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Associative memory in a pair of cortical cell groups with reciprocal projections

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Abstract

We examine the functional hypothesis of bidirectional associative memory in a pair of reciprocally projecting cortical cell groups. Our simulation model features two-compartment neurons and synaptic weights formed by Hebbian learning of pattern pairs. After stimulation of a learned memory in one group we recorded the network activation. At high synaptic memory load (0.14 bit/synapse) we varied the number of cells receiving stimulation input (input activity). The network "recalled" patterns by synchronized regular gamma spiking. Stimulated cells also expressed bursts that fascilitated the recall with low input activity. Performance was evaluated for *one-step retrieval* based on monosynaptic transmission expressed after ca. 35 ms, and for *bidirectional retrieval* involving iterative activity propagation. One-step retrieval performed comparably to the technical Willshaw model with small input activity, but worse in other cases. In 80% of the trials with low one-step performance iterative retrieval improved the result. It achieved higher overall performance after recall times of 60–260 ms. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

In a sparse bidirectional associative memory (BAM) with binary neurons it has been investigated whether bidirectionally iterated retrieval can improve upon the

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result of a single retrieval step [9]: While the naive BAM extension of the Willshaw model [14] failed, a modified BAM retrieval scheme was presented with substantially increased performance. The impact of this result with respect to information processing in reciprocally connected cortical cell groups was discussed in [10], but only a rough idea was provided as to how mechanisms of a more realistic neuronal network model could support such a more powerful bidirectional retrieval mode. In a previous simulation study with a two-compartment neuron network we examined the hypothesis that Hebbian learning in a network of cortical cells with high local connectivity can provide an efficient autoassociative memory function [12]. It was shown that the retrieved patterns were coded through coincident single spike events, agreeing with the so-called temporal coding assumption that has been postulated on the basis of recent experiments [3,8,1]. Besides cortical circuits formed by local connectivity, results from anatomical studies suggest the presence of another type of cortical circuits providing a strong internal coupling within a set of excitatory cells: a pair of cell groups that project reciprocally on each other. Such wiring schemes can be expected between cell groups of different cortical layers as well as between cell groups located in different cortical areas. The latter expectation is motivated by the following anatomical findings: (i) the majority of cortico–cortical connections have been reported to be reciprocal [2], and (ii) projections are patchy with patch sizes comparable to the size of cortical columns [6]. To examine possible computational functions of the reciprocal wiring scheme we use a simulation model similar as presented in [12].

2. Methods

In our simulations the behavior of excitatory cortical cells is described by a two-compartment neuron model [7]. This model is a reduced version of a 19-compartment cable model [11], segregating fast currents for sodium spiking into a soma-like compartment and slower calcium and calcium-mediated currents into a dendrite-like compartment.

We studied two reciprocally connected cell groups A and B of 50 cells, each using the same neuronal parameter settings as in [7]. Inhibition in each cell group was modeled by an inhibitory interneuron receiving input from all excitatory cells in the group. To mimique the effect of a population of interneurons it had a threshold-linear rate function and inhibited all excitatory cells with equal weights on their soma-compartment. Inhibitory synapses employed a fast GABA-ergic conductance change.

The excitatory connection strengths between the groups were modified by binary Hebbian learning of pairs of 0/1-patterns containing $k = 10$ ones at random positions in each cell group [12]. In this study we examined a network with 10 pattern pairs stored. The synaptic saturation is 0.3 which is approximately the maximum load possible in a Willshaw network of this size. Excitatory synapses terminated on the dendritic compartment and activated AMPA- and NMDA-currents [7]. Since memory patterns were small, EPSP-amplitudes in response to a single spike had to be scaled to relatively high values of a few mV (compare [4]). The inhibitory interneurons had a graded output, modeling the average firing rate in a pool of interneurons that control the total activity in their neighborhood [5,13].

During a retrieval experiment a subset of cells in group A with overlap to one memory pattern received depolarizing dendritic input. Contrasting the experiments in [12], the stimulation (Poisson processes) was restricted to a period of 25 ms, after that the input was turned off. We conducted experiments using stimulation subsets of different sizes and recorded the network activity over a 500 ms interval after stimulus onset. Although the variation in size covered a large range (between 2 and 20 stimulated cells) there was no external adjustment of parameters governing network inhibition. The model was completely symmetrical with respect to the two cell groups. No distinction was made between cell group A receiving stimulation input and cell group B receiving no direct stimulation, instead all neuron and network parameters were set to exactly the same values.

To judge retrieval performance we compared the activity configuration in cell group B with the memory pattern addressed by stimulation. To measure similarity we use the transinformation between network state and the memory pattern normalized by the information content of the latter (in our case 36 bits). This quantity will be referred to as retrieval quality or simply "quality" in the remainder.

3. Results

About 25–40 ms after stimulus onset the first synchronized wave of induced activity occurred in cell group B. Subsequently, the activity propagated back and forth through the reciprocal connections, influencing the activity configurations of the rhythmic synchronized spike events in both cell groups. The spike frequencies were in the gamma band (30–90 Hz). Although we observed spike synchronization within each cell group we did not find a phase locking between the groups. In the absence of stimulation we observed regular spiking of the neurons. During stimulation the neurons receiving the afferent input showed the tendency to burst. This tendency increased with decreasing size of the stimulated population (Fig. 1).

To judge the performance of the fastest possible response (we call this one-step retrieval since only monosynaptic activity propagation to cell group B is involved) we determined the quality maximum in the first wave of activity. To monitor the results provided by iterative activity flow between the cell groups (the bidirectional retrieval mode) we also detected the quality maximum over the whole recording sequence. The following figure shows the experimental results resolved for different stimulation conditions.

Diagrams (a) and (c) display the measured quality values. A quality equal to one corresponds to perfect retrieval. At the memory load examined it translates to a synaptic storage capacity of $0.295/2 = 0.15$ bit/synapse. The divisor of two is due to the fact that bidirectional transmission requires two biological synapses. Diagram (a) compares the first quality maximum with the performance of the Willshaw model (a feed-forward network with binary synapses) at the same memory load. The curve is computed for constant activity threshold setting using the theory from [9]. The fact that the quality

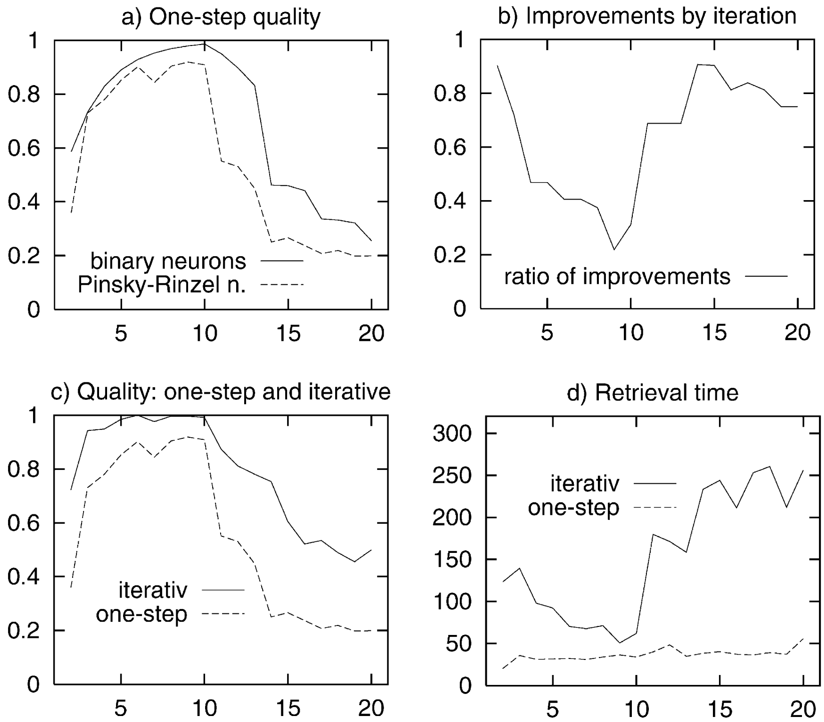

Fig. 1. Experimental results: The x-axes of the diagrams label the input activity, i.e., the number of cells that receive stimulation currents. At an input activity of ten the stimulation pattern was identical to one of the stored patterns, at lower or higher activities it deviated by miss or add errors, respectively. The curves show mean values of measured quantities averaged over 32 simulation runs.

curves stay somewhat below one indicates that load in both networks is near the maximum. The biological model is slightly worse (with a maximum capacity of $0.27/2 = 0.14$ bit/synapse), but at low input activities both performances are similar. However, for large input activities the biological model performance decays very rapidly. The question underlying diagram (b) is whether bidirectional activation cycles in the network can improve retrieval qualitity. In fact, for very small as well as in the entire range of high input activity the quality maximum is only computed by iterative retrieval. The diagrams (c) and (d) compare the qualities and retrieval times of one-step and iterative retrieval in the Pinsky–Rinzel neuron network: The iterative retrieval performs better in all cases. Most significantly, the inability of one-step retrieval to cope with high activity input can be significantly improved by iteration.

4. Conclusions

This paper investigated in simulation experiments with two-compartment neurons whether BAM can be a functional concept for reciprocally connected cortical structures. The experiments showed that robust associative completion of pattern pairs is possible in a pair of cell groups densely and reciprocally connected by synapses with Hebbian plasticity. As it turns out, this function does not even require the presence of local Hebbian connections. This computational function is robust against high deviations between stimulus patterns and memories to be recalled. The realistic neurons support this robustness by their tendency to burst in cases where the set of stimulated cells is small.

We evaluated the associative memory function provided by the first response occurring after 25–40 ms (in the cell group receiving no direct stimulation input) and after an iterative activity propagation process using the reciprocal connections. The first response performance was compared with the Willshaw model with constant activity threshold setting. For small sizes of input activity the performance is comparable, for large sizes the first response retrieval performs worse. In this biologically important case with spurious input activity bidirectional reverberation improved the retrieval result in roughly 80% of the simulation runs. Over the whole range of used stimuli, bidirectional retrieval yields an improved mean performance. For large input activities it not only outperforms one-step retrieval but even the Willshaw model. However, the mean retrieval time is prolonged to 60–260 ms depending on input activity. Since parameter settings in both cell groups were identical, the recall operation has no preference direction, i.e., the different roles of the cell groups are entirely determined by afferences.

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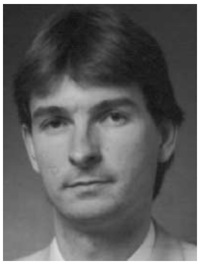
Thomas Wennekers studied Physics at the University of Düsseldorf, where he graduated in 1991. Afterwards he was a Ph.D. student at the C. & O. Vogt-Institute of Brain Research and Neuroanatomy in Düsseldorf, and—since 1992 — at the Department of Neural Information Processing in Ulm, where he received a Ph.D. in computer science in 1998. He currently is Research Scientist at the Max-Planck-Institute for Mathematics in the Sciences in Leipzig. His research interests are computational neuroscience and brain theory.



Friedrich T. Sommer graduated in Physics at University of Tübingen and received 1993 his Ph.D. from Düsseldorf University. After a postdoc time at University of Ulm he became in 1995 research associate at the Institutes of Medical Psychology and Neuroradiology in Tübingen. In 1997 he was awarded a DFG fellowship. In 1998 he was visiting scientist at MIT. Since 1999 he is principal investigator at University of Ulm leading a project developing analysis methods for functional neuroimaging (fMRI). Research interests also include analysis and optimization of formal associative memories, and large scale models of cortical activation.