Color vision in tree squirrels[1]

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Six tree squirrels were tested on a series of color discrimination problems utilizing various combinations of nine color filters ranging from 680 to 420 mu with intensity randomized. All animals reached criterion for all combinations by the 10th day of testing. These data support studies using indirect methods in demonstrating that tree squirrels possess color discrimination ability.

With the exception of the swine (Klopfer, 1966) and the antelope squirrel (Crescitelli & Pollack, 1965) there is little, if any, behavioral evidence of color vision in subprimate mammals. Whether or not this is due to the restricted number of animals that has been studied or, as comparative zoologists have emphasized, due to the arboreal habitat and diurnality serving as prime factors, is yet to be determined. If the latter is the case the tree squirrel is a logical animal to be studied.

The tree squirrel shares with the primates many common characteristics. In addition to its arboreal and diurnal behavior, the retina of the tree squirrel is composed of numerous small cones having a maximum density in the lateral posterior area. There appear to be no cells that can be identified unequivocally as rods (Polyak, 1957). Several investigators (Arden & Tansley, 1955; Weale, 1955; Dartnall, 1960; Tansley, Copenhaver, & Gunkel, 1961) have indirectly demonstrated the existence of color vision in several species of squirrels by the shape of spectral sensitivity curves. These studies employed such techniques as electroretinography, fundus reflectometery and direct absorption measurements from extracted pigment.

The present study was designed to provide a direct behavioral demonstration of color discrimination ability in the tree squirrel and thus, make possible a cross-verification of the existing physiological data.

Method

Six mature and experimentally sophisticated tree squirrels, four gray *(Sciurus carolinensis)* and two fox *(Sciurus niger)*, were used as Ss.

They were tested in an apparatus that consisted of a restraining cage and a test chamber which were separated by an opaque barrier and a glass shield The test chamber was divided into two compartments each backed by a top-hinged clear plastic response door that could be latched or left open. Inserted in the back of each door was a piece of milk glass and a mask made of black construction paper with a circular hole cut in the middle. Behind these doors there were reward chambers lined with white filter paper for the purpose of color absorption. Adjacent to each reward chamber was a moveable filter holder. Light

from slide projectors was projected through the filters onto the response doors to provide the discriminanda.

The stimuli were provided for by the use of nine Balzars interference filters (680, 600, 573, 550, 530, 490, 440, and 420 mμ) and five neutral density filters (0.2, 0.5, 1.0, 1.5 and 2.0 log units). All pairs of interference filters were physically equated for intensity and each interference filter was equated with a corresponding "gray."

Each S was tested on two sets of four problems for a total test series of eight problems. The first set of four problems involved a discrimination between two interference filters the intensities of which were varied every five trials around equated intensity values. The physical difference in wavelength decreased from Problem 1 to Problem 4.

The first three of the second set of four problems involved the pairing of each interference filter with a gray the intensity of which was randomly varied every five trials around a gray equal to the intensity of the color filter. The last problem consisted of a simple intensity discrimination.

Each S received a block of 50 trials per day until a criterion of 35 out of 50 was reached ($\alpha = 0.01$). The door on which the incorrect stimulus was projected was latched (both food wells baited) and the opaque screen was raised. After 5 sec the glass shield was raised and the animal was permitted to respond to one of the stimuli. A noncorrection procedure was employed. The trial was terminated after a response by lowering both screens. The position of the correct stimulus was changed according to a random sequence.

Results and Discussion

All Ss reached criterion on all problems by the 10th day of testing. The mean number of trials necessary to reach criterion for each filter combination in Problems 1-4 may be seen in Table 1. With one exception as the difference in wavelength between stimuli decreased, the number of trials to criterion increased. Performance on the second part of the experiment may also be seen in Table 1. Although the criterion was reached rapidly on these problems, it appears that wavelengths at 550 and 530 mμ were most difficult to discriminate while those at 490 and 465 mμ were most easy to discriminate.

In order to determine whether changing the relative intensity every five trials had any effect, Z scores were computed for each stimulus pair. Of the 18 pairs tested only one was significant; therefore, H_1 could not be rejected.

The data of the present experiment are consonant

Table 1. Mean Number of Correct Responses on the Final Day of
Testing and the Number of Days to Criterion

Problem	Mean No. of Correct Responses	Days to Criterion
620(R)-465(B)	37.5	7
620(R)-550(G)	35.3	5
550(G)-465(B)	37.5	5
550(G)-490(B)	38.5	8
600(R)-550(G)	36.5	9
465(B)-420(V)	35.0	9
600(R)-620(R)	35.0	10
550(G)-530(G)	37.5	10
490(B)-465(B)	35.5	10
680(R)-2.5 log units	35.5	4
620(R)-1.5 log units	36.5	3
600(R)-1.5 log units	36.0	4
573(G)-1.5 log units	37.5	3
550(G)-1.5 log units	36.0	5
530(G)-1.7 log units	39.0	4
490(B)-2.2 log units	36.0	2
465(B)-2.3 log units	37.5	2
440(V)-3.0 log units	37.0	3
420(V)-3.0 log units	39.0	3

with those of Crescitelli & Pollack (1965) for the antelope squirrel and add support to those studies using indirect methods to demonstrate color vision in certain species of squirrels.

The behavioral demonstration of color vision in the tree squirrel has many implications which are important both for comparative research and for theories of evolutionary development. Most of the earlier theories concerning the evolution of color vision have stressed the development of this mechanism solely within the primate order (Walls, 1942; Polyak, 1957). These theories have stated that the emergence of color detection mechanism within the mammalian class is contingent upon both arboreality and diurnality. The results of the present study reemphasize the importance of these characteristics by providing evidence of color discrimination ability in a subprimate mammal which is characterized by these qualities. This finding contributes to a functional as opposed to a taxonomical approach to the study of evolutionary processes.

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