Synfire chains with conductance-based neurons: internal timing and coordination with timed input

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Abstract

Synfire chain models store and retrieve hetero-associative sequences of firing patterns, thereby explaining basic aspects of the neuronal processing of temporal information. Existing models were based on McCulloch-Pitts or integrate & fire neurons and therefore neglect most physiological properties of real neurons. Here, we study a model with conductance-based neurons and both, hetero- and auto-associative couplings which support synfire vs. attractor activity, respectively. We show that the speed of synfire recall is influenced by slow neuronal variables and is sensitive to the ratio between auto- and heteroassociative synapses while quite insensitive to background activity. We then propose a bidirectional synfire model where the duration of states in a synfire chain is variable and can be coordinated by a timed but otherwise unspecific external signal.

Key words: Associative memory, sequence memory, synfire chains, timing of sequences, temporal neural processing.

1 Introduction

Learning and reproduction of temporal sequences of events seems one of the major tasks for the brain. Classical neural models for this task are synfire chain models [11,1] in which temporal sequences of patterns (synfire chains) are learned by storing associations between subsequent states in Hebbian synapses.

Another classical neural model is regaining influence in an ongoing debate about the relationsip between processing of temporal information and persistent neural activity that is observed in various brain regions: Attractor memories with auto-associative synaptic projections [8,4]. An early example is the pump of thought model by Braitenberg [3], which is basically an attractor memory network with dynamic threshold control.

In this study we focus on a model that combines principles of synfire and attractor models, a combination proposed before with formal neurons [5]. Existing synfire chain models with spiking neurons used units on the integrate & fire level. Here we use a simulation model with biologically more realistic conductance-based neurons. We investigate two network architectures, a single pool and a bidirectional network. Two items will be addressed. First we ask how the dynamics of synfire chains with conductance-based neurons depends on basic model parameters, such as the ratio of the strengths of hetero- and auto-associative projections or the level of background activity. Second, we propose a bidirectional model in which the timing of synfire chains can be coordinated with sensory inputs and other brain activity.

2 Methods

Compared to earlier synfire chain models with spiking neurons [2,10,9], our model has two main modifications. We use biophysically matched two-compartment neurons [6] and we include auto-associative synapses. The dendritic neuron compartment includes slow variables for the calcium level and calcium level dependent ion channels. The neurons are coupled by a synaptic matrix that resulted from a clipped Hebbian learning process. For a detailed description of this modeling approach, see [7]. The synfire chains used during synaptic learning consist of sparse random patterns.

We study two network architectures. A *single-pool network* of 200 fully connected neurons and a *bidirectional network* of two pools, 100 cells each, with auto-associative projections within the pools and heteroassociative projections between the pools. All neurons in a pool are connected to a single gradual neuron network mediating inhibition via GABA-A receptors.

The synfire chain used in the training of the single-pool network consisted of 10 patterns, each pattern containing 10 active neurons. In the bidirectional network the synfire chain included 18 patterns (9 in each pool) with 10 active neurons each. In the auto-associative connections within each pool 10 patterns were stored leaving in each pool one pattern that is not connected to the synfire chain.

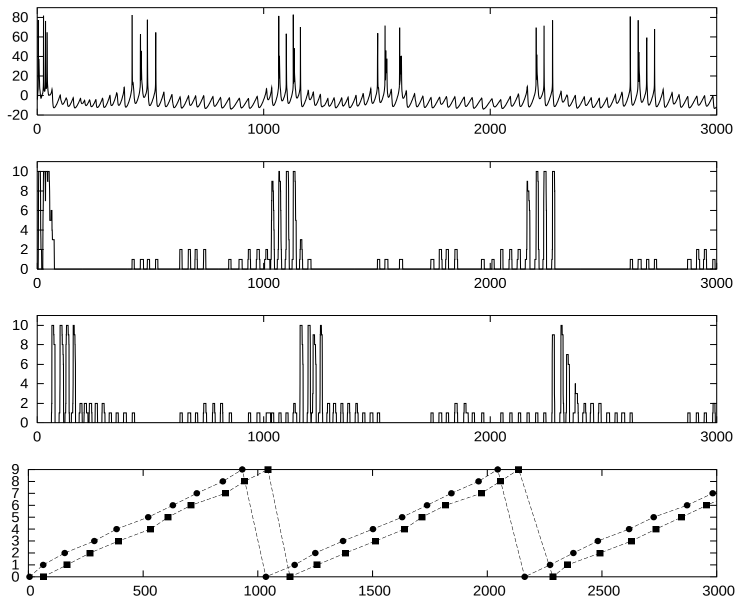

Fig. 1. *The upper trace displays the soma potential of one neuron after initiation of activity in pattern 0. The displayed neuron belongs to two patterns, # 0 and # 4. Second and third frames show pattern overlaps for patterns 0 and 1, respectively. The lowest diagram shows the starts (circles) and terminations (squares) of associative spindles for the patterns in the chain.*

3 Results

3.1 Single-pool network

Figure 1 summarizes the neural activity processes in the single-pool network with auto- and hetero-associative couplings of equal strength. There is rhythmic activity in the beta- to gamma-range, and repetiting spindle activity on a long scale. The middle traces show that patterns are retrieved in associative spindles consisting of brief excitatory-inhibitory activation cycles, cf. [7]. Spindles reveal a varying number of individual retrieval events (cf. Figs. 2 and 3). Note that spindles of different patterns can somewhat overlap in time.

In a first series of experiments we investigated how a shift in the ratio between auto- and hetero-associative connection strength impacts the timing of sequence retrieval. One can see in figure 2 that the recall speed of sequences can be changed by several orders of magnitude. For ratios near fifty percent the pace of sequence recall reaches a few hundreds of milliseconds (per stored synfire pattern).

A second series of experiments assessed how unspecific background activation can affect the timing of sequence recall. The experiments used the same

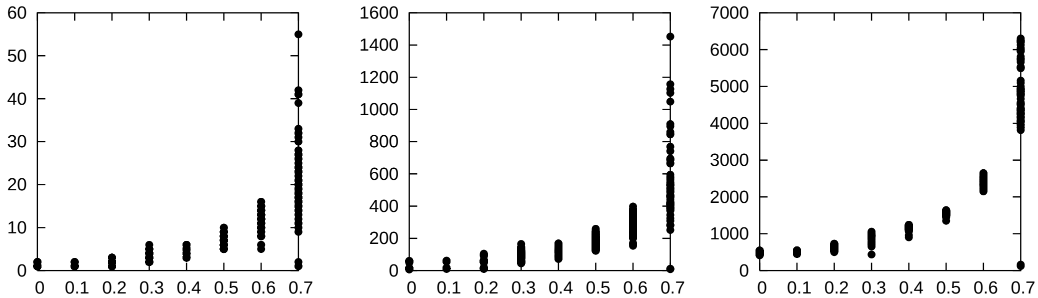

Fig. 2. *Influence of auto-associative connections on the timing of sequence recall. The total excitatory efficacy (auto + hetero) is kept at a fixed level and the x-axes display the fraction of the auto-associative connections. Left: Number of retrieval cycles per associative spindle. Middle: Duration of spindles in ms. Right: Total time through synfire chain consisting of 10 patterns.*

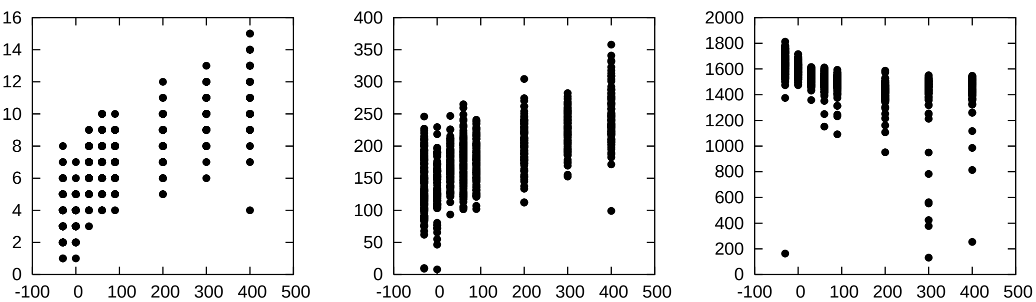

Fig. 3. *Impact of unspecific background activity on sequence retrieval. The x-axes display the level of background current into the somatic compartment of the PR-cells. The y-axes display the same time quantities as in figure 2. Symbols represent individual measurements of the displyed quantities in repeated simulations.*

parameters as in figure 2 but now with a fixed ratio between auto- and hetero-assocative connections of 0.5. The results are displayed in figure 3. Interestingly, the spindle duration (middle plot) and the number of retrieval events per spindle (left plot) increase only moderatly with background activity and the speed of sequence retrieval even slightly decreases (right plot). This is, because associative spindles of subsequent patterns increasingly overlap with growing background activty. As a consequence, a wide speed control of behavioral sequences would hardly be possible this way. The very short cycle times in the right plot (for instance at Is=300) result from retrieval errors that cause leaps in the sequence.

3.2 Bidirectional network

A question we wanted to address in this study is how the timing of sequence recall in a brain region can be influenced by neuronal input for the purpose of coordinating dynamic memory recall with other processes in the brain or in the environment. We saw in section 3.1 that background activity has no strong systematic effect on the synfire chain dynamics, whereas the ratio of auto-associative connections has a strong effect. Higher auto-associative couplings prolong the persistence of patterns. A similar effect would be achieved by an input that specifically stimulates currently active patterns. However, to use such input for timing would make the internal memory redundant since the external source would have to memorize the whole pattern sequence as well.

An idea how sequence speed could be controlled by input that does not stimulate the sequence itself will be demonstrated in an experiment with the bidirectional network. A control input is applied to one pool and stimulates the stored pattern that is unconnected to the synfire chain. The simulation sweep in figure 4 shows the time courses of the control input and the overlaps with stored patterns (for patterns in the pool not receiving control input). Without control input, the bidirectional recall of synfire chains is similar as in the single-pool network. As control input is applied at the end of the first cycle, the current pattern (# 9) is held as long as the control input lasts, much longer than the previous spindles following the intrinsic dynamics. After release of control input the synfire chain resumes and switches to pattern 1 which is then again prolonged by control input.

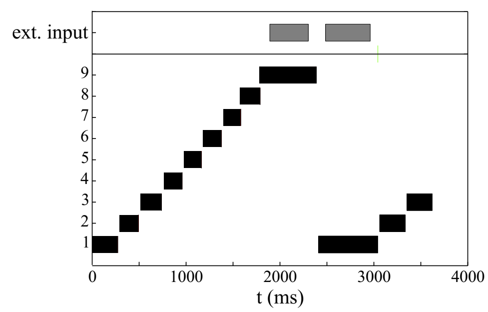

Fig. 4. *Synfire retrieval in the bidirectional network and the influence of input. The x-axis displays time. Black horizontal bars visualize the onset and duration of patterns retrieved in the first pool. The different patterns in the synfire chain are labeled on the y-axis. The upper grey bars visualize the time trace of the control input applied to the second pool.*

4 Conclusion

By simulation experiments we have investigated the dynamics of synfire chains in networks of biologically realistic conductance-based neurons. We found that while the intrinsic dynamics of synfire chains is insensitive to background activity it is strongly influenced by the strength of auto-associative synapses. The latter can slow down the switching between states and create persistent activity up to few hundreds of milliseconds, in a range that is relevant for temporal processing in behavior (syllable rhythm, voluntary movements, etc.).

Further we have proposed a bidirectional network model for sequence memory in reciprocally connected brain regions. In this model sequences are implemented in an interleaved fashion such that associations between two states in one region are mediated by states in the other region. In such a model the timing of sequences can be controlled by an unspecific input. If a particular synfire chain is active, state transitions can be halted by stimulating in one region a state that does not belong to the synfire chain. After input release the transition in the synfire chains resumes at the intrinsic pace. Thus, the pacing of an active synfire chain can be controlled by a timing signal, stemming either from from sensory input (sequence recognition) or from any structure in the brain responsible for timing (sequence execution).

References

[1] M. Abeles. *Corticonics: Neural Circuits of the Cerebral Cortex.* Cambridge University Press, Cambridge, UK, 1991.

[2] E. Bienenstock. A model of neocortex. *Network*, 6:179–224, 1994.

[3] Braitenberg. Cell assemblies in the cerebral cortex. In R. Heim and G. Palm, editors, *Theoretical approaches to complex systems*, pages 171–188. Springer, 1978.

[4] J. J. Hopfield. Neural networks and physical systems with emergent collectiv computational abilities. *Proceedings of the National Acadamy of Science (USA)*, 79:2554–2558, April 1982.

[5] D. Horn and M. Usher. Neural networks with dynamical thresholds. *Physical Review A*, 40:1036–1044, 1989.

[6] P. F. Pinsky and J. Rinzel. Intrinsic and network rhythmogenesis in a reduced Traub model for CA3 neurons. *Journal of Computational Neuroscience*, 1:39–60, 1994.

[7] F. T. Sommer and T. Wennekers. Modeling studies on the computational function of fast temporal structure in cortical circuit activity. *Journal of Physiology - Paris*, 94(5/6):473–488, 2000.

[8] W. K. Taylor. Electrical simulation of some nervous system functional activities. In *Information Theory, Vol. 3*, pages 314–328. Butterworths, 1956.

[9] T. Wennekers. Dynamics of spatio-temporal patterns in associative networks of spiking neurons. *Neurocomputing*, 32:597–602, 2000.

[10] T. Wennekers and G. Palm. Controlling the speed of synfire chains. *Lecture Notes in Computer Science*, 1112:451–456, 1996.

[11] W. A. Wickelgren. Context-sensitive coding, associative memory and serial order in (speech) behavior. *Psychological Review*, 76:1–15, 1969.