*LETTER* **Communicated by Misha Tsodyks**

# Modeling Synaptic Plasticity in Conjunction with the Timing of Pre- and Postsynaptic Action Potentials

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**We present a spiking neuron model that allows for an analytic calculation of the correlations between pre- and postsynaptic spikes. The neuron model is a generalization of the integrate-and-fire model and equipped with a probabilistic spike-triggering mechanism. We show that under certain biologically plausible conditions, pre- and postsynaptic spike trains can be described simultaneously as an inhomogeneous Poisson process.**

**Inspired by experimental findings, we develop a model for synaptic long-term plasticity that relies on the relative timing of pre- and postsynaptic action potentials. Being given an input statistics, we compute the stationary synaptic weights that result from the temporal correlations between the pre- and postsynaptic spikes. By means of both analytic calculations and computer simulations, we show that such a mechanism of synaptic plasticity is able to strengthen those input synapses that convey precisely timed spikes at the expense of synapses that deliver spikes with a broad temporal distribution. This may be of vital importance for any kind of information processing based on spiking neurons and temporal coding.**

## 1 Introduction

There is growing experimental evidence that the strength of a synapse is persistently changed according to the relative timing of the arrival of presynaptic spikes and the triggering of postsynaptic action potentials (Markram, Lübke, Frotscher, & Sakmann, (1997); Bell, Han, Sugawara, & Grant, 1997). A theoretical approach to this phenomenon is far from being trivial because it involves the calculation of correlations between pre- and postsynaptic action potentials (Gerstner, Kempter, van Hemmen, & Wagner 1996). In the context of simple neuron models such as the standard integrate-and-fire model, the determination of the firing-time distribution involves the solution of first-passage time problems (Tuckwell, 1988). These problems are known to be hard, the more so if the neuron model is extended so as to include biologically realistic postsynaptic potentials.

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We are going to use a neuron model, the spike-response model, which is a generalization of the integrate-and-fire model (Gerstner & van Hemmen, 1992; Gerstner, 1995; Kistler, Gerstner, & van Hemmen, 1997). This model combines analytic simplicity with the ability to give a faithful description of "biological" neurons in terms of postsynaptic potentials, afterpotentials, and other aspects (Kistler, et al., 1997). In order to be able to solve the first-passage time problem, the sharp firing threshold is replaced by a probabilistic spike-triggering mechanism (section 2). In section 3 we investigate conditions that allow for a description of the postsynaptic spike train as an inhomogeneous Poisson process, if the presynaptic spike trains are described by inhomogeneous Poisson processes too. Using this stochastic neuron model, we can analytically compute the distribution of the first postsynaptic firing time for a given ensemble of input spike trains in two limiting cases: for low- and high-firing threshold (section 4). Finally, in section 5 a model of synaptic plasticity is introduced and analyzed in the context of a neuron that receives input from presynaptic neurons with different temporal precision. We show analytically and by computer simulations that the mechanism of synaptic plasticity is able to distinguish between synapses that convey spikes with a narrow or a broad temporal jitter. The resulting stationary synaptic weight vector favors synapses that deliver precisely timed spikes at the expense of the other synapses so as to produce again highly precise postsynaptic spikes.

## 2 The Model

We will investigate a neuron model—the spike-response model—that is in many aspects similar to but much more general than the standard integrate-and-fire model (Gerstner & van Hemmen, 1992; Gerstner, 1995). The membrane potential is given by a combination of pre- and postsynaptic contributions described by a response kernel $\epsilon$ that gives the form of an elementary postsynaptic potential and a kernel $\eta$ that accounts for refractoriness and has the function of an afterpotential, so that

$$h_i(t) = \sum_{j,f} J_{ij}\epsilon(t - t_j^f - \Delta_{ij}) - \sum_f \eta(t - t_i^f). \tag{2.1}$$

Here, $h_i$ is the membrane potential of neuron $i$, $J_{ij}$ is the strength of the synapse connecting neuron $j$ to neuron $i$, $\Delta_{ij}$ is the corresponding axonal delay from $j$ to $i$, and $\{t_j^f, f = 1, 2, \ldots\}$ are the firing times of neuron $j$. Causality is respected if both $\epsilon(s)$ and $\eta(s)$ vanish identically for $s < 0$. Depending on the choice for $\epsilon$ and $\eta$, the spike-response model can reproduce the standard integrate-and-fire model or even mimic complex Hodgkin-Huxley-type neuron models (Kistler et al., 1997). A typical choice for $\epsilon$ is $\epsilon(t) = t/\tau_M \exp(1 - t/\tau_M)\Theta(t)$, where $\tau_M$ is a membrane time constant and

$\Theta$ the Heaviside step function with $\Theta(t) = 1$ for $t > 0$ and $\Theta(t) = 0$ elsewhere. As for the refractory function $\eta$, a simple exponential can be used, for example, $\eta(t) = \eta_0 \exp(-t/\tau_{\mathrm{ref}})\Theta(t)$.

Equation 2.1 could also be generalized so as to account for short-term depression and facilitation if the constant coupling $J_{ij}$ is replaced by a function of the previous spike arrival times at synapse $i \mapsto j$ (Kistler & van Hemmen, 1999). In this context, however, we will concentrate on situations where only a single spike is transmitted across each synapse, so that effects of short-term plasticity do not come into action.

The crucial point for what follows is the way in which new firing events are defined. Instead of using a deterministic threshold criterion for spike release, we describe the spike train of the postsynaptic neuron as a stochastic process with the probability density of having a spike at time $t$ being a nonlinear function $\nu$ of the membrane potential $h(t)$. If we neglect the effect of the afterpotential, $\eta = 0$, the spike train of neuron $i$ is an inhomogeneous Poisson process with rate $\nu = \nu(h_i)$ for every fixed set of presynaptic firing times $\{t_j^f, j \neq i\}$.

Spike triggering in neurons is more or less a threshold process. In order to mimic this observation, we have chosen the rate function $\nu(h)$ to be

$$\nu(h) = \nu_{\max}\Theta(h - \vartheta), \tag{2.2}$$

where $\nu_{\max}$ is a positive constant and $\vartheta$ the firing threshold. We note that $\nu_{\max}$ is not the maximum firing rate of the neuron, which is given by the form of $\eta(t)$, but a kind of a reliability parameter. The larger $\nu_{\max}$, the faster the neuron will fire after the threshold $\vartheta$ has been reached from below. The role of the parameter $\nu_{\max}$ is further discussed in section 4.

## 3 Noisy Input

For a fixed set of presynaptic spikes at times $\{t_j^f, j \neq i\}$ and a negligible afterpotential ($\eta = 0$), the membrane potential of neuron $i$ at time $t$ is uniquely determined and given by

$$h_i(t) = \sum_{j,f} J_{ij}\epsilon(t - t_j^f - \Delta_{ij}). \tag{3.1}$$

In this case, the spike train of neuron $i$ is a Poisson process with rate $\nu_{\max}$ for those time intervals with $h_i(t) > \vartheta$ and no spikes in between.

Things become more complicated if we include an afterpotential after each spike of neuron $i$ and if the arrival times of the presynaptic spikes are no longer fixed but become random variables too. We will not discuss the first point because we are mainly interested in the first spike of neuron $i$ after a period of inactivity. As a consequence of the second point, the membrane potential $h_i(t)$ is no longer a fixed function of time, but a stochastic process because every realization of presynaptic firing times $\{t_j^f, j \neq i\}$ results in a different realization of the time course of the membrane potential $h_i(t)$ as given through equation 3.1. The composite process is thus doubly stochastic in the sense that in a first step, a set of input spike trains is drawn from an ensemble characterized by Poisson rates $\nu_i$. This realization of input spike trains then determines the output rate function, which produces in a second step a specific realization of the postsynaptic spike train. The natural question is how to characterize the nature of the resulting postsynaptic spike train.

For an inhomogeneous Poisson process with rate function $\nu$, the expectation of the number $k$ of events in an interval $[T_1, T_2]$ is

$$\mathrm{E}\{k \mid \nu\} = \int_{T_1}^{T_2} \mathrm{d}t\, \nu(t). \tag{3.2}$$

If the rate function $\nu$ is replaced by a stochastic process, we have to integrate over all possible realizations of $\nu$ (with respect to a measure $\mu$) in order to obtain the (unconditional) expectation of the number of events,

$$\mathrm{E}\{k\} = \int \mathrm{d}\mu(\nu) \mathrm{E}\{k \mid \nu\} = \left\langle \mathrm{E}\{k \mid \nu\} \right\rangle_\nu = \int_{T_1}^{T_2} \mathrm{d}t\, \bar{\nu}(t), \tag{3.3}$$

with $\langle \cdot \rangle_\nu = \int \cdot\, \mathrm{d}\mu(\nu)$ and $\bar{\nu}(t) = \langle \nu(t) \rangle_\nu$. Hence, the composite process has the same expectation of the number of events as an inhomogeneous Poisson process with rate function $\bar{\nu}(t)$, which is just the expectation of $\nu(t)$. Nevertheless, the composite process is not equivalent to a Poisson process. This can be seen by calculating the probabilities of observing $k$ events within $[T_1, T_2]$. For a Poisson process with fixed rate function $\nu$, this probability equals

$$\mathrm{prob}\{k \text{ events in } [T_1, T_2] \mid \nu\} = \frac{1}{k!} \left[ \int_{T_1}^{T_2} \mathrm{d}t\, \nu(t) \right]^k \exp\left[ -\int_{T_1}^{T_2} \mathrm{d}t\, \nu(t) \right], \tag{3.4}$$

whereas for the composite process, we obtain

$$\begin{aligned} &\mathrm{prob}\{k \text{ events in } [T_1, T_2]\} && (3.5) \\ &\quad = \left\langle \mathrm{prob}\{k \text{ events in } [T_1, T_2] \mid \nu\} \right\rangle_\nu \\ &\quad = \sum_{n=0}^{\infty} \frac{(-1)^n}{k!\,n!} \left\langle \left[ \int_{T_1}^{T_2} \mathrm{d}t\, \nu(t) \right]^{n+k} \right\rangle_\nu \\ &\quad = \sum_{n=0}^{\infty} \frac{(-1)^n}{k!\,n!} \int_{T_1}^{T_2} \mathrm{d}t_1 \ldots \int_{T_1}^{T_2} \mathrm{d}t_{n+k} \left\langle \nu(t_1) \ldots \nu(t_{n+k}) \right\rangle_\nu . && (3.6) \end{aligned}$$

The last expression contains expectations of products of the rate function $\nu$ evaluated at times $t_1, \ldots, t_{n+k}$. Since the membrane potential $h$ is a continuous function of time, the rate function is (at least) piecewise continuous, and $\nu(t_i)$ and $\nu(t_j)$ with $t_i \neq t_j$ are in general not statistically independent. The calculation of correlations such as $C(t_i, t_j) := \langle \nu(t_i)\nu(t_j)\rangle - \langle \nu(t_i)\rangle\langle \nu(t_j)\rangle$ is thus far from being trivial (Bartsch & van Hemmen, 1998).

In the following we *approximate* the composite process by an inhomogeneous Poisson process with rate function $\bar{\nu}$. This approximation can be justified for large numbers of overlapping excitatory postsynaptic potentials (EPSPs), when, due to the law of large numbers (Lamperti, 1966), the membrane potential as a sum of independent EPSPs and thus the rate function $\nu(t)$ is almost always close to its expectation value $\bar{\nu}(t)$. The approximation is equivalent to neglecting correlations in the rate function $\nu$. That is, to good approximation (as we will see shortly), we are allowed to assume $\nu(t_1), \ldots, \nu(t_{k+n})$ to be independent for $t_i \neq t_j$, $i \neq j$. In doing so, we can replace the expectation of the product by the product of expectations under the time integrals of equation 3.5 and obtain

$$
\begin{aligned}
&\text{prob}\,\{k \text{ events in } [T_1, T_2]\} \\
&\quad = \sum_{n=0}^{\infty} \frac{(-1)^n}{k!n!} \int_{T_1}^{T_2} \mathrm{d}t_1 \ldots \int_{T_1}^{T_2} \mathrm{d}t_{n+k} \bar{\nu}(t_1) \cdot \ldots \cdot \bar{\nu}(t_{n+k}) \\
&\quad = \frac{1}{k!} \left[ \int_{T_1}^{T_2} \mathrm{d}t\, \bar{\nu}(t) \right]^k \exp\left[ - \int_{T_1}^{T_2} \mathrm{d}t\, \bar{\nu}(t) \right], \qquad (3.7)
\end{aligned}
$$

which is the probability of observing $k$ events for an inhomogeneous Poisson process with rate function $\bar{\nu}$ that is simply the expectation of the process $\nu$. The efficacy of this approximation remains to be tested. This is done throughout the rest of this article by comparing theoretical results based on this approximation with numerical simulations.

We now calculate $\bar{\nu}$ for neuron $i$. We assume that the spike train of the presynaptic neurons, labeled $j$, can be described by an inhomogeneous Poisson process with rate function $\nu_j$. A description of spike trains of cortical neurons in terms of inhomogeneous Poisson processes is appropriate for time windows below approximately 1 second (Rieke, Warland, de Ruyter van Steveninck, & Bialek, 1997), which is sufficient for our purpose. With these preliminaries we can calculate the first and the second moment of the distribution of the resulting membrane potential.

The average postsynaptic potential generated by a single presynaptic neuron with rate function $\nu_j$ is

$$
\left\langle \sum_f \epsilon(t - t_j^f) \right\rangle = (\nu_j * \epsilon)(t). \qquad (3.8)
$$

Here $*$ denotes convolution, that is, $(f*g)(t) = \int \mathrm{d}t'\, f(t')g(t-t')$. The second moment is (Kempter, Gerstner, van Hemmen, & Wagner, 1998, appendix A)

$$\left\langle \left[ \sum_f \epsilon(t - t_j^f) \right]^2 \right\rangle = \left[(\nu_j * \epsilon)(t)\right]^2 + \left(\nu_j * \epsilon^2\right)(t). \tag{3.9}$$

Returning to equation 3.1, we see that the expectation value $\bar{h}_i$ of the membrane potential and the corresponding variance $\sigma_i^2$ are given by

$$\bar{h}_i(t) = \mathrm{E}\{h_i(t)\} = \sum_j J_{ij}(\nu_j * \epsilon)(t) \tag{3.10}$$

and

$$\sigma_i^2(t) = \mathrm{Var}\{h_i(t)\} = \sum_j J_{ij}^2(\nu_j * \epsilon^2)(t). \tag{3.11}$$

Because of the central limit theorem, the membrane potential at a certain fixed time $t$ has a gaussian distribution, if there are sufficiently many EPSPs that superimpose at time $t$; (for an estimate by the Berry-Esseen inequality we refer to Kempter et al., 1998). Equipped with the gaussian assumption, we can calculate $\bar{\nu}(t)$,

$$\begin{aligned} \bar{\nu}(t) &= \int \mathrm{d}h\, \mathcal{G}[h - \bar{h}_i(t), \sigma_i(t)]\nu(h) \\ &= \frac{\nu_{\max}}{2} \left\{ 1 + \operatorname{erf}\left[ \frac{\bar{h}_i(t) - \vartheta}{\sqrt{2\sigma_i^2(t)}} \right] \right\}, \end{aligned} \tag{3.12}$$

with $\mathcal{G}$ being a normalized gaussian, $\mathcal{G}(h, \sigma) = (2\pi\sigma^2)^{-1/2} \exp\left[-h^2/(2\sigma^2)\right]$. We note that this is the first time that we have used explicitly the functional dependence (see equation 2.2) of the firing rate $\nu$ on the membrane potential $h$.

The result so far is that if the membrane potential is a sum of many EPSPs so that we can assume $h(t)$ to be gaussian distributed and the membrane potentials for different times to be independent, and if the effect of the afterpotential is negligible, then the postsynaptic spike train is given by an inhomogeneous Poisson process with rate function $\bar{\nu}$ as given by equation 3.12.

## 4 First Passage Time

In the previous section we discussed an approximation that allows us to replace the doubly stochastic process that describes the postsynaptic spike train by an inhomogeneous Poisson process with a rate function $\bar{\nu}$ that is independent of the specific realization of the presynaptic input. This approximation allows us to calculate the distribution of the first postsynaptic spike analytically.

The probability of observing no spikes in the interval $[t_0, t]$ is

$$\text{prob}\,\{\text{no spike in } [t_0, t]\} = \exp\left[-\int_{t_0}^{t} \mathrm{d}t'\,\bar{\nu}(t')\right], \tag{4.1}$$

and the density for the first firing time after time $t_0$ is

$$\begin{aligned} p_{\text{first}}(t) &= \frac{\mathrm{d}}{\mathrm{d}t}(1 - \text{prob}\,\{\text{no spike in } [t_0, t]\}) \\ &= \bar{\nu}(t)\exp\left[-\int_{t_0}^{t} \mathrm{d}t'\,\bar{\nu}(t')\right]. \end{aligned} \tag{4.2}$$

We are going to study the first-spike distribution (*first passage time*) in a specific context. We consider a single neuron having $N$ independent synapses. Each synapse $i$ delivers a spike train determined by an inhomogeneous Poisson process with rate function $\nu_i(t) = (2\pi\sigma_i^2)^{-1/2}\exp\left[-t^2/2\sigma_i^2\right]$, so that on average, one spike arrives at each synapse with a temporal jitter $\sigma_i$ around $t = 0$.

We can calculate the averaged rate function $\bar{\nu}$ for this setup,

$$\bar{\nu}(t) = \frac{\nu_{\max}}{2}\left\{1 + \operatorname{erf}\left[\frac{\sum_{i=1}^{N} J_i\bar{\epsilon}_i(t) - \vartheta}{\sqrt{2\sum_{i=1}^{N} J_i^2\overline{\epsilon_i^2}(t)}}\right]\right\}, \tag{4.3}$$

with expectation and variance being given as convolutions

$$\bar{\epsilon}_i(t) = (\nu_i * \epsilon)(t), \quad \text{and} \quad \overline{\epsilon_i^2}(t) = (\nu_i * \epsilon^2)(t). \tag{4.4}$$

The resulting density of the first postsynaptic spike is shown in Figure 1.

**4.1 High Threshold.** We calculate the density of the first postsynaptic spike explicitly for two limiting cases. First, we assume that the probability of observing at least one postsynaptic spike is very small,

$$\int \mathrm{d}t\,\bar{\nu}(t) \ll 1. \tag{4.5}$$

In this case, the neuron will fire, if it will fire at all, in the neighborhood of the maximum of the postsynaptic potential. We expand the terms involving the

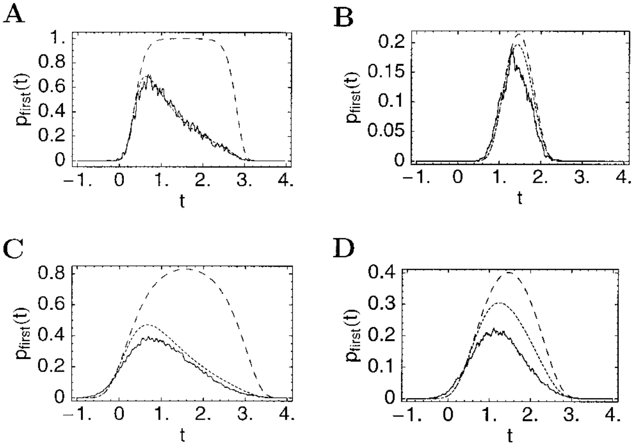

Figure 1: Plots to compare the density function for the first postsynaptic spike as reconstructed from simulations (solid line) with the analytical approximation using the averaged rate function of equation 4.3 (dotted line). The dashed line represents the mean rate $\bar{\nu}$. (A, B) $N = 100$ synapses with strength $J_i = 1/N$ receive spike trains determined by an inhomogeneous Poisson process with rate function $\nu_i = (2\pi\sigma^2)^{-1/2}\exp\left[-t^2/2\sigma^2\right]$ and $\sigma = 1$. The EPSPs are described by alpha functions $t/\tau\exp(1 - t/\tau)$ with time constant $\tau = 1$ so that the maximum of the membrane potential amounts to $h = 1$, if all spikes were to arrive simultaneously. The postsynaptic response is characterized by $\nu_{\max} = 1$ and $\vartheta = 0.5$ in *A* and $\vartheta = 0.75$ in *B*. Increasing the threshold obviously improves the temporal precision of the postsynaptic response, but the overall probability of a postsynaptic spike is decreased. (C, D) The same plots as *A* and *B* but for $N = 10$ instead of 100 synapses. The synaptic weights have been scaled so that $J_i = 1/10$. The central approximation that asserts statistical independence of the membrane potential at different times produces surprisingly good results for as little as $N = 10$ overlapping EPSPs.

membrane potential in the neighborhood of the maximum at $t_0$ to leading order in $t$,

$$\frac{\sum_{i=1}^{N} J_i\bar{\epsilon}_i(t) - \vartheta}{\sqrt{2\sum_{i=1}^{N} J_i^2\overline{\epsilon_i^2}(t)}} = h_0 - h_2(t - t_0)^2 + \mathcal{O}(t - t_0)^3 . \tag{4.6}$$

The averaged rate function $\bar{\nu}$ can thus be written

$$\begin{aligned}\bar{\nu}(t) &= \frac{\nu_{\max}}{2}\left\{1 + \operatorname{erf}\left[h_0 - h_2(t - t_0)^2 + \mathcal{O}(t - t_0)^3\right]\right\}\\ &= \bar{\nu}_0 - \bar{\nu}_2(t - t_0)^2 + \mathcal{O}(t - t_0)^3 ,\end{aligned} \tag{4.7}$$

with

$$\bar{\nu}_0 = \frac{\nu_{\max}}{2}\left[1 + \mathrm{erf}\,(h_0)\right], \qquad \text{and} \qquad \bar{\nu}_2 = \frac{\nu_{\max} h_2}{\sqrt{\pi}} \mathrm{e}^{-h_0^2}. \tag{4.8}$$

It turns out that for $-0.5 < h_0 < 0.5$, the averaged rate function $\bar{\nu}$ can be approximated very well by the clipped parabola

$$\bar{\nu}(t) \approx \begin{cases} \bar{\nu}_0 - \bar{\nu}_2 (t - t_0)^2, & \text{for } |t - t_0| < \sqrt{\bar{\nu}_0/\bar{\nu}_2}, \\ 0, & \text{elsewhere.} \end{cases} \tag{4.9}$$

Using this approximation, we can calculate the integral over $\bar{\nu}$ and obtain the distribution of the first postsynaptic spike,

$$p_{\text{first}}(t) = \left[\bar{\nu}_0 - \bar{\nu}_2 (t - t_0)^2\right] \exp\left[\frac{\bar{\nu}_2}{3}(t - t_0)^3 - \bar{\nu}_0 (t - t_0) - \frac{2\bar{\nu}_0}{3}\sqrt{\frac{\bar{\nu}_0}{\bar{\nu}_2}}\right] \\ \times \Theta\left(\sqrt{\frac{\bar{\nu}_0}{\bar{\nu}_2}} - |t - t_0|\right). \tag{4.10}$$

For $h_0 < -0.5$, however, a gaussian function is the better choice,

$$\bar{\nu}(t) \approx \bar{\nu}_{\text{post}} \mathcal{G}(t - t_0, \sigma_{\text{post}}), \tag{4.11}$$

with $\bar{\nu}_{\text{post}} = \sqrt{\pi \bar{\nu}_0^3/\bar{\nu}_2}$ and $\sigma_{\text{post}} = \sqrt{\bar{\nu}_0/(2\bar{\nu}_2)}$. Since $\bar{\nu}_{\text{post}} \ll 1$, we have

$$p_{\text{first}}(t) \approx \bar{\nu}(t). \tag{4.12}$$

**4.2 Low Threshold.** We now discuss the case where the postsynaptic neuron fires with probability near to one, that is,

$$1 - \int \mathrm{d}t\, \bar{\nu}(t) \ll 1. \tag{4.13}$$

In this case, the neuron will fire approximately at time $t_0$ when the membrane potential crosses the threshold, $h(t_0) = \vartheta$. We again expand the terms containing the membrane potential to leading order in $(t - t_0)$,

$$\frac{\sum_{i=1}^{N} J_i \bar{\epsilon}_i(t) - \vartheta}{\sqrt{2 \sum_{i=1}^{N} J_i^2 \bar{\epsilon}_i^2(t)}} = h_1 (t - t_0) + \mathcal{O}(t - t_0)^2, \tag{4.14}$$

and assume that the averaged rate function $\bar{\nu}$ is already saturated outside the region where this linearization is valid. We may therefore put

$$\bar{\nu}(t) = \frac{\nu_{\max}}{2}\left\{1 + \mathrm{erf}\left[h_1 (t - t_0)\right]\right\}, \tag{4.15}$$

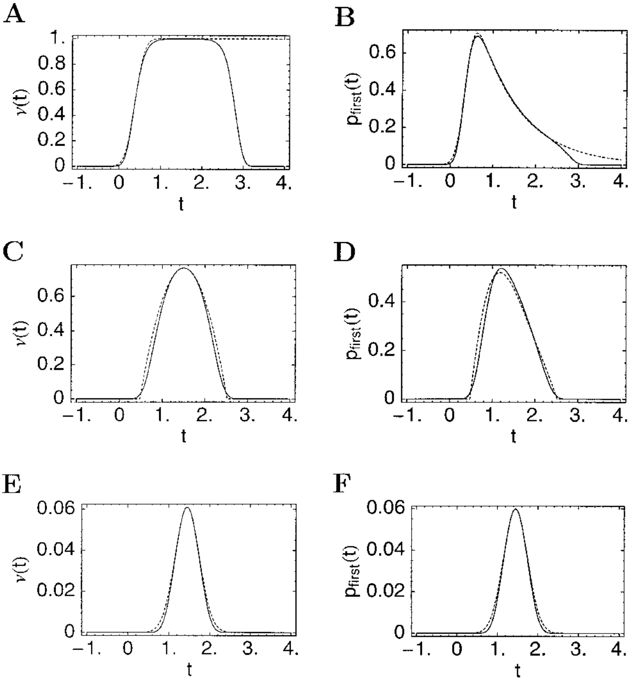

Figure 2: Approximation of the averaged rate function $\bar{\nu}$ (left) and the density of the first postsynaptic spike $p_{\text{first}}$ (right) for various threshold values. The solid line gives the numerical result; the dashed line represents the analytic approximation. (A, B) Approximation for low-threshold value ($\vartheta = 0.5$) as in equations 4.15 and 4.16. (C, D), Approximation by a clipped parabola for $\vartheta = 0.65$, as in equations 4.9 and 4.10. (E, F) Gaussian approximation for high-threshold values ($\vartheta = 0.8$); see equations 4.11 and 4.12. The number of synapses is $N = 100$; the other parameters are as in Figure 1.

and obtain for the density of the first postsynaptic spike,

$$p_{\text{first}}(t) = \bar{\nu}(t) \exp\left[-\bar{\nu}(t)(t - t_0) - \frac{\nu_{\max}}{2\sqrt{\pi}h_1} e^{-h_1^2(t-t_0)^2}\right]. \tag{4.16}$$

Outside the neighborhood of the threshold crossing, that is, for $|t - t_0| \gg h_1^{-1}$, $p_{\text{first}}$ can be approximated by

$$p_{\text{first}}(t) \approx \nu_{\max} e^{-\nu_{\max}(t-t_0)} \Theta(t - t_0), \qquad |t - t_0| \gg h_1^{-1}. \tag{4.17}$$

**4.3 Optimal Threshold.** As can be seen in Figure 2, the width of the first-spike distribution decreases with increasing threshold $\vartheta$. The temporal precision of the postsynaptic spike can thus be improved by increasing

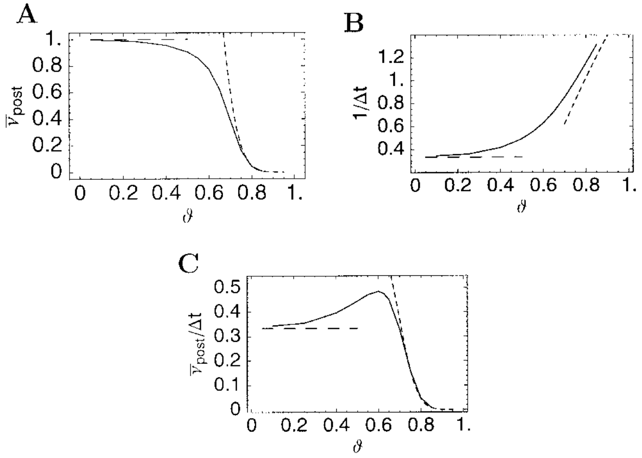

Figure 3: Reliability (A) and precision (B) of the postsynaptic firing event as a function of the threshold $\vartheta$. The neuron receives input through $N = 100$ synapses; for details, see the caption to Figure 1. Reliability is defined as the overall firing probability $\bar{\nu}_{\text{post}} = \int \mathrm{d}t\, p_{\text{first}}(t)$. Precision is the inverse of the length of the interval containing 90% of the postsynaptic spikes, $\Delta t = t_2 - t_1$ with $\int_{-\infty}^{t_1} \mathrm{d}t\, p_{\text{first}}(t) = \int_{t_2}^{\infty} \mathrm{d}t\, p_{\text{first}}(t) = 0.05\bar{\nu}_{\text{post}}$. *C* demonstrates that there is an optimal threshold in the sense that $\bar{\nu}_{\text{post}}/\Delta t$ exhibits a maximum at $\vartheta \approx 0.6$. The short and the long dashed lines represent the results obtained through the high- and the low-threshold approximations, respectively; See equations 4.18–4.20.

the firing threshold $\vartheta$. The overall firing probability of the postsynaptic neuron, however, drops to zero if the threshold exceeds the maximum value of the membrane potential. The trade-off between the precision of the postsynaptic response and the reliability, that is, the overall firing probability of the postsynaptic neuron, is illustrated in Figure 3. There is an optimal threshold where the expectation value of the precision, that is, the product of reliability and precision, reaches its maximum (Kempter et al., 1998).

A straightforward estimate demonstrates the functional dependence of precision and reliability on the various parameters. For high-threshold values, the density $p_{\text{first}}$ for the first postsynaptic spike can be approximated by a gaussian function with variance $\bar{\nu}_0/2\bar{\nu}_2$. The precision of the firing time is thus proportional to

$$\Delta t^{-1} \propto \sqrt{\bar{\nu}_2/\bar{\nu}_0} = \left(\frac{2h_2 e^{-h_0^2}}{\sqrt{\pi}\,[1 + \operatorname{erf}(h_0)]}\right)^{1/2}, \tag{4.18}$$

which depends solely on the time course of the membrane potential and is independent of $\nu_{\max}$. The reliability of the postsynaptic response amounts to

$$\bar{\nu}_{\text{post}} = \sqrt{\pi \bar{\nu}_0^3 / \bar{\nu}_2} = \nu_{\max} \left( \frac{\sqrt{\pi}[1 + \text{erf}\,(h_0)]^3}{8 h_2 \mathrm{e}^{-h_0^2}} \right)^{1/2}, \tag{4.19}$$

which is proportional to $\nu_{\max}$.

For low threshold, $p_{\text{first}}(t)$ is dominated by an exponential decay $\propto \mathrm{e}^{-\nu_{\max} t}$, resulting in a constant precision,

$$\Delta t^{-1} \approx \frac{\nu_{\max}}{3.00}, \tag{4.20}$$

and reliability close to unity.

## 5 Synaptic Long-Term Plasticity

There is experimental evidence (Markram et al., 1997) that the strength of synapses between cortical neurons is changed according to the relative timing of pre- and postsynaptic spikes. We develop a simple model of synaptic long-term plasticity that mimics the experimental observations. Using the densities for the first postsynaptic spike calculated in the previous section, we find analytic expressions for the stationary synaptic weights that result from the statistics of the presynaptic spike train.

**5.1 Modeling Synaptic Plasticity.** Very much in the thrust of the spike-response model, we describe the change of a synaptic weight as the linear response to pre- and postsynaptic spikes. Spike trains are formalized by sums of Dirac delta functions, $S(t) = \sum_f \delta(t - t^f)$, with a delta function for each firing time $t^f$. The most general ansatz up to and including terms bilinear in the pre- and postsynaptic spike train for the change of the synaptic weight $J$ is

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t} J(t) = \; & S_{\text{pre}}(t) \left[ \delta_{\text{pre}} + \int \mathrm{d}t'\, \kappa_{\text{pre}}(t') S_{\text{post}}(t - t') \right] \\ & + S_{\text{post}}(t) \left[ \delta_{\text{post}} + \int \mathrm{d}t'\, \kappa_{\text{post}}(t') S_{\text{pre}}(t - t') \right]. \end{aligned} \tag{5.1}$$

This is a combination of changes that are induced by the pre- ($S_{\text{pre}}$) and the postsynaptic ($S_{\text{post}}$) spike train. Furthermore, $\delta_{\text{pre}}$ ($\delta_{\text{post}}$) is the amount by which the synaptic weight is changed if a single presynaptic (postsynaptic) spike occurs. This non-Hebbian contribution to synaptic plasticity, which is well documented in the literature (Alonso, Curtis, & Llinás, 1990; Nelson, Fields, Yu, & Liu, 1993; Salin, Malenka, & Nicoll, 1996; Urban & Barrionuevo, 1996), is necessary to ensure that the fixed point of the synaptic strength can be reached from very low initial values and even zero postsynaptic activity (take $0 < \delta_{\text{pre}} \ll 1$) and to regulate postsynaptic activity (take $-1 \ll \delta_{\text{post}} < 0$). Finally, $\kappa_{\text{pre}}(s)$ ( $\kappa_{\text{post}}(s)$) is the additional change induced by a presynaptic (postsynaptic) spike that occurs $s$ milliseconds after a postsynaptic (presynaptic) spike. This modification of synaptic strength depends critically on the timing of pre- and postsynaptic spikes (Dan & Poo, 1992; Bell et al., 1997; Markram et al., 1997). Causality is respected if the kernels $\kappa$ vanish identically for negative arguments.

In order to restrict the synaptic weights to the interval $[0, 1]$, we treat synaptic potentiation and depression separately and assume that synaptic weight changes due to depression are proportional to the current synaptic weight $J(t)$, whereas changes due to potentiation are proportional to $[1 - J(t)]$, so that

$$\frac{\mathrm{d}}{\mathrm{d}t}J(t) = [1 - J(t)]\left[\frac{\mathrm{d}}{\mathrm{d}t}J(t)\right]^{\text{LTP}} - J(t)\left[\frac{\mathrm{d}}{\mathrm{d}t}J(t)\right]^{\text{LTD}} \tag{5.2}$$

with

$$\begin{aligned}\left[\frac{\mathrm{d}}{\mathrm{d}t}J(t)\right]^{\text{LTP/D}} &= S_{\text{pre}}(t)\left[\delta_{\text{pre}}^{\text{LTP/D}} + \int \mathrm{d}t'\, \kappa_{\text{pre}}^{\text{LTP/D}}(t')S_{\text{post}}(t - t')\right] \\ &\quad + S_{\text{post}}(t)\left[\delta_{\text{post}}^{\text{LTP/D}} + \int \mathrm{d}t'\, \kappa_{\text{post}}^{\text{LTP/D}}(t')S_{\text{pre}}(t - t')\right],\end{aligned} \tag{5.3}$$

and $\delta_{\text{pre/post}}^{\text{LTP/D}}, \kappa_{\text{pre/post}}^{\text{LTP/D}}(t') \geq 0$.

We are interested in the net change $\langle \Delta J \rangle$ of the synaptic weight integrated over some time interval and averaged over an ensemble of presynaptic spike trains,

$$\langle \Delta J \rangle = \left\langle \int \mathrm{d}t \left[\frac{\mathrm{d}}{\mathrm{d}t}J(t)\right]\right\rangle. \tag{5.4}$$

If synaptic weights change only adiabatically, that is, if the change of the synaptic weight is small as compared $J$ and $(1 - J)$, we have

$$\langle \Delta J \rangle = [1 - J(t)]\left\langle \Delta J^{\text{LTP}} \right\rangle - J(t)\left\langle \Delta J^{\text{LTD}} \right\rangle, \tag{5.5}$$

with

$$\begin{aligned}\left\langle \Delta J^{\text{LTP/D}} \right\rangle &= \left\langle \int \mathrm{d}t \left[\frac{\mathrm{d}}{\mathrm{d}t}J(t)\right]^{\text{LTP/D}} \right\rangle \\ &= \delta_{\text{pre}}^{\text{LTP/D}}\bar{\nu}_{\text{pre}} + \delta_{\text{post}}^{\text{LTP/D}}\bar{\nu}_{\text{post}} \\ &\quad + \int \mathrm{d}t \int \mathrm{d}t'\, \nu(t; t')\kappa^{\text{LTP/D}}(t; t'),\end{aligned} \tag{5.6}$$

where $\bar{\nu}_{\text{pre,post}} = \int \mathrm{d}t \nu_{\text{pre,post}}(t)$ is the expected number of pre- and postsynaptic spikes, and $\kappa^{\text{LTP/D}}(t; t') = \kappa^{\text{LTP/D}}_{\text{pre}}(t-t') + \kappa^{\text{LTP/D}}_{\text{post}}(t'-t)$ is the change of the synaptic weight due to a presynaptic spike at time $t$ and a postsynaptic spike at time $t'$. In passing we note that $\nu(t; t')\mathrm{d}t\mathrm{d}t'$ is the joint probability of finding a presynaptic spike in the interval $[t, t+\mathrm{d}t)$ and a postsynaptic spike in $[t', t'+\mathrm{d}t')$.

**5.2 Stationary Weights.** In the following we concentrate on calculating the stationary synaptic weights defined by

$$\langle \Delta J \rangle = 0 \qquad \Longleftrightarrow \qquad J = \frac{\left\langle \Delta J^{\text{LTP}} \right\rangle}{\left\langle \Delta J^{\text{LTP}} \right\rangle + \left\langle \Delta J^{\text{LTD}} \right\rangle}. \tag{5.7}$$

To this end, we return to the situation described at the beginning of Section 4 where a neuron receives input through $N$ independent synapses, each spike train being described by an inhomogeneous Poisson process with rate function $\nu_i$, and $1 \le i \le N$. We study a single synapse and assume that this synapse conveys (on average) one action potential with a gaussian distribution centered around $t = 0$ so that $\nu(t) = \mathcal{G}(t, \sigma_{\text{pre}})$. The synaptic weight of this synapse is denoted by $J$. Furthermore, we assume that the presynaptic volley of action potentials triggers at most one postsynaptic spike, as is the case, for instance, if postsynaptic action potentials are followed by strong hyperpolarizing afterpotentials. This assumption relieves us from the need to discuss the influence of the shape of the afterpotential $\eta$ because the postsynaptic spike statistic is now completely described by the first-passage-time $p_{\text{first}}$.

We discuss the case where the firing time of a single presynaptic neuron and the postsynaptic firing time are virtually independent. This might be considered as an approximation of the case where either the corresponding synaptic weight is small or the number of overlapping EPSPs needed to reach the firing threshold is large. The joint probability $\nu_i(t, t')$ of the firing of the presynaptic neuron $i$ and the first postsynaptic spike is then simply the product of the probabilities,

$$\nu_i(t, t') = \nu_i(t) p_{\text{first}}(t'). \tag{5.8}$$

We investigate a learning rule that is inspired by the observation that a synapse is weakened (depressed) if the presynaptic spike arrives a short time after the postsynaptic spike and is strengthened (potentiated) if the presynaptic spike arrives a short time before the postsynaptic spike and, thus, is contributing to the postsynaptic neuron's firing (Markram et al., 1997). We can mimic this mechanism within our formalism by setting

$$\kappa^{\text{LTP}}(t; t') = \epsilon^{\text{LTP}} \exp\left[-(t'-t)/\tau^{\text{LTP}}\right] \Theta(t'-t), \tag{5.9}$$

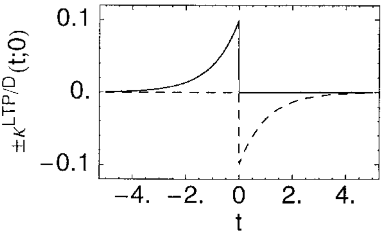

Figure 4: Synaptic plasticity based on the timing of pre- and postsynaptic spikes. The kernels $+\kappa^{\mathrm{LTP}}$ (solid line) and $-\kappa^{\mathrm{LTD}}$ (dashed line) describe the modification of synaptic strength as it is caused by the combination of a postsynaptic spike at time 0 and a presynaptic spike arriving at time $t$. See equations 5.9–5.10 with $\epsilon^{\mathrm{LTP}} = \epsilon^{\mathrm{LTD}} = 0.1$ and $\tau^{\mathrm{LTP}} = \tau^{\mathrm{LTD}} = 1$.

and

$$\kappa^{\mathrm{LTD}}(t;t') = \epsilon^{\mathrm{LTD}} \exp\left[-(t-t')/\tau^{\mathrm{LTD}}\right] \Theta(t-t'), \tag{5.10}$$

with $\epsilon^{\mathrm{LTP/D}} > 0$ and $\tau^{\mathrm{LTP/D}}$ as time constants of the "synaptic memory" (see Figure 4). Our choice of adopting exponentials to describe the kernels $\kappa^{\mathrm{LTP}}$ and $\kappa^{\mathrm{LTD}}$ is motivated by both biological plausibility and the need to keep the mathematical analysis as simple as possible.

With these prerequisites, we can calculate the mean potentiation and depression due to the correlation of pre- and postsynaptic spikes (cf. equation 5.6) for the limiting cases of high and low threshold. If we approximate the postsynaptic firing by a gaussian distribution (cf. equation 4.12),

$$p_{\mathrm{first}}(t) = \bar{\nu}_{\mathrm{post}} \mathcal{G}(t - t_0, \sigma_{\mathrm{post}}), \tag{5.11}$$

we find

$$\begin{aligned}
&\int \mathrm{d}t \int \mathrm{d}t'\, \nu(t;t') \kappa^{\mathrm{LTP}}(t;t') \\
&\quad = \epsilon^{\mathrm{LTP}} \int_{-\infty}^{\infty} \mathrm{d}t \int_{t}^{\infty} \mathrm{d}t'\, \mathcal{G}(t, \sigma_{\mathrm{pre}}) \bar{\nu}_{\mathrm{post}} \mathcal{G}(t' - t_0, \sigma_{\mathrm{first}}) \exp\left[-(t'-t)/\tau^{\mathrm{LTP}}\right] \\
&\quad = \frac{1}{2} \bar{\nu}_{\mathrm{post}} \epsilon^{\mathrm{LTP}} \exp\left[\frac{1}{2}\left(\frac{\sigma}{\tau^{\mathrm{LTP}}}\right)^2 - \frac{t_0}{\tau^{\mathrm{LTP}}}\right] \operatorname{erfc}\left[\frac{1}{2}\frac{\sqrt{2}\sigma}{\tau^{\mathrm{LTP}}} - \frac{t_0}{\sqrt{2}\sigma}\right],
\end{aligned} \tag{5.12}$$

and

$$\begin{aligned}
&\int \mathrm{d}t \int \mathrm{d}t'\, \nu(t;t') \kappa^{\mathrm{LTD}}(t;t') \\
&\quad = \frac{1}{2} \bar{\nu}_{\mathrm{post}} \epsilon^{\mathrm{LTD}} \exp\left[\frac{1}{2}\left(\frac{\sigma}{\tau^{\mathrm{LTD}}}\right)^2 + \frac{t_0}{\tau^{\mathrm{LTD}}}\right] \operatorname{erfc}\left[\frac{1}{2}\frac{\sqrt{2}\sigma}{\tau^{\mathrm{LTD}}} + \frac{t_0}{\sqrt{2}\sigma}\right],
\end{aligned} \tag{5.13}$$

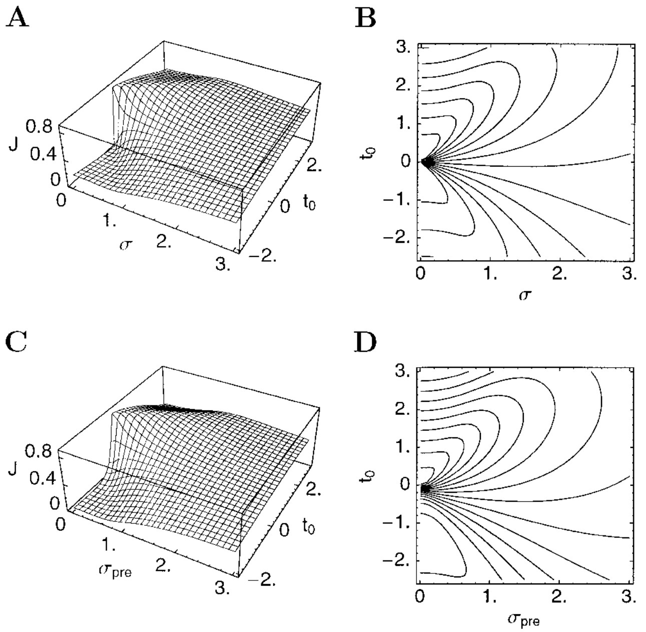

Figure 5: Stationary synaptic weights. (A) Three-dimensional plot of the stationary synaptic weight for high threshold as a function of $\sigma$ and $t_0$, where $\sigma^2 = \sigma_{\mathrm{pre}}^2 + \sigma_{\mathrm{post}}^2$ is the sum of the variances of pre- and postsynaptic firing time and $t_0$ the time between the arrival of the presynaptic spike and the firing of the postsynaptic action potential. (B) Contour plot of the same function as in *A*. (C, D) Plot of the stationary synaptic weight in the case of low-threshold $\vartheta$ as a function of the standard deviation $\sigma_{\mathrm{pre}}$ of the presynaptic firing time and the time $t_0$ when the expectation of the membrane potential reaches the threshold from below. The parameters used to describe synaptic plasticity are $\delta_{\mathrm{post}}^{\mathrm{LTD}} = 0.01$, $\delta_{\mathrm{pre}}^{\mathrm{LTP}} = 0.001$, $\delta_{\mathrm{pre}}^{\mathrm{LTD}} = \delta_{\mathrm{post}}^{\mathrm{LTP}} = 0$, $\epsilon^{\mathrm{LTP}} = \epsilon^{\mathrm{LTD}} = 0.1$, $\tau^{\mathrm{LTP}} = \tau^{\mathrm{LTD}} = 1$; See equations 5.2, 5.9, and 5.10.

with $\sigma^2 = \sigma_{\mathrm{pre}}^2 + \sigma_{\mathrm{post}}^2$. Using equation 5.7, we are thus able to calculate the stationary weight of a synapse that conveys a single action potential with a gaussian distribution with variance $\sigma_{\mathrm{pre}}^2$, given the postsynaptic spike at $t = t_0$ with variance $\sigma_{\mathrm{post}}^2$. This result is illustrated in Figure 5. If the variance of both pre- and postsynaptic spike is small, that is, $\sigma^2 = \sigma_{\mathrm{pre}}^2 + \sigma_{\mathrm{post}}^2 \ll 1$, the stationary weight is dominated by the kernels $\kappa^{\mathrm{LTP/D}}$: The weight is close to zero if the presynaptic spike occurs after the postsynaptic one ($t_0 < 0$) and close to unity if the presynaptic spike arrives a short time before the postsynaptic action potential ($t_0 > 0$). For large variances, this dependence on the timing of the spikes is smoothed, and the stationary weight is determined by the rates of pre- and postsynaptic spikes.

We obtain a similar result for low threshold if we approximate the postsynaptic firing time by an exponential distribution (cf. equation 4.17),

$$\begin{aligned}
&\int \mathrm{d}t \int \mathrm{d}t'\, \nu(t;\, t')\kappa^{\mathrm{LTP}}(t;\, t') \\
&\quad = \epsilon^{\mathrm{LTP}} \int_{-\infty}^{\infty} \mathrm{d}t \int_{\max(t,t_0)}^{\infty} \mathrm{d}t'\, \mathcal{G}(t,\, \sigma_{\mathrm{pre}})\nu_{\max} \mathrm{e}^{-\nu_{\max}(t'-t_0)} \mathrm{e}^{-(t'-t)/\,\tau^{\mathrm{LTP}}} \\
&\quad = \frac{\epsilon^{\mathrm{LTP}}\nu_{\max}}{\nu_{\max} + 1/\,\tau^{\mathrm{LTP}}} \left\{ \frac{1}{2} \exp\left[ \frac{1}{2} \left( \frac{\sigma_{\mathrm{pre}}}{\tau^{\mathrm{LTP}}} \right)^2 - \frac{t_0}{\tau^{\mathrm{LTP}}} \right] \right. \\
&\qquad \times \operatorname{erfc}\left[ \frac{\sigma}{\sqrt{2}\tau^{\mathrm{LTP}}} - \frac{t_0}{\sqrt{2}\sigma_{\mathrm{pre}}} \right] \\
&\qquad + \frac{1}{2} \exp\left[ \frac{1}{2} \left(\sigma_{\mathrm{pre}}\nu_{\max}\right)^2 + t_0\nu_{\max} \right] \\
&\qquad \left. \times \operatorname{erfc}\left[ \frac{\sigma_{\mathrm{pre}}\nu_{\max}}{\sqrt{2}} + \frac{t_0}{\sqrt{2}\sigma_{\mathrm{pre}}} \right] \right\}, \qquad (5.14)
\end{aligned}$$

and

$$\begin{aligned}
&\int \mathrm{d}t \int \mathrm{d}t'\, \nu(t;\, t')\kappa^{\mathrm{LTD}}(t;\, t') \\
&\quad = \frac{\epsilon^{\mathrm{LTD}}\nu_{\max}}{\nu_{\max} - 1/\,\tau^{\mathrm{LTD}}} \left\{ \frac{1}{2} \exp\left[ \frac{1}{2} \left( \frac{\sigma_{\mathrm{pre}}}{\tau^{\mathrm{LTD}}} \right)^2 + \frac{t_0}{\tau^{\mathrm{LTD}}} \right] \right. \\
&\qquad \times \operatorname{erfc}\left[ \frac{\sigma}{\sqrt{2}\tau^{\mathrm{LTD}}} + \frac{t_0}{\sqrt{2}\sigma_{\mathrm{pre}}} \right] \\
&\qquad - \frac{1}{2} \exp\left[ \frac{1}{2} \left(\sigma_{\mathrm{pre}}\nu_{\max}\right)^2 + t_0\nu_{\max} \right] \\
&\qquad \left. \times \operatorname{erfc}\left[ \frac{\sigma_{\mathrm{pre}}\nu_{\max}}{\sqrt{2}} + \frac{t_0}{\sqrt{2}\sigma_{\mathrm{pre}}} \right] \right\}. \qquad (5.15)
\end{aligned}$$

**5.3 Synaptic Weights as a Function of the Input Statistics.** We saw in the previous section that the stationary synaptic weights can be calculated as a function of the parameters characterizing the distribution of the pre- and postsynaptic spikes. The synaptic weights, on the other hand, determine the distribution of the postsynaptic spike. If we are interested in the synaptic weights that are produced by given input statistics, we thus have to solve a self-consistency problem.

The self-consistency problem can be solved numerically for the limiting cases of low and high threshold, where the distribution of the postsynaptic firing time is completely characterized by only a few parameters. That is, starting from a given vector $\boldsymbol{J}$ of synaptic couplings, we calculate the parameters that characterize the postsynaptic firing time using the results of section 4 in the limiting cases of high- and low-firing threshold. In a second step, we calculate the corresponding stationary synaptic weight vector $\overline{\boldsymbol{J}}$ as it is determined by the statistics of pre- and postsynaptic firing times; (cf. section 5.2). Finally, we solve the self-consistency equation $\boldsymbol{J} = \overline{\boldsymbol{J}}$ using standard numerics.

In the simple case where all synapses deliver spikes with a common statistics, the stable solution to the self-consistency equation is unique because the mean postsynaptic firing time is a monotone function of the synaptic weight. But if the synapses are different, say, with respect to the mean spike arrival time, the solution in general will no longer be unique.

We illustrate the solution of the self-consistency problem by means of an example and consider a neuron that receives spikes via $N$ independent synapses. Again, each presynaptic spike train is described by an inhomogeneous Poisson process with a gaussian rate $\mathcal{G}(t, \sigma_i)$ centered at $t = 0$. In contrast to our previous examples, the synapses are different with respect to the temporal precision $\sigma_i$ with which they deliver their action potentials.

Figure 6A shows the resulting synaptic weights if we start with two groups of presynaptic neurons that deliver action potentials with $\sigma_1 = 0.1$ and $\sigma_2 = 1.0$, respectively. The number of neurons contained in group 1 and group 2 are $n_1 = 20$ and $n_2 = 80$, respectively, but the results turned out to be insensitive to the actual numbers. (A more balanced ratio of synapses would shift the curve $J_1(\vartheta)$ slightly to the left). We compare the results obtained from the unique solution of the self-consistency equation with simulations of a straightforward implementation of the synaptic dynamics given in equation 5.2. The number of iterations required for the synaptic weights to settle down in the stationary values depends on the amplitude of the synaptic weight change described by $\delta^{\mathrm{LTP/D}}$ and $\epsilon^{\mathrm{LTP/D}}$ and on the amount of postsynaptic activity and, thus, on the firing threshold. With the parameters used in Figure 6, stationarity is usually reached in fewer than 1000 iterations.

Finally, a brief discussion of the results shown in Figure 6 is in order. For a high firing threshold, the synaptic weights of both groups are close to their maximum value because otherwise the neuron would not fire at all. This is due to the constant presynaptic potentiation $\delta_{\mathrm{pre}}^{\mathrm{LTP}} > 0$. For very low threshold, the postsynaptic firing is triggered by the first spikes that arrive at the neuron. These spikes stem from presynaptic neurons with a broad firing-time distribution (group 2). Spikes from group 1 neurons thus arrive mostly after the postsynaptic neuron has already fired and the corresponding synapses are depressed accordingly. This explains why synapses

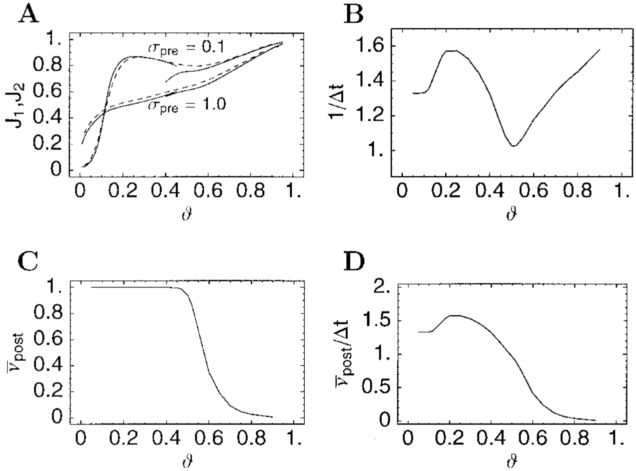

Figure 6: (A) Synaptic weights for a neuron receiving input from two groups of synapses. One group ($n_1 = 20$) delivers precisely timed spikes ($\sigma_{\rm pre} = 0.1$) and the other one ($n_2 = 80$) spikes with a broad distribution of arrival times ($\sigma_{\rm pre} = 1.0$). The synapses are subject to a mechanism that modifies the synaptic strength according to the relative timing of pre- and postsynaptic spikes, see equation 5.2. The upper trace shows the resulting synaptic weight for the group of precise synapses; the lower trace corresponds to the second group. The solid lines give the analytic result for either the low-threshold ($\vartheta < 0.4$) or the high-threshold ($\vartheta > 0.4$) approximation. The dashed lines show the results of a computer simulation. The parameters for the synaptic plasticity are the same as in Figure 5. (B, C, D) precision $\Delta t^{-1}$, reliability $\bar{\nu}_{\rm post}$, and efficiency $\bar{\nu}_{\rm post}/\Delta t$ as a function of the threshold $\vartheta$ for the same neuron as in *A*. See Figure 3 for the definition of $\bar{\nu}_{\rm post}$ and $\Delta t$.

delivering precisely timed spikes are weaker than group 2 synapses, unless the firing threshold exceeds a certain critical value.

The most interesting finding is that in the intermediate range of the firing threshold, synapses that deliver precisely timed spikes are substantially stronger than synapses with poor temporal precision. Furthermore, there is an optimal threshold at $\vartheta \approx 0.2$ where the ratio of the synaptic strengths of precise and unprecise synapses is largest. The firing of the postsynaptic neuron is thus driven mainly by spikes from group 1 neurons, and the jitter of the postsynaptic spikes is minimal (see Figure 6B).

## 6 Discussion

We have presented a stochastic neuron model that allows for a description of pre- and postsynaptic spike trains by inhomogeneous Poisson processes provided that the number of overlapping postsynaptic potentials is not too small. In view of the huge number of synapses that a single neuron carries on its dendritic tree and the number of synchronous excitatory postsynaptic potentials required to reach threshold—$10^4 \dots 10^5$ synapses and several tens of EPSPs—the approximations used seem to be justified. Since firing of a neuron is triggered by a large number of synchronous presynaptic action potentials, the postsynaptic firing time and the arrival time of a single presynaptic spike can be assumed to be independent and the correlation of pre- and postsynaptic firing times is readily calculated.

In addition to the spike-triggering mechanism, we have developed a model for synaptic long-term plasticity based on the relative timing of pre- and postsynaptic firing events. The dynamics of the synaptic weights can be analyzed in connection with the former neuron model. In particular, stationary synaptic weights can be calculated as limit states for a given ensemble of presynaptic spike trains. It turns out that this mechanism is able to tune the synaptic weights according to the temporal precision of the spikes they convey. Synapses that deliver precisely timed action potentials are favored at the expense of synapses that deliver spikes with a large temporal jitter. This learning process does not rely on an external teacher signal; it is unsupervised. Furthermore, there is only one free parameter that has to be fixed: the firing threshold $\vartheta$. It is conceivable that a small, local network of inhibitory interneurons could be entrusted with setting the firing threshold.

The result concerning the tuning of synaptic weights has two consequences that are open to experimental verification. First, it shows that neurons are able to tune their synaptic weights so as to select inputs from those presynaptic neurons that provide information that is meaningful in the sense of a temporal code. Second, this tuning ensures the preservation of temporally encoded information because noisy synapses are depressed and the neuron is thus able to fire its action potential with high temporal precision. We believe that this mechanism has clear relevance to any information processing based on temporal spike coding.

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