Correlational-Based Development of Disparity Sensitivity

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Abstract

A correlational-based model of development of disparity sensitivity is proposed. The weights between two one-dimensional input layers and a single cortical layer were modified by a linear Hebb rule using fixed correlation matrices both within and between eyes and fixed cortical connections. With local correlations, the delayed presentation of a slight amount of between-eye correlation led to the development of both binocular cortical cells with the left and right receptive fields aligned, i.e. zero disparity and monocularly dominated cells, which tended to have non-zero disparity preferences.

Introduction

The development of response properties of neurons in the mammalian visual cortex depends on visual experience during a critical period (1). This plasticity is dependent on the statistics of the pattern of neural activity on both the geniculocortical inputs and the cortical neurons themselves (2, 3, 4, 5).

The mechanism of depth perception has been extensively studied, and the disparity selectivity of cortical neurons probably plays a central role. Disparity is the relative difference in position in the two retinas on which an image is cast, and disparity sensitivity refers to the ability of cortical cells to detect relative image displacements between the two eyes. The random-dot stereogram showed that disparity is sufficient, although not necessary, to perceive depth (6). Many disparity selective neurons are maximally stimulated when presented with either

convergent, divergent, or zero disparity (7, 8). In this study we address the problem of how the disparity sensitivity of cortical neurons develops.

We assume that development of disparity sensitivity is activity dependent and driven by correlations both within and between the retinas. Several different models have been proposed exploring how visual cortex structures such as ocular dominance columns (9, 10, 11, 12) and orientation selectivity (13, 14) might develop by virtue of the correlations in retinal activity. In these models, orientation and ocular dominance are not explicitly specified but emerge through competition and cooperation for cortical synapse sites, with the more correlated cells reinforcing their synapses and the uncorrelated cells weakening theirs. We sought to identify the conditions that would allow the development of a population of cortical cells sensitive to a range of disparities within this simple framework. In general, we find that this type of model allows the development of cortical cells with a range of disparity selectivity and that by allowing development to occur in two phases, corresponding to prenatal and postnatal periods, the experimentally observed relationship between ocular dominance and disparity emerges (15, 16, 17).

Methods

Initial visual development was modeled with two one-dimensional input layers, representing the retinas of the left and right eyes, fully connected with synaptic weights to a one-dimensional cortical layer of the same size (Fig. 1). This is the same as in Miller et al. (10, 18) except that only a few columns of cortex were simulated, the arbor function of the retinal cells was flat, and the model was one-dimensional. Fixed lateral connections were used to represent the influence of one cortical cell on another.

A linear Hebb rule was used to model the changes in synaptic strength between the retinas and the cortex using correlations C^{LL} and C^{RR} within the eyes, and C^{LR} and C^{RL} between the eyes. A lower bound of zero was imposed on the weights. Weights were also normalized using a combination of subtractive and multiplicative procedures, thus keeping the total input to a cortical cell constant. A transition from predominately subtractive to multiplicative normalization was necessary to stabilize mixtures of both monocular and binocular cells.

The form of the correlation matrices as well as the fixed cortical interaction matrix were Gaussian. C^{LL} and C^{RR} were equal to each other and constructed such that each retinal point was locally correlated with its neighbors with a Gaussian distribution. C^{LR} and C^{RL} were also Gaussian and equal to each other but with four times the variance and 0.2 times the amplitude. The cortical interaction matrix, which represented fixed intracortical connections, was generated by a difference of short and long range Gaussians, giving a "Mexican hat" influence function. The width, or standard deviation, of each Gaussian function relative to the layer size was: 0.05 for the same-eye correlation
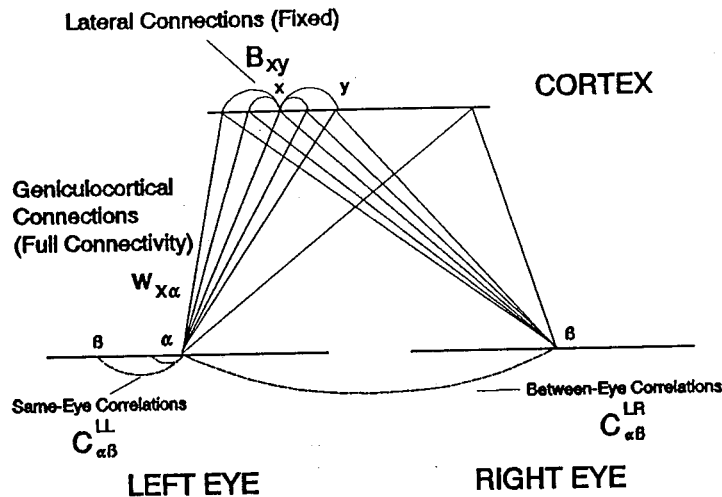
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Figure 1. Schematic diagram of the model of visual cortex development. The model consists of a one-dimensional layer for each eye fully connected to a one-dimensional cortex of the same size. The cortex also contained fixed lateral connections.

function; 0.10 for the between-eye function; and 0.05 for the positive component of the cortical interaction function and 0.15 for the negative component (but with 1/9 amplitude).

Binocularity is obviously necessary to develop disparity sensitive cells with a single cortical layer. Miller (10, 18) analyzed the development of ocular dominance, and Dayan and Goodhill (19) showed how binocularity could arise from between-eye correlations. However, there are two trade-offs. If the between-eye correlations are too small, all cells become monocularly dominated; conversely, if the between-eye correlations are too strong, then the cells all become responsive to both eyes, but with zero disparity. Although it is possible to balance both the same-eye and between-eye correlations and adjust the normalization procedure so that both monocularity and binocularity are equally favored, this is unstable. If between-eye correlations are introduced only after development has commenced, some cells will have progressed too far towards monocularity to be perturbed. The cortical interaction function does not affect this outcome and simply ensures that cortical cells are generally consistent with their neighbors. We therefore searched for conditions that would produce patches of relative ocular dominance, involving cells of nonzero but smoothly varying disparity, with boundaries of cells responsive to both eyes, but with zero disparity.

The amplitude of the correlation matrices was varied to model three different developmental paradigms. In the first model, the between-eye correlations were set to zero ($C^{LR}=C^{RL}=0$), corresponding to an animal whose visual cortex development is completely prenatal. In the second model, correlations were added between the eyes, which might occur in an animal whose visual cortex development is completely postnatal. The third model had two phases: one phase with only same-eye correlations, and the second with both same-eye and between-eye correlations, a circumstance in which visual cortex development has both prenatal and postnatal components. The amplitude of the between-eye correlation relative to the same-eye was, respectively in these three paradigms, 0.0, 0.2, and 0.2. Retinal and cortical layers had 60 cells each, and periodic boundary conditions were adopted to avoid edge effects. For all results reported here, initial weights were randomly assigned and ranged from 0.49 to 0.51, but the same results were obtained with a range of initial weights of 0.4 to 0.6. Computer simulations were run on a Sun SparcStation 2, a complete model taking 800 iterations, or three hours of run time, to develop to a stable pattern.
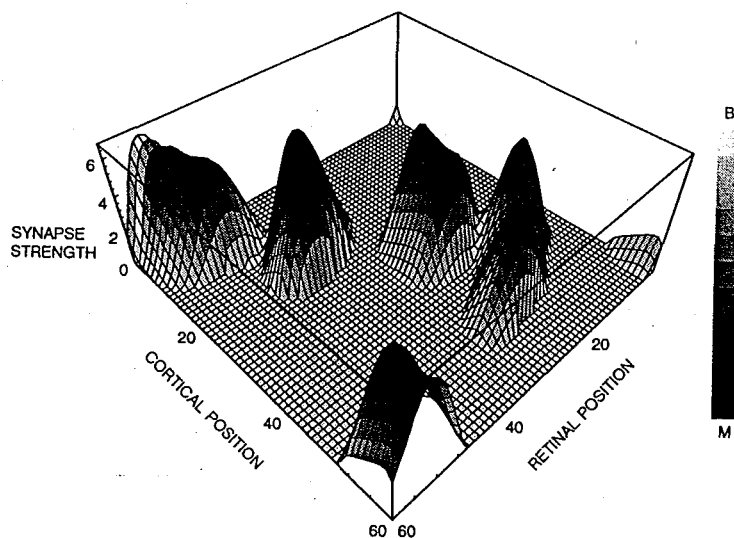

Figure 2. Final development of geniculocortical connections in a model with same-eye correlations only. The height represents the total input from a retinal location in both eyes to a cortical cell, while monocularity is given by shading.

Ocular dominance was calculated for each cortical cell as the difference between the total synaptic input from the right eye and the total synaptic input from the left eye. This was normalized to the total synaptic strength, which was constant. Ocular dominance for each cortical cell was defined by $(R-L)/(R+L)$ where R was the total input from the right eye and L was the total input from the left

eye. Thus ocular dominance ranged from -1.0 (completely dominated by the left eye) to 1.0 (completely dominated by the right eye). Disparity sensitivity for a given cortical cell was calculated by first determining the left and right receptive fields, including both the direct and intracortical inputs. The receptive fields were then summed at each retinal position and the peak response in the field noted. This was then repeated with successive shifts of the receptive fields, the shift with the maximum peak response representing the best disparity. It should be noted that this method cannot define disparity for completely monocular cells since shifting the receptive fields has no effect when one is uniformly zero.
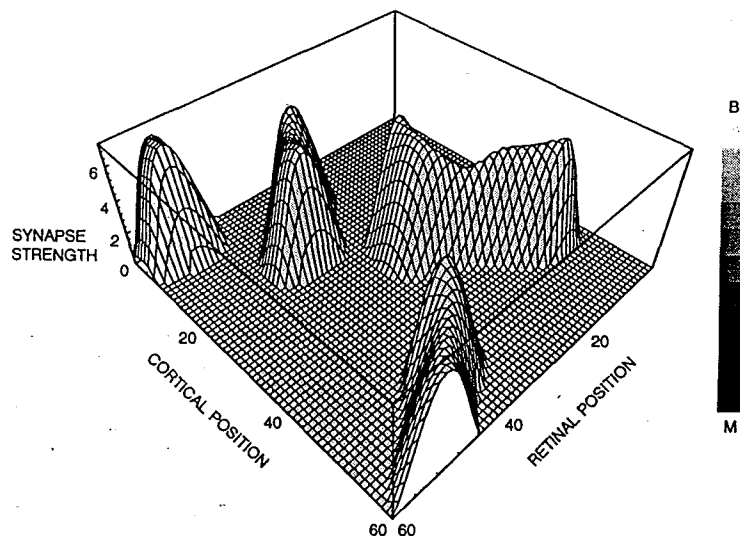

Figure 3. Final geniculocortical connections in a model with both same-eye and between-eye correlations throughout development. The presence of between-eye correlations early in development led to an exclusively binocular cortex.

Results

In geniculocortical development with same-eye correlations only, the first feature to appear was the localization of the receptive fields, which appears as peaks in Fig. 2. The scale of the peaks in the retinal direction was determined by the width of the correlation function and was seen to correspond to the Gaussian width of the same-eye correlations. As discussed by Miller (18), the cortical scale of the peaks was determined by the width of the cortical interaction function, which in these simulations was the same as the width of the same-eye correlations. The peaks were organized along diagonal bands, which reflected the tendency of the model to form topographics maps because of the cortical interaction function. In a mature network, nearly all the receptive fields were found to be monocular, illustrated by the dark peaks. Most of the cortical cells were completely dominated by one of the eyes, and the periodicity of ocular

dominance across the cortex corresponded to the width of the cortical interaction function. The presence of between-eye correlations throughout development led to a cortex full of binocular cells (Fig. 3). The ocular dominance was effectively 0.0 across the cortex, and most cells had zero disparity.
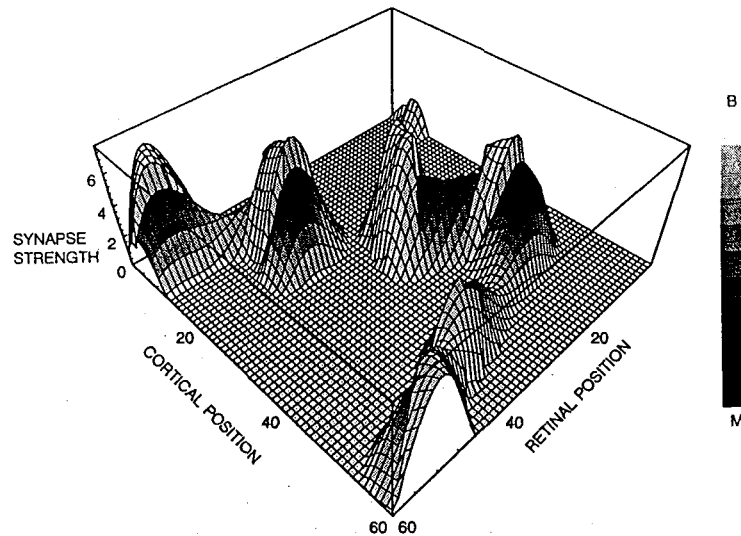

Figure 4. Final geniculocortical connections in a model with two-phase development. Initial same-eye correlations were followed by the addition of between-eye correlations, leading to the development of both monocular and binocular cells.

The two-phase development led to a mixture of both monocular and binocular cortical cells. Approximately half of the cortical cells were monocularly dominated, but there were zones of binocularity at the transition between left and right eye dominance (Fig. 4). The pattern of ocular dominance and disparity was similar to the other two paradigms but with a relatively even distribution of monocular and binocular cells. The scatter plot in Fig. 5 shows that the binocular cells tended to have zero disparity while the more monocular cells had nonzero disparity.

Discussion

The model of visual cortex development described here should be interpreted as a highly simplified representation of activity-dependent development. First, we made a number of architectural simplifications to reduce the complexity of a two-dimensional cortex to a one-dimensional problem; second, we have used a linear version of Hebb's rule of synapse modification. However, this model does address the experimental evidence of species-dependent differences of visual development. Monkeys have a high proportion of monocular cells in area 17, particularly layer IV, whereas cats are known to have predominantly
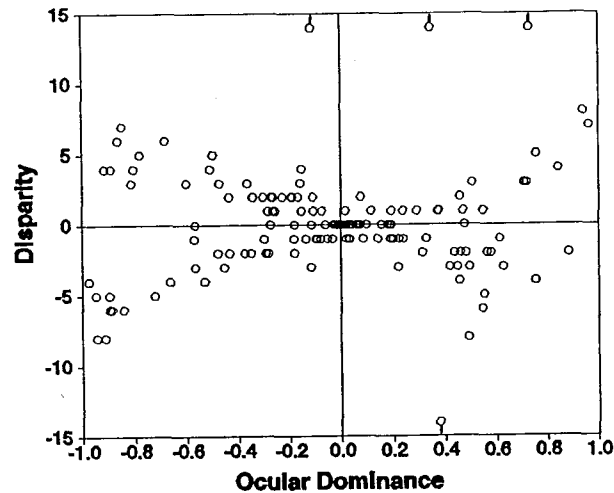
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Figure 5. Scatter plot of disparity vs. ocular dominance for three simulations using different initial conditions. There is a tendency for cells with balanced ocular dominance to have best disparities near zero.

binocular cells in area 17. Furthermore, the binocular cells in area 17 of the cat tend to be of the tuned excitatory type, i.e. cells with best disparity of zero (15). The species difference can be explained most simply by timing differences (Michael Stryker, personal communication). Primate visual cortex development begins prenatally and, according to our model, should be driven by locally correlated activities within each eye. However, between-eye correlations are not present, and so lead to monocular cortical cells. The cat, however, has a greater proportion of its visual development postnatally when binocular correlations are present because both eyes are stimulated similarly. Thus the cat is expected to have a greater proportion of binocular cells, and furthermore, these cells should have zero disparity if the cats' vergence apparatus is intact.

These predictions emerge from our model, as does the finding in the cat (15, 16, 17) that the binocular cells tend to have best disparity of zero, while the more monocular cells have less of a preference for zero disparity. In the linear Hebb model described here, we could only generate such a relationship between ocular dominance and disparity using a two-phase paradigm. Although it was possible to achieve a mixture of monocular and binocular cells with single-phase paradigms, such as those using same-eye anti-correlations (18), it was not possible to achieve a systematic relationship between ocular dominance and disparity similar to that obtained with the two-phase model. Our model is based on a number of simplifying assumptions; however, we believe that the main conclusions will hold for more general correlation-based models of development.

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