Multistability in Spiking Neuron Models of Delayed Recurrent Inhibitory Loops

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Definition and Examples of Multistability

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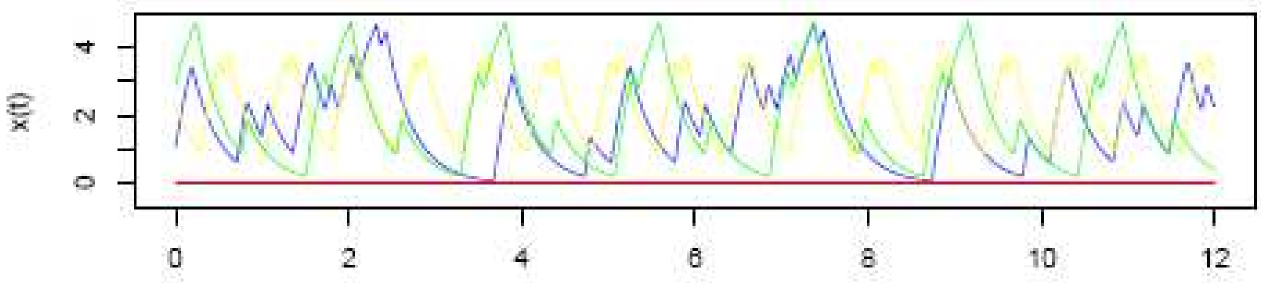
Considering a delay differential equation

$$\frac{dx(t)}{dt} = -\alpha x(t) + F(x(t-\tau))$$

$$F(x) = \begin{cases} c & \text{if } x \in [x_1, x_2]; \\ 0 & \text{otherwise } (x < x_1 \text{ or } x > x_2), \end{cases}$$

Background and Examples of Multistability

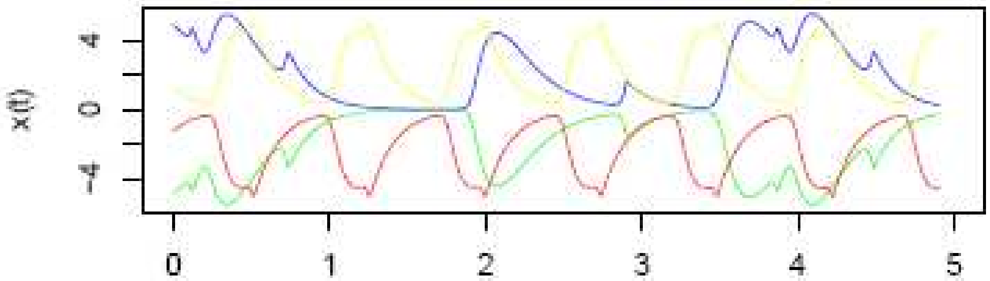
Losson found four coexisting attracting periodic solutions[a]



For Mackey-Glass delay differential equation

$$\frac{dx(t)}{dt} = -\alpha x(t) + \frac{\beta x(t-\tau)}{1 + x(t-\tau)^{10}}$$

There exist four coexisting attracting periodic solutions[b]

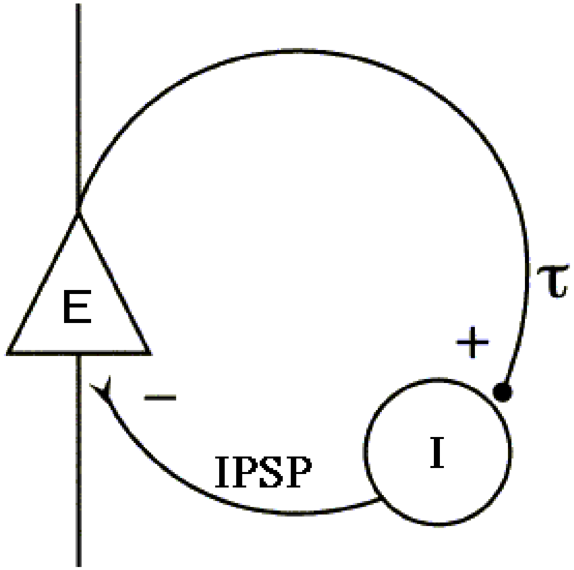


S.Richard Taylor PhD thesis

Recurrent Inhibitory Loops

Recurrent Inhibitory loop is the simplest neural network composed of two neurons: excitatory E and inhibitory I.

- Neuron E excites neuron I.
- In turn, neuron I delivers an inhibition to neuron E.
- There is a time lag τ.

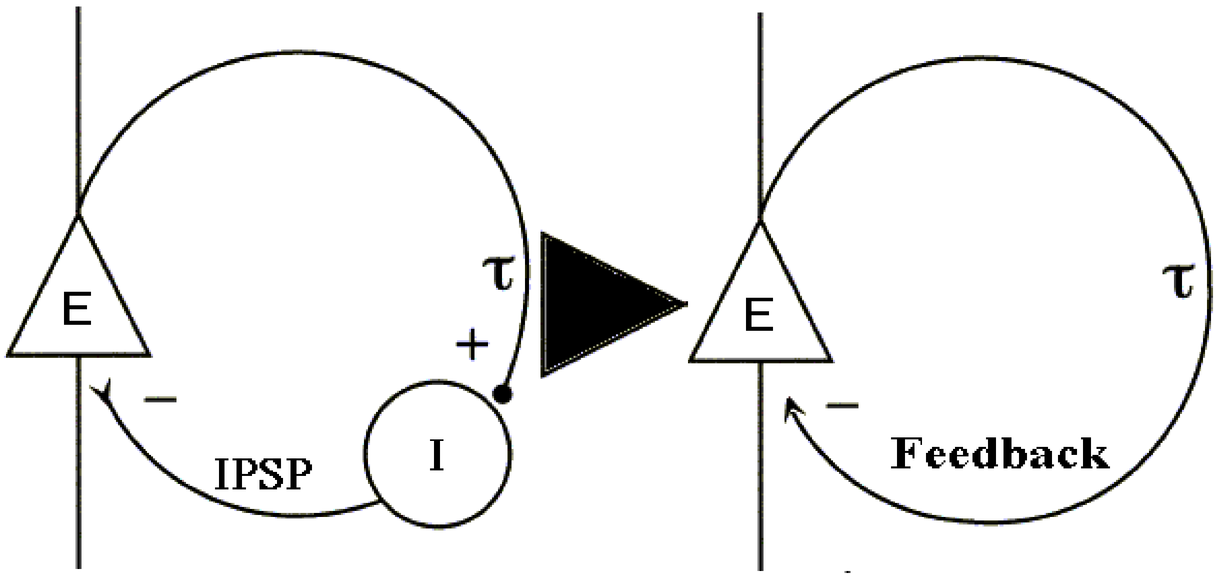


Recurrent inhibitory loop models

Conductance-based models: Hodgkin-Huxley model (HH)

$$Cx'(t) = -g_{Na}m^3h(x(t) - E_{Na}) - g_K n^4(x(t) - E_k) - g_L(x(t) - E_L) - F(x(t-\tau)) + I_s(t),$$

$$\begin{cases} m'(t) = \alpha_m(x)(1-m) - \beta_m(x)m, \\ n'(t) = \alpha_n(x)(1-n) - \beta_n(x)n, \\ h'(t) = \alpha_h(x)(1-h) - \beta_h(x)h\,. \end{cases} \quad \begin{cases} \alpha_n = \frac{0.1-0.01x}{\exp(1-0.1x)-1}\,, & \beta_n = \frac{0.125}{\exp(x/80)}\,, \\ \alpha_m = \frac{2.5-0.1x}{\exp(2.5-0.1x)-1}\,, & \beta_m = \frac{4}{\exp(x/18)}\,, \\ \alpha_h = \frac{1}{\exp(3-0.1x)+1}\,, & \beta_h = \frac{0.07}{\exp(x/20)}\,. \end{cases}$$



Recurrent inhibitory loop models

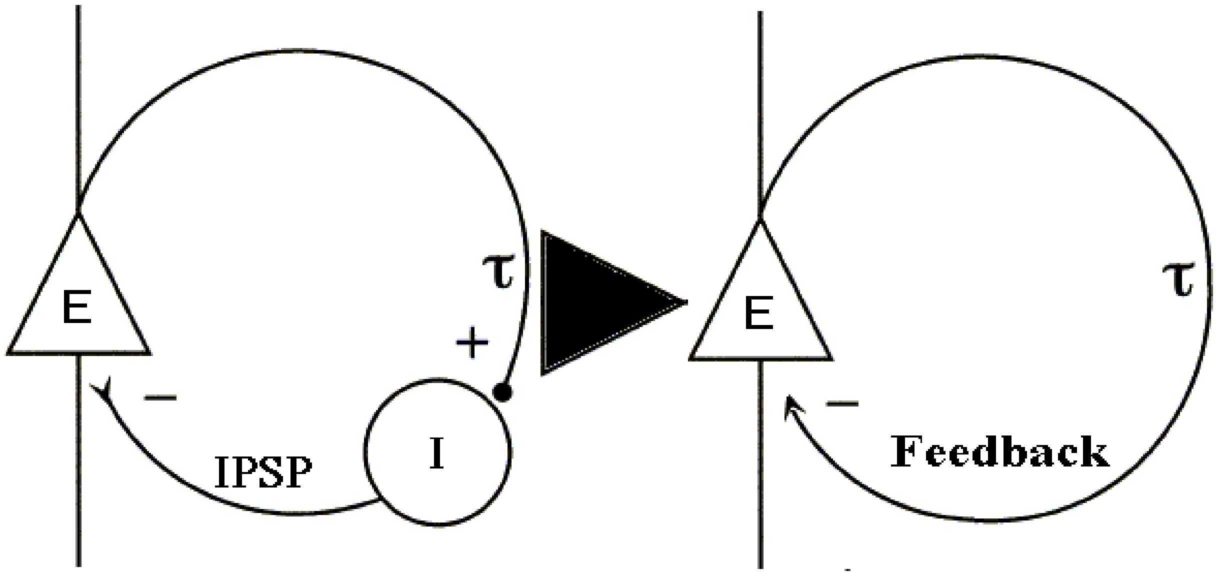
Phenomenological spiking neuron models : Integrate-and-fire models

- Linear integrate-and-fire model (LIF)

$$\frac{dx(t)}{dt} = -\beta x - F(x(t-\tau)) + I_s(t)$$

- Quadratic integrate-and-fire model (QIF)

$$\frac{dx(t)}{dt} = \beta(x-\mu)(x-\gamma) - F(x(t-\tau)) + I_s(t)$$



Comparison of three models

Hodgkin-Huxley model (HH)

$$Cx'(t) = -g_{Na}m^3h(x - E_{Na}) - g_K n^4(x - E_k) - g_L(x - E_L) - F(x(t - \tau)) + I_s(t)$$

Linear integrate-and-fire model (LIF)

$$\frac{dx(t)}{dt} = -\beta x - F(x(t - \tau)) + I_s(t)$$

Quadratic integrate-and-fire model (QIF)

$$\frac{dx(t)}{dt} = \beta(x - \mu)(x - \gamma) - F(x(t - \tau)) + I_s(t)$$

Our Objectives

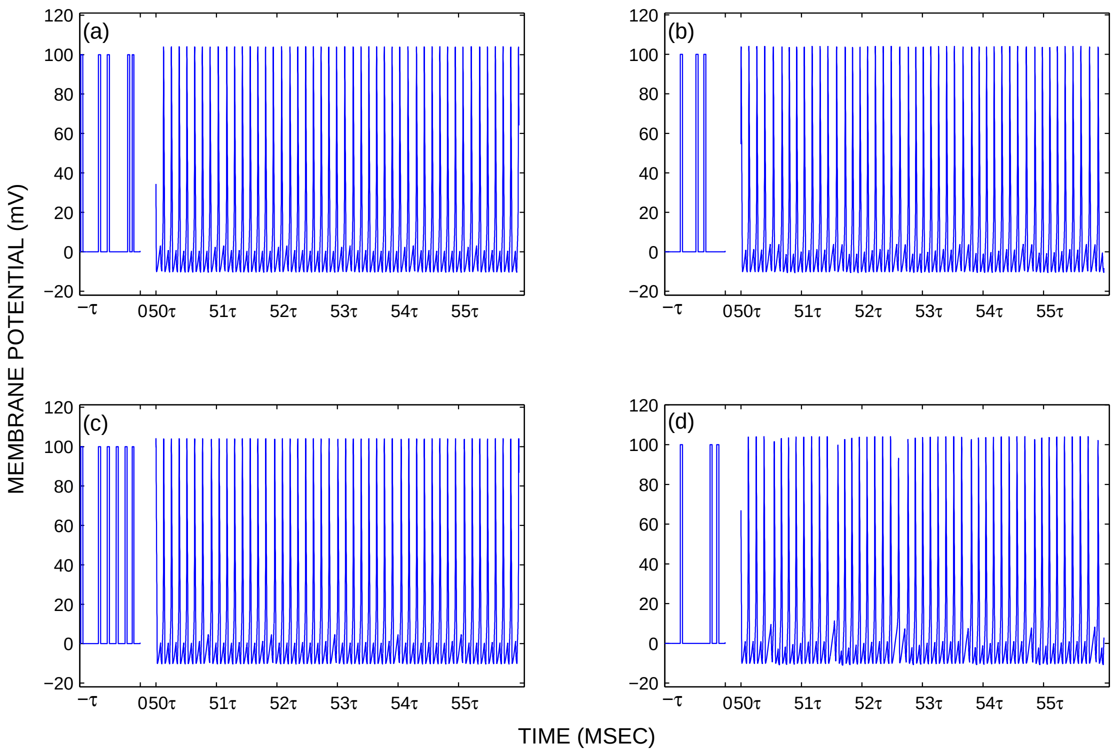
- Find the multiple attracting periodic solutions using Hodgkin-Huxley model (HH)
- Explain why integrate-and-fire models fail to generate the multistability
- Provide effective mechanisms for integrate-and-fire models to achieve multistability and increase the capacity of such two-neuron loop

Model Analysis and Simulation Results

Feedback function is a **monotonic** function

$$F(x) = \begin{cases} a & \text{if } x \geq \vartheta_1 \text{(threshold);} \\ 0 & \text{otherwise } (x < \vartheta_1). \end{cases}$$

For Hodgkin-Huxley model (HH) and $I_s = 10$, there exist four attracting periodic solutions.



Linear integrate-and-fire model (LIF)

Linear integrate-and-fire model (LIF)

$$\frac{dx(t)}{dt} = -\beta x - F(x(t-\tau)) + I_s(t)$$

When multistability happens, there are two necessary conditions

- $F(x)$ must be nonmonotonic.
- τ is longer than the intrinsic time scale of the control mechanism, i.e. $\tau > \alpha^{-1}$.

Reason of loss of multistability for LIF model

- Model is too simple
- Some biological functions and features of neurons can not be captured
  - Action potential (firing procedure)
  - Absolute refractory period
  - Rebound spike procedure

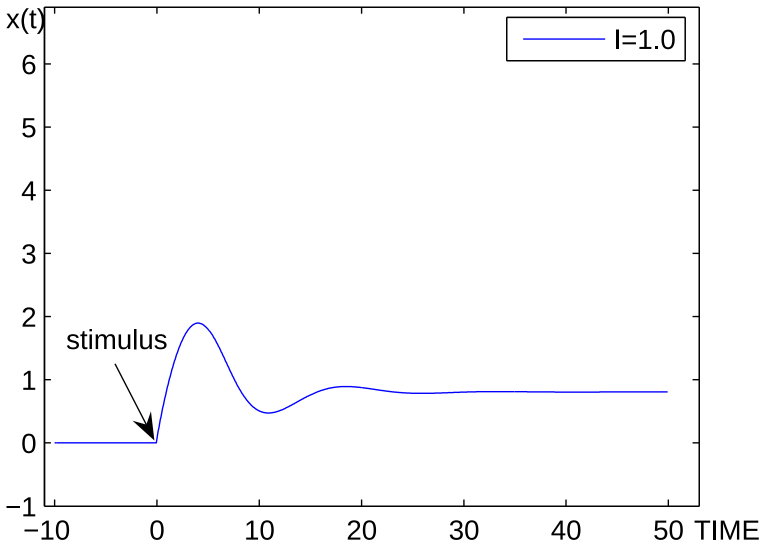
To solve the problem

- Incorporate the firing and rebound mechanisms as well as the absolute refractory period to linear integrate-and-fire model

Three biological functions and features of neurons

Firing procedure

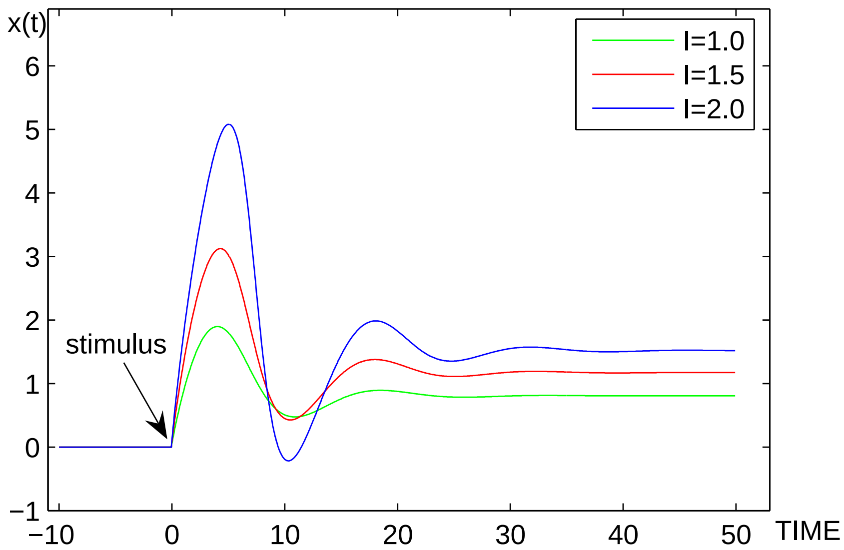
- Stimulus I_s causes the membrane potential to increase and approach its equilibrium.



Three biological functions and features of neurons

Firing procedure

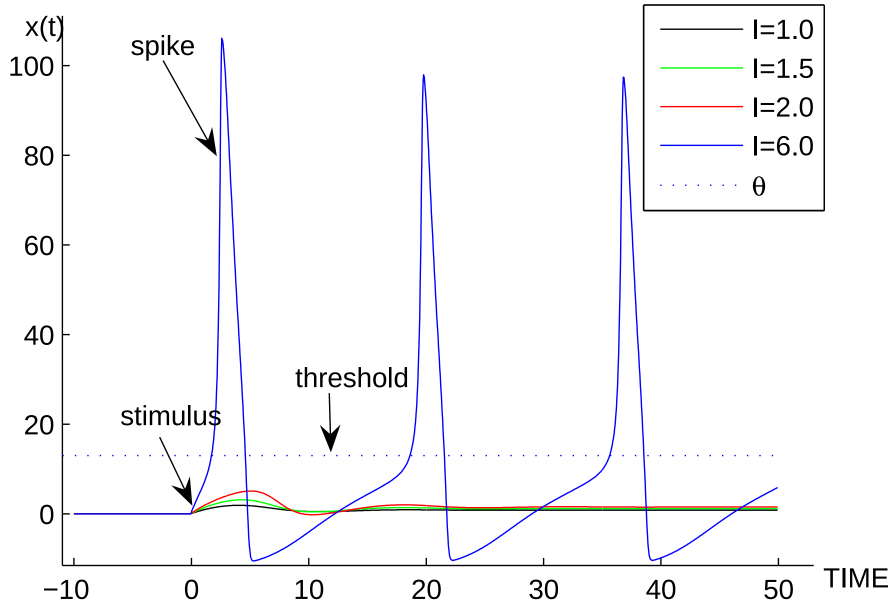
- Stimulus I_s causes the membrane potential to increases and approach its equilibrium.
- The larger I_s, the higher the membrane potential.



Three biological functions and features of neurons

Firing procedure

- Stimulus I_s causes the membrane potential to increases and approach its equilibrium.
- As I_s increases, the membrane potential increases.
- If the potential reaches certain threshold, the neuron fires and creates an action potential(spike). After firing, the membrane potential is reset to certain value.

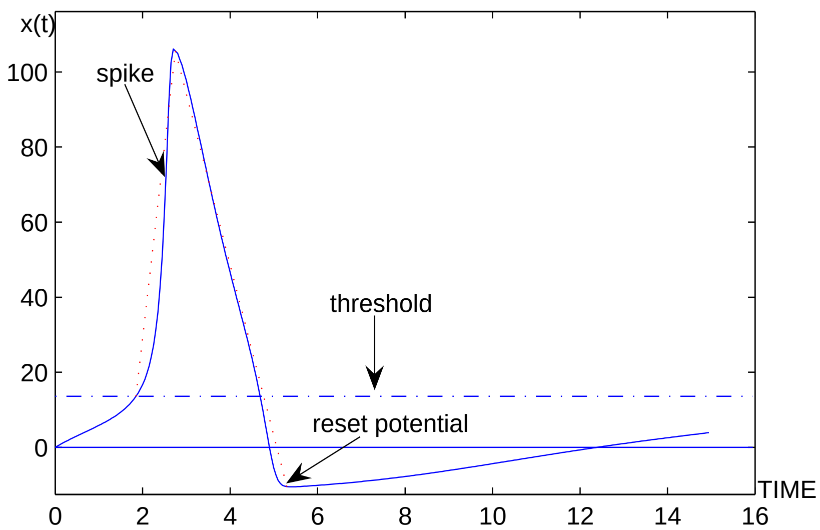


Three biological functions and features of neurons

Time course of firing procedure is approximated by a continuous linear function or a continuous exponential function

$$x_f(t) = \hat{x}_1(t) = \begin{cases} \vartheta_1 + \frac{c-\vartheta_1}{s_1-t_f}(t-t_f) & \text{if } t \in [t_f, s_1); \\ V_r + \frac{c-V_r}{s_2-s_1}(s_2-t) & \text{if } t \in [s_1, s_2], \end{cases}$$

$$x_f(t) = \hat{x}_2(t) = \begin{cases} \vartheta_1 e^{\alpha_1 (t-t_f)} & \text{if } t \in [t_f, s_1]; \\ e^{-\alpha_2 (s_2-t)} \left[\frac{V_r}{s_2-s_1}(t-s_1) + \frac{c\, e^{\alpha_2(s_2-s_1)}}{s_2-s_1}(s_2-t) \right] & \text{if } t \in (s_1, s_2], \end{cases}$$

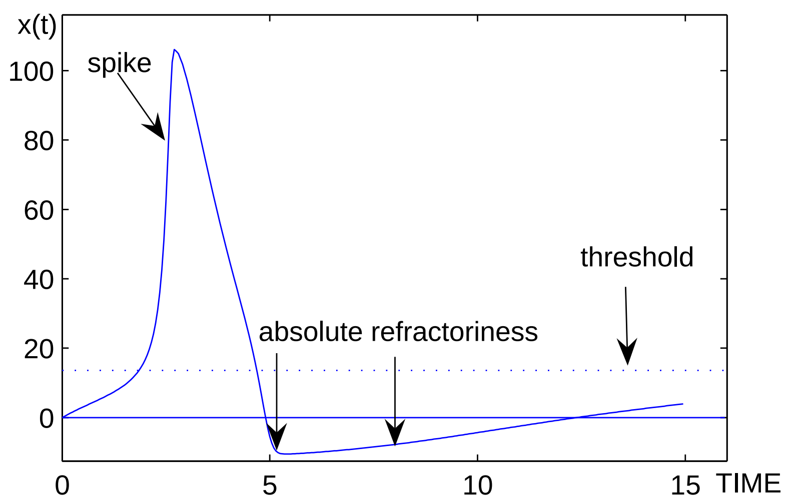


Three biological functions and features

Absolute refractory period

- After the firing of a spike, there is a short period called absolute refractoriness during which the neuron is not affected by any input at all.
- The membrane potential is described by

$$\frac{dx}{dt} = -\beta x, \quad \text{or} \quad x_{abs}(t) = V_r e^{-\beta(t-s_2)},$$

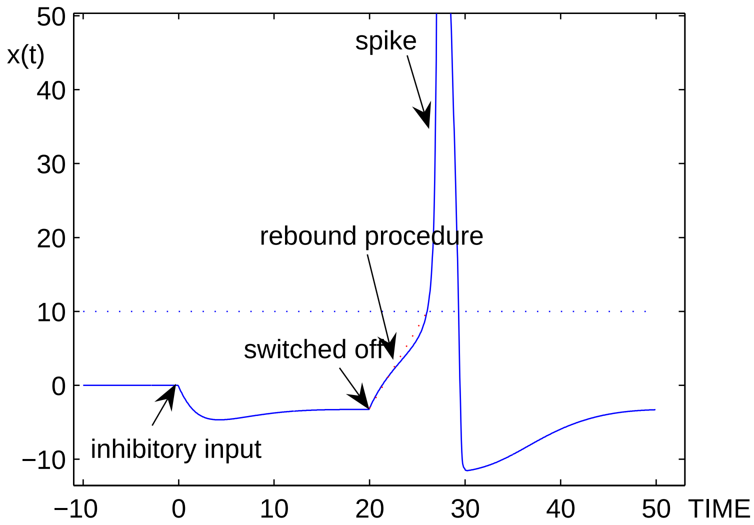


Three biological functions and features of neurons

Rebound procedure

- An inhibitory input causes the membrane potential to decrease
- The larger inhibitory input, the lower the membrane potential
- If the membrane potential is less than its rebound thresholds, once the input is switched off, an inhibitory rebound spike is generated.
- Time course of rebound spike is approximated by a continuous linear function

$$x_b(t) = \tilde{x}_1(t) = x_{t_b} + \frac{\vartheta_1 - x_{t_b}}{d_b}(t - t_b)$$



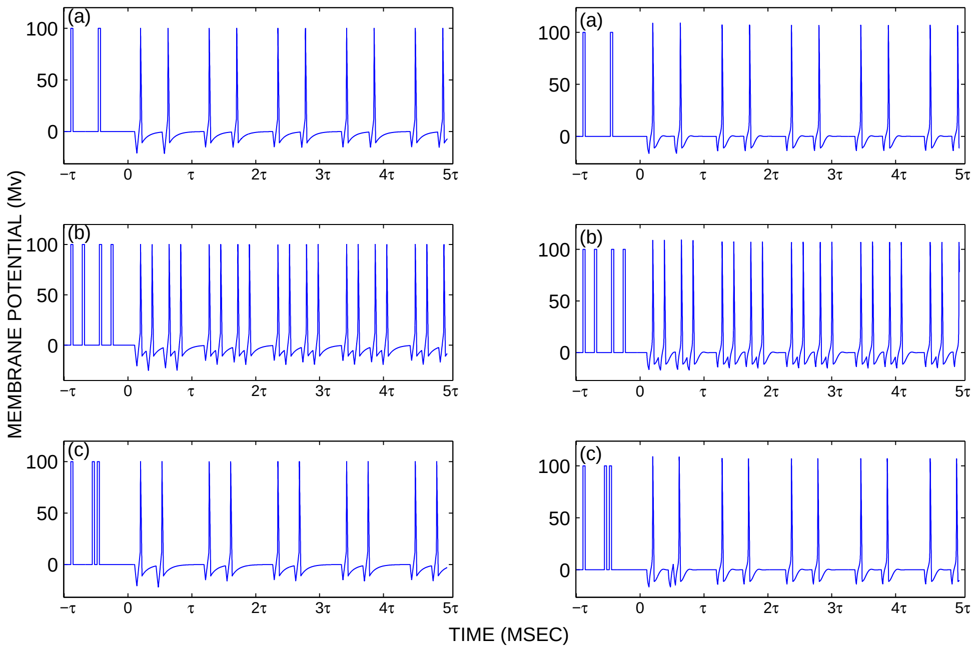
LIF model with three biological functions

In summary, linear integrate-and-fire model (LIF) with the special time courses

$$\frac{dx(t)}{dt} = -\beta x - F(x(t-\tau)) + I_s(t)$$

$$x(t) = \begin{cases} x_f(t) + x_{abs}(t) & \text{if } x(t) \geq \vartheta_1; \\ x_b(t) & \text{if } x(t_b) \leq \vartheta_2, \text{ input is switched off.} \end{cases}$$

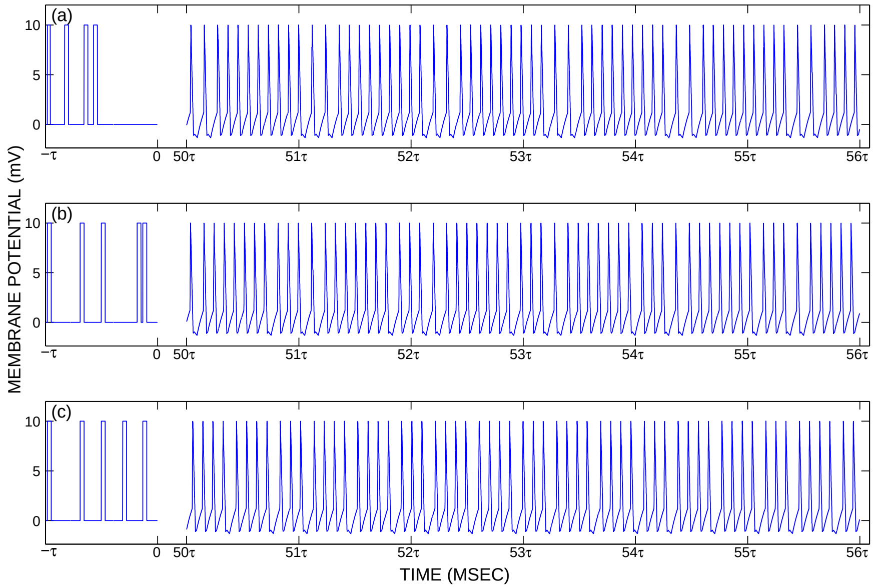
When $I_s = 0$, the simulation results



Model Analysis and Simulation Results

When $I_s = 0.38$, the numerical results show

- Generate a large number of attracting periodic solutions
- Increase the capacity of the stable patterns
- Two-neuron recurrent inhibitory loop exhibits the multistability

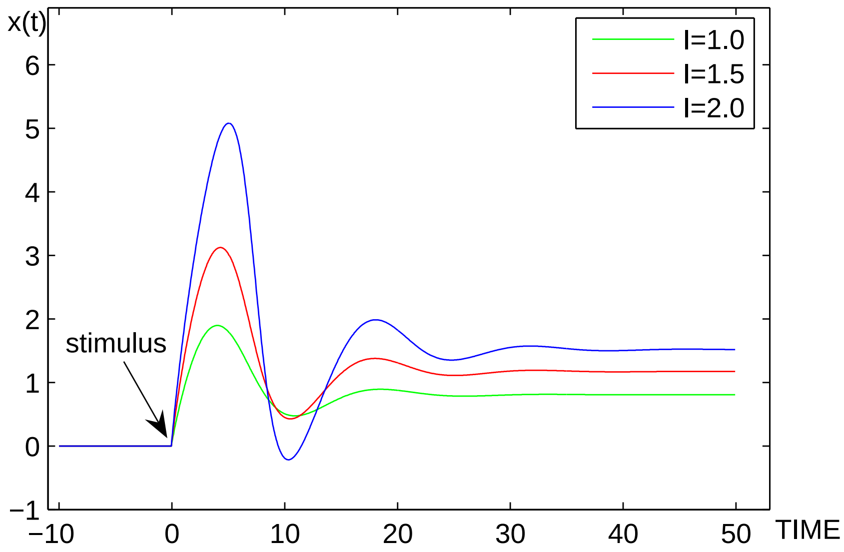


Disadvantage: The constructed linear time course of rebound spike does not seem to be consistent with the real path of rebound spike.

Quadratic integrate-and-fire model (QIF)

Reasons of using the quadratic integrate-and-fire model (QIF)

- Quadratic integrate-and-fire model solve the rebound spike problem by introducing a rebound equation.
- The relationship of the equilibrium state and applied stimulus is a quadratic function rather than a linear function.
- There is the similar relationship for the inhibitory input.



Quadratic integrate-and-fire model (QIF)

Quadratic integrate-and-fire model (QIF)

- Original equation

$$x'(t) = \beta(x - x_{rest})(x - x_F) + I_s(t)$$

- Rebound equation

$$x'(t) = \beta(x - x_I)(x - x_F) + I_s(t)$$

Quadratic integrate-and-fire model (QIF) for recurrent inhibitory loops

$$x'(t) = \beta(x - \mu)(x - \gamma) - F(x(t - \tau)) + I_s$$

$$\mu = \begin{cases} x_I & \text{if } x(t) < \vartheta_2\text{,input is switched off;} \\ x_{rest} = 0 & \text{otherwise.} \end{cases}$$

Once firing, the membrane potential is described by

$$x(t) = x_f(t) + x_{abs}(t),$$

$$\frac{dx_{abs}(t)}{dt} = \beta(x_{abs} - x_{rest})(x_{abs} - \gamma),\ t \in [t_2, t_2 + d_{abs}]$$

QIF model and Simulation Results

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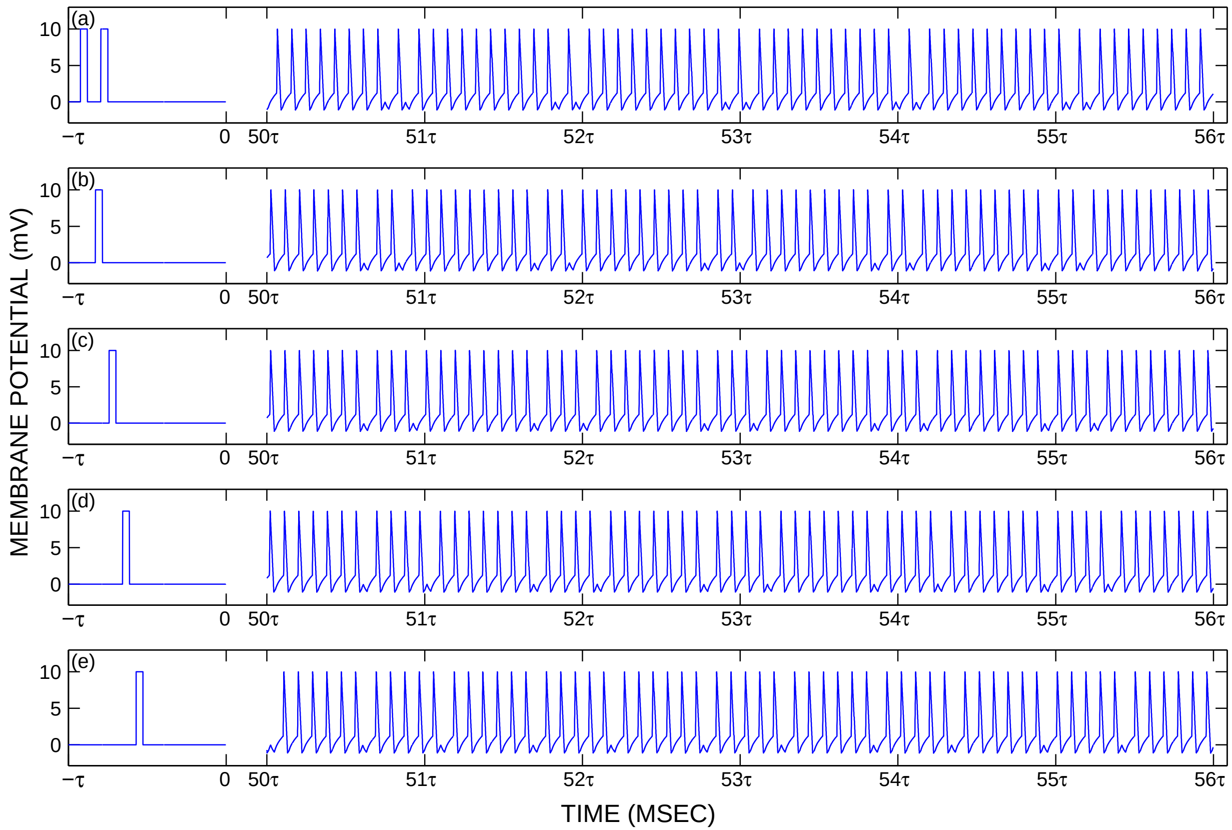

Conclusion

- Focus on the asymptotic behavior of the excitatory neuron in a recurrent inhibitory loop
- Emphasis on the capability of such a single loop to generate multiple stable patterns
- The key to multistability in phenomenological neuron model is the incorporation of the firing and rebound mechanisms as well as the absolute refractory period.
- Both simulation and analysis show that a recurrent inhibitory loop based on the quadratic integrate-and-fire model exhibits coexisting multiple attracting periodic solutions.