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Extraretinal Light Perception in the Sparrow IV. Further Evidence that the Eyes Do Not Participate in Photoperiodic Photoreception

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Summary. Photoperiodic testicular growth in House Sparrows (*Passer domesticus*) exposed to long days (16 hrs) of orange-red light (>600 nm) is exclusively controlled by extraretinal photoreceptors in the brain; the eyes are not involved. Careful reconsideration of previously published data from this and other bird species does not support a role for the eyes in photoperiodically significant photoreception.

Introduction

The brain has been shown by several ingenious experimental approaches to be directly involved as a receptor for photoperiodic reproductive events in a variety of bird species. The contribution of the eyes, if any, to photoperiodic photoreception has been a topic of considerable interest and experimentation. Employing an approach made possible by knowledge of the light intensity necessary for measurable gonadal growth in normal House Sparrows (*Passer domesticus*), Menaker *et al.* (1970) demonstrated that the eyes do not participate. Benoit has concluded from evidence accumulated from a long series of experiments with domestic ducks (*Anas platyrhynchos*) that the eyes contribute to but are not essential for the stimulation of testis growth by light (Benoit, 1964, 1970). He postulates that the retinal photoreceptor, unlike the brain receptor, is responsive to light only in the orange-red region of the spectrum.

Experiments presented here were designed to test the hypothesis of the existence of special red-sensitive retinal receptors for photoperiodism in the sparrow.

Methods and Materials

On 11 December, male House Sparrows were moved indoors from outdoor aviaries and caged in pairs under a LD 9:15 (100:0 lux) light cycle (Ken-Rad 40 watt daylight fluorescent bulbs). Initial controls were killed and testis weights measured. Half of the remaining birds were bilaterally enucleated (Menaker, 1968). Four experimental groups were then established; blind-clipped, blind-hooded, sighted-clipped, and sighted-hooded. Hooded birds had carbon black in aqueous suspension injected beneath the skin of the skull and their heads covered with Sudan Black B stain in collodion (cellulose nitrate in ethyl ether). The birds' beaks and eyes were not collodion treated, though the empty orbits of the blind-hooded birds were. The clipped groups had their head feathers removed with surgical scissors. All groups were

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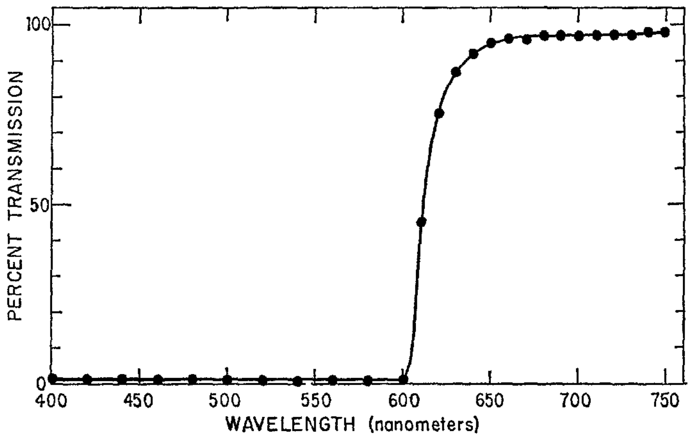

Fig. 1. Wavelength-transmission curve of the red plastic filter

exposed to LD 16:8 of red light on 13 January and the experiment was terminated 24 days later when the birds were killed and their testes weighed.

The experimental red light was provided by incandescent bulbs filtered by 0.125 cm transparent red plastic (Acrylite, American Cyanamid Co.). The filter wavelength-transmission curve as measured spectrophotometrically (Cary Model 14) is shown in Figure 1. Two light intensities, referred to as low and high, were utilized. To produce the low intensity light the voltage to 15 watt, 130 volt incandescent bulbs (Ken-Rad 15A15) was adjusted to supply 0.15 ergs/cm^2/sec of red light (600–700 nm) at perch height. The high intensity red light (990 ergs/cm^2/sec, 600–700 nm) was from 100 watt, 130 volt incandescent bulbs (Westinghouse) voltage adjusted to 107 volts. The light intensities were obtained by measuring the sources through three colored filters to determine an equivalent black body temperature which in turn was used to calculate the light energy fluxes. The procedure was checked with a calibrated Epply Radiometric Standard. A deviation of 9% was found from the calibrated values.

Results

The four experimental groups were designed to clearly demonstrate the locus of red light perception as measured by testicular growth. The blind-hooded birds presumably had no photoreceptors (i.e., eyeless with brain occluded) exposed to the light and thus served as a terminal control. The blind-clipped birds had only the brain exposed to light. The sighted-hooded group had only the eyes exposed to light, provided none reached the brain either through leaks in the hood or through the orbits or beak. In the sighted-clipped group light reached both the eyes and the brain.

The data presented in Table 1 indicate that at the low intensity of red light the eyes are not involved in photoperiodic photoreception. Only birds in which the extraretinal receptor was exposed (blind-clipped and sighted-clipped) show significant testis growth when compared with the initial controls. Furthermore, there is not even the suggestion of a difference between these two groups even though the eyes are present in one group and not in the other. The hooded birds, both blind and sighted, in which the brain was shielded from the red light, showed no significant testis growth.

Table 1. Effects of low intensity red light exposure of the eyes and/or the brain photoreceptor on the testis weight of sparrows

Group	Number	Testis weight[a]
Initial controls	16	4 ± 1
Blind-hooded	7	11 ± 7
Sighted-hooded	7	6 ± 1
Blind-clipped	8	235 ± 40
Sighted-clipped	10	243 ± 32

[a] Testis weights are means (combined weights of both testes in mg) of all birds in the group followed by the S.E.

Table 2. Effects of high intensity red light exposure of the eyes and/or the brain photoreceptor on the testis weight of sparrows

Group	Number	Testis weight[a]
Initial controls	16	4 ± 1
Blind-hooded	5	305 ± 65
Sighted-hooded	8	319 ± 43
Blind-clipped	6	302 ± 55
Sighted-clipped	8	341 ± 52

[a] Testis weights in mg as in Table 1.

All the birds, regardless of treatment, which were exposed to the high light intensity (Table 2) responded identically with significant testis growth. This result can only be due to the failure of the hooding technique to effectively shield the brain from light. For example, the hooded group without eyes (blind-hooded) showed as much testis growth as did any of the other groups. Light must be reaching the brains of these birds through the hooding or via some other route such as through the beak. No enhancement of testis growth occurred in any group under either light intensity merely because of the presence of the eyes.

At the end of the experiment the light attenuation capability of the hoods was determined by measuring the transmission of light through evacuated bird skulls. The hooding treatment reduced the light reaching the brain by an average factor of 2000 as compared to clipped birds. Although hooding effectively attenuated the light penetrating to the brains of birds exposed to the dim light, it was inadequate to shield hooded birds under the bright light.

Discussion

When subjected to various long day treatments, the testicular growth response of blind sparrows is indistinguishable from that of normal birds (Underwood and Menaker, 1970); these results offer no support to the case for retinal involvement. Indeed, other previous work with *Passer* (Menaker and Keatts, 1968; Menaker *et al.*, 1970) demands rejection of the retinal hypothesis and the results presented here make it untenable even in its special form (i.e., the involvement of red sensitive retinal receptors). Photoperiodic testicular growth in the sparrow is exclusively mediated by extraretinal photoreception. Evidence of extraretinal photoreception influencing reproductive events has also been reported in chickens (Harrison and Becker, 1969; Harrison, 1972; Ookawa, 1970a, b, c), male domestic ducks (Benoit, 1935a, b, c, 1937), Japanese quail (*Coturnix coturnix japonica*) (Oishi *et al.*, 1966; Kato *et al.*, 1967; Sayler and Wolfson, 1968; Oishi and Kato, 1968; Homma *et al.*, 1972; Oishi and Lauber, 1973a, b) and White-crowned (*Zonotrichia leucophrys*) and Golden-crowned Sparrows (*Z. atricapilla*) (Gwinner *et al.*, 1971; Turek, 1974). Utilizing orange and blue radioluminescent implants to stimulate testis growth in Japanese quail, Homma and Sakakibara (1971) showed that at least several areas of the brain are involved in photoperiodic photoreception (hypothalamus, optic lobe, olfactory lobe) but that implants into the eyes are ineffective in eliciting testis growth. The implants, however, emitted very dim light, perhaps too weak to adequately stimulate the retinal receptors postulated by Benoit, if indeed they exist.

Benoit believes that not only the photoreceptors located in the brain but also the retinae participate in gonadal photostimulation in the duck. Benoit's retinal hypothesis stems from experiments described in three papers (Benoit, 1938a; Benoit, Assenmacher and Walter, 1953; Benoit and Assenmacher, 1954). In two cases the experimental approach was similar; pairs of ducks (one intact and one with sectioned optic nerves) were exposed to various intensities of white light (Benoit, Assenmacher and Walter, 1953; Benoit and Assenmacher, 1954). Of a total of 10 comparable pairs, in seven cases the intact duck showed a stronger testis response. The differences between the blind and intact ducks of several of these seven pairs, however, were slight. The third experiment utilized a technically different approach (Benoit, 1938a). Benoit attempted to isolate the retinal receptors by depositing around the eye, in the posterior part of the orbit, slats or sheets of either opaque rubber, metal or blackened paraffin, in ducks with both sectioned and intact optic nerves. A black drape was placed over the ducks' heads and pierced with a hole at the level of the eye. The ducks were subsequently illuminated with red light. A total of seven ducks were used (four intact and three with sectioned optic nerves). The intact ducks showed approximately twice the testis development of the blinded ducks. It is likely, however, to be technically more difficult to prevent diffusion of the red light to brain photoreceptors in ducks with intact nerves since the placement of shields around an intact nerve would seem to prohibit the amount of shielding that could be accomplished if the optic nerve did not have to be respected. Even in the blind ducks some light diffused past the shielding since the blinded animals did show small but positive testis growth. Also, it is possible that the intact nerve could function as a physical light pipe to the brain photoreceptors thereby eliciting greater testis growth in intact ducks.

Early experiments by Benoit demonstrated that visible light in the orange-red region (617–740 nm) of the spectrum was the most effective in stimulating testis growth in intact ducks (Benoit and Ott, 1938, 1944; Benoit *et al.*, 1950a). In these experiments, at least at the higher intensities, the orange-red light must have stimulated both the putative retinal receptors and the deeper brain photoreceptors. Subsequently, Benoit attempted to define the action spectrum of the retinal photoreceptors by exposing intact ducks to low intensities of monochromatic light (Benoit and Assenmacher, 1966; Benoit *et al.*, 1966). At threshold intensities, Benoit reasoned, it would be unlikely that light would penetrate to the brain photoreceptors; only the retina would be stimulated. Utilizing this approach Benoit demonstrated that visible light in the red region of the spectrum was the most effective in stimulating testicular growth (maximum sensitivity 625–647 nm). The hypothetical receptors in the retina responsible for gonadal stimulation would then be separate from those involved in normal vision since the latter, as assayed by the pupillary reflex, are maximally sensitive in the yellow region of the spectrum (Benoit *et al.*, 1952).

Benoit finally attempted to show a clear dissociation between the retinal and brain photoreceptors by exposing intact ducks and ducks with sectioned optic nerves to low (0.045–293 ergs/cm^2/sec) intensities of monochromatic light in the red region (634–638 nm and 650 nm). According to his hypothesis the intact ducks should have shown a stronger response. Including controls, these experiments involved 277 ducks (cf. Tables 1 and 2 in Benoit, 1970). These experiments clearly failed to support the hypothesis of retinal involvement. Testicular growth in the blind ducks was as great as that shown by intact ducks. It is quite clear that brain receptors were stimulated even at the lowest levels of light energy. The reason that ducks are most sensitive to light in the orange-red region is simple; experiments utilizing not only ducks (Benoit, Assenmacher and Manuel, 1953; Benoit *et al.*, 1954a, b) but also other animals (Bachem and Reed, 1931; Danforth, 1930; Hawley *et al.*, 1940) show that visible light of the longer wavelengths more readily penetrates tissue and is, therefore, able to reach and stimulate the photoreceptors located in the brain.

We feel that the initial experiments of Benoit (Benoit, 1938a; Benoit, Assenmacher and Walter, 1953; Benoit and Assenmacher, 1954) do not conclusively show retinal involvement. The sample sizes were small and the differences may not be significant. Clearly, later attempts to stimulate only retinal receptors by using low levels of illumination and statistically significant numbers of ducks offer no support for retinal involvement (Benoit, 1970). The high sensitivity of the brain photoreceptors to red light demands extreme caution in interpreting the experiment involving isolation of the retinal receptors by depositing light shields behind the eyes of ducks with both sectioned and intact optic nerves (Benoit, 1938a). In view of the possible technical difficulties in providing complete shielding in intact ducks, the greater testis growth observed in the intact ducks might well be due to the diffusion of red light to brain photoreceptors. The difficulties involved in effectively shielding brains from red light are also amply demonstrated by our own data from House Sparrows (Table 2). Without the *a priori* assumption that the eyes are involved, Benoit's action spectrum data can most reasonably be interpreted as showing the response of only the brain photoreceptors. It seems likely that orange-red light is most efficacious in eliciting testis growth in both blind and intact ducks since orange-red light more readily penetrates to the brain. In this regard we note that visible light in the red, yellow, and blue regions of the spectrum are all effective in stimulating testis growth when directly applied by glass or quartz rods or tubes to the rhinencephalon, pituitary, or hypothalamus (Benoit, 1938a, b; Benoit *et al.*, 1950a, b). Although Benoit (1970) interprets this result as further evidence of a dissociation between the retina (which, according to his hypothesis is sensitive only to orange-red) and the brain receptors, it seems clear to us that the light intensities which were directly applied to the brain were all above threshold, making it impossible to determine the action spectrum of the brain photoreceptors.

Gwinner, Turek and Smith (1971) present equivocal evidence for a retinal role in the long day-induced events of the spring annual cycle in two species of migratory *Zonotrichia*. Exposed to a LD 16:8 low intensity light cycle (4 to 8 lux), less testicular growth, migratory fattening and restlessness (*Zugunruhe*) occurred in black collodion-hooded or india ink-injected birds than in clear collodion-hooded and normal birds. They concluded that extraocular photoreception is involved in the photoperiodic responses studied, but that the eyes are possibly of significance as well. Turek (1974) has recently completed studies of extraretinal photoreception in the breaking of the photorefractory period in Golden-crowned Sparrows. Photorefractory birds must experience short days before long days can again exert their stimulatory effect. He found that these birds have a photoperiodic light intensity threshold far lower than originally suspected. When normal and clipped (head feathers removed) photorefractory Golden-crowned Sparrows were exposed to long days of dim light (LD 16:8, 0.2 lux), the normal birds broke refractoriness and the clipped birds did not. Under long days of a higher light intensity (about 6.0 lux) both clipped and black collodion-hooded birds failed to break refractoriness. He cites two possible explanations; the eyes are involved at 6.0 lux but not at 0.2 lux, or more likely, that at a light intensity of 6.0 lux enough light, even in the hooded birds, still reaches the extraretinal photoreceptors to prevent termination of the refractory period, i.e., all the birds extraretinally perceived the long photoperiod at the higher light intensity. The latter interpretation would explain the observed gonadal growth in hooded birds reported earlier (Gwinner, Turek and Smith, 1971) without recourse to the assumption of retinal involvement. Turek concludes that photoreception in the Golden-crowned Sparrow during gonadal growth and in the refractory period is mediated by extraretinal photoreceptors and that the eyes probably play no significant role.

We have found that the hooding treatment is not only ineffective in shielding the brain from red light of 990 ergs/cm^2/sec (Table 2) but also from red light of a much lower intensity, 30 ergs/cm^2/sec (unpublished results). Our experiments with House Sparrows and the results of Gwinner, Turek and Smith with Golden-crowned and White-crowned Sparrows show that shielding techniques can be fruitful in dissociating retinal from brain photoreception but in addition emphasize that extreme caution must be observed. This approach is only effective at near threshold intensities of light. Above threshold, enough light may penetrate to the brain either through the hood itself or via some other route, such as through the chin or beak, to elicit testis growth.

Recently, it has been suggested that the termination of sexual activity by short days is dependent, in Japanese quail, on their having experienced long days prior to blinding (Homma *et al.*, 1972). Although we have shown that the eyes are not involved in gonadal recrudescence in sparrows, and find no support in the literature for the view that they are involved in the control of recrudescence in any other avian species, the data of Homma *et al.* (1972) suggest that the eyes may contribute in some fashion to the control of gonadal regression.

Somewhat surprisingly perhaps, the lateral eyes appear to play no role in the perception of light which photoperiodically stimulates gonadal recrudescence in birds. It is the brain that performs this task, but precisely where and how remain at present unknown.

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