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Vision in Drosophila I
Conversion of the retinal image into a stack of sensory maps;
Hereditary defects

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INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS

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VISION IN 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, from the incoming flow of visual information, a small portion of essential data 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 of the visual field (Fig. 1). Light-induced automatic gain control is found in all of these receptors. Contrast vision at 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 occur in mutants with defects in one of the two receptor systems (Fig. 2).
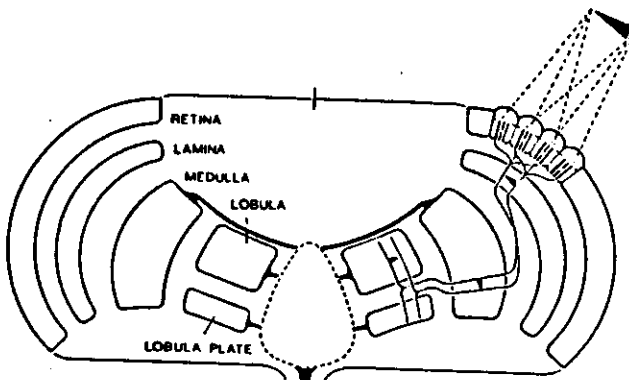

Fig. 1 Compound eyes and optic neuropile in a simplified horizontal section through the head of the fruitfly (width about 0.7 mm). Tip and base of the arrow heads illustrate the position of neighbouring sampling points in the visual field, the collection of light signals by the corresponding visual elements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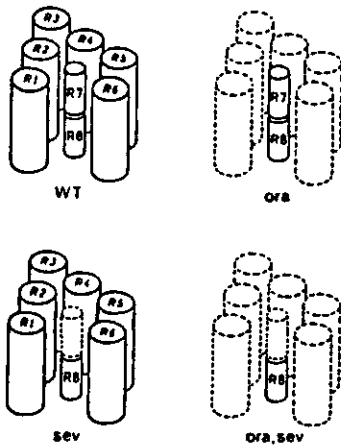
Genetic dissection of the visual system; Five examples

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 missing (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 wildtype 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 subsystem of axillary flight-control muscles (Fig. 3).

Sine oculis (*so*[1]; chromosomal position 2-57.1; history see Lindsley and Grell 1968) 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 wildtype. 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 breakpoint 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 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*. Translation-induced altitude control, and object-induced tracking, are not significantly impaired (Fig. 3).

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VISION IN DROSOPHILA II.
FLIGHT CONTROL BY EVALUATION OF THE MOVEMENTS OF FIGURE AND GROUND

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Resolution of movement into four directional components

The retinal signals processed in about 1400 'columns' of the visual system induce, in the retinotopic 'layers' of the lobula plate, 2-dimensional patterns of nervous activity which 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 the brain showing the stimulus-specific accumulation of ^{3}H-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, requires 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 by 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 given spatial wavelength λ (the angular width of a pair of stripes) and angular velocity w. Gradual decrease of λ inevitably leads into a domain of non-natural stimulation. Two effects are expected in this domain: (1) Inversion of the torque response due to incomplete resolution of the pattern at stripe widths $λ/2 < Δφ$, and (2) decrease of the response due to incomplete contrast transfer at stripe widths $λ/2 < Δρ$. The distance Δφ and the width Δρ, derived from the optomotor reactions in Fig. 1C correspond to the angular distance between nearest neighbours in the array of visual elements. Any improvement of the resolving power of the movement detecting system and of the acuity of its input elements would require a decrease of the distance Δφ and of the width Δρ, respectively. However, the product ΔφΔρ is proportional to the square root of the number of quanta per second received at a given illumination. This product cannot be
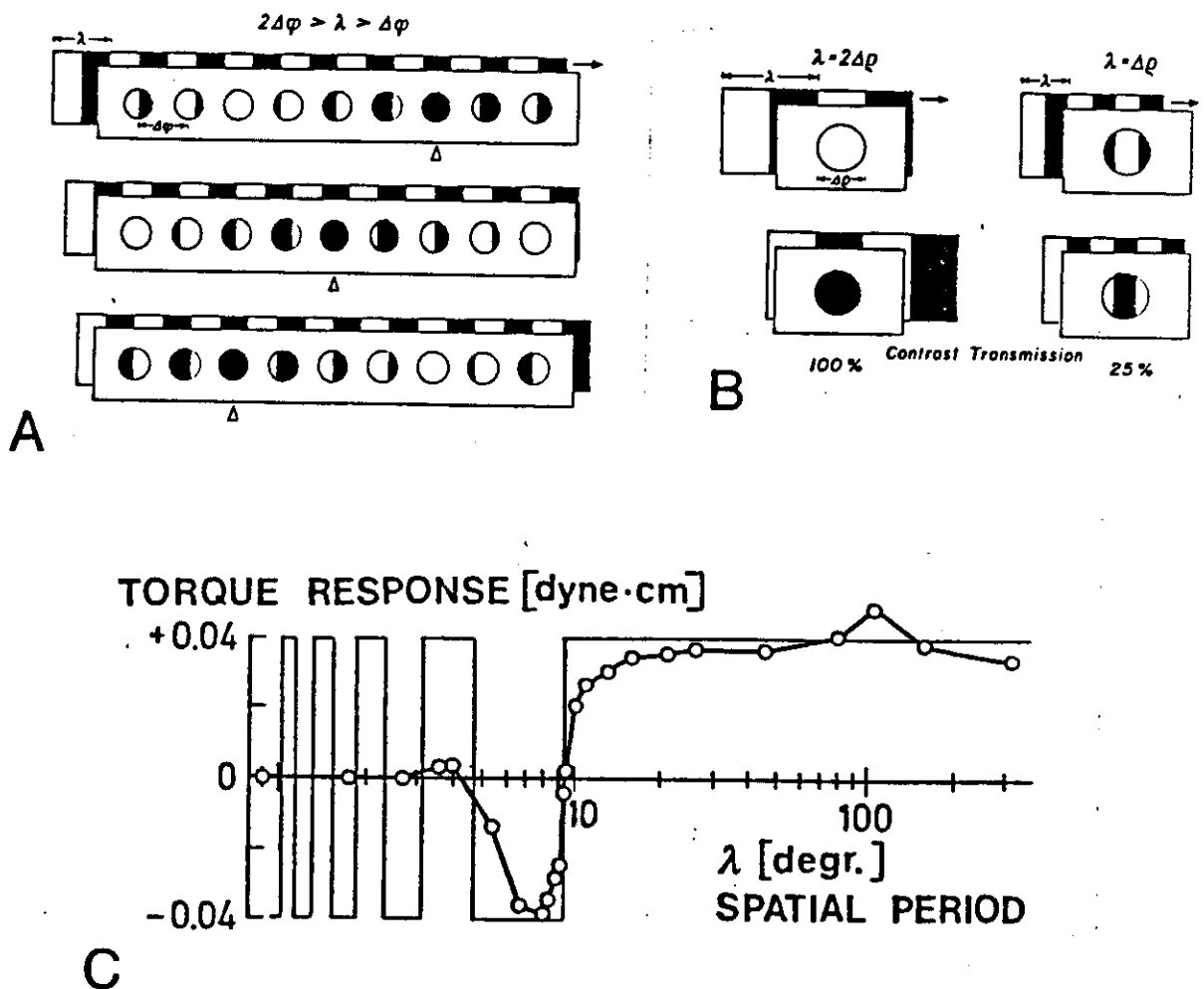
Fig. 1. A striped pattern described by its comparatively small period λ is moving in front of columnar visual fields which are characterized by their distance Δφ and width Δρ. Incomplete resolution of the pattern (A) and incomplete transfer of its contrast (B) invert the sign and decrease the magnitude 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.

reduced without loss of sensitivity at 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).

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 achieved by multiplication and subsequent temporal averaging of two input signals, G(t) and G(t-Δt) (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 entierely 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 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 vertical preferred direction enable the fly to control altitude, pitch and roll. Much work in contemporary fly research is focussed on the sophisticated systems required in order to recognize, select and pursue 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 of the wingbeat amplitudes. 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 a 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 center indicates preference of orientation towards the object (fixation). Maxima on either side result from preferred orientation in the opposite direction (anti-fixation). The angular speed of the bar was controlled by the difference between the wingbeat amplitudes on either side (Fig. 2B), or by the difference between the activities of a selected subsystem of flight-control muscles on either side (Fig. 2C). Object motion in 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 wildtype (WT) and in the mutant 'small optic lobes' (sol) are described in the legend of Fig. 2.
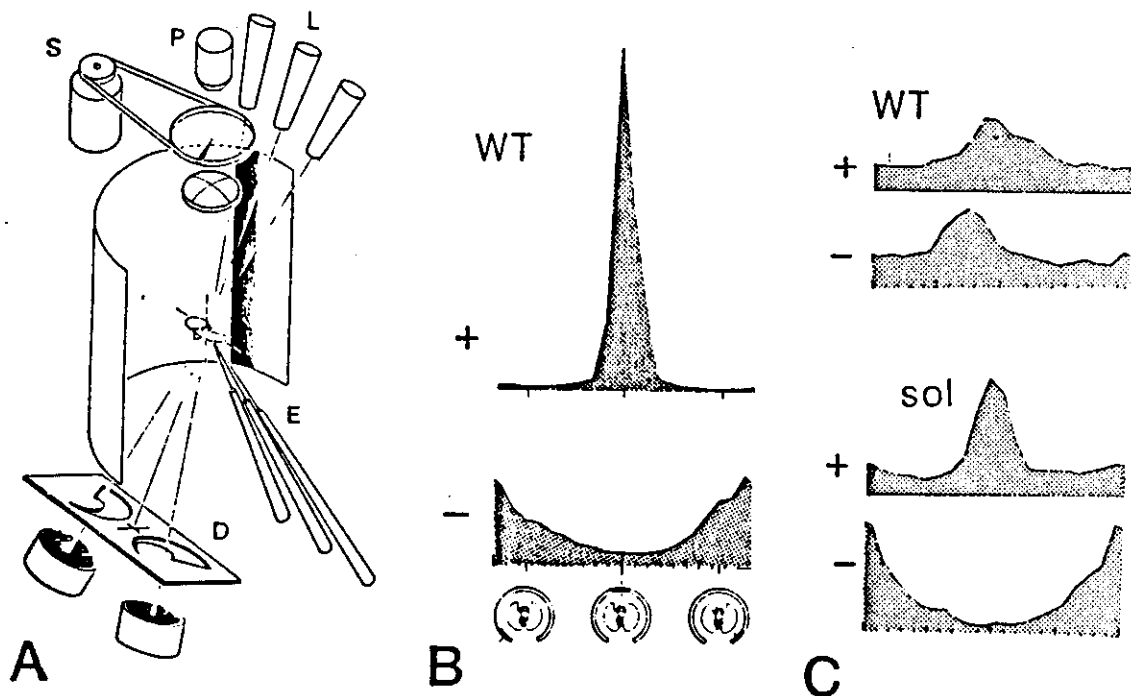
Fig. 2. (A) Flight simulator. Spotlights L were used to adjust the fly in the center, and to cast shadows of the beating wings onto contralateral mask openings of a photoelectric device D for the measurement of the intended turns. Micro-electrodes E were required to specify the contribution of selected muscular subsystems. The signals from D or E act on servomotor S which controls, by rotation of a circular diapositive between lamp and lens of projector P, the angular speed of a vertical bar on the (partly dissected) cylindrical screen. (B) Orientation in the flight simulator. Essential actions of the visual stimulus on the wingbeat amplitudes of the wildtype (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 wildtype 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 otherwise available responses 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 can not 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 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 wildtype. 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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VISION IN DROSOPHILA III.
FUNCTIONAL FLEXIBILITY; SEARCH AND CHOICE

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Dynamic depth perception: The influence of the 'ground' on the orientation towards a 'figure'

Fig. 1A shows *Drosophila* during stationary flight in the center of a panorama consisting of a 'figure' (a vertical bar) and a 'ground' (a random-dot pattern). The signals representing the intended turns of the tethered fly can be used to simulate course-control during free flight. This has been done, in the present experiment of 5 h duration, by exclusive rotation of the figure (FIG.) or simultaneous rotation of figure and ground (FIG.+GRD.). The histograms in Fig. 1B show, in temporal sequence from front to back, the relative time spent by the figure in different angular positions between 180° to the left and 180° to the right of the fixed forward direction. A maximum at the center indicates 'fixation' of the dark bar in the frontal visual field. The fly fixates the figure as long as the ground is at rest. The fixation is not sustained if the ground is following the moving figure (Götz 1983).

The striking influence of the ground on the orientation of the fly suggests two mutually exclusive explanations: The 'figure' is either invisible for the fly, or ignored by the fly, unless there is relative movement (movement parallax) between figure and ground. The use of movement parallax for figure-ground discrimination has been verified in larger flies. A model has been proposed which describes the essential phenomena on a cellular level of the visual system (Egelhaaf 1985, Reichardt and Poggio 1979, Reichardt et al 1983). However, the context-independent object fixation found in the mutant *optomotor-blind* favours the second explanation for the results of the present experiment: The wildtype probably suppresses the attractivity of a conspicuous visual object if it appears to be embedded in the visual

background. The movement parallax observed during free flight in a resting environment indicates the proximity of a visual object. Evaluation of this parallax enables the fly to distinguish figures of simular subjective size by their apparent distance. The results obtained in the flight simulator suggest preference and selection of the apparently nearest figure which might be attractive as a target or a landing site. This can not be explained by 'binocular depth perception'. We propose the term 'dynamic depth perception' to describe an application of movement parallax in *Drosophila* which is likely to increase its limited range of depth perception from millimeters to meters.
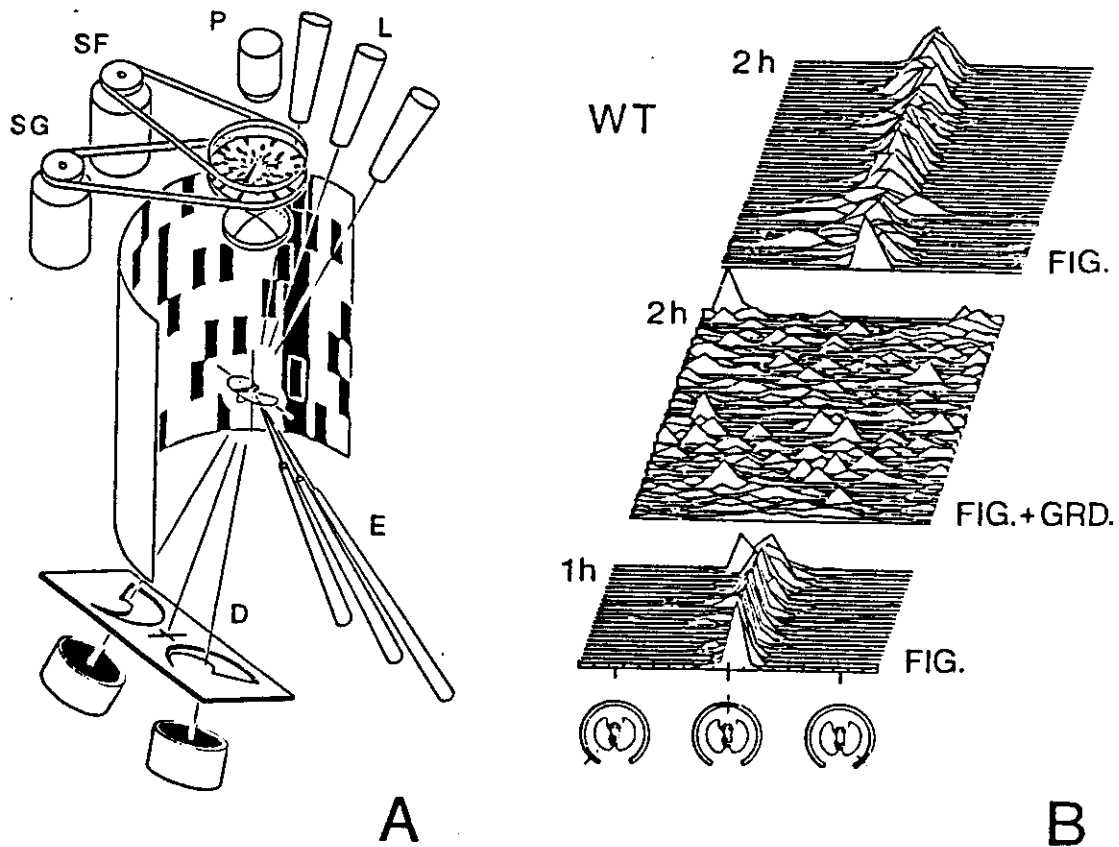
Fig. 1 (A) Flight simulator using the intended turns of a tethered fly to control, independently by the servomotors SF and SG, the angular speed of a vertical bar (FIG.) and a random-dot pattern (GRD.). For technical details see 'Vision in *Drosophila* II', legend of Fig. 2. (B) Series of histograms showing, in temporal sequence from front to back, the prefered position of the vertical bar in the visual field of a wildtype fly during 5 h of flight in the simulator. Course towards the figure prevails if the ground is at rest (FIG.). The attraction of the visual object subsides gradually if the ground is moving in conjunction with the figure (FIG.+GRD.). Relative movement between figure and ground indicates proximity of the figure, and seems to be used for 'dynamic depth perception' during free flight.

To investigate the choice between two objects, a wingless *Drosophila* mutant *vestigial (vg)* was allowed to walk on a circular platform surrounded by water. A scanning device recorded the track of the fly and the sequence of its runs towards a visual object on either side of the platform. The results shown in Fig. 2 are surprising: The number of approaches per object is almost completely independent of the particular size and shape of the visual stimulus. Equidistribution of these runs is achieved by sustained spontaneous alternation between the two objects. The fly keeps running to and fro for hours, a behaviour reminding on the indecision of Buridan's ass between two heaps of hay (Götz 1980, Bülthoff et al 1982).
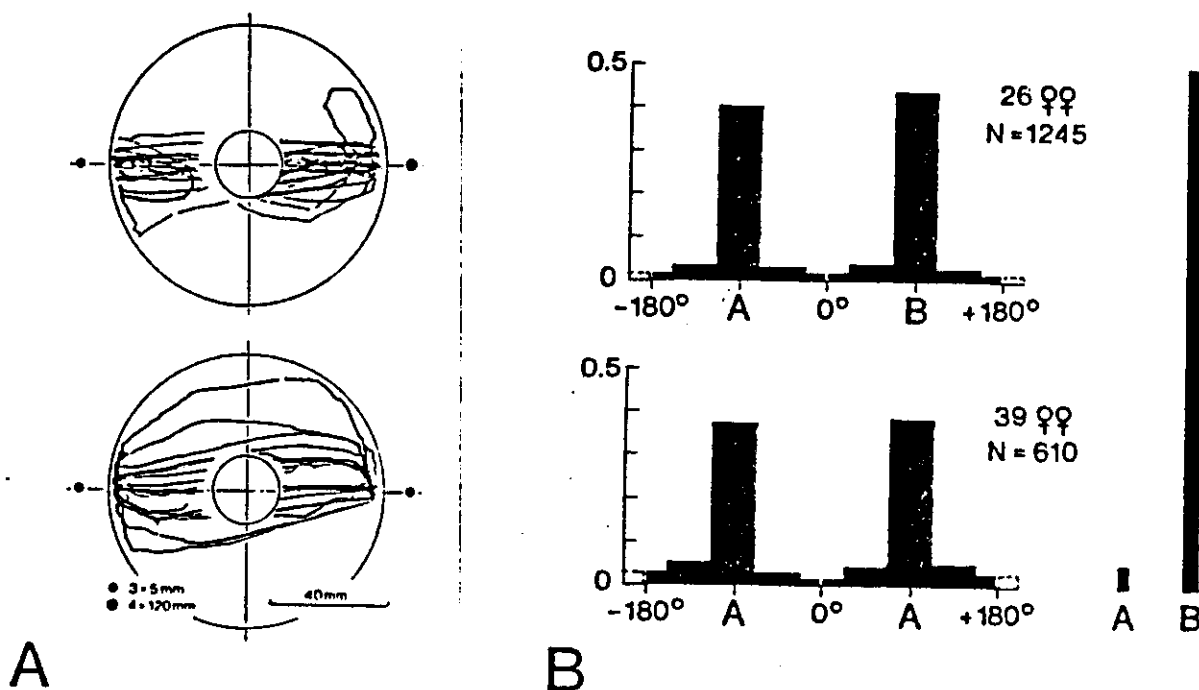

Fig. 2 Equidistribution of choice between competitive visual objects conceals the ability of pattern discrimination in Buridan's paradigm. (A) Tracks of two wildtype flies recorded for 200 s on a platform of 44 mm radius. The scanning device blanks the tracks within a central area and at velocities below 1 mm/s. The flies are running to and fro between inaccessible objects of different (top), or equal (bottom), size and shape. (B) Distribution of the direction of N passages from the center to the peripherie of the circular platform in the experiments shown on the left of the figure. The inset illustrates the relative size of the visual objects used in these experiments. Sustained spontaneous alternation between the targets equalizes the number of runs towards the objects on either side of the platform.

Exploration of a natural environment requires the discovery of rewarding sites in the midst of all sorts of visual landmarks. The present strategy prevents the fly from being 'captured' by an arbitrary non-rewarding object. The implications of this strategy may be of general interest: Many authors

have rated pattern recognition and learning in animals by comparison of the selection frequencies for different patterns. The proof of the statistical independence of successive choices is often missing. Sustained spontaneous alternation between the objects would conceal the ability for pattern discrimination in the results of these experiments.

The recurrent alternation between competitive targets in *Drosophila* resembles the recurrent alternation between competitive aspects of ambiguous figures in human perception, for instance the spontaneous depth reversal of the Necker cube: The underlying strategies of the entirely different brains help to overcome the preoccupation with arbitrarily selected interpretations of the retinal images.

Area-covering search in the absence of visual objects

Removal of sensory cues near the fly elicits area-covering search behaviour. The persistence of direction along the track can be described by the mean free path of a random-walk approximation. A fly on a circular platform is compelled to run, often for some time, along the outer boundary if the mean free path is sufficiently large to divert locomotor activity from the center to the surround. This effect is likely to explain the 'centrophobism' found in *Drosophila*. The mean radial distance of the track from the centre of the platform can be used to calculate the corresponding mean free path (Götz and Biesinger 1985a, b).

Area-covering search in *Drosophila* is obviously controlled by variation of the mean free path: Evaluation of the centrophobism has revealed a gradual increase of the persistence of direction during accomodation to a non-rewarding territory. The fly extends its radius of action, most probably in order to facilitate the detection of favourable districts in a natural environment. The control of the persistence of direction in the tracks of *Drosophila* can be disturbed: A few seconds of exposure to ether vapour are sufficient to increase the mean free paths by a factor of two, and to block the control mechanism irreversibly for the rest of the life of a fly.

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SEARCH AND CHOICE IN *DROSOPHILA*

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ABSTRACT

Search behaviour of the fruitfly in a choice between inaccessible targets, or 'figures', depends on the spatial and temporal context of the visual input. An account of the attempted flights and runs towards these figures was derived from the wingbeat control responses during tethered flight in a simulator, or obtained by automatic tracking during free walk in an arena. The present results demonstrate new aspects of search strategies in insects.

(1) At least three pairs of flight control muscles respond to displacements of the retinal images of *figure* and *ground*. Each pair contributes to fixation and tracking of a figure, and to stabilization of course and altitude with respect to the ground. Two pairs support a rigid strategy of *'instructional' fixation*. The third pair engages in a flexible strategy of *'operant' fixation* suitable to cope with artificially inverted displacements. Only 'instructional' fixation is found in the corresponding muscles of the mutant *'small optic lobes'*.

(2) Relative movement between figure and ground indicates the proximity of a figure, and seems to serve for long-range *depth perception* during free flight. Tethered flies prefer the nearest figure which might be attractive as a landing site. The attraction subsides gradually whenever the figure is moving in conjunction with the ground. Fixation of a figure requires up to 5 course-control manoeuvres/s, and can be maintained for 24 h of tethered flight in a simulator.

(3) Comparison of the number of 'runs' towards each of two inaccessible figures in the periphery of the arena has revealed a remarkable equidistribution of the frequencies of approach. The results suggest lack of preference even in a choice between two extremely different figures. The temporal sequence of the runs shows, however, that the equidistribution is achieved by *sustained spontaneous alternation* of the preferred target. In search for rewarding sites this strategy disengages the fly from continuous fixation of the nearest figure. The alternation of preference in *Drosophila* is reminiscent of sustained spontaneous depth reversal in human perception which helps to overcome one-sided interpretations of ambiguous figures such as the Necker cube. Alternation of preference may have concealed the ability for pattern recognition and learning in numerous experiments on vertebrates or invertebrates. To exclude this possibility one has to prove the statistical independence of successive choices.

(4) Area-covering search can be observed in the absence of sensory landmarks. Random-walk approximation of the search trajectories has revealed a reversible increase of the persistence of direction, or the 'mean free path', with the time spent under unfavourable condi-

tions. This strategy gradually extends the radius of search until the fly hits upon favourable sensory signals. Ether narcosis irreversibly increases the mean free path, and blocks its control for the rest of the life.

INTRODUCTION

The retinal image of the resting environment is an important reference system for the control of locomotion in *Drosophila melanogaster*. Displacements of this image are resolved, for instance, into a horizontal component which elicits course-control responses of the wings or legs, and a vertical component which elicits altitude-control responses of the wings. The properties of the responses have been investigated in numerous experiments on stationarily flying or walking flies (Bausenwein et al. 1986; Buchner 1976; Buchner et al. 1978; Bülthoff 1981; Bülthoff and Götz 1979; Bülthoff et al. 1982; Fischbach and Heisenberg 1981; Götz 1964, 1968, 1970, 1975, 1977, 1980, 1983a and b, 1985, 1987a and b; Götz and Biesinger 1985a and b; Götz and Buchner 1978; Götz et al. 1979; Götz and Wandel 1984; Götz and Wenking 1973; Heide 1983; Heide et al. 1985; Heisenberg and Buchner 1977; Heisenberg and Götz 1975; Heisenberg and Wolf 1984; Heisenberg and Wolf 1988; Mayer et al. 1988; Zanker 1988).

Fig. 1 shows *Drosophila* during free flight in a resting environment. The cylindrical surface illustrates the visual field of the eyes. Deviation from a straight course is accompanied by a displacement of the retinal image in the opposite direction. To counteract involuntary deviations, the fly tries to follow the displacements of the retinal image. This is done by an increase of the wingbeat amplitude on the outer side, and a decrease of the wingbeat amplitude on the inner side, of the intended turn (Götz 1968, 1983a and b). Course-control is extremely efficient: The fly responds to displacements as slow as 1 revolution/h, or as fast as 50 revolutions/s (Götz 1964). However, stabilization of the course with respect to the *ground* is only one aspect of flight control. Actually, the fly has to detect, approach and explore visual landmarks in search of rewarding sites. This requires *figure*-induced orientation (Götz 1983b; Heisenberg and Wolf 1984). The use of visual flight control for *fixation* and *tracking* of a figure, and for selection of a target according to its distance will be treated in the following two sections. Another section describes a strategy for the efficient exploration of competing targets on the ground. The last section covers search in the absence of sensory landmarks.
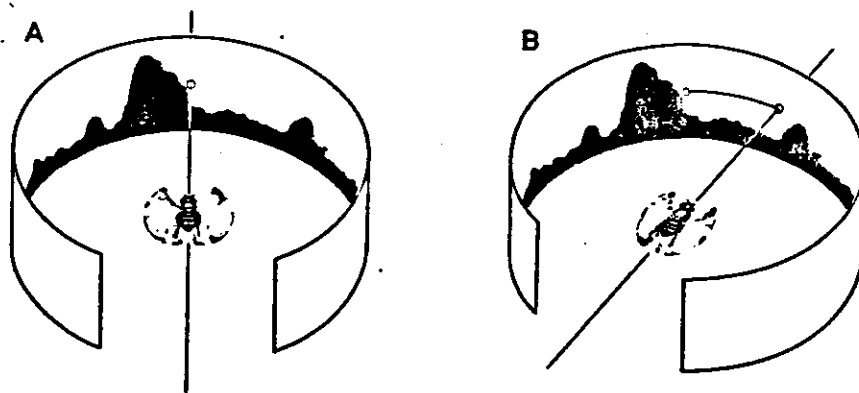

Fig. 1. Angular displacements of the surroundings within the visual field indicate a change in the direction of flight. The figure illustrates the retinal images received before (A), and after (B), a turn to the right. *Drosophila* is capable of stabilizing the retinal image in order to maintain a straight course. (From Götz 1975).

Flight control is achieved by up to 17 very small *control muscles* on either side of the bulky *power muscles* in the thorax of the fly. Fig. 2 shows four of these muscles which have been investigated in cooperation with G. Heide. Three muscles, the *basalar*, the *sternobasaler* and the *1st axillary muscle*, respond to visual stimulation and contribute to the control of both course and altitude. These muscles either increase or decrease the wingbeat amplitude of the fly (Götz 1983a and b, 1987b; Heide 1983; Heide et al. 1985).
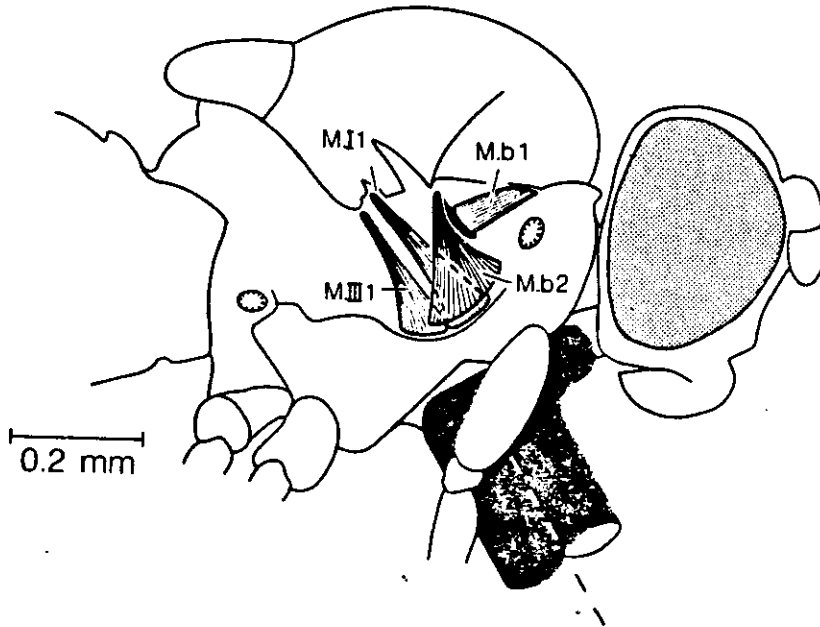

Fig. 2. Flight control muscles on the right side of the thorax of *Drosophila*. M.b1 basalar muscle, M.b2 sternobasalar muscle, M.I1 1st axillary muscle, M.III1 3rd axillary muscle. Redrawn from Zalokar 1947; notation according to Heide 1971. Head and thorax are affixed to the fly-holder (dark colour) of a flight simulator which allows to record the movements of the wings, and the activities of selected control muscles, under flight-induced visual stimulation.

Fig. 3A illustrates the tethered flight of *Drosophila* in a *flight simulator*. An infrared spotlight on either side casts a shadow of the beating wing onto the contralateral mask opening of an optoelectric device. This device measures the wingbeat amplitudes on either side. The difference of the wingbeat amplitudes represents the intended turn. The signal controls, by rotation of a circular transparency in a projector on top of the simulator, the angular speed of a bar on the cylindrical screen around the fly. One half of the screen is removed to show the details. The simulator allows the fly to manoeuvre the figure into arbitrary angular positions (Götz 1987a, b).

Fig. 3B gives an example of figure-induced orientation during 12 h of tethered flight in the simulator. The historgrams represent, in temporal sequence from front to back, the time spent by the figure in different angular positions between 180° to the left and 180° to the right of the fly's forward direction. A maximum at the centre indicates *fixation* of the figure in the frontal area of the visual field. Actually, this experiment has been continued for another 20 h, and fixation is encountered around the clock (Götz 1987a). Fixation requires continuous course control manoeuvres, like driving in heavy traffic. As an example, a

succession of course-control manoeuvres, recorded in a time period of 5 s, is given in Fig. 4. The upper traces show the beat amplitudes of the left and right wing, respectively. The lower traces the simultaneously recorded activities of the sternobasalar muscle on the left and on the right. Muscular activity is accompanied by an increase of the *ipsilateral* wingbeat amplitude. At least one pair of antagonists, the 1st axillary muscles, accounts for the simultaneous decrease of the *contralateral* wingbeat amplitude.
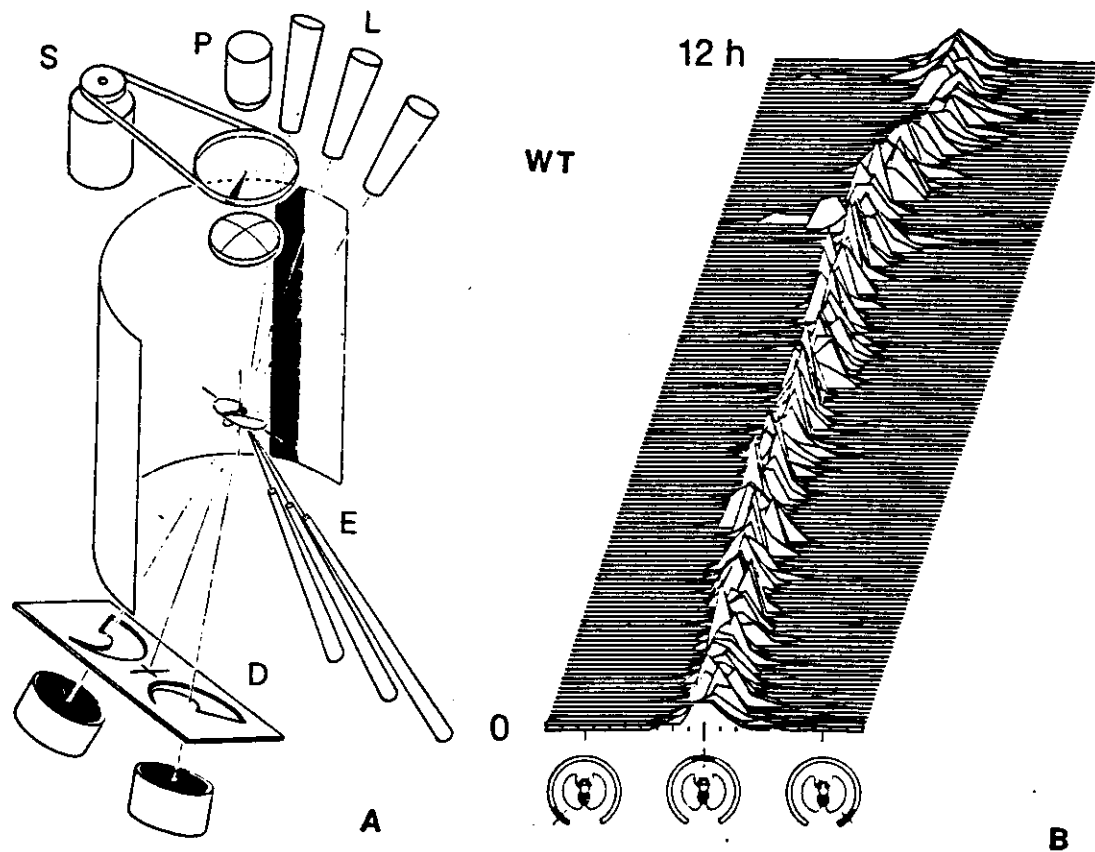

Fig. 3. (A) *Flight simulator* using the intended turns of the fly to investigate fixation and tracking of a *'figure'* during flight under stationary conditions. Spotlights L are required to adjust the tethered fly in the centre, and to cast shadows of the beating wings onto the contralateral mask openings of the optoelectric device D for the measurement of the intended turns. Micro-electrodes E on either side of the fly-holder can be inserted into selected pairs of flight control muscles to measure their contribution to the intended turns. The signals from either D or E act on servomotor S which controls, by rotation of a circular transparency between lamp and lense of a projector P, the angular speed of a vertical bar on a cylindrical screen. The diagram shows half of the screen on the left side of the fly. - (B) Figure-induced orientation during the first 12 h of an experiment in which tethered flight was sustained for 32 h with only short interruptions during feeding. The difference of the wingbeat amplitudes on either side was used to control the angular speed of the bar. The histograms represent, in temporal sequence from front to back, the time spent by the figure in different positions to the centre of the visual field. The maxima near the midline of the histograms demonstrate *'fixation'* of the figure in front of the fly.
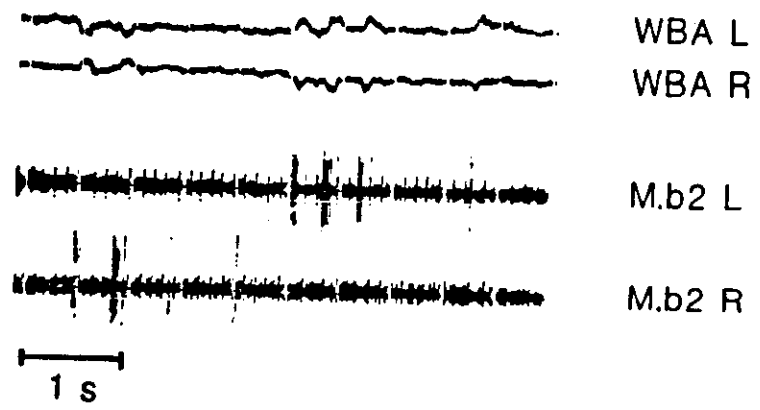
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figure in the flight simulator. Contraction of a sternobasalar muscle seems to increase the ipsilateral wingbeat amplitude. Simultaneous decrease of the contralateral wingbeat amplitude intensifies the manoeuvre.
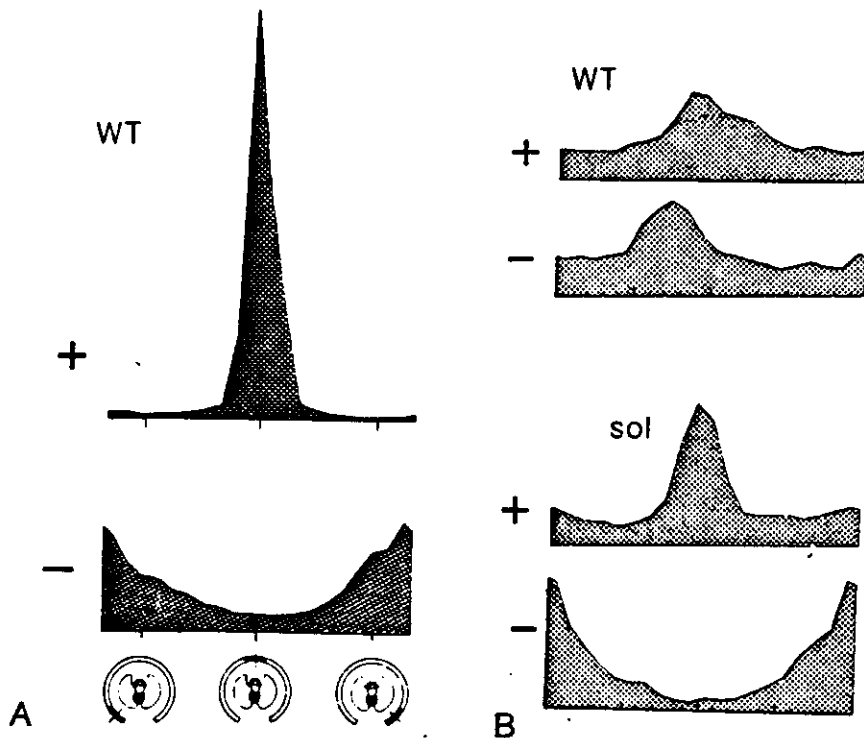

Fig. 5. Figure-induced orientation in the flight simulator. The histograms show the relative time spent by the figure in different positions with respect to the centre of the visual field. The results were obtained by continuous alternation between 'normal' conditions (+) where the figure is expectedly moving in the direction opposite to the intended turn, and 'inverted' conditions (-) where the figure is unexpectedly moving in the direction of the intended turn. - (A) Non-adaptive strategies of 'instructional' fixation prevail if the wingbeat signal is used to control the movements of the figure: the wild-type fly (WT) alternates between a course towards the figure under normal conditions, and a course away from the figure under inverted conditions. Flight time 1 h. - (B) The contribution of the pair of axillary muscles (M.I1) to the intended turns of the wild-type (WT; 6 flies, 10 h) revealed the existence of adaptive strategies of 'operant' fixation which are not confused by the inversion of the perceived movement (upper histograms). The corresponding muscular subsystem of the mutant 'small optic lobes' (sol; 2 flies, 5h) shows a relapse to non-adaptive strategies of 'instructional' fixation (lower histograms).

To simulate free flight under *normal* conditions, the wingbeat signal must be used to move the figure in 'counter-turn' direction around the fly. *Inversion* of the signal changes the *kinetic context* of the visual stimulus, and creates a situation which never occurred in the history of insect evolution. The histograms in Fig. 5A show the results of continuous alternation between *normal* (+), and *inverted* (-) conditions. The fly alternates, accordingly, between a course *towards* the figure, and a course *away* from the figure. Conclusion: Fixation of the figure obviously depends upon the kinetic context. The attempt to fixate the figure under inverted conditions produces the opposite effect (Götz 1983b; Heisenberg and Wolf 1984).

What happens if we pick up, by means of an electrode on either side of the fly in Fig. 2, the contribution of a single pair of flight control muscles, and use only this signal to move the figure around the fly? Of the three pairs of muscles investigated, so far, one was outstanding because of its unexpected properties: The pair of 1st *axillary* muscles. The histograms in Fig. 5B show these properties: In '*small optic lobes*' (*sol*), a mutant with reduced number of nerve cells in the 1400 columns of the visual neuropil (Fischbach and Heisenberg 1981; Heisenberg and Wolf 1984), the axillary muscles support a course *towards* the figure under *normal* (+) conditions, and a course *away* from the figure under *inverted* (-) conditions. The contribution of these muscles depends on the kinetic context. However, in the wild-type (WT), the axillary muscles support a course *towards* the figure, independent of the kinetic context. The contribution is not confused by the *inversion* of the perceived movement (Götz 1983b, 1985, 1987b).

The co-existence of non-adaptive and adaptive strategies of fixation in the wild-type has been confirmed by analysis of the torque response (Wolf and Heisenberg 1986). The results illustrate the versatility of the flight control system. It is tempting to speculate about the function of the nerve cells which are missing in the mutant and which do not seem to be required for the ordinary non-adaptive optomotor control of course and altitude in *Drosophila*.

CHOICE OF A FIGURE ACCORDING TO ITS PROXIMITY: DYNAMIC DEPTH PERCEPTION

The flight simulator in Fig. 6A presents, on its cylindrical screen, a bar-shaped *figure* and a dotted *ground*. The difference of the wingbeat amplitudes on either side can be used for moving figure and ground independently around the fly (Götz 1983b). The results in Fig. 6B, obtained during 5 h of tethered flight, show a striking effect of the *structural context* of the visual stimulus on the orientation of a fly which is allowed to control the angular speed either of the figure ('FIG.'), or of figure and ground simultaneously ('FIG. + GRD.'). Fixation is found as long as the figure is moving with respect to the ground. Almost no fixation is found as long as the figure is moving in conjunction with the ground. Two alternative explanations can be given under these conditions:

(1) Without relative movement between figure and ground, the figure will be *invisible*.

(2) Without relative movement between figure and ground, the figure will be *ignored*.

The movement-induced separation of figure and ground in the fly, and the corresponding transition from invisibility to visibility, is now well understood from the work of W. Reichardt and his group (Egelhaaf et al. 1988). However, the slow fading of fixation in the intermediate time period of the present experiment, and the absence of fading in a corresponding experiment on an optomotor-blind mutant (Götz 1983b), suggest that, in the present experiment, the conspicuous figure is still visible but actively ignored.
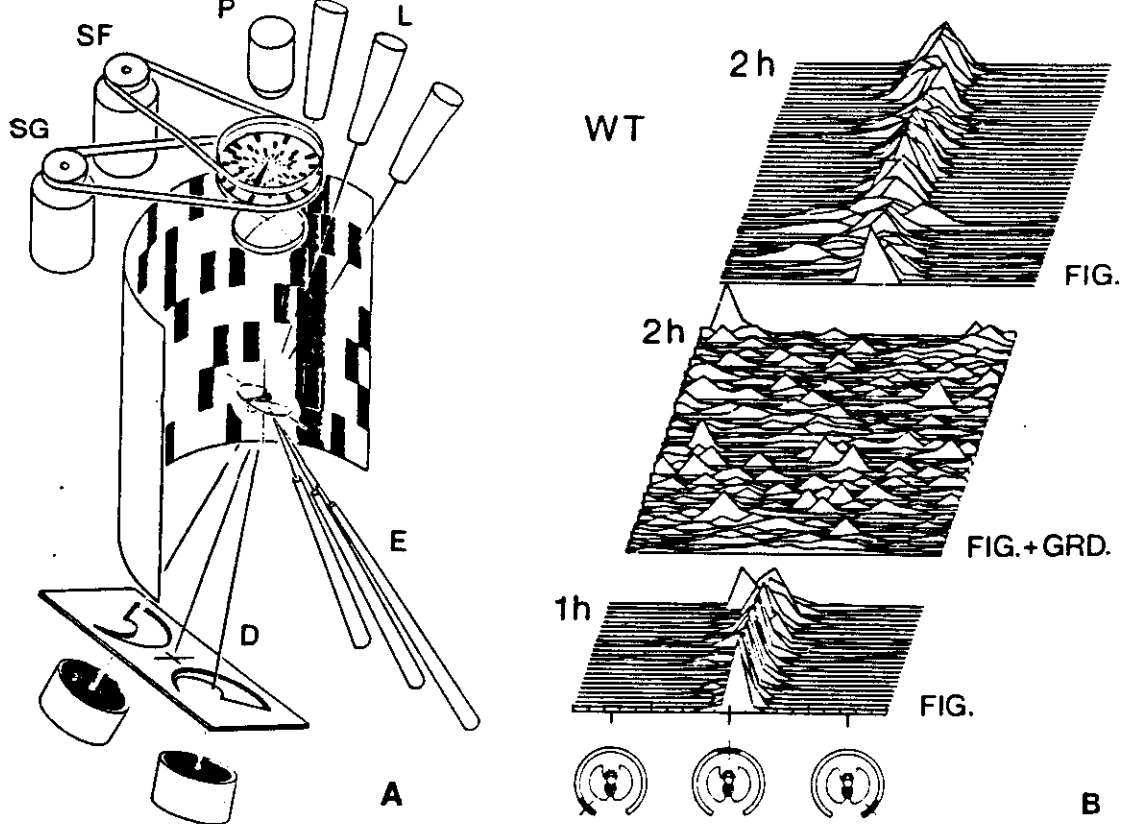
Fig. 6. (A) *Flight simulator* using the intended turns of a tethered fly to control, independently by servomotors SF and SG, the angular speed of a vertical bar (FIG.), and a random-dot pattern (GRD.). Technical details as described in Fig. 3A. - (B) Series of histograms showing, in temporal sequence from front to back, the preferred position of the vertical bar in the visual field of a wild-type fly during 5 h of flight in the simulator. Course towards the *figure* prevails if the *ground* is at rest (FIG.). The attraction of the visual object subsides gradually if the ground is moving in conjunction with the figure (FIG. + GRD.). Relative movement between figure and ground indicates proximity of the figure, and seems to be used for *'dynamic depth perception'* during free flight.

A tentative explanation of this phenomenon is given in Fig. 7. The two frames illustrate the displacement of figures in successive retinal images, received on a passage from left to right. *Near figures*, such as the *Drosophila* on the tip of the match-stick, are likely to become preferred targets because of the relative movement against the ground. *Remote figures* appear to be embedded in the ground and, therefore, do not elicit the attention of the fly.

Evaluation of the *structural context* enables the fly to distinguish figures of similar subjective size by their distance. This facilitates the exploration of visual landmarks and is likely to increase the limited range of *depth perception* in *Drosophila* from 'millimeters' to 'meters'.

Fig. 7. Successive aspects of a scenery seen by a fly on a passage from left to right. Near figures such as the *Drosophila* on the tip of the match-stick stand out because of their relative movement against the ground. '*Dynamic depth perception*' enables the fly to distinguish figures of the same subjective size by their distances which may be far beyond the range of stereopsis.

SEARCH AMONG COMPETING FIGURES: SPONTANEOUS ALTERATION OF THE PREFERRED TARGET

The continuity of the fixation response during the first 12 h of the experiment in Fig. 3B suggests that *Drosophila* would easily disclose its preference in a choice between two different figures. In Fig. 8 the fly is affixed to a sled, and is kept walking for about 12 h on a tread compensator (Götz and Wenking 1973; Götz 1977), a servo-controlled ball to hold the freely walking fly in a fixed position and orientation to the dotted pattern on either side. Preference, in this experiment, is given by the average curvature of the track in revolutions/pathlength towards the preferred pattern. In a choice between the one-dot-pattern and the multi-dot-pattern of the same luminous area we obtained, with 90 flies, a total pathlength of 3800 m. The average curvature was about 1 rev./2 m pathlength towards the multi-dot-pattern. This preference lasts throughout the experiment, is invariant to the reversal of contrast and amounts to only 3 percent of the optomotor course-control response obtained under similar conditions. Scaled to our bodily dimensions the average curvature would be 1 rev./km pathlength. The effect is significant, but clearly too small to justify the notion 'preference'.

It is conceivable that flies do not easily detect different numbers of elements in the two patterns. We have a similar problem with the *Minsky-Papert spirals* shown in Fig. 9. Our perception fails to inform us about the number of elements in these spirals. We need scrutiny to identify a single element in the spiral on the left, and two disjunct elements in the spiral on the right.
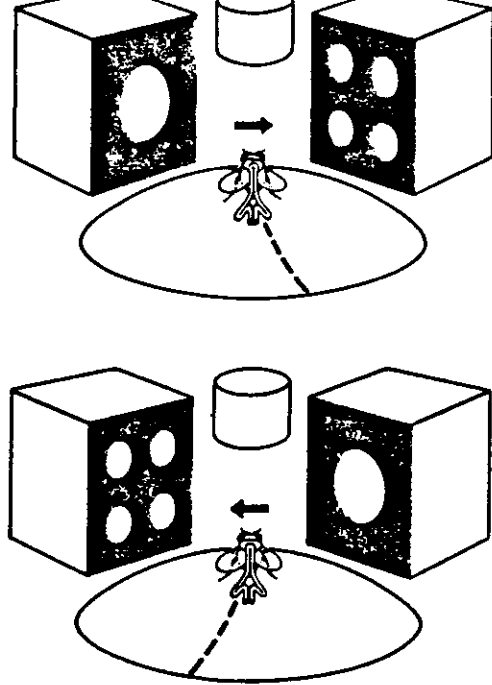
Fig. 8. Choice between differently dotted patterns of the same luminous area. The freely walking fly is held, for several hours, in a state of spontaneous fluctuation around a fixed position and orientation to the patterns on either side of a *tread compensator*. The cylindrical transducer on top of the compensator measures the translatory and rotatory displacements of a tiny sled of paramagnetic wire which is drawn by the fly. A sensor-controlled servo-system (not shown in the diagram) counteracts the displacements by appropriate rotation of a mercury-filled ball on which the fly is walking. Broken lines illustrate the track of the fly. The average curvature in revolutions/meter pathlength is read from counters on the shaft the servo-motors. To diminish the influence of locomotor bias the patterns were exchanged every 5 minutes. Arrows indicate the surprisingly weak preference of the multi-dot pattern.
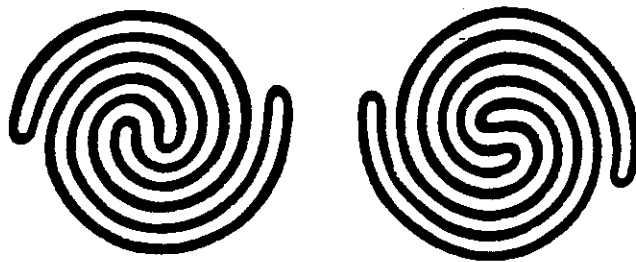

Fig. 9. The *Minsky-Papert spirals* illustrate a difficulty *Drosophila* may have with the discrimination of dotted patterns in the previous experiment. Scrutiny of a human observer is required to detect the actual number of unconnected picture elements: one in the spiral on the left, and two in the spiral on the right. (From Minsky and Papert 1969).

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different figures. The results of the arena-experiment in Fig. 10 support this conjecture. The frontal half of the illuminated wall of the arena is removed to show the circular disk, on which the fly is freely walking between two inaccessible figures. Shortened wings, and a water-filled moat around the disk, prevent its escape. An optical scanner is used to plot the track of the fly and to record its passages from the center of the disk to the different sectors in the periphery (Götz 1980; Bülthoff et al. 1982).
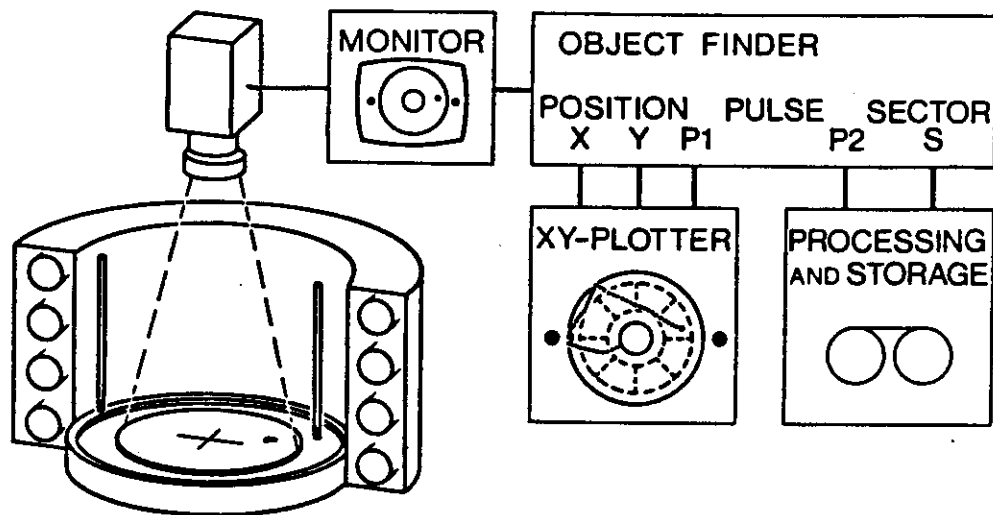

Fig. 10. *'Dipterodrome'* with opto-electrical scanner, used for the investigation of search strategies on the ground. The frontal half of the arena is cut away to show an elevated disk of 88 mm diameter on which the fly is freely walking between two inaccessible figures. Shortened wings, and a water-filled moat around the disk, prevent its escape. To plot subsequent XY-positions along the track of the fly, the 'object finder' delivers a regular sequence of plot pulses P1 as long as the fly is moving. The distances from the centre of the disk are averaged to obtain the mean radial distance R of the track. A pulse P2 indicates the passage from the centre to one of the eight sectors of a ring-shaped area in the periphery of the disk. This pulse activates the storage of the corresponding sector number S. (From Bülthoff et al. 1982).

Fig. 11A shows the frequency of runs into different directions. Two results characterize the behavior of *Drosophila*: (1) Runs towards the figure are particularly frequent. (2) Equidistribution of these runs is found not only in a choice between identical figures (F1, F1), but also in a choice between extremely different figures (F1, F2): If tested separately, figure F2 is about 10 times more attractive to the fly than figure F1. The lack of preference in a choice between these figures cannot be explained by insufficient perception: the fly evidently compensates for the difference in attraction of the figures.

Fig. 11B shows this strategy in action. Each of the diagrams represents the track of a fly which was running for 200 s on a circular disk, either between the identical figures F1 and F1, or between the extremely different figures F1 and F2. Near the center, the trajectories are blanked for technical reasons. The diagrams show that the equidistribution of the choices is achieved by *sustained spontaneous alteration* of the preferred target: the fly keeps running to and fro, between the figures, sometimes for hours. In one of the experiments a fly scored, within 7 hours of walk on the disk, 2500 alterations on a path of 220 m length (Bülthoff et al. 1982). The loop on the right of the upper diagram is one of the rare exceptions where a figure has been visited twice in succession. The results suggest two general conclusions:

(1) A strategy based on sustained spontaneous alteration of target facilitates the exploration of the visual environment in search of rewarding sites. The strategy prevents the fly from being captured by the nearest object. The effect of this strategy can be compared with sustained spontaneous depth reversal in human perception which helps to overcome one-sided interpretions of ambiguous figures such as the classical *Necker cube* shown in Fig. 12.

(2) Sustained spontaneous alteration of target may have concealed the ability for pattern discrimination and learning in numerous apparently 'unsuccessful' experiments on invertebrates as well as vertebrates. To exclude this possibility, one has to prove the statistical independence of successive choices. This has rarely been done in the past.
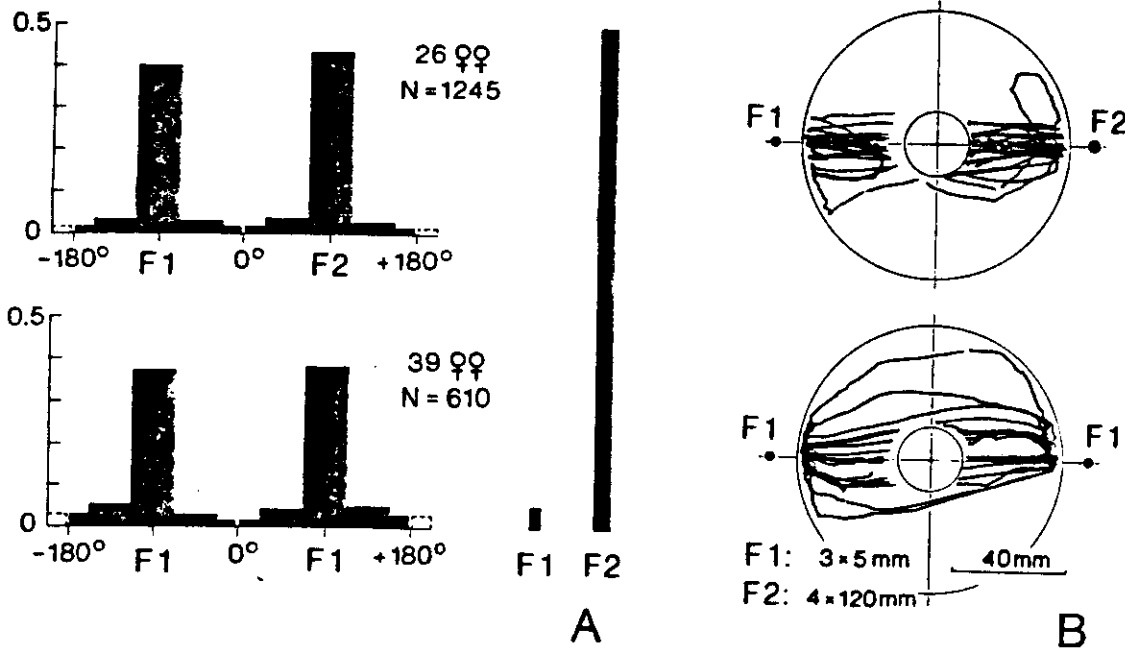

Fig. 11. Choices between inaccessible figures which are either identical (F1, F1, lower diagrams), or extremely different (F1, F2, upper diagrams). - (A) Relative frequencies of runs in different directions, obtained by evaluation of N passages from the centre to the periphery of the circular disk in the arena. Note the apparent lack of preference in the choice between different figures. - (B) Tracks of two flies which were running for 200 s on the circular disk. The scanning device obscures the tracks near the centre or at velocities below 1 mm/s. Equidistribution of the choices is achieved by *sustained spontaneous alteration* of the preferred target.

Fig. 12. The *Necker cube* is a classical example of sustained spontaneous depth reversal in human perception. The ambiguous figure is immediately seen in 3D. Spontaneous alteration between the aspect with the lower left square in front, and the aspect with the upper right square in front, prevents a preoccupation of the observer. Spontaneous alteration of the preferred target during search in the arena may serve similar purposes in *Drosophila.*
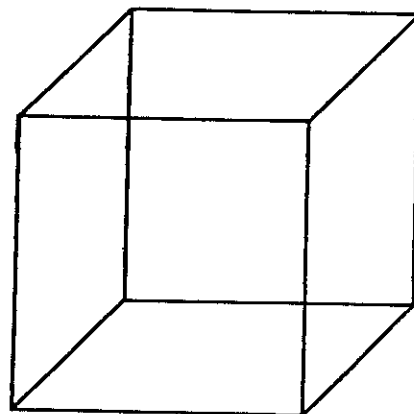
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Removal of sensory cues near the fly elicits area-covering search behaviour. The persistence of direction along the track can be described by the *mean free path* of a random-walk approximation. A fly on a circular platform is compelled to run, often for some time, along the outer boundary if the mean free path is sufficiently large to divert locomotor activity from the center to the surround. This effect is likely to account for the avoidance of the centre in experiments with *Drosophila* (Götz and Biesinger 1985a). Fig. 13 illustrates the mean radial distances R of three simulated random-walk tracks from the centre of the platform. The actual distance of a fly in an arena experiment can be used to calculate the corresponding mean free path (Götz and Biesinger 1985b).

Fig. 13. Random-walk approximation of area-covering search in the arena. The persistence of direction along the track of a fly explains the avoidance of the centre observed in the absence of sensory landmarks. The diagram indicates, in units of the radius of the circular disk, R_{max}, the expected relation between the *mean free path* and the *mean radial distance* of the track. An increase of the mean free path from zero to infinity is accompanied by an increase of the mean radial distance from $R = 2/3$ to $R = 1$. The computer-generated examples of random walk on a circular disk illustrate this transition: increasing portions of the tracks of 30 units total length are forced into orbits along the outer boundary.
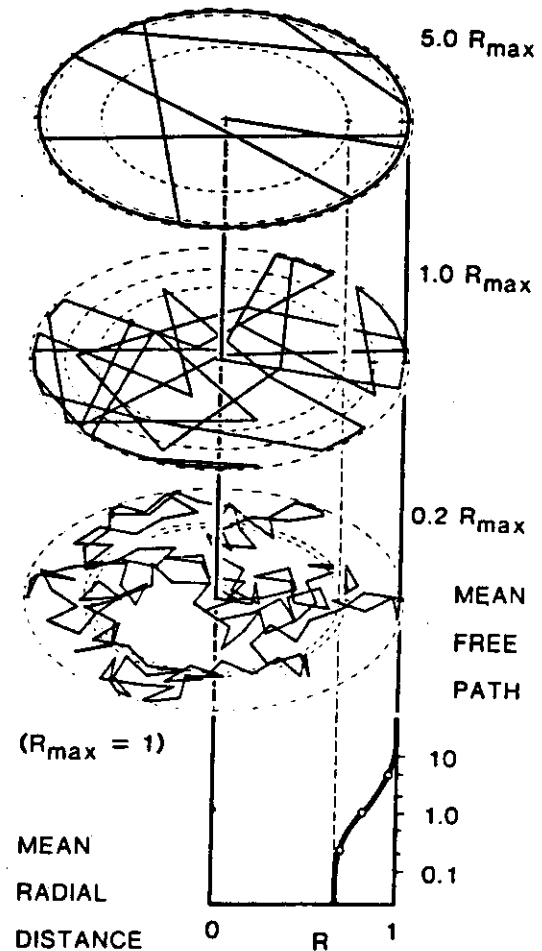
Area-covering search in *Drosophila* is obviously controlled by variation of the mean free path. Evaluation of the time course of centre avoidance in the arena has revealed a reversible gradual increase of the persistence of direction during accomodation to a non-rewarding territory. The *spontaneous centrophobia* of the fly extends its radius of search, most probably in order to facilitate the detection of favourable districts in a natural environment. The tracks of a completely blind mutant *sine oculis* (so) on the circular disk of the arena shown in Fig. 10 illustrate the transition from a comparatively low mean free path of about 17 mm at the beginning to an increased mean free path of about 180 mm after 20 min of area-covering search in the absence of visual cues (Fig. 14).

The control of the persistence of direction in the tracks of *Drosophila* can be disturbed by *ether-induced centrophobia*. A few seconds of exposure to ether vapour are sufficient to increase the initial mean free path by a factor of two, and to block the control mechanism irreversibly for the rest of the life of a fly. Fig. 15 shows the different tracks of a control fly and its sibling which received a very short ether narcosis 4 d before the experiment. Banana odour released from the inner compartment of the arena fails to hold a fly near the
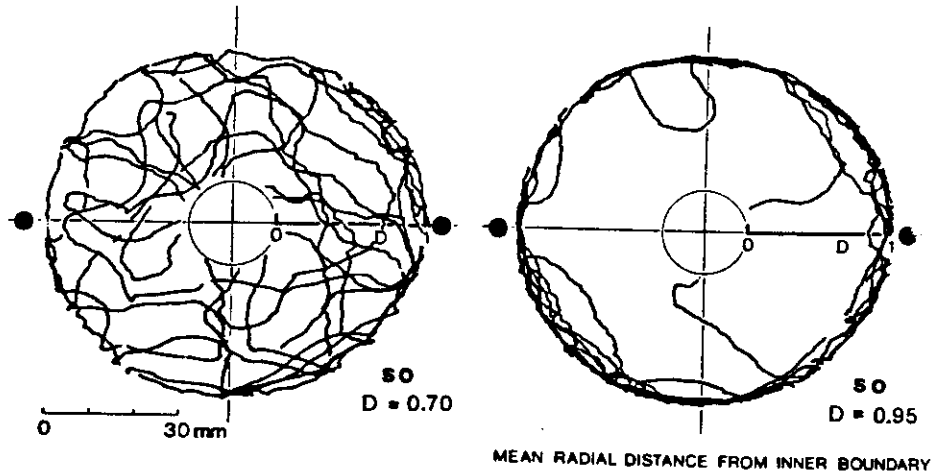
SO
D = 0.70

SO
D = 0.95

0   30mm

MEAN RADIAL DISTANCE FROM INNER BOUNDARY

Fig. 14. *'Spontaneous centrophobia'*, explained by an increase of the 'mean free path' during area-covering search in the arena. The diagrams show different tracks of a completely blind mutant *'sine oculis'* (*so*) which was freely walking between two inaccessible figures of 4 x 120 mm size. Each of the tracks represents 200 s of search, either at the beginning (diagram on the left) or at the end (diagram on the right) of a 20 min period of continuous locomotor activity on the circular disk. The blindness allows unnoticed removal of scent marks deposited by the fly. The scanning device obscures tracks near the centre or at velocities below 1 mm/s. Unlike the example in Fig. 13, the mean radial distance (D) of the fly is measured from the inner boundary of the scanning area. The 'mean free path' derived from these distances amounts to 17 mm at the beginning, and 180 mm at the end of the experiment. Increase of the mean free path facilitates the escape from unfavourable districts in a natural environment.
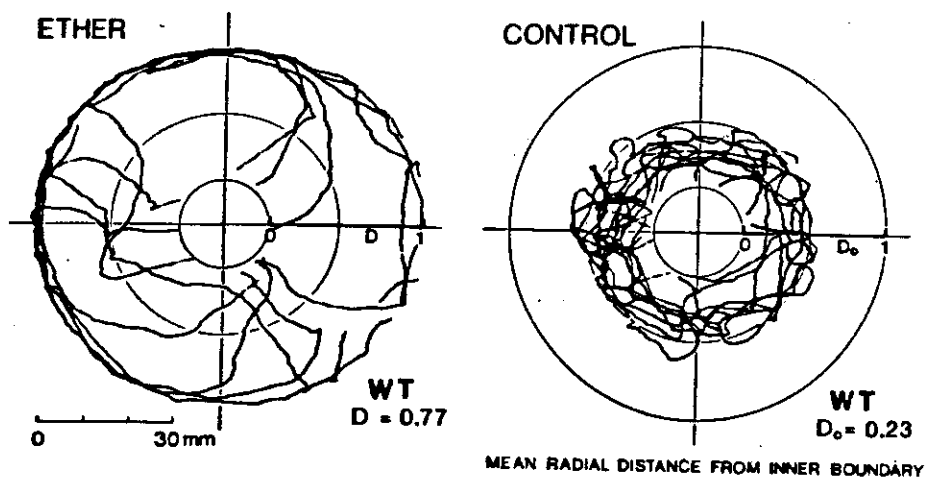

ETHER

CONTROL

WT
D = 0.77

WT
D_o = 0.23

0   30mm

MEAN RADIAL DISTANCE FROM INNER BOUNDARY

Fig. 15. *'Ether-induced centrophobia'*, a permanent change in area-covering search due to a mild ether narcosis 4 d before the experiment. The concentric circles indicate the outer boundary of the disk in the arena, and the invisible borders of a ringshaped inner compartment below the air-permeable floor from which banana odour is released at a constant rate of 2 ml/s. The diagrams represent the tracks of two 7 d old female siblings of a wild-type (WT) strain which have been reared under identical conditions. Each of the flies was running for 200 s on the disk. Tracks near the centre or at velocities below 1 mm/s were obscured. The mean radial distances of the test fly (D), and of the control fly (D_0), are measured from the inner boundary of the scanning area. Irreversible post-narcotic increase of the persistence of direction along the track seems to account for the translocation of search from the source of odour to the periphery of the disk. The translocation, confirmed in 806 trials, can not be explained by olfactory desensitization. (From Götz and Biesinger 1985a).

centre if the mean free path is sufficiently large compared with the radius of the disk. The olfactory cue and its substitutes, a visual attractant at the centre or a thermal repellent at the periphery, facilitate the demonstration of both 'spontaneous' and 'ether-induced' avoidance of the center. However, none of these cues is essential for the ether effect. Search control by variation of persistence in the track of a fly is compatible with observations in other insects.

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