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VISUAL RECEPTIVE FIELD ORGANIZATION OF SINGLE UNITS IN THE VISUAL CORTEX OF MONKEY†

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The receptive fields of 159 units in the visual cortex (area 17) of the rhesus monkey were mapped by moving a white or black disc in a scanning pattern on a tangential contrasting screen placed 57 cm from the animal. The area explored was 25° × 25°. Bars, edges, and other 'whole' stimuli, some of them colored, were used to determine the most effective stimulus parameters. The units recorded from were divided into fourteen groups. The most numerous groups of units were: disc, 26%; diffuse, 14%; fine, 13%; color-sensitive, 14%; and another group of units unresponsive to any stimuli, 36%. Behavioral analysis on five of the monkeys which were revived after the experiment show no significant correlation between classes of cells in a given animal and his performance in visual discriminations.

INTRODUCTION

Considerable study has been devoted to exploring the receptive fields of single cells in the visual cortex of the brain (Hubel and Wiesel, 1962, 1968; Spinelli and Barrett, 1969). For practical reasons most of these experiments have been done on subprimate mammals, despite the fact that one of the chief goals of these efforts is to reach a greater understanding of the mechanism of pattern perception in man. Our own research has followed this course with one exception: a major focus of our work has been on the neuroanatomical, gross electrophysiological and neurobehavioral analysis of visual pattern discrimination in monkeys (Pribram, Spinelli and Kamback, 1967; Spinelli, 1967a; Spinelli and Pribram, 1970). It seemed reasonable therefore to initiate a series of studies comparing the results of neural unit analysis in lower organisms (crabs, bees and cats) with those obtained in monkeys. Any trends discovered in such a phylogenetic comparison could, by extrapolation, become the basis for deeper inquiry into human perceptual processes.

To further this aim, several of the monkeys used for unit analysis in this experiment were revived after the 'acute' procedures and tested behaviorally on two simple visual discrimination problems. Some interesting and bewildering results were obtained in these monkeys, so they are presented more as a pique to curiosity than as a definitive result.

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METHODS

Because the methods used in this work have been described in previous papers (Spinelli, 1966; Spinelli, 1967b) they will be reviewed only briefly.

Subjects and Surgical Preparation

Twelve rhesus monkeys were used in these experiments. Surgery was kept to a minimum; under pentothal anesthesia the radial vein was cannulated with a small teflon catheter and a small opening made in the skull and dura. A solution of agar in saline was used to minimize brain pulsation. Intubation of the trachea was done through the mouth. After incisions and pressure points were carefully infiltrated with a solution of procaine in oil (Zyljectin) the animal's head was placed in a stereotaxic apparatus which leaves the visual field unobstructed. Anesthesia was then discontinued and gallamine triethiodide (Flaxedil) and saline were administered through the venous catheter by means of a continuous infusion pump. Artificial respiration was maintained by a constant-volume pump (stroke volume 50 to 75 ml, rate 20/min). Contact lenses were used to protect the corneas

and to correct for accommodation. Pupil size was controlled with atropine. Temperature of the animals was maintained at $38 \pm 0.5°C$.

Recording

Tungsten microelectrodes attached to a solid state source follower were used to record from single units as previously described (Spinelli, 1967b). An IGFET (Motorola 2N3796) was used as the active device.

Electrode placements are diagrammed in Figure 1. Most recordings were made from that part of area striata (17 of Brodman) to which the retinal fovea projects, i.e., a point some 5 mm below and just posterior to the ventral tip of the sulcus lunatus.

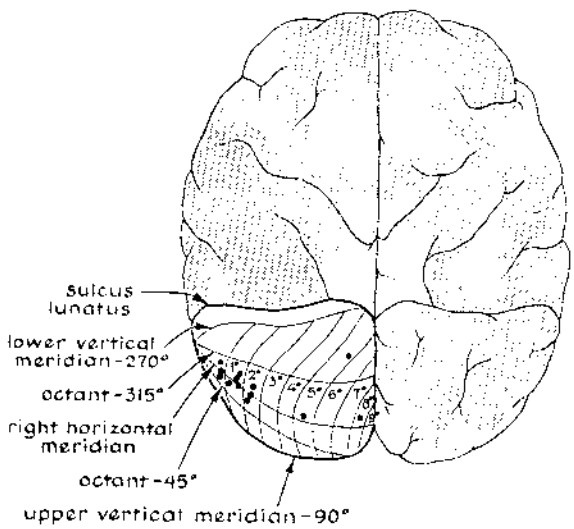

FIGURE 1 Recording sites for ten of the monkeys used in this experiment. The remaining penetrations were within a few millimeters of the lower tip of the lunate sulcus. Several passes were made on some monkeys.

Some explorations were made, however, along the visual meridians radiating out from the foveal projection to the posterior extremity of the hemisphere.

Visual Stimuli

Two types of analysis were performed on each unit whenever possible, 'real-life' stimulation and standardized mapping. 'Real-life' stimuli included white or colored bars and edges of differing sizes, either projected or held by a wand; hands and shadows of hands; discs of varying sizes and colors; light flashes generated by a Grass photo stimulator; slits of light projected onto a screen; and total dimming or brightening of the room. Colors were generated very simply by using Edmund #60,403 filters held in front of a projector or flashlight. No attempt was made to equate for brightness, though units were judged to be color-sensitive only if their responses to a given projected stimulus were several times greater with color filters than without the filters. Thus a unit had to have a stronger response to a colored stimulus than to a brighter white stimulus to be judged color-sensitive.

For standardized maps a disc was moved, under servo control, on a white or black tangential screen in a scanning pattern of 50 lines 25° long and 0.5° apart, to obtain $25° \times 25°$ receptive field maps. A map is constituted of 50×50 or 2,500 data points (Spinelli, 1967a). The screen was evenly illuminated by a tungsten filament lamp. Incident light was usually set at 20 lm/m^2 and scanning speed at 10°/sec, though all parameters could be varied.

Data Collection and Processing

Each unit was first tested with 'real-life' stimuli in an attempt to establish the best parameters for stimulation. Colored lights were used to get a first impression of color sensitivity; we did not use spectrally pure colors nor did we equate, except roughly, for brightness, but just looked to determine which cells would respond strongly to colored lights. It is therefore possible that the number of color-sensitive units reported here is smaller than the number of units which could be shown to be responsive to color with finer methods of analysis.

After this exploration the receptive field was mapped using a black spot (3% reflectance) of minimal size moving on a white screen (75% reflectance) in the four main directions: up-down, down-up, left-right, and right-left. The map was done first binocularly, then for the left and right eyes separately. A PDP-8 computer was used to generate the voltages fed to the X and Y servo systems and to count and store separately the spikes generated by the unit in each 0.5° space. Because the computer controlled both the stimulus display and the data counting, perfect isomorphism between visual and data space was assured. These maps form the basis of our classification of receptive field shapes.

From a mathematical standpoint these maps are convolutions of the receptive field 'shape' and the scanning stimulus shape (see Spinelli and Barrett,

1969, for definition); this interaction between two functions is closest to the receptive field 'shape' the more closely the scanning stimulus approaches the impulse function, i.e., a dot of vanishing size. Accordingly most of these maps were done with as small a disc as possible. The same criteria of clustering and repeatability were used in assessing the significance of the results reported here as were used previously (Spinelli and Barrett, 1969).

RESULTS

Data from 159 units investigated in some detail form the body of this report.

In presenting the results we will make comparisons with our earlier findings in the cat when applicable, and also with the findings of Hubel and Wiesel (1968), the only other study of receptive fields in the visual cortex of monkey.

Receptive Field Classes

Disc This group represents 26% of our sample. The characteristics of these units are similar to those described for the cat cortex (Spinelli and Barrett, 1969). Reasonably circular receptive fields with a diameter no greater than 5° were pooled in this group. Most of these units are binocularly activated. Figures 2 and 3 show two such units; in column A the unit was mapped binocularly; in columns B and C the left and right eyes respectively were mapped. Note the very shallow surround typical of cortical units with this type of receptive field, and the binocular activation of both units.

Diffuse Seventeen percent of all units are in this group. These units are similar to the diffuse units described in the cat, where they represent 21% of the sample. Their receptive fields are roughly circular with very ill-defined boundaries; the intensity of response is considerably weaker

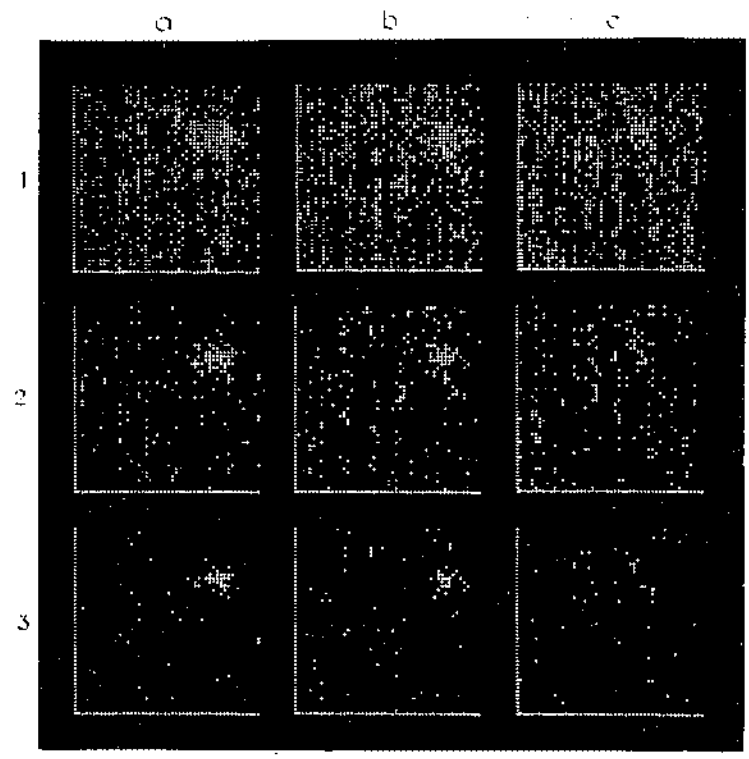

FIGURE 2 This figure shows a disc-shaped receptive field. In column 'a' the unit was mapped with both eyes open; in columns 'b' and 'c' with the left and the right eye respectively. Rows 1, 2 and 3 represent regions where the unit fired 1, 2, 3 times or more respectively.

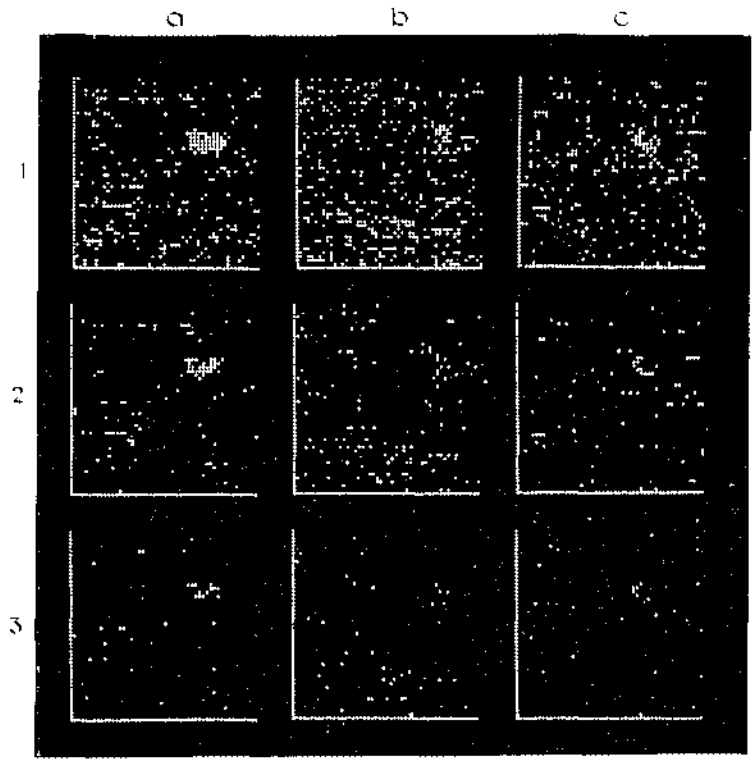

FIGURE 3 Disc-shaped receptive field. See Figure 2 for details.

than that of diffuse units in the cat. Figure 4 shows one such unit. These units probably correspond to the complex cells of Hubel and Wiesel (1968) (65% of their sample). They are not artifacts of poor optics, for well-defined receptive fields were often found on the same pass with diffuse fields.

Line Elongated receptive fields represent 14% of the sample, compared with 9.5% found by Hubel and Wiesel in monkey visual cortex, and with the 21% which we found in the cat. Of these units one-third responded in a sufficiently clear way to bars presented on the screen to enable us to classify them as line-chaped fields before mapping. Figure 5 shows a line-shaped receptive field.

Color Fourteen percent of the units responded much more strongly to a probing stimulus shown through a given color filter than to the identical white stimulus. This compares with the 10% of Hubel and Wiesel. Most of these units responded selectively and reciprocally to red and green or to blue and yellow, though a few had striking selectivities to colors such as fuchsia.

Direction Sensitive Only 6% of the units were classified as direction sensitive, compared with 17% in the cat (Spinelli and Barrett, 1969). Hubel and Wiesel (1968) comment on direction sensitivity, but give no estimate of its frequency. A unit was considered to be direction sensitive only if there was a null direction, i.e., no response to the spot. This criterion excludes units which respond most strongly to stimuli moving in one direction and least strongly to stimuli moving in the opposite direction. Uusually the receptive field was also classified according to the shape obtained with the spot moving in the preferred direction.

Flash Responsive Six percent of the sample gave clear responses to full-field flash. Hubel and Wiesel find practically no such units in the monkey. This compares with 75% flash-responsive units in the cat (Murata, Cramer and Bach-y-Rita, 1965).

Undefined This group represents 36% of our total sample. In general even the least selective units for color, direction, or orientation gave enough of a response to visual stimuli that one

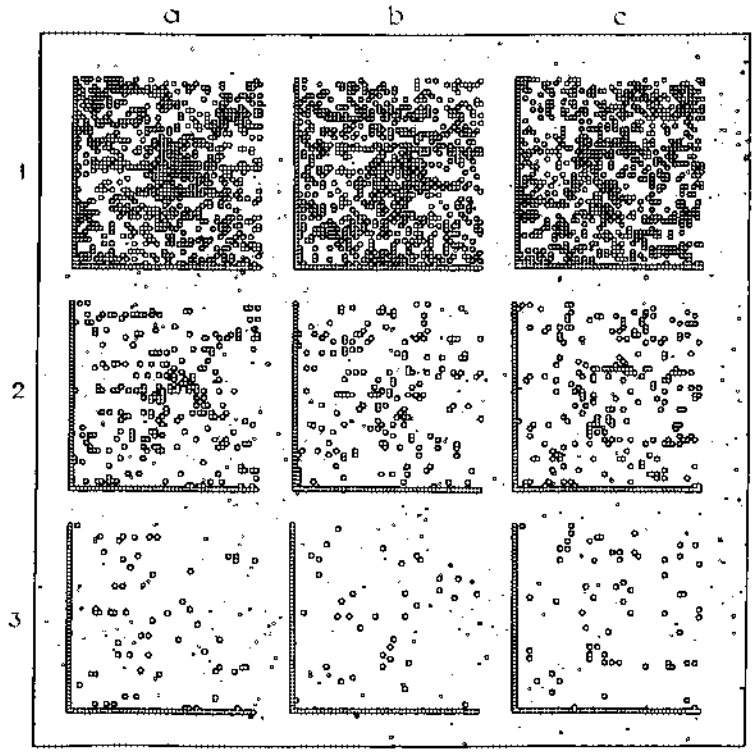

FIGURE 4 This figure shows maps of a unit's receptive field classified as diffuse. In column 'a' the unit was mapped with both eyes open; in columns 'b' and 'c' with the left and right eye respectively. Rows 1, 2 and 3 represent regions where the unit fired 1, 2, 3 times or more respectively.

could use this response to identify that stimulus configuration which would excite the unit maximally; but these units resisted all our attempts to drive them. They typically had clear, well-differentiated spikes with low but present background activity. There is no question that these units were not damaged; we could usually hold and test them for hours, and their spike shapes were normal.

Other Properties A few units had unusual properties: about 1% of the units responded also to non-visual stimuli, as opposed to 50% in the cat (Murata, Cramer and Bach-y-Rita, 1965; Spinelli,

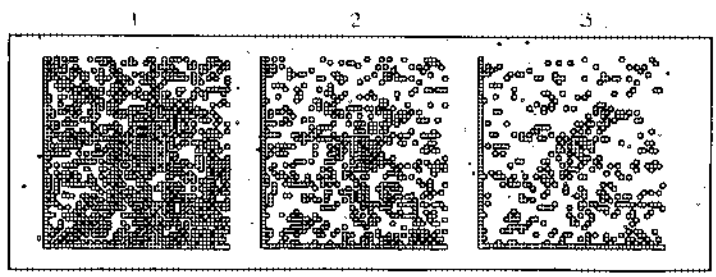

FIGURE 5 This figure shows a line-shaped diagonally oriented receptive field. The narrow diagonal inhibitory bar is especially clear at levels 2 and 3.

Starr and Barrett, 1968). One unit responded well to movement of objects regardless of shape or direction, one responded tonically to total level of illumination, one had a large inhibitory receptive field, and six had unstable receptive fields whose shape varied.

DISCUSSION

There are some fundamental differences between the results we obtained in the cat and in the monkey. A major and striking difference is that in the cat 164 of our units were responsive to visual stimuli and could be mapped with the method described above. In the monkey only 101 of the 159 units could be made to respond in spite of extensive tests with all imaginable stimuli. While it is certainly possible that our 'bag of tricks' did not contain any appropriate stimuli for these units, it is clear that the undefined units are not present in the cat, or are present only in very small numbers. In the monkey, the proportion of undefined receptive fields was highest at the foveal projection and became lower peripherally, suggesting that these undefined cells are more involved in the kinds of

TABLE 1

Monkey:	XI	316	302	324	341	356	355†	353	271	355†	351	352	354	Total	%‡	Cat
Class																
Color	0	0	0	0	0	3	5	3	3	2	2	1	3	22	14	
Line	2	3	2	0	2	0	0	1	2	1	2	1	4	20	13	20
Flash	0	2	0	0	1	0	0	1	0	2	0	2	2	10	6	75
Diffuse	1	2	0	0	1	0	2	3	1	4	0	7	2	23	14	21
Disc	1	1	1	1	1	2	5	4	7	6	2	6	5	42	26	44
Variable shape	1	0	3	0	0	0	0	0	0	1	1	0	0	6	4	
Undefined	9	0	6	11	8	5	1	3	2	3	8	1	1	58	36	1
Direction sensitive	1	0	2	1	2	0	0	0	0	0	3	0	0	9	6	17
Movement	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	
Touch	0	0	0	0	0	1	0	1	0	0	0	0	0	2	1	
Large inhibitory	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	
Background illumination	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	
Specific color	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	
Unidentified	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	
Total	14	6	11	13	13	10	10	13	13	15	14	15	12		159	165
Days to criterion in a color discrimination							21	1			1	9	2			
Days to criterion in a pattern discrimination							6	9			4	5	6			

† This monkey was prepared and recorded on two separate occasions.
‡ This column totals more than 100% because some cells had characteristics of more than one category.

processing characteristic of the foveal region. The most numerous classes in the cat were disc (44%), diffuse (21%), and line (20%). In the monkey the number of identifiable classes is greater, the most numerous classes being undefined (36%), disc (26%), diffuse (14%), and line (13%). All monkey unit classes are listed with the cat's for comparison in Table 1.

Some comments on the classification of receptive fields are in order. The classification scheme used here and by others is mainly naturalistic, but because we are trying to understand pattern recognition our in-depth analysis was aimed at systematic mapping. Classification simplifies description so that we can describe 14 groups instead of 159 units, focussing on some common characteristics of a group of cells and ignoring their differences. Shape or size, resting activity, direction sensitivity, etc., are used as criteria for classification. The classification scheme implies that the organism uses all the cells in a class equivalently, but this assumption is not necessarily true; thus the question arises whether the class boundaries are justified. Another assumption which must be questioned, as noted in a previous paper (Spinelli and Barrett, 1969), is the idea that units with very simple receptive field properties are earlier in the processing chain than units with more 'complex' properties.

In our experience there are considerable differences in class ratios between different kinds of animals; this is especially clear in a 'thin' analysis of a large number of units per animal. It should be possible to take advantage of these naturally occurring differences to assess the use made by the animal of a given class. To this end an 'in depth' analysis of each unit was made in some monkeys in this study and the number of units per animal limited to 15 or less.

Five of the monkeys used in the 'in depth' microelectrode study were revived at the end of the recording period (one of the monkeys was recorded from twice) and used subsequently for behavioral testing. This was carried out in a computer-controlled automated discrimination apparatus for discrete trial analysis (DADTA). The apparatus and training techniques have been detailed elsewhere (Pribram, 1969). In this experiment the monkeys were taught a color (red vs. green) and a pattern (1 vs. 0) discrimination. They were given 50 trials per day and brought to a criterion of 90% correct in 100 consecutive trials.

The results of the red–green and the 1–0 discriminations, expressed in days to criterion, are shown in the bottom two rows of Table 1. Performance of each monkey on the two tasks was compared to the percentage of five classes of receptive fields (diffuse, undefined, disc, line, and color-sensitive) sampled in his visual cortex. Then the behavioral and electrophysiological data were correlated across animals in order to determine relationships between performance on visual discriminations and proportions of various receptive field classes. The results were close to what would be expected by chance. In no case was there a monotonic relationship between performance of a monkey on a visual discrimination and frequency of a given class of receptive fields. Some weak relationships appeared, but because ten cases were considered these results could not be judged statistically valid.

These results should be viewed in combination with a behavioral study which was conducted on a set of cats in which ratios of receptive field classes were changed artificially (Hirsch and Spinelli, 1970). Behavioral testing indicated that animals possessing only vertically oriented receptive fields for one eye and horizontal fields for the other had no difficulty in interocular transfer of discriminations in which the orientation of features is the key element. Thus the availability of detectors *per se* cannot be crucial in determining the capacity to discriminate.

It seems inescapable, when one finds a unit which seems responsive only to a very specific stimulus to conclude that the unit is a detector for the stimulus. Yet we are still missing some crucial pieces of the puzzle. The characteristics of the system as a whole are not necessarily those recorded at the unit level. (By analogy, linear operations can be performed by digital computers.) Some assumptions are inherent in a method of analysis; sinusoidally modulated visual stimuli, in the temporal or spatial dimension, or maps generated by spot scans assume that the system can be treated as a linear processor. But bars, edges, and more complex stimuli assume nonlinear processing. From previous work we have reached the conclusion that, at least in the cat, visual cortex contains both cells which are committed to specific features of the visual image and cells which are not. We suggest that uncommitted cells could be considered part of a linear mechanism in contrast with the nonlinear mechanisms of the line detectors, and accordingly we used both methods in this analysis. In the rhesus monkey the number of types of units is greater, yet the broad distinction between cells uncommitted to specific features of the visual world and cells that are committed to specific features still applies. Moreover it has been shown in the cat (Campbell, Cleland and Cooper, 1968) that the selectivity of units with line-shaped receptive fields is quite broad. We find this to be true also in the monkey.

A lack of extreme receptive field specificity is probably adaptive. Our ability to see many colors with only three color pigments rests on a similar phenomenon; the spectral sensitivity curves of the pigments are very broad and overlap greatly. *Relative* activity determines the final sensation, thus allowing the perception of many more colors than the number of available pigments. If similar principles apply to pattern vision, then fewer types of units would be necessary, their absolute tuning would be nearly irrelevant, and, because recognition would be dependent on the activity of the whole rather than of a few selected units, the system would be less sensitive to disruption. The proposed theoretical resemblance of neural mechanisms of color and pattern vision, coupled with the experimental link of microelectrode studies and behavioral testing, shows promising new avenues for investigation.

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