J Comp Physiol (1981) 144:127–137

Journal of Comparative Physiology · A

The Photosensory Function of the Pineal Organ of the Pike (*Esox lucius* L.) Correlation Between Structure and Function

Jacky Falcón* and Hilmar Meissl

Max-Planck-Institut für Physiologische und Klinische Forschung, W.G. Kerckhoff-Institut, Parkstrasse 1, D-6350 Bad Nauheim, Federal Republic of Germany

Accepted May 2, 1981

Summary. Electrical recordings from the exposed pineal organ of the pike (*Esox lucius* L.) were performed in order to localize the photoreceptive structures. Extracellular recordings showed a maintained activity of nerve fibers from the pineal tract and of single neurons from the distal region of the pineal organ. At increasing levels of steady exposure to white light, the impulse frequency decreased. Illumination of the organ with wavelengths between 380 and 710 nm resulted in an inhibition of the spike activity (achromatic response), associated with slow graded responses (electropinealogram, EPG). Sensitivity curves exhibited maxima at 530 and 620 nm in the light adapted, and one maximum at 530 nm in the dark adapted organ. In rare occasions, inhibitory (λ_{max} 380 nm) and excitatory (λ_{max} 620 nm) responses were recorded from single ganglion cells (chromatic response). Some observations (dark adaptation curves; intensity-duration relationship) suggest that the spike potentials and graded responses are probably not generated by the same structures. Moreover, slow potentials without spike potentials were recorded from isolated medial regions of the pineal where no nerve cells are observed.

The pineal organ of the pike appears to be a functional photoreceptive organ that may act as a dosimeter of solar radiation, and as an indicator of daylength. The morphological differentiation of its epithelium is closely related to its function, no electrical activity being propagated from the medial region to the brain.

* Present address: Laboratoire de Biologie Cellulaire, L.A. CNRS 290, Université de Poitiers, U.E.R. Sciences, 40, Avenue du Recteur Pineau, F-86022 Poitiers Cédex, France

Abbreviation: EPG electropinealogram

Introduction

The epiphysis cerebri of fish is a direct photosensitive organ (Dodt 1973) that may also have a neuroendocrine function (see Falcón 1979a for references). Since indole compounds are synthesized in pineal photoreceptors, they might be considered as photoneuroendocrine elements (Oksche 1971).

In contrast to other teleost fishes, the epiphysis of the young pike exhibits regional differences in structure. (1) The organ can be divided into 3 morphologically different parts (Falcón 1979a; Fig. 1). (2) Typical cone-like photoreceptors were identified in the distal and proximal regions of the pineal, whereas partially rudimentary photoreceptors with degenerated outer segments and/or absence of synaptic contacts were mainly localized in the medial part (Falcón 1979b). (3) The number of nerve cells was high in the proximal part, low in the distal, and zero in the medial part (Falcón 1979c; Falcón and Mocquard 1979). (4) 5-hydroxytryptophan/5-hydroxytryptamine (5-HTP/5-HT) and monoamine oxidase (MAO) activity were mainly localized in the medial region (Falcón et al. 1980a). However, typical as well as partially rudimentary photoreceptors were seen to uptake labelled tryptophan (5-TP-^{3}H) and 5-HTP-^{3}H (Falcón et al. 1980b).

It was therefore suggested that only the distal and the proximal region convert photic information into electrical impulses, transmitted along nervous pathways to other parts of the brain. However, it is unknown if the partially rudimentary photoreceptors are still photoreceptive.

The following study was performed in order to complement the structural observations by electrophysiological recordings.

0340-7594/81/0144/0127/$02.20

Materials and Methods

Animals. Pikes (body length 10 to 50 cm) were obtained from a commercial hatchery and kept in oxygenated fresh water. The daily photoperiod was 12L/12D. Experiments were performed between October 1978 and July 1980.

Recording of Impulse Activity. Fifty animals were used for these experiments. The fishes were anesthetized with nembutal (pentobarbital natrium Abbott, subcutaneously applied in a single dose of 6 mg/100 g) and immobilized by an injection of tubocurarine chloride (Asta, 0.3 mg/100 g). The pineal was exposed by excising the overlying skin and removing the bone with a dental drill. In some control experiments the lateral eyes were removed. The animal was then placed in a trough, and covered by wet gauze. A continuous flow of oxygenated water of room temperature was provided through the gills. Platinum-iridium glass insulated microelectrodes, with a tip diameter of 5 µm, were used for recording. The active electrode was guided by means of a micromanipulator to the sites of recording and its position was adjusted until the maximum of activity was obtained. The indifferent electrode was placed on the skull. Potentials were amplified, displayed on an oscilloscope and monitored by a loudspeaker. In some preparations, histological marking of the recording sites was performed by electrolytical deposit of iron from steel microelectrodes (prussian-blue reaction; Morita and Bergmann 1971).

Recording of Slow Potentials. Slow potentials were recorded from 20 'in vitro' preparations. After decapitation, the organ was excised and covered with goldfish Ringer solution. After removal of the

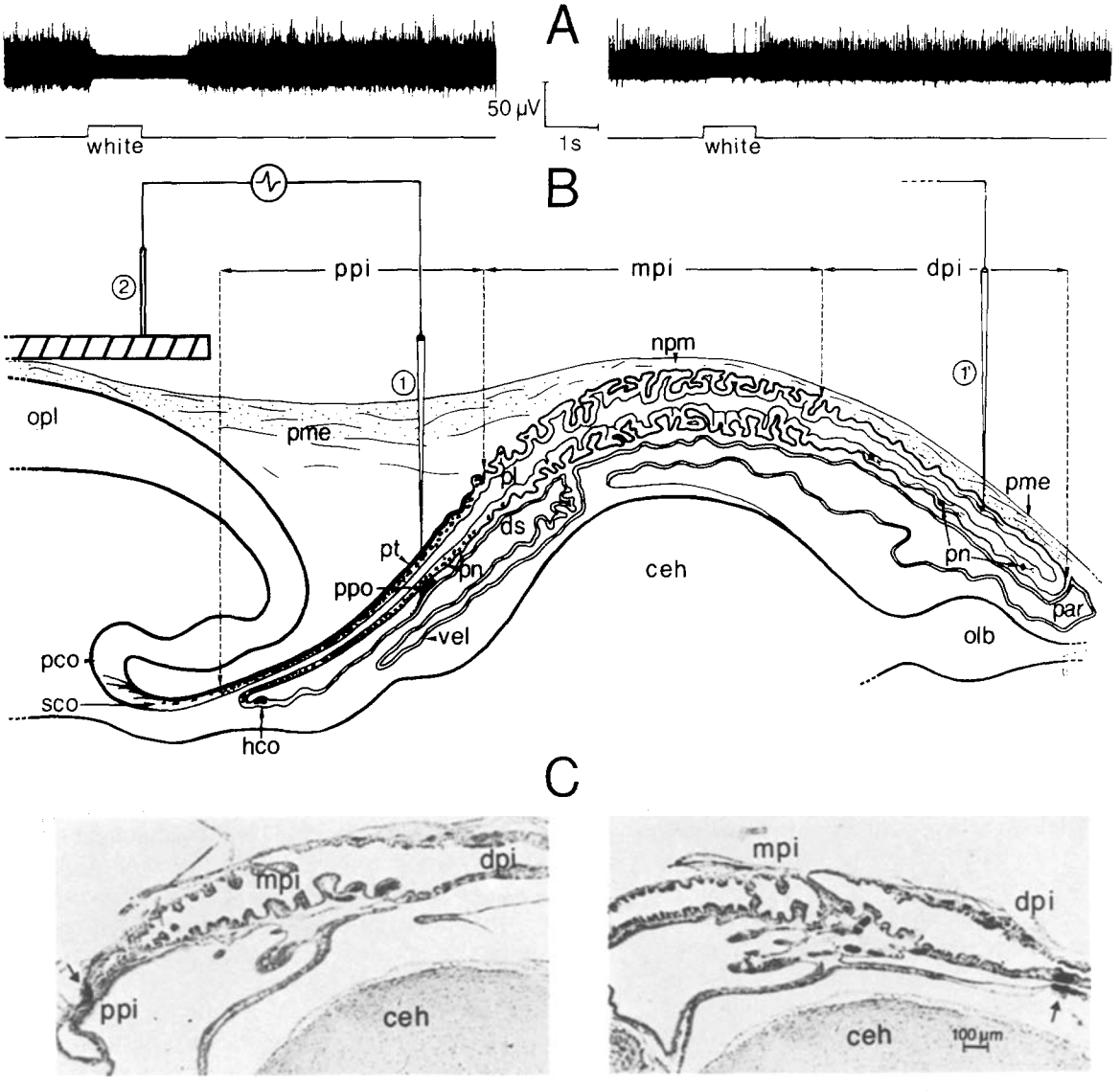

Fig. 1. **A** Nervous discharge recorded from the pike's pineal tract (left) and from a single cell of the distal part (right), inhibited by a 1 s stimulus of white light (2900 µW/cm²). **B** Sagittal section through the pineal organ. (1) and (1') sites of recording electrodes, (2) indifferent electrode; *dpi* distal pineal; *ds* dorsal sac; *hco* habenular commissure; *mpi* medial pineal; *npm* non-pigmented meninges; *olb* olfactory bulb; *opl* optic lobes; *par* paraphysis; *pco* posterior commissure; *pme* pigmented meninges; *pn* pineal neuron; *ppi* proximal pineal; *ppo* parapineal organ; *sco* subcommissural organ; *vel* velum transversum. **C** Histological sections showing electrolytical deposit of iron at the recording sites (arrows) in the dorsal wall of the proximal region, close to the pineal tract (left), and in the ventral wall of the distal region (right); eosin staining; ×60

meninges and dorsal sac, the isolated pineal was placed on a saline soaked filter paper. The cut end of the pineal stalk was lifted onto an Ag-AgCl cotton wick electrode. The indifferent electrode was in contact with the Ringer solution. In addition, 4 'in vivo' experiments were performed with the pineal organ being exposed as described in above. The responses were d.c. amplified, displayed on an oscilloscope and filmed.

Recordings from Isolated Parts of the Pineal. The proximal, medial and distal pineal regions (Fig. 1) of 9 pikes were separated by means of a razor blade. Potentials were recorded between 2 Ringer solution filled glass pipettes of 60 to 80 μm in diameter, inserted into Zn-$ZnSO_4$ electrodes. The glass tips were in contact with both sides of the ventral or dorsal epithelium. The d.c. amplified potentials were displayed on an oscilloscope, averaged by means of a computer and photographed. After the experiment, the tissues were fixed by 4% formalin and embedded in paraffin for histological control.

Stimulus. Stimuli were provided by a 150 W xenon arc. Two independent beams were available; wavelengths were controlled by Schott interference band filters (half band width 16 to 22 nm). For the attenuation of the light stimuli neutral density absorption filters were used.

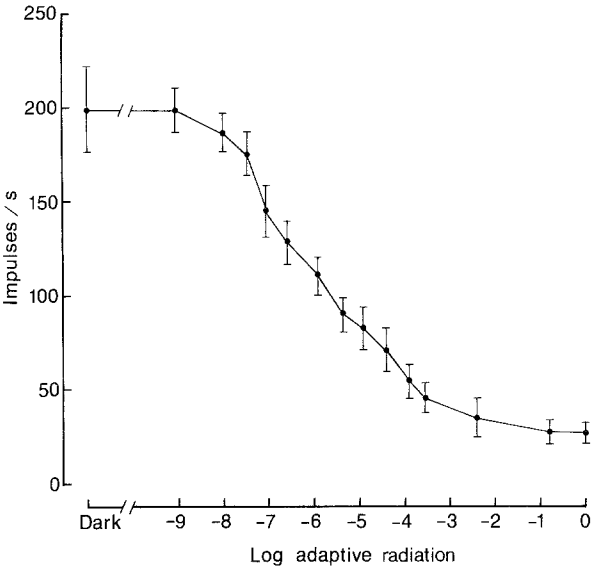

Fig. 2. Maintained nervous discharge (impulse/s) of the pike's pineal tract ($n=7$, mean values and standard deviation) during exposure to steady white light (abscissa O = 1300 μW/cm², about 10^3 cd/m²)

Results

Extracellular recordings from the exposed pineal showed a maintained spontaneous activity of fibers from the pineal tract and from single cells in the distal region (Fig. 1). No impulse activity could be recorded from the medial region. Illumination of the organ by white light resulted in an inhibition of the spike activity (Fig. 1A) associated with slow graded responses (Figs. 3A, B, 4C). Spike off responses were occasionally seen at the cessation of the stimulus.

Spike Discharges

The absolute threshold was determined by measuring the light energy necessary to obtain the first perceptible decrease of the discharge rate in a 3 hours dark adapted animal. For a white stimulus of 500 ms duration, a value of 2.5×10^{-5} lm/m² ($\simeq 8 \times 10^{-6}$ cd/m²) was obtained.

The firing rate of nerve fibers in the pineal tract was determined first after 2 h of dark adaptation, then during steady exposure to stepwise increased intensities of white light. A decrease of nerve impulses was seen which was almost linear between 10^{-5} and 0.3 cd/m² (Fig. 2). At low ($<10^{-6}$ cd/m²) and high (>100 cd/m²) levels of illumination the spontaneous discharge remained almost constant (cf. Morita 1966a).

Slow Potentials

Recordings from the pineal tract revealed, upon light stimulation, a monophasic response pattern (Figs. 3A, B, 4C). The shape of the EPG depended on the intensity and the wavelength of the stimulus and its duration as well as on the state of adaptation. The change of potential was slower in darkness than in the light adapted state (cf. Fig. 3A, B); otherwise, the shape remained unaltered, except for a long lasting d.c. component which was particularly seen at high stimulus strengths (Fig. 3B). For constant test flashes of increasing duration, both amplitude and duration of the responses increased up to a stimulus period of 2 to 4 s (Fig. 3A; see below). For stimuli of longer duration the mean amplitude of response remained nearly constant with a slow return of potential towards the base line upon cessation of the stimulus (Fig. 3A).

For test flashes of constant duration, the increase of stimulus intensity resulted in an increase of both amplitude and duration of response as well as in a shortening of the rise time and delay period (Fig. 3B). For stimuli intensities higher than 2.5 log above EPG threshold the amplitude of the response remained rather constant while the decline of potential after the stimulus occurred in 2 phases: an initial rapid phase followed by a slower one which outlasted the stimulus for many seconds (Fig. 3B).

In those experiments where both EPG and spikes were recorded the absolute threshold for the EPG was found to be similar as for the spike responses.

Spectral Sensitivity

Achromatic Response. Most of the nerve cells studied in the pike's pineal displayed maintained activity in darkness which was inhibited by light stimuli of all

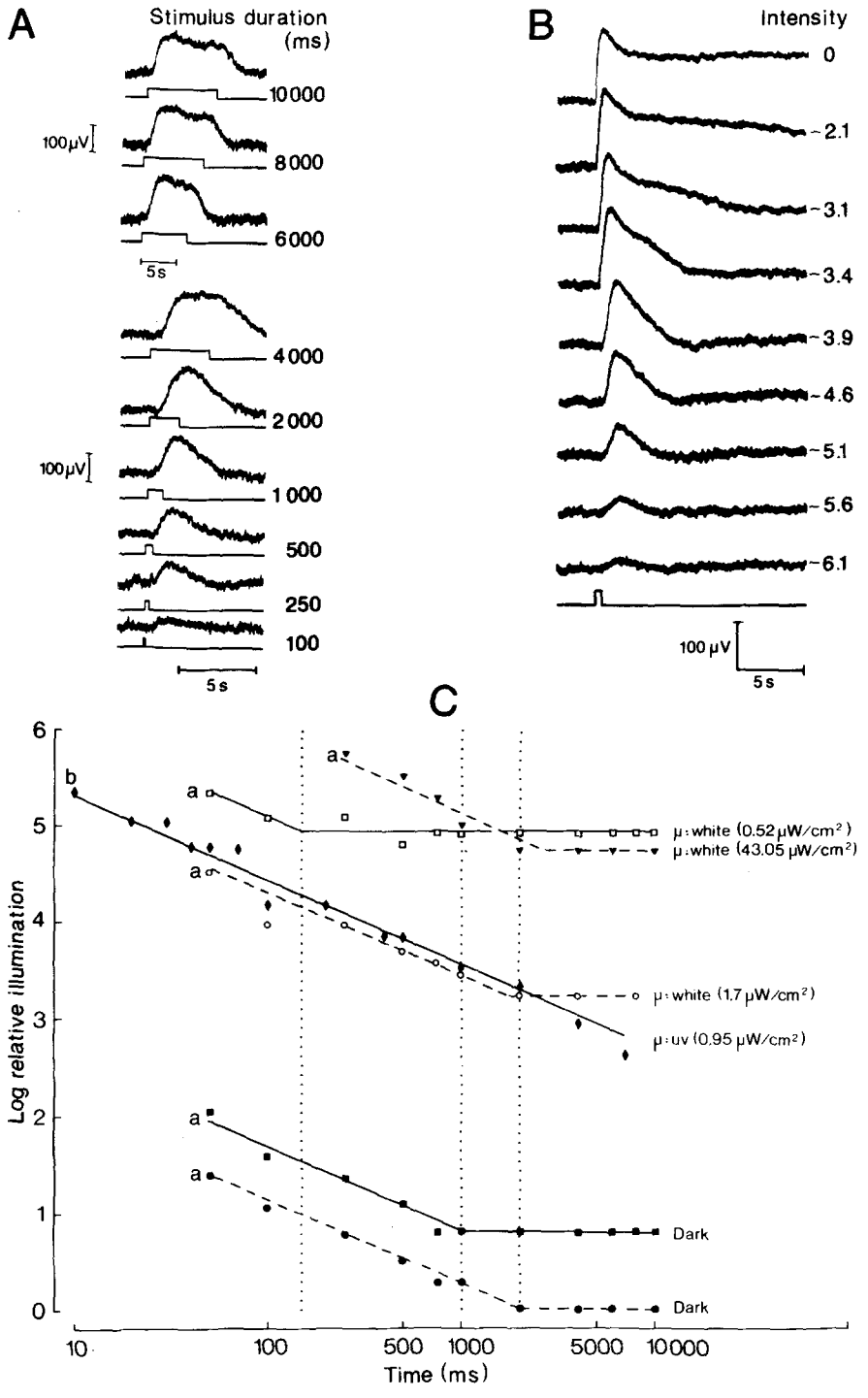

Fig. 3A–C. Responses to light of the pike's pineal organ. **A** EPG responses to constant test flashes (540 nm; 1.5×10^{-3} μW/cm²) of increasing duration. **B** EPG responses to constant test flashes (540 nm; 0.5 s) of increasing intensities (ordinate O = 97 μW/cm²). **C** Graph showing the relation between the duration (abscissa) and intensity (log values) of the light stimuli for a criterion response of the pineal. EPG data: dashed lines; spike data: lines drawn in full. Achromatic responses (a) were recorded to test stimuli of 520 nm in darkness or during steady exposure to white light as indicated; the excitatory component of the chromatic response (b) was recorded to test stimuli of 535 nm during conditioning with ultraviolet (362 nm) light

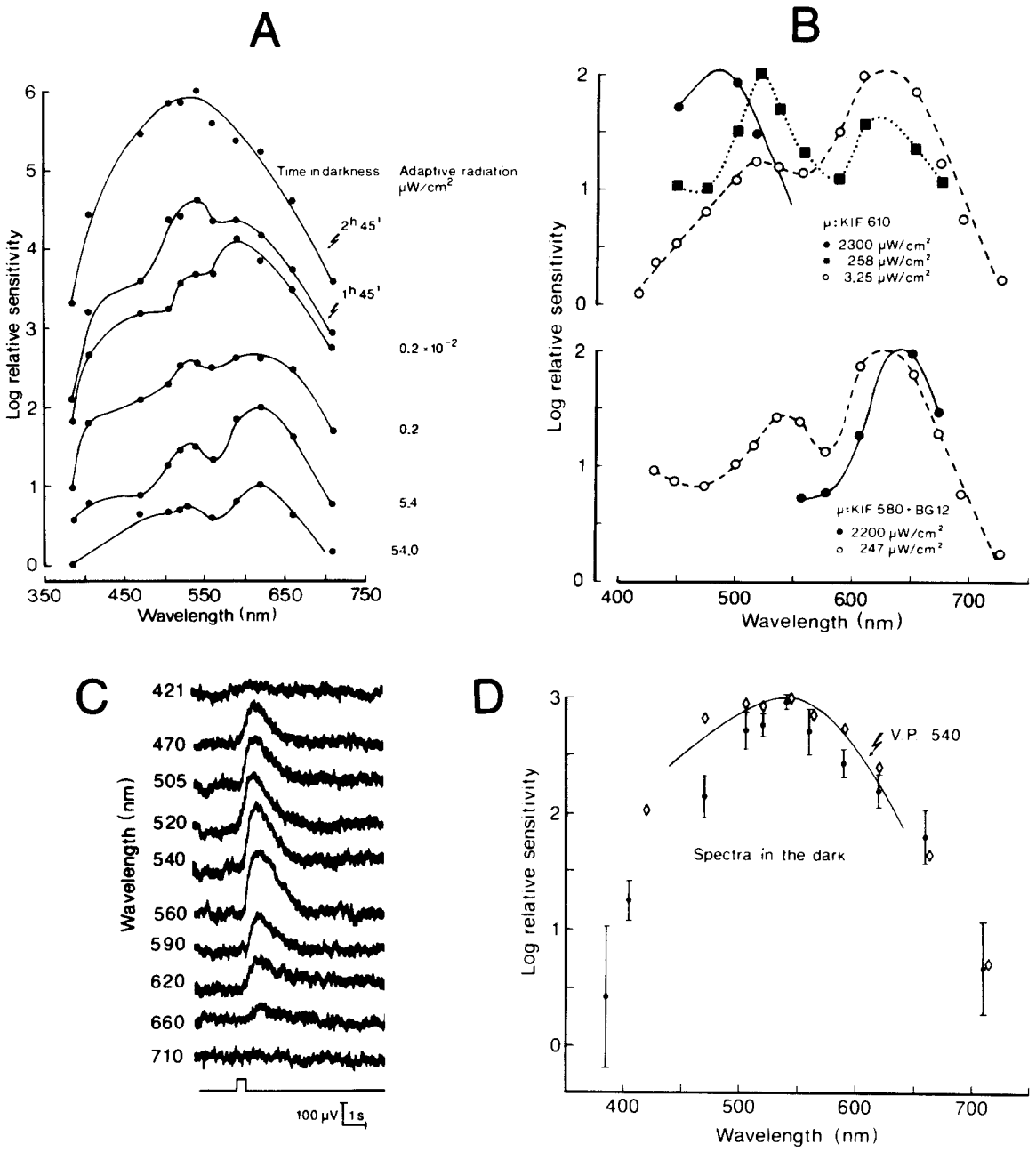

Fig. 4A–D. Achromatic response of the pike's pineal. **A** Relative spectral sensitivity curves (spike data) measured in darkness and during exposure to different levels of radiation (white light). **B** The same during chromatic adaptation to red (above, KIF 610) or to blue-green (below, KIF 580 + BG 12) light of different intensities. **C** Slow responses (EPG) of the dark adapted pineal to stimuli of different wavelengths carrying the same energy (1.3×10^{-3} μW/cm²). **D** Relative spectral sensitivity curves after several (3 to 5) h in darkness (● spikes; ◇ slow potentials; — Dartnall's nomogram V.P. 540 nm)

wavelengths between 380 and 710 nm (achromatic response). Accordingly, the slow potentials recorded had all the same polarity and did not change their polarity with wavelength (Fig. 4C).

In a series of experiments spectral sensitivity curves were determined by measuring the relative energy causing (i) the first perceptible inhibitory response (spikes) or, (ii) a constant response (EPG). Comparing the data obtained after several hours of dark adaptation (showing a single peak at about 540 nm) with those obtained during light adaptation, there is a shift of the maximum to longer wavelengths (620–640 nm) with a secondary peak in the green (530–540 nm, Fig. 4A). With exposure to stepwise decreasing intensities of white light, the high sensitivity to red light was gradually replaced by other wave-

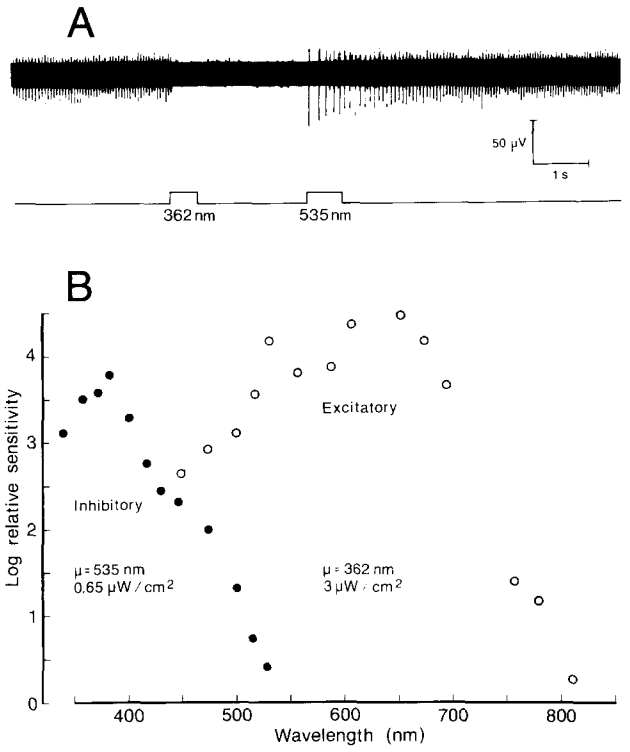

Fig. 5A, B. Chromatic response recorded from a single cell in the distal part of the pike's pineal organ. **A** Inhibition of the maintained discharge in response to ultraviolet (362 nm) light, and excitation in response to green (535 nm) light. **B** Relative spectral sensitivities of the inhibitory (dots) and excitatory (circles) thresholds during steady exposure to weak green and ultraviolet background, respectively

lengths, until, after 3 h of dark adaptation, sensitivity was highest in the green part of the spectrum (Fig. 4A, D). Selective adaptation to red or to blue-green light diminished or suppressed the peak in the red or the green part of the spectrum, respectively (Fig. 4B).

Chromatic Response. Only at very rare occasions the electrical activity of single nerve cells in the distal part of the pineal was inhibited by test lights of short wavelengths and increased by long wavelengths (chromatic response) causing a lasting change of the impulse pattern, persisting for many seconds (Fig. 5A). Inhibitory thresholds were lowest at 380 nm when measured against a weak green (535 nm) excitatory background, while the excitatory thresholds exhibited a minimum at 620 nm, as measured against a week background of ultraviolet light (362 nm, Fig. 5B).

Dark Adaptation

Slow Potentials. After a 30 min exposure to white light (1300 $\mu W/cm^2$) the EPG amplitude was seen to increase in darkness according to the flash intensity used, i.e., fast with high energy flashes and slower with test stimuli of lower intensities (Fig. 6A). Generally, during the first minutes in darkness the increase of the response amplitude was fast, and then became slower until it reached a maximum (depending on the flash intensity and the time interval in the dark). From these response curves, a conventional dark adaptation curve was drawn, similar to that obtained by the measurement of EPG thresholds (Fig. 6C), by plotting the intensity of the light flash (necessary for a small constant response) against time in darkness. No further changes occurred after 90 min in darkness.

The dark adaptation curves of the EPG differed from those obtained with spikes (see below) in that no knee could be detected; the experimental data were fitted (line drawn in full) by an equation of $Y = Ae^{-t/B} + Ce^{-t/D} + E$ ($A = -1{,}907$; $B = 23{,}554$; $C = -2{,}750$; $D = 1{,}486$; $E = 5{,}841$).

Spikes. For the spike data, the change of threshold after light adaptation to 1300 $\mu W/cm^2$ (about 10^8 times the dark threshold) consists of two branches, with a knee at their intersection (Fig. 6C) which appeared 20 to 40 min after the light was turned off (depending on the intensity and duration of the light adaptation period). In the beginning of dark adaptation the decrease of threshold was very rapid both for the red and the green test lights. There was distinct difference in threshold for the two test lights in favour of red one before the knee and green one after. The equation fitting the EPG data in (a) did not describe the dark adaptation curves obtained with inhibitory spike thresholds.

Increment Thresholds

Only spike data of the achromatic response were available in the determination of incremental thresholds. After 3 h of dark adaptation the inhibitory threshold was measured, then the organ was exposed to white light beginning from low to high levels of adaptive radiation and at each step the inhibitory thresholds were determined to flashes of 540 and 620 nm. The curves obtained were bisectioned with a knee at their intersection. At low levels of adaptive radiation the change of threshold was bigger for green than for red light, i.e., the organ became relatively more sensitive to red than to green light. At high levels of light exposure the loss of sensitivity was similar for both wavelengths.

Bloch's Law

Bloch's law states that for a visual threshold response the product of intensity and duration of test lights

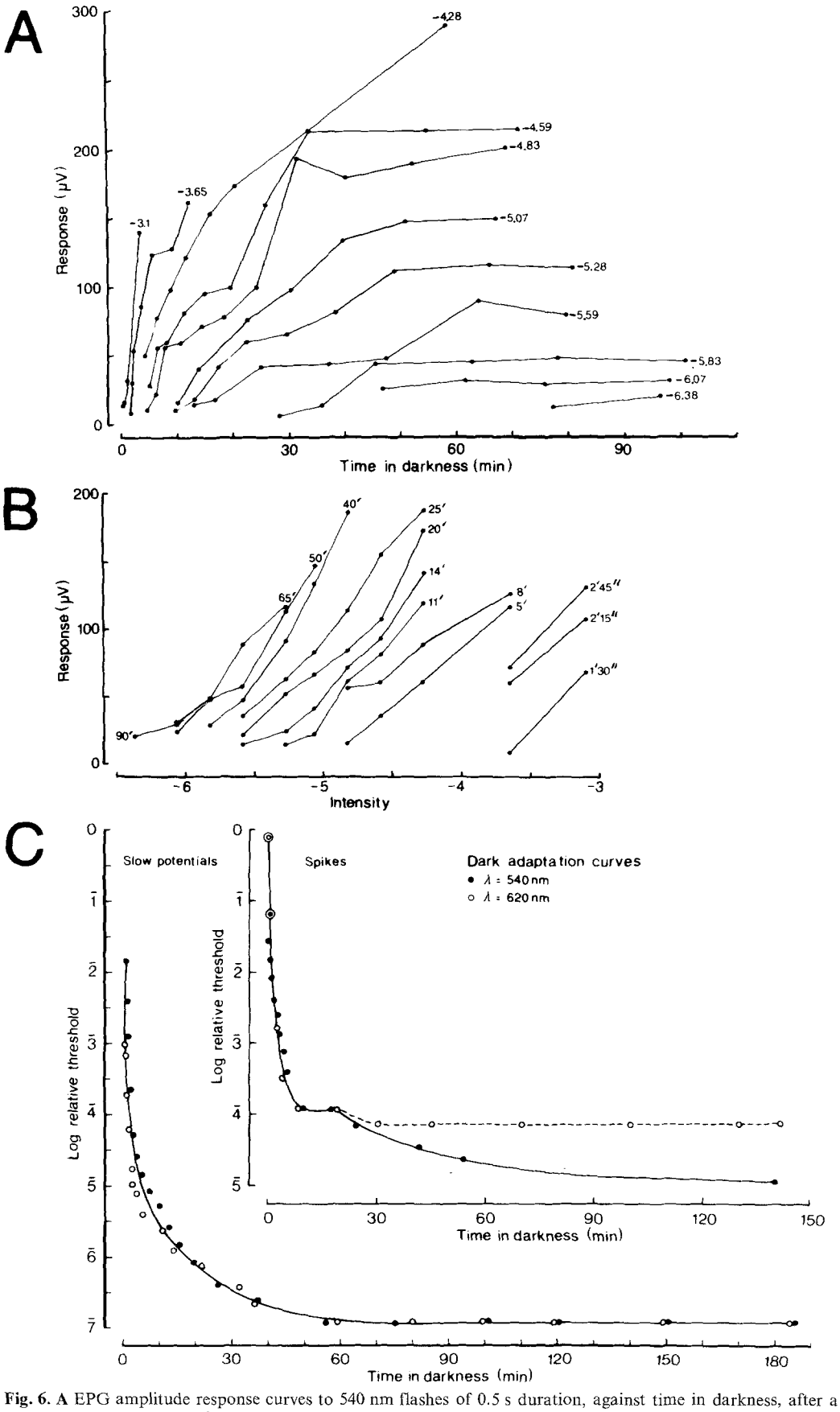

Fig. 6. **A** EPG amplitude response curves to 540 nm flashes of 0.5 s duration, against time in darkness, after a previous 30 min exposure to white light (1300 μW/cm²). Responses to flashes of equal intensities are interconnected by lines (ordinate O corresponding to 97 μW/cm²). **B** Amplitude response curve vs log flash intensity (derived from **A**) at different times in the dark. **C** Dark adaptation curves recorded after 30 min exposure to white light (of 1300 μW/cm²): *Slow potentials:* (EPG, 0.5 s stimuli); final dark thresholds to test flashes of 540 and 620 nm were superimposed along the ordinate. *Spikes:* (1 s stimuli); thresholds before the knee were made to coincide at the ordinate (measurements made at the end of the light adaptation period are shown by double contoured symbols)

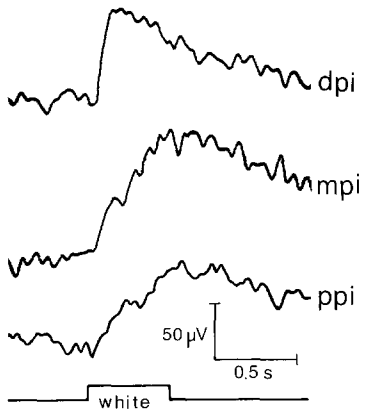

Fig. 7. EPG response recorded from distinct separated regions of the pike's pineal organ in vitro, in response to flashes of white light (2.9 mW/cm^2) and of 0.5 s duration in darkness; the recordings were made from distal (*dpi*), medial (*mpi*), and proximal (*ppi*) regions (8 responses averaged)

is constant up to a stimulus duration of 0.03 s in light adapted state and of 0.10 s after dark adaptation. For longer stimulus duration only the intensity determines the threshold.

Achromatic Response. For the EPG of the pike's pineal organ (Fig. 3C (a)) the product of intensity and duration was constant up to a critical period of 2 s (symbols connected by dashed line). This was seen after dark adaptation and during exposure to light. For longer stimuli, the product of intensity and duration of the stimulus increased.

For the inhibitory spike threshold (symbols connected by full lines) the critical duration of the intensity-duration relationship of the stimulus was different after dark adaptation and during exposure to light (Fig. 3C (a)). After dark adaptation it followed Bloch's law up to 0.75–1 s in the dark adapted, and up to 100–250 ms in the light adapted organ.

Chromatic Response. The intensity-duration relationship of the test stimulus for the chromatic response was studied for the excitatory threshold against a weak inhibitory (362 nm) background. The integration time for the response was more than 10 s (Fig. 3C/b).

Photosensitivity of the Pike's Pineal in vitro

In order to investigate the electrical activity of different regions of the isolated pineal, the organ was removed, and the distal and proximal parts were separated from the medial part where, according to Falcón (1979b) and Falcón and Mocquard (1979) only rudimentary photoreceptors are present without any ganglion cells.

Intense (2900 µW/cm^2) flashes of 0.5 s duration were applied in darkness, just after placing the electrodes. Under these conditions, slow potentials were recorded from all regions of the isolated organ (Fig. 7). The responses to flashes were abolished during exposure to strong light (1300 µW/cm^2), and recovered after cessation of the adapting light.

After dissection (removal of the meninges and dorsal sac) the shape of responses (amplitude, latency, rise time) varied strongly with the condition of the preparation and the position of electrodes. Therefore, the shape of potentials shown here should not be compared in all details, even when recorded from parts of the same organ. Histological controls showed for the medial part of the organ a folded epithelium, which is a typical feature of this region (Fig. 1).

Discussion

Functional Significance of the Photosensitivity

The results presented above indicate that the pineal organ of all pikes investigated is photosensitive. Additionally to the impulse discharges of nerve cells in the distal pineal region, and to nerve fibers in the proximal part, slow graded potentials were recorded from the pineal tract. The highly preserved structure of the pike's pineal organ is reflected by the low intensity dark threshold of about 10^{-5} lm/m^2 for both spikes and slow graded potentials, a value similar to that obtained in the dark adapted pineal of the trout (Morita 1966a).

Prominent in the pike's pineal light sensitivity is a maintained discharge that is inhibited by all wavelengths of the visible spectrum, i.e., an achromatic response. During steady exposure to light, the discharge of the pineal tract signals the level of illumination over a range of 8 log units. Although the spectral absorbance of the tissue covering the organ from above (skin, skull) was not measured, it did not attenuate the incident light by more than 0.5 log in the animals used. Thus, as for other pineal organs (Morita and Dodt 1965; Hamasaki and Esserman 1976) the pike's pineal organ may operate as a dosimeter of solar radiation, and as an indicator of daylength. It may thereby exert an influence on circadian and circannual biological rhythms.

The spectral sensitivity in the dark, and during exposure to white and chromatic light, as well as the changes of threshold during dark and light adaptation show the presence of two mechanisms in the pike's pineal, a red (λ_{max} = 620–640 nm) and a green (λ_{max} = 530–540 nm) one, resembling the Purkinje shift in the frog's epiphysis cerebri (Dodt and Morita 1964). This indicates a high degree of specialization.

Considering the diurnal variations of environmental illumination under water, the transmission spectrum at depths between 1 to 4 m is very broad during day time (Munz and McFarland 1977), thus permitting both the green and the red mechanism of the pike's pineal to operate. However, during twilight and after sunset, or just before sunrise, the longer wavelengths are strongly absorbed at this depth. Under such lightening conditions the pike's pineal exhibits a sensitivity change from the red to the green. This indicates a more complex mechanism as in the trout where a similar shift of sensitivity is lacking (Morita 1966a). This switching process puts the more sensitive of the two mechanisms in the photopic or in the scotopic range of illumination, thereby increasing the photoreceptive capacities of the pineal organ.

Only very rarely, nerve cells of the pike's pineal were found to produce chromatic response, i.e., cells which exhibited spike inhibition to short wavelengths ($\lambda_{max}=380$ nm) and excitation to long wavelengths ($\lambda_{max}=620$ nm). The number of such cells is probably very small in the pike's pineal. Evidence for this conclusion is provided by the EPG representing an average of all light sensitive elements stimulated, which in the pike exhibited an achromatic type of response whereas the EPG in the frog (Dodt and Heerd 1962; Baumann 1962) and in the lizard (Dodt and Scherer 1968) showed a chromatic type of response. So far, the pike's pineal behaves similarly to other teleosts, where chromatic units are very rare or even absent (Morita 1966a).

Origin of Slow Potentials

According to Hamasaki and Eder (1977) slow potentials represent mass potentials occurring in many neurons, while others (Morita and Dodt 1973; Donley and Meissl 1979) suggest that they are summated extracellular receptor currents. For the following reasons we exclude the EPG to be generated by nerve cells:

– Slow potentials were recorded in vitro from all parts of the pike's pineal organ, while nerve cells were scarce in the distal part, and absent in the medial one.

– Using glass electrodes for recording, the polarity of the EPG depended on the recording electrode position. Thus, as already seen in the pineal organ of the lamprey, the structures generating the graded potentials are oriented in respect to the site of the recording electrode, which is not seen in the case of the nervous elements.

– The time course of dark adaptation for pineal ganglion cell responses consists of two functions with a knee at their intersection. By contrast, the EPG dark adaptation curves can be described by the addition of two exponential terms, which do not produce a knee. Since the switching process effecting the change from the photopic to the scotopic level operates probably at the level of ganglion cells, the graded potentials should arise earlier (Donley and Meissl 1979).

– The time interval within the product of intensity and duration of the stimulus produces a constant response is different. While the EPG follows Bloch's law for periods up to 4 s in the dark adapted state, this relation holds only up to 1 s for the nerve discharges. Moreover, at photopic levels, the critical duration decreases considerably for the spikes while it remains constant for the EPG. A similar phenomenon was described earlier for the response of the frog's epiphysis (Donley and Meissl 1979).

– Application of aspartate, an agent which was found to isolate the PIII component of the lateral eye (Sillman et al. 1969), to the pike's pineal organ in vitro, increases the nervous discharges considerably without affecting the slow potentials (Meissl, unpublished observations).

All these observations indicate that the EPG and the spike responses are generated by different cell types. Considering that the interstitial cells are unresponsive to light, we conclude that the EPG represents the sum of extracellular receptor currents, generated by the photopic and scotopic elements of the epiphysis (Donley and Meissl 1979). If this conclusion is valid, the EPG is a direct and easy way to study the responses of pineal photoreceptors.

Functional Differentiation and Possible Photoneuroendocrine Transducers in the Pike's Pineal Organ

The absence of nerve cells in the medial part of the pike's pineal (Falcón and Mocquard 1979) explains why successfull recordings of spike discharges from this region were only exceptional, and probably originated from nerve axons from the distal part of the organ running towards the posterior commissure. We therefore assume that the medial part of the pineal organ is only secretory, while there is nervous and possibly secretory activity in the distal and proximal regions.

As in the lamprey (Meiniel and Hartwig 1980), the indole biosynthesis in the pike's pineal organ is probably directly affected by light. This assumption is supported by the observation that only a very small number of catecholaminergic fibers was seen in the surrounding tissues (Owman and Rüdeberg 1970; Falcón et al. 1980a). In mammals, the indole biosynthesis is indirectly affected by light through retinohypothalamic fibers, the suprachiasmatic nuclei, and

catecholaminergic nerve fibers originating in the superior cervical ganglion (Deguchi 1979; Rusak 1979). It was further suggested that in pineal sensory cells light might be converted into both electrical and neurohumoral outputs (Oksche 1971; Oksche and Hartwig 1975, 1979).

The present and previous findings (Falcón et al. 1980b) suggest that the typical photoreceptors in the distal and proximal parts of the pineal organ of the pike may act as photoneuroendocrine transducers. It is the new finding of this study that the partially regressed photoreceptors in the medial region of the pike's pineal seem still capable of photoreception. The question of photoreception by structures not classified as typical photoreceptors is a pertinent general one. In birds, typical photoreceptors could not be identified in the pineal organ (Collin 1971, 1976; Oksche 1971) and electrical recordings from the exposed pineal failed to demonstrate a direct photosensory function (Morita 1966b; Ralph and Dawson 1968). Nevertheless, a direct effect of light on the indole biosynthesis has been recently evidenced in the avian pineal organ (ref. in Deguchi 1979; Takahashi and Menaker 1979). The recordings of slow potentials from the isolated medial part of the excised pineal organ of the pike are in good agreement with these findings, and support the idea that partially rudimentary cells of this region are still capable of photoreception, even without conversion into an electrical output. Even if the isolation of the medial part was not perfect, the contribution of photoreceptors from the other parts of the organ cannot explain the strength of the responses recorded.

The conclusion that the typical and partially rudimentary photoreceptors of the pike's pineal organ are photoneuroendocrine transducers needs further investigation. Microelectrode recordings and a detailed study of neuroendocrine processes in the different parts of the organ would be suitable to elucidate the two possible functions of the photoreceptive structures. The pineal organ of the pike offers a suitable model for the study of photosecretory transduction.

We wish to thank Professor Dodt for helpful discussions and critical reading of the manuscript. J. Falcón was supported by a fellowship of the Max-Planck-Gesellschaft.

References

Baumann Ch (1962) Lichtabhängige langsame Potentiale aus dem Stirnorgan des Frosches. Pfluegers Arch 276:56–65

Collin JP (1971) Differentiation and regression of the cells of the sensory line in the epiphysis cerebri. In: Wolstenholme GEW, Knight J (eds) The pineal gland. Churchill Livingstone, Edinburgh London, pp 79–125

Collin JP (1976) La rudimentation des photorécepteurs dans l'organe pinéal des vertébrés. In: Raynaud A (ed) Mécanismes de la rudimentation des organes chez les embryons de Vertébrés. Colloques Internationaux du CNRS no 266, Paris, pp 393–407

Deguchi T (1979) Circadian rhythms of indolamines and serotonin N-acetyl-transferase activity in the pineal gland. Mol Cell Biochem 27:57–66

Dodt E (1973) The parietal eye (pineal and parietal organs) of lower vertebrates. In: Jung R (ed) Handbook of sensory physiology, vol VII/3B. Springer, Berlin Heidelberg New York, pp 113–140

Dodt E, Heerd E (1962) Mode of action of pineal nerve fibers in frogs. J Neurophysiol 25:405–429

Dodt E, Morita Y (1964) Purkinje-Verschiebung, absolute Schwelle und adaptives Verhalten einzelner Elemente der intrakranialen Anuren-Epiphyse. Vision Res 4:413–421

Dodt E, Scherer E (1968) Photic responses from the parietal eye of the lizard *Lacerta sicula campestris* (de Betta). Vision Res 8:61–72

Donley CS, Meissl H (1979) Characteristics of slow potentials from the frog epiphysis (*Rana esculenta*); possible mass photoreceptor potentials. Vision Res 19:1343–1349

Falcón J (1979a) L'organe pinéal du Brochet (*Esox lucius* L.). I. Etude anatomique et cytologique. Ann Biol Anim Biochem Biophys 19:445–465

Falcón J (1979b) L'organe pinéal du Brochet (*Esox lucius* L.). II. Etude en microscopie électronique de la différenciation et de la rudimentation partielle des photorécepteurs; conséquences possibles sur l'élaboration des messages photosensoriels. Ann Biol Anim Biochem Biophys 19:641–688

Falcón J (1979c) Unusual distribution of neurons in the pike pineal organ. In: Ariens Kappers J, Pévet P (eds) The pineal gland of vertebrates including man: Progress in brain research, vol 52. Elsevier/North-Holland Biomedical Press, Amsterdam New York, pp 89–91

Falcón J, Mocquard JP (1979) L'organe pinéal du Brochet (*Esox lucius* L.). III. Voies intrapinéales de conduction des messages photosensoriels. Ann Biol Anim Biochem Biophys 19:1043–1061

Falcón J, Juillard MT, Collin JP (1980a) L'organe pinéal du Brochet (*Esox lucius* L.). IV. Sérotonine endogène et activité monoamine oxydasique; étude histochimique, ultracytochimique et pharmacologique. Reprod Nutr Dévelop 20:139–154

Falcón J, Juillard MT, Collin JP (1980b) L'organe pinéal du Brochet (*Esox lucius* L.). V. Etude radioautographique de l'incorporation *in vivo* et *in vitro* de précurseurs indoliques. Reprod Nutr Dévelop 20:991–1010

Hamasaki DI, Eder DJ (1977) Adaptive radiation of the pineal system. In: Crescitelli F (ed) Handbook of sensory physiology, vol VII/5. Springer, Berlin Heidelberg New York, pp 497–548

Hamasaki DI, Esserman L (1976) Neural activity of the frog's frontal organ during steady illumination. J Comp Physiol 109:279–285

Meiniel A, Hartwig HG (1980) Indoleamines in the pineal complex of *Lampetra planeri* (Petromyzontidae). A fluorescence microscopic and microspectrofluorimetric study. J Neural Transm 48:65–83

Morita Y (1966a) Entladungsmuster pinealer Neurone der Regenbogenforelle (*Salmo irideus*) bei Belichtung des Zwischenhirns. Pfluegers Arch 289:155–167

Morita Y (1966b) Absence of electrical activity of the pigeon's pineal organ in response to light. Experientia 22:402

Morita Y, Bergmann G (1971) Physiologische Untersuchungen und weitere Bemerkungen zur Struktur des lichtempfindlichen Pinealorgans von *Pterophyllum scalare* Cuv. et Val. (Cichlidae, Teleostei). Z Zellforsch 119:289–294

Morita Y, Dodt E (1965) Nervous activity of the frog's epiphysis cerebri in relation to illumination. Experientia 21:221

Morita Y, Dodt E (1973) Slow photic responses of the isolated pineal organ of lamprey. Nova Acta Leopold 38:331–339

Munz FW, McFarland WN (1977) Evolutionary adaptations of fishes to the photic environment. In: Crescitelli F (ed) Handbook of sensory physiology, vol VII/5. Springer, Berlin Heidelberg New York, pp 193–274

Oksche A (1971) Sensory and glandular elements of the pineal organ. In: Wolstenholme GEW, Knight J (eds) The pineal gland. Churchill Livinstone, Edinburgh London, pp 127–146

Oksche A, Hartwig HG (1975) Photoneuroendocrine systems and the third ventrical. In: Knigge KM, Scott DE, Kobayashi H, Ishii S (eds) Brain endocrine interaction II. Karger, Basel, pp 40–53

Oksche A, Hartwig HG (1979) Pineal sense organs – components of photo-neuroendocrine systems. In: Ariens Kappers J, Pévet P (eds) The pineal organ of vertebrates including man: Progress in brain research, vol 52. Elsevier/North-Holland Biomedical Press, Amsterdam New York, pp 113–130

Owman C, Rüdeberg C (1970) Light, fluorescence, and electron microscopic studies on the pineal organ of the pike, *Esox lucius* L., with special regard to 5-hydroxytryptamine. Z Zellforsch 107:522–550

Ralph CL, Dawson DC (1968) Failure of the pineal body of two species of birds (*Coturnix japonica* and *Passer domesticus*) to show electrical responses to illumination. Experientia 24:147–148

Rusak B (1979) Neural mechanisms for entrainment and generation of mammalian circadian rhythms. Fed Proc 38:2589–2595

Sillman AJ, Ito H, Tomita T (1969) Studies on the mass receptor potential of the isolated frog retina. I. General properties of the response. Vision Res 9:1435–1442

Takahashi JS, Menaker M (1979) Physiology of avian circadian pacemakers. Fed Proc 38:2583–2588