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

Friedrich T. Sommer [a] Thomas Wennekers [b]

[a]*Redwood Neuroscience Institute*
1010 El Camino Real, Menlo Park, CA 94025, USA
email: fsommer@rni.org

[b]*Plymouth Institute of Neuroscience*
Centre for Theoretical and Computational Neuroscience
University of Plymouth, PL4 8AA Plymouth, UK
email: thomas.wennekers@plymouth.ac.uk

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.

Recently, another classical neural model has regained influence in a 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.

Earlier synfire chain models with spiking neurons [2,10,9] used units on the integrate & fire level and did not incorporate attractor memory. Here we investigate the combination of synfire chains and attractor memories [5] in biologically realistic neuronal networks with conductance-based neurons. We study two different network architectures, a single pool and a bidirectional network, see figure 1. First we ask how the characteristic time constants of synfire chains in the model depends on its basic 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

Our simulation model contains biophysically matched two-compartment neurons –Pinsky-Rinzel (PR) neurons– with a dendritic compartment including slow variables for the calcium level and calcium level dependent ion channels [6]. Pattern associations are stored in synapses with (clipped) Hebbian learning. For a detailed description of this modeling approach, see [7]. The synfire chains used for learning are sequences of sparse random patterns. The learned associations include transitions between patterns (hetero-associations) *and* auto-associative memory.
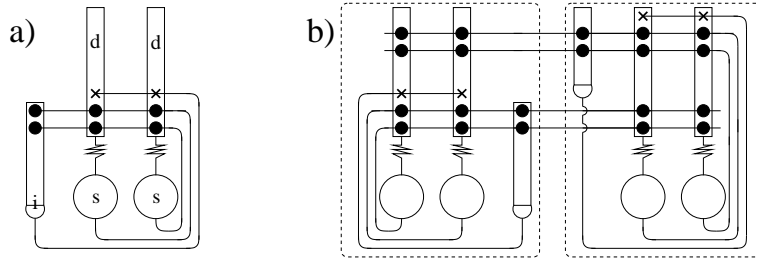

Fig. 1. *Network architectures.* **a)** *Single-pool network: (s,d) soma/dendritic compartment of excitatory cells, (i) inhibitory neuron, (●) excitatory Hebb synapse, (×) inhibitory synapse.* **b)** *Bidirectional network: each pool (within a dashed boundary) has individual inhibition.*

The network architectures we studied are depicted in figure 1. The *single-pool network* contained 200 fully connected neurons and the *bidirectional network*

100 cells in each pool. Inhibition within a pool through GABA-A receptors is modeled by a single gradual neuron. The synfire chain used for training of the single-pool network consisted of 10 patterns, each pattern with 10 active neurons. In the bidirectional network the synfire chain included 18 of these patterns with pattern transitions stored in the connections between the pools. Thus the stored sequence involved both patches in an interleaved fashion (9 patterns in each pool). Each pool contained an additional pattern stored in the auto-associative connections but unconnected to the synfire chain.

3   Results

Single-pool network: Figure 2 summarizes the 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. Overlaps with learned patterns b) and c) show that retrieval takes place through associative spindles formed by brief excitatory-inhibitory activation cycles, cf. [7]. Spindles reveal a varying number of individual retrieval events (cf. Figs. 3 and 4). Note that spindles of different patterns can somewhat overlap in time.
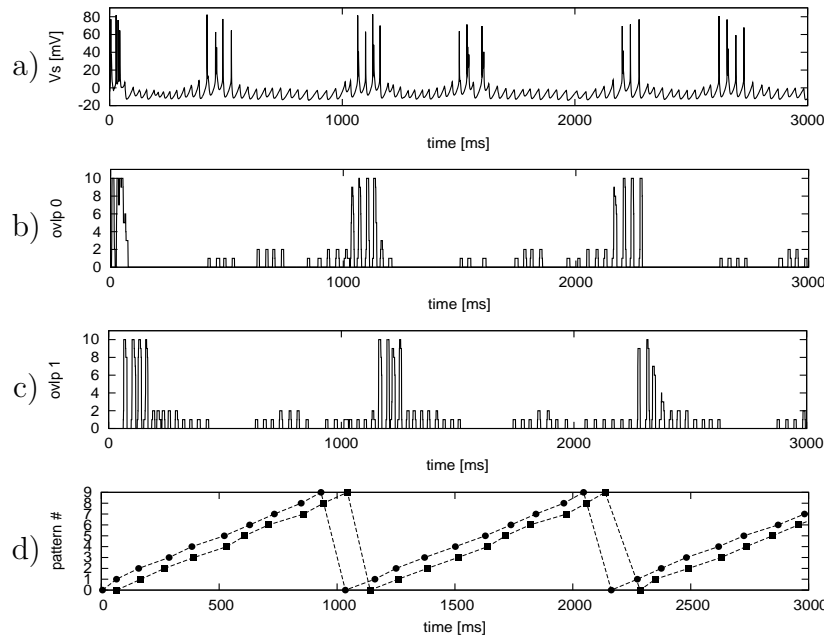

Fig. 2. **a)** *soma potential (mV) of a neuron (participating in pattern #0 and # 4) after initiation of activity in pattern #0.* **b)**, **c)** *overlaps for pattern #0 and #1 (# of active neurons common with a pattern). d) onsets (circles) and terminations (squares) of associative spindles for the patterns in the chain (#0 – #9).*

In a first series of experiments we investigated how a shift in the ratio be-

3

tween auto- and hetero-associative connection strength impacts the timing of sequence retrieval. Figure 3 shows that the recall speed of sequences can be changed by several orders of magnitude. For ratios near fifty percent the switching pace between patterns reaches a few hundreds of milliseconds.
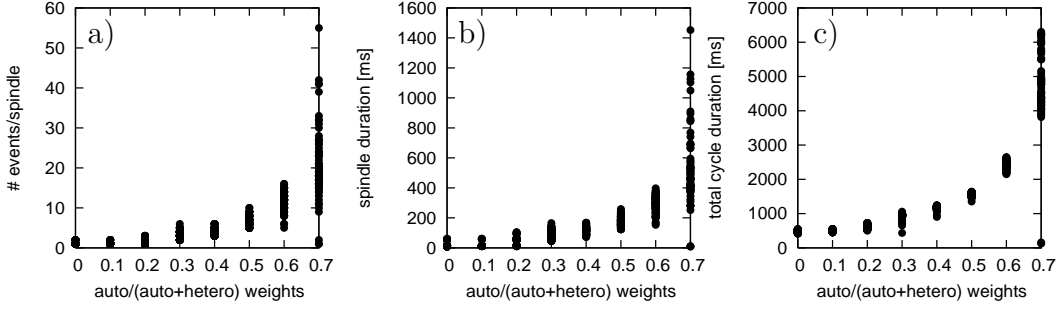

Fig. 3. *Auto-associative connections influence the timing of sequences.* **a)** *Number of retrieval cycles per associative spindle.* **b)** *Duration of spindles.* **c)** *Duration of synfire chain consisting of 10 patterns. The x-axes display the fraction of auto-associative efficacy. The total excitatory efficacy (auto + hetero) is constant.*

A second series of experiments assessed how unspecific background activation can affect the timing of sequence recall. The experiments used the same parameters as in figure 3 but now with a fixed ratio between auto- and hetero-assocative connections of 0.5. The quite moderate influence of background activity is displayed in figure 4. Interestingly, the spindle duration (b) and the number of retrieval events per spindle (a) increase with background activity whereas the total duration of sequences decreases (c). (The very short cycle times in (c), in particular at Is=300, result from retrieval errors that cause leaps in the sequence). The sequence duration decreases because associative spindles of subsequent patterns increasingly overlap in time as background activity is raised. This series of experiments suggests that variation of background activity cannot provide a wide speed control of recalled sequences.
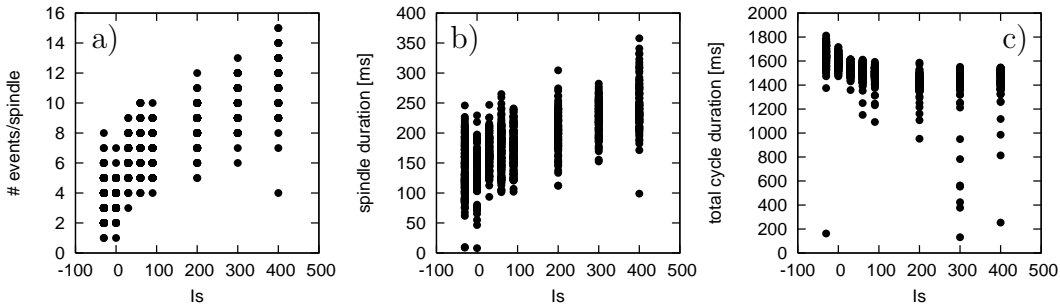

Fig. 4. *Impact of unspecific background activity on timing of sequence retrieval. The x-axes display the level of background current (I_s in $[10^{-8}A/cm^2]$) into the somatic compartment of the PR-cells. The plots* **a)**, **b)** *and* **c)** *display the same quantitites as in figure 3. Symbols represent individual measurements of the displayed quantities in repeated simulations.*

Bidirectional network: Timing of sequence transitions can be controlled by an unspecific neural input in a bidirectional network with a sequence stored

4

in an interleaved fashion, see section 2. The control input stimulates a pattern stored in one pool but unconnected to the synfire chain. The simulation sweep in figure 5 illustrates the recall process with and without control input. Shown are the time courses of control input and overlaps with stored 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.
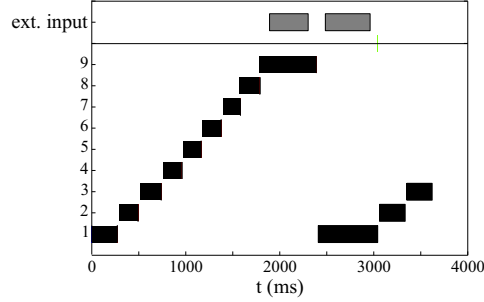

Fig. 5. *Synfire retrieval in the bidirectional network and the influence of input. Black traces visualize the onset and duration of patterns (#1 – #9) retrieved in the first pool. The different patterns in the synfire chain are labeled on the y-axis. The grey trace visualizes the control input applied 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 prolong the duration of 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.).

A further question of this study was how switching in a sequence stored in a brain region can be influenced by neuronal input for the purpose of co-ordinating dynamic memory recall with other processes in the brain or in the environment. As we saw in section 3, background activity has no strong systematic effect on sequence timing, however, the ratio of auto-associative connections has a strong effect. Stronger auto-associative couplings prolong the persistence of patterns but it is unclear how the coupling strengths could be influenced by other neural activity. A similar effect could be achieved by an input that specifically stimulates currently active patterns. However, a sequence model requiring such a timing input would be useless since the external source would have to memorize the whole pattern sequence as well.

As possible solution of the time control problem we propose sequences to be stored in several neuronal pools with intrinsic auto-associative and mutual hetero-associatie connections. For a reciprocal cortical pathway the concept is demonstrated in our bidirectional network model, where associations between two states in one region are mediated by states in the other region. Sequence transitions can be halted by input that supresses the sequence state in one region while leaving the state in the other region undisrupted. Thus, after the release of control input, the sequence resumes (at intrinsic pace). Our model demonstrates that pacing of synfire chains can be controlled by unspecific timing signals, either reflecting sensory input (sequence recognition) or input from other brain regions (coordinated sequence recall, 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 collective 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.