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Cone monochromacy and a reversed Purkinje shift in the gerbil

G. H. Jacobs and J. Neitz

Department of Psychology, University of California, Santa Barbara (California 93106, USA)
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Summary. Retinal spectral sensitivity of the gerbil (*Meriones unguiculatus*) shows that this animal has a unique photoreceptor complement: there is only a single class of cone and the spectrum for these receptors is peak shifted toward the short wavelengths relative to the spectra obtained from rods.
Key words. Gerbil; *Meriones unguiculatus;* photopigment spectra; cone monochromacy; Purkinje shift.

Based on the observation that nocturnal animals tended to have predominantly rod retinas whereas retinas of diurnal animals contained many cones, Schultze[1], in 1866, proposed the duplicity theory of vision. Over time the many characteristic differences in visual behavior between diurnal and nocturnal animals came to be causally linked to the differential presence of rods and cones. Among the tenets of classical duplicity theory are the ideas that a) the presence of cones implies a color vision capacity, and b) the change from rod-based to cone-based vision associated with transition from lower to higher ambient light levels is characterized by a shift in relative spectral sensitivity from shorter to longer wavelengths (the Purkinje shift)[2]. We have found that the visual system of a cricetid rodent, the gerbil (*Meriones unguiculatus*), provides striking exceptions to both of these generalizations; in this animal the change from rod- to cone-based vision is accompanied by a small shift in spectral sensitivity toward shorter wavelengths, and since there is only a single class of cone in the gerbil retina this animal must perforce lack color vision.

Observations of gerbil activity rhythms suggest a diurnal life style[3]. The gerbil retina contains both rods and cones. At the level of light microscopic examination these receptors appear generally similar in morphology to rods and cones found in other rodent retinas. Although no detailed counts of rods and cones have yet been made in the gerbil retina, the latter are plentiful; in the sections we have examined cones constitute as many as 20% of all photoreceptors.

Several functional properties of gerbil photoreceptors were examined by recording a retinal gross potential, the electroretinogram (ERG). ERGs were recorded from contact lens electrodes placed on the eyes of anesthetized animals. The stimuli were either single pulses (400 ms) of light delivered to the dark- or light-adapted eye or high frequency trains (50 Hz) of light pulses. Both adaptation and test lights were presented in Maxwellian view in the form of a circular spot subtending 53° on the retina. Details of the optical system, the recording system, and the procedures for recording ERGs have been published[4, 5].

We first determined the sensitivity of the eye to two different monochromatic lights (460 and 580 nm). The measurement was initially made in the completely dark-adapted eye and, subsequently, over a range of gradually

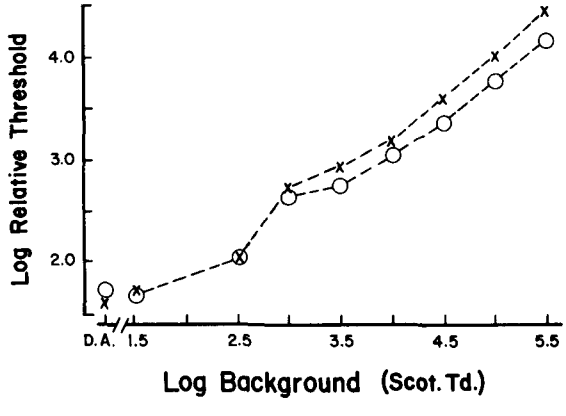

Figure 1. Increment thresholds for the gerbil determined from ERG measurements. Thresholds were measured for two test wavelengths, 460 nm (*o*) and 580 nm (*x*); each had a half-energy passband of 10 nm. At each of 9 background levels the test light intensity required to produce a b-wave response of constant amplitude (18 μV) was determined. These thresholds were first measured following 45 min of dark adaptation (left) and then on steady background lights (achromatic, 2850 K) of increasing intensity. The thresholds for the two test lights were adjusted by a constant amount sufficient to effectively superimpose them at low levels of adaptation. This same constant was then applied to the thresholds determined at all background levels. The test and background lights were circular spots subtending 50° on the retina. Retinal illuminance was determined by calculating the power in the adapting beam (per mm^2) for the gerbil retina and then converting this value to equivalent human scotopic trolands[14].

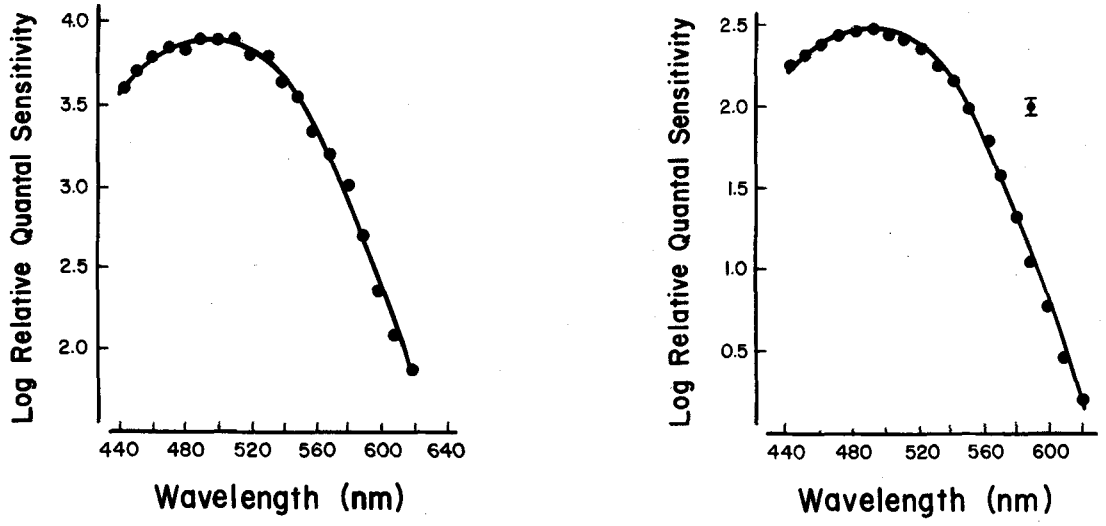

Figure 2. Spectral sensitivity of the gerbil determined by ERG measurements in dark-adapted (left) and light-adapted (right) animals. The data points for the dark-adapted eye (solid circles) were obtained by determining the intensity of a monochromatic light required at each of 19 wavelengths to produce a constant amplitude ERG (b-wave of 18 μV). To minimize the effects of any changes in the sensitivity of the eye over time, thresholds were alternately measured for a standard test light (500 nm) and, in turn, each of the other test wavelengths. Spectral sensitivity is then specified relative to that at the standard test wavelength. The continuous curve is that for the best fitting visual pigment nomogram[4, 5]. It has a spectral peak of 499 nm. Spectral sensitivity in the light-adapted eye was determined with ERG flicker photometry[4, 5]. The data points are mean values for six gerbils. The error bar shows the average amount of variation (+/−1 SD) across the 19 test wavelengths. The best fitting visual pigment nomogram (solid curve) has a spectral peak value of 493 nm.

increasing light-adaptation levels. In figure 1 the thresholds for the two test lights were adjusted by a constant value so that they superimposed when the eye was dark-adapted or adapted to very dim lights. With that same constant adjustment the thresholds continue to coincide until the adaptation light exceeds a value of about 3 log scot. td. Above that level, however, the threshold for the 580 nm lights is consistently relatively higher than that for the 460 nm light. The experiment shows, thus, that light adaptation causes the gerbil eye to shift in relative spectral sensitivity toward the shorter wavelengths, i.e., in a direction opposite to that typical of a Purkinje shift. Interestingly, the light level at which this shift begins to manifest itself is within about a half a log unit of the retinal illuminance at which human rods reach their saturation level[6].

Comparison of the size of the threshold differences for the two test wavelengths of figure 1 under conditions of dark and light adaptation suggests that the adaptation-dependent shift in spectral sensitivity in the gerbil is not very large. This was documented by measuring complete spectral sensitivity functions in the dark-adapted eye and in the highly light-adapted eye. The spectral sensitivity functions of gerbils that had been dark-adapted for 40 min were determined for the single pulse ERG. The resulting function for one animal (fig. 2, left) is best fitted by a visual pigment nomogram having a peak value of 499 nm. Peak values obtained for two other animals were 499 nm and 502 nm. The spectral sensitivity function of the light-adapted gerbil was determined using the procedure of ERG flicker photometry[4]. The average spectral sensitivity curve for six animals (fig. 2, right) is smooth in form and well fit by a visual pigment nomogram that has a peak value of 493 nm. The peak values for the individual spectral sensitivity functions for six animals all fell in the range 492–495 nm. The Purkinje shift in humans is characterized by a change in peak sensitivity toward the long wavelengths of some 50 nm. The analogous shift for the gerbil is in the opposite direction, and is about 6 nm in magnitude.

Other than an unusual spectral peak, gerbil cones have a number of functional properties that are similar to those seen in cones from other species: 1) ERG responses can be recorded with very rapidly flickering lights (e.g., 70 Hz), 2) a full spectral sensitivity function can be obtained when the eye is steadily adapted to a very bright (5.6 log td) light, and 3) only a brief time is required to recover photopic sensitivity following exposure to bright adaptation lights.

The photopic spectral sensitivity function of the gerbil (fig. 2, right) is well fit by a standard curve for a single photopigment suggesting that this retina contains only a single cone photopigment. If so, cone-based signals should behave univariantly[7]. This was examined by recording spectral sensitivity functions in the presence of intense chromatic adapting lights. The two spectral sensitivity functions of figure 3 were determined from ERG flicker photometry when the eye was concurrently adapted either to 440 nm (top) or 560 nm (bottom) lights. The intensities of these two adaptation lights were first adjusted to be equally effective, i.e., so that each raised the threshold for a photopic test light (25 Hz, 580 nm) by an additional 0.5 log units. In figure 3 the same curve has been fit to the sensitivity values obtained under the two

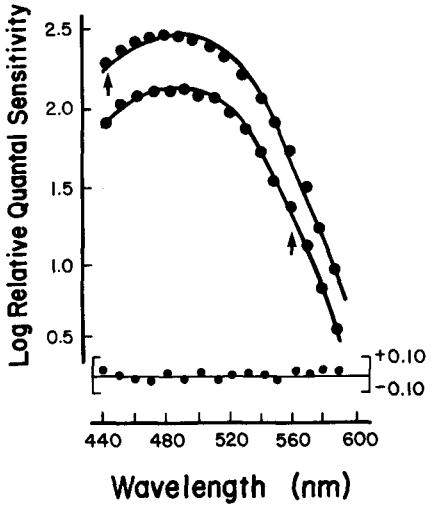

Figure 3. Spectral sensitivity functions for the gerbil determined under two conditions of intense chromatic adaptation. The top curve was obtained from ERG flicker photometry while the eye was concurrently exposed to a 460 nm light (wavelength indicated by arrow); the bottom curve is a similar function obtained from the same eye exposed to 560 nm light. The two functions are arbitrarily positioned on the sensitivity axis; the absolute differences in sensitivity for the two conditions are plotted logarithmically at the bottom. The curves drawn through the data points are the same for the two sensitivity curves.

adaptation conditions; both are equally well accounted for by this curve. The absolute differences in sensitivity under the two adaptation conditions are shown at the bottom of figure 3 these differences are small at all spectral locations (<0.10 log unit), and they vary unsystematically across the spectrum. This experiment, as well as several additional ones involving different adaptation and test conditions, yield a straightforward conclusion: the gerbil retina contains only a single class of cone. The gerbil is a cone monochromat and thus should lack any color vision. Among all mammals that have so far been adequately examined, apparently only the rat has a similar arrangement[8] and that a rodent, unlike the gerbil, has few cones and weak photopic vision.

Early investigations of visual pigments suggested that several clear distinctions could be drawn between pigments found in cones and rods[9]. Later, however, it became reasonable to think of all visual pigments as belonging to a single family in which individual members vary in opsin structure and in the positioning of absorption spectra[10]. The present results reinforce this view. For instance, the gerbil cone photopigment has a spectrum that is very similar, if not identical, to that of the human rod photopigment[11,12]. This fact suggests that the very disparate properties of human rod-based and gerbil cone-based signals (threshold sensitivity, temporal resolution, etc) must originate from characteristics of photoreceptors in which they are housed and in the neural networks that they innervate.

Both from measurements of the rod pigments of various fish species[10] and of the cone pigments of a number of different mammals[13], it appears that the absorbance spectra of vertebrate photopigments are not randomly positioned across the spectrum, rather, these pigment spectra tend to cluster at a number of discrete spectral positions. The interval difference between the spectral peaks of the adjacent pigment positions has been estimated to be about 6 nm[10,13]. The spectral separation between the peaks of the gerbil rod and cone pigments (fig. 2) is close to this value leading us to suggest that the two photopigments of the gerbil represent the minimal spectral shift that can be produced during the evolution of new photopigments.

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