



SMR.853 - 29

ANTONIO BORSELLINO COLLEGE ON NEUROPHYSICS

(15 May - 9 June 1995)

**"Processing of Visual Input in the Fruitfly *Drosophila* - I
Conversion of the Retinal Image into a Stack of Sensory
Maps; Hereditary Defects"**

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These are preliminary lecture notes, intended only for distribution to participants.

INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
 The Processing and Use of Sensory Information in Biological Systems
 Antonio Borsellino College on Neurophysics, Trieste, 15 May - 9 June 1995

**PROCESSING OF VISUAL INPUT IN THE FRUITFLY *DROSOPHILA*, I.
 CONVERSION OF THE RETINAL IMAGE INTO A STACK OF SENSORY MAPS;
 HEREDITARY DEFECTS**

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Information processing in the compound eye

Vision is limited by the properties of the eyes and by the capacity of the visual system. The hexagonal array of lenses and the combination of different photoreceptors in the compound eyes of the fruitfly select a small portion of essential data from the incoming flow of visual information for further processing in the optic lobes. About 86% of the visual environment of the fly is imaged onto the photoreceptors of about 1400 visual elements. Each of these elements uses 'neuronal optics' to collect the signals from 6 peripheral receptors (R1-6) and a tandem-like structure of 2 central receptors (R7+8) which belong to different ommatidia but happen to receive light from a common sampling point within the visual field (Fig. 1).

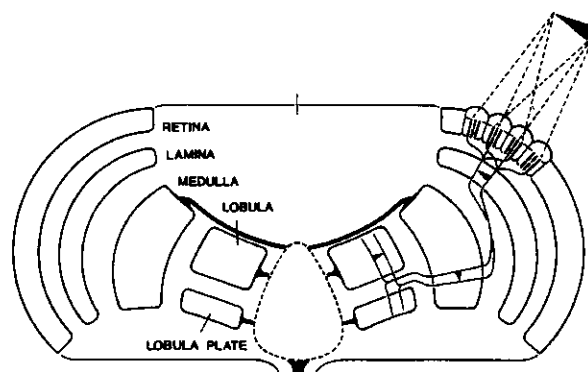


Fig. 1 Compound eyes and optic neuropile in a simplified horizontal section through the head of the fruitfly (width about 0.7 mm). Tip and base of the arrow heads illustrate the position of neighbouring sampling points in the visual field, the collection of light signals by the corresponding visual elements and the representation of the visual information in adjacent 'columns' of the optic lobes.

Light-induced automatic gain control is found in all of these receptors. Contrast vision in dim light is intensified by superposition of the signals from the light-sensitive receptors R1-6 which seem to be functionally equivalent to the 'rods' in the human retina. Colour vision requires sufficient illumination to activate the receptors R7+8 which seem to be functionally equivalent to the 'cones' in the human retina. Night-blindness or colour-blindness occurs in mutants with defects in one of the two receptor systems (Fig. 2).

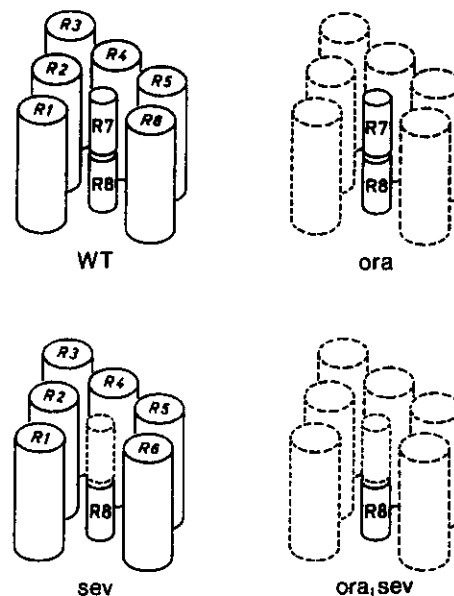


Fig. 2 Light-sensitive structures (rhabdomeres) of the eight photoreceptors in the ommatidia of the fruitfly. Wild type (WT), mutant *outer rhabdomeres absent* (*ora*), mutant *sevenless* (*sev*) and double-mutant combining the two defects (*ora; sev*). Movement perception is linked to the receptor system R1-6.

Neuronal structure of the visual system

At least half of the neurons in the CNS of *Drosophila* is found in the optic neuropile shown in Fig. 1. This neuropile consists of a 2-dimensional array of about 1400 'columns'. Each of these columns is the neuronal appendage of a visual element with direct access to local information from one of the sampling points of the visual field. Adjacent sampling points are represented by adjacent columns. From their origin in the 1st optic lobe (lamina) the columns ascend through the outer chiasma and the 2nd optic lobe (medulla) to the inner chiasm, where they split into branches passing through the two compartments of the 3rd optic lobe (lobula, lobula plate). On their way through the three lobes the columns penetrate 'layers' of tangential neurons. Each of these layers represents a retinotopic projection, or 'sensory map', of the visual field. The tangential neurons contribute to (1) the comparison, processing and summation of signals from different sampling points, (2) the connection of layers on

either side, and (3) the projection of visual information onto higher centres of the brain. Some mutants show the suppression of 'isomorphic sets' of neurons either in the columns or in the layers of the optic neuropile (Fig. 3). Comparison of the neuroanatomical defects and their behavioural correlates helps to reveal the functional architecture of the visual system in *Drosophila*.

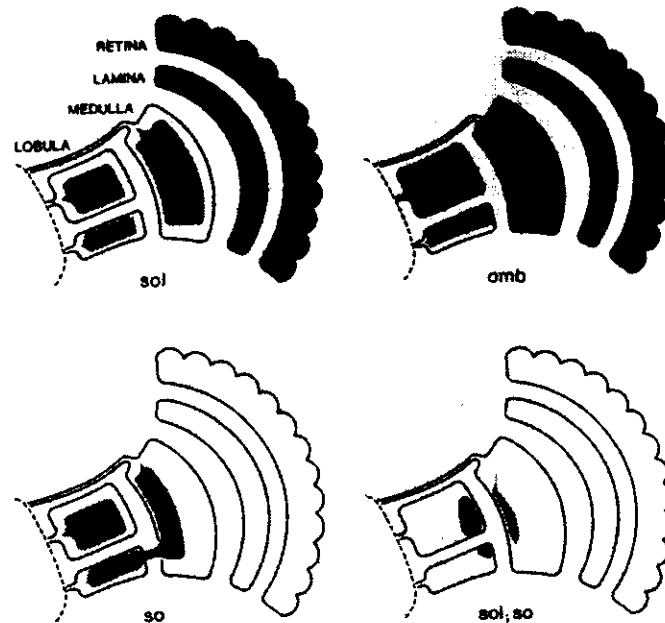


Fig. 3 Simplified horizontal section showing the right side of the visual system of the fruitfly. The contours indicate the cross-sections of the retina and the three optic lobes in the wild type. The dark areas represent the remaining retinal and nervous tissue in the mutants' *small optic lobes* (*sol*), *optomotor-blind* (*omb*), *sine oculis* (*so*) and the double-mutant combining the two complementary defects (*sol; so*).

Genetic dissection of the visual system; Five examples

Outer rhabdomeres absent (*ora*^{JK84}; chromosomal position 3-65.3; first described by Harris et al. 1976) suppresses photopigment synthesis and reduces the large rhabdomeres of the photoreceptors R1-6 to rudiments. Movement-induced reactions of the visual system and physiological activity in the corresponding 'layers' of the lobula plate are almost completely absent (Fig. 2).

Sevenless (*sev*^{LY3}; chromosomal position 1-33.4; first described by Harris et al. 1976) suppresses development of photoreceptor R7. This impairs the transfer of light signals to photoreceptor R8 which requires the rhabdomere of R7 as a light-guide. Deficient responses

in colour discrimination test. Movement-induced reactions of the visual system as in wild type flies (Fig. 2).

Small optic lobes (*sol*^{KS58}; chromosomal position 1-68; first described by Fischbach and Heisenberg 1981). About 50% of the isomorphic sets of columnar neurons in the medulla, lobula and lobula plate die during early pupal development. Movement-induced reactions of the visual system are normal in many respects. Relapse to pre-programmed optomotor responses in a sub-system of axillary flight-control muscles (Fig. 3).

Sine oculis (*so*¹; chromosomal position 2-57.1; history see Lindsley and Zimm 1992) causes degeneration of eye cells during early pupal development. Retina, lamina and distal medulla are absent or rudimentary. The proximal medulla and the lobula complex retain the columnar organisation of the neuropile in the wild type. However, more than 50% of the isomorphic sets of columnar neurons are missing in the mutant. Most of these sets seem to be different from the isomorphic sets missing in *sol*: Fischbach and Technau (1984) showed the almost complete elimination of columnar neurons in the double-mutant *sol*; *so* (Fig. 3).

Optomotor blind (*omb*^{H31}; chromosomal position close to the distal break-point of an inversion in the 1-4C region; first described by Heisenberg et al. 1978). Movement-sensitive giant tangential neurons of the horizontal system (HS) and the vertical system (VS) in the lobula plate are absent or rudimentary. The neurons of these systems are associated with rotation-induced optomotor reactions to yaw, pitch and roll which are deficient in *omb*. Neither translation-induced altitude control nor object-induced tracking are significantly impaired (Fig. 3).

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