

The finding that a lesion of some critical size is necessary to elicit a breakdown in performance indicates that the hippocampal cells which support prolonged titrating avoidance behavior are spread through the length of the hippocampus, rather than concentrated within a specified anterior or posterior location. The present data do not contribute to identifying the particular hippocampal cells which support the sort of "endurance" measured in this study. However, several studies showed that in monkeys lesions of the anterior hippocampus resulted in degeneration of the lateral septal nucleus and nucleus acumbens, whereas lesions of the posterior hippocampus resulted in degeneration of the medial portions of the septal nuclei. In squirrel monkeys all regions of the monkey hippocampus apparently project to the diagonal band, olfactory tubercle, anteroventral nucleus, and mammillary bodies (7). It remains unknown whether these diffusely projecting cells specifically affect endurance of task performance.

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## Behavioral Correlates of Constant Light-Induced Retinal Degeneration

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Exposure of albino rats to continuous, low-intensity illumination produces degeneration of photoreceptors. In this study adult albino rats that were housed in either cyclic light or constant light (440 lux) were tested on pattern discriminations, intensity discriminations, and color discriminations for at least 24 weeks. Rats showed a decreased ability to perform pattern discriminations after approximately 7 weeks in constant light and after 24 weeks in constant light their performance was near chance. However, intensity discriminations and color discriminations were not impaired during 24 weeks in constant light. The fact that the constant light-exposed rats could perform color discriminations suggests that at least two different visual pigments are transducing light in these animals, despite the fact that no intact photoreceptor cells were observed in the retinas of the constant light-exposed rats.

#### INTRODUCTION

Exposure of albino rats to continuous, low-intensity illumination produces degeneration of photoreceptors (14). Based on histological findings one might predict that albino rats exposed to constant light would be functionally blind. The results of two studies that were published simultaneously (1, 3) indicated that this was not the case. Those two papers reported that albino rats having severely degenerated retinas, resulting from exposure to constant light, were able to learn and perform visually guided tasks

Abbreviations: ERG—electroretinogram; LGN—lateral geniculate nucleus; VC—visual cortex.

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as well as control animals. A later study by Bennett *et al.* (5) indicated that after approximately 90 days in constant light there was a decrease in the ability of rats to perform a light-dark discrimination task. More recent studies (9, 16) showed that although rats with constant light-induced retinal degeneration can perform visually guided tasks, their visual thresholds are higher than those of control rats. Two different investigators recently suggested that residual cones are mediating visually guided behavior in light-exposed rats. La Vail (11), who used light microscopic and electron microscopic techniques, reported that cones were less sensitive than rods to light-induced degeneration. Cicerone (7) measured electroretinograms (ERGs) in light-exposed rats and found that the recovery of the ERG following light adaptation indicated that the photopic mechanism was more resistant to light-induced degeneration than the scotopic mechanism.

The behavioral experiments reported here correlated the visual capabilities of light-exposed rats with the response characteristics of cells in the lateral geniculate nucleus (LGN) and the visual cortex (VC), as reported in the following paper (10), and with the numbers and types of cells in the retina. The behavioral studies were designed to determine the time course of changes in the ability of rats exposed to constant light to perform pattern discriminations, color discriminations, and intensity discriminations. The data from these experiments were expected to show whether different types of visual capabilities deteriorated at similar or different rates in light-exposed rats.

## METHODS

Adult, female, albino rats of the Sprague-Dawley strain were housed in an environment of constant or cyclic light. The animals in cyclic light were exposed to 14 h of light followed by 10 h of dark in each 24-h period. The animals in the constant light group were housed in clear plastic cages having one GE F40CW 40-W fluorescent tube 50 cm above the bottom of the cage. In addition, the room lights (12 GE F40CW 40 W) were on continuously. The illumination, measured as incident light at the cage floor, was 40 fc (430 lux).

The animals were trained and tested in a gray experimental chamber that was 35.6 cm on a side. The testing chamber was in a dark room. During training and testing white noise was used to mask extraneous sounds. A clear Plexiglas nose panel, referred to as the start panel, was mounted on one wall of the experimental chamber. Behind the start panel was a rear projection system containing a variety of visual stimuli. On the opposite wall of the chamber were two nose panels (choice panels) with rear projectors behind them. Between the two choice panels was a pellet delivery

tube. All animals were pretrained to press the panels using traditional shaping methods. At the beginning of an experimental trial, a visual stimulus was projected onto the start panel. When the animal pressed the start panel the start stimulus was turned off and two stimuli were simultaneously projected onto the choice panels. If the animal pressed the panel in front of the positive stimulus it received a 48-mg food pellet reward. Pressing either choice panel turned off the visual stimuli and initiated a 10-s waiting period before the next trial. The visual stimulus projected onto the start panel was always the same as the stimulus that was rewarded when projected onto the choice panels, which were alternated from side to side, on successive trials, according to a Gellerman series (8). Eighteen different Gellerman series were used, and the series was changed each day. During training each animal received 30 trials per day and was trained until it had reached a criterion of 90% correct responses on 3 consecutive days. The automated equipment that controlled the testing sequence and recorded the animals' scores was in a room adjacent to the room containing the experimental chamber.

When an animal had reached criterion on all tasks on which it was to be trained, it was assigned to an experimental or a control group. If an animal was being tested on two different types of tasks, it was tested on each task on alternate weeks. An example of this would be to test pattern vision one week and color vision the next week, etc. This regimen of testing was used for at least 24 weeks on each rat in order to monitor any changes in the ability of experimental animals to perform the different types of visual discriminations.

A special testing procedure was used to test color vision. Rats were tested on their ability to discriminate between blue and red stimuli. The relative brightness of the blue and red stimuli was changed each day to prevent the rats from using brightness cues to make the discrimination. Seven different intensity pairs were used. Measurements of the spectra of the blue and red stimuli and estimations based upon rat photopic spectral sensitivity curves (13, 15) indicated that in two of the pairs the red stimuli should have appeared brighter than the blue stimuli, in one pair the blue and red stimuli should have appeared equally bright, and in the remaining pairs the blue stimuli should have appeared brighter than the red stimuli. By changing the relative brightness of the blue and red stimuli each day, it should have been impossible for the rats to use brightness cues to make the discrimination.

The pattern discriminanda consisted of horizontal or vertical stripes. The stripes were alternating black and white bars 3 mm wide, and the total flux of the two targets was equal. In the intensity discriminations the targets were white circles 3.5 cm in diameter.

The method of changing the stimulus intensity in both the color and in-

tensity discriminations was to insert resistors of different values in series with the projector bulb. This provided an easily reproducible method of changing the intensities. The method can be criticized, however, because changing the current through the incandescent light not only changes the intensity, but also can change the spectrum of the light emitted. To determine what effect this had on the color stimuli, the spectra were measured with an ISCO spectroradiometer (Model SR). The measurements indicated that there was a smooth and regular decrease in intensity from one stimulus to the next for the blue, red, and white stimuli. Based on these measurements, it is believed that the method of changing the intensity did not introduce a significant error that would invalidate the results of these studies.

At the conclusion of behavioral testing the rats were deeply anesthetized with Nembutal, and the eyes were removed for either paraffin or plastic embedding. The eyes were sectioned, stained, and examined to determine the degree of retinal degeneration. The details of the histological methods are reported in the following paper (10).

The data for any one behavioral task were analyzed by comparing the scores of the control animals with the scores of the constant light-exposed animals. The scores from each week were examined using a Kruskal-Wallis one-way analysis of variance. If the analysis of variance showed that the scores were significantly different at the 0.05 level, the rankings of the scores of the control animals were pooled, as were the rankings of the scores of the light-exposed animals. This information was then analyzed using a Kruskal-Wallis partitioning method to determine if the differences were between control animals and experimental animals or within one of the two groups (12).

## RESULTS

The behavioral studies were conducted in two phases. The first phase consisted of studies on the ability of light-exposed rats to discriminate between different patterns and between lights of different intensities. In the second phase, pattern discriminations, intensity discriminations, and color discriminations were tested.

Six animals were used in the first phase of experiments. The rats were trained initially on a pattern discrimination consisting of horizontal stripes vs. vertical stripes, with horizontal stripes being the positive stimulus. After reaching criterion on this task, the rats were assigned to either the experimental group (four rats) or to the control group (two rats). All animals were then tested on the pattern discrimination once every 5 days for at least 180 days. After 150 days of constant light, the scores of the experi-

mental rats had decreased to near chance (50%), indicating that they could no longer discriminate effectively between horizontal and vertical stripes (see Fig. 1).

At this point two of the experimental rats were tested to determine if they could discriminate between horizontal stripes at one choice panel and no stimulus at the other choice panel (see Fig. 2). Animal 8 performed only slightly above chance. Animal 13, however, learned the task immediately and scored 90% or above on 6 consecutive days. These two animals were then tested on vertical stripes (positive) vs. no stimulus. There was no change in animal 8's performance from the previous task. Animal 13 performed at approximately 55% correct responses for 4 days before learning the new task. This suggests that animal 13 might have had some residual capability for distinguishing horizontal stripes from vertical stripes, because it had difficulty learning the new task where a previously negative stimulus became a positive stimulus. On the other hand, it is also possible that the animal was somehow solving the latter discrimination using local flux cues. The eyes were then removed from these two animals and they were again tested to determine if there were any nonvisual cues which the animals could use to perform the task. In neither case did the animal's performance significantly vary from chance. Histological examination of the paraffin-embedded eyes of animals 8 and 13 confirmed that less than 0.3% of the photoreceptor nuclei remained compared to the number of photoreceptor nuclei in a similar section from the eye of a control rat. No intact photoreceptors were observed in the retinas of these two rats.

After 200 days of testing on the pattern task, animals 17 (control), 21, and 23 (experimental) were then tested on their ability to discriminate between white lights of different intensities. In the first pair of stimuli tested, one stimulus had an intensity that was 10% of the other stimulus. All rats reached a criterion of 90% correct responses in 20 trials within 4 days on this task. The intensity of the dimmer stimulus was then increased to approximately 25% of the brighter stimulus, and the rats were tested on this new pair of stimuli. This procedure was repeated each time a rat reached the criterion, raising the intensity of the dimmer stimulus by 10 to 15% relative to the brighter stimulus. If a rat failed to reach the criterion within 10 days but was still scoring above chance, the intensity of the dimmer light was again increased. In this way it was possible to determine how different the intensities of two lights had to be for the rats to be able to discriminate reliably between them. All three rats were able to discriminate at the criterion level, a stimulus at least 42% dimmer than another stimulus. If the dim stimulus was 28% dimmer than the other stimulus, the rats could perform above chance levels (at about 70%) but not at the criterion level. If

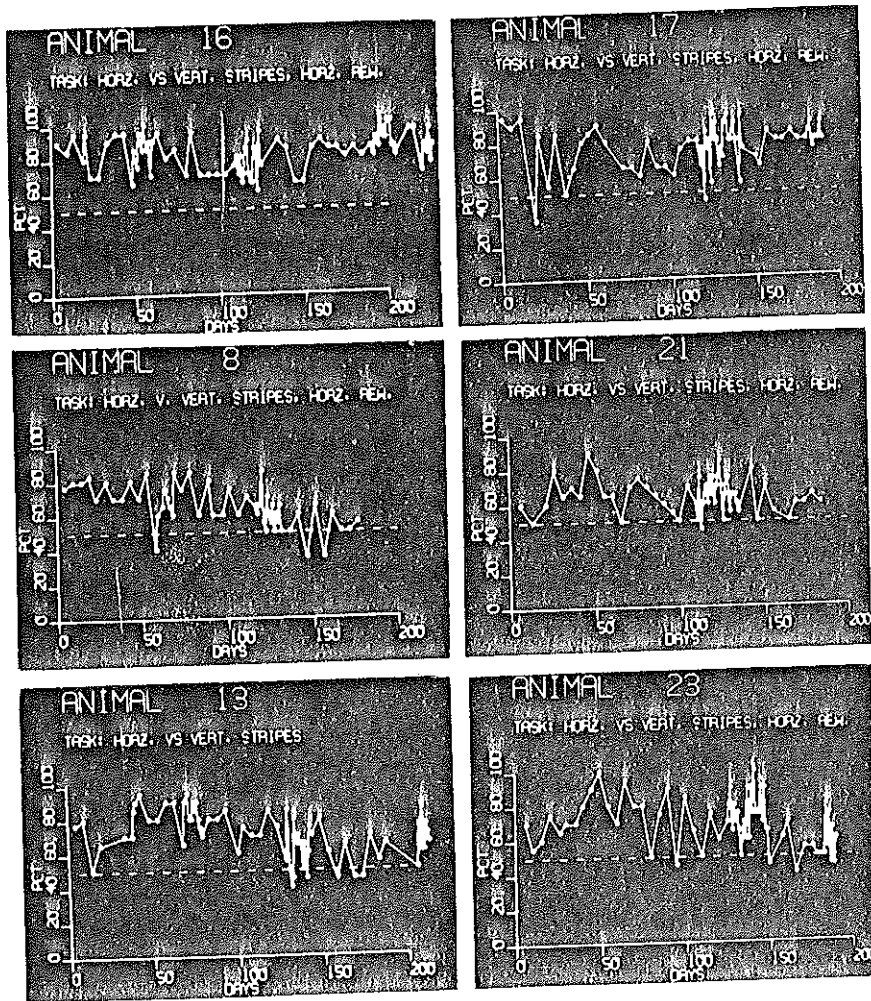


FIG. 1. Phase 1 studies on pattern vision: Horizontal stripes vs. vertical stripes. Scores of experimental and control animals tested on discriminating between horizontal and vertical stripes. Experimental animals were exposed to constant light beginning on day 0. Animal 16 served as the control for animals 8 and 13. Animal 17 served as the control for animals 21 and 23. The abscissa represents time in days. The ordinate indicates the percentage of correct responses in 20 trials per day. The dashed line indicates the 50% or chance level. After approximately 150 days of exposure to constant light, the scores of the experimental animals had decreased to near chance levels. See text for details.

the dim stimulus was only 19% dimmer than the other stimulus, the rats could not make the discrimination. Histological examination of the plastic-embedded retinas from the two experimental animals revealed a few nuclei

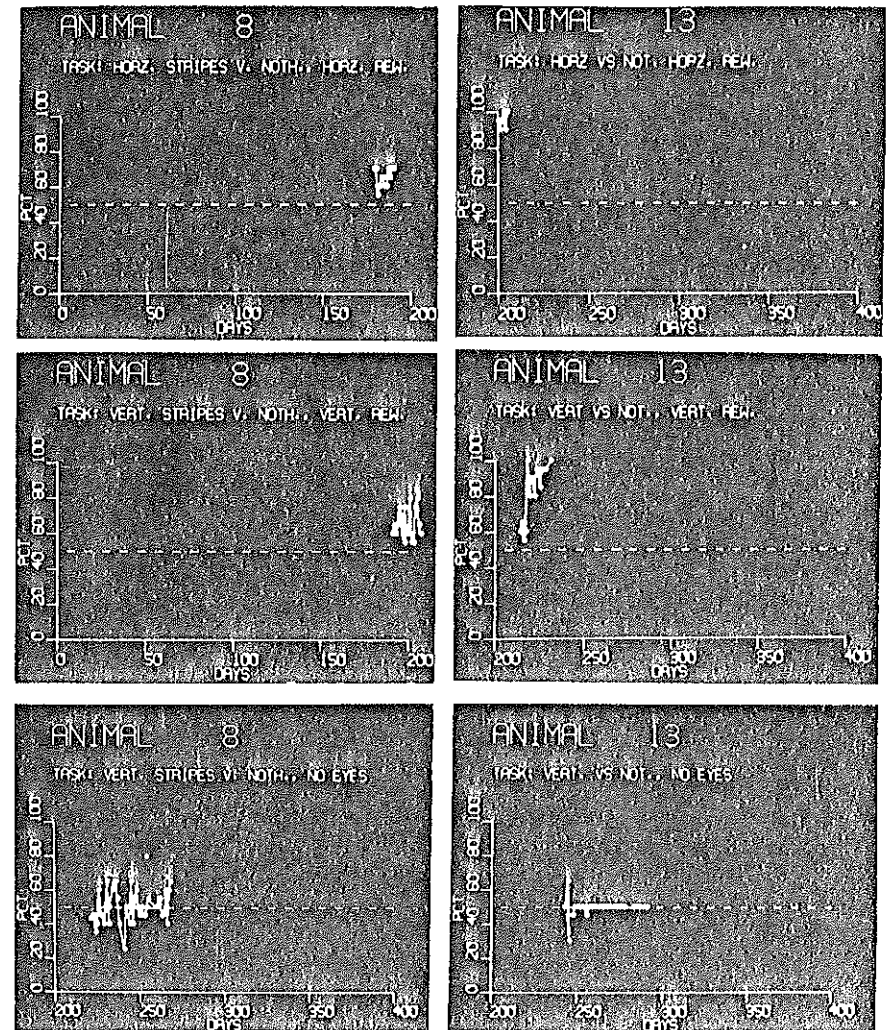


FIG. 2. Phase 1 control tests. Scores of two experimental animals tested on different tasks after long-term exposure to constant light. Upper graphs—discriminating between horizontal stripes and a blank panel; middle graphs—discriminating between vertical stripes and a blank panel; lower graphs—animals tested on vertical stripes vs. a blank panel after removal of the eyes. See text for details.

in the periphery of the retina that had the staining characteristics of photoreceptor nuclei, but, once again, no intact photoreceptors were observed.

The testing of animals 21 and 23 on intensity discriminations was continued to see if there were performance changes after even longer exposure

durations. The rats were tested 5 days a week, every other week, with one stimulus 40% dimmer than the other stimulus. After approximately 300 days of constant light exposure, it was necessary to increase the relative intensity differences between the stimuli for the rats to make the discriminations at the 90% level. After about 350 days the rats were unable to discriminate between the brightest white stimulus available for testing ( $2.1 \mu\text{W}/\text{cm}^2$  at the choice panel) and no stimulus.

In the second phase of the experiment, the testing regime was different from that used in the first phase. Eleven rats were trained on the pattern discrimination (horizontal vs. vertical stripes), and of these rats six reached the criterion (90% correct responses in 20 trials on 3 consecutive days) within 50 days of training. These six rats were then tested 5 days a week on this task every other week. The testing of these animals showed that whereas the performance of the control animals remained at a high level, the performance of the light-exposed animals decreased (Fig. 3). During the first week of exposure to constant light, there was a highly significant ( $P < 0.001$ ) decrease in the performance of the experimental animals. After 5 weeks in constant light, however, the scores of the experimental animals were not significantly different from controls. By contrast, 7 weeks of exposure to constant light again resulted in the scores of light-exposed animals being significantly lower ( $P < 0.05$ ) than those of the control animals. The scores of the light-exposed animals continued to decrease, so that after 23 weeks of exposure to continuous light the scores were only slightly above chance. These results confirm the results from the phase 1 experiments on pattern vision, in that exposure to constant light for long periods of time produces a decrease in the ability of rats to discriminate between horizontal and vertical stripes.

Four rats that failed to learn the pattern discrimination were tested for their ability to make intensity discriminations. Two rats were exposed to constant light and two were maintained in cyclic light. They were tested 5 days a week, every other week, on discriminating between two white stimuli, one 42% dimmer than the other. During 168 days in constant light, the two experimental animals showed no change in their ability to make this particular intensity discrimination at criterion levels.

The six animals used in the pattern discrimination and the four animals used in the intensity discriminations were also tested on alternate weeks for their ability to discriminate between blue and red stimuli. The relative brightness of the colored stimuli was changed daily to prevent the animals from using brightness cues to make the discriminations. The scores of six of the ten animals are shown in Fig. 4. With increased exposure durations there was an increase in the variability of the scores of the light-exposed animals, whereas the control animals' scores remained stable. An analysis

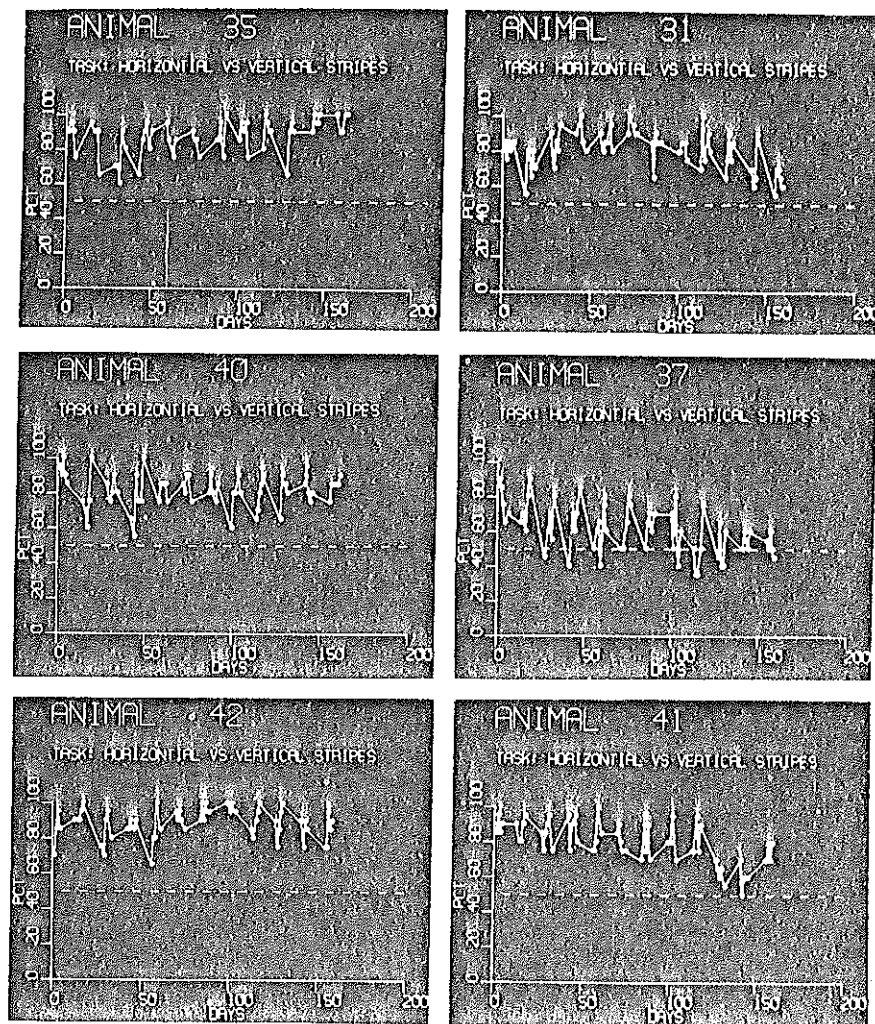


FIG. 3. Phase 2 studies on pattern vision: Horizontal stripes vs. vertical stripes. Scores of control animals and experimental animals from the second phase of testing. The animals were tested on discriminating between horizontal stripes and vertical stripes. Animals 35, 40, and 42 were housed in cyclic light, and animals 31, 37, and 41 were housed in constant light.

of the data showed that the light-exposed animals performed poorly on the days when they were tested on a task in which the intensity of the blue stimulus was low. On days when the experimental animals performed well, the intensity of the blue stimulus was relatively high.

After 168 days of testing, the 10 rats were examined to determine their

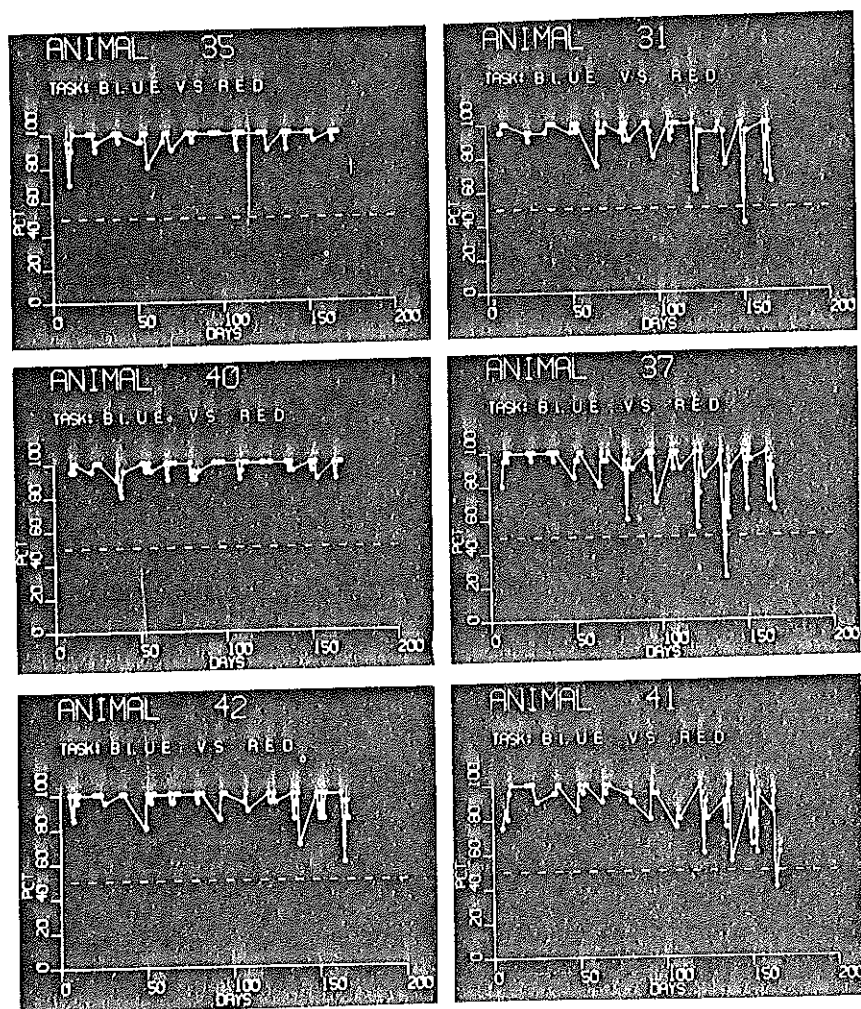


FIG. 4. Phase 2 studies on color vision. Scores of control animals and experimental animals from the second phase of testing on discriminating between blue and red stimuli. Animals 35, 40, and 42 were housed in cyclic light, and animals 31, 37, and 41 were housed in constant light.

visual thresholds for the blue and red stimuli. The rats were given 20 trials per day and were first tested on their ability to discriminate between a blue stimulus at one choice panel and no stimulus at the other panel. When each rat reached a criterion of 90% correct responses in 20 trials, the intensity of the blue stimuli was decreased by 10 to 15%. This procedure was continued until an animal was unable to discriminate between a given intensity of blue light at one panel and no stimulus at the other panel. It was found that the

control animals were able to discriminate all intensities of blue used in the color tests. The experimental animals were found to have increased thresholds in that they were unable to discriminate the two lowest intensities of the blue stimuli from no stimulus, whereas they could discriminate the higher two intensities of blue stimuli from no stimulus. In reference to the color tests discussed above, the correlation between the dimmest intensity of blue which an animal could discriminate from an unlit panel and the dimmest intensity of blue which the animal could discriminate from red was perfect. If the rat could not discriminate between a dim blue stimulus and the red stimulus, it could not discriminate between the same blue stimulus and no stimulus, and vice versa.

These 10 rats were also tested on their ability to discriminate between a red stimulus and no stimulus, with red being the positive stimulus. Because the red stimuli had always been negative for the rats, it might be difficult for them to perform this task. All animals were tested on red vs. a dark panel for 10 days, and the control and experimental animals performed similarly. During the first 10 trials of each day, an animal would perform poorly, scoring 4 to 6 correct. During the second 10 trials, however, it would do quite well, scoring 8 to 10 correct. Only two control rats reached a criterion of 90% correct in 20 trials within the 10 days of testing. To determine if dark adaptation was necessary for the rats to discriminate the red stimuli, two control rats and two light-exposed rats were placed in the dark experimental chamber for 5 min (approximately twice as long as the time in which a rat performs 10 trials) before the beginning of testing. This procedure did not increase the rats' scores for the first 10 trials. This suggests that the poor performance on the first 10 trials was not due to an incomplete dark adaptation. These data suggest that the rats could discriminate the red stimulus from no stimulus and that the red stimulus was above the rats' visual threshold.

Examination of the paraffin-embedded eyes of the constant light-exposed rats used in the second phase of the experiments revealed that the degeneration of the photoreceptors was virtually complete, cell nuclei with staining and size characteristics of photoreceptor nuclei being extremely rare. Figure 5 shows examples of retinas from a control rat and a rat exposed 6 months to constant light.

## DISCUSSION

The results from the studies on pattern vision showed that exposure to constant light for extremely long periods was required to produce significant changes in the discriminative abilities of rats. The time course of the decay of the rats' ability to discriminate between horizontal stripes and vertical stripes was similar in both phases of the study. This occurred

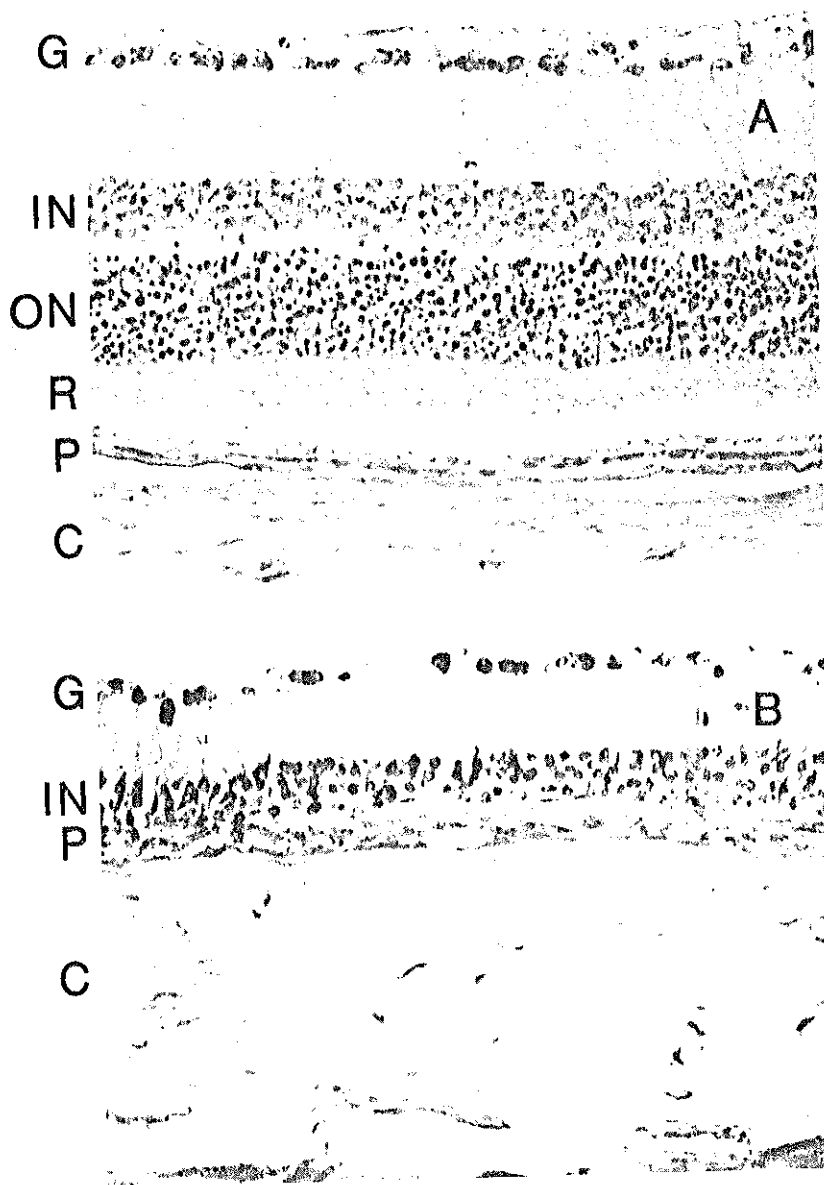


FIG. 5. Examples of paraffin-embedded retinas. A is from an animal housed in cyclic light and B is from an animal housed in constant light for 6 months. Note the absence of the outer nuclear layer and the receptor layer in B (G—ganglion cell layer, IN—inner nuclear layer, ON—outer nuclear layer, R—receptor layer, P—pigment epithelium, C—choroid).

despite the fact that the animals were tested on different schedules in the two different phases of the study.

The results of testing the two animals that had their eyes removed in the first phase of the study suggest that there were no nonvisual cues that would explain the above chance performance on two-choice discrimination tasks of the light-exposed animals. It will be recalled that those two animals were performing visual discriminations at levels above chance, even after massive photoreceptor destruction, but, as soon as their eyes were removed, their performance fell to chance levels.

These results are consistent with those of previous investigators, whose work suggested that very long exposure durations were required to reveal behaviorally determined visual deficits in constant light-exposed rats. For example, Bennett *et al.* (4, 5) found a decrease in the ability of rats to make light-dark discriminations after about 90 days in constant light, and Anderson and O'Steen (2) found no changes in the performance or learning rates on a pattern task in rats exposed to constant light for only 30 days. After 3 months of light exposure, rats were found to have increased thresholds for light detection by Weizenbaum and Colavita (16). One study (6) that showed a rapid decrease in the ability of rats to perform visual discriminations resulting from exposure to constant light used light that was at least six times more intense than that used in this study.

In the tests on color vision in rats exposed to constant light, it was found that there was a progressive decrease in the ability of the rats to discriminate between the dim blue stimuli and the red stimuli. The tests conducted after the rats had been 24 weeks in constant light showed that the dim blue stimuli, which they could not discriminate from red, were also the blue stimuli that were below their visual threshold. Tests also showed that the red stimuli were above their visual threshold. The tests on intensity discrimination in control and experimental animals revealed that the intensity of one white light had to be between 28 and 42% greater than a second white light for the rats to discriminate between them. One can conclude from this that if a rat was discriminating between two colors on a basis of brightness cues, then the apparent brightness of the two colors would have to be at least 30% different. However, the rats could discriminate blue from red as long as both the blue and red stimuli were above the rats' visual threshold, regardless of the relative intensity of the two stimuli. These facts, taken together, argue strongly that the rats were discriminating between blue and red on a basis of hue and not relative brightness. This is particularly true when one considers that the relative intensities of the colored stimuli were alternated on a daily basis and this procedure would confound any attempt of the rats to use brightness cues.

It is particularly interesting that the performance of the rats on a pattern task decreased dramatically as exposure time approached 24 weeks, although these same animals were still able to perform color discriminations. A statistical analysis of the scores of the three experimental rats that were tested both on pattern discriminations and color discriminations showed that after 140 days in constant light their scores on the pattern discriminations were significantly lower ( $P < 0.01$ ) than their scores on the color discriminations. Although Anderson and O'Steen (2) reported that rats exposed to constant light took more time to perform a pattern task than a black-white task, they found that the accuracy of the light-exposed rats was not impaired. Therefore, this is the first time that a differential effect of constant light on the accuracy of visual discriminations was reported. Of possibly greater significance is the fact that light-exposed rats could perform color discriminations at all. This would seem to indicate that there were at least two different visual pigments that were transducing light in the light-exposed rats. This observation may give support to the suggestions of LaVail (11) and Cicerone (7) that residual cone fragments might be mediating vision in light-exposed rats. Neurophysiological and histological studies that are reported in the following paper (10) suggest, however, that cone fragments are not the primary light-transducing element in light-exposed rats.

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