

Lateral Inhibition Underlying Suppression of Neuronal Activity and Sparse Coding

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Abstract—The functional importance of lateral inhibition in neural processing has been well documented, but the detailed mechanism is still hotly debated. In previous studies, we showed that lateral inhibition serves to decrease firing rates in neurons to the level corresponding to the best representation of stimuli. To further validate this hypothesis, we examine whether a sparse coding model is compatible with the response properties of cortical neurons, including orientation selectivity, cross orientation suppression and surround suppression. Simulation results demonstrate that the model can explain conflicting conclusions drawn from physiological experiments and give new insight into topological structure and information processing in the visual cortex.

Index Terms—sparse coding, lateral inhibition, orientation selectivity, cross orientation suppression, surround suppression

I. INTRODUCTION

The information processing mechanism of primary visual cortex (V1) has been intensively investigated both at the single-neuron level and the neuronal population level for several decades. Although many response properties of cortical neurons are well characterized now, such as orientation selectivity, cross orientation suppression and surround suppression, the neural mechanisms underlie these phenomena are still hotly debated. Ever since Hubel and Wiesel [1] first proposed a feedforward model for the orientation selectivity of V1 neurons [2], it has been argued whether orientation selectivity originates from excitatory convergence of lateral geniculate nucleus (LGN) afferents. This simple model predicted the tuning width of orientation selectivity should widen with increasing contrast of stimuli, which on the contrary is invariant [3], a phenomenon known as the contrast invariance of orientation selectivity. It was suggested that the lateral inhibition from neurons preferring different orientations helped to sharpen orientation selectivity [4], [5], which was supported by the so-called cross orientation suppression whereby the response of a V1 neuron to its preferred orientation is suppressed by null oriented stimuli [6], [7]. But measurements with intracellular recordings [8], [9] indicated that this kind of lateral inhibition could not be involved in cross orientation

suppression. In fact, a purely feedforward model with neurons having known nonlinear properties is sufficient to explain many response properties of V1 neurons [10]. However, a purely feedforward model is insufficient in accounting for some dynamic neuronal response properties [11]. Furthermore, the improved feedforward model predicts the loss of cross orientation suppression at low contrasts which is not the case for the responses of neuronal populations [12]. In summary, there are still some disagreements about the role of lateral inhibition in visual cortical processing (for review, see [13]).

Another phenomenon known as surround suppression, that is, the presence of stimuli in the non-classical receptive field (nCRF) of neurons can suppress their spiking responses, has attracted much interest in the last decade. Differently from cross orientation suppression, surround suppression is strongest when the stimulus in the nCRF has a parallel orientation (iso-orientation) and exhibits contrast dependent size tuning [14]. Moreover, the latency of surround suppression is much longer than the onset of the center response, and this cannot be explained by subcortical mechanisms. Horizontal connections have been thought to be the anatomical substrates for surround suppression [15]. However, the spatial extent [16] and propagation speed [17] of horizontal connections seems not to support the suppression induced by far surround stimuli.

With regard to information processing in visual cortex, Olshausen and Field [18] demonstrated that there are only two global objectives, that the representation error is small and that the representation is sparse, need to be optimized to yield the Gabor-like CRF profiles of simple cells. However, this model was found not able to produce the diverse distribution of receptive field structures as those obtained from physiological experiments [19]. Rehn and Sommer [20] then modified the model by introducing the hard sparseness constraint, meaning that the number of activated neurons rather than the neuronal activity is very limited when a stimulus is fed to the inputs. This new algorithm is fully successful in yielding essentially the same results as the physiological data and gives a clearer direction to the way in which V1 neurons form the sparse representation of a stimulus. There has been much experimental evidence indicating that sparse coding is a common strategy employed by sensory cortex. But the plausible neural mechanisms for sparse coding have seldom been considered so far (but see [21]).

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Broadly speaking, due to the lack of global information in the observations made in a very limited area, there is still a lot of confusion in understanding the response properties of cortical neurons. Then a possible solution could be determining the intrinsic neural mechanisms underlying these response properties of neurons by analyzing the coding properties of neuronal populations. In this paper, we investigate the global objective function of the sparse coding model by Rehn and Sommer [20], and then explore how the two objectives are achieved by neural network analysis.

II. HELPFUL HINTS

Consider the modified sparse coding model with the hard sparseness constraint, which can be expressed as:

$$\min\left\{\left(x - \sum_j a_j w_j\right)^2 + \lambda \|a\|_0\right\} \quad (1)$$

where x is the input pattern, w_j a basis vector with a_j being its coefficient, a the coefficient vector and λ the weight. The two terms correspond to the two global objectives of the model, which are to find the best representation and to guarantee the representation being sparse. Because the l_0 norm is non-differentiable, the optimization problem of (1) is difficult to solve. To make the problem tractable, the following alternative model is usually adopted:

$$\min\{\|a\|_0\} \text{ s.t. } \left(x - \sum_j a_j w_j\right)^2 < \varepsilon \quad (2)$$

with ε being the trade-off parameter. Compared with model (1), the major difference of the new model is that the two global objectives are treated separately. In this way, the objectives may be easily achieved through different neural mechanisms.

As for a neural network performing sparse coding, the input pattern x only activate few of the output neurons and then the information in x is encoded in the output values $\{y_j\}$ of these activated output neurons. Suppose we have selected a set of basis vectors $\{w_j\}$, then we consider how to determine the best representation $\hat{x} = \sum_j a_j w_j$ of x satisfying the representation error $\|x - \hat{x}\|_2 < \varepsilon$. As pointed out in [22], lateral inhibition plays a key role in sparse representation, by which cortical neurons not only compete with each other to represent the input signal sparsely but also cooperate with each other to make the representation more accurate. The responses of output neurons that correspond to the best representation are modified as follows:

$$y_j = Y_j - \sum_{k \neq j} \frac{w_k w_j}{\|w_k\|^2} w_k \quad (3)$$

where $Y_j = x \cdot w_j$, which is the output value of the j th activated output neuron at the condition of no other neurons being activated. By transposition, (3) is rewritten as:

$$\Delta Y_j = Y_j - y_j = \sum_{k \neq j} \frac{w_k w_j}{\|w_k\|^2} w_k \quad (4)$$

The above equation has the same form as the Hartline-Ratliff equation for lateral inhibition [23], [24]. The result is consistent with the direct measurement [23]. Equation (4) also shows that the more correlated the neurons are, the stronger the inhibitory connection between them is. This explains why the synaptic inhibition is primarily tuned to similar orientations [8]. And by such kind of lateral inhibition, the responses of neurons with similar orientation preferences are suppressed by each other resulting in the decrease in excitation, followed by the decrease in inhibition, from the large values $\{Y_j\}$ to the small ones $\{y_j\}$ (see (3)). The inhibitory interactions existing between the highly correlated neurons eliminate the probability that too many neurons exhibit very strong responses to a stimulus. This helps to reduce the redundancy in the representation and provides a solid foundation for sparse coding in the primate visual cortex.

Compared with the global objective of finding the best representation which is realized by lateral inhibition between the output neurons, the objective of minimizing the number of activated neurons may be achieved on the basis of the distributed computation in neural networks and the threshold activation level and spike firing of the neurons. When a stimulus is presented to the network, some output neurons are activated. Those that capture the major features of the stimulus will be activated first. Then they fire a spike to neighboring highly correlated neurons and delay their activation. Many of these neighboring neurons would receive too much lateral inhibition to be activated and then show no response to the stimulus. In this way, the stimulus is sparsely represented well enough by the large number of output neurons. At the same time, the activated output neurons fire spikes competitively with each other. Such a neural network, named a lateral inhibitory spiking neural network (LISNN), has been presented in [22].

III. FEEDFORWARD INTEGRATION FIELD

To further validate whether lateral inhibition is the general mechanism underlying various inhibitory effects of neuronal activity, we examine several correlated response properties of neurons. The model successfully explains the experimental results and gives insight into the topological structure and information processing in the visual cortex. But first of all, we would reconsider the concept of receptive field. Compared with the traditional definition of receptive field based on the responses of neurons to a stimulus, we care more about the structure that corresponds to the basis vector w_j . In the proposed LISNN model, V1 neurons in the output layer integrate signals from two different pathways: feedforward excitation from LGN inputs and lateral inhibition from intracortical circuits. We define the group of LGN cells converging to the same V1 neuron as the Feedforward Integration Field (FIF) of the V1 neuron. With this

definition, we can say that the basis vector w_j is composed of connection weights to the j th V1 neuron from the LGN cells in its FIF. From (3) we see that lateral inhibitory connections are strong between highly correlated neurons. So a strong lateral inhibitory connection between two V1 neurons implies that there must be a large spatial overlap of the coincident positive and negative regions of the FIFs of these two V1 neurons to make sure that $w_k \cdot w_j > 0$ is satisfied. It means: if surround suppression is caused by such cortical lateral inhibition, the FIFs of V1 neurons must be much larger than their CRFs so that they can overlap with each other. We give an illustration of the possible spatial distributions of FIFs in Fig. 1. In fact, the idea of overlapping basis vectors has been employed in other models [25], but no efforts were made to investigate the relationship between the larger FIF and the smaller CRF. We will show in the following that FIF is an important concept for our understanding of surround suppression.

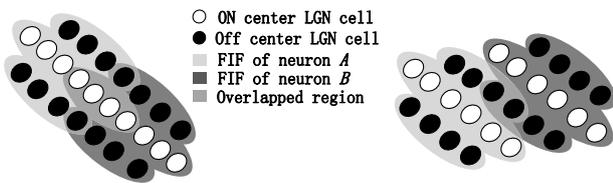


Figure 1. Illustration of the feedforward integration fields (FIFs) of neuron A and B, which are overlapped with each other.

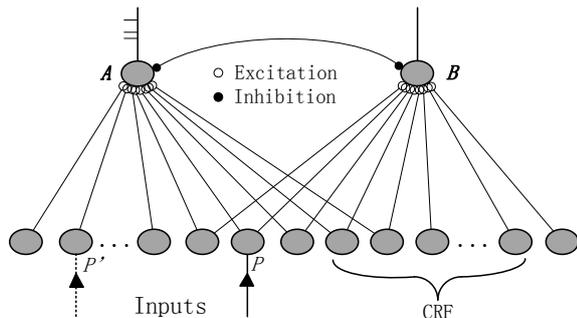


Figure 2. Illustration of the constriction of the response field of neuron B. Neuron A is activated first by the stimulus presented at point P, which is beyond the CRF of neuron B, and sends inhibitory signals to B through lateral inhibitory connections to suppresses its activity.

The prediction that FIFs are much larger than CRFs agrees with the findings that the blockade of GABA inhibition increases the receptive field size of neurons. This means the receptive field of neurons, which should actually be called the response field of neurons, is heavily reduced by lateral inhibition. The constriction of the response field of neurons from the larger FIF to the smaller CRF may occur as shown in Fig. 2. The stimulus presented in point P in the nCRF of neuron B elicits a spike in neuron A, which then sends an inhibitory signal to B to keep it silent. Such a mechanism could be responsible for the measurement that in strongly suppressed neurons the surround suppression arrives even earlier than the CRF excitation [17]. The spatial distribution of FIFs explains the finding that surrounds suppression caused by iso-oriented gratings is stronger from the ends of the CRF than from the CRF flanks [26].

Since the overlapped areas of FIFs are larger at the ends than at the flanks, neurons are more correlated with those in the end side regions than those in the flank side regions. In consequence, stimuli presented in the ends of the CRF elicit more lateral inhibition and then cause a stronger suppression.

The large overlapped FIFs make it possible for the far surround suppression to be mediated by horizontal connections. As can be seen in Fig. 2, whether a stimulus is presented in point P in the near surround or P' in the far surround, neurons integrating inputs from the surround (surround neurons, like neuron A) will be activated approximately at the same time. Then it sends inhibitory signals to neurons integrating inputs from the center (center neurons, like neuron B). As a result, the onset of suppression occurs almost simultaneously for both near surround and far surround no matter the stimulus is presented far beyond spatial extent of horizontal connections or not [17]. In this way, surround suppression can be evoked very fast by very far surround stimuli through horizontal connections. What is more, stimuli from further away, even beyond the FIFs of surround neurons, will suppress the activity of surround neurons and in turn slightly facilitate the responses of center neurons (see Fig. 3(B)). This phenomenon has been observed in some V1 neurons [27]. As for the contrast dependent size tuning of surround suppression [14], it may due to the suprathreshold activation of surround neurons. In order to activate surround neurons to suppress the response of center neurons, a smaller sized high contrast stimulus, as indicated by point S in Fig. 3(A) over which the center response decrease with the increasing stimulus diameter, is enough for the membrane potential of a surround neuron to exceed the threshold, while the size of a low contrast stimulus should be much larger.

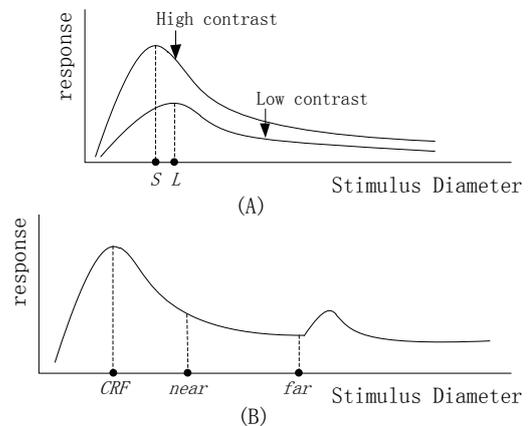


Figure 3. Size tuning of surround suppression. (A) For a high contrast stimulus to activate surround neurons to suppress the center response, the size of the stimulus corresponding to point S is smaller than that of the low contrast stimulus. (B) Stimuli from beyond the spatial extent of far surround suppress the activity of surround neurons and in turn slightly facilitate the center response.

IV. DISCUSSION

The presented model provides a good explanation for the appearance of Mexican-hat shaped tuning curve and

its dynamical parameters as shown in Fig. 4 [28]. If the FIF of a neuron best matches the input pattern x , let us say $x = \lambda w_k$, then the output value of this neuron is $y_k = \lambda \|w_k\|^2$ and the inhibition that other neurons received from this neuron can be calculated as follows:

$$I_{k,j} = \frac{w_k w_j}{\|w_k\|^2} (\lambda \|w_k\|^2) = y_j \quad (5)$$

That is, it will totally suppress the activity of these highly correlated neurons, whose responses then reach their minimum values R_{\min} . A sketch adapted from [29] of the average dynamics of $A = R_{\max} - R_{\min}$, R_{\min} and R_{orth} are shown in Fig. 5, from which we can see that there is a positive response in the early part of the time course indicating that V1 neurons tend to respond to a wide range of stimuli at first. Then there is a sharp downward slope of the response curves of R_{\min} and R_{orth} because of the arrival of lateral inhibition. A little while after the response of the neuron whose FIF best matches the input pattern reaches its maximum, lateral inhibition from this neuron is strongest, and R_{\min} and R_{orth} are driven to their minima.

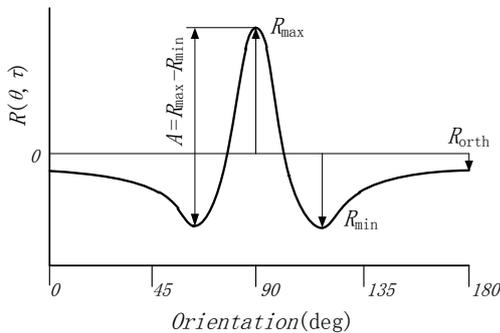


Figure 4. Mexican-Hat shaped tuning curve at a fixed time delay τ .

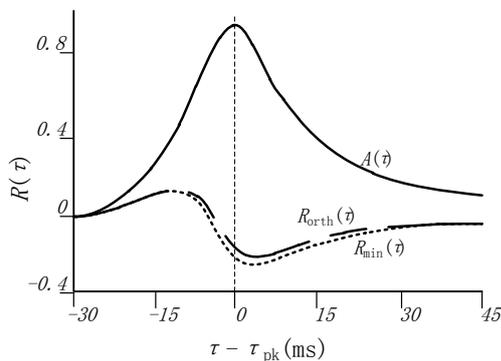


Figure 5. Plot adapted from Ringach *et al.* [29] showing the average dynamics of A , R_{orth} and R_{\min} illustrated in Fig. 4.

The main result of (5) indicates that there are strong inhibitory connections between highly correlated neurons. As discussed above, these neurons with similar preferences compete with each other and become more professional in representing stimuli. It seems the response of V1 neurons becomes restricted to a smaller but more structured region as the lateral inhibitory interactions increase. This process may lead to the observations that the presentation of stimuli in the nCRF increases neuronal response sparseness [30] and sharpens

orientation tuning of V1 neurons [27]. Compared with interactions between a center neuron and its surround neurons, lateral inhibitory interactions among the center neurons could be much broader because center neurons share a larger region of their FIFs. Inhibition can come from neurons with similar orientation preference. In some sharply tuned V1 neurons, these inhibitory signals are combined to produce the tuned suppression, centered near the preferred orientation of these neurons and broader than the tuned excitation [29]. When small lateral cortical patches from the recording pipette are inactivated, the recorded cells will shift their preferred orientation to the orientation of the inactivated site [31]. Such lateral inhibition provides a possible mechanism for cross orientation suppression. The negative response of neurons to some non-optimal oriented stimuli has been recorded, at the peak latency of which the suppression caused by lateral inhibition is strongest [11]. In fact, cross orientation suppression seems to result from the overall level of cortical activity [12]. This conclusion is reinforced by our finding that both cross orientation suppression and surround suppression can be viewed as an outcome of neuronal populations performing the same computational task.

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