Interaction of Neuronal I/O Functions with STDP

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SUMMARY

Spike timing-dependent synaptic plasticity (STDP) develops neural circuits through close interaction with the firing function of single neurons. Here, we investigate the neuronal firing function dependency of STDP about a single-compartment Hodgkin–Huxley (HH) model neuron and a leaky integrate-and-fire (LIF) model neuron. Computer simulation shows that the development of synaptic strength by synaptic input pairs with constant intervals depends on the firing function of the models. The more organized packet inputs also develop synaptic strength in a firing function-dependent manner, to realize specific information processing. These results suggest that in real biological systems too, STDP with the same time window will develop different neural circuits, depending on the neuronal firing functions. © 2006 Wiley Periodicals, Inc. Syst Comp Jpn, 38(1): 41–50, 2007; Published online in Wiley InterScience (www.interscience.wiley.com). DOI 10.1002/scj.20234

Key words: HH model neuron; LIF model neuron; STDP; inverse correlation function.

1. Introduction

It is known that the biological brain stores information by modifying effective strength of synaptic connections between neurons, or synaptic strength. The change of synaptic strength, which is called synaptic plasticity, has been believed to be induced on the basis of average firing frequencies of the pre- and postsynaptic neurons [1]. Recently, a new form of synaptic plasticity called spike-timing-dependent synaptic plasticity (STDP) has been reported and has attracted attention; synaptic plasticity depends not only on firing frequencies of pre- and postsynaptic neurons, but also on their exact firing timings with an asymmetrical time window [2–4]. Let the firing time of the presynaptic neuron be \( t_i \) and that of the postsynaptic neuron be \( t_{\text{post}} \). Then, it is reported that the synaptic coupling strength is enhanced if \( t_{\text{post}} - t_i > 0 \), and is suppressed if \( t_{\text{post}} - t_i < 0 \), as shown in Fig. 1.

It is apparent that STDP modifies synaptic strength through close interaction with the firing function of single neurons.
neurons [5]. For example, Gerstner and colleagues have shown that the sound phase-detection for azimuthal sound localization by barn owls is attained by the interaction between coincidence-detector neurons and STDP [6]. It is also known that the firing functions of neurons are not uniform, but differ greatly depending on the kind of neuron [7, 8]. Thus, even if there are two neural networks with entirely the same synaptic connections and an STDP time window with the same time constant, the two neural networks may develop quite differently if the neuronal firing functions are different.

Here, by the use of computer simulation, we investigate the firing function dependency of STDP about the single-compartment Hodgkin–Huxley (HH) model neuron and the leaky integrate-and-fire (LIF) model neuron, which are often used as abstract model neurons. The inverse correlation function, which represents the firing probability of a neuron in response to a synaptic input in random synaptic inputs, reveals that the LIF neuron is an integrator of inputs, whereas the HH neuron works as a coincidence detector. Two synaptic inputs with constant latencies in random synaptic inputs reveal that the modification of synaptic strength can be estimated from the inverse correlation function; the LIF neuron enhances the synaptic inputs that precede for a relatively long time, while the HH neuron enhances the synchronized synaptic input.

Then, we investigate the interaction between the neuronal firing function and STDP about the more organized inputs, packet inputs composed of synaptic input sequences with a constant interval. Synaptic strength distribution attained by the packet inputs also reflects the inverse correlation function, enhancing the preceding inputs with the respective time-constants of the neurons. Finally, the role of such interaction between neuronal firing function and STDP in information coding of local neuronal circuits is discussed.

2. Methods

In this study, two kinds of neuron, the LIF neuron and HH neuron, are considered, and the firing response to particular synaptic inputs, as well as the interaction with STDP, is discussed. The two kinds of model neuron used in the simulation and the update rule for the synaptic coupling strength are defined below.

2.1. LIF neuron

Let the membrane potential be $V$ (mV), the current accompanying the excitatory synaptic input be $I_{syn}^{ex}$ (pA), and the current accompanying the inhibitory synaptic input be $I_{syn}^{in}$ (pA). Then the behavior of the LIF neuron is described as follows [5]:

$$C_m \frac{dV}{dt} = \bar{g}_l (E_{rest} - V) + I_{syn}^{ex} + I_{syn}^{in}$$

Here $C_m$ (pF) is the membrane capacitance, $E_{rest}$ (mV) is the resting membrane potential, and $\bar{g}_l$ (nS) is the membrane conductance. Table 1 shows the values of these parameters. These parameters give a membrane time-constant of 20 ms. This model neuron does not have any firing mechanisms. Therefore, the threshold is set as $-53.9$ mV, and it is assumed that if the potential exceeds the threshold, the neuron fires and the potential returns to $-60$ mV.

In this study, 100 presynaptic neurons are connected to the model neuron through 20 inhibitory synapses ($i = 0$ to 19) and 80 excitatory synapses ($i = 20$ to 99) (Fig. 2). The input current $I_{syn}^{in}$ (pA) from the excitatory synapse and the input current $I_{syn}^{ex}$ (pA) from the inhibitory synapse are represented by the conductance with exponential decay and the equilibrium potential:

$$I_{syn}^{in} = g_{peak}^{in} \sum_{i=0}^{19} g_i(t)(E_{syn}^{in} - V)$$

$$I_{syn}^{ex} = g_{peak}^{ex} \sum_{i=20}^{99} g_i(t)(E_{syn}^{ex} - V)$$

$$g_i(t) = \sum_{j} W_i(t_j^i) \cdot g_{syn}(t - t_j^i)$$

$$g_{syn}(t) = \begin{cases} 0 & (t < 0) \exp\left(-\frac{t}{\tau_{syn}}\right) & (t \geq 0) \end{cases}$$

Here $g_{peak}^{ex}$, and $g_{peak}^{in}$ are the maximum conductance of excitatory and inhibitory synaptic inputs, respectively. $E_{syn}^{ex}$ (mV) and $E_{syn}^{in}$ (mV) are the equilibrium potentials of excitatory and inhibitory synaptic inputs, respectively. $t_j^i$ is the $j$-th firing time of presynaptic neuron $i$. $\tau_{syn}$ (ms) is the decay time constant of the conductance. $W_i(t)$ is the synaptic strength from presynaptic neuron $i$, which follows the update rule for synaptic strength (described later).

2.2. HH neuron

Let the membrane potential be $V$ (mV), the current accompanying the excitatory synaptic input be $I_{syn}^{ex}$ (pA), and the current accompanying the inhibitory synaptic input

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<td>$C_m$ (pF)</td>
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be $I_{syn}^{in}$ (pA). Then, the behavior of the HH neuron is described as follows [9]:

$$C_m \frac{dV}{dt} = I_{Na} + I_K + I_l + I_{syn}^{ex} + I_{syn}^{in} \quad (6)$$

Here $C_m$ (pF) is the membrane capacitance. The ionic currents $I_{Na}$, $I_K$, and $I_l$ are as follows:

$$I_{Na} = g_{Na} m^3 h (E_{Na} - V) \quad (7)$$

$$I_K = g_K n^4 (E_K - V) \quad (8)$$

$$I_l = g_l (E_l - V) \quad (9)$$

Here $g_{Na}$ (nS), $g_K$ (nS), and $g_l$ (nS) are the maximum conductances of Na+, K+, and Cl- channels, respectively, and $E_{Na}$ (mV), $E_K$ (mV), and $E_l$ (mV) are the equilibrium potentials. Table 2 shows the values of these parameters. $m$, $h$, and $n$ are gate variables taking values between 0 and 1, governed by the following dynamics:

$$\frac{dm}{dt} = \{ \alpha_m (1 - m) - \beta_m m \} \cdot 3^{(T - 6.3)/10} \quad (10)$$

$$\frac{dh}{dt} = \{ \alpha_h (1 - h) - \beta_h h \} \cdot 3^{(T - 6.3)/10} \quad (11)$$

$$\frac{dn}{dt} = \{ \alpha_n (1 - n) - \beta_n n \} \cdot 3^{(T - 6.3)/10} \quad (12)$$

$$\alpha_m = \frac{0.1 (V + 40)}{1 - \exp(-(V + 40)/10)} \quad (13)$$

Here $g_{peak}^{ex}$ (nS) and $g_{peak}^{in}$ (nS) are the maximum conductances of excitatory and inhibitory synaptic inputs, respectively, $E_{syn}^{ex}$ (mV) and $E_{syn}^{in}$ (mV) are the equilibrium potentials of excitatory and inhibitory synaptic inputs, and $t_{peak}$ (ms) is the peak time of the $\alpha$ function, and $W_i(t)$ is the synaptic strength from presynaptic neuron $i$.

2.3. Rule for updating synaptic strength by STDP

The LIF and HH model neurons have synaptic connections with 100 presynaptic neurons (Fig. 3). The initial...
The strength of the synapses is uniform \( W_i(t=0) = 1 \). The upper limit is set as 2 and the lower limit as 0. The synapses with index \( i = 0 \) to 19 are inhibitory, and the synaptic strength is not updated.

The simple exponential function shown in Fig. 1 is used as the time window of STDP, and the decay time constant is set as 15 ms. Letting the firing time of the presynaptic neuron be \( t_i \) (ms) and the firing time of the postsynaptic neuron be \( t_{\text{post}} \) (ms), the time window of STDP is defined as follows, using \( \Delta t = t_{\text{post}} - t_i \):

\[
\text{window}(\Delta t) = \begin{cases} 
\frac{P_\text{LTP}}{1000} \exp\left(-\frac{\Delta t}{15}\right) & (\Delta t \geq 0) \\
-\frac{P_\text{LTD}}{1000} \exp\left(-\frac{\Delta t}{15}\right) & (\Delta t < 0)
\end{cases}
\] (23)

The maximum change of synaptic strength by a firing is set as \( P_{\text{LTP}} = 3, P_{\text{LTD}} = 3.6 \) (LIF neuron), \( P_{\text{LTD}} = 3.15 \) (HH neuron). \( P_{\text{LTD}} \) has different values for the LIF neuron and the HH neuron, so that the average synaptic strength of excitatory synapses holds at approximately \( W_i(t) = 1 \) throughout the simulation.

The update of the synaptic strength is performed at the firing of the postsynaptic neuron for long-term potentiation (LTP), and at the firing of the presynaptic neuron for long-term depression (LTD). That is, letting the \( m \)-th firing time of a postsynaptic neuron be \( t_{\text{post}}^m \) (ms) and the \( n \)-th firing time of presynaptic neuron \( i \) be \( t_i^n \) (ms), the coupling strength \( W_i(t) \) changes as follows:

\[
\frac{dW_i(t)}{dt} = \sum_m \delta(t - t_{\text{post}}^m) \sum_n \text{window}(t_{\text{post}}^m - t_i^n)
+ \sum_n \delta(t - t_i^n - \Delta) \sum_m \text{window}(t_{\text{post}}^m - t_i^n)
\] (24)

Here \( \delta(\cdot) \) is Dirac’s delta function, and \( \Delta \) is a very small value [larger than the range of \( t \) for which \( \delta(t) \) has a value].

3. Results

3.1. Input–output function of LIF and HH neurons

First, with the fixed synaptic strength, the firing functions of the LIF and HH neurons are investigated (Fig. 4). A situation is assumed in which each presynaptic neuron fires randomly and independently at 40 Hz, that is, Poisson process input is given to the neuron.

Random synaptic inputs of 4000 Hz make the LIF neuron fire at 11.3 Hz and HH neuron fire at 13.5 Hz. Even if the input sequences are entirely the same, the membrane potential or the firing timing is totally different [Figs. 4(a) and 4(d)]. The difference is due to the fact that the LIF
neuron detects the threshold of membrane potential, but the HH neuron detects a more complex input structure [10].

In order to investigate more precisely the input–output function of each model neuron, the inverse correlation function $RC(\tau)$ is used [(b), (c), (e), and (f) of Fig. 4]. The inverse correlation function represents the relative probability of synaptic inputs at $\tau$ ms after a postsynaptic neuronal firing. It is defined as follows:

$$RC(\tau) = \frac{< \lambda_{in}(t)\lambda_{out}(t+\tau) > t_f - f_{in}f_{out}}{f_{in}} \quad (25)$$

Here $< \cdot >$, represents the time average of the variable inside the angle brackets, $\lambda_{in}(t)$ is the expected number of synaptic inputs in a unit time at time $t$, $\lambda_{out}(t)$ is the expected number of neuron firings in unit time at time $t$, and $f_{in}$ and $f_{out}$ are the average synaptic input frequency and the average firing frequency, respectively.

Figures 4(b) and 4(c) show that the firing probability of the LIF neuron increases for approximately 15 ms after an excitatory synaptic input, and the probability decreases after an inhibitory synaptic input with the similar time constant. On the other hand, the firing probability of the HH neuron increases in short period and the increase decays rapidly with oscillation. Thus, the neuron works as a coincidence detector. The differences in the firing function are considered to produce the different firing timing of the neurons, as shown in Figs. 4(a) and 4(d).

### 3.2. STDP in synaptic input pairs

We investigate the interaction of LIF and HH neurons, with different firing functions and consequently different firing timings, with STDP. A situation is assumed that the inputs from an excitatory synapse $i$ keep constant latencies with inputs from another excitatory/inhibitory synapse $j$, in which the other presynaptic neurons fire independently at 40 Hz. In other words, a situation is assumed in which excitatory–excitatory input pairs or excitatory–inhibitory input pairs are given [Fig. 3(a)].

For each latency from –16 ms to 16 ms in 1-ms steps, 100 s $\times$ 10 times trials were performed. The synaptic strength where input pairs are given is shown in Figs. 5(a) to 5(d). In both the LIF neuron and the HH neuron, the preceding inputs of excitatory–excitatory input pairs ($t_i - t_j < 0$) are enhanced and the following inputs ($t_i - t_j > 0$) are suppressed, while the preceding excitatory inputs of excitatory–inhibitory input pairs are suppressed and the following excitatory inputs are enhanced. These consequences are accounted for as follows. In the case of excitatory–excitatory input pairs, the preceding inputs tend to show LTP, due to the potentiation effect by the following input induced firing. On the other hand, the following inputs tend to show LTD, due to the depression effect by the preceding input induced firing. In the case of excitatory–inhibitory input pairs, the preceding excitatory inputs show LTD, due to the decrease of firing probability after the excitatory inputs by the following inhibitory inputs, and the following excitatory inputs show LTP, since the preceding inhibitory inputs decrease the firing probability before the excitatory inputs. It was further observed that the time constants for potentiation and depression in excitatory–excitatory input pairs differ in the LIF and HH neurons. In the HH neuron, just the synapses giving synchronized input pairs are potentiated [Figs. 5(a) and 5(c)].

Here, we show that the change of synaptic strength induced by the synaptic input pairs can be predicted by the inverse correlation function $RC(t)$ and STDP time window $\text{window}(t)$ (Fig. 6).

A synaptic input fluctuates firing probability, as given by the inverse correlation function. The firing probability fluctuation changes synaptic strength, because the fluctuation produces imbalance of potentiation and depression effects in STDP. Although the strength of synaptic inputs is not specifically affected by their own firing probability fluctuation since all of the synapses suffer from the same effect, the strength of synapses with accompanying inputs with a constant interval through other synapses show specific changes, as given by the following formulation. Here, the synaptic strength $W_i$ of synapse $i$ is affected by the input from synapse $j$ arriving at the interval $\Delta t = t_i - t_j$. The amount $\Delta W_i$ is given by the following convolution integral:

$$\Delta W_i = \int RC(t) \cdot \text{window}(t - \Delta t)dt \quad (26)$$

Here $RC(t)$ for excitatory inputs is used if the input from synapse $j$ is excitatory, and $RC(t)$ for inhibitory inputs is used if the input is inhibitory. The target synapse $i$ must be excitatory, since only the strength of excitatory synapses is changed.

The synaptic strength predicted by Eq. (26) is a very good match with the results of 100-s simulation, and the strength of the HH and LIF neurons is different [Figs. 5(e) to 5(h)]. In particular, in the range of $t_i - t_j > 0$ in excitatory–excitatory input pairs, $\Delta W$ of the LIF neuron has a long recovery time constant from weak depression, due to $RC(t)$ of the LIF neuron, whereas that of the HH neuron has a short recovery time constant with oscillation from strong depression, since $RC(t)$ of the HH neuron has a short decay time constant. $RC(t)$ of the HH neuron and the LIF neuron can explain the difference in changes of synaptic strength. Note that the change of synaptic strength reproduced from $RC(t)$ cannot account for the enhancement of synaptic connectiv-
Ity in the HH neuron when the excitatory–excitatory input pairs are synchronized with an interval less than 3 ms. This phenomenon, that the firing probability of the neuron is increased by more than the linear sum of $RC(t)$, is due to the nonlinear interaction of two synchronized synaptic inputs. This cannot be discussed in terms of the inverse correlation function.† As a result, the HH neuron has the function that enhances synchronously arriving excitatory–excitatory input pairs, and suppresses the excitatory inputs followed by other excitatory inputs within a short period.

### 3.3. STDP in synapse input packets

It can be seen in the case of synaptic input pairs with constant intervals that the changes of synaptic strength can be represented by the convolution of the inverse correlation function of the neurons and STDP. In order to investigate further the interaction between STDP and the firing mechanisms of the neurons for more organized synaptic inputs, the synaptic strength and the output spikes attained by packet inputs are observed [Fig. 3(b)].

The packet input is composed of successive firings of 40 presynaptic neurons at a 3-ms interval. The inputs are given through excitatory synapses with indices $i = 20$ to 60.

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†Such a change of firing probability due to the nonlinear interaction of two synaptic inputs can be handled by using higher-order cross-correlation, but is not discussed in this paper.

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Fig. 5. (a–d) Connectivity attained by 100-s paired input stimulation. The figures show the connectivity of excitatory synapse $i$ separated by the indicated time intervals with input synapse $j$. Every figure shows the average and standard deviation of 10 trials. Dotted lines show the connectivity of the other excitatory synapses. (e–h) Expected changes of connectivity $i$ derived by the convolution of STDP and reverse correlations. Dashed lines are potentiation effect, dashed-dotted lines are depression effect, and solid lines are the net effect. (a, b, e, f) LIF neuron. (c, d, g, h) HH neuron. (a, c, e, g) Synapse $j$ is excitatory. (b, d, f, h) Synapse $j$ is inhibitory.

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Fig. 6. Effect of input $j$ on the connectivity of input synapse $i$, where $\Delta t = t_i - t_j$. 

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It is assumed that the synapses fail to give inputs with a probability of 40%. The simulation period of each trial is set as 6000 s, and the packets are generated randomly at 4 Hz. Throughout the trials, random independent inputs are given at 30 Hz through all synapses, including the synapses that provide the packet inputs.

After trials for 6000 s, most of the synaptic strength $W_i(t)$ approaches the upper or the lower limit and comes to the equilibrium state (Fig. 7) [5]. In the stationary state, the synaptic input of the preceding arrival tends to be enhanced, but the synaptic input of the succeeding arrival tends to be suppressed, in both LIF and HH neurons. This is due to the property of STDP that the preceding input is enhanced in the excitatory synaptic input pair on the whole packet input.

The details of the synaptic coupling distribution differ greatly between the two neurons. In the LIF neuron, a constant number of preceding synaptic inputs are enhanced and the synapse providing the retarded input is strongly suppressed. In the HH neuron, on the other hand, only the synapse that provides the first input is selectively enhanced, and the other synapses are weakly suppressed.

The above difference is accounted for on the basis of the different behavior of STDP for the synaptic input pair. The HH neuron, which strongly enhances the synchronized input, first enhances a small number of preceding synapses. Because of the increase in the neuron firing probability by this enhancement, the synapses providing retarded inputs are successively suppressed. Since the time constant for suppression is not very long in the HH model neuron, the

![Fig. 7. Connectivity after packet input of 250, 500, and 6000 s. Nos. 0 to 19 (stems with dotted lines) are the connectivity of inhibitory synapses; Nos. 20 to 59 (stems with solid lines) are the connectivity of excitatory synapses with packet input, and Nos. 60 to 100 are the connectivity of excitatory synapses with no packet input. Dashed lines show the average of 30 trials. Left: LIF neuron. Right: HH neuron. The bottom figure shows the example of synapse input. Highlight dots are the constituents of an input packet.](image)
integrated suppression does not grow high. In the LIF neuron, in contrast, the preceding input is enhanced with a long time constant, and the suppression is integrated with a long time constant, strongly suppressing the remaining synapses. Because of these situations, clearly distinct synaptic coupling distributions are formed.

Finally, in order to investigate the effects of these different synaptic coupling strength distributions on neural information processing, the response firing characteristics of the neuron to the packet input before and after the modification of the synaptic coupling strength were observed (Fig. 8).

When the packet input was given before the modification of the synaptic coupling strength, the firing probability increased over the whole input time in the LIF neuron, while the firing probability changed only at the start and end of the input in the HH neuron [Figs. 8(a) and 8(b)]. These situations well reflect the features of the two kinds of neuron: namely, in the LIF neuron, the firing probability is increased when the absolute input frequency is increased, while the HH neuron fires in response to the change of the synaptic input frequency [10].

After the change of the synaptic coupling strength, on the other hand, the firing of the neuron for the preceding input is enhanced, and the firing intensity for the retarded input is suppressed and adjusted to the same level as the surrounding firing frequency, in both the LIF and HH neurons [Figs. 8(c) and 8(d)]. This is produced by the firing adjustment mechanism of STDP as follows. If the succeeding input is suppressed by the preceding firing beyond the surrounding firing frequency, the LTD effect of STDP is reduced on a relative basis, which enhances the following neuron firings. This increase in the firing frequency then enhances the LTP effect. By this process, the formerly suppressed synapse is reenhanced to the same level as the surrounding firing frequency.

After the modification of the synaptic coupling strength, the firing frequency decreases greatly as a whole in the LIF neuron, while the change in the HH neuron is not so remarkable. The reason is as follows. In the LIF neuron, the firing frequency is almost identical to the absolute input strength, and the coupling strength of the synapse for packet input must be reduced to 0 in order to suppress the firing by the succeeding packet input to the level of the surrounding firing frequency. As a result, the average excitatory coupling strength is decreased and the firing frequency as a whole is decreased in the LIF neuron. In the HH neuron, in contrast, the firing frequency does not necessarily correspond to the input strength, and a slight suppression suffices to lower the firing frequency of the succeeding packet to the surrounding firing frequency. This is another reason for the different synaptic coupling strength distributions in the HH neuron and the LIF neuron in Fig. 7.

The dashed lines in Fig. 7 and the histograms in Fig. 8 represent the averages of 30 trials, but large fluctuations are observed in the trials. However, in the real brain, it is expected that the postsynaptic neurons will receive the averaged signal as a sum of presynaptic firings when source neurons provide the similar firing sequences. Since the brain uses multiple neurons for processing single signals to keep redundancy, multiple neurons will receive the same packets and collaborate to provide output to the same postsynaptic neuron. Thus, the information received by the postsynaptic neuron is the same as the sum of multiple trials [11].

4. Conclusions

This study has demonstrated that the developments of neuronal circuits depend not only on the timing window of STDP, but also on the interaction of STDP with neuronal
firing functions. For the input pair with constant latencies, the LIF neuron, which detects a relatively long-term input, enhances preceding inputs with a long time window. On the other hand, the HH neuron, which is a coincidence detector, strongly enhances synchronized input pairs. The synaptic strength distributions of the two model neurons attained by more complex packet inputs also reflect the firing functions of the neurons, not only the STDP timing window.

The difference in neuronal firing functions implies a difference in the information processing of neuronal circuits. For example, the LIF neuron, which has a long integration time constant of synaptic inputs as shown in the inverse correlation function, must be robust to fluctuation of the firing timing, since the timing is strongly affected by noise inputs within the decay time constant. By contrast, the HH neuron, which functions as a coincidence detector, does not change the firing timing so much. These characteristics have recently been discussed as a problem of information coding in the firing time-series of neurons [11–14], and the present paper shows that the neuronal firing function affects not only the on-line information processing, but also the neuronal circuits formation.

Recent detailed studies have shown that the firing functions of single neurons are also varied by neuronal modulation and input frequency [15–17]. The biological brain may reconstruct the neuronal circuits by modifying the neuron firing function and interacting with STDP, for satisfying requirements in information processing.

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