Variable Discharge Pattern and Contrast Invariant Orientation Tuning of a Simple Cell: A Modeling Study

Akhil R. Garg  
Department of Electrical Engineering  
J.N.V. University Jodhpur, India  
E-mail: garg_akhil@yahoo.com

Basabi Bhaumik  
Department of Electrical Engineering  
Indian Institute of Technology New Delhi, India  
E-mail: bhaumik@ee.iitd.ac.in

Klaus Obermayer  
Department of Electrical and Computer Science  
Technical University Berlin, Germany  
E-mail: oby@cs.tu-berlin.de

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Abstract— The orientation tuning width of the spike response of neuron in V1 does not change with the contrast of input signals. It is also known that cortical neurons exhibit tremendous irregularity in their discharge pattern, which is conserved over large regions of cerebral cortex. To produce this irregularity in responses the neurons must receive balanced excitation and inhibition. By a modeling study we show that, if this balance is maintained for all levels of contrast, it results in variable discharge patterns of cortical neurons at all contrast and also in contrast invariant orientation tuning. Further, this study supports the role of inhibition in shaping the responses of cortical neurons.

Keywords—Database Orientation tuning, simple cells, complex cells, visual cortex

1. Introduction

Hubel and Wiesel [1] were the first to show that simple cells are tuned for orientation. They had suggested that simple cells in primary visual cortex acquire the property of orientation selectivity due to the structure of their receptive field (RF). The RF structure of these cells is composed of segregated elongated ON/OFF subfields; they proposed that RF structure of these cells is formed due to specific connectivity scheme, wherein ON-center LGN inputs have their receptive field (RF) centers aligned over the simple cell's ON sub-region, and similarly OFF-center LGN inputs have their RF centers aligned over the simple cell's OFF sub-region. Later experimental studies [2][3][4][5][6] confirmed such a connectivity scheme to exist between LGN cells and simple cells of primary visual cortex. However, with this connectivity scheme the width of orientation tuning curve of the cortical cell widens with the increase in the contrast of input stimulus [7][8][9]. Contrary to this, experimental studies show that the orientation tuning of simple cells in layer IV of mammalian primary visual cortex is contrast invariant [8][9][10]. Also, in the visual cortex the repeated presentations of an identical stimulus elicit a variable number of action potentials [11][12][13], and the time between successive action potentials (interspike interval) is highly irregular [13][14]. It was also shown that this irregularity reflects noise, relegating the signal carried by the neuron to a crude estimate of spike rate [8].

Although many modeling studies have been performed to analyze the mechanism of acquiring these two response properties, most of these studies were confined to explore only one of these properties. Here by a
modeling study we show that cortical cells can acquire both of these properties simultaneously. It has been shown that variable spiking can be achieved with the combination of excitatory and inhibitory inputs to a neuron and to produce highly irregular firing; the neuron must balance excitation with inhibition [13]. Also, in addition to the excitatory inputs simple cells receive inhibitory inputs [9]. Furthermore, recent experimental study [15] has shown the existence of two functionally distinct types of interneurons in layer IV providing inhibitory inputs to simple cells. One type is tuned for orientation and has RF structure similar to that of simple cells, and is therefore called as simple inhibitory cell [15][19]. The other type of interneurons is not tuned for orientation, and has RF structure similar to that of complex cells, and is called as complex inhibitory cells [15][19].

In the present work we critically examined how the feedforward inhibitory inputs due to these interneurons contribute to contrast invariant orientation tuning and to neural output pattern. We show that untuned inhibitory inputs due to complex type of inhibitory cells can be used to balance excitatory inputs to produce highly variable discharge pattern of cortical neurons and contrast invariant orientation tuning. As the contrast of input stimuli increases, there is an increase in the firing rate of LGN cells. This results in the increase of feed forward excitation, and the balance between the excitation and inhibition is disrupted. In order to maintain the balance, there should be some mechanism to simultaneous increase the inhibition with the increase in excitation. In our model we show that, if the outputs of the inhibitory interneurons are made to be dependent upon the average firing rates of the population of LGN cells for every stimulus condition, the inhibition increases automatically with the contrast increase and balances the increased excitation.

Our model resembles other models using inhibition for increasing orientation selectivity, but differs from such models. We use feed forward untuned inhibition rather than broadly tuned cross-orientation or feed forward phase-specific tuned inhibition. And we show that this also results in highly variable discharge pattern of cortical cells. The input from LGN to cortical cell not mediated by cortical excitatory cells is often termed as phase-specific tuned inhibition. In our model we show that, if the outputs of the inhibitory interneurons are made to be dependent upon the average firing rates of the population of LGN cells for every stimulus condition, the inhibition increases automatically with the contrast increase and balances the increased excitation.

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2. Material and Methods

Simple cell RF was modeled as a Gabor function [16], which is a two dimensional Gaussian multiplied by a sinusoid. The positive values of Gabor function were taken to be ON subregion yielding connection from ON type LGN cells, and negative values of Gabor function were taken to be OFF subregion yielding connection from OFF type LGN cells. The model simple cell in cortical layer was a single compartment, integrate-and-fire neuron that received synaptic input in the form of transient conductance changes at both excitatory and inhibitory synapses. The membrane potential of the model neuron then changes according to

\[
\tau_m \frac{dV}{dt} = V_{rest} - V(t) + G_{ex}(t)(E_{ex} - V(t)) + G_{in}(t)(E_{in} - V(t))
\]

with \(\tau_m = 20\text{ms}, V_{rest} = -70\text{mV}, E_{ex} = 0\text{mV},\) and \(E_{in} = -70\text{mV}\) [17]. \(E_{ex}\) and \(E_{in}\) are the reversal potentials for the excitatory and inhibitory synapses. \(V(t)\) is the membrane potential of the cortical cell at time step \(t\). Whenever the membrane potential of the cell reaches the threshold value of -54mV, it fires an action potential, and then the membrane potential is reset to -60mV. The synaptic conductance \(G_{ex}\) and \(G_{in}\) and their related peak conductance values are measured in the units of the leakage conductance value of the neuron, and are dimensionless. The values of individual peak excitatory conductance \(g_{eON}\) and \(g_{eOFF}\) are taken from the output of Gabor function, representing the ON/OFF regions of receptive field structure. In other words, individual peak synaptic conductance represents the synaptic strength between an LGN cell of a particular type located at a particular location and cortical cell. Whenever a particular ON/OFF type LGN cell fires, the corresponding peak synaptic conductance contributes to the value of total excitatory conductance. Each cortical cell also receives feedforward inhibition due to both complex and simple types of inhibitory cells. To study the effect of inhibition due to these cells individually we have modeled the inhibition separately.

2.1 Modeling of inhibition due to complex cells

Since the complex type of inhibitory cells are untuned for orientation, we assume that each cortical cell receives inhibition from \(N\) such cells; the synaptic strength of connection between each inhibitory cell and cortical cell is given by \(g_{in}\) (inhibitory peak synaptic conductance). Output of each of these inhibitory cells was in
the form of spikes generated by independent Poisson's process. The firing frequency used for generating spikes was made proportional to the LGN firing rates. Additionally, whenever any of the inhibitory cells fires in the form of spike, it contributes towards the value of total inhibitory conductance. Otherwise, inhibitory synaptic conductance decays exponentially as

\[ \tau_{ex} \frac{dG_{ex}}{dt} = -G_{ex}(t) + \sum_i g_{iex} A_{iex}^{ON} + \sum_k g_{kex} A_{kex}^{OFF} \]

\[ \tau_{in} \frac{dG_{in}}{dt} = -G_{in}(t) + \sum_j g_{jin} A_{jin}^{inh} \]

where \( \tau_{ex} = \tau_{in} = 5 \text{msec} \), and \( A_{iex}^{ON} \) and \( A_{kex}^{OFF} \) are the activity of \( i^{th} \) and \( k^{th} \) ON and OFF type LGN cells, and \( A_{jin}^{inh} \) is the activity of \( j^{th} \) inhibitory cell.

2.2 Modeling of inhibition due to simple type inhibitory cell

Simple-type inhibitory cells are tuned for orientation having elongated segregated ON/OFF regions in their RF structure. Also, these cells inhibit excitatory cells with similar orientation preference and antiphase RF structure [7]. In our model we assume that cortical cell has two RF structures, one for excitatory inputs and the other for inhibitory inputs. These RFs were generated using Gabor function, and the connecting strength between LGN cells and cortical cell was represented by peak synaptic conductances \( g_{iex}^{ON}, g_{iex}^{OFF}, g_{jin}^{ON}, \) and \( g_{jin}^{OFF} \). Their values were obtained from output of two Gabor functions, which were similar except the phase shift of 180 degrees in spatial domain. One Gabor function was for obtaining the excitatory connectivity strength, and the other for obtaining inhibitory connection strengths. Whenever a particular ON/OFF type LGN cell fires, the corresponding peak synaptic conductance contributes to the values of total excitatory and inhibitory conductance. Otherwise, both excitatory and inhibitory synaptic conductance values decay exponentially. Therefore,

\[ \tau_{ex} \frac{dG_{ex}}{dt} = -G_{ex}(t) + \sum_i g_{iex} A_{iex}^{ON} + \sum_k g_{kex} A_{kex}^{OFF} \]

\[ \tau_{in} \frac{dG_{in}}{dt} = -G_{in}(t) + \sum_j g_{jin} A_{jin}^{inh} \]

where \( \tau_{ex} = \tau_{in} = 5 \text{msec} \) and \( A_{iex}^{ON} \) and \( A_{kex}^{OFF} \) are the activity of the \( i^{th} \) and \( k^{th} \) ON and OFF type of LGN cells.

2.3 Balance of excitation and inhibition

The condition of balance between excitation and inhibition is that the mean value of the excitatory current and mean value of inhibitory current input to a cortical cell are same. Therefore, from Eq.(1) for \( V = V_m \), we get

\[ <G_{ex}> (E_{ex} - V_m) = -<G_{in}> (E_{in} - V_m) \]

\[ <G_{in}> = -<G_{ex}> \frac{(E_{in} - V_m)}{(E_{ex} - V_m)} \]

where, \( <G_{ex}> \) and \( <G_{in}> \) are the excitatory and inhibitory synaptic conductance values, which are temporally averaged for every stimulus condition and depend upon mean firing rate, the number and the value of peak synaptic conductance of excitatory and inhibitory inputs, respectively. Since \( E_{ex} \) and \( E_{in} \) are constants, on replacing \( (E_{ex} - V_m)/(E_{in} - V_m) \) by \( K \) in Eq.(4), we get

\[ <G_{in}> = K * <G_{ex}> \quad \text{where} \quad <G_{ex}> = n_{ex} <f_{ex}> g_{ex} \quad \text{and} \quad <G_{in}> = n_{in} <f_{in}> g_{in} \]

where \( n_{ex} \) and \( n_{in} \) are the total numbers of excitatory and inhibitory inputs, and \( <f_{ex}> \) and \( <f_{in}> \) are the average firing rates of these inputs, and \( g_{ex} \) and \( g_{in} \) are the values of the excitatory and inhibitory peak synaptic conductance values. If \( n_{ex}, n_{in}, g_{ex} \) and \( g_{in} \) are constants, we get \( <f_{in}>=K_1 <f_{ex}> \). This gives the relationship between average firing rates of excitatory and inhibitory inputs to maintain the balance between excitation and inhibition.

3. Results

3.1 LGN input to a simple cell

Moving sinusoidal gratings of different orientation and particular spatial frequency was used as an input stimulus. Circularly-symmetric center-surround LGN spatial receptive fields were used, and LGN firing was determined as the rectified linear filtering of input luminance. For a moving grating of a preferred orientation, a cortical cell receives LGN input varying in its strength with time. There are occasions when the phase of input
stimulus matches exactly with the phase of a cortical cell's RF structure in spatial domain. Under such condition, the cortical cell receives maximum input. On the other hand there are occasions when there is a phase difference of 180 degree between the phases of input stimulus and RF structure of a cortical cell, and the input received by the cortical cell under such condition becomes minimum. The perfect match between phases of input stimulus and RF structure is made when the dark portion of input stimulus coincides with OFF subregion of RF structure, and the bright portion of input stimulus coincides with the ON subregion of RF structure. Similarly the phase difference of 180 degrees is made when the dark portion of input stimulus coincides with ON subregion of RF structure, and the bright portion of input stimulus coincides with OFF subregion of the RF structure. For null orientation stimulus, dark and bright regions of input stimulus overlap with both ON and OFF subregions of RF structure at all times. Therefore, the input received by the cortical cells at all times is almost same.

If the value of threshold for spiking is greater than the maximum input received by cortical cell for null orientations and is less than the maximum input received by cortical cell for preferred orientation, the cortical cell becomes highly selective for orientation. With the increase in contrast of input stimulus, the mean rate of the individual LGN cell grows and therefore the mean input received by the cortical cell grows. This growth of mean input does not depend upon the orientation of input stimulus, and even a null oriented stimulus can elicit a high rate of LGN input at high contrast, even higher than the maximum input elicited by an input stimulus of preferred orientation at low contrast. Despite this simple cells respond to their preferred orientation even at a very low contrast, and often do not respond to null orientation even at high contrast, i.e., they show contrast invariant orientation tuning [8][10]. The reason is that in addition to this feedforward excitation the cortical cells receive inhibitory inputs, and in response to the visual stimuli the membrane potential strongly fluctuates but, on average, remains below the firing threshold because it combines excitation and inhibition.

If with the increase in contrast excitatory input to cortical cell increases due to increase in the firing rate of LGN cells but the inhibitory input does not change with change in the contrast of input stimuli, and if this increased mean input is above the cell’s firing threshold, even for the non preferred orientation of input stimulus the width of the tuning curve will widen. On the other hand, if somehow there is simultaneous increase in excitatory and inhibitory inputs with the increase in contrast such that the value of average membrane potential remains below the firing threshold for all the orientations of the input stimulus, this may lead to contrast invariant orientation tuning. This balance in the excitation and inhibition results in highly irregular firing patterns for cortical cells. A simple integrate-and-fire mechanism with balanced excitation and inhibition has been shown to produce such an irregular response [13]. Furthermore, in the balanced regime weak correlations caused by signals shared among inputs have a multiplicative effect in the input-output rate of postsynaptic neuron [18].

As mentioned earlier, recent experimental study [15] has shown two types of inhibitory cells with their output depending upon feed forward excitatory inputs. First question that arises immediately is whether the output of any one of these individually or in combination can balance the feed forward excitatory inputs? And secondly, how does it effect the orientation tuning property of a simple cell? In the following sections we examine the possible role of these inhibitory cells in shaping the response of the cortical cell.

![Figure 1](image)

Figure 1. (a) Spike response of a cortical cell. Each sub block represents the response for an input stimulus of different orientation. The contrast of input stimulus is always kept at 50%. (b) Tuning curves for different contrasts, excitation always balanced with inhibition in each case.
3.2 Complex type inhibitory cell and its role in shaping the response of the cortical cell

Experimental study has shown that one type of inhibitory cells in the primary visual cortex has the RF structure similar to those of complex-type excitatory cells [15]. These cells are not tuned for orientation and their responses do not depend upon the phase of input stimulus [15]. Therefore, in our modeling study we assumed \( N \) such cells providing inhibitory inputs in form of Poissonian spike trains of a particular rate to the cortical cell in question. To explore the possible role of these cells in shaping the cortical cell responses we studied three cases.

(i) Excitation always balanced by inhibition: The inhibition provided by these inhibitory cells always balance the feedforward excitation to keep the average membrane potential below the firing threshold for stimulus of any orientation and contrast. We achieve this by making the firing rate of inhibitory cells dependent on the LGN firing rate, which changes with contrast. This balance in excitation and inhibition leads to highly variable discharge pattern of cortical cell. In Figure 1(a) we have plotted, the spike response of the cell for stimulus of different orientation and fixed contrast of 50%. Each sub block in this figure represents the response for different orientations of input stimulus, and is for a time duration of 1500 mS. The RF structure of the cell was obtained using Gabor function, and the cell had the preferred orientation of 90 degrees due to this RF structure. As can be seen from the figure, the numbers of spikes for non-preferred orientations are either zero or at most one or two. For orientation that is preferred or close to preferred orientation there are a large number of spikes.

On repeating the trial the spikes in terms of timings and number are not reproducible, confirming that responses of the cortical cells are highly irregular. Therefore, we accumulated the number of spikes for a trial period of 1000 msec for each orientation and repeated the process 100 times, and obtained the average number of spikes. In Figure 1(b), the orientation-tuning curves of a cortical cell show the average number of spikes per second for each orientation for different contrast levels. Actually we showed 10 different orientations of input stimuli starting from 0 to 162 degrees with an increment of 18 degrees. The cell has a preference to a stimulus of 90 degrees orientation for different contrasts. At a particular time and preferred orientation the bright and dark portions of the grating stimuli align with the cortical cells ON and OFF subregions simultaneously. When the matching between the two is perfect, the total number of LGN cells to contribute to the membrane potential of cortical cell is larger. We indeed get contrast invariant orientation. On calculations we found it to be approximately 26 degrees for all contrasts, quite similar to the experimental studies. We also observed that the average value of membrane potential fluctuates, but remains below the firing threshold independent of stimulus orientation. This was achieved due to the balance in average excitatory and inhibitory inputs. The cell still spikes because the consistency of the responses and the relative time spent by the membrane potential above threshold for preferred orientation is much more than those for the stimulus of non-preferred orientations.

Figures 2 and 3 show the plots of average membrane potential, average excitatory current and average inhibitory current, respectively, of a cortical cell for an input stimulus of 50% contrast. For stimulus of any orientation average excitatory and inhibitory currents are the same in absolute amplitude and opposite in direction leading to average membrane potential to be always less than firing threshold. We also obtain large variations in the average membrane potential as observed experimentally in experimental studies.

(ii) Excitation balanced with fixed inhibition: If we fix the inhibition at a particular value, by keeping the firing rate of inhibitory cells constant and do not allow it to change with the contrast of input stimulus, as shown in Figure 4(a), the selectivity of cell changes from sharply tuned to broadly tuned as the contrast increase of the input stimulus. On increasing the firing rate of inhibitory cell so as to increase the amount of inhibition results in tuned response curves for high contrasts, but the response at lower contrast diminishes. This all suggest that the inhibition has to change with the contrast to produce contrast invariant orientation tuning.

(iii) Excitation Only: In Figure 4(b) the orientation tuning curves of the same cell are shown at different contrast of input stimulus with only feedforward excitation. With the increase in contrast the tuning width increases, suggesting its dependence on the contrast of the input stimuli. The cell response is also reproducible in terms of the number of spikes from trial to trial. This confirms that only feedforward excitation is not sufficient to produce contrast invariant orientation tuning or variable discharge pattern of the cortical cell.

Figure 2. Average membrane potential of a cortical cell for different orientation of input stimuli at 50 percent contrast.
3.3 Simple-type inhibitory cell and its role in shaping the response of the cortical cell

Experimental studies have shown that other than complex inhibitory cells there are other types of inhibitory cells present in primary visual cortex. One type has elongated and segregated ON/OFF regions in their RF structure similar to the RF structure of simple cells. These cells are also tuned for orientations, and are called as simple-type inhibitory cells [15]. Modeling studies [7][18] suggest these cells are providing inhibitory inputs to the excitatory simple cells and having similar preferred orientations with out-of-phase RF structure to the inhibitory cells. The role of these cells has been studied in great details by Troyer, et. al. [7]. The RF structure of the simple-type excitatory cortical cell can be separated into two RF structures, one for providing excitatory feedforward inputs and the other for providing inhibitory feedforward inputs to the cortical cell. The net input to the cortical cell is the difference of these two inputs.

Two RF structures are similar in all respects except the 180 degrees phase difference in spatial domain. For a moving sinusoidal grating of the preferred orientation, because of the 180 degrees phase shifts in two RFs, there would be instances when the cortical cell receives only excitatory input or only inhibitory inputs. The excitatory input becomes above the firing threshold, and the cell fires. On the other hand for the stimulus of non-preferred orientations the excitatory and inhibitory inputs are the same, and the net input remains below the firing threshold and cells do not fire. All this mechanism makes the cortical cells highly selective for orientation.

We repeated the conceptual model of Troyer, et. al. [7], and observe that, due to the out-of-phase in the two RF structures, the combination of inhibitory and excitatory inputs resulted in contrast invariant orientation tuning in Figure 5(a). On increasing the inhibitory contribution by increasing the synaptic strength for inhibitory inputs the cell becomes more sharply tuned as shown in Figure 5(b). This is quite obvious that the effect of inhibition is only at null orientations and the increase in inhibition makes the cell more sharply tuned.

The conceptual model assumes that the cortical cell RF can be separated in two RF structures, and the inhibition is coming before any spiking of the inhibitory cell. However, in reality the inhibition to cortical cell
will come due to the spiking of inhibitory cell. In an experimental study [15], these types of inhibitory cells are also well tuned for orientation and inhibiting the excitatory cells with similar orientation preference. These cells will not spike for stimulus of null orientation, and will not be able to provide inhibition needed for the contrast invariant responses. Also, for stimulus of preferred orientation, the time instances for the maximum or high values of inhibitory inputs at excitatory cells are quite different from the time instances for the maximum or high values of excitatory inputs at the cortical cells. This leads to large fluctuations in average value of membrane potentials, and disturbs the balance in excitation and inhibition for both null and preferred orientation.

3.3 Effect of various parameters on contrast invariant orientation tuning

We studied the effects of $\tau_m$, $\tau_{ex}$ and $\tau_{in}$ time constants for membrane potential, average excitatory and inhibitory currents on the response of the cortical cell for inhibitory inputs due to only complex type of inhibitory cells. We will discuss their effects one by one.

While keeping all the other parameters of the model, i.e., $g_{syn}$, $g_{ex}$, $\tau_{ex}$ and $\tau_{in}$ constants, we varied $\tau_m$ and observed its effect on the tuning properties of the cortical cell. In Figure 6, with the increase in the value of $\tau_m$, the tuning width of the cell decreases and the maximum number of spikes for all the orientations decreases, even when the input and the RF structure of the excitatory cell were the same. With the high value of $\tau_m$ the membrane potential of the cell varies slowly, and the changes in the membrane potentials are the results of cumulative changes in the input stimulus for a long duration of time. Since input stimulus is designed to provide the average membrane potentials below the threshold, the cell tends to fire less and its orientation selectivity decreases. On the other hand, if the time constant is low, the changes in the membrane potentials are due to cumulative changes in the input for short duration and on short time scales for stimulus of preferred orientation. There are instances when excitatory input is more than inhibitory inputs and making the cell to spike. Therefore the number of spikes is more for preferred orientation and the tuning width is also broad.

The $\tau_{ex}$ controls the excitatory synaptic conductance of the cell. By changing its value only we observed that small changes in the value of $\tau_{ex}$ lead to large changes in the firing rates. For slight increase in its value the firing rates of the cell increases for stimulus of all orientations. The tuning width also widens with increase in of $\tau_{ex}$ as shown in Figure 7(a). It is obvious that, due to large $\tau_{ex}$, the excitatory synaptic conductance changes slowly. Also, if it has already reached a high value, even a small value of input can lead to the firing. The effect of $\tau_{in}$ was just the opposite to $\tau_{ex}$. For slight increase in its value the firing rates decrease to all stimulus orientations. The tuning width also widens with decrease in the value of $\tau_{in}$ as shown in Figure 7(b). It is obvious that, due to the increase of $\tau_{in}$, the inhibitory synaptic conductance changes slowly. In such a case a larger value of new input is needed for the model cell to fire.

Figure 5. (a) Orientation tuning curve obtained using conceptual model of Troyer, et. al. [7]. (b) Orientation tuning curve with increased inhibition obtained using the same model.

Figure 6. Tuning curves for different values of $\tau_m$.

Figure 7.
3.4 Effect of spatial frequency of input stimulus on contrast invariant orientation tuning

To test the effect of spatial frequency on the tuning properties we varied the spatial frequency of the input stimulus keeping all the other parameters fixed. If the spatial frequency of the drifting grating does not match with the spatial preference of the cells (approximately given by the spatial frequency component of the Gabor filter, i.e., 0.5 cycles/degree), the tuning width of the cell widens for the spatial frequency less or more than the preferred spatial frequency in Figure 8. It can also be seen that the widening of the width is for low contrast values, and it remains the same with the increase in contrast. Therefore, the changes in the tuning curve are due to the changes in spatial frequency of the input stimulus, but are not dependent on the contrast of input stimulus.

4. Discussion

We have shown that out of two types of feedforward inhibition as observed by [15] in cat layer IV, only the feedforward inhibition from complex-type inhibitory cells, which are untuned for orientation, balances the feedforward excitation and results in almost constant value of average membrane potential. We also showed that, if this balance is maintained for all values of input contrast, it not only leads to irregular discharge patterns of cortical cell [12] at all contrast but also leads to the contrast invariant tuning.

Many approaches for achieving contrast invariance had been proposed earlier. Some authors suggested that contrast changes simply multiply the response of a cell obtained using linear model by a constant. [20] Changing this gain value gives rise to contrast invariant orientation tuning. Others [21][22] suggested that the width of orientation tuning is the emergent property of intra-cortical circuitry and is independent of the parameters of input stimulus, including stimulus contrast. Using narrowly-tuned excitatory and broadly-tuned inhibitory intra-cortical interactions, they showed that a cell emerges to sharply tuned even with weakly- tuned LGN inputs. Earlier Troyer, et. al. [7], had used simple-type inhibitory cells to produce contrast invariant orientation tuning. We argue that the role of such cells in producing the contrast invariant orientation tuning is very limited. Since they themselves are tuned for orientation, and on assuming that they also have contrast invariant orientation tuning, such cell will not fire at null orientations. Thereby, they will be unable to provide the required inhibition at null orientation to produce contrast invariant orientation tuning. Secondly, if we assume that these cells show contrast-dependent orientation tuning, they may provide the required inhibition at null orientations. However, for the stimulus of preferred orientation, the timing difference between the arrivals of the excitation and inhibition leads to large variations in the average value of membrane potential.

Figure 8. Tuning curves obtained at different contrast and spatial frequencies of the input stimulus of a cortical cell. The cell has a preferred orientation of 90 degrees.
However, these cells may be needed to explain the experimental findings that the inhibitory conductance to drifting bar or grating is approximately anti-phase to the excitatory conductance [8][19]. In their modeling work Lauritzen and Miller [19] showed the different roles of simple and complex type inhibitory cells in defining the response properties of a cortical cell. They could show that within limited parameter regime complex-type inhibitory cells could provide contrast-invariant orientation tuning. They also showed that simple-type inhibitory cells were helpful in defining spatial and temporal tuning properties. In our modeling study we have explicitly shown how the balance between excitation and inhibition is achieved at all contrast levels of input stimulus, which results in variable discharge patterns of the cortical cell as well as the contrast invariant orientation tuning. In comparison to their work the parameter regimes were not limited, since in our model inhibition also changes with contrast and is directly dependent on the firing rate of LGN cells. Related proposals were made in a model of monkey VI layer IV [23][24]. In these models all cortical cells, both excitatory and inhibitory, received simple-cell LGN input and inhibited dominated input from other nearby cells. This all resulted in phase non-specific feedforward input similar to what we have modeled using complex-type inhibitory cell. Our work is based on experimental finding of the existence of the feedforward inhibition [15].

Although there are not many such experimental studies, we argue that there must indeed be significant amount of feedforward inhibition, which should be fast and arrive on time so as to prevent the cortical cell to fire in response to the positive pulse of LGN input evoked by transient nonpreferred stimuli [19][25]. We have constructed a simple model that accounts for contrast invariant orientation tuning. In this model the untuned inhibition, dependent on feedforward input, plays a vital role in shaping the response of a cortical cell. Also, using this model we show that balance between excitation and inhibition leads to not only irregular discharge patterns of cortical neurons but also to contrast invariant orientation tuning. We have analytically derived the relationship needed between the firing rates of excitatory and inhibitory inputs to maintain this balance.

References

Variable Discharge Pattern and Contrast Invariant Orientation Tuning

A.R. Garg, B. Bhaumik, and K. Obermayer


Akhil R. Garg was born at Jodhpur in India, in 1968. He received his B.E. in Electrical Engineering in 1991 and M.E. (Control system) in 1997 from J.N.V. University Jodhpur, India. He joined as faculty at J.N.V. University in 1992. He was a DAAD fellow at the Department of Electrical Engineering and ComputerScience of the Berlin University of Technology, Germany, from 2002 to 2003. He is currently working as an Assistant Professor in the Department of Electrical Engineering. He is also doing Ph.D. as part-time research scholar from the Department of Electrical Engineering. I.I.T. Delhi. His current research interests are computational neuroscience, artificial neural networks and Control systems.

Basabi Bhaumik received her Ph.D. 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.

Klaus Obermayer was born in Ludwigsburg, Germany, in 1961. He received the Diplom degree in physics in 1987 from the University of Stuttgart, Germany, and the Dr. rer. nat. degree in 1992 from the Department of Physics, Technical University of Munich, Germany. From 1992 and 1993 he was a postdoctoral fellow at the Rockefeller University, New York, and the Salk Institute for Biological Studies, La Jolla, CA. From 1994 to 1995 he was member of the Technische Fakultät, University of Bielefeld, Germany. He became associate professor in 1995 and full professor in 2001 at the Department of Electrical Engineering and Computer Science of the Berlin University of Technology, Germany. He is head of the Neural Information Processing Group. His current areas of research are computational neuroscience, artificial neural networks and machine learning, and biomedical image processing.