Fast Analog Computation in Networks of Spiking Neurons Using Unreliable Synapses*

Thomas Natschläger and Wolfgang Maass

Inst. for Theoretical Comp. Science, Technische Universität Graz
Klosterwiesgasse 32/2, A-8010 Graz, Austria
email: (tnatschl, maass)@igi.tu-graz.ac.at

Abstract. We investigate through theoretical analysis and computer simulations the consequences of unreliable synapses for fast analog computations in networks of spiking neurons, with analog variables encoded by the firing activities of pools of spiking neurons. Our results suggest that the known unreliability of synaptic transmission may be viewed as a useful tool for analog computing, rather than as a "bug" in neuronal hardware. We also investigate computations on analog time series encoded by the firing activities of pools of spiking neurons.

1 Introduction

It has been demonstrated in [10] that biological neural systems involving 10 or more synaptic stages are able to carry out complex computations within 100 to 150 ms. Since the firing rates in these neural systems are typically well below 100 Hz and interspike intervals are highly variable [7] this cannot be be explained by models based on the encoding of analog variables through firing rates of spiking neurons. A possible explanation is a model where analog values are encoded in small temporal differences between the firing times of presynaptic neurons [10, 6]. However, these models do not provide satisfactory explanations for fast analog computation in neural systems where synaptic transmission is unreliable, as appears to be the case in cortical systems of most vertebrates, with *failure probabilities* ranging up to 0.9, see [2]. A more common type of coding encountered in vertebrate cortex is a population coding where information is encoded by fractions of neurons in various pools that fire within some short time interval (say, of length between 5 and 10 ms) [3]. Although there exists substantial empirical evidence that many cortical systems encode relevant analog variables by such space-rate code, it has remained unclear how networks of spiking neurons can *compute* in terms of such a code: If all neurons in a pool V have the same firing threshold and there are reliable synaptic connections from all neurons in pool U to all neurons in V with approximately equal weights, then all neurons $v \in V$ receive about the same input from U.

*Research for this article was partially supported by the ESPRIT Working Group NeuroCOLT, No. 8556, and the Fonds zur Förderung der wissenschaftlichen Forschung (FWF), Austria, project P12153. We also would like to thank Peter Auer for helpful discussions.

Hence, a firing of a fraction x of neurons in U will typically trigger almost none or almost all neurons in V to fire. Several mechanisms have already been suggested to achieve a smooth graded response in terms of a space-rate code in V instead of a binary "all or none" firing, e.g. strongly varying firing thresholds or a different number of synaptic connections from U for different neurons $v \in V$ [11]. Both option are not completely satisfactory, since firing thresholds of biological neurons appear to be rather homogeneous and a regulation of the response in V through the connectivity pattern seems to make it very difficult to implement changes due to some learning process. Furthermore, both options fail to spread activity over all neurons in V homogeneously, and hence would make the computation less robust against failures of individual neurons.

In section 2 we investigate the question which functions $\langle x_1, \ldots, x_n \rangle \to y$ can be computed by a network of spiking neurons if space-rate code is used to encode the analog variables $x_i \in [0,1]$ and $y \in [0,1]$.[1] The main result is that the output y encoded in a space-rate code in pool V of our model approximates a sigmoidal function $\sigma(\sum_i w_i x_i)$ for a proper sigmoidal function σ and proper weights $w_i \in \mathbb{R}$. In section 3 we investigate what *computations on times series* can be performed by our model. We show there that our model can be described as a linear filter with *infinite impulse response* (IIR).

2 A Model for Fast Analog Computation

We assume that n pools $U_1, \ldots, U_n$ consisting of N neurons each are given, and that all neurons in these pools have synaptic connections to all neurons in another pool V of N neurons.[2] The pools U_i encode the analog input variables $x_i \in [0,1]$ in a space rate code whereas pool V encodes the output y of the network in a space-rate code, i.e. during a short time interval (say of length 5 ms) a total of Nx_i (Ny) neurons fire in pool U_i (V) where each neuron fires only once [3]. In accordance with recent results from neurophysiology we assume that a spike from a neuron $u \in U_i$ triggers with a certain probability r_{vu} ("release probability") the release of some vesicles filled with neurotransmitter at one or several release sites of a connection between neurons $u \in U_i$ and $v \in V$. Data from [9, 2] strongly suggest that in the case of a release the amplitude of the resulting EPSP in neuron v is a stochastic quantity. Consequently, we model the amplitude of the EPSP (or IPSP) in the case of a release by a random variable (r.v.) a_{vu} with probability density function ϕ_{vu}. Our model also allows multiple release sites per synapse, as reported for example in [9]. Figure 1B shows an example of ϕ_{vu} for a synapse with 5 release sites.

Figure 1A illustrates the basic input/output behavior of our model. Shown are results of computer simulations of our model for $n = 6$ presynaptic pools U_i and a poolsize of $N = 200$ (black dots) and a plot of $\sigma(\sum_i x_i w_i)$ for a proper sigmoidal function σ (solid line).[3] We call w_i the "effective weight"

[1] Here and in the following the index i always runs from 1 to n.

[2] Our results remain also valid for connection patterns given by random graphs

[3] We used the spike response model [4] for our simulations. The parameter of the EPSP

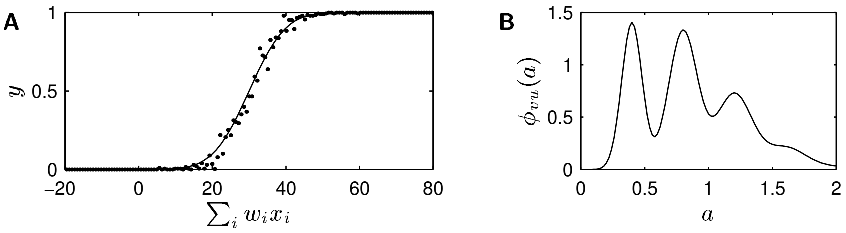

Figure 1: **A** Input/output behavior of our model for a poolsize of $N = 200$ and $\langle w_1, \ldots, w_6 \rangle = \langle 10, -20, -30, 40, 50, 60 \rangle$ for the "effective weights". Each dot is the result of a simulation of our model with an input $\langle x_1, \ldots, x_6 \rangle$ selected randomly from $[0,1]^6$ such that $\sum_i w_i x_i$ covers the range $[-20, 80]$ almost uniformly. The y-axis shows the fraction y of neurons in V that fire during a 5 ms time interval in response to the firing of a fraction x_i of neurons in pool U_i during a earlier time interval of length 5 ms. The solid line is a plot of the function $\sigma(\sum_i w_i x_i)$ as described at the end of section 2. **B** Example of a distribution function ϕ_{vu} of EPSP amplitudes as used for this simulations. This corresponds to a synapse with 5 release sites and a release probability of 0.4 (units are arbitrary).

from pool U_i to pool V. These simulations show that the output y given through the percentage of neurons in V that fire during a time interval I_{out} of length 5 ms approximates quite well the value $\sigma(\sum_i w_i x_i)$ for a sigmoidal "activation function" σ. Note that σ has not been implemented explicitly in our computational model. As we will show in the next paragraphs σ emerges *implicitly* through the large scale statistics of the firing activity.

We considered an idealized mathematical model (details have to be omitted from this abstract, but see [8]) where all neurons which fire in the pools U_i fire synchronously. We also assume that the probability that a neuron $v \in V$ fires can be described by the probability that the sum h_v of the amplitudes of EPSP's and IPSP's (these can be viewed as independent r.v.'s) resulting from firing of neurons in the pools $U_1, \ldots, U_n$ exceeds the firing threshold θ. We assume in this section that the firing rates of neurons in pool V are relatively low, so that the impact of their refractory period can be neglected, i.e. we assume that each neuron $v \in V$ is at rest.[4] Since h_v is the sum of a large number of independent r.v.'s the central limit theorem allows us to approximate the firing probability $\mathrm{P}\{h_v \geq \theta\}$ of a neuron $v \in V$ by $1 - \Phi(\theta; \mu_v, \sigma_v)$ where $\Phi(\cdot; \mu_v, \sigma_v)$ denotes the normal distribution function with mean μ_v and variance σ_v^2. According to our model we have $\mu_v = \sum_i \sum_{u \in U_i} x_i r_{vu} \bar{a}_{vu}$ and $\sigma_v^2 = \sum_i \sum_{u \in U_i} x_i r_{vu} \hat{a}_{vu} - x_i^2 r_{vu}^2 \bar{a}_{vu}^2$ where $\bar{a}_{vu}$ is the mean PSP amplitude $\int a \phi_{vu}(a) da$ and $\hat{a}_{vu}$ is the second moment $\int a^2 \phi_{vu}(a) da$. For sake of brevity we assume in this summary that μ_v and σ_v are the same for all $v \in V$ (see [8] for the general case), i.e. $\sum_{u \in U_i} r_{vu} \bar{a}_{vu} =: w_i$, $\sum_{u \in U_i} r_{vu} \hat{a}_{vu} =: \hat{w}_i$ and $\sum_{u \in U_i} r_{vu}^2 \bar{a}_{vu}^2 =: c_i$ for all neurons $v \in V$. In this case we can approximate the expected fraction of neurons which will fire in pool V by $1 - \Phi(\theta; \bar{\mu}, \bar{\sigma})$ ($\bar{\mu} = \sum_i w_i x_i$ and $\bar{\sigma} = \sum_i \hat{w}_i x_i - c_i x_i^2$) which grows smoothly with $\bar{\mu}$ like a sigmoidal function.

(IPSP) amplitude distribution function ϕ_{vu} (such as the number of release sites) and the release probabilities r_{vu} were drawn randomly from distributions reported in the literature.

[4] Such a model can be viewed as a synfire chain [1] with unreliable synapses.

The deviations of the data points in Fig. 1 from the sigmoidal function of $\bar{\mu}$ can be traced back to two independent sources of noise. One source are just stochastic fluctuations due to the finite poolsize of $N = 200$ which is guaranteed to vanish as $N \to \infty$. Another source of noise is of a more systematic nature: $\bar{\sigma}$ also depends on the inputs x_i in such a way that $1 - \Phi(\theta;\, \bar{\mu}, \bar{\sigma})$ is not purely a function of $\bar{\mu}$. It is shown in [8] that this type of noise already dominates the sampling noise for moderate pool sizes like $N = 200$. Thus if the system should have the property that the output y can be approximated by a sigmoidal function of $\bar{\mu}$ then also $\bar{\sigma}$ must be a function of $\bar{\mu}$. In the asymptotic analysis for $N \to \infty$ this can be achieved if (a) either r_{vu} or $\bar{a}_{vu}$ scale such that $w_i = \sum_{u \in U_i} r_{vu}\bar{a}_{vu}$ stays constant and (b) if there is a common constant $\gamma > 0$ such that $\hat{w}_i = \gamma w_i$ for all i. Under this conditions the terms $c_i = \sum_{u \in U_i} r_{vu}^2 \bar{a}_{vu}^2$ vanish if $N \to \infty$ and we get $\bar{\sigma} = \gamma\bar{\mu}$. Hence the term $1 - \Phi(\theta;\, \bar{\mu}, \gamma\bar{\mu})$ solely depends on $\bar{\mu}$. Conditions (a) and (b) indicate that it might be advantageous for such a neural system to use similar amplitude distributions ϕ_{vu} for different neurons $v \in V$ and to encode different weights w_i as well as weight changes by means of the release probabilities r_{vu} (for details see [8]).

A combination of excitatory and inhibitory pools U_i rises some complications because it is then impossible to satisfy $w_i = \gamma\hat{w}_i$ with a common constant $\gamma \neq 0$ for all i. This indicates that computations which involve positive as well as negative weights can not be carried out with the same precision as computations which involve just positive weights. However, simulation results like the one reported in Fig. 1 show that the qualitative behavior of our model is not disturbed even under the suboptimal condition of combining excitatory and inhibitory pools U_i. For the sigmoidal function in Fig. 1 we used $\sigma(\bar{\mu}) = 1 - \Phi(\theta;\, \bar{\mu}, C)$ with $C^2 = 0.5 \sum_i \hat{w}_i$ as sigmoidal function. In [8] more appropriate sigmoidal functions σ are investigated.

3 Analog Computation on Time Series

We now analyze the behavior of our computational model if the firing probabilities in the pools U_i change with time. Writing $x_i(t)$ $(y(t))$ for the probability that a neuron in pool U_i (V) fires during the t-th time window of length, say 2 ms, our computational model from section 2 maps a vector of n analog time series $\{x_i(t)\}_{t \in \mathbb{N}}$ onto an output time series $\{y(t)\}_{t \in \mathbb{N}}$.

As an example consider a network which consists of one presynaptic pool U_1 connected to the output pool V with the same type of synapses as discussed in section 2. In addition there are *feedback connections* between individual neurons $v \in V$. The results of simulations reported in Fig. 2 show that this network computes an interesting map in the time series domain: The space-rate code in pool V represents a sigmoidal function σ (like in section 2) applied to the output of a *bandpass filter*.

We also have analyzed the computational power of such networks of spiking neurons in the time-series domain (details have to be omitted from this summary, see [8]) using the spike-response model [4]. We model the effect on the

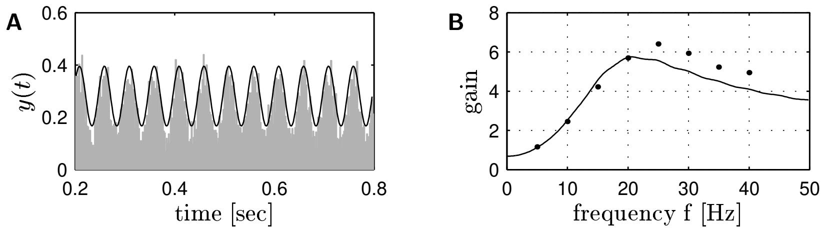

Figure 2: The gray shaded bars in panel A show the actual measured fraction of neurons which fire in pool V of the network described at the beginning of section 3 during a time interval of length 2 ms in response to a sin wave modulated activity in pool U_1 (not shown). The solid line is a plot of a sin function fitted to the simulation result. The amplitudes of such fits for various frequencies are used to construct empirically the frequency amplitude response (black dots in panel B) of the filter implicitly implemented by the network. This is in good agreement with the theoretical frequency amplitude response (solid line in panel B) given by $|H(e^{j2\pi f})|$ where $H(z)$ is the transfer function[6]of the filter in terms of the z-transform.

membrane potential of a neuron $v \in V$ at time t caused by a firing of a neuron $u \in U_i$ ($v \in V$) at a time k through a "response function" $\varepsilon_i(t-k)$ ($\rho_j(t-k)$, $j \in \{1 \ldots, m\}$), i.e. ε_i (ρ_j) models the effect of a "feedforward" ("recurrent") connection. In addition to the effective weights w_i between the pools U_i and pool V there are the effective weights $\tilde{w}_j$ of the recurrent connections. The effect on the membrane potential of a neuron $v \in V$ at time t caused by a firing of v itself at time k, i.e. the refractoriness, is modeled through the function $\eta(t-k)$.

We consider time series of the form $x_i(t) = x_0 + \tilde{x}_i(t)$ and $y(t) = y_0 + \tilde{y}(t)$ where the magnitudes of the signals $\tilde{x}_i(t)$ and $\tilde{y}(t)$ are rather small. If we furthermore assume that $x_i(t) = x(t)$ (hence $\tilde{x}_i(t) = \tilde{x}(t)$) for all i then we can approximate the output $\tilde{y}(t)$ of the network by $\tilde{y}(t) = \sum_{k=0}^{t} b_k \tilde{x}(t-k) - \sum_{k=1}^{t} a_k \tilde{y}(t-k)$ with $b_k = K \sum_i w_i \varepsilon_i(k)$ and $a_k = -K\eta(k) - K \sum_{j=1}^{m} \tilde{w}_j \rho_j(k)$.[7] This is the general form of an infinite impulse response (IIR) time invariant linear filter, see [5]. Note that the coefficients b_k (a_k) are determined by the weights w_i ($\tilde{w}_j$) of the feedforward (recurrent) connections and by the time course of the corresponding response functions $\varepsilon_i(k)$ ($\rho_j(k)$ and $\eta(k)$). Thus different sets of weights w_i and $\tilde{w}_j$ yield different IIR filters. Furthermore, if one assumes that the time course of PSPs (modeled by the response functions) can be changed it is not hard to proof that one can indeed choose *arbitrary* numbers b_k and a_k. Thus one can approximate any given IIR filter with a network of spiking neurons using space-rate coding.

[6]The transfer function of such filter in terms of the z-transformation is given by $H(z) = (\sum_{k=0}^{k_0} b_k z^{-k})/(1 + \sum_{k=1}^{k_0} a_k z^{-k})$.

[7]Note that there are no rigorous mathematical arguments for such an approximation. However, our simulation results (Fig. 2) show the high quality of this approximation.

4 Conclusions

In this article we have established important links between details of realistic models for biologic neurons and synapses and resulting large scale effects of such details for computations with populations of neurons. We have shown that the unreliability of synaptic transmission suffices to explain the possibility of fast analog computations on the network level. In particular the arguments of section 2 imply that the computation of arbitrary functions of the form $\langle x_1, \ldots, x_n \rangle \to y = \sigma(\sum_i w_i x_i)$, with inputs and output in space-rate code, can be carried out within 10 ms by a network of spiking neurons. Hence the universal approximation theorem for multilayer perceptrons indicates that *arbitrary continuous functions* $f : [0,1]^n \to [0,1]^m$ can be approximated with a computation time of not more than 20 ms by a network of spiking neurons with 3 layers.

We have also addressed the question which additional computational functions on the network level are possibly if one incorporates other important features of biological neurons and micro-circuits such as the refractory behavior of neurons and local recurrent connections. We have shown that through these features a rich repertoire of linear filters, especially IIR-filters, can be implemented on the level of space-rate coding in populations of neurons.

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