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Receptive-Field Characteristics of Neurons in Cat Striate Cortex: Changes With Visual Field Eccentricity

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SUMMARY AND CONCLUSIONS

1. Receptive-field properties of 214 neurons from cat striate cortex were studied with particular emphasis on: *a*) classification, *b*) field size, *c*) orientation selectivity, *d*) direction selectivity, *e*) speed selectivity, and *f*) ocular dominance. We studied receptive fields located throughout the visual field, including the monocular segment, to determine how receptive-field properties changed with eccentricity in the visual field.

2. We classified 98 cells as "simple," 80 as "complex," 21 as "hypercomplex," and 15 in other categories. The proportion of complex cells relative to simple cells increased monotonically with receptive-field eccentricity.

3. Direction selectivity and preferred orientation did not measurably change with eccentricity. Through most of the binocular segment, this was also true for ocular dominance; however, at the edge of the binocular segment, there were more fields dominated by the contralateral eye.

4. Cells had larger receptive fields, less orientation selectivity, and higher preferred speeds with increasing eccentricity. However, these changes were considerably more pronounced for complex than for simple cells.

5. These data suggest that simple and complex cells analyze different aspects of a visual stimulus, and we provide a hypothesis which suggests that simple cells analyze input typically from one (or a few) geniculate neurons, while complex cells receive input from a larger region of geniculate neurons. On average, this region is invariant with eccentricity and, due to a changing magnification factor, complex fields increase in size with eccentricity much more than do simple cells. For complex cells, computations of this geniculate region transformed to cortical space provide a cortical extent equal to the spread of pyramidal cell basal dendrites.

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INTRODUCTION

The pioneering work of Hubel and Wiesel (24, 25), over the past decade, has led to an intensive study of receptive-field characteristics of neurons in the cat striate cortex. However, nearly all of these studies have concentrated on cells with receptive fields located within 10° of the area centralis and very few (i.e., ref 27, 28) have commented on properties of cortical neurons associated with more peripheral parts of the visual field. None of the studies has dealt with either a wide range of peripheral receptive-field properties or systematic changes in these properties as field locations shift from the center to the periphery of the visual field.

Therefore, we studied and compared cortical neurons with receptive fields located throughout most of the visual field. In particular, we wished to answer the following four questions: *1*) Could neurons with peripheral receptive fields, including those in the monocular segment of the visual field, still be classified into the standard cell types of simple, complex, and hypercomplex (14, 24, 25, 35, 36)? *2*) Do receptive-field properties change with eccentricity in the visual field, and if so, how? *3*) Do any new or unusual properties appear in peripherally located fields? *4*) If present, how would such data on changes with eccentricity relate to similar changes described for X- and Y-cells of the dorsal lateral geniculate nucleus (23)?

As will be shown, the peripheral receptive fields for cortical neurons are qualitatively similar to those for the central visual area. However, these fields do demonstrate certain systematic changes with eccentricity. Their average size increases, and their selectivity for stimulus orientation and speed generally become poorer with increasing eccentricity; but

the pattern of ocular dominance and of preferred stimulus orientation plus direction stays nearly constant throughout the visual field. We also noted several interesting correlations between changes with eccentricity of X- and Y-cells on the one hand and simple and complex cells on the other.

METHODS

Preparation and recording

Striate cortical neurons were studied in 21 adult cats anesthetized with Fluothane for surgery and then maintained on N_2O/O_2 (70/30). They were paralyzed with gallamine triethiodide and artificially ventilated. End-tidal CO_2 was continuously monitored and kept at 3.5–4.0% by varying the stroke rate or volume of ventilation as needed.

Atropine and neosynephrine were topically applied to dilate the pupils and retract the nictitating membranes; zero-power contact lenses protected the corneas. Retinoscopy plus spectacle lenses, if needed, assured that the retinas were conjugate with the tangent screen 114 cm in front of the eyes. Retinoscopy was occasionally performed along a peripheral axis as well as a central one, and the differences in dioptric correction were usually 1 diopter or less. We rotated the stereotaxic apparatus around a vertical axis in order to plot peripheral receptive fields onto the same general region of the tangent screen, and corrections were applied to convert distances on the tangent screen to visual angles.

Varnished tungsten or stainless steel electrodes (5–25 MΩ at 500 Hz) were used to record extracellular activity of single neurons. Each receptive field was first plotted with hand-held stimuli. Background illumination was 0.6 cd/m² (i.e., in the cat's mesopic range; see ref 17), and stimulus illumination was approximately 1.5 log units above this. We occasionally plotted fields using dark discs and rectangles with higher background illumination. The plots consisted of the "minimal response field" (3), and properly oriented stimuli were used to map the excitatory part of the receptive field. A large, wide slit of light (4–8° or more) was typically used so that both the leading- and trailing-edge fields (see definitions below) could be separately determined. The slit was made sufficiently wide to minimize interactions in response to the leading and trailing stimulus edges (8). In addition to the minimal response fields, other characteristics examined were (see definitions below): preferred and range of stimulus orientation, preferred direction of stimulus movement, optimal and range of stimulus speed, ocular dominance, and spontaneous activity.

We also collected quantitative data by preparing average response histograms relating firing rate to stimulus position (Fig. 1). Techniques used for these histograms were those of Bishop and co-workers (9, 18, 27, 35). For cells with low spontaneous activity (i.e., most simple and some complex cells), histogram data were used to evaluate inhibitory portions of the receptive field by the method of monocular or binocular conditioning (9, 18).

Histological procedures

To control for penetrations that could possibly have passed outside of striate cortex, markers were placed at several recordings sites by passing current through the electrode tip; these aided in reconstruction of electrode tracks (see Fig. 14). With tungsten electrodes, the marks consisted of small lesions (10 μA for 10 s), and with stainless steel electrodes, they consisted of a stained iron deposit (16). Iron was deposited by passing 2 μA for 15 s through the electrode tip. Following the recording session, cats were transcardially perfused with saline followed by 10% formol-saline; in cats studied with stainless steel electrodes, a Prussian blue reaction was used to stain the deposited iron (16). The brains were stereotaxically blocked in the coronal plane, embedded in egg yolk, cut frozen at 40 μm, and stained with cresyl violet. All neurons of this study were located in the striate cortex.

Definition of terms

Defined below are some of the terms used in this paper:

LEADING (OR TRAILING) EDGE. We usually mapped receptive fields with slits of light which presented two contrast borders. As the slit moved through the field, the leading edge was the dark-to-light border and the trailing edge, the light-to-dark border.

LEADING- (OR TRAILING) EDGE FIELDS. These are the excitatory subregions of the receptive field which can be mapped with a single, moving edge. The leading-edge field is that portion through which movement of the leading edge evokes a response, and the trailing-edge field is analogously defined.

WIDTH. The width of an excitatory receptive field is the dimension along an axis perpendicular to the preferred stimulus orientation. A receptive field could include as many as four excitatory subregions (a trailing- and leading-edge field for each of the two directions of stimulus

movement). We characterized the size of a receptive field in terms of the width of the widest edge field. Interestingly, the widest edge field was always the edge field in which visual stimulation elicited the largest neuronal response.

Width instead of area has been used to characterize receptive-field size for the following reason. We frequently found that a response could not be elicited until the stimulus covered most of the field lengthwise, and this led to field lengths being measured as less than zero. Bishop and Henry (10) also noted this. For long, narrow fields, the use of width instead of area could be misleading, but such fields were infrequently encountered, whereas "negative area" fields were common.

DIRECTION SELECTIVITY AND PREFERRED DIRECTION. A cell displays direction selectivity if its response (in spikes per second) to one direction of stimulus movement is at least twice that to the opposite direction. The direction of stimulus movement eliciting the greatest response in such cells is the preferred direction.

ORIENTATION RANGE. The total angle of stimulus orientations to which a neuronal response could be elicited is the cell's orientation range. This value is roughly 4 times the value of the half-width at half-maximum response used by other workers to express orientation selectivity (19, 20, 37, 42, 48).

ORIENTATION SELECTIVITY. This is inversely related to orientation range. That is, a neuron which responds to a wide range of stimulus orientations has poor orientation selectivity, and vice-versa.

PREFERRED ORIENTATION. This is the stimulus orientation which evokes the best response (in spikes per second, unless otherwise indicated) from the cell. Our determination of preferred stimulus orientation for each neuron was usually indistinguishable from the orientation at the center of the orientation range.

OPTIMAL SPEED. This refers to the stimulus speed which evokes the best neuronal response. From histogram data, this best response can either be spikes per second or spikes per stimulus. With hand-plotting techniques, however, we probably measured optimal speed on the basis of a combination of spikes per second and spikes per stimulus (cf. ref 35).

PEAK RESPONSE. A modified version of the criteria of Bishop et al. (9) was used to measure peak neuronal response levels from histogram data. That is, spikes per second were averaged from the highest five bins within the receptive field. These bins did not have to be consecutive, and this allowed for a more representative measure from the brief, multiple peaks frequently encountered in complex cell histograms.

OCULAR DOMINANCE. Five classes were used to describe the relative excitatory influence of stimuli to either eye for each neuron. Class 1, driven by contralateral eye only; class 2, binocular but dominated by contralateral eye; class 3, equally driven by either eye; class 4, binocular but dominated by ipsilateral eye; class 5, driven by ipsilateral eye only.

RESULTS

Classification of units

Cells were classified as simple, complex, hypercomplex, etc., on the basis of the moving slit criteria of Pettigrew et al. (35) and Sherman et al. (42). Many were also classified by the criteria of Hubel and Wiesel (24). Hypercomplex cells were distinguished by their reduced responsiveness as the stimulus length was increased beyond the excitatory zone in one or both directions (10, 14, 25, 36). For simple and complex cells, the criteria are noted below in order of decreasing reliability (see ref 42 for details). *1.* Every simple and no complex cell has inhibitory sidebands flanking the discharge region (see Fig. 1 and ref 42). *2.* Leading- and trailing-edge fields (see definitions in METHODS) in simple cells are usually separated spatially, while in complex cells they overlap (42). *3.* At matched eccentricities, complex cells generally display poorer orientation selectivity than do simple cells (37, 48). *4.* At matched eccentricities, complex cells tend to have larger fields than do simple cells (35). *5.* At matched eccentricities, complex cells are relatively more responsive to higher stimulus speeds than are simple cells (32, 35).

The last three of the above criteria—field size, optimal stimulus speed, and orientation range (32, 35, 37, 48)—were derived from fields in or near the area centralis. As shown below, these parameters for cortical cells increase with increasing eccentricity, and thus they could not be used to classify peripheral fields. On the average, however, complex cells retain their relatively larger field size, higher optimal speed, and greater orientation range within each eccentricity group. Yet, because these properties for simple cells with peripheral fields often fall within the range of properties for more central complex fields, the position of each receptive field must be considered when using these criteria. As we have noted elsewhere (42), criteria

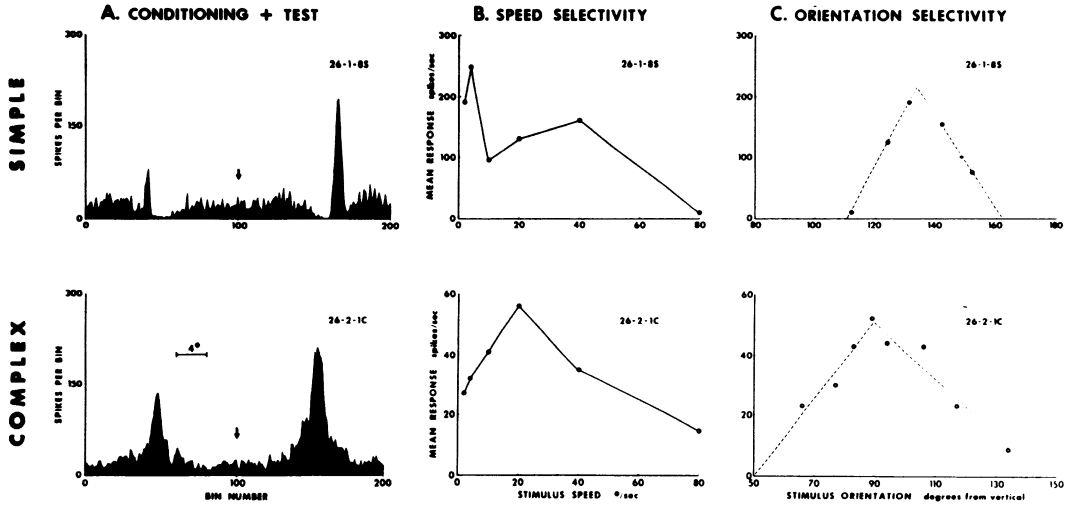

FIG. 1. Comparison of a typical simple and a typical complex cell showing receptive-field differences in sideband inhibition, speed selectivity, and orientation selectivity. The simple field (cell *26-1-8S*) was located 30° from the area centralis while the complex field (cell *26-2-1C*) was located 17° from the area centralis. The simple cell was unusual because its elicited discharge rate was much higher than typical for this cell type (35, 42). *A:* monocular conditioning of the simple cell by using two asynchronous stimuli, only one of which (test stimulus) was in synchrony with the histogram analyzer (9). This allowed the background activity to be artificially increased which, in turn, delineated the inhibitory zones next to the excitatory zone. The test stimulus was 1.0° wide by 10° long moving at 2°/s. The complex cell displayed spontaneous discharge and our study required only the test stimulus which was 0.5° wide by 10° long moving at 2°/s. Each 100 bins represent one direction of movement for the stimulus, and the arrow indicates the stimulus turn-around position. *B:* mean response for each unit determined at various stimulus speeds. Here, the stimulus for each cell was 6° wide by 10° long. *C:* mean response for each unit determined at various stimulus orientations. Stimulus speeds were 4°/s for the simple cell and 2°/s for the complex cell; the shapes were the same as in *B*.

based on inhibitory sidebands and single-edge field separation were invariant with eccentricity, and thus distinguish cortical cells with fields at all eccentricities.

A brief outline of our classification scheme for peripherally located fields follows (42). Within 10° of area centralis, fields were routinely classified by standard criteria (24, 35, 37, 48). We noted that within this region every simple field had inhibitory sidebands and the vast majority had spatially offset single-edge fields. No complex field in this central area had inhibitory sidebands and, except for a few cells which had only one detectable single-edge field, each had single-edge fields which overlapped. We found that peripheral fields with inhibitory sidebands (i.e., simple cells) nearly always had offset single-edge fields; fields without inhibitory sidebands (i.e., complex cells) had superimposed, single-edge fields. At matched peripheral eccentricities, the presumptive simple cells had better orientation selectivity, smaller fields, and lower optimal speeds than did complex cells. Finally, in this and another study (42), over 70 neurons (mostly with fields near area centralis but many with peripheral field locations) were also classified by the Hubel and Wiesel (24) criteria using stationary, flashing slits, and in no single case did a discrepancy arise between classification schemes. Thus, we depended mostly on the first two criteria listed above to distinguish between peripherally located simple and complex fields: these and/or the Hubel and Wiesel (24) criteria were applied to every peripheral receptive field. We did not systematically apply the original Hubel and Wiesel (24) tests to all cells because we found that many cortical neurons were unresponsive or poorly responsive to stationary, flashing stimuli, but nearly all responded to appropriate moving stimuli (42). While we have chosen the terminology of Hubel and Wiesel (i.e., "simple" and "complex") often without adhering to their criteria, we feel justified in doing so for reasons given above, and we feel this preferable to adopting new terminology.

Our sample of cortical units consequently consisted of 98 simple, 80 complex, and 21 hypercomplex cells. In addition, there were 22 presumptive geniculate fibers, two nonoriented cells, and 13 unmapped fields, giving a total of 236 neurons. Quantitative data in the form of

poststimulus time histograms were routinely taken for the cortical neurons. Many other neurons were held for insufficient time to allow unambiguous classification (testing for inhibitory sidebands is time consuming) and, except for Fig. 14, none of these are discussed further.

The 22 units classified as geniculate fibers were monocularly driven, had on- or off-centers with antagonistic surrounds, had moderate to high spontaneous activity, showed no orientation or direction selectivity, and had fiberlike action potentials (6). Two cells were classified as cortical nonoriented neurons since, in addition to lacking orientation selectivity, one was binocularly driven and the other had a receptive-field center which was unusually large (6.5°) for a geniculate neuron. Both of these neurons had cell-like action potentials (6). It is possible, even using these criteria, that these two neurons may have been fibers from the interlaminar layers of the lateral geniculate nucleus (39). While many of our cortical neurons responded to a very wide range of stimulus orientations, all but these two had a distinct preference for certain orientations. In addition to the two nonoriented cells, we found four others which responded to stimuli of any orientation, though they responded more briskly to a limited orientation range. Their remaining characteristics were those of complex cells, and they were classified as such. Whether or not these four are included in our complex cell population makes no fundamental difference to the conclusions derived below. Joshua and Bishop (27) classified 28% of cortical neurons as nonoriented; perhaps many of these included neurons with preferred orientations despite a large orientation range. Otherwise, the discrepancy between our data and theirs is difficult to explain.

Because cortical neurons have a columnar organization with respect to many receptive-field properties (24), a vertical electrode penetration typically encounters cells with similar properties. It is sometimes difficult to define the first field in a penetration, but successive fields are generally easier to plot. However, in our experiments, cells for which no receptive fields could be plotted were not always found at the start of a penetration. Most unmappable cells (11 of 13) were recorded between two other cells whose fields were well defined, and this should have made it relatively easy to find any fields present. Since we usually spent no more than 30–60 min attempting to locate a cell's receptive field, we cannot say definitely that these cells lacked responsive receptive fields. It should be emphasized that these 13 cells displayed no responses to either stationary, flashing stimuli, or moving stimuli. In the remainder of this paper we shall deal only with simple, complex, and hypercomplex cells.

Area centralis position

This study largely concentrated on the receptive-field changes with eccentricity from the area centralis. The center of the area centralis (fixation point) on the tangent screen was taken as 7.5° vertical and 16.0° horizontal to the center of the optic disc (27, 33). The eccentricity position of each of our fields has been calculated with respect to this inferred location of the area centralis.

For the 98 simple, 80 complex, and 21 hypercomplex cells, Fig. 2 shows the cell types, receptive-field locations, and preferred orientations; Fig. 3 shows the preferred directions of movement for the subset of 105 neurons (53%) with direction selectivity. Directionally selective neurons included 47 simple cells (59%), 45 complex cells (46%), and 13 hypercomplex cells (62%). We saw no clear relationship between eccentricity and either preferred orientation (Fig. 2) or direction (Fig. 3). Although Palmer and Rosenquist (34) found that most cells of the superior colliculus preferred stimuli moving away from the area centralis, they also reported no such preference among cortical neurons projecting to the colliculus.

Since the position of the area centralis, with respect to the optic disc, varies slightly among cats (27), there were probably errors of up to 2° in the calculated eccentricity values. In order to compare receptive fields at different eccentricities, we have grouped each field (based on the position of its geometric center) into one of five eccentricity ranges (cf. Figs. 9 and 13). These ranges are smaller nearer the area centralis than the periphery (i.e., 0–5° versus 20–45°). Therefore, with an error of up to 2°, we probably incorrectly grouped more neurons centrally than peripherally. This would lead to greater underestimation of monotonic changes with eccentricity for central than for peripheral receptive fields.

Simple and complex cells

Simple and complex cells predominated in our sample, and four characteristics of their receptive fields changed with eccentricity. These were their relative ratio, size, orientation selectivity, and preferred speed. Preferred orientation showed no appreciable change with eccentricity, and ocular dominance changed only near the edge of the binocular segment (i.e., at $> 30°$ eccentricity).

SIMPLE/COMPLEX RATIO. Figure 4 plots for

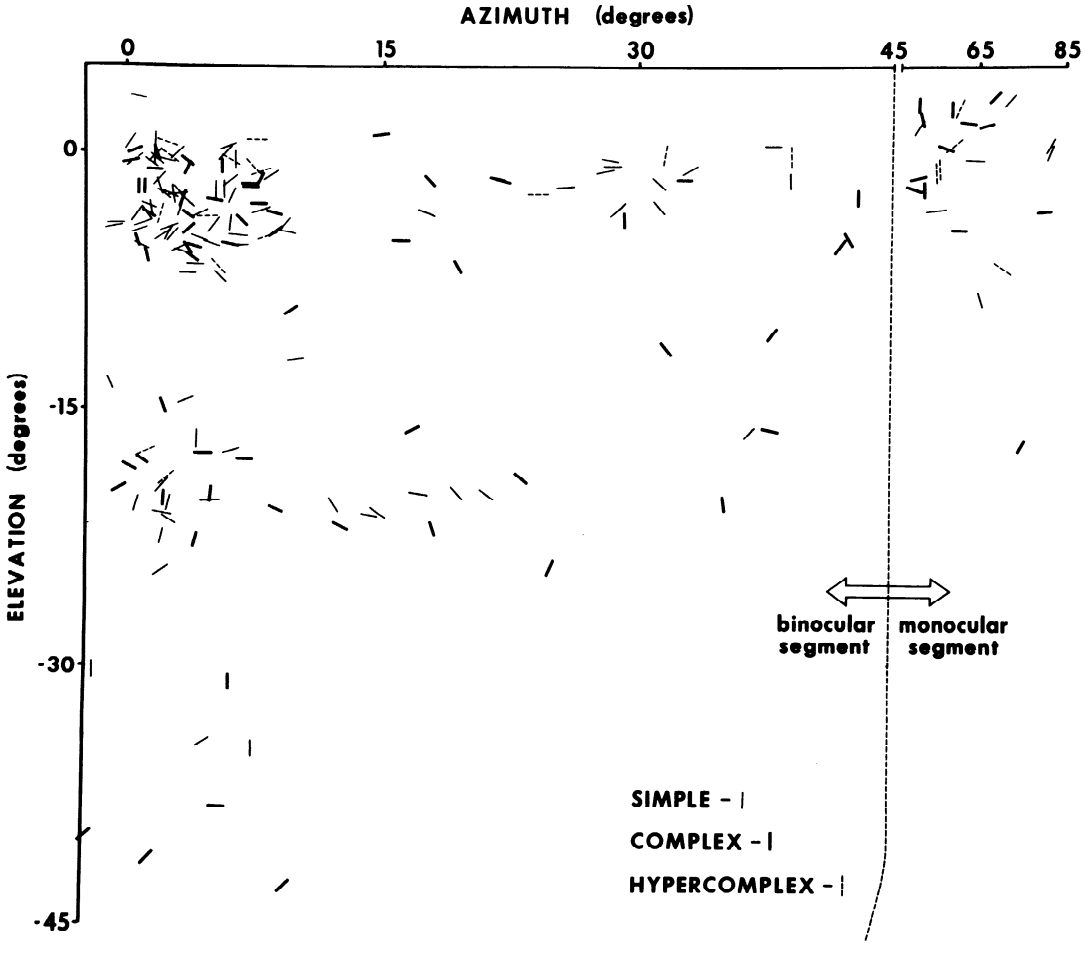

FIG. 2. Positions, types, and preferred orientations for all of the simple, complex, and hypercomplex receptive fields of this study. All fields from the left hemifield are presented as if they were at the corresponding location in the right hemifield. The border drawn between the monocular and binocular segments is that used by Sherman et al. (41). The preferred orientations are indicated by short line segments whose centers represent the receptive-field centers. Note both the lack of obvious pattern in the preferred orientations as well as the lack of change with eccentricity in average preferred orientation.

each eccentricity group the percentage of complex cells calculated from the combined total of simple and complex cells (other types were excluded). The figure also plots analogous data from lateral geniculate neurons (23) showing a similar change with eccentricity in the relative X- and Y-cell distribution.

SIZE. Figure 5 and Table 1, both of which were derived from hand plots, show that receptive fields become much larger as their positions become more eccentric. However, this change was considerably more evident for complex than for simple cells (Fig. 5*A*, *B*). Relative to complex cells, therefore, simple cells have fairly constant receptive-field sizes throughout the visual field. Note that the average size of cortical fields increases with eccentricity at a slope greater than that for either complex or simple cells; this is obtained because there is an increase in the proportion of complex fields at greater eccentricities as well as an increase in the size of the complex fields.

The receptive-field sizes derived from histograms correlated well with hand-plotted data though, as expected, the histograms revealed weak responses not shown by hand plotting. All but 2 of 31 field widths measured by histograms were consequently larger than those determined by hand plotting (Fig. 6).

ORIENTATION RANGE. The range of orientations over which each cell continued to respond also increased with eccentricity (Fig. 7). Since

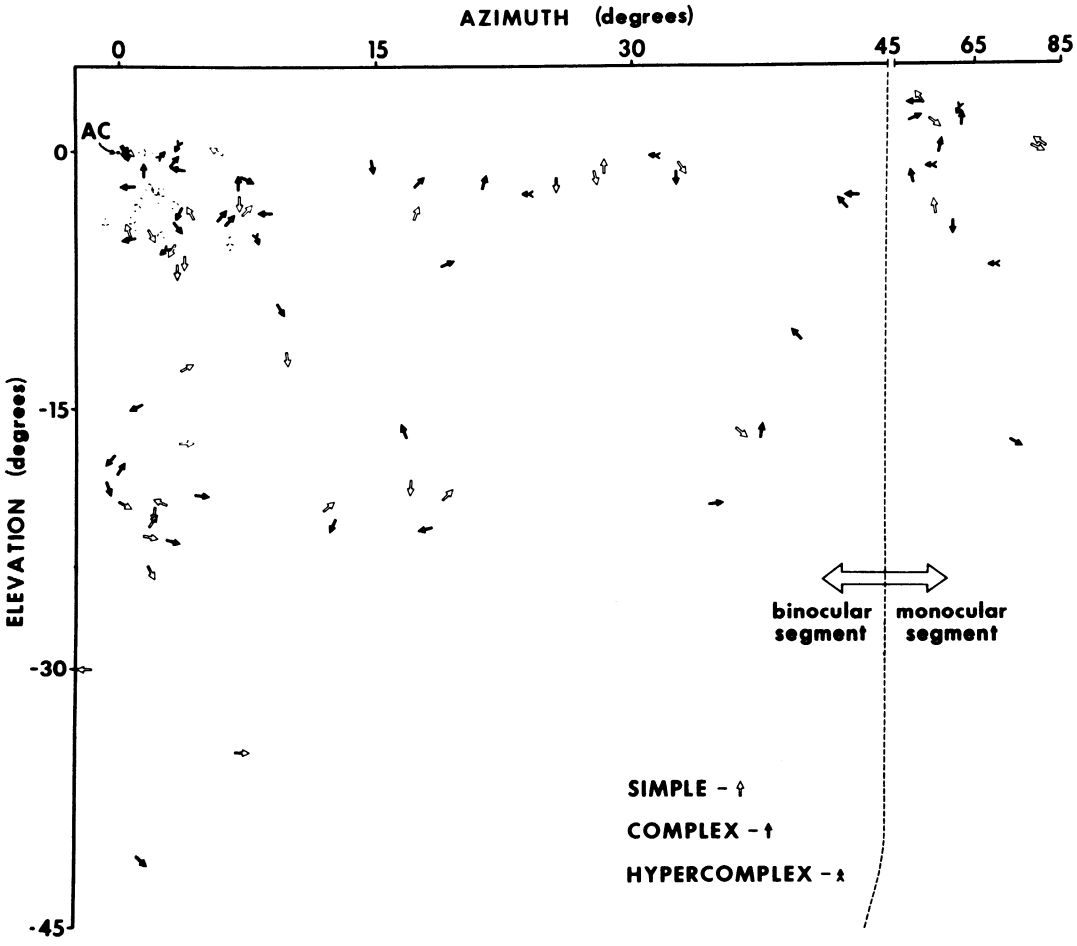

FIG. 3. Preferred directions of movement for the subset of 105 cells in Fig. 2 which demonstrated clear direction selectivity (see METHODS). No obvious relationship occurred between the pattern of direction selectivity and any portion of visual field (i.e., area centralis; cf. ref 34). AC, center of area centralis.

we found no cells which had orientation ranges between 180 and 360°, we felt that the four complex cells with orientation ranges of 360° were special cases and we did not include them in our averages for Fig. 7. None of these four fields were located within 10° of the area centralis. Again, note that complex cells displayed a greater eccentricity-related change in orientation selectivity than did simple cells. Figure 7 was drawn from hand-plotted data, but a satisfactory correlation existed between the orientation ranges measured by hand-plotting and histogram methods (Fig. 8). Seven cells were used in this comparison, with a mean difference of 16% between the methods.

PREFERRED ORIENTATION. To standardize our method for obtaining the value of the preferred orientation and to help minimize biases, such as the experimenter's tendency to orient stimuli vertically or horizontally which might produce a slight surplus of cells with these preferred orientations (20), we took the middle of the range of effective stimulus orientations as the pre-

TABLE 1. *Receptive-field widths of simple and complex cells within each eccentricity group*

Eccentricity, deg	Simple Field Widths, deg	Complex Field Widths, deg
0–5	0.72 ± 0.46 (28)	1.58 ± 0.84 (11)
5–10	0.89 ± 0.43 (25)	1.96 ± 1.35 (15)
10–20	1.17 ± 0.75 (10)	3.07 ± 1.93 (13)
20–45	1.07 ± 0.63 (27)	3.43 ± 2.20 (27)
45–90	1.37 ± 0.87 (8)	4.87 ± 4.50 (14)

Values are means ± SD. Numbers in parentheses represent the numbers of fields from which each set of values was derived.

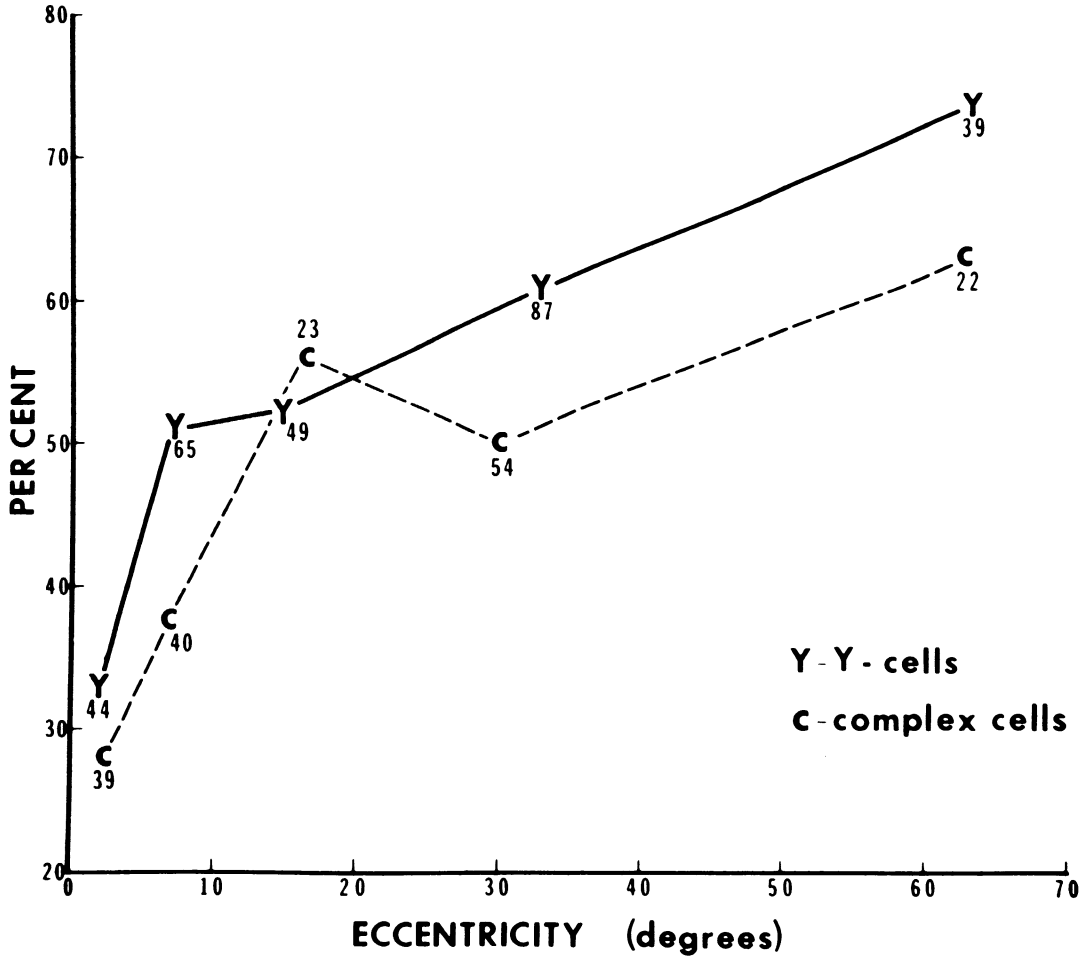

FIG. 4. Change with eccentricity in percentage of complex fields relative to simple fields. Each point represents the percentage of complex cells derived from the total number of simple and complex cells located within each of the five eccentricity groups (see text for these groups). The number of cells in each group is shown. Also shown are previously published data (23) from lateral geniculate neurons which gives the percentage of Y-cells similarly derived from the total number of X- and Y-cells within each eccentricity group.

ferred orientation (see METHODS). This may not always represent the preferred orientation (37) and, furthermore, the preferred orientation derived from histograms can vary slightly in time (19). With these limitations noted, our estimates of the preferred orientations did not appear to change with eccentricity (Fig. 9), since no statistically significant differences occurred among the eccentricity groups.

An "oblique effect" has been described for many animals in that thresholds for the detection of stimuli oriented near the principal (i.e., vertical and horizontal) meridians are lower than those for obliquely oriented stimuli (2). Rose and Blakemore (37), in a study of cat cortical neurons, found a possible correlation to this presumed oblique effect: namely, that orientation selectivity of simple cells was inversely related to the angular distance of the preferred orientation from the principal meridians. Note that this result cannot be explained in terms of the potential bias noted above (20). No such correlation was noted for complex cells. However, our data from the same visual area as that used by these authors (0–10°) shows no such significant correlation (Fig. 10). A significant difference exists between our sets of data ($P < 0.01$ on a transformation of r to z values), and we cannot easily explain this. Perhaps cats used by Rose and Blakemore had early environments relatively rich in stimuli along the prime meridians (12) while ours did not; our cats were ob-

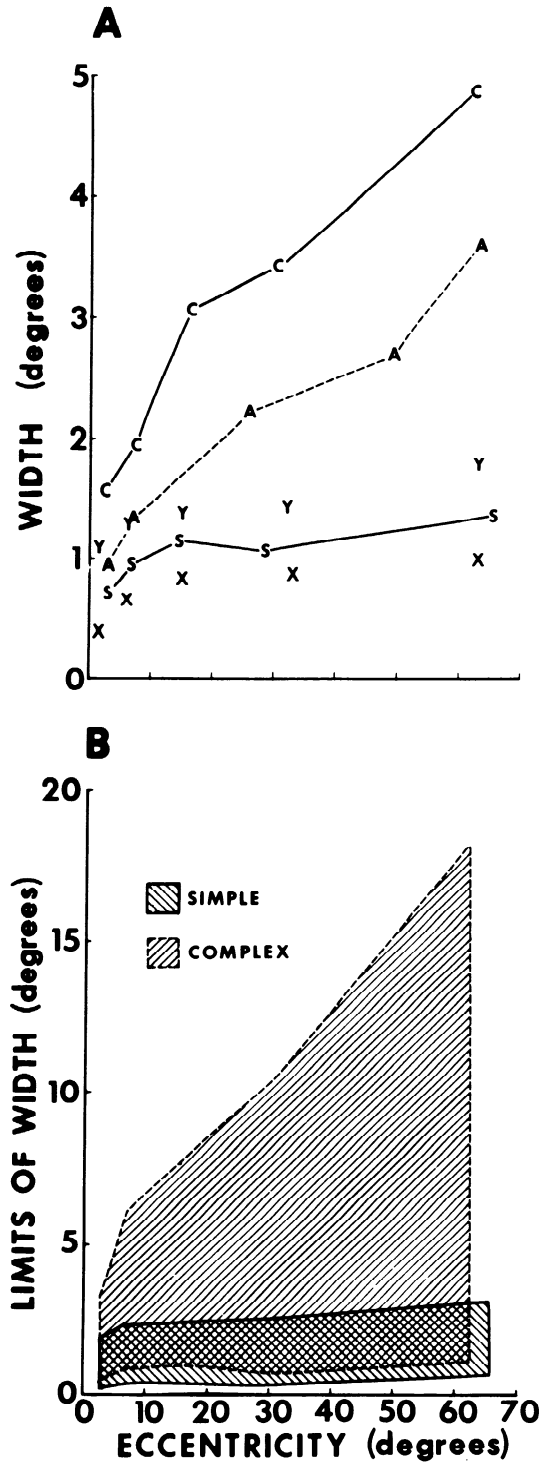

FIG. 5. Change of receptive-field width with eccentricity; data taken from hand-plotted fields. *A:* average widths in each of the five eccentricity groups for simple cells (S), complex cells (C), and the combined average for simple and complex cells (A). The data of Hoffmann et al. (23) for the average receptive-field center diameters of geniculate X- and Y-cells (X and Y, respectively) are also shown. *B:* total range or extent of simple and complex receptive-field widths in each eccentricity group.

tained as adults and we do not know the nature of their early environment. Although not illustrated, our data from complex and hypercomplex cells also showed no significant correlation for these parameters. Our results do support other evidence (11, 25, 27) that the cat does not have an oblique effect (however, see ref 20, 35).

SPEED SELECTIVITY. Consistent with the previous parameters, the stimulus speed which elicited the best response (in terms of spikes per second) increased with eccentricity (Fig. 11). Again, complex cells showed a greater increase than did simple cells. Figure 11 must be viewed with caution since it is derived from hand-plotted data and the correlation between hand-plotted and histogram data for optimal stimulus speed is relatively poor (Fig. 12). Of the 23 points in Fig. 12, 14 agree to within 3°/s, but these are for the slowest stimulus speeds (<20°/s). At higher speeds, hand-plotted estimates considerably undershoot histogram estimates. This probably reflects the weakness at high speeds of the hand-plotting method in distinguishing changes in firing rate from changes in spikes per stimulus (35). Both because of this greater underestimate of the higher preferred speeds with hand plotting and also because preferred speeds increase with eccentricity, Fig. 11 probably underestimates speed preferences for peripheral fields more than for central ones, and thus the rate of change with eccentricity is greater than shown in Fig. 11.

OCULAR DOMINANCE. Hubel and Wiesel (24) have described the binocular influences (ocular dominance) for cells of the central 10° of the visual field. We found essentially the same distribution of binocular influences for the central portion and throughout the binocular portion of the cat's visual field (Fig. 13). There were no differences in ocular dominance among the four eccentricity groups in the binocular segment ($P > 0.10$ on a χ^2 test), in agreement with the findings of Joshua and Bishop (27). However, we had the impression that the contralateral eye dominated receptive fields more strongly near the edge of the binocular segment. For example, at 30–40° eccentricity, 9 of 18 receptive fields were class 1, as opposed to only 22 of 131 with fields 0–30° eccentric, a significant difference ($P < 0.01$ on a χ^2 test). This could obtain from uncertainty in the location of the border

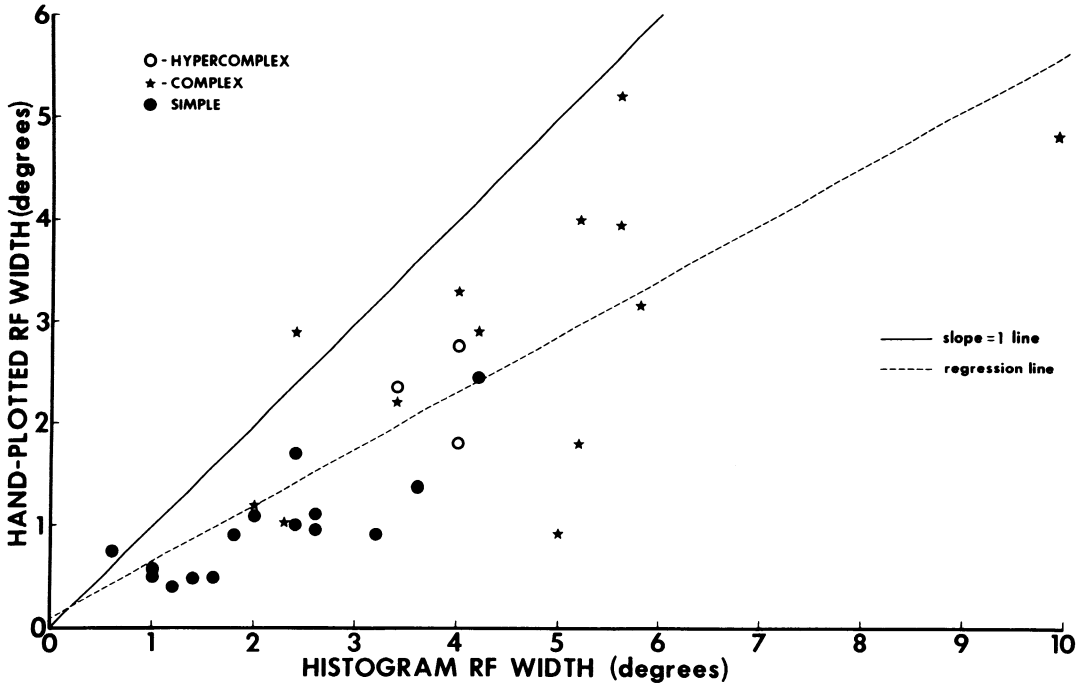

FIG. 6. Comparison of hand-plotted versus histogram-determined receptive-field (RF) widths. The width of each simple receptive field is that of the widest single-edge discharge field (see METHODS). The linear regression line for these 31 points has a slope of 0.55 ($r = 0.80$, $P < 0.001$). Note that, as expected, almost all of the hand-plotted widths are smaller than those widths determined by histograms.

between monocular and binocular segments and/or an irregular shape for this border.

Albus (1) has recently reported a change in ocular dominance with eccentricity for the receptive fields of simple but not complex cells; namely, simple fields within the central 4° are mostly driven by only one eye, whereas more peripheral simple fields are binocularly driven. We found no statistical difference between the ocular dominance distribution of simple and complex fields, nor did we find evidence for the change with eccentricity for simple fields as reported by Albus (1). No explanation can be offered now for this discrepancy beyond a restatement of our uncertainty (roughly 2°) in locating the area centralis. It may be that most of our simple fields included in the 0–5° grouping were indeed not within 4° of the area centralis.

Hypercomplex cells

A cell was classified as hypercomplex if its response to a short slit was clearly better than that to a longer slit (25), and 21 cells were classified as hypercomplex. They were found throughout the visual field including the monocular segment. While this number was not enough to draw firm conclusions concerning functional changes with eccentricity, the general trend for these cells was similar to that for simple and complex cells. That is, for the 21 hypercomplex cells we noted larger fields, greater orientation ranges, and faster preferred stimulus speeds at increasing distances from the area centralis; we saw no change with eccentricity in preferred orientation or ocular dominance.

A separation of hypercomplex cells into two groups called type I and type II has been described by Dreher (14). Types I and II hypercomplex cells have receptive fields much like simple and complex cells, respectively, both having the characteristic hypercomplex property of responding better to a stimulus of restricted length. Rose (36) has extended this with the recent suggestion that hypercomplex cells are simply one extreme of continuous spectra for simple and complex cells, each having varying degrees of inhibitory end zones. Thus, he argues that hypercomplex cells are not really a separate class of cortical cell. We noted in the 21 hypercomplex cells of this study that most of the characteristic field properties were much like those of simple or complex cells, and these

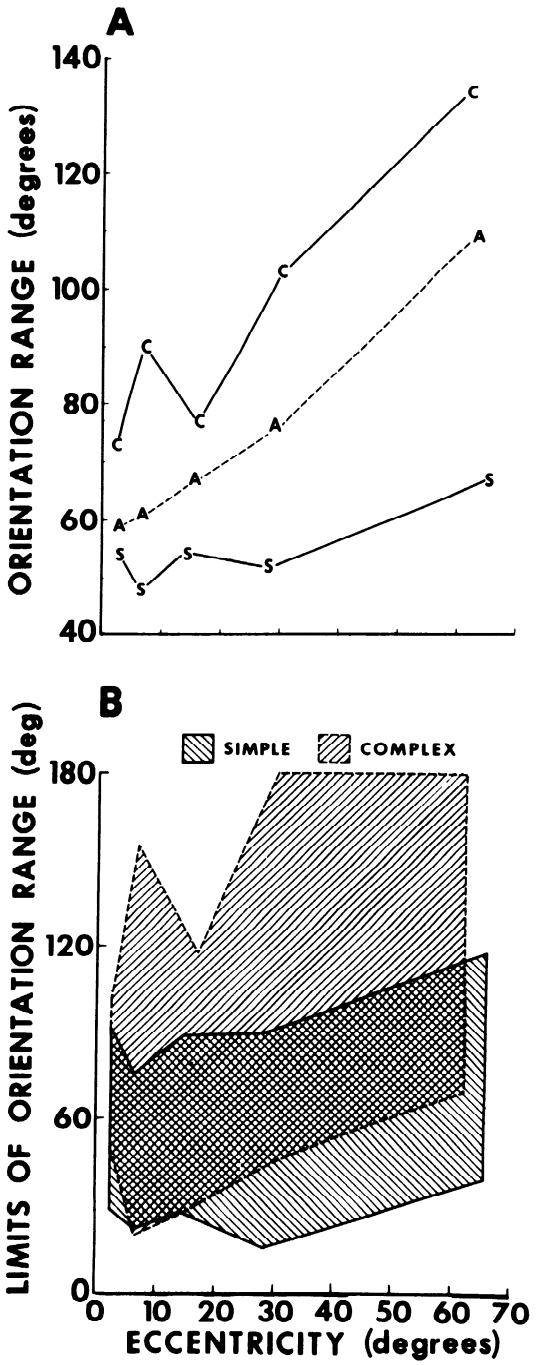

FIG. 7. Change with eccentricity in orientation ranges for simple and complex cells; data from hand-plotted fields. *A:* average orientation ranges in each of five eccentricity groups for simple cells (S), complex cells (C), and the combined average of simple and complex cells (A). *B:* extent of orientation ranges in each eccentricity group among simple and complex cells.

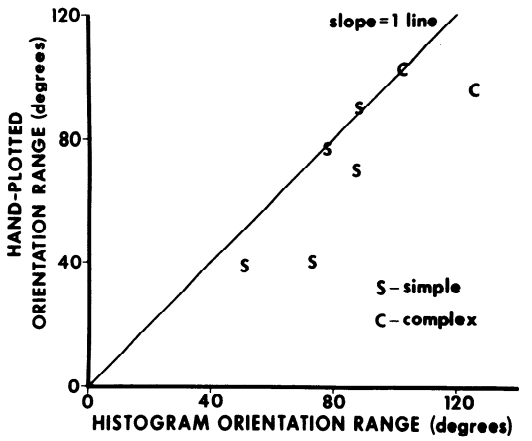

FIG. 8. Comparison of hand-plotted versus histogram-determined orientation ranges. Note that the hand-plotted ranges are either equal to or smaller than the histogram-determined ranges.

properties tended to change with eccentricity as did those of simple and complex cells. Ten of the cells classified as hypercomplex were like Dreher's type I cells; eight were like type II; two were lost before they could be categorized; and one had ambiguous features. Although not quantitively studied, there appeared to be a gradation of the responses among different hypercomplex cells—some cells would not respond at all to long stimuli, others responded nearly as well to long as to short stimuli, and the rest responded in an intermediate manner. Thus, our findings tend to support conclusions of Dreher (14) and Rose (36), and this raises the possibility that only two major classes of cells—simple and complex—reside in cat striate cortex.

Receptive fields in monocular segment

GENERAL PROPERTIES. It was apparent after only a few penetrations in the area of the splenial gyrus that the characteristics of receptive fields in the monocular segment of the visual field were qualitatively similar to those of the more central, binocular area. We found simple, complex, and hypercomplex cells; the receptive fields of these neurons had orientation ranges, optimal speeds, and sizes which were slightly larger on the average than more central receptive fields. For example, the largest receptive field seen in our study was a complex field located 53° lateral to the vertical midline with a width of 18°. Its orientation range was 180°, and it responded to stimulus speeds well over 200°/s. Furthermore, simple cells in the monocular segment showed clear inhibitory sidebands, as did their more central counterparts (see also

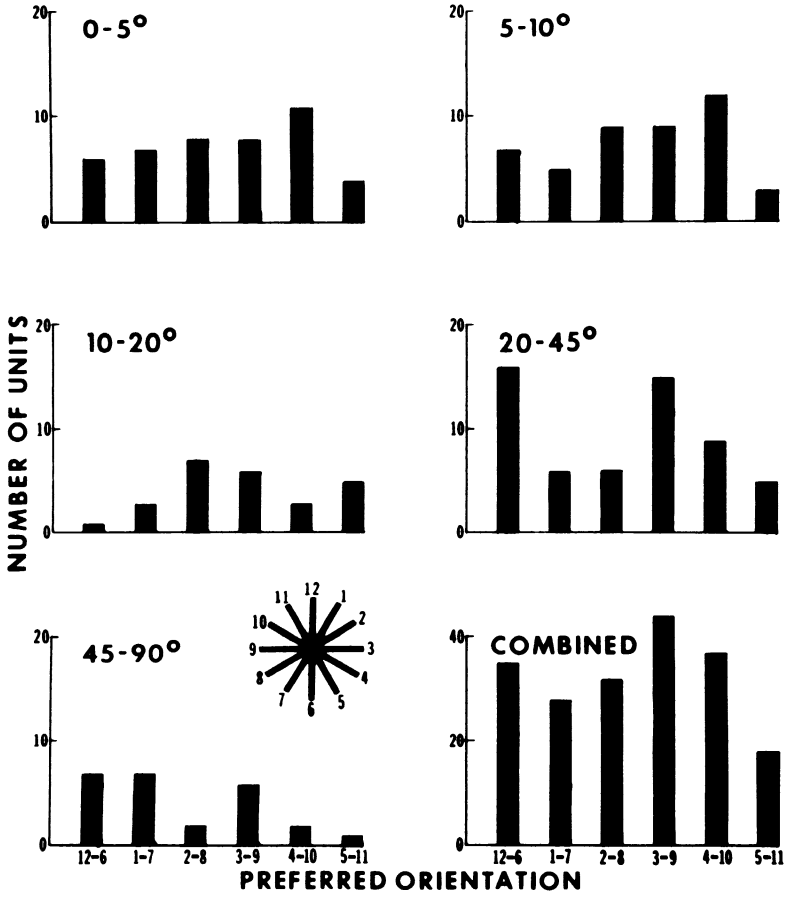

FIG. 9. Numbers of preferred orientations among the cortical cells for each of the five eccentricity groups plus a total for all cells. A preferred orientation of horizontal is a 3-9 position shown by the inset clockface, while vertical is 12-6, etc.

ref 42). The most peripherally located receptive field studied was a simple field 82° lateral to the vertical meridian, while the most lateral, binocular receptive field was 42° from the vertical meridian (see Fig. 1*A*). There were three monocular fields between 42 and 45° lateral to the vertical meridian, and these may have been in the monocular visual field. These three are thus represented by dashed lines in the upper portion of class 1 cells in the 20–45° group of Fig. 12. Our 45° separation point for the binocular and monocular portion of the visual field approximately corresponds to the separation shown by behavioral studies (40, 44) and used by Sherman et al. (41) for their study of geniculate neurons (see Fig. 2). There were other binocular units located up to 44° from the area centralis, but being low in the field they had vertical components which placed them within 42° of the vertical midline.

PREFERRED ORIENTATION. As indicated by Figs. 2 and 9, the population of fields in the monocular segment displayed the full range of preferred orientations. These data conflict with those of Kalia and Whitteridge (28) who reported that over half of the neurons in the cat's monocular segment of striate cortex preferred horizontally oriented stimuli. We are unable to explain this significant discrepancy ($P < 0.001$ on a χ^2 test).

SPLENIAL VISUAL AREA. Figure 14 reconstructs an electrode penetration placed at a 20° angle from vertical in order to sample cells sequentially with fields from the vertical meridian to the monocular segment. Nearly all of our successful explorations of the monocular segment were histologically verified and found to correspond closely to the cortical tissue as indicated in Fig. 14. Kalia and Whitteridge (28)

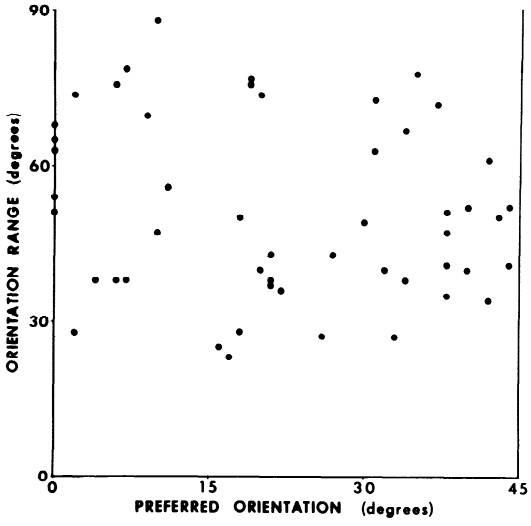

FIG. 10. Relationship between preferred orientation and orientation range for 50 simple cells (see text). The orientation range for each cell is plotted against the angular separation between the cell's preferred orientation and the nearest prime meridian (vertical or horizontal). Thus, points along the horizontal axis of the graph must fall between 0 and 45°. There is no statistically significant correlation between these two parameters ($r = -0.18$; $P > 0.1$).

suggest that splenial cortex also contains a nonstriate cortical area, the "splenial visual area." They reported that, as successive penetrations were placed mediolaterally through splenial cortex, field positions progressed to a peripheral limit and began to reverse stepwise toward the area centralis. We did not find evidence for such a reversal. We must emphasize, however, that if the splenial visual area were small we could easily have missed it.

Receptive-field correlations

Table 2 summarizes the major correlations of receptive-field characteristics from our data. Each of the two parts separately summarizes these correlations for simple and complex cells. Note that for complex receptive fields all but one of the correlations are statistically significant. Better correlations exist among the complex cell data than among those of simple cells. This may obtain because complex fields are actually less complicated, since they lack the inhibitory sidebands and offset edge discharge zones of simple fields.

The correlation of width with optimal speed in Table 2 agrees with the data but not the conclusion of Pettigrew et al. (35). They contend that there is no clear correlation for the data plotted in their Fig. 7 (receptive-field width versus optimal speed). We concluded from their data that a significant correlation existed ($r = 0.50$, $n = 90$, $P < 0.001$). However, the large amount of variation still unaccounted for tends

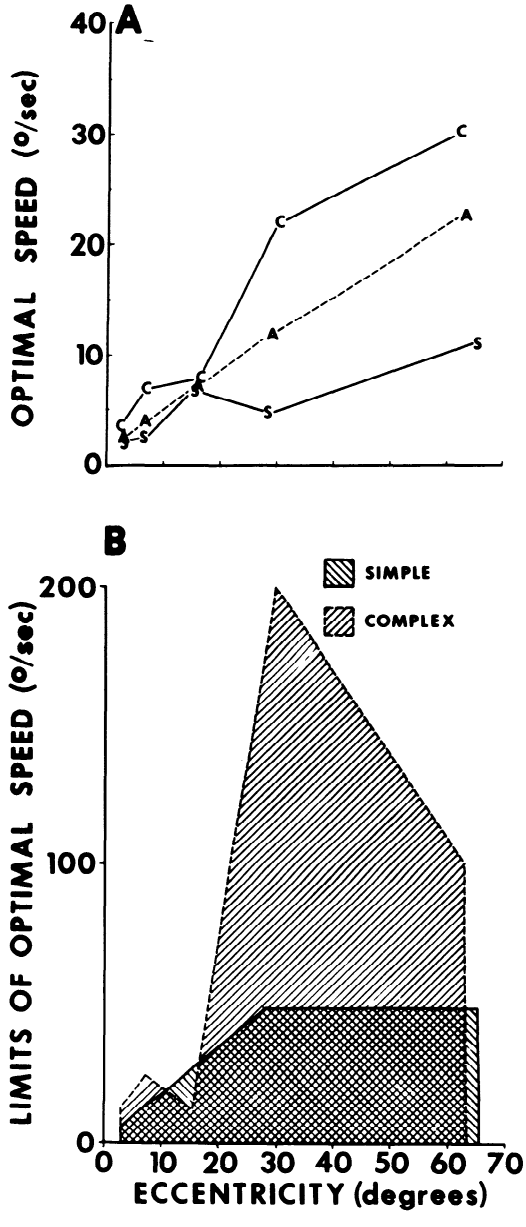

FIG. 11. Change with eccentricity in optimal stimulus speed for simple and complex cells; data from hand-plotted fields. *A:* average optimal speeds in each of the five eccentricity groups for simple cells (S), complex cells (C), and the combined average of simple and complex cells (A). *B:* extent of optimal speeds in each eccentricity group among simple and complex cells.

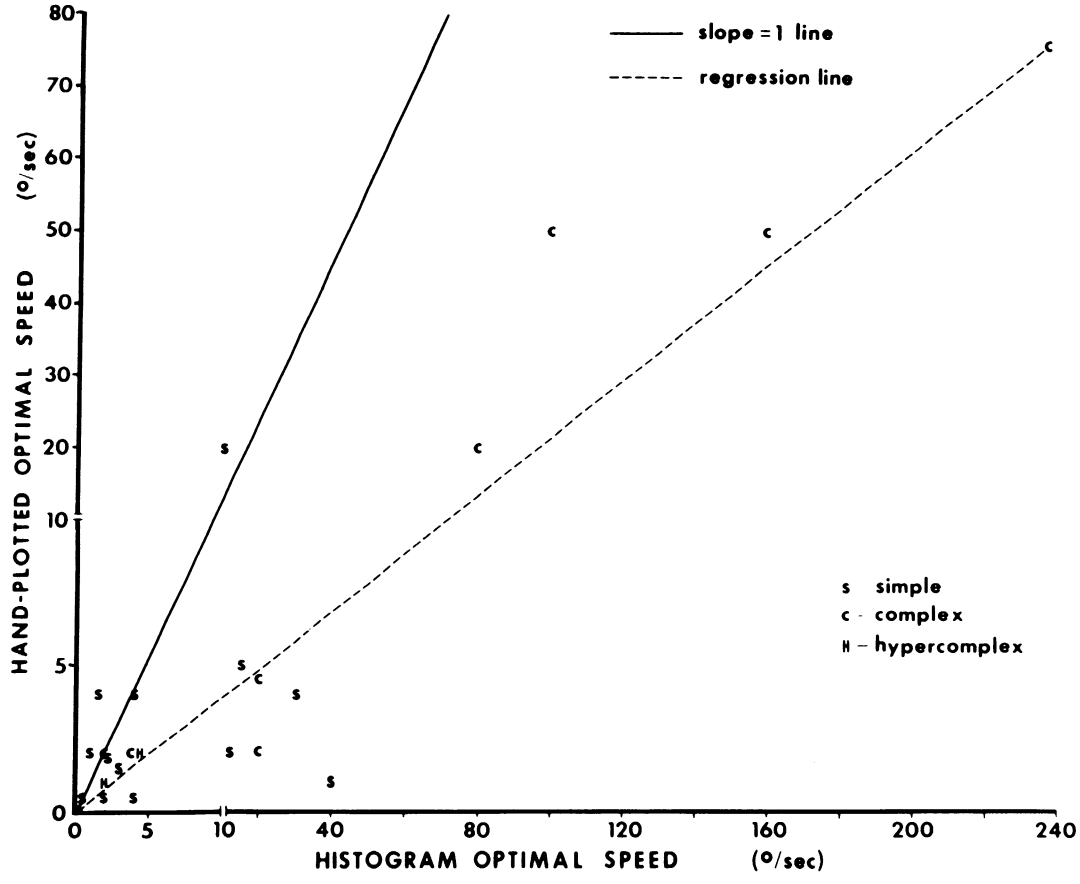

FIG. 12. Comparison of hand-plotted versus histogram-determined optimal speeds. Note that at the higher stimulus speeds (>20°/s) the hand-plotted estimates were always less than the histogram-determined speeds (see text).

to obscure this statistically significant correlation.

DISCUSSION

Changes with eccentricity

In this study of the receptive-field properties of cells located over a large portion of the cat's striate cortex, we have extended and confirmed the reports of previous authors that, with increasing eccentricity, there is a steady average increase of field size (24, 27), orientation range (27), and optimal speed (27). Also, simple fields become relatively less numerous with increasing eccentricity. It is certainly not surprising that peripheral receptive fields of neurons in the cat's striate cortex are not as finely tuned as those representing central vision. It is known that human acuity (15) and thresholds for stimulus speed (30) decline with increasing eccentricity. Although, to our knowledge, no analogous data exist for the cat, similar changes with eccentricity seem likely. For instance, Berkley (4) has concluded from cortical lesion studies that the cat's peripheral vision has less capacity to discriminate line orientation than does its central vision. The decreasing percentage of simple cells (whose fields are relatively more finely tuned) as well as the decreased specificity of all cells for stimulus size, orientation, and speed would contribute to this change with eccentricity. Despite these large quantitative changes in receptive-field properties with eccentricity, there were no obvious qualitative changes throughout the visual field, including the monocular segment.

Differences between simple and complex cells

Our data supplement previous studies (20, 24, 32, 35, 37, 48) which suggest that simple cells, on the average, have smaller fields, prefer

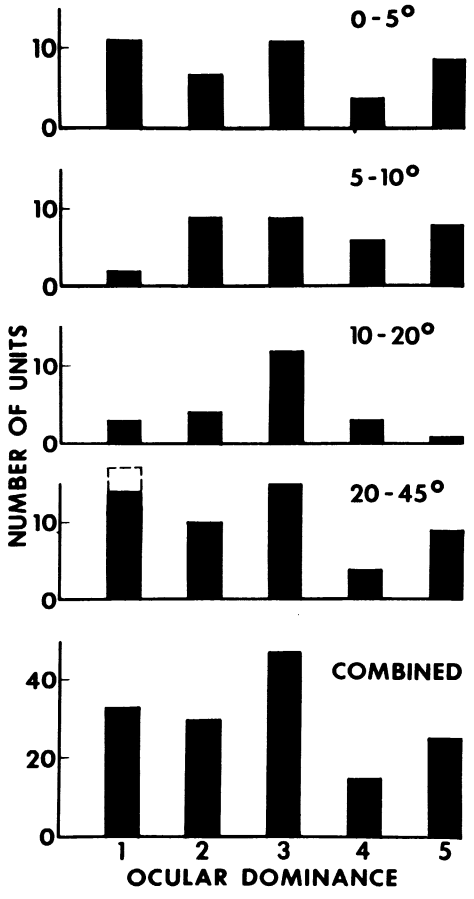

FIG. 13. Ocular-dominance distribution for each of the four eccentricity groups (monocular segment group excluded) plus the total for all units. For these eccentricity groups, there was no statistically significant change with eccentricity in ocular dominance ($P > 0.1$ on a χ^2 test). However, there was evidence for contralateral eye dominance near the edge of the binocular segment (see text). The dashed portion of class 1 cells in the 20–45° eccentricity group represents cells between 42 and 45°, which may have been in the monocular segment of the visual field. Ocular dominance classes are defined in METHODS.

slower stimuli, and display greater selectivity for stimulus orientation than do complex cells. Simple fields also have inhibitory sidebands not found in complex fields and they have more separation in their edge discharge fields than do complex cells (42). Our cell sample not only confirms these observations in the central 10° of visual field, but it also indicates that at matched locations many of these differences actually increase with eccentricity (see Figs. 5, 7, 11).

This is partly due to the fact that simple cells, when compared to complex cells, display impressive consistency in receptive-field properties throughout the visual field. Figure 15 elucidates this difference between cell types by plotting the linear regression lines for changes in field properties with eccentricity. The vertical scales have been adjusted so that the Y-intercepts coincide for the simple cell regression lines. The resultant pairs of regression lines for simple and complex cells are significantly different ($P < 0.05$, $P < 0.001$, and $P < 0.001$, respectively, for width, orientation range, and preferred speed) on a t test for slope differences. These data suggest fundamental differences between simple and complex cells, differences which might be partially explained by hypothetical differences in the nature of their afferentation as described below.

Afferents to simple and complex cells

As shown by Fig. 5*A*, receptive-field widths for simple cells closely parallel those for geniculate cells at all eccentricities. This is consistent with previous suggestions that one or a few geniculate neurons provide the excitatory input for each simple cell (8, 24, 25). Widths for complex cells, on the other hand, increase more rapidly than those for either simple or geniculate cells. Therefore, whether afferents to complex cells derive from geniculate neurons, simple cells, or a combination thereof (45), this suggests a different pattern of synaptic input for simple cells than for complex cells. One possible explanation is related to the concept of a magnification factor for the lateral geniculate nucleus and visual cortex, M_{LGN} and M_{VC}, respectively.

MAGNIFICATION FACTORS. M_{LGN}, in millimeters per degree, is defined as the linear distance across the geniculate surface required to map 1° of visual field. The neurons included in this region would be all of those whose receptive-field centers are bounded by the 1° of visual field (38). A similar definition applies to M_{VC} (5). Figure 16, which is drawn from data of other studies, shows that M_{LGN} and M_{VC} decrease monotonically with eccentricity in an essentially parallel fashion (or, as plotted, $1/M_{LGN}$ and $1/M_{VC}$ increase monotonically). That is, M_{LGN} and M_{VC} differ at all eccentricities only by a constant factor of approximately 5, which presumably represents the greater volume of cortex devoted to the same visual hemifield. Sanderson (38) has shown that the change in M_{LGN} with eccentricity results from the eccentricity change in retinal ganglion cell density, and presumably the retinal pattern also determines the eccentricity relationship of M_{VC}. Interestingly, S. V. Webb and J. H. Kaas (unpublished observations) found the same retinocortical rela-

TABLE 2. *Correlations for simple and complex cells among various parameters measured in this study*

	Simple Cells				Complex Cells			
	Eccentricity	Optimal mean response	Optimal speed	Orientation range	Eccentricity	Optimal mean response	Optimal speed	Orientation range
Field width								
n	98	18	85	91	80	16	54	65
r	0.32	0.29	0.28	0.17	0.28	0.66	0.53	0.41
P	<.001	>0.1	<0.01	>0.1	<0.01	<0.01	<0.001	<0.001
Orientation range								
n	90	18	81		80	14	47	
r	0.17	−.08	0.09		0.53	0.67	0.56	
P	<0.1	>0.1	>0.1		<0.001	<0.01	<0.001	
Optimal speed								
n	83	12			54	10		
r	0.42	0.15			0.49	0.73		
P	<0.001	>0.1			<0.001	<0.01		
Optimal mean response								
n	18				18			
r	0.11				0.37			
P	>0.1				<0.1			

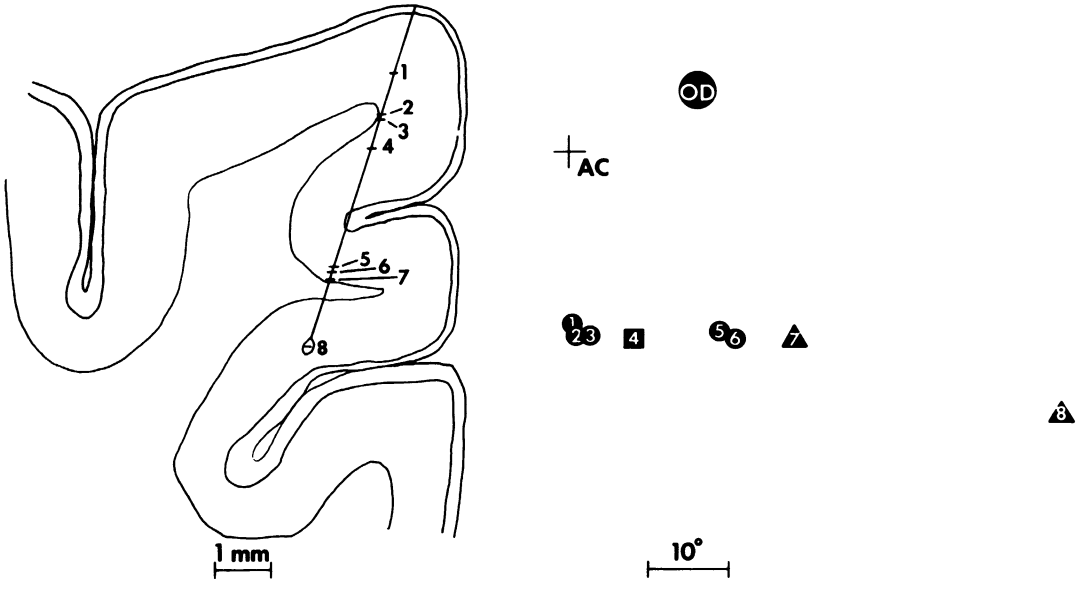

FIG. 14. Reconstruction of electrode position through the coronal plane 8.5 of the left hemisphere. On the left is a camera lucida drawing of a coronal section indicating the electrode track plus positions of each of eight neurons from which receptive-field data were acquired. Note that the electrode entered at a 20° angle from vertical. A stainless steel electrode was used, and the oval-shaped outline at the bottom of the track indicates the stained iron deposit (see METHODS). The eight field locations are indicated on the right in relation to the area centralis (AC) and right optic disc (OD). Among the fields are five simple cells (circles), one complex cell (square), and two cells lost before unambiguous classification could be achieved (triangles). Numbers in fields on the right refer to numbers along the electrode track on the left.

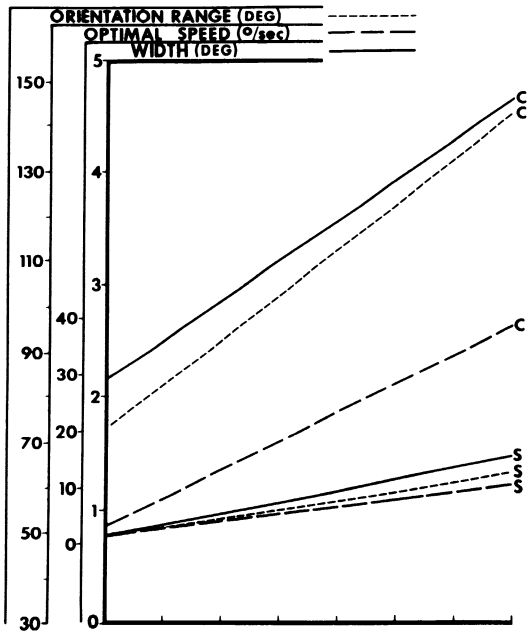

FIG. 15. Linear regression lines for width, orientation range, and optimal stimulus speed as a function of eccentricity. These lines have been calculated using all of the hand-plotted simple (S) and complex (C) cell data. The intersection points of the simple cell lines have been adjusted to coincide on the vertical axis of this graph in order to clearly show the divergence of the complex cell regression lines relative to the simple cell lines. The horizontal axis measures eccentricity from the area centralis, each vertical slash equally 10°.

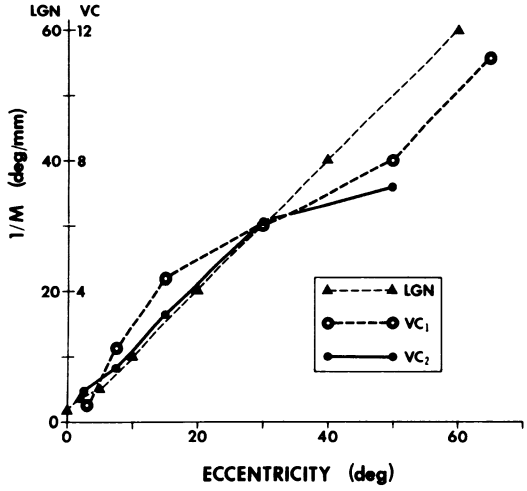

FIG. 16. Magnification factors for lateral geniculate and striate cortex. For convenience, we plotted the reciprocal of magnification factor, 1/M. The geniculate data were taken from Sanderson (38, 39), and the cortical data are a composite from Bilge et al. (solid line, VC_1; ref 5) and R. J. Tusa, L. A. Palmer and A. C. Rosenquist (dashed line, VC_2; personal communication). Note that the cortical and geniculate magnification factors differ only by a constant (approximately 5) which is presumably due to the cortical volume devoted to a hemifield being larger than the geniculate volume.

tionship in the owl monkey. In any case, note that, at least for the lateral geniculate nucleus, this monotonic decrease in magnification factor means that neighboring neurons representing the central visual fields have receptive fields with more overlap and less scatter than those representing peripheral visual fields (see Fig. 17).[1]

SIMPLE AND COMPLEX FIELD WIDTHS. Given this concept of magnification factor, it is now possible to consider a hypothesis which accounts for the relationship between eccentricity and field width for simple and complex cells. However, in addition to M_{LGN} and M_{VC}, several terms must first be defined. Figure 17, which depicts simple cells (S) as stellate and complex cells (C) as pyramidal (29), illustrates most of these terms. W_{LGN}, W_{VC}, W_{SIM}, and W_{CPX} are, for a given eccentricity, the mean field widths for geniculate, cortical, simple, and complex cells, respectively. D_{LGN} represents the mean linear distance across the lateral geniculate which bounds the centers of all geniculate neurons supplying the average cortical cell. An individual D_{LGN} runs across the lateral geniculate in a direction equivalent (in terms of the visuotopic map) to the visual-field direction along which the field width for the cortical neuron is measured. The underlying assumption below is that the receptive field of any neuron is simply that visual area which includes all of the receptive fields of its presynaptic neurons. One need only to define these presynaptic neurons (e.g., in the lateral geniculate)[2] to predict the cortical

[1] As a consequence of the change in M_{LGN} with eccentricity, there are more geniculate neurons available to map central areas than there are to map equivalent peripheral areas. This can be accomplished by: *a*) smaller individual fields centrally than peripherally, and/or *b*) more overlap and less scatter among a group of central fields than among a similar group of periheral fields. The increased size with eccentricity of individual geniculate neuronal fields (ref 23, 38; and Fig. 4) is insufficient to account for the M_{LGN} changes (38). Therefore, the indicated change in overlap and scatter must also occur. Sanderson (38) directly measured overlap and scatter of geniculate neuronal fields, and he found such a change with eccentricity.

[2] For simplicity, the hypothesis is drawn as if both simple and complex cells receive input directly and solely from geniculate cells, but the hypothesis in no

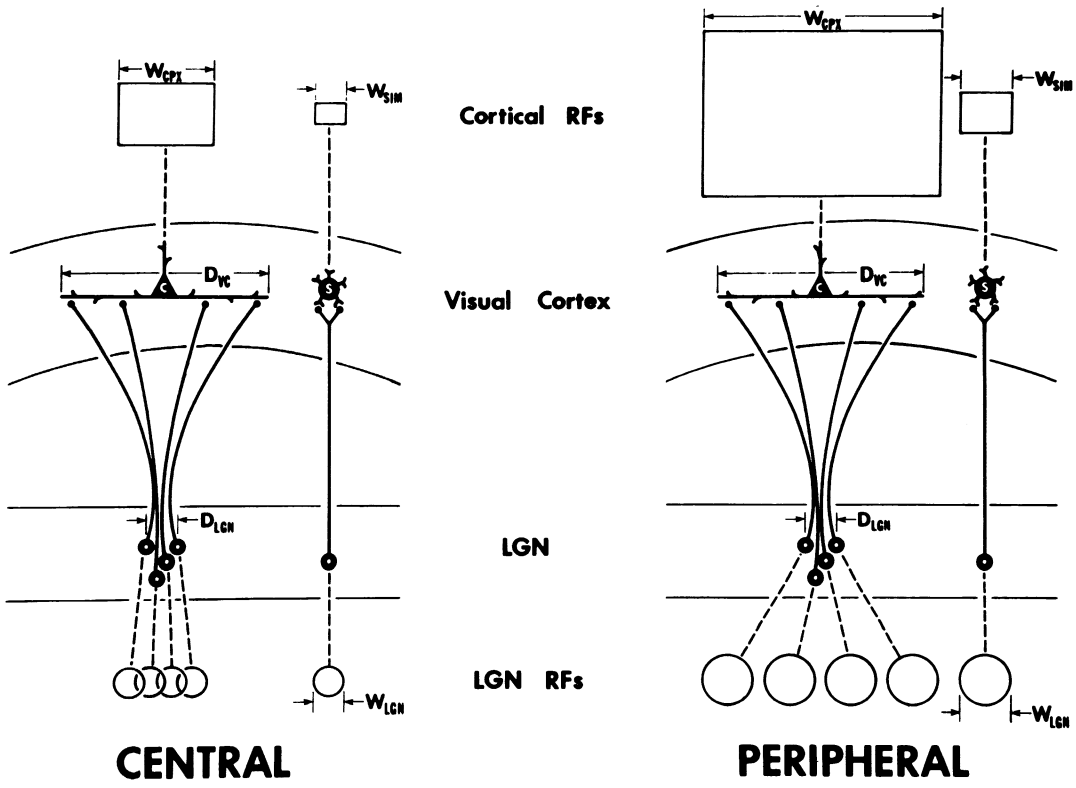

FIG. 17. Diagram of geniculostriate pathways for central and peripheral visual fields. A simple cell (labeled S) receives from a single geniculate neuron. However, a complex cell (labeled C) receives from a geniculate region, D_{LGN}, including four neurons (an arbitrary number); this geniculate region on average is one-fifth the extent of the complex cell's basal dendrites, D_{VC}. The receptive-field widths for the geniculate and cortical neurons are shown. Since only one geniculate cell projects to a simple cell, the simple field width, W_{SIM}, increases with eccentricity only as does the field width of its geniculate afferent, W_{LGN}. Because of a changing magnification factor resulting in less overlap and more scatter among neighboring geniculate cells mapping peripheral vision (38), complex field widths, W_{CPX}, increase with eccentricity at a faster rate than do those of the afferent, W_{LGN} (see text).

field width, and D_{LGN} plus W_{LGN} sufficiently defines these neurons. Therefore, the mean width of a cortical receptive field at a given eccentricity is determined by two components. One is D_{LGN}/M_{LGN}, but since magnification factor is defined in terms of receptive-field centers (see above and ref 38), W_{LGN} (the mean geniculate field width) must be added (actually one-half W_{LGN} at each end) to describe the entire extent of visual field mapped by the presynaptic neurons. Consequently,

$$W_{VC} = D_{LGN}/M_{LGN} + W_{LGN}$$

Other data (see above and ref 8, 24, 25) indicate that a single geniculate neuron frequently determines a simple cell's receptive-field width for a given contrast edge (see Fig. 7). If so, then D_{LGN} is zero, since it represents the extent of afferent geniculate neuronal centers, and

$$W_{SIM} = W_{LGN}$$

This relationship is in good agreement with the data of Fig. 5A. It predicts that the decreased overlap and increased scatter of geniculate neuronal fields with increased eccentricity play little or no role in simple field widths, since magnification factor is omitted as a determinant for simple fields. Instead, as indicated in Fig. 7, simple fields, on average, get wider with increasing eccentricity solely because the fields of their individual geniculate inputs get wider.

Mean field width at a given eccentricity for complex cells can similarly be determined by

way depends on this. A complex cell could well receive input only from simple cells to which the geniculate cells are presynaptic, but even though these presynaptic geniculate cells are now disynaptic to the complex cell, they still define its receptive field through the intermediary simple cells. Thus, with minor modification, the hypothesis fits both the serial and parallel processing theories (see text).

$$W_{CPX} = D_{LGN}/M_{LGN} + W_{LGN}$$

Figure 5A indicates that complex cells must have multiple inputs, and thus the magnification factor now plays a major role in determining complex widths. Figure 17 shows that since M_{LGN} decreases with eccentricity, the fields of neighboring geniculate neurons which represent central vision have more overlap and less scatter than those which represent peripheral vision (ref 38 and footnote 1). We suggest that this change in overlap and scatter, which is a direct consequence of a changing M_{LGN}, explains the large change in complex field widths with changing eccentricity.

From the data of Figs. 5A and 15, W_{CPX}, W_{LGN}, and M_{LGN} are known at various eccentricities, and we can thus solve for D_{LGN} in the above formula for complex cells by

$$D_{LGN} = M_{LGN} (W_{CPX} - W_{LGN})$$

Figure 18 shows that $1/M_{LGN}$ is highly correlated to $W_{CPX} - W_{LGN}$ ($r = 0.99, P < 0.001$), and that the slope of $1/M_{LGN}$ plotted against $W_{CPX} - W_{LGN}$ is roughly 70 μm. This in turn suggests that D_{LGN} for complex cells has a constant value, regardless of eccentricity, of approximately 70 μm. That is, on average, each complex cell samples from a 70-μm extent of geniculate neurons, either directly by receiving fibers from geniculate neurons along the 70-μm extent or indirectly via simple cells which are postsynaptic to these geniculate neurons.[2]

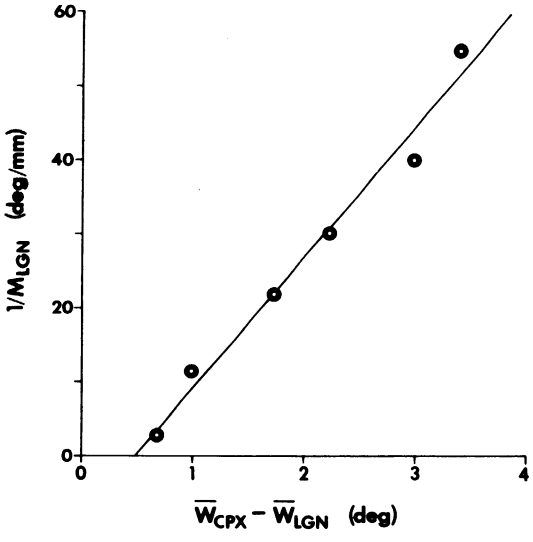

FIG. 18. Plot for each of five eccentricity groups of the reciprocal of geniculate factor, $1/M_{LGN}$, versus the average difference between field widths of complex cells and geniculate cells, $W_{CPX} - W_{LGN}$. These parameters are highly correlated ($r = 0.99$, $P < 0.001$), and the slope of the line of best fit is approximately 70 μm (see text).

Because M_{LGN} differs from M_{VC} only by a constant factor of approximately 5, D_{LGN} for complex cells can be equated with its cortical analog, D_{VC}, by

$$D_{VC} \cong D_{LGN} \times 5 \simeq 350\ \mu m$$

Interestingly, this value of 350 μm, which is derived solely from considerations of receptive fields and magnification factors, is the approximate average span of the basal dendritic arborization for pyramidal cells in cat visual cortex (43). Although perhaps coincidental, this suggests a strong structure-function relationship; namely, presynaptic (geniculate)[2] neurons project their axons toward the pyramidal (complex) cell, and the extent of axons intercepted relates closely to the span of the basal dendrites. For all pyramidal (complex) cells, the mean and range of values for this span is invariant with cortical location (i.e., related to eccentricity), and this results in a mean and range of receptive-field widths which depends heavily on magnification factor. Thus, even the variability in complex field widths (Fig. 5 and Table 1) could be a consequence of the variability among the sizes of pyramidal cell basal dendritic spans (43). We must emphasize an inherent weakness with the hypothesis. The structure/function relationship strongly rests on the assumption that pyramidal cells are the complex cells. Although Kelly and Van Essen (29) found a good correlation for this structure/function classification, the correlation was not perfect. However, the hypothesis could still be valid for the large subset of complex cells that are pyramidal.

Although this structure-function relationship for complex cells is hypothetical and based on sketchy data, it may prove useful in explaining properties in other parts of the visual system and perhaps in other sensory systems. For one example, McIlwain (31) has used an analogous approach to explain the eccentric distribution of receptive fields along vertical penetrations through the superior colliculus.

Serial and parallel processing

The preceding discussion strongly infers that simple cells receive a qualitatively different pattern of synaptic input than do complex cells. Two models have been advanced which separately or in combination might account for this difference. Hubel and Wiesel (24, 25) proposed a hierarchical, serial scheme for the geniculostriate system whereby information is processed through a single chain involving: geniculate cell to simple cell to complex cell to hypercomplex cell, etc. More recently, Stone and

co-workers (22, 23, 45–47; see also ref 13, 26) proposed an alternate scheme of parallel processing through two functionally distinct geniculostriate systems: *a*) geniculate X-cells to simple cells, and *b*) geniculate Y-cells to complex cells.[3] Stone and Fukuda (47) and Ikeda and Wright (26) suggested independently that X-cells might be required for high-resolution pattern vision, while Y-cells might be needed for motion detection and visuomotor orientation. Palmer and Rosenquist (34) have shown that cortical complex cells, which apparently receive afferents from geniculate Y-cells (22), project to the superior colliculus, and the colliculus seems to be involved in visuomotor orientations (44). It is, therefore, of interest to consider our data within the theoretical frameworks of both serial and parallel processing models.

As indicated previously, the changes in receptive-field properties with changing eccentricity can be accounted for by either model.[2] However, the difference in the pattern of these changes between simple and complex cells suggests the possibility of separate function for the two cell types, and separate function is a prediction of the parallel processing model (23, 26, 47). More support for parallel processing derives from the relative frequency pattern of complex cells. As recordings are made from geniculate neurons with more eccentric receptive fields, the relative percentage of Y-cells increases (23). This led Stone (discussion at end of ref 45) to predict a similar increase in the relative percentage of complex cells with increasing eccentricity. Figure 4 plots the relative percentages of geniculate Y-cells and cortical complex cells as a function of their field eccentricity. The relationship between the two functions is quite close, since a significant correlation obtains for the five pairs of data points ($r = 0.91$, $P < 0.01$). Although these data were predicted by the parallel processing model, it is important to note that the relationship is not inconsistent with the serial processing model (24, 25).

[3] Wilson and Stone (49) have recently provided evidence that the third major class of retinal ganglion cells, W-cells, are represented at the cortical level via geniculate neurons in the C laminae. Since no systematic data have yet been published for these geniculate neurons and since it is not yet known whether they project to simple and/or complex cells, the following discussion is limited to X- and Y-cell inputs to the striate cortex.

Conclusions

The data from this study suggest qualitatively different patterns of properties between simple and complex cells. Again, while not inconsistent with the model of serial processing, this view seems more aligned with parallel processing. We have suggested a hypothesis of different types of synaptic input to simple and complex cells which is consistent with our data that simple field properties, when compared with those of complex fields, remain fairly constant throughout the visual field. This, in turn, is consistent with the notion (26, 47) that the simple system might analyze quantitative stimulus details, whereas the complex system is more involved in stimulus detection and a relatively crude analysis of detail.

ACKNOWLEDGMENTS

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