Color Discrimination in the Cat

Abstract. *Red-green color discrimination by cats was demonstrated in a situation which effectively eliminated cues based on relative brightness. The persistence of the cat's response to cues based on brightness differences may help to account for the failure of previous experiments to show that cats can make behavioral color discriminations.*

The visual system of the cat presents a curious riddle. Anatomical structures and physiological functions requisite for color vision have been found, yet studies designed for the behavioral demonstration of color discrimination have been largely unsuccessful (*1*). The cat is usually considered functionally color-blind (*2*), although some positive results have been obtained in color discrimination experiments (*3*). Such results are frequently attributed to brightness, texture, or characteristics of the stimulus other than wavelength distribution. We have found evidence for color discrimination in the cat in an experimental situation which we believe to be free of the influence of cues other than the wavelength distribution of the stimuli. A brightness match between red and green was first obtained. This information was used to control brightness cues in the actual color discrimination study.

All training was carried out in a discrimination apparatus consisting of a starting box and 76-cm runway. Two adjacent opal plastic panels, hinged from the top, were placed at the end of the runway. The separate compartments behind the panels were backed with opal plastic. The panels were illuminated independently, each by one side of a stereo projector, through the backs of the compartments. The animals were trained to select and push open the correct panel in order to obtain a small piece of meat placed in a food dish in the compartment. The incorrect door was locked and correction of errors was permitted.

Four adult cats which had not been used for previous experiments were first trained to make a heterochromatic brightness discrimination. One panel was illuminated with red light (Kodak 25A filter) and simultaneously the other panel was illuminated with green light (Kodak 58 filter). Green and red illumination were varied from right to left in accordance with the Gellerman sequence (*4*). Brightness of the two wavelengths was also randomly presented in such a way that 50 percent of the time the luminance of the red light was greater than that of the green and 50 percent of the time the luminance of the green was greater than the red. This was accomplished by first estimating the relative luminance of the panels for the cats with each of the two color filters in the system. Calculations were based on the known characteristics of the sources; the transmittance of the color filters and the spectral response function for the cat as derived by Gunter (*5*). Results of these calculations indicated that with no neutral filters, the luminance of the green light would be greater than the red by a factor of 2. The transmittance of the green filter was therefore "equated" with that of the red by physically combining the green filter with a 0.3 neutral density filter. The luminance of either the red or the green light was then decreased, or made "darker" by the addition of a 1.0 neutral density filter.

Each cat was trained to select the darker panel independent of color or position. The training schedule consisted of five daily sessions each week with 48 trials per session. The criterion for successful learning was designated as 90-percent correct choices or more for three consecutive days. When this criterion of learning was reached, the luminance of the brighter panel was gradually reduced until the cat began to make errors—that is, demonstrated inability to distinguish consistently which of the two stimuli was the darker. Ten trials on the original dark positive schedule were given at the beginning of each session. The luminance of the brighter panel was then decreased by the addition of neutral density filters in 0.1-log unit steps. This procedure was carried out concurrently but independently for each of the two colors. Thus, on the first trial, if the red panel was brighter, luminance of this panel was decreased by adding a density of 0.1. If the cat chose the green panel, luminance of the red panel was decreased by an additional 0.1 log unit on the next trial for which the red panel was brighter. This procedure was continued until the cat chose the red panel—that is, made an "error." The luminance of the red panel was then increased by 0.2 log unit on the next trial for which it was supposed to be brighter. If the cat performed correctly on that trial the luminance was again decreased by 0.1 log unit. On each successive trial for which either color was brighter, the luminance of that color was decreased by 0.1 log unit after correct performance and increased by 0.2 log unit after incorrect performance. This method was continued until a consistent minimum difference between the luminance of each color was repeatedly reached over a period of 10 days for both red light being brighter and green light being brighter.

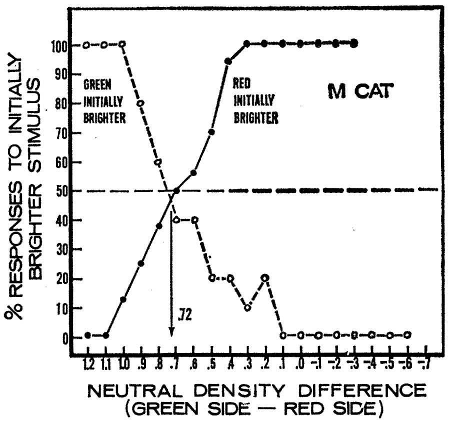

Fig. 1. The increasing percentage of responses of one cat to the initially brighter of two stimuli as its brightness is reduced by the addition of neutral filters. Cats were trained to respond to the dimmer of two simultaneously presented stimuli, regardless of color. Values on the abscissa represent neutral density on the green side minus neutral density on the red side.

At this point, the procedure was modified. Neither panel was locked. The cat was reinforced for responding to either side. Trials were continued in which additional neutral density filters in 0.1 steps were added to the side which had initially been brighter, until sufficient neutral density was added to effect a complete reversal of the cat's original preference. This was repeated on each of 10 days. Figure 1 illustrates the average increasing preference of one animal for the panel which originally had a greater luminance as its luminance was reduced by the addition of neutral filters. When the neutral density added to the green filter exceeded that added to the red filter by approximately 0.72 log unit, this animal showed almost equal probability of going to either the red or the green panel. Interpolated values of neutral density required with the green for 50 percent preference were 0.73, 0.71, and 0.68, for comparable determinations with three additional cats. It was therefore assumed that with the addition of a neutral density of 0.7 (rather than the 0.3 calculated from Gunter's data) to the green filter, transmitted light through the red filter and through the green-neutral combination would be of approximately equal brightness for the cats.

Two weeks later, three of the four original cats were trained to discriminate between red and green in the same apparatus. The fourth cat was replaced with another, cat T, which had not had brightness training. Two of the animals (M and T) were trained to approach the red panel and the other two (C and N) to approach the green. To render brightness an irrelevant cue, both red and green were presented at each of five luminances. This was accomplished by adding neutral filter values of 0, 0.2, 0.4, 0.6, or 0.8 to both the red filter and the green-neutral 0.7 combination. The range of luminance represented was approximately 3 to 20 millilamberts. Each degree of luminance of green was paired with every degree of luminance of red, resulting in 25 possible color-brightness combinations. Each of these was presented once with green on the left and once with green on the right in random sequence. The order of presentation was varied from day to day. This made a total of 50 presentations for each daily test session. For 20 of these presentations green was the darker of the two stimuli, for 20, red was the darker, and for the remaining 10 presentations, red and green were presumably of nearly equal brightness. Thus, if a cat were performing on the basis of a brightness discrimination or position, its performance with respect to color would be at a chance level. Performance of 90 percent or better on three successive days was adopted as a reasonable criterion for the demonstration of color discrimination.

After prolonged training, all four cats reached this criterion. Figure 2 shows the learning curves for two of these cats. Cat T, trained to approach red (red positive), started by achieving 42-percent correct responses and after 1450 trials demonstrated significant color discrimination between red and green. Cat N (green positive) started by getting 50-percent correct responses and reached the criterion after 1650 trials. Cat M (red positive) required 1750 trials and cat C (green positive) required 1350 trials to reach the criterion.

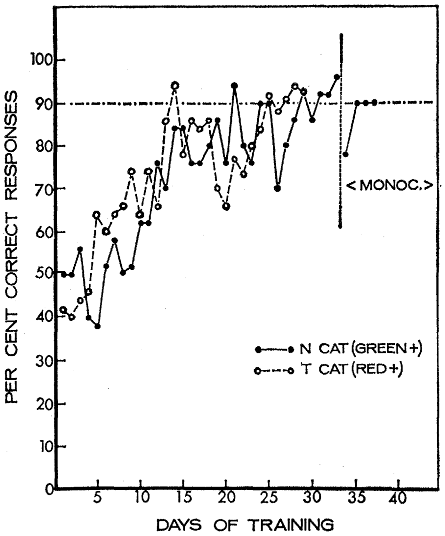

Fig. 2. Color discrimination learning curves for two cats. Cat N, trained on green positive, took 1650 trials to reach the criterion. Cat T, trained on red positive, took 1450 trials. Graph to right of vertical dotted line shows monocular performance of cat N after adaptation to a mask which exposed only the right eye.

The possibility that demonstrations of color discrimination in the cat might be the result of a difference in the apparent depth of surfaces illuminated in different colors has been suggested by Kohler (*6*). This follows from the possibility that differences in refraction of different wavelengths of light by the optical elements of the cat's eye might introduce binocular disparities which are dependent on wavelength. One method of checking this possibility is illustrated in Fig. 2. After cat N reached the criterion for color discrimination, it was adapted to a mask which occluded one eye. It was then tested monocularly for four successive days. The results (Fig. 2) afford a clear indication that color discrimination for the cat is not dependent upon binocular depth perception.

Analysis of the data trial by trial shows that at the beginning of training the cats made their choice on the basis of brightness differences rather than color. A cat would choose either the brighter or the darker of the two stimuli consistently for blocks of trials or even for a whole day's session, and then switch its response to the opposite brightness level for another series of trials. This alternation of response occurred several times and then gradually disappeared as response to the positive color cue improved. Position habits were seen infrequently, possibly because prior training with brightness matching had eliminated much of this behavior. An analysis of the color-brightness combinations for which errors were made on the three successive days on which the performance was 90 percent or more showed no systematic relation to relative brightness or position of red and green.

Additional training was given to the same cats with red and green of reduced saturation. It is of interest to consider briefly the results of this work, as they provide additional support to the results presented here. A preliminary experiment showed that the addition of rotating disks (2400 rev/min) with two open sectors to each beam of light, did not in any way disrupt the original color discrimination. Saturation was reduced by fastening a combination of neutral filters and the red or green filter over one of the open sectors in a disk, and neutral filters alone over the other open sector. The panels were thus illuminated with fused light from successive white and colored flashes at a rate of 80 per second. By varying the densities of neutral filters, it was possible to vary the relative contributions to total luminance of white and colored light. Training was continued with the desaturated red and green, varying brightness and position as in the original color discrimination training. When the contribution of colored light to total luminance was reduced to 50 percent, animals were able, with some additional training, to learn the discrimination. When the contribution of colored light was reduced to 10 percent, none of the animals learned the discrimination, even after 2000 trials. The average precentages of correct responses for the last 400 trials were: M, 58 percent; C, 62 percent; T, 59 percent; N, 52 percent. These results afford confirmation that color, and not some uncontrolled artifact, was the relevant variable in the initial color discrimination.

It is concluded from the results of these studies that cats have the ability to discriminate between red and green illumination without the aid of brightness cues. However, prolonged training is required to overcome the persistence with which the cat will respond to brightness cues. In many of the earlier studies for which negative results were reported there may have been simply an insufficient number of training trials. On the other hand, if methods used for establishing a brightness match between different colors are inadequate, an animal which is responding on the basis of brightness differences may appear to be making a successful color discrimination. This is particularly true if the range of brightness used includes both scotopic and photopic levels.

Even if the validity of the results and conclusions presented here is accepted, these results do not afford proof of any similarity between the underlying mechanisms for color discrimination in the cat and the mechanisms for color discrimination in other animals for which the capability is widely acknowledged.

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Sound-Evoked Potentials in Neocortex of Unanesthetized Opossum

Abstract. *Short-latency potentials are evoked by auditory stimuli at all loci of neocortex recorded from, including points in orbital-frontal, visual, and somatosensory areas. These potentials are similar in latency and wave form to responses obtained from the primary auditory projection area in higher mammals, but occur in widely varying spatial patterns.*

In eutherian mammals, anatomical and electrophysiological studies have shown that the sensory projection nuclei of the dorsal thalamus (medial geniculate, lateral geniculate, and ventral basal) send their axons to well-defined and restricted portions of the neocortex. Anatomical (*1*, *2*) and electrophysiological studies (*3*) with a metatherian mammal, the Virginia opossum, also indicate differential specialization of the neocortical areas with respect to sensory modality; that is, visual, auditory, and somatic areas can be differentiated. Results reported here, obtained by using the method of evoked potentials in the unanesthetized opossum, do not confirm the existence of a localized cortical auditory projection area. Instead, short-latency activity evoked by auditory stimuli appears in widely varying patterns over extensive regions of the neocortex.

Chronic implants of Nichrome wire electrodes, insulated except at their tips, were made in the neocortex of four opossums. In each animal, surface-to-white-matter pairs of electrodes were implanted at loci evenly distributed over the entire lisencephalic neocortex of one hemisphere. Electrode positions were verified histologically.

After recovery from surgery (about 2 weeks), animals were adapted to the sound-treated recording room and small shielded cage. With the opossum apparently at ease and fully adapted to the situation, bursts of clicks were presented to elicit the evoked potentials, which were displayed on a four-beam oscilloscope. Several daily recording sessions were given for each opossum.

Short-latency evoked potentials were recorded from all electrode positions in all opossums. No recording site was active all the time, but evoked potentials could always be elicited from some loci. Figure 1 shows typical examples of the short-latency evoked potentials obtained from opossum No. P1. The region from which auditory evoked potentials were recorded from this opossum while anesthetized with sodium pentobarbital is also indicated on Fig. 1. This restricted "auditory" area has been described previously (*3*) and corresponds with cytoarchitectural (*2*) and retrograde-degeneration (*1*) delineations.

In the awake opossum the same types of short-latency evoked potentials appear in "non-auditory" and classically defined "auditory" neocortex.

Patterns of evoked activity varied (i) in the onset latencies of the evoked potentials and (ii) in the spatial distribution of activity. Table 1 shows the distribution of latencies falling in the range below 20 msec in opossum Pl, a typical case. Slow waves with latencies greater than 20 msec were often evoked, but only the shorter-latency, faster wave forms are under consideration here. Classically defined auditory cortex does not differ significantly from other cortex with respect to latencies of evoked potentials.

Table 1. Observed onset latencies of evoked potentials in opossum No. P1.

Electrode position	Onset latencies (msec)														
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1								x	x						
2						x		x	x	x		x			
3								x	x		x				
4							x	x							
5			x					x	x	x					
6								x	x						
7			x					x	x			x			
8			x				x	x	x	x		x			
9						x		x	x	x					
10						x		x							
11									x		x	x			
12								x	x	x					

Table 2. Observed dissociations of evoked potentials for electrode pairs in opossum No. P1.

Positions, potentials present	Positions, potentials not present											
	1	2	3	4	5	6	7	8	9	10	11	12
1					x			x		x	x	
2	x		x		x	x	x	x		x	x	
3	x			x				x			x	
4	x	x	x					x			x	
5						x				x		
6		x			x							
7		x	x		x	x		x			x	
8	x	x					x			x	x	
9					x		x	x		x	x	
10						x			x			
11		x	x		x	x				x		x
12			x			x				x	x	