Electrophysiological Evidence for Rod and Cone-based Vision in the Nocturnal Flying Squirrel

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Summary. The flying squirrel (Glaucomys volans) is a strongly nocturnal rodent. Previous anatomical observations suggested that the retina of this animal contains some cone-like receptors in addition to large numbers of rods. Evidence for duplicity of function in this visual system was obtained from an examination of three indices of visual activity: the electroretinogram (ERG), the isolated PIII retinal response, and the visually evoked cortical potential (VECP). The spectral sensitivity of the dark-adapted flying squirrel is similar to that of other mammals—it has a 500 nm peak (Figs. 3, 8). Responses of the ERG and isolated PIII to flickering light indicate the operation of two processes (Figs. 4, 7), one of which is unable to follow flickering light at repetition rates above 10–15 Hz. Spectral sensitivity measurements reveal that these two processes have different spectral sensitivities. The photopic mechanism in the flying squirrel visual system has peak sensitivity at about 520 nm (Figs. 5, 7, 9). The effects of steady light adaptation are much more obvious in the cortical potentials than they are in the retinal potentials.

Introduction

In a recent survey of the structure of photoreceptors, Cohen (1972) pointed out that nearly all vertebrate retinas appear to contain two types of photoreceptors as distinguished by the form of their synaptic terminals. These terminals are described as spherular or pedicular in shape—the former is typically associated with rod photoreceptors, the latter with cones. Since there is an overwhelming body of evidence demonstrating the association of rods with scotopic vision, and that of cones with photopic vision, it is particularly interesting to note that even clearly nocturnal species appear to have a number of cone photoreceptors. Cohen (1972) suggests that these anatomical observations imply the presence of duplex vision in nocturnal species. There is evidence in support of this contention; for example, from work done on the rat. The retina of this
nocturnal rodent contains a small number of photoreceptors which appear to have some of the anatomical properties usually associated with cones (Sidman, 1958; Dowling, 1967). Evidence that these receptors provide at least some of the functional capacities typically associated with cones has been obtained in both physiological (Dodt and Echte, 1961; Green, 1973) and behavioral (Birch and Jacobs, 1975) studies. On the other side of the coin, recent research indicates that a group of highly diurnal animals, the ground squirrels, although previously believed to have all-cone retinas, in fact do not. Indeed, there are now both anatomical and electrophysiological results showing that at least four species of ground-dwelling sciurids have a small, but functional, rod system (Green and Dowling, 1975; West and Dowling, 1975; Jacobs, Fisher, Anderson and Silverman, 1976).

Taken together, these results on strongly nocturnal and strongly diurnal species suggest that most, perhaps all, mammalian retinas contain both rods and cones and thus provide all mammalian species with the potential for duplex vision. To further pursue this possibility, we have sought evidence for duplex vision in a strongly nocturnal rodent, the flying squirrel. Although not much appears to be known about vision in this species, naturalistic observations verify that this animal is nocturnal in behavior (MacClintock, 1970). And, as for other nocturnal species, Cohen (1972) has noted that the retina of this species contains a small number of cone-like photoreceptors in addition to large numbers of typical rods. To determine if these two types of photoreceptors provide the basis for duplex vision, several aspects of the electroretinogram (ERG) and the visually evoked cortical potential (VECP) of the flying squirrel were examined.

Materials and Methods

Experiments were performed on Southern flying squirrels (*Glaucomys volans*). Both sexes were used and all animals were adults.

Photic stimuli were obtained from a double-beam optical system. One beam of this system, usually employed as an adaptation light, originated from a tungsten-filament lamp. The other beam was produced by a Bausch and Lomb high-intensity grating monochromator with slits adjusted to yield a monochromatic light having a half-energy passband of 10 nm. The outputs from these two lights were converged at a beam splitter and the mixture of the two was focused in the plane of the animal's pupil to provide illumination of a central retinal field 40° in diameter. The intensities of the two beams were independently controlled through the use of neutral density filters. Electromagnetic shutters were located in the optical system so as to permit stimulation from either source separately or from a mixture of the two.

The flying squirrels were initially anesthetized by an intraperitoneal injection of a mixture of sodium pentobarbital (40 mg/kg) and chloral hydrate (60 mg/kg). Supplemental anesthesia was given as required. Normal body temperature was maintained during the experiment through the use of a circulating hot water heater. After the animals were placed in a stereotaxic head holder, the eyelid of the test eye was retracted and the pupil was dilated by topical administration of Cyclogyl (cyclopentolate hydrochloride). The other eye was covered with an opaque mask.

ERGs were recorded from insulated stainless steel electrodes inserted through the cornea just ahead of the limbus and into the posterior chamber of the eye. An indifferent electrode was sewn into the skin above the eye. ERG signals were differentially recorded through an amplifier having a bandpass of 0.2 to 1,000 Hz. The amplified signals were averaged with an Ortec 4623 Signal Averager. These averaged signals were read out through an X-Y plotter and ERG measure-