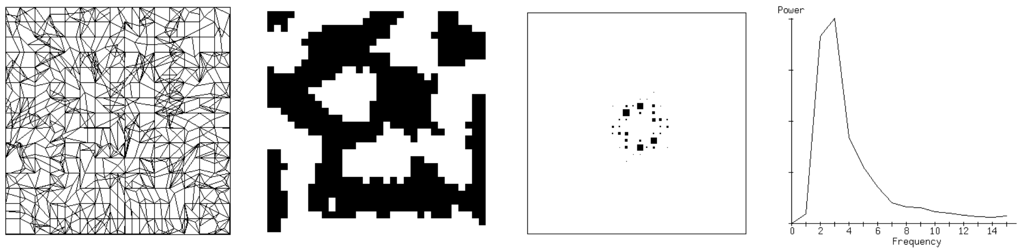
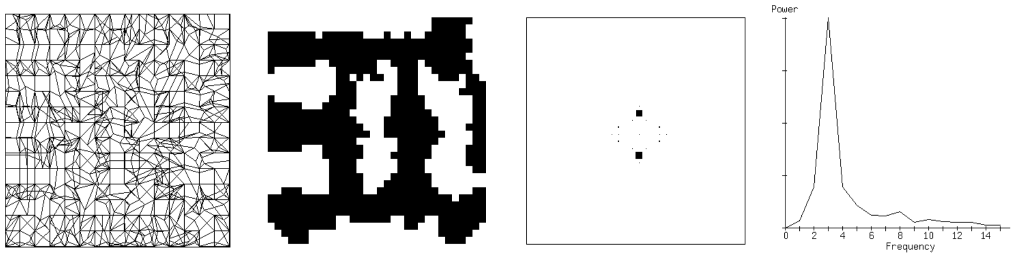
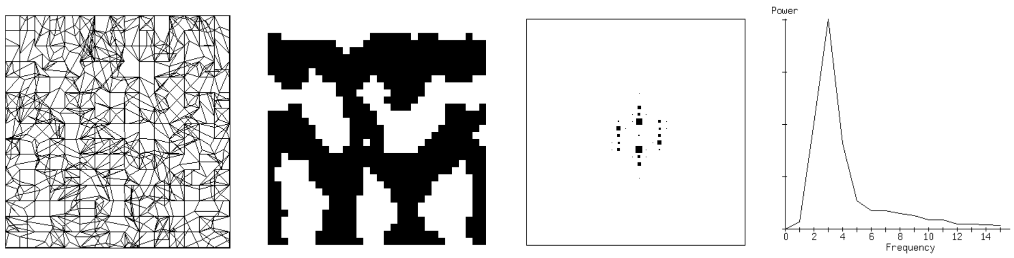
(a)



(b)



(c)



(d)

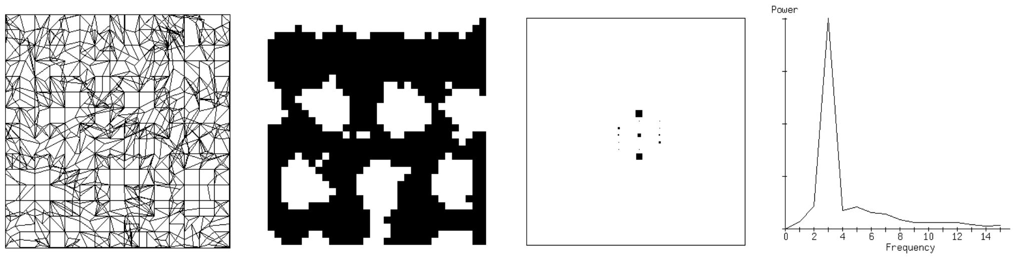


Figure 5.12: Effects of monocular deprivation - Kohonen-type algorithm. In all cases slow annealing and a separation of retinae of 0.2 was used. (a) Normal case. (b) Deprivation parameter = 0.8. (c) Deprivation parameter = 0.6. (d) Deprivation parameter = 0.4.

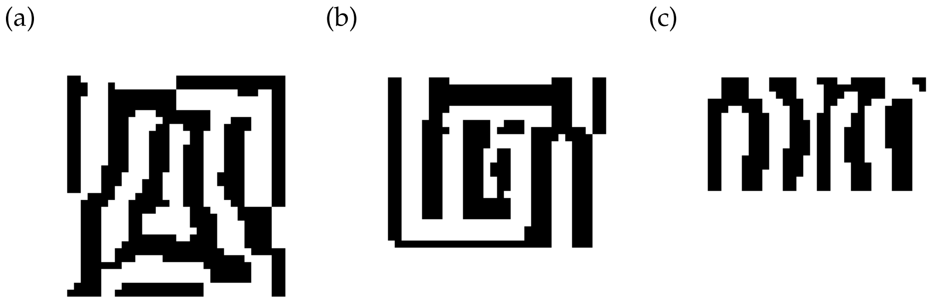


Figure 5.13: Testing the prediction of [LeVay et al 1985] regarding stripe orientation. (a) Normal case: 32×32 points in cortical sheet. (b) 32×24 points in cortical sheet. (c) 32×16 points in cortical sheet. It can be seen there is an increasingly strong tendency towards stripes oriented parallel to the short axis as the cortical sheet becomes more anisotropic. Slow annealing was used.

of ocular dominance in general. It would not be expected to occur in models where there is no consideration of topography (such as [Swindale 1980]), since the effect relies on the undesirability of "stretching", i.e. deformations in topography in certain directions.[3]

5.7 Discussion

We address the following three issues:

- **Representation:** What is the meaning of formulating the problem in these geometric terms, and what is its relationship to biology?
- **Algorithms:** How important is the choice of algorithm? How do the results (e.g. stripe width) depend on the parameters of the model?
- **Relation to other work:** What relation do both this representation and these algorithms bear to other models of topography and ocular dominance?

5.7.1 Representation and algorithms

The notion of a feature space containing the inputs it is desired to represent has been used extensively (see e.g. [Kohonen 1988]). However, a problem that always arises when dimensions having different meanings (such as orientation and position, or ocularity and position) are regarded as the axes of a feature space is that of how "distances" between these features are to be measured, and what such distances actually mean. It is not immediately clear in our case why distances in the ocularity dimension should contribute in exactly the same way as distances in the spatial dimensions. Two arguments can however be made to support this interpretation. Firstly, in the model we directly control the ratio of the separation of units within and between retinae: we assume that they can both be measured in the Euclidean metric, but not what their weightings should be. Secondly, due to our interpretation of distances as correlations, we are claiming that the two types of distance really are measuring the same kind of thing: the correlation between units, whether these units be in the same eye or in different eyes (the same argument also applies to an interpretation in terms of chemical concentrations).

We turn now to the issue of how it was chosen to situate points (retinal units) in the feature space. This brings us directly to the two assumptions mentioned in section 5.3 above. It should be emphasised that, given the correlational interpretation, these are empirical questions: their validity can (at least in principle) be determined by biological experiment. Assuming that there is a relationship between the position of units in feature space

[3]The hypothesis of [LeVay et al 1985] has also recently been tested in [Jones et al 1991]. They exactly minimized a measure of topographic distortion of mapping from two LGNs, and showed that boundary conditions had the predicted effect. However, they did not discuss how such an optimization could be carried out in the biological system, or what determines the width of the stripes in this framework.

and in physical space, and that the same ordering of units applies to both, is essential for the approach to ensure that a mapping that is topographic in feature space is also topographic in physical space. Whether this assumption is valid in reality depends on both the structure of the visual world and on the nature of spontaneous activity in the retina: as we saw in chapter 2, both play a part in map development. The statistics of natural scenes have been investigated in [Field 1987], who found the existence of correlations at all length scales (see also [Hancock et al 1992]. These correlations decrease with distance, as in the representation here. Similarly, [Mastronade 1989, Meister et al 1991] showed that spontaneous firing of retinal ganglion cells was correlated between neighbours and this correlation decreased with distance. It is clear the assumption that the correlation between two units is a function only of their separation in feature space (and hence physical space) is not true on a large scale, due to non-uniform sampling of the visual scene by the retina and non-uniform receptor density over large distances. However, on a local scale, which is the scale addressed in the simulation results presented above, the assumption may be approximately valid. Lastly we observe that the fact that the arrangement of points in feature space is highly regular (in contrast to for instance [Durbin & Mitchison 1990] and [Obermayer et al 1990] (discussed later), algorithms which choose points randomly in their respective feature space according to particular distributions) may be influencing the results. One elastic net experiment that was tried to investigate this was to randomly displace each retinal unit a small distance ($<< d$) from its initial location so as to break the symmetry. Although qualitatively the final stripe pattern was similar, there was a slight difference in the course of development. In the randomly displaced case, the cortical sheet did not become entirely flat, and vertical movement of cortical units during stripe formation was more gradual than in the undisplaced case.

Optimum stripe widths

The optimum stripe width (i.e. the pattern of visitation of retinal units by the cortical sheet that minimizes the sum of distances between neighbouring cortical units in feature space) can in theory be calculated directly for this representation for any combination of the parameters l and d. This was investigated for the one-dimensional case in [Goodhill & Willshaw 1990], where the following results were proved:

- The $\sqsupset$ path (i.e. the 1-D rope runs the entire length of one retina, then changes to the other retina and runs back in the opposite direction: the mapping segregates into non-overlapping regions) is the shortest path for $l > d$.
- Stripes of width 2 units gives the shortest path for $l < d$.
- Stripes of width n units have minimum length when

$$n = 1 + \frac{l^2}{d^2} \tag{5.8}$$

From this last result it follows that the Z path is always longer than the best striped path (the Z path is the counterpart of the $\sqsupset$ path, where now the topographies are laid out side by side rather than being reflected: the rope travels completely from one end of the left eye to the other, and then doubles back and travels the complete length of the right eye in the same direction).

We also note that the elastic net actually minimises distance in the L_2 norm. In this case the optimal stripe width is

$$n = \frac{2l}{d} \tag{5.9}$$

Comparing this with equation 5.8, we see that optimum stripe width increases more slowly with l/d in the L_2 norm than the L_1 norm.

It is difficult to generalize these calculations regarding stripe width to the two dimensional case of interest here, since there is now a much richer space of possibilities for the pattern of stripes, even assuming uniformity. However, it is clear that a similar argument for the generalization of the $\sqsupset$ path in 2-D also holds. Thus we have the significant result that for $l > d$, the case for all the simulation results presented in this chapter, the mapping corresponding to two non-overlapping regions always has a shorter path length than any striped mapping. Why do these algorithms not find these solutions? A possible explanation is that, for the range of l/d we have considered, the two retinae are cooperating over topography but competing over ocularity. Each pair of corresponding retinal units attempts to attract the cortical point(s) in the same topographic location.

5.7.2 Related work

The approach described in this chapter is related to work applying Kohonen's algorithm to a somewhat similar feature space. In [Kohonen 1988, Ritter & Schulten 1988] pictures are briefly presented of an elastic sheet deforming within a three-dimensional block of feature points regularly spaced through the volume of the block, with the suggestion that this could be related to ocular dominance stripe formation. However this is not pursued: this example is just given to illustrate their main point of "automatic selection of feature dimensions". Kohonen-type algorithms cause an elastic rope/sheet to align itself along the main axis/axes of variation in the feature space, with (small) deformations to take account of feature units not on this main axis/axes.

A detailed application of Kohonen's algorithm to a feature space similar to the one investigated here, and the orientation-position case of [Durbin & Mitchison 1990], has been undertaken in [Obermayer, Ritter & Schulten 1991, Obermayer, Blasdel & Schulten 1991]. Although the model was originally presented as a pattern-based competitive learning model [Obermayer et al 1990] (as in the model to be presented in chapter 6), recently these authors have placed greater emphasis on a more abstract, feature-mapping interpretation. This model has already been described in chapter 3. Two important differences between this model and the elastic model are that [Obermayer, Ritter & Schulten 1991] use a set of feature points located at random in the space, and also sometimes consider arbitrary degrees of dominance between the two eyes, as described in chapter 3, whereas we use only feature points which are entirely left-eye or right-eye.

5.8 Conclusions

We have shown that the elastic net and Kohonen-type algorithms can both form topography and ocular dominance from the same mechanisms, and we have investigated their behaviour over a range of parameters. Various measures of the quality of the maps produced have been defined, and these show that in general the elastic net performs slightly better than the Kohonen-type algorithm for parameters chosen such that the time taken by both algorithms is comparable. In addition we have demonstrated that both algorithms can successfully model the effects of monocular deprivation. The behaviour of the elastic net in the case of anisotropic boundary conditions has been shown to agree with the prediction of [LeVay et al 1985].