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The comparative physiology of extraocular photoreception

Introduction

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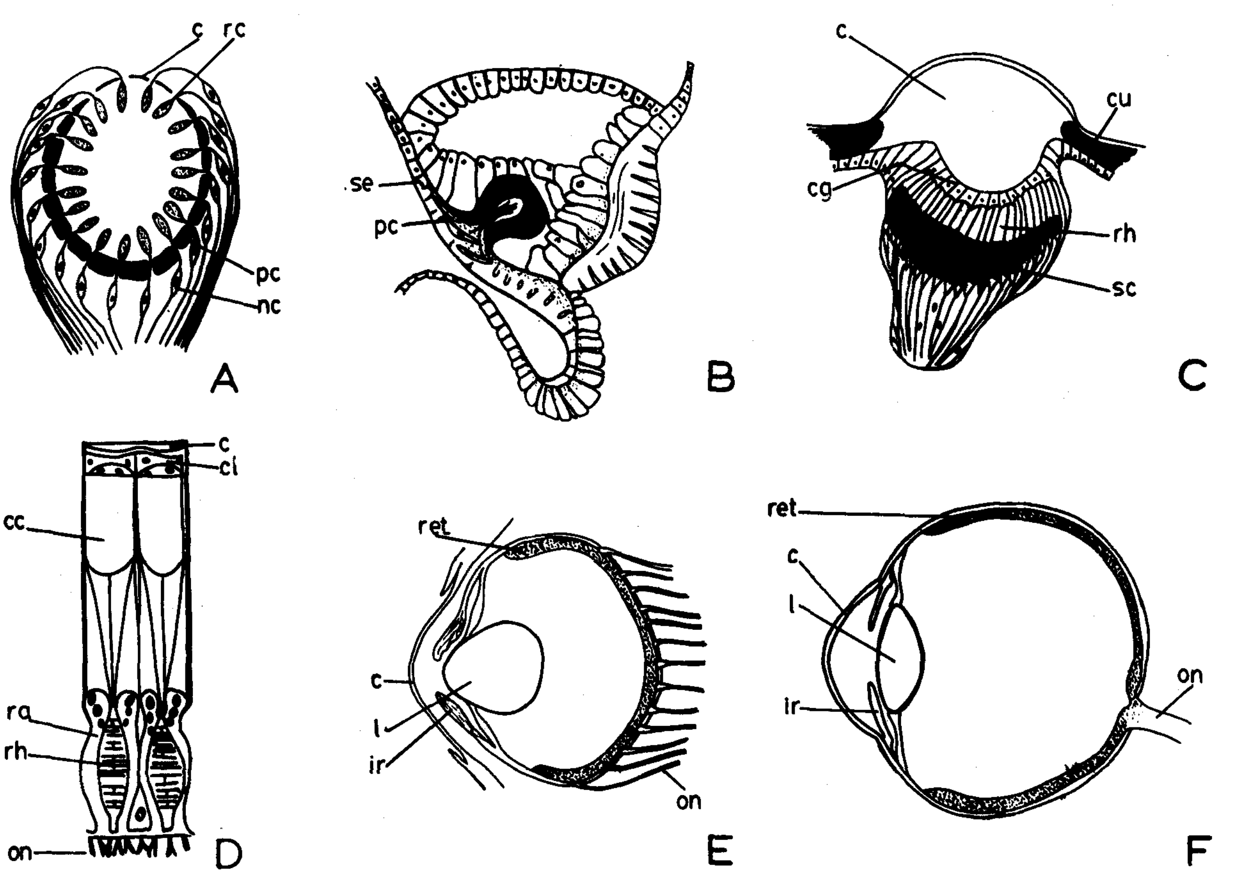
The perception of light is undoubtedly one of the most common sensory abilities found in animals. This is hardly surprising if one considers that the presence of light, in spite of variations with time of day, latitude and habitat, is a dominant aspect of the external milieu in which all, except a few, animals live. In order to use the information present in the visual environment most organisms possess well-developed photosensory organs which, their large variety notwithstanding, are collectively referred to as eyes. Ocular photoreception typically involves more than the mere transduction of photic energy. Particularly, many eyes possess a highly organized neural network to analyze the spatio-temporal structure of the visual world outside. For this purpose they have additional accessory systems including an image-forming apparatus and an oculomotor system.

Although some protozoans (e.g. the green flagellate, *Euglena*) have primitive photoreceptive systems, simple eyes are first encountered in jellyfish which possess cup-shaped ocelli containing a refractive structure and patches of pigment cells (fig., A). More specialized eyes are found in the Plathelminthes and the Annelids (fig., B). There is little dispute that these eyes can discriminate light intensities and allow the organism to orientate itself with respect to the direction of illumination. Complex visual processing, however, requires a more advanced degree of ocular development. Two major types of ocular photoreceptive organs have developed to achieve this: the compound eyes of arthropods and the camera-type eyes of molluscs and vertebrates (fig., D, E, F). In addition, the dorsal ocelli of insects exhibit many features of a primitive eye (fig., C). Compound eyes have genuine refractive structures: the lens and the crystalline cone. Through these light gains access to the photoreceptor cell (retinula) which can initiate nerve impulses in the optic fibers projecting to the brain. The camera-type eye is found in molluscs where it is most highly developed in the cephalopods. These eyes bear great resemblances to those of vertebrates: they both possess refractive structures (lens and cornea), an accessory image-forming apparatus in the form of an iris and pupil and an intricately organized retina (fig., E, F). It is a further characteristic of bilateral ocular photosensory systems that the eyes project to well-defined regions of the central nervous system where visual information is further processed and integrated with other sensory information.

In view of the predominant importance of ocular photoreception in all but the more primitive organisms the eyes have received much more attention from physiologists than extra-ocular photoreceptive systems. While the first experimental and theoretical studies of the human eye date back to Ibn al-Haytham (965-1039)[1] the earliest reports of photoreception mediated by photoreceptors of unknown localization, in the European minnow *(Phoxinus phoxinus)* and in amphibia, were published at the beginning of this century[2-4]. At present, however, many investigations have established the existence and functional importance of extraocular photoreceptors (EOP's) in both vertebrates and invertebrates. The classical method to demonstrate extraocular photoreception (EOP) involves the surgical removal of the eyes. With this technique it was shown that in blinded fishes, reptiles, and amphibia, positive and negative phototactic responses as well as pigmentary adaptation of the skin can still be evoked by light. A much more striking finding is that EOP's in many species ranging from molluscs to birds apparently mediate the effects of light on 2 particular functions: circadian rhythms and photoperiodic time measurement. In fact, the best generalization that can presently be made about EOP is that in all invertebrates and submammalian vertebrates which have been studied in this respect, it plays an important role in the entrainment of circadian rhythms to light-dark cycles and the effects of seasonally changing photoperiod on such functions as reproduction and migratory activity. Interestingly, circadian rhythmicity and photoperiodic time measurement are intimately related[5,6]. The ability to detect changes in daylength and the subsequent induction or termination of, for instance, testicular growth in birds or diapause in insects requires the presence of an entrained circadian pacemaker. In view of their well-established functional importance EOP's deserve attention not because they represent an exotic rarity of animals which predominantly rely on their eyes for visual perception but rather because they relay the most common aspect of the visual environment, the daily alternations between day and night, to those functions that critically depend on this information.

A natural starting point of the study of EOP's is to establish their localization. This has been attempted in a number of ways. When the eyes are removed putative photoreceptors elsewhere in the animal's body can subsequently be eliminated to study the effects of such lesions on photically induced responses. Thus, in insects the ocelli and different parts of the nervous system have been lesioned. In vertebrates destruction of the pineal end organ and epiphysis has been attempted since these represent well-known EOP's. Alternatively, the penetration of light into various body compartments can be blocked to establish if EOP is thereby eliminated. Von Frisch[2] and Benoit[7] were among the first to localize EOP's by direct illumination of circumscribed regions of the brain in vertebrates. The most recently developed technique for localized photostimulation involves the implantation of light-emitting diodes or radioluminescent probes. In general, these studies have all implicated neural structures as the site of EOP. In the invertebrates the indications are strong that the brain contains photoreceptors which mediate circadian rhythm entrainment and photoperiodic responses. In the special case of *Aplysia* individual photoreceptive neurones have been identified in the abdominal ganglion. Also in the vertebrates the central nervous system appears to be the major site of EOP. In particular, regions of the diencephalon in the vicinity of the third ventricle are most conspicuous. Deep brain photoreceptors are scattered throughout the diencephalon of lower vertebrates and birds while the pineal and the pineal end organs of lower vertebrates stand out as relatively highly developed photosensory structures. While in most vertebrates EOPs are present and serve similar functions as in invertebrates,



Schematic illustrations of various ocular photoreceptor organs. *A* Eye of a land planarian; *B* complex ocellus of a jelly fish; *C* dorsal ocellus of an insect; *D* ommatidia; *E* octopus eye; *F* generalized vertebrate eye.
Abbreviations: c, cornea; cc, crystalline cone; cg, cl, corneagenous cells; cu, cuticula; ir, iris; l, lens; nc, nerve cells; on, optic nerves; pc, pigment cells; ra, retinular cells; rc, retinal club; ret, retina; rh, rhabdome; sc, sense cells; se, sensory epithelium.

mammals have apparently lost the ability to perceive light extraretinally.

The localization of EOP's in invertebrates may not be so surprising in view of the fact that the central control of circadian rhythms and photoperiodic time measurement in molluscs and insects is also mediated by brain structures. In vertebrates, this correspondence between the site of the brain photoreceptors and the central neural mechanisms controlling these two functions is even more conspicuous. The pineal system, itself a photoreceptive structure, has been identified as an important component of the circadian pacemaker in lower vertebrates and birds[8]. The ventral diencephalon, moreover, contains the suprachiasmatic nuclei which are regarded as a putative circadian pacemaker in birds and mammals. Pinealectomy and lesions of the suprachiasmatic nuclei also abolish the animal's ability to respond to changing photoperiod[8]. Thus there seems to be a close structural relationship between EOP's and those regions of the diencephalon which utilize their photosensory capacity to respond to the daily illumination cycle and the seasonal lengthening and shortening of the photoperiod.

EOP's also present us with problems relating to the mechanisms of phototransduction and their morphological and anatomical organization. Unfortunately comparatively little is known about these more microscopic questions. In two cases, however, a detailed study at the cellular level has recently become possible: the photoreceptive neurones of the abdominal ganglion of *Aplysia* and the pineal and parietal organs of lower vertebrates. Here the photoreceptors are identified and can therefore be subjected to the full range of experimental techniques available to the photobiologist. In this way many details of the photochemistry and electrophysiology of these cells have been unravelled. In those instances where localization has as yet proved impossible, progress is being made with the microphotospectrometric analysis of tiny sections of brain tissue containing photoreceptor cells.

In the following papers many of the different aspects of EOP will be reviewed. The electrophysiological and photobiological study of 3 types of identified EOP's is discussed in the first three contributions. Andresen and Brown will summarize their work on the photosensitive neurones in the molluscan brain and demonstrate how nerve cells lacking the classical morphology of ocular photoreceptors transduce photic energy into a conductance change of their membrane. In the second and third papers the visual properties of diencephalic photoreceptors in the vertebrate brain are described by Hartwig and Oksche, while Dodt and Meissl review the neurobiology of another identified extraocular photoreceptive system in vertebrates: the pineal and parietal organs. The last three papers focus on the functional aspects of EOPs. Here their localization and function are reviewed for the invertebrates by Page and for the vertebrates by Underwood and Groos. In these two papers separate attention will be given to the importance of EOPs relative to that of the eyes. In the last review by Oliver and Baylé the special case of encephalic photoreception in birds will be discussed in detail.

The present review series demonstrates the functional significance of extraocular photoreception for a wide variety of species in which EOP's have been described. No doubt neurobiologists will direct increasing attention on extraocular photoreception extending our modest understanding presently reflected in this review series.

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Neurobiological aspects of extraretinal photoreceptive systems: structure and function*

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In vertebrates, photosensory systems that in part have been proven to mediate environmental photoperiodic cues synchronizing self-sustaining clock mechanisms have evolved from the matrix of the diencephalon along 3 different lines: a) lateral eyes and their retinohypothalamic projections, b) deep encephalic photoreceptors, and c) pineal sense organs (for references see Oksche and Hartwig[1]). In mammals, retino-