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 LGN input and explain improved visibility as an effect of enlargement of a stimulus.

1   Introduction

The studies examining the long-range spatial interactions in visual cortex propose that the cortical circuitry 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 patch. Furthermore, when the Gabor patch is elongated along the orientation axis the visibility of the patch is more prominent than elongation that is orthogonal to the orientation axis. As a result Polat and Norcia [8] have proposed summation pools that are hypothesized to be elongated. Note, however, that the response properties, such as orientation selectivity, spatial phase, etc., of the neurons located within these hypothesized summation pools 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 [11]. Local projections are, however, biased towards the iso-orientation domain [11]. Results by Yousef et al. [11] 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. The summed activity within these modules 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 (area 17). 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, which are excited by excitatory cells that are anticorrelated with the targets of the inhibitory simple cells. The proposed summation pools are mildly elongated along the orientation axis. The simulations show that the proposed summation pools

can indeed facilitate the weak 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 are designed as contrast edge detectors (composed of two elongated subregions with opposite sign). The 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 receptive field (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]. Furthermore, all units are tuned for the same spatial frequency of 1 cycle/degree [4].

The LGN input of the units is computed using a model developed by Troyer et al. [10].

3 Simulation Results

The simulations are divided into two parts. In the first part, the BCPNN incremental learning algorithm is used to develop the hypothesized layer 4 (area 17) summation pools. Later we address the question of whether or not these summation pools can indeed facilitate the weak 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. Note further that the weight matrix is symmetric. 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 value of all units inside a hypercolumn in absence of any 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.

The summation pool of the 'reference unit' is visualized in Figure 1A. Units that are correlated with the reference unit are connected to it through reciprocal excitatory connections (Fig. 1A, thick lines). The result of anticorrelation is inhibitory connection through a local inhibitory simple cell (Fig. 1A, 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. According to this scheme anticorrelated units can inhibit each other by local or long-range excitation of the inhibitory simple cells.

The strength of the excitatory connections between the reference unit and units having same orientation preference and absolute spatial phase as the reference unit tend to decrease along the axis that corresponds to the preferred orientation of the reference unit. Along the axis, which is orthogonal to the orientation preference of the reference unit, 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 (Fig. 1*A*). Relative spatial phase refers to the position of the ON- and OFF-subregions with respect to the center of a receptive field.

The local connections have higher amplitude than the 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 [11]). Thus, based on the connections made by the reference unit we hypothesize that the summation pools are highly heterogeneous. Finally, the area covered by the connections emerging from the reference unit is mildly elongated along the orientation axis of the reference unit.

We assume that the proposed summation pools can facilitate weak 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. 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 comes 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].

In the first part, the units receive both LGN input and cortical excitatory and inhibitory input (Fig. 1*B*). The LGN input is amplified and sharpened by the connections between the units, and hence all hypercolumns converge after 50 ms. In the second part, the units receive only LGN input, thus there are no connections between the units (Fig. 1*C*). The LGN input is not sufficient for the majority of the

hypercolumns to converge, since only those receiving maximum LGN input can detect the contrast edge. Note the difference in convergence speed between these two cases after 50 ms (five simulation steps). These simulations demonstrate how facilitation and suppression mediated by local and long-range horizontal connections can enhance and sharpen weak LGN input.

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 (area 17). 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, which are excited by excitatory cells that are anticorrelated with the targets of the inhibitory simple cells. The proposed summation pools are mildly elongated along the orientation axis.

The simulations show that the proposed summation pools can indeed facilitate the weak LGN input, 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 has not been addressed. Our intention is to investigate the effect of this property in the near future. It is, however, reasonable to assume that the

proposed elongated summation pools can explain reported differences in degree of improved visibility, which seems to be related to stimulus configuration.

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Fig. 1. Polar-plots organized as the network model, each one representing a hypercolumn module. The legend in *A* (top right) shows the orientation and the relative spatial phase of the units in each hypercolumn module. *A*, The summation pool of the 'reference unit', which is positioned in the middle hypercolumn (marked with an arrow). Thick lines are excitatory connections and thin lines correspond to inhibitory connections. Distance from the origin is proportional to the strength of the connection. *B*, Polar-plots showing normalized activities of the units in hypercolumn modules after 50 ms. Distance from the origin is proportional to the activity level. During this simulation the units receive input from both LGN and cortex. *C*, Same as *B*, but the units receive only LGN input. Note that only hypercolumns receiving strongest input do converge.

A   B   C