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A model for the formation of orientation columns

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[Plate 1]

A mathematical model is proposed to describe the formation of orientation columns in mammalian visual cortex. The model is similar in concept to that proposed for ocular dominance column formation (Swindale 1980), the essential difference being that orientation is a vector rather than a scalar variable. It is assumed that initially orientation selectivity is weak and randomly distributed, and that selectivity develops in such a way that the orientation preferences of neurons less than about 200 μm apart tend to change in a similar direction, whereas the preferences of cells further apart tend to develop in opposite directions. No hypotheses are made about the anatomical or physiological basis of these interactions, and it is not necessary to assume that they are the result of environmental stimulation, as with existing models for the development of orientation selectivity (see, for example, von der Malsburg, 1973).

The model reproduces the experimental data on orientation columns: roughly linear sequences of orientation change are produced, and these alternate unpredictably between clockwise and anticlockwise directions of change. Continuous sequences may span several 180° cycles of rotation. The sequences are generally smooth, but abrupt discontinuities of up to 90° also occur.

The iso-orientation domains for large orientation ranges (60–90°) are periodically spaced branching stripes that resemble those demonstrated in animals by the 2-deoxyglucose technique. The domains for narrower orientation ranges are periodically spaced but are more irregular in shape, though sometimes thin and elongated.

The model makes a number of predictions that can be tested experimentally. Of particular interest are the discontinuities in the orientation sequences: these should be distributed with a spacing roughly equal to, or half, that of the iso-orientation domains. Each should be surrounded by one or two complete sets of iso-orientation domains, and each may be associated with regions where cells are not orientation selective. These regions may be more extensive in younger animals, when the columns are at an intermediate stage of formation, and less numerous where the columns run parallel and unbranched over large areas.

INTRODUCTION

Two physiological properties of neurons in the mammalian visual cortex, ocular dominance and orientation preference, have a systematic and periodic representation on the cortical surface. Ocular dominance, the extent to which a neuron's

response is dominated by signals from the right or the left eye, is represented by alternating stripes or patches for the two eyes, with a repeat periodicity of about $800\ \mu\text{m}$ (Hubel & Wiesel 1962, 1968, 1972). Selectivity for the orientation of a line, or an edge stimulus, also varies systematically with lateral distance across the cortical surface. While neurons in the same vertical fascicle of tissue have closely similar orientation preferences, microelectrode recordings show that as the electrode

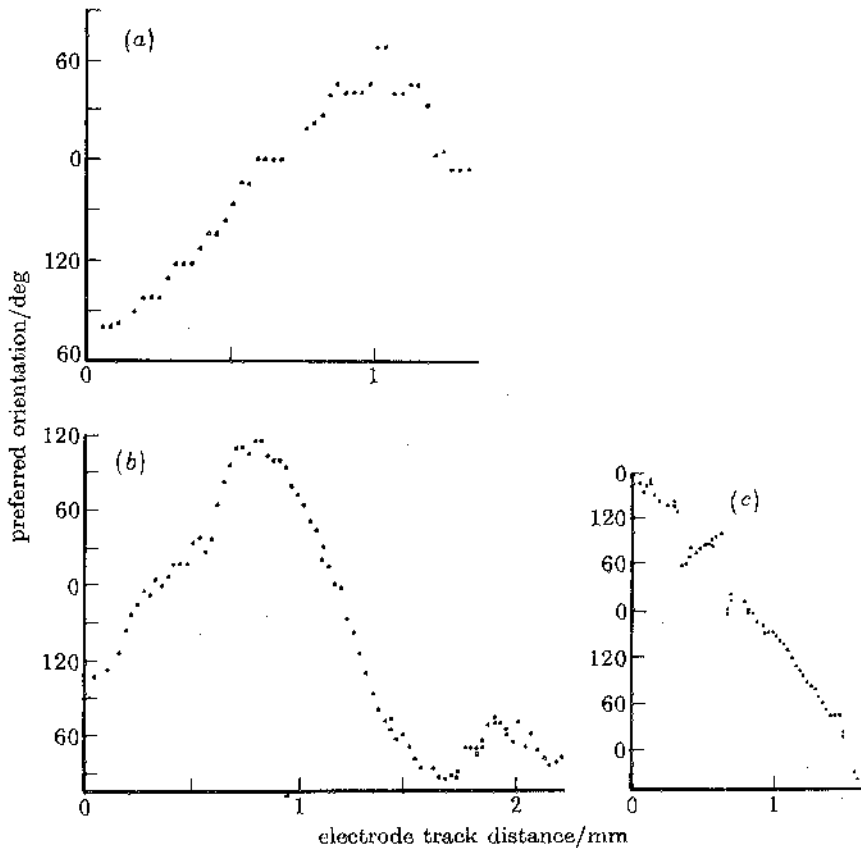


FIGURE 1. Graphs of preferred orientation against electrode track distance in single, nearly tangential penetrations through the striate cortex of monkeys (redrawn from Hubel & Wiesel (1974) and Wiesel & Hubel (1974)): (a) from a visually inexperienced $2\frac{1}{2}$ week old monkey; (b, c) from adults.

is moved laterally, the preferred orientation changes by gradual small amounts, with a 180° cycle of change being completed on average every $500\text{--}1000\ \mu\text{m}$ (Hubel & Wiesel 1968, 1974; Albus 1975; Humphrey & Norton 1980). Graphs of orientation against distance (figure 1) show nearly linear sequences of change, which may reverse unpredictably from a clockwise to an anticlockwise direction. Such one-dimensional maps of orientation do not allow one to predict the two-dimensional layout of regions representing a single narrow range of orientations. This can be demonstrated however, by using an activity label such as

2-deoxyglucose, which shows (figure 2) that regions of tissue containing neurons that are stimulated by, for example, moving vertical bars, are stripe-like, and spaced with a periodicity of about 500–600 μm in monkeys (Hubel *et al.* 1978; Humphrey *et al.* 1980) and about 1000 μm in the cat (Albus 1979).

There are few clues to the anatomical basis of orientation selectivity, and no structural correlate of a columnar organization has yet been identified. There is also little physiological information on how the columnar structure arises during embryonic and postnatal development. It is certain that orientation columns can

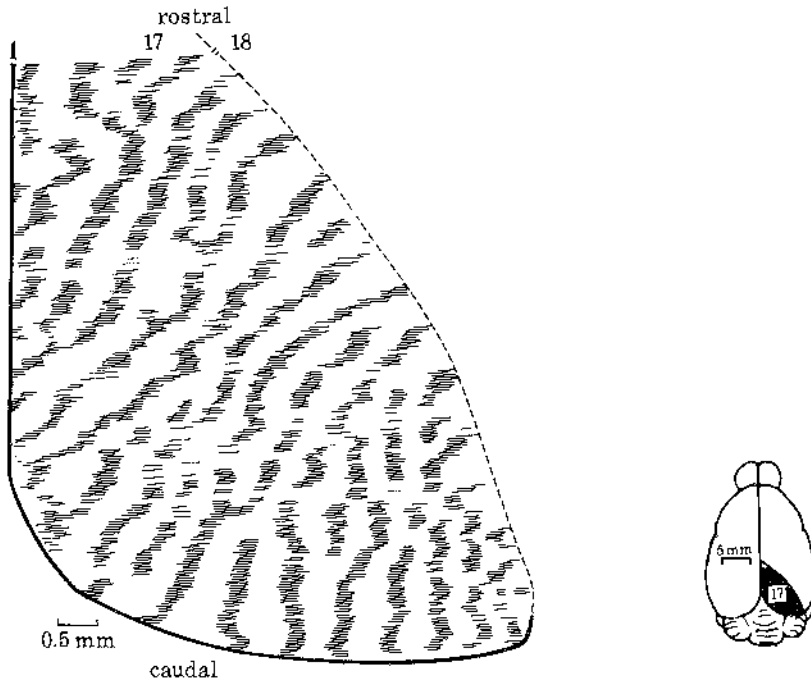


FIGURE 2. Dorsal view of the striate cortex of a tree shrew, showing the distribution of increased 2-deoxyglucose consumption caused by seeing moving vertical stripes. Shaded regions show the location of neurons whose orientation preferences are within about 30° of vertical (reproduced from Humphrey *et al.* (1980)).

form in the absence of visual experience, since neurons in area 17 of new-born monkeys are orientation selective and arranged in ordered sequences similar to those in adults (Wiesel & Hubel 1974). In visually inexperienced kittens, orientation-selective cells can be found (Hubel & Wiesel 1963; Sherk & Stryker 1976) and there is evidence that these form ordered sequences, as in adult cats, but it is also true that in many regions the cells are only weakly selective for orientation, if at all (Barlow & Pettigrew 1971), and form apparently random sequences (see discussion by Blakemore (1978) of the results of Sherk & Stryker). This suggests that in kittens, and perhaps in monkeys before birth, there is an initial stage of development where orientation selectivity is weak and randomly distributed, and that columnar structure emerges in parallel with responsiveness to visual stimuli

and selectivity for orientation. This view is supported by the results of recent 2-deoxyglucose experiments, which show that orientation columns are absent in 3 week old kittens (I. D. Thompson, M. Kossut and C. Blakemore, personal communication).

If this is true, there would be similarities with the way in which ocular dominance columns emerge from a nearly uniform mixture of synapses carrying signals from the right and left eyes (Rakic 1976, 1977; LeVay *et al.* 1978). In this case a competitive interaction between the two species of synapse, involving short and long range effects that differ in sign, is adequate to describe the formation of periodic striped domains of ocular dominance (von der Malsburg 1979; Swindale 1980). It is natural to wonder whether similar rules could be used to give a description of the way in which orientation columns form. One difference between the two types of column is that ocular dominance is a scalar variable (for example it is usually represented on a scale of values from 1 to 7), whereas orientation is a cyclic quantity which must be represented by a vector, or a complex number, if, for example, orientations are added to be averaged.†

Taking this difference into account, I show here that if there is a tendency for the orientation preferences of cells close to one another to develop in a similar direction, and for those of cells further apart to develop in different directions, columns will be formed with many of the properties observed in adult animals.

THE MODEL

Assumptions

An initial assumption is that the fine structure of the columns is not explicitly coded by genetic information. This implies that there is a stage in development, perhaps following cessation of cell division in the cortical plate, at which the future orientation preferences of nerve cells is undetermined. Following this, some form of interaction must take place that leads to the establishment of orientation selectivity either directly, by the formation of appropriate sets of connections, or, perhaps, indirectly, by means of some kind of chemical label that could later guide the formation of appropriate connections. In either case one might expect, by analogy with ocular dominance columns, that the requirements of continuity and periodicity in the representation would be met by an interaction in which neighbouring cells tended to take up similar orientations and cells further apart tended to take up different orientations. As with ocular dominance, the short range effects would ensure local similarity, while the long range effects would ensure periodicity.

Representation of orientation

The vector $\mathbf{z} = (a, b)$ will be used to represent orientation as a function of position \mathbf{r} on the cortical surface. The orientation of \mathbf{z} will be taken to represent

† If orientations are to be added together (e.g. if one is to consider the average of the orientations present in a single fascicle), then a scalar measure of angle is an inappropriate representation. For example one cannot usefully average four orthogonal orientations by adding the angles 0° , 90° , 180° and 270° and dividing by 4, since the result is dependent on an arbitrary choice of origin. If vector representations are used, e.g. $(0, 1)$, $(1, 0)$, $(-1, 0)$, $(0, -1)$ the average is the vector $(0, 0)$, and this is independent of the choice of origin.

the average of all the individual orientation preferences (or labels) of the neurons in a single vertical cylinder of cortical tissue about 30–50 μm in diameter. In the monkey, such cylinders of tissue each contain about 270 cells (Rockel *et al.* 1974), and it is probably reasonable to identify them with the vertical fascicles of cells visible in Nissl stained sections. There is some evidence to suggest that these fascicles may be unitary components of the orientation columns, since the orientation preferences of cells within a fascicle seem to be identical, whereas cells in adjacent fascicles usually have slightly different orientation preferences (Hubel & Wiesel 1974).

The magnitude, or modulus, of \mathbf{z} , $|\mathbf{z}| = (a^2 + b^2)^{1/2}$ is taken to be a measure of the strength of the organizing effect exerted by the neurons of one fascicle upon another. What $|\mathbf{z}|$ might represent in reality is uncertain, but it is reasonable to suppose that it will be large if all the neurons in a fascicle share the same orientation, and small if the orientations are different. Other factors might also contribute to $|\mathbf{z}|$: for example the physiological responsiveness of the individual cells in the fascicle, or the narrowness of their orientation tuning curves.

The angle formed by the vector $\mathbf{z} = (a, b)$ relative to the horizontal axis, is $\theta = \tan^{-1}(b/a)$. As it stands this is cyclic in the range of directions from 0–360°. However, orientation, in the sense in which the term is used in this paper and by visual physiologists in general, is a quantity that is cyclic over the range 0–180°. Thus orientations differing by 180° are indistinguishable, and this should be a property of the orientation represented by \mathbf{z} . There are two ways in which this requirement could be met by the model. One is to use the value $\theta' = \frac{1}{2}\theta$ as the external representation of orientation (i.e. for θ' to correspond to the values that an experimenter would assign to the columns) while the value θ remains internal to the model; θ' would thus be cyclic in the range 0–180°. The other way is to use the value of θ as it stands as the external representation of orientation, but, in analysing the output of the model, to treat values of \mathbf{z} differing in orientation by 180° as indistinguishable. This implies that though the mechanism of column formation does make such a distinction, such differences are simply not apparent (at present) to experimenters. (The possibility that a distinction might be made on the basis of differences in direction preference seems unlikely, for reasons given below.)

Computations

For the computations to be described below, the cortex was represented by a 64×64 array of vectors. Initially, small, randomly distributed orientations were assigned to each point. These might correspond, for example, with the slight random biases resulting from an initial, sparse set of connections made by geniculate afferents with cells in layer IV in the cat, or, in the monkey, by cells in layer IVc (which are non-oriented in adult animals) with cells outside that layer. Following this, the orientation biases increase and change direction, at rates given by $\partial\mathbf{z}/\partial t$. These rates are assumed to be not locally independent. Thus the direction and rate of change at one point will be determined by the orientations and magnitudes of surrounding points. In reality, such interactions would occur if nearby cells were competing for inputs from a set of presynaptic cells, and if the

selection of a subset of the available inputs by one, or a group of cells, were to bias the possible orientations that could be formed by selection from the remaining subsets available to nearby cells, or to alter the rates of growth of axons in nearby locations.

In the model, the variation of these interactions with lateral distance r between cells will be described by the function $w(r)$. It is difficult to suggest from physiological or anatomical considerations how w might vary with distance. The requirement that orientations should tend to become locally similar, however, suggests that w should be positive for short distances, meaning that nearby orientations will tend to change in the same direction, while the fact that less locally (e.g. for separations of 250–500 μm) orientations are dissimilar suggests that for these distances w should be negative.

For a representation where $\theta' = \frac{1}{2} \tan^{-1}(b/a)$, a negative value of w will imply a tendency for induced changes in orientation to differ by 90° , whereas if $\theta' = \tan^{-1}(b/a)$ the tendency will be for orientations to change in directions that differ by 180° . (It is possible for w itself to be a vector, implying a tendency for orientations to change towards a particular relative angle which changes smoothly with distance. This possibility will not be considered here, but the consequences are discussed in appendix 1.)

The overall rates of change of \mathbf{z} will be determined by making, for each point, a weighted sum of the surrounding orientations. Thus

$$\partial \mathbf{z} / \partial t = (\mathbf{z} * w) f(|z|), \quad (1)$$

where $f(|z|)$ is used to set an upper limit on the value of $|z|$. This would correspond probably to the stage at which all the neurons in a fascicle have the same preferred orientation and are optimally tuned and maximally responsive (although these latter properties might develop independently of the process of orientation column formation). This limit is set by having $f(|z|) \rightarrow 0$, as $|z| \rightarrow Z$, the maximum value of $|z|$. Suitable forms for $f(|z|)$ are thus

$$\left. \begin{aligned} f &= 1 & \text{if } |z| < Z, \\ f &= 0 & \text{if } |z| = Z, \end{aligned} \right\} \quad (2)$$

or

$$f = (Z - |z|) \quad (3)$$

which was more frequently used.

For most of the computations $w(r)$ was a difference of two gaussian functions,

$$w(r) = A e^{-\lambda_1 r^2} - B e^{-\lambda_2 r^2}, \quad (4)$$

with A , B , λ_1 and λ_2 positive constants, but other functions, such as a similar combination of two exponentials, were also used with satisfactory results. As with ocular dominance columns, it can be shown that the requirement for periodicity will be met provided that the Fourier transform of w has a positive maximum at a non-zero frequency (see appendix 1). Most functions that are positive near the origin and negative in other regions should satisfy this requirement. Thus the precise functional form of $w(r)$ is not a critical feature of the model. The values of λ_1 and λ_2 were adjusted so that the periodicity of the patterns produced would

be about equal to that in the monkey (570 μm), if points in the array represent regions of cortex about 30–40 μm apart.

Specification of conditions at the boundaries of the modelled region was avoided by treating opposite edges of the array as though they were adjacent to one another (i.e. as though the array was the unit cell in a repetitive two-dimensional pattern).

For most of the computations, the orientations represented by \mathbf{z} were initially distributed uniformly through 180° . In view of evidence suggesting that there is bias of orientation preferences in visually inexperienced kittens (Frégnac & Imbert 1978) and monkeys (C. Blakemore, personal communication) towards horizontal and vertical, some computations were performed with a similar bias present in the initial values of \mathbf{z} . The moduli of \mathbf{z} were normally distributed about zero with standard deviations that varied from 0.1 to 20% of Z . Variations within this range had little effect on the results. Iterations of the program were continued until $|\mathbf{z}| = Z$ for 99% or more of the points in the array.

RESULTS

The output of the model can be interpreted in two different ways, depending on whether the angle represented by \mathbf{z} is cyclic in the range 0 – 180° or 0 – 360° . In the latter interpretation, two iso-orientation domains are present for a single cycle of \mathbf{z} , and the periodicity is accordingly doubled. So that the spacing of the domains would be comparable in both cases, the linear dimensions of $w(r)$ were doubled. In other respects the computations performed were identical.

180° representation

In this form of the model, the orientation represented by \mathbf{z} is $\theta' = \frac{1}{2} \arctan(b/a)$, and the effect of the long range interactions is to make cells separated by distances of 250–500 μm take up orientations which, on average, are orthogonal.

The orientation sequences produced (figure 3) resemble those found in monkeys, consisting mainly of nearly linear clockwise or anticlockwise sequences of change, with unbroken sequences often spanning several 180° cycles. Reversals in the direction of rotation occur with no apparent regularity, and at no particular orientations. This is illustrated by figure 4, which shows the spatial distribution of clockwise change, relative to an upward direction of movement across the page. While regions of the array up to 1000 μm apart tend to share the same direction of rotation, continuous sequences of either type of rotation vary considerably in length. As in the monkey (figure 1c), smooth sequences are sometimes interrupted by sudden large shifts in orientation of up to 90° (figure 3c, e, g, h). Sometimes an entire short segment appears displaced from the main sequence by a constant 90° rotation (figure 3g).

Plots of the distribution of a complete half cycle of orientation (figure 5a) show periodically spaced, stripe-like regions that branch, similar in form to those observed in 2-deoxyglucose autoradiographs. Plots of the domains occupied by narrow ranges of orientation, with different colours representing different orientation ranges (figure 6), show that these occupy small and variously shaped regions, often with long narrow extensions. Domains for neighbouring ranges tend, as one

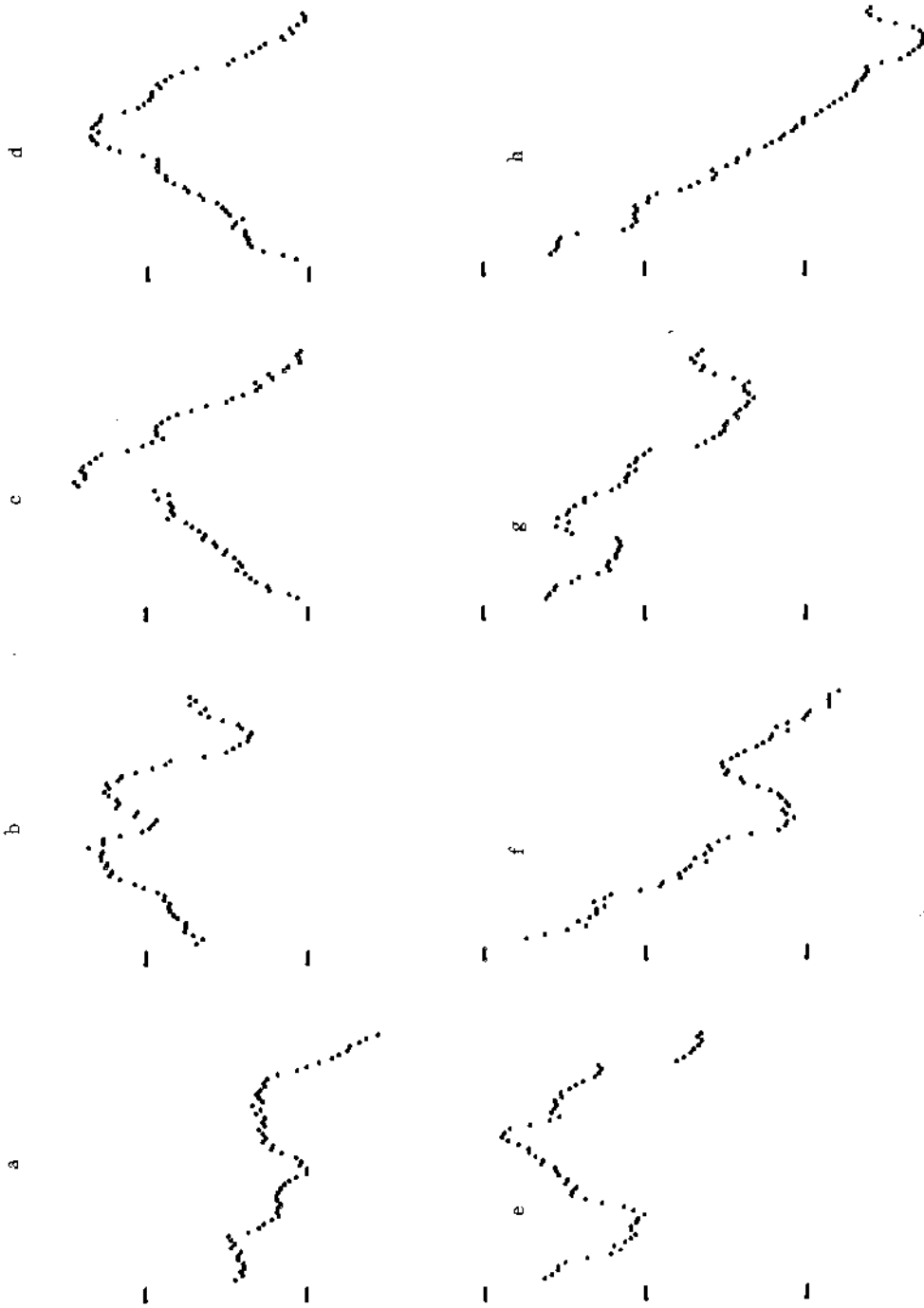


FIGURE 3. Modelled orientation sequences (cf. figure 1). Each is a plot of the orientations present in rows (marked a-h) of the array shown in figure 5. The assignment of a point to any particular cycle of the vertical orientation scale is arbitrary in principle; the convention adopted here is to position each point so that it is nearest to the preceding one. This means that two adjacent points can never be more than 90° apart. This convention has been followed in figure 1 with the exception of the second discontinuity in sequence c.

would expect, to share boundaries, whereas domains of non-adjacent ranges meet at points of discontinuity in the orientation sequences. It is thought that in reality these domains should be uniformly thin (Hubel & Wiesel 1974), although there is no direct evidence for this.

The discontinuities in the orientation sequences form points, or, if a lower threshold is chosen for their display, short narrow strips (figures 4, 5). These are

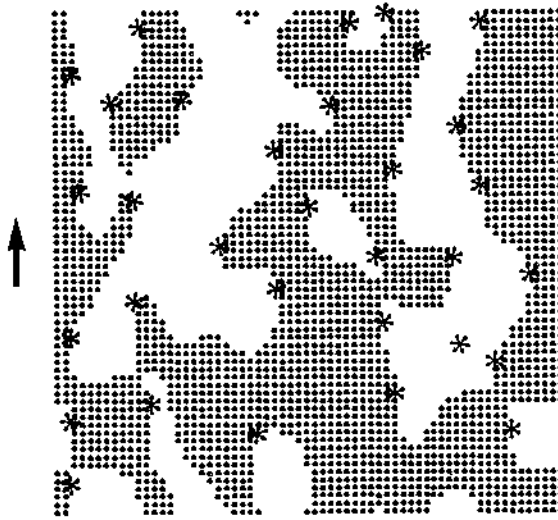


FIGURE 4. Regions of clockwise orientation change, relative to an upward direction of movement across the page (arrow), for the pattern of orientations shown in figure 6*a*. The asterisks mark the locations of discontinuities in the orientation sequences greater than 50° .

distributed with a periodicity about double that of the iso-orientation domains. Further examination shows that these regions are located at points where complete sets of orientation domains meet. The domains are organized in ordered sequences around the discontinuities: thus as a circuit in a given direction is made around each point, the sequence of orientations goes through a complete clockwise or anticlockwise cycle. It is easy to verify this by inspection of figure 6, if one first identifies the points where many different domains meet, and then notes the order of the colours around each point.

Topologically (see Elsdale & Wasoff 1976), these points can be characterized as half-rotation singularities with indices $+\frac{1}{2}$ or $-\frac{1}{2}$, according to whether the sequence of orientations goes through a complete 180° cycle in a clockwise or an anticlockwise sense as a circuit is made in a given direction around each singularity (figure 9*a*). Roughly equal numbers of positive and negative singularities occur in each pattern. The moduli of the vectors in the vicinity of the singularities behave untypically, in that they remain small for a long time after the moduli of most other points in the array have reached their upper limiting values (figure 9*a*). At an earlier stage in the formation of the pattern, these regions of low moduli are much more extensive in area. Thus the rate at which the moduli increase and the columns form is not uniform, but varies across the array, with a periodicity

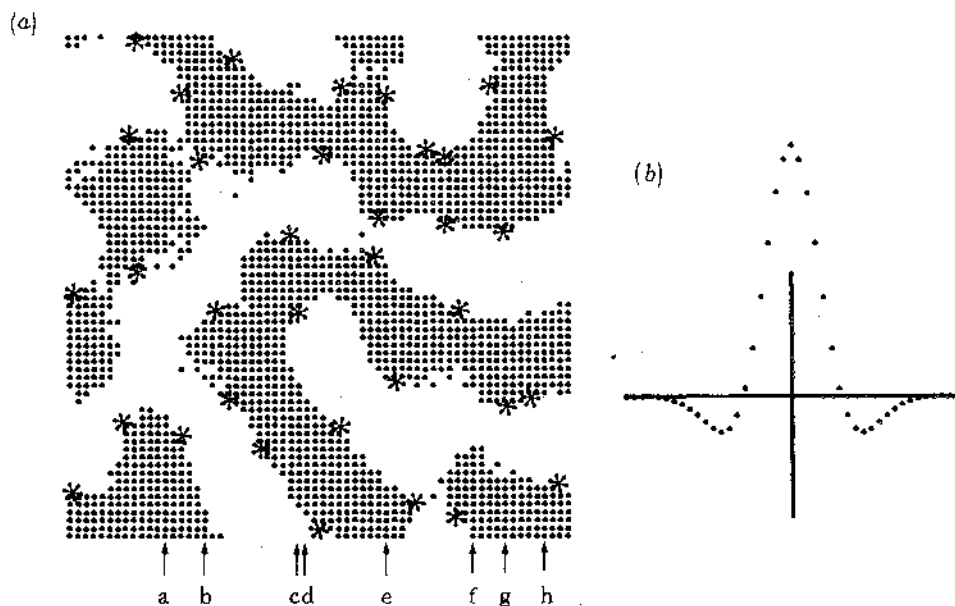


FIGURE 5. (a) Iso-orientation domains for a 90° orientation range in the 180° interpretation of the model. Orientation sequences from rows marked a–h are shown in figure 3. For this large orientation range the domains are branching stripes of fairly uniform width, with no preferred direction. Asterisks mark discontinuities in the orientation sequences. (b) The function $w(r)$ used to generate this pattern (to the same scale), and that of figure 6. In this case the initial standard deviation of $|z_0|$ was 20% of Z .

that is about double that of the columns. An explanation for this is given in appendix 2.

360° representation

In this form of the model it is assumed that the orientations represented by \mathbf{z} can take on values between 0 and 360° , but that, for the purposes of display and comparison with the experimental data, orientations differing by 180° should be regarded as indistinguishable. The long range interactions imply a tendency for cells separated by distances of 500–1000 μm to take up orientations that differ on average by 180° .

The orientation sequences produced (figure 7) are similar in their general properties to those produced by the 180° model, with the exception that fewer

DESCRIPTION OF PLATE 1

FIGURE 6. Modelled iso-orientation domains for the 180° version of the model, with colours in the cycle magenta, orange, yellow, green, blue, purple, magenta... representing adjacent orientation ranges. Each range is 30° wide. In (a) $w(r)$ was circularly symmetric, and the domains have no overall preferred direction. For (b) the central, positive area of $w(r)$ was elongated, and the domains run in the direction of elongation. The number of points where complete sets of domains meet is reduced as a result. In both cases the standard deviation of $|z_0|$ was 0.1% of Z .

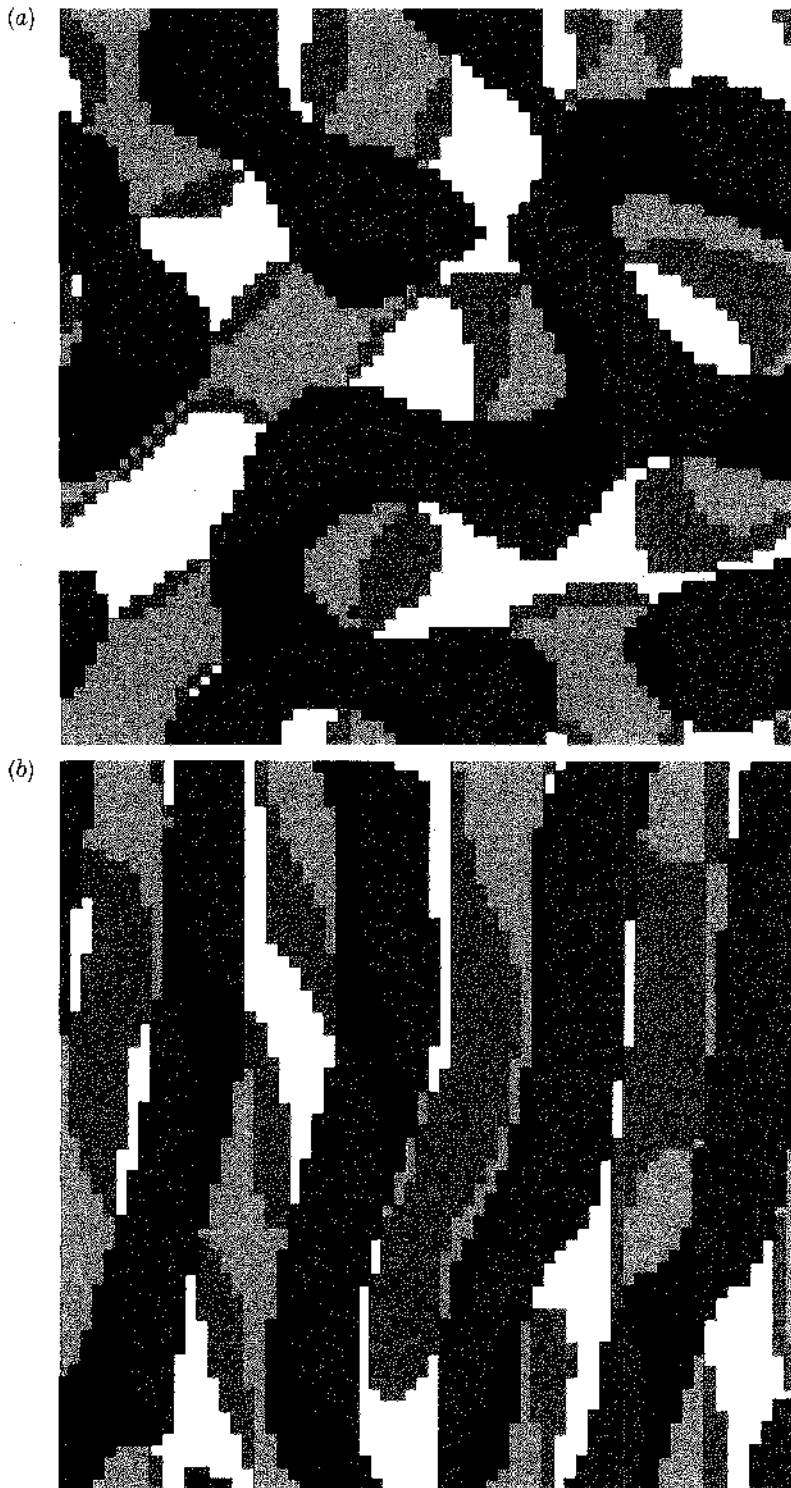


FIGURE 6. For description see opposite.

the moduli of z remain low, are recognizable as regions where orientation changes rapidly, and where clockwise and anticlockwise sequences about (figure 4). Their spacing is about equal to that of the iso-orientation domains. The sequence of orientations goes through a full 360° cycle in either a clockwise or an anticlockwise direction as a circuit is completed in a given direction around such points, which can thus be classified as full rotation singularities with indices of $+1$ or -1 (figure 9*b*).

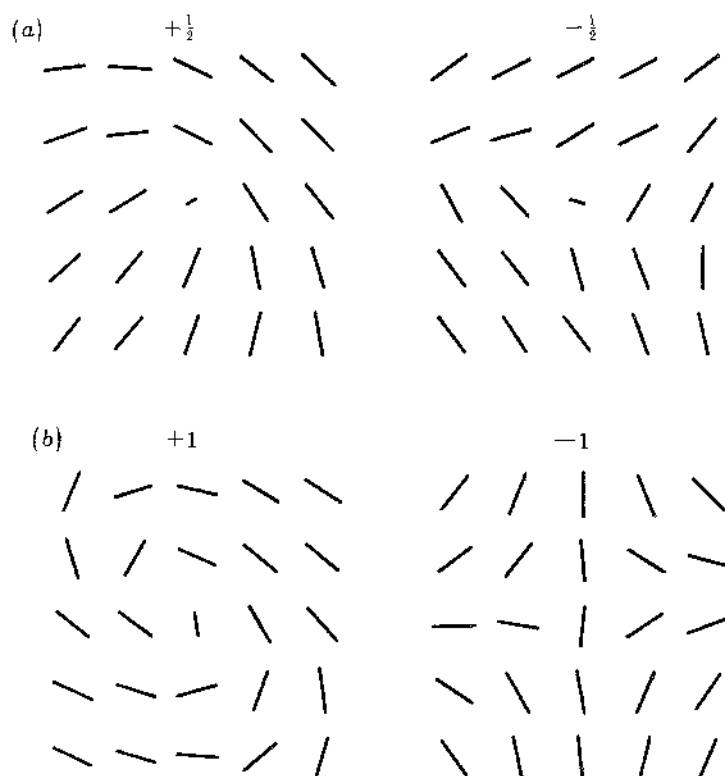


FIGURE 9. Orientation singularities produced in the 180° version of the model (a) and the 360° version (b). The length of the lines is proportional to $|z|$. (a) Taken from points in figure 5; (b) from figure 8.

Effect of changing w

The effects of changes in $w(r)$ on the behaviour of the orientation columns are similar to the effects on ocular dominance columns produced by changes in the corresponding function used to describe their formation (Swindale 1980). Deviations from circular symmetry produce changes in the direction of elongation of the domains: if the central positive region of $w(r)$ is elongated, the domains tend to follow the direction of the elongation (figure 6*b*); if the negative surround is elongated, the domains tend to run in the orthogonal direction. As a consequence of the domains becoming parallel and less frequently branched, the number of

points where complete sets of domains meet is reduced (figure 6*b*). Narrowing the central peak of $w(r)$ (e.g. by increasing the value of λ_1) leads to more irregular orientation sequences, with an increased frequency of alternation between clockwise and anticlockwise progressions.

A general requirement for stability (see appendix 1) is that the volume under $w(r)$ should be equal to or less than zero. If this is so, then the average of all the orientations in the array will have a stable equilibrium value of zero.

Initial conditions

Experimental evidence suggests that there is a tendency for the distribution of orientations in visually inexperienced kittens (Frégnac & Imbert 1978) and newborn monkeys (C. Blakemore & F. Vital-Durand, personal communication) to be biased towards horizontal and vertical. This anisotropy may persist to a slight degree in adult animals (Pettigrew *et al.* 1968; Kennedy & Orban 1979; Leventhal & Hirsch 1977; Blakemore *et al.* 1981).

Anisotropies in the initial distribution, \mathbf{z}_0 , of \mathbf{z} tended to decrease with time in the model. As one would expect, changes that alter the average of \mathbf{z}_0 tend to be reversed. Thus, for the 180° representation, it was found that an initial excess of horizontal orientations only, biasing \mathbf{z}_0 towards horizontal, was reversed in time by the development of an excess of vertical orientations (figure 10*a*). Thus in cats and monkeys a bias towards horizontal and vertical orientations might be the result of an initial bias for only one of these orientations.

Changes that leave the value of $\bar{\mathbf{z}}_0$ close to zero also tend to be reversed. Figure 10*b* shows that an initial excess of both horizontal and vertical orientations changes to a more uniform distribution with time. In contrast to this, it was noticed that an initially uniform distribution of orientations often changed during development to a distribution that was non-uniform (figure 10*c*). There were usually two broad peaks one half cycle apart. The orientations at which the peaks occurred were variable, which suggested that they were not a computational artefact.

DISCUSSION

The model described here is formally very simple; it appears to describe the existing experimental data adequately, and it suggests a number of further properties of orientation columns that can be looked for experimentally. It suggests that the mechanism responsible for the development of orientation selectivity may involve a particular type of lateral interaction but it has (so far) no suggestions to make about the actual mechanism, or the way in which visual experience might be involved. Most existing models for the development of orientation selectivity (see, for example: von der Malsburg 1973; Nass & Cooper 1975; Pérez *et al.* 1975) ascribe a primary role to visual experience. For example, von der Malsburg's model supposes that there are Hebb synapses in the cortex, short range excitatory and long range inhibitory connections between cortical cells, and oriented patterns of input from the retina resulting from visual experience. This leads to the formation of clusters where neighbouring cells have similar

orientation preferences. The spatial layout of these orientations was not studied in detail by von der Malsburg, but the resemblance suggests that it ought to be possible to realize the present model in terms of a similar mechanism based on visual experience and Hebb synapses. One problem faced by all such theories, however, is that they fail to account for the existence of organized sequences of orientation selective cells in newborn and visually inexperienced animals, since it

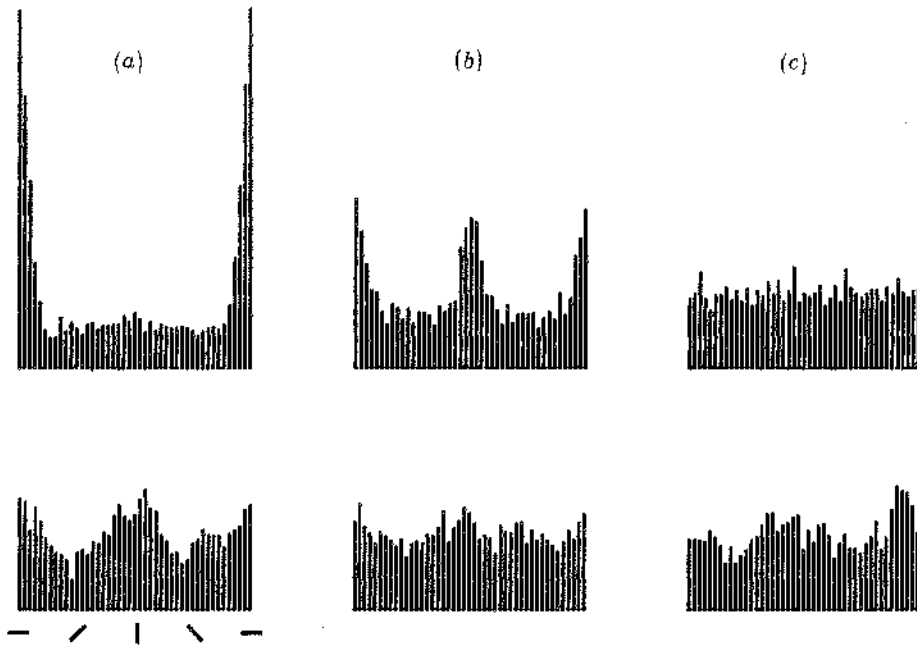


FIGURE 10. Histograms of the orientations of z , at the start of development (upper row) and at the finish (lower row). A 180° representation being assumed, each bin is 4° wide. The initial assignment of orientations was such that in (a) each point had a 50% probability of being normally distributed around horizontal, with a standard deviation of 8° , and a 50% probability of being uniformly distributed over the entire orientation range. In (b) 70% of the points were uniformly distributed and the remainder were normally distributed around horizontal or vertical, with a standard deviation of 15° . In (c) the distribution was uniform.

is unlikely that the required patterns of retinal (or geniculate) activity would occur before birth, or the time of eye opening.

An alternative to a model based on patterned electrical activity and modifiable synapses would be one based on chemical labels for different orientations. No such model has yet been proposed, but the present model might serve as a starting point for such a theory (e.g. the components of z might represent the concentration of two chemicals).

There are some similarities between the arrangements of orientations produced by the present model (most obviously in the version where a full 360° cycle of orientation is represented), and the arrangement postulated by Braitenberg & Braitenberg (1979). These authors speculated that orientations might be arranged

radially, like the spokes of a wheel, around 'centres' spaced roughly 500 μm apart. One could identify these 'centres' with the singularities of the present model whose spacing (in the 360° version of the model) is equal to the periodicity of the iso-orientation domains, and around each of which a complete and ordered cycle of orientation domains is arranged. However, in the present case, the arrangement of orientations is as likely to be tangential to the singularity as radial, or in any other orientation relative to lines radiating from the singularity. In the Braitenberg & Braitenberg model orientations change in a clockwise direction for clockwise movement around each centre, but in the present model centres where the orientation changes in an anticlockwise sense are equally common. The more restricted arrangement proposed by Braitenberg & Braitenberg predicts that regions of iso-orientation should be short elongated segments, whose direction of elongation should vary with the orientation represented, and this is not observed experimentally. For example, in the monkey (Hubel *et al.* 1978), the iso-orientation domains for vertical have no consistent orientation relative to either cortical or retinal coordinates. In the tree shrew (Humphrey *et al.* 1980) iso-orientation domains for both horizontal and vertical orientations run in the same direction (orthogonal to the border of area 17), a configuration that Braitenberg & Braitenberg admit they are unable to explain.

The lack of any dependence between orientation, and the configuration of the domain in which the orientation is represented, suggests that it is correct to exclude a type of model that has not so far been considered here, in which $w(\mathbf{r})$ is a vector field locally dependent on the orientation of \mathbf{z} . (This is the sort of model that might appropriately describe the interaction between an array of compass needles, where the magnetic field due to each needle is a function of the orientation of the needle.)

There is little evidence at present that suggests whether the 180° or the 360° representation is the more appropriate for the present model. The procedure of halving the angle formed by the vector \mathbf{z} with its coordinate axes to obtain a measure of orientation that is cyclic over a 180° rotation seems unnatural, though it is quite satisfactory as a computational device. One reason for preferring this form of the model to the alternative 360° representation is that the latter introduces a distinction between orientations differing by 180°, which it is supposed has not yet been made experimentally. The possibility that such differences could indicate differences in direction preference seems unlikely for several reasons. Although there is evidence of a columnar organization of direction preference in the cat (Payne *et al.* 1980), the representation in the cortex seems to be independent of orientation. Electrode penetrations show that sequences of continuous orientation change are often interrupted by 180° shifts in the preferred direction of stimulus movement. These shifts are much more frequent than the 180° shifts occurring in the 360° version of the present model, and this suggests that the mechanism responsible for continuity in the representation of orientation makes no distinction between cells whose direction preferences differ by 180°. Other physiological evidence suggests that direction and orientation selectivity develop independently. Direction selectivity can be abolished, leaving orientation selectivity apparently normal, by rearing kittens in a stroboscopically illuminated environment (Cynader & Chernenko 1976). In normal animals many orientation selective cells

are not direction selective, while, conversely, it is possible for cells, particularly in young kittens, to possess direction selectivity but not orientation selectivity (Barlow & Pettigrew 1971; Blakemore & Van Sluyters 1975).

Rigorous testing of the descriptive accuracy of the model is likely to be difficult. One possible approach would be to study the Fourier transforms of orientation sequences recorded from electrode penetrations in a series of developing animals, and to show that the transforms changed at rates given by equation (5a) (appendix 1). Apart from this, the model makes a number of predictions that, if confirmed, would provide circumstantial evidence in its favour. These are mainly the outcome of the computer simulations that have already been described, but they have a mathematical basis, which is outlined in appendix 2.

The rate at which the columns develop should fluctuate spatially, with a periodicity equal to, or double that of the iso-orientation domains. These fluctuations should be least evident in the initial and final stages of development. Physiological recordings should thus show spatially correlated variations in responsiveness or orientation tuning in animals at intermediate stages of column formation (e.g. in kittens 4–5 weeks old). A variation in responsiveness, if it exists, might also be demonstrable in deoxyglucose autoradiographs from animals stimulated with a complete range of orientations.

Discontinuities in the orientation sequences should be spaced on average with a periodicity comparable to or greater than that of the orientation domains. Where the domains run parallel to one another over large areas (as in the tree shrew) they may be expected to occur less frequently. Reconstructions from parallel electrode penetrations on either side of a discontinuity should show that it is surrounded by either a 180° cycle of orientations, in which case the discontinuities should be spaced with a periodicity double that of the domains, or a 360° cycle, in which case the spacing should be equal to that of the domains. (The spacing of the discontinuities shown in figure 1 supports the first of these predictions.)

Regions where orientation selectivity is poorly developed, or absent, may persist from the juvenile state, though reduced in area, in adult animals. Each should be associated with a discontinuity. If the regions are large, the discontinuity will be located somewhere along the edge, and the region as a whole will be surrounded by either a 180° or a 360° cycle of orientations. Opposite the discontinuity a neutral equilibrium prevails (see appendix 2) and orientations may vary randomly with position, or the response properties of the cells might be abnormal in other ways.

The recent results of Horton & Hubel (1981) are in general agreement with the foregoing predictions. Their experiments suggest that orientation columns coalesce in patches spaced with a periodicity comparable to, or slightly greater than, that of the orientation columns. In layers II and III of the cortex the patches are labelled by deoxyglucose, irrespective of the orientation of a visual stimulus, and physiological recording confirms that cells in these regions lack orientation selectivity (Hubel & Livingstone 1981). Horton & Hubel (1981) and Hendrickson *et al.* (1981) have also shown that the patches are aligned on the central regions of left and right eye ocular dominance stripes. This suggests that orientation columns and ocular dominance columns are not geometrically independent, as has

been assumed here, and some means should be sought to link the models that I have proposed for the two columnar systems.

APPENDIX 1

Here the behaviour of \mathbf{z} , and its space average $\bar{\mathbf{z}}$ are investigated, for the initial stages in development when $|z| \ll Z$. It is convenient to treat \mathbf{z} as the complex number $a + ib$. Ignoring the constant factor Z , equation (1) reduces to

$$\partial \mathbf{z} / \partial t = \mathbf{z} * w. \tag{5}$$

In frequency space this transforms to give

$$\partial \mathbf{Z} / \partial t = \mathbf{Z} W, \tag{5a}$$

where \mathbf{Z} and W are the Fourier transforms of \mathbf{z} and w respectively. This has the solution $\mathbf{Z} = \mathbf{Z}_0 \exp(Wt)$, where \mathbf{Z}_0 is the transform of \mathbf{z}_0 , the value of \mathbf{z} at $t = 0$. It is straightforward to show, as in the analogous model for ocular dominance columns (Swindale 1980), that the frequency for which W has a positive maximum will be the predominant spatial frequency of the iso-orientation domains. Note that the experimental observation that orientation changes linearly with distance implies a single spatial frequency in \mathbf{z} ; thus if $\theta = kr$, where k is a constant and r is distance, $\mathbf{z} = |z| [\cos(kr) + i \sin(kr)]$.

If w is complex, or not even symmetric, its transform will in general be complex. In this case equation (5) has the oscillatory solution $\mathbf{Z} = \mathbf{Z}_0 \exp(Ct) \exp(iDt)$, where C and D are the real and imaginary components of W . This suggests that in reality any complex component of w is small or absent.

Averaging both sides of equation (5) over space (or taking the value of its transform at $\nu = 0$) gives $\partial \bar{\mathbf{z}} / \partial t = \bar{\mathbf{z}} \bar{w}$, with the solution $\bar{\mathbf{z}} = \bar{\mathbf{z}}_0 \exp(\bar{w}t)$. Provided that \bar{w} (i.e. the volume under the function) < 0 the equilibrium state is $\mathbf{z} = (0, 0)$, whatever the initial value of $\bar{\mathbf{z}}_0$. This is true also for values of \mathbf{z} averaged over regions of space as small as, but not smaller than, the approximate spatial extent of w .

APPENDIX 2

Here it is shown that the rate of increase of $|z|$ will vary in space with a periodicity twice that of the iso-orientation domains. Where \mathbf{z} is a continuous function of position, there must exist regions where, except for configurations of \mathbf{z} that are unlikely to occur in practice, the value of $\mathbf{z} * w$, and the rate of change of $|z|$ will be zero or negative. These regions can be identified with the singularities where complete sets of orientation domains meet.

For any particular decomposition of \mathbf{z} into orthogonal components a and b , one has, from equation (1),

$$\partial a / \partial t = a * w f(|z|); \quad \partial b / \partial t = b * w f(|z|). \tag{6}$$

The modulus of \mathbf{z} is defined as $|z|^2 = a^2 + b^2$, and therefore

$$\partial |z| / \partial t = (1/|z|) [a \partial a / \partial t + b \partial b / \partial t].$$

Substituting from equation (6) gives

$$\partial|z|/\partial t = (1/|z|) [a(a * w) + b(b * w)]f(|z|). \quad (7)$$

Other than in the initial stages of pattern formation, the functions a and b will both contain a limited range of spatial frequencies, and these will tend to be preserved by convolution with w . In particular the positions of the zero crossings of a and b will tend to be preserved, and thus the signs of a , b and their convolution

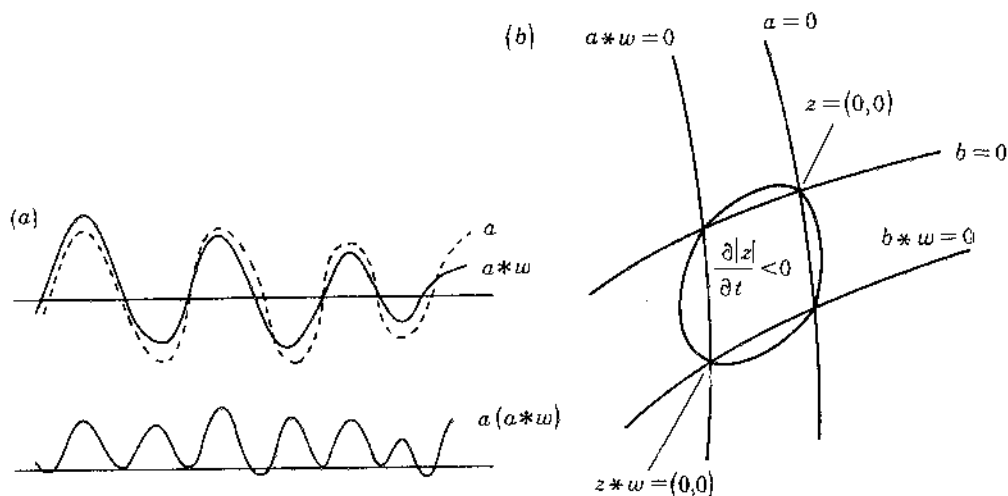


FIGURE 11

products $a * w$, $b * w$ will be similar. Thus in most regions, both $a(a * w)$ and $b(b * w)$ will be positive, but will fluctuate with a periodicity twice that of a and b (figure 11a); $|z|$ therefore increases at a rate that has a periodicity twice that of z .

There must inevitably be regions, at or near the zero crossings of a and $a * w$, where the value of $a(a * w)$ is zero or negative. Consider first the case where the zero crossings of a and $a * w$ coincide exactly; there will then be no positions where $a(a * w)$ is negative, but the zero values will, in two dimensions, form a set of curved lines. In an infinite or unbounded field these will form a set of closed loops defining the boundaries between domains for complete half cycles of orientation. A similar set of loops defining zero values of $b(b * w)$ exists; the intersections of the two sets of loops then define points where the values of z and $z * w$ are both zero. The distances between the points may be variable, but on average will be half the distance between iso-orientation domains. Configurations of z for which such intersections do not occur are unlikely if the initial values of z are random.

Note that these points are located at the intersection of two orthogonal domain boundaries, and that this is so however the boundaries are chosen (i.e. for any decomposition of z into orthogonal components). Each point therefore is surrounded by a complete set of orientation domains. Since a and b change continuously with position the domains will be ordered, and since for a single circuit around each point a and b will each have a single positive and negative phase, a single cycle of domains will be present.

The computations give results that are in agreement with these expectations, but it may be supposed that in reality these ideal conditions are less closely approached. More generally, it may be supposed that equilibrium conditions will not necessarily be reached, and that the zero crossings of a , b and their convolution products with w will not coincide exactly. In this case, regions where $a(a * w)$ and $b(b * w)$ are negative will be narrow bands, and the intersections will be small patches (figure 11*b*). Within these regions, $\partial|z|/\partial t$ will be negative; at the edges its value will be zero, and there will be a singularity where $z = (0, 0)$ at some position along the edge. This suggests that in the cortex discontinuities in the orientation sequences may be located at the boundaries of regions where orientation selectivity is poorly defined, because cells are either unresponsive or broadly tuned for orientation. At an opposite point along the edge of each patch, $z * w = 0$ and hence $\partial z/\partial t = 0$ and a neutral equilibrium prevails. At such points orientation might vary randomly with depth in the cortex, or the response properties of the cells might be abnormal in other ways.

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REFERENCES

- Albus, K. 1975 A quantitative study of the projection area of the central and paracentral visual field in area 17 of the cat. II. The spatial organization of the orientation domain. *Expl Brain Res.* **24**, 181–202.
- Albus, K. 1979 ¹⁴C-deoxyglucose mapping of orientation subunits in the cat's visual cortical areas. *Expl Brain Res.* **37**, 609–613.
- Barlow, H. B. & Pettigrew, J. D. 1971 Lack of specificity of neurones in the visual cortex of young kittens. *J. Physiol., Lond.* **218**, 98P–100P.
- Blakemore, C. 1978 Maturation and modification in the developing visual system. In *Perception. The handbook of sensory physiology*, vol. 8, pp. 376–436. Berlin, Heidelberg and New York: Springer-Verlag.
- Blakemore, C., Garey, L. J. & Vital-Durand, F. 1981 Orientation preferences in the monkey's visual cortex. *J. Physiol., Lond.* **319**, 78P.
- Blakemore, C. & Van Sluyters, R. C. 1975 Innate and environmental factors in the development of the kitten's visual cortex. *J. Physiol., Lond.* **248**, 663–716.
- Braitenberg, V. & Braitenberg, C. 1979 Geometry of orientation columns in the visual cortex. *Biol. Cybernetics* **33**, 179–186.
- Cynader, M. & Chernenko, G. 1976 Abolition of direction selectivity in the visual cortex of the cat. *Science, N.Y.* **193**, 504–505.
- Elsdale, T. & Wasoff, F. 1976 Fibroblast cultures and dermatoglyphics: the topology of two planar patterns. *Wilhelm Roux Arch. EntwMech. Org.* **180**, 121–147.
- Frégnac, Y. & Imbert, M. 1978 Early development of visual cortical cells in normal and dark-reared kittens: relationship between orientation selectivity and ocular dominance. *J. Physiol., Lond.* **278**, 27–44.
- Hendrickson, A. E., Hunt, S. P. & Wu, J.-Y. 1981 Immunocytochemical localisation of glutamic acid decarboxylase in monkey striate cortex. *Nature, Lond.* **292**, 605–607.
- Horton, J. C. & Hubel, D. H. 1981 Regular patchy distribution of cytochrome oxidase staining in primary visual cortex of macaque monkey. *Nature, Lond.* **292**, 762–764.
- Hubel, D. H. & Livingstone, M. S. 1981 Regions of poor orientation tuning coincide with patches of cytochrome oxidase staining in monkey striate cortex. *Soc. Neurosci. Abstr.* **7**, 357.

- Hubel, D. H. & Wiesel, T. N. 1962 Receptive fields, binocular interaction, and functional architecture in the cat's visual cortex. *J. Physiol., Lond.* **160**, 106-154.
- Hubel, D. H. & Wiesel, T. N. 1963 Receptive fields of cells in striate cortex of very young, visually inexperienced kittens. *J. Neurophysiol.* **26**, 994-1002.
- Hubel, D. H. & Wiesel, T. N. 1968 Receptive fields and functional architecture of monkey striate cortex. *J. Physiol., Lond.* **195**, 215-243.
- Hubel, D. H. & Wiesel, T. N. 1972 Laminar and columnar distribution of geniculo-cortical fibers in the macaque monkey. *J. comp. Neurol.* **146**, 421-450.
- Hubel, D. H. & Wiesel, T. N. 1974 Sequence regularity and geometry of orientation columns in the monkey striate cortex. *J. comp. Neurol.* **158**, 267-294.
- Hubel, D. H., Wiesel, T. N. & Stryker, M. P. 1978 Anatomical demonstration of orientation columns in macaque monkey. *J. comp. Neurol.* **177**, 361-380.
- Humphrey, A. L. & Norton, T. T. 1980 Topographic organisation of the orientation column system in the striate cortex of the tree shrew (*Tupaia glis*). I. Microelectrode recording. *J. comp. Neurol.* **192**, 531-547.
- Humphrey, A. L., Skeen, L. C. & Norton, T. T. 1980 Topographic organisation of the orientation column system in the striate cortex of the tree shrew (*Tupaia glis*). II. Deoxyglucose mapping. *J. comp. Neurol.* **192**, 549-566.
- Kennedy, H. & Orban, G. A. 1979 Preferences for horizontal or vertical orientation in cat visual cortical neurons. *J. Physiol., Lond.* **296**, 61P-62P.
- LeVay, S., Stryker, M. P. & Shatz, C. J. 1978 Ocular dominance columns and their development in layer IV of the cat's visual cortex: a quantitative study. *J. comp. Neurol.* **179**, 223-244.
- Leventhal, A. G. & Hirsch, H. V. B. 1977 Effects of early experience upon orientation sensitivity and binocularity of neurons in visual cortex of cats. *Proc. natn. Acad. Sci. U.S.A.* **74**, 1272-1276.
- von der Malsburg, Ch. 1973 Self-organisation of orientation sensitive cells in the striate cortex. *Kybernetik* **14**, 85-100.
- von der Malsburg, Ch. 1979 Development of ocularity domains and growth behaviour of axon terminals. *Biol. Cybernetics* **32**, 49-62.
- Nass, M. M. & Cooper, L. L. 1975 A theory for the development of feature detecting cells in visual cortex. *Biol. Cybernetics* **19**, 1-18.
- Payne, B. R., Berman, N. & Murphy, E. H. 1980 Organisation of direction preferences in cat visual cortex. *Brain Res.* **211**, 445-450.
- Pérez, R., Glass, L. & Shlaer, R. 1975 Development of specificity in the cat visual cortex. *J. math. Biol.* **1**, 275-288.
- Pettigrew, J. D., Nikara, T. & Bishop, P. O. 1968 Responses to moving slits by single units in cat striate cortex. *Expl Brain Res.* **6**, 373-390.
- Rakic, P. 1976 Prenatal genesis of connections subserving ocular dominance in the rhesus monkey. *Nature, Lond.* **261**, 467-471.
- Rakic, P. 1977 Prenatal development of the visual system in the rhesus monkey. *Phil. Trans. R. Soc. Lond. B* **278**, 245-260.
- Rockel, A. J., Hiorns, R. W. & Powell, T. P. S. 1974 Number of neurons through full depth of neocortex. *J. Anat.* **118**, 371P.
- Sherk, H. & Stryker, M. P. 1976 Quantitative study of orientation selectivity in visually inexperienced kittens. *J. Neurophysiol.* **39**, 63-70.
- Swindale, N. V. 1980 A model for the formation of ocular dominance stripes. *Proc. R. Soc. Lond. B* **208**, 243-264.
- Wiesel, T. N. & Hubel, D. H. 1974 Ordered arrangement of orientation columns in monkeys lacking visual experience. *J. comp. Neurol.* **158**, 307-318.