

RECEPTIVE FIELDS AND FUNCTIONAL ARCHITECTURE IN TWO NONSTRIATE VISUAL AREAS (18 AND 19) OF THE CAT¹

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TO UNDERSTAND VISION in physiological terms represents a formidable problem for the biologist. It amounts to learning how the nervous system handles incoming messages so that form, color, movement, and depth can be perceived and interpreted. One approach, perhaps the most direct, is to stimulate the retina with patterns of light while recording from single cells or fibers at various points along the visual pathway. For each cell the optimum stimulus can be determined, and one can note the characteristics common to cells at each level in the visual pathway, and compare a given level with the next.

From studies carried out in the cat it is clear that visual messages undergo considerable modification, within the retina and the lateral geniculate body, and especially within the striate cortex (16, 12, 10, 13). Retinal-ganglion and geniculate cells respond optimally to an appropriately placed spot of light of just the right size; a smaller or larger spot is less effective. Cells at these levels therefore register not simply the illumination of a region on the retina, but also the difference in illumination between a region and its surround. In the striate cortex cells are far more complex and diverse in their response properties. The great majority respond best to straight-line stimuli: for a given cell the optimum stimulus may be a white or dark line, or an edge separating light from dark. A line stimulus is effective only when shone in an orientation that is characteristic for the cell; there is typically no response when the stimulus is shone at 90° to the optimum orientation, and the range of orientations over which a response is evoked may be 30° or even less. Some cells prefer one inclination, others another, and we have no evidence that any one orientation, such as vertical or horizontal, is more common than another. For some cells, termed "simple," the exact position of the stimulus is critical: even a slight displacement of the line to a new position, without changing its orientation, produces a dramatic decrease in the response. These properties of simple cells are dictated by the arrangement of excitatory and inhibitory regions of the receptive field, as mapped with small-spot stimulation (10). The simplest assumption is that each of

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the simple cortical cells receives its input directly from a specific group of cells in the lateral geniculate body (13, text-Fig. 19). Other cells, termed "complex," respond to an appropriately oriented stimulus regardless of where in the receptive field it is positioned. These cells behave as though they received projections from a large number of simple cortical cells, all having the same receptive-field arrangement and orientation, but differing in the exact retinal positions of these fields (13, text-Fig. 20).

All of this suggests a highly specific and intricate set of cortical connections, first between the incoming geniculate axons and the simple cortical cells, and then between certain simple cells and certain complex ones. Strong indirect support for the specific connections between simple and complex cells comes from a study of cortical functional architecture. From single long microelectrode penetrations and from multiple short penetrations it can be shown that neighboring cells in the striate cortex usually have the same receptive-field orientation, and roughly the same receptive-field position. In fact, cells having the same receptive-field orientation are aggregated into regions of columnar shape extending from surface to white matter, with walls perpendicular to the cortical layers (13, 14). Such an arrangement means that the very cells that are supposed to be interconnected on physiological grounds—simple and complex cells with the same receptive-field orientation, and a certain small variation in receptive-field position—are in fact grouped together, and are therefore highly likely to be interconnected also on anatomical grounds. This columnar system presumably makes for great economy in length and number of interconnections.

A given small region of retina is thus represented in the striate cortex many times, first in a column representing one orientation, then in a column representing another. For the entire visual field such an analysis must require a very large number of columns, and an even greater number of cells. One can now begin to understand the dramatic increase in the number of cells as one goes from geniculate to striate cortex.

To pursue this work further it is obviously necessary to learn where the next steps in integration occur. The efferent connections of the cat striate cortex have not been worked out in any great detail, but a number of results in the cat and other species suggest that there are multiple projections, both cortical and subcortical. We have begun by looking at the cortex itself, first examining the cortical regions just lateral to the striate. These areas have long been suspected, on various grounds, of being involved in vision. The strongest physiological evidence for this was presented in 1941 by Talbot and Marshall (27). Stimulating the retinas with small spots of light, and recording evoked potentials, they mapped out in each hemisphere of the cat cortex two orderly topographic projections of the contralateral half-field of vision. The more medial of the two areas, which they termed "visual area I," seems from their maps to correspond roughly to the anatomically defined striate cortex; the lateral area, termed "visual II," has not yet been correlated with cytoarchitecture.

In the present study we explored the cortex from medial to lateral in

successive penetrations, crossing from visual I into Talbot and Marshall's visual II, and then continuing into what has proved to be a third distinct topographically organized visual area lying lateral to the second. We have called this region "visual area III."

In analyzing visual II and III we have followed our usual procedure of describing cells in terms of their responses to visual stimulation, attempting at the same time to build up a picture of cortical architecture by comparing the behavior of neighboring cells, and of cells recorded in sequence, in long penetrations. Our hope has been to learn how the next stages of integration make use of the input from cells of the striate cortex, and to find out whether the columnar plan of architecture that is present in the primary visual area holds also for higher areas. Finally, we have made a correlation of the three physiologically defined visual areas with the histological variations of the cortex as seen on Nissl- and myelin-stained sections, and have used the Nauta technique to establish that visual areas II and III actually receive direct projections from visual I.

METHODS

Seventeen cats were used. Procedures for preparing the animal, including anesthesia, immobilization of eyes, correction of refractive errors, and mapping of area centralis and optic discs on the projection screen, have all been described elsewhere (10, 11, 13). The retinas were stimulated by shining spots or patterns of light from a tungsten filament projector onto a wide movable tangent screen at 1.5 m. distance. Recordings were made in the light-adapted state. Background illumination was about 1.0 cd/m^2 , and stimuli were 0.5–1.5 log units brighter than the background. All recordings were made with tungsten micro-electrodes (8). In nine experiments (11 penetrations) a small hole was drilled in the skull over the right hemisphere, the dura incised, and a 19-gauge hollow stainless steel needle cemented into the hole with its lumen close to the cortex, to form a closed chamber; the electrode was hydraulically introduced through the needle. In each of the remaining eight experiments a number of penetrations were made through a modified Davies chamber (4) which was cemented onto the skull (14); the brain was photographed through a dissecting microscope and an enlarged print was used to indicate the points of entry of the electrode relative to cortical blood vessels. Forty-two penetrations were made in these mapping experiments. At the end of each experiment the brain was perfused with saline followed by formal-saline, the calvarium removed, and the brain photographed again. All brains were imbedded in celloidin, sectioned serially at 26μ ., and stained with cresyl violet (Nissl) or Loyez stain (myelin). In each penetration one or several lesions were made by passing direct current through the electrode (about $5 \mu\text{A}$. for 5 sec.). The lesions were used to reconstruct electrode tracks (9, 13). Destructive lesions for silver-degeneration studies by the Nauta method (22) were made in four cats with coarse electrodes (30 – 35μ . from end of insulation to tip); currents of the order of $10 \mu\text{A}$. were passed for 10 sec. In two cats lesions were made by stabbing the cortex with a 25-gauge hypodermic needle.

RESULTS

PART I. VISUAL AREAS I, II, AND III: PHYSIOLOGICAL MAPPING AND CORRELATION WITH HISTOLOGY

*Topographical representation*²

All of the 53 penetrations of the present experiments were made from the lateral, postlateral, and middle and posterior suprasylvian gyri, at

² Names of gyri and sulci used in this study are generally those of Winkler and Potter (31); they are illustrated in Fig. 37.

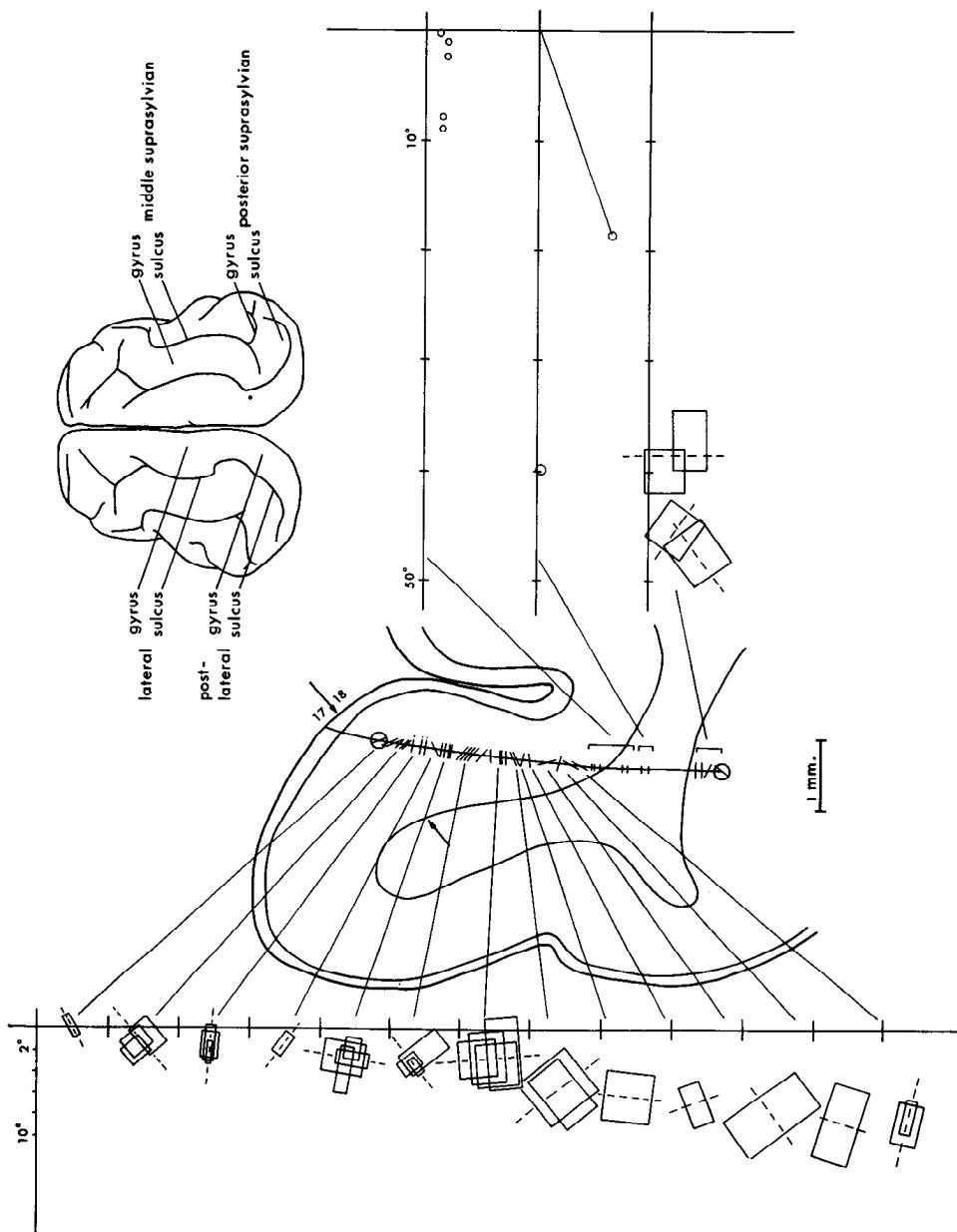


FIG. 1. Reconstruction of an electrode track which passed down along the medial wall of the right postlateral sulcus. Tracing of a coronal section through the postlateral gyrus is shown near the center of the figure. To the upper right is a tracing of a photograph of the dorsal view of the brain (anterior is to the top of the figure); point of entry of electrode is indicated by a dot. Electrode entered cortex close to the 17-18 boundary (i.e., the visual I-visual II boundary); and a lesion was made at the point where the first cells were recorded (indicated by a circle). A second lesion was made at the end of the penetration, in the upper bank of the splenial sulcus. Lines intersecting the electrode track indicate single

levels close to the junction or region of overlap of the lateral and postlateral sulci (Horsley-Clarke coordinates P 4.0-A 4.0). Topographic mapping was thus confined to regions of cortex in and lateral to the striate representation of the area centralis and parts of the visual field a few degrees below it. We have shown previously that in the course of a long penetration down the mesial (interhemispheric) segment of the lateral or postlateral gyrus parallel to the surface, the receptive fields of successively recorded cells tend gradually to move out into the contralateral half-field of vision (13: text-Fig. 13 and p. 134). The visual I representation of the midline (the vertical meridian) is located deep in the lateral bank of the postlateral gyrus at posterior levels, while more anteriorly it appears on the surface of the lateral gyrus close to where the postlateral sulcus ends, and then crosses the gyrus obliquely from lateral to medial. This line forms the lateral border of visual area I (compare the boundary between 17 and 18 in Fig. 37).

The cortical region lateral to visual I was first explored by making deep microelectrode penetrations along both walls of the postlateral sulcus. In the experiment illustrated in Fig. 1 the electrode tip passed obliquely along the entire medial wall of the sulcus, crossed the underlying white matter, and ended in the upper bank of the splenial sulcus. The positions of the receptive fields in the contralateral visual field are shown to the left of the figure. Each diagram shows one or several receptive fields in relation to the center of gaze (the area centralis projection), which is re-represented in each diagram by the crossing of the short horizontal lines and the long common vertical line. Fields of successive cells are shown on the same diagram if their orientations are the same, i.e., if they are located in the same column (see below). At the outset the cells had their receptive fields very close to the vertical meridian. As the electrode advanced from one cell to the next there were slight, more or less random fluctuations in field positions. Superimposed on these fluctuations one could detect a gradual trend outward, into the contralateral half-field of vision, so that deep in the postlateral

units; the longer lines, cells; the shorter, axons. Orientations of receptive fields of cells are indicated by the directions of these lines: a line perpendicular to track represents a vertical orientation; a line-plus-dot perpendicular to track represents a horizontal orientation. To the left, the position of each receptive field in the visual field is given with respect to the area centralis (center of gaze), which is indicated separately for every change of receptive-field orientation, by the intersection of the long common vertical line (the vertical meridian) and the short horizontal crossbars. Receptive-field orientations are shown by interrupted lines. The field of the first cell, oriented at 2:00, was thus about 5° below the area centralis, near the vertical meridian. (For technical reasons one cannot be sure that this field actually crossed into the ipsilateral field.) The next three cells had overlapping fields oriented at 1:30, slightly to the left of the first field, and overlapping it. Note the gradual drift of receptive fields away from the midline, so that the final ones recorded from area 18 lie almost 10° in the contralateral (left) visual field. All of the fields in 18 were complex. Geniculate axons in white matter, and cells in the suprasplenial gyrus, have fields whose positions are indicated in the same way, to the right of the figure. For convenience, fields of cortical cells are shown as rectangles; their precise borders were not always determined, but the diagrams by their width and length show accurately the optimum stimulus length, and the distance over which the stimulus was effective.

sulcus the fields had moved out about 8–10°. In the white matter a few geniculate axons were recognized by their clustered firing pattern (9, 12), and by the concentric center-surround arrangement of their receptive fields; some of the fields were located near the center of gaze, others in the far periphery. Finally, four cells recorded from suprasplenial striate cortex (i.e., from visual I) had their receptive fields 35–50° out in the contralateral visual field, close to the horizontal meridian.

In another experiment the postlateral sulcus was explored in its lateral bank at a slightly more posterior level (Fig. 2). The first cells had their receptive fields 15–20° out in the contralateral field of vision close to the horizontal meridian. As the electrode advanced down the bank there was a rapid inward drift in field position, so that halfway down the fields were

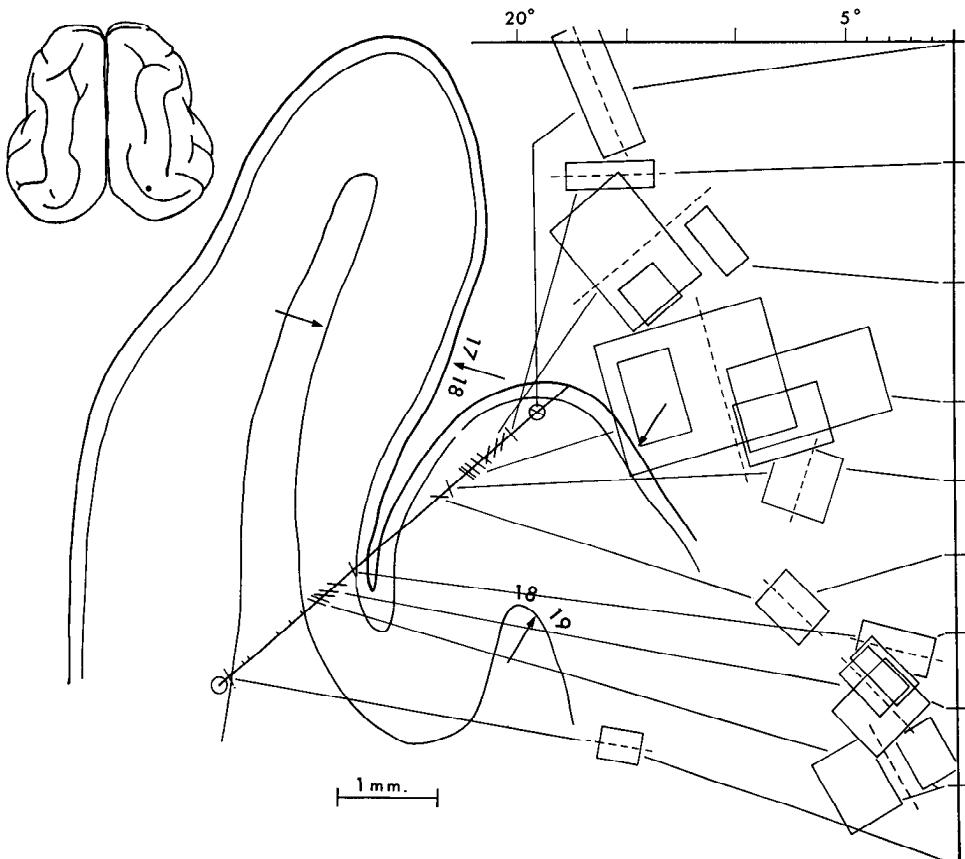


FIG. 2. Reconstruction of an electrode track that passed down the lateral bank of the postlateral sulcus, then through gray matter deep in the postlateral sulcus, and finally ended in area 17 (visual I) after crossing white matter. Of five axons recorded from white matter, four were from geniculate cells, and one was from a complex cortical cell. For conventions see legend of Fig. 1. Note how receptive fields move in toward the vertical meridian as the electrode moves medially across the cortex of visual II.

about 5–10° from the center of gaze. The electrode then crossed the sulcus to the opposite bank; here the fields of six cells were only about 5° out, and there was little or no detectable over-all drift as the full thickness of cortex was traversed, undoubtedly because this part of the penetration was almost perpendicular to the cortical layering. Several geniculate axons were recorded from white matter: their fields (not illustrated) were near the area centralis. Finally, a single cell recorded from the interhemispheric gray matter had its receptive field 17° out from the midline.

These two experiments suggest that as one proceeds laterally along the cortex, starting at the lateral margin of the primary visual area, the receptive fields of cells move out from the vertical meridian into the contralateral half-field of vision. This, together with other experiments to be illustrated below (Figs. 3, 29, 32), confirms the finding of Talbot and Marshall (27) that there is a topographically organized second visual area lateral to the primary one. Other characteristics of cells in visual II, such as field size and response properties, will be discussed below.

We were naturally interested in establishing the lateral boundaries of visual II, and in learning what lay beyond that area. The first of eight mapping experiments is illustrated in Fig. 3A. A series of four microelectrode penetrations was made at the level of the posterior end of the lateral gyrus, beginning about 2.5 mm. from the midline and working laterally. In the first penetration, two cells had receptive fields situated in the contralateral half-field of vision about 5° out from the midline. The second and third penetrations showed a clear progressive outward movement, establishing that these two penetrations (and probably also the first) were in visual II. In the fourth penetration most of the first 15 cells had tremendous receptive fields, some extending out as far as 60°. From cell 16 on, however, as the electrode advanced down the lateral bank of the gyrus, the receptive fields came to occupy positions closer and closer to the midline, indicating a reversal of the outward trend. At the same time there was an abrupt change in receptive-field size and response characteristics (to be discussed below). This experiment, which was subsequently confirmed in similar mapping experiments in 7 other animals (see for example, Fig. 31), indicates that there is a third topographically organized visual area lateral to the second. We term this area "visual III."

Some notion of the regions of cortex explored so far can be obtained from Fig. 37. The area centralis representation in visual III appears to be quite large, including much of the knee-like junction of the middle and posterior suprasylvian gyri. There is little doubt that visual III is arranged in a manner similar to visual I, in that as one proceeds forward along the cortex the receptive fields occupy progressively lower positions in the visual field. We have made no attempt to define physiologically the lateral borders of visual III, though in several short penetrations along the medial bank of the suprasylvian gyrus at the levels of Figs. 3 and 4 we failed to record responses to visual stimuli. At these levels, visual III would thus seem to occupy the

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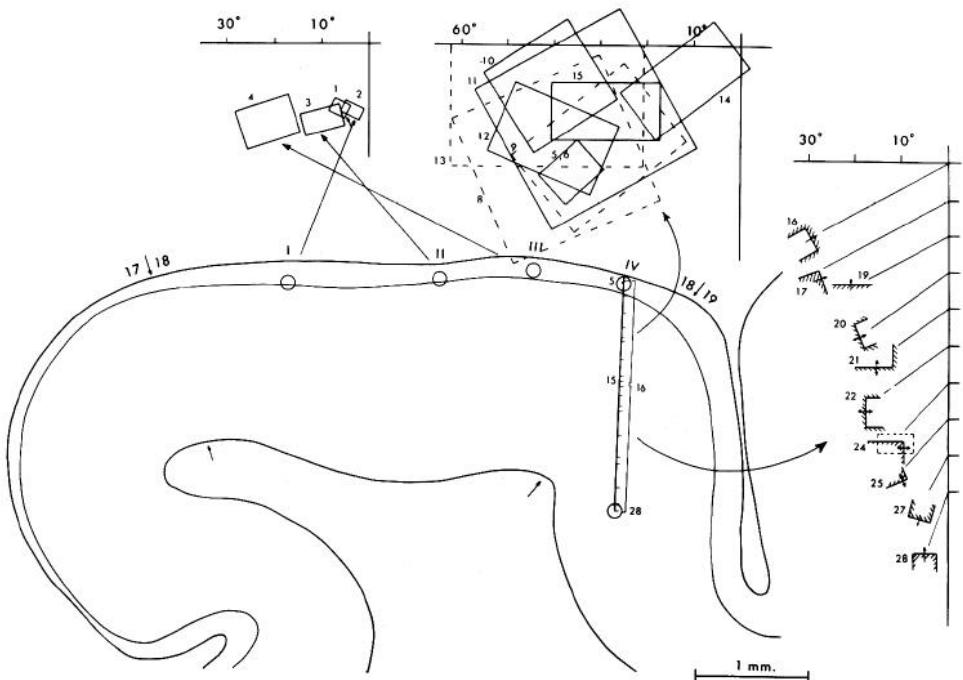
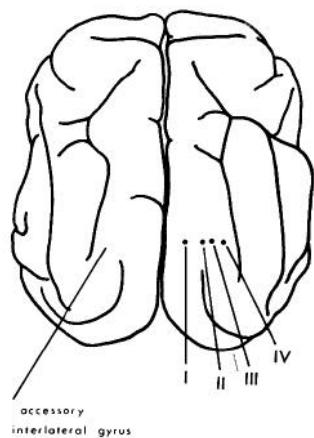
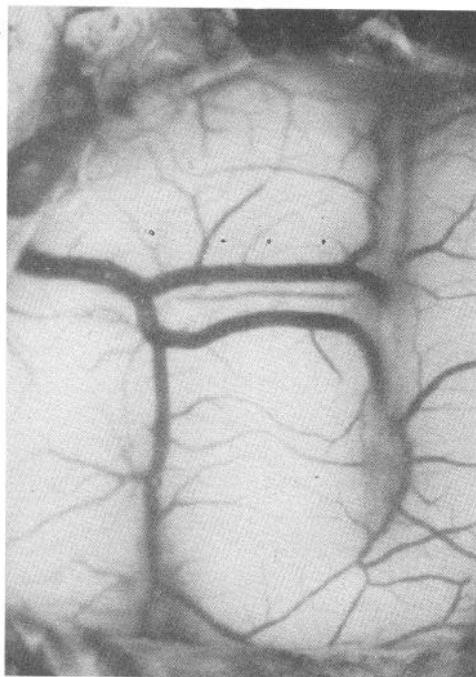
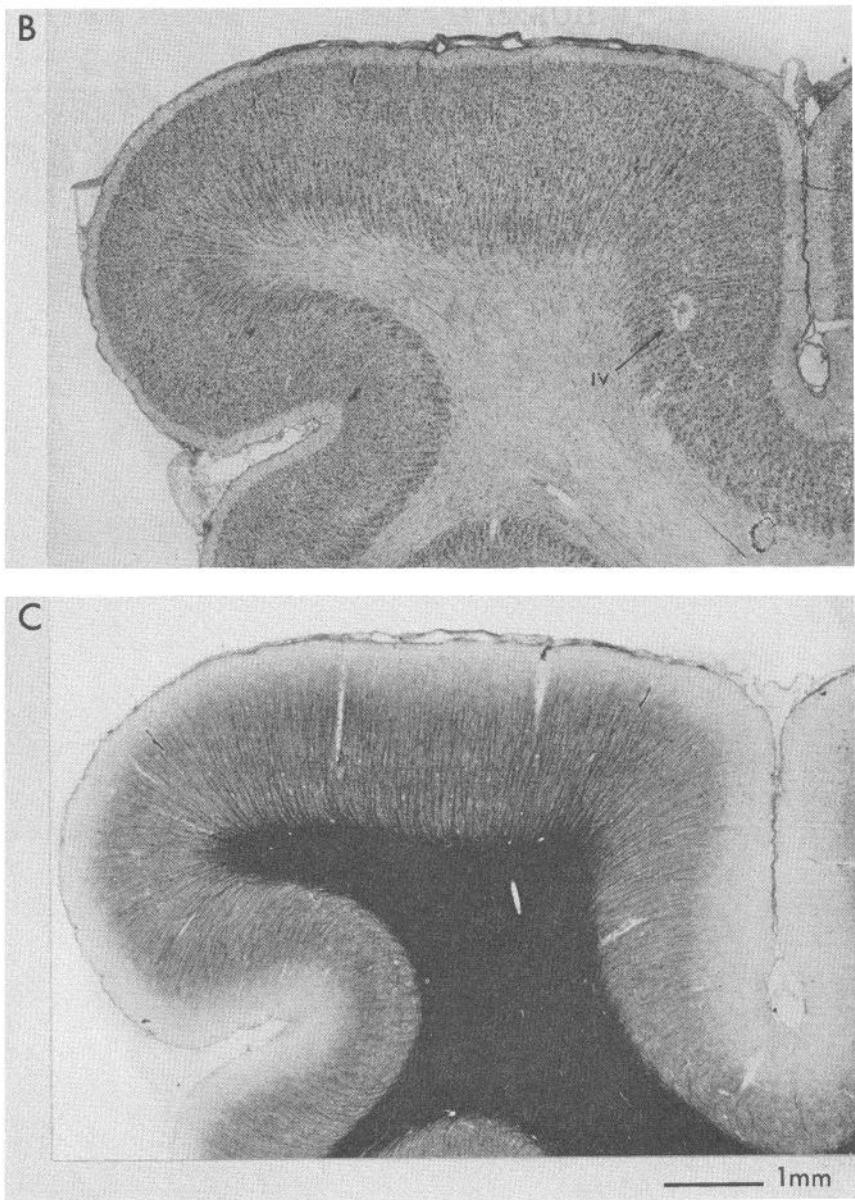


FIG. 3. A : four microelectrode penetrations through the right lateral gyrus near its posterior end. Points of entry are shown in brain tracing (upper right) and in a photograph of the exposed brain surface made at the beginning of the experiment (upper left; width of photograph, 8 mm.). Penetrations I, II, and III are superficial; in each of these a lesion was made at the positions of the first units recorded, and the electrode was then removed. Note that there was a progressive movement out into the contralateral visual field as the electrode moved laterally across 18. Penetration IV passed down along the lateral bank



of the lateral gyrus. Fields 1–15 of track IV illustrate the large size and wide scattering seen far out in 18. At cell 16 of track IV, the 18–19 (visual II–visual III) boundary, the fields began to move back toward the midline, and a high proportion were hypercomplex. Diagrams of fields 16–28 show the positions of the fields, and the optimum stimulus shape, orientation, and directions of movement. Cells 16, 20, and 22 responded to a light tongue on a dark background (a double-stopped edge); 27 and 28, to a dark tongue; 17, 24, and 25 to a dark corner on a light background; 21 to a light corner; and 19 (a complex cell) to an edge. The area over which a cell was driven was mapped carefully only for cell 24, and is shown by the interrupted rectangle. *B* and *C*: same experiment as Fig. 3A. Coronal sections through lateral gyrus; Nissl stain (cresyl violet) and myelin stain (Loyez). Same scale as coronal tracing in Fig. 3A. Arrow in Nissl section indicates second lesion of penetration IV. Note the lack of any dramatic transition in Nissl architecture between 17 and 18, and the very coarse myelination of radial fibers in 18.

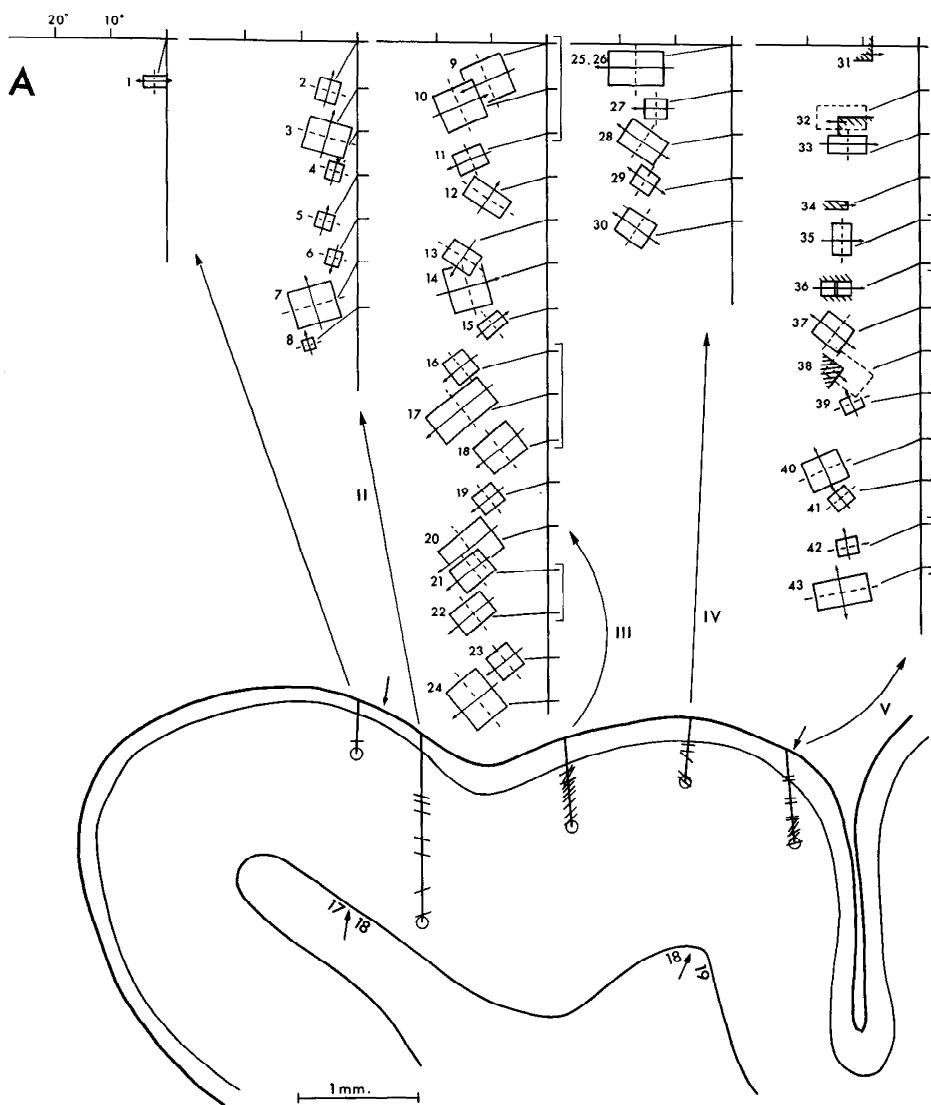
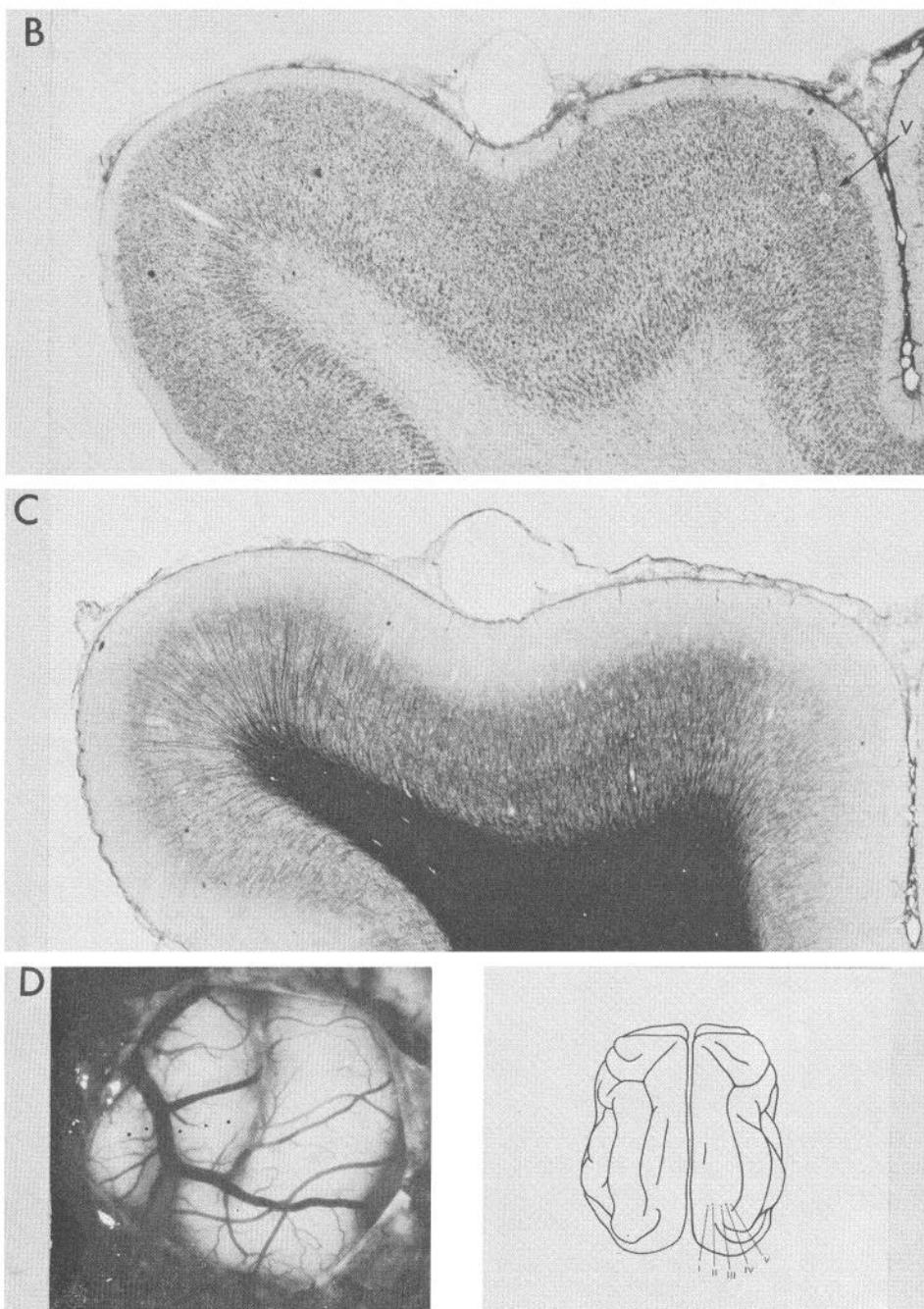


FIG. 4. *A*: reconstructions of five microelectrode penetrations in the lateral gyrus, from a single experiment. Conventions as in Figs. 1 through 3. Lines perpendicular to track represent a vertical receptive-field orientation for all penetrations except IV, where they indicate horizontal orientation. Note 1) how fields move progressively out as one moves laterally in area 18, but apparently no further, in this experiment, than 15–20° (penetration IV); 2) the relatively long sequences of cells with the same receptive-field orientations, in penetration III, which was almost perpendicular to the cortical surface; 3) the mixture of complex cells (rectangles) and hypercomplex cells (drawn with cross-hatching) in area 19. Cells 31, 32, and 38 responded to dark corners; 34 to a dark tongue (double-stopped edge); 36 to a double-stopped slit. Areas over which cells 32 and 38 responded are indicated by interrupted rectangles: the activating portion of field 36 is shown by the continuous rectangle. Arrow through receptive field indicates most effective direction of movement. *B* and *C*: Nissl-stained and myelin-stained coronal sections of lateral gyrus



in experiment of Fig. 4A. The Nissl section shows part of the electrode track and the lesion of penetration V. Note in the myelin section the coarse pattern formed by the radial fibers in area 18. D: left, photograph of cortical surface, showing entry points of the five penetrations. Right, tracing from photograph of brain surface; anterior is up.

entire lateral bank of the lateral gyrus (see area marked 19 in Fig. 37). A little further back visual III occupies the lateral half of the accessory inter-lateral gyrus (Fig. 37B), and extends over to the medial bank of the suprasylvian gyrus (see Fig. 29). Still further back (Fig. 37C; also Figs. 30 and 31) visual III begins in the medial wall of the posterior suprasylvian gyrus and extends laterally for an unknown distance.

In a few experiments involving a succession of penetrations from medial to lateral we failed to move far out into the periphery of the contralateral visual field while crossing visual II and III in succession. Figure 4 provides an illustration of this. Here as we proceeded laterally across the posterior part of the lateral gyrus the fields moved out in the usual manner, except that none of them extended further than about 15°; it seems unlikely that the entire remaining periphery could have been represented in the small unexplored area between penetrations IV and V. A similar experiment is illustrated in Fig. 29. It is thus our impression that the extreme lateral parts of the visual field may sometimes have no representation at these antero-posterior levels. It is as if the large regions of visual I, II, and III devoted to area centralis had crowded the lateral representations into more anterior and posterior parts of the cortex.

Correlation of the three visual areas with microscopic anatomy

An obvious question concerns the correlation of these three physiologically defined areas with cytoarchitectural subdivisions. The borders of areas 17, 18, and 19 were, accordingly, determined in Nissl- and myelin-stained sections of all the experimental brains, using slides that showed the electrode tracks and lesions. The criteria used were those given in a recent comprehensive study of the visual areas of the cat by Otsuka and Hassler (23). For determining both the medial and lateral borders of area 18 we have found especially useful the presence of large third-layer pyramidal cells in 18, and, in myelin-stained sections, the coarse, irregular, and often oblique pattern of fibers in the deeper cortical layers. In Figs. 1 through 4 and 29 through 32 the designations 17, 18, and 19 are based entirely on histological criteria.

A comparison of the physiologically defined visual areas I, II, and III with the anatomically determined 17, 18, and 19 has shown a remarkably exact correspondence. An example is shown in Fig. 3, where the border between visual II and III is precisely defined physiologically as occurring between cells 15 and 16. The correlation between this and the border between 18 and 19 seen on the myelin-stained section (Fig. 3B) is quite striking. In no case has there been any disagreement between physiological and anatomical findings. Moreover, our composite picture of the borders between visual I, II, and III from all experiments coincides well with the gross borders shown by Otsuka and Hassler (23: Fig. 8b), which are based on their own microscopic analysis.

PART II. RESPONSES OF SINGLE CELLS IN VISUAL AREAS II AND III

General comments

For every spontaneously firing cell in visual II and III, it was sooner or later possible to find a visual stimulus that evoked a response, unless the cell was badly injured or the cortex was in a pathologic state. By continuously stimulating the retina as the electrode advanced one could even activate and hence study a number of otherwise quiescent cells. There may, of course, be cells that neither fire spontaneously nor respond to visual stimuli. As in visual I (13), deepening the level of anesthesia suppressed spontaneous activity and made responses more sluggish, without, however, lowering the response specificity.

Outside of visual I no simple cells were found, and no axons with geniculate properties were encountered in gray matter. In visual II and III one can distinguish several distinct categories of cells. The first group contains cells that resemble complex cells of the striate cortex. A second large group consists of cells with more elaborate properties. All cells that exceed the complex type in the intricacy of their behavior we have called "hypercomplex," and within this group we distinguish lower order and higher order cells. The types of cells found in visual II and III are summarized in Table 1.

Complex cells

Complex cells were common both in visual II and visual III. In visual II they were in the overwhelming majority, forming 96% of the cells studied. This figure may, however, be misleading, since it includes cells recorded in early experiments done at a time when hypercomplex cells had not been recognized: 90% would probably be a closer estimate. In visual III, of 109 cells recorded, 46 (42%) were complex and 63 (58%) were hypercomplex.

Complex cells in visual II and III closely resembled those in visual I in their responses to retinal stimulation. Diffuse light or small circular spots evoked little or no response. A given cell was affected most by a line regardless of its precise position in the receptive field, provided the orientation was optimal; at 90° to the best orientation no responses were evoked. The preferred orientation differed from one cell to another, and there was no indication that any one orientation was more common than the others. If the adequate stimulus was a slit or a dark bar, its width was usually important: making it narrower or wider than some optimum usually rendered it ineffective. In the present context it is particularly worth emphasizing the effects of varying the stimulus *length*. A maximum response was obtained when the full length of a receptive field was covered; making the stimulus even longer had no additional effect, a result that is implicit in the term "receptive field," since we use this term in the sense of the entire region of the retina functionally connected with the cell. There was, in other words, simple summation of

stimulus effects over the entire receptive field along the direction of the field orientation. This was not true of the higher order cells to be described below.

Movement of an optimally oriented line stimulus in a direction perpendicular to the orientation was usually the most powerful way of activating a cell. The two directions of movement were not necessarily equally effective, and sometimes one direction of movement produced no response at all. The rate of movement was usually an important variable, since the cell's firing frequency tended to fall off sharply if the rate was less or greater than some

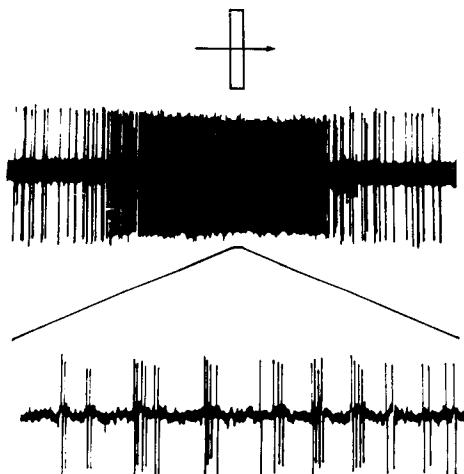


FIG. 5. Response of a complex cell, recorded from visual II, to a vertical $1^\circ \times 4^\circ$ slit moved slowly to the right at a speed of about $2^\circ/\text{sec}$. Stimulation of right (ipsilateral) eye; ocular-dominance group 5. Receptive field extended from the center of gaze out into the contralateral visual field for about 10° . A portion of the same response is shown with a faster sweep in the lower record, to illustrate the pattern of firing. Time, upper sweep, 10 sec., lower sweep, 200 msec. Background intensity, $0 \log_{10} \text{cd}/\text{m}^2$; slit, $1.3 \log_{10} \text{cd}/\text{m}^2$.

optimum. The most effective rates of movement varied from cell to cell, from about $0.1^\circ/\text{sec}$. up to about $20^\circ/\text{sec}$.

Figure 5 illustrates a type of cell commonly seen in both visual I and II. These cells fired rapidly, and in a characteristic pattern of very brief high-frequency bursts, as a line stimulus slowly crossed the receptive field. The cell of Fig. 5 was typical in that it responded when a slit was moved in one direction, but was neither excited nor inhibited by the reverse movement. (Edges or dark bars evoked only feeble responses). It was rare for a cell to be activated by movement in one direction and inhibited by movement in the reverse direction; one of the few convincing examples is shown in Fig. 6. Here the cell responded to a slit, bar, or either type of edge, with excitation to movement up and suppression of firing to movement down. Inhibition of this sort would, of course, tend to be overlooked in cells with a slow maintained rate of firing, and may be more common than our results suggest.

In visual II complex receptive fields tended to be larger than those in visual I. As in visual I, field size was loosely correlated with distance from the area centralis, a relationship that is illustrated in Fig. 7, where the area of each field is plotted against the distance of its geometric center from the area centralis. In some experiments in which visual II was explored from medial to lateral, receptive fields of successively recorded cells expanded in

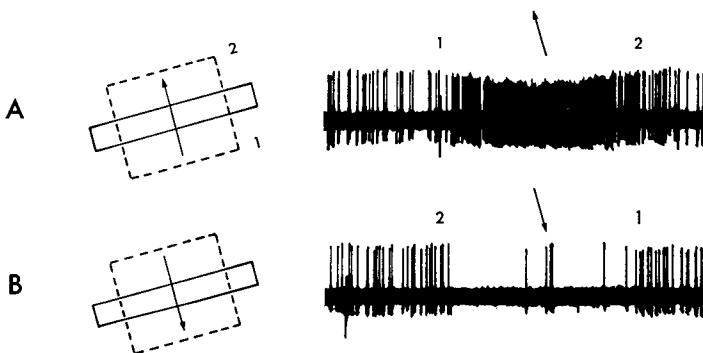


FIG. 6. Responses of another complex cell recorded in visual II, in the same penetration as the cell of Fig. 5. Stimulation of left (contralateral) eye, ocular-dominance group 3. Size of receptive field $3^\circ \times 4^\circ$. Upper record, optimally oriented slit, $6^\circ \times 1^\circ$, moved up across receptive field. Lower record, same slit, moved downward; note inhibition of resting discharge, beginning at 2, when slit enters field, and ending at 1, when it leaves. Rate of movement $0.5^\circ/\text{sec}$. Duration of sweeps, 10 sec. Stimulus intensities as in Fig. 5.

such a way, as they moved into the periphery, that their inner borders continued to extend medially almost to the vertical meridian. A field whose center was $30\text{--}40^\circ$ out thus came to occupy a large part of the contralateral visual field. As in visual I, all fields were confined entirely or almost entirely to the contralateral half-field of vision; many in fact stopped abruptly at the vertical meridian, and those that extended across it did so for such a small distance as to make it doubtful whether this represented a genuine encroachment on the ipsilateral field, or whether it was an artifact related to an error in estimation of the vertical meridian (see DISCUSSION).

Complex cells in visual III were similar in all respects to those found in the striate cortex. While no analysis was made of receptive-field size, as was done for visual II cells, we have the impression that the complex fields of visual III were similar in size to those of visual I.

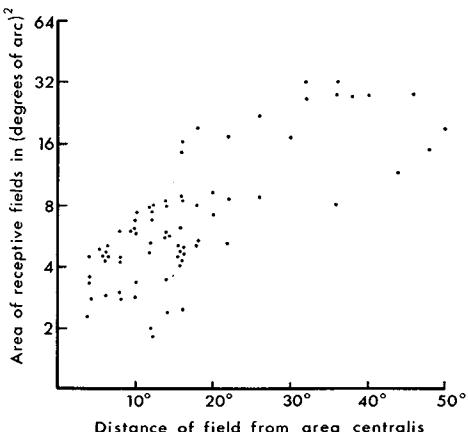


FIG. 7. Receptive-field areas in (degrees of arc) 2 of 72 cells in visual II, plotted against distance of the geometric center of each field from the area centralis.

Hypercomplex cells

Cells even more specialized than complex cells were present in both visual II and III. In visual II they formed about 5–10% of the population. In visual III they were much more numerous, comprising about half of the cells in some penetrations and almost all of them in others. A useful indication that an electrode had passed from visual II to visual III was the abrupt increase in the numbers of higher order cells. This is shown particularly well in Fig. 3, penetration IV.

We term these more complicated cells of areas 18 and 19 "hypercomplex." Cells in this group showed certain common features, but varied widely in

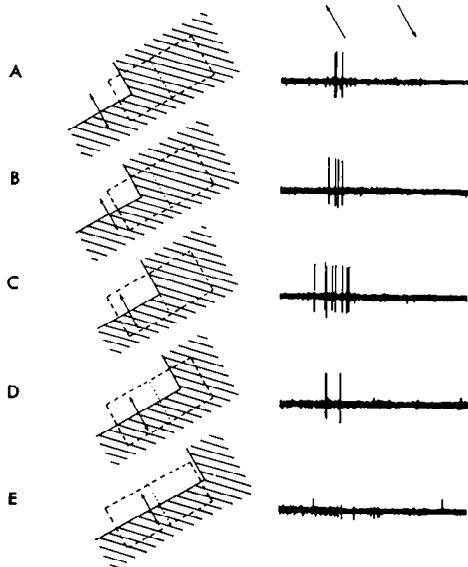


FIG. 8. Records from a hypercomplex cell in visual II (see Fig. 32, unit 7). Stimulation of right (ipsilateral) eye, ocular-dominance group 6. Receptive field, $2^\circ \times 4^\circ$, indicated by interrupted rectangle. Stimulus consisted of an edge oriented at 2:00, with dark below, terminated on the right by a second edge intersecting the first at 90°. Brighter regions, $1.3 \log_{10} \text{cd}/\text{m}^2$; dark areas, $0.0 \log_{10} \text{cd}/\text{m}^2$. A through C: up-and-down movement across varying amounts of the activating portion of the field; D-E: movement across all of the activating portion and varying amounts of the antagonistic portion. Rate of movement $4^\circ/\text{sec}$. Each sweep 2 sec.

other respects, both in the types of stimuli they responded to and in their apparent order of complexity. These common features and differences can best be described by several examples, and we shall begin by describing the responses of four lower order hypercomplex cells, and shall follow this with two examples of cells of higher order.

Lower order hypercomplex cells. Records of a hypercomplex cell in visual II are shown in Figs. 8 through 11 (see Fig. 32, unit 7). This cell responded best to a 2:00–8:00 edge with dark below, moved upward at about $2^\circ/\text{sec}$. over a circumscribed region as shown in Fig. 8C. The area over which responses were evoked, about $2^\circ \times 2^\circ$, is indicated roughly by the left half of the interrupted rectangle. As more and more of this area was stimulated the response steadily improved (Fig. 8, A through C). The orientation of the edge was critical, since changing it by more than 10° – 15° produced a marked decrease in the response, and a 30° change made the stimulus ineffective. Downward movement was entirely ineffective, as were small circular spots,

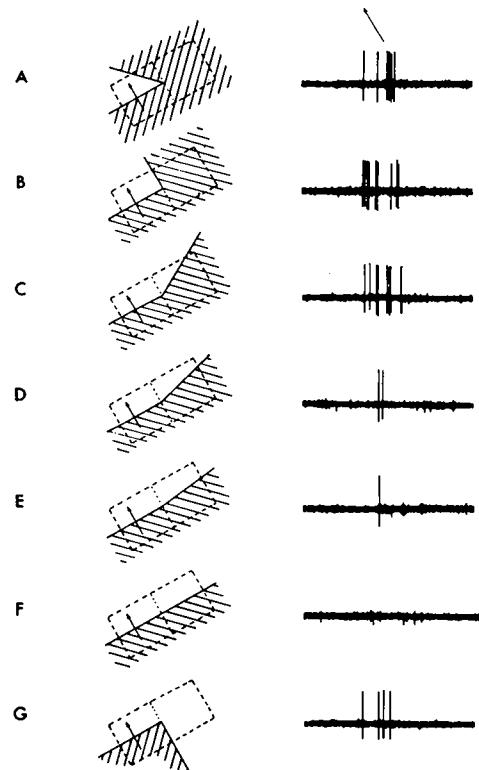
diffuse light, or up-and-down movement of an edge with dark above. The cell was driven by both eyes, the ipsilateral one giving the better responses (group 5).

From these responses alone one would conclude that this was an ordinary complex cell, responding to an edge at 2:00 with dark below, moved up. The situation was more complicated than that, however. The remainder of Fig. 8 shows that as more and more of the right half of the interrupted rectangle

FIG. 9. Same cell as in Fig. 8. Stimulation with two intersecting edges moved up across the receptive field as shown. Inhibition is maximum when the right (antagonistic) half of the receptive field is stimulated with an edge having the same orientation as the optimum edge for the left (activating) half (*F*). Duration of each sweep, 2 sec.

was included in the stimulus, simply by extending the edge further to the right, the response became progressively weaker, until it failed completely when the entire rectangular area was stimulated.

It would seem from Fig. 8 that this cell required as a stimulus an edge crossing the left half of the rectangular field, but also required that a similar edge should *not* simultaneously cross the right half. There are, however, several possible alternatives. Perhaps it was important to have the 11:00–5:00 edge come somewhere near the boundary between the two halves. Or perhaps it was necessary to have some kind of interruption in the continuity of the 2:00 edge at the boundary. The records of Figs. 9 through 11 allow one to eliminate some of these possibilities. In all of the records of Fig. 9, the left half of the interrupted rectangle was stimulated in the most powerful way; the orientation of the stimulus to the right was meanwhile varied through all possible angles. From the selection of records shown it is clear that the closer the orientation was to that of the left edge, the weaker was the response. Stimulating the right ("antagonistic") region thus effectively suppressed the response, provided the orientation of the edge crossing that region was not more than about 15° or so from the inclination that was optimal for the



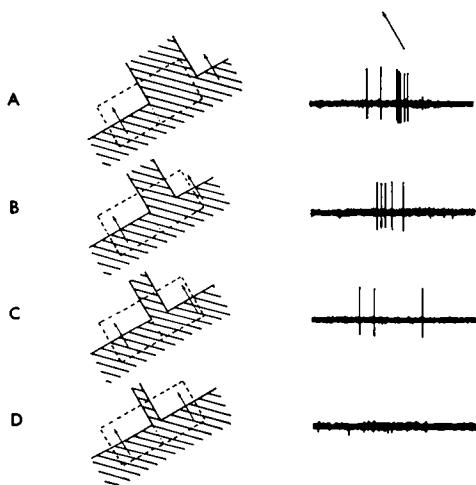


FIG. 10. Same cell as in Figs. 8 and 9. Each time an optimally oriented stopped edge is moved up across the activating (left) part of the receptive field at optimal speed ($2^\circ/\text{sec.}$), a second edge is simultaneously moved up to the right of the first, at varying distances. The antagonistic effect, first noted about 2° from the boundary between the two parts of the field, increases the closer the edge is to this boundary. Sweep duration, 2 sec.

left half. This represents an orientation specificity comparable to that of the left ("activating") region.

By stimulating the left and right subdivisions of the field separately, and varying the length of the right-hand stimulus, as shown in Fig. 10, it was found that the antagonistic region had roughly the same length as the activating. Records 10C and 10D suggest, moreover, that merely having a discontinuity near the dotted line dividing the rectangles, even in the form of an 11:00-5:00 edge, was not enough to make the 2:00 edge effective. This is further supported by the experiment of Fig. 11, in which a notch of varying width interrupted the edge. Here, moreover, one could map roughly the extent of the antagonistic area in the 11:00-5:00 direction, and show that it was roughly equal to the extent of the activating region.

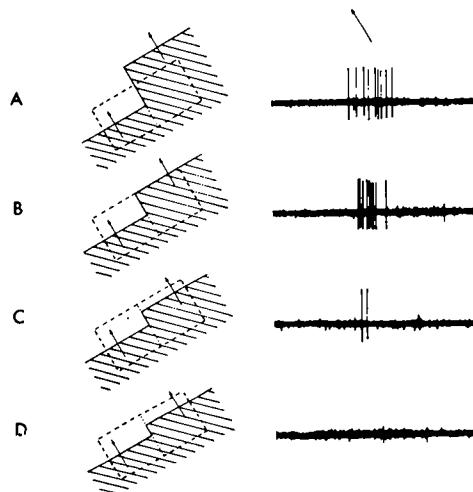


FIG. 11. Same cell as in Figs. 8 through 10. The two halves of the field are stimulated simultaneously by two edges separated by a step of varying height; antagonistic effects are first seen when the step equals the width of the field, and increase as the step is narrowed, to about $1/2^\circ$, after which no change is seen. Each sweep, 2 sec.

From these experiments the essential property of the cell seems to have been its responsiveness to a specifically oriented edge, provided the edge was limited in its length at one end (in this case the right). As to the extent of the edge to the left, the longer it was the better was the response, until it passed the left boundary of the interrupted rectangle; beyond that point the length made no difference. For convenience we shall refer to cells of this type as responding to a "stopped edge." A term such as "corner cell" has the disadvantage that the cell responded not to all corners, but to a particular class

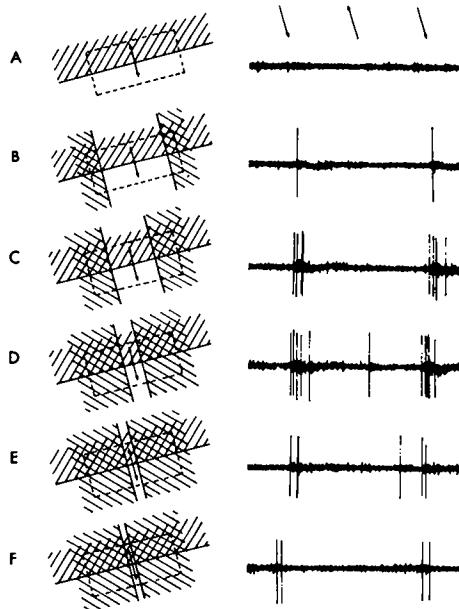


FIG. 12. Recordings from a cell in area 19 of the right hemisphere; stimulation of left eye. Receptive field about 8° below the center of gaze, about 13° long and 6° wide. Rapid ($30^\circ/\text{sec.}$) up-and-down movement of a long edge with dark above evoked no response (A). Responses to downward movement began to appear when the stimulus was limited in its length (B, C), and became maximal when a $2\frac{1}{2}^\circ$ -wide region in the center was stimulated (D), at which point an occasional response occurred even to upward movement. Further narrowing made the response weaker (E and F). Duration of each sweep, 1 sec.

of corners (those of Fig. 9, B and G) over a narrow range of orientations and positions.

A hypercomplex cell of a second type, this one recorded from visual III, is described in Figs. 12 through 15. It was driven from the contralateral eye only (group 1). It responded to an edge moved very rapidly down and to the right, but only if the region stimulated was restricted on both sides. In Fig. 12A, for example, moving a very long edge down gave no response. The edge became effective when it was shortened by blocking out both ends of the region being stimulated, and the responses increased until all but the center $2\frac{1}{2}^\circ$ was eliminated (Fig. 12, B and D). At this point there was not only a brisk response to movement down, but also a weak response to movement up. Further narrowing of the area stimulated reduced the response.

The $2\frac{1}{2}^\circ$ stimulus of Fig. 12D was most potent when it was oriented in a 2:00 direction. As shown in Fig. 13, a 30° change in either direction all but eliminated the response.

To assess the relative effectiveness of the end zones of the interrupted

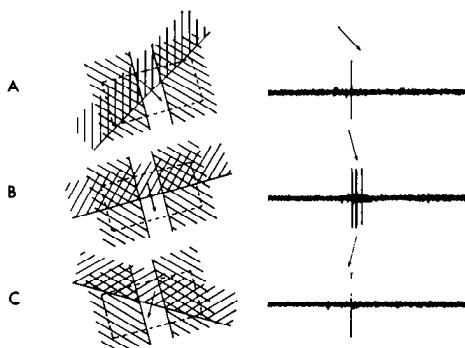


FIG. 13. Same cell as in Fig. 12. Effects of varying the orientation of the edge. Duration of each sweep, 1 sec.

rectangle in interfering with the response, each end was blocked off in turn (Fig. 14, A and B). Both end regions were clearly capable of antagonizing the responses, the right one somewhat more so than the left, and eliminating both produced the best response, with even an occasional impulse in response to upward movement. One can say that this field was "stopped" at both ends. The region stimulated could be constricted either by blocking off the end regions (as in Figs. 12 and 13; or 14, A through C) or by reducing the length of the edge (Fig. 14, D through F); when the length was reduced the optimum stimulus became a $2\frac{1}{2}^{\circ}$ tongue moved rapidly into the activating part of the field in a 11:00-5:00 orientation (Fig. 14F). The exact positioning of the stimulus was then highly critical, since introducing it even slightly to the left or right of the central region presumably meant reducing the activating area covered and at the same time including some of the antagonistic. This is shown in Fig. 15.

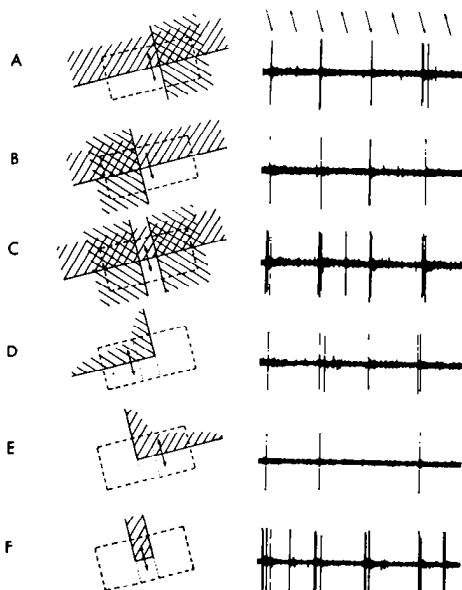


FIG. 14. Same cell as in Figs. 12 and 13. In A and B portions of the field to the right and left of the $2\frac{1}{2}^{\circ}$ -wide center are blocked separately, to show that the more important antagonistic region is to the right. The equivalent experiment is repeated in D and E, using dark corners. In F, which corresponds to C, a dark tongue is used instead of an edge blocked to either side; a dark tongue moved in from above (F) is equivalent to a light tongue moved out from below (C). Duration of each sweep, 2 sec.

For this cell and the previous one the receptive field, defined as the entire area functionally connected with the cell, is outlined by the interrupted rectangles. The fields so defined are subdivided into activating and antagonistic regions in a manner analogous to the excitatory and inhibitory parts of simple fields we have described in previous papers (10, 13). The terms "excitatory" and "inhibitory," if used for hypercomplex fields, must be understood in a more abstract way, since the effects of the regions do not add or subtract in any simple spatial sense, but only along a line parallel to the receptive-field axis (see DISCUSSION). For the cells described below (Figs. 16 through 20), interrupted rectangles are used to outline the excitatory (or activating) subdivision of receptive fields and the antagonistic regions are not shown.

The two cells just described responded best to edge stimuli. Two examples of cells responding to slits and dark bars are shown in Figs. 16 and 17 and

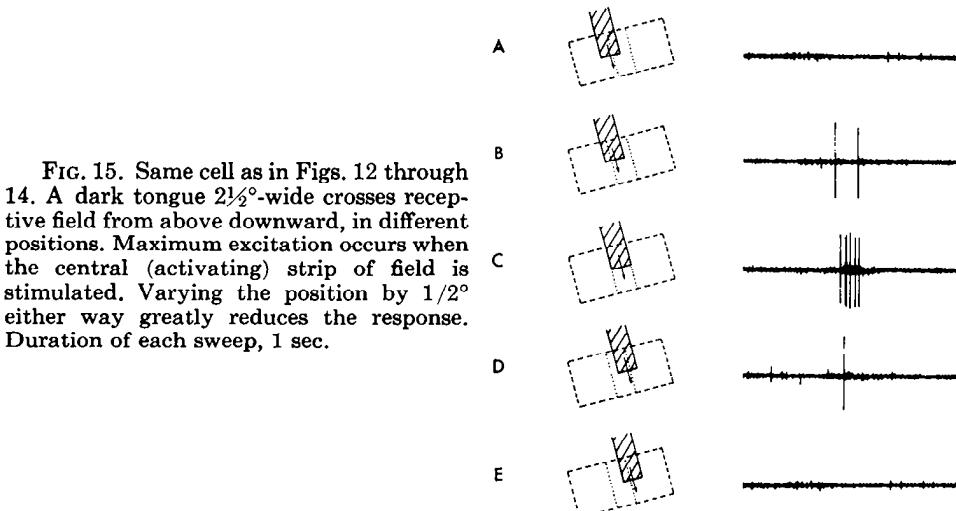


FIG. 15. Same cell as in Figs. 12 through 14. A dark tongue $2\frac{1}{2}^{\circ}$ -wide crosses receptive field from above downward, in different positions. Maximum excitation occurs when the central (activating) strip of field is stimulated. Varying the position by $1/2^{\circ}$ either way greatly reduces the response. Duration of each sweep, 1 sec.

Figs. 18 through 20. These cells were recorded in sequence from a single penetration of visual III in the right hemisphere (see Fig. 29, units 21 and 22). Unit 22, illustrated in Figs. 16 and 17, responded best to a slit $1/8^{\circ}$ wide and 2° long, oriented about 15° to the horizontal. It was driven by both eyes, but preferred the ipsilateral (group 5). Brisk responses were evoked with stationary stimuli: shining the slit anywhere within a $2^{\circ} \times 2^{\circ}$ region evoked an "on" response (Fig. 16, A through C), provided the orientation was within about $20-30^{\circ}$ of the optimum. At 90° to the optimum there was no response (Fig. 16D). A slit $1/8^{\circ}$ wide, as used in A through C, was clearly optimal, and this dimension was critical, since $1/16^{\circ}$ and $1/4^{\circ}$ evoked distinctly weaker responses, and $1/2^{\circ}$ was ineffective. Taken by themselves, these results would be typical for an ordinary complex cell. This cell, however, responded weakly or not at all to a $1/8^{\circ}$ slit extending several degrees beyond the excitatory region in both directions (Fig. 16E).

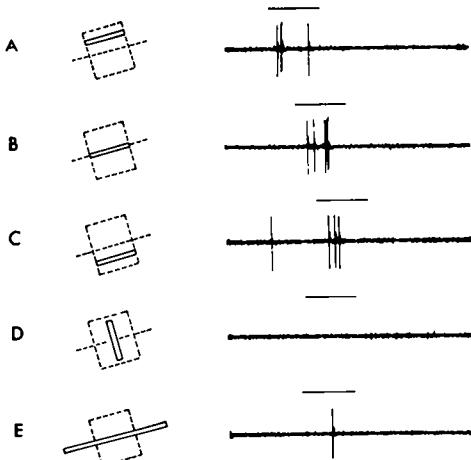


FIG. 16. Responses of a cell recorded in area 19, right hemisphere (see cell 22, penetration V, Fig. 29). Receptive field was 10° below and to the left of the center of gaze. Excitatory portion roughly $2^\circ \times 2^\circ$, represented by interrupted rectangle. A through C, stimulation with an optimally oriented slit, $1/8^\circ \times 2^\circ$, in various parts of receptive field in right (ipsilateral) eye. D: same slit, shone at 90° to optimum orientation. E: optimally oriented slit $5 1/2^\circ$ long, extending beyond excitatory region on both sides. For each record upper line shows when stimulus light was on. Duration of each sweep, 1 sec. Intensity of slit, $1.0 \log_{10} \text{cd}/\text{m}^2$; background, $0.0 \log_{10} \text{cd}/\text{m}^2$.

Responses to moving stimuli are shown in Fig. 17. Upward movement, not illustrated in Fig. 17, was about as effective as downward. The optimum rate was of the order of $3^\circ/\text{sec}$. By stimulating with slits extending beyond the excitatory region in one or both directions and for various distances, it was possible to compare the inhibitory capabilities of the two outlying regions and form some idea of their extent. From the responses shown in Fig. 17 we concluded that inhibitory areas were present at both ends, extending $2-3^\circ$ beyond the ends, with the left stronger than the right (Fig. 17, cf. B with D, or C with E).

Another cell, recorded just prior to the one described above, had many similar properties but several interesting differences (Figs. 18 through 20).

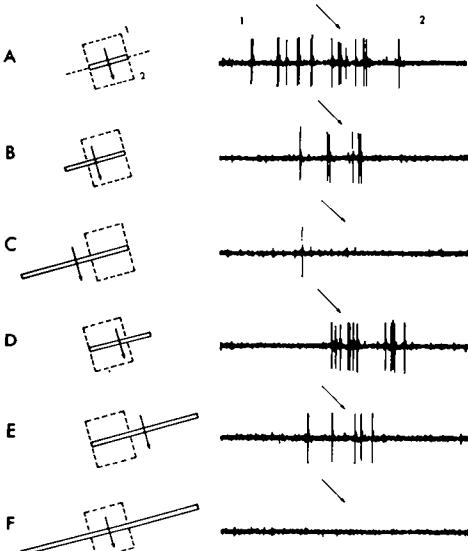
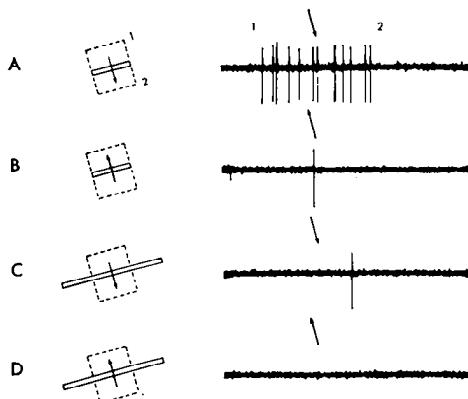


FIG. 17. Same cell as in Fig. 16. Responses to $1/8^\circ$ -wide slits of various lengths moved downward across receptive field at about $3^\circ/\text{sec}$. A: stimulation of activating part only; B through F: stimulation of activating part, as well as varying portions of the antagonistic flanks. Right flank is weaker than left. Sweep duration, 1 sec.

FIG. 18. Cell recorded near that of Fig. 16 and 17 (see Fig. 29, cell 21, penetration V). Receptive field 8° below and to the left of the center of gaze; activating portion, roughly 4° long and $3-4^\circ$ wide, denoted by the interrupted rectangle. Responses to up-and-down movement of a slit $1/8^\circ \times 3^\circ$ (A and B), and $1/8^\circ \times 8^\circ$ (C and D). Intensity of slit, $1.3 \log_{10} \text{cd/m}^2$; background, $0.0 \log_{10} \text{cd/m}^2$. Rate of movement about $3^\circ/\text{sec.}$; sweep duration 2 sec.



Like the last cell, it was driven from both eyes, but preferred the contralateral (group 3). It responded to a slit, and again the optimum width was $1/8^\circ$ and the orientation was about 15° to the horizontal. A moving stimulus was far more effective than a stationary one, and downward movement was more effective than upward over a range of about 4° . The optimum length was about 3° (Fig. 18, A and B). Extending the slit in both directions made it virtually ineffective (Fig. 18, C and D), showing that this cell, like the last,

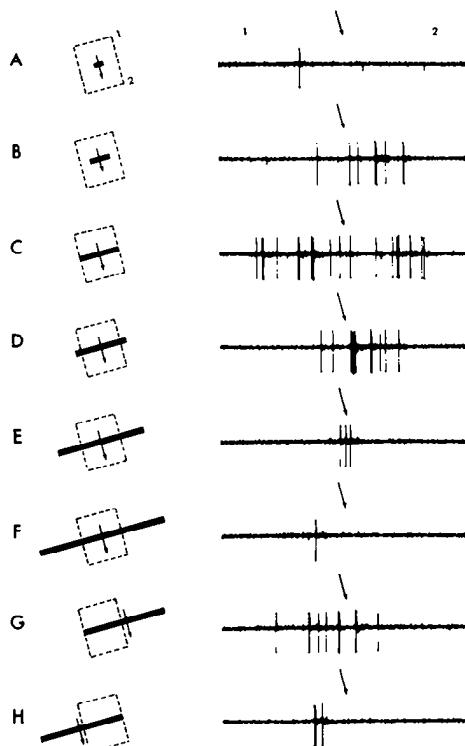


FIG. 19. Same cell as in Fig. 18. Responses to black bars, $1/8^\circ$ wide and of various lengths, moved down over various parts of the receptive field, as indicated to the left. Rate of movement about $2^\circ/\text{sec.}$ Intensity of bar, $0.0 \log_{10} \text{cd/m}^2$; surround, $1.3 \log_{10} \text{cd/m}^2$. Sweep duration, 2.5 sec.

was no ordinary complex one. Unlike the cell just described, it responded to a black bar at least as well as to a slit; the optimum dimensions were the same, as was the directional preference for downward movement. Figure 19 demonstrates summation within the confines of the activating part of the field and antagonism from the outlying parts, and it emphasizes how critical the optimum length can be. From Fig. 19, G and H, it seems that for this cell the left-hand antagonistic region was more powerful than the right-hand one.

The experiment of Fig. 20 was designed to measure how far the left antagonistic area extended, by stimulating the activating area with a downward-moving slit, at the same time moving down a second slit at varying distances to the left of the first. It would seem that most of the antagonistic region was within about $2\text{--}3^\circ$ of the activating region. In Fig. 20E we show that stimulation of the flanking region by itself was without effect. Perhaps this was because there was too little spontaneous activity for any inhibition to be apparent. A failure to respond to stimulation of an antagonistic region alone has been observed in all hypercomplex cells so far studied.

The four cells just described had in common a close resemblance to complex cells, except that their receptive fields were stopped at one or both ends. Hypercomplex fields, like complex ones, occurred in all orientations, with no

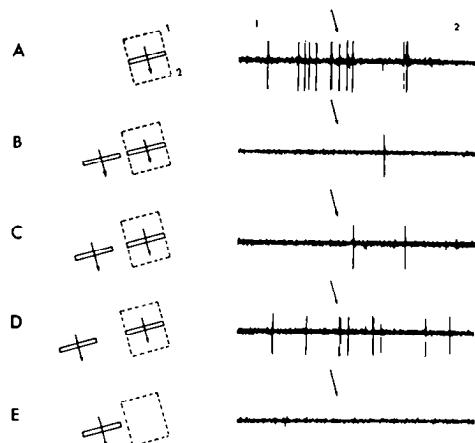


FIG. 20. Same cell as in Figs. 18 and 19. A: responses to slit $1/8^\circ \times 3^\circ$ moved down across the activating region. B through D: responses to two slits, $1/8^\circ \times 3^\circ$, one moved down across the activating region, the second moved simultaneously in the left flank, at varying distances from the first; E: second slit moved in flank, unaccompanied by the first. Sweep duration, 2 sec.

indication that one orientation was more common than any other. From these and other examples we find that the main types of ordinary complex cells—distinguished by whether they respond to slits, edges or dark bars, or any combination of these—all have their counterparts among the hypercomplex cells. A hypercomplex cell driven by edges may have its field stopped at one end (Figs. 8 through 11) or at both ends (Figs. 12 through 15). So far, hypercomplex cells activated by slits or bars (Figs. 16 through 20) have all had fields stopped at both ends. The frequency with which these various cell types were observed is shown in Table 1.

Higher order hypercomplex cells. Twelve hypercomplex cells recorded in visual III had properties that could not be described in these relatively simple terms. We have called such cells “higher order hypercomplex.”

One of the main characteristics of higher order cells was an ability to respond to two sets of stimuli with orientations 90° apart. Figures 21 and 22 show records of unit 2 in the experiment of Fig. 30. This cell responded to stimulation of either eye (group 5), to a 2:00 edge with dark above. With a stimulus stopped to the left (Fig. 21B) the cell responded to movement down

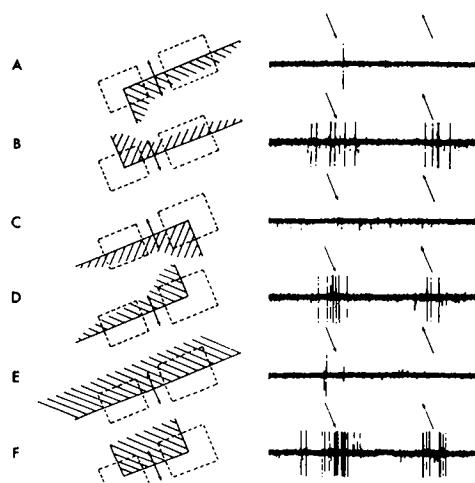
Table 1. 290 cells recorded in areas 18 and 19

Cell Type	Activated by	Visual II	Visual III
Complex	Edge	38	6
	Dark bar	12	12
	Slit	72	23
	Mixed	17	0
	Uncategorized	34	5
Total		173	46
Hypercomplex*	Edge		
	single-stopped (corner)	6	18
	double-stopped (tongue)	0	33
	Slit (double-stopped)	2	5
	Dark bar (double-stopped)	0	3
	Uncategorized	0	4
Total		8	63
Totals		181	109

* Eleven of the cells in visual III were classed as higher order hypercomplex.

or up throughout an oval area indicated roughly by the left interrupted rectangle. With the edge stopped to the right (Fig. 21D) the cell responded over a separate region suggested by the right interrupted rectangle. Corners made from an edge with dark below were almost ineffective (Fig. 21, A and C), as was an unstopped edge with dark above (Fig. 21E). A dark tongue 5° wide, combining the two corners of Fig. 21, B and D, evoked a very brisk response when it was moved in from above (Fig. 21F). The responses shown in B, D, and F were highly sensitive to the orientation of the stimulus, and fell off quickly if the orientation was changed by more than 10–15°. Up to

FIG. 21. Responses of a cell recorded in area 19, right hemisphere (see cell no. 2, Fig. 31). Receptive field 6° from center of gaze. Regions from which responses were evoked are indicated roughly by the two interrupted rectangles, of which the right was 3° × 4° in size. A right-angled corner with dark up and to the right (B) evoked responses when moved down or up over the left-hand region; no response was evoked in the right-hand region. A corner with darkness up and to the left evoked responses to up-and-down movement only over the right-hand region (D). Little or no response was obtained with corners with dark below (A and C), or with unstopped edges (E). A tongue (F), combining stimuli B and D, gave the most powerful responses. Rate of movement, about 0.5°/sec. Duration of each sweep, 20 sec. Intensities, shaded areas 0.0 \log_{10} cd/m²; background, 1.0 \log_{10} cd/m².



this point, then, the cell behaved in many respects like a lower order hypercomplex cell responsive to a double-stopped edge, such as that of Figs. 12 through 15. Considered in that way, the field would have a central activating region, presumably including most of the two rectangular areas and the region between them, flanked on both ends by antagonistic areas. It seems doubtful, however, whether such a simple arrangement could explain the properties of this cell. The relatively large regions over which corners evoked responses indicate that the points at which the edges were stopped were not very critical. This was not generally true for a lower order hypercomplex cell (cf. Fig. 15): usually the more of the activating region the stimulus covered the more active was the response, with a sharp dropoff in response as soon as the inhibitory region was invaded. In this cell the responses to each corner were, on the contrary, surprisingly vigorous and uniform over its own entire rectangle, suggesting a complexity of organization greater than that of any hypercomplex cells described up to now. A better example of this kind of behavior is provided by the cell to be described next (Figs. 23 through 26).

That the cell just described was complex in still another way is shown in Fig. 22. The cell responded vigorously when the corner used in Fig. 21D was

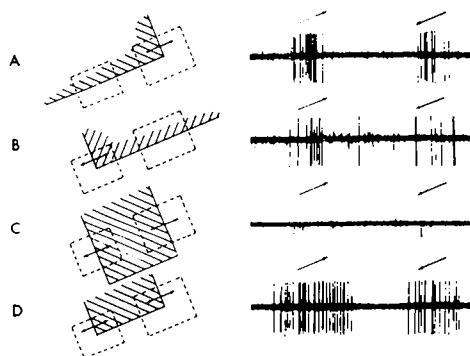


FIG. 22. Same cell as Fig. 21. Responses to movement down and to the left, and up and to the right, of corners with dark above (A and B); failure to respond to an unstopped dark bar (C); strong response to a dark bar stopped below (D), combining stimuli (A) and (B). Sweep duration, 20 sec.

moved down and to the left or up and right (Fig. 22A). Sidewise movement, like downward movement, evoked responses only when the stimulus corner was oriented as shown in Fig. 22, A and B; a change of 15–20° was enough to abolish the response. The range over which a response was evoked was very nearly the same as before, and is indicated by the same interrupted rectangle. The corner of Fig. 21B similarly evoked a brisk response when moved sidewise over the left-hand rectangular area, as shown in Fig. 22B. Combining the two stimuli by using a wide bar produced a very powerful response (Fig. 22D), whereas there was no response when the bar extended below the excitatory regions (Fig. 22C).

This cell would seem to combine the attributes of two sets of lower order hypercomplex cells, one set having a 2:00 receptive-field orientation, the other a 5:00 orientation. Such complicated cells, combining characteristics of two groups of lower order hypercomplex cells with orientations 90° apart,

seem to be much less common than ordinary lower order hypercomplex cells, in that we have seen only 11 of a total of 63 hypercomplex cells in visual III, and have found none in visual II. A high proportion (8 cells) were recorded in two of the penetrations (see Figs. 30 and 31), both of which were in the region of area centralis representation. The behavior of these cells can be better understood by considering responses of other neighboring cells recorded simultaneously or in the same penetration, a topic that is taken up in a later section (p. 261).

A second example of a higher order cell is shown in Figs. 23 through 26. Recorded in the same penetration as the last cell (see Fig. 30, unit 6), its

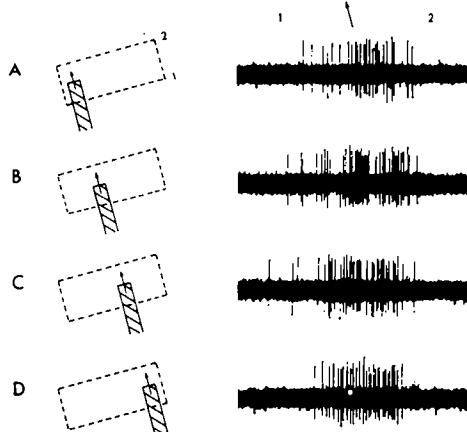


FIG. 23. Responses of a cell recorded in area 19, right hemisphere (see cell no. 6 of Fig. 31). Region from which responses were evoked, $4^\circ \times 1\frac{1}{2}^\circ$, are indicated approximately by the interrupted rectangle. Responses to a dark tongue $1/2^\circ$ wide introduced from below in four different positions, at a rate of about $0.5^\circ/\text{sec}$. Intensities as in Fig. 21. Duration of each sweep, 5 sec.

receptive field was in roughly the same region, and measured $4^\circ \times 1\frac{1}{2}^\circ$. A powerful response was evoked by an edge with dark below, inclined at 15° to the horizontal, stopped at both ends, and introduced into the field from below at a rate of about $1^\circ/\text{sec}$. The response was markedly reduced by changing the orientation by 20 – 30° . Although the field itself was 4° long, the optimum length of the stimulus edge was only $1/2^\circ$. Indeed, the most interesting feature of this cell was its ability to respond regardless of where along the 4° -long lower border of the field the stimulus was introduced (Fig. 23)—this despite the fact that an edge only slightly longer than $1/2^\circ$ was distinctly less effective, and a 2° edge evoked no response (Fig. 24). Active responses were evoked not only to a $1/2^\circ$ -long double-stopped edge, but also to a double-stopped slit or dark bar, whose optimal length was again $1/2^\circ$: the thickness of the stimulus was not critical provided it exceeded $1/4^\circ$.

This cell, then, had many features similar to the cell of Figs. 12 through 15, in responding to an appropriately oriented edge stopped at both ends: it differed in that it responded over a wide area of receptive field, whereas with the other cell there was a well-defined region from which responses were evoked, flanked by regions from which responses could be suppressed. Indeed, it is as if properties like those of the previous cell had been generalized

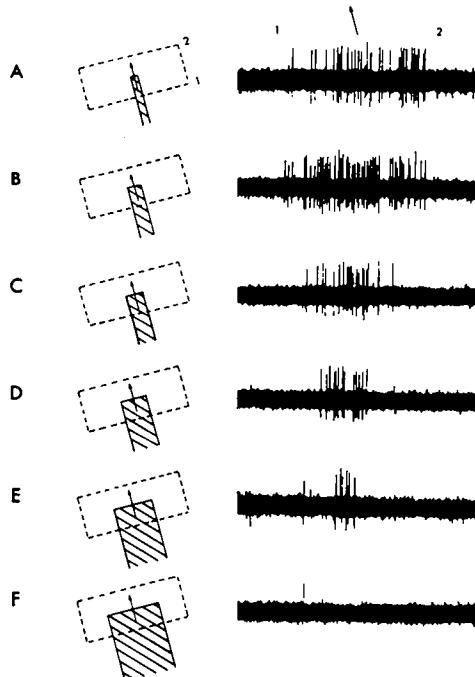


FIG. 24. Effects of varying the width of tongue, in cell of Fig. 23. Movement from below up over center of field at rate of 0.5°/sec. Widths, A through F, are $1/4^\circ$, $1/2^\circ$, $3/4^\circ$, 1° , $1\frac{1}{2}^\circ$, and 2° ; optimum width (B), $1/2^\circ$. Duration of each sweep, 5 sec.

over a considerable expanse of retina. This generalization was probably also a feature of the last cells (Figs. 21 and 22), though in that case it was perhaps not so clear. These two cells were also similar in their ability to respond to either of two stimuli 90° apart. A powerful response was obtained with a $1/4^\circ$ -wide slit or dark bar, oriented at 2:30 and introduced into the receptive field from the right at a rate of about $1^\circ/\text{sec}$. (Fig. 25); left-to-right movement gave a much weaker response. The stimulus worked regardless of the exact level

at which it crossed the field (Fig. 25, A through C). Yet a slit or dark bar 1° wide evoked no response (Fig. 25D). The orientation was again critical to within $15-20^\circ$; but, surprisingly, changing the orientation of the 11:30 leading edge by using instead a sharply pointed slit or bar did not lessen the potency of the stimulus, so that the important thing was probably the direction of movement of the stimulus, and not the orientation of the leading edge.

Finally, this cell showed a phenomenon that we have occasionally seen in complex cells as well as hypercomplex ones. As a stimulus was repeated time after time at intervals of 2-3 sec. it tended to become progressively less effective, until finally the cell failed to respond. For example, in Fig. 26 a $1/2^\circ$ tongue was brought in from below and moved up slowly through the field, and this was repeated once every 3 sec. After four stimuli the

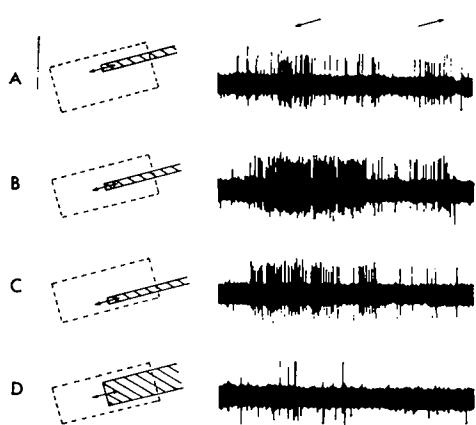


FIG. 25. Same cell as in Figs. 23 and 24. A through C: responses to a dark $1/4^\circ$ tongue moved across the field from right to left in various positions as shown, at a rate of $1^\circ/\text{sec}$. D: response to a 1° tongue moved across field. Duration of each sweep, 10 sec.

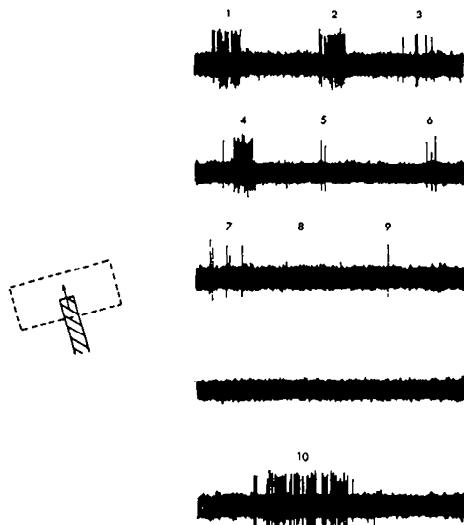
FIG. 26. Same cell as in Figs. 23 through 25. Continuous record. Dark tongue $1/4^\circ$ wide is moved up and down over center of field at $1^\circ/\text{sec.}$, and the stimulus is repeated every 2–3 sec. By the eighth or ninth repetition the cell is failing to respond. No stimulus is given for 10 sec. The tenth stimulus is then highly effective. Each sweep, 10 sec.

response began to fail, and after nine stimuli the cell had virtually stopped responding. Now no stimulus was delivered for about 10 sec. A new stimulus (10) introduced after this resting period was once more quite effective. If the dark bar was introduced each time in a different part of the field, there was no progressive decline in the response. If it was reintroduced repeatedly in the same place, as in Fig. 26, until the response faded, a brisk response occurred when it was suddenly introduced in a new place.

This kind of progressive decline in responsiveness has often been seen in complex cells in visual I and II. For example, many cells are strongly influenced by a critically oriented stationary line stimulus regardless of its position within the receptive field (13: text-Fig. 7). Such cells often fail to respond after several applications of the stimulus in the same place; changing the part of the field stimulated revives the response. In cells of this type, moving the stimulus generally produces a vigorous discharge, perhaps because new regions of the receptive field are being stimulated successively.

Binocular interaction

For most cells in visual II and III the receptive-field characteristics were worked out separately for each eye, and then both eyes were stimulated together. The results were very similar to those we have previously reported for cells in visual I (13). Most cells, though not all, were influenced independently from the two eyes. A cell that could be driven from both eyes always had receptive fields in corresponding positions in the two retinas, at least to within the limits of accuracy of the method: the two receptive fields thus occupied the same position in the contralateral visual field. The two receptive fields were of the same size and arrangement, so that whatever stimulus was the most effective in one eye—in form, orientation, and direction and rate of movement—was also the most effective in the other eye. Both stimuli together gave more vigorous responses than either applied alone. For a given cell the two eyes were not necessarily similar in their ability to evoke responses. Some cells responded equally well to the two eyes,



others favored the ipsilateral eye, still others the contralateral. A few cells responded only to one eye. Thus all shades of relative ocular dominance were found, from cells driven exclusively by the contralateral eye to those driven exclusively by the ipsilateral one. As in previous studies (13), we have divided cells into seven groups according to relative ocular dominance; these groups are defined in Fig. 28.

In Fig. 27 the relative influence of the two eyes was determined for two cells recorded simultaneously in visual area III. One cell was driven almost equally well from the two eyes, and was classed as group 4 (Fig. 27, A and

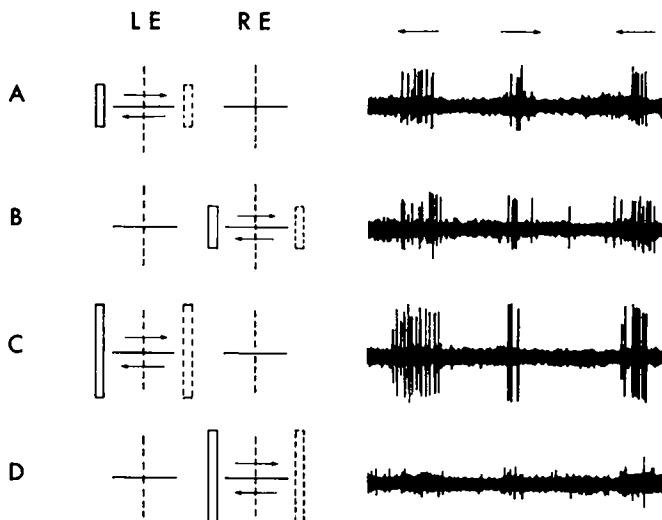


FIG. 27. Two cells simultaneously recorded from area 19; these were cells 35 (complex, large spikes) and 36 (hypercomplex, small spikes), in Fig. 4, penetration V. A and B: responses of the hypercomplex cell (no. 36) to a vertical slit, $\frac{1}{2}^\circ \times 2^\circ$, moved rapidly back and forth across the receptive field of the left eye (A), and the right eye (B); no response from the complex cell. C and D: movement of a slit $\frac{1}{2}^\circ \times 12^\circ$ produces no response from the hypercomplex cell, but a brisk response from the complex cell (no. 35), in the left eye only. Intensity of stimulus, $1.0 \log_{10} \text{cd/m}^2$; background, $0.0 \log_{10} \text{cd/m}^2$. Rate of movement about $20^\circ/\text{sec}$. Sweep duration, 1 sec.

B). The second cell, on the other hand, responded only from the left or contralateral eye and was placed in group 1. This record is an example of a simultaneous recording from a complex and a hypercomplex cell and will be referred to again.

One hundred and forty-nine of the cells in visual area II, and 89 of those in visual III, were categorized as to ocular dominance. The distribution of these cells among the seven different groups is given in Fig. 28, B and C. It will be seen that for both visual areas, cells driven by the two eyes (groups 2 through 6) form the great majority, and that cells favoring the contralateral eye (groups 1 through 3) exceed those favoring the ipsilateral (groups 5 through 7). Comparison with Fig. 28A shows a marked similarity between these histograms and the one obtained previously for visual I. In the histo-

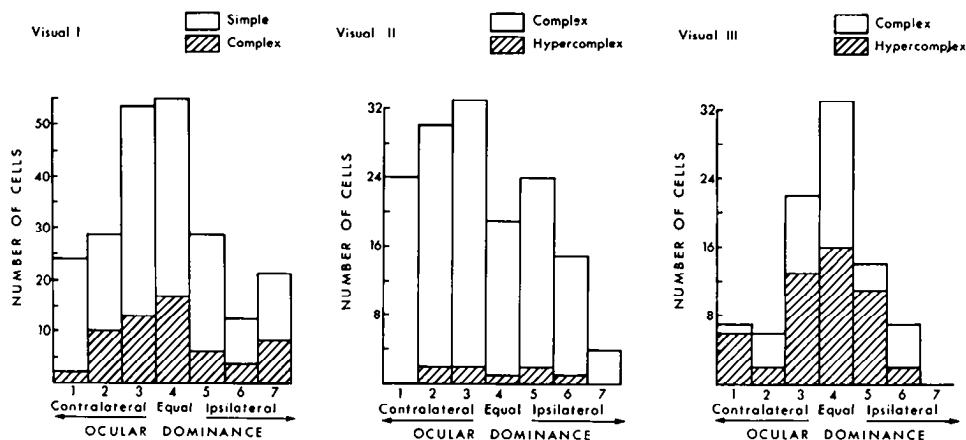


FIG. 28. Distribution according to ocular dominance of (A), 223 cells in visual I (13; text-Fig. 12), (B), 149 cells in visual II, and (C), 89 cells in visual III. Cells of group 1 are driven only by the contralateral eye; for cells of group 2 there is marked dominance of the contralateral eye; for group 3, slight dominance. For cells in group 4 there is no obvious difference between the two eyes. In group 5 the ipsilateral eye dominates slightly, in group 6, markedly; and in group 7 the cells are driven only by the ipsilateral eye.

grams for visual II and III the shaded area represents hypercomplex units. While one can say little about the ocular-dominance distribution of hypercomplex cells in visual II, in visual III the distribution of these cells seems to run parallel to that of the general population. It seems surprising that the functional separation of the two eyes should persist with so little change from one level to the next in the hierarchy, beginning with simple and then complex cells in visual area I, and proceeding to complex and then hypercomplex cells in visual III.

PART III. FUNCTIONAL ARCHITECTURE OF VISUAL AREAS II AND III

In this section we examine similarities between neighboring cortical cells, with the object of learning whether there are discrete regions of cortex throughout which the cells share certain receptive-field characteristics. As in previous studies (13, 14) we have proceeded by studying 1) sequences of cells in single penetrations, 2) unresolved background activity, and 3) multiple-unit recordings. The advantages and limitations of these three approaches have already been discussed (13).

Receptive-field orientation

Columns with single orientation. We were anxious to examine the receptive-field orientations of neighboring cells in visual areas II and III, since in visual I the relative constancy of receptive-field orientation from cell to cell forms the basis for the entire columnar system. Remarkably similar results were found in both areas of nonstriate visual cortex. At any stage in a penetration through gray matter the background activity of unresolved

single units was driven best by a line stimulus in a specific orientation, and was silent if the stimulus was oriented at 90° to that orientation. When a single cell was isolated its receptive-field orientation and the optimum orientation for the unresolved background activity almost always coincided. In all multiunit recordings (16 two-unit and 3 three-unit recordings) the cells studied together had identical receptive-field orientations. As the electrode advanced the optimum stimulus orientation for unresolved background activity and for isolated cells would remain constant for varying distances, and would then change abruptly. At the transition point there was either no clear preferred orientation or there were two preferred orientations, that of the cells in the region the electrode was leaving, and that of cells in the new region. Like area 17, areas 18 and 19 are thus subdivided into discrete regions in which cells have similar receptive-field orientations.

By observing distances between shifts in orientation as the electrode advanced in various directions through gray matter it was possible to assess the size and shape of these regions. In visual area II, examples of two oblique penetrations are seen in Figs. 1 and 2. The short sequences of cells between shifts in orientation—here the longest sequences contained only four to five cells—were typical of such oblique penetrations. On the other hand, in penetrations that were almost normal to the surface the sequences of cells with a similar orientation tended to be much longer. In the experiment of Fig. 4, penetration III was almost perpendicular to the cortex of area 18: here after three short sequences there was a relatively long one, containing all cells from no. 15 to no. 24. Other examples of penetrations more or less normal to the surface can be seen in Fig. 4, penetration II, where a sequence of five cells occupies a large part of the cortical thickness, and Fig. 29, penetration IV, with a sequence of four cells. From these and other experiments we conclude that visual area II, like visual I, is subdivided into discrete regions within which cells have a common receptive-field orientation. The variation of sequence lengths with obliquity of electrode path makes it very likely that here also the regions are columnar in shape and extend from surface to white matter, with walls perpendicular to the radial fiber bundles.

Similar results were found in visual III. Figure 4 shows an oblique penetration (V) containing four shifts of orientation and no very long sequences. Figure 29, on the other hand, shows a particularly long sequence of 15 cells occupying an entire penetration (V) that was very nearly perpendicular to the cortical layers. Thus here too there seems to be a distribution of cells in columns according to receptive-field orientation. (One important exception to this principle for columns in visual III will be discussed in the next section.)

In the striate cortex one finds within a single column both simple cells and complex cells in large numbers (13). In areas 18 and 19 there were both complex cells and hypercomplex cells in a single column. Examples of both types of cells in a single sequence can be found in Fig. 29, penetration IV (visual II), and penetration V (visual III). A clear demonstration can also be seen in Fig. 27, in which a complex cell and a hypercomplex one were

recorded simultaneously. A short slit, covering the entire activating portion of the hypercomplex cell's field, evoked a strong response from that cell (small spikes, *A* and *B*), but failed to activate the complex cell, presumably because it crossed only a small part of the complex cell's field. A long slit (*C* and *D*), on the contrary, crossed most or all of the complex cell's field and evoked a strong response from the complex cell; in so doing it crossed both the activating and antagonistic portions of the hypercomplex cell's field, and consequently evoked no response.

In visual I there was an indication that simple and complex cells were to some extent segregated by layers, since complex cells seemed to be virtually absent from layer 4 (13: text-Fig. 18). So far we have insufficient material to make a similar analysis of visual II and III, though from examples like that of Fig. 29 it seems that there is no strict segregation of complex and hypercomplex cells by layers.

Figure 29 illustrates one further point, that within a single column one can find representatives of all ocular-dominance groups; in this case the two cells belonged to groups 1 and 4. In penetration V of Fig. 29 the ocular-dominance groups of all of the cells (except 14, for which the grouping was not determined) are noted inside each receptive-field diagram; all groups from 2 to 6 were represented in the one column.

Columns with dual orientation. In PART II we have described hypercomplex cells of higher order that responded to stimuli in either of two orientations 90° apart. The relationship of these cells to neighboring ones, especially to complex and lower order hypercomplex cells, obviously presents a special case, since columns so far described have contained cells with a single common receptive-field orientation. The three penetrations in which cells with dual orientation were found were particularly interesting in that some of the lower order neighboring cells responded to one of the two orientations, while others responded to the other. A good example of this type of cell sequence can be seen in Fig. 30. Four of the first nine cells were hypercomplex, and each responded to two stimulus orientations, 2:30 and 11:30. Of the remaining five cells, no. 5 and no. 6 were hypercomplex and responded to dark bars with an 11:30 orientation, but not to stimuli oriented at 2:30. On the other hand, no. 7 (complex) and no. 8 (hypercomplex), responded to stimuli oriented in a 2:30 direction, but not to an 11:30 stimulus. Cells no. 6 and no. 7 were recorded simultaneously and had fields oriented 90° apart, an event that is exceedingly rare in visual I, occurring only at the boundary between two columns.

Another example is to be seen in the short sequence formed by cells 4 through 6 of Fig. 31. Here cell no. 4 responded to a 2:30 edge moved downward: the cell was hypercomplex, with the field stopped at both ends. Cell no. 5 responded to an edge oriented at 11:30 (i.e., 90° to the previous stimulus), and the field was stopped above and below. Cell no. 6, whose records are illustrated in Figs. 23 through 26, responded to *both* stimulus orientations (though it will be recalled that here there was some doubt as to just what it was about the horizontal tongue that activated this cell). In the same figure

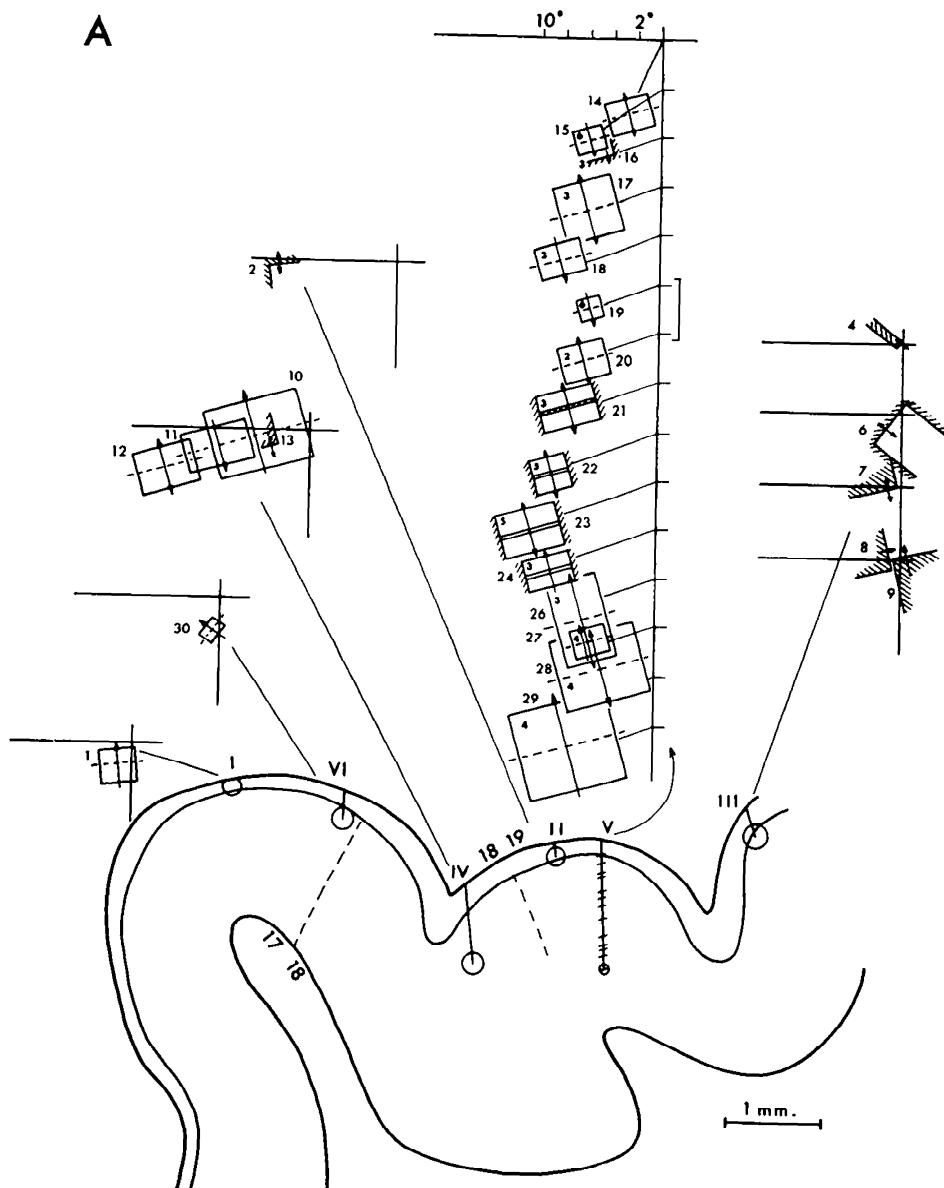
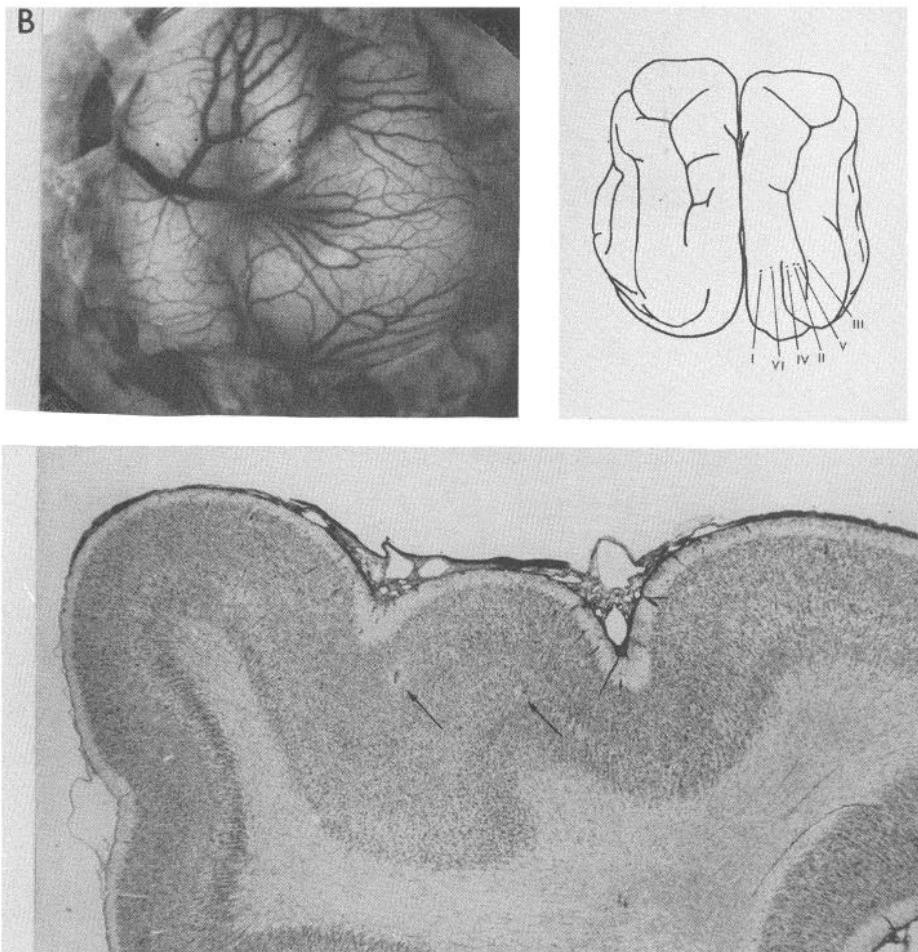


FIG. 29. A: six microelectrode penetrations through the right postlateral, accessory interlateral, and suprasylvian gyri, at a level indicated in the brain tracing (B, upper right). Points of entry were originally marked on the photograph of the exposed brain surface taken at the beginning of the experiment (B, upper left). Two of the lesions (IV and V) can be made out in the photomicrograph of a Nissl-stained section through this area (B, below); other lesions and electrode tracks appeared on adjacent sections. Conventions as in Figs. 1 through 4. Position and size of complex receptive fields are indicated by rectangles.

a similar sequence is formed by cells no. 1 to no. 3: cell no. 1 had a complex field oriented at 2:00, no. 2 was hypercomplex and responded to 2:00 and 11:00 orientations (described in Figs. 21 and 22), and no. 3, recorded simultaneously with no. 2, responded only to a 2:00 edge stopped on the left.

The few dual-orientation hypercomplex cells that we have studied (11 in all) have all occurred in sequences of this type. Such sequences may thus represent a different type of column, containing complex and hypercomplex



In penetration V, ocular-dominance groups are indicated in the upper left of each receptive field. Hypercomplex cells 7, 8, 9, and 13 responded to dark corners; 2 and 16 to light corners; 4 to a dark tongue; 6 to a light tongue; 21 responded to a double-stopped dark bar or slit; and 22–24 to double-stopped slits. For cells 21–24 the rectangles indicate the activating portion of the receptive fields. In this experiment note especially 1) the apparent absence of any far peripheral visual-field representation; 2) single columns traversed by penetrations IV and V; 3) cells 8 and 9 simultaneously recorded, fields oriented 90° apart.

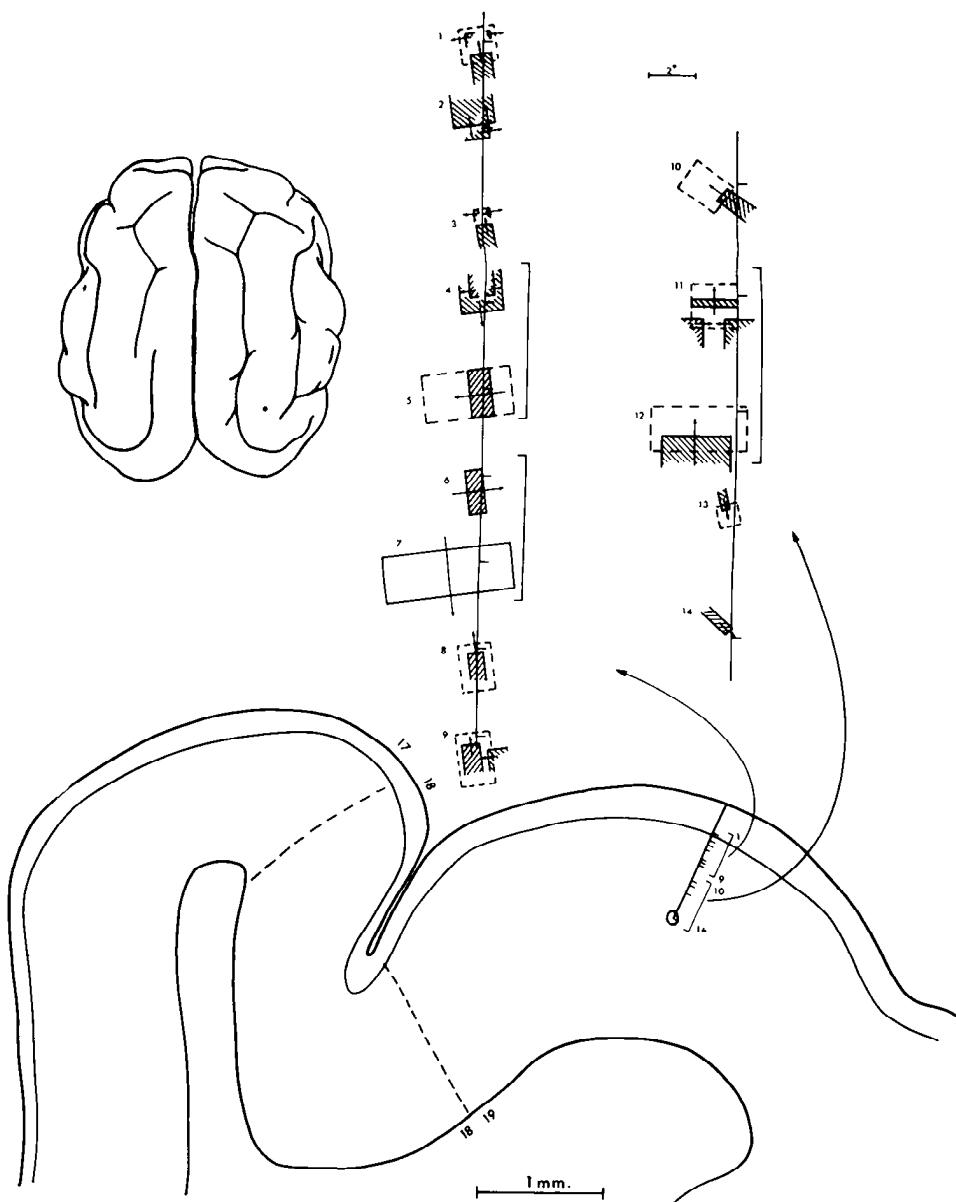


FIG. 30. Single penetration part way through visual III. All cells were hypercomplex, with double-stopped fields, except for no. 7, which was complex. First nine cells were apparently in the same column, within which orientations 2:30 and 5:30 were both represented. For hypercomplex cells, interrupted rectangles indicate roughly the regions from which responses were evoked, where these were mapped. Cells 1-4, 8-10, and 12-14 responded best to dark tongues; 5, 6, and 11 to double-stopped dark bars. Cells 4 and 5, 6 and 7, and 11 and 12 were simultaneously recorded pairs. All receptive fields were located in or near the area centralis. Whether any of these fields extended beyond the vertical meridian into the ipsilateral half visual field is uncertain.

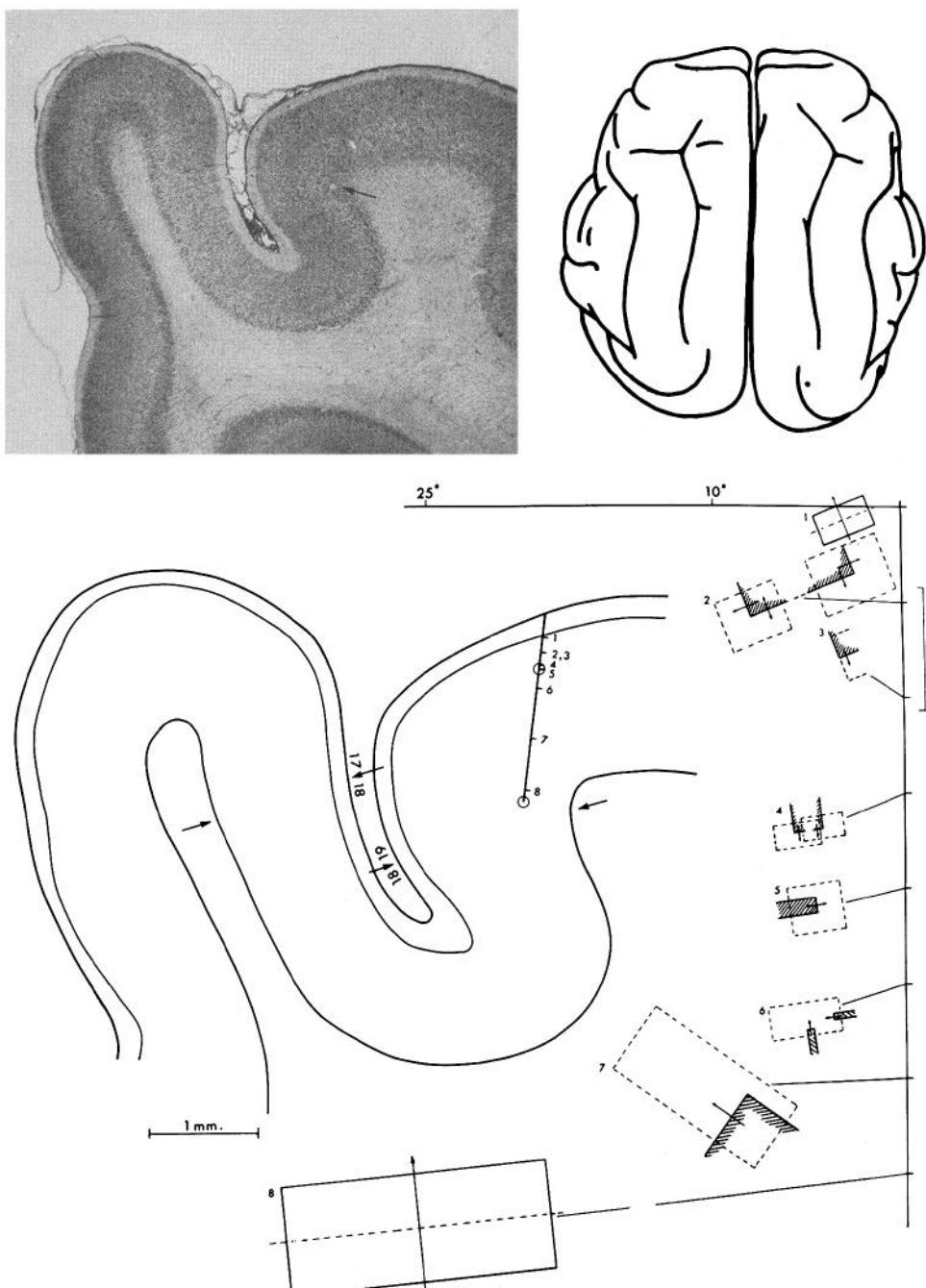


FIG. 31. Single oblique penetration through visual III. The deeper of the two lesions is shown in the Nissl section in upper left. Cells 1 and 8 were complex, 2-7 hypercomplex. Units 2 and 3 were recorded simultaneously. Conventions as in previous figures.

cells with either of two receptive-field orientations 90° apart, and also higher order complex cells responding to both stimulus orientations. If these columns are a distinct kind within visual III, it would be interesting to know whether they are scattered among the ordinary visual III columns, or are grouped together, as Figs. 30 and 31 would seem to suggest.

Relationship between neighboring columns. In most penetrations through visual areas II and III there was no obvious relation between receptive-field orientations of cells in neighboring columns. Just as in visual I, however (14), there were a few startling exceptions. In the experiment of Fig. 32 the electrode passed obliquely down the lateral bank of the postlateral gyrus, with the usual very gradual outward drift of receptive fields, typical for visual II, beginning in this case at about 10° and ending some 20° out from the area centralis. The shifts in orientation were meanwhile highly regular. Each shift was small and clockwise, except for the brief reversal in direction between cells 15 and 16, and the large shift in orientation between 13 and 14. We conclude that at least some groups of columns in visual II are organized in a regular way.

In this example one is struck by the minute widths of the columns, at least in the coronal plane: it is unusual to find a shift of orientation at almost every new unit (cf. Figs. 1 and 2, for example). It therefore seemed worth asking whether there might not be some relation between the shifts in orientation and the radial fiber bundles. Close examination of Nissl sections in the region between the middle and lower lesions suggested that there were in the order of 30 radial fiber bundles and associated cell fascicles. Within this area, between cells 15 and 25 (a distance of ca. 0.6 mm.), about 10 clockwise shifts in orientation were detected. Since there may have been more shifts in orientation than were actually observed, it is at least possible that each of the radially oriented anatomical subdivisions represented a column. The columns may thus be no more than about $20\ \mu$. across, though it is not known whether this would represent the diameter of a more or less circular cylinder, or, as seems more likely, the width of a slab-shaped structure of long, narrow cross section (14). No surface mapping has been done in visual II or III, but to judge from oblique microelectrode penetrations, the columns in these two areas, like those in visual I, can have cross-sectional diameters of up to about 0.5 mm.

Receptive-field position

As described in PART I, during an oblique penetration or in a penetration parallel to the cortical layers, the receptive fields of successively recorded cells tended to drift across the retina in an orderly fashion, in accordance with the topographical mapping of visual fields onto the cortex. In visual II and III, as in visual I (13), this topographic orderliness did not hold down to the cellular level. In proceeding from cell to cell in a single penetration the positions of successively mapped receptive fields were instead staggered in an apparently random way (Figs. 1 through 4, 29 through 31). Even in crossing

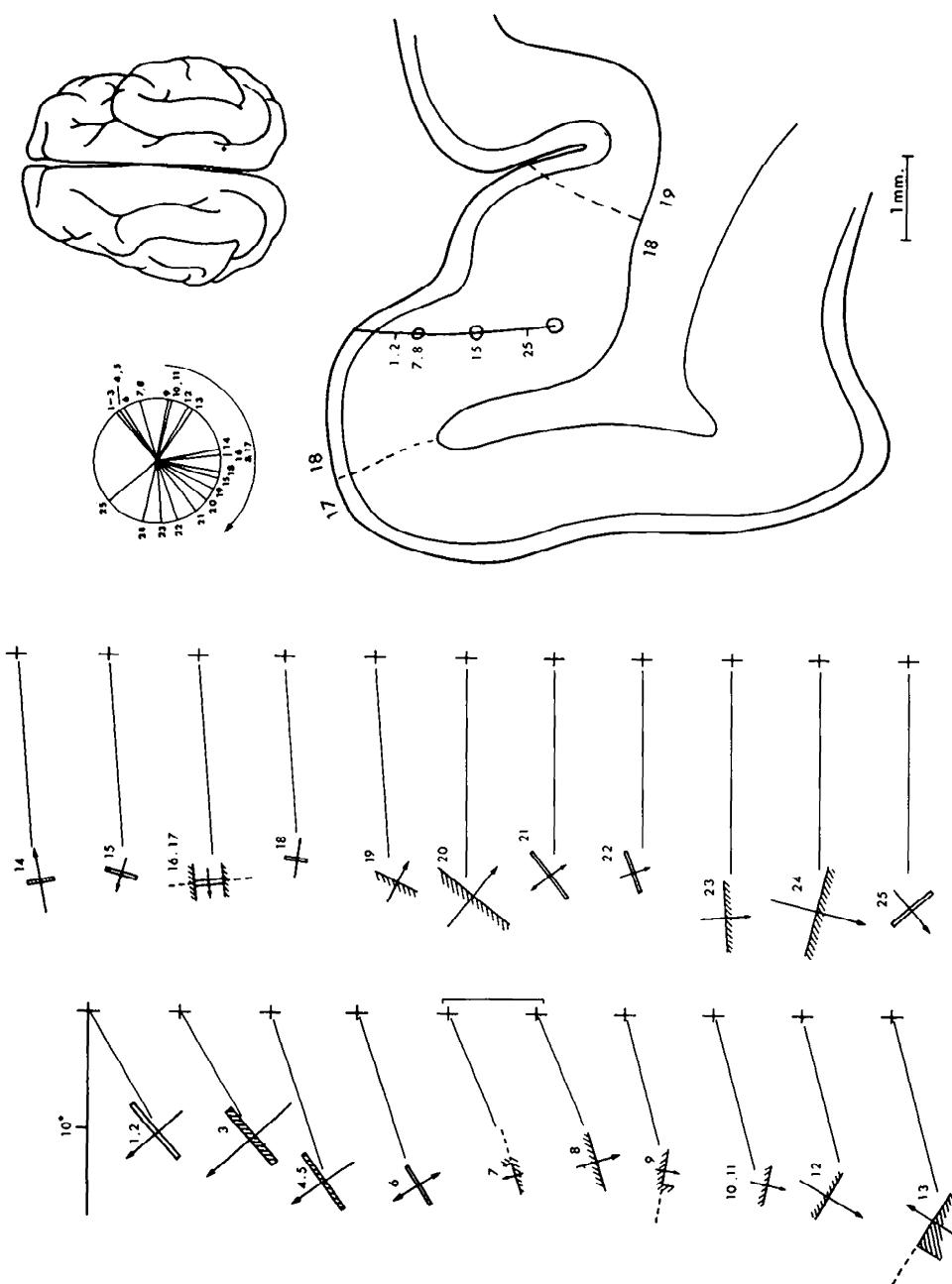
a single column or several columns there was never any clear change in average receptive-field position. Only in very long penetrations (Figs. 1 through 3, etc.), traversing many columns, was a net change in receptive-field position seen against the otherwise random staggering. In a penetration perpendicular to the surface, as the electrode advanced from surface to white matter, there was no net change in receptive-field position. When two or three cells were recorded simultaneously they had receptive fields in the same general part of the retina, differing slightly in their positions, but usually overlapping. The area over which fields of cells in a single column were dispersed in this apparently random way was of the same order as the area occupied by the largest receptive fields in the column. For a column in the part of the cortex representing the area centralis, the upper limit of receptive-field size was small (perhaps about 3°), and so was the variation in position; whereas in regions representing peripheral retina, field size and variation in position both tended to be larger. The correlation between field size and dispersion was especially impressive in visual area II, where peripheral receptive fields tended to be very large and widely scattered (see Fig. 3, upper part of penetration IV).

In summary, a column is defined as a region within which cells have a common receptive-field orientation (with the one exception described above). These cells differ in their ocular dominance, in the details of the organization of their fields, and, to a small extent, in the retinal positions of their fields. A given region of retina must be represented by a number of columns, corresponding to the different possible orientations. In experiments like that of Fig. 32 one can distinguish at least 10–15 orientations, so that this would be a possible lower limit for the number of columns required to represent any given small retinal area.

PART IV. PROJECTIONS FROM STRIATE CORTEX TO OTHER CORTICAL AREAS

The findings of the preceding sections are difficult to interpret without information on the interconnections of areas 17, 18, and 19. It would be especially desirable to know, for example, whether area 17 sends direct connections to 18 and 19. To learn more about the projections of 17 to other cortical areas we accordingly made small lesions in area 17 in six cats, and subsequently traced degenerating fibers by the method of Nauta and Gygax (22). In three cats the lesions were made in the interhemispheric segment of the lateral gyrus; in the other three they were made further back, in the medial aspect of the exposed part of the postlateral gyrus. To determine the boundaries of 17, 18, and 19, sections were stained at 1/2-mm. intervals with myelin and Nissl stains.

The results of an anterior lesion are illustrated in Figs. 33 and 34. In this experiment the cortex was simply stabbed with a 25-gauge hypodermic needle. The track began 1–2 mm. medial to the boundary between 17 and 18 (as determined from adjacent Nissl- and myelin-stained sections; Fig. 33A),



VISUAL AREAS II AND III IN THE CAT

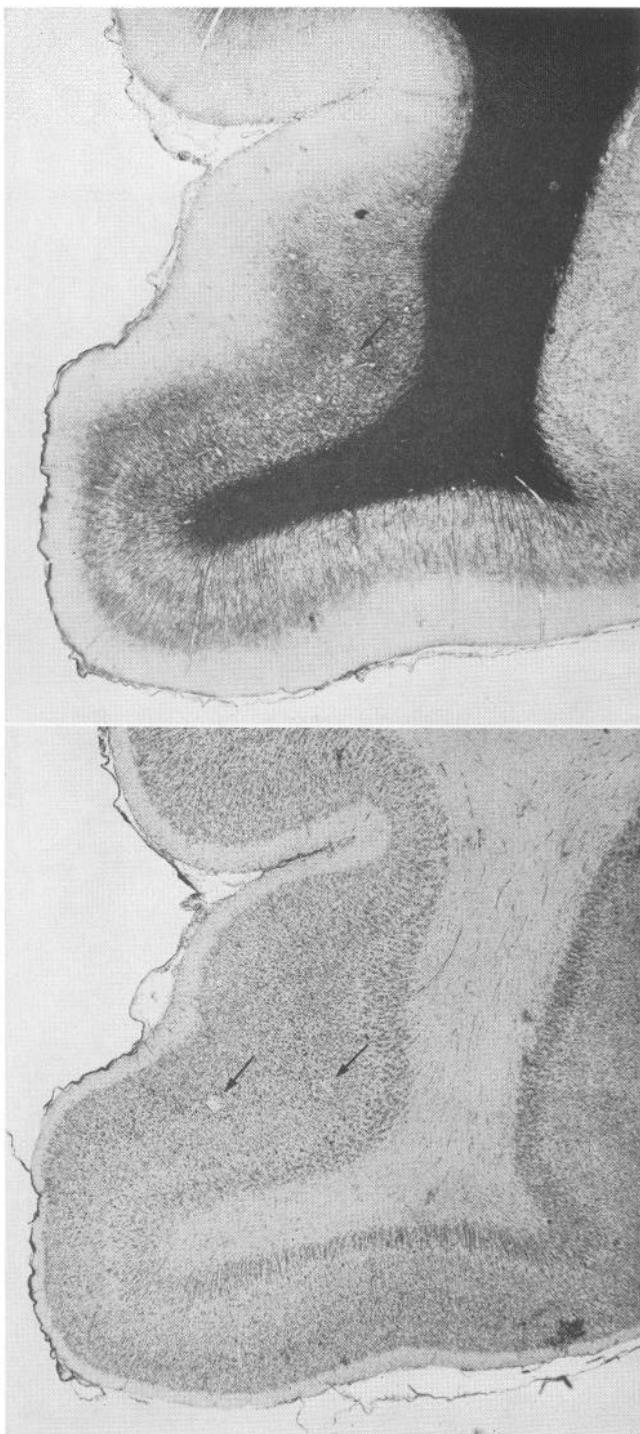


FIG. 32. Oblique penetration through visual II. The middle and final lesions are indicated by arrows on the Nissl section (lower left); this final lesion is also seen in the myelin section (lower right). In diagrams of complex receptive fields (1-6, 8, 10-12, 14, 15, 18-25) the length of a stimulus indicates the breadth of the field, the arrow indicates the field length and the preferred direction of movement, if any. For the hypercomplex receptive fields, the diagrams of the optimal stimulus suggest the breadth of the excitatory part of the field; the interrupted line, the breadth of the inhibitory area; the arrow, the field length and the preferred direction of movement. Note 1) the gradual tendency of fields to move out toward the periphery; 2) the steady systematic clockwise rotation of receptive-field orientation, illustrated in the circular diagram to the left of the tracing of the brain surface.

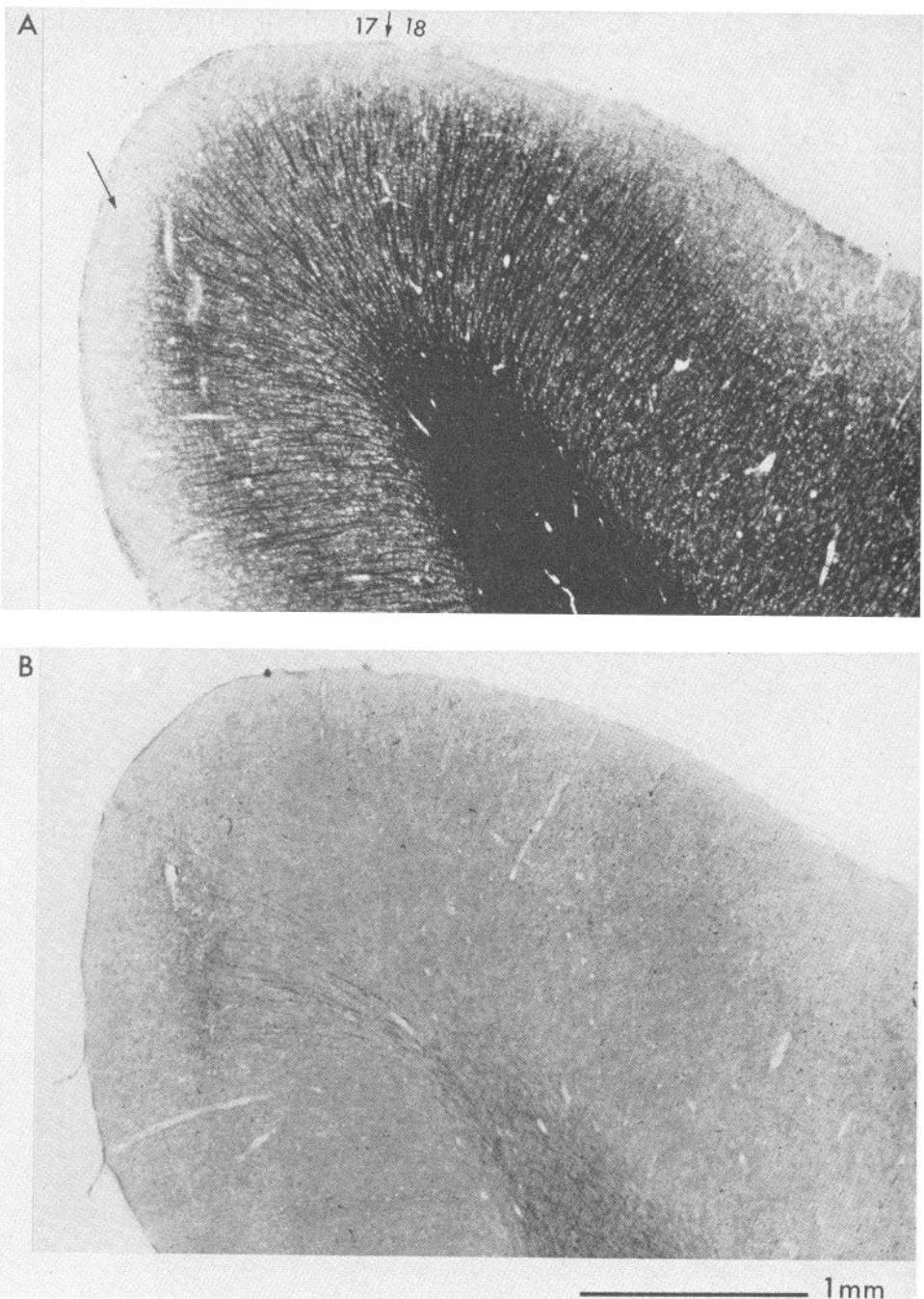


FIG. 33. A : myelin-stained section showing lesion in area 17, made for the purpose of studying degenerating fibers. Stab wound made by needle can be seen extending down medial aspect of lateral gyrus (arrow). Note also the transition between 17 and 18, indicated by coarser pattern of myelinated fibers. (Loyez stain.) B: Nauta stain of a section close to A, showing degenerating fibers leaving in the radial fiber bundles. Brain perfused 10 days after lesion was made.

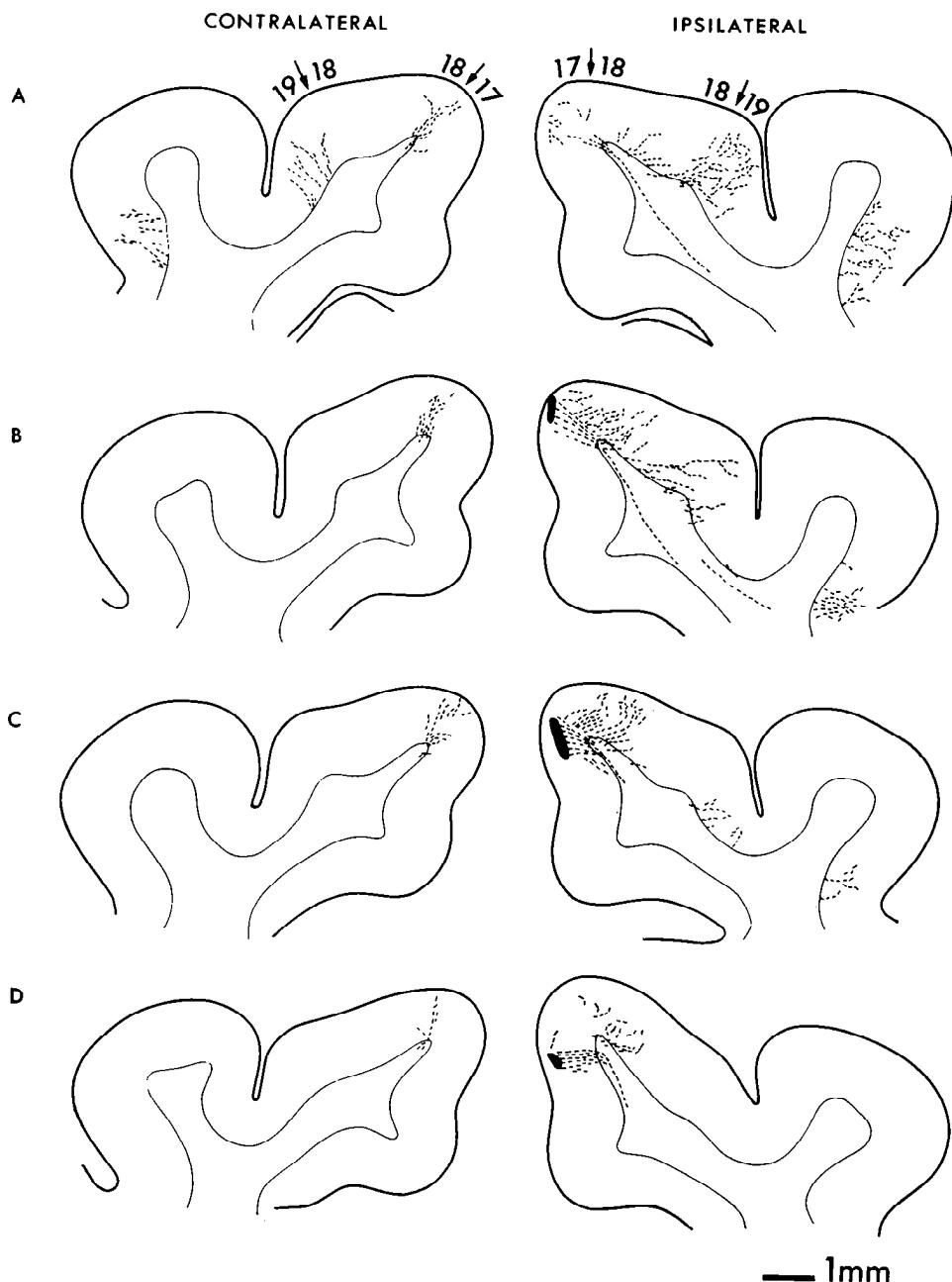


FIG. 34. Same brain as in Fig. 33. Camera-lucida tracings of degenerating fibers (broken lines) in lateral and suprasylvian gyri. Lesion is shown in B, C, and D as the black area in the right hemisphere. The four sections are taken approximately 750 μ . apart.

and extended for about 3 mm. in a direction almost tangential to the layers of the cortex. Silver stains showed degenerating axons in large numbers fanning out from the site of the lesion, many following the direction of the radial fiber bundles and proceeding toward white matter (Fig. 33B), many others streaking through the cortex toward area 18, seemingly by as direct a route as possible (Fig. 34, B and C). In serial sections some of the axons could be followed down through the white matter as far as the corpus callosum, and then across and up the other side; others were lost deep in white matter, and were presumed to be bound for subcortical structures. On the side of the lesion large numbers of degenerating axons were found in three areas: 1) A region confined to 18, extending laterally from a point close to the boundary between 17 and 18, along the lateral gyrus for about 1-2 mm.; axons could often be traced directly in single sections from the lesion to this area. 2) A region in the lateral wall of the lateral gyrus, well within area 19. 3) A region confined to the lateral wall of the suprasylvian gyrus, chiefly in its lower half. In each of these three areas the degeneration was maximal a few millimeters anterior to the site of the lesion, and extended for only several millimeters in an anterior-posterior direction. The fibers entered the cortex obliquely or even almost tangentially, showing no tendency to assume the orderly radial pattern that might be expected from examining Nissl- or myelin-stained sections of these regions. This contrasted strongly with the pronounced radial pattern of the fibers leaving area 17, shown in Fig. 33B. In the contralateral hemisphere degenerating fibers were found in the most medial millimeter or so of area 18. The border between 17 and 18 was not sharp enough, even in the myelin-stained sections, to exclude the possibility of some projections to contralateral 17. If any fibers did reach 17, they were confined to a small area near the 17-18 border; no fibers were seen on the medial (interhemispheric) segment. Thus there is no evidence for a set of connections linking homologous regions of 17 on the two sides (see DISCUSSION). Some contralateral projections were also found in 19 and in the lateral wall of the suprasylvian gyrus.

In the experiment of Figs. 35 and 36 an electrolytic lesion was made with a microelectrode deep in the cortex of the interhemispheric segment of the postlateral gyrus, in layers 5 and 6, well within area 17, probably in a portion receiving projections from the contralateral visual field 4-8° out along the horizontal meridian (13: text-Fig. 13). No recordings were made, and the electrode was withdrawn immediately after the current was passed. The resulting lesion was roughly $125\ \mu$. in diameter (Fig. 35A). Compared with acutely made electrolytic lesions (9), those in which several days elapsed before the death of the animal showed a dense infiltration with phagocytes and glial cells. At the level of the lesion there was again a massive outpouring of fibers directed radially toward white matter, and a much sparser group of fibers coursing through 17 in all directions for about 1-2 mm. tangentially and obliquely, extending superficially at least to the second layer. A few fibers heading down obliquely along the medial wall of the hemisphere

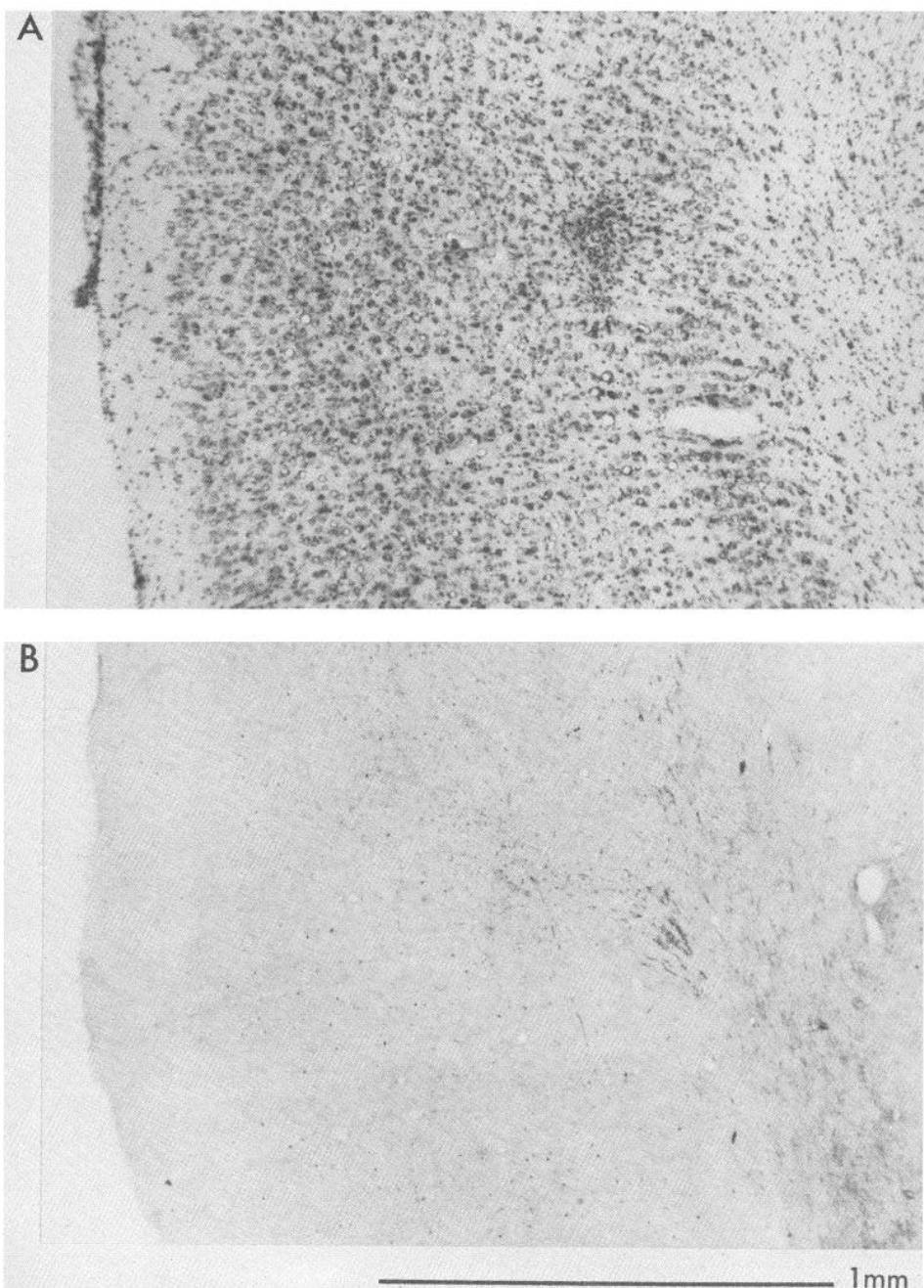


FIG. 35. A: Nissl-stained section showing electrolytic lesion in area 17, made for the purpose of tracing degenerating fibers. Eight days elapsed between making lesion and perfusing the animal. (Cresyl violet.) B: Nauta stain of section close to A, showing degenerating fibers leaving lesion along radial fiber bundles.

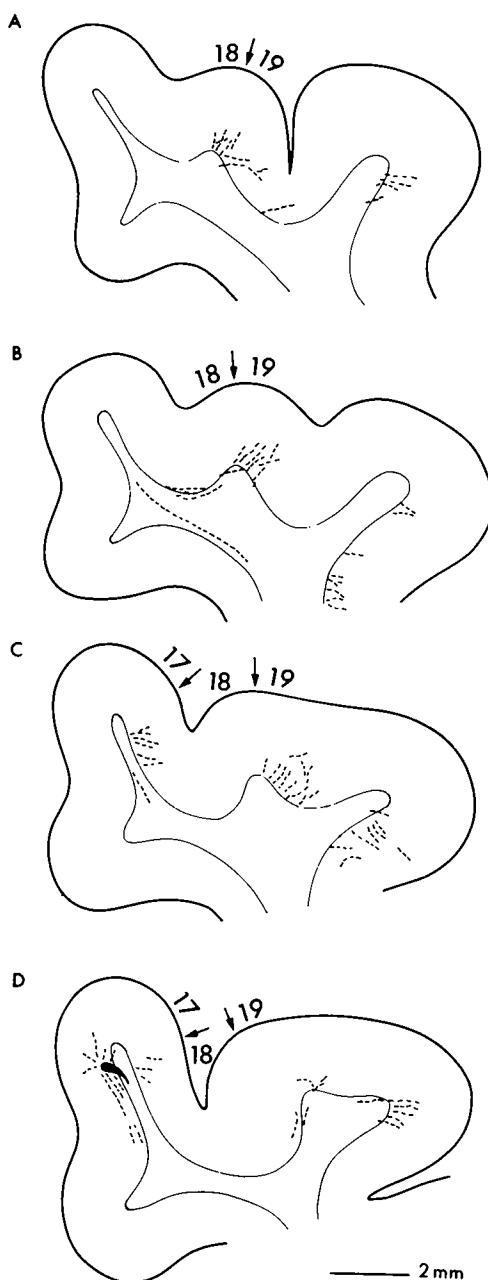


FIG. 36. Same brain as in Fig. 35. Camera-lucida tracings of degenerating fibers at four levels approximately 1.25 mm. apart. Levels A, B,—C and D correspond roughly to levels A, B, and C in Fig. 37.

appeared bound for white matter; otherwise there were no degenerating fibers in distant parts of area 17.

Again three discrete regions of cortex were found in the ipsilateral hemisphere, in area 18, area 19, and along the medial wall of the suprasylvian sulcus (Fig. 36). It is interesting to notice how the projection to 19 moves, in sections taken at progressively more posterior levels, from the lateral bank of the lateral gyrus (Fig. 36A) to the crest of the interlateral accessory gyrus (B), and finally to the medial part of the posterior suprasylvian gyrus (C). These are precisely the areas occupied by visual III in physiological experiments (Fig. 37). Thus studies of Nissl-stained and myelin-stained material and experiments with silver degeneration all correlate well with the physiological findings.

In posterior sections, fibers projecting to the lateral bank of the suprasylvian gyrus came to occupy a higher position in the sulcus, and the gap between this area and the degeneration in 19 narrowed so that the two almost coalesced. In both these regions the degeneration was again at a level slightly anterior to the lesion, and extended over an area of

cortex only a few millimeters in diameter. In this brain, stains of the contralateral hemisphere were unsatisfactory.

Almost identical results were obtained from the other four experiments. In summary, then, a given small region of area 17 gives cortical projections to at least three small discrete regions in the ipsilateral and contralateral

hemispheres; one in area 18, one in 19, and a third in a region of cortex occupying the lateral bank of the suprasylvian gyrus.

These results appear to be similar to those given in a preliminary account by Polley and Dirkes (25), except that they found degeneration in area 17 of the contralateral hemisphere. The findings are difficult to compare, however, without more detailed information on where their lesions were placed.

The projection to the lateral wall of the suprasylvian gyrus seems to involve precisely the area from which Clare and Bishop (1) recorded responses to stimulation of the optic nerve and the striate cortex (see also 5, 29). As to areas 18 and 19, we conclude that these are "higher" visual areas, in which messages from 17 are further elaborated. Whether 18 and 19 are interconnected, or whether they receive projections from other parts of the visual pathway (tectum, thalamus, etc.), are matters for future anatomical studies.

DISCUSSION

Cortical visual areas

To casual inspection one of the striking features of the cerebral cortex is its relative anatomical uniformity. It is true that there are occasional abrupt and obvious transitions, such as occur between somatic sensory and motor cortex, or in primates between areas 17 and 18. On the other hand, there are large areas in which variations in structure as seen with Nissl or myelin stains are more subtle, requiring considerable experience to distinguish genuine architectural variations from those produced by changes in cortical curvature, or small differences in the angle at which a gyrus or sulcus is sectioned. For this reason, the extent to which the cortex can be justifiably subdivided has been a matter of some dispute.

From the present study it is clear that some architectural subdivisions, subtle though they may be, are quite valid, reflecting differences both in connections and in function. We began by showing that in each hemisphere of the cat brain there are at least three precisely organized topographical projections of the contralateral half-field of vision. It turns out that these three physiologically defined areas, visual I, II, and III, are identical to the areas defined anatomically as 17, 18, and 19. Furthermore, from silver-degeneration studies it seems that two of the cortical areas to which 17 projects coincide with visual areas II and III. The boundaries between 17, 18, and 19 can thus be assessed by four independent methods, the Nissl-stain, the myelin-stain, silver-degeneration techniques (Nauta method), and physiological mapping. In the areas examined, the boundaries determined by all four methods are identical. These are summarized in Fig. 37, for three different antero-posterior levels.

In this paper we have used the terminology, "visual I, II, and III" and "areas 17, 18, and 19" more or less interchangeably, favoring the former when the context was a physiological one, and the latter when the context was anatomical. The designations 17 through 19 refer specifically to the

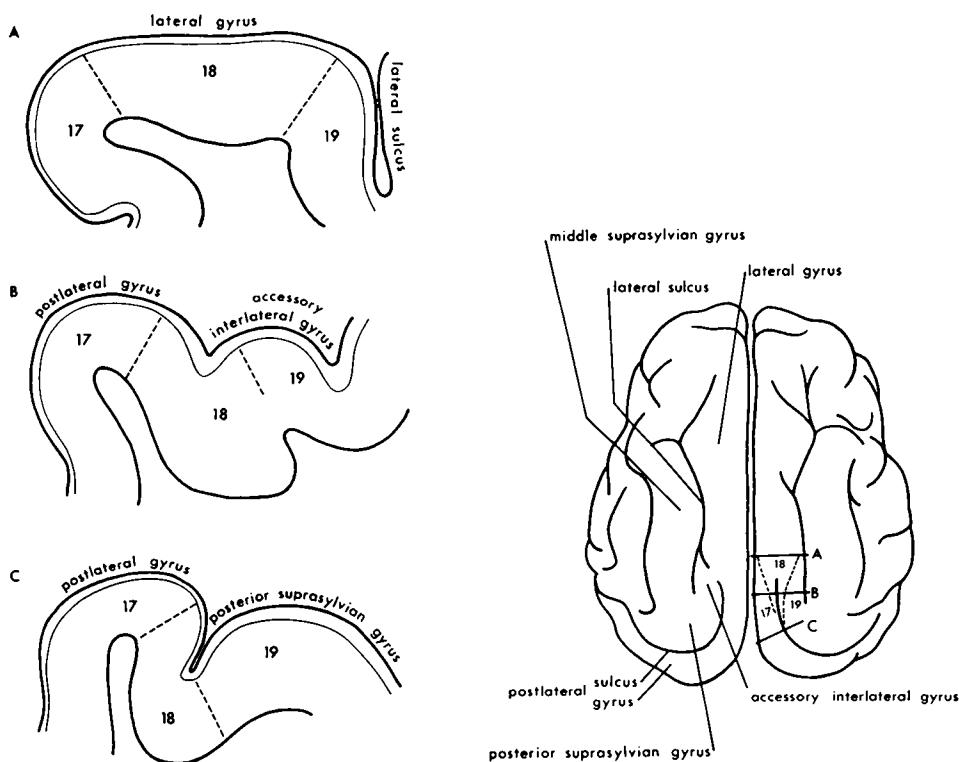


FIG. 37. Composite diagram showing coronal sections at three antero-posterior levels through visual areas I, II, and III (or 17, 18, and 19). Boundaries are based on several criteria, including histology as studied in Nissl- and myelin-stained sections, distribution of projections from area 17 to nonstriate visual cortex by the silver-degeneration technique, and physiological recordings.

regions anatomically defined by Otsuka and Hassler for the cat (23). The terms "occipital" and "preoccipital" have been avoided, since they seem inappropriate to the cat brain. "Peristriate" and "parastriate" are terms too easily confused to be useful. We use "area 17" and "striate cortex" interchangeably, since, even though this part of the cortex is not particularly striated compared with the primate area 17, there seems to be no doubt about the homology between the areas in cat and primate. The relationship between areas 18 and 19 in the cat, and the regions so designated in primates, is less clear; at present it would seem to depend mainly on the proximity of the regions to area 17, and on the large pyramidal cells in layer 3 of area 18. Future studies of anatomy and physiology should help to clarify the extent to which the areas in the two species are homologous. From preliminary experiments in spider monkeys (unpublished) it seems that area 18 is precisely arranged topographically, with the vertical-meridian representation bordering that of area 17, just as it does in the cat. Similar results have been reported for the squirrel monkey and the rhesus monkey by Cowey (2).

In the rabbit, visual areas I and II have been precisely mapped by the method of evoked potentials by Thompson, Woolsey, and Talbot (28). So far the two visual areas have not been correlated with cytoarchitectonics. As in the cat, visual II was situated anterolateral to visual I, with the vertical meridian projecting to the boundary between the two. Visual II was more extensive in the rabbit than in the cat, and there was a smaller region of binocular projection, reflecting the more lateral position of the rabbit's eyes.

We have limited our comparison between physiological mapping and cytoarchitecture to the part of the cat cortex indicated in Fig. 37. No studies were made of the posterior portions of 17, 18, and 19, where the superior visual fields presumably have their representation. Neither have we any information on the cortical area that adjoins 17 deep in the splenial sulcus, a region that Otsuka and Hassler designate as 19. For the present we tentatively assume that the entire visual II lies lateral to visual I; whether, as the cytoarchitectural studies suggest, some of visual III lies next to visual I in the splenial sulcus—i.e., whether some parts of the visual fields have their visual III representation there and not lateral to visual II—remains to be determined.

As many authors have stressed (20, 23), the lateral boundary of area 17 in the cat is often difficult to define sharply, especially in Nissl sections. Myelin stains are usually helpful, for in these the transition is seen as an abrupt coarsening of the radial efferent fibers (23; see also Figs. 3, 4, 32), and as an increase in the proportion of obliquely running fibers. The difficulty in pinpointing this 17-18 border, added to possible variations from cat to cat, probably accounts for the differences in position assigned to it by various neuroanatomists (cf., e.g., Figs. 2 and 3 in ref. 20). It is nevertheless agreed by most authorities, and can indeed be considered as established by Otsuka and Hassler (23), that the part of area 17 that extends over the dorsal surface of the brain occupies only a part of the width of the lateral gyrus, probably 1/3-1/4 depending on the antero-posterior level.

That such a small part of the lateral gyrus is striate cortex is worth emphasizing, because the region of maximal cortical evoked potential in response to a visual stimulus is probably *outside* area 17, as first pointed out by Doty (5). This area of maximum response appears to lie in 18, in the area of projection of the inferior visual fields, and cannot therefore be used as a guide to the position of the striate cortex. Studies involving stimulation or ablation of the visual areas, or recording from them, are therefore of limited value if the regions worked upon are not precisely determined by gross and microscopic anatomy.

The position of the lateral border of 19 is not clear, either from anatomical studies (23) or from the physiological mapping done so far. Our mapping of visual II agrees fairly well with the rough sketch of Talbot and Marshall (27), except for a few crosses which they show extending over to the exposed part of the posterior suprasylvian gyrus. The region designated as visual II in the diagrams of Woolsey (32), based, presumably, on the map of Talbot and

Marshall, seems to include most or all of what we would term visual III (area 19).

An additional comment may be made here concerning possible functions of visual II. For technical reasons related to difficulties in defining the area centralis to an accuracy of less than 1° or so, we cannot be sure whether or not the fields of cells in either 17 or 18 extend into the ipsilateral field of vision. Assuming for argument's sake that receptive fields of area 17 are entirely confined to the contralateral half-field, the fact that 18 receives projections from 17 of the opposite hemisphere suggests that some cells in 18 should have at least part of their receptive fields in the ipsilateral visual field. This would mean that 18 might have an important function in correlating the two half-fields of vision along the vertical meridian. In crossing the 17-18 border from medial to lateral there should thus be a slight additional movement of receptive fields past the midline and into the ipsilateral field, prior to a movement in the reverse direction. We have no evidence yet that this occurs. An absence of projections linking corresponding parts of area 17 in the two hemispheres would make good sense, especially for parts of 17 not adjoining 18, since it is difficult to imagine why cells having receptive fields in a particular part of the visual field should have connections with other cells in the contralateral hemisphere, with fields in a mirror position in the other half-field of vision. Previous studies of this subject, anatomical (26) and physiological (3, 6), have been somewhat contradictory, and it is hard to evaluate them because of changing notions about the exact definition and location of 17, 18, and 19 in the cat.

Schemes for elaboration of hypercomplex fields

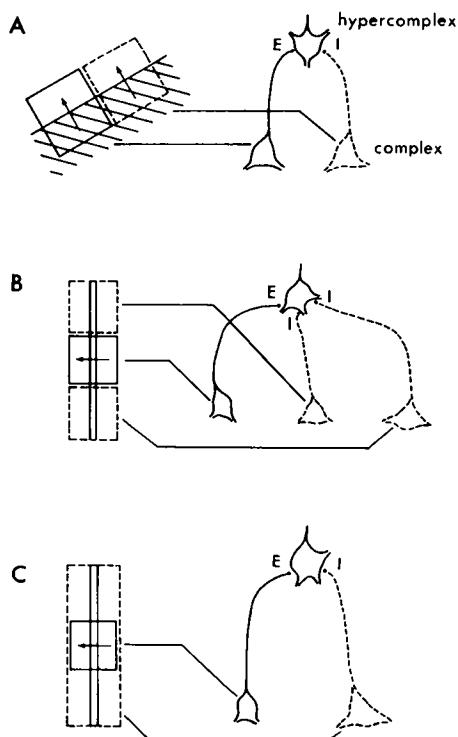
With areas 18 and 19 well established as anatomical and physiological entities, and with the evidence that area 17 sends strong projections to both of them, it is natural to ask what further processing of the visual messages takes place in 18 and 19. In both areas a proportion of cells seem to have properties identical to those of higher order cells of area 17—i.e., they have complex properties. Complex cells are in the great majority in visual II, and seem to form about half the population in visual III. In visual II the very large size of some receptive fields suggests that one cell may receive input from a number of fibers from the striate cortex. These incoming fibers would presumably all have the same receptive-field orientation and a similar preference as to form of stimulus (slit vs. bar, etc.); they would only need to differ from one another in their precise receptive-field positions. In visual III, on the other hand, complex cells did not differ in any obvious way from cells of visual I, so that one need not propose any extensive convergence of afferents onto complex cells.

Since the next step in complexity is represented by the hypercomplex cell, it seems reasonable to try to interpret hypercomplex properties by assuming that these cells receive their afferents from complex cells. To see how this might work, it may be useful to contrast complex properties with

hypercomplex. With complex cells the responses are more vigorous the longer the stimulus line, until the stimulus reaches the boundaries of the receptive field. Beyond this it makes no difference how long the stimulus is. There is, in other words, summation across the entire receptive field in the direction of the receptive-field orientation. With hypercomplex cells of lower order (Figs. 8 through 27) a similar summation occurs in one portion of the field, which can be loosely termed excitatory. If the stimulus extends beyond this part into inhibitory regions the response no longer increases, but, on the contrary, is suppressed, and a line crossing the entire receptive field is indeed usually ineffective. Here one can speak of excitatory and inhibitory subdivisions of a hypercomplex field, or perhaps better, an activating region and an antagonistic one, provided it is clearly understood that it is not simple illumination of these regions that determines whether the cell is excited or its response prevented. Each region by itself is typically complex, i.e., a cell responds when an appropriately oriented line (slit, bar, or edge) is shone or moved anywhere within the activating area, and the response is prevented with similar and simultaneous stimulation of the antagonistic region. Summation occurs in each region, in the sense that within one region the longer the line the greater its effect; mutual antagonism occurs in the sense that adequate stimulation of the activating region is offset by adequate stimulation of the opposing one. Summation and mutual antagonism thus occur only along the direction of the receptive-field orientation, and not in any simple spatial sense, as is so for simple cortical cells and cells at lower levels. In hypercomplex cells it is of course the similarity of the orientation of the two opposing subdivisions of the field that makes a long straight line ineffective, and a stopped line, properly placed and oriented, the most effective stimulus.

It is perhaps worth emphasizing this distinction between a pair of antagonistic regions within each of which simple areal 1 summation occurs, and a pair of antagonistic regions with more complex properties. It has recently been suggested that the retinal ganglion cells in the frog termed "convex edge detectors" by Lettvin and colleagues (17) have receptive fields with an excitatory center and an inhibitory surround (7). To judge from the accounts of Lettvin and co-workers it seems likely that if the fields in question have a center-surround organization it is only in some highly complex sense. They seem to be quite different from retinal ganglion cells or geniculate cells in the cat, and indeed they may have a complexity approaching that of hypercomplex cells in areas 18 and 19.

The properties of a hypercomplex cell are most easily explained by supposing that the afferents to the cell are complex, and that some synapses are excitatory and others inhibitory. It is only necessary to assume that the excitatory input is a complex cell (or perhaps more than one) with a receptive field identical in position and arrangement to the excitatory or activating part of the hypercomplex field, and that inhibitory inputs originate from complex cells with fields in the territory of the antagonistic flanks. This general scheme is illustrated in Fig. 38. The simplest case, that of a cell with



supplied by a single cell with a large field indicated by the entire interrupted rectangle. In either case (B or C), a slit covering the entire field of the hypercomplex cell would be ineffective. Scheme C requires that a slit covering but restricted to the center region be too short to affect the inhibitory cell.

its field stopped at only one end, is given in Fig. 38A; the cell could be the one illustrated in Figs. 8 through 11. Only two afferent cells are shown, an excitatory and an inhibitory, but there might be many of each type. In Fig. 38, B and C, two possible arrangements are suggested to account for the properties of a double-stopped hypercomplex cell (see Figs. 16 through 20, and 27). Figure 38B requires two inhibitory cells, or sets of cells, both complex, with their fields covering the two flanking areas. In an alternative scheme (Fig. 38C), the hypercomplex cell receives an excitatory input from a complex cell whose field covers the activating center, as before, and an inhibitory input from a single complex cell with a field having the same size and position as the entire hypercomplex field, both center and flanks. This arrangement could only work efficiently if the inhibitory afferent gave a good response to a long slit, but little or no response to a stimulus confined to the activating area. This was true for the complex cell (large spikes) of Fig. 27, which responded well to a large slit, but not to a small one. Except for the difference in ocular dominance, one might imagine that the two simultaneously recorded cells in Fig. 27 were interconnected, the complex cell sending inhibitory connections to the hypercomplex one.

FIG. 38. Wiring diagrams that might account for the properties of hypercomplex cells. A: hypercomplex cell responding to single stopped edge (as in Figs. 8 through 11) receives projections from two complex cells, one excitatory to the hypercomplex cell (E), the other inhibitory (I). The excitatory complex cell has its receptive field in the region indicated by the left (continuous) rectangle; the inhibitory cell has its field in the area indicated by the right (interrupted) rectangle. The hypercomplex field thus includes both areas, one being the activating region, the other the antagonistic. Stimulating the left region alone results in excitation of the cell, whereas stimulating both regions together is without effect. B: scheme proposed to explain the properties of a hypercomplex cell responding to a double-stopped slit (such as that described in Figs. 16 and 17, except for the difference in orientation, or the hypercomplex cell with small spikes in Fig. 27). The cell receives excitatory input from a complex cell whose vertically oriented field is indicated to the left by a continuous rectangle; two additional complex cells inhibitory to the hypercomplex cell have vertically oriented fields flanking the first one above and below, shown by interrupted rectangles. In an alternative scheme (C), the inhibitory input is

In the schemes just proposed, the highly specific properties of hypercomplex cells in 18 and 19 seem to demand highly specific sets of connections from lower order cells. Compelling evidence to support the schemes is given by the functional architecture of visual II and III. As we have shown, these areas, like visual I, are subdivided into columns each containing complex and hypercomplex cells with identical receptive-field orientations and a certain variation in receptive-field position—in short, the very cells that the physiology predicted should be interconnected. It is known from Golgi preparations of the cortex that cells within a region having the size and shape of a column would in fact be richly interconnected. As in area 17, then, the morphological anatomy, the functional architecture, and the single-cell physiology all seem to be completely consistent. The columns of areas 18 and 19, like those of 17, may be considered as functional units of cortex, there being many interconnections between cells of one column, far fewer between cells of adjacent columns. The main purpose of the aggregation of cells into columns is presumably an enormously efficient reduction in the lengths of these connections.

Hypercomplex cells of higher order

An even higher degree of complexity, and still another example of a correlation between response properties and functional architecture, is provided by the cells in area 19 that responded to two orthogonal stimulus orientations. The simplest mechanism for the dual receptive-field orientation would involve convergence upon the cell of two sets of afferent hypercomplex cells having their receptive-field orientations 90° apart. Cells with dual orientation seemed to occur within columns that also contained complex and lower order hypercomplex cells, some having one receptive-field orientation, others an orientation at right angles to the first. It seems, in fact, that here again the very cells that the physiological experiments suggest are interconnected are aggregated in columns. Perhaps it should be stressed, however, that our notions about these higher order cells and the columns containing them are tentative, based as they are on a very few cells (11 in all), in only three penetrations. Experiments with more cells and penetrations may help to settle a number of questions, especially the relation, within visual area III, between these columns and ones in which a single orientation is represented.

A second quite different type of higher order transformation was seen in several cells. The cell recorded in Figs. 23 and 24 responded best to a double-stopped edge with a sharply defined orientation and length (Fig. 24). This was no ordinary hypercomplex cell, however, since there was no division of its field into excitatory and inhibitory areas, and since it responded to movement over an area many times the width of the optimum stimulus (Fig. 23), so that the hypercomplex properties were, in a sense, generalized in the direction of the receptive-field orientation. (A similar generalization was probably also present, though to a lesser extent, in the higher order hypercomplex field of Figs. 21 and 22.) Such behavior could obviously be explained by imagining a convergence of many lower order hypercomplex

cells onto a cell of higher order, the afferent cells differing only with respect to the exact positions of the boundaries between centers and flanks. This convergence could occur in the same columns in which the lower order hypercomplex properties were elaborated.

The phenomenon of progressive attenuation of responses shown by this cell (Fig. 26) is one that we have seen from time to time in all three visual areas. Here it was clearly not a question of progressive unresponsiveness of the cell itself, since the responses came back as soon as the stimulus was introduced in a new part of the receptive field. Presumably the failure was somewhere along one particular pathway leading to the cell. Lettvin *et al.* (18) have found cells with somewhat similar behavior in the frog tectum.

Transformations in the three visual areas

We have already referred, in the first part of this DISCUSSION, to the relative structural uniformity of the cerebral cortex. It seems astonishing that neural aggregations so similar in organization can be concerned with functions so diverse as vision, audition, somatic sensation, and motor movements. It becomes important to learn whether the anatomical similarity of the different cortical areas reflects common functional features. For this reason it seems worth while to compare the different transformations that occur in visual areas I, II, and III.

In the striate cortex one can distinguish two successive processes of convergence, each involving many excitatory afferents. The convergence of incoming geniculate fibers onto a simple cell is apparently such that the cell responds maximally only when most of the excitatory afferents are simultaneously activated. A spot is a feeble stimulus, but a slit may be a powerful one; if the cell has connections with the two eyes, a maximal response occurs only when the eyes are stimulated together. The result of the process is an enormous increase in specificity, each cell requiring a particular stimulus position, shape, and orientation, and preferably stimulation of both retinas. This increased specialization is attained by an immense increase in the number of cells, and through multiple branching of the afferent fibers. At the next stage, from simple to complex cells in the striate cortex, the convergence is again excitatory, but with the difference that for activation of the complex cell only a small proportion of the afferents need be activated at any one time. For example, a slit becomes effective wherever it is shone within the receptive field, and, for reasons not clear, two parallel slits shone in the same receptive field seldom give a more powerful response than either by itself. On the other hand, sequential activation of the afferents by movement of a line across the field is generally a very powerful stimulus, perhaps partly because none of the antecedent cells has time to adapt. The transformation from simple receptive field to complex involves a generalization of one of the qualities of the stimulus, namely its orientation.

In 18 and 19 a still different mode of convergence takes place, apparently one in which excitatory and inhibitory influences come together on one cell.

Here the result is again to increase stimulus specificity, rather than to generalize. The hypercomplex cell does not necessarily respond to a properly oriented line crossing the receptive field; it accepts only a line that is appropriately terminated. A line covering the entire field presumably activates two processes that mutually cancel to an amazingly precise degree. This powerful mechanism for enhancing stimulus specificity has already been encountered in two different contexts in the mammalian visual system. In the retina, the geniculate, and the striate cortex, it is used to discriminate against diffuse light in favor of patterned stimulation; in the monkey retina it is used to enhance specificity of the response to certain monochromatic wavelengths at the expense of others and of white light. Analogous mechanisms involving inhibition are known to occur in the somatosensory and auditory systems.

The next step, shown in the example of Figs. 23 and 24, and seen so far only in a few penetrations in area 19, seems again to be one of convergence of excitatory afferents. For the higher order hypercomplex cell to respond, the line must now be properly oriented (sometimes with two possible orientations 90° apart) and limited in its extent, as before, but it need not necessarily be accurately specified as to position. Still more generalization has taken place, this time along a direction parallel to the receptive-field orientation, i.e., at right angles to the direction of generalization in the transformation from simple cells to complex. Here again the convergence must be such that one only need activate small sets of antecedent hypercomplex cells in order to activate the higher order cell. The transformation is thus analogous to that between simple and complex cells in the striate cortex. Indeed, there is an analogy between simple cells and lower order hypercomplex cells, with their centers and flanks and high specificity, and also between complex and higher order hypercomplex cells, in each of which generalization has taken place.

Though these transformations show certain similarities in their details they also exhibit a considerable variety, and there seems to be no doubt that impressive differences exist in the details of connections between one cortical area and the next. These differences are undoubtedly related to the cyto-architectural distinctions between the various areas. The common features are perhaps more fundamental—the occurrence of one or more intricate transformations between incoming and outgoing messages, taking place within a system of more or less independent columns with little lateral dissemination of information, and the possibility of explaining the transformations by simple, relatively well-known neural mechanisms like the nerve impulse, excitatory and inhibitory synapses, convergence, and so on, with the strong indication that the connections are not random, but highly specified.

The highly structured and specific nature of these connections raises the question of their origin, and in particular whether they are developmentally determined, or depend for their evolution on visual experience after birth.

For connections up to and including the striate cortex it is clear that the development is largely innate, since kittens shortly after birth and prior to any visual experience show virtually the same response specificity as is found in the adult (15). In some respects this seems quite natural, since at these levels in the visual pathway one is still dealing with what are undoubtedly building blocks of perception, elements that would hardly be expected to differ from individual to individual with experience (except for pathological early experience such as results from sensory deprivation (30)). If this reasoning is valid for the striate cortex, it is probably also valid for 18 and 19; one would expect to find the connections innately determined there too. The experiments have not yet been done.

Columnar organization of the cortex

The most conspicuous property common to the three visual regions is to be found not in the details of the transformations that occur there, but in the columnar organization. Although Lorente de Nó (19) had emphasized the richness of the radial connections and the relative paucity of horizontal connections in the cortex, Mountcastle (21) was the first to show that one area of cortex, the somatosensory, was organized in discrete columnar regions, and to enunciate the principle that the column was the elementary unit of organization. This notion was based on the anatomically known richness of connections between cells in a column, and the assumption that neighboring columns, containing cells that subserved entirely different sensory submodalities, were functionally independent. A demonstration of columnar organization in the primary visual cortex (13, 14) showed that this plan was not unique to the somatosensory system. In the striate cortex, furthermore, the subdivision into columns depended on more subtle criteria: not on the submodality of the afferents, but rather on the connections within the columns. The present study shows that the columnar organization is not confined to sensory receiving areas, but holds also for certain higher visual areas. Thus all four cortical areas in which functional architecture has been examined show a columnar organization; it would be surprising if other cortical areas were not similarly subdivided. It is perhaps worth noting that functional parcellations of gray matter nuclei have been found outside the cortex, for example by Poggio and Mountcastle (24) in the ventrobasal complex of the thalamus. These subdivisions, like columns in the somatosensory cortex, are defined by differences in submodality from one cell aggregate to the next. The lateral geniculate body provides an extreme example of an especially coarse aggregation of cells within an otherwise functionally uniform mass of gray matter: in the monkey the small-cell and large-cell portions of the geniculate are each parcellated into layers according to eye dominance. Perhaps it is a rule, in the central nervous system, for sets of cells that are interconnected to be grouped together, and separated from other similar groups with which they have few or no connections.

The most interesting aspect of columnar organization, in the visual sys-

tem at any rate, is the clear role that it appears to play in function. The concept of the column as a functional unit becomes more vivid when the transformations occurring within it are known, and it is realized that the segregated cells are just those that must be interconnected to explain the transformations. Far from being a mere aggregation of cells with common characteristics, the column emerges as a dynamic unit of function.

In the visual areas the columnar system can probably be looked on as a solution to the problem of dealing with three independent variables—two to specify a position on the retina, and the third for receptive-field orientation—in a structure, the cortex, that is in a sense two-dimensional. If there were four variables one might expect there to be two columnar systems, superimposed, as it were; this in fact appears to be the case in the monkey striate cortex where cortical subdivisions depending on ocular dominance are superimposed on the receptive-field orientation columns (unpublished).

So far nothing has been said of the horizontal cortical subdivisions into layers, divisions that are anatomically far more obvious than the vertical cytoarchitectonic subdivisions. In area 17 there are strong hints of physiological differences among layers (13), in that the fourth-layer cells seem to be almost exclusively simple. In 18 and 19 the results are even less clear. Part of the reason for our ignorance about the significance of layering is that in the cat the boundaries between layers are not always easy to find accurately in Nissl-stained sections. Moreover, most layers contain a variety of cell types, so that one cannot expect physiological properties of cells in one layer to be uniform. Finally, it is technically difficult to localize a particular cell along a given electrode track. For these reasons we have deferred a study of this aspect of the physiology, with the hope that the problem may be more easily undertaken in the monkey, where the layering is more clean-cut.

Implications for perception

It remains to discuss the possible implications of this work for an understanding of perception. This can be approached by asking what cells in a given area are responding to any particular part of an image. In the striate area cells respond to the contours of a form: most cells whose receptive fields lie entirely inside the homogeneous part of an image are uninfluenced, since for them the stimulus is in effect diffuse. A portion of the boundary of a figure will activate that population of complex cells whose receptive fields are not only crossed by the boundary but also oriented in the direction of the boundary. A segment of a curve will activate a complex cell best if the tangent to the curve does not greatly change its direction within the receptive field. The impression of the homogeneous interior of a figure as bright or dark is presumably derived from the activity of cells whose fields cover the boundaries, and from the lack of any signals from cells whose fields are entirely within.

Hypercomplex cells are still more selective. From these cells continuous straight boundaries, or boundaries that curve to a negligible degree within the confines of a receptive field, evoke no response. There must be discontinuities such as interruptions of a line or changes in direction. A simple image like a square activates only hypercomplex cells whose fields include the vertices, and then only if the receptive-field orientations are appropriate. Awareness of a straight edge may thus be derived from signals in hypercomplex cells activated by the ends of the edge, plus the failure of other hypercomplex cells to signal other directional changes in the edge. If perception of an entire line can arise solely from information on changes in direction one may have an explanation for the "completion" phenomenon, in which patients with an occipital lobe lesion perceive a line as uninterrupted even though it crosses the blind part of the visual field.

The hypercomplex cell can, in a sense, serve to measure curvature; the smaller the activating part of the field, the smaller the optimal radius of curvature would be. To term such cells "curvature detectors" seems unwise, however, since the term neglects the importance of the orientation of the stimulus, and does not capture the essential importance of a line stimulus to one region and the absence of a line stimulus to an adjacent, antagonistic region. Similar objections would apply to terms like "corner unit." The word "hypercomplex," while ugly and unwieldy, and perhaps also unwise in view of the possibility of finding even more complex cells, is at least relatively neutral.

Finally, it should perhaps be stressed that a proper understanding of the part played by any cell in a sensory system must depend not simply upon a description of the cell's responses to sensory stimuli, but also on a knowledge of how the information it conveys is made use of at higher levels. Just as one can better grasp the meaning of cells in the retina or geniculate, with their on-center or off-center fields, by knowing that such cells converge on the more specific cells of area 17, so an understanding of hypercomplex cells will be incomplete until we have a description of the cells they converge upon. How far such analysis can be carried is anyone's guess, but it is clear that the transformations occurring in these three cortical areas go only a short way toward accounting for the perception of shapes encountered in everyday life.

SUMMARY

In 1941 Talbot and Marshall (27) mapped the cat's visual cortex by recording slow potentials evoked by small-spot stimulation of the retina. In each hemisphere they found two separate but adjacent projections of the contralateral field of vision, which they termed visual areas I and II. In recordings from single cells we have confirmed these findings and have found a third systematic projection (visual III) of the contralateral visual field bordering on and lateral to visual area II. In crossing visual areas I, II, and III from medial to lateral, the corresponding receptive-field areas in the contralateral visual field moved progressively into the vertical meridian, then

out into the periphery of the visual field, and finally back into the vertical meridian. On correlating the areas so mapped with microscopic anatomy as seen in Nissl- and myelin-stained sections, we conclude that the three visual areas are identical to areas 17, 18, and 19, as defined in the cat by Otsuka and Hassler (23).

In experiments using silver-degeneration (Nauta) techniques, cells in area 17 (visual I) projected both to 18 and 19 bilaterally, suggesting that visual messages are transmitted from visual I to visual II and III for further processing.

Cells in visual areas II and III, like those in visual I, responded best to line stimuli such as slits, edges, and dark bars; for optimum response the orientation of the stimulus was critical. The great majority of cells in visual II and half of the cells in visual III were "complex," in the sense that we have used this term in visual I. Other cells, which we term "lower order hypercomplex," formed 5-10% of the cells in visual II and about half of those in visual III. Finally, a few cells in visual III with even more elaborate response properties were termed "higher order hypercomplex."

A lower order hypercomplex cell, like a complex one, responded either to a slit, an edge, or a dark bar, but the length of the stimulus had to be limited ("stopped") in one or both directions. The adequate stimulus was thus a critically oriented line stimulus falling within a given region of retina (the "activating" region), provided a similarly oriented line did not fall over an adjacent ("antagonistic") region. For a cell that responded to an edge limited at one end only, a powerful stimulus was thus a right-angle corner formed by two edges, one of which fell across the activating region in the optimum orientation, while the other fell on the boundary between the activating and the antagonistic regions. A lower order hypercomplex cell thus behaved as though it received inputs from two complex cells (or sets of cells), one excitatory to the cell, with a receptive field occupying the activating portion, and one inhibitory to the cell, having its field in the antagonistic portion.

Higher order hypercomplex cells, of which only 11 were studied, resembled lower order hypercomplex cells in requiring that a line stimulus be limited in length at one or both ends. The higher order cells, however, differed in responding to the line in either of two orientations 90° apart, and the point where the terminus of the line or edge fell within the receptive field was not necessarily critical. These hypercomplex cells behaved as though they had their input from a large number of lower order hypercomplex cells.

Visual areas II and III were both organized in columns which appeared to extend from surface to white matter, within which there were both complex and hypercomplex cells, all with the same receptive-field orientation, but differing in the precise position and arrangement of receptive fields. In visual II and III a single column thus contained hypercomplex cells and also the complex cells that on physiological grounds one would predict projected to the hypercomplex cells. In addition, in visual III there were columns in which some cells had one receptive-field orientation, others had an orienta-

tion at 90° to the first, and still others, higher order hypercomplex cells, responded to both these orientations. Again the cells that seem to be interconnected on physiological grounds are apparently all contained within a single column.

In visual II, as in visual I, some groups of columns were arranged in a highly ordered fashion: as one moved across the cortical surface, the orientation of the underlying columns changed in small regular steps. In other regions the shifts in orientation between neighboring columns appeared to be random in direction and variable in size, sometimes small but sometimes approaching 90°.

The majority of cells of visual II and III were driven from both eyes. A cell that was binocularly driven had fields in corresponding parts of the two retinas, which were, as far as one could tell, identical in their arrangements. Ocular dominance varied from cell to cell, ranging from cells that were driven only from the contralateral eye, through those driven equally well by the two eyes, to those driven exclusively by the ipsilateral eye. The distribution of cells according to relative ocular dominance was remarkably similar in the three visual areas, and in visual III the distribution of hypercomplex cells was similar to that of complex cells. Thus the partial functional separation of cells according to ocular dominance seems to be maintained as far centrally as area 19.

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