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Concluding remarks

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It is intriguing that in many species, including insects, molluscs and sub-mammalian vertebrates, that have well developed eyes for visual perception of spatial-temporal gradients, movement, etc., extraocular photoreceptors (EOP's) have been demonstrated. A phylogenetic discontinuity may be apparent in mammals, for adults at least lack extraocular photoreceptors, although there are reports of EOP's in some (e.g. rat) neonatal mammals.

Extraocular photoreceptors are localized within the CNS or are to be found in anterior tentacles and rhinophores of invertebrates. In vertebrates photoreceptors may be found in the pineal-parietal organ complex. These epiphysial regions share a common embryonic origin with the retina, each developing phylogenetically as diencephalic evaginations. It is probable that a circumscribed region of the diencephalic primordium is the only area to be found in vertebrates capable of forming photoreceptive cells. Encephalic EOP's have also been localized to a circumscribed ependymal area covering the antero-dorsal hypothalamus of sub-mammalian vertebrates.

Phylogenetically, there is a gradual transformation in function; the pineal complex, initially a photosensitive organ in primitive vertebrates, becomes a neuroendocrine organ whose activity is controlled in part by an indirect photic input in the mammals. This functional development is paralleled by structural transformations of pineal cells from photoreceptors (fish, amphibia) through rudimentary photoreceptor structures (birds) to secretory pinealocytes found in mammals. The extraocular photoreceptive cells resemble retinal photoreceptors in their morphology. It is noteworthy that the putative receptor cells associated with the deep encephalic EOP's in *Phoxinus phoxinus* are reminiscent of retinal (and pineal) photoreceptors at an early developmental stage.

Aplysia again provides neurobiology with a model system implicating calcium release as the primary event in the phototransduction mechanism of the photosensitive neurones located in the abdominal ganglia of this species. Alternative transduction mechanisms, for example, photosensitive enzymes or modulation of enzymes through photochromic co-factors, may also be significant. An important consideration with respect to deep encephalic photoreceptive mechanisms is that of light penetration and light absorption by tissue overlying the photopigment. There may be a scattering in the tissue or specific absorption by identified substances, e.g. hemoglobin and metanin. These factors determine the lower end of the photo-sensitivity range and the action spectrum, with longer wavelengths penetrating tissue better than shorter wavelengths in vertebrates.

The biological significance of extraocular photoreception may be appreciated on the basis of the spectrum of functions in which it plays a central role in both the invertebrates and vertebrates. Thus, EOP's may serve as a light-dosimeter, processing information related to environmental luminance levels. Such information has importance in light-induced (conditional) reflex skin coloration changes (e.g. in *Phoxinus phoxinus*) and phototactic response behaviors (e.g. *Alligator mississippiensis*). Extraocular photoreception assumes a central role in the regulation of photoperiodic behavior. This includes photic entrainment of circadian rhythmicity in the invertebrates, fish (e.g. *Anguilla anguilla*) and reptiles, photoperiodic control of gonadal growth in birds (e.g. *Passer domesticus*) and importance in photoperiodic time measurement, e.g. in invertebrates during metamorphosis when organized photoreceptors are absent or non-functional. A functional discontinuity again is apparent when considering mammalian photoperiodic behaviors for these appear to be regulated through the suprachiasmatic nuclei of the hypothalamus which is in receipt of a direct retinal input. For sub-mammalian species, at least, extraocular photoreceptors constitute an essential functional system complementing the 'retinal (ocular) visual system' in the analysis of the visual environment and in regulating the organism's response to it.