SPATIAL AND CHROMATIC INTERACTIONS IN THE LATERAL GENICULATE BODY OF THE RHESUS MONKEY[1]

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THE RECEPTORS AND NERVE CELLS that make up the visual pathway must convey and interpret information on both the form and the color of retinal images. In higher mammals little is known about the degree to which nerve cells are specialized for handling these types of information. In a visual stimulus the importance of spatial attributes, and especially of dark-light contours, first became obvious with the discovery by Hartline (20) of lateral inhibition in the *Limulus*, a type of study that was extended to mammals when Kuffler (28) demonstrated that the receptive fields of retinal ganglion cells in the cat are subdivided into a center and an opponent surround. The opponent principle, in which spatially separated excitatory and inhibitory regions are pitted against each other, has now been observed for retinal ganglion cells in the frog (1), the lizard (9), the rabbit (3), the rat (4), the ground squirrel (33), and the monkey (24). Similar effects have been seen in the lateral geniculate body and visual cortex in the cat (23, 25, 26), and also recently at these levels in the monkey.

In 1958 De Valois and his collaborators (15) observed geniculate cells in the macaque monkey that were excited by one set of wavelengths and inhibited by another, making it apparent that in higher mammals the spectral composition of the stimulus was also an important variable. Similar opponent-color effects have since been described in the primate at the level of the retinal ganglion cell (24), and in the visual cortex (34). In the cat the absence or rarity of opponent-color mechanisms (19, 36) may be related to an inferior ability to discriminate color (31, 32, 40); indeed since Svaetichin's (41) original observation of opponent-color responses in the fish retina (S-potentials), similar response patterns have been seen only in animals thought to have good color vision.

Given the existence of two opponent mechanisms in the monkey visual system, one for the spatial variable and the other for color, it is natural to ask whether these occupy the same channels, or are confined to separate groups of cells. In the goldfish it is clear from the work of Wagner, MacNichol, and Wolbarsht (43, 45) that opponent-color and opponent-spatial

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effects can be found in common retinal ganglion cells. In the monkey, with its great visual capacity, similar mechanisms are to be expected, perhaps in more developed form. The rhesus monkey was chosen for the work to be described because behaviorally its vision seems to be very similar to that of man(10). In this species, moreover, absorption spectra of the three cone types are possibly identical to those of man, with maxima at about 445, 535, and 570 mμ. (5, 30). Any knowledge of the receptor properties obviously makes it easier to interpret responses to color at more central levels of the nervous system.

The purpose of the present study was to examine in detail how cells respond to variations in stimulus size, shape, and wavelength. By working in various states of light and dark adaptation we also tried to learn something about the connections of rods and cones with single fourth-order cells. The decision to record from the geniculate was made because of the obvious interest in learning how cells function at an early stage of the visual pathway, especially the stage that forms the input to the striate cortex. We also hoped to learn more about the significance of the layering in this puzzling structure.

Some of the findings of the present paper have already been described in preliminary notes (27, 47).

METHODS

Sixteen monkeys were used, ranging in age from 1 to 3 years. Animals were anesthetized with intraperitoneal sodium Pentothal (35 mg/kg.), and additional doses of the drug were given at half-hour intervals. The head was held rigidly in a Horsley-Clarke stereotaxic apparatus (42). The eyes were immobilized with a continuous infusion of succinylcholine (20–40 mg/kg. per hour). For complete immobilization it was often necessary to give additional intramuscular injections of gallamine triethiodide (10 mg/hour). Pupils were dilated with 1% homatropine. Contact lenses were fitted to the corneas after measuring corneal curvature with a keratometer (Bausch & Lomb, type 71-21-35). Focus was checked at a distance of 1.5 m. (the distance from the eyes to the projection screen) with a slit retinoscope, and any necessary correction was made with supplementary lenses mounted in front of the animal's eyes. With a properly fitted contact lens, correction by more than ±1.0 diopters was seldom necessary.

For most work the animal faced a large white screen at a distance of 1.5 m. When receptive-field centers were smaller than about 10 min. of arc, the screen was moved back to a distance of 5 m., and the eyes refocused. The projected positions of the foveas and the optic discs of each eye were marked out on the screen by an opthhalmoscopic projection method (24, 42), which with our present instrument was accurate to within about 1/2°.

For work in the light-adapted state the screen was lit diffusely with a tungsten lamp at a distance of about 5 m. This background measured about 1.0 log cd/m^2, and the light impinging on the screen was bright enough so that fine print could easily be read and objects appeared normally colored. The spectral energy content of the background light is discussed below.

Stimuli consisted of spots of white light or monochromatic light projected onto the screen with a modified slide projector containing a 500-W. tungsten bulb. Stimulus durations of about 1 sec. were produced by a crude mechanical shutter. Monochromatic light was obtained by placing interference filters (Baird Atomic, B-1, half-bandwidth 7 mμ.) directly in front of the projection lens, which was far enough from the screen that the rays could be regarded as practically parallel. Sixteen filters gave wavelengths about 20 mμ. apart over the visible range (400–700 mμ.). Spots at the highest intensities available showed up brightly against the high mesopic background, at all but the longest and shortest wavelengths.

To calibrate the stimulator it was necessary to have a sensitive photometer whose spectral sensitivity was known. We used a Photovolt model 520M (Photovolt Corp., New

York City) with a photomultiplier tube type IP28 (RCA). The spectral-sensitivity curve of the individual tube was supplied by the manufacturer, and this was checked independently by comparing the set of photomultiplier readings for beams of monochromatic light at different wavelengths with readings made on a thermopile (Kipp and Zonen: Delft, Holland, model E-20). The light from the stimulator, having passed through the optical system consisting of slide projector, neutral density wedge, and an interference filter, was directed into the calibrated photometer. With the wedge at some constant setting, readings were made on the photometer for each interference filter, and these were converted into relative energy units and then into quanta. This set of numbers furnished corrections which, when added to the wedge reading, gave the relative energy of any monochromatic beam of light.

The system was calibrated for several projection lamps that had been in use for various periods, and no significant differences were found in the spectral energy content. Although the absorption spectrum of the glass part of the neutral density wedge was taken care of in the over-all calibration, the emulsion was not, since this differed in density for different settings. We therefore recalibrated the stimulator at wedge settings 2 log units apart. From 440 mμ. to 680 mμ. the curves were similar in shape to within 0.02 log units, for our purposes a negligible error. The interference filters together with their blocking filters were calibrated in a Beckman spectrophotometer to check bandwidth and center frequency. It was fortunate that these precautions were taken, since a number of filters were unacceptable and had to be replaced. The whiteness of the screen was examined by comparing readings made directly from the projector (as described above) with readings made upon light reflected from the screen. The reflectivity was constant to within 0.05 log units from 440 mμ. to 660 mμ.

The background lamp was run at less than its rated voltage, and was slightly yellow in appearance. To obtain a measure of its spectral energy content, photometer readings were made with the different interference filters interposed, and the results compared with those obtained when a standard lamp (U.S. Bureau of Standards, color temperature 2,854°K) was used as source. The two curves of energy versus wavelength when placed so as to cross at 540 mμ. deviated so that the background had a spectral content 0.14 log units below that of the standard lamp at 440 mμ., and 0.17 log units above it at 640 mμ.; deviations were proportionately less at intermediate wavelengths. The background was used at a fixed intensity for all measurements to be described, except in the studies of chromatic and dark adaptation, and in studies specifically designed to test the effects of varying background intensity and color temperature.

The animal's eyes were dark adapted by turning out the background light and waiting 1/4 to 1 hour before making further measurements. For chromatic adaptation the white background light was left on, and the monochromatic light from a second identical stimulator was directed so as to fill most of the screen. This light was intensely colored, and the areas of screen lit by it contrasted vividly with the parts lit only with the white light. The white background was kept on in order to keep the retinas light adapted, something that was especially important for chromatic adaptation at long wavelengths. The 1 sec. duration spot was superimposed upon both of these diffuse, steady adapting lights. In several cells we examined the effects of confining the monochromatic adapting light to the center or the surround of the receptive field.

Threshold stimulus intensities were determined by listening for a change in maintained firing while stimulating once every 5 sec., gradually raising or lowering the wedge setting to find the weakest intensity at which some change could be heard. For "on" responses the change took the form of an increase in firing rate while the light was on; for "off" responses it was either the burst of impulses on turning off the light or the suppression of firing while the stimulus was on, whichever was detected first. This procedure has the obvious disadvantage that auditory thresholds may vary with the listener, and may depend upon whether the response is excitatory or inhibitory and upon the amount of maintained activity. The method nevertheless usually gave results reproducible to within 0.1–0.2 log units, and had the advantages of convenience and speed, important in a survey the object of which was to make a variety of studies on each cell and to sample many cells. Many of the irregularities in the curves were probably due to the problems of threshold determinations, and, while more accurate curves would doubtless have been obtained by suitable averaging techniques, we do not feel that this would have changed any of our main conclusions.

Methods of recording have been described in detail elsewhere (21, 23). Tungsten microelectrodes were introduced through a closed chamber. The electrode was protected by a 19-gauge needle, which was stereotaxically inserted vertically until the tip came to rest 2 mm. above the lateral geniculate; the electrode was then advanced by a hydraulic driver. All recordings were extracellular. Criteria for distinguishing cells from fibers have been discussed elsewhere (22). One or two lesions were made in each track (21) and Nissl-stained sections of the formalin-fixed, celloidin-embedded brain were used to reconstruct the tracks. No cells were included in the study unless the track and lesions were histologically identified.

Procedure. When a single cell was identified the eyes were stimulated separately with white light (or with monochromatic light if white was ineffective), and the eye that did not drive the cell was then covered. With the white background light turned on the receptive field was found and the field-center size roughly estimated. Spectral sensitivities were determined by measuring the thresholds for monochromatic light at different wavelengths, first for small (center-size) spots and then for large. Log sensitivity (the negative of log threshold) was then plotted against wavelength. The spectral-sensitivity curves were used as a guide in making the choice of background wavelengths for chromatic adaptation and stimulus wavelength in plotting area-sensitivity curves. Finally, the measurements were remade in the dark-adapted state.

Note on anatomical terminology. The six layers of the lateral geniculate are conventionally numbered from ventral to dorsal, the most dorsal layer being the sixth. This system has the disadvantage that it can be confused with a second system, seldom if ever used today, in which the layers are numbered in the opposite direction. A second difficulty is that of remembering which layers receive input from the contralateral eye and which from the ipsilateral. In the present paper we introduce an alternative system of labeling the layers. The four dorsal, histologically identical small-cell layers we label "D," numbering them D_1 to D_4 from dorsal to ventral. The two ventral (large-cell) layers are labeled "V," and numbered from ventral to dorsal. The six layers in order of penetration from above by an electrode are therefore D_1, D_2, D_3, D_4, V_2, V_1. Reversing the numbering for the ventral layers makes the odd-numbered layers receive input from the contralateral eye, and the even-numbered layers from the ipsilateral. Separate numbering of the dorsal and ventral layers is consistent with the relative histological and physiological uniformity within each set, and the marked differences between them.

RESULTS

Eighteen penetrations were made in 16 monkeys, and 244 units were examined in enough detail to permit their categorization. Spectral sensitivities were determined in 49 of these cells for both large and small spots, and 25 of the 49 were also examined in the dark-adapted state. Physiologically the monkey geniculate turns out to be more complex than that of the cat, the difference being related mainly to a large variety of responses to colored light. In the 4 dorsal layers one can distinguish 3 main cell groups, which we designate type I, type II, and type III. Each of these contains several subgroups. In the ventral layers there are at least 2 major groups. Receptive fields of all of the cells had 1 common feature, that of circular symmetry, and the great majority (though not all) showed a concentric center-surround arrangement. No directional asymmetries were seen with stationary or moving stimuli, and no cells showed the types of complex behavior seen in the cat and monkey cortex. In these respects the geniculates of cat and monkey seem to be similar.

In the following paragraphs we first describe the properties of dorsal layer cells, considering the behavior of the three main groups, first in the light-adapted state and then in the dark-adapted state. Next, we discuss the

organization of the four dorsal layers, considering the distribution of different cell types within the layers and the size of receptive fields. Finally, we describe the cells of the two ventral layers.

DORSAL LAYERS

Type I cells: center-surround fields and opponent-color responses

Two hundred thirteen cells were recorded in the four dorsal layers. Of these, 164, or 77%, were classed as type I (see Table 1). A cell was placed in this group if it had a receptive field with an antagonistic center-surround arrangement and if the center and surround had different spectral sensitivities. These properties may best be illustrated by an example.

Figure 1 shows the responses of a type I cell situated in the most dorsal layer (D_1). A white spot illuminating the center of the field gave a brisk on-response (lower left record, Fig. 1); a white spot covering the entire receptive field gave no response.[2] A small red spot made by placing a 620-mμ.

Table 1. 213 cells recorded from the dorsal layers

Layer	Type I					Type II	Type III		Totals
	Red, on-center	Red, off-center	Green, on-center	Green, off-center	Blue, on-center		On-center	Off-center	
D_1	39 (45%)	11 (13%)	12 (14%)	2 (2%)	2 (2%)	4 (5%)	11 (13%)	6 (7%)	87
D_2	19 (37%)	8 (16%)	9 (18)%	5 (10%)		5 (10%)	2 (4%)	3 (6%)	51
D_3	10 (23%)	13 (30%)	6 (14%)	4 (9%)	1 (2%)	3 (7%)	1 (2%)	5 (12%)	43
D_4	7 (22%)	6 (19%)	8 (25%)	2 (6%)		3 (9%)	0	6 (19%)	32
Totals	75 (35%)	38 (18%)	35 (16%)	13 (6%)	3 (1%)	15 (7%)	14 (7%)	20 (9%)	
	164 (77%)					15 (7%)	34 (16%)		213

interference filter in front of the stimulator evoked a vigorous on-response. A large spot of the same intensity produced a similar response, neither weaker nor stronger. This suggested that the center was sensitive to light of long wavelength but that the periphery was not, since including it had no effect upon the response. A blue spot of center size evoked no consistent change in the irregular background discharges, whereas a large blue spot suppressed the maintained firing and evoked a brisk off-discharge. Thus within the receptive field only the surround was sensitive to short wavelengths.

In summary, the receptive field as examined by these rough tests appeared to have an excitatory center and an inhibitory periphery, with the center differentially sensitive to long wavelengths and the surround to short wavelengths. The responses to white light, seen in the lower records of Fig. 1, can now be understood as the resultant of the effects of long and short wavelengths. On the other hand, the responses to diffuse light, shown to the

[2] So far, these responses are typical for an on-center geniculate cell in the cat. However, using monochromatic light it became clear that the situation was more complex.

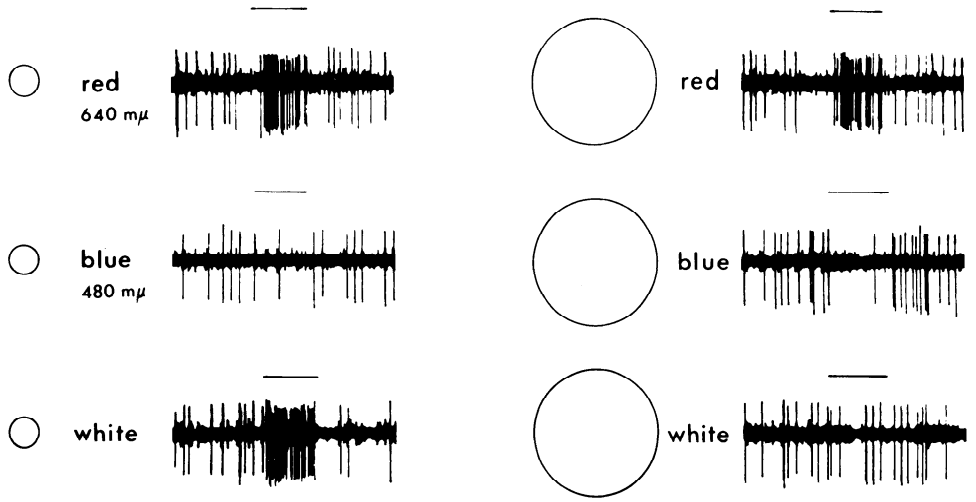


FIG. 1. Responses of a dorsal-layer geniculate cell to white and monochromatic light. Top line, *red*, 640 mμ.; middle line, *blue*, 480 mμ.; bottom line, *white*. *Left:* illumination of field center with 1/2° spot. *Right:* illumination of whole receptive field. Colored spots were produced by placing an interference filter in the beam of white light. They therefore contain far less energy than the white stimuli. Light-adapted state. Field center 19° from the fovea, 6° below the horizontal meridian. Recorded from layer D_1. Further studies of this cell are illustrated in Figs. 2–4.

right in the figure, suggest immediately that the cell was specialized to register color stimuli, and was not particularly interested in diffuse white light.

Measurements were made in this cell to determine spectral sensitivities of the center and surround, separately and together, and to establish more accurately the spatial distributions of the two systems. Here, as in every cell in which measurements were made, our first step was to determine sen-

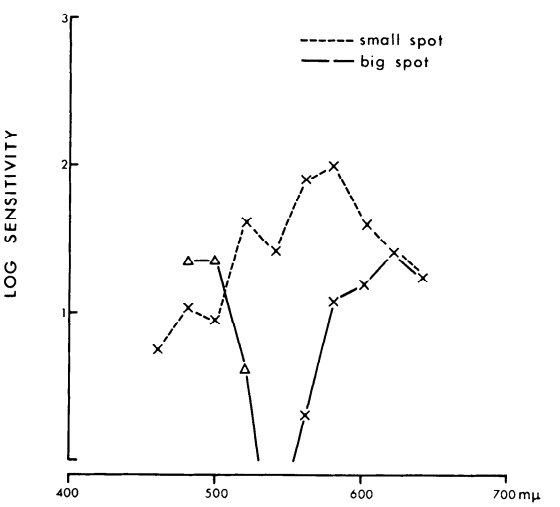


FIG. 2. Spectral sensitivity of the red on-center geniculate cell of Fig. 1. Relative sensitivities obtained by determining log reciprocal thresholds. Crosses = on-responses; triangles = off-responses. No response to 540 mμ. at any available intensity. Light-adapted state; stimuli are superimposed on a 1 cd/m² steady diffuse white background. (In this and other similar curves, points corresponding to "no response" are either omitted or plotted as circles slightly below zero on the log sensitivity scale.)

sitivities at different wavelengths, first for a center-size spot and then for a large one. This relatively simple procedure gave enough information to categorize the cell. In Fig. 2 sensitivities are shown for center-size spots with interrupted lines and for large spots with continuous lines; crosses designate on-responses and triangles off-responses. The peak sensitivity of the center system (interrupted lines) was at about 580 mμ. At long wavelengths the small-spot and large-spot curves almost coincided, reflecting the insensitivity of the periphery to red. As wavelength was progressively shortened, the influence of the inhibitory surround became more and more powerful. Thus between 560 and 600 mμ., sensitivities to large spots fell below those to small ones, indicating that over this range there was peripheral suppression. At 540 mμ., the neutral point, the two effects balanced and a large spot gave no response at any available intensity. At still shorter wavelengths the surround dominated the center and large spots evoked off-responses. This inhibitory limb of the curve for large spots might well have been displayed below the wavelength axis, but the use of a log sensitivity scale made this awkward. It will be noted that at 480 mμ. and 460 mμ. a bright center-size spot evoked an on-response. The small blue spot used in Fig. 1 was evidently below threshold for a response.

To determine the spectral sensitivity of the receptive-field periphery alone, the most direct method would be to use an annulus. Technically this was difficult because of the small center size, and we therefore studied the opposing systems separately by chromatic adaptation of the entire receptive field. With the white background still on to avoid dark adaptation, the screen was flooded with diffuse light at 640 mμ., a wavelength to which presumably only the center system was sensitive (Fig. 2). With this background the spectral sensitivity to large monochromatic spots, measured as before by observing the cell's transient response, is given by the curve labeled 640 in Fig. 3. Off-responses were now evoked from 460 mμ. to 580 mμ., and the peak response, though not well defined, was somewhere around 540 mμ. The effect of the adapting light in suppressing the center system was the same whether it was confined to the center or covered the entire receptive field, and in fact it now made no difference whether the stimulus was an annulus covering all but the center system, or a large spot. This curve was therefore taken to represent the spectral sensitivity of the surround. By using an adapting light at 460 mμ. the effectiveness of the surround region was differentially reduced, and under this condition the sensitivities to diffuse light (dotted line, labeled 460) were about the same as those obtained with a small spot, shown in Fig. 2. The mechanism underlying these differential adaptation effects is taken up in the DISCUSSION.

To measure the size of the receptive-field center, thresholds were determined for different spot sizes, first using red light at 640 mμ. and then green at 520 mμ. The area-sensitivity curve for the center system was made using a white background light. Because of the overlap of the two systems at short wavelengths, the field periphery was measured using, in addition to the

white background, a steady diffuse adapting light at 640 mμ. These values for stimulating and adapting wavelengths were chosen using information given in Fig. 3. The two area-sensitivity curves are shown in Fig. 4. Sensitivity to red light increased from 1/8° ,the smallest spot to evoke a response at any available intensity, to 1/2°, where it leveled off; 1/2° was therefore taken as the field-center size. The peripheral response to 520-mμ. light was first seen at 1°, and the curve leveled off at about 6°, which was taken to be the total field diameter. (Because of the differences in background light, the relative sensitivities of center and surround cannot be compared using these two curves.)

To sum up, the receptive field consisted of a 1/2° excitatory center with a spectral sensitivity peak in the high 500s, and a peripheral inhibitory zone

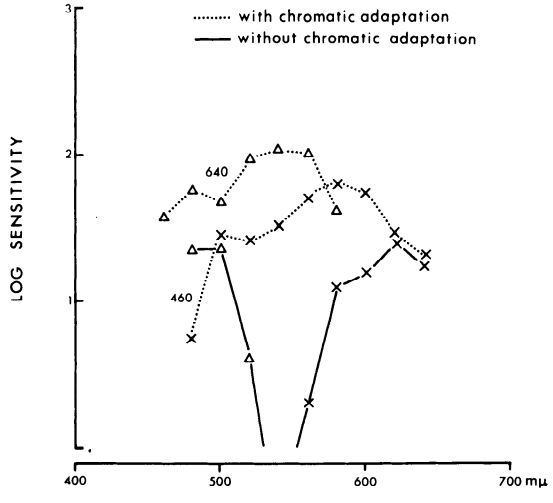


FIG. 3. Effects of chromatic adaptation on responses to diffuse light. Same cell as in Figs. 1 and 2. Continuous lines, reproduced from Fig. 2, show responses to large spots against the constant 1 cd/m² white background. A steady monochromatic diffuse 640-mμ. light was now added to the white background, and with large spot stimulation the sensitivities are given by the dotted curve marked 640. All responses from 460 mμ. to 580 mμ. were inhibitory (triangles). Similar chromatic adaptation with light at 460 mμ. resulted in the second dotted curve marked 460. All responses were now "on" (crosses), from 480 mμ. to 620 mμ., and the curve was roughly the same as that for center-size spots, shown in Fig. 2.

6° in outer diameter with maximum sensitivity in the mid-500s. Given three sets of cones with peak absorption spectra at about, 445, 535, and 570 mμ. (5, 30), the results at once suggest that the geniculate cell received excitatory input from the red-sensitive cones in the field center, and inhibitory input from green-sensitive cones in the periphery. This cell seems identical to the "red-green" type already described by De Valois and co-workers (12) in the monkey lateral geniculate body. De Valois was not concerned with spatial aspects of stimulation, but using chromatic adaptation and diffuse light stimulation he found that the two opponent systems had peak spectral sensitivities around 540 and 580 mμ.

As discussed below, it seems most likely that only red- and green-sensitive cones provided the input to this cell, but it is conceivable that the field periphery received contributions from the blue-sensitive cones also. Evidence that this cell received input from rods as well as cones is presented below, in the section on dark adaptation.

Subgroups within type I

The cell just described belonged to a subgroup which we term "red-on center, green off-surround." This was by far the commonest subgroup, there being 75 examples of a total of 213 dorsal-layer cells (35%). Assuming the existence of both on-center and off-center fields, and given three cone types, there are obviously many possible subgroups within type I. Besides the red on-center cell just described, we have seen four other varieties, several of which are described in the following paragraphs (see also Table 1).

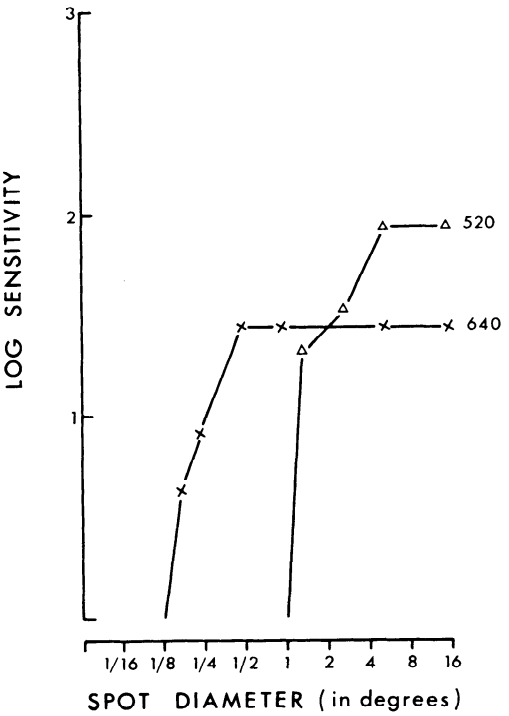


FIG. 4. Area-sensitivity curves for two wavelengths of monochromatic light. Same red on-center cell as in Figs. 1–3. Sensitivities were first determined for various sizes of spots at 640 mμ., against the usual white background. On-responses indicated by crosses. With 520-mμ., spots and a steady background of 640-mμ. diffuse light added to the white, off-responses were evoked (triangles). Inbhiitory effects with short wavelengths were seen only for spots 1° and over, and the effect leveled off at about 6°. Because of the difference in backgrounds the sensitivities of the two systems cannot be compared in this figure.

Thirty-eight cells (18% of 213) had fields of the "red off-center, green on-surround" type, an arrangement that was, in a sense, the reverse of that found in the cell just described. An example of one of these is given below in the section on dark adaptation. "Green on-center, red off-surround" was a combination that occurred in 35 of the 213 cells recorded in the dorsal layers (16%). Figure 5 shows spectral-sensitivity curves for a cell of this type; they are similar to the curves of Fig. 2, the two sets being roughly mirror images of one another. A "green off-center, red on-surround" combination was found for 13 cells (roughly 6%). Thus many examples were seen of the four possible red-green combinations. On the other hand, there were only three clear examples of type I cells that received a blue cone contribution. The cell of Fig. 6 had a field with a blue-sensitive on-center and a

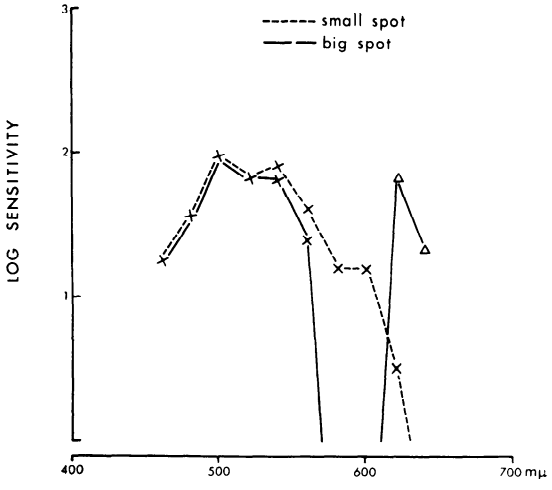


FIG. 5. Spectral sensitivities for small spots and large spots, in a "green on-center, red off-surround" cell recorded from layer D_2. Field center 10–12 min. in diameter, situated 10° from the fovea.

green-sensitive off-surround, the two opponent systems having spectral-sensitivity peaks at about 450 mμ. and 540 mμ. No examples were seen of cells receiving opponent inputs from blue- and red-sensitive cones.

To identify a particular cell as a member of one or another subgroup it was not necessary to make detailed measurements of the type just described. In order to classify enough cells to study the distribution of the different subtypes in the geniculate, some quick means of identification was necessary. Using white spots we usually first established the center-surround arrangement and the field-center position and size; then with monochromatic light

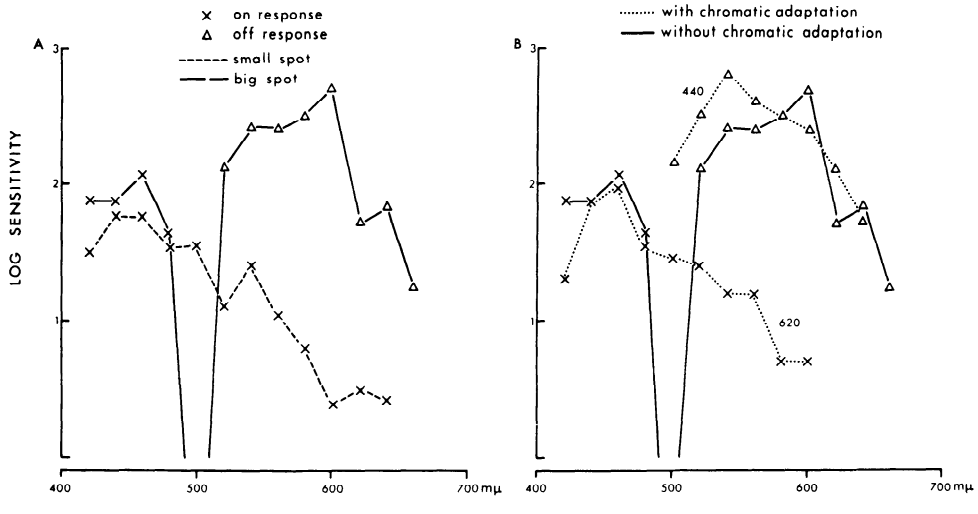


FIG. 6. Spectral sensitivities of a type I "blue on-center, green off-surround" cell recorded in layer D_2. Field center 1/2° in diameter, situated 9° from the fovea. *Left:* spectral sensitivities for small-spot and large-spot stimulation. *Right:* effect of chromatic adaptation at 620 mμ. and 440 mμ. upon the responses to large spots. Conventions as in Figs. 2–5.

peripheral suppression was compared at different wavelengths, and the neutral point determined. This gave enough information to identify the cell group. Detailed measurements, like those described above, were made in about one-fifth of the cells.

The balance between the center and surround systems varied from cell to cell, as reflected in the position of the neutral point and in the type of response, "on" versus "off," to white light. A cell-to-cell variation in the balance between opponent systems was far more prominent in type I cells than in type II.

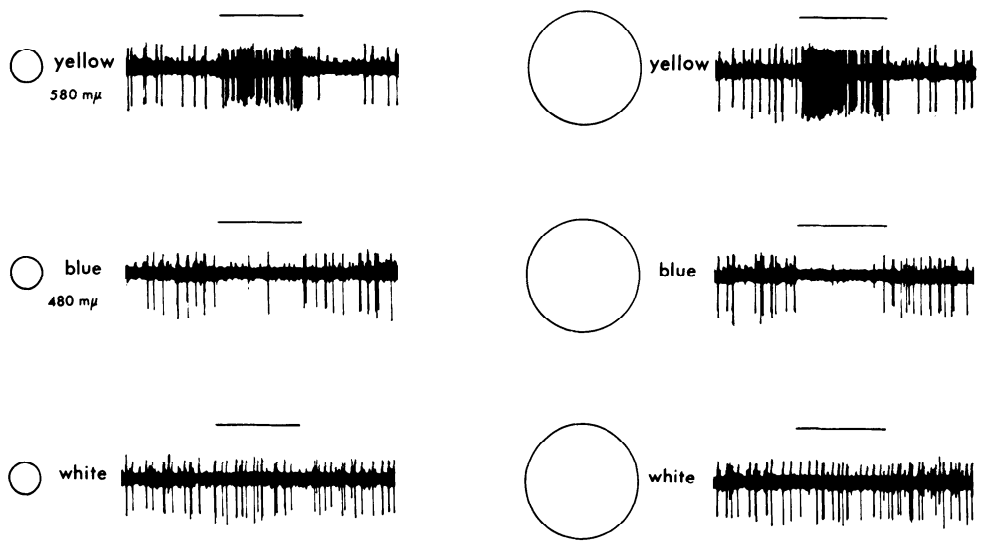


FIG. 7. Responses of a type II "blue-off, green-on" cell. Top line, *yellow*, 580 mμ.; middle line, *blue*, 480 mμ.; lower line, *white*. Small spots, 3/8° in diameter; large spots, 6° in diameter. Cell located in layer D_2, at the posterior tip of the lateral geniculate. Field 1/2° in diameter, about 1° from the fovea.

The neutral point of the individual type I cell varied also to some extent with the intensity and spectral composition of the "white" background light. To estimate roughly the importance of color balance we compared the neutral points of several type I cells before and after filtering the background light through Wratten 85 or 80B color-balance filters (Eastman Kodak Co., Rochester, N.Y.). These filters made the background distinctly yellowish or bluish, and yet changed the neutral point in either direction by less than about 10 mμ. Varying the intensity of the background with neutral density filters likewise tended to influence the neutral point, usually in a direction predictable from the response to diffuse white light.

Type II cells: opponent-color responses; no center-surround arrangement

Type II cells were in many respects the most remarkable of the dorsal layer cells. Like those of type I they showed opponent-color responses, but

their fields differed in having no trace of any center-surround arrangement. Only eight examples were seen and studied well enough to allow positive identification, suggesting that they are rather rare.

Responses of a typical type II cell are illustrated in Fig. 7. The receptive field occupied a region 1/2° in diameter, situated about 1° from the fovea. Within this area, on-responses were evoked by a 580-mμ. spot regardless of its exact size or position. As shown in the upper row of Fig. 7, large spots evoked more vigorous responses than small ones. A blue spot at 480 mμ. suppressed firing throughout the field, and again the effect was more marked the larger the spot (middle row). White light, containing much more energy

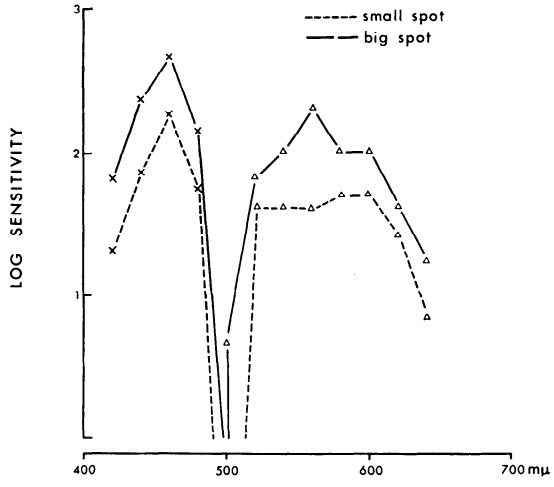


FIG. 8. Spectral sensitivities of a type II "blue-on, green-off" cell from layer D_2. Field 1/2° in diameter, 9° from fovea. Small spots were about 0.4° in diameter, large spots 10°.

than either of the monochromatic stimuli, evoked no obvious response regardless of the size or shape of the spot. The simplest interpretation of these findings is that the cell received input from two populations of cones, one excitatory and the other inhibitory, and that these two sets of receptors were distributed in an almost identical way throughout the circular 1/2° region.

Figure 8 gives the spectral sensitivities of a type II cell whose behavior was similar to that of the cell just described, but with responses of opposite sign, "on" to short wavelengths and "off" to long. Neither white light nor a 500-mμ. monochromatic light gave any obvious responses, again regardless of shape, position, or intensity. The interrupted lines refer to spots slightly smaller than the 1/2° field, and continuous lines correspond to 10° spots. The two curves were similar in shape and virtually parallel, the increased sensitivity to the larger spots reflecting spatial summation within the receptive field. The neutral point was at 500 mμ. for all spot sizes and shapes. These curves were thus quite different from the corresponding ones for type I cells (Figs. 2, 5, 6*A*), where the neutral point could be shifted from one end of the spectrum to the other by changing the region of the field that was stimulated.

The most direct evidence that the two opponent systems converging upon this cell had the same spatial distributions came from a comparison of area-sensitivity curves. Figure 9 shows two curves, one for on-responses using spots at 460 mμ., the other for off-responses to spots at 560 mμ. The curves were almost identical, indicating that the two systems were balanced throughout the field. On comparing area-sensitivity curves of type I cells (Fig. 4) with those of type II (Fig. 9), the difference in arrangement of receptive fields is obvious at a glance.

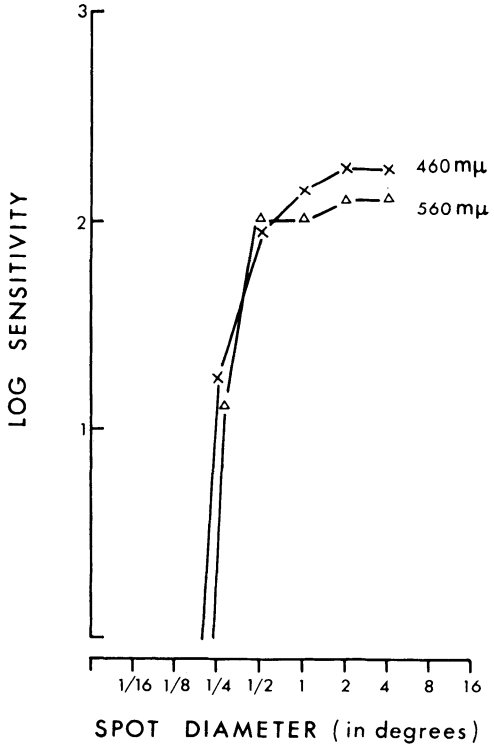


FIG. 9. Area-sensitivity curves for the cell of Fig. 8, for light at 460 mμ. (on-responses) and 560 mμ. (off-responses). Background in both cases white, 1 cd/m².

Chromatic adaptation was used in an attempt to obtain the spectral sensitivities of the two systems. Figure 10 shows the results of adapting *1*) with light at 440 mμ. and *2*) with light at 620 mμ. The two resulting curves (dotted) have their peaks at about 460 mμ. and 530 mμ., suggesting that the excitatory input was from blue-sensitive cones and the inhibitory input was from the green. That the two opponent systems had overlapping spectral sensitivities was confirmed by adapting with light at 500 mμ., i.e., light that was precisely at the neutral wavelength and evoked no response at any available intensity (cf. Fig. 8). Flooding the screen with this light, on top of the white background, produced a uniform suppression in sensitivity at all wavelengths, shown by the curves of Fig. 11.

The eight most thoroughly studied type II cells had properties practically

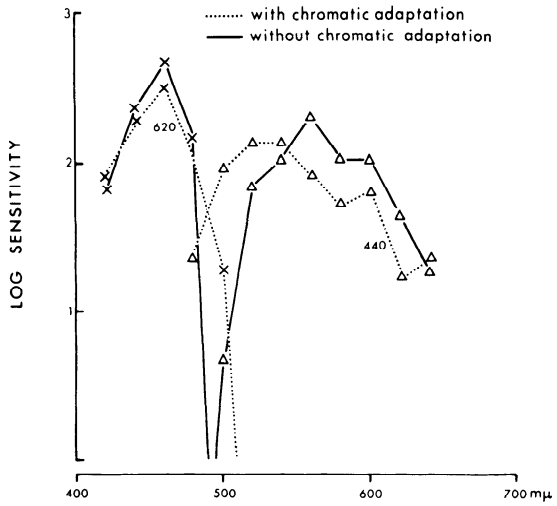


FIG. 10. Effects of chromatic adaptation on large-spot responses of the cell of Figs. 8 and 9. Adapting lights at 620 mμ. and 440 mμ.

identical to those of the two just described. All had neutral points at 500 mμ., with spectral sensitivities suggesting opponent inputs from both blue and green cones. In all these examples the spatial distributions of the opponent systems seemed to be identical. Besides these cells there was a group of seven that had neutral points at 600 mμ., and whose spectral sensitivities suggested opponent inputs from red and green cones. These cells were not thoroughly studied, and it is not clear whether any of them were truly type II cells, i.e., whether they had opponent systems with identical spatial distributions. The results we did obtain suggested that the two components of the receptive field had spatial distributions that overlapped but were not

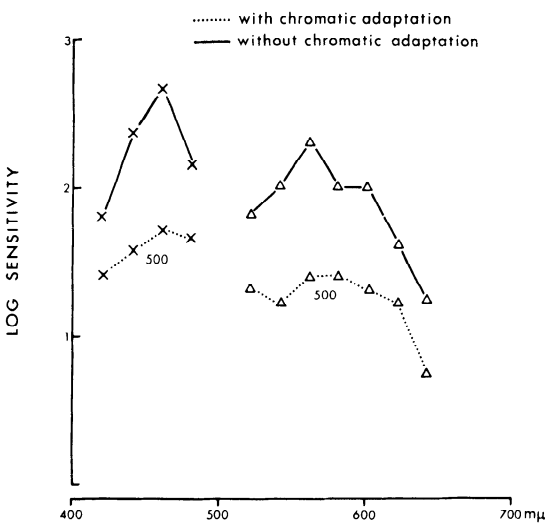


FIG. 11. Effects of chromatic adaptation with light at 500 mμ., the neutral wavelength, in the cell of Figs. 8–10. Though producing no response by itself, the adapting light lowered the sensitivity of the cell to stimulation at other wavelengths.

identical. The over-all size of the regions occupied by the opponent systems seemed to differ slightly, with the suggestion that one component (the excitatory or the inhibitory) prevailed in the center and the other toward the periphery. The arrangement may thus be similar to that described by Wolbarsht, Wagner, and MacNichol (49) for some goldfish retinal ganglion cells. These cells are for the time being classed as type II in Table 1.

Type III cells: no opponent-color mechanism

Of 213 cells recorded in the dorsal layers, 34, or 16%, were classed as type III cells. These were defined as cells showing no opponent-color re-

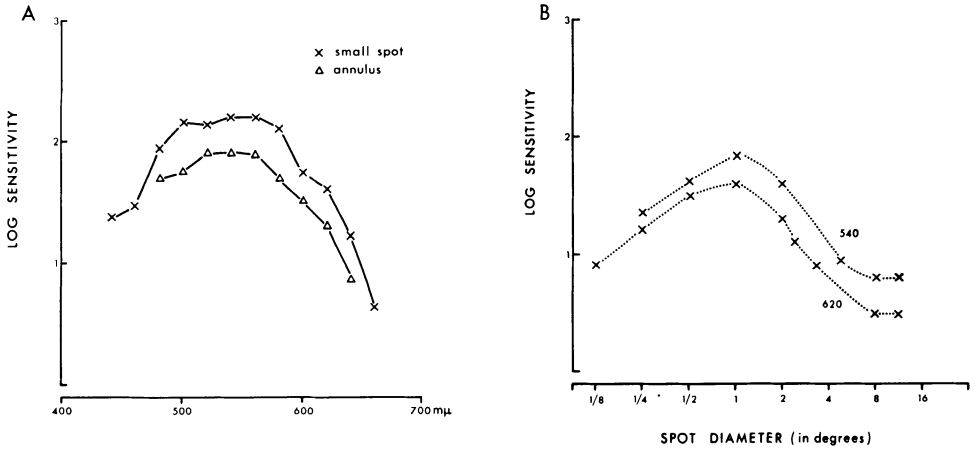


FIG. 12. Type III cell with an on-center 1° in diameter, located 25° from fovea. Recorded from layer D_1. *A:* spectral sensitivities to small spots 1° in diameter, and annuli with inner diameter 1°, outer diameter 8°. Light-adapted state. *B:* area-sensitivity curves at two wavelengths, 540 mμ. and 620 mμ.

sponses. Receptive fields were subdivided into center and concentric surround, some centers being excitatory and others inhibitory. In most cells there was moderate or marked peripheral suppression, with little or no response to diffuse light, but in some the effect of the periphery was small or even negligible. For all cells, however, the peripheral suppression was the same at all wavelengths.

Figure 12 shows some results from a typical type III on-center cell. In Fig. 12*A* spectral sensitivities are given for the on-responses evoked by a 1° center spot (crosses), and off-responses from a 1°–8° annulus covering all of the receptive field except the center area (triangles). The two curves are nearly parallel, showing that there was little or no difference in the spectral sensitivities of the two opposing systems. This would mean, as a corollary, that peripheral suppression should be just as pronounced at all wavelengths, and this was directly demonstrated by further measurements. Figure 12*B* shows area-sensitivity curves made at two different wavelengths, 540 mμ.

and 620 mμ. For each wavelength the sensitivity increased (spatial summation) for spots up to about 1°, the diameter of the field center. Sensitivity then decreased progressively (peripheral suppression) up to 5° or 6°, where it leveled off, indicating the outer boundary of the field. The shapes of the two curves are almost identical. This result is to be contrasted with that obtained for a type I cell in Fig. 4, in which entirely different area-sensitivity curves were obtained at two different wavelengths, and with that for a type II cell shown in Fig. 6 in which the curves were identical, but the responses were of opposite sign. Behavior of this type III cell in the dark-adapted state is discussed below.

It is probably easiest to understand the behavior of a type III cell by supposing that it receives an excitatory input from cones in one part of the receptive field (center or surround) and inhibitory input from the remainder, and that in these two sets of cones the relative representations of the three cone types are the same. From cell to cell the relative contributions of the three cone types doubtless differ, since the spectral-sensitivity curves of different cells have different peaks. This has long been known to be so for retinal ganglion cells in the cat (19), which resemble type III cells in most respects. Type III cells are probably the same as the nonopponent broad-band cells described in the rhesus monkey by DeValois (11). Further evidence that more than one cone type supplies these cells has been obtained by chromatic adaptation studies (Fig. 20*B*).

To sum up the properties of these dorsal-layer cells, there seem to be three rather sharply defined types: type I with center-surround receptive fields, in which center and opposing surround have different spectral sensitivities; type II with two opposing systems having different spectral sensitivities and identical spatial distributions; and type III with opponent center and surround systems having the same spectral sensitivity. In addition, a few cells seem to have properties somewhere between those of type I and type II, but these have not been thoroughly studied.

Cells of all three types had the interesting property that on-off responses were rare. This is in marked contrast to retinal ganglion cells and geniculate cells in the cat (26, 28) and to retinal ganglion cells of the goldfish (48), where on-off responses are often seen when opponent systems are simultaneously stimulated. The absence of on-off responses in the monkey presumably indicates that the on-system and the off-system have similar time courses, excitation in one always being opposed by inhibition in the other.

Dark adaptation

We were naturally interested in learning whether all types of geniculate cells were connected to both rods and cones, or whether some were connected to rods and others to cones. Twenty-five cells were therefore observed and categorized first in the light-adapted state and then after dark adapting the eyes for 15–20 min.

Type I cells. Not all cells in this group were affected in the same way by

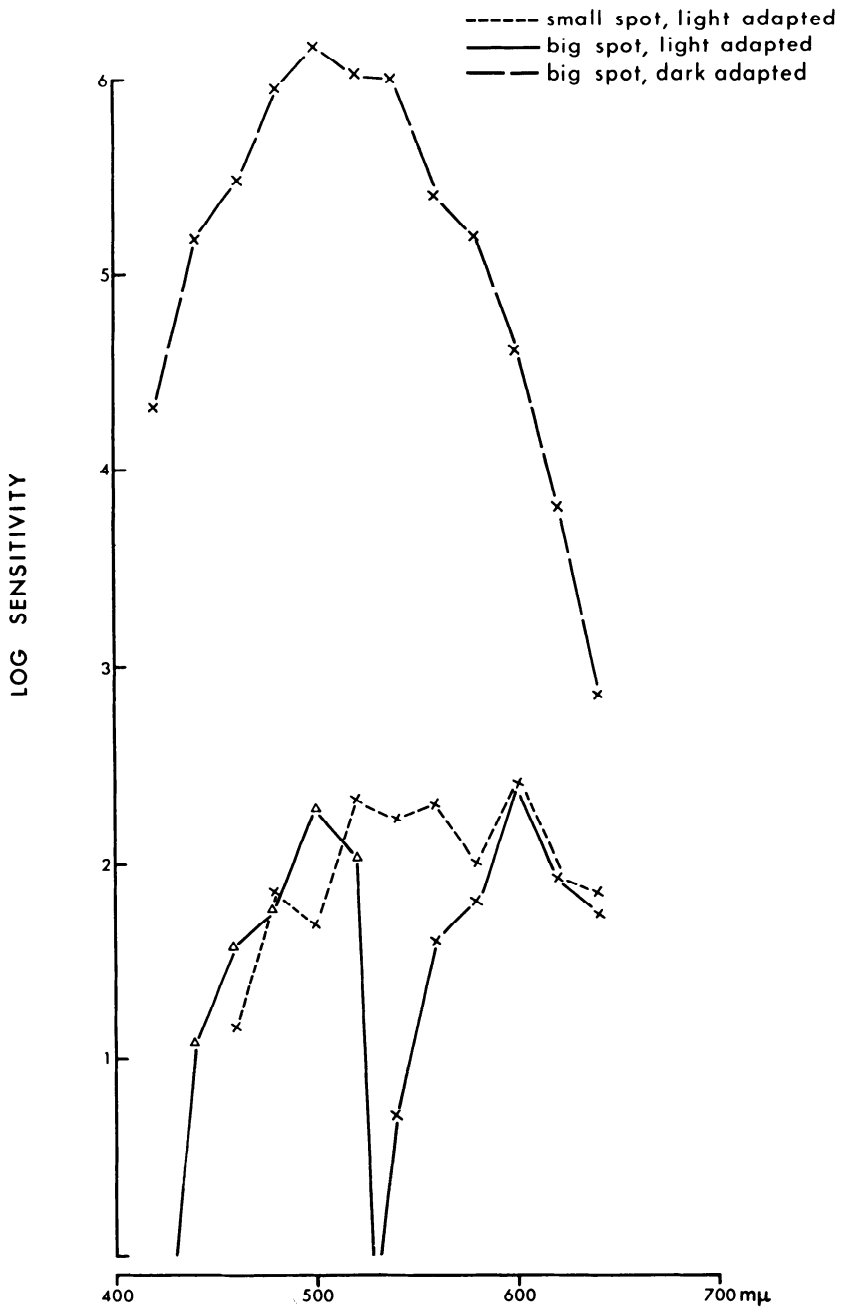


FIG. 13. Dark-adaptation effects in a type I red on-center cell in layer D_4. Field center 1/2° in diameter, situated 19° from the fovea. Lower curves show spectral sensitivities to small and large spots in the usual way (cf. Figs. 2, 5, and 6), with a 1 cd/m^2 white background light. Eliminating practically all the background for 15 min. produced the marked increase in sensitivity and shift in the maximum on-response sensitivity toward the short wavelengths shown for big spots by the upper curve. All responses were now "on" in type. Note that for wavelengths below 520 mμ., responses to large spots were "off" in light adaptation, "on" in dark adaptation. As far as one could tell the change occurred immediately upon switching the background light on or off.

dark adaptation. An example of one pattern of adaptation is given in Fig. 13. The cell was a typical red on-center, green off-surround, similar to the cell of Figs. 1–4 (which, in fact, reacted to dark adaptation in the same way). After 15 min. dark adaptation the cell's sensitivity increased by about 4 log units, as shown in Fig. 13 by the interrupted curve. With diffuse light, on-responses were now obtained throughout the spectrum, with peak sensitivity at about 500 mμ. Our own thresholds for perceiving the spot with dark-adapted eyes agreed to within a few tenths of a log unit with those obtained for the cell. Moreover, for all wavelengths below about 620 mμ. the spot appeared colorless at threshold intensities and for the first few log units above threshold.

We conclude that this cell received input from rods as well as from cones. Thresholds were the same in the dark-adapted state for a center-size spot and for diffuse light, indicating that any rod contribution from the surround was not detectable at levels of intensity that were capable of stimulating the cell from the field center. Unfortunately the periphery of the field was not tested at suprathreshold scotopic levels, so that we do not know whether the cell made connections with rods in the field periphery.

The shift in response patterns between the two states of adaptation took place very quickly, this being especially obvious when the change in background reversed the response type from "on" to "off" and vice versa. Thus for the cell of Fig. 13, diffuse light at 500 mμ. gave off-responses with the background turned on, and on-responses with the background off. Here the response type reversed with a delay too short to be detected on rough testing, but certainly no more than a few seconds. It should be emphasized that the background in the light-adapted state was probably not intense enough to produce much bleaching of rod pigments; with a high photopic background the rods would undoubtedly have taken several minutes to reassert themselves.

Four of the 17 type I cells examined in the dark-adapted state had input from rods, showing similar increases in sensitivity and a Purkinje shift. In all four the response evoked from the center in dark adaptation ("on" or "off") corresponded to the center-type response in light adaptation. There was no obvious change in field-center size with dark adaptation, and stimuli that were threshold for the center seemed to have no influence on the periphery.

The remaining 13 type I cells showed neither a Purkinje shift nor any comparable increase in sensitivity on dark adaptation. The red off-center cell of Fig. 14 is an example. Spectral-sensitivity curves for small spots and for diffuse light were typical for red off-center cells. The diffuse-light curves are plotted in Fig. 14*A* in the light-adapted state and after 15 min. of dark adaptation. Each opponent system increased in sensitivity by roughly 1 log unit, and there was little difference in the cells' behavior, with peripheral suppression occurring at intermediate wavelengths as before. The thresholds of our own dark-adapted eyes were several log units lower than those of the

cell, and it was interesting to observe that the cell began reacting to the stimuli at about the intensities at which the spot first appeared colored.

While making the determinations on this cell we noticed a second, simultaneously recorded unit of lower spike amplitude, which turned out to have a much lower threshold, one close, in fact, to that of our own dark-adapted eyes. A spectral-sensitivity curve of this cell was made for comparison, and

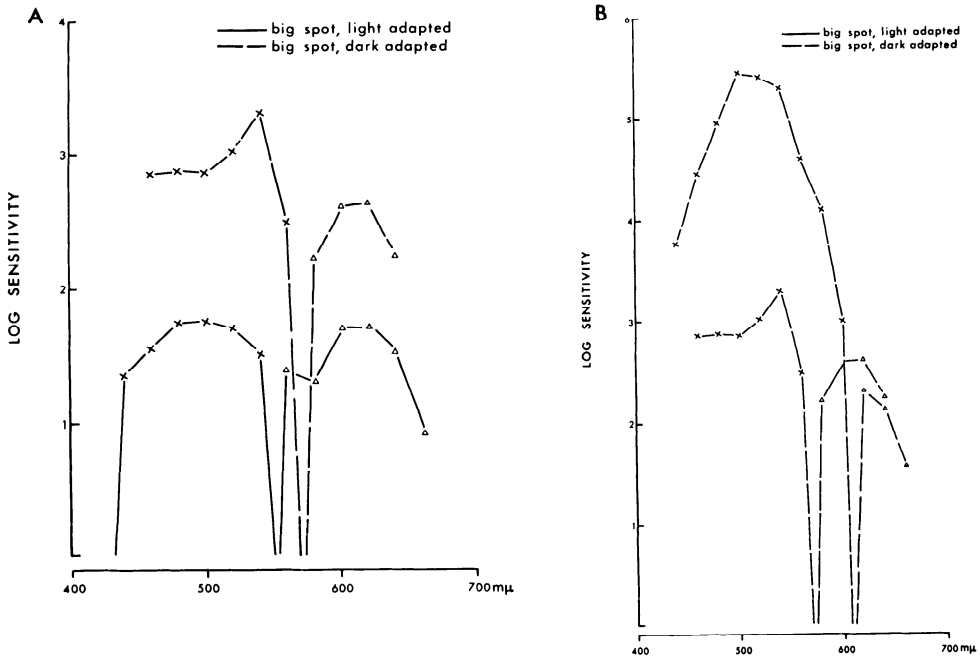


FIG. 14. Effects of dark adaptation in a type I cell with a red sensitive off-center 3 1/2° from the fovea. Recorded from layer D_2. Center size was 1/4° and the whole field was about 4° in diameter. *A*: spectral sensitivities for large spots before and after dark adaptation. Both systems increased in sensitivity, but only by about 1 log unit. *B*: comparison of dark-adaptation effects in the cell of *A* with that of a simultaneously recorded green on-center, red off-surround cell. Though studied under identical conditions, one cell has sensitivity some 2 log units greater than the other.

is shown in Fig. 14*B*. Thresholds were as much as 2 log units lower than those of the first cell, with peak sensitivity at about 520 mμ. This type I cell was a green on-center. It seems clear from this that cells with only cone input can exist side by side in the geniculate with cells having both rod and cone connections.

To sum up these results, some geniculate type I cells have connections with rods and cones, as manifested by about a 4 log unit increase in sensitivity, a disappearance of opponent-color effects at scotopic stimulus levels, and a shift in peak spectral sensitivity to the low 500s. Others show none of these changes and appear to make connections with cones only, even though

having their fields outside of the fovea, where rods are abundant. The relative frequency of cells with and without rod input is not at all clear, but presumably it varies with position of receptive fields in the visual field, so that a thorough study would require a generous sampling from different parts of the geniculate.

Type II cells. Two type II cells were examined with the eyes dark adapted. In both there was an increase ins ensitivity of about 0.5–1 log unit

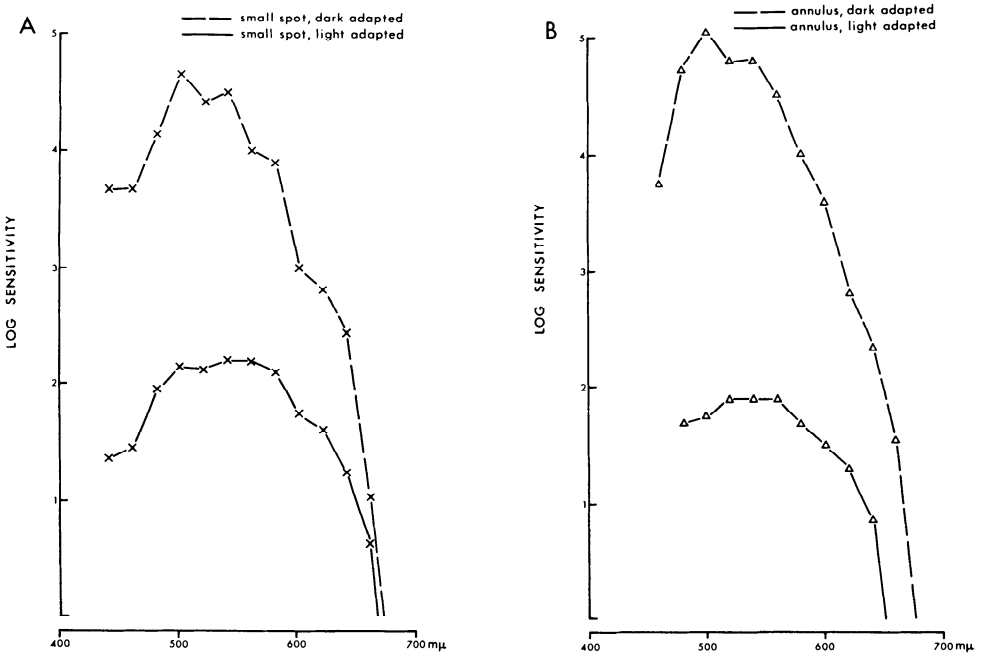


FIG. 15. Effects of dark adaptation in the cell of Fig. 12. *A*: on-responses to 1° spots. *B*: off-responses to an annulus, inner and outer diameters 1° and 6°, respectively. A suprathreshold 1° white spot was directed steadily on the field center during these measurements, so that thresholds are not strictly comparable with those of *A*.

for both systems, with no change in neutral point, suggesting a lack of any rod input. (It is worth noting that once again changing the white background light produced some change in sensitivity, even though white light, like the 500-mμ. light, evoked no response itself.)

Type III cells. Of the four dorsal-layer type III cells tested, two showed only a slight increase in sensitivity with no Purkinje shift, suggesting that they lacked connections with rods. The other two cells increased markedly in sensitivity and showed a clear shift in spectral sensitivity. One of these, an on-center cell, was studied in some detail. The results for the light-adapted state have already been given in Fig. 12. There it was shown that center and surround had practically identical spectral sensitivities and that peripheral suppression was the same at two widely separated wavelengths.

When the eyes were dark adapted the threshold fell by over 2 log units (Fig. 15). At stimulus intensities just above threshold a large spot gave a weaker response than a small spot, indicating that rods fed into the cell from both center and surround, in opponent fashion. For a center-size spot the spectral sensitivity, shown by dotted lines in Fig. 15*A*, had a peak in the low

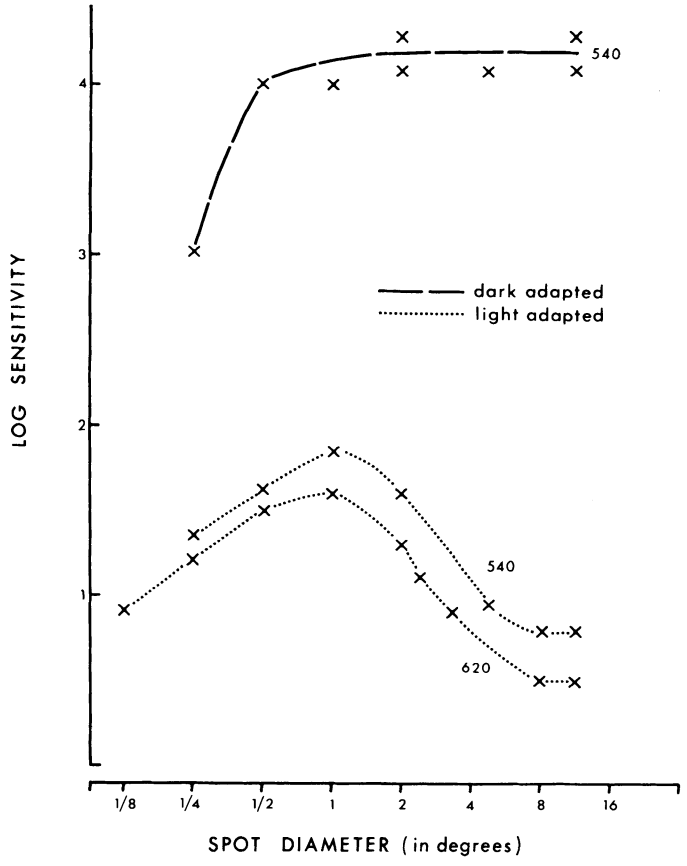


FIG. 16. Area-sensitivity curves for the cell of Figs. 12 and 15. Lower curves, light-adapted state for spots at 540 mμ. and 620 mμ. (redrawn from Fig. 12*B*). Upper curve, dark-adapted state.

500s, being displaced to the short end of the spectrum compared with the light-adapted curve. Stimulation of the surround alone failed to evoke any response. If, however, a just-suprathreshold white spot was directed on the center and left there, monochromatic stimuli now evoked clear peripheral responses in the form of suppression of firing with off-discharges. Thresholds for these responses at different wavelengths are shown in the upper, interrupted curve of Fig. 15*B*. Again there was a marked threshold decrease with a clear Purkinje shift giving further evidence that rods from the periphery of the field were connected to the cell.

On comparing the area-sensitivity curves for light and dark adaptation in Fig. 16, it appears that the field-center size remained about the same in the two states, yet to our surprise the contribution of the periphery was not evident, there being no decline in sensitivity for large spots. Stimuli that were just suprathreshold, on the other hand, evoked much stronger responses from the center than from the whole receptive field, indicating that the surround made an important contribution, and that its threshold was in fact

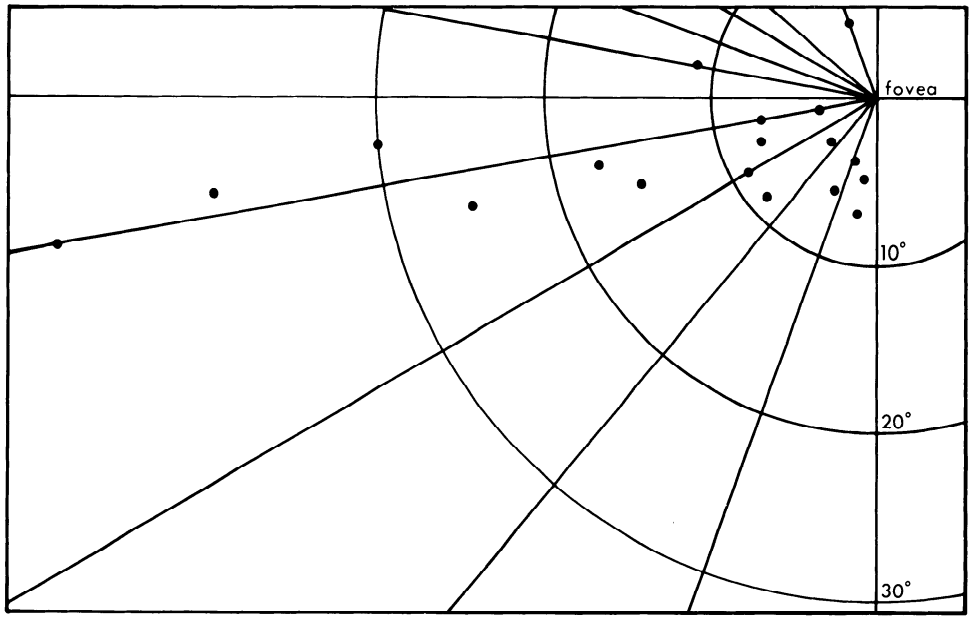


FIG. 17. Regions of visual fields explored in 18 penetrations of the lateral geniculate. Each dot represents the average visual-field position of the receptive fields in a single penetration. Most penetrations were normal to the geniculate layering, so that there was little variation in the positions of the individual receptive fields.

not much higher than that of the center. Once more it was as if some activation of the center was necessary before the peripheral effect could manifest itself.

In summary, of four type III cells tested in dark adaptation, two had rod input from both center and surround and two appeared to lack rod input.

Distribution of cell types in the dorsal layers

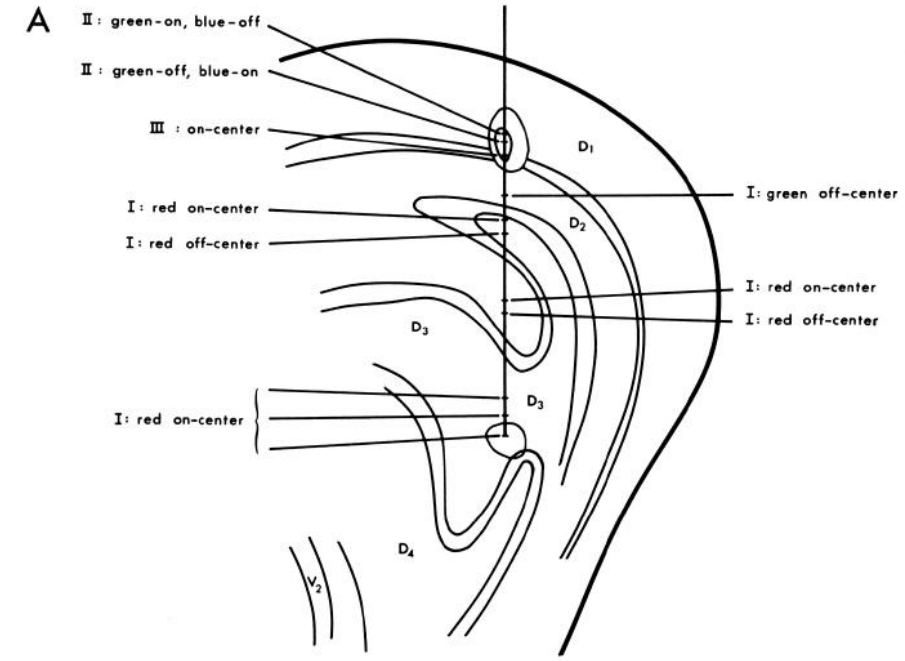
Topographical considerations. It is well known from the anatomical work of Clark and Penman (7) and Polyak (38) that the contralateral half-visual fields are mapped in an orderly way upon the six geniculate layers. The six maps are in register, with layers D_1, D_3, and V_1 connected to the contralateral eye and D_2, D_4 and V_2 to the ipsilateral (see METHODS for discussion of terminology). While no attempt was made at a complete or detailed map-

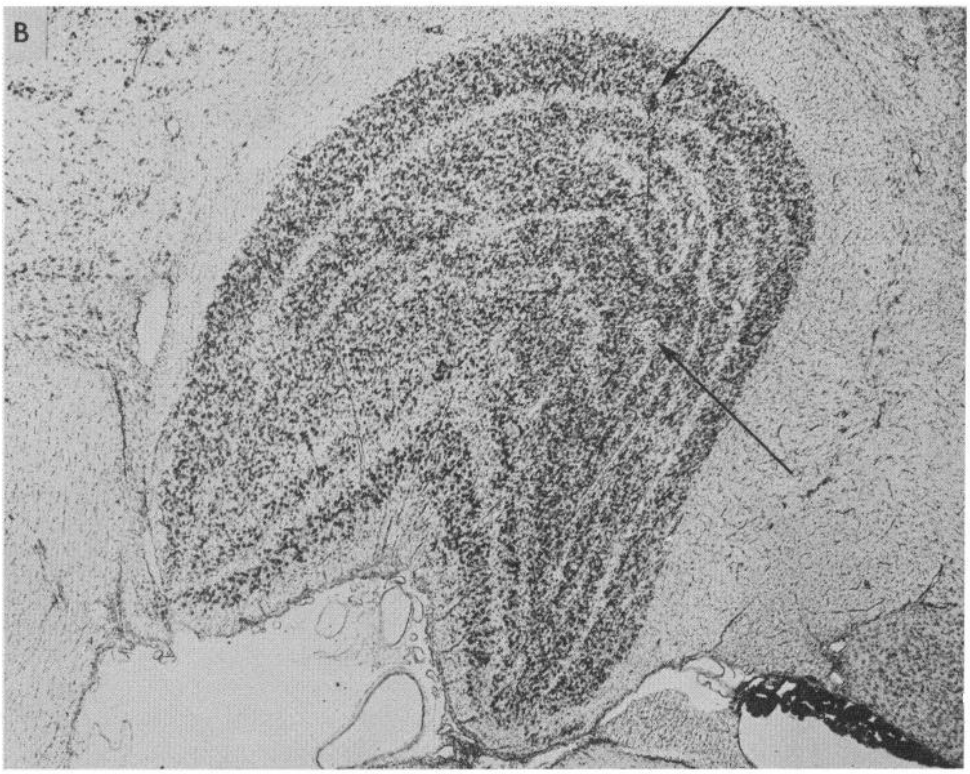
ping in the present experiments, our results are in good agreement with the anatomy. The topographical representation is clearly a precise one: the receptive fields were small and restricted, and for simultaneously or successively recorded cells they either overlapped or were close together. As the electrode advanced through a layer in a radial direction there was no over-all drift in receptive-field positions of successively recorded cells, only a slight variation in position, even in long sequences. In very oblique penetrations there was always a steady drift in receptive-field positions, superimposed, as in the cortex (26), upon a small, apparently random staggering in field position. Figure 17 indicates the parts of the visual field explored. Each dot represents the average position of the receptive fields observed in a given penetration. The positions of these dots taken together reflect the parts of the lateral geniculate studied. Eleven of the 19 penetrations were made in areas serving retinal regions within 10° of the fovea. No recordings were clearly established as having been made in the area representing the fovea, but a few cells had fields that were at most within a degree or two of the center.

A fairly typical track reconstruction is shown in Fig. 18, an example chosen partly because it illustrates the danger of relying heavily on shifts from one eye to the other in estimating the electrode position with respect to the different layers. In this experiment one might have concluded from the eye shifts that the penetration terminated in V_1, the most ventral layer, instead of layer D_3. In fact, had the penetration continued in the same direction through the interlocking folds it would have passed through D_2 three times instead of once, and would never have reached the ventral layers.

Distribution of cell types in the dorsal layers. It was obviously important to learn whether the various cell types were evenly distributed throughout the four dorsal layers. The results are summarized in Table 1. The sampling of cells was largest for layer D_1 and progressively smaller for each of the other layers, because many penetrations were discontinued before the deeper layers were reached. To allow for this, the number of cells in a particular layer is given also as a per cent of the total number of cells in that layer, so that in comparing the different layers it is the percentages that are important.

Table 1 shows that all major cell types were represented in both pairs of dorsal layers, indicating a lack of any rigid separation of functional groups. There was some unevenness in the distribution of red on-center cells, these being almost twice as common in the dorsal two layers as in the middle two. On the other hand, the red off-center cells were about twice as common in the middle layers. We are nevertheless hesitant to accept what appears at first glance to be a statistically significant result for reasons having to do with the distribution of cells within each layer. Within a given layer there was no obvious systematic segregation of the different cell types, yet as the electrode advanced from cell to cell there were frequent sequences in which one subtype occurred two to six times in a row. As might be expected, this was most often seen with red on-center cells, for these were the most com-


A
II: green-on, blue-off
II: green-off, blue-on
III: on-center
I: red on-center
I: red off-center
I: red on-center
D1
D2
D3
D3
D4
V2
I: green off-center
I: red on-center
I: red off-center


B

mon. Clearly even a slight tendency toward grouping makes one cautious about interpreting the relatively small samples represented by Table 1. Meanwhile one can sum up the table by saying that *1*) no group of cells is confined to any layer or pair of layers; *2*) red on-center cells, red off-center cells, green on-center cells, and green off-center cells are all represented in all four layers; and *3*) the two dorsal layers are perhaps richer than the middle two in red on-center cells and poorer in red off-center cells.

Sizes of receptive-field centers. Cell centers ranged in diameter from 2 min. of arc up to about 1°. Distributions of type I cells according to field-center size are given in Fig. 19, with separate histograms for on-center (left) and off-center (middle). On comparing the two histograms, it can be seen that, though the size ranges overlapped, on-centers tended to be smaller than off-centers, and in fact all of the very small field centers (1/32° to 1/16°) were "on" in type. This agrees with our previous observations in spider monkey optic nerve (24). The relative proportions of red-center and green-center cells (shaded versus unshaded) were about the same for all center sizes. Fields of type III cells (Fig. 19, right) tended to be larger than those of type I, though again the size ranges overlapped. For both type I and type III cells there was a loose correlation between field-center size and distance from fovea. The smallest centers, 1/32° to 1/16°, were all within 10° of the fovea. Type II fields ranged in size from 1/4° to 1°, and were found as close as 2° from the fovea and as far out as 12°.

VENTRAL LAYERS

Thirty-one cells were recorded from the ventral layers. The sampling was relatively small because many penetrations either did not reach the ventral layers or missed them entirely (Fig. 18), and because the ventral layers are relatively thin. Cells in these layers fell into two main groups: those of the first resembled type III cells in the dorsal layers; cells in the second group were different from any seen in the dorsal layers, and are termed type IV cells.

Ventral-layer type III cells

As with dorsal-layer type III cells, both on-centers (7 cells) and off-centers (14 cells) were seen. By definition, a cell in this group responded in

FIG. 18. *A:* reconstruction of an electrode track through right lateral geniculate. Coronal section. Electrode track is shown entering layer D_1 and ending in layer D_3; lesions made near the beginning of the penetration and at the end are outlined as irregular ovals. Short lines intersecting the electrode track show the positions of cells studied during the penetration. Labels indicate, by their position to left or right of figure, whether cells were recorded from contralateral or ipsilateral eye. Distance from entry of track into geniculate to end of track was about 1.5 mm. *B:* one of the Nissl sections from which the track was reconstructed, showing lesions (arrows) and first part of electrode track (outlined by inflammatory reaction).

the same way ("on" versus "off") to a spot of a given size or shape for all effective wavelengths, and showed the same degree of peripheral suppression over the entire spectrum. Most cells were unresponsive, or virtually so, to diffuse light, peripheral suppression being practically complete for white

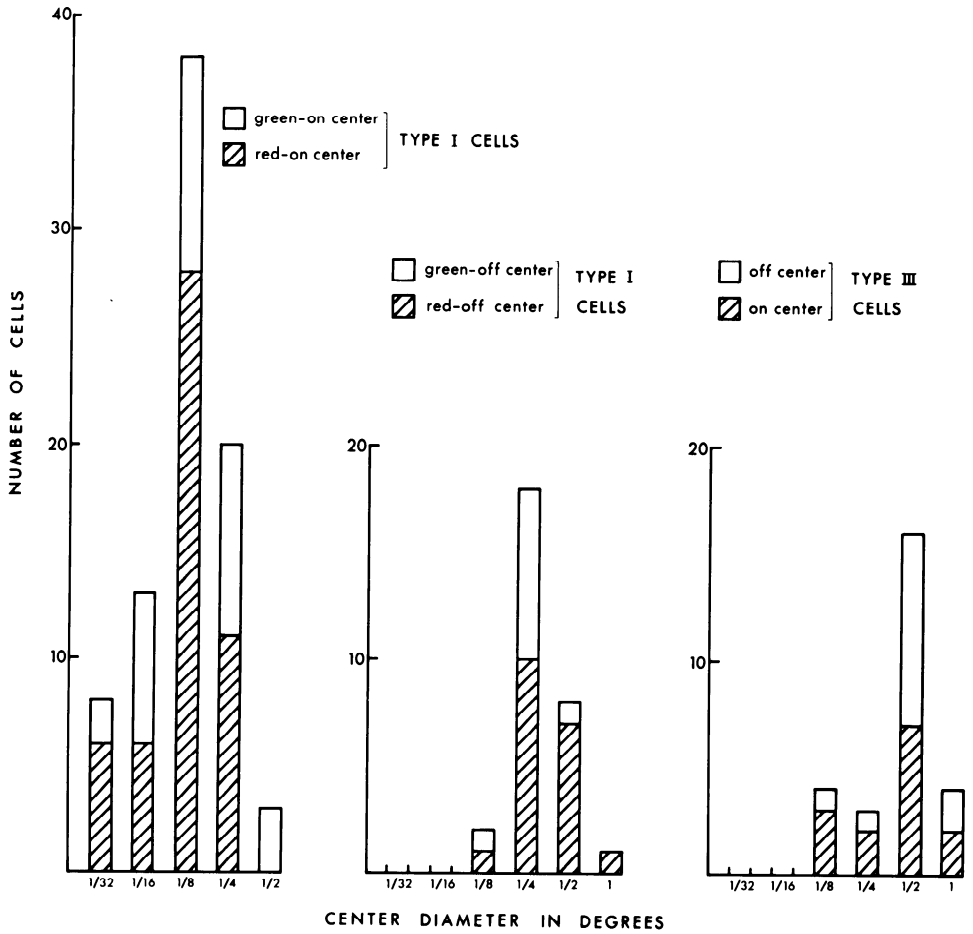


FIG. 19. Distribution of geniculate cells with respect to size of field centers. *Left* and *middle* histograms: type I cells. *Right:* type III cells.

light and all wavelengths of monochromatic light, and at all available intensities.

An off-center type III cell was examined to learn whether more than one cone type contributed to the receptive field. To estimate center and surround dimensions, sensitivity (reciprocal threshold) was plotted against spot size for white stimuli in the light-adapted state (Fig. 20*A*). Peripheral suppression was complete at 6–8° spot diameter, sensitivity falling by over 3 log units from the maximum at 1/2°. Next, spectral sensitivity was determined

for spots just under center size (Fig. 20*B*). After adapting the field center with light at 640 mμ., threshold measurements were repeated for stimuli at 480, 520, and 620 mμ. The effect of the steady adapting light, shown by the arrows, was to reduce sensitivity at all three wavelengths, but more for the long than the short. This result is just what one would expect if the cell received contributions from more than one type of cone in the field center, in a nonopponent system.

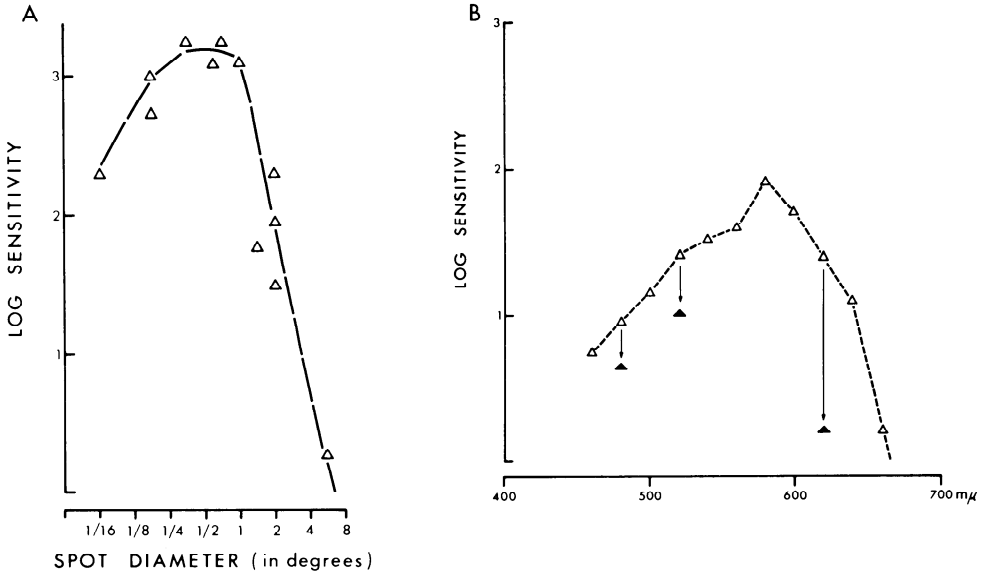


FIG. 20. Off-center type III cell recorded in light-adapted state from layer V_2. Field center 6° from fovea. *A*: area-sensitivity curve for white light stimuli, showing field-center size to be about 1/2°, and overall field at least 6–8° in diameter. *B*: spectral sensitivity plotted for 3/8° spots. Empty triangles, off-responses with the usual white background. Filled triangles, three measurements made in the presence of 640-mμ. diffuse steady background. Decline in sensitivity is greater for long wavelengths than for short, suggesting that more than one type of cone had a nonopponent connection with the cell.

Dark adaptation was not done for any ventral-layer type III cells, so that we have no information about the possible contribution of rods to these cells. The fields were found as close as 3° from the fovea and as far out as 12°. Center diameters ranged from 1/8° to 1/2°. Sampling was too small to allow any comparison of field-center sizes in ventral as opposed to dorsal layers.

Type IV cells

Type IV cells, of which 10 were studied in detail, were quite unlike anything seen in the dorsal layers, or in the cat retina or geniculate. A typical example is illustrated in Fig. 21*A*. As with every cell in this group the receptive field was concentric in type, with an excitatory center and an inhibitory surround. There was active maintained firing. Small spots evoked on-dis-

charges with sensitivities shown by the rather broad upper (interrupted) curve. These responses were poorly sustained, lasting for a few seconds or less. To large spots the responses were most unusual: at short and medium wavelengths (violet through yellow) there was no effect at any intensity, i.e., peripheral suppression was complete. In the red, however, the influence of the surround actually predominated over that of the center, and the maintained activity was suppressed by large spots. The cessation of firing, unlike the center response, was well maintained, usually lasting as long as the light was left on. The effect required relatively high intensities, especially for complete suppression of firing. There was summation over a tremendous

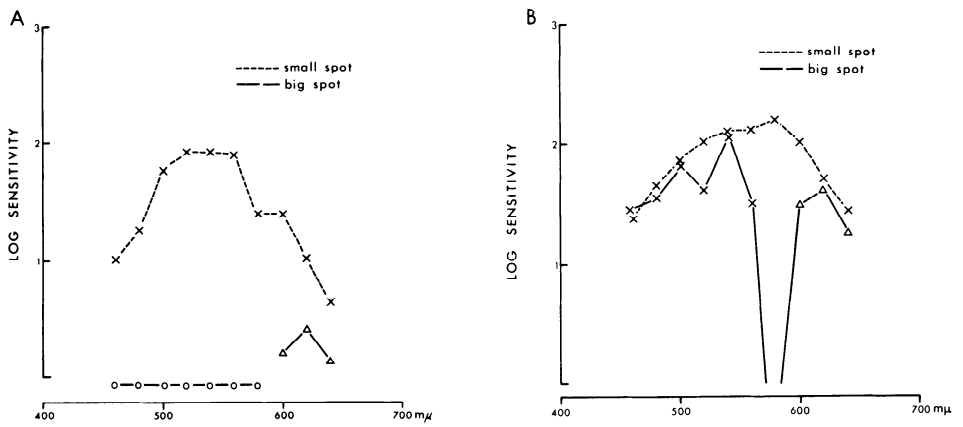


FIG. 21. *A:* typical type IV cell, with brief on-responses to small spot stimulation, sustained suppression of maintained firing to large spots, but only at long wavelengths. At wavelengths up to 600 mμ. no response could be evoked with large spots. Field center 1/2° in diameter, situated 11° from fovea. Recorded from layer V_2. *B:* type IV cell with no obvious peripheral suppression at short wavelengths, but otherwise similar in properties to the cell illustrated in *A*. Field center 1/4°, 12° from fovea. Layer V_1.

area, in some cases with clear differences in the effects of a 20° and a 25° spot. White light acted like red, producing a sustained suppression of firing with no marked off-discharge but, rather, a simple resumption of the maintained firing.

Cells of this type seemed to be plentiful. One of the common signs that the electrode had entered the ventral layers was the nearly complete suppression of unresolved background activity by diffuse light, especially diffuse red light, in contrast to the general activation of the background by small spots. These are the only cells we have seen in which surround prevailed over center with white light, or where there was this center-surround difference in temporal adaptation.

A few cells had properties somewhat different from those just described. For the cell of Fig. 21*B* the surround system seemed to be not only richer than the center in red cone concentration, but also poorer in green or green plus blue. At wavelengths up to the mid-500s the surround had no discernible

influence, while at wavelengths beyond 580 mμ. the sustained surround effect dominated and was apparent even at relatively low stimulus intensities. Diffuse white light was ineffective or evoked a weak on-response. It is thus clear that opponent-color cells occur in the ventral layers, though they seem rare. Too few have been seen to justify their classification as type I cells, or as a separate group.

Two type IV cells were studied after dark adaptation. One of these was the cell of Fig. 21*A*. In both there was an increase in sensitivity of about 1 log unit for all responses, with no obvious change in any of the qualitative behavior just described. Sensitivities were many log units below that of our own dark-adapted eyes. These two cells thus seemed not to have any significant rod input.

Discussion

In this study the object was to learn how information on form and color of a stimulus is handled at an early stage in the central nervous system. Given two opponent processes in the monkey, a chromatic and a spatial, it seemed important to learn whether these existed in independent pathways or were combined in common cells. The answer seems to be that both things occur: some cells are mainly concerned with form, others mainly with color, while the majority handle both variables at the same time. In the case of color, as originally shown by De Valois (10, 11), a cell may be excited by one group of cones and inhibited by another group with a different spectral sensitivity, so that white light covering a large retinal area and stimulating both groups of cones may evoke little or no response. For the spatial variable the receptors may excite or inhibit a cell, depending on retinal position, with the result that diffuse light has little effect regardless of wavelength (24). In any given cell one or both of these mechanisms may be found. Both opponent mechanisms seem aimed at increasing the specialization of single cells, in the direction of color as opposed to white, or spatial contrast as opposed to diffuse light. Thus the existence of inhibitory mechanisms leads to the surprising result that the optimum response of a cell in the visual pathway is not obtained by stimulation of all of the receptors—in general that is the least efficient stimulus. For the cell to respond optimally a particular set of receptors must be activated, the set varying from one cell to the next. The function of a structure like the geniculate can thus be studied by asking how the receptors are categorized into set and subsets by the different cells.

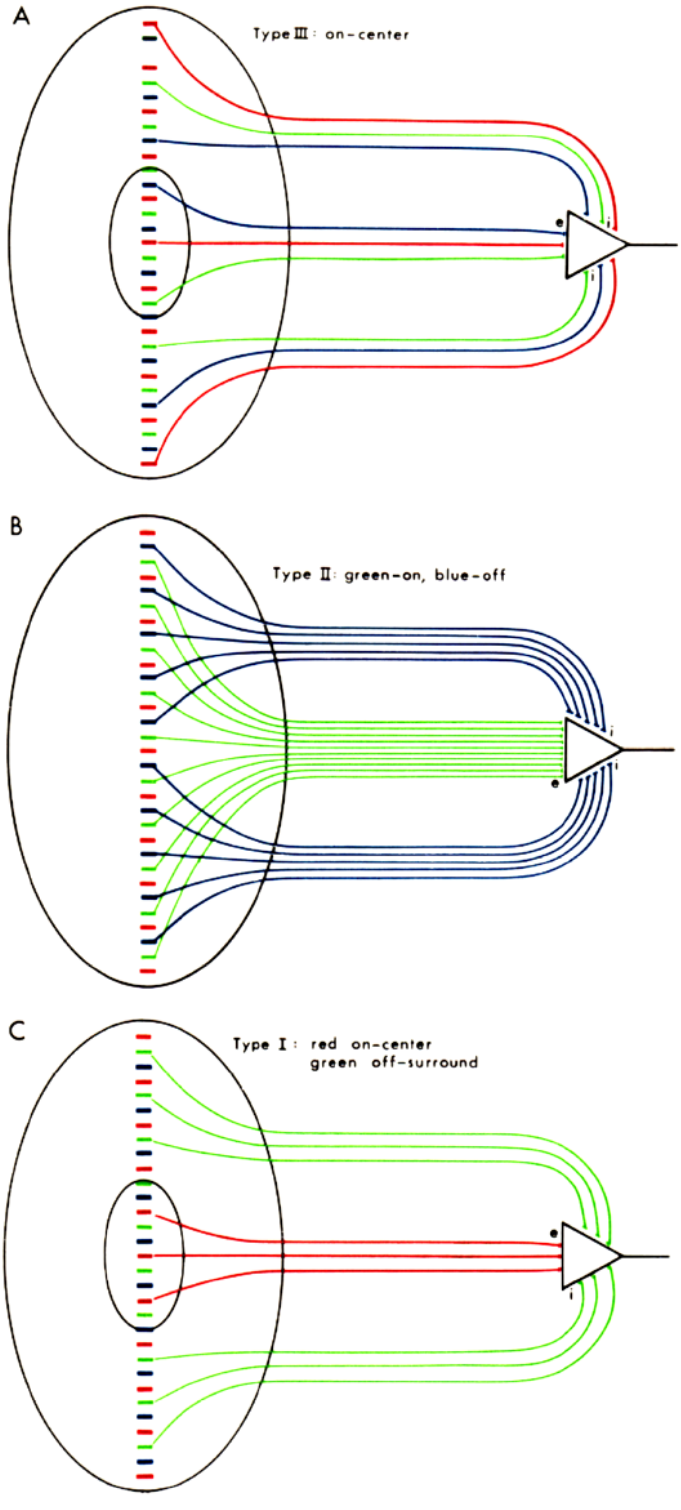
The findings can be summed up by saying that in the light-adapted state practically all cells are influenced by two antagonistic sets of connections, one excitatory and the other inhibitory. Depending upon the details of these connections, three main cell types can be distinguished. For type III cells the opponent inputs take origin from two groups of receptors that are spatially separated into center and surround. A given cell is generally supplied by cones of more than one type, and the relative proportions of the three cone types are the same for center and surround, though from cell to cell

they undoubtedly differ. This is shown diagrammatically in Fig. 22*A* for a type III on-center cell; here a cell is considered to receive excitatory input from cones in the field center, with the red-, blue-, and green-sensitive cones represented in the ratio of 1:1:1, and inhibitory input from peripherally located cones in the same ratio. (For simplicity, intervening synaptic stages are omitted, as are the rods.) Type III cells presumably represent an elementary step in form analysis, registering not simply the general level of illumination but rather comparing light that falls on one retinal region with that falling on the immediate surround. This is done to a large extent irrespective of wavelength. For these cells unevenness of illumination is a powerful stimulus, and diffuse light tends to be inadequate.

For type II cells the scheme is just the converse: opponent sets of receptors of different spectral sensitivities are distributed in identical fashion throughout the same retinal area. The cell of Fig. 22*B* receives excitatory input from green-sensitive cones over the entire receptive field, and inhibitory input from blue cones throughout the same region; over all parts of the receptive field the proportion of excitatory to inhibitory cones is constant. Thus these cells react mainly to unevenness of spectral energy distribution, and diffuse light is as good a stimulus as an optimally placed spot.

For type I cells, finally, the two sets of receptors are not only spatially segregated but also have different spectral sensitivities. The red on-center cell of Fig. 22*C* is supplied by the red-sensitive cones from the field center, and the green-sensitive cones from the periphery. The properties of the other two cell types are thus combined in the type I cell, which deals with black-white images in the same way as the type III cell does, but for diffuse light or parts of images lacking spatial intensity gradients has all of the wavelength-discriminating ability of the type II cell. In sum, diffuse light is to the type III cell what white light is to the type II, and what diffuse white light is to the type I.

FIG. 22. *A*: proposed contribution of cones to a type III on-center cell. Three types of cones are illustrated by colors and, for simplicity, receptors are shown only along a line through the field center. Cones project to the cell, via intervening synapses which are not shown, and activation of those in the center of the receptive field leads to excitation of the cell (e), those in the periphery to inhibition (i). The three cone types from the center are arbitrarily shown as being present in the ratio of 1:1:1, and this ratio is the same for the periphery. *B*: schematic representation of a type II cell, receiving excitatory input from green-sensitive cones and inhibitory input from the blue. The relative contributions of the two afferent cone types are the same in all parts of the receptive field. *C*: representation of a type I cell receiving excitatory input from red-sensitive cones in the field center and inhibitory input from green-sensitive cones in the periphery. Note that in these figures "i" is used simply to imply that light falling on the cone leads to an increased tendency toward cessation of firing of the cell. This could depend on an inhibitory synapse at any stage in the path from receptor to geniculate cell, and need not imply active inhibition at the geniculate cell itself.


A
Type III: on-center
e
i
i
B
Type II: green-on, blue-off
i
e
i
C
Type I: red on-center
green off-surround
e
i

The schemes proposed in Fig. 22 must be considered tentative, with several details still unsettled. The first of these concerns the relative contribution of the three cone types. While the simplest assumption consistent with the experimental evidence is that each opponent-color cell receives input from two of the cones, it is often difficult to be sure that the third cone does not also contribute. Cells that we regard as receiving opponent inputs from red and green cones could, for instance, receive contributions from the blue-sensitive cones along with the green. The result would be to broaden the spectral sensitivity of the short-wavelength system and displace the peak even further to the short-wavelength end of the spectrum. Since, in fact, the spectral sensitivity of the short-wavelength system in these cells generally has its peak in the mid-500s, falling off markedly by the mid-400s, the contribution of the blue cones must at most be a minor one. But if the ratio of green cones to blue in the input to the short-wavelength system were the same as it is in the local cone population the contribution of the blue cones would be hard to detect, for even outside the fovea there are probably far fewer blue cones than green ones.

The situation is different in the case of the blue-versus-green opponent cells (a few type I cells and most of the type II). Here the problem is to tell whether or not the red cones as well as the green contribute to the long-wavelength system, and in what proportion. This is not easy, since the two cones have extensively overlapping spectral sensitivities. Thus whether the green cones make up the entire contribution to the long system, or just half of it, will determine whether the spectral-sensitivity peak is at 540 mμ. or 560 mμ., a subtle difference for techniques as coarse as those used in this study.

Finally, there is the possibility of opponent-color cells having one system fed by green cones and the other by red cones plus blue cones. The result would be two neutral points, a cell being excited at intermediate wavelengths and inhibited at the long and short ends of the spectrum, or the reverse. So far we have not seen any cells of this type, though they should be easy to recognize. De Valois and Jones (13), recording also from the macaque geniculate, have reported finding such cells, but the results may not necessarily have to be interpreted in terms of three cone inputs, since with the eyes dark adapted a contribution from rods would seem possible. For example, a "red off-center, green on-surround" cell with inhibitory rod input, a type we have seen, might well masquerade as a "purple-off, green-on" cell if examined only in the scotopic state.

A second qualification to the interpretations implied by Fig. 22 concerns the arrangement of the receptive field of type I cells. The problem can best be approached by comparing our results in the monkey geniculate with a similar study made in the goldfish retina by Wagner, MacNichol, and Wolbarsht (43–45, 48, 49). The comparison reveals some striking similarities but also certain differences in the details of receptive-field organization. In the goldfish some cells showed no opponent-color effects, but had center-surround receptive fields of the type described by Kuffler (28) (type III

in the present study). Other cells showed opponent-color responses, but in these the opponent systems overlapped instead of being distributed on the retina in a center-surround manner. The two systems had sensitivities that were maximal in the field center, but tapered off toward the periphery at different rates so that the effects of one predominated in the center and those of the other in the surround.

One might ask whether in the monkey the fields of type I cells are not also organized as two partially overlapping opponent systems with different spatial distributions. Experimentally, it is difficult to obtain a clear answer to this. As a rule the size of receptive-field centers of type I cells is very small relative to the size of the whole field, so that a spot of center-size placed anywhere in the periphery evokes no response at any wavelength or intensity. On the other hand, a small spot in the center evokes only center-type responses regardless of wavelength. Thus if the opposing system is activated at all from the center, its effects are apparently outweighed. In the goldfish, on-off responses indicate that opposing systems are being simultaneously activated, but in the monkey these mixed responses do not occur—either one system is dominant and completely submerges the other or the two mutually cancel and no response is seen. In any case, a distinction between overlapping and nonoverlapping arrangements seems of theoretical rather than practical importance in the monkey, given the small size of field centers relative to the total field size. The scheme suggested in Fig. 22 seems to us the simplest consistent with the results. If, as seems likely on anatomical grounds, there are ganglion cells in or near the fovea whose field centers are supplied by single cones, then the receptive-field periphery of such cells must obviously be annular. Type II cells have overlapping opponent systems, but with the important difference that the sensitivities of the two systems have the same spatial distribution. No such cells have been reported in the goldfish. Possibly the model proposed by Wolbarsht *et al.* (49) might apply in the monkey to the relatively rare red-green opponent cell that seems to combine features of the type I and type II cells (see RESULTS section, under *Type II cells*).

Here a comment may be made on the organization of center-surround fields of types I and III. The descriptions in this and other papers may give the impression that the center and surround of a concentric receptive field are roughly equal and opposite in their influence on a cell. This is not strictly so. Peripheral responses are often difficult to evoke with annular stimuli alone, especially in the lateral geniculate of the cat and monkey. This has also been noted for retinal ganglion cells in the rabbit (3). Nevertheless it is clear that the periphery is highly effective, since a large spot evokes a weaker response (excitatory or inhibitory) than a small one, and often evokes none at all. In cells of the cat geniculate diffuse light has on the average less effect than it does at the retinal ganglion cell level (25), reflecting an increase in the potency of the receptive-field periphery; yet, compared with retinal cells, geniculate cells respond especially grudgingly to annuli. This is true

both for on-center and off-center cells. Apparently the more potent the surround is in suppressing the center effects the more difficult it is to obtain a response from the surround alone. One can, however, always obtain a response from the periphery by first shining a spot steadily on the center and then turning on and off the annulus—it was necessary, for example, to use this device to obtain a spectral-sensitivity curve for the field surround in the dark-adapted type III on-center cell of Fig. 15*B*. The reciprocal phenomenon does not seem to occur, in that a center stimulus is not made more effective by shining a steady annulus in the periphery. It is as though the surround system could only exert its effects provided the center system was also activated. As indicated below, this peculiarity may help explain the difficulty in demonstrating peripheral effects at threshold in the dark-adapted state. The point to be emphasized is that the center and surround of concentric receptive fields seem to function in quite different ways, the effects of the surround working, as it were, through the center.

Chromatic adaptation. The importance of neural mechanisms in light and dark adaptation is well recognized and has most recently been emphasized by Rushton (39) and Dowling (16); they found, by very different methods, that within a wide range of intensities the amounts of pigment actually bleached were too small to account for the observed large changes in sensitivity. In the present experiments the rapid recovery from the rather moderate intensities of adapting lights likewise suggests that neural mechanisms are important: the effects of chromatic adaptation on opponent responses subside within seconds of the time the adapting light is turned off, rather than after several minutes as one would expect if it were solely a matter of pigment bleaching and regeneration. It is thus likely that chromatic adaptation involves a change in the stimulus-response relationship in one opponent system without any equivalent change in the other, the effect presumably occurring at some point prior to the convergence of the two systems. In the cat it is well known that the response to an intermittent white stimulus of constant intensity declines as the white background is turned up. Presumably in the monkey the decline in sensitivity with chromatic adaptation is similar in nature but the effect is selective, being confined to one of the opponent systems.

These remarks apply to chromatic adaptation of the type employed in our experiments, in which the intermittent stimulus is superimposed upon a steady adapting light. Obviously the mechanisms would be quite different if the adapting light were first turned out and then the stimulus applied. We have avoided this method because of the complications involved in stimulating during the transient off-effects following the change in background.

Dark adaptation. That rods and cones may converge on single retinal ganglion cells in the cat was shown first by Granit (19) and later confirmed by Barlow, FitzHugh, and Kuffler (2). In the monkey similar conclusions have been reached by Gouras (18). From the results of De Valois (10,

15) in the rhesus geniculate it seems clear that some lateral geniculate cells receive input from rods and cones, and others from cones only. Our findings confirm those of De Valois, and further show that cells with fields clearly outside of the rod-free fovea may receive input from rods and cones, or from cones only. Indeed, to our surprise, the majority of cells recorded from the 10° parafoveal region received no rod input. We have seen no examples of cells with connections to rods but not to cones. As shown in Fig. 14*B*, two cells can exist side by side, one with a powerful rod input and the other with none. This, then, is still another example of the striking specificity of connections seen already in the geniculate in other contexts.

In the present work we were particularly interested in the receptive-field organization of cells that receive both rod and cone input. In the type I cell the receptive fields in the dark-adapted and light-adapted states had about the same center size, and in all cells the center responses were the same (on versus off) in the two states. The question of whether the receptive-field periphery supplies rods as well as cones in type I cells is still not answered, and while it is true that at threshold no effects were seen from the periphery, this was also the case in the type III cell of Fig. 15*B*, which turned out to have a clear input from rods in the periphery.

It seems that some type III cells receive rod contributions and others do not. In the one well-studied cell the rods from the center were excitatory and those from the surround inhibitory, and the same was true for the cones, so that there was no basic difference in the field arrangement in the two states. Only at threshold did the surround fail to manifest itself (Fig. 16), perhaps, as discussed above, because of the necessity for having some center activation for the surround to work upon.

The dark-adaptation effects in type III cells are in some ways similar to those obtained in the cat by Barlow, FitzHugh, and Kuffler (2). They found that rods project onto single retinal ganglion cells, producing excitatory effects from the center and inhibitory effects from the surround, or the reverse. After some hours of adaptation the surround effects were no longer detectable, not only from area-threshold measurements but also on comparing small and large spots as much as several log units above threshold. In these cells both center and surround increased in sensitivity as the rods became effective in dark adaptation, but ultimately the center sensitivity considerably exceeded that of the periphery. As shown in Fig. 15, no such center-periphery differences were seen in the monkey. This suggests a possible difference in dark-adaptation mechanisms in the two species, which would not be surprising since the cat is a nocturnal animal.

Just as with chromatic adaptation, the change in spectral sensitivity occurred within a second or less of the time that the background light was turned off. This would surely not have been so had our background been a high photopic one. The quickness of the change, from responses dictated primarily if not entirely by cones to responses due to rods, suggests that neural mechanisms were chiefly involved.

Distribution of cell types in the lateral geniculate body. The significance of the layering in the geniculate has puzzled anatomists and neurophysiologists for many years, and a number of theories have been proposed, notably those of Clark (6) and Walls (46). In the present study one of our main objectives was to learn whether cells as categorized by receptive-field organization differed from layer to layer. It was no surprise to find the biggest disparity between the four dorsal layers and the two ventral, given the glaring histological dissimilarities in the two sets of layers. Distributions of cell types were entirely different, there being no typical type I or type II cells in the ventral layers, and no type IV cells in the dorsal. Among the four dorsal layers the only difference, besides the obvious one related to ipsilateral and contralateral eyes, was in the distribution of the type I subgroups, the red on-centers being somewhat more common in the dorsal two layers than in the middle two, and the red off-centers somewhat less common. Both groups were nevertheless clearly represented in both pairs of layers. The lack of any fundamental differences in response properties of cells in these four layers once more fits well with the lack of any distinguishing histological features.

Our results are to some extent inconsistent with those of De Valois and co-workers (14), who concluded that cells are segregated into three groups by response type, with on-responses occurring in the two most dorsal layers (D_1 and D_2 in our terminology), on- and off-responses in the middle two, and off-responses (with inhibition during the stimulus) in the ventral layers. With respect to the ventral layers our findings actually are not in disagreement, since practically all of the cells we have observed were either unresponsive to diffuse light or, in the case of type IV, were inhibited. Nevertheless, type IV cells are, ironically, on-center in type, having a periphery that dominates in diffuse light, and type III contains both on-center and off-center, so that it would be misleading to continue speaking of the ventral layer cells as "off" or "inhibitory."

The middle pair of layers was shown by De Valois *et al.* (14) to contain predominantly opponent-color cells, giving on-responses or off-responses to diffuse light depending on wavelength. Our results confirm this. On the other hand, the dorsal pair of layers was initially described as containing on-cells, which constituted at first "the overwhelming majority" (14) and later 75% (13) of the cells. These cells were originally thought to be narrow band "modulators" of five types, but subsequently, as a result of using chromatic adaptation, they were found to have opponent-color properties (12). Our results show that the majority of dorsal-layer cells are opponent color in type and tend to suggest that there are more on-center cells than off-center in these two layers, though off-center cells are certainly quite common.

Anatomically and physiologically, the significance of the layering of the lateral geniculate body continues to be obscure. Anatomically, one would like to learn more about the afferent supply and the efferent projections of the different layers: whether, for example, ventral-layer and dorsal-layer

cells receive projections from separate classes of retinal ganglion cells, and whether the axons of the dorsal layers have cortical terminations different from those of ventral layers. The present physiological study, like that of De Valois and collaborators (13), fails to bear out either the trichromatic theory of Clark (6) or the photopic-scotopic theory of Walls (46). What one can say in summary is that in the dorsal four layers the cells are predominantly of the opponent-color type, at least for the part of the geniculate representing parafoveal parts of the retina, whereas in the ventral two layers the importance of color seems to be reduced.

Sizes of receptive fields. The smallest field centers measured in the present work were of the order of 2 min. of arc, which would correspond to about 10 μ. on the retina. These receptive fields were all type I, suggesting that the center was supplied by one type of cone only. The intercenter distance between cones is 2.0–2.5 μ. in the central part of the human fovea and, to judge from Østerberg's drawings, it is probably several times larger 1° from the center of the fovea (35, 37, 38). The smallest field centers were thus supplied by a few cones at the most, and possibly some were made up of one cone only, though more careful measurements would be necessary to establish that. No area-threshold measurements were made on these cells so the exact size of field centers and surrounds are not known, but it is clear that the peripheries were orders of magnitude larger than the centers.

Functions of the lateral geniculate. It should be emphasized that the present study tells us little about the part the lateral geniculate plays in vision. The electron microscope leaves no doubt that something more than a one-to-one relationship exists between optic fibers and geniculate cells (8), and it would be most interesting to know what physiological interactions these complex connections subserve. We have no reason to think that the classes of cells we have described for the geniculate do not also exist in the optic nerve, since opponent-color responses have been described in the spider monkey optic nerve (24), and several fibers which we recorded from the optic tract in the present work were not obviously different in their properties from geniculate type I cells. It is true that in the spider moneky optic nerve opponent-color cells were not nearly as common as in the rhesus geniculate, but this was probably related to the species difference and to the large area of visual fields explored in the spider monkey rather than to any difference between retina and geniculate. The exact function of the monkey geniculate is probably more subtle. In the cat there are clear differences between responses of geniculate cells and those of retinal ganglion cells, one contribution of the geniculate being a more precise adjustment of the balance between field center and surround, with decreased effectiveness of diffuse light (25). Similar kinds of interactions may well occur in the monkey but, if so, a different type of study will probably be required to reveal them.

There are, finally, some obvious correlations between the responses observed in the geniculate and perceptual phenomena. Given a cell whose receptive field is organized in center-surround fashion, and supposing, for

simplicity, that diffuse light is ineffective, illuminating the field center with a white spot of a particular intensity can produce excitation or inhibition depending on whether the surround is simultaneously illuminated with a brighter or dimmer white light. There is a compelling parallel between these responses and one's impression of the spot as "white" or "black," and it is hard to think that the two events are not in some way related. Type I and type III cells are of course equally capable of mediating these black-white sensations. In the case of color there is a similar parallel between the virtual ineffectiveness of diffuse white light in opponent-color cells of type I or II, and the addition of complementary colors to produce the sensation "white." This involves the assumption that a necessary condition for a white sensation is a failure of an opponent-color cell to respond. Here the type II cells would seem to play the more important part, since in these the responses depend predominantly on stimulus wavelength and to a much smaller extent on stimulus geometry.

One is naturally inclined to ask whether a similar parallel can be made between spatial color-induction effects or the spatial-color effects described by Land (29) and the behavior of the type I cell. Surprisingly, it turns out that type I cells are of no direct help. The responses to a centered red spot are not enhanced by simultaneously shining green in the surround, since for type I cell this amounts to the same thing as using diffuse white light. For color contrast in this situation one would seem to require something like a red on-center green on-surround, a field type we have not so far seen. On the other hand, as already indicated, the type I cell is as good a candidate as the type III for the mediation of black-white contrast mechanisms. It may be that color contrast effects are not dealt with at a retinal or geniculate level at all, but only in the cortex. This would be consistent with the finding that Land's effects can occur when the two images are presented binocularly (17), which suggests that the necessary machinery is present in the cortex—though of course it does not rule out its existence at lower levels as well.

SUMMARY

In the visual system of primates, mechanisms exist for the analysis of both spatial and chromatic qualities of a retinal image. The present study was designed to examine these processes at the lateral geniculate level in the rhesus monkey. Extracellular recordings were made from 224 cells while stimulating the retina with spots of light of various sizes and wavelengths, and in various states of light and dark adaptation.

In the four dorsal (small cell) layers three types of cells were distinguished. Type I cells were by far the most common. In the light-adapted state they had concentrically arranged receptive fields which were divided into an excitatory or inhibitory center and an opponent surround, the center and surround having different spectral sensitivities. With diffuse light stimuli they showed opponent-color responses, giving on-responses to one set of wavelengths, off-responses to another set, and no response at some interme-

diate wavelength—the "neutral point." Chromatic-adaptation studies suggested that the cell had connections with one of the three types of cones in the field center, and another in the surround. Five varieties were seen, in order of frequency: *1*) red on-center, green off-surround; *2*) red off-center, green on-surround; *3*) green on-center, red off-surround; *4*) green off-center, red on-surround; and *5*) blue on-center, green off-surround. All type I cells behaved in the same way to white light, showing the usual center-surround arrangement seen in the retina or geniculate in the cat. On-off responses were rare or absent.

Type II cells made up a small minority of the dorsal-layer cells. They lacked any center-surround receptive-field arrangement, but gave opponent-color responses over all regions of the receptive field and had a 500-mμ. neutral point that was independent of stimulus geometry. These cells behaved as though they received opponent inputs from two sets of cones with identical distributions over the retina. Two types were seen: green-on, blue-off, and green-off, blue-on. A few cells seemed to have opponent connections with green and red cones. Here the two cone types were distributed throughout overlapping regions, but one set of cones seemed to predominate in the field center and the other in the surround.

Type III cells had concentrically arranged on-center or off-center receptive fields, the center and surround having identical spectral sensitivities. A large spot evoked a weaker response than a small one regardless of wavelength. These cells probably received input from cones of several types, the proportions of the three types being the same for the field center as for the surround.

A number of cells with fields outside the fovea were studied also in the dark-adapted state. Some type I cells behaved as though they had no connections with rods, while others showed clear evidence for rod input, giving a 4 log unit increase in sensitivity with a shift in the peak sensitivity to a point near 500–520 mμ. Opponent-color effects were no longer seen, and center-type responses occurred over the entire spectrum except at high stimulus intensities in the red. At threshold levels of intensity these responses were evoked from the field center only, so that whether they receive input from rods in the field periphery is still uncertain. Two type II cells examined in dark adaptation showed no evidence for rod connections. Of four type III cells two lacked a rod input, and the other two had rods feeding in from center and surround, forming opponent systems just as in the light-adapted state; for these cells scotopic thresholds were practically the same for center and surround.

All of the cell types were seen in both pairs of dorsal layers, and there were no differences in distribution of cell types in these four layers except for a suggestion that red on-center cells were more common in the two dorsal layers than in the two middle, and red off-center cells less common. Field-center sizes were generally smaller for type I cells than for type III, and among type I cells on-centers tended to be smaller than off-centers. Field

centers were smaller the closer they were to the fovea, the smallest being 2 min. of arc in diameter, for fields 1° or 2° from the fovea; the largest were around 1°. Fields of type II cells ranged in diameter from 1/4° to 1°.

Ventral-layer cells were of two kinds. The first seemed similar to type III as described above. The second, termed type IV, had concentrically arranged on-center fields with a very large off-surround whose spectral sensitivity was displaced to the red with respect to the center. With red light, and generally also with white, the receptive-field periphery prevailed over the center, so that diffuse light produced a well-maintained suppression of the background firing.

In summary, a wide variety of cell types are present in the monkey geniculate. Some are concerned mainly with spatial variables, others with color, but most are able to handle both variables. Some have connections both with rods and cones and others with cones only.

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