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Receptive Fields of Opponent Color Units in the Optic Nerve of the Ground Squirrel

Abstract. *When mapped with white light, each receptive field consisted either of an excitatory ("on") center and a concentric inhibitory ("off") surround, or of the reverse arrangement. Monochromatic stimuli revealed that each receptive field was composed of two mutually antagonistic components (one excitatory, one inhibitory) which had different spectral sensitivities and different spatial distributions. For some units the two chromatic components had identical spatial distributions.*

Dowling has presented anatomical and physiological evidence that the photoreceptor layer of the ground squirrel (*Citellus mexicanus*) is composed only of cones (*1*). Since cones are used exclusively for diurnal vision and, in some animals, for color vision, the question naturally arises as to whether the ground squirrel possesses any neural mechanism for color discrimination. Dowling found only one visual pigment (maximum absorption at 523 nm) present in the cones (*1*), which would indicate that the ground squirrel has no color vision. However, he has informed me that his method of analysis prevented detection of any visual pigments with absorption curves in the blue region of the spectrum (wavelengths shorter than 490 nm). Therefore, I proceeded, with monochromatic spots of light, to study the receptive fields of single optic nerve fibers in the ground squirrel. Some units (24 of 124 studied; 19 percent) were found to transmit opponent color information; that is, light of short wavelengths (blue) had an effect opposite to that of longer wave lengths (green). A recent behavioral study confirms that the ground squirrel can distinguish blue from other colors or white light (*2*).

The methods employed in this study were described in the previous report (*3*). In these experiments monochromatic stimuli were produced by inserting Baird-Atomic interference filters into the light paths of the two slide projectors.

When the receptive fields of these units were mapped with white light, they invariably consisted of pure "on" or pure "off" field centers (1.0° to 4.5° diameter) and concentric antagonistic surrounds. The responses to white light were always weak and phasic. However, when monochromatic light was used to stimulate the field centers, a new and startling pattern of responses was revealed. A single unit which was exclusively "on" center or "off" center to white light became either "on" or "off" center, depending upon the wavelength of the stimulus. Some fibers were excited by green light and inhibited by blue light, while others behaved in the opposite manner. Inhibition was seen only when a unit was spontaneously active and, in the absence of such activity, only an "off" response was observed.

Units excited or inhibited by green light gave the same type of response to yellow or red light; there was never any evidence of red-green antagonism. In this respect the ground squirrel is very similar to a protanope, a red-blind human being (*4*).

When the receptive field center of one such opponent color unit was illuminated with a spot of white light, there was a slight inhibition of the resting activity, followed by a weak "off" response (Fig. 1*B*). With the intensity of the light set as in Fig. 1*B*, a blue interference filter (462 nm) was placed in the light path. The centered blue spot completely abolished the resting activity and elicited a strong "off" response, followed by the return of the spontaneous firing (Fig. 1*C*). Thus, the blue spot was much more effective than the white in inhibiting the fiber's resting activity. On the other hand, a centered green spot (528 nm) evoked a strong excitatory ("on") discharge that persisted throughout the period of illumination (Fig. 1*D*).

As illustrated in Fig. 2, the responses of other color-coded units were often just the reverse. This particular fiber gave a weak "off" response when the center of the receptive field was stimulated with a spot of white light (Fig. 2*A*). However, a centered green spot (540 nm) of the same size produced a much stronger "off" response (Fig. 2*B*). Conversely, illumination of the field center with a blue spot of light (480 nm) evoked a vigorous "on" response with a maintained discharge that lasted throughout the period of illumination (Fig. 2*C*).

Preliminary results indicated that the green- and blue-responsive components had peak sensitivities at about 540 nm and 462 nm, respectively. In studying the electroretinogram of this and other squirrels, a number of investigators have found spectral sensitivity functions with peaks close to one or both of the above wavelengths (*1*, *5*). A blue-green stimulus (499 nm) occasionally produced an "on-off" re-

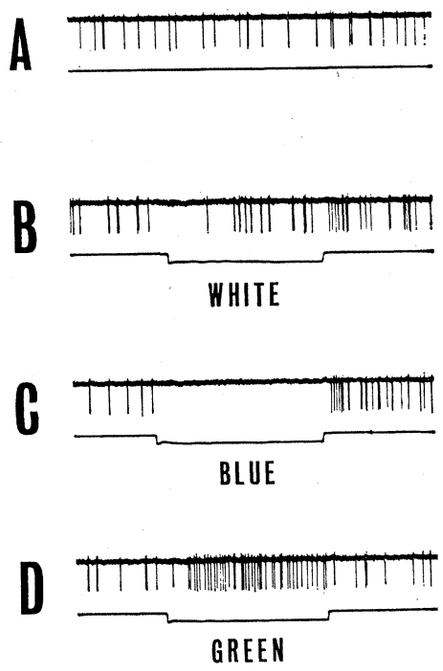

Fig. 1. Green-excitatory, blue-inhibitory fiber. Field center, 3° in diameter. (*A*) Resting activity in the dark. (*B*) A centered 3° spot of white light slightly depressed the resting activity and evoked a small "off" response. (*C*) Centered 3° blue spot (462 nm) completely inhibited the resting activity and elicited a stronger "off" response than in *B*. (*D*) Centered 3° green spot (528 nm) evoked a strong excitatory ("on") response that persisted throughout the period of illumination. Stimuli were not of equal energy. Luminance of white light stimulus, 2.5 $\log_{10}$ cd/m^2; luminance of background, 0.5 $\log_{10}$ cd/m^2. In *B*, *C*, and *D* the downward deflection of the lower (photocell) trace indicates the 1-second period of illumination. Spikes retouched for clarity.

sponse but usually it had no effect (Fig. 2*D*), which indicates that this is the approximate spectral region where excitation is canceled by inhibition. Protanopes have a neutral point at about 495 nm (*4*).

Projection of green and blue spots together revealed an antagonistic interaction between the two color components. This was to be expected, since white light, a mixture of all spectral colors, was a less effective stimulus than monochromatic light. Selective chromatic adaptation abolished the antagonism and thereby revealed the presence of two independent components underlying the opponent color mechanism. Strong chromatic adaptation at one end of the spectrum always selectively depressed the component at that end, and increased the sensitivity of the other, nonadapted component. Because its antagonist was depressed, the nonadapted component was responsive to a greater range of wavelengths and its spectral sensitivity curve was shifted toward 500 nm.

Antagonism was always observed when both the blue and green spots were positioned at least partially within the field center. Sometimes there was no interaction when one spot was placed in the field center and the other was positioned in the surround. Therefore, either the spatial distributions of the two chromatic components coincided with the field center as mapped with white light or the intensity of the monochromatic light was insufficient to stimulate the relatively insensitive surround.

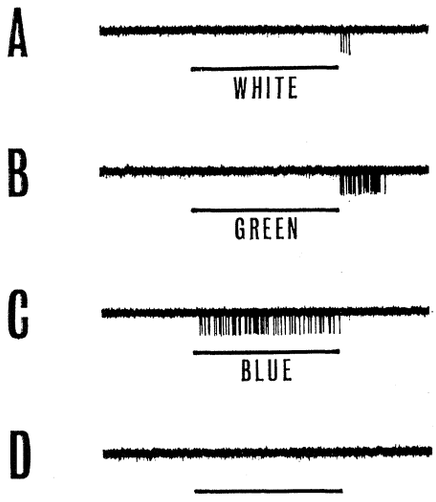

Fig. 2. Blue-excitatory, green-inhibitory fiber. Field center, 2°. (*A*) Centered 2° spot of white light evoked an "off" response. (*B*) Centered 2° spot of green light (540 nm) elicited a greater "off" response than in *A*. (*C*) Centered 2° spot of blue light (480 nm) produced a strong excitatory ("on") response that persisted throughout the period of illumination. (*D*) A centered 2° spot of blue-green light (499 nm) evoked no response. Stimuli were not of equal energy. See Fig. 1 for the luminance of the white spots and the background. Black bars indicate the 1-second period of illumination. Spikes retouched for clarity.

To test these two alternatives, I positioned small spots of light (15 to 30 minutes of arc) of long (540 nm) or short (462 nm) wavelengths in different parts of the receptive field and thereby mapped the spatial distributions of the blue- and green-responsive areas. This method demonstrated (i) that the responses to green and blue spots were always of the opposite type, regardless of the size, position, or intensity of the stimulus, and (ii) that the receptive fields were so organized that one chromatic component (blue) extended farther radially than the other (green).

The responses of a color-coded fiber to white and monochromatic spots of different sizes are illustrated in Fig. 3. With white light stimulation the unit was "on" center, with an antagonistic surround (Fig. 3, *A* and *B*). The fiber gave "on" responses to centered green spots of light and "off" responses to centered blue spots. A green spot which just covered the plotted center evoked the strongest "on" response (Fig. 3*C*). Smaller green spots produced weaker discharges and ones larger than the field center elicited equal responses (Fig. 3*D*). However, the maximum "off" response to blue light was produced by a spot about twice the diameter of the field center (Fig. 3*F*). Smaller blue spots produced weaker "off" responses (Fig. 3*E*) and ones larger than 3° gave equal responses.

The greatest antagonism between the responses to a green spot and a blue spot occurred when both stimuli were positioned within the field center. There was less antagonism when the blue spot was moved into the surround, but remained tangent to the field center. Finally, when the blue spot was placed even farther out in the surround, there was no interaction between the two color systems. On the other hand, the green spot had to be in the center of the receptive field to antagonize the blue center response. In other words, the spatial distribution of the blue-responsive system included both the center and surround of the receptive field, while the green-responsive component was confined to the field center.

It was often impossible to bring out a surround response to blue light, except by selective chromatic adaptation of the field center. When the center of the receptive field was continuously illuminated with a green spot, a centered blue annulus evoked a surround response. When the field center was not illuminated with the green spot, the blue annulus often produced no response. Presumably, the green light was selectively light adapting the green-responsive component (reducing its sensitivity) and simultaneously raising the sensitivity of the blue-responsive system.

Recent evidence indicates that there is a second type of opponent color unit. For the first and the second types, the peak sensitivities of the two antagonistic processes were in the green (540 nm) and blue (462 nm) regions of the spectrum. However, in the second type the spatial distributions of the two chromatic components were identical and coincided with the responsive area mapped with white light.

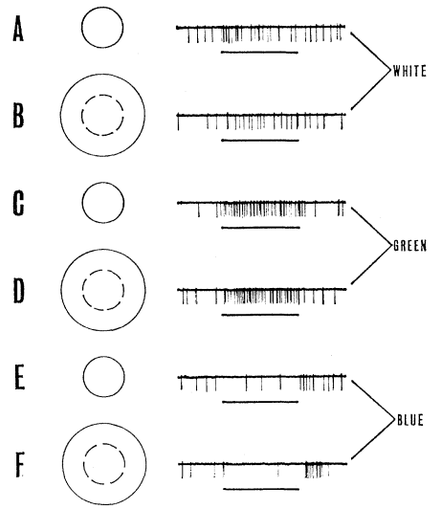

Fig. 3. Responses of an opponent color unit to white and monochromatic spots of different sizes; the two chromatic components had different spatial distributions. Field center, 1.5°. (*A*, *B*) Excitatory responses to centered 1.5° (*A*) and 3° (*B*) white spots. Note much smaller response in *B* due to light falling on the antagonistic surround. (*C*, *D*) Essentially equivalent excitatory responses to centered 1.5° (*C*) and 3° (*D*) spots of green light (540 nm. (*E*, *F*) Inhibitory responses to centered 1.5° (*E*) and 3° (*F*) spots of blue light (462 nm). Note stronger inhibition and greater "off" response in *F* as compared to *E*. Stimuli were not of equal energy. See Fig. 1 for the luminance of the white spots and the background. Black bars indicate the 1-second period of illumination. Spikes have been retouched for clarity.

The blue component did not extend farther radially than the green. Because the highly yellow lens of the ground squirrel's eye strongly absorbs those wavelengths shorter than about 500 nm, there is the possibility that the intensity of the blue light was insufficient to stimulate an existing, but very insensitive, surround. Nevertheless, because of evidence to be described in a paper in preparation, it seems quite certain that these latter receptive fields represent a second class of opponent color units.

The opponent color receptive fields of the ground squirrel are similar to those of some retinal ganglion cells in the goldfish (*6*) and to those of some cells in the lateral geniculate nucleus of the monkey (*7*). A comparision of the opponent color receptive fields of these three animals will be made in a paper now in preparation.

The present report, together with the previous one (*3*), further substantiates the statement that highly sophisticated neural integrations occur within the retina of the ground squirrel. No other mammalian retina is known to process both movement and color information to such a great extent. It is important to remember that all of this complex neural coding takes place before any visual information is transmitted through the optic nerve to the brain.

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Postsynaptic versus Presynaptic Inhibition in Antagonistic Stretch Reflexes

Abstract. *Motoneurons of the cat gastrocnemius-soleus muscle were studied intracellularly with conventional glass micropipettes. Each of these motoneurons was made to fire repetitively by stretch of its own muscle (gastrocnemius-soleus), and by current injected through the impaling microelectrode. By comparing the amount of inhibitory influence from antagonistic stretch of posterior biceps on the repetitive firing in these two different situations, an estimate could be obtained of the relative contribution of postsynaptic inhibition in this type of antagonistic stretch reflex. Even when the experimental conditions were such as to favor presynaptic inhibition, only strong postsynaptic inhibitory effects were seen; presynaptic inhibition was not found.*

Presynaptic reduction in the potency of the excitatory inflow to spinal motoneurons from muscle afferents was reported by Frank and Fuortes (*1*). They found that the monosynaptic excitatory postsynaptic potential recorded intracellularly from gastrocnemius motoneurons was sometimes reduced in size by a volley in the hamstring afferents. Moreover, the inhibitory hamstring volley alone produced no hyperpolarization or change in excitability of the postsynaptic membrane. Later, Frank (*2*) proposed two possible explanations of these findings: (i) the excitatory inflow had been influenced by the hamstring volley before arriving at the motoneuron postsynaptic membrane, or (ii) interaction between the excitatory and inhibitory volleys occurred within the motoneuron but at a distant site where the effect of the inhibitory volley alone could not be detected by the microelectrode that impaled the soma of the cell.

Eccles and co-workers (*3*) have used the similarities between depression of excitatory postsynaptic potentials and the amount of depolarization at the primary afferent terminals to argue for the existence of presynaptic inhibition. The depolarization of the presynaptic terminals is postulated to decrease the amplitude of the action potentials propagated into these terminals and thus to diminish the amount of transmitter substance liberated. Presynaptic inhibition has also been reported to differ from the previously known spinal postsynaptic inhibitions in its pharmacological properties (*4*). However, postsynaptic inhibitions which, like presynaptic inhibition, are resistant to strychnine have recently been described in spinal motoneurons (*5, 6*). In addition, the peripherally activated, postsynaptic, strychnine resistant inhibitions are removed by picrotoxin (*6, 7*) held to be a specific antagonist of presynaptic inhibition (*4*).

This study was undertaken to gain information about the relative contribution of postsynaptic inhibition in spinal motoneurons when muscle stretch is used as a stimulus.

A motoneuron, which is fired repetitively by autogenetic muscle stretch (meaning stretch of its own muscle), reduces its rate of firing in response to antagonistic muscle stretch (*8*). This inhibition may reflect a combination of events occurring at the motoneuron postsynaptic membrane, at the presynaptic excitatory terminals, and at interneuronal relays. The excitability change occurring at the postsynaptic membrane may be caused by true postsynaptic inhibition or by a removal of background excitation, and can be assessed from the reduction in motoneuron discharge rate when firing is produced solely by passing a constant depolarizing current through the impaling microelectrode tip, thus bypassing the primary afferent terminals. By comparing the amount of inhibition in these two different situations, that is, synaptically induced firing and firing induced by injected currents, an estimate can be obtained of the relative contribution of postsynaptic excitability changes.

The measurements were collected from 18 cats, which were anesthetized with pentobarbitone (35 to 40 mg/kg) and immobolized by gallaminetriethiodide (Flaxedil, Abbott). The posterior biceps and gastrocnemius-soleus muscles in the left hind limb were freed and strings were tied to the cut distal tendons so as to be able to stretch the muscles by weights. The lumbar cord was exposed and transected at L_2. Except for the ipsilateral L_7 dorsal root, the spinal cord was bilaterally de-afferented from L_5 and below. The ipsilateral L_7 (often also S_1) ventral root was cut, and the peripheral stump was stim-