# A Correlational Model for the Development of Disparity Selectivity in Visual Cortex that Depends on Prenatal and Postnatal Phases

Gregory S. Berns; Peter Dayan; Terrence J. Sejnowski

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# A correlational model for the development of disparity selectivity in visual cortex that depends on prenatal and postnatal phases

GREGORY S. BERNS, PETER DAYAN, AND TERRENCE J. SEJNOWSKI*

Howard Hughes Medical Institute, Computational Neurobiology Laboratory, Salk Institute for Biological Studies, P.O. Box 85800, San Diego, CA 92186-5800

**ABSTRACT**    Neurons in the visual cortex require correlated binocular activity during a critical period early in life to develop normal response properties. We present a model for how the disparity selectivity of cortical neurons might arise during development. The model is based on Hebbian mechanisms for plasticity at synapses between geniculocortical neurons and cortical cells. The model is driven by correlated activity in retinal ganglion cells within each eye before birth and additionally between eyes after birth. With no correlations present between the eyes, the cortical model developed only monocular cells. Adding a small amount of correlation between eyes at the beginning of development produced cortical neurons that were entirely binocular and tuned to zero disparity. However, if an initial phase of purely same-eye correlations was followed by a second phase of development that included correlations between eyes, the cortical model became populated with both monocular and binocular cells. Moreover, in the two-phase model, binocular cells tended to be selective for zero disparity, whereas the more monocular cells tended to have nonzero disparity. This relationship between ocular dominance and disparity has been observed in the visual cortex of the cat by other workers. Differences in the relative timing of the two developmental phases could account for the higher proportion of monocular cells found in the visual cortices of other animals.

The development of visual cortex in mammals depends on electrical activity in the geniculostriate pathway both prenatally and during a postnatal critical period (1–5). Several models have been proposed to account for how the properties of cortical neurons such as ocular dominance (OD) (6–9) and orientation selectivity (10, 11) might develop through activity-dependent plasticity. Most assume that correlational mechanisms determine which synapses are created and which subsequently survive. In their simplest forms, synapses change strength according to the correlations between presynaptic and postsynaptic activity (12). In this study we sought conditions that allow cortical cells to develop selectivity for binocular disparity.

Depending on the distance from the plane of fixation, objects cast images on the left and right retinae with various disparities. Some cells in the primary visual cortex respond maximally to stimuli at this plane (which corresponds to zero disparity), others to stimuli nearer (positive disparity, by convention) or farther (negative disparity) (13–15). Disparity-sensitive cells can be classified as either simple or complex, depending on the nature of their response (15, 16). In this paper we modeled only simple cells, for which displacement between the receptive fields of the two eyes may underlie disparity tuning (16). A consistent relationship has been observed between the disparity sensitivity of cells and the monocularity (i.e., degree of responsiveness to stimulation from just one eye), more binocular cells tending to have disparities closer to zero (15–19).

We have studied the relationship between OD and disparity sensitivity in a simple Hebbian model which is capable of generating a range of stable monocular and binocular cells. The general constraints on our model were dictated by the anatomy of the geniculocortical projection, the intracortical connectivity, and the pattern of correlations likely to be present along input fibers to visual cortex early in development. By the Hebbian mechanism, a cortical cell can ultimately have substantial connections from both eyes if the correlations between the inputs from the eyes are high, corresponding to zero disparity. Conversely, if a cortical cell has a weaker connection from one eye than the other, then it can sustain weaker correlations between the inputs, as in nonzero disparity. We found these conditions to obtain in a model with two phases of development: the first, prenatal, phase, with monocular input correlations, and the second, postnatal, phase having binocular correlations.

## METHODS

**The Model.** Initial visual development was modeled with two one-dimensional input layers, representing the retinae of the left and right eyes, fully connected with synaptic weights to a one-dimensional cortical layer of the same size (Fig. 1). Fixed lateral connections were used to represent the influence of one cortical cell on another. This was the same as in Miller *et al.* (7, 20) 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.

A linear Hebb rule, together with the normalization discussed below, was used to model the changes in synaptic strength between the retinae and the cortex. The effective change at each iteration, after averaging over input patterns (21), was given by

$$\Delta w_{x\alpha}^{L} = \lambda \sum_{y} \sum_{\beta} K_{xy}(w_{y\beta}^{L}C_{\alpha\beta}^{LL} + w_{y\beta}^{R}C_{\alpha\beta}^{LR})$$

$$\Delta w_{x\alpha}^{R} = \lambda \sum_{y} \sum_{\beta} K_{xy}(w_{y\beta}^{L}C_{\alpha\beta}^{RL} + w_{y\beta}^{R}C_{\alpha\beta}^{RR}), \qquad [1]$$

where $w_{x\alpha}^{L}$ was the strength of the synapse connecting retinal position $\alpha$ in the left eye to cortical position $x$; $\lambda$ was a rate constant; $K$ was the cortical interaction matrix which governed the influence of one cortical cell over another, defined by $K = (I - B)^{-1}$, where $I$ was the identity and $B$ was the cortical connection matrix; $C^{LL}$ and $C^{RR}$ were matrices representing the correlations in input activity within geniculocortical cells representing either left or right eyes; and $C^{LR}$ and $C^{RL}$ were corresponding matrices representing correlations between right and left eyes. Weights were not allowed to become negative, and any weight that became zero was frozen at that value—i.e., making $\Delta w = 0$, which effectively removed it from further development.

Abbreviation: OD, ocular dominance.
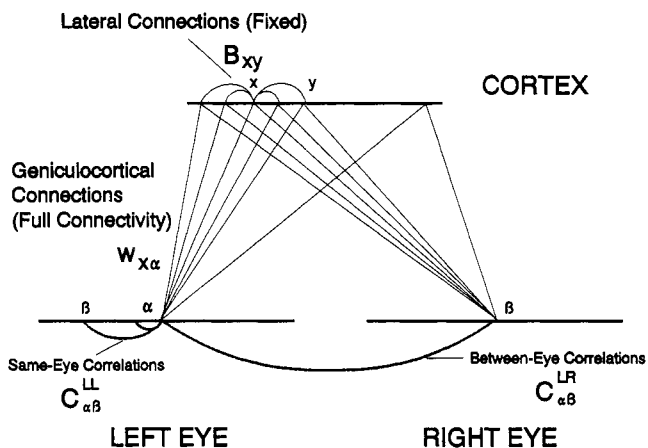*To whom reprint requests should be addressed.

FIG. 1. Schematic diagram of the model of visual cortex development. The model consists of a one-dimensional layer for each eye, positions in which are given by $\alpha$, fully connected to a one-dimensional cortex of the same size, positions in which are given by $x$. The geniculocortical connections are excitatory only, and the strengths of the synapses, given by $w_{x\alpha}$, are modifiable by a linear Hebb rule. The cortex also contains fixed lateral interactions, given by the matrix $B_{xy}$, which can be either excitatory or inhibitory. Activity correlations are illustrated as either same-eye, $C^{LL}$, or between-eye, $C^{LR}$, and are given by Gaussian functions of various amplitudes.

The form of the correlation matrices as well as the fixed cortical interaction matrix was Gaussian. $C^{LL} = C^{RR}$ and $C^{LR} = C^{RL}$, but the between-eye correlations, when used, were taken to have 4 times the variance and ⅕ of the amplitude of the same-eye correlations. The cortical interaction matrix 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 function; 0.10 for the between-eye function; and 0.05 for the positive component of the cortical interaction matrix and 0.15 for the negative component (but with ⅑ amplitude).

**Normalization.** A combination of subtractive and multiplicative normalization was used, forcing the total input weight to a given cortical cell to be constant and so preventing weights from growing without bound. An amount given by

$$\frac{1}{N} \sum_\alpha (\Delta w_{x\alpha}^L + \Delta w_{x\alpha}^R) \qquad [2]$$

was subtracted from each input to cortical cell $x$, where $N$ was the total number of inputs (120 in our simulations), with the exception that weights that would become less than 0 after the subtraction were frozen at 0. All weights were then multiplied by a factor to keep constant their sum in the face of this lower limit. As more weights became zero, the subtractive step played a lesser part, and the final, multiplicative, step played a greater one. Thus, there was a gradual transition from purely subtractive constraints early in development to predominantly multiplicative constraints later in development, which was separate and independent of the prenatal/postnatal correlation changes. Miller *et al.* (7, 20) used almost pure subtractive normalization, employing the number of nonzero weights rather than $N$ in Eq. 2 and also an upper bound on the weights. K. Miller (personal communication) has pointed out that another way to achieve a mixture of OD would be to have constant weak binocular correlations, wholly subtractive normalization, and top limits to synaptic weights.

**Simulations.** Retinal and cortical layers had 60 cells each, with periodic boundary conditions 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 to develop to a stable pattern (with $\lambda = 0.0025$).

The amplitudes of the correlation matrices were varied to model three different developmental paradigms. In the first, between-eye correlations were set to zero ($C^{LR} = C^{RL} = 0$), corresponding to an animal for which the development of the visual cortex is completely prenatal. In the second, correlations were added between the eyes, as for an animal with completely postnatal development. The third had two phases: one phase with only same-eye correlations, and the second with both same-eye and between-eye correlations, modeling development with 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.
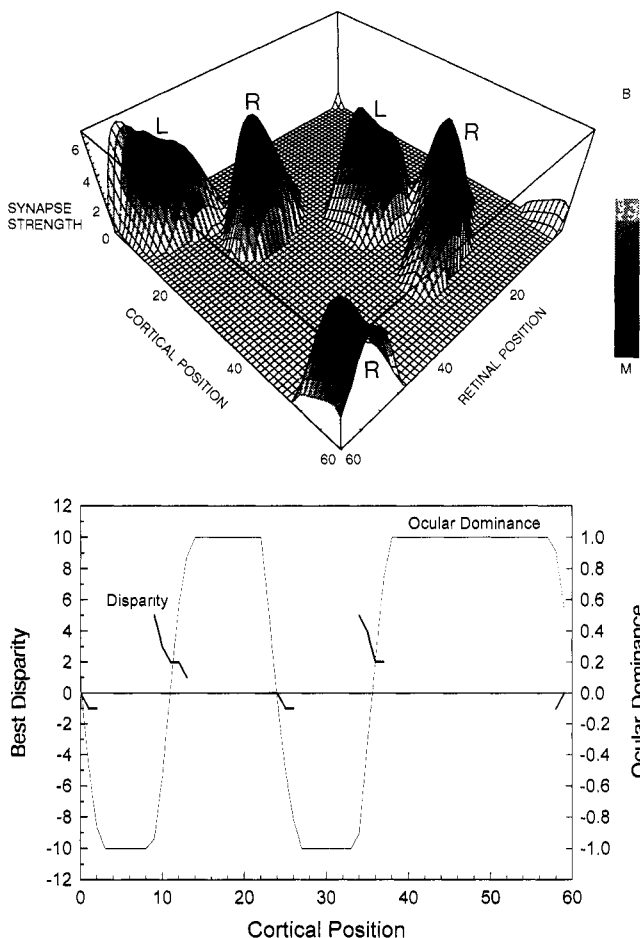


FIG. 2. Response properties of geniculocortical connections in a model without any between-eye correlations at 800 iterations. (*Upper*) The $x$-axis represents retinal cell position, while the $y$-axis represents cortical position. The total synaptic input from a given retinal location in both eyes to a given cortical cell is represented by height above the $xy$-plane. The shading represents the degree of monocularity/binocularity, ranging from completely monocular (black) to evenly binocular (white). Left or right eye dominance is correspondingly indicated. (*Lower*) Pattern of both OD and disparity sensitivity across the cortex. Most cells were monocularly dominated by either the left or right eye and thus lacked well-defined disparity sensitivities.
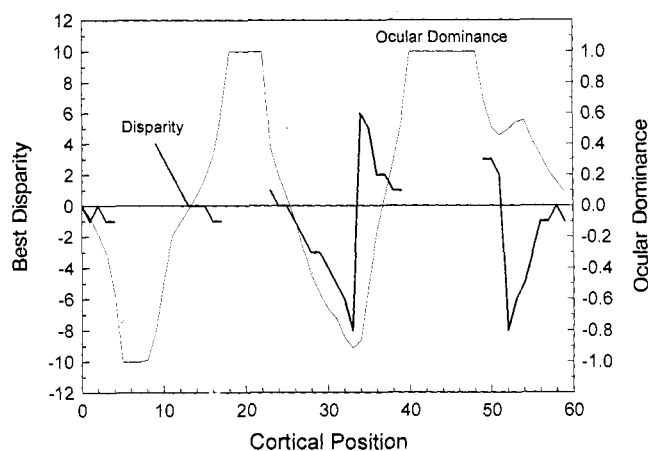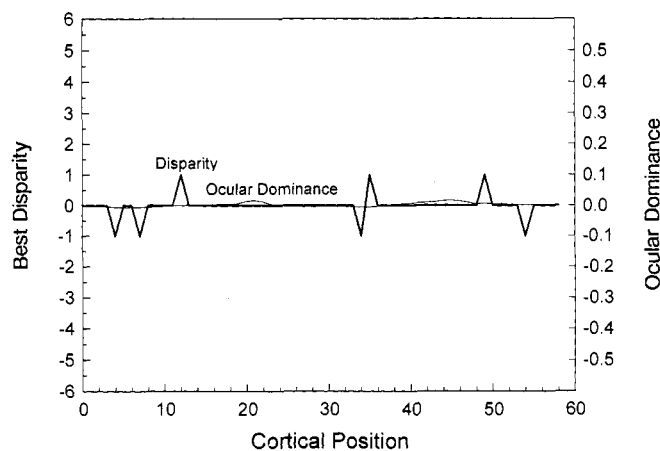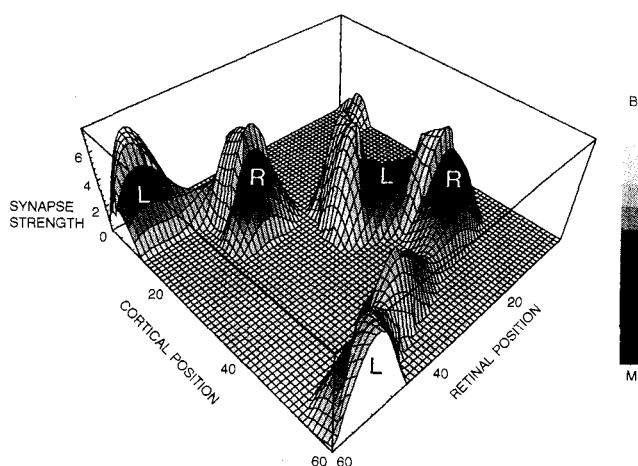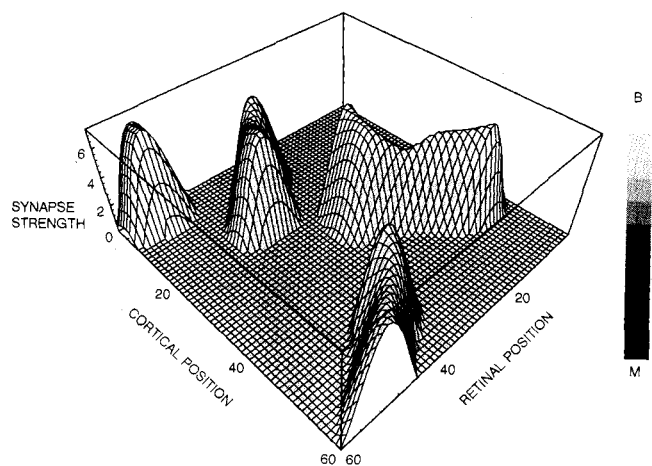
FIG. 3. Response properties of cortical neurons in a model that included both same-eye correlations and between-eye correlations throughout development. (*Upper*) Geniculocortical connections after 400 iterations. The presence of between-eye correlations early in development led to an exclusively binocular cortex—i.e., no OD. (*Lower*) Pattern of both OD and disparity sensitivity. Both OD and disparity were found to be clustered around 0 (no OD and aligned receptive fields).

Ocular dominance was calculated for each cortical cell as $(R - L)/(R + L)$, where $R$ was the total input from the right eye and $L$ was the total input from the left eye, and the normalization factor $(R + L)$ was kept constant as the weights changed. Thus OD ranged from $-1.0$ (completely dominated by the left eye) to 1.0 (completely dominated by the right eye). The disparity sensitivity of each cortical cell was calculated as the relative distance between the peak weights of the left and right receptive fields of that cortical cell (including the effects of the other cortical cells by way of the intracortical connections). Disparity was undefined for purely monocular cells when this method was used.

## RESULTS

In geniculocortical development with same-eye correlations only, the first feature to appear was the localization of the receptive fields, as seen in Fig. 2. The width of the receptive fields in the retinal direction was determined by the width of the correlation function. As discussed by Miller *et al.* (7), the cortical scale of the receptive fields was determined by the characteristic width of the cortical interaction matrix, which in these simulations was the same as the width of the same-eye correlations and which resulted in the tendency to form topographic structures evident as the diagonal bands.

FIG. 4. Response properties of cortical neurons in a model with two-phase development. (*Upper*) Geniculocortical connections in which initial same-eye correlations were followed by the addition of between-eye correlations (at 175 iterations) led to the development of a cortex containing both monocular and binocular cells, shown here at 400 iterations. The binocular cells were found in the transition zones between left and right eye dominance. (*Lower*) Pattern of both OD and best disparity sensitivity and their relationship to each other. The pattern of OD resembled that of Fig. 3, but there were more binocular cells in the transition zones. The cells in the transition zones also tended to have aligned receptive fields as seen in the concordance of zero-crossings of OD and zero disparity. Note also the large jumps or fractures in the best disparity.

After development with same-eye correlations only, nearly all the receptive fields were found to be monocular (illustrated by the dark peaks in Fig. 2 *Upper*). Most of the cortical cells were completely dominated by one of the eyes, and the periodicity of OD across the cortex corresponded to the width of the cortical interaction matrix (Fig. 2 *Lower*). The presence of between-eye correlations throughout development led to a cortex full of binocular cells (Fig. 3 *Upper*). The OD was effectively 0.0 across the cortex, and most cells had zero disparity (Fig. 3 *Lower*).

The two-phase development led to a mixture of 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 *Upper*). The pattern of OD and disparity (Fig. 4 *Lower*) 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 tended to have nonzero disparity. There was a statistically significant direct relationship between absolute disparity and
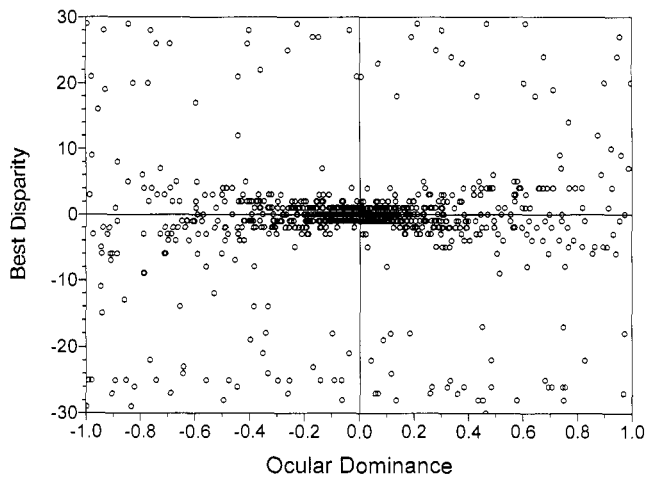
FIG. 5.    Scatter plot of best disparity vs. OD for 20 simulations, using different initial conditions. Binocular cells tended to have best disparities near zero, whereas relatively monocular cells had nonzero disparity sensitivity. This relationship was statistically significant under linear regression ($r^2 = 0.19$, $P < 0.0001$) and matched previous experimental data (19).

absolute OD ($r^2 = 0.19$, $P < 0.0001$). The receptive fields and disparity tuning of a typical binocular cell and monocular cell are shown in Fig. 6. Disparity sensitivity and OD were both

distributed in a topographically organized manner across the cortex. Sharp transitions or fractures in the disparity map tended to occur at the centers of OD columns, as in Fig. 4 *Lower*.

## DISCUSSION

The results from our model suggest that the range of disparity-sensitive cells results from the prenatal competition between the eyes, and the results are then partially reversed after birth. In the simulations with exclusively same-eye correlation, only monocular cortical cells were observed to develop. In the simulations with sufficient between-eye correlations present throughout development, the cortex became homogeneously binocular, and all the cells had essentially a best disparity of zero. However, when development was divided into two phases, the first phase having no between-eye correlation and the second phase having both same-eye and between-eye correlation, the model developed both monocular and binocular cells. The binocular cells, which occurred at the transition between left and right eye dominance, tended to have a best disparity of zero, while the more monocular cells had less of a preference for zero disparity. Indeed, this relationship between OD and disparity has been experimentally observed in the cat (15-19). Freeman and Ohzawa (22) have recently found that the proportion of monocular cells in the cat visual cortex decreases during the first few weeks after birth, and there is a concomitant
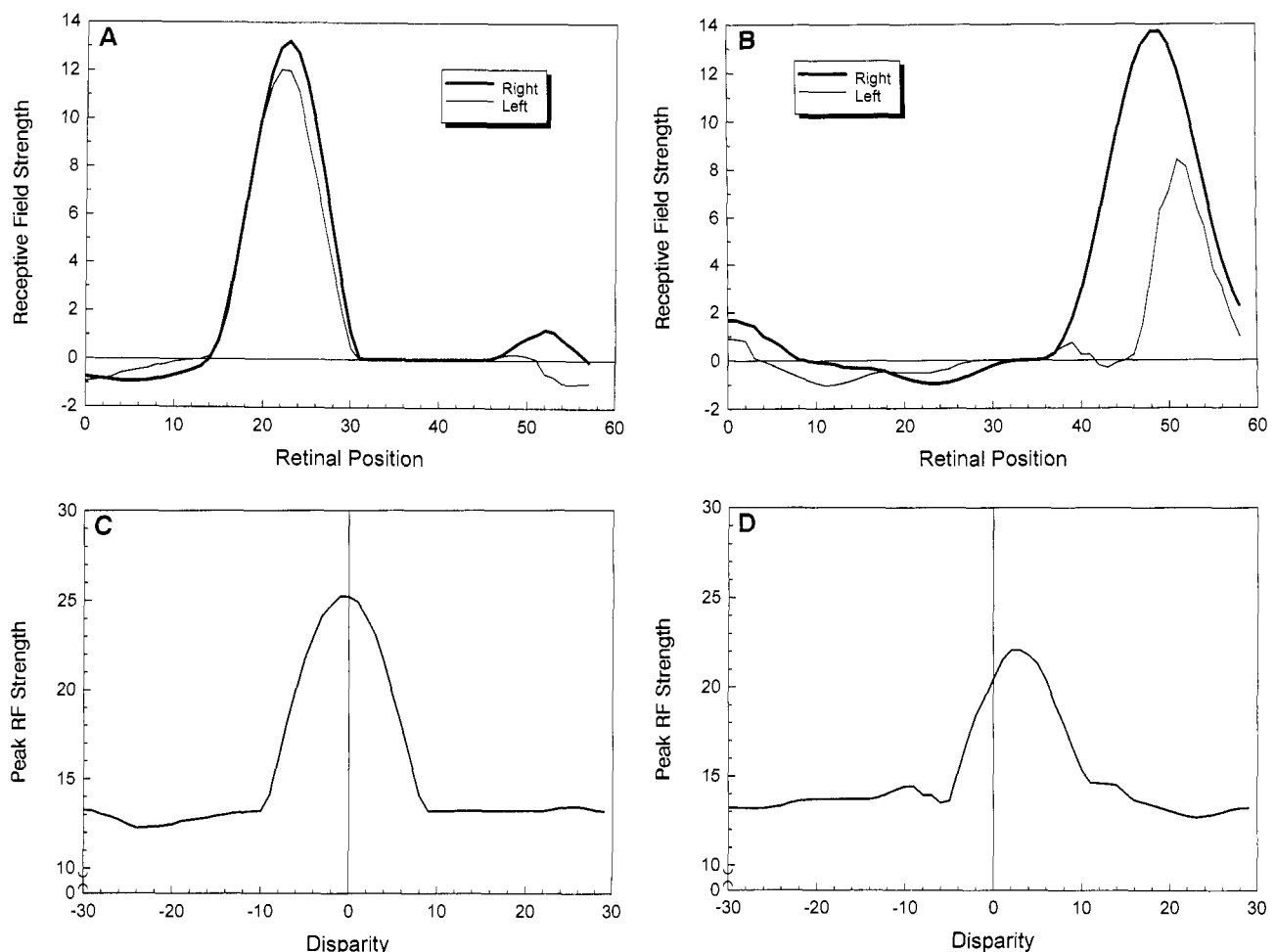


FIG. 6.    Receptive fields and disparity tuning curves for cells in a mature network using a two-phase paradigm. (*A*) Receptive fields of a typical binocular cell in the two-phase paradigm. (*B*) Receptive fields of a relatively monocular cell. (*C*) Disparity tuning curve for the receptive fields (RFs) shown in *A*. (*D*) Disparity tuning curve for the receptive fields shown in *B*. The best disparity of the binocular cell was nearly zero, while the more monocular cell had a best disparity of four.

increase in tuned cells. The proportion of monocular cells in the primary visual cortex of monkeys is greater than that in cats. This could be explained by our model if we assume that the visual cortex of monkeys is more mature at birth than is cat cortex. The differences in the visual cortex architecture of various species might be explained by differences in maturity of the cortex at birth (Michael Stryker, personal communication). Furthermore, our model predicts that fracture zones in the disparity map should occur at the center of OD columns, just like fractures in the orientation map (23–25). Although the latter have been reported and predicted, we are not aware of any experimental observations on the arrangement of disparity-tuned cells.

Many neurons in the visual cortex are selective to vertical as well as horizontal disparities (14, 15). For example, LeVay and Voigt (19) presented disparity-tuning curves perpendicular to the axis defining the best orientation of the neuron, which typically has a vertical component. Our one-dimensional model of horizontal disparity does not include a vertical dimension. We have extended our model to two dimensions and have found, in preliminary simulations, the same relationship between disparity and OD, that is, binocular cells have aligned receptive fields. Furthermore, relatively monocular cells can have components of both horizontal and vertical disparity sensitivity, depending on the nature of the between-eye correlations.

The model is obviously simplified from both biological and mathematical viewpoints. In particular we are not claiming to have modeled details of how cortical cells in different layers actually calculate disparity, such as their subunit structure (26). Also, there is evidence for mechanisms, such as long-term potentiation (5), that would support Hebbian synaptic plasticity as required by our model. However, our normalization procedures, like others, are unsatisfactory insofar as they are not based on known biological mechanisms. We believe that the main conclusions of our simplified model— i.e., that the relationship between disparity sensitivity and OD can develop by means of correlational mechanisms, will hold for more complete correlational models that take these details into account. The more general lesson is that distinct phases of development, which are characterized by both changes in the input patterns and freezing of some connection strengths, may produce neurons with complex response properties while preserving uniform learning mechanisms.

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