crystallization of the motor pattern some control mechanism other than auditory feedback takes over and becomes adequate to maintain its organization. There are thus several pathways impinging upon the development of song patterns in the white-crowned sparrow, including acoustical influences from the external environment, acoustical feedback from the bird's own vocalizations, and perhaps nonauditory feedback as well.

Cultural transmission is known to play a role in the development of several types of animal behavior (*5*). However, most examples consist of the reorientation through experience of motor patterns, the basic organization of which remains little changed. In the development of vocal behavior in the white-crowned sparrow and certain other species of song birds, we find a rare case of drastic reorganization of whole patterns of motor activity through cultural influence (*6*). The process of acquisition in the white-crowned sparrow is interesting in that, unlike that of some birds (*7*), it requires no social bond between the young bird and the emitter of the copied sound, such as is postulated as a prerequisite for speech learning in human children (*8*). The reinforcement process underlying the acquisition of sound patterns transmitted through a loudspeaker is obscure.

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Mangabey x and b Wave Electroretinogram Components: Their Dark-Adapted Luminosity Functions

Abstract. *The temporal separation of* x *and* b *components in the electroretinogram of the dark-adapted eye of the sooty mangabey,* Cercocebus torquatus atys, *permits an uncomplicated calculation of luminosity functions. Flicker electroretinogram studies indicate enhancement of the photopic blue sensitivity.*

The electroretinogram (ERG) comprises several individual components which have been treated in great detail by several authors (*1–3*). Our paper concerns the two major corneal positive components, the x and b waves. Motokawa and Mita (*4*) were the first to discover an early positive wave in the response to brief flashes of red light, which they called the x wave. In subsequent investigations Adrian (*5*) showed that the x wave had a considerably shorter latency than the b wave and was photopic in nature. Armington (*6*) related the x wave to red sensitivity, demonstrating that in man the spectral sensitivity function of the x wave fits the CIE (Comm. Intern. de l'Éclairage, ICI) photopic function only in the deep red. The ERG from the dark-adapted primate eye is usually dominated by the b component, which has been related to rod function and rhodopsin. The smaller x wave can usually be seen in response to flashes of light of long wavelength, but appears, if it can be detected at all, only as a notch in the leading edge of the rising b wave at wavelengths shorter than about 590 mμ. However, the ERG of the dark-adapted eye of the sooty mangabey, *Cercocebus torquatus atys*, reveals a distinct separation of the x and b components of the response at all wavelengths; this permits direct determination of the spectral sensitivity of both components.

The four adult mangabeys used in this study were lightly anesthetized and placed in a stereotaxic instrument. A silver–silver chloride ring electrode was placed around the limbus of each eye. The left eye was covered and the right pupil was dilated with a 1 percent solution of cyclopentalate hydrochloride; the lids were retracted. The animal was placed in a light-tight, electrically shielded box and aligned in the optical system in a manner that placed the final lens focus on the node of the eye, presenting the animal with a Maxwellian view subtending about 20 degrees of visual angle.

The light source was a 6-volt, 18-amp tungsten ribbon filament bulb. The filament image was condensed and focused on a point aperture. The diverging beam from the point source was collimated, passed through appropriate filters, and then refocused on the node of the animal's eye. An electrically operated flag-shutter interrupted the beam at the point aperture. Flickering light with a light-to-dark ratio of 1:1 was provided by inserting at the aperture an episcotister driven by a constant-speed motor. Various combinations of disks and motors provided any desired flicker rate from 2 to 35 cy/sec. Single-flash studies were conducted, with a stimulus duration of 200 msec. Interstimulus intervals were 1 minute or greater, depending on the intensity series. Light composed of narrow-band wavelengths was provided by interference filters or Wratten color filters. Flash intensity was controlled with neutral-density filters. All filters were calibrated with a spectrophotometer and equated for equal energy transmission in the construction of luminosity curves. The filters used gave test flashes at eight spectral points with peak band pass at 452, 490, 505, 538, 576, 606, 633, and 646 mμ.

The ERG was displayed on four

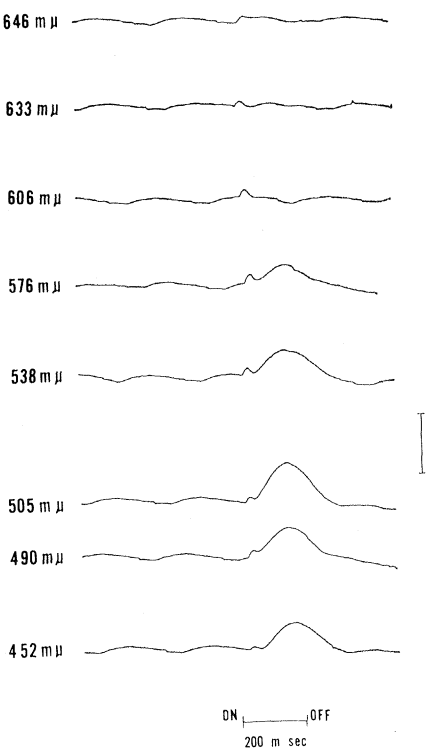

Fig. 1. Electroretinogram of the dark-adapted mangabey eye to a series of equal energy stimuli; animal No. 2.

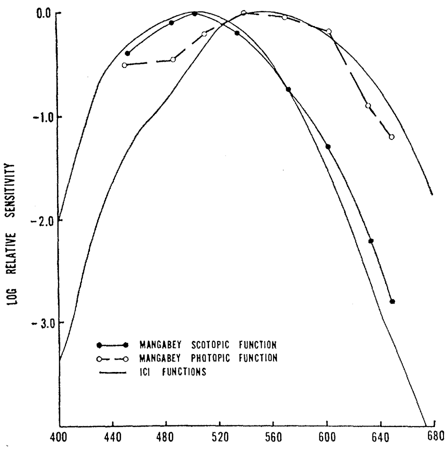

Fig. 2. Spectral sensitivity functions of the mangabey compared with the CIE (ICI) scotopic and photopic functions; data from averages of four animals.

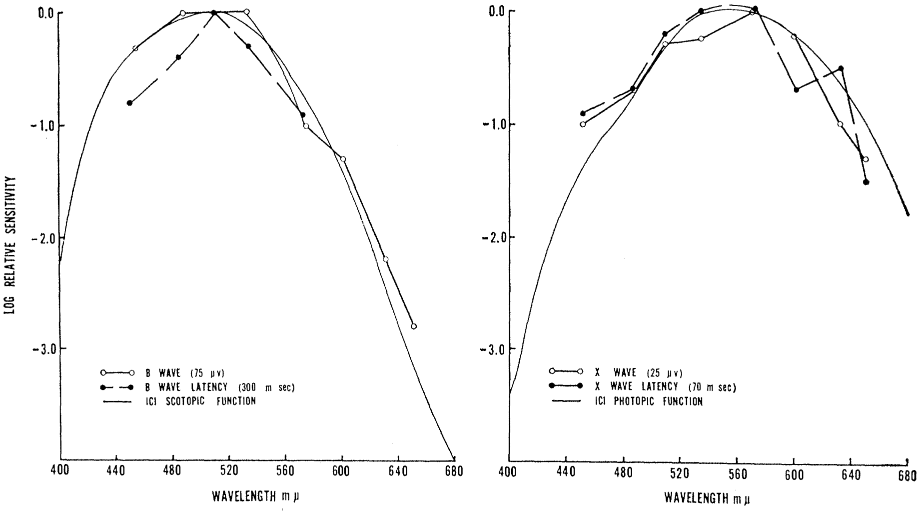

Fig. 3. Spectral sensitivity curves for the *x* wave and *b* wave derived from response magnitude/intensity and response peak latency/intensity curves; animal No. 4. ICI, CIE.

channels of a conventional ink writer at different amplifications in order to display all components of the response. The resistance-capacitance (*RC*) time constant was 1 second on all channels. Signal distortion resulting from a-c coupling was minimal in the early phases of the response. A direct-coupled monitor was used to test for distortion, and the major discrepancy was found in the decay time of a response to a signal flash of duration nearly equal to or longer than the *RC* time-constant of the amplifier. The fifth channel displayed the output of a photocell that was illuminated by the stimulus beam when the shutter opened; it functioned as a signal marker.

A series of responses of the dark-adapted eye to an equal energy spectrum is presented in Fig. 1. An early positive wave that precedes the *b* wave is seen at each point tested. At this intensity the average peak latency of the *x* wave was about 70 msec; of the *b* wave, about 190 msec. Responses were recorded across three log units of intensity for each of the eight spectral points tested. Plots of response magnitude as a function of stimulus intensity were constructed for each wavelength. A criterion magnitude was chosen that intercepted each curve in the linear portion of the function, and the relative intensity values of the intercepts were corrected for equal energy transmission of the filters and plotted as a luminosity function.

The method of Armington and Biersdorf (*7*) was used to construct response magnitude functions for flickering light, of different wavelengths and intensity compositions, for a number of flicker frequencies. When spectral sensitivity curves were constructed for the average magnitude of 20 consecutive responses starting 2 seconds after stimulus onset, the flicker of 4 cy/sec yielded the same spectral sensitivity curve as the *b* wave, and the flicker of 20 cy/sec yielded the same spectral sensitivity curve as the *x* wave. Because of the high degree of agreement between the data collected by the two techniques, the functions for *b* wave and flicker of 4 cy/sec and for *x* wave and flicker of 20 cy/sec were summed (Fig. 2). Each point in the data represents the average of many responses from all four monkeys.

The *b* wave and 4 cy/sec flicker luminosity functions show good agreement with the CIE scotopic function; the slight elevation in the long wavelengths probably reflects measurement error. Figure 1 shows that the *b* wave is difficult to detect and measure at wavelengths greater than 600 mμ.

The major departure of the *x* wave and 20 cy/sec flicker luminosity function from the CIE photopic standard is in the short wavelengths; the discrepancy at 452 mμ is 0.89 log unit. Heightened sensitivity in the short wavelengths is not unusual in luminosity curves; it has been found in both behaviorally determined curves (*8*) and luminosity functions determined from the ERG (*9*).

The extreme separation of the *x* and *b* components in the dark-adapted ERG of the mangabey allows the construction of peak latency by intensity curves for both positive components of the response. For example, the mean peak latency of the *x* wave for all wavelengths and intensities used was 70 msec; of the *b* wave, 300 msec. The mean latencies were used as the criterion measure instead of a response magnitude, and an equal latency luminosity plot was constructed for animal No. 4 for both the *x* and *b* waves. Figure 3 shows the equal response luminosity function and the equal latency luminosity function for the *x* wave and the *b* wave. Both sets of curves are compared with the appropriate CIE function. There is enhanced sensitivity in the short wavelengths for both the equal response plot and the equal latency plot. This evidence from the mangabey eye indicates that the blue sensitivity enhancement so frequently seen in luminosity functions is of photopic origin.

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