Biological Modeling of Neural Networks

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

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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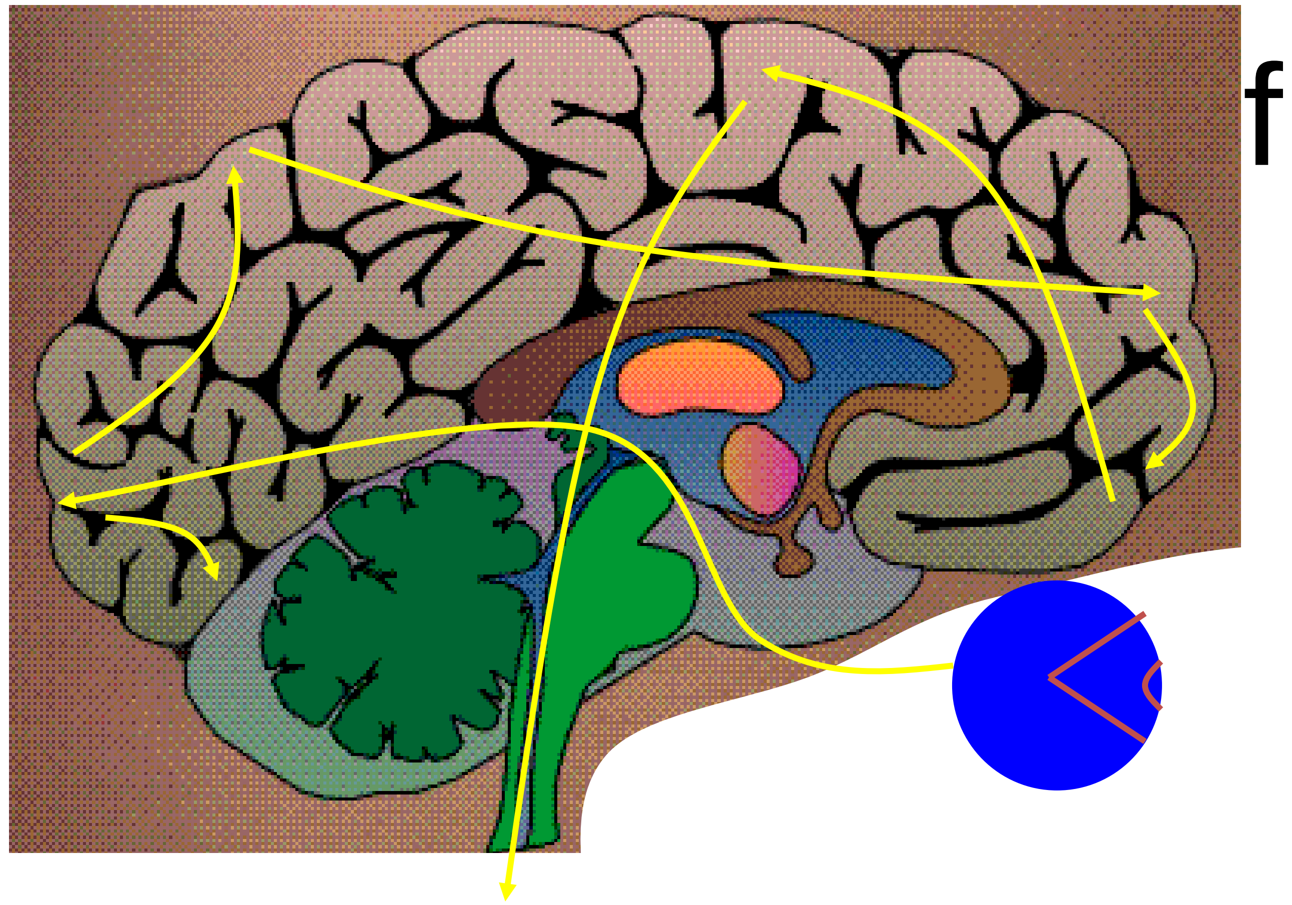
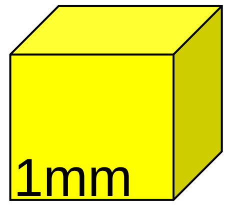
Neuronal Dynamics – 1.1. Neurons and Synapses/Overview

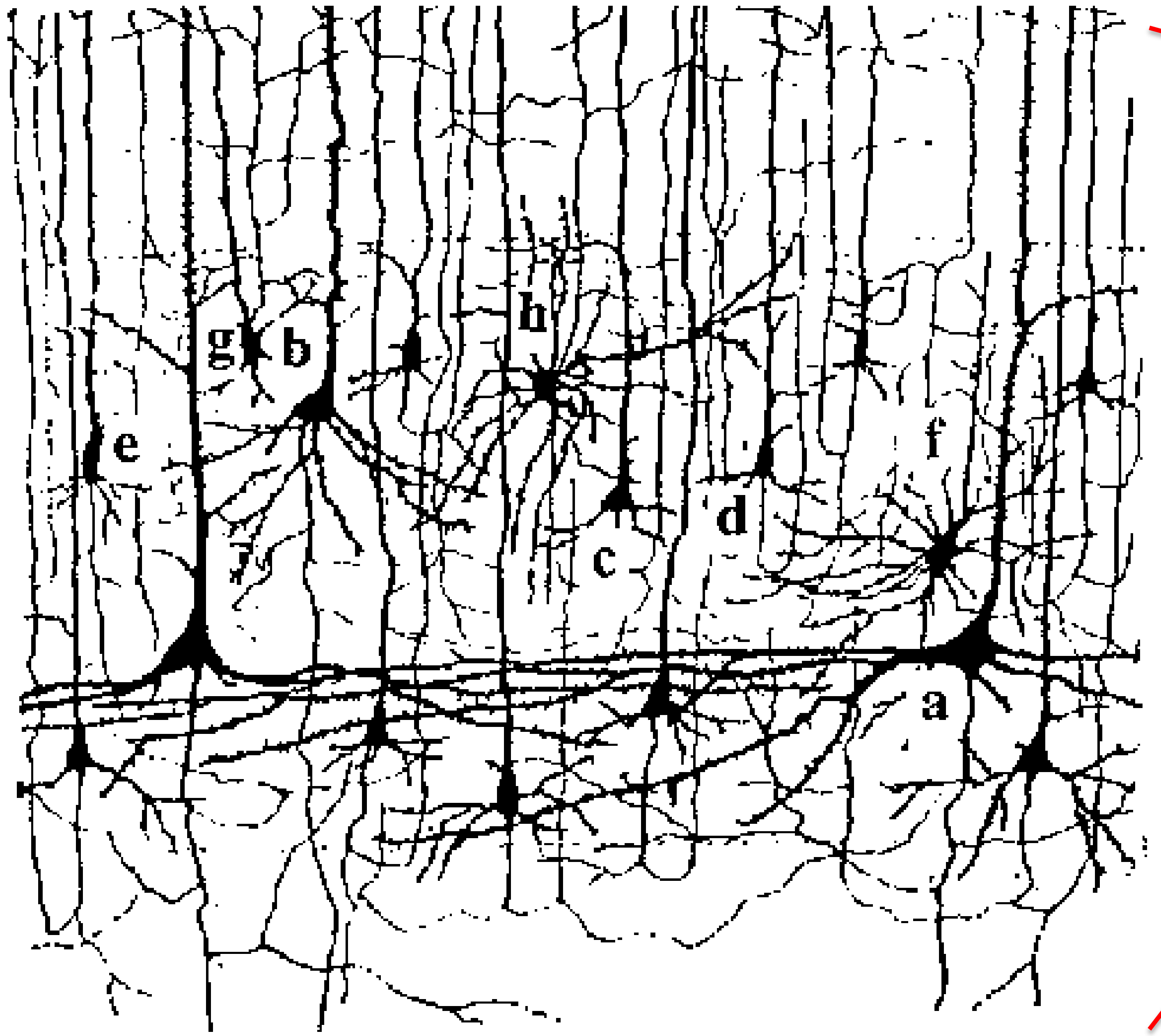
How do we recognize?
Models of cogntion
Weeks 10-14

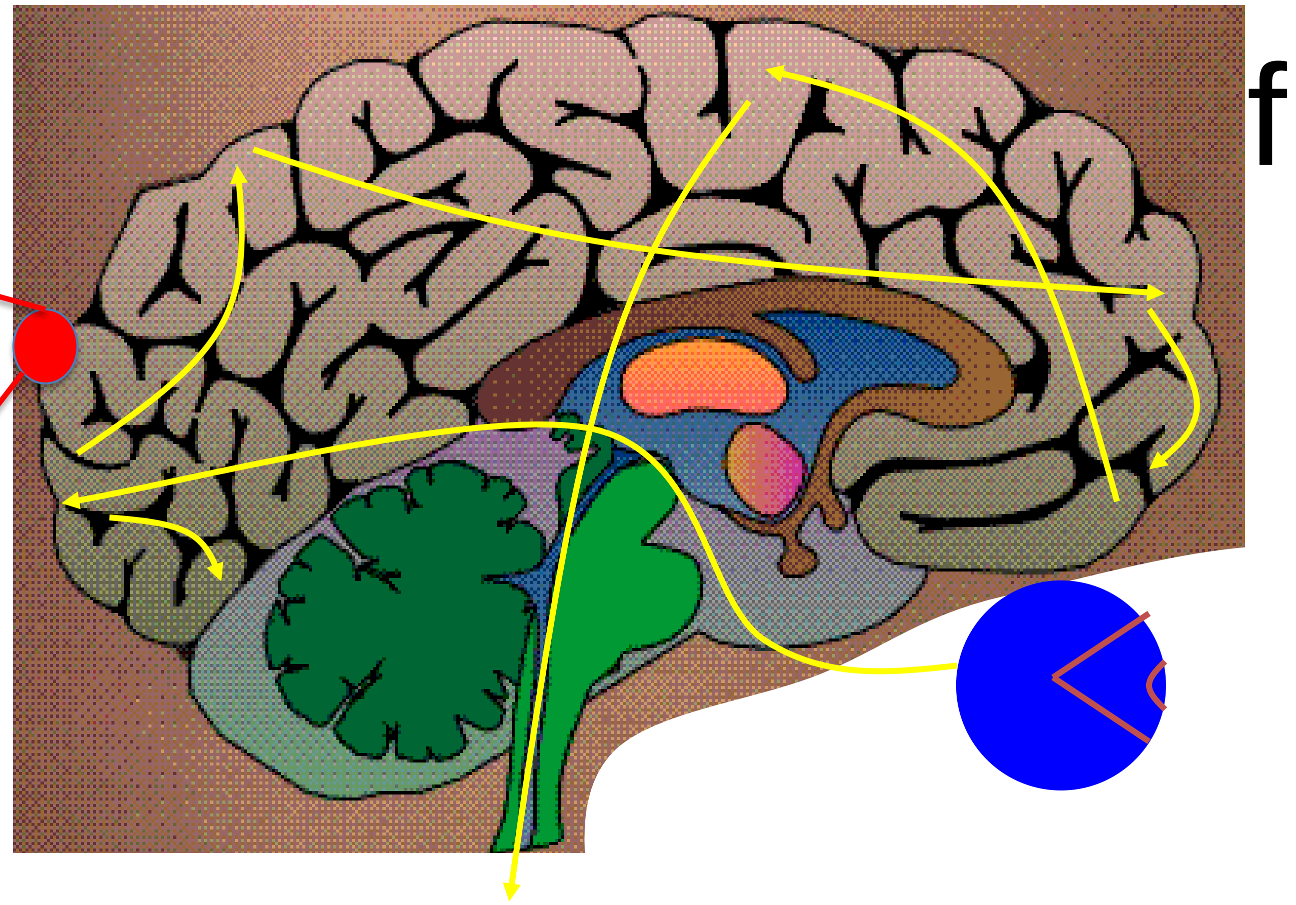


Neuronal Dynamics – 1.1. Neurons and Synapses/Overview



10 000 neurons
3 km wires



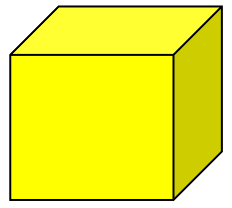


motor
cortex

frontal
cortex

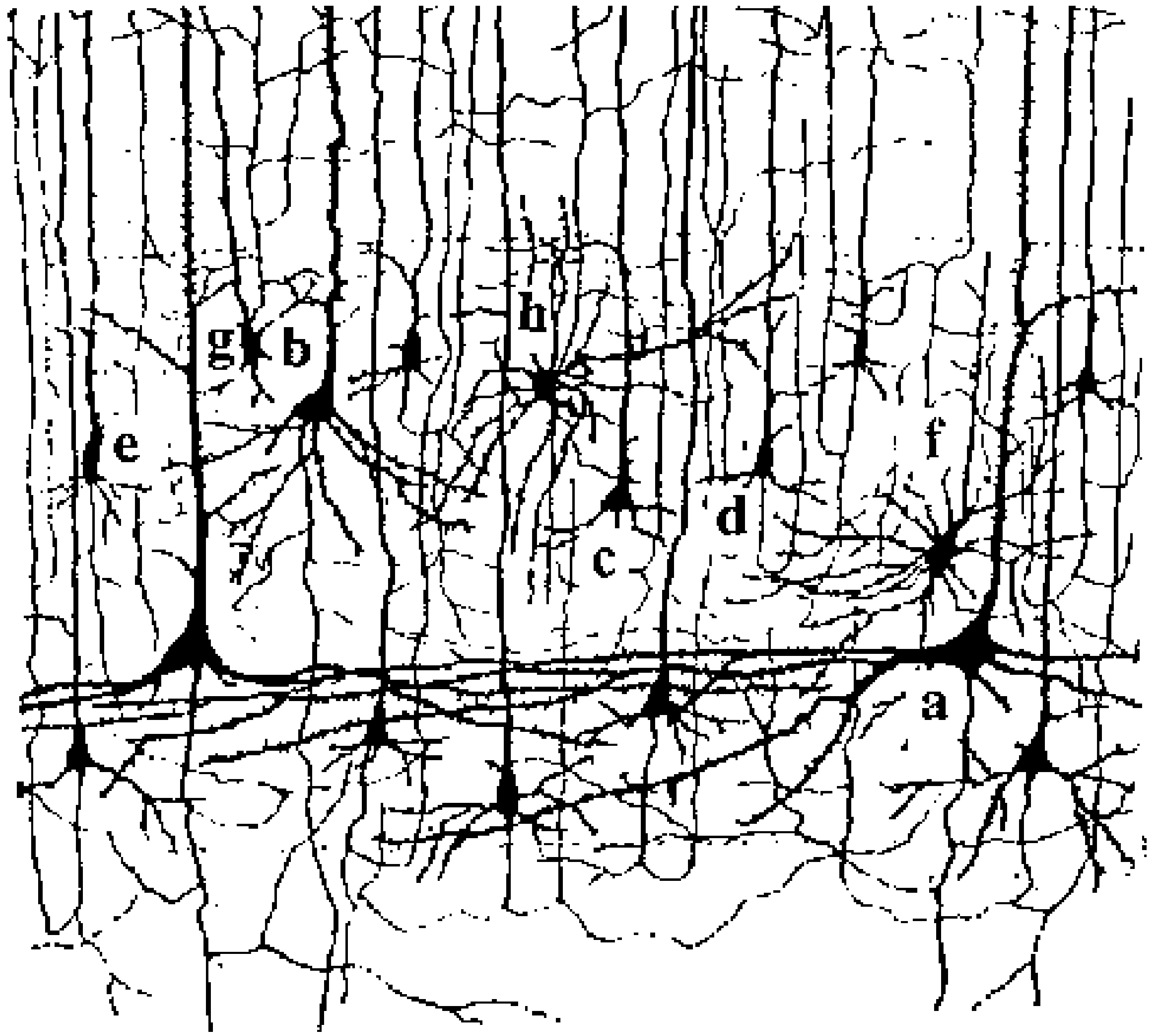
to motor
output

Neuronal Dynamics – 1.1. Neurons and Synapses/Overview



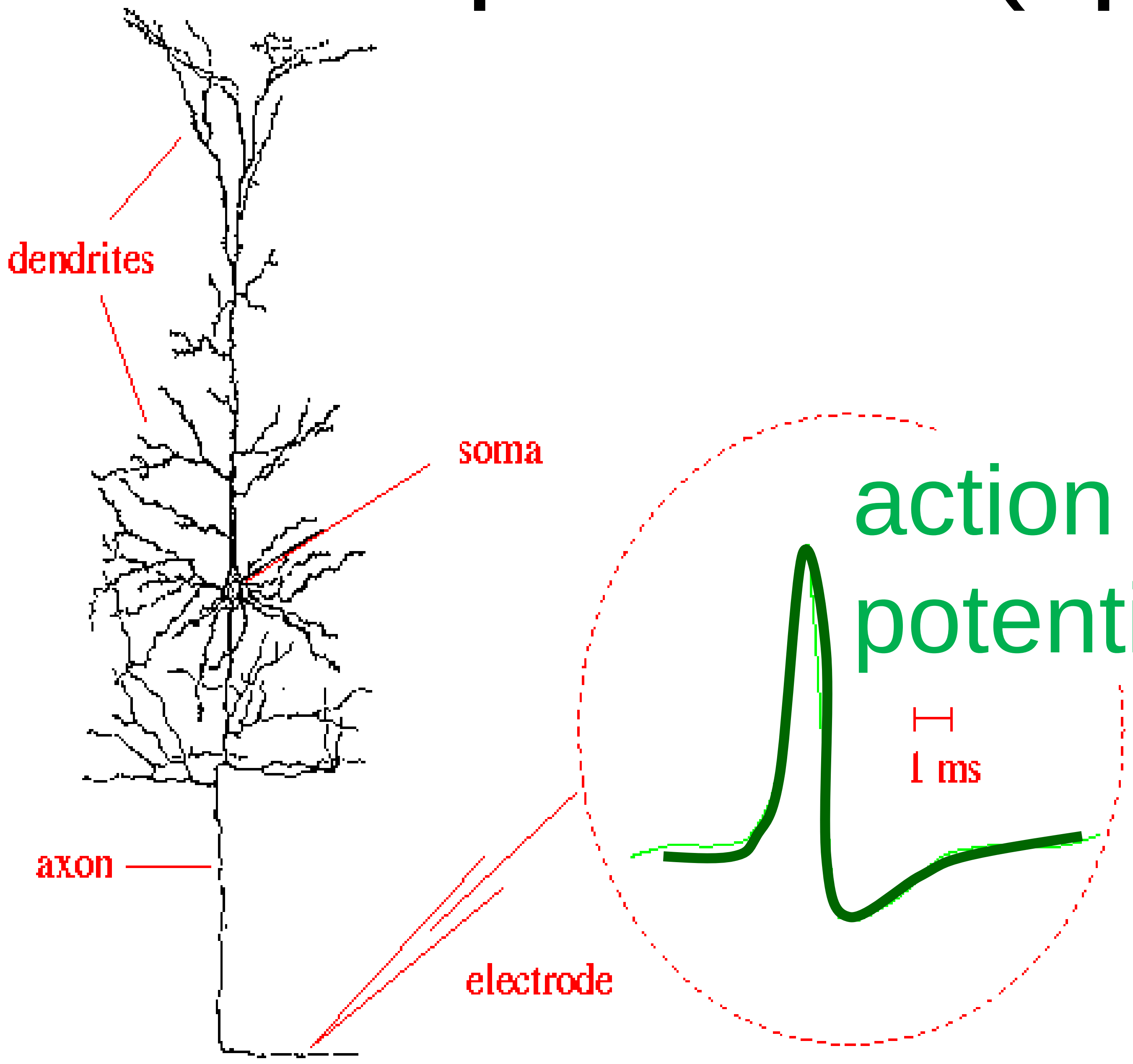
1mm

10 000 neurons
3 km wire



Ramon y Cajal

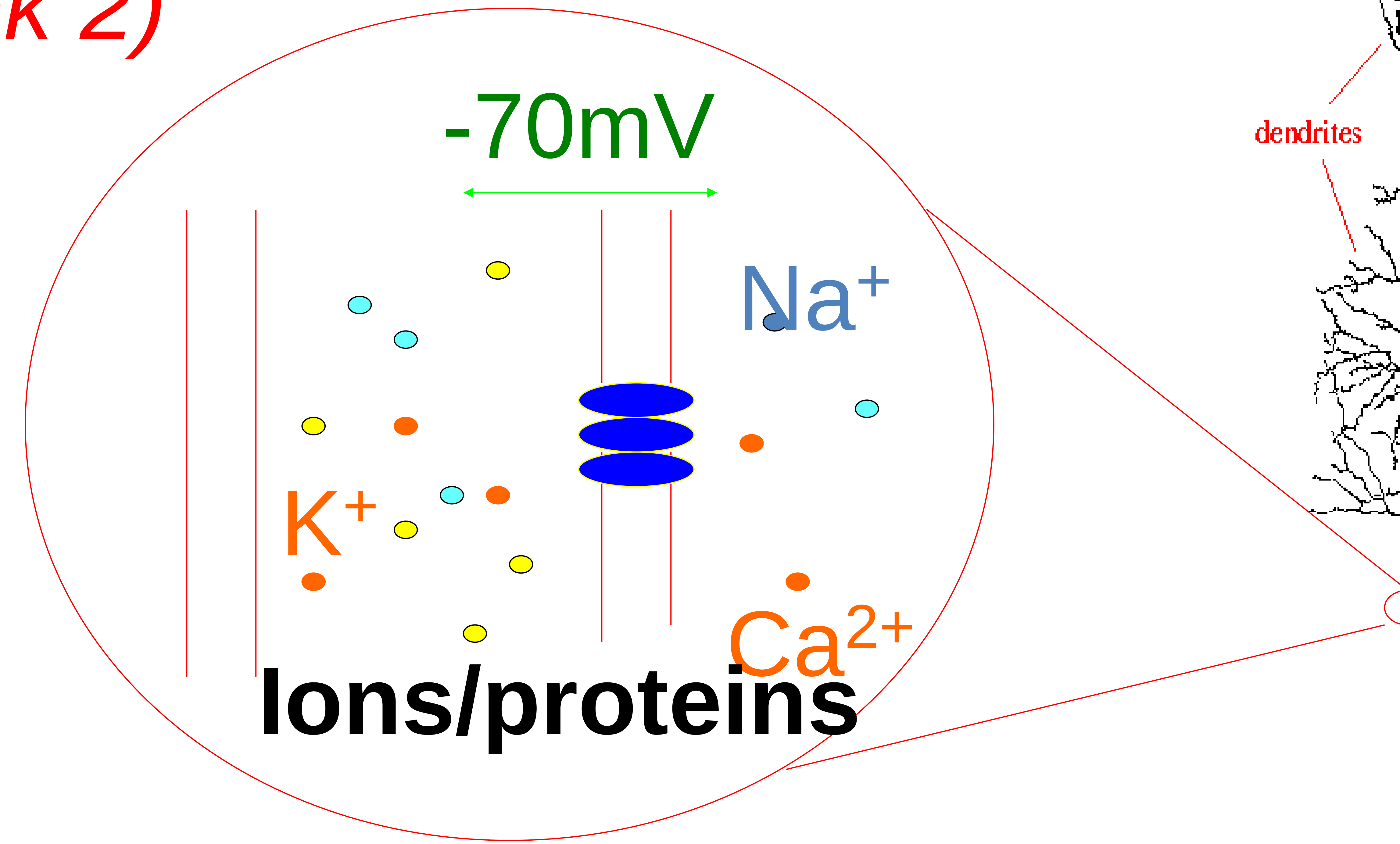
Signal:
action potential (spike)

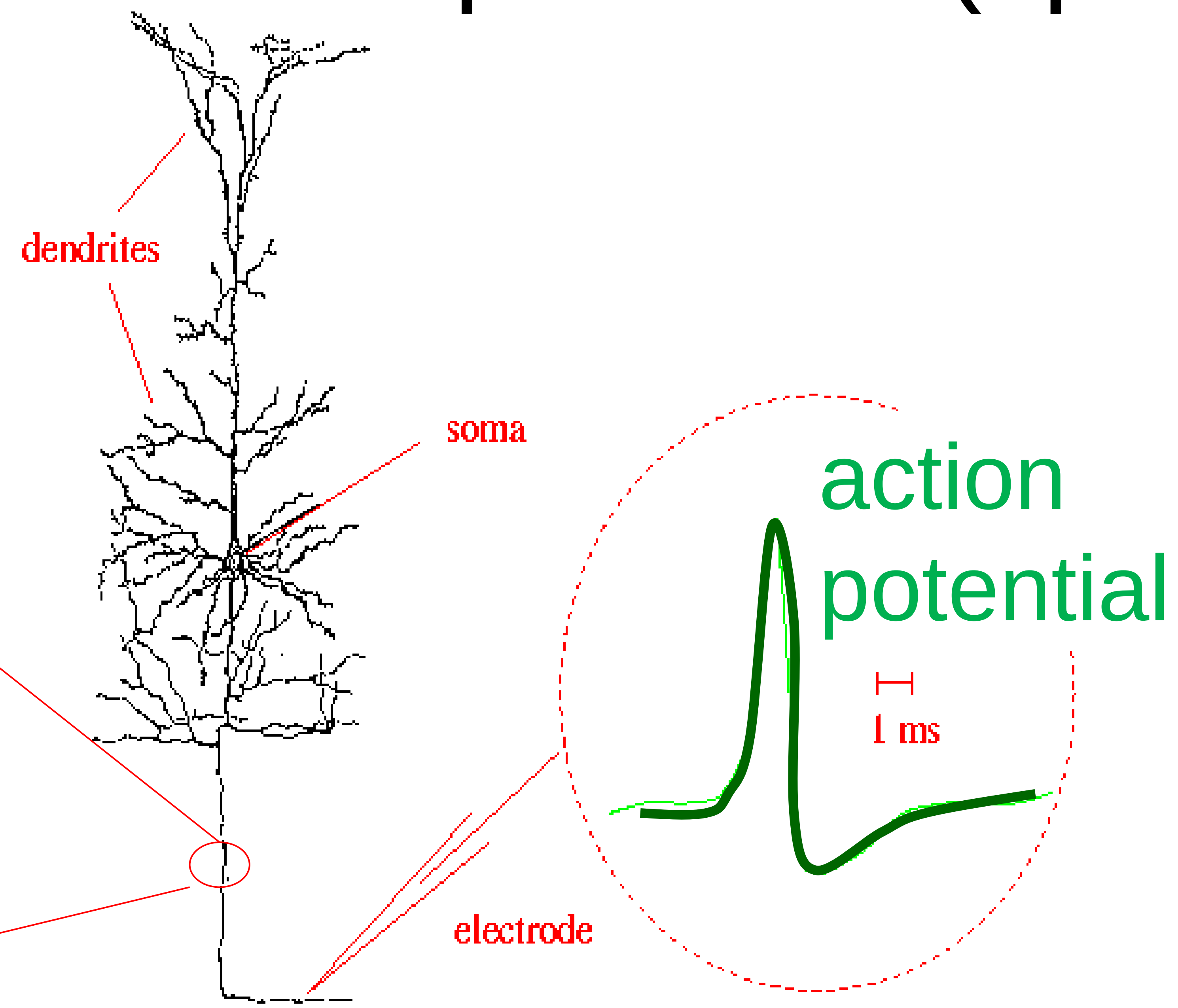


Neuronal Dynamics – 1.1. Neurons and Synapses/Overview

Hodgkin-Huxley type models:
Biophysics, molecules, ions
(week 2)

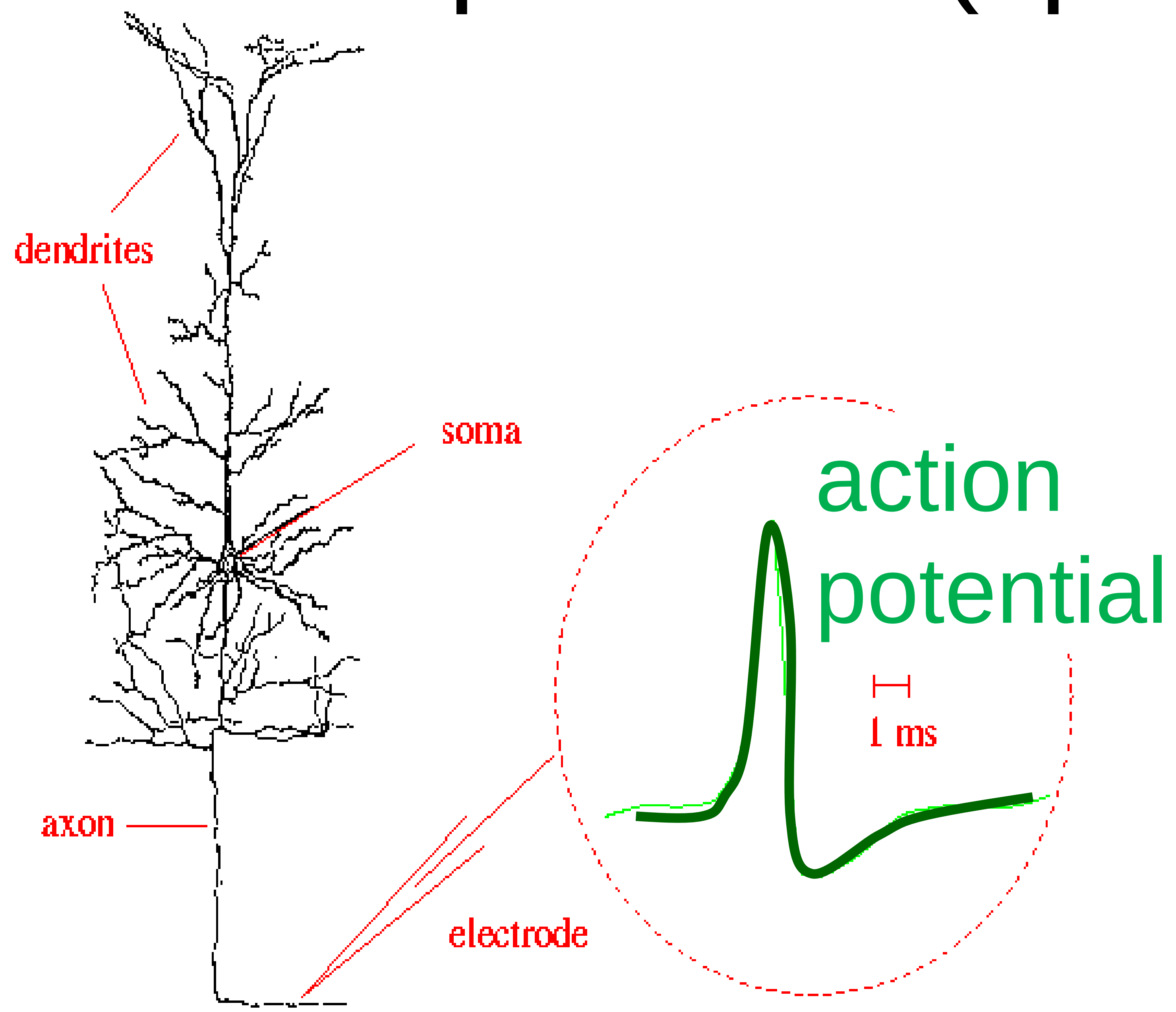
Signal:
action potential (spike)





Neuronal Dynamics – 1.1. Neurons and Synapses/Overview

Signal:
action potential (spike)

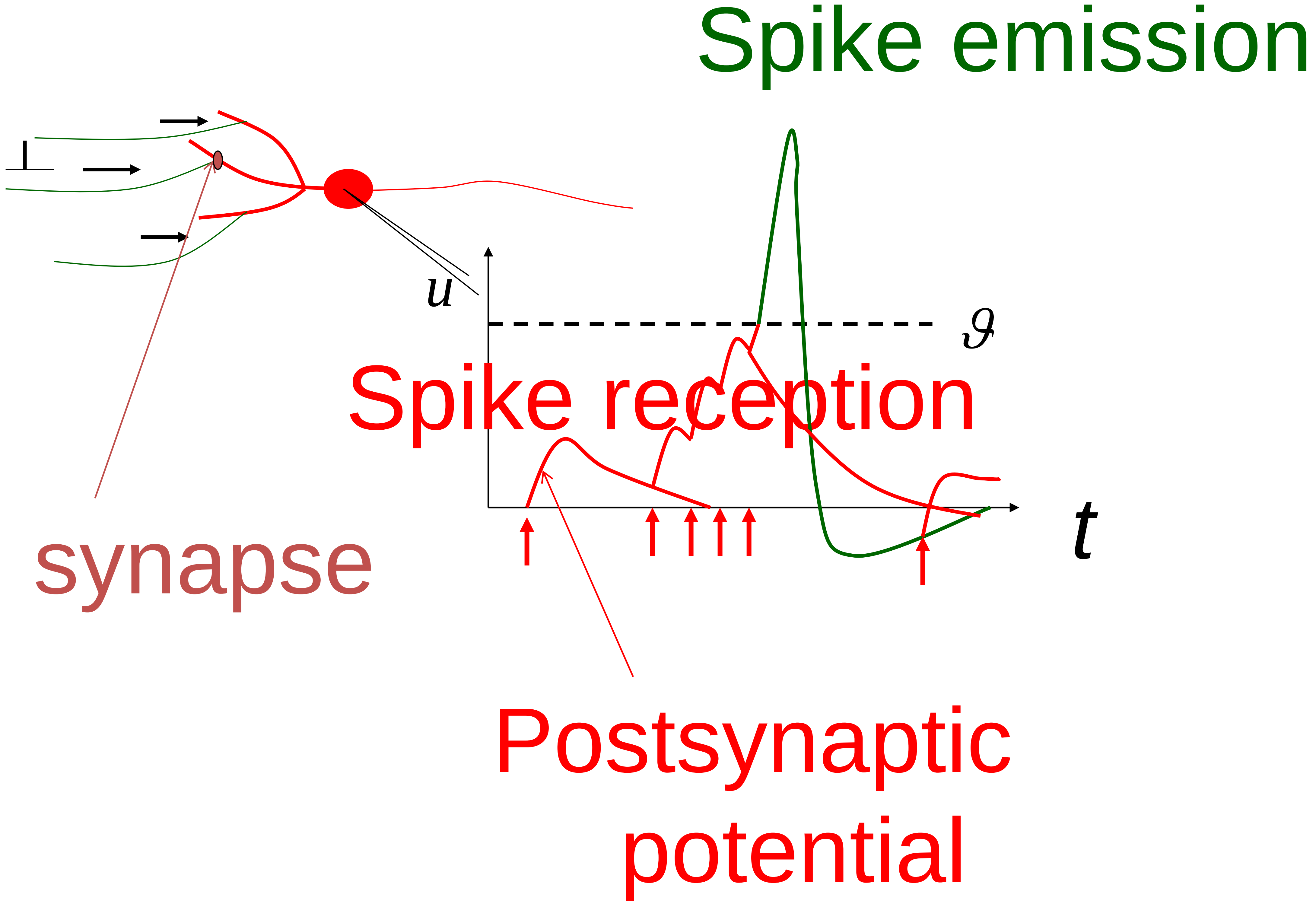


Neuronal Dynamics – 1.1. Neurons and Synapses/Overview

Integrate-and-fire models:

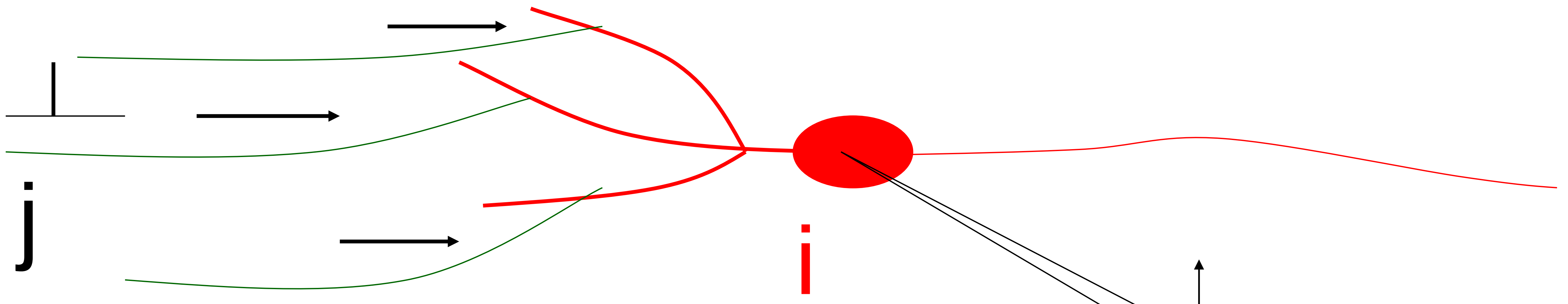
Formal/phenomenological

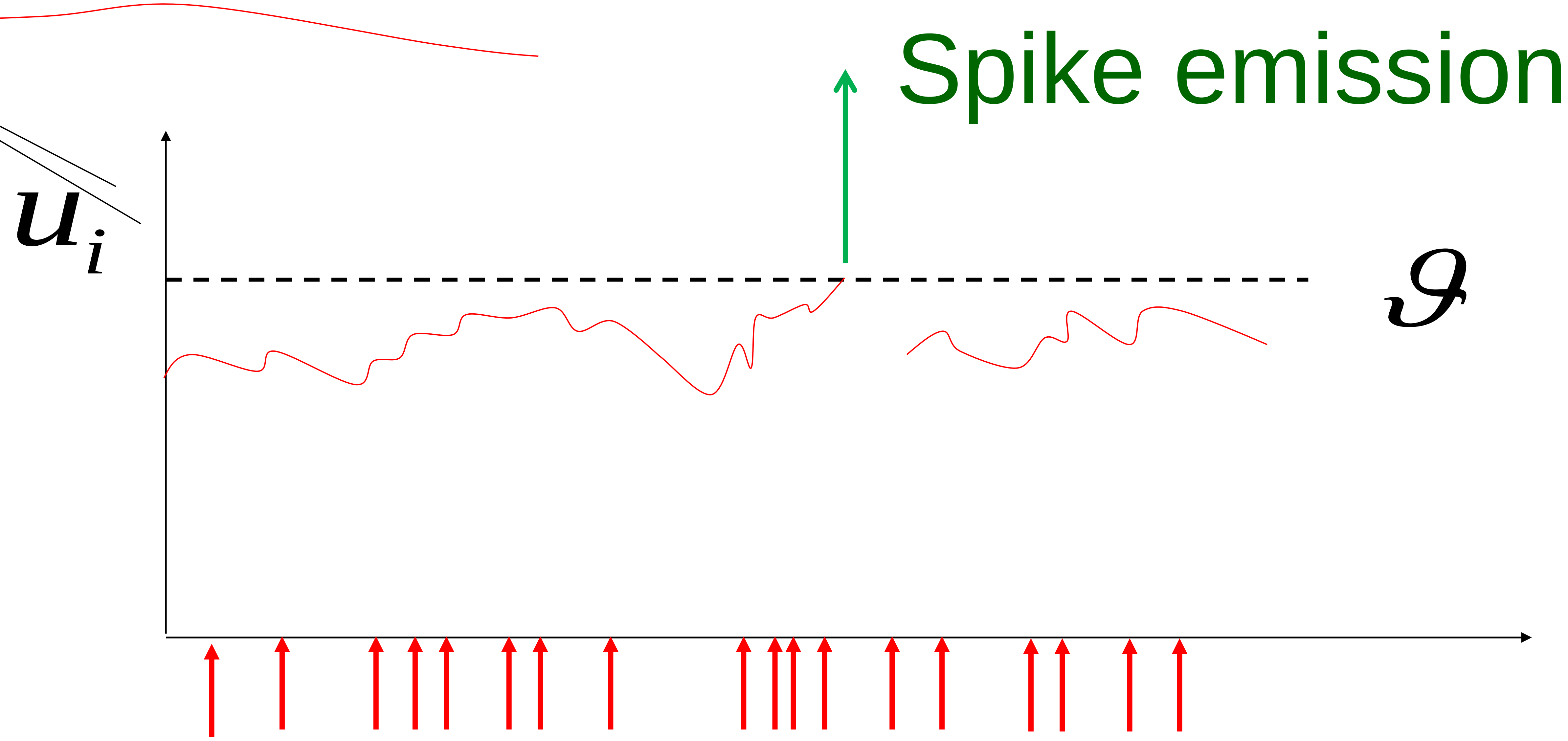
(week 1 and week 6+7)



-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

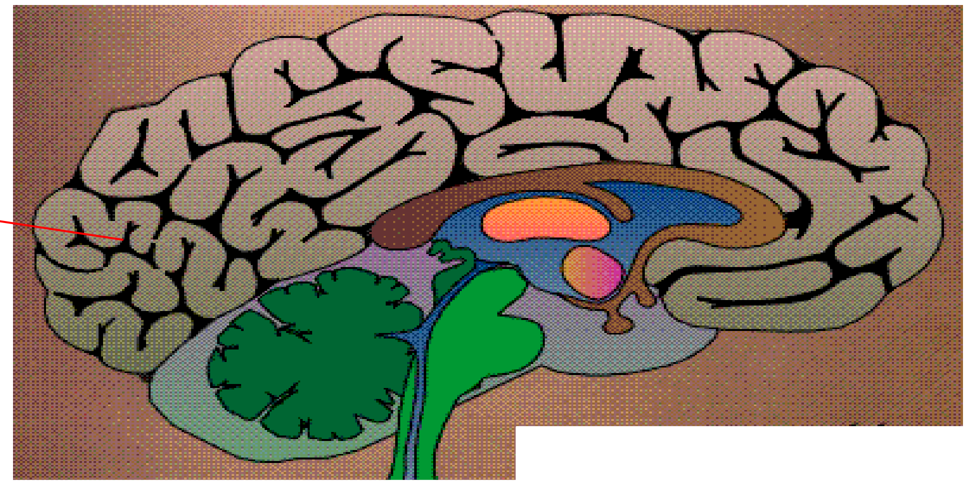
Spontaneous activity *in vivo*

What is noise?

What is the neural code?

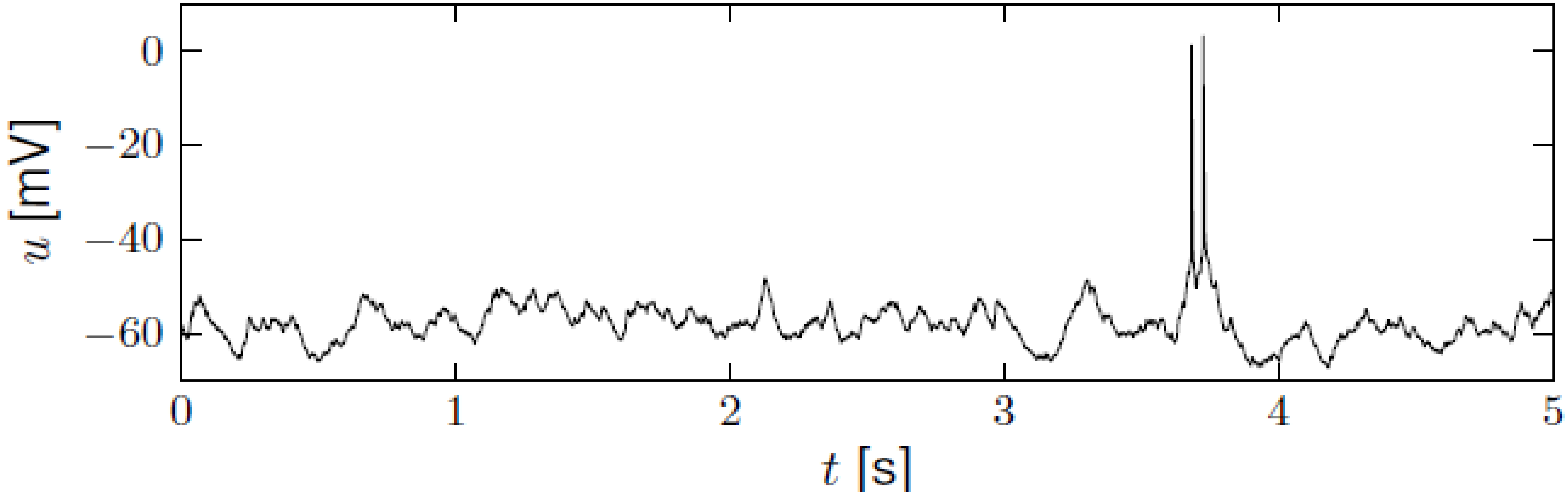
(week 8+9)

electrode



Brain

awake mouse, cortex, freely whisking,



Crochet et al., 2011

Neuronal Dynamics – 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!

Neural Networks and Biological Modeling – 1.1. Overview

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 Dendrites**

Week 5,6,7: **Associative Memory, Learning, Hebb, Hopfield**

Week 8,9: **Noise models, noisy neurons and coding**

Week 10: **Estimating neuron models for coding and decoding**

Week 11-14: Networks and cognitions

Neural Networks and Biological modeling

Course: Monday : 9:15-13:00

A typical Monday:

1st lecture 9:15-9:50

1st exercise 9:50-10:00 ← *paper and pencil*

2nd lecture 10:15-10:35

2nd exercise 10:35-11:00 ← *paper and pencil*

3rd lecture 11:15 – 11:40

3rd exercise 12:15-13:00 ← *paper and pencil OR interactive toy examples on comput*

have your laptop with you

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

http://lcn.epfl.ch/ *moodle.eplf.ch*

Neural Networks and Biological Modeling

Questions?

Week 1 – part 2: The Passive Membrane

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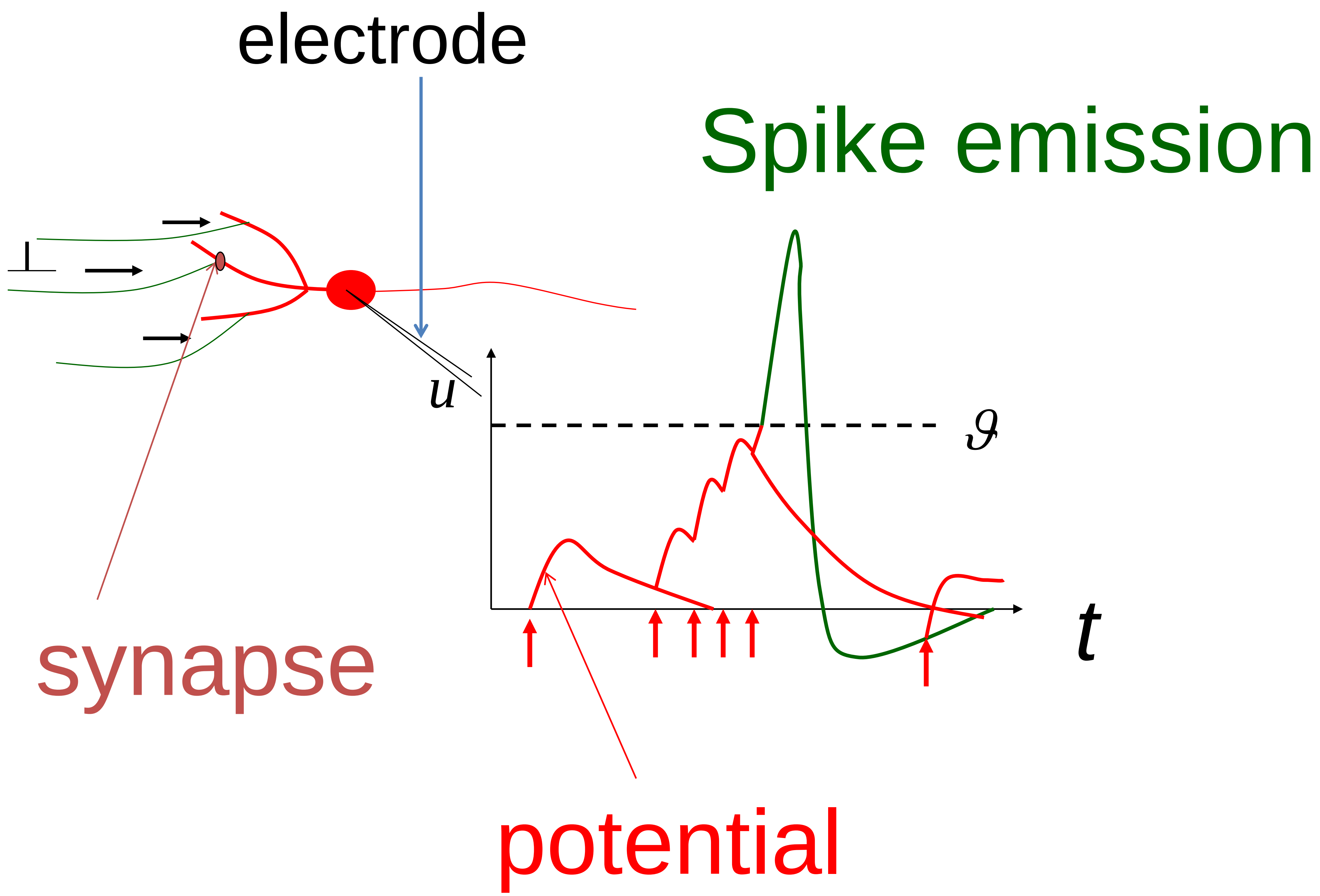
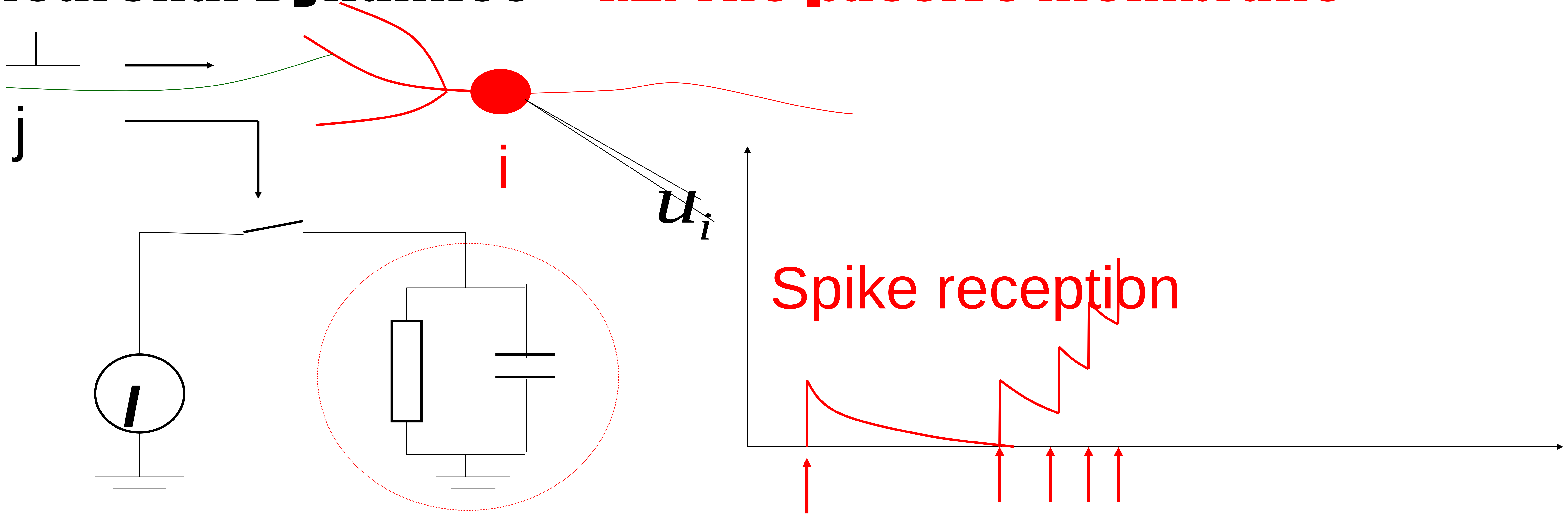
Neuronal Dynamics – 1.2. The passive membrane



Integrate-and-fire model

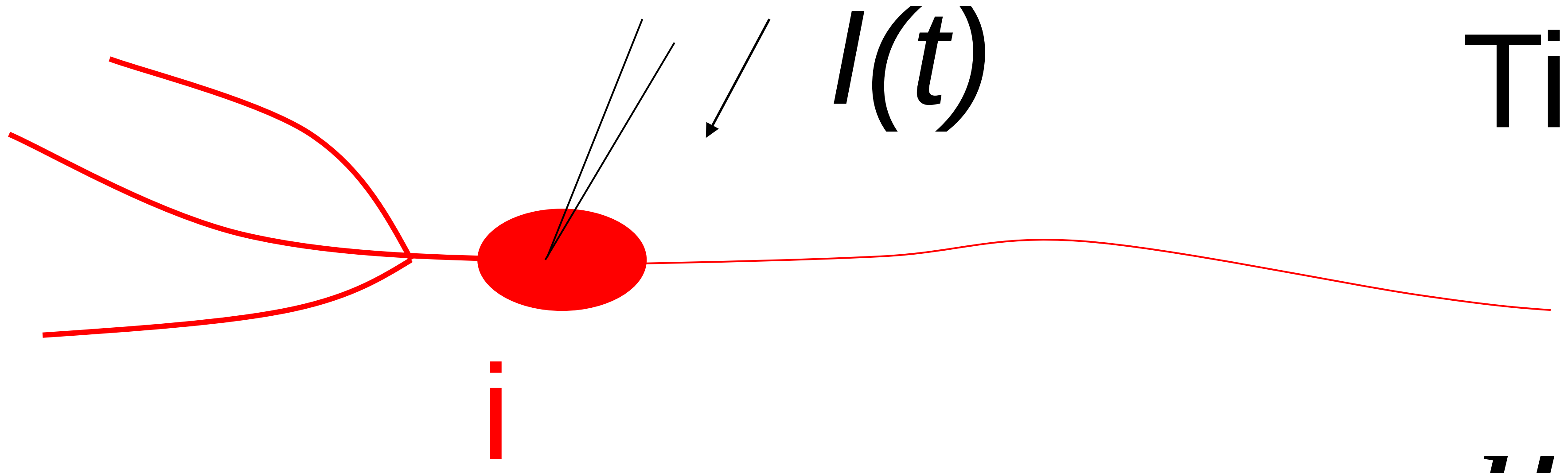
Neuronal Dynamics – 1.2. The passive membrane



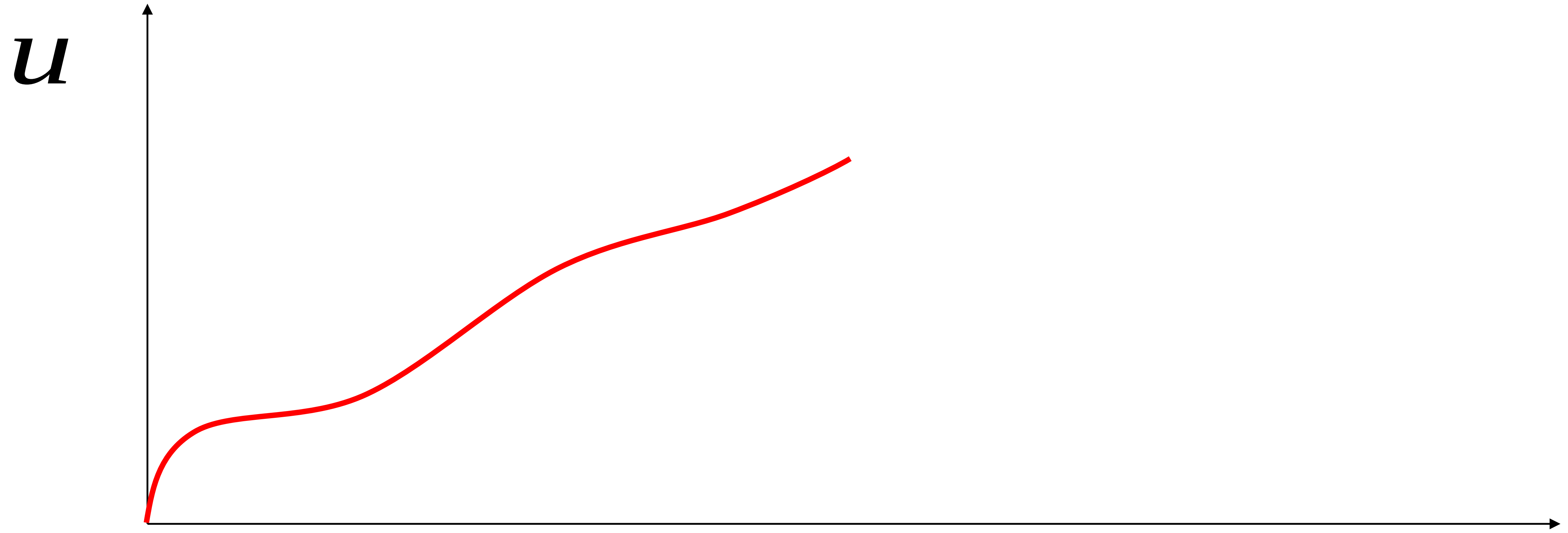
Subthreshold regime

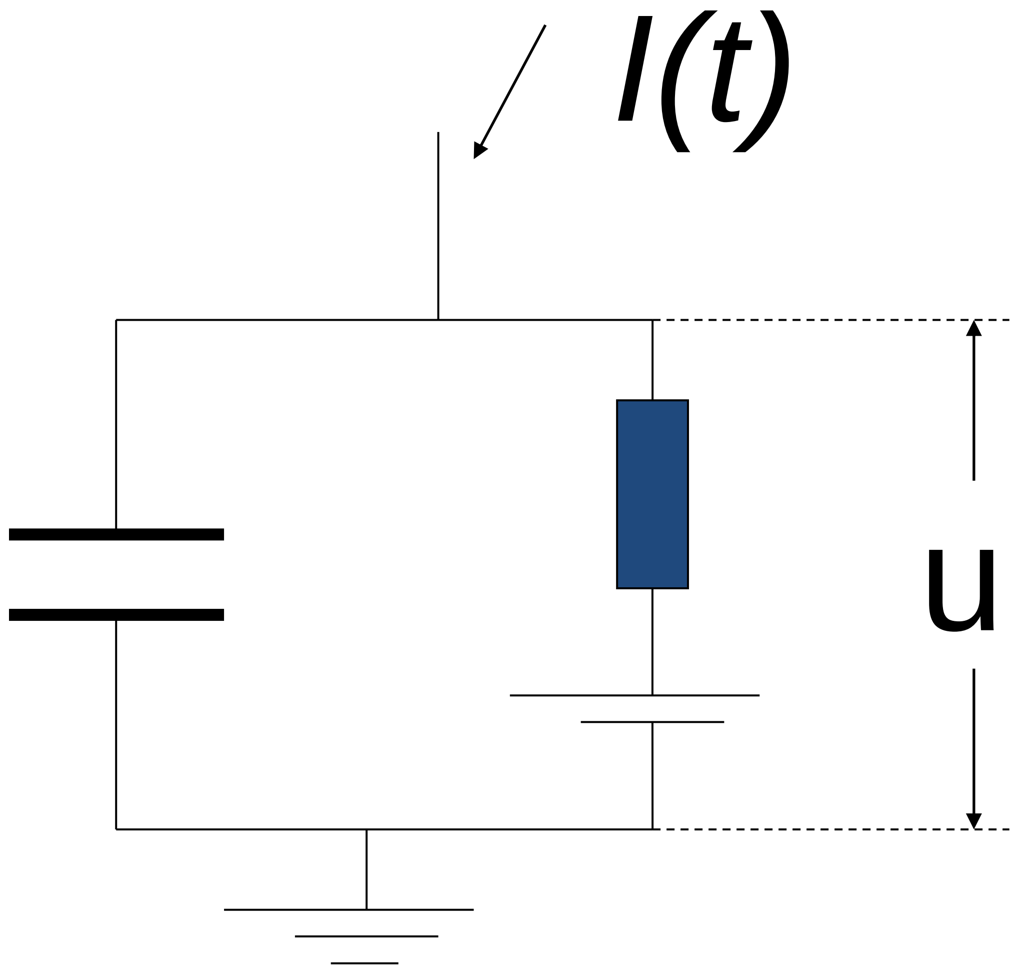
- linear
- passive membrane
- RC circuit

Neuronal Dynamics – 1.2. The passive membrane



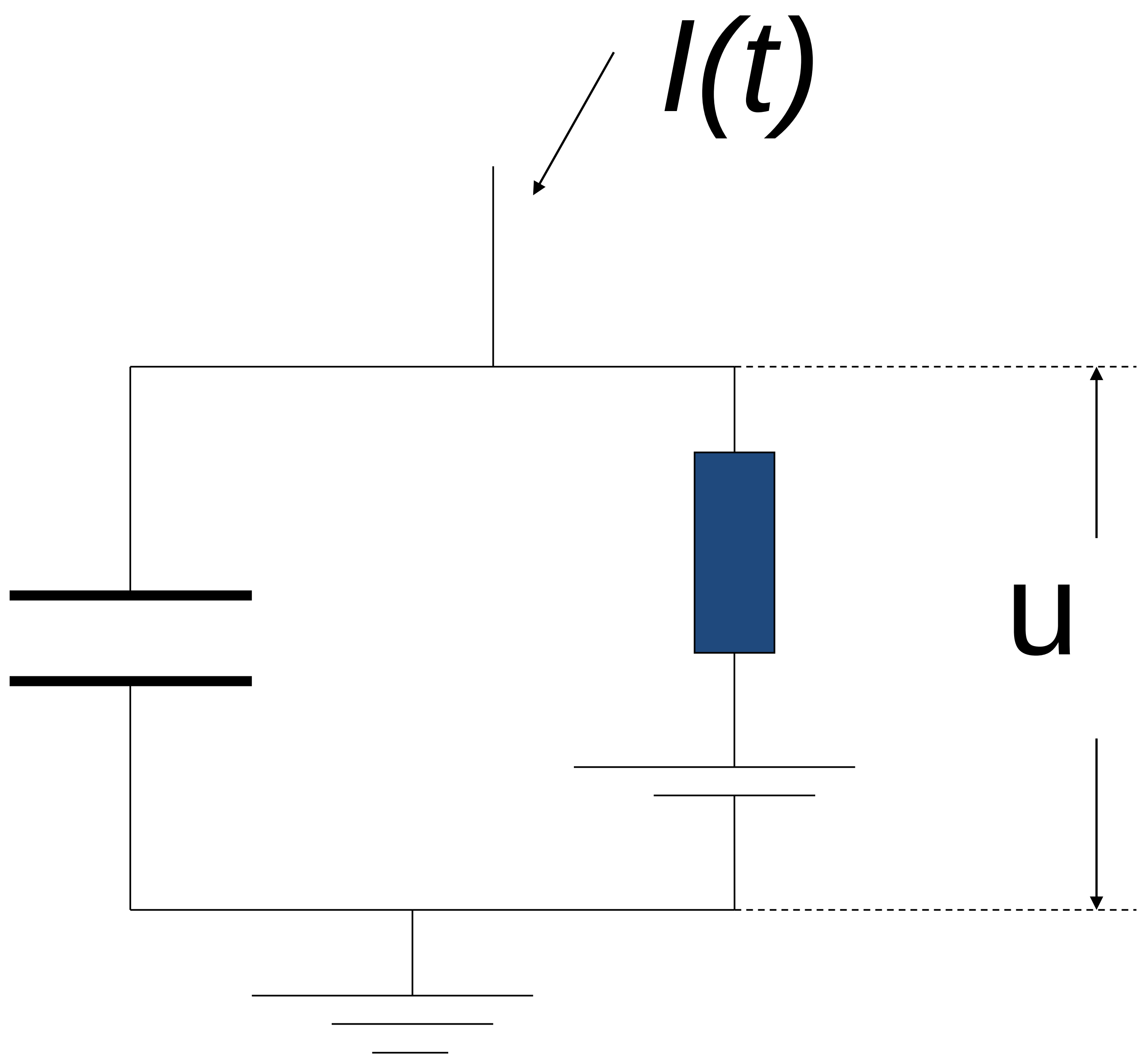
Time-dependent input



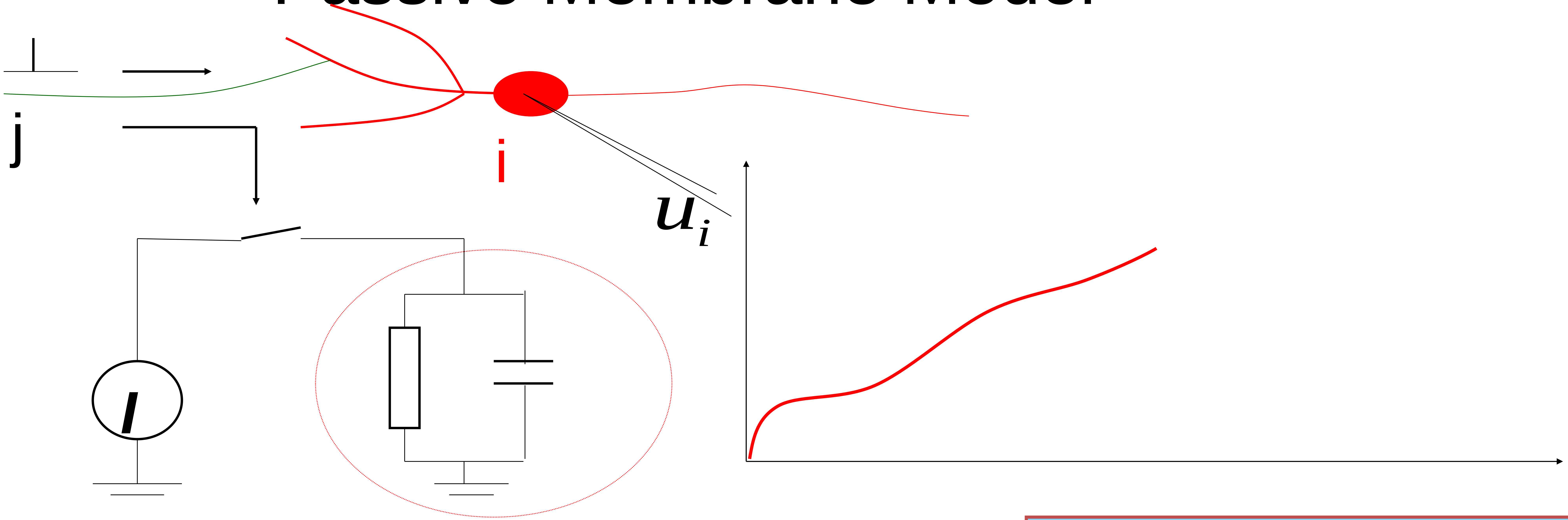


Math development:
Derive equation

Passive Membrane Model



Passive Membrane Model



Math Development: Voltage rescaling

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

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

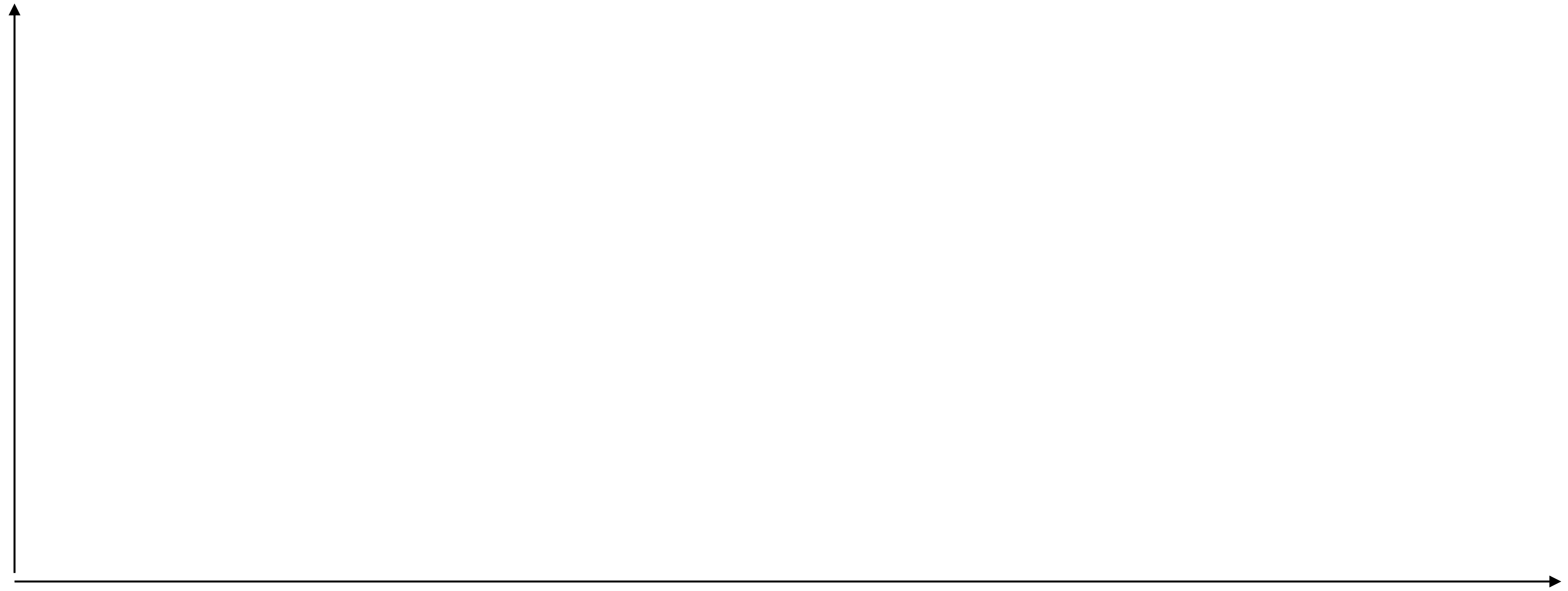
Passive Membrane Model

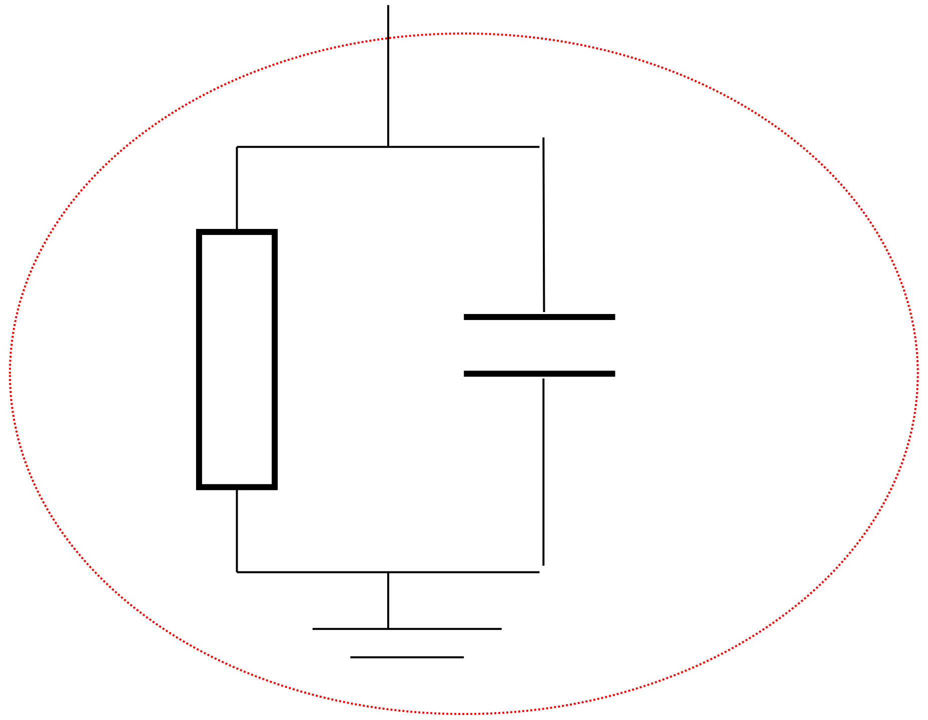
$$\tau \cdot \frac{d}{dt}u = -(u - u_{rest}) + RI(t)$$

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

Passive Membrane Model/Linear differential equation

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

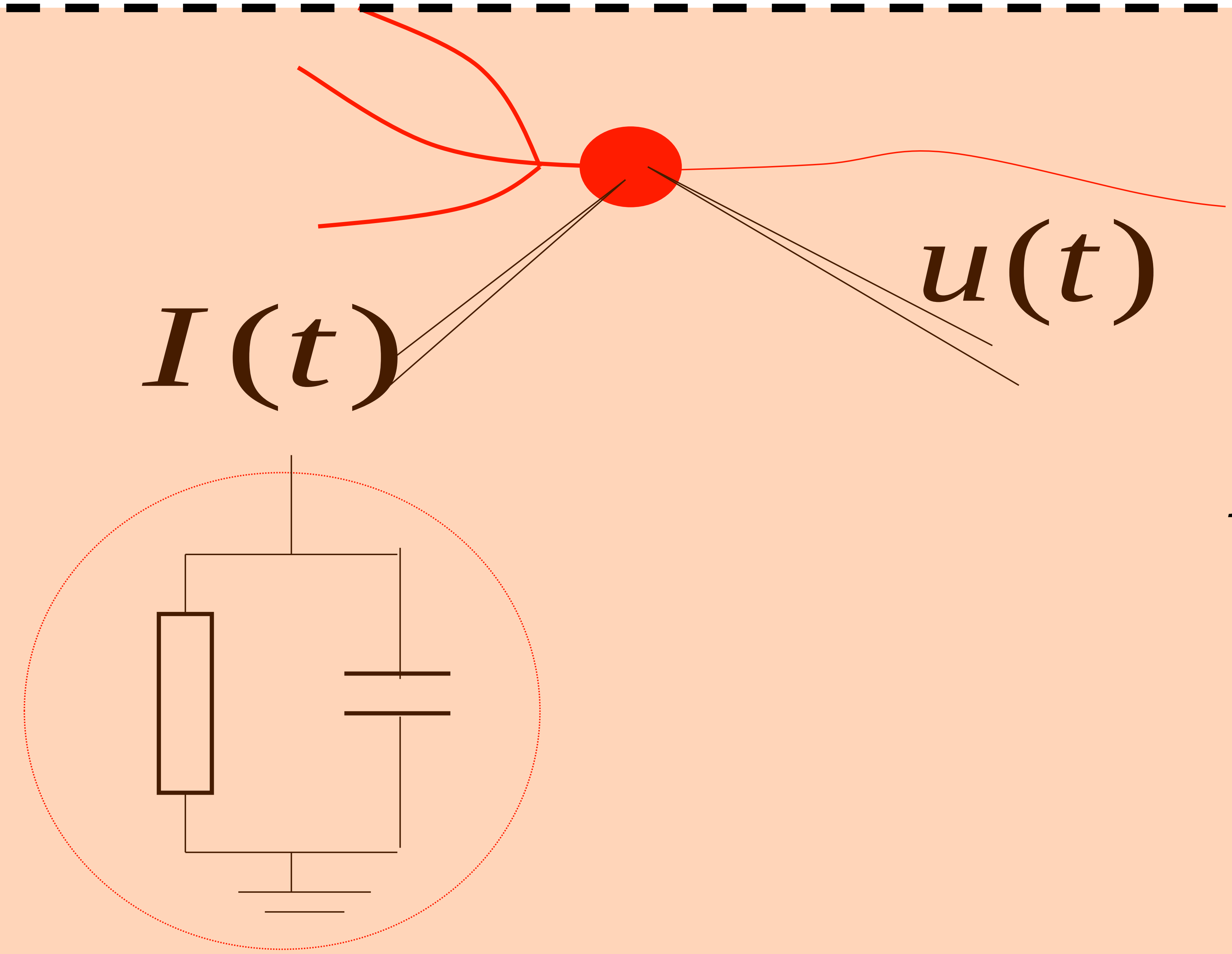


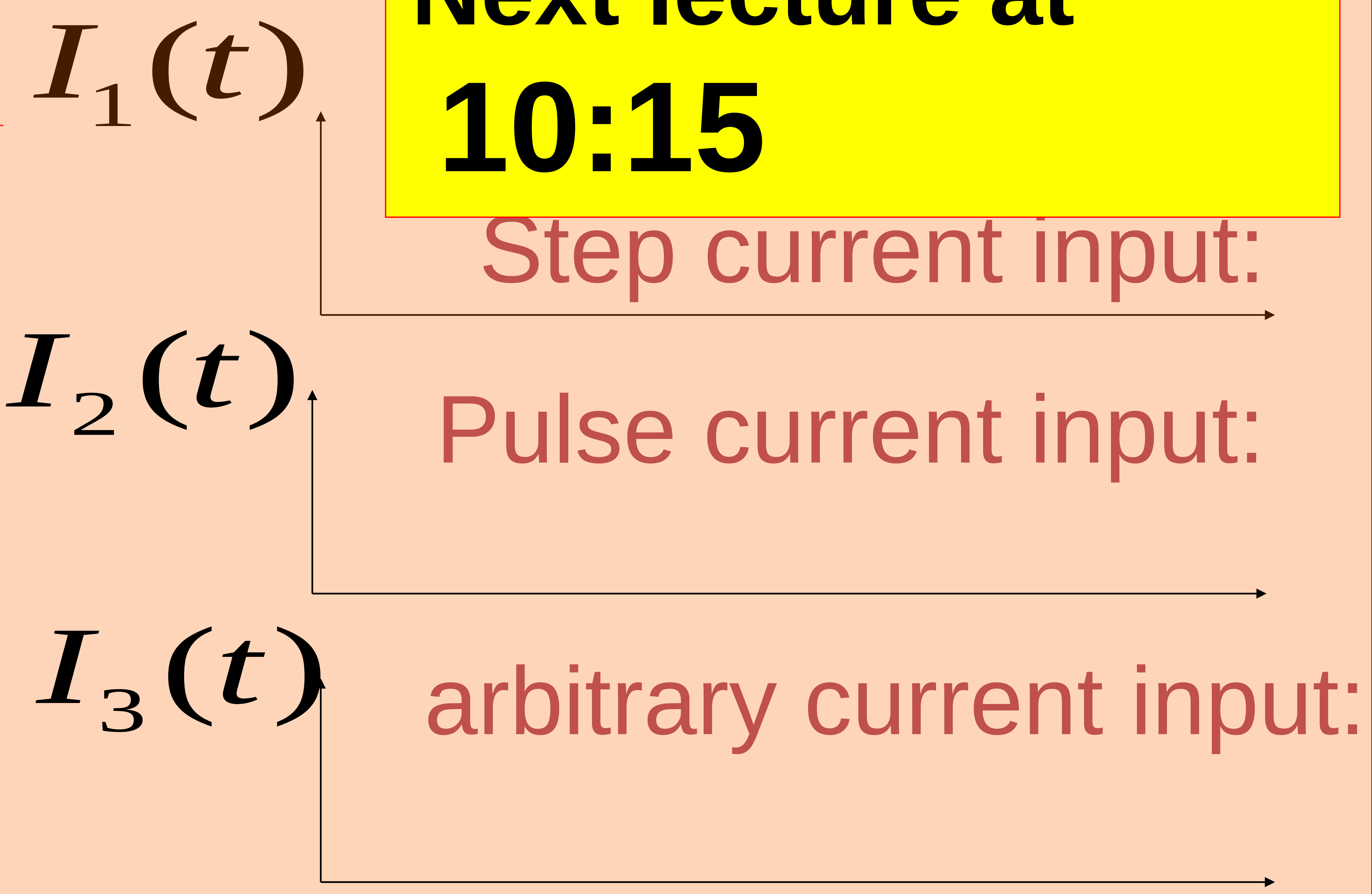


Free solution:
exponential decay

Neuronal Dynamics – Exercises NOW

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



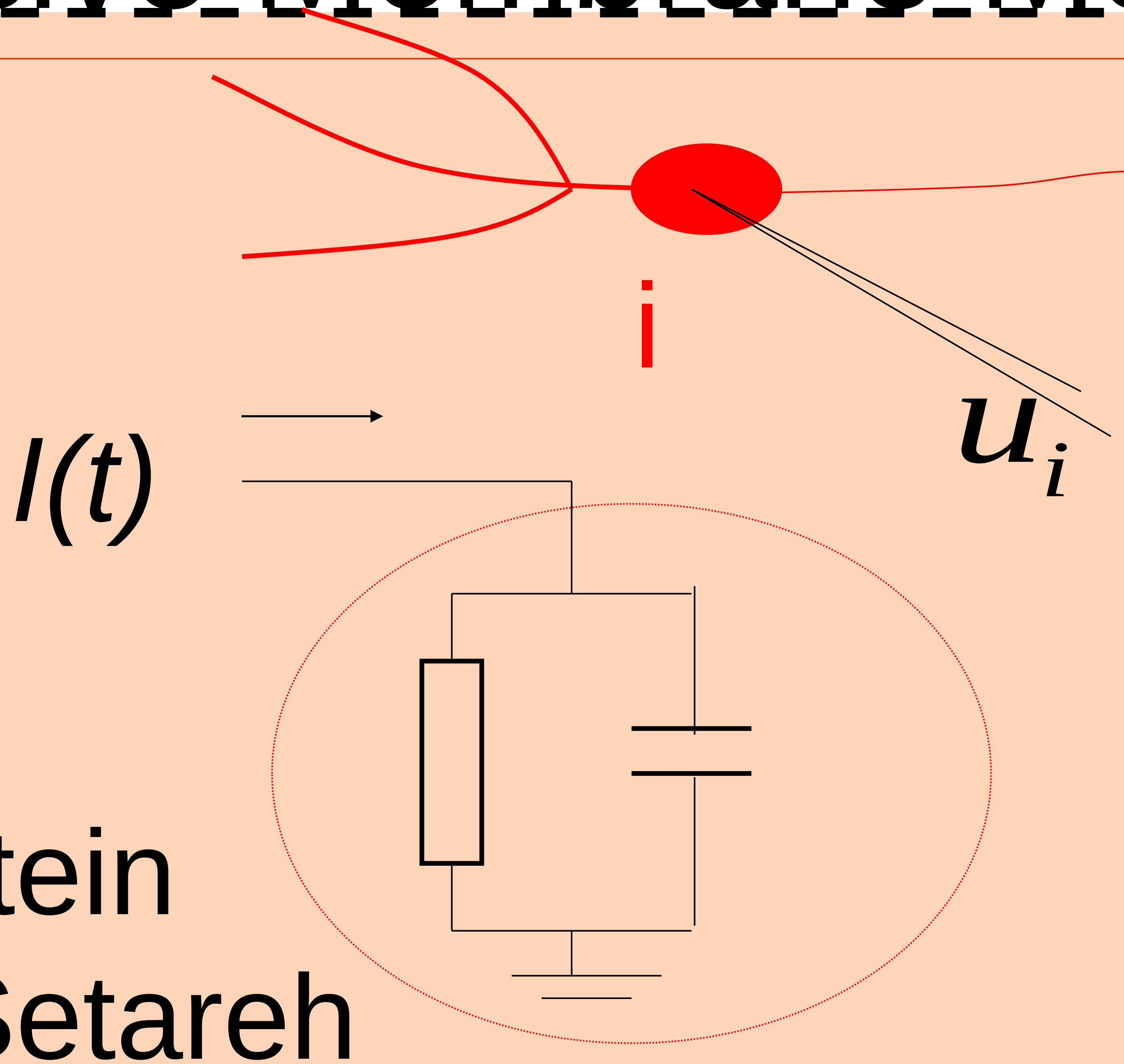


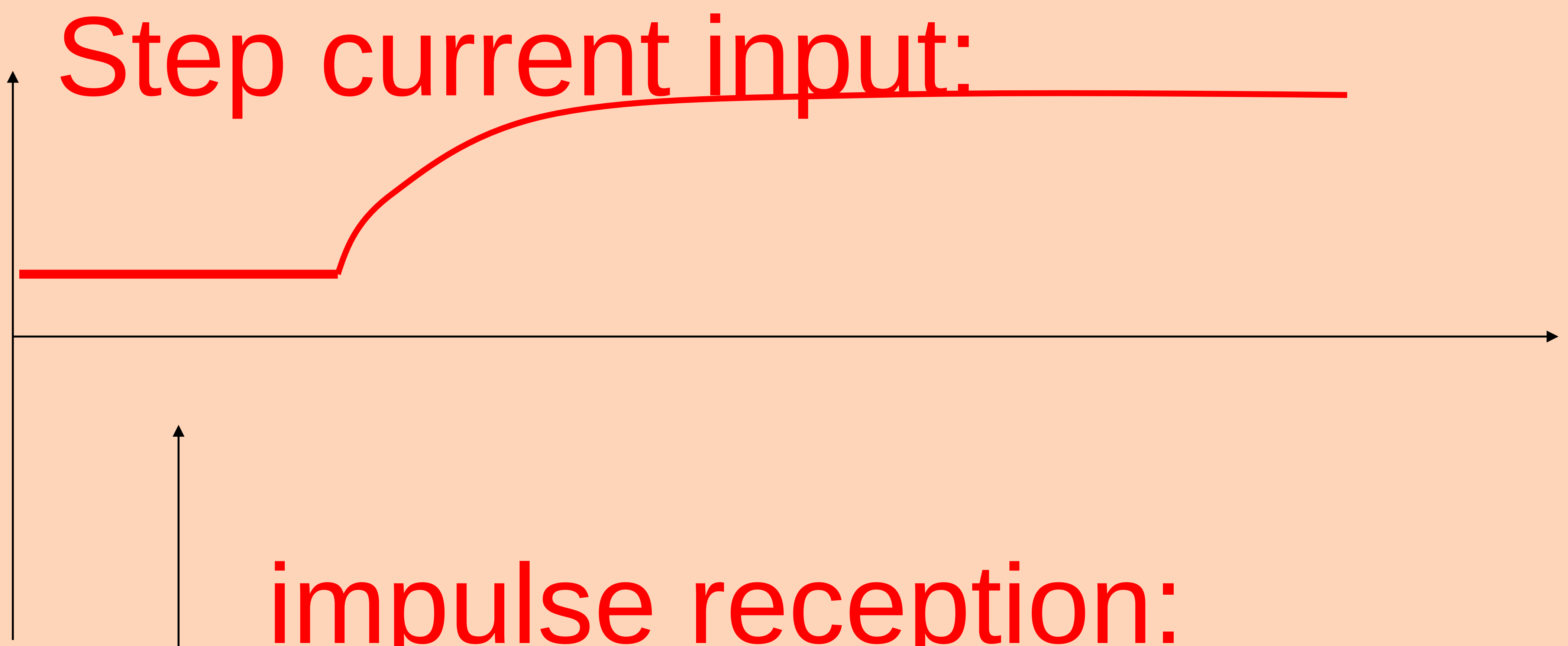
$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$

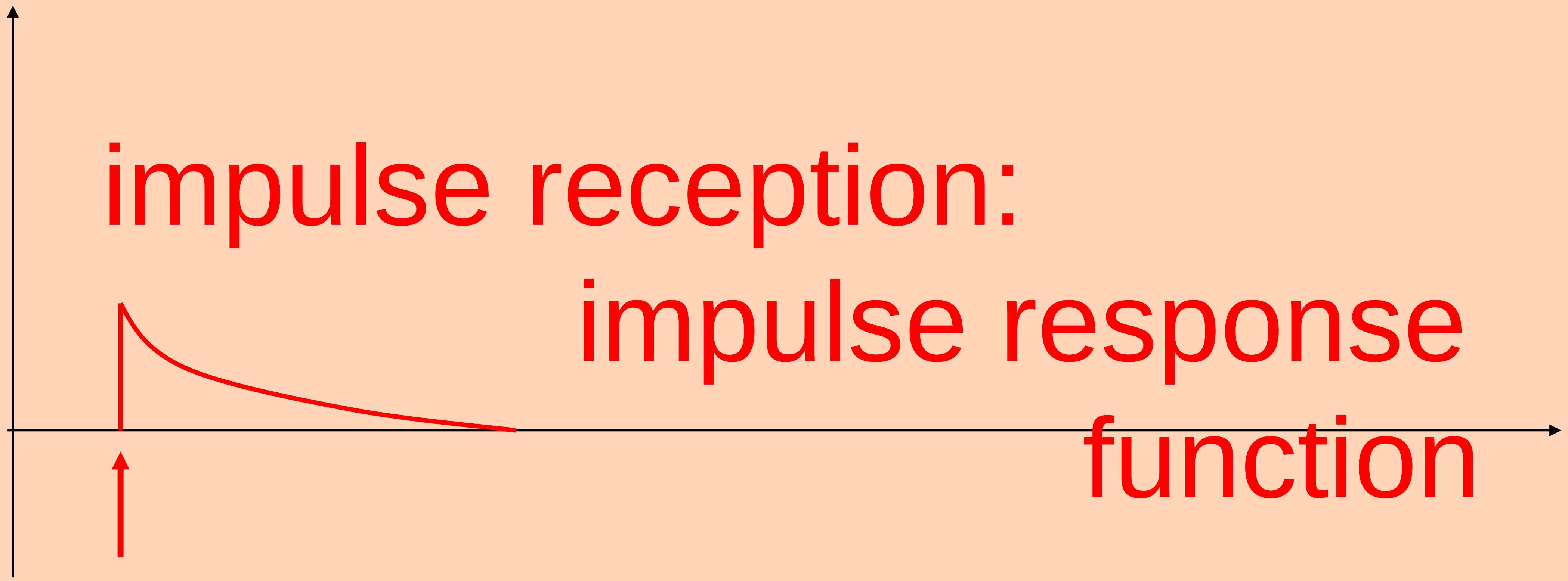
$$\tau \cdot \frac{d}{dt} V = -V + RI(t); \quad V = (u - u_{rest})$$

Calculate the voltage, for the 3 input currents

Passive Membrane Model – exercise 1 now







TA's:

Carlos Stein

Hesam Setareh

Samuel Muscinelli

Alex Seeholzer

Linear equation

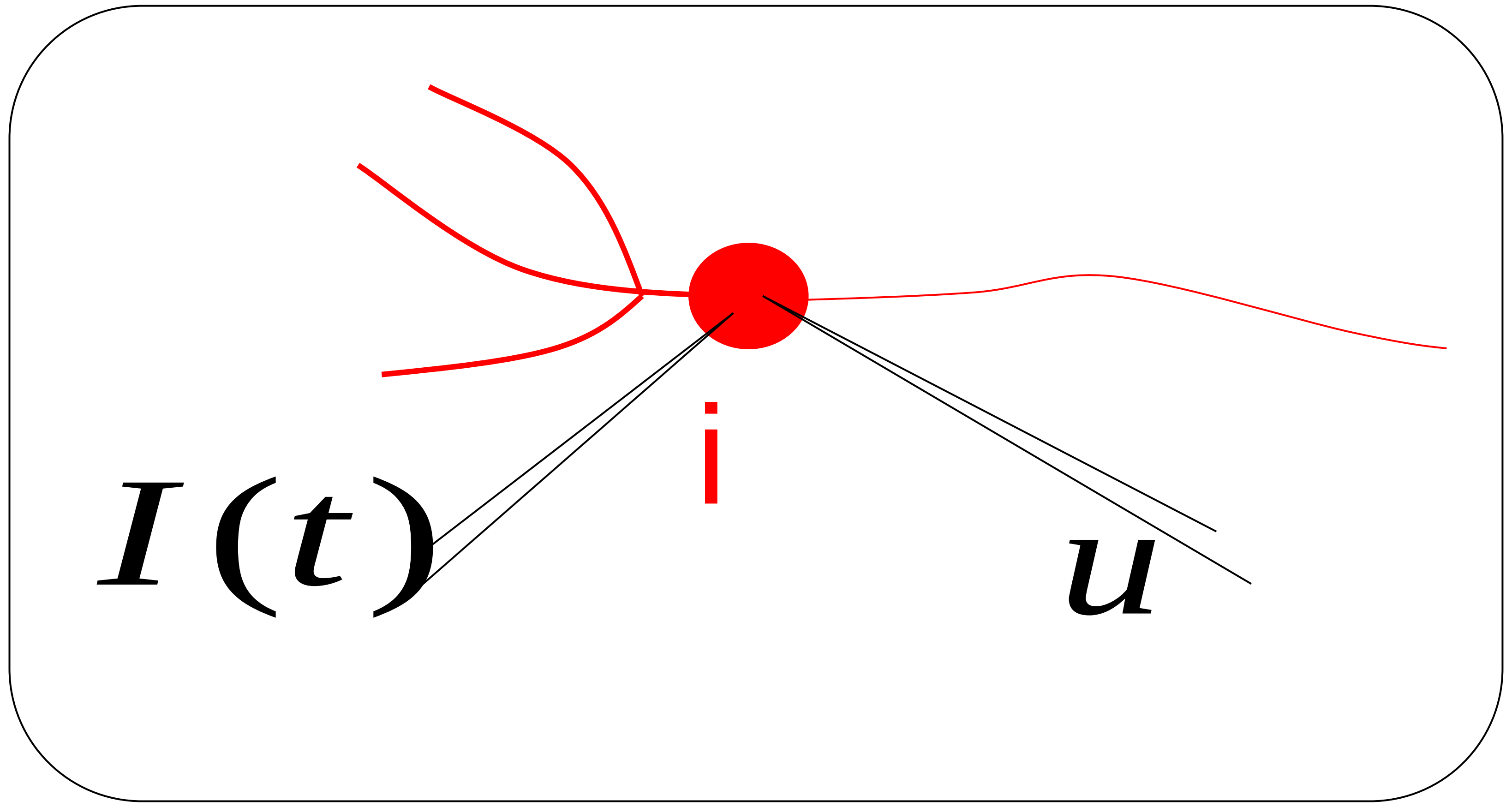
$$\tau \cdot \frac{d}{dt}u = -(u - u_{rest}) + RI(t)$$

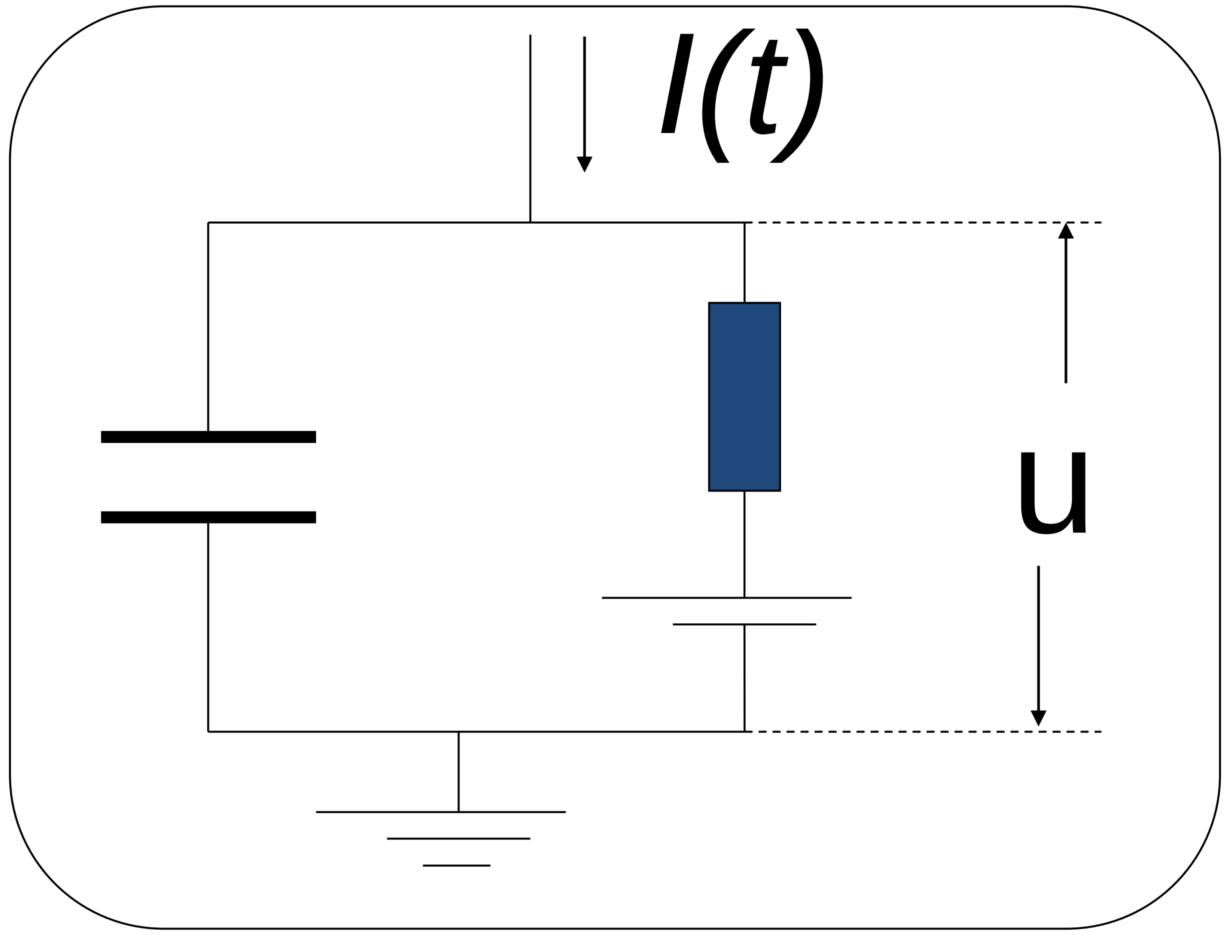
Start Exerc. at 9:47.

Next lecture at

10:15

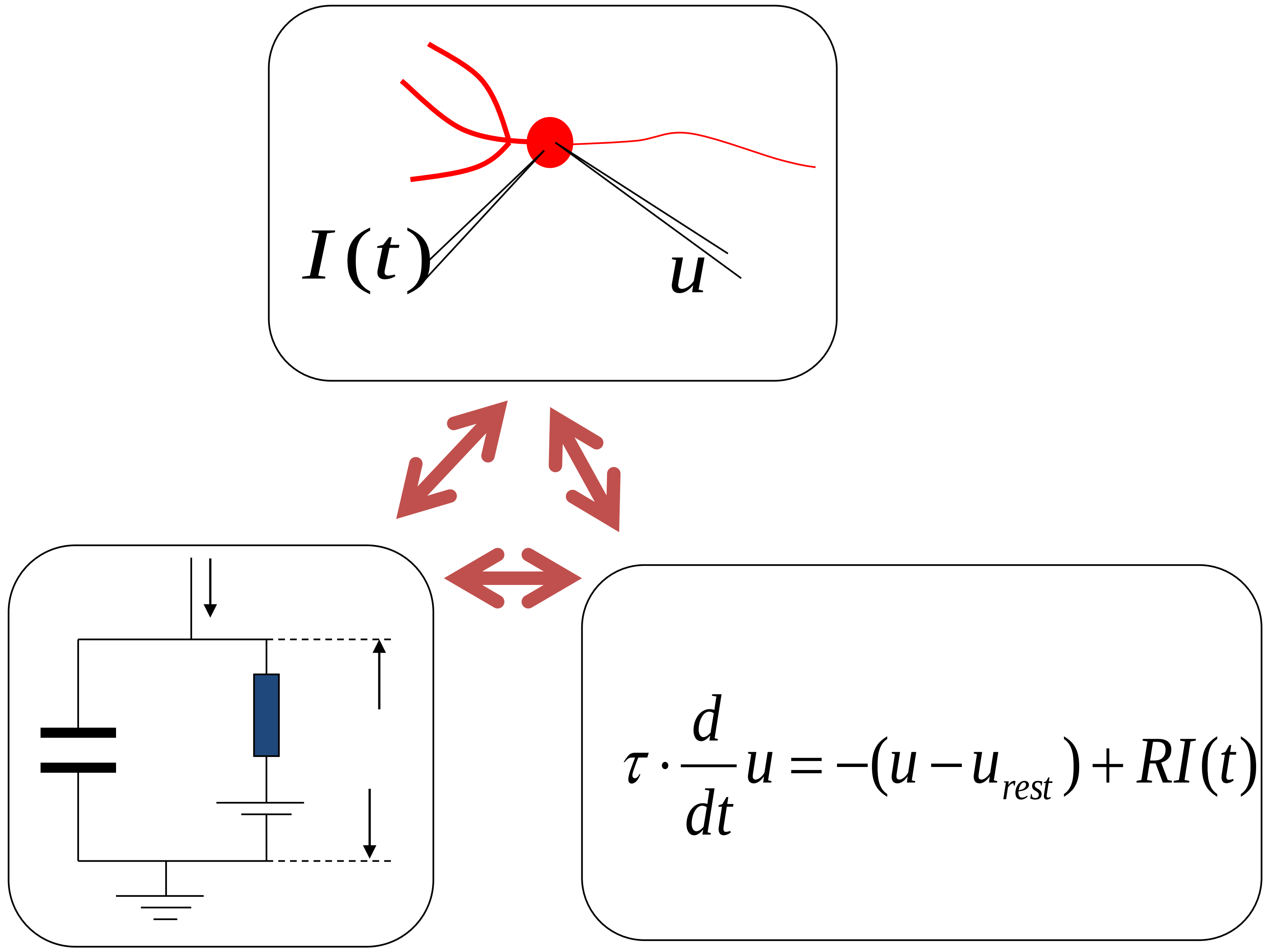
Triangle: neuron – electricity - math





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

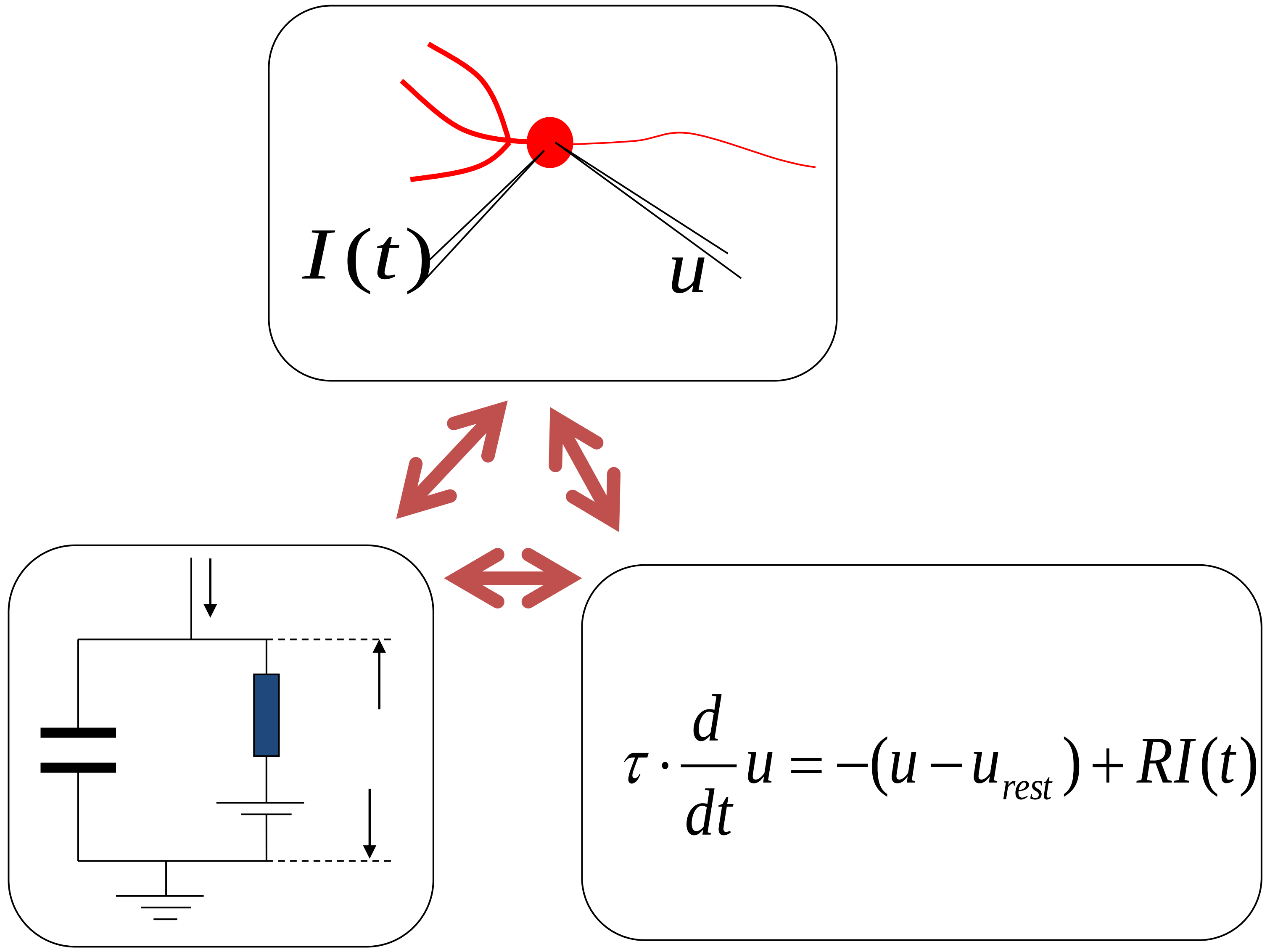
Pulse input – charge – delta-function



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

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

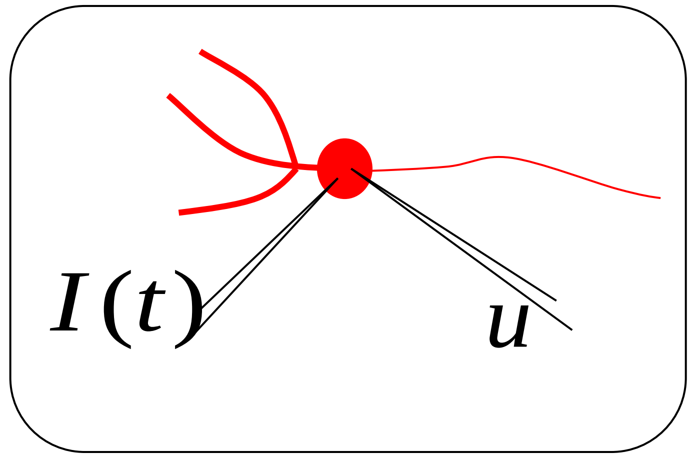
$$u(t) = u_{rest} + \int_{-\infty}^{t} \frac{1}{C} e^{-(t-t')/\tau} I(t')dt'$$

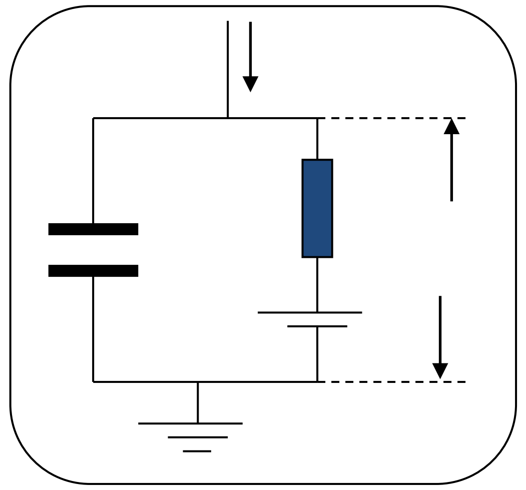
Single pulse

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

you need to know the solutions of linear differential equations!

Passive membrane, linear differential equation

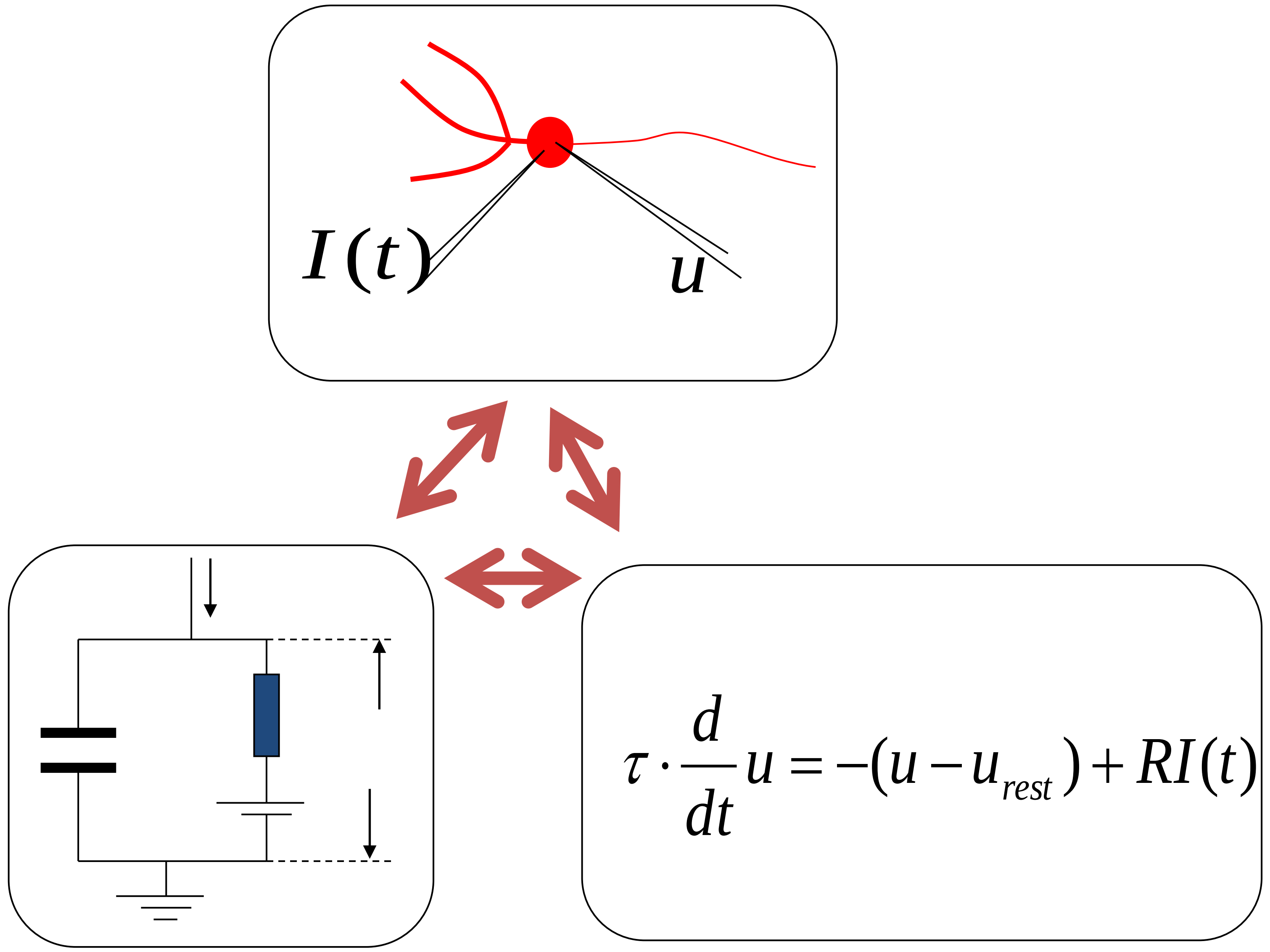




$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$

Passive membrane, linear differential equation

If you have difficulties, watch lecture 1.2detour.



Three prerequisits:

-Analysis 1-3

-Probability/Statistics

-Differential Equations or Physics 1-3 or Electrical Circuits

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

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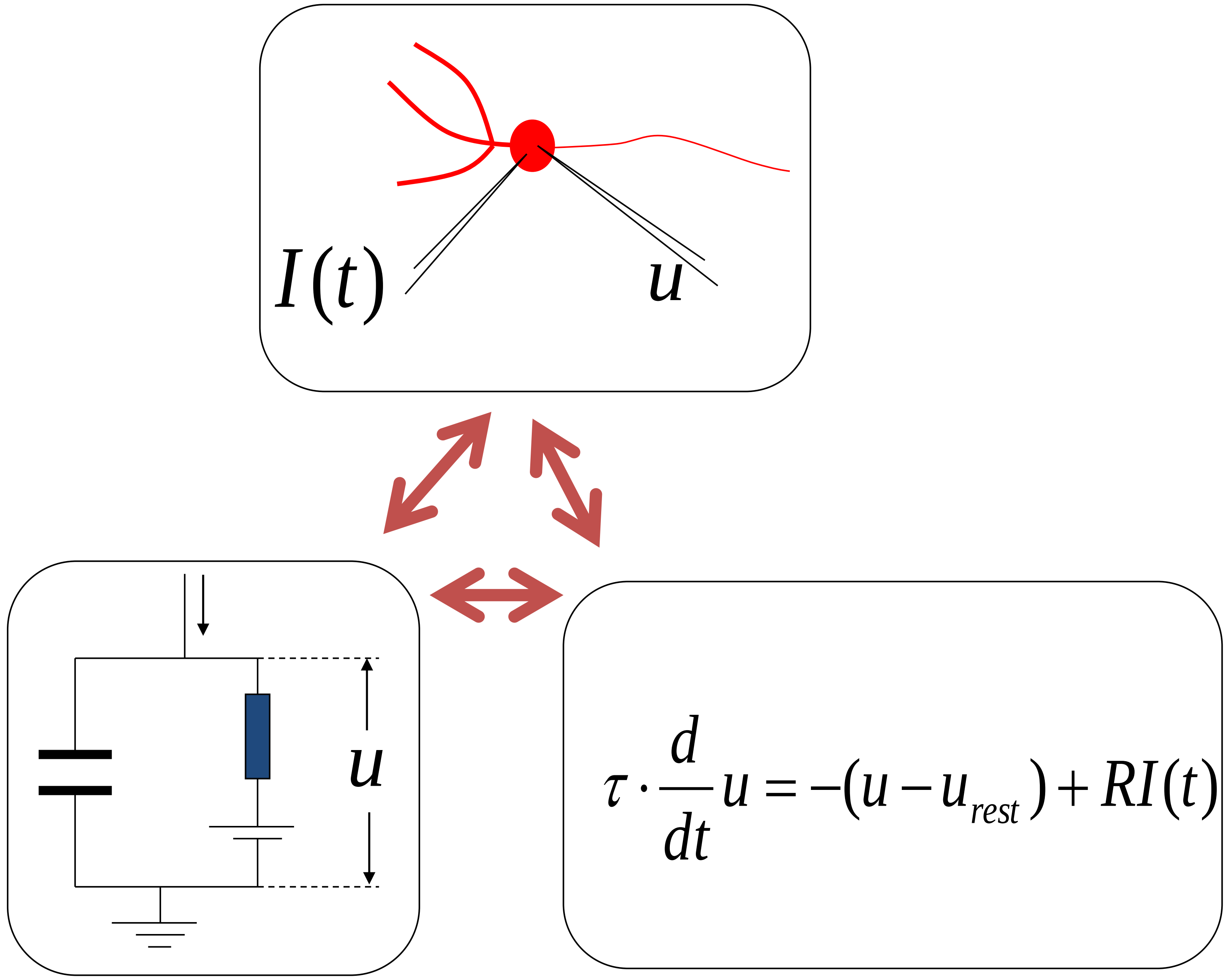
- √ 1.1 **Neurons and Synapses:** Overview
- √ 1.2 **The Passive Membrane**
  - Linear circuit
  - Dirac delta-function
  - Detour: solution of 1-dim linear differential equation
- 1.3 **Leaky Integrate-and-Fire Model**
- 1.4 **Generalized Integrate-and-Fire Model**
- 1.5. **Quality of Integrate-and-Fire Models**

Neuronal Dynamics – 1.3 Leaky Integrate-and-Fire Model

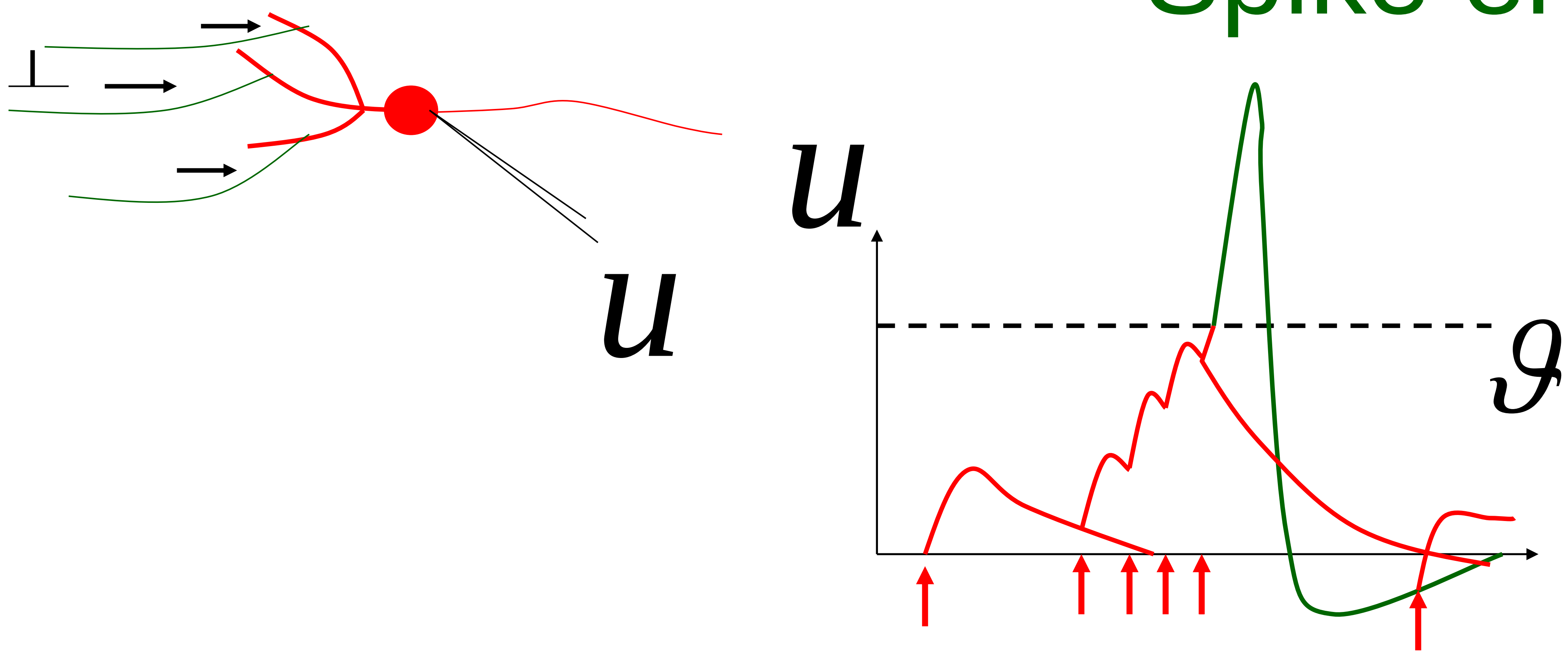
$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$



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

Neuronal Dynamics – Integrate-and-Fire type Models

Spike emission



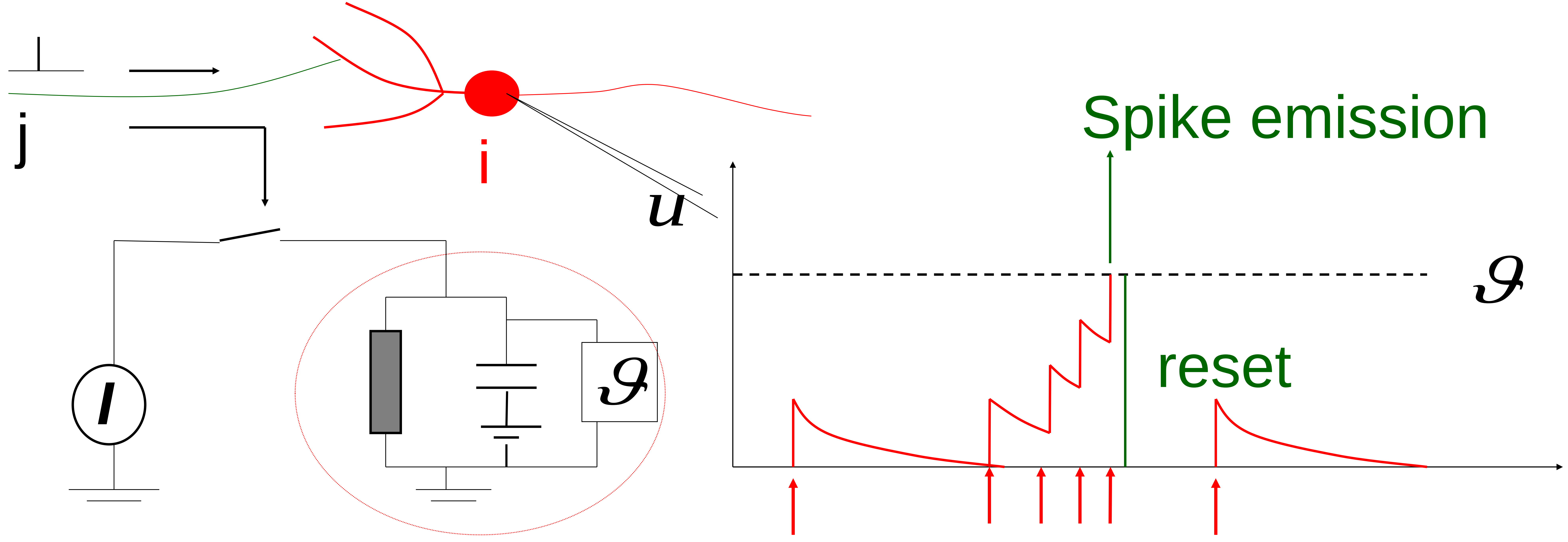
Input spike causes an EPSP
= excitatory postsynaptic potential

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

Leaky Integrate-and-Fire Model

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

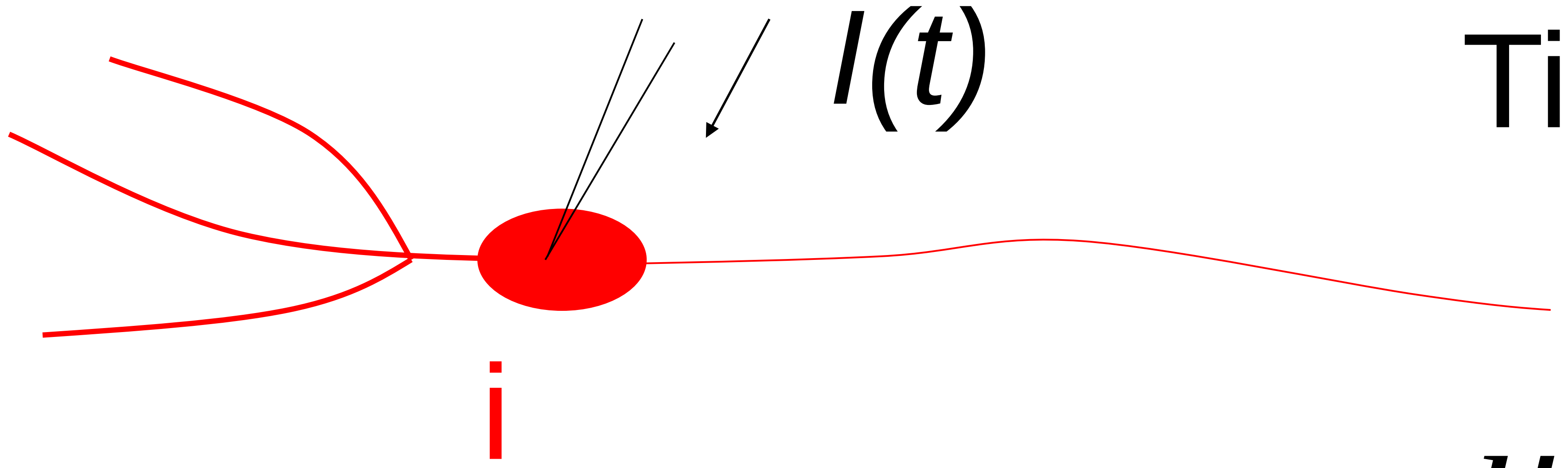
Neuronal Dynamics – 1.3 Leaky Integrate-and-Fire Model



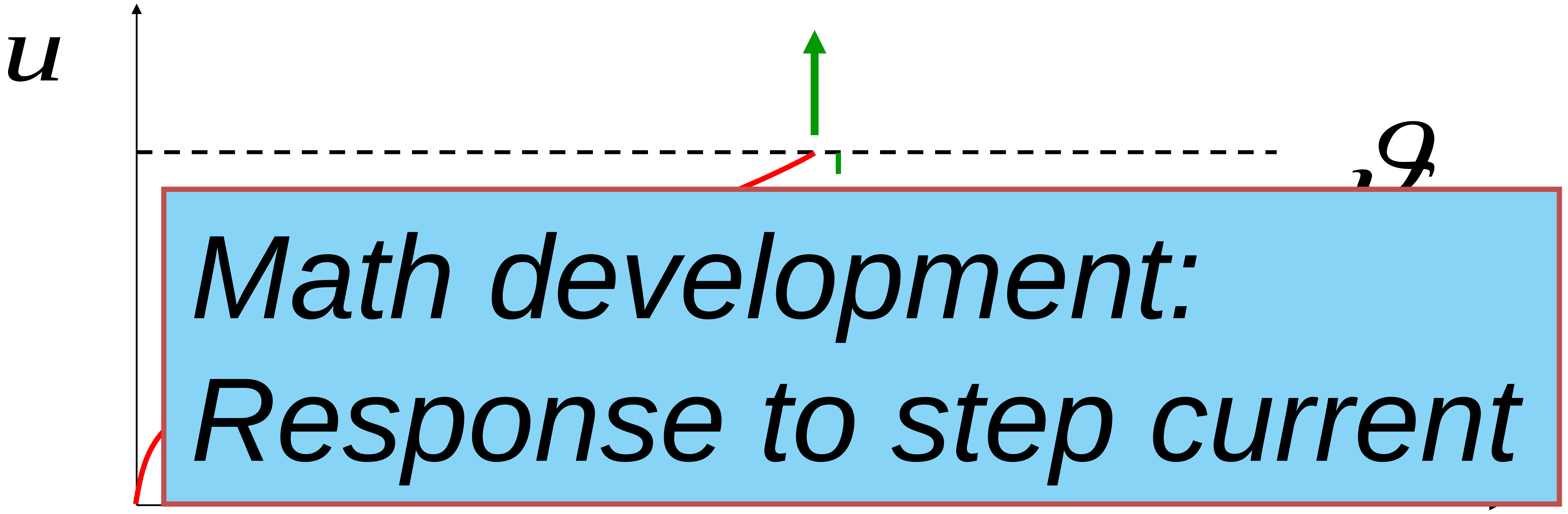
$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$ linear

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

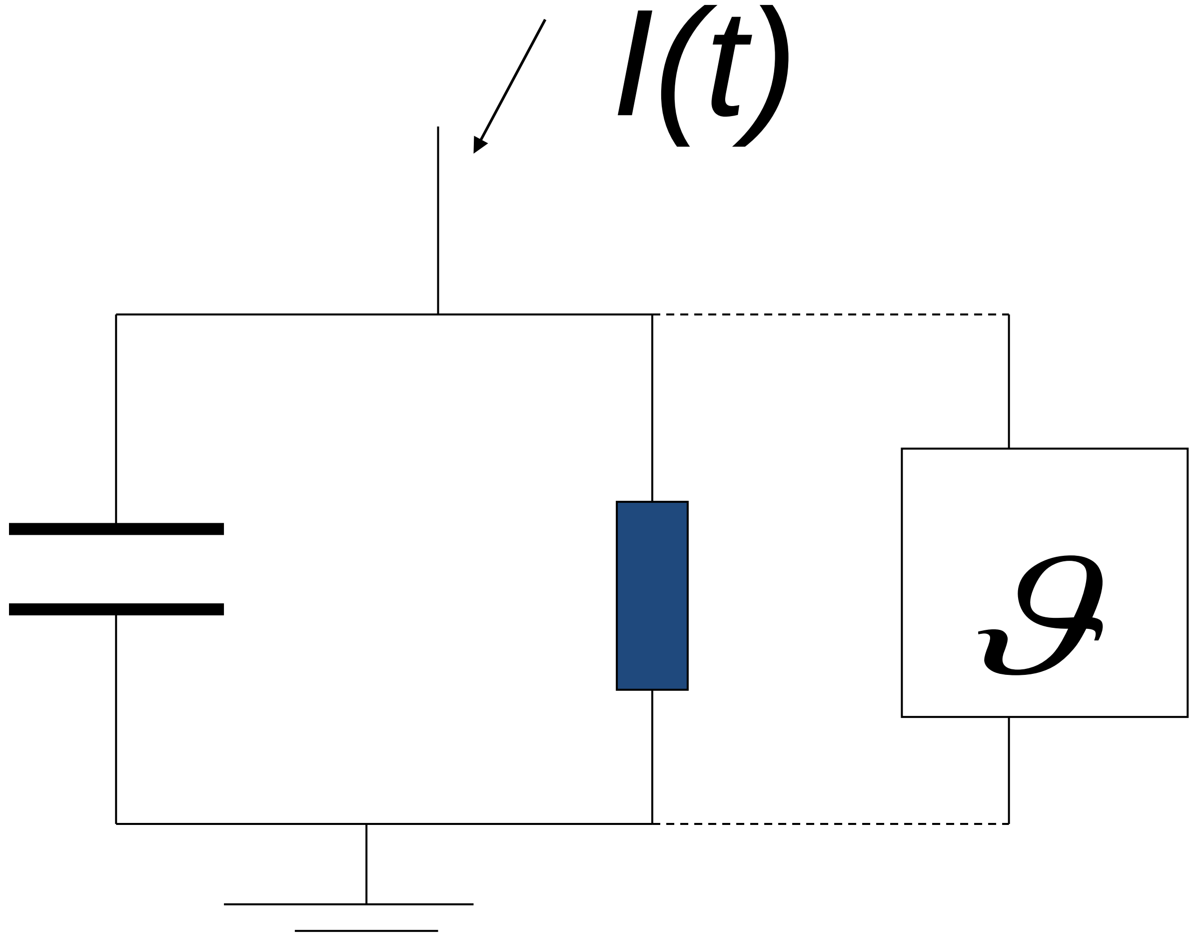
Neuronal Dynamics – 1.3 Leaky Integrate-and-Fire Model



Time-dependent input



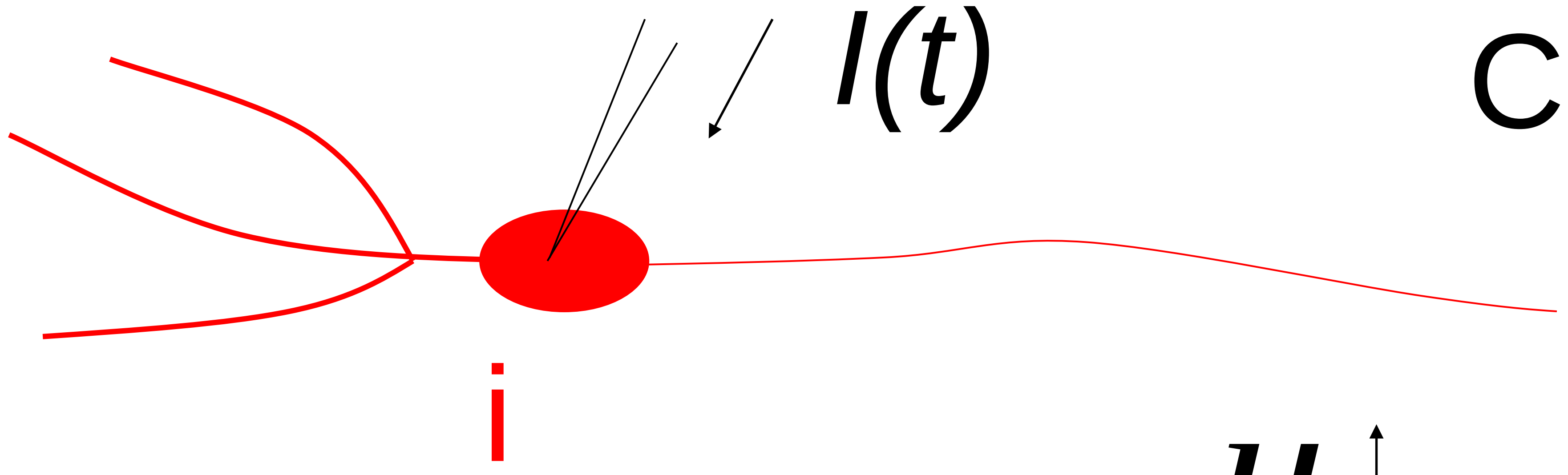
Math development:
Response to step current

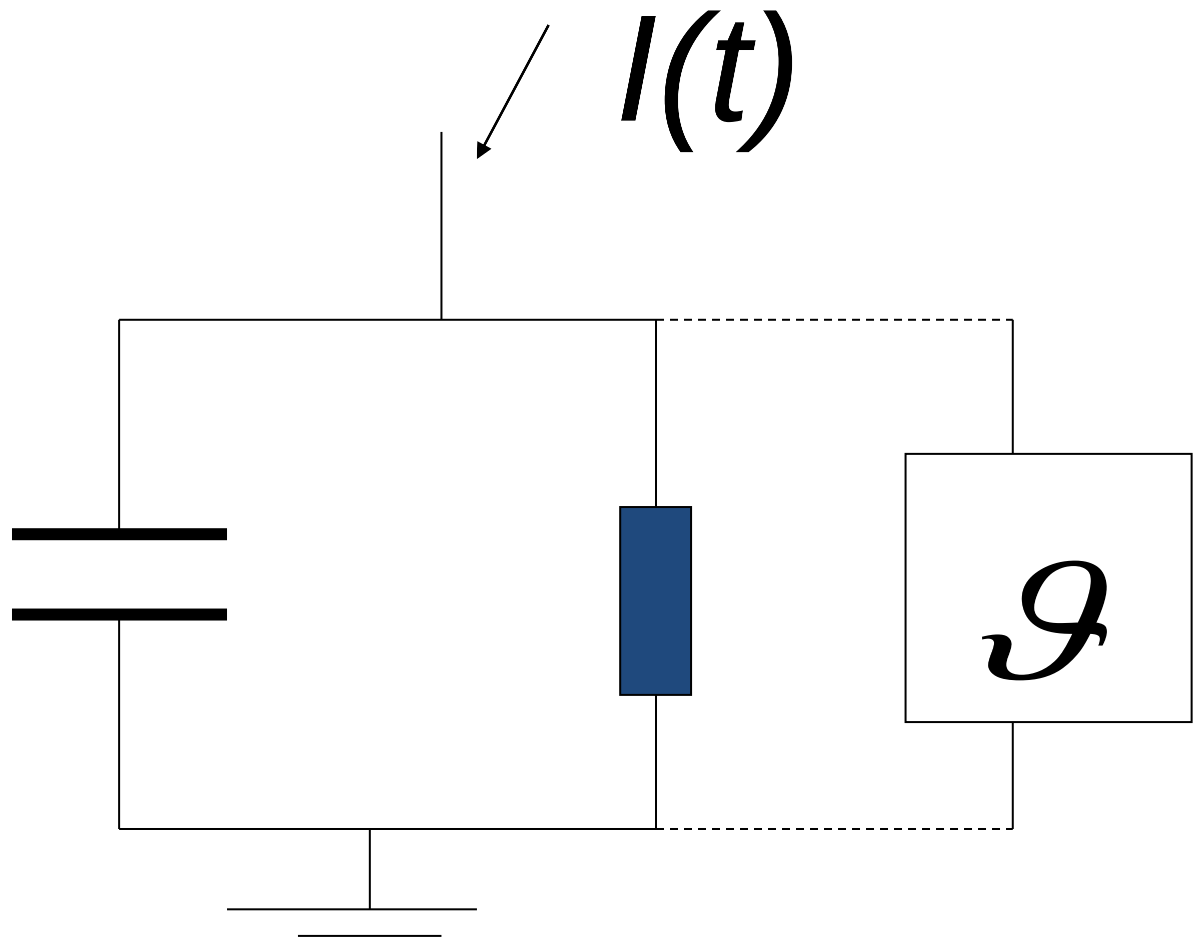


-spikes are events
-triggered at threshold
-spike/reset/refractoriness

Neuronal Dynamics – 1.3 Leaky Integrate-and-Fire Model

CONSTANT input/step input





Leaky Integrate-and-Fire Model (LIF)

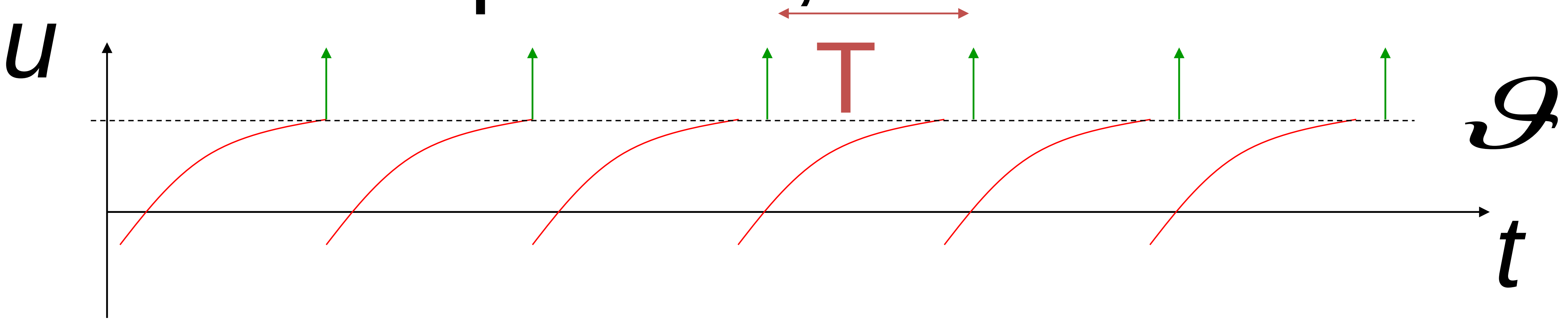
$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI_0$$

LIF

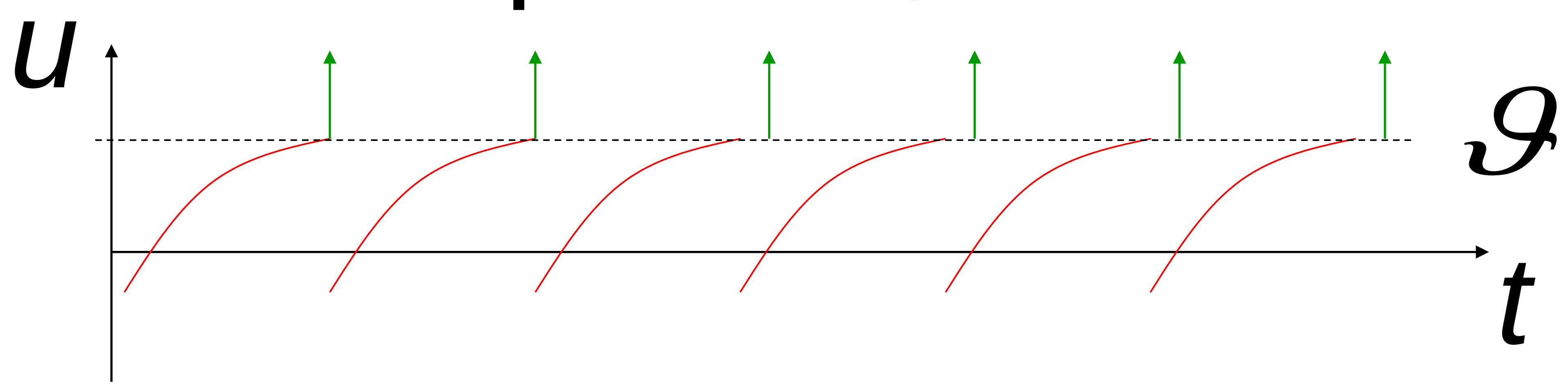
If $u(t) = \vartheta \Rightarrow \quad u \to u_r$

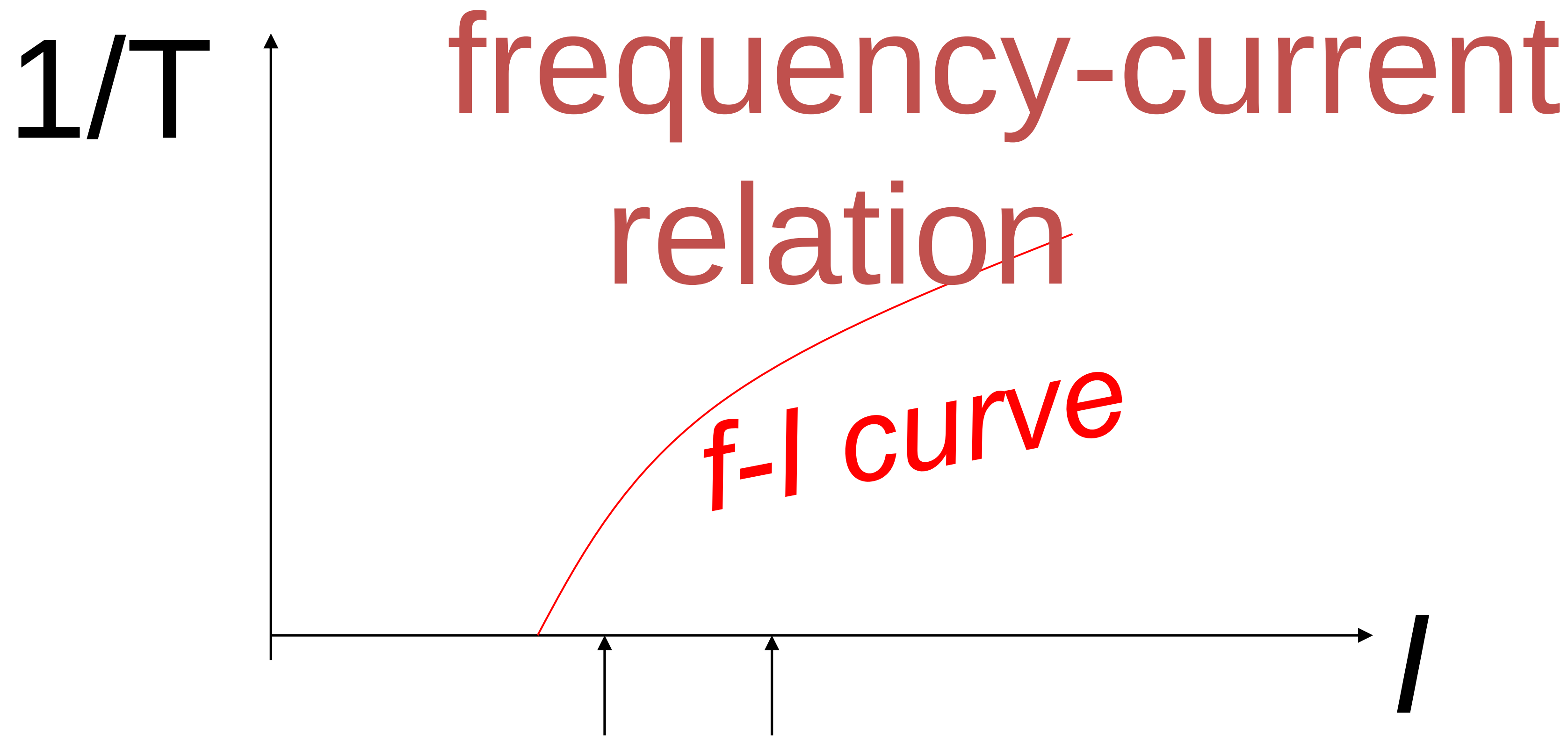
'Firing'

Repetitive, current I_0



Repetitive, current $I_1 > I_0$

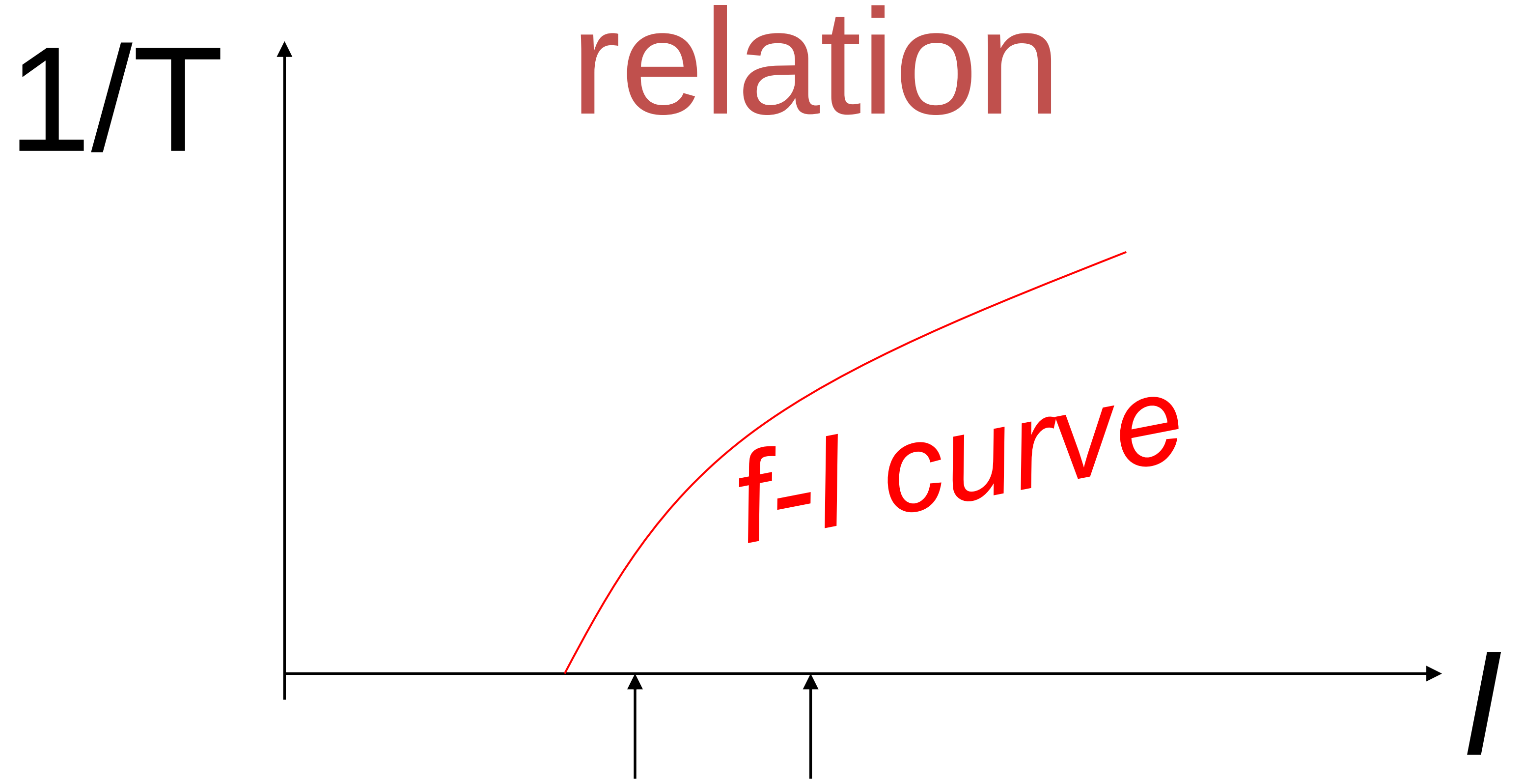




Neuronal Dynamics – First week, Exercise 2

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

frequency-current relation

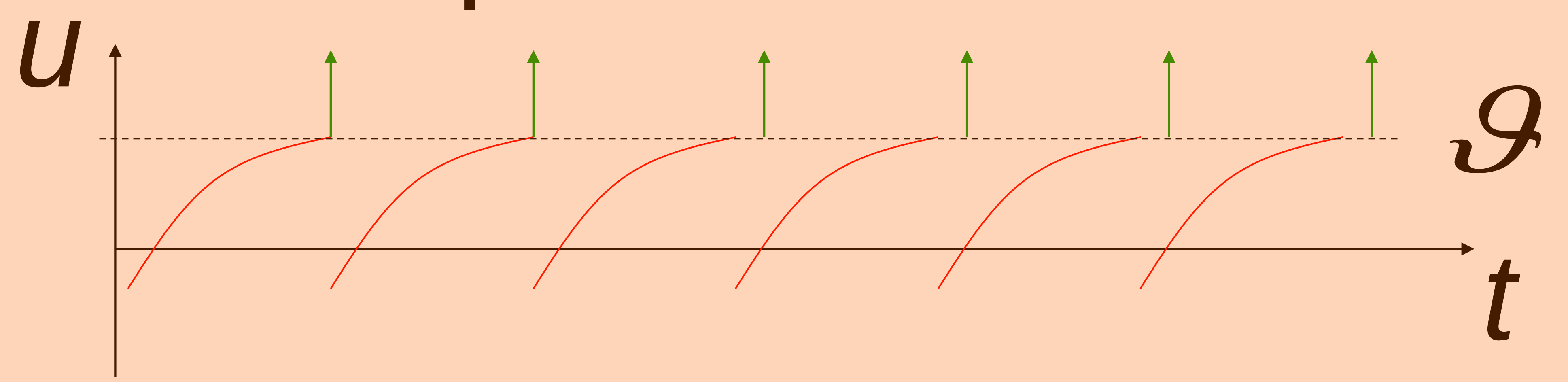


EXERCISE 2 NOW: Leaky Integrate-and-fire Model (LIF)

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

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?

repetitive



Start Exerc. at 10:55.
Next lecture at 11:15

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

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

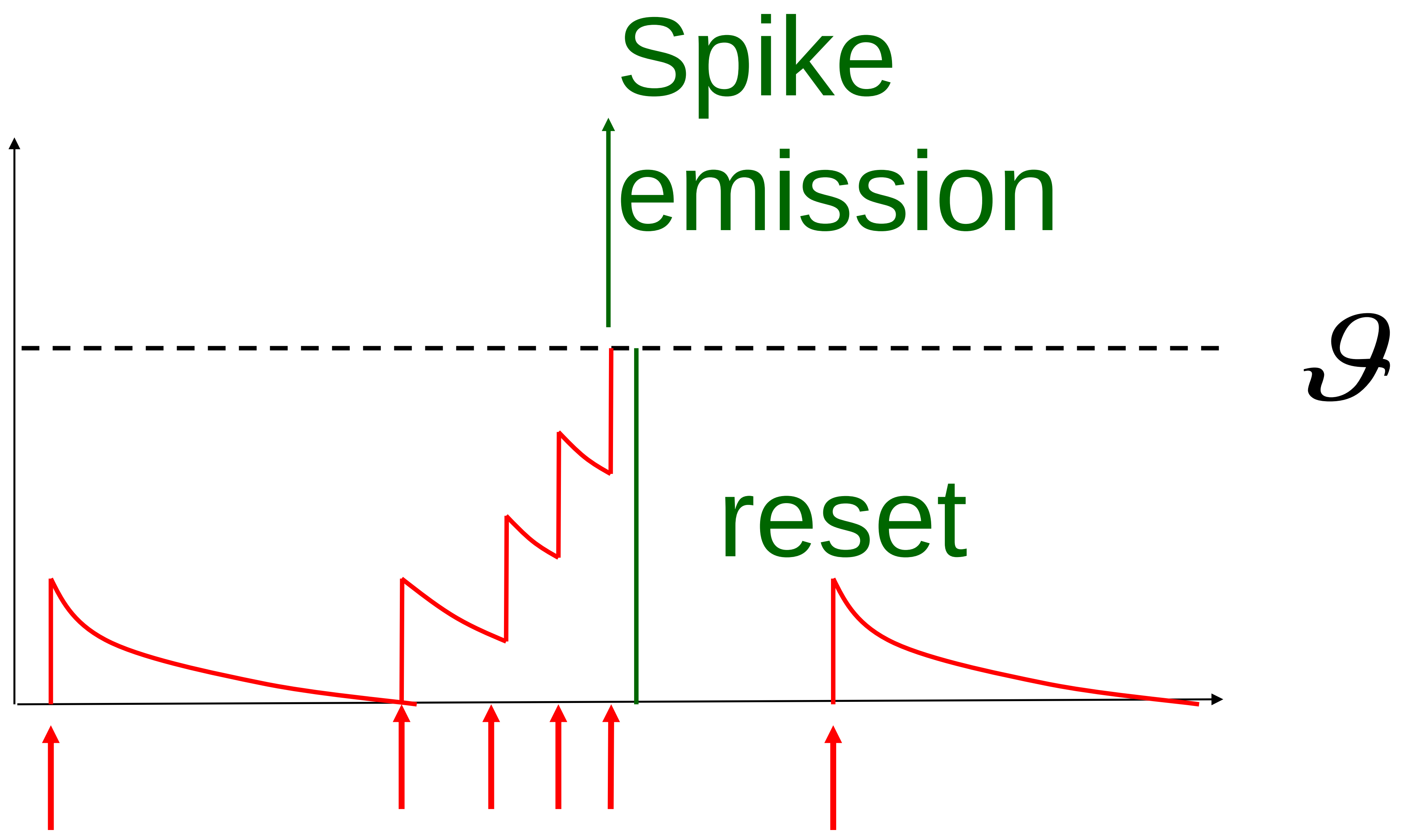
Neuronal Dynamics: Computational Neuroscience of Single Neurons

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

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Neuronal Dynamics – 1.4. Generalized Integrate-and Fire



Integrate-and-fire model

LIF: linear + threshold

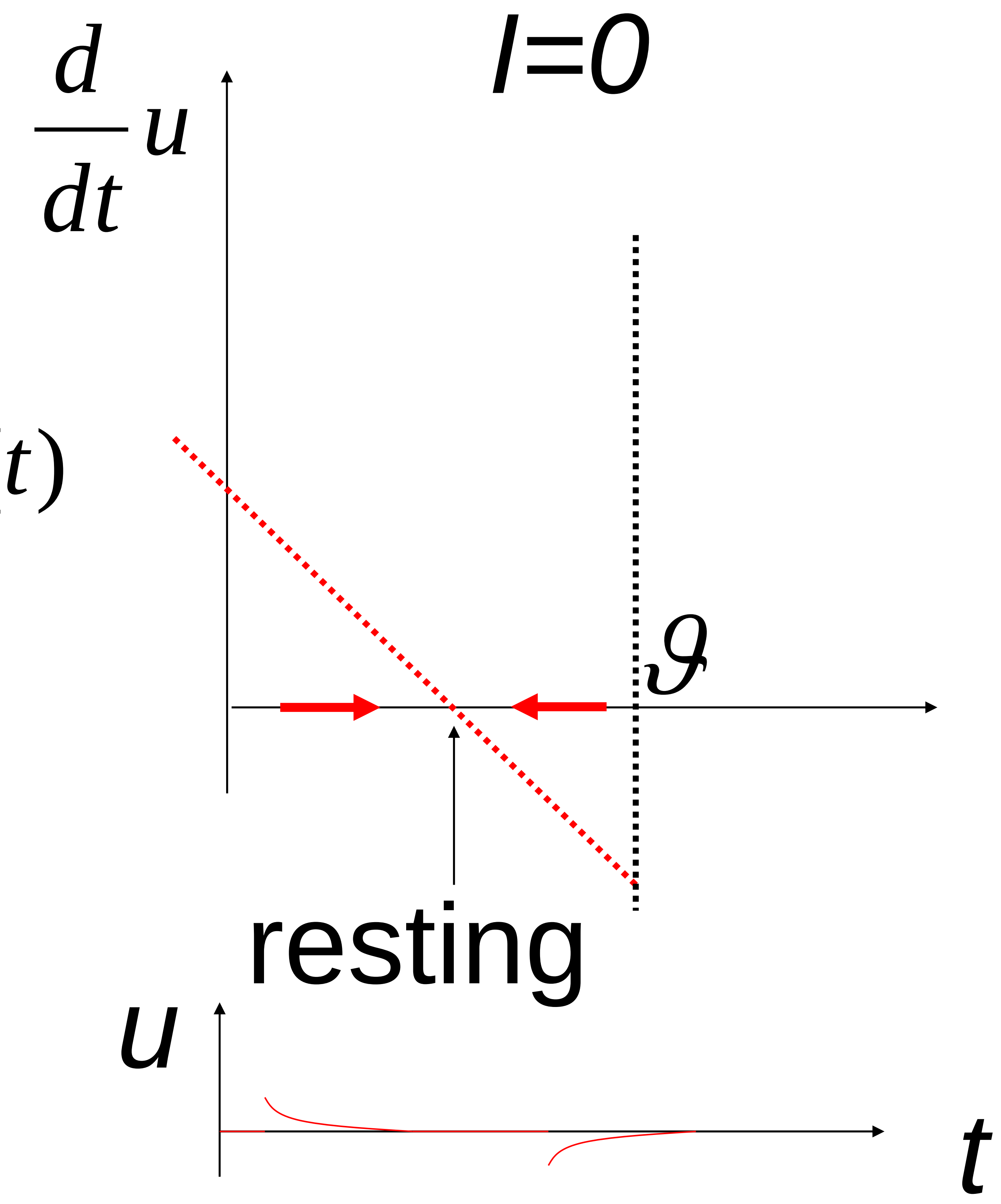
Neuronal Dynamics – 1.4. Leaky Integrate-and Fire revisited

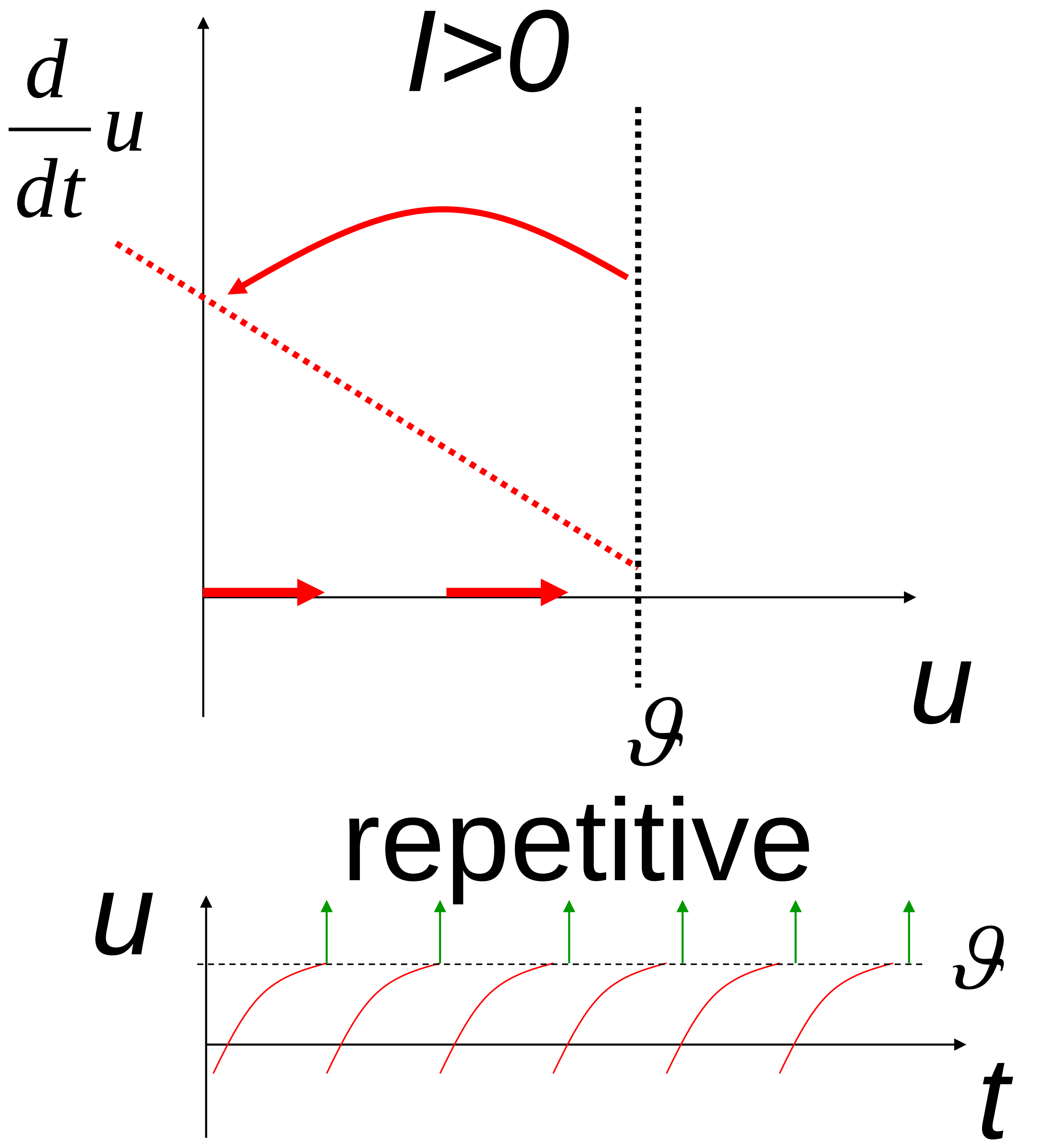
LIF

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

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

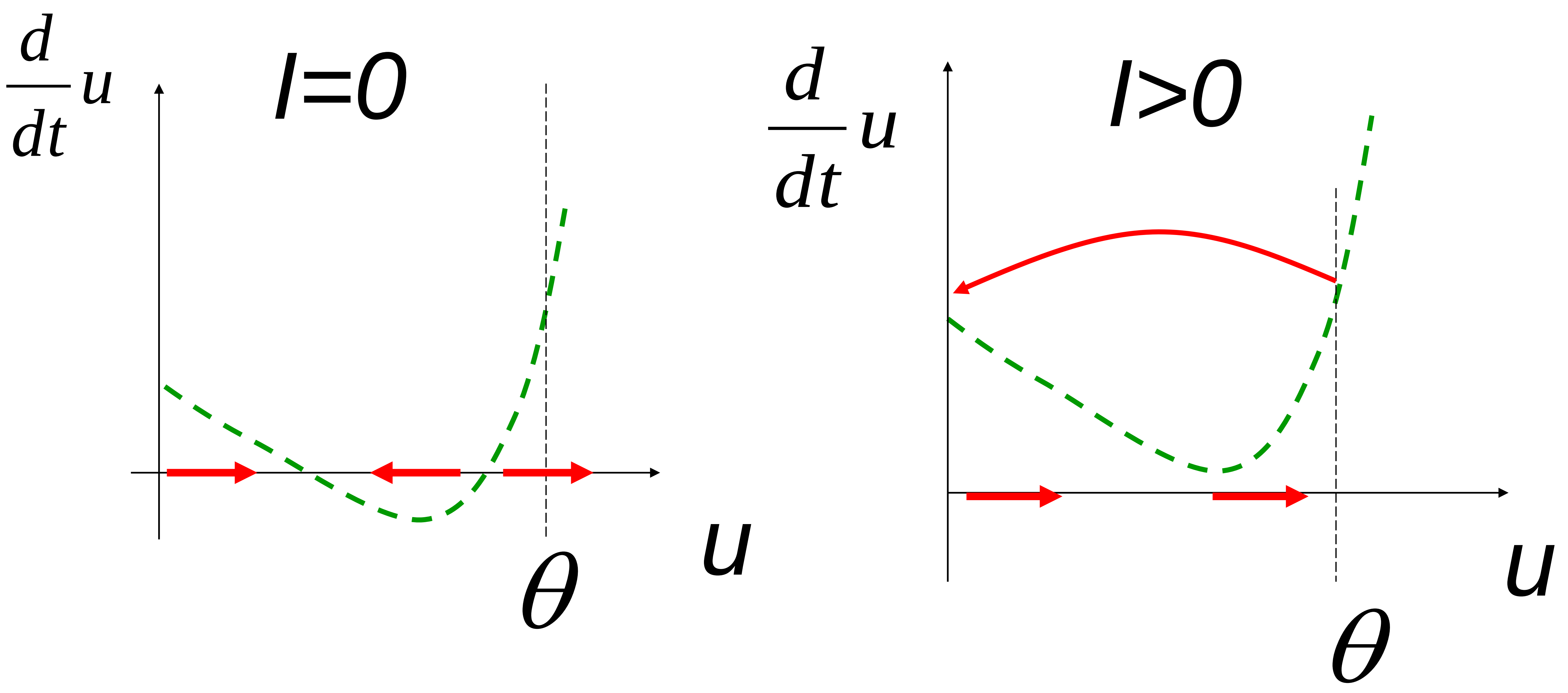
Nonlinear Integrate-and-Fire

NLIF

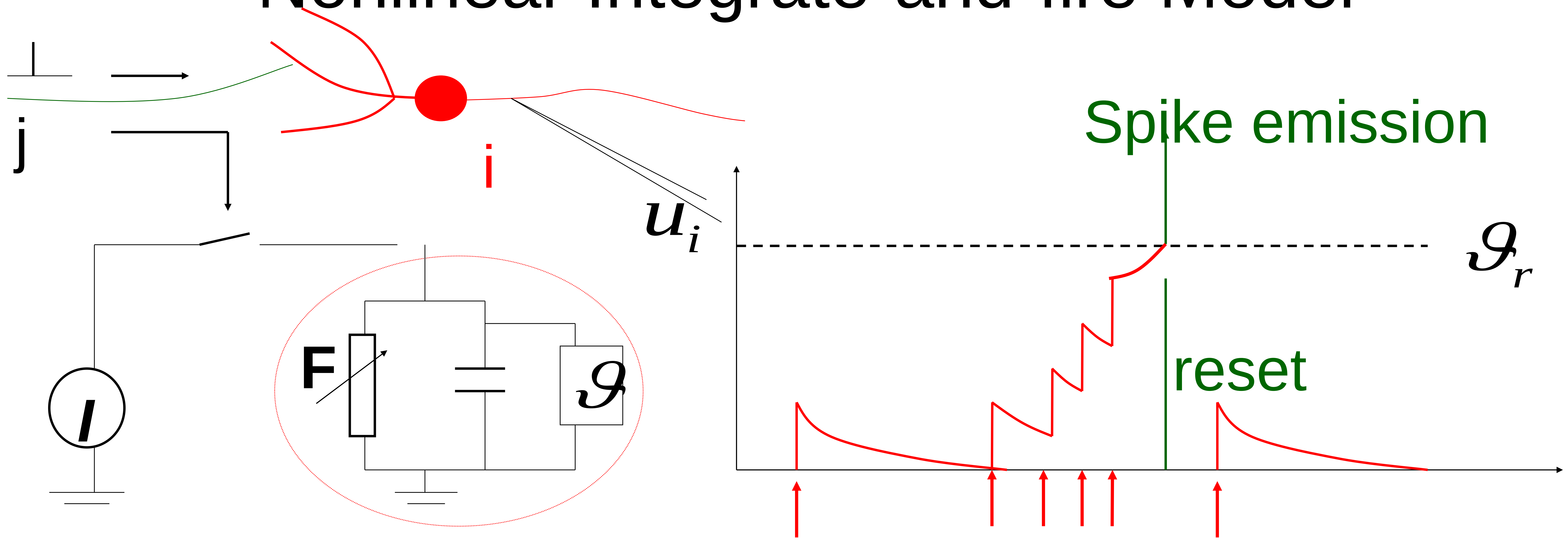
$$\tau \cdot \frac{d}{dt}u = F(u) + RI(t)$$

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

$$u \rightarrow u_r$$



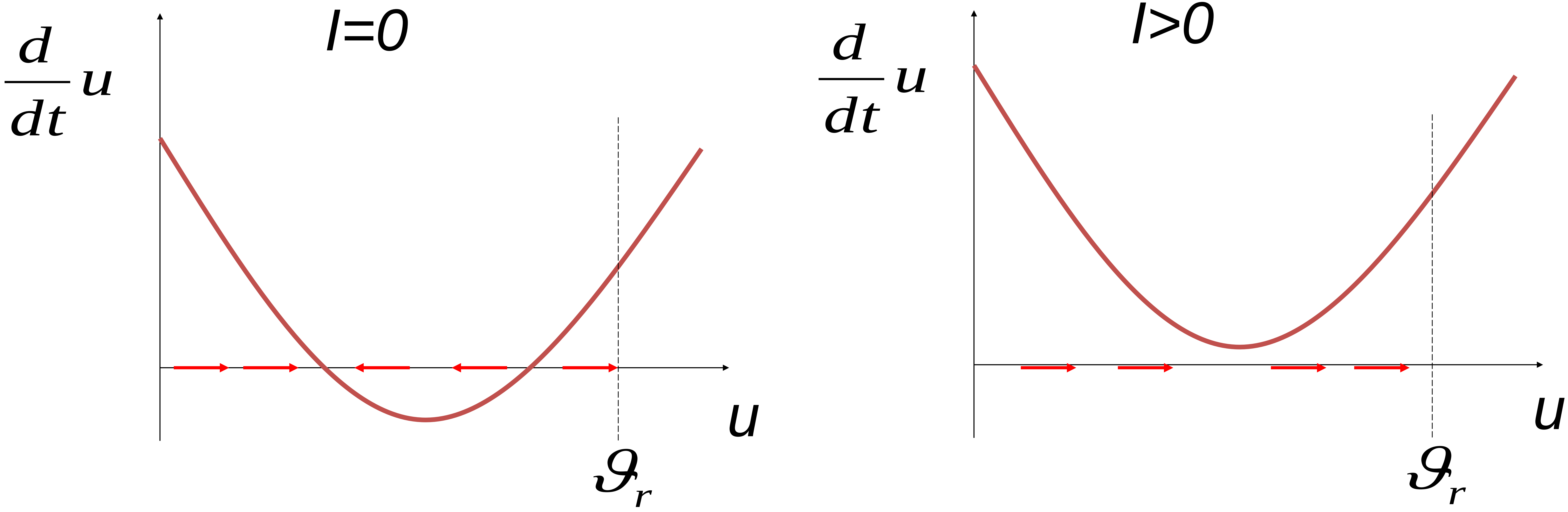
Nonlinear Integrate-and-fire Model



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

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

Nonlinear Integrate-and-fire Model



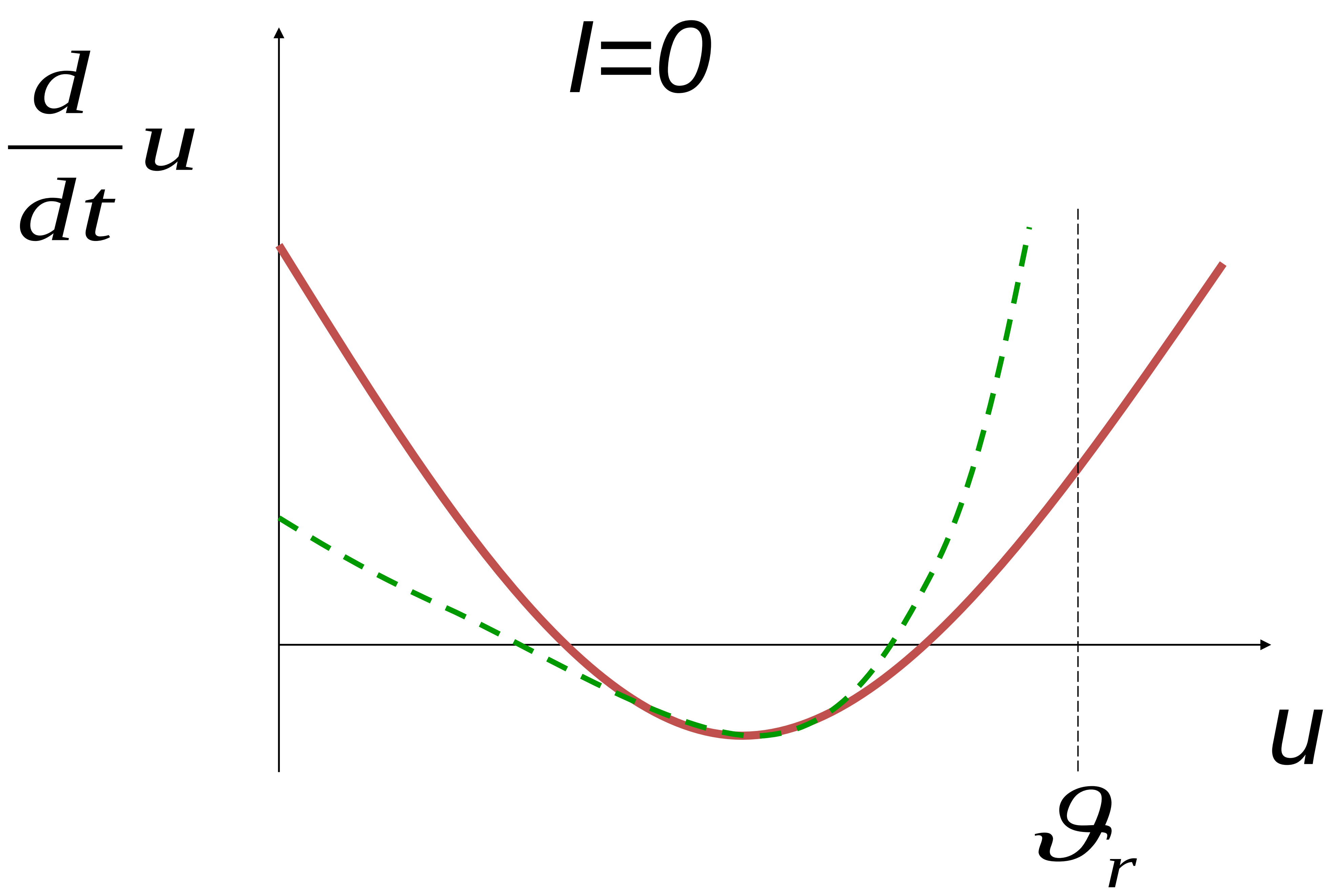
$$\tau \cdot \frac{d}{dt}u = F(u) + RI(t)$$ NONlinear

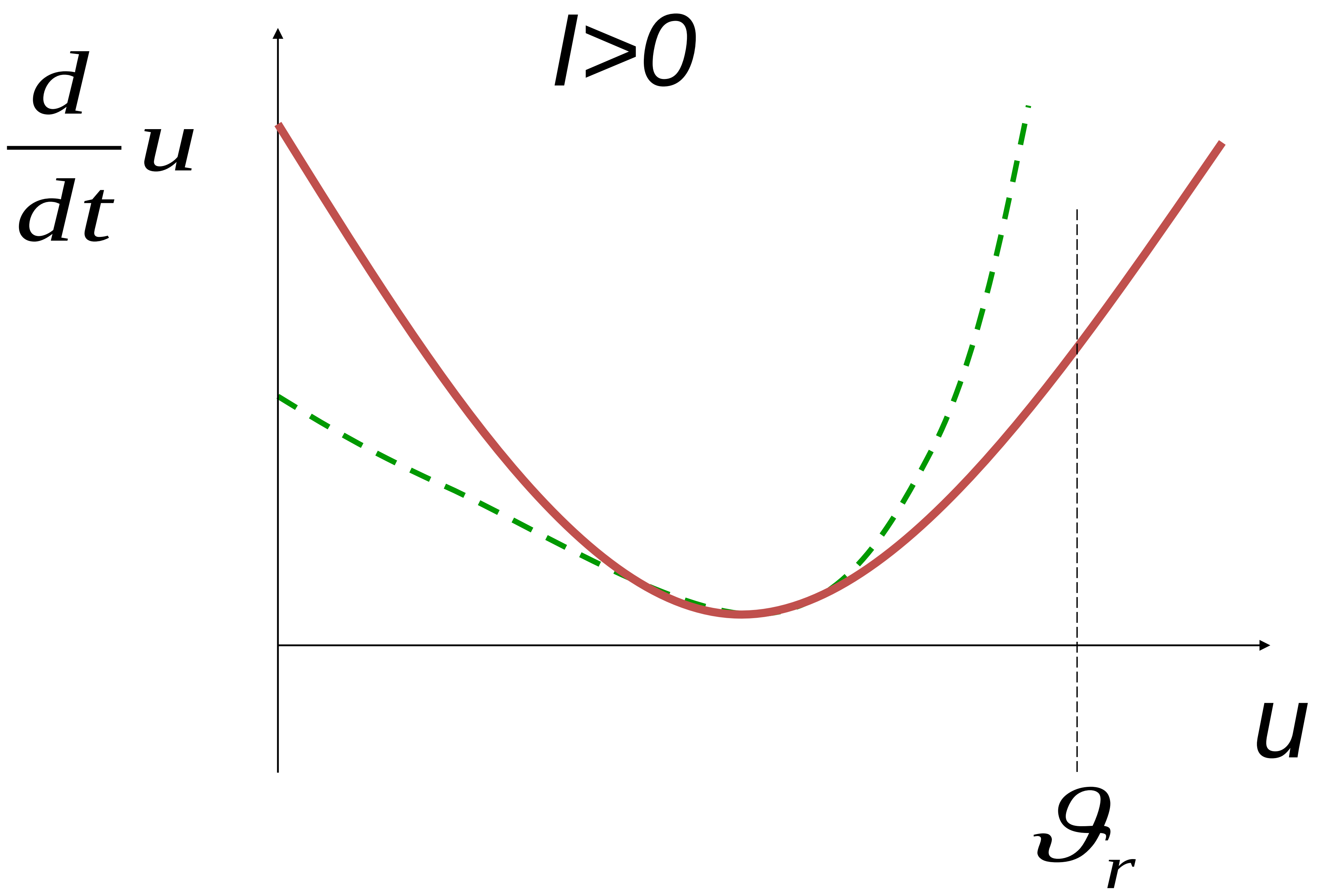
$$u(t) = \vartheta_r \Rightarrow$$ Fire+reset threshold

Quadratic I&F:

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

Nonlinear Integrate-and-fire Model





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

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

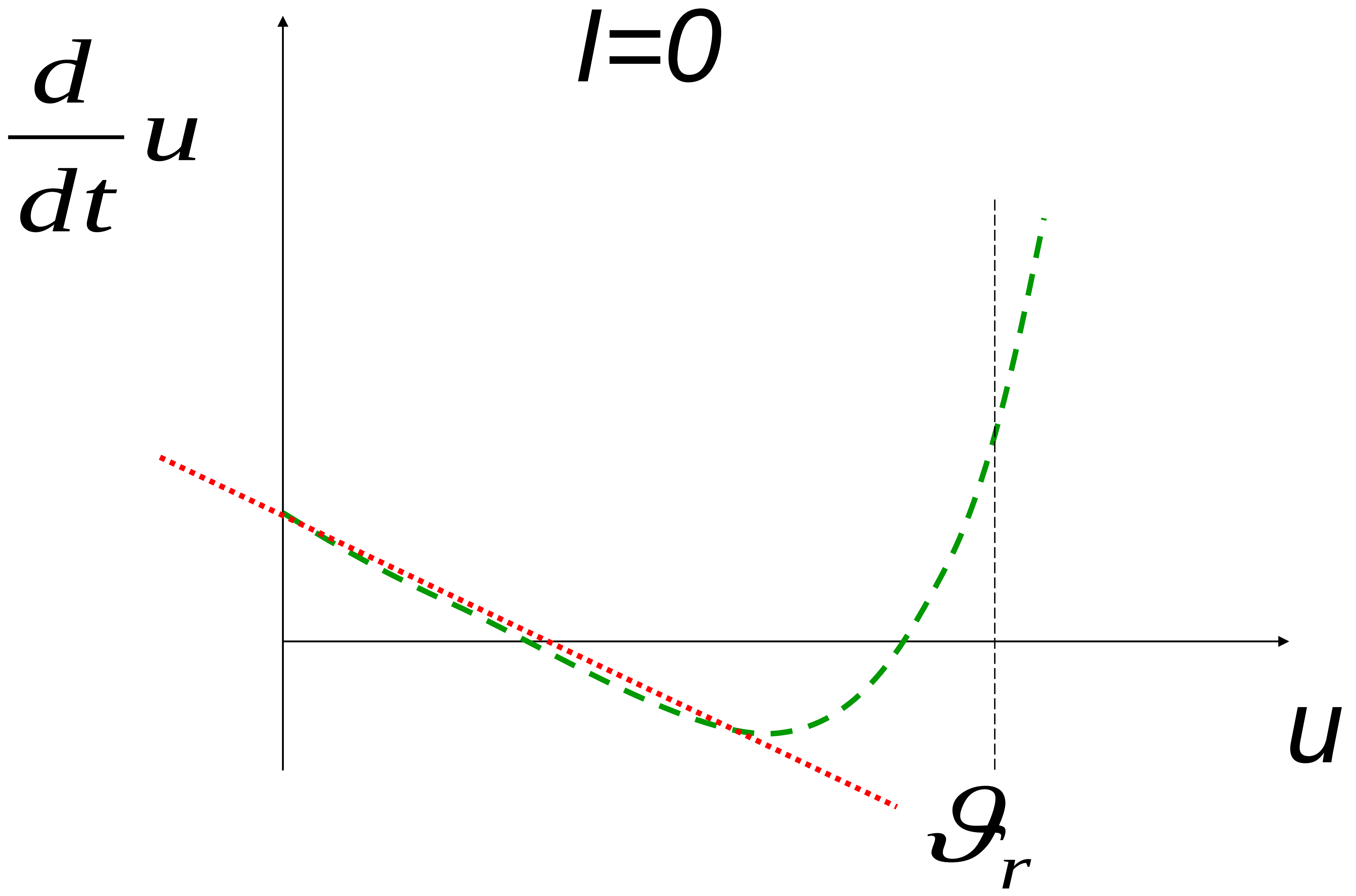
Quadratic I&F:

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

exponential I&F:

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

Nonlinear Integrate-and-fire Model



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

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

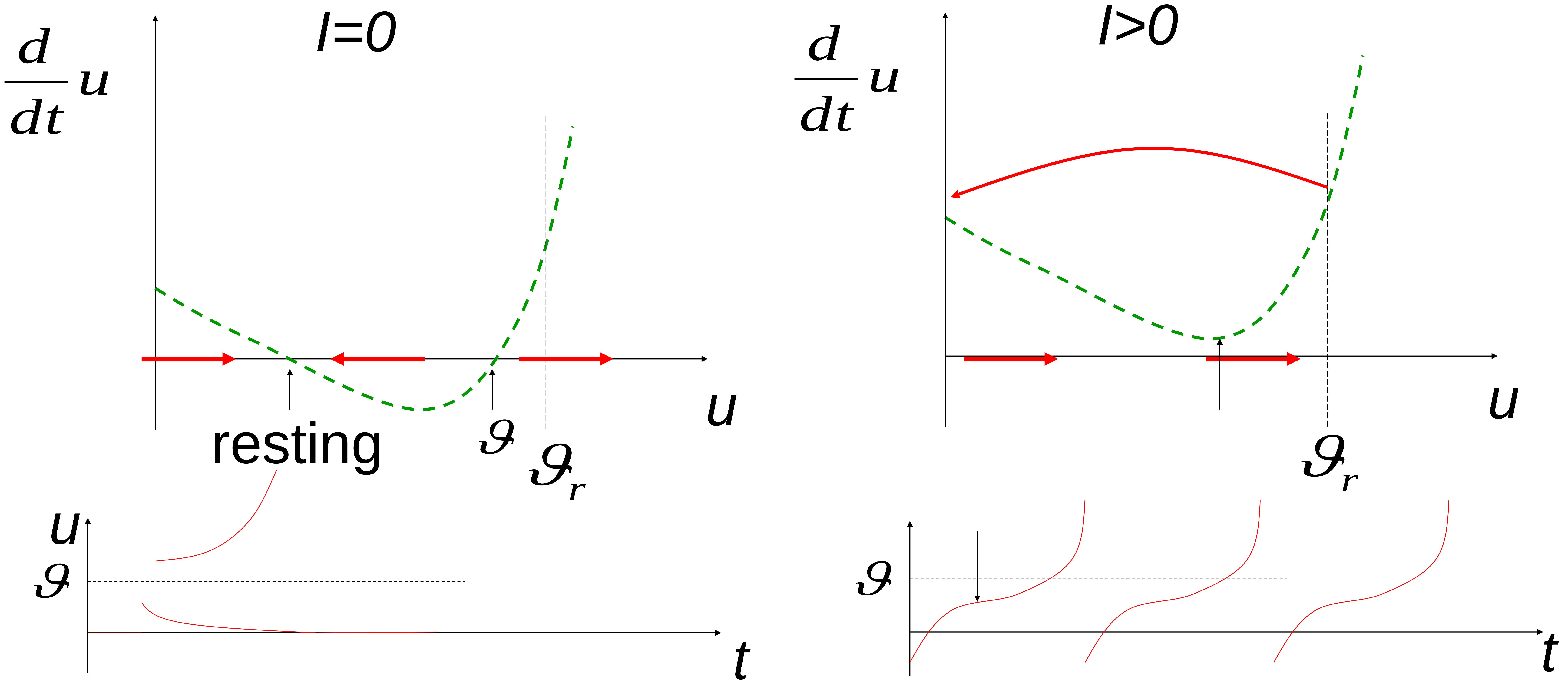
NONlinear

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

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

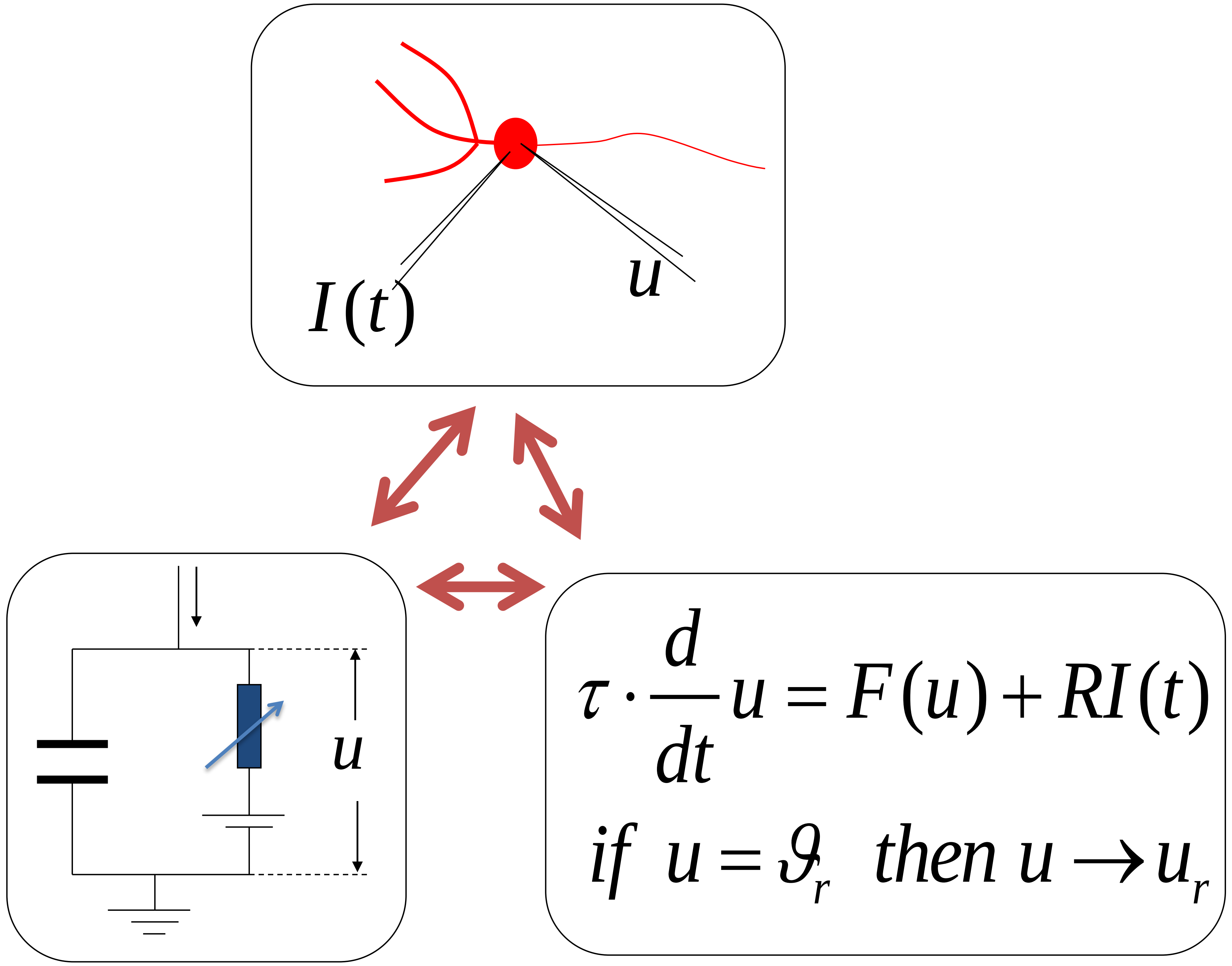
1.2 The Passive Membrane
- Linear circuit
- Dirac delta-function

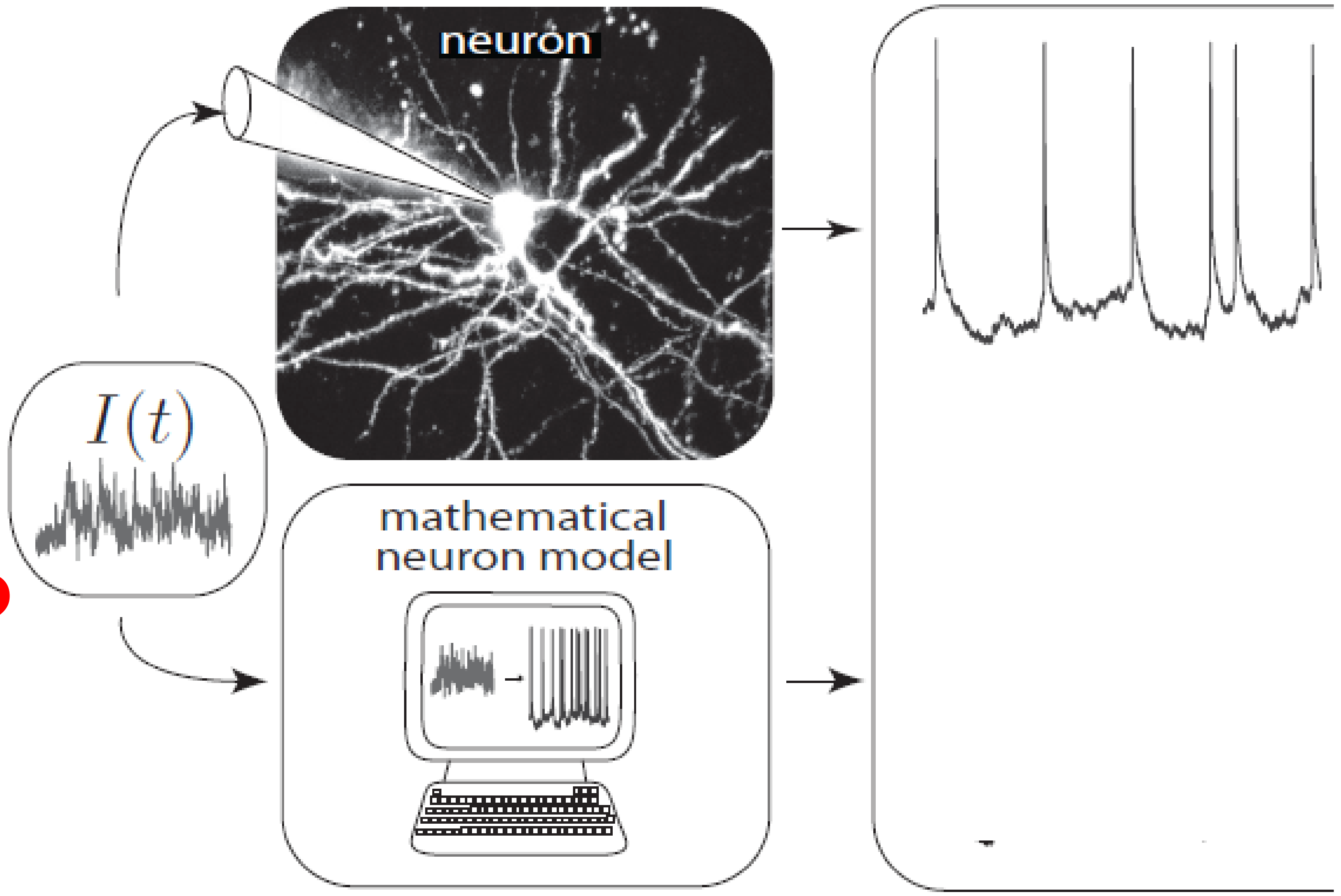
√ **1.3 Leaky Integrate-and-Fire Model**

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

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

Can we compare neuron models with experimental data?

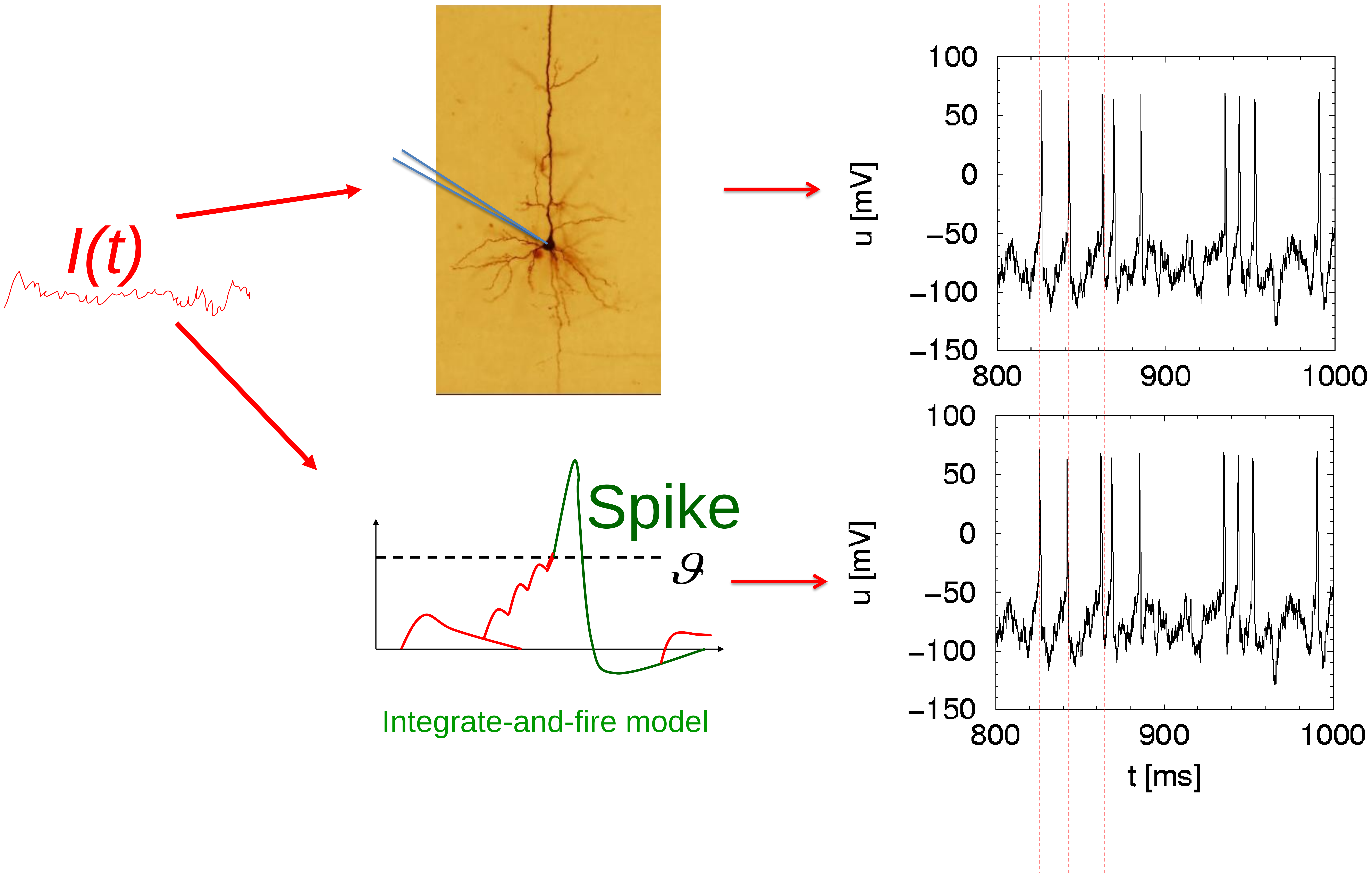




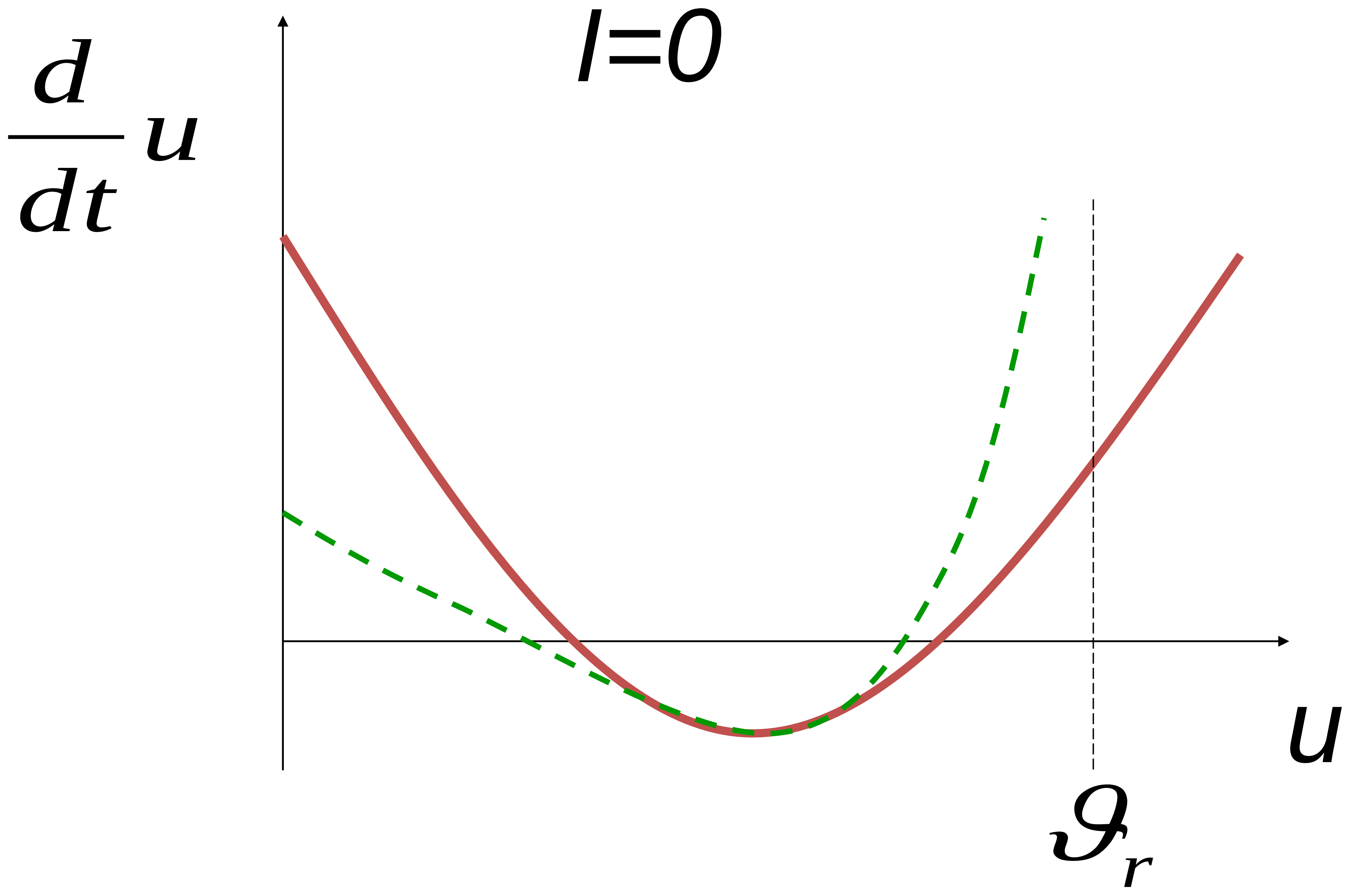
What is a good neuron model?

Can we compare neuron models with experimental data?

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



Nonlinear Integrate-and-fire Model



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

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

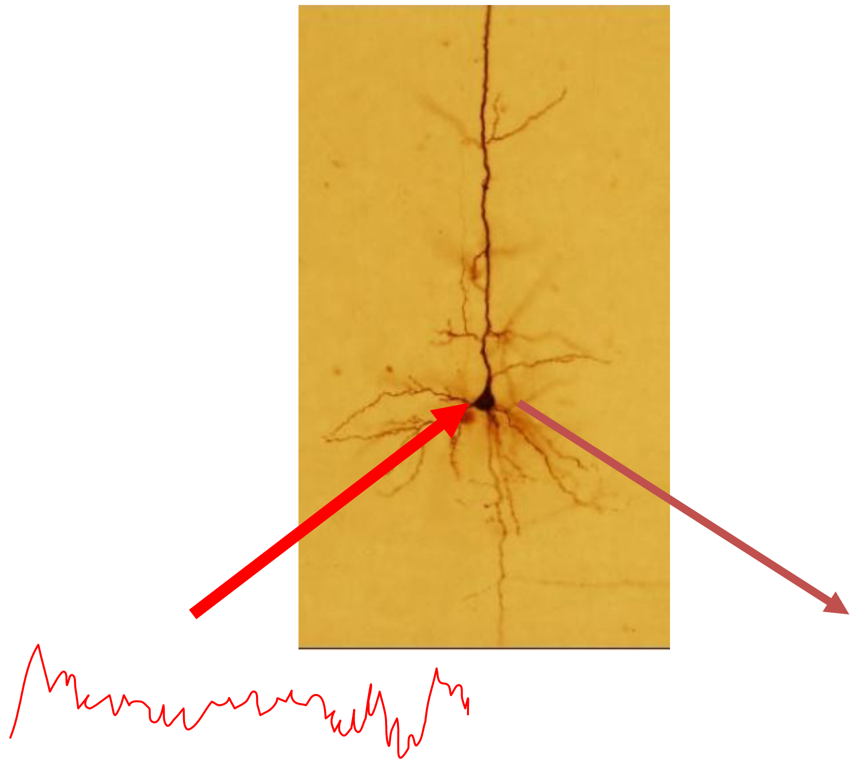
$$u(t) = \vartheta_r \Rightarrow \text{ Fire+reset}$$

Quadratic I&F:

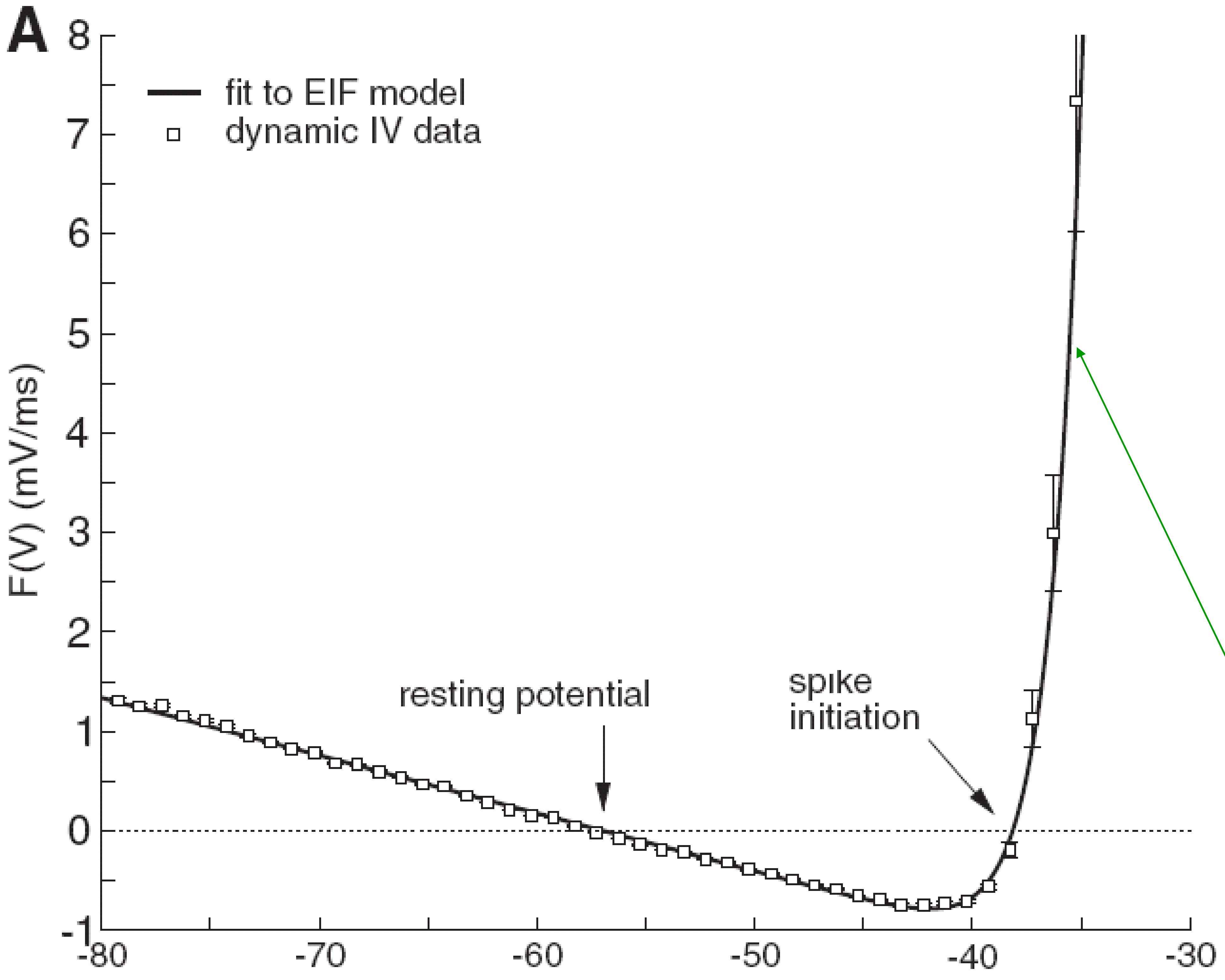
$$F(u) = c_2(u - c_1)^2 + c_0$$

exponential I&F:

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



I(t)



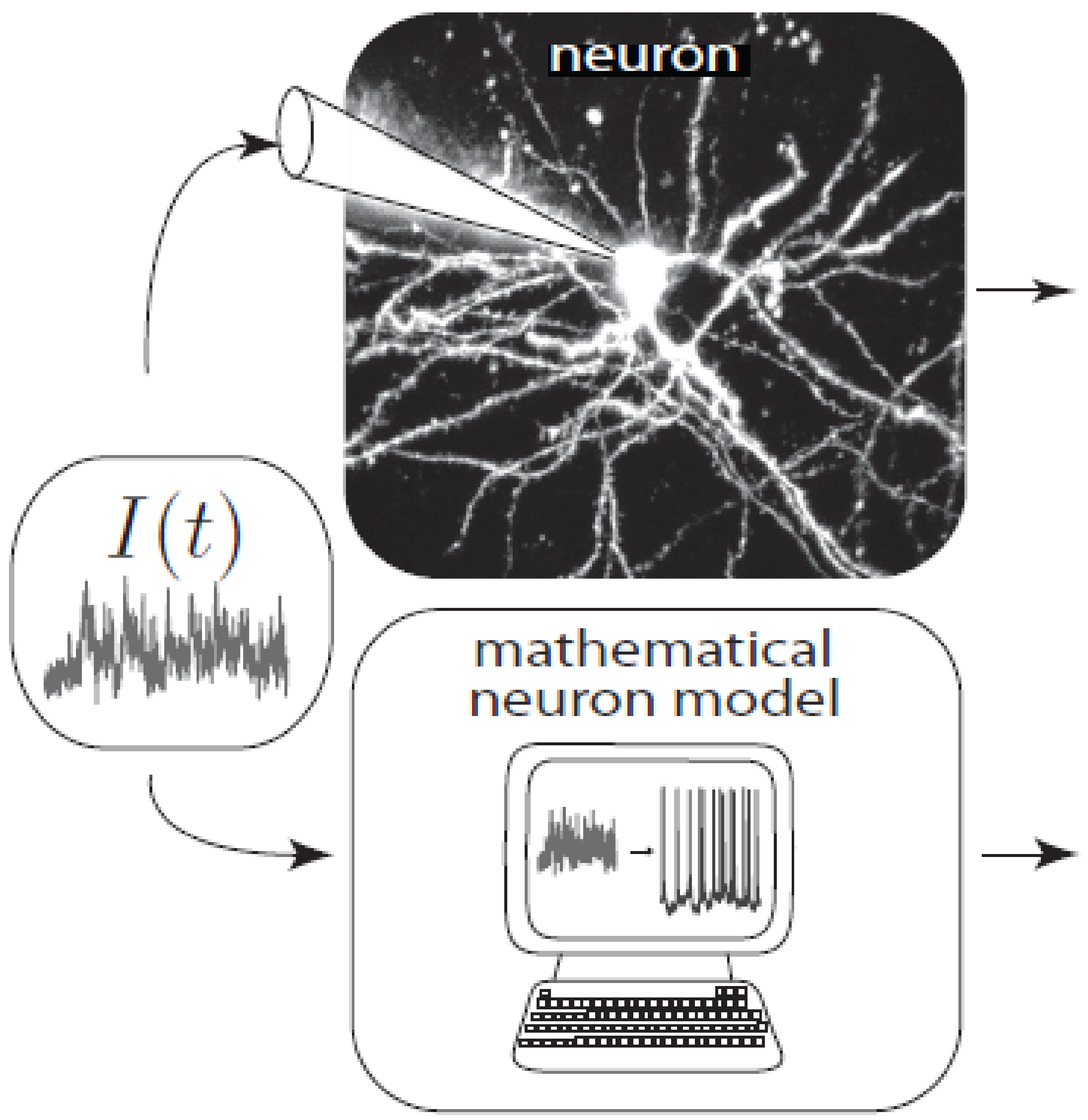
$$F(u) = -(u - u_{rest}) + \Delta \exp\left(\frac{u-\vartheta}{\Delta}\right)$$

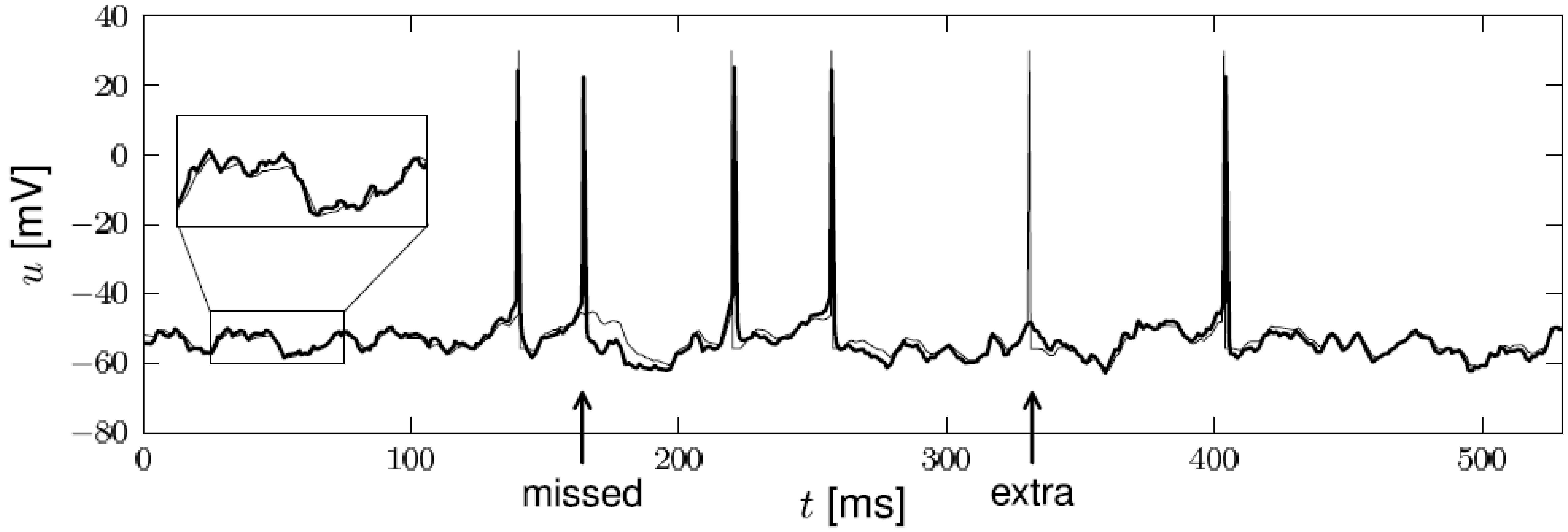
u [mV]

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

Badel et al., J. Neurophysiology 2008

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





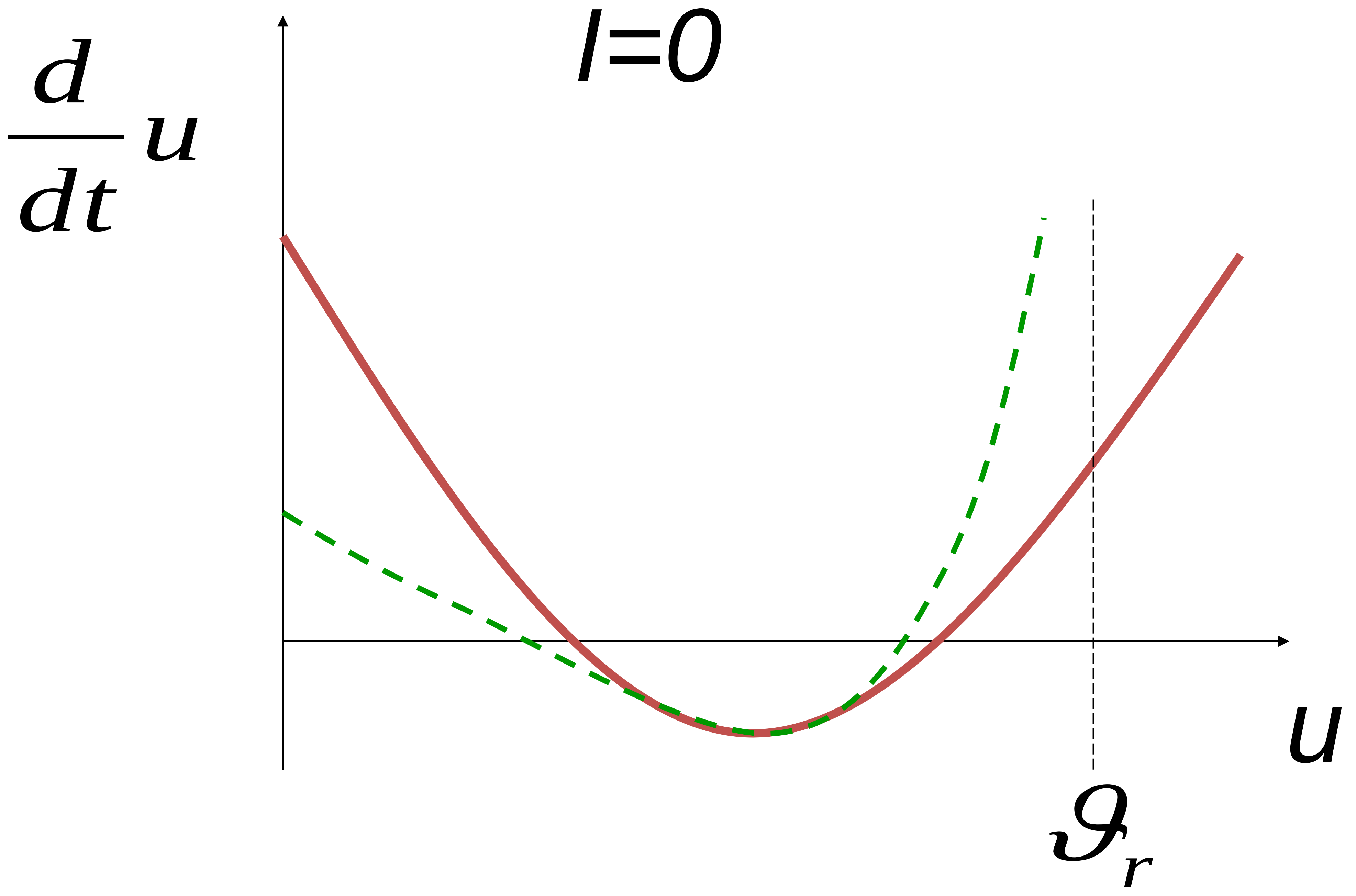
Nonlinear integrate-and-fire models
are good

Mathematical description → prediction

Computer ecercises:
Python

Need to add
- adaptation
- noise
- dendrites/synapses

Neural Networks and Biological - Exercise 3



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

Homework!

Neuronal Dynamics – 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.

Neuronal Dynamics –

THE END

MATH DETOUR SLIDES

Week 1 – part 2: Detour/Linear differential equation

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

Neuronal Dynamics:
Computational Neuroscience of Single Neurons

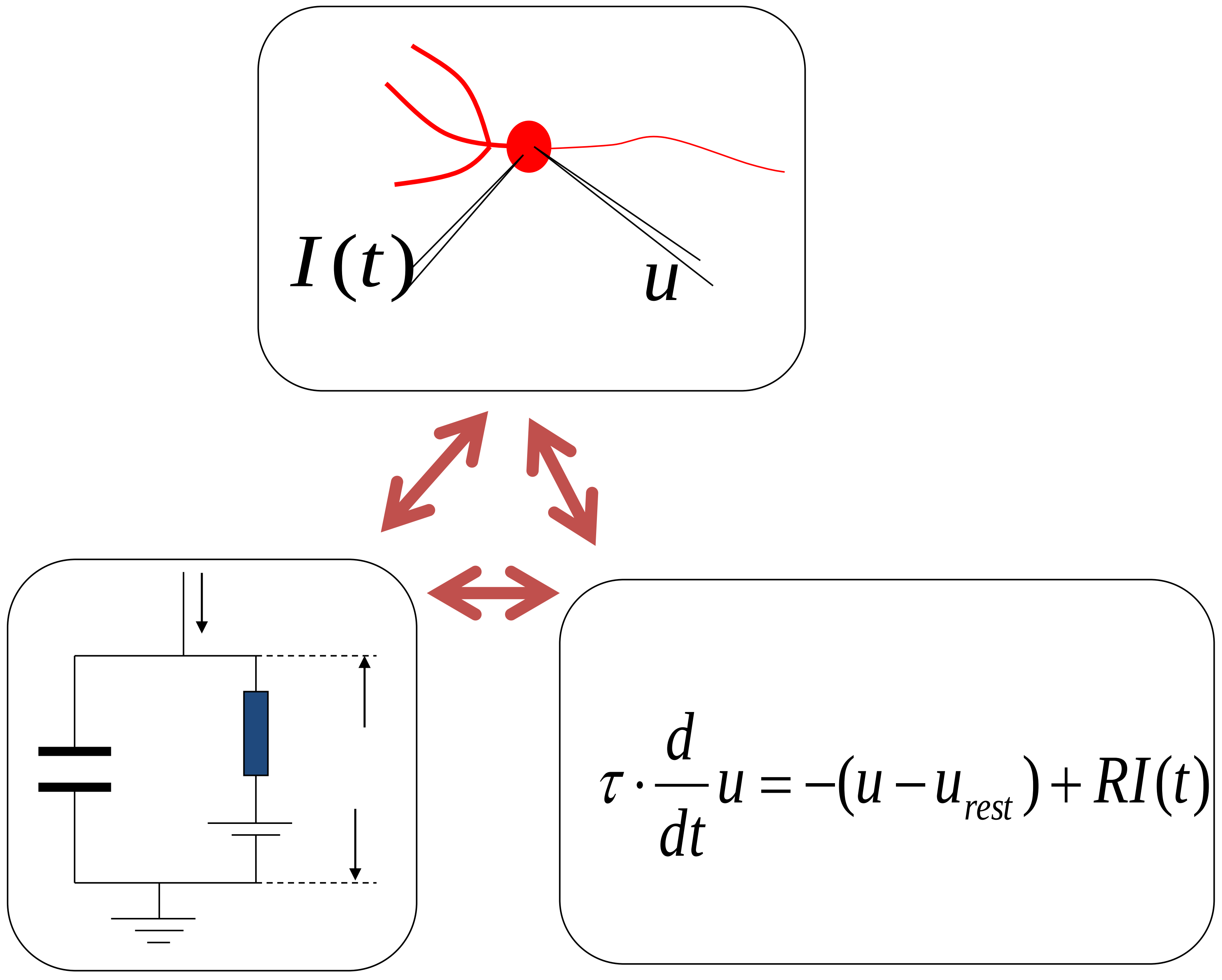
Week 1 – neurons and mathematics: a first simple neuron model

Wulfram Gerstner

EPFL, Lausanne, Switzerland

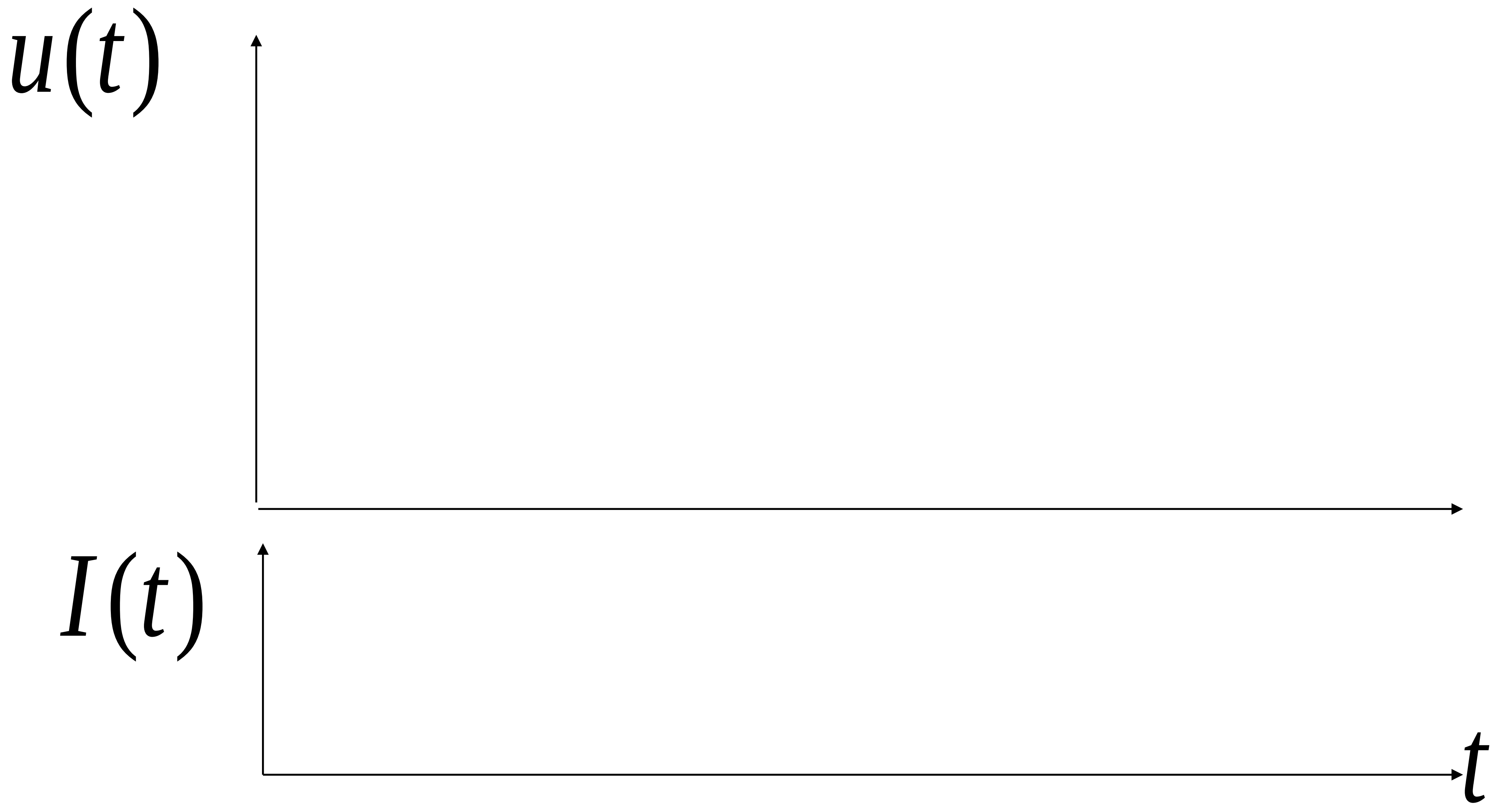
Neuronal Dynamics – 1.2Detour – Linear Differential Eq.

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

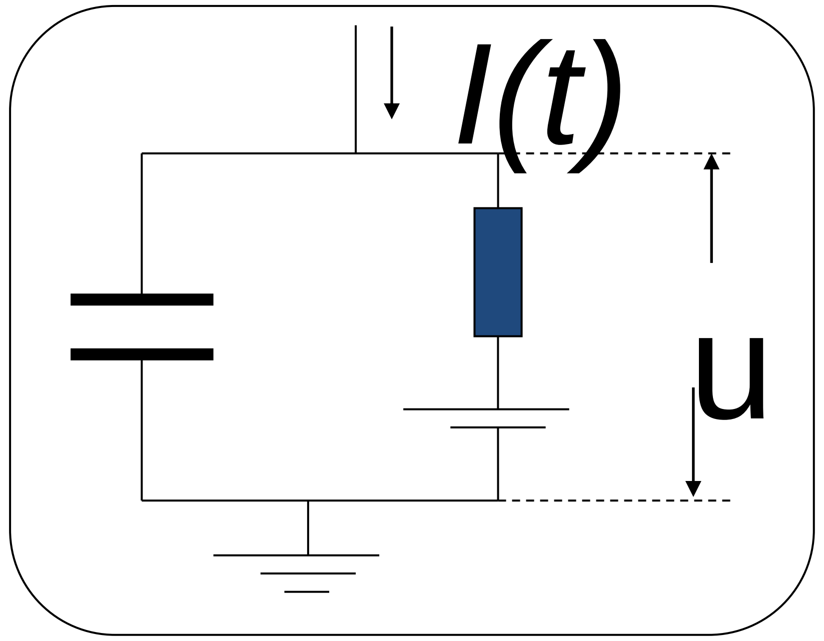


Neuronal Dynamics – 1.2Detour – Linear Differential Eq.

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

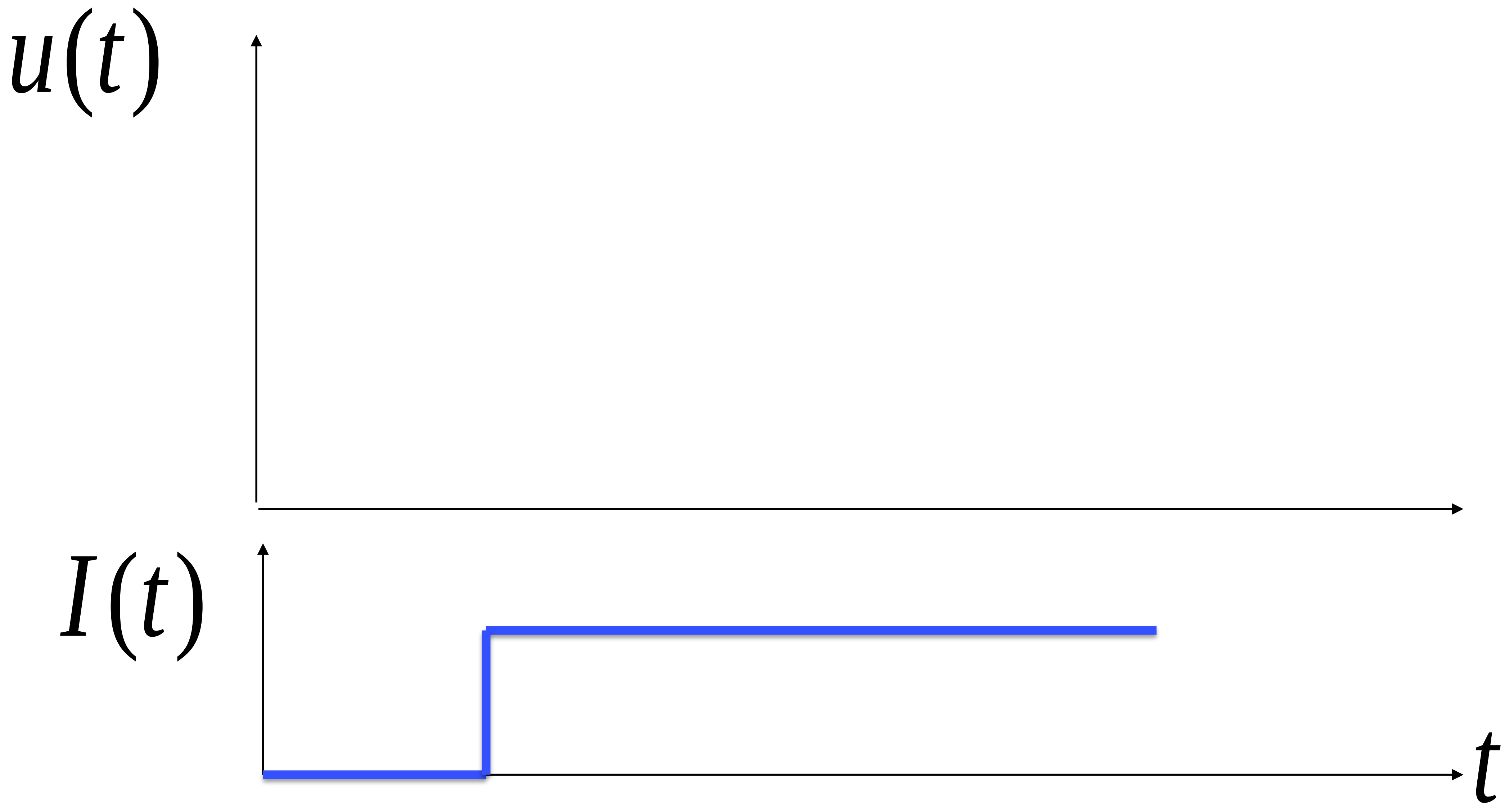


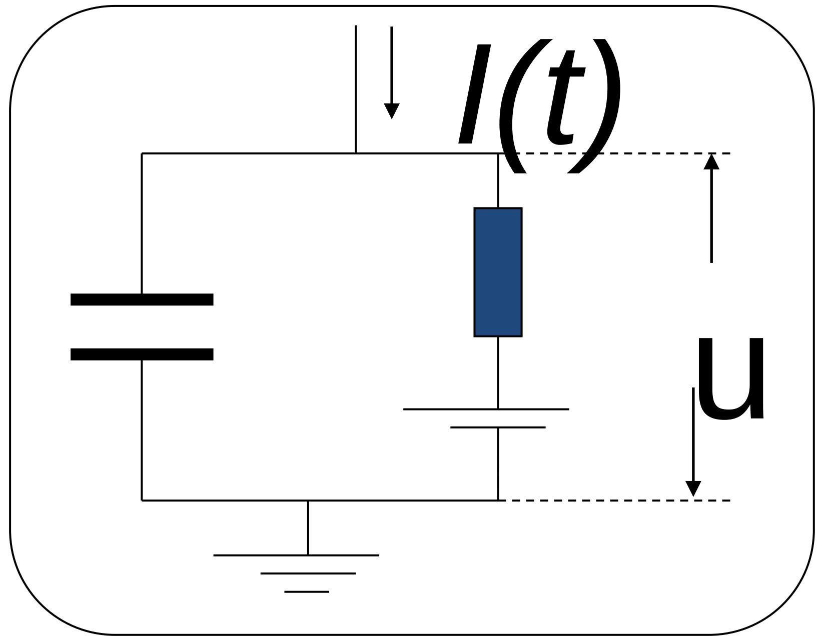
Math development:
Response to step current



Neuronal Dynamics – 1.2Detour – Step current input

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





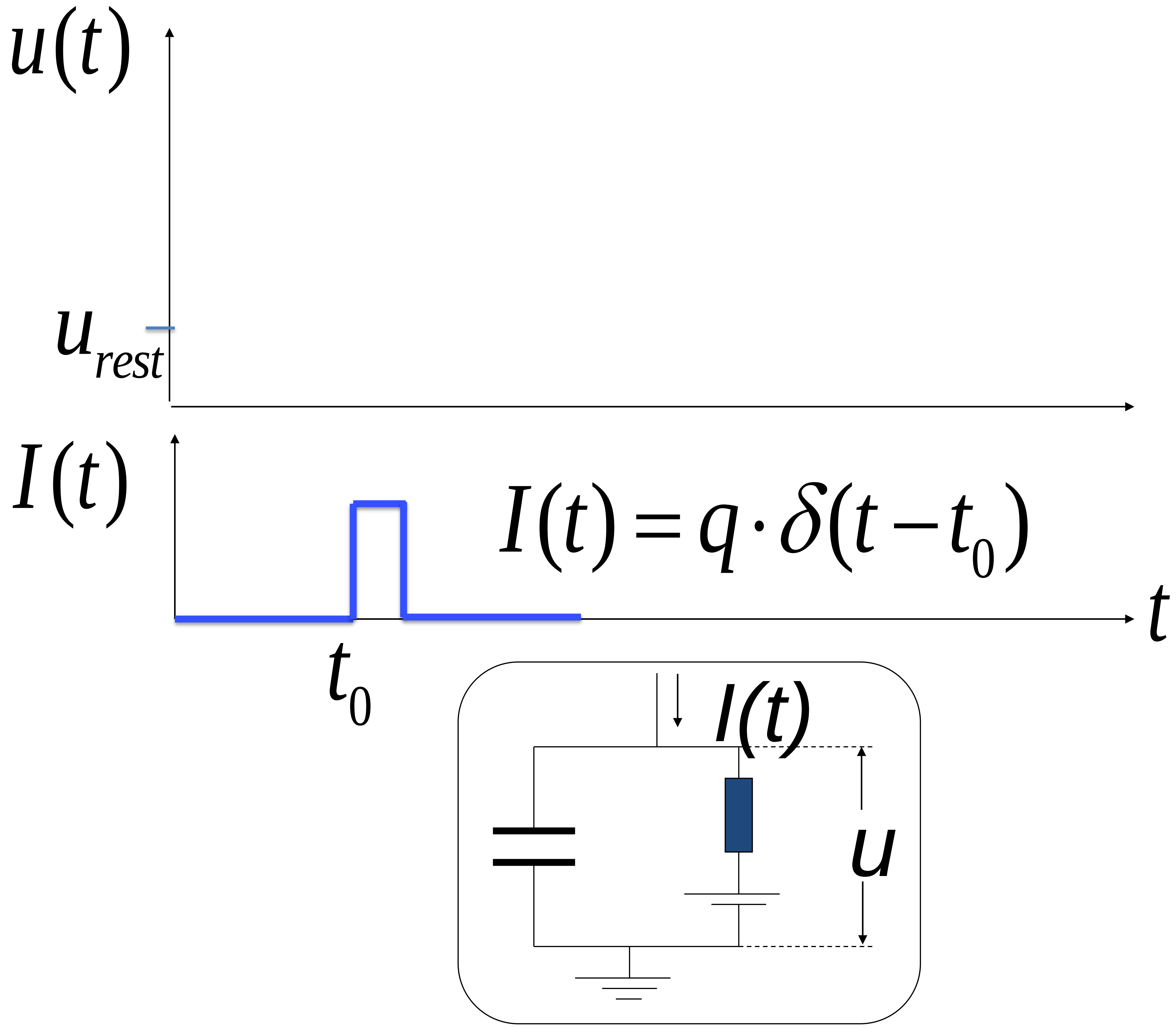
Neuronal Dynamics – 1.2Detour – Short pulse input

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

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

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

Math development: Response to short current pulse

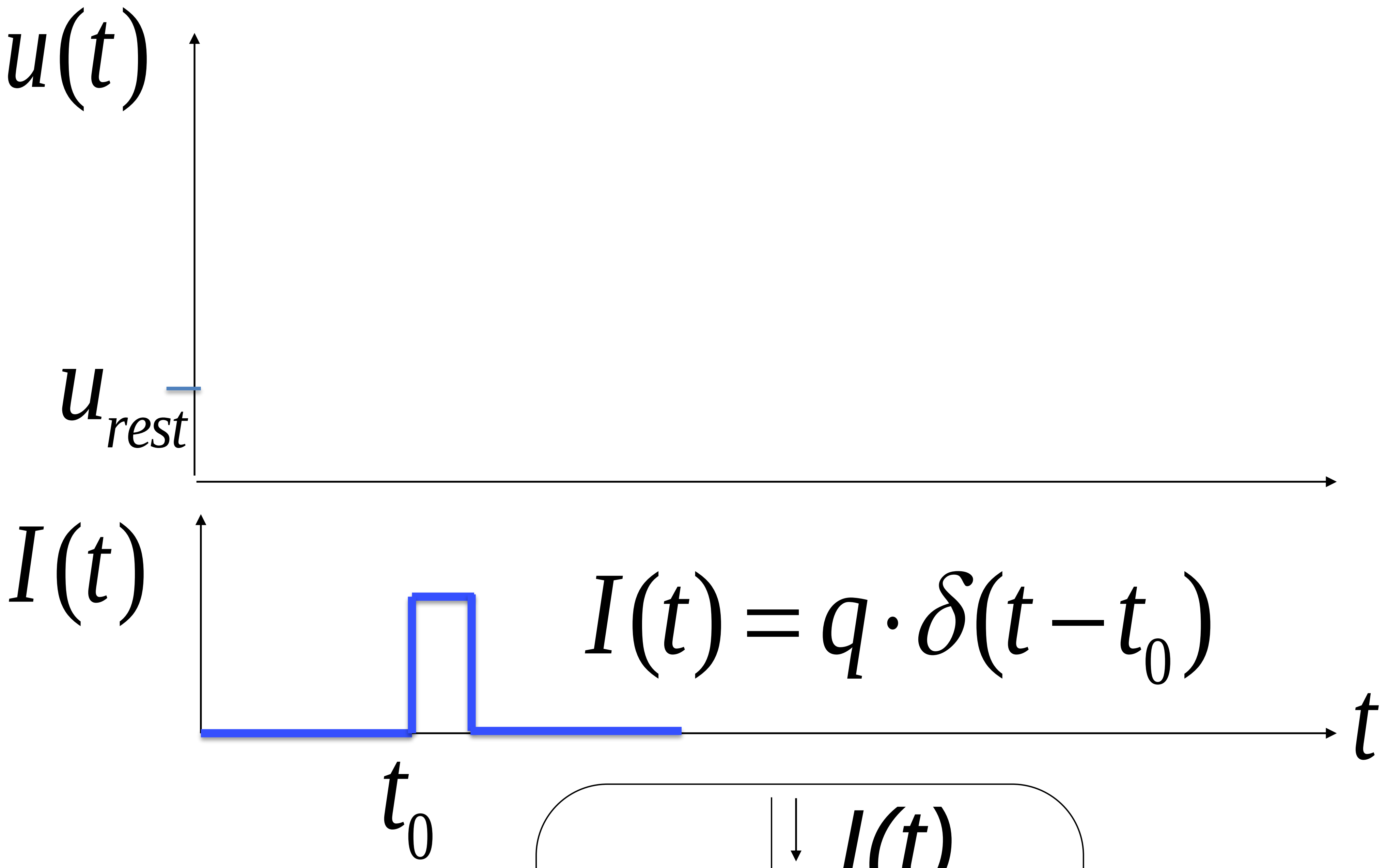


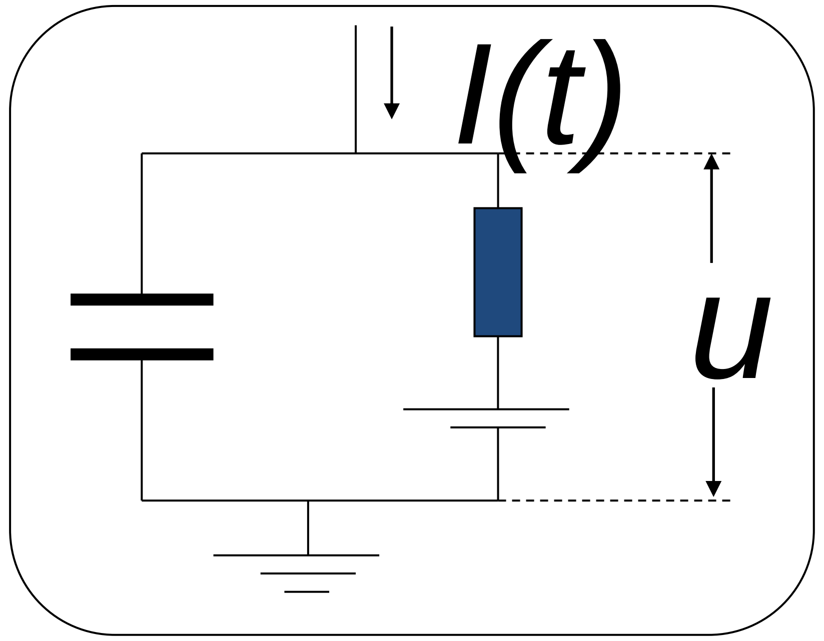
Neuronal Dynamics – 1.2Detour – Short pulse input

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

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

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





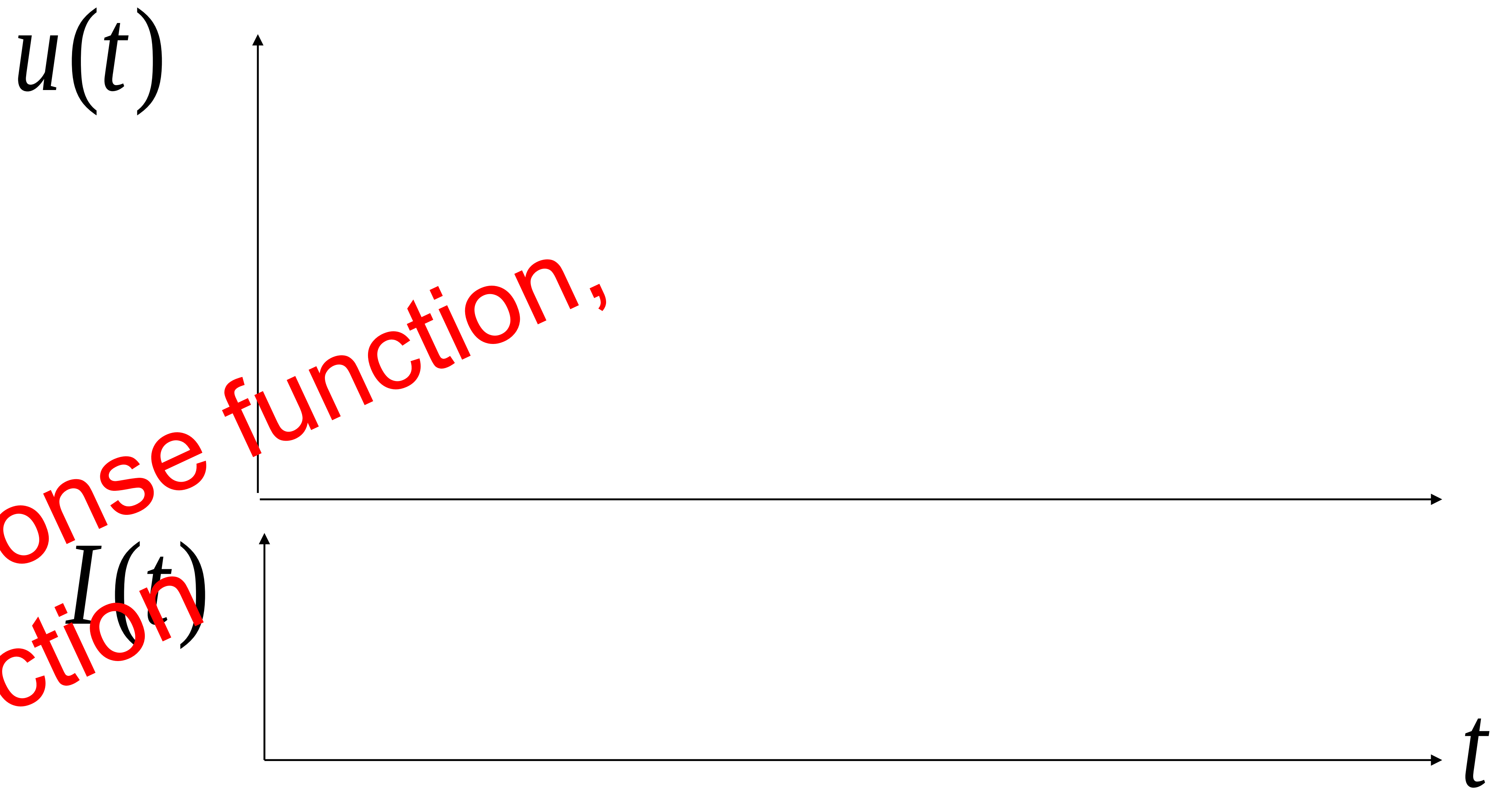
$$u(t) = u_{rest} + \frac{q}{C} e^{-(t-t_0)/\tau}$$

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:

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

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 – 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!

Neuronal Dynamics – Exercises 1.2/Quiz 1.2

*If you don't feel at ease yet, spend **10 minutes** on these mathematical exercises*