Organization of Primary Visual Cortex (Area 17) in the Ferret

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ABSTRACT
Anatomical and electrophysiological mapping techniques were used to determine topographic organization and arrangement of ocular dominance columns in the primary visual cortex of ferrets. From its border with area 18 on the posterior lateral gyrus, area 17 extends around the caudal pole of the hemisphere and over the splenial gyrus to the caudal bank of the splenial sulcus. The visuotopic map is oriented with the insonat lines approxi- mately parallel to the long axis of the posterior lateral gyrus and the associative lines approximately perpendicular to the insonat lines. Central azimuths are represented on the posterior lateral gyrus and peripheral azimuths are represented on the splenial gyrus; the inferior visual field maps medially and the superior visual field maps laterally. As in other
species, the representation of the central visual field is expanded.
The ferret has a considerable degree of binocular vision. Receptive fields driven through the ipsilateral eye extended more than 20° into the contra-
larateral visual field. Within the region of area 17 corresponding to the binoc-
ular portion of the visual field, tritiated proline injected into one eye transneuronally labelled an ipsilateral projection as a series of patchy bands roughly complementary to the labelled contralateral projection. Physiological ocular dominance columns were evident as well in that neu-
rons and groups of neurons recorded in this region showed clustered ocular
dominance preferences. Most single neurons studied were binocularly driven.

Key words: ocular dominance columns, topography, visual field map.

This study describes the anatomical and physiological organization of the primary visual cortex (area 17) of the normal adult ferret (Mustela putorius furo). Interest in the ferret and mink visual systems previously has concentrated on the retinotopic projection because of the availabil-
ity of a catalog of color orientation mutations that correlate with altered routing of ganglion cell axons to the dorsal lateral geniculate nucleus (dLGN) (Guillery, '71; Sanderson et al., '74; Otero-dorier et al., '73) and visual cortex (Ittung and Guillery, '80). More recently, the ferret has appeared to be a potentially valuable subject for the study of early visual development because of the relative immaturity of its vi-

sual system at birth (Linden et al., '78; Guillery et al., '86; McConnell, '86; reviewed in Jackson and Hickey, '80). Knowledge of the normal, adult organization is prerequi-
ts to further investigations into geniculostriate and cortical
development.
In the present study we have located and mapped area 17 in the ferret and have compared its anatomical and phys-
iological organization to that of area 17 in another carni-
vore, the cat. Our results disclose the size, position, and topography of area 17 in the ferret and the segregation of the two eyes' inputs to layer IV in a system of ocular dominance columns. Some of these findings have appeared in abstract form (Law and Stryker, '83).

MATERIALS AND METHODS
Physiological recordings
Animals and surgery. Adult ferrets (700-900 g) obtained from Marshall Farms (North Rose, NY) were initially an-
esthetized with 0.9 ml/kg i.m. of a mixture of ketamine (50 mg/ml) and acepromazine (0.5 mg/ml) and were given atro-
pine sulfate (0.2 mg/kg) to prevent mucus accumulation in

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the trachea during surgery. After intravenous and tracheal cannulation, anesthesia was maintained at surgical levels by using sodium thiopental (10–30 mg/kg, i.v.). The animals were placed in a modified stereotaxic holder on a feedback-controlled heating pad that maintained body temperature at 37.2°C, and a heart rate monitor was connected. The scalp was then retracted, and the portions of the skull and dura overlying area 17 were removed. In general, area 17 was made accessible by a large craniotomy extending from Horsley-Clarke anterior—2 mm to the caudal pole of the hemisphere (approximately Horsley-Clarke—8 mm), and from Horsley-Clarke lateral—medial 2 mm to the lateral margin of the skull (approximately Horsley-Clarke 11 mm). A skull screw was then placed over the hemisphere contra-lateral to that studied electrophysiologically, and the electroencephalogram (EEG) was monitored throughout the remainder of the experiment. Intravenous thiopental sodium was administered at the first sign of desynchronization of the EEG.

Following surgery, a photograph of the exposed brain surface, to be used for noting the sites of electrode penetrations with respect to blood vessel landmarks, was taken and printed at 20–35 x. Pressure points and wound margins were infiltrated with lidocaine, and neuromuscular blockade was induced with pancuronium bromide (0.1 mg/ hour, i.v.). Thereafter the animals were ventilated with a mixture of nitrous oxide and oxygen (3:1) at a rate and stroke volume that maintained expired peak CO2 between 3.8 and 4.4% and peak inspiratory pressure less than 17kPa. Anesthesia was supplemented by injecting thiopental (approximately 2 mg/kg, hour, i.v.) as necessary. Pupils were then dilated with 2% atropine sulfate and the nictitating membranes were retracted with 10% solution of phenyl-ephrine hydrochloride before contact lenses of the appropriate refractive power were fitted.

**Topographic organization.** The topographic organization of area 17 was examined by making extracellular recordings from single neurons and small clusters of neurons and relating their receptive-field positions to the locations of the corresponding recording sites within the posterior lateral gyrus. Recordings were made with electrophrodes tungsten elec-

trodes insulated to impedances of 700 kQ to 3 Mfl with Stoker-Mudjae luscar (Huel, 571). Visual responses of neu-

rons at each recording site were studied by projecting small rectangles of light from a hand-held lamp onto a tangent

screen placed 570 mm from the eyes directly in front of the

animal or at an angle of 60° to the midline. Electro-

lytic lesions (4–6 μA cathodal for 4–6 seconds) marked the locations of many of the electrode penetrations, thus allow-

ing us to determine the locations of the unmarked penetra-

tions by interpolation. In addition, at the end of many recording sessions, injections of the dye fast green were made into the cortex to serve as additional markers.

Two different types of microelectrode penetrations were used in one approach, electrode penetrations were made either normal to the surface of the brain, spaced at 300–

500-μm intervals on a square grid, or on a vertical axis along rostrocaudal rows spaced at 1.5-mm intervals, with penetration spaced at 500-μm or 1.2-mm intervals within a row. The entry points of the penetrations were recorded on photographs of the cortical surface with blood vessels as reference points. The electrodes were advanced vertically in 100-μm steps until layer IV was encountered. Affronts from the lateral geniculate nucleus contributed to the multi-unit activity recorded within layer IV and could be recog-

nized by their brisk responses to non-oriented, rapidly moving stimuli. Receptive fields were always determined through the dominant eye at each recording site, and were usually determined through each eye. After recording in layer IV, the electrode was advanced and receptive fields were often plotted again within layer VI.

The electrode was then advanced through the white mat-

ter until the ventral tip of gray matter was recognized by a change in background activity. Within the ventral tier, receptive fields were plotted at recording sites in layer VI and again in layer IV. Because of the folding of the cortex, vertical electrode penetrations are not normal to the lami-

nate in the ventral tier of gray matter. Some of the more caudal penetrations traversed almost parallel to the lami-
nae within the caudal bank of the superior sulcus, and recording sites were spaced at 100-μm intervals here.

In the second approach, microelectrode penetrations were made more nearly tangential to the cortical surface at an-
gles of 30–60° from the vertical. Such long penetrations allowed us to examine the shift of receptive field locations with small (50–200 μm) changes in electrode position. In two cases, electrodes were angled 45–60° in a parasagittal plane, with the recordings made at 100-μm intervals as the electrode advanced rostrally. In another case, a 30° angle in the coronal plane was used to allow access to the very most lateral portions of the posterior lateral gyrus.

**Boundary area 18.** The boundary between areas 17 and 18 was determined physiologically by making rostro-

caudal rows of vertical microelectrode penetrations spaced at 200-μm intervals. The 17/18 border was defined by changes in receptive field size and neuronal response properties and by the reversal of the progression of receptive field positions (Huel and Wiesel, 52, 55, Tusa et al., 79). Electrorlytic lesions made at the physiologically defined bor-

der in each row of penetrations guided our search for the anatomical features that might be used to define the bound-

aries of area 17.

**Visual response properties.** The receptive field proper-

ties of ocular dominance, preferred orientation, preferred direction of movement, and the distribution of surround was noted at most recording sites. The relative strength of each eye’s multunit response was judged qualitatively to fall into one of seven categories analogous to those defined by Huel and Wiesel (62) for single units.

In ten animals, higher-impedance electrodes were used to study single neurons in area 17. Findings from these ani-

mals on ocular dominance are included in this report.

Quantitative findings on orientation selectivity and other receptive-field properties will be presented elsewhere.

A scalar index was used to describe the bias toward one eye or the other in each animal’s ocular dominance distri-

bution. (Huel et al., 79.) This contralateral bias index (CBI) was calculated according to the following formula:

\[ CBI = 100 \times \left(1 - \frac{(2)(x^2) - (2)(x^2) + (x^2)}{2(x^2)} \right) \]

where hold numbers (1–7) equal the number of units in each ocular dominance group, and \( x \) equals the total number of visually responsive units. This index takes a value of 100 for exclusive dominance of the contralateral eye, a value of 0 for equal dominance of the two eyes, and a value of 0 for exclusive ipsilateral dominance. This index reflects the
"weight" of the ocular dominance distribution toward one eye or the other.

Histology. At the completion of the recording session, animals were given lethal doses of pentobarbital (50-80 mg/kg, i.v.) and perfused intracardially with 1 M phosphate-buffered saline followed by 4% paraformaldehyde in 0.1 phosphate buffer (pH 7.2-7.4). The head was postfixed by immersion in fixative solution for several days, after which the brain was blocked and sectioned at 30 or 40 μm in a plane containing the electrode tracks. Cresyl violet stains were used to locate electrode tracks and marking lesions. Transneuronal autoradiographic tracing of the geniculocortical projection (see below) was carried out in two of the animals studied physiologically, and a variety of other stains (see below) were used to examine the 17/18 border region.

Camera lucida drawings and photomicrographs were made of sections containing electrode tracks. Recording sites were assigned by referring to the Horsley-Clark's coordinates of the electrode penetrations, microdrive readings at the lesion sites, and the locations of the dye marks. For the purpose of map reconstruction, recording sites were projected to cortical layer IV along the radial columns of cells evident in Nissl-stained sections.

The receptive field position at each recording site was noted on the photographs and drawings. The locations of these receptive fields were related to the fixation point for each eye and expressed as two azimuths, azimuth and elevation, on a spherical polar coordinate system (Bishop et al., '90). The fixation point azimuth was determined by using the method of Sanderson and Sherman ('71). The fixation-point elevation was placed 3.5° below the projection of the optic disc in order to make the cortex maps consistent with the maps of the lateral geniculate nucleus (LGN) (Zahs and Stryker, '86). The uncertainty in assigning the true fixation-point elevation will be discussed below.

Map reconstruction: graphically unfolding the cortex

From coronal sections. In one animal studied physiologically we used a two-dimensional reconstruction technique (following Van Essen and Maunsell, '80) to obtain an overview of the visual map. To make this flattened map from serial 40-μm coronal sections, we began at the most caudal section through layer IV and traced every tenth section at the level of layer IV, aligning each section relative to its neighbor. To maintain this alignment accurately, we split the most rostral sections at the lateral and medial edges and temporarily aligned the ventral and dorsal halves separately. After completing the reconstruction, the azimuth and elevation of each receptive field center were noted at the position on the reconstruction of the projection of each recording site onto layer IV. Isomargin and iso-elevation lines were then drawn over the flattened cortical reconstruction.

From parasagittal sections. In two animals prepared in parasagittal section, drawings of reconstructed electrode penetrations were used to create unfolded representations of areas 17 and neighboring visual areas after building a physical three-dimensional model. In these reconstructions, data from four to ten serial 40-μm sections were collapsed onto a drawing of a single section. Sections were selected for drawing at approximate 1-mm intervals. Drawings were mounted on cardboard and assembled in accurate three-dimensional register. Strips of foil were then laid along the border between layers IV and V, and the positions of the recording sites were projected radially onto these strips.

For all but the most medial and most lateral sections, the width of the strip of foil was the average distance between the section and its two neighbors of the series. Since, for both animals, the mapped region extended approximately to the medial border of area 17, the width of the most medial strip was chosen to be half the distance between the two most medial sections. For one animal (S15), electrode penetrations had been placed quite far laterally, and recording sites were found in the sharply curved region of cortex, where the parasagittal plane is nearly tangential to the plane of layer IV. A tracing was made of the most lateral section of the series from S15, and this tracing was superimposed along an interhemispheric cut hinged at the caudal pole. In the second animal, sections containing recording sites did not extend as far laterally, and the most lateral section was represented as a strip half the width of the distance between it and its nearest neighbor of the series.

The strips were then laid flat and aligned so the caudal poles of the sections were in the correct relative anterior-posterior positions. Isomargin and iso-elevation lines were drawn by connecting recording sites with receptive fields having the same azimuths or elevations, respectively. In drawing these lines, interpolations were sometimes made. For example, a higher-elevation line might be drawn between recording sites with receptive field elevations of 9° and 11°.

Anatomy

Antoniological features characterizing area 17. The boundaries of area 17 were delineated anatomically by using three techniques. Cresyl violet staining allowed visualization of the laminar structure of the cortex through which the 17/18 border could be discerned. Fiber staining carried out by using the Weil method was used to distinguish area 17 from 18 on the basis of differences in the caliber of myelinated axons innervating specific laminae. Finally, transneuronal autoradiography (Wiesel et al., '74) was carried out in five ferrets to trace the projection from the LGN to area 17. In five ferrets, we injected 2 μCi 3H-proline (specific activity 40 Ci/Mmol, New England Nuclear NET-323) dissolved in 7-25 ml sterile saline into the vitreous humor of the right eye by using a 33-gauge needle. From 30-μm sections from these animals, we made a horizontal, parasagittal, frontal plane, coated with Kodak NTB-2 emulation, and developed 3-8 weeks later. Autoradiographic labelling of the visual cortex was sufficiently intense to be visible at low magnification in darkfield but not brightfield optics.

Flattened preparations. In two animals that were not used for microelectrode studies, the posterior neocortex was physically flattened before sectioning by using the method described by Ciavarra and Montero ('74) so that large regions of area 17 could be seen in a single section. These animals were first perfused with phosphate-buffered saline followed by brief perfusion with 2% glutaraldehyde in 0.1 M phosphate buffer (pH 7.4). The posterior half to two-thirds of the two cortical lobes were quickly removed and the dura was peeled off. The pia covering the deeper sulci was cut and some internal white matter was removed. Two cuts were made at the posterior lateral and medial margins to facilitate the unfolding of the ventral aspect of the posterior lateral gyrus. The cortices were placed between sili-
were hardened in fixative in the flattened state for 2-7 days. The corneas were then embedded in a gelatin-alumina mixture before sectioning at 40 µm and autoradionuclide imaging. 

Area and volume measurements. The total surface area of area 17 was calculated by using two different methods. In the two methods, for which complete fiducial maps were prepared from serial parasagittal sections, the area count was performed by the planimeter defined area 17 was a simply measured by a Summers digitizer. A second measure of the total area of area 17 in the plane of layer IV was calculated from fluorescence micrographs of the volume of layer IV divided by its average thickness. The volume of layer IV in area 17 was measured with the aid of a complete series of parasagittal autoradiographic sections taken at intervals of 100 µm in two animals in which one eye had been injected with 2 µCi [3H]proline 1-2 weeks prior to perfusion. In some sections, layer IV stands out as a dense labeled band over the entire extent of area 17 (see for example, Fig. 5). The outline of each band on the side contralateral to the eye that had been injected, including the slightly labeled gap that corresponds to the unlabeled ipsilateral eye's ocular dominance patches, was traced in the camera lucida at a high magnification of 15X. The area of the outlined bands was measured with a planimeter digitizer connected to the PDP/23 computer for planimetry. The sum of these areas, multiplied by the spacing between sections, was taken to be the volume of layer IV in area 17. The surface area of area 17 in the plane of layer IV was then calculated by dividing this volume by the average thickness of layer IV measured in sections that intersected the plane at right angles.

This method of calculating surface area assumes a constant thickness of layer IV. This assumption has been verified in other species (Van Essen and Maumon, '82) and is confirmed by our repeated measurements in the ferret. It has the virtue that it accounts properly for the property of layer IV that is cut in oblique or tangential section without the need for making adjustments to the planimeter with which the planes were marked in that in the sections were cut. The area estimated by the second technique included both contralateral and ipsilateral eye patches. The fraction of layer IV devoted to the ipsilateral eye was estimated from volume measurements of the density labeled labeled to those in the planimeter with which the planes were marked in that in the sections were cut. The area estimated by the second technique included both contralateral and ipsilateral eye patches. The fraction of layer IV devoted to the contralateral eye was estimated from volume measurements of the density labeled labeled to those in the planimeter with which the planes were marked in that in the sections were cut.

The relative areas occupied by the contralateral eye patches and the contralateral eye patches were estimated from the flattened cortices illustrated in Figure 15. The projection of the ipsilateral eye patches delineate the region in which the two sides were to be compared. Labelled and unlabeled areas within this region of area 17 in the two hemispheres were then measured. This reconstruction was performed in a projection period of ocular dominance patches. Comparables portions of the binocular region in the two hemispheres were outlined, and the period was measured in the direction normal to the elongate course of the patches at random, approximately 1-mm, intervals within this region.

**Fig. 15.** The location of area 17 on the surface of the ferret brain. The isocortex at the level of the medial prefrontal cortex have been removed. A: Lateral view showing the visual field projection onto area 17. B: Anterior view showing the visual field projection onto area 17. C: posterior view showing the visual field projection onto area 17. D: Relation of the superficial appearance of area 17 to its appearance in section. The left hemisphere was cut in the parasagittal plane at the levels shown in the heavy arrowheads in B, the cortex lateral to the cut was removed, and the cut surface was outlined. Contours of these figures section 4 of figure 15. Fig. 16. The postparietal and occipital sulci have been outlined on the left hemisphere in parts B and C. D: anterior; E: dorsal; L: lateral; P: posterior.
as easily defined. Along electrode penetrations that ran oblique to the cortical surface, the preferred orientations of successively encountered units changed gradually and progressively. In the middle cortical layers, from which the mapping data reported here were principally obtained, most multiple-unit responses were dominated by one eye, implying that the eye preferences of simultaneously recorded units were similar.

Topographic organization of area 17
A single representation of the contralateral visual field was found within area 17 of the ferret. Physiological mapping techniques were used to record from single and multiple units within much of area 17 in eight ferrets. The centers of the receptive fields plotted in four of these mapping experiments are drawn in Figure 2 to illustrate the extent of the visual field represented in area 17. Receptive fields of units in area 17 dominated by the contralateral eye were found with azimuths as great as 135° and elevations ranging from at least -40° to +70° degrees. Ipsilaterally dominated units (indicated by open circles in Fig. 2) were found only in the central portion of the visual field. The ferret’s binocular visual field was found to extend to at least 30° azimuth in the superior visual field and to at least 20° azimuth in the inferior visual field. This estimate of the extent of the binocular visual field is consistent with

Fig. 2. Monocular and binocular segments of the visual field represented in area 17. Closed and open symbols indicate receptive fields of units responding to stimulation through the contralateral and ipsilateral eyes, respectively. Receptive fields illustrated are from mapping experiments in four animals (including FH and PW of Figs. 4 and 7). Azimuth and elevation are indicated in degrees.
that found in mapping studies of the LGN (Zahs and Stry- kor, '80).

Reconstruction of map from cortical sections. In initial mapping experiments, rows of electrode penetrations were made in the cortical plane, and the brain was sectioned in that plane as well. Within each section, the more medial penetration sites represented more inferior portions of the visual field. For the dorsal surface at least, the more caudal sections at a given intermedial position represented more peripheral portions of the visual field. However, for the major portion of area 17, lying beyond the dorsal surface, it was difficult to appreciate the organization of the visuotopic map from such sections.

In order to gain a sense of the overall organization and continuity of the visuotopic map, it is desirable to "unfold" the cortex to view it as a flat sheet. We did not find it possible to reconstruct electrode penetrations in a cortex that had been physically unfolded. However, it was possible to graphically unfold the cortex after locating recording sites in sections. The visuotopic map over a portion of area 17 from which recordings were obtained in one ferret is reconstructed in Figure 3 by using Van Essen and Maun- sell's ('80) technique as described in Materials and Meth- ods. The positions of marking lesions (made during the recording experiment and shown in Fig. 3A by filled circles) were placed on this reconstructed surface and the locations of remaining recording sites were inferred from these landmarks. Figure 3B shows isoluminance and isoelevation lines drawn on the basis of receptive-field positions at these re- cording sites. On the dorsal surface (shown in the top half of Fig. 3B) more peripheral fields were located progres- sively more caudally and inferior fields progressively more medially. On the ventral (tensorial) surface (shown in the bottom half of Fig. 3B) intermedial organization was simi- lar while receptive fields continued to progress peripherally as the surface continued ventrally and medially.

Reconstruction of map from sagittal sections. The major portion of area 17 was found in the previous experiments to lie on the tensorial surface of the splenial gyrus. Because this surface is inclined only slightly from the coronal plane, the contours of the map sections obtained in area 17 were on the other hand, nearly normal to the surface of area 17 over most of its extent (except for the relatively small amount of area 17 lying at the lateral and medial edges of the hemisphere). For this reason, our most extensive analysis was conducted on material sectioned in the sagittal plane.

Receptive fields were determined at 143 sites in 54 elec- trode penetrations in one animal (F91) and at 134 sites in 41 penetrations in a second animal (F91). Electrode pene- trations were then reconstructed from serial parasagittal sections stained by a Nissl method. Figure 4 shows the centers of the receptive fields of the multiet clusters recorded in F91. Because the location of area 17 is more easily seen in autoradiographically labelled sections than in Nissl-stained sections, the mapping data from F91 were superimposed on a series of labelled sections from another animal. This animal had received an injection of 3H-proline into one eye a week prior to a terminal recording experi- ment in which the boundary between areas 17 and 18 was determined electrophysiologically. The locations corre- sponding to the recording sites from the more extensive mapping experiment in Figure 4 were placed in these sec- tions, illustrated in Figure 5, by using the Horsley-Clarke coordinates of each site. The position of the 17/18 border and the receptive-field elevations confirmed, respectively, the correct anterior-posterior and lateral-medial place- ments of the mapping data onto the sections.

Within parasagittal sections like those shown in Figure 5, area 17 may be traced caudally from its boundary with area 18 around the caudal pole and then rostromedially along the splenial gyrus onto the caudal bank of the splen- ial sulcus. Receptive-field locations of units encountered along such a route follow an arc from central and inferior to peripheral and superior in the contralateral visual hemi- field. The elevations of receptive fields increase and the area become steeper in more lateral sections.

These parasagittal sections were also graphically un- folded (as described in Materials and Methods) in order to convey a sense of the overall organization of the map in area 17. The unfolded map constructed from F91 is shown in Figure 6. Features of the visuotopic map in area 17 are apparent in this reconstruction. Isoluminance lines run roughly parallel to each other and are crossed at approxi- mately right angles by isoelevation lines. In this animal, the region of area 17 representing the central 10-15° of azimuth occupies approximately 2 mm on the dorsolateral surface of the posterior lateral gyrus. The most peripheral visual field (azimuth as large as 120°) maps to the crown of the splenial gyrus.

Although the pattern illustrated in Figures 4-6 from animal F91 above was the most common, in some animals the precise position of area 17 on the cortical hemisphere differed by more than 3 mm from this case. Such variability in position is significant when one considers that the entire extent of area 17 along the representation of the horizontal meridian is no more than 10 mm.

This variability is illustrated by data from another case, F91. The receptive-field centers of the sites recorded in this animal are shown in Figure 7. Figure 8 shows the corre- sponding unfolded map. This figure illustrates the less fre- quently observed, but not rare, case, in which area 17 is shifted back so that only the central 5° of azimuth are represented on the dorsal surface of the cortex, and the very far periphery (azimuth larger than 85°) comes to be repre- sented in the same region of the plane. In this case (not illustrated, less common than those above, area 17 appeared to be shifted as much as 1.5 mm rostrally) to the position occupied in the case illustrated in Figures 4-6.

Size of area 17

The size of area 17 was measured in two independent ways as described in Materials and Methods. After label- ling the geniculo-cortical projections by transneuronal au- toradiography, the volume of layer IV was measured from a complete series of sections and was then divided by the average thickness of layer IV measured in sections normal to the cortical surface to yield an estimate of surface area in the plane of layer IV. In one 890-g female analyzed by this method, area 17 occupied 76.7 mm². In another 890-g female, area 17 occupied 85.7 mm².

In two other ferrets, the region of area 17 studied electro- physiologically was measured on the flattened maps illus- trated in Figures 6 and 8. For these measurements, area 17 was bounded dorsorostrally by the representation of the vertical meridian (9° isoluminance line), mediolaterally by the most medial section containing recording sites, and laterally by the most lateral section containing recording sites. The rostromedial boundary was somewhat arbitrarily drawn as a line skirting the most rostromedial recording sites in
Fig. 4. The receptive-field centers of 143 multunit clusters recorded in area 17 and neighboring visual areas in ferret FS1. Locations marked with circles are receptive fields of sites recorded in area 17; locations marked with squares are receptive fields of sites recorded in area 18; locations marked with triangles are fields recorded in other visual areas. Numbers and letters within the symbols refer to recording sites shown in Fig. 5 and 6. The receptive field at the site marked by a 8° azimuth, +60° elevation is designated as being from “other visual areas” in Figures 4 and 6 on the basis of the response characteristics of the units recorded at the site. This site appears to be well within area 17 on the section illustrated, an artifact of superimposing data on this particular representative section.

Fig. 3. Flattened representation of area 17 in one ferret showing the organization of the visual map. A. Serial coronal sections were reconstructed by using a two-dimensional mapping technique (modified from Vosbruch and Manford, 1968). Sections were cut for reconstruction at the positions indicated by the arrow in the inset, and the dorsal and ventral halves were aligned separately. Electrolytic lesion and penetration sites (filled circles) confirmed the alignment and allowed the estimation of the locations of many other penetration sites (open circles). B, Descention (shaded) and insinuation (dotted) lines describe the organization of the map over the flattened cortical surface. More peripheral fields are located progressively more caudally and wrap around the ventral surface of the gyrus. The inferior portion of the visual world maps medially, D, dorsal, V, ventral, L, lateral; M, medial; WM, white matter.
Fig. 5. Mapping data from the experiment illustrated in Figure 4 have been superimposed on a series of parasagittal sections through ferret cortex, which are oriented in the same plane as the sections of Figure 4. Sites are indicated by squares, circles and triangles. Sites that were found to be located in layer IV or beneath the pial surface are shown as open symbols. Sites in layer III are shown as filled symbols. Sites that were located in the sulcal region are shown as filled triangles. Sites that were located in the fissural region are shown as filled circles. Sites that were located in the subpial region are shown as filled squares. Sites that were located in the subarachnoid space are shown as open circles. Sites that were located in the subpial region but were not associated with a sulcal or fissural landmark are shown as open squares. Sites that were located in the subpial region but were not associated with a sulcal or fissural landmark and were not associated with a subarachnoid space are shown as open triangles.

Fig. 6. Flattened representation of area 17 and neighboring visual areas constructed from the mapping data displayed on the sections of Figure 5. Circles indicate recording sites in area 17; squares indicate sites in area 19; and triangles show sites in more ventral visual areas. These symbols correspond to the sites in Figure 5 and the receptive fields in Figure 4. Thin solid lines are isoluminant dashed lines are isoluminant. Heavy lines mark the caudal pole and sulci of the occipital lobe.
Magnification factor

An expanded representation of the central visual field is seen in the flattened maps of Figures 6 and 8. In Figure 6, for example, the central 30° of azimuth maps to an area of cortex (30 mm²) greater than that representing the peripheral 90° (24 mm²).

From the flattened maps, a greater area of cortex also appears to be devoted to the inferior visual field (51 mm²) than to the superior visual field (26 mm²), but this conclusion depends on the assignment of the fixation point elevation. The assignment of elevations in the cortical maps was made consistent with previous published maps of the LGN (Zeki and Stryker, '80). This assignment was on the basis of the distribution of geniculate receptive-field sizes as a function of elevation, a function that varied little between -30 and +20° of elevation. Inspection of the flattened cortical maps reveals that the elevations near -10° have the most expanded representation, suggesting that the true horizontal meridian may be closer to the elevation labelled -10° in the maps than to that labelled 0°. If the line labelled -10° represents the projection of the horizontal meridian more accurately than the line labelled 0°, then the representation of the superior visual field (31 mm²) is somewhat larger than that of the inferior visual field (22 mm²). This issue will be considered in the Discussion.

The expanded representation of the central visual field may be expressed quantitatively as the magnification factor (Daniel and Whitteridge, '61). Area magnification fac-
tors were calculated as described in Materials and Methods. Because of the spacing of the electrode penetrations during the recording sessions, as well as the expansion of the central visual field which occurs in the visuotopic map in area 17, smaller areas of the visual field were represented in areas of cortex measured in the central representation than in the peripheral representation. Areas of cortex devoted to 5° × 5° areas of the visual field were measured for the region of area 17 representing 0–20° of azimuth and 0–20° of elevation. For the region representing 20–50° azimuth and 0–20° to +25° elevation, areas of cortex measured representing areas of the visual field not exceeding 50°. For azimuths greater than 50° or elevations less than –20°, the cortical representations of visual field areas not exceeding 100° were measured.

Figure 8A shows a scatter plot and best-fitting smooth curve of the relation between magnification factor and eccentricity, defined as the square root of the sum of the squares of azimuth and elevation. In calculating eccentricity, 10° was added to the values of elevation shown on the maps, since the data presented here suggest that the –10° isoelevation line is closer to the true representation of the horizontal meridian than is the 0° line. Magnification falls off quite gradually by this analysis, in which azimuthal and elevational changes are combined. Magnification also changes gradually as a function of an azimuth, as shown in Figure 8B. Values on the abscissa indicate the center of the visual field areas represented. Magnification remains fairly constant across the central 25° of azimuth and then declines steadily. This trend, ob-
The border between areas 17 and 18 was delineated both physiologically and anatomically.

**Physiology.** Microelectrode recordings made in two ferrets to define the rostral border of area 17 on the posterior lateral gyrus revealed a reversal in the visual-field representation similar to that across the 17/18 border in other species. Figure 9B shows three examples of this transition. At successive electrode positions from rostral to caudal along row A, for example, fields 1–3 moved from peripheral to more central portions of the visual field while receptive fields recorded in the more caudal penetrations 3–6 reversed the direction of progression and moved back toward the periphery of the contralateral visual field. We take this progression of receptive-field positions to be evidence that the more rostral penetrations were within area 18 and the more caudal ones within area 17. Note also that, as in other species, receptive fields in area 18 were considerably larger than those in area 17. Possibly as a result of the large receptive fields, neurons and neuron clusters within area 18 responded much better to extremely rapid motion than did neurons in area 17. These changes in receptive-field size and character always occurred within 500 μm of the point at which the progression in receptive-field position reversed (rows B and C of Fig. 10). Electrolytic marking lesions were made at the points of transition between areas 17 and 18 (marked with asterisks in the inset). These lesions allowed us to identify the physiologically defined border in histologic sections (see Fig. 12D below).

**Normal anatomy.** In the cat four features visible in the normal anatomy of the visual cortex are useful in locating the border between areas 17 and 18 (Otsuka and Hassler, 1965). Area 17 contains fewer large pyramidal cells in layer III; 2) at the border between 17 and 18, a cluster of large pyramidal cells is often found; 3) layer IV is nearly twice as thick within area 17 as within area 18; and 4) coarse bundles of myelinated fibers are more prominent within area 18. The Nissl preparation shown in Figure 12D illustrates
the third of these features clearly, and the first two may be seen with some study. Figure 11 shows a Weil myelin preparation that illustrates the fourth feature. All of these features that distinguish area 17 from area 18 in the cat appear to be useful as well in the ferret.

**Experimental anatomy.** Transneuronal autoradiographic labelling of the geniculo-cortical projection was also helpful in defining the 17/18 border. Figure 12A shows a low-magnification dark-field photomicrograph of a parasagittal section through the region of the 17/18 border. Area 17 in the ferret receives a projection from the dLGN that is densely labelled with the transneuronal method; the projection to area 18 is labelled very much more lightly and possibly not throughout its full extent. The vertical white
Fig. 11. Nissl stain of parasagittal section through ferret visual cortex. Dotted line shows pial surface; area 17 to right of white arrow; area 18 to left. As in cat, sparse bundles of myelinated fibers are more prominent in area 18. Dorsal is up; medial is to right; scale bar equals 200 μm.

Fig. 12. The 17/18 border. A: Low-power darkfield photomicrograph of a parasagittal section through the visual cortex contralateral to an eye which had been injected with FMG. Note dense labelling (light) of layer IV within area 27. Region between vertical white lines enlarged in B. Enlargement of autoradiograph in A showing the 17/18 border region. Electrolytic lesions (white arrows) mark 17/18 border defined physiologically. Note expansion of labelling into upper and lower layers between asterisks, extending less than 1 mm (blue) into area 17 and less than 2 mm into area 18. C: Micrograph shown in A photographically superimposed to demonstrate the expansion of labelling into upper and lower layers near the 17/18 border and extension of weak labelling of layer IV into area 18. B: Nissl stain of serial section adjacent to serially shown in A-C. Electrolytic lesion (black arrow) marks physiologically defined border between areas 17 and 18. Nissl stain reveals histological transition between the two areas. The lines on the photomicrograph delineate the six cortical layers, demonstrating greater thickness of layer IV in area 17 (right side). Scale bars equal 1 mm. A, anterior; B, dorsal; P, posterior; V, ventral.
bars in Figure 12A delineate the region shown in higher magnification in Figure 12B. The adjacent section, containing an electrolytic lesion (arrow) made at the physiologically determined border, is shown in a Nissl preparation in Figure 12D. This lesion confirms that the physiological 17/18 border is where the dense label ends.

Close examination of the autoradiographs revealed the unexpected finding that the transneuronal label was distributed more widely within the upper and lower layers in the 1–2 mm near the 17/18 border than within either area 17 or 18. Figure 12C is a print of the same photomicrograph shown in 12A, exposed for a longer time in order to make visible the increased density of grains in layers II, III, V, and VI near the 17/18 border. This is more clearly seen in the high-magnification darkfield photomicrograph of Figure 12E. Labelling considerably above background was observed in all cortical layers within the region shown between the two asterisks in 12B.

Ocular dominance columns in area 17

Anatomy. Intracranial injections of \(^{14}\)H-proline followed by transneuronal autoradiography revealed a pattern of ocular dominance patches within area 17. Transneuronally labelled geniculoocortical terminations were found to fill layer IV of the contralateral hemisphere of area 17 continuously in more peripheral representations corresponding to the monocular segment of the visual field and with a patchy distribution in the representation of the binocular segment of the visual field. In the ipsilateral hemisphere, the labelling was confined to patches within the posterolateral pole roughly complementary to patches seen in the other hemisphere. Figure 13 shows the transneuronal labelling of the two hemispheres in coronal sections taken about 1.8 mm from the caudal pole. Note the patchy labelling of layer IV and the particular clarity of the patches on the ipsilateral side, in which faint patchy labelling is also seen in layer VI.

The overall nature of the geniculoocortical termination pattern is best seen in the reconstructions in Figure 14 and 15. Figure 14 is an expanded reconstruction of serial horizontal sections. The right eye of the animal from which those sections were made was injected with \(^{14}\)H-proline 11 days prior to perfusion. In this figure drawings of sections from the cortex contralateral to the injected eye are arrayed above those from the ipsilateral hemisphere such that the caudal portions of each reconstruction abut, allowing the complementary pattern of the patches to become more evident. The widths of the ipsilateral eye patches varied between 200 and \(1,500 \mu\text{m}\) when viewed in the horizontal plane.

Figure 15 shows the labelled regions from a ferret in which the visual cortex was physically flattened (see Materials and Methods) before sectioning parallel to the plane of the flattened surface. Tracings of serial sections from this brain were superimposed to make this reconstruction, which makes visible the rather striped pattern of ocular dominance patches. The period of the ocular dominance patches measured in this brain was \(850 \pm 25 \mu\text{m}\) (SEM).

Fig. 15. Ocular dominance patches in coronal section through area 17 following transneuronal transport of \(2 \text{ nCi} \) of \(^{14}\)H-proline injected into right eye. Left (contralateral) hemisphere shown on left; right (ipsilateral) hemisphere shown on right. Dorsal is up, medial is toward the middle; scale bar equals 1 mm.
Fig. 14. Expanded reconstruction of ocular dominance patches in horizontal sections. Hemispheres contralateral to an eye that had been injected with 3H-proline is shown above ipsilateral hemisphere. Areas of these autoradiographic label are drawn in black while lightly labeled areas appear stippled. Note complementary nature of labelling pattern in the two hemispheres patches appear on (ipsilateral) side where holes occur in the otherwise uniform labelling of the contralateral hemisphere. Note also that ocular dominance patches occur only in the portion of area 17 representing medial visual fields. R, rostral; C, caudal; M, medial; L, lateral.

Fig. 15. Pattern of autoradiographic labelling in layer IV of physically flattened visual cortex from a ferret that had received intracarotid injection of 3H-proline. Tracings reconstructed from serial sections nearly tangential to flattened layer IV. The most posterior portions of each hemisphere were only partially flattened, and therefore the fidelity of the reconstruction is less accurate in these regions. The reconstruction thus appears in four parts and the alignment of such as the four parts is shown by individual axes. Axes with solid lines indicate the orientation of the central, flattened portion of the hemisphere, while the axes with broken lines show the orientation of the partially flattened, posterior portions. Labels as in Figure 14. Note that many centres correspond to more strongly elongated ocular dominance patches. Note also that ipsilateral patches are narrower than contralateral patches.
In two transneurally labelled brains studied in sagittal section, the ipsilateral eye patches occupied 15% and 14% of the total volume of layer IV in areas 17, while the contralateral eye patches occupied 88% of the total volume. The ipsilateral projection thus represents approximately 17% of the volume of the contralateral projection.

Even within the binocular segment, transneurally labelled geniculo-cortical afferents serving the contralateral eye occupied a greater portion of area 17 than did those serving the ipsilateral eye: the labelled contralateral eye bands in Figures 3 and 15 tended to be wider than the gaps separating these bands, and wider as well than the labelled bands in the ipsilateral hemisphere. The volume of layer IV occupied by the afferents serving each eye within the most binocular segment (region extending halfway from the 17/18 border to the beginning of the monococular segment) was measured on a series of autoradiographically labelled coronal sections. Approximately 77% of the most binocular region of the contralateral hemisphere was occupied by label while only 49% of the corresponding region was labelled ipsilaterally. The sum of these two figures, 126%, would indicate that there is some degree of overlap between afferents serving the two eyes. The absolute magnitude of this overlap is difficult to determine from such autoradiographic material because of the somewhat arbitrary definition of “border” of the labelled patches, when, in fact, grain density declines gradually rather than abruptly (see LeVay et al. [78]). The relative values of 77 and 49% coverage by the contralateral and ipsilateral geniculo-cortical afferents are, however, probably genuine, as they were drawn by using the same criterion. These values would suggest that even within the binocular segments there should be a substantially greater influence of the contralateral than the ipsilateral eye. Physiological findings below are in accord with this suggestion.

Physiology. The relative efficacy of the eye was assumed physiologically within the binocular portion of the ferret visual cortex. Single units in area 17 with receptive fields within 10° of the vertical meridian were usually driven binocularly. Figure 16 shows an ocular dominance histogram compiled by using the seven-point scale of Hubel and Wiesel ([62] from 220 single units in ferret receptive field centers between +20 and −30° elevation and <15° azimuth) recorded in ten ferrets. The overall greater dominance of the contralateral eye is evident from this histogram: about twice as many units favored the contralateral eye as favored the ipsilateral eye (contralateral bias index = 66, see Materials and Methods). This histogram, which consisted most of the mapping data, eye preference was much more marked, and responses were purely monocularly driven at 60° of the binocular segment recording sites. The relative field coverage is illustrated in Fig. 9. The multimodal data revealed that the two eyes are much more nearly equal in their influence within 10° of the vertical meridian (contralateral bias index = 59) than in more peripheral parts of the binocular representation (contralateral bias index = 78). More than four times as many recording sites were dominated by the contralateral eye as by the ipsilateral eye in peripheral portions of the binocular representation while the corresponding figure was less than four times for the central 10°. The above data in confirmation with the above findings also showed that eye preference was also evident physiologically. Recording sites within a penetration normal to the surface tended very strongly to have the same eye preference. Neighboring penetrations also tended to be similar in eye preference.

Discussion

Topographic organization

Electrophysiological mapping techniques were used to determine the topographic organization of primary visual cortex in ferrets. From its border with area 18 on the posterior lateral gyrus, area 17 extends around the caudal pole of the hemisphere and over the splenial gyrus to the caudal bank of the splenial sulcus. The visuomotor map is oriented with the isoinnominat lines approximately parallel to the long axis of the posterior lateral gyrus and the isolevelation lines approximately perpendicular to the isoinnominat. Cen-

tral azimuths are represented on the posterior lateral gyrs and peripheral azimuths are represented on the splenial gyrus; the inferior visual field maps medially and the su-

perior visual field maps laterally.

How much of area 17 was mapped in this study? An estimated 80% of area 17 was mapped electrophysiologically in each of the two animals from which maps were constructed from parasagittal section. This value is based on a comparison of the mapped areas to the area of area 17 defined by transneuronal labelling. The unmapped area includes the ventromedial splenial gyrus and the ventral portion of the caudal bank of the splenial sulcus. It can be inferred from Figures 6 and 8 that this region of area 17 contains the representation of the supratemporal visual field. The extent of the visual field represented in area 17 is best illustrated in Figure 2. Receptive fields of units in area 17 have been found with azimuths as great as 135° and elevations ranging from at least −40 to +70°.

Use of maps. These mapping experiments were undertaken in part to provide a guide for future studies of ferret area 17. Figures 4–6 should aid the neurophysiologist in relating locations in the visual field to sites in the cortex.

Fig. 16. Ocular dominance histogram compiled from recordings of 220 single units in ten ferrets. Histogram plate percentage of units in each of seven ocular dominance groups defined by Hubel and Wiesel ([62]; group 1 (sensitive for units driven exclusively through contralateral (ipsilateral) eye; group 2 (weakly dominated by the contralateral (ipsilateral) eye, group 3 (faintly for units weakly dominated by the contralateral (ipsilateral) eye; group 4 (faint) for units driven nearly equally by the two eyes. Number of units in each bar of histogram is indicated above the bar.)
In order to locate a site in the cortex representing a known location in the visual field, the physiologist should refer to Figure 4 to find the receptive number of the receptive field closest to the desired visual field location. The reference number can then be used to find the corresponding cortical site in the paraocular sections of Figure 5 or in the flattened representation of area 17 in Figure 6. Similarly, to find the receptive field of a recording site more rapidly when the Henley-Clarke coordinates of that site are known, the physiologist should first refer to Figure 5 to get the receptive number of the appropriate receptive field, next look at the flattened representation in Figure 6 to find the approximate azimuth and elevation of that receptive field, and finally refer to Figure 4 for a more precise location of the receptive field. When it is necessary to adjust an electrode position, the following guidelines may be helpful. Caudal movement of the electrode results in a peripheral-superior (the main effect of the electrode movement on the receptive-field location being given first) shift in the receptive fields of sites recorded on the dorsal surface of area 17 and in a central shift in the receptive fields of sites on the tentorial surface. Lateral movement of the electrode results in a superior-central shift in the receptive-field location for sites recorded on either surface.

Comparison with the cat

The cat and ferret have in common the general plan of the carnivore visual system and geniculocortical projection (Sanderson, 174). The two species have similar tapetal retina, and a similar classification of retinal ganglion cells into α, β, and γ types has been made on anatomical grounds (Vitek et al., 95). The two species differ in that the ferret's retina has much smaller, more laterally placed eyes, a much less pronounced area centralis, and a stronger visual streak than does the cat (Vitek et al., 95). Receptive fields in the ferret are also substantially larger than in the cat, as predicted from the angular subtense of retinal ganglion cell dendritic fields, and the ferret has less overlap between fields and appears to have an ipsilaterally directed α-cell projection (Vitek et al., 95, Zaha and Stryker, 95). Several features of ferret visual cortex are similar to the cat and differ from those of the monkey, indicating the laminar patterns of staining for cytochrome oxidase and acetylcholine and the extent of cortical connections (Rockland, 95). The segregation of ON- and OFF-center cells in ferret LGN and cortex also differs from cat, although it is similar to the monkey (Sanderson, 174; LeVay and McConnell, 92; Stryker and Zaha, 93; LeVay et al., 93; Zaha and Stryker, 93).

Topographic organization

The topography of ferret area 17 may be compared to that of the cat, a much more widely studied carnivore. Figure 17 schematically compares the position and organization of the cat and ferret visual cortex. The organization of area 17 in the cat shown in Figure 17A is redrawn from Tsui et al. (78). In both figures iso-elevation lines appear as dotted lines, while isomuism lines are solid. In the cat, the fixation point (the intersection between the vertical and horizontal meridians) occurs at the center of the dorsal surface of the hemisphere at the junction of the lateral and posterior lateral gyri (asterisk). In the ferret, the representation of the fixation point occurs more laterally and ventrally, approximately two-thirds of the way down the dorsal surface of the posterior lateral gyri (asterisk). Because of its caudal aspect, the cat's brain could be made to resemble the ferret's brain by spreading the caudal poles upward and outward from a hinge at the dorsal midline. The tentorial surface of area 17 in the ferret thus plays the role of the medial bank of area 17 in the cat.

The ferret's visual field extends farther along the horizontal meridian than does the cat's, as would be expected from the ferret's more laterally placed eyes. Recording sites were found in ferret area 17 with receptive fields having azimuths as great as 135°, the cat's visual field extends to the 90° azimuth.

Magnification

There is an expanded representation of the central visual field within area 17 of the ferret. Such central magnification has been described in the cat as well (Tsui et al., 78). However, cortical magnification factor changes much more gradually as a function of azimuth in ferrets than in cats, probably reflecting the ferret's visual streak (Vitek et al., 95; Henderson, 90) vs. the cat's well-developed central area (Stone, 78). In cats, cortical magnification factor appears to be determined by the gradient of retinal ganglion cell density (Tsui et al., 78). However, central magnification in macaque striate cortex appears to be greater than that which would be predicted on the basis of retinal ganglion cell densities or LGN volumes (Malpeli and Baker, 79). This study pro-
video insufficient data to estimate the precise extent to which magnification factors in ferret cortex are determined by retinal ganglion cell densities. However, magnification factor in cortex does change in parallel with ganglion cell density in retina: cortical magnification factor changes more rapidly as a function of elevation than as a function of azimuth, just as retinal ganglion cell density changes more rapidly along the inferior-superior axis than along the naso-temporal axis (Vitek et al., '85). The similarity between the fraction of the LGN devoted to the ipsilateral eye (12%, 16%, and 19% in three cases studied by Zahn and Stryker, '85) and the fraction of cortical layer IV occupied by affor- dants serving each eye (14% and 18%) in the two cases presented suggests that magnification changes little between LGN and cortex.

Monocular and binocular segments. The binocular seg- ment of the visual field is smaller in ferret than in cat, in accordance with the more lateral placement of the ferret's eyes. The binocular field in the cat encompasses up to 45° on each side of the vertical meridian (Sanderson et al., '91). Based on the sample of receptive fields illustrated in Figure 2, the ferret's binocular visual field extends to at least 30° azim- uth in the superior visual field and to at least 20° azimuth in the inferior visual field. This estimate of the extent of the binocular visual field is consistent with that found in mapping studies of the LGN (Zahn and Stryker, '85).

The binocular segment occupies about half of the visual cortex in the ferret, leaving a large and accessible monocu- lar segment. By contrast, in the cat, only a rather inaccessible 16% of area 17 is devoted to the monocular segment of the visual field (Tan et al., '79). Thus, the ferret may provide an excellent model system for investigations of binocular interactions and future studies that will compare the organizations of the monocular and binocular representations.

Ocular dominance columns. The present study provides anatomical and physiological evidence that binocular re- gions of area 17 are arranged into a pattern of ocular dominance columns that extend approximately back to the primary visual cortex (Shatz et al., 1977). These columns are more or less continu- ous and tend to be elongated in the rostrocaudal direction— roughly perpendicular to the border with area 18 over much of the dorsal surface of the posterior lateral gyrus. These data differ from the cat in the smaller extent of the cortex in which they occur and in the greater degree of imbalance between the sizes of the two eyes' columns. In the cat, Shatz and Stryker ('79) measured the contralateral patches to be 33% larger than the ipsilateral patches while the present results show a 97% difference in size in the ferret. Rockland ('84) has used transneuronal transport of wheat germ agglutinin-conjugated horseradish peroxidase to reveal ocular dominance patches in the ferret, and McConnell and LeVay ('84) have evidence for them in a closely related species, the mink.

Relation to intrinsic cortical connections. Rockland ('84) has found that local projections labeled retrogradely by injections within area 17 of the ferret appear as multiple patches in coronal section. Reconstructions of these patches reveal retrogradely labeled bands on the dorsal surface of the posterior lateral gyrus (Rockland, '85), reminiscent of earlier findings on tree shrew and pri- mate (Rockland et al., '82; Rockland and Lund, '85). The similar course of ocular dominance bands in present results is consistent with the possibility that these patches might be related to the ocular dominance system in the ferret, although the present findings do not, of course, exclude other possibilities. Patches that may be similar in area 15 of the cat appear to be related to orientation rather than to ocular dominance columns (Matsumura et al., '80), while in the tree shrew, no strict relation between such patches and decoretrogradely-labeled orientation columns was evident (Rockland et al., '82). Further work will be required on the organization of orientation columns in the ferret to resolve this point.

Elevation of the fixation point. Consideration of cortical magnification factors suggests that the true fixation point elevation is below that assigned in Figures 2-8. In this study, the fixation point was chosen to make the cortical maps consistent with maps of the LGN previously published (Zahn and Stryker, '85). When con- structing the geniculate maps, the fixation point elevation was placed 3.5° above the elevation of the projection of the optic disc on the basis of the elevation of the smallest receptive fields found in two geniculate mapping experi- ments. There was, however, little change in the sizes of geniculate receptive fields between elevations 3° below to 10° above the optic disc projection, leaving the precise ele- vation of the fixation point relatively uncertain. We noted in our attempts to locate the fixation point more precisely by relating the location of area centrals to the locations of retinal ganglion cells with known receptive fields. In two animals, we attempted to label retinal gang- lion cells corresponding to known regions of the visual field by making horseradish peroxidase injections within the LGN at sites with physiologically defined receptive fields. When the retinas of these animals were prepared in flat mount, we found that both the widespread extent of the retrograde ganglion-cell labelling and the imprecision in locating area centrals on the basis of its higher cell density resulted in a broad range of estimates of location of the fixation point. Since these experiments failed to define the location of the fixation point more precisely than had our geniculate recordings, we do not illustrate them here.

Because of the presence of a visual streak, it is, however, reasonable to assume that magnification factor in ferret area 17 is greatest along the representation of the horizontal meridian. If this assumption is valid, the real fixation point elevation is approximately 12° below that assigned in the figures, or 15° below the elevation of the optic disc projection. This location is well within the range of elevations provided by a consideration of geniculate receptive field sizes and the results of the retinal labelling experimen- tations. This estimate is also consistent with that expected from relating the isofield white whole maps of Vitek et al. ('85) to the extents of the visual field observed in our studies of the cortex and LGN (Zahn and Stryker, '85).

Neighboring visual areas. During these experiments, electroretinogram penetrations were made into visually responsive areas rostral to area 17. Areas were distinguished by differences in the most effective stim- uli for eliciting responses and by reversals in the vertebral map when penetrations crossed from one area to another. Two visual areas were encountered rostral to area 17. Both of these areas are present on the dorsal surface of the posterior lateral and lateral gyrus; these areas are presumably homologous to areas 18 and 19. Visual responses were also recorded on the caudal bank of the medial sulcus rostral to area 17. This area may be analo-
Border with area 18

Direct geniculocebrothal input, as revealed in the present study by transneuronally transplanted label following an eye injection of 2H-proline, goes primarily to area 17 in the ferret, although a very much weaker projection also can be observed in layer IV of at least part of area 18. The border region between areas 17 and 18 can be visualized in the ferret by using the same criteria applied to the cat (O'Leary, 41; Otsuka and Hassler, 192; LeVay and Gilbert, 176): that is, bundles of coarse myelinated fibers appear to enter area 18; layer IV in area 18 is half as thick as layer IV in area 17; larger pyramidal cells are often seen at the border; and area 17 contains fewer large pyramidal cells, especially in layers V and VI. Thus, the border between areas 17 and 18 can be identified in normal histological sections. Rockland (130) has shown that an acetylcholinesterase stain also reveals the border between areas 17 and 18 with particular clarity; the low levels in layer IV of area 17 stand out.

The 17/18 border in the ferret has one feature not prominent in many other species. Transneuronal autoradiography of the visual cortex following an injection into one eye reveals weak labelling above background of layers II, III, V, and VI, as well as IV, extending less than 1 mm into area 17 and about 2 mm into area 18 (Fig. 6). Such a pattern of labelling appears not to be present in the mouse (Drager, 740), a gray squirrel (Webber et al., 77), cat (Shatz et al., 77), Shih tzu and Shihkyo, 78), baby monkey (Hube et al., 76), and squirrel monkey (Kanai et al., 76), whereas monkey (Hube et al., 70), or monkey sequence (Hube and Wiesel, 77), although if it were present but fainter in the ferret, it might well have failed to show up on the published autoradiograms. Figure 2 of Hube et al. (79) is drawn with a slight suggestion of a similar pattern of labelling. However, it is possible to determine from the literature whether this is a general finding in the tree shrew. The significance of this finding is unknown, but a differential distribution of transneuronally labelled fiber to the border region between areas 17 and 18 in the ferret and the tree shrew may reflect the presence of some other input unique to this border region.

The transneuronally labelled geniculocebrothal projection to layer IV of area 18, as compared to the label in area 17, appears from the results to be much less strong in the ferret than it is in the cat (Shatz et al., 77). The gray squirrel (Webber et al., 77) is the only species we have found in the literature in which a pattern of labelling similar in this respect to that in the ferret appears.

Unresolved questions

The present experiments focused on topographic organization and on occipito-dorsal columns. It will also be of interest to determine whether the receptive-field classes that are recognized in the visual cortex in the cat are similar in other binocular mammals are present in ferrets. Experiments on this question and on the organization of orientation columns in the ferret are in progress (Waltzman and Stryker, in preparation).

A particularly interesting question regarding the columnar organization of ferret visual cortex concerns the arrangement of its ON and OFF-center geniculotha inputs. ON and OFF-center responses are segregated into subfields within the LGN (Stryker and Zha, 130). The projection of these sublaminae onto the cortex takes the form of patches reminiscent of ocular dominance patches in layer IV (Zha and Stryker, 38); in the ferret, LeVay et al. (37), in the mink). We hope to understand the development and functional significance of such an organization.

The lack of a (spatially directed microcell population in the ferret raises questions about parallel X and Y pathways, their development, and effects of deprivation (Vick et al., 755). Areas 18 in the cat is thought to receive exclusively Y-type geniculothal input originating from the retinal X-cells (Sherman, 75). This is difficult to reconcile with the present finding that area 18 in the ferret has properties similar to those of the corresponding area in the cat, including cells driven by the ipsilateral eye. An answer to this difficulty for the cortex is that there appear to be cells with Y-like morphology and physiological properties in layer AI of the LCN, leaving open the question of the retinal inputs to these geniculothal cells (LeVay et al., 97).

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Ferret VISUAL cortex.