

Classification of Receptive Field Properties in Cat Visual Cortex*

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Summary. The properties of the receptive fields of visual cortex neurons of cats were studied manually and by a computer controlled system using single lines, double lines and multiple lines (gratings). The multiple selectivities of each of the receptive fields studied make it necessary to abandon the concept that each cell functions as a feature detector. Instead, an attempt was made to classify the receptive field properties with the aim to delineate the transfer functions (of the total networks) served by each property. When tested with *one-line* stimulus, cells with simple receptive field properties differed from cells with complex receptive field properties as to their velocity selectivity (simple: 1° to 3°/s; complex: 4° to 10°/s), spontaneous activity (lower for cells with simple properties), optimal firing rate (lower for cells with simple properties) and receptive field size (smaller for cells with simple properties) but not for orientation and direction selectivity. When tested with a *2-lines* moving stimulus, the responses of cells with simple properties were facilitated by the progressive separation of the lines whereas the responses of cells with complex receptive field properties were inhibited. When multiple lines, i.e. *gratings*, were used, an equivalence between simple and X properties and complex and Y properties was shown, while the sustained/transient classification proved to be independent of the simple/complex (X/Y) classification. Thus, receptive field properties can be classified into three categories: one reflects the input to the receptive fields; a second deals with the interactive

properties of the fields; while a third appears more related to the overall properties of the network.

Key words: Visual properties – Visual cortex – Receptive fields – Spatial frequency – Interactive properties

Almost every textbook of physiology, of psychology, and of physiological psychology describes the cells composing the visual cortex as feature detectors (e.g. Hilgard et al. 1979). This description is based on the discovery by Hubel and Wiesel (1959) that such cells respond considerably more briskly when a cat, rabbit or monkey are shown bars of light presented in certain orientations than when presented spots or flashes of light. This discovery takes added meaning from the fact that below the cortex, spots rather than lines are the more effective stimulus (e.g. Kuffler 1953; Hammond 1972).

As Creutzfeldt and Ito have noted (1968), certain problems arise, however, when these findings are interpreted to mean that the cells of the visual cortex are *detectors* of lines. A detector is characterized by an output which *uniquely* specifies the input which is detected. No such unique relationship between lines presented in preferred orientation and the output of cells in the visual cortex has been established. Quite the contrary: such cells have also been shown to respond to (i.e. their output varies with) changes in luminance, direction of motion, velocity of motion, color, and when moving spots rather than lines are used as stimuli (Spinelli et al. 1970). Some of these same cells are responsive even to non-visual stimuli: e.g., they are selectively tuned to a band width of auditory frequency (Spinelli et al. 1968) and on the basis of evidence obtained from potentials recorded with small macroelectrodes perhaps to other stimuli

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such as panel presses and reward contingencies as well (Pribram et al. 1967).

Nonetheless, as shown by the mappings made with moving spots referred to above, the receptive fields of cells in the visual cortex are elongated and oriented, properties which distinguish them from those recorded in the visual system below the cortex. The question therefore arises as to the functional significance of such elongated and selectively oriented visual receptive fields. In addition to the feature detector interpretation, two proposals have been made: (1) The elongated fields function to provide sensitivity to edges (e.g. Bishop and Henry 1972; Henry 1977); and (2) the elongated fields represent tuned spatial filters (e.g. Campbell and Robson 1968).

The proposal that the cells of the visual cortex compose tuned spatial filters stems in part from the finding that the fine grain of their receptive fields may contain inhibitory side bands (Hubel and Wiesel 1959; Spinelli and Barrett 1969; Spinelli et al. 1970; Pollen et al. 1971; Glezer et al. 1973). Such side bands (surrounds) also characterize the circular receptive fields of cells in the lateral geniculate nucleus (Hammond 1972), thus the filter characteristics are not limited to cortex.

Recently, de Valois has tested these three proposals and shown that bar width is not an effective dimension in changing the output of cells in the visual cortex (Albrecht et al. 1980). Further, edges per se fail to delimit the orientation selectivity of these cells. This was shown by defining the orientation selectivity of a cell with use of gratings and then substituting checkerboards or plaids. In every case, the complex stimulus had to be rotated so that the major axis of the Fourier transform of the pattern was aligned with the orientation selectivity of the cell which was no longer maximally stimulated by the edges composing the pattern (De Valois et al. 1979).

Conceiving the function of cells in the visual cortex as composing spatial filters rather than bar or edge detectors raises several problems. Hubel and Wiesel in their original discovery distinguished four classes of cells: concentric, simple, complex and hypercomplex (Hubel and Wiesel 1959). All subsequent investigators have readily identified the concentric, simple and complex properties of cells according to the definitions that initially delineated them. More difficulty has been encountered with the hypercomplex category, however (see e.g. Spinelli et al. 1970; Schiller et al. 1976). Thus, Henry in a comprehensive review of the work of the Canberra group (1977) notes that "In the striate cortex of the cat, hypercomplex cells . . . are extremely rare; as few as ten in several thousand isolated neurons have

been detected in our laboratories." In part, this may be due to the fact that the methods used in such studies were inappropriate to engage the hypercomplex selectivity, but the more likely reason, as Henry points out, is that the presence of end zone inhibition (the characteristic of hypercomplexity) "may be associated with any type of excitatory region covering the full spectrum of simple and complex cells."

Two additional distinctions in receptive field properties of cells in the visual system were initiated by Enroth-Cugell and Robson (1966). One distinction rested on the sustained or transient nature of the response to a luminance stimulus and the other on the linearity or nonlinearity of the response when presented with gratings shown in phase and in counter-phase.

The classification of responses of cells in the visual system as linear and nonlinear fits the proposal that these cells perform the functions of spatial filters. The description of the distinction between simple and complex cells is also consonant with the linear-nonlinear distinction since simple cells show clear inhibitory side bands in their receptive fields, whereas complex cells do not. Enroth-Cugell and Robson had shown that, at the optic nerve, units that responded linearly also, as a rule, responded transiently while those that responded nonlinearly also, as a rule, gave a sustained response.

These results gave promise of a convergence of characteristics such that simple cells could be considered sustained responders making up the linear element in a spatial filter. This ready interpretation has been made implicitly in a number of studies and reviews (e.g. Breitmeyer and Ganz 1976) despite the fact that more recent studies have shown the sustained-transient dimension to be more complex (see e.g. Cleland and Levick 1972; Fukuda and Stone 1974) even at the retinal level and that such convergence of characteristics may not hold at the cortex (Ikeda and Wright 1974).

The studies presented in this paper were undertaken to investigate to what extent a convergence of classifications might properly hold. The experiments were part of a systematic program in which quantitative computer controlled techniques were utilized, first with single spots (Spinelli 1966; Spinelli and Pribram 1966; Spinelli and Barrett 1969) then with double spots (Phelps 1973) followed by multiple spots (visual white noise - Sutter 1976). In the present experiments single lines, double lines and multiple lines (gratings) were used, often with the same cell. Many of the results confirm those which have by now been reported by others where different techniques were used in each experiment. The current experiments were performed in conjunction with

Table 1. Classification of properties of striate cortex receptive fields

	Simple			Complex			Uncategorized			Statistical Value
	No. of cells	X	SD	No. of cells	X	SD	No. of cells	X	SD	
Orientation (degrees)	17	58.35	18.49	51	58.86	40.81				$t = 0.24$ NS
Velocity (degrees/s)	17	1.91	1.85	51	6.87	4.32				$t = 5.67$ $p < 0.01$
Spontaneous firing rate (spikes/s)	78	2.15	2.35	95	3.60	3.45	47	8.83	8.79	$F = 38.7$ $p < 0.001$
Optimal firing rate (spikes/s)	83	12.87	14.79	124	21.89	20.70	48	17.73	18.15	$F = 5.94$ $p < 0.01$
Receptive field size (No. of bins)	33	1.96	1.33	65	3.77	2.19	47	4.06	1.75	$F = 13.72$ $p < 0.01$

those reported in Lassonde et al. (1981) and suggest a direction that can be taken in answering the provoking problems of classifying the various functional characteristics of receptive fields in the visual cortex.

One-Line Experiment

Methods

Data were collected from 14 adult cats weighing 2–4 kg. Under deep general anesthesia (Nembutal, 18 mg/kg), the animals were implanted with a recording chamber designed and built in our laboratory (Pitito et al. 1976). The microelectrodes were lowered with a stereotaxic microdrive inside the chamber according to the coordinates used by Spinelli and Pribram (1966), i.e. 2–6 mm posterior to the interaural line and 0.5 to 1.5 mm lateral to the midline. Recording was accomplished by securing the head in a holder fixed to the skull by dental cement. This system permitted painless and stable immobilization of the head without the use of carbars, avoiding surgical preparation during the actual recording sessions.

Before a unit was analyzed with the computerized mapping technique, it was initially addressed with black (white) paper lines of various widths pasted on white (black) cardboard. A streak retinoscope was then used to define more precisely the sensitivities of the unit. The receptive fields were plotted on a white enamel screen at 1 m (Movshon et al. 1978a–c). These plots allowed us to position a computer controlled oscilloscope vis-a-vis the receptive field; the oscilloscope was placed 57 cm away from the eyes of the animal so that each cm on the screen would correspond to one degree of visual angle. Eye dominance for the unit was determined and the non-dominant eye occluded. Using the streak retinoscope, final adjustments were made so that the cell's receptive field center coincided with the center of the oscilloscope screen.

The stimulus on the oscilloscope face consisted of one line whose length could be adjusted. This line could be moved in any orientation, direction and velocity by a computer (PDP-8) which also recorded the unit's response to the stimuli. The directional and orientational sensitivity of all units was measured by collecting

36 histograms of a unit's response to a single white line on a gray background moving in each of 36 directions in 10° increments. The lines used were 0.05° wide and were displayed on P4 (white) phosphor 57 cm from the cat. Diffuse white background luminance, provided by tungsten filament flood lamps directed at the off-white room walls, was set between -1.5 and -1.0 log cd/m². Lines were presented on this background with a contrast of 0.91. All luminance measurements were made with a MacBeth 6800 photometer. Stimuli were presented in each direction and orientation only once before presenting the next stimulus orientation. Similarly, second and subsequent presentations at any orientation occurred only after all other orientations had been presented first, thus interlacing the stimulus directions. Any long term changes in cell activity were in this manner averaged into all histograms. This technique was termed the "multiple histogram technique" by Henry et al. (1973). The computer stored responses from different stimulus orientations separately. Tuning curves describing orientation versus response were usually bell-shaped with half-widths varying from ±30° to ±60° about the optimum orientation.

Results

Prior to any quantitative investigation, 257 cells were examined by manual stimulation and acoustic recording techniques and classified as showing simple or complex characteristics according to the criteria proposed by Hubel and Wiesel (1962) and Pettigrew et al. (1968). The simple property was assigned to receptive fields which could be subdivided into parallel excitatory and inhibitory regions; the complex property was assigned to receptive fields that tended to be larger and give "on-off" responses to a line flashed at any position. Ninety-seven receptive fields were classified as showing "simple" properties, 128 as showing complex properties, while the properties of 32 receptive fields could not be categorized in either class.

One hundred and forty-four of these cells were then tested using a computer controlled moving light bar displayed on an oscilloscope face in 5° increments in all of 360° of orientation. No significant differences were found between receptive fields showing simple and complex properties with regard to mean width of their orientation tuning curve (see Table 1) or their directional selectivity. However, only 14% of the receptive fields mapped were symmetrically bidirectional and only 16% were completely unidirectional. The remaining 70% of the receptive fields responded to both directions but showed a distinct preference for one of them. These results are similar to those obtained by Spinelli, Pribram and Bridgeman using computer controlled spot stimuli in an earlier study (1970).

Velocity sensitivity was tested by moving the bars at different speeds in the preferred orientation: 22% of the receptive fields showed velocity selectivity. Of these, simple receptive fields were found to respond best to velocities ranging from 1–3°/s, whereas complex receptive fields responded preferentially to velocities ranging from 4–10°/s. As can be seen from Table 1, these differences were reliable to a 0.01 level of statistical significance.

A receptive field profile was obtained on the same 144 cells by moving a line across the entire receptive field in the preferred orientation, in the preferred direction, and at the preferred velocity. This profile produced a post-stimulus histogram from which a quantitative estimate of receptive field (RF) size could be derived by the following formula:

$$RF = V \times T$$

where V equals the velocity of the line moving through the field and T equals the number of bins times the bin width. As can be seen from Table 1, receptive fields with simple properties have reliably narrower RF's than receptive fields showing complex properties, while uncategorized receptive fields show the widest fields. This difference was statistically significant at the 0.01 level.

The average discharge produced by the unit over its receptive field was also calculated and recorded as the "optimal" firing rate of the cell. As shown in Table 1, cells with complex receptive fields have a considerably higher optimal firing rate (spikes/s) than those with simple receptive fields, a difference which reaches the 0.01 level of statistical significance. Cells with uncategorized fields fall in between.

In order to assay the spontaneous activity of each unit (as a control for optimal firing rate), a blank display of the mean background luminance of the oscilloscope was presented for the same period as that used for stimulus presentation (180 s). Table 1

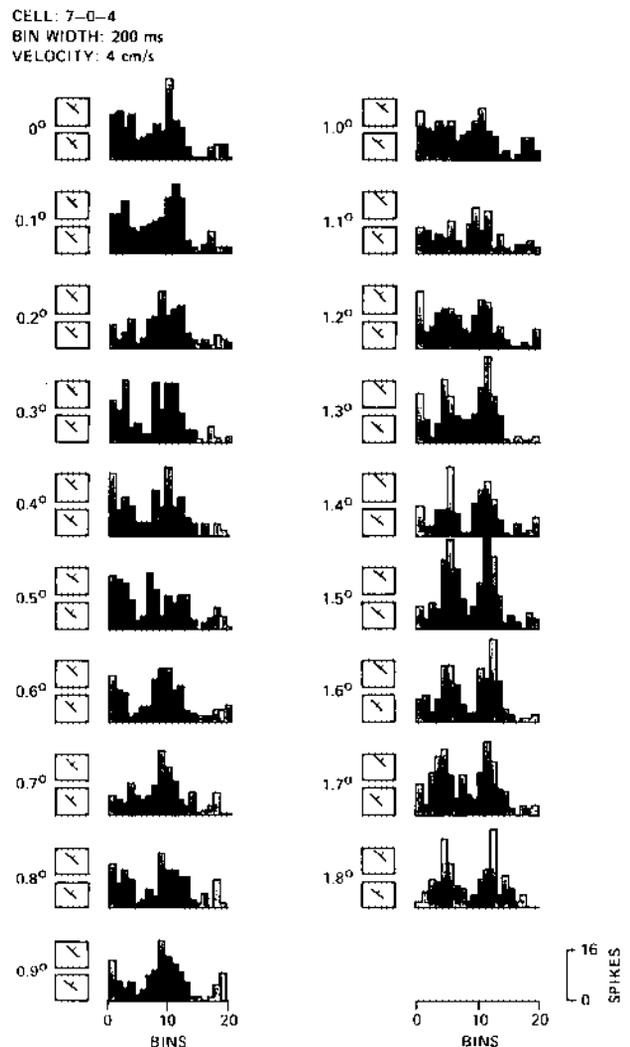


Fig. 1. Discharge pattern of a unit in the visual cortex presented with a 2-line stimulus of various separations ($0-1.8^\circ$) moving in the preferred direction and orientation with the preferred velocity. The number to the left represents the separation (in $^\circ$) of the 2 lines; the bar in each square represents the preferred orientation and direction of the unit. Ordinate: response discharge in spikes/s; abscissa: position of the 2-line stimulus as they move across the field (bin width: 200 ms)

records that cells whose receptive fields show simple properties have a reliably lower spontaneous firing rate than do cells whose receptive fields show complex properties, while uncategorized cells generally showed the highest spontaneous rate. These differences also reach the 0.01 level of statistical significance.

Two-Line Experiment

Methods

There are regions *within* the receptive field which, while not able to provoke a discharge on their own, can nevertheless facilitate or

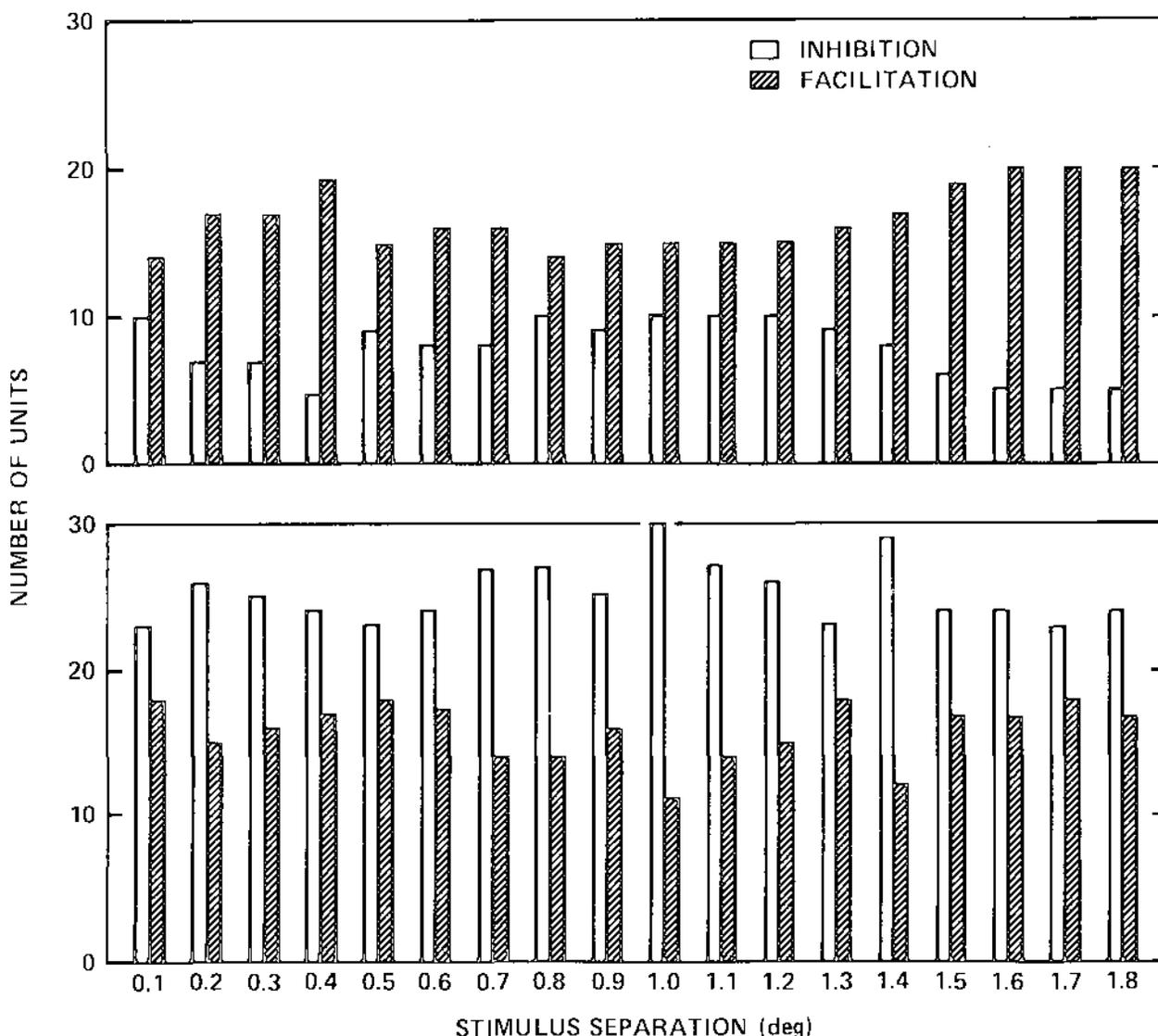


Fig. 2. Graph of the facilitation and inhibition produced by a pair of lines moving at the preferred orientation in the preferred direction with preferred velocity. Abscissa: progressive separation of the lines in degrees of visual angle; ordinate: number of cells showing facilitation and inhibition. Above, cells with simple properties; below, cells with complex properties

inhibit a discharge produced by simultaneous stimulation of another region of the field (Henry et al. 1973; Movshon et al. 1978). In order to study these regions, 86 additional units were examined with two moving parallel lines with separations ranging from 0–1.8° presented on the oscilloscope face with a luminance contrast of 0.83. The two lines were always moving in the preferred orientation and direction at the preferred velocity which had been previously determined by the neuron's response to single lines. The length of the line was also kept optimal for obtaining a maximum response for the particular unit being examined. Post stimulus time histograms (PSTH) were then repeatedly (five separate scans) collected for each separation using multiple histograms to plot cell activity at a number of different separation distances. Each PSTH was plotted, the number of spikes/scan being the ordinate and the position of the lines on the oscilloscope face being the abscissa.

The total response of the cell as described by its histogram when the two lines were superimposed was taken as baseline. For

each degree of separation the unit's response was considered facilitated when its total response increased by one standard deviation and inhibited when decreased by this amount.

Results

Figure 1 shows the effect of stimulus separation on the response of one such unit. The separations range from 0–1.8° in 0.1° increments and each histogram represents one such increment. At separation 0.8° there is a decrease in the response histogram and at 1.5°, the separation is big enough so that each line evoked its own comparable response which is maintained for the remainder of the run. These results were consistent with previous findings (Phelps 1975).

The 86 receptive fields were classified in terms of whether their overall response was facilitated (increased by one standard deviation) or inhibited (decreased by one standard deviation) by the double moving-line. As shown in Fig. 2, simple receptive fields show an overall facilitation to the various separations of the moving double-lines, especially when the separation between the lines is 0–0.6° and 1.2–1.8°; these two zones of marked facilitation are separated by an intermediate region (0.7–1.1°) where fewer receptive fields show facilitation. Complex receptive fields give a different picture; overall, their responses are inhibited by the two-line separation. Once again, however, the two zones (0–0.6° and 1.2–1.8°) are separated by an intermediate zone (0.7–1.1°) in which a somewhat greater number of cells show inhibition. Only 4% of the cells sampled showed *no* facilitation or inhibition.

Multiple Line (Spatial Frequency) Experiments

Method

As in the single and double line experiments all stimulus patterns were generated by means of a Tektronix 604 display monitor with a P-6 (fast, reasonably white) phosphor. In *all* these experiments, mean luminance (measured with a MacBeth 6800 photometer and directly determined with a PIN photodiode) was 5.4 cd/m² and the Michelson contrast

$$\frac{\text{maximal luminance} - \text{minimal luminance}}{\text{maximal luminance} + \text{minimal luminance}} \text{ was } 0.20.$$

Stationary sinusoidal gratings were generated in the traditional way as described by Campbell and Green (1965). A triangular wave at 500 kHz serving as a vertical deflection signal, provided uniform luminance in the vertical direction. The horizontal deflection was driven by a sawtooth at ca. 330 Hz which was triggered by zero transitions of the periodic intensity signal.

Sinc-wave drifting grating of any periodic luminance profile were generated by a technique in which the displayed grating was shifted horizontally and was reset after one full cycle of displacement. A special circuit was designed which automatically tailored a sawtooth signal from its period to maintain a constant angular drift velocity (cycles per second) independent of the spatial frequency of the grating. This design made it possible to adjust the parameters for drifting gratings with only two controls: (1) Keeping the angular drift velocity constant, the period of the grating could be changed over a range of two decades by adjusting the frequency of the signal generator for intensity without appearance of glitch. (2) Keeping the period of the grating constant, the drift velocity could be adjusted over a range of 1 : 20 without glitch. The drift velocity used in the experiment was 2 Hz.

To obtain a sinusoidal reversal of a stationary grating, the intensity signal had to be modulated at 100% modulation with a slow sinc wave signal. This was achieved with an IC four quadrant multiplier. A trigger pulse was derived from the modulating signal for the synchronization of a C.A.T. computer. This made it possible to record spike histograms locked into the reversal cycle.

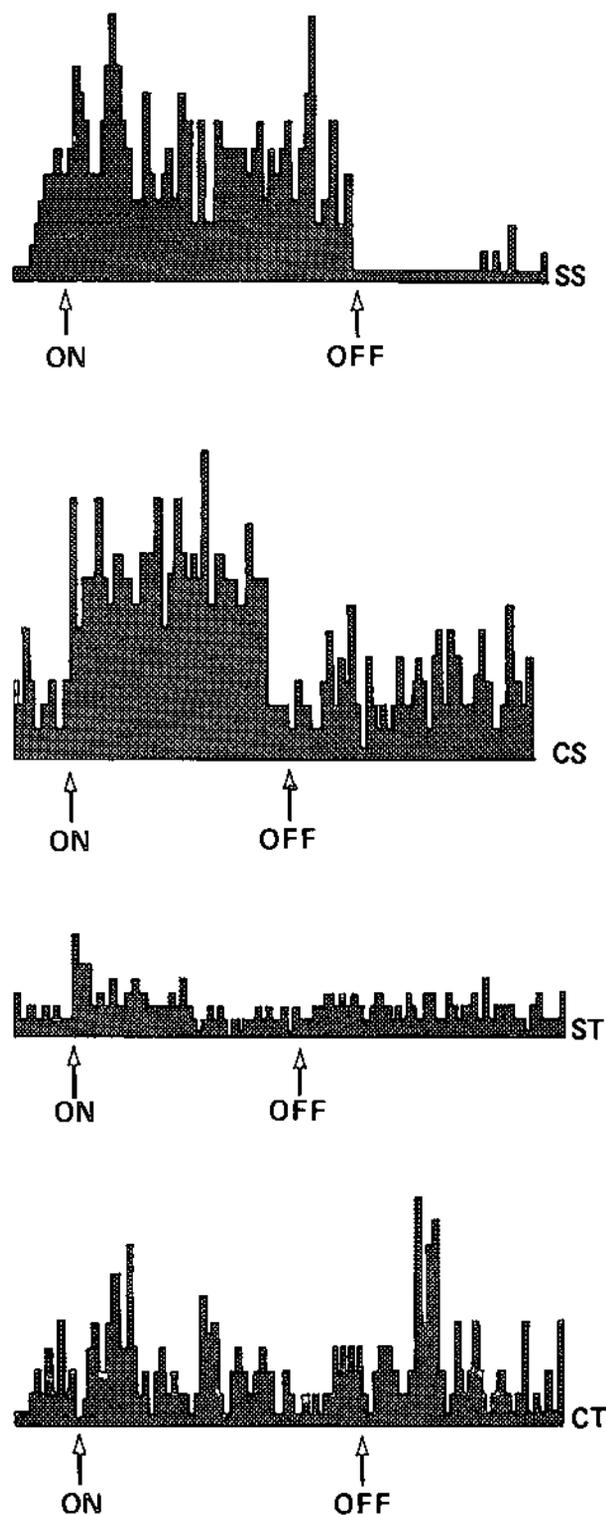


Fig. 3. Examples of the responses defined as sustained and as transient of cortical units shown stationary gratings. SS: simple-sustained; CS: complex-sustained; ST: simple-transient; CT: complex-transient. ON: stimulus ON for 4 s; OFF: stimulus OFF for 4 s. See text for details

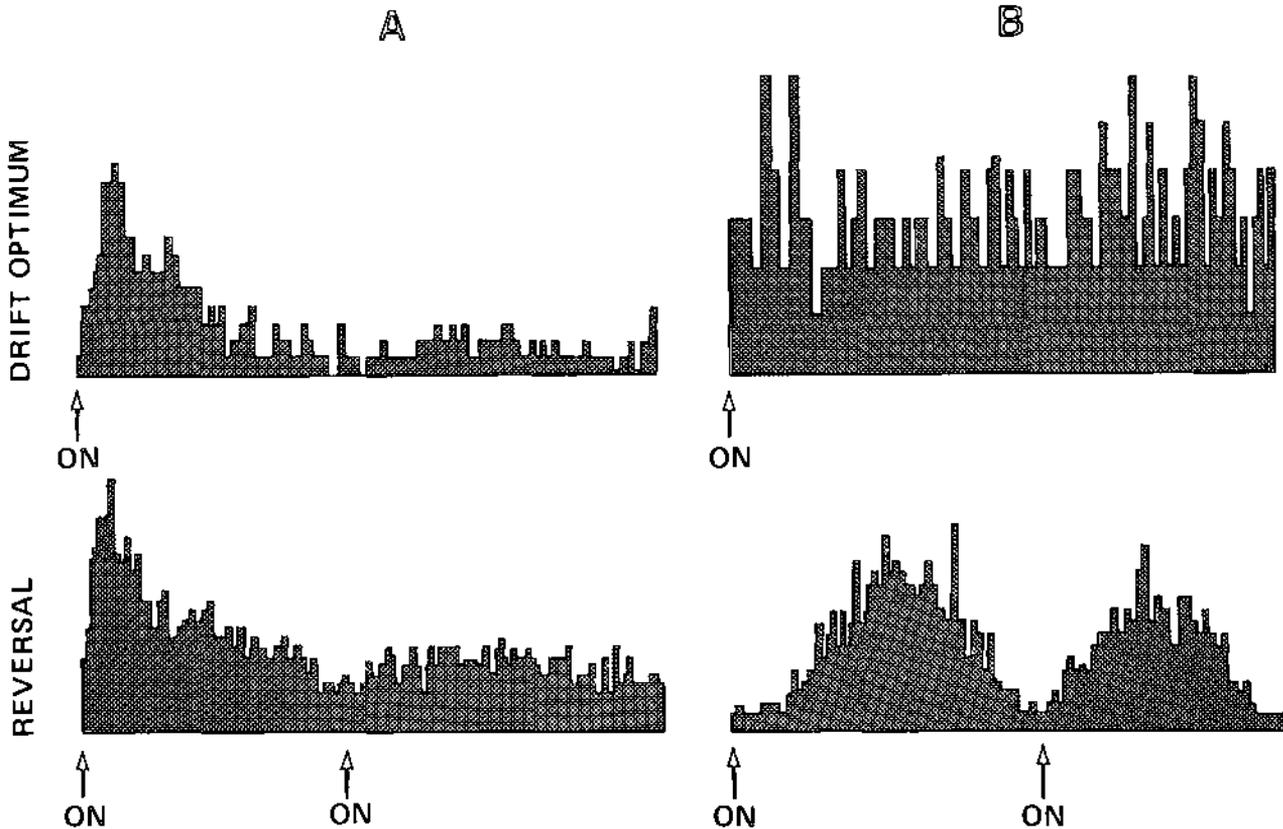


Fig. 4A, B. Discharge patterns of units in the visual cortex presented with drifting and flashing stationary gratings. The upper diagrams show responses to drifting gratings. A shows the type of response (initial only) that defines a "simple" property of cells. B shows the type of overall response that defines a "complex" property. The lower diagrams show responses to stationary gratings flashed in phase and counterphase. A shows the type of response that defines a "linear" property of cells (response to one phase but not to counterphase) while B shows the type of response that defines a nonlinear property (response to both phase and counterphase). The optimal spatial frequency for unit A is 0.7 c/deg , for unit B is 0.8 c/deg

The average luminance remained constant over a reversal cycle. The signal was reversed at a rate of 16 alternations/s (8 Hz).

To measure the temporal structure of the on-off response, a pattern to which the cell responded well was periodically switched on and off by a simple timer circuit. Again a trigger pulse for the C.A.T. computer was used, marking the beginning of every on-off cycle. The off-pattern was a dark screen, while the on-pattern was chosen to be a stationary grating of a spatial frequency corresponding to the peak of the tuning curve derived from drifting gratings. Two settings were used for the on-off cycle: 1 s on - 1 s off; and 4 s on - 4 s off.

Results

Tuning curves were drawn for each cell as follows. Cell responses to drifting (2 Hz) gratings were collected over a 50 s period for each of ten sine wave gratings (spatial frequency = 0.2-2.0 cycles per degree of visual angle). The firing rate was determined by means of a spike converter which counted the number of spikes over the 50-second collection period; and one 50 s baseline count was taken in the

absence of visual stimulation. Gratings were presented in random order. The curves obtained from these collections were then smoothed to decrease erratic cell responses by averaging each point with the two next to it. The peak response of the smoothed curve was then set equal to one, and the remaining points converted into decimal fractions of that peak. The resultant set of points was then plotted on log-log paper. All tuning curves were suprathreshold since optimal direction, velocity and frequency stimulation were determined and used (see below).

Of the 115 additional receptive fields investigated in this part of the study, 55 were classified as simple and 58 as showing complex properties according to the criteria previously described for manual-aural mapping.

In addition, 82 receptive fields were analyzed according to their sustained/transient properties. Determination was made by collecting post stimulus time histograms of response to a four second ON -

four second OFF presentation of the optimal spatial frequency grating at 0° phase angle. Four seconds periods were found to be representative in preliminary tests using a range of one to seven seconds. Forty-three receptive fields showed a return of the firing discharge to the spontaneous level within 4 s of stimulation and were thus classified as transient responders, whereas 39 receptive fields still responded with 3–4 spikes/s above mean spontaneous firing level at the end of this period and were thus classified as sustained responders. These sustained and transient responses could be collated with the simple and complex properties of the receptive fields according to hand-held mapping: 19 showing sustained properties were simple and 20 complex; of those showing transient properties 15 were simple and 28 were complex. In agreement with the results of Ikeda and Wright (1974), four different combinations of properties were therefore identified: simple-sustained (SS, $n = 19$), complex-sustained (CS, $n = 20$), simple-transient (ST, $n = 15$) and complex-transient (CT, $n = 28$). Post stimulus histograms obtained for each of these combinations are illustrated in Fig. 3.

Next, quantitative, computer controlled mapping was performed with sine wave gratings presented at preferred orientation (direction and velocity, if drifted) and optimal (peak) frequency with luminance and contrast above threshold in an attempt to identify the linear and nonlinear properties of these receptive fields. Two criteria were used in order to distinguish linearity (X) from nonlinearity (Y). Receptive field properties were classified as X, (1) if the cells responded to a grating positioned in the preferred orientation and drifting in the preferred direction by a modulation of their discharge frequency and (2) if the cell responded to a phase reversing (16/s) stationary optimally oriented grating pattern linearly, i.e., at only one phase angle (0° or 180°). By contrast, receptive field properties were classified as Y if the cells responded to a grating similarly positioned and drifting in the preferred direction by an overall increase of their average discharge and if they responded to the optimally oriented phase reversing stationary pattern non-linearly, i.e., at more than one spatial phase (e.g. 0° and 180°). An example of X and Y type receptive fields is shown in Fig. 4. The first part of Fig. 4 shows the modulated response of the X type to a sinusoidally moving grating. On the other hand, the Y type gives an unmodulated response to the same stimulus. The second part of Fig. 4 represents the response to a stationary grating whose phase angle was either 0° or 180° . Notice that the X receptive field is characterized by a response to only one of the two phase

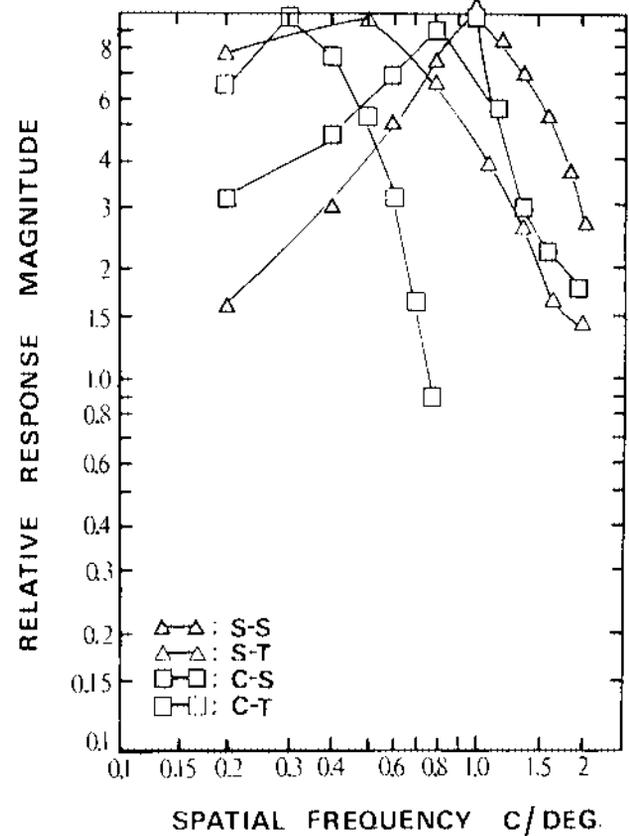


Fig. 5. Examples of spatial frequency tuning characteristics of cells showing combinations of properties: SS: simple-sustained; ST: simple-transient; CS: complex-sustained; CT: complex-transient; Abscissa: spatial frequencies in c/deg; ordinate: relative response magnitude

Table 2. Range of peak spatial frequencies

Properties	Range of peak spatial frequencies
Simple	0.2–1.4 cycles/degree
Complex	0.2–1.8 cycles/degree
Linear	0.2–1.2 cycles/degree
Nonlinear	0.2–1.8 cycles/degree
Sustained	0.2–1.6 cycles/degree
Transient	0.2–1.8 cycles/degree
Simple-sustained	0.2–1.4 cycles/degree
Simple-transient	0.2–1.2 cycles/degree
Complex-sustained	0.2–1.6 cycles/degree
Complex-transient	0.2–1.8 cycles/degree

angle presentations whereas the Y receptive field is characterized by a uniform response to both presentations.

Of a total of 47 cells studied in this fashion, 14 receptive fields were classified as having X properties by both criteria and 33 were categorized as having Y properties. There was no instance in which the properties of a receptive field were classified differ-

Table 3. Mean spontaneous activity and optimal firing rate of cells also showing simple, complex, linear, nonlinear, sustained, and transient properties

	Simple	Complex	Linear	Nonlinear	Sustained	Transient
Number of cells	55	58	14	33	39	43
Mean spontaneous activity (spikes/s)	3.19	4.42	3.94	4.61	5.57	2.78
Standard deviation (spontaneous activity)	2.43	5.5	1.58	6.7	9.72	8.13
Mean optimal firing rate (spikes/s)	9.96	16.15	10.22	17.66	12.96	14.69
Standard deviation (optimal firing rate)	9.27	10.49	10.43	11.82	9.1	11.09

ently by the two criteria. Further, all 33 showing Y properties also showed complex receptive fields as determined by manual mapping whereas out of 14 receptive fields showing X properties, 12 were characterized by simple properties and two showed complex properties. These results suggest an equivalence between simple and X properties, on the one hand, and complex and Y properties on the other. Despite this observation, the simple/complex and X/Y classifications were handled separately in an attempt to discern differences among the receptive field groups in peak responses to spatial frequency and width of tuning curve.

No significant difference in peak frequency were found between receptive fields with simple and complex properties ($X^2_{(2)} = 3.23$, $p < 0.1$), nor between receptive fields with X and Y properties ($X^2_{(2)} = 1.5$, $p < 0.5$), nor between receptive fields with sustained and transient properties ($X^2_{(2)} = 1.18$, $p < 0.5$), nor was there any difference in peak frequency for property classes in combination ($X^2_{(6)} = 4.44$, $p < 0.5$). Furthermore, receptive fields classified in this fashion were not found to differ in the range of peak spatial frequencies, except that those with simple and X properties responded over a slightly narrower range of spatial frequencies. These results are summarized in Table 2. Note that these results were obtained with suprathreshold stimulation.

Widths of the tuning curve for each receptive field type were measured (in cycles per degree) between the two points at 50% of the suprathreshold peak response. The width of a tuning curve was judged to be narrow if the response had fallen to half-amplitude of the peak response within one octave of spatial frequency.

No significant differences in narrowness of tuning curves were found between receptive fields with simple and complex properties ($X^2_{(1)} = 0.68$, $p > 0.25$), nor between those with X and Y properties ($X^2_{(1)} = 0.44$, $p > 0.5$), nor between those with

sustained and transient properties ($X^2_{(1)} = 0.013$, $p > 0.95$) nor among the four classes in combination ($X^2_{(3)} = 2.37$, $p > 0.75$).

As a control the spontaneous firing rate of each cell was collected over a period of 50 s to a blank display of the mean luminance of the background illumination of the oscilloscope. Similarly the response of each cell to a drifting grating pattern of optimal frequency, orientation, direction and velocity was collected over a period of 50 s. The mean spontaneous activity and the mean optimal firing rate of cells showing each of the different classes of properties are reported in Table 3.

It can be seen once again that the properties "X" and "simple" are alike in that the cells which show them have a lower spontaneous activity and firing rate than those classified as "Y" and "complex" which are alike. Cells with sustained responses on the other hand, show a higher spontaneous discharge but a lower optimal firing rate than those with transient responses ($F = 2.01$, $p > 0.1$).

Discussion

The results of the studies reported here, as well as those of the many others in the literature, make it clear that characterization of cells based on a response to any single stimulus dimension or feature has become untenable. Such responses cannot be taken in isolation from the wealth of other reactivities of the cells being studied (see especially the series of comprehensive studies and analyses by Schiller et al. 1976). Rather, an attempt must be made to systematize the variety of selectivities by classifying them with the view that such classification can aid in understanding the transfer functions served by each class.

Classification was initiated by Hubel and Wiesel (1962) who proposed a distinction between simple and complex receptive fields on the basis of differ-

ences in the internal structure of the field: "simple" fields showed parallel regions of opposite sign (e.g., an elongated excitatory center with inhibitory flanks) while "complex" fields presented an apparently more homogeneous structure. The results of the current quantitative *single line experiments* show that preferred orientation and direction of movement are independent of these distinctions. On the other hand, cells with simple receptive fields respond best to velocities of 1–3°/s while cells with complex receptive fields preferred a faster velocity of 4–10°/s to produce an optimal firing rate. Furthermore, the spontaneous firing rate of cells with complex fields is almost twice that of cells with simple properties.

The results of the single line experiment thus suggest a method for analyzing receptive field properties that could be usefully extended: some properties are independent of the simple-complex categorization while others are not. In the results of these initial experiments the independent properties appear to delineate the overall external influences on the structure of a cell's receptive field, influences which define stimulus parameters such as preferred orientation and direction of movement. The properties that relate to the simple-complex distinction, on the other hand, appear to describe differences in the cell's responses due to the internal interactive structure and function of the receptive field.

The interactive properties were examined specifically in the *two line experiments*. The results of these experiments showed, as might be expected from the work of Hubel and Wiesel (1962), Cleland and Levick (1972), Andrews and Pollen (1979), and of Bishop and Henry (1972) that simple receptive fields are characterized by definitely separate "zones" of augmentation and reduction of responsiveness often with a neutral region between. The overall mode of response of cells with such simple receptive fields to such moving stimulus is, however, facilitatory. Complex receptive fields, on the other hand, display inhibitory interactions leading to reduced responsiveness over a much wider region. Pollen and Feldon (1979) used a moving single narrow slit similar to ours, and Movshon, Thompson and Tolhurst (1978a–c) used flashing rather than moving lines at various separations and obtained results complementary to ours.

They suggest and our two-line interaction data support their suggestion that complex receptive fields as well as simple receptive fields have a recognizable internal structure that is characterized by these internal interactions. The difference in the mode of interactive processing between simple and complex fields suggests an additional conclusion. If one takes as a simplifying assumption that the afferent input to

the receptive field is primarily excitatory and that lateral interactions are primarily inhibitory as proposed by Bishop et al. (1971), and by Creutzfeldt et al. (1974), support would be obtained for the hypothesis that simple receptive fields are determined to a large extent by input while complex receptive fields are more influenced by lateral connectivities among their dendritic structures, i.e. by dendrodendritic interactions.

In accord with the findings of others (Campbell and Robson 1968; Enroth-Cugell and Robson 1966; Movshon et al. 1978a–c; De Valois et al. 1978; De Valois et al. 1979; Albrecht et al. 1980; Schiller et al. 1976) *multiple line (grating) experiments* have provided a most powerful tool for quantitatively measuring, analyzing and classifying the properties of receptive fields in the visual system.

With regard to the interactive properties of receptive fields these were determined by the use of stationary sine wave gratings when spatial phase was reversed and by sine wave gratings drifted across the field in the preferred orientation and direction. Two populations of receptive fields were distinguished by these quantitative methods: One population responded by modulating their response to the drifting grating and responding linearly, i.e., to only one phase (0° or 180°) to the stationary grating. This type of receptive field property was labeled "X" because Enroth-Cugell and Robson (1966) defined such linear responses in "X" units of the periphery. By contrast, another population of fields labeled "Y" was characterized by an overall increase in response to the drifting grating and a nonlinear response to the stationary grating (i.e., both 0° and 180° produced a response). Movshon et al. (1978a–c), using similar techniques, also distinguished these two populations of receptive fields. In our experiments, these criteria defined populations which were practically the same as those defined by hand held and computer controlled single-line stimuli as "simple" and "complex" (only two out of 47 cells failing to match).

An additional dimension has been added to attempts to classify the properties of cells in the visual system by those who noted that the response to stimulation of some cells is "sustained" while that of others is "transient" (Barlow and Levick 1969; Cleland and Levick 1972). Many investigators (Dreher et al. 1976; Fukuda and Stone 1974; Fukuda and Sugitani 1974; Stone and Dreher 1973; Wilson et al. 1976) have assumed that the sustained response is what Enroth-Cugell and Robson described as modulated ("X") while the transient response is unmodulated ("Y"). This correspondence was brought into question, however, by Stone and Hoffman (1971), at least for cells in the visual cortex, and our results

clearly show that the modulated (linear) – unmodulated (nonlinear) and sustained-transient classes are independent of each other and *not* coordinate. These results also support those obtained by Ikeda and Wright (1974) who concluded that the simple/complex classification was different from the sustained/transient. Thus, the results of our experiments and those of others establish the independence of these two dimensions at the cortex. The sustained-transient classification appears to reflect basic differences in the durational properties of the response output of visual cells; the modulated-unmodulated classification appears to reflect differences in the spatial configuration (overall linearity) of the receptive field.

Conclusion

The results of the experiments reported here and those of the many studies reported in the vast literature on receptive field properties of cortical cells in the visual system, make it imperative to abandon the conception that such cells are feature detectors. Instead, these results indicate that each cell shows multiple feature selectivities and that some of these selectivities can be grouped into classes. Thus, in the results of the experiments reported here (and supported by the results obtained in a companion series of experiments utilizing the effects of intracerebral stimulation on receptive field properties – see Lassonde et al. 1981) three classes of selectivity could be tentatively discerned: One reflects the external input to the field, another the interactive properties of its receptive field, and a third appears more to characterize the output properties of that field.

In view of the fact that the output of a cortical cell is not uniquely determined by any single input (i.e. the cell is not a detector) it seems preferable to begin to characterize the results of unit analysis in terms of the properties of the network of cortical cells rather than to attempt to classify single cells. A beginning was made in this direction by Henry (1977) when, as noted in the introduction, he stated that the hypercomplex property “may be associated with any type of excitatory region covering the full spectrum of simple and complex cells.” However, in his comprehensive review, Henry persisted in labeling cells in an attempt to classify them rather than their properties. The presentation of results of the current experiments attempts to overcome this natural tendency. An effort was made to provide a more viable approach to the problems of unit analysis by classifying receptive field network properties rather than cell types.

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Note Added in Proof

These studies have recently been extended to include single cell recordings. Bridgeman (1980) has shown that recordings from units in the visual cortex of monkeys tested in a metacontrast task reveal task as well as stimulus relationships. The changes in firing pattern come some 200-400 ms after stimulus onset - at approximately the time the P_{300} is recorded with cross electrodes.