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Electrical parameters influence on the dynamics of the Hodgkin–Huxley liquid state machine

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ABSTRACT

The model of mammalian cortical hypercolumn was simulated using liquid state machines built of simple Hodgkin–Huxley neurons. The influence of cell electrical parameters on the system dynamics was investigated. The systematic analysis of the hypercolumn separation ability in the function of time constants, cell membrane capacitance, resistance, Hodgkin–Huxley equilibrium potential and sodium and potassium channel conductances was performed. Optimal ranges of time constants for the most effective computational abilities of the model were estimated.

1. Introduction

In this article the results of the Hodgkin–Huxley (HH) neural networks [1] simulations will be studied. The aim of the research presented herein was to perform the detailed analysis of the electrical parameters influence on the fundamental properties of liquid state machines (LSM).

The cortex is built of neurons organised in microcircuits [2] which form columns and the function of each column depends on its location in the brain. The theory of liquid computing and LSM originates from Maass and Markram and was firstly presented in [3]. They showed that neural microcircuits tend to behave in a way similar to that of liquids.

The methods used for the analysis of neural liquids dynamics are, however, different from the typical, physical approach to real liquids. But similarly to the real liquids—neural microcircuits can reach an almost infinite number of states as a result of an almost infinite number of perturbations. The behaviour of LSM (or cortical column–neural microcircuit) dynamics in some way resembles the behaviour of some lake calm surface being disturbed by stones dropped into the water [3]. In the liquid computing theory—the specialised expert (called readout) can derive the history of stimulation by observing the current state of the 'liquid'. Cortical microcircuits turn out to be very good 'liquids' for computing on perturbations. They are characterised by the large diversity of elements, neurons, synapses, the large variety of mechanisms and time constants characterising their interactions, involving recurrent connections [3]. The model of liquid state machine (LSM) is based on a strict mathematical framework that guarantees, under ideal conditions, universal computational power [3].

In original Maass' works the simple integrate-and-fire (IF) neurons were used. It is predictable that the ideas of liquid computing can be easily moved to the machines built of more complicated HH cells. However, there was no detailed research done on the influence of e.g., time constants and other HH parameters on the general dynamics of the LSM-based systems.

This paper will present the results of our experiments with varying electrical parameters of HH neurons used for the construction of a simple, cortical model including ensemble of the LSMs.

Computational investigation of the electrical parameters influence on the dynamics of neural networks is important in compartmental modelling and building new theories [4]. Till now there is no good and complementary theory basing on the genetic, molecular and cellular foundations explaining the autism spectrum disorder (ASD) [5]. Simulations presented herein may help in improving Posner's model of shifting attention [4] by implementing into it biologically realistic HH neurons.

2. The model

The network used for simulations can be treated as the simple model of mammalian visual system [6]. The idea of liquid computing calls for architecture consists of two main modules

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[7,8]. That is why the input device called 'retina' and the neural hypercolumn–'liquid' were implemented.

The models consisting of thousands of HH neurons [1] are power consuming and for the reason of easy parallelisation, the discussed structure was built on the basis of square-shaped networks with the borders being powers of 2.

The retina is built on the 16×16 square-shaped grid and can be easily divided into 64 patches (2×2) or 16—with the patch dimension 4×4 or 4 (by analogy with the patch dimension 8×8 cells) depending e.g., on the level of variety of the structure we want to model or the number of processors we have available for simulations. Each patch is connected with one of its corresponding HHLSM columns in the following way: each retinal cell of the given patch is connected with all neurons of the lateral geniculate nucleus (LGN—which in nature is the primary relay centre for visual information received from the retina of the eye) of the corresponding column. Retinal cells are connected only with the excitatory channels of LGN. The weight of these connections is set to $w=2$. The retinal cells are not connected with one another.

Typical HHLSM consists of 1024 cells put on a $8 \times 8 \times 16$ grid. There are layers arranged in each column (Fig. 2) and the set of columns simulates the hypercolumn (or the liquid, but one should remember the lake surface comparison and physicists working on liquids usually do not agree with this statement). There is no L1 layer in the scheme. We reserved it for so-called 'readout' often used in Maass' works [3] which can be e.g., artificial neural network and can be used for more profound analysis of the liquid dynamics. The LGN layer is built on the $8 \times 8 \times 1$ grid and all the other layers are arranged on the $8 \times 8 \times 3$ grids. In each layer all the neurons are connected with one another and there are 80% of excitatory connections and 20% of inhibitory connections. But for the connection of layers we use only the neurons from the "bottom" of one layer and the "top" of the other one. Inside the layers the full-connection is arranged. However, the probabilities of excitatory and inhibitory connections creation are the same. There are recurrent connections from the layer L6 to LGN in each column. In addition, layers L6 of particular columns are connected in the same way with LGNs of other HHLSMs, simulating the corticothalamic feedback. Intercolumn connections are presented in Fig. 1 by the arrow. The rule of these connections is set as follows: the column N sends the signal to the column $N+1$ and the last column is not transmitting its activity anywhere. Each connection in the model is characterised with 'delay' parameter ($d=10^{-4}$ s) and random weight ($w \in [0,5]$). In original Maass'-works there were no arranged layers. There is no real need to implement layers in order to observe liquid computing phenomena. Nevertheless, such a structure of the columns was chosen to be closer to biology in some way. The layers and connections that we implemented imitate the real structures. So, we can treat the hypercolumn as a very simplified part of periodic structure of the visual cortex.

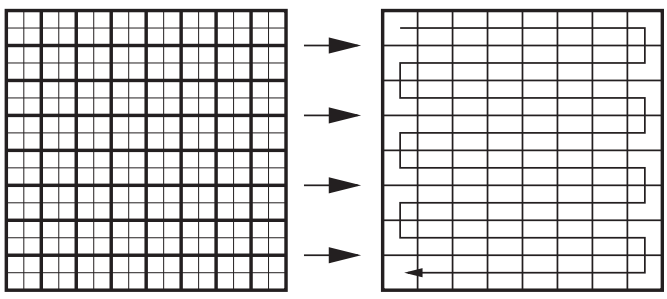

Fig. 1. The model of simulated visual system with 64 patches. The arrow represents the connections of HHLSM columns (for detail see text).

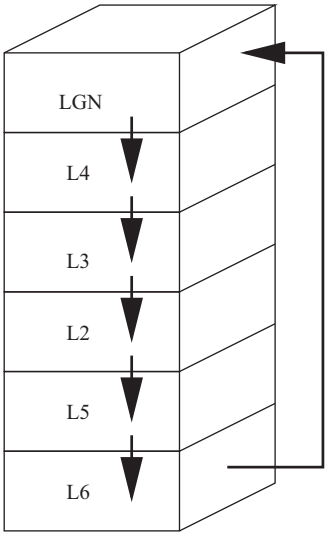

Fig. 2. The structure of HHLSM as the fundamental microcircuit of the simulated hypercolumn.

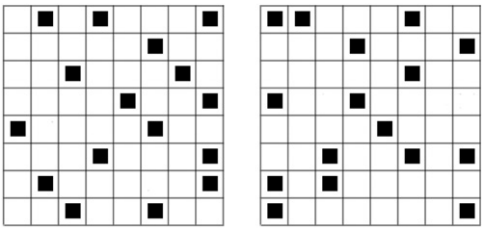

Fig. 3. A typical couple of input patterns stimulating 25% patches of the retina (in this case for the model 64k).

All simulations described in this paper were performed using the parallel version of GENESIS 2.3 [9,10] on the local cluster. For detail of the machine see Appendix A. The neurons used in the model were relatively simple HH cells—for detail see Appendix B.

3. Results

We investigated two models: consisting of 16 HHLSMs (16,384 HH neurons) called 16k and 64 HHLSMs (65,536 neurons) called 64k. One should remember that there are also additional 256 retinal cells in each model.

Chosen patches on the retina were stimulated by changing in time randomly generated impulses with mean frequency of 200 Hz. That means that in each case the input pattern was not only geometrically different but also characterised by varying in time dynamics of stimulation. In original Maass' works we usually have one stimulating neuron connected to 30% of randomly chosen neurons of the column [3]. In comparison, our model is a bit more sophisticated. The exemplary couple of input patterns stimulating the retina is shown in Fig. 3.

Up to $T=1000$ ms of biological activity of the systems was simulated.

The state of the hypercolumn is defined by a multidimensional vector with the binary coordinates: 0 for a neuron that is not active and 1 for an active one in a given interval of time e.g., in the discussed simulations $t_i=10$ ms. The 'dead-state' corresponds to the hypercolumn with all inactive neurons. The number of vector elements is equal to that of neurons in the hypercolumn (16,384 or 65,536), HHLSM (1024) or retina (256). Having recorded the activity of the model for different stimulation one can calculate

the Euclidean distance $d(u,v)$ of two vectors $\vec{u}(t)$ and $\vec{v}(t)$ representing two liquid states changing in time:

$$d(u,v) = \|\vec{u}(t) - \vec{v}(t)\| = \sqrt{\sum_{i=1}^{N} (u_i - v_i)^2}. \quad (1)$$

The state of the liquid may be then redefined as the distance of the disturbed hypercolumn from its vector being in the dead state:

$$u = \|\vec{u}(t) - \vec{0}\| = \sqrt{\sum_{i=1}^{N} (u_i)^2}. \quad (2)$$

In each case a difference in the states of the liquid was observed for different retinal stimulations. Fig. 4 presents such distances from the dead-state calculated for the retina and the hypercolumn. The results were collected for typical retinal patterns in the 500 ms simulation in the 64k model. The retina was divided into 64 patches and each patch consisting of 4 neurons, 25% of patches (giving 16) were stimulated. All cells of the stimulated patch are connected to the above mentioned random spike generators. That means that in the discussed example the stimulation comes from 80 synapses (four per one patch), so the state of the retina is maximal, calculated as $\sqrt{80}$ and equal to about 8.9 as shown in Fig. 4. It is a typical behaviour of LSM. HH neurons provide the model with many additional parameters that may have significant influence on its separation abilities. Using the Euclidean distance defined in such a way probably is not the best solution, while HH neurons are spiking, however, even such a simple method can show that the discussed structures have separation abilities. The method of calculating the distance was inspired by the distance measures used in [3]. For sure, the frequency of HH spiking neurons depends on their time constants, defined in the model as

$$\tau = C_m \cdot R_m. \quad (3)$$

This must have influence on the states that the hypercolumns get, and this leads to the dependence of HHLSM separation ability on electrical parameters of particular cells. In Figs. 5 and 6 we present the soma activity of selected and isolated cells from the hypercolumn which were stimulated only by the input. The time constant of these cells was different in each case. The value of τ was manipulated by C_m tuning (Fig. 5) and R_m (Fig. 6). The plots Figs. 4 and 5 are different which made us investigate the influence of both C_m and R_m on the dynamics of the systems. Note that the values of R_m and C_m in the HH model are given in ohms and farads per square meter. In this paper, however, we will stick to SI units. At the examination both the membrane capacitance and the resistance of the dendrites were taken into account. For detail see Appendix B. The decrease of separation ability can be observed with the C_m parameter growth. Fig. 7 presents the state difference of the hypercolumn calculated from the results of 64k model simulations. The membrane capacitance C_m was changing from 10 mF to 20 mF. It is predictable behaviour as the neurons with larger time constants have in general longer times of spikes integration. In addition we investigated the influence of the so-called equilibrium potential E_m [10] on the separation ability of

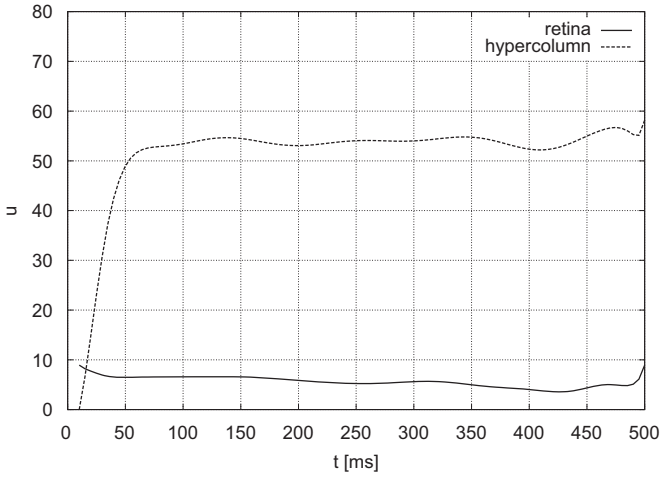

Fig. 4. The states of the retina and hypercolumn for two different input patterns. 25% of retinal cells were stimulated in the 64k model.

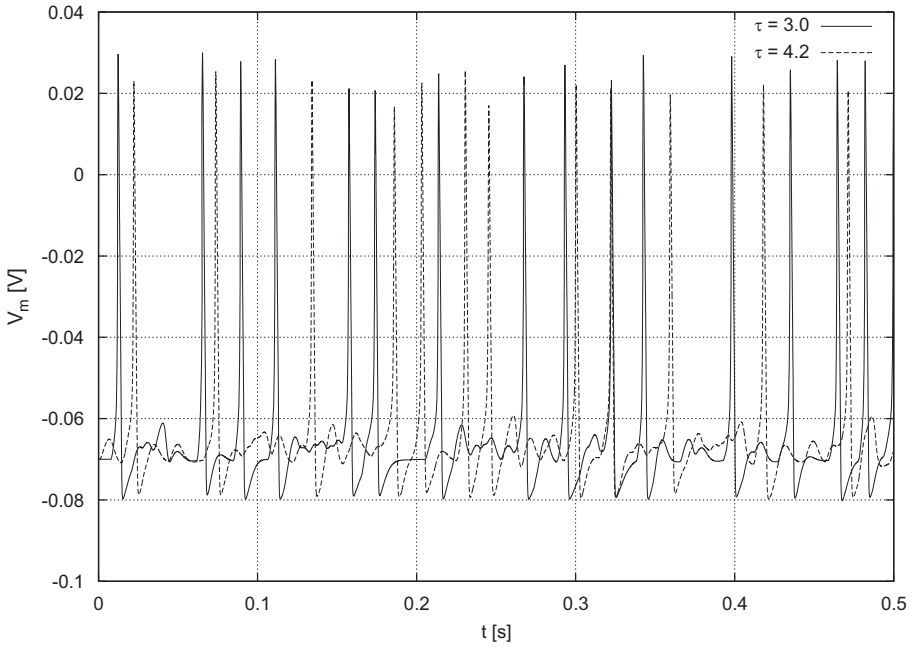

Fig. 5. The example of HHLSM soma activity for two different values of time constants. The cell was stimulated only by the retinal input. The time constants were changing by manipulating only the C_m parameter. In this case C_m=9 mF for τ = 3.0 ms and C_m=12.6 mF for τ = 4.2 ms. R_m = 333 mΩ.

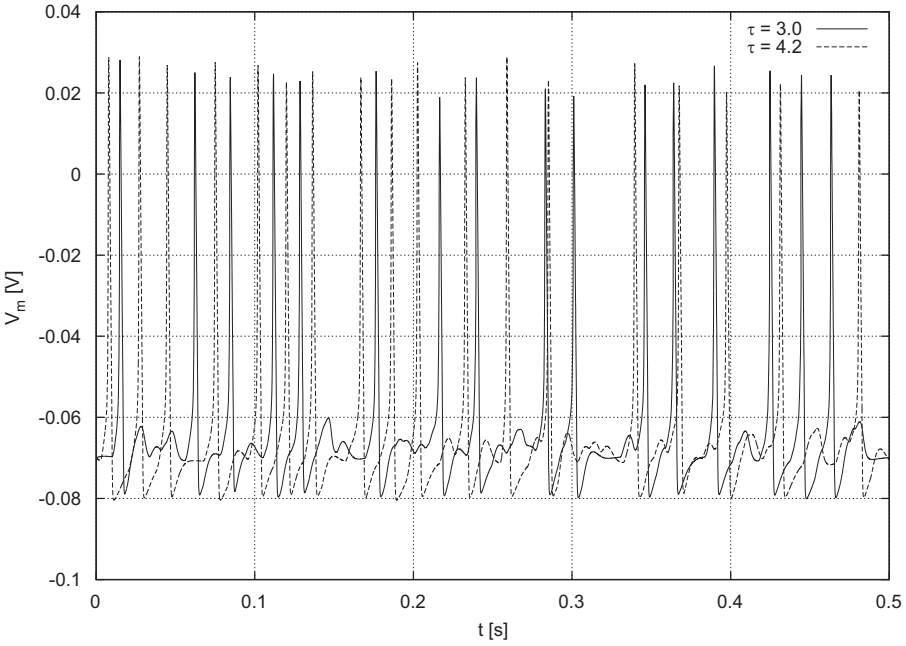

Fig. 6. The example of HHLSM soma activity for two different values of time constants. The cell was stimulated only by the retinal input. The time constants were changing by manipulating only the R_m parameter. In this case $R_m = 300$ mΩ for $\tau = 3.0$ ms and $R_m = 420$ mΩ for $\tau = 4.2$ ms. C_m=10 mF.

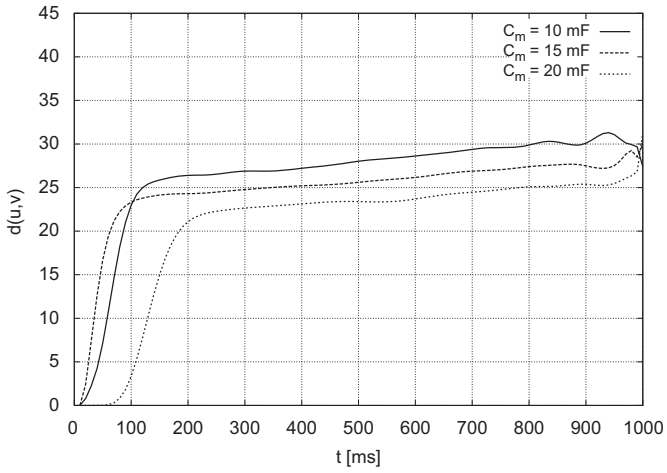

Fig. 7. The 64k hypercolumn liquid-state distance for two different patterns stimulating the retina and changing the membrane capacitance C_m. Decrease of separation ability observed with the C_m growth. (For detail see text.)

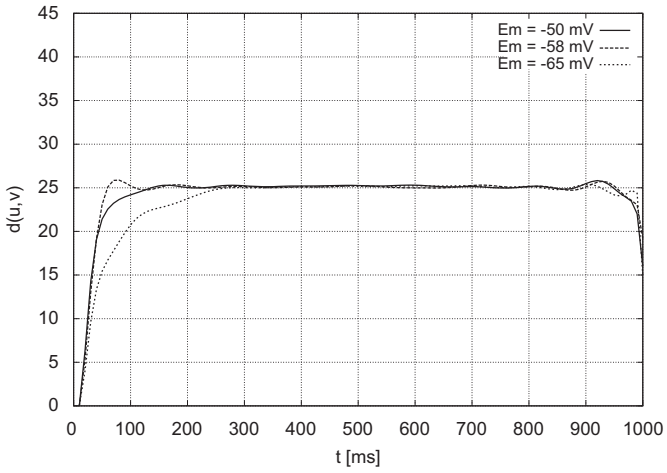

Fig. 8. The 64k hypercolumn liquid-state distance for two different patterns stimulating the retina and changing the HH equilibrium potential E_m. No change in distance was observed. (For detail see text.)

LSM and no significant influence on the general hypercolumn dynamics was observed (Fig. 8). Exceeding the verge parameters of E_m led the hypercolumn to the permanent dead-state. In Fig. 9 the trend of hypercolumn separation ability as a function of time constant is presented. It was already shortly reported in [11] that for the relatively long times of simulated biological activity of the system ($T > 150$ ms) the separation ability is on the satisfactory level, however, a decrease can be observed for the time constants $\tau > 5$ ms. For $T < 150$ ms a strong decrease takes place when τ grows. Of course, the longer the T-time is the greater difference of states can be observed. The optimal value of τ is around 3.5 ms.

The presented model of hypercolumn works in a synchronous mode. The most interesting processes can be observed in the first 100–200 ms. Immediately after the network dynamics is dominated by recurrent signals. The changes of the state are very small and the separation algorithm is not working as effectively as at the beginning of simulation. The difference of states fluctuates around the constant level and a kind of stable state is observed. However, the hypercolumn is ready for next computations after some time needed for relaxation. This is one of the most significant features of the 'liquid computing' paradigm: the same structure can process almost an infinite number of varying in time inputs giving the adequate answers for stimulations in each case [11]. In the next series of experiments we checked the dependence of the separation ability on both the capacitance and resistance of the neural membrane but set independently. In order to accomplish this we run 200 simulations of 16 k model, 100 per one stimulation pattern and for the selected pairs of C_m and R_m. We checked all combinations of the time constants calculated for $C_m \in [10\text{ mF}, 19\text{ mF}]$ and $R_m \in [174\text{ mΩ}, 330\text{ mΩ}]$. The set of adequate pairs from the mentioned ranges of parameters can be represented as the product of two matrices:

$$C_m = [10, 11, 12, 13, 14, 15, 16, 17, 18, 19]^T \text{ [mF]} \quad (4)$$

and

$$R_m = [330, 300, 275, 254, 236, 220, 206, 194, 183, 174]\ [\mathrm{m}\Omega] \quad (5)$$

giving the time constant matrix:

$$\tau = \begin{bmatrix} 3.30 & 3.00 & 2.75 & 2.54 & 2.36 & 2.20 & 2.06 & 1.94 & 1.83 & 1.74 \\ 3.63 & 3.30 & 3.02 & 2.79 & 2.60 & 2.42 & 2.27 & 2.13 & 2.01 & 1.91 \\ 3.96 & 3.60 & 3.30 & 3.05 & 2.83 & 2.64 & 2.47 & 2.33 & 2.20 & 2.09 \\ 4.29 & 3.90 & 3.57 & 3.30 & 3.07 & 2.86 & 2.68 & 2.52 & 2.38 & 2.26 \\ 4.62 & 4.20 & 3.85 & 3.56 & 3.30 & 3.08 & 2.88 & 2.72 & 2.56 & 2.44 \\ 4.95 & 4.50 & 4.12 & 3.81 & 3.54 & 3.30 & 3.09 & 2.91 & 2.74 & 2.61 \\ 5.28 & 4.80 & 4.40 & 4.06 & 3.78 & 3.52 & 3.30 & 3.10 & 2.93 & 2.78 \\ 5.61 & 5.10 & 4.67 & 4.32 & 4.01 & 3.74 & 3.50 & 3.30 & 3.11 & 2.96 \\ 5.94 & 5.40 & 4.95 & 4.57 & 4.25 & 3.96 & 3.71 & 3.49 & 3.29 & 3.13 \\ 6.27 & 5.70 & 5.22 & 4.83 & 4.48 & 4.18 & 3.91 & 3.69 & 3.48 & 3.31 \end{bmatrix} \quad (6)$$

with all values given in milliseconds.

Note that all parameters are chosen in such a way that on the diagonal of the matrix the time constant $\tau = 3.3$ which is the initial value in the cells used in most GENESIS tutorials and models [10].

In Fig. 10 the state distance (or separation ability) is presented for each value of τ from the matrix (6). The slight decrease of state distance can be observed following the increase of R_m and C_m. However, the plot in Fig. 10 allows us to estimate the optimal ranges of resistance and capacitance as follows:

$$10\ \mathrm{mF} < C_m < 15\ \mathrm{mF} \quad (7)$$

and

$$236\ \mathrm{m}\Omega < R_m < 330\ \mathrm{m}\Omega. \quad (8)$$

When these two crucial parameters take such optimal values, the separation ability of the HHLSM is the best. For other values the liquid computing efficiency is not as effective as it could be.

In the 64k model we investigated the influence of the sodium and potassium channel conductances on the separation abilities of HHLSM. Originally $G_{Na}=1200$ S, $G_K=360$ S and in our simulations we varied them by 20%.

In Fig. 11 one can see that changing the value of G_{Na} leads to some visible increase of separation ability, however the states of the liquid seem to be less stable than in the original case of $G_{Na}=1200$ S.

In Fig. 12 the liquid state difference for the varying G_K parameter is presented. We observe the worse separation than in the natural case when $G_k=360$ S and at least at this moment

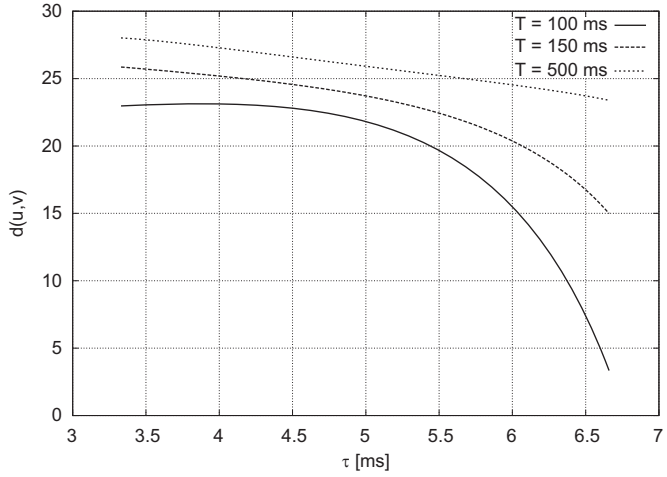

Fig. 9. The separation ability as a function of time constant τ for two different patterns stimulating the retina in the model 64k and different time of biological activity simulation.

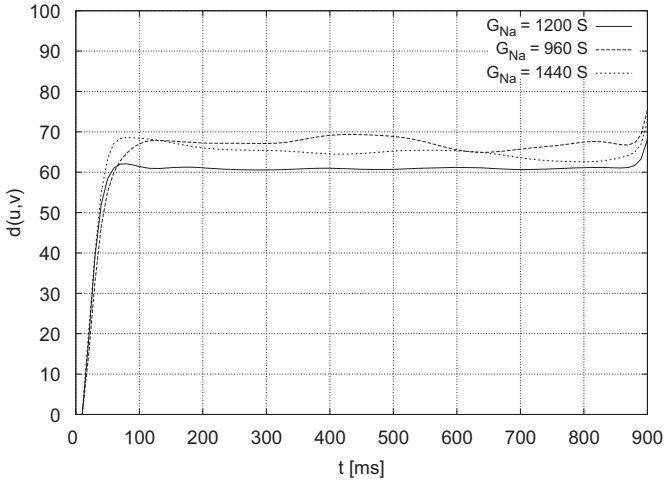

Fig. 11. Separation ability as a function of sodium channel conductance for the model 64k and the time of simulated biological activity $T=900$ ms.

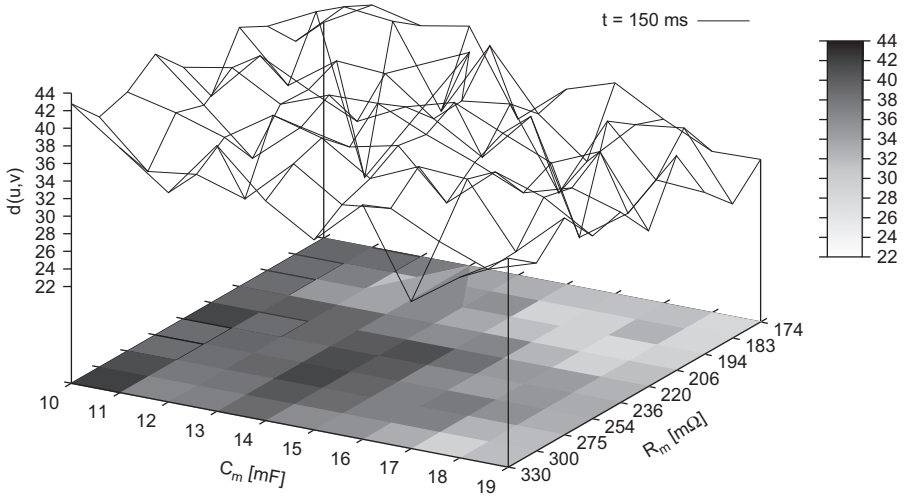

Fig. 10. Separation ability as a function of cell membrane resistance and capacitance for the model 16k and the time of simulated biological activity $T=150$ ms.

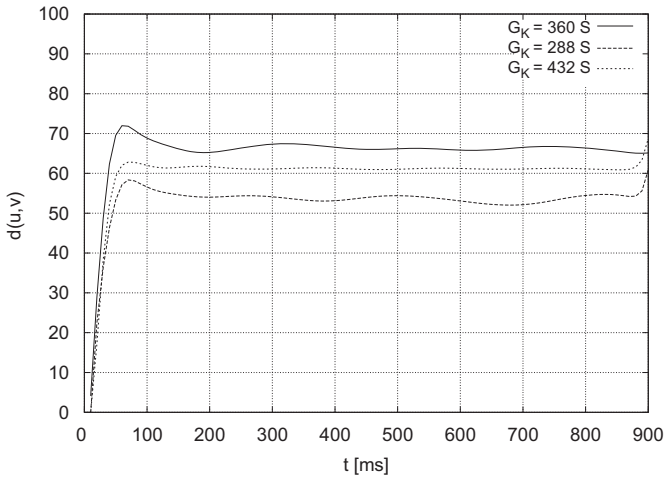

Fig. 12. Separation ability as a function of potassium channel conductance for the model 64k and the time of simulated biological activity $T=900$ ms.

there is no reason to manipulate the potassium channel conductance in simulations.

4. Conclusions

Hodgkin–Huxley liquid state machines were simulated in the model of mammalian cortical hypercolumn. The main objective of the research presented in this paper was to perform the systematic analysis of cell electrical parameters influence on the fundamental property of liquid computing—the separation ability.

We showed, based on the dynamics of single cells, that the time constant must be meaningful while creating LSMs of the biologically realistic Hodgkin–Huxley neurons. Later we proved that with the increase of C_m the separation ability decreases. This led us to the analysis of the neural liquid dynamics in the function of cells time constants depending firstly only on the value of C_m.

The influence of equilibrium potential and sodium and potassium channels conductances was also checked and we concluded that there is a possibility of improving the separation ability by manipulating the G_{Na} parameter.

Finally we investigated the difference of hypercolumn states for both varying parameters C_m and R_m. Finding the optimal ranges of parameters for liquid computing seems to be important. Since now it is possible to create models consisting of most effective and biologically realistic neurons.

Maass in his studies [3] concentrated mainly on much simpler neurons. We have also some experience in investigation of LSMs built of different and simpler than HH models of cells [12,13]. It should be outlined that the smaller the HH neuron time constant is, the closer it is than the IF unit. Such IF neurons were originally used in the Maass' works. Nevertheless, the HH model introduces to the theory much more parameters like e.g., ionic channel conductances and this implies that further investigation of HHLSM is in demand. From the point of view of our research it is also important to investigate more profoundly the origin and role of non-linear and self-organised behaviour already found in the models [14–17].

Finally, analysis and simulation of neural systems with use of biological models is crucial for understanding functionalities of the whole brain [18]. New trends in neurocybernetics hopefully will lead us to the explanation of phenomena concentrated around mind, intelligence and cognition [19–21]. That is why the research of the systems not built not classical neural networks is so important and justified.

Acknowledgements

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Appendix A. Simulation environment

The local cluster used for most of the simulations discussed in this contribution is built of eight machines and one additional machine—the so-called "access node". Each machine has two Intel(R) Xeon(R) quad-core processors (CPU E5320 @ 1.86 GHz Xeon) with 8 GB of RAM. The cluster works under control of Ubuntu 8.04 LTS and 2.6.24-26-server. kernel version. The model is simulated in the parallel version of GEneral NEural SImulation System GENESIS 2.3. A gcc v. 4.2.4 compiler was used for the general system configuration.

Appendix B. Hodgkin–Huxley neurons details

Both retina and hypercolumn consist of multicompartmental neurons with two dendrites (each built of one compartment), a soma, and an axon. The dendrites contain synaptically activated excitatory and inhibitory channels and the soma has voltage activated HH sodium and potassium channels. The behaviour of each compartment is equivalent to that of an electrical circuit [10]. During the process of network creation, the dendrite to which particular synapse was connected was chosen randomly, with equal probability of 50%. The topology of dendrites was not taken into consideration, neurons were connected by weights chosen at random. Axon was simulated only as a simple delay line. The model of synapse in GENESIS is realised by a function of weight and delay parameters. The alpha functions reflecting changes of synaptic channel conductances is permanently built in simulator and broadly described in [10].

Such a simple HH neurons were used because of the numerical restrictions and time consuming simulations. Most often networks consisting of thousands of cells use less power consuming models of neurons. However, in our model we had an opportunity to investigate the most numerically sophisticated HH neuron. In future we plan to investigate networks with smaller number of more complicated units.

Thus originally each circuit was characterised by a typical of the GENESIS group of parameters which are as follows: resistances $R_a=0.3\,\Omega/m^2$, $R_m=0.33333\,\Omega/m^2$, capacity $C_m=0.01$ F/m^2, and potential $E_m=0.07$ V. For the soma compartment $E_k=0.0594$ V and for the dendrite $E_k=0.07$ V. Conductance for each type of ionic channels is chosen to be: $G_K=360\,\Omega^{-1}$ and $G_{Na}=1200\,\Omega^{-1}$. These parameters originate from neurophysiological experiments [10] and are chosen to make the model biologically more realistic. The soma has a circular shape with the diameter of 30 μm, dendrites and axon are cable like with the length of 100 μm.

When changing the time constants and other electrical parameters the C_m, R_m, G_{Na}, G_K and E_m values were manipulated.

All the other parameters are chosen as suggested by the GENESIS authors to simulate the behaviour of the biological-like neurons [10]. More details concerning the HH model can be found elsewhere [10,1].

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