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# Participation of the Green-Sensitive Receptor in the Cat Retina in Light Discrimination

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**In behavioral experiments the participation of the green-sensitive receptor of the cat retina in color discrimination was examined. In paired presentation of color stimuli using the method of conditioned feeding movement, in 3 cats the authors discovered a differentiated reaction to stimuli which identically excited both the red-sensitive and the blue-sensitive receptors and differed from each other only in excitation of green-sensitive receptors. The fact that such a differentiated reaction can be elaborated indicates that the visual system of the cat contains a green-sensitive receptor and that these animals may actively use it in their behavior.**

Key words: color vision, green-sensitive receptor, cat, behavior.

In the last thirty years our concepts of the color differentiation capacities of the cat have undergone a substantial evolution. Right up to the 1960's the capacity of cats for light differentiation were doubted. This was based on the results of behavioral experiments in which the researchers

were not able to elaborate a differentiation reaction to color [11, 12, 16]. However, subsequently it emerged that cats can be taught after all to solve problems in color differentiation [3, 4, 14, 15, 19].

As a result of the first electrophysiologic studies of the visual system of the cat [8, 10] the suggestion arose that the basis of color differentiation in these animals may be two light-sensitive receptors: the rod photoreceptors, governed by rhodopsin, and the longer-wave, red-sensitive cones. Such a concept of separate scotopic and photopic visual systems with little connection to each other [2, 8] corresponds well with the fact that in cat behavior it is difficult to develop color differentiation. However, subsequently the existence of a second, blue-sensitive, cone receptor was demonstrated [5,9,17,21]. And, finally, again on the basis of electrophysiologic experiments [6, 18], the hypothesis was put forth that in the cat retina there exist not two, but three cone receptors. The third, a green-sensitive cone receptor, has approximately the same spectral sensitivity as

the rods.<sup>1</sup> Thus, in accord with these data, a cat must not only have the capacity for light differentiation, but even may be a trichromat.

The goal of the present study was to test the participation of the green-sensitive receptor in color differentiation in the cat in behavioral experiments. The most simple approach for this purpose would be to attempt to develop a differentiating reaction to stimuli that are identical both for the blue-sensitive and the red-sensitive receptors and differ only in excitation of the green-sensitive receptors. However the task is complicated by the fact that we do not know the curves of spectral sensitivity of the cat receptors with sufficient precision. This leads to some error in calculation of their stimuli. As a result, one cannot be certain that the stimuli used are precisely balanced in excitation of blue- and red-sensitive receptors, and, consequently, that the cat in his choice is not prompted by small (uncontrollable) differences in stimuli in excitation of these two receptors.

It would be possible to solve this problem in conditions of unavoidable imprecision in determination of receptor exciters if the cat is taught to pay no attention to small differences in color. For this purpose it is necessary to use not two stimuli, to which correspond two points in the color space, but two groups of stimuli that differ mainly in excitation of the green-sensitive receptor and fall in two different local areas of the color range. The dimensions of these regions should be more obvious than the possible inaccuracies in assessment of excitations of blue- and red-sensitive receptors. If it is possible to teach the cat to differentiate any stimulus from one region of the color space from any stimulus from the other region, then it would be possible to confirm that the green-sensitive receptor of the cat participates in the processes of color differentiation.

### Method

As stimuli in our experiments we used uniformly colored mat-finish paper measuring 15 × 15 cm, illuminated by an incandescent lamp. Their reflection spectra were measured on the SF-10 spectrophotometer. Using spectral reflection coefficients ( ), we calculated the relative excita-

tion of R, G, and of three cat receptors in response to illumination reflected by the paper, according to the following formulas:

$$R = a_R \int_{400}^{750} S(\lambda) \rho(\lambda) r(\lambda) d\lambda,$$

$$G = a_G \int_{400}^{750} S(\lambda) \rho(\lambda) g(\lambda) d\lambda,$$

$$B = a_B \int_{400}^{750} S(\lambda) \rho(\lambda) b(\lambda) d\lambda,$$

where S( ) is the spectrum of illumination, taken to be equal to the spectrum of the standard source A MKO1931; r( ), g( ) and b( ) are the curves of the spectral sensitivity of the receptors in the cat eye; the standardizing multiples a<sub>R</sub>, a<sub>G</sub> and a<sub>B</sub> were selected so that for an ideally white surface in which ( ) = 1, the values of the corresponding color coordinates were equal to 100.

The three numbers obtained – R, G and B – determine the color of the stimulus in a given illumination for the cat's system of color vision (in the event that it is a trichromat). Color may be prerepresented by a point in the corresponding three-dimensional color space or in some projection of it. In the instance where the cat does not have a green-sensitive receptor (is a dichromat), the value of the coordinate G is insubstantial, the color of the stimulus is characterized only by a pair of numbers: R and and may be prerepresented by a point of two-dimensional (dichromatic) color space.

The curves of spectral sensitivity of the cat eye receptors were calculated according to Dartnall's nomogram [7] for absorption spectra that correspond to light-sensitive pigments. The light transmission spectrum for the cat lens was also calculated [20].

The pigment absorption spectrum of the green-sensitive cones and rods of the cat (rhodopsin) has a maximum of approximately 500 nm [8] and correlates well with Dartnall's nomogram. The position of the maximums of the two remaining receptors is less precisely known, in the literature most often the values 450 and 555 nm are given [6, 9, 21]. However, taking into account the possible inaccuracy of the data obtained in

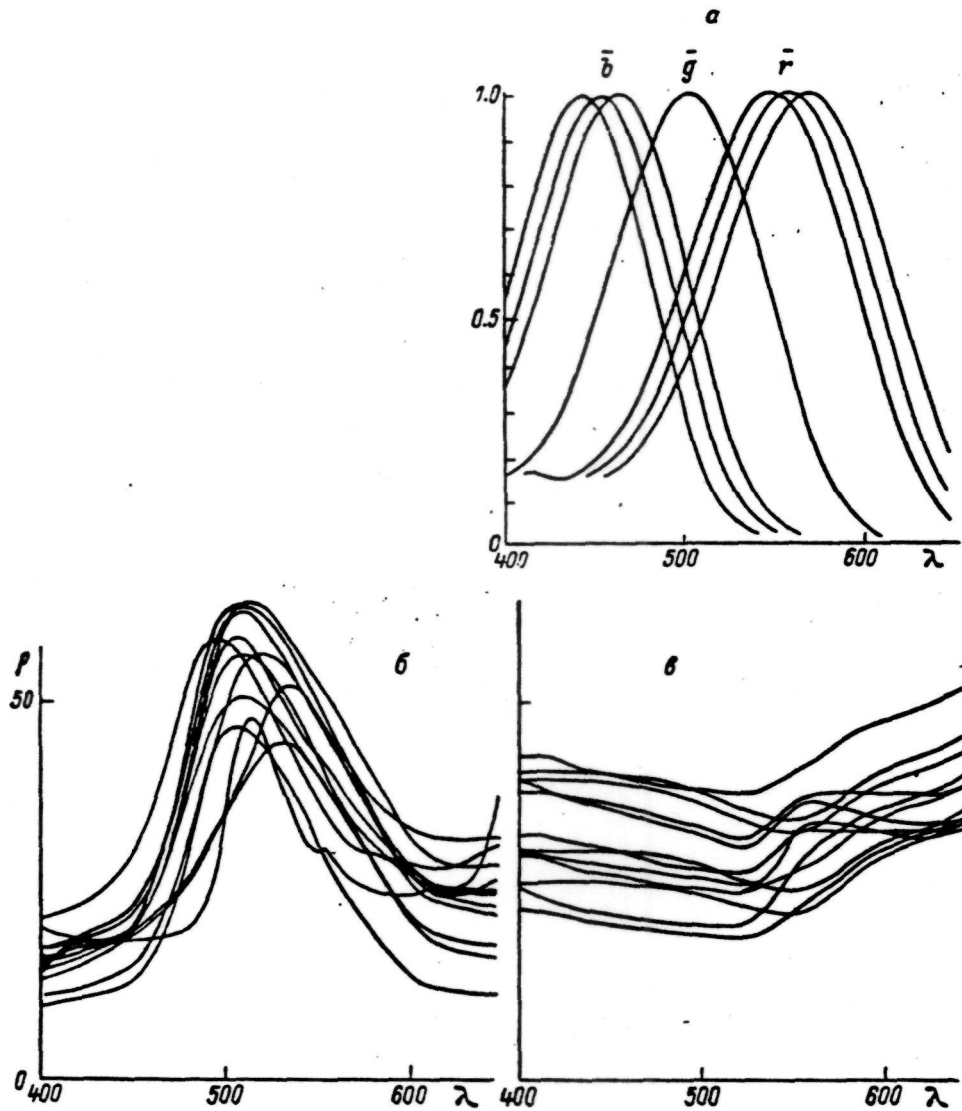


Fig. 1. Suggested curves of the relative spectral sensitivity of cat eye receptors (a) and the spectral reflection coefficients (in %) of green (b) and purple (c) stimuli.

electrophysiologic experiments, for each of these receptors three sensitivity curves were used in the calculations. The mean of these had maximums at 450 and 555 nm, and the ( $f_{max}$ ) of the two remaining curves differed by  $\pm 10$  nm (Fig. 1,a). The values for the coordinates R and  $f_{max}$  calculated according to these curves enable determination of the limits of scatter of these values caused by the imprecision of our values  $f_{max}$  for the cat receptors, possible deviations of their curves of spectral sensitivity from the nomogram curves [8], as well as by some deviations of the spectrum of

the applied light source from the spectrum of light source A.

Two groups of 12 stimuli were prepared, which differed in excitation of the green-sensitive receptor: green stimuli strongly reflecting in the green region of the spectrum (Fig. 1,b), and purple stimuli having weak reflection in the same region of the spectrum (Fig. 1,c). In their remaining two color coordinates these stimuli little differed from each other. Fig. 2,a presents the positions of the colors of the stimuli used in the dichromatic plane RB. The indefiniteness of the values of the color coordinates R and  $f_{max}$  does not allow a

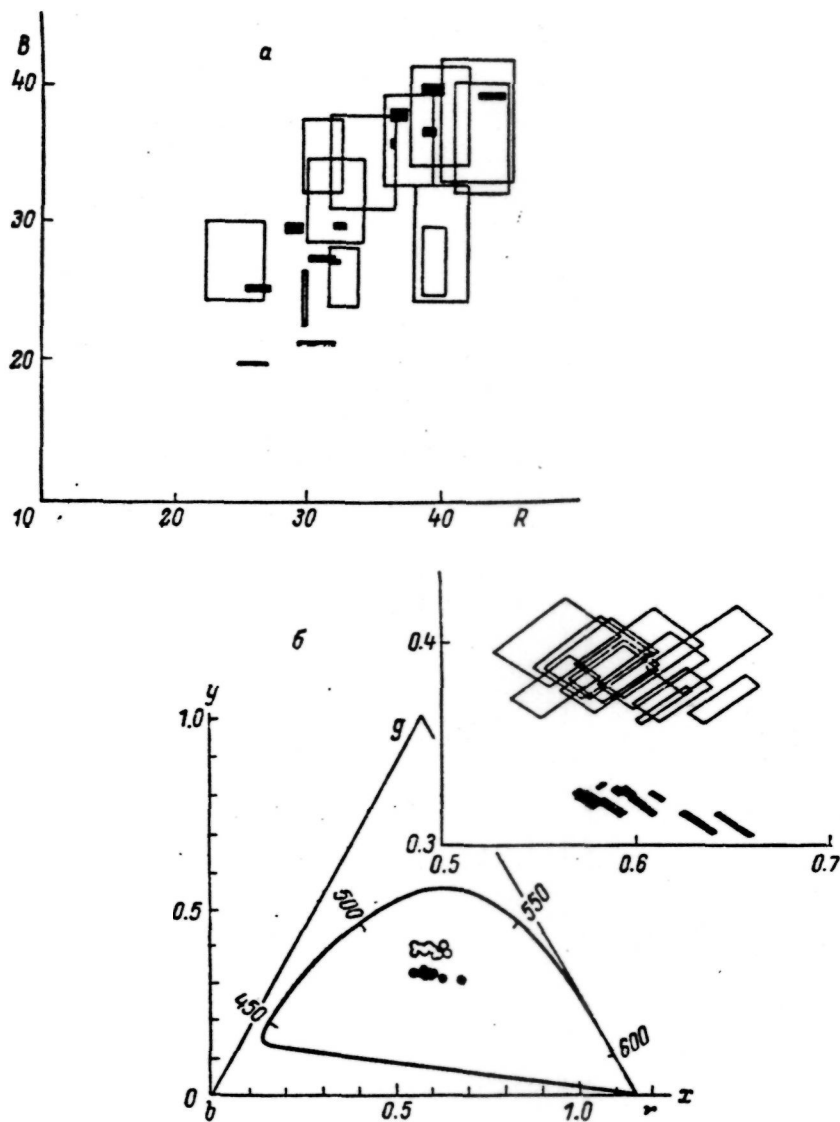


Fig. 2. Position of the stimulus colors in the color space of the cat.

a - Projection to the dichromatic coordinate plane RB; the rectangles are the limits of the possible dispersal of color coordinates of green (white rectangles) and purple (black rectangles) stimuli, b - Central projection to the diagram of coloricity for the system of color vision of the cat in the color triangle centered relative to the standard source A MKO 1931. Lines of spectral and purple colors are plotted; the central part of the diagram is presented in the inset, where the possible dispersal of the coordinates of coloricity of these same stimuli is shown with quadrangles.

precise indication of the position of the stimulus color. Therefore, in the drawing each stimulus corresponds to a certain rectangular area of the color space in which the color of a given stimulus may fall. As can be seen from the drawing, the

purple and green stimuli occupied one area of the dichromatic plane RB. The light of achromatic (gray) surfaces, reflecting from 20 to 45% of the incident light, should fall in the same region. Therefore, for the dichromatic cat, which does not

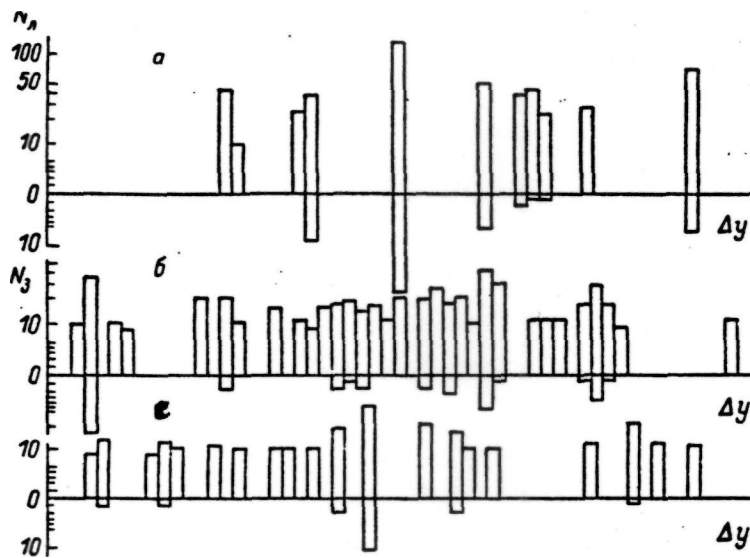


Fig. 3. Results of testing of three cats trained to select purple stimuli when presented in a pair with green.

The diagram shows the results of testing for these pairs, in which the stimuli were differentiated by the cats at a significance level of 0.01. The height of the columns corresponds to the number of selections; above - purple, below - green stimulus in a pair. Other explanations are in the text.

have a green-sensitive receptor, our purple and green stimuli should appear almost identically gray in color, slightly differing mainly in brightness. At the same time, in the three-dimensional color space of the cat, because of the differences in the green coordinate, these groups of stimuli occupied two substantially different areas (Fig. 2,b).

Behavioral experiments were set up on 3 adult cats (1 female and 2 males) using the conditioned feeding motion method. The experiments were carried out in a cage with a starting box, partitioned off by a raisable door. At a distance of 110 cm from this door, on the opposite side of the cage in its lower left and right corners there were two feeders. 70 cm away from each other were rectangular openings measuring  $15 \times 11$  cm, and closed by vertically rising transparent doors made of organic glass. The wall itself was pasted over with white paper, while behind the transparent doors were placed the stimuli - colored pieces of paper. The whole scene was illuminated by a 100 watt in-

candescent bulb. The intensity of the light on the surface of the stimuli was approximately 25 lux.

The procedures for training and testing already trained cats consisted of the following: Two stimuli were simultaneously presented to the cat: a fortified purple stimulus and a differentiated green stimulus. The triggering signal was opening the door of the starting box. The cat was supposed to rush to the feeder behind which a purple stimulus was presented, and, having opened the door of the feeder by pressing it with a paw or muzzle, gain access to the piece of meat. If the wrong door was chosen, it did not open, and the cat was driven into the starting box without fortification. Before the tests meat was placed in both feeders. The cats were presented with stimuli approximately 20 times per day. The interval between the starts was approximately 2 min. The stimuli changed places in a certain sequence, which ruled out the possibility of development of some kind of simple strategy, a type of preference for one side or sequential change of direction.

The training usually was conducted with one pair of stimuli until achievement of a statistically reliable level of difference. In the testing various combinations of purple and green stimuli were presented from our group, in which each purple was presented in combination with many different green stimuli. This ruled out the possibility of choices being made only because of brightness, inasmuch as in some pairs the purple stimulus was brighter, and in some others darker, than the green stimulus or any of the possible light-sensitive receptors of the cat. The degree of reliability of the difference was assessed for each pair of stimuli separately. We considered the stimuli reliably differentiated by the cat if the hypothesis of their equally probable selection was repudiated with a significance level of 0.01.

### Results of the Investigation

One of the cats used in the experiments (female N) had preparatory experience: over the course of 8 months she worked in several different arrangements with other stimuli of similar colors. By the time she was tested in our experimental arrangement she had achieved an 85% level of differentiation. Without additional training, testing in the new arrangement for green-purple pairs from our set (Fig. 1, b, c) gave the following results: The cat was presented with 30 different pairs of stimuli. The total number of presentations of these pairs was 630. A purple (fortified) stimulus was selected in 555 cases, which comprise 88% of the total number of selections. The number of presentations of 11 pairs was sufficient to confirm that the purple stimulus in them was reliably preferred over the green. The remaining pairs were presented fewer times; in none of these pairs did the cat show a preference for the green stimulus.

The results of this series are presented in Fig. 3, a. In this diagram for definiteness the pairs are arranged according to the degree that the components of their stimulus differ in relative excitation of the green-sensitive receptor-according to difference in the coordinate  $y$  on the diagram of chromaticity (Fig. 2, b). The height of the columns in Fig. 3 is proportional to the number of selec-

tions: above - purple, below - green stimulus in each pair presented.

Cat Sh. had not been used previously in experiments. He was trained in the work for over 1 month. The training was carried out on a pair comprised of the brightest purple and brightest green (Fig. 1, b, c). In the process of training he received 240 presentations. Having become accustomed to discriminating purple and green stimuli received in this pair, he was transferred to other pairs practically without additional training. A total of 48 different pairs were presented to him in the test series of experiments. Of the total number of 656 presentations, green stimuli were selected a total of 57 times and purple 599, which makes up 91% correct reactions; 32 pairs were presented a sufficient number of times for confirmation of the fact that the purple stimulus was reliably preferred over the green. The results of the experiments undertaken on this cat are presented in Fig. 3, b.

Cat M. had not been used in experiments prior to this. He was trained for approximately 3 weeks. In the process of training he received over 200 presentations of one pair of stimuli, after which the green stimulus was replaced with another, brighter one, and this pair was presented to him for an additional 100 times. In the test series 27 pairs were shown. The total number of presentations was 360, of which in 332 cases the purple was chosen and in 28 cases - green, which comprises 92% correct choices. In 20 pairs of purple stimuli there was a reliable preference for green. The results of this series are presented in Fig. 3, c.

### Discussion of the Results

With respect to color vision in the cat, in the literature there has been a long-standing opinion that it is rather difficult to develop a reaction to color in this animal, and on this basis it was concluded that color has a secondary importance in the cat's life. In actual fact, in the first successful experiments it was necessary to give up to 1600 presentations in order to develop a reliable differentiated reaction to color [19]. Subsequently, however, this number steadily declined, and in our experiments with cats fewer than 400 presentations were required (see also [1]). In part this was

determined by the selection of animals according to ability to be trained in an experimental situation, since not all cats are equally trainable. We even had cats which could not be trained at all to discriminate purple stimuli from green. However, this does not at all mean that the cat's green-sensitive receptor did not participate in the processes of color discrimination. The fact of the matter was, as a special test series revealed, this cat also could not be trained to discriminate blue stimuli from orange, which obviously differ in excitation of other receptors of the system of color vision of the cat.

Also essential for successful training of cats in color discrimination are the angular dimensions of stimuli, a fact to which Loop and co-authors were the first to turn their attention [14]. Cats were successfully trained in those experiments where stimuli with large angular dimensions were used, or, as in our experiments, the animals had the opportunity to approach closely to the stimuli, in this manner regulating their angular dimensions for themselves.

The capacity of the cat to be trained to differentiate specially selected purple stimuli from green, which was demonstrated in our experiments, indicates that these animals in solving color discrimination problems actively make use of green-sensitive receptors in their behavior, insofar as the remaining two receptors can provide discrimination of these colors. The mesopic lighting conditions in these experiments do not permit an answer to the question of whether this receptor is determined by the work of the assumed green-sensitive cones [6] or whether we are dealing with rods. However, a hypothesis of the participation of rods in color discrimination in the cat was advanced by Daw and Pearlman [8] at the time that only one long-wave cone receptor was known and otherwise it was impossible to explain the capacity for color discrimination. Insofar as at the present time it has been shown that in the cat retina there are green-sensitive cones, drawing upon rods to explain its color vision seems superfluous

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