The findings presented in Figs. 1 and 2 support the idea that, with respect to transmitters, two types of amacrine cells exist in the mud puppy retina. Each of these cells is inhibitory to on-off ganglion cells, but it is not certain whether there are significant physiological differences between the ganglion cells sensitive to strychnine and those sensitive to picrotoxin (or bicuculline). In the rabbit, intravenous injections of strychnine and picrotoxin had selective effects on the properties of ganglion cell receptive fields. Picrotoxin blocked motion selectivity, whereas strychnine blocked some features of other types of ganglion cells. Wyatt and Daw (*13*) concluded, as we do here, that different glycine- and GABA-releasing amacrine cells are required to explain these results.

Since most on-off ganglion cells are sensitive to both glycine and GABA, the fact that a particular cell is almost entirely influenced by one or the other implies a high degree of spatial separation in the operation of the two transmitters. It is possible that spatial separation could be based on differences in receptor distribution between dendrite and soma. Alternatively, isolation of synaptic elements by glial processes, aided by glial uptake of amino acid transmitters, could serve as a spatial buffering mechanism to maintain relative independence in transmitter systems. It seems unlikely, however, that the spatial separation of GABA and glycine action is complete. In all recordings, GABA and glycine antagonists enhanced light-evoked responses regardless of whether the agent abolished the IPSP's. Input resistance measurements show that this enhancement is associated with an increase in input resistance of the cell. It is possible, therefore, that both glycine and GABA are released in the dark, and light-evoked increases are superimposed on a continuous low level of transmitter release (*14*). A mechanism that could account for this release is suggested by experiments which demonstrated that amacrine cells are depolarized in the dark by an excitatory transmitter released by the hyperpolarizing bipolar cell (*15*). This possibility implies a subtle control system which is influenced by states of dark and light adaptation and regulates the efficiency of synaptic input to the ganglion cells.

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11. Both GABA and glycine affect amacrine and bipolar cells and one type of unidentified neuron. The action of GABA and glycine is differential with respect to bipolar cells. The depolarizing bipolar cell is more sensitive to GABA and the hyperpolarizing bipolar cell is more sensitive to glycine.
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14. Figure 1 shows that the initial action of GABA and glycine antagonists results in enhancement of EPSP's and IPSP's before any blocking action is evident. Since the intracellular recordings are probably from the soma of ganglion cells, it is possible to explain these results by assuming that the increased resistance reflects a block of continuous GABA or glycine action at the level of the soma, which initially enhances the EPSP's and IPSP's. As the antagonists diffuse to the dendrites, the primary site of synaptic input, IPSP block is obtained.
15. R. F. Miller and R. F. Dacheux [*J. Gen. Physiol.* **67**, 639 (1976)] suggested that both on-off amacrine cells and ganglion cells receive excitatory input from depolarizing and hyperpolarizing bipolar cells. The onset of a light stimulus results in an EPSP in the ganglion cell mediated by the depolarizing bipolar cell, followed by an amacrine-mediated IPSP. At the termination of a light stimulus the sequence is repeated, but the EPSP at off is mediated by the hyperpolarizing bipolar cell.
16. Supported by NIH grant EY 00844.
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10 March 1977; revised 2 May 1977

Interactions Between Rod and Cone Systems in the Goldfish Retina

Abstract. *Signals from both the rod and the cone receptor systems converge upon the same retinal ganglion cell, but only one or the other of these systems appears to be effective at any particular level of adaptation. In this report we provide evidence that the change from one receptor system to the other is not simply due to the two systems having nonoverlapping dynamic ranges; rather, there is a distance-dependent interaction between the two systems.*

It is generally accepted that in the vertebrate retina cones mediate vision under conditions of high background luminance, while rods are responsible for vision under dark adapted conditions. However, the way that the visual system accomplishes the transition from one receptor system to the other is not completely understood. One mechanism that probably plays a part in the switch from rod to cone vision is rod saturation (*1*). However, with an active process such as a nonlinear inhibitory interaction (*2*) between the two receptor mechanisms, increased cone activity could reduce the contribution of the rod system.

Experiments investigating the nature of the interaction between rods and cones have yielded inconsistent results. Whitten and Brown (*3*) found that the range of light intensities that evoked responses from both rod and cone systems in the monkey retina was greatly increased by introduction of barbiturate anesthetic, which seems to depress lateral interactions in the retina. The effects of barbiturate anesthesia are very complex, however, and it is possible that the increased dynamic range of the rods was due directly to the drug, rather than being a result of release from inhibition. Other evidence for an inhibitory interaction comes from studies of monkey ganglion cell responses (*4*), but similar experiments performed on cats failed to reveal anything except a linear summation of rod and cone signals (*5*). Psychophysical studies of rod-cone interaction have also yielded equivocal results, with some experimenters claiming evidence for an inhibitory rod-cone interaction (*6*) and others concluding that the two systems act independently of each other (*7*).

A nonlinear inhibitory interaction between rods and cones in the retina should be apparent in ganglion cell responses, since the two systems have combined at or before this level in the

retina (*8*). If such an interaction exists, it would probably be mediated through a lateral pathway in the retina, as suggested by Whitten and Brown (*3*). Such an interaction would most likely be distance dependent; that is, inhibition should be greatest when the rod and cone receptors being stimulated are located very close to each other, while it should be minimized when spatially separate areas within the same ganglion cell receptive field are stimulated. We investigated this possibility for ganglion cells in the goldfish retina. The goldfish was chosen as the experimental animal because it possesses a duplex retina, as well as a cone system that can be stimulated exclusively of other receptors (*9*).

Extracellular ganglion cell responses were recorded with platinum-iridium microelectrodes placed in the optic tract of intact, self-respiring goldfish (*Carassius auratus*). The fish were immobilized by lesioning the spine and by rigidly clamping the rostral edge of the cranial opening through which the electrodes were advanced into the brain. With this preparation the fish can breathe normally, thus avoiding the problems of maintaining the proper respiratory state of the retina encountered when either isolated retina or artificially respired curarized preparations are employed (*10*).

The analytical method used to investigate the combination of signals from rods and cones was based on the two-stimulus summation technique employed by Levine and Abramov (*11*). One assumption upon which the Levine and Abramov analysis of results from two-stimulus experiments is based is that two different pathways, which are functionally independent up to some point of retinal processing, are being stimulated. This can be accomplished either by stimulating one receptor system in two distinct locations or by, as in this study, stimulating two different receptor systems. Two stimuli were chosen such that one excited cones and the other rods. The cone stimulus was a light of 710 nm, and the rod stimulus was a light of 522 nm. (For evidence that these two stimuli actually were rod and cone specific, see below.) Thresholds for each stimulus were determined by feeding the amplified spike train into a loudspeaker, and finding the weakest stimulus that evoked an audible response when flashed repetitively for 1 second in every 5. For each stimulus (presented as a 1-second flash), responses were recorded over a range of light levels from its threshold to about 1.5 log units above threshold. Responses were also recorded to the two stimuli presented simultaneously over the same range of light levels. These data were plotted with log stimulus attenuation on the abscissa and response on the ordinate, and smooth curves (stimulus response curves) were drawn by eye to fit the data (see Fig. 1). When both stimuli were presented together, they were always paired such that the strengths of each stimulus were the same relative to their respective thresholds.

The stimulus response curves for the two stimuli presented both separately and together were used to generate a response summation plot (*11*), which compares the arithmetically summed responses to each stimulus presented separately with the response obtained when the two stimuli were presented together (physiological sum). For each light level (relative to the threshold of each stimulus) the arithmetic sum of the responses to each stimulus is presented on the abscissa (Rr + Rc), and the physiologically summed response to the same stimuli presented simultaneously is plotted on the ordinate (Rr + c).

If the response to illumination is linear at and after the point at which the receptor systems first interact, the response summation plot will be a straight line with a slope of 1. Different types of nonlinearities will affect this plot in different ways; for example, a nonlinear inhibitory lateral interaction will cause a depression to a slope of less than 1 (*11*). Depression from unit slope does not necessarily imply lateral interactions as opposed to other nonlinearities; to identify lateral interactions we make use of the expected feature that the strength of interaction should be a function of the lateral distance between the interacting systems. That is, we may minimize lateral interactions by separating the stimuli in space, and maximize the interactions by overlapping the stimuli. Any *difference* between response-summation curves derived under these two conditions may be assumed to be due to the difference in strength of the lateral interactions.

We used two different pairs of stimuli, with one pair such that both the rod and cone stimuli fell on the same retinal area (spatially overlapped configuration) and the other pair such that the cone stimulus fell on a different retinal area (separated configuration). The stimuli were four-bladed pinwheels concentric with the center of the receptive field; the diameters of the stimuli were chosen to maximize the response of the cell. If there is a distance-dependent lateral inhibition between rods and cones, for any given cell the response summation function derived from the spatially overlapped stimulus configuration should lie below the

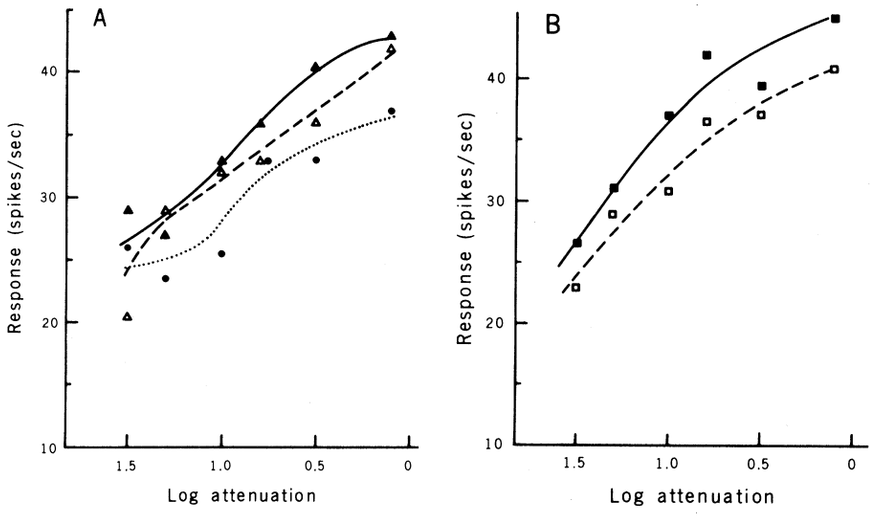

Fig. 1. (A) Stimulus response curves derived from one cell during separate stimulation by the 522-nm rod stimulus (circles) and the 710-nm cone stimulus (open and solid triangles). The stimuli were presented singly. The scaling of the relative stimulus strengths of the rod and cone stimuli is described in the text. The dotted curve is drawn by eye to fit the responses to the rod stimuli. The solid triangles represent data taken when the rod and cone stimuli fell on different retinal areas, and the open triangles represent data taken when the cone stimulus was rotated to fall on the same area as the rod stimulus. The solid curve has been drawn through the solid triangles, while the dashed curve has been drawn to fit the open triangles. (B) Stimulus response curves for same cell as in Fig. 1A for rod and cone stimuli presented simultaneously in both the spatially separated and overlapped configurations. Solid squares represent data from the separated stimulus configuration; the solid curve has been drawn by eye to fit the data. Open squares are data taken when stimuli were overlapped; the dashed curve has been drawn to fit these data.

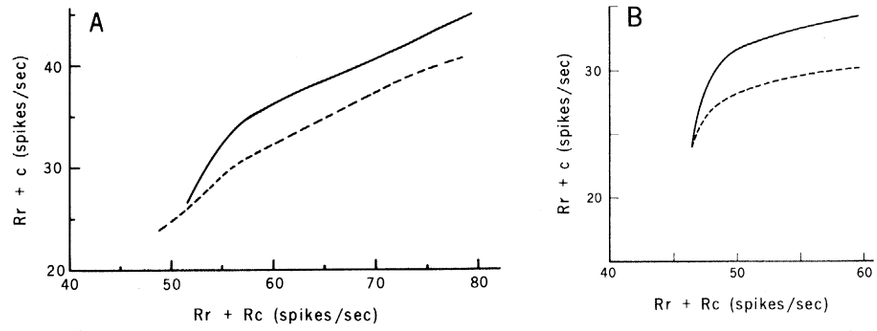

Fig. 2. (A) Response summation plots generated from the stimulus response curves presented in Fig. 1, A and B. The top curve (solid line) comes from the stimulus response curves taken in the spatially separated stimulus configuration for single (Fig. 1A) and simultaneous (Fig. 1B) presentations. For any given stimulus attenuation, the responses to the rod and cone stimuli presented singly are estimated from the solid and dotted curves in Fig. 1A, added together, and plotted against the value of the solid (simultaneous) curve from Fig. 1B at that same intensity. The bottom response summation curve (dashed line) is calculated in the same way from the dashed and dotted curves in Fig 1A and the dashed curve in Fig. 1B. (B) Response summation plots generated from another cell. The solid line represents the separated configuration, while the dashed line represents the overlapped configuration.

function derived from the separated stimulus configuration.

To confirm that the 522-nm stimulus actually was specific for rods, the course of dark adaptation was traced by determining the threshold for the 522-nm stimulus at various times after exposure to a large, bright adapting flash. For all six cells for which dark adaptation was traced, the dark adaptation curve tended to level off between 8 and 13 minutes after the adapting flash; threshold then began to decrease further, and generally dropped an additional 1.5 log units. It is generally agreed that the earlier plateau of a dark adaptation function represents the threshold of the cone system, while the subsequent drop in threshold is due to the more slowly adapting rods. Thus, the 522-nm stimulus should affect only rods for attenuations ranging from dark-adapted threshold to approximately 1.5 log units above that threshold. That the 710 nm stimulus was in fact stimulating cones predominantly was deduced from the absorption spectrum for the rod pigment of the goldfish (*12*). The rod pigment should be about 3 log units less sensitive to light at 710 nm than light at 522 nm. Our observed differences at absolute threshold are approximately 1.5 log units, implying that rods are not responsible for the response at both wavelengths. From the two points discussed above, it may be seen that each of the two stimuli excites one receptor type exclusively over a range of about 1.5 log units before the other type should begin to intrude.

Two-stimulus summation experiments using both spatially overlapped and separated stimulus configurations were performed against a dark background on 12 dark-adapted cells. The responses to the 710-nm stimulus and to the 522-nm stimulus were always of the same polarity (*13*), that is, both caused an increase in firing at the onset of the stimulus ("on"-center cells) or at stimulus offset ("off"-center cells). Eleven of the cells were off-center cells, and one was an on-center cell (*14*). For the on-center cell, the response measure was the total number of spikes during the 1-second stimulus; for the off-center cells, total number of spikes in the first second after stimulus offset was taken as the response.

Response summation plots for two cells are shown in Fig. 2, and the stimulus-response curves from which one of these plots was derived is shown in Fig. 1. For both of these cells, as for the ten of the 11 off-center cells and the one on-center cell, the response summation functions derived from stimulation when rod and cone stimuli were spatially separated lie above the functions derived from stimulation with the spatially overlapped configuration (*15*). From this, we may conclude that in the goldfish retina there is a distance-dependent interaction between rod and cone receptor systems. Signals from rods and cones do not simply sum; on the other hand, the more active system does not totally suppress the other. It should be noted that a comparison of two response summation functions does not give information about the absolute strength of interaction; rather, it represents the difference in magnitude of the interaction between the two stimulus configurations.

There are five possible retinal levels at which the interaction we have described might originate: receptors, horizontal cells, bipolar cells, amacrine cells, and ganglion cells. At the receptor level, interreceptor electrical connections between rods and cones have been described anatomically (*16*), but there are no known chemically mediated synapses between receptors. It is therefore unlikely that there is an inhibitory interaction between receptors; however, an electrical interreceptor facilitation, such as that seen in the cat and the turtle (*17*), could be responsible for the effect we have described at the ganglion cell level (*18*).

Horizontal cells have been suggested by Whitten and Brown (*3*) as mediators of a rod-cone interaction, but, as pointed out above, their results can be explained in other ways. Evidence against horizontal cells mediating an interaction comes from anatomical and physiological studies which indicate a complete separation of the rod and cone systems at this level (*19*).

Both amacrine and bipolar cells are likely candidates for mediators of rod-cone interactions. In fish, rod bipolar cells receive input from both rods and principal cones (*20*). Amacrine cells also provide a possible site for a distance-dependent rod-cone interaction, as at least one type of amacrine cell receives inputs from both rods and cones, and feeds back onto both rod and cone bipolar cells (*21*).

Finally, interactions at the ganglion cell level have been invoked to explain rod-cone interactions; in particular, it has been suggested that differences in the latencies of the two receptor systems allow the earlier-arriving cone signals to suppress rod signals (*4*). Such a mechanism cannot explain our results, because there should be no differences in the relative latencies for our two stimulus conditions. Moreover, we believe rod-cone interactions are unlikely at this level because the rod and cone signals have been mixed prior to the ganglion cell.

In summary, we believe we have demonstrated a nonlinear interaction between the rod and cone systems. The functional significance of this interaction is to shorten the range of light levels over which both the rod and cone systems are active. Thus, this interaction provides a mechanism for an abrupt changeover from rod to cone vision without totally relying on the cone system to become active just as the rod system saturates.

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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.
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17 June 1977

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.

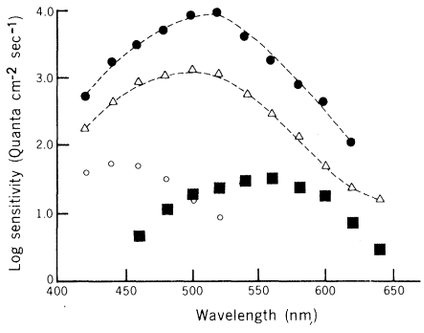

Fig. 1. Spectral response curves from retinal ganglion cells. Inputs from cone systems with peak sensitivities (λ_{max}) of 450, 500, and 555 nm as well as the 500-nm λ_{max} rod system. All three cone systems (○, on-surround, light-adapted X cell; ■, on-center, light-adapted Y cell; and △, on-surround, 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