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Published on: 01 Jan 1977 - Journal of Comparative Physiology A-neuroethology Sensory Neural and Behavioral Physiology (SPRINGER HEIDELBERG)

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Published in:
Journal of Comparative Physiology A

DOI:
[10.1007/BF00605402](https://doi.org/10.1007/BF00605402)

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
1977

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Citation for published version (APA):

Snyder, A. W., Stavenga, D. G., & Laughlin, S. B. (1977). Spatial Information Capacity of Compound Eyes. *Journal of Comparative Physiology A*, 116(2), 183-207. <https://doi.org/10.1007/BF00605402>

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Spatial Information Capacity of Compound Eyes

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Received September 28, 1976

Summary. The capacity of the compound eye to perceive its spatial environment is quantified by determining the number of different pictures that can be reconstructed by its array of retinula cells. We can then decide on the best compromise between an animal's capacity for fine detail and contrast sensitivity. The theory accounts for imperfect optics, photon noise, and angular motion limitations to acuity.

1. There is an optimum parameter $p = D\Delta\phi$, where D is the facet diameter and $\Delta\phi$ is the interommatidial angle, for each mean luminance, angular velocity and mean object contrast. We find that this value of p is approximately that found by Snyder (1977) for threshold resolution of a sinusoidal grating at the ommatidial sampling frequency.

2. A diffraction limited eye ($D\Delta\phi \cong \lambda/\sqrt{3}$) is the optimum design only for those animals that are active in the brightest sunlight, and have a region of their eye that normally experiences low angular velocity, otherwise it is better to have a larger $D\Delta\phi$. λ is the wavelength of light in vacuum.

3. The design of the fly *Musca* is consistent with that of an animal with high angular velocity.

I. Introduction

In this paper we attempt to determine the design of a compound eye that optimises the animal's *spatial* acuity or *spatial* resolving power. Clearly, the optimum design depends on the range in environmental intensities experienced by the animal, its mean velocity and the preferred acuity task. Previous calculations of eye parameters have neglected the intensity of light as well as the animal's velocity and are based on either two point resolution or resolution of a sinusoidal grating (examples include Mallock, 1894, 1922; Barlow, 1952; Mazokhin-Porshnyakov, 1969; Kirschfeld, 1976). Goetz (1965) has presented an analysis for finding the ratio (acceptance angle/interommatidial angle) but has not included the dependence on intensity. More recently Snyder (1977a) has determined the parameters of the compound eye as a function of intensity and velocity but for sinusoidal

gratings as the acuity task. Since sinusoidal gratings are unnatural, one might sensibly question the relevance of results derived from them.

The purpose of this paper is to develop a quantitative measure of an animal's resolving power (*the spatial information capacity*) that is based on a generalized acuity task and then to determine the parameters of the eye that maximise this measure. To accomplish this, we introduce intuitive concepts of information theory as developed by us originally for the study of vertebrate eyes (Snyder et al., 1977). The formulation leads to an understanding of the compromise an animal must strike between contrast sensitivity and spatial resolving power.

II. Concept of an Animal's Spatial Information (Picture Reconstructing) Capacity

An eye must reconstruct its spatial environment from an array of intensity measurements, each measurement provided by an individual ommatidium. It is convenient to view this spatial quantization as a two-dimensional mosaic or checkerboard, i.e. a picture constructed from many smaller elements. Thus the number of ommatidia per field of view sets the capacity of the eye for fine detail.

The fine detail of a picture is lost if there is inadequate contrast between the various elements. Accordingly, the capacity of the eye for contrast sensitivity is determined by the number of *different* intensity levels that can be discriminated by an array of ommatidia. At first it might be thought that an infinite number of different intensity levels can be distinguished; however we show below that the quantum nature of light, i.e. photon noise, sets a lower limit to the number that is reliably distinguished. The more photons captured by the ommatidia, the greater the number of intensity levels and thus the greater the contrast sensitivity of the animal. In other words, both space and intensity are quantized by the eye.

Now it is clear that (for a given eye size) as the number of ommatidia per field of view increases, the potential of the eye for resolving fine detail also increases, but there must be fewer photons available for each of the ommatidia and hence a smaller number of recognizable intensity levels. Because of this unavoidable competition between the capacity of the eye for fine detail on one hand and the capacity for contrast sensitivity on the other, what is the most appropriate number of ommatidia per field of view? The answer clearly depends on the number of available photons, but some measure of acuity performance is required. A natural metric is the number of *different* pictures that can be reconstructed by the mosaic of ommatidia, i.e. by the many elements that make up each picture. Assuming that there are n_p ommatidia per field of view, each one with *one* of n_i possible intensity levels, the *maximum* number of pictures that can be reconstructed by the ommatidia is $n_i^{(n_p)}$. Now it follows from the classical arguments of information theory (Goldman, 1953; Pierce, 1961) that the logarithm of the *maximum* number of *different* pictures that can be reconstructed, per field of view, by the ommatidia is the *spatial information capacity of the eye*, denoted here as H .

$$H = \ln n_i^{(n_p)} = n_p \ln n_i \quad (1)$$

Table 1. List of important symbols

p	=eye parameter
$p = D \Delta\phi = D^2/R = R(\Delta\phi)^2$; [μm].
	At the diffraction limit $p = \lambda/2$ (square lattice); $p = \lambda/\sqrt{3}$ (hexagonal lattice)
$\Delta\phi$	=interommatidial angle
$\Delta\phi = D/R$; [radians] in formulae, [degrees] in figures
D	=facet diameter, assumed to be equal to the entrance pupil diameter; [μm]
R	=(local) eye radius; [μm]
f	=distance from distal tips of rhabdom to posterior nodal point
$\Delta\rho_r$	=effective angular diameter of the rhabdom [radians]. Includes possible additional light gathering due to crystalline cone; when not present $\Delta\rho_r = d_{\text{Rh}}/f$, where d_{Rh} is the rhabdom diameter
$\Delta\rho$	=width of the angular acceptance function of the photoreceptor retinula cell at 50% sensitivity; [radians]. $\Delta\rho^2 = (\lambda/D)^2 + (\Delta\rho_r)^2$
v_s	=sampling frequency; i.e. highest spatial frequency that can be reconstructed by the array of ommatidia; [radians]
$v_s = 1/2 \Delta\phi$	(square lattice); $v_s = 1/\sqrt{3} \Delta\phi$ (hexagonal lattice)
v_{c0}	=cutoff frequency, i.e. highest spatial frequency passed by the optics of an individual ommatidium
$v_{c0} = D/\lambda$, in case of diffraction limit; [radians] $^{-1}$
λ	=wavelength of light in vacuum; [μm]
v	=angular velocity; [radians] [s] $^{-1}$ in formulae, [degrees] [s] $^{-1}$ in figures
\bar{C}	=mean contrast of a random two-dimensional distribution of light intensity in the object world (see Fig. 2)
\bar{N}	=mean number of photons absorbed by each photoreceptor of an array of photoreceptors, per integration time of the eye, due to a uniform source, infinite in extent.
(1) $\bar{N} = \hat{I}(D\Delta\rho_r)^2$	
(2) \hat{I}	=intensity parameter
$= 0.89 \varepsilon A t \bar{I}_0$	
(3) \bar{I}_0	=mean number of photons per second entering the entrance pupil per square μm per steradian of field; [s] $^{-1}$ [μm] $^{-2}$ [s] $^{-1}$
(4) ε	=quantum efficiency, i.e. the fraction of photons entering the pupil that are counted by the photoreceptors
(5) $A t$	=integration time (effective shutter time) of the eye; [s]
M_l	=modulation transfer function (MTF) of lens-pupil = [$\exp\{-3.56(v\lambda/D)^2\}$]
M_r	=MTF of rhabdom = [$\exp\{-3.56(v\Delta\rho_r)^2\}$]
$M = M_l M_r$	= $\exp\{-3.56(v\Delta\rho)^2\}$
H	=information capacity per unit solid angle of object field, defined here to be the natural logarithm of the number of different pictures that can be reconstructed by an array of ommatidia at the level of the retinula cells
(1) $H = n_p \ln n_i$; [s] $^{-1}$ in formulae, [degrees] $^{-2}$ in figures
(2) n_p	=number of ommatidia per solid angle of object field; [s] $^{-1}$ in formulae, [degrees] $^{-2}$ in figures
(3) n_i	=number of different intensity levels that can be distinguished by the photoreceptor array

$$\text{Spatial information capacity} = (\text{no. of ommatidia per field of view}) \\ \times \ln (\text{no. of different intensity levels})$$

where \ln is to the base e . By using the logarithm of the number of pictures, we preserve the intuitive notion that doubling the number of ommatidia per field of view n_p , doubles the spatial information capacity H of an eye.

Having established the essential concept, we next relate n_p and n_i to the physical parameters of the compound eye.

The number of ommatidia per square radian of object space n_p is

$$n_p = 1/(\Delta\phi)^2 \quad (2)$$

assuming for simplicity that the ommatidia are arranged in a square lattice, where $\Delta\phi$ is the interommatidial angle in radians.

III. Number of Intensity Levels that can be Distinguished Reliably by the Mosaic of Ommatidia

The number of intensity levels n_i that can be reliably distinguished by the ommatidia is limited by noise, ultimately due to the quantum nature of light, i.e. photon noise, and by imperfect optics, ultimately due to the wave nature of light, i.e. by diffraction. We first consider the limitation of photon noise.

1. Limitation of Photon Noise to the Number of Discriminable Intensity Levels n_i

Because of the random nature of photon emission and absorption, a uniform light source (infinite in extent) appears non-uniform to an array of ommatidia, as shown in Figure 1. The standard deviation σ_{noise} in photon counts across an infinite array of ommatidia is

$$\sigma_{\text{noise}} = \sqrt{\bar{N}} \quad (3)$$

where \bar{N} is the mean number of photons captured by the individual rhabdoms per integration or shutter time of the eye (Barlow, 1964; Rose, 1973). Because of this $\sqrt{\bar{N}}$ uncertainty in the interpretation of a photon count, there is only a finite number of intensity levels n_i that can be distinguished with certainty by the ommatidia.

We suppose here that the intensity levels need be separated by $2\sigma_{\text{noise}}$ intervals to be reliably discriminated, i.e. the standard deviation of one level just meets the standard deviation of the neighboring level. This is the usual reliability criterion for communication systems and is analogous to assuming that the threshold signal to noise ratio is unity (see Appendix B). Thus, n_i is found by determining the number of intervals of width $2\sigma_{\text{noise}}$ that can fit into a given range of mean object intensity. This intuitive procedure gives the *maximum* number of intensity levels that can be reliably distinguished (Carlson, 1975).

We are reminded that our expression for spatial information capacity H , given by Equation (1), is based on the *maximum* number of pictures that ommatidia can reconstruct. It is convenient to know what distribution of object

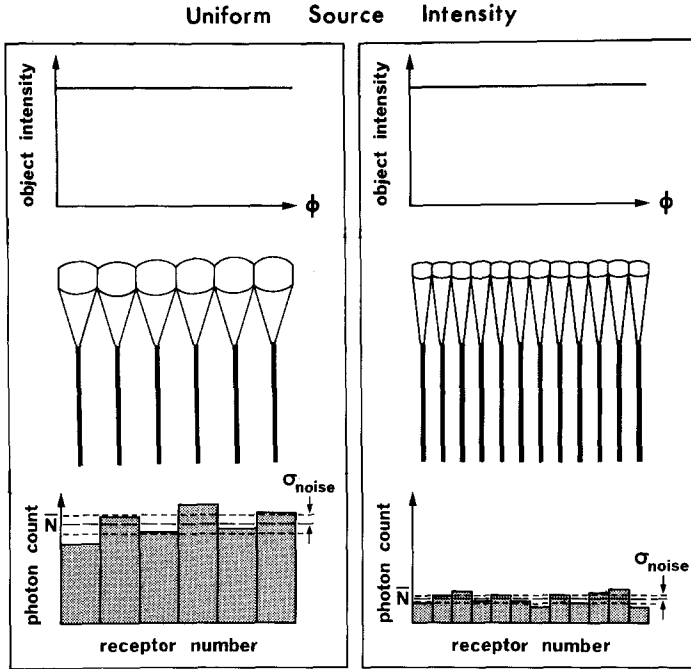


Fig. 1. The fluctuation in photon counts across the photoreceptors (in one integration time) due only to the random arrival of photons (photon noise). The object is a two dimensional uniform source, infinite in extent (see Fig. 3)

intensities would produce this maximum. From information theory (e.g. Pierce, 1961) we learn that a random scene fulfils the requirement, i.e. a scene containing objects of random contrast and random size (or identical size at random distances from the eye). Such a scene is the epitome of the unexpected since every spatial frequency has equal importance. The spatial information capacity H of an eye is therefore equivalent to the amount of information that it can extract from a random scene. Accordingly, we determine the number of possible contrast levels that exist when the object intensity is random as in Figure 2.

In the absence of photon noise, the standard deviation σ_{sig} in photon counts, due to the random scene in Figure 2, is

$$\sigma_{\text{sig}} = \bar{N} \bar{C} \quad (4)$$

where \bar{N} is the mean number of photons absorbed by the rhabdoms of the individual ommatidia and \bar{C} is the mean contrast of the object intensity distribution. In the presence of noise (Fig. 3), twice the standard deviation in photon counts is given by $2(\sigma_{\text{sig}}^2 + \sigma_{\text{noise}}^2)^{1/2}$, remembering that variances and not standard deviations must be summed (Goldman, 1953). Dividing this expression by $2\sigma_{\text{noise}}$ gives the number n_i of possible intensity levels

$$n_i = \{1 + \sigma_{\text{sig}}^2 / \sigma_{\text{noise}}^2\}^{1/2} \quad (5a)$$

$$= \{1 + \bar{N} \bar{C}^2\}^{1/2} \quad (5b)$$

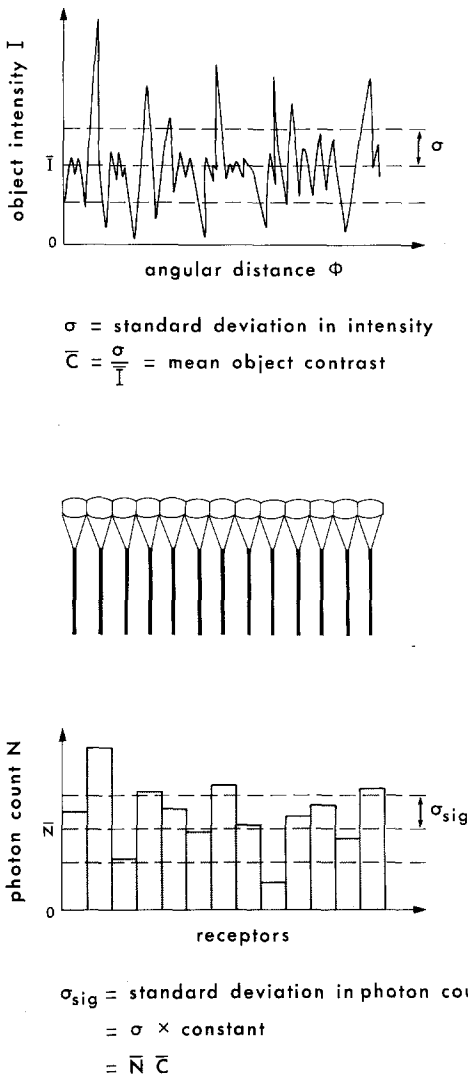


Fig. 2. Spatial distribution of photon counts by an array of ommatidia due to a random distribution of object intensity. The effect of noise has been intentionally neglected but is included in Figure 3

assuming photon noise is the only limitation. We next examine how imperfect optics modify this result.

2. Limitations of Imperfect Optics Plus Photon Noise to the Number of Discriminable Intensity Levels

In order to appreciate how imperfect optics limits the number of intensity levels we must first discuss some basic concepts of optical filtering (Goodman, 1968). The most useful way to quantify the effect of imperfect optics is by the demodula-

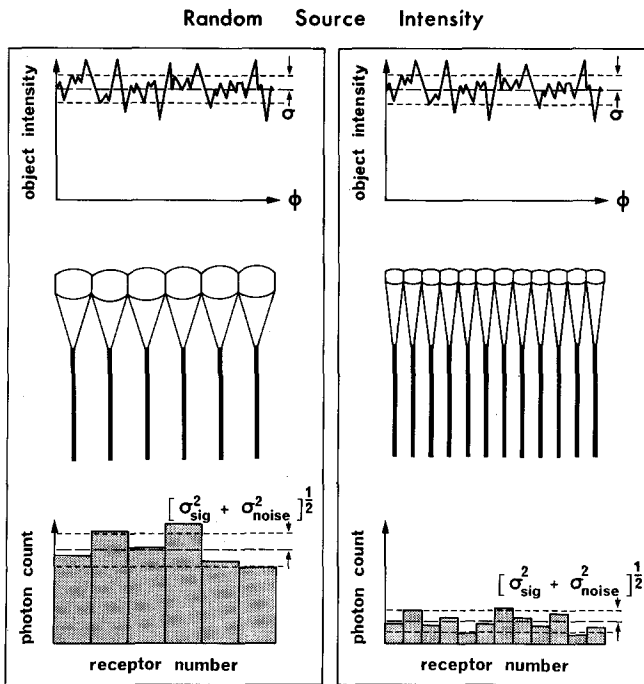


Fig. 3. The effect of noise on the spatial distribution of photon counts by an array of ommatidia due to a random distribution of object intensity. Ommatidia with larger facets accept more photons than those with smaller facets (assuming nearly equal focal lengths in both cases) so that their signal to noise ratio is greater

tion of a spatial sinusoid as it passes through each component part of the visual system (Fig. 4). In particular we use the modulation transfer function $M(v)$ or MTF to characterize the modulation of a spatial sinusoid of unity amplitude and frequency v after passing through all components. Figure 4 shows the MTF at the photoreceptor level. The MTF of the lens-pupil is $M_l(v)$, while the MTF of the finite diameter of the rhabdom is $M_r(v)$. Thus, as shown in Figure 4, the modulation that appears across the array of retinula cells is a quantized version of mM_lM_r , where m is the object contrast or modulation.

It is intuitive, from Figure 5, that the interommatidial angle sets the highest spatial frequency v_s that can be reconstructed by the array of ommatidia. We call v_s the sampling frequency of the ommatidia, where

$$v_s = \text{sampling frequency} = 1/2\Delta\phi \quad (6)$$

assuming a square array of ommatidia. The case of a hexagonal lattice of visual axes is discussed by Snyder (1977a, b).

A random distribution of object intensities contains all spatial frequencies, equally weighted (O'Neill, 1963). Using Fourier analysis of random distributions, we have shown (Snyder et al., 1977) that the presence of imperfect optics reduces the number of possible intensity levels n_i from that given by Equation

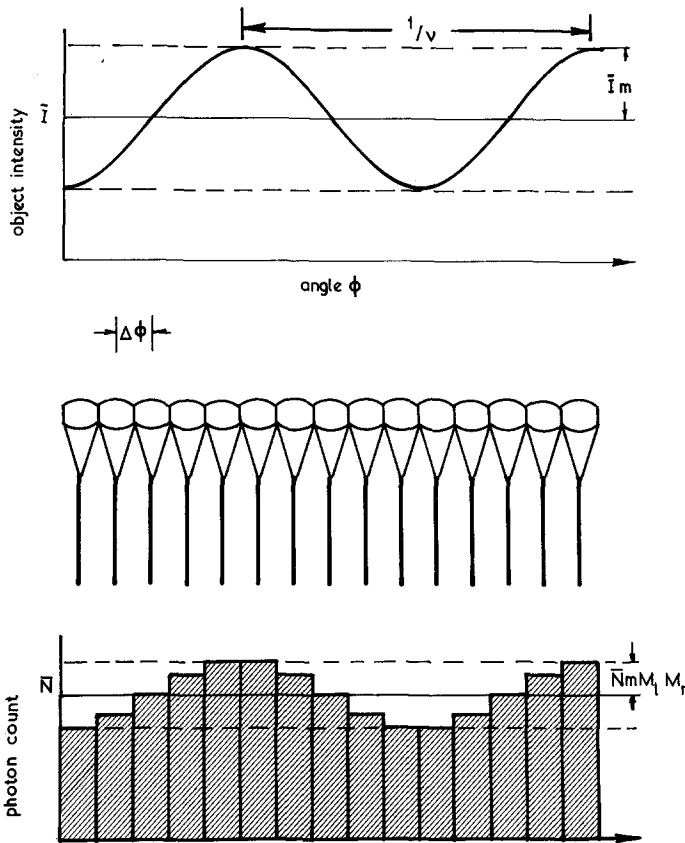


Fig. 4. Demodulation of a sinusoidal grating by an array of ommatidia. The object modulation is m , the modulation transfer function of the lens and the rhabdom are M_l and M_r respectively. The modulation in photon counts hence is $m M_l M_r$.

(5b) to

$$n_i = \{1 + \bar{N} \bar{C}^2 M(v_s)\}^{1/2} \quad (7)$$

where $M = M_l M_r$. The greater v_s , the smaller M and hence the fewer the number of intensity levels that can be distinguished.

3. Expressions for the MTF $M(v)$

We assume that the lens-pupil is diffraction limited (Kirschfeld and Franceschini, 1968) for which case the MTF of the lens-pupil M_l is the Fourier transform of the diffraction intensity pattern of a circular aperture (Goodman, 1968) and approximated well by the Gaussian function (rev. Snyder, 1976a, b).

$$M_l(v) = e^{-3.56 \left(v \frac{\lambda}{D}\right)^2} \quad (8)$$

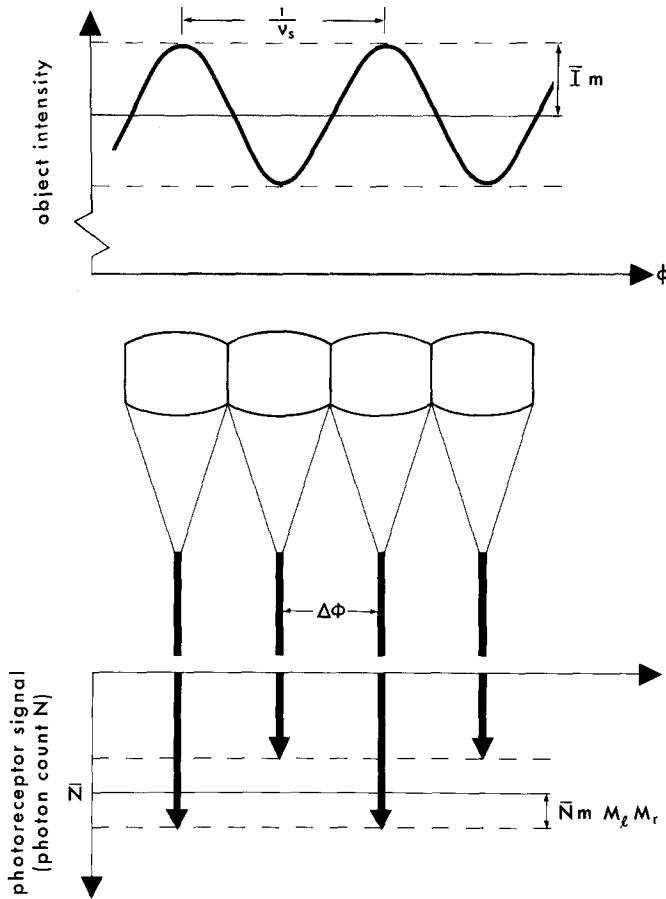


Fig. 5. Highest spatial frequency v_s that can be reconstructed by a square array of ommatidia, where M_l and M_r are the MTF's of the lens pupil and the rhabdom respectively

where λ is the wavelength of light in vacuum and D the entrance pupil diameter, assumed here to be the diameter of the facet.

The MTF of the rhabdom M_r is given by the Fourier transform of the rhabdom's light capture profile (in isolation from the lens-pupil) which includes possible light funnelling due to the crystalline cone. Snyder (1977a) has shown that a Gaussian approximation is suitable for M_r so that

$$M_r(v) = e^{-3.56(v\Delta\rho_r)^2} \quad (9)$$

where $\Delta\rho_r$ is the effective angular diameter of the rhabdom. The *minimum* value of $\Delta\rho_r$ equals the angular diameter of the rhabdom.

We can now specify the MTF at the level of the retinula cells due to a sinusoid at the ommatidial sampling frequency v_s . From Equations (6), (8) and (9)

$$M(v_s) = M_l(v_s) M_r(v_s) = e^{-0.89\left(\frac{\Delta\rho_r}{\Delta\phi}\right)^2} \quad (10)$$

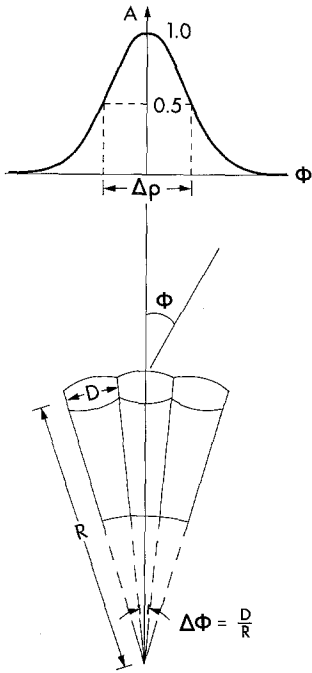


Fig. 6. Angular acceptance function of an ommatidium. The halfwidth $\Delta\rho$ is at 50 % sensitivity. D is the facet diameter, R is the eye radius, and $\Delta\phi$ the interommatidial angle

where, $\Delta\rho$, the width of the photoreceptor cell angular sensitivity function at 50 % sensitivity (Fig. 6), is given by (Snyder, 1977 a)

$$(\Delta\rho)^2 = (\lambda/D)^2 + (\Delta\rho_r)^2. \quad (11)$$

The highest spatial frequency passed by the optics of an individual ommatidium is called the cutoff frequency ν_{co} , and is defined by $M(\nu_{co})=0$. If the optics is limited by diffraction only, i.e. $\Delta\rho_r \ll \lambda/D$, then (Goodman, 1968)

$$\nu_{co} = \text{cutoff frequency} = D/\lambda. \quad (12)$$

This is the highest spatial frequency passed by an individual ommatidium when the entire optical system is diffraction limited. Allowing for limitation due to a finite rhabdom diameter, the highest spatial frequency is effectively reduced to $\nu_{co} \simeq 1/\Delta\rho$ as discussed by Snyder (1977a, b).

4. Expression for the Mean Number of Photons Absorbed

If we let \bar{I}_0 be the mean number of photons entering the eye per square radian of object field per $(\mu\text{m})^2$ per second, ε the fraction of this number that is absorbed by the rhabdom, Δt the sampling time of the eye, then $\bar{N} = \bar{I}_0 \varepsilon \Delta t$ times the pupil

area $D^2 \pi/4$, multiplied by the solid angle that the rhabdom subtends in object space. Assuming the rhabdom has a Gaussian acceptance profile of half width $\Delta \rho_r$, we find (Snyder, 1977 a)

$$\bar{N} = \hat{I} (D \Delta \rho_r)^2 \quad (13)$$

where the intensity parameter \hat{I} is defined in Table 1.

IV. Optimum Eye Parameters for Maximum Spatial Information Capacity of Compound Eyes

1. Mathematical Expression for Information Capacity H

We can now express the spatial information capacity of compound eyes H given by Equation (1) in terms of the animal's physical parameters. From Equations (1), (2), (7), (10), (11) and (13)

$$H = \left(\frac{1}{\Delta \phi} \right)^2 \ln \{ 1 + \bar{N} \bar{C}^2 M(v_s) \}^{1/2} \quad (14a)$$

$$= \frac{1}{2(\Delta \phi)^2} \ln \left[1 + \bar{C}^2 \hat{I} (D \Delta \rho_r)^2 e^{-0.89 \{ (\frac{\lambda}{D \Delta \phi})^2 + (\frac{\Delta \rho_r}{\Delta \phi})^2 \}} \right]. \quad (14b)$$

Our purpose is to find the optimum parameters D , $\Delta \rho_r$ and $\Delta \phi$, i.e., those that maximise an animal's information capacity H for any given mean intensity \hat{I} and contrast \bar{C} .

2. Optimum Rhabdom Acceptance Angle $\Delta \rho_r$

The information capacity H given by Equation (14b) is maximised when

$$\Delta \rho_r = 1.06 \Delta \phi. \quad (15)$$

This is the optimum rhabdom acceptance angle. Substituting this optimum value of $\Delta \rho_r$ into Equations (11) and (14b) leads to

$$\frac{\Delta \rho}{\Delta \phi} = \left\{ \left(\frac{\lambda}{D \Delta \phi} \right)^2 + 1.12 \right\}^{1/2}, \quad (16)$$

for the ratio of the acceptance angle $\Delta \rho$ to the interommatidial angle $\Delta \phi$, and

$$H = \frac{1}{(\Delta \phi)^2} \ln \{ 1 + 0.37 \bar{N} \bar{C}^2 M_l(v_s) \}^{1/2} \quad (17a)$$

$$= \frac{1}{2(\Delta \phi)^2} \ln \{ 1 + 0.41 \bar{C}^2 \hat{I} (D \Delta \phi)^2 e^{-0.89 (\frac{\lambda}{D \Delta \phi})^2} \} \quad (17b)$$

for the spatial information capacity H of the eye.

From this expression, we see that $D \Delta \phi$ is the determinant of H given a certain contrast intensity parameter $\bar{C}^2 \hat{I}$.

3. Optimum Facet Diameter D and Interommatidial Angle $\Delta\phi$

The facet diameter D and interommatidial angle $\Delta\phi$ are related by geometry to the *local* radius R of the eye (Fig. 6)

$$D = R \Delta\phi. \quad (18)$$

We emphasize that in general compound eyes are neither spherical nor are D and $\Delta\phi$ constant over the eye. However, the parameter p ,

$$p = \frac{D^2}{R} = R(\Delta\phi)^2 = D \Delta\phi, \quad (19)$$

is nearly constant over a substantial portion of many eyes, including the honeybee (Kuiper and Leutscher-Hazelhoff, 1965), the fly *Musca* (Stavenga, 1975) and numerous compound eyes of insects native to Australia (Horridge, 1976). This parameter p is also a principle determinant in maximizing H in Equation (17b) as we have noted above. We emphasize however that the *absolute* resolving power of an eye is determined by $\Delta\phi$ and not by p .

Provided there is sufficient luminance, the ommatidia can reconstruct the highest frequency passed by the optics when the ommatidial sampling frequency ν_s equals the cutoff frequency ν_{co} of the optics. From Equations (6) and (12) we find that there is no advantage in having the interommatidial angle $\Delta\phi < \lambda/2D$, so that

$$p \geq \lambda/2 \quad (20)$$

for a square lattice of ommatidia. Thus, with $\lambda = 0.5 \mu\text{m}$, the minimum value of $p = 0.25 \mu\text{m}$. This is the well known case of a diffraction limited compound eye.

Distinction between R and D Constant Cases. We can solve Equation (17) subject to two different constraints: i) the R constant case where we ask for the optimum eye parameter p for a *given* local eye radius R ; ii) the D constant case where we ask for the optimum eye parameter p for a *given* facet diameter D . The mathematics associated with these two cases is discussed further in Appendix A and B.

The R constant case is particularly meaningful for a spherical eye or for large portions of eyes constrained to have a particular radius. With the assumption that the fovea is specialized for high resolving power, then the fovea should have relatively large facet diameters D . Many diverse factors determine D , including the behavioral necessity of achieving a certain acuity over a specified field of view, the corneal area and the number of supportable photoreceptors.

Information theory, as presented here, cannot account for these factors; however, *given* a diameter for neighboring facets, it can determine the interommatidial angle $\Delta\phi$ and the angular light capture area $\Delta\rho_r$ of the rhabdom that gives the greatest number of pictures per unit angle. Thus, the D constant case is applicable to the foveal region of compound eyes.

In Figure 7 we have plotted the optimum eye parameter p vs the mean light intensity parameter \hat{I} for various mean object contrasts. It is necessary for $\log \hat{I} \bar{C}^2$ to be greater than 7 for the R constant case and greater than 5 for the

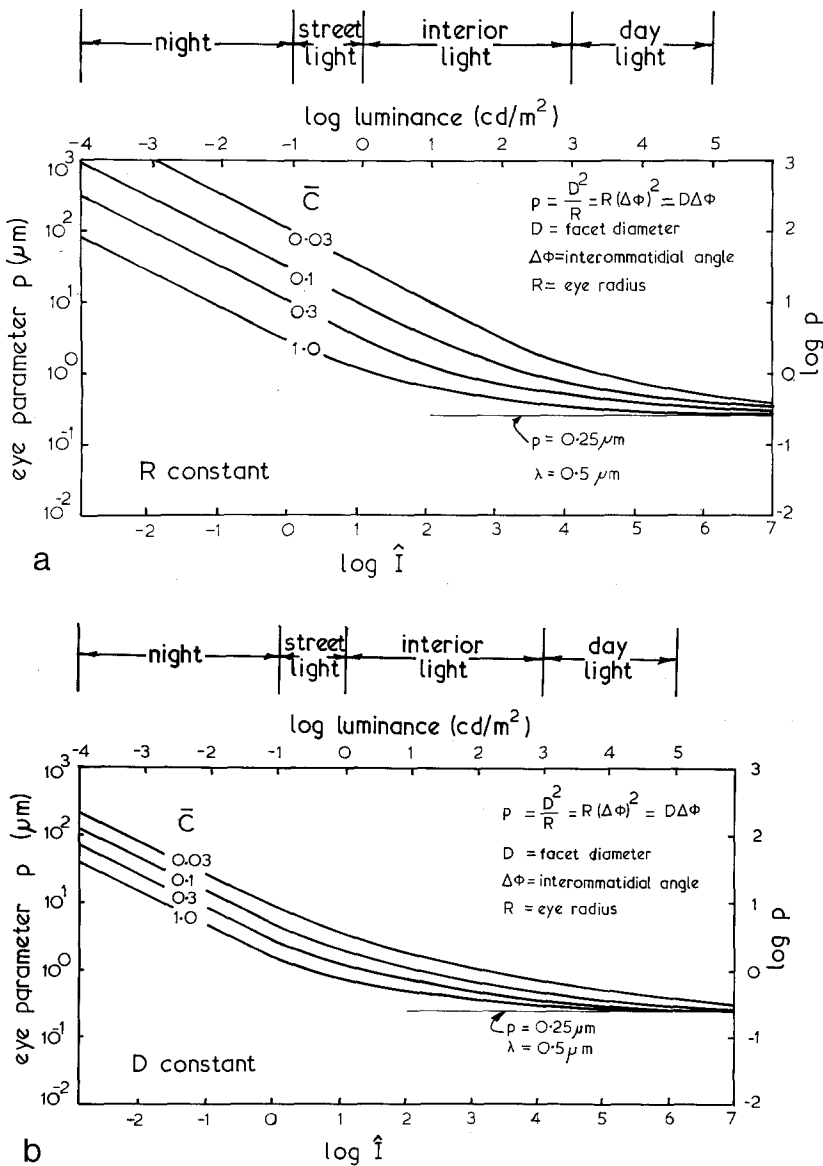
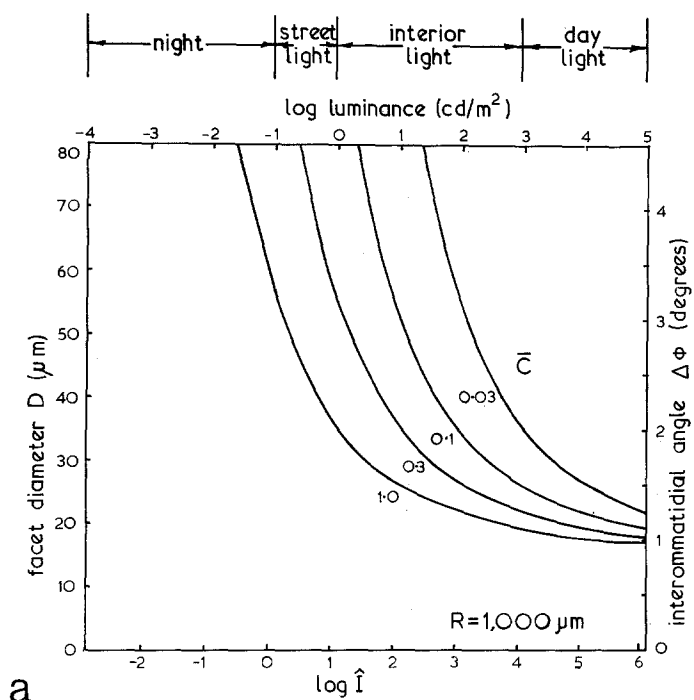
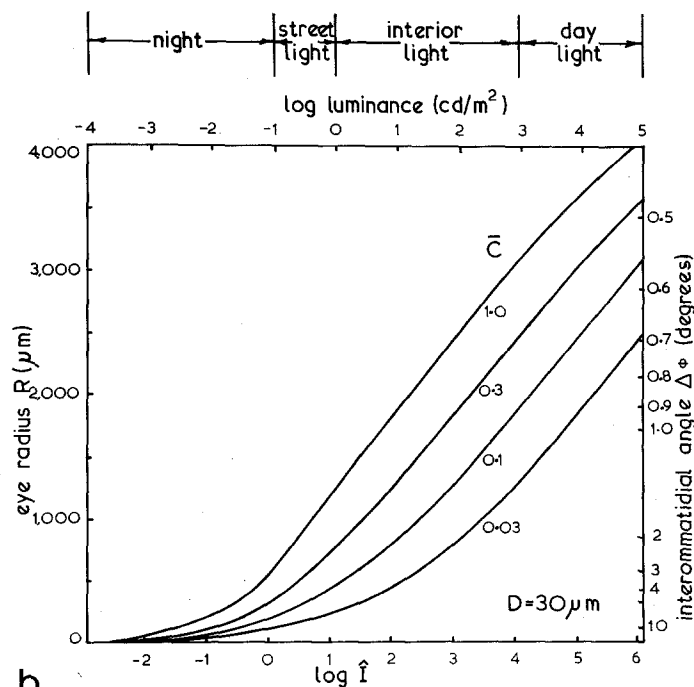


Fig. 7a and b. The optimum value of the eye parameter p as a function of the light intensity parameter \hat{I} at different mean contrasts \bar{C} . The conversion from \hat{I} to luminance in candelas per square meter is given in Appendix C. **a** and **b** give the case for R and D constant respectively

D constant case in order to have a diffraction limited eye, i.e. one with $p = \lambda/2$ to be at optimum (see also Appendix B). When $\hat{I}\bar{C}^2$ is lower than this minimum, the optimum eye has p greater than $0.25 \mu\text{m}$. A hexagonal lattice of ommatidia requires the same $\hat{I}\bar{C}^2$ to reach the diffraction limit, which is then $p = \lambda/\sqrt{3}$, or $0.29 \mu\text{m}$ if $\lambda = 0.5 \mu\text{m}$ (Snyder, 1977 a).



a



b

Fig. 8. a Facet diameter D and interommatidial angle $\Delta\phi$ necessary for maximum information capacity at given intensity parameter \hat{I} and mean contrast \bar{C} for the case when the eye radius R is $R = 1000 \mu\text{m}$. **b** Eye radius R and interommatidial angle $\Delta\phi$ necessary for maximum information capacity when the facet diameter is held constant at $D = 30 \mu\text{m}$

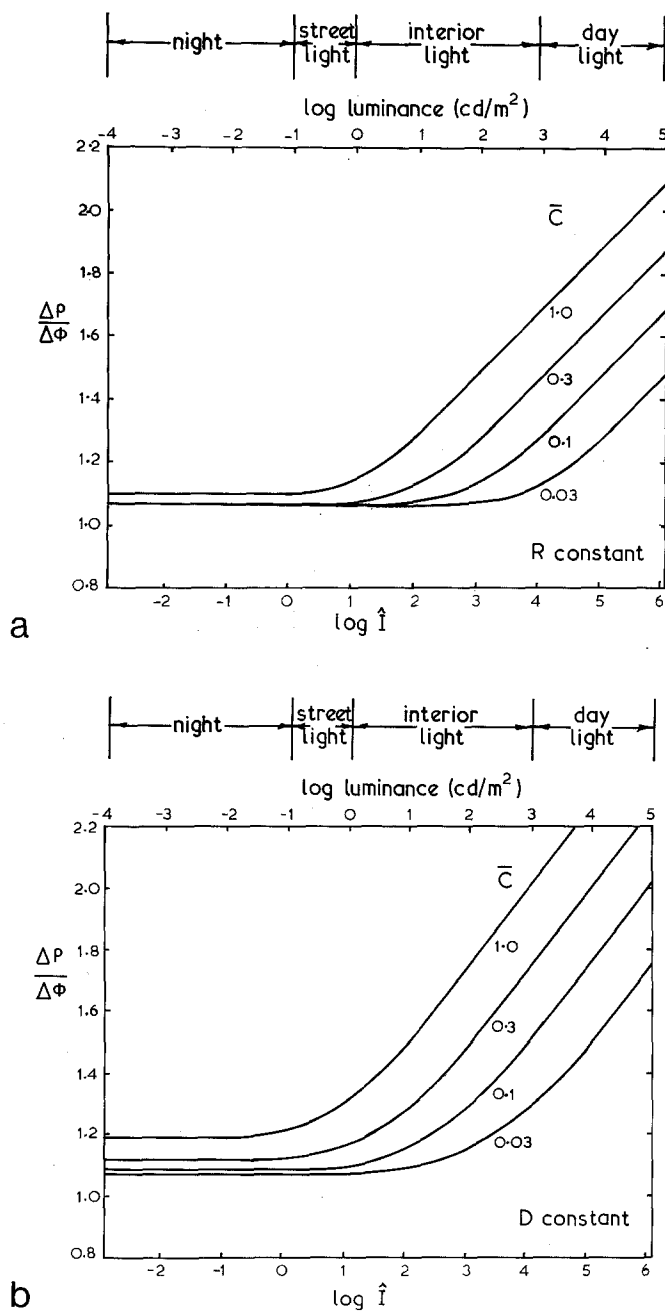


Fig. 9. The value of the ratio $\Delta \rho / \Delta \phi$ necessary to maximise the information capacity

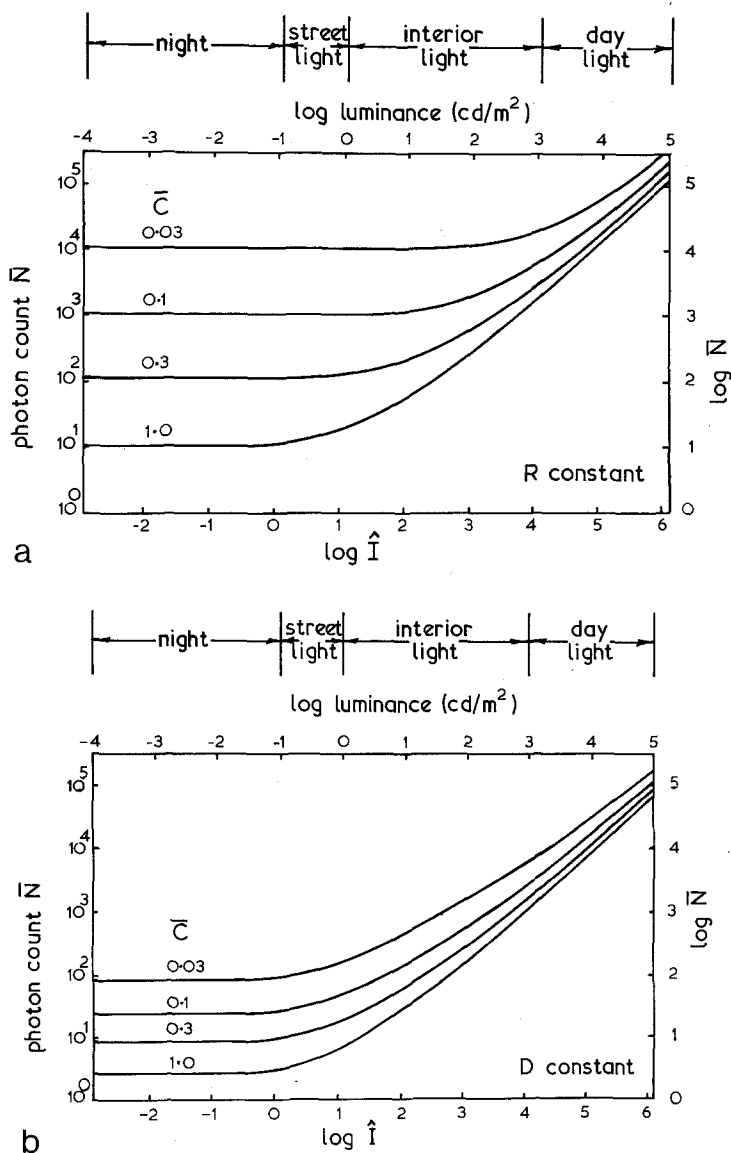


Fig. 10a and b. Mean photon count \bar{N} , per integration time of the eye, by the individual ommatidia when the information capacity is maximum for the case the R is constant a and D is constant b

In Figure 8 the optimum values of the facet diameter D and eye radius R are also shown explicitly. The optimum ratio $\Delta\rho/\Delta\phi$ also depends on the intensity of light as shown in Figure 9. (The ratio $\Delta\rho/\Delta\phi$ has been discussed by Goetz (1965) and Wehner (1975) as a determinant of eye design.) In Figures 10 and 11 we also show the mean photon count \bar{N} and the maximum H associated with the optimum eye parameter p .

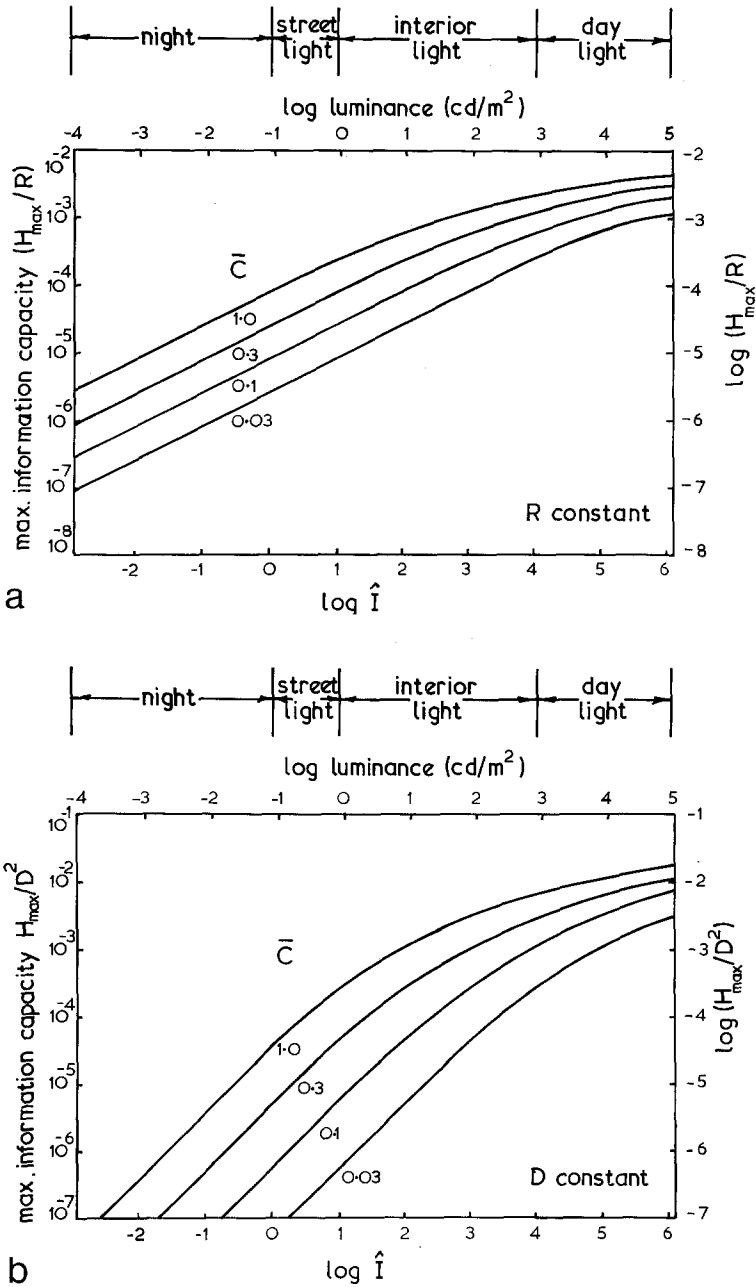


Fig. 11. The maximum information capacity H_{\max} , i.e., H for the optimum eye parameter p (Fig. 7). When eye radius R is constant H_{\max}/R is given uniquely by intensity parameter \hat{I} and mean contrast \bar{C} ; when facet diameter D is constant it is H_{\max}/D^2 , see Appendix B. The dimension of H_{\max}/R is $[\text{degrees}]^{-2} [\mu\text{m}]^{-1}$ and of H_{\max}/D^2 $[\text{degrees}]^{-2} [\mu\text{m}]^{-2}$.

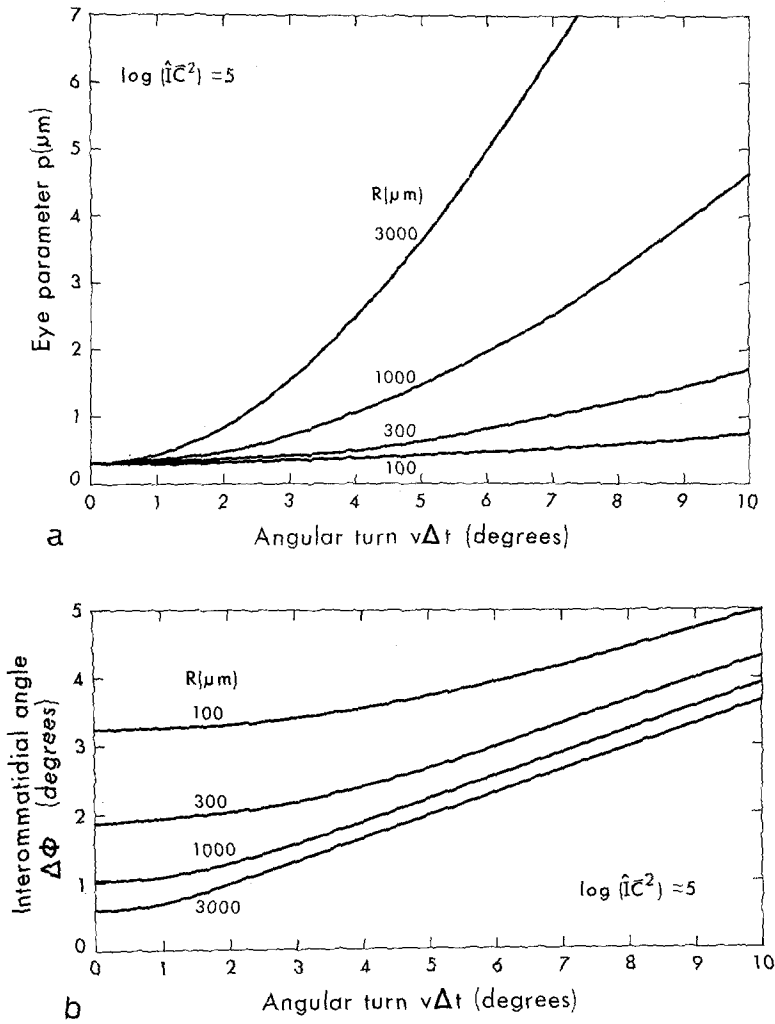


Fig. 12. The eye parameter p and interommatidial angle $\Delta\phi$ necessary to maximise the information capacity when the animal is undergoing angular velocity v relative to the object world. The integration time is Δt . We have assumed the intensity of light is that of a bright sunny day $\log(\hat{I}C^2) = 5$

4. Effect of Angular Motion on Determining the Optimum Eye Parameters

The presence of angular motion produces an additional spatial uncertainty of the amount $v\Delta t$, where v is the angular velocity and Δt the integration time of the eye. Snyder (1977 a) has shown that the effect of motion on spatial resolution is accounted for by a simple modification of Equation (11) of the form

$$(\Delta\rho)^2 = (\lambda/D)^2 + (\Delta\rho_r)^2 + (v\Delta t)^2 \quad (21)$$

so that the expression for information capacity Equation (17a) becomes

$$H = \frac{1}{2(\Delta\phi)^2} \ln \left\{ 1 + 0.37 \bar{N} \bar{C}^2 M_I(v_s) e^{-0.89 \left(\frac{v \Delta t}{\Delta\phi} \right)^2} \right\}. \quad (22)$$

Thus, the presence of a finite angular velocity is equivalent to a reduction in the intensity contrast parameter $\hat{I} \bar{C}^2$. This is demonstrated in Figure 12, which shows that the optimum eye parameter p and the interommatidial $\Delta\phi$ must increase as the angular velocity v increases. A fly undergoing fast angular turns is from the point of view of acuity placing itself in a dimmer or greyer environment.

IV. Discussion

1. Philosophy of Information Capacity

An animal views the spatial environment as a picture reconstructed by an array of retinula cells. This picture has two fundamental determinants: fine detail and contrast. The fine detail of the picture is set by the number of ommatidia per field of view, while the contrast depends on the light intensity and the quality of the optics, since it is limited by photon noise and imperfect optics. The smaller the interommatidial angle $\Delta\phi$, the greater the capacity of the eye for fine detail; however, as $\Delta\phi$ decreases so must the contrast sensitivity. This is because the imperfect optics (ultimately diffraction limited) degrades the higher spatial frequencies that are sampled by the ommatidia more than the lower frequencies. If the decrease in $\Delta\phi$ is accompanied by a decrease in facet diameter, there is an additional reduction in estimated or perceived contrast because fewer photons are then absorbed and pupil diffraction increases. Consequently, contrast and fine detail are interrelated, an increase of one coming at the expense of a decrease in the other. How is one to decide on which to value more? We have used a criterion for determining the *optimum* value of the parameters of the compound eye based on maximising the number of *different* pictures that an array of ommatidia can reconstruct from a random scene. Thus, for a given mean luminance and contrast, there is an optimum facet diameter D and interommatidial angle $\Delta\phi$ and angular rhabdom diameter, $\Delta\rho_r$.

One might sensibly question the relevance of using a random scene as the acuity task for eye design. It is quite true that no natural scene is ideally random for then it could not have discernable detail. However, the virtue of a random scene is that it places equal emphasis on all spatial frequencies. Although an animal never sees a random scene at any one instant, over the course of time it is exposed to a wide spectrum of spatial frequencies so that to specialize to any one spectral region is artificial.

In Figure 13 we have compared our optimum eye design, based on the criterion of extracting the maximum information from a random scene, with that based on the criterion for optimum resolution of a sinusoidal grating at the ommatidial sampling frequency $v_s = 1/2\Delta\phi$ (Snyder, 1977 a).

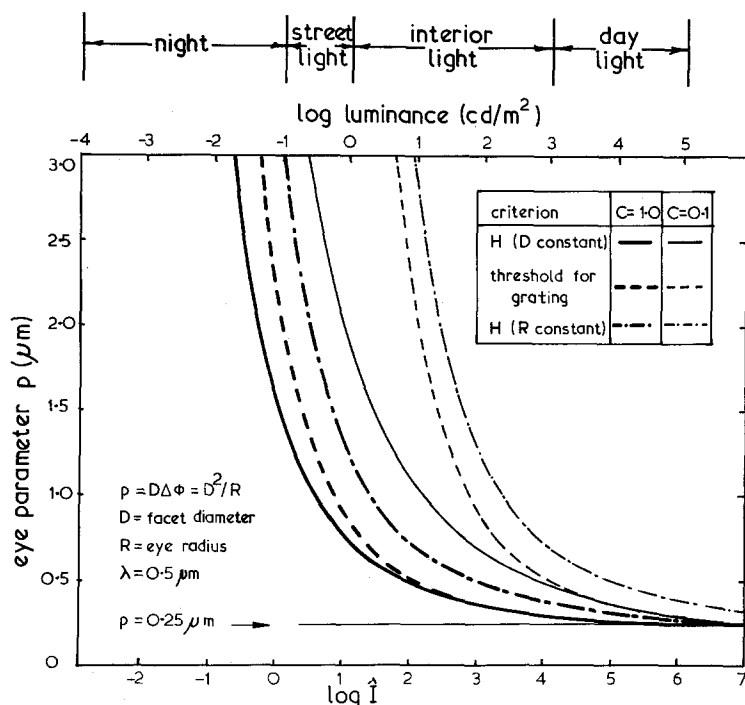


Fig. 13. Comparison of optimum p values based on three different criteria: information theory holding D or R constant and threshold resolution of a sinusoidal grating at the ommatidial sampling frequency

The two are similar, in the limit of high intensity and contrast. The reason is that the information capacity H of equation (1) is more sensitive to changes in n_p than in n_i (provided $n_i \geq 2$) so that a greater H is achieved by having a comparatively larger n_p than n_i , i.e. fine spatial detail is more important than contrast sensitivity in the limit of high contrast and intensity. The results of Figure 13 for sinusoidal gratings were obtained by taking the highest spatial frequency that can be resolved at a fixed signal to noise ratio equal to unity i.e. the minimum detectable contrast. Thus, the two different acuity tasks demand similar retinal designs because both give precedence to fine spatial detail over contrast sensitivity.

Finally, we note that both of the acuity tasks discussed above involve an extended and continuous distribution of object intensities, i.e., the sinusoidal grating and the random distribution of object intensity are infinite in extent. Had the acuity task been resolution of isolated points, to take an extreme example, the optimum eye design criteria is different with the facet diameter D playing a role more like p in the analysis presented here (Snyder, 1977 a, b).

2. Neural Pooling

In the text we showed that, if an eye is to be at *optimum* for a range of environmental intensity and contrast, there must be a range both in the parameter p and the angular rhabdom diameter $\Delta\rho_r$ across the eye. When p is uniform across the eye, there is an alternative effective strategy involving neural pooling.

In its simplest form neural pooling can be treated as an exact analogue of photoreceptors by assuming that pools do not overlap. Thus the light gathering capacity (see Equation 13) of a neural ommatidium is proportional to D_n^2 , where $D_n = R\Delta\phi_n$ is the effective diameter of the neural ommatidium and $\Delta\phi_n$ is the angle between adjacent neural ommatidia. There are $n_p = (1/\Delta\phi_n)^2$ neural ommatidia per square radian of object space with a sampling frequency v_s equal to $1/2\Delta\phi_n$. Making these changes in Equations (1) and (14a) gives the information capacity H of an array of neural ommatidia. We find that H is maximised if the angular diameter of the rhabdom $\Delta\rho_r$ varies as the neural interommatidial angle, i.e. $\Delta\rho_r = 1.06\Delta\phi_n$. Furthermore, we find that the information capacity *decreases* by widening the acceptance angle of an ommatidium unless this widening occurs together with neural pooling.

We are reminded that the information capacity is the capacity of an eye to perceive a white noise pattern. However, if the environment contains predominantly low spatial frequency components, it is advantageous to open up the acceptance angle with decreasing intensity (Laughlin, 1975, Snyder, 1977a).

A more detailed evaluation of strategies for dark adaptation is given by Snyder (1977a).

Finally, we note an important difference between the effect of neural pooling in lens and apposition compound eyes. The image due to neural pooling in lens eyes is in theory no different from that found by larger photoreceptors. However, the image due to neural pooling in a compound eye is worse than that formed by larger ommatidia, even though the light gathering capacity is identical. The reason is that larger ommatidia have less pupil diffraction.

3. Comparisons of Theory with Existing Eyes

We have found that the diffraction limited eye ($p = \lambda/2$) is optimum only for animals that are exposed to the brightest sunlight and have regions of the eye that normally experience low angular velocity. For these animals, the eye parameter $p = \lambda/2$ for a square lattice of ommatidia and $p = \lambda/\sqrt{3}$ (or $p = 0.29\text{ }\mu\text{m}$ when $\lambda = 500\text{ nm}$) for a hexagonal arrangement of ommatidia. This limit is very nearly reached in the foveas of the Australian sand wasp *Bembix* and the dragonfly *Hemicordula tau* (Horridge, 1976). Both of these animals hover when examining their prey. By comparison the dragonfly *Zyxomma*, active only before dawn and after dusk, has measured p values of 1.0–1.5 (Horridge, 1976) and this is consistent with our theoretical predictions (Fig. 7).

On the other hand, the fly *Musca* is active in rather bright conditions, yet, throughout most of its eye, $p \approx 1.3\text{ }\mu\text{m}$ (Stavenga, 1975), i.e., about 4.5 times greater than the diffraction limit. According to Figure 7 $p = 1.3\text{ }\mu\text{m}$ is the optimum design for an animal that is active in the late afternoon and at dusk. However, when we account for the high angular velocity habits of *Musca*, which conservatively turns 360° per second (see Land and Collett, 1974), we estimate, with $\Delta t = 20\text{ ms}$ that $v\Delta t = 7.2^\circ$ and thus, with $R \approx 700\text{ }\mu\text{m}$ and Figure 12 a, $p \approx 1\text{ }\mu\text{m}$ appears to be indeed reasonable. In other words, high angular velocity is equivalent to a low intensity-contrast environment (Snyder, 1977a).

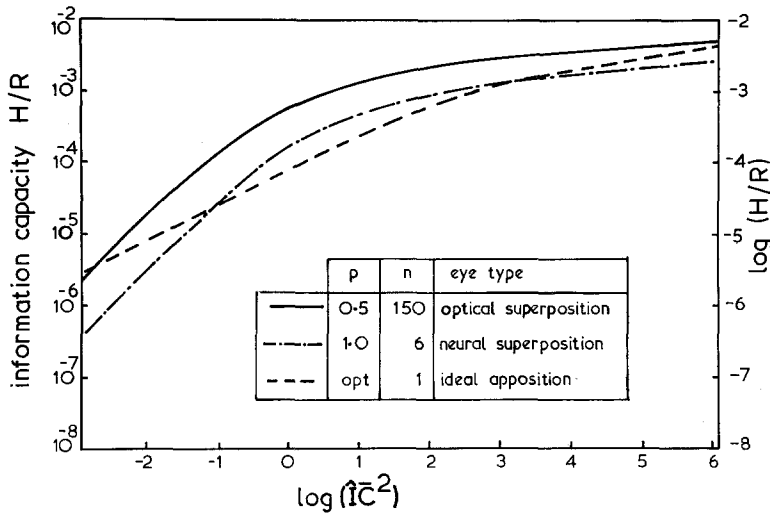


Fig. 14. Comparison of the maximum information capacities for an ideal apposition eye, an ideal optical superposition eye, and *Musca*, a neural superposition eye

In conclusion, we have compared the information capacity H of a hypothetical ideal apposition and ideal optical superposition eye with that of *Musca*. The apposition eye is assumed to have an enormous range of p values to accommodate the optimum under *all* contrast-intensity conditions. The optical superposition eye is assumed to be diffraction limited with 150 participating facets and $p = 0.6 \mu\text{m}$ constant over the whole eye. The fly *Musca* is assumed to have $p = 1.3 \mu\text{m}$ constant over the entire eye and a neural summation advantage of $6\bar{N}$. Figure 14 shows the comparison.

The ideal optical superposition eye is the best of the three but probably the results are inapplicable at high intensities (where the lens-pupil function limits acuity), because we have not accounted for the aberrations of the effective aperture formed by the 150 recruited ommatidia. Within a restricted region of intensity and contrast the neural superposition eye is better than the ideal apposition eye. Thus, the neural improvement of photon capture by a factor of 6 significantly compensates for the high p values found in this animal.

Appendix A. Optimum Eye Parameters when Facet Diameter D is Held Constant

When D rather than R is held constant in the process of finding the parameters that maximise the spatial information capacity of the eye, we must allow for some modifications not presented in the text.

The expression for the number of intensity levels n_i given by Equation (7), is inaccurate for $\bar{N} < 10$. A more uniformly valid expression is (Snyder et al., 1976)

$$n_i = \left\{ 1 + \frac{(\bar{N} \bar{C})^2}{N + 1} M(v_s) \right\}^{1/2}. \quad (\text{A.1})$$

In the R constant case, the optimum value of \bar{N} is greater than 10 for all situations of interest, so this modification is unnecessary. In the *high* intensity region it is also unnecessary for the D constant case.

We have determined the optimum parameters for the D constant case by maximising H as represented by Equation (1), when n_p is given by Equation (2) and n_i by Equation (A.1). In this case $\Delta\rho_r$ is slightly intensity dependent, but over the region of interest $\Delta\rho_r \simeq 1.1\Delta\phi$.

Appendix B. High Intensity Limit of Information Capacity

When the intensity is *high*, we can express the information capacity H , given in Equation (17b), by

$$H = (R/2p) \ln \{0.41 \bar{C}^2 \hat{I} p^2 e^{-0.89(\lambda/p)^2}\}, \quad (\text{B.1})$$

for the R constant case and

$$H = (D^2/2p^2) \ln \{0.41 \bar{C}^2 \hat{I} p^2 e^{-0.89(\lambda/p)^2}\}, \quad (\text{B.2})$$

for the D constant case.

1. R Constant Case

Finding the p that maximises Equation (B.1) leads to

$$\ln \{0.41 \bar{C}^2 \hat{I} p^2 e^{-2.67(\lambda/p)^2}\} = 2, \quad (\text{B.3})$$

or by noting the definitions of \bar{N} and $M_i(v_s)$

$$\ln \{0.37 \bar{N} \bar{C}^2 M_i^3(v_s)\} = 2, \quad (\text{B.4a})$$

$$\bar{N} \bar{C}^2 M_i^3(v_s) = 20. \quad (\text{B.4b})$$

The diffraction limit is given by $v_s = v_{co}$ or $p = \lambda/2$. Substituting $p = \lambda/2$ into the above expression leads to

$$\log \bar{N} \bar{C}^2 = 5.94 \quad (\text{B.5})$$

for the *minimum* number of photons to have the diffraction limit be the optimum design or equivalently when $\lambda = 0.5 \mu\text{m}$

$$\log \hat{I} \bar{C}^2 = 7.09. \quad (\text{B.6})$$

2. D Constant Case

Finding the p that maximises Equation (B.2) leads to an analogous set of equations;

$$\ln \{0.41 \bar{C}^2 \hat{I} p^2 e^{-1.78(\lambda/p)^2}\} = 1, \quad (\text{B.7})$$

$$\ln \{0.37 \bar{C}^2 \hat{I} M_i^2(v_s)\} = 1, \quad (\text{B.8})$$

$$\bar{N} \bar{C}^2 M_i^2(v_s) = 7.35. \quad (\text{B.9})$$

Substituting $p = \lambda/2$ into these expressions gives the minimum conditions neces-

sary for the diffraction limit to be the optimum design, when $\lambda = 0.5 \mu\text{m}$

$$\log(\bar{N} \bar{C}^2) = 3.96 \quad (\text{B.10})$$

$$\log(\hat{I} \bar{C}^2) = 5.11. \quad (\text{B.11})$$

Appendix C. Conversion of \hat{I} to Luminance

Using our table of symbols,

$$\hat{I} = 0.89 \varepsilon \Delta t \bar{I}_0. \quad (\text{C.1})$$

According to Wyszecki and Stiles (1967), p. 226,

$$\bar{I} = L \cdot A \cdot (\lambda/V'_\lambda) \cdot 8.8 \cdot 10^9 \quad (\text{C.2})$$

where \bar{I} is the mean number of quanta *per second* entering the ommatidium per square degree of field, A apparent area in $(\text{mm})^2$, L the luminance of the field in candelas per m^2 , λ the wavelength in cm and V'_λ the CIE relative luminous efficiency curve (for scotopic vision).

We take $\lambda = 5 \cdot 10^{-5} \text{ cm}$ so that $V'_\lambda = 0.98$, $A = (\pi/4) D^2 \cdot 10^{-6}$, $\bar{I}_0 = \bar{I} (4/\pi D^2) (180/\pi)^2$, so that $\bar{I}_0 = 1.47 \cdot 10^3 L$ and

$$\hat{I} = 1.31 \times 10^3 (\varepsilon \Delta t) L. \quad (\text{C.3})$$

With $\varepsilon = 0.5$ and $\Delta t = 2 \cdot 10^{-2} \text{ s}$ (20 ms) as representative values

$$\log \hat{I} = \log L + 1.11. \quad (\text{C.4})$$

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