Quantitative Assessment of the Local and Long-Range Horizontal Connections within the Striate Cortex

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Abstract

We present a quantitative assessment of the local and long-range horizontal connections within two separate models of layer 4 and layer 2/3 of the striate cortex. Connections between the orientation minicolumns, building the models, are developed during exposure to visual input. Layer 4 long-range horizontal connections target all orientation domains in a balanced manner, whereas local connections are biased towards the iso-orientation domain. However, both local and long-range horizontal connections of the layer 2/3 network are biased towards the iso-orientation domains. We hypothesize that the patchy layout of the layer 2/3 long-range connections is a consequence of excitatory cells targeting mainly other excitatory cells located in distal iso-orientation domains. Furthermore, both networks demonstrate dense local and sparse distal connectivity.

1. Introduction

The columnar organization of the neocortex [6,15] is one of the most influential findings in neuroscience [16]. Hubel and Wiesel [15] found that the striate cortex (primary visual cortex) is composed of orientation minicolumns each one comprising some hundreds of excitatory cells and a smaller number of inhibitory interneurons of different kinds. Vertical penetration of the cortex showed that contrast edge orientation is coded such that the cells in each orientation minicolumn respond selectively to a broad range of orientations. Furthermore, orientation selectivity was shifted smoothly during horizontal penetration. One decade earlier, Hubel and Wiesel [1] addressed the fundamental question of the orientation selectivity of the cortical cells. The proposed model of orientation selectivity, which is known as the 'feedforward' model, relies heavily on the arrangement of the thalamic afferents. According to this arrangement, the ON-center LGN cells converge on the ON-subregions of a simple cell's receptive field (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 the thalamocortical circuitry. However, some of the orientation selectivity properties are not possible to predict by the feedforward model [3]. Contrast invariance of orientation tuning is one such example. As contrast increases the height of the response curve increases while the width remains almost constant [21]. Furthermore, the psychophysical studies examining the long-range spatial interactions within the visual cortex clearly demonstrate that the cortical circuitry plays a major role in cortical cell responses. Polat and Norcia [5] demonstrated that elongation of a Gabor patch along the orientation axis results in facilitation of the responses of the cells in visual cortex, probably as an effect of summation fields.

Since the discovery of the patchy layout of the layer 2/3 long-range horizontal connections [13], the layout and the function of intracortical connections have started to drawn more attention. It is now widely accepted that the long-range horizontal connections of the superficial layers are a prominent feature of the visual cortex [7–14]. More recent studies on a variety of species have confirmed the patchy, iso-orientation biased, layout of these connections [7,8,10,12]. A study by Kisvárday et al. [10] shows that 56.2% of the excitatory local connections target the iso-orientation (±30º) domain. Oblique- (±30–60º) and cross-orientation (±60–90º) domains receive 28.4 and 15.3 per cent of the connections respectively. Long-range connections show a similar pattern, i.e. 40.0% of them descending from the injection site are targeting the iso-orientation domains, 36.9% the oblique-, and 23.1% the cross-orientation domains. Same study reveals also that only 30% of the excitatory connections from an injection site, in area 17 of cat, are defined as distal (>0.5 mm), and thus the majority of the connections target nearby cells. A recent study by Chisum et al. [8] reveals the fall-off in bouton

A

90°

45°   135°

0°

B

C

0.2

0.15

0.1

0.05

0

Connection strength (fraction)

−100   −50   0   50   100
Orientation (degree)

D

0.25

0.2

0.15

0.1

0.05

0

Cell composition (fraction)

−90 −75 −60 −45 −30 −15 0 15 30 45 60 75 90
Orientation (degree)
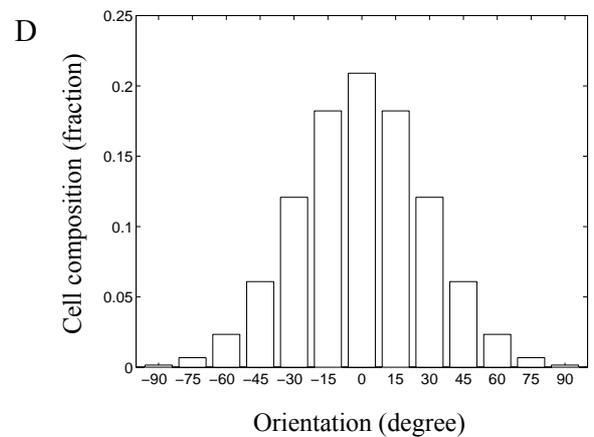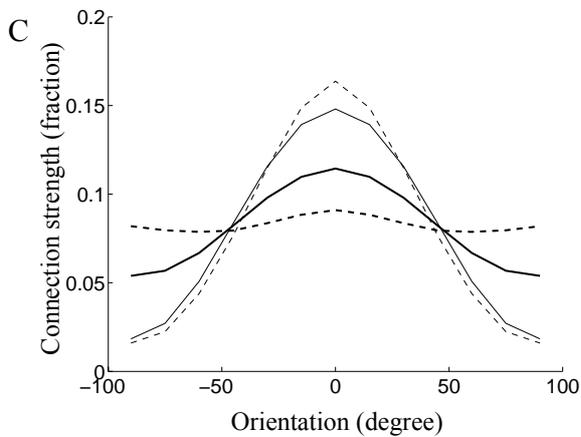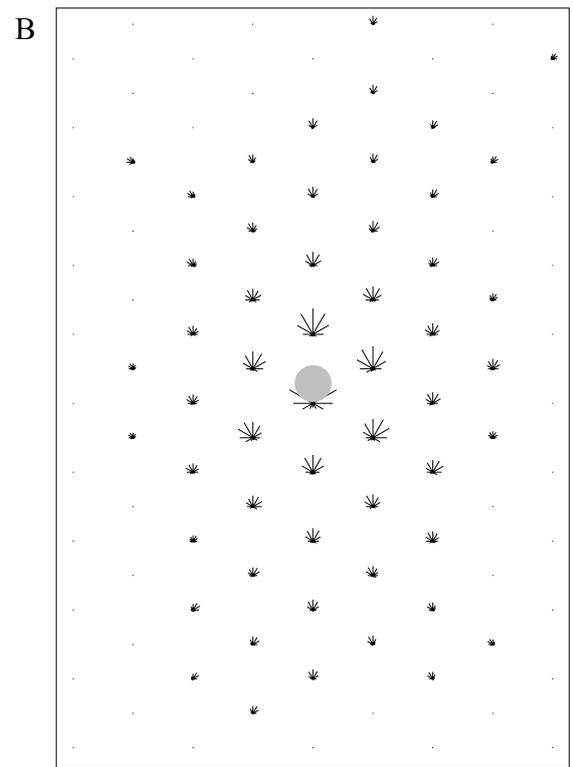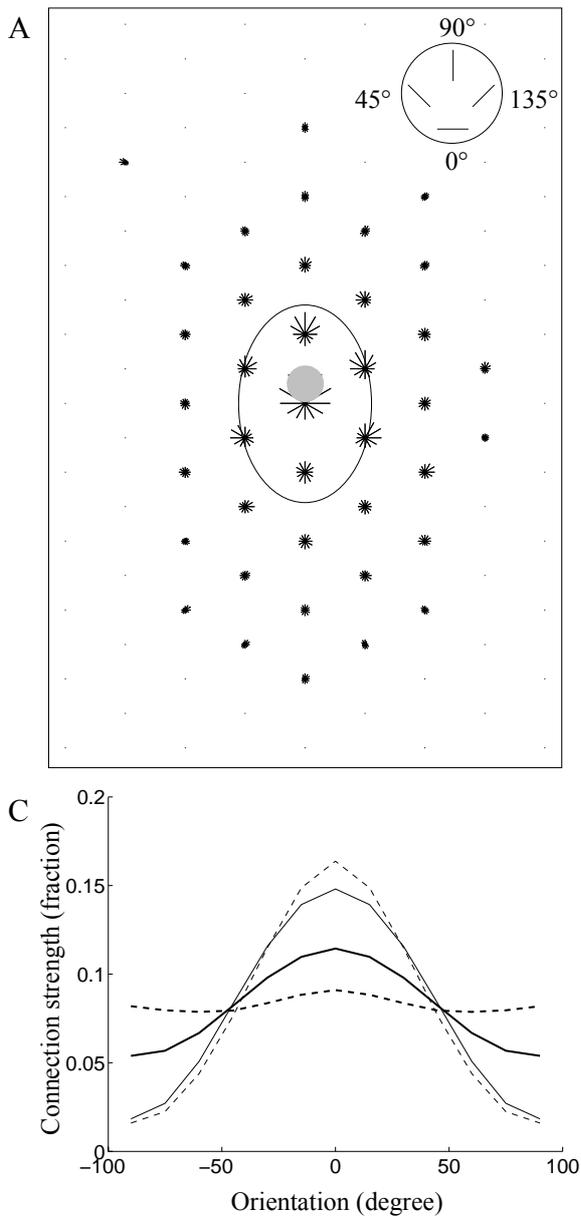
Figure 1. *A*, Layer 4 network connections, which originate from the abstract injection positioned at 90º (illustrated with a gray circle), visualized by 9x11 polar-plots organized as the network model. Each polar-plot represents a hypercolumn module. The legend (top right) shows the orientation of the units in each polar-plot, consequently the relative spatial phases are ignored. Distance from the origin is proportional to the strength of the connection. The oval marks the RFs of units detecting vertical lines inside the host hypercolumn. We see that these units' RF overlap with many other hypercolumns, and hence indicate strong overlap between RF of units situated in neighboring hypercolumns. Note the elongated shape of the long-range connections. *B*, Same as *A* but for the layer 2/3 network connections. *C*, Fraction of the layer 4 local (solid thick line) and long-range (dashed thick line) connections as a function of the deviation from the mean orientation selectivity at the abstract injection site. Long-range connections are equally distributed, whereas local connections are biased towards the iso-orientation domain. Furthermore, both layer 2/3 local (solid thin line) and long-range (dashed thin line) connections are biased towards the iso-orientation domains. *D*, Composition of the abstract injection sites for layer 4 and layer 2/3 networks. Spread of orientations inside these regions correspond roughly to that of an iso-orientation domain and is less than those in *C*.

distribution as a function of distance from an injection site. Number of boutons along the preferred axis is down to 15% of the maximum only 0.7 mm from the injection site. At 1.4 mm the number of boutons is roughly 5% of the maximum. The decrease along the orthogonal axis is even more dramatically. Thus, axial specificity of the layer 2/3 long-range connections is prominent. Chisum et al. [8] show that the dramatic fall-off with distance implies that most long-range connections are between neurons for which the RFs overlap by at least 50%. Furthermore, the long-range horizontal connections are to be responsible for the summation field of the neurons. Chisum et al. [8] observe also the similarity between the elongated RF and axial specificity of the long-range connections.

Surprisingly, the long-range horizontal connections found in the layer 4 have drawn much less attention. Layer 4 is the main recipient of the thalamic input, and the simple cells found in the cat layer 4 are well tuned for orientation [1,2]. Thus, the interplay between the orientation map and the layout of long-range connections is essential for understand the origins of orientation selectivity. The findings suggest that the layout of the layer 4 long-range horizontal connections is different from those found in the superficial layers [8,10,11,14]. Their extent is only 50% of the long-range connections of the superficial layers [10]. Furthermore, Yousef et al. [11] found that layer 4 long-range connections (of area 18) are hardly biased towards iso-orientation domains. 35.4% of the connections (>740 μm) targeted the iso-orientation domain. Oblique- and cross-orientation domains received 33.7% and 30.9% of the connections respectively. The pattern shown by the local connections (<740 μm) is different. The local iso-orientation domain receive 60.0% of the connections, while 22.0% of the connections are targeting the oblique- and 18.0% the cross-orientation domains. Note that as much as 40% of the local connections are targeting oblique- and cross-orientation domains. Inhibitory long-range horizontal connections extent only one third to one half of the excitatory network, and the excitatory ones out number them. Thus majority of the long-range connections are considered to be excitatory in both layer 4 and layer 2/3 [10]. It seems that independent of the layer, the excitatory long-range horizontal connections are neither random nor restricted to iso-orientation domains. Consequently cross talk between different orientation domains is a prominent feature of both the layer 4 and the superficial layers.

The Bayesian Confidence Propagation Neural Network (BCPNN) has been developed in analogy with the known generic cortical structure [24]. This is an abstract neural network architecture in which each unit corresponds to a cortical minicolumn. The learning rule is based on Hebb's ideas on synaptic plasticity and emergence of cell assemblies [26]. Thus, correlated activity reinforces the connections between the units. Anti-correlated activity results in weakening of a connection, and emergence of an inhibitory one. The network is partitioned into hypercolumn-like modules and the summed activity within each hypercolumn is normalized to one. A biologically plausible model of a hypercolumn module based on the BCPNN was presented recently [28].

A quantitative assessment of the local and long-range horizontal connections within two separate models, of layer 4 and superficial layers, of the striate cortex is presented. Long-range horizontal connections of the layer 4 network target all orientation domains in a balanced manner, whereas local connections are biased towards the iso-orientation domain. The pattern shown by the layer 2/3 network is different. Both local and long-range horizontal connections are biased towards the iso-orientation domains. We hypothesize that the patchy layout of the layer 2/3 long-range connections is a consequence of excitatory cells targeting mainly other excitatory cells located in distal iso-orientation domains. Both networks demonstrate dense local and sparse distal connectivity as a result of fall-off with distance. Furthermore, tests with contrast edges indicate that both layer 4 and layer 2/3 networks can detect contrast edges, which have low contrast. However, these tests need to be verified quantitatively.

2. Network Model

As stated before the columnar organization of the striate cortex [15] is the main influence of our network model. We hypothesize that V1 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 one representing a unique orientation. The network model used during the simulations consists of 99 (9x11) hypercolumns arranged to form a hexagonal array. 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 5.6x8.1 mm. The distance between the RF centers of two adjacent hypercolumns corresponds to 0.5° of visual angle (at 5° of eccentricity [19]). The visual field covered by the model is 4.5x7.3°. 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 axial specificity of the 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 observed during the simulations.

Each layer 4 hypercolumn consists of 24 units, representing 12 orientations. The difference in orientation selectivity between two successive units inside a model hypercolumn is 15°. Observe that having this configuration, we represent every orientation twice with two so-called anti-correlation units. These anti-correlation units represent the same orientation. But they have opposite relative and absolute spatial phases, so that the units' subfields with opposite sign overlap. 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 analyze the same spot of the visual field. Furthermore, as shown by the oval, which represents RFs of units detecting vertical lines, there is a strong overlap between the RF of units situated in neighboring hypercolumns (Fig. 1*A*). The RFs of the units are designed as contrast edge detectors, and hence are composed of two subregions with opposite sign. Orientation tuning of the LGN input is 40º at half-width at half-height [20], suggesting a subfield aspect ratio of 3:1. The RF width is 1º [19], and hence the RF height is 1.5º. 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].

The inhibition is mediated by local interneurons. Recently, Hirch et al. [4] reported inhibitory simple cells, which have good orientation tuning, and complex inhibitory cells that are untuned for orientation. We assume that the inhibitory simple cells can mediate local inhibition to excitatory simple cells. We hypothesize further that the opponent inhibition theory proposed by Ferster [22] can explain the local circuitry of inhibitory and excitatory simple cells. Opponent inhibition implies that the presynaptic inhibitory simple cell has opposite absolute spatial phase as the postsynaptic excitatory cell. Furthermore, the cells' subfields with opposite sign overlap, i.e. they have opposite relative spatial phase. We hypothesize that the inhibitory complex cells reported by Hirch et al. [4] can regulate the total activity of the excitatory cells in a region, which corresponds to a hypercolumn.

3. Simulation Results

The simulations are divided into two phases. During the first phase, we intent to show that the incremental BCPNN learning rule can develop a network that quantitatively resembles layer 4 local and long-range connectivity. During the second phase, the objective is to show that layer 2/3 local and long-range connectivity can

be derived based on the results from the first phase and additional simulations.

The incremental BCPNN learning rule [24] develops the fully connected recurrent network of units. The result is a weight matrix, which contains information on the degree of correlation between pairs of units located in the different regions of the network. Briefly, the incremental BCPNN learning rule 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, anti-correlation between two units will result in an inhibitory connection (via a local inhibitory interneuron [4,22]). We assume that the excitatory long-range connections can mediate long-range inhibition through local inhibitory interneurons. We hypothesize that interneurons can inhibit excitatory simple cells in their close surroundings as proposed by the opponent inhibition theory [22]. If units are uncorrelated, the weight will fluctuate around zero value. Thus, the weight between two units is a measure of the correlation between them during the training sequence. The weight matrix is symmetric, and hence can be interpreted both as connections from one unit to all units in the network, and connections from all units into one. 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 RFs. 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 mean activity of an arbitrary unit inside a hypercolumn in absence of 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 incremental BCPNN learning rule. The contrast of the stimulus is 100%, though the effect of high noise in combination with the normalization procedure lowers this level considerably.

Recently we reported the behavior of a layer 4 network similar to the current network [25]. We saw that the long-range connections have facilitory effect on the

units. This result was in line with the elongated summation pools proposed by Polat et al. [27]. The network could detect a noisy contrast edge much faster in presence of the intracortical connections. As revealed by the weight matrix, the modular specificity of the long-range connections targeting excitatory cells was prominent. Cross-orientation domains were inhibited through excitatory long-range connections targeting local inhibitory interneurons. However, quantitative values on corticocortical connections reported by Yousef et al. [11] and others are based on connections from cells located inside an injection site, which can be 200–400 µm across, i.e. roughly an iso-orientation domain. Inside such a patch we find cells with a broad range of orientation preferences. Note that the information available as the weight matrix is fundamentally different from the data on the connections from an injection site. As a consequence, an abstract injections site, which corresponds to a typical iso-orientation domain, is constructed (Fig. 1D). Spread of orientation preferences inside an orientation minicolumns is also an important factor while constructing an abstract injection site. Note that Murphy and Sillito [17] reported that orientation selectivity could vary 9–18° inside an orientation minicolumn. To enable a quantitative assessment, the connections originating from the abstract injection site are divided into local connections, i.e. connections to the units inside the so-called host hypercolumn, and long-range connections, i.e. connections to units located in all other hypercolumns. The abstract injection site is located inside the host hypercolumn. Connection strengths from this abstract injection site is defined as the weighted sum of connections from each one of the units participating in the connection. The size of this weight corresponds to a fraction that defines the occurrence of neurons with a given orientation selectivity inside the injection site, which has the size of an iso-orientation domain (Fig. 1D). The strength of the connections is visualized as polar-plots (Fig. 1A). Connections to distal hypercolumns, which are >15% of the connections within the host hypercolumn are plotted and used during the quantitative assessment. Calculations show that 43.3% of the local connections target the iso-orientation domain (Fig. 1C). Oblique-orientation domain's share of the local connections is 33.1%, and the cross-orientation domain receives 23.6% of the local connections. However, the distribution of the excitatory long-range connections differs prominently. Only 35.5% are targeting the iso-orientation domains. The oblique- and cross-orientation domains receive, respectively, 32.4 and 32.1 per cent of the connections. These values are close to reported values of Yousef et al. [11]. To test the parameter dependencies, the abstract injection site was set to infinity, i.e. nearly the whole model. The distributions were almost equal for all three orientation domains, both for local and distal connection. Iso-

orientation domains were targeted by 34.6% of the connections, while 33.7 and 31.7 per cent of the connections targeted oblique- and cross-orientation domains respectively.

The patchy layout of the layer 2/3 long-range connections is investigated by a series of simulations. The layer 2/3 network used during the simulations has similar set up as the previous networks, which were used to investigate the layer 4 connectivity. However, now the units have complex cell RFs, and hence only 12 units are needed in each hypercolumn instead of 24 as earlier. Input to a complex cell unit is defined as the sum of rectified inputs to the anti-correlation unit pairs, found in the layer 4 network, having the same orientation selectivity as the complex cell unit. Note that the anti-correlation pairs have same orientation selectivity but opposite relative spatial phase, i.e. they detect the same orientation but opposite phase. We hypothesize that the patchy layout of the layer 2/3 network is, at least partially, a consequence of excitatory cells targeting mainly other excitatory cells located in distal iso-orientation domains. To test this hypothesis the excitatory connections targeting the inhibitory interneurons are removed (Fig. 1B). The distribution of the long-range connections from the abstract injection site is 58.4% to iso-, 31.4% to oblique- and 10.2% to cross-orientation domains (Fig. 1C). Local connections show a similar pattern. The iso-orientation domain receives 54.3% of the connections. Oblique- and cross-orientation domains receive 33.4 and 12.3 per cent respectively. Kisvárday et al. [10] report a similar distribution for the local connections, whereas the long-range connections reported by Kisvárday et al. [10] are less orientation specific.

The fall-off with distance for both layer 4 and layer 2/3 networks is less than the reported values by Chisum et al. [8]. We found that the degree of overlap between RFs of units situated in adjacent hypercolumns is one decisive factor that controls the degree of fall-off. When the distance between the RF centers of two adjacent hypercolumns increased, the extent of the long-range connections is reduced (not shown here). A consequence of the fall-off with distance is dense local and sparse distal connectivity demonstrated by both networks. Furthermore, the elongated shape of the long-range connections of both networks matches well the RF aspect ratio of the units. These findings are in line with the reported similarities between RF shape and the extent of the long-range connections by Chisum et al. [8]. Furthermore, preliminary results indicate that both networks can detect low contrast (15%) stimulus, defined as contrast edge. However, to confirm this observation and investigate the optimal extent of the long-range

horizontal connections, in relation to the RF sizes and shapes, additional simulations must be carried out.

4. Discussion

We presented a quantitative assessment of the layer 4 and layer 2/3 local and long-range horizontal connections based on two separate models. Our results show that layer 4 long-range horizontal connections target all orientation domains in a balanced manner, whereas layer 4 local connections are biased towards the iso-orientation domain. However, the layer 2/3 network is significantly different. Both local and long-range horizontal connections of the layer 2/3 network are biased towards the iso-orientation domains. We hypothesize that the patchy layout of the long-range connections is a consequence of excitatory long-range connections targeting mainly other excitatory cells located in distal iso-orientation domains. Furthermore, the fall-off with distance results in dense local and sparse distal connectivity for both networks. Preliminary results indicate that the layer 2/3 network, like the layer 4 network, can detect low contrast stimulus. We intend to confirm this observation by further simulations in the near future. The optimal extent of the long-range horizontal connections, in relation to the RF sizes and shapes, needs also be investigated more carefully.

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