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Arbitrary Elastic Topologies and Ocular Dominance

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The elastic net, which has been used to produce accounts of the formation of topology-preserving maps and ocular dominance stripes (OD), embodies a nearest neighbor topology. A Hebbian account of OD is not so restricted—and indeed makes the prediction that the width of the stripes depends on the nature of the (more general) neighborhood relations. Elastic and Hebbian accounts have recently been unified, raising a question mark about their different determiners of stripe widths. This paper considers this issue, and demonstrates theoretically that it is possible to use more general topologies in the elastic net, including those effectively adopted in the Hebbian model.

1 Introduction

Durbin and Willshaw's (1987) elastic net algorithm for solving the traveling salesperson problem (TSP) is based on a method for developing topology-preserving maps between the eye and brain (or lateral geniculate nucleus and cortex) due to von der Malsburg and Willshaw (1977) and Willshaw and von der Malsburg (1979). The elastic algorithm inspired a host of similar ones aimed at different optimization tasks, one of which is this topology problem, augmented by two associates—forming ocular dominance stripes and orientation selective cells (Goodhill and Willshaw GW 1990; Durbin and Mitchison 1990).

Simić (1990, 1991) and Yuille (1990) looked at the relationship between elastic algorithms and Hebbian inspired ones (Hopfield and Tank 1985), showing that both mechanisms could be viewed as optimizing the same functions, albeit implementing differently the constraints (for the TSP, that each city should be visited exactly once). More recently, Yuille, Kolodny, and Lee (YKL 1991) repeated the feat and aligned elastic and Hebbian (Miller, Keller, and Stryker, MKS 1989) accounts of ocular dominance.

The elastic net for the TSP consists of a set of points on a computational rubber band, pulled by forces toward the cities that have to be visited and by tension. The energy in a stretched rubber band is proportional to the square of its extension, which is incorrect for modeling the length of a tour (proportional just to the extension, in this model),

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but Durbin (cited as a personal communication in Yuille 1990) suggests that changing the elastic net to use the absolute distance rather than its square is infelicitous. Hopfield and Tank's (1985) model does in fact use the actual distances, and so, as they lucidly discuss, Simić's and Yuille's match between the elastic and Hebbian algorithms is not perfect.

The nature of the topologies is even more mysterious in the match between Hebbian and elastic algorithms for ocular dominance. Topology enters MKS' model through a cortical interaction function, which involves more than just the nearest neighbors. Conversely, these are the natural topology for the elastic version. This is one factor leading to an apparent difference between the predictions of MKS and GW. MKS suggested that the width of ocular dominance stripes is governed by the width of the cortical interaction function, whereas GW predicted that it is dependent on the relative correlations within and between the two eyes.

This paper considers the issue by examining the two models of ocular dominance. The next section reviews YKL's analysis, and Section 3 looks at generalizing the nearest neighbor topology, testing the generalization in a one-dimensional version of ocular dominance.

2 Yuille, Kolodny, and Lee's Analysis

YKL unify the two models through the medium of a single cost function, which defines a generalized deformable model:[1]

$$\begin{aligned} E\left[\mathcal{V}^L, \mathcal{V}^R, Y\right] &= \sum_{ia} \left\{ \mathcal{V}^L_{ai} \left|\mathbf{x}^L_i - \mathbf{y}_a\right|^2 + \mathcal{V}^R_{ai} \left|\mathbf{x}^R_i - \mathbf{y}_a\right|^2 \right\} \\ &\quad + \frac{\nu}{2} \sum_a \left|\mathbf{y}_a - \mathbf{y}_{a+1}\right|^2 \end{aligned} \tag{2.1}$$

where $\mathcal{V}^L_{ai}$ and $\mathcal{V}^R_{ai}$ are the variables matching the ith unit in the left and right eyes (more correctly lateral geniculate nucleus layers), respectively, to the ath unit in the cortex, $\mathbf{x}^L_i$ and $\mathbf{x}^R_i$ are the retinal "positions" of the ith unit in the left and right eyes, $\mathbf{y}_a$ is the "position" of the ath unit in the cortex, and $Y \equiv \{\mathbf{y}_a\}$. As GW and YKL say, these "positions" are defined somewhat abstractly; however, they are intended to capture something like the correlations between the firings of the retinal and cortical units. ν is a constant that governs the relative weighting of the first term, which measures how close, correlationally, matching cells are, and the second term, which measures how close neighboring cortical cells are. This cost function owes its power of unification to having both matching $\mathcal{V}$ and continuous Y variables.

The constraint on both retinal and cortical fields on a solution—that each cell should have a unique partner—is effectively duplicated in these

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[1] For convenience, this paper will look at the one-dimensional versions of the various tasks. Extensions to the second dimension are straightforward, but messy. Also, YKL separate out the retinotopy dimension—whereas it is incorporated here into the continuous variables $\mathbf{x}$ and Y. MKS arbor functions are also neglected.

two sets of variables.[2] Minimizing E subject to these constraints leads to the optimal map. Hebbian and elastic methods are effectively different ways of minimizing this function, imposing different constraints in different manners on the way to deriving a solution. Both use Hopfield and Tank's key insight for the TSP that the constraints need not *all* hold throughout the optimization process, so long as they are guaranteed to be satisfied by the time the algorithm terminates.

The reduction to an elastic net comes from eliminating the $\mathcal{V}^L$ and $\mathcal{V}^R$ variables using a Gibbs trick. The probability of a particular assignment of $\mathcal{V}$ and Y is declared to be proportional to $e^{-\beta E[\mathcal{V}^L,\mathcal{V}^R,Y]}$, and these terms are summed over the set of $\mathcal{V}^R$ and $\mathcal{V}^L$ that satisfy the partial constraint that each cell in the cortex maps to a unit in either the left or the right eye, but not both. The resulting elastic energy function is[3]

$$\begin{aligned} E_{\text{eff}}[Y] &= -\frac{1}{\beta}\sum_a \log\left\{\sum_i e^{-\beta|\mathbf{x}_i^L-\mathbf{y}_a|^2}+e^{-\beta|\mathbf{x}_i^R-\mathbf{y}_a|^2}\right\} \\ &\quad + \frac{\nu}{2}\sum_a |\mathbf{y}_a-\mathbf{y}_{a+1}|^2 \end{aligned} \tag{2.2}$$

Note that the topology term survives this reduction intact, since it does not depend on the $\mathcal{V}$.

The alternative to eliminating the $\mathcal{V}$ variables is to eliminate the Y. YKL do this by regarding $E[\mathcal{V}^L,\mathcal{V}^R,Y]$ as a quadratic form in Y, which has a minimum at $Y_*[\mathcal{V}^L,\mathcal{V}^R]$. Imposing the normalization constraint (see MKS) that each cortical cell receives a constant weight from the retina:

$$\sum_i \mathcal{V}_{ai}^L+\mathcal{V}_{ai}^R = 1 \quad \forall a \tag{2.3}$$

gives

$$(\mathcal{I}+\nu\mathcal{T})Y_*^T = \mathcal{V}^L X^{L^T}+\mathcal{V}^R X^{R^T}$$

where $X^L=\{\mathbf{x}_i^L\}$ and $X^R=\{\mathbf{x}_i^R\}$, and

$$\mathcal{T}_{ab}=\begin{cases} 2 & a=b \\ -1 & a=b+1 \\ -1 & a=b-1 \\ 0 & \text{otherwise}\end{cases}$$

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[2] In terms of these variables: for each a, one of the collection over i of $\{\mathcal{V}_{ai}^L,\mathcal{V}_{ai}^R\}$ should be 1 and all the rest 0, and for each i the same should be true of the collection over a. Also, for each a, $\mathbf{y}_a$ should be the same as one $\mathbf{x}_i^L$ or $\mathbf{x}_i^R$, and for each i, there should be different a_1 and a_2 such that $\mathbf{y}_{a_1}=\mathbf{x}_i^L$ and $\mathbf{y}_{a_2}=\mathbf{x}_i^R$.

[3] Here and throughout, boundary conditions are avoided by assuming toroids and using modulo arithmetic.

embodies the toroidal nearest neighbor topology. Therefore, at the minimum

$$Y_*^T = (\mathcal{I} + \nu\mathcal{T})^{-1}\left(\mathcal{V}^L X^{L^T} + \mathcal{V}^R X^{R^T}\right)$$

where the inverse exists for $\nu > 0$. Substituting back into equation 2.1, imposing the constraints in equation 2.3, and ignoring terms that do not depend on the $\mathcal{V}$, gives

$$\begin{aligned} E\left[\mathcal{V}^L, \mathcal{V}^R\right] &= \frac{1}{2}\sum_{abij}\Big\{(\mathcal{I} + \nu\mathcal{T})_{ab}^{-1}\mathcal{V}_{ai}^L\mathcal{V}_{bj}^L\left|\mathbf{x}_i^L - \mathbf{x}_j^L\right|^2 \\ &\quad + (\mathcal{I} + \nu\mathcal{T})_{ab}^{-1}\mathcal{V}_{ai}^R\mathcal{V}_{bj}^R\left|\mathbf{x}_i^R - \mathbf{x}_j^R\right|^2 \\ &\quad + 2(\mathcal{I} + \nu\mathcal{T})_{ab}^{-1}\mathcal{V}_{ai}^L\mathcal{V}_{bj}^R\left|\mathbf{x}_i^L - \mathbf{x}_j^R\right|^2\Big\} \end{aligned} \tag{2.4}$$

MKS' Hebbian system regards the output o_a of cortical cell a as coming partly from the input from the two eyes i^L and i^R through the connection matrix, $[\mathcal{V}^L i^L + \mathcal{V}^R i^R]_a$, and partly from the other cortical cells $[\mathcal{D}o]_a$ (MKS call $\mathcal{C} \equiv (\mathcal{I} - \mathcal{D})^{-1}$ the cortical interaction function):

$$\begin{aligned} o &= \mathcal{V}^L i^L + \mathcal{V}^R i^R + \mathcal{D}o \\ &= (\mathcal{I} - \mathcal{D})^{-1}\left(\mathcal{V}^L i^L + \mathcal{V}^R i^R\right) \end{aligned} \tag{2.5}$$

Hebbian learning changes $\mathcal{V}_{aj}^L$ proportional to $\langle o_a i_j^L\rangle$, where the angle brackets represent an averaging process. Defining

$$D_{jk}^{LL} = \langle i_j^L i_k^L\rangle, \quad D_{jk}^{RR} = \langle i_j^R i_k^R\rangle, \quad \text{and} \quad D_{jk}^{LR} = \langle i_j^L i_k^R\rangle$$

YKL show that the $\mathcal{V}$ are moving down the gradient of

$$\begin{aligned} E_{\mathrm{MKS}}\left[\mathcal{V}^L, \mathcal{V}^R\right] &= -\frac{1}{2}\sum_{abij}\Big\{(\mathcal{I} - \mathcal{D})_{ab}^{-1}\mathcal{V}_{ai}^L\mathcal{V}_{bj}^L D_{ij}^{LL} \\ &\quad + (\mathcal{I} - \mathcal{D})_{ab}^{-1}\mathcal{V}_{ai}^R\mathcal{V}_{bj}^R D_{ij}^{RR} \\ &\quad + 2(\mathcal{I} - \mathcal{D})_{ab}^{-1}\mathcal{V}_{ai}^L\mathcal{V}_{bj}^R D_{ij}^{LR}\Big\} \end{aligned} \tag{2.6}$$

Compare equations 2.4 and 2.6. YKL argue that for the intent of comparing minima, one can identify $K - |\mathbf{x}_i^L - \mathbf{x}_j^L|^2$ with D_{ij}^{LL} and similarly for D_{ij}^{RR} and D_{ij}^{LR}, for some constant K. Therefore, if $-\mathcal{D} = \nu\mathcal{T}$, these two expressions will have the same interesting minima—so, provided that the constraints are properly satisfied during learning, they should lead to the same ultimate solution.[4] Note that this can make the effective correlations negative at some distance, which, as MKS discuss, allows correlation width to determine stripe width in their model.

The cortical interaction function calculated from $\mathcal{T}$ (using $\nu = 3/4$) is shown in Figure 1. Although YKL show that this is enough to pro-

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[4] YKL actually derive a different condition for matching—that $\xi\mathcal{T} = (\mathcal{I} - \mathcal{D})^{-1}$ for some constant ξ. The truth of this would appear to depend on $\sum_{aij}\mathcal{V}_{ai}^L\mathcal{V}_{aj}^R|\mathbf{x}_i^L - \mathbf{x}_j^L|^2$, and the similar expressions for $\mathcal{V}^R\mathcal{V}^R$ and $\mathcal{V}^R\mathcal{V}^L$, being constant over the $\mathcal{V}$ that satisfy the partial constraints.

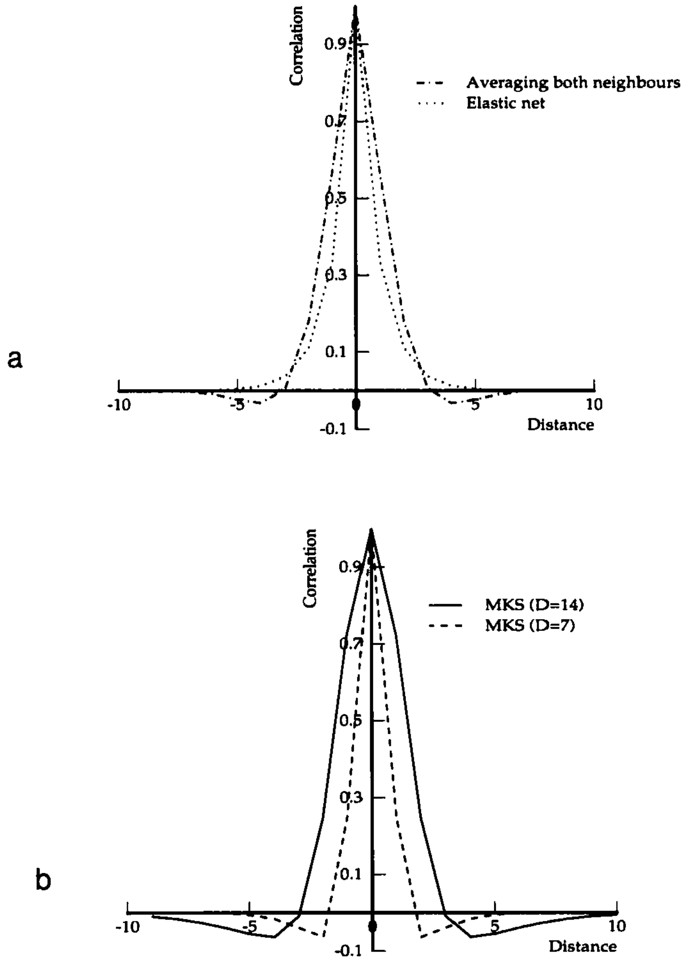

Figure 1: Cortical interaction functions. (a) Elastic topologies. (b) MKS topologies.

duce interesting ocular dominance stripes, it is clearly not the same as MKS' cortical interaction function, which is shown in the same figure. One reason why elastic and Hebbian models make different predictions about the factors determining stripe widths is also obvious—the cortical interaction function corresponding to the elastic topology is immutable. The next section considers alternatives.

3 Generalizing Elastic Topologies

The shape of the interaction function comes from the term $\sum_a |\mathbf{y}_a - \mathbf{y}_{a+1}|^2$ in equation 2.1. A more general quadratic form for this is

$$\sum_{ab} \mathcal{S}_{ab} \mathbf{y}_a^T \mathbf{y}_b = \mathrm{tr}\left\{Y^T Y \mathcal{S}\right\} \tag{3.1}$$

For instance, if $\mathcal{S} = \mathcal{T}$, then this reduces to exactly the same expression as in equation 2.1. Note also that this formulation is sufficiently general as to model the case of two-dimensional retinas and cortex, although it does not extend to nonquadratic cases such as the length rather than the square of the length for the TSP.

Such a change has little effect on the elastic energy function from equation 2.2, which becomes

$$E_{\mathrm{eff}}[Y] = -\frac{1}{\beta} \sum_a \log\left\{\sum_i e^{-\beta|\mathbf{x}_i^L - \mathbf{y}_a|^2} + e^{-\beta|\mathbf{x}_i^R - \mathbf{y}_a|^2}\right\} + \frac{\nu}{2} \mathrm{tr}\left\{Y^T Y \mathcal{S}\right\}$$

However, differentiating E as a quadratic form to eliminate the Y leads to

$$(\mathcal{I} + \nu\mathcal{S}) Y_*^T = \mathcal{V}^L X^{L^T} + \mathcal{V}^R X^{R^T}$$

assuming that $\mathcal{S}$ is symmetric. If $\mathcal{S}$ also has a similarity property such that $\sum_b (\mathcal{I} + \nu\mathcal{S})_{ab}^{-1}$ does not depend on a,[5] then substituting back in gives the energy function

$$\begin{aligned} E\left[\mathcal{V}^L, \mathcal{V}^R\right] &= \frac{1}{2} \sum_{abij} \left\{ (\mathcal{I} + \nu\mathcal{S})_{ab}^{-1} \mathcal{V}_{ai}^L \mathcal{V}_{bj}^L \left|\mathbf{x}_i^L - \mathbf{x}_j^L\right|^2 \right. \\ &\quad + (\mathcal{I} + \nu\mathcal{S})_{ab}^{-1} \mathcal{V}_{ai}^R \mathcal{V}_{bj}^R \left|\mathbf{x}_i^R - \mathbf{x}_j^R\right|^2 \\ &\quad \left. + \ 2(\mathcal{I} + \nu\mathcal{S})_{ab}^{-1} \mathcal{V}_{ai}^L \mathcal{V}_{bj}^R \left|\mathbf{x}_i^L - \mathbf{x}_j^R\right|^2 \right\} \end{aligned}$$

As above, setting $\mathcal{D} = -\nu\mathcal{S}$ to unify the elastic and Hebbian energy functions allows Hebbian modeling of arbitrary elastic topologies and vice versa.

One way of generating elastic topologies is to consider them in terms of an estimation problem. Say that $\sum_b \mathcal{E}_{ab} \mathbf{y}_b$ is an estimate of $\mathbf{y}_a$. Then, the total square estimate error is

$$\sum_a \left|\mathbf{y}_a - \sum_b \mathcal{E}_{ab} \mathbf{y}_b\right|^2 = \sum_{ab} [(\mathcal{I} - \mathcal{E})^T (\mathcal{I} - \mathcal{E})]_{ab} \mathbf{y}_a^T \mathbf{y}_b$$

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[5] This holds if the topology is the same over the whole cortex.

Comparing this with equation 3.1 shows that $\mathcal{S} = (\mathcal{I}-\mathcal{E})^T(\mathcal{I}-\mathcal{E})$. $\mathcal{T}$ can be generated this way, by making $\mathcal{E}_{a(a+1)} = 1$ and the remaining components 0. Another example comes from estimating $\mathbf{y}_a$ as the average of both its neighbors, that is, setting

$$\begin{aligned} \mathcal{E}_{ab} &= \frac{1}{2}\begin{cases} 1 & b = a+1,\ b = a-1 \\ 0 & \text{otherwise} \end{cases} \\ &\Longrightarrow \mathcal{S}_{ab} = \frac{1}{4}\begin{cases} 6 & b = a \\ -4 & b = a+1,\ b = a-1 \\ 1 & b = a+2,\ b = a-2 \\ 0 & \text{otherwise} \end{cases} \end{aligned} \tag{3.2}$$

whose associated cortical interaction function more closely resembles the MKS Mexican hats (see Fig. 1). Note that although for any $\mathcal{E}$ there is a unique associated $\mathcal{S}$ and therefore $\mathcal{C}$, the same is not true the other way around. Symmetric $\mathcal{S}$ will only have a square root if all its eigenvalues are positive, and it is easy to generate seemingly plausible $\mathcal{C}$ for which this is not the case.

MKS generated their $\mathcal{C}$ as

$$\mathcal{C}_{ab} = e^{-\frac{|a-b|^2}{(\kappa D)^2}} - \frac{1}{9}e^{-\frac{|a-b|^2}{(3\kappa D)^2}} \tag{3.3}$$

where $\kappa = 1/7.5$ and $D = 7$ was the width of their arbor function (the number of cortical cells to which a retinal cell would connect). Changing D changes the length scale of the cortical interaction, and so changes the optimal stripe width. Figure 1 shows graphs of the elastic net cortical interaction function, the Mexican hat one from equation 3.2, and two generated from MKS—one with $D = 7$ and one with $D = 14$.

One way to test the generalized topology terms is to use them in the cost function of equation 2.1 and to consider the optimal stripe width for the ocular dominance maps this defines.[6] It is convenient to study the one-dimensional case, since the interesting optima are just "Z" folds, as in the left-hand side of Figure 2 (after GW). Maps inspired by the sideways "U" shape on the right-hand side of the figure will, in many cases, have lower costs than these—however, they are ruled out as the cortex does not traverse the retinas appropriately. Given particular spatial locations of the retinal cells, it is straightforward to calculate the cost per unit length of Z-folds of varying widths—the width that minimizes this is the one both Hebbian and elastic algorithms should find.

GW show that the optimal width of a stripe for the basic elastic topology is $2l/d$, where l is the separation of the two retinas and d is the distance between two cells within a retina. Simulations verified this, using the elastic net topology $\mathcal{T}$. Note that increasing l increases $|\mathbf{x}_i^L - \mathbf{x}_j^R|^2$ in the third term of equation 2.4, leaving the other distance terms unaltered.

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[6] If the appropriate constraints are satisfied, one of the equivalent equations such as 2.4 can also be used.

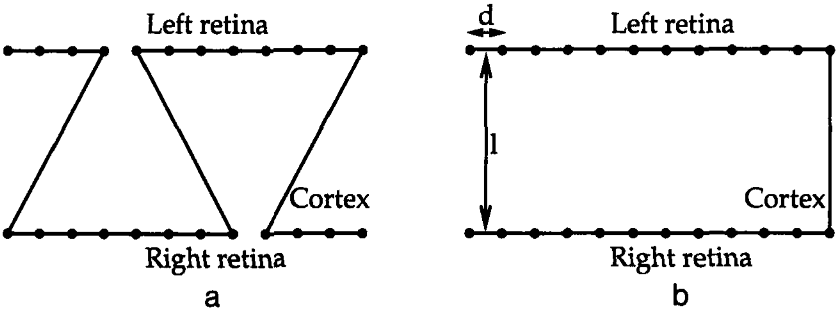

Figure 2: One-dimensional ocular dominance maps. (a) "Z"-fold stripes. (b) Optimal map.

For the MKS topology, the optimal width should increase with D, the length scale of the cortical interaction function. The analysis above suggests that it should also increase with l, given the common energy function. Both of these are demonstrated in Figure 3, which shows how the optimal Z-fold stripe width w varies with both l and D. With the exception of the patch for low l and high D, this is monotonic in both variables.

Note that as D increases, the matrix C becomes increasingly singular, which forces implausible constraints on the cortical connectivity. Also small stripes are favored for large D and small l, since they benefit more from the negative contributions from the influences of widely separated cells than they lose through the cost of switching between the retinas. In fact the cost function becomes at least trimodal in the width of the stripes in this regime; one optimum is at the minimum stripe width, another is at the sideways "U" of Figure 2, and the third is at the width that would preserve monotonicity in Figure 3.

4 Discussion

It is natural to wish to incorporate more extensive topologies into the elastic net than the nearest neighbor one with which it is presently endowed. One particular motivation for this comes from the apparent conflict between the predictions of stripe width from the elastic and Hebbian theories of the development of ocular dominance. However it is important in other cases such as graph matching in von der Malsburg's (1981) correlation theory of brain function. In this, fine scale temporal correlations in the firing of cells in a field are determined by the topology of the object being represented on that field, and inference consists of matching

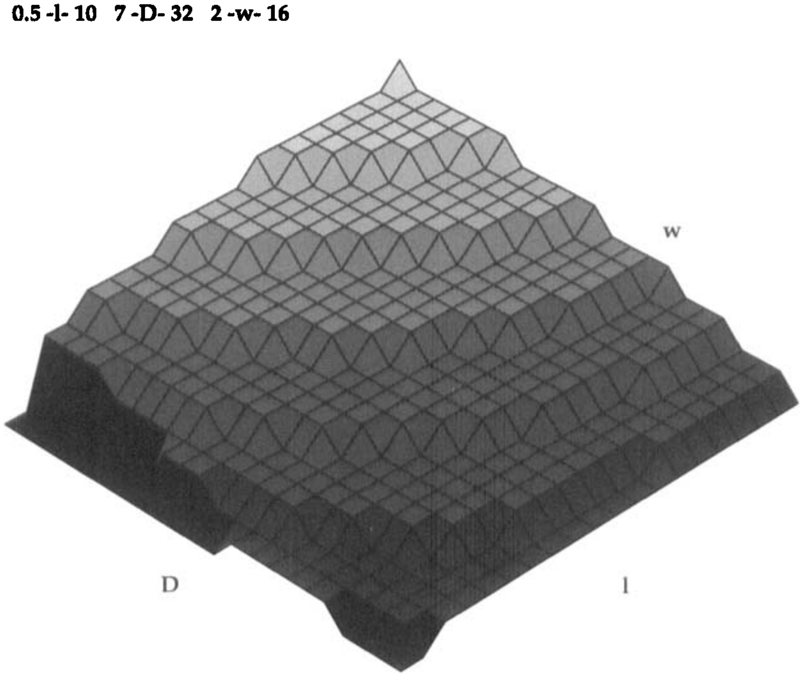

Figure 3: Optimal Z-fold stripe width w versus length scale D of the cortical interaction function and distance l between the retinas. The cost function values E were calculated from equation 2.4, replacing $(\mathcal{I}+\nu\mathcal{T})^{-1}$ with C generated using equation 3.3.

this graph with an isomorphic one on another field. If the fine scale temporal correlations embody more than nearest neighbor correlations (and inference will be faster if they do), then describing this process in elastic terms will require a more general topology too.

This paper has used the formalism of generalized deformable models to consider how general topologies fit into an elastic net framework. It demonstrates that this is effective by showing how the optimal stripe widths theoretically change with changing cortical length scales. However, it does remain to be seen which of the alternatives lead to stable elastic algorithms. Designer topologies are as simple to specify as designer error functions, and it will be interesting to see if there is an equivalent wealth of well-motivated examples.

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