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

MARGARET I. LAW, KATHLEEN R. ZAHS, AND MICHAEL P. STRYKER
Department of Physiology, University of California, San Francisco, California 94143-0444

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 isoazimuth lines approximately parallel to the long axis of the posterior lateral gyrus and the isoelevation lines approximately perpendicular to the isoazimuths. 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 contralateral visual field. Within the region of area 17 corresponding to the binocular 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 gaps in the labelled contralateral projection. Physiological ocular dominance columns were evident as well in that neurons 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 retinogeniculate projection because of the availability of a catalog of coat color mutations that correlate with altered routing of ganglion cell axons to the dorsal lateral geniculate nucleus (dLGN) (Guillery, '71; Sanderson et al., '74; Oberdorfer et al., '77) and visual cortex (Huang and Guillery, '85). 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 visual system at birth (Linden et al., '81; Guillery et al., '85; McConnell, '85; reviewed in Jackson and Hickey, '85). Knowledge of the normal, adult organization is prerequisite 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 physiological organization to that of area 17 in another carnivore, 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 into 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 anesthetized with 0.8 ml/kg i.m. of a mixture of ketamine (50 mg/ml) and acepromazine (0.5 mg/ml) and were given atropine sulfate (0.2 mg/kg) to prevent mucus accumulation in

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M.I. Law's present address is Dept. of Biology, The Exploratorium, 3601 Lyon St., San Francisco, CA 94123.

Address reprint requests to Dr. M.P. Stryker, Dept. of Physiology, University of California, San Francisco, CA 94143-0444.

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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 37.5°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-posterior −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 contralateral 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×. 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 peak expired CO₂ between 3.8 and 4.4% and peak inspiratory pressure less than 1kPa. 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 a 10% solution of phenylephrine 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 electropolished tungsten electrodes insulated to impedances of 700 KΩ to 3 MΩ with Stoner-Mudge lacquer (Hubel, '57). Visual responses of neurons 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 either directly in front of the animal or at an angle of 60° to the midline, Electrolytic lesions (4–6 μA cathodal for 4–6 seconds) marked the locations of many of the electrode penetrations, thus allowing us to determine the locations of the unmarked penetrations 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-mm intervals, with penetrations spaced at 500-μm or 1-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. Afferents from the lateral geniculate nucleus contributed to the multi-unit activity recorded within layer IV and could be recognized by their brisk responses to non-oriented, rapidly moved 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 matter until the ventral tier 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 laminae in the ventral tier of gray matter. Some of the more caudal penetrations travelled almost parallel to the laminae within the caudal bank of the splenial 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 angles 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 with area 18.** The boundary between areas 17 and 18 was determined physiologically by making rostrocaudal 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 (Hubel and Wiesel, '62, '65; Tusa et al., '79). Electrolytic lesions made at the physiologically defined border in each row of penetrations guided our search for the anatomical features that might be used to define the boundaries of area 17.

**Visual response properties.** The receptive field properties of ocular dominance, preferred orientation, preferred direction of motion, and preferred sign of contrast were noted at most recording sites. The relative strength of each eye’s multiunit response was judged qualitatively to fall into one of seven categories analogous to those defined by Hubel and Wiesel ('62) for single units.

In ten animals, higher-impedance electrodes were used to study single neurons in area 17. Findings from these animals 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 distribution (Reiter et al., '86). This **contralateral bias index (CBI)** was calculated according to the following formula:

\[
CBI = 100 \times \frac{(1-7) + (2/3) \times (2-6) + (1/3) \times (3-5) + n}{(2 \times n)},
\]

where bold numbers (1–7) equal the number of units in each ocular dominance group, and n 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 50 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 time of the recording session, animals were given lethal doses of pentobarbital (50–80 mg/kg, i.v.) and perfused intracardially with 0.1 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 geniculo cortical 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-Clarke 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 angles, azimuth and elevation, on a spherical polar coordinate system (Bishop et al., '62). 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 Sherman, '85). 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 more rostral sections at the lateral and medial edges and straightened and 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. Isoazimuth and isoelevation 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 area 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 (F81), 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 F81, and this tracing was opened along an anteroposterior 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 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. Isoazimuth and isoelevation 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 10° isoelevation line might be drawn between recording sites with receptive field elevations of 9° and 11°.)

**Anatomy**

**Anatomical 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 discriminate 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 the visual cortex. Ten to 12 days before perfusing these ferrets, we injected 2 mCi 3H-proline (specific activity 40 Ci/mM, 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. Frozen 30-μm sections from these animals were taken in the horizontal, parasagittal, or coronal plane, coated with Kodak NTB-2 emulsion, 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 Olavarria and Montero (‘84) 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 corners to facilitate the unfolding of the ventral aspect of the posterior lateral gyrus. The cortices were placed between sili con-coated glass slides separated by 1–2-mm spacers and
Magnification factors. Areal magnification factors were derived from measurements on the two flattened maps prepared from parasagittal sections. Each area of cortex defined by a pair of isoazimuth lines and a pair of isoelevation lines was measured; areas bounded by isoazimuth or isoelevation lines drawn from long interpolations between recording sites were excluded from these calculations. This area value was then divided by the area of visual field represented in that area of cortex to give the areal magnification factor in units of square millimeters of cortex per square degree of visual field.

RESULTS

Location of area 17

Area 17 occupies about 80 mm² on the most caudal portion of the neocortex of the ferret. This position, revealed by physiological mapping studies and a variety of anatomical procedures, is illustrated in Figure 1. Area 17 wraps around the crown of the posterior lateral gyrus at the posterior pole of the hemisphere, traverses the occipitotemporal sulcus (Lockard, '85) and splenial gyrus, and terminates on the caudal bank of the splenial sulcus. The occipitotemporal sulcus is a shallow sulcus that takes the same position with respect to area 17 as the suprasplenial sulcus in the cat (Tusa et al., '78). This sulcus is not always apparent in parasagittal sections through the cortex, and its rostral extent varies greatly among animals. The splenial gyrus forms the tentorial surface of area 17.

The orientation of the visuotopic map in area 17 is also shown in Figure 1. The representation of the vertical meridian forms the dorsal rostral border of area 17 and is seen as a line that roughly follows the contour of the posterior lateral gyrus. The exact rostrocaudal position of this line varies among animals and may extend dorsally onto the lateral gyrus. Inferior elevations are represented dorsomedially along this line and superior elevations map ventrolaterally. Isoazimuth lines are oriented nearly parallel to the long axis of the posterior lateral gyrus, and isoelevation lines run roughly perpendicular to the isoazimuth lines.

Visual responses

The responses to visual stimuli of neurons in area 17 of the ferret were remarkably similar to those described in the cat (Hubel and Wiesel, '62). Most single neurons in the cellular layers of the cortex were orientation-selective and responded optimally to moving stimuli. Receptive fields had sharp and easily defined borders and were typically a few to a few tens of degrees square in area.

Units recorded simultaneously had similar orientation selectivities and largely overlapping receptive fields. The receptive field of a multiple-unit cluster was similar in area to that of a single unit, and the receptive-field position was

Fig. 1. The location of area 17 on the surface of the ferret brain. The brainstem at the level of the medulla and the cerebellum have been removed. A: Lateral view showing the visual field projection onto area 17. Solid lines indicate isoazimuths and dashed lines indicate isoelevations. Labelling of sulci and gyri after Lockard ('85). B: Caudalateral view of area 17. C: Caudomedial view of area 17. D: Dorsal view of area 17. E: Relation of the surface appearance of area 17 to its appearance in section. The left hemisphere was cut in the parasagittal plane at the level shown in by the heavy arrowheads in B, the cortex lateral to the cut was removed, and the cut surface was outlined. Compare this figure to section 4 of Figure 5. The occipitotemporal and splenial sulci have been outlined on the left hemispheres in parts B and C. A, anterior; D, 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 38° 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 F81 and F91 of Figs. 4 and 7). Azimuth and elevation are indicated in degrees.
that found in mapping studies of the LGN (Zahs and Stryker, '85).

**Reconstruction of map from coronal sections.** In initial mapping experiments, rows of electrode penetrations were made in the coronal 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 lateromedial 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 Essens and Maunsell's ('80) technique as described in Materials and Methods. 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 isoazimuth and isolevel lines drawn on the basis of receptive-field positions at these recording sites. On the dorsal surface (shown in the top half of Fig. 3B) more peripheral fields were located progressively more caudally and inferior fields progressively more medially. On the ventral (tentorial) surface (shown in the bottom half of Fig. 3B) lateromedial organization was similar while receptive fields continued to progress peripherally as the surface continued rostrally and ventrally.

**Reconstruction of map from sagittal sections.** The major portion of area 17 was found in the previous experiments to lie on the tentorial surface of the splenial gyrus. Because this surface is inclined only slightly from the coronal plane, coronal sections of area 17 cut it very obliquely. Sagittal sections, on the other hand, were 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 electrode penetrations in one animal (F81) and at 134 sites in 41 penetrations in a second animal (F91). Electrode penetrations were then reconstructed from serial parasagittal sections stained with a Nissl method. Figure 4 shows the centers of the receptive fields of the multiunit clusters recorded in F81. Because the location of area 17 is more easily seen in autoradiographically labelled sections than in Nissl-stained sections, the mapping data from F81 were reconstructed in Figure 3 by using Van Essens and Maunsell's ('80) technique as described in Materials and Methods. 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 isoazimuth and isolevel lines drawn on the basis of receptive-field positions at these recording sites. On the dorsal surface (shown in the top half of Fig. 3B) more peripheral fields were located progressively more caudally and inferior fields progressively more medially. On the ventral (tentorial) surface (shown in the bottom half of Fig. 3B) lateromedial organization was similar while receptive fields continued to progress peripherally as the surface continued rostrally and ventrally.

**Size of area 17**

The size of area 17 was measured in two independent ways as described in Materials and Methods. After labeling the geniculocortical projections by transneuronal autoradiography, 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 860-g female analyzed by this method, area 17 occupied 76.7 mm². In another 890-g female, area 17 occupied 87.2 mm².

In two other ferrets, the region of area 17 studied electrophysiologically was measured on the flattened maps illustrated in Figures 6 and 8. For these measurements, area 17 was bounded dorsorostrally by the representation of the vertical meridian (0° isoazimuth line), medially by the most medial section containing recording sites, and laterally by the most lateral section containing recording sites. The rostroventral boundary was somewhat arbitrarily drawn as a line skirting the most rostroventral recording sites in
Figure 3

A

B
Fig. 4. The receptive field centers of 143 multiunit clusters recorded in area 17 and neighboring visual areas in ferret F81. 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 area(s). Numbers and letters within the symbols refer to recording sites shown in Figures 5 and 6. The receptive field at the site marked 8g (8° azimuth, +40° 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 Van Essen and Maunsell, '80). Sections were split for reconstruction at the positions indicated by the arrow in the inset and the dorsal and ventral halves were aligned separately. Electrolytic lesions and penetration sites (filled circles) confirmed the alignment and allowed the estimation of the locations of many other penetration sites (open circles). B: Isoelevation (dashed) and isoazimuth (solid) lines describe the organization of the map over the flattened cortical surface. More peripheral fields are located progressively more caudally and wrap around the tentorial surface of the gyrus. The inferior portion of the visual world maps medially. D, dorsal; V, ventral; L, lateral; M, medial; WM, white matter.

area 17, except for the region between rows 2 and 6 in Figure 6, where the 120° isoazimuth was used as the boundary. The areas so measured were 54 mm² in F81 and 52 mm² in F91. The mapping experiment in F81 did include slightly more of the far peripheral visual field than did the experiment in F91. These areas represent an underestimate of the size of area 17, because they include only the regions studied electrophysiologically. In the case of F81, it was possible to estimate the area not included in the electrophysiological map from the extent of transneuronal label. In this case, the total area of area 17 was found to be 65 mm².
Figure 5 continued
Fig. 5. Mapping data from the experiment illustrated in Figure 4 have been superimposed on a series of parasagittal sections through ferret cortex. Sections have been transneuronally labelled after an injection of tritiated proline into the contralateral eye and are shown in darkfield. Layer IV of area 17 is seen as a labelled band in these sections. For each section, locations corresponding to the recording sites from the more extensive mapping experiment of Figure 4 are indicated by the letters. Recording sites were in layer IV; letters mark the top of the projection line containing the recording site. The receptive-field position for each site is shown in Figure 4 and is designated by a reference number for the section (number in white circle) postscripted with the letter marking the recording site. Number beneath the reference number is the Horsley-Clarke lateral-medial coordinate of the section. Arrows point to the caudal pole and the edge of the splenial sulcus, where applicable.

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 18; and triangles show sites in more rostral visual area(s). These symbols correspond to the sites in Figure 5 and the receptive fields in Figure 4. Thin solid lines are isoaazimuths; dashed lines are isoelevations. Heavy lines mark the caudal pole and edge of the splenial sulcus.
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 (34 mm²) than to the superior visual field (20 mm²), but this conclusion depends on the assignment of the fixation-point elevation. The assignment of elevations in the cortical maps was made to be consistent with previously published maps of the LGN (Zahs and Stryker, '85). This assignment was on the basis of the distribution of geniculate receptive-field sizes as a function of elevation, a function that changed 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 (23 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). Areal 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 $5^\circ \times 5^\circ$ areas of the visual field were measured for the region of area 17 representing $0-20^\circ$ of azimuth and $-20^\circ$ to $+25^\circ$ of elevation. For the region representing $20-50^\circ$ azimuth and $-20^\circ$ to $+10^\circ$ elevation, areas of cortex were measured representing areas of the visual field not exceeding $100^\circ$.

Figure 9A 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, $10^\circ$ was added to the values of elevation shown on the maps, since the data presented here suggest that the $-10^\circ$ isoelevation line is closer to the true representation of the horizontal meridian than is the $0^\circ$ 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 azimuth, as shown in Figure 9B. Values on the abscissa indicate the center of the visual field areas represented. Magnification remains fairly constant across the central $25^\circ$ of azimuth and then declines steadily. This trend, ob-
Fig. 9. Areal magnification factors in area 17 of the ferret. A: Areal magnification vs. eccentricity. Pooled data from F81 and F91. Smooth curve is the second-order polynomial that best fits these points. A single datum (eccentricity = 3.5, magnification factor = 7.48) has been omitted from this figure to save space, but this point was included when fitting the curve. B: Areal magnification vs. azimuth. Mean and standard error of the mean (SEM) at each azimuth were calculated from the pooled data from F81 and F91 at all elevations. Number above each error bar is the number of areas that contributed to the mean. C: Areal magnification vs. elevation. Mean and SEM at each elevation were calculated from the pooled data from F81 and F91 at all azimuths.

served when data are pooled across elevations as shown, is also present when magnification factor vs. azimuth is plotted for a series of elevations (not shown).

Figure 9C shows magnification factor plotted as a function of elevation. Magnification is greatest at −12.5° and decreases sharply above and below this elevation. When magnification factor vs. elevation is plotted separately for each of a series of azimuths placed at 5° intervals, a series of curves with peaks at −12.5° is obtained (data not shown).

The 17/18 border

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 10 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 histological 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, '62); 1) 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 geniculocortical 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

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Fig. 10. Electrophysiological determination of the 17/18 border. Photographic inset on right shows the surface of an adult ferret brain in the region mapped. Inset at lower left shows dorsal view of left hemisphere (compare to Fig. 1D); box indicates area shown in photographic inset; scale bar = 2 mm. Entry points of 19 of 63 penetrations made in this region are indicated in three rows: A, B, and C. Numbers in each row indicate penetration sites that correspond to numbered receptive fields to the left. Receptive fields in row B are shown hatched. Asterisks on photograph mark the 17/18 border as defined by the reversal of direction of progression of receptive field positions. Note larger size of area 18 receptive fields (e.g., A1 and A2). C, caudal; L, lateral; M, medial; R, rostral; LS, lateral sulcus; SS, suprasylvian sulcus.
Fig. 11. Weil 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, coarse bundles of myelinated fibers are more prominent in area 18. Dorsal is up; caudal 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 3H-proline. Note dense labelling (light) of layer IV within area 17. Region between vertical white lines enlarged in B, B: Enlargement of autoradiograph in A showing the 17/18 border region. Electrolytic lesion (white arrow) marks 17/18 border defined physiologically. Note expansion of labelling into upper and lower layers between asterisks, extending less than 1 mm into area 17 and less than 2 mm into area 18. C: Micrograph shown in A photographically overexposed 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. D: Nissl stain of serial section adjacent to section 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; D, 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 12B. 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.** Intraocular injections of \(^{3}\)H-proline followed by transneuronal autoradiography revealed a pattern of ocular dominance patches within area 17. Transneuronally labelled geniculocortical 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 geniculocortical 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 these sections were made was injected with \(^{3}\)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 \(\mu\)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 820 \(\mu\)m \(\pm\) 25 \(\mu\)m (SEM).

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Fig. 13. Ocular dominance patches in coronal section through area 17 following transneuronal transport of 2 mCi of \(^{3}\)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 section. Hemisphere contralateral to an eye that had been injected with $^{3}$H-proline is shown above ipsilateral hemisphere. Areas of dense autoradiographic label are drawn in black while lightly labelled 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 central 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 intracocular injection of $^{3}$H-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 each of the four parts is shown by individual axes. Axes with solid lines indicate the orientation of the central, flattened portion of the hemispheres, while the axes with broken lines show the orientation of the partially flattened, posterior portions. Labels as in Figure 14. Note the nearly continuous, rostrocaudally elongated ocular dominance patches. Note also that ipsilateral patches are narrower than contralateral patches.
In two transneuronally labelled brains studied in sagittal section, the ipsilateral eye patches occupied 15 and 14% of the total volume of layer IV in area 17, while the contralateral eye patches occupied 90% of the total volume. The ipsilateral projection thus represents approximately 17% of the volume of the contralateral projection.

Even within the binocular segment, transneuronally labelled geniculocortical 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 13 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 monocular 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 "borders" 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 geniculocortical 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 two eyes was assessed 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 (all 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).

In multunit recordings from layer IV, which constituted most of the mapping data, eye preference was much more marked, and responses were purely monocularly driven at 68% of the binocular segment recording sites (visual field coverage illustrated in Fig. 2). The multunit 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 twice for the central 10° of azimuth. A clustering of neurons according to 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 visuotopic map is oriented with the isoazimuth lines approximately parallel to the long axis of the posterior lateral gyrus and the isoelevation lines approximately perpendicular to the isoazimuths. 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.

**How much of area 17 was mapped in this study?** An estimated 83% 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 superior peripheral 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.

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**Fig. 16.** Ocular dominance histogram compiled from recordings of 220 single units in ten ferrets. Histogram plots percentage of units in each of seven ocular dominance groups defined by Hubel and Wiesel ('62): group 1 (seven) for units driven exclusively through contralateral (ipsilateral) eye; group 2 (six) for units strongly dominated by the contralateral (ipsilateral) eye; group 3 (five) for units weakly dominated by the contralateral (ipsilateral) eye; and group four for units driven nearly equally through 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 reference 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 parasagittal 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 Horsley-Clarke coordinates of that site are known, the physiologist should first refer to Figure 5 to get the reference 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-inferior 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 geniculate lamination (Sanderson, '74). The two species have similar tapetal retinas, and a similar classification of retinal ganglion cells into α, β, and γ types has been made on anatomical grounds (Vitek et al., '85). The two species differ in that the ferret 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., '85). 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 a smaller fraction of β cells and apparently lacks an ipsilaterally directed α-cell projection (Vitek et al., '85; Zahs and Stryker, '85). Several features of ferret visual cortex are similar to the cat and differ from those of the monkey, including the laminar patterns of staining for cytochrome oxidase and acetylcholinesterase and the extent of callosal connections (Rockland, '85). The segregation of ON- and OFF-center cells in ferret LGN and cortex also differs from cat, although it is similar to the mink (Sanderson, '74; LeVay and McConnell, '82; Stryker and Zahs, '83; LeVay et al., '87; Zahs and Stryker, '88).

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 cortices. The organization of area 17 in the cat shown in Figure 17A is redrawn from Tusa et al. ('78). In both figures iso-elevation lines appear as dotted lines, while isoazimuth lines are solid. In the cat, the fixation point (the intersection between the vertical and horizontal meridians) occurs at the caudal-medial aspect 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 dorsolateral surface of the posterior lateral gyrus (asterisk). Viewed from 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 ferrets. Such central magnification has been described in the cat as well (Tusa 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., '85; Henderson, '85) vs. the cat's well-developed area centralis (Stone, '78).

In cats, cortical magnification factor appears to be determined by the gradient of retinal ganglion cell density (Tusa 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, '75). This study pro-
provides 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 nasotemporal 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 Zahs and Stryker, '85) and the fraction of cortical layer IV occupied byafferents serving that eye (14 and 15% in the two present cases) suggests that magnification changes little between LGN and cortex.

**Monocular and binocular segments.** The binocular segment 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, '71). Based on the sample of receptive fields illustrated in Figure 2, the ferret's binocular visual field extends to at least 38° 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 that found in mapping studies of the LGN (Zahs and Stryker, '85).

The binocular segment occupies about half of the visual cortex in the ferret, leaving a large and accessible monocular segment. By contrast, in the cat, only a rather inaccessibly 13% of area 17 is devoted to the monocular segment of the visual field (Tusa et al., '78). 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 regions of area 17 are arranged into a pattern of ocular dominance columns similar to those observed in the cat (Shatz et al., '77). These columns are more or less continuous 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 columns differ from those in 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' patches. In the cat, Shatz and Stryker ('78) measured the contralateral patches to be 33% larger than the ipsilateral patches while the present results show a 57% difference in size in the ferret. Rockland ('84) has used transneuronal transport of wheat germ agglutinin conjugated to 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 labelled retrogradely by injections within area 17 of the ferret appear as multiple patches in coronal section. Reconstructions of these patches reveal rostrocaudally elongated bands on the dorsal surface of the posterior lateral gyrus (Rockland, '85), reminiscent of earlier findings on tree shrew and primate (Rockland et al., '82; Rockland and Lund, '83). 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 18 of the cat appear to be related to orientation rather than to ocular dominance columns (Matsubara et al., '85), while in the tree shrew, no strict relation between such patches and deoxyglucose-labelled 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 (Zahs and Stryker, '85). When constructing the geniculate maps, the fixation point elevation was placed 3.5° below 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 experiments. There was, however, little change in the sizes of geniculate receptive fields between elevations 34° below to 16° above the optic disc projection, leaving the precise elevation of the fixation point relatively uncertain.

We failed in our attempts to locate the fixation point more precisely by relating the location of area centralis to the locations of retinal ganglion cells with known receptive fields. In two animals, we attempted to label retinal ganglion 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 retrograde ganglion-cell labelling and the imprecision in locating area centralis 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 experiments. This estimate is also consistent with that expected from relating the retinal whole mount data of Vitek et al. ('85) to the extents of the visual field observed in our studies of the cortex and LGN (Zahs and Stryker, '85).

**Neighboring visual areas**

During these experiments, electrode penetrations were made into visually responsive areas rostral to area 17. Areas were distinguished by differences in the most effective stimuli for eliciting responses and by reversals in the visuotopic map when penetrations crossed from one area to another. Two visual areas were encountered rostral to area 17 on the dorsal surface of the posterior lateral and lateral gyri; these areas are presumed to be areas 18 and 19. Visual responses were also recorded on the caudal bank of the splenial sulcus rostral to area 17. This area may be analo-
gous to area 20b in the cat, described by Tusa et al. ('78) as being located in the posterior portion of the splenial sulcus abutting the representation of the upper visual field in area 17. Alternatively, it may be analogous to the splenial visual area of Kalia and Whitteridge ('73).

**Border with area 18**

Direct geniculocortical input, as revealed in the present study by transneuronally transported label following an eye injection of 3H-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, '62; LeVay and Gilbert, '76): 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 layer V, than area 18. Thus, the border between areas 17 and 18 can be identified in normal histological sections. Rockland ('85) 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 mouse (Drager, '74), a gray squirrel (Weber et al., '77), cat (Shatz et al., '77; Shatz and Stryker, '78), bush baby (Hubel et al., '76), owl monkey (Kaas et al., '76), squirrel monkey (Hubel et al., '76), or rhesus monkey (Hubel and Wiesel, '77), although if it were present but fainter than in the ferret, it might well have failed to show up on the published autoradiographs. Figure 2 of Hubel ('75) shows a tree shrew with a slight suggestion of a similar pattern of labelling. However, it is not 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 geniculocortical fibers 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 geniculocortical projection to layer IV of area 18, as compared to the label in area 17, appears from the present results to be much less strong in the ferret than it is in the cat (Shatz et al., '77). The gray squirrel (Weber 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 ocular dominance columns. It will also be of interest to determine whether the receptive-field classes that are recognized in primary visual cortex in the cat and 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 (Waitzman 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 geniculate inputs. ON- and OFF-center responses are segregated into sublaminae within the LGN (Stryker and Zahs, '83). The projection of these sublaminae onto the cortex takes the form of patches reminiscent of ocular dominance patches in layer IV (Zahs and Stryker, '88, in the ferret; LeVay et al., '87, in the mink). We hope to understand the development and functional significance of such an organization.

The lack of an ipsilaterally directed α-cell projection in the ferret raises questions about parallel X and Y pathways, their development, and effects of deprivation (Vitek et al., '85). Area 18 in the cat is thought to receive exclusively Y-type geniculate input originating from the retinal α-cells (Sherman, '85). 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 A1 of the LGN, leaving open the question of the retinal inputs to these geniculate cells (Esguerra et al., '87).

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