Biological Modeling of Neural Networks

Wulfram Gerstner
EPFL, Lausanne, Switzerland

TAs in 2020:
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COURSE WEBPAGE:
Moodle

Week 1: A first simple neuron model/neurons and mathematics
Week 2: Hodgkin-Huxley models and biophysical modeling
Week 3: Two-dimensional models and phase plane analysis
Week 4: Two-dimensional models, type I and type II models
Week 5,6: Associative Memory, Hebb rule, Hopfield
Week 7-10: Networks, cognition, learning
Week 11,12: Noise models, noisy neurons and coding
Week 13: Estimating neuron models for coding and decoding: GLM
Week x: Online video: Dendrites/Biophysics
Week xx: Density equations
LEARNING OUTCOMES

• Solve linear one-dimensional differential equations
• Analyze two-dimensional models in the phase plane
• Develop a simplified model by separation of time scales
• Analyze connected networks in the mean-field limit
• Formulate stochastic models of biological phenomena
• Formalize biological facts into mathematical models
• Prove stability and convergence
• Apply model concepts in simulations
• Predict outcome of dynamics
• Describe neuronal phenomena

Transversal skills

• Plan and carry out activities in a way which makes optimal use of available time and other resources.
• Collect data.
• Write a scientific or technical report.
Biological Modeling of Neural Networks

Written Exam (70%) + miniproject (30%)

Miniproject consists of 3 extended computer exercises, of which you have to hand in 2 (first one is easier, recommended)

Textbook:
http://neuronaldynamics.epfl.ch/

Video:
https://lcnwww.epfl.ch/gerstner/NeuronalDynamics-MOOC1.html
https://lcnwww.epfl.ch/gerstner/NeuronalDynamics-MOOC2.html
Welcome back to EPFL!!

Today: Course in BS 170

BS 170 for the first week, but
INM 200 for the rest of the semester
Week 1 – neurons and mathematics: a first simple neuron model

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Reading for week 1: NEURONAL DYNAMICS
- Ch. 1 (without 1.3.6 and 1.4)
- Ch. 5 (without 5.3.1)

1.1 Neurons and Synapses: Overview
1.2 The Passive Membrane
  - Linear circuit
  - Dirac delta-function
1.3 Leaky Integrate-and-Fire Model
1.4 Generalized Integrate-and-Fire Model
1.5. Quality of Integrate-and-Fire Models
Biological Modeling of Neural Networks

1.1 Neurons and Synapses: Overview

1.2 The Passive Membrane
- Linear circuit
- Dirac delta-function

1.3 Leaky Integrate-and-Fire Model

1.4 Generalized Integrate-and-Fire Model

1.5 Quality of Integrate-and-Fire Models
How do we recognize things?
Models of cognition
Weeks 5-10
10,000 neurons
3 km of wire
10,000 neurons
3 km of wire

Signal:
action potential (spike)

Ramon y Cajal
Neuronal Dynamics – 1.1. Neurons and Synapses/Overview

Hodgkin-Huxley type models: Biophysics, molecules, ions

(week 2)

Signal: action potential (spike)

-70mV

Ions/proteins: Na⁺, K⁺, Ca²⁺
Neuronal Dynamics – 1.1. Neurons and Synapses/Overview

Signal:
action potential (spike)
Integrate-and-fire models: Formal/phenomenological (week 1 and week 7-9)

- spikes are events
- triggered at threshold
- spike/reset/refractoriness
Noise and variability in integrate-and-fire models

Output
- spikes are rare events
- triggered at threshold

Subthreshold regime:
- trajectory of potential shows fluctuations

Output
- spikes are rare events
- triggered at threshold

Subthreshold regime:
- trajectory of potential shows fluctuations

Random spike arrival
Neuronal Dynamics – membrane potential fluctuations

Spontaneous activity *in vivo*

What is noise?
What is the neural code?

(week 11-13)

awake mouse, cortex, freely whisking,

Lab of Prof. C. Petersen, EPFL

_Crochet et al., 2011_
A cortical neuron sends out signals which are called:

- [ ] action potentials
- [ ] spikes
- [ ] postsynaptic potential

In an integrate-and-fire model, when the voltage hits the threshold:

- [ ] the neuron fires a spike
- [ ] the neuron can enter a state of refractoriness
- [ ] the voltage is reset
- [ ] the neuron explodes

The dendrite is a part of the neuron:

- [ ] where synapses are located
- [ ] which collects signals from other neurons
- [ ] along which spikes are sent to other neurons

In vivo, a typical cortical neuron exhibits:

- [ ] rare output spikes
- [ ] regular firing activity
- [ ] a fluctuating membrane potential

Multiple answers possible!
Biological Modeling of Neural Networks

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Biological modeling of Neural Networks

Course: Monday : 9:15-13:00

A typical Monday:
1st lecture 9:15-9:50
  1st exercise 9:50-10:00
2nd lecture 10:15-10:35
  2nd exercise 10:35-11:00
3rd lecture 11:15 – 11:40
  3rd exercise 11:45-12:40

Course of 4 credits = 6 hours of work per week
  4 ‘contact’ + 2 homework

have your laptop with you

paper and pencil

paper and pencil

paper and pencil

OR interactive toy examples on computer

moodle.epfl.ch
Biological Modeling of Neural Networks

Week 1 – part 2: The Passive Membrane

1.1 Neurons and Synapses:
   ✔ Overview

1.2 The Passive Membrane
   - Linear circuit
   - Dirac delta-function

1.3 Leaky Integrate-and-Fire Model

1.4 Generalized Integrate-and-Fire Model

1.5. Quality of Integrate-and-Fire Models

Week 1 – neurons and mathematics:
a first simple neuron model

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Neuronal Dynamics – 1.2. The passive membrane

Integrate-and-fire model
Neuronal Dynamics – 1.2. The passive membrane

Subthreshold regime
- linear
- passive membrane
- RC circuit
Neuronal Dynamics – 1.2. The passive membrane

Time-dependent input

Math development: Derive equation (Blackboard)
Passive Membrane Model

\[ I(t) \]

\[ u \]
Passive Membrane Model

\[ \tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t) \]

\[ \tau \cdot \frac{d}{dt} V = -V + RI(t); \quad V = (u - u_{rest}) \]
Passive Membrane Model

\[ \tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t) \]

\[ \tau \cdot \frac{d}{dt} V = -V + RI(t); \quad V = (u - u_{rest}) \]
Passive Membrane Model/Linear differential equation

$$\tau \cdot \frac{d}{dt} V = -V + RI(t);$$

Free solution: exponential decay
Neuronal Dynamics – Exercises NOW

Start Exerc. at 9:47. Next lecture at 10:15

Step current input:

Pulse current input:

arbitrary current input:

Calculate the voltage, for the 3 input currents

\[
\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)
\]

\[
\tau \cdot \frac{d}{dt} V = -V + RI(t); \quad V = (u - u_{rest})
\]
The voltage across a passive membrane can be described by the equation

$$\tau \frac{du}{dt} = -(u - u_{\text{rest}}) + RI(t). \quad (1)$$

1.1 Step current

Consider a current $I(t) = 0$ for $t < t_0$ and $I(t) = I_0$ for $t > t_0$. Calculate the voltage $u(t)$, given that the neuron is at rest at time $t_0$. (Hint: Instead of solving the differential equation explicitly, try to construct the response to the step current along the lines: What is the value of $u(t)$ for $t < t_0$? What is the asymptotic value of $u(t)$ for $t \gg t_0$? What is the functional form and time scale of the transition?)

1.2 Pulse current

Consider a current pulse

$$I(t) = \begin{cases} 0 & \text{for } t < t_0 \text{ and } t > t_0 + \Delta, \\ q/\Delta & \text{for } t_0 < t < t_0 + \Delta, \end{cases} \quad (2)$$

where $\Delta$ is a short time and $q$ is the total electrical charge.

Consider first $\Delta = 0.1\tau$, and then $\Delta = 0.05\tau$, $\Delta = 0.025\tau$. Sketch the input current pulse and the voltage response. What happens in the limit $\Delta \to 0$? (Hint: Use $e^{-x} \approx 1 - x$ for $x \ll 1$.)

1.3 Delta function

The Dirac delta function can be defined by the limit of a short pulse:

$$\delta(t - t_0) = \lim_{\Delta \to 0} f_\Delta(t) \quad \text{where} \quad f_\Delta(t) = \begin{cases} 1/\Delta & \text{for } t_0 - \Delta < t < t_0 + \Delta, \\ 0 & \text{otherwise}. \end{cases} \quad (3)$$

Convince yourself that the integral $\int_{t_1}^{t_2} \delta(t - t_0) \, dt$ is equal to one if $t_1 \leq t_0 < t_2$ and vanishes otherwise.

Express $I(t)$ in Eq. 1 using the $\delta$-function for the case that an extremely short current pulse arrives at time $t_0$. Pay attention to the units!

1.4 General solution

Assuming that before a given time $t_0$ the current is null and the membrane potential is at rest, derive the general solution to Eq. (1) for arbitrary $I(t)$. Express $I(t)$ in Eq. 1 using the $\delta$-function for the case that an extremely short current pulse arrives at time $t_0$. Pay attention to the units!
Passive Membrane Model – exercise 1 now

Step current input:

\[ \tau \cdot \frac{d}{dt} u = - (u - u_{rest}) + RI(t) \]

impulse reception:

impulse response function
\[ \tau \cdot \frac{d}{dt} u = -(u - u_{\text{rest}}) + RI(t) \]
Pulse input – charge – delta-function

\[ u(t) \]

\[ I(t) \]

\[ I(t) = q \cdot \delta(t - t_0) \]

Pulse current input
Dirac delta-function

\[ I(t) = q \cdot \delta(t - t_0) \]

\[ \int_{t_0-a}^{t_0+a} \delta(t - t_0) \, dt = 1 \]

\[ f(t_0) = \int_{t_0-a}^{t_0+a} f(t) \delta(t - t_0) \, dt \]
Neuronal Dynamics – Solution of Ex. 1 – arbitrary input

\[ \tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t) \]

Arbitrary input
\[ u(t) = u_{rest} + \int_{-\infty}^{t} \frac{1}{c} e^{-\frac{(t-t')}{\tau}} I(t') dt' \]

Single pulse
\[ \Delta u(t) = \frac{q}{c} e^{-\frac{(t-t_0)}{\tau}} \]

you need to know the solutions of linear differential equations!
Passive membrane, linear differential equation

\[ \tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t) \]
Passive membrane, linear differential equation

If you have difficulties, watch lecture 1.2detour.

Three prerequisites:
- Analysis 1-3
- Probability/Statistics
- Differential Equations or Physics 1-3 or Electrical Circuits

https://lcnwww.epfl.ch/gerstner/NeuronalDynamics-MOOC1.html
LEARNING OUTCOMES

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• Predict outcome of dynamics
• Describe neuronal phenomena

Transversal skills

• Plan and carry out activities in a way which makes optimal use of available time and other resources.
• Collect data.
• Write a scientific or technical report.

Look at samples of past exams

Use a textbook, (Use video lectures) don’t use slides (only)

miniproject
Biological Modeling of Neural Networks

Written Exam (70%) + miniproject (30%)

Miniproject consists of 3 extended computer exercises, of which you have to hand in 2

Textbook:

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Video:

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Questions?

This is **not** a course on

Deep learning or Artificial neural networks

→ Deep Learning, master EE, (*Fleuret*)
→ Artificial NN, master CS, (*Gerstner*)
Summary of Section 1.1 and 1.2.
Neurons emit spikes (action potentials) which are short standardized events in the form of voltage pulses. Spikes are emitted at the firing threshold. Below the threshold the electrical behavior is often well characterized by a linear differential equation (math) corresponding to an RC circuit (electricity) or to a passive membrane (biology). We will often in this class walk along the triangle that connects math with electricity and biology. This class has a strong focus on mathematical modeling of the biological phenomena. Differential equations, Dirac-delta pulses, and their link to biology are important concepts. The time constant of an RC circuit is $\tau=RC$. 
1.1 Neurons and Synapses:
Overview

1.2 The Passive Membrane
- Linear circuit
- Dirac delta-function
- Detour: solution of 1-dim linear differential equation

1.3 Leaky Integrate-and-Fire Model

1.4 Generalized Integrate-and-Fire Model

1.5 Quality of Integrate-and-Fire Models
Neuronal Dynamics – 1.3 Leaky Integrate-and-Fire Model

\[ \tau \cdot \frac{du}{dt} = -(u - u_{\text{rest}}) + RI(t) \]
Simple Integrate-and-Fire Model:
- passive membrane
- + threshold

Leaky Integrate-and-Fire Model:
- output spikes are events
- generated at threshold
- after spike: reset/refractoriness

Input spike causes an EPSP = excitatory postsynaptic potential

Spike emission
Neuronal Dynamics – 1.3 Leaky Integrate-and-Fire Model

\[ \tau \cdot \frac{d}{dt} u = -(u - u_{\text{rest}}) + RI(t) \]

\[ u(t) = \mathcal{G} \Rightarrow \text{Fire+reset} \quad u \rightarrow u_r \]

linear

threshold

Spike emission

reset
Neuronal Dynamics – 1.3 Leaky Integrate-and-Fire Model

-Time-dependent input

-Math development: Response to step current

- spikes are events
- triggered at threshold
- spike/reset/refractoriness
Consider the linear differential equation
\[ \tau \cdot \frac{d}{dt} x = -x + x_c \]
with initial condition \[ at \ t = 0 : x = 0 \]

The solution for \( t > 0 \) is

(i) \[ x(t) = x_c \exp(t / \tau) \]

(ii) \[ x(t) = x_c \exp(-t / \tau) \]

(iii) \[ x(t) = x_c [1 - \exp(-t / \tau)] \]

(iv) \[ x(t) = 0.5x_c [1 + \exp(-t / \tau)] \]

You will have to use the results: response to constant input/step input again and again

Week 1 – Quiz 2.

Take 90 seconds:
Neuronal Dynamics – 1.3 Leaky Integrate-and-Fire Model

CONSTANT input/step input
Leaky Integrate-and-Fire Model (LIF)

\[ \tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI_0 \]

If \( u(t) = \mathcal{I} \Rightarrow u \rightarrow u_r \)

Repetitive, current \( I_0 \)

Repetitive, current \( I_1 > I_0 \)

‘Firing’

frequency-current
relation

f-I curve
Neuronal Dynamics – First week, Exercise 2

\[ \tau \cdot \frac{du}{dt} = -(u - u_{\text{rest}}) + RI(t) \]

frequency-current relation

f-l curve
Exercise!
Calculate the interspike interval $T$ for constant input $I$.
Firing rate is $f=1/T$.
Write $f$ as a function of $I$.
What is the frequency-current curve $f=g(I)$ of the LIF?

LIF \[ \tau \cdot \frac{du}{dt} = -(u - u_{rest}) + RI_0 \]

If firing: \[ u \rightarrow u_r \]

assume: \[ u_r = u_{rest} \]

repetitive

Start Exerc. at 10:53.
Next lecture at 11:15
Exercise 2: Integrate-and-fire model

Consider the model of Eq. (1) with a threshold at \( u = \vartheta > u_{\text{rest}} \). If the membrane potential reaches the threshold, the neuron is said to fire and the membrane potential is reset to \( u_{\text{rest}} \). The injected current is a step of magnitude \( I_0 \):

\[
I(t) = \begin{cases} 
0 & t \leq t_0 \\
I_0 & t > t_0 
\end{cases}
\]

2.1 What is the minimal current to reach the threshold, assuming \( u(t = 0) = u_{\text{rest}} \)?

2.2 At what time will the voltage first reach the threshold?

2.3 Calculate the firing frequency \( f \) as a function of \( I_0 \).

The function \( g(I_0) \) which gives the firing frequency as a function of the constant applied current is called gain function.
Summary of Section 1.3.
The leaky integrate-and-fire neuron model is the combination of a passive membrane (linear differential equation) with a threshold. The moment when the potential hits the threshold defines the firing time of a spike. Immediately after firing the voltage is reset to a lower value (not necessarily to the resting potential).

For the leaky integrate-and-fire model, the gain function (frequency of firing for constant input, as a function of input strength) can be calculated analytically. The firing frequency decreases with decreasing input. If the constant input is below a critical value no firing can occur. This value defines the rheobase current threshold. For the leaky integrate-and-fire model the rheobase current threshold can be predicted from the voltage threshold and the model parameters R and C.
Week 1 – part 4: Generalized Integrate-and-Fire Model

Biological Modeling of Neural Networks

Week 1 – neurons and mathematics: a first simple neuron model

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1.1 Neurons and Synapses: Overview
1.2 The Passive Membrane
  - Linear circuit
  - Dirac delta-function
1.3 Leaky Integrate-and-Fire Model
1.4 Generalized Integrate-and-Fire Model
1.5. Quality of Integrate-and-Fire Models
Neuronal Dynamics – 1.4. Generalized Integrate-and-Fire Model

Integrate-and-fire model

LIF: linear + threshold
Neuronal Dynamics – 1.4. Leaky Integrate-and-Fire revisited

LIF

\[ \tau \frac{du}{dt} = -(u - u_{\text{rest}}) + RI(t) \]

If firing:
\[ u \rightarrow u_{r} \]

If \( I = 0 \):

If \( I > 0 \):

resting

repetitive
Neuronal Dynamics – 1.4. Nonlinear Integrate-and-Fire

**LIF**

\[
\tau \cdot \frac{du}{dt} = -(u - u_{rest}) + RI(t)
\]

**NLIF**

\[
\tau \cdot \frac{du}{dt} = F(u) + RI(t)
\]

If firing:

\[
u \rightarrow u_{reset}\]
Neuronal Dynamics – 1.4. Nonlinear Integrate-and-Fire

Nonlinear Integrate-and-Fire

NLIF

$$\tau \cdot \frac{du}{dt} = F(u) + RI(t)$$

firing: \( u(t) = \theta \Rightarrow u \rightarrow u_r \)
Nonlinear Integrate-and-fire Model

\[ \tau \cdot \frac{d}{dt} u = F(u) + RI(t) \]

\[ u(t) = \mathcal{I}_r \Rightarrow \text{Fire+reset threshold} \]
Nonlinear Integrate-and-fire Model

\[ \tau \cdot \frac{du}{dt} = F(u) + RI(t) \]

NONlinear

\[ u(t) = G_r \Rightarrow \text{Fire+reset threshold} \]
Nonlinear Integrate-and-fire Model

\[ \frac{d}{dt} u = F(u) + R I(t) \]

\[ u(t) = \mathcal{G}_r \implies \text{Fire+reset} \]

\[ F(u) = c_2 (u - c_1)^2 + c_0 \]

exponential I&F:

\[ F(u) = -(u - u_{rest}) + c_0 \exp(u - \mathcal{G}) \]
Nonlinear Integrate-and-fire Model

\[ \tau \cdot \frac{d}{dt} u = -(u-u_{rest}) + RI(t) \]

\[ u(t) = \mathcal{I}_r \Rightarrow \text{Fire+reset threshold} \]

exponential I&F:

\[ F(u) = -(u-u_{rest}) + c_0 \exp(u - \mathcal{I}) \]
Nonlinear Integrate-and-fire Model

Where is the firing threshold?

\[ \tau \cdot \frac{d}{dt} u = F(u) + RI(t) \]
Summary of Section 1.4.
Nonlinear integrate-and-fire models with a nonlinear function $f(u)$ of the voltage $u$ are excellent models of spiking behavior. The exponential integrate-and-fire (EIF) model is linear for low voltage, but combines it with an exponential nonlinearity for large voltages. The quadratic integrate-and-fire (QIF) is symmetric for low and large voltages. The LIF has a linear function $f(u) = u - u_{rest}$. All generalized integrate-and-fire models have a voltage reset after a spike. For constant input, the zero-crossings of the function $f(u)$ define stationary states.

We distinguish two important stimulation paradigms: (i) stimulation with short current pulses (Dirac delta pulses) – such pulses correspond to an initial condition on the voltage axis; (ii) stimulation with constant current – such stimuli correspond to a vertical shift of the function $f(u)$. We find in both EIF and QIF that the minimal current for spike initiation depends on the stimulation protocol.
Week 1 – part 5: How good are Integrate-and-Fire Model?

Biological Modeling of Neural Networks

Week 1 – neurons and mathematics: a first simple neuron model

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- 1.1 Neurons and Synapses:
  Overview
- 1.2 The Passive Membrane
  - Linear circuit
  - Dirac delta-function
- 1.3 Leaky Integrate-and-Fire Model
- 1.4 Generalized Integrate-and-Fire Model
  - where is the firing threshold?
- 1.5. Quality of Integrate-and-Fire Models
  - Neuron models and experiments
Neuronal Dynamics – 1.5. How good are integrate-and-fire models?

Can we compare neuron models with experimental data?

\[ \tau \cdot \frac{d}{dt} u = F(u) + R I(t) \]

if \( u = \varphi \), then \( u \to u_r \)
1.5. How good are integrate-and-fire models?

What is a good neuron model?

Can we compare neuron models with experimental data?
Neuronal Dynamics – 1.5. How good are integrate-and-fire models?

$I(t)$

Integrate-and-fire model

Spike
Nonlinear Integrate-and-fire Model

\[ \tau \cdot \frac{d}{dt} u = F(u) + RI(t) \]

\[ u(t) = \mathcal{I} \Rightarrow \text{Fire+reset} \]

Can we measure the function \( F(u) \)?

Quadratic I&F:

\[ F(u) = c_2 (u - c_1)^2 + c_0 \]

Exponential I&F:

\[ F(u) = -(u - u_{\text{rest}}) + c_0 \exp(u - \mathcal{I}) \]
1.5. How good are integrate-and-fire models?

\[
\frac{du}{dt} - \frac{1}{C} I(t) = F(u) \frac{1}{\tau}
\]

\[
F(u) = -(u - u_{\text{rest}}) + \Delta \exp \left( \frac{u - \theta}{\Delta} \right)
\]

Badel et al., J. Neurophysiology 2008
Neuronal Dynamics – 1.5. How good are integrate-and-fire models?
Nonlinear integrate-and-fire models are good

Mathematical description → prediction

Need to add
- adaptation
- noise
- dendrites/synapses

Computer exercises: Python
Biological Modeling of Neural Networks

http://neuronaldynamics.epfl.ch/

Textbook:

Lecture today:
- Chapter 1
- Chapter 5

Exercises today:
- Install PYTHON for Computer Exercises
- Exercise 3, on sheet

Videos (for today: ‘week 1’):
\[
\tau \cdot \frac{d}{dt} u = F(u) + RI(t)
\]

I=0

Homework!
Exercise 3: Integrate-and-fire models

The general form of an integrate-and-fire model is

$$\frac{du}{dt} = F(u) + \frac{RI(t)}{\tau}$$  \hspace{1cm} (4)$$

where $F(u)$ is an appropriate function and $I(t)$ is the injected current. Three popular choices for the function $F$ are the following (see Fig. 1):

Leaky integrate-and-fire $F(u) = -\frac{u - u_{\text{rest}}}{\tau}$

Quadratic integrate-and-fire $F(u) = k \frac{(u - u_{\text{rest}})(u - u_{\text{th}})}{\tau}$

Exponential integrate-and-fire $F(u) = -\frac{(u - u_{\text{rest}}) + \Delta e^{\frac{u_{\text{th}} - u_{\text{rest}}}{\Delta}}}{\tau}$

3.1 Identify the resting potential $u_{\text{rest}}$ and the spike threshold $u_{\text{th}}$ in Fig. 1.

3.2 Consider three different values $u_1$, $u_2$, and $u_3$ for the voltage such that (i) $u_1$ is below $u_{\text{rest}}$ (the resting potential), (ii) $u_2$ is between $u_{\text{rest}}$ and $u_{\text{th}}$ (the spike threshold), and (iii) $u_3$ is above $u_{\text{th}}$ (see Fig. 1). For the three models described above, determine qualitatively the evolution of $u(t)$ when started at $u_1$, $u_2$, and $u_3$, assuming that the external input $I(t) = 0$.

- For $u(t = 0) = u_1$, the voltage increases/decreases slowly/rapidly.
- For $u(t = 0) = u_2$, ........................................
- For $u(t = 0) = u_3$, ........................................

3.3 Why is $u_{\text{rest}}$ called the resting potential? What is the role of $u_{\text{th}}$?

3.4 Consider the two voltage traces shown in Fig. 2(b) (top) in response to a step current (bottom). Using the graphs in Fig. 2(a), determine which of the two models was used to generate each trace.
Summary of Section 1.5.
The exponential integrate-and-fire (EIF) model is an excellent model of spike initiation in neurons. [And better than the QIF which is ‘too symmetric’].
The quality of a neuron model can be measured by predicting spikes for new input that was used to optimize the model parameters. Further improvements of generalized integrate-and-fire models are possible and involve (i) noise in the spike generation process and (ii) adaptation.
First week – References and Suggested Reading


Selected references to linear and nonlinear integrate-and-fire models
First week

THE END (of main lecture)

MATH DETOUR SLIDES
(for online VIDEO)
Neuronal Dynamics: Computational Neuroscience of Single Neurons

Week 1 – neurons and mathematics: a first simple neuron model

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EPFL, Lausanne, Switzerland

Week 1 – part 2: Detour/Linear differential equation

✓ 1.1 Neurons and Synapses:
   Overview

✓ 1.2 The Passive Membrane
   - Linear circuit
   - Dirac delta-function
   - Detour: solution of 1-dim linear differential equation

1.3 Leaky Integrate-and-Fire Model
1.4 Generalized Integrate-and-Fire Model
1.5 Quality of Integrate-and-Fire Models
Neuronal Dynamics – 1.2Detour – Linear Differential Eq.

\[
\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)
\]
Neuronal Dynamics – 1.2 Detour – Linear Differential Eq.

\[ \tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t) \]

Math development: Response to step current
Neuronal Dynamics – 1.2 Detour – Step current input

\[ \tau \cdot \frac{du}{dt} = -(u - u_{\text{rest}}) + RI(t) \]

\[ u(t) \]

\[ I(t) \]

\[ t \]
Neuronal Dynamics – 1.2 Detour – Short pulse input

\[ u(t) = u_{\text{rest}} + RI_0 \left[ 1 - e^{-(t-t_0)/\tau} \right] \]

short pulse: \((t-t_0) \ll \tau\)

**Math development:**
Response to short current pulse

\[ \tau \cdot \frac{d}{dt} u = -(u - u_{\text{rest}}) + RI(t) \]

Math development:
Response to short current pulse
Neuronal Dynamics – 1.2 Detour – Short pulse input

\[ u(t) = u_{\text{rest}} + RI_0 \left[ 1 - e^{-(t-t_0)/\tau} \right] \]

short pulse: \( (t-t_0) \ll \tau \)

\[ \tau \frac{d}{dt} u = -(u - u_{\text{rest}}) + RI(t) \]

\[ u(t) = u_{\text{rest}} + \frac{q}{C} e^{-(t-t_0)/\tau} \]

\[ I(t) = q \cdot \delta(t-t_0) \]
**Neuronal Dynamics – 1.2 Detour – arbitrary input**

Single pulse

\[ u(t) = u_{rest} + \frac{q}{C} e^{-(t-t_0)/\tau} \]

Multiple pulses:

\[ u(t) = u_{rest} + \int_{-\infty}^{t} \frac{1}{C} e^{-(t-t')/\tau} I(t') dt' \]

\[ \tau \frac{du}{dt} = -(u - u_{rest}) + RI(t) \]
Neuronal Dynamics – 1.2 Detour – Greens function

Single pulse
\[ \Delta u(t) = q \frac{1}{C} e^{-(t-t_0)/\tau} \]

Multiple pulses:
\[ u(t) = u_{\text{rest}} + [u(t_0) - u_{\text{rest}}] + \int_{t_0}^{t} \frac{1}{C} e^{-(t-t')/\tau} I(t')dt' \]

\[ \tau \cdot \frac{d}{dt} u = -(u - u_{\text{rest}}) + RI(t) \]

Impulse response function,
Green’s function
Neuronal Dynamics – 1.2 Detour – arbitrary input

\[
\tau \cdot \frac{d}{dt} u = -(u - u_{\text{rest}}) + RI(t)
\]

Arbitrary input
\[
u(t) = u_{\text{rest}} + \int_{-\infty}^{t} \frac{1}{c} e^{-(t-t')/\tau} I(t')dt'
\]

Single pulse
\[
\Delta u(t) = \frac{q}{c} e^{-(t-t_0)/\tau}
\]

If you don’t feel at ease yet, spend 10 minutes on these mathematical exercises
And quiz 2 in week 1.

you need to know the solutions of linear differential equations!