

The influence of neural activity and intracortical connectivity on the periodicity of ocular dominance stripes

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Received 26 March 1998, in final form 1 June 1998

Abstract. Several factors may interact to determine the periodicity of ocular dominance stripes in cat and monkey visual cortex. Previous theoretical work has suggested roles for the width of cortical interactions and the strength of between-eye correlations. Here, a model based on an explicit optimization is presented that allows a thorough characterization of how these and other parameters of the afferent input could affect ocular dominance stripe periodicity. The principle conclusions are that increasing the width of within-eye correlations leads to wider columns, and, surprisingly, that increasing the width of cortical interactions can sometimes lead to narrower columns.

1. Introduction

In cats, monkeys and humans, layer 4 of the primary visual cortex (V1) is divided up into alternating regions dominated by input from the left and right eyes (e.g. Hubel and Wiesel 1977). These regions segregate from a spatially uniform pattern during development (Rakic 1976, LeVay *et al* 1978). A characteristic feature of the segregated pattern is its strongly regular periodicity. Which biological variables determine this periodicity?

Recent experimental data suggest a role for the correlational structure of neural activity. Löwel (1994) showed that kittens raised with divergent strabismus have wider ocular dominance stripes than normal kittens. Comparison of the patterns of ocular dominance stripes in normal squirrel monkeys seen by Horton and Hocking (1996a) with those in strabismic squirrel monkeys seen by Livingstone (1996) reveals substantially wider stripes in the strabismic case. Tieman and Tumosa (1997) compared the periodicity of ocular dominance stripes in kittens raised with alternating monocular exposure (AME) with normal kittens, and found that the AME group had wider stripes, though to a lesser degree than in the strabismic case. The crucial parameter that is altered in all these cases is that the strong correlations normally present between activity in the two eyes are reduced. This effect of between-eye correlations on stripe periodicity was first explicitly predicted for the strabismic case by Goodhill (1993) (see also Goodhill and Willshaw 1990), though it was also implicit in the elastic net model of Goodhill and Willshaw (1990), and has since been observed in several other models (e.g. Sirosh and Miikkulainen 1997). Recent preliminary data have also suggested an influence on stripe periodicity of the spatial extent of lateral connections in the cortex (Hensch and Stryker 1996). Such an effect was previously observed in many models, for instance those of Swindale (1980), Miller *et al* (1989), Goodhill (1993), and

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the elastic net (Dayan 1993). For comprehensive reviews of models, see Erwin *et al* (1995) and Swindale (1996).

Despite this apparently good match between theoretical models and experimental findings, a more extensive theoretical investigation of the ways in which correlated activity could combine with intracortical connections to determine stripe periodicity has not been performed. One problem with attempting a thorough characterization of the parameter space is that in so-called high-dimensional models, such as Miller *et al* (1989) and Goodhill (1993), segregation is often quite sensitive to the parameters. For instance, as shown by Bauer *et al* (1997), there are combinations of between-eye correlation strengths and cortical interaction widths for which segregation fails in a model like that of Goodhill (1993), and thus the periodicity that would result in this case cannot be determined (see also Dayan and Goodhill 1992). By contrast, in so-called low-dimensional or feature space models, such as those of Goodhill and Willshaw (1990) and Obermayer *et al* (1992), segregation is more or less guaranteed. A different problem, however, arises: these models do not allow arbitrary variations in the correlational structure of the inputs. The only degree of freedom is the position of feature points, and so, for instance, the spatial extent of within-eye correlations cannot be altered independently of the spatial extent of different-eye correlations (for further discussion see Goodhill *et al* 1996).

An alternative approach which avoids these problems, though limited in other ways to be described, is one based on a more abstract optimization principle. A qualitative argument in the experimental literature, formalized by Jones *et al* (1991), has been that the ocular dominance map is an attempt to optimally trade off competing desires: for neighbouring points within each eye to be represented nearby in the cortex, and for corresponding points between the two eyes to also be represented nearby in the cortex. Since the most correlated inputs are expected to be neighbouring points in one eye and corresponding points between the two eyes, this argument can be expressed more generally in the terms that highly correlated inputs should be represented close together. However, with rare exceptions such as the model of Jones *et al* (1991), which was concerned with the overall map and took stripe periodicity to be fixed, an explicit optimization of an objective function measuring this trade-off has not been theoretically explored. This is understandable: such a model puts forward no mechanism to explain how the optimization is performed biologically, it addresses only the outcome of the segregation process rather than the dynamics of segregation itself, and such an optimization presents a severe computational challenge. The tendency in the theoretical literature has rather been to investigate biologically motivated mechanisms that are more computationally tractable. However, this is at the expense of the limitations described above, and leaves open many questions regarding how certain parameters interact to determine ocular dominance stripe periodicity.

In this paper a one-dimensional optimization model is used to thoroughly characterize the effects of four parameters on ocular dominance stripe periodicity. These are: the spatial extent of within-eye correlations, the spatial extent of between-eye correlations, the strength of between-eye correlations relative to within-eye correlations, and the spatial extent of lateral interactions in the cortex. Effects of some of these parameters alone have been explored in particular models as discussed above. The present complete investigation of this four-dimensional parameter space in an optimization framework reproduces some of these results. However, it also reveals that there are parameter regimes where surprising effects can occur: for instance, domains where *increasing* the extent of lateral connections *decreases* the width of stripes. This characterization also leads to specific novel predictions regarding the outcome of particular rearing paradigms on ocular dominance stripe periodicity. In particular, the model predicts that dark-reared, binocularly deprived

and strabismically-reared kittens should all have slightly different ocular dominance stripe periodicities, due to the different spatial statistics of retinal activity that each of these rearing paradigms entail.

2. Optimization model

2.1. Objective function

The objective function optimized is the C measure introduced by Goodhill *et al* (1995) (see also Goodhill and Sejnowski (1996, 1997)). This is defined as follows:

$$C = \sum_{i=1}^N \sum_{j<i} F(i, j)G(M(i), M(j)) \quad (1)$$

where i and j label points in the input space of retinal points (N in total), and M is the mapping to the cortex so that $M(i)$ and $M(j)$ label the cortical cells which represent input points i and j respectively. $F(i, j)$ gives the similarity between points i and j in the input space, and $G(M(i), M(j))$ gives the similarity between the representations of those features in the cortex. It can be shown that, if a perfectly topographic mapping from the input space to the output space exists, then maximizing C will find it (Goodhill *et al* 1995). The C measure provides a way to unify several different approaches to topography, which can then all be interpreted in this common framework simply as different choices of the F and G functions. Approaches falling in this class (see Goodhill and Sejnowski (1996, 1997) for further details) include the elastic net, Kohonen's (1982) self-organizing map (via the quasi-objective function for this algorithm introduced by Luttrell (1990, 1994)), the generalization of Luttrell's objective function proposed by Mitchison (1995), the model of Miller *et al* (1989) (see section 5), metric multidimensional scaling (Torgerson 1952), minimal wiring (Durbin and Mitchison 1990), and dynamic link matching (Bienenstock and von der Malsburg 1987a, b). The C measure is thus an appropriately general function to optimize here.

In the present context, F gives the form of the correlations within and between eyes. Following Miller *et al* (1989), the within-eye correlation is assumed to be

$$F(i, j) = e^{-d_{ij}^2/\sigma_S^2}$$

where the subscript S refers to 'same eye'. In the one-dimensional case d_{ij} is assumed to be $i - j$, i.e. retinal points are assumed to be evenly spaced, unit distance apart. Left and right eye correlations are taken to be identical. Again following Miller *et al* (1989), the between-eye correlation is assumed to be

$$F(i, j) = M_D e^{-d_{ij}^2/\sigma_D^2}$$

where $0 \leq M_D < 1$ is the magnitude of between-eye correlations relative to same-eye correlations (D refers to 'different eye'). i and j now label points in different eyes, and d_{ij} is the distance from point j to the point corresponding to i . G is like the neighbourhood function in Kohonen's self-organizing map, and is related to the end result of the iterative application of a kernel of short-range excitation and global inhibition in this patch of cortex to yield a single activity bubble (Wiskott and Sejnowski 1998). In the model this has the form

$$G(i, j) = e^{-d_{ij}^2/\sigma_C^2}$$

where $d_{ij} = i - j$ and the subscript C refers to 'cortex'. The above notation is summarized in table 1.

Table 1. Notation for the optimization model.

Parameter	Meaning
$F(i, j)$	Correlation between retinal points i and j
$G(i, j)$	Similarity between cortical points i and j
M_D	Ratio of strength of between- to same-eye correlations
σ_S	Spatial scale of same-eye correlations
σ_D	Spatial scale of between-eye correlations
σ_C	Spatial scale of cortical similarity
N	Number of retinal points (equals number of cortical points)

2.2. Performing the optimization

A total of 24 points are considered, 12 in each eye. There are thus of the order of $24! \approx 10^{23}$ possible mappings in total. Optimization by exhaustive search is impractical, and instead the heuristic technique of simulated annealing was used (Kirkpatrick *et al* 1983). This performs gradient descent/ascent in an objective function, but allows occasional steps in the wrong direction so that the solution is less likely to get stuck in a local optimum. The probability of taking a step in the wrong direction is controlled by a ‘temperature’ parameter that is gradually reduced. The parameters used were as follows (van Laarhoven and Aarts 1987). The initial map from retinal to cortical points was random, and the initial temperature was three times the average difference in cost between random maps. At each step, a candidate move consisted of interchanging a random pair of points in the map. This move was accepted with 100% probability if it improved the value of the objective function, or with a probability determined by the temperature if it did not. Once the sooner of 24 000 candidate moves had been generated or 2400 moves accepted, the temperature was multiplied by 0.998. The procedure was terminated when no moves were accepted out of 24 000 candidates at the same temperature. In each case the best of five runs was chosen from different starting conditions. Using these parameters, the results in table 2 took approximately 30 hours to generate on a 195 MHz SGI Octane workstation, i.e. each case took about 3 minutes.

3. Results

The parameter values investigated were $\{\sigma_S, \sigma_D, \sigma_C\} = \{1.0, 2.0, 3.0\}$, and $M_D = \{0.0, 0.2, 0.4, 0.6, 0.8\}$, a total of 135 cases in all. Results are shown in table 2. In many cases the optimal map is the complete segregation of the two eyes into two adjacent regions. Sometimes these are traversed in the same direction (this will be referred to as a Z map), sometimes in opposite directions (referred to as a \square map). For striped solutions, the following general trends can be seen (note that in each case a change in the parameter can also leave stripe width unchanged):

- (i) Increasing σ_S increases stripe width.
- (ii) Increasing σ_D decreases stripe width.
- (iii) Increasing M_D decreases stripe width.
- (iv) Increasing σ_C decreases stripe width

An exception to trends (iii) and (iv) occurs in row 6. Here increasing M_D *increases* stripe width, and increasing σ_C (through rows 4–6) *increases* stripe width. Both these exceptions would disappear if the last two maps in row 6 were of width 1 rather than 2.

Table 2. One-dimensional maps produced by the optimization procedure for all parameter combinations. σ_S = spatial scale of same-eye correlations, σ_D = spatial scale of between-eye correlations, σ_C = spatial scale of intracortical interactions, M_D = relative strength of between-eye correlations. ‘Row’ is an arbitrary label to facilitate indexing into the table. Note that the aspect ratio of the pictures is arbitrary, and does not represent a parameter of the model.

Row	σ_S	σ_D	σ_C	$M_D = 0.0$	$M_D = 0.2$	$M_D = 0.4$	$M_D = 0.6$	$M_D = 0.8$
1	1.0	1.0	1.0					
2	1.0	1.0	2.0					
3	1.0	1.0	3.0					
4	1.0	2.0	1.0					
5	1.0	2.0	2.0					
6	1.0	2.0	3.0					
7	1.0	3.0	1.0					
8	1.0	3.0	2.0					
9	1.0	3.0	3.0					
10	2.0	1.0	1.0					
11	2.0	1.0	2.0					
12	2.0	1.0	3.0					
13	2.0	2.0	1.0					
14	2.0	2.0	2.0					
15	2.0	2.0	3.0					
16	2.0	3.0	1.0					
17	2.0	3.0	2.0					
18	2.0	3.0	3.0					
19	3.0	1.0	1.0					
20	3.0	1.0	2.0					
21	3.0	1.0	3.0					
22	3.0	2.0	1.0					
23	3.0	2.0	2.0					
24	3.0	2.0	3.0					
25	3.0	3.0	1.0					
26	3.0	3.0	2.0					
27	3.0	3.0	3.0					

These two cases were therefore re-run using a much slower annealing schedule than would have been practical for the whole 135 cases, to test for the possibility that these represent local rather than global minima. However, the result remained unchanged.

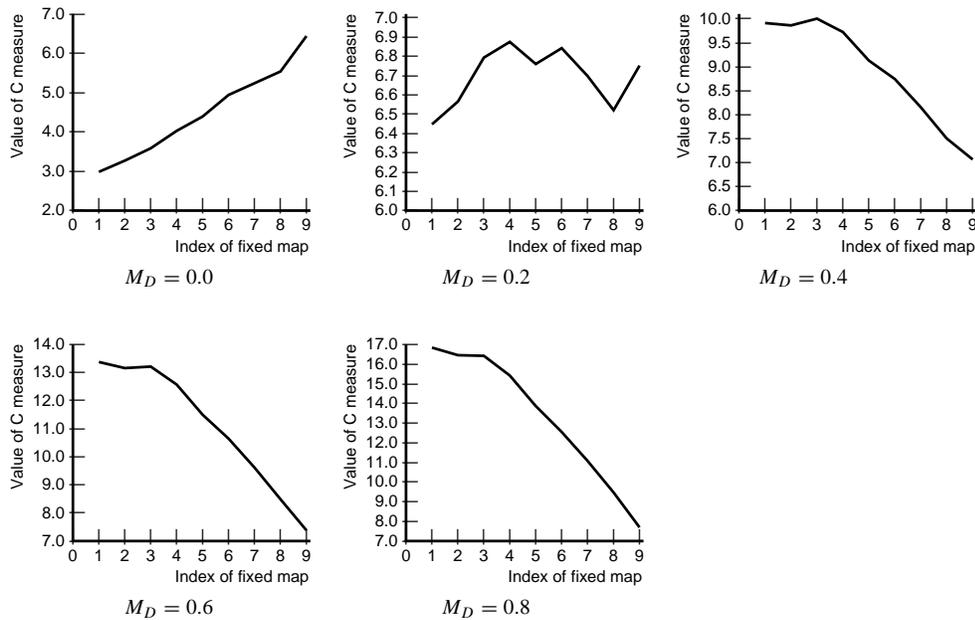


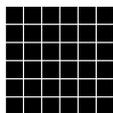
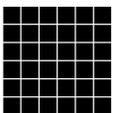
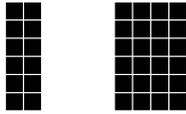
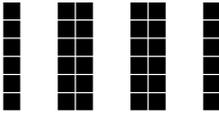
Figure 1. Variation in the value of C over the set of fixed maps for row 5 of table 2 ($\sigma_S = 1.0$, $\sigma_D = 2.0$, $\sigma_C = 2.0$). Note that the vertical scales are different in each graph, since values of C are not comparable between different sets of parameters.

In order to test whether the map found in each case was at least the optimal striped mapping, the best values of C found in each case were compared with the value of C calculated for nine fixed maps of increasing stripe width, numbered as follows. 1: width 1 (e.g. row 3, $M_D = 0.2$ in table 2). 2: width '1.5' (row 12, $M_D = 0.6$). 3: width 2 (row 1, $M_D = 0.4$). 4: width '2.5' (row 5, $M_D = 0.2$). 5: width 3 (not seen in table 2). 6: width 4 (row 14, $M_D = 0.6$). 7: width '4.5' (row 27, $M_D = 0.6$). 8: width 6 (not seen in table 2). 9: the \square map. Figure 1 shows some examples of how the value of C varies over this set of fixed maps for row 5 of the table. In every case except two in the table, the fixed maps were never better than the result found by the optimization. The two exceptions are row 15 with $M_D = 0.4$, and row 23 with $M_D = 0.8$: in both cases the map of form \square is slightly better.

The general trends displayed in table 2 can be qualitatively understood as follows. As σ_S increases, points which are increasingly widely separated within an eye become significantly correlated. One would therefore expect longer stretches of cortex which represent the same eye, i.e. wider stripes. As M_D or σ_D increase, the overall degree of correlation between the two eyes increases, and one would expect an increasing desire to keep corresponding and close-to-corresponding points within the eyes close together in the cortex, i.e. narrower stripes. As σ_C increases, on the one hand one would expect a wider interaction in the cortex to lead to wider stripes (as observed in many other models). On the other hand, however, if the two eyes are correlated then a wider cortical interaction makes it favourable to bring together in the cortex close-to-corresponding points in the two eyes, whereas this might not have been favourable before, thus leading to narrower stripes. It is interesting that the usual behaviour in the table is that increasing σ_C leads to narrower stripes, opposite to the trend commonly observed in models.

An important question is the degree to which these one-dimensional periodicity results scale up to two dimensions, as in other algorithms such as the elastic net (Goodhill and Willshaw 1990, Goodhill 1992). Two-dimensional simulations were therefore also performed for the parameters of row 14 in table 2 (as an example of a case with three well-defined periodicities). Two retinæ of size 6×6 (72 points in all) mapped to a cortex of size 12×6 . Simulated annealing parameters were as before, except that the maximum number of candidate moves was 72 000, the acceptance limit was 7200 moves, and only one run was performed for each set of parameters (each case took several hours to run). Note that there are now more than 10^{100} possible states, compared to 10^{23} in the one-dimensional case. Results are shown in table 3. Stripes run parallel to the short axis of the cortex, as expected (Jones *et al* 1991), and the periodicity of the one-dimensional case is generally reproduced. An exception is for $M_D = 0.4$, where the map seen in row 15 of table 2 occurs instead of the map in row 14.

Table 3. Two-dimensional results for the parameters of row 14 of table 2. Two retinæ of size 6×6 mapped to a cortex of size 12×6 . The periodicities of the one-dimensional case are generally reproduced.

$M_D = 0.0$	$M_D = 0.2$	$M_D = 0.4$
		
$M_D = 0.6$	$M_D = 0.8$	
		

4. Analysis

In order to help understand the trends seen in table 2, it is useful to consider a simpler case that can be explicitly analysed. For extremely short-range cortical interactions similarity in the cortex is effectively only nearest neighbour, and it is approximately true that $G(i, j) = 1$ if i and j are neighbours and 0 otherwise. This is roughly the case when $\sigma_C = 1.0$, which applies to rows 1, 4, 7, 10, 13, 16, 19, 22 and 25 in table 2. Now analytical formulae for the value of C as a function of the three remaining parameters σ_S , σ_D and M_D can straightforwardly be derived and compared. The analytical results well predict the simulation results, giving intuitive insight into how the parameters interact in the optimization.

First consider the \square mapping. The value of C of this map, C_{\square} , is

$$C_{\square} = (N - 2)e^{-1/\sigma_S^2} + M_D \tag{2}$$

(since there are $N - 1$ segments in each eye where $G(i, j) = 1$ and $F(i, j) = e^{-1/\sigma_S^2}$, and one ‘crossover’ segment where $G(i, j) = 1$ and $F(i, j) = M_D e^{-0/\sigma_D^2}$). The value of C for

the Z map, C_Z , is

$$C_Z = (N - 2)e^{-1/\sigma_S^2} + M_D e^{-(N/2-1)^2/\sigma_D^2}. \quad (3)$$

For $N = 24$ the second term of the right-hand side of equation (3) is effectively zero, and thus $C_{\square} > C_Z$ in all cases except when $M_D = 0$, when they are equal. From table 2 it can be seen that the two maps occur with about equal frequency when $M_D = 0$, but that the Z map is never seen when $M_D > 0$, as expected.

Consider now the set of striped mappings and refer to their C -values as $C_s(n)$, where s indicates that the mapping is striped and n indicates the stripe width. The following expressions can be derived:

$$C_s(1) = \frac{N}{2}M_D + \left(\frac{N}{2} - 1\right)M_D e^{-1/\sigma_D^2} \quad (4)$$

$$C_s(2) = \frac{N}{2}M_D + \left(\frac{N}{2} - 1\right)e^{-1/\sigma_S^2}. \quad (5)$$

The general expression for $n \geq 2$ is

$$C_s(n) = \frac{N}{2} \left[2 \left(1 - \frac{1}{n}\right) e^{-1/\sigma_S^2} + \frac{M_D}{n} \left(e^{-f(n)/\sigma_D^2} + e^{-g(n)/\sigma_D^2} \right) \right] \quad (6)$$

where

$$f(n) = g(n) = \left(\frac{n-2}{2}\right)^2 \quad \text{for } n \text{ even}$$

$$f(n) = \left(\frac{n-1}{2}\right)^2 \quad g(n) = \left(\frac{n-3}{2}\right)^2 \quad \text{for } n \text{ odd.}$$

When is a striped map better than the \square map? Consider stripes of width 2 (the reason for this will become apparent shortly). $C_s(2) > C_{\square}$ when $M_D > e^{-1/\sigma_S^2}$, and thus $\sigma_S = 1.0$ requires $M_D > 0.37$. This expectation is confirmed in rows 1, 4 and 7 of table 2, where the \square map is preferred for $M_D \leq 0.2$, but a striped map is preferred for $M_D \geq 0.4$.

When is the map of stripes of width 1 better than the map with stripes of width 2? $C_s(1) > C_s(2)$ when

$$M_D > e^{(1/\sigma_D^2 - 1/\sigma_S^2)}.$$

Since $M_D < 1$, the above inequality can never hold, and thus stripes of width 1 are never favoured, when $\sigma_S > \sigma_D$. This expectation is confirmed in table 2. For the case of $\sigma_S = 1.0$, $\sigma_D = 2.0$, the inequality requires that $M_D > 0.47$. This expectation is confirmed in row 4 of table 2, where width 2 is optimal for $M_D = 0.4$, but width 1 is then preferred for $M_D = 0.6$ and $M_D = 0.8$. For the case of $\sigma_S = 1.0$, $\sigma_D = 3.0$, the inequality requires that $M_D > 0.41$. This expectation is again confirmed, in row 7. For the case of $\sigma_S = 2.0$, $\sigma_D = 3.0$ (row 16), the inequality requires that $M_D > 0.87$. As expected, stripes of width 1 are no longer seen.

When are stripes of greater width local maxima of C ? Setting $dC_s(n)/dn = 0$ does not yield analytically tractable expressions. However, more direct methods can be used: there is a local maximum at n if $C_s(n-1) < C_s(n) > C_s(n+1)$. Using equation (6), conditions can be derived on M_D for this to be true. For n odd, we obtain the condition $M_D^1 < M_D < M_D^2$ where $M_D^1 = M_D^2$; that is, there are no local maxima at odd values of $n \neq 1$. For n even, we also obtain $M_D^1 < M_D < M_D^2$ where now

$$M_D^1 = \frac{2e^{-1/\sigma_S^2}}{ne^{-[(n-4)/2\sigma_D]^2} - (n-2)e^{-[(n-2)/2\sigma_D]^2}}$$

$$M_D^2(n) = M_D^1(n+2).$$

As M_D decreases, maxima for larger values of n become apparent, though the range of M_D for which they exist becomes small. Note however that a completely segregated map is always the global maximum, except when $M_D > e^{-1/\sigma_s^2}$, when $n = 2$ or $n = 1$ are globally optimal as noted above. Thus as M_D decreases $n = 2$ first becomes a local optimum, then the position of the local optimum shifts to larger n . It is apparent from the table that broader stripes can be optimal for $\sigma_C > 1.0$. Unfortunately the above analysis cannot easily be extended to the case of broader cortical interactions, since now each $C_s(n)$ contains many more terms and cannot be so conveniently analytically compared.

5. Discussion

5.1. Effectiveness of the optimization procedure

Since a heuristic rather than exact optimization procedure was used, it cannot be ruled out that some of the results in table 2 (in addition to the two exceptions already noted) might represent local rather than global optima of the objective function. However, there are at least four reasons to have confidence that at least many of the other entries are indeed global optima. Firstly, as shown in section 4 above, the simulation results exactly match those expected from direct calculations when these are applicable. Secondly, similar optimization parameters were found to produce optimal or close to optimal solutions for related problems where the optimal solution was explicitly known (Goodhill and Sejnowski 1996, 1997). Thirdly, a closer investigation of some particular cases (row 6 as described above) revealed no changes in the solution using substantially more generous annealing parameters. Fourth, fixed maps of a range of periodicities were never found to improve on the solution found by optimization, except for the two cases already noted.

5.2. Relation to other models

One intention of the present work is to reveal which aspects of the behaviour of other models can be simply understood by an optimization argument, and which aspects rely on model-specific details. Direct comparisons can be made with several models which fall within the class of C -measure optimizations. (Mitchison (1991) also used optimization arguments to address the formation of striped maps; however, the objective function used in this case was quite different from the C -measure, and intracortical rather than afferent projection patterns were optimized.)

The concern of Jones *et al* (1991) was to explain the overall directional flow of stripes in the striate cortex. Formalizing an intuitive idea of LeVay *et al* (1985), they showed that optimizing an objective function that attempts to keep neighbouring and corresponding points in each eye nearby can reproduce some differences in the pattern between cats and monkeys. The effect arises due to the different shapes of the primary visual cortex in each case. Their formulation of this problem can be expressed as a maximization of C when

$$F(i, j) = \begin{cases} 1 & i, j \text{ neighbouring, corresponding} \\ 0 & \text{otherwise} \end{cases}$$

and

$$G(i, j) = \begin{cases} 1 & i, j \text{ first or second nearest neighbours} \\ 0 & \text{otherwise.} \end{cases}$$

For two-dimensional retinæ and cortex they found a solution such that if $F(i, j) = 1$ then $G(M(i), M(j)) = 1, \forall i, j$, which is achieved when stripes have a width of one[†]. The effect on periodicity of varying F and G was not investigated.

The elastic net, a low-dimensional feature space model originally formulated for the travelling salesman problem (Durbin and Willshaw 1987), was first applied to the formation of ocular dominance stripes by Goodhill and Willshaw (1990). Here, dissimilarities (not similarities) are given by

$$F(i, j) = \begin{cases} |i - j|^2 & i, j \text{ in same eye} \\ |i - j - N/2|^2 + l^2 & i, j \text{ in different eyes} \end{cases} \quad (7)$$

assuming that indices $1, \dots, N/2$ give points in one eye and indices $N/2 + 1, \dots, N$ give points in the other eye. l can be thought of as inversely related to the strength of between-eye correlations (see Yuille *et al* 1996 for discussion). $G(i, j)$ is given by

$$G(i, j) = \begin{cases} 1 & i, j \text{ neighbouring} \\ 0 & \text{otherwise.} \end{cases} \quad (8)$$

The globally optimal mapping (i.e. minimum of C , since F now gives dissimilarities rather than similarities) when $l > 1$ is to keep the eyes entirely separate in the cortex, whereas for $l < 1$ the globally optimal map is stripes of width $n = 2$ (Goodhill and Willshaw 1990). However, there is also a local minimum for a striped map, analogous to the present model, where the interdigitations have width $n = 2l$ (Goodhill 1992). By varying the value of l it is thus possible to smoothly vary the periodicity of the locally optimal striped map. However, an important difference with the present model is that in equation (7) the dissimilarities increase without limit with distance, whereas in the present model the similarities tend to zero with distance. Thus in the present model the extra cost of stripes one unit wider rapidly becomes negligible, whereas for equation (7) this extra cost continues to increase by ever larger amounts. As $n \rightarrow \infty$, $C_s(n) \sim C_{\square}$ for the similarities defined in the present model (i.e. there is the same cost for traversing the two blocks in the same direction as in the opposite direction), whereas for the dissimilarities defined by equation (7) there is quite a different cost in these two cases. That F and G should tend to a bounded value as i and j become ever more distant neighbours is biologically more reasonable than that they should be potentially unbounded. Dayan (1993) showed how to properly introduce neighbourhood relations of more general form into the elastic net, and completely characterized stripe width as a function of both l and cortical interaction width. Although width was mostly monotonic with these variables, non-monotonicity as a function of interaction width was found for very high correlation. In the present model an insufficient number of values of cortical interaction width were investigated to see such an effect if it exists; however, it is interesting that increasing cortical interaction width can cause stripe width to both increase and decrease in the elastic net model.

Luttrell's (1990) quasi-objective function for the Kohonen (1982) algorithm can be expressed in the present case using the same F as for the elastic net, but with a G that is a Gaussian function of distance in the cortex (Goodhill and Sejnowski 1997). However, since the width of G is usually continuously reduced during the simulation of the Kohonen algorithm it is hard to determine how this width affects stripe periodicity.

Miller (1998) and Elliott *et al* (1998) have recently discussed an objective function for

[†] This was obtained by an exact optimization using an algorithm for subgraph isomorphism, which unfortunately cannot be directly extended to the present model.

models of neural development that has the form

$$E = -\frac{1}{2} \sum_{x,y,\alpha,\beta} S(x, \alpha) I(x, y) C(\alpha, \beta) S(y, \beta) \quad (9)$$

where x and y label neurons in an afferent space such as the retina or the LGN; α and β label neurons in a target space such as the cortex; $I(x, y)$ gives the effective interaction between target neurons x and y ; $C(\alpha, \beta)$ gives the correlation between afferent neurons α and β ; and $S(x, \alpha)$ and $S(y, \beta)$ give the connection strengths between afferent and target neurons. This same objective function is optimized by the models of both Miller *et al* (1989) and Elliott *et al* (1996), though with differences in the form and interpretation of the terms in the function, and the way in which constraints on the synaptic strength variables are enforced (Miller 1998, Elliott *et al* 1998). When only one-to-one maps between input neurons and target neurons are allowed, and there are assumed to be the same number of input and target neurons, the minimization of equation (9) reduces to the maximization of the C -measure (see Wiskott and Sejnowski (1998) for further discussion of the mathematical relationships between different models). Ocular dominance stripe periodicity in the full Miller model is determined by the peak of the power spectrum of the cortical interaction function, or the afferent arbor diameter, whichever gives the smallest stripe width. Behaviour in the present model appears quite different: stripe periodicity is finite even though cortical interactions are all positive (so that the peak of the power spectrum is at zero), and stripe periodicity can be greater than one even though the arbor width is effectively one. The latter is because, unlike the Miller model, the present model allows flexibility in the topography of the mapping. In Miller's model corresponding points in each eye are restricted to the same small region of the cortex; since every retinal point must possess territory in the cortex, stripes cannot be wider than the width of this region.

5.3. Biological relevance

A striking feature of table 2 is how often a completely segregated map is the optimal solution. This would appear somewhat problematic for a model purporting to account for interdigitated stripes. However, the analysis and simulation results show that, even when this is true, there is often also a local minimum for interdigitated stripes. In reality it is likely that the overall topography of the V1 map is specified by molecular cues such as gradients. Recent data from the retinotectal (Cheng *et al* 1995, Drescher *et al* 1995) and hippocampalseptal (Gao *et al* 1996) systems show that gradients of receptors of the Eph family are expressed in the input structure, while matching gradients of Eph ligands are expressed in the output structure (for reviews see Friedman and O'Leary 1996, Flanagan and Vanderhaeghen 1998). The interaction of these gradients during development may subserve topographic map formation (e.g. Goodhill 1998), at least in a crude form. Later activity then refines the map (reviewed in Udin and Fawcett 1988, Goodhill 1992). Such an overall topographic bias would exclude completely segregated patterns, and favour instead locally optimal striped patterns. This bias would be hard to include explicitly in the present optimization model. In some models topography is hard-wired (e.g. Miller *et al* 1989), whereas in others it emerges from the dynamics of the algorithm (e.g. Goodhill and Willshaw 1990).

The model presented here allows a more complete investigation of the interaction of parameters determining stripe periodicity than is possible in other models. This leads to some specific biological predictions, as follows:

1. Decreasing correlation between the two eyes, as in strabismus or monocular deprivation, (almost) always increases stripe width. This effect is also seen in several other models, and thus constitutes a very robust theoretical result.
2. Increasing the width of lateral interactions in the cortex can cause both increases and decreases in stripe width, depending on the other parameters. This contrasts surprisingly with most previous models, which predict only increases in stripe width.
3. Increasing the spatial extent of within-eye correlations increases stripe width.

As discussed in section 1, there is already experimental evidence supporting prediction 1. The experimental data relating to prediction 2 are so far preliminary, consisting only of an abstract (Hensch and Stryker 1996). The third prediction is not easy to test experimentally. It would be hard to actually measure the value corresponding to σ_S in the retina or lateral geniculate nucleus, and even harder to measure σ_D . A simpler approach would be to compare stripe widths between dark-reared (DR), binocularly deprived (BD) and strabismic kittens. In each case it should be true that $M_D \approx 0$, leaving only the parameters σ_S and σ_C in the model. It would be convenient to assume that σ_C is the same in each of these three cases so that σ_S is the only varying parameter, but this may not be true if σ_C is even partly determined by activity-dependent mechanisms. σ_S is now determined by the characteristic correlation width of spontaneous retinal activity in the DR case, by spontaneous activity modulated by illumination through the eyelids in the BD case (see e.g. Krug and Thompson 1997), and by the statistics of natural scenes in the strabismic case. The model predicts that stripe width may be different in these cases. Unfortunately it is not possible to be more precise without knowing the actual values of σ_S and σ_C . In addition, the effect of different values of σ_S between the three cases may be small. Since there is natural variability in stripe width between different macaque monkey individuals (Horton and Hocking 1996b) (though apparently less in the case of the cat (Löwel 1994)), it might therefore be difficult to examine enough animals to produce statistics sufficient to definitively address this question, unless for instance clones can be compared.

Acknowledgments

I thank Laurenz Wiskott for very stimulating discussions, and the anonymous referees for many helpful comments on an earlier version. This work was supported by DOD grant DAMD17-93-V-3018.

References

- Bauer H-U, Brockmann D and Geisel T 1997 Analysis of ocular dominance pattern formation in a high-dimensional self-organizing-map model *Network: Comput. Neural Syst.* **8** 17–33
- Bienenstock E and von der Malsburg C 1987a A neural network for the retrieval of superimposed connection patterns *Europhys. Lett.* **3** 1243–9
- 1987b A neural network for invariant pattern recognition *Europhys. Lett.* **4** 121–6
- Cheng H J, Nakamoto M, Bergemann A D and Flanagan J G 1995 Complementary gradients in expression and binding of Elf-1 and Mek4 in development of the topographic retinotectal projection map *Cell* **82** 371–81
- Dayan P S 1993 Arbitrary elastic topologies and ocular dominance *Neural Comput.* **5** 392–401
- Dayan P S and Goodhill G J 1992 Perturbing Hebbian rules *Advances in Neural Information Processing Systems 4* ed J E Moody, S J Hanson and R P Lippman (San Mateo, CA: Morgan Kaufmann) pp 19–26
- Drescher U, Kremoser C, Handwerker C, Loschinger J, Noda M and Bonhoeffer F 1995 In-vitro guidance of retinal ganglion-cell axons by RAGS, a 25 KDa tectal protein related to ligands for Eph receptor tyrosine kinases *Cell* **82** 359–70
- Durbin R and Mitchison G 1990 A dimension reduction framework for understanding cortical maps *Nature* **343** 644–7

- Durbin R and Willshaw D J 1987 An analogue approach to the travelling salesman problem using an elastic net method *Nature* **326** 689–91
- Elliott T, Howarth C I and Shadbolt N R 1996 Axonal processes and neural plasticity. I: Ocular dominance columns *Cerebral Cortex* **6** 781–8
- 1998 Axonal processes and neural plasticity: a reply *Neural Comput.* **10** 549–54
- Erwin E, Obermayer K and Schulten K 1995 Models of orientation and ocular dominance columns in the visual cortex: a critical comparison *Neural Comput.* **7** 425–68
- Flanagan J G and Vanderhaeghen P 1998 The ephrins and Eph receptors in neural development *Ann. Rev. Neurosci.* **21** 309–45
- Friedman G C and O'Leary D D M 1996 Eph receptor tyrosine kinases and their ligands in neural development *Curr. Opin. Neurobiol.* **6** 127–33
- Gao P-P, Zhang J-H, Yokoyama M, Racey B, Dreyfus C F, Black I B and Zhou R 1996 Regulation of topographic projection in the brain: Elf-1 in the hippocampal system *Proc. Natl Acad. Sci. USA* **93** 11161–6
- Goodhill G J 1992 *Correlations, Competition and Optimality: Modelling the Development of Topography and Ocular Dominance* Cognitive Science Research Paper CSRP 226, University of Sussex, also available from www.giccs.georgetown.edu/~geoff
- 1993 Topography and ocular dominance: a model exploring positive correlations *Biol. Cybern.* **69** 109–18
- 1998 Gradients for retinotectal mapping *Advances in Neural Information Processing Systems 10* ed M I Jordan, M J Kearns and S A Solla (Cambridge, MA: MIT Press) pp 152–8
- Goodhill G J and Löwel S 1995 Theory meets experiment: correlated neural activity helps determine ocular dominance column periodicity *Trends Neurosci.* **18** 437–9
- Goodhill G J, Finch S and Sejnowski T J 1995 *Quantifying neighbourhood preservation in topographic mappings* Institute for Neural Computation Technical Report Series, No. INC-9505, November 1995, also available from www.giccs.georgetown.edu/~geoff
- 1996 Optimizing cortical mappings. *Advances in Neural Information Processing Systems 8* ed D S Touretzky, M C Mozer and M E Hasselmo (Cambridge, MA: MIT Press) pp 330–6
- Goodhill G J and Sejnowski T J 1996 Quantifying neighbourhood preservation in topographic mappings *Proc. 3rd Joint Symp. on Neural Computation (University of California, San Diego and California Institute of Technology)* (Pasadena, CA: California Institute of Technology) vol 6, pp 61–82, also available from www.giccs.georgetown.edu/~geoff
- 1997 A unifying objective function for topographic mappings *Neural Comput.* **9** 1291–304
- Goodhill G J and Willshaw D J 1990 Application of the elastic net algorithm to the formation of ocular dominance stripes *Network: Comput. Neural Syst.* **1** 41–59
- Hensch T K and Stryker M P 1996 Intracortical interactions regulate ocular dominance column segregation *Soc. Neurosci. Abstr.* **22** 1729
- Horton J C and Hocking D R 1996a Anatomical demonstration of ocular dominance columns in striate cortex of the squirrel monkey *J. Neurosci.* **16** 5510–22
- 1996b Intrinsic variability of ocular dominance column periodicity in normal macaque monkeys *J. Neurosci.* **16** 7228–39
- Hubel D H and Wiesel T N 1977 Functional architecture of the macaque monkey visual cortex *Proc. R. Soc. (Lond.) B* **198** 1–59
- Jones D G, Van Sluyters R C and Murphy K M 1991 A computational model for the overall pattern of ocular dominance *J. Neurosci.* **11** 3794–808
- Kirkpatrick S, Gelatt C D and Vecchi M P 1983 Optimization by simulated annealing *Science* **220** 671–80
- Kohonen T 1982 Analysis of a simple self-organizing process *Biol. Cybern.* **44** 135–40
- Krug K and Thompson I D 1997 Visual driving of cortical neurons through the unopened eyes of neonatal ferrets *Soc. Neurosci. Abstr.* **23** 1665
- LeVay S, Connolly M, Houde J and Van Essen D C 1985 The complete pattern of ocular dominance stripes in the striate cortex and visual field of the macaque monkey *J. Neurosci.* **5** 486–501
- LeVay S, Stryker M P and 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** 223–44
- Livingstone M 1996 Ocular dominance columns in New-World monkeys *J. Neurosci.* **16** 2086–96
- Löwel S 1994 Ocular dominance column development: strabismus changes the spacing of adjacent columns in cat visual cortex *J. Neurosci.* **14** 7451–68
- Luttrell S P 1990 Derivation of a class of training algorithms *IEEE Trans. Neural Networks* **1** 229–32
- 1994 A Bayesian analysis of self-organizing maps *Neural Comput.* **6** 767–94
- Miller K D 1998 Equivalence of a sprouting-and-retraction model and correlation-based plasticity models of neural development *Neural Comput.* **10** 529–47

- Miller K D, Keller J B and Stryker M P 1989 Ocular dominance column development: Analysis and simulation *Science* **245** 605–15
- Mitchison G 1991 Neuronal branching patterns and the economy of cortical wiring *Proc. R. Soc. (Lond.) B* **245** 151–8
- 1995 A type of duality between self-organizing maps and minimal wiring *Neural Comput.* **7** 25–35
- Obermayer K, Blasdel G G and Schulten K 1992 Statistical-mechanical analysis of self-organization and pattern formation during the development of visual maps *Phys. Rev. A* **45** 7568–89
- Rakic P 1976 Prenatal genesis of connections subserving ocular dominance in the rhesus monkey *Nature* **261** 467–71
- Sirosh J and Miikkulainen R 1997 Topographic receptive fields and patterned lateral interaction in a self-organizing model of the primary visual cortex *Neural Comput.* **9** 577–94
- Swindale N V 1980 A model for the formation of ocular dominance stripes *Proc. R. Soc. (Lond.) B* **208** 243–64
- 1996 The development of topography in the visual cortex: a review of models *Network: Comput. Neural Syst.* **7** 161–247
- Tieman S B and Tumosa N 1997 Alternating monocular exposure increases the spacing of ocularity domains in area 17 of cats *Visual Neurosci.* **14** 929–38
- Torgerson W S 1952 Multidimensional scaling, I: theory and method *Psychometrika* **17** 401–19
- Udin S B and Fawcett J W 1988 Formation of topographic maps *Ann. Rev. Neurosci.* **11** 289–327
- van Laarhoven P J M and Aarts E H L 1987 *Simulated Annealing: Theory and Applications* (Dordrecht: Reidel)
- Wiskott L and Sejnowski T 1998 Constrained optimization for neural map formation: a unifying framework for weight growth and normalization *Neural Comput.* **10** 671–716
- Yuille A L, Kolodny J A and Lee C W 1996 Dimension reduction, generalized deformable models and the development of ocularity and orientation *Neural Networks* **9** 309–19