Generalized Bienenstock–Cooper–Munro rule for spiking neurons that maximizes information transmission

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Maximization of information transmission by a spiking-neuron model predicts changes of synaptic connections that depend on timing of pre- and postsynaptic spikes and on the postsynaptic membrane potential. Under the assumption of Poisson firing statistics, the synaptic update rule exhibits all of the features of the Bienenstock–Cooper–Munro rule, in particular, regimes of synaptic potentiation and depression separated by a sliding threshold. Moreover, the learning rule is also applicable to the more realistic case of neuron models with refractoriness, and is sensitive to correlations between input spikes, even in the absence of presynaptic rate modulation. The learning rule is found by maximizing the mutual information between presynaptic and postsynaptic spike trains under the constraint that the postsynaptic firing rate stays close to some target firing rate. An interpretation of the synaptic update rule in terms of homeostatic synaptic processes and spike-timing-dependent plasticity is discussed.

Methods and Models

Spiking-Neuron Model. We consider a stochastically spiking-neuron model with refractoriness. For simulations, and also for some parts of the theory, it is convenient to formulate the model in discrete time with step size $\Delta t$, i.e., $t^k = k \Delta t$. However, for the ease of expression and with respect to a comparison with biological neurons, it is more practical to turn to continuous time by taking $\Delta t \to 0$. The continuous time limit is indicated in the following formulas by a right arrow ($\to$). The postsynaptic neuron receives input at $N$ synapses. A presynaptic spike train at synapse $j$ is described in discrete time as a sequence $x_j^k (k = 1, \ldots, K)$ of zeros (no spike) and ones (spike). The upper index $k$ denotes time bin $k$. Thus, $x_j^k = 1$ indicates that a presynaptic spike arrived at synapse $j$ at a time $t^k$ with $t^{k+1} \leq t^k < t^k$. Each presynaptic spike evokes a PSP of amplitude $w_j$ and exponential time course $e(t - t^k)$ with time constant $\tau_m = 10$ ms. The membrane potential at time step $t^k$ is denoted as $u(t^k)$ and calculated as the total PSP

$$u(t^k) = u_r + \sum_{j=1}^{N} \sum_{n=1}^{k} w_j e(t^k - t^n) x_j^n + \sum_{j} w_j e(-t^k).$$

[1]

where $u_r = -70$ mV is the resting potential. The probability $p^k$ of firing in time step $k$ is a function of the membrane potential $u$ and the refractory state $R$ of the neuron,

$$p^k = 1 - \exp[-g(u(t^k)) R(t^k) \Delta t] = g(u(t^k)) R(t^k) \Delta t,$$

[2]

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Abbreviations: BCM, Bienenstock–Cooper–Munro; LTP, long-term potentiation; LTD, long-term depression; PSP, postsynaptic potential.

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where $\Delta t$ is the time step and $g$ is a smooth increasing function of $u$. Thus, the larger the membrane potential, the higher the firing probability. For $\Delta t \to 0$, we may think of $g(u)R(i)$ as the instantaneous firing rate, or hazard of firing, given knowledge about the previous firing history. We focus on nonadapting neurons where the refractoriness $R$ depends only on the timing of the last postsynaptic spike, but the model can be easily generalized to include a dependence on earlier spikes as well. More specifically, we take for the simulations

$$ R(i) = \frac{(t-i-\tau_{\text{abs}})^2}{\tau_{\text{refr}}} + \frac{(t-i-\tau_{\text{abs}})}{\tau_{\text{refr}}} \Theta(t-i-\tau_{\text{abs}}), \quad [3] $$

where $i$ denotes the last firing time of the postsynaptic neuron, $\tau_{\text{abs}} = 3$ ms is the absolute refractory time, and $\tau_{\text{refr}} = 10$ ms is a parameter characterizing the duration of relative refractoriness. The Heaviside function $\Theta(x)$ takes a value of one for positive arguments and vanishes otherwise. With a function $R(i)$ such as in Eq. 3 that depends only on the most recent postsynaptic spike, the above neuron model has renewal properties and can be mapped onto a spike-response model with escape noise (9). Except for Fig. 2, we take throughout the paper $g(u) = r_0 \log(1 + \exp((u-u_0)/\Delta u))$ with $u_0 = -65$ mV, $\Delta u = 2$ mV, and $r_0 = 11$ Hz. This set of parameters corresponds to in vivo conditions with a spontaneous firing rate of $\approx 1$ Hz. The function $g(u)$ and the typical firing behavior of the neuron model are shown in Fig. 1A. For Fig. 2, we consider the case $\tau_{\text{abs}} = \tau_{\text{refr}} = 0$ and an instantaneous rate $g(u) = \{10$ ms $+ [1/g(u)]\}^{-1}$ with $g(u)$ as above i.e., the neuron model exhibits no refractoriness and is defined by an inhomogeneous Poisson process with maximum rate of 100 Hz; compare Fig. 1A. Integration of all equations is performed in MATLAB on a standard personal computer by using a time step $\Delta t = 1$ ms.

**Spike Trains.** The output of the postsynaptic neuron at time step $t^k$ is denoted by a variable $y^k = 1$ if a postsynaptic spike occurred between $t^{k-1}$ and $t^k$ and 0 otherwise. A specific output spike train up to time bin $k$ is denoted by uppercase letters $Y^k = \{y^1, y^2, \ldots, y^k\}$. Because spikes are generated by a random process, we distinguish the random variable $Y^k$ by using boldface characters from a specific realization $\tilde{y}^k$. Note that the lowercase variable $y^k$ refers always to a specific time bin, whereas the uppercase variable $Y^k$ refers to a whole spike train. Similar remarks hold for the input: $X$ is the random variable characterizing the input at all synapse $1 \leq j \leq N$; $X^k$ is a specific realization of all input spike trains up to time $t^k$; $X^j_i = \{x_{i1}, x_{i2}, \ldots, x_{ik}\}$ a specific realization of an input spike train at synapse $j$, and $x_{ik}$, its value in time bin $k$. For given presynaptic spike trains $X^k$ and postsynaptic spike history $Y^k$, the probability of emitting a postsynaptic spike is described by the following binary distribution:

$$ P(y^k|Y^{k-1}, X^k) = (\tilde{\rho}^k)^{y^k}(1 - \tilde{\rho}^k)^{1-y^k}, \quad [4] $$

since $y^k \in \{0, 1\}$. Analogously, we find the marginal probability of $y^k$ given $Y^{k-1}$

$$ P(y^k|Y^{k-1}) = (\tilde{\rho}^k)^{y^k}(1 - \tilde{\rho}^k)^{1-y^k}, \quad [5] $$

where $\tilde{\rho}^k = \langle \rho^k \rangle_{y^k=1}$ and $\langle \cdot \rangle_{y^k=1} = \Sigma y^k \cdot P(X^k|Y^{k-1})$.

From probability calculus, we obtain the conditional probability of the output spike train $Y^k$ given the presynaptic spike trains $X^k$,

$$ P(Y^k|X^k) = \prod_{i=1}^k P(y^i|Y^{i-1}, X^i), \quad [6] $$

and an analogous formula for the marginal probability distribution of $P(Y^k)$. With Eqs. 4 and 6, we have an expression for the probabilistic relation between an output spike train and an ensemble of input spike trains.

**Mutual Information Optimization.** Transmission of information between an ensemble of presynaptic spike trains $X^k$ of total duration $K\Delta t$ and the output train $Y^k$ of the postsynaptic neuron can be quantified by the mutual information (24)

$$ I(Y^k, X^k) = \sum_{Y^k, X^k} P(Y^k, X^k) \log \frac{P(Y^k|X^k) P(X^k)}{P(Y^k)} . \quad [7] $$

While it is easier to transmit information if the postsynaptic neuron increases its firing rate, firing at high rates is costly from the point of view of energy consumption and also difficult to implement by the cells biophysical machinery. We therefore optimize information transmission under the condition that the firing statistics $P(Y^k)$ of the postsynaptic neuron stays as close as possible to a target distribution $\hat{P}(Y^k)$. With a parameter $\gamma$ (set to $\gamma = 1$ for the simulations), the quantity we maximize is therefore

![Fig. 1.](image-url)
synaptic efficacies $w_j$ is expected value of refractory variable $x_j$ evaluated at $30$ Hz throughout the paper except for Fig. 2) modulated by the firing frequency $L$.

![Fig. 2. Relation to BCM rule. (A) The function $\phi_{\text{post}}$ of the BCM learning rule Eq. 16 derived from our model under assumption of Poisson firing statistics of the postsynaptic neuron. A value of $\phi_{\text{post}} > 0$ for a given postsynaptic rate $\rho_{\text{post}}$ means that synapses are potentiated when stimulated presynaptically. The transition from depression to potentiation occurs at a value $\phi$ that depends on the average firing rate $\rho_{\text{post}}$ of the postsynaptic neuron (blue $\rho_{\text{post}} = 10$ Hz; green $\rho_{\text{post}} = 20$ Hz; red $\rho_{\text{post}} = 30$ Hz). B. The threshold $\delta$ as a function of $\rho_{\text{post}}$ for different choices of the parameter $\gamma$, i.e., $\gamma = 0.5$ (purple); $\gamma = 1$ (black); $\gamma = 2$ (orange).]

$L = H(Y^k; X^k) - \gamma D(P(Y^k)||\hat{P}(Y^k)),$

where $D(P(Y^k)||\hat{P}(Y^k)) = \sum_{Y_k} P(Y_k) \log(P(Y_k)/\hat{P}(Y_k))$ denotes the Kullback–Leibler divergence (24). The target distribution is that of a neuron with constant instantaneous rate $\hat{g}$ (set to $\hat{g} = 30$ Hz throughout the paper except for Fig. 2) modulated by the refractory variable $R(t)$, i.e., that of a renewal process.

The main idea of our approach is as follows. We assume that synaptic efficacies $w_j$ can change within some bounds $0 \leq w_j \leq w_{\text{max}}$ so as to maximize information transmission under the constraint of a fixed target firing rate. To derive the optimal rule of synaptic update, we calculate the gradient of Eq. 8. Applying the chain rule of information theory (24) to both the mutual information $I$ and the Kullback–Leibler divergence $D$, we can write $L = \sum_{k=1}^L \Delta L^k$ where

$$\Delta L^k = \left( \log \frac{P(y^k|y^{k-1}, x^k)}{P(x^k|y^{k-1})} - \log \frac{P(y^k|y^{k-1}, x^k)}{P(x^k|y^{k-1})} \right)_{y, x, t}.$$  

with $\sum_{x, t} = \sum_{x_1, \ldots, x_k} P(X^k; Y^k)$. Assuming slow changes of synaptic weights, we apply a gradient ascent algorithm to maximize the objective function and change the synaptic efficacy $w_j$ at each time step by $\Delta w_j^k = \alpha(\partial \Delta L^k/\partial w_j)$ with an appropriate learning rate $\alpha$. Evaluation of the gradient (see Supporting Text, which is published as supporting information on the PNAS website) yields

$$\Delta w_j^k = \alpha(C_j f(t^j - \gamma G^2))_{y, x, t},$$

with three functions $C_j$, $F$, and $G$, described in the following.

First, with $\rho'$ denoting the derivative of $\rho$ with respect to $u$, the quantity

$$C_j^k = \sum_{l=k-k_a}^{l=k} \sum_{u=1}^l \varepsilon(t^l - t^u) x_j^u \rho_{j}^{\rho' t} \rho' \left[ y^l - 1 - \rho y^l \right]$$

is a measure that counts coincidences between postsynaptic spikes ($y_l = 1$) and the time course of PSPs generated by postsynaptic spikes ($x_j^u = 1$) at synapse $j$, normalized to an expected value $C_j^k_{y, x, t} = 0$. The time span $k_a$ of the coincidence window is given by the width of the autocorrelation of the spike train of the postsynaptic neuron (see Supporting Text and Fig. 6 which are published as supporting information on the PNAS website). The term

$$F^k = \log \frac{P(y^k|y^{k-1}, X^k)}{P(x^k|y^{k-1})} = y^k \log \frac{\rho^k}{\rho} + (1 - y^k) \log \frac{1 - \rho^k}{1 - \rho}$$

compares the instantaneous firing probability $\rho^k$ at time step $k$ with the average probability, $\bar{\rho}$ and, analogously, the term $G^k = \log(P(y^k|y^{k-1})/P(x^k|y^{k-1}))$ compares the average probability with the target value $\bar{\rho}$.

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Results

We analyzed information transmission for a model neuron that receives input from 100 presynaptic neurons. A presynaptic spike that arrives at time $t^j(i)$ at synapse $j$ evokes an excitatory PSP of time course $\varepsilon(t - t^j(i))$. The amplitude $w_j$ of the postsynaptic response is taken as a measure of synaptic efficacy and subject to synaptic dynamics. Firing of the postsynaptic neuron is more likely if the total PSP $u(t) = u_t + \sum_j w_j \varepsilon(t - t^j(i))$ is large; however, because of refractoriness firing is suppressed after a postsynaptic action potential at time $t^j$ by a factor $R$, which depends on the time since the last postsynaptic spike; see methods for details.

Maximizing the mutual information between several presynaptic spike trains and the output of the postsynaptic neuron can be achieved by a synaptic update rule that depends on the presynaptic spike arrival time $t^j(i)$, the postsynaptic membrane potential $u_t$, and the last postsynaptic firing time $t^j$. More precisely, the synaptic update rule can be written as

$$\frac{dw_j(t)}{dt} = \alpha C_j(t) B_{\text{post}}(t - \delta)$$

where $C_j$ is a measure sensitive to correlations between pre- and postsynaptic activity, and $B_{\text{post}}$ is a variable that characterizes the state of the postsynaptic neuron (see Methods and Models). $\alpha$ is a small learning parameter. We note that in standard formulations of Hebbian learning, changes of synaptic efficacies are driven by correlations between pre- and postsynaptic neurons,
similar to the function $C_j(t)$. The above update rule, however, augments these correlations by a further postsynaptic factor $B_{\text{post}}$.

This postsynaptic factor $B_{\text{post}}$ depends on the firing time of the postsynaptic neuron, its refractory state, the membrane potential $u$ by means of the instantaneous firing intensity $g(u)$, and on its past firing history by means of $g(t)$. The postsynaptic factor can be decomposed into two terms: the first term compares the instantaneous firing intensity $g(u)$ with its running average $\bar{g}(t)$ and the second term compares the running average with a target rate $\bar{g}$. Thus, the first term of $B_{\text{post}}$ measures a running average of the postsynaptic rate. The function $\phi$ in Eq. 16 shown in Fig. 2 is characteristic for the BCM learning rule (12). Our approach by information maximization predicts a specific form of this function that can be plotted either as a function of the instantaneous firing rate $\nu_{\text{post}}$ or as a function of the total PSP $\nu_{\text{post}} = \bar{g}_2^{-1}(\nu_{\text{post}})$, in close agreement with experiments (2, 13). Moreover, because information maximization was performed under the constraint of a fixed target firing rate, our approach yields automatically a sliding threshold of the form postulated in ref. 12, but on different grounds. Thus for neurons without refractoriness, i.e., a pure rate model, our update rule for synaptic plasticity reduces exactly to the BCM rule.

An application of rate models to stimulation paradigms that vary on a time scale of tens of milliseconds or less has often been questioned because an interpretation of rate is seen as problematic. Our synaptic update rule is based on a spiking-neuron model that includes refractoriness and that captures properties of much more detailed neuron models well (25). The learning rule for spiking neurons has a couple of remarkable properties that we explore now.

First, we consider a pattern discrimination task in a rate coding paradigm. Patterns are defined by the firing rate $x_{\text{pre}}$ of 25 presynaptic neurons ($x_{\text{pre}} = 2, 13, 25$, and 40 Hz for patterns, 1–4, respectively) modeled as independent Poisson spike trains. The remaining 75 synapses received uncorrelated Poisson input at a constant rate of 20 Hz. Each second, a pattern was chosen stochastically and applied during 1 sec. Those synapses that received pattern-dependent input developed strong efficacies close to the maximal value $w_{\text{max}} = 1$, whereas most of the other 75 synapses developed weaker ones; compare Fig. 3. However,
of correlated inputs (Fig. 4A). The rate of the output neurons reflects the modulation of their respective inputs (Fig. 4B). To summarize, the synaptic update rule derived from the principle of information maximization drives neurons to spontaneously detect and specialize for groups of coherent inputs. Just as in the standard BCM rule, several output neurons (with different specialization) are needed to account for the different features of the input.

Fig. 5. Spike–spike correlations. The \( n = 100 \) synapses have been separated into four groups of 25 neurons each (group A, \( 1 \leq j \leq 25 \); group B, \( 26 \leq j \leq 50 \); group C, \( 51 \leq j \leq 75 \); group D, \( 76 \leq j \leq 100 \). All synapses were stimulated at the same rate of 20 Hz. However, during the first 15 min of simulated time, neurons in groups C and D were uncorrelated, whereas the spike trains of the remaining 50 neurons (groups A and B) had correlations of amplitude \( c = 0.1 \), i.e., 10% of the spike arrival times were identical between each pair of synapses. After 15 min, correlations changed so that group A became correlated with C, whereas B and D were uncorrelated. After 45 min of simulated time, correlations stopped, but stimulation continued at the same rate. (A) Upper) Evolution of all 100 weights (red, potentiated; blue, depressed). (Lower) Average mutual information per bin as a function of time. In the absence of correlations \((t > 45 \text{ min})\), mutual information is lower than before, but the distribution of synaptic weights remains stable. (B) Nine postsynaptic neurons \( 1 \leq i \leq 9 \) with membrane potential \( u_i(t) \) are stimulated as discussed in \( A \) and project to a readout unit with potential \( h(t) = \sum_{j=1}^{100} w_{ij}(t) - \theta \) where the sum runs over all output spikes \( m \) of all nine neurons. Mean membrane potentials are \( \bar{u} \) and \( \bar{h} \), respectively. The fluctuations \( \sigma_w^2 = \sum_{ij} (w_{ij}(t) - \bar{w}_{ij})^2 \) of the PSPs (blue line, top graph) and those of the readout potentials \( \sigma_h = \langle (h(t) - \bar{h})^2 \rangle \), green line) are correlated (Lower) with the mutual information and can serve as neural signal.
of a readout neuron further down the processing chain (Fig. 5B). Thus, information that is potentially encoded in millisecond correlations in the input can be detected, enhanced, transmitted, and read out by other neurons.

Discussion

The synaptic update rule discussed in this paper relies on the maximization of the mutual information between an ensemble of presynaptic spike trains and the output of the postsynaptic neuron. As in all optimization approaches, optimization has to be performed under some constraint. Because information scales with the postsynaptic firing rate, but high firing rates cannot be sustained by the biophysical machinery of the cell over long times, we imposed that, on average, the postsynaptic firing rate should stay close to a desired firing rate. This idea is consistent with the widespread finding of homeostatic processes that tend to push a neuron always back into its preferred firing state (22). The implementation of this idea in our formalism gave naturally rise to a control mechanism that corresponds exactly to the sliding threshold in the original BCM model (12). While derivations of the BCM model from optimality concepts (23, 19) or statistical approaches (26) are not new, our approach gives another perspective on the concept of a sliding threshold.

Our derivation extends the BCM model, which was originally designed for rate models of neuronal activity to the case of spiking-neuron models with refractoriness. Spiking-neuron models of the integrate-and-fire type, such as the one presented here, can be used to account for a broad spectrum of neuronal firing behavior, including the role of spike–spike correlations, interspike interval distributions, coefficient of variations, and even timing of single spikes; for a review, see ref. 9. The essential ingredients of the spiking neuron model considered here were (i) PSPs generated by presynaptic spike arrival, (ii) a heuristic spiking probability that depends on the total PSP, and (iii) a phenomenological account of absolute or relative refractoriness. The synaptic update rule depends on all three of these quantities. While we do not imply that synaptic potentiation and depression of real neurons are implemented the way it is suggested by our update rule, the rule shows nevertheless some interesting features.

First, in contrast to pure Hebbian correlation driven learning, the update rule uses a correlation term modulated by an additional postsynaptic factor. Thus, presynaptic stimulation is combined with a highly nonlinear function of the postsynaptic state to determine the direction and amplitude of synaptic changes. The essence of the BCM rule (presynaptic gating combined with nonlinear postsynaptic term) is hence translated into a spike-based formulation.

Second, the spike-based formulation of a synaptic update rule should allow a connection to spike-timing-dependent plasticity (5, 6) and allow its interpretation in terms of optimal information transmission (27–29). Given the highly nonlinear involvement of postsynaptic spike times and PSP in the optimal synaptic update rule, a simple interpretation in terms of pairs or pre- and postsynaptic spikes as in many standard models of synaptic plasticity (30, 31) can only capture a small portion of synaptic plasticity phenomena. The optimal learning rule suggests that nonlinear phenomena (32–35) are potentially highly relevant.

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Supporting Text

**Evolution of the Average Synaptic Update Rule**

In this appendix, we evaluate the derivative of Eq. 9 in the main text, i.e., we need to calculate

$$\frac{\partial}{\partial w_j} \left\{ \log \frac{P(y^k | Y^{k-1}, X^k)}{P(y^k | Y^{k-1})} - \gamma \log \frac{P(y^k | Y^{k-1})}{P(y^k | Y^{k-1})} \right\}_{Y^k, X^k}. \quad [1]$$

Before we start, let us recall some notation. The average of an arbitrary function $f_w$ with arguments $x$ and $y$ is by definition

$$\langle f_w(x,y) \rangle_{x,y} = \sum_x \sum_y p_w(x,y) f_w(x,y) \quad [2]$$

where $p_w(x,y)$ denotes the joint probability of the pair $(x,y)$ to occur and the sum runs over all configurations of $x$ and $y$. The subscript $w$ indicates that both the probability distribution $p_w$ and the function $f_w$ may depend on a parameter $w$.

By definition, we have $p_w(x,y) = p_w(y | x)p(x)$ where $p(x)$ is a given input distribution and $p_w(y | x)$ the (parameter-dependent) conditional probability of generating an output $y$ given $x$. Hence, Eq. 2 can be transformed into

$$\langle f_w(x,y) \rangle_{x,y} = \sum_x p(x) \sum_y p_w(y | x)f_w(x,y) = \left\{ \sum_y p_w(y | x) f_w(x,y) \right\}_x \quad [3]$$

If we now take the derivative with respect to the parameter $w$, the product rule yields two terms

$$\frac{\partial}{\partial w} \langle f_w(x,y) \rangle_{x,y} = \left\{ \sum_y p_w(y | x) \frac{\partial}{\partial w} f_w(x,y) \right\}_x \quad [4]$$

$$+ \left\{ \sum_y p_w(y | x) \left[ \frac{\partial}{\partial w} \log p_w(y | x) \right] f_w(x,y) \right\}_x$$

The first term contains the derivative of the function $f_w$, whereas the second term contains the derivative of the conditional probability $p_w$. We note that Eq. 4 can also be written in the form

$$\frac{\partial}{\partial w} \langle f_w(x,y) \rangle_{x,y} = \left\{ \frac{\partial}{\partial w} f_w(x,y) \right\}_{x,y} + \left\{ \left[ \frac{\partial}{\partial w} \log p_w(y | x) \right] f_w(x,y) \right\}_{x,y} \quad [5],$$

i.e., as an average over the joint distribution of $x$ and $y$. This formulation will be useful for the problem at hand.

The gradient in Eq. 1 contains several terms and for the moment we pick only one of these. The others will then be treated analogously. Let us focus on the term $\langle \log P(y^k \mid Y^{k-1}, X^k) \rangle_{Y^k, X^k}$ and apply steps completely analogous to those
leading from Eqs. 2-5.

\[
\frac{\partial}{\partial w_j} \langle \log P(y^k | Y^{k-1}, X^k) \rangle_{y^k, X^k} = \left\langle \frac{\partial}{\partial w_j} \log P(y^k | Y^{k-1}, X^k) \right\rangle_{y^k, X^k} + \left[ \frac{\partial}{\partial w_j} \log P(Y^k | X^k) \log P(y^k | Y^{k-1}, X^k) \right]_{y^k, X^k}
\]

[6]

We now evaluate the averages using the identity

\[
\langle y^k, X^k \rangle = \left\langle \langle y^k, X^k \rangle \right\rangle_{y^k, X^k} \].

We find that the first term on the right-hand side of Eq. 6 vanishes, since

\[
\left\langle \frac{\partial}{\partial w_j} \log P(y^k | Y^{k-1}, X^k) \right\rangle_{y^k, X^k} = \sum_{y^k \in \{0,1\}} \frac{\partial}{\partial w_j} \left[ \log P(y^k | Y^{k-1}, X^k) \right] P(y^k | Y^{k-1}, X^k)
\]

\[
= \frac{\partial}{\partial w_j} \left[ \sum_{y^k \in \{0,1\}} P(y^k | Y^{k-1}, X^k) \right] = 0
\]

[7]

because of the normalization of probabilities. The same argument can be repeated to show that \(0 = \langle \frac{\partial}{\partial w_j} \log P(y^k | Y^{k-1}) \rangle_{y^k, X^k} \). The reference distribution \( \hat{P}(y^k | Y^{k-1}) \) is by definition independent of \( w_j \).

Hence, the only term that gives a nontrivial contribution on the right-hand side of Eq. 6 is the second term. With an analogous argument for the other factors in Eq. 1, we have

\[
\frac{\partial}{\partial w_j} \left[ \log \frac{P(y^k | Y^{k-1}, X^k)}{P(y^k | Y^{k-1})} - \gamma \log \frac{P(y^k | Y^{k-1})}{P(y^k | Y^{k-1})} \right]_{y^k, X^k}
\]

\[
= \left[ \frac{\partial \log P(Y^k | X^k)}{\partial w_j} \right] \left[ \log \frac{P(y^k | Y^{k-1}, X^k)}{P(y^k | Y^{k-1})} - \gamma \log \frac{P(y^k | Y^{k-1})}{P(y^k | Y^{k-1})} \right]_{y^k, X^k}
\]

[8]

An identification of the factors \( C, F, \) and \( G \) in the main text is straightforward. From Eq. 4 in the main text we have

\[
\log P(y^k | Y^{k-1}, X^k) = y^k \log(\rho^k) + (1 - y^k) \log(1 - \rho^k)
\]

[9]

Hence, we can evaluate the factors

\[
F^k = \log \frac{P(y^k, Y^{k-1}, X^k)}{P(y^k, Y^{k-1})} = y^k \log \frac{\rho^k}{\pi^k} + (1 - y^k) \log \frac{1 - \rho^k}{1 - \pi^k}
\]

\[
G^k = \log \frac{P(Y^k | y^k, Y^{k-1})}{P(Y^k | y^k, Y^{k-1})} = y^k \log \frac{\pi^k}{\rho^k} + (1 - y^k) \log \frac{1 - \pi^k}{1 - \rho^k}
\]

Furthermore, we can calculate the derivative needed in Eq. 8 using the chain rule from Eq. 6 of the main text, i.e.,
which yields

\[
\frac{\partial \log P(Y^k \mid X^k)}{\partial w_{lj}} = \frac{\partial}{\partial w_{lj}} \sum_{j=1}^{k} \log P(y_j \mid Y^{i-1}, X^i) \tag{11}
\]

\[
= \sum_{i=l}^{k} \left[ \frac{y_j}{\rho^j} - \frac{1 - y_j}{1 - \rho^j} \right] \rho^j \sum_n \varepsilon(t' - t^n) x^n_j \tag{12}
\]

We note that in Eq. 8 the factor \( \frac{\partial}{\partial w_{lj}} \log P(Y^k \mid X^k) \) has to be multiplied with \( F^k \) or with \( G^k \) before taking the average. Multiplication generates terms of the form \( \langle y^i y^k \rangle_{x^i x^k} = \langle \langle y^i y^k \rangle_{x^i} \rangle_{x^k} \) For any given input \( X^k \), the autocorrelation \( \langle y^i y^k \rangle_{x^i x^k} \) with \( l < k - a \) of the postsynaptic neuron will have a trivial value

\[
\langle y^i y^k \rangle_{x^i x^k} = \langle y^i \rangle_{x^i} \langle y^k \rangle_{x^k} \quad \text{for} \quad k - l > k_a \tag{13}
\]

where \( k_a \Delta t \) is the width of the autocorrelation. As a consequence

\[
\left[ \frac{y_j}{\rho^j} - \frac{1 - y_j}{1 - \rho^j} \right] (F^k - \gamma G^k) \tag{14}
\]

Hence, for \( k - l > k_a \), we can truncate the sum over \( l \) in Eq. 12, i.e.,

\[
\sum_{l=1}^{k} \to \sum_{l=k-k_a}^{k} \quad \text{which yields exactly the coincidence measure} \ C_j \text{ introduced in the main text; cf. Eq. 11 in the main text, and which we repeat here for convenience}
\]

\[
C_j = \sum_{l=k-k_a}^{k} \left[ \frac{y_j}{\rho^j} - \frac{1 - y_j}{1 - \rho^j} \right] \rho^j \sum_n \varepsilon(t' - t^n) x^n_j \tag{15}
\]

From Averages to an Online Rule

The coincidence measure \( C_j \) counts coincidences in a rectangular time window. If we replace the rectangular time window by an exponential one with time constant \( \tau_c \) and go to continuous time, the summation \( \sum_{l=k-k_a}^{k} \) in

Eq. 15 turns into an integral \( \int_0^{\infty} dt' \exp[-(t-t')/\tau_c] \ldots \) which can be transformed into a differential equation

\[
\frac{dC_j(t)}{dt} = -\frac{C_j(t-\delta)}{\tau_c} + \sum_f \varepsilon(t-t'_f) S(t) \left[ \delta(t-\hat{i}-\delta) - g(u(t)) R(t) \right] \tag{16}
\]

cf. Eq. 15 in the main text. Based on the considerations in the previous paragraph, the time constant \( \tau_c \) should best be chosen in the range
Similarly, the average firing rate $\bar{\rho}(t) = \bar{g}(t) R(t)$ can be estimated using a running average

$$\tau_\pi \frac{d\bar{g}(t)}{dt} = -\bar{g}(t) + g(u(t))$$

[17]

with time constant $\tau_\pi$.

In Fig. 6, we compare the performance of three different update schemes in numerical simulations. In particular, we show that (i) the exact value of the truncation of the sum in Eq. 15 is not relevant, as long as $k_\Delta t$ is larger than the width of the autocorrelation; and (ii) that the online rule is a good approximation to the exact solution.

To do so, we take the scenario from Fig. 3 of the main text. For each segment of 1 s, we simulate 100 pairs of input and output spike trains. We evaluate numerically Eq. 8 by averaging over the 100 samples. After each segment of 1 second (=1,000 time steps) we update the weights using a rule without truncation in the sum of Eq. 15. We call this the full batch update; compare Fig. 6 (Top).

Second, we use the definition of $C_j^t$ with the truncated sum and repeat the above steps; Fig. 6 (Middle). The truncation is set to $k_\Delta t = 200$ ms which is well above the expected width of the autocorrelation function of the postsynaptic neuron. We call this the truncated batch rule.

Third, we use the online rule discussed in the main body of the paper with $\tau_\pi \tau_c = 1$ s; Fig. 6 (Bottom).

Comparison of top and center graphs of Fig. 6 shows that there is no difference in the evolution of mean synaptic efficacies, i.e., the truncation of the sum is allowed, as expected from the theoretical arguments. A further comparison with Fig. 6 Bottom shows that updates based on the online rule add some fluctuations to the results, but its trend captures nicely the evolution of the batch rules.

**Supplement to the Pattern Detection Paradigm**

In Fig. 3, we presented a pattern detection paradigm where patterns defined by input rates were chosen randomly and applied for one second. After learning, the spike count over one second is sensitive to the index of the pattern. Fig. 7A shows the histogram of spike counts for each pattern. Optimal classification is achieved by choosing for each spike count the pattern which is most likely. With this criterion 81 percent of the patterns will be classified correctly.

The update of synaptic efficacies depends on the choice of the parameter $\gamma$ in the learning rule. According the the optimality criterion in Eq. 8 of the main text, a high level of $\gamma$ implies a strong homeostatic control of the firing rate of the postsynaptic neuron whereas a low level of $\gamma$ induces only a weak homeostatic control. In order to study the role of $\gamma$, we repeated the numerical experiments for the above pattern detection paradigm with a value of $\gamma = 100$ instead of our standard value of $\gamma = 1$. Fig. 7B shows that the output firing rate is still modulated by the pattern index, the modulation at
\( \gamma = 100 \) is, however, weaker than that at \( \gamma = 1 \). As a result, pattern detection is less reliably with 45 percent correct classification only. We note that this is still significantly higher than the chance level of 25 percent.
Figure 6: Evolution of the synaptic efficacies for the pattern detection paradigm of Fig. 3 during the first 10 minutes of simulated time. Red: mean synaptic efficacy of the 25 synapses that received pattern-dependent input rates. Blue: mean synaptic efficacy of the remaining 75 synapses. The batch update rule (top), the truncated batch rule (middle) and the online rule (bottom) yield comparable results.

Second, we use the definition of $C_j^k$ with the truncated sum and repeat the above steps; Fig. 6 (middle). The truncation is set to $k_a \Delta t = 200$ms which is well above the expected width of the autocorrelation function of the postsynaptic neuron. We call this the truncated batch rule.

Third, we use the online rule discussed in the main body of the paper with $\tau_C = 1$s; Fig. 6 (bottom).

Comparison of top and center graphs of Fig. 6 shows that there is no difference in the evolution of mean synaptic efficacies, i.e., the truncation of the sum is allowed, as expected from the theoretical arguments. A further comparison with Fig. 6 bottom shows that updates based on the online rule add some fluctuations to the results, but its trend captures nicely the evolution of the batch rules.
Figure 7: Pattern detection. A Histograms of spike counts $n_{sp}$ over one second (horizontal axis, bin size 2) during presentation of pattern 1 (dark blue), pattern 2 (light blue), pattern 3 (yellow), and pattern 4 (red). Vertical scale: number of trials $n$ with a given spike count divided by total number $N_p$ of trials for that pattern. B Spike count during one second (mean and variance) for each of the four patterns with a parameter value $\gamma = 1$ (light blue) and $\gamma = 100$ (dark blue). The values for $\gamma = 1$ are redrawn from Fig. 3.