Noisy Spiking Neurons with Temporal Coding have more Computational Power than Sigmoidal Neurons

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Abstract

We exhibit a novel way of simulating sigmoidal neural nets by networks of noisy spiking neurons in temporal coding. Furthermore it is shown that networks of noisy spiking neurons with temporal coding have a strictly larger computational power than sigmoidal neural nets with the same number of units.

1 Introduction and Definitions

We consider a formal model SNN for a **s**piking **n**euron **n**etwork that is basically a reformulation of the spike response model (respectively leaky integrate and fire model) without using δ-functions (see [Maass, 1995] or [Maass, 1996] for further background).

An SNN consists of a finite set V of *spiking neurons*, a set $E \subseteq V \times V$ of *synapses*, a *weight* $w_{u,v} \geq 0$ and a *response function* $\varepsilon_{u,v} : \mathbf{R}^+ \to \mathbf{R}$ for each synapse $\langle u, v\rangle \in E$ (where $\mathbf{R}^+ := \{x \in \mathbf{R} : x \geq 0\}$) , and a *threshold function* $\Theta_v : \mathbf{R}^+ \to \mathbf{R}^+$ for each neuron $v \in V$.

If $F_u \subseteq \mathbf{R}^+$ is the set of *firing times* of a neuron u , then the *potential* at the trigger zone of neuron v at time t is given by

$$P_v(t) := \sum\nolimits_{u:\langle u,v\rangle \in E} \ \sum\nolimits_{s \in F_u : s < t} w_{u,v} \cdot \varepsilon_{u,v}(t-s) \ .$$

In a noise-free model a neuron v fires at time t as soon as $P_v(t)$ reaches $\Theta_v(t-t')$, where t' is the time of the most recent firing of v . One says then that neuron v sends out an "action potential" or "spike" at time t .

For some specified subset $V_{in} \subseteq V$ of *input neurons* one assumes that the firing times ("spike trains") F_u for neurons $u \in V_{in}$ are not defined by the preceding convention, but are given from the outside. The firing times F_v for all other neurons $v \in V$ are determined by the previously described rule, and the output of the network is given in the form of the spike trains F_v for a specified set of *output neurons* $V_{out} \subseteq V$.

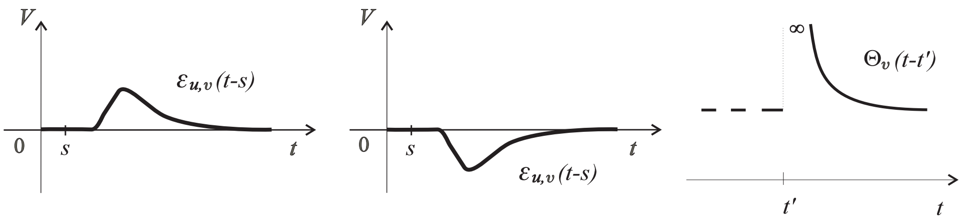

Figure 1: Typical shapes of response functions $\varepsilon_{u,v}$ (EPSP and IPSP) and threshold functions Θ_v for biological neurons.

We will assume in our subsequent constructions that all response functions $\varepsilon_{u,v}$ and threshold functions Θ_v in an SNN are "stereotyped", i.e. that the response functions differ apart from their "sign" (EPSP or IPSP) only in their delay $d_{u,v}$ (where $d_{u,v} := \inf \{t \geq 0 : \varepsilon_{u,v}(t) \neq 0\}$) , and that the threshold functions Θ_v only differ by an additive constant (i.e. for all u and v there exists a constant $c_{u,v}$ such that $\Theta_u(t) = \Theta_v(t) + c_{u,v}$ for all $t \geq 0$) . We refer to a term of the form $w_{u,v} \cdot \varepsilon_{u,v}(t-s)$ as an excitatory respectively inhibitory postsynaptic potential (abbreviated: EPSP respectively IPSP).

Since biological neurons do not always fire in a reliable manner one also considers the related model of *noisy spiking neurons*, where $P_v(t)$ is replaced by $P_v^{noisy}(t) := P_v(t) + \alpha_v(t)$ and $\Theta_v(t-t')$ is replaced by $\Theta_v^{noisy}(t-t') := \Theta_v(t-t') + \beta_v(t-t')$. $\alpha_v(t)$ and $\beta_v(t-t')$ are allowed to be arbitrary functions with bounded absolute value (hence they can also represent "systematic noise").

Furthermore one allows that the current value of the difference $D(t) := P_v^{noisy}(t) - \Theta_v^{noisy}(t-t')$ does not determine directly the firing time of neuron v, but only its current *firing probability*. We assume that the firing probability approaches 1 if $D \to \infty$, and 0 if $D \to -\infty$. We refer to spiking neurons with these two types of noise as "noisy spiking neurons".

We will explore in this article the power of *analog* computations with noisy spiking neurons, and we refer to [Maass, 1995] for results about *digital* computations in this model.

2 Fast Simulation of Sigmoidal Neural Nets with Noisy Spiking Neurons in Temporal Coding

So far one has only considered simulations of sigmoidal neural nets by spiking neurons where each analog variable in the sigmoidal neural net is represented by the *firing rate* of a spiking neuron. However this "firing rate interpretation" is inconsistent with a number of empirical results about computations in biological neural systems. For example [Thorpe & Imbert, 1989] have demonstrated that visual pattern analysis and pattern classification can be carried out by humans in just 100 ms, in spite of the fact that it involves a minimum of 10 synaptic stages from the retina to the temporal lobe. [de Ruyter van Steveninck & Bialek, 1988] have found that a blowfly can produce flight torques within 30 ms of a visual stimulus by a neural system with several synaptic stages. However the firing rates of neurons involved in all these computations are usually below 100 Hz, and interspike intervals tend to be quite irregular. Hence one cannot interpret these analog computations with spiking neurons on the basis of an encoding of analog variables by firing rates.

On the other hand experimental evidence has accumulated during the last few years which indicates that many biological neural systems use the *timing* of action potentials to encode information (see e.g. [Bialek & Rieke, 1992], [Bair et al., 1994]).

We will now describe a new way of simulating sigmoidal neural nets by networks of spiking neurons that is based on *temporal coding*. The *key mechanism* for this alternative simulation is based on the well known fact that EPSP's and IPSP's are able to *shift* the firing time of a spiking neuron. This mechanism can be demonstrated very clearly in our formal model if one assumes that EPSP's rise (and IPSP's fall) *linearly* during a certain initial time period. Hence we assume in the following that there exists some constant $\triangle > 0$ such that each response function $\varepsilon_{u,v}(x)$ is of the form $\alpha_{u,v} \cdot (x - d_{u,v})$ with $\alpha_{u,v} \in \{-1, 1\}$ for $x \in [d_{u,v},\, d_{u,v} + \triangle]$, and $\varepsilon_{u,v}(x) = 0$ for $x \in [0, d_{u,v}]$.

Consider a spiking neuron v that receives postsynaptic potentials from n presynaptic neurons $a_1, \ldots, a_n$. For simplicity we assume that interspike intervals are so large that the firing time t_v of neuron v depends just on a single firing time t_{a_i} of each neuron a_i, and Θ_v has returned to its "resting value" $\Theta_v(0)$ before v fires again. Then if the next firing of v occurs at a time when the postsynaptic potentials described by $w_{a_i,v} \cdot \varepsilon_{a_i,v}(t - t_{a_i})$ are all in their initial *linear* phase, its firing time t_v is determined in the noise-free model for $w_i := w_{a_i,v} \cdot \alpha_{a_i,v}$ by the equation $\sum_{i=1}^{n} w_i \cdot (t_v - t_{a_i} - d_{a_i,v}) = \Theta_v(0)$, or equivalently

$$t_v = \frac{\Theta_v(0)}{\sum_{i=1}^{n} w_i} + \frac{\sum_{i=1}^{n} w_i \cdot (t_{a_i} + d_{a_i,v})}{\sum_{i=1}^{n} w_i} \tag{1}$$

This equation reveals the somewhat surprising fact that (for a certain range of their parameters) spiking neurons can compute a *weighted sum* in terms of *firing times*, i.e. *temporal coding*. One should also note that in the case where all delays $d_{a_i,v}$ have the same value, the "weights" w_i of this weighted sum are encoded in the "strengths" $w_{a_i,v}$ of the synapses and their "sign" $\alpha_{a_i,v}$, as in the "firing rate interpretation". Finally according to (1) the coefficients of the presynaptic firing times t_{a_i} are automatically *normalized*, which appears to be of biological interest.

In the simplest scheme for temporal coding (which is closely related to that in [Hopfield, 1995]) an analog variable $x \in [0, 1]$ is encoded by the firing time $T - \gamma \cdot x$ of a neuron, where T is assumed to be independent of x (in a biological context T might be time-locked to the onset of a stimulus, or to some oscillation) and γ is some contrast that is determined in the proof of Theorem 2.1 (e.g. $\gamma = \Delta/2$ in the noise-free case). In contrast to [Hopfield, 1995] we assume that both the inputs *and* *the outputs* of computations are encoded in this fashion. This has the advantage that one can *compose* computational modules.

We will first focus in Theorem 2.1 on the simulation of sigmoidal neural nets that employ the piecewise linear "linear saturated" activation function $\pi : \mathbf{R} \to [0,1]$ defined by $\pi(y) = 0$ if $y < 0$, $\pi(y) = y$ if $0 \leq y \leq 1$, and $\pi(y) = 1$ if $y > 1$. The Theorem 3.1 in the next section will imply that one can simulate with spiking neurons also sigmoidal neural nets that employ *arbitrary* continuous activation functions. Apart from the previously mentioned assumptions we will assume for the proofs of Theorem 2.1 and 3.1 that any EPSP satisfies $\varepsilon_{u,v}(x) = 0$ for all sufficiently large x, and $\varepsilon_{u,v}(x) \geq \varepsilon_{u,v}(d_{u,v} + \Delta)$ for all $x \in [d_{u,v} + \Delta, d_{u,v} + \Delta + \gamma]$. We assume that each IPSP is continous, and has value 0 except for some interval of $\mathbf{R}$. Furthermore we assume for each EPSP and IPSP that $|\varepsilon_{u,v}(x)|$ grows at most linearly during the interval $[d_{u,v} + \Delta, d_{u,v} + \Delta + \gamma]$. In addition we assume that $\Theta_v(x) = \Theta_v(0)$ for sufficiently large x, and that $\Theta_v(x)$ is sufficiently large for $0 < x \leq \gamma$.

Theorem 2.1 *For any given $\varepsilon, \delta > 0$ one can simulate any given feedforward sigmoidal neural net N with activation function π by a network $\mathcal{N}_{N,\varepsilon,\delta}$ of noisy spiking neurons in temporal coding. More precisely, for any network input $x_1, \ldots, x_m \in [0,1]$ the output of $\mathcal{N}_{N,\varepsilon,\delta}$ differs with probability $\geq 1 - \delta$ by at most ε from that of N. Furthermore the computation time of $\mathcal{N}_{N,\varepsilon,\delta}$ depends neither on the number of gates in N nor on the parameters ε, δ, but only on the number of layers of the sigmoidal neural network N.*

We refer to the Appendix for details of the somewhat complicated proof. One employs the mechanism described by (1) to simulate through the firing time of a spiking neuron v a sigmoidal gate with activation function π for those gate-inputs where π operates in its linearly rising range. With the help of an auxiliary spiking neuron that fires at time T one can avoid the automatic "normalization" of the weights w_i that is provided by (1), and thereby compute a weighted sum with *arbitrary* given weights. In order to simulate in temporal coding the behaviour of the gate in the input range where π is "saturated" (i.e. constant), it suffices to employ some auxiliary spiking neurons which make sure that v fires exactly once during the relevant time window (and not shortly before that).

Since inputs and outputs of the resulting modules for each single gate of N are all given in temporal coding, one can compose these modules to simulate the multilayer sigmoidal neural net N. With a bit of additional work one can ensure that this construction also works with *noisy* spiking neurons. ∎

3 Universal Approximation Property of Networks of Noisy Spiking Neurons with Temporal Coding

It is known [Leshno et al., 1993] that feedforward sigmoidal neural nets whose gates employ the activation function π can approximate with a single hidden layer for any $n, k \in \mathbf{N}$ any given continuous function $F : [0,1]^n \to [0,1]^k$ within any $\varepsilon > 0$ with regard to the L_∞-norm (i.e. uniform convergence). Hence we can derive the following result from Theorem 2.1:

Theorem 3.1 *Any given continuous function $F : [0,1]^n \to [0,1]^k$ can be approximated within any given $\varepsilon > 0$ with arbitrarily high reliability in temporal coding by a network of noisy spiking neurons (SNN) with a single hidden layer (and hence within 20 ms for biologically realistic values of their time-constants).* ∎

Because of its generality this Theorem implies the same result also for *more general schemes of coding analog variables by the firing times of neurons*, besides the particular one that we have considered so far. In fact it implies that the same result holds for any other coding scheme C that is "continuously related" to the previously considered one in the sense that the transformation between firing times that encode an analog variable x in the here considered coding scheme and in the coding scheme C can be described by uniformly continuous functions in both directions.

4 Spiking Neurons have more Computational Power than Sigmoidal Neurons

We consider the *"element distinctness function"* $ED_n : (\mathbf{R}^+)^n \to \{0,1\}$ defined by

$$ED_n(s_1,\ldots,s_n) \;=\; \begin{cases} 1\,, & \text{if } s_i = s_j \text{ for some } i \neq j \\ 0\,, & \text{if } |s_i - s_j| \geq 1 \text{ for all } i,j \text{ with } i \neq j \\ \text{arbitrary}, & \text{else}\ . \end{cases}$$

If one encodes the value of input variable s_i by a firing of input neuron a_i at time $T_{in} - c \cdot s_i$, then for sufficiently large values of the constant $c > 0$ *a single noisy spiking neuron v can compute ED_n* with arbitrarily high reliability. This holds for any reasonable type of response functions, e.g. the ones shown in Fig. 1. The binary output of this computation is assumed to be encoded by the firing/non-firing of v . Hair-trigger situations are avoided since no assumptions have to be made about the firing or non-firing of v if EPSP's arrive with a temporal distance *between* 0 and c .

On the other hand the following result shows that a fairly large sigmoidal neural net is needed to compute the same function. Its proof provides the first application for Sontag's recent results about a new type of "dimension" d of a neural network N , where d is chosen maximal so that *every* subset of d inputs is shattered by N . Furthermore it expands a method due to [Koiran, 1995] for using the VC-dimension to prove lower bounds on network size.

Theorem 4.1 *Any sigmoidal neural net $\mathcal{N}$ that computes ED_n has at least $\frac{n-4}{2} - 1$ hidden units.*

Proof: Let $\mathcal{N}$ be an arbitrary sigmoidal neural net with k gates that computes ED_n. Consider *any* set $S \subseteq \mathbf{R}^+$ of size $n-1$. Let $\lambda > 0$ be sufficiently large so that the numbers in $\lambda \cdot S$ have pairwise distance ≥ 2 . Let A be a set of $n-1$ numbers $> \max\,(\lambda \cdot S) + 2$ with pairwise distance ≥ 2 .

By assumption $\mathcal{N}$ can decide for n arbitrary inputs from $\lambda \cdot S\ \cup A$ whether they are all different. Let $\mathcal{N}_\lambda$ be a variation of $\mathcal{N}$ where all weights on edges from the first input variable are multiplied with λ. Then $\mathcal{N}_\lambda$ can compute any function from S into $\{0,1\}$ after one has assigned a suitable fixed set of $n-1$ pairwise different numbers from $\lambda \cdot S \cup A$ to the last $n-1$ input variables.

Thus if one considers as *programmable* parameters of $\mathcal{N}$ the factor λ in the weights on edges from the first input variable and the $\leq k$ thresholds of gates that are connected to some of the other $n-1$ input variables, then $\mathcal{N}$ shatters S with these $k+1$ programmable parameters.

Since $S \subseteq \mathbf{R}^+$ of size $n-1$ was chosen *arbitrarily*, we can now apply the result from [Sontag, 1996], which yields an upper bound of $2w+1$ for the maximal number d such that *every* set of d different inputs can be shattered by a sigmoidal neural net with w programmable parameters (note that this parameter d is in general much smaller than the VC-dimension of the neural net). For $w := k+1$ this implies in our case that $n-1 \leq 2(k+1)+1$, hence $k \geq (n-4)/2$. Thus $\mathcal{N}$ has at least $(n-4)/2$ computation nodes, and therefore at least $(n-4)/2-1$ hidden units. One should point out that due to the generality of Sontag's result this lower bound is valid for all common activation functions of sigmoidal gates, and even if $\mathcal{N}$ employs heaviside gates besides sigmoidal gates. ∎

Theorem 4.1 yields a lower bound of 4997 for the number of hidden units in any sigmoidal neural net that computes ED_n for $n = 10\,000$, where 10 000 is a common estimate for the number of inputs (i.e. synapses) of a biological neuron. With the same method one can show that even if one takes nonlinear effects in dendritic integration and realistic weight-sizes of a biological neuron into account, the resulting model for a spiking neuron can still compute analog functions in temporal coding for which hundreds of hidden units would be needed on any sigmoidal neural net (see [Maass, 1996]).

Finally we would like to point out that to the best of our knowledge Theorem 4.1 provides the largest known lower bound for *any* concrete function with n inputs on a sigmoidal neural net. The largest previously known lower bound for sigmoidal neural nets was $\Omega(n^{1/4})$, due to [Koiran, 1995].

5 Conclusions

To the best of our knowledge Theorems 2.1 and 3.1 provide the only theoretical model for analog computations in network of spiking neurons that is consistent with experimental results on the maximal computation speed of biological neural systems. As explained after Theorem 3.1, this result holds for a large variety of possible schemes for encoding analog variables by firing times.

These theoretical results hold *rigorously* only for a rather small time window of length γ for temporal coding. However a closer inspection of the construction shows that the actual shape of EPSP's and IPSP's in biological neurons provides an automatic adjustment of extreme values of the inputs t_{a_i} towards their average, which allows them to carry out rather similar computations for a substantially larger window size. It also appears to be of interest from the biological point of view that the synaptic weights play for temporal coding in our construction basically the same role as for rate coding, and hence the *same* network is in principle able to compute a closely related analog function in *both* coding schemes.

We have focused in our constructions on feedforward nets, but our method can for example also be used to simulate a Hopfield net with graded response by a network of noisy spiking neurons in temporal coding. A stable state of the Hopfield net corresponds then to a firing pattern of the simulating SNN where all neurons fire at the same frequency, with the *"pattern"* of the stable state encoded in their phase differences.

The theoretical results in this article may also provide additional goals and directions for a new computer technology based on *artificial* spiking neurons.

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Appendix (can be ignored)

Proof of Theorem 2.1: Let $\pi_\gamma : \mathbf{R} \to [0,\gamma]$ be the activation function defined by $\pi_\gamma(y) = 0$ if $y < 0$, $\pi_\gamma(y) = y$ if $0 \leq y \leq \gamma$, and $\pi_\gamma(y) = \gamma$ if $y > \gamma$. In view of the scaling of analog variables $x \in [0,1]$ by the factor γ in the here considered encoding of x by a firing time $T - \gamma \cdot x$, it is more convenient to simulate (instead of gates with activation function π and this encoding) gates with activation function π_γ and an encoding of $s \in [0,\gamma]$ by a firing time $T - s$. Note that one has $\pi(\sum_{i=1}^n r_i x_i) = \frac{1}{\gamma} \cdot \pi_\gamma(\sum_{i=1}^n r \cdot \gamma x_i)$ for arbitrary $r_i, x_i \in \mathbf{R}$.

Thus we simulate an arbitrary π_γ-gate G, for some $\gamma > 0$, which computes a function $f_G : [0,\gamma]^n \to [0,\gamma]$. Let $r_1, \ldots, r_n \in \mathbf{R}$ be the weights of G. Then we have

$$f_G(s_1,\ldots,s_n) = \begin{cases} 0 & , \quad \text{if} \quad \sum_{i=1}^n r_i \cdot s_i < 0 \\ \sum_{i=1}^n r_i \cdot s_i & , \quad \text{if} \quad 0 \leq \sum_{i=1}^n r_i \cdot s_i \leq \gamma \\ \gamma & , \quad \text{if} \quad \sum_{i=1}^n r_i \cdot s_i > \gamma \end{cases}$$

for arbitrary inputs $s_1, \ldots, s_n \in [0,\gamma]$.

For the sake of simplicity we will first consider a simulation that employs spiking neurons *without* noise (i.e. $\alpha_v = \beta_v = 0$ and each neuron v fires whenever $P_v(t)$ crosses $\Theta_v(t - t')$ from below). Afterwards we will describe the changes that are needed in this construction for the general case of *noisy* spiking neurons.

We construct for a given π_γ-gate G and for an arbitrary given parameter $\varepsilon > 0$ with $\varepsilon < \gamma$ a network $\mathcal{N}_{G,\varepsilon}$ of spiking neurons that approximates f_G with precision $\leq \varepsilon$, i.e. the output $\mathcal{N}_{G,\varepsilon}(s_1,\ldots,s_n)$ of $\mathcal{N}_{G,\varepsilon}$ satisfies $|\mathcal{N}_{G,\varepsilon}(s_1,\ldots,s_n) - f_G(s_1,\ldots,s_n)| \leq \varepsilon$ for all $s_1,\ldots,s_n \in [0,\gamma]$.

In order to be able to scale the size of "weights" according to the given gate G we assume that $\mathcal{N}_{G,\varepsilon}$ receives an additional input s_0 which is given like the other input variables $s_1,\ldots,s_n$ in temporal coding. Thus we assume that there are $n+1$ input neurons $a_0,\ldots,a_n$ with the property that a_i fires at time $T_{in} - s_i$ (where T_{in} is some constant).

We construct a spiking neuron v in $\mathcal{N}_{G,\varepsilon}$ that receives $n+1$ PSP's $h_0(t),\ldots,h_n(t)$ from the $n+1$ input neurons $a_0,\ldots,a_n$, which result from the firing of a_i at time $T_{in} - s_i$. In addition v receives some auxiliary PSP's from other spiking neurons in $\mathcal{N}_{G,\varepsilon}$, whose timing depends only on T_{in} .

The firing time t_v of this neuron v will provide the output $\mathcal{N}_{G,\varepsilon}(s_1,\ldots,s_n)$ of the network $\mathcal{N}_{G,\varepsilon}$ in temporal coding, i.e. v will fire at time $T_{out} - \mathcal{N}_{G,\varepsilon}(s_1,\ldots,s_n)$ for some T_{out} that does not depend on $s_1,\ldots,s_n$. Let $w_{a_i,v}$ be the weight of the synapse from input neuron a_i to neuron v, $i = 0,\ldots,n$. We assume that the "delay" $d_{a_i,v}$ between a_i and v is the same for all input neurons $a_0,\ldots,a_n$, and we write d for this common delay. Thus we can describe for $i = 0,\ldots,n$ the impact of the firing of a_i at time $T_{in} - s_i$ on the potential at the trigger zone of neuron v at time t by the EPSP or IPSP $h_i(t) = w_{a_i,v} \cdot \varepsilon_{a_i,v}(t - (T_{in} - s_i))$, which has on the basis of our assumptions the value

$$h_i(t) = \begin{cases} 0 & , \quad \text{if} \quad t - (T_{in} - s_i) < d \\ w_i \cdot (t - (T_{in} - s_i) - d) & , \quad \text{if} \quad d \leq t - (T_{in} - s_i) \leq d + \Delta \ , \end{cases}$$

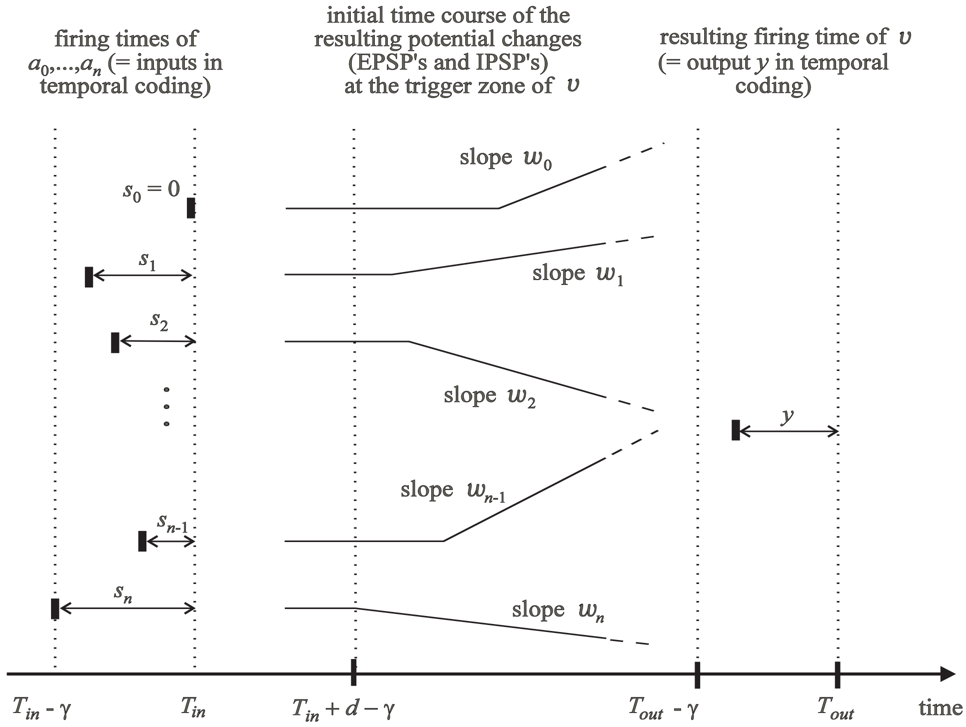

Figure 2: Illustration regarding the simulation of a sigmoidal gate by a spiking neuron v in temporal coding

where $w_i = w_{a_i,v}$ in the case of an EPSP and $w_i = -w_{a_i,v}$ in the case of an IPSP.

We assume that neuron v has not fired for a sufficiently long time, so that its threshold function $\Theta_v(t-t')$ can be assumed to have a constant value $\Theta_v(0)$. Then if no noise is present, the time t_v of the next firing of v can be described by the equality

$$\Theta_v(0) = \sum\nolimits_{i=0}^{n} h_i(t_v) \;=\; \sum\nolimits_{i=0}^{n} w_i \cdot (t_v - (T_{in} - s_i) - d) \;\;, \tag{2}$$

provided that

$$d \le t_v - (T_{in} - s_i) \le d + \Delta \;\; \text{for} \;\; i \;=\; 0, \ldots, n \;\; . \tag{3}$$

We assume from now on that a fixed value $s_0 \equiv 0$ is chosen for the extra input s_0. Then (2) is equivalent to

$$t_v \;=\; \frac{\Theta_v(0)}{\sum_{i=0}^{n} w_i} \;+\; T_{in} \;+\; d \;-\; \frac{\sum_{i=1}^{n} w_i \cdot s_i}{\sum_{i=0}^{n} w_i} \;\; . \tag{4}$$

This t_v satisfies (3) if $-s_j \;\le\; t_v - T_{in} - d \;\le\; \Delta - s_j$ for $j = 0, \ldots, n$, hence for any $s_j \in [0, \gamma]$ if

$$0 \;\le\; \frac{\Theta_v(0) - \sum_{i=1}^{n} w_i \cdot s_i}{\sum_{i=0}^{n} w_i} \;\le\; \Delta - \gamma \;\; . \tag{5}$$

We set $w_i := \lambda \cdot r_i$ for $i = 1, \ldots, n$, where $r_1, \ldots, r_n$ are the weights of the simulated π_γ-gate G, and $\lambda > 0$ is some not yet determined factor (that we will later choose sufficiently large in order to make sure that neuron v fires closely to the time t_v given by (4) even in the presence of noise). We choose w_0 so that $\sum_{i=0}^n w_i = \lambda$. This implies that (4) with

$$T_{out} := \frac{\Theta_v(0)}{\lambda} + T_{in} + d$$

is now equivalent to

$$t_v \;=\; T_{out} - \sum\nolimits_{i=1}^n r_i \cdot s_i \;, \tag{6}$$

and (5) is equivalent to

$$0 \;\leq\; \frac{\Theta_v(0)}{\lambda} \; - \sum\nolimits_{i=1}^n r_i \cdot s_i \;\leq\; \Delta - \gamma \;. \tag{7}$$

Hence, provided that γ, λ and $\Theta_v(0)$ are chosen in relationship to Δ so that

$$\gamma \;\leq\; \frac{\Theta_v(0)}{\lambda} \;\leq\; \Delta - \gamma \;, \tag{8}$$

we have satisfied (5), and therefore achieved that the firing time t_v of neuron v provides in temporal coding the output $f_G(s_1, \ldots, s_n) = \sum_{i=1}^n r_i \cdot s_i$ of the simulated π_γ-gate G for all inputs $s_1, \ldots, s_n \in [0, \gamma]$ with $\sum_{i=1}^n r_i \cdot s_i \in [0, \gamma]$.

In order to simulate G also for $s_1, \ldots, s_n \in [0, \gamma]$ with other values of $\sum_{i=1}^n r_i \cdot s_i$, we make sure that v fires at a time with distance at most ε to $T_{out} - \gamma$ if $\sum_{i=1}^n r_i \cdot s_i$ is larger than γ, and that v fires with distance at most ε to time T_{out} if $\sum_{i=1}^n r_i \cdot s_i < 0$. For that purpose we add inhibitory and excitatory neurons which fire at times that depend on time T_{in}, but not on the input $s_1, \ldots, s_n$. The activity of these auxiliary inhibitory and excitatory neurons may also shift the firing time t_v of v if $\sum_{i=1}^n r_i \cdot s_i \in [0, \gamma]$, but at most by ε.

According to the previously described construction we have by (6) that $t_v = T_{out}$ if $s_i = 0$ for $i = 1, \ldots, n$ (and therefore $\sum_{i=1}^n r_i \cdot s_i = 0$). Furthermore the parameters have been chosen so that (3) is satisfied for this case, which implies that each of the PSP's $h_i(t)$ is at time T_{out} for $s_i = 0$ still within the initial segment of length Δ of its first non-zero segment. This implies that for *any* value of $s_i \in [0, \gamma]$ the PSP $h_i(t)$ is at time $T_{out} - \gamma$ not further advanced than the end of the initial segment of length Δ of its first non-zero segment. Thus

$$|h_i(t)| \leq |w_i \cdot (t - (T_{in} - s_i) - d)| \;\leq\; |w_i| \cdot (T_{out} - \gamma - (T_{in} - \gamma) - d) \;\leq\; |w_i| \cdot \Delta$$

for all $t \leq T_{out} - \gamma$ and all $s_i \in [0, \gamma]$. This implies that for *any* $s_1, \ldots, s_n \in [0, \gamma]$ (even if $\sum_{i=1}^n r_i \cdot s_i \notin [0, \gamma]$) we have $|\sum_{i=0}^n h_i(t)| \leq W \cdot \Delta$ for all $t \leq T_{out} - \gamma$, where $W := \sum_{i=0}^n |w_i|$.

Hence in order to prevent a firing of v before time $T_{out} - \gamma$, it suffices to employ auxiliary neurons in $\mathcal{N}_{G,\varepsilon}$ which send IPSP's to v that lower the potential at the trigger zone of v during the interval $[T_{out} - \gamma - \Delta\, ,\, T_{out} - \gamma]$ by more than $W \cdot \Delta - \Theta_v(0)$. In general these IPSP's will also influence the potential at the trigger zone of v shortly *after* time $T_{out} - \gamma$. Since these auxiliary IPSP's will be independent of the input $s_1, \ldots, s_n$, they may delay the firing of v even in the case where $\sum_{i=1}^n r_i \cdot s_i \in [0, \gamma]$. In order to approximate the given π_γ-gate G with an error of at most ε , we assume that these auxiliary IPSP's have vanished at the trigger zone of v by time $T_{out} - \gamma + \varepsilon$. It is obvious that all these conditions can be achieved with a sufficient number (and/or "weights") of auxiliary synchronized IPSP's from inhibitory neurons in $\mathcal{N}_{G,\varepsilon}$ whose firing time depends only on T_{in}. This can be satisfied using only our rather weak assumption that each IPSP is continuous and of value $\neq 0$ before it eventually vanishes.

We now want to make sure that v fires at the latest by time $T_{out} - \gamma + \varepsilon$ if $\sum_{i=1}^n r_i \cdot s_i > \gamma - \varepsilon$. Since all auxiliary IPSP's have vanished by time $T_{out} - \gamma + \varepsilon$, we have $P_v(T_{out} - \gamma + \varepsilon) = \sum_{i=0}^n h_i(T_{out} - \gamma + \varepsilon)$. Hence it suffices to show that the latter is $\geq \Theta_v(0)$. Consider the set I of those $i \in \{1, \ldots, n\}$ with $r_i > 0$, i.e. those i where $w_{a_i,v} \cdot \varepsilon_{a_i,v}(t)$ represents an EPSP. By choosing suitable values s_i' in the interval $[0, s_i]$ for $i \in I$ and by setting $s_i' := s_i$ for $i \in \{1, \ldots, n\} - I$, one can achieve that $\sum_{i=1}^n r_i \cdot s_i' = \gamma - \varepsilon$. According to (6) the potential P_v reaches the value $\Theta_v(0)$ at time $T_{out} - \gamma + \varepsilon$ for the input $\langle s_1', \ldots, s_n' \rangle$, and according to (3), (5), (7), (8) each PSP $w_{a_i,v} \cdot \varepsilon_{a_i,v}$ is at time $T_{out} - \gamma + \varepsilon$ still within Δ of the beginning of its non-zero phase. If one now changes s_i' to s_i for $i \in I$, the EPSP $w_{a_i,v} \cdot \varepsilon_{a_i,v}$ will be advanced in time by $s_i - s_i' \in [0, \gamma]$. Hence each of the EPSP's $w_{a_i,v} \cdot \varepsilon_{a_i,v}$ for $i \in I$ is for input s_i at time $T_{out} - \gamma + \varepsilon$ within $\Delta + \gamma$ of the beginning of its rising phase. Since we assume that $w_{a_i,v} \cdot \varepsilon_{a_i,v}(t) \geq w_{a_i,v} \cdot \varepsilon_{a_i,v}(d + \Delta)$ for all $t \in [d + \Delta, d + \Delta + \gamma]$, $P_v(T_{out} - \gamma + \varepsilon)$ has for input $\langle s_1, \ldots, s_n \rangle$ a value that is at least as large as for input $\langle s_1', \ldots, s_n' \rangle$, and therefore a value $\geq \Theta_v(0)$. This implies that in the case $\sum_{i=1}^n r_i \cdot s_i > \gamma - \varepsilon$ the neuron v will fire within the time interval $[T_{out} - \gamma\ , T_{out} - \gamma + \varepsilon]$.

In an analogous manner we can achieve with the help of EPSP's from auxiliary excitatory neurons in $\mathcal{N}_{G,\varepsilon}$ (whose firing time depends only on T_{in}, not on the input values $s_1, \ldots, s_n$) that neuron v fires at the latest at time T_{out}, even if $\sum_{i=1}^n r_i \cdot s_i < 0$. The preceding analysis implies that for any value $s_i \in [0, \gamma]$ and any $t \leq T_{out}$ the absolute value of the PSP $w_{a_i,v} \cdot \varepsilon_{a_i,v}(t)$ can be bounded by $|w_{a_i,v}| \cdot \rho$, where $\rho := \sup\{|\varepsilon_{a_i,v}(t)| : i \in \{0, \ldots, n\}$ and $t \in [d\ , d + \Delta + \gamma]\}$ is the maximum absolute value that any $\varepsilon_{a_i,v}(t)$ for $i = 0, \ldots, n$ can reach during the initial segment of length $\Delta + \gamma$ of its non-zero segment. Since we have assumed that the absolute value of these functions $\varepsilon_{a_i,v}(t)$ grows during $[d + \Delta, d + \Delta + \gamma]$ not faster than during their linear segment $[d, d + \Delta]$, we can set $\rho := \Delta + \gamma$. Consequently we can derive for any $t \leq T_{out}$ and any values $s_1, \ldots, s_n \in [0, \gamma]$ the bound $|\sum_{i=0}^n h_i(t)| \leq \sum_{i=0}^n |w_{a_i,v}| \cdot \rho = W \cdot \rho$. Thus it suffices to make sure that EPSP's from auxiliary neurons in $\mathcal{N}_{G,\varepsilon}$ reach the trigger zone of neuron v shortly after time $T_{out} - \varepsilon$, and that their sum reaches a value $\Theta_v(0) + W \cdot \rho$ by time T_{out}. Then for any values of $s_1, \ldots, s_n \in [0, \gamma]$ the potential $P_v(t)$ will reach the value $\Theta_v(0)$ at the latest by time T_{out}, causing a firing of v by time T_{out} . These auxiliary EPSP's will in general have the side-effect that they slightly advance for inputs $s_1, \ldots, s_n \in [0, \gamma]$ with $\sum_{i=1}^n r_i \cdot s_i \in [0, \varepsilon]$ the firing time t_v , but the firing time will stay *within* the interval $[T_{out} - \varepsilon, T_{out}]$.

We assume that $\inf\{\Theta_v(x) : x \in (0, \gamma]\}$ is so large that v cannot fire *more* than once during $[T_{out} - \gamma\, , T_{out}]$. Hence our construction makes sure that v fires *exactly once* during $[T_{out} - \gamma\, , T_{out}]$ for any inputs $s_1, \ldots, s_n \in [0, \gamma]$. In the following we will denote this firing time t_v of v by $T_{out} - \mathcal{N}_{G,\varepsilon}(s_1, \ldots, s_n)$.

We have now shown that under the assumption that no noise influences the firing time t_v of neuron v, we have $|\mathcal{N}_{G,\varepsilon}(s_1,\ldots,s_n) - f_G(s_1,\ldots,s_n)| \leq \varepsilon$ for all $s_1,\ldots,s_n \in [0,\gamma]$. If one plots the variable $y = \mathcal{N}_{G,\varepsilon}(s_1,\ldots,s_n)$ which neuron v outputs in temporal coding as a function of $\sum_{i=1}^n r_i \cdot s_i$, one sees that the effective "activation function" σ of this implementation of the π_γ-gate G has the form indicated in Figure 3: Like the piecewise linear activation function π_γ of the simulated

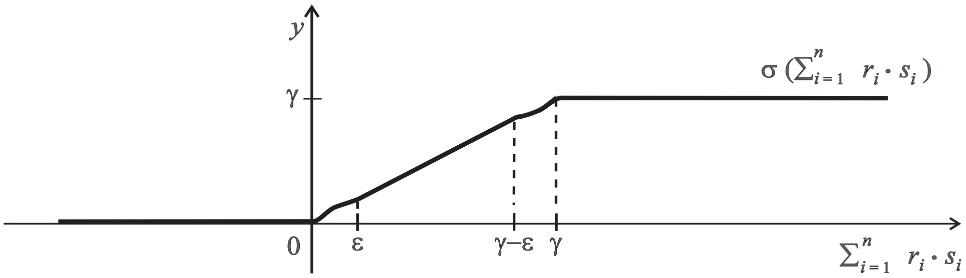

Figure 3: The resulting "activation function" σ of the implementation of a sigmoidal gate in temporal coding.

gate G, this activation function σ is linear in the intervals $(-\infty, 0]$, $[\varepsilon, \gamma-\varepsilon]$, $[\gamma, \infty)$. However in contrast to π_γ it connects these linear segments by smooth segments in the intervals $[0, \varepsilon]$ and $[\gamma-\varepsilon, \gamma]$, whose precise shape depends on the exact shape and size of the previously discussed auxiliary EPSP's and IPSP's.

We will now consider the general case where the firing time t_v of v is subject to two types of *noise*, as described in section 1. We show that by choosing the parameter λ in our preceding construction sufficiently large, we can achieve that in spite of these two types of noise the actual firing time $\tilde{t}_v$ of neuron v will be arbitrarily close to the previously considered "deterministic firing time" t_v of neuron v, with probability arbitrarily close to 1.

Assume that some arbitrary $\varepsilon, \delta > 0$ are given. In the preceding construction we had chosen values $w_i := \lambda \cdot r_i$ for the strengths of the synapses to neuron v, where $\lambda > 0$ was some not yet determined factor. According to (6) a change in the value of this parameter λ can only result in a shift of t_v by an amount that is independent from the input variables $s_1,\ldots,s_n$. Furthermore if one chooses $\Theta_v(0)$ in dependence of λ so that $\Theta_v(0) = \lambda \cdot \tilde{c}$ for some constant $\tilde{c}$, the resulting firing time t_v is completely independent from the choice of λ . On the other hand the parameter λ occurs as a factor in the term $\sum_{i=0}^n \lambda \cdot r_i \cdot |\varepsilon_{a_i,v}(t-(T_{in}-s_i))| = \sum_{i=0}^n h_i(t)$ in the potential $P_v(t) = \sum_{i=0}^n h_i(t)$ (we ignore the effect of auxilary PSP's for the moment). Hence by choosing λ sufficiently large one can make sure that in the deterministic case $P_v(t)$ has an arbitrarily large derivative at the time t_v when it crosses $\Theta_v(t-t')$.

Furthermore if we choose γ, λ, and $\Theta_v(0)$ so that (8) can be replaced by

$$2\gamma \;\leq\; \frac{\Theta_v(0)}{\lambda} \;\leq\; \Delta - \gamma - \varepsilon \;, \tag{9}$$

then it is guaranteed that the linearly increasing potential $P_v(t)$ (with slope proportional to λ) will rise with the same slope throughout the interval $[t_v - \gamma\,, t_v + \varepsilon]$.

If we now keep this setting of the parameters, but replace the deterministic neuron v by a stochastic neuron v that is subject to the two types of noise that were specified in section 1, the following can be observed. If $|\alpha(t)| \leq \alpha$ and $|\beta(t)| \leq \beta$ for all t , then the time interval around t_v during which $P_v(t)$ is within the interval $[\Theta - \alpha - \beta \, , \Theta + \alpha + \beta]$ becomes arbitrarily small for sufficiently large λ .

Furthermore if λ is sufficiently large (and $\Theta_v(0)$ is adjusted along with λ so that $\frac{\Theta_v(0)}{\lambda} = \tilde{c}$ for some constant $\tilde{c} > 0$ that is independent of λ), then $P_v(t)+\alpha+\beta-\Theta_v(0)$ is arbitrarily negative during $[T_{out} - \gamma \, , \, t_v - \varepsilon]$. Thus the probability that v fires during $[T_{out} - \gamma \, , \, t_v - \varepsilon]$ can be brought arbitrarily close to 0. In addition, by making λ sufficiently large one can achieve that $P_v(t) - \alpha - \beta - \Theta_v(0)$ is arbitrarily large throughout the time interval $[t_v + \varepsilon/2 \, , \, t_v + \varepsilon]$. Hence the probability that v fires by time $t_v + \varepsilon$ can be brought arbitrarily close to 1.

If one increases the number (respectively weights) of the previously described auxilary PSP's in an analogous manner, one can achieve for the here considered noisy neuron model that with probability $\geq 1 - \delta$ the neuron v of the here constructed network $\mathcal{N}_{G,\varepsilon,\delta}$ fires exactly once during $[T_{out} - \gamma \, , \, T_{out}]$, and at a time $\tilde{t}_v = T_{out} - \mathcal{N}_{G,\varepsilon,\delta}(s_1, \ldots, a_n)$ with $|\mathcal{N}_{G,\varepsilon,\delta}(s_1, \ldots, a_n) - f_G(s_1, \ldots, s_n| \leq 2\varepsilon$, for all $s_1, \ldots, s_n \in [0, \gamma]$.

The previously described construction can easily be adapted to allow shifts in the arrival times of auxiliary PSP's at v of up to $\varepsilon/2$. Hence we can allow that these PSP's also come from *noisy* spiking neurons.

In order to simulate an arbitrary given feedforward network N of π_γ-gates with precision ε and probability $\geq 1 - \delta$ of correctness, one applies the preceding construction separately to each gate G in N. For any given $\varepsilon, \delta > 0$ one determines for each π_γ-gate G in N (starting at the output gates of N) suitable values $\varepsilon_G, \delta_G > 0$, so that in order to approximate N within ε with probability $\geq 1 - \delta$ it suffices that each gate G in N is approximated within $2\varepsilon_G$ with probability $\geq 1 - \delta_G$ by a network $\mathcal{N}_{G,\varepsilon_G,\delta_G}$ of noisy spiking neurons. In this way one can achieve that the network $\mathcal{N}_{N,\varepsilon,\delta}$ of noisy spiking neurons that is composed of these networks $\mathcal{N}_{G,\varepsilon_G,\delta_G}$ approximates in temporal coding with probability $\geq 1 - \delta$ the output of N within ε , for any given network input $x_1, \ldots, x_m \in [0, \gamma]$.

This implies the claim of Theorem 2.1 because of the relationship between π-gates and π_γ-gates that we had described at the beginning of this proof. ∎