Study of spatial frequency selectivity and its spatial organization in the visual cortex through a feedforward model

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Abstract

A purely feedforward model has been shown to produce realistic simple cell receptive fields that show smooth transitions between subregions and fade off gradually at the boundaries [2]. Here we show that the modeled cells also capture a wide range of spatial frequency properties of cortical cells. The shape and size of the subregions in the receptive field is found to be an important parameter in determining the frequency selectivity of the cell. The spatial frequency maps obtained through the model show a continuous distribution of spatial frequency preference across the modeled cortex and pinwheels co-localize with the extrima of the spatial frequency domains.

Keywords: spatial frequency selectivity; feedforward model; simple cells; spatial frequency map

1 Introduction

Visual cortical neurons are selective for not only the position and orientation of an input stimulus but also for its spatial frequency content. At any given eccentricity cells selective for a range of orientations and spatial frequencies [6] can be found. Cortical cells exhibit band-pass frequency characteristics with spatial bandwidths varying considerably among cells [17,1,11]. Orientation tuning and spatial frequency selectivity being amongst the two prominent properties of cortical cells, their dependence on and relationship to one another has motivated a large body of experimental work [17,6,12,10]. A columnar organization for the spatial frequency preferences has been observed using both the 2DG staining [13] and the optical imaging [9] techniques. The spatial frequency preferences are organized into domains that form a map that is locally continuous across V1.

Some of the computational models have studied both the orientation and spatial frequency tuning in cortical cells. Among these are the ring model proposed by Bressloff and Cowan [4] and the correlation-based model of Troyer et al. [14]. While Bressloff and Cowan's model suggests the need for cortico-geniculate feedback to obtain faithful spatial-frequency representation in cortical neurons. In the model of Troyer et al. [14] frequency tuning is mainly driven by the LGN inputs despite the presence of strong intra-cortical inhibition. Orientation tuning width in their model reduces monotonically with increasing spatial frequency as has been observed in cat cortical cells [16,17,8]. However, neither of these models discusses the spatial organization of frequency preferences on the cortical surface.

We have proposed a feedforward neurotrophic model for the formation of simple cell receptive fields [2]. Receptive field development in the model is determined by diffusive cooperation and resource limited competition guided axonal growth and retraction in the geniculocortical pathway. The receptive fields generated through the model resemble experimentally measured receptive fields for simple cells with well segregated ON and OFF subregion. This paper, aims to study the selectivity of the modeled receptive fields for spatial frequency of the input stimulus. Modeled cortical cells are selective to a wide range of spatial frequencies lying between 0.3 c/deg to 1.04 c/deg (mean is 0.49

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c/deg). Being a purely feed-forward model, the dependence of spatial frequency selectivity on the spatial structure of the receptive fields has been explored. The spatial organization of the frequency selectivity on the modeled cortical surface has also been studied. Spatial frequency maps obtained through the model show a continuous distribution of spatial frequency preference across the modeled cortex.

2 The feedforward model for the formation of simple cell RFs

Model Assumptions: For the formation of simple cell RFs, we have proposed a model based on competition for neurotrophic factors and cooperation among near neighbors through diffusion [2]. The model is based on biologically plausible assumptions of: (a) Competition for a pre-synaptic resource where a pre-synaptic cell has a fixed amount of resource to distribute among its branches. This would constrain the number of axonal branches a neuron can maintain. A role for presynaptic resources was first suggested for elimination of polyneuronal innervations in neuromascular system [18]; (b) Competition between axons for target space. The axons are competing for neurotrophic factors, growth or survival promoting factors, released by the postsynaptic cells upon which the axons innervate. Competition for target space or post-synaptic competition is used in all models for development of ocular dominance and; (c) Diffusive cooperation between near neighbor (i) cortical cells and (ii) same type of i.e. ON-ON and OFF-OFF LGN cells. Studies on Long-term potentiation LTP have shown the generation of diffusible signals at the active synapses leads to strengthening of the nearby synapses. Diffusive spread of signals also provides local anti-correlation between ON and OFF LGN cells.

No synaptic weight normalization is used. Both cooperation and competition determine the strength of synapses in the model. Fixed resources are used for both pre and postsynaptic competition. Such competition among synapses for finite resources, such as receptor or a trophic factor controlling the number of synapses have been observed [19]. The cooperation among neighboring cells can occur through release and uptake of diffusible factors [3].

Model architecture and equations: The model consists of three hierarchical layers: retina, LGN and cortex. All the layers are modeled as regular two-dimensional arrays. Both retina and LGN comprise of two distinct (ON and OFF) layers of size 30x30. Cortex consists of one layer of 50x50 spiking cells based on the SRM model of Gerstner [7]. Retinal and LGN cells are modeled as center surround gaussian filters with fixed one to one connectivity from retina to LGN. A cortical cell receives thalamic projections (both ON and OFF) from a 13x13 region centered symmetrically about its corresponding retinotopic position in the LGN. Initial synaptic strengths are very weak and randomly organized. Time evolution of synaptic strengths represents cortical development and is achieved through the following differential equation for weight updation.

$$\frac{\partial \mathrm{W}_{\mathrm{IJ}}^{+}}{\partial \mathrm{t}} = (\gamma_1 - \mathrm{K}_1)(\gamma_2 - \mathrm{K}_2)\,\mathbf{A}_{\mathrm{R}}\; \mathrm{W}_{\mathrm{IJ}}^{+} + \mathrm{D}_{\mathrm{L}} \frac{\partial^2 \mathrm{W}_{\mathrm{IJ}}}{\partial \mathrm{J}^2} + \mathrm{D}_{\mathrm{C}} \frac{\partial^2 \mathrm{W}_{\mathrm{IJ}}}{\partial \mathrm{I}^2} \qquad (1)$$

where, W_{IJ}^{+} (W_{IJ}^{-}) represents the strength of the connection from the ON-(OFF) center LGN cell at position J in LGN layer to the cortical cell at position I in the cortical layer. $W_{IJ} \in \{W_{IJ}^{+}, W_{IJ}^{-}\}$. $K_1^2 = \Sigma_{P=1}^{NXN} (W_{PJ}^{+})^2$, is the sum square of synaptic strength of all branches emanating from the LGN cell at the location J. γ_1 represent fixed presynaptic resources available in the LGN cell at location J. The term $(\gamma_1 - K_1)$ enforces competition for resources among axonal branches in a LGN cell. Similarly the term $(\gamma_2 - K_2)$ enforces competition among LGN cells for target space in the cortex. $K_2^2 = \Sigma_{P=1}^{MXM} (W_{IP})^2$ is the sum of the square of synaptic strength of all branches of LGN cells converging on the cortical cell at location I. γ_2 represent fixed postsynaptic resources available in the cortical cell at location I. A_R is the arbor function. Arbor function determines the number of synapses being modified. A trapezoidal window has been used as arbor function, where in the window height reduces as one moves towards the periphery of the window. D_L and D_C are the

diffusion in the LGN and cortex respectively. MxM and NxN are the sizes of the LGN and the cortex respectively. A similar equation is used for updating W_{IJ}^{-}.

3 Simulation Results

Simple cell receptive fields are obtained by simulating the differential equation for weight updating. The simulation details have been presented in [2]. The properties of the simple cells thus developed are evaluated by measuring their responses to moving sinusoidal gratings of 50% contrast at orientations lying between 0^o and 180^o and spatial frequencies lying between 0.25 and 2 c/deg. The study on orientation selectivity of the modeled cells has been presented in [2]. Here we report the spatial frequency selectivity and its spatial organization in the modeled cortex.

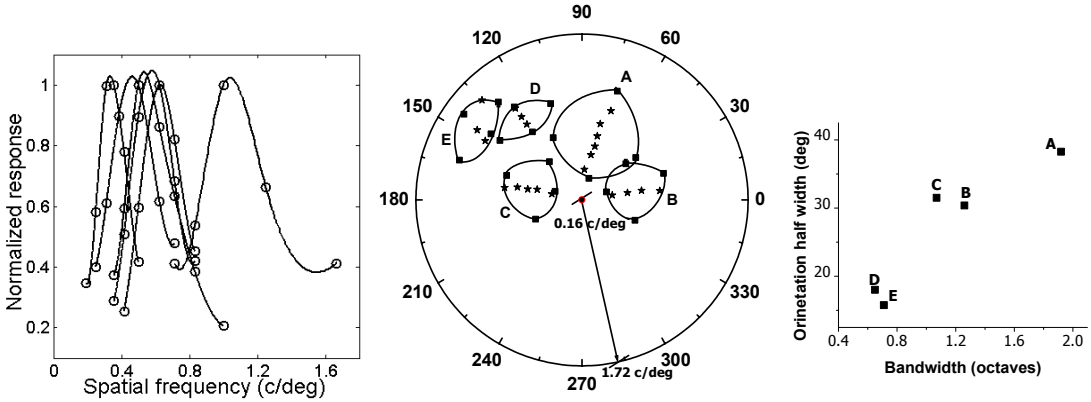


Figure 1(a) Spatial tuning curves at the preferred orientation for a few representative cells from our simulation. (b) Two-dimensional polar plots of five representative cells (marked A to E) are shown. The four half amplitude points for each cell are marked with filled squares. Stars indicate the input spatial frequencies for which the cells show an orientation-tuned response. (c) Cartesian plot between the spatial frequency bandwidth and orientation half width

3.1 Spatial frequency selectivity in modeled cells

The modeled cells have been able to capture the different spatial frequency properties observed in cortical simple cells. The cells show selectivity for a wide range of spatial frequencies. The optimal spatial frequency (f_o) for the cells varies by about 1.2 octaves, ranging from 0.3c/deg to 1.04 c/deg. The mean optimal frequency for the cells was 0.49c/deg (S.D. 0.16). In cats, optimal spatial frequency has been found to range from 0.3-1.8c/deg [1] and 0.2-2.0 c/deg [11]. In monkey's the observed ranges are much higher, 0.5-15 c/deg [6]. The spatial tuning bandwidth varied considerably amongst cells. The tuning widths varied from 0.65 octaves to 2.25 octaves with an average tuning width of 1.16 octaves (S.D. 0.47). This matches with the experimentally reported average tuning bandwidth of 1.3$\pm$0.3 octaves [1] and 1.0$\pm$0.2 octaves [11]. Figure 1(a) shows the spatial tuning curves for a few selected cells.

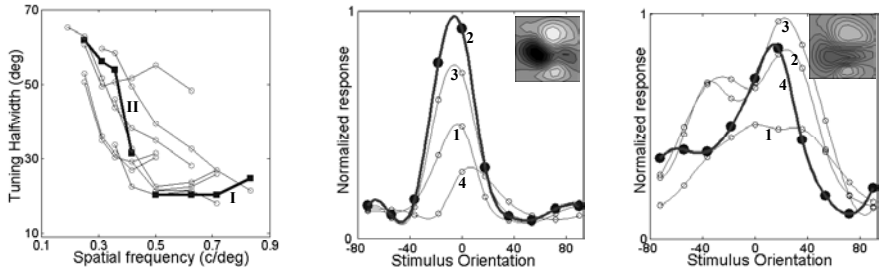
Orientation specificity and spatial frequency specificity are strongly correlated. The cells that are sharply tuned to orientation are also generally narrowly tuned to spatial frequency. De Valois et al [6] showed with the help of polar plots that cortical cells have localized spatial frequency response. They noted the half amplitude points on the orientation and spatial frequency-tuning curves and plotted them on the polar axes, with orientation as the angle, and frequency as the distance from the center. The cortical cells respond to stimuli bounded by the region formed by these four half amplitude points thus acting as local two-dimensional spatial-frequency filters. Figure1(b) shows polar plots for five representative cells from our simulations. Polar plots marked A,B and C show cells with wide orientation tuning and wide spatial frequency tuning, while the cells marked D and E have sharp orientation tuning and narrow spatial tuning width. Accompanying Cartesian plot between the spatial frequency bandwidth and orientation half width in Figure1(c) clearly brings out the strong correlation between the spatial frequency tuning and orientation tuning. On the polar plot for each

cell the spatial frequencies for which the cell shows an orientation tuned response have been marked with stars. It can be observed in Figure1(b) that the preferred orientation is independent of stimulus spatial frequency as observed for cortical cells in cats [10] and monkeys [17].

3.1.1 Sharpening of Orientation tuning with spatial frequency

Significant sharpening of orientation selectivity with increasing spatial frequency has been observed for simple cells[16, 8]. This has been attributed to the inhibiton that cortical cells receive from LGN cells [16], which themselves show orientation biases at higher spatial frequencies [15]. The model presented here is a purely feedforward model with excitatory connections and the modeled LGN cells do not have any orientation bias, yet the modeled cells exhibit sharpening of orientation tuning with spatial frequency. Our study shows that this can be attributed to the distribution of synaptic strengths within the receptive field of a simple cell.

The orientation tuning of the cells was studied as a function of spatial frequency of the input sinusoidal grating (Figure 2(a)). For some cells orientation tuning improves by as much as 30-40 deg with the spatial frequency while for others orientation tuning varies by at best 4-10 deg with the spatial frequency. Figure 2 (b)&(c) show the RFs and orientation tuning plots at various spatial frequencies for two cells, one from each category. Both the cells have the same preferred orientation of 0^o. The two cells differ with regards to (i) their preferred spatial frequency, and (ii) degree of change in orientation tuning with the spatial frequency. These differences are attributed to the strength and distribution of synaptic weights. The cell in Figure 2(b) responds optimally at a higher spatial frequency of 0.63 c/deg and its orientation tuning stays nearly constant (4 deg. variation) with spatial frequency. The cell has stronger and clustered synaptic strengths. A grating just wide enough to cover the central region corresponding to large weights will cause the cell potential to rise above the threshold causing the cell to fire. The cell in Figure 2(c) has weaker (about 2.7 times lower) and dispersed synaptic strengths. So the contributions from even the small weights lying at the periphery of the sub-regions become significant. Hence, maximum response is achieved only at a lower frequency of 0.36 c/deg, when the summation region is bigger. It shows a drastic improvement in orientation tuning from 61.88^o to 31.4^o with increasing spatial frequency due to reduced summation area.



(a) (b) (c)

Figure 2 (a) Orientation tuning half width as a function of spatial frequency of the input stimulus. The curves shown in thick lines, marked I and II, are for the cells whose orientation tuning curves and RFs are shown in (b) and (c) respectively. (b)-(c) Orientation tuning curves are marked 1,2,3,4 in the ascending order of the spatial frequency for the respective figures. The curves in thick lines are at the frequency at which the cell had the best tuning response. For the cell in (b), minimum-tuning width is obtained at the optimal frequency i.e. 0.63 c/deg (curve 2) but for the cell in (c) tuning is poor at the optimal frequency i.e. 0.36 c/deg (curve 2) and as the frequency increases.

3.2 Spatial frequency maps

In the last decade, optical imaging of intrinsic signals has been used by various groups to examine the structure of spatial frequency maps. It has been observed that the spatial frequency preferences are organized into domains that form a map that is locally continuous across V1. For these domains different arrangements have been suggested: binary [9], pinwheel [4] and clustered [10]. Though these arrangements are debatable, yet the common observation among these studies has been that the pinwheel centers co-localize with the extrima of the spatial frequency domains [10]. The arrangement of frequency preferences on the modeled cortex was studied. The spatial frequency maps obtained through the model showed that nearby cells prefer similar spatial frequencies and are clustered together to form domains that are locally continuous. Figure 3 shows a spatial frequency map obtained through the model. The contour

plot of the corresponding orientation map for the modeled cortex is also shown. The pinwheels are mostly found to co-localize with the extrima of the spatial frequency domains as observed in experiments.

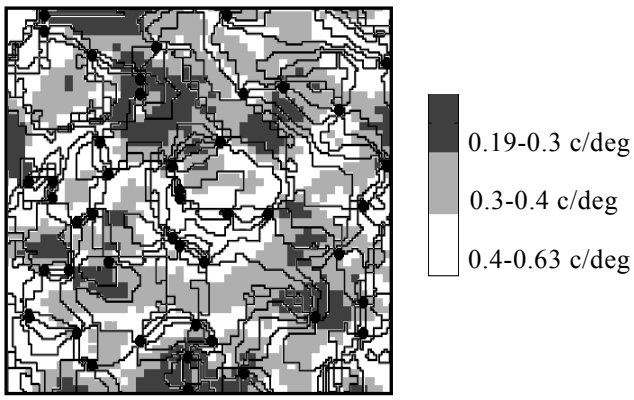


Figure 3 Spatial frequency map for one of the simulated cortices along with orientation contour map of the same cortex..

4 Discussion

The simple cells developed through the model [2] capture a number of experimentally observed spatial frequency characteristics of cortical simple cells such as (i) localized 2D spatial-frequency responses, (ii) preferred orientation being independent of spatial frequency and (iii) strong correlation between orientation specificity and spatial frequency specificity. The cells show preference for a range of spatial frequencies (0.3-1.04 c/deg). Observed frequency ranges are lower than experimentally observed ranges. Spatial bandwidths were found to vary considerably among cells. Reduction in orientation tuning widths with increasing spatial frequency for some cells indicates towards a role played by the distribution of synaptic strengths in the receptive fields in determining the frequency characteristics of the cells. The spatial frequency maps obtained through the model show domains selective to a continuous range of the spatial frequencies.

The model presented is a purely feedforward model and incorporates only X-cells in the LGN; that too of one size only. Our results indicate that spatial preference in the cortical cells could simply be due to the distribution of synaptic strengths in the cells receptive fields.

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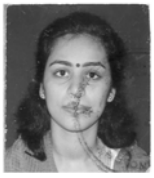

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