Chapter 7

Conclusions

7.1 Introduction

We first summarize the main points made in the thesis. We then present a more detailed comparison of the models we have addressed, paying particular attention to the terms of reference set out in the introduction. Directions for future work are suggested.

7.2 Summary of the main points

- Motivations: Experimental data from the natural system suggests that topography and ocular dominance can arise from the same developmental mechanisms. Despite this, previous models for topography or ocular dominance have tended not to simultaneously address both issues in a satisfactory way.

- We therefore discussed several models of visual development from the point of view of (a) whether they could form topography and ocular dominance from the same mechanisms, (b) to what extent they could be interpreted biologically, (c) whether they could form appropriate maps in the presence of positive correlations between the two eyes, and (d) the extent to which the morphology of model stripes matched that of natural stripes. These were a correlational model [Miller et al 1989], an elastic net model [Goodhill & Willshaw 1990], a model based on a particular version of Kohonen's self-organizing feature map algorithm, and a competitive model which explicitly considered the presentation of a sequence of input patterns.

- A perturbation analysis of Miller's model of ocular dominance showed that binocular solutions can be favoured over monocular solutions if small correlations are introduced between the eyes or if there are negative correlations within each eye. The model is also not stable to perturbative differences in the correlations within the two eyes.

- We demonstrated that both the elastic net and a new Kohonen-type algorithm can produce topography and ocular dominance from the same developmental mechanisms. Considering the development of topography and ocular dominance as an optimization problem, we formulated various different ways of assessing the quality of the maps produced. With respect to these metrics it was shown that the elastic net generally produces better results than the Kohonen-type algorithm for comparable amounts of computation. The numerical methods of evaluating the map generally agreed with qualitative assessments of stripe morphology. Both algorithms were shown to correctly predict the results of monocular deprivation. Stripe width in both models is governed by a parameter we interpret to be the ratio of the strength of correlation within and between retinae.

- A particular type of competitive model in conjunction with a suitable weight normalization rule can simultaneously produce topography and ocular dominance from biologically plausible mechanisms. In particular, distributed patterns of activity can be presented simultaneously in the two retinae, which allows investigation of the influence of positive correlations between the eyes on stripe width. It was found that stripe width is *decreased* by increasing the strength of correlations between the eyes, and *increased* by increasing the spread of lateral interactions in the cortex. This behaviour combines aspects of both Miller's and the elastic net and Kohonen-type models.

7.3 Comparison of models

7.3.1 Topography and ocular dominance

The elastic net, Kohonen-type and competitive model each produce topography and ocular dominance from the same mechanisms, without any additional assumptions. It is not clear whether Miller's model is capable of this: we discuss this further below. One interesting difference is that in Miller's model refinement does not guarantee the development of dominance, whereas in the others receptive field refinement and the development of ocular dominance proceed hand in hand, driven by the same mechanisms.

7.3.2 Biological plausibility

Miller has discussed in some detail how the mechanisms and parameters of his model can be interpreted biologically [Miller 1989, Miller et al 1989, Miller 1990(a), Miller 1990(b), Miller & Stryker 1990]. However, it is interesting to compare Miller's presentation with that of Linsker's for a similar model [Linsker 1986, Linsker 1988]. Linsker lays greater emphasis on the *simplicity* of the model, and the fact that it attempts to reproduce the behaviour of the natural system using a minimal number of rules. He refers to these rules as "biologically plausible", without attempting a more detailed justification. The elastic net and Kohonen-type models are more algorithmic in nature, although they can be interpreted as implementing Hebbian-type rules. Although we have identified distances as correlations in the representation of the problem used by these models, this has not been rigourously justified. The competitive model has the advantage that it is expressed in terms of a succession of inputs rather than averaged correlations: furthermore, these patterns are distributed and simultaneous in both retinae. However, certain assumptions are made regarding the mechanisms of competition and cooperation in the cortex, the plausibility of which has not been addressed.

7.3.3 Input Correlations

We have shown that monocularity in Miller's model begins to break down when there are positive correlations between the eyes. Our interpretation of distances in feature space as representing correlations suggests that the elastic net and Kohonen-type algorithms can form appropriate maps for positive cross-eye correlations. The competitive model gives appropriate maps for a range of positive correlations between the two eyes. Since it is driven by a succession of input patterns rather than the regular correlations of the elastic and Kohonen-type models, a much wider range of correlational structure can be investigated in this model. In the elastic net, Kohonen-type and competitive models stripes become narrower as the two eyes become more correlated, which is expected from intuitive arguments.

7.3.4 Stripe morphology

It is difficult to compare stripe morphology for the different models beyond the general statement that the segregated regions in each of the models are long, thin, and of roughly uniform width. There are a number of problems with making more detailed comparisons between the models. Firstly, Miller used periodic boundary conditions, which we have not used for the elastic and competitive models. Secondly, due to various technical features of the models, the stripes presented tend to be of different thicknesses. Thirdly, all these simulations are on a small scale.[1] However, we have seen that of the models for which simulation results are presented in this thesis, the elastic net tends to produce the most regular stripes (i.e. the most sharply-peaked power spectrum of the fourier transform), especially for small separations of the two retinae.

It is also difficult to make detailed comparisons with the natural system for reasons of scale. Whereas in all the models presented stripe width is generally just a few units across, in the natural system stripes can be many tens or hundreds of cells wide, and so comparisons with, for instance, the way the stripes terminate are not particularly meaningful. However, one area of stripe morphology where progress has been made in this thesis is of showing, as suggested by [LeVay et al 1985], that anisotropic boundary conditions can lead to an overall orientation for the stripes. A related issue to this is the degree to which the elastic and competitive models succeed in producing a "good" map. We have investigated this for the elastic net compared to a Kohonen-type algorithm, and also for the competitive model.

The elastic net and Kohonen-type algorithm reproduce the results of monocular deprivation without requiring any adjustments in the parameters apart from a reduction in strength for one eye. Monocular deprivation can be modelled in Miller's framework, but it is necessary to alter the form of the afferent normalization mechanism. Deprivation has not yet been investigated in the competitive model. However, it should be pointed out that, since it uses a similar afferent normalization mechanism to Miller's model, it is likely that similar adjustments to this will need to be made.

[1] Note that all the 40×40 arrays of cortical units presented by Miller have a border of 15×15 units which are repeated: this was done to demonstrate continuity across the edges of his array.

7.4 Further work

7.4.1 Miller's model

We have been able to point to some of Miller's experimental results that support certain aspects of the perturbation analysis presented in this thesis. However, a more thorough empirical investigation is needed, in particular of the effect of positive correlations between the eyes, which Miller does not discuss. A more direct empirical comparison with the elastic, Kohonen-type and competitive models would also be useful.

Our analysis only considers the addition of very small correlations. An analytic investigation of more general cases would be of interest, although it is not immediately clear how to go about this. As a starting point larger perturbations could be investigated empirically.

So far the analysis of Miller (e.g. [Miller 1989]) has only considered first-order terms - a linear approximation. It would be interesting to analyse the role of higher-order terms, as was done for different but related systems in [Turing 1952] and [Häussler & von der Malsburg 1983].

The largest outstanding question regarding Miller's model is its ability or otherwise to form a topographic map. A fixed topography was assumed in all the simulation results Miller presented for his model: each cortical unit saw a 7×7 window of those presynaptic units directly below it, with connection strengths multiplied by the arbor function. We now consider what would happen if each cortical unit initially had non-zero connections to *all* units in the presynaptic sheet, and there was no arbor function making each unit in the postsynaptic sheet specific for the presynaptic units directly below it. There are two issues. Firstly, would receptive fields refine: that is, would the majority of connection strengths for each cortical unit go to zero leaving attention focussed on a small region of the presynaptic sheet? Secondly, would the regions that each cortical unit focussed on progress in an orderly way across the LGN in moving across the cortical sheet?

Some of Miller's simulation results are relevant to the first question. In [Miller et al 1989] the development of receptive fields for a number of individual cortical units is shown. Refinement occurs over time: eventually non-zero weights are restricted to a significantly smaller region than the original 7×7 window. Miller explains this [Miller 1990(a), pages 295–296] as being due to inputs in the centre of the receptive field having more correlated neighbours than inputs in the periphery (assuming the correlations are a decreasing function of distance). However, this seems to suggest that without the fixed topography, all cortical units would refine attention on the centre of the presynaptic sheet. In particular, there is no competitive pressure to learn different features. This makes the second question irrelevant.

To make these arguments more precise it might be possible to analyse this extended system in terms of its eigenvectors. The correlation matrix to be considered is now for the whole presynaptic sheet, rather than just the presynaptic region defined by the arbor function. Assuming gaussian correlations of range significantly less than the width of the presynaptic sheet, this correlation matrix would take the form of a gaussian "blur" down the leading diagonal (for the one-dimensional case), with zeros away from the neighbourhood of the leading diagonal. It might also be possible to investigate the spatial layout of these refined receptive fields by including the cortical iteration matrix in the eigenvector calculation, thus calculating both receptive field form and location for the whole set of cortical units simultaneously. We review below some very recent work that is relevant to this question.

7.4.2 The elastic net and Kohonen-type models

In the one-dimensional case of the elastic net model investigated in [Goodhill 1988, Goodhill & Willshaw 1990], it is possible to calculate explicitly which are the shortest paths, and thus to compare simulation results with these optimal results. It would be interesting to attempt similar calculations for the two-dimensional case. Although the general case is hard, it may be possible to compare analytically the sum D of distances between neighbouring points in the cortical sheet of certain general forms, such as parallel stripes of fixed width, a checker-board pattern, and the two-dimensional equivalent of the $\sqsupset$ path. This would enable us to see whether there are significantly shorter paths that the elastic net and Kohonen-type algorithm avoids, and whether these shorter paths represent patterns that are closer or otherwise to biological reality. It might also reveal something about the D-value of stripes with and without twists and turns. On the same theme it would be interesting to see the result of applying a more standard TSP algorithm to this optimization problem, to address again to what extent the elastic net and Kohonen-type algorithm are restricted to finding only a class of possible solutions.

There is an outstanding question as to why the elastic net but not the Tea Trade model is capable of forming stripes. A detailed comparison of the mathematics underlying both models might answer this, and in addition shed light on the correct biological interpretation of elastic net parameters.

A difficulty in the biological interpretation of the elastic net is that it is hard to see how the regularization term relates to a more realistic cortical interaction function as used in Miller's model. A similar problem applies to the version of neighbourhood updating used in the Kohonen-type algorithm. Recent analysis has begun to make this clearer [Dayan 1992].

A more accurate expression for the dependence of k_s on the parameters of the model could be found by following the techniques employed in [Durbin et al 1989]. k_s corresponds to the first bifurcation of the energy function, i.e. the first time E has more than one minimum. Due to the highly regular arrangement of retinal units, this occurs for a much lower value of k than in the TSP case where cities are usually arranged more randomly, and so E develops a very large number of minima very quickly. In [Durbin et al 1989] the value of k at the first bifurcation was found by calculating the smallest eigenvalue of the Hessian matrix: when this is zero, the system bifurcates. This method could be applied to the ocular dominance case by writing down the Hessian matrix for the feature space of retinal units used here.

There are problems with knowing precisely what is being compared in chapter 5 between the elastic net and Kohonen-type algorithms. Firstly, it is not known whether the energy functions each optimizes have the same minima, so that the difference in results is only to do with differing abilities of the algorithms to optimize, or whether the energy functions actually have different minima. Secondly, our comparison of equal run times is obviously rather crude, being highly implementation-dependent. Further theoretical work might begin to answer these questions. Also, it would be interesting to compare the algorithms for even slower annealing.

7.4.3 Competitive model

An important feature of the competitive model is that in general, the effect of arbitrary input patterns can be investigated. In particular, it would be possible to use fragments of (suitably preprocessed) real images. Following [Barrow 1987], retinal and LGN processing could be simply modelled as a convolution with a difference of gaussians. This pre-processing would introduce negative components in the inputs, which are not allowed in the model as it is presently formulated, but this could perhaps be dealt with by separating on and off channels as in for example [Barrow & Bray 1992].

A mathematical analysis of the model would be enlightening from several points of view. Firstly, it would be interesting to know the precise analytical relationship between stripe width and the parameters of degree of correlation between the two eyes and extent of lateral interactions in the cortical sheet. Secondly, analysis might make it clearer how the model relates to Miller's and the elastic net, and also to the model of [Obermayer, Ritter & Schulten 1991]. It might be possible to apply some of the mathematical techniques of [Obermayer, Blasdel & Schulten 1991, Obermayer, Ritter & Schulten 1991] to this model, which would help to reveal the mathematical differences between presenting localized and distributed patterns of activity. One length parameter that could be expected to have an effect on stripe width is σ_r, the range of correlations within each retina. For the simulations presented here this was fixed at $\sigma_r = 1.5$: generally less than or approximately equal to the values used for σ_c, the range of the cortical interaction function. We might expect the case $\sigma_r > \sigma_c$ to produce interesting results, since now the correlations in the retinae "overflow" the range of lateral interactions in the cortex. For instance, in Amari's (monocular) model it was found that this regime led to a break-up of the previously smooth map into columnar microstructures [Takeuchi & Amari 1979]. In addition, the ability of the model to account for the results of monocular deprivation, i.e. a reduction in the strength of the input from one eye, needs to be investigated.

The biological plausibility of the model would be enhanced by adopting an explicit interaction function in the cortex as in for instance [Willshaw & von der Malsburg 1976] (and Miller's model), rather than the Kohonen approximation used up to now. However, a problem with this would be the large additional computational burden this would impose on an already computationally-intensive algorithm.

7.4.4 Unification of elastic and correlational models

We now review some very recent work [Yuille et al 1991(a), Yuille et al 1991(b)] that points to a mathematical link between the elastic net model and Miller's correlational model. The suggestion is that both can be derived from a more general objective function for the topography and ocular dominance problem, in a very similar way to that in which the elastic net and Hopfield and Tank's algorithm can be derived from a more general objective function for the TSP. [Yuille et al 1991(a)] suggest that an appropriate "generalized deformable model" for this problem has cost function

$$\begin{aligned} E[V^L, V^R, y, B] &= \sum_{i,j,a,b} V^L_{(ij)(ab)}\{|x^L_{ij} - y_{ab}|^2 + (B_{ab} - h)^2\} \\ &\quad + \sum_{i,j,a,b} V^R_{(ij)(ab)}\{|x^R_{ij} - y_{ab}|^2 + (B_{ab} + h)^2\} \\ &\quad + \nu \sum_{a,b}\{(B_{a+1,b} - B_{ab})^2 + (B_{a,b+1} - B_{ab})^2\} \\ &\quad + \tau \sum_{a,b}\{|y_{a+1,b} - y_{ab}|^2 + |y_{a,b+1} - y_{ab}|^2\}. \end{aligned} \tag{7.1}$$

The x's represent retinal points: these are laid out in a grid for each retina. The y's represent points in a cortical sheet, and the B's represent the ocularity of each cortical point. y and B are both continuous variables. The V's are matching variables that specify which cortical points are matched to which retinal points. These are initially conceived to be binary variables, but become continuous under a statistical mechanics interpretation for finite temperature. The first two terms impose the matching constraints and the last two terms impose smoothness of the B and y fields. In [Yuille et al 1991(a)] it is shown that eliminating the V fields leads to an elastic net type energy function. It is also suggested that eliminating the B and y fields leads to a model closely related to Miller's.

The most interesting aspects of this work from our point of view are the following:

- It addresses the question as to the true nature of the relationship between Miller's model and the elastic net (cf [Goodhill & Willshaw 1990]).
- In order to identify the model derived by eliminating the B's and the y's with Miller's model, it is necessary for [Yuille et al 1991(a)] to explicitly identify distances with correlations: in particular their analysis suggests that the correlation between x_i and x_j should be $K - |x_i - x_j|^2$, where K is a constant. This agrees with the interpretation of distances as correlations we have adopted so far.
- Since the elastic model can produce topography by the same mechanism as ocular dominance, it may be possible to use this analysis to address theoretically the question of whether a correlational mechanism can produce topography. This is not considered in [Yuille et al 1991(a)].
- Extensions of this work provide insight into the relationship between the regularization term of the elastic model and cortical interaction functions, and show how more general neighbourhood terms may be included in the elastic net [Dayan 1992].

However, there are a number of technical errors and ambiguities in [Yuille et al 1991(a)] that need to be addressed. In addition, it would be interesting to see if the Kohonen-type algorithm and the competitive model can also be subsumed under this framework. Examples are given in [Yuille 1990] of generalized deformable models for competitive-type models of various phenomena.

7.4.5 Experimental issues

This thesis highlights a number of questions about the natural system which have not been answered experimentally. One of the most important of these here is the form of correlations between the two eyes. Various experiments have investigated the form of correlations resulting from spontaneous correlations *within* an eye (e.g. [Arnett 1978, Ginsburg et al 1984, Mastronade 1989, Meister et al 1991]). However, there are a number of problems with exploring the correlations *between* eyes. Firstly, such correlations are not likely to be produced by spontaneous firing: only in response to real visual input, and are thus much harder to measure. Secondly, it would be necessary to very closely match the positions of cells in the two eyes/lateral geniculate nuclei that were recorded from.

We have predicted that stripe width could be affected by the strength of the correlations between the two eyes. Thus it would be interesting to try to detect changes in stripe width in response to artificially induced strabismus.

Since this severly reduces the extent of correlations between the two eyes, we predict an increase in stripe width. Although the effects of strabismus on the degree of dominance of individual cells has been investigated extensively, the effect on stripe width has not been examined (D. Hubel, Personal Communication). It would also be interesting to try and investigate the effect on stripe width of the cortical interaction function. One possibility might be to attempt to pharmacologically alter the form of lateral interactions in the cortex/tectum.

Two interesting questions which (as far as the author is aware) have not been answered experimentally are whether (a) there is any detailed similarity between the patterns of stripes in the two hemispheres, and (b) there is any similarity between the patterns in closely related individuals. Answers to both these would help to illuminate the extent to which the detailed form of the pattern is determined by genetic as opposed to environmental factors.

7.4.6 Measures and morphology

As we have already suggested, in order for work in this area to progress it is necessary to have better ways of evaluating the output of models, in terms of the degree of topography of the map produced, and the degree to which stripe morphology matches that of the natural system. The latter requires a more careful characterization of natural stripes than has hitherto been performed. It will also be necessary to decide, out of the many possible features of this morphology that could be considered, which are the *key* features that should be used to constrain theoretical models.

7.4.7 Balancing models

A set of proposals regarding stripe formation that has not been properly addressed theoretically are the balancing models as discussed in chapter 3. Although these address only the interaction between topography and ocular dominance rather than the reason individual cells become ocularly dominant, a proper theoretical investigation could help to clarify a number of important issues. For instance, which kinds of patterns are produced by what kinds of mechanisms or interactions between mechanisms, and which classes of objective functions give patterns of stripes when minimized.

7.5 Summary: principal contributions

To conclude, we list the principal contributions made by this thesis.

- We have shown that computational models can be formulated in which topography and ocular dominance naturally arise from the same developmental mechanisms.
- We have shown analytically that the addition of perturbing correlations in Miller's model of ocular dominance leads to an instability, and an increased tendency to produce binocular rather than monocular units, thus highlighting a weakness of correlational models in general.
- We have addressed a number of issues related to elastic net and Kohonen-type models of ocular dominance, including the extent to which various measures of optimality imply good stripe morphology, and have shown that these models can naturally account for the results of monocular deprivation.
- We have introduced a new model based on a competitive mechanism, in which for the first time topography and ocular dominance are able to develop in the presence of distributed activity simultaneously in the two eyes. Stripe width in this model can be influenced by both the degree of correlation between the eyes and the extent of lateral interactions in the cortex. The former influence represents a novel prediction regarding the determiners of stripe width in the natural system.

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