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Brain photoreceptors for the photo-induced testicular response in birds*

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Gonadal function in many birds is stimulated by visible radiations, and daylength constitutes a primary source of information for controlling the reproductive cycle; this was first demonstrated by Rowan[1]. Testicular development depends upon the gonadotropic activity of the hypothalamic-adenohypophyseal system (review in Baylé[2]), and two hypothalamic regions in particular participate in the neuroendocrine control of gonadotropic secretion: the infundibular complex and the anterior-preoptic area. The mechanisms by which birds perceive light in order to induce gonadotropin release are discussed in this report.

Originally, it was thought[3] that the photoreceptors for photoperiodic gonadal responses in birds were located in the testes themselves and in the skin of the foot. However, artifical lighting of the whole body, except for the head which was covered by a black hood, did not induce the photosexual reflex in ducks[4] and sparrows[5,6]. Therefore, it was assumed that the eyes contain the photoreceptors, and Benoit concluded from a long series of experiments that the eyes do indeed contribute to the stimulation of testicular growth by light. When, for example, the retinal photoreceptors were isolated by slats of opaque rub-

ber, by blackened paraffin placed in the posterior part of the orbit[7], and by a black hood placed over the duck's head leaving a hole at eye level, testes development in intact ducks was approximately twice as great as that in the ducks blinded by optic nerve transection. Likewise, testicular growth was found to be significantly greater in intact than in enucleated mallards submitted to feeble illumination[8,9]. Other researchers are also of the opinion that information from retinal receptors participates in photoperiodically induced testicular growth and regression in *Coturnix*[10,11] and *Zonotrichia*[12]; however, results of a series of investigations[13-15] make it improbable that such is the case in the house sparrow: The gonads did not respond to light when India ink was injected under the skin of the head, even if the eyes were intact.

We recently re-investigated this problem[16]. Small disc-shaped pellets (0.6 mm in diameter, 0.2 mm thick) of radioluminous material (RLM) were inserted bilaterally in the anterior chamber of the eyes of quail subjected to short days. Two weeks later, testicular weight was noted (fig. 1). Inserting RLM pellets in the eyes of intact birds led to testicular enlargement and red RLM (620 nm; 0.015 cd/m^2; 25-10^{-8}W) was much more effective than green RLM (530 nm; 0.029 cd/m^2; 58-10^{-8}W). In contrast, testes remained quiescent after RLM was placed in the anterior chamber of the quail whose optic nerve had been severed. In the same species, no testicular growth occurred after intraocular orange RLM implantation[10,17]. The main difference with our own experiment seems to lie in the exact location of the RLM pellets, i.e., the posterior chamber vs the anterior chamber of the eye. Insertion of RLM plates in the posterior chamber possibly resulted in severe retinal disturbances. Since testicular responses to anterior chamber RLM implants were suppressed by sectioning optic nerve fibers (fig. 1), there is no doubt that retinal signals, by themselves, stimulate gonadotropin release.

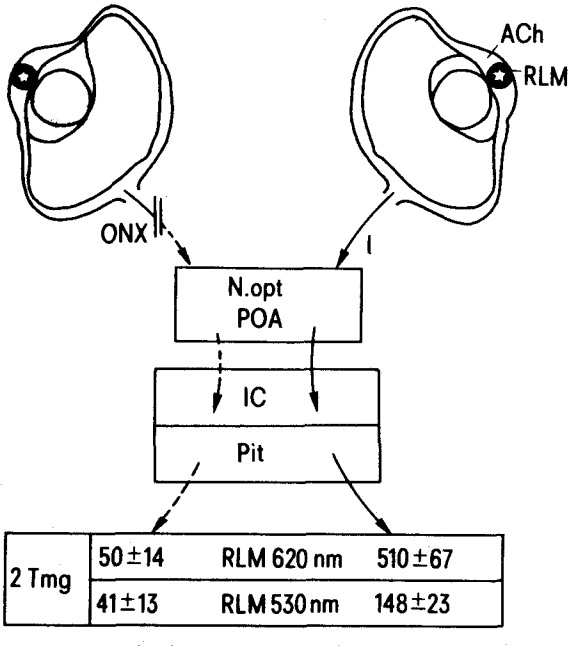

Figure 1. Retinal photoreceptors and photoinduced testicular growth (combined testes weight, in mg). Radioluminous pellet (RLM) was inserted in the anterior chamber (ACh) of the eye. In intact (I) birds, retinal information stimulated the gonadotropic axis. The involvement of retinal photoreceptors was demonstrated by the testicular quiescence in blinded (ONX) quail. Red RLM (620 nm) was much more effective than green RLM (530 nm). IC = infundibular complex. N.opt = nucleus opticus principalis thalami. Pit = pituitary. POA = preoptic-anterior hypothalamus.

There is positive evidence for a direct retino-hypothalamic projection to the suprachiasmatic region in hens, ducks, sparrows and pigeons (review in Oksche[18]). Moreover, horseradish peroxidase injection in the preoptic-anterior hypothalamic region of quail resulted in intracellular labeling of ganglion cells of the retina[19]. Infundibular projections arising from suprachiasmatic and preoptic areas have also been demonstrated in quail[20].Therefore, morphological as well as physiological data argue that retinal photoreceptors can participate in gonadal photostimulation, at least in the quail and duck.

In any event, the eyes are not essential for photoperiodically induced testicular growth. Long daylengths continue to induce testes development even after total severance of the optic nerves or removal of both eyes in a variety of birds species (see section 1), thus much effort has been devoted to localize the extraretinal photoreceptors and to determine how they are involved in the photosexual response.

1. Location of extraretinal photoreceptors: surgical approach

Blinding does not prevent long days from stimulating testicular growth in the drake[4,21], chicken[22,23], quail[24-26], sparrow[27,28], canary[29] and white-crowned sparrow[12,30]. Surgical removal of the telencephalic structures does not suppress the photosexual reflex in quail[31].

It has been reported that hypothalamic deafferentation does not suppress the photoinduced testicular growth in quail[32], however conflicting data have been presented in this regard. In some experiments total deafferentation of the tuberal region completely blocked photic gonadostimulation[33,34] although the infundibular nuclear complex seemed to retain some autonomous capacity to secrete low levels of LH-RH[35]. Horseradish peroxidase injection in the infundibular complex of intact quail allowed us to observe labeled cells in various brain regions. Absolutely no cellular labeling could be detected outside the deafferenting border after surgical isolation of the infundibular complex but testicular growth was still induced by environmental photostimulation[20]. Therefore, we conclude that the infundibular island has

Table 1. Combined testes weight (mg) in intact (I), blinded (ONX), hemispherectomized (HM) and infundibular complex deafferented (IC-DAF) quail

Group	I (n:12)	ONX (n:12)	HM (n:6)	IC-DAF (n:12)
Photoperiod				
6 L:18 D	38±3.2	26±6	30±4.1	40±7.0
18 L: 6 D	2170±211	2051±23	1350±153	1384±209

intrinsic and autonomous properties both of photoresponsivity and of stimulating gonadotrophin secretion.

2. Location of extraretinal photoreceptors: direct illumination of discrete brain regions

Light applied directly on the hypothalamus through a glass tube[36,37] or a quartz rod, 4 mm in diameter[7,38-40] exerted a strong effect on testicular growth in ducks. Of course, the large size of the light-conducting rod that was used in these experiments did not allow the precise localization of the deep photoreceptors, and more recently[41], glass optic fibers (0.3 mm in diameter) have been implanted within the hypothalamus. Positive testicular responses were obtained when light, at a low energy level, was directed into the paraventricular nucleus and the infundibular complex. Significant testicular enlargement was induced by directing more light energy onto the suprachiasmatic region and the median eminence.

A similar technique was applied in the white-crowned sparrow[42]. Intracranial implantation of light-transmitting fibers allowed the illumination of small areas of the brain. The most effective sites of illumination lie in the basal hypothalamus and in the tuberal region and were not affected by bilateral optic nerve transection of the optic nerve. The anterior hypothalamus does not appear to be photosensitive and the effectiveness of photostimulation in regions which are in close proximity to the ventromedial hypothalamus and infundibular nucleus, such as the region of the optic chiasma and optic tract and of the oculomotor nerve, may be explained by the spreading of the light. Indeed, the effects of light from the tip of the glass fiber can be exerted anywhere within the cone which subtends within the nervous tissue.

Recently, light-emitting diodes were fixed in parietal, retroocular or interorbital positions[10]. The effects on testicular growth in quail depended upon both their location and the wavelength, orange-red light being markedly more effective than green-yellow radiations. These results are quite similar to those observed using radioluminous material (RLM) as a means of stimulating the encephalic photoreceptors. Inorganic paint is excited by beta irradiation from tritium contained in the binder, and emits self-luminescence. Application of orange RLM to the skin of the head of male quail prevents testicular regression when the daily photoperiod is shortened from LL to 8L:16D, but green RLM is without effect on testes size[43,44]. In other investigations[45], orange or green RLM coated onto a polyethylene disc (10 mm) was placed on the surface of the skull of quail entrained on 'short days'. LH secretion was found augmented in quail with large amounts of orange RLM and caused maximum rates of testicular growth. Green paint was without effect. The reason that birds are sensitive to orange and not to green is probably that light of the longer wavelengths more readily penetrates tissues and can reach the photoreceptors located in the brain[46]. For this reason it has been difficult to determine the threshold of the deep photoreceptors since we do not know the rate of absorption of photons between the light-emitting RLM and the cerebral photosensitive elements.

A more accurate experimental approach, in so far as the location of encephalic photoreceptors is concerned, has been that of implanting the RLM. Oval plates (1.5×1.0×0.8 mm) of orange or blue RLM were inserted in the fissura longitudinalis cerebri (FLC) of quail reared in 'short days'[17]. The brightness of this RLM was less than 0.1 cd/m^2. Orange (580 nm) RLM insertion in the FLC, adjacent to the hypothalamic area, led to rapid testicular development. Orange RLM implantation in the orbital cavity, near the optic foramen, also resulted in a positive testicular response. When blue RLM was implanted, either in the FLC or behind the eyes, positive testicular responses were observed only in 1 out of 13 and 1 out of 11 birds, respectively. Testicular growth was also promoted following orange RLM implant in the ventromedial hypothalamus and the infundibular area of male quail kept under 8L:16D[10,17].

Table 2 summarizes data from various experiments[48-52]. Quail were reared under short daily photoperiods (6L:18D) except for the photostimulated controls (18L:6D). Green (530 nm) RLM was

Table 2. Combined testes weight (2 Tmg), plasma testosterone (Tt) and LH levels in intact (I) or hypothalamic deafferented (DAF) quail bearing green RLM implants in the infundibular (IC), preoptic (POA), paraolfactory (POL) or neostriatal (NS) area. n = number of birds, RM = non luminescent ^{3}H material

Group (n)	Photoperiod	Implant	2 Tmg	Tt ng/10 ml	LH ng/ml
I (15)	6 L:18 D	-	77±19	0.7±0.03	0.4±0.01
I (15)	18 L:6 D	-	1839±221	24±3.0	4.5±0.6
IC (10)	6 L:18 D	RM	63±15	-	-
IC (10)	6 L:18 D	RLM	1841±272	23±1.3	3.9±0.4
IC (10)	D:D	RLM	2017±54	-	-
DAF-IC (10)	6 L:18 D	RLM	1403±227	19±2.7	3.2±0.7
DAF-IC (10)	18 L:6 D	-	1565±188	-	-
POA (10)	6 L:18 D	RLM	81±22	1.4±0.6	0.9±0.2
POL (10)	6 L:18 D	RM	37±6	2.3±0.5	-
POL (10)	6 L:18 D	RLM	764±83	9.4±0.6	-
NS (10)	6 L:18 D	RLM	42±8	-	-

implanted in the infundibular complex (IC), the preoptic area (POA), the paraolfactory lobe (POL) and the neostriatum (NS). In some birds, IC implants were placed in the deafferented basal hypothalamus. The effects of direct illumination of the infundibular complex on gonadal function are always positive in spite of technical (optic fibers or RLM implants) or species (duck, white-crowned sparrow or quail) differences. This result can be taken as evidence for an intrinsic photosensitivity and gonadotropic responsiveness of neuronal populations located in the basal hypothalamus. Moreover, one can see from table 2 that RLM placement in the deafferented infundibular complex continues to promote testicular growth. At this point, we think it valuable to note that comparison of parasagittal diagrams of the diencephalic region in both *Zonotrichia*[42] and *Coturnis*[20,50] indicates that our hypothalamic islands include not only the infundibular nucleus but also the entire ventromedial hypothalamus and even the caudal part of the supraoptic region. Moreover, as to the effectiveness of infundibular RLM beads in birds held either in complete darkness (DD) or in 'short days' (6L:18D), no cumulative effect of local permanent photostimulation of the hypothalamus and of photoperiodic environmental lighting can be detected. At least, beta irradiation per se has no effect on the gonadotropic axis.

As to RLM placement in the preoptic-anterior hypothalamic area (POA), no positive testicular response can be observed (tables 2 and 3). Illumination of the anterior hypothalamus of *Zonotrichia* through optic fibers is also ineffective[42] although moderate testicular development was reported in ducks using high light intensity[41]. It was suggested above that preoptic anterior hypothalamic neuronal clusters might be involved in the photosexual reflex partly as a target network for retinal information.

RLM induces a marked enlargement of testes when pellets are placed in the paraolfactory area. The fact that the paraolfactory area is labeled after infundibular injection of horseradish peroxidase[20] led us to compare the localization of these labeled neurons in quail to the rhinencephalic region which was photostimulated directly in drakes[53], resulting in testicular growth, and to hypothesize that these two regions might be analogous. Actually, placement of small discs of RLM in the paraolfactory lobe of quail results in gonadotropic stimulation. Implantation of solid RLM spheres (0.8 mm in diameter) in the olfactory bulb of quail induced testicular growth in more than 50% of implanted birds[47]. However, placement of small beads of RLM in the rhinencephalon had no effect[10]. Other areas of high photosensitivity include the optic lobe[47], the nucleus rotundus[42], the region dorsal and posterior to the anterior commissure[10,17] and some parts of the midbrain[54]. In contrast, no photosensitivity could be detected by illuminating the optic tectum, the region of the posterior commissure, the area of the tractus septo-mesencephalicus and various parts of the cerebrum such as the Wulst region[10], and the neostriatum[52].

Table 3. Testicular response (weight of both testes in mg) to continuous illumination of extraretinal photoreceptors

Photo-period	RLM	Duration 14 days POA	POL	IC	9 days IC
6 L:18 D	620 nm	28±4	1549±183	1900±292	737±61
	530 nm	53±3	764±83	1521±107	507±29
18 L:6 D	-	2200±300			761±87

Although the pineal organ has been suggested as a site of photoreception, it does not appear to act as a photoreceptor for gonadal growth in birds. The effects of pinealectomy and of melatonin injection were reviewed recently[55]. In quail, local lighting of the pineal with orange RLM did not induce gonadal growth[17,47]. With the use of large amounts of radioluminous paint, however, a stimulatory effect of continuous light was evidenced, but the testicular weight was not significantly lower in pinealectomized quail than that in intact ones[44]. One earlier report[56] suggested that the pineal body could serve as a photoreceptor for the photosexual reflex in *Coturnix* since the testicular growth that was induced by RLM application on the skull was suppressed after pinealectomy.

Experiments summarized in table 3 were undertaken in order to test the spectral and temporal responsiveness of deep photoreceptors. Green (530 nm) or red (620 nm) light-emitting pellets were implanted in either the infundibular complex (IC) or the paraolfactory lobe (POL). RLM implants were also placed in the preoptic-anterior hypothalamus which is not photosensitive and therefore served as controls. Testicular weights were measured 9 or 14 days later.

The hypothalamic spectral sensitivity is wider than that of the retina. When light is introduced directly to the hypothalamus of ducks via a quartz rod, all visible wavelengths stimulate testicular growth[7,39,40,57]. Data from table 3 indicate that red RLM is moderately more effective that green RLM in stimulating infundibular photoreceptors. The difference between red and green effectiveness appears to be more significant at the paraolfactory level of *Coturnix*.

It is well known[58] that testicular growth in birds subjected to a daily stimulatory environmental photoperiod is a logarithmic function of time. It was also found (table 3) that the testes enlargement following continuous lighting of the infundibular complex was significantly higher after 14 than after 9 days of treatment.

On the whole therefore, one can propose that extraretinal photoreceptors for photoperiodically induced testicular growth are concentrated mainly in

the mediobasal hypothalamus. These photosensitive elements which are not morphologically distinguishable[59] have a wide spectral sensitivity and are part of a neuronal network responsible for the release of gonadotropin releasing factor. The other hypothalamic region involved in the photosexual reflex lies more rostrally (suprachiasmatic-preoptic area) and does not appear to contain photosensitive elements although it does serve as a target organ for retinal photic information. Extraretinal photoreceptors are also demonstrable in the paraolfactory lobe and their relationships with the gonadotropic hypothalamus are explored in table 4. Green RLM was placed, bi- or unilaterally, in the paraolfactory lobe. Half of the implanted birds were left intact. The remaining half was subjected to paraolfactory hypothalamic disconnection (a thin blade was lowered at anterior coordinate +7.5[60] rostral to the tractus septo-mesencephalicus, and a see-saw motion of the blade into the frontal plane allowed complete sectioning of the brain). Bilateral disconnection was performed in bilaterally implanted quail. Unilateral (homo- or contro-lateral) disconnection was performed in unilaterally implanted quail. Autopsy occurred 12 days later. Birds were held in short daily photoperiods except for photostimulated controls (18L:6D, testicular weight = 1.420 ± 67 mg).

The gonadal response to paraolfactory local photostimulation is suppressed after interrupting all the neural links between the paraolfactive lobe and the hypothalamus[52]. Moreover, paraolfactory projections to the hypothalamus are mainly contralateral[61]. The physiological role that might be played by the photosensitive elements in the paraolfactory lobe is unknown. It seems that, in intact quail, photic energy is detected by some rhinencephalic neurons and changed into neural signals that are conveyed to the contralateral gonadotropic hypothalamus.

3. Electrophysiological investigations on extraretinal photoreceptors

There have been few attempts to record electrophysiological correlates of the effects of photic stimulation on the deep photoreceptors that are involved in photoperiodically induced testicular development.

Flash-evoked potentials were recorded[62] in unanesthetized, chronically prepared quail from the photosensitive area of the infundibular complex (i.e., infundibular nucleus and ventromedial nucleus, after Oksche[63]). Infundibular responses to flashes are characteristic and homogeneous (table 5).

Their latency is longer than in the optic chiasma and shorter than in other hypothalamic regions. Changing the environmental lighting pattern from 6L:18D to 18L:6D shortens the latency of the infundibular responses, but testosterone treatment has the same effect. No response can be recorded after bilateral optic nerve transection.

Infundibular flash-evoked potentials proceed from retinal photoreceptors and seem to be testosterone-dependent. It follows that they cannot be taken as direct correlates of deep photoreceptor activity. Retinal signals can be conveyed to infundibular neurons through indirect pathways involving anterior hypothalamic or dorsal thalamic relays[64]. However, the homogeneity and constancy of flash-induced infundibular responses and their characteristic latency may be explained by the special role played by the infundibular complex in the photoperiodically induced gonadotropic activity, even if flash stimuli do not provide a normal functional trigger to this system.

In order to obtain functional characteristics of deep photosensitive elements, multiple unit activity (MUA) was recorded from neuronal pools located in the infundibular complex, in chronically maintained birds which were resting but awake. All records were obtained in scotopic conditions[65-67]. Experimental groups are indicated in table 6. Intact (I) and blinded (ONX) quail were subjected to either 'short' or 'long days'. Radioluminous (RLM) or radio non luminescent material (RM) was implanted in the infundibular complex of 'short-day' reared quail. We are well

Table 4. Testicular response (mg) to local stimulation of paraolfactory photoreceptors after paraolfactory hypothalamic disconnection

RLM implants	Intact	Disconnection		
		Bilateral	Contra-lateral	Homo-lateral
Bilateral	486 ± 21	28 ± 2	-	-
Unilateral	359 ± 30	-	24 ± 5	240 ± 17

Table 5. Amplitude (μV) and latency (msec) of flash-evoked potentials in the infundibular complex (IC), optic chiasma (OC) or non photosensitive hypothalamus (NPH) of intact or blinded (ONX) male quail

Treatment	Photoperiod	Flash-evoked potentials					
		IC		OC		NPH	
		μV	msec	μV	msec	μV	msec
Intact (32)	6 L:18 D	25-30	14.3 ± 0.3	40-50	7.6 ± 0.5	0-30	18-22
Intact (32)	18 L:6 D	25-30	12.2 ± 0.2	40-50	7.3 ± 0.7	0-30	18-22
Testosterone 250 μg/day (18)	6 L:18 D	25-30	12.4 ± 0.4	40-50	7.5 ± 0.6	0-30	18-22
ONX (6)	18 L:6 D	0	-	0	-	0	-

Table 6. Effects of repetitive (1 cps) flash stimulations on multiunit activity (MUA) recorded from the photosensitive hypothalamic area for 200 sweeps of 1 sec

Photoperiod	6 L:18 D				18 L:6 D	
Group	I (10)	ONX (15)	RM (20)	RLM (20)	I (10)	ONX (15)
Spontaneous MUA/200 sec	335±38	229±19	340±26	201±25	185±15	162±21
Flash-altered MUA/200 sec	797±166	223±27	658±30	169±18	133±24	138±17

aware that MUA is somewhat difficult to interpret, partly due to the possibility of exploring heterogeneous neuronal populations with semi-microelectrodes (10–15 µm in tip diameter). However, since stereotaxic coordinates for microelectrode lowering are exactly the same as for the RLM implantation which resulted in testicular growth, one can assume that MUA records ought to characterize, at least in part, the photoreceptor activity of photosensitive infundibular elements.

Flash-altered MUA is compared to spontaneous basal firing rates in various experimental groups. Infundibular MUA is markedly increased after flash stimulation in non-photostimulated quail (136 and 94% increase in intact an RM implanted 'short-day' birds). This important response to photic stimulation can be observed during the whole sweep (1 sec) following flash lighting (50 µsec; 400 lx), with a maximum at approximately 250 msec. This positive response of infundibular MUA to flash is completely suppressed and even tends to be reversed in photostimulated birds (18L:6D: 26% decrease; RLM: 16% decrease). No response could be detected after blinding the animals.

It appears, therefore, that flash-induced variations of firing rates in the photosensitive area of the hypothalamus result from retinal photoreceptors. However, the magnitude and even the increment or diminution of these responses are influenced by the environmental light regimen. We suggest that these effects are exerted directly on the deep extraretinal photoreceptive area since they can be observed in the mere presence of RLM local photostimulating pellets.

Spontaneous MUA is much lower in blinded than in intact non-photostimulated quail (32%) but this effect of optic nerve transection disappears in birds kept under long daily photoperiods. We observed here again the clearcut effect of the retinal photoreceptors on infundibular firing rates, complemented by the modulating influence of the deep infundibular photoreceptors.

Environmental as well as deep local photostimulation lead to markedly decreased infundibular MUA as compared to values found in non-photostimulated birds (45% and 41% decrease respectively). This effect can be observed not only in intact but also in blinded quail. Infundibular MUA is 30% lower in 'long-day' than in 'short-day' ONX animals. Once again, this influence may be mediated through deep extraretinal receptors located in the infundibular complex.

Quite different results were noted by recording the effect of acute or chronic lighting on the preoptic MUA[68]. For example, preoptic multiunit activity, on the whole, is markedly reduced after a flash of light, but there is an increase in firing rates (about 6 times) occuring within the first milliseconds after flash stimulation. Thereafter, MUA is lower than the spontaneous level for approximately 250 msec. These alterations of preoptic firing rates observed after flash-stimulation are completely suppressed if the optic nerves are severed. The early peak in firing of preoptic neuronal populations, which is much earlier than that found in the infundibular region (latency: 20 msec vs 250 msec) is comparable to the response exhibited by the optic tectum.

Data in table 7 present further evidence that deep hypothalamic photosensitive elements can be directly triggered by environmental lighting. To follow this up, the frequency of discharge in the infundibular photosensitive area was obtained during the light phase (09.00–15.00 h) and part of the dark phase (15.00–21.00 h) of quail in short photoperiods (6L:18D). Intact quail exhibited higher MUA levels during the morning than during the afternoon (44%). Bilateral severance of optic nerves did not affect this difference which must be caused therefore by illumination of extraretinal photoreceptors from outside, in the absence of any retinal information.

Investigations on the responsiveness of paraolfactory neuronal clusters, using the same semi-microrecording technique, are now in progress. It seems[61] that paraolfactory photoreceptors also behave rather specifically and independent of retinal information with respect to environmental lighting.

On the other hand, recording pineal multiunit activity from unanesthetized quail indicates that light influences the pineal MUA[69–71]. Flash stimulations induce a marked decrease in pineal activity but this inhibitory effect disppears after optic nerve section. Pineal firing rates are lower in photostimulated birds than in non-photostimulated quail except for those

Table 7. Spontaneous infundibular MUA in intact and blinded quail kept in short days (6 L_{9-15}:18 D): dark vs light phase differences

Time of the records	09.00–15.00 h (light phase)	13.00–21.00 h (dark phase)
Intact (12)	398±40	224±37
ONX (20)	301±27	180±18

that had been blinded. The effects of light on pineal MUA appear therefore to be mediated exclusively through retinal photoreceptors.

Conclusion

The location and participation of extraretinal deep photoreceptors for photoperiodically induced testicular growth are schematized in figure 2. Light radiations penetrate the brain tissues to reach and stimulate the extraretinal deep photoreceptors located in the infundibular complex and in the paraolfactive lobe. In turn, deep photoreceptors lead the infundibular (and eventually preoptic-anterior) neurosecretory cells to produce and release GnRH into the hypophyseal portal system. Besides the optic projections onto the visual system[64], retinal information is conveyed to the preoptic-anterior hypothalamus and can interfere with the gonadotropic function. Retinal and extraretinal photoreceptors might also cooperate to provide the circadian and circannial components involved in measuring the duration of daylength. There seems little doubt that other parts of the neuronal machinery within the brain are also involved in regulating this system; crucial, for one, are the thalamic projections to the infundibular area.

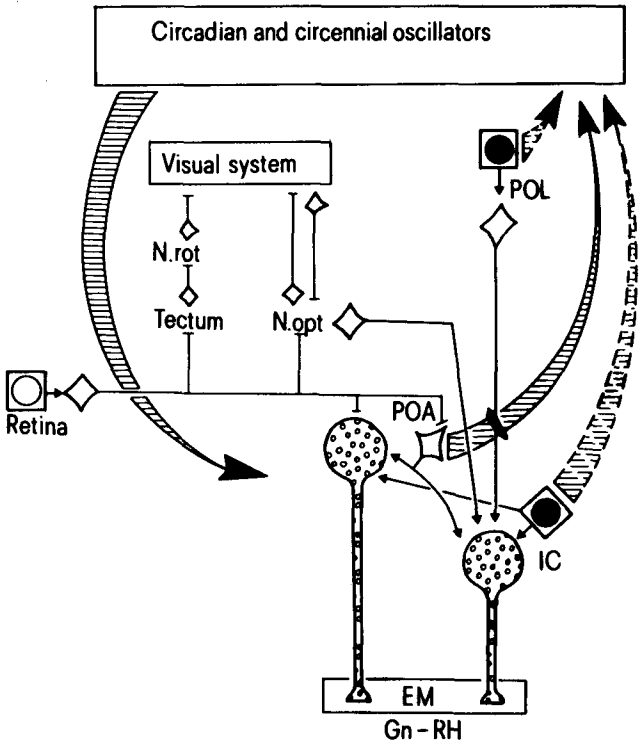

Figure 2. Photoreceptor involvement in photoperiodically induced testicular development. See text for further explanation. ■: Extraretinal photosensitive elements; ⊡: retinal photoreceptors. EM = median eminence; Gn-RH = gonadotropin releasing hormone; IC = infundibular complex: N.rot = nucleus rotundus; N.opt = nucleus opticus principalis thalami; POA = preoptic-anterior hypothalamus; POL = paraolfactive lobe.

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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.