Layout and Function of the Intracortical Connections within Layer 4 of Cat Area 17

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Abstract

A patch of layer 4 of cat area 17 has been modeled. The developmental network model is based on the modular structure of the neocortex. Connections between the orientation minicolumns, building the network model, are developed during exposure to visual input. The network model captures some of the known properties of the layer 4 of cat area 17. Local connections are dense, whereas distal connections are sparse. Both local and distal inhibition is mediated by inhibitory simple cells, which target excitatory cells that are located in their close surroundings and have opposite absolute and relative spatial phase. Excitatory local connections seem to be biased towards the iso-orientation domain. However, there is a strong crosstalk between all orientation domains made by the excitatory long-range horizontal connections. Furthermore, the excitatory long-range horizontal connections are mildly elongated along the orientation axis. We hypothesize that this network layout can give a simple explanation to the psychophysical experiments demonstrating response facilitation as a result of elongation of a Gabor patch along the orientation axis.

1 Introduction

Orientation selectivity of the striate cells populating the primary visual cortex (area 17 of cat, area V1 of monkey) is one of the most investigated issues in visual neuroscience [3,21]. The feedforward model, proposed by Hubel and Wiesel [1], was the first attempt to explain the origin of the orientation selectivity of the striate cells. It was proposed that orientation selectivity of neurons classified as simple cells was a consequence of the synaptic input from the LGN. According to this arrangement, the ON-center LGN cells project to the ON-subregions of a simple cell's receptive fields (RF). The OFF-subregions of a simple cell were constructed in the same way by the OFF-center LGN cells (see also [2]). Still today the Hubel and Wiesel feedforward model serves as a model of thalamic input to neocortex.

However, some of the properties related to the orientation selectivity are not possible to predict by a pure feedforward model [3–8]. Especially the psychophysical studies [4–8] examining the long-range spatial interactions in visual cortex clearly demonstrate that the cortical circuit plays a major role in altering the responses of the striate cells. Polat and Norcia [5] demonstrated that elongation of a Gabor patch along the orientation axis results in facilitation of the responses of the striate cells. As a result, Polat and Norcia [5] propose elongated summation pools.

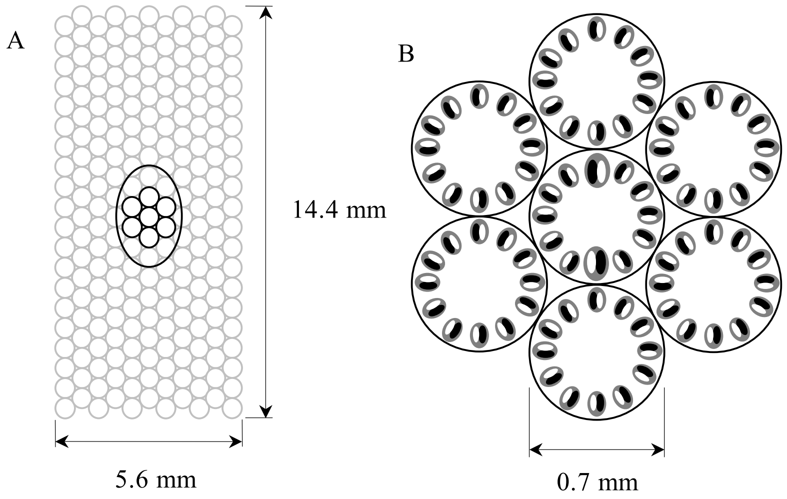

Figure 1. *A*, The network model consists of an 11x20 hexagonal array of hypercolumn modules. The oval illustrates the RF of the magnified units, positioned in the hypercolumn in the center in Fig. 1*B*. These units detect vertical lines but have opposite absolute and relative spatial phases. We see that these units' RF overlap with many other hypercolumns, and hence indicate strong overlap between RF of units situated in neighboring hypercolumns. *B*, A sub-network consisting of seven hypercolumns. Inside each hypercolumn 12 units are placed. Every hypercolumn figure is also a polar plot (see polar-plots in Fig. 2). The units indicate the positions in the polar-plot.

The excitatory long-range horizontal connections are a prominent feature of the visual cortex [9–14]. These connections can extend for several millimeters on cortex surface. Local connections are defined as connections between neurons located inside an area as big as a hypercolumn (<500 µm). Especially the layer 2/3 excitatory long-range horizontal connections have been subject to intense study since the discovery of their patchy layout [13]. More recent studies have confirmed the patchy, iso-orientation biased, layout of these connections [10,12]. The patches do, however, vary in size. Kisvárday et al. [10] report that the patch size can vary between 200 and 1000 µm in area 17 of cat. Observe that an iso-orientation domain is roughly 400–600 µm in diameter. These values indicate that the patches are heterogeneous. Differences in orientation preferences between striate cells up to 90º inside such a patch are not unusual. Furthermore, according to Kisvárday et al. [10], also the local connections prefer the iso-orientation domain, i.e. the local connections show same connectivity patterns as the long-range horizontal connections. Schmidt et al. [12] do also report axial specificity of the excitatory long-range horizontal connections. Later we will see that this anisotropy, also shown by our network model, can explain some of the observations described above [4–8].

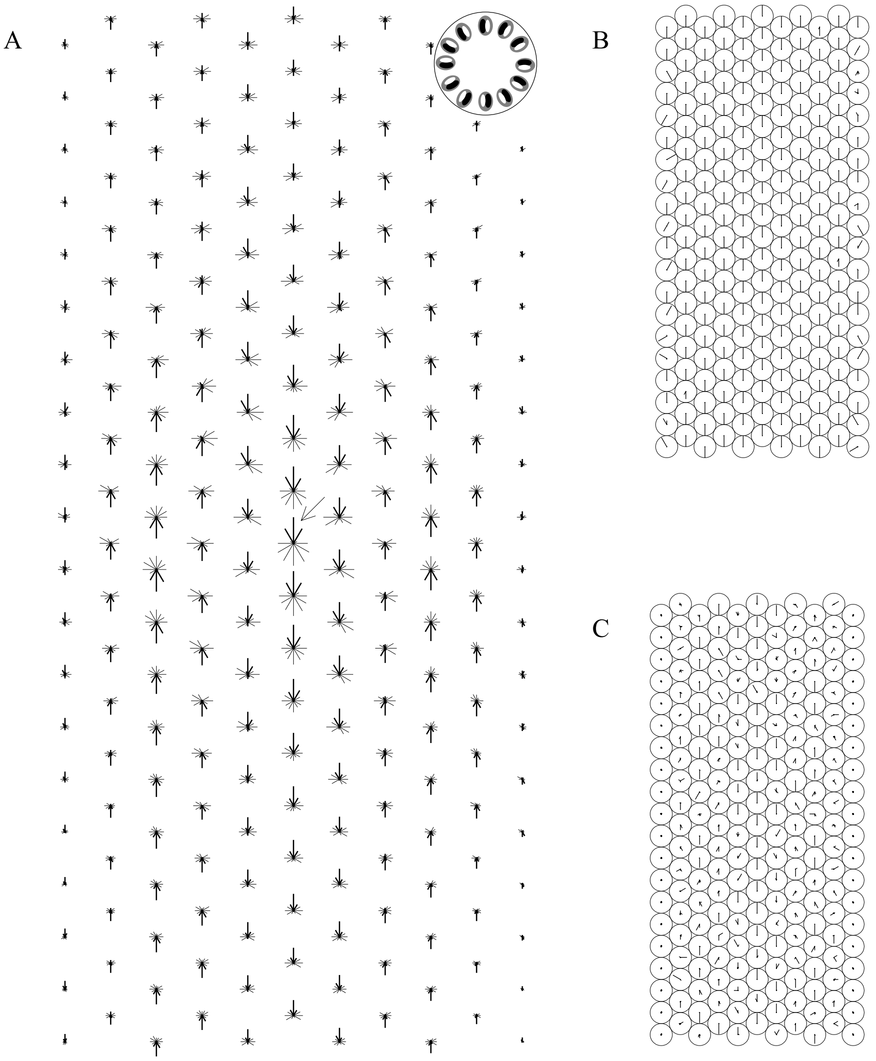

Figure 2. Polar-plots organized as the network model, each one representing a hypercolumn module. The legend in *A* (top right) shows the orientation and the relative spatial phase of the units in each polar-plot representing a hypercolumn module. *A*, Projections of the 'reference unit', which is positioned 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 both

thalamic and cortical input. *C*, Same as *B*, but the units receive only thalamic input. Note that only hypercolumns receiving strongest input, those in the middle column, do converge.

On the contrary, the excitatory long-range horizontal connections found in layer 4 have drawn less attention [11,14]. However, the study by Yousef et al. [11] reveals some of the layer 4 excitatory long-range horizontal connections' properties. This study indicate that these connections are not, or very little, biased towards iso-orientation domains. The excitatory long-range horizontal connections to iso-, oblique- and cross-orientation domains are almost equal in distribution. However, local connections are still biased towards the iso-orientation domain. It seems that independent of the layer, the excitatory long-range connections are neither random nor restricted to iso-orientation domains. We can therefore assume that crosstalk between different orientation domains is a prominent feature of both layer 4 and layer 2/3. This belief is also supported by the experiments described above [4–8].

According to the findings by Hubel and Wiesel [15] the primary visual cortex has a modular structure (for a recent review see [16]). 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 striate cells in each orientation minicolumn respond selectively to a broad range of orientations. A recent study by DeAngelis et al. [17] reveal the degree of invariance of response variables like orientation, spatial frequency and relative spatial phase. Orientation was highly clustered, closely followed by spatial frequency. One response variable did, however, not show any evidence of clustering, namely, the relative spatial phase. Furthermore, an orientation hypercolumn contains orientation minicolumns with response properties distributed over all angles, and thus represents the local edge orientation pertinent to a given point in visual space.

The Bayesian Confidence Propagation Neural Network model (BCPNN) has been developed in analogy with the known generic cortical structure [25]. This is an abstract neural network model in which each unit corresponds to a cortical minicolumn. The network is partitioned into hypercolumn-like modules and the summed activity within each hypercolumn is normalized to one. We hypothesize that normalization can be carried out by large basket cells [28]. We assume that these cells inhibit an area that corresponds to a hypercolumns.

A patch of layer 4 of cat area 17 has been modeled. This developmental network model is based on the modular structure of the neocortex. BCPNN incremental learning algorithm develops the connections between the units. The correlation-based network captures some of the known properties of area 17 of cats, such as dense local and sparse distal connectivity. The network has two different types of interneurons. Large basket cells are responsible for keeping the total activity within a hypercolumn constant. The second group of interneurons, the inhibitory simple cells, mediate local and distal inhibition through targeting excitatory cells that are located in their close surroundings and have opposite absolute and relative spatial phase (relative to the interneuron). Excitatory local connections seem to be biased towards the iso-orientation domain. However, excitatory long-range horizontal connections target all orientation domains in a balanced manner, thus there is a strong crosstalk between all orientation domains. Note however that some of the targets of the long-range horizontal connections are excitatory cells, whereas some are inhibitory simple cells, since the network is correlation-based. Furthermore, the excitatory long-range horizontal connections are mildly elongated along the orientation axis, most likely as a result of the stimulus configuration. During the learning phase the stimuli were contrast edges. Note that on the contrary to layer

2/3, there has not been any report on axial specificity of the layer 4 long-range horizontal connections. Nevertheless, we believe that the network behavior supports the existence of elongated summation pools in visual cortex, and gives a simple explanation for how it might be carried out within area 17. There are a variety of feedforward and recurrent models of area 17 (see review [3]), however, very few of them address the questions related to response facilitation as a consequence of elongated summation pools. Recently, Grossberg and Raizada [31] modeled perceptual grouping based on long-range horizontal interactions within area 17. In that model, layer 2/3 complex cells are responsible for contrast-sensitive perceptual grouping.

2 Network Model

As stated before the columnar organization of the primary visual cortex [15] is the main influence of our network model. We hypothesize that area 17 is composed of repetitive structures, i.e. orientation minicolumns. We assume further that the orientation minicolumns can be grouped around hypothetical centers, the so-called pinwheels [18], to form modules we refer to as hypercolumns. We hypothesize that a hypercolumn can be built from a finite number of orientation minicolumns each representing a unique orientation (Fig. 1*B*). The network model used during the simulations consists of 220 (11x20) hypercolumns arranged to form a hexagonal array (Fig. 1*A*). The diameter of the circular hypercolumns, and thus the distance between two adjacent hypercolumns is 0.7 mm [19]. The size of the network model in cortical dimensions is 5.6x14.4 mm (Fig. 1*A*). The distance between the RF centers of two adjacent hypercolumns corresponds to 0.2^o of visual angle (at 2^o of eccentricity [19]). The visual world covered by the model is 2.4x5.4^o. Note that the modeled cortical patch and hence the visual field covered by the network model is elongated. This shape was chosen after observing the mildly elongated shape of the excitatory long-range horizontal connections, and having the computational limitations in mind. However no artifacts related to corner effects due to the elongated shape of the network model was noticed during the simulations.

Each hypercolumn consists of 12 units, representing 6 orientation minicolumns (Fig. 1*B*). The difference in orientation preference between two successive units inside a model hypercolumn is 30°. Observe that having this configuration, we represent every orientation twice with two so-called anticorrelation units. These anticorrelation units represent same orientation. However, they have opposite absolute and relative spatial phases, so that their subfields with opposite sign overlap. The magnified RF figures inside the middle hypercolumn are detecting vertical lines and have opposite absolute and relative spatial phases (Fig. 1*B*), thus they qualify as anticorrelation pairs.

The RF centers of the units belonging to a model hypercolumn are positioned in the center of their host hypercolumn. As a consequence of this arrangement the units belonging to a hypercolumn are analyzing the same spot of the visual field. The RF of the units are designed as contrast edge detectors, and hence composed of two elongated subregions with opposite sign (Fig. 1*B*). Orientation tuning of the LGN input is 40^o at half-width at half-height [20], suggesting a subfield aspect ratio of 3:1. The RF width is 1^o [19], and hence the RF height is 1.5^o. Figure 1*A*. shows how a RF, in this case belonging to the units located in the middle hypercolumn detecting vertical lines (Fig. 1*B*), are related to the rest of the network. We can see that there is an overlap between the RF:s of these two units and the rest of the network. Furthermore, all units are tuned for the same spatial frequency of 1 cycle/degree [19]. The thalamic input of the units is computed using a model developed by Troyer et al. [23].

3 Simulation Results

The simulations are divided into two parts. Firstly, BCPNN incremental learning algorithm [15] is used to train the fully connected recurrent network of units. The objective is to see if the BCPNN algorithm can develop a network that resembles the primary visual cortex [9–14]. Later we address the question of whether or not this network can explain some of the reported psychophysical observations, especially those related to response facilitation [5].

Briefly the BCPNN incremental learning algorithm behaves in the following way. If two units are correlated during a time step, the connection between them strengthens. This corresponds to the creation of an excitatory connection. However, anticorrelation between two units will result in an inhibitory connection (via a local inhibitory interneuron [26,27]). Hirsh and colleagues [26] have reported that there are inhibitory simple and complex cells in cat area 17. Furthermore, according to the study by Ferster [27] interneurons mediate inhibition between excitatory simple cells, which have opposite absolute spatial phase. Based on the results by Ferster [27] and Hirsh et al. [26] we assume that interneurons inhibit excitatory cells located in their close surroundings. We hypothesize further that the interneurons and their postsynaptic excitatory cell targets have overlapping receptive fields and opposite absolute spatial phases, relative each other. The implication of this scheme is that any given excitatory cell can, through an interneuron, inhibit another excitatory cell. Note that both local and distal inhibition can be mediated by these interneurons, since excitatory cells located in an arbitrary place can target an interneuron. Kayser and Miller [22] have proposed a similar model called the opponent inhibition model based on [27]. Their model assumes, however, that exclusively excitatory cells that have similar receptive field profile, i.e. same orientation preference and same absolute spatial phase, target the interneurons. Kayser and Miller [27] also assumed that the excitatory cell's receptive field and its inhibitory target's receptive field coincide in visual space. Hypothetically the whole network is local and can be located within an orientation minicolumn.

According to the BCPNN incremental learning algorithm, if units are uncorrelated, the connection value will fluctuate around zero value. This means that the weight between two units is a measure of the correlation between them. From this follows also that the weight matrix is symmetric, and hence can be interpreted both as projections from one unit to all units in the network, and projections from all units into one. Note that normalization limits the total activity within a hypercolumn to one. This is done mathematically by dividing activity level of each unit within a hypercolumn by the total activity of its host hypercolumn. It is, however, assumed that large basket cells are responsible for normalization within area 17 [28].

Training of the fully connected network lasts for 1000 simulation steps. The time step is defined as 1 second, and hence the simulation duration corresponds to 1000 seconds. The learning rate, which defines the degree of weight modification, is 0.005 [15]. At every time step, the activity levels of the units are initiated with a new arbitrary contrast edge stimulus. The position and the orientation of the stimulus are sampled from a uniform distribution. The stimulus width is 1º, and its spatial frequency is 1 cycle/degree. Observe that for convenience the width and the spatial frequency of the stimulus is the same as that of the RF.

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. 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. Later the activity levels are normalized so that the sum of activities in each hypercolumn is equal to one, as required by the BCPNN incremental learning algorithm. The contrast of the stimulus is 100%, though the effect of high noise in combination with the normalization procedure lowers this level considerably.

We see that in general the local connections do have higher amplitude than the long-range horizontal connections. This indicates strong local and sparse distal connectivity (Fig. 2*A*). The developed network is correlation-based and incorporates a second group of interneurons (after the large basket cells), which are hypothesized to be the inhibitory simple cells described by Hirch et al. [26] (see also [27]).

Not surprisingly, the 'reference unit' is most correlated with itself (Fig. 2*A*). Units that are correlated excite each other (Fig. 2*A*). Units that are anticorrelated (not only anticorrelation pairs) inhibit each other through inhibitory simple cells, which have opposite absolute and relative spatial phase compared to their postsynaptic targets (Fig. 2*A*). We hypothesize that these interneurons could be driven by both local and distal excitatory cells that are anticorrelated with the targets of the interneurons. We assume further that the connection strengths between the inhibitory simple cells and their excitatory targets are constant.

The mildly elongated shape (along the orientation axis) of the connections made by the reference unit reveals the axial specificity of the excitatory long-range horizontal connections (Fig. 2*A*). This result is in agreement with the results of Schmidt et al. [12] and others on layer 2/3 of several species. Note however that the layer 4 network seems to be less elongated than layer 2/3.

As shown by Yousef et al. [11], all distal orientation domains are targets of the long-range horizontal connections. The connection matrix shows that, some of the excitatory long-range horizontal connections are targeting excitatory cells located in iso-orientation domains, whereas others are targeting local interneurons positioned in all three orientation domains (2*A*). Obviously there is an intense crosstalk between all orientation domains, made by the excitatory long-range horizontal connections. Note further that the inhibitory long-range horizontal connections are not the subject of study, since all long-range horizontal connections are considered to be excitatory.

A more detailed analysis of the excitatory long-range horizontal connections uncovers the type of these connections. We see that the strength of the excitatory connections between the reference unit, and units having same orientation preference and absolute (and relative) spatial phase tend to decrease along the axis, which corresponds to the preferred orientation of the reference unit. Along the orthogonal axis, connection type is switched from excitatory to inhibitory, as an effect of anticorrelation (Fig. 2*A*). Note also that again along the orthogonal axis, the reference unit is correlated with the units having opposite relative spatial phases, but similar absolute spatial phases (Fig. 2*A*). These observations indicate that units with similar absolute spatial phases excite each other. DeAngelis et al. [17] showed recently that relative spatial phase did not show any evidence of clustering, and local pooling across simple cells with different spatial phases was proposed to improve signal quality. These ideas support the connectivity pattern between the iso-orientation domains.

Above, we showed that the network captures important properties of the connection pattern found within area 17. In the second part of the simulations, we will see if this network can predict some of the psychophysical effects especially those related to elongated summation pools in visual cortex [5]. But first, a brief explanation of the balance between the excitatory cortical input and the thalamic input received by the units. Chung and Ferster [20] reported that cortical suppression left only 46% of the visually evoked response of the striate cells receiving monosynaptic input from the thalamus. This balance is preserved in our network model such that at 100% contrast the input to a unit is 46% of maximum theoretical input, and the cortical input is scaled accordingly. The maximum theoretical input is defined as the strongest excitatory input that is possible to receive by a unit from the rest of the network. Normally distributed noise with a standard deviation of 10% of the maximum theoretical input is added to the total input of every unit. The simulation time step is 10 ms, and the 'membrane time constant' of the units is 50 ms [15].

The simulation consists of two phases. During these both phases the stimulus is a vertical contrast edge, positioned in the center of the network. This stimulus is identical to the stimuli used during the training of the network. In the first phase, the units receive both thalamic input and cortical excitatory and inhibitory input (Fig. *2B*). The thalamic input is amplified by the cortical connections and all hypercolumns are converging after 50 ms, even those receiving weak input. In the second phase, the units receive only thalamic input (Fig. *2C*). However, the thalamic input is not sufficient for the majority of the hypercolumns; only those receiving maximum thalamic input can converge. Note the difference in convergence speed and quality between these two cases after 50 ms. The role of excitatory long-range horizontal connections in sharpening of the responses of the units receiving weak thalamic input is evident.

The experiment by Polat and Norcia [5] shows that elongation of a Gabor patch along the orientation axis results in facilitation of the responses of the striate cells in visual cortex. As a result, elongated physiological summation pools are proposed. We hypothesize that the mildly elongated shape of the long-range horizontal connections along the orientation axis (Fig. 2*A*) can explain the facilitation described by Polat and Norcia [5]. Furthermore, pooling across simple cells with different, in our network model opposite, relative spatial phases might also play an important role improving signal quality [17]. Finally, we presume that at least qualitatively, the simulations show the facilitatory effect of the excitatory long-range horizontal connections (Fig. 2B and 2C).

4 Discussion

A patch of layer 4 of cat area 17 has been modeled. This developmental network model is based on the modular structure of the neocortex. BCPNN incremental learning algorithm develops the connections between the units. The correlation-based network captures some of the known properties of area 17 of cats, such as dense local and sparse distal connectivity. The network has two different types of interneurons. Large basket cells are responsible for keeping the total activity within a hypercolumn constant. The second group of interneurons, the inhibitory simple cells, mediate local and distal inhibition through targeting excitatory cells that are located in their close surroundings and have opposite absolute and relative spatial phase (relative to the interneuron). Excitatory local connections seem to be biased towards the iso-orientation domain. However, excitatory long-range horizontal connections target all orientation domains in a balanced manner, thus there is a strong crosstalk between all orientation domains. Note however that some of the targets of the long-range horizontal connections are excitatory cells, whereas some are inhibitory simple cells, since the network is correlation-based. Furthermore, the excitatory long-range horizontal connections are mildly elongated along the orientation axis, most likely as a result of the stimulus configuration. During the learning phase the stimuli were contrast edges. Note that on the contrary to layer 2/3, there has not been any report on axial specificity of the layer 4 long-range horizontal connections. Nevertheless, we believe that the network behavior supports the existence of elongated summation pools in visual cortex, and gives a simple explanation for how it might be carried out within area 17.

During the learning phase exclusively contrast edges stimuli were used. We believe that this affected the layout of the local and long-range horizontal connections significantly. One obvious question is how other types of stimuli like sinusoidal gratings or other shapes might affect the layout of these connections. Our intention is to address this question in the near future.

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