WHAT CAUSES EDGE FIXATION IN WALKING FLIES?

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Summary

The orientation of freely walking flies (female *Lucilia cuprina*) to lines and stripes in a circular arena is described. The following observations were made.

1. The flies walked straight towards a dark line using the frontal eye region, but a pale line on a dark background was only weakly attractive.

2. In bright conditions flies walked in a curved line towards a black–white edge, the path being convex towards the dark side of the border. The curves indicated that the flies were heading for a point about 5–10° to the dark side of the edge.

3. In dim conditions the edge of a dark region was not especially attractive and flies headed towards any point in the dark area.

These observations can be accounted for by assuming that the fly walks towards the darkest region in its visual field (scototaxis). In bright conditions the edges of a dark region become more attractive than its centre. This change could be explained if lateral inhibition creates a 'Mach-band' effect, making the edges appear darker than the centre. Thus, fixation behaviour in walking *Lucilia* females seems to be a simple taxis.

Introduction

Most visual behaviour, including fixation and figure–ground discrimination in the fly, cannot be supported by simple linear computation (Poggio and Reichardt, 1976). However, as Wehner (1987) has emphasized, the apparent computational complexity of a behavioural problem can be exaggerated unless we look carefully at the question being asked of the world. In general, object fixation requires non-linear processing of second or higher order (Pick, 1974; Poggio and Reichardt, 1976). Here we argue that the simpler question: 'where is the darkest point in the visual field?', involving essentially linear processing, can account for much of the behaviour of a walking fly. We also speculate about how neural processing at early stages of vision could affect the answer to the question.

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Materials and methods

We describe the behaviour of freely walking female blowflies *Lucilia cuprina* of the laboratory strain SWT (standard wild type) from CSIRO stocks aged 2–8 days. One test was also carried out using flies originating from a wild population on Flinders Island, Tasmania. The flies were prevented from flying by waxing the base of the wings. Sometimes the eyes were painted with red matt enamel (Humbrol), which stuck well but could easily be lifted off with forceps once dry. After preparation, flies were left for at least 2 h before testing.

During experiments a single fly was placed in the centre of a white cardboard arena 0.5 m in diameter with 0.6 m high walls. Patterns, constructed using black and white paper, or paper of calibrated mean reflectance (Letratone), were fixed to the arena's wall. A projector (150 W quartz–halogen bulb), placed directly above, lit the arena with a cone of light and illuminated the walls nearly uniformly. The projector was focused on the white floor of the arena, but direct illumination of the floor was blocked by a black disc in the image plane, rendering floor and walls roughly equal in brightness. The luminance of the arena wall was measured with a Pentax spotmeter. For most experiments this was $500\,\mathrm{cd\,m^{-2}}$, but lower luminances were used in experiments comparing the responses to stripes of different contrast polarity (see Fig. 3). Low light intensities were investigated using luminances of $5\,\mathrm{cd\,m^{-2}}$ and $0.05\,\mathrm{cd\,m^{-2}}$. Before testing, flies were screened for competence in fixation by placing a vertical black stripe 25 mm wide (the angular subtense at the centre of the drum is the usual description given of the target size; in this case 6°). The fly was released from under a Petri-dish cover, ensuring that its initial position was arbitrary, and allowed to walk freely. About half the flies made directly for the stripe on most occasions. Good fixators alone were used for further experiments, but no fly was rejected after it had passed the initial screening procedure. Fixators could usually be recognized by their tendency to rotate on the spot before walking decisively towards the chosen target. Poor fixators walked at random, often in spirals, around the arena. Agitated flies ran quickly as soon as they were released, and hence were left to settle between each trial run. Successive runs by a given fly followed a rather stereotyped course. The basis for this stereotypy is unknown, but olfactory cues or secondary landmark learning cannot be ruled out. This stereotyped behaviour complicated the use of statistical procedures to validate results, but the main findings were quite clear. To minimize the tendency of flies to follow a stereotyped path, and to control against illumination artefacts the position of the stripe was altered by 90° or 180° after the completion of five runs. A run was counted when the fly had walked to within 10 mm of the drum wall. A trial was completed when the fly had been tested once in each of two or four quadrants. Each experiment described here is based on runs from four or more flies.

Runs were recorded in one of two ways. Either the distribution of runs was obtained by scoring the 10° sector in which the fly crossed a circle 230 mm in diameter, or more precise paths were followed by single-frame analysis of video records. Further analysis of these trajectories was made by hand-fitting logarithmi

spirals or tangents (see Fig. 1). A logarithmic spiral is the trajectory expected if a fly walks forward maintaining a constant angular bearing with respect to an edge. Taking the edge as the origin of a polar coordinate system (r,θ), with θ (rad) being measured clockwise with respect to the drum tangent at the edge directed towards the dark side, the trajectory can be described by the equation:

$$r = r_0 \exp[(\theta - \theta_0)/k],$$

where (r_0, θ_0) are the polar coordinates specifying the initial position of the walking fly, and $k = \tan\phi$, where ϕ (rad) is the angular bearing of the edge. We refer to ϕ as the curvature parameter (Fig. 1).

Results

Fixation of a line

After a period of searching by rotating on the spot, or of undirected wandering, flies fixated and ran *straight* towards a 1.5° black line (Fig. 1). They often finished by walking straight up the line itself. The direct route followed (Fig. 1) implies that the front of the eye was used for fixation, and if the eye was covered leaving only the front seven facet rows (and ocelli) exposed good fixation was maintained (Fig. 2A). In contrast, flies with the front 7–10 rows of facets covered, but the rest of the eye uncovered, were unable to fixate a 6° stripe (Fig. 2B; controls Fig. 2C). These results show that the front of the eye, within about 10° of the midline (Land and Eckert, 1985), is used for line fixation by *Lucilia* females.

Contrast polarity

The effect of contrast polarity on fixation and tracking behaviour has been little studied, with a dark target on a pale ground being the usual stimulus configuration (but see Reichardt, 1970, 1973). We found a marked effect of contrast polarity on the tendency of flies to fixate a 6° stripe. After adjustment to give the same mean luminance ($50\,\mathrm{cd\,m^{-2}}$), a black stripe on a white background was much more attractive than a white one on a black background (Fig. 3A). Similarly, at lower contrast (40%) when flies were given a choice between 3° wide stripes set 150° apart (background $250\,\mathrm{cd\,m^{-2}}$), they were much more strongly attracted to a dark than to a pale line (Fig. 3B). These findings imply that scototaxis (attraction to darkness) plays a significant role in the fixation of narrow stripes. Even when flies headed for the pale line they did not run directly up the centre of the target but veered off to one side. A similar bimodal distribution of attractiveness about a pale line has been shown for moths (Preiss and Kramer, 1984). The standard wild type strain (SWT) of *Lucilia cuprina* is a laboratory stock, but has been maintained to resemble the wild phenotype. Experiments with flies from stocks recently caught in the wild indicated a similar preference for a low-contrast dark stripe (20 out of 40 runs) over a pale stripe (8 out of 40) to that seen in SWT. Twelve of the 40 runs by the four wild-caught flies tested were not directed (within 10°) towards either stripe.
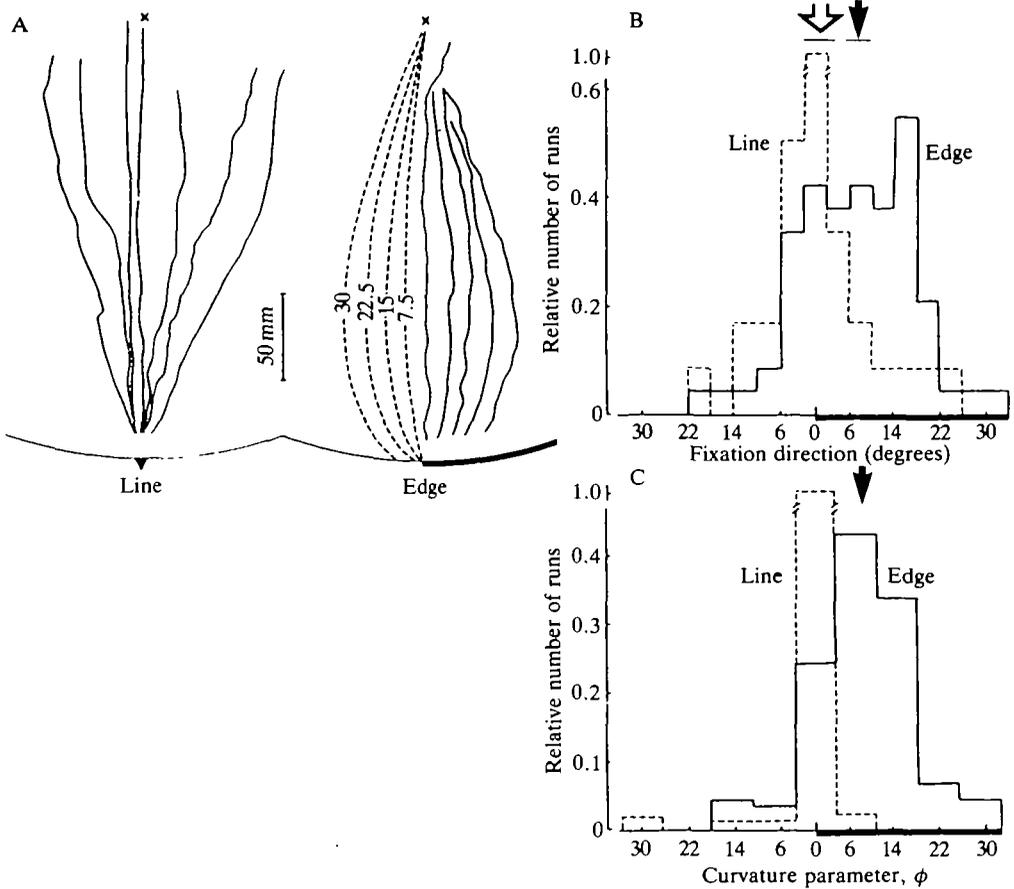
Fig. 1. (A) Selected paths run by flies, traced from video film, towards a line (left) and towards the edge of a 90° stripe (right). The brightness of the wall was 500 cd m⁻². Curves plotted as dashed lines are logarithmic spirals plotted for four different values of the curvature parameter ϕ, corresponding to fixation points lying 7.5–30° from the edge, or fixating the edge with the corresponding lateral eye region. Only runs which finished within 2 cm of the edge (1 cm in from the drum wall) are analysed. These runs correspond roughly to those falling within the 10° sector closest to the edge (Fig. 4A), about 50 % of all runs. (B) Histogram of the angle to the edge (solid line) or to the 2° line (dashed line) to which the tangents to paths projected at 130 mm from the drum wall (10 flies, 73 runs to the edge; five flies, 35 runs to the line). Solid and open arrows give means for runs to the edge (7.5° on the dark side of the edge) and the line (0.4°), respectively, and bars give 95 % confidence estimates for the mean. Bar heights are normalized to the proportion heading directly for the line. (C) Histogram of the curvature parameter ϕ for runs to an edge (solid line) and a line (dashed line), respectively; positive angles are those to the right of the line or to the dark side of the edge. Mean angle to an edge (+8.5°) is arrowed. Note the very large proportion of runs straight towards the line (88 % of total), with no evidence of the bimodal distribution to be expected if the target were fixated laterally. The curvature parameter is estimated by matching the path with a logarithmic spiral (Fig. 1A).
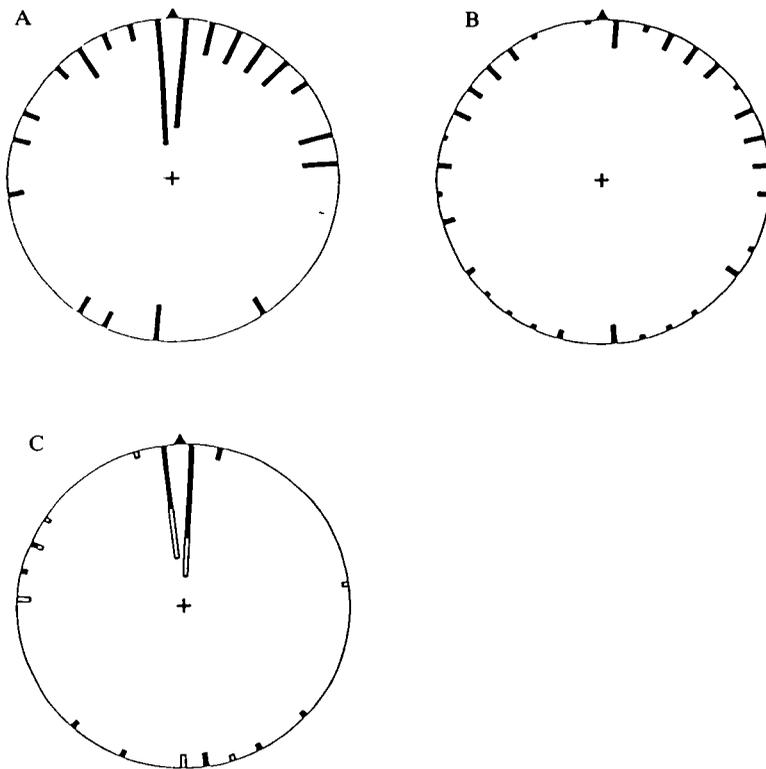
Fig. 2. Runs towards a 6° wide stripe (triangle) in bright conditions. Bar height is proportional to the number of runs crossing each 10° sector at a radius of 230 mm. Five runs were made in each of two quadrants by each fly. (A) Runs by four flies, with both eyes painted leaving only the front seven facet rows exposed towards a black line. 40 runs, normalized to the most frequently selected sector. (B) Runs by four flies (40 runs) with the front seven facet rows occluded. Virtually no fixation occurs. The histogram is normalized to the proportion heading for the most selected sector in controls. (C) Controls (55 runs) before application of the paint (solid bars) for all flies, and after its removal for two (open bars).

Fixation of an edge

Just as they seemed to prefer to walk towards a dark line, *Lucilia* were attracted by larger dark regions: flies nearly always walked towards a dark quadrant and avoided a white quadrant (Fig. 4). At $500\,\mathrm{cd\,m^{-2}}$ and $5\,\mathrm{cd\,m^{-2}}$ the edges of the regions were strongly preferred, whilst in dim conditions, with a luminance of $0.05\,\mathrm{cd\,m^{-2}}$, edge preference disappeared and the flies headed towards an arbitrary point in the dark area (Fig. 4).

Walking towards edges was less precise than walking towards a line (Fig. 1). Some individuals appeared to ignore the edges and head for the centre of the stripe, but most finished close to the edge. However, analysis of all the filmed paths which finished within 20 mm of the edge (at 10 mm inside the wall) (Fig. 1) shows that the flies walked in a curved path which was convex towards the dark
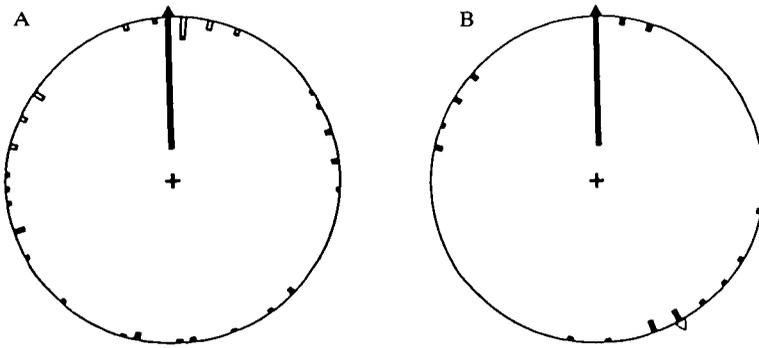
Fig. 3. The effect of contrast polarity on the attractiveness of stripes. (A) Comparisons of runs for four flies towards 6° black stripes (solid bars) and white stripes (open bars), both with a mean luminance of 50 cd m^{-2}. 40 runs in each condition, normalized to the proportion heading for the black bar. There is no doubt that at least one fly sometimes made for the white line, but she consistently veered off to the side of the target instead of running up its centre, as is typical for a black stripe. Other flies usually moved in arbitrary spirals in the presence of a white stripe, whilst all ran directly towards the black stripe. (B) Relative attractiveness of a dim and a bright stripe (3° wide) of lower contrast (40 %) at a mean luminance of 250 cd m^{-2}. In this experiment five flies were given a choice between a pale line (open triangle) and a dark line (solid triangle) set 150° apart (to prevent confusion with antifixation). As with the high-contrast stripes (A) there was clear evidence of attraction to the pale stripe, but the dark stripe is 5–10 times more attractive.

side of the edge. The degree of curvature was quite variable but projecting a tangent from the path at 13 cm from the wall, or fitting the path with a logarithmic spiral – the curve expected if flies maintain a constant bearing to the edge (see Materials and methods) – suggests that the flies headed for a point between 5° and 10° inside the edge (estimates of the mean heading, based on tangent projection and curve fitting, are 7.5° and 8.5° to the edge, respectively).

Discussion

Line fixation

Several different mechanisms appear to be used for fixation and tracking by insects (see e.g. Geiger, 1981; Preiss and Kramer, 1984). Here we argue that edge and line fixation by walking female *Lucilia* can be accounted for by a single strategy: to head for the darkest point in the visual field. This accounts for the preference for a dark line over a light one (Fig. 3), a preference which is also seen in tethered flying *Musca* (Reichardt, 1970), except perhaps at lower contrasts (Reichardt, 1973; see Fig. 3B). This sensitivity to contrast polarity is one of two points where our findings differ from those of others, urging caution in their generalization. The other important difference between our own and previous findings in both flying (Reichardt, 1973) and walking (Horn and Fischer, 1978
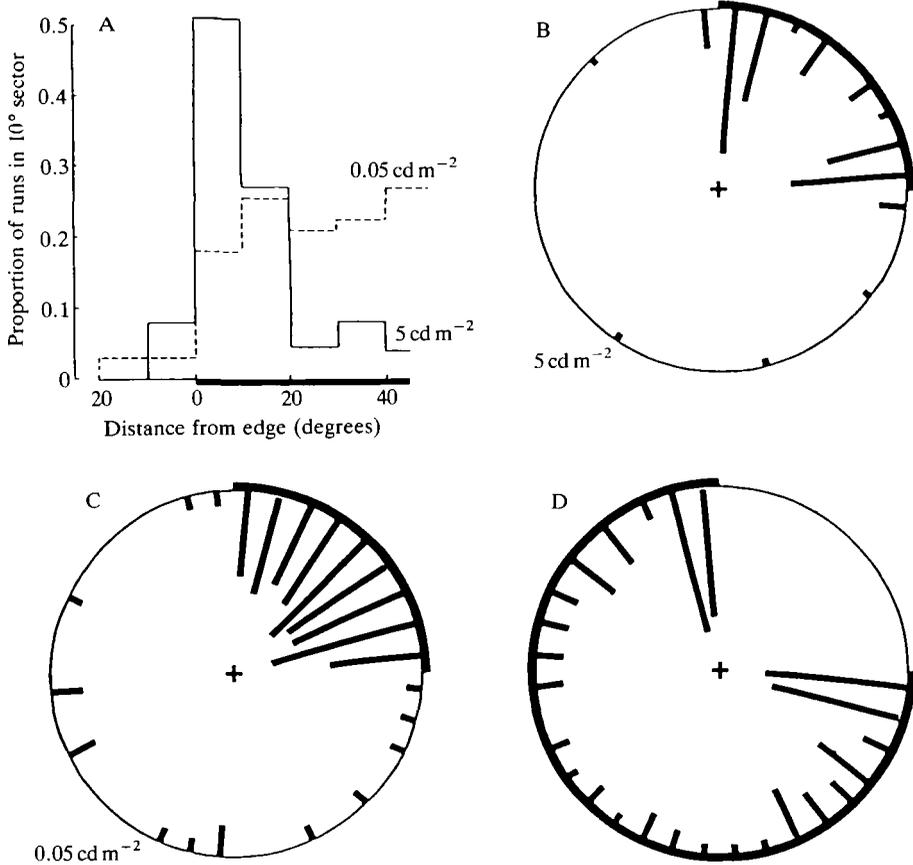
Fig. 4. Plots of the 10° sector in which paths crossed the 230 mm radius relative to the edges of stripes subtending 90° at the arena's centre. (A) Histogram of the proportion of runs with a dark quadrant (B,C) falling in each 10° sector at 230 mm radius with the mean brightness of the walls either 5 cd m^{-2} (solid line) or 0.05 cd m^{-2} (dashed line). Five runs in each quadrant by each of eight flies in the bright condition, and by four of these in the dim condition. Runs to the right-hand edge are reflected about the midline of the stripe to give aggregated data relative to the edge (0°). (B) Plot of runs for four flies with a dark quadrant with the mean luminance of the arena at 5 cd m^{-2}. Bar heights of runs are normalized to the most frequently selected 10° sector. (C) Runs of the same four flies at 0.05 cd m^{-2}. (D) Runs by six flies (120 runs total) with a white quadrant and the mean luminance of the arena at 5 cd m^{-2}.

Wehner, 1981, p. 391) flies is in the effects of blinding different parts of the visual field. We find that the front 10° of the visual field are necessary and sufficient to support fixation of a dark line (Fig. 2), whereas earlier work indicates that a region 20° lateral (and in flying flies ventral) is most important for fixation. Analysis of path trajectories (Fig. 1) supports our suggestion that the front of the eye is used for line fixation. Female *Lucilia* have a negligible binocular overlap (Land and Eckert, 1985) and, if a lateral region of the eye were used for fixation, we would

expect the flies to walk along one of two curved paths depending on which eye was seeing the target (they did not walk sideways). Such curved paths are clearly seen, for instance, in line fixation by the ladybird (*Coccinella*) (Collett, 1988), where it has convincingly been shown that motion in a lateral region (beyond 45°) is critical in eliciting fixation. *Lucilia* walk straight towards a fixated line (Fig. 1) with no evidence for a bimodal distribution of path curvatures or of zig-zag paths corresponding to alternate lateral fixation, first by one eye and then by the other. The directness of the path indicates that very little image motion is needed to stimulate the fixation mechanism. These differences in the eye region used and the trajectory followed are clearly consistent with our suggestion that fixation by walking *Lucilia* is mediated by a mechanism which directs fixation to the region in the scene which appears darkest, giving scototactic behaviour. The postulated mechanism differs from others described elsewhere, where motion is of paramount importance.

Edge fixation

The flies were seen to run straight towards a line, but to follow a curved path to an edge (Fig. 1). As previously noted (Varjú, 1976; Wehner, 1972), the curve is convex towards the dark side of the boundary, but ends near the border [see Horn and Fischer (1978) who find that flies head for a region distributed symmetrically about an edge]. Two general hypotheses could explain these results: either two competing processes are occurring, namely edge fixation and scototaxis (preference for dark regions), or the dark side of a border is intrinsically attractive.

If, as we assume, edge fixation is mediated by the same mechanism as line fixation (Figs 1,3), and the fly walks directly towards the most attractive point in the visual field, then the curved paths imply that the fly heads for a point 5–10° to the dark side of the edge (Fig. 1). One alternative explanation for the curved trajectories, already questioned for line fixation, is that the boundary itself is fixated by a lateral eye region (Horn and Fischer, 1978; Wehner, 1981). However, since paths are usually convex towards the dark side of an edge (Figs 1,4) there must be an element of scototaxis. Thus, with this alternative hypothesis we need two competing mechanisms: fixation with a lateral region of the eye, and scototaxis.

Similar results to ours have been obtained by Varjú (1976) in the beetle *Tenebrio molitor* and by Preiss and Kramer (1984) in the moth *Lymnatria dispar*. These authors make a good case for an interaction between fixation and scototaxis, accounting for the curved paths by postulating that the relative attractiveness of an edge increases as its retinal slip and hence apparent motion increases, as also suggested for line fixation by the ladybird (Collett, 1988). However, as we have stressed, there seems to be a difference between the mechanism of line fixation seen here and that observed in other studies upon flies and ladybirds. Our observations press for a different view from Varjú's, which is less dependent on retinal slip to account for the curved paths. As already mentioned, a white stripe is much less attractive than a black stripe (Fig. 3), and when flies do walk towards the

white stripe they appear to veer away to its sides, instead of climbing up the centre of the target. This emphasizes that contrast polarity remains dominant in the fly, and fixation induced by relative motion does not supersede scototaxis at any stage. Parenthetically, we note that, in principle, curvatures of the paths will differ depending upon whether retinal slip or attraction to darkness is the basis for fixation. If motion is important the fixation angle should increase gradually, depending on the gain of the response. In contrast, for a scototaxis (with border enhancement by lateral inhibition, as discussed below), a constant fixation angle would be expected. However, our data are not sufficiently accurate to make this comparison worthwhile.

As further evidence that scototaxis underlies fixation by walking *Lucilia*. we find that the edge taxis disappears at light levels around $0.1\,\mathrm{cd\,m}^{-2}$, well above the minimum of about $3\times10^{-5}\,\mathrm{cd\,m}^{-2}$ (limited by photon noise) required to elicit optomotor behaviour (Fermi and Reichardt, 1963). For *Drosophila*, in experiments similar to ours, the allure of vertical edges compared with the centre of a stripe disappears when the stripe height drops below 40° (Wehner, 1972). Instead, *Drosophila* heads randomly into the dark region. This suggests that proximity to an edge (in this case horizontal), rather than relative movement, may be most important for attracting walking flies. Thus, we contend that a single, essentially linear, process to find the darkest region (giving scototaxis), with a front-end mechanism that emphasizes edges, deserves consideration alongside other models of 'fixation' behaviour (e.g. Poggio and Reichardt, 1976; Varjú, 1976; Geiger, 1981).

Is there a role for lateral inhibition?

One obvious mechanism that will enhance the signal at an edge is lateral inhibition (Ratliff, 1965) to give an effect resembling Mach bands at the edge, and we suggest that a single simple mechanism in which the fly heads for the darkest point in a 'neural image' filtered by lateral inhibition can account for our observations as well as some others in walking flies. The *Lucilia* female heads directly for a dark line, but she essentially ignores a white line. Mach bands are one of several human visual illusions in which the apparent contrast at borders is enhanced because the dark side of the border appears darker and the light side lighter than contiguous dark and light areas further from the edge. It has been suggested that Mach bands are attributable to lateral inhibition in the retina (e.g. Ratliff, 1965; Cornsweet, 1970), and the analogy drawn here is at this level, although this view may be simplistic (see, for example, Morrone and Burr, 1988). In particular, humans do not see Mach bands at isolated step edges. Whilst the 'contrast' of the edge is enhanced by the inhibition, the fly ignores the structure *per se* but makes for the centre of the darkest region, which we estimate to be between 5° and 10° from that edge (Fig. 1). There is little or no lateral inhibition in the dark-adapted fly lamina (Dubs, 1982; Laughlin and Osorio, 1989), and theory as well as observation of lateral inhibition in other species predicts a more ubiquitous reduction of lateral inhibition in the dark-adapted fly visual system.

There are, for instance, very marked increases in spatial and temporal inhibition in locust medulla cells on light adaptation (D. Osorio, unpublished observations). A decline in lateral inhibition would lead to a corresponding loss of attractiveness of edges at low light levels, which we have seen (Fig. 4). At present we cannot ascribe the proposed inhibition to any particular ganglion; lateral inhibition in the lamina is likely to be strongest between adjacent ommatidia, and would probably give maximum enhancement within 5° of an edge (see also M.V. Srinivasan, R.B. Pinter and D. Osorio, in preparation).

By simplifying the 'algorithm' used for edge fixation (if that is the function of this behaviour) the fly pays a penalty. The Mach band is a weak stimulus compared with an edge, and this could cause a lability in performance which would not be expected if fixation were subserved by other mechanisms (e.g. Geiger, 1981). However, in natural conditions where large uniform dark areas are rare the scototactic response may be quite stable. As we might expect, not only is edge fixation lost in dim conditions, but also the scatter for paths within and between individual *Lucilia* was larger than for line fixation. In *Drosophila*, edge fixation is also highly variable, being evident in some experiments (Wehner, 1972), but not in others, possibly depending upon the strain (Coombe and Heisenberg, 1986; P.E. Coombe, personal communication). Additionally, as mentioned above, *Drosophila* edge fixation is markedly dependent on the perceived height of the bar: unless a bar is more than 40° in height flies ignore its edges (Wehner, 1972). Here, we postulate a mechanism for *Lucilia*, with a receptive field width (for the excitatory centre of a simple centre–surround unit) of between 5° and 10° (Fig. 1). Given the larger interommatidial angle in *Drosophila* (about four times that in *Lucilia*: Hardie, 1985), it is quite possible that, in Wehner's (1972) experiment with a low bar, lateral inhibition from the horizontal edges masked the attractive 'bands' from the vertical edges. These observations all point to a subtle interplay between 'edge fixation' and scototaxis: an interplay which we suggest occurs in low-level processing, rather than between higher-order commands as suggested by Varjú (1976) for *Tenebrio*.

The function of lateral inhibition

Lateral inhibition is a familiar mechanism in early vision (e.g. Ratliff, 1965) whose function can be seen in two fundamentally different ways: either to enhance the appearance of borders (Ratliff, 1965), or to decorrelate the retinal signal, and to make it more robust against noise introduced at higher levels (Srinivasan *et al.* 1982). Whereas the first view attributes particular importance to certain features, such as edges and boundaries, the second emphasizes the role of early vision in transforming the retinal image to make optimal use of limited neural bandwidth (Barlow, 1961). According to this second view, no one feature should take precedence over any other. The mechanism of edge fixation postulated here implies that the appearance of lateral inhibition on light adaptation influences the fly's behaviour by altering the relative attractiveness of the edges and the interiors of dark regions. From this perspective, it seems that the effect of inhibition is not

discounted by higher-order interpretation, as would be desirable if the mechanism were purely for ideal signal transmission. Irrespective of its real (evolutionary) function, we argue that lateral inhibition can 'enhance' the perception of an edge in the fly.

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