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Visual Receptive Field Organization of Single Units in the Cat's Visual Cortex

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The receptive fields of 165 cells in the primary visual cortex (area 17) of cats were mapped by moving a small white or black disc (0.5°) in a scanning pattern on a tangential contrasting screen placed at 57 cm from the cat; bars and edges were also used as more complex stimuli. An area $25 \times 25^\circ$ was explored by the moving stimulus. The screen was positioned to allow optimum mapping of units activated by images falling on the area centralis of both eyes. High resolution maps were obtained by automated stimulus control and data collection. Various levels of illumination, speed and direction of scan were used. The data show that the great majority of the units, over 90%, are binocularly activated. This fact, combined with standard criteria, leaves no doubt that the units recorded were cortical cells. The spontaneous firing rate was very low, less than 2/sec, for most units; somewhat higher rates were shown by units with diffuse receptive fields. The receptive fields mapped with the small disc were divided in the following classes; disc shaped, constituting 44% of the total sample; diffuse: 21%; bars and edges: 20%; composite: 12%; and unclassified: 3%. Of the units studied 17% were direction sensitive; more specifically, 16% of the disc shaped; 25% of the diffuse; 10% of the bars and edges; and 24% of the composite receptive fields showed direction sensitivity. Further analysis using bars and edges as stimuli, under either manual or servo control essentially confirms Hubel and Wiesel's data with regard to units with elongated or diffuse receptive fields. On the other hand, units with disc-shaped receptive fields seem to be uncommitted to specific features of the visual image suggesting that linear mechanisms might play a substantial role in the processing of visual information.

Introduction

One of the most striking manifestations of animal and human behavior is the recognition of visual patterns and the apparent ease with which it takes place, regardless of the exact position of forms in the visual space. The brain mechanisms underlying this aspect of behavior have, therefore, not surprisingly, been the object of much investigation and speculation by psychologists and physiologists (1-4, 9-11, 14, 18-20).

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In other fields, too, the general question of pattern recognition has received considerable attention, especially from the applied sciences laboratories as the quest for simple mechanisms, capable of performing pattern recognition is intensified in view of important practical applications (16); this work is of interest to us because it demonstrates whether schemes that might have seemed likely or reasonable at first glance are in fact possible.

In a previous paper, one of us (18) described receptive fields of single retinal ganglion cells whose activity and response to the scanning movement of a small spot on a tangential contrasting screen, was recorded from their axon in the optic nerve. In the present work the same method was used to examine the visual receptive fields of single units in the primary visual cortex of the cat. We felt that this work was needed to help us understand the use made by the visual cortex of the activity received from the retina via the lateral geniculate body.

When mapping the receptive field of a unit that is only one in a network of interacting cells it is possible to collect a great deal of information about the unit itself, but no direct information is gained about the connectivity of the system. A variety of methods have been developed to trace functional connections in the visual pathway, i.e., its functional anatomy. At the macroscopic (macroelectrode) level the work of Talbot and Marshall (22) and of others after them (7) is an example of how successful this approach can be; at the microscopic (microelectrode) level the number of potential connections becomes suddenly so enormously great that the possibility of tracing neuronal connections in a network and of defining its logical operations—much as an engineer would trace an unknown electronic circuit with the help of a probe—becomes an extremely difficult problem.

The response pattern to visual stimuli of single units in the visual cortex has been studied previously (3, 10, 11, 13) in an effort to infer the functional anatomy of the underlying system. Most of these studies, for technical reasons, were limited to the most responsive central regions of the receptive field. Detailed, quantitative, wide-angle maps of receptive fields of single units in the visual cortex of the cat, of resolution comparable to those available for retinal ganglion cells (18) are thus not available in the literature. This paper reports some initial experiments carried out to meet this need in the hope that better, more objective methods of classification will be possible.

Methods and Materials

The methods used in this work, except for some minor modifications, have been described in great detail in a previous paper (18). They will therefore be described only briefly at this time.

Preparation. Thirty adult cats were used. Surgery, consisting of cannulation of the radial vein and trachea and of a small opening in the skin and skull to allow penetration of the microelectrode at the selected cortical locus (anterior 0, lateral 0.5–1.5 stereotaxic coordinates), was performed under intravenously injected thiopental sodium anesthesia. All incisions and pressure points were then infiltrated with a solution of procaine in oil (Zyljectin); this local anesthetic has been found, when used with human patients, to remain active for several days. The cat's head was then placed in a stereotaxic apparatus that leaves the visual field free, and anesthesia was discontinued. A solution of agar in saline was used to minimize brain pulsation. Paralysis of the animal was obtained with gallamine triethiodide (Flaxedil), given intravenously at the dose of about 50 mg/hour. Possible residual eye movements were looked for, in some experiments, with a method similar to the one described by Rodieck *et al.* (17) and found to be absent. Artificial respiration was maintained by a constant volume pump (stroke volume: 50 ml, rate 20/min). The nictitating membrane was retracted by the instillation of a few drops of phenylephrine hydrochloride (Neo-Synephrine) and the pupils dilated with homatropine (Isoptohomatropine). Contact lenses were used to protect the corneas and to correct for accommodation. In some experiments the pupils were left in their normal state; it was found that this did not change the nature of the results. Temperature of the animal was maintained at 38 ± 0.5 C.

There are some aspects of this preparation that require comment. (a) The state of the corneas and cleanliness of the lenses are, of course, very important and easily maintained in satisfactory condition. (b) Thiopental sodium is a short acting barbiturate that should not be used over extended periods of time because of the accumulation of metabolic byproducts. Local anesthetics, in turn, are reabsorbed in the general circulatory system and have to be used in sufficient amounts, to be sure, but with caution. (c) Last, but foremost, is the state of the cortex. This depends on the general state of the animal, which should always be optimal, and on the care taken in opening the skull: The slightest push on the cortex is sufficient, in an acute preparation where only hours are available for recovery, to alter its state. In our experience the first sign of a moderately deteriorated preparation is a decrease or disappearance of the resting activity which, though of a very low frequency, is present in most units.

Recording. The activity of units located in the primary visual cortex was recorded with tungsten microelectrodes attached to a solid state source-follower (18). The great majority (about 90%) of the units studied were located in the left posterior lateral gyrus: 0.5–1.5 mm from the medial border A 0 in stereotaxic coordinates. The area centralis projects to this region (15, 22); thus, most of these units are sensitive to regions of the visual

space at, or near, the visual axis (6). Penetrations of the microelectrode were never deeper than 2 mm; at the end of a penetration a small lesion was produced by passing current through the microelectrode; histological examination verified that all penetrations were within the cortex.

Visual Stimuli. A tangential white or black screen (reflectance: White 75%, black 3%) placed at about 57 cm from the cat's eye was used. At this distance 1 cm is equal to approximately 1° . On this screen a small contrasting disc 0.5° in diameter, or other stimuli, could be moved with uniform speed under servo control in a scanning pattern of 50 lines 25° long and 0.5° apart over a $25 \times 25^\circ$ square, to obtain two-dimensional maps of receptive fields shapes. The activity generated by the unit during each 0.5° of movement was collected separately, thus, a map consists of 50×50 or 2500 data points. The screen was evenly illuminated by a tungsten filament lamp. The level of incident light could be varied from 2 to 200 lm/m^2 . Scanning speed and direction could also be controlled.

Data Collection and Processing. A small general purpose computer (PDP-8) was used to generate the voltages necessary to drive the servo systems over the scanning pattern and to count the spikes generated by the unit being mapped. As already said, each map generated a matrix of 2500 numerical values in the memory of the computer from which it could be stored on digital tape for further processing. Individual scans, integral contours, or isometric display could be shown and photographed on an oscilloscope face.

Some Comments on Data Collection and Processing. The mapping of ganglion cells' receptive fields with this method has shown that the best way to view the data is by the use of integral contour displays. This means displaying on an oscilloscope only those points where activity exceeded an arbitrarily selected value. The high resting activity of ganglion cells and their vigorous responses to the moving spot made it possible to use integral contour displays two or three standard deviations above or below the mean background activity to show excitatory or inhibitory regions, respectively, of high statistical significance (18). This brute-force approach cannot be used with maps of visual cortex receptive fields because of the much smaller resting activity and the irregularity of its burst. Significance of the data in this case was ascertained mainly by criteria of repeatability and clustering. The laws of combinatorics here, clearly show that the chance the same clustering of points will repeat itself on two separate maps is very, very small.

Results

Data from 165 units, investigated in detail, will form the body of this report. The unit investigated was first stimulated by manually moving on the screen small contrasting discs, annuli, bars, and edges in various directions

and at different speeds. This gave a gross idea of the most effective stimulus parameters. The receptive field of the unit was then mapped with both eyes opened (spot diameter 0.5° , scanning speed $10^\circ/\text{sec}$, white spot on black background or vice versa, incident light on the screen: 20 l m/m^2 ; white reflectance 75%, black 3%) using the scanning direction to which the unit fired most. Then each eye was mapped in turn from left to right, right to left; down-up and up-down. By this procedure receptive field shape, direction, sensitivity, and data concerning the nature of convergence were sought. The entire procedure was then repeated after changing the screen from black to white and the spot from white to black. The effects of different levels of illumination and scanning speeds were also analyzed. Not all of the parameters could be studied in all units; analysis was therefore started on those parameters to which the cell seemed most sensitive, i.e., if a unit showed direction sensitivity in the preliminary examination, this parameter was investigated first. After mapping the receptive field with the disc, a number of units were studied by moving a contrasting bar on the screen in the same scanning pattern that was used for the disc. These latter maps then, are representations not of the receptive field, but of the loci where presence of a moving bar activates or inhibits the cell and how much. This same line of reasoning, of course, can be applied to the maps obtained with the small spot. All units recorded from, except one, could be mapped with the small disc; most of them were binocularly activated. As the number of binocularly activated geniculate units is negligible (9), binocularity was used as the main criterion of corticality of a given unit; to distinguish cellular from fiber activity standard criteria were also taken into account (5).

Shape of Receptive Fields

Receptive fields are usually described in terms of their geometrical and functional attributes (parameters); this custom will be followed here, but the "shape" of a receptive field is, in a sense, an abstraction. Geometrical and functional attributes are the result of the underlying anatomical structure interacting with the mapping stimulus. The same unit, e.g., if direction sensitive, will show different receptive field "shapes" when mapped with a moving spot of minimum size depending on the scanning direction and a different shape yet will be obtained by using stationary flashing spots. Units with inhibitory and excitatory areas of different relative potency will have different resting activity depending on total level of illumination with consequent possible changes in receptive field size and shape. A complete description of the receptive field of a given unit would require a set of mathematical or logical statements defining the output transfer functions over the pertinent parameters, much the same as it is done by Hartline and Ratliffe (8) for the eccentric cells in the *Limulus* eye or by engineers for ac-

tive and passive elements in electronic networks. As this approach is as yet impossible for a variety of reasons illustrated in the discussion, the units recorded in this study were divided in a number of classes on the basis of some of their more obvious characteristics. These were: Shape or size of the receptive field, when mapped in the preferred direction; resting or background activity; and direction sensitivity. Most units were binocularly activated. The receptive fields from the two eyes were usually, but not always, similar in shape and functional properties. Resting activity was present in most units, but at a very low level—less than 2/sec. Units with diffuse receptive fields had higher resting activity—about 5–10/sec.

Disc-shaped Receptive Fields. Receptive fields with a reasonably circular center not exceeding 5° in diameter were classified as disc-shaped. Usually a very extensive and very shallow, often asymmetric, inhibitory region surrounds the center bringing the total diameter of the field to 20 or more degrees. Figure 1 shows the disc-shaped receptive fields of a binocularly activated unit mapped at $10^\circ/\text{sec}$ with the white spot moving horizontally on the black background; in column *a* both eyes were open; in columns *b* and *c* the left eye and the right eye, respectively, were open. Row 1, for all maps, shows regions where the units fired one time or more, and row 2, regions where the units fired two times or more, (firing frequency = 40/sec or greater).² In Fig. 2 the receptive fields for the left eye of 12 units of this class are shown. All these units were activated from the two eyes with about equal strength. In some units the inhibitory area is lobated producing a "clover leaf" effect. In Fig. 2, 3*a* shows such a unit. In all, the disc-shaped fields constituted 44% of the total sample. In general, scanning speed or level of illumination, within the limits valid for retinal ganglion cells, did not affect markedly receptive field shapes. About 16% of these units displayed direction sensitivity, namely, the receptive field would map best with the white or black spot moving in a given direction, and not at all in the opposite one, with intermediate degrees of clarity in intermediate positions. It was somewhat surprising to find that the receptive fields from the two eyes were quite often located in nonhomotopic retinal regions. In Fig. 3 a unit detected in the same animal and penetration of Fig. 1 shows that the

² It was found initially that most units seem to map best with a scanning speed of 5–10°/sec, and most of the integral contour displays shown in the figures were obtained by mapping units at the speed of 10°/sec, 20 lm/m² unless otherwise specified. This means that each spot on a map represents activity generated during 0.5° and 50 msec. It would seem that slower speeds should, within the limits set by adaptation, generate better maps because of the longer sample time spent in each 0.5° of arc. This is indeed the case, provided that no shift occurs in the spontaneous activity of the unit half way through the map. Long-term periodic changes in the spontaneous activity of cortical units are often encountered; to minimize this and also to allow maximum exploration of all parameters, 10°/sec rather than 5°/sec was preferentially used.

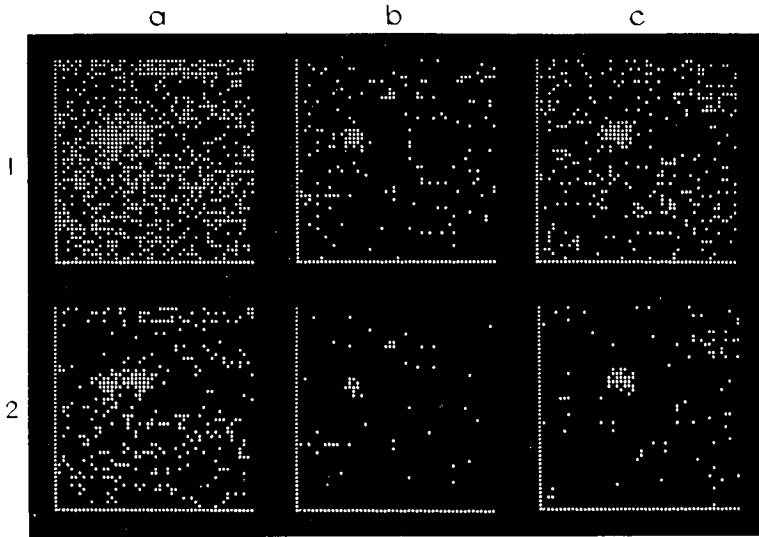


FIG. 1. Integral contour displays from a unit with disc-shaped receptive fields. In column *a* both eyes were open; in columns *b* and *c* the receptive fields from the left and right eye, respectively, were mapped. Firing levels of displays in row 1, 1 or greater; in row 2, 2 or greater.

distance between the receptive fields from the two eyes, as shown in *1a* where the unit was mapped with both eyes open, is quite different from the distance between the two receptive fields of Fig. 1.

The relative strength of the receptive fields from the two eyes was found to differ for different units on a continuum from exclusively monocular activation to units that were activated equally by either eye. The "weaker" receptive field could be either smaller or of about the same size but fainter.

Diffuse. This type of field, constituting 21% of the sample, differs from the disc-shaped only on some aspects: They are roughly circular or oval in shape, with ill-defined borders and the diameter of the excitatory area is usually greater than 10° , with very shallow, wide and irregularly shaped inhibitory regions around it. There are some reasons for distinguishing this type of receptive field from the disc ones even though it is difficult to say if the differences are critical and the distinction meaningful or if these receptive fields should be considered just an extreme variation of the disc ones. (a) One-fourth of these units or 25% are also direction sensitive, a substantially greater percentage than for the disc shaped. (b) There seems to be a discontinuity in the receptive field sizes. (c) Some preliminary recordings from the medial border of the lateral gyrus at A 7 show that this type of field becomes much more frequent moving away from the region where the area centralis projects. (d) Background activity is usually, but not al-

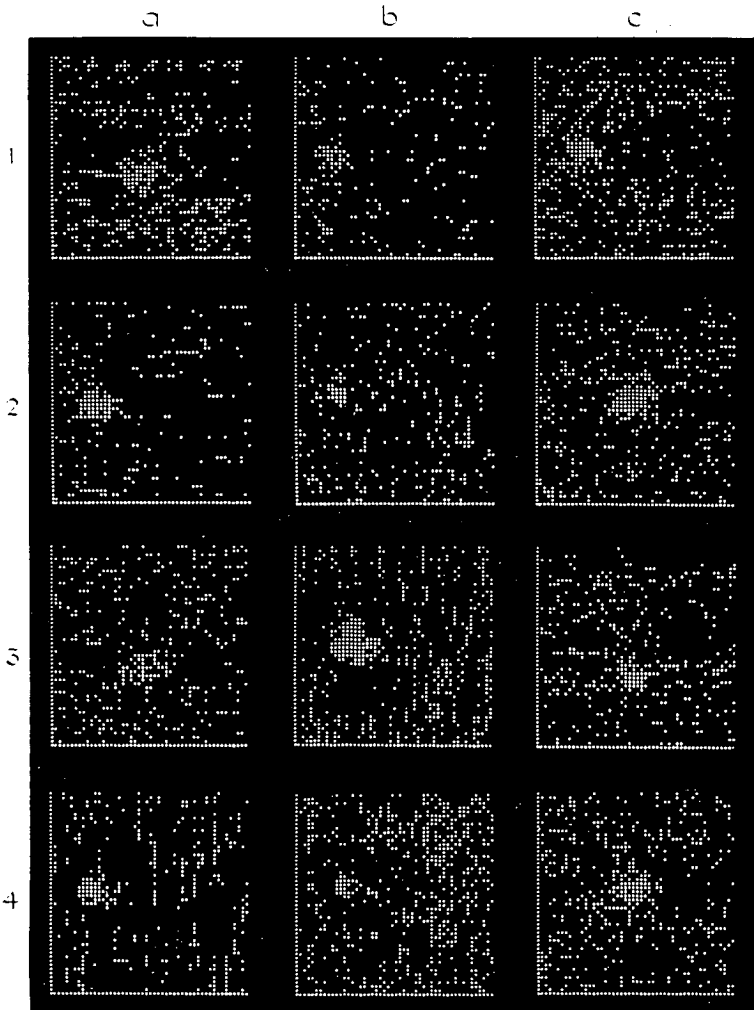


FIG. 2. Receptive fields classified as disc-shaped for the left eye of 12 units. All these units could be activated from either eye with about equal strength, i.e., their response was binocularly coherent. Notice the wide inhibitory areas around the centers. Notice also that the inhibitory areas are often lobated suggesting that a small number of optic radiation fibers whose receptive fields would be still partly visible, are converging onto some of these units from near regions by simple proximity rules.

ways, greater for this type of unit than for the units with disc-shaped receptive fields. Figure 4 shows a diffuse receptive field; in column *a*, the left eye was mapped, in column *b* the right eye was mapped with the spot moving vertically. In row 1 the level of the integral contour display is 1 or more, in row 2, it is 2 or more.

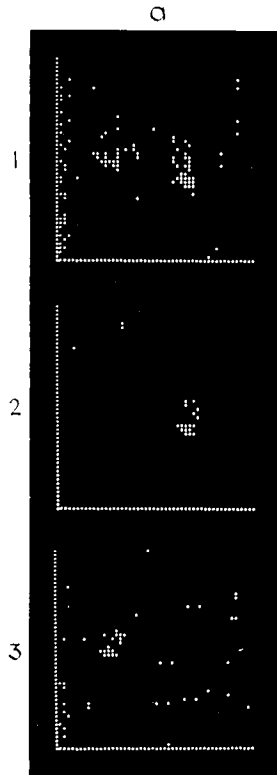


FIG. 3. Integral contour displays from a unit whose receptive fields were mapped with both eyes open in 1a; the right eye open only in 2a; and the left eye only in 3a. This unit was found in the same penetration of the unit of Fig. 1. Notice the difference in separation between the receptive fields for the eyes of the two units.

Bars and Edges. The receptive fields of 20% of the units recorded from the primary visual cortex of cats at A 0, 0.5–1.5 mm from the medial border of the posterior lateral gyrus were of the elongated type described by Hubel and Wiesel as “simple” (10). Figure 5 shows a unit belonging to this class. The firing level of all contour displays in this figure is 1 or greater. In Fig. 5, 1a, the unit’s receptive field from the left eye was mapped with the spot moving horizontally and in 2a with the spot moving vertically. It can be readily seen from 1a that the overall activity of this unit is very small and that only a few spikes are generated in the region of the receptive field, which, instead, is clearly revealed by scanning in the vertical direction. The “shape” of the receptive field, in 2a, is that of a horizontal inhibitory bar, with a strong excitatory upper flank and weak excitation on the lower flank and sides. In 3a a vertically oriented bar 1° wide and 4° long was

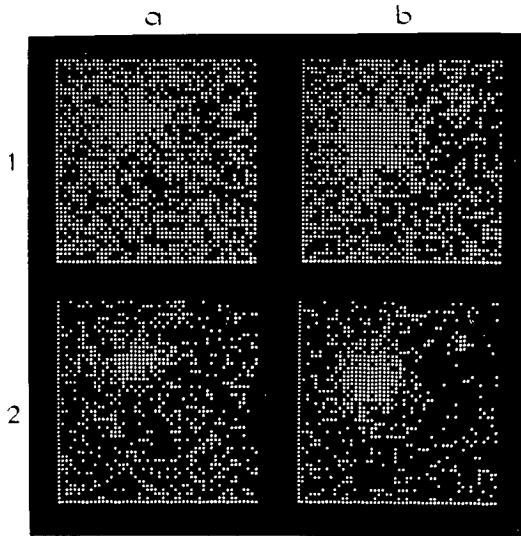


FIG. 4. A diffuse type of receptive field is shown in this figure. In *a* column *a*, the left eye was open, in column *b* the right. Levels of displays in row 1, 1 or greater; in row 2, 2 or greater. Notice the higher level of activity of this unit as compared with the units of Fig. 2.

used to scan the field horizontally; in *4a* the bar was oriented horizontally and made to scan the field vertically; strong responses are generated for this latter condition only. Note that in *3a* no clear responses were generated at any time, i.e., not even during those two or three scans when the lower end of the bar was passing through the excitatory region only, at H 23 (compare this map with *1a*). What this means is that the unit responds more selectively to the bar, namely, more responses are generated by the bar in the preferred direction and fewer in the nonpreferred than by the spot. A combination of elongated shape and direction sensitivity seems required in explaining the behavior of this unit. The behavior of this unit should be contrasted with that of the unit in Fig. 6. Here in the *a* column the receptive field of the unit from the left eye was scanned horizontally; in the *b* column, vertically; a spot was used in row 1 (level displayed, 1 or greater; in row 2, 2 or greater) and a bar $1 \times 4^\circ$ in row 3 (level of display, 1 or greater; in row 4, 2 or greater) the long axis of the bar was kept orthogonal to the direction of movement. In this case, scanning the unit with a bar simply produces more activity both in the preferred vertical orientation and in the non preferred horizontal orientation. Another example of elongated receptive field is shown in Fig. 7 (level displayed, 1 or greater).

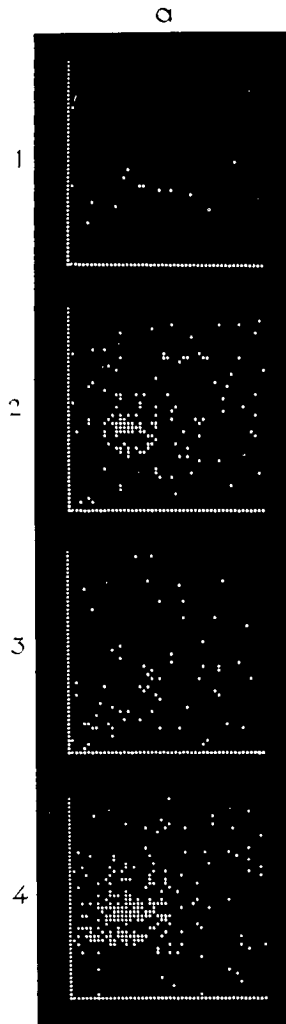


FIG. 5. A bar-shaped receptive field is shown in this figure. In *1a* the spot was used in a horizontal scan; in *2a*, a vertical scan. In *3a* and *4a* a bar 1° and 4° long, orthogonal to the direction of movement was used for a horizontal and vertical scan, respectively. (See text for details.)

Composite. This type of receptive field (12% of the total) is similar to the diffuse ones in that it covers large areas of the visual field typically over 10° in diameter, but it differs from the diffuse in the microstructure of the responsive area which instead of being smooth shows a number of sharp intermixed excitatory and inhibitory areas. Figure 8 shows a map from a unit

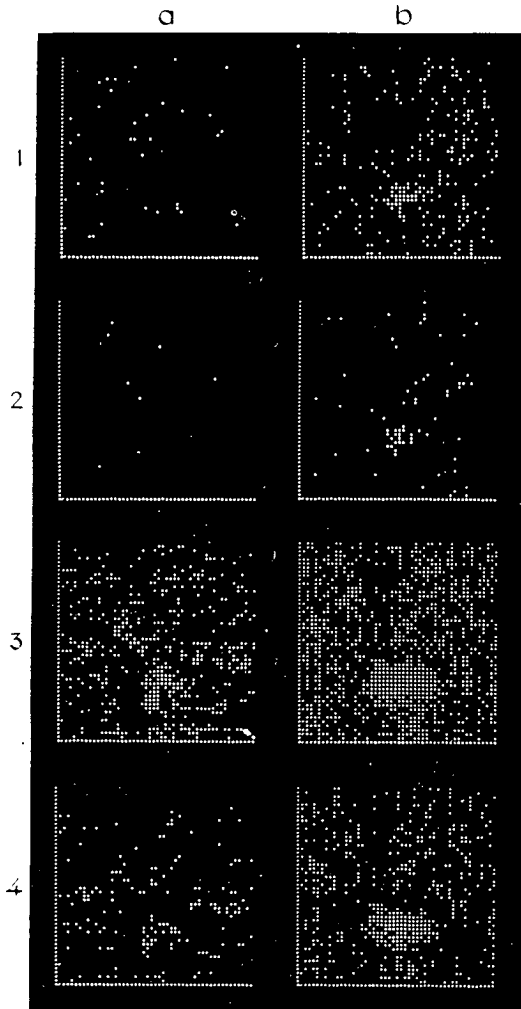


FIG. 6. A bar-shaped receptive field is shown in row 1, spot moving horizontally in *1a*, and vertically in *1b*; firing levels in row 1, 1 or greater; in row 2, 2 or greater. In row 3 a bar 1° wide and 4° long, orthogonal to the direction of movement was used; direction of movement for the bar was vertical in *3b* and horizontal in *3a*; firing levels in row 3, 1 or greater; in row 4, 2 or greater.

of this type mapped with the spot moving vertically, (level displayed, 1 or greater).

Others. A small number of units (3%) displayed highly unstable receptive fields. Their characteristics will not be described here.

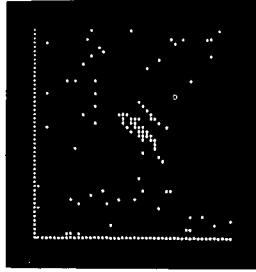


FIG. 7. Bar shaped receptive field. Direction of scan: Vertical. Firing levels: 1 or greater.

Changes in the Stimulus Parameters

Illumination. The level of light incident on the display was typically 20 lm/m^2 . This level of illumination seemed to be best for most units. Figure 9 shows the receptive fields of two units, in column *a* and *b*, and the effect of changing the total level of illumination from 2 lm/m^2 in row 1, to 20 and 200 lm/m^2 in rows 2 and 3. Level of integral contour display is 1 or greater in all maps. The effect of changing the level of illumination was in general relatively minor.

Scanning Direction. Seventeen per cent of all units fired maximally when scanned in a preferred direction and very little or not at all in the opposite way, intermediate levels of responsiveness being encountered with intermediate directions of scan: 16% of the disc shaped; 10% of the bar shaped; 25% of the diffuse; and 24% of the composite units were found to be sensitive to the direction of scan. In Fig. 10, 1 *a* (firing level displayed for all maps is 1 or greater), the diffuse receptive field for the right eye of a binocularly activated unit was scanned vertically and in 2*a*, horizontally; the responsivity of the unit drops sharply for the nonpreferred direction, the horizontal, so that the receptive field becomes practically invisible on the

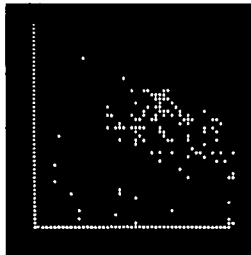


FIG. 8. Composite type of receptive field. Notice the presence of several sharp line-shaped excitatory regions with a 45° orientation. Firing levels: 1 or greater.

map. In *1b* and *2b*, the disc-shaped receptive field for the left eye of a unit that was also binocularly activated was scanned horizontally from right to left (*1b*) and from left to right (*2b*); no response is visible when scanning was from left to right. In *1c* and *2c* the receptive field for the right eye of the same unit as is in the *b* column was mapped in the same fashion. Again it can be seen that the unit is best activated when scanning is from right to left. The general finding is that the binocularly activated direction sensitive units display the same direction sensitivity from either eye.

Scanning Speed. This parameter was investigated only in so far as necessary to determine the angular speed at which units would map best. This was found to be $5 - 10^\circ$ for most units. An occasional unit required greater or smaller speeds; but this was such a rare finding that we felt that a parametric analysis of scanning speeds on each unit was (within the framework of this study) unwarranted. In general, then, it can be said that the opti-

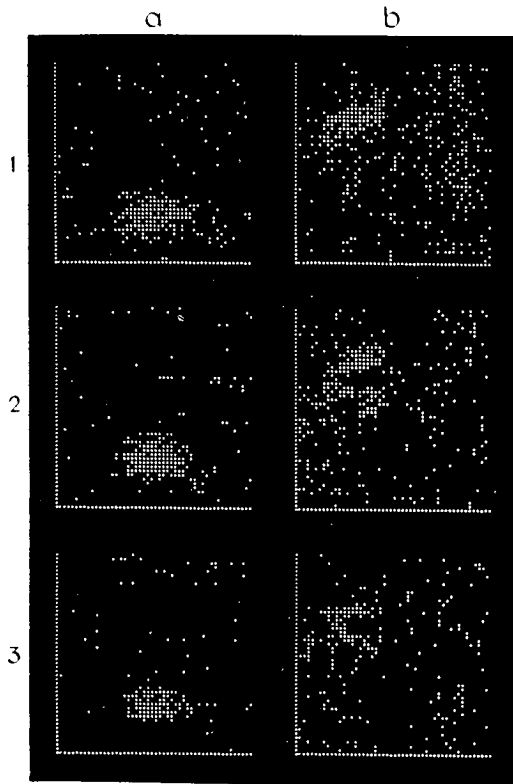


FIG. 9. The effect of changing the total level of illumination from 2 lm/m^2 to 20 lm/m^2 and 200 lm/m^2 —rows 1, 2, and 3—in the receptive field of two units is shown in columns *a* and *b*. Firing levels: 1 or greater in all maps.

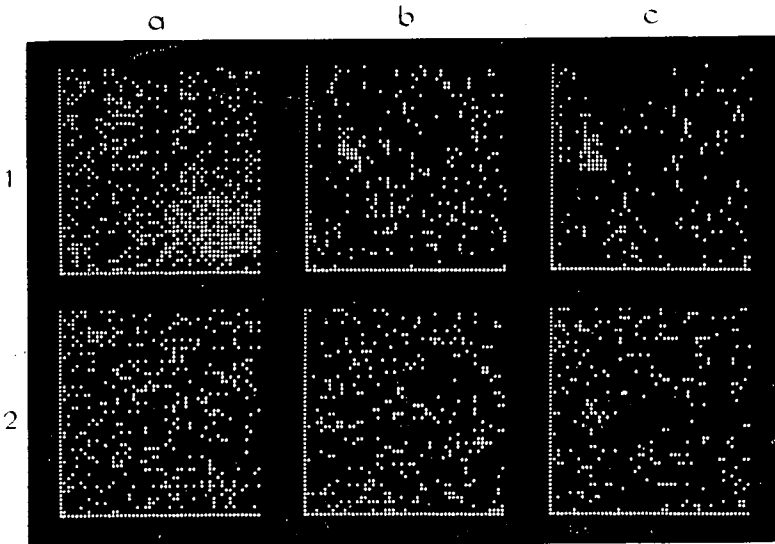


FIG. 10. In 1a the receptive field for the right eye of a unit, classified as having diffuse receptive fields, was mapped with the spot moving vertically, and in 2a with the spot moving horizontally. In 1b and 1c are shown maps for the left and right eye, respectively, of a unit classified as having disc-shaped receptive fields obtained with the spot moving horizontally from left to right, and in 2b and 2c with the spot moving from right to left. Notice the disappearance of the responsive area from the map when the spot is moving in the nonpreferred direction. All levels of displays: 1 or greater.

imum speed for cortical units is nearly identical with the optimum mapping speed for retinal ganglion cells. The fact that the best sampling time for "clearest" receptive fields seems to be about 50—200 msec is, of course, related to the activity decay time of retinal ganglion cells (18). The above considerations provide a physiological basis for the finding that fixation times seem to have also a 50—200 msec range, i.e., after a saccade the eye lingers long enough to obtain the maximum benefit of time averaging, but little enough to avoid adaptation.

Reversing the Background. In the retina, "on" regions of ganglion cell receptive fields are changed to "off" regions (12) and vice versa in their response pattern when background and stimulus reflectances are reversed; this does not happen for most of the cortical cells with which this was tried, i.e., excitatory regions brought out by mapping a unit with a white disc on a black background remain excitatory when mapped with a black disc on a white background. There is some tendency for the maps to be clearer when the white background is used, indicating a greater ratio between unit response and spontaneous activity. A disc-shaped unit mapped with a white and black background is shown in Fig. 11.

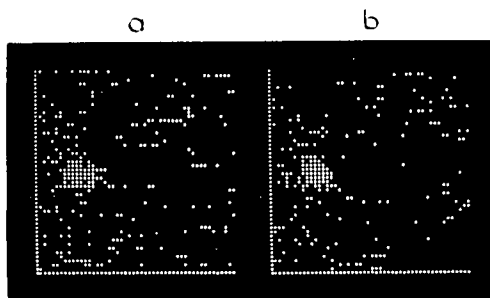


FIG. 11. The receptive field for the right eye of a unit classified as having disc-shaped receptive fields was mapped with the white spot moving horizontally on a black background in *a*, in *b* the map was repeated with a white background and black spot. Notice essentially similar excitatory region for both maps. Notice also the slightly sharper borders of the excitatory region in *b*.

General Remarks Concerning Receptive Fields Organization and Comparison with Previous Findings

Binocular Disparity. One of the most immediately apparent and puzzling results—at the time we were unaware of Barlow's findings (3)—was the fact that, on the maps done with both eyes open, the distance in degrees between the receptive fields of binocularly activated units, while constant for the same unit in a variety of conditions, was not the same for different units in the same animal (Figs. 1 and 3); this prevailed even when different units were recorded in the same pass of the microelectrode through the visual cortex. Specifically, the great majority of the units had receptive fields that were "closer" than they should have been if they had zero binocular disparity, i.e., if their receptive fields had been in homonymous retinal positions. This result is, thus, in agreement with Barlow's findings (3) and in contrast with Hubel and Wiesel's (10) statement that all binocularly activated cells had receptive fields in homonymous retinal positions. This aspect of receptive field organization was investigated by us only in so far as was necessary to establish that residual eye movements were not responsible for the results.

Disc-shaped Receptive Fields. The possibility that receptive fields appearing disc-shaped on our maps did not fully reveal the potential of the units investigated was tested by scanning the receptive field region with bar and edges and other stimuli much as has been described by other authors (10, 11, 13). This type of analysis did not reveal any more than could have been predicted by taking spatial summation and direction sensitivity (for those units that showed it) into account.

Diffuse and Composite. The large size of these receptive fields and the microstructure of the composite ones suggest that a great deal more con-

vergence is taking place on these units than on smaller disc-shaped ones. The characteristics of some of these receptive fields make them somewhat similar to the complex field described by Hubel and Wiesel (10). Thus, the diffuse and composite receptive fields that are also direction sensitive as in Fig. 10 generate, when stimulated in the same way, responses similar to the ones shown in Fig. 8 of Hubel and Wiesel (10).

Binocular Coherence. It has already been mentioned that the receptive fields from both eyes for most units were usually, but not always, similar in their properties. The units of Fig. 12 illustrate this phenomenon. In 1 *b* a

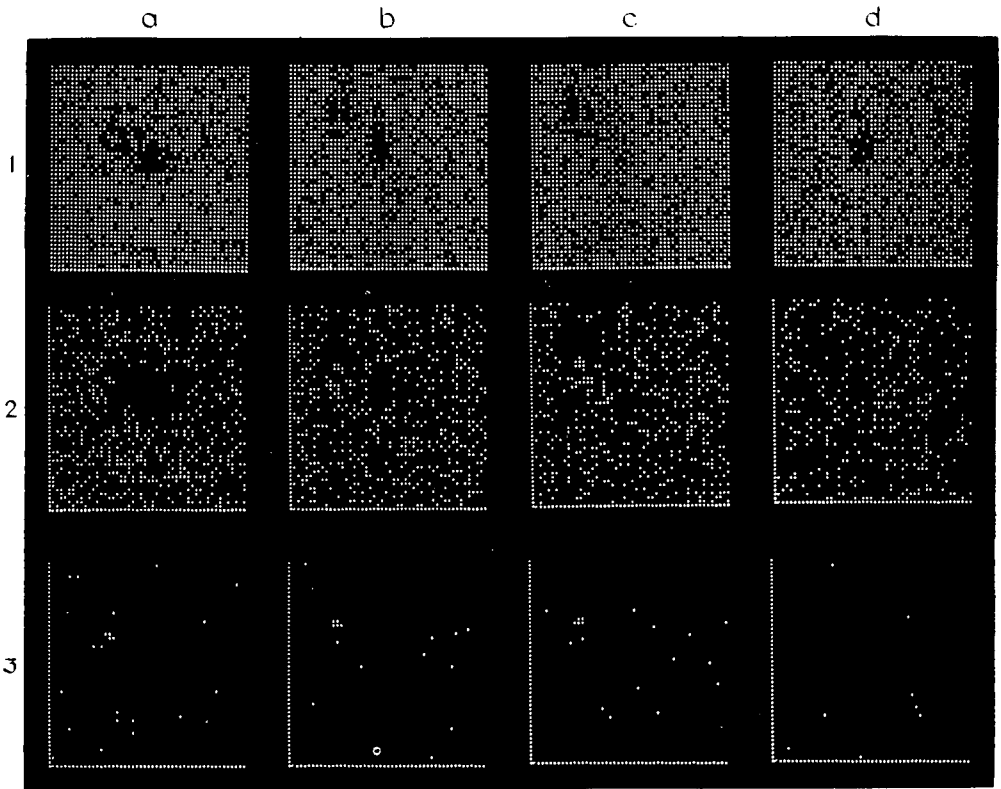


FIG. 12. Two examples of two very similar units which are not coherent with regard to shape of receptive fields. In 1*b* the receptive fields of a unit were mapped with both eyes open: Level of integral contour display in 1*b*, 1 or greater; in 2*b*, 2 or greater; in 3*b*, 3 or greater; the unit was mapped again with the left eye only open in 1*c*, and with the right eye only open in 1*b*. Notice that the excitatory region is present only for the left eye's receptive field. In 1*a* another unit, found in the same penetration and very similar to the one just described was mapped with both eyes open. Levels of integral contour displays in row 1, 1 or greater; in row 2, 2 or greater; in row 3, 3 or greater.

low level integral contour display (1 or greater) is shown of the map that was generated by scanning the unit with the spot moving vertically and with both eyes open. It can be clearly seen from this level that the receptive field for the left eye is formed by an inhibitory region surrounding a small excitatory disc-shaped center. The excitatory region can be more clearly seen in *2b* and *3b* corresponding to higher levels of integral contour display, 2 and 3 or greater, respectively. Note that the receptive field for the right eye does not contain an excitatory center, in *1c*, *2c* and *3c*, the left eye only was mapped and again one can see that the inhibitory region, which is about 3 or 4° wide and 4 to 5° long contains an excitatory center. In *1d*, *2d* and *3d* the right eye only was mapped and here one can see that the inhibitory region for the left eye, does not contain an excitatory center, thus confirming the map obtained with both eyes open. In the *a* column another unit, very similar to the one described above, in the lack of an excitatory region for the right eye, but with stronger inhibitory areas was mapped with both eyes open; levels of displays in rows 1, 2, and 3 are 1, 2, and 3 or greater, respectively.

Discussion

The first major conclusion that can be drawn from the results is that the cells on the primary visual cortex of cats (area 17) do not respond exclusively to line or edge stimuli. Second, the binocular coherence of cortical units receptive fields, namely, the degree of similarity of the parameters measured for each receptive field in the two eyes, is not too good for some of the parameters; for example: Retinal homotopicity, size and strength of the two receptive fields are not coherent for most units. Shape and direction sensitivity showed the highest level of coherence, but even in this case a few units showed striking differences such as absence of one of the components in one of the fields, as in Fig. 12. Third, the surround of most of the receptive fields extends, even though weak, over wide areas. Fourth, the most numerous population is that of the disc-shaped receptive fields.

These findings also suggest a number of possibilities concerning the role of receptive field organization in the processing of visual patterns. Note in this respect, that a great percentage of receptive fields are unaffected by reversing background and stimulus reflectances. This might be important in the recognition of patterns, which can take place irrespective of background illumination or color. The relative stability of the receptive field shape and function with changes of scanning direction, speed and level of incident light, also furthers this point.

Nature of Convergence of Optic Radiation onto Cortical Cells. A number of suggestions have been advanced concerning the functional connections between optic radiation fibers and cells in the visual cortex (10, 13). The

most detailed hypothesis has been provided by Hubel and Wiesel (10). It states essentially that lateral geniculate cells with receptive fields located on a line of the visual world converge in an excitatory or inhibitory fashion (or both) onto the same cortical cell. The evidence for this comes from the experimental finding that there are cells in visual cortex with line-shaped receptive fields. Other possibilities have been suggested by Leicester (13). The finding of units as the one in Fig. 2, at 3a, suggest to us that, at least in the case of the disc-shaped receptive fields, it is possible that convergence takes place from the nearest optic radiation fibers in a uniform way. In other words, the clover-leaf aspect of the inhibitory surround for some of these cells suggests a convergence from few fibers so that the residual lateral geniculate units' receptive fields are still visible. Clearly, many more radiation fibers converge on units that do not show this phenomenon, or on units with very large receptive fields. We are not clear at this point about the nature of possible interactions between cortical cells, and it is apparent at least to us, that much more work would be required before the definitive functional anatomy of visual cortex can be known with a reasonable degree of confidence.

Comparison with Data from Previous Authors. A question of considerable interest concerns the presence or absence of units with circularly shaped receptive fields in the primary visual cortex. On this the literature is divided. Hubel and Wiesel (10) stated that "all" the cortical units they recorded from in area 17 had elongated receptive fields and exhibited strong specificity to bars or edges with specific orientations either in specific positions in the visual field ("simple" receptive fields), or over larger areas ("complex"). Baumgartner, Brown, and Schulz (4) on the other hand, have found that about 50% of their cortical units were concentrically organized and about 20% had characteristics that made them similar to the units described by Hubel and Wiesel.

There is no question in our minds that at least 44% of the units we recorded from in area 17 of the cats in our experimental group have disc-shaped receptive fields; in other words, this is a conservative estimate. The fact that these units could be binocularly activated (9) combined with standard criteria (5) leaves no doubt that they were cortical cells. Only 20% of the units had receptive field shapes such that they could be identified with Hubel and Wiesel simple cells, and about 10% of the total sample had characteristics that, for some stimulus conditions, could identify them with complex cells. Thus, our data are somewhat in between that reported by Baumgartner *et al.* (4) and that reported by Hubel and Wiesel (10). Two possibilities come to mind concerning the disc-shaped receptive fields. One would be that the difference is apparent and is due to mapping the

receptive fields with a moving rather than a stationary spot. Though the two methods may not produce identical results this explanation seems unlikely: First, because Baumgartner *et al.* (4) did obtain similar results by using stationary stimuli and second, because Hubel and Wiesel (10) stated that, at least for simple fields, responses to moving bars could be predicted from the arrangements of excitatory and inhibitory regions and vice versa; moreover, as can be seen in Figs. 5 and 7, the method we used has no difficulty in identifying units with elongated receptive fields. Thus, a more likely explanation would be that some of the units that Hubel and Wiesel discarded as geniculate units (10) were indeed cortical and that an undetermined fraction of the units they had left uncategorized—about a third of the total—had disc-shaped receptive fields.

Baumgartner's idea (4) that "a qualitative change in the organization of visual afferent units does not first occur between the lateral geniculate body and the cortex, but rather between cortical units" is also somewhat unsatisfactory in its implication that 50% of the units in visual cortex, where the number of units handling the sensory inflow becomes suddenly enormous, are only relays for lateral geniculate units. The fact that nonvisual systems have substantial and specific effect (19) on the activity of at least some of the units with disc-shaped receptive fields in the visual cortex, combined with the sudden increase in cell population seems to indicate that a crucial stage in the processing of visual information has been reached when the optic radiations meet the cortex.

The crucial question, then, centers on whether units with line-shaped receptive fields are to be considered "detectors of lines" and nothing else, i.e., nonlinear elements; or as operators with more or less linear-transfer characteristics capable of responding to a great variety of stimuli in different ways. It seems clear that the first alternative is excluded by the fact that these units can be mapped with small stationary or moving spots even though spatial summation makes them fire most to an object that has the same shape of their receptive field, i.e., a line. The possibility remains that the next element in the processing chain, has sufficiently high threshold, so that it fires only to the maximum discharge from a line element. If this were the case, a number of cells should be found that do not respond at all to a moving spot. This is not the case: Of the 165 units analyzed in this study, all but one responded to small moving spots and could be mapped with the method used in this work. In the case of the unit that could not be mapped by using the small disc it was also impossible to elicit any response from the unit to moving bars and edges in a variety of orientations or to any other stimulus that was tried; it seems, therefore, probable that the unit was in some way damaged.

This does not mean that some units could not be considered to be "detectors." Indeed, as has been pointed out by others (2, 14), it seems highly adaptive for an organism to possess units which will detect unequivocally certain items of information without excessive demands from the point of neuronal circuitry. Thus, motion and direction sensitive units probably do just that, i.e., alert the organism that something is moving in the environment and in which direction so that appropriate oculomotor tracking or scanning reactions can take place. A different set of problems is encountered when dealing with units which probably have to do with some stage of pattern recognition; here perceptual constancies have to be taken into account and it is just one part of this facet of information processing, namely, transitional invariance, that theoretical constructs, as, for instance the complex cells proposed by Hubel and Wiesel (10) are supposed to handle. This means that there are units that, e.g., respond to a line in the same orientation over a range of spatial positions. The difficulty here is that these responses are not identical (see for example, Hubel and Wiesel, Ref. 10, Fig. 4) over the different positions. It would be necessary to say that the next stage is not bothered by all this variability and that a line is detected no matter how the unit fires, but this is just the opposite of what has been postulated to get rid of the less strong responses caused by nontrigger features of stimuli.

The reason all this is important is that there should be some clearly defined and acceptable heuristic techniques to determine if a unit is a detector so that one does not waste time in meaningless parametric analysis; on the other hand, if the unit is part of a network, i.e., of a kind similar to the one found in the Limulus eye, then quantitative, parametric analysis is necessary to determine interactions among units and the transfer function of the network as a whole.

Implications for Pattern Recognition. Recognition of a visual pattern, say a capital *A*, takes place regardless of exact position or orientation in the visual space, ambient illumination, size, small mutilations or wiggles in the character, etc. Yet subjective experience and psychological work (1) point to the fact that the particularities of each experience are not lost; in other words, the different orientation or position, etc., is also detected. Thus, we disagree with schemes that attempt to explain perceptual constancies by just dumping information. A reasonable possibility, at this time, seems that a population of detectors exists with the function of extracting basic information from the visual world: Motion, direction of motion, orientation and size, and position in the visual field could be detected by cells committed to these specific features. On the other hand, a more numerous population of uncommitted cells would be required to convey the uniqueness of each sensory experience. Note that, while engineers working at pattern recognizing

machines have on one hand shown the tremendous efficiency of feature extractors when the symbol set is known, they have, on the other hand, found a necessity for information processing circuitry which is uncommitted to any specific feature (21).

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