The Absolute Sensitivity of Lens and Compound Eyes

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Lens Eyes, Compound Eyes, Absolute Sensitivity

The numbers of light quanta available to photoreceptors of lens- and different types of compound eyes are calculated on the basis of photometric considerations. It is shown that the results depend upon the situation in the optical environment: For point-like lightsources such as stars receptors in compound eyes generally receive considerably less numbers of light quanta compared *e. g.* with the human eye. This is due to the small sizes of the ommatidial facets. For extended optical surroundings, however, the numbers of quanta reaching the receptors in typical insect compound eyes of the apposition type are comparable to those in the human eye. In this respect the optical superposition eye of nocturnal insects like *Ephestia* is an exceptional case, where there is an improvement in the numbers of quanta reaching the receptors by a factor 100 to 1000 compared to the eyes of bee or man.

The absolute size of the diameter of facets in compound eyes in general is small compared to the diameter of the pupil in lens eyes. That is, the diameter of the facet of a fly's or bee's ommatidium is approximately 0.025 mm; the diameter of the pupil of the dark adapted human eye, however, can be as large as 7 mm, which makes its area larger by a factor of approximately 10^5 times. Due to this fact, it is generally accepted that the number of light quanta available to the photoreceptors in insects is small compared to that available to animals with lens eyes [1–3]: Animals with compound eyes are assumed to have a rather poor absolute sensitivity.

This in fact is true if one considers the situation of animals looking at distant, point-like objects like stars. In a diffraction-limited lens system, the number of light quanta q, incident at the lens surface, will be distributed over the Airy pattern in the focal plane. The diameter D of the disc of the Airy distribution is

$$D \propto f/A\,, \tag{1}$$

which means that eyes of the same "f-number" A/f, given by the ratio of the pupil diameter and the focal length, produce Airy discs of the same size (Fig. 1). The number of light quanta per unit time q, distributed over the Airy pattern, will increase in such conditions with the square of the pupil size:

$$q \propto A^2\,. \tag{2}$$

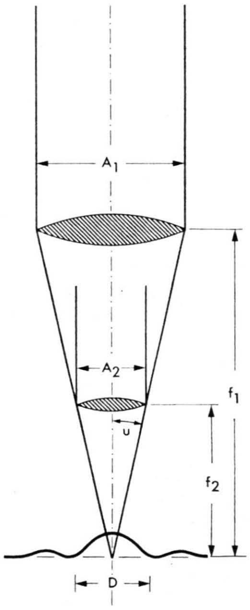

Fig. 1. The absolut diameter D of Airy's disc in the focal plane of a converging lens depends upon the ratio of pupil diameter A and the focal length f, irrespective of the absolute size of A.

This means in fact that an insect eye with small facets is in principle a poor device for the detection of point-like objects like stars, even if its dioptric system has an f-number similar to that of a lens eye. This argument, as those derived below, is based on purely photometric considerations. Factors such as light losses in the dioptric media, different photopigment concentrations in outer segments or rhabdomeres, possible existence of a tapetum and so on are not taken into account.

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In natural conditions, animals normally do not look at stars but at extended optical surroundings in which every point emits or reflects light quanta. For a distant optical environment the mean number of quanta, dq, available per unit time and per area dF in the focal plane of a lens will be *

$$\mathrm{d}q \propto \mathrm{d}F \sin^2 u \approx \mathrm{d}F \sin^2 \frac{A}{2f} \approx \mathrm{d}F \frac{A^2}{4f^2}, \quad (3)$$

where u is the maximum possible value of the angle between the optical axis and a ray originating at the image point and passing through the lens, as shown in Fig. 1 (see *e.g.* Levi[4]). If the luminance is homogenous within the acceptance angle of a receptor with diameter δ, one arrives at

$$q_{\mathrm{r}} \propto \delta^2 \sin^2 u \approx \frac{A^2}{4f^2} \delta^2. \quad (4)$$

This equation shows that the number q_{r} of quanta available per receptor per unit time depends not on the pupil size A but on the f-number A/f, or more precisely, on the angle u. As a consequence, a receptor with diameter δ will receive the same number of quanta when located within a vertebrate retina or an insect retinula, provided that the f-number is the same in both cases. The physical interpretation of this result is that the reduction in the number of quanta due to the small lens diameter in the insect ommatidium is compensated for by an increased area in the optical surround from which the receptor collects light.

There have been several types of compound eyes developed in evolution, their performance with respect to the two situations as discussed above will be compared.

Within the classical apposition eye[5], light entering the cornea facet will be absorbed by photopigment of visual cells primarily within the same ommatidium (Fig. 2 a). The dioptric system acts as a converging lens which projects a reversed image in its focal plane where the photopigment containing parts of the receptors, the rhaddomeres, are located with their distal endings. Light concentrated by the dioptrics onto the distal endings of either individual or of several fused rhabdomeres travels down these structures, which act as light guides, due to their relatively high refractive index. Thus, light will be partially absorbed by the photopigment. This type of compound eye is realized for instance in the compound eye of the bee.

Some data of human and insect eyes are collected in the Table. The ratio of the pupil areas in man and bee is approximately 10^5, which makes the human eye according to Eqn (2) a better device for the detection of stars. To ratio of 10^5 is so large that it seems hard to imagine that bees are able to detect stars at all. For one knows that humans are, in optimal conditions, able to detect stars down to the sixth magnitude class. The brightest "star" (with exception of the moon and the sun), Venus, is only a factor of 10^4 brighter than stars of the sixth class. Therefore even Venus should be below the threshold of visibility of a bee, assuming a similar absolute sensitivity of the receptors in man and bee.

If one compares however the situation for an extended optical surround, one easily finds that the rhabdome of a bee receives approximately the same number of quanta as will be accepted by a human receptor, since q_{r}, which is proportional to the product of $\delta^2 \cdot \sin^2 u$ is approximately the same for both species.

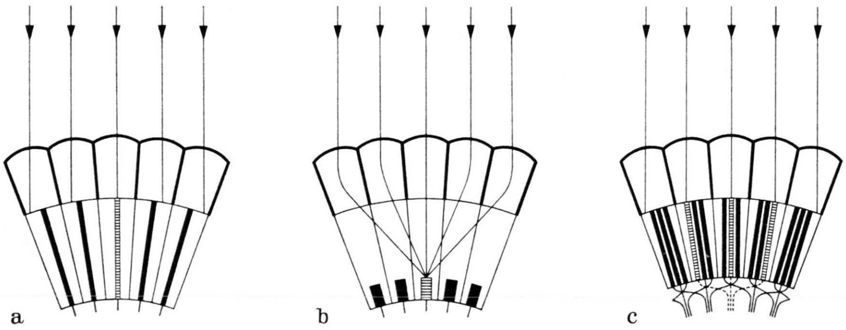

Fig. 2. Three different types of compound eyes, schematically. a: Classical apposition eye, b: Optical superposition eye, c: Neural superposition eye[8].

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* It is assumed that the optical environment has a Lambertian radiation pattern, that lenses are aplanatic and that image media have the same refractive index.

Table. Data of human and insect eyes.

		Man	Bee	Fly *(Musca)*	Moth *(Ephestia)*	
Pupil diameter A (Effective pupil diameter $\bar{A}$)	[mm]	7×10^0 (a)	2.5×10^{-2} (c)	2.5×10^{-2} (e)	2.0×10^{-2} (g)	(2.3×10^{-1})
Focal length f (Effective focal length $\bar{f}$)	[mm]	2.3×10^1 (a)	6.0×10^{-2} (c)	5.0×10^{-2} (e)	2.4×10^{-2}	(7.6×10^{-2})
Receptor diameter δ (Equivalent receptor diameter δ^*)	[μm]	$1-2 \times 10^0$ (b)	$1-2 \times 10^0$ (d)	$1-2 \times 10^0$ (f)	(1.5×10^0)	8×10^0 (h)
A^2 ($\bar{A}^2$)	[mm^2]	4.9×10^1	6.2×10^{-4}	6.2×10^{-4}	4×10^{-4}	(5.3×10^{-2})
$\tan u = A/2f$ ($\tan \bar{u} = \bar{A}/2f^2$)		1.5×10^{-1}	2.1×10^{-1}	2.5×10^{-1}	4.2×10^{-1}	(1.5×10^0)
u ($\bar{u}$)	[deg]	8.7×10^0	1.2×10^1	1.4×10^1	2.3×10^1	(5.7×10^1)
$\sin u$ ($\sin \bar{u}$)		1.5×10^{-1}	2.0×10^{-1}	2.4×10^{-1}	3.8×10^{-1}	(8.3×10^{-1})
$\sin^2 u$ ($\sin^2 \bar{u}$)		2.3×10^{-2}	4.2×10^{-2}	5.9×10^{-2}	1.5×10^{-1}	(7.0×10^{-1})
$\delta^2 \sin^2 u, \bar{u}$ ($\delta^* \sin^2 u$)		$2.3-9.1 \times 10^{-2}$	$4.2-17 \times 10^{-2}$	$5.9-24 \times 10^{-2}$	(3.3×10^{-1})	4.5×10^1

References. a: 11; b: 12; c: Kirschfeld, unpublished; d: 13; e: 14; f: 15; g: 10; h: 16.

A second type of compound eye (optical superposition eye) is characterized by the fact that parallel light, entering several facets, is directed to one and the same rhabdome (Fig. 2 b). Accordingly, the dioptric system must be more complicated, projecting an erect image in the plane of the rhabdomes [5–7].

For a point-like object the number of quanta q_r available to the receptors might be estimated on the basis of a schematic diagram as presented in Fig. 3, which defines an "effective" aperture $\bar{A}$ and an "effective" focal length $\bar{f}$ of the optical superposition eye of a moth, *Ephestia*. By means of Eqn (2) one arrives at

$$q \propto \bar{A}^2. \tag{5}$$

where $\bar{A}^2$ is approximately equal to $N A^2$, and N is the number of facets that contribute to the illumination of one rhabdome. This means that for a point-like object, the number of quanta available to the photoreceptors is increased by approximately a factor of N compared with an apposition eye, the facets of which have a diameter A. Since N in the optical superposition eye of the moth is approximately 100 (Kunze [6]), one finds this type of eye improved by a factor of 100. This number holds, of course, as long as one assumes that all facets involved in the illumination of one rhabdome give the same contribution, which in reality might be somewhat overestimated. But even if one assumes the factor 100, the *Ephestia* eye is still worse by a factor of 10^3 compared with a human eye. It might be just able to make the brightest "stars" visible to a moth.

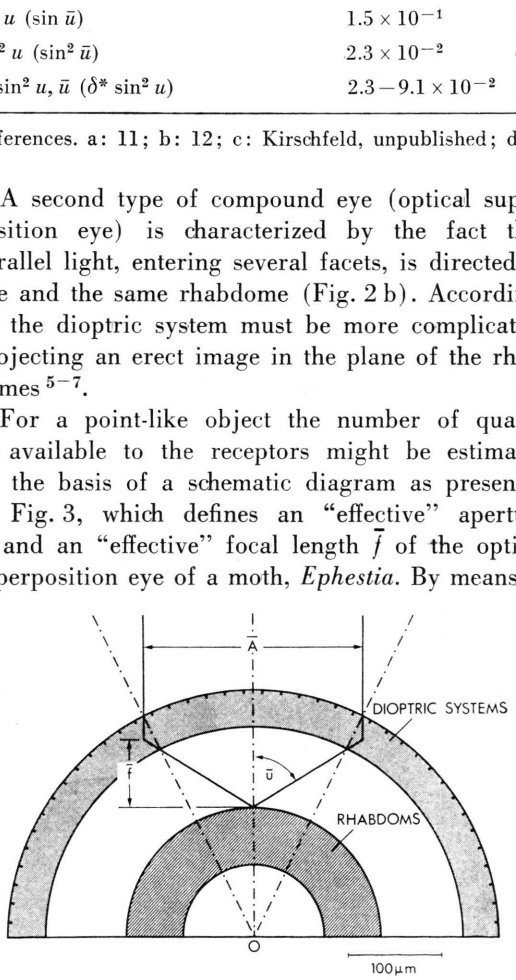

Fig. 3. Schematic diagram of the optical superposition eye of the moth *Ephestia*. Anatomical dimensions according to Umbach [10]. The "effective" aperture $\bar{A}$, the "effective" focal length $\bar{f}$ and the aperture angle $\bar{u}$ have been constructed according to the observations of Kunze [6] that the glow in the *Ephestia* eye has a diameter of approximately 13 facets.

If one calculates the number of quanta dq per area dF we find according to Eqn (3)

$$dq \propto dF \sin^2 \bar{u}, \tag{6}$$

where $\bar{u}$ is the "effective" aperture angle as defined in Fig. 3.

The size of the aperture angle of a moth eye calculated with $\bar{A}$ and $\bar{f}$ according to Fig. 3 is exceptionally high and bigger by a factor of approximately 5 than in the eyes of man or bee. This increases the number of quanta per area in the plane of the receptors by a factor of approximately 25. But in the moth, the diameter δ of the rhabdome is 8 μm[16] and therefore is bigger by a factor of 4 to 8 than in the apposition eye of the bee. The total gain is therefore 16 to 64 times 25 or 400 to 1600. This means that the advanlage of the optical superposition eye compared with a bee's eye is more prominent for *extended* optical surrounds, where the gain factor becomes approximately 1000.

It can be shown (Fig. 4) that the increased diameter of the rhabdome in the moth eye is not detrimental to the contrast transfer of this eye: The acceptance angle $\Delta\varrho$ is the same for a thin rhabdome of diameter δ^*, located in the focal plane of L_1, and for the big rhabdome (diameter $\delta = (b/q)\delta^*$), located in the "effective" focal plane.

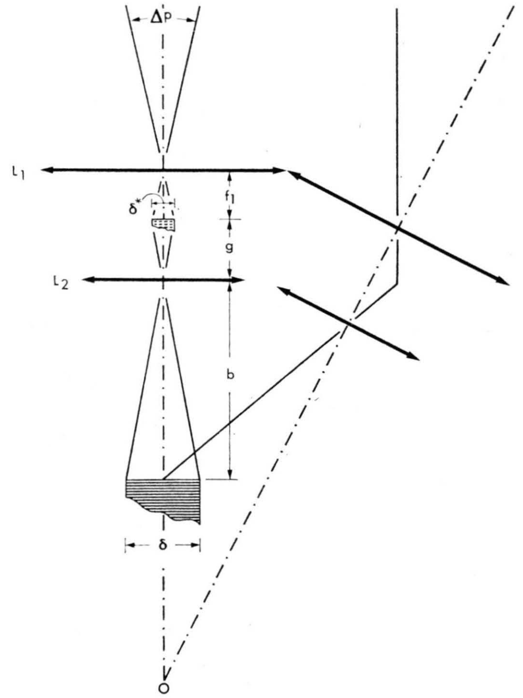

Fig. 4. Beam path in the dioptric systems of an optical superposition eye, schematic, not to scale. If a rhabdome was located in the focal plane of a lens L_1, it would accept light from an angle $\Delta\varrho$; a rhabdome located in the image plane of the lens L_2 will cover the same angle $\Delta\varrho$, if its diameter is increased by a factor b/g (g and b: object and image distances as defined in the figure). The argument is based on geometric-optical considerations; diffraction is not taken into account.

Comparing the moth eye with the human eye, the numbers in the Table show that for point-like objects the number q of quanta per receptor is smaller by a factor of 1000 than in the human eye (ratio of $A^2/\bar{A}^2$); for an extended optical surround, however, this number is *bigger* by more than a factor of 100. Only for an extended optical environment does the moth eye become more sensitive than a human eye, as far as photometric arguments are considered.

Finally the performance of a third type of compound eye that has been analyzed in some detail will be mentioned, the so-called "neural" superposition eye. This eye is characterized by the fact that the rhabdomeres of the receptors in individual ommatidia are not fused together as *e. g.* in the bees eye, but that they are isolated from each other. This has as a consequence that the optical axes of the receptors within each ommatidium diverge, and also that the optical axes of 7 receptors within 7 different ommatidia (in special eye regions: Optical axes of 9 receptors of 9 ommatidia) are parallel to each other[8, 9] (Fig. 2 c). The numbers of light quanta, available to the rhabdomeres, as determined by Eqns (2) and (4) will be the same as the number of quanta available to a rhabdome in the classical apposition eye with a fused rhabdome. Since 7 rhabdomeres of 7 different ommatidia (in special eye regions up to 9 rhabdomeres of 9 different ommatidia) always collect light quanta from one and the same area of the environment, the number of light quanta from this area, available to the visual system, will be increased by a factor of 7 (or 9 respectively) in this type of compound eye. This factor holds for both cases, point-like objects as well as extended optical surroundings.

The considerations as shown above demonstrate that the rhabdomes in the apposition eye and the rhabdomeres in the neural superposition eye will receive in a "natural" environment, numbers of light quanta per unit time of the same order of magnitude as the receptors in the human eye. In the optical superposition eye, the receptors are expected to receive numbers of light quanta per unit time that are higher by a factor of at least 100 than in the human eye, as far as photometric arguments are considered.

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