Simplified neuron models II:
Izhikevich model & Firing-rate models

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Outline

Izhikevich model

From spiking neurons to firing-rate models

Rate dynamics of LIF neurons with strong synapses
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Rate dynamics of LIF neurons with strong synapses
2D reduction of the Hodgkin-Huxley model

Different reductions of the HH model

\[ C \dot{V} = I - \bar{g}_K n^4 (V - E_{K^+}) - \bar{g}_{Na} m^3 h (V - E_{Na^+}) - g_L (V - E_L) \]

\[ \dot{n} = (n_\infty (V) - n) / \tau_n (V) \]

\[ \dot{m} = (m_\infty (V) - m) / \tau_m (V) \]

\[ \dot{h} = (h_\infty (V) - h) / \tau_h (V) \]

to 2-dimensional systems of the form

\[ \dot{x} = f(x, y) \]

\[ \dot{y} = g(x, y) \]
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- example: “\( I_{Na+,p} + I_{K+} \) model” (\( x = V, y = n \))
  - removal of Na\(^+\) inactivation, i.e. \( h = 1 \)
  - assuming instantaneous Na\(^+\) activation, i.e. \( m = m_\infty \)

\[ \Rightarrow \quad C \dot{V} = I - \bar{g}_{K+} n^4 (V - E_{K+}) - \bar{g}_{Na+} m_\infty^3 (V - E_{Na+}) - g_L (V - E_L) \]

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- Many reductions have in common that \(x\) is a fast voltage \((V)\) and \(y\) a slow recovery variable (e.g. \(n\) or \(h\)).
Phase plane

- **V-nullcline:** curve defined by $\dot{V} = 0 = f(V_0, n_0)$

  \[
  0 = I - \bar{g}_K n_0^4 (V_0 - E_{K^+}) - \bar{g}_{Na} m_\infty^3 (V_0 - E_{Na^+}) - g_L (V_0 - E_L)
  \]

  \[
  n_0 = \left( \frac{I - \bar{g}_{Na} m_\infty^3 (V_0 - E_{Na^+}) - g_L (V_0 - E_L)}{\bar{g}_K (V_0 - E_{K^+})} \right)^{1/4}
  \]

- **n-nullcline:** curve defined by $\dot{n} = 0 = g(V_0, n_0)$

  \[
  0 = (n_\infty(V_0) - n_0) / \tau_n(V_0) \quad \Leftrightarrow \quad n_0 = n_\infty(V_0)
  \]
Izhikevich model

- decision "to spike or not to spike" is made close to left minimum of $V$-nullcline (resting state)

- approximation of dynamics in the vicinity of the resting state

\[
\dot{V} = \tau_{\text{fast}} \left( p \left( V - V_{\text{min}} \right)^2 - (u - u_{\text{min}}) \right)
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\[
\dot{u} = \tau_{\text{slow}} \left( s \left( V - V_0 \right) - u \right)
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- $V$ can escape to infinity $\leadsto$ action-potential upstroke

\[ \text{reset system when membrane potential reaches } V_{\text{max}} (V, u) \rightarrow (V_{\text{reset}}, u + u_{\text{reset}}) \text{ when } V = V_{\text{max}} \]

- note: only 4 dimensionless parameters $a$, $b$, $c$, $d$
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- rescaling:

\[
\begin{align*}
\dot{v} &= I + v^2 - u \\
\dot{u} &= a(bv - u) \\
\text{if } v \geq 1, \text{ then } v &\rightarrow c, \ u \rightarrow u + d
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Izhikevich model

- model can mimic both *integrators* and *resonators* (by appropriate choices of parameters)
Izhikevich model

- model can mimic both *integrators* and *resonators* (by appropriate choices of parameters) ... and a large variety of different neuron types
Outline

Izhikevich model

From spiking neurons to firing-rate models

Rate dynamics of LIF neurons with strong synapses
Firing-rate models

Stimulus

Presynaptic spikes

 Postsynaptic spikes
Firing-rate models

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Presynaptic spikes

Postsynaptic spikes

▶ variable (stochastic) spike times
Firing-rate models

- variable (stochastic) spike times
- description of (trial-averaged) responses by firing rates
Firing-rate models

Stimulus

Response firing rate

Presynaptic spikes

Postsynaptic spikes

- variable (stochastic) spike times
- description of (trial-averaged) responses by *firing rates*
- description of firing-rate dynamics by *firing-rate models*
Firing-rate models

Stimulus

Presynaptic spikes

Response firing rate

Postsynaptic spikes

- variable (stochastic) spike times
- description of (trial-averaged) responses by firing rates
- description of firing-rate dynamics by firing-rate models
Firing-rate models

Decomposition of stimulus $a(t)$ and response rate $r(t)$ into constant and time-dependent components:

$$a(t) = a_0 + a_1(t) \quad \text{and} \quad r(t) = r_0 + r_1(t)$$
Firing-rate models

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Stationary (constant) response

Activation function

Stationary response

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$$r_0 = f(a_0)$$
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Stationary (constant) response

Nonstationary (time-dependent) response

**Activation function**

**Impulse response**

\[
r_0 = f(a_0)
\]

\[
r_1(t) = (a_1 * h_0)(t)
\]
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**Stationary (constant) response**

**Nonstationary (time-dependent) response**

Activation function

Impulse response

Transfer function

Stationary (constant) response

Nonstationary (time-dependent) response

### Activation function

- Input rate $a_0$
- Response rate $r_0 = f(a_0)$

### Impulse response

- Input $a(t)$
- Impulse response $r(t) = (a_1 \ast h_0)(t)$

### Transfer function

- Frequency $f$
- Impulse response $R_1(f) = A_1(f)H_0(f)$
**Firing-rate models**

Decomposition of stimulus $a(t)$ and response rate $r(t)$ into constant and time-dependent components:  

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Stationary (constant) response

Nonstationary (time-dependent) response

**Activation function**

Stationary response

Nonstationary response

**Impulse response**

Stationary response

Nonstationary response

**Transfer function**

Stationary response

Nonstationary response

▶ Combination of stationary and nonstationary response properties:

$$r(t) = f\left((a * h)(t)\right) \quad \text{('linear-nonlinear model')}$$
Rate models in NEST

\[ X(t) = X_0 + \int_{t_0}^{t} a(s, X(s)) \, ds + \int_{t_0}^{t} b(s, X(s)) \, dW(s) \]

- more general model:
  - explicit time dependence
  - stochastic input: Wiener process \( W(t) \) (Brownian motion)

- second integral defined as Itô integral:

\[
\int_{t_0}^{t} Y(s) \, dW(s) := \lim_{n \to \infty} \sum_{i=1}^{n} Y_{i-1} \cdot (W_i - W_{i-1})
\]

with \( Y_i = Y(t_0 + i \cdot \frac{t-t_0}{n}) \) and \( W_i = W(t_0 + i \cdot \frac{t-t_0}{n}) \)

rather than Stratonovich integral

\[
\int_{t_0}^{t} Y(s) \circ dW(s) := \lim_{n \to \infty} \sum_{i=1}^{n} \frac{Y_{i-1} + Y_i}{2} \cdot (W_i - W_{i-1})
\]
Firing-rate models

- can create networks of rate neurons
Firing-rate models

- can create networks of rate neurons
- often difficult to relate rate model parameters to neuronal and synaptic characteristics

Examples:
- complex single-neuron dynamics
- synaptic dynamics
- strong synaptic weights

Parameters such as $f(\cdot)$ and $h(t)$ can—in principle—be obtained from:
- experiments
- mathematical analysis of specific neuron and synapse models
- simulation studies

However,:
- requires controlled stimulation of synapses
- possible only under simplifying assumptions
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Markram et al. (2004)
Firing-rate models

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Rate dynamics of LIF neurons with strong synapses
The early visual system

Sketch of the early visual pathway (Dayan & Abbott, 2001)
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The early visual system

- single ganglion-cell spikes can elicit spikes in thalamic relay cells
- transfer ratio up to 50% (Ruksenas et al., 2000; Ozaki & Kaplan, 2006)

connections between ganglion and relay cells are strong

(Cleland et al., 1971)
The early visual system

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- Remark:
  - In neocortex: wide distribution of synaptic weights
  - Considerable fraction of cortical synapses is not weak (postsynaptic potentials up to several mV)
The early visual system

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- considerable fraction of cortical synapses is **not weak** (postsynaptic potentials up to several mV)
Model and setup

- neuron model: leaky integrate-and-fire
- synapse model: $\alpha$-function shaped currents with amplitude $w$
- input: spike trains with sinusoidal firing rate $a(t) = a_0 + a_1 \sin(2\pi ft)$
- response rate fitted by $r(t) = r_0 + r_1 \sin(2\pi ft + \varphi)$

For a wide range of

- input parameters: $f$, $a_0$, $a_1$
- neuron and synapse parameters: $w$, $\tau_s$, $\tau_m$
Stationary response (constant input)

- Increase in stationary response rate $r_0$ with synaptic weight $w$
- Transfer ratio $r_0/a_0 < 1$ even for strong weights
Nonstationary response (sinusoidal input)

▶ measured transfer function

\[ H(f) = \frac{r_1(f)}{a_1} \cdot e^{i\varphi(f)} \]

well fitted by a 1st-order low-pass filter

\[ \tilde{H}(f) = \frac{\gamma}{1 + if/f_c} \]

with cutoff-frequency \( f_c \) and low-frequency gain \( \gamma \)

↷ exponential impulse response

\[ h(t) = \frac{\gamma}{\tau} \begin{cases} e^{-t/\tau} & t \geq 0 \\ 0 & t < 0 \end{cases} \]

with time constant \( \tau = 1/(2\pi f_c) \)

↷ rate dynamics

\[ r(t) = f((a \ast h)(t)) \]

equivalent to

\[ \tau \dot{u} = -u(t) + \gamma a(t), \quad r(t) = f(u(t)) \]
Nonstationary response (sinusoidal input)

- **cutoff frequency** $f_c$
  - slightly increases with synaptic weight $w$ for small to moderate weights
  - jumps to high values at critical weight $w_{\text{crit}}$

- **low-frequency gain** $\gamma$
  - increases with synaptic weight $w$
  - is fully explained by slope of activation function
Prediction for non-sinusoidal stimuli

A. $w < w_{\text{crit}}$

B. $w > w_{\text{crit}}$

C.

D.
Literature


- Hahne et al. (2017), *Integration of continuous-time dynamics in a spiking neural network simulator*, Front Neuroinform 11:34

- Nordlie et al. (2010), Rate dynamics of leaky integrate-and-fire neurons with strong synapses, Front Comput Neurosci 4:149