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14. The reason we find a preponderance of off-center cells is not known. Other reports of relative proportions of on- and off-center goldfish ganglion cells range from approximately equal [N. Daw, *J. Physiol.* **197**, 567 (1968)] to proportions similar to what we report (*11*).
15. These response summation functions were generated from the smooth stimulus response curves because of the high variability present in the individual data points. Nevertheless, the effects we describe for the smooth curves can generally be discerned when the response summation function is generated directly from the raw data. As a further test of the validity of our conclusions we compared the difference in the responses under the two stimulus configurations (separated or overlapped) when the stimuli were presented simultaneously versus the difference in the summed responses when the rod and cone stimuli were presented singly. This comparison tests whether the differences observed as a function of stimulus configuration when the stimuli are simultaneously presented are significantly greater than the random differences that are induced when the individual stimuli are presented separately. A paired *t*-test, calculated for all 12 cells at all stimulus attenuations, showed this difference to be highly significant ($t = 3.401$, d.f. = 85, $P < .001$).
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18. If nearby receptors combined their responses locally through gap junctions, the nonlinearity inherent in the receptor function itself would produce ganglion cell responses to two stimuli close together that would be smaller than if they were separated.
19. In the cat, it has been shown that the axon of the horizontal cell is too long and thin to be useful in transmitting information by electrotonic conduction, so that the cell is effectively broken up into independent rod and cone portions [R. Nelson, A. V. Lützow, H. Kolb, P. Gouras, *Science* **189**, 137 (1975)]. In fish, there are separate rod and cone horizontal cell systems [W. K. Stell, *Am. J. Anat.* **121**, 401 (1967)], which have been shown not to have direct connections with each other [A. Kaneko, *J. Physiol.* **213**, 95 (1971)].
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Trichromatic Vision in the Cat

Abstract. *Many cat retinal ganglion cells (types X, Y, and W) have inputs from three separate cone systems. Those with peak sensitivities at 450 and 555 nanometers have been previously shown. A λ_{max} cone with a peak sensitivity of 500 nanometers can be differentiated from other cones by spectral sensitivity and from rods by receptive field differences, functioning above rod saturation levels, and by cone-rod breaks in the dark-adaptation curves. The similarity of the three-cone cat retina to the extramacular retina of the rhesus monkey suggests that the cat may have photopic trichromatic vision.*

The original electrophysiological demonstrations of color discrimination in the cat by Granit (*1*) were later questioned, largely because no equivalent psychophysical evidence could be found (*2*). Some success was later achieved in training cats to discriminate colors after many trials (*3*, *4*). Recently Daw and Pearlman showed some opponent color responses in the lateral geniculate with 450-nm and 555-nm cone systems, although neurons connected to the 450-nm cone system were found only rarely (*4*). The discrepancy between the abundance of color mechanisms found by Granit and the paucity or limited range of such mechanisms as reported by others (*4*-*6*) has remained unresolved. In the search for new data, we have examined the retina by electrophysiological techniques and have found abundant evidence for three separate cone systems at the ganglion-cell level.

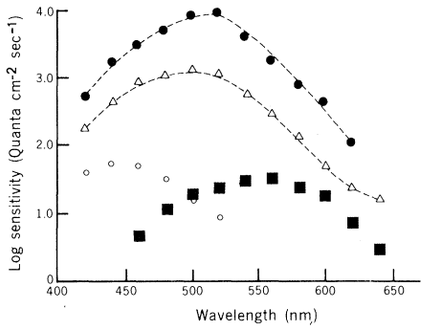

Fig. 1. Spectral response curves from retinal ganglion cells. Inputs from cone systems with peak sensitivities (λ_{max}) of 450, 500, and 555 nm as well as the 500-nm λ_{max} rod system. All three cone systems (○, on-surround, light-adapted X cell; ■, on-center, light-adapted Y cell; and △, on-surround, light-adapted W cell) can be found at photopic light levels well above rod saturation (*11*), but the rod system (●, on-surround, dark-adapted W cell) is found only at low light levels after prolonged dark adaptation. For the X cell, 0.0 log units of sensitivity equals 9.0×10^{13} quanta cm^{-2} sec^{-1} (38 μW cm^{-2} at 500 nm) with a Wratten filter No. 15 background at 6.3×10^{3} quanta cm^{-2} sec^{-1} (20 μW cm^{-2}) on the retina. For the Y cell, 0.0 log units of sensitivity equals 3.5×10^{14} quanta cm^{-2} sec^{-1} with a Wratten filter No. 47A background at 1.3×10^{13} quanta cm^{-2} sec^{-1} (5.1 μW cm^{-2}) on the retina. For the W cell, 0.0 log units of sensitivity equals (i) 3.5×10^{15} quanta cm^{-2} sec^{-1} in the light-adapted state with a Wratten filter No. 30 background at 4.1×10^{13} quanta cm^{-2} sec^{-1} and (ii) 8.8×10^{1} quanta cm^{-2} sec^{-1} in the dark-adapted state with no background. All radiation values refer only to the spectral band between 420 and 660 nm.

A Maxwellian-view optical system was used in order to provide the necessary intensity for spectrally limited background illumination as well as spatially localized test patterns. A simple projection system was added to an optical stimulator previously described by Wagner *et al.* (*7*). The animal preparation and recording methods were conventional. Cats were anesthetized with ether, and 5 percent lidocaine was applied to all incisions and pressure points. Paralyzing agents, gallamine triethiodide and curare, were introduced into a cannulated forelimb vein. The animal was intubated and then artificially ventilated with a mixture of 70 percent nitrous oxide and 30 percent oxygen. An application of 1 percent atropine dilated the eye and paralyzed accommodation. The eye was immobilized with a retaining ring sutured to the sclera. Levick-style tungsten-in-glass microelectrodes (*8*) were advanced into the eye through an incision in the sclera in order to make extracellular recordings from isolated retinal ganglion cells. Vigorously responding "off"- (or "on"-) center cells which had on (off) inhibition to a spot flashed in the center were classified as X if they maintained a response to a centered light spot (on center) or dark spot (off center), as long as the light was on; they were classified Y if their response was phasic, that is, if the firing returned to a maintained level in 2 seconds or less. These classifications are based on the scheme used by Stone and Fukuda and by Cleland *et al.* (*9*), which grew from (but may not exactly correspond to) Enroth-Cugell and Robson's linear (X) and nonlinear (Y) terminology (*10*). Cells that responded sluggishly and lacked postexcitatory inhibition were classified as W if they had large fields, slow activity, and low-frequency action potentials with long time constants (*9*). It was impossible to confidently classify almost half of the cells according to these

rules (*11*). This large number of unclassified cells represents to a large extent our own desire to follow the classification scheme rigidly. Any cell that did not correspond exactly to the rules was not labeled. The problem of classification of retinal ganglion cells in the cat retina is a hotly debated subject (*12*), and our work at present does little to clarify it.

Threshold spectral sensitivity curves were plotted in both the center and the surround with various spectral backgrounds. Three independent cone systems were present with peak sensitivities at 450, 500, and 555 nm (Fig. 1). All ganglion cells examined received input from at least two of these cone types. Contributions from all three cone systems were found in X, Y, and W classes. In general the contributions were additive, but in an occasional ganglion cell, the various inputs were antagonistic. The cone type most often found has a spectral sensitivity peak at 555 nm and was found in the center and surround of most ganglion-cell receptive fields. The 450-nm cone system can be easily isolated with an intense yellow background and was found in about half of the ganglion cells sampled. The spectral sensitivity of the 450- and 555-nm cone systems corresponds to those previously described (*5*).

To our knowledge, the cone system peaking near 500 nm has not been previously reported. Its spectral sensitivity is similar to that of the rod. It can be differentiated from the rod response because it responds when the intensity of the background is well above the rod saturation level (*13*). Also, at photopic levels a number of cells have a prominent 500-nm response in the surround across at least 2 log units of background intensity, whereas no responses from the antagonistic 500-nm system are evident in the center. After dark adaptation, these cells exhibit both center and surround responses with the same (rod) spectral sensitivity. Furthermore, some cells have the same spectral sensitivity in the light-adapted and dark-adapted states and produce a dark-adaptation curve that shows a typical cone-rod break (Fig. 2). In these cells, the spectral sensitivity curve in the light-adapted state has a peak absorption near 500 nm (Fig. 1); the spectral sensitivity after lengthy dark adaptation has a similar peak. During dark adaptation, the threshold sensitivity to test lights at 460, 500, and 620 nm showed a constant relative relationship appropriate for a spectral sensitivity peaking near 500 nm. This result indicates that the spectral sensitivity remains unchanged during dark adaptation, in contrast to the change in the cone-rod break time as a function of the stimulus wavelength as shown with a 555-nm cone and a 500-nm rod combination (dashed lines, Fig. 1). A word of caution is necessary at this point. We have assumed that the receptor responsible for the peaking of the photopic input near 500 nm is a cone; however, we have not anatomically identified this receptor. It is possible, although unlikely, that a special type of rod could retain its sensitivity at photopic levels as well as dark-adapt in a conelike manner. The important point is that this receptor, whatever its anatomical attributes, is functionally equivalent to a cone, and we will denote it as such for convenience.

The 500-nm cone system contributes to a majority of the ganglion-cell receptive fields, in either the center or the surround, usually in both. Usually the 500-nm and the 555-nm cone systems are additive (on with on, off with off), with the center always opposed to the periphery. In contrast, the 450-nm cone system appears to lack the concentric spatial opponency usually found in the 500-nm and 555-nm cone systems. The 450-nm cone will have the same influence as the other cone or cones in one part (center or surround) of a receptive field; but in the other part, it will have no influence, or an opponent one, to the other cones in that part of the receptive field.

The differential spatial organizations of the contributions of these three cone types in retinal ganglion-cell receptive fields provide a basis for trichromatic vision in the cat. In many ways the functional organization of the ganglion cells in the cat retina resembles that reported in the monkey by Gouras (*14*). Confirmation of this interpretation is added by Kolb and her associates by a description of the anatomical similarity between the cat retina and the paramacular monkey retina (*15*). Perhaps with the techniques of chromatic and spatial isolation combined with dark adaptation, a similar triple-cone organization may be found in other mammals, for example, the ground squirrel (*16*), usually regarded as color-deficient.

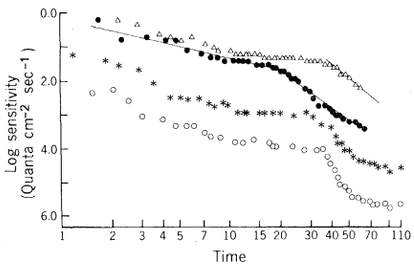

Fig. 2. Dark-adaptation curves for retinal ganglion cells. The Y-cell on-center curves (●, 500 nm; △, 620 nm) show the course of dark adaptation for a 555-nm λ_{max} cone system that shifts its spectral sensitivity into a 500-nm λ_{max} rod system after dark adaptation. The shift to the rod response is influenced by the wavelength of the test stimulus. With a 620-nm test stimulus, the cone system is more sensitive than the rod system for nearly 40 minutes; with a 500-nm test stimulus, the rod becomes more sensitive than the cone within 25 minutes. The W-cell on-surround dark-adaptation curves (○, 500 nm; ⁎, 620 nm) show a 500-nm λ_{max} cone system coupled to a 500-nm rod system. There is no change in spectral sensitivity with dark adaptation, although a clear rod-cone break can be seen at about 35 minutes. Changes in the wavelength of the stimulating light do not influence the time of the rod-cone break. This result confirms that there is not a change in spectral sensitivity accompanying the shift from cone to rod types of ganglion-cell responses. The spectral responses of the W cell before and after dark adaptation are shown in Fig. 1. The spectral response curve of the Y cell in the dark-adapated state resembles the dark-adapted W cell in Fig. 1, and in the light-adapated state, the Y cell in Fig. 1. The Y cell was light-adapted for 6 minutes with Wratten filter No. 30 at 4.3×10^{14} quanta cm^{-2} sec^{-1}, and the W cell with a Wratten filter No. 30 at 2.6×10^{14} quanta cm^{-2} sec^{-1} for 15 minutes. For the Y cell, 0.0 log units on the sensitivity scale is 3.5×10^{12} quanta cm^{-2} sec^{-1}; for the W cell, 7.0×10^{14} quanta cm^{-2} sec^{-1}. The 500-nm background curves ● and ○ have been displaced upward 0.6 log unit for comparison purposes. All radiation values refer to the spectral band between 420 and 660 nm.

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11. Fifty-four cells were sufficiently tested to allow complete categorization with all input spectral sensitivity and dark-adaptation characteristics

available. Approximately 33 percent were X category, 25 percent were Y, 6 percent were W, and about 40 percent were unclassified. All cells had input from the 555-nm cone system. More than 85 percent had inputs from the 500-nm cone system. Approximately 50 percent had input from the 450-nm cone system. No striking patterns have yet been identified in the distribution of any particular cone system among the on-center or off-center types in each category.
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The Photographic Determination of Group Size, Composition, and Stability of Coastal Porpoises (*Tursiops truncatus*)

Abstract. *During a 21-month study, 53 individual bottle-nosed porpoises were recognized by photographs of their dorsal fins. They traveled in small subgroups (mean size = 15) composed of a stable core of five animals plus other individuals that varied greatly from sighting to sighting.*

Little research has been done on the group composition and dynamics of wild porpoises (*1*). This lack results in part from the difficulty of sighting and resighting porpoise groups in the open ocean, and in part from the difficulty of identifying individuals within a group. While studying South Atlantic bottle-nosed porpoises (*Tursiops truncatus*), which periodically came within sighting distance of the Argentine coast (42°23′S, 64°3′ W), we developed a simple photographic technique to record individuals by their natural markings.

The trailing edge of a bottle-nosed porpoise's dorsal fin is very thin and is readily tattered during the animal's life. Since this tissue apparently does not regenerate, prominent nicks and scars that have lasted more than 2 years are seen on almost all animals (Figs. 1 and 2). As well, pigment spots and bite marks made by conspecifics are often found on the dorsal fin and elsewhere, but these usually last for only about 6 months to 1 year.

From August 1974 through March 1976, *T. truncatus* passed by our land observation point on 191 of 433 days on which observations were made. On approximately 150 days, we took 35-mm still camera photographs (with lenses ranging from 50 mm to 1000 mm in size) of individual porpoises from land, from a small rubber boat (3.5-meter Zodiak), or both. We took more than 15,000 photographs, from which we identified 53 ani-

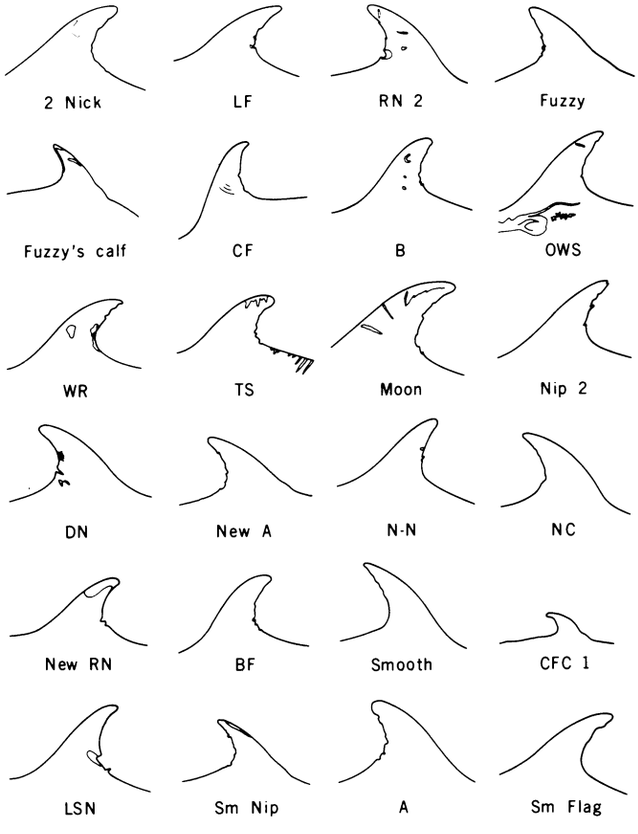

Fig. 1 (left). A sample of 24 fin variations found within the population. Lines within the fin boundaries represent light pigment spots or scar tissue. Fig. 2 (right). Three individual porpoises followed photographically through time. Compare these fins with the corresponding line drawings of Fig. 1. The fin shape and trailing edge nicks appear to be relatively stable.