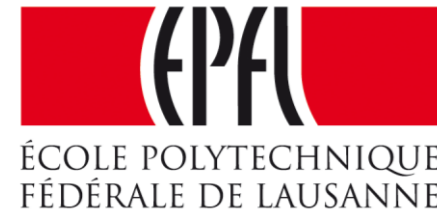


# Week 9 – adaptation and firing patterns



## Biological Modeling of Neural Networks:

### Week 9 – Adaptation and firing patterns

Wulfram Gerstner

EPFL, Lausanne, Switzerland

#### 9.1 Firing patterns and adaptation

#### 9.2 AdEx model

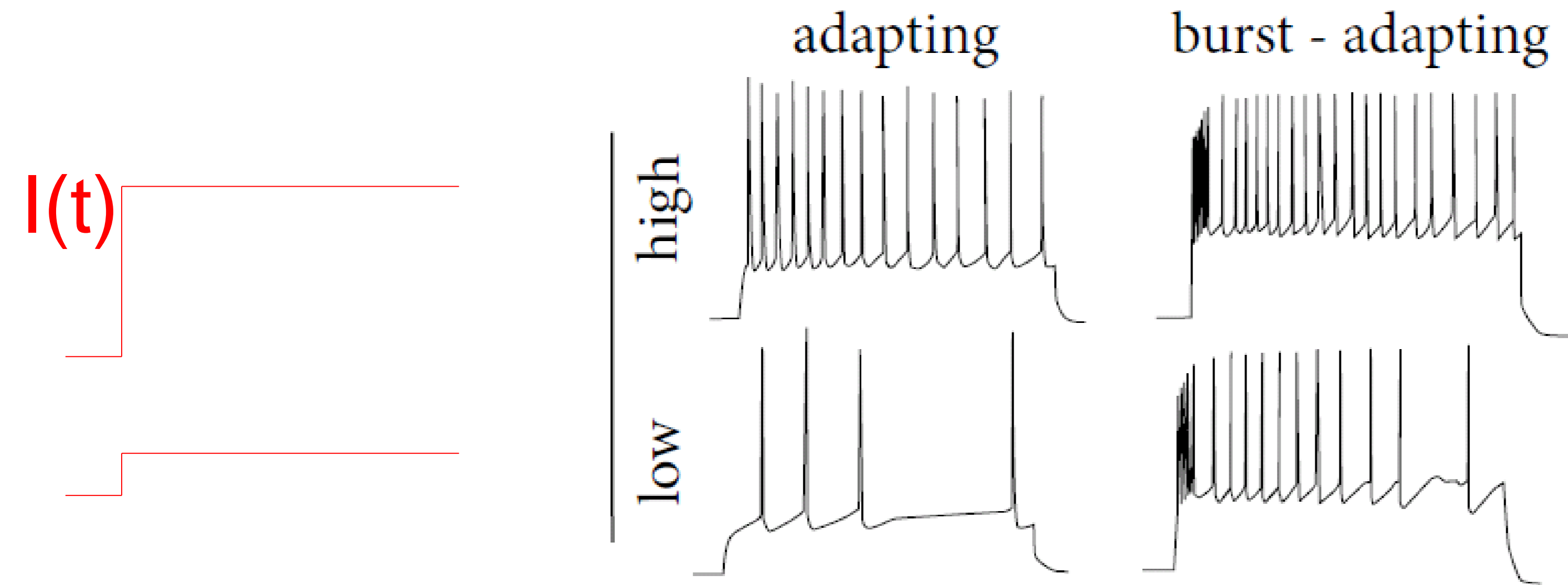
- Firing patterns and adaptation

#### 9.3 Spike Response Model (SRM)

- Integral formulation

# Neuronal Dynamics – 9.1 Adaptation

## Step current input – neurons show adaptation

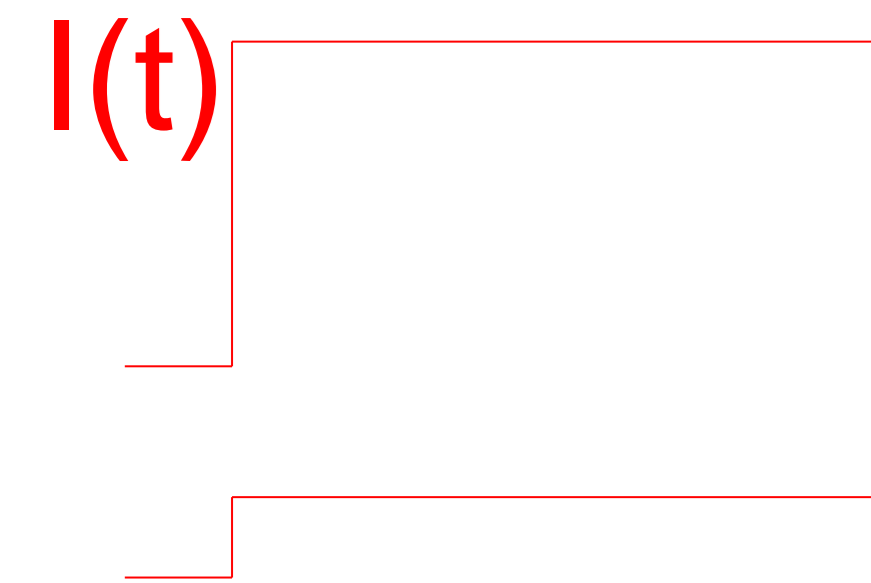
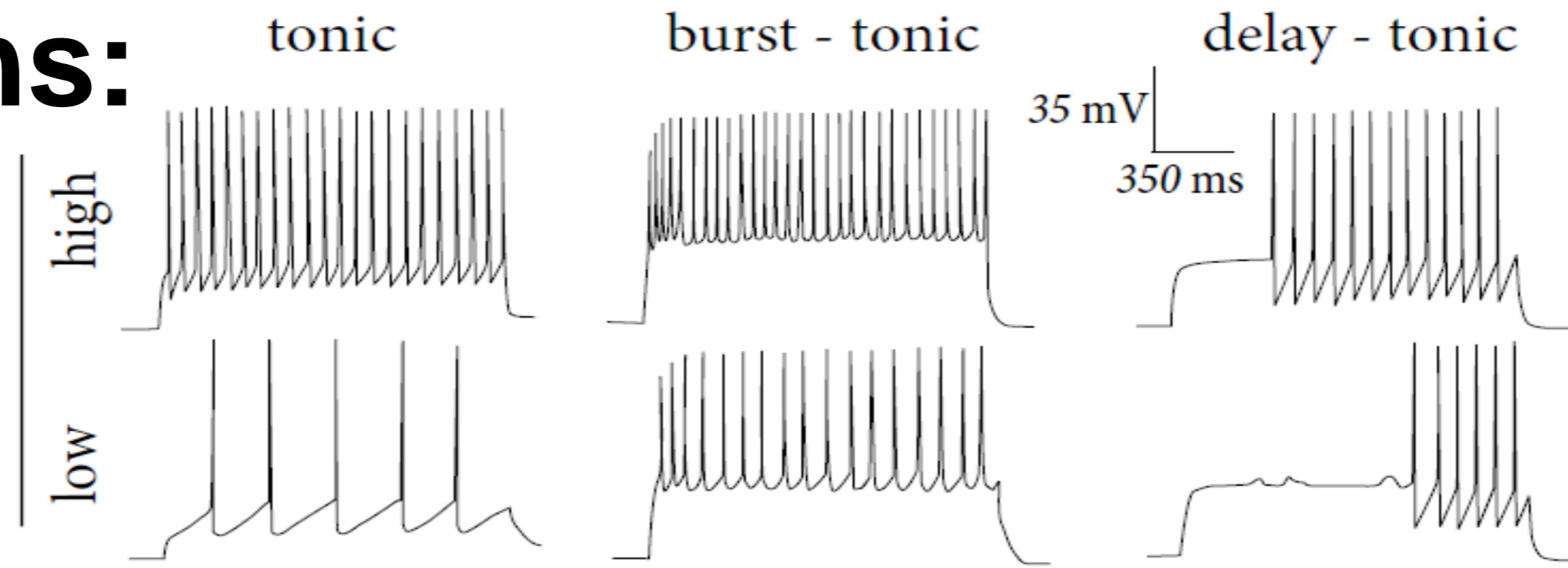


*Data:  
Markram et al.  
(2004)*

**1-dimensional (nonlinear) integrate-and-fire model cannot do this!**

# Firing patterns:

Response to  
Step currents,  
*Exper. Data,*  
*Markram et al.*  
*(2004)*



# Week 9 – adaptation and firing patterns



## Biological Modeling of Neural Networks:

### Week 9 – Adaptation and firing patterns

Wulfram Gerstner

EPFL, Lausanne, Switzerland

9.1 Firing patterns and adaptation

9.2 AdEx model

- Firing patterns and adaptation

9.3 Spike Response Model (SRM)

- Integral formulation

# Neuronal Dynamics – 9.2 Adaptive Exponential I&F

Add adaptation variables:

Blackboard !

$$\tau \frac{du}{dt} = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \mathcal{I}}{\Delta}\right) - R \sum_k w_k$$

$$\tau_k \frac{dw_k}{dt} = a_k (u - u_{rest}) - w_k + b_k \tau_k \sum_f \delta(t - t^f)$$

Exponential I&F  
+ 1 adaptation var.  
= AdEx

**SPIKE AND  
RESET**

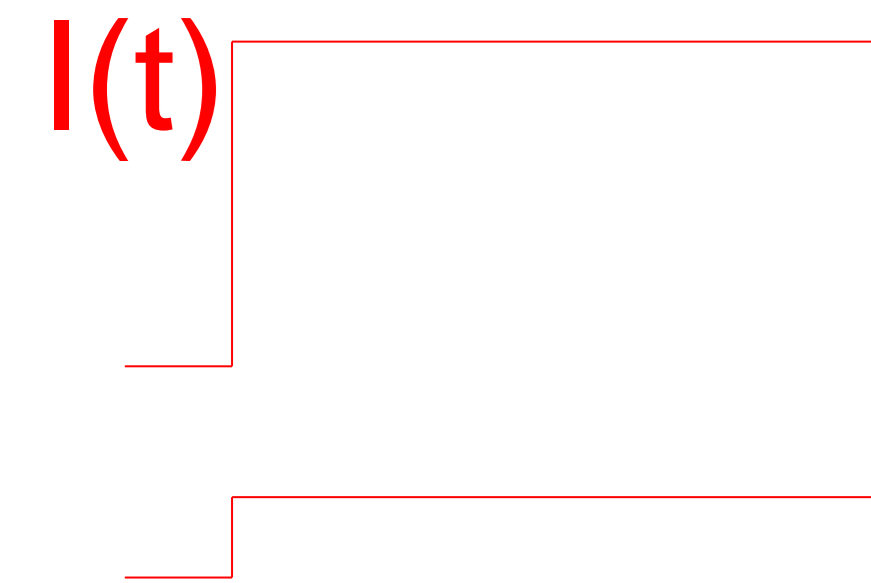
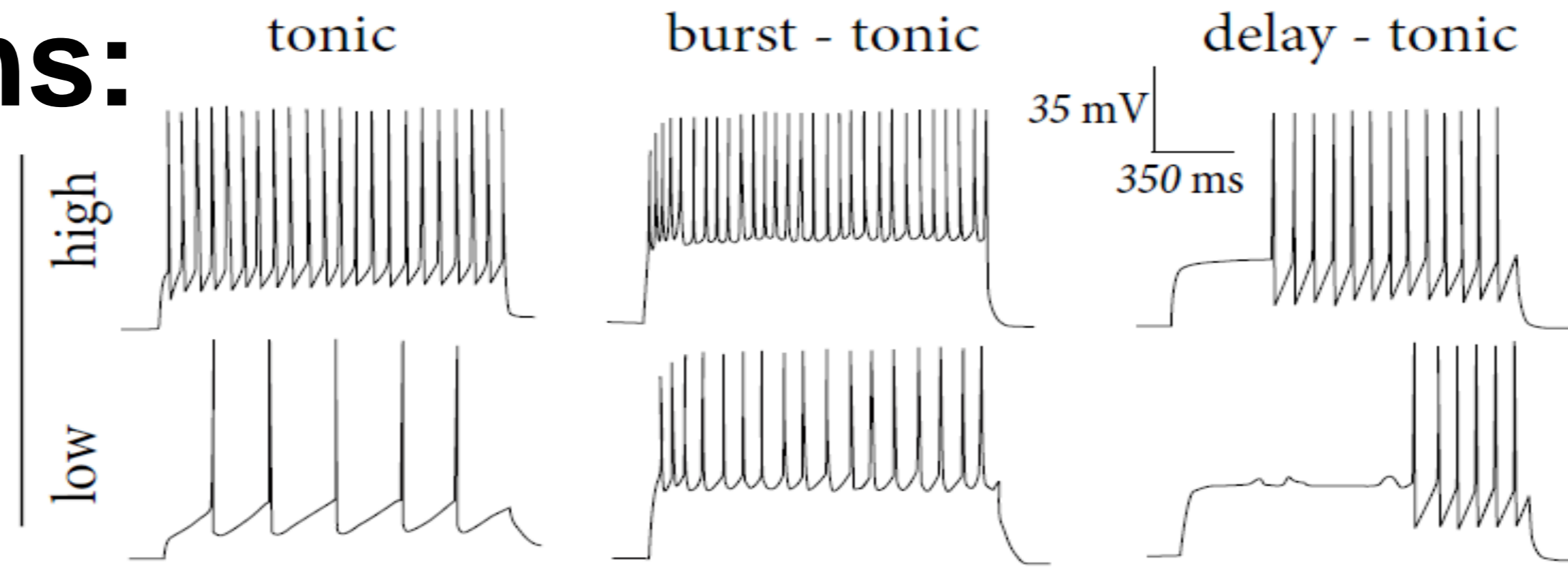
after each spike  $w_k$   
jumps by an amount  $b_k$

If  $u = \theta_{reset}$  then reset to  $u = u_r$

*AdEx model,  
Brette & Gerstner (2005):*

# Firing patterns:

Response to  
Step currents,  
*Exper. Data,*  
*Markram et al.*  
*(2004)*

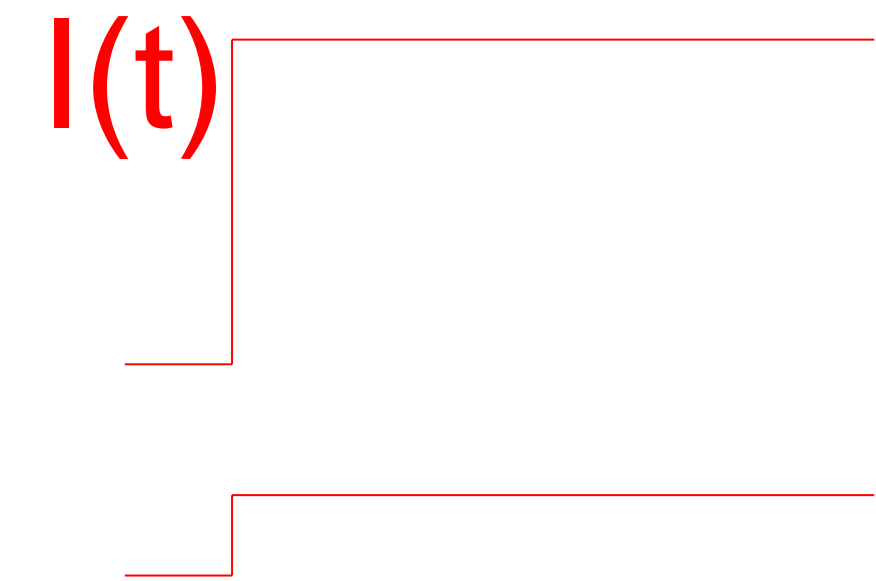
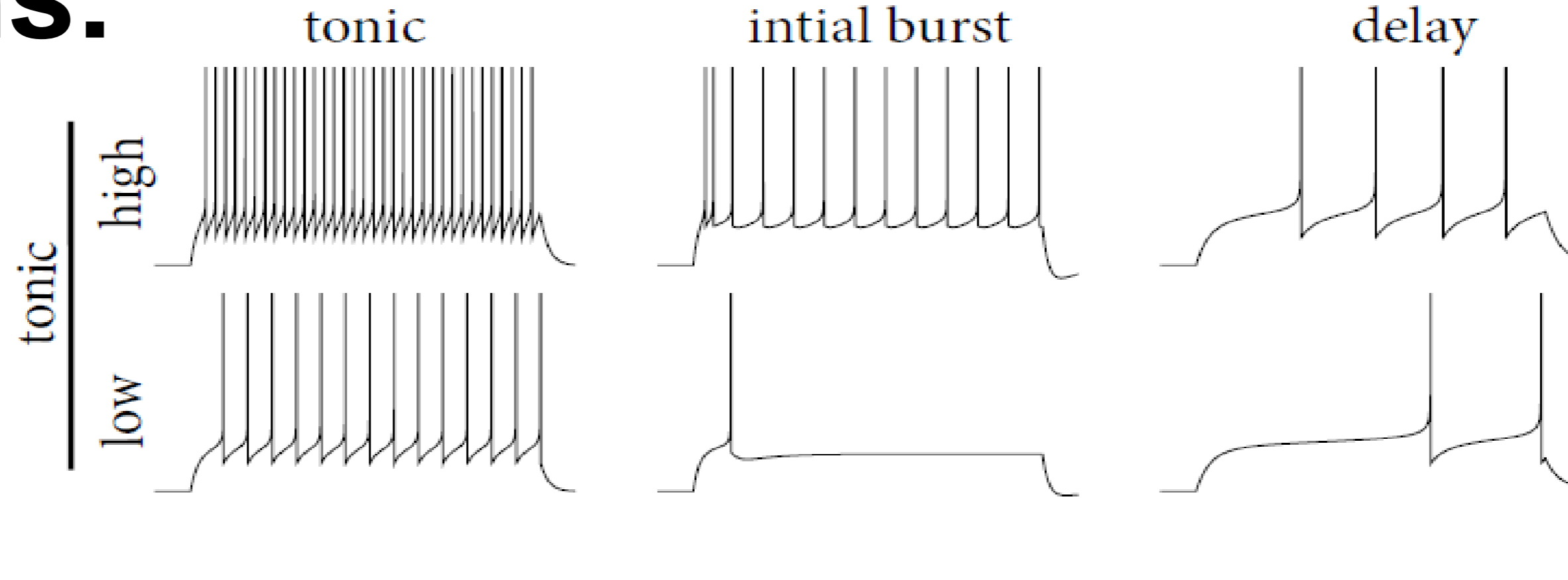


# Firing patterns:

Response to  
Step currents,  
**AdEx Model,**  
**Naud&Gerstner**

ERN

INITIATION PATTERN



*Image:*  
*Neuronal Dynamics,*  
*Gerstner et al.*  
*Cambridge (2002)*

# Neuronal Dynamics – 9.2 Adaptive Exponential I&F

$$\tau \frac{du}{dt} = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \mathcal{G}}{\Delta}\right) - R w + R I(t)$$
$$\tau_w \frac{dw}{dt} = a (u - u_{rest}) - w + b \tau_w \sum_f \delta(t - t^f)$$

**AdEx model**

**Phase plane analysis!**

Can we understand the different firing patterns?



# Neuronal Dynamics – Quiz 9.1. Nullclines of AdEx

$$\tau \frac{du}{dt} = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \mathcal{I}}{\Delta}\right) - R w + R I(t)$$

$$\tau_w \frac{dw}{dt} = a (u - u_{rest}) - w$$

**A - What is the qualitative shape of the w-nullcline?**

- constant
- linear, slope a
- linear, slope 1
- linear + quadratic
- linear + exponential

**B - What is the qualitative shape of the u-nullcline?**

- linear, slope 1
- linear, slope 1/R
- linear + quadratic
- linear w. slope 1/R+ exponential

1 minute

Restart at 9:38

# Week 9 – part 2b : Firing Patterns



## Biological Modeling of Neural Networks:

### Week 9 – Optimizing Neuron Models For Coding and Decoding

Wulfram Gerstner

EPFL, Lausanne, Switzerland

#### 9.1 What is a good neuron model?

- Models and data

#### 9.2 AdEx model

- Firing patterns and adaptation

#### 9.3 Spike Response Model (SRM)

- Integral formulation

#### 9.4 Generalized Linear Model

- Adding noise to the SRM

#### 9.5 Parameter Estimation

- Quadratic and convex optimization

#### 9.6. Modeling in vitro data

- how long lasts the effect of a spike?

# AdEx model

after each spike  
 $u$  is reset to  $u_r$

$$\tau \frac{du}{dt} = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \mathcal{G}}{\Delta}\right) - R_w + RI(t)$$

$$\tau_w \frac{dw}{dt} = a (u - u_{rest}) - w + b \tau_w \sum_f \delta(t - t^f)$$

after each spike  
 $w$  jumps by an amount  $b$

parameter  $a$  – slope of  $w$ -nullcline

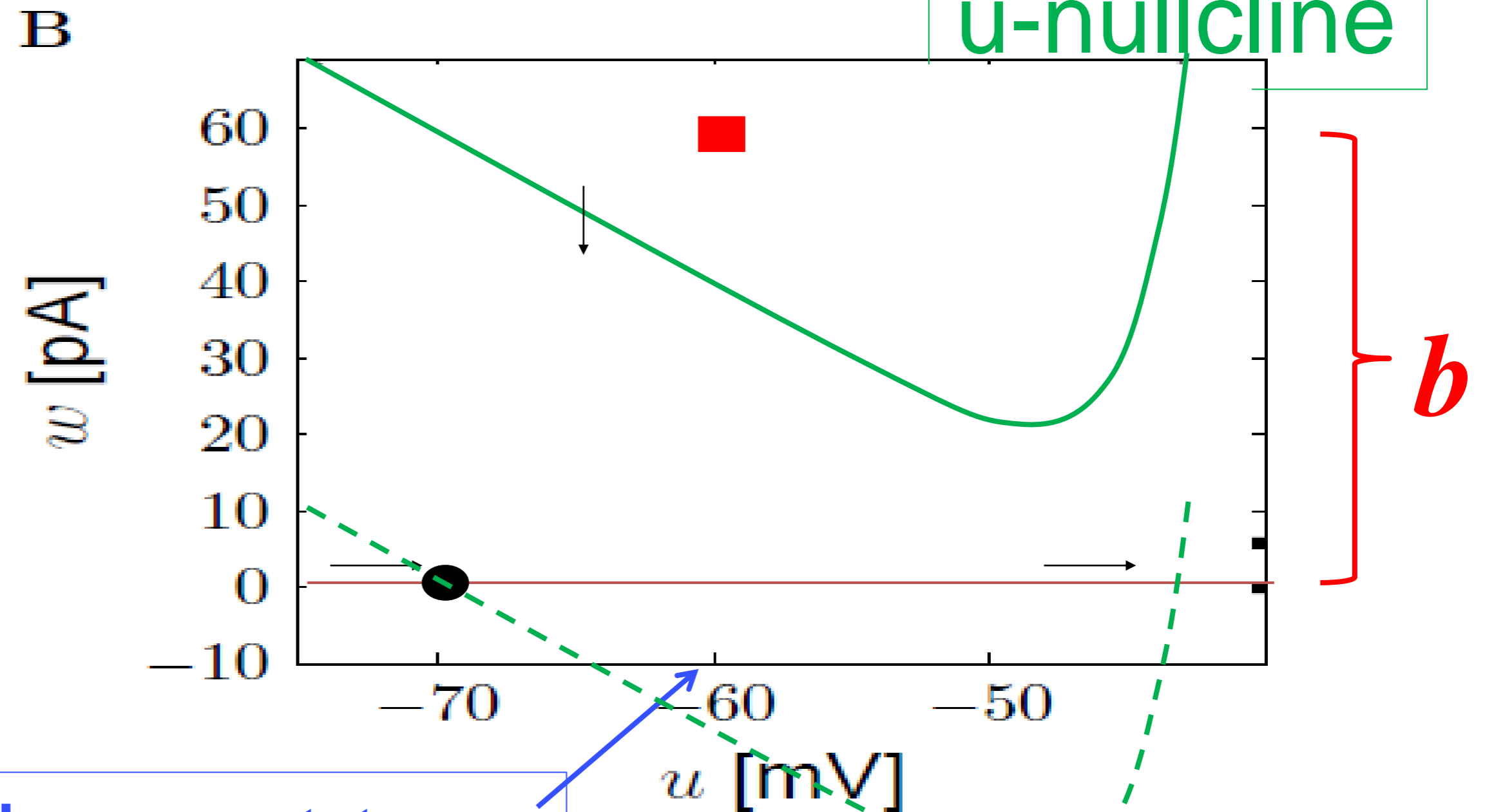
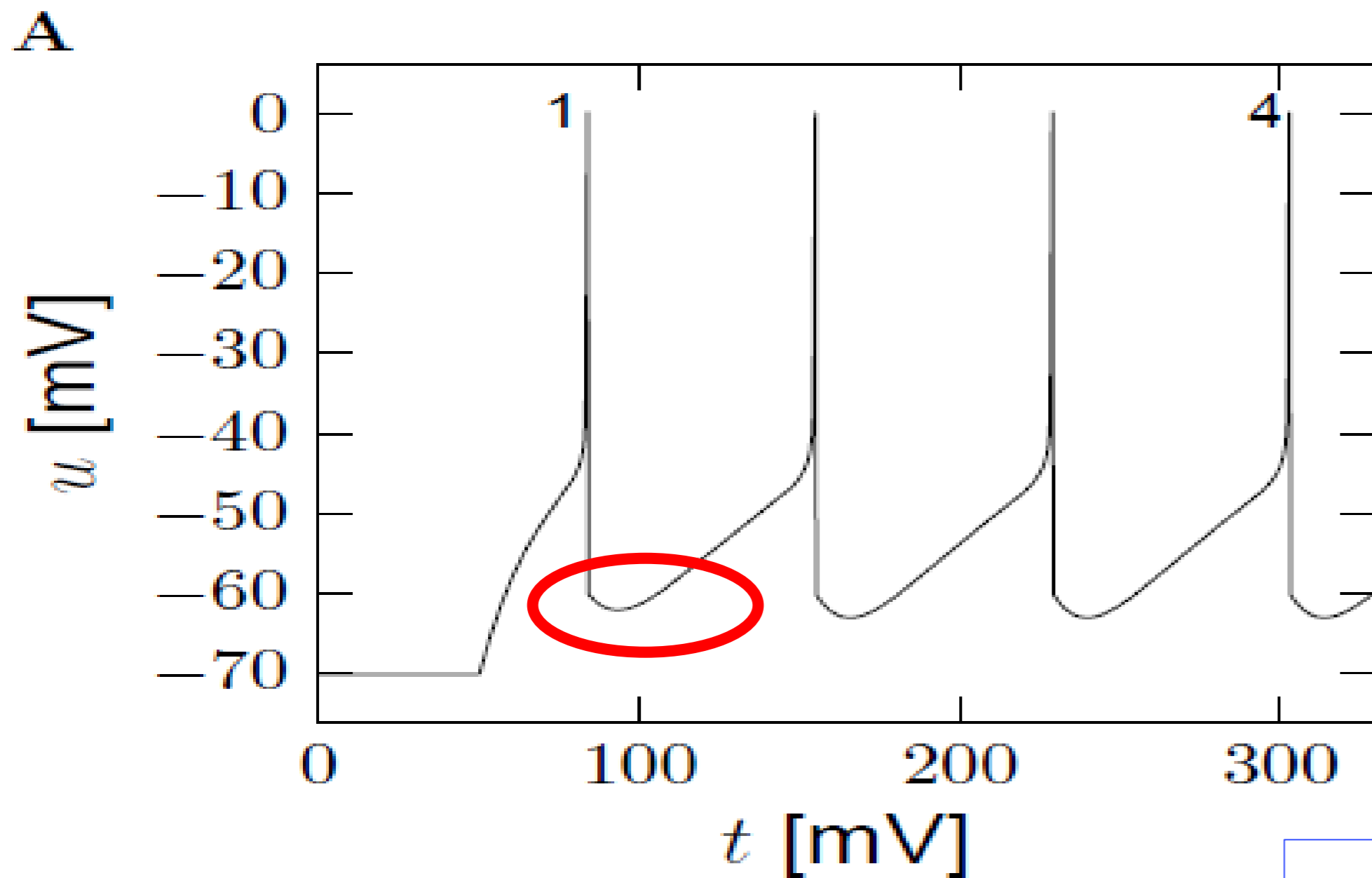
Can we understand the different firing patterns?

# AdEx model – phase plane analysis: **large $b$**

$$\tau \frac{du}{dt} = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \mathcal{G}}{\Delta}\right) + w + RI(t)$$

$$\tau_w \frac{dw}{dt} = a (u - u_{rest}) - w + b \tau_w \sum_f \delta(t - t^f)$$

**$a=0$**



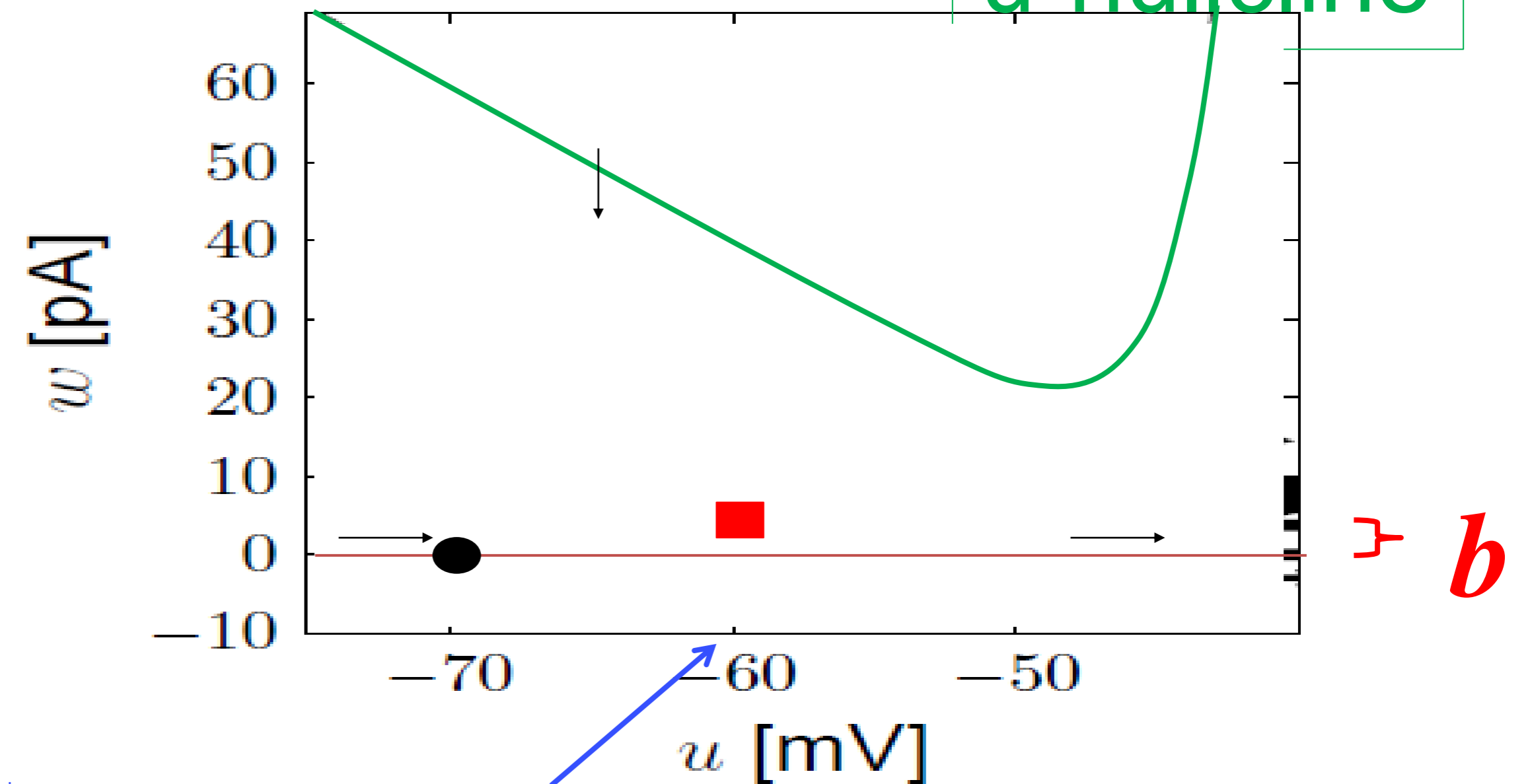
# AdEx model – phase plane analysis: **small $b$**

$$\tau \frac{du}{dt} = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \mathcal{I}}{\Delta}\right) + w + RI(t)$$

$$\tau_w \frac{dw}{dt} = a (u - u_{rest}) - w + b \tau_w \sum_f \delta(t - t^f)$$

**adaptation**

D



$u$  is reset to  $u_r$

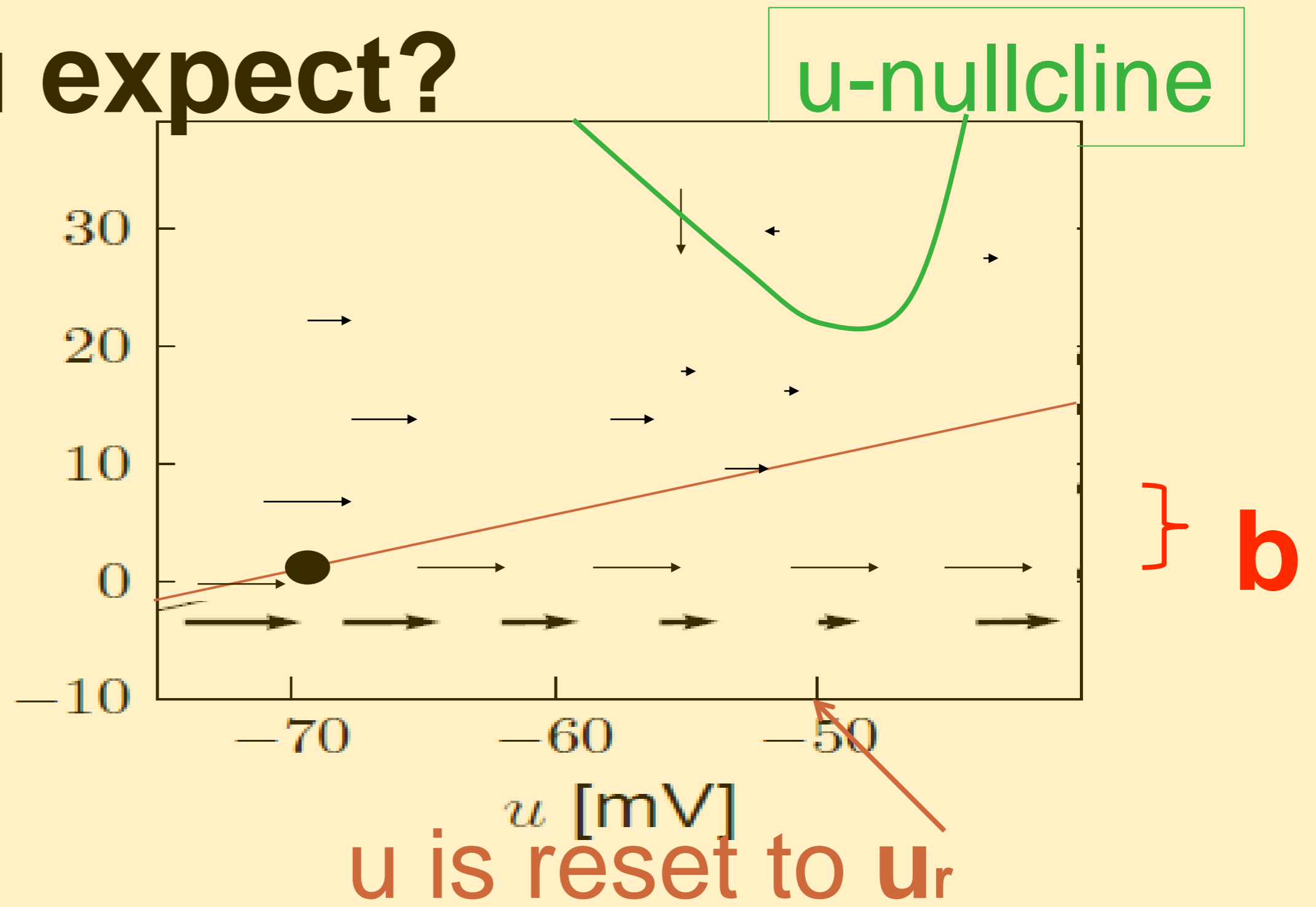
# Quiz 9.2: AdEx model – phase plane analysis

$$\tau \frac{du}{dt} = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \mathcal{G}}{\Delta}\right) + w + RI(t)$$

$$\tau_w \frac{dw}{dt} = a (u - u_{rest}) + b \tau_w \sum_f \delta(t - t^f)$$

What firing pattern do you expect?

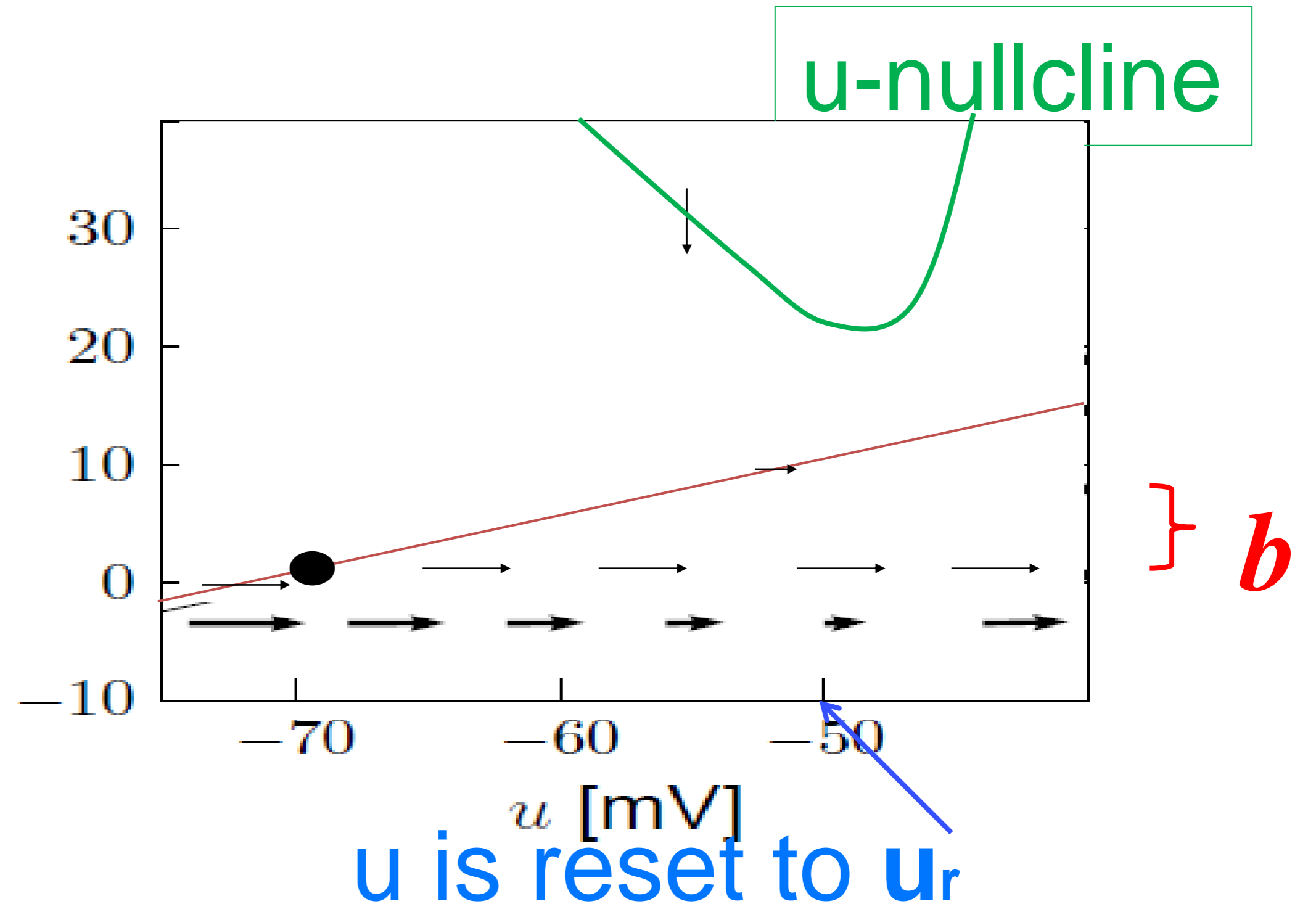
- (i) Adapting
- (ii) Bursting
- (iii) Initial burst
- (iv) Non-adapting



# AdEx model – phase plane analysis: $a > 0$

$$\tau \frac{du}{dt} = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \mathcal{G}}{\Delta}\right) + w + RI(t)$$

$$\tau_w \frac{dw}{dt} = a(u - u_{rest}) - w + b \tau_w \sum_f \delta(t - t^f)$$



# Neuronal Dynamics – 9.2 AdEx model and firing patterns

after each spike  $u$  is reset to  $u_r$

$$\tau \frac{du}{dt} = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \mathcal{I}}{\Delta}\right) - R w + R I(t)$$

$$\tau_w \frac{dw}{dt} = a (u - u_{rest}) - w + b \tau_w \sum_f \delta(t - t^f)$$

after each spike

$w$  jumps by an amount  $b$

parameter  $a$  – slope of  $w$  nullcline

**Firing patterns arise from different parameters!**

*See Naud et al. (2008), see also Izhikheich (2003)*



# Neuronal Dynamics – Review: Nonlinear Integrate-and-fire

$$(1) \quad \tau \frac{du}{dt} = f(u) + RI(t)$$

(2) If  $u = \theta_{reset}$  then reset to  $u = u_r$

Best choice of  $f$ : linear + exponential

$$\tau \frac{du}{dt} = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \mathcal{I}}{\Delta}\right)$$

**BUT: Limitations – need to add**

- ✓ -Adaptation on slower time scales
- ✓ -Possibility for a diversity of firing patterns
- Increased threshold  $\mathcal{I}$  after each spike
- Noise

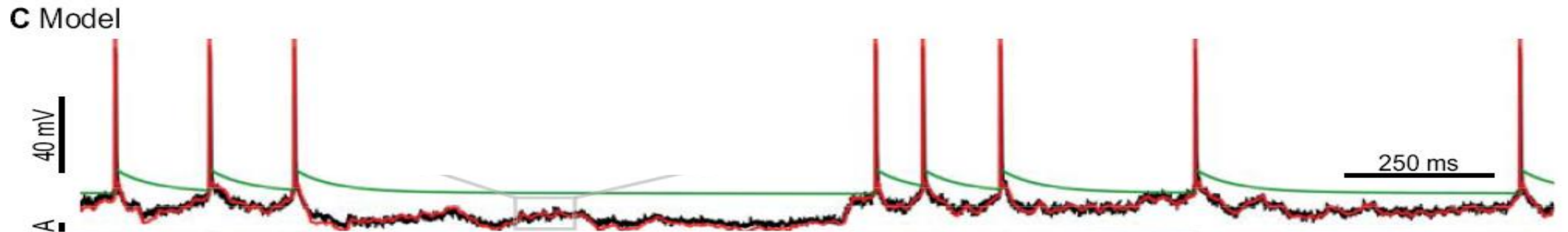
# Neuronal Dynamics – 9.2 AdEx with dynamic threshold

Add dynamic threshold:

$$\tau \frac{du}{dt} = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \mathcal{I}}{\Delta}\right) - R \sum_k w_k + RI(t)$$

Threshold increases after each spike

$$\mathcal{I} = \theta_0 + \sum_f \theta_1 (t - t^f)$$



# Neuronal Dynamics – 9.2 Generalized Integrate-and-fire

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

*If  $u = \theta_{reset}$  then reset to  $u = u_r$*

**add**

- ✓ -Adaptation variables
- ✓ -Possibility for firing patterns
- ✓ -Dynamic threshold  $\mathcal{I}$
- Noise

# Week 9 – part 3: Spike Response Model (SRM)



## Biological Modeling of Neural Networks:

### Week 9 – Optimizing Neuron Models For Coding and Decoding

Wulfram Gerstner

EPFL, Lausanne, Switzerland

#### √ 9.1 What is a good neuron model?

- Models and data

#### √ 9.2 AdEx model

- Firing patterns and adaptation

#### 9.3 Spike Response Model (SRM)

- Integral formulation

#### 9.4 Generalized Linear Model

- Adding noise to the SRM

#### 9.5 Parameter Estimation

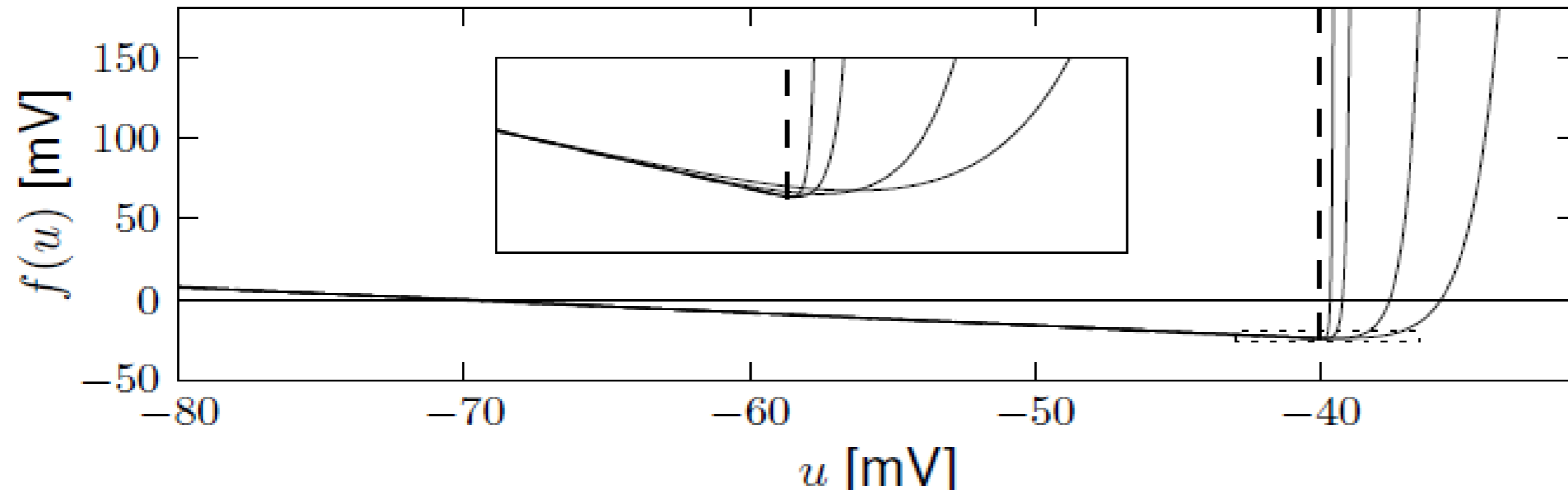
- Quadratic and convex optimization

#### 9.6. Modeling in vitro data

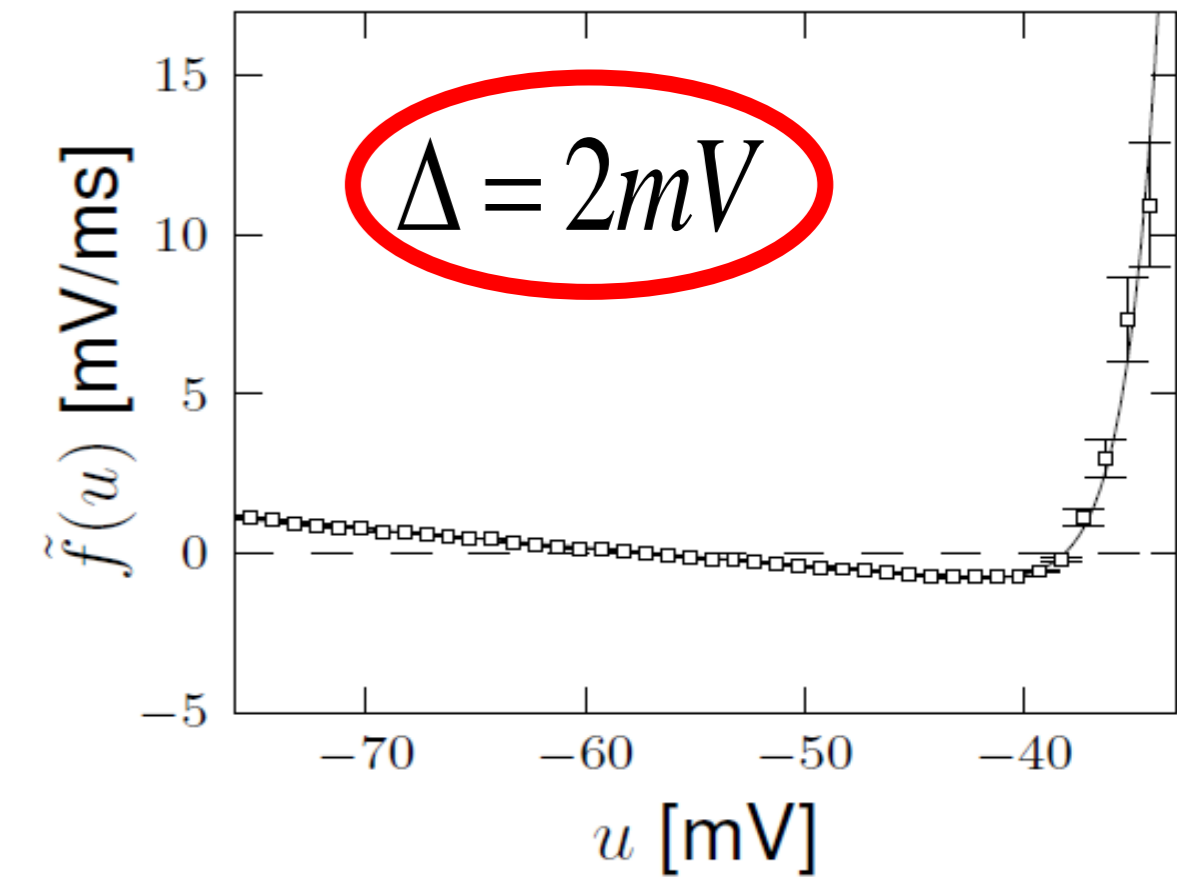
- how long lasts the effect of a spike?

# Exponential versus Leaky Integrate-and-Fire

$$\tau \frac{du}{dt} = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \mathcal{I}}{\Delta}\right) + RI(t)$$



*Badel et al (2008)*  
A



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

Reset if  $u = \mathcal{I}$

**Leaky Integrate-and-Fire:  
Replace nonlinear kink by threshold**

# Neuronal Dynamics – 9.3 Adaptive leaky integrate-and-fire

$$\tau \frac{du}{dt} = -(u - u_{rest}) - R \sum_k w_k + RI(t)$$

$$\tau_k \frac{dw_k}{dt} = a_k (u - u_{rest}) - w_k + b_k \tau_k \sum_f \delta(t - t^f)$$

SPIKE AND  
RESET

after each spike

$w_k$  jumps by an amount  $b_k$

If  $u = \mathcal{G}(t)$  then reset to  $u = u_r$

Dynamic threshold

# Neuronal Dynamics – 9.3 Adaptive leaky I&F and SRM

$$\tau \frac{du}{dt} = -(u - u_{rest}) - R \sum_k w_k + RI(t)$$

$$\tau_k \frac{dw_k}{dt} = a_k (u - u_{rest}) - w_k + b_k \tau_k \sum_f \delta(t - t^f)$$

Adaptive  
leaky I&F

**Linear equation → can be integrated!**

$$u(t) = \sum_f \eta (t - t^f) + \int_0^\infty ds \kappa(s) I(t - s)$$

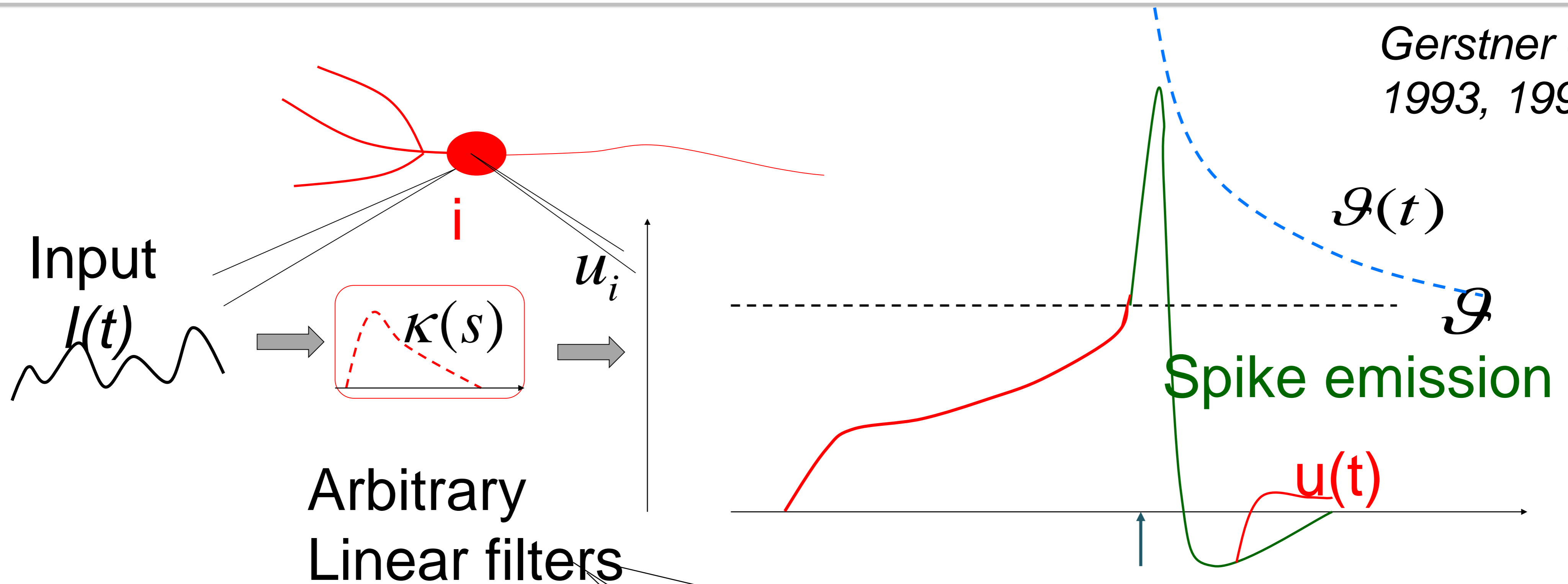
$$\mathcal{G}(t) = \theta_0 + \sum_f \theta_1 (t - t^f)$$

**Spike Response Model (SRM)**  
Gerstner et al. (1996)



# Neuronal Dynamics – 9.3 Spike Response Model (SRM)

Gerstner et al.,  
1993, 1996



potential

$$u(t) = \sum_{t'} \eta(t-t') + \int_0^\infty \kappa(s) I(t-s) ds + u_{rest}$$

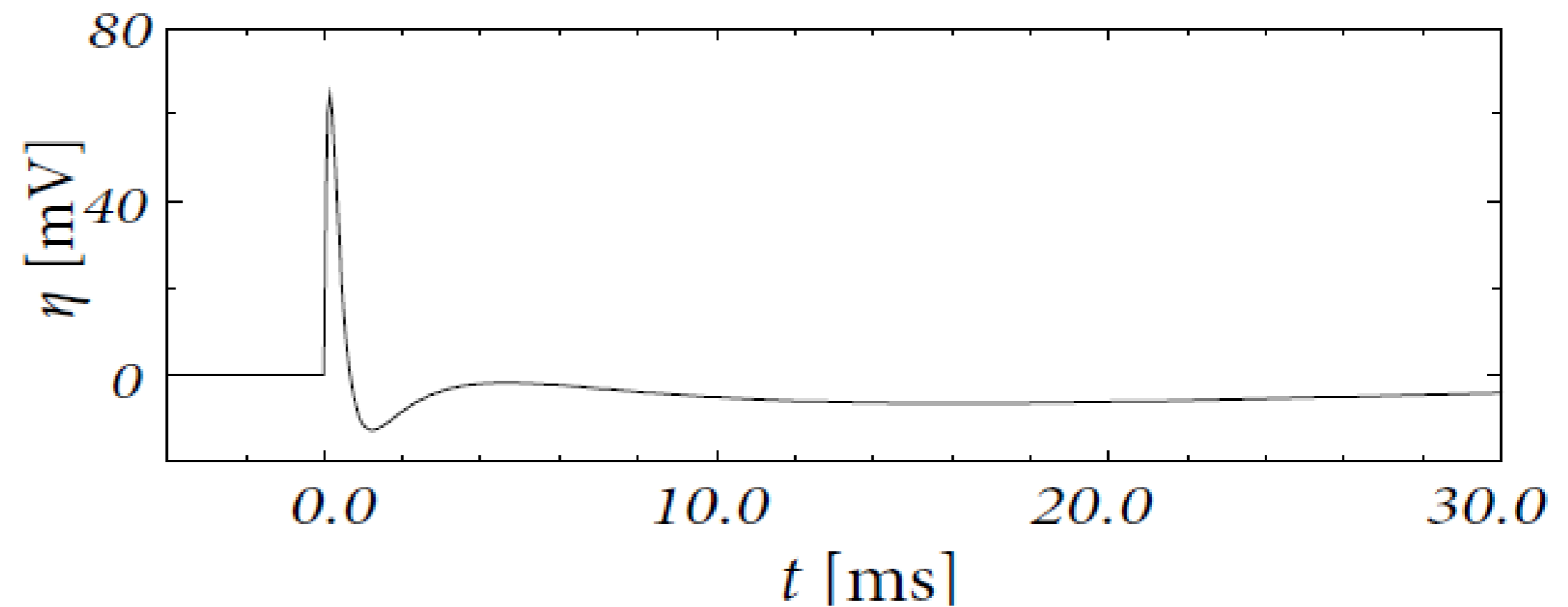
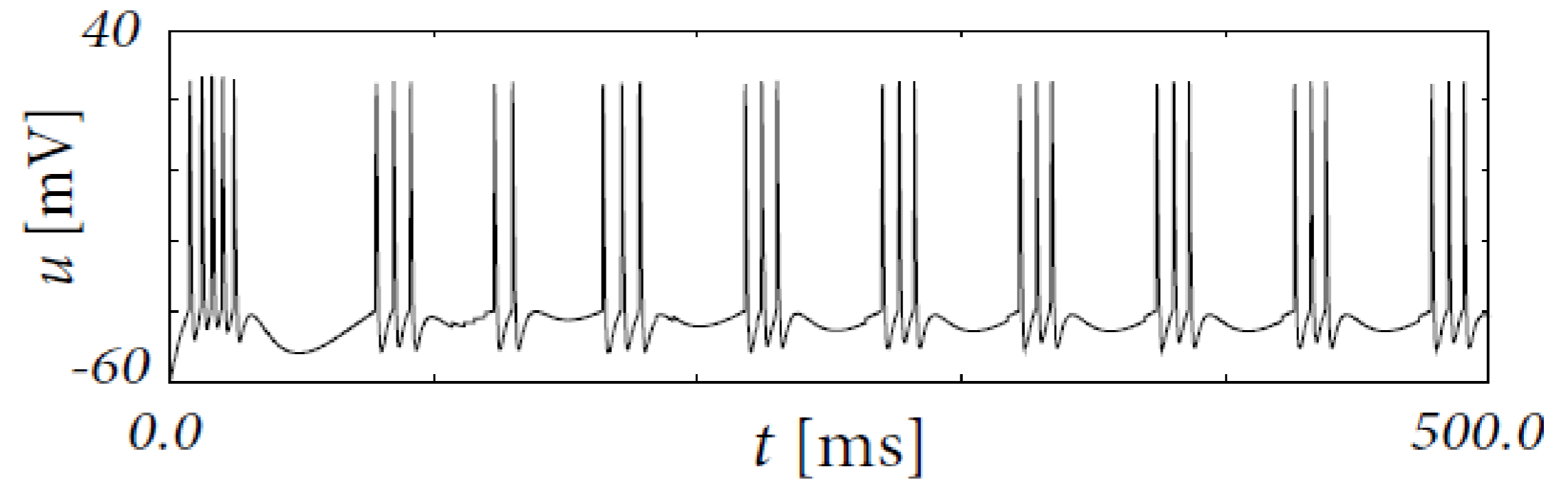
threshold

$$\mathcal{G}(t) = \theta_0 + \sum_{t'} \theta_1(t-t')$$



# Neuronal Dynamics – 9.3 Bursting in the SRM

SRM with appropriate  $\eta$   
leads to bursting



$$u(t) = \sum_f \eta(t - t^f) + \int_0^\infty ds \kappa(s) I(t - s) + u_{rest}$$
$$u(t) = \int_0^\infty ds \eta(s) S(t - s) + \int_0^\infty ds \kappa(s) I(t - s) + u_{rest}$$

# Exercise 1: from adaptive IF to SRM

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

If  $u = \mathcal{I}$  then reset to  $u = u_r$

$$\tau_w \frac{dw}{dt} = -w + b \tau_w \sum_f \delta(t - t^f)$$

Next lecture  
at 9:57/10:15

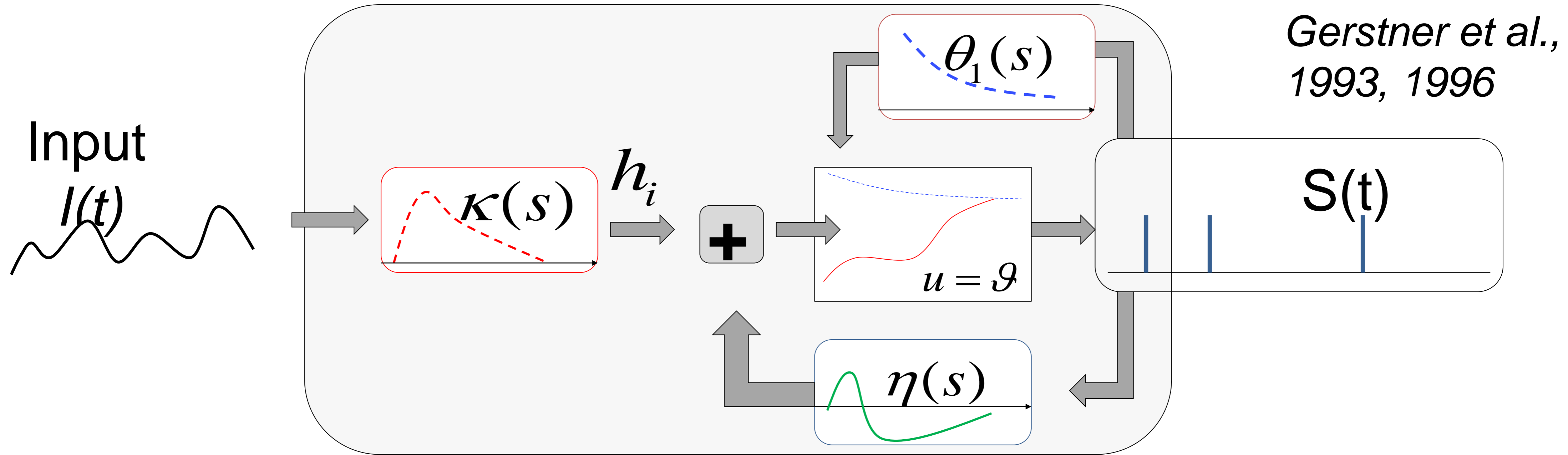
Integrate the above system of two differential equations so as to rewrite the equations as

**potential**  $u(t) = \int_0^{\infty} \underline{\eta(s)} S(t-s) ds + \int_0^{\infty} \underline{\varepsilon(s)} I(t-s) ds + u_{rest}$

**A – what is  $\underline{\eta(s)}$  ?** (i)  $x(s) = \frac{R}{\tau} \exp(-\frac{s}{\tau})$  (ii)  $x(s) = \frac{R}{\tau_w} \exp(-\frac{s}{\tau_w})$

**B – what is  $\underline{\varepsilon(s)}$  ?** (iii)  $x(s) = C[\exp(-\frac{s}{\tau}) - \exp(-\frac{s}{\tau_w})]$  (iv) **Combi of (i) + (iii)**

# Neuronal Dynamics – 9.3 Spike Response Model (SRM)



potential

$$u(t) = \sum_{t'} \eta(t-t') + \int_0^\infty \kappa(s) I(t-s) ds + u_{rest}$$

threshold

$$\mathcal{G}(t) = \theta_0 + \sum_{t'} \theta_1(t-t')$$

firing if

$$u(t) = \mathcal{G}(t)$$

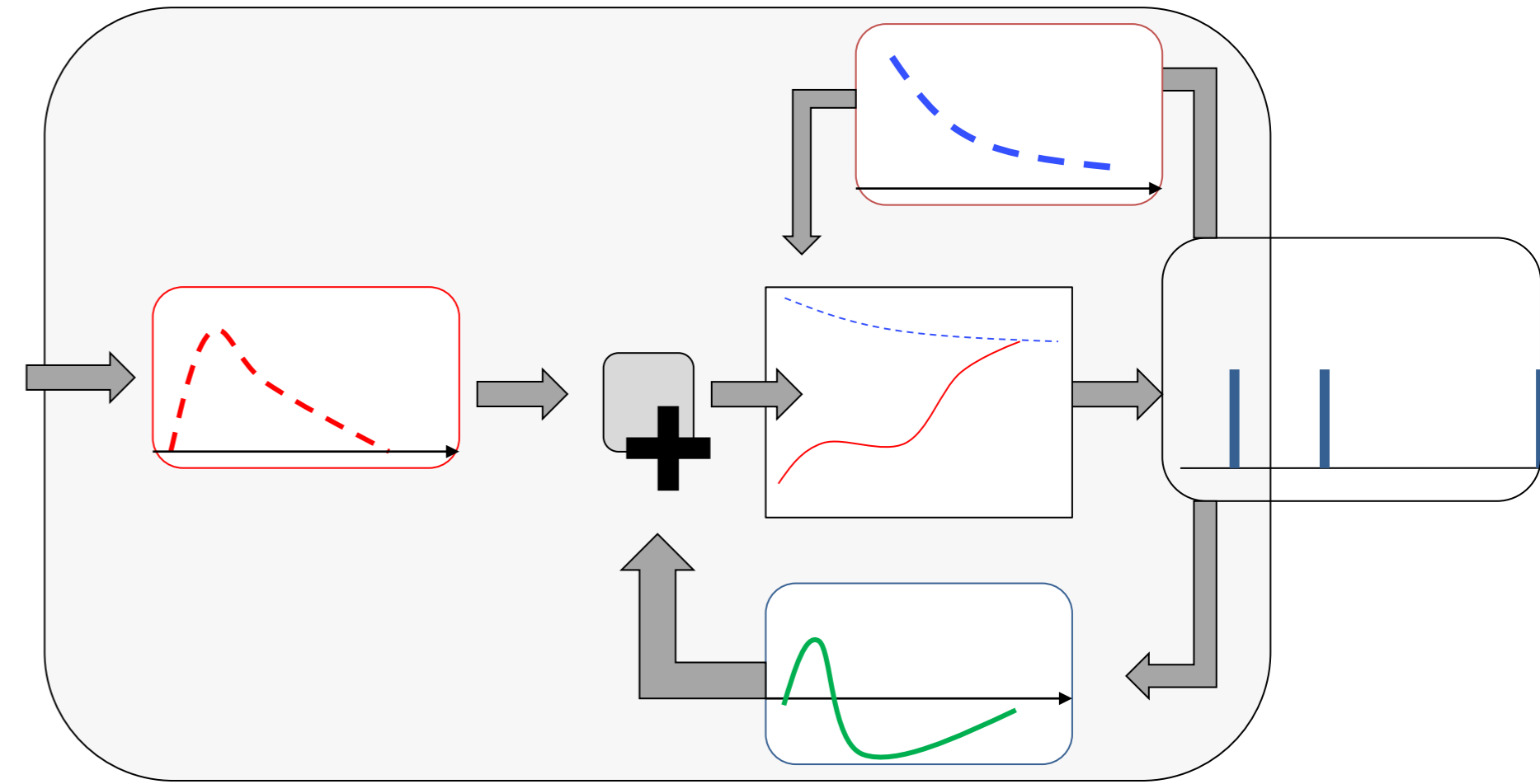
# Neuronal Dynamics – 9.3 Spike Response Model (SRM)

potential

$$u(t) = \sum_{t'} \underline{\eta(t-t')} + \int_0^\infty \underline{\kappa(s)} I(t-s) ds + u_{rest}$$

threshold

$$\mathcal{G}(t) = \theta_0 + \sum_{t'} \underline{\theta_1(t-t')}$$



Linear filters for

- input
- threshold
- refractoriness