Evidence of color vision in a diurnal prosimian, *Lemur catta*

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Two *Lemur catta* were tested in a WGTA on three two-choice color discrimination problems involving paired comparisons of red, green, and blue. Four illumination combinations between the two discriminanda served to make brightness irrelevant, hue being the only salient cue. All color problems were learned within criterion limits of 21 out of 25 correct choices during 16 consecutive test sessions, indicating good color vision for this diurnal prosimian.

Investigations of the primate visual system have found that both Old World and New World monkeys demonstrate color vision mediated by trichromatic mechanisms (Grether, 1939; Miles, 1958a, b; Jacobs, 1963; DeValois & Jacobs, 1968). The tree shrew, *Tupaia glis*, has been shown to have dichromatic color vision (Shriver & Noback, 1967; Polson, 1968; Snyder, Killackey, & Diamond, 1969). However, the Tupaiids have an equivocal taxonomic status, since they possess phylogenetic characteristics which are transitional between those of the primates and the insectivores.

Walls (1942) suggested that human color vision evolved within the primate order and probably developed independently from that of the lower vertebrates. However, color vision has not been adequately demonstrated in a recognized diurnal prosimian. It would, therefore, appear desirable to provide a more extensive test of color vision in a prosimian such as the diurnal lemuroid, *Lemur catta*, the "ring-tail" lemur. The previous studies of discrimination by diurnal prosimians between colored stimuli have yielded equivocal results, and adequate controls for brightness cues were not always utilized (Bierens de Haan & Frima, 1930; Glickman, Clayton, Schiff, Guritz, & Messe, 1965; Davis, Leary, Steven, & Thompson, 1967).

Morphological investigations of the retinal configuration of *Lemur catta* have presented a nocturnal neural network with relatively small numbers of cones (von Castenholtz, 1965; Rohen & von Castenholtz, 1967; Ordy & Samorajski, 1968). Although the photoreceptors are predominantly rod-like, a functional cone mechanism (the prerequisite necessary to mediate color vision) has been demonstrated neurophysiologically (Ordy & Samorajski, 1968).

However, not all species possessing cones have been found to have color vision. The presence of chromatic mechanisms, as shown by neuroanatomical or

neurophysiological evidence, does not mean that an animal can use color information or that it relies on chromaticity rather than alternative cues, such as brightness. Therefore, all a priori judgments of the presence of color sense in a species with a photopic mechanism must be supplemented by the essential test: a behavioral evaluation of color vision. Hence, the present study was undertaken to establish the potential for color vision in a recognized diurnal prosimian, *Lemur catta*, and to cross-verify existing physiological and anatomical data.

METHOD

The Ss were two sexually mature *Lemur catta*, a male and a female. The behavioral tests for color vision were carried out in a modified Wisconsin General Testing Apparatus (WGTA). The S in the test cage was separated from two foodwells located on a sliding test tray by two movable sheets of Plexiglas, one clear and one opaque, each of which could be raised or lowered independently in a guillotine fashion. Each foodwell was covered by a displaceable swing-away lid of stiff nongloss white cardboard. Two standard 35-mm slide projectors were positioned above the foodwells, such that each light beam was reflected off a mirror and directed onto the swing-away lids as 2½-sq-in. spots of light.

Kodak Wratten gelatin filters were used to vary the spectral composition of the two stimuli. The color specification numbers were 24 (red), 61 (green), and 47 (blue). The dominant wavelengths of these colors were 615, 536, and 470 nm, respectively. Independent variations in brightness of either discriminative stimulus were produced by means of Kodak Wratten neutral density filters (No. 96).

Initially, a shaping procedure was used to train the lemurs to reach through the bars of the test cage in order to obtain a preferred food reward, raisins, placed in the foodwells covered by the swing-away lids. During this phase of the experiment, the S was simultaneously presented with a nonvaried hue combination of positively reinforced bright blue and nonreinforced dim red. The right-left position of the two discriminanda was randomized to avoid the formation of a position habit. Criterion during shaping was at least 21 out of 25 correct responses on each of the four daily testing sessions for 4 consecutive days.

Subsequently, after criterion was reached, three two-choice hue discrimination problems were presented in the following combinations with their respective reinforcement values: (1) blue-positive vs red-negative, (2) blue-positive vs

*Appreciation is expressed to J. Mark Ordy, Tulane University Delta Regional Primate Center, Covington, Louisiana, for supplying the animals used and for his assistance in the completion of this study.

green-negative, and (3) green-positive vs red-negative. Differential reinforcement with the preferred food was used to establish one of the two colors as the positive cue. The S's basic task was to select the positively reinforced color from the nonreinforced color in each pair of the three two-choice color combinations. As in the shaping procedure, both colors were presented simultaneously and their right-left position was randomized according to the Gellerman series (1933).

The critical control for all studies of color discrimination is based on the elimination of brightness as a possible cue. Therefore, four brightness combinations were used for each hue discrimination problem as follows: The positive color stimuli were projected at intensities greater than, less than, and approximately equal to—at high and low levels of illumination—that of the negative stimuli. The range of brightness levels employed sought to assure that any discrimination based on brightness cues was reduced to near chance levels.

Table 1 presents the illuminance readings of the discriminanda for each problem as measured at the level of the test tray.

Four test sessions a day were given. The first test session of each day was administered while the S was approximately 12-h food deprived. Each test session consisted of 25 trials with the two discriminanda presented at one of the four brightness combinations. The brightness combinations were used in a counterbalanced order; hence, each S received 100 trials a day, each 25-trial block consisting of a different illuminosity combination.

The criterion for successful discrimination was set at 21 out of 25 correct responses in each test session for 16 consecutive sessions (84% correct responses). A discrete-trial procedure was used. Testing was conducted in a darkened sound-attenuated room. On each trial, a raisin was placed in the appropriate foodwell, the swing-away lid replaced, and the test tray moved forward. One well-cover lid was illuminated with the positive stimulus, the other by the negative stimulus. The opaque

Plexiglas door was raised and the lemur was permitted to view the discriminanda through the transparent Plexiglas. Following a 3-sec delay, this latter door was raised, permitting the S to make a response. A noncorrection procedure was used. However, if the S responded to the same foodwell more than four times in succession, in order to discourage the formation of a position habit, the correct stimulus appeared on the opposite side on the next trial and continued to appear there until the lemur had made two successive responses on that side. After a response had been made, or in 45 sec in the event of no response, the trial was terminated by lowering both doors. An intertrial interval of 15 sec was interposed between each trial. The testing session for each lemur lasted approximately 45 min. The intersession interval was 2-3 h.

With successive trials, the white well-covers sometimes became soiled during the testing session since the lemurs' responses necessitated repeated contact with them. Therefore, to eliminate the possibility of the soiled swing-away lids serving as secondary cues, they were replaced before the start of every testing session. Auditory masking was provided by the forced-air blowers of the slide projectors. Olfactory cues were minimized by rubbing both foodwells with raisins prior to each testing session. Brightness controls having already been considered, color appeared to be the only consistently rewarded cue.

RESULTS AND DISCUSSION

The behavioral color tests indicated that both lemurs discriminated the positive color from the nonreinforced color for each pair of the three color combinations independently of the four brightness combinations to a statistically significant criterion of 21 out of 25 correct choices during 16 consecutive test sessions over a 4-day period ($p < .001$). The male lemur attained the criterion of discrimination on each color problem in 4 days or 400 trials. Color discrimination by the female lemur during the behavioral testing was somewhat less consistent. Although the female S required only 400 trials to attain criterion performance for the blue-positive vs red-negative discrimination, the blue-positive vs green-negative combination required 900 trials, and the green-positive vs red-negative discrimination required 725 trials to attain the criterion level of performance. An analysis of variance indicated that neither of the lemurs' performances was significantly influenced by the various brightness combinations, the test days, the three color problems, or by their interactions. A summary of the color discrimination tests for the two lemurs is presented in Table 2. The paradigm employed in the present study indicates that *Lemur catta* apparently learned to make a discrimination based upon differences in spectral composition. The range over which brightnesses were varied argues that hue was the only salient cue.

However, it would, perhaps, be of additional value to attempt to provide an explanation regarding the differences in performance between the two lemurs. Their previous testing history indicated that they were not experimentally naive, both Ss having been used in visual acuity studies employing a runway apparatus (Ordy & Samorajski, 1968). In addition, the female lemur, who was found to be a much more difficult

Table 1
Illuminance Readings Measured at the Level of the Test Tray

Problem I: Blue (+) vs Red (-)*		
Illuminance Combination**	Blue (fc)	Red (fc)
$B_H \cong R_H$	1.21	1.14
$B_H > R_L$	1.21	.22
$B_L < R_H$	.29	1.14
$B_L \cong R_L$	.29	.22
Problem II: Blue (+) vs Green (-)		
Illuminance Combination	Blue (fc)	Green (fc)
$B_H \cong G_H$	1.21	1.10
$B_H > G_L$	1.21	.26
$B_L < G_H$	.29	1.10
$B_L \cong G_L$	.29	.26
Problem III: Green (+) vs Red (-)		
Illuminance Combination	Green (fc)	Red (fc)
$G_H \cong R_H$	1.20	1.05
$G_H > R_L$	1.20	.20
$G_L < R_H$	.12	1.05
$G_L \cong R_L$	.12	.20

*Plus (+) and minus (-) signs indicate positively reinforced and nonreinforced colors, respectively.

**H and L refer to high and low levels of illumination, respectively, used with the hue.

animal to handle than the more docile male, had also been subjected to the placement of corneal electrodes in the determination of electroretinogram/critical flicker frequency values (Ordy & Samorajski, 1968). To what extent their previous experimental history or any differences in personality might be reflected in their error scores can only be speculative. However, even during the initial shaping procedure, which required only a simple brightness discrimination, the female made a substantially greater number of errors before reaching criterion. Finally, it should be noted that during the testing of the third color discrimination problem (green vs red), the female developed an illness which necessitated discontinuing testing for a period of over 2 months to insure that she had completely recovered before testing was resumed. Subsequently, she was reshaped employing only brightness differences between the colors used in the third problem. It is unknown whether, or to what extent, the initial onset of the illness interfered with the performance of the S in the previous problem (blue vs green) in which the greatest number of errors was committed.

On the other hand, the relatively low total number of errors in the performance of the male lemur is suggestive of a more sophisticated tester. Moreover, since brightness was varied in blocks of 25 trials, it is possible that a brightness cue may have been utilized and contributed to the performance of the S within blocks. However, on one half of the illuminance combinations, the two hues were closely matched at both high and low levels of illumination. This would have tended to compromise the performance of the S and, since it did not occur, it tends to reinforce the likelihood that color was, in fact, the salient cue.

The evidence for color vision in this diurnal lemur serves to expand and strengthen earlier studies which explored the potential for color vision in diurnal prosimians. The behavioral demonstration of color discrimination also affirms previous neurophysiological evidence for a retinal photopic mechanism in *Lemur catta* (Ordy & Samorajski, 1968). The neuroanatomical evidence of retinal duplicity, albeit the predominance of rod-like photoreceptors (von Castenholtz, 1965; Rohen & von Castenholtz, 1967; Ordy & Samorajski, 1968), likewise concurs with the present behavioral findings.

This investigation may permit certain cautious conclusions to be drawn with respect to the phylogenetic development of color vision in primates. The study provides additional evidence that all primates, including man, the anthropoid apes, the diurnal New World monkeys, the diurnal Old World monkeys, and the diurnal prosimians, have the potential for color vision. Assuming that the early lemuroid progenitor had the ability to sense color, the present study lends weight to Walls's assertion that the development of human color vision occurred within the primate order. It is also

Table 2
Summary of Behavioral Color Tests of Two
Subjects of the Diurnal Prosimian, *Lemur catta*

S	Two-Choice Color Discrimination	Total Number			Percent Correct
		TS	P	E	
Male	Blue (+) vs Red (-)*	16	400	5	98.75†
	Blue (+) vs Green (-)	16	400	10	97.50
	Green (+) vs Red (-)	16	400	5	98.75
Female	Blue (+) vs Red (-)	16	400	5	98.75
	Blue (+) vs Green (-)	36	900	55	93.89
	Green (+) vs Red (-)	29	725	39	94.62

Note—TS = testing sessions, P = presentations, E = errors.
*Plus (+) and minus (-) signs indicate positively reinforced and nonreinforced colors, respectively.

†According to the binomial test, the probability of obtaining 21 correct choices out of 25 trials by chance is less than .001 when $P = Q = \frac{1}{2}$ (Siegel, 1956).

possible that the early lemuroids did not have color vision, in which case the implication would be that this ability evolved independently for these prosimians.

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(Received for publication February 14, 1974;
accepted May 21, 1974.)