

On the Complexity of Learning for Spiking Neurons with Temporal Coding¹

Wolfgang Maass

Institute for Theoretical Computer Science, Technische Universität Graz,

Klosterwiesgasse 32/2, A-8010 Graz, Austria

E-mail: maass@igi.tu-graz.ac.at

and

Michael Schmitt²

Lehrstuhl Mathematik und Informatik, Fakultät für Mathematik,

Ruhr-Universität Bochum, D-44780 Bochum, Germany

E-mail: mschmitt@lmi.ruhr-uni-bochum.de

Spiking neurons are models for the computational units in biological neural systems where information is considered to be encoded mainly in the temporal patterns of their activity. In a network of spiking neurons a new set of parameters becomes relevant which has no counterpart in traditional neural network models: the time that a pulse needs to travel through a connection between two neurons (also known as delay of a connection). It is known that these delays are tuned in biological neural systems through a variety of mechanisms. In this article we consider the arguably most simple model for a spiking neuron, which can also easily be implemented in pulsed VLSI. We investigate the Vapnik–Chervonenkis (VC) dimension of networks of spiking neurons, where the delays are viewed as programmable parameters and we prove tight bounds for this VC dimension. Thus, we get quantitative estimates for the diversity of functions that a network with fixed architecture can compute with different settings of its delays. In particular, it turns out that a network of spiking neurons with k adjustable delays is able to compute a much richer class of functions than a threshold circuit with k adjustable weights. The results also yield bounds for the number of training examples that an algorithm needs for tuning the delays of a network of spiking neurons. Results about the computational complexity of such algorithms are also given. © 1999 Academic Press

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² Corresponding author. This research was carried out while M. Schmitt was with the Institute for Theoretical Computer Science at the Technische Universität Graz.

1. INTRODUCTION AND DEFINITIONS

During the last few years the paradigms for computation in biological neural systems have undergone drastic changes. With the help of refined experimental techniques it has been learned that information is not only encoded in the *firing rates* of biological neurons, but often also in the *temporal patterns* of their firing. Whereas threshold circuits and sigmoidal neural networks provide a suitable model for neural computation based on *rate coding*, i.e. in terms of firing rates, they cannot be used for modelling neural computation based on *temporal coding*, i.e. in terms of temporal patterns of neuronal activity. In order to model temporal patterns of activity, one has to consider networks consisting of a different type of computational unit: spiking neurons, or leaky integrate-and-fire neurons, as they are commonly called in biophysics and theoretical neurobiology.

We will focus in this article on a simple version of the spiking neuron model (“spiking neurons of type A” in the terminology of Maass, 1997b). This model allows us to study some fundamental new learning problems that arise in the context of computation with temporal coding. Since the model is sufficiently simple, the basic aspects of this new mode of computation are not obscured by the myriad of additional subtleties and complications that occur in a more detailed neuron model. In addition, this simple model for a spiking neuron has the advantage that it provides a link to silicon implementations of spiking neurons in analog VLSI (see, e.g., Maass and Bishop, 1999).

1.1. The Model for a Spiking Neuron

We consider a *spiking neuron* v that receives inputs in the form of short pulses, also known as *spikes*, from n input neurons a_1, \dots, a_n . We assume that there exists for $i = 1, \dots, n$ a connection from a_i to v with weight $w_i \in \mathbb{R}$ and delay $d_i \in \mathbb{R}^+$ (where $\mathbb{R}^+ = \{x \in \mathbb{R} : x \geq 0\}$). We treat time as a continuous variable. For simplicity we assume that if the input neuron a_i *fires*, i.e. emits a spike, at time t_i , this causes a rectangular pulse in v of the form $h_i(t - t_i)$ with

$$h_i(x) = \begin{cases} 0 & \text{for } x < d_i \text{ or } x \geq d_i + 1, \\ w_i & \text{for } d_i \leq x < d_i + 1. \end{cases}$$

We assume that the neuron v fires as soon as the sum $P_v(t) = \sum_{i=1}^n h_i(t - t_i)$ of these pulses reaches a certain threshold θ_v . More precisely, the firing time of v is defined to be the smallest value t such that $P_v(t) \geq \theta_v$; if no such t exists then v does not fire.

In a biological context the pulses h_i are called *postsynaptic potentials*. They model the effect of a firing of neuron a_i on the *membrane potential* $P_v(t)$ at the trigger zone of v . The firing threshold θ of a biological neuron depends on the time which has passed since its last firing. For simplicity we assume here that the neuron has not fired for a while (say at least 20 ms), so that its firing threshold has returned to its *resting value* θ_v .³

³ There is some discussion among neurobiologists whether the sign of a synaptic efficacy w_i can change in the course of a learning process. This issue will not be relevant for the results of this article.

The model is a simple version of a leaky integrate-and-fire neuron. In contrast to more complex models (see e.g., Tuckwell, 1988; Gerstner, 1995; Maass, 1997a), it models a pulse as a step function, rather than as a continuous function of a similar shape. Pulses of this shape are actually very common in silicon implementations of networks of spiking neurons (Murray and Tarassenko, 1994; Maass and Bishop, 1999).

A spiking neuron of this type was called a “spiking neuron of type A” in Maass (1997b). In this article we will refer to it simply as a *spiking neuron*.

1.2. Temporal Coding

A spiking neuron may be viewed as a digital or analog computational element, depending on the type of temporal coding that is used. For *binary coding* we assume that input neuron a_i fires at time 0 if it encodes a 1, and that it does not fire at all if it encodes a 0. Correspondingly, we assume that v outputs a 1 if it fires as a result of this input from a_1, \dots, a_n , and that v outputs a 0 if it does not fire. For binary coding we do not make any requirements on the timing of its firing, when v outputs a 1.

For *analog coding* we assume that a_i encodes a real number $t_i \in \mathbb{R}^+$ by firing at time t_i . The output value of v is the time t_v when it fires (or $t_v - T$ for a suitable constant T if one wants to scale the real-valued output of v into a specific range). In the case that v does not fire, we assume that this encodes some fixed analog output t_0 (e.g., $t_0 = 0$).

We will consider both types of coding in this article. Moreover, the type of coding for the inputs may differ from that for the output; e.g., analog coding for the inputs and binary coding for the output may occur. In some cases, the proof of a result for binary coding implies a corresponding result for analog coding or vice versa. We then prove the result for that type of coding for which it is more difficult and explain afterward how to obtain the corresponding result for the other type.

We view in the following the delays d_i as “programmable parameters” of a neuron, in addition to the weights w_i of its synapses. This is reasonable since in biology many mechanisms are known that can change the effective delay between two neurons. One well-known mechanism is the selection of a few synapses out of an initially very large set of synapses between two neurons. Some other biological mechanisms for changing the effective delay between two neurons are discussed in (Agmon-Snir and Segev, 1993; Gerstner *et al.*, 1996).

Our results about the VC dimension of a spiking neuron are complementary to those achieved in (Zador and Pearlmuter, 1996). In that article the integration time constant and the threshold were viewed as the only variable parameters of a spiking neuron, whereas the effect of variable delays was not addressed.

1.3. Complexity of Learning

In this article we investigate the complexity of learning for a spiking neuron within the framework of *probably approximately correct learning*, or *PAC-learning* for short. For detailed definitions of this paradigm we refer the reader to (Anthony

and Biggs, 1992; Blumer *et al.*, 1989; Valiant, 1984). In Section 2 we estimate the computational power and the sample complexity of a single spiking neuron. We give upper and lower bounds for its computational power when using binary coding in terms of several classes of Boolean functions. The sample complexity is analyzed in terms of the *Vapnik–Chervonenkis dimension*, or *VC dimension* for short. As the main result of this section we show that for binary and analog coding the VC dimension of the corresponding function class is $\Theta(n \log n)$. It is well known that the VC dimension of a function class gives fairly tight bounds on the sample complexity, i.e. the number of training examples needed, for PAC-learning this class. According to (Haussler, 1992), these estimates of the sample complexity in terms of the VC dimension hold even for agnostic PAC-learning, i.e. in the case when the training examples are generated by some arbitrary probability distribution. In particular, these bounds remain valid when the training examples are not generated by a spiking neuron.

In Section 3 we consider feedforward networks of spiking neurons. We show that such networks can have a VC dimension that is quadratic in the number of delays that are programmable. Interestingly, this bound equals the quadratic lower bound for sigmoidal networks in terms of the number of weights due to (Koiran and Sontag, 1997). We further show that this bound is asymptotically tight by proving that any feedforward network of spiking neurons has a VC dimension that is at most quadratic in the number of its edges. Moreover, this upper bound holds even if all delays, weights, and thresholds are programmable and even for analog coding of the inputs. The proof of this bound relies on a well-known and far-reaching result by (Goldberg and Jerrum, 1995).

In Section 4 we investigate the computational complexity of PAC-learning using a particular spiking neuron as the hypothesis class. We show that for any bounded set of at least two delay values the consistency problem for the corresponding hypothesis class is NP-complete. This implies that there are no efficient PAC-learning algorithms for these hypothesis classes unless the complexity classes RP and NP are equal. The intractability results presented in this section have consequences also for the case of agnostic PAC-learning. According to known results (Kearns *et al.*, 1994b; Höffgen *et al.*, 1995), polynomial-time agnostic PAC-learning with some hypothesis class \mathcal{H} is possible only if the minimizing disagreement problem for \mathcal{H} is in RP. Now, for each hypothesis class \mathcal{H} the consistency problem for \mathcal{H} can be solved in polynomial time if the minimizing disagreement problem for \mathcal{H} can be solved in polynomial time. (More precisely, there is an easily definable polynomial-time reduction from the consistency problem to the minimizing disagreement problem.) Therefore, polynomial-time agnostic PAC-learning is not possible for the hypothesis classes considered in this section, provided that $\text{RP} \neq \text{NP}$.

The final section 5 contains some concluding remarks and discussion.

2. COMPUTATIONAL POWER AND VC DIMENSION OF A SINGLE SPIKING NEURON

We first introduce some notation. The class of Boolean functions that can be computed by a spiking neuron with n binary coded inputs and a binary coded output is

denoted by $\mathcal{S}_n^{\text{bb}}$ (where “bb” stands for “binary input and binary output”). Correspondingly, $\mathcal{S}_n^{\text{aa}}$ is the class of functions from \mathbb{R}^n to \mathbb{R} that can be computed by a spiking neuron with analog coding of the inputs and the output. The subclass of $\mathcal{S}_n^{\text{aa}}$ restricted to Boolean output values encoded in binary is denoted by $\mathcal{S}_n^{\text{ab}}$.

We use a similar notation for the threshold gate and for the sigmoidal gate: A threshold gate, also known as a perceptron or a McCulloch–Pitts neuron, with inputs x_1, \dots, x_n has weights w_1, \dots, w_n , where w_i is associated with x_i for $i = 1, \dots, n$ and a threshold θ . It outputs 1 if $w_1x_1 + \dots + w_nx_n \geq \theta$; otherwise 0. By $\mathcal{T}_n^{\text{bb}}$ we denote the class of Boolean functions that can be computed by a threshold gate. A threshold gate with real-valued inputs and binary-valued output corresponds to a half-space over \mathbb{R}^n . We denote the corresponding function class by $\mathcal{T}_n^{\text{ab}}$. The sigmoidal gate is a neuron model that computes functions from \mathbb{R}^n to \mathbb{R} . We assume that it calculates its output value by applying the standard sigmoidal function $1/(1 + e^{-y})$ to the sum $w_1x_1 + \dots + w_nx_n - \theta$. We denote the corresponding function class by $\mathcal{T}_n^{\text{aa}}$.

For assessing the computational power of a spiking neuron in the Boolean domain it turns out that it is useful to consider two further classes of Boolean functions: the first one is a special type of disjunctive normal form (DNF); the second one is a disjunction of linearly many threshold gates. The class $\mu\text{-DNF}_n$ is the class of Boolean functions, each of which can be written as a DNF formula over n variables where each variable occurs at most once. By $\text{OR-of-}O(n)\text{-}\mathcal{T}_n^{\text{bb}}$ we denote the class of Boolean functions that can be computed by a disjunction of $O(n)$ threshold gates.

2.1. Computational Power

It is obvious that in the case of binary coding a spiking neuron has at least the computational power of a threshold gate; just assume that all delays d_i are equal. However, it is easy to see that its computational power is strictly larger. In order to characterize its power more precisely we compare it with the Boolean function classes defined above. The following theorem clarifies the relationships among these classes. It shows that a spiking neuron with binary coding can also compute any function in $\mu\text{-DNF}$. On the other hand, it can be simulated by a disjunction of linearly many threshold gates. The results are graphically depicted in Fig. 1.

THEOREM 2.1. (a) $\mathcal{T}_n^{\text{bb}} \not\subseteq \mu\text{-DNF}_n$ for all $n \geq 3$.

(b) $\mu\text{-DNF}_n \not\subseteq \mathcal{T}_n^{\text{bb}}$ for all $n \geq 4$.

(c) $\mathcal{T}_n^{\text{bb}} \subseteq \mathcal{S}_n^{\text{bb}}$ for all n , and $\mathcal{T}_n^{\text{bb}} \neq \mathcal{S}_n^{\text{bb}}$ for all $n \geq 4$.

(d) $\mu\text{-DNF}_n \subseteq \mathcal{S}_n^{\text{bb}}$ for all n , and $\mu\text{-DNF}_n \neq \mathcal{S}_n^{\text{bb}}$ for all $n \geq 3$.

(e) $\mathcal{S}_n^{\text{bb}} \subseteq \text{OR-of-}O(n)\text{-}\mathcal{T}_n^{\text{bb}}$. More precisely, each function in $\mathcal{S}_n^{\text{bb}}$ can be computed by an OR of $2n - 1$ threshold gates. For $n \geq 2$, however, there exist functions computable by an OR of two threshold gates that are not in $\mathcal{S}_n^{\text{bb}}$.

Proof. All proofs are straightforward. We give evidence of the inequality claims by presenting for each of them a function that separates the two classes involved for

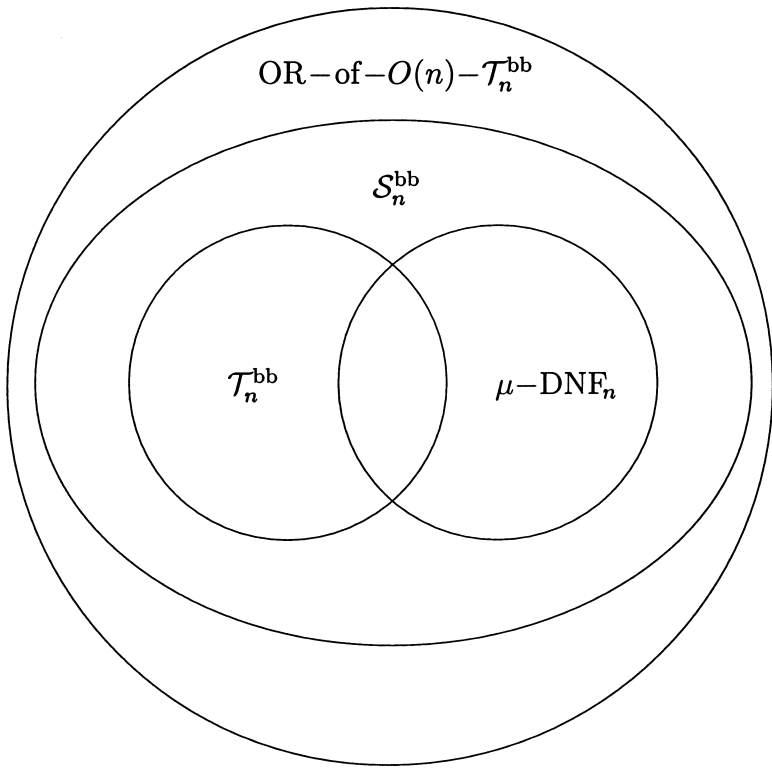


FIG. 1. Upper and lower bounds for the computational power of a spiking neuron in the Boolean domain as established in Theorem 2.1.

the smallest n . It is then easy to obtain a separating function also for higher values of n .

(a) The function $(x_1 \wedge x_2) \vee (x_1 \wedge x_3) \vee (x_2 \wedge x_3)$, which is 1 if and only if the input vector contains at least two 1's, can obviously be computed by a threshold gate. Assume that it can be written as a μ -DNF $_3$ formula. Then this formula either contains an AND clause with only one variable or it consists of at most one AND clause, both of which contradict the definition of the function.

(b) Consider the μ -DNF $_4$ formula $(x_1 \wedge x_2) \vee (x_3 \wedge x_4)$. Assuming that it can be computed by a threshold gate implies that $w_1 + w_2 \geq \theta$ and $w_3 + w_4 \geq \theta$, but also that $w_1 + w_3 < \theta$ and $w_2 + w_4 < \theta$. All four inequalities together form a contradiction.

(c) The inclusion is obvious. For the inequality consider the function in (b) which can be computed by a spiking neuron as follows: Choose equal values for delays which belong to the same AND clause and take care that pulses from different AND clauses do not overlap. This is also the general way of computing a μ -DNF formula by a spiking neuron, which is the first claim of (d).

(d) For the inclusion see (c). For the inequality consider the function $(x_1 \wedge x_2) \vee (x_2 \wedge x_3)$ which is in $\mathcal{S}_3^{\text{bb}}$: Choose delays such that the pulses for x_1 and x_3 do not overlap but that those for each pair x_1, x_2 and x_2, x_3 do overlap. It is easy to see that this function cannot be written as a μ -DNF $_3$ formula.

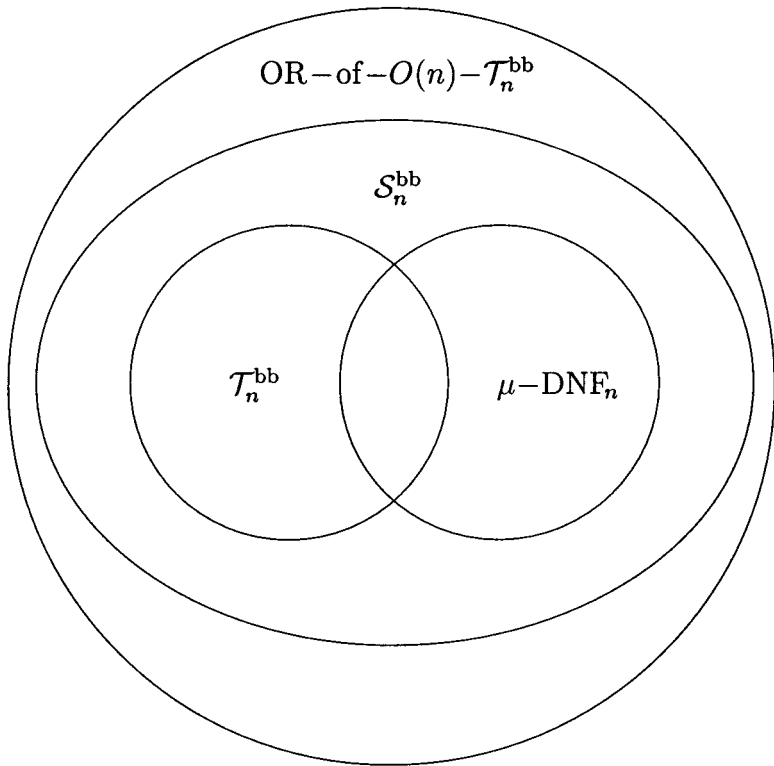


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The weights are defined as $w_i = 1$ for $1 \leq i \leq m + 2^k$, and the threshold is $3/2$. The delays for the last 2^k inputs are fixed in such a way that pulses for inputs from different components $b_A, b_{A'}$, where $A \neq A'$, do not overlap. (For instance, integer values $\{0, \dots, 2^k - 1\}$ would do this.)

It remains to show that S can be shattered. Let $S' \subseteq S$. The delays for the first m inputs are specified as follows: For each $i \in \{1, \dots, m\}$ define the set

$$A'_i = \{j \in \{1, \dots, k\} : \mathbf{s}^{i,j} \in S'\} \quad (2)$$

and choose the delay for the i th input equal to the delay of input $b_{A'_i}$. Now consider an arbitrary $\mathbf{s}^{i,j} \in S$. Since the threshold is $3/2$, the neuron fires if and only if inputs i and $b_{A'_i}$ both receive a 1. By means of (1), this holds if and only if $j \in A'_i$, and hence by means of (2), if and only if $\mathbf{s}^{i,j} \in S'$. ■

We have assumed binary coding of the input values in the proof of Theorem 2.3. However, the result can be shown to hold also for analog coding of the input values at the cost of adding an extra input with value 0. Its weight is chosen such that all pulses from inputs that encode 0 are cancelled. This weight can also be kept fixed because all elements of S constructed in the proof have the same number of 0s.

2.3. Upper Bound for the VC Dimension

The lower bound of Theorem 2.2 holds for a very restricted spiking neuron with fixed weights and integer delays. The following surprising result shows that this bound is asymptotically tight, even if the delays and weights range over arbitrary real numbers.

THEOREM 2.4. *The VC dimension of a spiking neuron with n analog coded inputs and binary coded output is $O(n \log n)$.*

The following statement is an immediate consequence of Theorems 2.2 and 2.4. It summarizes the results of this section in terms of the function classes computed by a spiking neuron.

COROLLARY 2.5. *The classes $\mathcal{S}_n^{\text{bb}}$ and $\mathcal{S}_n^{\text{ab}}$ have VC dimension $\Theta(n \log n)$.*

In the proof of Theorem 2.4 we will use the following result which is a consequence of Theorem 2 in (Cover, 1965)⁴ and Proposition A2.1 of (Blumer *et al.*, 1989).

LEMMA 2.6. *Let m hyperplanes in \mathbb{R}^n passing through the origin be given, where $m \geq n$. They partition \mathbb{R}^n into at most $2(em/(n-1))^{(n-1)}$ different regions.*

Proof. By Theorem 2 of (Cover, 1965), m hyperplanes through the origin partition \mathbb{R}^n into at most $2 \sum_{k=0}^{n-1} \binom{m-1}{k}$ different regions. By Proposition A2.1(iii) of (Blumer *et al.*, 1989), $2 \sum_{k=0}^{n-1} \binom{m-1}{k} \leq 2(e(m-1)/(n-1))^{(n-1)}$ for $m \geq n$. ■

⁴ This reference is frequently cited when using this result. Cover himself, however, attributes the first proof of this theorem to (Schläfli, 1901).

Proof of Theorem 2.4. The proof is structured as follows: We first estimate the number of dichotomies induced by a spiking neuron on an arbitrary finite set $S \subseteq \mathbb{R}^n$ of cardinality m . This will result in the upper bound on the number of dichotomies

$$2(4emn)^n \cdot 2(2em)^n. \quad (3)$$

Then the assumption that S is shattered by a spiking neuron, i.e. that all 2^m dichotomies can be computed, will lead to the bound $m = O(n \log n)$ and, hence, to the claimed result.

The computation of a spiking neuron can be considered in the following way: Given an input vector and a delay vector, at most $2n - 1$ intervals on the time axis have to be considered in order to determine whether the neuron fires. These intervals are specified by the starting and ending points of the n pulses. With each interval there is associated a subset of the weights corresponding to the set of pulses that are active during this interval. The neuron fires if within some interval the sum of the weights in the associated subset reaches the threshold.

In order to prove (3), we first estimate the number of different delay vectors that have to be considered. For each fixed $\mathbf{s} = (s_1, \dots, s_n) \in S$, the space \mathbb{R}^n of delay vectors $\mathbf{d} = (d_1, \dots, d_n)$ is partitioned into regions by hyperplanes of the form

$$s_i + d_i + y = s_j + d_j + z,$$

where $y, z \in \{0, 1\}$, depending on whether the term corresponds to a starting or ending point of a pulse. Taking into account all values for $i, j \in \{1, \dots, n\}$ and $y, z \in \{0, 1\}$ we derive that there are at most $(2n)^2$ such hyperplanes for each fixed \mathbf{s} . They partition \mathbb{R}^n into regions of delay vectors that are equivalent with regard to the computation of the neuron on input vector \mathbf{s} . If one partitions \mathbb{R}^n by at most $m \cdot (2n)^2$ hyperplanes that arise for all $\mathbf{s} \in S$, the resulting regions consist of delay vectors \mathbf{d} that are equivalent with regard to all input vectors $\mathbf{s} \in S$. Estimating the number of different regions, one has to take into account that the hyperplanes do not necessarily pass through the origin. But the number of different regions of \mathbb{R}^n generated by $m \cdot (2n)^2$ arbitrary hyperplanes is at most as large as the number of different regions of \mathbb{R}^{n+1} generated by $m \cdot (2n)^2$ hyperplanes that all pass through the origin. By Lemma 2.6 this partition consists of at most $2(4emn)^n$ different regions. Hence, for inputs from S it suffices to consider these many delay vectors.

Now we show that for each fixed delay vector at most $2(2em)^n$ many weight vectors need to be considered. The upper bound (3) follows then from this number and the bound on the number of different delay vectors. For each fixed input vector $\mathbf{s} \in S$ and each delay vector \mathbf{d} there are at most $2n - 1$ hyperplanes that have to be considered corresponding to the intervals during which there are active pulses. Each hyperplane is characterized by a subset of $\{w_1, \dots, w_n\}$ and by the threshold θ_v . If for the given \mathbf{s} and \mathbf{d} two weight vectors of the spiking neuron result in different outputs, then these outputs must be different for one of the intervals and, hence, for the hyperplane corresponding to this interval. Consequently, the number of regions of the space \mathbb{R}^{n+1} of weights w_1, \dots, w_n and threshold θ_v is not larger than the number of regions that arise from at most $2n - 1$ hyperplanes. Taking into account

all $\mathbf{s} \in S$, the space \mathbb{R}^{n+1} is partitioned by at most $m \cdot (2n - 1)$ hyperplanes that all pass through the origin. By Lemma 2.6 the number of different regions that arise from these hyperplanes is bounded by $2(2em)^n$. From this (3) follows.

Finally, the following claim implies the bound $O(n \log n)$ for the VC dimension and, hence, the statement of the theorem.

Claim. The VC dimension of $\mathcal{S}_n^{\text{ab}}$ is at most $8n \log(2n)$ for all $n \geq 8e^2$.

Assume that S has cardinality m and is shattered by $\mathcal{S}_n^{\text{ab}}$. Hence, all 2^m dichotomies of S can be computed by a spiking neuron. Then (3) implies

$$\begin{aligned} 2^m &\leq 2(4emn)^n \cdot 2(2em)^n \\ &= 4(8e^2m^2n)^n \\ &\leq 4(mn)^{2n}, \end{aligned}$$

where we have used the assumption $n \geq 8e^2$ for the last inequality. Taking logarithms on both sides yields

$$m \leq 2n \log(mn) + 2,$$

which implies

$$m \leq 2n(\log(mn) + 1). \tag{4}$$

For any $m \geq \log n$ there is a real number $r \geq 1$ such that $m = r \log(rn)$. (This can easily be seen from the fact that for arbitrary n the function $q_n: [1, \infty) \rightarrow [\log n, \infty)$ defined by $q_n(z) = z \log(zn)$ is 1-1 and onto.) Substituting $m = r \log(rn)$ on both sides of (4) yields

$$\begin{aligned} r \log(rn) &\leq 2n(\log(rn \log(rn)) + 1) \\ &= 2n(\log(rn) + \log(\log(rn)) + 1) \\ &\leq 2n(\log(rn) + \log(rn/2) + 1), \end{aligned}$$

where the last inequality follows from $\log(rn) \leq rn/2$. (This requires $rn \geq 4$ which is guaranteed by the assumption $n \geq 8e^2$.) Hence, we have

$$r \log(rn) \leq 4n \log(rn).$$

Dividing both sides by $\log(rn)$, which is positive due to $rn \geq 8e^2$, we get

$$r \leq 4n,$$

which implies

$$r \log(rn) \leq 4n \log(4n^2).$$

Resubstituting $m = r \log(rn)$ for the left-hand side and rearranging the right-hand side yields

$$m \leq 8n \log(2n),$$

as claimed. This completes the proof of Theorem 2.4. \blacksquare

The bound (3) can also be used to estimate the number of Boolean functions that can be computed by a spiking neuron. Substituting $m = 2^n$ yields the bound $2^{O(n^2)}$. Combining this with the lower bound $2^{\Omega(n^2)}$ of (Muroga and Toda, 1966) for $\mathcal{F}_n^{\text{bb}}$ and our Theorem 2.1(c), we get the upper and the lower bounds almost matching.

COROLLARY 2.7. *There are $2^{\Theta(n^2)}$ many Boolean functions computable by a spiking neuron with binary coding of the inputs.*

For the case of binary coding the analysis can even be made simpler, because the factor $2(4emr)^n$ in (3), which is a bound on the number of delay vectors that have to be considered, can be replaced by a bound that is easier to obtain. One observes that for a set $S \subseteq \{0, 1\}^n$ of input vectors each delay needs to take on at most n^2 many different values. Hence, it is sufficient to consider at most $2^{2n \log n}$ many delay vectors. Thus, one derives the upper bound $2^{n^2 + O(n \log n)}$ for the number of Boolean functions. This result is particularly interesting in the light of the fact that there are at most 2^{n^2} many different functions in $\mathcal{F}_n^{\text{bb}}$ (Muroga, 1971).

2.4. Pseudo Dimension

When analyzing the PAC-learnability of real-valued function classes the *pseudo dimension* plays a similar role as the VC dimension does for binary-valued function classes (Haussler, 1992). Following the terminology of (Macintyre and Sontag, 1993) we say a set $\{\mathbf{s}^1, \dots, \mathbf{s}^m\} \subseteq \mathbb{R}^n$ is *H-shattered* by a class \mathcal{F} of real-valued functions if there exist real numbers x^1, \dots, x^m such that every dichotomy of $\{(\mathbf{s}^1, x^1), \dots, (\mathbf{s}^m, x^m)\}$ is induced by some function of the form $(\mathbf{s}, x) \mapsto \text{sign}(f(\mathbf{s}) - x)$ for some $f \in \mathcal{F}$. (Here $\text{sign}(x)$ denotes the function which outputs 1 if $x \geq 0$, otherwise, 0.) Analogously to the VC dimension, the pseudo dimension of \mathcal{F} is defined as the largest number m such that there is a set of m elements that is H-shattered by \mathcal{F} . Obviously, if \mathcal{F} contains only binary-valued functions then its pseudo dimension is equal to its VC dimension.

Using known results about the pseudo dimension (see, e.g., Haussler, 1992) it is easy to derive that the class $\mathcal{F}_n^{\text{aa}}$ has pseudo dimension $n + 1$, which is equal to the number of programmable parameters. From our definitions for binary and analog coding in Subsection 1.2 it follows immediately that a set which is shattered by a spiking neuron with binary coding of the output is also H-shattered by a spiking neuron with analog coding of the output. Hence, by Theorem 2.2 the pseudo dimension of the class $\mathcal{S}_n^{\text{aa}}$ is $\Omega(n \log n)$. Thus, the pseudo dimension of a spiking neuron is significantly larger than the pseudo dimension of a sigmoidal gate, even when the delays are the only adjustable parameters of the spiking neuron. The following result shows that this lower bound is asymptotically tight.

THEOREM 2.8. *The pseudo dimension of a spiking neuron with n analog coded inputs and analog coded output is $O(n \log n)$.*

Proof. We follow the same lines of reasoning as in the proof of Theorem 2.4; i.e., we first estimate the number of dichotomies that are induced on a set $S = \{(\mathbf{s}^1, x^1), \dots, (\mathbf{s}^m, x^m)\} \subseteq \mathbb{R}^{n+1}$ by the functions $(\mathbf{s}, x) \mapsto \text{sign}(f(\mathbf{s}) - x)$ for $f \in \mathcal{S}_n^{\text{aa}}$.

For each fixed $(\mathbf{s}, x) \in S$, the space \mathbb{R}^n is partitioned into regions of equivalent delay vectors \mathbf{d} by hyperplanes of the form

$$s_i + d_i + y = s_j + d_j + z$$

and

$$s_i + d_i + u = x,$$

where $u, y, z \in \{0, 1\}$, depending on whether the term corresponds to a starting or ending point of a pulse. For all $(\mathbf{s}, x) \in S$ together we thus obtain at most $m \cdot ((2n)^2 + 2n) = m \cdot 2n(2n + 1)$ hyperplanes that define regions of delay vectors that are equivalent with regard to the computation on S . We bound the number of these regions by the number of regions of \mathbb{R}^{n+1} that arise from $m \cdot 2n(2n + 1)$ hyperplanes passing through the origin. These are by Lemma 2.6 at most $2(2em(2n + 1))^n$ different regions. Hence, for inputs from S it is sufficient to consider these many delay vectors.

Now, for each fixed delay vector the upper bound $2(2em)^n$ on the number of weight vectors can be derived as in Theorem 2.4. Multiplying both bounds, we have that the number of dichotomies that are induced on S by the functions $(\mathbf{s}, x) \mapsto \text{sign}(f(\mathbf{s}) - x)$ is at most

$$2(2em(2n + 1))^n \cdot 2(2em)^n.$$

If all dichotomies of S are induced then this bound must be greater than or equal to 2^m . From this we obtain the claimed result $m = O(n \log n)$ by a calculation which is analogous to that in Theorem 2.4 and omitted here. ■

We summarize the results on the pseudo dimension for a spiking neuron obtained in this section.

COROLLARY 2.9. *The class $\mathcal{S}_n^{\text{aa}}$ has pseudo dimension $\Theta(n \log n)$.*

3. VC DIMENSION FOR NETWORKS OF SPIKING NEURONS

We consider feedforward networks of spiking neurons (SNNs), where the structure, or architecture, of a network is defined in terms of an underlying directed acyclic graph. The network inputs and outputs can encode Boolean or analog values as in the preceding section. The output of an internal gate is assumed to be an analog variable encoded through the timing of its output spike. The following lower bound for the VC dimension of an SNN in terms of the number of delays

equals the quadratic lower bound in terms of the number of weights due to (Koira and Sontag, 1997), which holds for sigmoidal neural networks. The agreement between these two bounds is somewhat surprising, since the settings and the constructions are quite different. The result shows in particular that the VC dimension of an SNN with k adjustable delays can be substantially larger than the VC dimension of any threshold circuit with k adjustable weights.

THEOREM 3.1. *For each n one can construct a feedforward SNN \mathcal{N} with $O(n)$ edges that has VC dimension $\Omega(n^2)$. This even holds if all weights and thresholds remain fixed.*

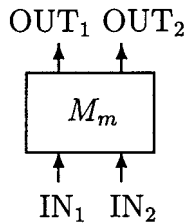
Proof. For any given $n \in \mathbb{N}$ we construct an SNN \mathcal{N} with $O(n)$ edges that has VC dimension at least n^2 . The essential building blocks of \mathcal{N} are modules M_1, \dots, M_n (see Fig. 4). The task of module M_m is to read out (and remove) the most significant bit b_m from any m -bit number $\langle b_1, \dots, b_m \rangle$ that is presented to M_m in the form of the delay of an input pulse⁵ at its first input port IN_1 (see Fig. 2). This delay with value $d = \sum_{i=1}^m b_i 2^{i-n-1}$ is measured relative to the arrival time of a second input pulse that enters M_m at the other input port IN_2 of M_m . The scaling of the delay d by 2^{-n} ensures that in the following the nonfixed delays, that is, those parts that depend on $\langle b_1, \dots, b_m \rangle$, all have values less than 1. (Note that $m \leq n$.) We will first describe the details of module M_m for $m = 1, \dots, n$, and then show how the desired SNN \mathcal{N} can be constructed with the help of these modules.

We fix some arbitrary constants $\Delta \geq 1/2$ and $\Delta', \Delta'' \geq 0$, which determine the fixed internal delays of connections inside the modules M_1, \dots, M_n . Assume that M_m receives at IN_1 a single pulse at time $d = \sum_{i=1}^m b_i 2^{i-n-1}$ (for arbitrary $b_1, \dots, b_m \in \{0, 1\}$) and at IN_2 a single pulse at time 0. The output port OUT_1 of M_m (see Fig. 2) will then emit a single spike at time $\Delta + \Delta' + \Delta'' + \sum_{i=1}^{m-1} b_i 2^{i-n-1}$ (note that the most significant bit b_m has been removed from this delay representation), and the output port OUT_2 of M_m will emit a spike if and only if $b_m = 1$; in the case that $b_m = 1$, a spike will be emitted from OUT_2 at time $\Delta + \Delta' + \sum_{i=1}^{m-1} b_i 2^{i-n-1}$.

We construct module M_m as a feedforward SNN consisting of four neurons (see Fig. 3). All weights on edges inside M_m have values from $\{-1, 1\}$. The thresholds have value $1/2$. Neuron v in M_m fires at most once. This firing happens during the time interval $[0, \Delta + 1)$ if and only if the pulse from IN_1 (which arrives at v at time $d + \Delta - 2^{m-n-1}$) arrives strictly before the pulse from IN_2 (which arrives at time Δ). Hence v fires during $[0, \Delta + 1)$ if and only if $d - 2^{m-n-1} < 0$, which holds if and only if $b_m = 0$. If v fires during $[0, \Delta + 1)$ it does so at time $d + \Delta - 2^{m-n-1}$. If $b_m = 1$ then $d - 2^{m-n-1} \geq 0$. If $d - 2^{m-n-1} > 0$ then v fires at time $\Delta + 1$, because the positive pulse from IN_1 is still present when the negative pulse from IN_2 expires at time $\Delta + 1$.

Since according to our construction (see Fig. 3) neuron u in M_m fires in any case at time $d + \Delta - 2^{m-n-1}$, neuron u' will fire if and only if v does not fire at time

⁵ To make this proof easier to read we identify a spike received by some neuron with the rectangular pulse it generates in the neuron.

FIG. 2. Module M_m .

$d + \Delta - 2^{m-n-1}$. Thus u' (which provides OUT_2) fires if and only if $b_m = 1$. Furthermore, if u' fires it does so at time $\Delta + \Delta' + d - 2^{m-n-1}$, which equals $\Delta + \Delta' + \sum_{i=1}^{m-1} b_i 2^{i-n-1}$ in the case $b_m = 1$.

Thus neuron v' (which provides OUT_1) receives in the case $b_m = 1$ a positive pulse from u' at time $\Delta + \Delta' + \Delta'' + \sum_{i=1}^{m-1} b_i 2^{i-n-1}$, a negative pulse from IN_2 at time $\Delta + \Delta' + \Delta'' + 2^{m-n-1} + 1$, and possibly a positive pulse from v at time $\Delta + \Delta' + \Delta'' + 2^{m-n-1} + 1$. Hence if $b_m = 1$ the neuron v' fires at time $\Delta + \Delta' + \Delta'' + \sum_{i=1}^{m-1} b_i 2^{i-n-1}$. Furthermore, this will be its only firing, since the subsequent positive pulse that possibly arrives from v coincides with the negative pulse from IN_2 . In the case $b_m = 0$ the neuron v' receives no pulse from u' , but a positive pulse from v arrives at time $d + \Delta - 2^{m-n-1} + \Delta' + \Delta'' + 2^{m-n-1} = \Delta + \Delta' + \Delta'' + \sum_{i=1}^{m-1} b_i 2^{i-n-1}$. Since the negative pulse from IN_2 arrives strictly after that time, neuron v' fires exactly once at time $\Delta + \Delta' + \Delta'' + \sum_{i=1}^{m-1} b_i 2^{i-n-1}$ in the case $b_m = 0$. Thus neuron v' fires

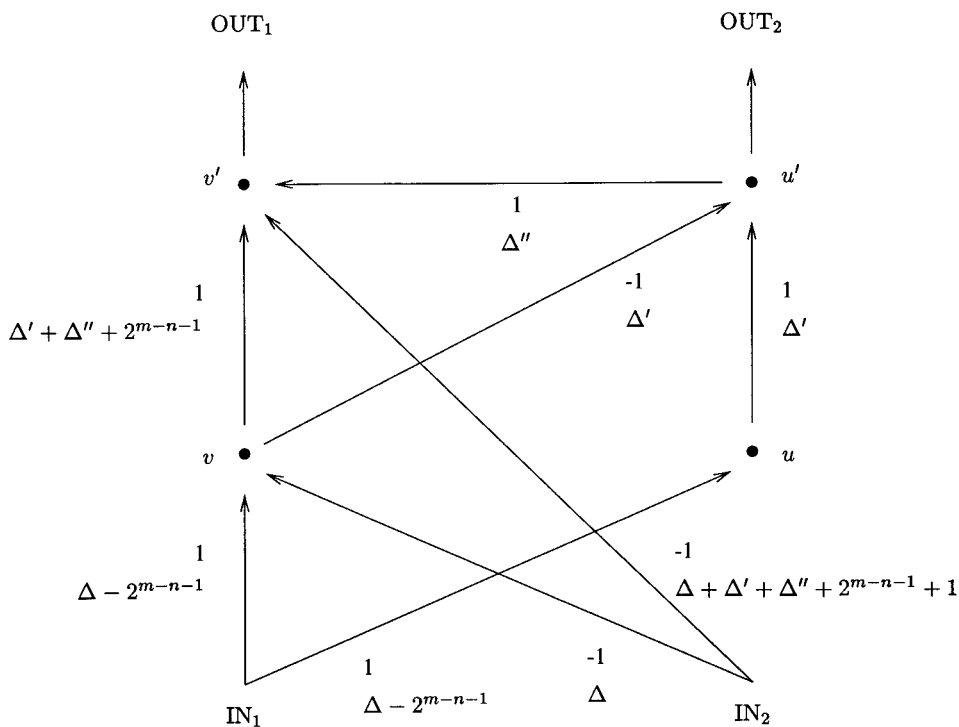


FIG. 3. Realization of module M_m with spiking neurons. For each connection the value of its weight (from $\{-1, 1\}$) as well as the value of its delay are indicated.

from IN_1 of M_j to its first neurons. The delays d_1, \dots, d_n from the network inputs x_1, \dots, x_n are assumed to be the only programmable parameters of the network. The network is constructed so that by assigning suitable values to these parameters d_1, \dots, d_n it shatters the set $D = \{\mathbf{e}_k: k = 1, \dots, n\}^2$, where $\mathbf{e}_k \in \{0, 1\}^n$ is the k th unit vector (with a 1 in the k th component and 0s elsewhere). An input vector $\langle \mathbf{e}_k, \mathbf{e}_i \rangle \in D$ is presented to the network by sending at time 0 an input spike to the network inputs x_k and y_i (as well as to the network input marked 1).

Consider some arbitrary given set $D' \subseteq D$. For $k \in \{1, \dots, n\}$ we define the k th delay d_k for this given set D' by $d_k = \sum_{i=1}^n b_i^k 2^{i-n-1}$, where the bits b_i^k are defined by

$$b_i^k = \begin{cases} 1, & \text{if } \langle \mathbf{e}_k, \mathbf{e}_i \rangle \in D', \\ 0, & \text{otherwise.} \end{cases}$$

We show now that with this choice of d_1, \dots, d_n for any input vector $\langle \mathbf{e}_k, \mathbf{e}_i \rangle$ with $k, i \in \{1, \dots, n\}$ the output neuron H of the network \mathcal{N} fires if and only if $\langle \mathbf{e}_k, \mathbf{e}_i \rangle \in D'$. Since for $\langle \mathbf{e}_k, \mathbf{e}_i \rangle$ among the network inputs x_1, \dots, x_n only x_k receives an input pulse, the module M_n receives at its input port IN_1 a pulse from G at time $1 + d_k$, where $d_k = \sum_{i=1}^n b_i^k 2^{i-n-1}$. Furthermore, module M_n receives at its input port IN_2 a pulse at time $\alpha_n = 1$. According to our construction the module M_n will then emit at its output port OUT_1 a spike at time $\Delta + \Delta' + \Delta'' + \sum_{i=1}^{n-1} b_i^k 2^{i-n-1} + 1$. It can be shown by induction on $n - m$ that for any $m < n$ the module M_m will receive at its input port IN_1 a pulse from M_{m+1} at time $(n - m) \cdot (\Delta + \Delta' + \Delta'') + \sum_{i=1}^m b_i^k 2^{i-n-1} + 1$ and at IN_2 a pulse at time $\alpha_m = (n - m) \cdot (\Delta + \Delta' + \Delta'') + 1$. This implies that for any $m \in \{1, \dots, n\}$ module M_m will emit at OUT_2 a spike if and only if $b_m^k = 1$. If it is emitted, this happens at time $(n - m) \cdot (\Delta + \Delta' + \Delta'') + \Delta + \Delta' + \sum_{i=1}^{m-1} b_i^k 2^{i-n-1} + 1$. The neuron G_m will receive this pulse at time $(n - m) \cdot (\Delta + \Delta' + \Delta'') + \Delta + \Delta' + \sum_{i=1}^{m-1} b_i^k 2^{i-n-1} + 2$. In addition, if $m = i$ (where $\langle \mathbf{e}_k, \mathbf{e}_i \rangle$ is the input vector) neuron G_m will receive at time $\beta_m = (n - m) \cdot (\Delta + \Delta' + \Delta'') + \Delta + \Delta' + 2$ a pulse from network input y_m . Since G_m has a firing threshold of value 2 it will fire if and only if both pulses arrive at G_m , i.e., if and only if $m = i$ and $b_m^k = 1$. Hence, G_m fires if and only if $m = i$ and $\langle \mathbf{e}_k, \mathbf{e}_i \rangle \in D'$. Furthermore, by construction the output neuron H of network \mathcal{N} fires if and only if at least one of the neurons G_1, \dots, G_n fires. Hence, H fires if and only if $\langle \mathbf{e}_k, \mathbf{e}_i \rangle \in D'$.

Thus we have shown that \mathcal{N} with the programmable parameters d_1, \dots, d_n shatters the set $D = \{\mathbf{e}_k: k = 1, \dots, n\}^2$ of cardinality n^2 . ■

COROLLARY 3.2. *It is impossible to give an upper bound for the VC dimension of an SNN with fixed weights in terms of the number n of its delays that are adjustable.*

The proof of Corollary 3.2 follows immediately from the preceding construction. One chooses any $m \in \mathbb{N}$ and constructs a network $\mathcal{N}_{n,m}$ similar to Fig. 4 with $O(n + m)$ edges and VC dimension at least $n \cdot m$ that has just n adjustable delays d_1, \dots, d_n , so that $\mathcal{N}_{n,m}$ can read out the first m bits of any d_i with the help of m modules M_1, \dots, M_m and additional inputs y_1, \dots, y_m . Note that the delays in M_1, \dots, M_m are not required to be adjustable.

The following result, which employs a bound from (Goldberg and Jerrum, 1995), shows that the lower bound of Theorem 3.1 is optimal.

THEOREM 3.3. *Consider an SNN \mathcal{N} with rectangular pulses where all delays, weights, and thresholds are programmable parameters, and let l be the number of edges. Then the VC dimension of \mathcal{N} is $O(l^2)$, even for analog coding of the inputs.*

Proof. Assume without loss of generality that the output of the network is coded in binary. Let l be the number of edges and let k be the number of programmable parameters of the network, hence $k = O(l)$. The behavior of the network, i.e. whether its output neuron fires or not, can be described by a Boolean formula $\Phi_{k,n}$ that involves as variables the k programmable parameters and the n input variables of the network. To decide whether the output neuron fires we consider all possible paths from an input neuron to the output neuron. There are at most $2^{O(l)}$ such paths. This leads to a Boolean formula $\Phi_{k,n}$ containing $s = 2^{O(l)}$ distinct atomic predicates, where each predicate is a polynomial inequality of degree $d = 1$ over $k + n$ variables. According to Theorem 2.2 of (Goldberg and Jerrum, 1995), the VC dimension of the class of functions described by this formula is at most $2k \log(8eds) = O(l^2)$. ■

4. COMPUTATIONAL COMPLEXITY OF DELAY LEARNING

In order to investigate the computational complexity of learning within the PAC framework one has to specify which class of hypotheses the learner may use. In one setting studied in the literature the learner is allowed to output hypotheses from some polynomial-time evaluable hypothesis class (see, e.g., Kearns *et al.*, 1994a, for a definition). If the class $\bigcup_{n \geq 1} \mathcal{S}_n^{\text{bb}}$ were PAC-learnable by such a hypothesis class then according to Theorem 2.1(d) the same result would hold for the class μ -DNF. Polynomial learnability of μ -DNF in this setting, however, implies polynomial learnability of the more general class DNF as (Kearns *et al.*, 1994a) have shown. It is one of the major open problems in computational learning theory whether DNF can be learned in polynomial time by some polynomial-time evaluable hypothesis class.

In this section we consider the complexity of PAC-learning when only hypotheses from $\mathcal{S}_n^{\text{bb}}$ may be used by the learner, a setting also known as *proper* PAC-learning. This appears to be the more adequate assumption for the analysis of learning for a single spiking neuron.

We investigate the computational complexity of the consistency problem for a spiking neuron which is defined as follows: Given a set of labelled examples from $\{0, 1\}^n \times \{0, 1\}$, does there exist a function in $\mathcal{S}_n^{\text{bb}}$ that is consistent (i.e., that does agree with) all examples?

In the following we show that this problem is NP-complete for a spiking neuron that may choose its delay values only from the set $\{0, 1\}$. A spiking neuron with two delay values and binary coding is only slightly more powerful than a Boolean threshold gate, which can be thought of as a spiking neuron with only one delay value. Therefore, this intractability result appears to be optimal in a certain sense. Moreover, the proof shows that the result also holds when the weights and the threshold are kept fixed.

THEOREM 4.1. *The consistency problem for a spiking neuron with delays from $\{0, 1\}$ is NP-complete.*

The proof is by a reduction from 3SET-SPLITTING (Garey and Johnson, 1979), a problem which was also used in (Blum and Rivest, 1992) for intractability results concerning certain two-layer networks of threshold gates. In fact, the problem considered here seems to be closely related to the consistency problem for the AND of two threshold gates analyzed in (Blum and Rivest, 1992). However, their reduction cannot be used here in a straightforward manner (e.g., by flipping the labels to change the AND into an OR), because due to our Theorem 2.1(e) the OR of two threshold gates is not equivalent to a spiking neuron with delays from $\{0, 1\}$.

Proof of Theorem 4.1. The problem is in NP because the delay values are binary and the weights can be bounded polynomially in size. The latter is shown similarly, as in the case of threshold gates.

To prove NP-hardness we define a polynomial-time reduction from 3SET-SPLITTING, which is the problem to decide for an instance (U, C) , where U is a finite set and C is a collection of subsets of U such that $|c| = 3$ for all $c \in C$, if there exists a partition U_0, U_1 of U such that all $c \in C$ satisfy $c \not\subseteq U_0$ and $c \not\subseteq U_1$.⁶

Let (U, C) be given and $n = |U|$. The set of examples is defined as $S = S^+ \cup S^- \subseteq \{0, 1\}^{2n} \times \{0, 1\}$, where the elements of S^+ and S^- are labelled by 1 and 0, respectively. For a set $I \subseteq \{1, \dots, 2n\}$ we denote by 1_I the binary vector of length $2n$ that has 1s exactly at the positions in I .

- Let $1_\emptyset \in S^-$.
- For each $u_i \in U$ let $1_{\{2i-1, 2i\}} \in S^+$.
- For each $c \in C$ where $c = \{u_i, u_j, u_k\}$ let $1_{\{2i-1, 2i, 2j-1, 2j, 2k-1, 2k\}} \in S^-$.

Obviously, there is a function computable in polynomial time that maps each (U, C) to the corresponding S . We show now that (U, C) has a set splitting if and only if there exists a function in $\mathcal{S}_{2n}^{\text{bb}}$ with binary delays that is consistent with S .

(\Rightarrow) Assume that (U, C) has a set splitting $\beta: U \rightarrow \{0, 1\}$ (i.e., $u_i \in U_j$ iff $\beta(u_i) = j$). Define the weights w_1, \dots, w_{2n} and threshold θ_v as

$$\left. \begin{array}{l} w_{2i-1} = 1 \\ w_{2i} = -2 \end{array} \right\} \quad \text{for } i = 1, \dots, n; \theta_v = 1/2.$$

Define the delays d_1, \dots, d_{2n} as

$$\left. \begin{array}{l} d_{2i-1} = \beta(u_i) \\ d_{2i} = 1 - \beta(u_i) \end{array} \right\} \quad \text{for } i = 1, \dots, n.$$

This spiking neuron is consistent with S : For input 1_\emptyset it does not fire because $\theta_v > 0$. For each $1_{\{2i-1, 2i\}}$ one of the two active inputs generates a pulse of height 1, hence the output is 1. For each $1_{\{2i-1, 2i, 2j-1, 2j, 2k-1, 2k\}}$ corresponding to a $c \in C$

⁶ Strictly speaking, the restriction of SET-SPLITTING as defined in (Garey and Johnson, 1979) allows that $|c| \leq 3$. However, it is straightforward to define a reduction that avoids subsets of cardinality 2.

there is associated with each delay value at least one of w_{2i}, w_{2j}, w_{2k} . Hence, for both delay values the corresponding potential cannot be larger than 0.

(\Leftarrow) Assume that the spiking neuron is consistent with S . Let g be the threshold function which has threshold θ_v , the weights assigned to delay value 0, and where the weights of delay value 1 are replaced by 0. Define $\beta: U \rightarrow \{0, 1\}$ as

$$\beta(u_i) = g(1_{\{2i-1, 2i\}}).$$

We claim that β is a set splitting of (U, C) . Assume the contrary. Then there exists $c \in C$, $c = \{u_i, u_j, u_k\}$ and $b \in \{0, 1\}$ such that

$$\beta(u_i) = \beta(u_j) = \beta(u_k) = b.$$

(i) If $b = 1$ then $g(1_{\{2l-1, 2l\}}) = 1$ for each $l \in \{i, j, k\}$. Because 1_{\emptyset} is a negative example and g is a threshold function this implies $g(1_{\{2i-1, 2i, 2j-1, 2j, 2k-1, 2k\}}) = 1$. Hence, the neuron fires on the input vector corresponding to c , in contradiction to the definition of S .

(ii) If $b = 0$ then consider the threshold function g' consisting of the weights assigned to delay value 1. Accordingly, g' must output 1 on input $1_{\{2l-1, 2l\}}$ for each $l \in \{i, j, k\}$ (because the label is 1 and g outputs 0). The label of 1_{\emptyset} then implies that g' outputs 1 on input $1_{\{2i-1, 2i, 2j-1, 2j, 2k-1, 2k\}}$. It follows that the neuron fires on this input in contradiction to the definition of S .

Finally, (i) and (ii) imply that β is a set splitting of (U, C) . ■

The fact that the weights need not be modifiable in the previous proof leads to the following stronger result.

COROLLARY 4.2. *The consistency problem for a spiking neuron with binary delays and fixed weights is NP-complete.*

In a similar way, NP-completeness can be shown for the case that the delays are allowed to take on values from a bounded set $\{0, \dots, k-1\}$ where $k \geq 3$. The reduction is from GRAPH- k -COLORABILITY and is basically a modification of the reduction used in (Anthony and Biggs, 1992) for the AND of k threshold gates. Again, the weights and the threshold can also be kept fixed. Combining this with Theorem 4.1 we get the result.

COROLLARY 4.3. *For each $k \geq 2$, the consistency problem for a spiking neuron with delays from $\{0, \dots, k-1\}$ is NP-complete. This holds also for a spiking neuron with fixed weights.*

The results presented in this section refer to a spiking neuron where the number of delay values is bounded. While it is easy to see that the consistency problem is in NP even when the number of delay values is allowed to grow with the number of inputs (see, e.g., the discussion at the end of Subsection 2.3), NP-hardness for this case is still not established.

5. CONCLUSIONS

We have investigated a new type of computational model where a set of parameters becomes quite relevant that plays little or no role in other models: transmission delays. We have shown that these new parameters have an even larger impact on the richness of the class of Boolean functions that can be computed by a spiking neuron than those parameters that are traditionally considered to be the main “programmable parameters” of a neuron: the “weights” of its synapses. We have shown that the VC dimension of a single spiking neuron is superlinear in the number of delays that can be varied and that the VC dimension of a network of spiking neurons can grow quadratically with the number of adjustable delays.

Both of these lower bounds hold already for the most simple version of a spiking neuron, or network of spiking neurons respectively, where all pulses have a rectangular shape. However, our constructions make only rather weak use of the particular form of the pulses considered in this article and they are likely to be transferable to models with biologically more realistic pulse shapes. These lower bounds are complemented by matching upper bound results, which hold (in terms of the total number of programmable parameters) even if delays *and* weights can be varied simultaneously. Furthermore, these upper bounds hold even in the case of analog network inputs, whereas the lower bounds are valid already in the Boolean case. Hence, we get tight bounds for either type of network input.

We have also shown that the learning complexity of a single spiking neuron is surprisingly large, in particular it is much larger than the learning complexity of a single threshold gate. Just like the corresponding result for multilayer threshold circuits, this should not be interpreted as saying that supervised learning is impossible for a spiking neuron. However, it tells us that it will become quite difficult to formulate rigorously provable positive learning results for spiking neurons.

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