Receptive Field Organization of Ganglion Cells in the Cat's Retina

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The response of retinal ganglion cells to a scanning disc was recorded from their axons in the optic nerve. A 25 × 25 deg region of the visual field with the fixation point at its approximate center was mapped. Units with receptive fields (RF) outside this region were discarded; 145 RF were mapped in a variety of conditions. Of the fields mapped, 110 were center activated or center suppressed, with a surround of the opposite sign. These concentrically organized RF were divided into two subclasses: concentric-a, in which the surround was a complete annulus; and concentric-b, in which the surround was present only on leaving the center even at very low (0.39 deg/sec) scanning speeds. A total of seven bar- and edge-shaped RF had different sizes and orientations and were somewhat similar to the line and edge-shaped RF described by Hubel and Wiesel in the visual cortex of the cat. A group of eight units which were center activated and had no inhibitory surround was found. They had the characteristic of maintaining an increased rate of discharge after the disc had passed through the center, provided that the disc moved at moderate speed (5 deg/sec) and remained in the vicinity of the center. These units were referred to as "presence detectors." Twenty units were left unclassified. Scanning the RF at different speeds and at different levels of ambient light had relatively small effects on the shape of the RF analyzed. The relatively small percentage of nonconcentric RF in the cat's retina indicates that much analyzing remains to be done at higher levels. On the other hand, these findings, combined with previous findings of units sensitive to direction of movement and light flux in the cat's retina, indicate that considerably more processing of the visual image is performed at the retinal level than hitherto suspected.

Introduction

The neural structures of the eye convert patterns of light falling on the retina into firing patterns of nerve fibers in the optic nerve. The operations performed by these structures can be modified by nonvisual stimuli (21, 22, 27) or by electrical stimulations in parts of the brain stem and cortex (6, 19, 20). This series of experiments, many performed in this laboratory, proved difficult to interpret, suggesting that a more detailed and quantitative analysis of retinal functions was needed. A method was therefore sought and

devised to display the results more completely and readily so that critical analysis could be undertaken. Toward this end, computer-constructed three-dimensional maps of the organization of visual receptive fields of the cat's retinal ganglion cells were recorded.

Kuffler (11), using small stationary flashing spots of light, described two types of ganglion cells in the cat's retina. One type increased firing rate when the spot was turned on, the other when the spot was turned off the central area of the field. In each case the central area is surrounded by an annulus shaped region giving the opposite response. Rodieck and Stone (15, 16) have shown that these fields can be mapped as well by using moving spots; these investigators essentially confirmed Kuffler's findings and reported no units with other properties. Similar units have been described in the spider monkey (9). The discovery of direction sensitive-units in rabbit (3) and pigeon retinas (13) and more recently of direction-sensitive units (22, 23) and of flux-detecting units (22) in cat's retina suggests that a reexamination of the cat's retina might prove useful; these reports reopen the question as to whether retinal coding of input (3, 12, 14) is a general biological principle. If the retina of "higher" mammals is simply a mosaic of "on" center and "off" center transducers from which more complex detectors have to be built up in more central visual structures (10), the organization of the visual systems of these animals would differ in important respects from that of other vertebrates. To investigate this question, the receptive fields of visual units were mapped by moving stimuli. Velocities, direction and contrast were varied and different levels of ambient illumination were used. The results reveal the existence of receptive fields that cannot be reduced to the concentric schema. A preliminary report of some of the findings detailed here has been presented elsewhere (18).

Method

Preparation. Twenty adult cats were used. Thiopental sodium was injected intravenously in amounts sufficient to obtain anesthesia. The radial vein and the trachea were then cannulated. An incision was made in the skin over the skull and a small trephine hole opened in the skull and dura. All incision and pressure points were infiltrated with a solution of procaine (Zyljectin) in oil; this local anesthesia remains active for several days. The cat's head was then placed in a stereotaxic apparatus that leaves the visual field free, and the skin flap was secured to a metal ring above the animal's head. A solution of agar in saline was used to minimize brain pulsation. At this point in the procedure, thiopental sodium anesthesia was discontinued and the animal paralyzed with gallamine triethiodide (Flaxedil) given in doses of about 50 mg/hr, i.v. Saline and glucose were also given as required. Artificial respiration was maintained by a Harvard apparatus pump model

607 (stroke volume: 100; respirator rate: 25 min). During this period, the corneas of both eyes were kept well moistened with instillations of homatropine (Isopto-Homatropine) and phenylephrine hydrochloride (Neo-Synephrine); contact lenses were then applied to the corneas for protection and to correct for accommodation. An artificial pupil, 1 to 3 mm in diameter, was used in most of the experiments. Great care was taken when applying the lenses that their surface remained perfectly clean; the state of the cornea was also checked routinely to assure that no deterioration was taking place.

Recording. An array of four tungsten microelectrodes was lowered stereotaxically and their tips aimed at the intracranial end of the optic foramen. Solid-state source followers (22) were directly mounted above the microelectrodes; the output of the source followers was then conventionally amplified and fed to a Schmitt trigger before further processing. Only units that left no doubt about being single units, and with receptive fields falling within the area scanned, were mapped.

Visual Stimuli. The stimulus display system consisted of a flat (tangential) screen 35 cm high by 45 cm long, placed about 57 cm from the eye; at this distance 1 cm on the screen subtends about 1 deg at the eye. On this screen thin black or white cardboard could be easily attached to produce a background of wanted reflectance (Fig. 1); a contrasting black or white disc, 0.5 deg in diameter, was mounted on a small magnet which was held in position on the screen by another similar magnet behind the screen. The position of the magnet behind the screen was in turn controlled by the servomechanisms of an X-Y plotter (Mosely 2DR-2). Close tolerances and appropriate shapes for the magnets are necessary to avoid slippage between them; the supporting screen had a thickness of 1 mm; slippage proved negligible. The screen was evenly illuminated by a tungsten-filament lamp. The level of the incident light could be varied from 2 lm/m^2 to 200 lm/m^2. The reflectance of the disc and background used on the screen was: white 75%, black 3%. In other experiments a disc 0.2 deg in diameter whose luminance could be controlled was used. This allowed one to vary the gradient between disc and background over an extended range. The disc position and movements on the screen could be controlled by simply feeding appropriate voltage functions to the x and y servo-amplifiers. A Weston illumination meter 756 was used to measure illumination levels.

Data Gathering and Processing. A small general-purpose computer was used to gather and process the data (PDP-8). A program was designed to achieve the following: (*i*) Generate the voltage functions for the x and y servo-amplifiers necessary to move the disc in a scanning pattern that covered a 25 by 25 deg region of the visual space. The scanning pattern consisted of fifty 25-deg horizontal (H) scans from left to right, or right to left spaced 0.5 deg vertically and starting with the bottom scan. At the end

of a scan the disc was rapidly returned to the starting position and lifted 0.5 deg. No data were collected during the return of the disc; 1.5 sec were allowed between scans. Alternatively the scans could be made in the vertical (V) direction from down to up or up to down starting with the left-most
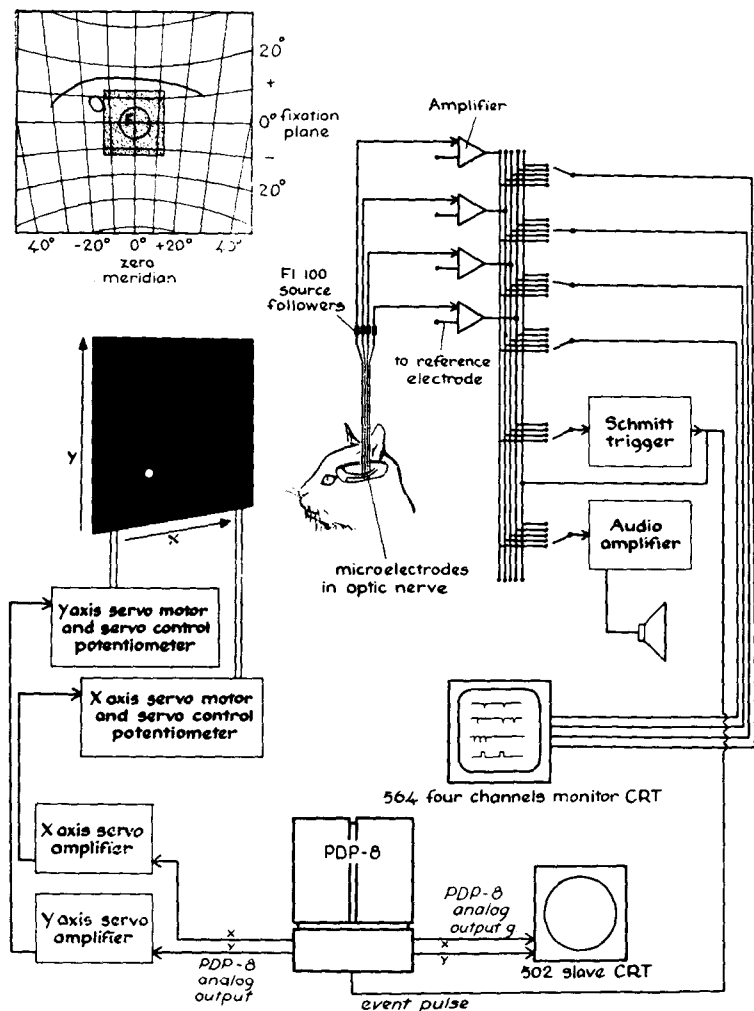

FIG. 1. Flow diagram of the experimental setup. The inset at the top left of the figure indicates the position of the optic disc (small oval) in respect to the region of retina that was scanned (dotted square). The solid curve line represents the most commonly found lower edge of the tapetum. F represents the approximate position of the fixation point.

scan. (*ii*) Control the speed of movement during an H or a V scan. (*iii*) Count and store in separate memory gates the number of spikes produced by the optic nerve unit being recorded during 0.5-deg segments, so that subsequently a matrix of 50 × 50 data points could be generated from the store. (*iv*) Print out the numerical values of the 2500 data points, or of any H or V scan. (*v*) Display on the oscilloscope face any of the H or V scans. (*vi*) Show the whole matrix as an isometric display. (*vii*) Display two-dimensionally, only those points at which the recorded activity was above or below a given value.

A separate program furnished by Digital Equipment Corporation was used to perform statistical computations.

Some Comments on Data Collection and Display. The method described here is not different in principle from the one described by the Bishop group (5). The isometric display of Fig. 2 is directly comparable to the complete

FIG. 2. Isometric display of a concentric off-center receptive field, same unit as in Fig. 3.

tri-dimensional plot shown in Rodieck and Stone's Fig. 6 (15). This is the way in which each field was mapped in this work. While the isometric display presents all the data collected in one map, it was found that a partial presentation of the data in the form of integral contour displays (Fig. 3) or single scan response histograms (Fig. 15) conveys a more immediate idea of what the shape of a receptive field is.

To this end, integral contour displays, selected on the basis of their statistical significance, were used to determine the shape of receptive fields and are almost exclusively shown. It was also found unnecessary to average the data of repeated maps even though the program for data collection allows it. The reason for this is probably due to the long time (0.1 sec) during which the activity of a unit is sampled in a standard map (5 deg/sec). A capital B will be used to indicate the mean background activity of a unit in number of pulses per memory gate. (Note that the background frequency in

pulses per second is equal to B/t, t being the time during which the disc moves 0.5 deg. By knowing the SD and assuming a normal distribution, it is then easy to assess the probability that a point, appearing on an integral contour display taken at a given level, is part of the background. This probability is down to 0.001 when the level of the integral contour is $B \pm 3$ SD. While the distribution is not gaussian it approximates a unimodal distribution enough to make this type of analysis satisfactory.
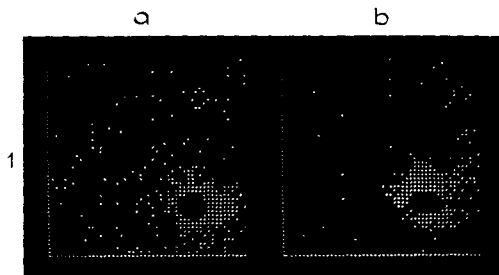

FIG. 3. Integral contour displays of a concentric-a field. Background in pulses per memory gate (B) $B = 0$. The white dots represent regions where the firing level of the unit was 1 or greater. In 1a the field was mapped with the disc moving horizontally; in 1b with the disc moving vertically. Scanning speed: 5 deg/sec; incident light: 20 lm/m^2; disc size: 0.5 deg; white disc on black background. In this and following integral contour displays the vertical and horizontal axes represent 25 deg.

Terminology. Bishop's methods (5) were used to determine the projection of various retinal landmarks on the tangential screen and his system C of spherical polar coordinates was used. Bishop's terminology is therefore used throughout except when otherwise specified. To simplify description, I will refer to "shape" of a receptive field as the combination of (*i*) that cluster of points which are significantly *above* the mean background level of firing of the unit and of (*ii*) that cluster of no points which is displayed when all points which are significantly *below* the mean background level of the firing of the unit are shown on a contour map. An H or V scan will be followed by a number indicating its position on the map. The number increases from bottom to top for the H scans and from left to right for the V scans.

Results

TYPES OF RECEPTIVE FIELDS

The receptive fields of 145 units were mapped in a variety of conditions. To simplify description, the types of receptive fields found will be described first; the effects of varying speed, direction, contrast and ambient illumination will be described in the second section of the results. Not all fields could be

mapped in all conditions. A total of 600 maps was collected, corresponding to 1,500,000 data points. A variety of receptive field shapes was observed; they will be described in order.

Concentric-a. Two main types of concentric fields were found; the first kind will be referred to as concentric-a and corresponds most closely to the receptive fields described by Kuffler and by Rodieck and Stone (11, 15, 16). Figures 2 and 3, $B = 0$, show an example of this type of organization: A central region, off in this case, more or less circular, is surrounded by a region of opposite sign. The shape of this particular receptive field, and of receptive fields of this kind, remains substantially constant over wide ranges of scanning speed or of ambient illumination, and is relatively independent of the scanning direction. Figure 4 shows the map of an on-center field, $B = 5.5$,
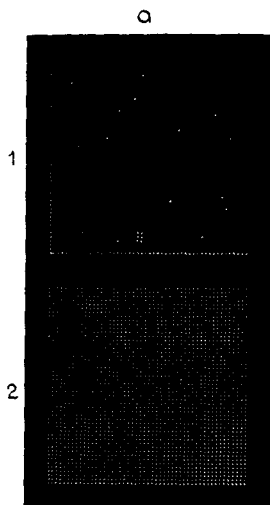

FIG. 4. Integral contour displays of a concentric-a field; $B = 5.5$, SD (standard deviation) $= 1.2$. In 1a: 9 or greater; level in 2a: 4 or greater. The receptive field of this unit was mapped with the disc moving horizontally. All other stimulus parameters are the same as in Fig. 3. In 1a the excitatory regions of the field are shown, in 2a the inhibitory ones.

SD $= 1.2$. These fields were mapped with a white 0.5 deg disc against the black background; incident light on the screen was 20 lm/m², scanning speed 5 deg/sec. Figure 5 shows another concentric-a field, $B = 1.2$, SD $= 0.6$, mapped with the same parameters; this particular field is interesting because of its great size and because it shows that the surround region can be made up of more than one component—two in this case. Ten receptive fields of this kind were found.

Concentric-b. The great majority of fields that can be identified as concentric have a shape which is not independent of the scanning direction. Figures 6 and 13, $B = 1$, $sd = 0.5$, show the map of an off field of this kind. It differs from a concentric-a field in that the surround is present only
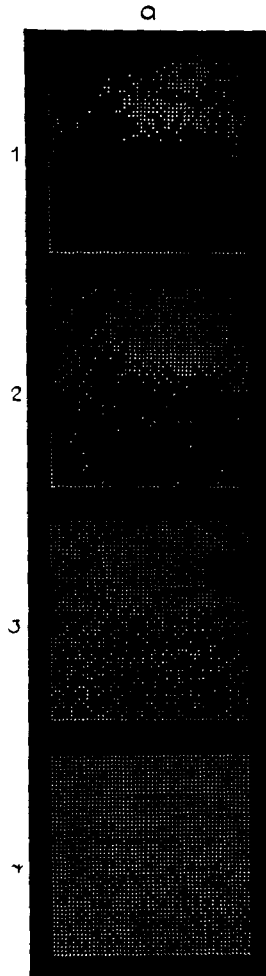

FIG. 5. The same stimulus parameters of Fig. 3 were used in mapping the receptive field of this unit. The disc was moving horizontally. $B = 1$, $sd = 0.5$; the levels are: 4a:1, 3a:2, 2a:3, 1a:4 or greater. Note the small off center which is best shown in 4a and the very large surround, best seen in 2a and 3a. It can be seen in 1a that the surround is not homogeneous.

in leaving the center of the field; changing the direction of the scan will
therefore change the position of the surround (Figs. 6 and 13). To simplify
description, the surround on entering or leaving the field will be called in-
surround and out-surround, respectively. Rodieck and Stone (15) noted that
the response of the surround on entering a concentric field (component a in
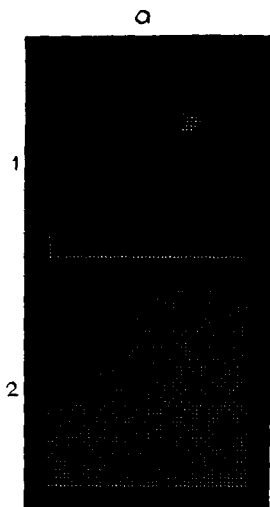

FIG. 6. The receptive field of this unit was mapped with the same stimulus parameters
used in Fig. 3; the disc was moved horizontally. $B = 1$, $sd = 0.5$; the levels are: 1a:4,
2a:1 or greater.

their response histograms) is usually but not always present and that it is
sufficient to decrease the scanning speed to obtain a more "symmetric" re-
sponse. In the present experiments, the difference persists. The shape of the
concentric-b fields remains essentially constant over wide ranges of trans-
formations of the stimulus and it is not sufficient to decrease scanning speed
to elicit the in-surround. The lowest speed that was tried was 0.39 deg/sec;
this speed compares with 10 deg/sec normally used by Rodieck and Stone
(15) or with the 2.5 deg/sec of their lowest speed. But it was still not possible
to have in- and out-surrounds of equal strength (Fig. 15). An examination
with flashing stationary spots showed that this last method would not have
distinguished the two types of receptive fields. In all, 100 concentric-b fields
were found.

The concentric-a and b fields have characteristics that make their identifi-
cation easy and immediate: they display a generally circular shape of the
center, with a complete surround or with an hemi out-surround. However, a
number of receptive fields do not conform to this kind of organization.

Bar and Edges. Bar- and edge-shaped receptive fields having different orientations and sizes were found. Figures 7a, b and 8 show examples of a bar-shaped receptive field mapped at 20 lm/m², 5 deg/sec, $B = 5.2$, $SD = 0.9$. These fields have characteristics which are somewhat similar to the "simple"
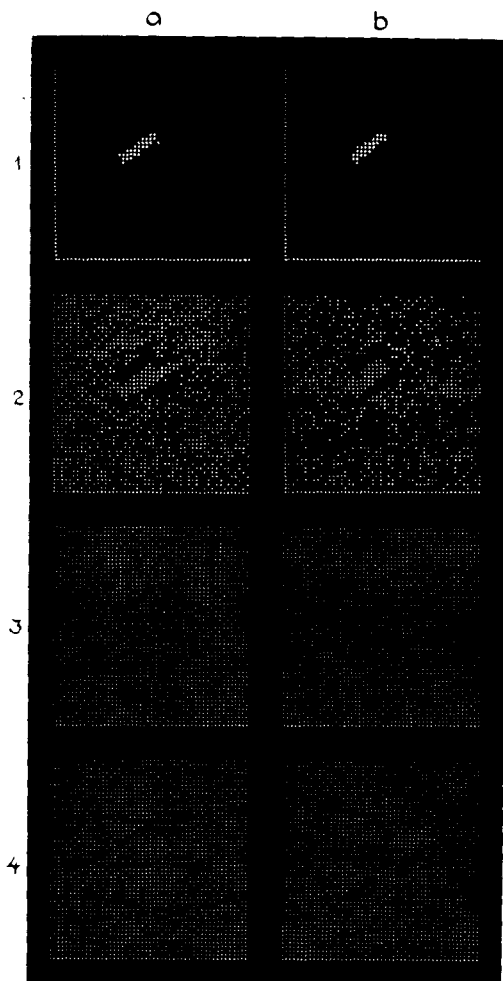

Fig. 7. The receptive field of this unit was mapped with the disc moving vertically in a and horizontally in b. All the other stimulus parameters were the same as in Fig. 3. $B = 5.2$, $SD = 0.9$. The levels are: 4a, 4b: 2; 3a, 3b: 3; 2a, 2b: 6; 1a, 1b: 10 or greater. Viewing of the data at different levels allows one to identify different features in the maps. The 2a level for example shows that there is an inhibitory surround on all sides of the bar-shaped excitatory component (1a) even though the inhibition is stronger on leaving the excitatory component than on entering it (4a and 4b).

receptive fields described by Hubel and Wiesel (10) for single units recorded
from the visual cortex of the cat. Bar- and edge-shaped receptive fields of
unusual size were also found. Some of these fields were mapped using higher
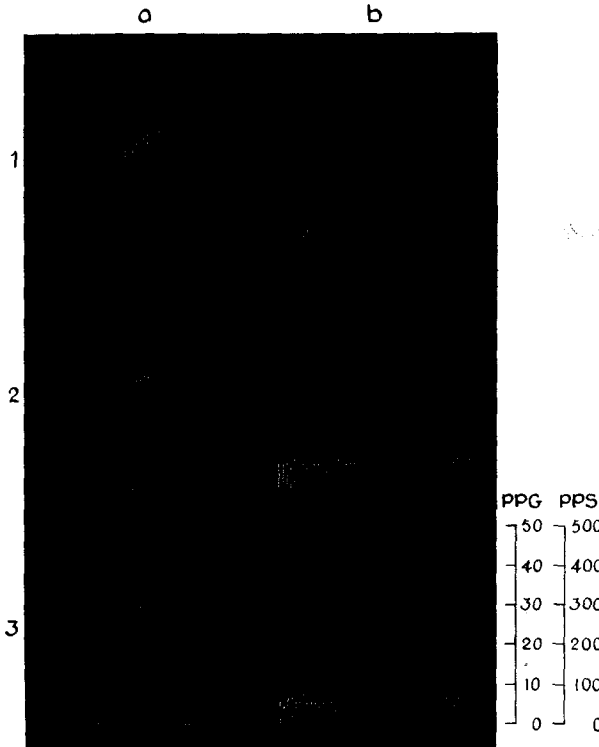contrast stimuli (18) but they can be demonstrated even by the much

Fɪɢ. 8. In this figure single vertical scans at the positions indicated by the vertical
marker (V17, V21, V24) are shown in 1b, 2b and 3b from the same map as in Fig. 7a. The
level of the integral contour display in 1a, 2a and 3a is 9 or greater. The calibration for the
single scans is in pulses per gate (ppG) and in pulses per second (ppS). The vertical
scans in 1b and 3b show that the excitatory component is just as strong at the two
extremes of the bar as it is in the middle.

smaller gradients used in most of these experiments. Some of these fields were
of a composite kind, namely, there is a big region either bar- or edge-shaped,
with a smaller secondary cluster of increased or decreased firing, either in
or near the big region. Figure 9 shows a map from a unit of this kind, mapped
at 20 lm/m², 5 deg/sec, $B = 0.4$, sᴅ $= 0.5$; this unit is interesting because it
is possible to compare the firing rates of the region immediately around what
one might have considered an off center with the firing rates of regions

several degrees away; it can be seen that the highest firing rates at H_6 and H_{43} are in the same range as that of H_{29}. It is clear that these fields exceed the boundaries of the scanning system. Their extent and properties have yet to be completely elucidated. Figure 10 shows two smaller fields of this type, mapped at the same level of incident light. Seven fields of this kind were found.
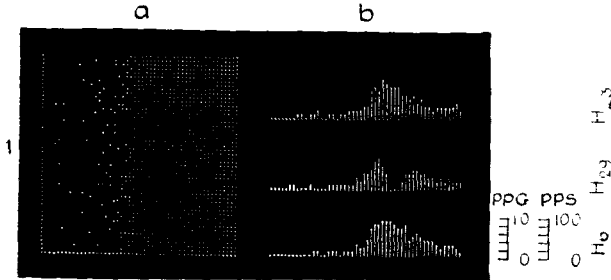

FIG. 9. The receptive field of this unit was mapped with the disc moving horizontally; all the other stimulus parameters are the same as in Fig. 3. $B = 0.4$, $sp = 0.5$. In 1a an integral contour display is shown, level: 2 or greater. In 1b three single scans at H_6, H_{29} and H_{43} show the response of the unit in ppG and ppS.
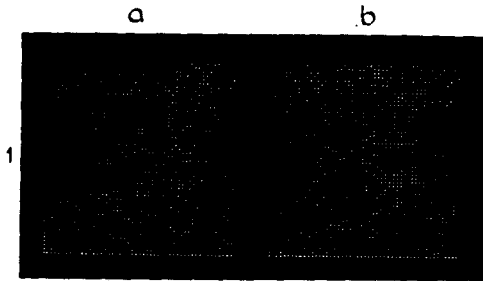

FIG. 10. Two units with slightly oblique edge-shaped receptive fields are shown. The unit in 1a had $B = 2$; the unit in 1b had a $B = 5$. The integral contour displays are shown at those levels, respectively.

Presence Detectors. A group of eight units was found with the characteristic that after the disc had passed through the center, the unit would "follow" the stimulus for some time. Figures 11a and 11b show one such unit, mapped at 20 lm/m², 5 deg/sec, $B = 3.3$, $sp = 1.1$. That the "following" is not simply a matter of prolonged afterdischarges can be proven in two ways: (*i*) When a white disc is manually placed on the center and then removed entirely from the visual field the afterdischarge disappears in a few hundred milliseconds. (*ii*) When the field is scanned at higher speeds, the "following" disappears. The map of Fig. 11c was done at 20 lm/m², 16.6 deg/sec,

$B = 0.9$, sd $= 0.7$. If prolonged afterdischarges were the cause of the excitatory streaks of Fig. 11a, one would expect them to show up even more at this faster scanning rate. This is not the case, indicating that "following" takes place only for stimuli moving at moderate speeds. No inhibitory surround can be demonstrated in these fields.
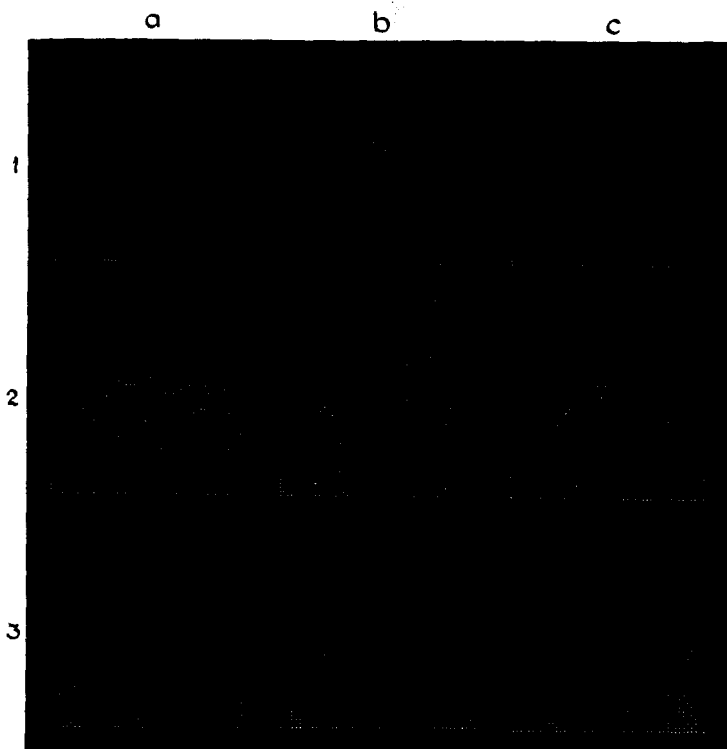

FIG. 11. This figure shows different levels of three maps performed on the same unit. In a the disc moved horizontally; in b and c, vertically. Scanning speed: 5 deg/sec in a and b, 16.6 deg/sec in c. $B = 3.3$, sd $= 1.1$ in a and b; $B = 0.9$, sd $= 0.7$ in c. The levels are 1a:8; 2a:5; 3a:2; 1b:8; 2b:5; 3b:2; 1c:4; 2c:3; 3c:1 or greater. Note the heightened firing level of the unit after the disc goes through the center as shown in 2a and 2b. Note also the absence of inhibitory surround shown in 3a, 3b and 3c. There was no similar sustained increased firing when the field was scanned at 16.6 deg/sec. All the other stimulus parameters remained the same as in Fig. 3.

Others. Odd shaped receptive fields are especially well demonstrated when using higher light gradients between disc and background, and for the time being, no attempt to analyze them will be made. The Discussion will deal with the problem of stray light. Figure 12 shows one such field mapped with

different gradients, $B = 4.7$, SD $= 1.5$. These fields will be referred to as "composite" because several components seem to make up their shape.

CHANGES IN THE STIMULUS PARAMETERS

The Effect of Speed. Rodieck and Stone (15) found that the change in unit firing caused by a small spot of light turned on or off in its receptive
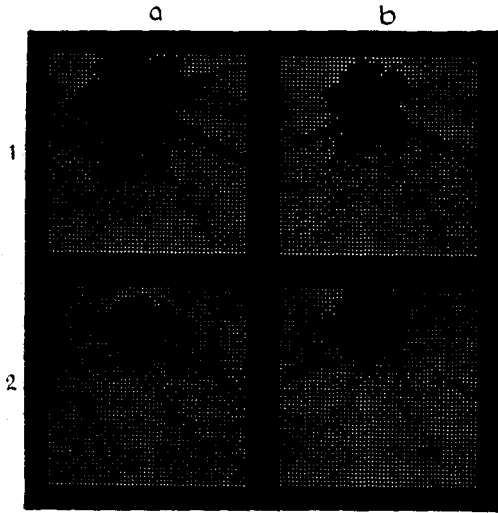

FIG. 12. The receptive field of this unit was mapped with the disc at 1.3, 11 and 44 cd/m² in 1a, 1b and 2a, respectively. The disc was 0.2 deg in diameter and was moved vertically. Background level was kept constant at 0.02 cd/m². Scanning speed: 5 deg/sec, $B = 4.7$, SD $= 1.5$. In 2b the field was scanned horizontally with the disc at 11 cd/m². All integral contour display levels are at 3 SD or greater. The receptive field size decreases with decreasing contrast, but some of the inhibitory bars are present even at the lowest contrast.

field has an exponential-like decay, with a time constant of 25 to 45 msec. It follows that there is an optimal speed for mapping the true firing pattern of the field. The signal to background firing level noise ratio becomes poorer, both for speeds which are too low because of adaptation (this holds true independently of what factor or factors are responsible for adaptation) and for speeds which are too high because of afterdischarge. Figure 13 (same unit as Fig. 6) shows a concentric-b off field ($B = 0.8$, SD $= 0.7$) mapped vertically at different speeds (20 lm/m²). Numerical computations show that the best signal to noise ratios are obtained at speeds from 5 to 10 deg/sec. Figure 14 shows the effect of different speeds on a concentric-a field; same unit as Fig. 5 mapped vertically. In Fig. 15 a concentric on-center
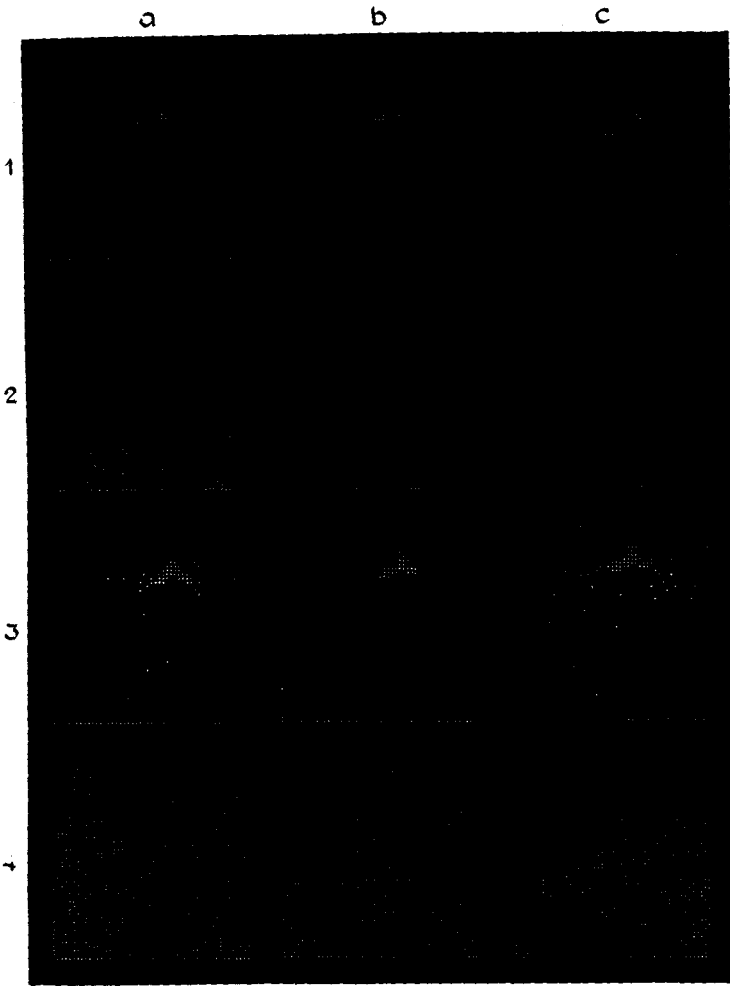
Fig. 13.   The receptive field of this off center unit was mapped six times at various speeds with the 0.5-deg disc moving vertically. Incident light: 20 lm/m²; 1a and 2a are two integral contour displays from the same map done at 1.6 deg/sec. The other scanning speeds are: 1b and 2b: 2.5 deg/sec; 1c and 2c: 5 deg/sec; 3a and 4a: 10 deg/sec; 3b and 4b: 16.6 deg/sec; 3c and 4c: 25 deg/sec. The levels of the displays in 1a, 1b, 1c, 3a, 3b and 3c are 3 sp above background. Notice that the surround is present only on leaving the center at all speeds. This unit is the same as in Fig. 6. The levels of the displays in 2a, 2b, 2c, 4a, 4b and 4c are set at one count or more per gate. Regions on the map devoid of white dots represent regions where the unit never fired. The off center is best seen in 2a and 2b.

field was mapped horizontally at the standard speed of 5 deg/sec, $B = 4.6$, $SD = 1.1$. The H_6 scans on the right show the response of the unit for speeds of 5, 0.78, and 0.39 deg/sec. Even at this extremely low speed it is impossible to obtain more than a suggestion of in-surround. This particular

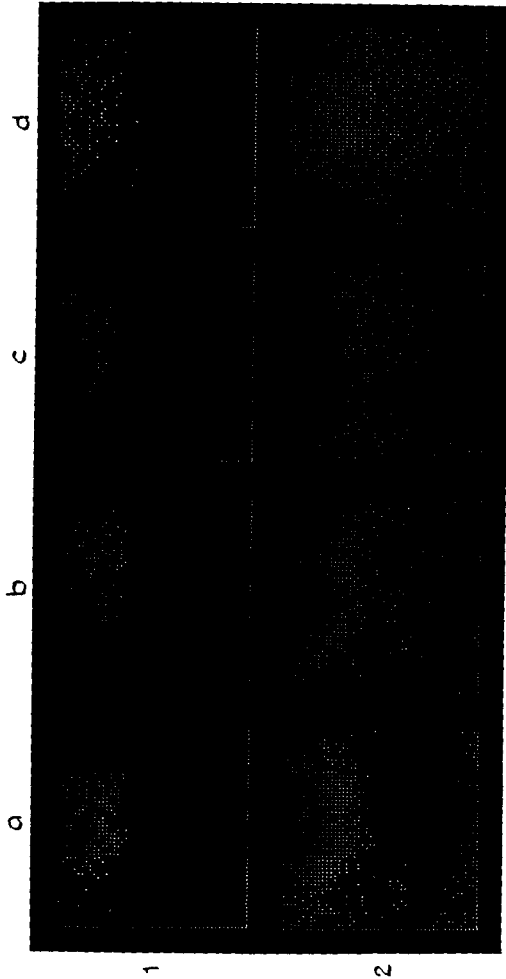FIG. 14. The receptive field of this unit (same unit as in Fig. 5) was mapped four times at various speeds with the 0.5-deg disc moving vertically. Incident light: 20 lm/m². The scanning speeds are: in a: 2.5 deg/sec, in b: 5 deg/sec, in c: 10 deg/sec, in d: 16.6 deg/sec. The levels of the displays are: in row 1: 3 SD above background; in row 2: 4 counts for 2a, 2 for 2b, 2 for 2c and 1 for 2d or greater.

field was a good candidate for the test because a very weak in-surround is present at 5 deg/sec.

The Effect of Light Level. The characteristics of most fields varied little over the range of ambient illumination that was explored. Typically the
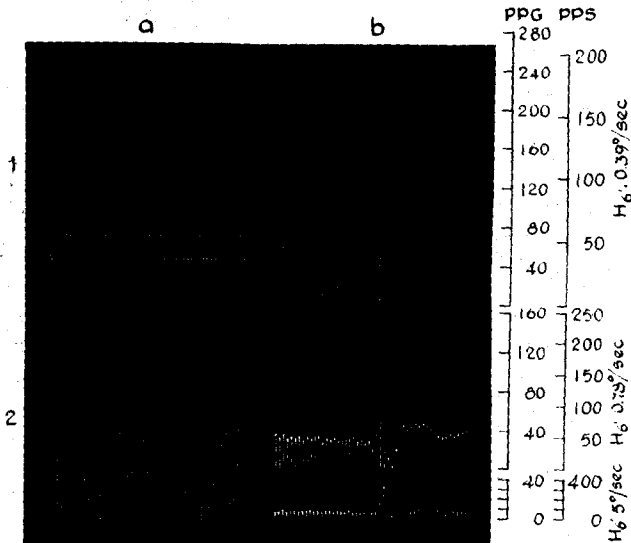

Fig. 15. The receptive field of this unit was mapped first with the same parameters used in Fig. 3, disc moving horizontally. $B = 4.6$, sp $= 1.1$. The displays in 1a and 1b are from this map. The levels are for 1a: 10 or more, for 2a: 5 or more. The level of 2a is set at background to evidence the weak in-surround. In b, single scans taken at H_6, as shown by the marker, are displayed. Different scanning speeds were used. Starting from the bottom: 5 deg/sec, 0.78 deg/sec, 0.39 deg/sec, calibration in ppG and ppS. Note that as the scanning speed becomes lower there is a tendency for the field to become more symmetrical, but that even at the slowest rate, complete symmetry is not achieved. The setting in of adaptation is also demonstrated by the lowered frequency of discharge for the center at these very low scanning speeds.

receptive field of a unit was mapped at 2, 20 and 200 lm/m² in that order, about 10 min being allowed for light adaptation. Figure 16 shows a concentric-a field mapped in these three conditions. The background activity of this unit changes from $B = 1.4$, sp $= 0.9$ at 2 lm/m² to $B = 0.2$, sp $= 0.4$ at 20 lm/m² and further to $B = 1.3$, sp $= 0.7$ at 200 lm/m². Barlow, Fitzhugh and Kuffler (2) found that the surround disappears at very low levels of illumination, i.e., when dark adaptation is nearly complete. The lowest level of luminance used in these experiments was 2.10^{-2}cd/m². At this level surrounds are still present. A closer analysis of the data presented in Fig. 15 shows that for this unit, and this also applies to other
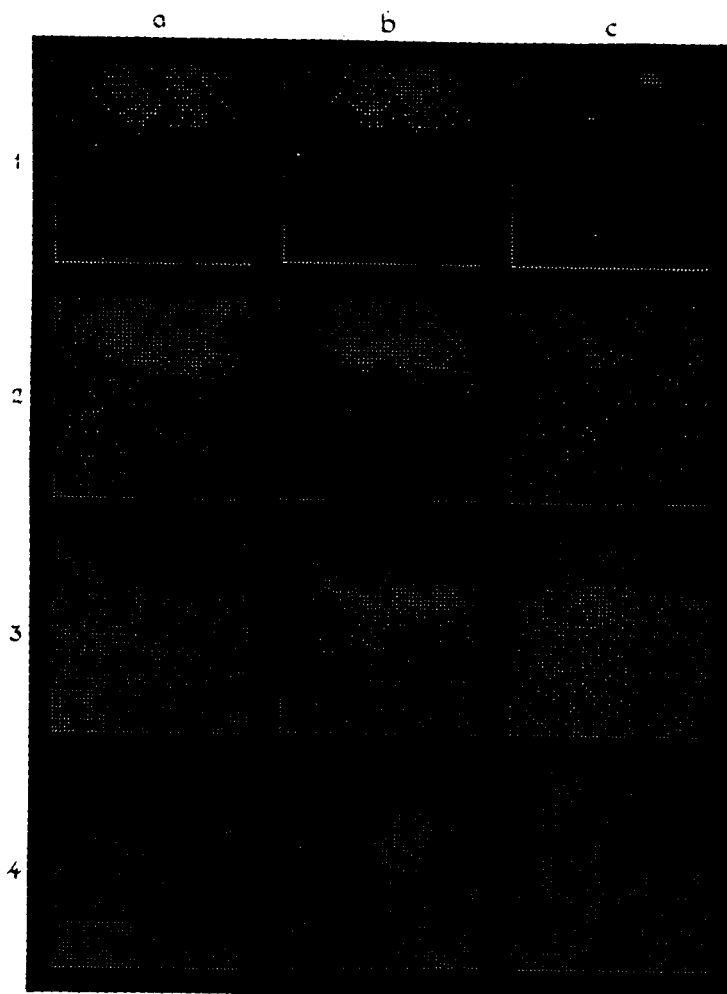
FIG. 16. The receptive field of this unit (same unit as in Fig. 5) was mapped with the disc moving vertically, scanning speed: 5 deg/sec, at three levels of incident light. In row a, 2 lm/m² were used, $B = 1.4$, SD $= 0.9$; in row b, 20 lm/m² were used, $B = 0.2$, SD $= 0.4$; in row c, 200 lm/m² were used, $B = 1.3$, SD $= 0.7$. The levels are: 4 in row 1, 3 in row 2, 2 in row 2 and 1 in row 4. Note the better definition of the surround at 20 lm/m² of incident light.

units even though the level might be different, there seems to be an optimum level of illumination at which signal to noise ratios are best. Thus at 2 lm/m² and at 200 lm/m², the surround is weaker than at 20 lm/m². Figure 17 shows a concentric-b field that exhibits essentially the same behavior:

$B = 3.4$, sd $= 1.1$; $B = 3.1$, sd $= 1.1$; $B = 0.9$, sd $= 0.7$; at 2, 20 and 200 lm/m², respectively.

Stimulus Gradient. Kuffler (11) found that increasing the intensity of the exploring spot seems to extend the receptive field of retinal ganglion cells. This suggests that one should use strong stimulus-background gradients
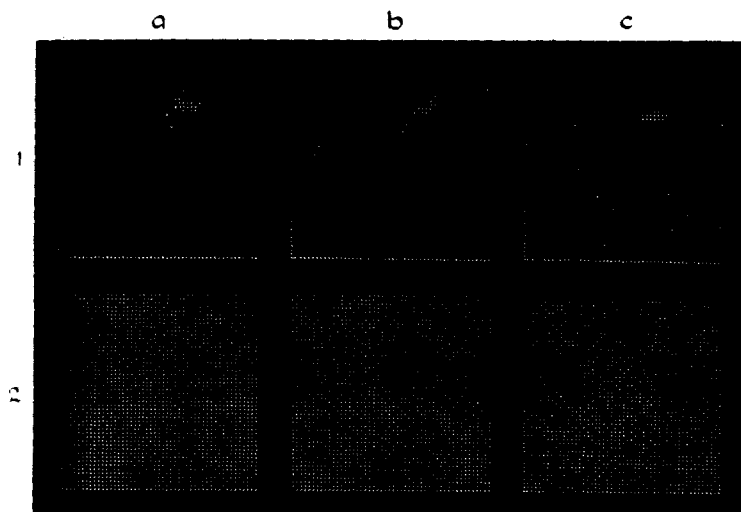

Fig. 17. The receptive field of this unit was mapped with the disc moving vertically, scanning speed: 5 deg/sec at three levels of incident light. In row a, 2 lm/m² were used, $B = 3.4$, sd $= 1.1$; in row b, 20 lm/m² were used, $B = 3.1$, sd $= 1.1$; in row c, 200 lm/m² were used, $B = 0.9$, sd $= 0.7$. The levels are 3 sd above background in row 1, 2 counts in 2a and 2b, 1 or greater in 2c.

to demonstrate the total extent of the field, i.e., those regions where the receptor density is low. Forty units were examined using a 0.02 cd/m² background and a 0.2-deg disc whose luminance could be increased up to 200 cd m². At these higher gradients concentric fields are obtained as a rule, but it is easy to obtain receptive field shapes of great size and odd shapes (18). Some of these field shapes suggest possible functions, but it is perhaps more profitable to show one of these fields mapped with different contrasts. Figure 12 shows a composite field mapped with the spot at 1.3, 11 and 44 cd m². The background was kept constant at 0.02 cd/m² and the field was scanned vertically. While the main round body of the field decreases in size rather regularly with decreasing contrast, the position of some of the boundaries changes very little. Some of the spokes are present even at the lowest gradient used. A horizontal mapping of the same field done with the spot at 11 cd m² shows essentially the same field shape as was obtained when the field was vertically mapped at the same gradient. As

already noted, edge and line shaped receptive fields originally found at
4 log units of contrast were also found at 1.4 log units and with an ambient
level of illumination of 2 to 200 lm/m².

Discussion

Optics, The Reflective Tapetum and the Problem of Stray Light. As the
interest was to map receptive fields located in or near the area centralis,
the center of the stimulus display system was aligned with the presumed
visual axis. The axis intersects the tangential screen 12.3 deg up and 2.5 deg
lateral from the perpendicular [normal to a frontal plane that goes from
the eye under examination to the screen, $\gamma F = +12.3$, $\delta F = -2.5$ deg in
Bishop, Kozak and Vakkur's terminology (5); see also Fig. 6 of Bishop's
paper]. The scatter of these values is small compared with the area scanned,
so that one can be sure that the area centralis is within the scanned region. A
reversible ophthalmoscope was also used to determine the position of the
optic disc in relation to the area scanned. The inset of Fig. 1 gives an
idea of the relative position of the optic disc and of the fixation point (F).

Extreme care was taken to maintain the cornea in optimal conditions
during surgery and in assuring that the contact lenses were clean. An artificial
pupil 1-3mm in diameter was used most of the time. While this improves
resolution somewhat, its presence or absence did not change the shape of
the receptive fields. This finding is in agreement with other authors (3).
Also in agreement with others (3, 5, 15) is the finding that perfect refraction
of the eye was not necessary; the smallest receptive field that was found
in this work was 3 deg, so that a slight blurring of the image would be of
no great consequence. The sharpness of the boundaries in most mapping
insures that refraction was within satisfactory limits.

In scanning a given part of the retina a fraction of the photons forming
the image of the white scanning disc is reflected. This fraction depends on
the reflectance of the structures that are successively illuminated. The
question has been raised (4), and it is, of course, worth considering, that
stray light might be a source of artifact in that the total amount of light
reflected inside the eye, and therefore the light falling on receptive fields
removed from the image proper, varies as a function of the reflectance of
the structures traversed by the image. This, of course, could lead to spurious
mappings. In other words, one could be mapping reflected light falling on
a receptive field outside the scanned area. These considerations apply
primarily to the fields mapped with high contrasting stimuli (0.2 deg, 200
cd/m² disc, 0.02 cd/m² background). A simple precaution was taken from
the beginning, namely, to map always the same general area of the retina;
fields outside this area were rejected. Thus, any artifact due to different
reflectance of different structures should appear in all maps in the same

positions. The most active region of a receptive field was always located first by waving a dimly-lit bulb in front of the cat. The "center" of the receptive field is thus located and always appears on the map. Possible artifacts should appear as extra regions of lower firing rate than the "center" and always in the same positions while the position of the center should vary from unit to unit. Such artifacts were not discovered. Concentric fields were often found near or in exactly the same region of the retina, where only moments before, fields with no trace of concentric organization had been plotted.

Quantitative considerations also seem to exclude stray light as a candidate for artifact. Consider a 0.2-deg circular image near the area centralis. (Perfect refraction is immaterial to the following argument because the total light energy in the image would not be changed by blurring.) If one assumes that the tapetum is a uniform diffuser (17, 26) then Lambert's cosine law will apply, i.e., the intensity of the reflected light will be proportional to the cosine of the angle made with the normal. It can then be shown (25) that every part of the inner surface of a sphere is equally illuminated by the flux reflected from any given portion of the spherical surface, a principle which is made use of in the photometric integrator. It is then a question of considering the ratio between the surface of the image and the surface of a sphere whose radius of curvature is equal to the posterior nodal distance. The relative fluxes and the reflectance of the tapetum also have to be taken into account.

The following formula formalizes these relationships:

$$\frac{2 \pi r^2(1 - \cos \frac{1}{2} \theta)}{4 \pi r^2} \times 10^4 \times 0.44 \approx \frac{1}{304},$$

where $r = 12.5$ (24), $\theta = 0.2$ deg. 10^4 is the illumination of the image relative to the illumination of the background on the retina and 0.44 is the reflection coefficient for the tapetum (26). The amount of light added to the background is thus $1/304$. Thresholds for just noticeable differences at this background level are about $1/15$ (4). It seems, therefore, that there is just not sufficient change due to reflected light, even if the spot moved from the tapetum to a point of 0 reflectance. The maximum gradient that one can use is thus determined by the threshold for just noticeable differences and by the size of the image.

The Effect of Scanning Speed. The overwhelming impression was that speed, except in the extremes, is not a factor in determining the shape of the receptive fields. Analysis of the data shows that there is an optimal speed around 10 deg/sec at which signal to noise ratios are best. That an optimum speed should exist could have been deduced from the data of

previous workers. Delays and afterdischarges (15) set the upper limit beyond which signal to noise ratio becomes poor. Further increase in scanning speed would ultimately produce responses similar to those produced by a flash of light. Adaptation in turn sets the lower limit beyond which further lowering of the scanning speed would result in greater and greater background levels as compared with signal changes. These findings, of course, do not exclude the possibility that units which are sensitive to the speed of angular displacement exist and have gone undetected in this study.

The Effect of Background Illumination. The inhibitory and the excitatory regions of receptive fields can be compared to the — and + inputs of an operational amplifier; in an ideal system a common mode signal should not affect the output level or the gain; in reality, if the inputs are connected to two photocells, and if the rejection ratio of the amplifier is not too good, common-mode signals will change the level of the output and there will be apparent and real changes in gain determined by the response curve of the photocells and by the maximum swing that is permissible to the output.

Barlow, Fitzhugh and Kuffler (2) found that many ganglion cells will, given time, return to their original firing level after a change in background illumination. That this return is often only partially complete can be seen from Figs. 12 and 13 and has also been demonstrated by other authors (11). An imblance between the excitatory and the inhibitory areas is most likely responsible for this result. A consequence of this imbalance is that there is a region of optimal signal to noise ratio for most units. In general, the changes in the response to a white disc on a black background, produced by changing the level of incident light from 2 to 200 lm/m^2, are relatively small. The amount of change is greater going from 20 to 200 lm/m^2 than from 2 to 20 lm/m^2 of incident light.

Nature of the Surround. The assumption that the surround is a symmetrical dome shaped single component with an opposite sign independent from the center (16) seems to be true only in special cases, i.e., in the concentric-a fields. Even in this class, surrounds with more than one component can be demonstrated. Strong and very-long lasting interactions between the center and the surround of the concentric-b fields have been shown. Even more complex is the situation for the bar and edge detectors, the composite fields and the follower units. At this time it is hard to do more than to point out that different relationships between excitatory and inhibitory regions must underlie the determination of the surround in the different classes of fields.

Types of Receptive Fields Found and Retinal Coding. The work of Letvin (12) and Maturana, et. al. (14) on the frog's eye and of others (3, 10, 13, 21, 23) in different animals or at different levels in the visual pathway, or both, has brought to the attention of physiologists that in the visual system

different units respond best to different features of the visual stimuli. That qualities are segregated at the receptor had been known for a long time in other sensory systems, i.e., auditory, somatic, etc. Yet in the retina of the cat, the only kind of receptive fields that had been found were, until recently, the concentric on and off center as described by Kuffler (11). Rodieck and Stone (15) showed that these fields could be mapped by using moving stimuli. More recently, Stone (23) was able to demonstrate direction-sensitive units and Spinelli and Weingarten (22), direction-sensitive units and flux detectors. The present results show that contrary to expectation, the retinal unit responses of the cat show a great deal of complexity; bar and edge detectors can be demonstrated as well as follower units, flux and direction detectors, and odd-shaped composite fields. Even concentric fields appear to be made up of two subclasses.

This evidence suggests that the retina of the cat is not a simple repeater, but that coding of visual information is performed at least in part at this level. The law of spatial summation, confirmed in the retina by various authors (1. 7, 8, 16) makes it inescapable that ganglion cells with receptive fields of different shapes will be optimally activated by different features of the retinal image. What these features are is a matter for speculation. Units with bar- and edge-shaped receptive fields have been called bar and edge detectors, respectively, on the basis that a cell will be optimally stimulated by an image that has the same shape and size of the receptive field (10). From an engineering point of view, of course, a detector is usually a very narrow band device, i.e., an infrared detector will not react to blue or to yellow. The tendency thus has been, by engineering-conscious physiologists. to emphasize the "specificity" of "convexity detectors" (12), "line detectors" (10) and so on. In reality, the specificity of these detectors is rather poor. For example, the simple line and edge detectors in the cat's cortex can be mapped with small spots (10), direction detectors give on-off responses to flashing spots (3) and so on. The lack of extreme specificity is probably very useful. The reason we can see so many colors rests on this very fact: the spectral sensitivity curves of the pigments are very, very broad and overlap greatly. Three "perfect" detectors would allow us to see only these three wavelengths.

On the basis of the evidence reported here, it might prove profitable to think of the various classes of receptive fields as the letters of a simple visual pattern alphabet, from which a more complex set of analyzers is then built up at the cortical level (10). The relative constancy of the receptive field shapes under most circumstances assures that similar visual patterns are repeatedly coded into the same letters in the same animal, though the receptive-field classes that make up the letters may be different in different species or even from animal to animal.

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