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Quantitative Studies of Single-Cell Properties in Monkey Striate Cortex. IV. Corticotectal Cells

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SUMMARY AND CONCLUSIONS

1. The receptive-field properties of corticotectal cells in the monkey's striate cortex were studied using stationary and moving stimuli. These cells were identified by antidromic activation from the superior colliculus.

2. Corticotectal cells form a relatively homogeneous group. They are found primarily in layers 5 and 6. These cells can usually be classified as CX-type cells but show broader orientation tuning, larger receptive fields, higher spontaneous activity, and greater binocular activation than CX-type cells do in general. A third of the corticotectal cells were direction selective.

3. These results suggest that the cortical input to the superior colliculus is not directly responsible for the receptive-field properties of collicular cells. We propose that this input has a gating function in contributing to the control of the downflow of excitation from the superficial to the deep layers of the colliculus.

INTRODUCTION

Changes in the response patterns of single cells in the superior colliculus to visual stimulation have been observed after ablation or cooling of the visual cortex in several species. After ablation of visual cortex, cells of the superficial gray and stratum opticum of the colliculus in the cat lose their normal binocularity, direction selectivity, and responsiveness to movement (13). Palmer and Rosenquist (6, 7) have characterized the response properties of those cells in striate cortex of the cat which project to the superior colliculus. They found that all cortical cells responding antidromically to stimulation of the superior colliculus fell into Hubel and Wiesel's (3) complex or hypercomplex categories. These cells were found in layer 5 and were more likely to be strongly binocular and direction selective than the entire population of

complex cells; they were also more likely to be broadly tuned for stimulus orientation. The authors hypothesized that the qualities lost after visual cortex ablation are supplied to the superior colliculus by the corticotectal projection.

In monkeys, after ablation or reversible cooling of visual cortex, a different pattern appears in the superior colliculus (12). One observes only subtle changes in the response patterns of the superficial layers of the superior colliculus and the ocular dominance of most cells is unaffected. By contrast, in the deeper layers, single cells become unresponsive to visual stimulation. It appears that the pathway through visual cortex is crucial for the integrity of the deeper collicular layers.

In this study we undertook to investigate the properties of those cells in area 17 of the monkey which project to the superior colliculus. This investigation had two aspects. First, we wished to clarify further the role the superior colliculus has in eye movement and vision by analysis of the type of information relayed to it by the visual cortex. Second, we had hoped that knowledge of the nature of striate cortex output may help to further delineate cell classes within this area and lead to a better understanding of visual cortex.

METHODS

Cortical units activated antidromically by superior colliculus stimulation were studied in 34 monkeys. The surgical preparation for this procedure has been described in the first paper of this series (8). A cortical well with a double eccentric setting which permitted multiple electrode penetrations was implanted over the parafoveal region of striate cortex. Most cortical electrode penetrations in these animals were made perpendicular to the cortical surface. A trephine hole was drilled in the skull overlying the superior colliculus, the dura was removed, and a microelectrode enclosed in a 19-gauge needle was lowered to a point 6 mm above the

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Horsley-Clarke stereotaxic coordinates for the superior colliculus at a 10° angle from the vertical. This electrode was used for both stimulation and recording. The electrode was lowered until the surface of the superior colliculus was contacted and then lowered 0.5 mm to maximally contact incoming corticotectal fibers. An effort was made to align the receptive fields of superior colliculus and striate cortex, since various studies have shown the corticotectal projection to be topographically organized (4, 5). When stimulation through the superior colliculus electrode antidromically activated a unit in cortex, the vertical position of the superior colliculus electrode was adjusted until the stimulation threshold was at a minimum. The stimulation pulse was a 0.05-ms monophasic negative-going square wave of 0.2–0.8 mA.

Antidromically activated units were identified by their constant latency of reponse to supra-threshold collicular stimulation and by their consistent response to high rates of collicular stimulation. In some animals lesions were made in the visual cortex at the level of antidromically activated units by passing 5–20 μA of the direct current through the cortical microelectrode for 5–20 s. At the end of the experiment the animals were perfused with 10% formal saline and the brains were prepared with the Nissl stain.

The computer-driven stimulus displays and data-collection system have been described in the previous papers (8–10). The response variables studied and computed for the antidromically activated units were:

1) Orientation tuning function. An estimate of the width of orientation tuning for a bar swept through the receptive field was calculated from a smoothed orientation-response curve between ordinate values of maximum response/√2 (9).

2) Stimulus-length specificity ratio (end stopping). The ratio of cell response to a 6.4° bar to the optimal length bar was calculated (8) using the formula:

$$100 - \frac{6.4^\circ \text{ bar response}}{\text{optimal response}} \times 100$$

3) Spontaneous activity. Averaged spontaneous activity in 10 1-s sampling periods to no visual stimulus was obtained in conjunction with the end-stopping measures.

4) Direction specificity. The mean number of spikes elicited with moving edges in each of the two directions independent of contrast was calculated using the formula:

$$\frac{L \rightarrow + D \rightarrow}{L \leftarrow + D \leftarrow} \times 100$$

with the smaller number in the numerator. Low

values, therefore, refer to direction-specific cells; high values, to bidirectional cells.

5) Contrast specificity. A ratio of the number of spikes elicited by light and dark edges swept through the receptive field, regardless of direction, was calculated using the formula:

$$\frac{\Sigma L}{\Sigma L + \Sigma D} \times 100$$

A value of 0 indicates light-edge preference; a value of 50, no contrast dependence; and a value of 100 dark-edge preference.

6) Interaction between contrast and direction. Interaction between contrast and direction was calculated with the formula:

$$\frac{[L \rightarrow + D \leftarrow] \text{ or } [L \leftarrow + D \rightarrow]}{\text{total } L + D}$$

A value of 0 indicates strong preference for a particular contrast pattern and direction and a value of 50 indicates no interaction.

7) Flash contrast preference. This measure is represented by a ratio of the averaged response to an optimally oriented light bar flashed on and off in the receptive field. The formula,

$$\frac{\text{on-response}}{\text{on-response} + \text{off-response}} \times 100$$

was used. A value of 100 indicates sensitivity to light increment only; a value of 50, equal responses to light increment and light decrement; and a value of 0, preference for light decrement.

8) Receptive-field width. The width of the response in degrees to a moving edge was measured at the half-way point between the base line and the peak of the response (8).

9) Binocularity. Binocularity was determined by using the 1–7 ocular dominance range, as defined by Hubel and Wiesel (2), where 1 = monocular, contralateral eye, 4 = equally driven in both eyes, and 7 = monocular, ipsilateral eye.

RESULTS

Eighty-nine corticotectal cells (C-T) were identified by their constant latency of response to collicular stimulation. Ten superimposed traces of the response of one such cortical unit to collicular stimulation appear in Fig. 1A. The average response latency to collicular stimulation was 4.6 ms; the distribution of latencies observed appears in Fig. 1B. No systematic difference in unit properties was correlated with response latency. For suprathreshold stimulation no significant change in latency was observed on varying current intensity. Conduction velocity averaged 8 m/s; the fastest velocity observed was 19 m/s; the slowest was 3 m/s.

All of the C-T sites marked with electrolytic

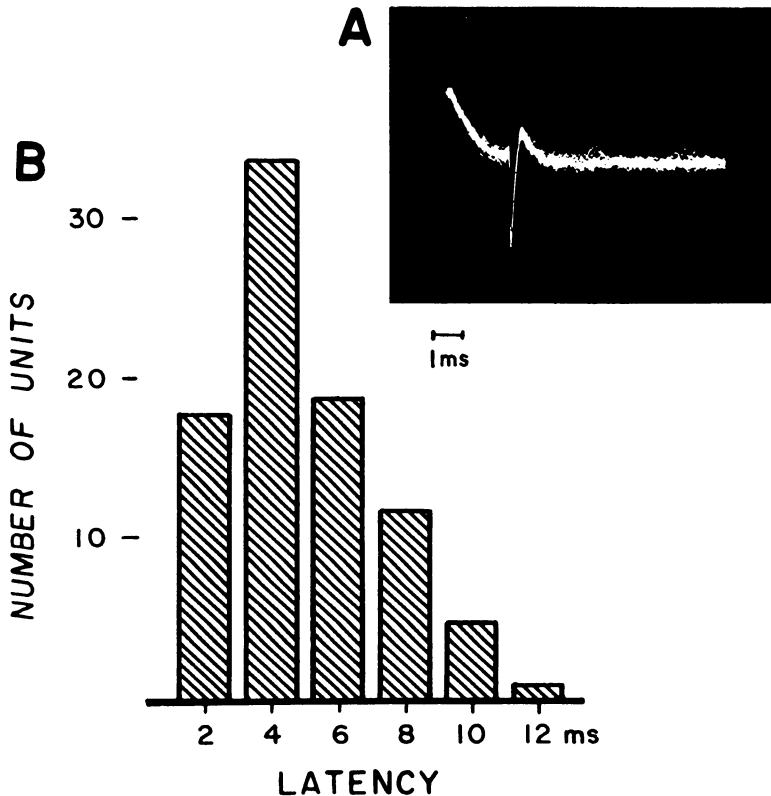


FIG. 1. *A*: corticotectal cell antidromically activated from the superior colliculus; 10 repeated sweeps triggered by an electric pulse to the superior colliculus. *B*: distribution of response latencies of corticotectal cells to antidromic activation from the superior colliculus.

lesions and most of those which were estimated (8) were in layers 5 and 6. Depth estimations and calculations along tangential passes, both of which are less accurate than direct marking, did place a few of the C-T cells in the lower part of layer 4.

Of the 89 C-T units observed, 50 were isolated sufficiently to permit study of their properties. For our analyses we did not assign C-T cells into the S-type and CX-type cell groups discussed previously (8-10); our principal interest was to determine if a functional criterion, such as projection to the superior colliculus, would yield cell-group classifications congruent with those based on cell-response criteria. S-type cells were defined as those oriented cells whose receptive fields had one or more distinct regions within each of which a response could be elicited only to light increment or to light decrement; CX-type cells were defined as those oriented cells which have a unified activating region within which a response could be elicited to both light increment and decrement. We found that the majority of C-T cells could be classified as CX-

type cells, but that 20% could not be classified so because of lack of orientation selectivity. No C-T cell could be classified as an S-type cell. Other cell properties such as larger receptive-field size, higher spontaneous activity, and greater binocular activation than the average CX-type cell, suggested that C-T cells may represent a subgroup of the CX population.

In addition, an effort was made to study cells that were recorded near C-T cells but were not themselves antidromically activated. The purpose of this comparison was to determine the relationship the group of C-T units had to the population of units in the same cortical region. The NC-T group includes CX, S, and unclassified units. Although a large proportion of the C-T and NC-T units could be classified as CX type, they were excluded from the CX group for these particular analyses. Finally, we also compared C-T cells with those CX-type cells in laminae V and VI which could not be antidromically activated from the colliculus.

The aim of these comparisons is to assess the relative contributions of projection site, laminar

localization, and cell response to the categorization of cell types and to the understanding of the organization of visual cortex.

Spatiotemporal organization of receptive fields of corticotectal cells

The responses of a representative C-T cell to a single edge moving across the receptive field in its optimal orientation is shown in Fig. 2. This was a direction-selective cell with a large receptive field. The cell responded in the same manner to light and dark edges and the response areas overlapped. Left-to-right movement excites the cell; movement in the opposite direction demonstrates a small degree of inhibition followed by excitation. The location of the maximum point of inhibition corresponds to the center of the excitatory region for left-to-right movement. Using cell-response criteria this cell would have been classified as a CX-type cell.

A quantitative comparison of the receptive-

field size of corticotectal cells appears in Fig. 3. Histograms of receptive-field width measured for C-T, CX-type, S-type, and NC-T units were determined as already described in the previous papers (8-10). Corticotectal units typically had large receptive fields as measured by both moving and flashing stimuli. They had a larger mean field width, 0.79° , than any other cell group. The width of the receptive field of C-T cells was similar to that of other CX-type cells in the same region of cortex. C-T cells all had receptive-field widths which were greater than 0.3° , and 28.5% of them had fields larger than 1° . In the population of NC-T cells, 16% had fields larger than 1° ; while in the overall populations of CX-type cells in our sample, only 6% had fields this large.

The histograms in Fig. 2 show that this particular cell was strongly directional. Since in the superior colliculus of the monkey directional cells are extremely rare (0-6%), we were interested in determining what the distribution of directionality is among corticotectal cells. The

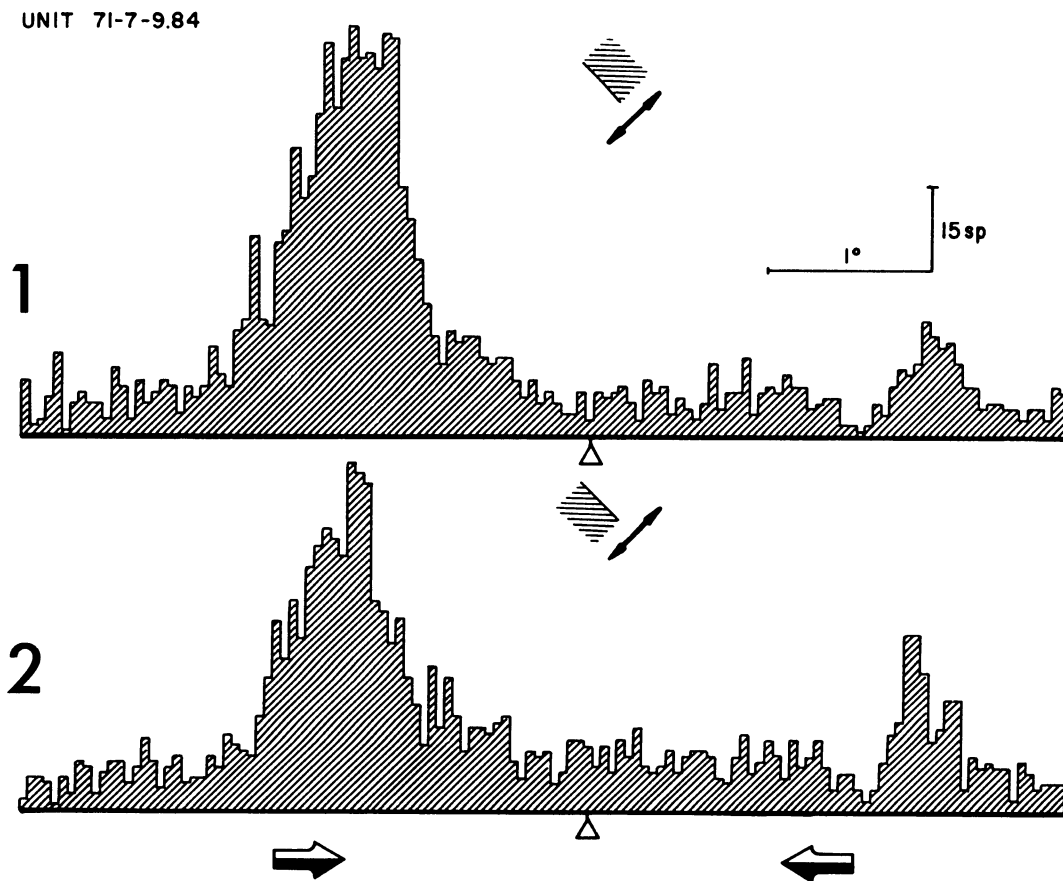


FIG. 2. Stimulus-response histogram of a corticotectal cell to moving edges; 30 repeated presentations at $2^\circ/s$ velocity. 1: light edge in up direction, dark in the other. 2: dark edge in up direction, light in the other.

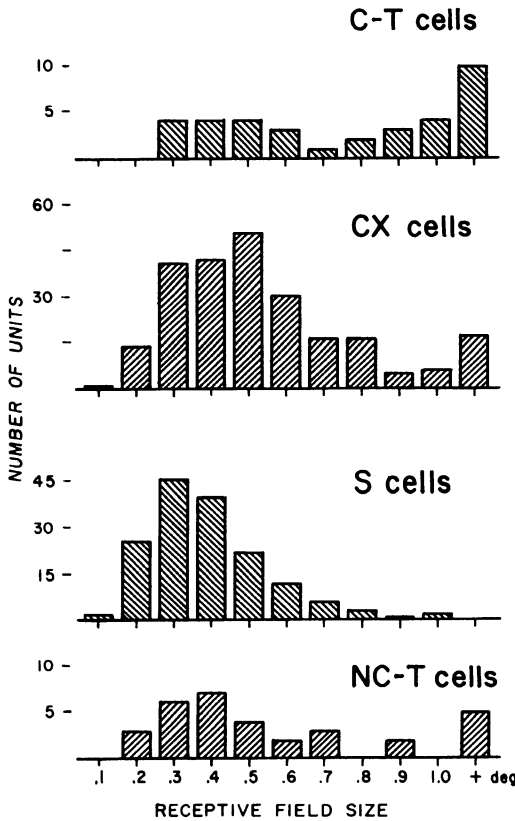


FIG. 3. Distribution of receptive-field sizes for C-T (N = 35), CX (N = 231), S (N = 160), and NC-T (N = 28) cells.

results of this are shown in Fig. 4. C-T units showed nearly the complete range of direction selectivity. There is, however, a slight skewing of the curve toward lack of direction preference relative to the CX-type cells and NC-T cells; 31% of C-T cells showed direction selectivity using 50 as the cutoff on the directionality index. By comparison, these values were 39% for CX-type cells, 65% for S-type cells, and 40% for NC-T cells. Only the difference of C-T and S-type cells reaches significance at the 5% level on a proportion test.

The data obtained with moving stimuli of opposite contrast edges (Fig. 2) also provide a measure of contrast independence and a measure of the interaction between contrast and direction. Cumulative data on these two measures appear in Fig. 5. Both of these measures suggest that the corticotectal cells are similar to CX-type cells; they show approximately the same range of contrast dependence and contrast-direction interaction as do the cells which were classified as CX type. Likewise, they resemble NC-T cells, although the NC-T group contains some

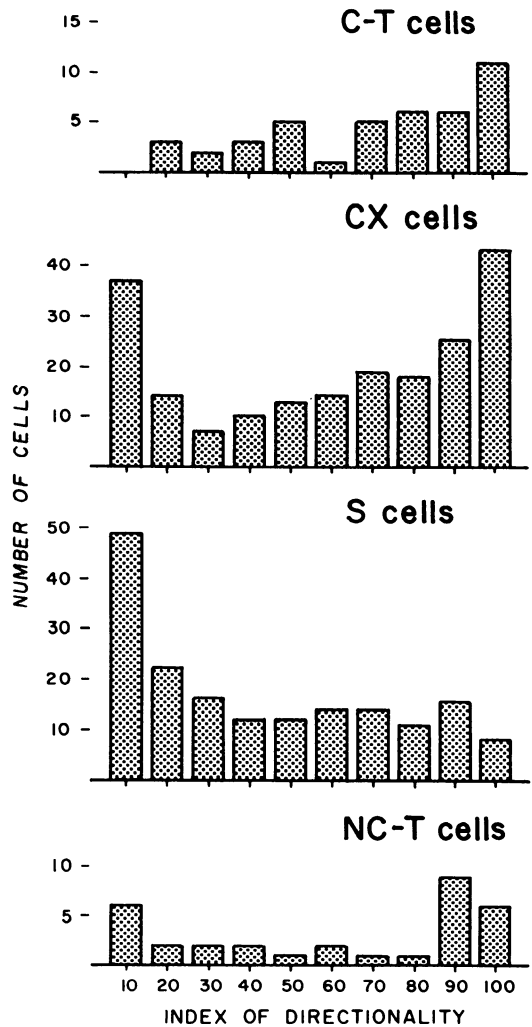


FIG. 4. Direction selectivity of C-T (N = 42), CX (N = 167), S (N = 173), and NC-T (N = 32) cells. Unidirectional cells have low values, bidirectional cells have high values. Index of directionality is 100 times the total response in the worse direction of stimulus movement divided by the total response in the better direction.

cells which are highly contrast and interaction selective.

Stimulus length and end stopping

The measure of inhibition along the axis of orientation has served as a basic measure in the cat to classify cells as hypercomplex (3). Work on the monkey has suggested that the attribute of end stopping is not one which can be used readily to discern such a class of cells (8). Instead, this attribute varies in a relatively continuous manner forming a unimodal distribution,

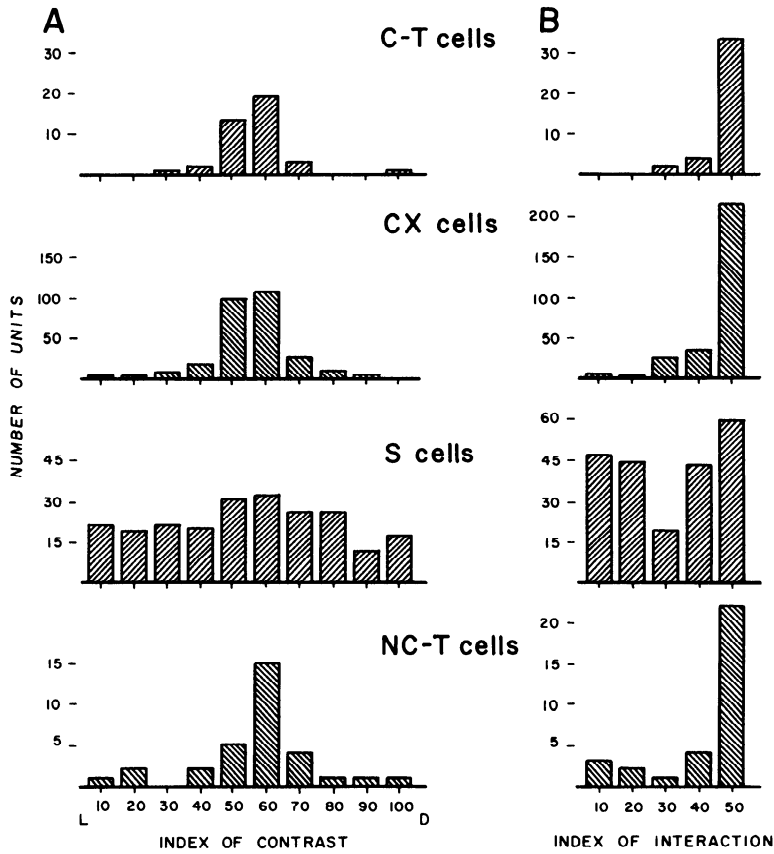


FIG. 5. A: distribution of the index of contrast dependency for C-T (N = 50), CX (N = 277), S (N = 213), and NC-T (N = 32) cells calculated using the formula: (total response to light edges/total response to all edges) × 100. B: distribution of the index of interaction between contrast dependence and directionality for C-T (N = 39), CX (N = 270), S (N = 200), and NC-T (N = 32) cells. Formula: (L→ + D←) or (L← + D→)/ total L + D.

with end stopping being more prominent in the upper than in the lower cortical layers. We found this same unimodal distribution of end stopping in C-T cells. This is shown in Fig. 6. This finding supports the view that end stopping varies in a relatively continuous manner since here we have a population of cells which all have in common the site to which they project.

Orientation tuning

A cumulative distribution of orientation tuning appears in Fig. 7. Corticotectal units are, in general, broadly tuned, more broadly tuned than CX, S, and NC-T cells; in addition, 20% of the cells possess no orientation selectivity. This measure demonstrates one problem when cells are classified qualitatively on the basis of response measures: the C-T cells are not bimodal in regard to orientation selectivity, but rather show a distribution ranging from broad orientation selectivity to no selectivity. It may be ar-

gued that the requirement that CX-type cells be orientation specific applies an artificial restriction in the classification of C-T cells. Even broad orientation tuning in corticotectal cells is curious since in the superior colliculus, none of the cells

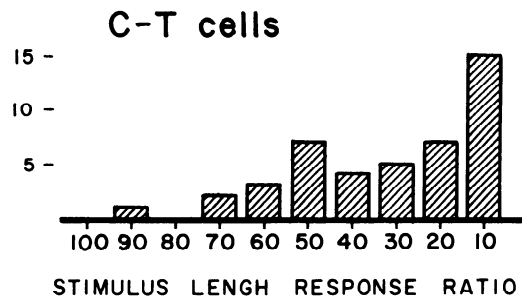


FIG. 6. Distribution of stimulus-length specificity for C-T (N = 44) cells. Index is derived by the formula: 100 - (6.4° bar response/optimal response) × 100.

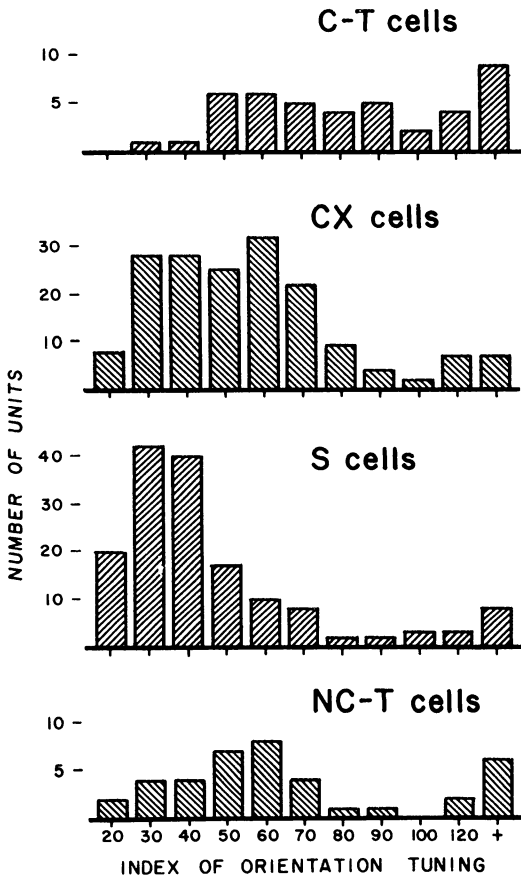


FIG. 7. Distribution of orientation tuning specificity for C-T (N = 45), CX (N = 202), S (N = 151), and NC-T (N = 34) cells.

studied have shown such an attribute (1, 11). It appears that the attributes of both orientation and direction selectivity of the corticotectal cells are not transmitted to the cells in the colliculus.

Ocular dominance

The ocular-dominance distribution of corticotectal cells appears in Fig. 8. From this figure it is evident that C-T cells tend to be strongly binocular. In our sample there was no cell which was monocularly driven. The ocular-dominance histogram of C-T cells most closely resembles the CX-type unit histogram. In fact, a greater proportion of C-T cells is driven well through both eyes (categories 3-5) than CX-type cells, and this difference is statistically significant at the 0.02 level (χ^2).

Spontaneous activity

Corticotectal cells showed considerably more spontaneous activity than did other cells in striate cortex. The cumulative histogram for this

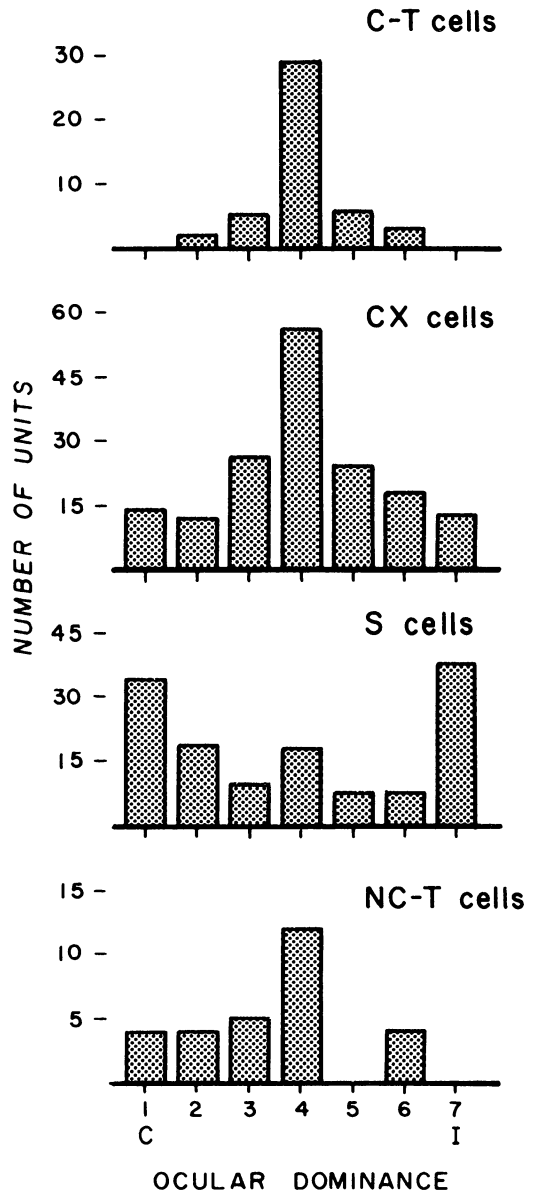
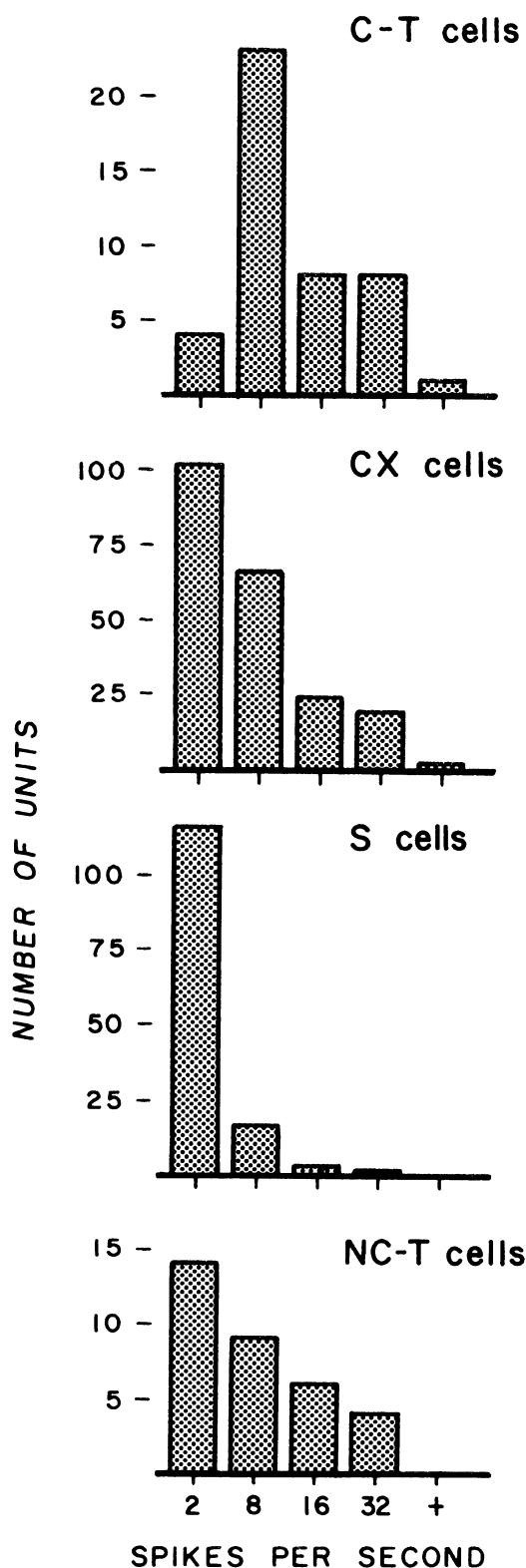


FIG. 8. Distribution of ocular dominance for C-T (N = 45), CX (N = 168), S (N = 135), and NC-T (N = 29) cells.

measure appears in Fig. 9. The average response of these cells was 9.2 spikes/s. This attribute of the corticotectal cells is also interesting since the cells in the superior colliculus under identical conditions of recording show very low spontaneous activity. This observation further suggests that this projection cannot be thought as a simple, direct excitatory input to collicular cells.

In summary, C-T units were more broadly tuned for orientation, more spontaneously ac-



tive, more binocularly activated, and had larger receptive fields than the other types of cortical units studied. On all these measures C-T units resemble CX-type cells most closely.

Those units which were recorded near the antidromically activated C-T units did not form a homogeneous cell group; this population (NC-T) included CX-type, S-type, and unclassified units. As a group, the NC-T units did not resemble the corticotectal cells any more closely than did the CX-type units (Fig. 3-9).

In a further effort to determine the subpopulation of cortical cells to which C-T units could be assigned, we compared the response properties of layer 5 and 6 CX-type cells with C-T cells for orientation tuning, spontaneous activity, binocularity, and receptive-field size. These comparisons appear in Fig. 10. The spontaneous activity and field sizes of layers 5 and 6 CX-type cells were quite similar to those exhibited by the C-T units. C-T units are more broadly tuned for orientation, however, even if one disregards those C-T units which are not oriented. Finally, C-T units show a somewhat greater degree of binocular interaction than lower layer CX-type cells, although this difference is quite small.

DISCUSSION

The antidromically activated cortical units we have studied form a rather homogeneous population of an easily recognizable cell type among the variety of cortical neurons. The majority can be classed as CX-type neurons; that is, oriented cells which have a unified activating region within which a response can be elicited to both light increment and light decrement. It is important to note, however, that C-T cells represent one extreme within the CX group in that they show higher spontaneous activity, broader orientation tuning, larger receptive fields, and greater binocular interaction than the average population of CX-type cells. C-T units resemble layer 5 and 6 CX-type cells more closely but still show broader orientation selectivity and slightly more binocular interaction.

Of the C-T units, 20% did not show orientation selectivity or appeared only slightly selective and were not classified as CX-type cells. The remaining response properties did not differ from the other C-T units, however, which suggests that orientation selectivity may form a continuum with nonselectivity. Thus, if one chooses a functional group criterion rather than a cell-response criterion, the traditional dichotomy of

FIG. 9. Distribution of spontaneous activity for C-T (N = 44), CX (N = 214), S (N = 137), and NC-T (N = 33) cells.

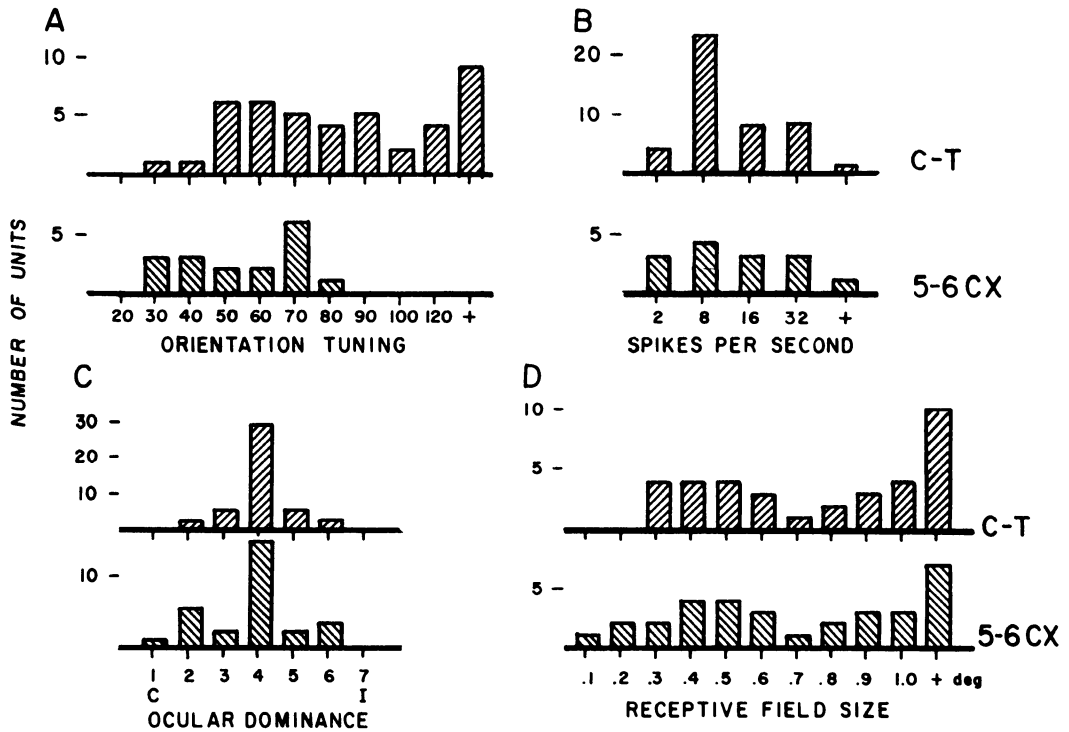


FIG. 10. Distribution for orientation tuning (A), spontaneous activity (B), ocular dominance (C), and receptive-field size (D), comparing C-T cells with those CX-type cells in layers 5 and 6 which do not project to the superior colliculus.

oriented/nonoriented may become a less important index of cortical function.

It is interesting that the C-T units in the monkey seem similar to those described by Palmer and Rosenquist (6) in the cat, despite the differences in unit discharge properties of collicular units in the cat. The corticotectal units in cat and monkey show a high degree of binocular interaction, large receptive fields which appear homogeneous to flashed and moving stimuli, and some cells show direction selectivity. Monkey corticotectal units appear to be more broadly tuned for orientation than those in the cat.

In their work on the cat, Palmer and Rosenquist (6) proposed a simple convergence model suggesting that the corticotectal projection may supply those properties which are lost to the superficial layers of the superior colliculus after cortex ablation. These are binocularity, direction selectivity, and response to movement. Such a model does not easily explain the results obtained in monkeys. After ablation or cooling of visual cortex in the monkey, cells of the superficial gray maintain their essential properties, such as sensitivity to movement, degree of binocularity, lack of direction selectivity, and presence of a suppressive surround. Relatively

large receptive-field size, binocularity, and the presence of a suppressive surround are qualities common to both the superficial superior colliculus units and C-T units. Directionality, orientation tuning, and the degree of spontaneous activity, however, are not in common with collicular cells. A high degree of convergence on collicular cells could get rid of the former two. A problem remains, however, for spontaneous activity which, with a great deal of convergence, would become extremely large (900 spikes/s on the average for a convergence of 100 cells). Therefore, it must be assumed that collicular cells either have a high-response threshold or are strongly clamped down by inhibitory mechanisms. One might conjecture that only considerable spatiotemporal summations of spikes can override this inhibition.

The relationship between the response characteristics of C-T units and the units of the deeper collicular layers is not so clear. These units are eye-movement related and lose their visual receptive fields after cortical ablation or cooling. These may be the units which, in the paralyzed preparation, have been described as erratic or habituating; some prefer jerky, square-wave movement; other respond in a sus-

tained manner to novel stimuli. None of the C-T units studied possess properties similar to these, which makes the simplest sort of convergence model untenable. We propose an alternative hypothesis which states that the corticotectal projection does not confer specific receptive-field properties on the deep collicular units, but rather gates the flow of information from the

superficial layers of the colliculus to the deep collicular layers.

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