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

Mona Mathur, Basabi Bhaumik[*†]
Department of Electrical Engineering, Indian Institute of Technology, Delhi, Hauz Khas, New Delhi-110016, India

Abstract

A purely feedforward model has been shown to produce realistic simple cell receptive fields (RFs) 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, size and number of the subregions in the RF 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 largely co-localize with the extremes 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. Cortical cells exhibit band-pass frequency characteristics with varying spatial bandwidths [13,1,9]. 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 [13,4,10,8]. The spatial frequency preferences are organized into domains that form a map that is locally continuous across V1. The present model addresses both issues of the spatial frequency map formation as well as details of

[*] Corresponding author.Email address: bhaumik@ee.iitd.ac.in [†] This work is sponsored by Department of science and Technology, Ministry of Science and Technology, India.

individual cell orientation and frequency selectivity. Two computational models have earlier studied orientation and spatial frequency tuning [3,11] in individual cell. Neither of these models addresses the issue of the spatial organization of frequency preferences on the cortical surface nor provides population statistics on spatial frequency response. While Bressloff and Cowan [3] suggest the need for cortico-geniculate feedback to obtain faithful spatial-frequency representation in a cortical neuron, Troyer et al's [11] correlation based model shows that frequency tuning in cortical neurons is mainly driven by the LGN inputs despite the presence of strong intra-cortical inhibition.

We have proposed a feedforward neurotrophic model based on diffusive cooperation and resource limited competition for the formation of simple cell RFs [2]. The modeled RFs resemble experimentally measured RFs for simple cells with well segregated ON and OFF subregion. This paper, aims to study the selectivity of the modeled RFs for spatial frequency of the input stimulus. Modeled cortical cells are selective to a wide range of spatial frequencies. Being a purely feed-forward model, the dependence of spatial frequency selectivity on the spatial structure of the RFs 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

The feedforward model consists of three hierarchical layers: retina, LGN and cortex and has been presented at length in [2]. 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. 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.

$$\frac{\partial W_{IJ}^{+}}{\partial t} = (\gamma_1 - K_1)(\gamma_2 - K_2)\,A_R\,W_{IJ}^{+} + D_L\frac{\partial^2 W_{IJ}}{\partial J^2} + D_C\frac{\partial^2 W_{IJ}}{\partial I^2} \qquad (1)$$

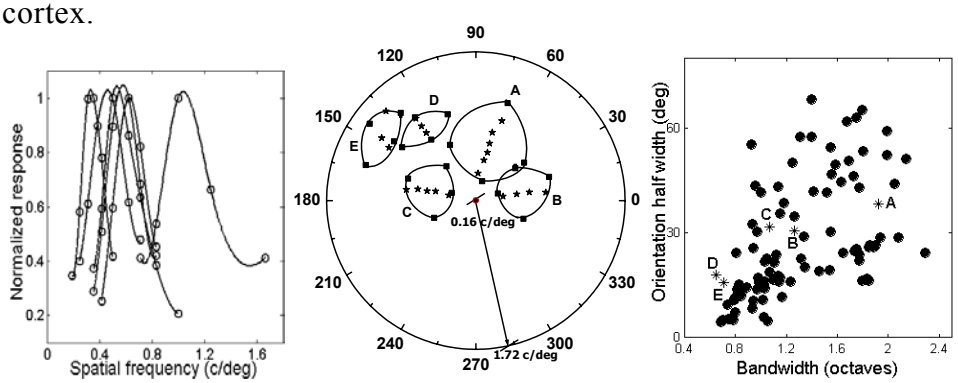
where, W_{IJ}^{+} (W_{IJ}^{-}) represents the strength of the connection from the ON-(OFF) center LGN cell at position J in LGN layer to the cortical cell at position I in the cortical layer. $W_{IJ} \in \{W_{IJ}^{+}, W_{IJ}^{-}\}$. $K_1^2 = \Sigma_{P=1}^{NXN}(W_{PJ}^{+})^2$, is the sum square of synaptic 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 constants in the LGN and the cortex respectively. MxM and NxN are the sizes of the LGN and the cortical layer respectively. A similar equation is used for updating W_{IJ}^-.

3 Simulation Results

Simple cell RFs 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 0.13 and 2 c/deg. The study on the effects of D_L, D_C and A_R on the RF formation and orientation selectivity of the

modeled cells has been discussed in detail in [2] along with role of aspect ratio in determining orientation selectivity. Here we report the spatial frequency selectivity and its spatial organization in the modeled cortex.



(a) (b) (c)

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 half amplitude points on spatial and orientaion tuning curve for each cell are marked with filled squares. Stars indicate the input spatial frequencies for which the cells show an orientation-tuned response. The alignment of star marks indicates that the preferred orientation is independent of stimulus spatial frequency as reported in cats [8] and monkeys [13]. (c)Cartesian plot between the spatial frequency bandwidth and orientation half width. The data points marked with stars and labeled A-E are for the cells shown in (b).

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. For constant RF sizes, cells with more number of subfields (i.e. smaller subregions width) are found to be selective for higher spatial frequency [1]. In our simulations with constant RF size, LGN diffusion constant (D_L) is the primary model parameter that determines the number of subregions in a cell's RF. For D_C=0.3 and $\gamma_1=\gamma_2=1$ the number of subfields reduces from five for D_L=0.025 to only two for D_L=0.075 [2] and the optimal spatial frequency (f_o) reduces from 1.04 cycles/degree to 0.33

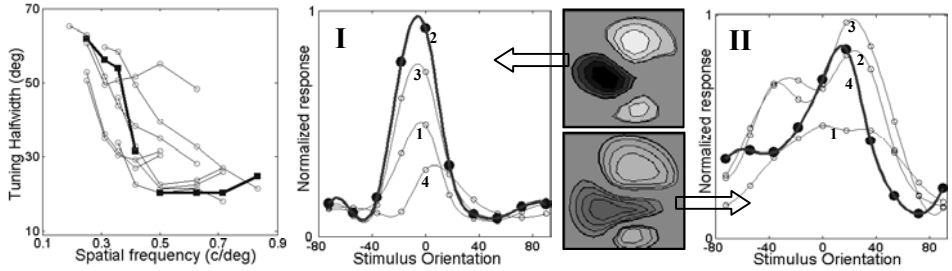
cycles/degree. In our simulated cells, f_o is inversely related to twice the subfield width and agrees with reported results [5]. f_o (Figure 1(a)) for the cells varies by about 2.45 octaves (0.19-1.04 c/deg). In cats, f_o has been found to range from 0.3-1.8c/deg [1] and 0.2-2.0 c/deg [9]. The spatial tuning widths varied considerably from 0.65-2.25 octaves with an average of 1.16 octaves (S.D. 0.47), matching closely with reported average bandwidth of 1.3 ± 0.3 octaves [1] and 1.0 ± 0.2 octaves [9].

De Valois et al [4] showed with the help of polar plots that cortical cells have localized spatial frequency responses. Polar plots for simulated cells Figure 1(b) showed similar localization of their frequency responses. Polar plots marked A, B and C show cells with wide orientation tuning and wide spatial frequency tuning, while the plots marked D and E show cells with sharp orientation tuning and narrow spatial tuning width. Orientation specificity and spatial frequency specificity are well correlated. The cells that are sharply tuned to orientation are also generally narrowly tuned to spatial frequency [13]. Accompanying Cartesian plot between the spatial frequency bandwidth and orientation half width in Figure1 (c) clearly brings out this correlation.

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 [12, 6]. This has been attributed to the inhibition that cortical cells receive from LGN cells

[12], which themselves show orientation biases at higher spatial frequencies. The model presented here is a purely feedforward model and the modeled LGN cells do not have any orientation bias, yet the modeled cells exhibit sharpening of orientation tuning with spatial frequency (Figure 2). For some cells, orientation tuning improves by as much as 20-40^o with the spatial frequency while for others orientation tuning varies by at best 4-10^o with the spatial frequency. 70% of the simulated cells belong to either of these two groups. Cells with 20-40^o improvements in tuning have f_o < 0.425 c/deg. To study this difference in behavior, two cells were taken (marked I and II), one from each group having the same preferred orientation of 0^o and equal number of subregions (D_L=0.075 for both the cells) in their RFs. However, LGN resource γ_1 is five times larger in cell I. This resulted in difference in (i) strength of their synapses and (ii) subfield width. The cell in Figure 2(b) has stronger synapses with a subfield of width 0.92^o and f_o = 0.63 c/deg whereas the cell in Figure 2(c) has weaker synaptic strengths (2.7 times lower) and a larger subfield width of 1.58^o and lower f_o = 0.36 c/deg. The weaker synapses spread over a wider subfield make the orientation tuning of the cell poor at lower frequencies. As the frequency increases the width of the input grating reduces, and the response reduces more at the orthogonal orientations than at the preferred orientation, resulting in a drastic improvement in orientation tuning from 61.88^o to 31.4^o with increasing spatial frequency.



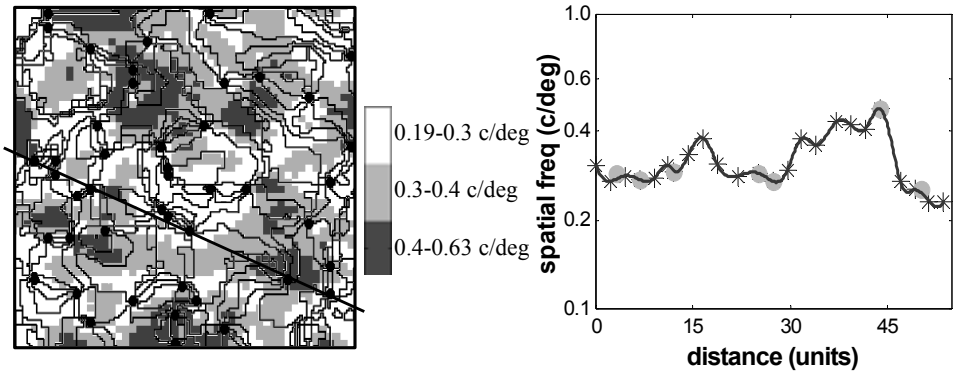
(a) (b) (c)

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 cells. The curves in thick lines are at the frequency at which the cell had the best tuning response.

3.2 Spatial frequency maps

Study of spatial frequency preferences across the cortical surface has shown that 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 [7], pinwheel [3] and clustered [8]. Though these arrangements are debatable, yet the common observation among these studies has been that the pinwheel centers co-localize with the extremes of the spatial frequency domains [8]. Our analysis of data from [8] (see Figure 6 in [8]) shows that though pinwheel centers largely co-localize with the extremes of the spatial frequency domains, about 27% pinwheel centers are located in the mid frequency range in the frequency map. Figure 3 shows a spatial frequency map obtained through our model. The contour plot of the corresponding orientation map for the modeled cortex is also shown. The pinwheels are mostly (73.33%) found to co-localize with the extremes of the spatial frequency domains and 26.67% pinwheels lie in the mid frequency range. A plot

of spatial frequency variation along the line marked in black in Figure 3(a) is shown in Figure 3(b). Cortical diffusion, D_C, ensures that near neighboring cells have similar receptive fields and orientation preferences [2]. Spatial frequency profile in general shows locally smooth transition with occasional abrupt transitions as reported in [8]. The domain size for smooth transition increases with increasing values of D_C.



(a) (b)

Figure 3(a) Spatial frequency map for one of the simulated cortices along with orientation contour map of the same cortex. (b) Distribution of spatial frequencies as a function of the distance along the line shown on the frequency map. Pinwheels falling on the line are marked with gray circles and the data points lying on the line are marked with stars.

4 Discussion

The simple cells developed through the model [2] capture a number of experimentally observed spatial frequency characteristics of cortical simple cells as well as spatial frequency map. The model presented is a purely feedforward model and incorporates only of X-cells in the LGN; that too of one size only. Our results indicate that spatial

preference is determined by subfield width and the distribution of synaptic strengths within it.

References

1. B.W. Andrews, D.A. Pollen, Relationship between spatial frequency selectivity and receptive field profile of simple cells, J. Physiol. 287 (1979) 163-176.
2. B. Bhaumik, M. Mathur, A Cooperation and Competition Based Simple cell Receptive Field Model and Study of Feed-forward Linear and Nonlinear Contributions to orientation selectivity, J. Comp. Neurosci. 14 (2003) 211-227.
3. P.C. Bressloff, J.D. Cowan, SO(3) symmetry breaking mechanism for orientation and spatial frequency tuning in visual cortex, Phys. Rev. Lett. 88 (2002) 078102.
4. R.L. De Valois, D.G. Albrecht, L.G. Thorell, Spatial frequency selectivity of cells in macaque visual cortex, Vision Res. 22 (1982) 545-559.
5. J.L. Gardner, A. Anzai, I. Ohzawa, R.D. Freeman, Linear and nonlinear contributions to orientation tuning of simple cells in the cat's striate cortex, Vis. Neurosci. 16 (1999) 1115-1121.
6. P. Hammond, C.J.D. Pomfrett, Influence of Spatial frequency on tuning and bias for orientation and direction in the cat's striate cortex, Vis. Res. 30 (1990) 359-369.
7. M. Hübener, D. Shoham, A. Grinvald, T. Bonhoeffer, Spatial relationship among three columnar systems, J. Neurosci. (1997) 9270-9284.
8. N.P. Issa, C. Trepel, M.P. Stryker, Spatial Frequency maps in cat visual cortex, J. Neurosci. 20 (2000) 8504-8514.
9. L. Maffei, A. Fiorentini, The visual cortex as a spatial frequency analyzer. Vis. Res. 13 (1973) 1255-1267.
10. D.J. Tolhurst, I.D. Thompson, On the variety of spatial frequency selectivities shown by neurons in area 17 of the cat, Proc. R. Soc. Lond. B. 213 (1981) 183-199.
11. T.W. Troyer, A.E. Krukowski, N.J. Priebe, K.D. Miller, Contrast-invariant orientation tuning in cat visual cortex: Thalamocortical input tuning and correlation-based intracortical connectivity, J. Neurosci. 18 (1998) 5908-5927.
12. T.R. Vidyasagar, J.A. Siguenza, Relationship between orientation tuning and spatial frequency in neurons of cat area 17, Exp. Brain Res. 57 (1985) 628:631.
13. M.A. Webster, R.L. De Valois, Relationship between spatial-frequency and orientation tuning of striate cortex cells, Opt. Soc. Am. A. 2 (1985) 1124-1132.

Dr. Mona Mathur received her B.E. in Instrumentation and Control Engineering from NSIT, Delhi. She received her masters and PhD from the Department of Electrical Engineering at the Indian Institute of Technology, New Delhi. Her research interests are in the areas of computational Neuroscience and analog VLSI design.

Dr. Basabi Bhaumik received her PhD and M. Tech in Electrical Engineering from Indian Institute of Technology, Kanpur and BE in Electronics and Telecommunication from Jadavpur University, Calcutta. She joined the faculty in Indian Institute of Technology, Delhi in 1980. She is currently a professor in the Department of Electrical Engineering. Her research interests are in the areas of Biological Neural Networks and Analog /Mixed Signal VLSI Design.