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Topographic relations between ocular dominance and orientation columns in the cat striate cortex

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Summary. In the visual cortex of four adult cats ocular dominance and orientation columns were visualized with (^{3}H)proline and (^{14}C)deoxyglucose autoradiography. The two columnar systems were reconstructed from serial horizontal sections or from flat-mount preparations and graphically superimposed. They share a number of characteristic features: In both systems the columns have a tendency to form regularly spaced parallel bands whose main trajectory is perpendicular to the border between areas 17 and 18. These bands frequently bifurcate or terminate in blind endings. The resulting irregularities are much more pronounced in the ocular dominance than in the orientation system. The periodicity of the columnar patterns was assessed along trajectories perpendicular to the main orientation of the bands and differed in the two columnar systems. The spacing of the ocular dominance stripes was significantly narrower than the spacing of orientation bands. The mean periodicity of a particular columnar system was virtually identical in the two hemispheres of the same animal but it differed substantially in different animals. However, the spacing of orientation columns covaried with that of the ocular dominance columns, the ratios of the mean spacings of the two columnar systems being similar in the four cats. The superposition of the two columnar systems revealed no obvious topographic relation between any of the organizational details such as the location of bifurcations, blind endings and intersections. We suggest the following conclusions: 1. The developmental processes generating the two columnar systems seem to obey the same algorithms but they act independently of each other. 2. The space constants of the two systems are rigorously specified and appear to depend on a common variable. 3. The main orientation of the bands in both columnar systems is related to a) the representation of the vertical meridian, b) the anisotropy of the cortical magnification factor, and c) the tangential spread of intracortical connections.

Key words: Columns – Visual cortex – Orientation – Ocular dominance – Maps – Cat – Development

Introduction

The clustering of neurones with similar response properties is a basic principle of cortical organization (Mountcastle 1957; Hubel and Wiesel 1962). In the primary visual cortex of mammals, such clustering has been demonstrated for functional properties such as eye and orientation preference (Hubel and Wiesel 1962, 1963, 1974; Albus 1975). These receptive field properties are similar in neurones located within columns that extend perpendicular to the cortical lamination. In topological studies, ocular dominance (OD) columns have usually been visualized by selective labeling of the terminal fields of geniculate afferents associated with either the ipsi- or the contralateral eye (Hubel and Wiesel 1972), and iso-orientation (OR) columns have been mapped with the 2-deoxyglucose (2-DG) method (Hubel et al. 1977b). Three-dimensional reconstructions of these columnar systems revealed common principles of organization but also marked species differences. In the rhesus monkey, OD-columns form a regular system of parallel bands whose main orientation is perpendicular to the boundary between striate and prestriate cortex (Hubel and Wiesel 1969; Wiesel et al. 1974; Hubel and Freeman 1977) while OR-columns appear as "swirling stripes with many bifurcations and blind endings" (Hubel et al. 1977b, 1978). No obvious topographical relationship be-

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Offprint requests to: S. Löwel (address see above) tween the two columnar systems could be identified (Hubel et al. 1978) in these anatomical studies. However, a recent investigation with optical imaging of visual cortical activity suggested a correlation between the two columnar systems in the monkey (Blasdel and Salama 1986). Sudden changes in preferred orientation, the so-called "fractures", were found either to be centered over OD-columns or to intersect the boundaries of adjacent columns at right angles.

In the three shrew, the afferents from the two eyes terminate in different layers (Hubel 1975) so that this animal does not possess OD-columns. However, the OR-columns are particularly well developed and form a system of regularly spaced bands whose topographical organization resembles closely that of the OD-columns in rhesus monkey (Skeen et al. 1978; Humphrey et al. 1980). The main orientation of these bands is again perpendicular to the border between areas 17 and 18. In the cat striate cortex, both OR-columns and OD-columns tend to form bands, or at least elongated slabs, and there are indications that their main orientation is perpendicular to the 17/18 border (Stryker et al. 1977; Shatz and Stryker 1978; LeVay et al. 1978; Albus 1979; Singer 1981; Singer et al. 1981; Löwel et al. 1987; Löwel and Singer 1987b). Thus, the cat appears to have two well developed columnar systems which tend to form bands. We expected that the analysis of their topographic relationship would provide indications not only on the processes which control the development of the columnar arrangements but also on some principles of cortical map formation.

Methods

Surgical procedures

We examined the topographic organization of OD- and OR-columns in the striate cortex of four normally reared adult cats weighing 2.4, 3.1, 1.3 and 1.2 kg. We visualized OD- and OR-columns according to the autoradiographic methods described first by Wiesel et al. 1974 and Hubel et al. 1977b. For transneuronal labeling of OD-columns we injected the left (cats C1+C2) or right (cats C3+C4) eye with 2–2.5 mCi (^{3}H)proline (injected volume 100 µl (cats C1+C2), 50 µl (cat C3) and 25 µl (cat C4)). For surgery the cats were anaesthetized with a mixture of ketamine-chloride (15–20 mg/kg) and xylazin hydrochloride (10 mg/kg) i.m. Two to three weeks later we prepared the same cats for the labeling of OR-columns with (^{14}C)2-DG. We induced anaesthesia as before but now maintained anaesthesia with nitrous oxide (70% N_2O/30% O_2), supplemented by small doses of Nembutal (cats C1+C2) i.v. The cats were either fixed in the stereotaxic instrument (C1+C2) as usual or they were fixed with a metal bar cemented to their skull (C3+C4) which allowed the removal of the eye, ear and mouth bars. Subsequently, the animals were paralyzed with hexcarbacholinbromide (Imbretil, i.v.) and artificially respirated. Body temperature and CO_2-content of the expired air were maintained at 38° C and 3.8%, respectively. ECG and EEG were monitored for the control of anaesthesia.

The nictitating membranes were retracted with Neosynephrine and the pupils dilated with atropine-sulphate. After having protected the corneae with black contact lenses, containing artificial pupils of 2 mm in diameter, the major retinal landmarks were plotted with a fundus camera on a translucent tangent screen positioned 0.57 m (cats C3+C4) or 1 m (cats C1+C2) in front of the eye plane. We determined the refraction of the eyes and corrected with additional spectacle lenses if necessary. We then let two to nineteen hours elapse (C1:2, C2:3, C4:5.5, C4:19) during which the above physiological parameters were maintained. Subsequently, we intravenously injected 200 µCi/kg (^{14}C)2-DG (Amersham, specific activity 310 mCi/mmol) for cats C1 and C2, or 370 µCi/kg and 120 µCi/kg for cats C3 and C4, respectively, and began the light stimulation. In cats C1+C2 the light stimulus consisted of a grating of vertically oriented black and white stripes of variable width and spacing. This pattern drifted right- and leftwards in alternation whereby the angular velocity varied between 5 deg and 15 deg/s. Cats C3+C4 were visually stimulated with logarithmic square wave gratings (spatial frequency: 0.08 cycles (c)/degree (deg) –1.5 c/deg). The velocity of the movement changed continuously between 1.6 deg/s and 30 deg/s. Visual stimulation of cats C1, C2, C3 was binocular, while that of cat C4 was monocular through the right eye (injected eye).

Histological procedures

After 50–58 min of light stimulation we sacrificed the animals with an overdose of Nembutal i.v., quickly removed the brains and prepared blocks from the occipital poles of both hemispheres. The blocks of cats C1+C2 were placed directly on the precooled (–80° C) tissue holders of the cryostate. Before the blocks were completely frozen, which took about two minutes, we inserted three needles to obtain guidelines for later reconstruction. We then cut 30 µm thick serial sections parallel to the horizontal plane at a cryostate temperature of –15° C and stretched the sections on slides by brief melting. The liquid phase was kept as short as possible by refreezing the sections on carbon dioxide ice. The sections were then stored at –40° C and alternating sections were selected for (^{14}C) and (^{3}H)autoradiography. For visualization of the (^{14}C)2-DG distribution we exposed the sections for 3½ weeks at –40° C on AGFA-Mamoray film (T3). For the demonstration of the (^{3}H)proline distribution, sections were dried to increase adhesion and then fixed in 4% formaldehyde. After having been washed in distilled water for elimination of radioactive 2-DG they were passed through ascending and descending alcohol. After drying they were covered with photographic emulsion (NTB 3 Kodak) and exposed for 7 weeks. Some of the sections exposed to X-ray film were stained with Thionine after exposure for later assessment of area boundaries.

The brains of cats C3 and C4 were processed in a different way: Their occipital poles were flat-mounted prior to freezing (technique described in detail in Freeman et al. 1987, see also Löwel et al. 1987). To provide landmarks for later superposition three holes were melted in the flat-mounts with warm needles. Subsequently, 26 µm thick serial sections were cut parallel to the cortical surface at a cryostate temperature of –12 to –15° C. The sections were then mounted on glass slides and immediately dried on a hot plate at +80° C. All sections were then exposed for 3 weeks at +4° C on AGFA-Mamoray T3-film for visualization of the (^{14}C)2-DG uptake pattern. For the demonstration of the (^{3}H)proline distribution the sections were then fixed as described for the horizontal sections. In contrast to the latter they were not dipped, but exposed to LKB-Ultrofilm for 8 weeks. Comparison of the (^{14}C)autoradiographs with the corresponding (^{3}H)autoradio-

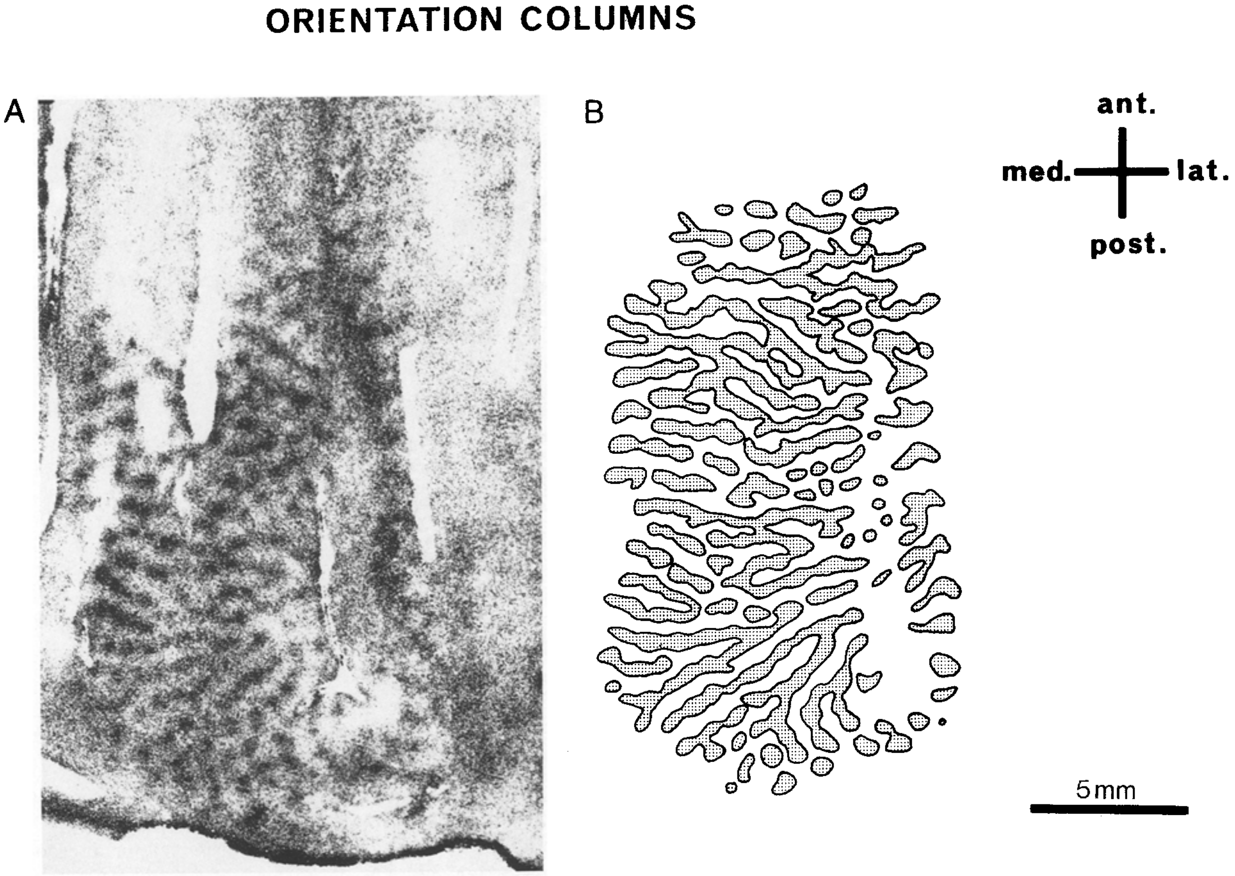

Fig. 1A, B. Reconstruction of the topographical distribution of increased 2-DG uptake in areas 17 and 18 of the right visual cortex of cat C4. The animal was stimulated monocularly with horizontal logarithmically spaced contours. **A** Autoradiograph of flat-mounted sections through the unfolded right visual cortex (two adjacent sections superimposed) showing (^{14}C)2-DG labeled iso-orientation (OR) bands. **B** Hand-drawing of the 2-DG pattern, obtained from superimposed, flat-mounted serial sections through all cortical layers. Abbreviations: ant. = anterior, post. = posterior, lat. = lateral, med. = medial

graphs and with the Nissl-stained sections revealed that the histological procedures had not caused any noticeable shrinkage of the mounted sections. The natural landmarks as well as the needle-tracks remained precisely superimposable.

Reconstruction of ocular dominance and orientation columns in serial horizontal sections

For the reconstruction of the OR-columns we projected the (^{14}C)autoradiographs on transparent paper and made 6.7 fold enlarged drawings. For the reconstruction of OD-columns we made drawings from the tritium labeled slides using a camera lucida. For a first examination we copied the enlarged drawings onto translucent perspex sheets and mounted these between perspex plates, using the needle holes as guidelines for correct superposition. This gave a comprehensive view of the OR- and OD-columns, respectively, but superimposing the two systems in the same reconstruction led to blurring of all details. Therefore, we reconstructed and superimposed the columnar systems graphically. This procedure gave satisfactory results for most parts of striate cortex but the projection of the three-dimensional columnar pattern onto the two-dimensional reconstruction plane risked the introduction of distortions, especially in regions of curvatures and sulci. We therefore excluded the posterior extremity of the lateral gyrus and in one cat, in which the superior suprasplenial sulcus was pronounced, we excluded also the deep parts of this sulcus in the reconstruction of the medial bank.

Reconstruction of ocular dominance and orientation columns in flat-mounts

Each single (^{14}C)autoradiograph of the flat-mounted sections was copied with a magnification of 4.2 on film. For contrast enhancement, the magnified negatives of two serial sections were superimposed using the three needle holes as guidelines and contact copies were made from these montages. Thereafter hand-drawings were made on transparencies from each of the contact copies, all drawings from one visual cortex were superimposed, again using the needle holes as guidelines, and the resulting pattern was redrawn.

For the reconstruction of OD-columns the (^{3}H)autoradiographs were photographically reproduced with the same magnification (×4.2). Although we had flat-mounted the cortex, single sections never covered the full extent of the labeled layer. Two reasons are likely to account for this finding: First, we may have not managed to completely flat-mount the cortex and second, the different thickness of the cortex at the crest of gyri and at the bottom of sulci may cause some minor undulations even in layer

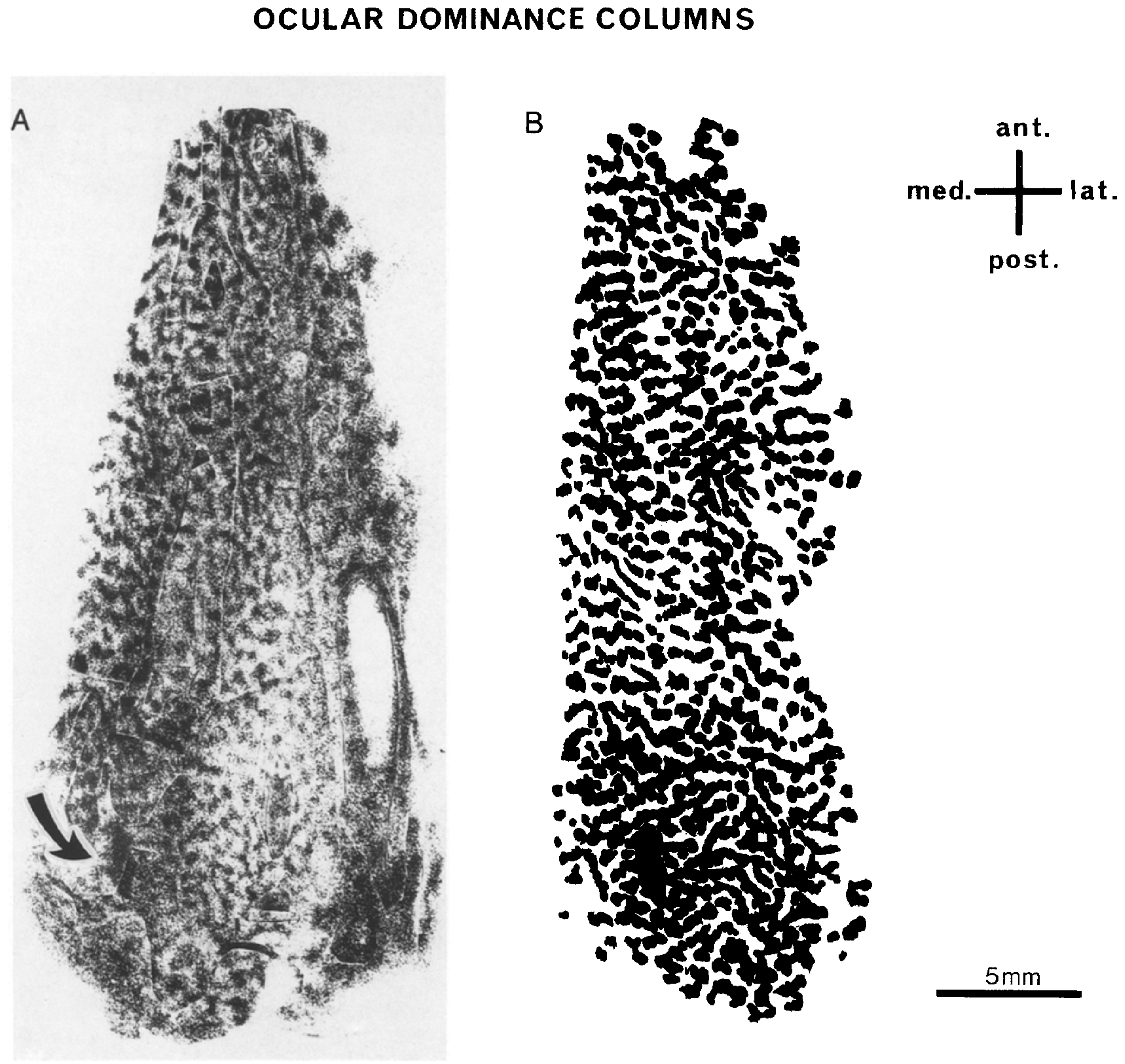

Fig. 2A, B. Reconstruction of the (^{3}H)proline labeled ipsilateral eye columns in layer IV of the right visual cortex of cat C4. **A** Photomontage from autoradiographs of serial flat-mount sections. The homogeneously labeled oval area in the posterior part of area 17 is the representation of the optic disc of the contralateral eye (see arrow). **B** Graphical reconstruction of the ocular dominance (OD) columns. Abbreviations as in Fig. 1

IV of a flat-mount. In order to obtain the complete pattern of OD-columns, a photomontage of all label-containing regions was made, using the needle holes as guidelines for the correct superposition of serial sections. The resulting pattern was redrawn on transparent paper. To check for the precision of the photomontage similar drawings were made from single sections and compared with the composite drawing. The topographic relations of the two columnar systems were then analyzed by graphical superposition.

Quantifications

The mean spacing of columns was measured in two different ways: In cats C1, C2 and C3, the distances between the bands were measured in the enlarged reconstructions along lines separated by 5 mm. These lines were roughly parallel to the 17/18 border. In cats C3 and C4, single autoradiographs were in addition analyzed with a digital image processing system (Imago II, Compulog). The density distribution of the X-ray films were coded in digital units, ranging from 1 to 256. Average columnar spacing was determined by one-dimensional Fourier analyses along vectors perpendicular to the main orientation of the bands.

Results

The 2-DG autoradiograph in Fig. 1 shows OR-bands in the unfolded right visual cortex of cat C4. In

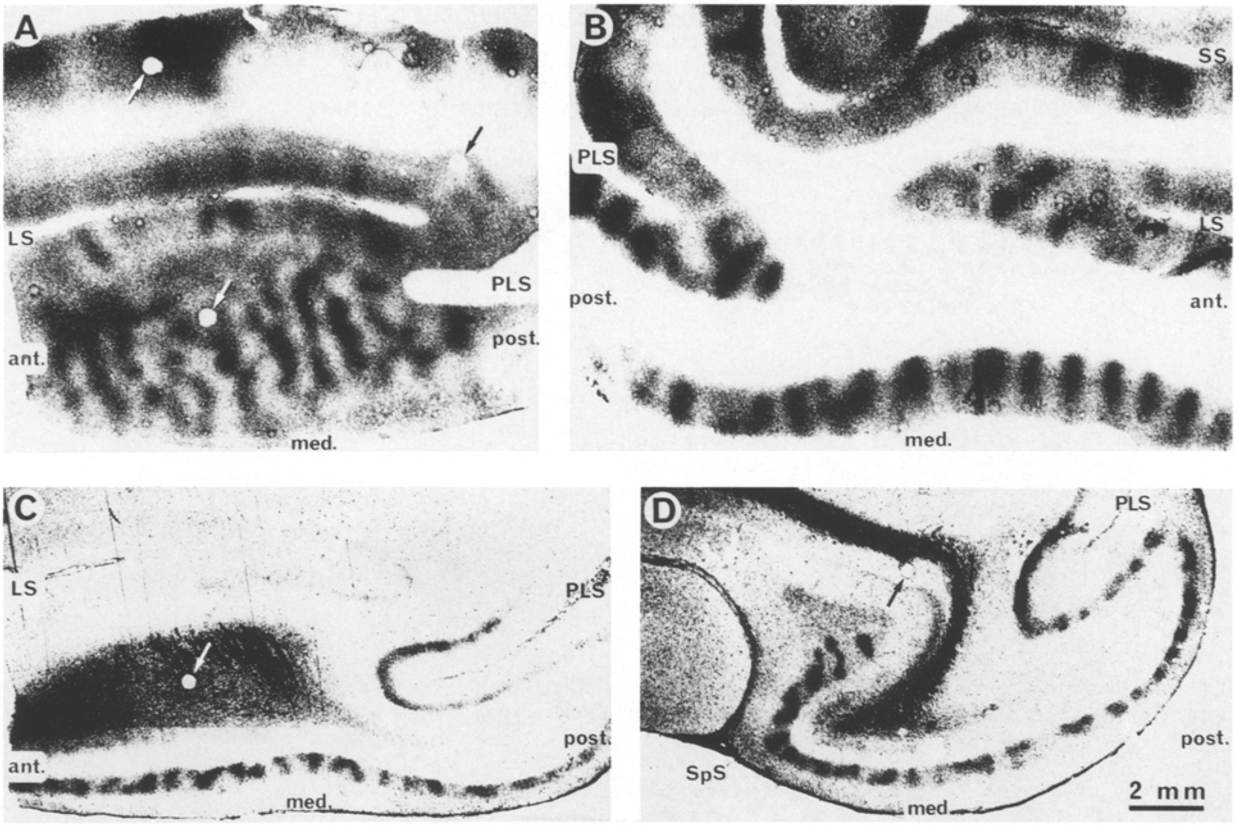

Fig. 3A–D. Autoradiographs of single horizontal sections through the occipital pole of cats C1 and C2. **A, B** (^{14}C)2-DG labeled OR-columns resulting from stimulation with vertically oriented contours. **C, D** (^{3}H)proline labeled OD-columns in the hemispheres contralateral to the injected eye. Sections **A** and **C** are from cat C2 and section **B** and **D** from cat C1. The superficial section **A** is tangential to the cortical lamination over a large region of the dorsal crest of the lateral gyrus; accordingly the OR-bands can be followed over several mms. Deeper sections **B–D** are orthogonal to the cortical lamination and show the columnar arrangements in the medial bank (med.) of the lateral gyrus. As shown in **B**, most OR-columns extend uniformly throughout all cortical layers. The OD-columns in **C** and **D** are typically restricted to layer IV. In the depth of the postero-lateral sulcus (PLS) the labelling of the terminals from the contralateral eye becomes continuous reflecting the monocular segment of the visual field (**C, D**). The needle-holes that served as landmarks for the reconstruction are indicated by arrows. Abbreviations as in Fig. 1 and: LS: lateral sulcus, PLS: postero-lateral-sulcus, SS: suprasylvian sulcus, SpS: splenial sulcus

agreement with previous evidence (Albus 1979; Singer 1981; Löwel et al. 1987) the OR-columns extend through the entire cortical thickness and tend to form parallel bands whose principal orientation is perpendicular to the presumed representation of the vertical meridian. In the posterior part of area 17 the bands run in a more rostro-caudal direction, so that their trajectories remain essentially perpendicular to the medial and posterior boundary of area 17. Clearly visible are the periodic variations of the optical density along OR-bands, that we have described previously as beads (Löwel et al. 1987). Noteworthy in relation to previous results, the organization of the monocularly induced activity-pattern shown in Fig. 1 does not differ significantly from that of binocularly induced patterns (Löwel et al. 1987). The only difference is a somewhat lower contrast between the OR-bands and the background in the former as compared to the latter.

The (^{3}H)proline labeled OD-columns were restricted to a tissue layer that comprised about 12–14 serial flat-mount sections and were located at a depth of 550 to 900 μm from the cortical surface. A photomontage of these OD-columns is shown in Fig. 2 for the same hemisphere of cat C4 that also served for the illustration of the OR-columns in Fig. 1. The homogeneously labeled elongated area corresponds to the representation of the optic disc of the contralateral non-injected eye.

In addition to the flat-mount preparations we analyzed the two columnar systems in graphical reconstructions from serial horizontal sections in two cats. The autoradiographs in Fig. 3 show examples of the columnar systems as they appeared in single horizontal sections. Based on this material we obtained complete reconstructions of OD- and OR-columns from the medial bank of area 17 in both hemispheres of cats C1+C2 and from the dorsal

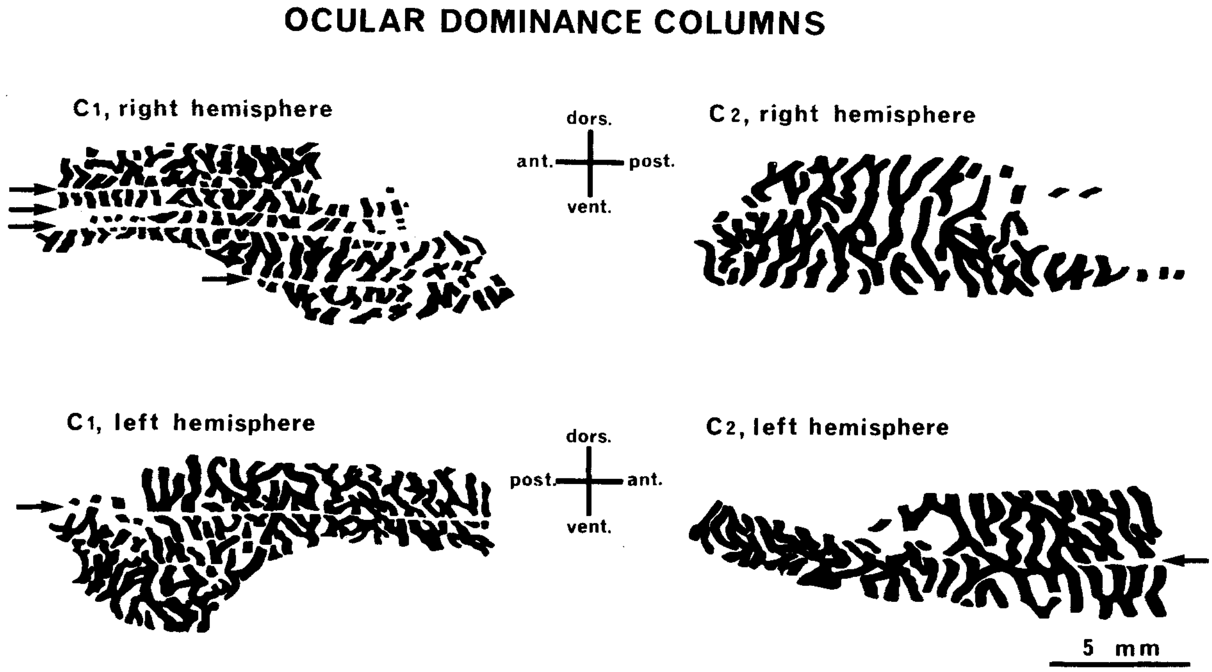

Fig. 4. Graphical reconstruction of OD-columns from the medial bank of striate cortex of cats C1 and C2. The arrows indicate sites where reconstruction was hampered because of faulty sections or because of unclear geometry in the vicinity of the superior splenial sulcus

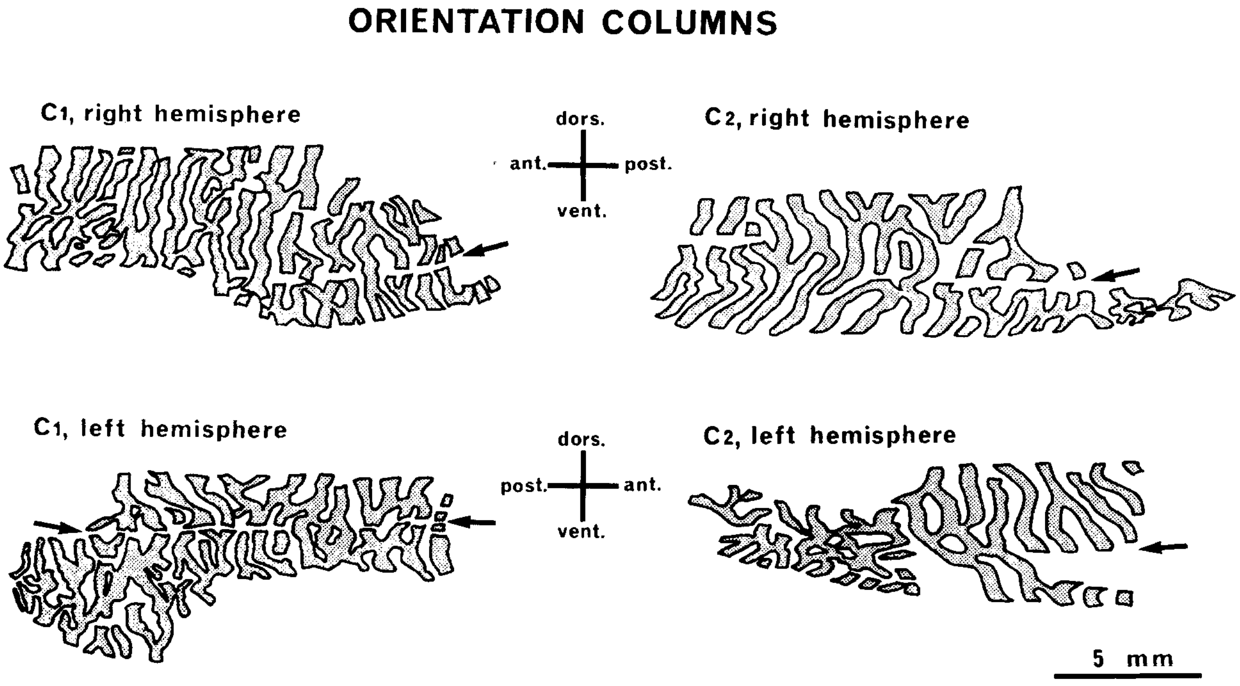

Fig. 5. Graphical reconstruction of OR-columns from the medial bank of striate cortex of cats C1 and C2. The arrows indicate sites where reconstruction was hampered because of faulty sections or because of unclear geometry in the vicinity of the superior splenial sulcus

surface of the lateral gyrus from the left hemisphere of cat C1. The reconstructions of the dorsal crest of the other hemispheres remained incomplete because too few tangential sections were available from layer IV for reliable reconstructions of the OD-columns.

The reconstructions from the medial banks of cats C1+C2 are shown in Figs. 4 and 5. In these, the columnar systems, in particular the OD-columns, appear more regular than in the directly reproduced whole mounts. The reason is that in these graphical

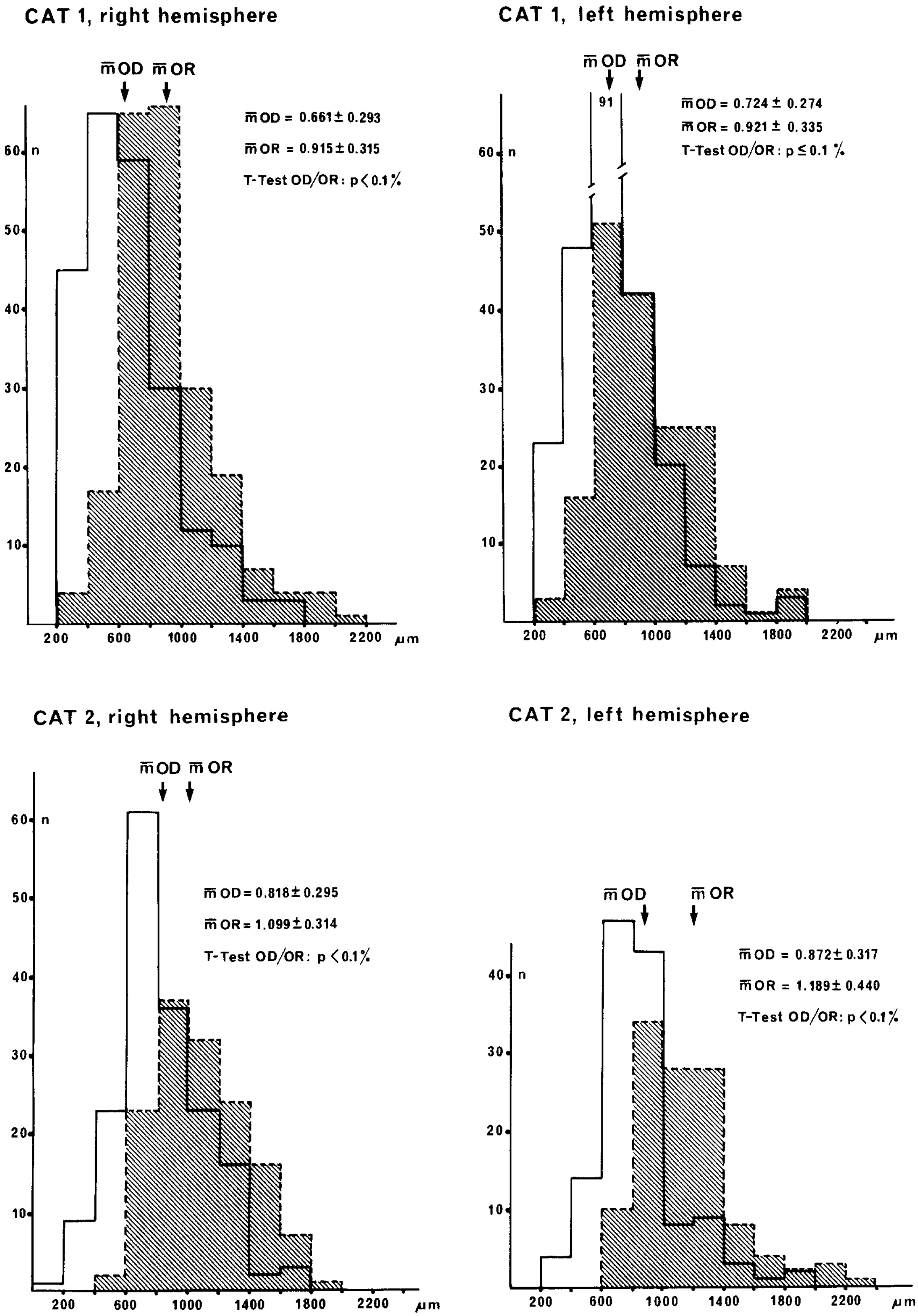

Fig. 6. Histograms of the distances between adjacent OD-bands (uninterrupted outlines) and neighbouring OR-bands (interrupted outlines, hatched planes) in cats C1 and C2. Abscissa: peak to peak distance between adjacent bands; Ordinate: number of observations in the various distance classes

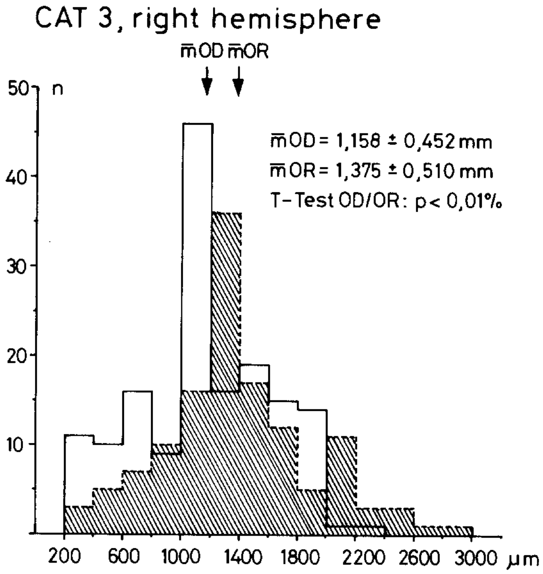

Fig. 7. Histogram of the distance between adjacent OD-bands and neighbouring OR-bands in the right hemisphere of cat C3

representations intensity modulations within the columnar systems were not considered.

As in the whole mounts, the global organizational features of the two columnar systems resemble each other. Both tend to form regularly spaced elongated slabs whose main orientation is perpendicular to the 17/18 border and parallel to the frontal plane. However, as in the whole mounts, the tendency to form bands is much less pronounced for OD- than for OR-columns.

Deviations from the main trajectories of the bands occur mainly at bifurcations and can then attain angles of up to 90 deg. In general, the irregularities of the columnar arrangements caused by bifurcations and blind endings are most pronounced in areas where the cortical sheet is bent as e.g. close to the posterior pole of the lateral gyrus.

Comparison between the corresponding reconstructions from the four hemispheres of cats C1+C2 reveals that the coarse structure of the columnar patterns is rather similar although the tendency of columns to form continuous bands is less marked in cat C1 than in cat C2.

In cats C1+C2, we determined the average spacing between each of the OR- and OD-bands by measuring the interband distance (from center to center) along a grid of parallel lines whose orientation was perpendicular to the main orientation of the bands. In both cats, the average interband distance was surprisingly similar in the two hemispheres: For iso-orientation bands it was 915 µm and 920 µm in cat C1 and 1100 µm and 1190 µm in cat C2 (Fig. 6). In the two tailed T-test the averages from the two cats differed at the $p < 0.1\%$ level while intraindividual interhemispheric differences were not significant. In area 17 of all four hemispheres the spacing of OD-bands was found significantly narrower than that of OR-bands. It was 660 µm and 725 µm in cat C1 and 820 µm and 870 µm in cat C2 (Fig. 6). Again, the interhemispheric differences were not significant but the averages of the two animals differed at the $p < 0.1\%$ level.

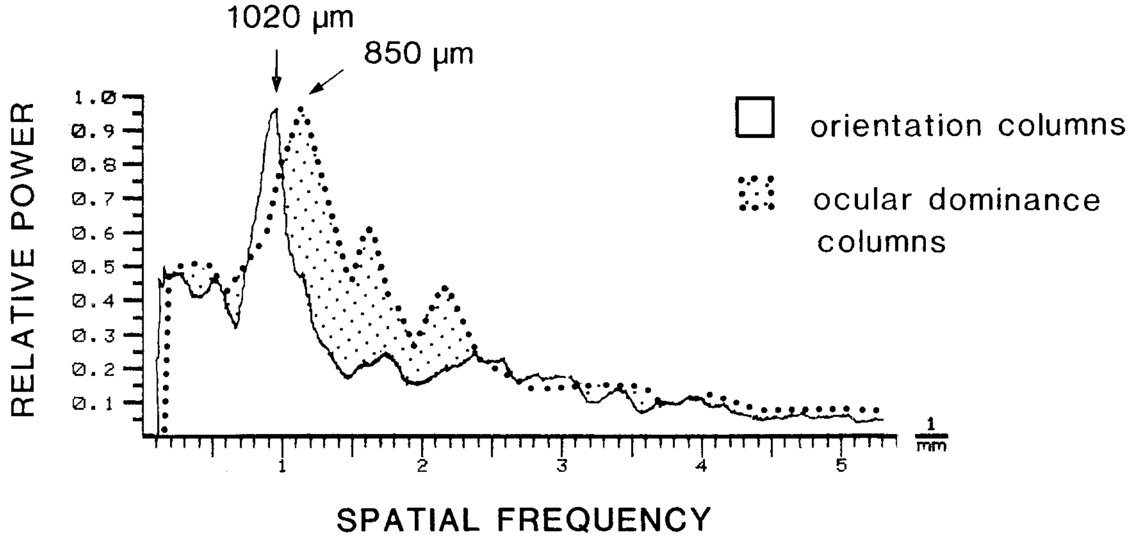

Fig. 8. One-dimensional Fourier analyses of the spatial organization of the OD- and OR-bands in cat C4. The x-axis represents spatial frequency in cycles/mm, the y-axis, the relative power of spectral components. All curves represent averages of measurements along seven parallel vectors perpendicular to the main trajectories of the two columnar systems. The graphs represent the Fourier-spectra in single (^{3}H)proline (dotted line and plane) and (^{14}C)2-DG (solid line) autoradiographs that were obtained from the same section

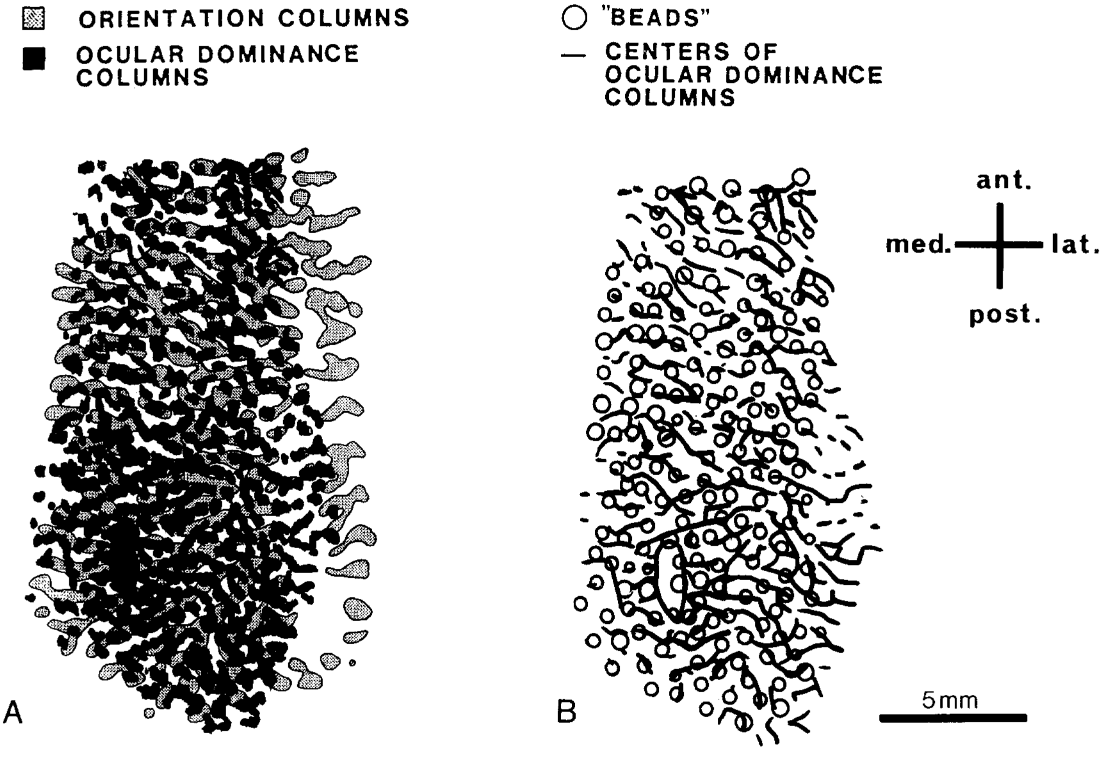

Fig. 9. **A** Graphical superposition of OD-columns (filled profiles) and OR-columns (dotted profiles) in the flat-mount of the right visual cortex of cat C4. The superposition is based on the reconstructions of the columnar systems as shown in Figs. 1B and 2B. **B** Superposition of the graphically determined centers of OD-bands (solid line) and of the beads of OR-bands (open circles) in the same flat-mount

Measurements of the spacing of OR- and OD-bands in the flat-mounts of cats C3 and C4 revealed very similar results. In cat C3, the measurement was performed by the same technique as in cats C1 and C2 (Fig. 7). Although the absolute values of the average spacing (OD = 1.16 mm, s.d. = 0.45, OR = 1.38 μm, s.d. = 0.51) were higher than in the other cats, the OD-bands again had a smaller average distance than the OR-bands ($p < 0.01$).

In cat C4, we made one-dimensional Fourier analyses along vectors perpendicular to the main orientation of both OR- and OD-bands to determine their main spatial frequencies. In order to analyze large regions of the flat-mounts we averaged the measurements along several parallel vectors. In the right visual cortex of cat C4 the average spacing of OR- and OD-bands was 1020 μm and 850 μm, respectively (Fig. 8), confirming again the narrower spacing of OD-columns.

Interindividual comparison reveals that the periodicities of OD- and OR-columns covary. Despite the large interindividual variations in columnar periodicity the ratios between the mean spacing of OD- and OR-columns were remarkably similar in different animals. These ratios were 0.72 and 0.78 in the right and left hemispheres of cat C1, 0.74 and 0.73 in the corresponding hemispheres of cat C2, 0.84 in cat C3 and 0.83 in cat C4.

Topographic relations between orientation and ocular dominance columns

Figures 9A and 10 show the graphical superposition of the OR- and OD-columns that were displayed singly in Figs. 1 and 2 and 4 and 5, respectively. In addition, we related the location of the 'beads', the regions of increased optical density in OR-bands, to the graphically determined centers of the OD-bands (Fig. 9B).

As is to be expected from the different space constants of the two columnar systems there is no fixed phase relation between the two columnar grids. Visual examination of their graphical superposition also reveals that there is no correlation between the locations of bifurcations and blind endings in the two systems nor is there any indication for a fixed spatial relationship between the beads in OR-bands and the OD-columns. This apparent independence of the two columnar systems is also reflected by the spatial

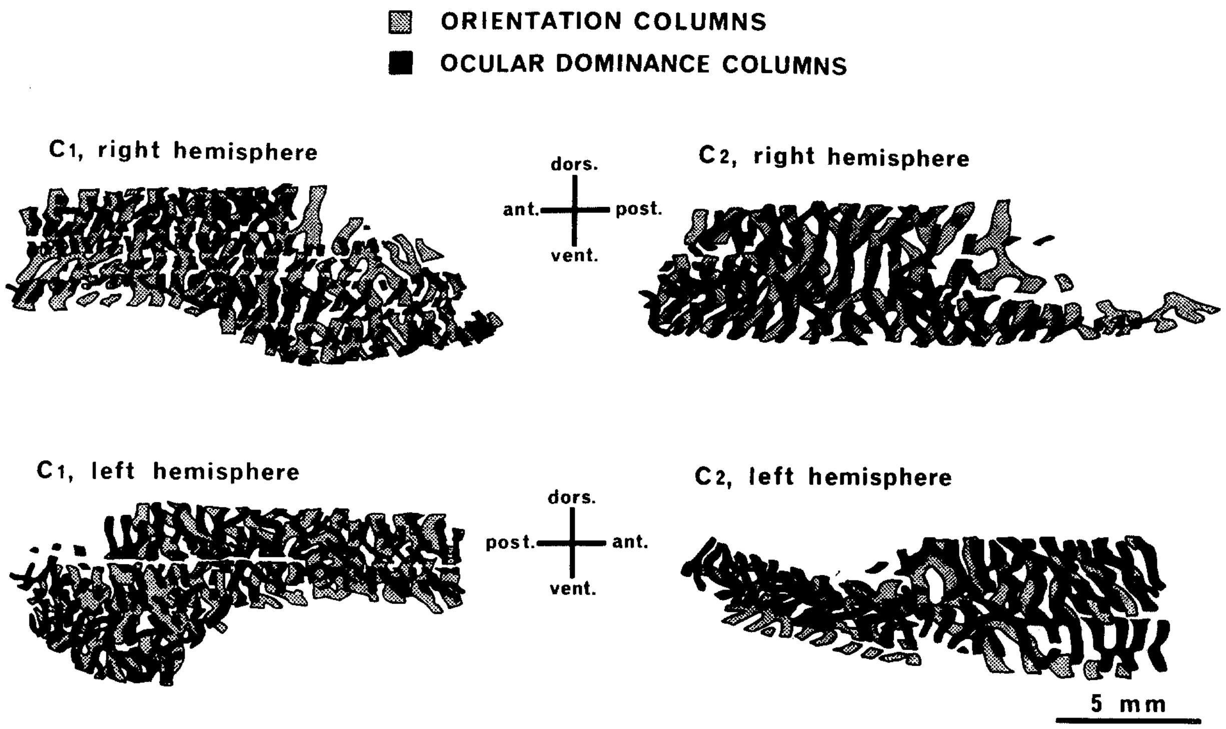

Fig. 10. Graphical superposition of OD-columns (filled profiles) and OR-columns (dotted profiles) in cats C1 and C2. These superpositions are based on the reconstructions of the two columnar systems as shown in Figs. 4 and 5

distribution of the zones of overlap. In regions were both columnar systems show a high degree of regularity these zones retain a banded pattern as it is expected from the interference between grids with similar orientation but different spatial frequencies. In regions, where the columnar patterns are arranged less orderly, the orientation of the respective columnar bands are rarely parallel and on occasions are even orthogonal to each other. Here the zones of overlap have a more patchy appearance. Hence, the zones of overlap of the two columnar systems exhibit a pattern which is expected from the superposition of two patterns which share the same basic features of internal organization but are otherwise independent of each other.

Interestingly, the monocularly induced OR-bands in cat C4 do not coincide with the OD-bands. The detailed analysis of this unexpected finding would go beyond the scope of this article and is the subject of a study in progress (see Löwel and Singer 1987a in this context).

Discussion

Methodological considerations

Before discussing the relations between OD- and OR-columns we would like to emphasize that in this as in most other studies the two columnar systems have been visualized with different techniques. The OR-columns were mapped with the 2-DG technique and most likely reflect the topographic distribution of neuronal elements which share a particular functional property (Schoppmann and Stryker 1981). The OD-columns, by contrast, were labelled with the transneuronal transport method and hence show the topographic distribution of axon terminals. Although there is a good correlation between the location of neurones with a particular eye preference and the termination pattern of the afferents from the two eyes (Hubel et al. 1977a; LeVay et al. 1978) it needs to be kept in mind that we are comparing a functional map with an anatomical map.

Another problem related to the comparison of the two columnar systems arises from the possibility that the processing for (^{3}H)autoradiography caused shrinkage or other distortions of the sections. Since all sections were frozen and mounted prior to processing we are confident, however, that this is not a major source of errors. As mentioned in the Methods section our controls revealed no noticeable difference between the (^{14}C)- and the (^{3}H)autoradiographs. Further support comes from the finding that the spacing of OD- and OR-columns, respectively, was nearly identical in the two hemispheres of the same animal. Since we had processed the blocks from the two hemispheres of the same animal as independently as the blocks of different animals, this demonstrates that variations due to shrinkage or other deformation must have remained small. This result is one of the reasons why we believe that the observed differences between the various cats reflect true differences of organization and not methodological variations.

Comparison of the two different reconstruction techniques suggest the following conclusion. General features of the columnar systems are adequately represented in the reconstructions from serial sections. However, both the details of the fine-grain organization such as intensity modulations as well as global features that emerge only when extensive regions are inspectable simultaneously, are accessible only with the flat-mount technique. Serial reconstructions nevertheless remain indispensable as a control for possible distortions due to unfolding. In the present experiments, this control revealed that flattening did not appear to introduce major distortions of cortical geometry.

Interhemispheric and interindividual comparison of columnar organizations

Comparison of the columnar patterns in the six hemispheres suggests that certain features of columnar organization are strictly specified and show very little interhemispheric and interindividual variability while others appear to be accidental. Features of the first type are: Firstly, the trend of the columns to form bands, secondly, the principal orientation of these bands and thirdly, the average spacing of the bands.

Bands or patches

The band-like pattern of the OR-columns as it emerged from the present reconstructions ressembles closely the patterns described in previous analyses (Albus 1979; Singer 1981; Löwel et al. 1987). The tendency of OD-columns to form bands is slightly more pronounced in the present than in earlier reconstructions (Shatz et al. 1977; Le Vay et al. 1978). The comparison of the two columnar systems in our reconstructions confirms that the tendency to form bands is less marked for the OD- than for the OR-columns and also differs in different animals. In addition, the flat-mount preparations revealed that this tendency varies in different regions of area 17. Reconstructions of only a selected area of the visual cortex do not suffice to reveal the degree of order inherent in the global pattern. This may account for the fact that our present analyses suggest more regularity in the two columnar systems than earlier reconstructions, in particular with respect of the tendency of columns to form bands with defined trajectories (Shatz et al. 1977; Le Vay et al. 1978).

Columnar trajectories and cortical magnification

The second consistent feature of both columnar systems is that the trajectories of the bands tend to be orthogonal to the cortical representation of the vertical meridian. Deviations from this general trend occur in posterior regions of area 17 close to the occipital poles. Here, the bands appear to be arranged less orderly and some of them take a more rostro-caudal course.

With regard to the preferential orientation of the trajectories of the bands, it is interesting that in striate cortex of all species investigated so far, both OR- and OD-columns – if they form bands at all – share this feature of organization. The bands are always orthogonal to the 17/18 border and only in more peripheral representations of the visual field they assume other directions (for citations see Introduction). Even in these peripheral regions the trajectories of the bands tend to show a systematic relation with area boundaries, usually being orthogonal to the latter. Theories about the self-organization of columnar systems actually predict that the structural and functional anisotropies of area boundaries determine the trajectories of the bands in the described way (Swindale 1980; von der Malsburg and Cowan 1982). Occasionally, we observed that OR-bands cross the 17/18 border without changing their course. Thus, while the anisotropies of this boundary may influence the orientation of the bands they do not seem to prevent the aggregation of cells which share the same functional properties. If, as the respective theories assume, this aggregation is mediated by horizontally spreading activity, this would imply that the tangential intracortical connections such as e.g. the collaterals of pyramidal cell axons continue across the 17/18 border. To our knowledge this problem has not been investigated systematically.

The fact that the two eyes and the different orientations are represented in a succession of stripes which are roughly parallel to the frontal plane implies an anisotropy in retino-cortical mapping. Since each point in visual space ought to be covered by a complete set of OD- and OR-columns, the cortical representation of a particular retinal area must extend further in directions orthogonal to the columnar bands than in directions that are parallel to the bands. The consequence should be an anisotropy of the cortical magnification factor in the sense that relatively more cortical tissue is devoted to the representation of vectors parallel to the vertical than parallel to the horizontal meridian. A recent 2-DG mapping experiment in the cat visual cortex (Löwel et al. 1987) has provided direct evidence for such an anisotropy in the cortical representation of the horizontal (HM) and vertical meridian (VM). Following retinal stimulation with a Maltese-cross pattern relatively more cortical tissue was activated in meridians parallel to the VM than to the HM. The elongated shape of the optic disc representation in Fig. 2 of this study is further confirmation for this anisotropy in the cortical magnification factor. An investigation of the retino-cortical correspondence in rhesus monkey has provided indications for a similar anisotropy in this species (Tootell et al. 1982). It thus appears as if the fixed relations between area boundary and columnar trajectories lead to a fixed relation between the anisotropy in cortical magnification and the representation of the vertical meridian. This could account for the fact that both in cat and monkey striate cortex (Le Vay et al. 1985) the retinal map is stretched along the representation of the vertical meridian. Because of the partial decussation of the optic nerves, the cortical representation of the vertical meridian is coincident with the boundary of the map. If, as appears to be the case, columnar trajectories tend to be orthogonal to boundaries and if magnification factors are greater along vectors orthogonal to the main trajectories of functional columns, the long axis of the cortical area should always be parallel to the representation of the vertical meridian.

The anisotropy of retino-cortical mapping is probably causally related also to the anisotropy in the spread of tangential intracortical connections. These reach further in the sagittal than in the frontal plane (Creutzfeldt et al. 1977). Hence, tangential fibers, whose course is parallel to the vertical meridian and perpendicular to the columnar bands are on the average longer than those running parallel to the bands. This is precisely what one expects if these tangential fibers were to mediate interactions which are isotropic with respect to retinal or visual field coordinates.

The spacing of bands

The third parameter of the columnar systems that appears to be strictly specified is the spacing of the bands. For each of the two columnar systems this spacing is surprisingly similar in the two hemispheres of the same animal. The average spacing of corresponding columnar systems differed, however, in the four cats by about 45%. Despite this absolute difference in columnar periodicity, the ratios between the spacing of OR-columns and the spacing of OD-columns were again nearly the same in the four hemispheres. These results suggest three conclusions: Firstly, the space constant of a particular columnar system appears to be characteristic for a particular brain but it can vary between animals at least within a range of 45%. Secondly, since the space constants of the two columnar systems differ significantly in all hemispheres, the substrate interactions which lead to the formation of the two systems must have different space constants. This suggests that different cell populations are involved in the formation of the two systems. Thirdly, since the space constants of the two columnar systems covary, the space constants of the respective substrate interactions probably depend in turn on a common variable. This variable is characteristic for a particular brain and could be related e.g. to the average span of horizontal excitatory and/or inhibitory interaction or to the total size of area 17. It is conceivable that the total number of OD- or OR-bands is similar in each of the animals while the size of area 17 varies. Our data are compatible with this hypothesis. Area 17 of cat C4 is smaller than that of cat C3 and the spacing of OD- and OR-bands in the former is narrower than in the latter. However, the analysis of more animals is needed to draw any firm conclusions.

The argument that the substrates of the two columnar systems might consist of different cell populations with different space constants for horizontal interactions is in agreement with other evidence. OD-columns are likely to result from competitive interactions between LGN fibres (Hubel et al. 1977a; Shatz and Stryker 1978) whereby these interactions are mediated via target cells of geniculo-cortical afferents (Cynader and Mitchell 1977; Rauschecker and Singer 1979). The development of OR-columns by contrast is likely to involve activity-dependent competition between intracortical pathways originating from orientation selective cells in layer IV (Singer et al. 1981). Comparing our results to those obtained in the monkey suggests further that there is perhaps a relation between the space constant of a particular columnar system and the continuity of the bands. In the cat, the OR-bands are spaced more widely than the OD-bands and are more regular than the latter. In the monkey, the conditions are reversed and OR-columns only occasionally form continuous bands. This might signify that larger space constants for horizontal interactions do not only lead to a wider spacing of the bands but also allow for a greater continuity within functionally coherent subsystems.

Another reason for the greater coherency of OR-bands in the cat may be that additional columnar systems are mapped in the monkey striate cortex which are lacking in the cat. Such is suggested by the existence of regularly spaced 'blobs' of increased cytochrome oxidase activity in monkey but not in cat striate cortex (Wong-Riley 1978; Horton and Hubel 1981). These blobs correspond to columns containing cells with concentric receptive fields, are not orientation selective but do process color information (Hubel and Livingstone 1981; Livingstone and Hubel 1984), and appear to result from the intercalation of an additional geniculo-cortical projection to lower layer III. In monkeys, stimulation with diffuse light alone (squirrel monkey) or parallel stripes of different orientations (squirrel and macaque monkey) produces inhomogenous 2-DG distributions, that correspond to the cytochrome oxidase patches (Humphrey and Hendrickson 1983). The presence of these zones of high metabolism complicates the interpretation of 2-DG autoradiographs in monkeys since it renders the distinction between stimulus-induced and background metabolic activity difficult.

In the cat, organizational features that show a high degree of interhemispheric and interindividual variability are the locations of the start and stop points of the bands, the sites of bifurcations and the directions of the curvings which occur in the outer regions of striate cortex. These irregularities of the columnar pattern are particularly frequent in regions where the cortical sheet undergoes deformations due to curvatures. This suggests that the expression of these features is accidental and perhaps related to anisotropies of the cortical sheet such as they result e.g. from variations of the cells' packing density.

Topographic relation between ocular dominance and orientation columns

The graphical superposition of the two columnar systems failed to show correlations beyond the degree that is expected to result from the superposition of independent but similarly organized patterns. Neither start and stop points or bifurcations showed any fixed relation nor were the beads of the OR-columns related to the centers or borders of OD-bands. In areas, where both columnar systems are organized less regularly, the bands of the two systems crossed each other with various angles and on occasions were even perpendicular to each other. Thus, although the two columnar systems share numerous features of their organization they appear to be independent. This has important implications with regard to the developmental processes which generate the columnar systems. The algorithms and the boundary conditions for the formation of columnar arrangements appear to be very similar in the two systems. However, the development of OD- and OR-columns seems to occur independently.

Therefore, we propose as a unifying interpretation of our findings that the neuronal interactions leading to the association of functionally coherent neurones follow the same principles in both columnar systems but involve different cell populations. Whether the recently demonstrated correlation between regions of rapid change in orientation preference (fractures) and OD-bands in the monkey striate cortex (Blasdel and Salama 1986) is a species-specific feature or reflects a general principle of visual cortex organization that escaped our present analysis can only be decided with further experimentation.

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