The Relationship between Visual Acuity and Illumination in the Fly, *Lucilia sericata*

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The variation in visual acuity with illumination has been studied by monitoring the extracellular response of direction sensitive motion detecting neurons to a drifting sine wave grating displayed upon an oscilloscope spreen. Acuity reaches a maximum value of 0.46 cycles/degree at luminances above 1.0 cd/m^2 and decreases gradually over a 3.8 log unit attenuation in intensity to a minimum value of 0.05 cycles/degree. The results have been compared with theoretical acuity curves for the coupound eye with various dark adaptation mechanisms. The analysis indicates that a major strategy of dark adaptation in the fly is a process involving intensity-dependent neural summation of signals from photoreceptors having different visual axes.

In dim light the human visual system suffers a marked loss in temporal and spatial resolution [1, 2]. It is presently accepted that this loss reflects the action of dark adaptation mechanisms which compensate for restrictions placed upon signal detection at low intensities by the quantal nature of light [3]. Thus at the expense of resolving fine detail in time and space, the retina functions in photon-scarce situations by integrating signals for longer times over larger areas. Several investigators have reported that the fly, too, exhibits reduced temporal [4] and spatial [5, 6] acuity in low light, but the significance of this in the context of dark adaptation has remained unsettled [7]. New insight into this important problem has been provided, however, by recent theoretical considerations of the effect of different dark adaptation mechanisms upon the spatial resolving power of the compound eye [8].

The major aim of the present work was to obtain experimentally the relation between visual acuity and luminance in the sheep blowfly, *Lucilia sericata*, and then to compare our results with the theoretical performance of a compound eye given various dark adaptation strategies. We were specifically interested in addressing the problem of which strategies the fly might use and how effective, in terms of increased photon capture, a particular strategy might be.

The acuity task used in our experiments was the resolution of a high contrast ($I_{\max} - I_{\min}/I_{\max} + I_{\min} = 0.89$) computer-generated sine wave grating displayed upon an oscilloscope (Dvorak and French, in prep.). To determine if a given sinusoidal spatial frequency was detected we took advantage of the well know optomotor reaction. The fly, and indeed most arthropods will follow the movement of a striped drum or grating if the pattern can be resolved. Rather than measure this following response, however, we monitored the activity of neurons which mediate it. These extensively-studied cells, the lobula plate giant fibres, (for example, see refs [9–11]) have a strong directional selectivity and can be repeatedly driven from a resting activity of a few spikes per second to a sustained level of over 150 spikes per second by a grating which drifts in the preferred direction (Fig. 1). All cells

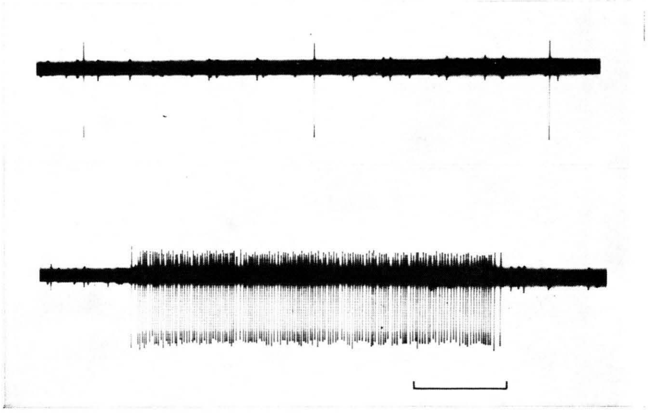

Fig. 1. Extracellular activity of a direction-sensitive motion detecting unit. The upper trace shows the spontaneous activity of the neuron in the presence of a stationary grating, while the lower trace illustrates a typical response evoked when a high contrast grating is caused to drift. (Mean luminance: 1.0 cd/m^2; spatial frequency: 0.2 cycles/degree; contrast: 0.75; drift rate: 1 cycle/sec; calibration: 250 msec).

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in this study were of the same functional type, that is, they were maximally responsive to horizontal, progressive (lateral-to-medial) movement presented to the contralateral compound eye and had very wide visual fields.

The animal was positioned in a light-tight arena such that the anterior, medial part (field center: 25° lateral from the frontal head axis in the equatorial plane) of the contralateral compound eye viewed the stimulus, which was masked to a circular aperture subtending 50° at the eye. Extracellularly-recorded action potentials were amplified and displayed in the conventional manner and passed through a Schmidt trigger to a PDP/1103 computer. A visual acuity curve (highest resolvable spatial frequency vs. mean luminance) was obtained as follows: at a given mean luminance the grating was stationary for 1 second and then drifted, at 1 cycle/sec., for 1 second. This was repeated 25 times. Spikes elicited during the stimulus run were counted by the computer and displayed on a C.R.T. screen as an averaged response histogram. The computer was also programmed to calculate and display the mean and standard deviation of firing levels associated with the stationary and drifting conditions. Following this, the frequency of the spatial sinusoid was increased and the procedure repeated until the resolution limit was found [12]. The mean luminance was then attenuated via quartz neutral density filters placed directly in front of the eye, and the animal was allowed 20 minutes to adapt to the new intensity level. During the adapting period the grating contrast was set to zero to rule out any possible effects of sine wave adaptation.

Experimental Results

The solid curve in Fig. 2 shows the observed variation in visual acuity with mean luminance for 21 female flies, all of the same generation. Visual acuity, *i. e.* the highest resolvable sinusoidal spatial frequency, is given as the normalized term, $\nu \Delta\Phi$ (where $\Delta\Phi$ is the interommatidial angle), and is plotted against the logarithm of the mean luminance, L (cd/m^2). The filled circles represent the mean and the error bars show 1 standard deviation. Acuity reaches a maximum value of 0.46 cycles/degree (spatial wavelength = 2.2°) at levels above 2.0 cd/m^2 and decreases gradually over a 3.8 log unit attenuation in intensity to a minimum value of 0.05 cycles/degree (spatial wavelength = 20°). This represents approximately a factor of 10 change. It was never possible to evoke responses at mean luminances lower than 1.6×10^{-4} cd/m^2, and hence, the curve stops abruptly at this point.

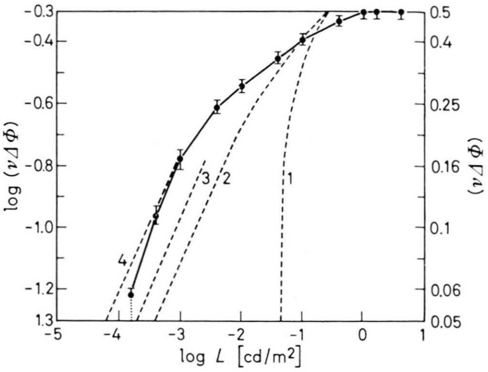

Fig. 2. The variation in visual acuity with mean luminance in the fly, *Lucilia sericata*. Visual acuity (highest resolvable sinusoidal spatial frequency, ν) is given as the normalized term, $\nu \Delta \Phi$, and is plotted against the logarithm of the mean luminance, L (cd/m^2). The solid curve shows the experimental results from 21 female flies, all of the same generation. (The filled circles show the mean, $\bar{x}$, and the error bars represent 1 standard deviation, s). The numbered curves were derived theoretically as described in the text. Curve 1 is for a compound eye with no dark adaptation mechanisms. Curve 2 illustrates the variation in visual acuty with luminance for an eye with neural pooling. Curve 3 shows neural pooling together with a 1.5 times increase in the photoreceptor acceptance angle, $\Delta\varrho$, and Curve 4 is for neural pooling together with a 1.5 times increase in $\Delta\varrho$ and a factor of 3 increase in integration time, Δt.

Theory

The numbered curves in Fig. 2 illustrate the theoretical variation in spatial resolution *vs* luminance for a compound eye with different dark adaptation strategies. The curves are derived from relationships set forth in Snyder [8], and the reader is referred to that work for a detailed treatment of the problem. Here, we present only a summary of the theoretical analysis. (See Table I for a definition of parameters.)

The theory assumes a compound eye which is spherical with ommatidia that have identical facet diameters and applies to photoreceptors which are limited in their performance by the particle nature of light (photon noise) only. Threshold is taken to be that when the signal-to-noise ratio, SNR, across the photoreceptor mosaic is unity. This is consistent with the threshold criterion set in the experiments outlined above [13].

Table I. List of important symbols.

p = eye parameter $= D\,\Delta\Phi = D^2/R = R(\Delta\Phi)^2$; [$\mu$m]. At the diffraction limit $p = \lambda/2$ (square lattice); $p = \lambda\sqrt{3}$ (hexagonal lattice).

$\Delta\Phi$ = interommatidial angle $= D/R$; [radians] in formulae, [degrees] in figures.

D = facet diameter, assumed to be equal to the entrance pupil diameter; [μm].

R = (local) eye radius; [μm].

λ = wavelength of light in vacuum.

$\Delta\varrho$ = width of the angular acceptance function of the photoreceptor retinula cell at 50% sensitivity; [radians].

SNR = signal to noise ratio.

m = modulation (or contrast) of sinusoidal grating.

$\tilde{m}$ = m/SNR.

$\bar{N}$ = mean number of photons absorbed by each photoreceptor of an array, per integration time of the eye, due to a uniform source, infinite in extent.
- (1) $\bar{N} = \hat{I}(D\,\Delta\varrho_{\mathrm{r}})^2$;
- (2) $\hat{I}$ = intensity parameter $= 0.89\,(\varepsilon\,\Delta t)\,\bar{I}$;
- (3) I = mean number of photons per second entering the entrance pupil per square μm per steradian of field; $[\mathrm{sr}]^{-1}\,[\mu\mathrm{m}]^{-2}\,[\mathrm{s}]^{-1}$;
- (4) ε = quantum efficiency, *i. e.* the fraction of photons entering the pupil that are counted the photoreceptors;
- (5) Δt = integration time (effective shutter time) of the eye; [s].

L = luminance (cd/m^2).

ν = sinusoidal spatial frequency (cycles/deg.).

Values for parameters defined in Table I are:

$\mathrm{SNR} = 1 \qquad m = 1 \qquad \tilde{m} = 1$

$\hat{I} = 0.89\,(\varepsilon\,\Delta t)\,L$

$\log \hat{I} = 1.1 \log L$ (equation (14), Snyder [8])

$\varepsilon = 0.5$

$\Delta t = 20$ msec

$p = 0.7\,\mu$m (mean value for *Lucilia,* frontal eye region along equatorial plane; Dvorak and Ribi (in prep.)

$\Delta\varrho = 1.0°$ (light-adapted value for retinula cells in frontal eye region near equator; R. Hardie, unpub. results).

1. No dark adaptation mechanisms (Fig. 2, curve 1)

For a compound eye with no dark adaptation mechanisms we start with equation (B 2) of Snyder [8].

$$\nu\,\Delta\Phi = 0.56\,\frac{\{\log \hat{I}\tilde{m}^2 + \log 0.56\,p^2\}^{1/2}}{\{0.56 + (\lambda/p)^2\}^{1/2}} \qquad \text{(B 2)}$$

and express it as

$$\nu\,\Delta\Phi = 0.56\,\sqrt{\log L + 0.6}\,. \qquad (1)$$

After correcting for neural superposition [14], we arrive at the defining equation

$$\nu\,\Delta\Phi = \{0.56\,\sqrt{\log L + 0.6}\} - 0.78\,. \qquad \text{(1 a)}$$

2. Neural pooling (Fig. 2, curve 2)

We now consider the case where signals from photoreceptors with different visual axes are summed neurally, and the summation process is intensity-dependent or varies across the retinal mosaic. Equation (B 4) of Snyder [8].

$$\tilde{m}^2\,\hat{I} = 7.1\left(\frac{\nu\,\Delta\Phi}{p}\right)^2 \mathrm{e}^{7.08(\nu\Delta\Phi)^2\{0.46 + (\lambda/p)^2\}} \qquad \text{(B 4)}$$

can be simplified and expressed as

$$L = (\nu\,\Delta\Phi)^2\,\mathrm{e}^{7.1(\nu\Delta\Phi)^2}\,. \qquad (2)$$

Making the correction for neural superposition, we obtain the defining equation

$$L = \{(\nu\,\Delta\Phi)^2\,\mathrm{e}^{7.1(\nu\Delta\Phi)^2}\} - 0.78\,. \qquad \text{(2 a)}$$

Discussion

It is clear from a comparison of the experimental visual acuity curve with Curve 1 (Fig. 2) that *Lucilia* must have effective dark adaptation mechanisms at work. We are reminded that Curve 1 illustrates the optimum performance of a compound eye having ideal photodetectors, p and $\Delta\varrho$ values as measured for *Lucilla* and no means of dark adaptation: the experimental results represent a 2.5 log unit improvement, at the lowest luminance ($L_{\min}$), upon this case.

What mechanisms of dark adaptation might *Lucilia* employ? An obvious strategy and one used in the vertebrate retina, is to pool signals from individual photoreceptors having different visual axes, thus, many receptors can act functionally as one larger receptor. Curve 2 (Fig. 2) shows what effect this strategy would have if it alone were operating in *Lucilia.* It is apparent that neural pooling offers a significant improvement upon the no dark adaptation case, however, before the actual effectiveness of this strategy can be assessed, we must consider the possibility of large changes in the eye parameter, p and/or the photoreceptor acceptance angle, $\Delta\varrho$. Either of these would be useful dark adaptation mechanisms. For example, if there existed a wide range in p values over the eye, this would be analogous to a photographic emulsion with many different sizes of silver grains and would certainly extend the operating range of the visual system. (For detailed accounts of the role of the eye parameter in the performance of the compound eye see Horridge [18] and Snyder *et al.* [19].) Furthermore, any marked widening of $\Delta\varrho$ would improve function at low light levels by allowing individual photoreceptors an increased photon-capture area.

The measured range in p for *Lucilia*, frontal eye region along the equatorial plane, is $0.5-0.8\,\mu$m (Dvorak and Ribi, in prep.). Substituting $p=0.5$ μm into equations (B 2) and (2 a) given above and solving results in a shift of the neural pooling curve 0.15 log units to the right at $L_{\min}$. Setting $p=0.8$ μm has virtually no effect at all upon Curve 2. From this analysis it is evident that for a variation in p to be an effective means of coping with a wide range in light levels the values must vary considerably more than they do in *Lucilia.*

If we now consider widening $\Delta\varrho$, we note that dark-adapted values measured for retinula cells in the frontal eye region in *Lucilia* average about 1.5°, whereas light-adapted values lie between 1.0° and 1.2° (R. Hardie, unpub. results). If we take the minimum $\Delta\varrho$ to be 1.0° and the maximum to 1.5°, in other words, assuming $\Delta\varrho$ increases by a factor of 1.5 during dark adaptation, we can estimate how much aditional photon capture this represents. From Snyder [8] we argue that, at low intensities, the compound eye with the neural pooling strategy obeys the $\sqrt{\overline{N}}$ law of an ideal photodetector array, so

$$\nu \, a \sqrt{\overline{N}} \tag{3}$$

and, from Eqns (12 a), (12 b) and (13) of Snyder [8] we find that

$$\overline{N} \, a \, L \, \Delta t (\Delta\varrho)^2 \, . \tag{4}$$

This means that the mean number of photons, $\overline{N}$, absorbed by each photoreceptor in the array varies as the square of the photoreceptor acceptance angle, $\Delta\varrho$. The observed change in $\Delta\varrho$ in *Lucilia* is therefore equivalent to a $(1.5)^2=2.25$ increase in $\overline{N}$. Such an increase is shown graphically by Curve 3 (Fig. 2), which represents the asymptote of the neural pooling curve shifted to the left $\log_{10}$ of 2.25 or 0.35 log units. These results strongly suggest that a widening of $\Delta\varrho$ with decreasing light is not of particular significance as a dark adaptation mechanism in *Lucilia.*

Having now dealt with the problem of ranges in p values and allowing for the neural pooling strategy to be combined with a 1.5 increase in $\Delta\varrho$, we see that Curve 3 still lies to the right of the experimental visual acuity curve. There are two possible reasons for this. Firstly, it could be argued that or value for quantum capture efficiency, ε, is too small. We chose $\varepsilon=0.5$ and it were, in fact, nearer to 1.0 this would shift Curve 3 to the left. However, estimates of this parameter in blowfly [20] and locust [21] have arrived at a value of 0.6 to about 0.7. If we allow $\varepsilon=0.6$ or 0.7 and recalculate the neural pooling curve, we find an insignificant change. The only remaining explanation has to do with integration time, Δt. Obviously, if Δt increases as luminances decreases this will result in increased photon capture. We can estimate the effect of increasing Δt by again referring to relationship (3), above, which shows that $\overline{N}$ is directly proportional to integration time. From studies of the temporal frequency response as a function of luminance in blowfly photoreceptors [4] it may be concluded that Δt could increase by a factor of 2 to 4. In our analysis, Δt was taken to be 20 msecs; if we now increase this to 60 msecs, this implies a factor of 3 increase in $\overline{N}$. We have shown this in Curve 4 (Fig. 2) which is the asymptote of the neural pooling curve with $\Delta\varrho=1.5°$ and $\Delta t=60$ msec. Notice that Curve 4 fits the lower intensity part of the experimental visual acuity curve rather well.

The results given here are consistent with the hypothesis that the fly has a combination of dark adaptation mechanisms, and the most significant of these, in terms of increased photon capture, appears to be a process involving intensity-dependent spatial summation. Put another way, our study indicates that, as with the human, the retinal mosaic of the fly becomes functionally coarser as luminance drops. Unfortunately, our demonstration of neural pooling is an indirect one: we have not given proof of summing, nor have we investigated actual methods of summing. Still, we feel the work has merit in its present form because it represents the first clear indication that neural spatial summation actually occurs in an invertebrate visual system.

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[12] We refer to the mean firing rate occurring in the stationary stimulus condition as, $\bar{x}_A$ and the standard deviation about this mean as, s_A. Similarly, for the drifting stimulus condition we have $\bar{x}_B$ and S_B. The resolution limit is taken to be the highest sinusoidal spatial frequency which satisfies the condition

$$(\bar{x}_A + s_A) \leqq (\bar{x}_B - s_B).$$

[13] Using the same definitions of terms as given in Footnote 12 we take the signal in our experiments to be, $(\bar{x}_B - s_B)$, and the noise to be, $(\bar{x}_A + s_A)$. The criterion for threshold detectability in the experiments is that when the signal is equal to (or greater than) the noise. This is a signal-to-noise ratio of 1 [14].

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[15] Most insects have a fused rhabdom, *i. e.*, the rhabdomeres (the photopigment-containing part of the photoreceptor cells) of the 6–8 retinula cells in an ommatidium are united to form a common lightguide. However, fly has an unfused type rhabdom. As a consequence, 7 rhabdomeres from 7 different ommatidia are always directed to one and the same point in space. Furthermore, the photoreceptor axons of 6 of these rhabdomeres all project to the same point in the first optic ganglion. This is known as neural superposition (see Kirschfeld [16, 17] for a detailed discussion). Thus, in our theoretical calculations $\bar{N}$ is actually $6\bar{N}$ and this is taken into account by subtracting 0.78 (which is the log of 6) from $\log L$ values defined in Eqs (1) and (2), above.

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