Invertebrate superposition eyes-structures that behave like metamaterial with negative refractive index

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The superposition eyes of moths and lobsters are described with the geometrical optics for a refractive surface between two media, where the refractive index of the image space is negative. Consequently, the eye power and the object focal length are negative, whereas the image focal length is positive. The F-number is also negative, but the sign is irrelevant for calculations of the light sensitivity, because that depends on F^2. [DOI: 10.2971/jeos.2006.06010]

1 Introduction

Exner [1, 2] distinguished two ways of imaging by compound eyes, apposition and superposition. Apposition eyes are utilised by most diurnal insects (bees, butterflies, dragonflies) and crustaceans (crabs) [3]-[6]. Superposition eyes are common among nocturnal insects (moths, beetles) and crustaceans (krill, lobsters), although several examples of diurnal insects (neuropterans, skippers, diurnal moths) with superposition eyes are known [3, 7, 8]. Compound eyes consist of ommatidia, which are more or less arranged in a hemisphere. Generally, an ommatidium's facet lens forms, together with the associated crystalline cone, the imaging optics that projects incident light onto the photoreceptors. The light-sensitive organelles of the photoreceptors, the rhabdomeres, which contain the visual pigment and the phototransduction apparatus, constitute the rhabdom. Depending on the quality of the imaging optics as well as the size and location of the rhabdom, the photoreceptors of a compound eye receive incident light from a narrow spatial field [5, 6]. In most apposition eyes, the rhabdomeres of an ommatidium are fused, so that the rhabdom acts as a single optical waveguide, which receives light via one single facet lens and crystalline cone. The rhabdom is then contiguous with the proximal tip of the cone. In superposition eyes, a rhabdom receives light via numerous facet lenses and crystalline cones, the number of which depending on the species. The number also depends on the state of light/dark adaptation, as the light flux is commonly regulated by movable sheets of screening pigments, which block the light traversing the so-called clear zone in between the crystalline cones and the rhabdom layer. The large number of facet lenses contributing to a superposition image creates an aperture that is much wider than that of a single facet lens, and this endows superposition eyes with a principal advantage over the apposition eyes: their enhanced light sensitivity allows vision at low light levels [4, 9]. The differences in imaging methods between apposition and superposition eyes are reflected in the different constructions of the optical elements. The material of facet lens and crystalline cone of both

eye classes is usually non-uniform, but especially in the so-called refracting superposition eyes, of many crustaceans, beetles, and moths, a major refractive index gradient perpendicular to the axis exists in the cones. This causes a severe redirection of obliquely incident light, similarly as occurs in an astronomical (or Kepler) telescope [1]-[10], shown in Figure 1.
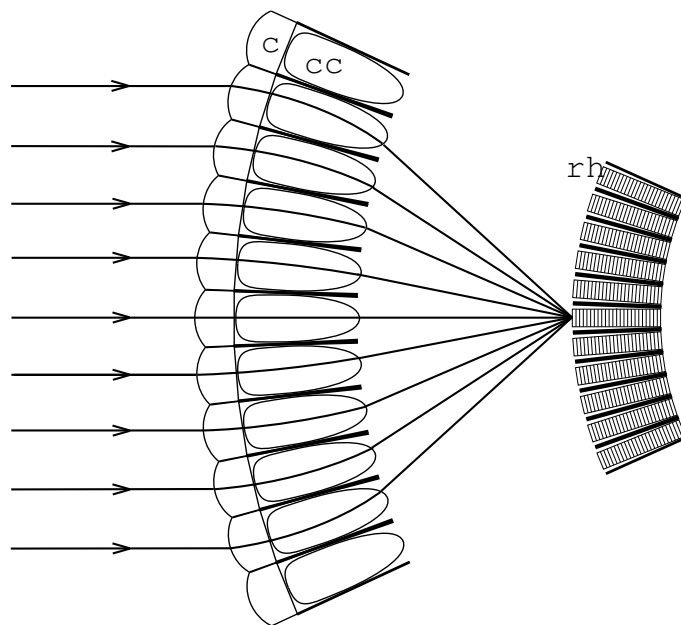

FIG. 1 Diagram of an ideal refracting superposition eye. A parallel light beam enters the eye via several facet lenses and is focused on a single rhabdom owing to the gradient refractive index in the crystalline cones. c: corneal facet lens; cc: crystalline cone; rh: rhabdom.

In the second type of superposition eye, the reflecting superposition eyes of decapods, the cones only have a shallow, longitudinally changing refractive index, but here the reflecting walls of the square-cylindrical cones cause the redirection of obliquely incident light [3, 6, 11]. In the third type,

the parabolic superposition eye of some crabs, a lens is combined with a parabolic mirror [4]. Compound eyes have inspired technical applications. Artificial apposition eyes mimicking bee eyes were recently made by Lee and Szema [12]. The discovery of the optical principles of the reflecting superposition eye stimulated the development of sensitive x-ray telescopes, for instance using square-channel microchannel plates, nicknamed lobster eye telescopes [13]. Chapman and Rode [14] presented a geometrical optics treatise of spherically curved, reflective arrays for x-ray applications, elaborating on the optical aberrations of these systems. They noticed that the curved medium has a refractive index of −1. The aim of the present paper is to present a more general - and more simple- geometrical optics description of superposition eyes, so to clarify the special properties of the principal points and focal distances of superposition eyes, which has so far been under-illuminated in the literature on superposition eyes. This study complements a wave-optical analysis, where it was shown that partial coherence plays an important role in superposition eye imaging [15].

2 IMAGING BY A SPHERICAL SURFACE

The refracting superposition eye, diagrammatically shown in Figure 1, can be considered as a special case of imaging by a spherical surface between two media with different refractive indices. Two classical cases of elementary geometrical optics theory are a convex and a concave spherical surface, which form the boundary between object and image space with refractive indices n and n' (Figures 2a,b).

N' are the nodal points, and n and n' are the refractive indices. The principal points coincide with the vertex of the surface. f=FH=N'F' and f'=FH=H'F' are the object and image focal lengths. α is the angle of incidence of a light ray, and β is the angle of refraction, or the exit angle. **a** A convex surface, like that of the cornea of the human eye, with radius R>0, that separates media with refractive indices 0<n<n'. The focal lengths are positive: f>0 and f'>0. **b** A concave surface, with radius R<0, separating media with 0<n<n'. The focal lengths are negative: f<0 and f'<0. **c** A convex surface, like that of a superposition eye, with radius R>0, between media with n>0 and n'<0. The object focal length is negative, f<0, and the image focal length is positive, f'>0. The angles of incidence and refraction have here opposite signs, in contrast with cases **a** and **b**, where they have the same sign. **d** A superposition eye where the tip of a rhabdom is positioned in the image focal point F' (see case **c**). The geometrical acceptance angle of the rhabdom, $\Delta\rho_r$, is determined by the rhabdom diameter. With nodal points coinciding with the eye's centre of curvature, $\Delta\rho_r$ is smaller than $\Delta\phi$, the interommatidial angle. The figures are drawn with n=1 in **a**-**c**, n'=1.5 in **a** and **b**, and n'=-1.5 in **c**.

Both object and image space of an axial geometrical optics system are characterised by three cardinal points: the focal points F and F', the principal points H and H', and the nodal points N and N' [16]-[18]. The optical system is characterised by its power, $P = n/f = n'/f'$, where f and f' are the focal lengths of object and image space, with f=FH= N'F' and f'=FN=H'F'. For a spherical refracting surface between two media, object and image principal points coincide with the surface vertex, and object and image nodal points coincide with the centre of curvature of the surface (Figure 2).

The power of a spherical, refracting surface, with radius of curvature R, between two media with refractive indices n and n' is $P = (n' - n)/R$. In a normal optical system, the refractive indices n and $n' \geq 1$, and thus for a convex spherical surface ($R > 0$) between two media with $n < n'$, it follows that $P = (n' - n)/R > 0$, and then both object and image focal lengths are positive, $f > 0$ and $f' > 0$ (Figure 2a). For a concave surface ($R < 0$) with $n < n'$, the power $P < 0$, and then both $f < 0$ and $f' < 0$ (Figure 2b).

3 ANGULAR MAGNIFICATION AND NEGATIVE REFRACTIVE INDEX OF SUPERPOSITION EYES

The dioptrics of a single ommatidium of a refractive superposition eye acts as an astronomical telescope [1, 2]. This instrument consists of two confocal lenses, with positive focal lengths f_1 and f_2. An incident parallel beam leaves it also as a parallel beam, but a positive angle of incidence α results in a negative exit angle β (Figure 2c), which are related to each other by tan β/tan α=-m, where $m = f_2/f_1 > 0$ [19]. In the paraxial, small-angle approximation this becomes β/α=-m, or, the angular magnification is negative. The paraxial form of Snell's law for a boundary between two media with refractive indices n and n' is β/α=n/n' (Figures 2a,b), and thus the assembly of corneal facet lenses and attached cones of a refracting superposition eye can be conceived as a convex, spherical surface separating two media with refractive indices n and n', the ratio of which equals n/n'=-m. In other words, whereas the refractive index of the object medium of superpo-
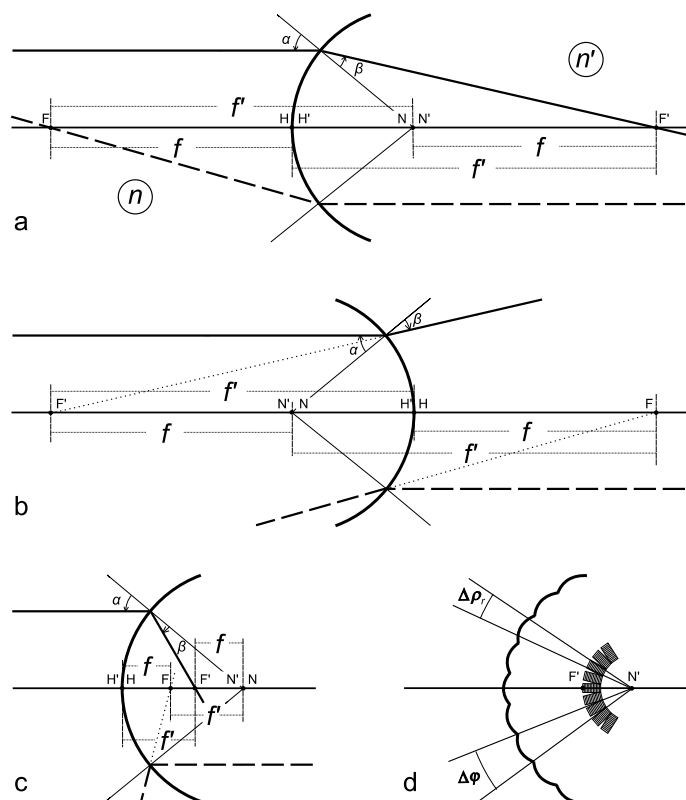
FIG. 2 Geometrical optics of a spherical surface between two media. F and F' are the focal points of object and image space, H and H' are the principal points, and N and

sition eyes is positive ($n > 0$), the refractive index of the image medium is negative, $n' = -n/m < 0$. (For the reflecting superposition eye of lobsters, the refractive index value is –1 [14].) In his analysis of the refracting superposition eye of the firefly beetle, *Lampyris*, Exner [1, 2] already noticed the similarity of the expression for the angular magnification $\beta/\alpha=m$ with the paraxial form of Snell's law, $\beta/\alpha=n/n'$, but he neglected the negative sign.

The implicit assumption of the geometrical optics treatment given above is that all parallel incident light rays converge on the image focal point. A spherical refractive surface of a medium with a constant refractive index, or, a constant angular magnification, suffers from spherical aberration, however. To let all rays hit one and the same focal point at a distance r from the eye's centre of curvature (Figure 3), the angular magnification must slightly vary with the angle of incidence α, according to $m(\alpha)=(1/\alpha)\arctan[2\alpha/(\alpha^2+2w/r)]$, with w the clear zone width [15].
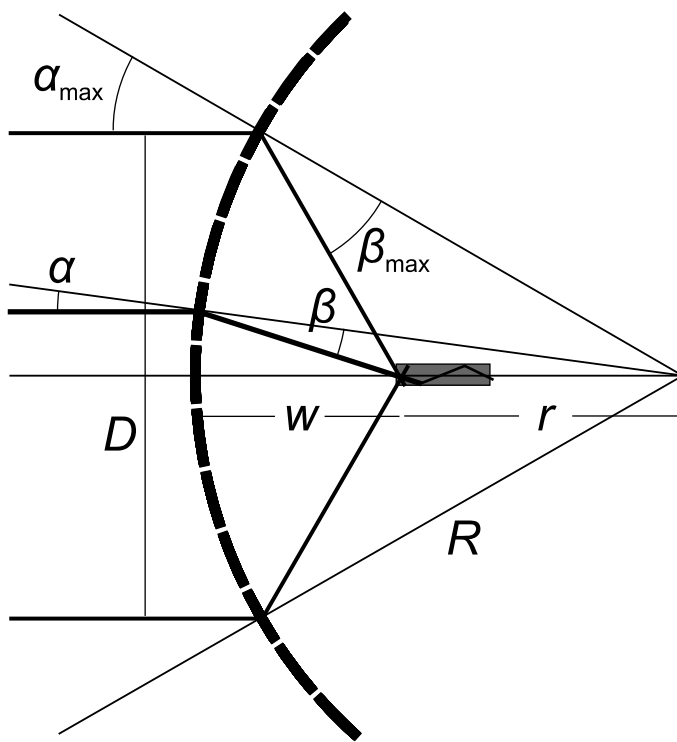

FIG. 3 Diagram of an ideal superposition eye, where a parallel incident beam is focused at the light receiving rhabdom. R is the radius of curvature of the eye. w is the width of the clear zone, and $r=$-f is the distance between the image focal plane of the superposition eye and the centre of curvature of the eye. α is the angle of incidence, and β is the exit angle. α_{max} is the maximum angle of incidence of a light ray that contributes to the superposition image, and β_{max} is the corresponding maximum exit angle. $D = 2R\sin\alpha_{max}$ is the diameter of the superposition aperture.

Experimental data show that for superposition eyes w/r is between about 0.5 and 1, and then the expression for the angular magnification appears to be well approximated by $m(\alpha) = 1/(w/r + \alpha^2)$.

McIntyre and Caveney [19] measured for the superposition eyes of three dung beetle species the distance of the surface of the rhabdom layer to the centre of curvature of the eye (r, Figure 3) and stated this to be approximately equal to the posi-

tive focal distance f, erroneously neglecting the negative sign. Furthermore they measured the clear zone width, w, and calculated the angular magnification for a number of angles of incidence by ray tracing [19]. The calculated angular magnifications appear to deviate somewhat from the angular magnifications calculated with the above formula, using the measured w and r values (see also [19]). Consequently, the focus will be imperfect. A distributed focus will result in a broadened visual field of the photoreceptors, and thus cause a sub-optimal spatial resolution of the eye. Imperfect imaging is apparently acceptable for the dung beetles, which are active at low light levels.

4 OBJECT FOCAL LENGTH AND F-NUMBER

For a superposition eye with n and $R > 0$, and $n' < 0$, the power $P = (n' - n)/R < 0$. Consequently, it follows from $P = n/f = n'/f'$ that $f < 0$ and $f' > 0$, that is, whereas the image focal length is positive, the object focal length is negative (Figure 2c). The consequence of superposition eye media behaving as metamaterial with a negative refractive index is that the object focal length of a superposition eye has a negative value. This has so far been overlooked. For instance, Land et al. [20] rightly emphasised that the object focal length of the superposition eye is the distance out from the eye centre to the image plane, but they nevertheless took f to be positive, see also [6, 19]. Furthermore, Land and Nilsson [6] state that classical superposition eyes have a single nodal point located at the eye's centre of curvature, which is only correct when it is read to mean that there is a single point where the two nodal points coincide, see also [21].

The focal length is an important parameter determining the acceptance angle of visual photoreceptors. The acceptance angle, $\Delta\rho$, is for apposition eyes approximately equal to $\Delta\rho_r = D_r/f$, where D_r is the diameter of the receptor when its light receiving end coincides with the focal plane of the facet lens [18]. A similar expression holds for superposition eyes, but here f has to be replaced by $-f$ (see Figure 2d). The spatial resolution of superposition eyes is given by the interreceptor angle, which in general corresponds to the interommatidial angle $\Delta\phi = D_l/R$, where D_l is the facet lens diameter and R the eye radius (Figure 2d, [3]-[7]). The extraordinary hummingbird hawkmoth has a refracting superposition eye with locally more rhabdoms than facets, however, and thus spatial sampling occurs at angles smaller than $\Delta\phi$ [21].

The focal length features also prominently in expressions for the brightness of optical systems, or in the light sensitivity of eyes, because the light flux density is proportional to $(D/f)^2$, where D is the diameter of the eye's entrance pupil (Figure 3). D/f is called the relative aperture and its inverse, $F = f/D$, is the F-number, a value frequently used in the visual literature. Imaging systems have usually a positive focal length, yielding a positive F-number, and presumably positive F-numbers have therefore been calculated for superposition eyes. However, the F-number values $F = 1.2, 0.8$, and 0.6 determined for the dung beetles *O. westermanni*, *O. alexis* and *O. aygulus* [19] have to be $F = -1.2, -0.8$, and -0.6. The F-number of superpo-

sition eyes is extraordinarily small (that is, its absolute value), which causes the high sensitivity of these eyes. The sensitivity increases when the distance of the rhabdom surface layer to the centre of curvature of the eye, r, decreases (Figure 3 , [8]). This means an increase of the aperture size D (Figure 3), because experiments show that the maximal exit angle of refractive superposition eyes, β_{max} (Figure 3), is approximately constant (25-30°, [19]). However, a decrease in r means an increase in the clear zone width, w, which means an increase in idle image space, and an animal will only pay this prize when sensitivity is at a premium. Therefore, only nocturnal animals will employ superposition eyes with a small F-number, whilst diurnal animals will increase the (absolute values of the) F-number so to minimise the clear zone width, as is the case in day-active moths [22].

ACKNOLEDGMENTS

References

[1] S. Exner, *Die Physiologie der facittirten Augen von Krebsen und Insecten* (Deuticke, Leipzig, 1891).

[2] [2S. Exner, *The physiology of the compound eyes of insects and crustaceans (translated by R.C. Hardie)* (Springer, Berlin Heidelberg, 1989).

[3] M.F. Land, "Optics and vision in invertebrates", *Handb. Sens. Physiol. Vol. VII/6B*, pp. 472-592, (Springer, Berlin Heidelberg New York, 1981).

[4] D. E. Nilsson, *Facets of vision* D.G. Stavenga and R.C. Hardie, eds., pp. 30-73, (Springer, Berlin Heidelberg New York, 1989).

[5] E.J. Warrant and P.D. McIntyre, "Arthropod eye design and the physical limits to spatial resolving power" Prog. Neurobiol. **40**, 413-461 (1993).

[6] M.F. Land and D.-E. Nilsson, *Animal eyes* (Oxford University Press, Oxford, 2002).

[7] P. Kunze, "Apposition and superposition eyes", *Handb. Sens. Physiol. Vol. VII/6A*, pp. 442-502, (Springer, Berlin Heidelberg New York, 1979).

[8] V.B. Meyer-Rochow and J. Gal, "Dimensional limits for arthropod eyes with superposition optics" Vision Res. **44**, 2213-2223 (2004).

[9] E.J. Warrant and P.D. McIntyre, "Limitations to resolution in superposition eyes" J. Comp. Physiol. A **167**, 785-803 (1990).

[10] P. Cleary, G. Deichsel, and P. Kunze, "The superposition image in the eye of *Ephestia kühniella*" J. Comp. Physiol. **119**, 73-84 (1977).

[11] K. Vogt, "Zur Optik des Flusskrebsauges" Z. Naturforsch. C **30**, 691 (1975).

[12] L.P. Lee and R. Szema, "Inspirations from biological optics for advanced photonic systems" Science **310**, 1148-1150 (2005).

[13] J.R.P. Angel, "Lobster eyes as X-ray telescopes" Astrophys. J. **233**, 364-373 (1979).

[14] H.N. Chapman and A.V. Rode, "Geometric optics of arrays of reflective surfaces" Appl. Opt. **33**, 2419-2436 (1994).

[15] D.G. Stavenga, "Partial coherence and other optical delicacies of lepidopteran superposition eyes" J. Exp. Biol. **209**, 1904-1913 (2006).

[16] M. Born and E. Wolf, *Principles of optics* (Pergamon Press, Oxford New York 1975).

[17] K.P. Bryceson and P. McIntyre, "Image quality and acceptance angle in a reflecting superposition eye" J. Comp. Physiol. **A 151**, 367-380 (1983).

[18] D.G. Stavenga, "Angular and spectral sensitivity of fly photoreceptors. II. Dependence on facet lens F-number and rhabdomere type in *Drosophila*" J. Comp. Physiol. A **189**, 189-202 (2003).

[19] P.D. McIntyre and S. Caveney, "Graded-index optics are matched to optical geometry in the superposition eyes of scarab beetles" Phil. Trans. R. Soc. Lond. B **311**, 237-269 (1985).

[20] M.F. Land, F.A. Burton, and V.B. Meyer-Rochow, "The optical geometry of euphausiid eyes" J. Comp. Physiol. A **130**, 49-62 (1979).

[21] E. Warrant, K. Bartsch, and C. Günther, "Physiological optics in the hummingbird hawkmoth: A compound eye without ommatidia" J. Exp. Biol. **202**, 497-511 (1999).

[22] M.F. Land, "The resolving power of diurnal superposition eyes measured with an ophthalmoscope" J. Comp. Physiol. A **154**, 515-533 (1984).