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# Computing with Stochastic Dynamic Synapses

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## Abstract

In most neural network models, synapses are treated as static weights that change only on the slow time scales of learning. In fact, however, synapses are highly dynamic, and show use-dependent plasticity over a wide range of time scales. Moreover, synaptic transmission is an inherently stochastic process: a spike arriving at a presynaptic terminal triggers release of a vesicle of neurotransmitter from a release site with a probability that can be much less than one. Changes in release probability represent one of the main mechanisms by which synaptic efficacy is modulated in neural circuits.

We propose and investigate a simple model for stochastic dynamic synapses that can easily be integrated into common models for neural computation. We prove through rigorous theoretical analysis and computer simulations that a stochastic dynamic synapse can respond with a large variety of different release patterns to different spike trains, even if they represent the same firing rate. Furthermore we show that a spiking neuron gains additional computational power through the use of dynamic synapses, and we explore new learning issues that arise in this context.

## 1 Introduction

The dominant paradigm for modeling neural computation is static. The activity of a computing element is typically represented as a scalar, usually interpreted as the "average firing rate"—the number of spikes in some relatively long time window. Synaptic connections are likewise modeled as static "weights" that change only on

the slow time scale of learning. Such models effectively ignore the wide range of time scales over which biophysical mechanisms act in real neural circuits.

Most real neural circuits consist of spiking neurons. Experimental evidence is accumulating from diverse systems—from flies [Bialek et al., 1991] to monkeys [Burracas et al., 1996]—that the precise timing of spikes can be used to encode information. There is growing recognition that the mean rate approximation for the activity of a spiking neuron may be inadequate, and that the “neural code” may make use of the fine temporal structure of spike trains. Computation with spiking neurons is only beginning to be explored [Zador and Pearlmuter, 1996, Maass, 1997].

Neurons communicate via synapses that are dynamic and stochastic. When a spike arrives at a presynaptic terminal, it sometimes triggers the release of a neurotransmitter-filled packet or vesicle of neurotransmitter from a release site, but it also sometimes fails to trigger a release [Katz, 1986]. Only when a vesicle is released does the signal from the presynaptic neuron propagate to the postsynaptic neuron. The probability that a presynaptic action potential fails to elicit a postsynaptic response is different at different synapses, and in the hippocampus can be 0.9 or higher [Allen and Stevens, 1994]. Moreover, release probability at a synapse is strongly modulated by the recent history of activity at that synapse. This modulation occurs through a variety of distinct biophysical mechanisms including paired-pulse facilitation and paired-pulse depression [Zucker, 1989]. Abbott and colleagues have adopted a phenomenological approach based on previous models of short-term plasticity at the neuromuscular junction [Magleby, 1987]. However, their model accounts only for the average probability across a population of synapses.

In what follows, we will be interested in the computational implications of release probability that is modulated at individual release sites. For this we must consider the biophysical mechanisms underlying the modulation of probability at individual release sites. We assume that release probability is determined by two distinct processes: facilitation, and depression. Facilitation in our model depends on the number of spikes that arrive at the presynaptic terminal. This is consistent with a mechanism in which the facilitation is determined by the amount of calcium that has entered the presynaptic terminal [Zucker, 1989], which in turn depends on the number of spikes that invade the presynaptic terminal. Depression in our model depends on the number of vesicles actually released by the synapse; such a dependence could arise for example if depression was the result of depletion of the pool of readily releasable vesicles [Dobrunz and Stevens, 1997].

We assume that time is discretized into small time intervals (with a length of, say, 1 millisecond). A synapse  $S$  carries out computations on spike trains, more precisely on trains of spikes that arrive at the presynaptic terminal. We represent each spike train as a binary sequence  $x_1 \dots x_T \in \{0, 1\}^T$ , where  $x_t = 1$  indicates that a spike arrives at time  $t$ . We will denote the interspike interval between the  $j$ th and  $(j + 1)$ st spike by  $I_j$ . The output of the synapse is also represented as a binary sequence  $z_1 \dots z_T \in \{0, 1\}^T$ , where  $z_t = 1$  indicates that the synapse has released a vesicle at time  $t$ . For simplicity we assume in this abstract that  $z_t = 1$  occurs only if  $x_t = 1$ , i.e. “spontaneous” synaptic release is not taken into account. We will describe the action of synapse  $S$  on a spike train  $\underline{x}$  by a sequence  $\underline{p} \in \{R, F\}^R$  for

$K = \sum_{i=1}^T x_i$ , where  $p_k = R$  (or  $p_k = F$ ) indicates that spike number  $k$  in  $x_1 \dots x_T$  did (or did not) trigger release of a vesicle at this synapse.

We focus on a model for synaptic computation that has in its simplest form two internal variables  $C$  and  $V$  that govern its release probability. The values of  $C, V$

at time step  $t$  are denoted by  $C_t, V_t, t = 1, 2, \dots$ . These variables will only assume nonnegative values. The variable  $C$  models in an abstract way internal synaptic processes that support presynaptic facilitation, such as concentration of  $Ca^{+}$  in the presynaptic terminal. The variable  $V$  models in an abstract way internal synaptic processes that support presynaptic depression, such as depletion of the pool of readily releasable vesicles. The current values of these variables depend on  $x_1, \dots, x_t$  and on internal parameters  $\Theta_C, \Theta_V, c_1, c_2, v_1, v_2, \alpha, \beta$ . We assume that the values of  $C_{t+1}, V_{t+1}, x_{t+1}$  for  $t = 0, 1, 2, \dots$  evolve according to the following rules:

$$(1) \quad C_{t+1} = c_1 \cdot x_{t+1} + C_t \cdot c_2$$

$$(2) \quad V_{t+1} = v_1 \cdot x_t + V_t \cdot v_2$$

If  $x_{t+1} = 0$  then  $x_{t+1} = 0$ . If  $x_{t+1} = 1$  then one sets  $x_{t+1} = 1$  with probability  $\sigma(\alpha \cdot (C_{t+1} - \Theta_C)) \cdot \sigma(\beta \cdot (\Theta_V - V_{t+1}))$ , else  $x_{t+1} = 0$ . The function  $\sigma: \mathbb{R} \rightarrow [0, 1]$  that occurs in this rule is some suitable squashing function, for example  $\sigma(y) = \frac{1}{1 + e^{-y}}$ . In the limit  $\alpha, \beta \rightarrow \infty$  this stochastic rule for release approaches the deterministic rule

$$x_{t+1} = \begin{cases} 1 & , \text{ if } C_{t+1} \geq \Theta_C, V_{t+1} \leq \Theta_V \text{ and } x_{t+1} = 1 \\ 0 & , \text{ otherwise.} \end{cases}$$

All variables and parameters can assume only values  $\geq 0$ . We set  $C_0 = V_0 = x_0 = 0$ . The parameters  $c_2, v_2$  assume only values in  $(0, 1)$ . Hence they give rise to an exponential decay of  $C$  and  $V$  according to (1), (2). The case  $C_0 = V_0 = 0$  is the case where the internal state of the synapse does not change before the first spike arrives (i.e. the initial state is a steady state for the variables  $C$  and  $V$ ). For a biological synapse this is approximately realized if no spike has arrived for a fairly long time period. In this case one can set  $c_1 = v_1 = 1$  without loss of generality. To see this one can formally replace  $C_t$  by  $C_t/c_1$ ,  $\Theta_C$  by  $\Theta_C/c_1$ ,  $V_t$  by  $V_t/v_1$ ,  $\Theta_V$  by  $\Theta_V/v_1$ . Since  $c_1$  and  $v_1$  have now been eliminated, we can write  $c, v$  instead of  $c_2, v_2$  in the following. We can then characterize a stochastic dynamic synapse with 6 parameters  $c, \Theta_C, v, \Theta_V, \alpha, \beta$ .

It is well established that synapses may have several different mechanisms for paired-pulse facilitation and depression [Zucker, 1989]. These can be taken into account within our framework by introducing more variables  $V_t, V_t', V_t'', \dots, V_t^{(k)}$  and  $C_t, C_t', C_t'', \dots, C_t^{(k)}$  with separate thresholds and time courses (i.e. decay factors). The release probability at step  $t$  is in this extended model given by

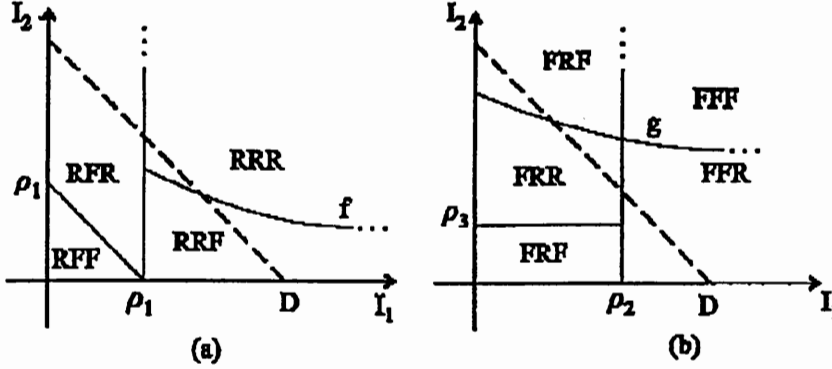
$$\max_{i=0, \dots, k} (\sigma(\alpha^{(i)} \cdot (C_t^{(i)} - \Theta_C^{(i)}))) \cdot \prod_{j=0}^k \sigma(\beta^{(j)} \cdot (\Theta_V^{(j)} - V_t^{(j)})) .$$

However for the sake of simplicity we will focus in this abstract — unless explicitly stated otherwise — on the case where a synapse has just two internal variables  $V_t, C_t$ . From the mathematical point of view our model for a stochastic dynamic synapse is closely related to the common model for a leaky integrate-and-fire neuron. The input-dependent variable  $C$  corresponds to the membrane potential of a neuron model, and the use-dependent variable  $V$  corresponds to a function that models refractory effects in a mathematical neuron model. Furthermore both  $C$  and  $V$  are subject to exponential decay, corresponding to the common decay of EPSP's and refractoriness in mathematical neuron models. Hence from an abstract point of view one may view a stochastic dynamic synapse as a dual "neuron" that receives just a single spike train as input but which may have substantially larger time constants. Hence in contrast to a neuron, a dynamic synapse cannot integrate over "space". But it can integrate over "time" at several scales.

## 2 The Range of Possible Synaptic Responses

**Theorem 2.1** For any spike train  $x_1 \dots x_T \in \{0, 1\}^T$  with 3 spikes and for any given pattern  $p \in \{R, F\}^3$  one can set the parameters  $c, \Theta_C, v, \Theta_V$  of a stochastic dynamic synapse so that its release pattern for input  $x_1 \dots x_T$  is  $p$  (with arbitrarily high probability for  $\alpha, \beta \rightarrow \infty$ ).

The proof of Theorem 2.1 is illustrated in Figure 1. By changing  $c, \Theta_C, v, \Theta_V$  one can move the boundaries of the 8 release patterns in such a way that the given point  $(I_1, I_2)$  with the two interspike intervals  $I_1, I_2$  of the spike train  $x_1 \dots x_T$  belongs to an area with the given release pattern  $p$ .



**Figure 1:** Expected response of a stochastic dynamic synapse with fixed parameters  $c, \Theta_C, v, \Theta_V$  to a spike train consisting of 3 spikes with interspike intervals  $I_1, I_2$ . (a) shows a typical distribution of release patterns in the case where the first spike triggered release. This occurs if  $\Theta_C < 1$ . The parameter  $\rho_1$  is defined through the equation  $v^{\rho_1-1} = \Theta_V$  and the function  $f$  assigns to each  $I_1 \geq \rho_1$  the unique  $I_2$  with  $v^{I_1+I_2-1} + v^{I_2-1} = \Theta_V$ . (b) shows a typical distribution of release patterns if the first spike did not trigger release. The parameters  $\rho_2$  and  $\rho_3$  are defined through the equations  $c^{\rho_2} + 1 = \Theta_C$ ,  $v^{\rho_3-1} = \Theta_V$ , and the function  $g$  assigns to each  $I_1$  the unique  $I_2$  with  $c^{I_1+I_2} + c^{I_2} + 1 = \Theta_C$ .

The diagonals  $I_1 + I_2 = D$  (dashed lines) in Figure 1 demonstrate that for a fairly wide range of values for  $D$  a synapse with fixed parameters can have three different likely release patterns (with different numbers of releases) even for spike trains consisting of 3 spikes with the same distance  $D$  between the first and third spike. Hence the "efficacy" of a synapse in our model can neither be viewed as a fixed nor as a purely rate-dependent percentage of releases. Instead it depends on the specific pattern of interspike intervals in the presynaptic spike train.

The following result shows that our synapse model can also exhibit a wide variety of responses for spike trains of length 4. However it also exhibits a constraint on the structure of likely release patterns in our model. Surprisingly this constraint holds even for the extended model of a synapse with additional internal variables with different time courses.

**Theorem 2.2** For any spike train  $x_1 \dots x_T \in \{0, 1\}^T$  with 4 spikes and any given pattern  $p \in \{R, F\}^4$  except  $RFRR$  one can set the parameters  $c, \Theta_C, v, \Theta_V$  of a

stochastic dynamic synapse so that its release pattern for input  $x_1 \dots x_T \in \{0, 1\}^T$  is  $\underline{p}$  (with arbitrarily high probability for  $\alpha, \beta \rightarrow \infty$ ).

The release pattern RFRR cannot be realized by a stochastic dynamic synapse with high probability for any setting of its internal parameters provided that the relation  $I_1 > I_3$  holds for the first and third interspike interval in the spike train  $x_1 \dots x_T$ . This holds even for synapses with any finite number of internal variables  $C_i, C'_i, \dots, C_i^{(k)}$  and  $V_i, V'_i, \dots, V_i^{(k)}$  with arbitrary individual decay factors  $c, c', \dots, c^{(k)}, v, v', \dots, v^{(k)}$ , thresholds  $\Theta_C, \Theta'_C, \dots, \Theta_C^{(k)}, \Theta_V, \Theta'_V, \dots, \Theta_V^{(k)}$ , and constants  $\alpha, \alpha', \dots, \alpha^{(k)}, \beta, \beta', \dots, \beta^{(k)}$ . ■

**Remark 2.3** The release pattern RFRR can be realized with the help of multiple synapses between two neurons: If 3 different synapses receive the same spike train  $\underline{x}$  with 4 spikes, one can always set their parameters so that exactly one of these synapses is likely to release for the first, third and fourth spike, but none of them is likely to release for the second spike.

### 3 Synaptic Pattern Discrimination

We have demonstrated that according to our model a synapse can have many different likely release patterns for spike trains with different interspike intervals, even with one fixed parameter setting. The following result shows there exists in fact a relatively simple on-line algorithm for adjusting the parameters of a synapse in such a way that the synapse acquires some given release-patterns  $\underline{p} \in \{R, F\}^3$  for different spike trains with 3 spikes. We assume that an arbitrary finite set  $S$  of pairs  $(\underline{x}, \underline{p})$  is given with spike trains  $\underline{x}$  with 3 spikes, and arbitrary  $\underline{p} \in \{R, F\}^3$ . We assume that an arbitrary finite range of allowed values has been fixed for each of the 4 parameters  $c, \Theta_C, v, \Theta_V$ .

The statement of the following result is reminiscent of the well-known Perceptron Convergence Theorem, although the context is very different. The following result guarantees the convergence of an on-line algorithm SL to a solution just on the basis of the assumption that there exists a solution.

**Theorem 3.1 (Synapse Convergence Theorem for Spike Trains with 3 Spikes).** Assume that  $S$  is an arbitrary finite set of pairs  $(\underline{x}, \underline{p}) \in \{0, 1\}^3 \times \{R, F\}^3$ , where each spike train  $\underline{x}$  contains 3 spikes. We assume that there exist values  $\delta, \bar{\Theta}_C, \bar{v}, \bar{\Theta}_V$  with the property that for any  $(\underline{x}, \underline{p}) \in S$  a synapse with these parameter values responds with the release pattern  $\underline{p}$  to the spike train  $\underline{x}$  with arbitrarily high probability for  $\alpha, \beta \rightarrow \infty$ .

With the on-line learning algorithm SL any synapse (with arbitrary initial parameter values) can learn to respond to spike train  $\underline{x}$  with release pattern  $\underline{p}$ , simultaneously for all  $(\underline{x}, \underline{p}) \in S$ . SL adjusts the parameters of a stochastic dynamic synapse after each time when the synapse produces a release pattern  $\underline{q} \neq \underline{p}$  for a spike train  $\underline{x}$  with  $(\underline{x}, \underline{p}) \in S$ . This algorithm SL converges in the sense that at most a fixed number of parameter adjustments are needed for any finite and infinite sequence of presentations of examples from  $S$  (with arbitrary repetitions).

The learning algorithm SL consists of a few simple rules each involving at most 2 of the 4 parameters. Details cannot be given in this abstract due to space constraints. ■

## 4 Distinguishing Poisson Spike Trains

We demonstrate in Figure 2 that a stochastic dynamic synapse is able to distinguish even among relatively long Poisson spike trains  $x, y \in \{0, 1\}^{100}$  with the same density.

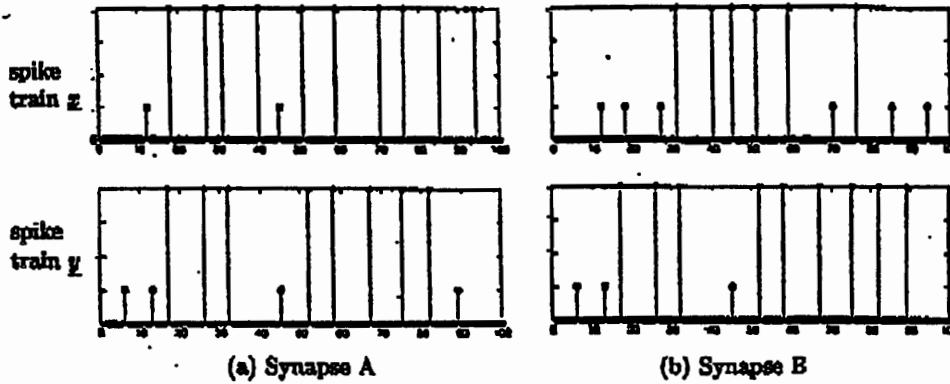


Figure 2: Two Poisson spike trains  $x$  and  $y \in \{0, 1\}^{100}$  with the same density can yield different percentages of releases in two synapses A and B that have slightly different parameter values. Releases are indicated by long bars, failures by short bars. Both  $x$  and  $y$  consist of 12 spikes. Synapse A (with  $c = 0.9, \Theta_C = 1.52, v = 0.94, \Theta_V = 1.7$ ) releases for  $x$  16.67% more spikes than for  $y$ ; see panel (a). Synapse B (with  $c = 0.87, \Theta_C = 1.46, v = 0.94, \Theta_V = 1.78$ ) releases for  $x$  25% fewer spikes than for  $y$ , see panel (b).

## 5 On the Computational Power of a Neuron with Dynamic Synapses

We show that the computational power of a spiking neuron with stochastic dynamic synapses is strictly larger than that of a spiking neuron with traditional "static" synapses. Let  $T$  be a some given time window, and consider the computational task of detecting whether at least one of  $n$  presynaptic neurons  $a_1, \dots, a_n$  fire at least twice during  $T$  ("burst detection").

**Theorem 5.1** *A spiking neuron  $v$  with stochastic dynamic synapses can solve this burst detection task (with arbitrarily high reliability). On the other hand no spiking neuron with static synapses can solve this task (for any assignment of "weights" to its synapses; we assume that transmission delays are  $\leq O(T)$ ).*

To prove the positive part of this result one sets the parameters of  $n$  excitatory synapses from  $a_1, \dots, a_n$  in such a way that they respond with high probability to any spike train of length  $\leq T$  with a release pattern that starts with FR. Set the firing threshold of neuron  $v$  so low that it fires upon receiving at least one EPSP from any of these synapses.

The negative part of Theorem 5.1 is proven indirectly via contradiction. ■

**Remark 5.2** This burst detection task is closely related to computing the Boolean function  $F_n(x_1, y_1, x_2, y_2, \dots, x_n, y_n)$  from  $\{0, 1\}^{2n}$  into  $\{0, 1\}$  which gives output 1 if and only if  $x_i + y_i \geq 2$  for some  $i \in \{1, \dots, n\}$ . We have shown that any feedforward sigmoidal neural net needs to have  $\Omega(n^{1/2})$  "neurons" to compute this function  $F_n$ . Hence one may argue that "burst detection" is a non-trivial computational task for a neural network.

## 6 Conclusions

We have introduced a simple model for stochastic dynamic synapses which makes it possible to explore the role of synaptic dynamics in the context of neural computation and learning. Our results about the diversity of possible synaptic responses, synaptic pattern discrimination, and adaptation of synaptic parameters throw new light on a number of fundamental issues regarding neural computation, learning and coding.

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