Table 1. Radiometric age data for shells from Tomales Bay, California, and Cape Blanco, Oregon.

Sample	Apparent age (10^3 yr)		Probable age (10^3 yr)
	C^{14}	Th^{230}/U^{234}	
Tomales Bay			
L–768C	>37	55 ± 5	$\geqq 50$
L–720A	34.5 ± 3	55 ± 3	$\geqq 50$
Cape Blanco			
L–720C	35 ± 2.5	35 ± 2	$\geqq 33$

immediately east of the San Andreas fault, the axis of which extends along Tomales Bay; hence there may have been displacement, as indicated by Weaver (*2*, p. 133).

A collection of mollusks was made by one of us (H.G.R.) in March 1962. The best material came from a point near the north end of the bay (locality 1 of Johnson, at an elevation of 3 meters). The shells were exceedingly fresh in appearance and consisted mainly of the species reported by previous investigators. The most abundant were *Macoma nasuta* Conrad, *Lucina nuttalli* Conrad, *Nassarius fossatus* Gould, *N. mendicus* Forbes, *Olivella biplicata* Sowerby, *Polinices reclusianus* Deshayes, and *Mitrella carinata* Hinds.

Shell beds from the vicinity of Cape Blanco, Oregon, have been studied by Diller, Martin, Baldwin, Addicott, and others (*5*). The shells occur in a deposit of terrace sand and gravel resting on a wave-cut platform south of the cape. The fossils were regarded by Martin as "recent forms deposited under cold water conditions." Baldwin regarded the shells as belonging to the Elk River beds, while Addicott retained the term Elk River for the underlying, gently deformed beds of Late Pliocene (?) age and assigned the shells to overlying terrace deposits of late Pleistocene age. The shell beds are locally horizontal and in other places slightly tilted. Baldwin believes that they date from late to post-Pleistocene, and Addicott regards them as late Pleistocene.

The locality was visited in March 1962 by one of us (H.G.R.), and material was submitted to Lamont Geological Observatory for age determination. The following species were the most common: *Saxidomus nuttali* Conrad, *Schizothaerus nuttali* Conrad, *Cardium* sp., and *Olivella baetica* Carpenter.

Several samples were dated by both C^{14} and Th^{230}/U^{234} methods (Table 1). Sample L-720A consisted of the pelecypod *Lucina nuttalli* (Conrad) from Tomales Bay; L-768C consisted of shell fragments from the same locality; L-720C consisted primarily of fragments of *Cardium* from Cape Blanco.

As pointed out by several workers (*6*), finite ages greater than about 25,000 years old obtained from carbonate materials should be considered minimum ages. The same is likely to be true of Th^{230}/U^{234} ages of mollusks (*7*) unless these ages can be otherwise verified. In the case of the material from Cape Blanco, the apparent agreement of two minimum ages does not necessarily provide proof for the validity of the 35,000 year age. We can only conclude that the samples are at least 33,000 years old.

More information is available for the Tomales Bay locality. One sample is greater than 37,000 years old, by the C^{14} method. Both yield apparent ages of 55,000 years by the Th^{230}/U^{234} method. The most probable age is greater than 50,000 years and these two samples could easily have been deposited during the last interglacial stage or earlier. Neither locality is very late Pleistocene or postglacial.

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21 March 1966

Receptive Fields of Directionally Selective Units in the Optic Nerve of the Ground Squirrel

Abstract. *These units responded vigorously to stimuli moving entirely across their receptive field centers in one direction (preferred) and not at all when the direction of motion was reversed (null). The directional selectivity was the result of an inhibitory mechanism which prevented responses to null movements. Surrounding each field center was a concentric antagonistic region produced by a second inhibitory mechanism.*

The purpose of the experiments reported here was to determine the nature and organization of the receptive fields of single optic nerve fibers in a mammal with an all-cone retina. The methods were similar to those used by others (*1*). The ground squirrel (*Citellus mexicanus*) was anesthetized with sodium pentobarbital, fitted with a tracheal cannula, and positioned in a stereotaxic head holder. The right pupil was dilated and accomodation relaxed with 1 percent atropine; a contact lens covered the cornea. The right eye of the animal faced a large screen upon which stimuli were projected from two tungsten-filament slide projectors. (See figure captions for luminances of stimuli and background.) A refracting lens brought the reflected stimuli into focus on the retina.

Gold-plated tungsten microelectrodes (*2*) were used to record from single fibers. The "pencil point" recording area widened from less than 0.5 μm in diameter to 10 to 15 μm over a length of about 25 μm. All of the optic nerve fibers are myelinated and of nearly the same diameter, so it is very unlikely that the electrodes were selectively recording from certain fibers and not from others. The discharges of a single fiber could be influenced by light stimulation over only a restricted area of the visual field. This area, defined as the receptive field, was mapped on sheets of paper attached to the screen (*3*).

The majority of the optic nerve fibers in the ground squirrel (78 of 124 studied; 63 percent) had concentric receptive fields like those of the cat's retinal ganglion cells. However, a second class of fibers (22; 18 percent) exhibited a selective sensitivity to the direction of

image movement. The rabbit is the only other mammal known to possess directionally selective units at the optic nerve level (*4*, *5*).

These fibers gave "on-off" responses to illumination of a roughly circular area of the visual field defined as the field center. The field centers were small (0.5° to 1.0° in diameter; 1° of visual angle corresponds to approximately 115 μm on the ground squirrel's retina). Each field center was surrounded by a concentric inhibitory area; illumination confined to the inhibitory surround never evoked any response. Because of these inhibitory regions, the fibers were unresponsive to changes in diffuse illumination.

An example of a directionally selective unit is illustrated in Fig. 1. An exploring spot of white light (15′) evoked an "on-off" response anywhere in the center of the receptive field. No responses could be obtained by illumination of the area outside of the field center with stationary or moving spots of any size. A centered spot of white light evoked an "on-off" response (Fig. 1*A*), but the same spot elicited a far greater response when it was moved entirely across the receptive field in a particular direction (preferred direction of motion; Fig. 1*B*). When the direction of motion was reversed, there was no response (the null direction; Fig. 1*B*). Movement of the spot along a path perpendicular to the preferred-null axis evoked either no response or weak, but equal, responses for either direction of motion (Fig. 1*C*). When a black spot on a white background was moved in the preferred direction, the directional selectivity of the unit remained unchanged (Fig. 1*D*). The preferred direction of motion also remained the same for moving black or white bars or slits as well as black-white edges, no matter which edge was leading (Fig. 1, *E* and *F*). Thus, these units were truly directionally selective in their responses to moving stimuli.

The directional selectivity of these units to moving stimuli could not be predicted on the basis of their responses to stationary stimuli. The smallest available stimulus (2.5′) failed to reveal any excitatory or inhibitory subdivisions within the field center. Therefore, the directionally selective response was not simply the result of the stimulus moving from an inhibitory area into an excitatory zone. On the contrary, the same directional selectivity applied for motion anywhere within the entire field center. The response to a small (10′ to 15′) white or black spot moving in the preferred direction began as soon as the stimulus had crossed the perimeter of the field center and continued until it passed across the opposite border. Directionally selective responses were evoked when small spots (2.5′ to 5.0′) positioned within the field center were moved short distances (5′ to 10′) back and forth in the preferred-null direction.

For motion in the preferred direction nearly all units responded to speeds as slow as 0.1°/sec and as high as 20° to 30°/sec, above which there was no response. Continuous movement of a white or black spot in the null direction usually yielded no response (Fig. 1, *B* and *D*). Occasionally, a few spikes were evoked when a spot was moved very slowly (about 0.1° to 0.3°/sec) in the null direction (*5*). Because the directionally selective fibers exhibited little or no resting activity, it was not possible to determine whether a single spot moved in the null direction had an effect opposite (inhibitory) to that produced by movement in the preferred direction (*5*).

However, other experiments did reveal that the directional selectivity of these units was controlled by an inhibitory mechanism:

1) When two small spots (5′ to 10′) were positioned tangentially along the preferred-null axis and within the field center, each alone produced an "on-off" response. When the two spots were flashed consecutively in the preferred sequence of motion, each spot evoked a response, but, for the opposite (null) sequence, only the first flash evoked a

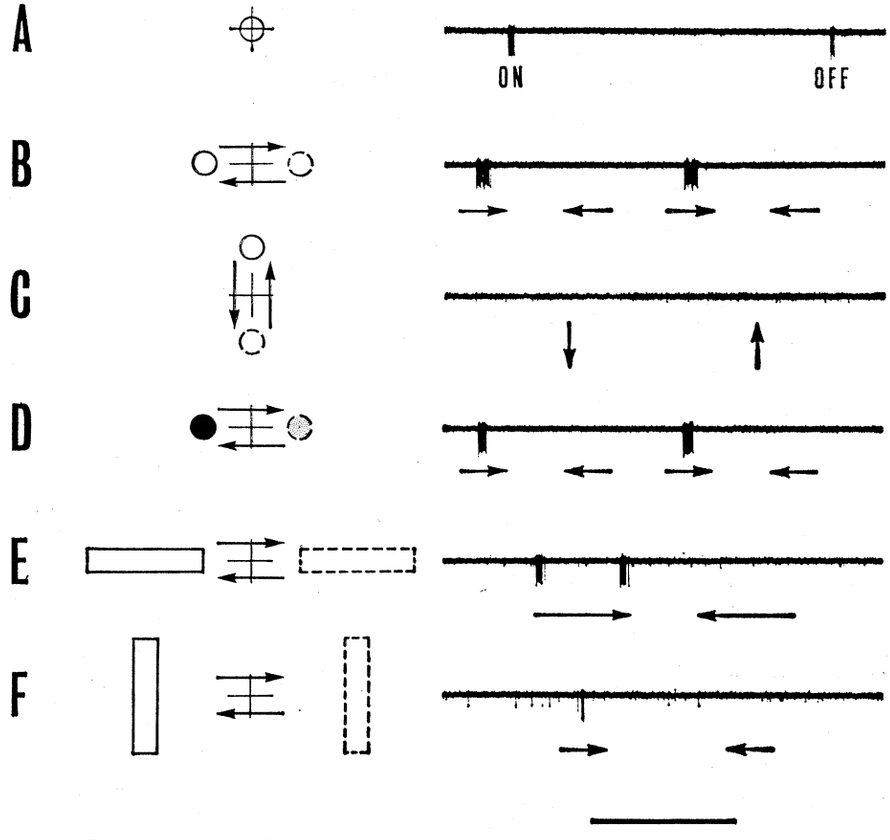

Fig. 1. Responses of a directionally selective unit. Field center (1°) indicated by a cross. (*A*) "On-off" response to a centered spot (0.5°) of white light. (*B*) Same spot moved horizontally through the field center from left to right and then back; unit responded only to left-to-right motion. (*C*) Same spot evoked no response when moved vertically through the field center. (*D*) When a black spot (0.5°) on a white background (same intensity as light in *A*, *B*, and *C*) was moved horizontally through the field center, it elicited the same type of directionally selective response as seen in *B*. (*E*) When a slit (0.5° by 7.0°) was oriented parallel to the direction of its horizontal motion through the field center, its leading and trailing edges evoked responses, but only for left-to-right movement. (*F*) After the same slit had been rotated through 90°, it elicited a slight motion response, but again only for left-to-right movement. Luminance of white stimuli, 2.0 $\log_{10}$ cd/m^2; luminance of background, 0.0 $\log_{10}$ cd/m^2. Rate of motion in all cases, about 10°/sec. Black bar at the bottom of the figure represents 1 second. Spikes retouched for clarity.

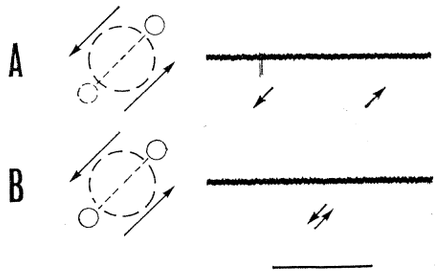

Fig. 2. Reponses of a directionally selective unit to two spots passing simultaneously through the field center, one spot moving in the preferred and the other in the null direction. Interrupted circle indicates the size of the field center (1°); each exploring spot, 15′. (*A*) Response to a single spot moved through the field center from 2:30 to 8:30 (preferred direction) and back. (*B*) Two spots moved simultaneously along the same path, but in opposite directions, through the field center; no response because of cancellation of excitatory and inhibitory effects. Luminance of stimuli and background same as in Fig. 1. Rate of motion, about 12°/sec. Black bar at the bottom of the figure represents 1 second. Spikes retouched for clarity.

response. In the latter case, the first flash inhibited any response from the second. Thus, the sequence of changes in illumination of points along the preferred-null axis determines the response to a moving stimulus.

2) When a spot was moved in interrupted steps in the preferred direction through the field center, there was a strong response throughout each period of motion. When a spot was moved in the same manner in the null direction, there was a small initial response each time the spot began to move, but none during the remainder of the movement. Presumably the inhibition had subsided before each succeeding null movement was initiated and, when the null movement began, inhibition was delayed with respect to excitation; therefore, a few spikes were evoked.

From 1) and 2) it is clear that whenever the level of illumination changes at any point within the field center, inhibition spreads laterally from that point in the null direction. The response to successive stimuli will depend upon their position in the field center and their time of application.

3) When two white spots simultaneously entered the field center, one spot moving in the preferred direction and the other in the null direction, no motion response was evoked (Fig. 2). Motion in the preferred direction only had an excitatory effect, while motion in the null direction only had an inhibitory effect, which could not be demonstrated in the absence of spontaneous activity (Fig. 2*A*). Therefore, simultaneous motion of the two spots in opposite directions did not elicit any response (Fig. 2*B*) because the excitatory and inhibitory effects canceled each other. Similar results were obtained in a study of directional movement detectors in the pigeon's retina (*6*).

The mechanism and intraretinal location of this inhibitory system will be discussed in a paper now in preparation.

The responses of a directionally selective fiber were also strongly inhibited by illumination of the area surrounding the field center. The threshold was higher for responses to stimuli which simultaneously covered both the field center and the surround compared to that for stimuli which covered only a portion or all of the field center. An example of the effects of simultaneous illumination of the center and surround is illustrated in Fig. 1. A slit with its long axis oriented in the direction of preferred motion evoked responses when the leading and trailing edges passed over the field center (Fig. 1*E*). When the direction of motion was reversed, there was no response. Motion of the slit in the preferred direction evoked about half as many spikes as did a spot of light of the same width (0.5°) moved in the same direction and at the same speed (Fig. 1, *B* and *E*). Thus, even though an edge was moving over the field center, the remainder of the slit was illuminating the surround and thereby inhibiting the motion response. Rotating the slit through 90° and passing it in the preferred direction across the field center elicited a directionally selective response which was weaker than for the original orientation, presumably because a greater part of the inhibitory surround was then illuminated (Fig. 1*F*).

When two projectors were used simultaneously to stimulate the center and surround of the receptive field, the presence of a concentric inhibitory area was even more obvious. The "on-off" response to a spot of light positioned within the field center (Fig. 3*A*) was completely inhibited by placing a second large spot in the surround and tangent to any point along the perimeter of the field center (Fig. 3*B*). The vigorous response to the preferred motion of the small spot (Fig. 3*C*) was strongly suppressed when the surround was illuminated (Fig. 3*D*).

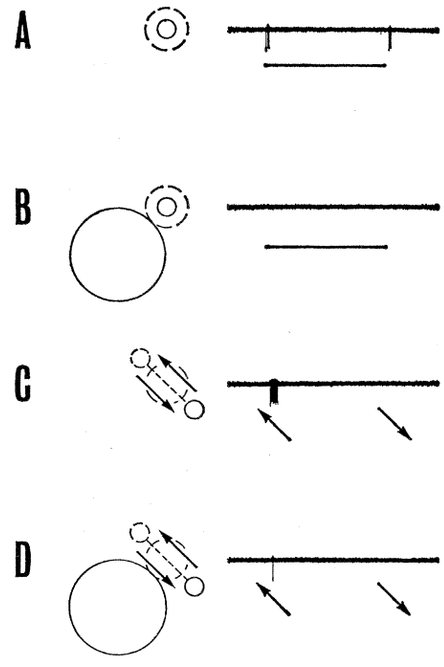

Fig. 3. Antagonism of the center response of a directionally selective unit by illumination of the inhibitory surround. The interrupted circle indicates the size of the field center (1°); exploring spot, 30′. (*A*) "On-off" response to the centered exploring spot. (*B*) Complete inhibition of the stationary ("on-off") response by continuous illumination of the inhibitory surround with a large spot (9°) placed tangent to the field center. (*C*) Directionally selective response to the exploring spot moved from 4:30 to 10:30 (preferred direction) and back. (*D*) Almost complete suppression of the motion response by placement of the large spot (9°) as in *B*. Luminance of stimuli and background same as in Fig. 1. In *A* and *B* the black bars indicate the 1-second period of illumination; in *C* and *D* the rate of motion was about 10°/sec. Spikes retouched for clarity.

The direction of preferred motion varied from unit to unit with no indication that one orientation was more prevalent than another. The receptive fields of the directionally selective fibers were scattered randomly throughout the visual field. Finally, there was no obvious relationship between the orientation of the preferred-null axes and the positions of the receptive fields in the visual field.

The above results demonstrate that complex neural integration of visual information occurs within the retina of the ground squirrel. The evidence presented in the following report (*7*) substantiates this statement.

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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-

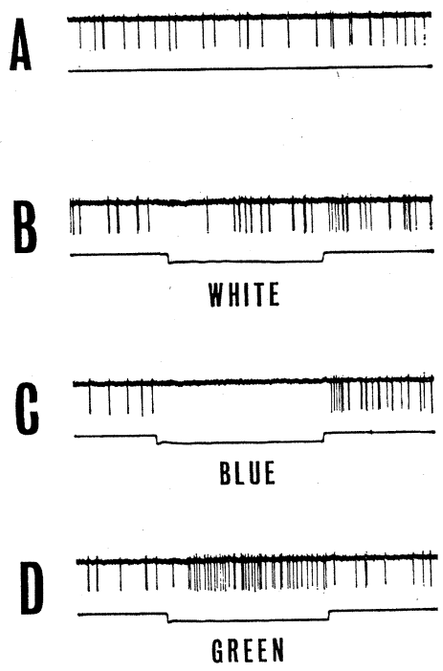

Fig. 1. Green-excitatory, blue-inhibitory fiber. Field center, 3° in diameter. (*A*) Resting activity in the dark. (*B*) A centered 3° spot of white light slightly depressed the resting activity and evoked a small "off" response. (*C*) Centered 3° blue spot (462 nm) completely inhibited the resting activity 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.