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BALANCED NETWORKS OF SPIKING NEURONS WITH SYNAPTIC ADAPTATION

John Hertz, Andrius Bernotas,
Andrea Fazzini, Thomas Lauritzen,
Sergio Solinas

NORDITA
Blegdamsvej 17
DK-2100 Copenhagen Ø
Denmark

{hertz,bernotas,fazz,tzl,sergio}@nordita.dk

Background

Van Vreeswijk and Sompolinsky suggested that asynchronous random neuronal firing in cortical networks could result from a self-consistent balance between excitation and inhibition. Here, we

1. extend their theory to integrate-and-fire neurons,

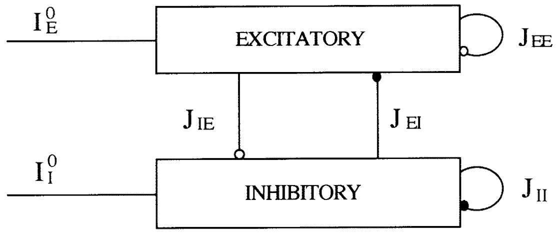
2. simulate balanced networks for both integrate-and-fire and Hodgkin-Huxley neurons, and

3. add synaptic adaptation.

We find

- stable balanced, asynchronous firing for suitable parameter ranges in all cases.

Integrate-&-Fire Model



Synapses (a, $b = 1$: excitatory; $= 2$: inhibitory):

$$J_{ab}^{ij} = \frac{J_{ab}}{\sqrt{K}} \qquad (J_{ab} = \mathrm{O}(1), \;\; J_{12}, J_{22} < 0)$$

with probability K/N; otherwise $J_{ab}^{ij} = 0$.
External inputs:

$$\hat{I}_a^0 = \sqrt{K} I_a \qquad (I_a = \mathrm{O}(1))$$

Membrane potentials u_a^i:

$$u_a^i = \sqrt{K} I_a + \sum_{b=1}^{2} \sum_{js} J_{ab}^{ij} \Theta(t - t_b^{js}) \mathrm{e}^{-(t - t_b^{js})/\tau}$$

$\tau =$ membrane time const
$t_b^{js} =$ time of sth spike of neuron j in pop b
($\Theta(x) = 1$ for $x > 0$; $\Theta(x) = 0$ for $x < 0$)

Mean Field Theory

Mean membrane potentials:

$$u_a(t) = \sqrt{K}\left[I_a + \sum_b J_{ab}\int_{-\infty}^{t} \mathrm{d}t' \mathrm{e}^{-(t-t')/\tau} r_b(t')\right]$$

with population rates $r_a(t)$.

Variances:

$$\alpha_a(t) = \sum_b J_{ab}^2 \int_{-\infty}^{t} \mathrm{d}t' \mathrm{e}^{-2(t-t')/\tau} r_b(t')$$

In steady state:

$$\begin{aligned}
u_1 &= \sqrt{K}(I_1 + J_{11} r_1 \tau + J_{12} r_2 \tau) \\
u_2 &= \sqrt{K}(I_2 + J_{21} r_1 \tau + J_{22} r_2 \tau) \\
\alpha_1 &= \tfrac{1}{2}(J_{11}^2 r_1 \tau + J_{12}^2 r_2 \tau) \\
\alpha_2 &= \tfrac{1}{2}(J_{21}^2 r_1 \tau + J_{22}^2 r_2 \tau)
\end{aligned}$$

$r_a\tau$: dimensionless rates (spikes per membrane time const)

$u_a^i(t)$: random walk, correlation time τ

$\Longrightarrow$ first passage time problem.

Rates:

$$r_a\tau = H\left(\frac{\theta_a - u_a}{\sqrt{\alpha_a}}\right)$$

($\theta_a =$ threshold for population a.)

Low rate limit (Tuckwell):

with $x = (\theta_a - u_a)/\sqrt{\alpha_a} >> 1$,

$$H(x) \approx \frac{x}{\sqrt{2\pi}} \mathrm{e}^{-\frac{1}{2}x^2}$$

For unsaturated firing ($r_a\tau \neq 0, 1$), $u_a = \mathrm{O}(1)$:

$$I_a + \sum_b J_{ab} r_b \tau = 0$$

Solve for r_a:

$$\begin{pmatrix} r_1\tau \\ r_2\tau \end{pmatrix} = (\det \mathsf{J})^{-1} \begin{pmatrix} J_{12}I_2 - J_{22}I_1 \\ J_{21}I_1 - J_{11}I_2 \end{pmatrix}$$

Conditions for $0 < r_a\tau < 1$:

$$\det \mathsf{J} > 0, \qquad |J_{22}|I_1 > |J_{12}I_2, \qquad J_{21}I_1 > J_{11}I_2$$

Stability Analysis

From

$$r_a(t)\tau = H\left(\frac{\theta_a - u_a(t)}{\sqrt{\alpha_a(t)}}\right)$$

with $r_a(t) = r_a^0 + \delta r_a(t)$,

$$\begin{aligned}
\delta u_a(t) &= \sqrt{K}\sum_b J_{ab}\int_{-\infty}^{t} \mathrm{e}^{-(t-t')/\tau}\delta r_b(t') \\
\delta \alpha_a(t) &= \sum_b J_{ab}^2\int_{-\infty}^{t} \mathrm{e}^{-2(t-t')/\tau}\delta r_b(t')
\end{aligned}$$

Fourier transform linearized equations:

$$\delta r_a(\omega) = \frac{-H_a'\sqrt{K}}{\sqrt{\alpha_a}}\sum_b \frac{J_{ab}\delta r_b(\omega)}{1 - \mathrm{i}\omega\tau}$$

with H_a' evaluated at $(\theta_a - u_a)/\sqrt{\alpha_a}$.
Back to time domain:

$$\left(\tau\frac{\mathrm{d}}{\mathrm{d}t} + 1\right)\delta r_a(t) = \frac{-H_a'\sqrt{K}}{\sqrt{\alpha_a}}\sum_b J_{ab}\delta r_b(t)$$

(Same as S-vV).
Growth/relaxation rates O($\sqrt{K}$)

Stability condition (K large): matrix

$$R_{ab} = \frac{H'_a}{\tau\sqrt{\alpha_a}} J_{ab} \equiv y_a J_{ab}$$

must have positive eigenvalues $\Longrightarrow$

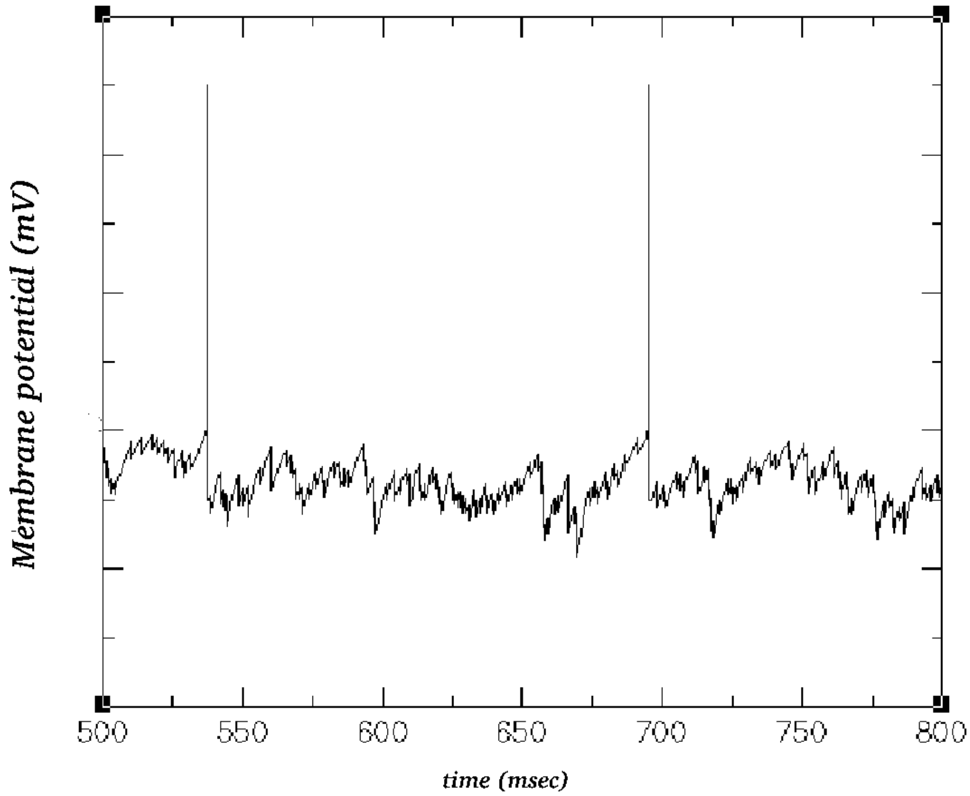
1. $\det \mathsf{J} > 0$ (already required for balance), and

2. (from $\mathrm{Tr}\,\mathsf{J} > 0$)

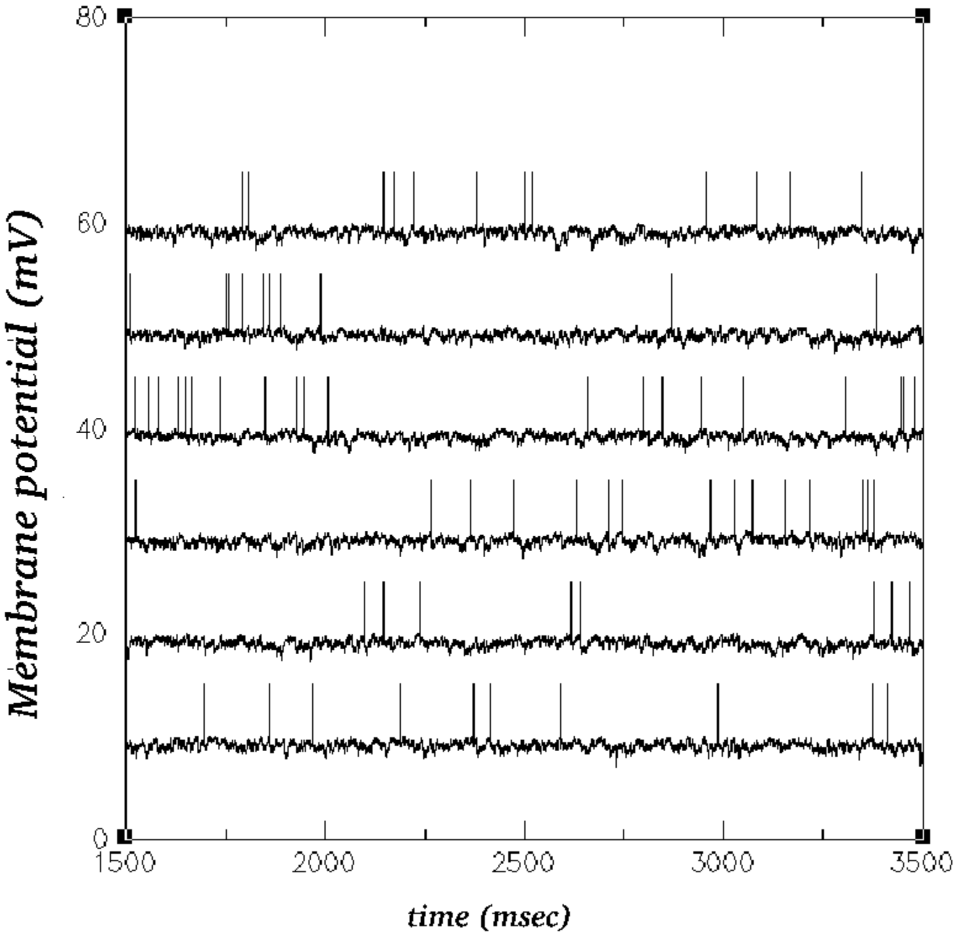
$$|J_{22}| > \frac{\sqrt{\alpha_2} H'_1}{\sqrt{\alpha_1} H'_2} J_{11}$$

Simulations with spiking neurons

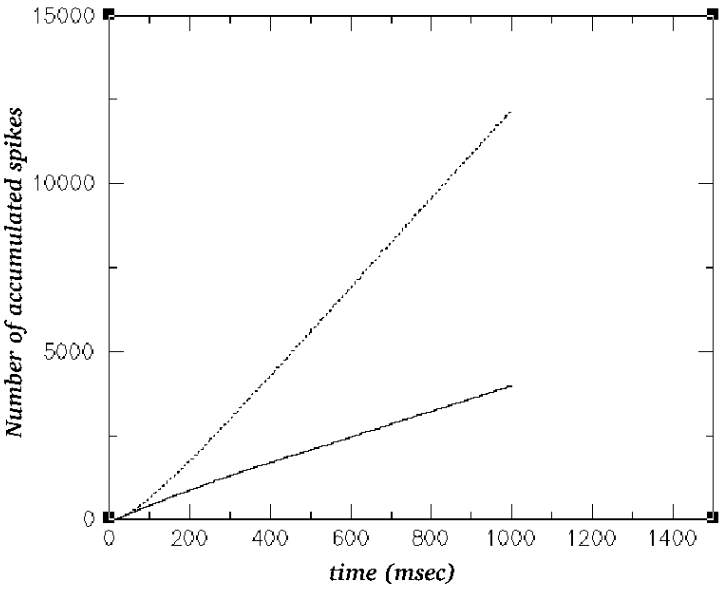
I & F: $N_1 = N_2 = 1500$, $\tau = 8$ ms, one neuron:



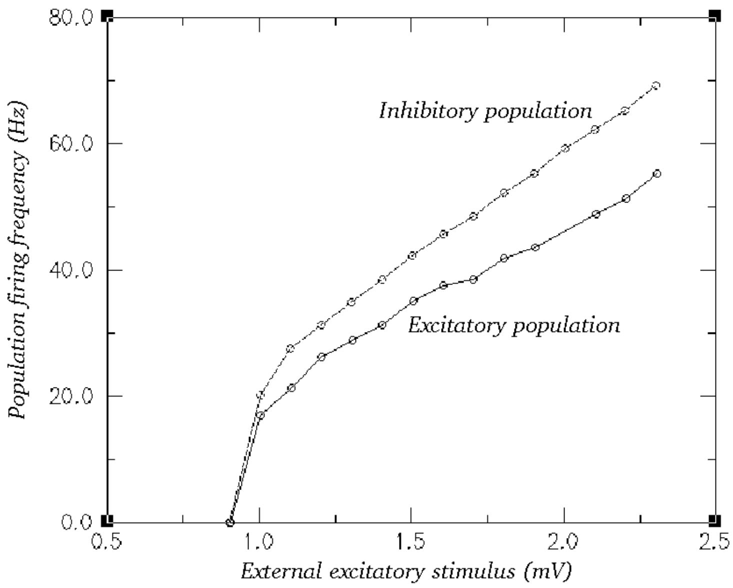
Brownian motion in effective quadratic potential below threshold, spike when $u_a^i(t)$ reaches threshold asynchronicity, 6 neurons:



Evidence for constant rates: total accumulated spikes vs time:



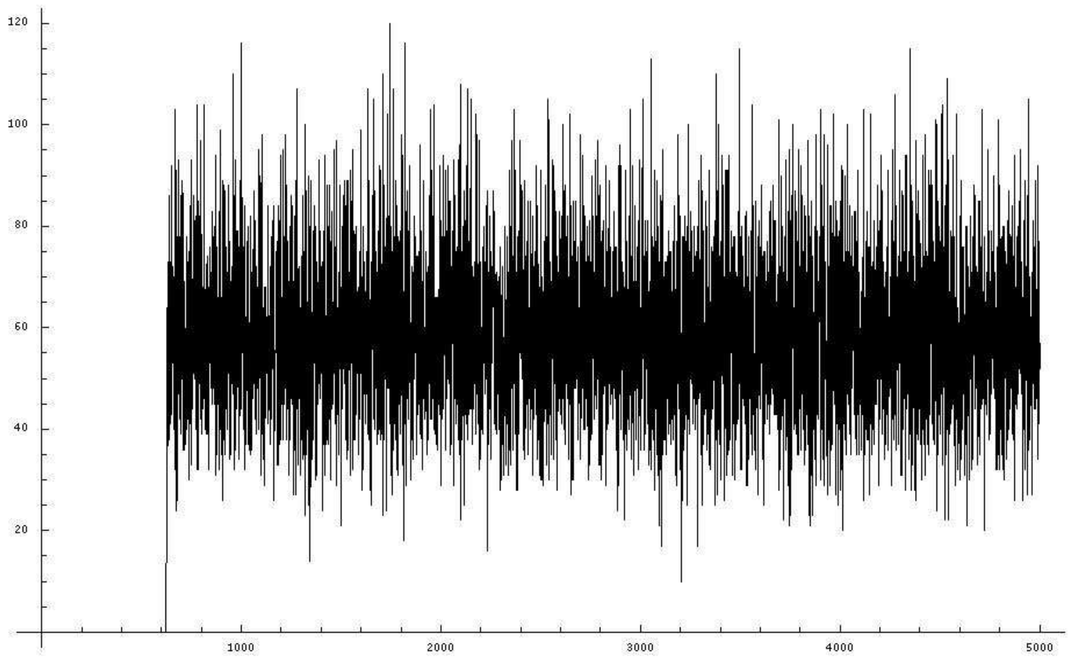
Rates vs external drive I_1 (I_1/I_2 fixed):



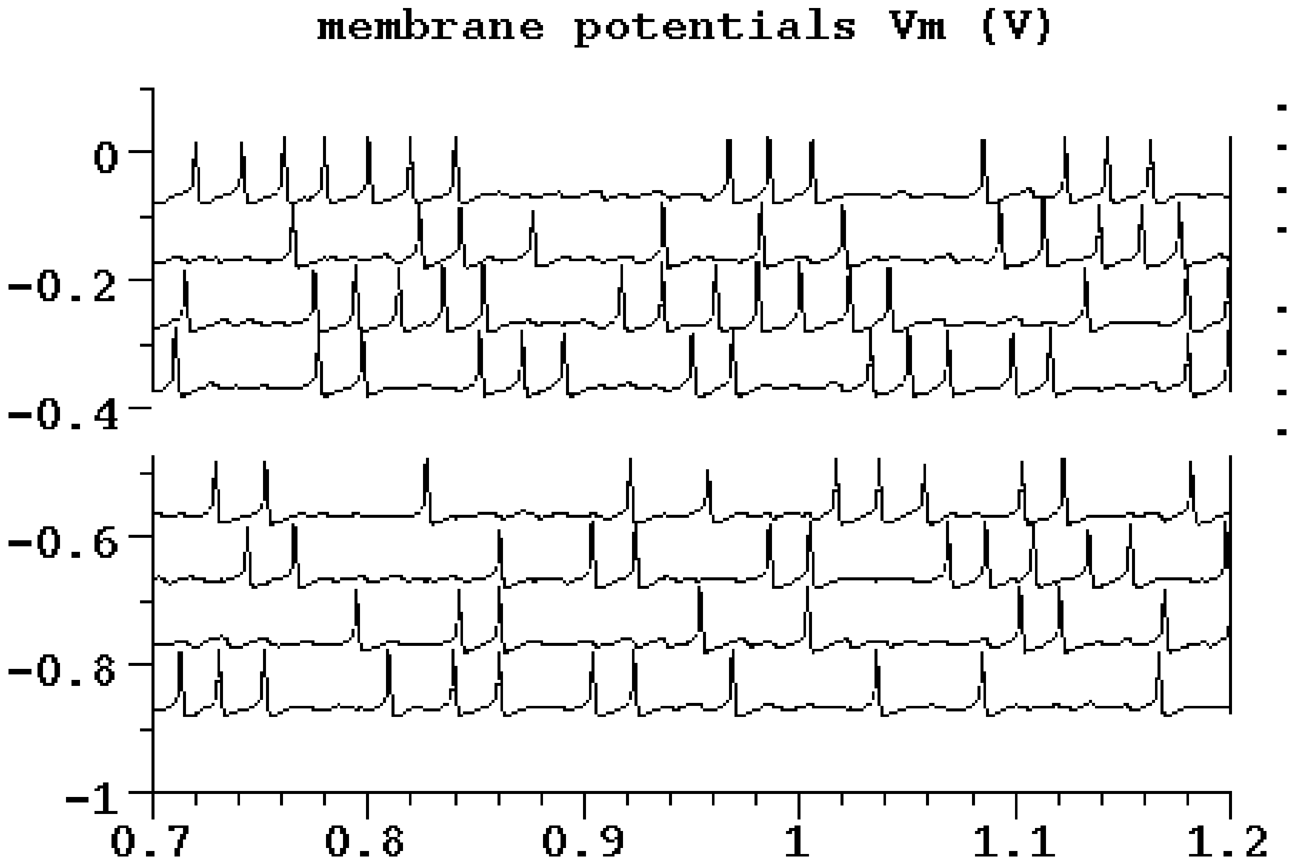
Deterministic chaos:

Compare evolution of two copies of the network after 1 neuron in 1 copy is forced to fire prematurely.
normalized Hamming distance

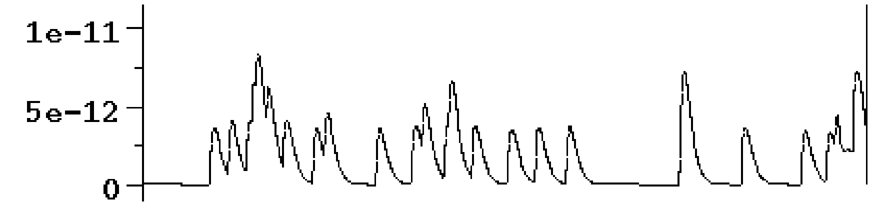
$$D(t) = \frac{1}{N} \sum_i [S_i^0(t) - S_i^1(t)]^2.$$



Hodgkin-Huxley neurons (250 + 250):

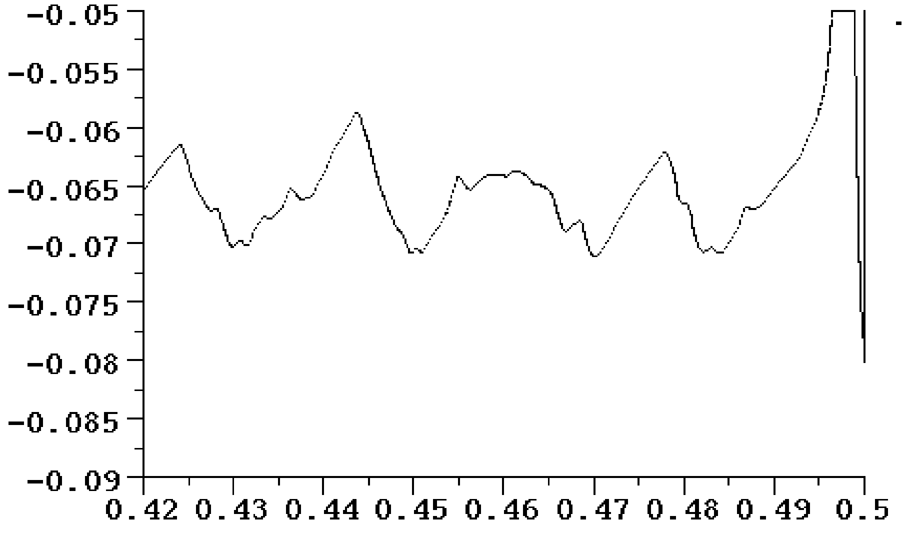


excitatory currents:

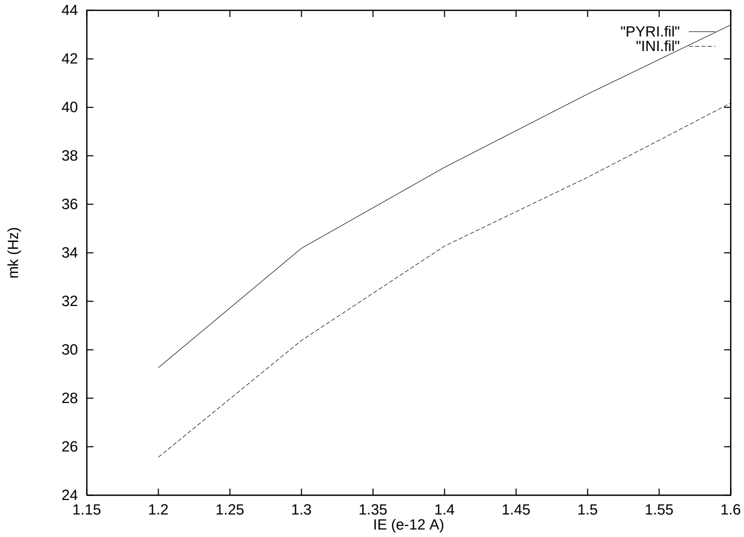


inhibitory currents:

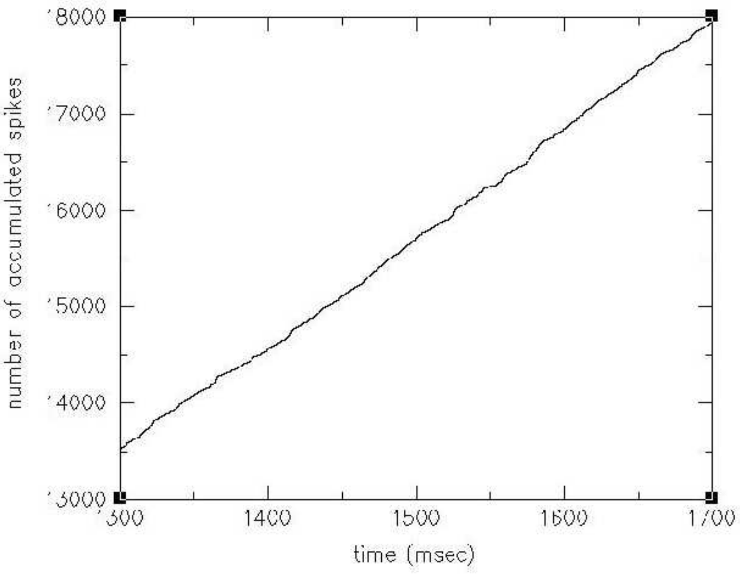
membrane potential



rates as a function of I_E:



Cumulative firings vs time:



Synaptic adaptation

Depression:

After presynaptic spike, $J \to fJ$.
Between spikes, relax toward J_0 with relaxation time $\tau_\mathrm{d} \sim 500$ ms.

With presynaptic firing rate r, on average

$$\frac{\mathrm{d}J}{\mathrm{d}t} = \frac{J_0 - J}{\tau_\mathrm{d}} - r(1-f)J$$

Steady state:

$$\bar{J} = \frac{J_0}{1 + (1-f)r\tau_\mathrm{d}}$$

$\Longrightarrow$ If an asynchronous state with rate r is stable for a given J in net without depression, try simple compensation

$$J_0 = [1 + (1-f)r\tau_\mathrm{d}]J$$

But is the system stable?

Example: depression of J_{11}

Linearize the MF equation for r_1,

$$\left(\frac{\mathrm{d}}{\mathrm{d}t} + \frac{1}{\tau}\right) \delta r_1(t) \;=\; \frac{-H_1' \sqrt{K}}{\tau\sqrt{\alpha_1}}[\bar{J}_{11}\delta r_1(t) \;+\; r_1 \delta J_{11}(t) + J_{12}\delta r_2(t)]$$

(eqn for δr_2 unchanged), and the J equation:

$$\left(\frac{\mathrm{d}}{\mathrm{d}t} + \frac{1}{\tau_{\mathrm{d}}}\right) \delta J_{11} = -(1-f)[\bar{J}_{11}\delta r_1 + r_1 \delta J_{11}]$$

$\Longrightarrow$ 3×3 stability matrix:

$$\mathsf{R} = \begin{pmatrix} y_1 \bar{J}_{11} & y_1 J_{12} & y_1 r_1 \\ y_2 J_{21} & y_2 J_{22} & 0 \\ \frac{(1-f)\bar{J}_{11}}{\sqrt{K}} & 0 & \frac{(1-f)r_1 + 1/\tau_{\mathrm{d}}}{\sqrt{K}} \end{pmatrix}$$

with $y_a = \frac{H_a'}{\tau\sqrt{\alpha_a}}$.
Note: elements of upper-left 2×2 block are O(1); elements in bottom row are $O(1/\sqrt{K})$

Perturbation theory $(K \gg 1)$

Changes in eigenvalues are $O(1/\sqrt{K})$, negligible for fast modes (rate relaxation).
$\Longrightarrow$ instability only if perturbations of J_{11} are unstable.

Change in relaxation rate for J_{11}

$$\begin{aligned}
&\approx -\sqrt{K} R_{31} \langle 1|\mathsf{R}_0^{-1}|1\rangle R_{13} \\
&= -\sqrt{K} \cdot \frac{(1-f)\bar{J}_{11}}{\sqrt{K}} \cdot \frac{y_2 J_{22}}{y_1 y_2 \det \bar{\mathsf{J}}} \cdot y_1 r_1 \\
&= \frac{(1-f) r_1 \bar{J}_{11} |J_{22}|}{\det \bar{\mathsf{J}}} > 0,
\end{aligned}$$

with R_0 the 2×2 stability matrix without synaptic adaptation
i.e. *enhanced stability*

Find enhanced stabilization with depression of *any* J_{ab}

Facilitation

After presynaptic spike, $J \to J + \hat{f}(J_{\mathsf{max}} - J)$. Between spikes, relax toward J_0 with relaxation time τ_{f}.

With presynaptic firing rate r, on average

$$\frac{\mathrm{d}J}{\mathrm{d}t} = \frac{J_0 - J}{\tau_{\mathsf{f}}} + r\hat{f}(J_{\mathsf{max}} - J)$$

Steady state:

$$\bar{J} = \frac{J_0 + r\hat{f}\tau_{\mathsf{f}} J_{\mathsf{max}}}{1 + r\hat{f}\tau_{\mathsf{f}}}$$

Linearized equation:

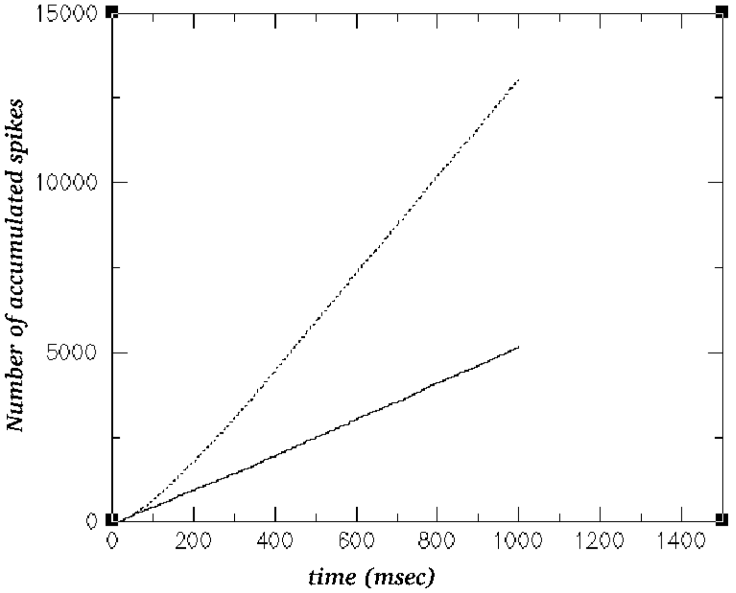
$$\left(\frac{\mathrm{d}}{\mathrm{d}t} + \frac{1}{\tau_{\mathsf{f}}}\right)\delta J = -\hat{f}[\bar{J}\delta r + r\delta J]$$

Same form as for depression $\Longrightarrow$

Enhanced stability with either depression or facilitation of any kind of synapse

Simulations with synaptic depression

cumulative spikes vs time:



rates vs external drive: