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LOW SPIKING RATES IN A NETWORK WITH OVERLAPPING ASSEMBLIES

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Introduction

In a recurrent artificial neural network (ANN) of the Hopfield type [1] the units are generally in either of the two extreme states, fully active or inactive. Given that the instantaneous firing rates of nerve cells, or local groups of such cells, are analogous to activity levels of the ANN units, this pattern of activity can be compared to experimental data. From experimental *in vivo* recordings it is clear that cortical pyramidal cells rarely operate at high frequencies (200–300 Hz), but rather at lower levels, *e.g.* 20–60 Hz [2]. The discrepancy in rates has been one of the strongest arguments against attractor network models of cortical associative memory previously put forward, see *e.g.* [3], [4] and [5].

Several authors have addressed this problem and proposed mechanisms for obtaining low activity levels in attractor ANNs, see *e.g.* [6]. The work presented here is a continuation of a recent study [7] where low firing rates in a population of mutually connected pyramidal cells were produced by introducing strongly saturating synapses. When the effect of a neuromodulator affecting the adaptation was simulated, after-activity could be produced. Here we show that this low rate is also possible in a network were overlapping patterns are stored. The network shows pattern completion, noise tolerance and rivalry as in earlier studies [3]. The "reaction times" for these processes are short as before.

The Cell and Network Model

In this study we have used the general purpose simulator, SWIM, intended for numerical simulation of networks of biologically realistic model neurons. Details of the mathematical model used in SWIM can be found in [8, 9] and parameter values used in [7].

The excitatory regularly spiking type cell, RS, is intended to simulate a neocortical pyramidal cell [10]. It could represent *e.g.* a cell of lamina II/III. To separate synaptic inputs of different origin there are three dendritic compartments for the apikal dendrite and one for the basal dendrite. The soma diameter is sampled from a normal distribution with a mean of $21\mu m$.

For the fast spiking inhibitory interneuron, FS, much less data is available [10]. Essentially it is a non-adapting, fast spiking small cell with a small dendritic tree. The soma diameter is sampled from a normal distribution with a mean of $7\mu m$.

The conductance of the Ca-dependent K channel may be affected by several monoamine neuromodulators as well as by acetylcholine [11], thereby changing the adaptation properties of the cell. To model the influence of the modulator, the conductance through the Ca-dependent K channels was multiplied by a factor (KCa) in the range 0 to 1 [7].

The model synapses used here are described in [7]. The excitatory RS-RS and RS-FS glutamate synapse is of a mixed kainate/AMPA and NMDA type with equally large peak amplitude postsynaptic potentials (PSP) for each type alone. The inhibitory FS-RS synapse is assumed to use GABA (or possibly glycine). The synapses are saturating corresponding to a full saturation of the postsynaptic receptor pool by one presynaptic activation [7]. With the saturating synapses the spike rates are relatively low also when an assembly is fully active.

The simulated network was comprised of fifty RS and fifty FS-cells. It can be seen as composed of fifty pairs with one excitatory cell and one inhibitory interneuron each [3], fig. 1. The interneuron receives input from excitatory cells in other pairs and inhibits its companion excitatory cell. The RS-RS synapse was located on the medial apikal compartment and the RS-FS synapse on the dendritic compartment. The FS-RS synapse was placed on the soma. Values for synaptic strengths were adopted from a recurrent Bayesian ANN [12] trained with 8 random patterns with 8 active units in each. Pairs of patterns shared between 0 and 3 units. The Bayesian learning rule produced excitatory synapses within the patterns and inhibitory ones between them.

Simulation Results

The simulations were made on a DECsystem 5000/200 UNIX workstation. A time step of $50\mu s$ was used. In all network simulations the system was run for 1 s simulated time before the experiment started (to reach "steady state" conditions). With a stimulation we will mean a current injection for 50 ms to the soma of a pyramidal cell.

The mechanisms behind low-rate after-activity in this model has been analyzed in [7]. In a recurrent network like this, an equilibrium situation is at hand when the firing frequency of the cells, f_{out}, equals the firing frequency, f_{in}, required to drive the cells to produce this output. Our neocortical pyramidal cell gives a "log shaped" input-output relation, which intersects the equilibrium line $f_{in} = f_{out}$ once. This is where stationary fix point activity, in the absence of any external input, may occur. To study the influence of different synaptic properties, we carried out a simulation in which an isolated postsynaptic cell was driven by a number of noisy synaptic inputs. This setup allowed us to determine the shape of the $f_{in} - f_{out}$ curve and the point of intersection with the $f_{in} = f_{out}$ line. With summing synapses the stable intersection point was at a

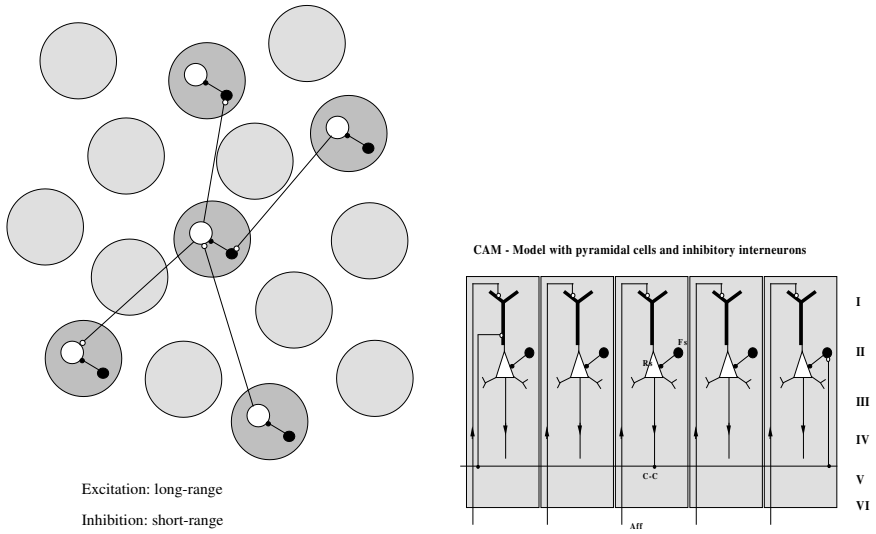

Figure 1: Left: Five pairs belonging to three different assemblies, with the three lower ones belonging to the same assembly. Right: Synaptic connectivity for a pair (middle) connecting to one pair in the same assembly (left), and a different assembly (right).

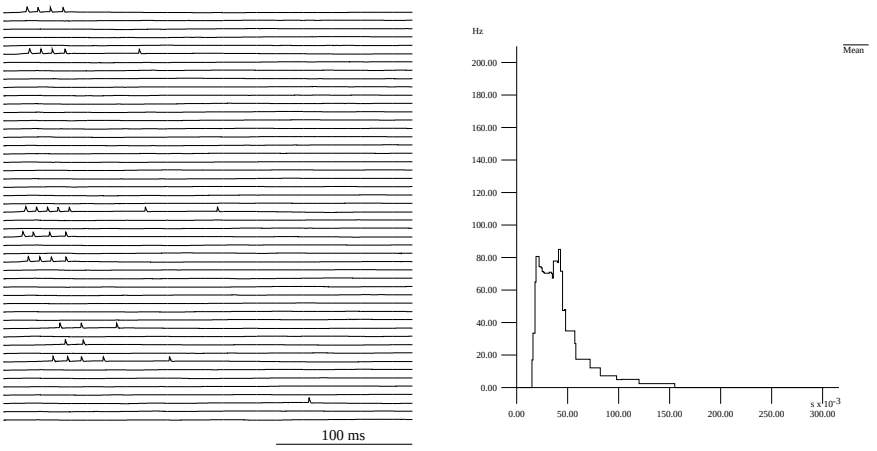

Figure 2: Left: Soma membrane potential for the 50 RS-cells. Simulated time 300 ms. Active assembly consists of cells 1, 6, 25, 28, 31, 39, 41, 43 from top. Current injection for 50 ms to the first six of these. Right: Mean frequency in the active assembly.

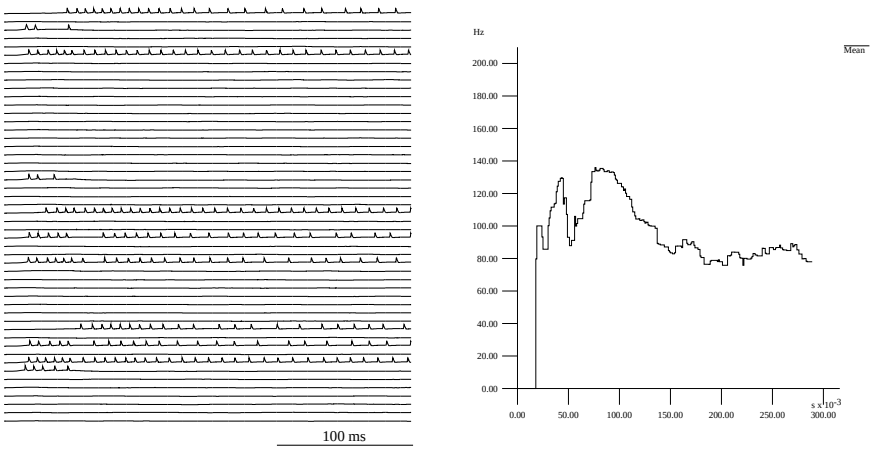

Figure 3: Pattern completion and noise tolerance. Left: Soma membrane potential for the RS-cells. Simulated time 300 ms. Stimulated cells are 3, 6, 21, 28, 31, 41, 43, 44 from top. Active assembly consists of cells 1, 6, 25, 28, 31, 39, 41, 43 from top. Right: Mean frequency in the active assembly.

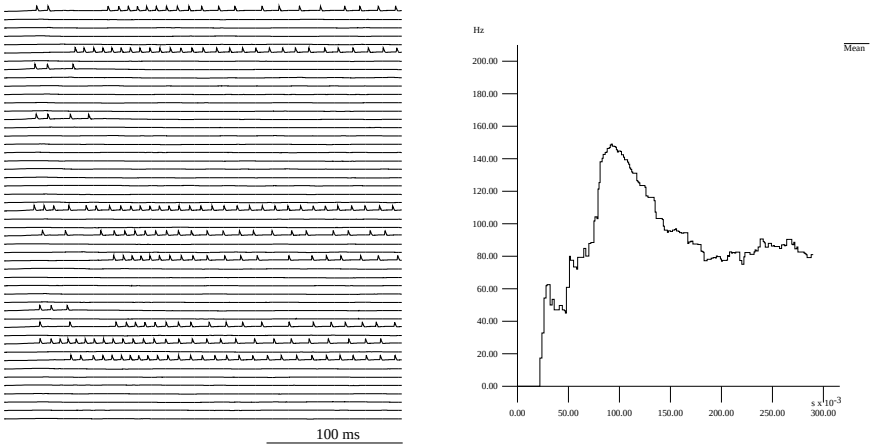

Figure 4: Rivalry leading to one winning assembly. Left: Soma membrane potential for the RS-cells. Simulated time 300 ms. Stimulated cells in one of the assemblies are 1, 25, 28, 41, 43 and in the other 8, 14, 39, all counted from top. Right: Mean frequency in the winning assembly.

frequency value of some 110 Hz. With saturating synapses the point may be significantly lower, about 70 Hz, the precise value being dependent on synaptic strength and closing time constants. It is the time constant of the synapse that affects the slope of the input-output curve and gives this low intersection point.

When a majority of the cells in an assembly are stimulated they will activate the remaining non-stimulated assembly members, fig.2 (*pattern completion*). Too few (one or two) stimulated cells results in no secondary activation (*noise tolerance*).

If neuromodulator application of *e.g.* serotonin is simulated the burst will continue with *low rate* after-activity after stimulation has ceased, fig.3. Pattern completion is here stronger and initial frequency somewhat larger than without modulator. The minimum rate of the after-activity is dependent on assembly size. With the small assembly here it is about 80 Hz, but with a larger size of 200 cells about 55 Hz [7]. Despite that all assemblies have overlap with some other assemblies, the activity is confined to one assembly at a time and is not spreading due to lateral inhibition (*pattern separation*). It is necessary to tolerate an overlap as this is a requirement for acceptable storage capacity (number of stored and reliably recalled patterns).

In figure 3 five cells in one assembly and three random cells were stimulated. The randomly activated cells are suppressed (*noise tolerance)*. The three missing cells in the assembly are completed (pattern completion). The time required to complete a pattern is relatively short, 40–100 ms, fig.3, 4. This corresponds to some 3–10 spikes per cell. A *short "reaction time"* is an important feature of these recurrent networks. As discussed in [3] the network can give a stable pattern within the time suggested by psychophysical reaction time experiments.

When parts of two patterns are stimulated simultaneously, the lateral inhibition between assemblies leads to *competition and rivalry* phenomena, fig.4. As before, modulator application enables after-activity. A winning pattern shuts down the other ones and completes its missing members and shows low rate after-activity. Also here reaction times are relatively short.

Conclusion

In this study we show that low rate sustained after-activity can be obtained in a simulated network with overlapping assemblies. The low rate is achieved by assuming that the synapses in the network are of a saturating type. The associative memory operations remain intact: After-activity is produced when the application of a monoamine neuromodulator is simulated. The network gives pattern completion of incomplete input and shows noise tolerance. Despite the overlap, the activity of one assembly does not spread to others. The time to reach a complete pattern, the "reaction time", is 40–100 ms, *i.e.* only some 3–10 spikes per cell. When parts of two patterns are presented simultaneously a rivalry process can lead to full completion of one pattern and suppression of the other.

Acknowledgments

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References

[1] Hopfield, J., "Neural networks and physical systems with emergent collective computational abilities," Proc. Natl. Acad. Sci. USA, vol. 79, 1982, pp. 2554–2558.

[2] Abeles, M., Vaadia, E., and Bergman, H., "Firing patterns of single units in the prefrontal cortex and neural network models," Network, vol. 1, 1990, pp. 13–25.

[3] Lansner, A. and Fransén, E., "Modelling Hebbian cell assemblies comprised of cortical neurons," Network, vol. 3, 1992, pp. 105–119.

[4] Hasselmo, M. E., Anderson, B. P., and Bower, J. M., "Cholinergic modulation of cortical associative memory function," J. Neurophysiol., vol. 67, 1992, pp. 1230–1246.

[5] Amit, D. J., Evans, M. R., and Abeles, M., "Attractor neural networks with biological probe records," Network, vol. 1, 1990, pp. 381–405.

[6] Amit, D. J. and Tsodyks, M. V., "Quantitative study of attractor neural network retrieving at low spike rates: I. substrate–spikes, rates and neuronal gain," Network, vol. 2, 1991, pp. 259–273.

[7] Fransén, E. and Lansner, A., "Low spiking rates in a population of mutually exciting pyramidal cells," 1994. (Submitted).

[8] Wallén, P., Ekeberg, Ö., Lansner, A., Brodin, L., Tråvén, H., and Grillner, S., "A computer-based model for realistic simulations of neural networks. II: The segmental network generating locomotor rhythmicity in the lamprey," J. Neurophysiol., vol. 68, 1992, pp. 1939–1950.

[9] Tråvén, H., Brodin, L., Lansner, A., Ekeberg, Ö., Wallén, P., and Grillner, S., "Computer simulations of NMDA and non-NMDA receptor-mediated synaptic drive — sensory and supraspinal modulation of neurons and small networks," J. Neurophysiol., vol. 70, 1993, pp. 695–709.

[10] McCormick, D. A., Connors, B. W., and Lighthall, J. W., "Comparative electrophysiology of pyramidal and sparsely spiny stellate neurons of the neocortex," J. Neurophysiol., vol. 54, no. 4, 1985, pp. 782–806.

[11] Nicoll, R. A., Malenka, R. C., and Kauer, J. A., "Functional comparison of neurotransmitter receptor subtypes in mammalian central nervous system," Physiol. Rev., vol. 70, no. 2, 1990, pp. 513–565.

[12] Lansner, A. and Ekeberg, Ö., "A one-layer feedback, artificial neural network with a Bayesian learning rule," Int. J. Neural Systems, vol. 1, no. 1, 1989, pp. 77–87.