

2.9 The Resolution of Lens and Compound Eyes

K. KIRSCHFELD

2.9.1 Introduction

Two distinctly different types of eyes have been highly developed in evolution: lens eyes (= camera eyes) in vertebrates, some molluscs and arachnids and compound eyes in arthropods. Based on his comparative studies of the optical properties of compound and lens eyes, Exner (1891) concluded that both types of eyes are optimally adapted for different functions: lens eyes with their high angular resolution seem to more useful for pattern recognition, whereas the compound eyes, with their poor resolution, are thought to be specialized for movement perception. This view is still generally accepted (see the textbooks of Scheer, 1969, Kaestner, 1972). Furthermore, the small facet diameters of the ommatidia in compound eyes seem to cause a poor absolute sensitivity (Exner, 1891; Barlow, 1952; Kirschfeld, 1966; Prosser and Brown, 1969; Snyder et al., 1973). Some insects are said, however, to have higher temporal resolution than humans (Autrum, 1948).

Irrespective of the mentioned disadvantages of compound eyes - poor resolution and sensitivity - many more individual animals as well as animal species are equipped with compound rather than with lens eyes, since even the number of known insect species ($\sim 10^6$) is at least 10 times larger than that of vertebrates (Weber and Weidner, 1974). Though primitive lens eyes (the ocelli) are also common to many insects, these must not be as useful as compound eyes since evolution has clearly favored the latter.

If it is true that both types of eyes are adaptations for different functions, we expect that the world as seen through a compound eye looks different from the world observed by a lens eye. Information on the optical environment available from both types of eyes should be different at the receptor level.

We will consider in this chapter if this is really the case. In order to illustrate the situation we will answer the questions of what would a compound eye look like if it had the optical performance of a human eye, and how a lens eye with the performance of the compound eye of a fly would need to be constructed.

2.9.2 Subjective Resolution

There is no doubt that the absolute resolution of compound eyes is far inferior to that of lens eyes. The angular distance between stripes of a striped pattern that is just able to induce an optomotor turning response must be larger than approximately 2° in the fly (Eckert, 1973), whereas under optimal conditions the "minimum separabile" in man is $0.6-1.8 \times 10^{-2}$ degrees (Buddenbrock, 1952).

These variations in performance do not necessarily reflect differences between the various principles according to which lens and compound eyes are realized. It might be due rather to the fact that the eye of such a small animal as a fly is just much smaller than a human eye. It may be more germane in terms of function to compare acuity relative to eye size or, biologically relevant as well, to animal size instead of absolute resolution, since, as we will see below, physical dimensions of an animal's eye place severe restraints upon its performance.

Angular resolution as determined by physiological methods apparently is dependent on the quality of the dioptrics of an eye ("optical resolution") as well as on the angular separation $\Delta\phi$ of the receptors ("anatomical resolution"). The resolution of the whole visual system has been determined with physiological methods. Test objects have been striped patterns or two point sources, the critical distances of which have been determined. These numbers, here called "physiologically resolution ϵ ", have been measured for many animal species. They characterize the performance of eyes sufficiently well for our purpose and will be used for comparison, even if they do not give such a precise description as the modulation transfer or linespread functions which are known only for a few species.

Fig. 1 relates experimentally determined values of anatomical ($\Delta\phi$) and physiological (ϵ) resolution to body height, H , for several species of animals.

We find in the first order a simple interrelationship between resolution ($\Delta\phi$ or ϵ) and body height H :

$$\Delta\phi \approx \epsilon = k \frac{1}{H} \text{ [deg]}, \quad (1)$$

where k is a factor of proportionality. For most of the animals listed in Fig. 1, k is between 0.2 and 3 deg x cm.

Whereas $\Delta\phi$ and ϵ in degrees are measures for an absolute spatial resolution, we may use k in deg x cm as a measure for "subjective resolution", the resolution being the better the smaller k . If two animals have the same subjective resolution, this means that for the same "subjective distance" of an object the same number of points per object area are scanned or resolved, where subjective distance is measured not in units of centimeters but in units of body height. For example, if we ($H \approx 2$ m) look at a fly in a distance of 5 m we resolve this fly into the same number of points as a fly ($H \approx 2$ mm) looking at another fly from a distance of 5 mm.

Eq. (1) is only a first-order approximation of the data of Fig. 1. There are, in fact, interesting deviations from this relationship. For instance, of all the larger animals, birds have the smallest value of k , that is the highest subjective resolution. The bat *Myotis* and the jumping spider *Metaphidippus* represent two extreme cases of low and high "subjective resolution". These facts will be considered again when we have developed a concept that allows an interpretation of the data on the basis of the performances of idealized lens and compound eyes.

The data suggest that smaller animals are adequately endowed even with a smaller absolute resolution because they have sufficient "subjective resolution". This is reasonable because small animals are concerned with objects in closer proximity than are large animals. At these shorter distances, a small animal can then resolve the same objects as well as can a larger animal at a greater distance. On the other hand,

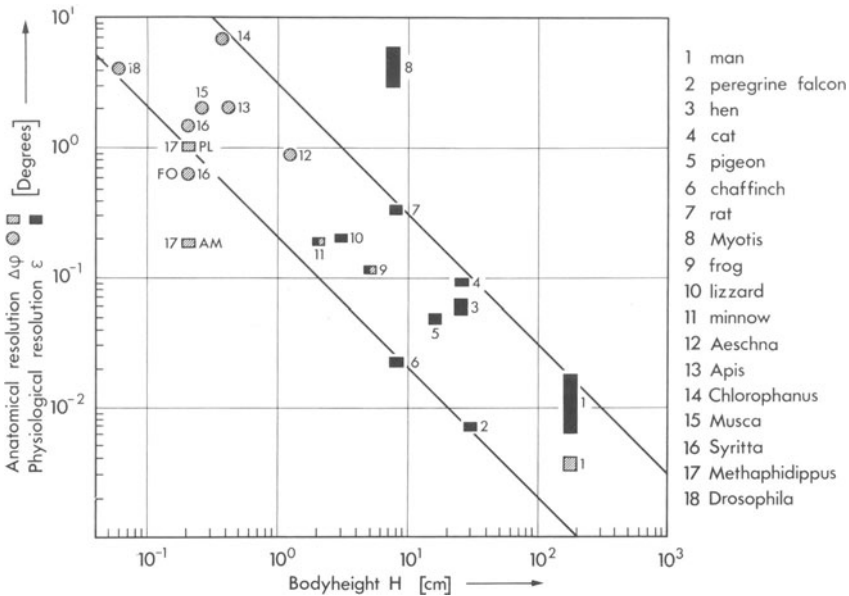
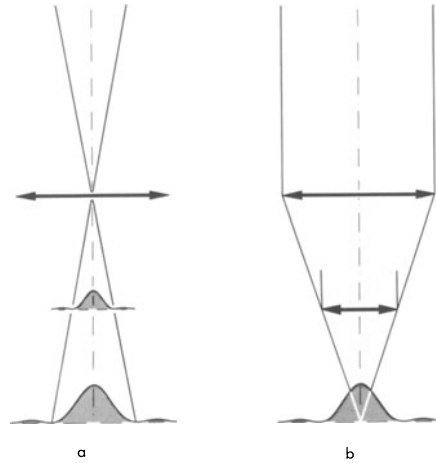


Fig. 1. Anatomical ($\Delta\phi$) and physiological (ϵ) resolution as a function of body height H of different animals. Circles: data from animals with compound eyes, rectangles: data from animals with lens eyes. The numbers indicate species and source of the data (1, 2, 3, 5, 6, 8, 9, 11, Buddenbrock, 1952; 4, 7, 10, Penzlin, 1970; 12, del Portillo, 1936; 13, Kirschfeld, 1973; 14, Hassenstein, 1951; 15, Kirschfeld and Franceschini, 1968; 16, Collett and Land, 1975; 17, Land, 1969; 18, Götz, 1965). The body height H (center of eyes above ground) has been estimated on the basis of the size of the animals according to Garms (1969) as far as vertebrates are concerned, or it was measured directly in the insects. For the jumping spider Metaphidippus resolution of antero-medial AM eyes as well as of postero-lateral eyes PL is indicated. For the hoverfly Syritta the resolution in the front region of the male is indicated by FO ("fovea"). The two lines of slope -45° indicate $k = 0.2$ and 3.0 deg x cm respectively

it means that within the limits of the scatter of the points in Fig. 1, the whole visual environment is poorer in detail for smaller animals.

From the data it appears that "subjective resolution" for all animals varies approximately over one order of magnitude while the range of body height spans three orders of magnitude, irrespective of whether the animal uses a lens or a compound eye. This analysis, therefore, suggests that, contrary to popular belief, the practical resolution of compound eyes is comparable to, rather than worse than, that of lens eyes. The difference in absolute spatial resolution seems to be due not so much to the fact that these animals have compound rather than lens eyes, but to the fact that these animals are so small. This begs the question as to why only relatively small animals are equipped with compound eyes, whereas all known large animals have lens eyes. In order to interpret these facts we will consider the factors that limit the angular resolution in lens as well as in compound eyes.

Fig. 2a and b. Graphical representation of Eq. (2). Double arrows: lenses, dotted: intensity distributions in the focal planes of the lenses. a) The angular size of Airy's disk depends only on the diameter of a lens, irrespective of its focal length. b) The absolute size of Airy's disk depends only on the ratio A/f , irrespective of the focal length of a lens



2.9.3 Physical Parameters Limiting Angular Resolution

2.9.3.1 The Diffraction Limit

An absolute limit to resolution of any eye is set by its optical resolution; information that is not transmitted by the dioptrics is irretrievably lost and cannot be restored by neural mechanisms. An upper limit of optical resolution is easily estimated if the dioptric is made by a lens system. In this case optical resolution is limited by Fraunhofer diffraction of light.

It has been shown that at small pupil sizes optical resolution in the human eye is basically diffraction limited (Campbell and Gubisch, 1966). The dioptric systems of the ommatidia of compound eyes are also lenses or lens systems, which in the cases that have been analyzed in some detail are also diffraction limited (e.g. Kirschfeld and Franceschini, 1968; Franceschini and Kirschfeld, 1971). It appears justified, therefore, to introduce diffraction as limiting the optical resolution of lens and compound eyes. From this point of view all eyes considered here are "lens eyes". Hence it would be more precise to call the "lens eye" a single lens eye (or single camera eye) and the compound eye a "multiple lens eye". Nevertheless, we will use the common terminology.

In the focal plane of a perfect lens system with circular aperture of diameter A the Fraunhofer diffraction image of a pointlike object at infinite distance may be characterized by the radius Δr of Airy's disk, that is the central zone of the diffraction image, included within the first diffraction minimum. We have the equations

$$\Delta r = 1,22 \frac{\lambda}{A} \quad [\text{rad}] \quad (2a)$$

$$r = \Delta r f = 1,22 \frac{\lambda}{A} f \quad [\text{mm}], \quad (2b)$$

where λ is the wavelength of light in the image medium, f is the focal length. Small Δr means better optical resolution. Δr , in angular units, depends only upon the pupil diameter and is independent of the focal length, whereas r , measured in units of length, depends only upon the ratio f/A , that is the "f-number" of the system (Fig. 2).

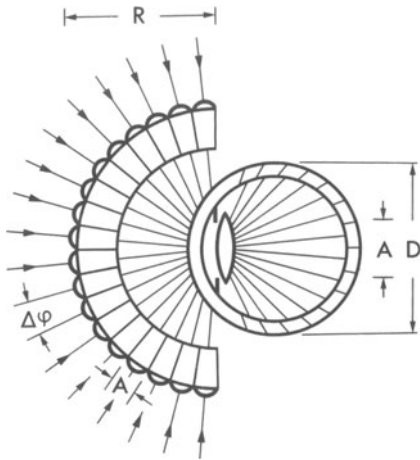


Fig. 3. Schematic diagram of a lens and a compound eye. $\Delta\phi$: divergence angle between neighboring receptors (anatomical resolution). A : diameter of the pupil or facet lens, respectively, D : diameter of the lens eye, R : radius of the compound eye

2.9.3.2 The Maximal Lens Diameter of an Eye

Diffraction limited optical resolution is determined by the aperture of the lens. If we characterize the size of an eye by its diameter D (Fig. 3), we find that the diameter A of its lens is

$$A = c_1 \times D, \quad (3)$$

where $c_1 (\leq 1)$ characterizes the relative size of the lens.

Compound eyes differ basically in design from lens eyes in that the ommatidial aperture can never be made as large as the diameter of the whole eye, since there must be space to accommodate many separate ommatidia (Mallock, 1922; Barlow, 1952; de Vries, 1956; Götz, 1965). In the compound eye the equation

$$A \approx \Delta\phi R \quad (4)$$

must be applied, where R is the radius of the eye and $\Delta\phi$ the angle between neighboring ommatidia, as can be derived directly from Fig. 3.

2.9.3.3 The Anatomical Resolution of an Eye

The overall angular resolution of any eye depends not only upon its optical resolution but also upon the angular separation $\Delta\phi$ of the receptors. Intuitively one might expect that there could be a constant, optimal ratio for all eyes between optical and anatomical resolution: anatomical resolution might be matched to the optical one in order to just transmit the information available from the dioptric system. Higher anatomical resolution would serve no purpose while lower resolution would sacrifice some of the qualities of the dioptrics. The latter statement is true only if the eye makes use of the information available to the receptors at one and the same time, i.e. if there is no temporal scanning. This is assumed for the moment; temporal scanning will be considered later.

The Rayleigh resolution-criterion, usually applied to telescopes, was often used when discussing the acuity of eyes. More recently such questions have been discussed using a formalism based on information

theory, which appears to be less arbitrary than the older approaches (e.g. Barlow, 1965; Westheimer, 1972a).

It is well known that a lens of finite size can transmit spatial frequencies only to an upper limit f_o and $f_o = A/\lambda$ [lines/radian] with incoherent illumination. Shannon (1949) has shown that all the information available in such a band-limited function is obtained if the values of the function are known at sampling intervals $\Delta\phi_s$. The size of $\Delta\phi_s$ is related to the highest spectral (= Fourier) component f_o of the function by

$$\Delta\phi_s = \frac{1}{2f_o}. \quad (5)$$

Thus for our optical system

$$\Delta\phi_s = \frac{\lambda}{2A} \text{ [rad]}. \quad (6)$$

$\Delta\phi_s$ gives the angular separation of independently acting receptors necessary in order to transmit all the information available from the dioptric system¹. Introducing Δr from Eq. (2a) instead of A gives

$$\Delta\phi_s = \frac{\Delta r}{2,44} = g\Delta r. \quad (7)$$

Fig. 4a is a graphical representation of this equation. It shows that approximately 5 receptors must scan the diameter of Airy's disk or approximately 20 receptors its area according to Eq. (7), in order to transmit the angular information available.

2.9.4 Eyesize and Resolution

2.9.4.1 Lens Eyes

For the sake of simplicity let us consider first so-called "isometric" animals: animals which are exact scale models of each other. Then the diameter D of the eye will be proportional to the body height H . The relation between optical resolution $1/\Delta r$ and body height H , becomes according to Eqs. (2a) and (3)

$$\frac{1}{\Delta r} = \frac{C_1 D}{1.22 \lambda} = \frac{C_2 H}{1.22 \lambda} \text{ [rad}^{-1}\text{]} \quad (8)$$

where C_1 and C_2 are constants of proportionality. This means, that larger body height and the accompanying larger eyesize yield better (diffraction limited) optical resolution for any given wavelength of light, since $\Delta r \times H$ for isometric animals is constant.

These elementary considerations rationalize the experimental finding that subjective resolution is in first approximation constant for all animals with lens eyes. It is not surprising, however, that in reality there is variation of resolution for a given H , since the assumptions inherent in Eq. (8) are not always valid. For instance, eye size and pupil diameter may either exceed the average or fall below it in some

¹In this paper we use only the simplest concepts from sampling theory and do not concern ourselves with the effects of aperture shapes and sampling lattices. Such refinements do not change the general conclusions presented here.

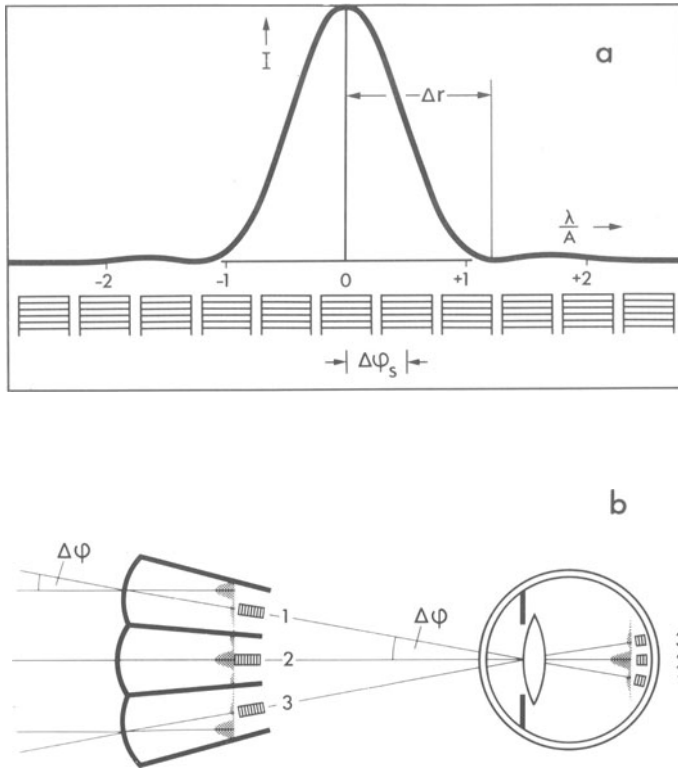


Fig. 4a and b. a) Array of receptors with angular separation $\Delta\phi_s = \Delta r/2.44$ in the focal plane of a lens eye. According to Shannon's sampling theorem receptors with this separation could transmit all the information available from the lens as far as angular resolution is concerned. The Airy pattern is shown to illustrate its size relative to the receptors. b) In the compound eye (classical apposition type) we have not one Airy pattern projected from a point source onto a retina with many receptors as in the lens eye. Instead in several ommatidia Airy patterns from the point source are projected, each covering the single rhabdom by a different angle. The relative position of the receptors 1 to 3 to the Airy pattern is basically the same, however, in the two types of eyes. Therefore, Eq. (7) can also apply to the compound eye. In this schematic diagram $\Delta\phi$ is greater than $\Delta\phi_s$

species. In addition resolution may not always be diffraction limited as assumed in Eq. (2). Some of the variations of the subjective resolution shown in Fig. 1 reflect special adaptations. That birds (with the exception of the domesticated hen) usually have a better resolution than mammals of similar size is explained by their relatively large eyeballs (see Walls, 1967, Fig. 70), and might have to do with the fact that rapidly moving animals need better eyes. The antero-medial (AM) eyes of the jumping spider *Metaphidippus* with their exceptionally high subjective resolution ($k \approx 0.05 \text{ deg} \times \text{cm}$, Fig. 1) is also explained by their large relative eye size with an aperture of one sixth and a focal length of one quarter of the body height (Land, 1969). The resolution of the smaller posterolateral (PL) eyes is within the range of other animals. The below average subjective resolution of the bat *Myotis* ($k \approx 30 \text{ deg} \times \text{cm}$) apparently has to do with the bats reliance on echolocation, which works even in the dark and is, therefore, of greater functional value for such an animal,

active at night, than is vision. Nevertheless, these exceptions need not invalidate the general rule that appears to hold for the majority of species.

2.9.4.2 Compound Eyes

By combining Eq. (2a), which describes the eyes as diffraction limited, with Eq. (4), which introduces the geometrical arrangement of the ommatidia in compound eyes, and Eq. (7), which claims an optimal matching between optical and anatomical resolution (comp. Fig. 4b) we obtain

$$\frac{1}{\Delta r} = \left[\frac{gR}{1.22 \lambda} \right]^{1/2} \left[\text{rad}^{-1} \right]. \quad (9)$$

That is: in contrast to the diffraction limited lens eye, where the resolution is proportional to eye size (Eq. (8)), we find in the diffraction limited compound eye that the resolution increases only with the square root of the size of the eye (Mallock, 1894; Barlow, 1952; de Vries, 1956; Kuiper and Leutscher-Hazelhoff, 1965) or, if eye size and body height are proportional, to the square root of body height H.

If we look in Fig. 1 at the subjective resolution of animals with compound eyes we again find that it is better in flying insects than e.g. in the usually slowly moving snout beetle *Chlorophanus*. The highest subjective resolution of the selected animals with compound eyes is found in the hover fly *Syrirta*. The male has a specialized foveal region FO in the front of the eye with increased angular resolution ($k \approx 0.12$). The high resolution in *Syrirta* is explained by the fact that it has eyes which are exceptionally large compared to its body size.

2.9.5 Minimal Size of a Lens Eye

Diffraction and, hence, the absolute size of the aperture A of the lens poses an absolute limit to the angular resolution of any eye. A further question is what determines the minimal size of an eye, given an absolute optical resolution and, hence, aperture size. The aperture size defines a resolution $1/\Delta r$. Since we match the anatomical resolution to the optical one according to Eq. (7) the angular distance of the receptors must remain constant if we reduce an eye in size, keeping the aperture constant. Therefore the receptor diameter must be reduced. The small eye and the large one superimposed in Fig. 5, therefore, show basically the same performance; angular resolution as well as absolute sensitivity are principally the same. The latter is due to the fact that the mean number of light quanta q from an extended optical environment available per receptor and time unit is given by

$$q \sim B \frac{A^2}{f^2} \delta^2, \quad (10)$$

where B is the mean brightness, f the focal length of the dioptric system and δ the diameter of the receptors (Rodieck, 1973; Kirschfeld, 1974). Since $A \times \delta/f$ is constant for the small and the large eye as well this is also the case for q.

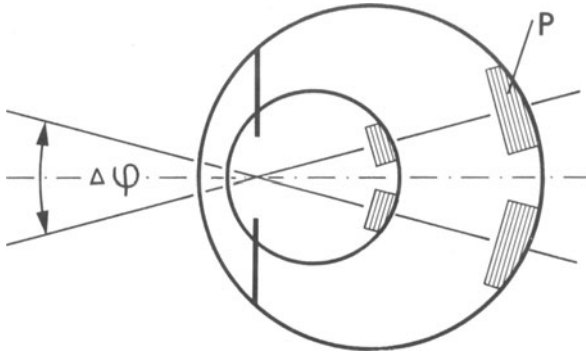


Fig. 5. A diffraction limited lens eye with given pupil diameter theoretically can be reduced in size without losses in angular resolution $\Delta\varphi$ or in absolute sensitivity as long as the diameter of the receptors is reduced proportional to the focal length of the system. A lower limit is reached, however, if the diameter of the receptors becomes so small that they are no longer able to work independently of each other due to optical cross talk. This appears to be at receptor diameters and distances of approx. 1-2 μm , given the realized refraction indices of receptors and surrounding media. P: Photoreceptors

There are, obviously, several factors that pose a limit to reduction of the eye size. For example, the f -number f/A of the lens must be reduced more and more with reducing the size of the eye which might introduce difficulties in its construction as far as aberrations are concerned (cf. Westheimer, 1972b). Second, there is clearly a lower limit to the photoreceptor diameter set by the size of nuclei, mitochondria, etc. A basic limit, however, seems to be posed by the wave properties of light.

By acting as light guides, outer segments and rhabdomeres are able to increase the total amount of light absorbed by increasing the optical path length. If light guides are too small, however, most of the light will travel along the outside of the light guide and, therefore, cannot be absorbed by the visual pigment inside. That is, the "optical diameter" is larger than the anatomical one. Furthermore, problems of optical cross-talk become serious in small waveguides (Snyder, 1975). This means that the receptors are no longer able to act independently of each other, a condition necessary if the sampling theorem (Eq. (5)) is applied. Lastly, the acceptance angle of the waveguide (directivity) becomes smaller as their size is reduced, which prevents the receptors from making use of a small f -number of the dioptrics. This reduces angular resolution as well as absolute sensitivity. The actual size to which receptors may be reduced depends basically upon the waveguide parameter

$$V = \frac{\pi \delta}{\lambda_0} \sqrt{n_1^2 - n_2^2} \quad (11)$$

where n_1 , n_2 are the refractive indices of the waveguide and its surround respectively, λ_0 is the wavelength of light in vacuum and δ the diameter of the waveguide, that is the outer segment or rhabdomere. The problems mentioned become serious if V becomes smaller than 2 to 3. Since the difference between n_1 and n_2 cannot be increased beyond some limit with the substances (lipoproteins and water respectively) available to the receptor cells, δ cannot be reduced beyond some limit.

This limit is, given realistic differences $n_1 - n_2$ of 0.02 to 0.04, in the order of 1 to 2 μm . Thus, the minimal "grainsize" for a biological retina cannot be reduced below this value.

From this point of view the high concentration of membranes in the photopigment containing structures of outer segments and rhabdomeres may not only provide a means to increase the photopigment concentration within these structures thus increasing the number of photons absorbed, but also to increase their refractive index so that the grain of the retina may be as fine as possible.

Though there is a lower limit of photoreceptor-diameter, determined by waveguide properties, receptors could be larger than this limit. However, optimum resolution could not be achieved in this case without also making the eye larger in order to maintain the matching between optical and anatomical resolution. It seems reasonable, therefore, that the eyesize with a given absolute aperture A has been reduced by evolution just to the point where the minimal receptor diameter that allows the receptors to act independently is reached. This can be realized as we have seen without any loss of angular resolution (Fig. 5) as well as absolute sensitivity.

These general arguments show that a more or less constant receptor diameter for all eye sizes is a functionally adequate adaptation. They explain why the absolute size of retinal elements only varies within narrow limits however large or small a lens eye may be (Walls, 1967). For instance the diameter δ of cones in the human fovea is in the order of 1-2 μm . Surprisingly this is also just the diameter of the rhabdomeres in the compound eye of the fly (receptors 1 to 6: 2 μm , receptors 7 and 8: 1 μm , Boschek, 1971). Every individual fly ommatidium with a retinula composed of 8 receptors with 7 rhabdomeres, all acting as independent waveguides (Kirschfeld, 1967), may be considered in this context as a lens eye, which explains the convergence. In compound eyes of the classical apposition type which have only one rhabdom per ommatidium acting as one single waveguide it is of course not the cross-talk between receptors that is limiting. Here the relative increase of the "optical diameter" compared with the anatomical one and the consequences for absorption as well as angular resolution (Pask and Snyder, 1975) are the main limiting factors.

Realizing that there exists a lower limit to the size of receptors, determined by the difference of the refractive indices between receptors and surrounding medium, one is able to calculate an optimal f-number of a diffraction limited lens eye, which is still useful with respect to the angular resolution of the system. Considering the case of an optimal matching between the "graininess" of the retina (anatomical resolution) and the optical resolution, one finds from Eq. (7) with the angular separation δ/f of the receptors $\approx \Delta\varphi_s$

$$\Delta r \approx 2.44 \frac{\delta}{F} \quad (12)$$

combined with Eq. (2a) one arrives at

$$\frac{f}{A} \approx \frac{2\delta}{\lambda} \quad (13)$$

which determines the smallest useful f-number. Introducing $\lambda = 0.37 \mu\text{m}$ (wavelength λ_o of light = 0.5 μm , refractive index $n = 1.34$) and $\delta = 1-2 \mu\text{m}$ yields f/A in the range of 5 to 10. Smaller f-numbers are of no use to any eye with respect to angular resolution. This holds as long as temporal scanning does not come into play. Smaller f-numbers might be advantageous, however, by increasing the absolute sensitivity.

2.9.6 Realized Lens and Compound Eyes

2.9.6.1 Human Eye

Optical measurements on human eyes have shown that diffraction is a limiting factor for optical resolution only at small pupil sizes. If the pupil dilates, other aberrations of the lens become more and more limiting. The best optical resolution occurs at a pupil diameter A of 2.4 mm (Campbell and Gubisch, 1966). According to Eq. (2a) the diameter of Airy's disk at this pupil size is 1.30 min of arc ($\lambda = 0.37 \mu\text{m}$).

The diameter of a cone in the human fovea is 1 to 2 μm (Buddenbrock, 1952) which corresponds to 0.2 to 0.4 min of arc, a value considerably less than the diameter of Airy's disk. This cone diameter corresponds nicely, however, to the angle $\Delta\varphi_s$ given by Eq. (7) to 0.27 min of arc for the optimal sampling interval. If signals of individual cones in the fovea act independently of one another, and if their signals are processed independently with respect to spatial resolution, the anatomical resolution of the human eye is sufficient to transmit all the spatial frequencies that pass the dioptric system. Optical and anatomical resolution are fitted according to Shannon's sampling theorem.

2.9.6.2 Fly's Eye

The radius at the front region of the eye of a *Musca* female is approximately 600 μm . By means of Eqs. (2a), (7) and (9) we calculate a value of $\Delta\varphi_s = 1.0^\circ$ and of $A = 11 \mu\text{m}$ ($g = 1/2.44$; $\lambda = 0.37 \mu\text{m}$). Actual measured values are $\Delta\varphi = 2.3^\circ$ and $A = 24 \mu$. This means that the anatomical resolution $\Delta\varphi$ is worse than it could be theoretically for a purely diffraction limited compound eye of the same size approximately by a factor of two. The deviation, though greater than the limit of experimental error, is not so large as to merit detailed discussion here.

2.9.7 Comparison of the Angular Resolution of Lens and Compound Eyes

Using the principle of the preceding sections we can determine how a compound eye might look if it were to have the same angular resolution as a human eye, and also the minimal size of a lens eye, with angular resolution equivalent to that of a fly's eye.

As we have seen, the human lens eye has its best resolution at a pupil size of 2.4 mm. Since its diameter is 24 mm, C_1 becomes 0.1. Fig. 6 shows the relationship between resolution of lens and compound eyes and their size (Eqs. (8) and (9)). It can be seen easily that a lens eye of $D = 24$ mm corresponds to a compound eye of radius $R = 31$ m ($\lambda = 0.37 \mu\text{m}$).

This means that a diffraction limited compound eye with the same angular resolution must be enormous (Fig. 7a). However, the calculation is somewhat erroneous for we know that the optimum resolution of the human eye is only confined to a rather small foveal region, decreasing rapidly with increasing angular distance α from the fovea (Fig. 8). This means that we can reduce the size of the "equivalent" compound eye by reducing A and R with increasing angular distance from the "fovea". The result is a compound eye of elongated shape with a long axis of 31 m (Fig. 7b). Its size can be reduced, however, still further, without loss of resolution. Since the radius is drastically

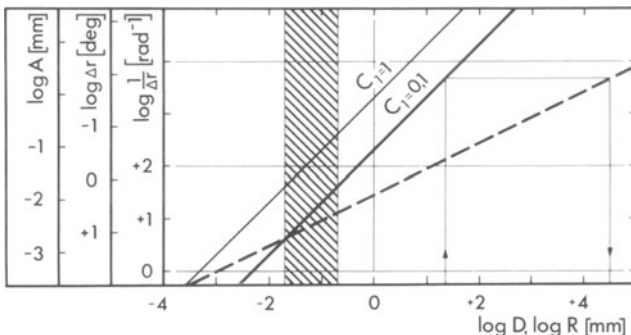


Fig. 6. Graphical representation of Eqs. (8) and (9). Ordinate: Pupil diameter A , size of Airy's disk Δr and resolution $1/\Delta r$. Thick continuous line: ordinate parameters of the lens eye as a function of its diameter D . The ratio C_1 was chosen to 0.1 which represents the case valid for the human eye at optical resolution (pupil size 2.4 mm). Thin continuous line: $c_1 = 1$. Interrupted line: ordinate parameters for the compound eye as a function of its radius R . Hatched area: size of photo-receptors (lengths 20 μm to 200 μm). Arrows: indicate that a human eye of diameter $D = 24$ mm ($\log D = 1.38$) with $c_1 = 0.1$ corresponds to a compound eye of radius $R = 3.1 \times 10^4$ cm ($\log R = 4.49$)

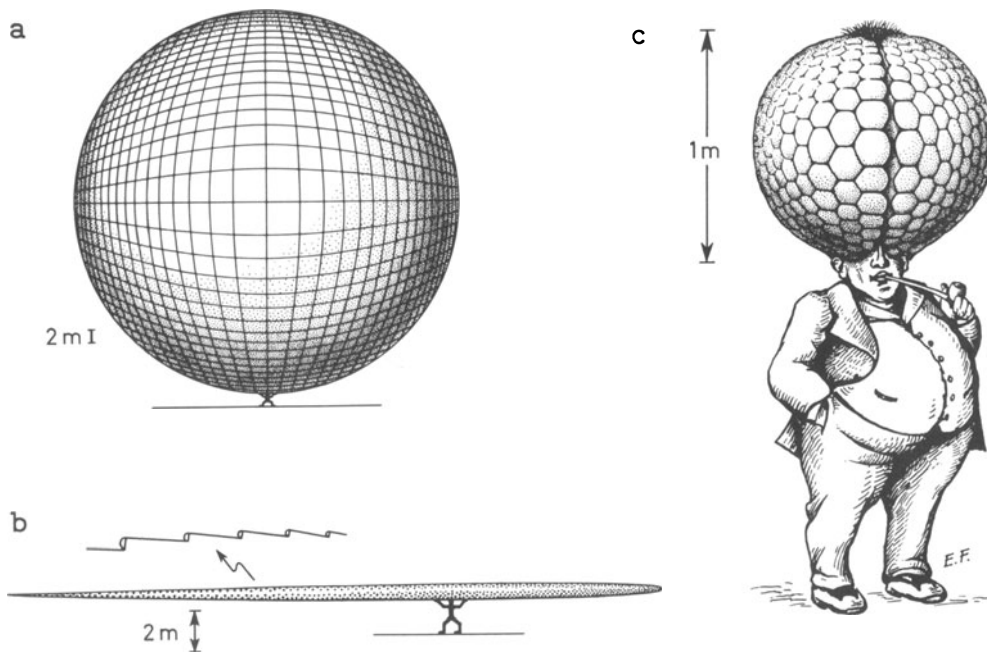


Fig. 7a-c. Human being equipped with compound eyes instead of lens eyes. (a) Compound eye with the same resolution as a diffraction limited lens eye with $A = 2.4$ mm. (b) The decrease in angular resolution with distance from the fovea has been taken into account. (c) Compound eye with the overall resolution of a human eye and of minimally possible size. The minimal surface necessary for all facets has been calculated and the size of the hemispheres has been determined so that the surface just allows space for all of the facets. Facet size not to scale, instead of the 100 facets per eye 10^6 should have been drawn

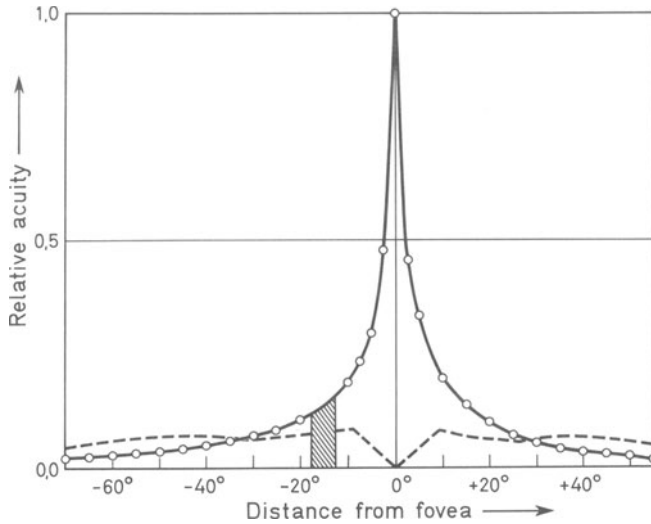


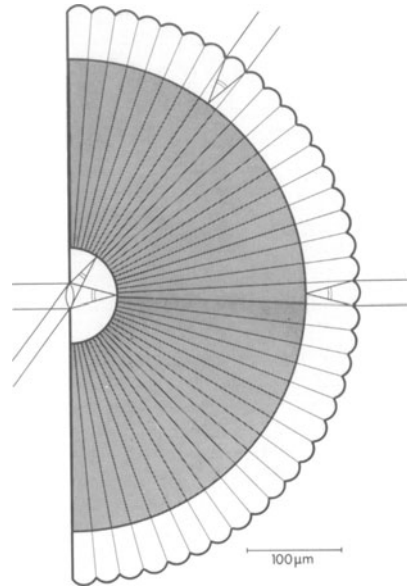
Fig. 8. Relative angular resolution of the human eye at different angular distances from the fovea as determined psychophysically by Wertheim. (From Rein Schneider, 1956). Circles: photopic system. Interrupted line: scotopic system. Hatched: blind spot

changing with angular distance of the fovea, most of the eye surface is not used for the entrance of light (inset Fig. 7b). If we calculate the integral only over the surface of all facets, we determine the surface the eye must have available at the minimum for the entrance of light into the ommatidia.

At angular distance α from the fovea the facets of size $A(\alpha)$ form a ring of radius $R(\alpha) \sin \alpha$ and thus contribute to the corneal surface an area ΔO given by $\Delta O(\alpha) = 2\pi A(\alpha)R(\alpha) \sin \alpha$. $1/\Delta \phi = \pi R/180A$ gives the number of ommatidia rings per degree. Integrating over $\Delta O/\Delta \phi$ from 0 to 90° finally results in the total surface O . It comes out to be $1.7 \times 10^6 \text{ mm}^2$. A hemisphere with equivalent surface has a radius R of 0.52 m (Fig. 7c). And this is the minimal size that a diffraction limited compound eye with human angular resolution must have. It is impossible to reduce its size further without loss in angular resolution.

The size of a lens eye equivalent to that of a fly's compound eye might be estimated as follows: the diameter A of the lens must be $24 \mu\text{m}$ in order to have the same absolute optical resolution as found in a fly's ommatidium. This aperture has to be combined with a minimal focal length of $50 \mu\text{m}$ which is necessary to match the absolute size of Airy's disk to the 1 to 2 μm diameter of the rhabdomeres in the same way as in the fly's eye. The lens and the vitreous body alone therefore would provide a lens eye of diameter $50 \mu\text{m}$. However, for such a small eye the size of the receptors must be considered. If we want to have the same total absorption within the photoreceptors of the hypothetical fly eye, we need receptors of a length equivalent to those in the real *Musca* compound eye that is of $200 \mu\text{m}$. As seen in Fig. 9, it is now the size of the receptors, which determines the actual diameter of the equivalent lens eye, and this yields a total diameter of some $500 \mu\text{m}$. However, the lens eye shown in Fig. 9 would be considerably less efficient than the real compound eye of the fly. High resolution combined with high light gathering power could be reached only in a small foveal area since aberrations of the lens in extra foveal regions would probably become serious. Furthermore, the actual light gathering power in the *Musca* compound eye is, due to a special arrangement of receptors in the ommatidia, higher by a factor

Fig. 9. Comparison of a lens and compound eye, both equivalent in angular resolution to that of a fly's compound eye. Lens eye vitreousbody and ommatidial dioptric-system (clear) are drawn at the left- and right-hand side of the receptors (stippled) of 200 μm length respectively. Lens and facets have the same diameter of 24 μm in order to give the same optical resolution as in the fly's eye. It can be seen that the size of the compound eye is somewhat bigger than the lens eye, in both cases the size is basically determined by the receptors, however. The compound eye has the advantage that angular resolution and light-gathering power do not decrease with increasing angular distance of the "fovea" of the eye, as it is usually the case in lens eyes due to aberrations of the lens



of 7 compared to the light gathering power defined by the area of the single facet (Kirschfeld, 1967). This means that the estimate of a diameter D of some 500 μ for the equivalent lens eye is too low. And even such there is no considerable difference in size.

2.9.8 Temporal Scanning

In contrast to the poor absolute resolution of compound eyes some insects, especially flies, have a rather high temporal resolution (Autrum, 1948). The frequency-response curve of their photoreceptors falls down to 10% of the maximal value at 150 cps (Zettler, 1969). Intracellular photoreceptor recordings of warmblooded animals are not available for comparison. Flicker-threshold response-curves determined psychophysically in man in bright-adaptation show a decay of sensitivity to 10% of the maximum at 65 cps (Kelly, 1961). This indicates that fly-eyes are by a factor of 2 to 3 faster than the human visual system. One might ask if this higher temporal resolution can be used to increase angular resolution by means of temporal scanning.

In the human, temporal scanning in principle is not expected to increase angular resolution. The fitting between optical and anatomical resolution according to the sampling theorem (9.6, this chapter) ensures that all the information passing the dioptrics in principle might be transmitted by the foveal receptors already in stationary conditions. This is in accordance with the finding that angular resolution determined under stabilized image conditions is the same as that determined in nonstabilized conditions (e.g. Westheimer, 1972b). It explains also why the f -number of approximately 10 in the human for optimal resolution just fits the minimal f -number as calculated above.

As we have seen there is some mismatch between optical and anatomical resolution in the fly. Even if not considerable this leaves the possibility of improvement of angular resolution by temporal scanning. Resolution then depends not only on the number of points that are scanned simultaneously by the eye, but also upon the sequence of signals that are elicited in the receptors if eye and surround are shifted relative to each other. The facets of diameter $24 \mu\text{m}$ in the fly's eye yield a $\Delta\phi_s$ (Eq. (6), $\lambda = 0.37 \mu\text{m}$) of 0.5° . This is by a factor of 4 better than the actually measured divergence angle $\Delta\phi$ between receptors which is approximately 2° . Temporal scanning, therefore, in principle can improve the angular resolution up to 0.5° . The high temporal resolution of the receptors could help the animal to carry out a short time scanning process.

In general, angular resolution may be improved by temporal scanning up to the limit set by the aperture size of the dioptric system. The ratio between optical resolution $1/\Delta r$ in man and fly is, therefore, given according to Eq. (2a) by $A_{\text{man}} = 2.4 \text{ mm} / A_{\text{fly}} = 24 \mu\text{m} = 100$ and cannot be reduced by high temporal resolution combined with special neural mechanisms in the fly.

2.9.9 Discussion

The above considerations show that lens eyes are apparently the better solution for large animals. These animals need high absolute angular resolution and in this case lens eyes need considerably less space than compound eyes. However, in small animals with poor absolute (but still adequate subjective) resolution the space needed for lens and compound eyes becomes comparable, especially if the eyes are so small that the size of the receptors and not that of the dioptric systems become a limiting factor. This explains why lens and compound eyes fit the relation between bodysize and resolution (Fig. 1) to the same degree, since compound eyes are realized only in small animals.

For small animals, compound eyes seem to be rather advantageous as far as size of visual field and distribution of angular resolution over the visual field are concerned. A single lens for the whole visual field gives high resolution only in a foveal region, since for practical lenses increasing angular distance from the fovea is usually accompanied by greater aberrations. Also it might well be that small animals with a poor absolute resolution could not tolerate a resolution still considerably worse at angles off the "fovea": this might bring predators out of the range of visibility, for example.

What the brain does with the information available from the receptors depends upon the logic of its wiring diagram. If we compare the numbers of neurons in those parts of the brain which seem to be directly related to vision we find 5×10^5 in the fly (neurons of the retina and the three optic ganglia; Campos-Ortega, pers. comm.) and 7×10^8 in man (retina, geniculate body and cortical areas 17 to 19; Blinkov and Glezer, 1968). This difference of a factor of approximately 10^3 is, indeed, considerable. If we relate the absolute numbers of neurons to the number of points resolved by the eyes (4×10^5 in man; Steinbuch, 1965, and 6×10^3 in the fly; Braitenberg, 1967) we arrive at 2×10^3 neurons per point discriminated in man and at 100 neurons per omnium in the fly. There is still an obvious difference of a factor of 20. But this difference is not so high as to lead us to expect from the outset different ways of processing of visual information in vertebrates and in insects.

Exner's (1891) statement that lens eyes seem to be more useful for pattern recognition whereas compound eyes are specialized for movement perception is no longer supported by the knowledge we have today of the optical properties of the two types of eyes. The image projected by a lens eye at the receptor level is not so different from that in a compound eye, as far as resolution is concerned, to support such a conclusion. And the belief that compound eyes have a poor absolute sensitivity as mentioned in the introduction, is also not justified (Rodieck, 1973; Kirschfeld, 1974).

Without any doubt there are differences between lens and compound eyes. Discrimination of E-Vector orientations of linearly polarized light seems to be a domain of animals with compound eyes. But what the differences are cannot be derived in general terms from the optical performance of the eyes or from the gross anatomy. And with increasing understanding of how visual systems work, it might transpire that the differences between the visual systems of animals with lens and compound eyes are smaller than was initially believed.

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2.9.10 References

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