Biological Modeling of Neural Networks

Wulfram Gerstner

EPFL, Lausanne, Switzerland

TA in 2018:

Vasiliki Liakoni

Chiara Gastaldi

Bernd Illing

new Mooc,
Inverted classroom

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**

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

Look at samples of past exams

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.

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

miniproject

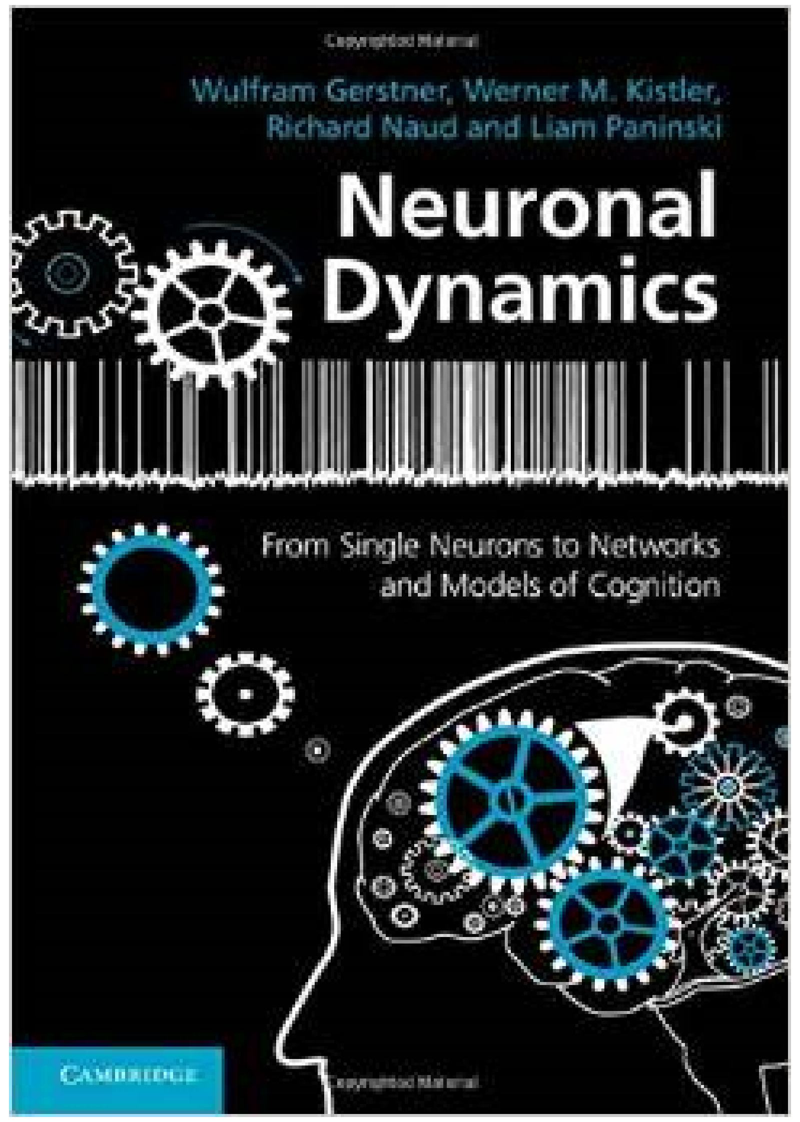
Biological Modeling of Neural Networks

Written Exam (2/3)
+ miniproject (1/3)

Miniproject consists of
three extended computer exercises

http://neuronaldynamics.epfl.ch/

Textbook:



Videos (for half the material):

http://lcn.epfl.ch/~gerstner/NeuronalDynamics-MOOC1.html

+ new mooc lectures as we go along

Welcome back to EPFL!!

Biological Modeling of Neural Networks

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

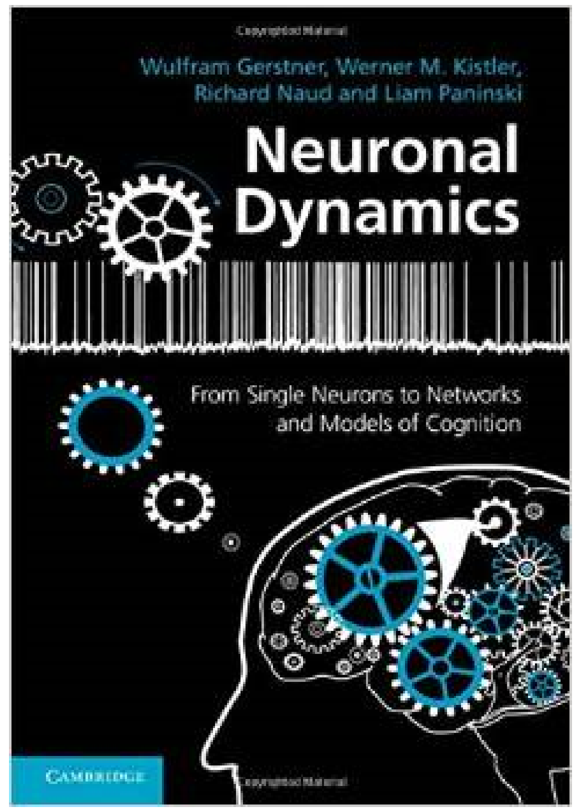
Week 1 – neurons and mathematics: a first simple neuron model

Wulfram Gerstner

EPFL, Lausanne, Switzerland

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

Cambridge Univ. Press



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

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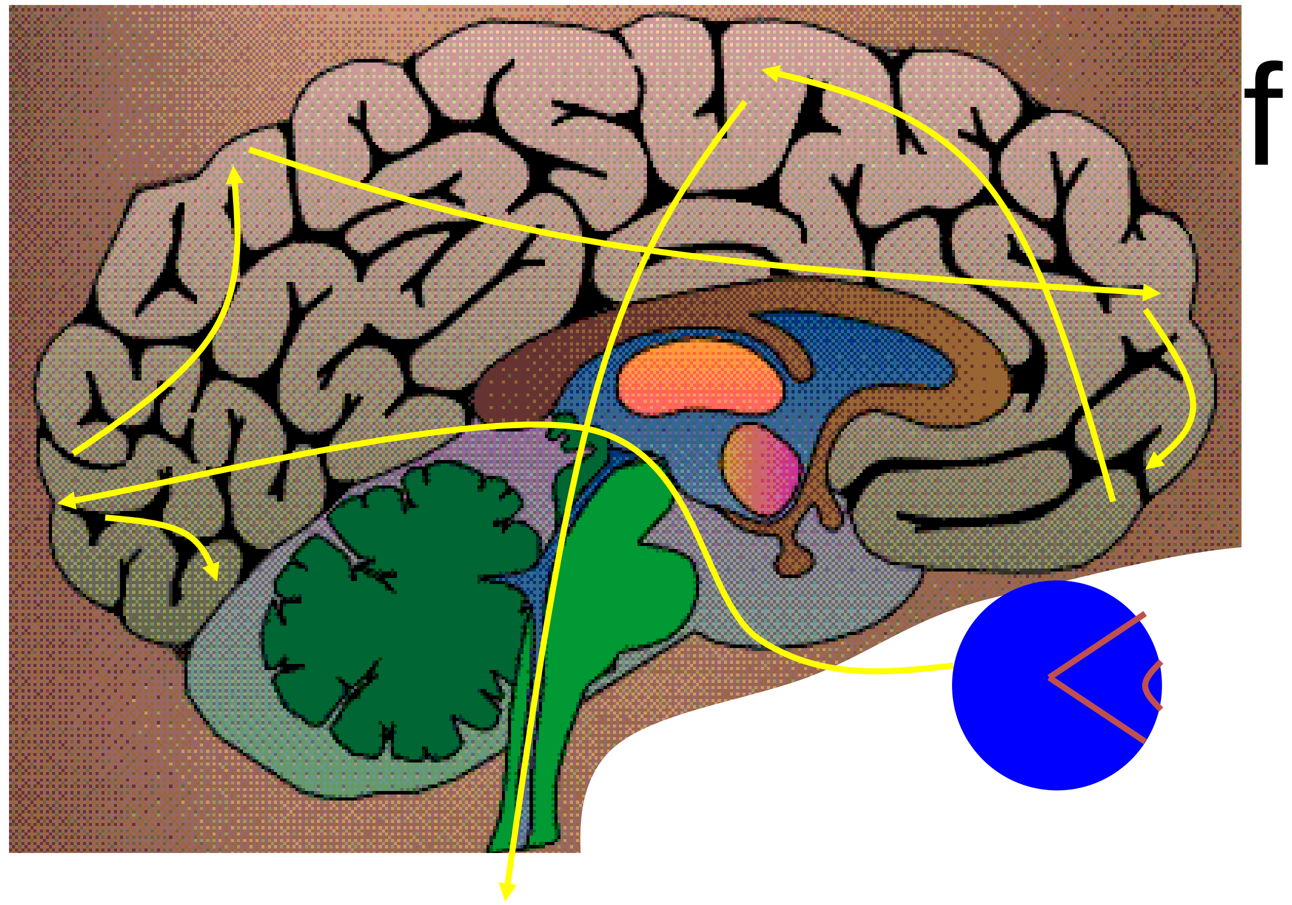
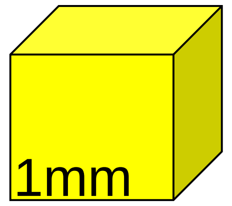
Neuronal Dynamics – 1.1. Neurons and Synapses/Overview

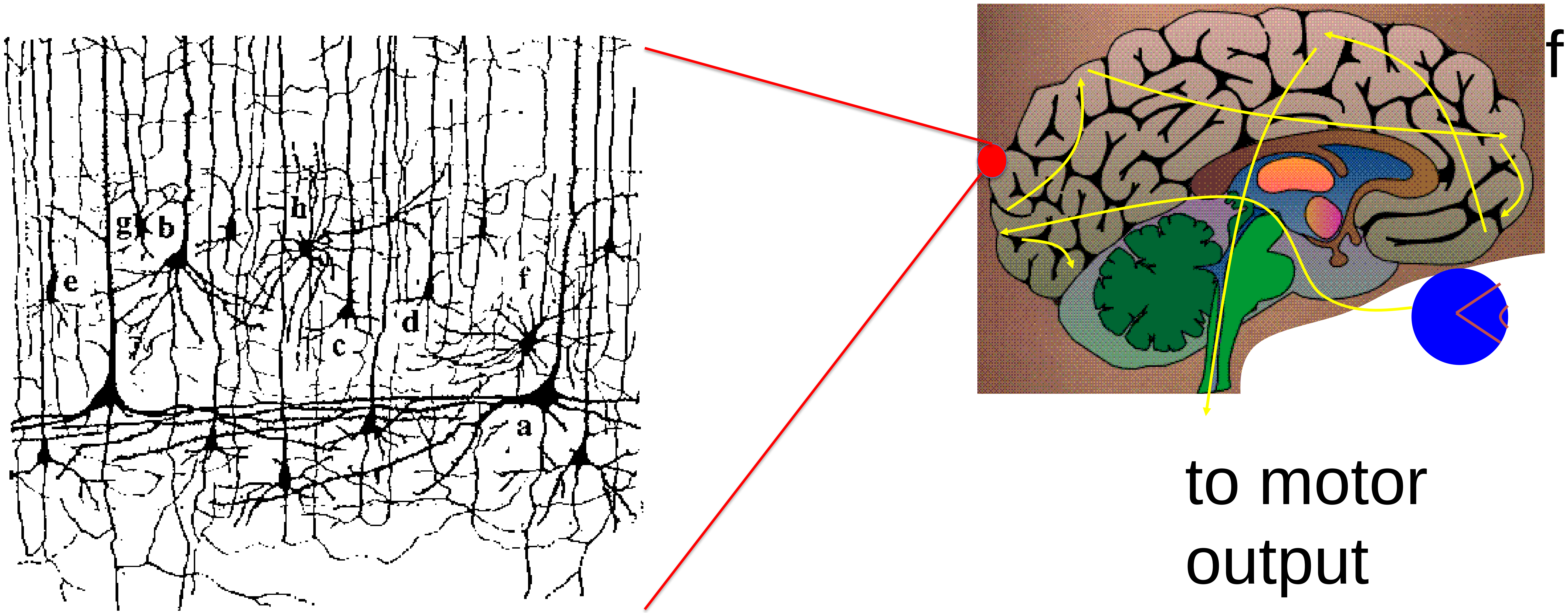
How do we recognize things?
Models of cognition
Weeks 10-14



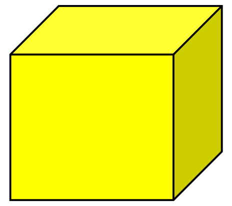
Neuronal Dynamics – 1.1. Neurons and Synapses/Overview



10 000 neurons
3 km of wire

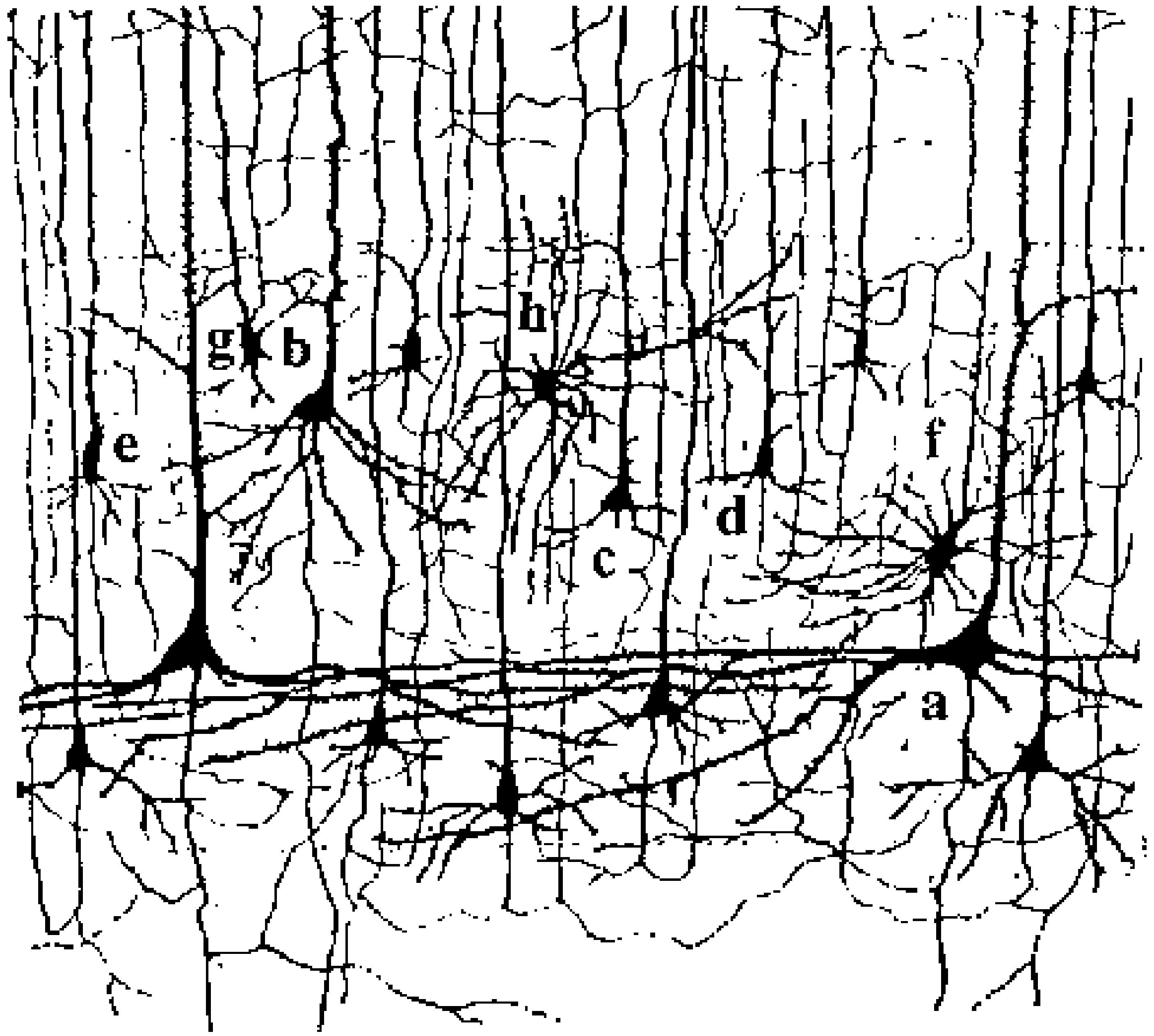


Neuronal Dynamics – 1.1. Neurons and Synapses/Overview



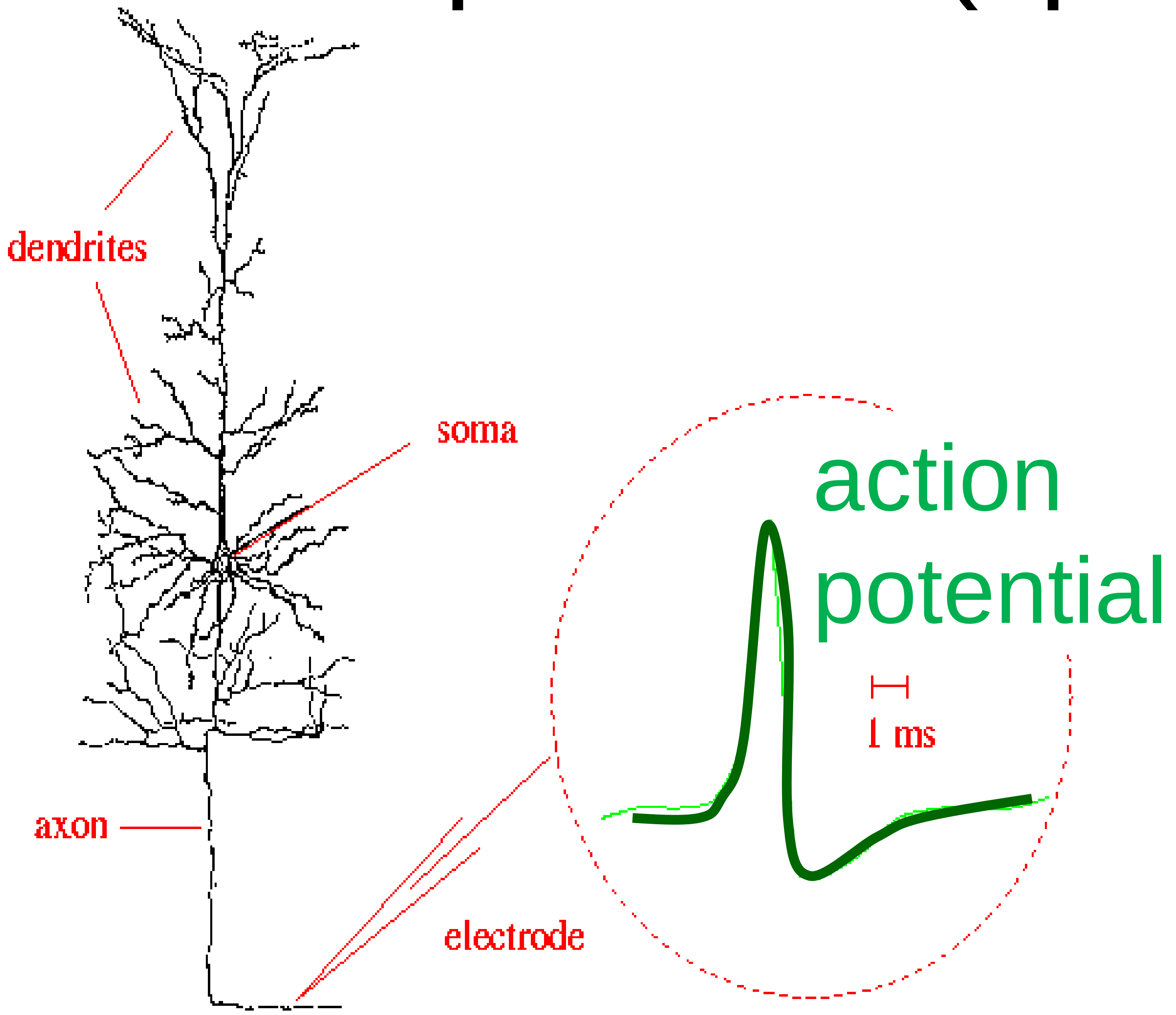
1mm

10 000 neurons
3 km of wire



Ramon y Cajal

Signal:
action potential (spike)



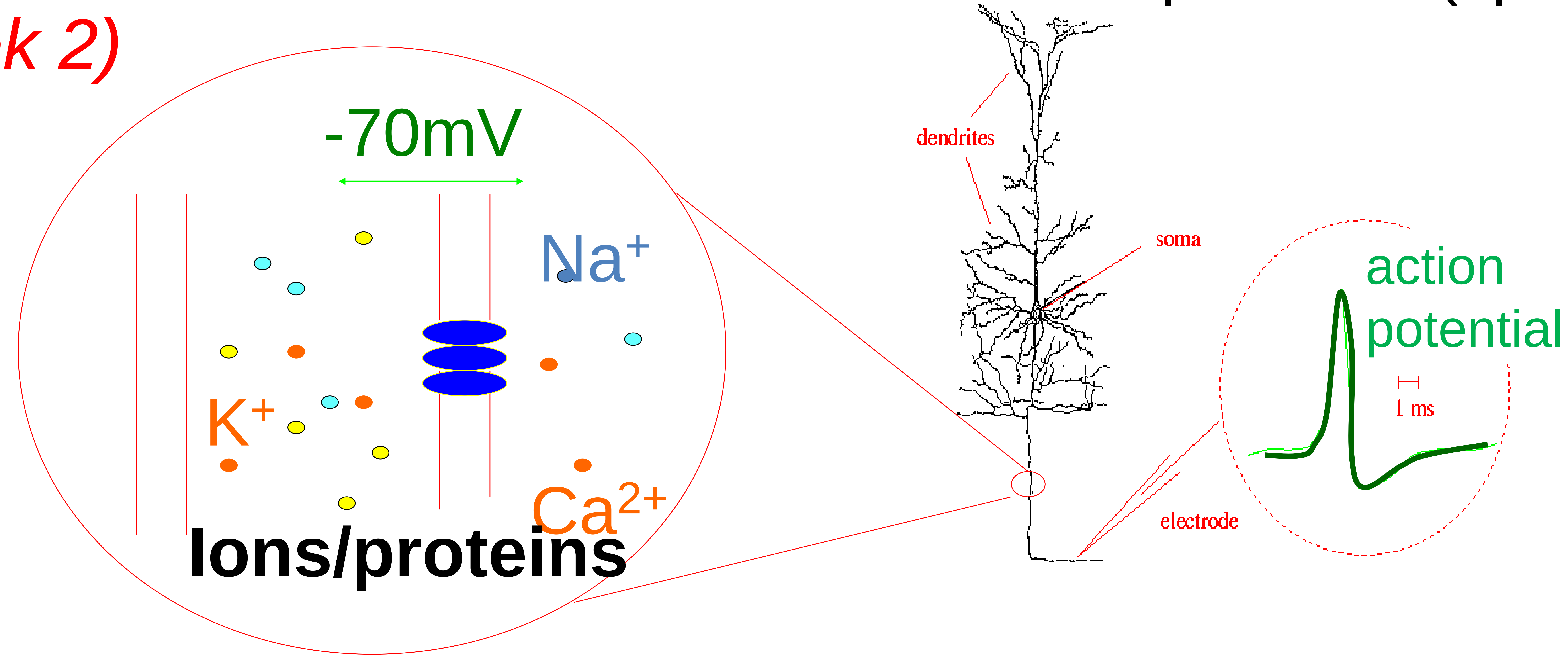
Neuronal Dynamics – 1.1. Neurons and Synapses/Overview

Hodgkin-Huxley type models:

Biophysics, molecules, ions

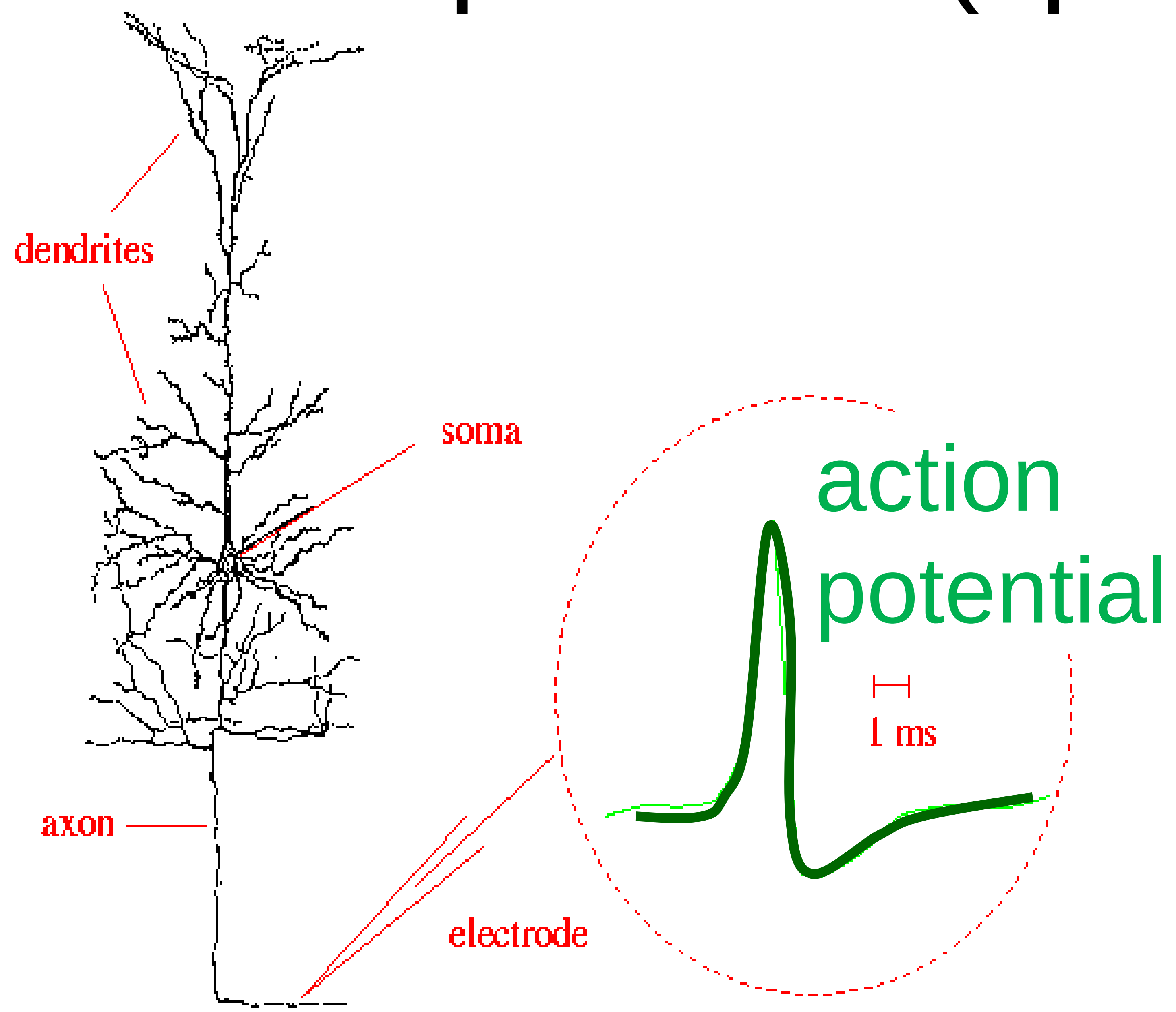
(week 2)

Signal:
action potential (spike)



Neuronal Dynamics – 1.1. Neurons and Synapses/Overview

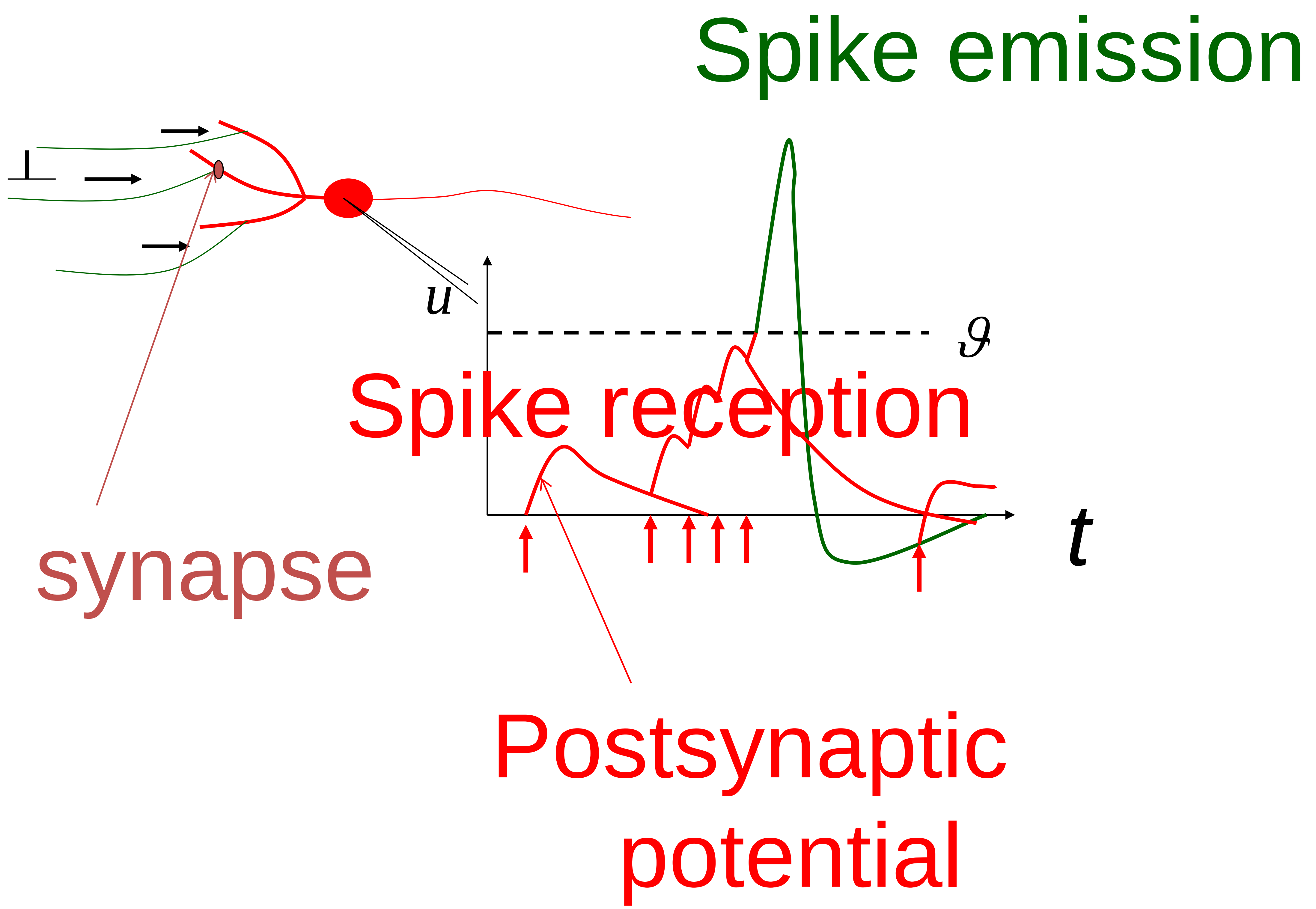
Signal:
action potential (spike)



Integrate-and-fire models:

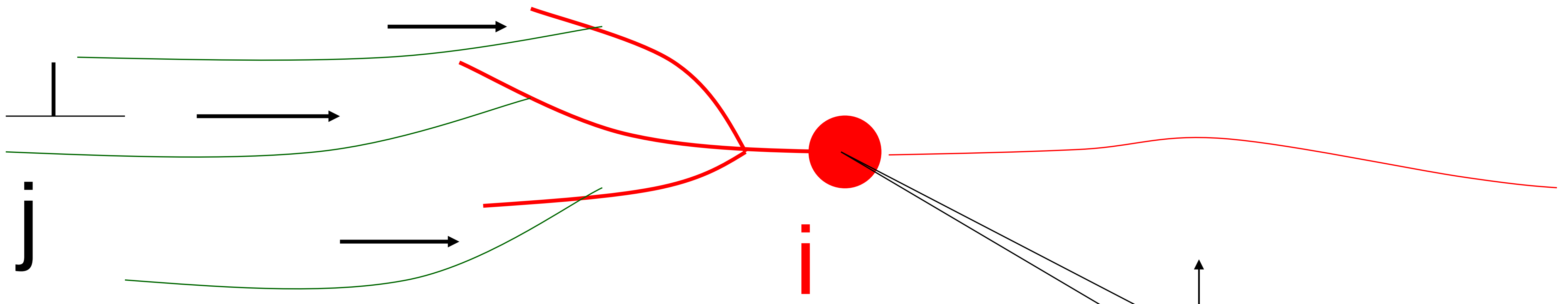
Formal/phenomenological

(week 1 and week 7-9)



-spikes are events
-triggered at threshold
-spike/reset/refractoriness

Noise and variability in integrate-and-fire models



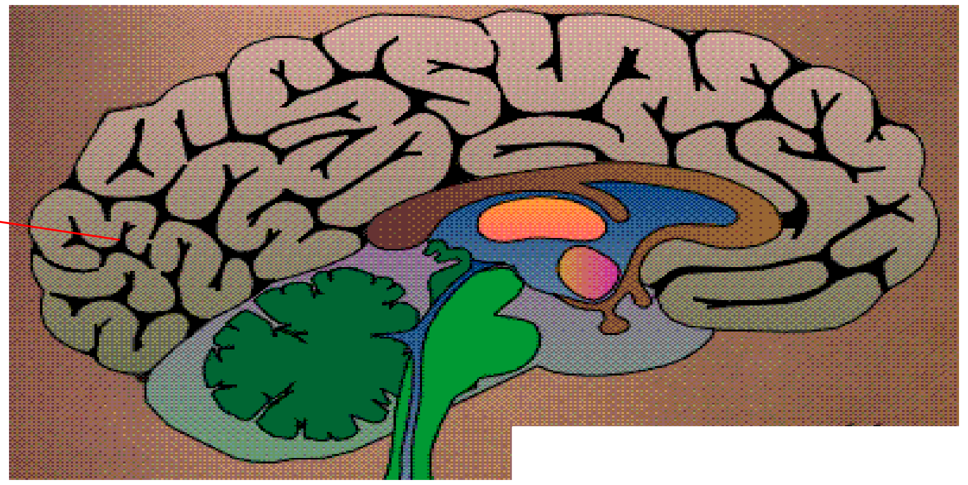
Output
-spikes are **rare** events
-triggered at threshold

Subthreshold regime:
-trajectory of potential shows fluctuations

Neuronal Dynamics – membrane potential fluctuations

Spontaneous activity *in vivo*

electrode



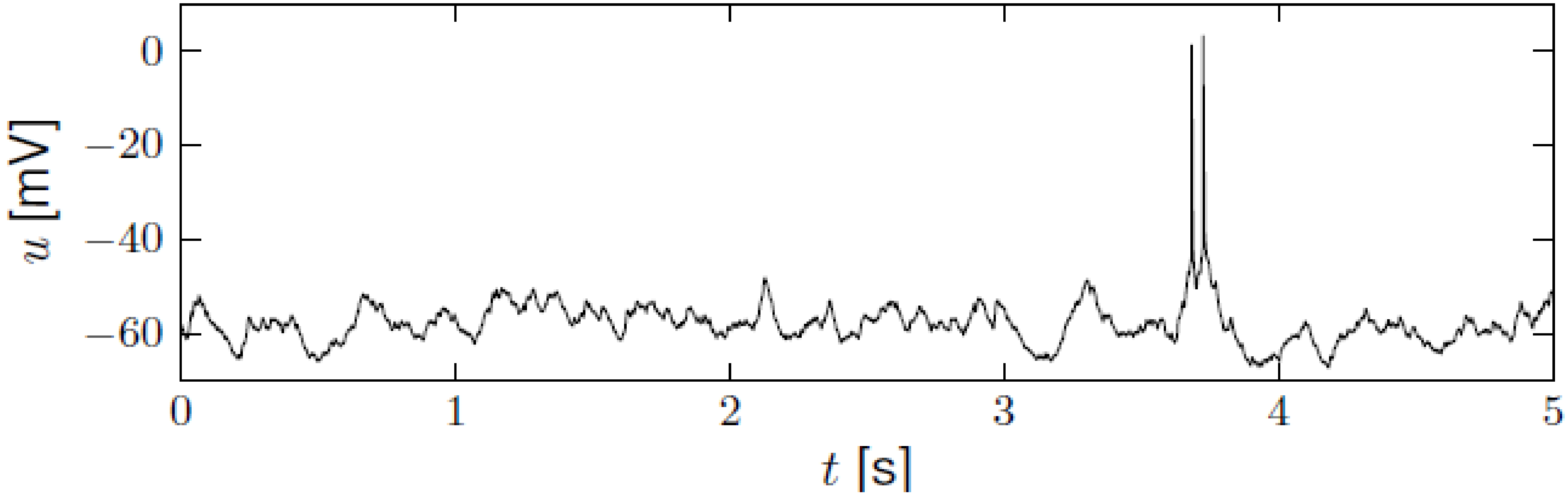
Brain

What is noise?

What is the neural code?

(week 7-9)

awake mouse, cortex, freely whisking,



Lab of Prof. C. Petersen, EPFL

Crochet et al., 2011

Biological Modeling of Neural Networks – Quiz 1.1

A cortical neuron sends out signals which are called:
- [ ] action potentials
- [ ] spikes
- [ ] postsynaptic potential

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 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

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

have your laptop with you

paper and pencil

paper and pencil

paper and pencil OR interactive toy examples on computer

Course of 4 credits = *6 hours of work per week*
4 'contact' + 2 homework

http://lcn.epfl.ch/~gerstner/

moodle.eplf.ch

Week 1 – part 2: The Passive Membrane

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Biological Modeling of Neural Networks

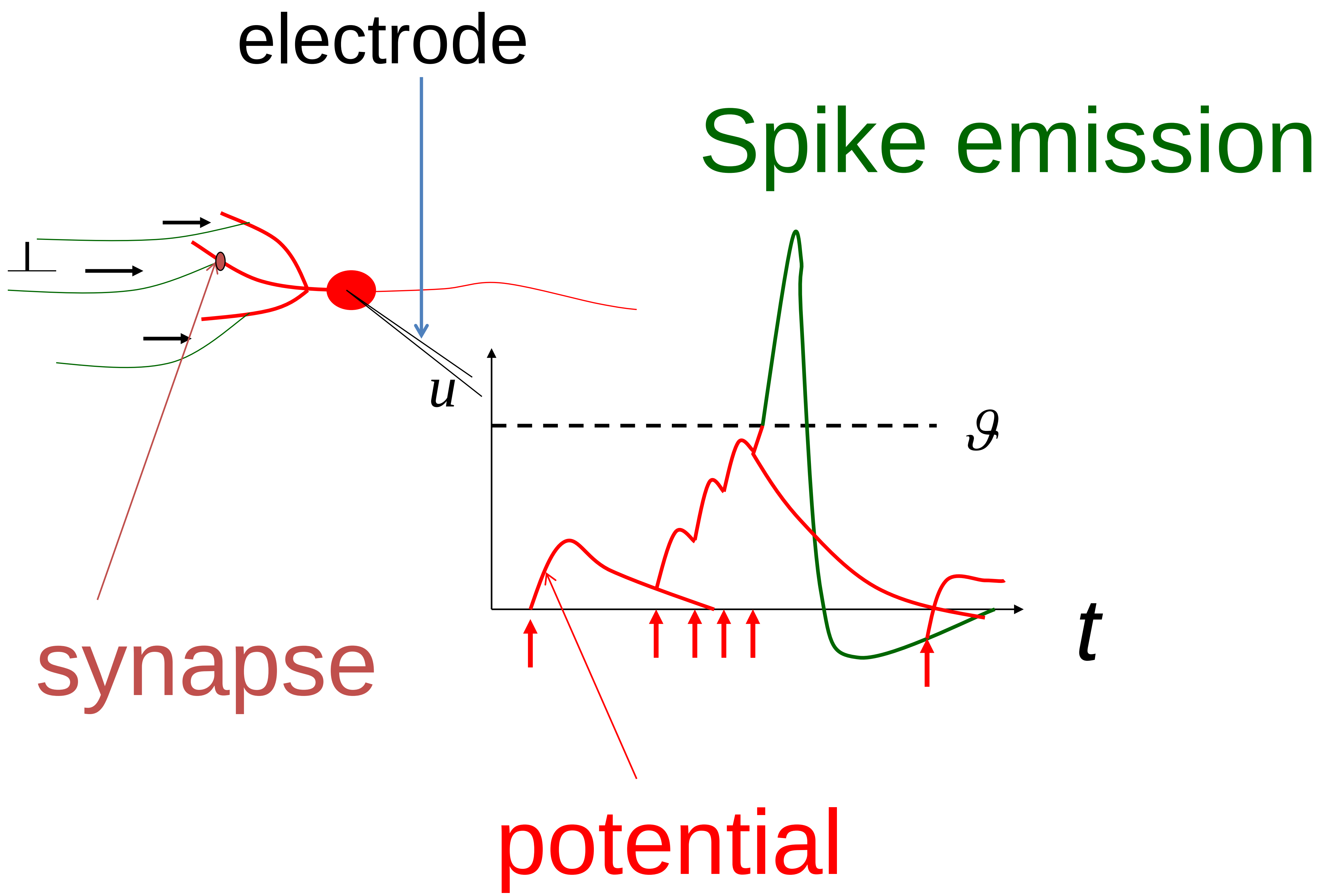
Week 1 – neurons and mathematics:

a first simple neuron model

Wulfram Gerstner

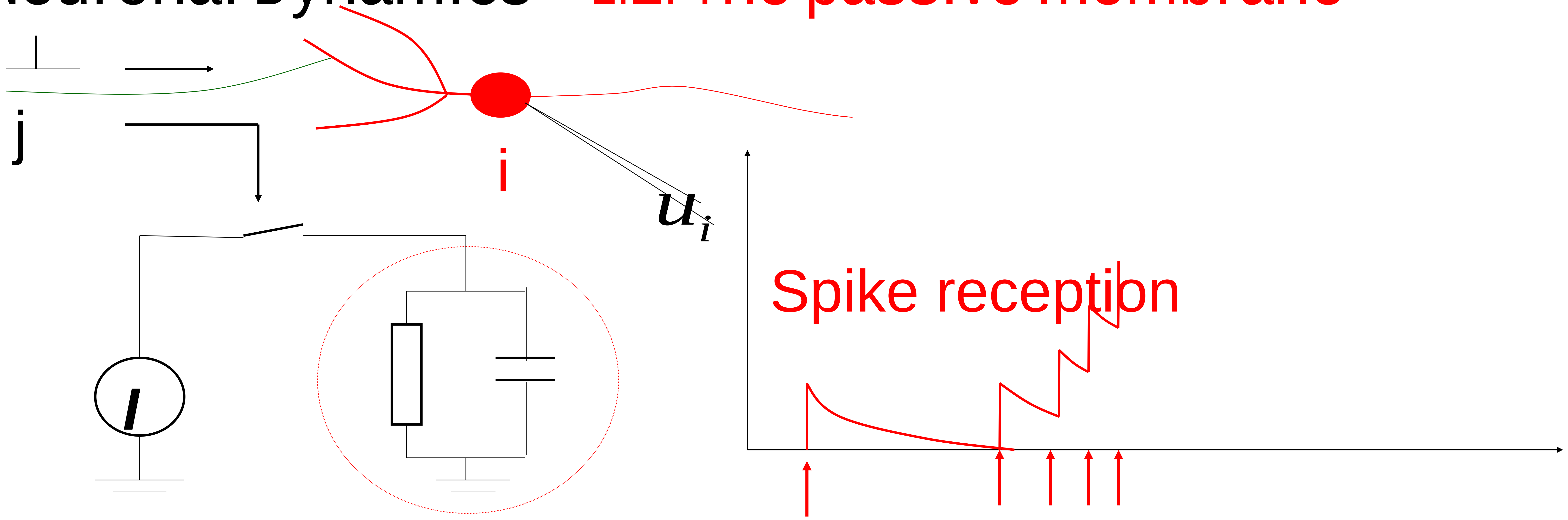
EPFL, Lausanne, Switzerland

Neuronal Dynamics – 1.2. The passive membrane



Integrate-and-fire model

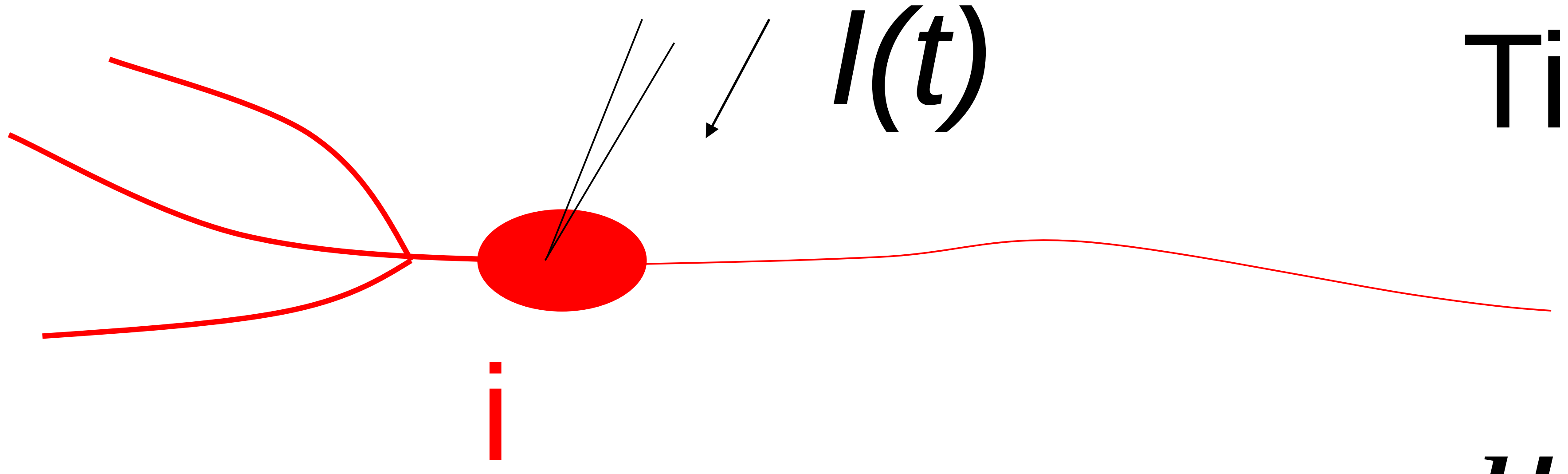
Neuronal Dynamics – 1.2. The passive membrane



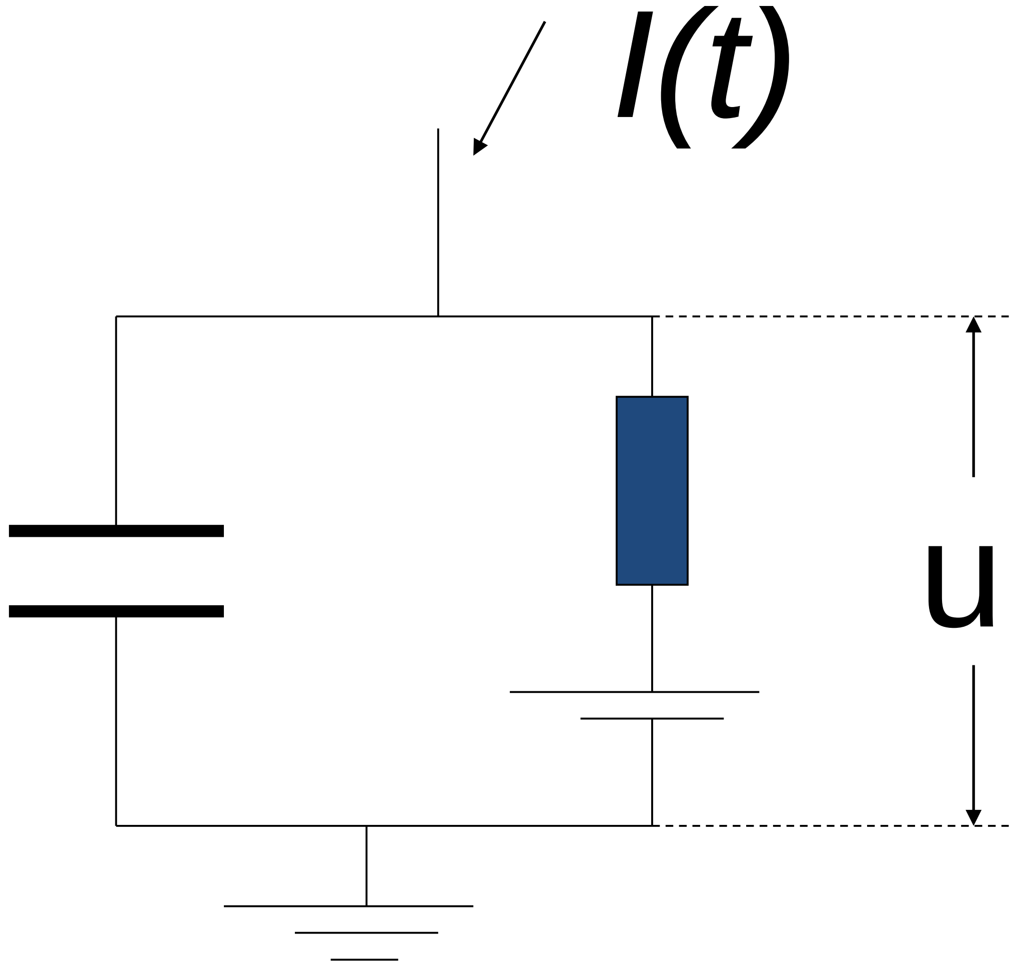
Subthreshold regime

- linear
- passive membrane
- RC circuit

Neuronal Dynamics – 1.2. The passive membrane

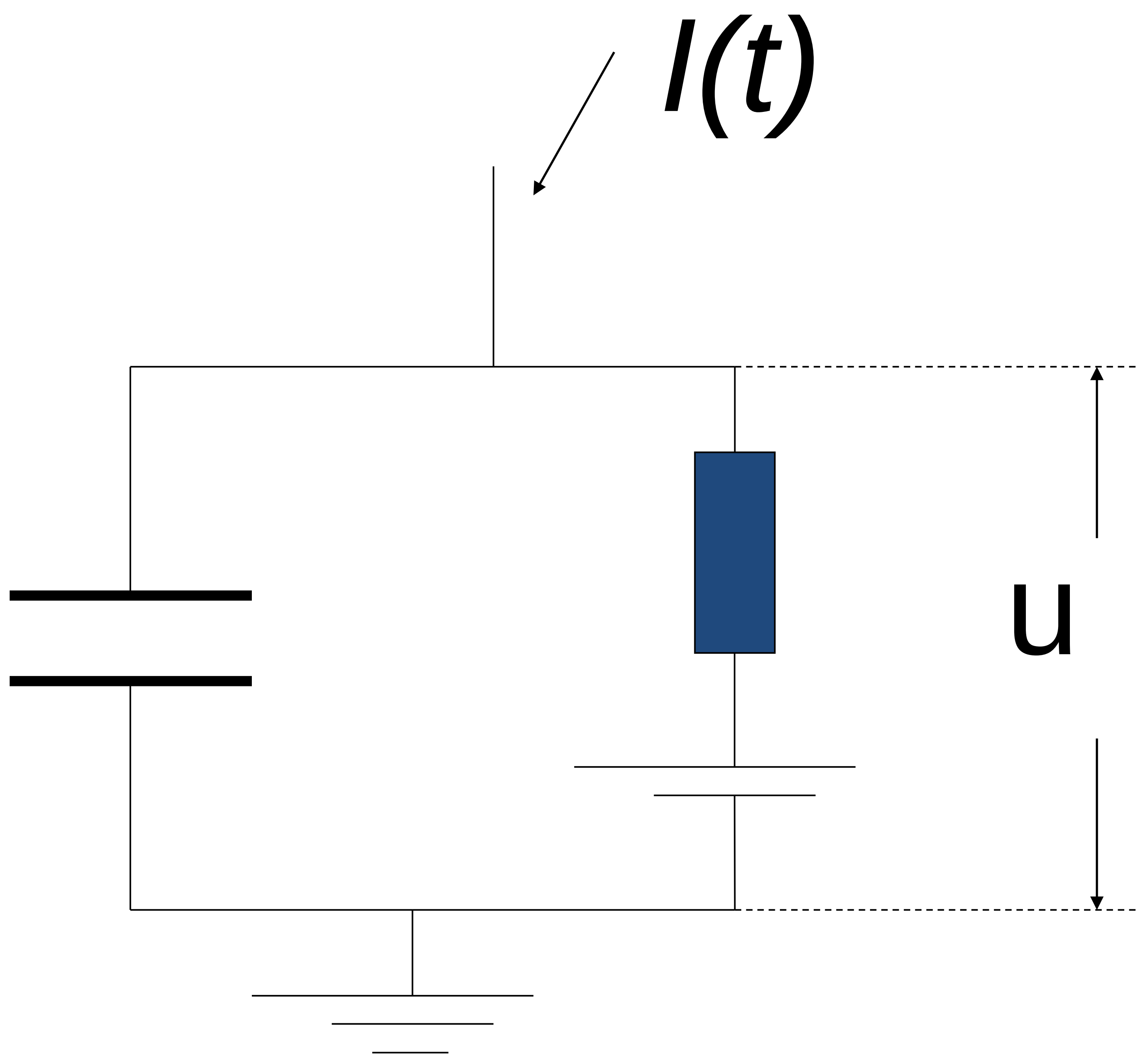


Time-dependent input

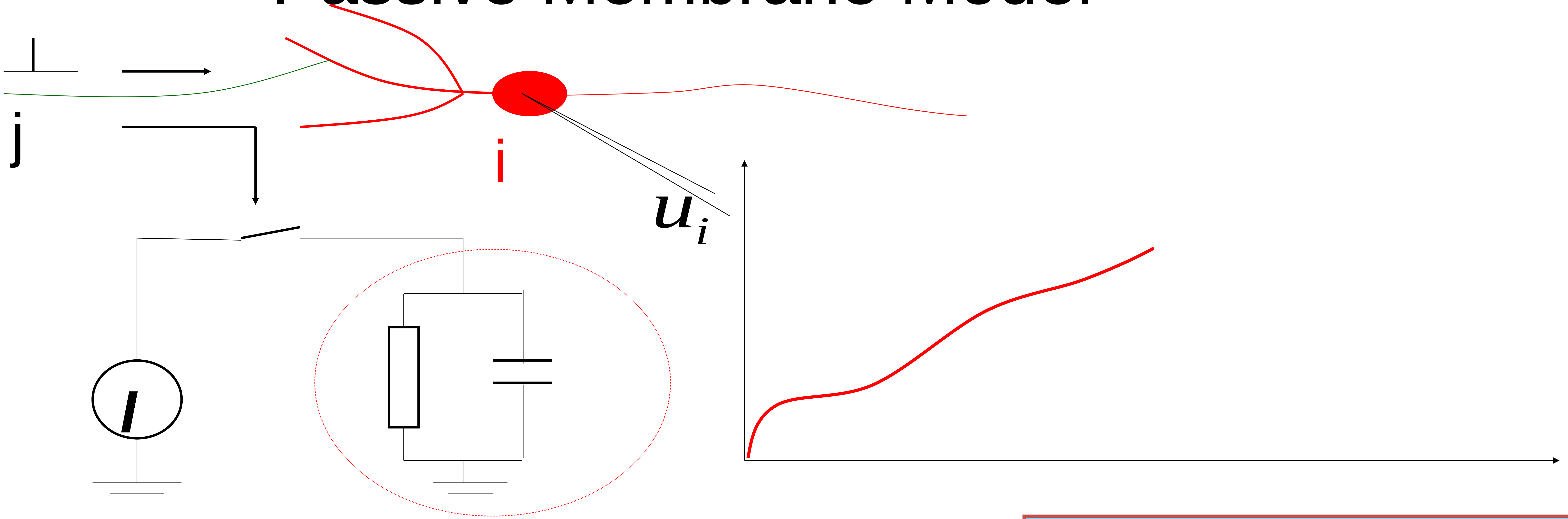


Math development:
Derive equation
(Blackboard)

Passive Membrane Model



Passive Membrane Model



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

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

Math Development: Voltage rescaling (blackboard)

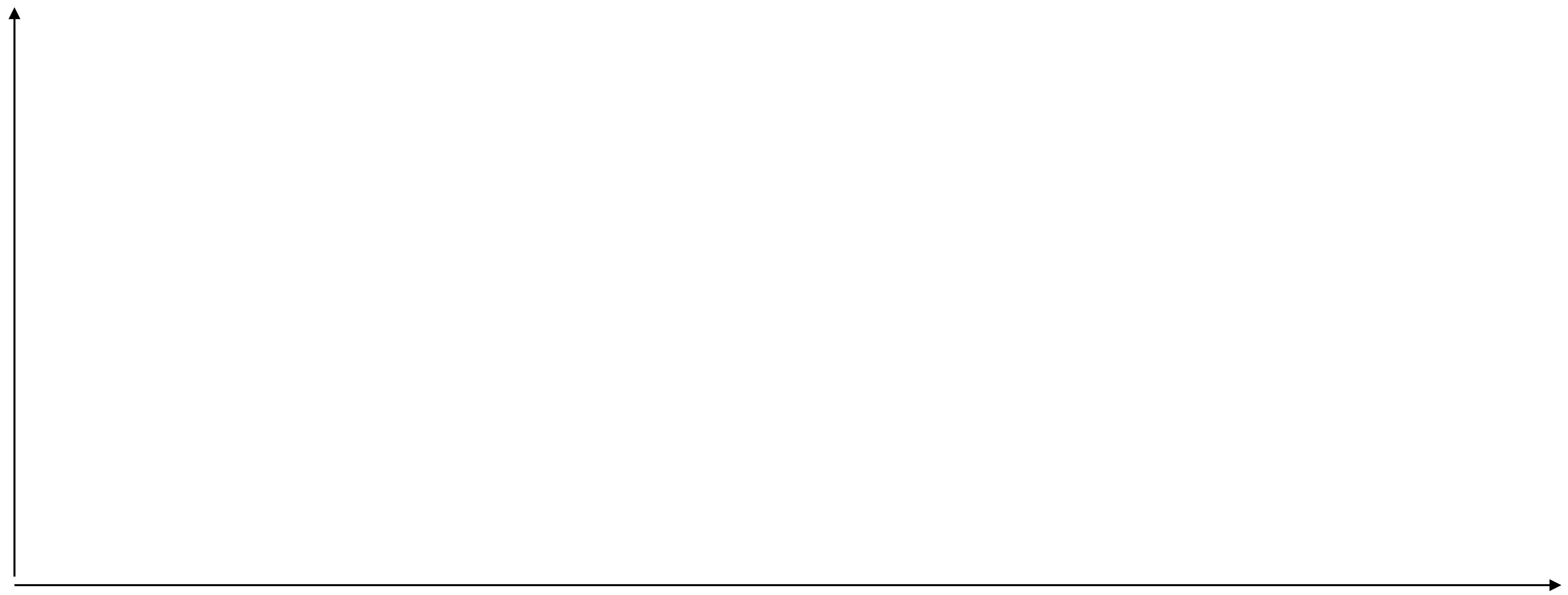
Passive Membrane Model

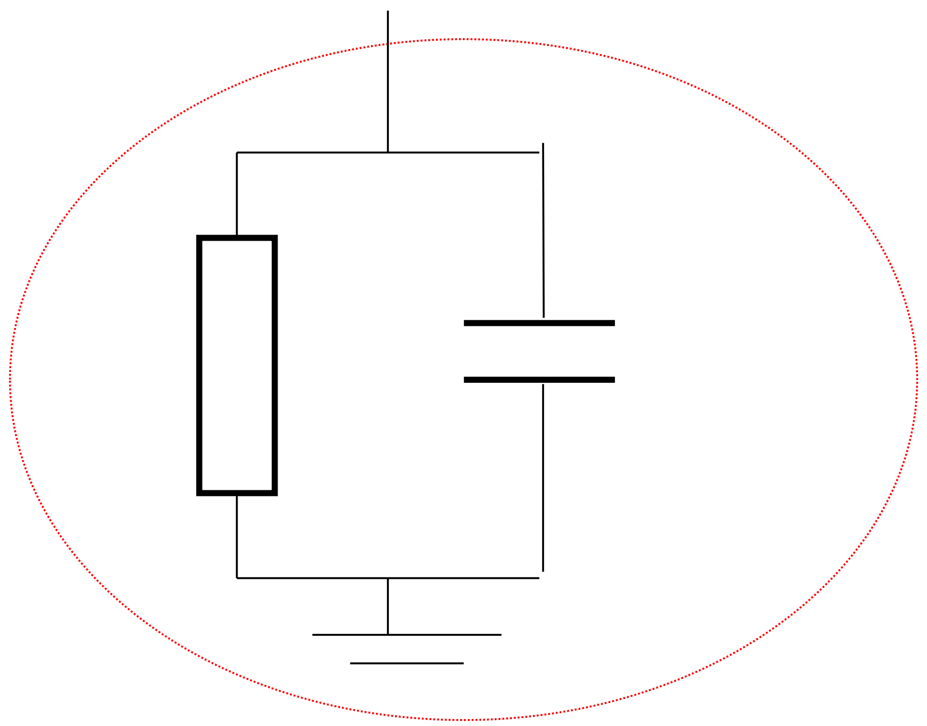
$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$

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

Passive Membrane Model/Linear differential equation

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

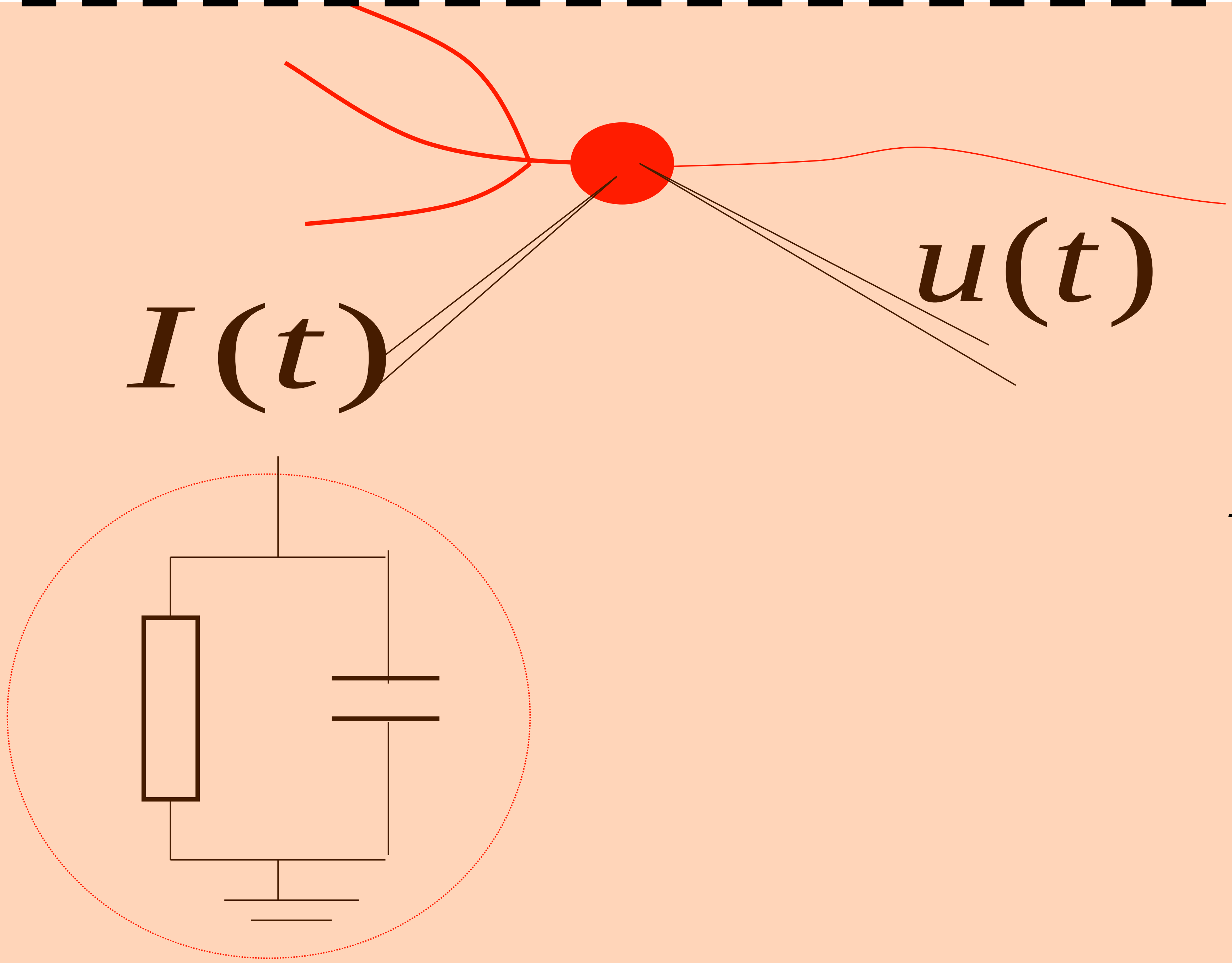


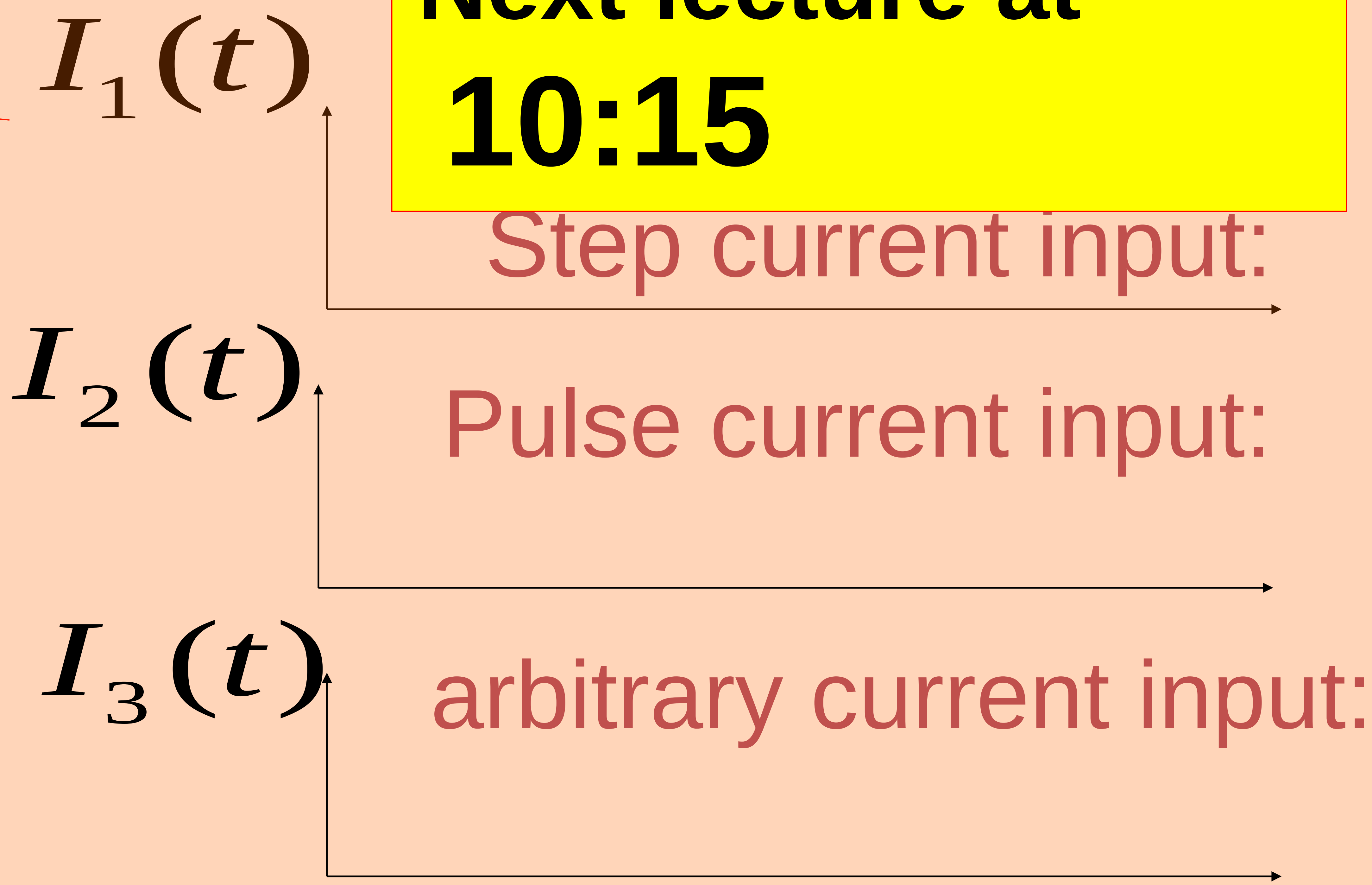


Free solution:
exponential decay

Neuronal Dynamics – Exercises NOW

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



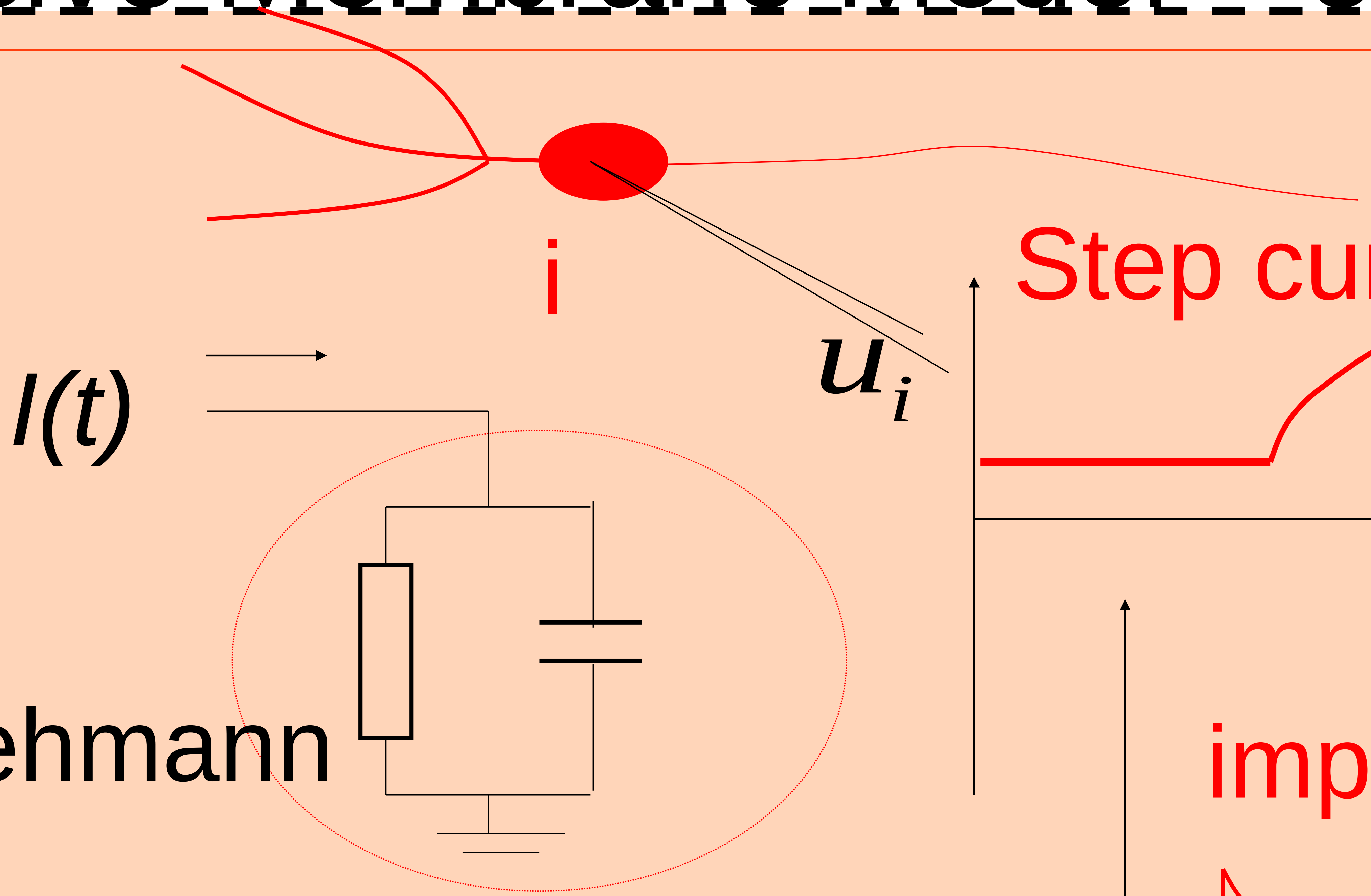


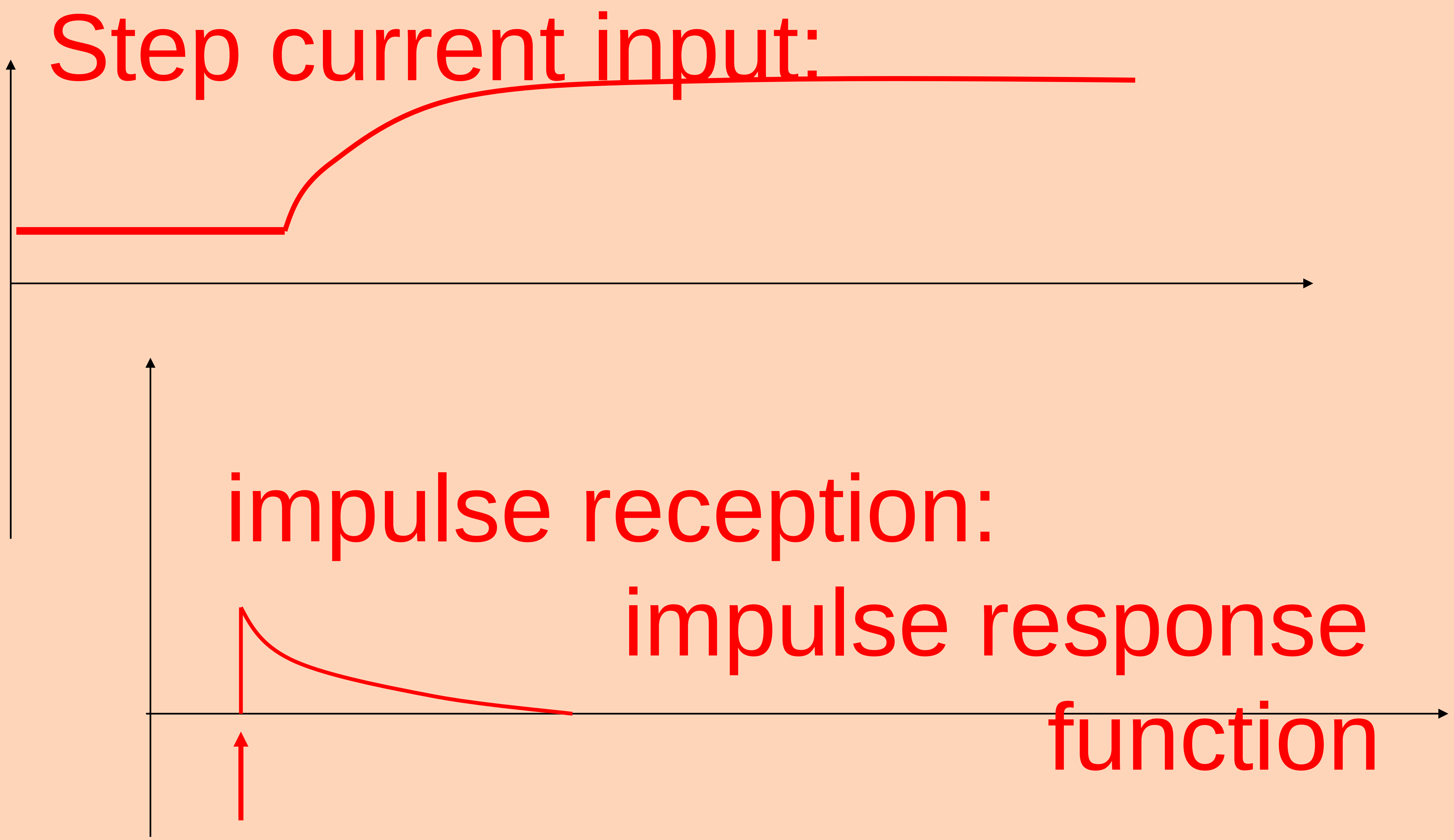
$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$

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

Calculate the voltage, for the 3 input currents

Passive Membrane Model – exercise 1 now





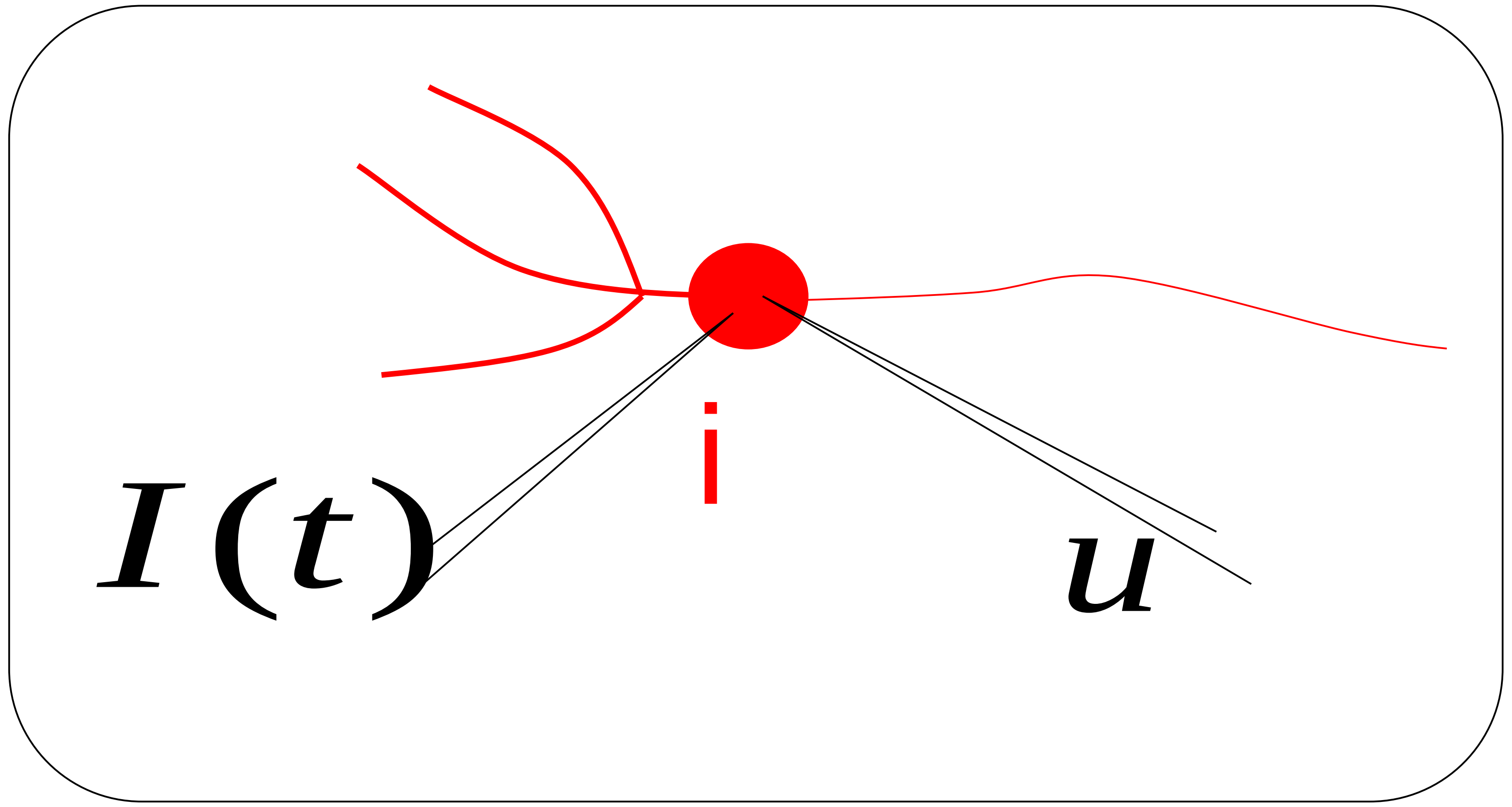
TA's:
Marco Lehmann

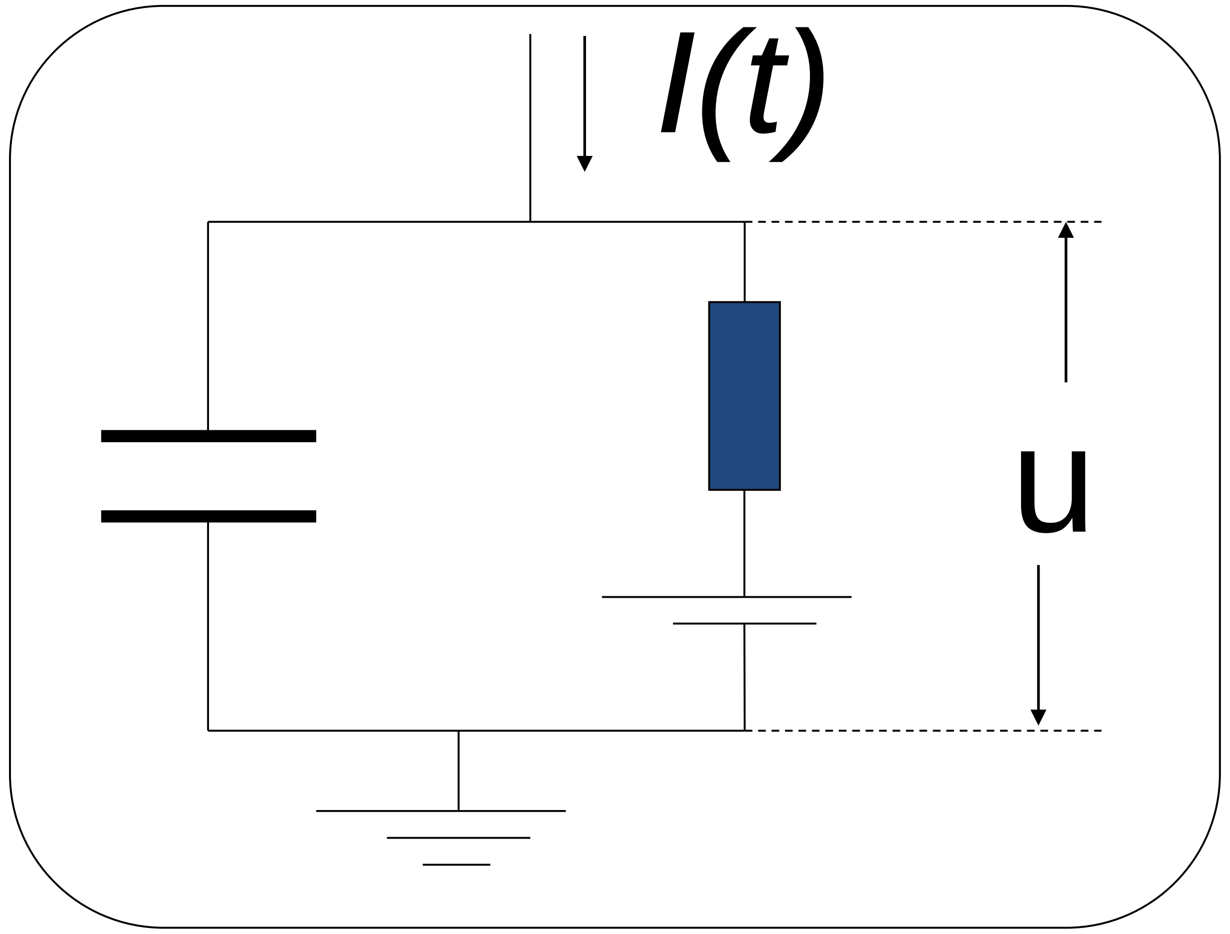
Linear equation

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

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

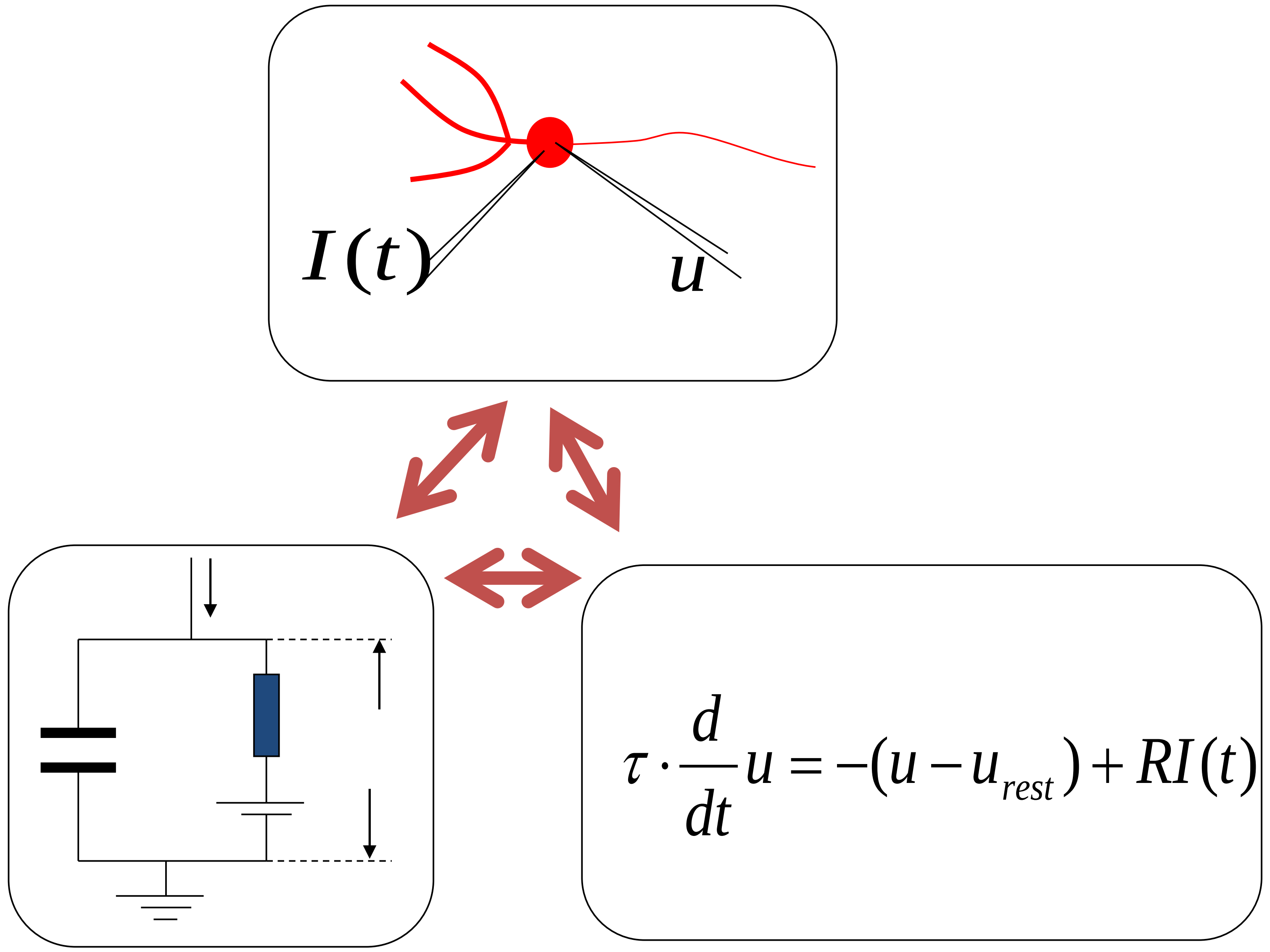
Triangle: neuron – electricity - math





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

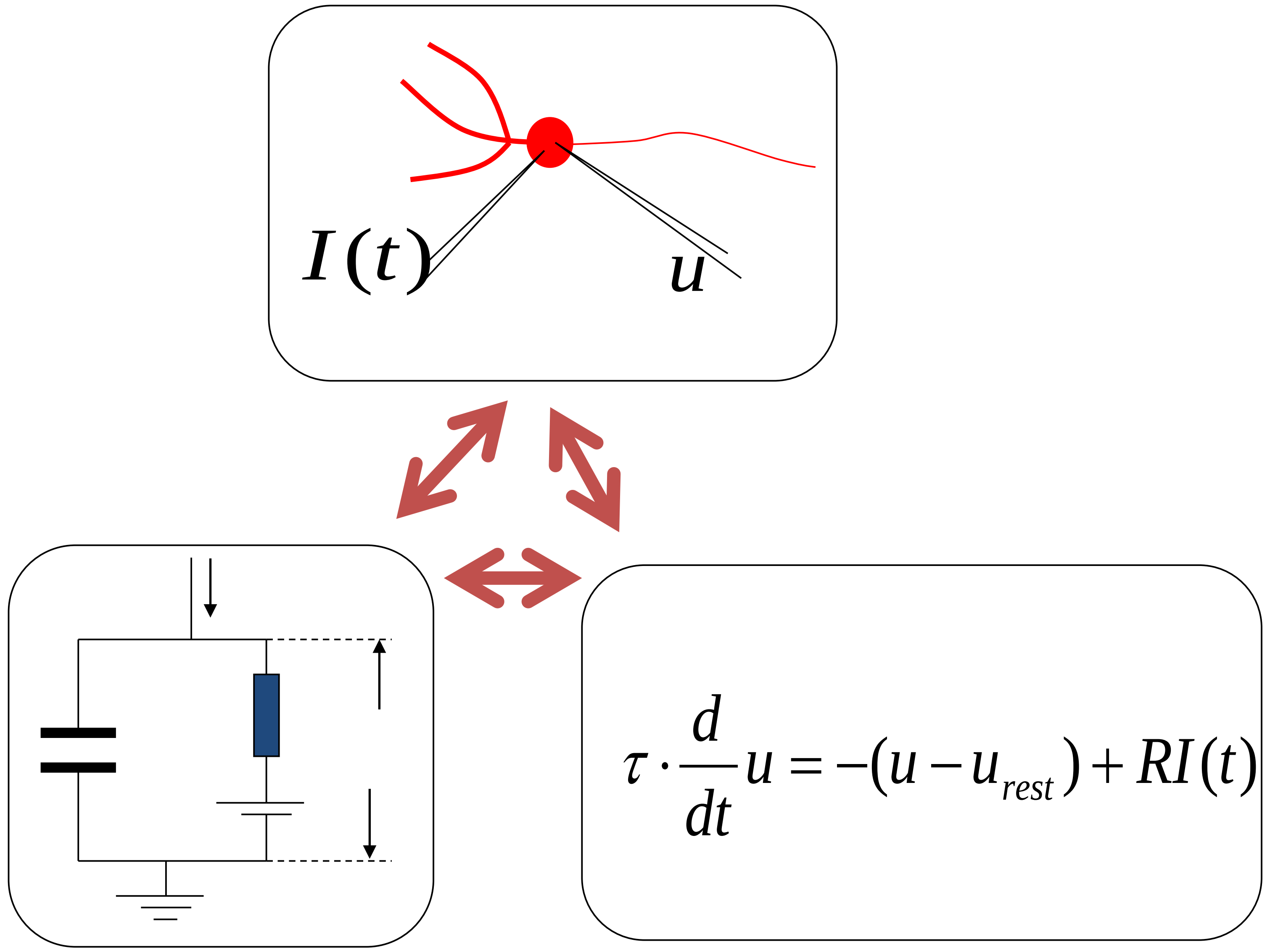
Pulse input – charge – delta-function



$$I(t) = q \cdot \delta(t - t_0)$$

Pulse current input

Dirac delta-function



$$I(t) = q \cdot \delta(t - t_0)$$

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

$$f(t_0) = \int_{t_0 - a}^{t_0 + a} f(t)\, \delta(t - t_0)\, dt$$

Neuronal Dynamics – Solution of Ex. 1 – arbitrary input

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

Arbitrary input

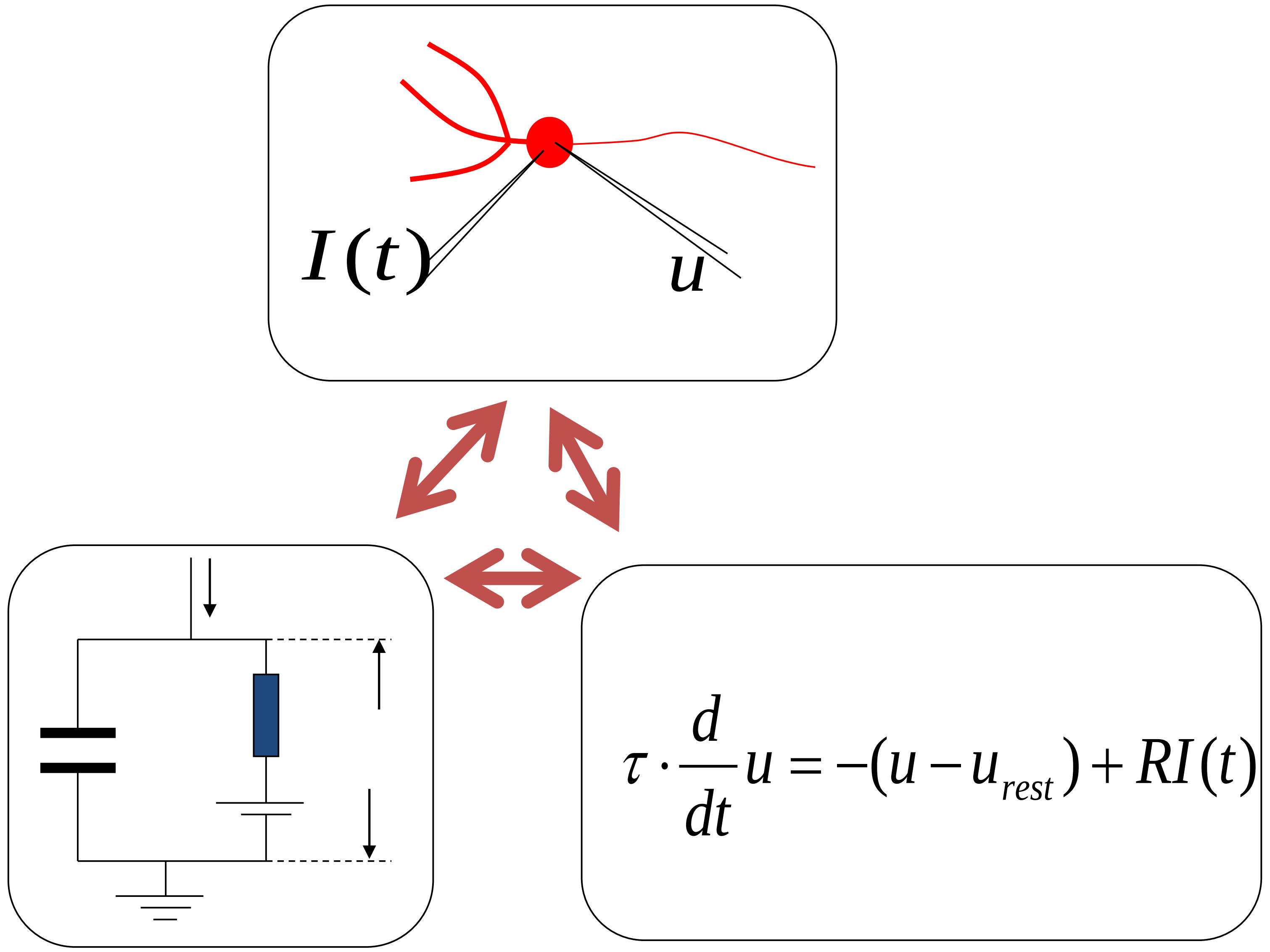
$$u(t) = u_{rest} + \int_{-\infty}^{t} \frac{1}{C} e^{-(t-t')/\tau} I(t')dt'$$

Single pulse

$$\Delta u(t) = \frac{q}{C} e^{-(t-t_0)/\tau}$$

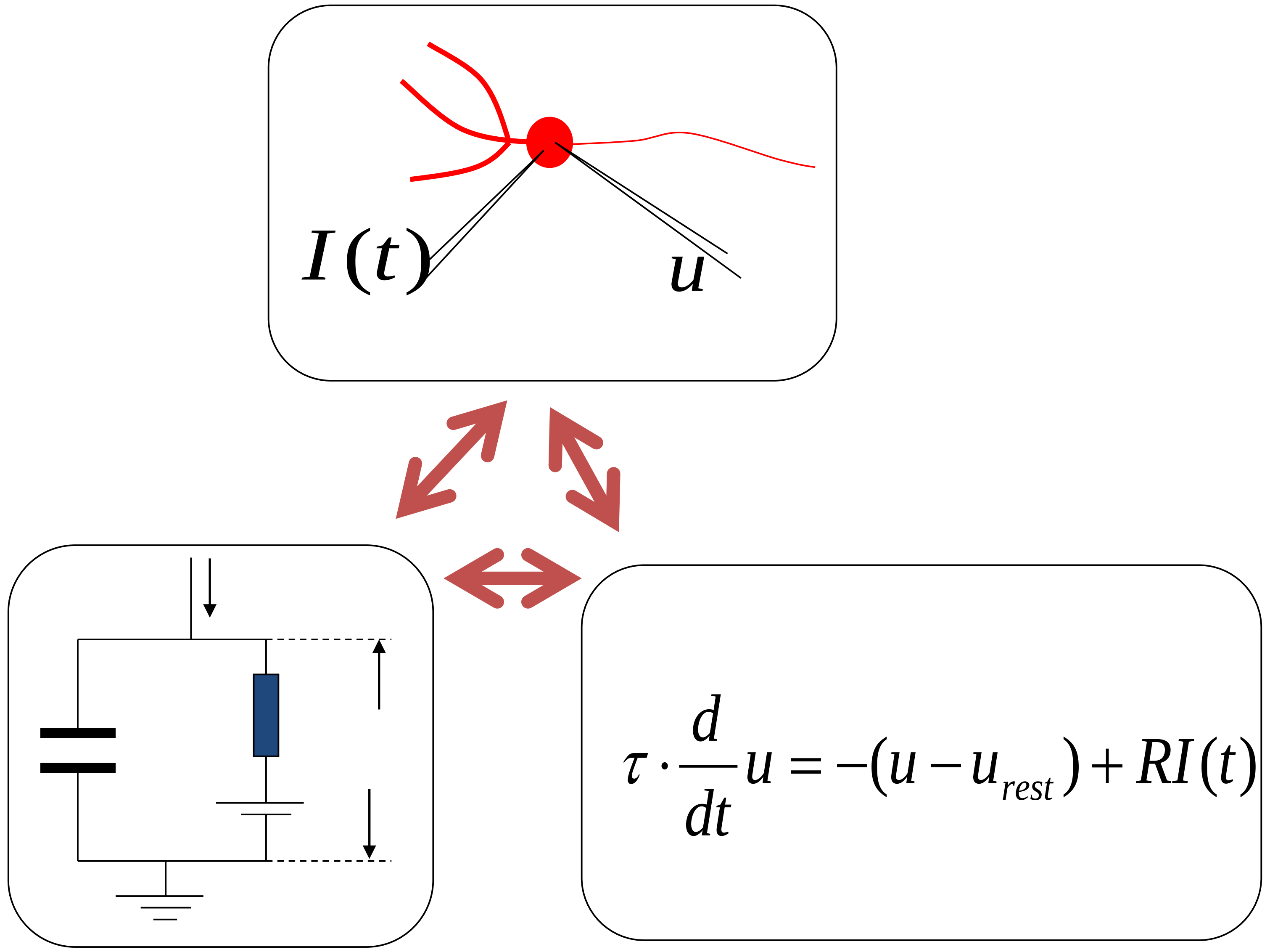
you need to know the solutions of linear differential equations!

Passive membrane, linear differential equation



Passive membrane, linear differential equation

If you have difficulties, watch lecture 1.2detour.



Three prerequisits:

-Analysis 1-3

-Probability/Statistics

-Differential Equations or Physics 1-3 or Electrical Circuits

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+ miniproject (1/3)

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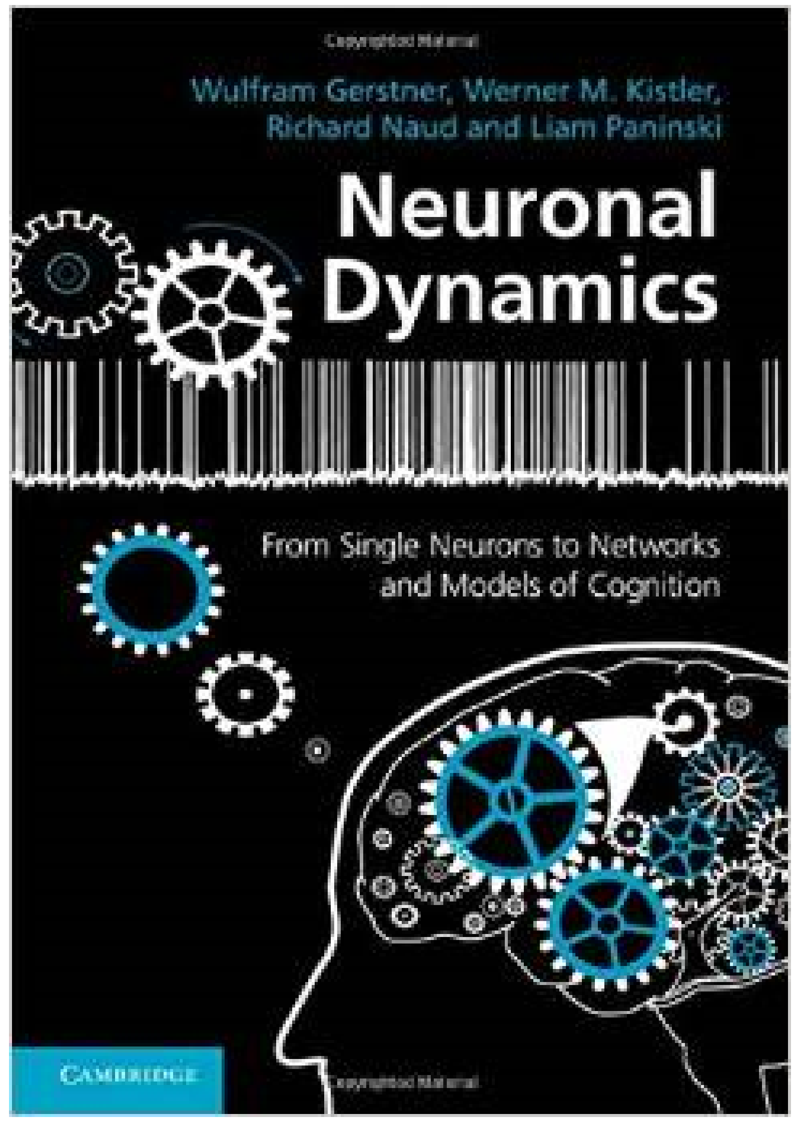

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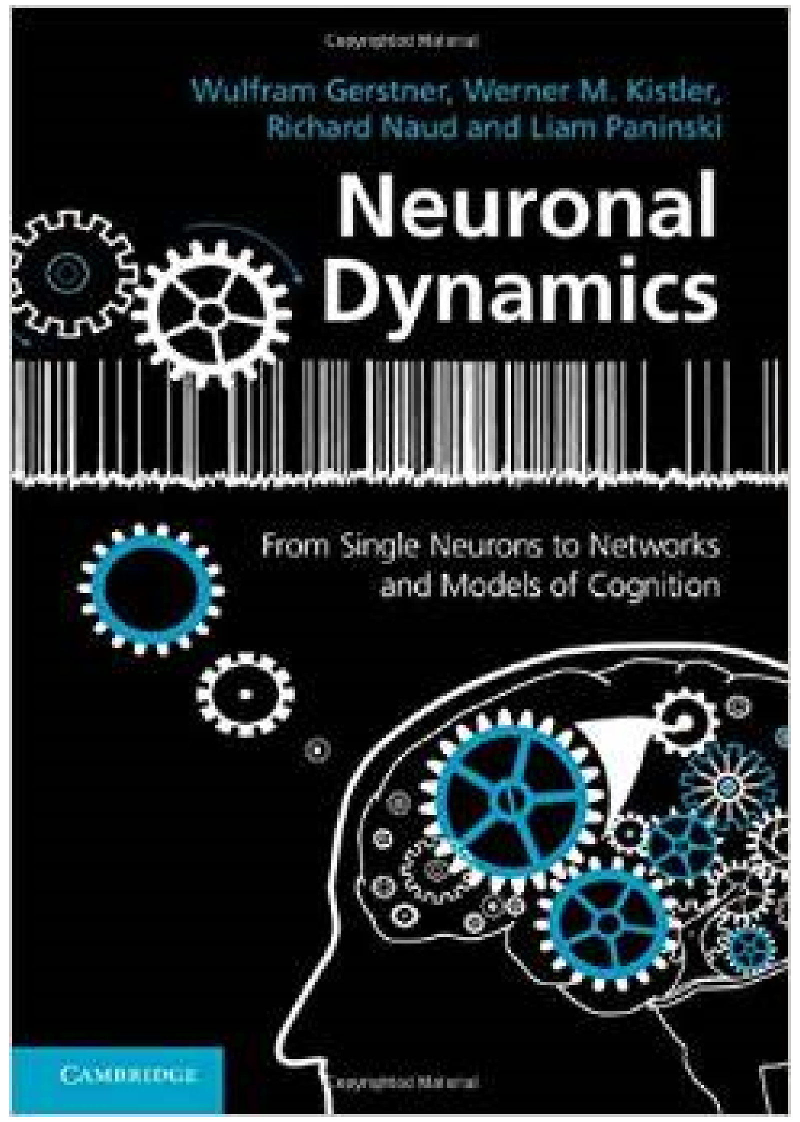

Questions?

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Week 1 – part 3: Leaky Integrate-and-Fire Model

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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
- Detour: solution of 1-dim linear differential equation

$\boxed{\text{1.3 Leaky Integrate-and-Fire Model}}$

1.4 Generalized Integrate-and-Fire Model

1.5. Quality of Integrate-and-Fire Models

Neuronal Dynamics – 1.3 Leaky Integrate-and-Fire Model

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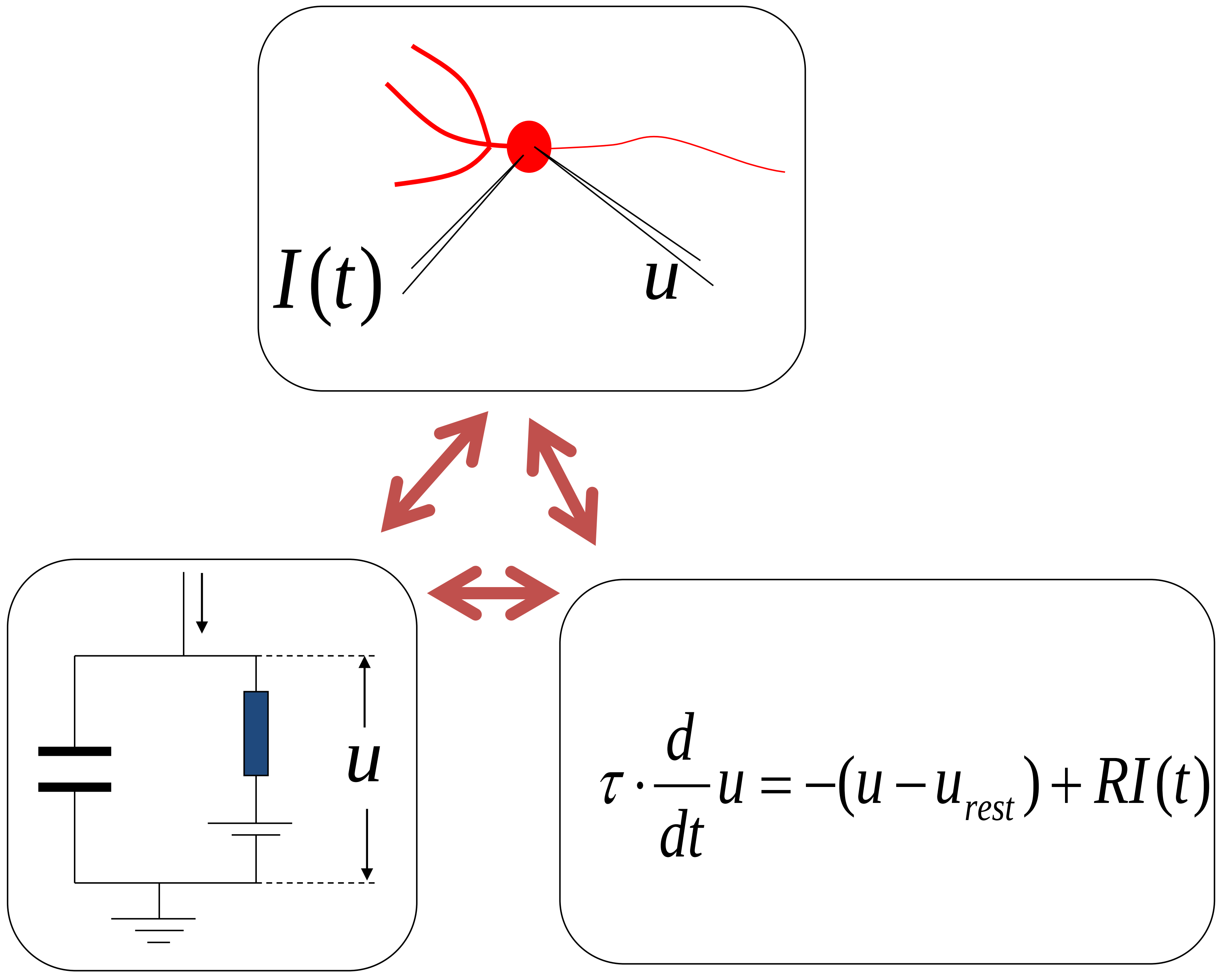
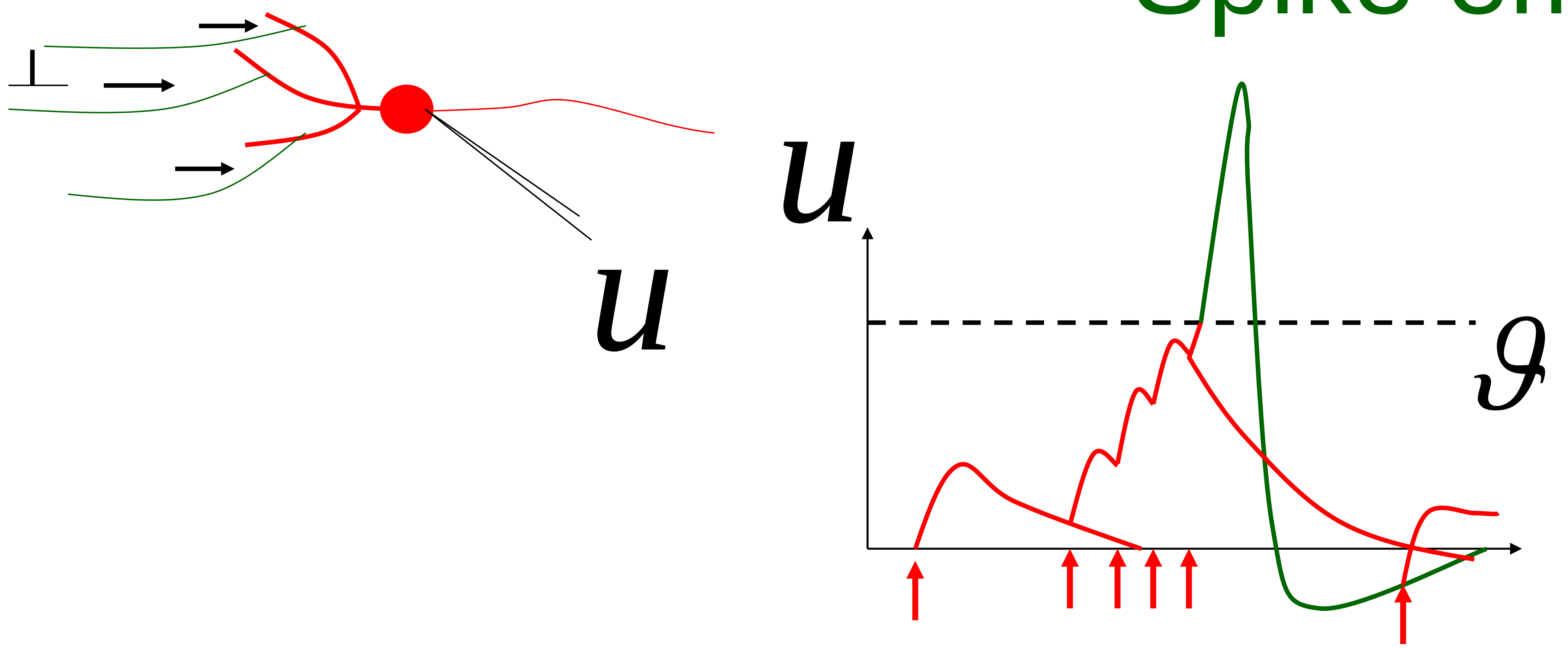


Neuronal Dynamics – Integrate-and-Fire type Models

Spike emission



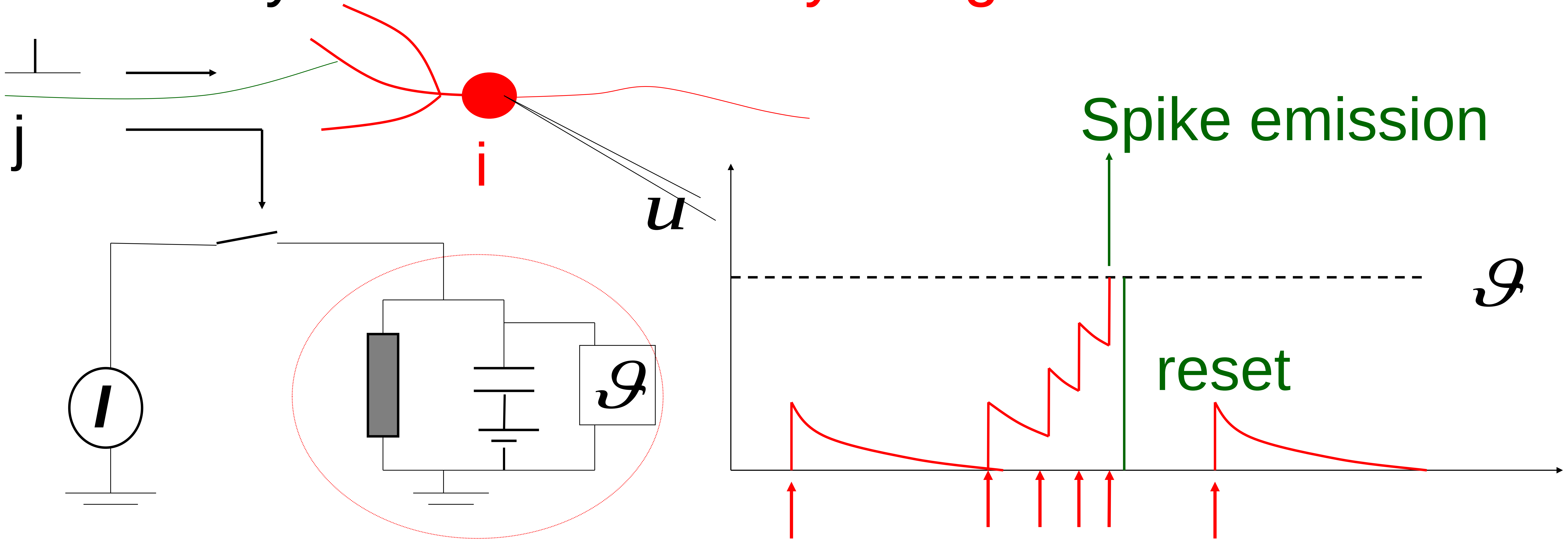
Input spike causes an EPSP
= excitatory postsynaptic potential

Simple
Integate-and-Fire Model:
passive membrane
+ *threshold*

Leaky Integrate-and-Fire Model

-output spikes are events
-generated at threshold
-after spike: reset/refractoriness

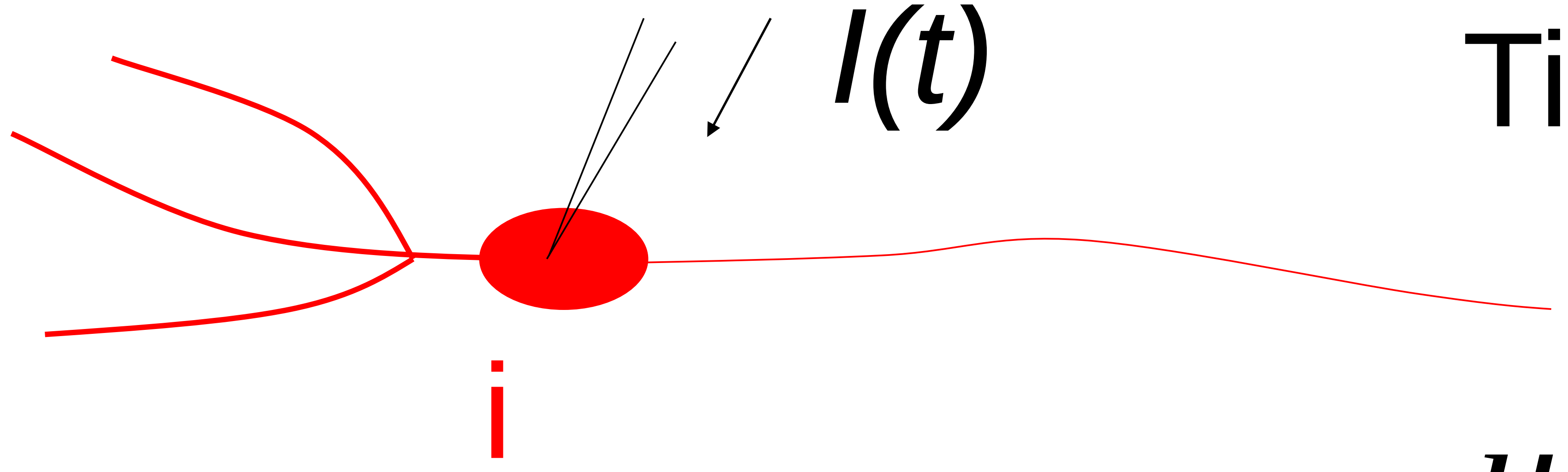
Neuronal Dynamics – 1.3 Leaky Integrate-and-Fire Model



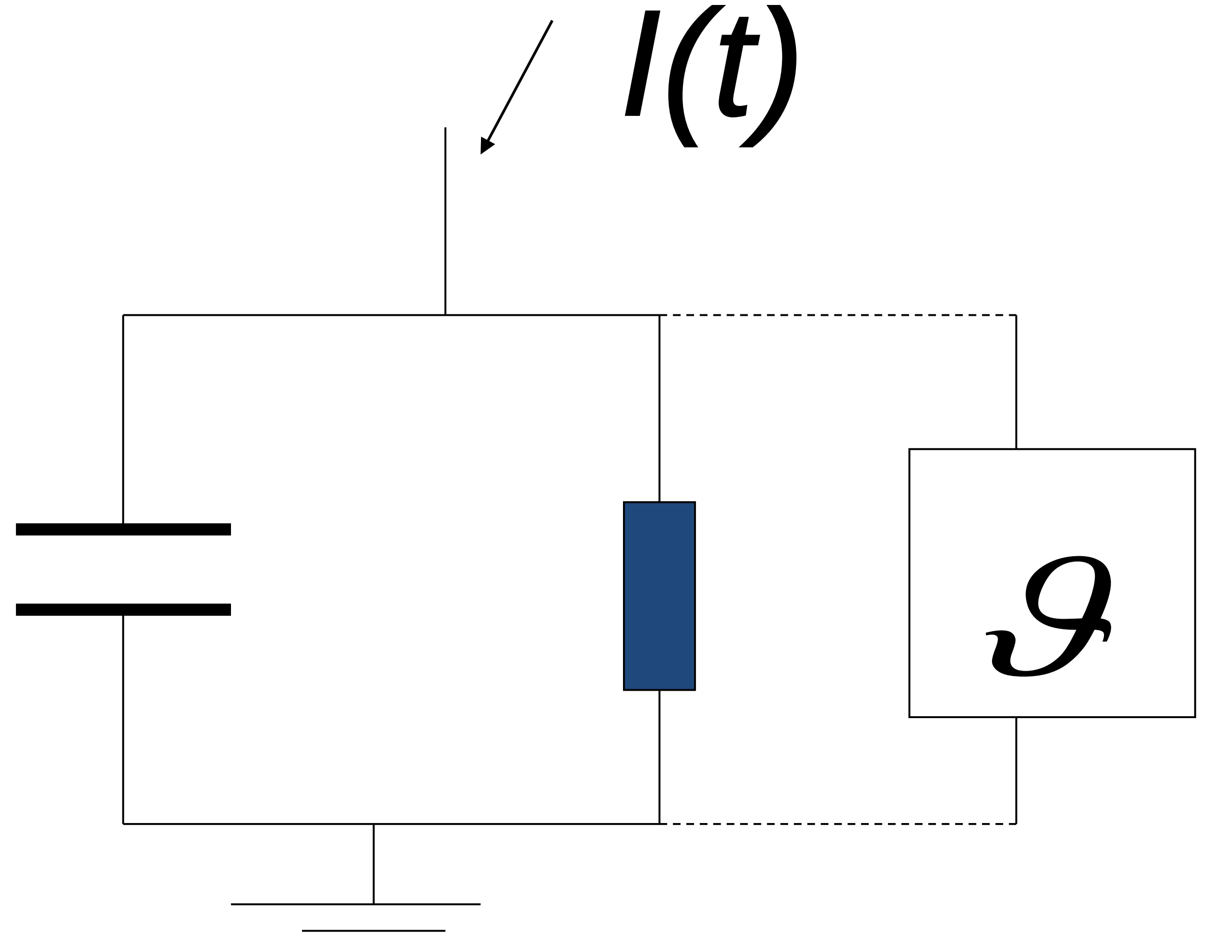
$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$ linear

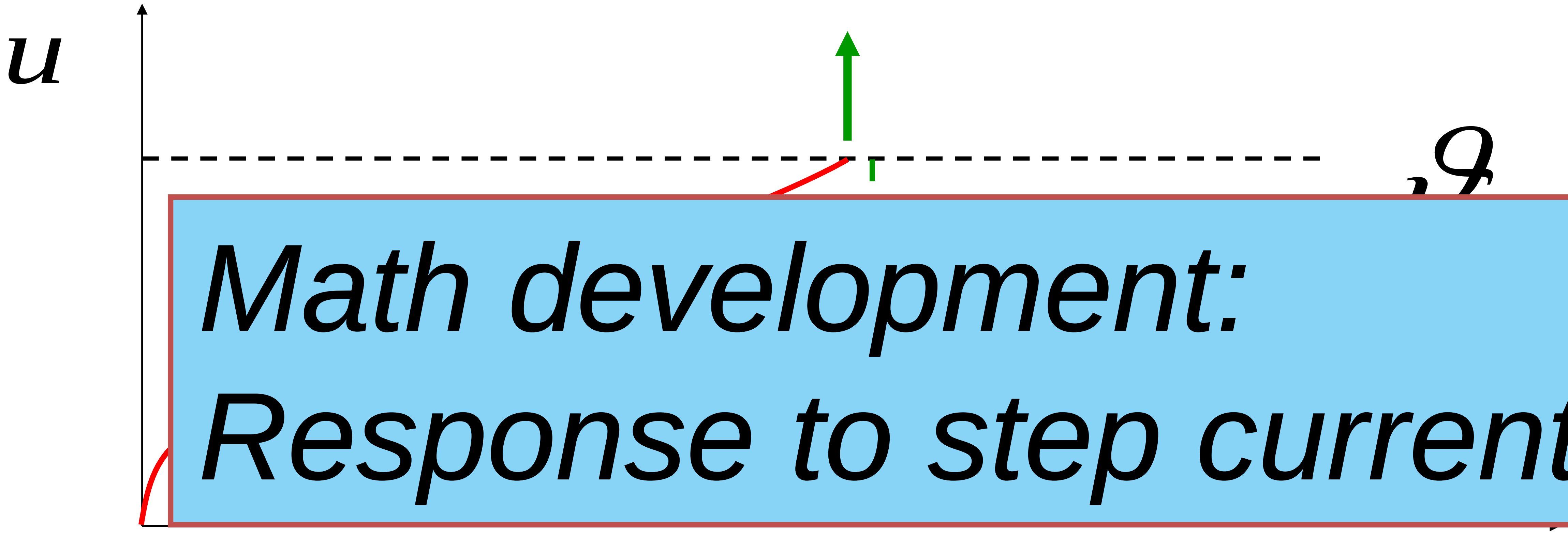
$u(t) = \vartheta \Rightarrow$ Fire+reset $u \rightarrow u_r$ threshold

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

Week1 – Quiz 2.

Take 90 seconds:

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) $x(t) = x_c \exp(-t/\tau)$

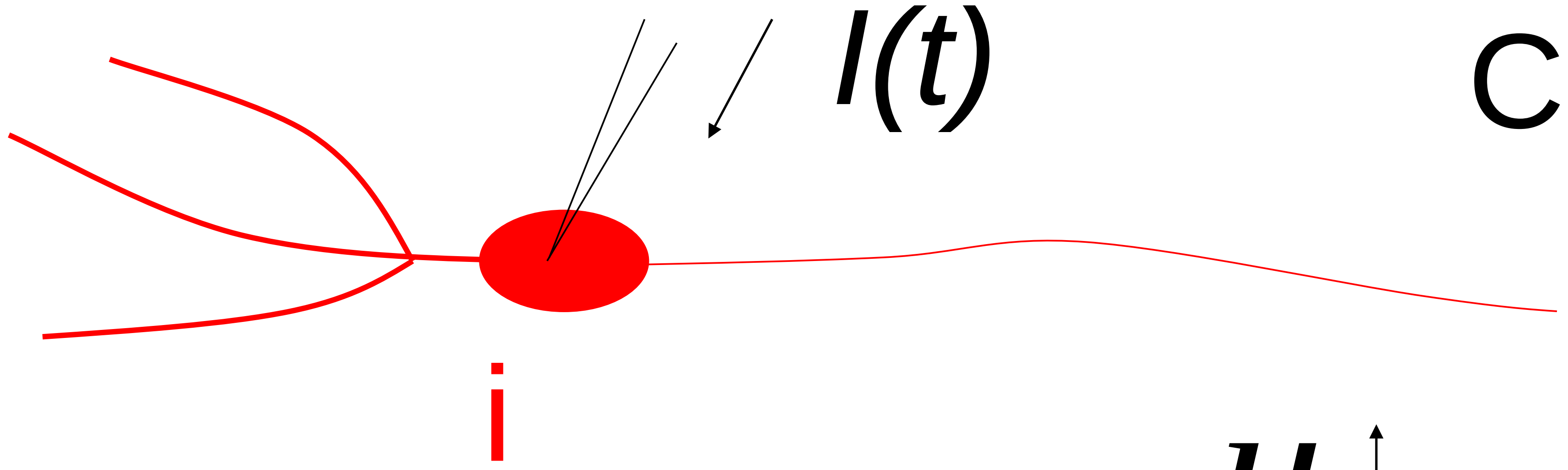
(iii) $x(t) = x_c[1 - \exp(-t/\tau)]$

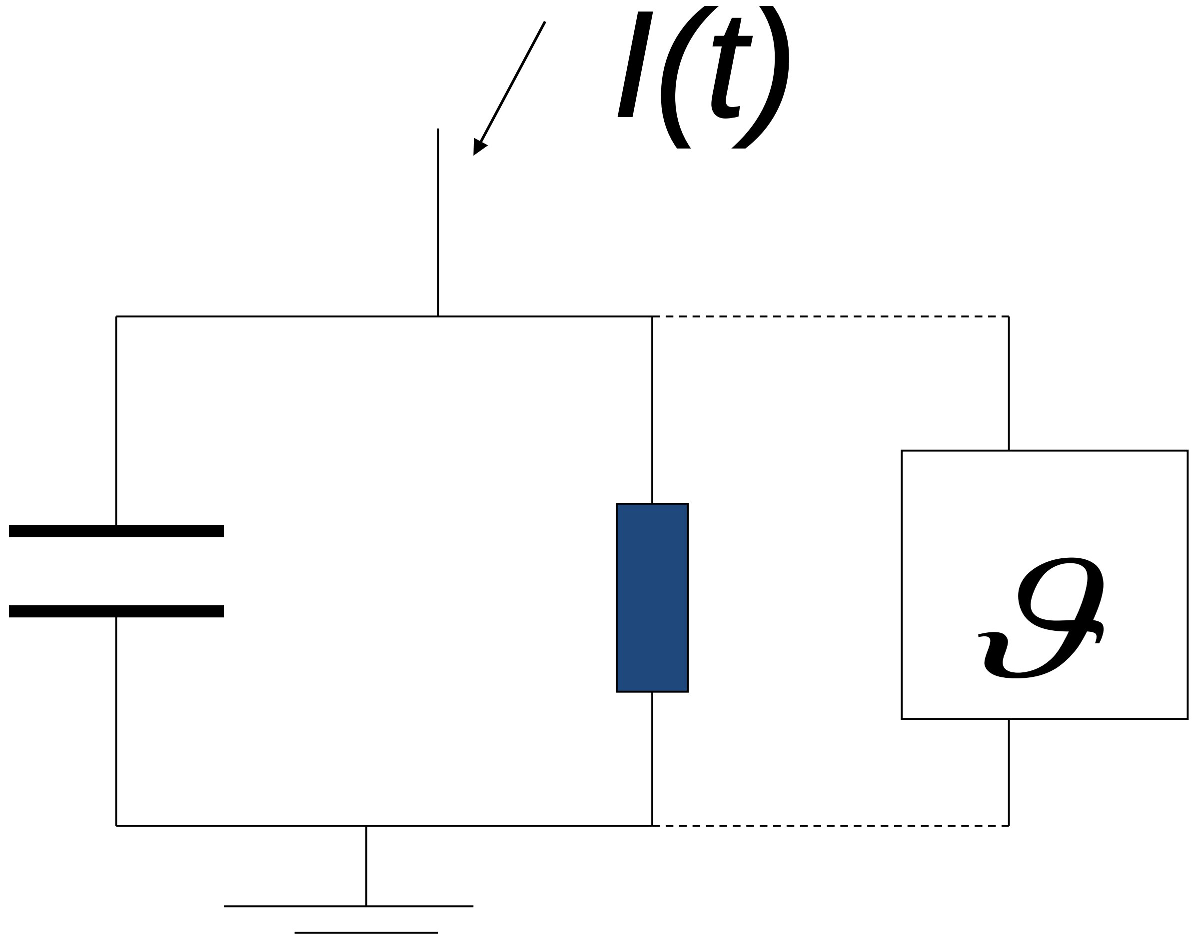
(iv) $x(t) = 0.5x_c[1 + \exp(-t/\tau)]$

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

Neuronal Dynamics – 1.3 Leaky Integrate-and-Fire Model

CONSTANT input/step input





Leaky Integrate-and-Fire Model (LIF)

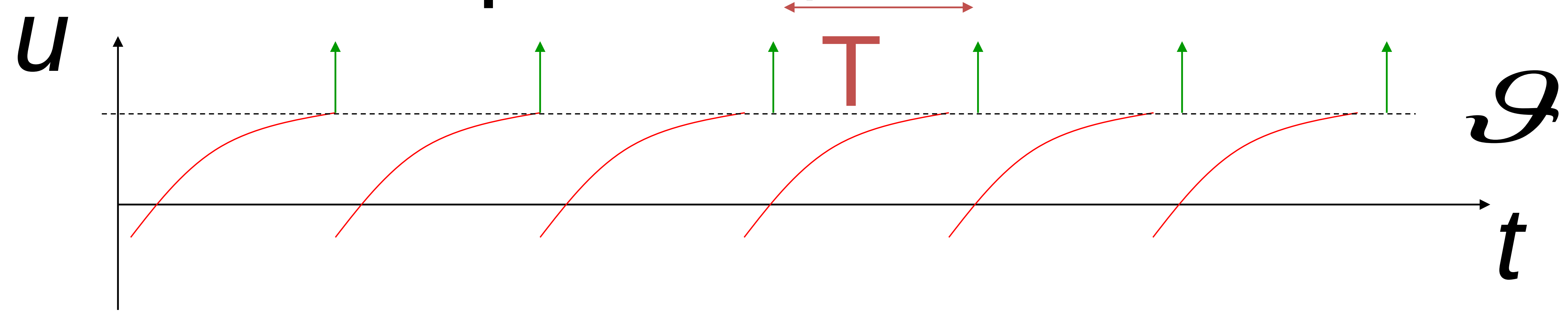
$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI_0$$

LIF

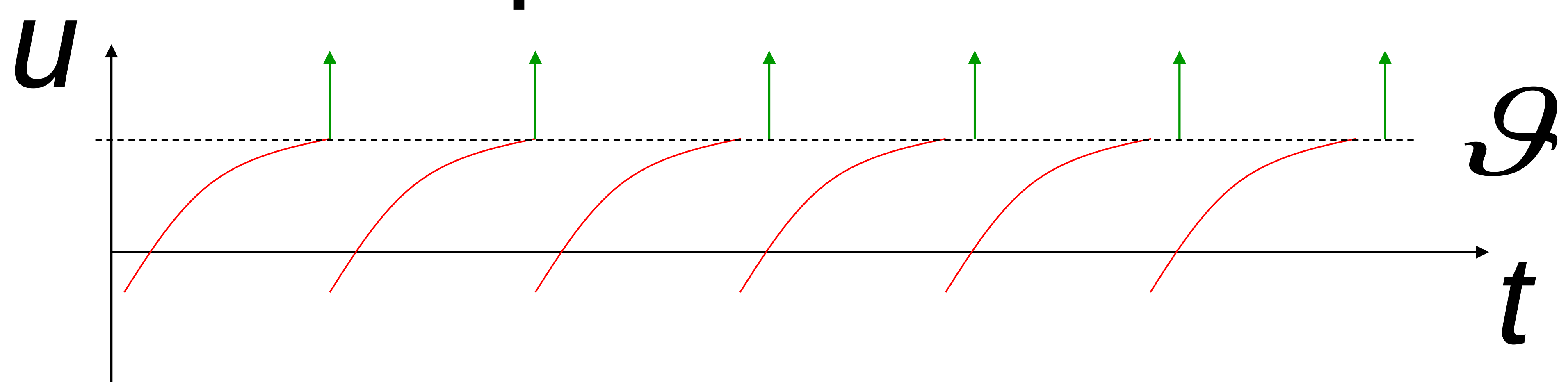
If $u(t) = \vartheta \Rightarrow \quad u \to u_r$

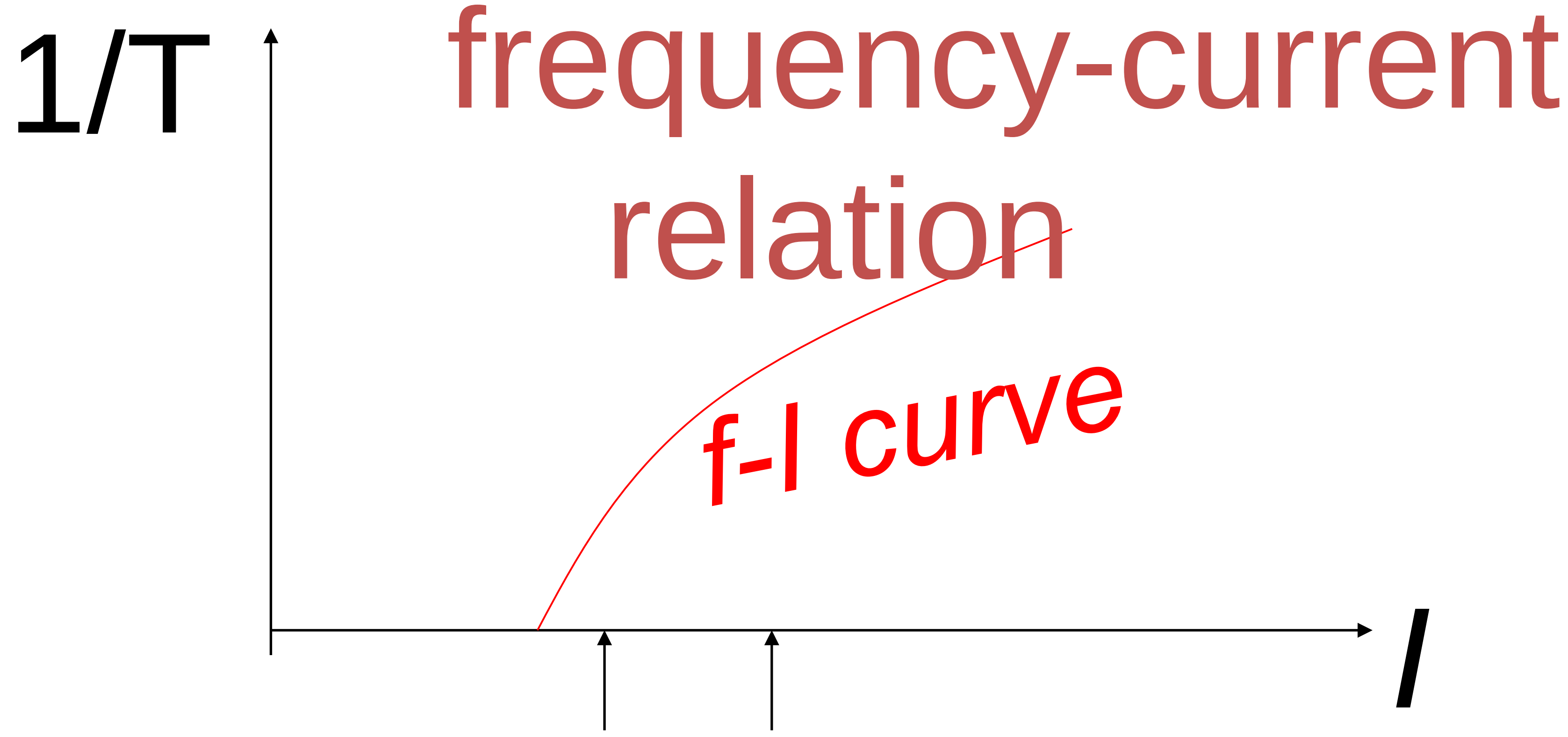
'Firing'

Repetitive, current I_0



Repetitive, current $I_1 > I_0$

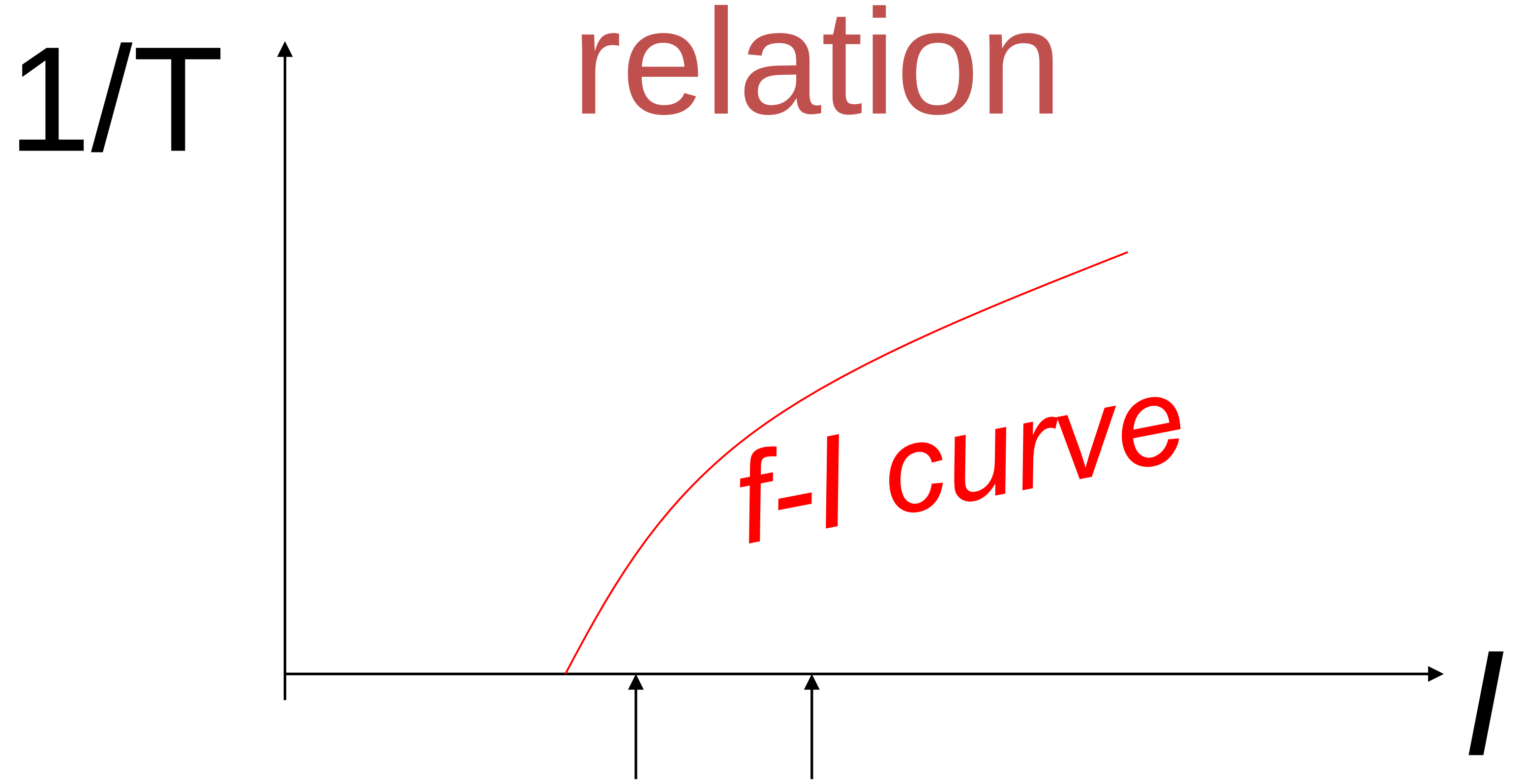




Neuronal Dynamics – First week, Exercise 2

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

frequency-current relation

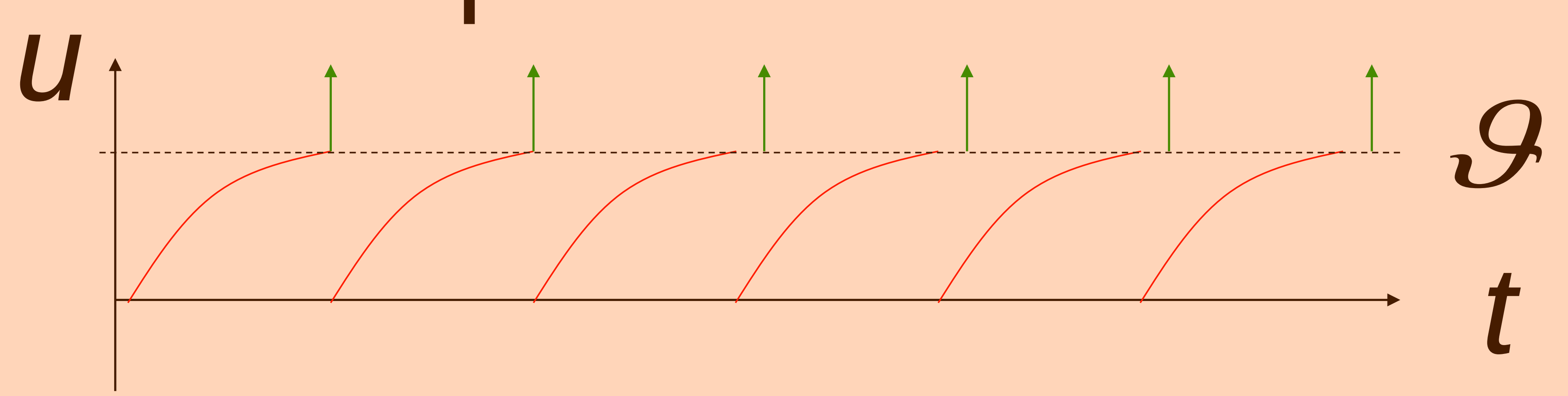


EXERCISE 2 NOW: Leaky Integrate-and-fire Model (LIF)

LIF $\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI_0$ If firing: $u \rightarrow u_r$

$assume: \; u_r = u_{rest}$

repetitive



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?

Start Exerc. at 10:53.
Next lecture at 11:15

Week 1 – part 4: Generalized Integrate-and-Fire Model

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Biological Modeling of Neural Networks

Week 1 – neurons and mathematics:

a first simple neuron model

Wulfram Gerstner

EPFL, Lausanne, Switzerland

√ 1.1 Neurons and Synapses:

Overview

√ 1.2 The Passive Membrane

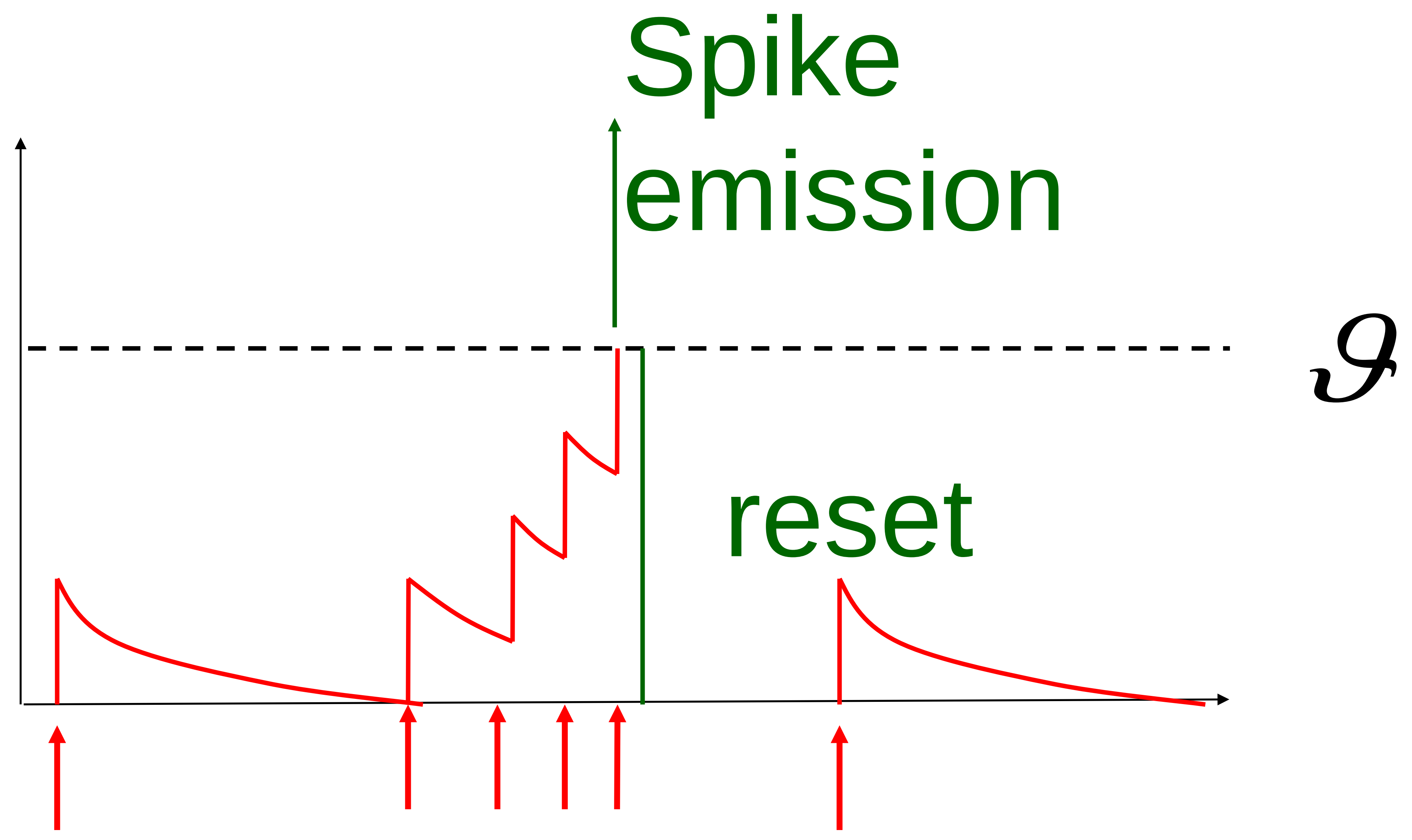
- Linear circuit
- Dirac delta-function

√ 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



Integrate-and-fire model

LIF: linear + threshold

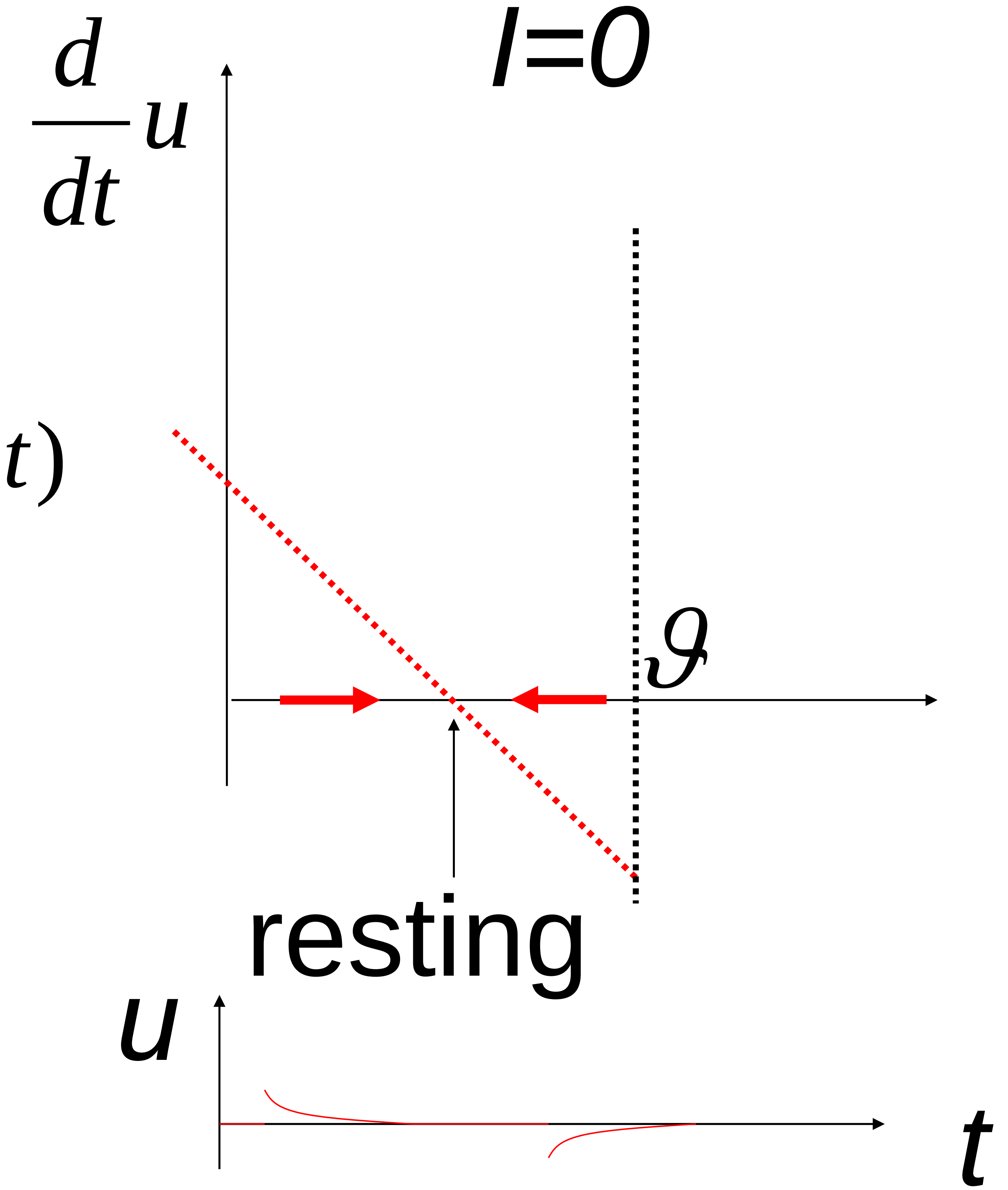
Neuronal Dynamics – 1.4. Leaky Integrate-and Fire revisited

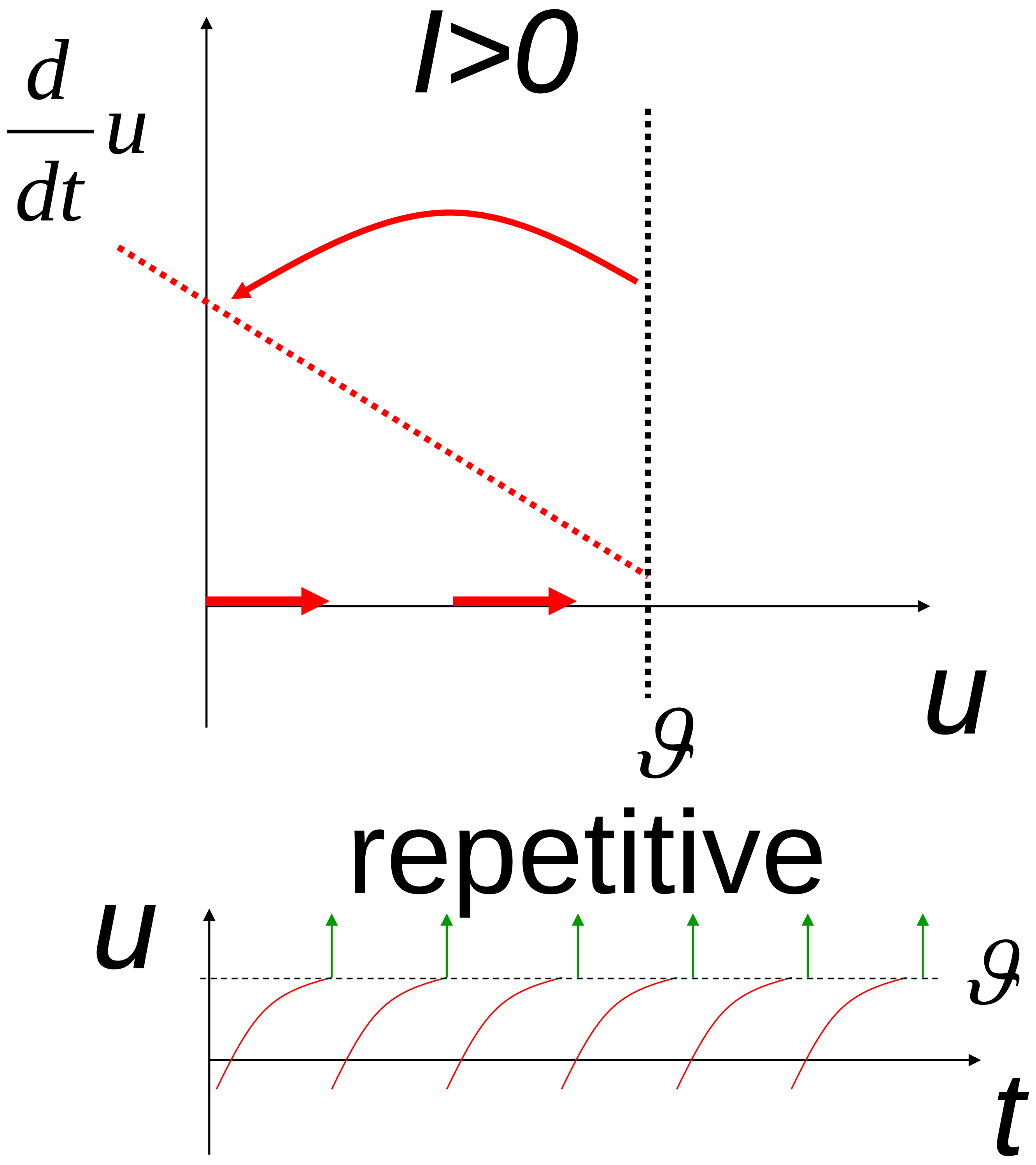
LIF

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

If firing:

$$u \to u_r$$





Neuronal Dynamics – 1.4. Nonlinear Integrate-and Fire

LIF

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

NLIF

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

If firing:

$$u \rightarrow u_{reset}$$

Neuronal Dynamics – 1.4. Nonlinear Integrate-and Fire

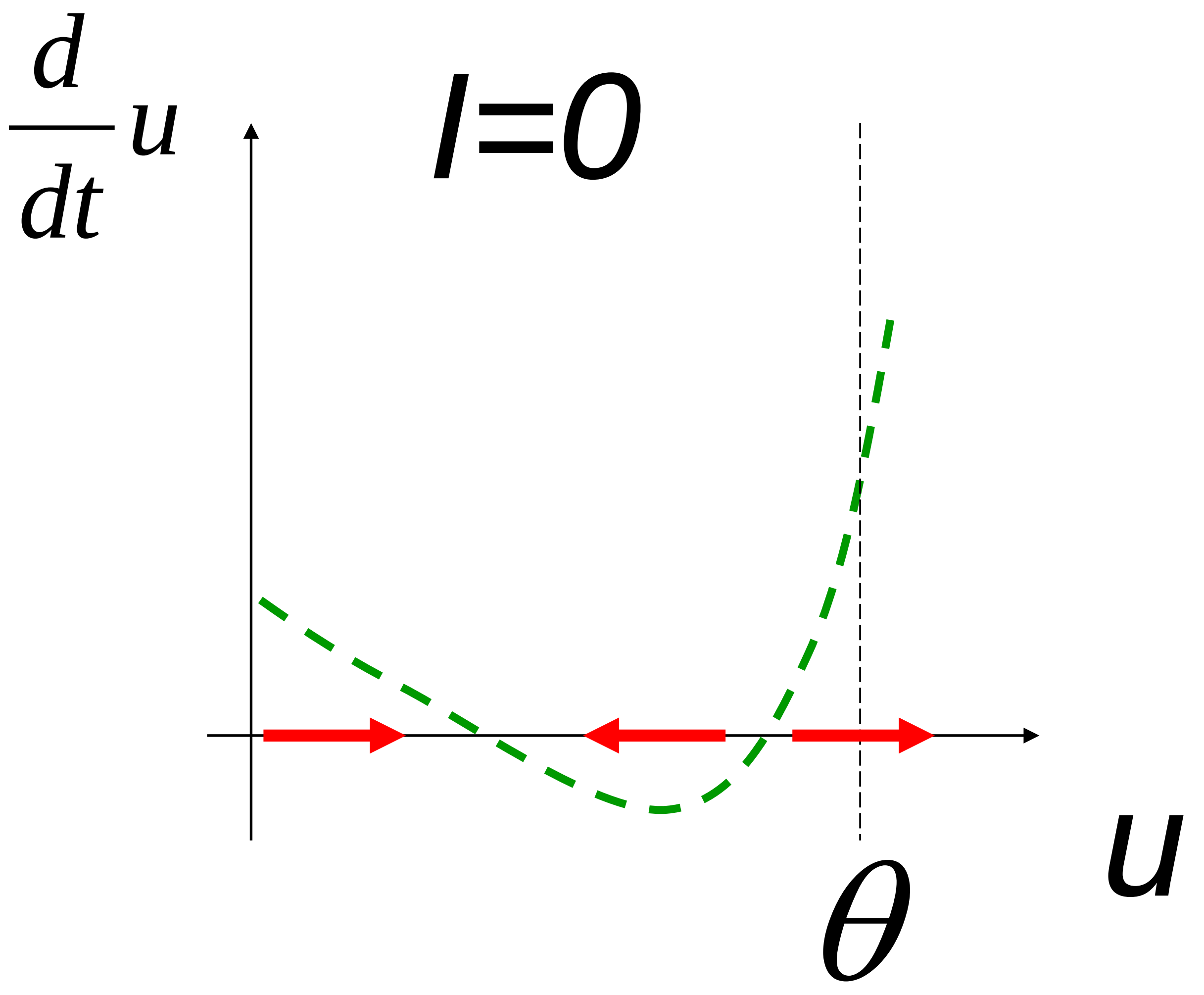
Nonlinear Integrate-and-Fire

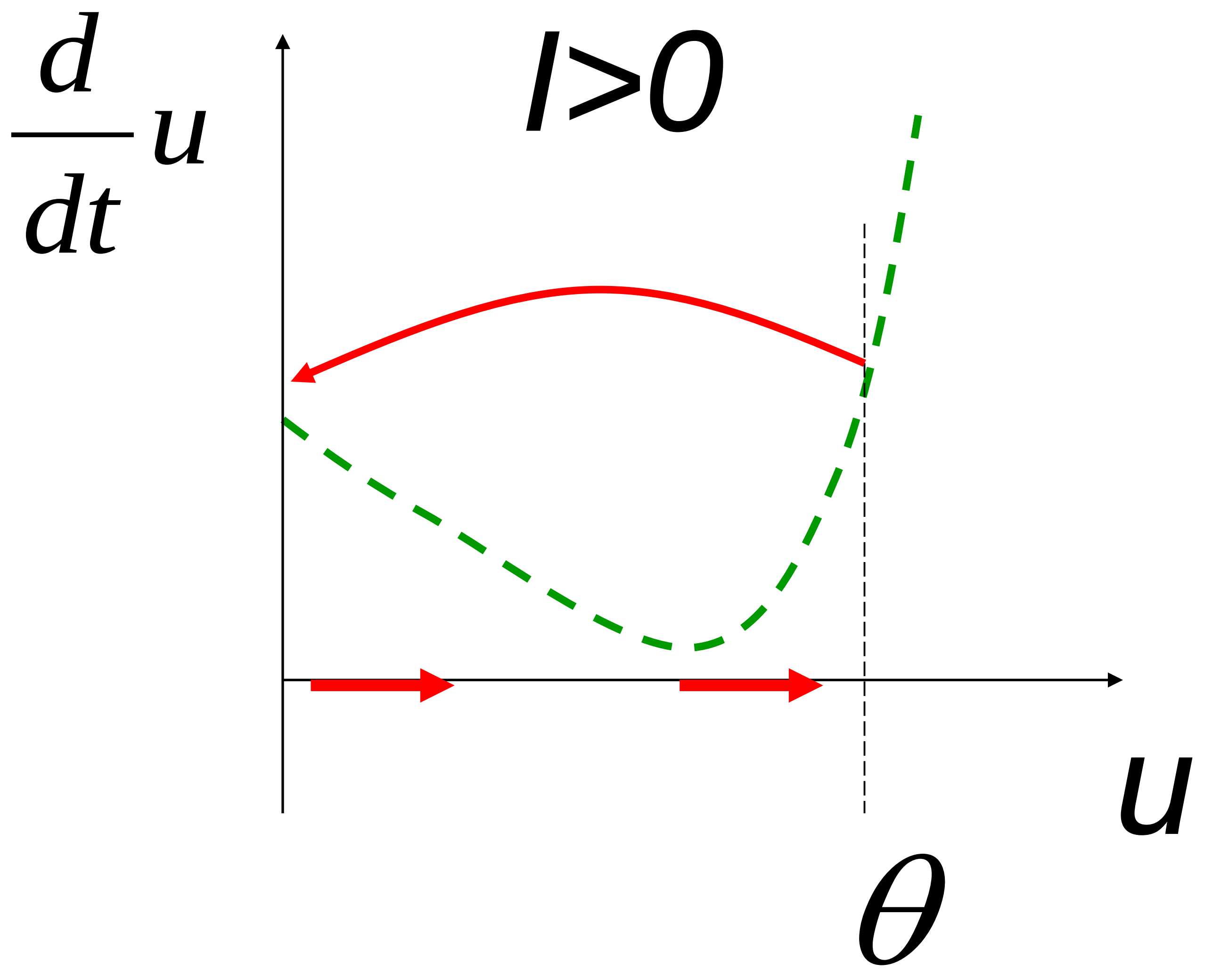
NLIF

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

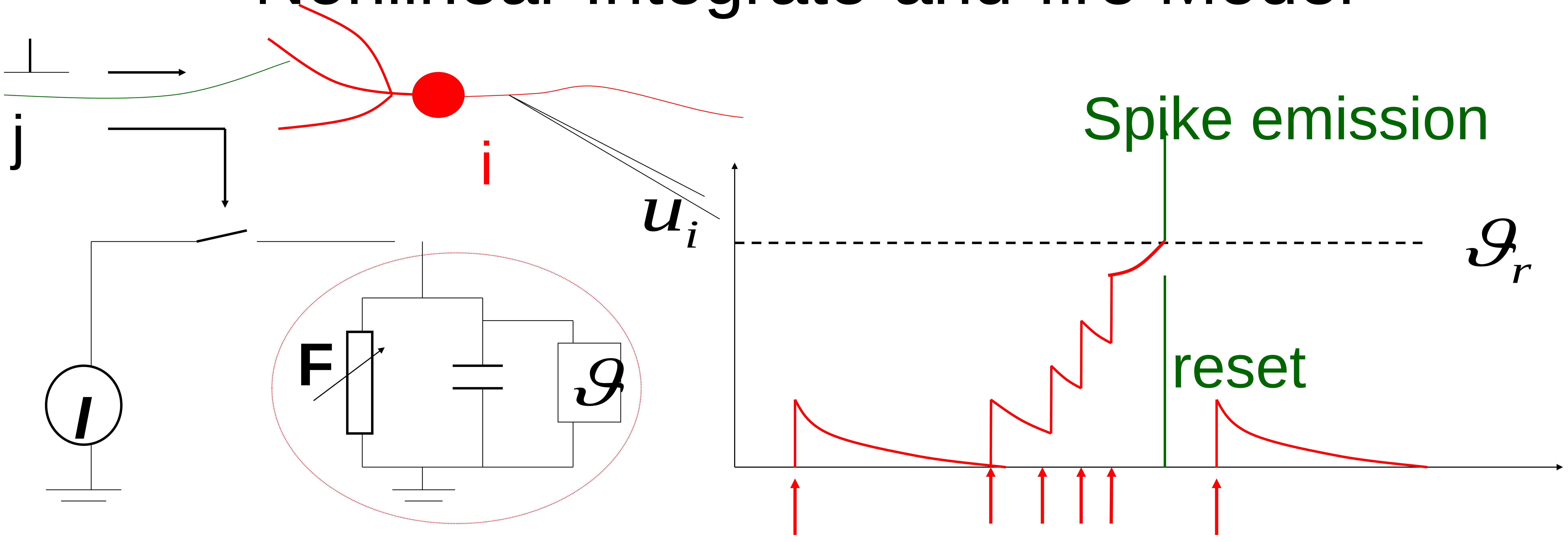
firing: $u(t) = \theta \Rightarrow$

$$u \rightarrow u_r$$





Nonlinear Integrate-and-fire Model



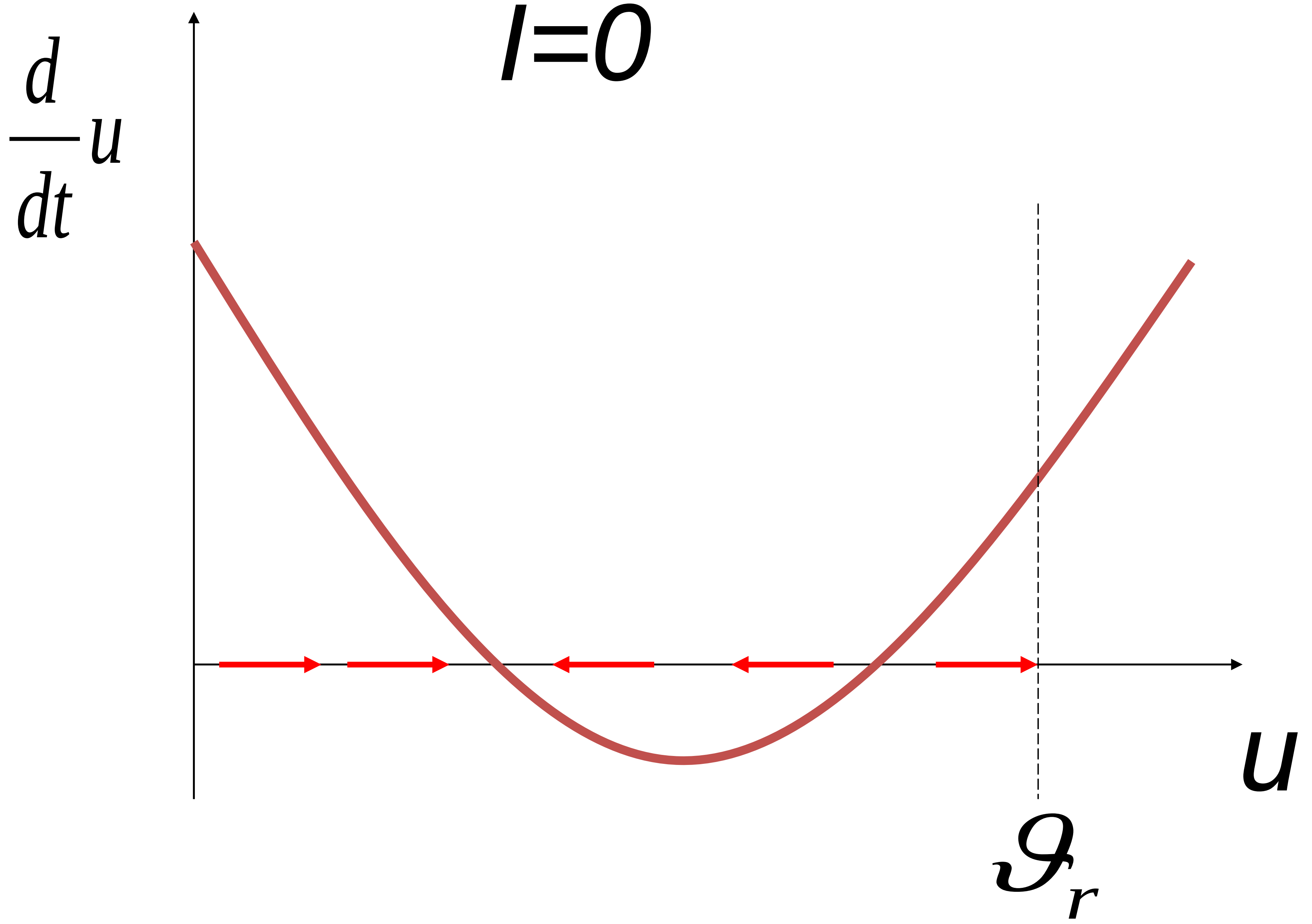
$$\tau \cdot \frac{d}{dt}u = F(u) + RI(t)$$

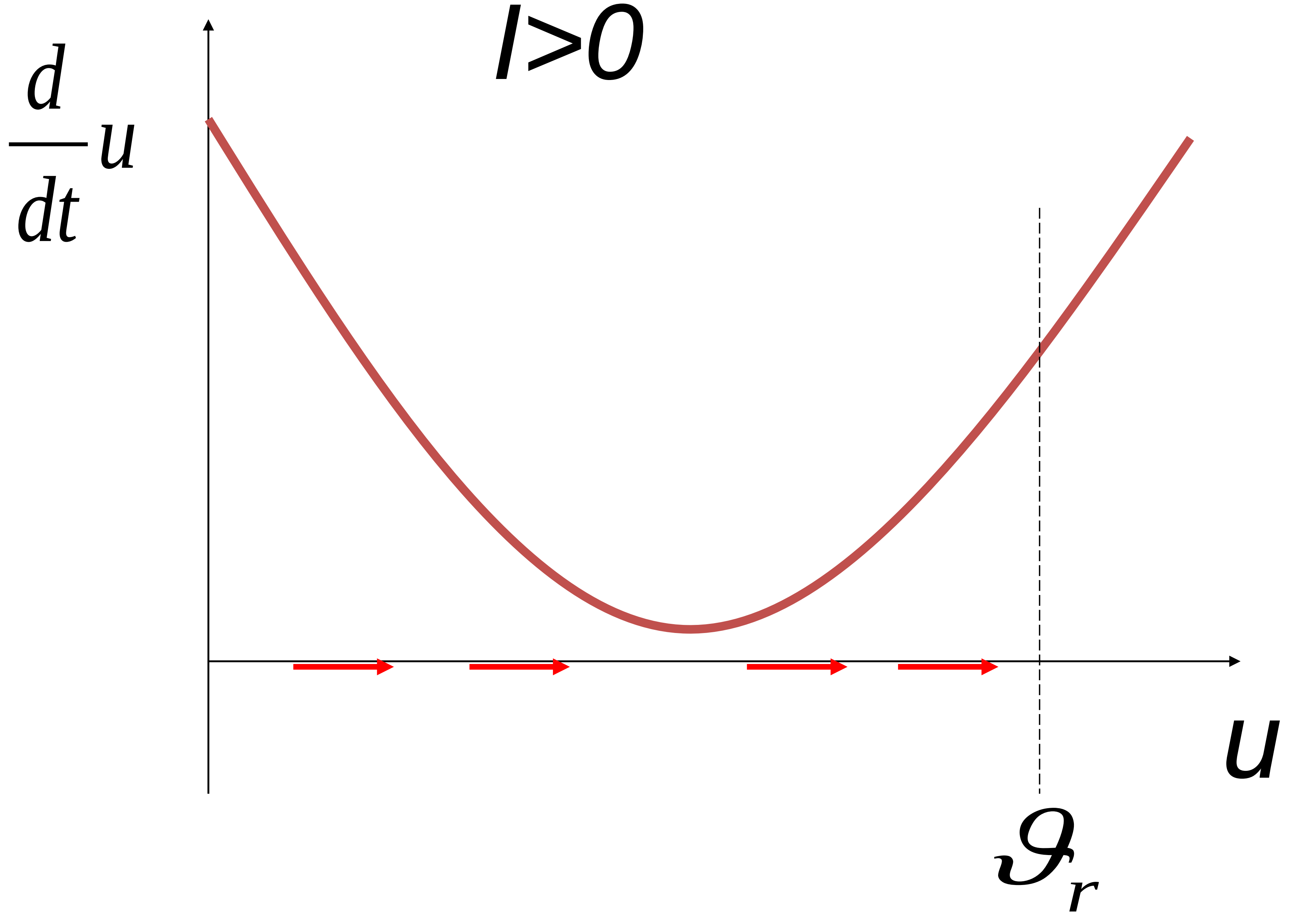
NONlinear

$$u(t) = \vartheta_r \Rightarrow$$

Fire+reset threshold

Nonlinear Integrate-and-fire Model





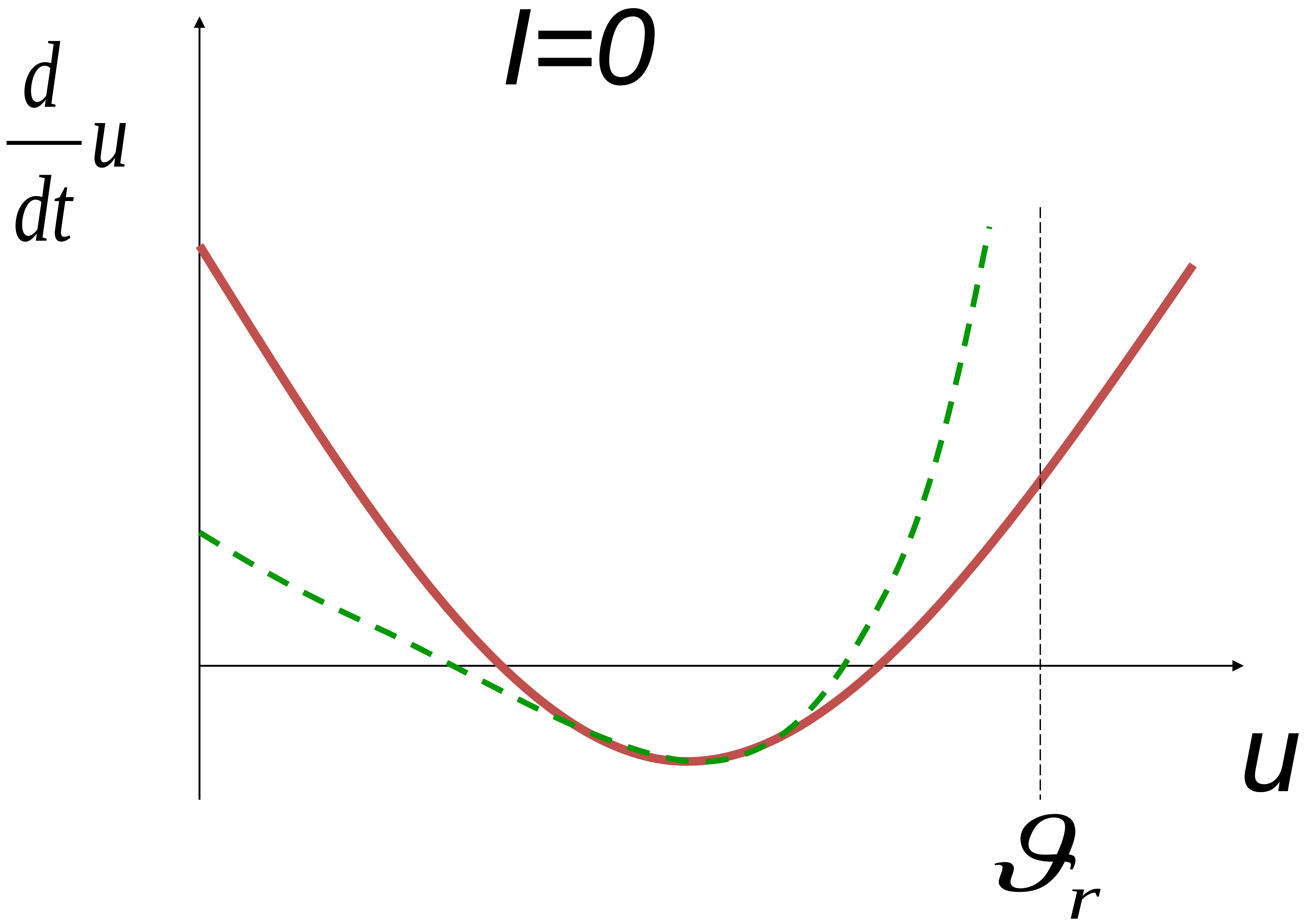
$$\tau \cdot \frac{d}{dt}u = F(u) + RI(t)$$ NONlinear

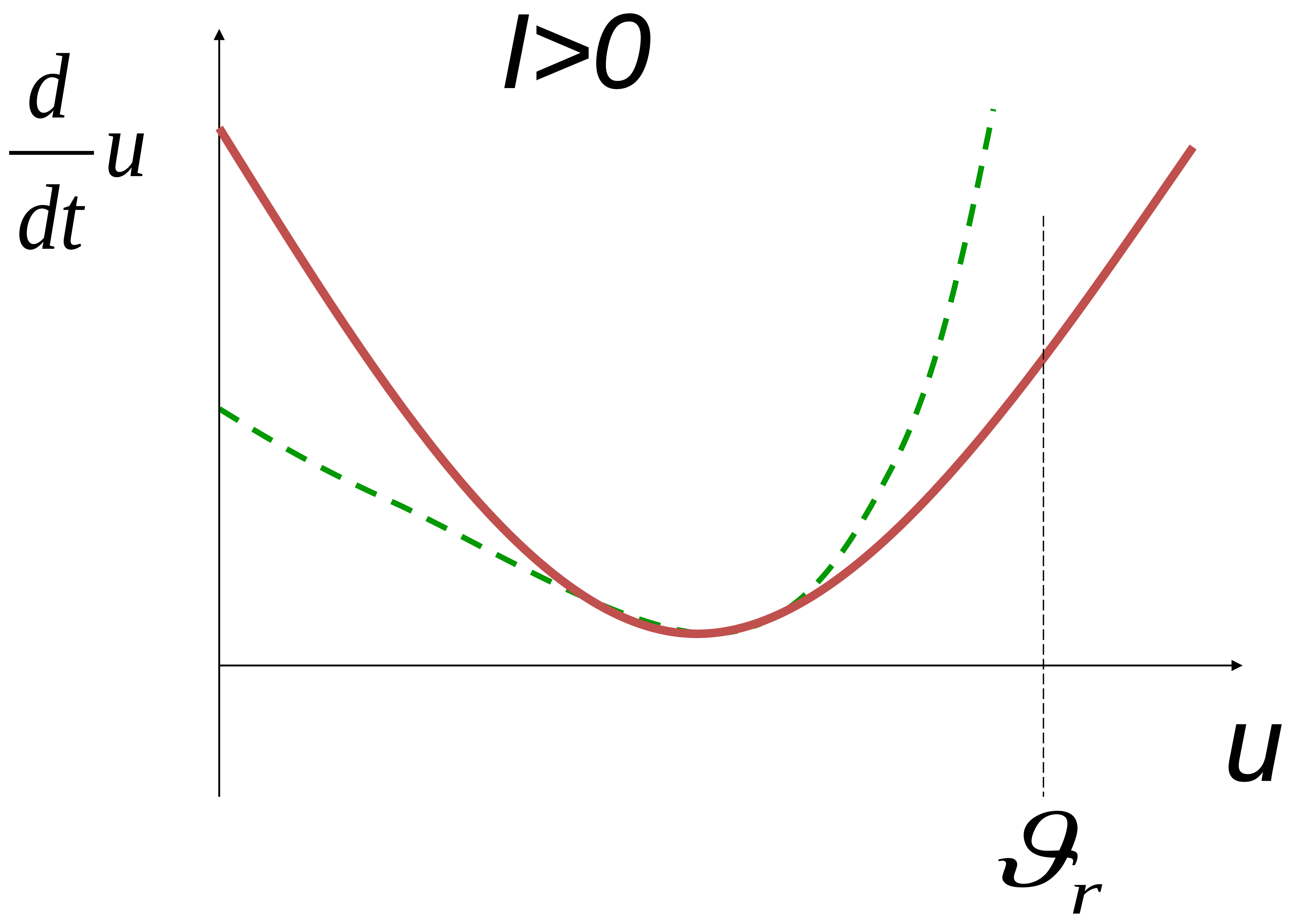
$$u(t) = \vartheta_r \Rightarrow$$ Fire+reset threshold

Quadratic I&F:

$$F(u) = c_2(u - c_1)^2 + c_0$$

Nonlinear Integrate-and-fire Model





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

$$u(t) = \vartheta_r \Rightarrow$$ Fire+reset

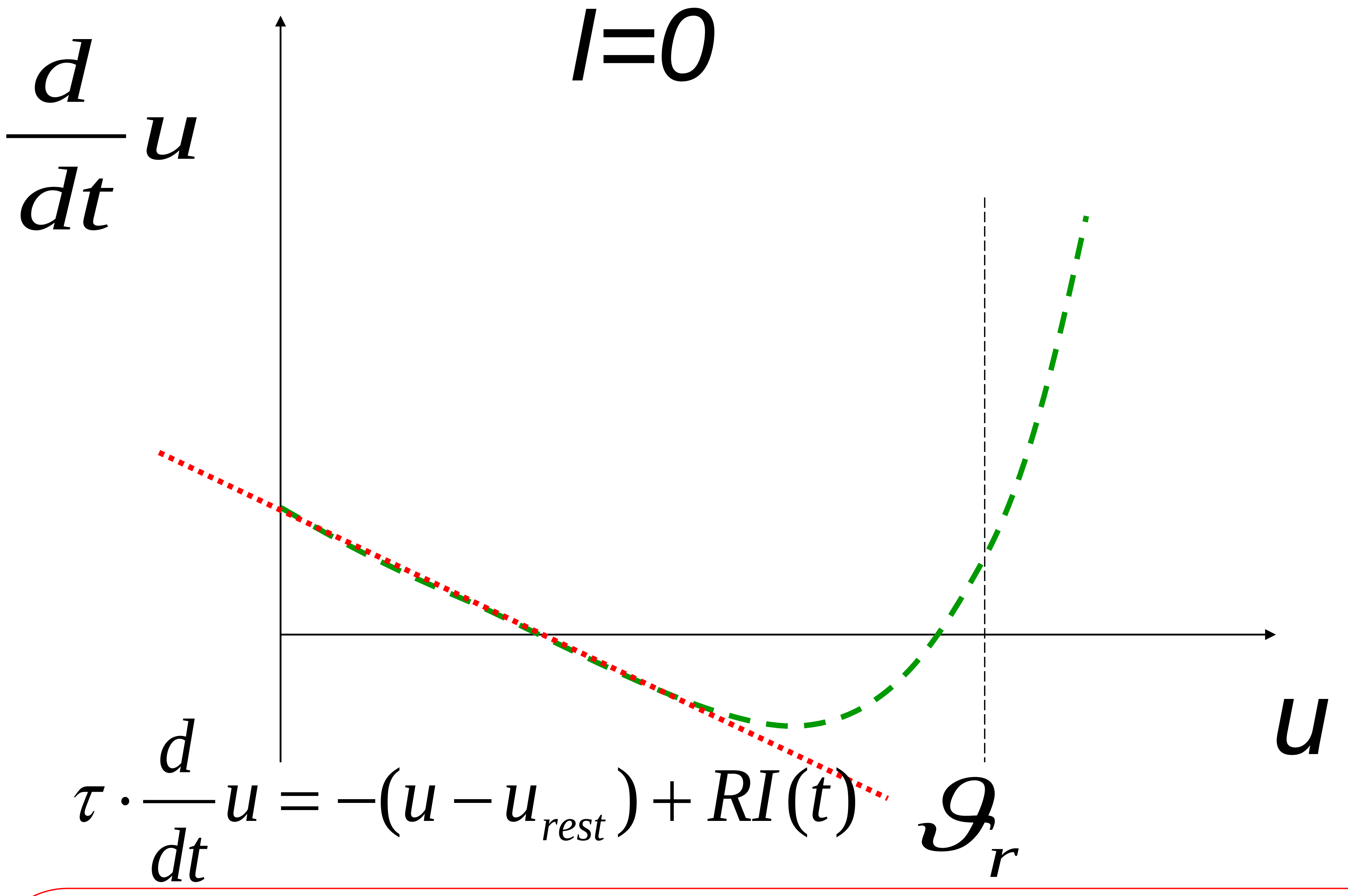
Quadratic I&F:

$$F(u) = c_2(u - c_1)^2 + c_0$$

exponential I&F:

$$F(u) = -(u - u_{rest}) + c_0 \exp(u - \vartheta)$$

Nonlinear Integrate-and-fire Model



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

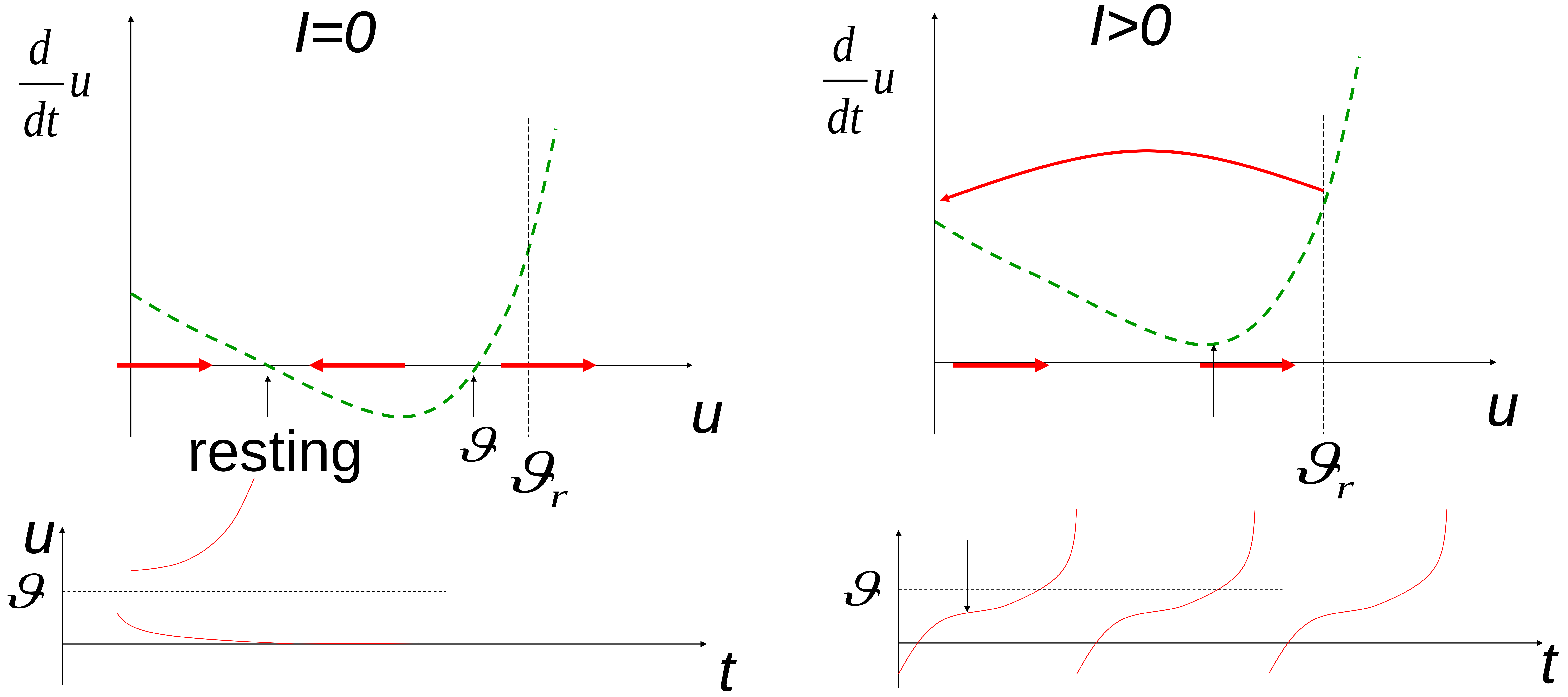
$$u(t) = \vartheta_r \Rightarrow$$ Fire+reset threshold

exponential I&F:

$$F(u) = -(u - u_{rest}) + c_0 \exp(u - \vartheta)$$

Nonlinear Integrate-and-fire Model

Where is the firing threshold?



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

Week 1 – part 5: How good are Integrate-and-Fire Model?

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

Biological Modeling of Neural Networks

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

Wulfram Gerstner

EPFL, Lausanne, Switzerland

√ 1.1 Neurons and Synapses:
Overview

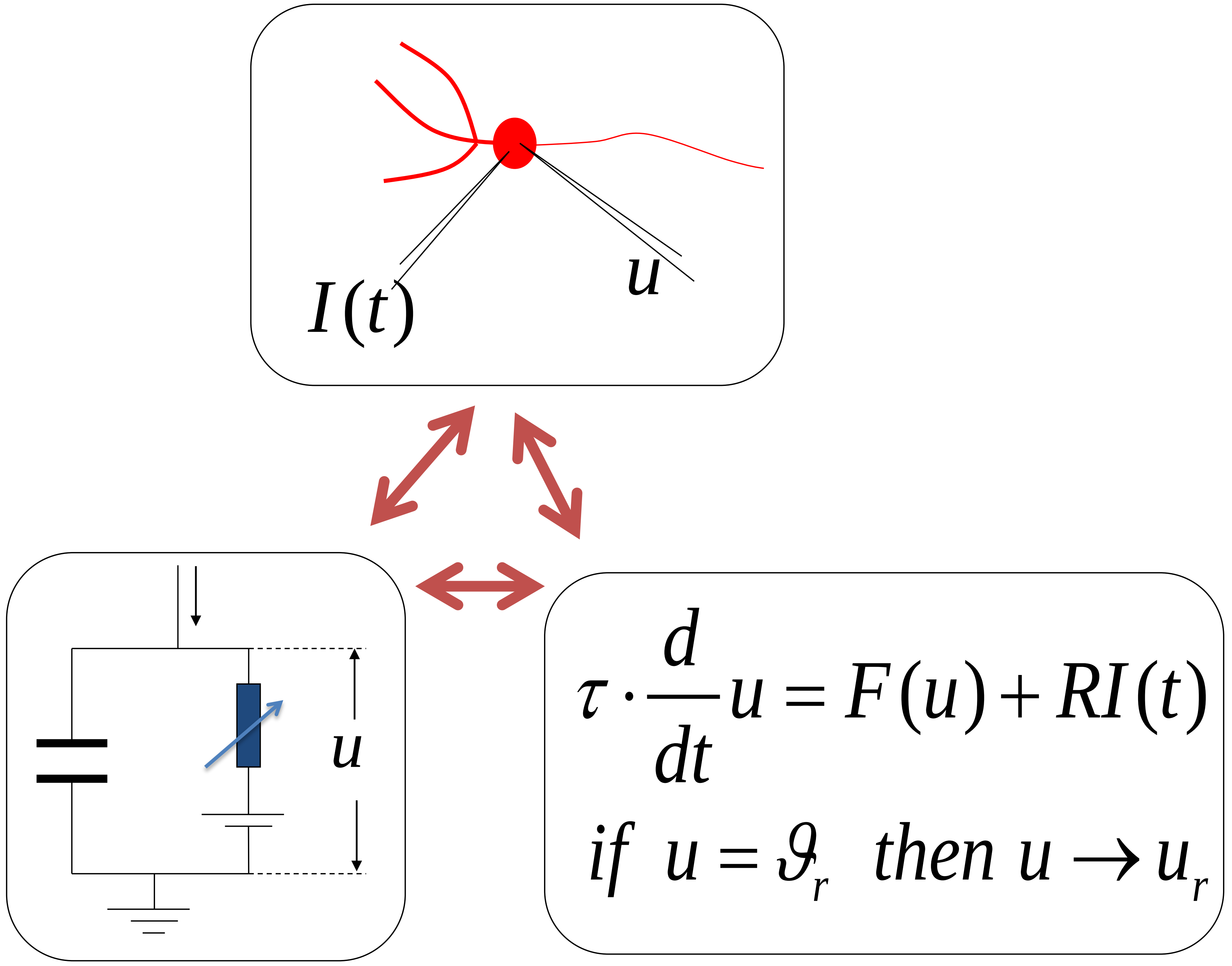
1.2 The Passive Membrane
- Linear circuit
- Dirac delta-function

√ 1.3 Leaky Integrate-and-Fire Model

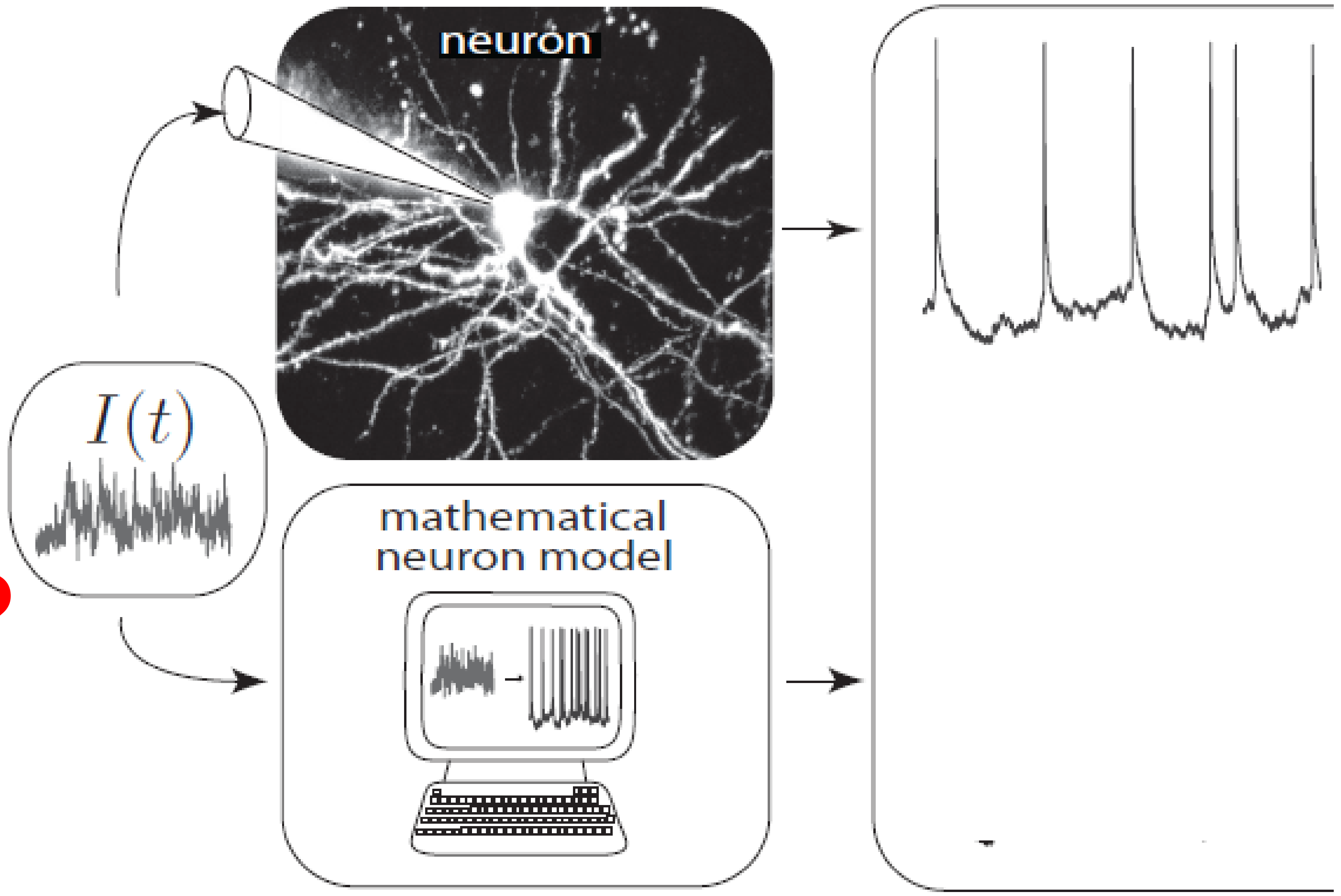
√ 1.4 Generalized Integrate-and-Fire Model
- where is the firing threshold?

1.5. Quality of Integrate-and-Fire Models
- Neuron models and experiments

Neuronal Dynamics – 1.5.How good are integrate-and-fire models?



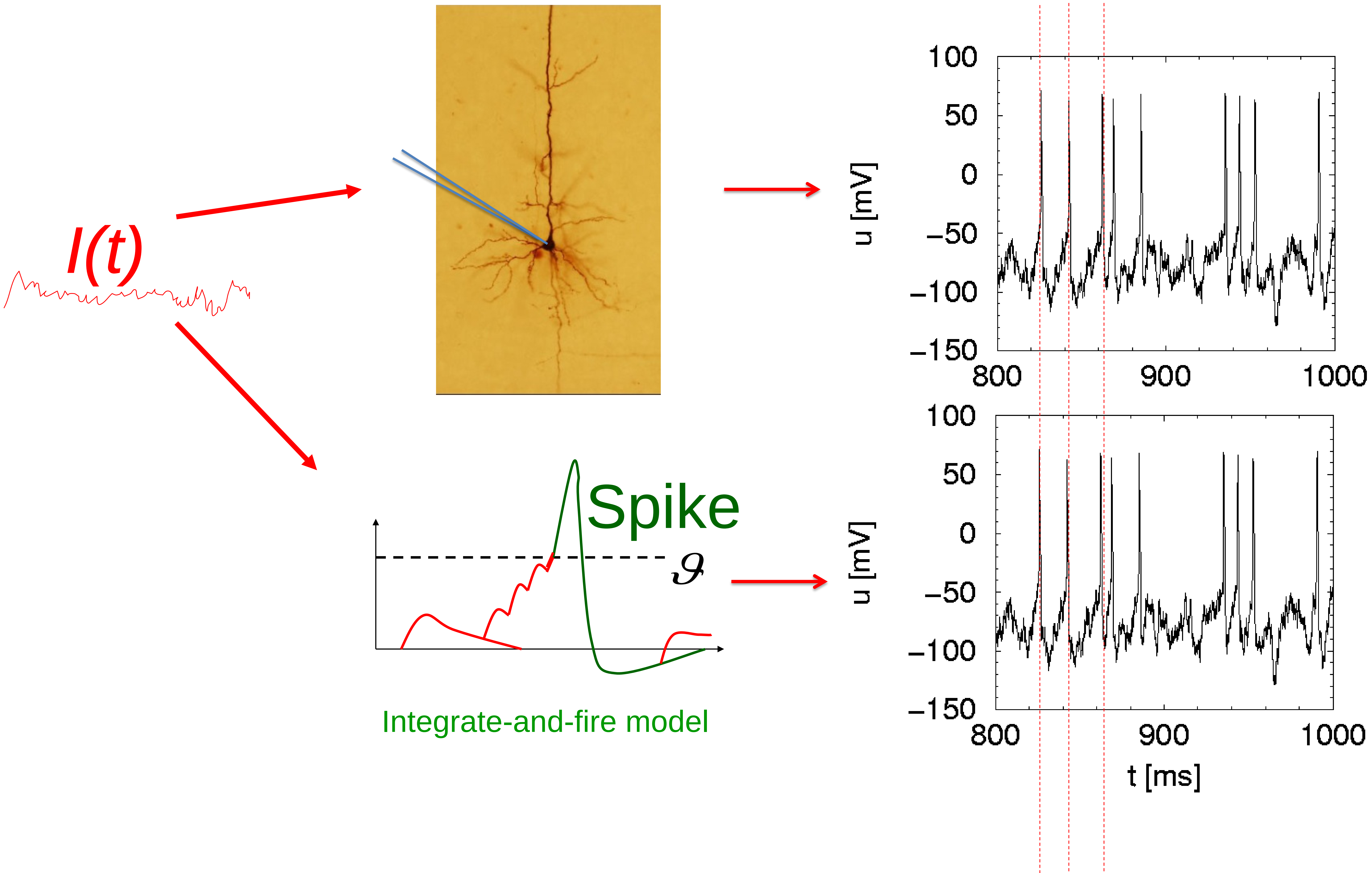
Can we compare neuron models with experimental data?



What is a good neuron model?

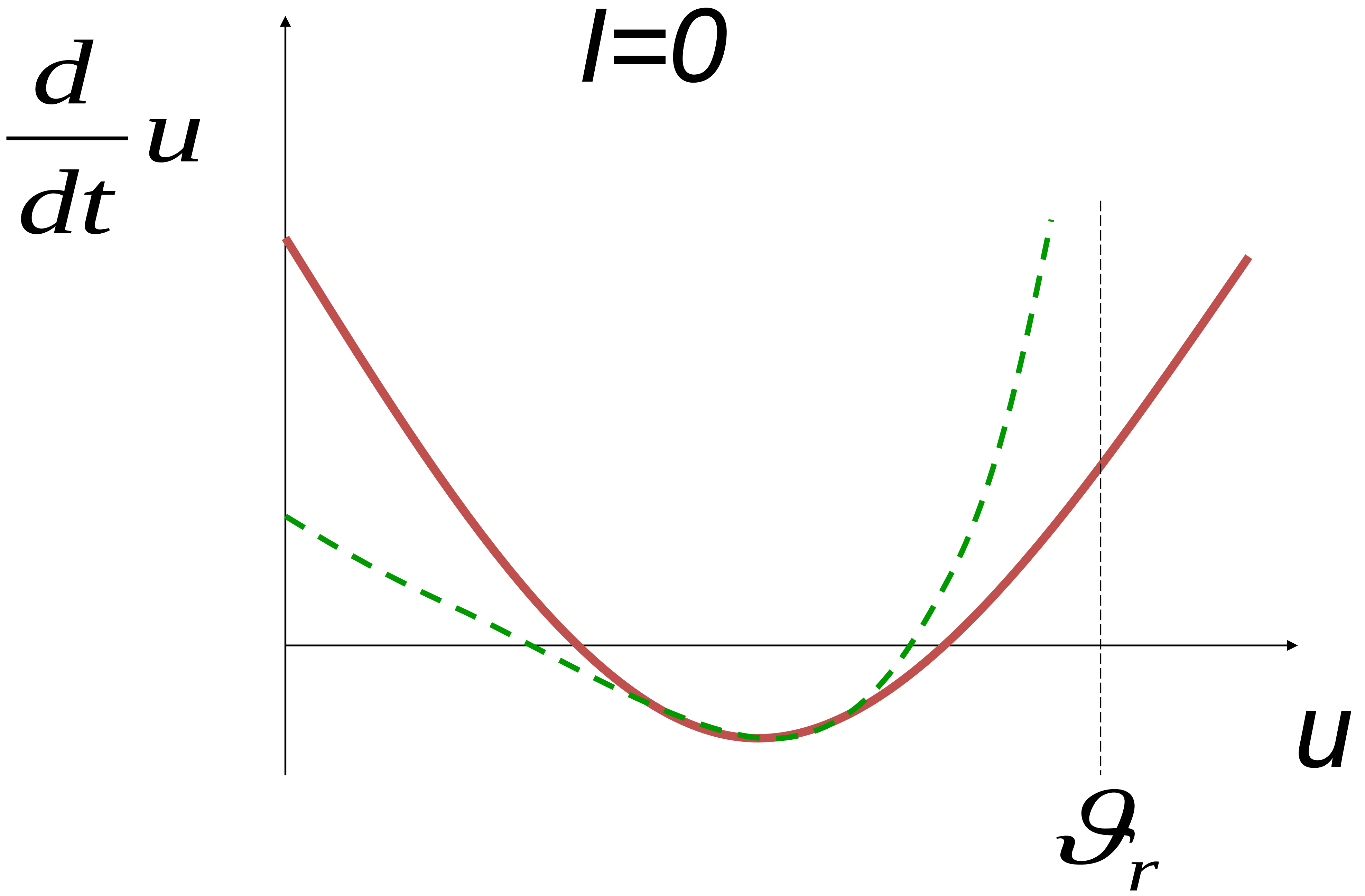
Can we compare neuron models
with experimental data?

Neuronal Dynamics – 1.5.How good are integrate-and-fire models?



Integrate-and-fire model

Nonlinear Integrate-and-fire Model



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

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

$$u(t) = \vartheta_r \Rightarrow \text{ Fire+reset}$$

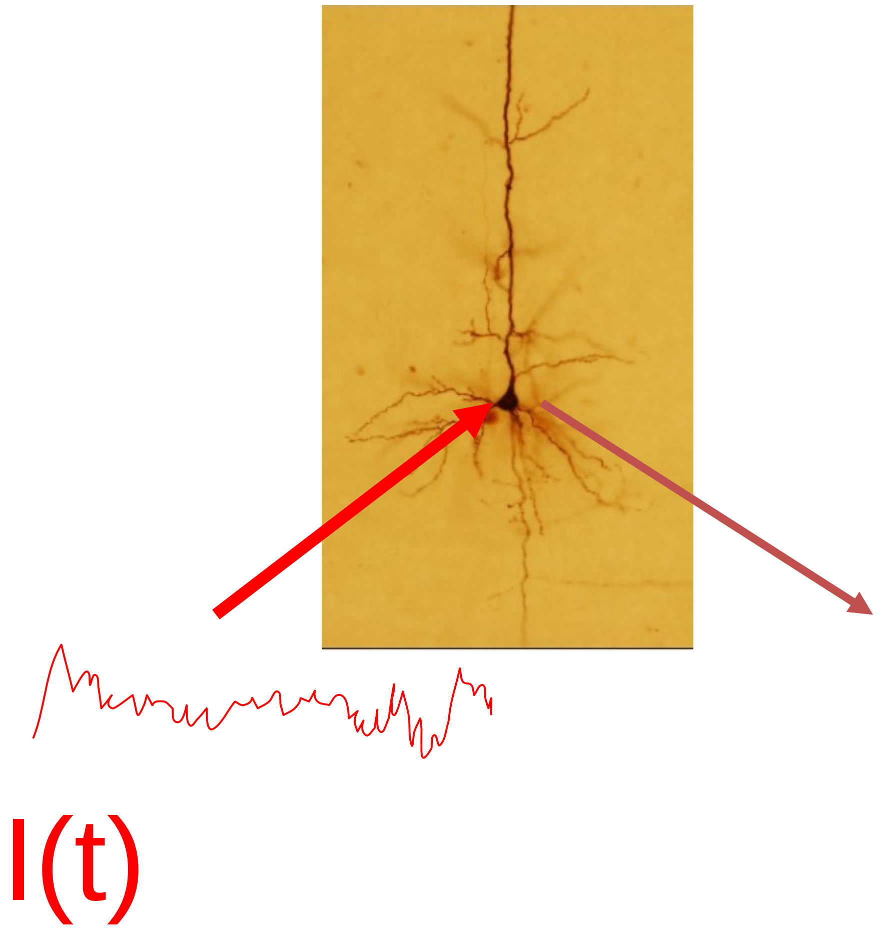
Quadratic I&F:

$$F(u) = c_2 (u - c_1)^2 + c_0$$

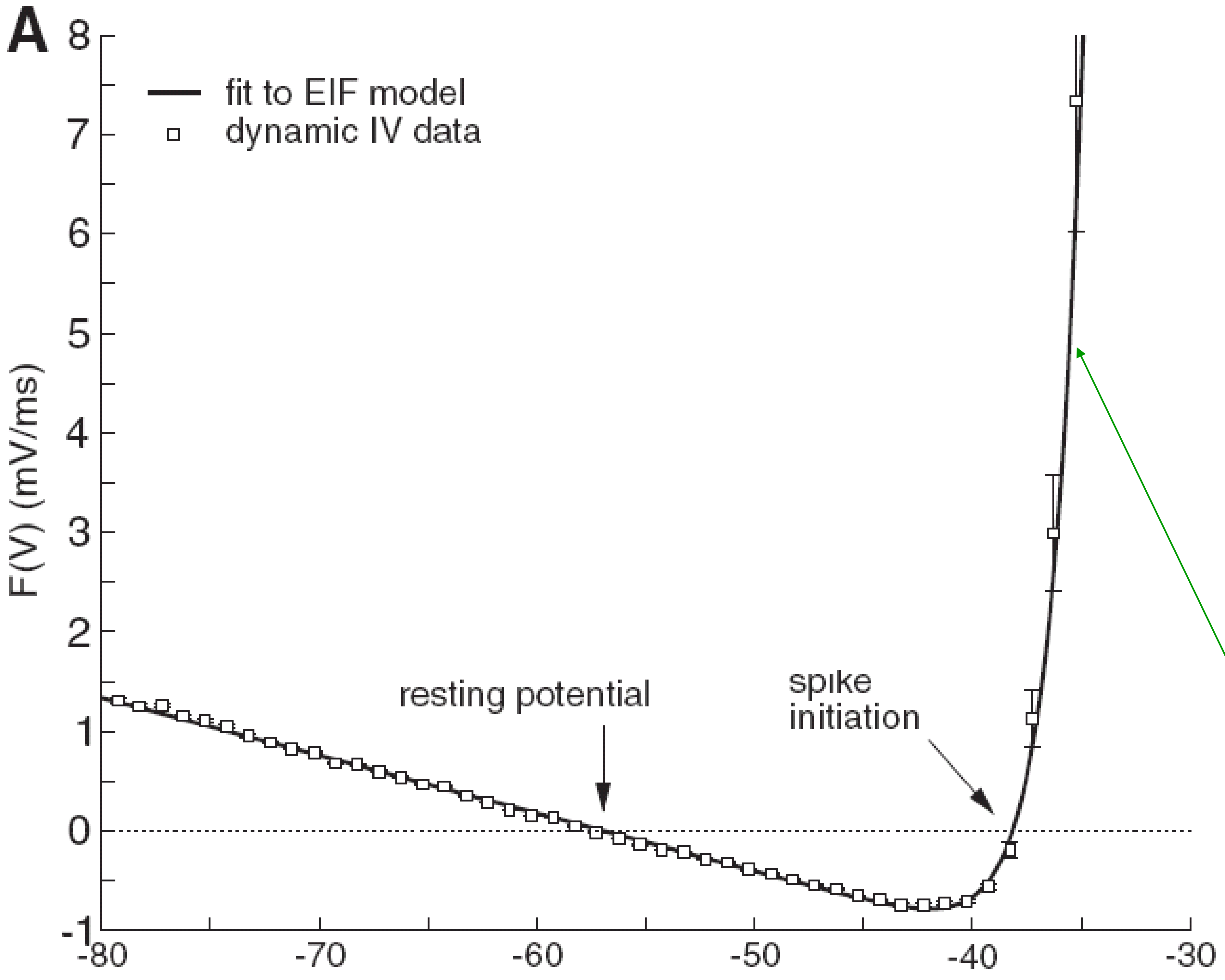
exponential I&F:

$$F(u) = -(u - u_{rest}) + c_0 \exp(u - \vartheta)$$

Neuronal Dynamics – 1.5.How good are integrate-and-fire models?



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

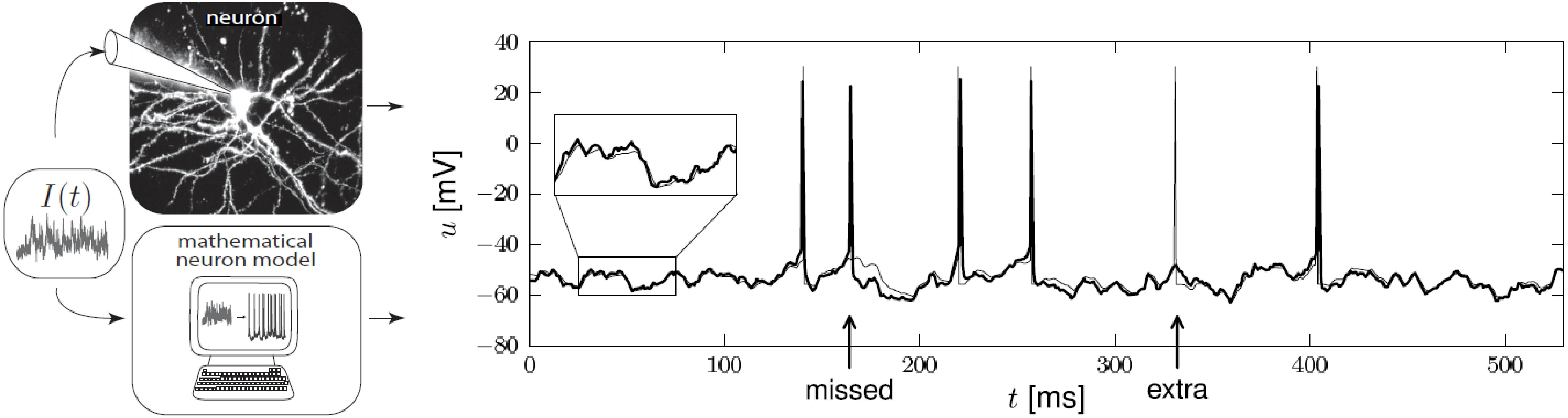


$$F(u) = -(u - u_{rest}) + \Delta \exp\left(\frac{u-\vartheta}{\Delta}\right)$$

u [mV]

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

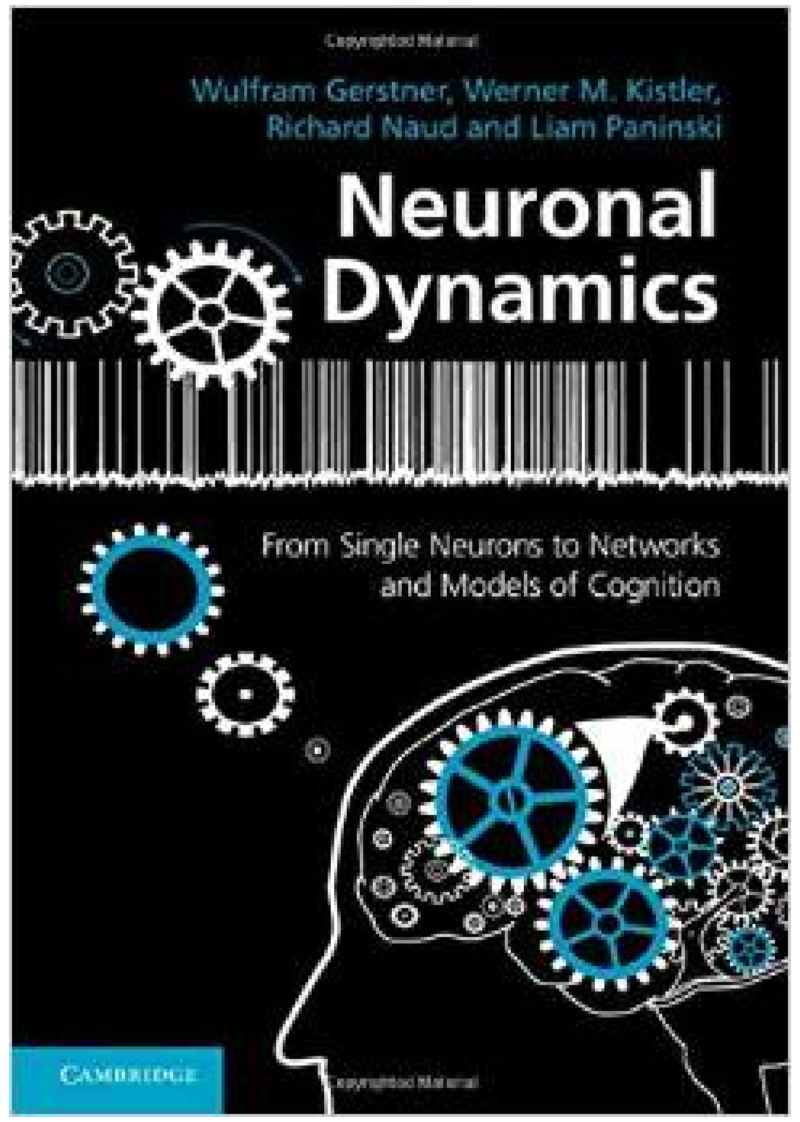
Need to add
- adaptation
- noise
- dendrites/synapses

Computer ecercises:
Python

Biological Modeling of Neural Networks

http://neuronaldynamics.epfl.ch/

Textbook:



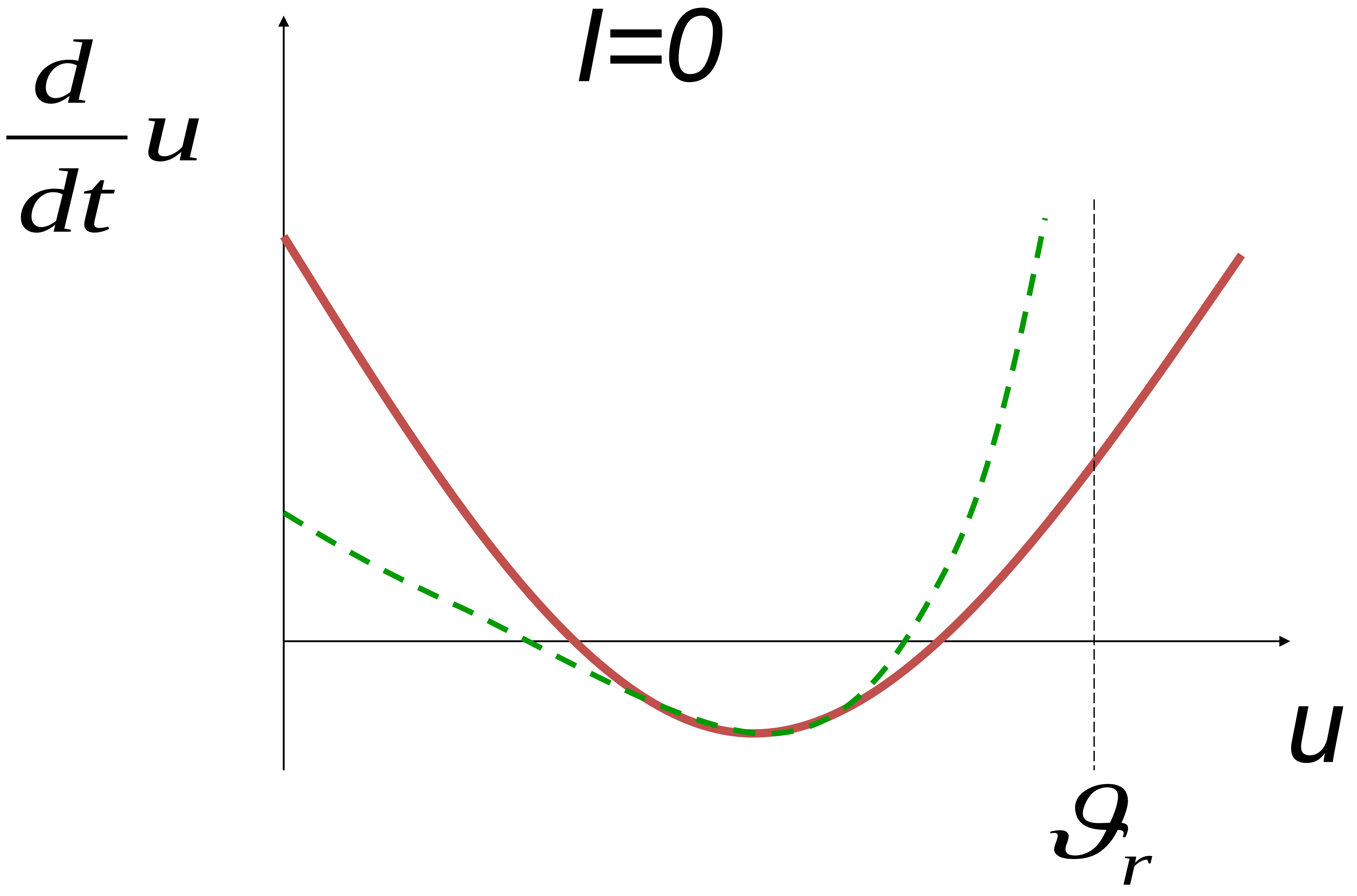
Lecture today:
-Chapter 1
-Chapter 5

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

Videos (for today: 'week 1'):

http://lcn.epfl.ch/~gerstner/NeuronalDynamics-MOOC1.html

Biological Modeling of Neural Networks – week1/Exercise 3



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

Homework!

First week – References and Suggested Reading

Reading: W. Gerstner, W.M. Kistler, R. Naud and L. Paninski, *Neuronal Dynamics: from single neurons to networks and models of cognition.* Chapter 1*: Introduction*. Cambridge Univ. Press, 2014

Selected references to linear and nonlinear integrate-and-fire models
- Lapicque, L. (1907). *Recherches quantitatives sur l'excitation electrique des nerfs traitee comme une polarization.* J. Physiol. Pathol. Gen., 9:620-635.
-Stein, R. B. (1965). A theoretical analysis of neuronal variability. Biophys. J., 5:173-194.
-Ermentrout, G. B. (1996). *Type I membranes, phase resetting curves, and synchrony*. Neural Computation, 8(5):979-1001.
-Fourcaud-Trocme, N., Hansel, D., van Vreeswijk, C., and Brunel, N. (2003). *How spike generation mechanisms determine the neuronal response to fluctuating input.* J. Neuroscience, 23:11628-11640.
-Badel, L., Lefort, S., Berger, T., Petersen, C., Gerstner, W., and Richardson, M. (2008). Biological Cybernetics, 99(4-5):361-370.
- Latham, P. E., Richmond, B., Nelson, P., and Nirenberg, S. (2000). *Intrinsic dynamics in neuronal networks. I. Theory.* J. Neurophysiology, 83:808-827.

First week

THE END (of main lecture)

MATH DETOUR SLIDES (for online VIDEO)

Week 1 – part 2: Detour/Linear differential equation

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Neuronal Dynamics:
Computational Neuroscience of Single Neurons

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

Wulfram Gerstner
EPFL, Lausanne, Switzerland

√ 1.1 Neurons and Synapses: Overview

√ 1.2 The Passive Membrane
- Linear circuit
- Dirac delta-function
- $\boxed{\text{Detour: solution of 1-dim linear differential equation}}$

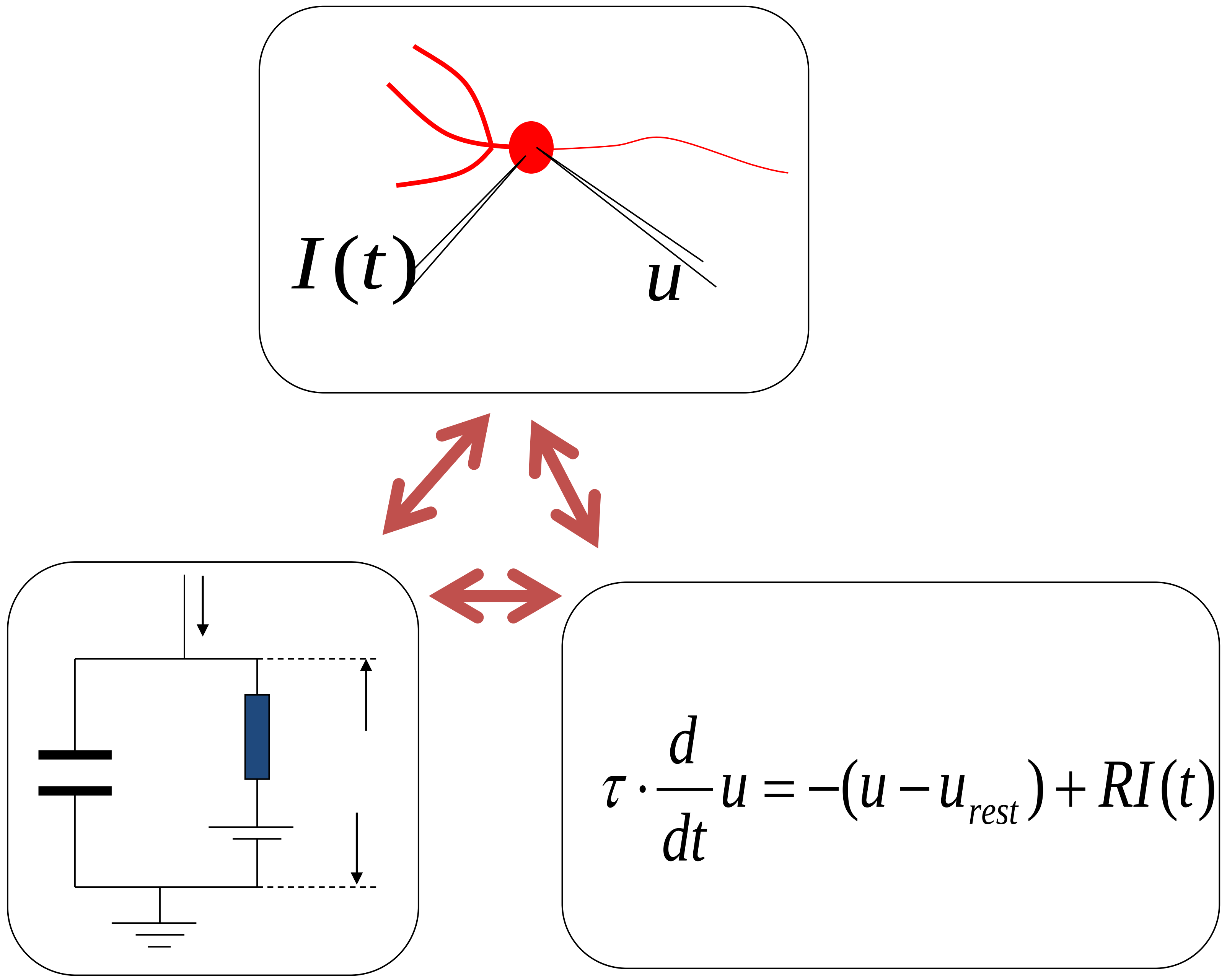
1.3 Leaky Integrate-and-Fire Model

1.4 Generalized Integrate-and-Fire Model

1.5. Quality of Integrate-and-Fire Models

Neuronal Dynamics – 1.2Detour – Linear Differential Eq.

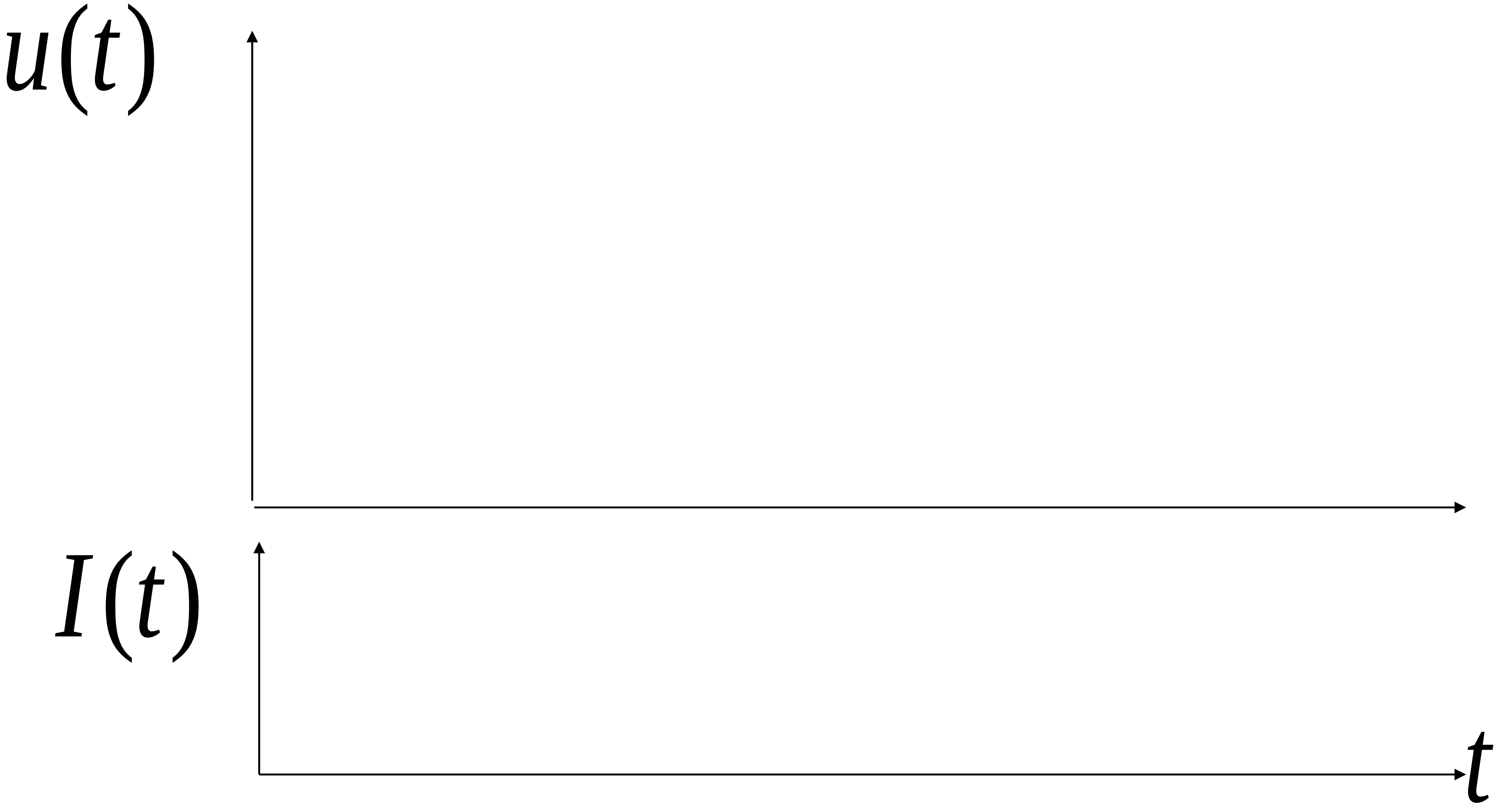
$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$

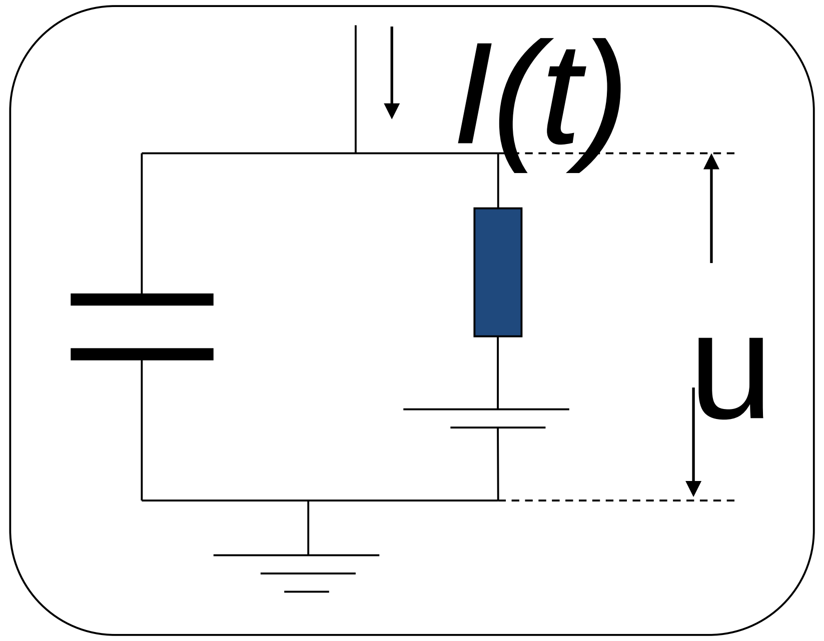


Neuronal Dynamics – 1.2Detour – Linear Differential Eq.

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

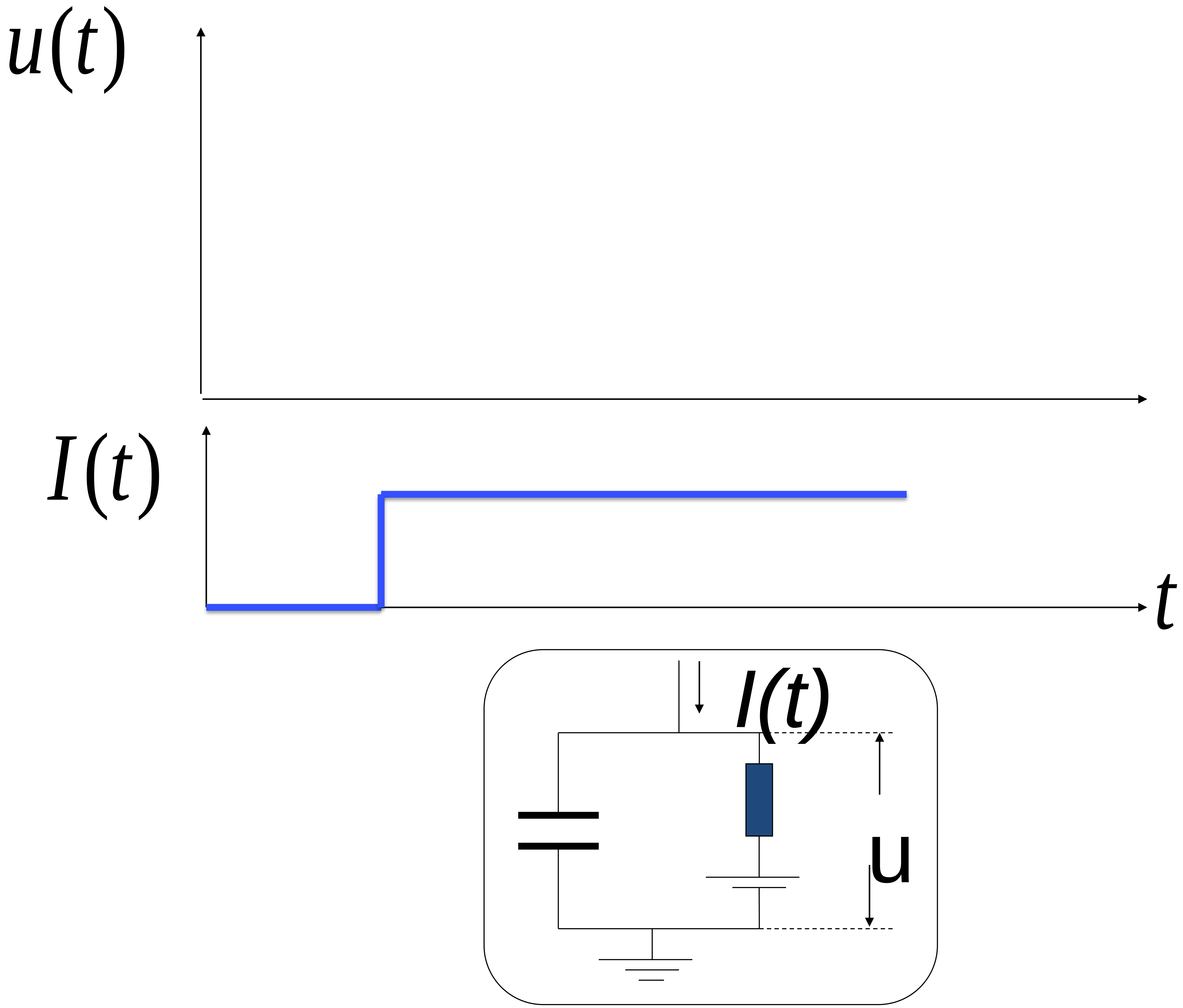
Math development:
Response to step current





Neuronal Dynamics – 1.2Detour – Step current input

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

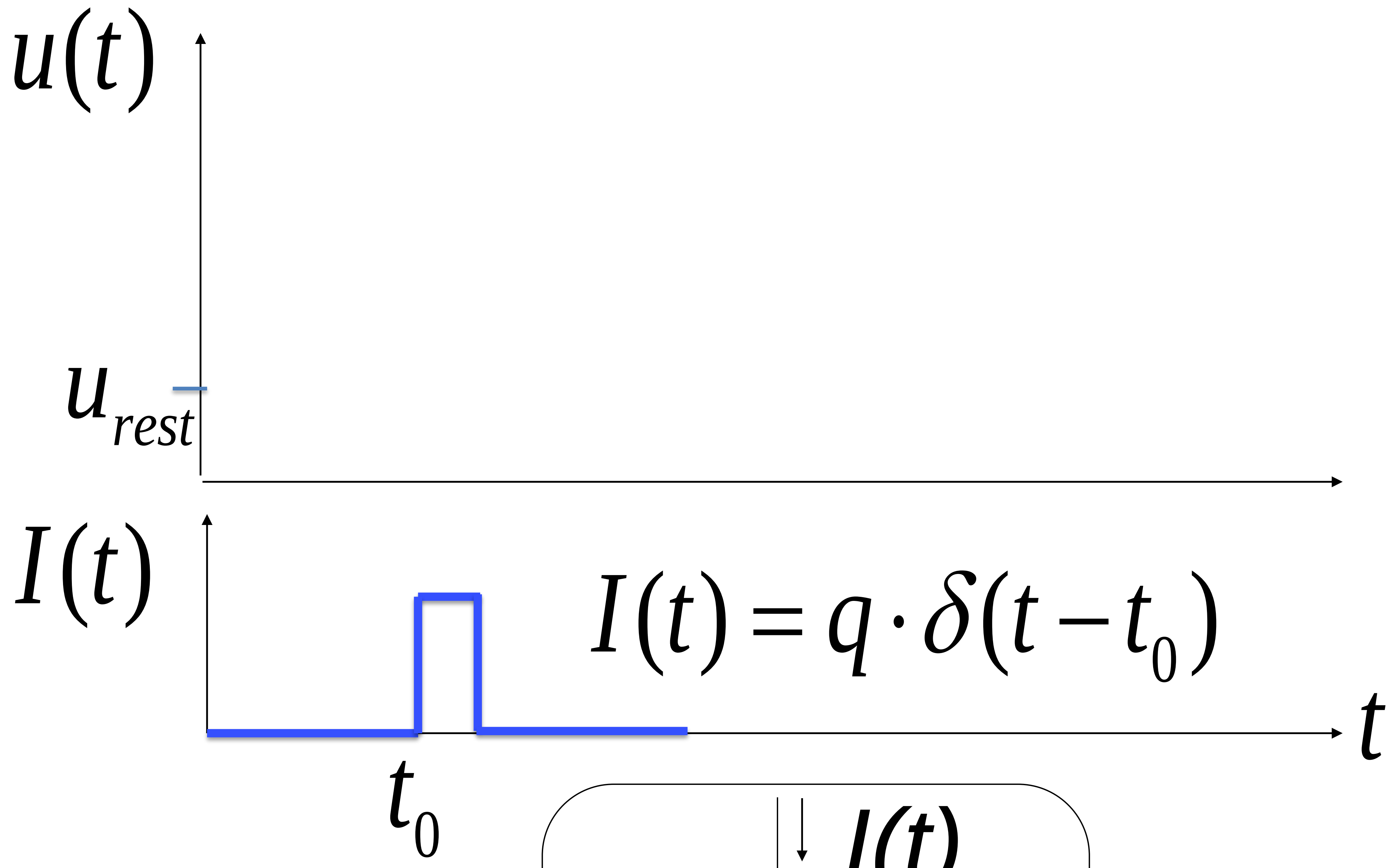


Neuronal Dynamics – 1.2Detour – Short pulse input

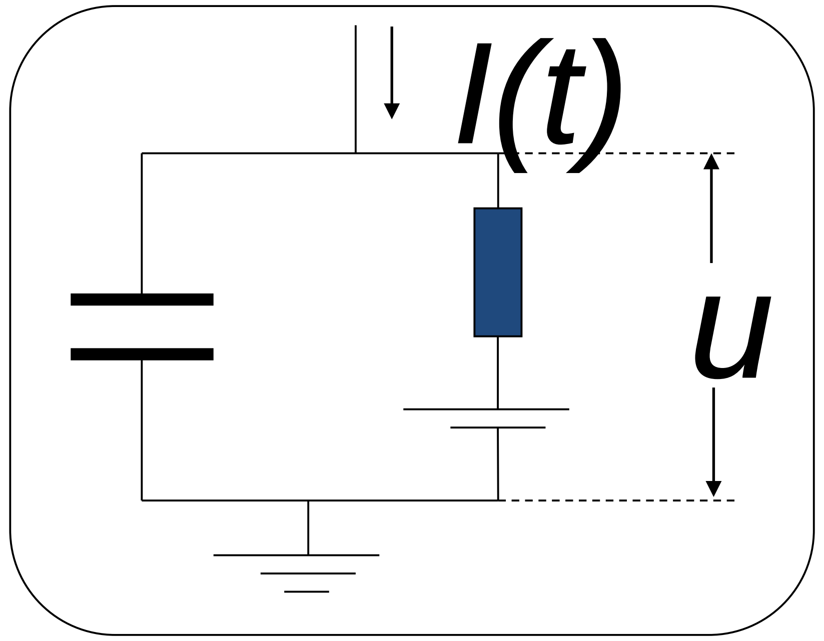
$$u(t) = u_{rest} + RI_0\left[1 - e^{-(t-t_0)/\tau}\right]$$

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

short pulse: $(t - t_0) << \tau$



Math development: Response to short current pulse

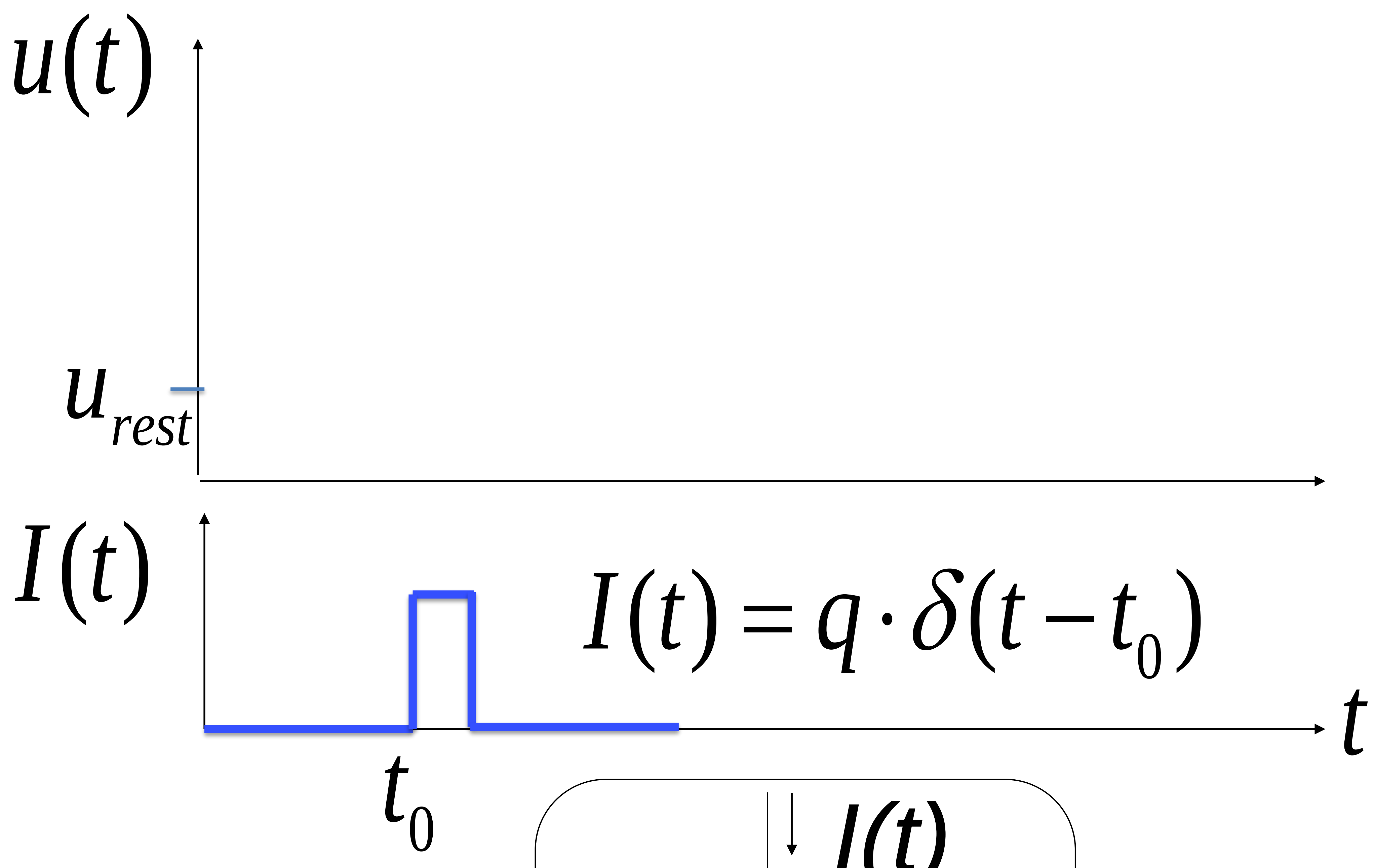


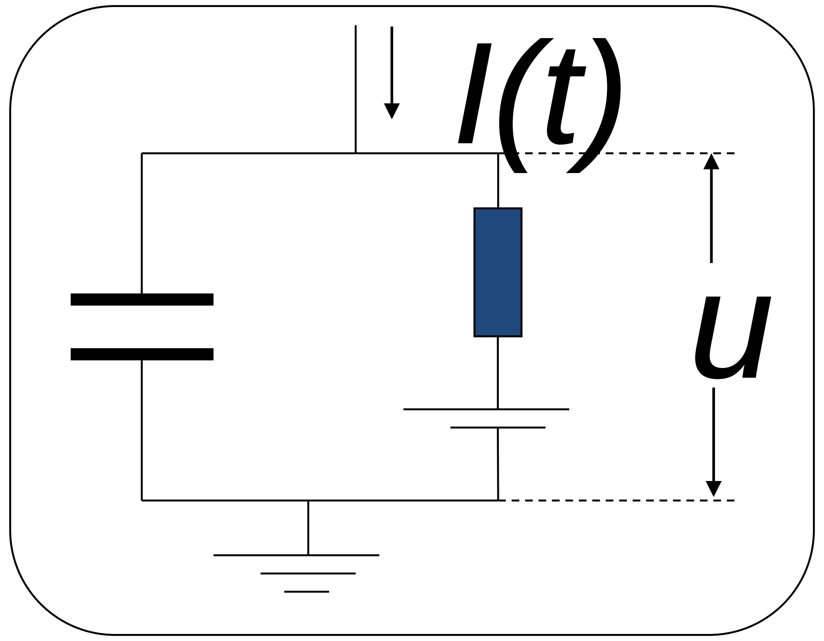
Neuronal Dynamics – 1.2Detour – Short pulse input

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

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

short pulse: $(t - t_0) << \tau$





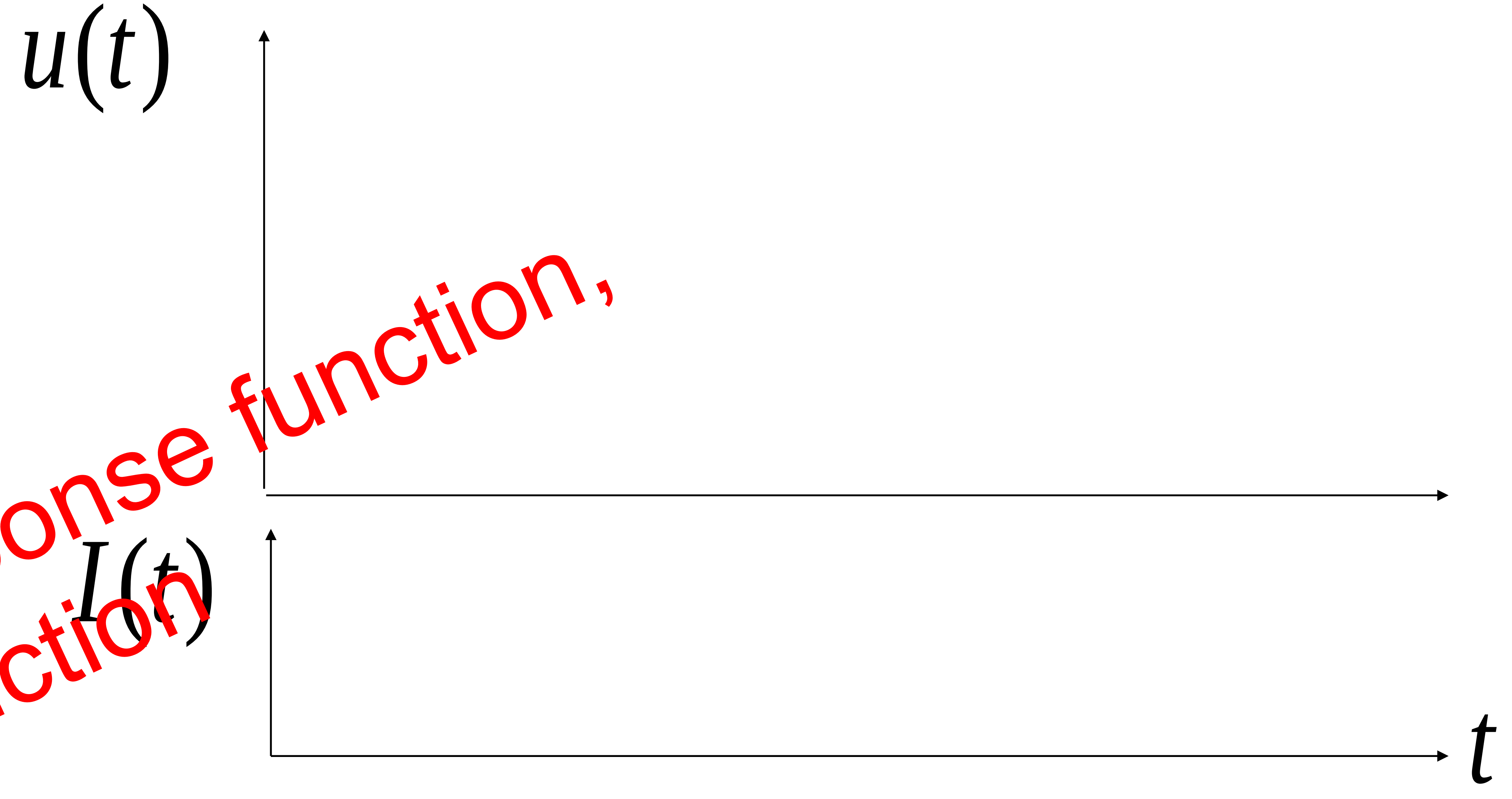
$$u(t) = u_{rest} + \frac{q}{C}e^{-(t-t_0)/\tau}$$

Neuronal Dynamics – 1.2Detour – arbitrary input

Single pulse

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

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



Multiple pulses:

Impulse response function,
Green's function

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

Neuronal Dynamics – 1.2Detour – Greens function

Single pulse

$$\Delta u(t) = q\frac{1}{C}e^{-(t-t_0)/\tau}$$

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

Multiple pulses:

Impulse response function,
Green's function

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

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

Neuronal Dynamics – 1.2Detour – arbitrary input

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

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

Arbitrary input

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

Single pulse

$$\Delta u(t) = \frac{q}{c} e^{-(t-t_0)/\tau}$$

you need to know the solutions of linear differential equations!