Coexistence of linear zones and pinwheels within orientation maps in cat visual cortex

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Revealing the layout of cortical maps is important both for understanding the processes involved in their development and for uncovering the mechanisms underlying neural computation. The typical organization of orientation maps in the cat visual cortex is radial; complete orientation cycles are mapped around orientation singularities. In contrast, long linear zones of orientation representation have been detected in the primary visual cortex of the tree shrew. In this study, we searched for the existence of long linear sequences and wide linear zones within orientation preference maps of the cat visual cortex. Optical imaging based on intrinsic signals was used. Long linear sequences and wide linear zones of preferred orientation were occasionally detected along the border between areas 17 and 18, as well as within area 18. Adjacent zones of distinct radial and linear organizations were observed across area 18 of a single hemisphere. However, radial and linear organizations were not necessarily segregated; long (7.5 mm) linear sequences of preferred orientation were found embedded within a typical pinwheel-like organization of orientation. We conclude that, although the radial organization is dominant, perfectly linear organization may develop and perform the processing related to orientation in the cat visual cortex.

Neurons in areas 17 and 18 of the cat visual cortex respond prominently to oriented contours, as was shown by Hubel and Wiesel (1–3). These neurons are also selective for a specific preferred orientation. Furthermore, neurons with similar preferred orientations are clustered together into columns of tissue perpendicular to the cortical surface. Parallel to the cortex, the preferred orientation changes continuously in most locations, forming orientation maps (1–3). For reviews regarding the organization of functional maps within the visual cortex and their corresponding theoretical models, see refs. 4 and 5, respectively. In this paper, we explore the patterns of orientation maps parallel to the surface of the cat visual cortex.

Determining the layout of orientation maps is important for two main reasons. The structure of the maps may shed light on the mechanisms underlying their formation that take place during development. In addition, the emerging organization at the end of cortical development is likely to be optimal for carrying out the specific computations within the relevant visual areas. Thus, a detailed description of adult cortical maps may enhance our understanding of the neural implementation of early visual processing.

The pattern of orientation maps has been the subject of many studies. In electrode penetrations tangential to the cortical surface, incremental steps are accompanied by incremental shifts in preferred orientation (2–3, 6). The rate of change of preferred orientation differs for different penetrations. Based on these observations, Hubel and Wiesel (7) suggested that the values of preferred orientation are constant along one axis whereas they continuously change along the orthogonal axis. They concluded that orientation preference might be represented in a continuous sequence of parallel elongated bands (7). Iso-orientation bands were indeed subsequently demonstrated by using the 2-deoxyglucose technique (8, 9). Narrow bands of heightened activity in response to a single orientation were observed in tangentially cut sections of cortex. These bands

could be interpreted as evidence for a linear arrangement. However, the interpretation of such 2-deoxyglucose patterns may not be straightforward, particularly if the bands appear to have a beaded appearance (9). In addition, several studies, both theoretical (10–16) and experimental (17, 18), suggested an alternative organization in which the domains of preferred orientation are arranged radially around orientation centers. The controversy regarding the type of organization seemed to be resolved by using the method of optical imaging of intrinsic signals. In contrast to the studies that used 2-deoxyglucose, optical imaging made it possible to image the cortical response to several orientations. Thus, this technique allowed orientation preference maps to be computed, rather than merely the pattern of response to a single orientation demonstrated by the 2-deoxyglucose technique. Furthermore, the reliability of the functional maps obtained by using the intrinsic signal has been repeatedly verified by means of single- and multi-unit electrical recordings (e.g., ref. 19). Using optical imaging, Bonhoeffer and Grinvald did notice small cortical regions with perfect linear organization (e.g., Fig. 2B and the top left panel of Fig. 3B in ref. 20). However, they established that in most locations iso-orientation domains are patches organized in "pinwheels" around singularity points referred to as orientation centers (20–22). Using the same technique, Bosking *et al.* (23) demonstrated long, linear, continuous sequences of orientation preference in area 17 of the tree shrew. Their finding raised the possibility of existence of species-specific differences that may account for the emergence of the two different layouts of orientation maps.

Here, we reexamined the organization of orientation preference maps in cat area 18 and along the border between areas 17 and 18. Optical imaging of intrinsic signals (24) was used to image the responses of different neuronal populations. In several instances, we observed wide linear zones as well as long linear sequences of preferred orientation. We thus conclude that linear organization of preferred orientation coexists together with the predominant radial organization in the cat visual cortex.

Materials and Methods

The methods are described here in outline only. Details of the procedures have been previously described (19, 21, 25).

Animals. The skull was opened above the portion of area 18 that occupies the lateral gyrus by drilling two semicircular holes centered at Horsley-Clark ∼ A4. The imaged area extended from 1 to 5 mm away from the midline. Fifteen anesthetized paralyzed cats and kittens (10 weeks old) were used. No age-dependent differences were detected.

Optical Imaging. Two different systems were used for imaging based on intrinsic signals. One system, introduced by Ts'o *et al.* (26), utilizes a slow-scan charge-coupled device camera (Photometrics, Tucson, AZ). The other is a differential video data acquisition system (IMAGER 2001, Optical Imaging, Eden Prairie, MN). The light used to illuminate the cortex was passed through interference filters of different wavelengths, with peak transmission ranging from 605 to 690 nm.

Visual Stimuli. The cats were stimulated binocularly using high-contrast rectangular-wave gratings with a spatial frequency of 0.15–0.18 cycles per degree and a temporal frequency of 2.5–6.0 Hz. The duty cycle used for the grating pattern ranged from 33 to 50%. The set of stimuli included eight differently oriented gratings, each of which moved in two opposite directions, orthogonal to the orientation. The set of stimuli spanned the full orientation spectrum at a resolution of 22.5°.

Analysis of Functional Maps. Data analysis was carried out by using the MATLAB software package (Mathworks, Natick, MA) run on an IBM RISC System/6000 workstation. The first step in the data analysis was to sum the frames acquired for each visual stimulus. Several types of analyses were then used for the presentations throughout the manuscript.

Single-Condition Maps. To obtain an "orientation single-condition map," the cortical image obtained during stimulation with a specific orientation was divided by the image of the sum of responses to all of the different orientation stimuli ("cocktail blank"). High-pass filtering was then applied, using an isotropic Gaussian ($\sigma = 500$ μm of cortical distance). The resulting image represents the pattern of specific activity evoked by the specific condition.

Vectorial Analysis. For comprehensive analysis of the organization of iso-orientation domains, the responses to eight different orientations of the grating stimuli were summed vectorially on a pixel-by-pixel basis (26–28), after low-pass filtering of the single-condition maps [using an isotropic Gaussian ($\sigma = 70$ μm)]. An "angle map" shows the angle of the resulting vectors by means of color-coding. A "polar map" records information about both preferred angle and magnitude of preference.

Results

Linear Zones Within Orientation Maps along the Border Between Areas 17 and 18.

To study the functional organization of cat areas 17 and 18 with respect to orientation, cats were presented with oriented gratings that spanned the full orientation spectrum (180°). Fig. 1*A* illustrates one of the eight orientation single-condition maps. Dark zones represent cortical areas that preferentially responded to a pattern of gratings whose orientation was parallel to the left oblique (135°). The activated zones were elongated, with the major axis of elongation approximately orthogonal to the border between areas 17 and 18. The responding domains appeared at approximately equal intervals. This organization suggested that a linear sequence of preferred orientation might have been represented parallel to the analyzed part of the cortex. To test this hypothesis, we computed the pixel-wise vectorial sum of responses to the different orientations (Fig. 1*B*). The values of preferred orientation changed continuously across more than three complete cycles of orientation, confirming that the organization was approximately linear. These values were mapped to a strip, 4.8 mm long, along the border between areas 17 and 18. The mean correlation coefficient of orientation preferences as a function of distance was 0.996 ± 0.003 (averaged across the rows of Fig. 1*B*). The average rate of change of orientation as computed by linear
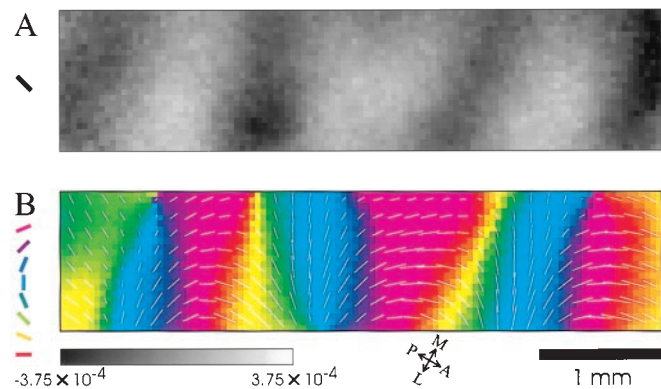
Fig. 1. A linear sequence of orientation preference along the border between areas 17 and 18. The set of visual stimuli included eight differently oriented gratings, moving in both directions orthogonal to the orientation. (*A*) Pattern of cortical response to a single grating pattern, presented in the format of a single-condition orientation map. Dark zones represent cortical areas that preferentially responded to the orientation as marked to the left of the image (135°). The activated zones are elongated and appear at similar intervals. (*B*) "Angle" representation of the orientation map obtained from the same part of cortex. The preferred orientation at any location is color-coded according to the color code presented to the left of the image. Superimposed are short lines that represent the local preferred orientation and the magnitude of preference by their angle and length, respectively. The preferred orientation changes continuously in an approximately linear manner parallel to the long dimension of the image obtained along the 17/18 border. In contrast, preferred orientation is approximately constant in a direction orthogonal to the border. The scale of gray levels represents the fractional changes of the pattern of response presented in *A*. A, anterior; P, posterior; M, medial; L, lateral. (Bar = 1 mm.) Similar conventions are used in subsequent figures.
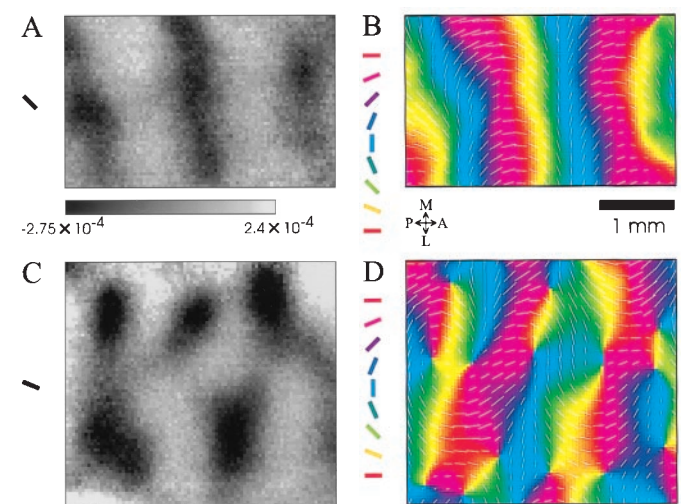

Fig. 2. A linear zone of orientation representation in cat area 18. (*A*) Pattern of response to a single grating pattern with orientation of 135°. The image was obtained from the anterior part of area 18. The pattern of activated (dark) domains is elongated approximately parallel to the ML axis. The activated domains appear at approximately identical intervals along the PA axis. (*B*) Angle representation of the orientation map obtained from the same part of the cortex. Zones with iso-orientation preference consist of slabs elongated parallel to the ML axis. The values of preferred orientation change continuously in an approximately linear manner along the PA axis. *C* and *D* depict the results obtained from an adjacent posterior part of area 18 of the same hemisphere. The presentation format in *C* and *D* is identical to that used in *A* and *B*, respectively. The cortical zones activated by a single oriented grating have a beaded appearance. The preferred orientation is organized in elongated iso-orientation domains, located around 15 orientation centers (*D*).
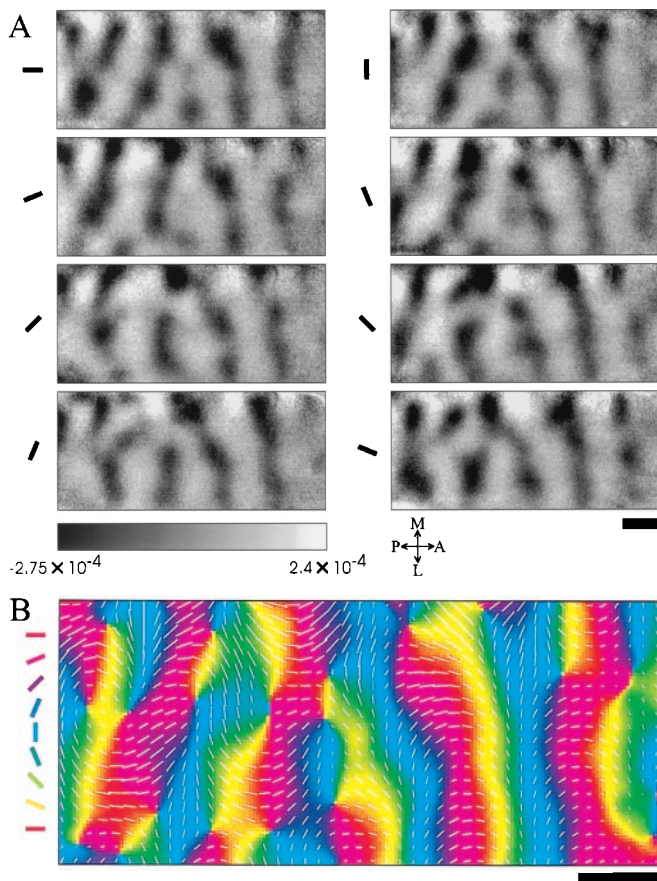
Fig. 3. Relationship between the patterns of response to individual oriented gratings and the organization of orientation preference. The results depicted here were obtained from the cat used for the maps shown in Fig. 2. (*A*) Patterns of response to individual grating patterns. Within the posterior part of the presented image, the cortical zones activated by a single oriented grating have a beaded appearance. In contrast, more anteriorly, the pattern of activated domains is elongated approximately parallel to the ML axis. (*B*) Angle representation of the orientation map from the same part of cortex. Within the posterior part of the presented image, the preferred orientation is organized in elongated iso-orientation domains, located around orientation centers. More anteriorly, zones with iso-orientation preference are organized as slabs elongated parallel to the ML axis. The values of preferred orientation change continuously in an approximately linear manner along the PA axis.

regression was 1.98 ± 0.25 radians/mm (one cycle mapped to 1.58 mm). Orthogonal to the 17/18 border, the orientation preferences remained approximately constant. We thus concluded that instances of linear organization for orientation exist along the border between areas 17 and 18.

Linear Zones Within Orientation Preference Maps in Cat Area 18. To determine whether linear organization for orientation is exclusive to the border between areas 17 and 18, we obtained orientation maps from the anterior part of area 18 of a different cat. Fig. 2*A* shows the pattern of domains activated by gratings oriented parallel to the left oblique. Three of these domains have an elongated shape, with the elongation approximately parallel to the medio-lateral (ML) axis. The responding domains appeared at approximately equal intervals, as in the case presented in Fig. 1. The corresponding organization for orientation (Fig. 2*B*) consisted of a sequence of orientation preferences that changed continuously along the postero-anterior (PA) axis. The organization for orientation was approximately linear over more
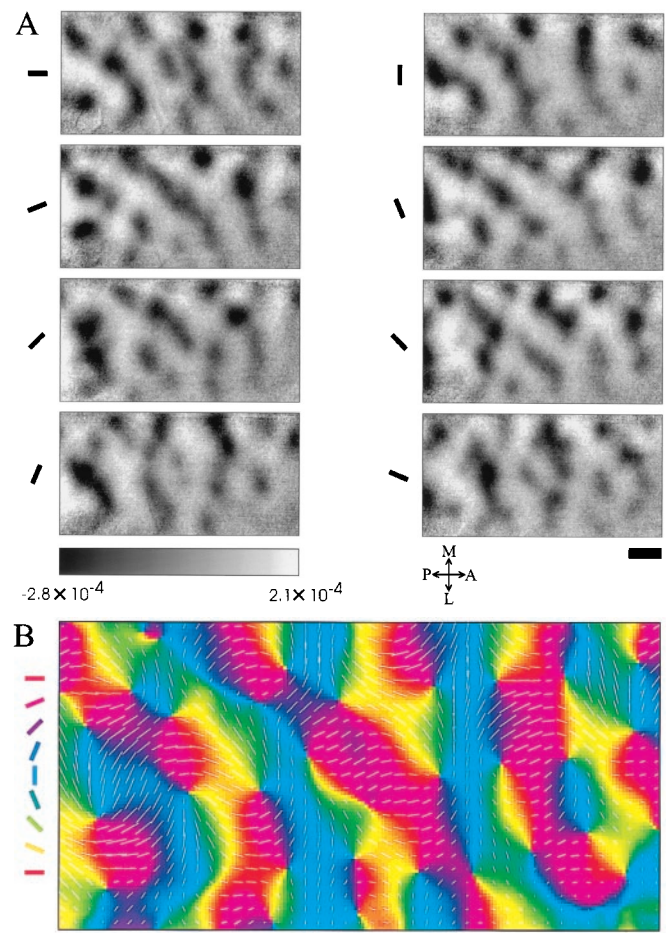

Fig. 4. A beaded pattern of domains activated by individual gratings corresponds to a radial organization of preferred orientation. *A* and *B* show orientation single-condition and orientation angle maps, respectively. The results were obtained from cat area 18. In this cat, the dominant appearance of domains within the single-condition orientation maps is beaded, although an elongated pattern is occasionally seen as well. Iso-orientation domains appear as elongated patches organized radially around orientation centers.

than two full cycles of the orientation domains (mean correlation 0.997 ± 0.02; average rate 2.02 ± 0.16 radians/mm, corresponding to one orientation cycle mapped to 1.55 mm). No orientation centers appeared in a cortical region 3.5 × 2.3 mm wide. We thus concluded that linear zones of orientation preference appear within area 18 as well.

To determine whether the choice of organization (linear or radial) for orientation is exclusive and identical across area 18, we obtained orientation maps from the posterior part of area 18 of the same cat. The pattern of cortical response to one of the gratings is shown in Fig. 2*C*. The pattern was beaded, thus differing markedly from the pattern of elongated domains obtained from the anteriorly adjacent cortex. The corresponding organization for orientation was radial (Fig. 2*D*). The domains of preference for individual orientations were somewhat elongated, with the axis of elongation almost parallel to the ML axis. However, these elongated domains were organized radially, around orientation centers. Fifteen orientation pinwheels were distributed in the presented 3.5 × 3.0-mm wide part of cortex. We concluded that the organization for orientation is not necessarily identical across area 18 but that adjacent zones of radial and linear organizations may coexist.
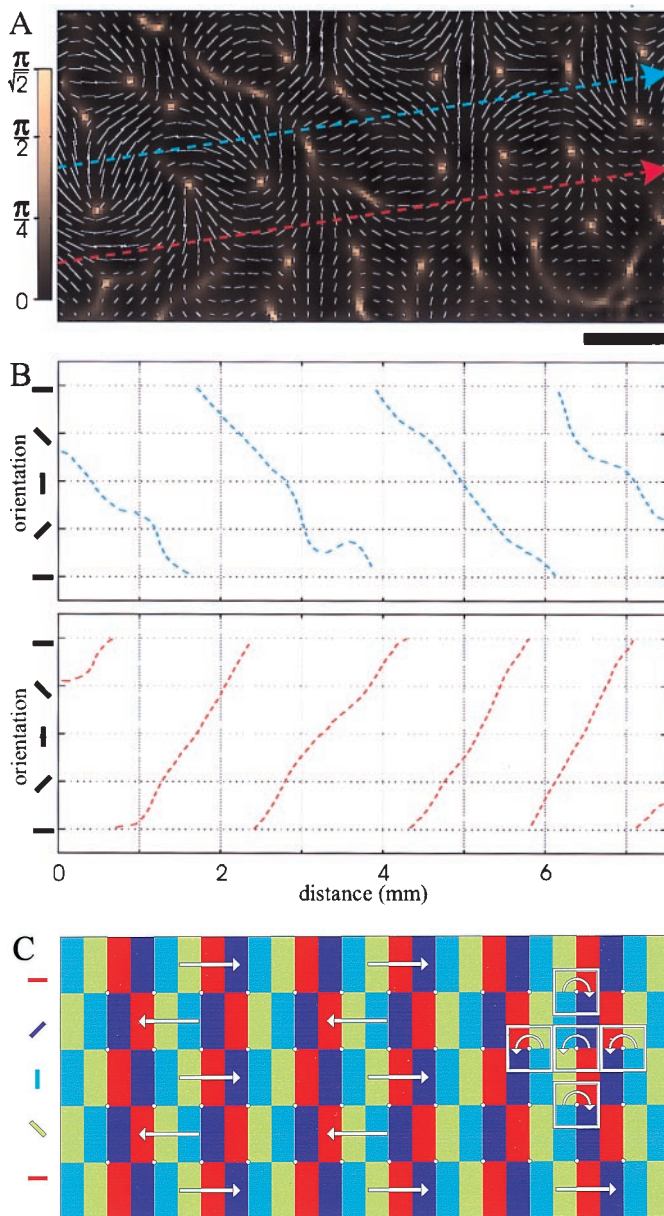
Fig. 5. Long linear sequences of orientation preference within an organization of the radial type. (*A*) The local preferred orientation and the magnitude of preference are shown in a format of short lines polar map (the area shown here is the same as that depicted by the angle map shown in Fig. 4*B*). In the background is the pattern of magnitude of the orientation gradient. The point-like bright regions indicate the pinwheel centers; the organization here is of the radial type. Blue and red lines represent the tracks along which sequences of orientation were sampled for presentation in *B*. The orientation singularities are distributed approximately along straight lines, parallel to the two marked lines. (*B*) Blue and red curves stand for the orientation preferences along the blue and red lines in *A*. Along these lines, the preferred orientation changes in an approximately linear manner, yet in opposite rotation direction within the space of orientation. (*C*) Cartoon of a crystal-like orientation preference map showing overlap between perfectly radial and perfectly linear organizations. The map is shown at a resolution of 45° (four colors). Orientation centers are distributed along rows and columns across the map. The chirality (clockwise or counter clockwise change of orientation) of pinwheels located in the same row is identical. Singularities located along adjacent rows are of opposite chirality. Linear sequences of orientation run parallel to and in between the horizontal lines formed by the orientation centers. The orientation preference along adjacent linear sequences changes in opposite rotation directions within the orientation space. This cartoon demonstrates that infinitely long linear sequences of orientation may be embedded within a crystal-like orientation map organized radially.

Patterns of Response to Individual Gratings Correlated with Linear or Radial Organization. In the previous section, we demonstrated both radial and linear organization for orientation preference. Along with these two types of organization, two instances of patterns of response to a single orientation were presented: a beaded pattern corresponding to the radial organization and a pattern of elongated domains corresponding to the linear organization. To test the dependence of the organization for orientation on the patterns of domains activated by individual gratings, we analyzed the patterns of response to all orientations. Fig. 3 shows the results obtained from the cat that was used for the maps presented in Fig. 2. As described above, the linearly organized part of the map appeared in the anterior (anterolateral) portion of the part of area 18 that occupies the lateral gyrus whereas radial organization was seen in the posterior part of that area (Fig. 3*B*). The response patterns for the individual oriented stimuli are shown in Fig. 3*A*. Elongated responding domains appeared infrequently in the posterior part of the imaged area (e.g., the second image, representing the response to orientation 22.5°). Instead, this part of the imaged area was dominated by a beaded appearance of the activated domains. In contrast, elongated responding domains dominated the anterolateral part of the patterns. Single responding domains with a patchy appearance were also found (e.g., the most anterior patch of the last image, representing the response to orientation 157.5°), but these were rare: a beaded appearance of a pattern as a whole was missing in this region. Based on these qualitative observations, we concluded that a linear or radial organization for orientation is correlated, respectively, with an elongated or beaded pattern of domains activated by individual gratings.

To verify this conclusion, we analyzed the organization for orientation obtained from a different cat. The format used for the presentation of Fig. 4 is identical to that for Fig. 3. Although elongated domains were occasionally seen (e.g., the central part of the second image), the overall patterns of response to single oriented stimuli were beaded. The beaded patterns of response to individual orientations gave rise to a typical radial organization for orientation in area 18. Elongated iso-orientation domains were observed in the map (e.g., the red domain in the center of Fig. 4*B*). However, these elongated domains touched two or more orientation singularities. Thus, the typical orientation map in cat area 18 presented here is consistent with the correlation between type of organization and response pattern of the domains activated by single gratings, as indicated above.

Long Linear Sequences of Orientation Preference Within an Organization of the Radial Type. In the previous sections we demonstrated both types of organization for orientation, radial as well as linear. The shown representative examples were from regions of the cortex that did not overlap. Might there be instances of radial and linear zones that intermix? By definition, orientation singularities cannot exist within large linear zones, where orientation changes linearly along one axis while remaining constant along the orthogonal axis. Is it possible that long, linear sequences of orientation preferences coexist within a predominantly radial organization for orientation?

To determine whether such phenomena exist, we sampled the values of preferred orientation along lines within the orientation map. The polar map in the form of short lines in Fig. 5*A* was obtained from the same piece of cortex shown in Fig. 4*B*. In the background is the map showing the magnitude of the orientation gradient. The bright point-like regions are the orientation singularities. The blue and red parallel lines (7.5 mm long) mark the tracks along which values of preferred orientation were sampled. Orientation singularities were distributed on both sides of each track. The orientation centers close to the two tracks were located along approximately straight lines. The blue and red axes were chosen in an orientation parallel to the approximately

straight lines that emerged as a result of the distribution of singularities. The corresponding sequences of preferred orientation are plotted in Fig. 5B. The curves are almost perfectly linear, with opposite rotations (clockwise and counterclockwise) of incremental steps within the orientation space. The correlation coefficients for orientation vs. distance were −0.9984 and 0.9973, and the rates of change were −1.45 and 1.93 radians per millimeter of cortex for the blue and red tracks, respectively. We concluded that long linear sequences of preferred orientation may coexist within radial organizations for orientation in cat area 18.

To further explore the topology of overlapping linear as well as radial organizations for orientation, we composed a hypothetical orientation map. The cartoon model presented in Fig. 5C is reminiscent of the map of orientation organization presented in Figs. 4B and 5A. Orientation centers, in which zones of the four presented orientations meet, are distributed evenly across the map; thus, the nature of the organization is radial. Linear sequences of orientation run parallel to and in between the horizontal lines along which the singularities are distributed. The composed organization is highly regular and may repeat itself infinitely (other mosaic arrangements of radial organization may be proposed that produce linear zones of a variable degree). Thus, we concluded that infinitely long linear sequences of orientation may coexist topologically within a perfect radial organization for orientation.

Discussion

Linear Zones Within Orientation Maps. In this study, we demonstrated the existence of large regions in cat visual cortex in which preferred orientation is organized in iso-orientation bands, 1.0–2.5 mm long. Orthogonal to the axis of elongation of these bands, we found linear sequences of orientation preference almost 5 mm long (Figs. 1 and 2). Elongated iso-orientation domains are frequently encountered in area 18 (17, 21). However, these elongated domains are usually organized radially, as in the typical map presented in Fig. 4. The wide linear zones shown in Figs. 1 and 2 are infrequent, as they appear in ≈10% of the cases.

A similar description applies to the border between areas 17 and 18 of the cat. Parallel iso-orientation bands that lie orthogonal to this border are frequently encountered (refs. 9 and 29; Fig. 1). In most of the cases, however, these bands are organized around orientation singularities (22, 29). Linear zones along the 17/18 border are more common in area 17 of the tree shrew, where elongated iso-orientation domains intersect the border at right angles (23, 30, 31) (linear zones are also common at the caudal edge of the dorsal portion of area 17 of the tree shrew). Parallel iso-orientation bands that lie close to the border with area 18 have also been detected in area 17 of the squirrel monkey (32). The data obtained from the three mentioned species indicate that linear sequences of orientation preference are common along the border between area 17 and area 18. Thus, this border might induce a boundary condition that biases the organization for orientation in favor of linearity.

A similar boundary condition, induced by the peripheral edge of area 17, may apply to differences in the organization between central and peripheral parts of area 17 in the cat. These differences have been shown in a recent study presented in an abstract form: Rathjen et al. (33) demonstrated that the layout of orientation maps in peripheral representations is more anisotropic than in foveal representations.

Altogether, it seems likely that the mechanisms underlying the development of iso-orientation domains enforce a combination of two patterns of orientation maps: radial and linear. In one extreme, the radial pattern is dominant whereas linear zones are narrow and short. This pattern is common in macaque V1 (25, 34–37) and in the exposed part of cat area 17. In the opposite extreme (e.g., Figs. 1 and 2), wide linear zones prevail. In patterns common in cat area 18 (e.g., Figs. 4 and 5), both components are expressed: pinwheels and singularities are intermixed with elongated iso-orientation domains and long linear sequences of orientation preference.

Continuity and Coverage. Along the linear sequences demonstrated in this study, one cycle of orientation is mapped on average to 1.7 mm parallel to the cortex (Figs. 1, 2, and 5). This extent is significantly longer than the average cortical orientation cycle length of 1.25 ± 0.13 reported by Swindale et al. (17), based on 21 orientation maps from cat area 18. This difference suggests that in linear organizations the length of cortex devoted to an orientation cycle exceeds the cortical length devoted to similar cycles organized radially.

Most models of the visual cortex topography are based on the principle of maximizing a combination of continuity and completeness (38–41). Hubel and Wiesel suggested that their "ice-cube" model is based on the need of the cortex to ensure that all combinations of eye and orientation preference are represented within a volume of tissue no larger than a cortical point image (6, 7). Thus, the principles of continuity and coverage underlie their model as well. The linear zones within orientation maps demonstrated in this study are consistent with the "ice-cube" model of Hubel and Wiesel (7). Do they obey the principles of continuity and coverage? The point image diameter in cat area 17 is ≈2.7 mm (42). In area 18 of the same species, the point image—measured as twice the standard deviation in receptive field center positions—is estimated as 0.6 mm along the ML axis and 1.2 mm along the PA axis (43). The linear zones that we encountered in cat area 18 were all organized such that preferred orientation remained constant along the ML axis and changed linearly along the PA axis. The average cycle length (1.7 mm) fits within the point image diameter in cat area 17, as defined by Albus (42). It also fits within the point image along the PA axis of area 18, assuming a less strict definition of the point image than that given by Cynader et al. (43). Thus, these linear zones obey the principles of continuity and coverage as formulated by Hubel and Wiesel (6).

A typical elongation of iso-orientation domains along the ML axis of cat area 18 is reported here, as well as in previous studies (17, 21). We suggest that the axis of elongation is not a coincidence, as elongation along the PA axis would make the mapping inconsistent with the principle of continuity. The magnification along the PA axis, 2–5 times the magnification along the ML axis, enables a change in both orientation preference and retinotopy along the PA axis while still obeying the continuity principle. According to our hypothesis, the relatively small point image along the ML axis facilitates a change in retinotopy alone, preserving the orientation preference constant along the elongated iso-orientation domains. We thus suggest that the typical elongation of iso-orientation domains in cat area 18 exists to maintain the principles of continuity and coverage.

The same principles may explain the linear zones next to the border between areas 17 and 18 (see previous section). The visual space is represented in a mirror image across the border. We hypothesize that, to have maximal continuity in terms of both retinotopy and orientation, elongated iso-orientation domains develop across the border. Linear sequences of orientation exist along the border, to maintain continuity and coverage.

Mechanistic and Topological Considerations. What is the principle that determines whether orientation domains will be organized radially or in linear zones? A common principle in models of cortical maps is the use of mechanisms that are equivalent to band-pass filtering of white noise (44). An unoriented (isotropic) band-pass filter, which represents a kernel with a center-surround structure, creates a simulated pattern of domains of

similar preference with a beaded appearance. An oriented (anisotropic) band-pass filter produces elongated domains, with the major axis of elongation parallel to the elongation of the kernel. By applying a threshold to the pattern of elongated domains, Rojer and Schwartz (44) produced binary maps. Avoiding the threshold operation would result in continuous, approximately linear mapping, consistent with the linear patterns of orientation demonstrated in our study.

We showed here that radial organization for orientation and long linear sequences of orientation coexist in cat area 18 (Fig. 5). Topologically, infinitely long linear sequences of orientation may be embedded within orientation maps of the radial type, with the average density of singularities [see Fig. 5C here, and the crystal-like ice-cube model (Fig. 3 in ref. 25), based on experimental data from the primary visual cortex of the macaque monkey (36)]. Linear sequences of orientation preference, up to 7.5 mm long and embedded among orientation singularities as shown here, are rare. A more common feature, seen along lines in area 18 that avoid singularities, comprises linear sequences of orientations 1–2 mm long. At the end of these sequences, the course of change in orientation reverses, as demonstrated by Hubel and Wiesel (6) in monkey area 17. Examples of this feature are seen in Fig. 2D (green zone in upper part), Fig. 3B (blue zone in upper right part), and Fig. 4B (magenta zone in center; blue zone in upper central part). At the point of change, it is common to encounter a reversal in orientation change in the orthogonal axis as well. The location of reversal in rotation within the orientation space corresponds to the "saddle-point" defined by Obermayer and Blasdel (37). It remains to be seen whether long linear sequences of orientation represent the rare instances in which stochastic occurrences of saddle-points fail to appear, or whether linear orientation representation mediates a specific functional role.

Concluding Remarks. We have demonstrated the existence of wide linear zones and of long linear sequences of orientation preference within orientation maps of the cat visual cortex. Linear zones of preferred orientation were detected along the border between areas 17 and 18, as well as within area 18. Long linear sequences were found embedded within orientation maps of the radial type. Moreover, we demonstrated that infinitely long, linear sequences of orientation preference may be embedded within a perfect crystal-like orientation map organized radially. In conclusion, although the dominant organization for orientation is radial, instances of long linear sequences and wide linear zones do exist in the cat visual cortex. These findings suggest that the differences between linear and radial arrangements may not be large in terms of optimizing "cost functions" during development and optimizing the processing efficiency related to shape perception. Further research on the mechanism determining the type of organization may reveal the principles underlying the development of cortical maps and their functional significance.

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