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Computer simulation of inhibition-dependent binding in a neural network

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Abstract

Reverberating dynamics of neural network is modeled on PC in order to illustrate possible role of inhibition as binding controller in the network. The network is composed of binding neurons. In the binding neuron model [BioSystems 48 (1998) 263], the degree of temporal coherence between synaptic inputs is decisive for triggering, and slow inhibition is expressed in terms of the degree, which is necessary for triggering. Two learning mechanisms are implemented in the network, namely, adjusting synaptic strength and/or propagation delays. By means of forced playing of external pattern, the network is taught to support dynamics with disconnected and bound patterns of activity. By choosing either high, or low inhibition, one can switch between the disconnected and bound patterns, respectively. This is interpreted as inhibition-controlled binding in the network.

Keywords: Binding; Inhibition; Learning; Neural network

1. Introduction

Information about the external world reaches brain being distributed in space and time. It is well distributed over the sensory pathways of different modalities. Moreover, different features of a compact in space and time signal of definite modality can be represented by means of activities in separate neuronal populations (Giard et al., 1995). At the same time, during perception separate portions of information are some way brought together to represent coherent objects. Mechanisms which ensure that separate pieces of information represented as disjointed in space and time neuronal activities produce impression of single coherent object are known as feature linking, or binding mechanisms (Llinás et al., 1994; von der Malsburg, 1999). Similar situation is with the storage of conceptual knowledge and its retrieval (Damasio, 1989). In this case, it is proposed (Tranel et al., 1997) that the retrieval starts in high-order association cortices and sub-cortical nuclei as activation of multiple spatially segregated sites in which the knowledge pertinent to a particular concept is stored in a non-explicit form. These activities in turn evoke activities in early sensory cortices as well as in motor structures giving explicit images of a concept being retrieved.

Thus, the recruitment of some intermediary regions due to time-locked activities in another regions seems to be essential for binding (Damasio et al., 1996). This process may happen at different spatial scales. For conceptual knowledge, the scale is comparable with the dimension of brain. For perception of elementary components of visual image, it could be the size of a few columns in the visual cortex (Eckhorn et al., 1988). The spatially smallest version of binding has been proposed for interpretation of information processing in a single neuron (Vidybida, 1998). In this

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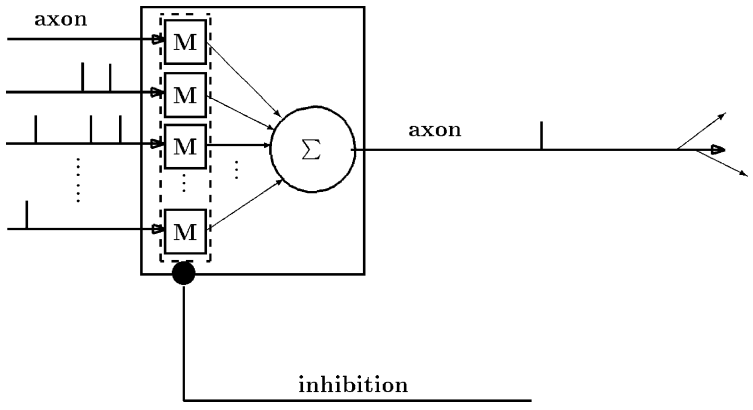

Fig. 1. The binding neuron. The memory block M for each input, mimics the EPSP finite lifetime. It stores input spike during period of time W, and then forgets it. If the total number of input signals taken with their weights exceeds the threshold value BT, the cell fires a spike. Slow inhibition is expressed in terms of the W: the higher is the inhibition, the narrower is the W. The total number of inputs into a single cell depends on the connection pattern in the network.

case (Fig. 1), the spatial scale is delimited by the set of synaptic inputs into a single cell. If a number of inputs comes temporally coherent,[1] the cell fires a spike, which is interpreted as binding of temporally coherent inputs into a single event (the output spike). For a single cell, it is proposed that slow inhibition could be a factor that effectively controls this type of binding (Vidybida, 1998).

In this paper, the neuronal model of Fig. 1 is utilized for constructing a simple neuronal network. The reverberating dynamics of this network is studied by means of computer simulation. The dynamical pattern in which some geometrically intermediate region is recruited into firing due to activity in adjacent regions is interpreted as a model for binding in this network, because after the recruitment, the domain of activity becomes spatially connected. The purpose of this paper is to demonstrate that slow inhibition could control this type of binding in the network under consideration.

2. Methods

The network composed of cells described in Fig. 1 has been modeled by means of C++ programming language and run on PC with time-step $\mathrm{d}t = 0.1$ ms. Here are the details of the model used.

2.1. Single cell

Single neuron model is based on the previously made numerical simulation of Hodgkin–Huxley-type neuron stimulated from multiple synaptic inputs (Vidybida, 1996). This model is realized as a unit with a number of inputs for receiving signals from other neurons, and an output for sending spikes to other neurons (Fig. 1). The exact number of inputs depends on connection pattern and varies from 4 for the case of the nearest neighbor connections to $N-1$ for fully connected network of N neurons. Any received input signal is stored (memorized) in the cell during period W after which it is forgotten. The temporal memorization mimics the temporal behavior of the excitatory post-synaptic potential (EPSP). The width W can be adjusted for any input. Reduction of W can be interpreted as increasing of inhibition (Vidybida, 1998). Here the W is chosen from the range 1–4 ms. The cell is realized in such a way that the W may be different for different cells, and for different inputs in a single cell, but in this work the W is changed uniformly for all inputs in all cells. Each input has its own weight (synaptic strength), which can be changed during learning (see below). The summation block ($\sum$ in Fig. 1) evaluates at any moment of time the total amount of excitation stored

[1] For a fixed number, n, of incoming into a neuron spikes, their degree of temporal coherence, TC, is defined in (Vidybida, 1998) as $\mathrm{TC} = 1/(t_n - t_1)$, where t_1, t_n are the arrival times of the first and the last spike, respectively.

in the cell, which is the sum of all memorized inputs signals taken with their weights. If the excitation reaches the binding (firing) threshold (BT), the cell fires a spike and then stays in refraction for 0.9 ms. Each cell has additional external input the strength of which just exceeds BT (not shown in Fig. 1). As a result, a single spike arriving through the external input triggers the cell immediately. This enables a possibility to play external patterns of activity which are used for teaching (learning).

2.2. Axon

Each axon is realized as a program unit characterized by the two cells which are connected by this axon. Also, it has its own length, which is equal to the distance between the cells it connects. Axon receives signal from its input cell, propagates it with velocity v and eventually pumps it into its output cell through the cell's synaptic input. At any moment of time, axon either propagates a spike, or is waiting for a spike from its input cell.

2.3. Network, general

The spatial structure of network is fixed as a plane structure. For constructing the network in a computer memory, the total number of neurons, N should be specified. All N units are arranged in a square lattice of rectangular shape. The number of units in a row and in a column of the rectangular are proportional to given numbers H and V, respectively. Depending on the numbers N, H, V, the last row in the square lattice can be left incomplete.

In order to specify exact physical parameters of inter-neuronal connections, the propagation speed in an axon, v is fixed. The propagation delay between any two nearest neighbor units, d_p is fixed as well. This allows to calculate the lattice constant a (the distance between two nearest neighbor units) as $a = vd_p$. With the exact value of a, one can determine geometrical distance between any two units.

Axonal connection pattern is imposed as follows. A maximal admitted delay, D is specified. If D is equal or exceeds the propagation time along the diagonal of the rectangular which represents the network, then any two cells are connected with two identical axons propagating in opposite directions. Otherwise, only axons with delays which are less or equal to D are retained. For example, if $D = d_p$, then only the nearest neighbors will be connected. After construction, it is possible to specify additionally which connections in the net should be excitatory, and which are inhibitory.

During runtime, the program allows to pause the network dynamics and to make some manipulations with its structural and dynamical properties and then run the dynamics further. Namely, it is possible to choose two subsets of neurons and to lock or unlock all axons, which connect any neuron from one subset with any other neuron from the another subset. Axons propagating from one subset to the another one and those propagating in the opposite direction can be manipulated separately. Also, it allows to play compulsory external patterns of activity. Patterns should be described by specifying which groups of cells have to fire at each moment of time during the presence of external drive, e.g. as in Table 1.

2.4. Network, realization

A network of 15 × 15 binding neurons has been used for modeling reverberating dynamics. The prop-

Table 1
Firing pattern used for teaching

Time (ms)											
0	0.2	0.4	0.6	0.8	1.0	1.2	1.4	1.6	1.8	2.0	2.1
Cell #											
79	64	34	49	36	37	38	40	39	69	84	–
80	65	50	35	51	52	53	54	55	70	85	–
144	159	174	175	173	172	171	170	169	154	139	–
145	160	190	189	188	187	186	184	185	155	140	–

Four cells in each table column are triggered at the moment specified above this column. When the table is exhausted, it is fed to the network again until the teaching time is exhausted. The cells are numbered as shown in Fig. 2.

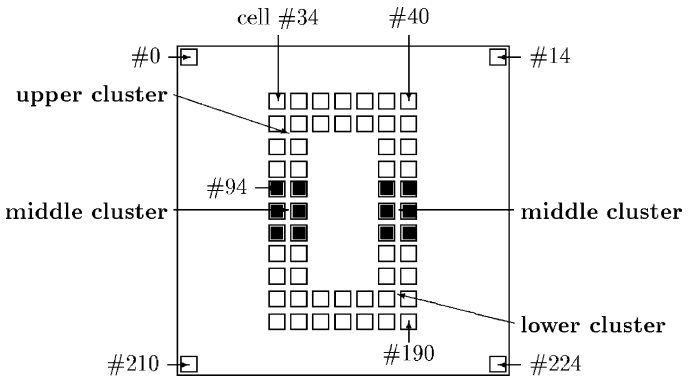

Fig. 2. Domains in the network, which display spatially bound/unbound activity depending on the level of inhibition. Neurons shown in black belong to the middle clusters. These clusters start firing for low inhibition and become silent for the inhibition made high. Cells outside of the O-shaped domain (only four of them are displayed) remain silent during all stages of simulation.

agation speed, v was set to 10 m/s. Propagation delay between the nearest neighbors is equal to 1 ms. This results in a square-shaped network with the square edge length equal to 140 mm. Connections with delay less or equal to 4 ms are retained in the network ($D = 4$ ms). This brings about the connectivity pattern in which a cell can be connected by reciprocal connections with up to 48 neighbors, provided its location is far enough from the square boundary. The binding threshold, BT = 300. The synaptic strength is initially set to 10.

Connections from the O-shaped region, which is shown in Fig. 2, to the remaining part of the network are chosen inhibitory. This prevents activity in the O-shaped region from spreading over the remaining part of the network. As this is the only purpose of inhibition in this pull of connections, its concrete realization does not matter in this work. All connections inside of the O-shaped region are excitatory. In its initial state, the network is at rest. This means that all axons are free of spikes, all cells are free of input signals, and not in their refractory states. The pattern used to drive the network (see Table 1) triggers only neurons in the O-shaped region. In this case the firing activity is unable to spread outside of the O-shaped region. Thus, for dynamical states which are studied here, the remaining part of the network may be considered as cut from the O-shaped region, even if for another tested driving patterns (not shown here) intensive reciprocal dynamical interaction between the both parts may happen.

2.5. Learning

Two types of learning are implemented in the network. Both can be switched on and off during the runtime. The first one is the Hebbian learning for adjusting of synaptic strength. If the synaptic learning mode is switched on, then every time the cell is triggered, the synaptic strength is advanced by 1 for those synapses which have contributed to this triggering.

The second one is adjusting the propagation (synaptic and/or axonal) delays. If this mode is switched on, then the cell receives a synaptic input during its refractory period then the delay in corresponding input is reduced by dt. A possible biological counterpart of this learning rule is discussed in Gerstner et al. (1996).

Both learning modes are useful for teaching the network to play a certain dynamical pattern. For this purpose, a text file should be prepared in which the order in which the cells must fire is specified. This file can be fed into the network during the runtime. Each cell in this case receives input through the additional external input which triggers cell independently of contribution from other inputs. After sessions of teaching, the network is able to play dynamics which may resemble the pattern used for teaching (see Section 3).

It appeared in preliminary experiments that a network of this type with uniform patterns of synaptic strengths and axonal connections, all of which are excitatory, is not suitable to play prolonged dynamics

in which some parts of network are silent. Instead, the activity either spreads over the entire network, or dies out within tens of milliseconds. But, to discuss binding, one needs to have in the network both spatially bound and unbound patterns of activity, which are stable in a sense. One possibility is to make inhibitory all connections from one part to another one (see Section 2.4). Another possibility is to teach the network to play dynamics with activity in a limited domain. This is possible by means of playing a compulsory pattern in a domain of the network with connections to the remaining part being locked, and with learning switched on. This allows to modify connections in the domain in such a way that it becomes able to support dynamics which in a sense is not very suitable for spreading further after unlocking the locked axons. Both approaches were used here in combination.

3. Results

The network was taught to support the dynamical pattern of sustained activity in which 12 neurons in the middle clusters of the O-shaped region (Fig. 2) are silent. For this purpose, axons propagating spikes from the upper and lower clusters to the middle ones were locked during the teaching sessions. The network was forced to play an external pattern which consists in serial firing of groups of neurons in the upper and lower clusters (see Table 1). In the first teaching session the synaptic weights were modified, in the second one, additionally the propagation delays were modified. Sessions duration was 100 and 200 ms. In the third session, the network was run freely for 100 ms with both learning mechanisms enabled. During the sessions, slow inhibition was low, which is expressed in the value $W = 4$ ms for each cell. Initial state for

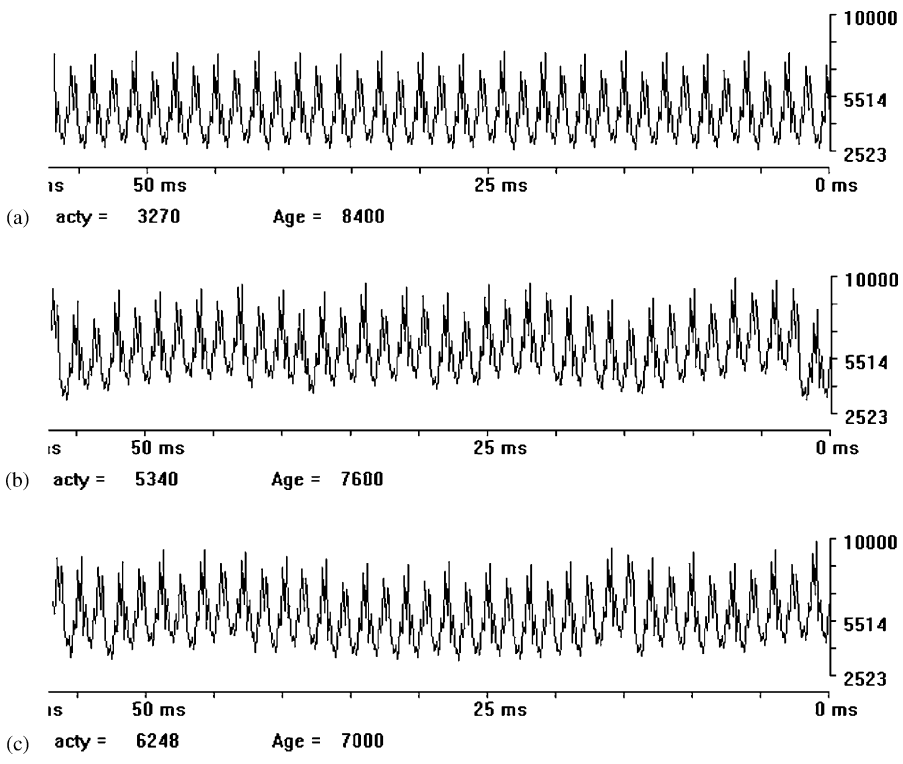

Fig. 3. The network integral activity during free runs with (a), $W = 1$ ms, (b), $W = 4$ ms, and, (c) with W interchanging from 1 to 4 ms and back every 20 ms. In (c) periods 0–20 ms, and 40–60 ms correspond to $W = 4$ ms, period 20–40 ms corresponds to $W = 1$ ms. The integral activity (acty) at any moment of time (age) is calculated as sum of total amounts of excitation stored in each cell and all spikes in axons at this moment of time. Age is displayed in 0.1 ms units. Exact values of age displayed in the panels correspond to point '0 ms' at the horizontal axis. Points to the left correspond to earlier moments. Note periodicity in (a) with period 9 ms.

Fig. 4. (a–c) The individual cells activity during the same periods of free run as in Fig. 3 panels a–c, respectively. The short horizontal bars mark cells refractory period. In the panels, cells are numbered along the vertical axis, single pixel corresponding to a single cell. In the (b) panel, positions of cells #34, #94 and #190 are pointed by arrows, for clarity. In (c) periods 0–20, and 40–60 ms correspond to $W = 4$ ms, periods 20–40, and 60–80 ms correspond to $W = 1$ ms.

any next session was the final state of the previous one.

After the teaching sessions both learning mechanisms were disabled. If one allows the network to run freely after this with the locked axons staying locked, the activity pattern in this run resembles that used for teaching in the following sense. The pattern shown in the Table 1 represents a clockwise rotation of activity around the center of the O-shaped region. In this free run activity, elements of rotation are discriminable as well, even if exact timing of firing deviated from the pattern used for teaching.[2] Also, the network integral activity (see Fig. 3) has oscillations similar to that in the third session of teaching.

But, if the locked axons are made unlocked at the end of the teaching sessions, then the dynamics brings about activity in the middle clusters. Namely, cells in the middle clusters start firing 10 ms after beginning of the run, and the all 12 cells are entrained into firing during next 5 ms. If during this bound activity the inhibition is made high by choosing $W = 1$ ms, the cells in the middle clusters stop firing during first 3 ms, while activity in upper and lower clusters remains stable. The switching between unbound and bound patterns of activity due to changed inhibition is reproducible in the course of running dynamics (Fig. 4). Namely, by setting $W = 1$ ms one gets the middle clusters silent (Fig. 4a and c), and by setting $W = 4$ ms one gets firing

[2] Several teaching protocols were tested preliminary in order to obtain a network which can support sustained firing in a limited domains. In some of them post-teaching activity was quiet similar to that used for teaching, but this similarity deteriorates with time.

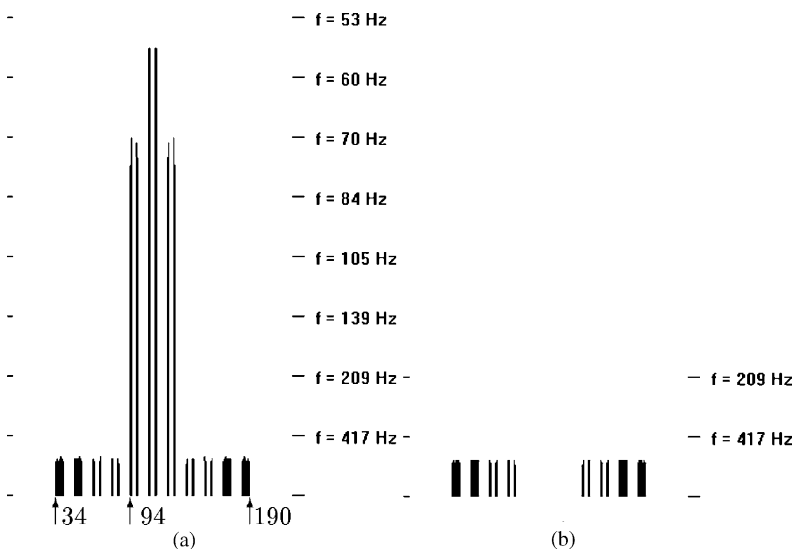

Fig. 5. Interspike intervals for active cells in the network for low (a) and high (b) inhibition. The time interval between the last spike and the previous one is shown for each cell as vertical bar with height proportional to duration of the interval; its inversed value is specified in Hz. a and b correspond to $W = 4$ and 1 ms, respectively. The cells are numbered along the horizontal axis, single pixel corresponding to a single cell. Positions of cells #34, #94 and #190 are pointed by arrows for clarity. The absence of bar in some position means that corresponding to this position, neuron was silent during period of observation.

in the middle clusters (Fig. 4b and c). In the Fig. 5, the time interval between most recent spike and the previous one is shown for each cell as vertical bar, its length proportional to the interval. The absence of bar at some place means that the cell corresponding to this place was silent during time of observation. Thus, data from Fig. 5 as well demonstrate that for high inhibition the domain of activity is unbound (disconnected), while for low inhibition the domain becomes bound (connected) due to activity in the middle clusters.

4. Conclusions and discussion

The purpose of this paper was to discuss the binding phenomenon and its inhibition-dependence in a simple model neural network. The network is composed of cells of special type—the binding neurons. Slow inhibition in the network is expressed in terms of binding window in each cell, as it was discussed earlier (Vidybida, 1998). The binding neuron is chosen here as it has transparent information-processing functionality and is simple for programming. This model is derived from results obtained numerically for the Hodgkin–Huxley-type neuron (Vidybida, 1996). The dynamical features observed here, depend equally on the individual cell construction and the connectivity pattern in the network as well as on the inhibition paradigm adopted. Taking into account that binding neuron comprises in simplified form some features of Hodgkin–Huxley neuron, one can expect that qualitative behavior of this network should remain the same if individual units of the network are replaced by the H–H model, or leaky integrator.

By means of trials and fails, a specific teaching protocol has been found. After applying this protocol, the network becomes able to play two patterns of reverberating dynamics. In the first pattern, the neuronal activity is confined within two spatially disconnected domains. In the second one, the region of activity consists of the two above domains connected by intermediate domains into a bound image. Raising slow inhibition switches from the bound pattern to the disconnected one, while lowering inhibition restores the bound pattern back, Fig. 4. This is interpreted as switching between bound and unbound images by means of slow inhibition.

It is difficult to offer possible physiological implications of the model considered. The paper is aimed to discuss a possible physical mechanism, which may

underlie binding. The binding itself may happen at different levels of activity which may include different number of cells. The case of very large number of cells may allow/require description in terms of continuous media, with individuality of cells washed out. In any case, such dynamical feature as entrainment into firing initially silent parts of network due to convergent stimulation from other parts must be present in a model, because this feature is suggested by physiological observations (see Section 1).

The choice of visually clear images of activity, as in Fig. 2, for the purpose of illustrating binding can be explained as follows. Whether activity in a neuronal population is treated as bound or unbound depends on which device reads out from the population. If it is another neuronal population with specific connection pattern, then two activities which are visually similar, but have a difference discriminable by the reading population, might be classified in the reading population as bound and unbound. As in this work the terminal recipient of activity pattern is visual system of a researcher, the two patterns must be visually interpretable as connected and disconnected ones in order to be able to illustrate binding.

Mechanisms of binding may have different physical nature in different cases. First, it could be of temporal nature (Eckhorn et al., 1988; Engel et al., 1991; Vidybida, 1998), second, it could be mainly of spatial nature, as discussed in Section 1, third, it could be of complex spatio-temporal nature. In this paper, only a spatial variant of binding is discussed, yet the network constructed is suitable to study the mechanisms of all three types. For this purpose, it is necessary to modify the network by means of suitable teaching in such a way, that it becomes able to support dynamical patterns which are bound and unbound in temporal or spatio-temporal sense.

Finally, it should be mentioned that sometime the binding idea is not accepted as being pertinent to information processing (e.g. Reisenhuber and Poggio, 1999). In principle, there are no scientific limitations for deriving all higher brain functions immediately from activities in individual neurons. The binding concept is useful if one wishes to discuss higher functions in terms of intermediate levels of neuronal activity. For this purpose, further elucidation of physical nature of binding might be useful.

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