans (Wada 1974a, b; Wunderer and Smola 1982). Based on the figure of 776 ommatidia per eye for *Drosophila* (Ready et al. 1976), this region comprises 3.2% of the total number of ommatidia. The amount of the *Drosophila* eye devoted to polarized light detection is thus comparable to the amounts calculated for other insects (*Apis*, 2.5%; *Cataglyphis*, 6.6%: Wehner 1982, 1989; *Calliphora*, 3.2%: Wada 1974b).

Long axons from these specialized dorsal marginal photoreceptors cross over each other at the first optic chiasma and project to synaptic targets in the two most peripheral R7 and R8 terminal layers of the dorsal posterior medulla (Fig. 3). In *Calliphora erythrocephala*, the only other dipteran species for which such data are available, the synaptic terminals of these cells occupy approximately three target rows in the equivalent region of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the medulla neuropil and extend slightly deeper into the medulla than adjacent nonmarginal R7 and R8 terminals (Strausfeld and Wunderer 1985; Nässel et al. 1988). In addition, these cells in *Calliphora* were found to possess thickened axons and enlarged club-shaped terminals. Homologous morphological specializations of these photoreceptor neurons in *Drosophila* are suggested by the more pronounced β-galactosidase staining observed for their axons and terminals relative to those of nonmarginal *Rh3*-expressing R7 cells. In *Drosophila*, the marginal cell terminals do not penetrate noticeably deeper into the medulla than their nonmarginal neighbors, but subtle differences in depth may be obscured by their enhanced β-galactosidase staining (cf. Fig. 2E). A subset of the dorsal marginal ommatidia in *Calliphora* have also been found to project axons in an unusual "double pseudocartridge" arrangement consisting of 12 peripheral axons and 4 central axons of two adjacent ommatidia (Wunderer and Smola 1982). If the dorsal marginal ommatidia of *Drosophila* participate in similar pseudocartridge formation, the close apposition of central photoreceptor axons could also contribute to their enhanced staining.

An alternative explanation for the axonal staining differences observed in *Drosophila* is that the *Rh3* promoter is simply more active in dorsal marginal R7 and R8 cells than in nonmarginal *Rh3*-expressing R7 cells. This explanation seems unlikely for two reasons. First, we do not see such staining differences between the cell bodies of marginal and nonmarginal *Rh3*-expressing photoreceptors (Fig. 2B and D; see also Fortini and Rubin 1990). Second, a quantitative analysis of expression levels of the *Rh3* promoter fragments used in P[*Rh3.2600lacZ*] and P[*Rh3.343lacZ*] has shown that head-specific promoter activites are consistently reduced to ~10% of their wild-type levels when assayed in sev^{d2} flies (Fortini and Rubin 1990). Since a wild-type eye contains ~275 *Rh3*-expressing photoreceptor cells (0.3 × [776 total R7 − 25 marg R7] + 50 marg R7/R8) whereas a *sevenless* eye contains ~25 *Rh3*-expressing R8 cells, comparable *Rh3* promoter activities may be in-

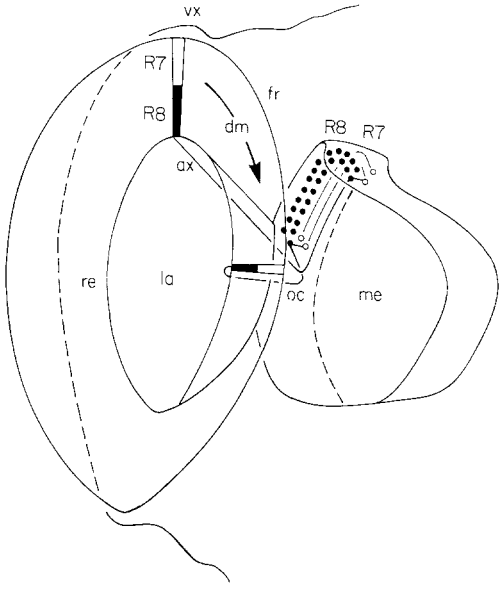

Fig. 3. Diagram of the optic lobe projection pattern of polarization-sensitive photoreceptor cells in *Drosophila melanogaster*. A single row of ~25 ommatidia located along the extreme dorsal anterior eye margin contains specialized *Rh3*-expressing R7 and R8 cells; for clarity, only the two ommatidia that define the anterior and posterior limits of this region are shown. These specialized photoreceptors project axons to the two most peripheral R7 (*open circles with fine connecting lines*) and R8 (*solid circles*) synaptic target layers of the dorsal posterior medulla (*dm* dorsal margin; *re* retina; *la* lamina; *me* medulla; *oc* optic chiasma; *ax* R7/R8 axons; *vx* vertex; *fr* frons)

Fig. 2A–O. Histological analysis of wild-type and *sevenless Rh3-lacZ* transgenic fly compound eye and optic lobe structures. **A** Horizontal section through wild-type P[*Rh3.2600lacZ*]1 medulla (*me*) and lamina (*la*) neuropil showing two localized sets of dorsal marginal R7 and R8 synaptic terminals (*circled*) that together flank a discontinuous line of nonmarginal *Rh3*-expressing R7 cell terminals (*R7*). Micrograph is oriented with *anterior* at *top*. Additional staining between and to the right of the *two small arrows* is due to the characteristic swelling of photoreceptor axons prior to entering the medulla (Fischbach and Dittrich 1989). *Inset:* A higher magnification view of the posterior (bottom in **A**) set of circled dorsal marginal terminals showing two R7 (*solid arrows*) and two R8 (*open arrows*) terminals. **B** Horizontal section through the dorsalmost retina (*re*) and medulla (*me*) of wild-type P[*Rh3.2600lacZ*]2 showing dorsal marginal R8 cells (*R8m;* between *open arrows*) and nonmarginal *Rh3*-expressing R7 cells (R7; between *solid arrows*) in the retina as well as marginal synaptic terminals (between *arrowheads*) in the medulla. Micrograph is oriented with *anterior* at *bottom*. **C** Sagittal section through the medulla (*me*) of wild-type P[*Rh3.343lacZ*]2 revealing a region of intensely stained marginal synaptic terminals along the dorsal posterior medulla (between *open arrows*) and more faintly stained axons (regions with *asterisks*) and terminals (indicated by *arrowheads*) of nonmarginal *Rh3*-expressing R7 cells. Micrograph is oriented with *dorsal* at *top, anterior* to the *right; la* lamina. **D** Horizontal section through compound eye and optic lobes of wild-type P[*Rh3.2600lacZ*]2 stained for 20 h. Two dorsal marginal R8 cells (*two black arrows*) and nonmarginal *Rh3*-expressing R7 cells display staining in the retina (*re*). Marginal cell axons (*two white arrows*) and synaptic terminals (*two arrowheads*) of the peripheral lamina (*la*) and medulla (*me*), respectively, stain more intensely than those of nonmarginal cells present in the more central lamina and medulla neuropil (*bracketed region*). Micrograph is oriented with *anterior* at *top*. **E** Horizontal section at higher magnification through the dorsal posterior medulla of wild-type P[*Rh3.2600lacZ*]2 stained for 20 h. *Arrowhead* indicates intensely stained synaptic terminals of marginal photoreceptor cells; *bracketed region* contains stained nonmarginal *Rh3*-expressing R7 cell terminals; *two small arrows* indicate region of axon swelling between the optic chiasma (*oc*) and medulla (*me*) as in **A**. Micrograph is oriented with *anterior* at *top*. **F–N** Consecutive serial sections through dorsal retina and optic lobe tissues of sev^{d2}; P[*Rh3.2600lacZ*]1, proceeding from posterior (**F**) to anterior (**N**) medulla neuropil; all micrographs are oriented with *dorsal* at *top*. *Solid arrowheads* in **F, I** and **N** indicate marginal R8 cell synaptic terminals; *open arrows* in **K** indicate a row of marginal R8 axons projecting through the plane of section at the optic chiasma; *R8 bracket* in **I** refers to the R8 cell body in the retina (*re* retina; *la* lamina; *me* medulla). **O** Schematic sagittal view of a *D. melanogaster* retina (*re*) and underlying medulla (*me*), showing the approximate locations of the oblique sagittal sectioning planes in **F** and **N**. The shaded portion of the retina corresponds to the dorsal marginal region (*dm*) and the solid area of the medulla denotes the specialized marginal photoreceptor synaptic target region (*dors* dorsal; *ant* anterior). **A, C, F–N** ×250; **A** *inset* ×800; **B** ×200; **D** ×160; **E** ×400

ferred for marginal versus nonmarginal *Rh3*-expressing photoreceptor cells.

Specific labeling of dorsal marginal R7 and R8 cells in *Rh3-lacZ* transgenic *Drosophila* should facilitate the identification of their postsynaptic interneurons in the medulla responsible for relaying information about the polarized light content of the sky to higher-order processing centers of the optic lobes and central brain. Transsynaptic cobalt migration in *Calliphora* has revealed that these photoreceptor cells are coupled to an assembly of columnar neurons, which extend to marginal zones of the ipsilateral lobula and lobula plate. Long columnar neurons originating in the lobula marginal zone project, in turn, to the equivalent regions of the contralateral lobula and medulla, implying that each of these optic lobes receives inputs from the dorsal marginal field of both eyes (Strausfeld and Wunderer 1985). Although the interneurons postsynaptic to polarization-sensitive photoreceptor cells have yet to be identified in *Drosophila,* certain neural cell types are apparently restricted to optic lobe regions subserving the dorsal frontal visual field, including particular columnar neurons of the medulla and long heterolateral columnar neurons connecting both lobulae via the great commissure (Fischbach 1983; Fischbach and Dittrich 1989). These heterolateral neurons of *Calliphora* and *Drosophila* may mediate interocular transfer of polarized light directional cues, which has been demonstrated to occur in foraging ants (Wehner and Müller 1985).

Two studies have shown that *Drosophila* is apparently able to orient with respect to linearly polarized light (Stephens et al. 1953; Wolf et al. 1980). However, in both studies the polarotactic response was elicited primarily by light stimuli in the visible range. Furthermore, the more recent study claims that the dorsal and ventral eye regions are equally sensitive to *e*-vector direction and that the R7 and R8 photoreceptor cells make no significant contribution to polarized light detection (Wolf et al. 1980). The results of these behavioral studies are difficult to reconcile with our description of a presumably polarization-sensitive dorsal eye margin in *Drosophila* characterized by highly specialized R7 and R8 cells containing the purely UV-absorbing *Rh3* opsin (Harris et al. 1976; Zuker et al. 1987). Our data suggest that polarized light orientation in *Drosophila* might best be tested with a UV stimulus in experimental paradigms based upon those which have already been used successfully to demonstrate such abilities in bees and ants (Wehner and Strasser 1985; Fent 1986; Wehner 1989). Finally, the neuroanatomical similarity of the *Drosophila* dorsal eye margin to the equivalent eye regions of other insect species raises the possibility of using the powerful molecular and genetic techniques available for the fruit fly to investigate common mechanisms of insect polarized light navigation.

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