

Development of Spectral Mechanisms in the Ground Squirrel Retina Following Lid Opening*

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Summary. The retina of the California ground squirrel (*Spermophilus beecheyi*) contains three classes of photopigments ($\lambda_{\max} = 440, 500, 525$ nm). From optic nerve recordings it was previously discovered that the effectiveness of signals from the 440 nm cone increase gradually over the weeks following lid opening. In this experiment several features of the electroretinogram (ERG) were examined to assess developmental changes in signals originating in the outer retina. As judged by threshold sensitivity, suprathreshold responsivity, or adaptability, the contribution of the 525 nm mechanism reaches its adult level two to three weeks after lid opening. The 500 nm mechanism appears to have a similar developmental time course. The development of the 440 nm mechanism was tracked using a chromatic adaptation measure. So indexed, the time required for this mechanism to reach its adult status was much greater than that for the other two mechanisms (70–80 days vs 40–45 days of age). The relatively slow development of effectiveness of the 440 spectral mechanism appears to reflect events occurring in the outer retina.

Key words: Visual development – Ground squirrel – Electroretinogram – Spectral mechanisms

Introduction

The California ground squirrel (*Spermophilus beecheyi*) has a heavily (ca. 90%) cone-dominated retina (Jacobs et al. 1976; Long and Fisher 1983) which appears to contain three classes of photopig-

ments. Two of these have absorbance peaks at about 440 and 520–525 nm (Jacobs and Tootell 1981). These provide the basis for a dichromatic color vision roughly similar to human protanopia (Anderson and Jacobs 1972). The third photopigment has an absorbance peak at about 500 nm. Its influence can be seen only under relatively restricted sets of stimulus conditions, and there is reason to believe that it is principally, although perhaps not exclusively, contained in the small population of rods (Jacobs and Tootell 1979).

In a recent study of the development of response properties of single optic nerve fibers in young California ground squirrels we found that the spectral mechanisms appear not to develop at the same rate. Whereas about 30% of all optic nerve fibers in the adult animal receive some input from the 440 nm cone, only about one third that proportion can be detected at about three weeks after lid opening (McCourt and Jacobs 1983). From that time onward, the proportion of units receiving inputs from 440 nm cones increases gradually until the adult organization is reached at about 75–80 days after birth. Over this same period no obvious developmental changes could be detected in the influence of the 525 nm cone. The strong implication of these results is that the mechanisms which provide the basis for color vision in this animal develop gradually during early life. This study left ambiguous the locus of this developmental effect. One possibility noted (McCourt and Jacobs 1983) was that the gradual development of the effectiveness of the 440 nm mechanism might reflect the fact that optic nerve fibers receiving inputs from 440 nm cones simply grow more slowly, and thus the developmental change reflected an inability to record from those fibers until they reached some criterion size.

The influences of all three spectral mechanisms in the California ground squirrel can be seen in a retinal

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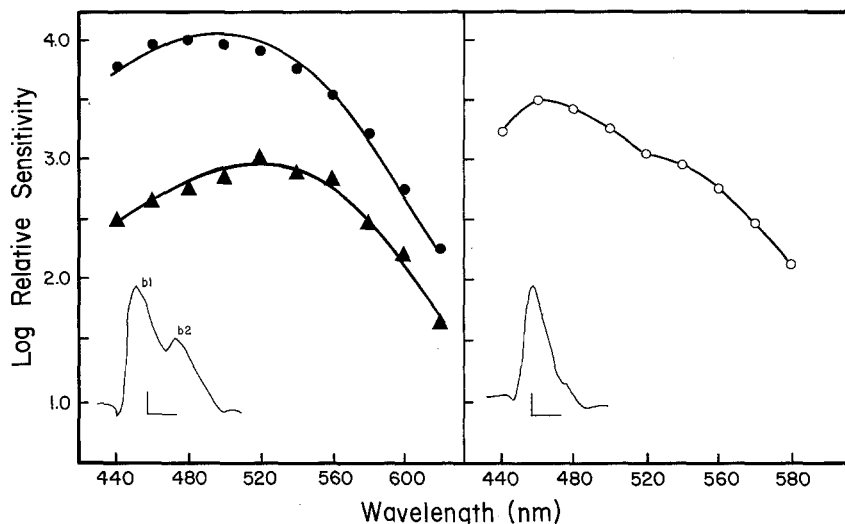


Fig. 1. Spectral sensitivity functions obtained from the b-wave of the ERG of the California ground squirrel. Left panel: The inset shows an ERG recorded from the dark adapted eye (test light = 540 nm; calibration bars = 75 ms and 10 μ V). Note the clear separation of the b-wave into faster and slower components. The spectral sensitivity functions for these two components are shown above. The values have been corrected for preretinal absorbance in this species (Yolton et al. 1974). At the top is the spectral sensitivity function for b2. The continuous curve drawn through the data points is that for the best-fitting visual pigment nomogram (Ebrey and Honig 1977). It has a sensitivity peak of 502 nm. The lower function shows the spectral sensitivity of the b1 component. The best fitting curve drawn through those data points has a peak at 520 nm. The two functions are arbitrarily positioned on the sensitivity axis. Right panel: The inset shows an ERG recorded from the light-adapted eye of a California ground squirrel (test wavelength and calibration same as left). Note that the b2 component is not observable under these conditions. The spectral sensitivity function shown at the top is that for b1 obtained under conditions where the eye was being concurrently adapted to an intense chromatic light (wavelength = 605 nm; Corneal irradiance = 6.89 $\text{mW}\cdot\text{cm}^{-2}$)

gross potential, the electroretinogram (ERG), which originates at locations distal to the ganglion cell layer (Rodieck 1973). In the experiments reported here we have examined the development of several aspects of this potential to see if there are developmental changes in the spectral mechanisms or not.

Materials and Methods

Subjects

Pregnant California ground squirrels (*Spermophilus beecheyi*) were locally trapped. Fourteen animals were derived from two litters. Most animals were tested at least twice during development.

Rearing Conditions

Pregnant animals were placed in large cages where they nested. Food and water were provided *ad libitum*. The illumination provided in the cages was identical to that of the white light condition used in the previous experiment (McCourt and Jacobs 1983). Light came from overhead fluorescent lamps (30 W Cool White) run on a 12 h dark: 12 h light daily cycle. The illuminance from these lights, as measured at the cage floors with a Weston low-level illumination meter, ranged from 194 to 237 lux.

Recording

Ground squirrels were anesthetized with sodium pentobarbital (75 mg/kg). They were positioned in a stereotaxic instrument and

the test eye was dilated by topical application of atropine sulfate (0.04%). Normal body temperature was maintained through the use of a circulating hot water heater.

ERGs were recorded using a Burian-Allen contact lens electrode. The output from this electrode was differentially amplified (amplifier passband = 0.2–1000 Hz) and responses were averaged with an Ortec 4623 Averager. The averaged responses were written out on an X/Y plotter for later analysis.

Stimulation

A three-beam Maxwellian view optical system was used: the output was a circular spot 44° in diameter. The test stimulus originated from a Bausch and Lomb high-intensity grating monochromator (half-energy passband = 10 nm). The other two beams came from tungsten-iodide lamps. The characteristics of these lights were controlled by inserting Kodak Wratten color filters and neutral density step filters in the beams. In this experiment one of these beams was used to provide an adaptation light. All of the beams contained high-speed electromagnetic shutters (Uniblitz) which were controlled from a specially designed digital timer.

ERGs were recorded under several stimulus conditions. To measure absolute sensitivity, animals were initially dark adapted for a period of at least 30 min following which dim 400 ms flashes of monochromatic light were presented at a rate of 6/min. Responses to a total of at least 20 such flashes were averaged for each intensity/wavelength combination. We first recorded responses to dim stimuli, and then gradually increased intensity in steps of 0.3 log unit to examine suprathreshold responsivity. To examine the effects of chromatic adaptation, the responses to two test lights, 595 and 470 nm, were recorded. Complete intensity/response functions were derived for each of these test lights under two conditions of chromatic adaptation, a homochromatic condi-

tion (e.g., 595 nm test with 595 nm adaptation) and a heterochromatic condition (e.g., 595 nm test with 470 nm adaptation). The appropriate adaptation lights were continuously present. As measured at the cornea, these adaptation lights had the following irradiances: 595 nm ($0.98 \text{ mW}\cdot\text{cm}^{-2}$); 470 nm ($0.83 \text{ mW}\cdot\text{cm}^{-2}$). Responses to a reference light were periodically recorded throughout the session to assure that no systematic changes in sensitivity had occurred.

Results

Indices of Spectral Mechanisms in the Ground Squirrel ERG

It was noted that contributions from all three of the ground squirrel spectral mechanisms can be seen in the ERG under the appropriate sets of stimulus conditions. We first describe the grounds on which these separations are made.

The ERG of the California ground squirrel, like that of other ground squirrels (antelope ground squirrel – Crescitelli 1961; golden-mantled ground squirrel – Jacobs et al. 1980; thirteen-lined ground squirrel – Raisanen and Dawis 1983) often has two prominent b-wave components (Jacobs and Tootell 1979). The inset in the left of panel Fig. 1 shows an ERG recorded from the eye of a dark-adapted ground squirrel. The separation of the b-wave into faster (implicit time $< 75 \text{ ms}$) and slower (implicit time $> 75 \text{ ms}$) components is obvious. This separation of waveform is most apparent for test lights of 500 nm or longer, for lights of low to moderate intensity, and for recordings made from dark-adapted eyes. The spectral sensitivities of the generators of b1 and b2 are different. Earlier it was shown that the spectral sensitivity of the b1 component in the California ground squirrel is close to that of photopigments having absorbance peaks at 520 to 525 nm,¹ while the spectral sensitivity for b2 is well fit by a curve having a 500 nm peak (Jacobs and Tootell 1979). The spectral sensitivity functions shown in Fig. 1 illustrate this fact: under those conditions where these two b-wave components can be seen, b1 and b2 may be used as indices of the 525 and 500 nm spectral mechanisms respectively.

In the light-adapted eye and/or with intense stimulus lights, the slower b-wave component, b2, is

no longer seen (see inset in the right panel of Fig. 1). Rather, under these conditions, the b-wave is dominated by the earlier peak and its spectral sensitivity is that of the 525 nm mechanism. Under some special stimulus conditions, however, it can be shown that the 440 nm mechanism also contributes to the b1 component of the ground squirrel ERG. If, for instance, spectral sensitivity is measured for b1 while the eye is concurrently adapted to an intense long-wavelength light, a peak appears in the spectral sensitivity function at about 460 nm. The spectral sensitivity function in the right panel of Fig. 1 illustrates this result. The degree to which the 440 and 525 nm mechanisms jointly contribute to b1 can be indexed quantitatively by comparing the responses of the eye to short and long wavelength lights under conditions of both short and long-wavelength adaptation. The procedure is conceptually similar to one developed to assess the magnitude of chromatic adaptation effects in human subjects (Boynton and Wagner 1961). Figure 2 provides an example of the method. Shown are ERG intensity/response functions recorded from the eye of an adult California ground squirrel using test lights of 595 and 470 nm. To the left are the functions for these two lights obtained when the eye was adapted to a 595 nm light. These two functions have been slid laterally by an amount sufficient to superimpose them. The functions to the right are responses obtained to the same test lights when the eye was adapted to a 470 nm light. The same lateral positioning of the two functions was used in this second case, the logic being that if only a single spectral mechanism contributes to the response the two functions should again superimpose. They do not, indicating that more than one spectral mechanism contributes to the b1 response under these conditions. The magnitude of the lateral separation of the two curves at the right in Fig. 2 can be used as an indication of the size of the differential adaptation achieved. In the case shown in Fig. 2, the adaptation effect was substantial, 0.40 log units. We used this chromatic adaptation procedure as a means of determining to what extent the 525 and 440 nm mechanisms jointly contribute to the b1 component of the ERG of young ground squirrels.

Development of the 525 nm Mechanism

Postnatal visual development in the California ground squirrel is relatively slow with lid opening occurring at between 30 to 35 days after birth (Fitch 1948; McCourt and Jacobs 1983). The two litters used in this experiment had lid openings at 32 days of

1 There is some uncertainty about the precise location of the peak of this mechanism in the California ground squirrel. Estimates based on behavioral measurements (Jacobs 1978), and on electrophysiological results (Jacobs et al. 1976; Jacobs and Tootell 1981) yielded peaks at 525 nm. More recent measurements from single unit recordings (unpublished) and the ERG (see Fig. 2) suggest the peak is at 520 nm. For brevity, in this report it is called the 525 nm mechanism

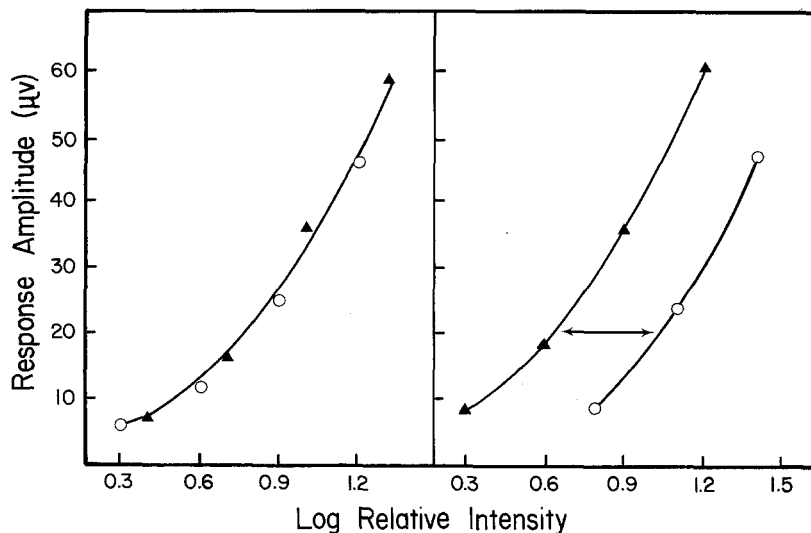


Fig. 2. Demonstration of differential chromatic adaptation of the b1 component in the ERG of the California ground squirrel. The left panel shows intensity/response functions for two monochromatic lights, 470 nm (○) and 595 nm (▲). These were obtained while the eye was continuously adapted to a 595 nm light. The responses to these two test lights were slid along the intensity axis by an amount sufficient to superimpose them. To the right are intensity/response functions for the same two test lights recorded while the eye was adapted to a 470 nm light. The lateral positioning of the two functions is the same as for the Left panel, but they no longer superimpose. The magnitude of the residual separation of the two functions at a criterion voltage of 20 μ V (arrow) was used as an index of the degree of differential chromatic adaptation achieved under these conditions

age. ERGs could first be reliably recorded two to three days after lid opening. At that time the ERG was low amplitude, insensitive, and easily habituated. It was however possible to measure the thresholds for the b1 response in the dark-adapted eye for two test wavelengths, 500 and 600 nm. This procedure was repeated on other animals at various times over the next two weeks. The results are shown in Fig. 3 which plots b1 thresholds (5 μ V criterion) for 500 and 600 nm lights for each of these young animals. Shown to the right in Fig. 3 are similar results obtained from eleven adult ground squirrels tested in the same manner. It is apparent that the b1 threshold reaches its adult level within six to ten days after lid opening. Note in Fig. 3 that the difference in threshold to the two lights is the same for each for the young animals as for the adults. Each thus shows the sensitivity difference predicted by the operation of the 525 nm mechanism.

The development of the b1 response to suprathreshold stimuli was also examined. In this case responses were recorded to moderately intense monochromatic light delivered to the dark adapted eye. The intensity of this light was such that in the adult ground squirrel it produced ERG responses about 80% of the maximum obtainable. The results from animals tested from three days after lid opening to four months of age are shown in Fig. 4. Although, initially, only small b1 responses were recorded to this suprathreshold light, amplitude grew rapidly in size toward the adult standard. Individual variability in these responses makes somewhat difficult a precise statement of the age at which these responses reach their adult level, but it appears that the b1 response

amplitudes are fully adultlike by at least 50 days of age. Beyond that age, no further systematic changes were seen.

The development of a third property of the 525 nm mechanism, its ability to adapt to bright lights, was also examined. To do so we measured the size of the threshold elevation produced under a condition favorable for adapting and stimulating the 525 nm mechanism – a 595 nm test light with a 595 nm adaptation light. This threshold was compared to the threshold for the 525 nm mechanism in its dark adapted state. The results are shown in Fig. 5. Shown to the right in Fig. 5 is the average adaptation effect produced under these conditions in six adult ground squirrels. Note that the adaptation effect was substantial in that the adapting light increased the threshold of the 525 nm mechanism by more than 2.2 log units. The bars to the left in Fig. 5 show analogous adaptation occurring in the 525 nm mechanism in young ground squirrels. It is apparent that from the first day at which it was possible to make this measurement (age 42 days) the adaptation effect was as large as it is in the adult animal, and from that time onward no other changes in the adaptation property can be seen.

These three indices of the development of the b1 component of the ground squirrel ERG show that the 525 nm mechanism develops rapidly toward its adult level following lid opening. That status is reached at slightly different times depending on whether thresholds, adaptation properties, or suprathreshold responses are examined, but, in any case, the 525 nm mechanism is indistinguishable from that of the adult by the time these animals reach 50 days of age.

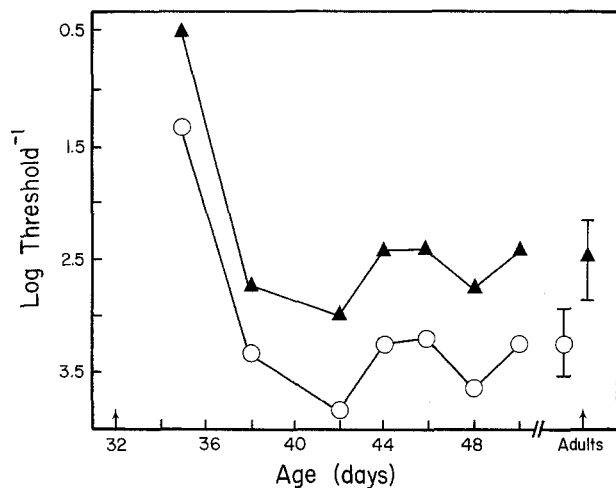


Fig. 3. Developmental changes in the threshold of the b1 component of the ERG of the California ground squirrel. Thresholds ($5 \mu\text{V}$ criteria) were determined for two lights, 500 nm (\circ) and 600 nm (\blacktriangle), in the dark adapted eyes of young and adult California ground squirrels. The time of lid opening is indicated by the arrow to the left. To the right are results of threshold measurements obtained from eleven adult ground squirrels tested in an identical manner (mean ± 1 SD)

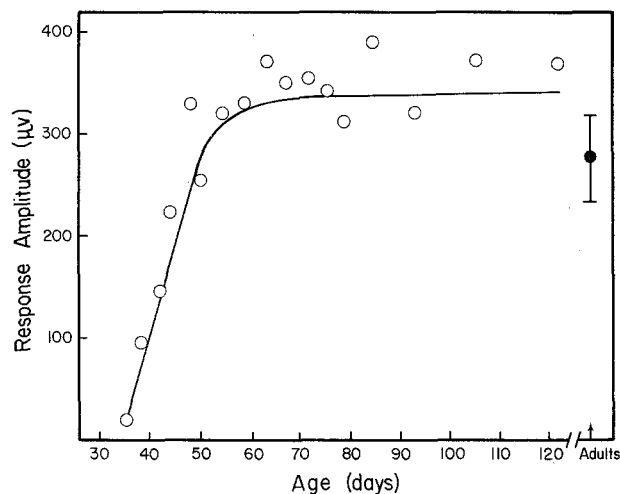


Fig. 4. Development of the b1 response to suprathreshold stimuli. Each data point shows the average response recorded from a young ground squirrel to a 500 nm test light ($22.6 \mu\text{W}\cdot\text{cm}^{-2}$) delivered to the dark adapted eye. Lid opening was at 32 days. To the right are results obtained from six adult ground squirrels (mean ± 1 SD) identically tested. The continuous line was fit by eye to the data points

Development of the 500 nm Mechanism

Because of the variability in its appearance, and the relatively restricted sets of stimulus conditions under which it is apparent, it is more difficult to obtain

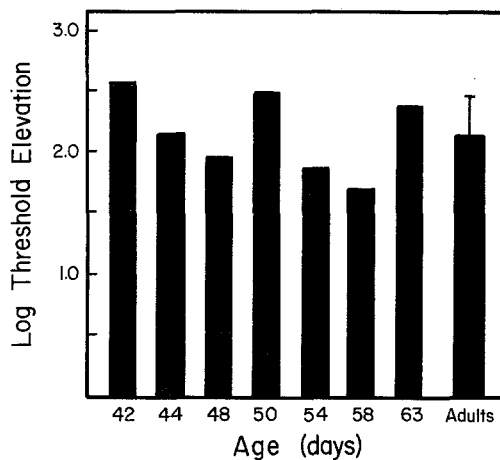


Fig. 5. Adaptability of the b1 component of the ground squirrel ERG. Plotted is the magnitude of the elevation in threshold ($5 \mu\text{V}$ criterion) for a 595 nm test light recorded when the eye was steadily adapted to a 595 nm light (corneal irradiance = $0.98 \text{ mW}\cdot\text{cm}^{-2}$) relative to the threshold for that same test light in the dark adapted eye. To the right is shown the threshold elevation for six adult ground squirrels (error bar = 1 SD). Note that the size of the adaptation effect was not significantly different for young and adult animals

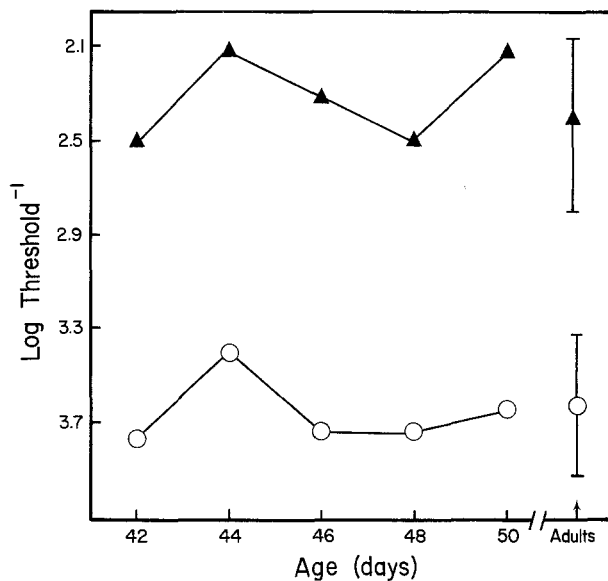


Fig. 6. Thresholds ($5 \mu\text{V}$ criterion) for the b2 component of the ground squirrel ERG. The test lights were 500 nm (\circ) and 600 nm (\blacktriangle). To the right are mean b2 thresholds (± 1 SD) recorded from eleven adult ground squirrels. The youngest animal tested was ten days beyond the time of lid opening

measurements of the early development of the b2 component of the ground squirrel ERG. It was detected in ERGs recorded a few days after lid opening, but reliable threshold measurements could first be obtained about ten days after that event, at

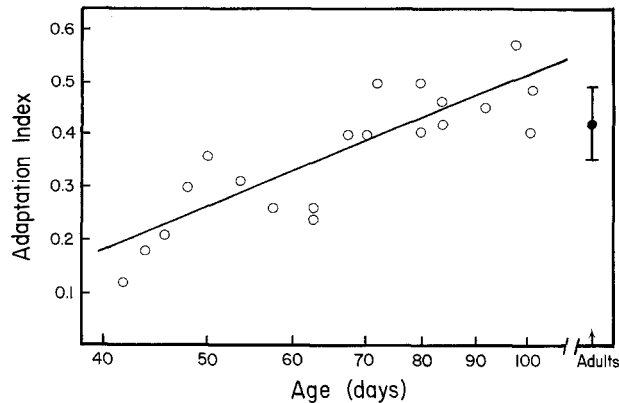


Fig. 7. Development of differential chromatic adaptation in the ground squirrel. Each open circle shows the size of the adaptation effect obtained from one ground squirrel. These values were obtained using the procedure illustrated in Fig. 2 and explained in the text. To the right are analogous results obtained from seven adult ground squirrels (mean \pm 1 SD). The straight line was best fit by the method of least squares ($r = 0.83$, $df = 18$, $p < 0.01$)

42 days of age. At that time the threshold values for b2 were indistinguishable from those of the adult. This is illustrated Fig. 6 which shows also from that time onward there were no further changes in b2 threshold. Note that the threshold differences for the two test lights in the young animals were the same as in the adult indicating that the mechanism being measured indeed had the spectral sensitivity of a 500 nm photopigment.

By its very nature it was not possible to obtain any indications of possible suprathreshold developmental changes in the b2 component of the ground squirrel ERG. However, comparisons of behavior at threshold suggest that the 500 nm mechanism develops over a time course not significantly different from that described above for the 525 nm mechanism.

Development of Differential Chromatic Adaptation

As demonstrated above, input to the b1 component from both the 440 and 525 nm mechanisms can be shown to occur under the appropriate conditions of chromatic adaptation. In the very youngest animals tested (< 40 days old) only vague indications of differential chromatic adaptation were seen. The first good measurements of the effect were obtained about ten days after lid opening, at which time however the size of the effect was small. From that point onwards the magnitude of the chromatic adaptation effect increased progressively. Results of this measurement are shown in Fig. 7 which plots the size

of the chromatic adaptation effect as a function of the age of the animal. The increase in this index is well described by an exponential growth function. As measured in this way, the chromatic adaptation property does not achieve its adult status until ground squirrels are 75–80 days old; that is, about seven weeks after the time of lid opening. Individual animals tested repeatedly over this period showed the same developmental trend in the chromatic adaptation index as is apparent from the group data. For instance, an animal tested at 46, 67, 93 and 121 days of age had adaptation effects of 0.21, 0.40, 0.46 and 0.46 respectively.

Discussion

There is both electrophysiological (Jacobs and Tootell 1981) and behavioral (Anderson and Jacobs 1972) evidence indicating that the vast majority of cones in the retina of the California ground squirrel contain a photopigment having a λ_{max} of about 525 nm. This study used the ERG to index the development of retinal mechanisms which receive input from this cone class. The results are consistent – as judged either by threshold sensitivity, by its adaptation properties, or by suprathreshold responsivity, this mechanism is immature immediately following lid opening, but from that time forward rapidly grows toward its adult status. The time course of development may be slightly different for the three properties, being more protracted for the development of suprathreshold response than for the other two indices. However, by all of these criteria, the contribution of the 525 nm mechanism to the ERG is fully mature by the time ground squirrels reach 50 days of age.

The development of the 500 nm mechanism in the ground squirrel retina is more difficult to study with the ERG. In particular, it was not possible to examine any features of the development of the suprathreshold characteristics of this mechanism. However, threshold sensitivity of the 500 nm mechanism could be measured, and it is clear that by about 10 days after lid opening this mechanism in the young ground squirrel has already reached its adult sensitivity. In this sense the development of the 500 nm mechanism appears coincident with that of the 525 nm mechanism.

Development of retinal gross potentials has been studied in several other species. None of these investigations appear to have been concerned specifically with spectral mechanisms, but some interesting

parallels between the results reported here and in other cases may be noted. B-wave thresholds reach their adult level in the ground squirrel by 8 to 10 days after the time of lid opening (Figs. 2 and 5). A very similar time course following lid opening has been reported for the development of the rat b-wave (Dowling and Sidman 1962; Birch and Jacobs 1979; Fulton and Graves 1980) and the cat late receptor potential (Tucker et al. 1979). In each of these latter cases this is a time period during which there are dramatic growth changes in the photoreceptors themselves (Weidman and Kuwubara 1968; Tucker et al. 1979), and this is likely also to be true for the ground squirrel. In both cat and rat other characteristics of retinal gross potentials follow different maturational time courses. For instance, the period required to reach maximum amplitude responses in the cat (Tucker et al. 1979) and to show the full range of adaptational properties in the rat (Fulton and Graves 1980) are more protracted than the time required to achieve maximal dark-adapted sensitivity. These features, like the development of maximum b-wave amplitude in the ground squirrel (Fig. 3) are species specific, and probably dependent on synaptogenesis in the outer retina as well as on changes occurring in the photoreceptor mosaic.

The manner in which different spectral mechanisms contribute to the ERG is not well understood. There is evidence from several mammalian species to indicate that, along pathways leading to the ERG generators, (a) there is a significant amplification of the strength of the signal originating in the short wavelength cones (Norren and Baron 1977; Raisanen and Dawis 1983) and, (b) that both excitatory and inhibitory interactions occur between different subsets of cone classes (Norren and Baron 1977; Valeton and Norren 1979; Zrenner 1983). The measurements of the third spectral mechanism in the ground squirrel retina are indirect so it is uncertain if the developmental change observed reflects maturation of the 440 nm cones directly, or of the sites of interaction of the outputs from this cone class with signals from the 525 nm cones, or both of these events. Whatever the case, however, it is apparent that the input from the 440 nm mechanism to the ERG continues to develop substantially after any developmental changes can be detected in the other two spectral mechanisms (80 days for the 440 nm mechanism versus not more than 50 days for the 500 and 525 nm mechanisms).

The timing of the developmental changes in the ground squirrel ERG are of particular interest in light of observations of the development of the response properties of optic nerve fibers. As noted previously, the proportion of such fibers receiving

inputs from the 440 nm cone increases gradually during early life achieving its adult level at 75–80 days of age (McCourt and Jacobs 1983). That figure is identical to the present indication of the time at which the 440 nm mechanism reaches its adult status as indexed by the b-wave of the ERG. It thus seems likely that the limiting factor in the growth of optic nerve spectral opponency is developmental change occurring at the level of the bipolar cells or earlier. In the case of the development of input from the 440 nm mechanism to the optic nerve it was observed that the time required to reach adult status was significantly dependent on the nature of the photic environment in which the ground squirrel was reared (McCourt and Jacobs 1983). Whether a similar dependence holds for the ERG remains to be seen.

Finally, there is an intriguing similarity between the electrophysiological indications of the development of the short wavelength mechanism in the ground squirrel and behavioral measurements of chromatic adaptation in human infants. Pulos et al. (1980) found that in two to three month old infants the short wavelength mechanism is less developed than the other spectral mechanisms. Our results lead to the same conclusion about the short wavelength mechanism in the young ground squirrel. It has been known for some time that there are a number of important ways in which the short wavelength mechanism in the mammalian visual system differs from the other spectral mechanisms (for a recent review, see Mollon 1982). Results from both human infants and young ground squirrels suggest that ontogeny belongs on this list.

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