

Recurrent Inversion of Visual Orientation in the Walking Fly, *Drosophila melanogaster*

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Summary. Movement-induced visual orientation in flies depends largely upon predictable responses which establish simple “optomotor balance” or complex “pseudo search” in the appropriate visual environment. Less conspicuous course diverting spontaneous actions of the flies become important in pattern-induced visual orientation. The apparently stochastic spontaneous actions of the housefly *Musca domestica* still allow powerful probabilistic predictions of orientation during stationary flight (Reichardt and Poggio 1981). The predominance of non-stochastic spontaneous actions such as “body saccades”, focussing and shift of “visual attention”, plasticity of response components etc. in the fruitfly *Drosophila melanogaster* (Heisenberg and Wolf 1979–1980) accounts for complementary behavioural options which reduce the relevance of probabilistic predictions of orientation in this fly.

The conjecture of “complementary options” is based on a striking antagonism between orientation towards a visual object (fixation), and orientation in the opposite direction (anti-fixation), in the walking fly. Forced choice in a multiple-Y-maze quite definitely elicits fixation in the wild type, and anti-fixation in the “optomotor blind” mutant *omb*^{H31} (Fig. 3). However, these effects cannot be attributed to a continuous predominance of attraction in the wild type and repulsion in the mutant. This is shown under comparable conditions of free choice in an arena: The flies of either strain alternate between fixation and anti-fixation of an inaccessible visual object (Fig. 4a), and keep running to and fro between two of these objects in “Buridan’s paradigm” (Fig. 4b, c), even if the objects are not alike (Fig. 4d). The sequence of approach, retreat and transition may be repeated a few thousand times to

the point of exhaustion (Fig. 5). The process resembles the recurrent alternation of ambiguous figures such as the Necker cube in human perception. The recurrent transition between competitive objects counteracts the accumulation of spontaneous preferences, and is likely to explain the apparent lack of pattern-discrimination under operant and non-operant conditions of continued free choice in *Drosophila*. The conspicuous dichotomy of fixation and anti-fixation in the same environment is, as yet, incompatible with the phenomenological theory of visually controlled orientation in larger flies.

Introduction

Pseudo Search, Random Search, Quantum Search

A prominent sensory cue for the control of locomotion in the fruitfly, *Drosophila melanogaster*, is the displacement of the retinal images of stationary landmarks. The rotatory and the translatory components of the displacement are retrieved by orderly arrays of thousands of direction specific movement detectors in the visual ganglia of the nervous system. The information is conveyed, over separate channels, to the thoracic ganglion where it is used to counteract the retinal displacement of the surroundings by control of the output at appropriate sites of the motor system. Most of the experiments on tethered flies refer to optomotor course control, or the suppression of unintended turning during locomotion in an open environment. “Pseudo search”, the induction of unintended turning, is an inherent by-product of optomotor course control in the proximity of visual landmarks which are moving past the fly. Predictability

Abbreviation: S.E.M. standard error of the mean

distinguishes "pseudo search" from intended turning due to "spontaneous actions" (Götz 1975a, 1980).

Preference for a particular orientation within an open environment is not expected if the fly is surrounded by a sufficiently homogeneous distribution of visual landmarks. A cluster of landmarks, however, may acquire the character of a visual object which is likely to elicit orientation in a preferred direction. Pattern-induced orientation in flies is achieved by a number of different strategies. The strategy of "smooth fixation" has been described by a phenomenological theory which seems to account for much of the non-hovering flight orientation in *Musca*, *Calliphora* and *Fannia* (Reichardt and Poggio 1981). "Smooth fixation" is accomplished by a peculiar asymmetry of the course control responses which favours back-to-front movements of the fluctuating retinal image. The asymmetry thus induces turning of the fly towards the visual object, fixation of the object in the frontal visual field and also tracking of a mobile object. The corresponding probability of different orientations the fly may take with respect to one or more visual objects can be calculated from the asymmetry of visually induced course-diverting torque, the fluctuation of superimposed spontaneous torque, and the relation between torque and turning. The fluctuation of endogenous torque of a smoothly fixating fly is apparently due to "random search", a continuous sequence of stimulus-invariant stochastic spontaneous actions. The stochastic properties of these actions facilitate probabilistic prediction of the attraction profile of a given environment. Almost continuous object fixation is found, as expected, in stationary flight with a single visual object of appropriate size and contrast.

In frequently hovering or cruising flies such as *Syritta* (Collett and Land 1975a, b), and *Drosophila* (Heisenberg and Wolf 1979; Wolf and Heisenberg 1980; Bülthoff et al. 1980) "smooth" fixation is, most probably, a temporary strategy of minor importance: Pattern-induced orientation is achieved mainly by non-stochastic "spontaneous actions" known as "saccadic" turning or "quantum search". In *Drosophila*, a saccade is accompanied by selective suppression of the visual course control response which would otherwise inhibit the spontaneous turning. The strategy of "saccadic" course control enables the fly to maintain an arbitrary direction of flight with respect to a visual object. A dark object on a bright background is stabilized either in front of the fly (fixation) or, more often, in intermediate positions between front and rear (non-fixation). Conversely, a bright object on a dark

background is held preferentially to the rear of the fly (anti-fixation). Adaptability of spontaneous "quantum search" is the predominant character of "saccadic" course control.

Comparison of the optomotor responses of wing stroke and leg stroke in *Drosophila* suggests a remarkable autonomy of the control systems used in different modes of locomotion (Götz and Wenking 1973; Götz et al. 1979). If "saccadic" course control were a specific requirement of hovering flight then one would not necessarily expect "quantum search" in the walking fly. Pattern-induced orientation on the ground has been carefully documented by evaluation of the *initial choice* of *Drosophila* in numerous arena experiments (Wehner and Horn 1975; Horn 1978). The attraction profiles obtained in different visual environments are compatible with "smooth" fixation or similar strategies based on "random search". For some years we tried to assay pattern discrimination under operant and non-operant conditions of *continued choice* in freely or stationarily walking flies. Results have not been published because of the as yet inexplicable metamorphosis of the attraction profiles during these experiments (Bülthoff 1980, 1981). Only a minor fraction of the difference between the initial attraction of any two objects persists throughout an experiment of several hours duration. This residual preference is invariant to the time and also to the reversal of contrast (Götz 1971, 1980), but does not seem to represent the most important strategy of pattern-induced orientation in the walking fly.

In the present paper we try to show that guided orientation towards visual objects is only one aspect of pattern-induced behaviour. Withdrawal from these objects by transition to the opposite behavioural strategy may be equally important for *Drosophila*. To corroborate this conjecture we compared freely walking flies of a wild type (*WT*) and an optomotor blind mutant (*omb*^{H31}) in two different choice experiments. We hope to prove the existence of complementary strategies of *fixation* and *anti-fixation* in the walking fly, and to demonstrate "quantum search" at the recurrent transition between these strategies. We suggest that apparent inconsistencies of pattern-induced orientation in different experimental paradigms can be explained by the temporal sequence of the alternating strategies.

Materials and Methods

Forced Choice Method. To assay the orientation behaviour of *Drosophila* under conditions of forced choice a comparatively large horizontal array of Y-mazes has been assembled into a

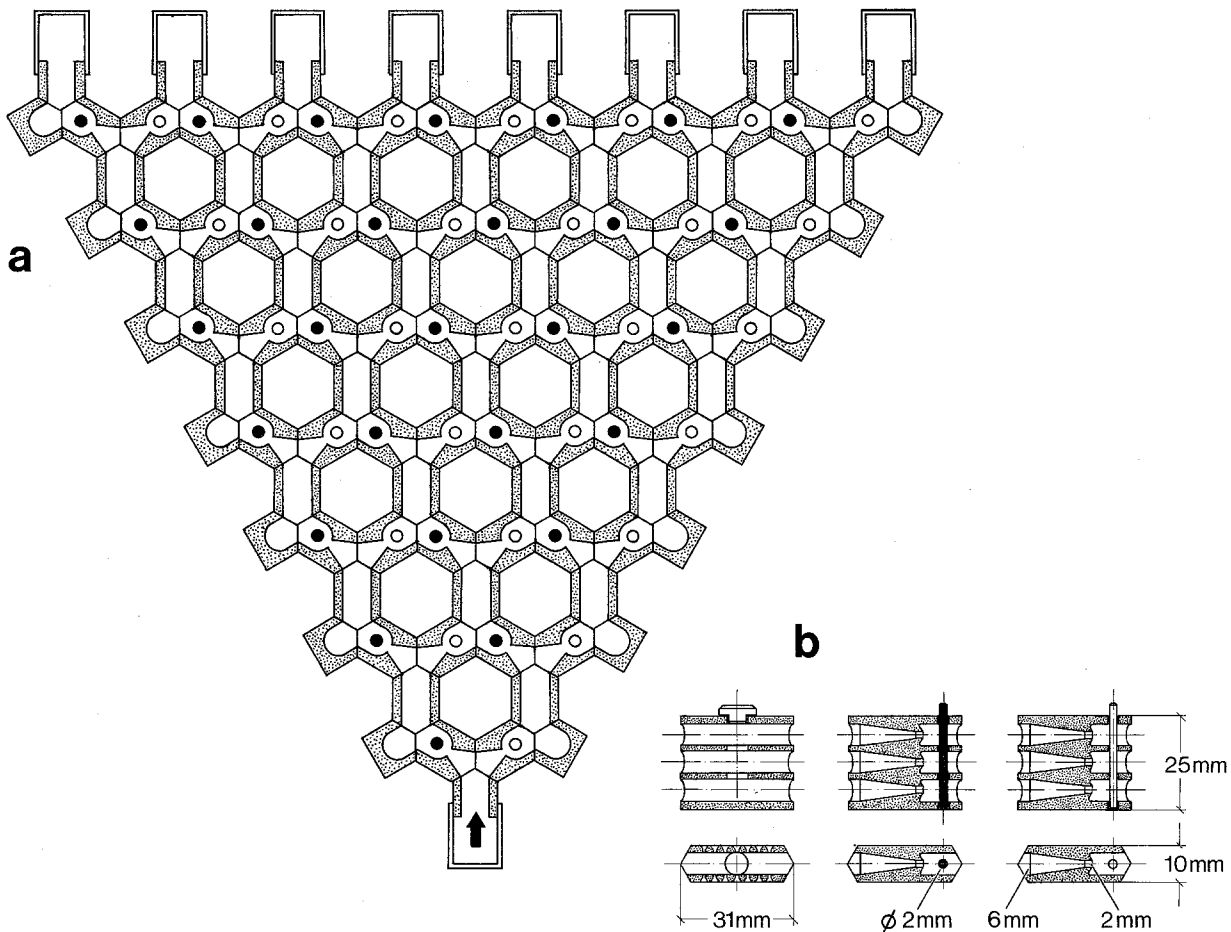


Fig. 1 a, b. Simplified scheme, and actual components, of a multiple-Y-maze used in the forced choice experiment. **a** Horizontal section of an array comprising only 7 of the 14 choice levels of the actual maze. **b** Building blocks of a choice element. The three components are made of light-diffusing plexiglass. The particular structure allows the passage of the maze in three interconnected storeys and the exchange of air. The decision to go left or right depends on the brightness of the circular section of the rod behind the narrow hole of the “rectifying” nozzles which prevent the flies from running in opposite direction through the maze

“Galtonian Board”. Figure 1 shows the design of the three translucent building blocks of a Y-shaped choice element. It further illustrates the assembly of 28 choice elements in a board comprising 7 consecutive rows, or choice levels, at which the walking fly has to decide to go either to the left or to the right. Our experimental array actually consists of 105 choice elements, or 14 choice levels. The multiple-Y-maze is currently used to select fixation-deficient mutants of *Drosophila* (Bülthoff, 1982a, b). As shown in the figure the flies are allowed to run the maze in three interconnected storeys. This is to increase the turnover rate and to avoid clogging.

On arrival at a decision point in the centre of any choice element the flies are confronted with a funnel-shaped nozzle on either side. The nozzles serve as “rectifiers” preventing the flies from running in the opposite direction through the maze (Hirsch 1959). Through the narrow hole of 2 mm diameter at the far end of the nozzles a fly can see a circular segment of either a black, or a transparent, rod of 2 mm diameter. Each segment covers about 0.1% of a hemisphere. This is equivalent to the receptive field of only one of the 700 visual elements in the retina of the corresponding eye. The smallness of the visual target is an important feature of the choice elements: presence or absence of the dark segment has almost no effect on the mean luminance, or on the phototactic attraction, of the corresponding side.

The forced choice behaviour is assayed in a number of tests, each with about 300 flies. While the interior of the maze is held at constant temperature (ca. 24°C) and luminance (ca. 1,000 cd/m²), the flies are released from an empty culture cell to the first choice element. After 14 consecutive choices a fly arrives in one of the 15 end cells where it receives food and awaits counting. About 90% of the flies arrive within 16 h. The missing flies die “en route”. They are found in about equal proportions before the first choice element and further on in the maze, a few of the latter sticking in the nozzles.

The comparatively small influence of component-specific, illumination-specific and strain-specific asymmetries on the choice of the flies is further eliminated by application of the following procedure between subsequent tests: (1) Disassembly of the maze and cleaning of the components in a dishwasher, (2) random permutation and turnover of corresponding components during reassembly of the maze, and (3) alternation of the side of the dark object within the choice elements by appropriate distribution of the removable rods. To simplify the presentation of the results the diagrams in Fig. 3 arbitrarily refer to the situation in Fig. 1 where the dark object is shown on the left side.

Free Choice Method. To investigate the orientation behaviour under conditions of free choice a fly with shortened wings is

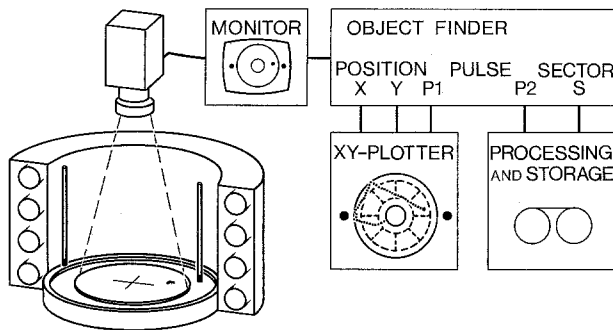


Fig. 2. Video scanning device used for automatic tracking of a walking fly during free choice between two visual landmarks. The fly is placed on an elevated platform in the centre of the illuminated area. Shortened wings and a water-filled "moat" prevent its escape. The actual position on the circular platform is encoded, simultaneously, in rectangular and in polar coordinates. The object finder provides the necessary signals to plot the trajectory of the fly and to count the number of passages, from centre to periphery, through 8 different sectors of a ring-shaped area

allowed to walk for about 200 s on an elevated disk of 44 mm radius in the centre of the arena in Fig. 2. The light diffusing inner wall of the arena, and the surrounding dc-driven toroid-shaped fluorescent lamps, are cut away to show the position of both the water-filled "moat" which prevents the fly from escaping, and the rod-like landmarks on either side which appear as dark objects in 54 mm distance from the centre on the homogeneously illuminated background of about 400 cd/m². Depending on the diameter and height of the black section of these landmarks the objects are either 4 × 120 mm bars which cover about 1%, or 3 × 5 mm spots which cover about 0.1% of the corresponding hemispheres on either side of the disk. The spots resemble the stimuli encountered in the multiple-Y-maze of Fig. 1: The apparent size of the dark spot seen from the centre of the disk is equivalent to the size of the dark segment seen from the centre of the choice elements. To investigate the attractiveness of a single object a slightly modified disk is used in the experiments of Fig. 4a. The dark spot is placed in the centre of this disk, and is made inaccessible to the flies by a surrounding water-filled "pond" of 15 mm radius.

The track of the fly is recorded by a video scanning device which has been developed in co-operation with H. Wenking. The video system consists of an inexpensive electronic camera (Philips LDH 26), equipped with a 2/3" plumbicon image converter tube to increase the tracking speed. The rectangular co-ordinates X and Y of the fly are derived from the time lag between the onset of the corresponding deflections of the scanning beam and the first encounter of an object-specific video signal. Digital devices for the sample-and-hold-operation of the tracking system (Fleischer and Pflugradt 1977) have been replaced by simple analog components (Harris Semiconductor, HA1-2425-5). Analog technique is also sufficient for on-line calculation of $R^2 = X^2 + Y^2$ where R denotes the radial distance of the fly from the centre of the disk. Comparison of R with preset radial distances is used to blank all of the visual signals outside of the tracking region $R_{\min} \leq R \leq R_{\max}$, and to define, within this region, the inner and outer boundaries of a ring-shaped district. The broken lines in Fig. 2 indicate the subdivision of this district into eight sectors which are easily distinguished by the three signs of X, Y and X-Y, respectively.

To plot subsequent XY-positions along the track the object finder delivers a regular sequence of plot pulses P₁ as long as the

fly is moving. Simultaneous averaging of the corresponding radial distances R yields the mean radial distance \bar{R} of a track as shown in Fig. 4a. An occasional pulse P₂ indicates a passage, from centre to periphery, through one of the eight sectors of the ring-shaped area. This pulse is used to record code S of the corresponding sector. Off-line evaluation of the data yields histograms of the passages as shown in Fig. 6. In other modes of operation the object finder has proved useful for the analysis of locomotor irregularities in *Drosophila* (Götz and Biesinger, in preparation).

Results

The present account refers to experiments on pattern-induced orientation in the *Drosophila* wild type "Berlin" (WT), and in M. Heisenberg's mutant "optomotor blind" (*omb*^{H31}) which has been derived from this stock by mutagenesis (Heisenberg and Götz 1975; Heisenberg and Buchner 1977; Heisenberg et al. 1978; Blondeau and Heisenberg 1982). The lobula plate neurons homologous to the movement-sensitive giant H- and V-cells in the visual systems of *Calliphora* and *Musca* are significantly reduced or missing in this mutant. Concomitantly, the movement-induced course control response is severely diminished. Pattern-induced orientation in the stationarily flying mutant is disturbed, mainly in that "saccadic" spontaneous actions are missing. "Smooth" fixation still operates, but has to await a chance of "catching" a visual object in the position-sensitive frontal area of the visual field. A dark vertical bar is rarely "caught" in less than a few seconds after presentation outside of this area. This may explain the predominance of non-fixation for comparatively short periods of initial choice in the walking mutant, and the predominance of fixation for comparatively long periods of continued choice in the flying mutant. The electroretinogram, and the movement-induced responses of altitude control and landing, seem to be essentially intact in *omb*^{H31}.

Pattern-Induced Orientation in the Maze

Figure 3 summarizes the results obtained under conditions of forced choice in the maze experiment. The black columns show the fraction of the N flies which made 14 consecutive choices on their way to one of the 15 end cells of the multiple-Y-maze. The histograms arbitrarily refer to the situation where the dark object appears on the left side of the choice elements. The staircase functions represent the best approximation of the experimental data by a binomial distribution. This type of distribution is expected if the probability P of approaches to the dark object is constant for all of the N flies and all of the consecutive choices. The deviation of the

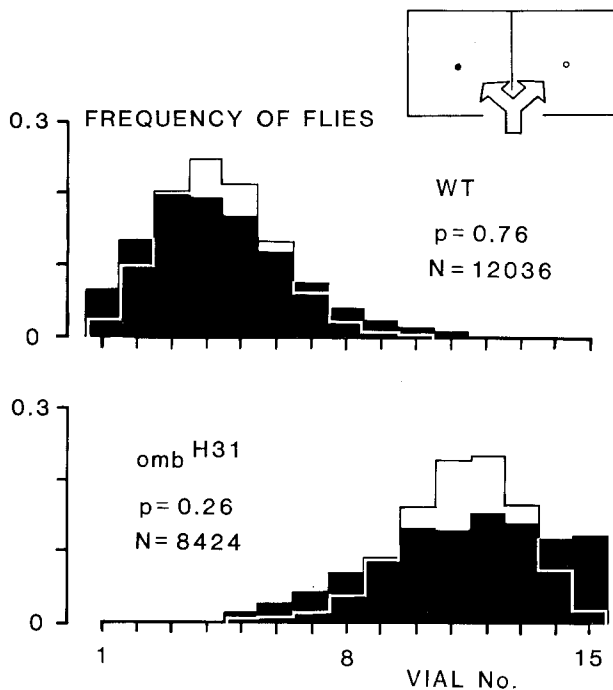


Fig. 3. Pattern-dependent forced choices of the walking *Drosophila* wild type (WT) and "optomotor blind" mutant (*omb*^{H31}) in the maze experiment. The inset illustrates the apparent size of the dark object in comparison to the bright background as seen from the centre of the Y-shaped choice elements. The object is arbitrarily shown in its left-hand position which underlies the presentation of the result. The distribution of the relative numbers of flies in the end cells (black columns), and the fitted binomial distribution (staircase function), refer to 14 consecutive choices of the N flies of either strain. The fraction of choices towards the object is given by the probability *P*. Approximation of *P* = 0.5 is expected in the absence of pattern-induced effects, and is found in object-blind mutants. The present results revealed the antagonism between "fixation" in the wild type and "anti-fixation" in the mutant

experimental data from the fitted curves corresponds to a comparatively moderate fluctuation of the probabilities in the two strains.

(1) Individual differences seem to account for most of the fluctuation of the probabilities *P*. Groups of flies selected for positive, or negative, deviation in the first test also maintained their respective deviation in a second test. The mutant is less homogeneous than the wild type.

(2) Sex-specific differences between the average probabilities *P* are comparatively small both in the wild type (females 0.75 ± 0.01 S.E.M., males 0.79 ± 0.01 S.E.M.), and in the mutant (females 0.26 ± 0.01 S.E.M., males 0.30 ± 0.02 S.E.M.).

(3) Species-specific lateral bias to the left side of the maze would account for positive deviation of the probabilities *P* if the dark object is shown on the left side, or for negative deviation of similar

magnitude if the dark object is shown on the right side of the choice elements. The observed deviation in the wild type (0.02 ± 0.01 S.E.M.), and in the mutant (0.00 ± 0.02 S.E.M.), is negligible in comparison to the "leftism" of *Drosophila* in other mazes (Murphey 1965; Hay 1975; Heisenberg and Götz 1975).

(4) Inconspicuously slow drift of the average probabilities *P* has prevailed during the last four years both in the wild type (+0.01/year), and in the mutant (+0.02/year). Evolution within the mutant strain has been proposed to explain a slow drift of the movement-induced responses in *omb*^{H31} (Blondeau and Heisenberg 1982).

All of the strain-specific components of the deviation from "binomial" behaviour in the maze are negligibly small and do not require further consideration in the present account.

The essential result from the forced choice experiments is the striking discrepancy between the pattern-induced responses of wild type and mutant. The wild type approaches the dark object in 76% of all choices. The result confirms the well established fixation behaviour of this strain. The chance of obtaining a score of $P \geq 0.76$ without any preference for visual objects is below 10^{-12} in the present experiment. The mutant *omb*^{H31}, on the other hand, approaches the dark object in only 26% of all choices. This is evidence for an unexpected trait of anti-fixation behaviour. The chance of obtaining a score of $P \leq 0.26$ in the absence of this trait is well below 10^{-4} in the present experiment. The result is remarkable for several reasons:

(1) The anti-fixation response of the mutant equals the fixation response of the wild type in reliability and strength.

(2) Anti-fixation in *Drosophila* has been associated, so far, with the avoidance of repellent configurations such as a bright vertical bar on a dark background (Heisenberg and Wolf 1979; Wolf and Heisenberg 1980). Occasional anti-fixation of otherwise attractive configurations (e.g. a dark vertical bar on a bright background) fits into the directional distribution of non-fixation during "saccadic" course control, and does not justify different labeling. No particular tendency towards anti-fixation has been observed in the flying mutant.

(3) Sizeable anti-fixation is evidently incompatible with the phenomenological theory of "smooth" fixation (Reichardt and Poggio 1981), and does not seem to occur under conditions of initial choice in the walking wild type (Wehner and Horn 1975; Horn 1978), and the walking mutant (Heisenberg et al. 1978).

(4) In a mutant such as *omb*^{H31} one expects degradation rather than inversion of the normal responses. The inversion of the optomotor effect on the walking speed in a genetically defective strain of *Drosophila* may appear as an exception to the rule (Götz 1975b). However, this inversion is likely to result from a shift of balance between the simultaneous optomotor responses of acceleration on the outer side, and deceleration on the inner side, of a curved trajectory.

A convincing interpretation of the results in Fig. 3 must resolve the present inconsistencies of orientation under conditions of forced choice in the maze, and free choice in the arena.

Pattern-Induced Orientation in the Arena

The probability of approach to the dark object in the maze is appropriate to characterize strain-specific orientation effects such as fixation in the wild type and anti-fixation in the mutant. However, the underlying strategies of orientation cannot be specified without recourse to the trajectories of the walking flies in the corresponding experiment. The choice elements in the maze are inaccessible to scrutiny "in situ". We therefore compared the trajectories of the wild type, and the mutant, in the vicinity of a visual object similar to the dark segment shown in the maze. The trajectories, and their mean radial distance from the object, were recorded for about 200 s under conditions of continued free choice in the arena (Fig. 2). The results shown in Figs. 4–6 refer to the reactions of female flies with shortened wings. Males react similarly under the same conditions.

The arrangement in Fig. 4a simulates the panorama seen from various positions within a choice element in the maze. The dark spot in the centre of the arena is surrounded by a ring-shaped platform between two water barriers. A fly on the platform thus maintains a radial distance $R_{\min} \leq R \leq R_{\max}$ to the object, where $R_{\min} = 15$ mm and $R_{\max} = 44$ mm. These parameters establish the identity of the retinal images received during passages either from R_{\max} to R_{\min} in the arena, or from the centre of a choice element to the far end of the nozzle in front of a target.

The mean radial distance \bar{R} of the trajectories in the arena can be used to assay the average attraction of the dark spot under conditions of continued free choice. The broken circles hidden in the two trajectories in Fig. 4a correspond to $\bar{R}_0 = 31.7$ mm, the expected mean radial distance in the absence of attraction. To calculate \bar{R}_0 we assumed constant density of the trajectories across the platform (Götz

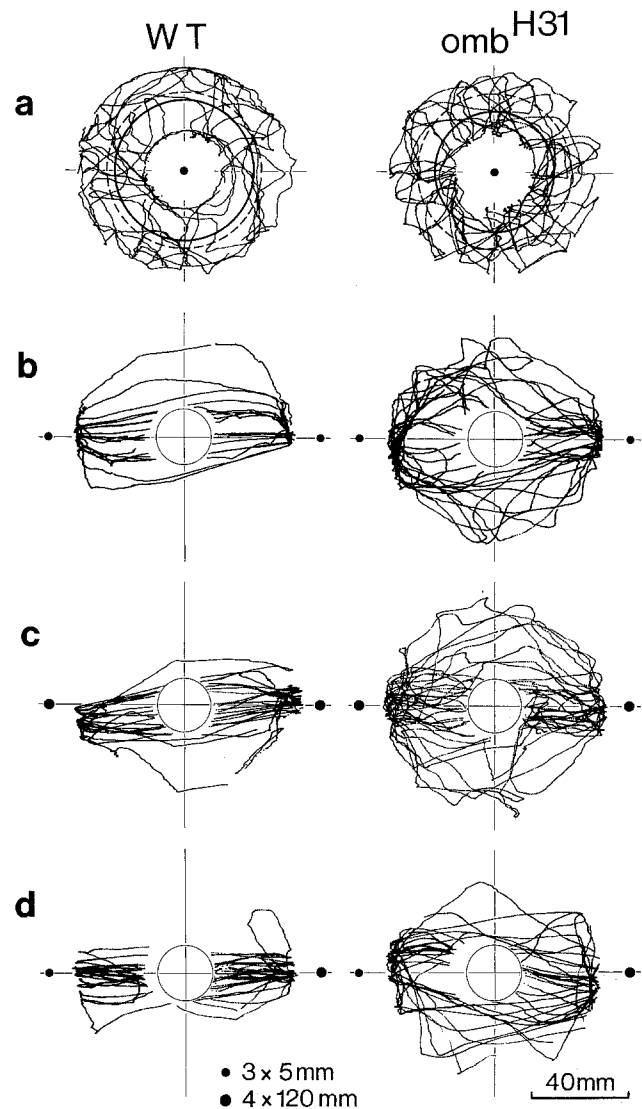


Fig. 4a–d. Pattern-dependent free choices of the walking *Drosophila* wild type (*WT*) and "optomotor blind" mutant (*omb*^{H31}) in arena experiments with one visual object in the centre of an annular platform, or two visual objects in the periphery of a circular platform. *Dots* indicate type, position and width of the inaccessible dark objects. Each of the diagrams represents the path of a female fly, recorded for ca. 200 s within a ring-shaped tracking region of the "isolated" platform. Blanks "en route" correspond to walking speeds below 1 mm/s. The mean radial distance in the presence (*solid circle*), and absence (*broken circle*), of a dark spot in the centre illustrates the average attraction exerted on 12 flies of either strain (a). The trajectories show the conversion of fixation into anti-fixation upon arrival at the water barrier in front of a visual object. The recurrent transition between two objects in "Buridan's paradigm" is surprisingly invariant to changes in their size and shape: The flies keep running to and fro between two spots of 5 mm height (b), two vertical bars of 120 mm height (c), and even a combination of these objects (d)

and Biesinger, in preparation). The object in the centre of the arena is either attractive if $\bar{R} < \bar{R}_0$, or repellent if $\bar{R} > \bar{R}_0$ or neutral if $\bar{R} = \bar{R}_0$. The most plausible hypothesis to be tested attributes fixation in the wild type to the predominance of attraction, and anti-fixation in the mutant to the predominance of repulsion, in the vicinity of a dark object. Actually, this hypothesis is incompatible with the experimental results: The solid circles in Fig. 4a represent the mean radial distances of the wild type ($\bar{R}_{WT} = 28.5 \pm 0.9$ mm S.E.M.), and the mutant ($\bar{R}_{omb} = 24.4 \pm 0.8$ mm S.E.M.), each obtained from the trajectories of 12 flies. The deviation of these distances from \bar{R}_0 corresponds to a moderate predominance of attraction in both strains. (The attraction is even significantly stronger in the mutant than in the wild type). This is evidence against the present hypothesis. The average attraction established under conditions of continued free choice in the arena is similar in the two strains and does not account for the antagonistic responses in the maze.

The trajectories of the flies of either strain have more in common than their bias towards the object. The two examples in Fig. 4a show a conspicuous preference for passages between the inner and outer barrier of the platform which is not observed in the absence of visual stimulation. The flies approach, and leave, the barriers in a roughly radial direction. Circling around the inaccessible visual target in the centre is frequently observed upon arrival at the inner barrier. Throughout this period the flies remain oriented towards the centre. The failure to reach the target seems to activate a sudden change in behaviour: Fixation of the target ceases, and anti-fixation begins, usually with a U-turn of the flies which are now leaving for the outer barrier. After several seconds of anti-fixation, and occasional exploration of the periphery, the next approach is due to occur, and so on. The recurrent inversion of orientation is not conditional on the use of water barriers. Similar results were obtained also in experiments with heat barriers invisibly embedded in the floor of the arena (Einighammer, unpublished). The flies spend much time in fixation and anti-fixation, and do not seem to become increasingly indifferent to the visual stimulus.

The arena experiment has shown the existence, and close association, of the two antagonistic responses of fixation and anti-fixation in freely walking flies of either strain. The dissociation of these responses in the forced choice experiment in Fig. 3 is obviously due to the particular conditions in the maze such as sudden confrontation with the dark object, and locomotor impediment in the

choice elements. Arrival in a new environment actually establishes fixation as the preferred initial choice of the wild type, and anti-fixation as the preferred initial choice of the mutant. The experimental evidence is derived from the trajectories of 31 female flies during the first 10 s in the arena. Immediately after release from the tip of a suction capillary the flies do not show strain-specific differences in the averages of both the initial delay of locomotion (about 1 s), and the initial turning (about 90°). However, the chance of fixation at the first passage across the platform is about $P = 0.7$ in the wild type, and about $P = 0.3$ in the mutant. These figures resemble the results of the forced choice experiment in Fig. 3: The delayed transition to object fixation in the mutant appears sufficient to explain the predominance of anti-fixation in the choice elements of the maze.

Buridan's Paradigm

The recurrent alternation between fixation and anti-fixation of inaccessible objects is more explicitly seen in arena experiments with identical targets on either side of the platform. The results in Fig. 4b refer to the experiment shown in Fig. 2. A female fly of either strain was released in the electronically blanked centre of the circular platform, and the trajectories were recorded for about 200 s. The apparent size of the dark spot on either side corresponds to the visual field of only one of the ca. 1,400 visual elements, or neurommatidia, of a fly in the centre of the platform. The spot covers about 20 visual elements at its nearest position, and about 1/4 of a visual element at its most distant position, from the fly. A spot in the latter position is a faint point-like object of low contrast. Free choice between the two identical spots seems to be as perplexing to *Drosophila* as it was to Buridan's ass in the early 14th century. The flies of either strain keep running to and fro, between the spots, for the duration of the experiment. This behaviour involves (1) approach towards one of the spots, (2) inversion of orientation on arrival at the barrier in front of this spot, (3) retreat from this spot, and (4) approach towards the faintly visible spot on the other side of the platform. Transition from fixation to anti-fixation is likely to occur during the regular U-turns in front of the target on either side. The complementary transition back to fixation is not seen in the present experiment as it cannot conceivably divert the trajectory of passages between an object behind and an object in front. The flies keep running along the direct line between two objects even if this line is a marginal chord of the

circular platform. The trajectories of the wild type, and the mutant, are comparatively similar and cannot be explained by the phenomenological theory of visual orientation in larger flies.

Is the recurrent inversion of orientation conditional on point-like objects such as the dark spots used in the previous experiments? To answer this question we repeated the experiment in Fig. 2 with a dark vertical bar on either side of the platform. So far, vertical bars have been the preferred objects in experiments on pattern-induced fixation and tracking in flies. The apparent size of a bar corresponds to the field of 10 visual elements of a fly in the centre of the platform. This is about ten times the size of the dark spot used before. The bar covers about 60 visual elements at its nearest position, and about 5 visual elements at its most distant position from the fly. The results are shown in Fig. 4c. Free choice between two identical bars elicits similar sequences of approach, retreat and transition as in the previous experiment. The alternation between fixation and anti-fixation in Buridan's paradigm is surprisingly invariant to size and shape of the identical objects used so far.

Is the recurrent inversion of orientation conditional on the identity of the two visual objects in Buridan's paradigm? The results in Fig. 4d refer to the trajectories between a dark spot on the left side and a dark vertical bar on the right side of the platform. These objects exert different attraction during the initial choice in *Drosophila* (Wehner 1981, pp. 386–422; Mimura 1982). Yet the flies keep patrolling to and fro, between incongruent objects, as they did in choice experiments with identical objects. Unlike Buridan's ass, the flies are not "caught" by the more attractive target. The continuous transition between entirely different objects obscures the invariant constituents of pattern preference. This explains the apparent lack of pattern discrimination under operant and non-operant conditions of continued free choice in *Drosophila*.

The trajectories in Fig. 4b–d demonstrate the recurrent inversion of orientation for a comparatively short period of about 200 s. To investigate the persistence of this effect we recorded the trajectory of a wild type female for several hours of almost uninterrupted locomotion between a dark spot on either side of the platform. (Once in a while the fly leaped into the moat and had to be placed back onto the platform by means of a suction capillary). Figure 5 shows a sequence of 24 samples, each representing about 200 s of the trajectory. The samples were taken in 15 min intervals for the first 6 h of the experiment. The fly was fed for about 1 min,

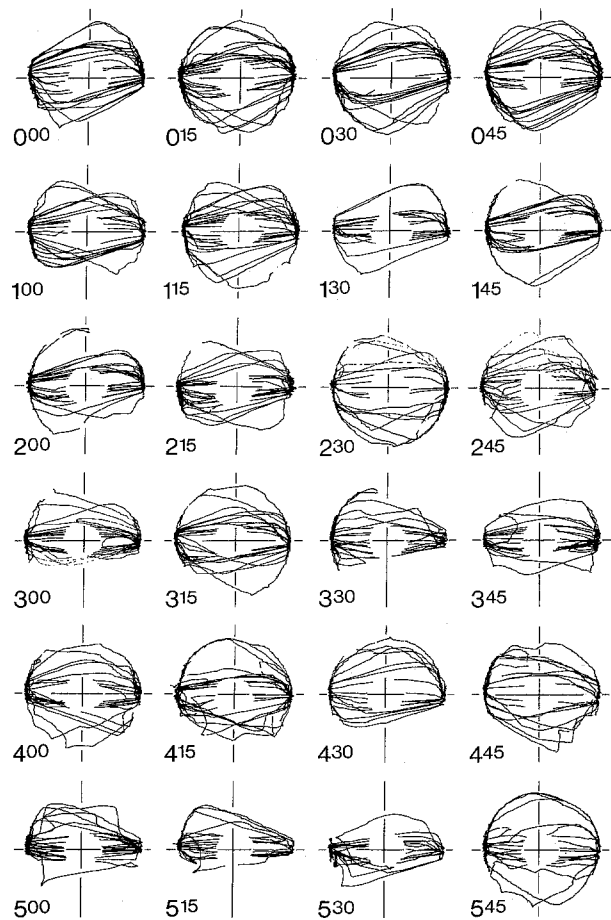


Fig. 5. Recurrent transition of a female *Drosophila* wild type between two inaccessible dark spots in "Buridan's paradigm". The experiment shown on the left side of Fig. 4b was repeated for more than 6 h to demonstrate the almost continuous alternation between fixation and anti-fixation in a single fly. Each of the samples represents ca. 200 s of the trajectory at a given time (h, min) after release of the fly in the arena. Transition between the objects can go on for very long time without significant decline

and the experiment was continued for another hour. The results were not significantly different from those obtained before the break. Within 7 h the fly covered about 220 m traversing the platform. Arrival at the barrier in front of a dark spot, and subsequent inversion of orientation, occurred about 2,500 times in a single experiment. The alternation between fixation and anti-fixation of inaccessible visual objects in Buridan's paradigm seems to be one of the most persistent behavioural traits found so far in *Drosophila*.

At least three objections might be raised against the conclusions drawn from the results in Figs. 4 and 5:

(1) Vision might not be the essential link in the orientation behaviour of the flies in the present experiment.

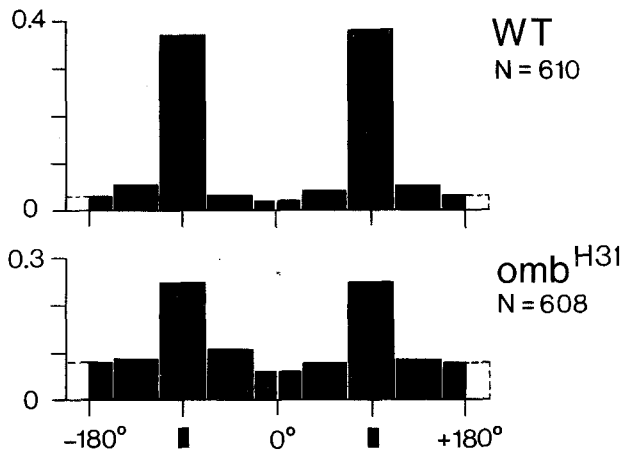


Fig. 6. Histograms of continued free choices of the *Drosophila* wild type (WT, 39 flies), and “optomotor blind” mutant (*omb^{H31}*, 39 flies), between two dark spots in the paradigm shown in Fig. 4b. The distribution of the direction of N passages from the centre to the periphery of the circular platform in the arena refers to the actual position of the objects which is continuously changed to avoid chemosensory feedback from the traces of earlier passages. The histograms demonstrate recurrent fixation of the inaccessible objects in both strains. The distribution of the corresponding passages back to the centre is not significantly different from the depicted results. The dark spots used throughout these experiments simulate the panorama seen from various positions within the choice elements in the maze. The retinal images correspond to only one of the 1,400 visual units of a fly in the centre of either the platform or the choice element. The images increase in equal proportion if the flies run to the barrier in front of the object

(2) Passages between the two objects in Buridan’s paradigm might be stabilized by chemosensory feedback received from earlier traces.

(3) Selected samples of trajectories of a few flies might not be sufficient to infer the recurrent inversion of orientation in *Drosophila*.

However, the following investigation corroborates the previous conclusions. Visual perception is a necessary prerequisite for both approach and retreat of the fly: Effects such as fixation and anti-fixation in Figs. 4 and 5 are completely missing in the blind mutant “*sine oculis*” (*so*) which has been checked for the absence of photoreceptors (Götz 1980). The precautions against chemosensory artifacts include rinsing of the platform between trials, and repeated displacements of the surrounding objects during the trials: Figure 6 shows the results obtained by automatic tracking and off-line evaluation of the first 200 s of the trajectories of 39 females of the wild type (WT), and 39 females of the mutant (*omb^{H31}*). The trajectories were recorded in alternating sequence, and refer to a dark spot on either side of the rinsed platform. The histograms represent the fraction of the N passages, from centre to periphery, through the eight sectors of the ring-

shaped area shown by the broken lines in Fig. 2. Preference for the two opposite sectors in front of the visual objects is compatible with the trajectories in Buridan’s paradigm. However, the present experiment was essentially modified in order to counteract possible effects of chemosensory feedback: After eight passages to the periphery the objects were automatically placed in front of another pair of opposite sectors of the ring-shaped area in Fig. 2. Simultaneously, the object finder fitted the co-ordinates to the new position of the visual objects. The trajectories obtained under these conditions correspond to those in Fig. 4b. The continuous transition between the two objects in the previous experiments can be attributed neither to chemosensory feedback nor to anomalous features of the selected samples in Figs. 4 and 5.

Histograms similar to those in Fig. 6 have been used to demonstrate pattern-induced fixation in the wild type (Wehner and Horn 1975; Horn 1978), and non-fixation in the mutant (Heisenberg et al. 1978). The available results refer to the initial choice upon arrival in the centre of the arena. The histograms obtained under conditions of continued choice in the present experiment demonstrate recurrent fixation of inaccessible visual objects by the walking flies of either strain. Actually, almost each of the N runs to the periphery is followed by a run back to the centre. These runs demonstrate recurrent anti-fixation of inaccessible visual objects. The histograms of the runs from the centre to the periphery shown in Fig. 6 are almost identical with the histograms of the corresponding runs in opposite directions.

Discussion

The variety of meaningful cues in the visual world provides a fly with a choice of reference systems for guided orientation. Withdrawal from guidance is an important constituent of the repertoire of visually induced responses in *Drosophila*. Withdrawal is passively achieved by “pseudo search”, an inherently predictable collapse of optomotor course control in the proximity of landmarks which are moving past the fly. The strategies of active withdrawal comprise the continuous “random search” due to random fluctuation of the course diverting endogenous torque, and the discontinuous “quantum search”, due to uniform “body saccades”. The regular U-turns performed upon arrival at an inaccessible visual object are, most likely, examples of “quantum search” in the walking mode.

The continuous alternation between the complementary strategies of fixation and anti-fixation in the walking fly accounts for apparent inconsistencies of guided orientation in different experimental paradigms. The alternation is remarkably independent of the visual stimulus, and is not disturbed in the optomotor blind mutant *omb*^{H31}. Why then do we find mutant-specific responses of anti-fixation in the maze experiment, and non-fixation in an earlier arena experiment (Heisenberg et al. 1978), where the wild type runs consistently towards the visual target? The present results suggest that the arrival in a new environment establishes fixation as the preferred initial choice of the walking wild type, and anti-fixation as the preferred initial choice of the walking mutant. The initial responses seem to account for the behaviour in the choice elements of the maze. The delayed transition from anti-fixation to fixation in the walking mutant may have produced a mixture of antagonistic responses (apparent non-fixation) during the initial choice in the earlier arena experiment. The comparatively low chance of "catching" an object in the position-sensitive frontal area of the visual field still explains the delayed transition to object fixation in the walking mutant, but fails to explain the instant anti-fixation in these flies.

Free choice between two identical objects on either side of the arena is particularly suited to demonstrate the recurrent alternation between approach and retreat in the walking fly. Buridan's name has been assigned to this paradigm to emphasize the analogy with the indecision of his famous ass in the vicinity of two identical heaps of hay (Götz 1980). Yet the ultimate in indecision is shown by *Drosophila* which keeps patrolling to and fro, even if the two objects exert conspicuously different attraction during the initial choice of the fly. This behaviour illustrates the extremely transient nature of visual attraction in *Drosophila*. Failure of the attempt to assay the constituents of pattern preference under conditions of continued choice in the arena may be attributed to the close association of fixation and anti-fixation in the walking fly. The otherwise powerful experimental scheme of free choice between different patterns cannot be successfully applied under these conditions.

What is disadvantageous for the experimenter may be advantageous for the fly: Exploration of the visual environment helps to discover rewarding objects in the midst of all sorts of visual landmarks. The strategy of approach, retreat and transition found in *Drosophila* probably increases the chance of such discovery by acceleration of the search

process. Moreover, the induced alternation between fixation and anti-fixation prevents the fly from being captured by the predominant visual attractiveness of an arbitrary non-rewarding target near its course. It is tempting to compare the recurrent transition between competitive objects in *Drosophila* with the recurrent alternation of the competitive aspects of ambiguous figures in human perception. The regularity and persistence of quantum search in the fly strikingly resembles the regularity and persistence of ambiguity effects such as reversal of perspective depth of a Necker cube (Attneave 1971). Quantum search as well as depth reversal help to overcome the preoccupation with only one aspect of the visual world. The strategies used to achieve this goal seem to have much in common.

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