Photoreception in Marine Invertebrates[1]

Thomas W. Cronin

*Department of Biological Sciences, University of Maryland Baltimore County,
Catonsville, Maryland 21228*

Synopsis. In order for photoperiodic phenomena to be expressed by any animal, the organism must possess some sort of photoreceptor. This may be in the form of an eye or an extraocular receptor, and the invertebrate phyla illustrate fantastic diversity in design of either receptor type. While all the major invertebrate phyla possess photoreceptor organs of one type or another, the best-studied groups are those with highly complex eyes. These include the crustaceans, the molluscs, and some polychaete annelids. Many species in these groups possess eyes having extreme sensitivity, good spatial resolution, and in some cases multiple spectral channels. In a few taxa, the eyes are known to provide input to circadian oscillators, which suggests that they may also be employed for measurement of photoperiod. Extraocular photoreceptors include dermal and ganglionic sense organs, which also feed into circadian systems in numerous invertebrates, from cnidarians to molluscs and arthropods.

INTRODUCTION

The presence of photoperiodic phenomena in an organism necessarily implies that it possesses photoreceptors. Normally, when we consider photoreception we think of visual receptors, or eyes; but extraocular photoreceptors—those which are not associated with the eyes at all—are also common among invertebrates. In many cases these receptors, as well as the principal eyes, are known to affect circadian rhythm expression, and thus they may also be involved in the systems which direct photoperiodic phenomena. The close connection between circadian and photoperiodic processes has been reviewed by Bünning (1973) and Saunders (1976).

Photoreceptors, especially eyes, are designed to provide animals with a variety of information. Complex eyes may supply their owners with data concerning the following features of the visual field: light intensity, spectral distribution, spatial distribution (images), polarization pattern, and temporal distribution (movement, flicker, or duration). Although any or all of these could in principle be used to measure photoperiod, I will initially concentrate on properties of invertebrate photoreceptors most closely relevant to photoperiod measurement: spectral sensitivity and absolute sensitivity. Later in this review, I will provide an overview of design and function of invertebrate eyes and extraocular receptors, including some of their known effects on circadian rhythms. As much as possible, and in keeping with the theme of the symposium, I will restrict examples to marine invertebrates. Several comprehensive reviews of invertebrate photoreception, especially vision, have recently appeared; see Autrum (1979, 1981a, b) and Ali (1984).

VISUAL SENSITIVITY

Spectral sensitivity

Spectral sensitivity measurements have been obtained from a reasonable cross section of marine invertebrates, and I present representative data in Table 1. Three principal methods have been used to gather these data: measurement of action or response spectra for photoresponses of planktonic animals (Phototaxis); measurement of the electrical responses of receptors, either in the whole eye using the electroretinogram (ERG), or extracellularly on the optic nerve (Optic nerve), or in single receptor cells (Single cell); and measurement of absorption spectra of visual pigments either in solution (Pigment extract) or in isolated receptor cells by microspectrophotometry (MSP). I have also included action spectral results for a few cases of dermal light sensitivity, obtained behaviorally (B) or electrophysiologically (EP).

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TABLE 1. *Spectral sensitivity maxima of photoreceptor systems of marine invertebrates.* *

Phylum Class	Species	Spectral sensitivity (max)	Method	Habitat	Source
Annelida					
Polychaeta	*Nereis mediator*	480	ERG	Intertidal	Yingst *et al.,* 1972
	Odontosyllis enopla	510–520	ERG	Coastal	Wilkens and Wolken, 1981
	Torrea candida	400, 560	ERG	Coastal	Wald and Rayport, 1977
Mollusca					
Gastropoda	*Aplysia* sp.	500	Optic nerve	Coastal	Jacklet, 1980
	Aplysia californica	470	Extraretinal (EP)	Coastal	Andresen and Brown, 1979
Bivalvia	*Tridacna maxima*	360, 490, 540	Single cell	Coral reef	Wilkens, 1984
Cephalopoda	*Octopus vulgaris*	475	Pigment extract	Coastal	Hara *et al.,* 1967
	Loligo peali	493	Pigment extract	Coastal	Hubbard and St. George, 1957
	Todares pacificus	480	Extraretinal (PE)	Deep sea	Hara and Hara, 1979
Arthropoda					
Xiphosura	*Limulus polyphemus*	360, 530	ERG	Coastal	Chapman and Lall, 1967
Crustacea					
Cirripedia	*Balanus balanoides* (nauplius)	510–530	Phototaxis	Coastal	Barnes and Klepal, 1972
Copepoda	*Acartia tonsa*	450–520	Phototaxis	Estuarine	Stearns and Forward, 1984
Stomatopoda	*Squilla mantis*	535–555	Single cell	Coastal	Schiff, 1963
Euphausiacea	*Euphausia superba*	485	Pigment extract	Deep sea	Denys and Brown, 1982
Decapoda	*Homarus americanus*	515	MSP	Coastal	Bruno *et al.,* 1977
	Palaemonetes vulgaris	390, 540	ERG	Estuarine	Wald and Seldin, 1968
	Callinectes sapidus	440, 508	Single cell	Estuarine	Martin and Mote, 1982
Echinodermata					
Asteroidea	*Asterias amurensis*	504	Extraretinal (B)	Coastal (?)	Yoshida and Ohtsuki, 1966

* This table is not intended as an exhaustive catalog of available data, but includes results chosen as representative. See text for further explanation. Abbreviations: ERG, electroretinogram; EP, electrophysiological assay; PE, pigment extract; MSP, microspectrophotometry; B, behavioral assay.

Table 1 reveals that marine invertebrates as a group are reasonably restricted in their spectral sensitivity range. Only a few examples exist in which the principal spectral maxima fall outside the limits of 450–550 nm, and no included species has a peak beyond 560 nm. This is in contrast to marine fishes, which frequently possess visual pigments with λ_{max} (the wavelength of maximum absorption or sensitivity) above 600 nm. In fishes, these long-wavelength pigments are probably devoted to contrast vision (McFarland and Munz, 1975) or to visual communication (O'Day and Fernandez, 1974; Levine et al., 1980). Some insects (butterflies) do have red-absorbing rhodopsins (Bernard, 1979); their apparent absence in marine invertebrates may imply visual requirements different from those of either marine vertebrates or butterflies.

In the marine environment, teleost piscine visual pigments are often placed so as to maximize sensitivity to the wavelength range actually available in the habitat of the particular species (Lythgoe, 1972; McFarland and Munz, 1975). Can the same be said of marine invertebrates? Dartnall (1975) has demonstrated that maximal photon fluxes for various water types at 10 m depth fall into the following wavelength ranges: turbid coastal water (similar to estuarine waters), λ_{max} (the wavelength of maximum flux) = 590 nm, half-band pass (HBP, the wavelength values at 50% of the peak) = 550–630 nm; typical coastal water, λ_{max} = 540 nm, HBP = 490–610 nm; typical oceanic waters (including clearest coastal types), λ_{max} = 525 nm, HBP = 460–590 nm; and clearest oceanic waters, λ_{max} = 510 nm, HBP = 440–600 nm. The trend is to shorter wavelengths of peak photon flux and broader curves as one moves offshore. Because of the monochromating effects of water, all of these functions shift to shorter wavelengths and narrower bandwidths with increasing depth; thus at 100 m in the clearest ocean water, λ_{max} = 475 nm and HBP = 440–500 nm. These values suggest that coastal/estuarine invertebrates should have spectral sensitivity λ_{max} at 550–590 nm, while in the open ocean, the λ_{max} of species living near the surface should be near 510 nm and that of deep-water species about 480 nm.

Goldsmith (1972) concluded that for marine crustaceans there is a fairly consistent match between the photic environment and visual pigments. With the phyletically more diverse data of Table 1, we can reach essentially the same conclusion, though there appears to be more variation among invertebrates than among fishes in the same habitat (Lythgoe, 1972). No invertebrate species seems to have a particularly poorly matched photoreceptor system.

Note that many invertebrates have a second sensitivity maximum in the short-wavelength or ultraviolet region. The significance of this peak is not clear; in some cases it may be used in hue discrimination (Hyatt, 1975), while in others it may offer contrast sensitivity or simply broaden spectral sensitivity. At present we have virtually no information concerning the influence of either the long- or short-wavelength system on photoperiodic phenomena. For only one invertebrate species (a cockroach) is there any information on spectral sensitivity for circadian rhythm entrainment (Mote and Black, 1981). The cockroach has two spectral channels, with λ_{max} near 365 and 500 nm. Resetting of the circadian clock is accomplished primarily by the 500 nm channel, while the 365 nm system may be weakly inhibitory. If marine animals with two spectral sensitivity maxima have similar physiology, the short-wavelength system may be less likely to be involved in circadian rhythm entrainment or photoperiodism.

Visual pigments

The spectral sensitivity function of a photoreceptor is largely a reflection of the absorption spectrum (or spectra) of the visual pigments which it contains. Among the marine invertebrates, visual pigments are well characterized only in the crustaceans and cephalopods. In both of these groups, the visual pigments are packed into the membranes of rhabdomeric photoreceptor cells (see below).

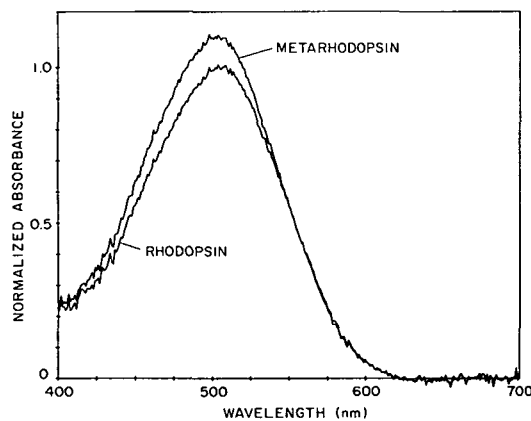A distinctive characteristic of known invertebrate visual pigments is their for-

FIG. 1. Absorption spectra of the 2 components of the visual pigment system of the stomatopod crustacean, *Squilla empusa*. The dark-adapted eye contains only the rhodopsin. Metarhodopsin is produced when the rhodopsin absorbs light, and a subsequent light absorption can convert it back to the rhodopsin. Only the rhodopsin → metarhodopsin transition leads to perception of light.

mation of a thermally stable photoproduct (metarhodopsin) upon conversion of the visually active form (rhodopsin). Once formed, the metarhodopsin may be photoconverted back to rhodopsin, and thus may be recycled many times; however, only the rhodopsin → metarhodopsin transition leads to visual excitation. The absorption spectra of the rhodopsin and metarhodopsin of a stomatopod crustacean are illustrated in Figure 1. As is typical for invertebrate visual pigments in general, the metarhodopsin has a greater peak absorption coefficient than the rhodopsin, and the two pigments have spectra of very similar shape but with different wavelength maxima.

The presence of stable metarhodopsins has two consequences of interest to us here. First, the presence of the metarhodopsin can alter the spectrum of ambient light as it passes down the photoreceptor (Goldsmith, 1978). In fact, it is the absorption characteristics of the metarhodopsin and even more particularly the other photostable accessory pigments in the vicinity of each photoreceptor cell that are principally responsible for the departure of the photoreceptor's spectral sensitivity curve from the absorption spectrum of the rho-

dopsin (Goldsmith, 1978; Stowe, 1980a). (Note that a heterogeneous distribution of screening pigments can provide the capacity for hue discrimination in a retina containing a single visual pigment. See Kong *et al.*, 1980 and Leggett, 1979.)

The other effect caused by the presence of a stable metarhodopsin is the impediment presented to the process of dark adaptation. Invertebrates seem to lack enzymatic systems for directly regenerating rhodopsin from metarhodopsin (Cronin and Goldsmith, 1984; Schwemer, 1984). In order to restore the photopigment content of the photoreceptors to 100% rhodopsin, it appears that at least the arthropods and probably molluscs as well must regularly replace their photoreceptor membranes and thus insert newly synthesized rhodopsin. As will be described later in this paper, the membrane turnover events are commonly associated with the ambient light : dark cycle, and obviously could be tied to mechanisms for measuring photoperiod.

An aspect of invertebrate visual pigments that has only recently emerged is the unexpected variety of chromophoric groups that attach to invertebrate opsins to form the visual pigment. Previous results with extracts from retinas encouraged the assumption that the chromophore of all invertebrate rhodopsins would turn out to be 11-*cis* retinal, a derivative of Vitamin A₁ (Goldsmith, 1972). Vogt (1983, 1984) recently published results demonstrating that in some insect orders (Diptera, Lepidoptera) the visual pigment chromophore is actually 3-hydroxyretinal. Suzuki and coworkers have since discovered 3-dehydroretinal (a vitamin A₂ derivative) in crayfish eyes (Suzuki *et al.*, 1984). Both sets of results are of special interest since these novel chromophores produce absorption spectra shifted along the wavelength axis relative to rhodopsin, and it will be exciting to learn whether some of the visual pigments of marine invertebrates possess unsuspected chromophores.

Absolute sensitivity

The definition of absolute threshold depends on the process of interest; an ani-

mal's threshold for vision and for entrainment to circadian synchronizers may not only differ from each other but also from the threshold inducing photoperiodism. Therefore, measurements of thresholds must be based upon some biological expression of the process being considered; this usually involves making use of some aspect of behavior. For example, environmental photic thresholds (quanta cm^{-2} sec^{-1}) for eliciting phototactic orientation in some planktonic crustaceans range from 3.8 × 10^{10} for nauplius larvae of the barnacle *Elminius modestus* (Barnes and Klepal, 1972), through 2.5 × 10^{11} for zoea larvae of the crab *Rhithropanopeus harrisii* (Forward et al., 1984), to 2.8 × 10^{11} for the copepod *Acartia tonsa* (Stearns and Forward, 1984). For comparison, the human limit for detection of a large dim source when fully dark adapted is 3.0 × 10^4 quanta cm^{-2} sec^{-1} (Pirenne and Denton, 1952).

While the dark-adapted human does much better than any small crustacean, these data may not readily extend to thresholds for photoperiodism. In the single published study on photic entrainment of an invertebrate circadian clock, Mote and Black (1981) determined the threshold to be 1.6 × 10^2 quanta cm^{-2} sec^{-1} for a species of cockroach, corresponding to the entrance of 5 photons into each eye per second—an incredible sensitivity. If their results are at all generalizable, the only marine animals which are beyond the day : night cycle must possess very inefficient photoreceptors indeed, or must live at a great depth.

INVERTEBRATE PHOTORECEPTORS

Probably all marine invertebrates have some photosensitivity, although many species have no recognized light-sensitive organs. A few phyla, such as the Bryozoa, have few or no known photoreceptors at all. Most species have at least some simple cephalic organs which serve to detect the location of light stimuli, and I shall refer to such organs as eyes. Extraocular photoreceptors are then those which occur elsewhere in the body or which are clearly unspecialized for providing even a rudi-

mentary discrimination of the direction of light. An overall view of the distribution of photoreceptor types is given in Table 2.

Photoreceptor cells may be conveniently grouped into two types (see Eakin, 1972), both of which typically have extensive proliferation of plasma membrane. The distinction between the two classes depends upon the presence of cilia: the ciliary type of photoreceptor cell has its photosensitive membrane derived from or associated with cilia, while the rhabdomeric type does not. The evolution and functional significance of photoreceptor design at the cellular level is unclear (see Westfall, 1982), and I will not go into the controversy here. However, in Table 2 I have noted the type(s) of photoreceptor cell characteristic of each phylum.

Eye design in lower invertebrates

Among the invertebrate phyla below the annelids which possess specialized light-sensitive organs, most have simple eyecups. These are groups of photosensitive cells set into a circular pit which is shielded by pigment granules (Fig. 2A). Although eyecups cannot form even a blurred image, they do permit the discrimination of the direction of a light source by localizing its shadow on the retinal surface (Fig. 2B). Pigment cups may be improved by the addition of a lens (Fig. 2C), but it is unlikely that these lenses are very effective (Land, 1981). Annelid eyes also are usually eyecups, but a few families of polychaetes have merged groups of eyecups to produce a simple form of compound eye (see Land, 1981). Alciopid polychaetes have evolved beautiful image-forming eyes not unlike vertebrate or cephalopod molluscan eyes. These animals are also specialized in that they have multiple photopigment systems, which may be an adaptation for the perception of depth (see Wald and Rayport, 1977).

Eye design in higher protostomes

The two highest protostomous phyla, the Mollusca and the Arthropoda, have developed eyes that rank among the best in the animal kingdom. Each group, however, has found its unique path to optical excellence.

Table 2.　*Diversity of photoreceptors of marine invertebrates.* *

Phylum Class	Eyes	Extraocular photoreceptors
Cnidaria	Pigment cups (C)	Dermal
Platyhelminthes	Pigment cups (C, R)	?
Nemertea	Pigment cups (R)	Cerebral
Rotifera	Pigment cups (R)	Cerebral
Nematoda	Pigment cups (R)	?
Annelida		
Polychaeta	Pigment cups (R), pigment tubes (R), lens eyes (R)	Cerebral, dermal
Mollusca		
Placophora	Pigment cup "shell eyes" (R) over valves	
Gastropoda	Pigment cups (R), lens eyes (C, R)	Dermal, ganglionic
Bivalvia	Pigment cups (R), pigment tubes (R), lens eyes (R)	Cerebral, dermal
Cephalopoda	Large pinhole eyes (R), lens eyes (R)	Epistellar body
Arthropoda		
Xiphosura	Nauplius and compound eyes (R)	Ventral photoreceptor
Crustacea		
Branchiopoda	Nauplius and compound eyes (R)	
Isopoda	Compound eyes (R)	
Amphipoda	Compound eyes (R)	
Ostracoda	Nauplius and compound eyes (R)	
Copepoda	Nauplius eyes (R), simple lens eyes (R)	
Cirripedia	Nauplius eye (R), compound eye (R)	
Stomatopoda	Nauplius eye (R), compound eyes (R)	
Euphausiacea	Nauplius eye (R), compound eyes (R)	
Decapoda	Nauplius eye (R), compound eyes (R)	Cerebral, caudal
Bryozoa	—	?
Echinodermata	Pigment cups (R)	Dermal
Chaetognatha	Pigment cups (C)	
Chordata		
Urochordata	Pigment cups (C)	

Eyes are considered to be directionally sensitive, cephalic photoreceptor organs. *Extraocular photoreceptors* have poor or no directional sensitivity, and are usually not restricted to the cephalic region. Abbreviations: C, ciliary; R, rhabdomeric.

Most molluscs continue to "view" the world through simple eyecups (see Land, 1984a for a recent review). However, some gastropod species have good eyes; for example, *Littorina littorea* has a lens eye that can form a very high-quality image in air (Hamilton *et al.*, 1983). Heteropod prosobranchs have wonderful eyes that scan vertically. They thus form images optically in the horizontal plane and *temporally* in the vertical plane (Land, 1982)! This method of seeing is unique in biological imaging systems. (There are a few retinas that seem to scan in all planes, and thus apparently build up the entire image as a time series, and some radio telescopes temporally scan in one plane, assisted by the earth's rotation. Some digitizing television cameras operate analogously to heteropod eyes; they scan a linear diode array through an optically focussed image.)

Bivalves usually make do without any particular ocular organs, though most probably do have light sensitivity on the mantle edge or in one or more ganglia. One marine bivalve, the scallop *Pecten maximus* (and probably other species of scallop), has proven itself the exception by evolving a spectacular set of several dozen non-cephalic eyes which ring the mantle margin. These form a reasonably sharp image on the retina using a combination lens-mirror optical system (Land, 1965, 1978; Fig. 3A). Scallops may have the only eyes which perform like a Schmidt astronomical camera, and they have its advantage of excellent light-gathering ability for the aperture. How the animal coordinates
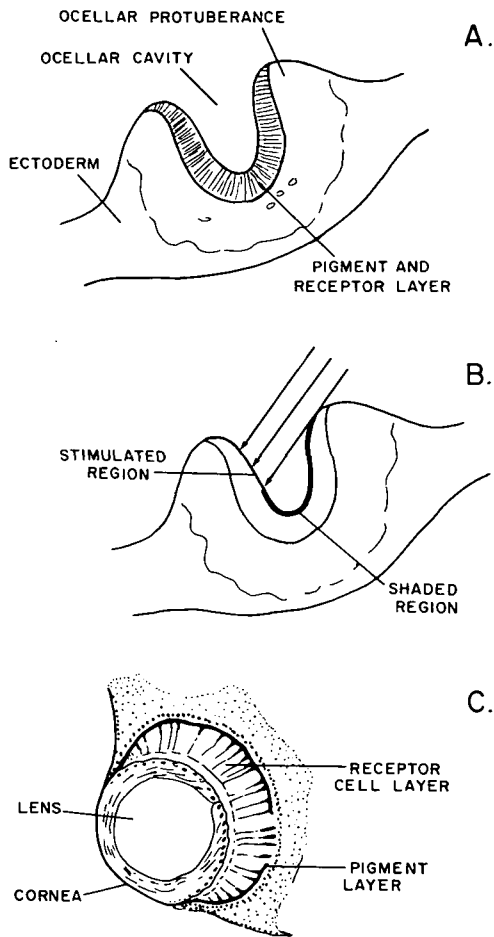
FIG. 2. Eyecup eyes from coelenterates. A. The simple eyecup of the hydromedusan *Spirocodon saltatrix*, consisting of a layer of photoreceptor cells lining the bottom of a U-shaped pit and extending from a pigment layer (after Toh *et al.*, 1979). B. Operation of the eyecup. The pigment layer causes a shadow to fall on the receptor layer, the location of which is related to the direction of light. C. A more specialized cubomedusan eyecup, which has added a lens. The function of the lens is unknown (after Pearse and Pearse, 1978).

FIG. 3. Molluscan eyes. A. The refracting-reflecting eye of the scallop. The image forms on the retina, just behind the lens. Defocussed light therefore first passes through the retina, degrading image contrast (after Land, 1978). B. Pinhole eye of *Nautilus* (vertical section). A fairly well-resolved, but very dim, image falls on the retina, which is the region located between the arrows (after Muntz and Raj, 1984). C. Refracting eye of *Octopus*. The high-quality lens forms a sharp retinal image. Retinal illumination is influenced by changes in the area of the pupil, and focussing occurs by longitudinal movements of the lens (after Wells, 1962).

input from 60 independently mobile, image-forming photoreceptors gives one something to think about; probably they act as glorified shadow detectors.

Perhaps the most impressive eyes of all invertebrates are to be found in the cephalopod molluscs (Fig. 3B, C). Here, inverted images are formed on a large retina containing closely packed receptor cells. The system is reminiscent of the vertebrate
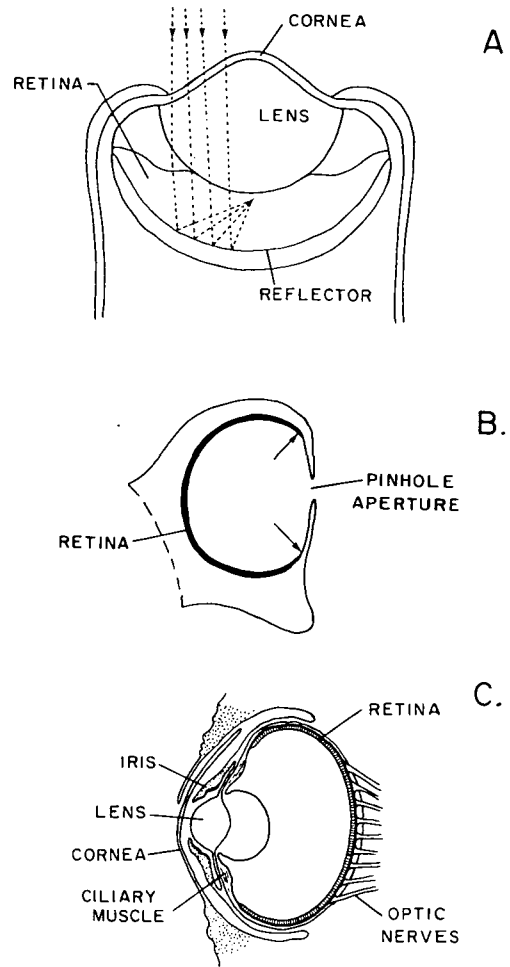
design, but has several fundamental differences in the details of its construction. Unlike the vertebrate case, the retina is *direct*, meaning that the individual receptor cells face the interior of the spherical eye, and the incoming light need not cross overlying neural layers before reaching them.
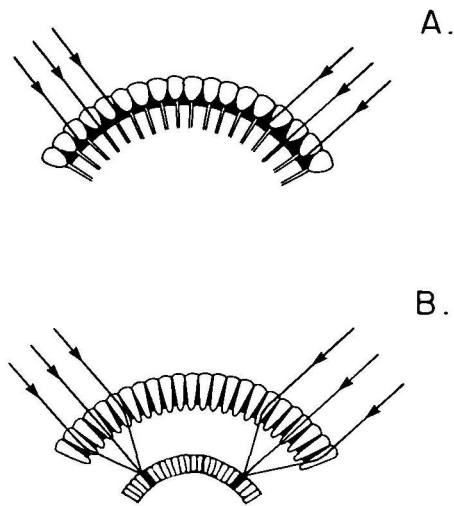
FIG. 4. Optical design in crustacean compound eyes. A. The apposition principle. Each receptor receives light through its individual cornea. The rhabdoms which would be stimulated by light from two directions are indicated. B. The superposition principle. Receptors are separated from the focussing elements by a clear zone, and each receptor may receive light through numerous corneal facets. Note that in both A and B, erect images form (both after Land, 1980).
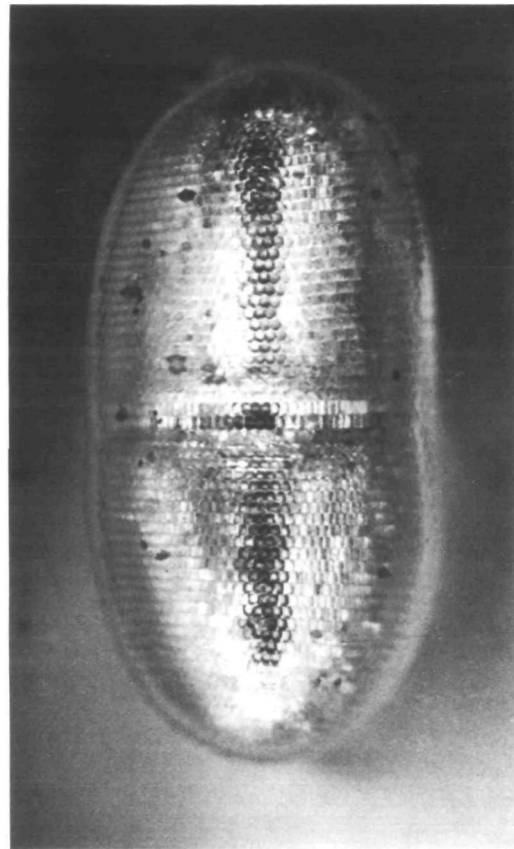

FIG. 5. The unusual apposition eye of *Squilla empusa*. In this eye, the visual field directly in front is sampled by independent groups of ommatidia in the top half, the bottom half, and the central band. The black specks on the surface of the eye are droplets of paint sprayed on in my laboratory to act as markers for mapping the eye.

Also, cephalopod photoreceptors are rhabdomeric (all vertebrates have ciliary photoreceptors), and their microvilli are properly oriented to permit discrimination of plane-polarized light. The large eye of *Nautilus* is famous as the epitome of a biological "pinhole camera" (Fig. 3B). It forms fairly sharp, if very dim, images (Muntz and Raj, 1984). However, as Land (1984a) has remarked, virtually any optical device at all behind the pinhole would improve both resolution and retinal illuminance, and it is puzzling that the design has withstood hundreds of millions of years of evolutionary time. Eyes of most squids, octopuses, and cuttlefish are of conventional camera design (Fig. 3C) and form excellent, bright images.

Arthropods have generally taken a different route to imaging their world; they build compound eyes from hundreds or thousands of independent optical units. Crustacean vision has been reviewed in some detail recently (Shaw and Stowe, 1982; Land, 1984b; Cronin, 1986), and in any event is far too complex and diverse to be discussed at length here. The xiphosauran *Limulus polyphemus* has, of course, for years provided vision scientists with an accessible and manipulable set of photoreceptors, and it is still serving the field with grace.

Compound eyes form erect, compound images, so that the top of the visual field is imaged onto the top of the eye itself. The optical array may operate in one of two ways (Fig. 4). Either each ommatidium acts as an independent radiometer for light collected in its visual field (the apposition design, Fig. 4A), or the imaging elements of numerous ommatidia may superimpose their focussed rays onto a small patch of
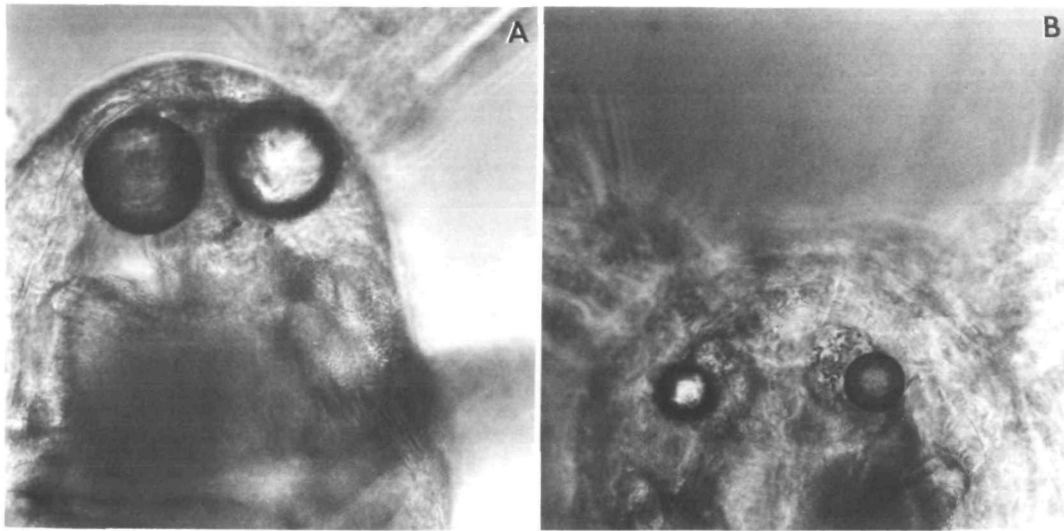
FIG. 6. The relatively large lensed eyes of the pontellid calanoid copepod, *Labidocera aestiva*. There is a striking dimorphism between the adult male (A) and female (B) type of eye. The cuticular lens of the male has a diameter of about 85 μm, while the female's lens is $\approx$40 μm in diameter. The reason for the dimorphism is unexplained; perhaps it is related to mating behavior in this species. In *L. aestiva* females, different types of eggs are produced in different photoperiods (Marcus, 1982).

receptors (the superposition type, Fig. 4B). The former design usually achieves greater resolution; the latter, greater image brightness. Probably the most specialized compound eyes of any arthropods are to be found in the stomatopod crustaceans (mantis shrimps, Fig. 5). These stalked, independently operated receptors may have as many as 3 different areas of the same eye looking at the same point in space (Horridge, 1978), providing a potential capacity for range finding in a single eye.

In many crustacean species, including whole taxa, compound eyes are not found. The large deep-sea ostracod *Gigantocypris* has 2 relatively huge collecting mirrors that produce low-resolution, but greatly intensified, images (Land, 1978). Copepods occasionally have exotic eyes, and these occur particularly among some Cyclopoid families as well as in the pontellid calanoid copepods. The odd double-lensed scanning eyes of *Copilia* and similar genera were recently discussed by Land (1981), who has also published photographs of the large, sexually dimorphic dorsal eyes of *Labidocera acutifrons* (Land, 1984b). The American pontellid *Labidocera aestiva*, which

exhibits photoperiodism, has a similar sexual dimorphism (Fig. 6). The ways in which *Labidocera* uses its eyes, and the reason for the dimorphism, are unexplained.

Eye design in higher deuterostomes

Other than the vertebrates, no deuterostome group has evolved eyes of any great competence. Echinoderms have never had high-quality eyes; they manage either with numerous eyecups on their extremities or with more generalized dermal light-sensitive receptors. A similar situation exists among the urochordates, although it is not known whether they have extraocular receptors. Chaetognaths have pigment-cup eyes that are noteworthy for their involvement in the animal's orientation and vertical migration behavior (Goto and Yoshida, 1984) and for their unique lamellar receptor membrane organization (Goto *et al.*, 1984).

Invertebrate extraocular photoreceptors

Many invertebrates, whether or not they possess any organs clearly definable as eyes, have a nonspecific diffuse light sense (Yoshida, 1979). In some cases, there may

be photoreceptors in specific ganglia, such as the caudal photoreceptor of decapod crustaceans (Wilkens and Larimer, 1976). This type of sensation may lead to such sophisticated behavior as the covering responses of various sea urchins, and it is likely based on photopigments closely similar to the visual pigments. In view of the involvement of extraocular photoreception in controlling (or at least influencing) circadian rhythms of diverse groups of invertebrates (reviewed by Bennett, 1979), photoperiodic phenomena of marine invertebrates may also frequently be under the influence of extraocular systems.

CIRCADIAN PROCESSES

As is true of many other aspects of vision science, the only invertebrate visual systems that have been subjected to a detailed analysis of light : dark cyclic effects are molluscan and arthropod eyes. Not surprisingly, in these organs there is a daily cycle of structural change in the photoreceptor membrane which is under both exogenous and endogenus control. What had not been expected is the sheer magnitude of the changes which occur in some species over the diel cycle, and the influence which the central nervous system exerts over them. It is likely that these membrane cycles are necessary for the renewal of visual pigment in rhabdomeric membranes (Cronin and Goldsmith, 1984).

Photoreceptor membrane turnover in crustaceans was reviewed by Waterman (1982) and new research has added considerable detail since then. Eguchi and Waterman (1967) first described a crustacean membrane synthesis-degradation sequence, in the crab *Libinia emarginata*. This landmark study was restricted to the effects of light and dark adaptation, and it revealed that degradation of rhabdomal microvillar membrane was greatest in the light. This paper also first described the sequence of cytological effects which occur during microvillar membrane degradation.

Recent research shows that some crabs are particularly impressive in their ability to restructure their photoreceptor membranes on a daily basis. *Callinectes sapidus* more than doubles its rhabdomeric mem-

branes between noon and night (Toh and Waterman, 1982), and the grapsids *Grapsus grapsus* and *Leptograpsus variegatus* have daily cycles of astonishing amplitude: their nocturnal rhabdoms are 20 times as large as diurnal ones (Nässel and Waterman, 1979; Stowe, 1980b). Moreover, *Leptograpsus*, at least, synthesizes this huge rhabdom completely *de novo* in a massive event occurring within an hour of onset of dark (Stowe, 1981). At dawn, the rhabdoms are reduced to their daytime size by pinocytosis at the microvillar bases followed by digestion of the removed membrane; thus, much of the membrane synthesized at dusk survives only a few hours.

Control of this cycle of synthesis and degradation of membrane is under investigation, but it is clear that the changes of light intensity associated with dawn and dusk are necessary for the greatest amplitude. On the other hand, both synthesis and breakdown will occur in constant light (synthesis) or constant dark (degradation), but after a delay and at a lower level than in light : dark (Stowe, 1982, 1983). The source of the central control is not known, and decapod crustacean eyes probably do not receive efferent input, but the synthetic event occurs in intact animals or isolated eyestalks with similar physiology (Stowe, 1982). Unknown also is whether the membrane cycle will continue to be expressed in constant conditions, or whether it is an "hourglass" type of event which requires daily resetting.

The invertebrate system in which the interplay of central and external cues is best understood is the compound eye of *Limulus polyphemus*. *Limulus* sheds virtually all its rhabdomeric microvilli each dawn and within the hour synthesizes (or at least inserts) a new batch of photoreceptor membrane (Chamberlain and Barlow, 1984). This event requires the occurrence of dawn (or lights-on), and will not happen in constant dark. In addition, the eye must receive efferent input from the brain for at least 3 to 5 hours to be primed for the turnover sequence (reviewed in Barlow and Chamberlain, 1980). Here, the brain's output of efference is known to be circadian (Barlow and Chamberlain, 1980).

Some molluscs have cycles of membrane synthesis and breakdown, but little is known about their physiology. Abalone, when kept in a 12 hr:12 hr light: dark cycle, produce long and regular microvilli during the dark phase which subsequently shed or break down in the light; the effects of constant conditions have not been investigated (Kataoka and Yamamoto, 1981). *Octopus ocellatus* undergoes similar changes, and the appearance characteristic of the light- or dark-adapted state simply becomes more pronounced with prolongation of the light or dark (Kataoka and Yamamoto, 1983), so the cephalopod case may differ from crustaceans.

The daily turnover of photoreceptor membrane leads directly to altered visual sensitivity (Williams, 1983), and even when primarily under environmental control this or accompanying daily events could provide input for day-length measuring systems. Among these auxiliary cycles are the well known rhythm of crustacean accessory pigment migration (reviewed by Kleinholz, 1961 and by Autrum in Autrum, 1982*b*), the daily change in angular sensitivity of compound eye ommatidia due to photomechanical changes (Barlow and Chamberlain, 1980; Leggett and Stavenga, 1981), and the circadian retinal sensitivity rhythm (Larimer and Smith, 1980). Study of the latter, in particular, has revealed a truly complex arrangement of oscillators and coupling mechanisms all operating in concert; time measurement would probably be a trivial task for such a system.

CONCLUSIONS

In this brief review there has not been space to provide more than a taste of the variety of structures and processes which characterizes invertebrate photoreception. I have been successful in my presentation if I have helped the reader become aware of some of the ways in which the various invertebrate phyla are able to keep themselves informed about their photic environments. If I have encouraged him or her to turn to the more thorough reviews mentioned in the introduction, so much the better. Invertebrate photoreceptors frequently are superbly adapted to pack

high sensitivity and fine resolution into a very small unit, in some ways outperforming anything the vertebrates have come up with. They yet hold many surprises for us.

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