A Model of the Summation Pools within the Layer 4 (Area 17)

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Abstract

We propose a developmental model of the summation pools within the layer 4. The model is based on the modular structure of the neocortex and captures some of the known properties of layer 4. Connections between the orientation minicolumns are developed during exposure to visual input. Excitatory local connections are dense and biased towards the iso-orientation domain. Excitatory long-range connections are sparse and target all orientation domains equally. Inhibition is local. The summation pools are elongated along the orientation axis. These summation pools can facilitate weak and poorly tuned LGN input and explain improved visibility as an effect of enlargement of a stimulus.

Keywords: Visual cortex; Summation pools; Horizontal connections; Response facilitation; Bayesian confidence propagation neural network

1 Introduction

Studies examining long-range spatial interactions in visual cortex show that cortical circuit plays a major role in altering the responses of the neurons. As demonstrated by Polat and Norcia [8] enlargement of a Gabor patch stimulus results in increased visibility of the stimulus. Furthermore, elongation of the stimulus along the orientation axis of the neurons results in more prominent visibility than elongation that is orthogonal to the orientation axis. Consequently, summation

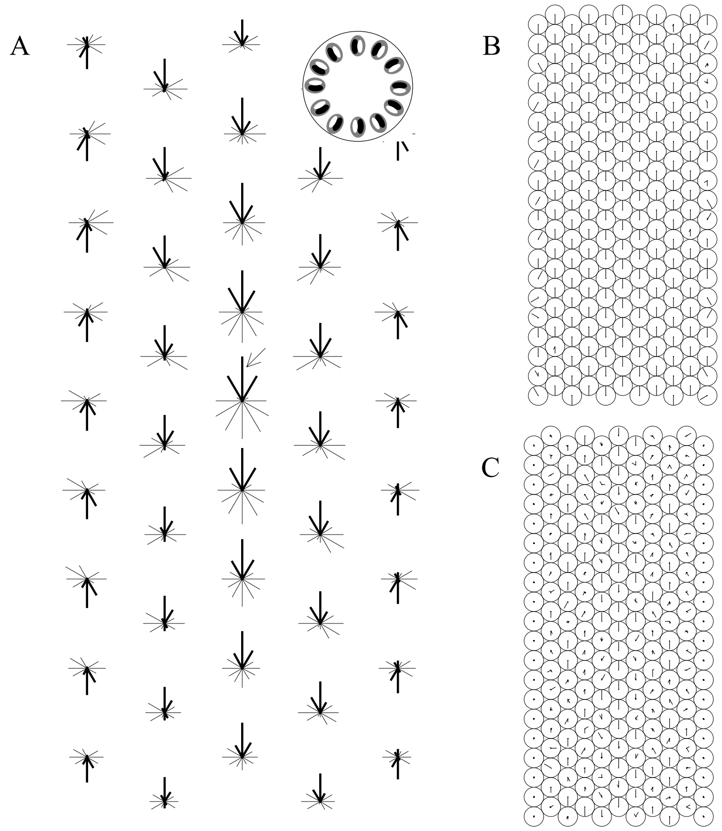

Fig. 1. Polar-plots organized as the network model, each one representing a hypercolumn. The legend in *A* shows the orientation and the relative spatial phase of the units in each hypercolumn. *A,* Central part of the reference unit's summation pool is shown. This unit (marked with an arrow) is located in the hypercolumn that is in the middle of the network. Thick lines represent excitatory connections, thin lines correspond to inhibitory connections. Distance from the origin is proportional to the strength of the connection. *B*, Normalized activities after 50 ms. Distance from the origin is proportional to the activity level of a unit. Units receive input from the LGN and the network. *C*, Units receive solely LGN input. Note that only hypercolumns receiving maximum LGN input can converge after 50 ms.

pools, which are hypothesized to be elongated, have been proposed [8]. However, response properties, such as orientation selectivity, spatial phase and frequency, etc., of the neurons that are found within a neuron's summation pool are not entirely known. It is neither clear in which cortical layers these pools might be located.

In layer 4 of cat primary visual cortex the excitatory connections target the distal (>0.74 mm) iso- (±30º), oblique- (±30–60º) and cross-orientation (±60–90º) domains equally [12]. Local projections are, however, biased towards the iso-orientation domain [12]. Results by Yousef et al. [12] indicate that the hypothesized summation pools within the visual cortex [8] might be composed of neurons situated in all orientation domains.

According to the findings by Hubel and Wiesel [6,7] the primary visual cortex has a modular structure. It is composed of orientation minicolumns each one comprising some hundreds of excitatory cells and a smaller number of inhibitory interneurons of different kinds. Contrast edge orientation is coded such that the neurons in each orientation minicolumn respond selectively to a broad range of orientations.

The Bayesian Confidence Propagation Neural Network model (BCPNN) [9] has been developed in analogy with the modular structure of the primary visual cortex [6,7]. This is an abstract neural network model in which each unit corresponds to an orientation minicolumn. The network is partitioned into hypercolumn-like modules (referred to as hypercolumns in the text). Summed activity within these hypercolumns is normalized to one. Earlier a biologically plausible implementation of normalization has been proposed [2].

A developmental model of the summation pools within the layer 4 (area 17) based on cat data is proposed. This model is in line with the modular structure of the neocortex and captures some of the known properties of the layer 4. Excitatory local connections are dense and biased towards the iso-orientation domain. Excitatory long-range connections are, however, sparse and target all orientation domains equally. Inhibition is local and is mediated by inhibitory simple cells. Proposed summation pools are mildly elongated along the orientation axis. Simulations show that the proposed summation pools can facilitate weak and poorly tuned LGN input, and hence explain improved visibility as an effect of enlargement of the stimulus.

2 Network Model

The network model used during the simulations consists of 220 (11x20) hypercolumns arranged to form a hexagonal array (Fig. 1*A*). Each hypercolumn consists of 12 layer 4 (area 17) units. Their receptive fields (RF) are designed as contrast edge detectors (composed of two elongated subregions with opposite sign). Difference in orientation preference between two successive units inside a hypercolumn is 30°. Note that every orientation is represented twice with two units, which have opposite absolute spatial phase (their subfields with opposite sign overlap). Absolute spatial phase refers to the position of the ON- and OFF-subregions with respect to the visual field.

The RF centers of the units belonging to a hypercolumn are positioned in the center of their host hypercolumn. The distance between the centers of two adjacent hypercolumns is constant throughout the network model and corresponds to 0.2º of visual angle (at 2º of eccentricity [4]). The visual world covered by the model is 2.4x5.4º. The RF width is 1º [4] and the height is ~1.5º indicating strong overlap between units positioned in neighboring hypercolumns. Orientation tuning of the LGN input is ~40º at half-width at half-height [1]. The LGN input is computed using a model developed by Troyer et al. [11]. All units are tuned for the same spatial frequency of 1 cycle/degree [4].

3 Simulation Results

The simulations are divided into two parts. During the first part, BCPNN incremental learning algorithm is used to develop hypothesized layer 4 summation pools. Later we address the question of whether or not these summation pools can facilitate weak and poorly tuned LGN input, and hence improve visibility as reported in [8].

The BCPNN learning algorithm is correlation based, thus if two units are correlated during a time step the connection between them strengthens. Anticorrelation results in an inhibitory connection via a local inhibitory interneuron. Excitatory connections are reciprocal, since the weight matrix is symmetric. For this network configuration training of the fully connected network lasts for 1000 simulation steps, where every step corresponds to 1 second. The learning rate, which defines the degree of weight modification, is 0.005 [9]. At every time step, the activity levels of the units are initiated using a new contrast edge stimulus, whose position and orientation are sampled from a uniform distribution. Its width is 1º, and spatial frequency is 1 cycle/degree.

Noise is added to the activity levels through several steps. First, a normally distributed noise with a standard deviation of 10% of the so-called bias value is added. The bias value is defined as the activity level of units inside a hypercolumn in absence of stimulus. Later, the activity levels are rectified so that all negative activity levels are set to zero, and a 5-10% uniform distribution noise is added to all units to simulate the background activity. The activity levels are normalized so that the sum of activities in each hypercolumn is equal to one. The contrast of the stimulus is 100%, though the effect of high noise in combination with the BCPNN normalization procedure lowers this level considerably.

Central part of the reference unit's summation pool is visualized in Figure 1*A*. Units that are correlated with the reference unit are connected to it through reciprocal excitatory connections (Fig. 1*A*, thick lines). The result of anticorrelation is inhibitory connection through a local inhibitory simple cell (Fig. 1*A*, thin lines). Ferster [5] has shown that inhibitory simple cells inhibit excitatory simple cells that are located in their close surroundings if they have opposite absolute spatial phase. Based on the proposed scheme [5] it is hypothesized that anticorrelated units can inhibit each other by local or long-range excitation of the inhibitory simple cells.

Strength of the excitatory connections between the reference unit and the units, which have the same orientation preference and absolute spatial phase as the reference unit, tends to decrease along the axis that corresponds to the preferred orientation of the reference unit (Fig. 1*A*). Along the orthogonal axis the connection type switches from excitatory to inhibitory (Fig. 1*A*). Thus, along this axis the reference unit becomes correlated with the units that have opposite relative spatial phase, but similar absolute spatial phase. Relative spatial phase refers to the position of the ON- and OFF-subregions with respect to the center of a RF.

Local connections have higher amplitude than long-range horizontal connections (Fig. 1*A*). This indicates strong local and sparse distal connectivity within the summation pool. As reported earlier, based on a similar network model [3], the excitatory long-range horizontal connections target all three distal orientation domains equally, whereas local connections are biased towards the iso-orientation domain (see also [12]). Thus, based on the connections made by the reference unit we hypothesize that the summation pools are highly heterogeneous with respect to orientation preference. Finally, the area covered by the connections emerging from the reference unit is mildly elongated along the orientation axis (This property is not shown in Fig. 1*A*). This effect is due to the stimulus used during the training.

We assume that the proposed summation pools can facilitate weak and poorly tuned LGN input, and hence improve visibility as reported in [8]. We show this through computer simulations that consist of two parts. During the simulations the stimulus is a vertical contrast edge, positioned in the center of the network model (see the legend in Fig. 1*A*. The RF at 12 o'clock represents the unit that is tuned to this stimulus). This stimulus is identical to the stimuli used during the training of the network. During the simulations 46% of the total excitatory input of a unit is from the LGN, whereas the rest is intracortical input [1]. The simulation time step is 10 ms, and the 'membrane time constant' of the units is 50 ms [9]. A hypercolumn has converged when the activity of its units is below <1% of a unit's maximum activity level. Maximum activity of a unit is 1.0 (all other units in its host hypercolumn are silent). The second requirement for convergence is that a unit dominates the hypercolumn, i.e. its activity is >0.9. This will occur after a number of simulation steps, since the model is a recurrent attractor network.

During the first simulation, units receive input from both the LGN and the other units within the network model (Fig. 1*B*). During this simulation the LGN input is amplified and sharpened by the connections between the units. As a result almost all hypercolumns converge after 50 ms. Note that in the middle three columns of hypercolumns the lines from the origin point upwards (Fig. 1*B*). This illustrates that the hypercolumns located in these three columns converge to the unit, which prefers the stimulus. During the second simulation, connections between the units are removed and compensated by stronger LGN input. As shown in Figure 1*C*, LGN input alone is not sufficient for the majority of the hypercolumns to converge. Note that only those hypercolumns that receive maximum LGN input converge. This is due to the attractor properties of the network.

Reported results on convergence pattern and relative speed (Fig. 1*B-C*) are rather independent of the parameter choices. Qualitatively similar results have been achieved with different values on simulation time step, membrane time constant, network size and shape, RF size, RF overlap between units located in adjacent hypercolumns, stimulus contrast used during training and retrieval, orientation tuning, contrast gain, etc.

4 Conclusions

We propose a developmental model of the summation pools within the layer 4 (area 17) based on cat data. The model is in line with the modular structure of the neocortex and captures some of the known properties of the layer 4. Excitatory local connections are dense and biased towards the iso-orientation domain. Excitatory long-range connections are, however, sparse and target all orientation domains equally. Inhibition is local and is mediated by inhibitory simple cells. Proposed summation pools are mildly elongated along the orientation axis.

Simulations show that the proposed summation pools can facilitate input from the weak and poorly tuned LGN, and hence explain improved visibility as an effect of enlargement of the stimulus. During the simulations the effect of the elongated shape of the proposed summation pools on network performance has not been addressed. It is reasonable to assume that elongated summation pools can explain reported differences in degree of improved visibility, which seems to be related to stimulus configuration [8]. Our intention is to investigate this effect in the near future in the framework of a laminar model, since elongated summations pools are more likely to be found in the superficial layers [10].

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