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**“Processing of Visual Input in the Fruitfly *Drosophila* - II
Motion Parallax between Figure and Ground Helps to Select
Accessible Targets”**

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

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**PROCESSING OF VISUAL INPUT IN THE FRUITFLY *DROSOPHILA*, II.
MOTION PARALLAX BETWEEN FIGURE AND GROUND HELPS TO SELECT
ACCESSIBLE TARGETS**

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Resolution of movement into four directional components

The retinal signals processed in about 1400 'columns' of the visual system induce 2-dimensional patterns of nervous activity in the retinotopic 'layers' of the lobula plate. These patterns seem to represent different components of movement within the visual field of the fruitfly. 'Sensory maps' for backward, forward, upward and downward movement have been identified on autoradiographs of the brain showing the stimulus-specific accumulation of ³H-deoxyglucose metabolites in the activated array of tangential neurons (Buchner and Buchner 1984). The anatomical counterparts of these neurons in larger flies are accessible for electrophysiological investigation (Hausen 1981). The computation of the patterns of activity within the 'sensory maps' and the evaluation of these patterns for the optomotor control of course and altitude during free flight require only a few percent of the neurons of the CNS. This portion of the nervous system is aptly described as a parallel array of neuronal processors providing special information for both the control of locomotion with respect to the visual environment and the discrimination, tracking and pursuit of selected visual objects.

Resolving power and acuity of the movement-detecting system

Movement-induced visual orientation is accomplished by evaluation of the directional components of drift within the retinal image of the surroundings. This requires direction-specific neuronal interactions between contiguous columns of the visual system. The columnar input is characterized by the angular distance $\Delta \phi$ and the angular width $\Delta \rho$ of the visual fields (Fig. 1A, B). The stimulus used to determine the respective parameters of the movement-detecting system consists of a continuous sequence of dark and bright stripes of a given spatial wavelength λ (the angular width of a pair of stripes) and angular velocity w . Gradually decreasing λ inevitably leads into a domain of non-natural stimulation. Two effects

are expected in this domain: (1) an inversion of the torque response due to incomplete resolution of the pattern at stripe widths $\lambda/2 < \Delta \phi$, and (2) a decrease in the response due to incomplete contrast transfer at stripe widths $\lambda/2 < \Delta \rho$. Distance $\Delta \phi$ and width $\Delta \rho$ derived from the optomotor reactions in Fig. 1C correspond to the angular distance between nearest neighbours in the array of visual elements. Any improvement in the resolving power of the movement-detecting system and in the acuity of its input elements would require a decrease in the distance $\Delta \phi$ and in the width $\Delta \rho$, respectively. However, the product $\Delta \phi \Delta \rho$ is proportional to the square root of the number of quanta per second received at a given illumination. This product cannot be reduced without loss of sensitivity in dim light. The ratio $\Delta \phi / \Delta \rho$ is not fixed by this condition. Optimum imaging requires a ratio close to 1. This ratio has been found in the movement-detecting system of *Drosophila* (Götz 1965, Buchner 1984).

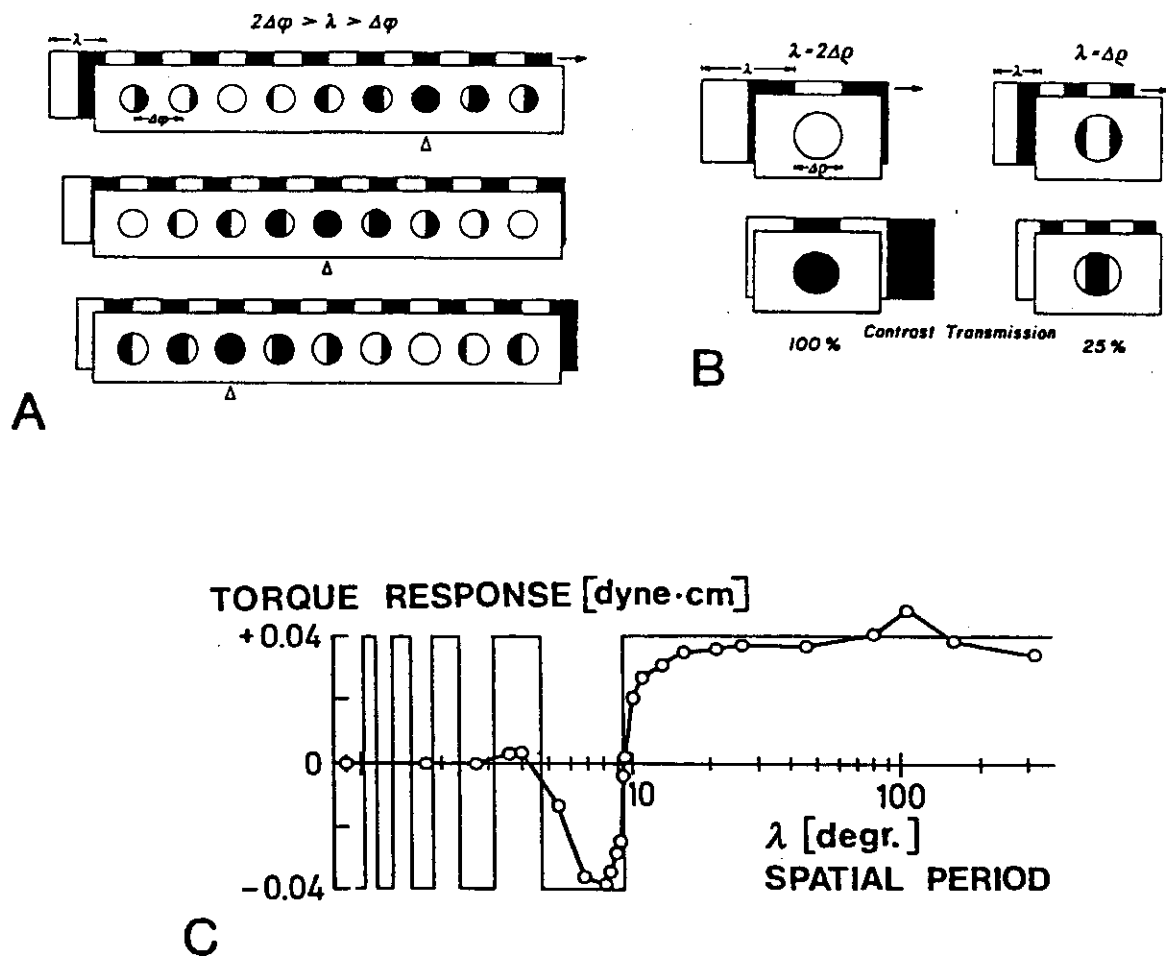


Fig. 1. A striped pattern described by its comparatively small period λ is moving in front of columnar visual fields which are characterized by their distance $\Delta \phi$ and width $\Delta \rho$. Incomplete resolution of the pattern (A) and incomplete transfer of its contrast (B) invert the sign and decrease the magnitude of the optomotor course-control response (C). The results have been used to determine both resolution and acuity of the movement-detecting system in the fruitfly.

Networks of elementary movement detectors

The properties of the elementary movement detectors have been analysed in some detail (Buchner 1984, Bülthoff and Götz 1979, Götz 1965, 1972, 1980, 1983a, Heisenberg and Wolf 1984). The steady-state responses of the detectors are adequately described by a correlation model of the Reichardt-Hassenstein type (Poggio and Reichardt 1976, Reichardt and Poggio 1976), where the interaction is calculated by multiplication and subsequent temporal averaging of two input signals, $G(t)$ and $G(t-\Delta t)$ (first-order autocorrelation). The model is representative of all 'simple' movement detectors which do not require more than the theoretical minimum of two input units in second-order non-linear interaction. Models of this type are equivalent in their steady-state responses, and seem to be sufficient to describe the properties of entirely different movement detection systems such as the direction-selective retinal ganglion cells in vertebrates (Torre and Poggio 1978).

Movement-induced flight control

Drosophila responds to moving landmarks in almost any part of the visual field. This requires the integration of signals from movement detectors in different eye region. The integration seems to be remarkably simple: the course-control response is proportional to $N_{CW} - N_{CCW}$ if the same pattern is moving clockwise within a zone comprising N_{CW} visual elements, and simultaneously counterclockwise in a zone comprising N_{CCW} visual elements. The algebraic sum of the contributions of an array of movement detectors seems to determine the course-control response. However, aimless course control is only one aspect of flight behaviour. Detector fields with vertically oriented direction enable the fly to control altitude, pitch and roll. Much work in contemporary fly research is focused on the sophisticated systems required for the recognition, selection and pursuit of moving objects.

Object-induced flight control: instructional and operant orientation

At least 3 of the 17 non-fibrillar flight-control muscles on either side of the *Drosophila* thorax convert movement-specific visual information into optomotor reactions in the amplitude of the beating wings. Each pair of these muscles contributes not only to the stabilization of course and altitude with respect to the surroundings, but also to the fixation of prominent objects in the frontal area of the visual field (Götz 1983a, b, Heide 1983).

Object-induced orientation has been investigated in the flight simulator shown in Fig. 2A, which allows the tethered fly to manoeuvre a dark vertical bar into arbitrary angular positions between 180° left and 180° right of the fixed course. The histograms in Fig. 2B, C show the relative time spent by the object in sectors of 18° bin-width. A maximum at the centre indicates preference of orientation towards the object (fixation). Maxima on either side result from preferred orientation in the opposite direction (antifixation). The angular speed of the bar was controlled by the difference between the wingbeat amplitudes on each side (Fig. 2B), or by the difference between the activities of a selected subsystem of flight-control muscles

on each side (Fig. 2C). Object motion in the opposite direction of the intended turns simulates the expected sensory feedback (+). Inversion of the expected feedback (-) creates artificial conditions which do not occur in a normal environment. Alternation between these options has revealed different strategies of object-induced orientation in *Drosophila* (Götz 1985, Wolf and Heisenberg 1986). The results obtained in the wild type (WT) and in the mutant '*small optic lobes*' (*sol*) are described in the legend to Fig. 2.

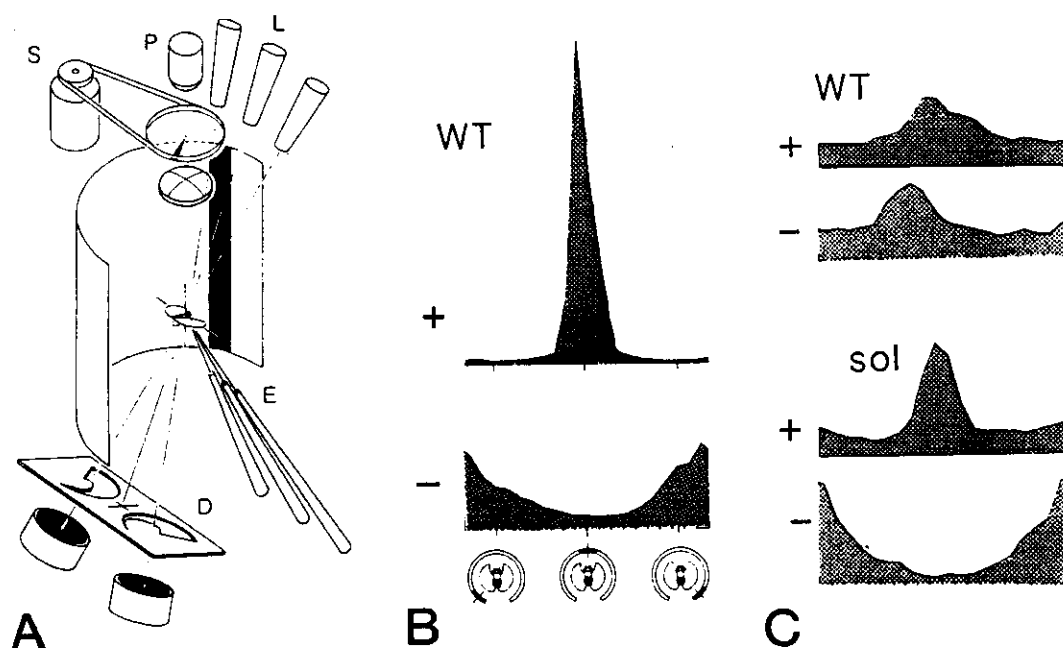


Fig. 2. (A) Flight simulator. Spotlights L were used to adjust the fly in the centre, and to cast shadows of the beating wings onto contralateral mask openings of a photoelectric device D for the measurement of the intended turns. Micro-electrodes E were required to specify the contribution of selected muscular subsystems. The signals from D or E act on servomotor S which controls the angular speed of a vertical bar on the (partly dissected) cylindrical screen by rotating a circular diapositive between the lamp and lens of projector P. (B) Orientation in the flight simulator. Essential actions of the visual stimulus on the wingbeat amplitudes of the wild type (WT) are programmed to achieve 'instructional' object fixation if the conditions are comparable with free flight (+). Anti-fixation is the expected consequence of signal inversion (-). (C) The flexibility of 'operant' object fixation enables a subsystem of axillary flight control muscles in the wild type to cope with signal inversion. Relapse to 'instructional' object fixation was found in the corresponding subsystem of the mutant '*small optic lobes*'.

'Instructional' orientation results from preprogrammed course-control responses to the signals received from a moving object. These responses prevail in the combined actions of the

course-control system (Fig. 2B) and in at least two of its subsystems: a pair of basalar flight-control muscles (b1 in Heide's nomenclature), and a pair of sterno-basalar flight-control muscles (b2). In a third subsystem, a pair of anterior 1st axillary flight-control muscles (I1), the instructional responses of the muscles b1 and b2 seem to be replaced by a more flexible approach to object fixation (Fig. 2C): the 'operant' orientation established in the WT experiment is likely to be explained by a trial-and-error strategy based on 'nearness of the goal', a non-directional visual instruction which cannot be confused by the inversion of the perceived object motion (Wolf and Heisenberg 1986). The results in Fig. 2 show both the functional coexistence and the structural separation of 'instructional' and 'operant' strategies.

A 50-percent decrease in the number of columnar neurons of the proximal optic lobes does not seem to impair the essential responses to visual stimulation in the mutant '*small optic lobes*'. The optomotor control of course and altitude and a number of related reactions are surprisingly normal in this mutant (Fischbach and Heisenberg 1981, Götz 1983b, Heisenberg and Wolf 1984). The missing subsystem of columnar neurons seems to have different functions in the visual system of the wild type. One of these functions could be to recruit the 'instructional' circuits of the visual system for flexible strategies of the brain. The relapse to 'instructional' orientation in one of the muscular subsystems of *sol* (Fig. 2C) does not eliminate 'operant' strategies from the nervous system; the mutant can still be trained to invert the action of the course-control system if this is made conditional to object fixation (Götz 1983b).

The present example illustrates the contribution of mutants to the analysis of structure and function in the brain of *Drosophila*. Other mutants have been used, for instance '*optomotor-blind*' to distinguish movement-induced from object-induced orientation, and '*outer rhabdomeres absent*' as well as '*sevenless*' to allocate these responses to the light-sensitive subsystem of the rhabdomeres R1-6 (Heisenberg and Wolf 1984).

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