The line operator satisfies the commutation relation
\[ [\hat{a}, \hat{a}^\dagger] = \hat{1} \]
with the sum factor equal to the cyclic product
\[ \hat{a} \hat{a}^\dagger \hat{a}^\dagger = \hat{1} \hat{a}^\dagger \hat{a}^\dagger \hat{a}^\dagger \hat{a} \]
where \( \hat{a} \) and \( \hat{a}^\dagger \) are the annihilation and creation operators, respectively.

The Hamiltonian operator is given by
\[ \hat{H} = \hat{a}^\dagger \hat{a} \]
and the energy levels are determined by the eigenvalues of \( \hat{H} \).

In a second quantization formalism, the field operators are expressed in terms of the creation and annihilation operators.

The two-body interaction is given by the operator
\[ \hat{V}_{\text{int}} = \hat{a}^\dagger \hat{a}^\dagger \hat{a} \hat{a}^\dagger \]
and the total Hamiltonian is the sum
\[ \hat{H}_\text{tot} = \hat{H} + \hat{V}_{\text{int}} \]

We report here the experimental results of two models.
neurons. We consider two types of activity-dependent couplings: (1) an excitatory synapse with STDP, and (2) an excitatory synapse with inverse STDP. Through STDP \( g(t) \) changes by \( \Delta g(t) \) which is a function of the time difference \( \Delta t = t_{\text{post}} - t_{\text{pre}} \) between the times of post- and presynaptic spikes. We use the additive update rule

\[
\Delta g(t) = \begin{cases} 
G(\Delta t) = A \text{sgn}(\Delta t) \exp(-\gamma |\Delta t|) 
\end{cases}
\]

for STDP, and \( \Delta g(t) = -G(\Delta t) \) for inverse STDP. We used \( A = 0.004 \mu S \) and \( \gamma = 0.15 \text{ms}^{-1} \).

We studied the synchronization properties of this coupled system by setting the autonomous period of the postsynaptic neuron to 15 ms, then evaluating the actual period of its oscillation \( T_2 \) as a function of the imposed autonomous oscillation period \( T_1 \) of the presynaptic neuron. In Fig. 1 we show \( T_1/T_2 \) as a function of \( T_1 \) in two cases: (a) a synaptic coupling with constant strength 0.008 \( \mu S \) and (b) a synaptic coupling with inverse STDP. In the later case the steady-state coupling strength depends on the ratio of neuronal frequencies (c). Its average over all \( T_1 \) values is 0.002 \( \mu S \), which is much lower than the strength in the case of constant coupling.

In Fig. 1a we see the familiar ‘Devil’s Staircase’ associated with frequency locking domains of a driven nonlinear oscillator. Only frequency locking with ratios 1:1, 2:1, 3:1, and 4:1 leads to synchronization plateaus with significant width. In Fig. 1b we see that the synchronization domains are substantially broadened due to activity-dependent coupling, especially for \( T_1/T_2 = 1 \). Some synchronization plateaus exhibit multistability, which we confirmed by observing the associated hysteresis. These results show that even a weak, but adaptive connection with strength that is determined dynamically is able to greatly enhance and enrich synchronization.

We also studied the robustness of this enhanced synchronization in the presence of noise by adding zero mean, Gaussian, white noise to the membrane currents of each neuron. We examined the behaviour of the system with RMS noise amplitudes \( \sigma = 0.01, 0.05, 0.1, \) and 0.5 nA.

For \( \sigma = 0.01 \) nA no phase-locking plateaus were destroyed. At \( \sigma = 0.05 \) nA the 4:1 plateau became distorted. Larger \( \sigma \) sequentially eliminated synchronization plateaus until only the 1:1 plateau remained. The 1:1 plateau was seen for all \( \sigma \). In Fig. 2 we illustrate the effect of the noise on synchronization when \( \sigma = 0.1 \) nA with (a) constant and (b) inverse STDP coupling. While in (a) most of the plateaus have disappeared, in (b) the 1:1, the 2:1 and even the 3:1 frequency locking regimes remained. In sharp distinction to classical synchronization, frequency locking through activity-dependent coupling is significantly more robust in the presence of noise.

To understand the mechanisms behind such a remarkable robustness we studied the diffusion of oscillation phase caused by noise. For \( \sigma = 0.5 \) nA in Fig. 3a we show that in the case of 1:1 synchronization and coupling with constant strength 0.008 \( \mu S \) noise-induced phase diffusion results in \( 2\pi \) phase slips that destroy synchronized state. Quite contrary Fig. 3b shows that in the case of activity-dependent coupling phase slips are absent and the phase difference does not increase. In this particular case the strength of coupling varied around the mean of 0.0064 \( \mu S \) with standard deviation of 0.0026 \( \mu S \).

In Fig. 4 we plot the average rate of phase slips for different amplitudes of the noise. In line with the above observation we see that in the case of activity-dependent coupling (dashed line) phase slips are suppressed in a wide range of noise amplitudes. We argue here that this suppression of phase slips is the primary mechanism responsible for robustness of synchronization mediated by activity-dependent coupling. After the introduction of a discrete map model we will discuss this mechanism in more detail.

We also considered synchronization through an activity-dependent synapse in the interesting case when the presynaptic neuron produces bursts of spikes and the postsynaptic neuron spikes irregularly. We found that synchronization through an STDP synapse is very fast, even a few spikes are enough for the frequency locking to establish itself. Neurons in the same set up with constant coupling synchronize much more slowly and only if the strength of the connection is appropriate for the given ratio of their frequencies. Hence, activity dependent synapses allow adaptation on the run: synchronizing a postsynaptic neuron to the firing properties of its presynaptic partner.
To understand the above results in a general way we have constructed a discrete time map model of periodic generators with STDP-like coupling. This map accounts for the dependence of the coupling strength on the activity of generators. Take $T_1$ and $T_2$ as the autonomous periods of the first and second generators. As a result of unidirectional coupling, the period of the second generator will change by some amount $\Delta T$ each time it receives a spike from the first generator. Assuming initial phases to be $0$, the time of the $n+1$-st spike of the first generator and $m+1$-st spike of the second generator are taken to satisfy

$$
\theta_{n+1}^{(1)} = \theta_{n+1}^{(1)} + T_1^{(1)}
$$

$$
\theta_{m+1}^{(2)} = \theta_{m+1}^{(2)} + \Delta T_{m,n},
$$

(6a)

(6b)

where $n$ and $m$ are such that $\theta_{n+1}^{(1)} \leq \theta_{m+1}^{(2)} \leq \theta_{n+1}^{(1) + 1}$. In general, $\Delta T_{m,n}$ would be a function of $T_1^{(1)}$, $T_2^{(1)}$, $\theta_{n+1}^{(1)}$, $\theta_{m+1}^{(2)}$, and the coupling strength $g_{m,n}$. We argue that the two main variables here are $\theta_{n+1}^{(1)}$, $\theta_{n+1}^{(2)}$, and $g_{m,n}$.

In the simplest case $\Delta T_{m,n}$ can be approximated by

$$
\Delta T_{m,n} = g_{m,n} F(\theta_{n+1}^{(1)} - \theta_{m+1}^{(2)}).
$$

(7)

where the function $F(x)$ is the analog of a phase response curve [13] for our model. To obtain results quantitatively comparable with our neuronal model, we fit it by a non-negative quadratic function that describes phase response of our model neurons: $F(x) = 835 + 63x - 9x^2$ for $0 \leq x \leq T_2^{(1)}$ and 0 otherwise. $g_{m,n}$ obeys the inverse STDP update rules:

$$
g_{m+1,n} = g_{m,n} - G(\theta_{m+1}^{(2)} - \theta_{n+1}^{(1)})
$$

(8a)

$$
g_{m,n} = g_{m,n-1} - G(\theta_{m}^{(2)} - \theta_{n}^{(1)})
$$

(8b)

In Fig. 2 we show the Arnol’d Tongues calculated for the map (6-8) in the case of (a) constant and (b) inverse STDP coupling. As with the model neurons, we see that activity-dependent coupling greatly enlarges the zones of synchronization.

This discrete map can be further analyzed to find its fixed points corresponding to $n = m$ synchronization and to examine their stability. We present here only the case of $1:1$ synchronization. Then $m = n$, and the system of equations (6-8) can be written in the following simple form:

$$
\tau_{n+1} = \tau_n + T_1^{(1)} - T_2^{(2)} + g_n F(\tau_n)
$$

$$
g_{n+1} = g_n - G(\tau_{n+1} - \tau_{n+1}) - G(\theta_{n+1}^{(2)})
$$

(9a)

(9b)

where $\tau_n = \theta_{n+1}^{(1)} - \theta_{m+1}^{(2)}$. The fixed points of (9) are given by $\theta_n^{(1)} = (T_2^{(1)} - T_1^{(2)}) / F(\tau_n)$ and $\tau_n = T_1^{(2)} / 2$. Stability calculations show that for such $F(\tau)$ and $G(\tau)$ these fixed points are stable. The second fixed point illustrates that activity-dependent coupling introduces a new limitation on the relationship between the phases of two oscillators. It is this limitation that causes the suppression of phase...
slips under the influence of noise. Detailed analysis shows that in the course of noise-affected synchronization the strength of activity-dependent coupling adjusts dynamically to keep this phase relationship close to satisfaction and, hence, suppresses phase slips.

In conclusion, we have analyzed the effects of activity-dependent coupling on synchronization properties of coupled neurons. We showed that such coupling results in a substantial extension of the temporal synchronization zones, leads to more rapid synchronization and makes it much more robust against noise. The enlargement of synchronization zones means that with STD-like learning rules the number of synchronized neurons in a large heterogeneous population may increase. In fact, this is an aspect of the popular idea due to Hebb [14]. It is supported by the results in [15, 16] which indicate that the coherence of fast EEG activity in the gamma band increases in a process of associative learning.

Based on our discrete map model results, we argue that the particular details of the signal-generating devices (e.g. neurons) and their connections (e.g. synapses) are not essential and the obtained results have general applicability. In fact, we observed similar phenomena of robust and enhanced synchronization in computer simulations of other types of periodic generators (such as Van-der-Pol and β-oscillators) with STD-like activity-dependent coupling.

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[12] The following values were used: $g_L = 0.027 \, \mu S$, $E_L = -64 \, mV$, $E_{Na} = 50 \, mV$, $g_{Na} = 7.15 \, \mu S$, $g_K = 1.43 \, \mu S$, $E_K = -95 \, mV$, $\alpha = 10 \, m/s^{-1}$, $\beta = 0.2 \, m/s^{-1}$, $C = 1.43 \times 10^{-4} \, \mu F$, $\alpha_{m} = 0.5 \times (1 - (1 - m))$, $\beta_{m} = 1.28 \times 10^{-4} \, \mu F$, $\alpha_{h} = 0.28 \times 10^{-4} \, \mu F$, $\beta_{h} = 0.128 \times 10^{-4} \, \mu F$.