neuroReport

NeuroReport 3, 73–76 (1992)

Development of orientation columns via competition between ON- and OFF-center inputs

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DEVELOPMENT of orientation-selective receptive fields in primary visual cortex of higher mammals can occur through activity-dependent competition between ON-center and OFF-center inputs. This competition yields orientation and spatial-frequency-selective 'simple cells' if the dark activity of ON (or OFF)-center inputs is best correlated with that of other ON (or OFF)-center inputs at small retinotopic separations and with that of OFF (ON)-center inputs at larger separations. Features of cat and monkey cortical organization emerge, including continuous and periodic arrangement of preferred orientation across the cortex. A new feature, systematic variation of receptive field spatial phase, is predicted. Experimental tests of this hypothesis are proposed.

Key words: Simple cell; Hebb synapse; Receptive field; Visual cortex; On-center; Off-center; Spatial frequency; Spatial phase; Cat; Monkey

Introduction

Most neurons in primary visual cortex of many mammalian species respond best to light/dark borders of a particular orientation.[1] The inputs these neurons receive from the lateral geniculate nucleus (LGN) are not orientation selective; they respond equally to bars of all orientations and well to non-oriented stimuli. The origin of cortical orientation selectivity remains unsolved.

Many processes in the developing nervous system involve segregation of two input populations, apparently via activity-dependent synaptic competition.[2] These include the segregation of left- and right-eye inputs to the LGN and the visual cortex[2,3] and of ON- and OFF-center inputs to the LGN.[4] These segregations are *between* postsynaptic cells; each cell eventually receives only a single type of input.

ON- and OFF-center inputs converge onto individual cortical cells.[1,5–7] Simple cells, a class of oriented cells,[1] show segregation of ON- and OFF-center inputs *within* their receptive fields. These fields consist of adjacent, non-overlapping, oriented regions alternately receiving ON-center and OFF-center excitatory input.[1,5,8,9]

It is proposed that orientation selectivity arises through activity-dependent synaptic competition between ON-center and OFF-center inputs to cortex (in cats, from LGN; in monkeys, from non-oriented cortical layers). In an appropriate parameter regime, this leads to segregation *within* cortical receptive fields, orientation-selective simple cells and periodic orientation columns. Abstracts of this work[10] and brief discussions of this hypothesis[2,3,11,12] have appeared.

I use a mathematical framework developed previously that describes a class of correlation based mechanisms of synaptic competition, including Hebbian synapses.[2,3,13,14] Either form of segregated outcome can result, depending on the correlations in input activities.[2,3,13] Segregation between postsynaptic cells is exemplified by ocular dominance segregation: if inputs from one eye are best correlated with one another, the left-eye and right-eye inputs become segregated onto different postsynaptic cells. Segregation of two input types *within* receptive fields occurs if, at small retinotopic separations, inputs of like types are best correlated, but at larger retinotopic separations opposite-type inputs are best correlated, and this change occurs at retinotopic separations smaller than an arbor radius (the radius over which inputs initially contact a single cortical cell).

I have studied competition between ON-center and OFF-center inputs to cortex under the hypothesis that this second type of correlation structure (a 'Mexican hat' structure) exists in their dark activity when orientation selectivity develops. This hypothesis is motivated by receptive field structure (Fig. 1).

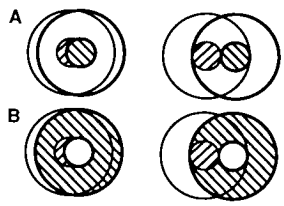

FIG. 1. **Correlations between ON- and OFF-center receptive fields at varying retinotopic separations**: Stripes signify On regions, white OFF regions. **A**: Two ON-center receptive fields (RFs). Left: At small retinotopic separations ON-centers overlap and OFF-surrounds overlap, hence the cells would be likely to frequently receive common input and be well correlated. Right: At larger retinotopic separations, ON-center of each RF overlaps OFF-surround of the other, so poor correlation or anticorrelation is expected. **B**: Two RFs of opposite center-types. The situation is reversed from A. Left: anticorrelation is expected. Right: ON-center overlaps ON-surround and OFF-center overlaps OFF-surround, so better correlation is expected than at similar separation in A. Thus, a Mexican hat structure is plausible: one in which ON (or OFF)-center inputs are best correlated with ON (OFF)-center inputs at small retinotopic separations, but best correlated with OFF (ON)-center inputs at larger retinotopic separations within an arbor radius. Measurements of dark activity in adult cat retina[21] found that, when receptive field centers overlap, ON-cells are correlated with ON-cells and OFF with OFF (A left), and ON-cells are anticorrelated with OFF (B left). At larger separations, zero correlation was found. The increased strength of the receptive field surround in the LGN vs. the retina makes plausible an extension of correlations to further retinotopic separations in the LGN, with changed sign.

Materials and Methods

The equation studied[13,14] is

$$\frac{d}{dt}S^{ON}(\mathbf{x},\boldsymbol{\alpha}) = \lambda A(\mathbf{x}-\boldsymbol{\alpha})\Sigma_{y,\beta}I(\mathbf{x}-\mathbf{y})$$
$$[C^{ON\text{-}ON}(\boldsymbol{\alpha}-\boldsymbol{\beta})S^{ON}(\mathbf{y},\boldsymbol{\beta}) + C^{ON\text{-}OFF}(\boldsymbol{\alpha}-\boldsymbol{\beta})S^{OFF}(\mathbf{y},\boldsymbol{\beta})].$$

A is the arbor function, I the intracortical interaction function, C the correlation functions, S the synaptic strengths, $\mathbf{x},\mathbf{y}$ two-dimensional postsynaptic locations, and $\boldsymbol{\alpha}$, $\boldsymbol{\beta}$ two-dimensional presynaptic location and λ a constant. The equation for OFF synaptic strengths is identical after exchange of 'ON' and 'OFF' everywhere. Growth of a synapse is determined by the sum of influences from all other synapses; influence exerted depends on strength (S), correlation with the influenced (C), and effect across cortex via intracortical connections and/or diffusion of modulatory factors (I). The arbor function (A) tells the number of synapses receiving this influence. While the equations are linear, they may accurately describe early development of the difference between ON- and OFF-center synaptic strengths under biological nonlinearities.[14] To ensure that development is competitive[15,16] subtractive constraints[13] conserve the summed synaptic strength over each postsynaptic cell.[17] Labelling the right side of the above equation $LS^{ON}(\mathbf{x},\boldsymbol{\alpha})$, the constraint modifies that equation to read

$$\frac{d}{dt}S^{ON}(\mathbf{x},\boldsymbol{\alpha}) = LS^{ON}(\mathbf{x},\boldsymbol{\alpha}) - [A(\mathbf{x}-\boldsymbol{\alpha})/2\Sigma_{\beta}A(\mathbf{x}-\boldsymbol{\beta})]\Sigma_{\beta I=(ON,OFF)}LS^{I}(\mathbf{x},\boldsymbol{\beta}).$$

In simulations, a cortical output layer and ON- and OFF-center input layers are represented by two-dimensional grids of 31 × 31 cells. Each input cell connects to the 97 cortical cells within a circle of diameter 11 grid intervals centered at the retinotopically corresponding cortical cell. Each synaptic strength $S^{I}(\mathbf{x}-\boldsymbol{\alpha})$ was initially chosen from a random distribution uniform between $0.8A(\mathbf{x}-\boldsymbol{\alpha})$ and $1.2A(\mathbf{x}-\boldsymbol{\alpha})$. Each developed under the constrained equation until it reached 0 or $4A(\mathbf{x}-\boldsymbol{\alpha})$, at which point no further change in a synapse was allowed. The maximum strength and mean initial strength set the size of the final receptive fields, die to the conservation rule. Methods of simulation as described in reference 13.

Results

A typical development, using purely excitatory intracortical connections, is illustrated in Fig. 2. A 3 by 3 patch of cortical cells develops oriented receptive fields with distinct, cleanly segregated ON (white) and OFF (black) subregions (Fig. 2A). A 20 by 20 set of mature receptive fields (Fig. 2B) demonstrates the variety and continuity[1,18–20] of final receptive fields. Where orientation remains constant across a group of cells, there is often a systematic change in spatial phase (the region of the receptive field occupied by ON or OFF inputs respectively). Cells with very low preferred spatial frequencies have poor orientation selectivity and in some cases are the centers of vortex-like or 'pinwheel' arrangements of preferred orientation.[18–20] There is a periodic arrangement of ON-dominated and OFF-dominated regions, reminiscent of afferent segregation in minks and ferrets.[2]

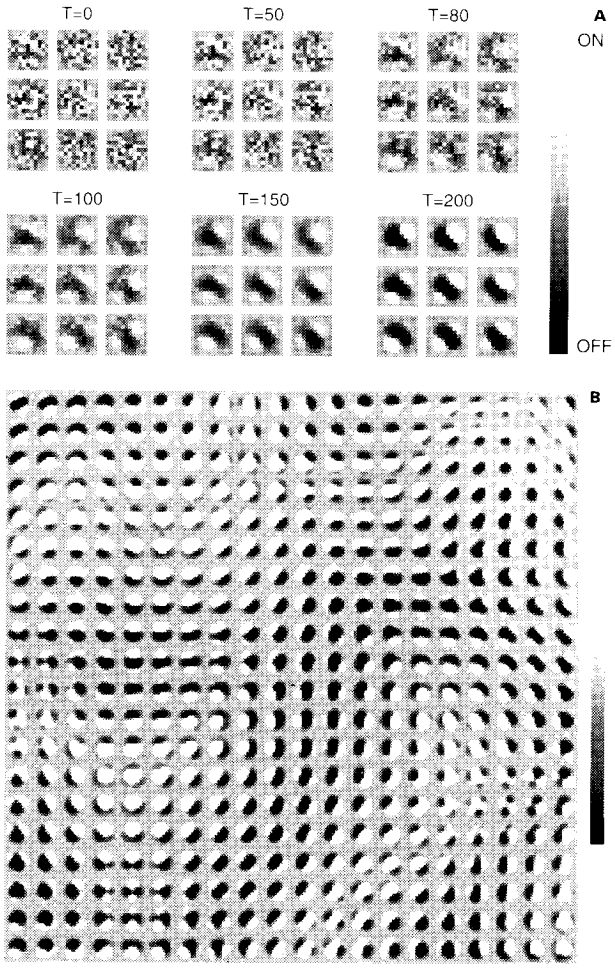

FIG. 2. **Development of orientation selectivity**: Results from a single simulation. **A**: Development of receptive fields (RFs) of 3 × 3 patch of cortical cells (T = 0 is initial condition; T, the number of iterations). Each square represents the input to a single cortical cell; 3 × 3 blocks of squares represent inputs to the same 3 × 3 patch of cortical cells at different developmental times. **B**: The final (T = 200) RFs of a 20 × 20 patch of cortical cells; format as in A except space separating RFs has been removed. In A and B: greyscale indicates difference between strength of ON-center and OFF-center synaptic input to a single cortical cell, from each of the 11 × 11 input positions that connect to that cell (corners of 11 × 11 RFs do not form connections and remain grey). White: ON-dominance; black: OFF-dominance; grey: equality. Images at each timestep have been scaled to use full dynamic range of the greyscale. Maximum difference D and maximum synaptic strength S in A: $T = 0$: $D = 0.37$, $S = 1.2$; $T = 50$: $D = 0.46$, $S = 1.54$; $T = 80$: $D = 0.66$, $S = 1.92$; $T = 100$: $D = 1.07$, $S = 2.32$; $T = 1.50$ and 200 (and B): $D = S = 4$. Functions used described in Fig. 3 legend.

The model cortical maps, both of preferred orientation and its gradient (rate of change), qualitatively resemble actual cortical maps (Fig. 3). Thus, the hypothesis is sufficient to robustly (Fig. 3 legend) account for aspects of cortical organization without further assumptions.

The model predicts that the mean preferred spatial

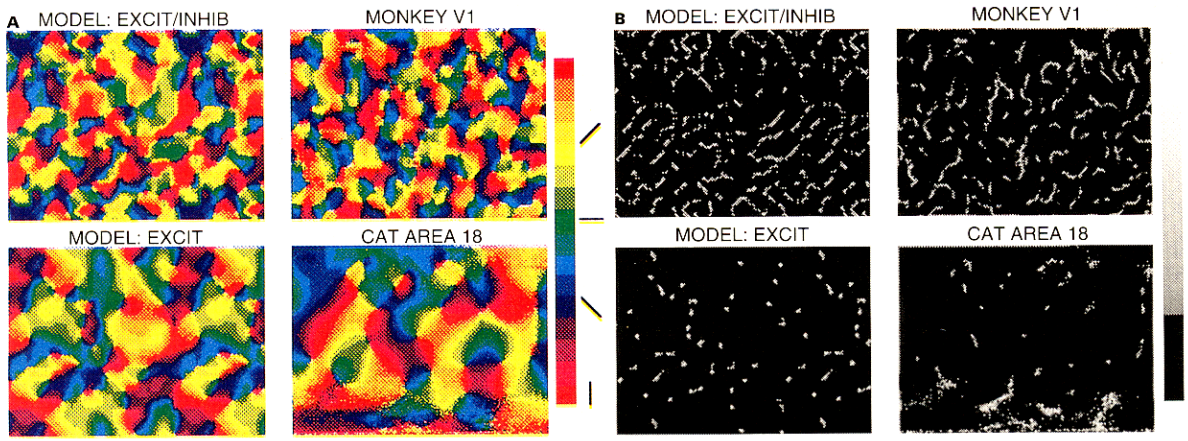

FIG. 3. **Comparison of model results to monkey and cat visual cortex**: Cortical maps obtained with the model compared to maps obtained from monkey VI by Dr. D. Ts'o, and cat area 18 by Drs. T. Bonhoeffer and A. Grinvald. **A**: Maps of preferred orientation, shown as hue. **B**: Maps of gradient (rate of change) of preferred orientation, computed from maps in A. Regions of high gradient (rapid change) are white. The model maps assume only local excitatory interactions in cortex ('excit') or such interactions surrounded by more distant inhibitory interactions ('excit/inhib'). 'Excit' is same simulation as Fig. 2 (T = 200). In cat and 'excit' model cortex, spatial periods are larger, and regions of rapid orientation change (high gradient) are largely confined to points corresponding to 'pinwheels' of orientation.[20] In monkey and 'excit/inhib' model cortex, spatial periods are narrower and regions of rapid change tend to be linear,[18] although pinwheels are also present. Experimental maps: 3.2 × 4.3 mm. Model maps matched in size by placing simulation results on grid four times finer in each dimension, and linearly interpolating intermediate values. One grid interval in model is 92 μm, in experimental maps. This corresponds to arbors with diameter about a millimeter, and intracortical excitation over a radius of roughly 200 μm. Both model cortices developed from identical initial conditions, for ease of comparing results. Results are robust, remaining qualitatively and roughly quantitatively (in spatial period of orientation domains) similar across initial conditions. Simulations used periodic boundary conditions: wrap around can be seen. Orientations shown on linear scale (16 equal steps of angle). Gradient greyscale linear from 0 (black) to maximum gradient in a given cortex (white), except values less than 25% of maximum also set to black. Model gradients computed from interpolated orientation maps. Gradient maxima, in degrees/pixel, are 72 and 75 for model, 97 for monkey, 119 for cat. Experimental maps in A produced by Drs. Tso, Bonhoffer and Grinvald using optical recording of intrinsic signals as in references.[19,20] Dr. Tso's data is unpublished; cat cortex was published in[20]. I thank all three researchers for allowing me use of their data. Functions used: Define $G(\boldsymbol{x},r) = \exp(-|\mathbf{x}|^2/(rR)^2)$, where $R = 5.5$ is the arbor radius; and $\delta(\boldsymbol{x}) = 1$ if $\mathbf{x} = 0$, and 0 otherwise. Intracortical interaction function $I(\boldsymbol{x}) = [a + (1 - a)\delta(\boldsymbol{x})][G(\mathrm{x},r_1) - kG(\boldsymbol{x}, 3r_1)]$, set to zero for $|\mathbf{x}| > x_1$. $a = 1/2$, $r_1 = 0.4$. 'excit': $k = 0$, $x_1 = 2.5$; 'excit/inhib': $k = 1/9$, $x_1 = 7.5$. Parameter a introduced because, for a Hebbian mechanism, intracortical interaction is of form $I(\boldsymbol{x}) = \delta(\boldsymbol{x}) + B(\boldsymbol{x}) + \Sigma_{\boldsymbol{y}} B(\boldsymbol{x}-\boldsymbol{y})B(\boldsymbol{y}) + \ldots$ where B describes connectivity between cortical cells.[13,14] ON-ON correlation function $C^{\mathrm{ON\text{-}ON}}(\boldsymbol{x}) = G(\boldsymbol{x}r_c) - (1/9)G(\mathbf{x}, 3r_c)$; $C^{\mathrm{ON\text{-}OFF}} = -0.5^{\mathrm{ON\text{-}ON}}$, $r_c = 0.28$ ('excit') or $r_c = 0.2$ ('excit/inhib'). Arbor function $A(\boldsymbol{x})$ is proportional to area of overlap of two circles, radii 5 and 2.5, with centers separated by $|\boldsymbol{x}|$ (a crude model of overlap of geniculocortical terminal arbors and cortical dendritic arbors), set to zero for $|\boldsymbol{x}| > 5.5$. Preferred orientations of model receptive fields assessed as orientation of sine wave grating that gave best response, where response of cell at x to grating with wave number k, phase φ is $\Sigma\alpha[S^{\mathrm{ON}}(\boldsymbol{x},\alpha) - S^{\mathrm{OFF}}(\boldsymbol{x},\alpha)] \sin[2\pi\mathrm{k}\text{-}\alpha/11)+\varphi]$. This does not model temporal summation in response to a moving bar or thresholds for postsynaptic response, which would sharpen orientation selectivity, or effects of intracortical synapses. Timestep: $\lambda\Delta t = 0.0012$ ('excit') or 0.0019 ('excit/inhib'); doubling of size causes almost no change. Parameter dependence: results are very robust. Arbitrarily large increase of r_1 and x_1 leads to little change in 'excit'; moderate increase leads to little change in 'excit/inhib'. Decrease of r_1 leads to narrower orientation domains. Setting $a = 1$ is similar to moderately increasing r_1. Increase of x_1 alone is without effect. Degree of orientation selectivity peaks at $r_c = 0.25$ for this arbor function; substantial increase of r_c leads to all-ON or all-OFF receptive fields; substantial decrease leads to receptive fields with many ON/OFF regions whose orientations may vary and wander. Within well-oriented regime, orientation map changes smoothly as r_c or arbor function varies, remaining similar in domain size and qualitative appearance for moderate changes.

frequency of cells is that which maximizes the Fourier transform of $(C^{\mathrm{ON\text{-}ON}} - C^{\mathrm{ON\text{-}OFF}})$.[2] The simplest assumption is that this maximum spatial period twice the diameter over which like-center retinal cells have positive correlation. This predicts preferred spatial frequency in cat area 17 (assuming X-cell inputs) of 0.5 cycles/degree at 10° eccentricity[21] which agrees with measurement.[22]

Discussion

The present hypothesis can be experimentally tested in several ways; negative results would falsify it. A Mexican-hat correlation structure should exist between ON- and OFF-center inputs in the pre-orientation layer at the appropriate developmental time. Orientation-selective cells should not form if all neural activity in the retinae, LGN or cortex is blocked sufficiently early in development, or if the Mexican-hat correlation structure is abolished without abolition of neural activity.

The cortical organization of orientation depends on both the competitive hypothesis and the model of intracortical interactions, so alternative outcomes could arise from the hypothesis. However, for any interactions pairs of cortical cells with excitatory or inhibitory interactions tend to develop correlated or anticorrelated receptive fields, respectively[2] (this may explain opponent inhibition[8,9]). The correlation of simple cell receptive fields depends on the retinotopic postions of ON- and OFF-subregions (Fig. 4). Thus, the organization of preferred orientation is determined by distance-dependent coupling between receptive fields depending on orientations and spatial phases. The simple model of intracortical interactions used here yields steady shifts of spatial phase across cortex among similarly oriented cells (Fig. 2B). More generally, experimental studies of the simultaneous maps of orientation, spatial phase and retinotopic position of simple cells are needed to understand orientation maps alone.

A model for activity-dependent development of orientation selectivity was first proposed by von der Malsburg,[17] using one input type and oriented input

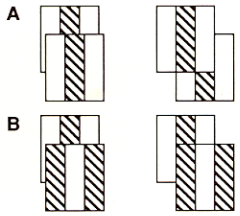

FIG. 4. **Correlations between cortical receptive fields at varying retinotopic separations**: **A**: Two receptive fields (RFs) with identical orientations and spatial phase. Left: At small retinotopic separations, the RFs have overlapping ON-regions and overlapping OFF-regions. Hence, they would be expected to be well correlated in their activities. Right: At larger retinotopic separations perpendicular to the orientation axis, the ON-regions of one RF overlap the OFF-regions of the other, so the two RFs are maximally anticorrelated. **B**: Two RFs with identical orientations but opposite spatial phases. The relationships of A are reversed: the two RFs are anticorrelated at small retinotopic separations (left), but correlated at larger retinotopic separations perpendicular to the orientation axis (right).

activity patterns. Such models do not account for segregation of inputs within receptive fields, ignore spatial phase, and have difficulty explaining development of orientation selectivity in the absence of vision. Models proposing distance-dependent coupling between receptive fields determined only by their orientations[23] share the first two limitations.

A symmetry-breaking scenario, in which a circularly symmetric but spatially oscillating correlation function leads developmentally to non-circularly symmetric, spatially structured receptive fields, was first demonstrated by Linsker[24] (analyzed in [11]). He used a single input type but with both positive and negative synaptic strengths; this differs biologically and dynamically from the present model.[14] Development of orientation selectivity was studied only on single, isolated cortical cells, depended on tight tuning of a parameter that fixed the percentage of positive synapses in the final receptive field, and occurred only in the late, nonlinear stage of development where model results may be altered by biological nonlinearities.[11,14] Cortical organization was studied only when all receptive fields have identical spatial phase. In the present model synapses are exclusively excitatory, and intracortical interactions cause segregated subregions to become oriented in early, linear development without additional parameters.

Tanaka independently proposes a relationship of ON/OFF competition to orientation.[25] In his model, competition leaves each cortical cell with exactly one LGN input (unlike actual cortical cells[5]). Cortical receptive fields are defined as the convolution of this input arrangement with the intracortical interaction function. Assuming rough retinotopy, this yields oriented receptive fields when ON and OFF inputs segregate in cortical patches like ocular dominance patches, since then the convolution is not circularly symmetric. Formation of such patches does not require a Mexican hat correlation function. Tanaka's mechanism involves breaking of symmetry in the pattern of inputs to different cortical cells, rather than to single cortical cells. It has a 'bootstrap' problem: at least some of the cortical cells must initially respond to their non-oriented LGN input.

Conclusion

It is proposed that Orientation selectivity can develop through an activity-dependent competition between ON- and OFF-center inputs. Spatial frequency selectivity and other cortical response features emerge. The hypothesis is strongly testable. It suggests novel experimental investigations, and a new principle for organizing the cortical map of orientation based on a coupling between orientation and spatial phase of receptive fields. Segregation within receptive fields, like that between receptive fields, can be understood as an outcome of correlation-based synaptic competition. Thus, competition of both left-and right-eye inputs[13] and of ON- and OFF-center innervations, in both LGN and cortex, may be studied within a unified framework, encompassing both separation and early convergence of these information streams, and accounting for many striking features of the visual pathway.

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ACKNOWLEDGEMENTS: Michael Stryker and Christof Koch provided facilities and support for this research. Michael Stryker and David MacKay provided many useful discussions. Supported by an N.E.I. Fellowship and by a Human Frontiers Science Program Grant to M.P. Stryker (T. Tsumoto, Coordinator), and by a Caltech Division of Biology Fellowship. Simulations performed at San Diego Supercomputer Center.

Received 20 November 1991; accepted 29 November 1991