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7. Duration is defined as time from loss of righting reflex to return of the reflex twice within 30 seconds, measured to the nearest minute. Sleep variables such as room temperature, extraneous sounds, food intake, and ethanol concentrations were adequately controlled.
8. Intraventricular injections in the mice were by the methods of R. A. Harris, H. H. Loh, and E. L. Way [*J. Pharmacol. Exp. Ther.* **195**, 488 (1975)] and W. G. Clark, C. A. Vivonia, and C. F. Baxter [*J. Appl. Physiol.* **25**, 319 (1968)].
9. Artificial cerebrospinal fluid was prepared by the method of D. Palaić, I. H. Page, and P. A. Khairallah [*J. Neurochem.* **14**, 63 (1967)]. Pilot studies showed no consistent or significant effects on sleeping time of injection versus sham puncture, osmolarity, or *p*H, when a fixed injection volume of 5 μl was used.
10. The dose-response relationship in rats was seen with calcium chloride (2 to 8 μmole/kg) given intraventricularly 30 minutes before a dose of ethanol (3.5 g/kg). These and related results have been reported by C. K. Erickson, L. K. Beck, K. L. Duensing, and R. M. Huff [*Abst. Soc. Neurosci.* **3**, 290 (1977)].
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14. Attempts to enhance sleeping time induced by pentobarbital by the administration of calcium have given equivocal results, as reported in Erickson *et al.* (*10*).
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23. We thank Bill Brant and Larry Beck for technical assistance on the treadmill apparatus, and the following for generous supplies of drugs: H. R. Besch (verapamil), R. J. Hosley (Eli Lilly & Company) (A23187), and W. E. Scott (Hoffman-La Roche Inc.) (X537A). The work was supported by research grants AA 01417 (C.K.E.) and a Pharmaceutical Manufacturers Association Foundation research starter grant (R.A.H.).

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Cat Color Vision: The Effect of Stimulus Size

Abstract. *Adult cats were trained to discriminate blue from green and gray. Although the cats could discriminate the intensity of stimuli whose areas ranged from 33 to 0.36 square centimeters they could not discriminate color when the stimulus was 0.36 square centimeter ($<$ 20° visual angle). This influence of stimulus size may account for both positive and negative results of previous studies.*

The color vision capability of the cat has been an issue of debate for over half a century. Early investigators (*1–3*) concluded that cats were color blind, but more recent studies (*4–6*) have clearly indicated that cats can discriminate some differences in wavelength distribution. What remains unclear is why the positive findings were difficult to obtain.

We were encouraged to address this question because of certain improvements in the behavioral testing procedures for the cat (*7*) and a simplification of procedures necessary to demonstrate color discrimination (*8*). The testing procedures proved to be effective for training normal adult cats to discriminate colors, and stimulus size emerged as a variable of critical importance.

Four untrained adult cats were maintained at 80 percent of their weight when given free access to food, and were trained to press either of two clear Plexiglas response panels with their noses for a reward of diluted beef baby food (*7, 9*). Visual stimuli were then rear projected onto a viewing screen positioned 1.5 cm behind the response panels. The cats were first trained to press the panel in front of the brighter of two blue (Kodak CC50 B) patches of light [area 4.5 cm^2 (*10*)]. Only responses to the correct (brighter) stimulus were reinforced, and the position of the brighter stimulus was varied in a haphazard fashion. After they had mastered the intensity discrimination (200 trials per day, four consecutive days at $\geq$ 80 percent correct or two consecutive days at $\geq$ 90 percent correct), cats A and B were trained to discriminate blue from gray [Kodak CC50 B versus neutral densities (ND) of log 0.0, 0.5, or 1.2] and cats C and D were trained to discriminate blue from green (Kodak CC50 B versus CC50 G). In the blue versus gray discrimination the blue stimulus transmitted more light at all wavelengths from 400 to 700 nm, 400 nm for blue versus ND 0.0 and less light at all wavelengths for blue versus ND 1.2. In the blue versus green discrimination, on half of the trials blue transmitted more light than green at every wavelength, and on the other half of the trials the reverse was true (*8*). For both discriminations and all brightness relations the blue stimulus was correct and its position was varied in a haphazard fashion. Thus, a cat could not reliably select the blue stimulus on the basis of brightness or position (*10*).

Although all four cats rapidly learned the intensity discrimination (mean, 13.25 sessions) after 50 sessions of testing on either color discrimination, none of the cats had reached the 80 percent correct level of performance; they all gave a stable performance of 65 to 70 percent correct, that is, better than chance but less than criterion. This mediocre performance was maintained through changes in stimulus intensity, contrast, and pupil dilation. However, when the size of the stimuli was increased to an area of 32.5 cm^2 there was a dramatic improvement in the performance of cats A, B, and C (*11*), two of them quickly reaching the 90 percent correct level and the third stabilizing around 75 to 80 percent correct. Cat C, which was learning the blue versus green discrimination, was then transferred to blue versus gray, and cats A and B, which were discriminating blue from gray, were transferred to blue versus green. All three cats maintained high levels of performance ($>$ 80 percent correct) that indicated their ability to discriminate blue from green or gray (*8*).

We then returned cats A, B, and C to the blue versus green discrimination and began a systematic manipulation of stimulus size. A method of limits was employed so that each day a cat was given 70 trials at each of four stimulus sizes. Ascending and descending series were conducted on alternate days. After 5 days (1400 trials) of color and stimulus-size testing the cats were retrained on the originally learned intensity discrimination until criterion performance was reached (mean, 4.3 sessions). Stimulus size was then manipulated as for the color discrimination for an additional five testing sessions. As shown in Fig. 1, these cats were able to discriminate color (80 to 90 percent correct) when the stimuli were 84 to 32.5 cm^2, but their performance became progressively worse as stimulus size decreased (around 55 percent correct when the stimuli were 0.36 cm^2). These changes in stimulus size had no effect upon our ability to discriminate between the blue and green stimulus. Manipulation of stimulus size over the same range had no effect upon the cats' ability to perform the intensity discrimi-

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nation. Although there were some individual differences in the ability of the animals to discriminate color when the stimulus size was changed, the influence of stimulus size was apparent in all three animals (*12*).

We were also interested in the extent to which our results might explain both positive and negative findings of previous studies on color discrimination in the cat. Although most previous investigators (*1–6*) have used stimuli as large or larger than those of this study there has been considerable variation in the distance from the stimuli at which the cats have had to make a discrimination. All studies in which the cats were allowed unrestricted approach to the stimuli gave positive results (*4, 6*). Studies in which the Wisconsin General Test Apparatus or similar apparatus was used gave both positive (*5*) and negative (*1, 3*) results, but it is difficult to estimate the cats' response distance in these studies.

Of the three negative findings on cat color vision (*1–3*) the most difficult to explain has been the work of Gunter (*2*). Gunter's cat color discrimination experiment was the fourth in a series of papers describing investigations of the cat's absolute visual threshold, scotopic, and photopic spectral sensitivities (*13*). The findings of these first three studies have been confirmed in detail and indicate that Gunter's cats were well-trained observers. Although Gunter's square stimuli were 58 cm^2, the cats had to select the correct stimuli from a distance of 22.9 cm. Thus the stimuli subtended a visual angle of approximately 19°. At the viewing distance of this study a visual angle of 19° represents a stimulus size of approximately 1 cm^2 (*14*), a size at which our cats could not perform the discrimination at criterion levels.

The results of this and past studies indicate that although cats can discriminate color, they can do so only if the stimulus subtends a fairly large visual angle. This finding raises two interesting questions. First, what is the neurological basis of this "deficit" and second, what were the selective pressures or vacuums which account for this perceptual handicap.

It is generally believed that color information in the mammalian visual system is encoded by color-opponent receptive field organization (*15*). Color opponent receptive fields are common in diurnal species with large populations of retinal cones (*16*) but are infrequently encountered in the cat (*17*) which has comparatively lower cone densities than a diurnal primate (*18*). That the cat's low cone densities may necessitate large stimuli to discriminate color raises the question of whether a similar effect occurs in human peripheral retina which has cone densities comparable to the cat's area centralis, a possibility already entertained by others (*19*).

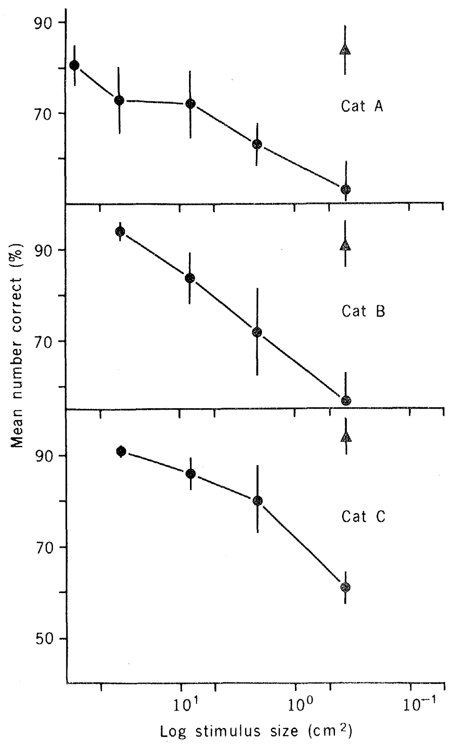

Fig. 1. Performance (mean number correct) as a function of stimulus size for intensity (triangles) and color (circles) discriminations. Bars represent 1 standard deviation. Each data point is based on 350 trials.

Because the cats in our study were making their discriminations very close to the stimuli (*14*), our larger stimuli probably represent the smallest absolute sizes for which the cat can discriminate color, that is, objects about the size of a credit card. Thus, it seems unlikely that any of the cat's prey are discriminable by color at the distance that stalking often begins. Whether this strips some cryptically colored prey of their concealment advantage when dealing with a cat is an interesting possibility.

In conclusion, it appears that color is probably an aspect of the cat's visual experience but the sensation is most likely confined to large or close objects, that is, apples are red but cherries are gray (*20*).

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10. Stimulus pairs were constructed by placing appropriate combinations of Kodak color-compensating filters and neutral density filters side by side in one 35-mm slide holder and projecting these from a carousel slide projector onto a rear projection screen (Polacoat Glass-Cat, 3M Company). Position of the correct stimulus was determined by arrangement of the filters on a particular slide. The size of stimulus viewed by the cat was controlled by obstructing part of the projected image. Slide to viewing screen distance was held constant at 57 cm.

    The color discrimination test has been considered in detail by Kicliter and Loop (*8*), and the blue versus green stimuli were the same as those described in table 1 in (*8*). The blue versus gray stimuli are new to this study but the control of brightness rests upon the same principles.

    In order to reduce the likelihood of the cats responding to inhomogeneities or patterns, for example, dust spots, on the slides the projected images were defocused and a total of at least 20 stimulus pairs, that is, 40 different stimuli, were utilized for each discrimination. Also, the slide sequence was changed during criterion level performance on the first color discrimination to eliminate the possibility that the animals had memorized the sequence. In addition to these procedural controls for fallacious color discrimination we think that the animals criterion level transfer from blue versus green to blue versus gray and vice versa indicates that their performance was based on a wavelength discrimination.

    Stimuli were calibrated with a Tektronix J16 photometer/radiometer for irradiance (probe J6502) and luminance (probe J6503). Spectral irradiance measurements were obtained with Corion interference filters. The luminance of the unfiltered light was 403 cd/m^2. The luminance in the intensity discrimination was 30.1 cd/m^2 versus 0.51 cd/m^2. The irradiance of the various stimuli in the color discrimination was measured from 400 to 700 nm in 20-nm steps.
11. The performance of cat D was unaffected by increasing stimulus size despite 30 sessions of training on the larger stimuli. When retested on the intensity discrimination this cat continued to perform very poorly and had apparently adopted a complex and counterproductive spatial strategy. This cat has been excluded from the data analysis.
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