Investigation of Feedback Connections Effect of a Spike Timing Neural Network Model of Early Visual System

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***Abstract*—The paper aims at design of a biologically plausible model of human visual system using spike timing neuron models. The first two stages of visual information processing include eye photoreceptors, relay structure called Lateral geniculate nucleus (LGN) and V1 area of visual cortex. Although most of models consider recurrent connections only within V1 area, there is biological evidence that feedback connections from V1 to LGN also exist. Here we started with the commonly accepted "push-pull" structure of V1/LGN model and upgraded it with excitatory feedback from V1 to LGN as well as with a structure of feedback inhibitory neurons – an interneuron and a Thalamic reticular nucleus (TRN) neuron. The model was implemented in NEST simulator. Effects of connection strength as well as the feedback structure (with or without an interneuron and TRN) were investigated by simulations of the model fed with realistic stimulus as input – patterns of moving dots.**

Keywords—spike timing neural network, integrate and fire neuron, early visual system, NEST simulator

I. INTRODUCTION

From centuries the scientists were curious to understand the functioning of the finest and complicated natural control system of living creatures – the brain. Nowadays huge amount of evidence about structure and functioning of different brain areas is accumulated. Among these the visual system attracted a lot of attention since it is one of the major sensory processing and information collecting systems.

Numerous neurophysiological findings from in-vivo experiments with mammals (cats, rats, monkeys etc.) as well as from humans [1, 2, 3] led to a commonly accepted hierarchical model of the visual system [4, 5]: the light sensor (eye) converts the incoming stimulus into electrical signal that propagates through the optic nerve to the next layer – the thalamus; here a structure of neurons called lateral geniculate nucleus (LGN) acts as a relay station between the retina and the next layer of neural cells – the primary visual cortex (V1).

Individual neurons in these three layers (retina, LGN, and V1) receive and process information from spatially closer regions from the previous layer (or visual field for the retina layer), called receptive fields. Besides the inter-layer connections, lateral connections between spatially closer neurons from the V1 layer also exist. In dependence on whether a given connection enhances or depresses the receiving neuron activity, connections were considered to be exciting or inhibiting. There are several topological structures of the primary visual system [6] among which [3, 7] is commonly accepted. It is based on in-vivo experimental results reported in [34] and since then numerous researchers adopted this structure. Although by far most models of early visual system do not consider feedback connections between LGN and V1 areas, experimental evidence about their existence was obtained by many researchers. Based on exhaustive review of existing knowledge, a structure of such feedback composed of interneurons and Thalamic reticular nucleus (TRN) was proposed in [8].

Commonly used artificial neural networks use simple neuron models representing mean firing rate of structures of biological neurons. They use sigmoid nonlinearity as activation function. Another modelling direction accounts in details for chemical reactions underlying the neural information processing [4, 9] and led to development of spike timing models of neural cells described by systems of differential equations [10]. Since these models needed a lot of computational resources, they were rarely used for practical applications. However, contemporary advance in computer technologies and powerful software packages like NEST [11] and NeuCube [12] allowed to simulate quite big neuronal structures as a step towards development of biologically plausible brain models. Since the NEST simulator [11] is an open source library that allows simulation of hierarchical structures of thousands of neurons with complex dynamics and variety of dynamical connections, we adopted it in our research.

In our preliminary research [13] we adopted the neuronal structure proposed in [3, 7, 14] to develop a biologically plausible model of primary visual system without feedback connections among the structures. In addition to previous work

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we also designed biologically plausible orientation map of the V1 receptive fields and investigated some of its parameters. Here we advanced further the model with feedback connections between V1 and LGN layers according to the structure proposed in [8]. Our aim was to investigate the effect of inclusion of the interneurons and TRN into feedback of the model.

Simulations were carried out by feeding of a natural visual stimulus to the model consisting of moving dots scenarios generated to test human reactions during performance of visual tasks. The obtained results suppose that the main role in the feedback played interneurons while the TRN affects less the firing rates of neurons in V1 layer.

The rest of the paper is organized as follows: section 2 describes the model structure and its parameters; section 3 describes the simulation investigations and the obtained results; the paper finishes with concluding remarks and directions for future work.

II. Model Structure

The model structure, adopted from [7], is shown on Fig. 1. It consists of three layers of neurons following the hierarchical structure of early visual system: retina receptors, LGN and V1. Neurons in each layer are positioned on two-dimensional regular grid. In addition, each LGN neuron has attached a feedback structure composed of an interneuron and a TRN neuron as in [8]. The feedback to each LGN neuron comes from the areas in V1 to which it is connected in forward direction. All blue lines denote inhibitory connections while the red ones – excitatory connections.

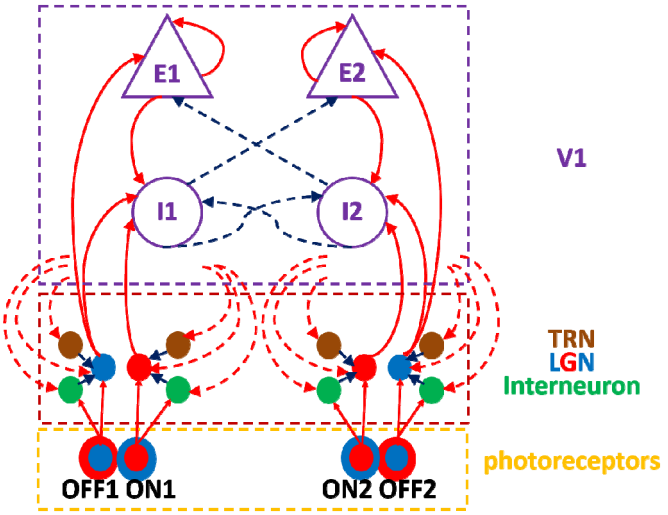

Fig. 1. Model structure with feedback connections from V1 to LGN directly and via interneurons (green) and TRN neurons (brown).

According to Fig. 1 we have two layers of photo-receptors/LGN neurons. Here each photoreceptor/LGN layer consists of 400 cells placed on a regular gird of size 20x20, covering a visual field with diameter of 7.5 deg. Both layers have identical positions of ON and OFF receptors placed in alternating order. The number of retinal ganglion and LGN neurons is the same since each photoreceptor cell is connected to its corresponding LGN neuron as well as to the corresponding interneuron. Their positions are relative to the visual scene.

As in [13], the V1 layer consists of 1000 neurons in total, separated into four groups – two exciting (E1 and E2) and two inhibiting (I1 and I2) populations. According to [3, 7] the ratio exiting/inhibiting neurons should be 4/1. Hence in our model the size of each excitatory population is 400 neurons while the size of each inhibitory population is 100 neurons. All neurons of the V1 layer are placed on regular grids of size 20x20 and 10x10 neurons respectively for excitatory and inhibitory groups. These grids are overlapped at the same plane of the V1 layer. Thus the inhibiting neurons are dispersed among bigger group of exciting neurons. The next section describes the used neuron models for each layer.

Each LGN neuron receives feedback from all neurons in the layer V1 to which it is connected by feedforward connections. There are three types of feedbacks: directly from V1, via interneuron and via TRN neuron. In our model each LGN neuron has its corresponding interneuron and TRN neuron.

A. Neuron Models

As it was proposed in [7], we used the model of photoreceptors from [3] to transform the visual stimuli to continuous electric current while for both LGN and V1 layers we used leaky integrate-and-fire neurons whose output signal has discrete form of spike trains. However, in contrast to [7], where identical spike-timing models were used for both LGN and V1 neurons, we decided to chose the different models from the NEST 2.12.0 library [11]. In addition, the interneurons and TRN neurons were modelled by the same spike timing equations like neurons in V1 layer.

1) Retina Photoreceptors

Following models in [3] the activity of photoreceptors in retina are modeled as spatiotemporal filter that is convolved with the visual stimuli. The spatial component of the filter has center-surround form. It is defined as difference of two Gaussian functions as in [7, 14]. Fig. 2 represents example of on center – off surround (ON) and off center – off surround (OFF) spatial components of such filters.

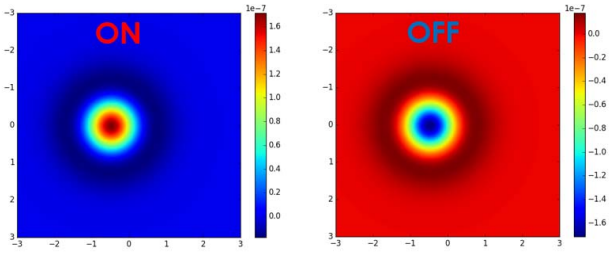

Fig. 2. Examples of spatial components of ON and OFF receptive fields of LGN neurons.

The temporal component has bi-phasic profile determined by difference of two Gamma functions [3, 7, 14]. The convolution of the spatio-temporal kernel with the moving visual stimuli transforms the images falling on the retina to

electrical signal that is generating input current for the corresponding LGN neuron.

2) LGN Neurons

For the LGNs we used the proposed in [15] model whose parameters were determined from in-vivo experiments. The models equations are as follows:

$$C\frac{dV}{dt} = -G_L(V - V_L) - G_E(V - V_E) - \\ - G_I(V - V_I) - G_A(V - V_A) \quad (1)$$

Here C is capacity of neuron cell membrane, V is membrane potential, G_L is leakage conductance, G_E and G_I are the conductances of total excitatory and inhibitory synaptic inputs respectively, G_A is the conductance of the potassium-mediated after hyperpolarization ion channel and V_L, V_E, V_I and V_A are the corresponding reversal potentials. The conductances (denoted here by G_X where X stands for E, I and A respectively) are time dependent on the moments of incoming spikes. For more detailed equations see [15]. The excitation input to the LGN neuron comes from retina photo-receptors in the form of generating current produced by the first layer of the model.

3) Model of V1, Interneurons and TRN Neurons

For this layer we chose the same model as in [7], proposed in [15]. The model equations are:

$$C\frac{dV}{dt} = -G_{rest}(V - V_{rest}) + I_{syn} \\ I_{syn}(i) = \sum_j w_{ij} y_{ij}(t) \quad (2)$$

Here C is capacity of neuron cell membrane, V is membrane potential, G_{rest} is the membrane conductance at resting state V_{rest} and I_{syn} is the synaptic current that is modeled as sum of postsynaptic currents from all neurons j connected to a given neuron i according to the equation (2). The parameter w_{ij} determines the absolute strength of the synaptic connection. The factor y_{ij} describes the contribution to a synaptic current of neuron i of the postsynaptic currents from neurons j that is determined by a dynamic system of equations from [16].

B. Connections

In the retina there are two types of receptive fields in dependence on whether corresponding neuron firing is enhanced by positive or negative difference between light intensity at a given spot and its surrounding. Since in awake animals eyes are constantly moving, the neurons in visual processing layers react strongly to sudden transitions in the level of image illumination, i.e. they accumulate temporal as well as spatial information from the observed world. LGN neurons have similar receptive fields like the connected to them retinal cells. They respond best to circular spots of light surrounded by dark background or dark spots surrounded by lighter background. Neurons in V1 layer respond best to elongated light or dark bars or to boundaries between light and dark regions (edges). Hence due to the shape of their receptive fields neurons in primary visual cortex are orientation and directionally selective, i.e. they respond more strongly to elongated stimuli moving in one direction than in the other.

1) Feedforward connections from LGN to V1

As in [3, 7], neurons from V1 layer have elongated receptive fields defined by a Gabor probability function [14], shown on Fig. 3.

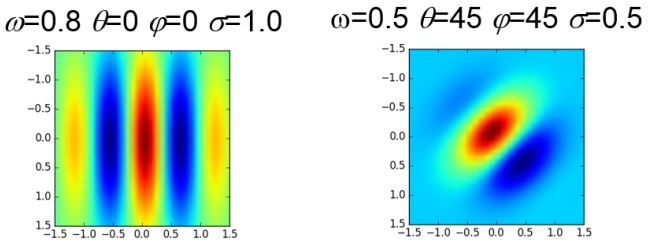

Fig. 3. Receptive fields of V1 neurons, defined by Gabor functions with different parameters, defining frequency ω, orientation θ, phase φ and variance σ.

Each neuron from V1 layer has its own orientation and phase parameters that determine its orientation selectivity. The maps containing the orientations and phases of all neurons within a layer define its columnar structure. In [7] these maps were generated randomly. However, as it was observed by neurophysiological investigations, the orientation maps in mammalian brains have ”pinwheel-structure”. Among the proposed approaches [17, 18, 19, 20] for mathematical design of such a structure, [20] is a relatively new and easily implemented one. That is why we used it to design orientation and phase maps in our model in our previous work [13]. First experiments showed that bigger size stimuli were detected by wider receptive fields of V1 neurons with respect to LGN layer while orientation of smaller stimuli was properly recognized by thicker orientation columns in V1 layer. Since our stimuli used to test the model are small dots and therefore, they contain high frequencies, here we used high spatial frequency to generate orientation structure of V1, as shown on Fig. 4.

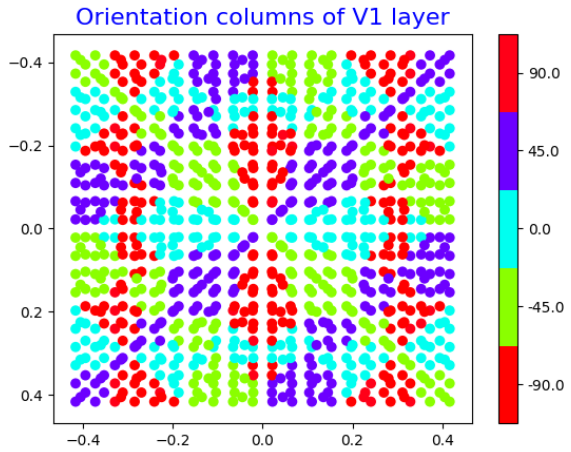

Fig. 4. Columnar organization of V1 layer. The color legend is related to orientation of the neurons.

We used five different orientations and phases in the range [-90;+90]° and [-180;+180]° respectively to model the characteristics of V1 neurons but the approach is applicable to any number of orientations and phases.

2) Lateral Connections in V1

The lateral connections between the four groups of neurons within the first layer of visual cortex have structure presented on Fig. 1. Their absolute values are determined on the basis of neuronal correlations by their positions, phases and orientations. For this aim Gabor correlation was used. The sign of a connection weight depends on whether it is excitatory (positive) or inhibitory (negative). Besides, as in [7], neurons forming inhibitory populations connect preferentially to neurons having a receptive field phase difference of around 180°.

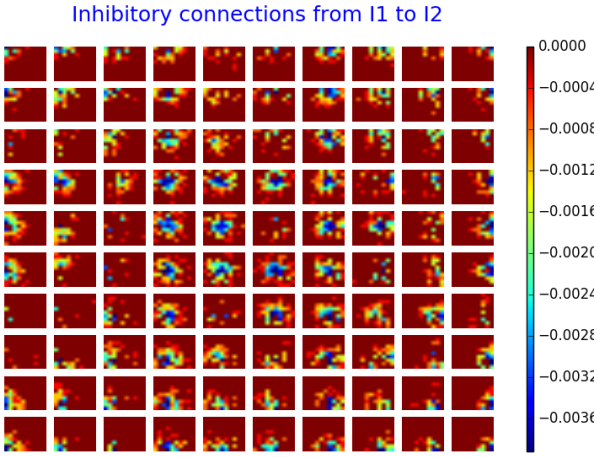

Fig. 5. Example of lateral connections between neuron groups (I1 and I2) in V1 layer.

In our model we defined frequencies and standard deviations of Gabor filters for lateral connections so as to obtain approximately circular receptive fields for all neurons in the layer. An example of obtained lateral connections is shown on Fig. 5.

3) Feedback Connections from V1 to LGN

The feedback connections from V1 to LGN neurons were chosen to have the value proportional to the corresponding feedforward connections from LGN to V1.

We tested several negative values for the inhibitory connections from interneurons and TRN to LGN, described further in the simulation results.

III. Simulation Results

We tested the designed in this way model by presenting a moving dot stimuli. Each stimulus is a movie consisting of 50 frames with 50 dots whose positions vary from frame to frame. Each frame was shown for 33.4 ms on the computer screen. An example of the first and last frame of such a stimulus is shown on Fig. 6.

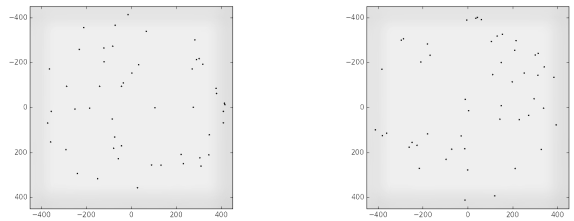

Fig. 6. First (left) and last (right) frame of a stimulus. Red and blue colors denote different values of intensity of the corresponding pixels on the screen.

This kind of stimuli is typical for psychophysiological experiments aimed to evaluate the process of decision making based on motion information. The participants had to keep fixation during the stimulus presentation and to indicate by an eye movement the perceived position of the center of radially moving dot patterns. More detailed information about the experiment and data collected are given in [21]. The final aim of our research is to develop a biologically plausible model of the brain structures responsible for the control of eye movements of humans, starting from visual perception of the stimuli (early visual system in the brain) and finishing with the brain structures responsible for making decisions. Thus the final aim of this research is to compare the developed model with real experimental data collected during psychophysiological tests with human volunteers.

A. Spiking Activity of V1 Layer

In the present work we fed into the model the visual stimulus and recorded the spiking activity in V1 layer. We tested five different configurations of feedback connections from V1 to LGN: no feedback (Fig. 7); feedback directly to the LGN neurons (Fig. 8); feedback to LGN and via interneuron (Fig. 9); feedback to LGN and via TRN (Fig. 10); feedback through interneuron, TRN and LGN together with three different combinations of values of the strength of feedback connection weights (Fig. 11-13). In all figures the dot colors "code" the orientation preference of the V1 neurons with identifier numbers (IDs) varying from 1 to 1000.

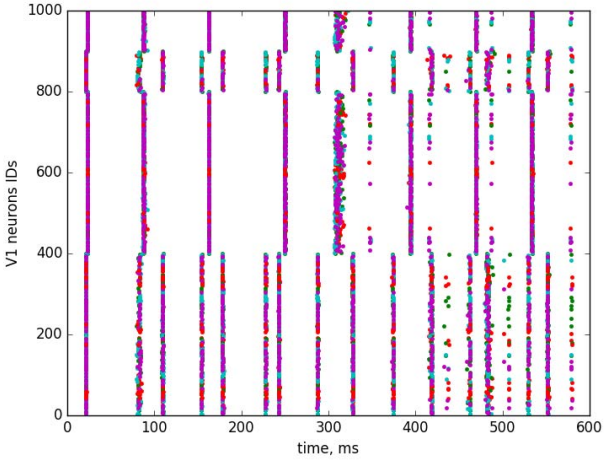

Fig. 7. V1 spiking activity without feedback from V1 to LGN area (case 1 from Table I).

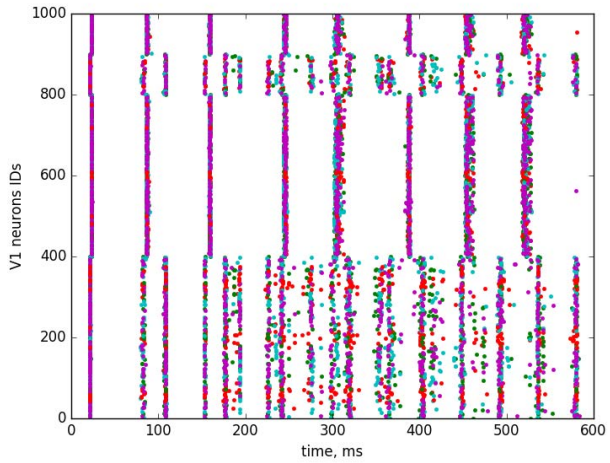

Fig. 8. V1 spiking activity with direct feedback from V1 to LGN.

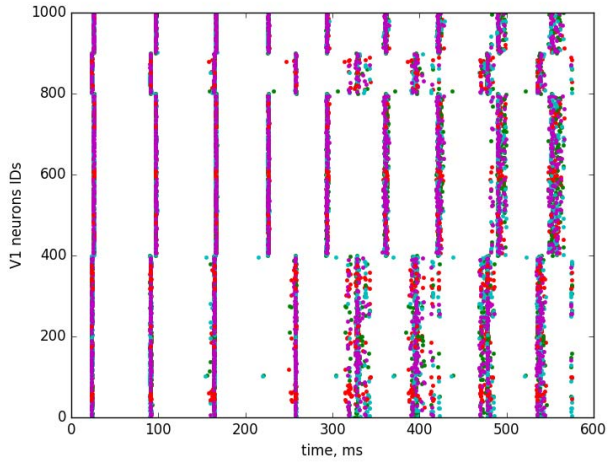

Fig. 9. V1 spiking activity with direct feedback from V1 to LGN and via interneuron.

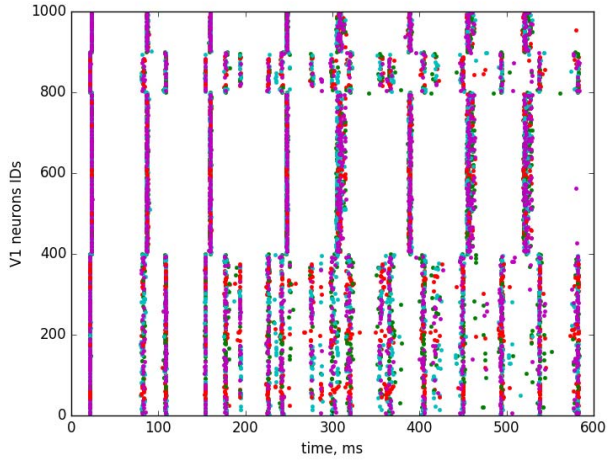

Fig. 10. V1 spiking activity with direct feedback from V1 to LGN and via TRN neuron.

For simulations on figures 8-10 the strength of direct feedback connections from V1 to LGN was proportional to the strength of corresponding feedforward connections scaled by 0.05. The strength of the inhibitory connections from interneurons and TRN was -1.0 for all of these figures.

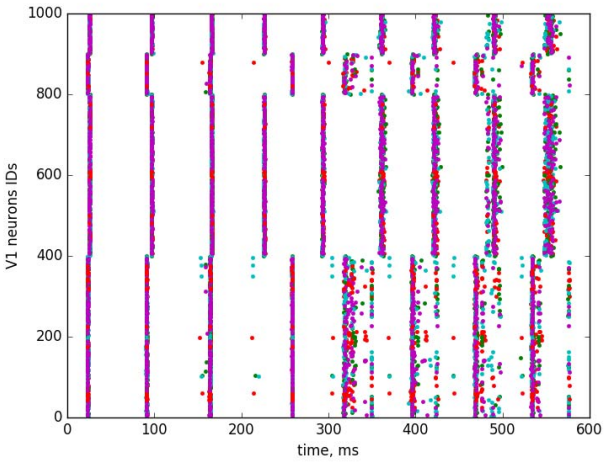

Fig. 11. V1 spiking activity with full set of feedback connections from V1 to LGN and via interneuron (case 5 from Table I).

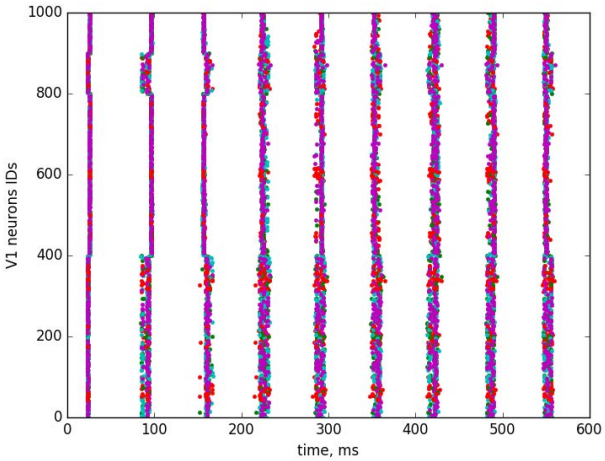

Fig. 12. V1 spiking activity with full set of feedback connections from V1 to LGN and via interneuron and TRN neuron (case 6 from Table I).

Figures 11-13 compare spiking activity of V1 with different strengths of full set of feedback connections. Spiking activity on Fig. 11 was obtained with strength of direct feedback connections proportional to the strength of corresponding feedforward connections scaled by 0.05 and strength of the inhibitory connections from interneurons and TRN of -1.0.

Fig. 12 represents the V1 spiking activity with strength of direct feedback connections proportional to the strength of corresponding feedforward connections scaled by 0.5 and strength of the inhibitory connections from interneurons and TRN of -1.0.

The spiking activity presented on Fig. 13 was obtained using the strength of direct feedback connections proportional to the strength of corresponding feedforward connections scaled by 0.05 and the strength of the inhibitory connections from interneurons and TRN was -0.5.

Table I summarizes the mean firing rates of groups of neurons having identical orientation preferences as well as number of spikes and number of neurons in each group.

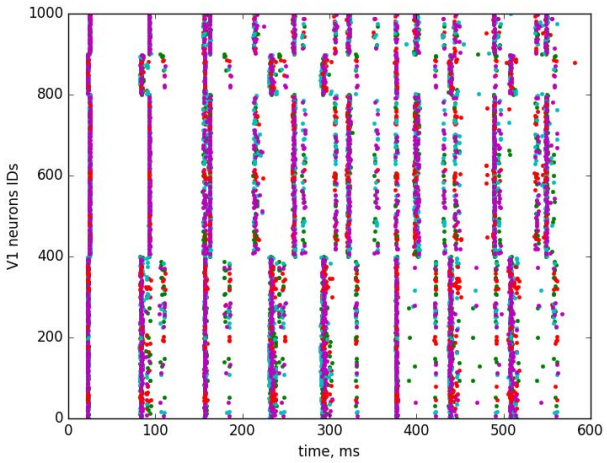

Fig. 13. V1 spiking activity with full set of feedback connections from V1 to LGN and via interneuron and TRN neuron (case 7 from Table I).

TABLE I. FIRING RATES AND NUMBER OF SPIKES IN V1 FOR ALL CONSIDERED STRUCTURES AND FEEDBACK CONNECTIONS

№	Case	θ	-45°	-0°	+45°	+-90°
		$N_{neurons}$	252	248	252	248
1	no feedback	FR	8.032	8.028	8.02	8.055
		Spikes	1992	2023	1989	1830
2	V1 to LGN	FR	7.969	7.988	7.988	7.960
		Spikes	1980	2013	1981	2006
3	only Interneuron	FR	8.488	8.476	8.496	8.488
		Spikes	2105	2136	2107	2139
4	only TRN	FR	7.992	8.004	8.008	7.968
		Spikes	1982	2017	1986	2008
5	All, scaling 0.05/-1.0	FR	8.504	8.488	8.504	8.492
		Spikes	2109	2139	2109	2140
6	All, scaling 0.5/-1.0	FR	9.0	9.0	9.0	9.0
		Spikes	2232	2268	2232	2268
7	All, scaling 0.05/-0.5	FR	8.032	8.035	8.036	8.015
		Spikes	1992	2025	1993	2020

From the figures 7-13 we observed that presence of feedback connections between LGN and V1 areas increased asynchrony in moments of spiking of neurons with different orientations. However increase of the strength of the feedback connections (Fig. 12, case 6 from Table I) also led to more synchronized spiking of all V1 neurons similar to that of the model without feedback connections (Fig. 7).

Comparing results from Table I we conclude that the model without feedback shows slightly higher firing rates and spike numbers than the model with direct feedback from V1 to LGN only. But the standard deviation of the firing rates between groups of neurons with different orientation preferences is higher for the model with feedback connection that suggests higher orientation selectivity.

The increased strengths of all kind of feedback connections (from V1 to LGN, interneurons and TRN as well as from interneurons and TRN to LGN) increase the firing rates and spike numbers as well as the standard deviations of firing rates between groups having different orientation preferences. This implies better orientation selectivity.

The inclusion of interneuron between V1 and LGN in the feedback has similar effect as the increase of feedback connection strength while presence of TRN neuron only leads to identical increase of firing rates of all orientation groups due to increased number of spikes.

Comparison between models having only interneuron, only TRN neuron or both of them with the same strength of feedback connections showed no significant difference between firing rates but in the case of full set of feedback connections the number of spikes increases. Hence although it seems that TRN neuron in feedback has no significant influence in comparison with interneuron effect, it contributes to increasing of spikes number in all cases.

IV. CONCLUSIONS

In conclusion, the simulation results demonstrated the importance of feedback connections between V1 and LGN areas especially with respect to the ability of the model to distinguish stimuli with different orientations. The presence of feedback connections has modulatory effect on the selectivity of V1 neurons.

Our next aim is to upgrade the model with layers sensitive to direction and speed of moving stimuli (MT and MST areas in the brain) and of neuron groups responsible for eye movements, and especially saccade generation (LIP neurons structure in the brain). In addition, the feedback from MT to V1 and LGN neurons will also be tested.

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