Compound eyes: old and new optical mechanisms

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Over the last twenty years classical views of how compound eyes work optically have undergone a series of overhauls. Exner’s central concept of an optically inhomogeneous lens cylinder has survived, and such devices are now made commercially. He was wrong, however, about some crustacean eyes. They produce images by a mirror mechanism that was not discovered until 1975, and which now shows promise as an optical system capable of development.

In 1891 Sigmund Exner produced a monograph on the optical mechanisms of insect and crustacean eyes that was a landmark not only in biology, but also in optical theory. The problem at that time was the image formation in many animals with compound eyes was not comprehensible in terms of conventional spherical surface refraction, as in a simple lens. This is particularly true of aquatic insects and crustaceans, where there is only a negligible refractive index difference between external and internal media so that ray-bending by a curved cornea is minimal, and also in those eyes whose corneal surfaces are flat anyway—some mantids, for example. Exner’s solution was ingenious and unconventional. He proposed that the optical elements of many compound eyes behaved as ‘lens cylinders’, that is, cylinders with a graded refractive index, densest along the axis and declining in an approximately parabolic manner towards the outside. Such structures have the property that a non-axial ray, striking the end of the cylinder normally, will be refracted continuously towards the axis (Fig. 1d, e). In fact, if the gradient is right, all parallel rays will be refracted to the same point on the axis, and parallel rays at an angle to the axis will be focused in the same plane, but slightly to one side. In other words, an inhomogeneous flat-ended cylinder would behave very much like an ordinary converging lens in its image-forming properties.

Inhomogeneous lenses were not an entirely revolutionary proposal, even in Exner’s day. Matthiessen1 had already proposed that the lenses of fish eyes had a variable refractive index, highest in the centre. He used this to explain why fish lenses had a much shorter focal length than a homogeneous lens with the same central refractive index (this would be about 4 radii, whereas real lenses have a focal length of about 2.55 radii, a figure that has come to be known as Matthiessen’s ratio). It also

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Fig. 1 Compound eye types and their optical components. a. Apposition eye; b, refraction superposition eye; c, reflecting superposition eye; d, apposition lens cylinder with focus at proximal tip; e, superposition (double length) lens cylinder; f, perspective and top view of ray path through a square cell in a reflecting superposition eye. a, d, e are based on Exner1; c is modified from Land2, f from Vogt3.
explained why fish lenses are free of spherical aberration, which would otherwise be severe. Speculation about the properties of optically inhomogeneous media goes back to Maxwell, who "stimulated apparently by the contemplation of his breakfast herring" (ref. 5), devised a fish-eye universe with the alarming property that all rays emitted from a particular point returned to it, after passing through a conjugate image4. Much of Exner's work was based on two animals which he chose for their differences and experimental convenience. They are the king crab (Xiphosura) *Limulus*, and the glowworm *Lampyris*.

**Limulus**

*Limulus* has a smooth cornea behind which is a series of ingrowths of the cuticle (Fig. 2a), each of which abuts onto a cluster of receptors. Exner found that there was an inverted image at the tip of each such ingrowth (Fig. 2c), and because of the smooth cornea concluded that this had to be produced by lens-cylinder focusing. In one particularly telling experiment he cut a parallel-sided slice through one of these structures, and showed that this still acted as a converging lens, though of longer focal length. Exner's lens-cylinder explanation of *Limulus* optics was challenged recently by Levi-Setti *et al.*7, who suggested that focusing might occur not by inhomogeneous refraction, but by reflection from the walls of each projection. They pointed out that the shape of the projections resembled that of an 'ideal collector', a reflecting device originally designed by Winston8 for the collection of faint radiation. However, such devices produce erect, not inverted images, and furthermore, the refractive index gradient in the *Limulus* cornea, measured by interference microscopy (Fig. 2b), is precisely that required for lens-cylinder optics9, so that Exner's mechanism survived the challenge.

**Superposition images**

*Limulus* has an apposition eye, that is, one in which each receptor cluster has its own private optics, and receives an image from a small solid angle of external space (Fig. 1a). Many nocturnal insects and crustaceans have eyes with a similar superficial appearance, but a quite different optical structure (Fig. 1b), known as superposition eyes. They are characterized anatomically by a wide zone of clear material between the superficial optics and the receptor layer, which usually forms a hemisphere with a radius of curvature about half that of the eye itself10,11. One group of insects with eyes of this kind are the glowworms and fireflies (Lampyridae) and these have the useful feature that the optical elements are physically part of the cornea, so that by simply cleaning out the interior of the eye the optics of the whole array can be studied. Exner did this, and found that instead of a series of inverted images at the cone tips there was just one erect image. This image was formed by the array as a whole and lay relatively deep, in approximately the position occupied by the retina. I have repeated Exner's observation (Fig. 3), as have others12,13. Unfortunately, it is not easy to see an image in most insect eyes with 'clear-zones', moths for example, because the optical elements of the crystalline cones are separate from the cornea and the array does not survive the abuse of cleaning. In choosing *Lampyris*, and for that matter *Limulus*, Exner clearly knew what he was doing.

The explanation Exner gave for superposition image formation is shown in Fig. 1b and c. Essentially, parallel light entering many facets superimposes in the image region, and because the whole system is symmetrically the overall result is an erect image. For superposition to occur it is clear that each optical element must behave as an inverter—a telescope with an overall magnification of −1. Parallel rays entering each element are redirected in such a way that the emergent beam makes the same angle with the element's axis as the entering beam, but, unlike the situation in a simple lens, the emergent beam lies on the same rather than the opposite side of the axis (Figs 1c and 3b, c).

There are two ways in which such a device could be made: as a conventional telescope made from two curved surfaces, with a focus in the middle, or from a pair of lens cylinders like those in *Limulus* but placed end to end. The former alternative is possible in theory but in insects the refractive indices are too low and the curvatures inadequate for this to be the correct interpretation. Exner chose the double-length lens-cylinder explanation for *Lampyris*. Rays are brought to a focus by the first half of the element, then unfocused and inverted by the second half. The correctness of this interpretation has now been verified for fireflies14, some other beetles15,16, moths17, skipper butterflies18 and ephusaid crustaceans19, in each case by examining sectioned crystalline cones using interference microscopy and confirming the existence of an appropriate refractive index gradient (Fig. 4).

Exner did, however, make one serious mistake. He generalized his mechanism to all eyes with a similar structure. Figure 1b admits of one other explanation and that is that the optical elements are simply plane mirrors (Fig. 1c). I shall return to this later.

**Man-made lens cylinders**

Commercial interest in inhomogeneous cylindrical lenses did not begin until the late 1960s, and the thrust was not to produce devices with compound eye-like properties, but to make optical fibres that transmitted images, as opposed to simply transmitting intensity. It is clear that an extended lens cylinder will keep imaging and re-imaging an object placed against its end at regular intervals along its length (Fig. 3d), and this ability could potentially be used to convey at least as much information per unit cross-sectional area as the alternative; this would be an expensive coherent light-guide array. The exact refractive index gradient that an image-transmitting lens cylinder should have was worked out in the mid-1950s by Fletcher, Murphy and Young20 who, incidentally, also derived the refractive index gradient for a Matthiessen fish lens. They give the following relationship between distance between loci (2F), axial refractive index (n0) and refractive index (n) at a radial distance (r) from the axis

\[ n = n_0 \left(1 - \frac{1}{2} a^2 r^2 + \frac{5}{24} \frac{a^4}{r^4} - \frac{35}{128} \frac{a^6}{r^6} + \frac{63}{256} \frac{a^8}{r^8} + \cdots + \frac{E_n (ar)^{2n}}{(2n)!} \right) \]

where \( a = \pi / 2F \), and \( E_n \) are the Euler numbers. If one ignores all terms beyond the \( r^2 \) term, the refractive index gradient

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**Fig. 2** Eye of *Limulus*. *a*, Crystalline cones projecting inwards from cornea. *b*, Interference micrograph of thin section of a cone. The fringe distortion is proportional to the local refractive index. Scale bar 100 μm. *c*, Inverted images of an arrowhead at the tips of the crystalline cones. (From Land5.)
Problems, and the light-guide heresy

During the 1960s, when commercial lens cylinders were at last being developed, their biological counterparts almost suffered extinction, as the following quotations show. Of lens cylinders: "It seems very doubtful if 'lens cylinder' properties will ever be found in a compound eye and therefore it would probably be better to discard the idea." (ref. 12). And of superposition optics: "There is no reason to suppose that this is true for any compound eye, and there are several reasons, given above, why the superposition image of the firefly is no more than an artifact of the cleaned retina." (ref. 27).

The revolt against Exner’s principal ideas began with some careful observations by Kuiper13, showing that in certain crustacean eyes there are no important refractive index variations in the crystalline cones, a conclusion subsequently verified by interference microscopy14,15. This would seem to rule out both lens-cylinder optics and superposition imagery. In their place, Kuiper suggested that the important optical elements in this kind of eye were tracts or threads which crossed the clear zone, conveying images from lens systems in the region of the cornea to the deep-lying receptors. In support of this idea, he pointed out that these higher-index light-guide-like structures often became lined with pigment in the light-adapted eye, the function of which was to ‘bleed’ light out of the light guides by bringing high-refractive index material into contact with their sides. Effectively, Kuiper was suggesting that superposition eyes, in crustaceans at least, were really apposition eyes with a ‘longitudinal pupil’ mechanism for protecting the eye against high light intensities, rather than a superposition mechanism for increasing sensitivities at low intensities. Further support for this idea seemed to come from an interference microscope study by Allen16, who claimed that in the hornworm moth the crystalline cones had a refractive index that was constant to less than 1%, and that the threads traversing the clear zone had an index of 1.523 (which would make them solid). These observations have not been confirmed, and indeed all subsequent work on insect superposition eyes17-20, including moths, has led to opposite conclusions11.

The present position is a satisfactory compromise. Most, if not all, insect eyes with clear zones do behave as proper Exner-type superposition eyes in the dark, with the threads that cross the clear zone interfering only minimally with the ray paths that contribute to the focused image. However, the effect of light adaptation is to cause pigment movement into the clear zone.
reflecting image-forming rays to the tract of thread joining each facet to its corresponding receptor bundle. Kuiper's light-bleeding mechanism, as well as simple pigment screening, probably both occur\(^{31,32}\) and the net effect is that eyes with superposition optics at night have apposition optics by day. In moths one can watch this change happening. When suddenly illuminated in the dark, there is a large patch of 'glow' or eye-shine corresponding to the whole pupil of the superposition system, illuminated from within by light reflected from a tapetum behind the receptors (Fig. 5d). Exposure to light causes this patch to shrink to not much more than one facet, as pigment migrates inward and intercepts the oblique rays that would go to form the superposition image\(^{32}\).

There remains, however, the problem that started the controversy. What happens in crustacean eyes without lens cylinders?

**Reflecting superposition optics**

Klaus Vogt provided an answer in a short note on crayfish eyes\(^{33}\). "Rays from an object point entering through different facets are superimposed not by refracting systems as in other superposition eyes but by a radial arrangement of orthogonal reflecting planes which are formed by the sides of the crystalline cones and purine layers surrounding them.\(^{34}\) Without being aware of Vogt's paper I reached the same conclusion about the eyes of a deep-sea shrimp\(^{35}\). If one looks at Exner's original figure\(^{1,1}\) it is clear that the elements he drew could equally well be replaced by plane mirrors (Fig. 1a, c), and this is precisely what happens in certain crustacea, specifically the long-bodied decapods (shrimps, prawns, crayfish and lobsters, but not the true crabs). The structure of their eyes is very much like that of insect superposition eyes—a peripheral array of optical elements, a wide clear zone and a deep-lying hemispherical retina. They ought, anatomically, to be superposition eyes. The crucial difference is that the 'crystalline cones' are not crystalline—they are jelly-like with a refractive index of about 1.42—and neither are they conical. They are square in surface view (Fig. 5a, d), as shown perfectly accurately in Grenacher's plate of 1879 (ref. 35) (Fig. 5b).

There is an elegant reason that eyes that use mirrors must have square facets. Figure 1c shows a two-dimensional diagram of an image-forming mirror array, but the question is: of what three-dimensional array would this be a section? One possibility is that it is a section of an axially symmetrical arrangement of mirror parallel strips (Fig. 6a). Clearly, this will form an image of a distant point source located on the axis of the structure, but equally clearly it will not form an image of light originating from any other direction; the strips will not so much focus light as get in the way of it. What is required is an array that will behave like the strip arrangement, but for all directions. An array of square corners will do this. The reason is that a pair of mirrors at right angles to each other behave as though they were a single mirror that is always normal to the plane of the incident ray (Figs 1f and 6b): the complete angle through which the ray is reflected must add up to 180°. (One occasionally encounters corner mirrors in clothes shops—it is impossible to escape from one's image by moving around them.) Thus, provided most light entering the eye encounters two faces of each mirror box, all ray paths to the focus will be essentially identical to those of the two-dimensional diagram\(^{29,30,32}\). For a large-aperture eye like that of a crayfish each mirror box should be about twice as deep as it is wide, for the double reflection conditions to be met.

Not all eyes of the reflecting superposition type actually have mirrors. In the shrimp *Palaeomonetes*, for example, reflection occurs at the faces of the mirror box by total internal reflection. With a refractive index of 1.41 inside the box, and a fluid outside with an index of about 1.33, the critical angle for total internal reflection is 71°, that is, rays making angles of up to 19° with the box wall will be reflected. This restricts the eye's effective pupil to about one-third of the eye diameter. To increase the boxes are lined with a specular mirror in both crayfish and deep-sea shrimp. The mirrors are composed of a three-layer sandwich of one-quarter wavelength-thick plates alternating with a fluid layer\(^{32}\), which is a common way for natural mirrors to be produced\(^{38,39}\). The nature of the material of the plates is not known in the crayfish, but in a penaeid shrimp it is the pteridine isoxanthopterin\(^{40}\).

A final refinement of the crayfish optical mechanism was found recently by Bryceson\(^{41}\). She noticed that each facet of the cleaned cornea is actually a long focus lens, with a focal length in water approximately equal to the distance from cornea to receptors (Fig. 5c). This has two implications. It means that the pencil of light passing through each mirror box is prefocused, so that it reaches the receptors as a fine beam, thereby improving image resolution. It also means that when the eye is in the light-adapted condition and each receptor only receives light from its 'own' facets; the focusing ensures a resolved image on that receptor and hence a narrow field of view. Interestingly, Kuiper had noticed inversed images in his original study\(^{36}\).

**Phylogeny and ontogeny**

Mirror boxes with a hexagonal cross-section do not reflect light as shown in Fig. 1f and 6b, and so cannot be used in reflecting superposition eyes. Therefore, hexagonally facetted eyes do not use this mechanism, whereas square-faceted eyes probably do. Corneal geometry can thus be used as a reliable indication of an eye's optical type, and, since this is likely to be an evolutionary conservative character, of its ancestry as well\(^{32,44}\).

An examination of the higher crustacea show that square-faceted eyes are found only in the Decapoda, and there only in the long-bodies forms. The crabs (Brachyura) and hermit-crabs (Anomura), have hexagonally facetted eyes of the apposition type, without a clear zone\(^{43,45}\). Equally interesting is the fact that the euphausiids, the shrimp-like krill usually grouped with the decapods in the super-order Eucarida, have both hexagonal facets and a clear zone. These eyes are very similar in their construction to the reflecting superposition eyes of molluscs, and indeed their bullet-like crystalline cones bend light in the same way as in insect superposition eyes\(^{45}\) and have a lens cylinder.
suggestions that the euphausiids and decapods are unrelated. Any one character is perhaps as fallible as any other as an evolutionary guide, but at least for eyes one can make the claim that once a design that works well has evolved it is most unlikely to be abandoned for an equally complicated but functionally equivalent one, as, for example, reflecting versus refracting superposition optics.

Although the decapods are alone among crustacea in possessing square-faceted eyes, there may be one possible parallel in insects. Horridge and Maclean have described the eye of the Australian mayfly *Atalophlebia*, which has entirely square facets in its dorsal eye (in males the eyes are divided), square homogeneous crystalline cones and a wide clear zone. The optics are not well understood, but this ought to be a reflecting superposition eye. By contrast, the common European mayflies (*Cloeon*) have hexagonal facets and presumably refracting superposition optics. The Ephemeroptera are again a taxonomically difficult group, and it will be interesting to see whether eye structure is helpful here as well.

**X-ray telescopes and other applications**

Both types of superposition eye represent image-forming systems equivalent in many ways to conventional lenses and mirrors, but which have so far found few applications in optical technology. It is almost true to say that they have not properly been invented. In the case of reflecting superposition devices it is clear that the task of making a large number of appropriate lens cylinders and aligning them accurately probably is not worth the effort, but for a reflecting system this is not necessarily true. One could imagine the construction of a reflecting array from strips of sheet metal, cut so as to interlock, or from a casting that was subsequently plated (there is a problem in trying to cover a sphere with squares—basically it cannot be done—but both geographers and lobstermen have found ways round it). Such structures could have wide apertures, like crustacean eyes, and serve in applications like solar collectors, where condensing power rather than resolution is at a premium, or as emitters they could be useful for making large collimators, lighthouse lenses for example.

If the pupil is restricted, much higher resolution can be achieved, and it is this form that has produced the only important application so far, as an X-ray telescope. X rays cannot be focused by refraction or by reflection at near normal incidence, which has meant that existing X-ray telescopes are all based on grazing incidence optics utilizing nested surfaces. Their design is basically similar to the tilted strips in Fig. 6a, and they suffer from the same drawback, a very narrow field of view. Angel realized that the use of square cells as reflectors eliminates this problem, and has designed a telescope with a spatial resolution of 30 arc s. This degree of resolution is achieved by making the reflecting cells very long—about 100 times their width. Because they are reflecting devices, square-cell surfaces are usable over large parts of the electromagnetic spectrum, and provided the manufacturing problems can be overcome they should have a wide range of uses.

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4. Maxwell, J. C. *Collected Works 1, 76–78 (1854).*
43. Land, M. F. in Making Sense of Sense Organs (ed. Laverack, M. S.) (Blackie, Glasgow, in the press).