REVIEW ARTICLE

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[1] 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 that 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[2]. 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. 1*d*, *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. Matthiessen[3] 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

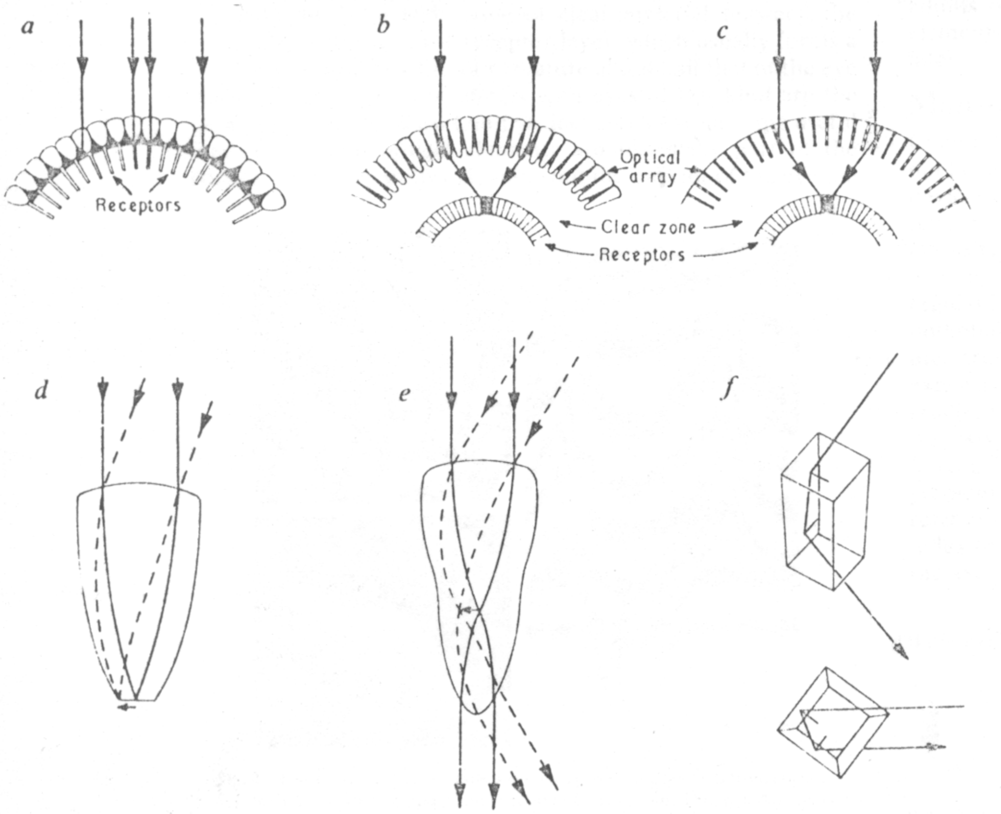

Fig. 1 Compound eye types and their optical components. *a*, Apposition eye; *b*, refracting superposition eye; *c*, reflecting superposition eye; *d*, apposition lens cylinder with focus at proximal tip; *e*, superposition (double length) lens cylinder; *f*, perspective and top view of ray path through a square cell in a reflecting superposition eye. *b*, *d*, *e* are based on Exner[1]; *c* is modified from Land[34]; *f* from Vogt[37].

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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[4], 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 image[4–6].

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. 2*a*), 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. 2*c*), 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 Winston[8] 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. 2*b*), is precisely that required for lens-cylinder optics[9], 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. 1*a*). Many nocturnal insects and crustaceans have eyes with a similar superficial appearance, but a quite different optical structure (Fig. 1*b*), 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 itself[10,11]. 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 others[12,13]. Unfortunately, it is not easy to see an image in most insect eyes with 'clear-zones', moths for example, because the optical elements (or 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.

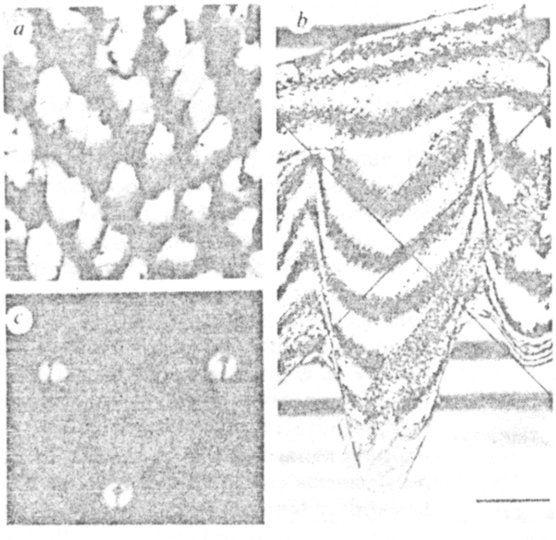

Fig. 2 Eye of *Limulus*. *a*, Crystalline cones projecting inwards from cornea. *b*, Interference micrograph of thin section of a cone. The fringe distortion is proportional to the local refractive index. Scale bar 100 μm. *c*, Inverted images of an arrowhead at the tips of the crystalline cones. (From Land[9].)

The explanation Exner gave for superposition image formation is shown in Fig. 1*b* and *e*. Essentially, parallel light entering many facets superimposes in the image region, and because the whole system is spherically symmetrical 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 1*e* and 3*b*, *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[1] 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 fireflies[14], some other beetles[15], moths[16], skipper butterflies[17] and euphausiid crustaceans[18], 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 1*b* admits of one other explanation and that is that the optical elements are simply plane mirrors (Fig. 1*c*). 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. 3*d*), 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 Young[19] who, incidentally, also derived the refractive index gradient for a Matthiessen fish lens. They give the following relationship between distance between foci ($2F$), axial refractive index (n_0) and refractive index (n_r) at a radial distance (r) from the axis

$$n_r = n_0 \operatorname{sech}(\pi r/2F)$$

This expression can be expanded[20] to give

$$n_r = n_0\left(1 - \tfrac{1}{2}a^2r^2 + \tfrac{5}{24}a^4r^4 - \tfrac{61}{720}a^6r^6 + \cdots + \frac{En}{(2n)!}(ar)^{2n} \cdots\right)$$

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

Fig. 3 Optics of refracting superposition eyes. *a*, Julia Cameron's portrait of Charles Darwin rephotographed through the cleaned cornea of a firefly. The eye was suspended in a hanging drop of water with the cornea in air. The image is erect, and the face is about 0.1 mm across. *b*, Bending of a light beam by a natural double length lens cylinder, a crystalline cone from a euphausiid crustacean. The beam is made visible with fluorescein and is 30 μm wide (from ref. 45). *c*, Light beam bent in a similar manner by a man-made SELFOC glass lens cylinder. Compare with the light paths in Fig. 1*b* and *e*. *d*, Lens cylinders also have the property of imaging an object at intervals of $2F$ (see text). The photograph shows the word 'are' with the same SELFOC as in *c* placed over the 'e'. The 'e' is re-imaged, inverted, at the upper end of the lens cylinder.

becomes a parabola, and it was this parabolic approximation that Exner's brother, Karl[21], derived in connection with biological lens cylinders (Fig. 4). Attempts to manufacture lens cylinders have also been made using diffusion processes which give rise naturally to parabolic gradients. In the 1960s attempts were made to use gas mixtures to produce lenses and waveguides[22]. Then in 1968 a glass lens cylinder (SELFOC) was produced and patented in Japan. It was made by heating a thallium-rich flint glass in a molten salt (KNO_3, at 500 °C) which leached out and replaced the heavy metal ions from the outside, thereby reducing the refractive index from 1.542 in the centre to 1.517 at the periphery[23,24].

More recently, plastic lens cylinders have been made by heating a high refractive index rod of soft polymerized plastic (diallyl isophthalate, $n = 1.57$) in a bath containing the monomer of a low index plastic (methylmethacrylate, $n = 1.49$)[25,26]. This gives a usable refractive index range that is similar to that of the glass lenses.

The future of man-made lens cylinders is unclear. They have good imaging properties over short distances—through one or two serial images (Fig. 3*d*)—but then aberrations of various kinds tend to degrade the image. The higher-order terms in the expansion for n_r begin to become important, as does the fact that non-paraxial rays require a somewhat different index gradient from paraxial rays[20]. Chromatic aberration also accumulates, although this can be offset to some degree by a suitable choice of materials[26]. Given these problems, as well as those of manufacture, it is likely that aligned fibre bundles offer better prospects for long-distance image transmission than focusing lens cylinders. There should, however, be many other applications for versatile lens-like systems of very small dimensions.

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 Kuiper[12], showing that in certain crustacean eyes there are no important refractive index variations in the crystalline cones, a conclusion subsequently verified by interference microscopy[28,29]. 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 Allen[30], 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 eyes[14–17], including moths, has led to opposite conclusions[11].

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,

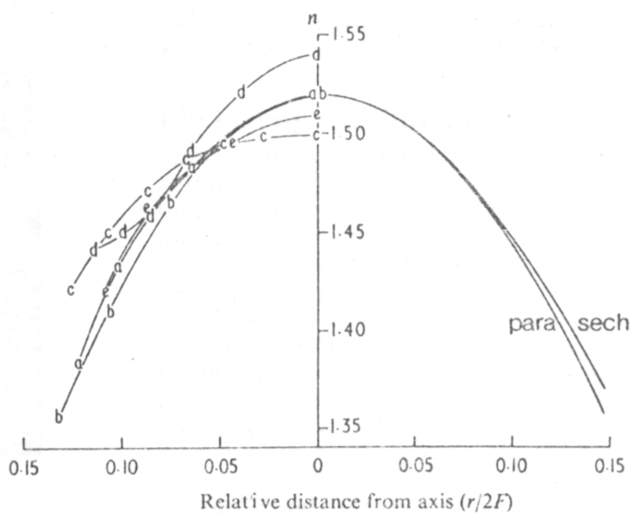

Fig. 4 Comparison of theoretical (right) and measured (left) refractive index distributions through crystalline cones. The theoretical curves show the difference between the Fletcher *et al.* equation[19] and Exner's parabolic approximation. Measured data are from: *a*, a euphausiid[18]; *b*, a firefly[14]; *c*, a moth[16]; *d*, a skipper butterfly[17]; *e*, *Limulus*[9]. The gradients have been normalized by taking the cone length as $2F$ for superposition eyes (*a*–*d*), and F in the case of the apposition eye of *Limulus* (*e*).

confining 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. 5*d*). 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 the 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." Without being aware of Vogt's paper I reached the same conclusion about the eyes of a deep-sea shrimp[34]. If one looks at Exner's original figure[1,11] it is clear that the elements he drew could equally well be replaced by plane mirrors (Fig. 1*b*, *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. 5*a*, *d*), as shown perfectly accurately in Grenacher's plate of 1879 (ref. 35) (Fig. 5*b*).

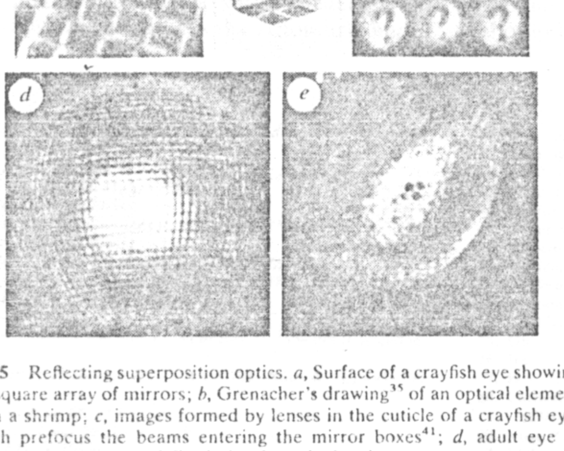

Fig. 5 Reflecting superposition optics. *a*, Surface of a crayfish eye showing the square array of mirrors; *b*, Grenacher's drawing[35] of an optical element from a shrimp; *c*, images formed by lenses in the cuticle of a crayfish eye, which prefocus the beams entering the mirror boxes[41]; *d*, adult eye of *Palaemonetes varians*, fully dark adapted, showing square symmetry and patch of eye-shine corresponding to the superposition pupil; *e*, 1st instar larva of *Palaemon serratus*, showing hexagonal symmetry and a small black pseudo-pupil characteristic of apposition eyes.

There is an elegant reason that eyes that use mirrors must have square facets. Figure 1*c* 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 tilted circular strips (Fig. 6*a*). 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 1*f* and 6*b*): 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[29,36,37]. 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 *Palaemonetes*, 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 this 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 tissue fluid[37], 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 pennaeid 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. 5*c*). 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' facet[42], the focusing ensures a resolved image on that receptor and hence a narrow field of view. Interestingly, Kuiper had noticed inverted images in his original study[12].

Phylogeny and ontogeny

Mirror boxes with a hexagonal cross-section do not reflect light as shown in Fig. 1*f* and 6*b*, and so cannot be used in reflecting superposition eyes. Therefore, hexagonally faceted 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[43,44].

An examination of the higher crustacea shows 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), but interestingly not the squat-lobsters (also Anomura), have hexagonally faceted eyes of the apposition type, without a clear zone[43,44]. 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 refracting superposition eyes of moths, and indeed their bullet-like crystalline cones bend light in the same way as in insect superposition eyes[45] and have a lens cylinder-

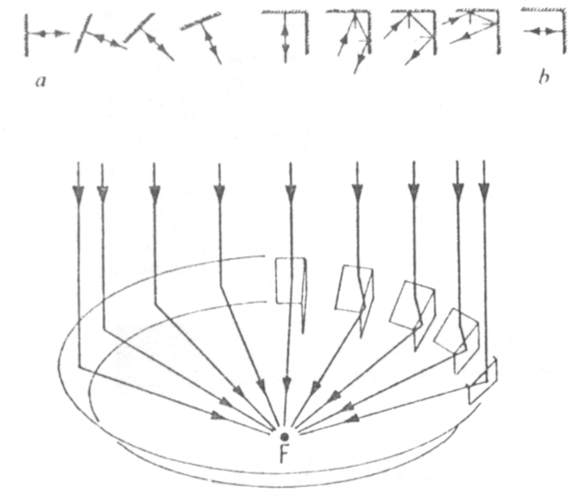

Fig. 6 A superposition focus can be formed either by set of tilted circular strips of mirror (*a*, left) or by a surface made of corner reflectors (*b*, right). Corner reflectors behave as though they are single mirrors at right angles to the plane of the incident ray (inserts above) so that the ray paths are almost the same as for the strips.

like refractive index profile[18]. The mysids (Peracarida), which look very much like euphausiids but differ from them in having a brood-pouch, also have refracting superposition eyes, although other peracaridans have apposition eyes. In the last century the euphausiids and mysids were grouped together as the Schizopoda, and my guess is that that grouping more accurately reflected their evolutionary affinity.

The decapods with reflecting superposition eyes do not start life that way (Fig. 5*e*). In their larval stages they have hexagonally faceted eyes with a typical apposition structure. In *Palaemonetes* it is not until about moult 15, when the animal is almost adult, that the facets square off and the superposition mechanism comes into operation. Presumably, the apposition type of eye is adequate for the upper ocean where the planktonic larvae live, just as it is in the light-adapted adults, but the deeper, dimmer waters the adults inhabit on maturity make it advantageous to use superposition optics, with their much greater light-gathering power. Larval crabs have eyes just like larval shrimps: the main developmental difference is that adult crab eyes retain the larval optical design. Again this makes sense, since most of them are shallow water or even terrestrial forms and would not need the superposition mechanism. It is as though the crab eye is derived from the crayfish eye by neoteny, the final developmental stage having been omitted.

This is somewhat perplexing for taxonomists. Eye structure links the mysids and euphausiids, which contemporary taxonomy does not. The reflecting superposition mechanism links all the long-bodied decapods, which are currently split between the Natantia and Reptantia[46] or the Dendrobranchiata and Pleocyemata[47]. It splits the galatheids (squat lobsters) from the pagurids (hermit crabs) and so divides the Anomura, and it suggests 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[48] 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 refracting 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 lobsters 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[49,50]. 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. 6*a*, and they suffer from the same drawback, a very narrow field of view. Angel[49] 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.

1. Exner, S. *Die Physiologie der facettierten Augen von Krebsen und Insecten* (Deuticke, Leipzig, 1891).
2. Horridge, G. A. & Duelli, P. *J. exp. Biol.* **80,** 165–190 (1979).
3. Matthiessen, L. *Pflügers Arch. ges. Physiol.* **21,** 521–528 (1886).
4. Maxwell, J. C. *Collected Works* **1,** 76–78 (1854).
5. Pumphrey, R. J. in *The Cell and the Organism* (eds Ramsay, J. A. & Wigglesworth, V. B.) 193–208 (Cambridge University Press, 1961).
6. Cornbleet, S. *Microwave Optics,* 121–132 (Academic, London, 1976).
7. Levi-Setti, R., Park, D. A. & Winston, R. *Nature* **253,** 115–116 (1975).
8. Winston, R. *J. opt. Soc. Am.* **60,** 245–247 (1970).
9. Land, M. F. *Nature* **280,** 396–397 (1979).
10. Horridge, G. A. (ed.) in *The Compound Eye and Vision of Insects,* 255–298 (Clarendon, Oxford, 1975).
11. Kunze, P. in *Handbook of Sensory Physiology* Vol. VII/6A (ed. Autrum, H.) 441–502 (Springer, Berlin, 1979).
12. Kuiper, J. W. *Symp. Soc. exp. Biol.* **16,** 58–71 (1962).
13. Eltringham, H. *Trans. R. ent. Soc. Lond.* **79,** 1–49 (1919).
14. Seitz, G. *Z. vergl. Physiol.* **62,** 61–74 (1969).
15. Meyer-Rochow, V. B. in *The Compound Eye and Vision of Insects* (ed. Horridge, G. A.) 299–313 (Clarendon, Oxford, 1975).
16. Hausen, K. *J. comp. Physiol.* **82,** 365–378 (1973).
17. Horridge, G. A., Giddings, C. & Stange, G. *Proc. R. Soc.* B**182,** 457–495 (1972).
18. Land, M. F. & Burton, F. A. *J. exp. Biol.* **82,** 395–398 (1979).
19. Fletcher, A., Murphy, T. & Young, A. *Proc. R. Soc.* A**223,** 216–225 (1954).
20. Rawson, E. G., Herriott, D. R. & McKenna, J. *Appl. Opt.* **9,** 753–759 (1970).
21. Exner, K. *Ann. phys. Chem.* **28,** 111–116 (1886).
22. Berreman, D. W. *Bell. Syst. Tech. J.* **43,** 1476–1479 (1964).
23. Uchida, T., Furukawa, M., Kitano, I., Koizumi, K. & Matsumara, H. *IEEE J. Quantum Electronics QE-6,* 606–612 (1970).
24. Koizumi, K., Ikeda, Y., Kitano, I., Furukawa, M. & Sumimoto, T. *Appl. Opt.* **13,** 255–260 (1974).
25. Ohtsuka, Y. *Appl. Phys. Lett.* **23,** 247–248 (1973).
26. Iga, K. & Yamamoto, N. *Appl. Opt.* **16,** 1305–1310 (1977).
27. Horridge, G. A. *Proc. R. Soc.* B**171,** 445–463 (1969).
28. Carricaburu, P. in *The Compound Eye and Vision of Insects* (ed. Horridge, G. A.) 236–254 (Clarendon, Oxford, 1975).
29. Vogt, K. *Z. Naturforsch.* **32c,** 466–468 (1977).
30. Miller, W. H., Bernard, G. D. & Allen, J. L. *Science* **162,** 760–767 (1968).
31. Walcott, B. in *The Compound Eye and Vision of Insects* (ed. Horridge, G. A.) 20–33 (Clarendon, Oxford, 1975).

32. Höglund, G. in *The Functional Organization of the Compound Eye* (ed. Bernhard, C. G.) 77–101 (Pergamon, Oxford, 1966).
33. Vogt, K. *Z. Naturforsch.* **30c**, 691 (1975).
34. Land, M. F. *Nature* **263**, 764–765 (1976).
35. Grenacher, H. *Untersuchungen über das Sehorgan der Arthropoden, insbesondere der Spinnen, Insecten und Crustacean* (Vanderhoeck & Ruprecht, Göttingen, 1879).
36. Land, M. F. *New Scient.* No. 1175, 10–13 (1979).
37. Vogt, K. *J. comp. Physiol.* **135**, 1–19 (1980).
38. Land, M. F. *Prog. Biophys. molec. Biol.* **24**, 75–106 (1972)
39. Land, M. F. *Scient. Am.* **239**, 126–134 (1968).
40. Zyznar, E. J. & Nicol, J. A. C. *J. exp. mar. Biol. Ecol.* **6**, 235–248 (1971).
41. Bryceson, K. *J. exp. Biol.* (in the press).
42. Kleinholz, L. H. in *The Physiology of Crustacea* Vol. II (ed. Waterman, T. H.) 133–169 (Academic, New York, 1961).
43. Land, M. F. in *Making Sense of Sense Organs* (ed. Laverack, M. S.) (Blackie, Glasgow, in the press).
44. Fincham, A. A. *Nature* **287**, 729–731 (1980).
45. Land, M. F., Burton, F. A. & Meyer-Rochow, V. B. *J. comp. Physiol.* **130**, 42–62 (1979).
46. Borradaile, L. A. *Ann. Mag. nat. Hist.* Ser. 7, **19**, 457–486 (1907).
47. Glaessner, M. F. in *Treatise on Invertebrate Paleontology* Part R., Vol. 2 (ed. Moore, R. C.) 399–566 (University of Kansas and Geol. Soc. Am., 1969).
48. Horridge, G. A. & McLean, M. *Proc. R. Soc.* **B200**, 137–150 (1978).
49. Angel, J. R. P. *Astrophys. J.* **233**, 364–373 (1979).
50. Hartline, B. K. *Science* **207**, 47 (1980).