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## A model for the formation of ocular dominance stripes

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The paper describes a model of competition that explains the formation of the ocular dominance stripes found in layer IVc of cat and monkey visual cortex. The main proposal is that synapses exert effects on the growth of other synapses, and that these effects extend over distances of at least 600  $\mu\text{m}$  and vary in magnitude and sign within this distance. Interactions between like type synapses are assumed to be stimulating for distances up to about 200  $\mu\text{m}$ , and inhibitory for distances of 200–600  $\mu\text{m}$ . The reverse is true of interactions between synapses of opposite eye type, where the effects are inhibitory for distances up to about 200  $\mu\text{m}$  and stimulating for longer ones. The interactions are assumed to be circularly symmetric. Growth of, for example, right eye synapses at one point will therefore (a) encourage local growth of right eye synapses and inhibit local growth of left eye synapses and (b) encourage growth of left eye synapses and inhibit growth of right eye synapses in an annular ring surrounding the point of initial increase. At the start of development, right and left eye synapses are assumed to be intermixed randomly within layer IVc. Computer simulations show that a wide variety of conditions incorporating these assumptions will lead to the formation of stripe patterns. These reproduce many of the morphological features of monkey ocular dominance stripes, including Y- and H-type branches and terminations, the tendency for stripes to run at right angles into the boundaries of the pattern, and to narrow at branch points.

The model can explain the effects of monocular deprivation on stripe morphology if it is assumed that the effectiveness of deprived eye synapses in determining rates of growth locally is reduced. The existence of a critical period for these effects can be explained if it is assumed that lateral growth of terminals does not occur, and that some factor such as a limited availability of postsynaptic sites decreases the rate of growth of synapses as their density approaches a maximum.

The model can be generalized to account for pattern formation in other systems, such as zebra or mackerel skin, where similar striped patterns occur. In this context, the simplest model based on diffusion that will produce a pattern of stripes requires that one cell type should secrete two substances, one of which stimulates growth or differentiation of its parent cell type and has a low rate of diffusion or is rapidly inactivated, and another that inhibits growth or differentiation and either has a higher rate of diffusion or is less rapidly inactivated.

A preliminary account of some of these results has appeared elsewhere (Swindale 1979).

## 1. INTRODUCTION

When electrophysiological recordings are made from the visual cortex of cats and monkeys, cortical neurons are found to vary in the relative extent to which they can be driven by stimuli given to the right or the left eye. Neurons that are close together or in the same radial column of cortical tissue tend to share a preference for stimuli given to a particular eye, and this preference varies system-

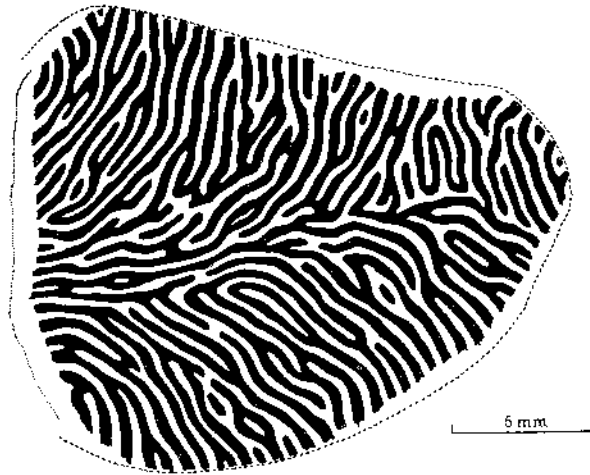


FIGURE 1. A reconstruction of the pattern of ocular dominance stripes in area 17 of a macaque monkey, made from a series of sections cut in a plane tangential to the cortical surface and stained by a reduced-silver technique (LeVay *et al.* 1975). This reveals narrow pale bands at points of transition between right and left eye-dominated cortex, so that the pattern of columns can be reconstructed. Regions receiving input from one eye are shaded black in the figure; the unshaded areas between the stripes receive their input from the other eye. The dashed line is the border between area 17 and 18. (Taken from Hubel & Wiesel 1977.)

atically with lateral distance in the cortex: left and right eye-dominated regions alternate with a periodicity of 700–800  $\mu\text{m}$  (Hubel & Wiesel 1962, 1968). An explanation for this phenomenon can be found in the way in which the two eyes' inputs, relayed separately by the different laminae of the lateral geniculate nucleus, are distributed within layer IVc of the cortex (figure 1): if the terminals conveying input from one eye are labelled selectively (e.g. by injecting a radioactive tracer into the eye), the distribution of label, viewed from a direction normal to the cortical surface, is not uniform, but forms a pattern of stripes that are individually about 350  $\mu\text{m}$  wide, separated by gaps of the same width (Hubel & Wiesel 1972; Wiesel *et al.* 1974; LeVay *et al.* 1975; Shatz *et al.* 1977). Individual stripes may divide to form Y- or H-type branches, and may change direction without branching, or end blindly. The gaps between the stripes have the same morphological properties as the stripes themselves, and it can be inferred that they are occupied by unlabelled input from the other eye (LeVay *et al.* 1975).

The implication that this segregation of the inputs to the two eyes is responsible for the physiological variations in ocular dominance has been confirmed by experiments that show an exact correspondence between the locations and boundaries of columns predicted from anatomical data and determined by electrophysiological recording (LeVay *et al.* 1975; Hubel *et al.* 1977; Shatz & Stryker 1978).

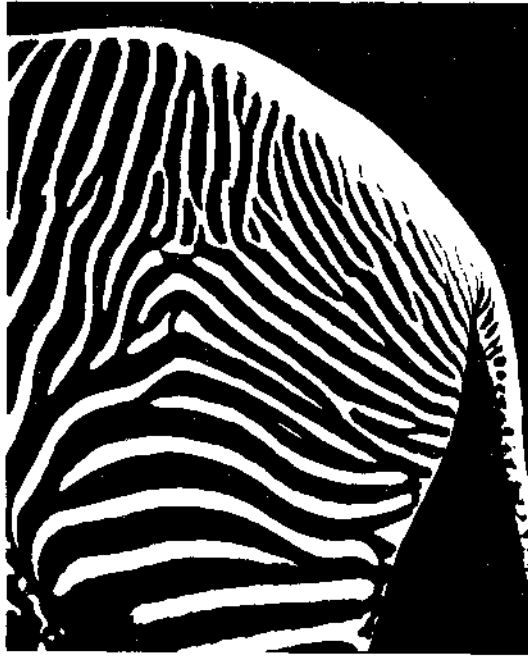


FIGURE 2. The stripes on the rear flank of a zebra. (Redrawn from a photograph in Strache (1959).)

It is remarkable that the ocular dominance stripes found in the monkey striate cortex closely resemble patterns that can be found elsewhere in nature. Comparisons with the stripes on zebras (figure 2) and fingerprints have been made (Hubel & Wiesel 1977), while similar patterns occur, for example, on male cuttlefish, on mackerel, bird feathers and many species of tropical fish. In all of these patterns the stripes display an apparent randomness in the location of branches and terminations, a tendency to narrow in width at branch points, and a tendency to run at right angles into the boundaries of the pattern. These resemblances suggest that there is some underlying formal similarity in the mechanisms that give rise to the patterns, and if this is so, it should be possible to formulate a model of the development of the pattern in the cortex without needing to make detailed assumptions about the underlying cortical physiology. The purpose of this paper is to suggest one such possible model; as a consequence it is also able to suggest how similar patterns could be formed in other systems.

## 2. THE MODEL

The starting point for the ideas to be expressed here is the model put forward by Hubel *et al.* (1977) to explain the effects of abnormal early visual experience on the development of the ocular dominance stripes. In both the cat and the monkey the pattern is formed at around, or shortly after, the time of birth. Six weeks before birth in the monkey, the inputs from the two eyes are uniformly intermixed within layer IVc of the visual cortex (Rakic 1976, 1977). One week before birth a periodicity in the distribution of afferents is apparent, although the inputs still overlap everywhere; by six weeks of age, separation into non-overlapping stripes is almost complete (Hubel *et al.* 1977). Abnormal visual experience can alter the characteristics of the final pattern if it occurs while the stripes are forming. Removal, or closure, of one eye shortly after birth for a period of 7 or more weeks causes the stripes conveying input from that eye to become narrow in width, while conversely, those from the normal eye expand (Hubel *et al.* 1977; Shatz & Stryker 1978). No such effects occur when similar procedures are carried out in animals more than about 2 months old, when segregation is already complete (Hubel *et al.* 1977).

Hubel *et al.* explained these results with the suggestion that during development there is competition between left and right eye terminals in the cortex, so that if in any region one set of terminals predominates numerically over the other the inferior set decreases in number and is eventually eliminated. Given two initially overlapping sets of projections, with periodic, out of phase fluctuations in density, this process should lead to segregation into non-overlapping stripes of equal width. Depriving one eye of vision might put it at a disadvantage in the competition, so that at the edges of a presumptive stripe, the input to that eye, though numerically still superior to that from the normal eye, would be rejected. This would explain why the deprived eye stripes become narrow and the normal stripes wider. As well as accounting for the effects of monocular deprivation, the hypothesis explains why deprivation effects become progressively less severe as segregation proceeds, and why binocular deprivation is without apparent effect (Wiesel & Hubel 1974). However, it is not certain that a purely local interaction of this sort could account for the initial stages in segregation, when a uniformly intermixed distribution of inputs changes to one with well defined periodic fluctuations in density. Ideally a model ought to be able to account for all stages of segregation, and in what follows I show that an extension of the ideas of Hubel *et al.* can do this.

In this model, I propose that the effects that a synapse exerts on the growth of other synapses are not local, but extend over space, varying in both magnitude and sign. Thus the effects on growth may be positive or negative, depending on distance. There are four types of interaction to take into account: effects on growth exerted between synapses of the same eye type (R-R and L-L interactions); and effects exerted between synapses of opposite eye type (R-L and

L-R interactions). These effects can be described quantitatively by a total of four functions  $w_{RR}$ ,  $w_{RL}$ ,  $w_{RL}$  and  $w_{LR}$ , which describe how the effects on growth produced by each type of synapse considered in isolation from others vary with distance. It is a general feature of the model that  $w_{RR}$  and  $w_{LL}$  are positive for short distances (0–200  $\mu\text{m}$ ) and negative for larger ones (200–600  $\mu\text{m}$ ), while the reverse is true for  $w_{RL}$  and  $w_{LR}$ .

The region of space within which  $w_{RR}$  and  $w_{LL}$  are positive and  $w_{RL}$  and  $w_{LR}$  are negative will be referred to as region E (this region is not necessarily the same

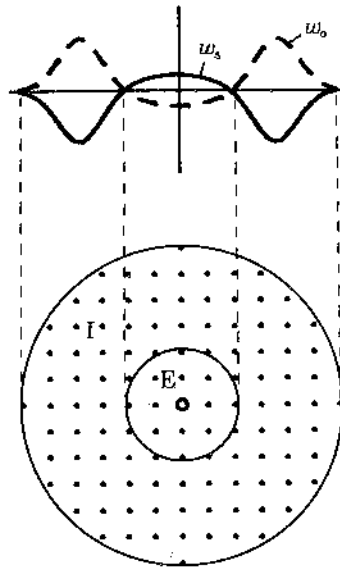


FIGURE 3. The functions  $w_s$  (dotted line) and  $w_o$  (continuous line) used to generate the pattern shown in figure 4, graphed as a function of radial distance. The bottom half of the figure shows their projection onto a part of the array used to represent the cortex. The dots represent points approximately 100  $\mu\text{m}$  apart from one another. The points shown are those whose associated synaptic densities influence the rate of growth of synapses at the central point, represented by a circle.

for all four functions, but will be assumed to be so for simplicity), while the surrounding region, in which the functions have an opposite sign, will be referred to as region I. All the functions are assumed to be zero for distances greater than 600  $\mu\text{m}$ , and all are assumed to be radially symmetric. If the inputs from the two eyes behave in the same way (which may not be the case in monocular deprivation), then  $w_{RR} = w_{LL}$  and  $w_{RL} = w_{LR}$ . When this is the case,  $w_s$  will be used to represent  $w_{RR}$  and  $w_{LL}$ , and  $w_o$  to represent  $w_{RL}$  and  $w_{LR}$  (figure 3). (The subscripts s and o are intended to signify same and opposite type interactions respectively.)

Various means can be envisaged by which synapses could come to exert distance-dependent effects on the growth of other synapses. If Hebb synapses are involved (as Malsburg & Willshaw (1976) suggest) effects on growth might depend on a

combination of various probabilities, e.g. that two synapses are in contact with the same postsynaptic cell, that they belong to the same axon, or that they are driven by similar regions of the retina. These probabilities are likely to vary with lateral distance between synapses. Alternatively, synapses could release chemicals that diffuse through tissue and exert stimulating and inhibitory effects on the growth of other synapses (this is discussed in appendix 2). Different types of mechanism would be expected to imply different functional forms for  $w_{RR}$  etc., but since the results of the model are to a large extent independent of the precise forms chosen (see below) the model allows considerable scope in interpretation in terms of more specific mechanisms.

To summarize, the extra features of the model that have been introduced can be expressed as follows: (1) synapses of opposite eye type not only inhibit each other's growth locally (in this case for distances of up to 200  $\mu\text{m}$ ) as proposed by Hubel *et al.* (1977) but also reinforce each other's rate of growth if situated greater than 200  $\mu\text{m}$  apart; and (2) synapses of one eye type compete among themselves, so that a local excess of one eye type will encourage further local growth of synapses of that type, but will discourage the growth of similar synapses if they are more than 200  $\mu\text{m}$  distant.

The postulated effects on growth represent the effects of individual synapses considered in isolation from others. To find the rates of growth at a point in the cortex, the effects of all surrounding left and right eye synapses have to be taken into account. This is done by making a locally weighted sum of the surrounding left and right eye synaptic densities, with the weights being given by the functions  $w_{RR}$ , etc. If  $n_R(\mathbf{r})$  and  $n_L(\mathbf{r})$  represent the densities of right and left eye synapses respectively at a position  $\mathbf{r}$  on the cortical surface (the cortex will be regarded as a two-dimensional sheet of tissue for this purpose), then the rate of growth of right eye synapses will be determined by a function  $s(\mathbf{r})$ , where

$$s_R(\mathbf{r}) = \int_{E, I} \int \{n_R(\mathbf{r} - \mathbf{r}_1) w_{RR}(\mathbf{r}_1) + n_L(\mathbf{r} - \mathbf{r}_1) w_{LR}(\mathbf{r}_1)\} d\mathbf{r}_1. \quad (1)$$

This is more conveniently written with the conventional notation for convolution. Thus,

$$s_R = n_R * w_{RR} + n_L * w_{LR}. \quad (1a)$$

The corresponding equation for left eye synapses is

$$s_L = n_L * w_{LL} + n_R * w_{RL}. \quad (2)$$

Other factors will limit the rates of growth  $\partial n_R / \partial t$  and  $\partial n_L / \partial t$  of right and left eye synapses:  $n_R$  and  $n_L$  cannot be negative, and there must exist an upper limit,  $N$ , to their density in the cortex. Thus, in general,

$$\partial n_R / \partial t = s_R f(n_R), \quad (3)$$

where  $f(n_R) = 0$  for  $n_R = 0$  and  $n_R = N$ . Thus, a suitable form for  $f(n_R)$  is

$$f(n_R) = n_R(N - n_R) \quad (4)$$

or, alternatively,

$$f(n_R) = k, \quad \text{where} \quad \begin{cases} k = 1 & \text{if } 0 < n_R < N \\ k = 0 & \text{if } 0 \geq n_R \geq N \end{cases}, \quad (5)$$

with similar relations holding for  $n_L$  and  $s_L$  throughout. Both of the possibilities (4) and (5) yield similar results in practice. Physiologically, these equations imply two things: (a) that once synapses of a given eye type have disappeared from a region they can never reappear, i.e. that lateral growth of terminals does not occur; and (b) that some factor such as the availability of postsynaptic sites reduces the rate of growth of synapses as the density increases.

For many of the computations it was further assumed that the sum of the densities of left and right eye synapses is constant throughout the cortex, i.e. that  $n_R + n_L = N$  everywhere. This will be the case if there exists a fixed and uniform number of postsynaptic sites in the cortex that are always occupied by either left or right eye synapses. Since  $n_R$  and  $n_L$  can no longer vary independently, this necessarily implies that  $w_{RR} = -w_{RL}$  and  $w_{LL} = -w_{LR}$ . The resulting simplification of the model is further discussed in appendix 1. In practice the results are essentially the same as with the less simple case.

Computer solutions of the above equations were obtained with the inputs to the cortex represented by pairs of values assigned to points in a two-dimensional array. These points represent regions of cortex each approximately 100  $\mu\text{m}$  apart in a direction parallel to the cortical surface. It was assumed that the initial mean densities of left and right eye synapses,  $\bar{n}_L$  and  $\bar{n}_R$ , were the same, with a variance equal to their mean numerical value. The actual numbers likely to be involved are not known, but, if layer IVc is about 200  $\mu\text{m}$  thick, then the data for the cat (no comparable data is available for the monkey) given by Garey & Powell (1971), Cragg (1975) and LeVay & Gilbert (1976) suggest that numbers in the range  $10^4$ – $10^5$  would probably be appropriate. The value most commonly used was  $1.5 \times 10^4$ ; however, in most cases the amplitude of the initial fluctuations in input is not critical. For models where  $n_R + n_L = N$  the initial distribution was assumed to be binomial with a variance =  $0.25N$ .  $N$  normally had the value  $3 \times 10^4$ .

For the majority of the computations the functions  $w_{RR}$  etc. all had the same general form:

$$w(r) = A \exp(-r^2/d_1) - B \exp\{-(r-h)^2/d_2\}, \quad (6)$$

where  $r$  is radial distance in units of 100  $\mu\text{m}$ , and  $A$ ,  $B$ ,  $d_1$ ,  $d_2$  and  $h$  are constants. Often  $h$  was zero. Many other functions satisfying the general requirements of the model (i.e. that  $w_{RR}$  and  $w_{LL}$  should be positive for short distances and negative for longer ones, with the reverse being true for  $w_{RL}$  and  $w_{LR}$ ) were also tried, and performed equally well (to the extent that the patterns produced were visually similar). These included, for example: a 'top hat' function, for which  $w_s = 1$  for  $r \leq 2$ , and  $-1$  for  $6 > r > 2$ , with  $w_0 = -w_s$ ; combinations of two exponential (rather than Gaussian) functions; and solutions to a steady state



diffusion equation (as outlined in appendix 2). In appendix 1 mathematical arguments are given that suggest why this should be so.

### 3. RESULTS

When the model is put into action in the form of a computer program, patterns like that shown in figure 4 develop. Figure 3 shows the functions  $w_s$  and  $w_o$  used to generate the pattern. As the inputs are changed with successive iterations of the program, the initial randomness disappears; blotches and stripes develop, and these eventually organize into a pattern of branching stripes that is stable to repeated further iterations of the program. These are remarkably similar to those observed in the monkey, and, on a small scale, almost every feature present in the pattern in the monkey can be observed in the artificial stripes. Further points of resemblance are that in both types of pattern stripes often narrow in width at branch points (a feature that can be observed in other patterns, such as mackerel and zebra stripes), and both types of stripe may show fluctuations in width along the length of the stripe. When this occurs the fluctuations tend to have the same periodicity as the spacing of the stripes. (Neither of these features is evident in the reconstruction of figure 1, but they can be seen in autoradiographs, e.g. fig. 8*b* in Hubel *et al.* (1978).) One difference between the two types of pattern is that the computer stripes are usually less constrained in the degree to which they take on a predominant local orientation, i.e. they change direction more frequently than do ocular dominance stripes. A possible reason for this is considered in section 4.

A wide variety of forms of  $w_s$  and  $w_o$  leads to the formation of stripes. The principal restriction on the possibilities is derived from the requirement that the values of  $s_R$  and  $s_L$ , averaged over space, should be close to zero. If this is so, then the average rates of growth of  $n_R$  and  $n_L$  will also be close to zero. This requirement will be satisfied if  $\bar{w}_s + \bar{w}_o \approx 0$ , where  $\bar{w}_s$  and  $\bar{w}_o$  represent the averages of  $w_s$  and  $w_o$  over space (i.e. the volumes under the functions). If  $\bar{w}_s + \bar{w}_o \ll 0$  the inputs will disappear everywhere; conversely, if  $\bar{w}_s + \bar{w}_o > 0$  segregation will fail to occur and the inputs will be distributed everywhere. This latter behaviour is interesting in view of the fact that within layer IVc of some New World species of monkey both left and right eye inputs are uniformly distributed (Hendrickson *et al.* 1978; Hendrickson & Wilson 1979). Also interesting is that, if  $\bar{w}_s + \bar{w}_o < 0$ , narrow

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FIGURE 4. A pattern of stripes produced by a computer. Figures give the age of the pattern in program iterations. A point is displayed wherever the input from a given eye predominates over the other. In the final pattern more than 97% of the points are occupied exclusively by input from one eye. The number of such points increases most rapidly between the 80th and 160th iterations of the program, which for a monkey would probably correspond to a period shortly after birth. For this pattern a constant total density of synapses was assumed, with  $w_s (= -w_o)$  given by equation (6), with  $A = 0.3$ ,  $B = 1.0$ ,  $d_1 = 5.0$ ,  $d_2 = 1.4$  and  $h = 3.7$ .

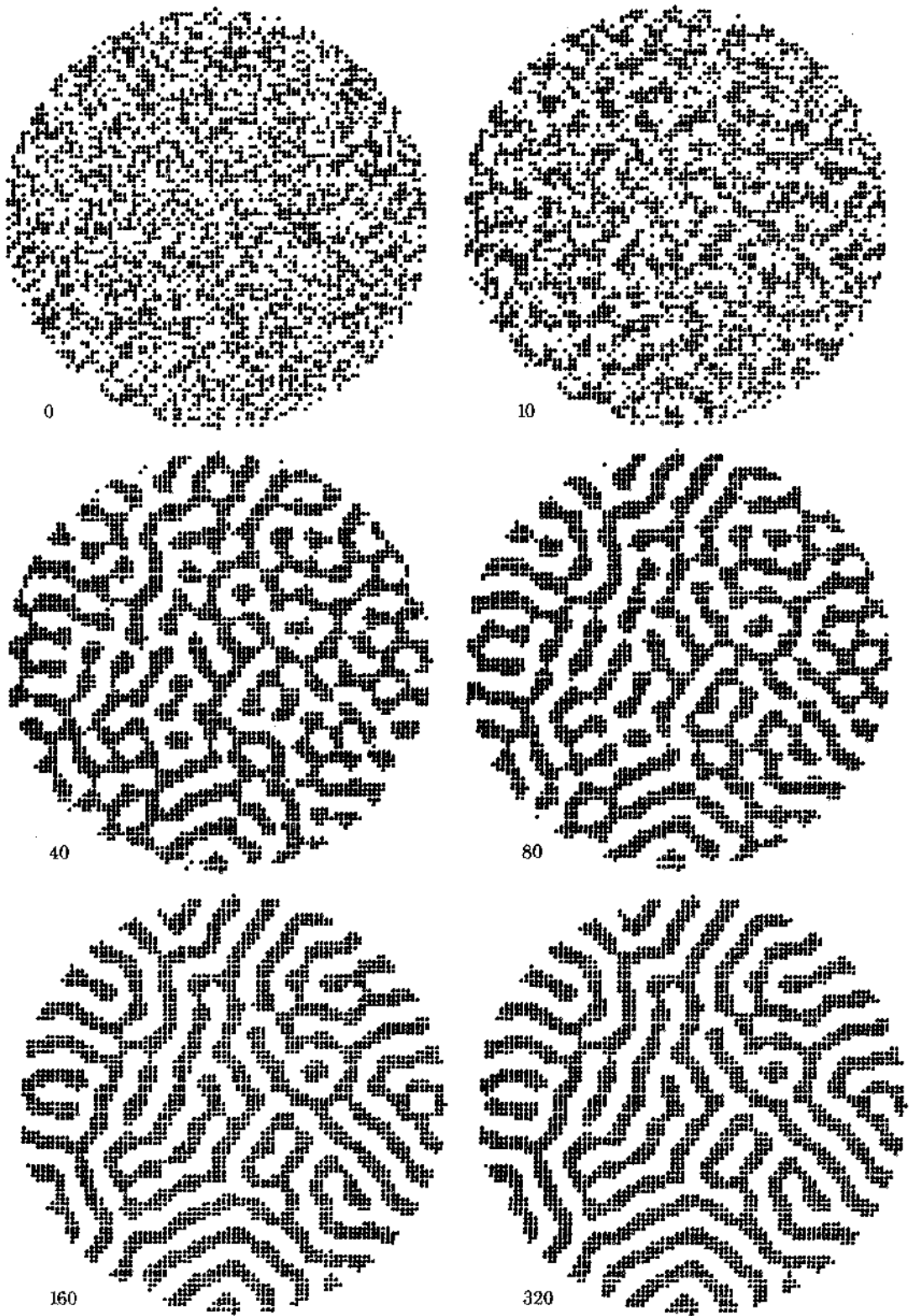


FIGURE 4. For description see opposite.

uniform gaps appear between the stripes. This may actually be the case in the macaque monkey, since silver stains reveal a lower density of fibres at points of transition between left and right eye-dominated cortex (LeVay *et al.* 1975). If  $\bar{w}_s = -\bar{w}_o$  (as is necessarily the case when the total density of synapses is constant) then the restrictions on the possible shapes that the functions can take will be least severe (see appendix 1 for further discussion of this). For example, both  $w_s$  and  $w_o$  can be zero within region E (implying an absence of short range effects), provided that  $w_o$  is positive in region I and  $w_s$  negative. It is also possible for  $w_s$  to be zero everywhere (implying that competition only occurs between synapses of opposite eye type), provided that  $\bar{w}_o \approx 0$ .

If the magnitudes of  $w_s$  and  $w_o$  are small in region E and large in I, then the stripes become more regular in width, and branch less frequently: H formations disappear and the tendency to narrow at branch points becomes pronounced. If the converse is true, and the magnitudes of  $w_s$  and  $w_o$  are large in E and small in I, then the stripes become irregular in width and branch frequently. If both functions are zero in region I (i.e. if long range interactions are absent) then segregation occurs in the form of large irregular patches.

Departures from radial symmetry in  $w_s$  and  $w_o$  alter the directions in which the stripes run. If region E is elongated there is a marked tendency for the stripes to run in the direction of elongation; if I is elongated then the stripes run perpendicular to this direction. This has an interesting consequence for points near the boundaries of the array, where the parts of regions E and I that extend over the boundary no longer have any determining effect on the behaviour of the stripes. Region I is effectively elongated and, as a result, the stripes in this region become orientated in a direction perpendicular to the border (figure 4). This is a striking feature of the stripes in the monkey, as well as those of zebras and mackerel.

#### 4. EFFECTS OF GROWTH OF THE CORTEX

It is interesting to consider the possible effects of growth of the striate cortex as a whole on stripe morphology. The striate cortex presumably enlarges substantially in area during the weeks before birth, when the columns are beginning to form, while an increase in area of about 20% is known to occur between birth and adulthood (Hubel *et al.* 1977). The periodicity of the columns is less in pre-natal monkeys than in adults (Rakic 1976), which suggests that the space constants of the interaction simply enlarge in parallel with the expansion of the cortex. However, if growth of the cortex is anisotropic, i.e. if there is an overall expansion in one direction, while the interactive forces between synapses remain radially symmetric, then there could be effects on the direction in which the final stripes run. This expectation was confirmed by simulations where the array in which the stripes were forming was slowly elongated (figure 5). The effects on the stripes are pronounced and clearly not due to a simple stretching of the pattern. The

stripes always run in the direction of the expansion, and this is unaffected by changes in the shapes of  $w_s$  and  $w_o$ . It is likely that any anisotropy in the expansion of the cortex during growth will be similar over rather large areas of cortex, and this may perhaps contribute to the observed uniformities in the orientations of the stripes.

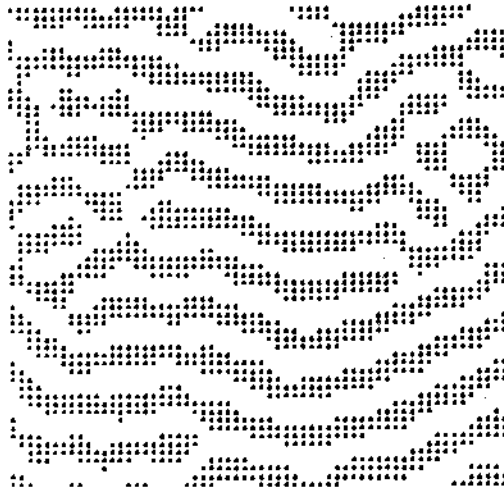


FIGURE 5. The effect of simulating a unidirectional expansion of the cortex while the stripes form. The functions  $w_s$  and  $w_o$  remain unchanged in shape while this happens. The array was expanded in the horizontal direction by 20%, and this expansion was completed before the period of peak turnover of synapses. For this pattern  $n_R$  and  $n_L$  could vary independently;  $w_s$  was given by equation (6), with  $A = 1.0$ ,  $B = 0.9$ ,  $d_1 = 3.0$ ,  $d_2 = 10.0$ , and  $h = 0$ ; for  $w_o$ ,  $A = -1.0$ ,  $B = -1.0$ ,  $d_1 = 4.0$ ,  $d_2 = 10.0$ , and  $h = 0$ .

### 5. MONOCULAR DEPRIVATION

It is natural to suppose that these effects result from a change in the relative effectiveness of the two eyes in determining the rates of growth of cortical synapses, i.e. that  $w_{RR} \neq w_{LL}$  and  $w_{RL} \neq w_{LR}$ , and that these changes will consist in a reduction of (a) the ability of the deprived eye to inhibit the local growth of opposing normal eye synapses and/or (b) the extent to which growth of deprived eye synapses cooperatively encourages similar local growth. These are both reductions in the magnitudes of short-range effects, i.e. those taking place within region E, so that this explanation is essentially the same as that proposed by Hubel *et al.* (1977). The alternative possibility is that interactions due to the deprived eye are increased in strength in region I, but this seems less likely, though the immediate consequences would be the same.

When such changes are made in the model, either at the start of, or during, segregation, the normal eye enlarges its territory at the expense of input from the 'deprived' eye. Two types of change can occur: if deprivation takes place before

the main features of the final pattern have emerged, circular islands of label, which have about the same width and spacing as normal stripes, are left embedded in a complementary pattern of input from the normal eye; however, if the stripes are induced to take on a predominant local orientation, e.g. by elongating the

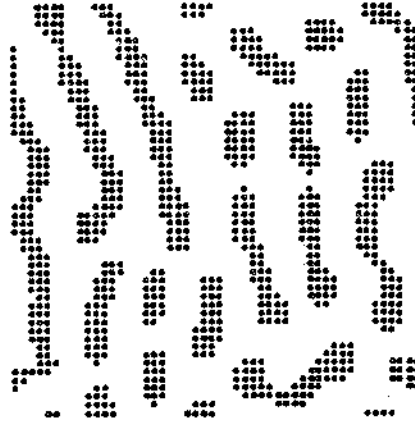


FIGURE 6. Simulated monocular deprivation. A constant total density of synapses was assumed, so that  $n_R = n_L$ ;  $w_{RR} = -w_{RL}$  and  $w_{LL} = -w_{LR}$ . The magnitudes of the central parts of the functions  $w_{RR}$  and  $w_{RL}$  were reduced by about 70% during the period of maximum turnover of synapses. Following this the functions were restored to their normal value while segregation continued to completion. The stripes were constrained to run in a uniform direction by slowly expanding the array during the earliest stage of segregation. This was complete by the time deprivation was started. Before and after the deprivation,  $w_{RR}$  and  $w_{LL}$  were given by equation (6), with  $A = 1.0$ ,  $B = 0.31$ ,  $d_1 = 3.0$ ,  $d_2 = 10.0$ , and  $h = 0.0$ ; for the period of deprivation,  $w_{RR}$  and  $w_{RL}$  were altered by reducing the value of  $A$  to 0.5.

array in which they form, or if the deprivation is initiated at a late stage in segregation, then the deprived stripes narrow in width while the normal ones expand (figure 6).

The model itself has a critical period for these effects (figure 7), which coincides with the period of segregation. Such a relation is implied by equation (4), and thus in turn by the physiological assumptions on which this equation is based. In the model, segregation will be complete when  $n_R$  and  $n_L$  are everywhere either zero or equal to  $N$ . When this is the case the pattern is stable to changes in the value of  $s(\mathbf{r})$  produced when the functions  $w_{RR}$  etc. are altered, since  $f(n) = n(N - n) = 0$  everywhere, and  $\partial n / \partial t = s(\mathbf{r})f(n)$ .

Further simulations have shown that the model behaves in a way suggested by the results of Movshon & Blakemore (1974), Movshon (1976) and Blakemore *et al.* (1978): the effects of initial deprivation can be reversed by reversing the changes made to the two eyes (so that the initially deprived eye is normal, and vice versa), if these changes are made before segregation is complete. The effect

is much less if equality is merely restored to the two eyes after the deprivation (cf. Hubel 1978): the extent to which 'binocular vision' is effective in reversing initial deprivation depends on the initial values of  $\bar{w}_s$  and  $\bar{w}_o$  (see appendix 1); if the values are close to zero then the procedure may have very little effect.

Simulated binocular deprivation has the effect of delaying segregation and thus prolonging the critical period of the model (figure 7).

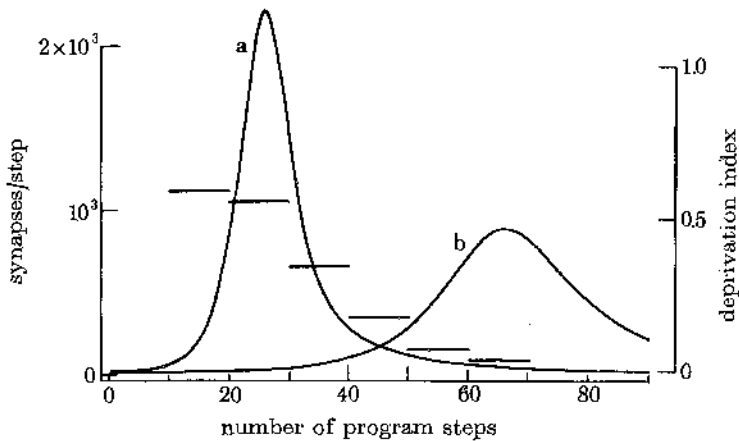


FIGURE 7. The effects on segregation of simulated monocular and binocular deprivation as a function of time. The two curves show how the total turnover of synapses changes (a) normally and (b) during binocular deprivation. The horizontal bars indicate periods of simulated monocular deprivation; their height indicates the magnitude of the effects, produced on a scale from 0 to 1; 0 indicates equality in the total number of left and right eye synapses; 1 indicates complete absence of one type of synapse.

## 6. WHY DO STRIPES FORM?

Since there is no way of predicting with certainty, other than by computer simulation, that equations (1)–(4) have a solution that is a pattern of stripes, no satisfactory answer can be given to this question at present. However, qualitative arguments can be given that at least make the result seem plausible. In appendix 1, I give quantitative arguments for supposing that the resulting pattern will have a well defined periodicity determined by the form of  $w_s$  and  $w_o$ , but no firm conclusions about what form the pattern will take can be drawn from these arguments.

Suppose that the values of  $n_R$  and  $n_L$  are the same everywhere, with no initial variance, and, for simplicity, suppose that  $w_s = -w_o$ . Then  $s_R$  and  $s_L$  will be zero everywhere, and growth will be absent. The system is now in an unstable equilibrium. Suppose that at one point the value of  $n_R$  is increased by a small amount. Within a surrounding region the size of E,  $s_R$  will become positive and  $s_L$  negative, while in the surrounding annular region I,  $s_R$  will be negative and  $s_L$  positive.

This therefore will induce growth of  $n_R$  in a spot surrounding the point of initial increase, and growth of  $n_L$  in a ring surrounding the spot. This in its turn will induce the growth of  $n_R$  in a surrounding ring, and the final pattern will be a set of alternating concentric rings of  $n_R$  and  $n_L$ . A more complicated initial disturbance will of course lead to a more complicated final pattern, but it is reasonable to suspect that alternating stripes will also be present.

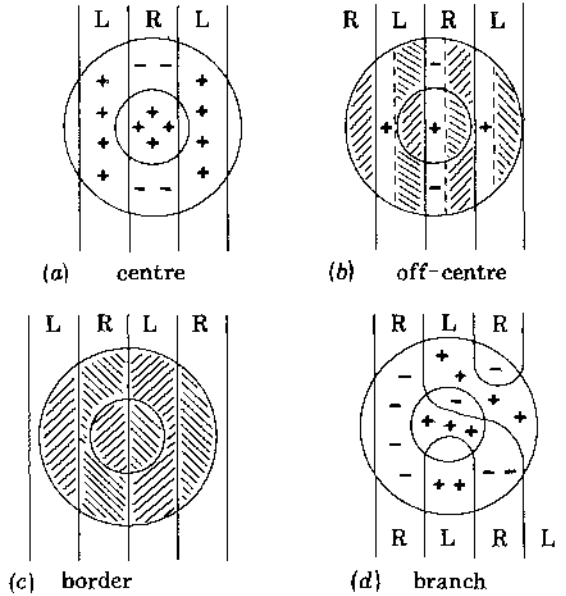


FIGURE 8. This illustrates the stability of a final pattern of stripes and branches, where segregation is complete and  $n_R$  and  $n_L = 0$  or  $N$  everywhere. Shaded areas represent regions from which contributions to the values of  $s_R$  and  $s_L$  cancel by symmetry. See text for further explanation.

A second argument is based on the fact that segregation divides the area that the inputs initially occupy into two regions, each of which is half of the initial area. Given that the same rules apply to both eyes, both regions should possess the same topological properties. This is true for a pattern of branching stripes, but not for alternative divisions into two equal areas, for example, into a set of disconnected spots embedded in a complementary honeycomb-like matrix.

It is possible to show diagrammatically that stripes, including branches, are a possible stable solution of equations (1)–(3). Figure 8 illustrates this. The requirement for stability is that the result of the operation defined by equations (1) and (2) should yield a value of  $s_R$  that is positive wherever right eye input is present, and a value of  $s_L$  that is similarly positive wherever left eye input is present. Figure 7a shows the contributions from surrounding left and right eye synapses to the value of  $s_R$  in the centre of the stripe. The two concentric circles represent regions E and I; within E, right eye synapses make a positive contribution to

$s_R$ ; outside  $E$ , left eye synapses occupy the larger part of the area of  $I$ , and so the contribution from  $I$  to the value of  $s_R$  is positive overall. Thus  $s_R$  is large and positive in the centre of a right eye stripe. The remainder of the figure illustrates, in turn, how  $s_R$  remains positive near the edge of a stripe, is zero at the edge of a stripe, and is still positive in the centre of a branch. This final part of the figure illustrates the effect of the magnitude of the centre weighting on the morphology of the branches: an  $H$  configuration in the right eye input would not be stable unless the centre weighting was large enough to overcome the extra inhibition produced by joining the two adjacent right eye stripes.

## 7. DISCUSSION

The essential ideas of this paper can be expressed simply but adequately as two rules of interaction between left and right eye synapses: (1) if synapses of one eye type predominate locally, i.e. within a circular region about 200  $\mu\text{m}$  in diameter, that type of synapse will increase in number at the expense of the other type; however, (2) this increase will be reduced or reversed if the same type of synapse predominates in a surrounding annular region 200–600  $\mu\text{m}$  distant. These rules can be used to provide an explanation for pattern formation in other systems, such as the zebra, and in appendix 2 a brief account of this application of the model is given. In addition to accounting for the normal morphology of ocular dominance stripes, the model lends itself to a simple explanation for the effects of monocular deprivation and for the existence of a critical period for these effects. The explanation for monocular deprivation is similar to that proposed by Hubel *et al.* (1977): the deprived eye is presumed to lose its effectiveness in determining rates of growth locally. The critical period can be explained if it is assumed that lateral growth of terminals does not occur, and that some factor such as a limited availability of postsynaptic sites reduces the competitively induced rate of growth of synapses as their density approaches a maximum.

There are similarities between this mechanism and other models that have been put forward to explain ocular dominance column formation (Malsburg & Willshaw 1976; Malsburg 1979). These are less general in scope than the present model and, consequently, make more assumptions about the properties of cortical neurons and their inputs. One of the models (Malsburg & Willshaw 1976) invokes features such as short range excitatory and long range inhibitory connections between cortical neurons, anticorrelations in the impulse activity of the two retinas, spatially correlated retinal inputs, and Hebb synapses in the cortex. The other model (Malsburg 1979) postulates the existence of local similarities in sets of presynaptic chemical markers that are transported via synapses into their postsynaptic cells, through which they propagate laterally. Synapses are then strengthened or weakened on the basis of similarity in the pre- and postsynaptic sets of markers. Computer simulations show that these assumptions are sufficient



to account for the segregation of inputs into alternating stripes, although it has not been shown that other features, such as branches or boundary-induced changes of direction, can be reproduced. It seems probable though that both models will lead to interactions between synapses that are similar in kind to those postulated here. The models are valuable, therefore, in providing possible physiological interpretations of the more general rules in this paper.

Other theories of pattern formation, based on diffusion (Turing 1952) and autocatalytic production of activator and inhibitor substances (Gierer & Meinhardt 1972; Meinhardt & Gierer 1974), have not so far been successfully applied to patterns of the sort discussed here (see Bard & Lauder 1974; Bard 1977). Despite this, these models are not conceptually dissimilar from the present one. The idea of short-range activation coupled to a longer-range inhibition is used by Gierer & Meinhardt in a very similar way, while if the present model is interpreted in terms of a diffusion mechanism (see appendix 2) there are considerable resemblances with Turing's theory, since the diffusion of two substances with different diffusion constants and/or inactivation rates is involved. The differences may lie more in the way in which certain constraints are built into the present theory, an important one being that diffusional gradients (if part of the mechanism) should always be at, or close to, equilibrium.

Despite the general form of the model, it does have a number of predictions to make. Most of these derive from experimental results showing that monocular deprivation, if it occurs while the columns are in the process of segregation, alters the morphology of the stripes from both eyes, the normal eye enlarging its territory at the expense of the deprived eye. A consequence of the explanation proposed for this effect, that for, e.g. right eye deprivation, the central regions of  $w_{RR}$  and  $w_{RL}$  become reduced in magnitude, is that binocular deprivation will delay the overall rate of segregation (see figure 7). Another consequence of binocular deprivation, if it reduces the magnitudes of all the functions  $w_{RR}$  etc. in their central regions, is that the final pattern of stripes will be abnormal, with a reduced incidence of H formations and an increased tendency for stripes to narrow at branch points (see section 3). At present there is no anatomical evidence that relates to either of these possibilities.

A related prediction concerns the correspondence between the period of segregation and the critical period. Such a correspondence is implicit in the model (providing an alternative to the explanation suggested by Kasamatsu & Pettigrew (1976)) and is observed experimentally (Hubel *et al.* 1977; LeVay *et al.* 1978). Binocular deprivation, therefore, if it prolongs segregation, should also prolong the critical period. Indirectly, behavioural (Timney *et al.* 1978) and electrophysiological evidence (Cynader 1979) obtained from the cat supports this prediction: the effects of monocular deprivation, judged by loss of visual acuity or by loss of cortical neurons driven by the deprived eye, are much more severe in cats reared for 10 months in the dark than in normal animals of that age. Con-

versely, any procedure that accelerates segregation (strabismus seems a likely candidate for this) should shorten the critical period.

It has been suggested by Mitchell *et al.* (1978) that a competitive mechanism cannot solely determine the effectiveness of the two eyes in driving cortical neurons, since an initially deprived eye can regain its influence on cortical neurons as a result of a subsequent period of binocular visual experience. During this period neither eye can have a competitive advantage over the other, and thus, it is argued, other factors must operate to restore equality of input. However, a competitive mechanism can explain this behaviour (see appendix 1). Given equality in the behaviour of the two eyes, the system described by equations (1)–(4) has a natural equilibrium in which the two eyes are equally represented; eye closure causes the system to tend to a new equilibrium, but restoration of equality to the two eyes restores the equilibrium to its initial value, to which the system can return. (However, under certain conditions, discussed in appendix 1, the time course of this return may be prolonged.) Another way of putting the argument would be to say that even if both eyes are open, one eye can effectively be at a competitive disadvantage if it maintains a greater than normal density of terminals in the cortex (which would be the case after monocular deprivation).

A word may be said about the pattern of ocular dominance columns in the cat. These develop, like those of the monkey, from an initially overlapping and even distribution of synapses (LeVay *et al.* 1978). At an intermediate stage of segregation, the density of the projections (measured from grain counts in radioautographs) fluctuates roughly sinusoidally (in agreement with the prediction of the linearized approximation to the model discussed in appendix 1). However, in the adult cat the distribution is still roughly sinusoidal, though with some degree of flattening of the peaks and troughs of the distribution. This contrasts with the square-wave pattern seen in the monkey, which the model explains by the assumption that the upper limits to synaptic density are set by some very local constraint, e.g. the density of available postsynaptic sites, which is presumably uniform throughout the cortex. A possible explanation for the difference between the two species could be that in the cat the limits to synaptic growth are not set by local constraints but by some other factor, for example, the density of incoming fibres. If it is these that have a square-wave distribution, then the boundaries of the columns estimated from counts of synaptic density would not be sharp, since a single fibre can distribute synapses throughout a surrounding region of cortex that is several hundred micrometres in diameter (Ferster & LeVay 1978).

The ocular dominance columns of cats and monkeys are not the only examples in which the neural inputs to a structure have a periodic, or stripe-like, distribution. In the rhesus monkey, for example, inputs to the frontal association, limbic and motor cortices (Goldman & Nauta 1977*a*), the caudate nucleus (Goldman & Nauta 1977*b*), the putamen (Künzle 1975) and the colliculus (Hubel *et al.* 1975) all show periodic fluctuations in density, and form patterns of stripes

or disconnected spots, or a complementary pattern of nearly continuous input interrupted by gaps. Similar patterns can be found in the cat colliculus (Graybiel 1975, 1978*a, b*) and can be induced artificially in the tecta of three-eyed frogs (Constantine-Paton & Law 1978). As described in section 5, the model can reproduce this range of patterns; whether spots, gaps or stripes are formed depends on the degree of asymmetry in the behaviour of the two competing inputs (i.e. the extent to which  $w_{RR} \neq w_{LL}$  and  $w_{RL} \neq w_{LR}$ ). If the hypothesis put forward in this paper is correct, it may be that all of these patterns develop as a result of competitive interactions that involve effects taking place over distances comparable with the periodicity of the pattern. Similar interactions may, in fact, be implicated wherever striped patterns with the morphological properties discussed here are found in nature.

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#### APPENDIX 1

Here, the behaviour of a linear approximation to the model is considered, for the case where the total density of right and left eye synapses remains constant, that is,  $n_R + n_L = N$  everywhere. Since  $n_R$  and  $n_L$  do not vary independently, it is convenient to use the single variable  $a = n_R - n_L$  to represent synaptic density; thus,  $n_R = (N + a)/2$  and  $n_L = (N - a)/2$ . Since neither  $n_R$  nor  $n_L$  can have negative values,  $a$  can have a range of values between  $-N$  and  $N$ . Since  $n_R + n_L$  is constant,  $\partial n_R / \partial t = -\partial n_L / \partial t$ , which implies that  $w_{RR} = -w_{RL}$  and  $w_{LL} = -w_{LR}$ . Equations (1)-(4) then reduce to

$$\partial a / \partial t = (a * w + K) (N - a) (N + a), \quad (7)$$

where  $w = w_{RR} + w_{LL}$  ( $= -w_{RL} - w_{LR}$ ), and  $K = N^*(w_{RR} - w_{LL})$ , a constant, which, except during monocular deprivation, when  $w_{RR} \neq w_{LL}$ , will be zero.

At the start of segregation,  $n_R \approx n_L$  everywhere, and thus  $a \approx 0$ . For small deviations of  $a$  from zero,  $(N - a) (N + a) \approx N^2$ , and so

$$\partial a / \partial t \approx N^2(a * w + K). \quad (8)$$

This equation can be solved by transformation into Fourier space, and this allows one to deduce the conditions that  $w$  must satisfy if a spatially periodic pattern is to be generated. Denoting the transforms of  $a$  and  $w$  by  $A(v)$  and  $W(v)$  respectively, where  $v$  is frequency, and assuming equality of the two eyes, so that  $K = 0$ , equation (8) transforms to give  $\partial A / \partial t = N^2 A W$ , which has the solution  $A = A_0 \exp(N^2 W t)$ , where  $A_0$  is the transform of  $A$  at time  $t = 0$ . If  $A$  is initially randomly distributed, all frequencies will initially be present in  $A_0$ .

The effect of multiplication by  $\exp(N^2Wt)$  is to cause one of these frequencies, that for which  $W$  is a maximum, to predominate over others. The ratio in the amplitudes of two frequencies  $\nu_1$  and  $\nu_2$  is  $A(\nu_1)/A(\nu_2) = \{A_o(\nu_1)/A_o(\nu_2)\} \exp\{W(\nu_1) - W(\nu_2)\}t$ . This ratio tends to infinity as  $t \rightarrow \infty$  for arbitrarily small positive difference between  $W(\nu_1)$  and  $W(\nu_2)$ , provided that  $A_o(\nu_1) \neq 0$ . Thus, provided that  $W$  has a positive and single-valued maximum, a single frequency should predominate in the final pattern. It seems reasonable to suppose that the effect of the nonlinearities that have been neglected is mainly to introduce higher harmonics of this frequency, which cause the sharp transitions present in the final pattern. Calculations have confirmed that the maximum of  $W(\nu)$  does accurately predict the periodicity of the computed stripes.

This analysis suggests that the existence of a positive maximum in the Fourier transform of  $w$  is a sufficient condition for the formation of a pattern characterized by the existence of a predominant spatial frequency. This requirement will clearly be satisfied by a large class of functions, with the exception of those where the maximum is at zero frequency, implying an absence of periodicity in the final pattern. These exceptions probably include most, if not all, of those functions whose shape could be interpreted to imply the existence of only one type of short-range interaction between synapses, rather than the two postulated here.

The response of the system described by equation (8) to changes in  $w$  and  $K$  resulting from monocular and binocular deprivation can also be predicted. Here, one is interested in the value of  $a$  averaged over space,  $\bar{a}$ , which gives a measure of the preponderance of one eye's input over the other. Integrating both sides of equation (8) over space gives  $\partial\bar{a}/\partial t = N^2(\bar{a}\bar{w} + K)$ , which has the solution

$$\bar{a} = \bar{a}_0 \exp(N^2\bar{w}t) + (K/\bar{w}) [\exp(N^2\bar{w}t) - 1], \quad (9)$$

where  $\bar{a}_0$  is the space average of  $a$  at time  $t = 0$ . Note: that in either normal vision or binocular deprivation,  $K = 0$ ; that deprivation of either, or both, eyes will make  $\bar{w}$  more negative (since the central positive regions of  $w_{RR}$  and  $w_{LL}$  are reduced in magnitude); and that  $K$  will be negative for right-eye deprivation and positive for left-eye deprivation. For positive values of  $\bar{w}$  the initial equilibrium  $\bar{a}_0$  is unstable; this suggests that in reality  $\bar{w} \leq 0$ . For the case in which  $\bar{w} < 0$ , the system tends to a stable equilibrium  $\bar{a} = -K/\bar{w}$ . The larger the magnitude of  $\bar{w}$ , the faster this equilibrium is reached. For  $K = 0$ ,  $\bar{a} = 0$ , i.e.  $\bar{n}_R = \bar{n}_L$ , with an equal representation of both eyes. If  $K$  is made negative (i.e. for right eye deprivation), the equilibrium value of  $\bar{a}$  becomes negative, i.e.  $\bar{n}_R < \bar{n}_L$ . The change will be reversed by making  $K$  positive (i.e. by subsequent monocular left-eye deprivation) or by restoring  $K$  to zero (i.e. by opening both eyes). This latter effect will have a slower time course than reverse suturing, however, because  $\bar{w}$  will be less negative after reopening, and terms in  $\exp(N^2\bar{w}t)$  in equation (9) will tend to zero more slowly. If  $\bar{w}$  is normally close to zero, then reopening can be

expected to be almost without effect. Electrophysiological studies suggest that this is so in the monkey (Hubel 1978) but not in the cat (Mitchell *et al.* 1977; Olson & Freeman 1978).

#### APPENDIX 2

The model can be generalized to account for pattern formation in other systems. For example, the functions  $w_s$  and  $w_o$  can be related to effects on growth or differentiation produced by the diffusion of active substances secreted by the cell types that constitute the pattern. Suppose that at the start of development presumptive elements of the final pattern (e.g. black pigment cells, or their precursors) are scattered randomly over a two-dimensional surface, with a density  $n(\mathbf{r})$ . Suppose that each cell releases into its surroundings a growth-stimulating substance with a short range of effect (due to a low rate of diffusion, or rapid inactivation) and an inhibitory substance with a longer range of effect. The effects on growth due to each cell will vary with distance from the cell and, at equilibrium, can be described by a function  $w(\mathbf{r}) = C_E - \beta C_I$ , where  $\beta$  is a positive constant and  $C_E$  and  $C_I$  are concentrations of the stimulating and inhibitory substances respectively;  $w(\mathbf{r})$  will then be positive for short distances and negative for longer ones. Provided that growth is slow compared to the time course of equilibrium by diffusion, growth at any point will be given by

$$\partial n(\mathbf{r})/\partial t = f(n) n(\mathbf{r}) * w(\mathbf{r}), \quad (10)$$

where  $f(n)$  describes the response of the cells to a stimulus to grow. When two interacting cell types are present, the equations describing the system are the same as those proposed for ocular dominance stripe formation. However, the simpler system described by equation (10) yields similar patterns (as the resemblance to equation (7) would suggest). Computer solutions have been obtained with  $f(n)$  given by equation (3), with  $n$  initially normally distributed about means varying in different instances from  $0.1N$  to  $0.9N$ , and with  $C_E$  and  $C_I$  obtained as equilibrium solutions to the steady-state diffusion equation  $D d^2C/dr^2 = kC$ , where  $D$  is the diffusion constant and  $k$  is the rate of removal or inactivation of  $C$ , and with a constant source of  $C$  at  $r = 0$ . Depending on the values of  $D$ ,  $k$  and  $\beta$  used, the patterns formed range from small, disconnected spots to branching, regularly spaced stripes with the appearance and properties of the stripes already described.

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