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The pineal and parietal organs of lower vertebrates

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In addition to deep encephalic photoreceptive areas, the principal site of extraocular photoreception in lower vertebrates seems to be the pineal complex. During phylogenetic development the morphological appearance of the pineal complex reveales striking differences among different species. A remarkable phenomenon is the continuous change from a photoreceptor organ to an indirectly photosensitive secretory organ with a transformation from a photoreceptor cell type (in lower vertebrates) to the secretory pinealocyte (in mammals). The great diversity in the anatomical and ultrastructural appearance of the pineal system is also reflected by the great number of functions in which it has been implicated. These include bodily changes as skin pigmentation, phototaxis, orientation, locomotion, metabolic and thermoregulatory responses and other rhythmical events which were attributed to the pineal. The present review compares the physiological performance of the pineal system of lower vertebrates in regard to their photoreceptive capacities.

Structural outline

Almost all vertebrates possess an intracranially located pineal organ, synonymously called the pineal gland or epiphysis cerebri. An extracranial part - the frontal organ (Stirnorgan), the parietal organ, or parietal eye - is found in anurans and in lizards. The frontal (parietal) organ is connected to the epiphysis by the frontal (parietal) organ nerve; a pineal tract projects from the epiphysis to other brain structures. Nerve fibers from the frontal organ were shown to form only a small part of the pineal tract[1-3]. Ultrastructurally, the pineal complex contains photoreceptive sensory cells resembling the retinal cones of the lateral eye[4-7], showing multiple membrane invaginations of their outer segments. They are shorter in length and contain a smaller number of discs compared to retinal photoreceptors[8]. The outer segments display a scattered arrangement and protrude into the pineal lumen, which communicates with the cerebrospinal fluid of the third ventricle. The majority of the receptor outer segments project in horizontal direction, arranged parallel to the roof of the bony skull[9,10].

Other cellular elements of the pineal system are nerve cells and interstitial (supportive or glia) cells. Two types of nerve cells were identified by means of the acetylcholinesterase (AChE) reaction in the pineal complex of anurans: multipolar cells - possibly interneurons - and pseudounipolar cells sending their axons into the pineal tract[11]. AChE preparations do not provide evidence for the presence of horizontal and bipolar cells in the frog's pineal organ. The amacrine-like multipolar cells of the pineal organ

might be interneurons displaying a mechanism different from that of retinal amacrine cells[11].

Tissue absorbance in front of the pineal complex

Presupposition for a photoreceptive function is that light reaches the visual pigment in the outer segments of photoreceptors. Light that is absorbed, scattered or reflected by the tissue overlying the pineal does not contribute to photoreception. In lower vertebrates which have developed an extracranial portion of the pineal system, the photoreceptor organ has a superficial position in the integument near the innermost skin layers (frontal organ in anurans) or between the parietal bones closely beneath the surface of the skull (parietal eye in Lacertilia). In the frog's frontal organ light penetrates the outer translucent skin layers (Stieda's spot) before entering the photosensitive structures. Measurements of the light absorbance of the frog's skin revealed that about 50% of light incident from above is absorbed in this area[12] in *Rana temporaria*. In the lizard's parietal eye more than 20% of the incident white light reaches the photoreceptor cells[13]. Moreover, the position outside the skull favors transmission of light to the pineal complex to serve specialized tasks such as the perception of ultraviolet and/or polarized light.

The situation for the intracranially located epiphysis is different. In some fishes, the bones of the skull form a pineal window[14], i.e., they have less pigmented zones that enable light penetration. In several species of sharks these structures permit up to seven times more light to enter the brain cavity when compared to the surrounding tissue[15]. About 10% of the incident light is transmitted through such a pineal window in young trouts[16]. In amphibians the intracranial pineal organ is covered by the bony skull and deeply pigmented skin, and thus highly protected from the incident light. In *Rana* about 0.1–0.3% of the light falling on the skull overlying the pineal area penetrates into the cranium[16]. In reptiles the corresponding values of light transmittance are 0.01 in *Iguana* and 0.2 in *Lacerta*[17], but for some wavelengths much lower in the presence of abundant blood vessels on top of the epiphysis. Measurable quantities of radiant energy penetrate also the skull of birds[18] and mammals[19].

Beside the absolute number of photons the spectral transmission of the tissue covering the photoreceptor organ determines the effective light input. In a number of vertebrates longer wavelengths (according to the absorption spectrum of hemoglobin) penetrate the tissue in front of the diencephalon about 1000 times more effectively than shorter wavelengths[20]. In the turtle *Pseudemys scripta elegans* about 2 log units of the incident light are absorbed between 600 and 700 nm, but nearly 5 log units at 450 nm. Thus, in this species the operating range of the photosensitive structure is limited to photopic conditions[21]. In larger sized animals, transmission of light to the deeply located pineal organ is low and, due to the rich blood supply of the organ, becomes finally insignificant. This causes a demand to translocate light reception from the epiphysis to the lateral eye as realized in higher vertebrates in the evolution of species[22].

Neuro-photoreceptive mechanisms of the pineal system

Maintained activity. Electrophysiological studies of pineal systems demonstrating extraocular photoreception in lower vertebrates include fishes (Cyclostomata, Chondrichthyes, Teleostei), amphibians (Anura) and reptiles (Lacertilia, Chelonia). All lower vertebrates investigated so far show signs of light-modulated electrical activity in the deeply located diencephalic structures of the epiphysis cerebri. The most common type of activity seen is a maintained discharge of nerve cells or fibers in the absence of external stimuli. The only stimulus effectively changing the frequency of this discharge is light[23]. Steady illumination decreases the maintained activity almost linearly with the logarithm of light intensity. This relationship holds over a range of 5–6 log units in the epiphysis of the frog[24] and the pike[25] and of approximately 4 log units in the turtle[21]. The frog's frontal organ changes its maintained activity over a range of at least 6.0 log units[26]. Thus, both components of the pineal complex operate over a wide range of light intensities thereby providing messages to the brain related to the ambient light level.

If the pineal is exposed to light flashes, instead of constant illumination, two types of response are recorded from the pineal complex. One consists of an opposed colour mechanism, i.e., of inhibition upon illumination by stimuli of short wavelengths and excitation to light of longer wavelengths (chromatic response). The other type is not colour coded and responds similarly to light of all wavelengths by a decrease of the firing rate or complete inhibition of the maintained discharge followed by an off-response after the end of stimulation (achromatic or luminance response).

Chromatic response

The chromatic response mechanism consists of inhibitory responses to short wavelengths and excitatory responses to medium and longer wavelengths. The 2 effects interact and the response to a given light stimulus depends on the wavelength and energy of previous illumination[12,27,28]. In fishes and frogs the inhibitory component is most sensitive to UV light (λ_{max} 355 nm)[12,25], and in lizards to blue light (λ_{max} 450 nm)[13]. The excitatory component is strongest in the green (λ_{max} 515–520 nm, frogs and lizards) and in the red (λ_{max} 620 nm, in the pike) region of the spectrum. The relation of threshold

energies between the inhibitory and the excitatory components varies, the inhibitory component being about 2 log units more sensitive in frogs, whereas dominance of the excitatory component is seen in the lizard. Thus, the net output of the frontal and parietal organ depends on the balance between opposite inhibitory and excitatory processes in response to the particular spectral composition of the incident light[12,29]. This balance provides a sensitive means for the assessment of variations in the spectral composition of day-light, where cyclic variations occur both in spectral composition and light energy. Thus, daily changes in the constituent parts of the visible spectrum shift the chromatic response to another state of activation. The nervous mechanism of such interactions in the pineal may be realized by 2 different receptor populations making synaptic contacts with a common ganglion cell using different (inhibitory and excitatory) transmitters[27], photointerconversion of 2 states of a single visual pigment employing only one type of receptor[30,31] or - more probably - by functionally polarized interneurons which transfer information from one cone system to another[32,33].

Achromatic (luminance) response

The inhibitory action of light to all wavelenghts in the visible and UV spectrum is the most common response of the pineal. The great majority of cells in the epiphysis and about half of the fibers in the frog's frontal organ nerve respond in this way. The response differs considerably from the chromatic response with respect to the absolute threshold, spectral sensitivity and the adaptation process. The lowermost light threshold of the achromatic response, measured so far in a dark adapted frog epiphysis, is at 3.6×10^{-6} lm/m^2 [34], which is of the same order as the light threshold of the isolated retina of the dark adapted frog's eye[35]. This indicates a highly developed nervous organization with a high degree of convergence of numerous sensory cells to one nerve cell[36]. The corresponding light threshold for the chromatic response, which exhibits a smaller but distinct sensitivity change during dark adaptation[29] is several log units above that of the achromatic response[12]. The illumination of bright sunlight is of 10^5 lm/m^2 [37], which is about 10^{11} times higher than the intensity threshold after dark adaptation of the achromatic response of the epiphysis. With constant illumination of the frog's pineal organ, full inhibition of the maintained discharge of the epiphysis cerebri occurred at a level of illumination between 2 and 8 lm/m^2 [24]. If the threshold measurements obtained from the exposed diencephalon are corrected for tissue absorbance by 3 log units the light threshold of the pineal organ in situ is still 2 log units below the luminance of full moonlight.

In some species, the spectral sensitivity of the response shows striking similarities to the spectral sensitivity of their lateral eyes. Using microspectrophotometric techniques a visual pigment was identified in the frog's frontal organ after bleaching at λ_{max} 550-580 nm[38] which is close to the sensitivity maximum of the achromatic response of pineal nerve fibers[12], and epiphyseal photoreceptors of adult *Rana temporaria* contain the visual pigment 502[38] like the accessory cones of the frog's retina. It was therefore concluded that the red cones of the epiphysis serve a scotopic apparatus[38]. With electrophysiological methods a spectrosensitivity was found matching the absorption spectrum of rhodopsin in the dark adapted epiphysis and with iodopsin while light adapted[34]. Electrical recordings from the pike's pineal organ show the presence of a green (λ_{max} 530 nm) and a red photopigment (λ_{max} 620 nm) during light adaptation and of only a green one in the dark adapted state[25], resembling the Purkinje shift of the frog's epiphysis[34]. Surprisingly, such a shift has not yet been observed in the frog's frontal organ where the achromatic response usually displayed an action spectrum at 560 nm. In lampreys the Purkinje shift is accompanied by a change of the type of response, i.e., the inhibitory effect of light on the maintained discharge (λ_{max} 525 nm) is replaced during light adaptation (which inhibits the maintained activity) by off-discharges (λ_{max} 590 nm) at the end of the light flash[39].

The comparison between retinal and pineal spectral properties suggests close relations between pineal photoreceptors and retinal cones. Small deviations in the action and absorption spectra will probably be eliminated if improved techniques will be at disposal for the measurement of the absorption spectra of pineal cells. Therefore it is tempting to assume that the retinal and pineal photoreceptors developed parallel mechanisms in evolution.

Slow potentials. In addition to the impulse discharge of ganglion cells and nerve fibers illumination of the pineal complex evokes slow (graded) potential changes analogous to the electroretinogram, and is accordingly called the electropinealogram (EPG). The potentials were recorded from the lizard's parietal eye[13,40] as well as from the frog's frontal organ[41] and from the epiphysis of fishes[25,42] and frogs[43].

Chromatic as well as achromatic (luminance) responses are reflected in these potentials. In the chromatic EPG the direction of change parallels the impulse activity, viz., a positive potential at the recording electrode in the parietal eye produced by a blue test light is associated with impulse inhibition, a negative deflection in response to medium and longer wavelengths with nervous excitation[13]. Similar changes occur in the frontal organ of *Rana temporaria:* UV radiation and light of shorter wavelengths elicit a slow potential opposite in direction to that evoked by longer wavelengths[41], i.e., the polarity of the EPG changes with wavelength, if chromatic units

are present. The pineals of lamprey[39] and pike[25] respond to various wavelengths with unidirectional (positive) slow potentials despite the fact that some chromatic units are present. It was therefore concluded that the EPG of the lamprey mainly reflects the activity of the achromatic units, the most common type of response seen.

For the origin of the EPG several candidates are available: photoreceptor cells, neural as well as supportive elements. The slow potentials may arise from ganglion cells as summated postsynaptic potentials spread electrotonically to the electrode[27] or from the photoreceptors as summated extracellular currents[39,43]. Recordings from pineal photoreceptors of some teleosts[42,44] are in favour of the latter suggestion, showing intracellular potentials similar in direction, shape and time course to the EPG. Confirming evidence for the receptor origin of the EPG also comes from in vitro recordings from the dissected median part of the pike's pineal organ[25] where nerve cells are absent[45]. A more detailed discussion is given elsewhere[43].

Early receptor potentials. Using intraretinal microelectrodes fast summated potentials were recorded after an intense light flash[46]. This so-called early receptor potential (ERP) is characterized by an extremely short latency, and has been observed in all vertebrate and invertebrate eyes investigated so far[47]. It is probably generated by the direct action of light on the visual pigment in the outer segments of photoreceptors and produced by charge displacements within the pigment molecule. In mixed retinae, the ERP is generated mostly by cones[48] and, therefore, of particular interest for research of the pineal photoreceptors which are cone-like in structure.

So far, rapid photoresponses in response to brief, high intensity flashes were obtained from the epiphysis of *Rana catesbeiana* and *Rana esculenta*[49] and from the pineal organ of the pike[50]. The response appeared without detectable latency, and its shape resembled the ERP of the lateral eye. Upon repetitive stimulation the potential was greatly diminished and abolished after bleaching the visual pigment. A photoresistant potential component described for the eye cup was not seen in the ERP of the epiphysis cerebri because of the lack of melanin pigment in the pineal organ. The similarity between the ERP of the pineal and the retina is evident also in the ERP action spectra. However, the ERP of the frog's dark adapted retina is dominated by a visual cone pigment with a maximal absorption at about 570–580 nm[48,51] while the action spectrum of the frog's pineal ERP is highest at about 500 nm[49]. A 2nd mechanism contributing to the ERP in the frog's retina is apparent during adaptation to red light showing a maximum at shorter wavelengths[51]. For comparison the action spectra of the pike's pineal and retinal ERP display 2 maxima at 530 and 620 nm[50].

Central projection of pineal nerve fibers

The nervous projection of pineal organs of lower vertebrates has been investigated so far only in a few species of teleosts, anurans and lizards[52]. In *Salmo* the projections of pinealofugal (afferent) nerve fibers were followed with histological methods using iontophoresis of cobalt chloride for staining. The pineal tract was found to project over an extensive sensorimotor area in the brain with terminations in the parapineal organ, the lateral habenular nucleus, the area praetectalis, the di- and mesencephalic periventricular grey, the nucleus of Darkschewitsch, the dorsal tegmentum and probably the preoptic nucleus[53]. In anurans, the pineal tract was found to project to the pretectal area and the periventricular grey[1], the regions of termination of the frontal organ nerve corresponding to those of the pineal tract[54].
In lacerta a well-developed parietal nerve connects the parietal eye with the left lateral habenular nucleus. Fibers of the pineal tract extend toward the periventricular layer, yet the sites of termination were not identified[55]. Recent investigations applying horseradish peroxidase to the parietal eye of adult lacerta revealed projections to the dorsolateral nucleus of the thalamus, the periventricular hypothalamic area, the preoptic hypothalamic and telencephalic regions and the pretectal area[56]. The terminations of the parietal eye partially overlap with those of the optic nerve.

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