Week 7 – part 1 : Models and data

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

Neuronal Dynamics:
Computational Neuroscience of Single Neurons

Week 7 – Optimizing Neuron Models For Coding and Decoding

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Week 7 – part 1 : Models and data

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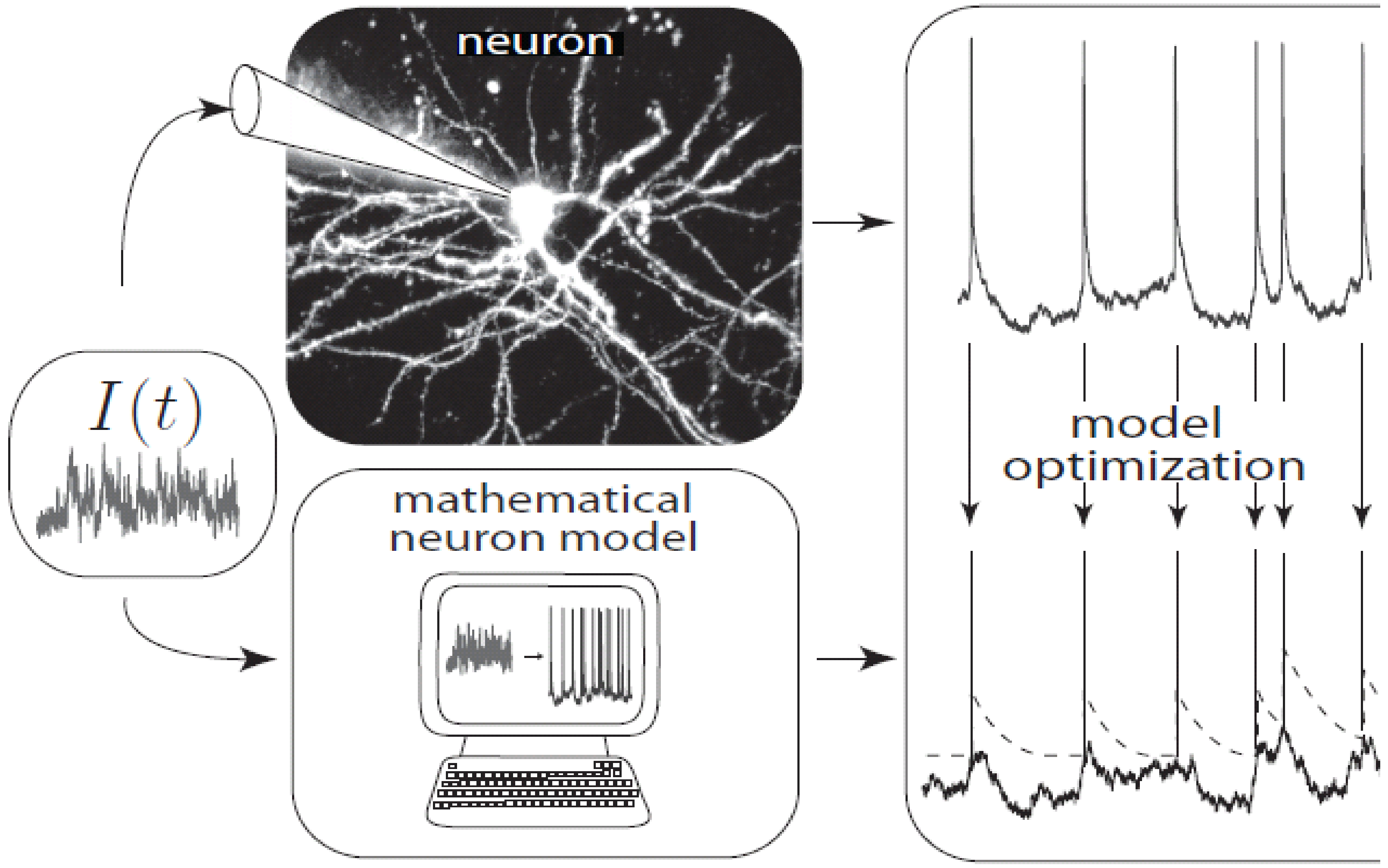
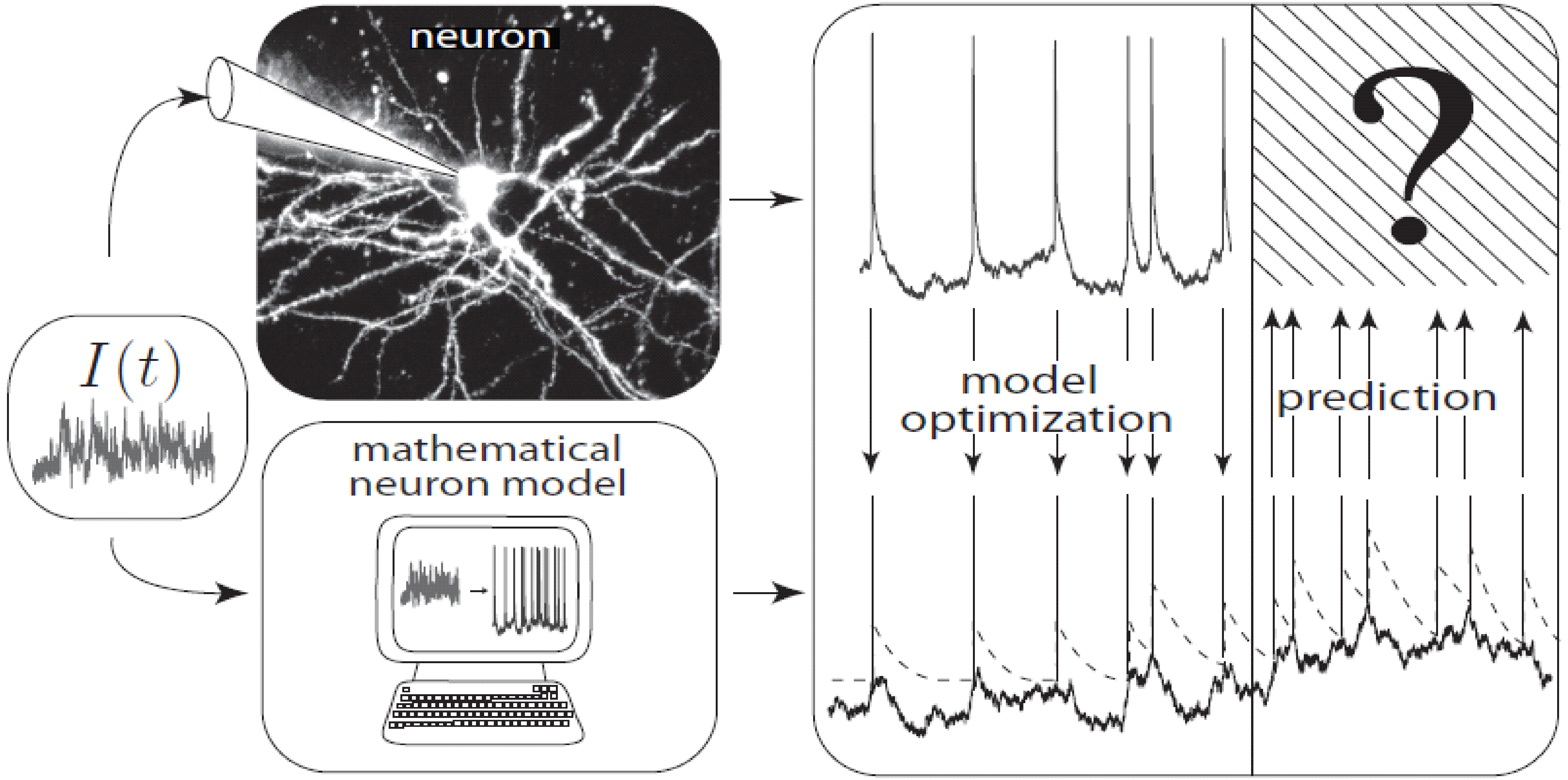


-What is a good neuron model?

-Estimate parameters of models?

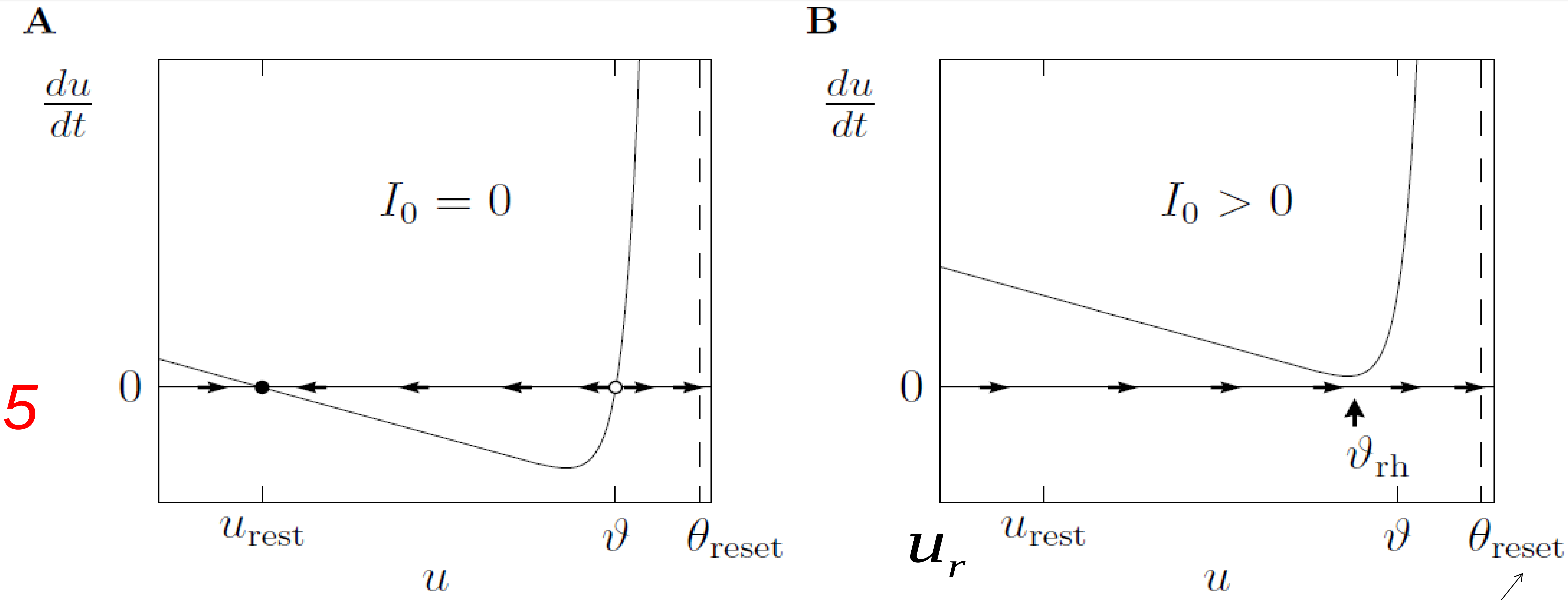
Neuronal Dynamics – 7.1 What is a good neuron model?



A) Predict spike times
B) Predict subthreshold voltage
C) Easy to interpret (not a 'black box')
D) Flexible enough to account for a variety of phenomena
E) Systematic procedure to 'optimize' parameters

Neuronal Dynamics – Review: Nonlinear Integrate-and-fire

See:
week 1,
lecture 1.5



u_r

$$\tau \frac{du}{dt} = f(u) + R\,I(t)$$

What is a good choice of **f** ?

If $u = \theta_{reset}$

then reset to

$$u = u_r$$

Neuronal Dynamics – Review: Nonlinear Integrate-and-fire

(1) $$\tau \frac{du}{dt} = f(u) + R\,I(t)$$

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

What is a good choice of ***f*** ?

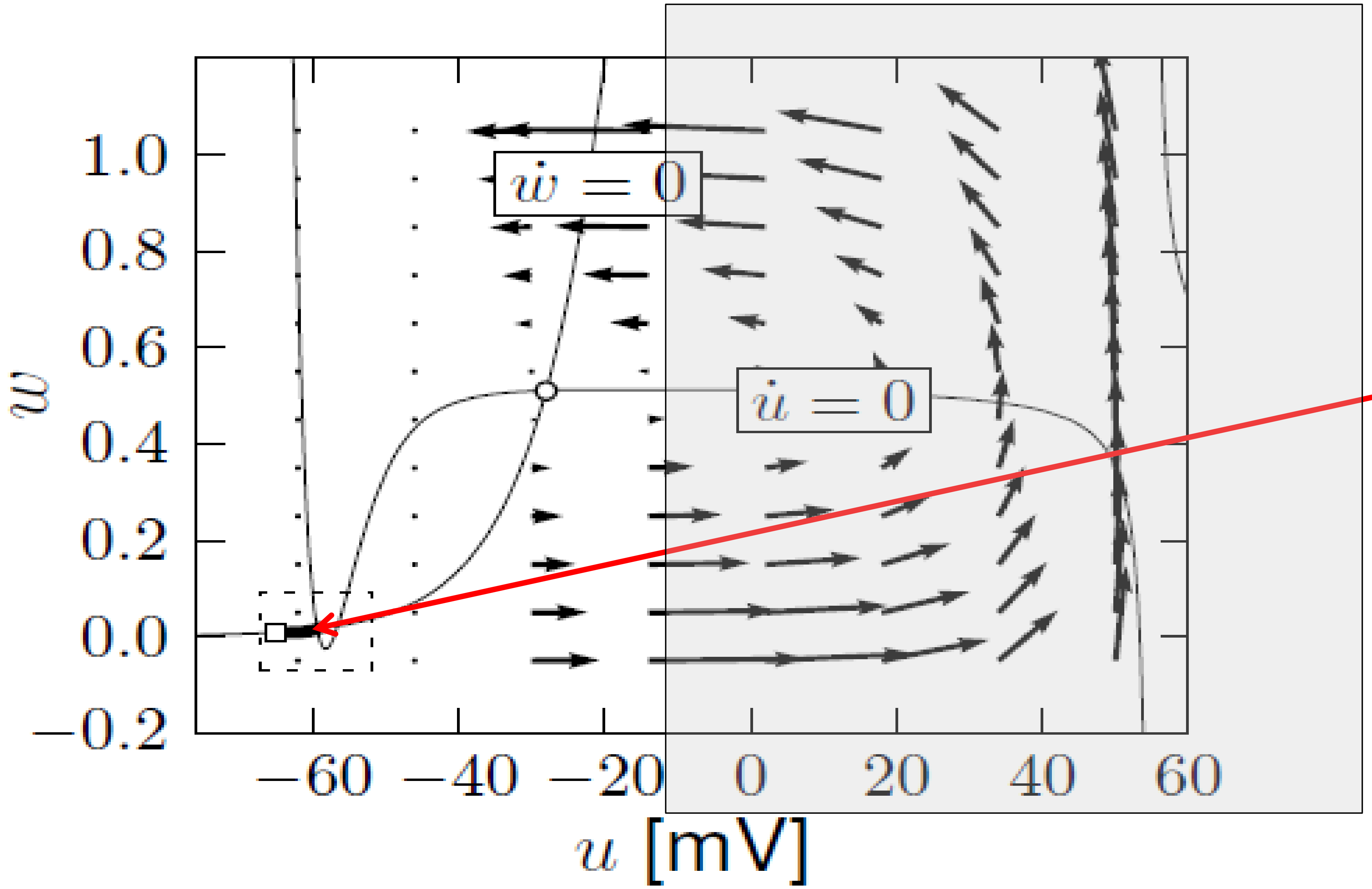
(i) Extract *f* from more complex models

(ii) Extract *f* from data

Neuronal Dynamics – Review: Nonlinear Integrate-and-fire

(i) Extract f from more complex models

$$\tau \frac{du}{dt} = f(u) + R\,I(t)$$



A. detect spike and reset

resting state

Separation of time scales:
Arrows are nearly horizontal

Spike initiation, from rest

$w \approx w_{rest}$

See week 4:
2dim version of
Hodgkin-Huxley

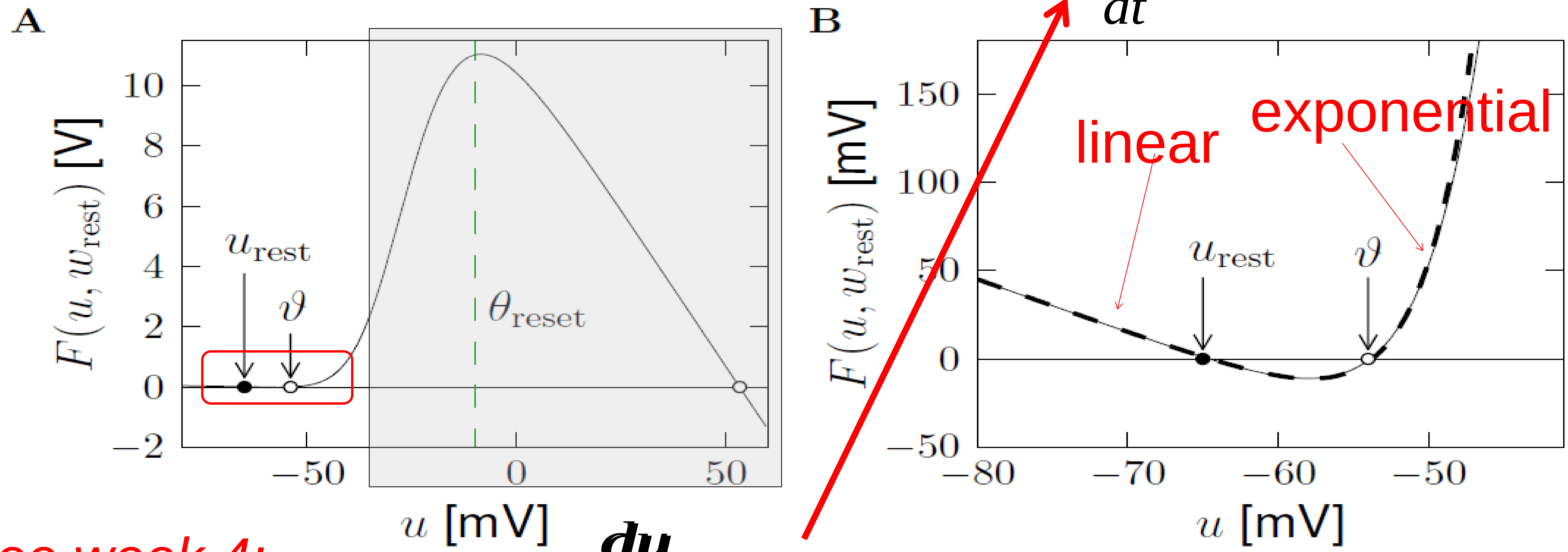
$$\tau \frac{du}{dt} = F(u,w) + R\,I(t)$$

$$\tau_w \frac{dw}{dt} = G(u,w)$$

B. Assume $w = w_{rest}$

Neuronal Dynamics – Review: Nonlinear Integrate-and-fire

(i) Extract f from more complex models $\tau \frac{du}{dt} = f(u) + R\,I(t)$



See week 4:
2dim version of
Hodgkin-Huxley

$$\tau \frac{du}{dt} = F(u, w_{rest}) + R\,I(t)$$

Separation of time scales

$$\tau_w \frac{dw}{dt} = G(u, w) \longrightarrow w \approx w_{rest}$$

Neuronal Dynamics – Review: Nonlinear Integrate-and-fire

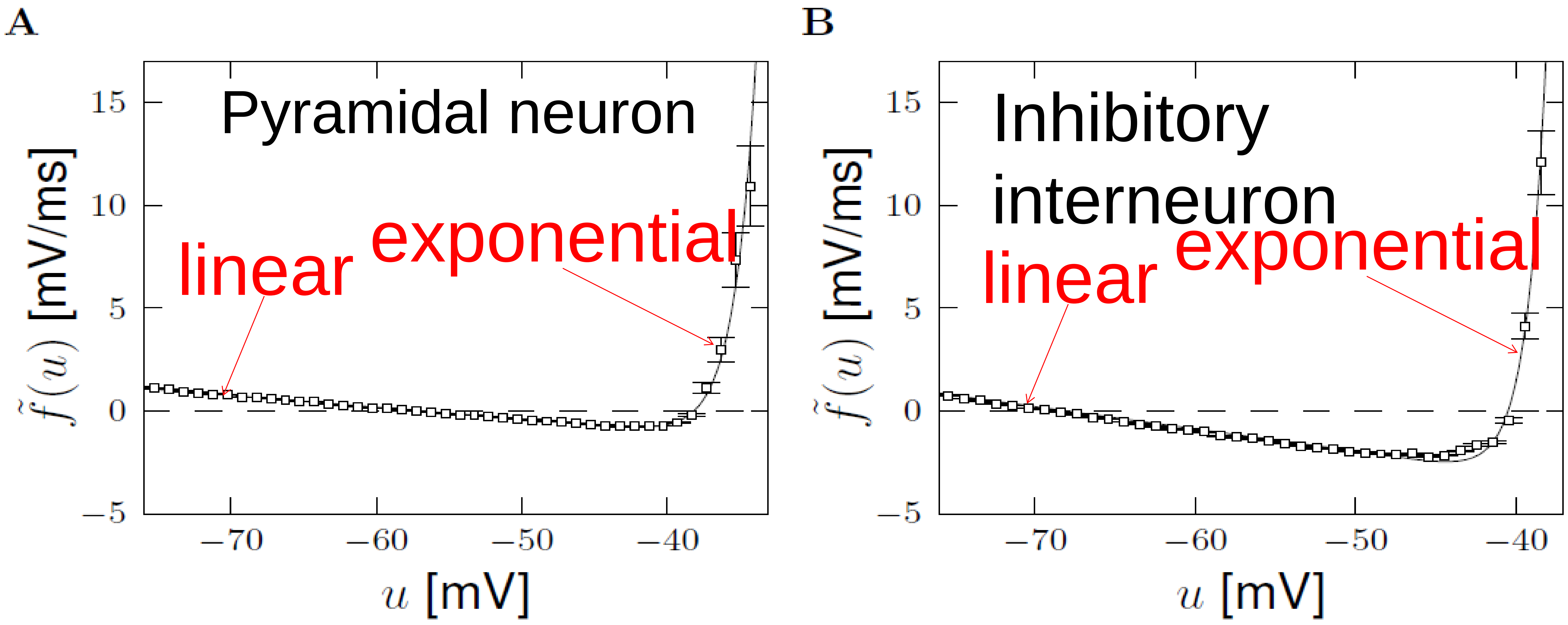
(ii) Extract *f* from data *Badel et al. (2008)*

$$\tau \frac{du}{dt} = f(u) + R\,I(t)$$

$$\tilde{f}(u) = \frac{f(u)}{\tau}$$

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

Exp. Integrate-and-Fire, *Fourcaud et al. 2003*



Badel et al. (2008)

Neuronal Dynamics – Review: Nonlinear Integrate-and-fire

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

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

Best choice of ***f*** : linear + exponential

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

BUT: **Limitations – need to add**

-Adaptation on slower time scales

-Possibility for a diversity of firing patterns

-Increased threshold ϑ after each spike

-Noise

Neuronal Dynamics – Quiz 7.1.

The exponential integrate-and-fire model

[ ] can be extracted from data

[ ] can be extracted from two-dimensional neuron model under the assumption of a separation of time scales

[ ] has a linear and an exponential term in the voltage equation

[ ] accounts for adaptation

[ ] accounts for bursting

Week 7 – part 2a : AdEx: Adaptive exponential integrate-and-fire

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Week 7 – part 2a : AdEx: Adaptive exponential integrate-and-fire

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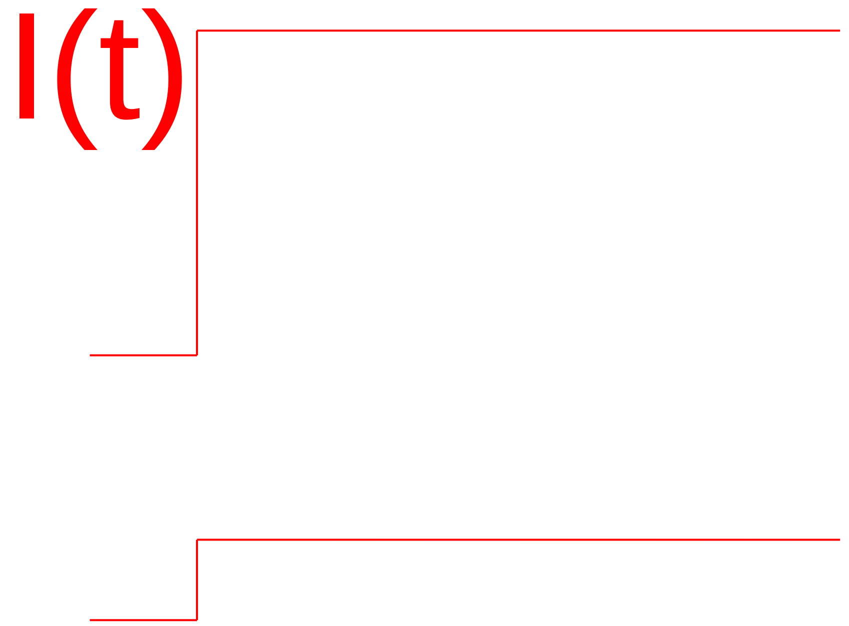
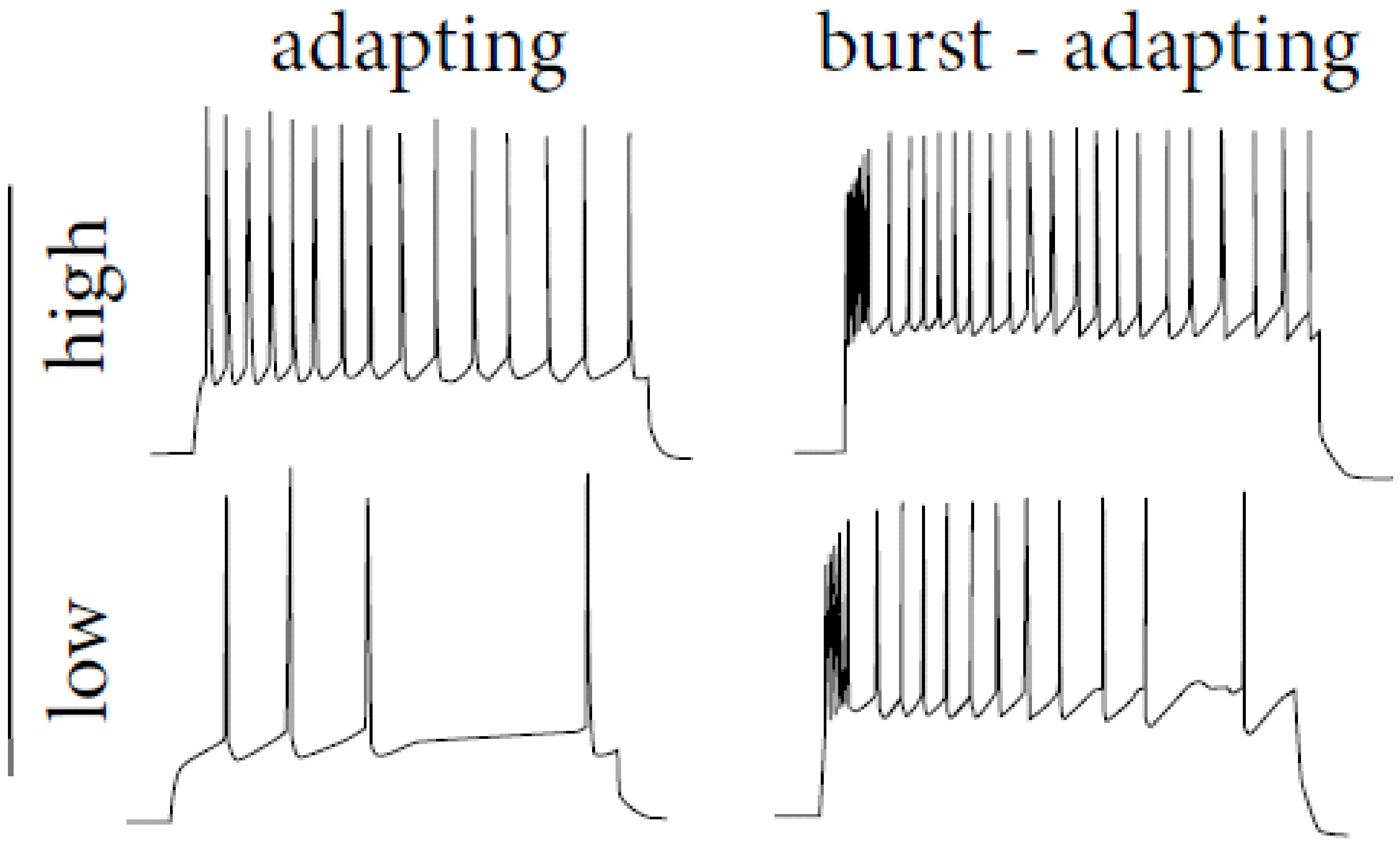
Step current input – neurons show adaptation





Data:
Markram et al.
(2004)

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

Add adaptation variables:

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

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

Exponential I&F
+ **1 adaptation** var.
= AdEx

SPIKE AND RESET

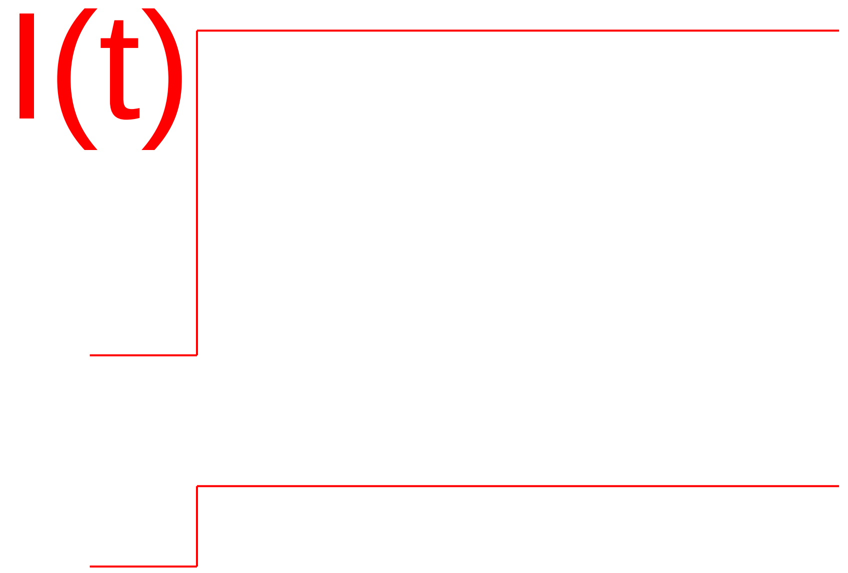
after each spike w_k jumps by an amount b_k

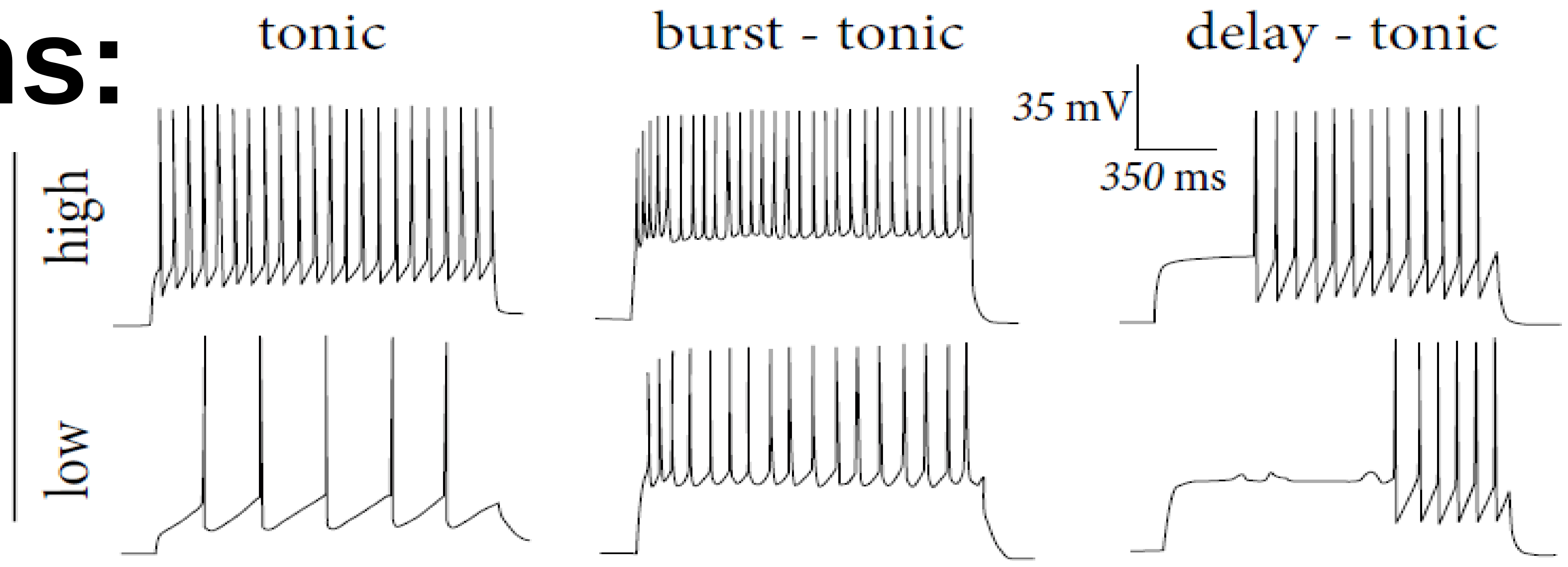
$If \quad u = \theta_{reset} \quad then \quad reset\ to\ u = u_r$

AdEx model, Brette&Gerstner (2005):

Firing patterns:

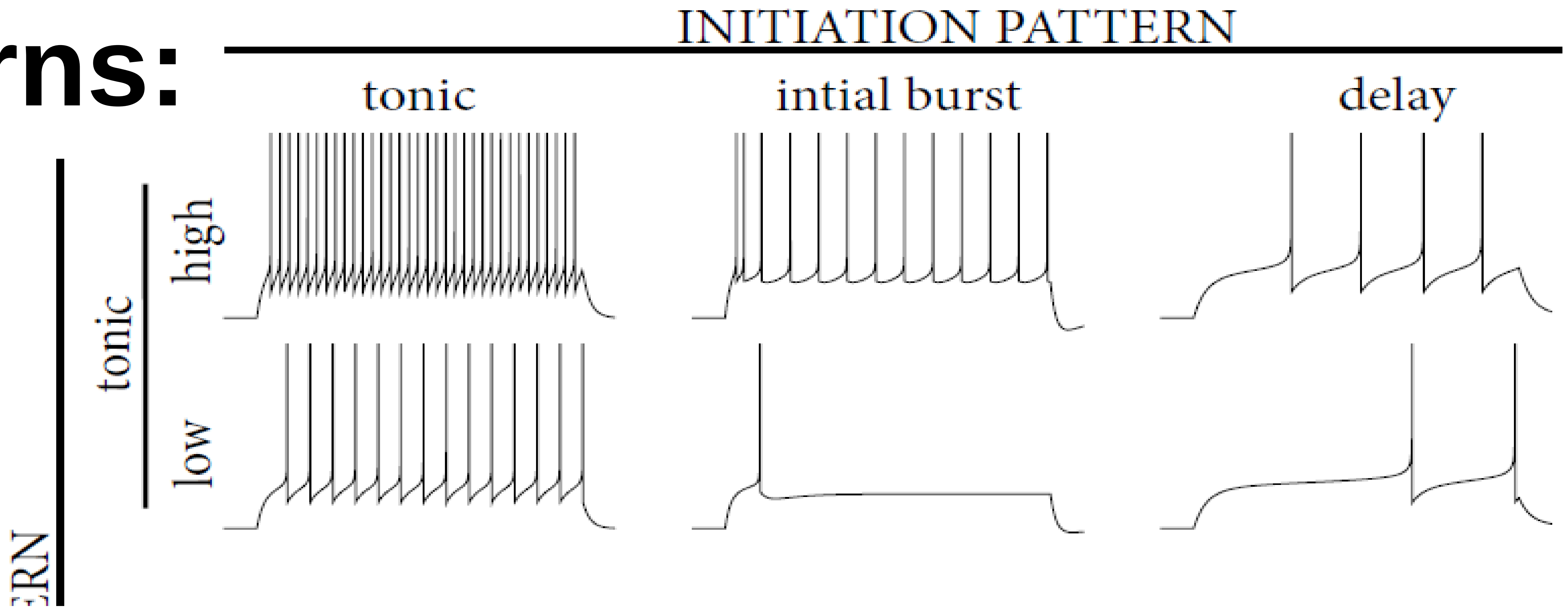
Response to
Step currents,
Exper. Data,
Markram et al.
(2004)





Firing patterns:

Response to
Step currents,
AdEx Model,
Naud&Gerstner



I(t)

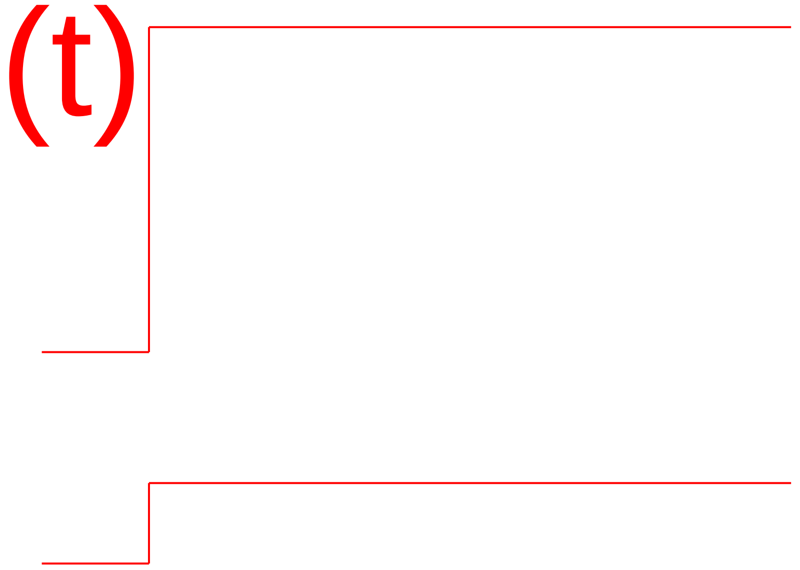


Image:
Neuronal Dynamics,
Gerstner et al.
Cambridge (2002)

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

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

AdEx model

Phase plane analysis!

Can we understand the different firing patterns?

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

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

-linear + exponential
-adaptation variable

→ Various firing patterns

Neuronal Dynamics – Quiz 7.2. Nullclines of AdEx

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

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

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 w-nullcline?

[ ] linear, slope 1
[ ] linear, slope 1/R
[ ] linear + quadratic
[ ] linear w. slope 1/R+ exponential

Week 7 – part 2b : Firing patterns and phase plane analysis

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Week 7 – part 2b : Firing patterns and phase plane analysis

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7.1 What is a good neuron model?
- Models and data

7.2 AdEx model
- Firing patterns and analysis

7.3 Spike Response Model (SRM)
- Integral formulation

7.4 Generalized Linear Model
- Adding noise to the SRM

7.5 Parameter Estimation
- Quadratic and convex optimization

7.6. Modeling in vitro data
- how long lasts the effect of a spike?

7.7. Helping Humans

AdEx model

after each spike
u is reset to **u**$_r$

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

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

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

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

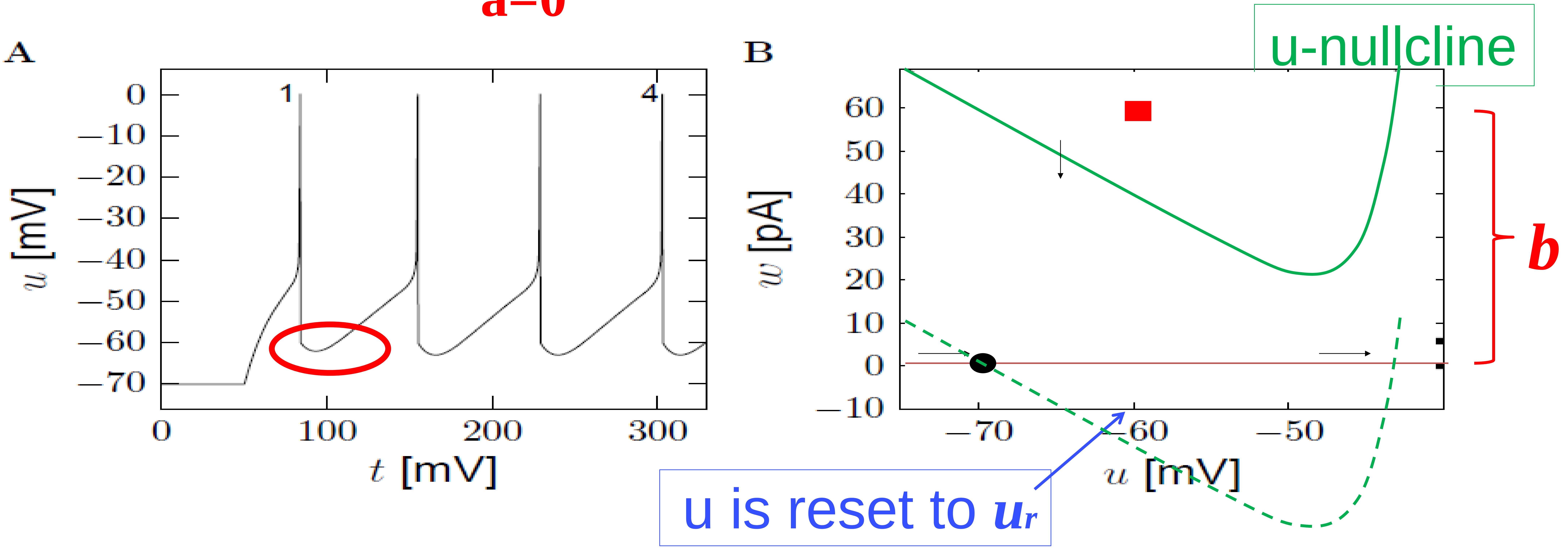
Can we understand the different firing patterns?

AdEx model – phase plane analysis: large *b*

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

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

a=0

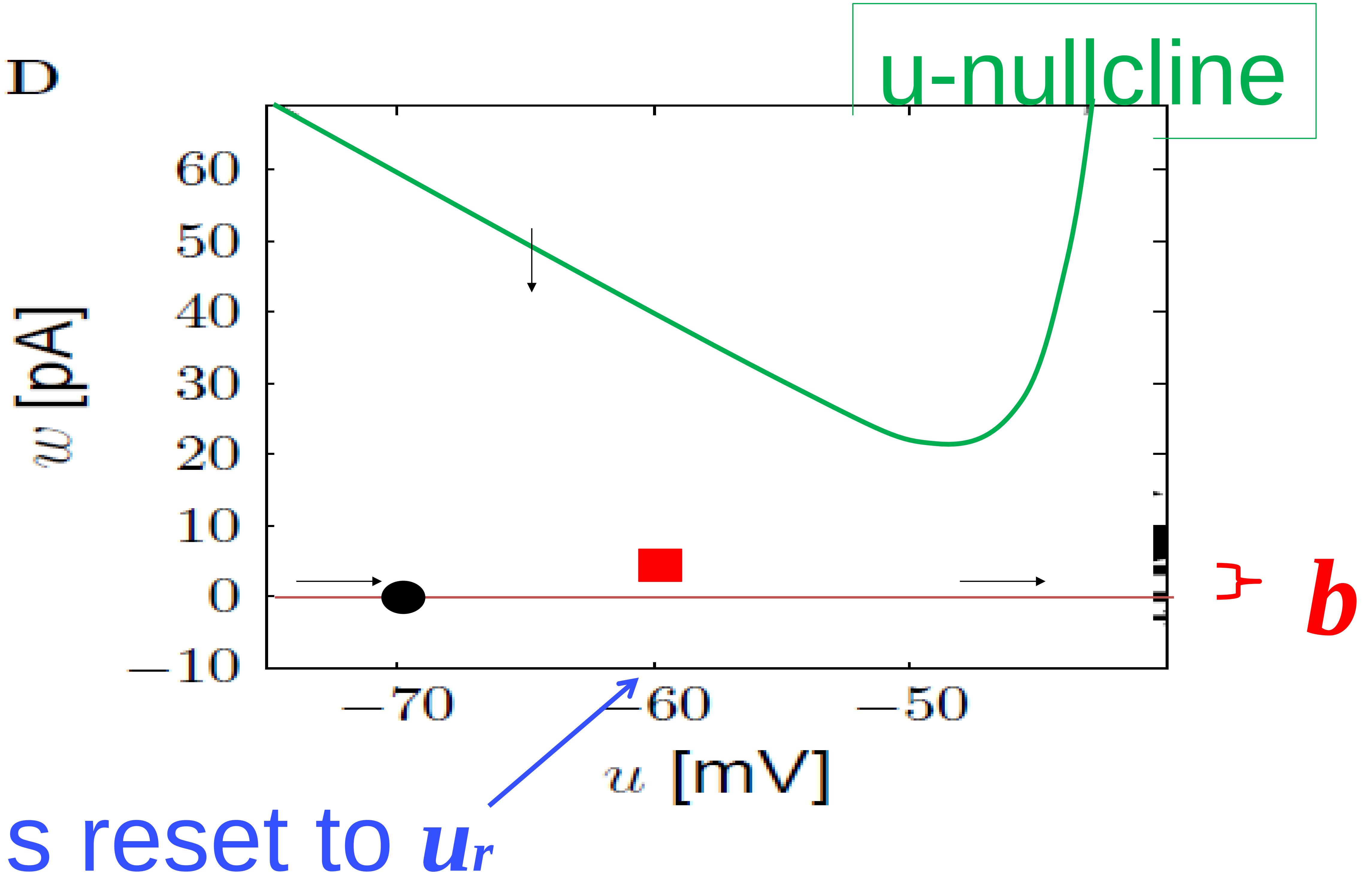


AdEx model – phase plane analysis: small *b*

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

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

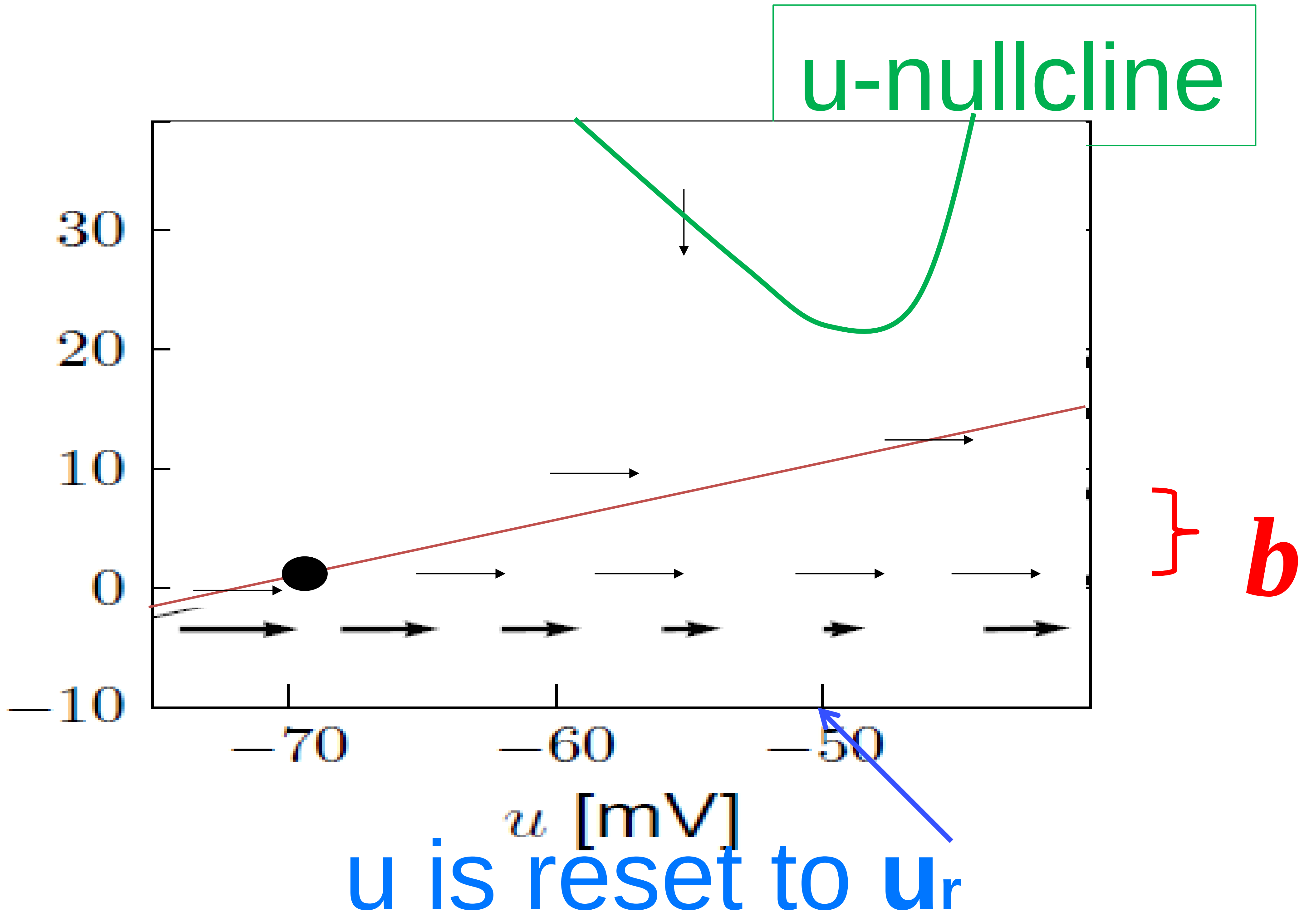
adaptation



AdEx model – phase plane analysis: a>0

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

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



Neuronal Dynamics – 7.2 AdEx model and firing patterns

after each spike u is reset to u_r

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

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

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 Izikhevich (2003)

Neuronal Dynamics – Review: Nonlinear Integrate-and-fire

(1) $$\tau \frac{du}{dt} = f(u) + R\,I(t)$$

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

Best choice of ***f*** : linear + exponential

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

BUT: **Limitations – need to add**

✓ -Adaptation on slower time scales

✓ -Possibility for a diversity of firing patterns

-Increased threshold ϑ after each spike

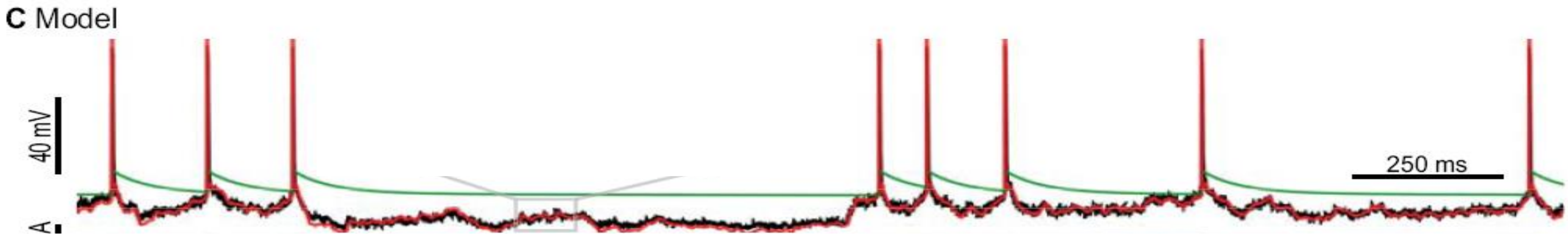
-Noise

Add dynamic threshold:

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

Threshold increases after each spike

$$\boxed{\vartheta = \theta_0 + \sum_f \theta_1(t - t^f)}$$



$$\tau \frac{du}{dt} = f(u) + R\,I(t)$$

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

add

√ -Adaptation variables
√ -Possibility for firing patterns
√ -Dynamic threshold ϑ
-Noise

Neuronal Dynamics – Quiz 7.3. Nullclines for constant input

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

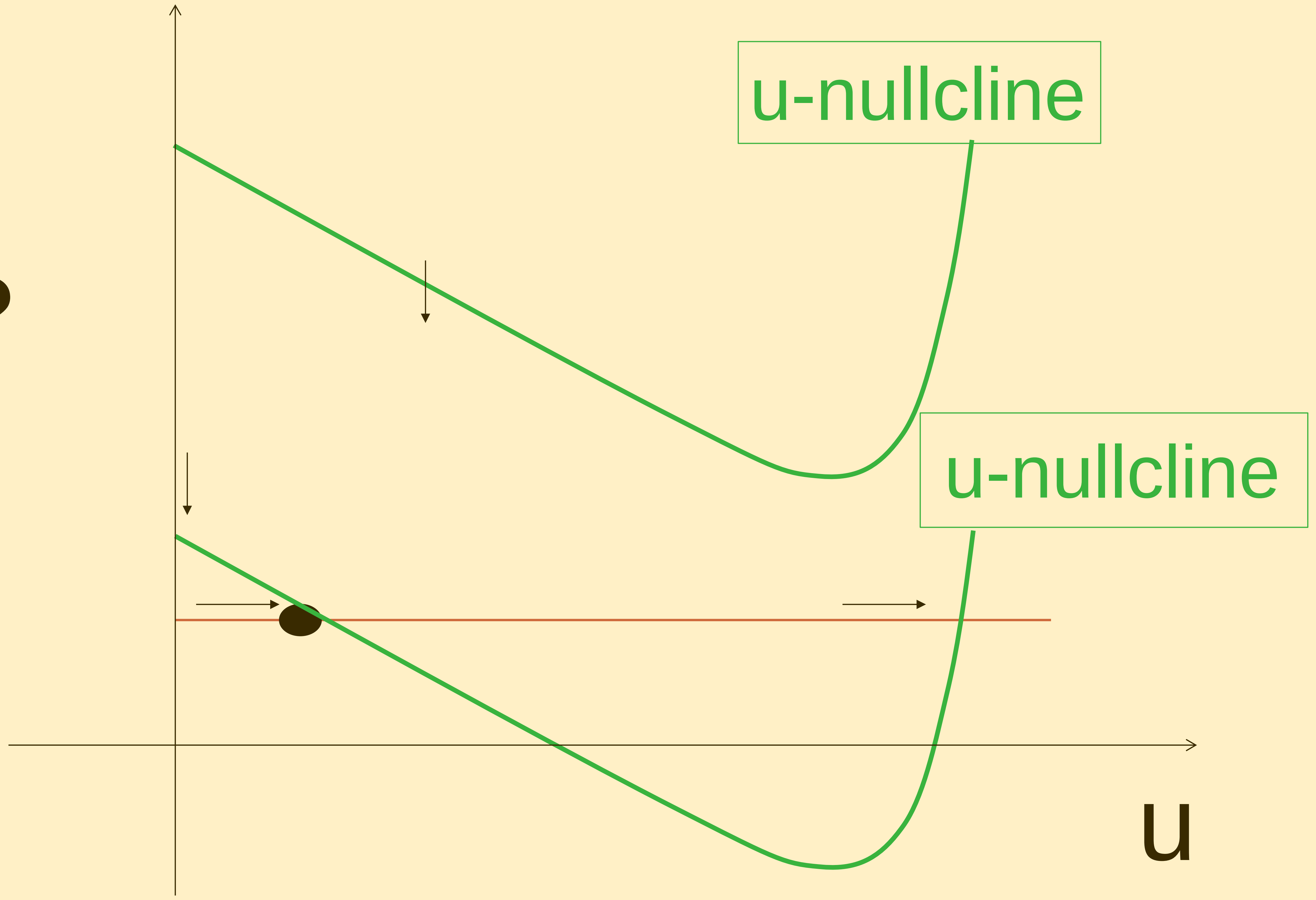
$$\tau \frac{dw}{dt} = \cancel{a\ (u - u_{rest})} - w + b\ \tau \cancel{\sum_f \delta(t - t^f)}$$

a=0

Only during reset

What happens if input switches from I=0 to I>0?

[ ] u-nullcline moves horizontally
[ ] u-nullcline moves vertically
[ ] w-nullcine moves horizontally
[ ] w-nullcline moves vertically



Week 7 – part 3 :Spike Response Model (SRM)

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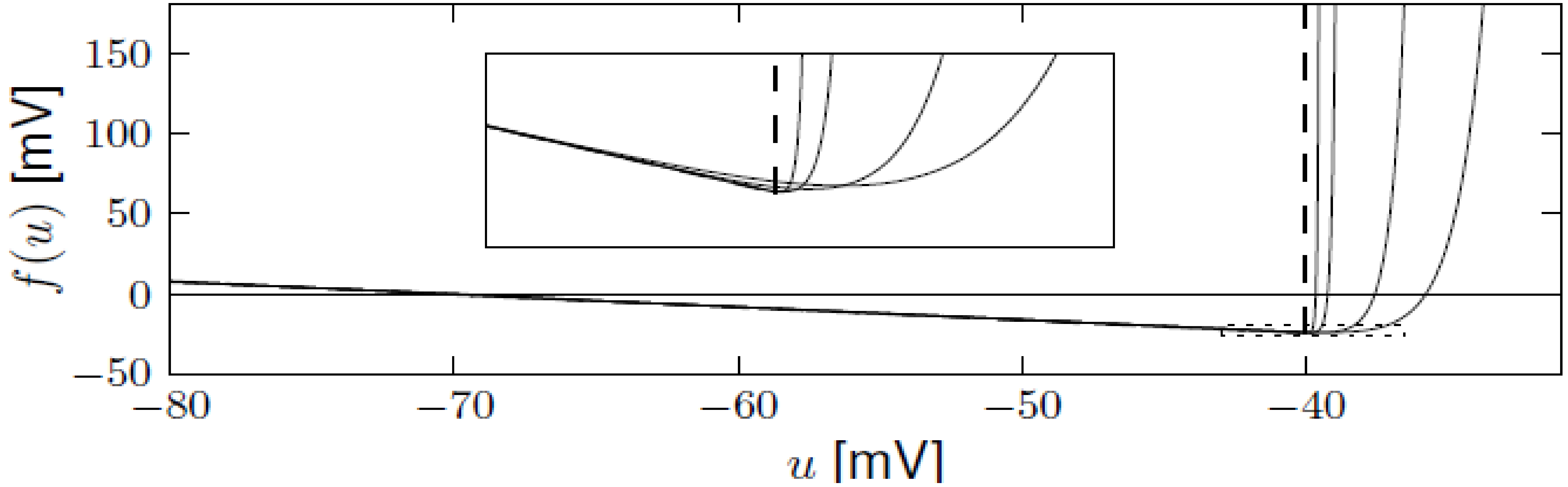
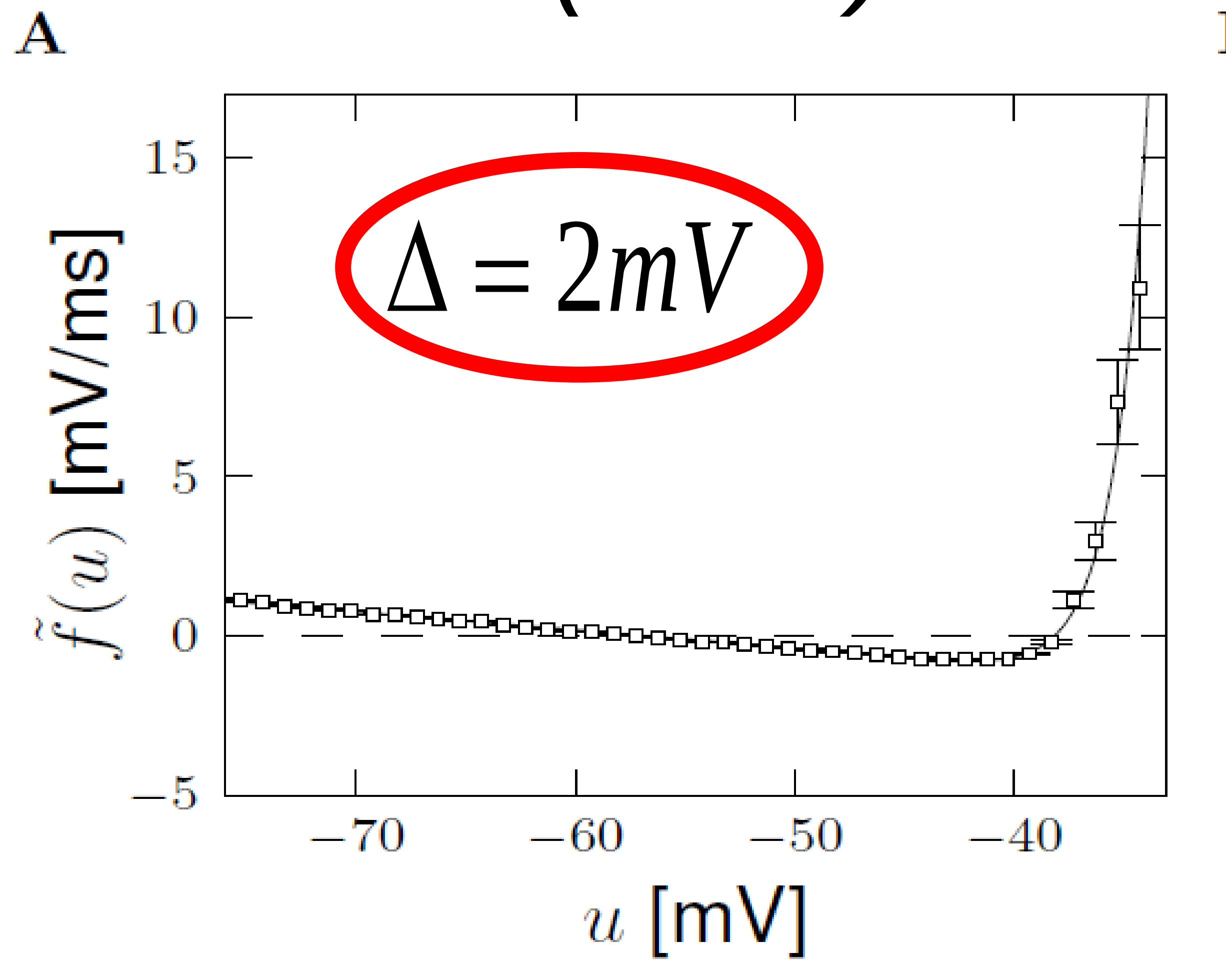
Exponential versus Leaky Integrate-and-Fire

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

Badel et al (2008)





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

Reset if u= ϑ

Leaky Integrate-and-Fire

Neuronal Dynamics – 7.3 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

$If \quad u = \vartheta(t) \quad then \quad reset\, to\; u = u_r$

Dynamic threshold

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

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

Adaptive
leaky I&F

Linear equation → can be integrated!

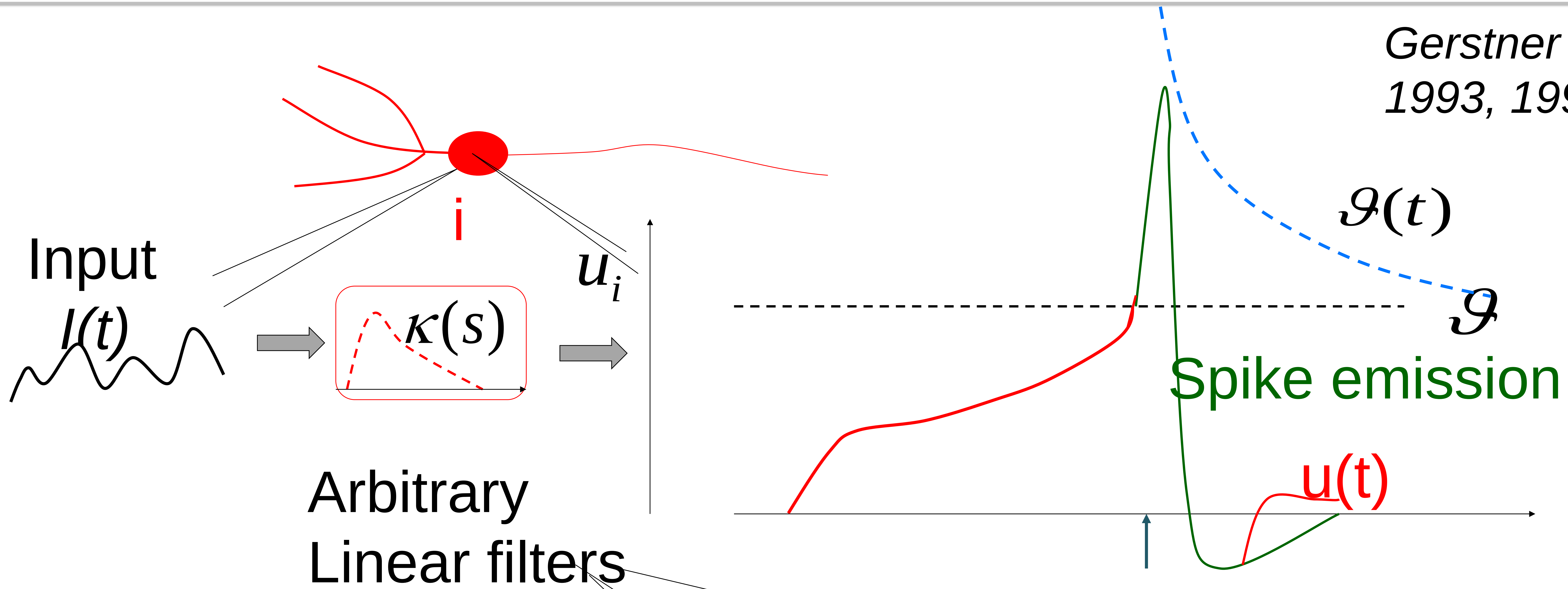
$$u(t) = \sum_f \eta\,(t - t^f) + \int_0^\infty ds\,\kappa(s) I(t - s)$$

$$\vartheta(t) = \theta_0 + \sum_f \theta_1(t - t^f)$$

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

Neuronal Dynamics – 7.3 Spike Response Model (SRM)

Gerstner et al., 1993, 1996



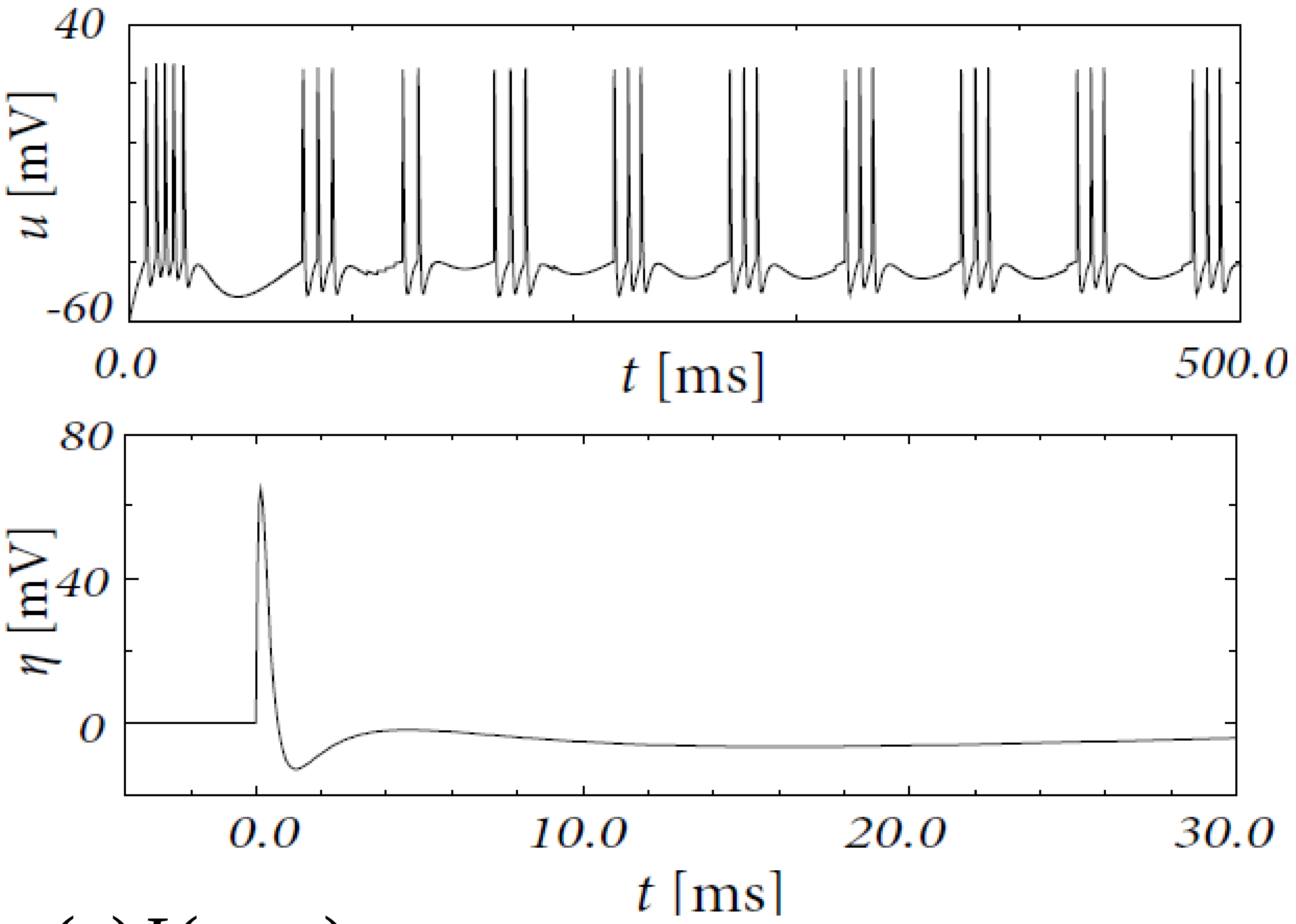
potential

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

threshold

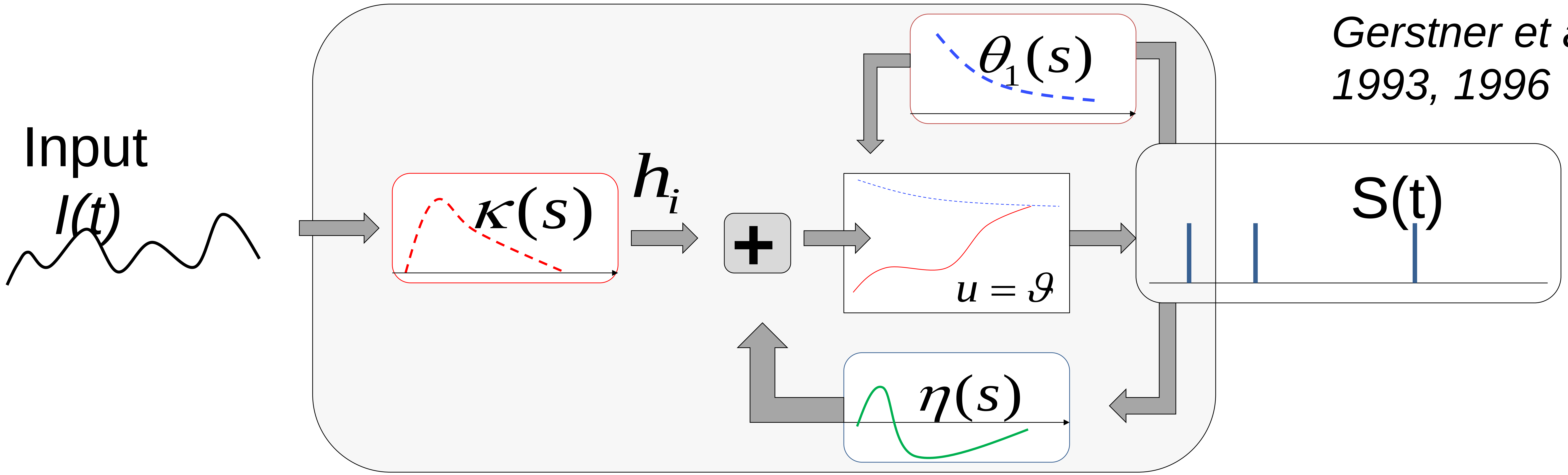
$$\vartheta(t) = \theta_0 + \sum_{t'} \theta_1 (t - t')$$

SRM with appropriate η leads to bursting



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

Neuronal Dynamics – 7.3 Spike Response Model (SRM)



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

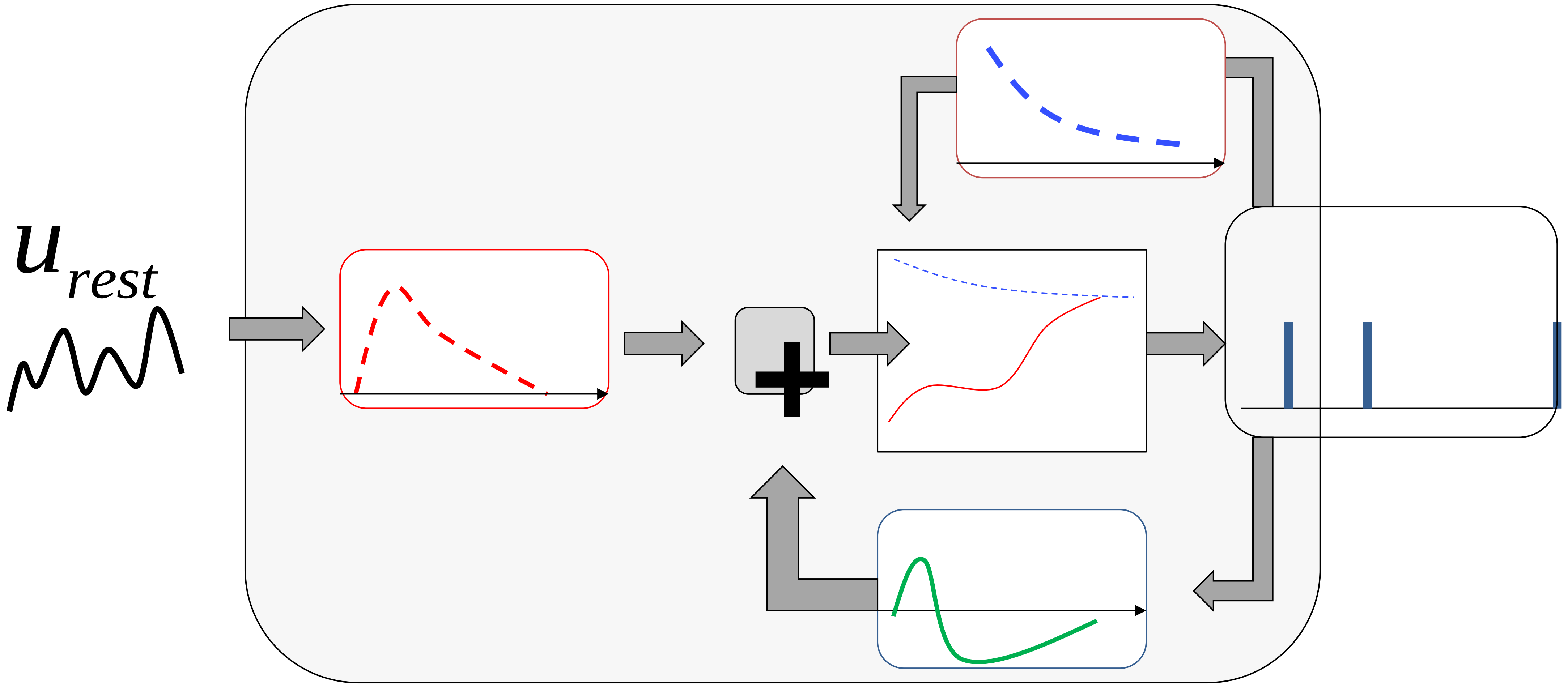
threshold $$\vartheta(t) = \theta_0 + \sum_{t'} \theta_1(t - t')$$

firing if $$u(t) = \vartheta(t)$$

Neuronal Dynamics – 7.3 Spike Response Model (SRM)

potential

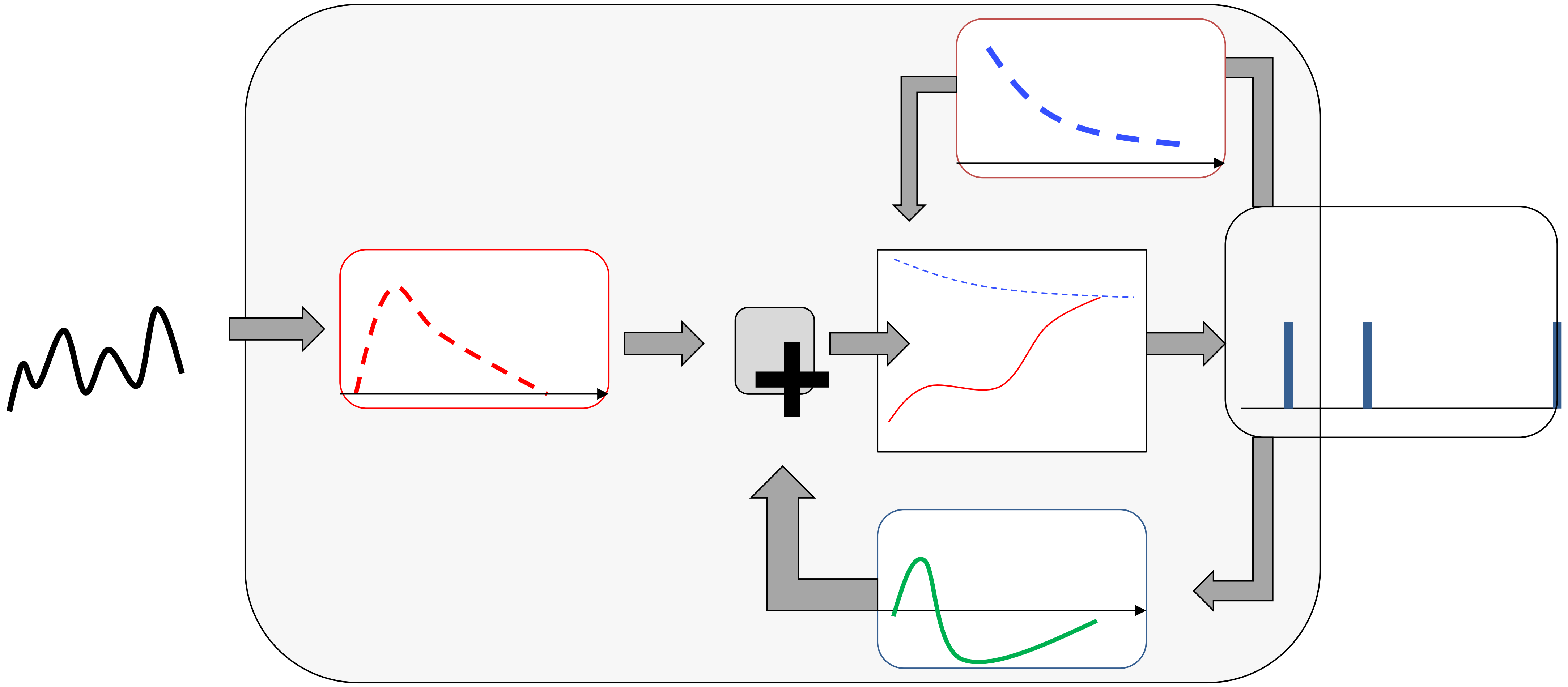
$$u(t) = \sum_{t'} \eta(t-t') + \int_0^\infty \kappa(s) I(t-s) ds + u_{rest}$$



threshold

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

Linear filters for
- input
- threshold
- refractoriness



Linear filters for

- input
- threshold
- refractoriness

Exercise 4: from adaptive IF to SRM

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

$$If \quad u = \vartheta \ then \quad reset\, to\ u = u_r$$

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

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

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

A – what is $\eta(s)$ **?**

B – what is $\varepsilon(s)$**?**

(i) $x(s) = \frac{R}{\tau} \exp(-\frac{s}{\tau})$ **(ii)** $x(s) = \frac{R}{\tau_w} \exp(-\frac{s}{\tau_w})$

(iii) $x(s) = \frac{b R \tau \tau_w}{\tau - \tau_w} [\exp(-\frac{s}{\tau}) - \exp(-\frac{s}{\tau_w})]$ **(iv) other**

Week 7 – part 4 :Generalized Linear Model (GLM)

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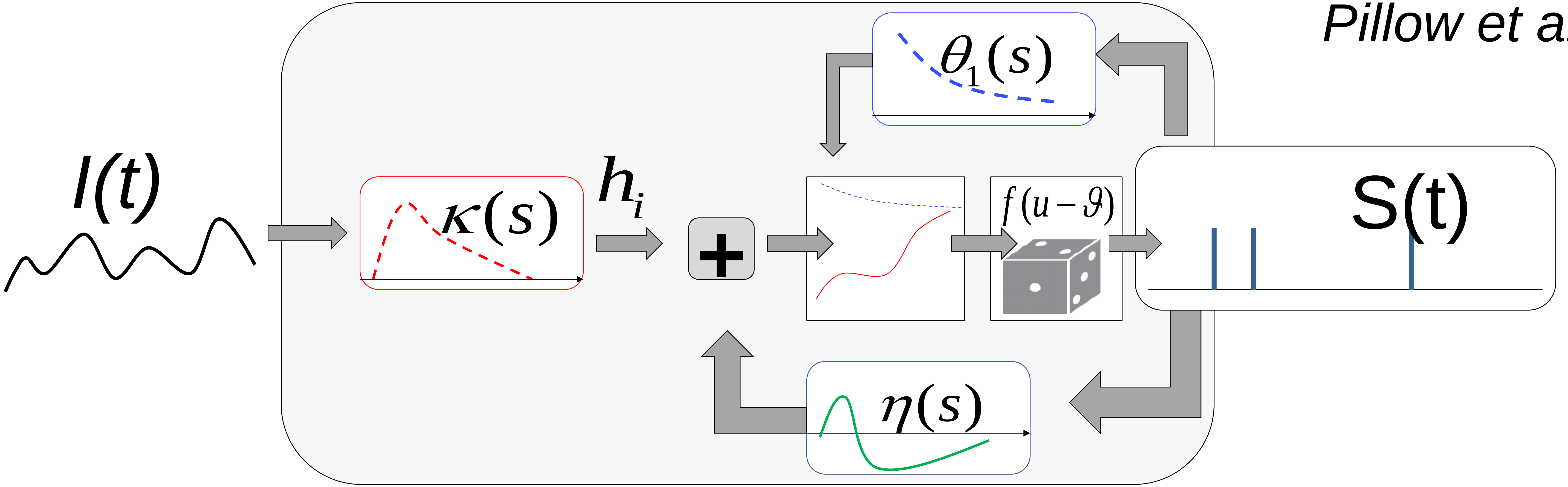
Spike Response Model (SRM)
Generalized Linear Model GLM

Gerstner et al., 1992,2000
Truccolo et al., 2005
Pillow et al. 2008



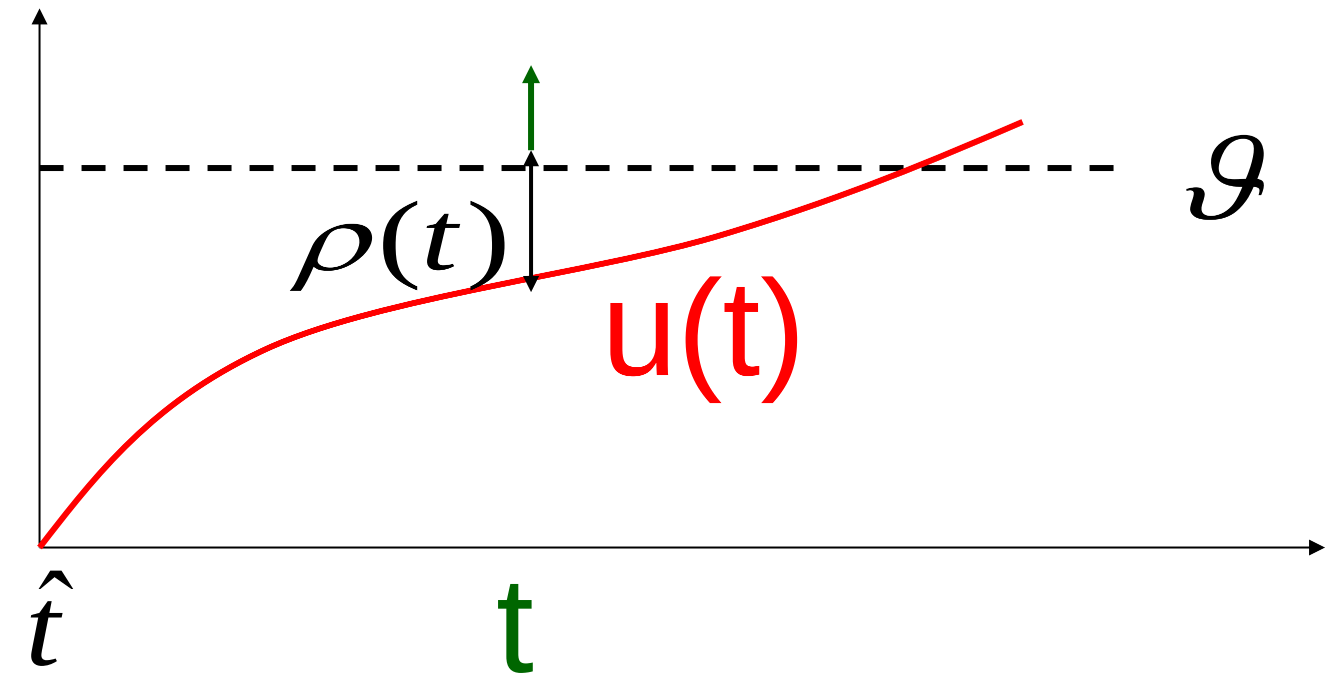
potential $u(t) = \int \eta(s) S(t-s) ds + \int_0^\infty \kappa(s) I(t-s) ds + u_{rest}$

threshold $\vartheta(t) = \theta_0 + \int \theta_1(s) S(t-s) ds$

firing intensity $\rho(t) = f(u(t) - \vartheta(t))$

Neuronal Dynamics – review from week 6: Escape noise

escape process

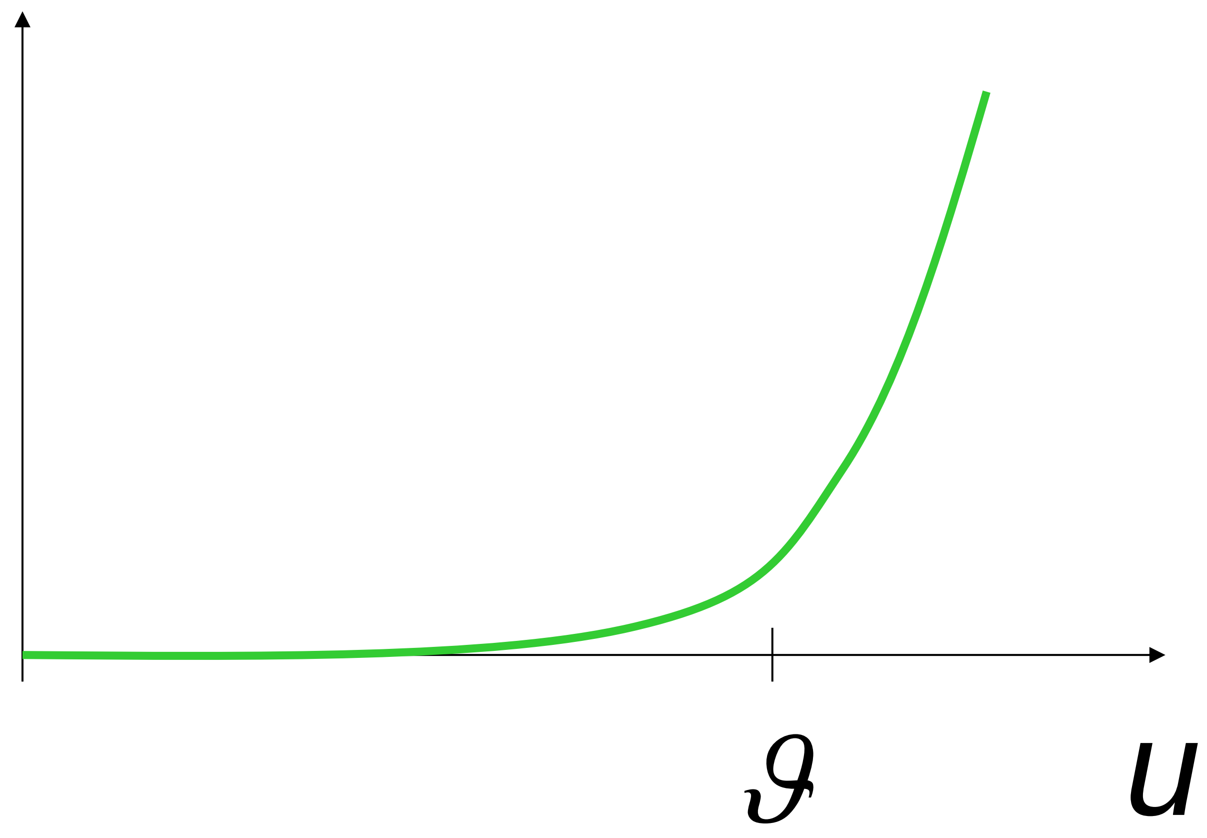


escape rate

$$\rho(t) = \frac{1}{\Delta}\exp\left(\frac{u(t)-\vartheta}{\Delta}\right)$$

escape rate

$$\rho(t) = f(u(t)-\vartheta)$$



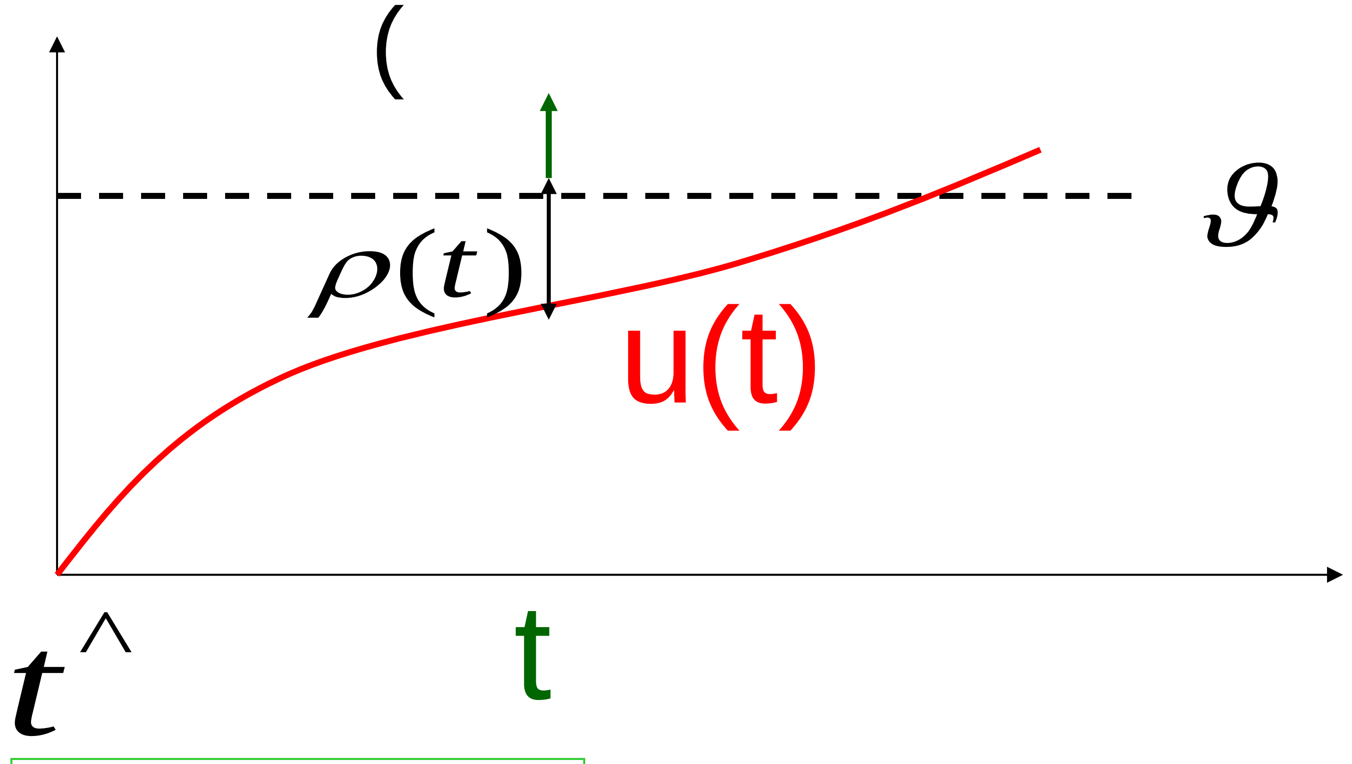
Example: leaky integrate-and-fire model

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

$$\text{if spike at } t^f \Rightarrow u\left(t^f+\delta\right) = u_r$$

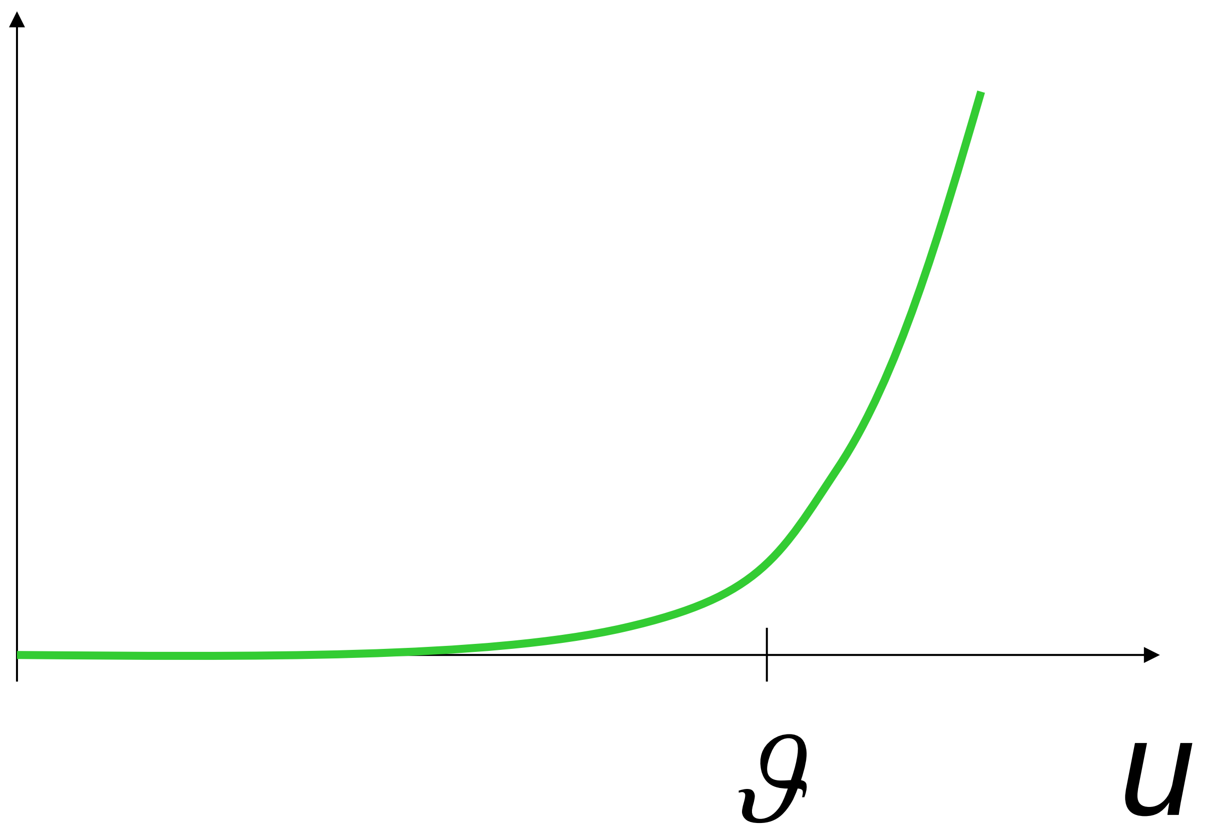
Neuronal Dynamics – review from week 6: Escape noise

escape process



escape rate

$$\rho(t) = f(u(t) - \vartheta(t))$$



Survivor function

$$\frac{d}{dt} S_I(t|\hat{t}) = -\rho(t)\, S_I(t|\hat{t})$$

$$S_I(t|\hat{t}) = \underbrace{\exp\left(-\int_{t^\wedge}^{t} \rho(t')\,dt'\right)}$$

Interval distribution

$$P_I(t|\hat{t}) = \underbrace{\rho(t)}_{\text{escape rate}} \cdot \underbrace{\exp\left(-\int_{t^\wedge}^{t} \rho(t')\,dt'\right)}_{\text{Survivor function}}$$

Good choice

$$\rho(t) = f(u(t) - \vartheta(t)) = \rho_0 \exp\left[\frac{u(t) - \vartheta(t)}{\Delta u}\right]$$

$$S(t) = \sum_f \delta(t - t^f)$$

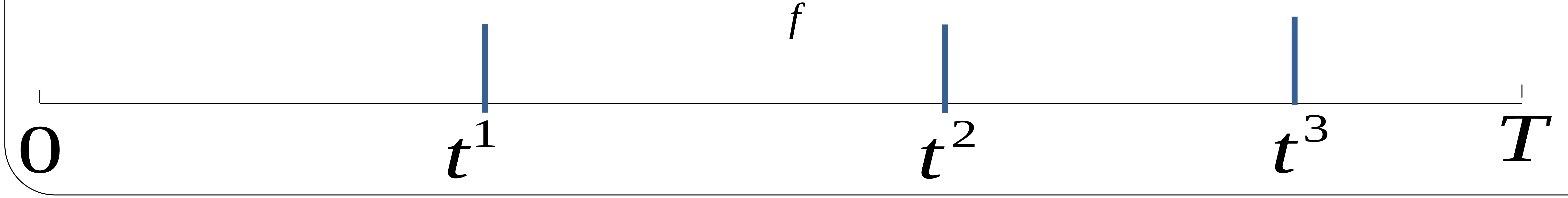
Measured spike train with spike times $t^1, t^2, \ldots t^N$

Likelihood L that this spike train could have been generated by model?

$$L(t^1, \ldots, t^N) = \exp\left(-\int_0^{t^1} \rho(t')dt'\right)\rho(t^1) \cdot \exp\left(-\int_{t^1}^{t^2} \rho(t')dt'\right) \ldots$$

Neuronal Dynamics – 7.4 Likelihood of a spike train

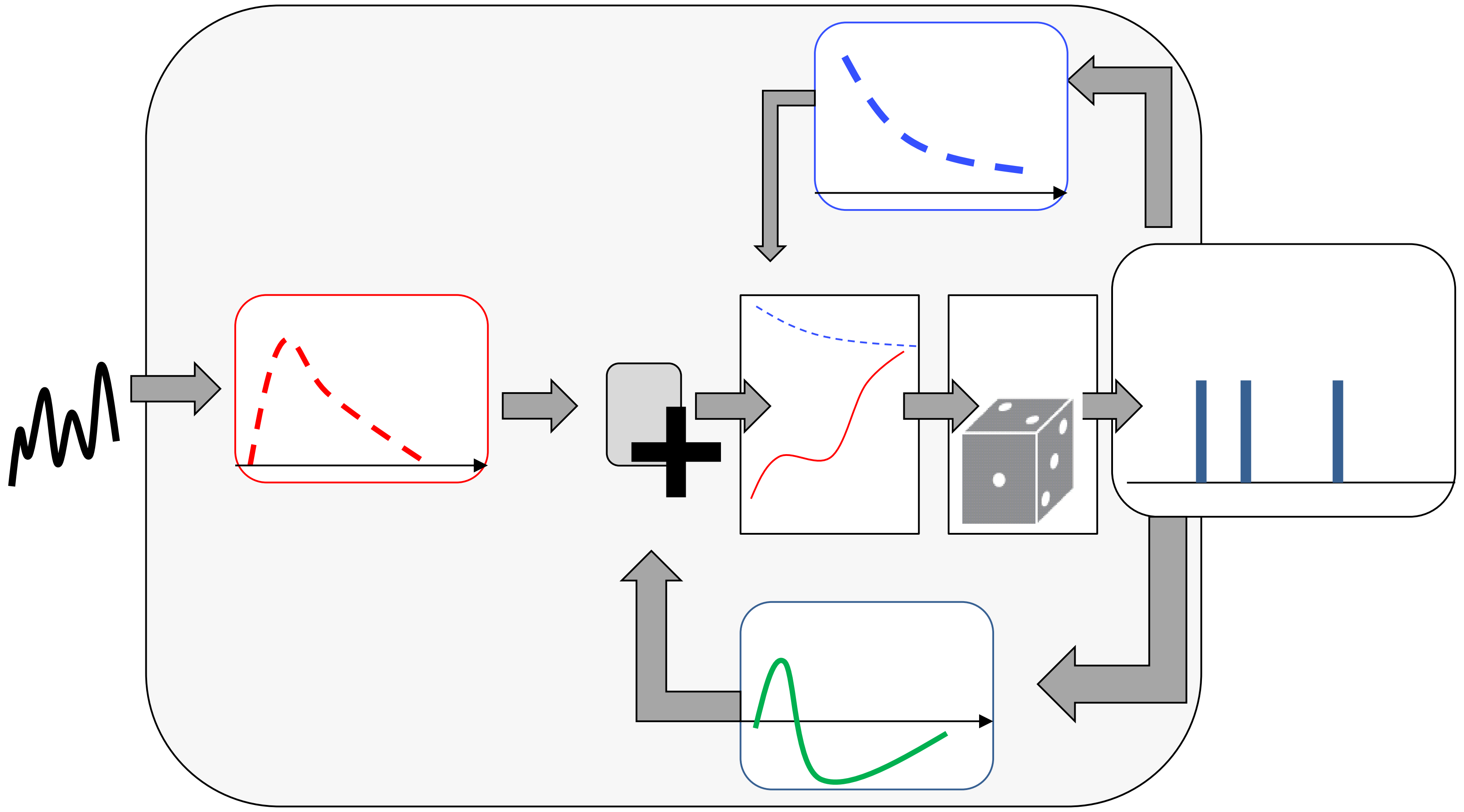
$$S(t) = \sum_f \delta(t - t^f)$$



$$L(t^1, \ldots, t^N) = \exp\left(-\int_0^{t^1} \rho(t')dt'\right)\rho(t^1) \cdot \exp\left(-\int_{t^1}^{t^2} \rho(t')dt'\right)\rho(t^2) \ldots \cdot \exp\left(-\int_{t^N}^{T} \rho(t')dt'\right)$$

$$L(t^1, \ldots, t^N) = \exp\left(-\int_0^{T} \rho(t')dt'\right)\prod_f \rho(t^f)$$

$$\log L(t^1, \ldots, t^N) = -\int_0^{T} \rho(t')dt' + \sum_f \log \rho(t^f)$$



-linear filters
-escape rate
→likelihood of observed spike train

Week 7 – part 5 : Parameter estimation

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

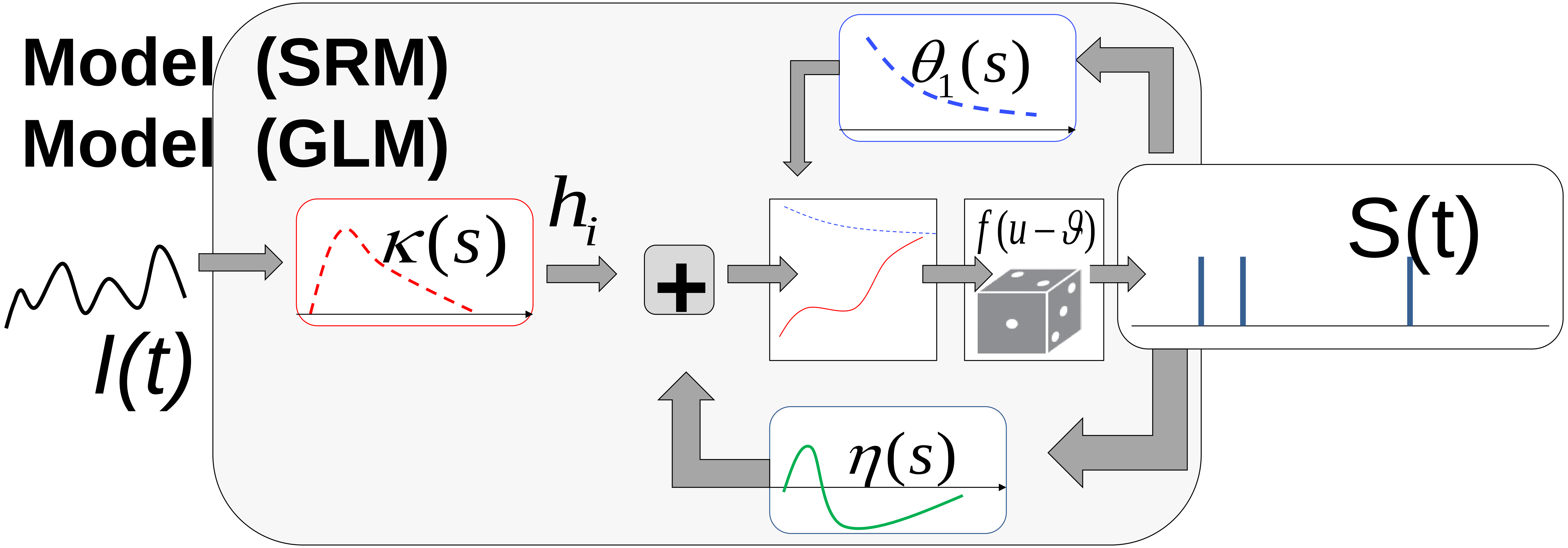
Neuronal Dynamics:
Computational Neuroscience of Single Neurons

Week 7 – Optimizing Neuron Models For Coding and Decoding

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Spike Response Model (SRM)
Generalized Lin. Model (GLM)



Subthreshold potential

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

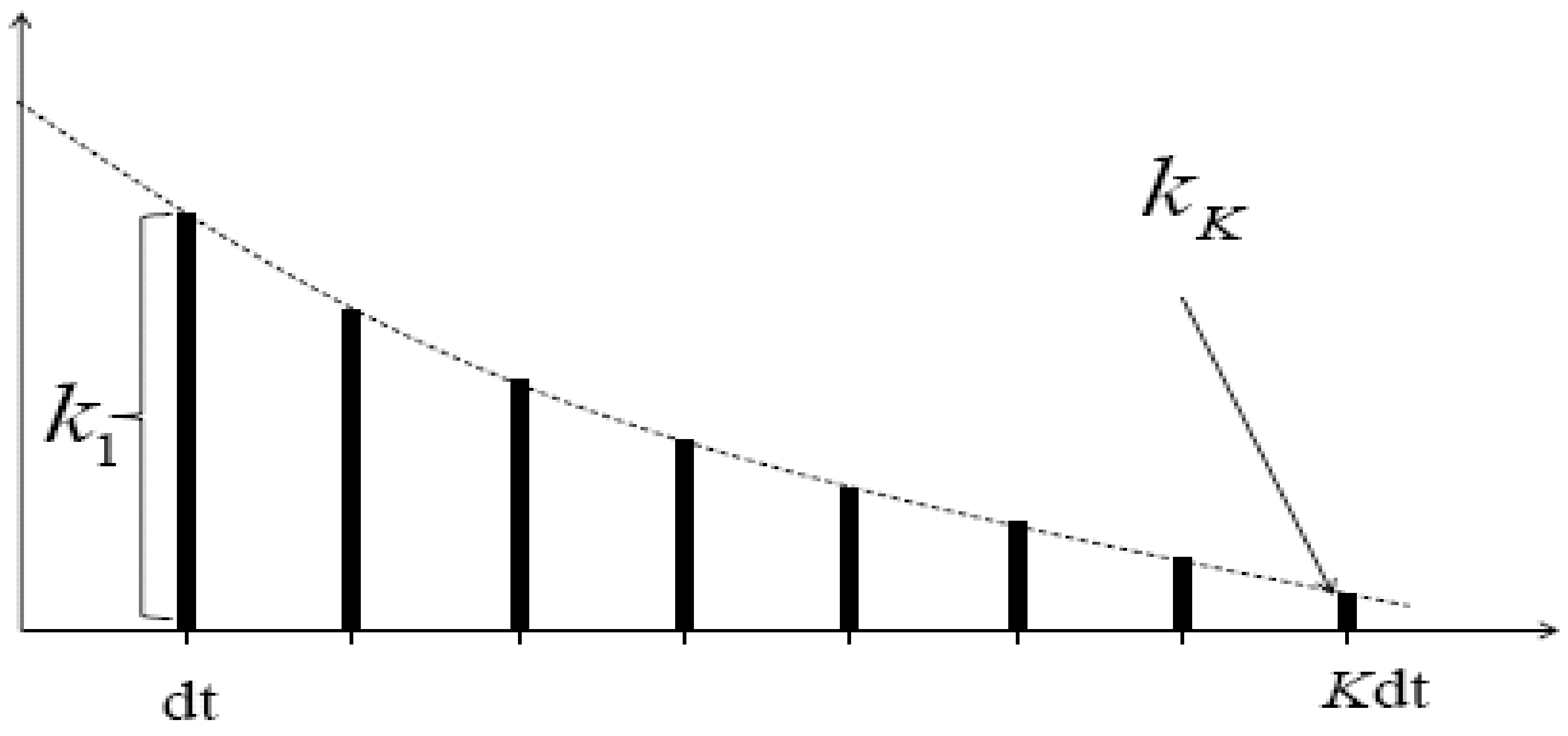
known spike train known input

Linear filters/linear in parameters

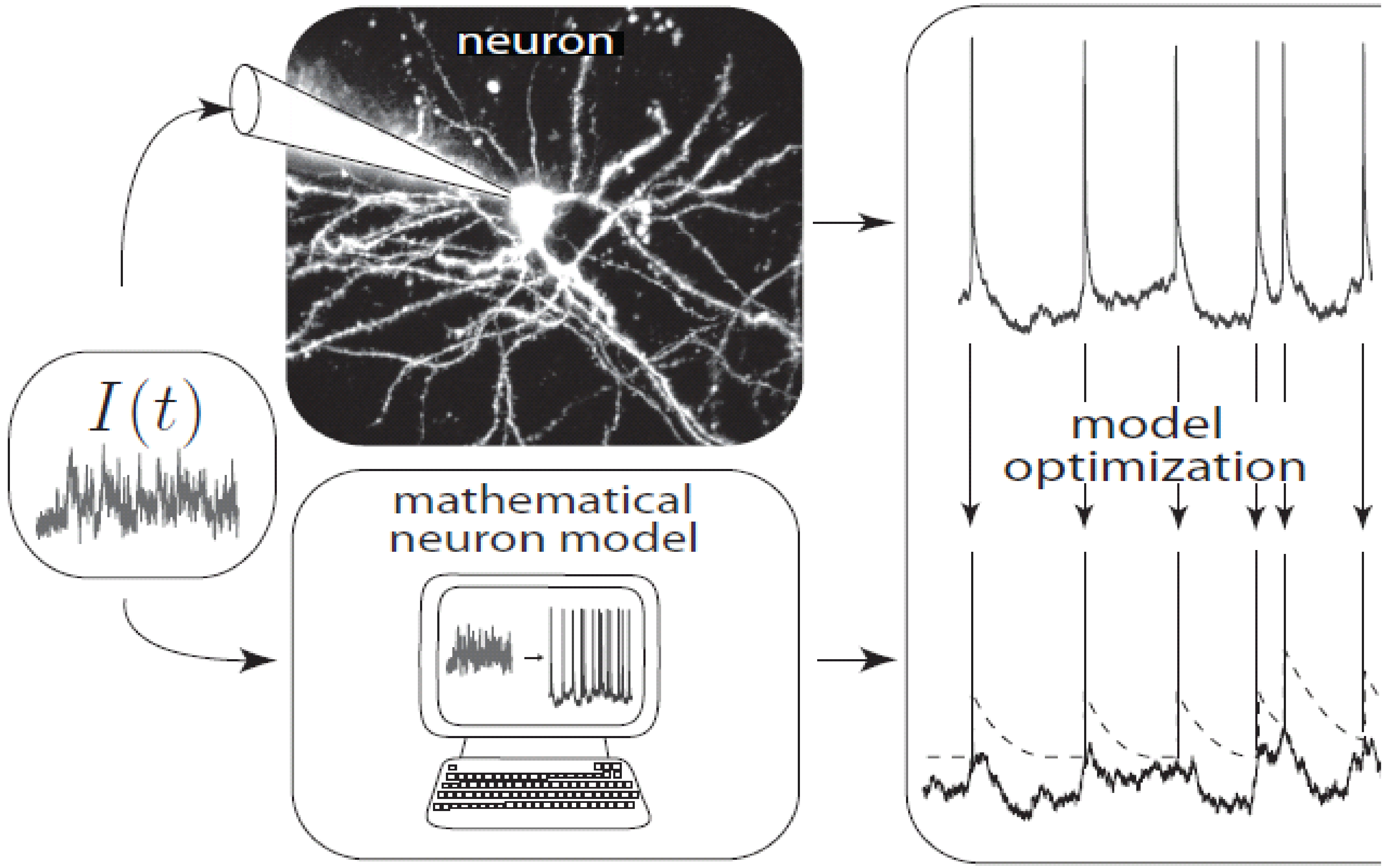
Linear in parameters = linear fit = quadratic problem

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

$$u(t_n) = \sum k_k I_{n-k} + u_{rest}$$



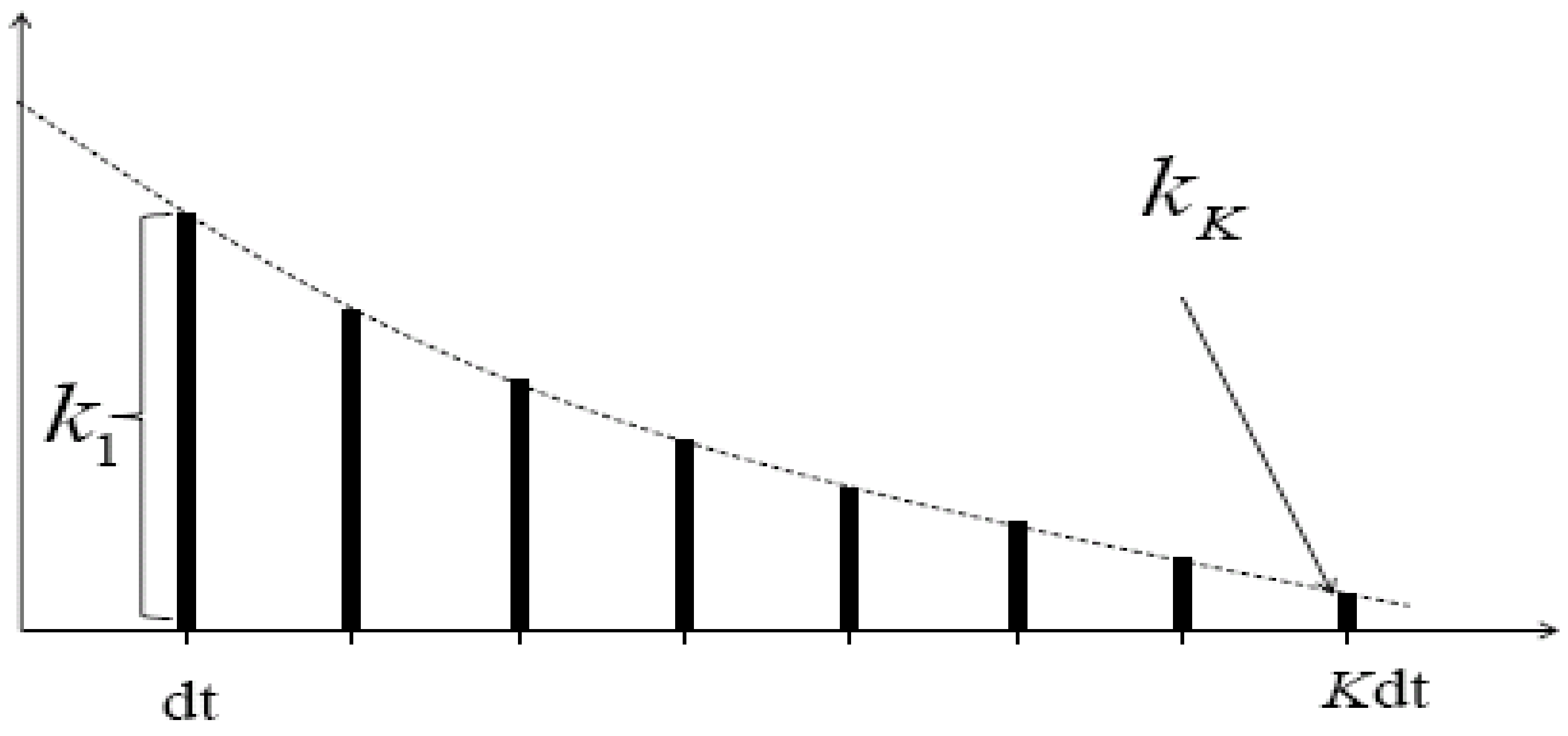
comparison model-data

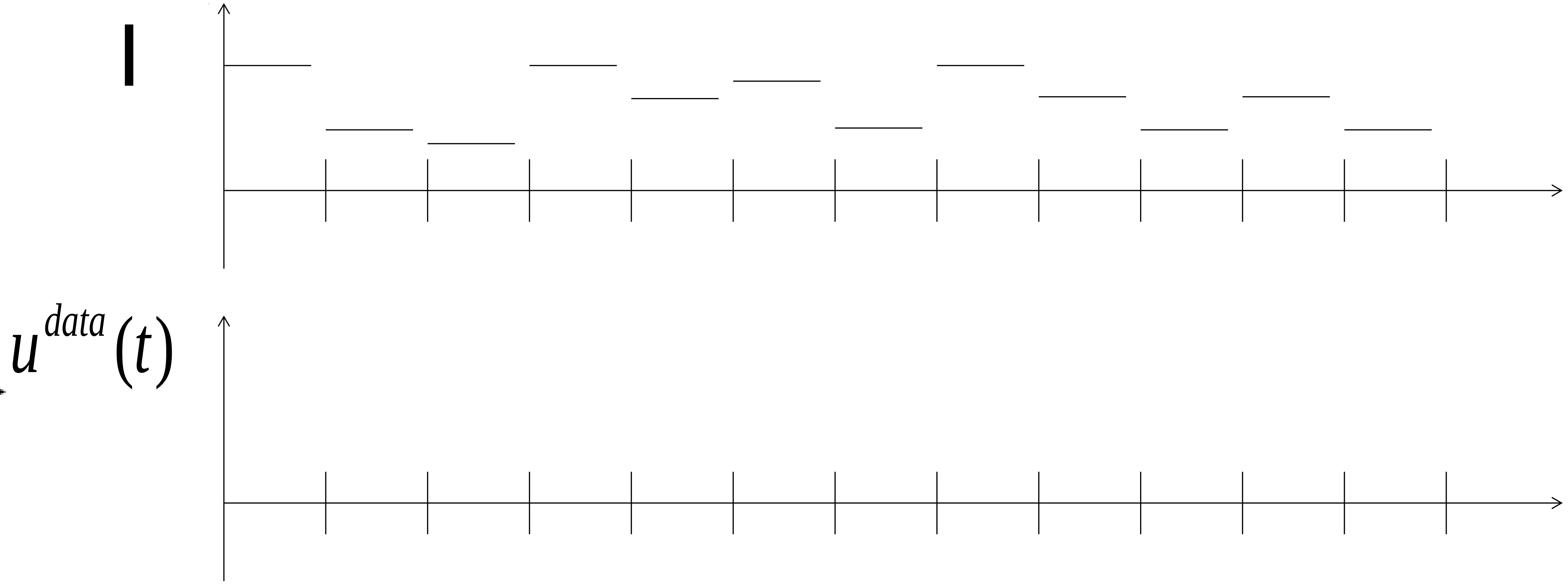


Linear in parameters = linear fit

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

$$u(t_n) = \sum k_k I_{n-k} + u_{rest}$$





$$E = \sum_n [u^{data}(t_n) - \sum_{k=1}^{K} k_k I_{n-k} - u_{rest}]^2$$

Linear in parameters = linear fit = quadratic optimization

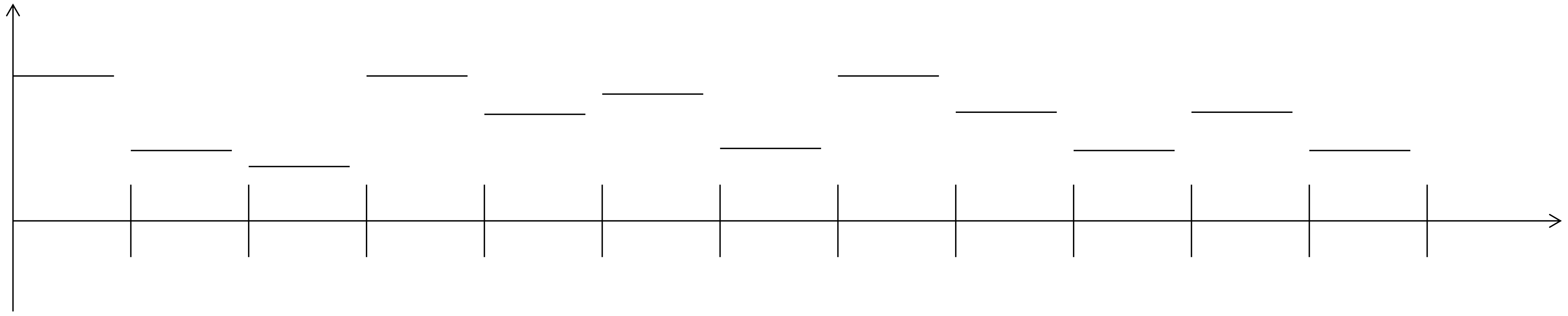
Model

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

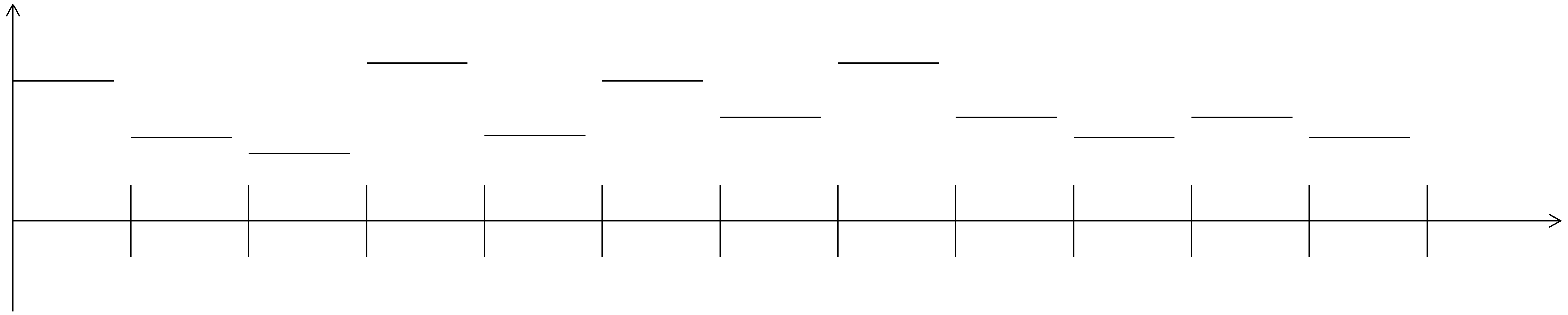
$$u(t_n) = \sum_k k_k \, I_{n-k} + u_{rest}$$

Data $u^{data}(t)$

I



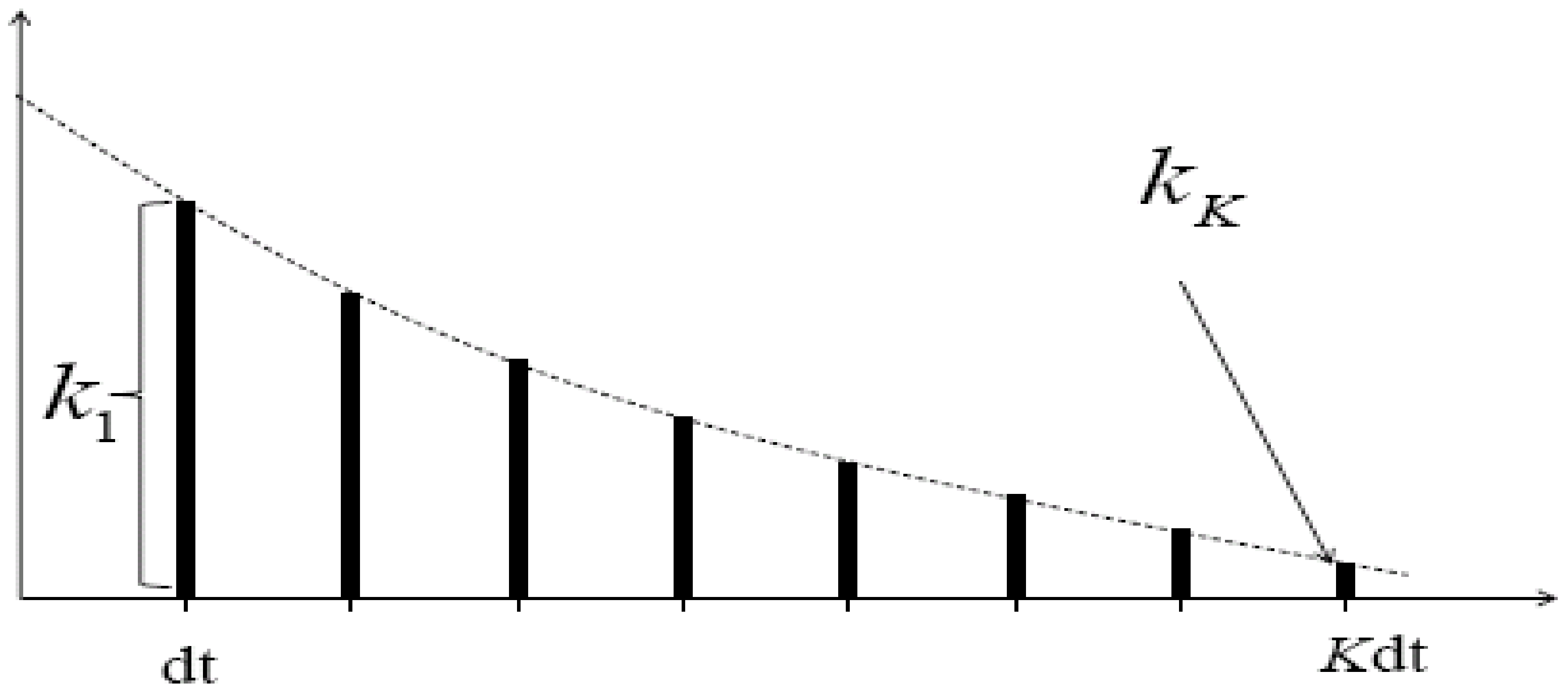
$u^{data}(t)$



$$E = \sum_n [u^{data}(t_n) - \sum_{k=1}^{K} k_k \, I_{n-k} - u_{rest}]^2$$

Vector notation

$$u(t_n) = \sum_k k_k I_{n-k} + u_{rest}$$



$$u(t_n) = \vec{k} \cdot \vec{x}_n$$

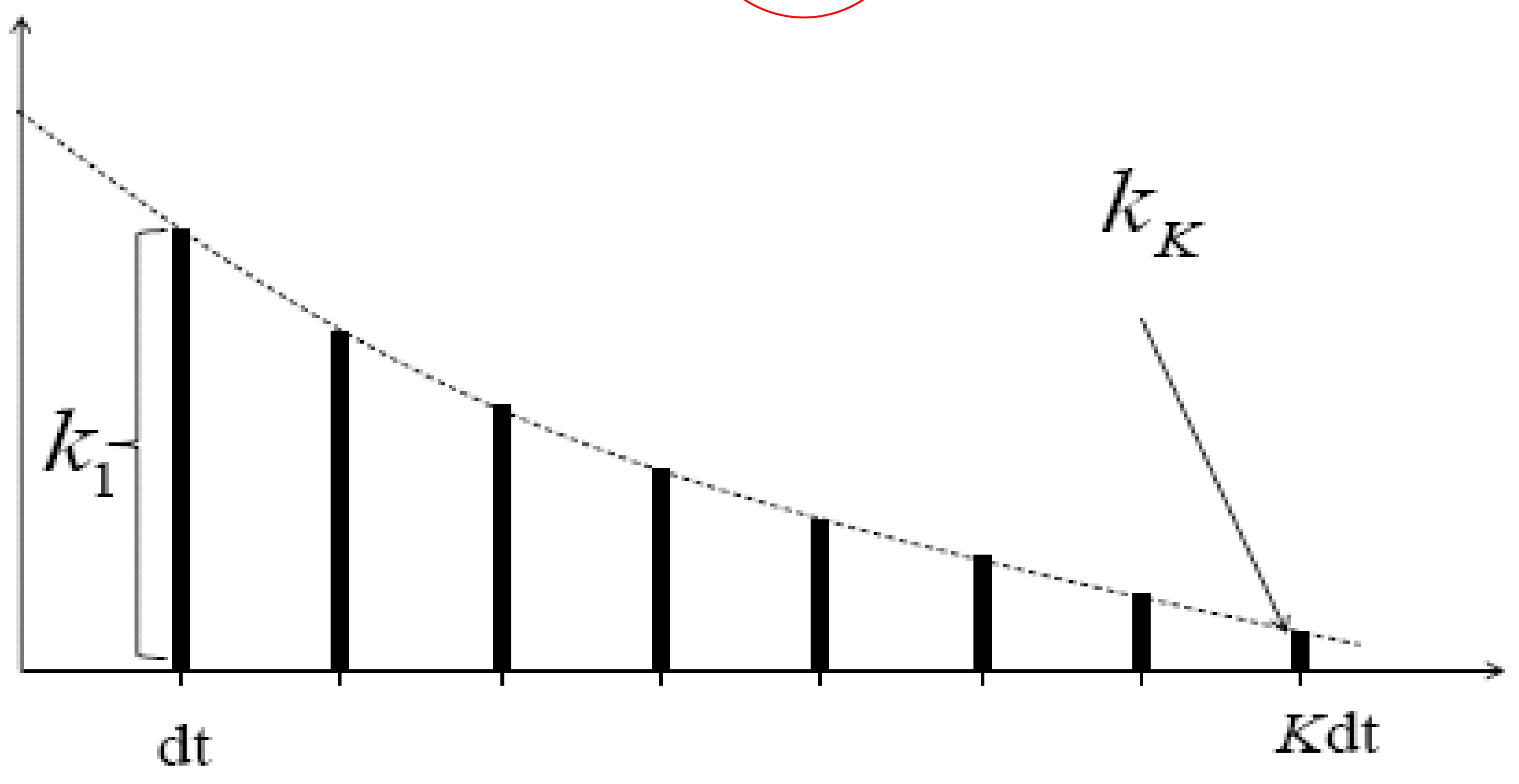
$$E = \sum_n [u^{data}(t_n) - \sum_{k=1}^{K} k_k I_{n-k} - u_{rest}]^2$$

Linear in parameters = linear fit = quadratic problem

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

$$u(t_n) = \sum k_k\, I_{n-k} + u_{rest}$$

$$u(t_n) = \vec{k} \cdot \vec{x}_n$$



$$\begin{array}{c|c}
\text{time} \backslash \text{input } \vec{\mathbf{x}} & \begin{array}{ccccc} x_1 & x_2 & x_3 & \dots & x_K \end{array} \\
\hline
\begin{array}{c} t=K+1 \\ t=K+2 \\ t=K+3 \\ . \\ . \\ . \\ t=T \end{array} &
\begin{pmatrix}
I_K & I_{K-1} & I_{K-2} & \dots & I_1 \\
I_{K+1} & I_K & I_{K-1} & \dots & I_2 \\
I_{K+2} & I_{K+1} & I_K & \dots & I_3 \\
 & & & & \\
 & & & & \\
 & & & & \\
I_T & I_{T-1} & I_{T-2} & \dots & I_{T-K+1}
\end{pmatrix} \mathrm{d}t
\end{array}$$

$$E = \sum_n \left[u^{data}(t_n) - \sum_{k=1}^{K} k_k\, I_{n-k} - u_{rest}\right]^2$$

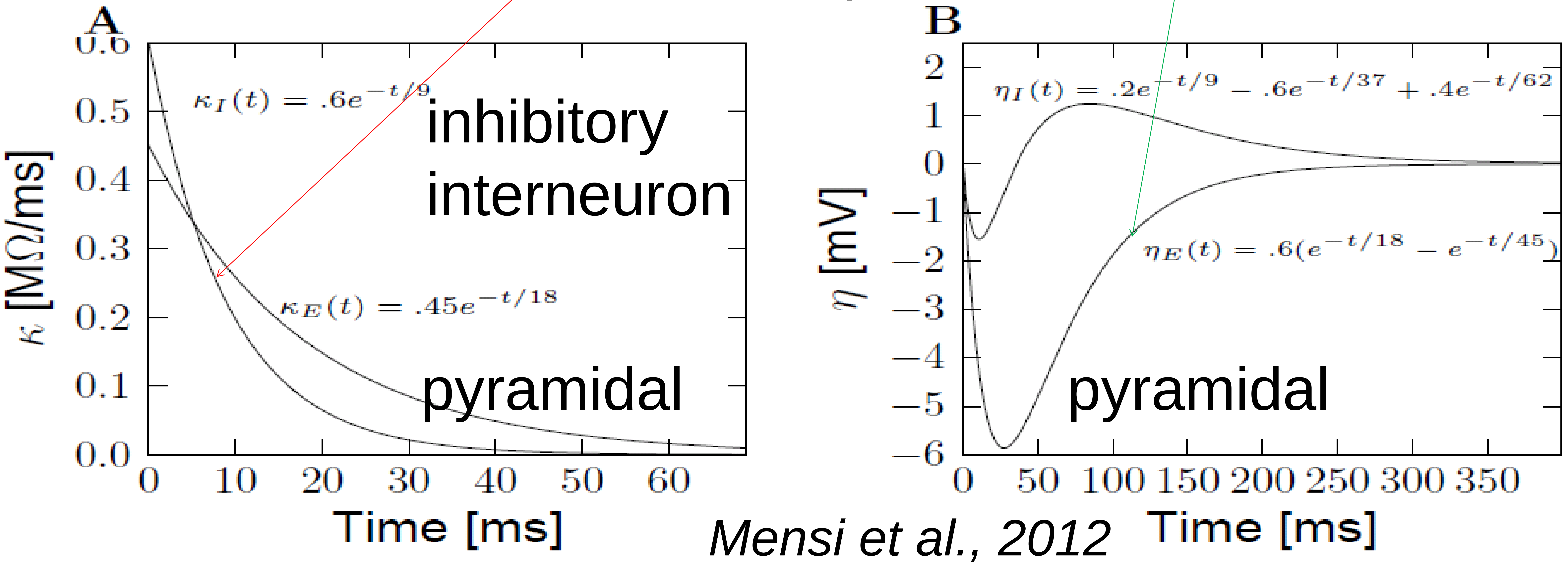
Neuronal Dynamics – 7.5 Extracted parameters: voltage

Subthreshold potential

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

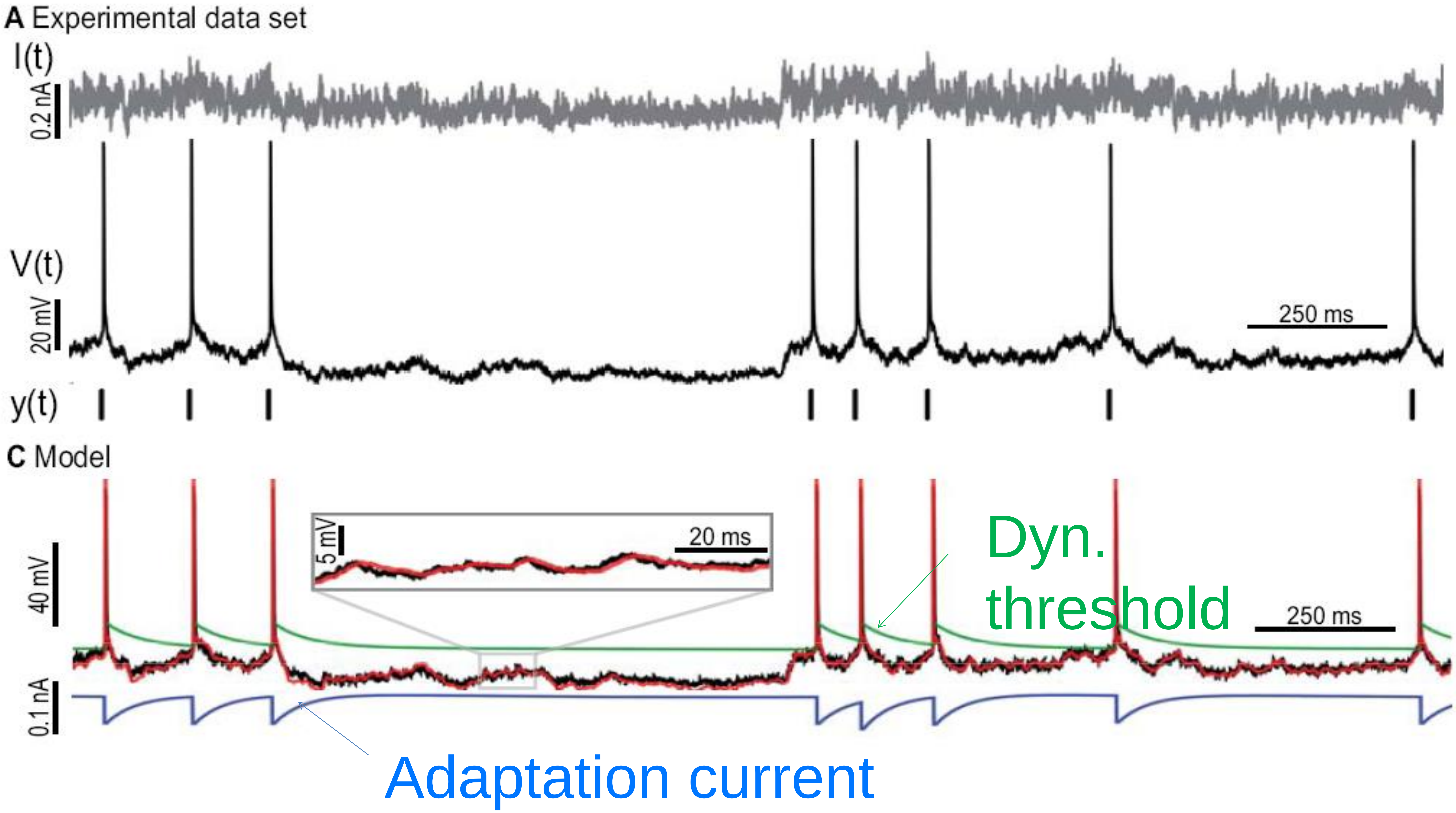
known input

known spike train



Mensi et al., 2012

Fitting models to data: so far ‘subthreshold’

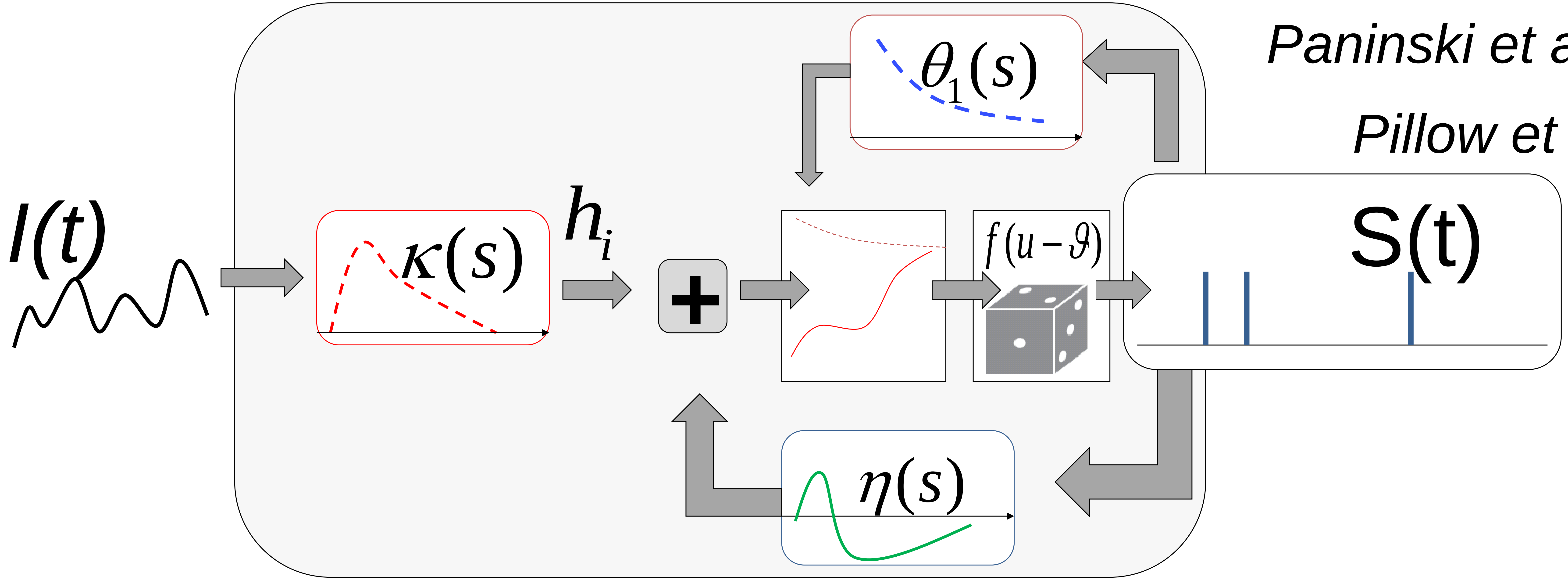


Neuronal Dynamics – 7.5 Threshold: Predicting spike times

Jolivet&Gerstner, 2005

Paninski et al., 2004

Pillow et al. 2008



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

threshold $\vartheta(t) = \theta_0 + \int \theta_1(s) S(t-s) ds$

firing intensity $\rho(t) = f(u(t) - \vartheta(t))$

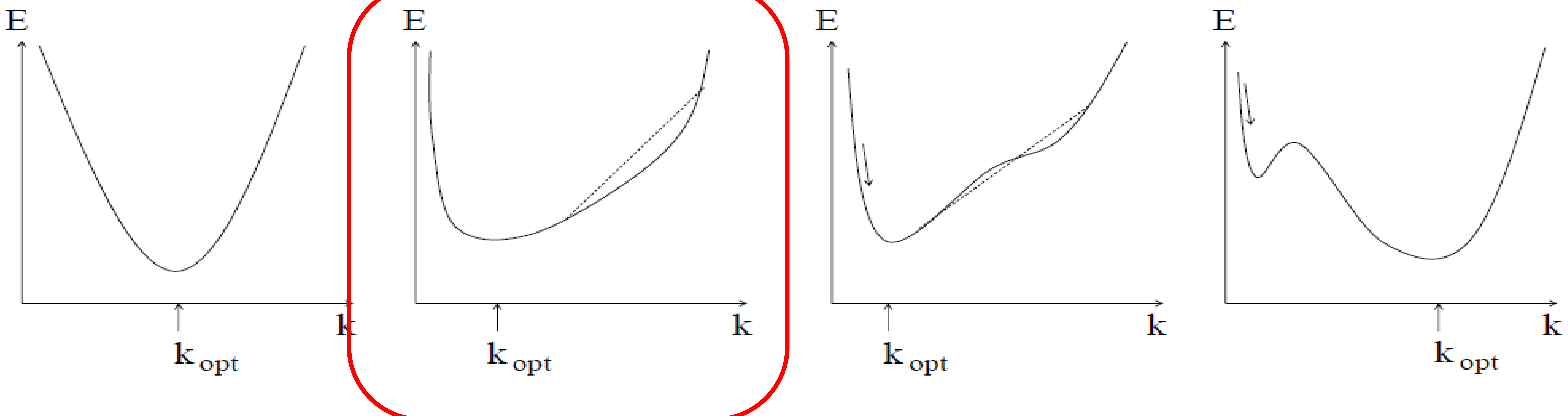
Neuronal Dynamics – 7.5 Generalized Linear Model (GLM)

$$\log L(t^1,\ldots,t^N) = -\int_0^T \rho(t')dt' + \sum_f \log\rho(t^f) = -E$$

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

threshold $\vartheta(t) = \theta_0 + \int \underline{\theta_1(s)} S(t-s)ds$

firing intensity $\rho(t) = f(u(t) - \vartheta(t))$



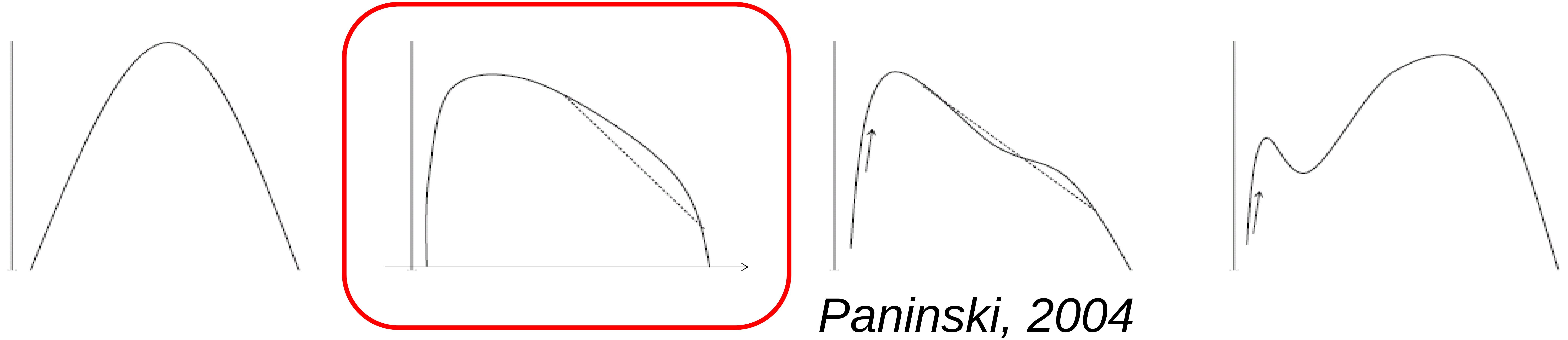
Neuronal Dynamics – 7.5 GLM: concave error function

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

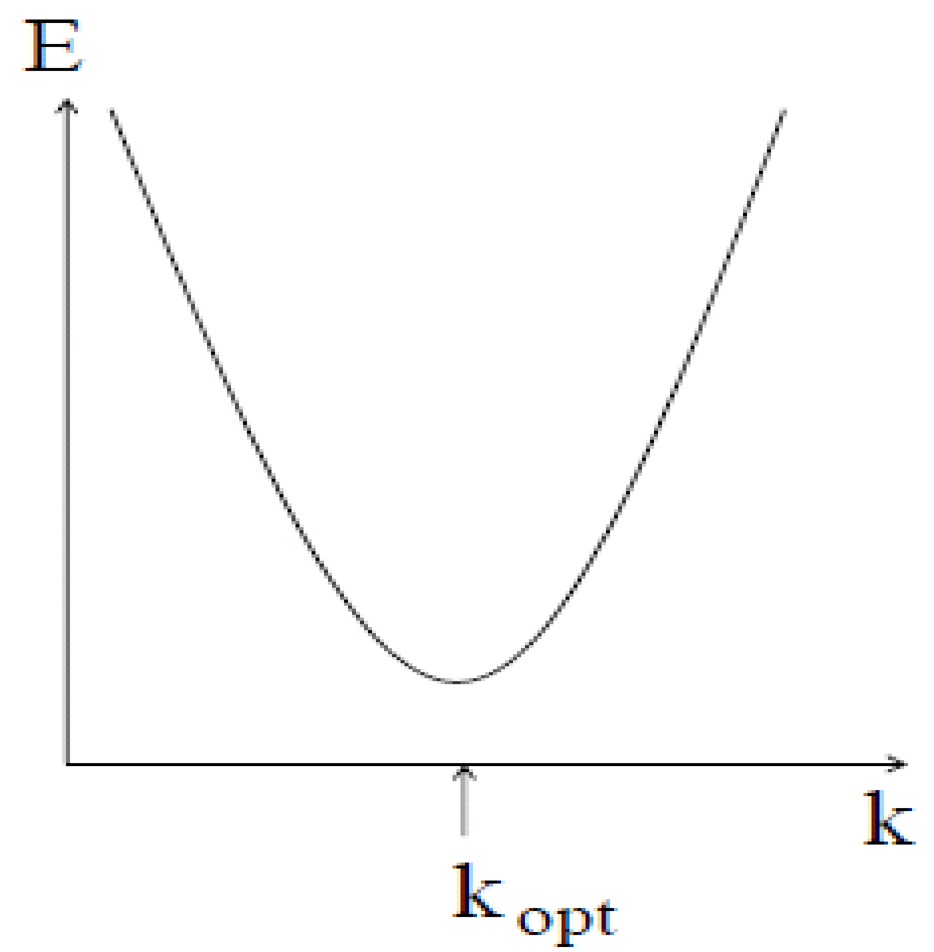
threshold $\vartheta(t) = \theta_0 + \int \underline{\theta_1(s)} S(t-s)ds$

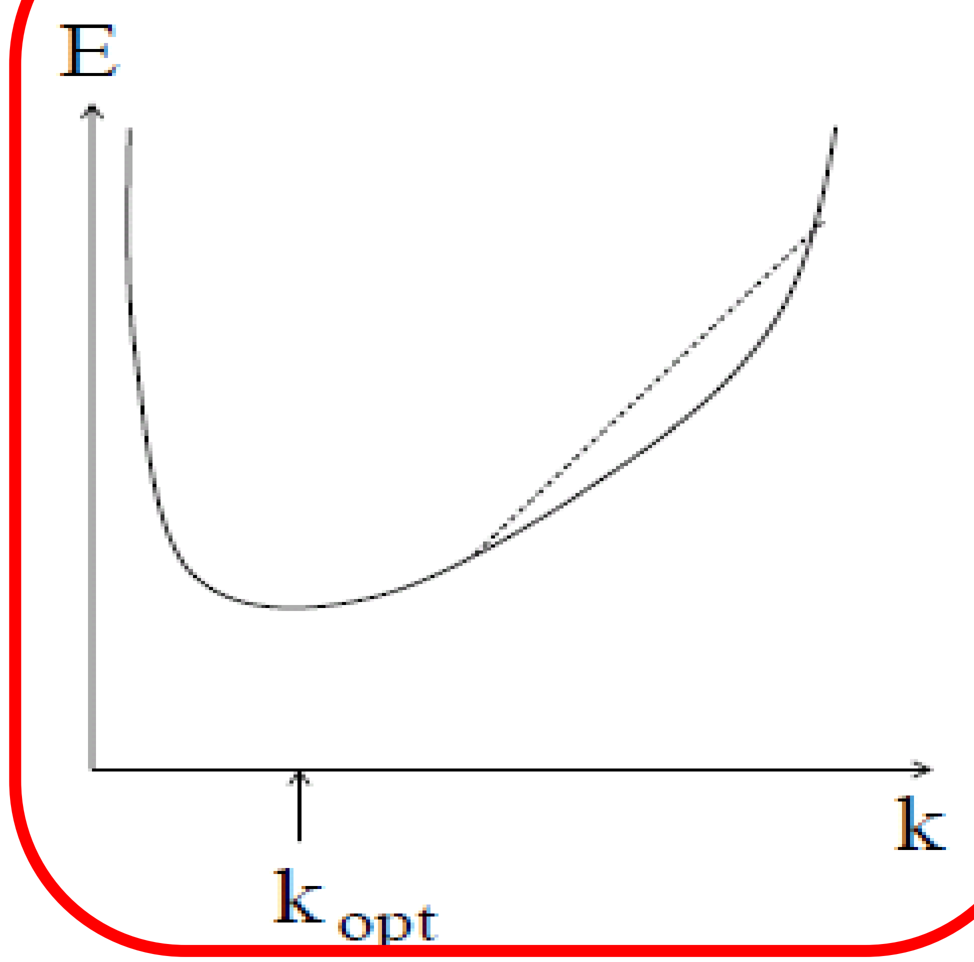
firing intensity $\rho(t) = f(u(t) - \vartheta(t))$

$$\log L(t^1, \ldots, t^N) = -\int_0^T \rho(t')dt' + \sum_f \log \rho(t^f)$$



Paninski, 2004





Voltage/subthreshold

- linear in parameters
  → quadratic error function

Voltage/subthreshold

- nonlinear, but GLM
  → convex error function

Exercise 5 NOW: optimize 1 free parameter

Model

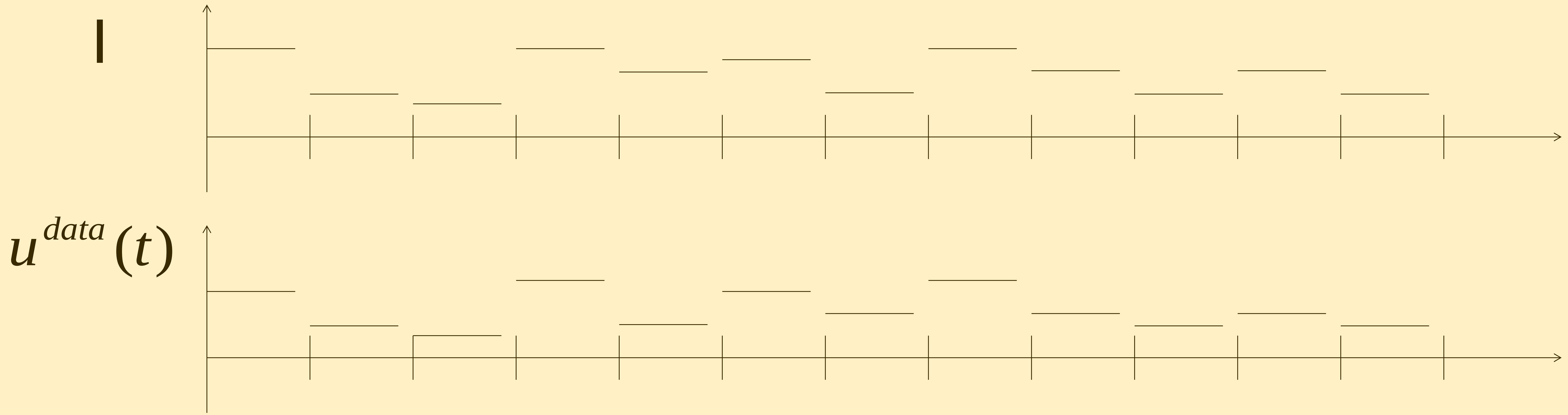
$$u_n = RI_n$$

Data

$$u^{data}(t_n)$$

Optimize parameter R, so as to have a minimal error

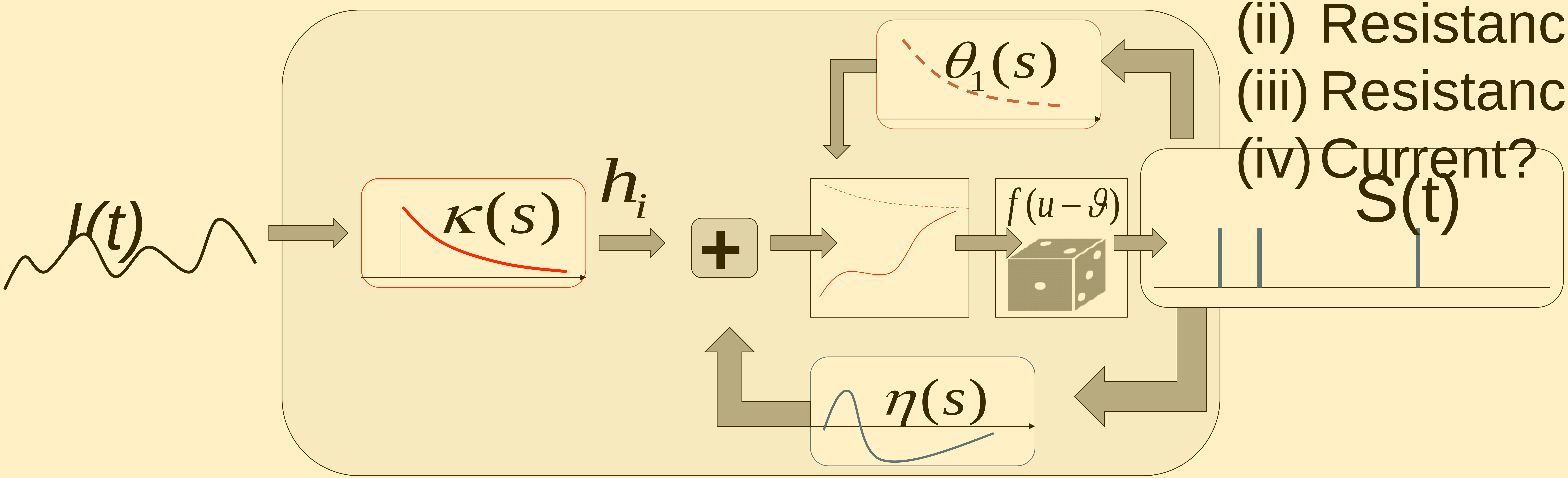
$$E = \sum_n [u^{data}(t_n) - RI_n]^2$$



Exercise 6 NOW – question 1:

What are the units of $\kappa(s)$?

(i) Voltage?
(ii) Resistance?
(iii) Resistance/s?
(iv) Current?



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

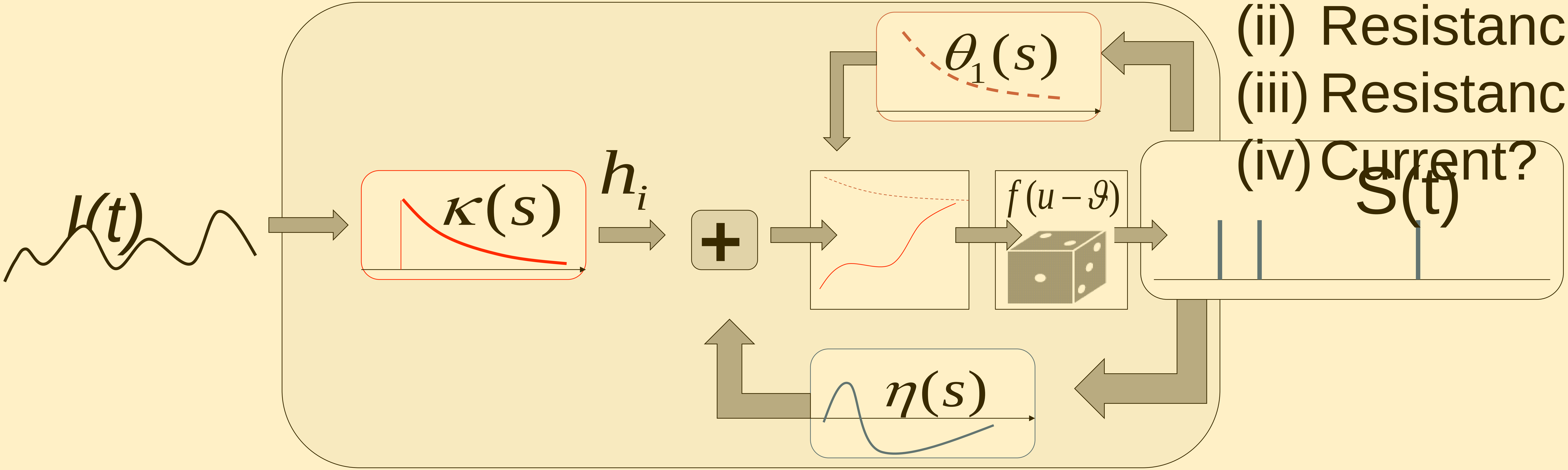
threshold $\vartheta(t) = \theta_0 + \int \theta_1(s) S(t-s) ds$

firing intensity $\rho(t) = f(u(t) - \vartheta(t))$

Exercise 6 NOW – question 2:

What are the units of $\eta(s)$?

(i) Voltage?
(ii) Resistance?
(iii) Resistance/s
(iv) Current?



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

threshold $\vartheta(t) = \theta_0 + \int \underline{\theta_1(s)} S(t-s)ds$

firing intensity $\rho(t) = f(u(t) - \vartheta(t))$

Week 7 – part 6 : Parameter estimation

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Neuronal Dynamics:
Computational Neuroscience of Single Neurons

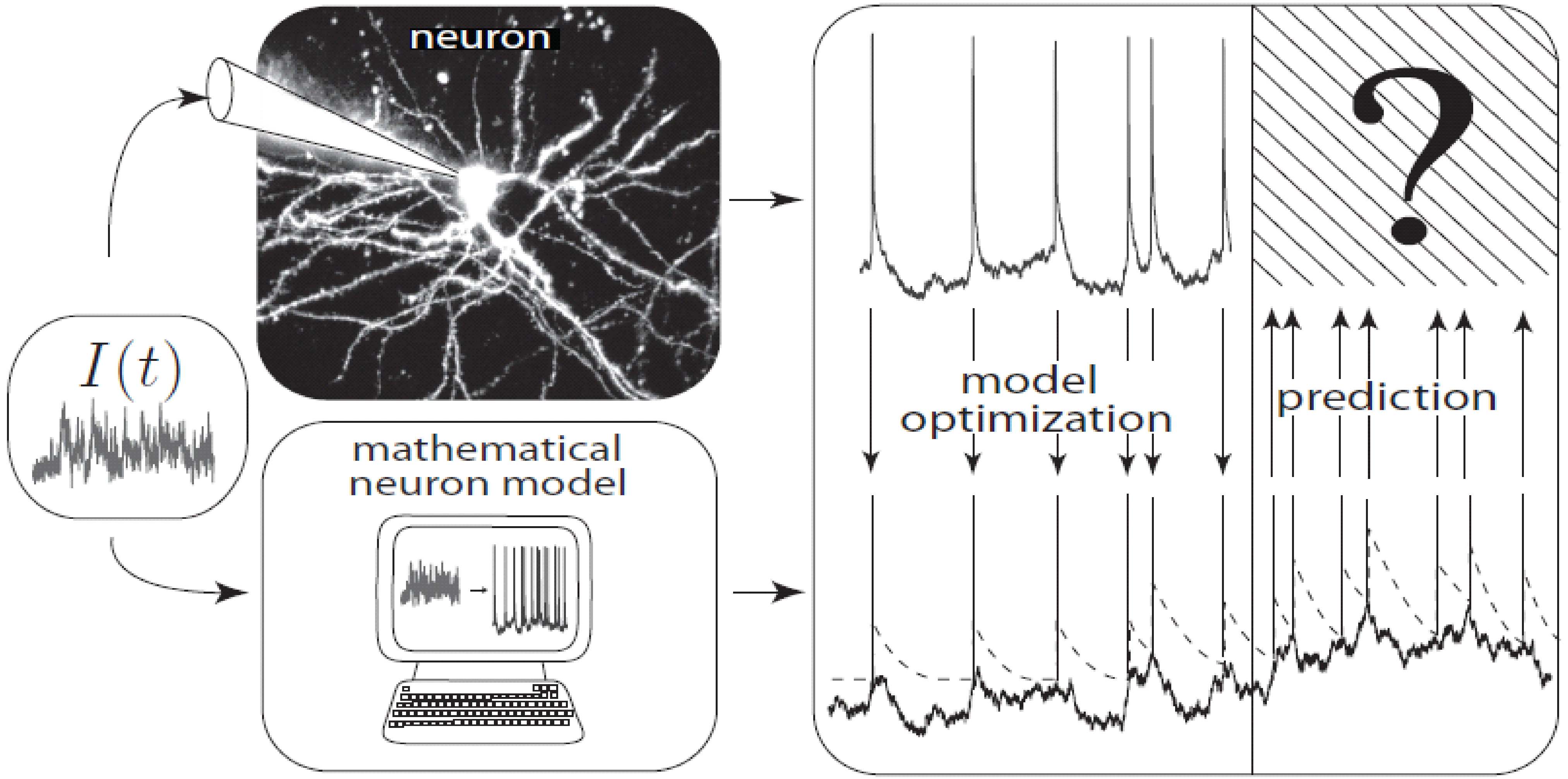
Week 7 – Optimizing Neuron Models For Coding and Decoding

Wulfram Gerstner

EPFL, Lausanne, Switzerland

- 7.1 What is a good neuron model?
  - Models and data
- 7.2 AdEx model
  - Firing patterns and analysis
- 7.3 Spike Response Model (SRM)
  - Integral formulation
- 7.4 Generalized Linear Model (GLM)
  - Adding noise to the SRM
- 7.5 Parameter Estimation
  - Quadratic and convex optimization
- 7.6. Modeling in vitro data
  - how long lasts the effect of a spike?
- 7.7. Helping Humans

comparison model-data



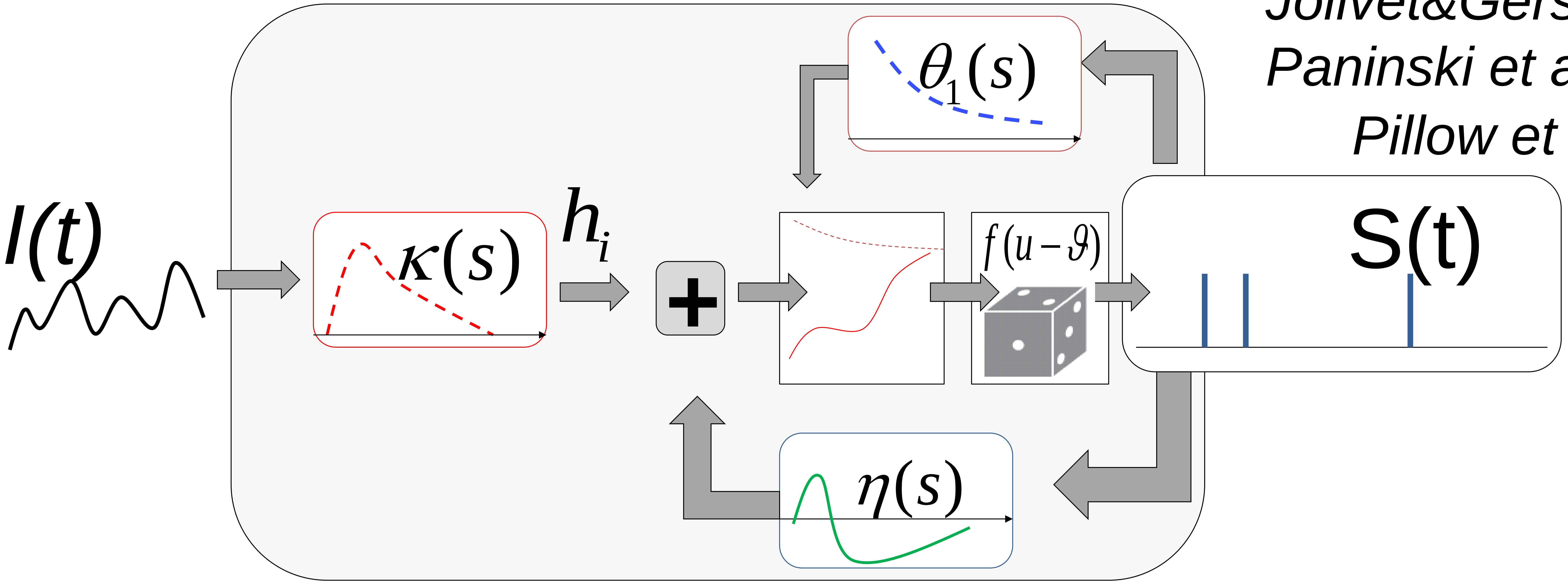
Predict

-Subthreshold voltage

-Spike times

Neuronal Dynamics – 7.6 GLM/SRM with escape noise

Jolivet&Gerstner, 2005
Paninski et al., 2004
Pillow et al. 2008



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

threshold $\vartheta(t) = \theta_0 + \int \theta_1(s) S(t-s)ds$

firing intensity $\rho(t) = f(u(t) - \vartheta(t))$

Neuronal Dynamics – 7.6 GLM/SRM predict subthreshold voltage

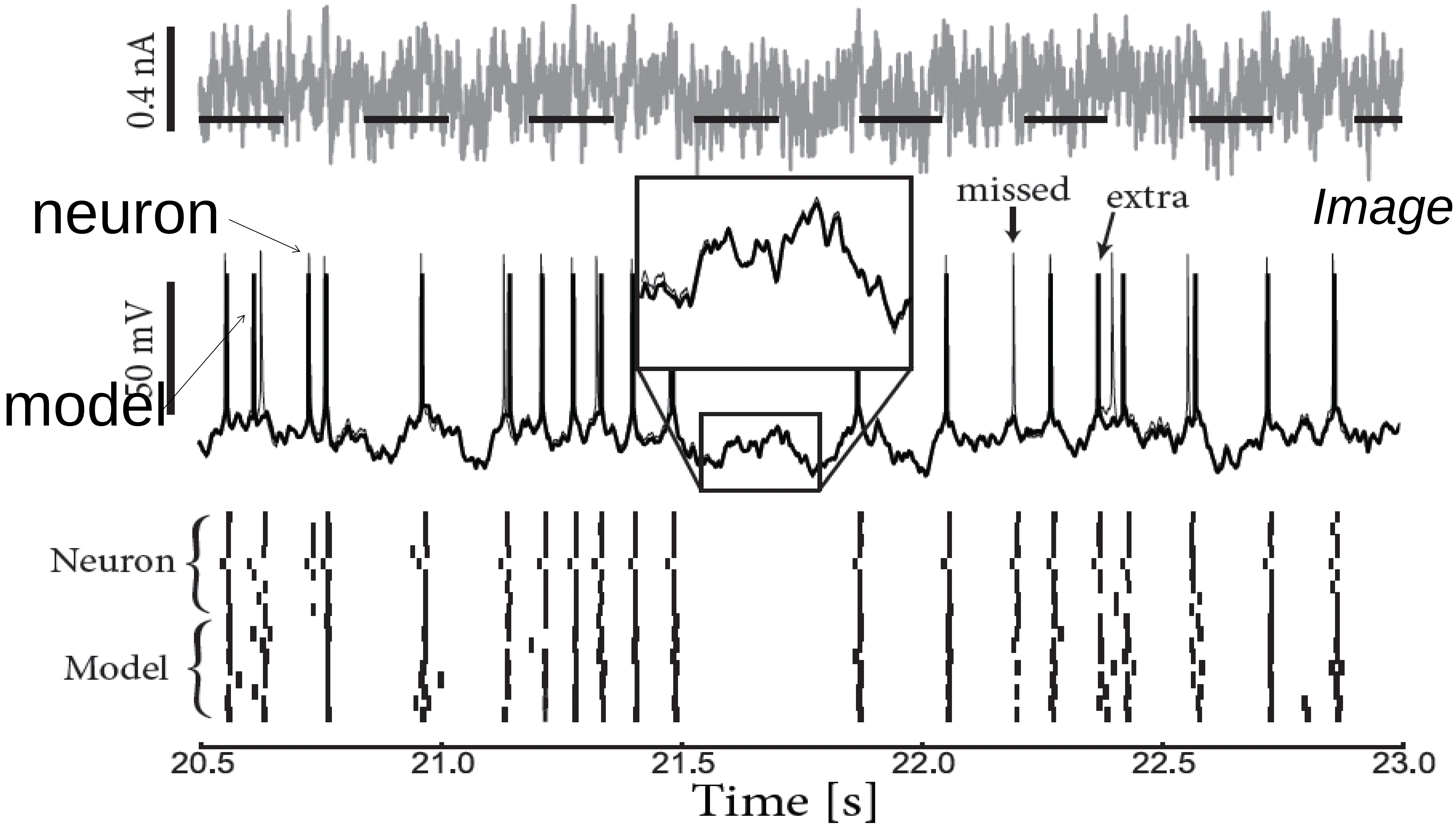
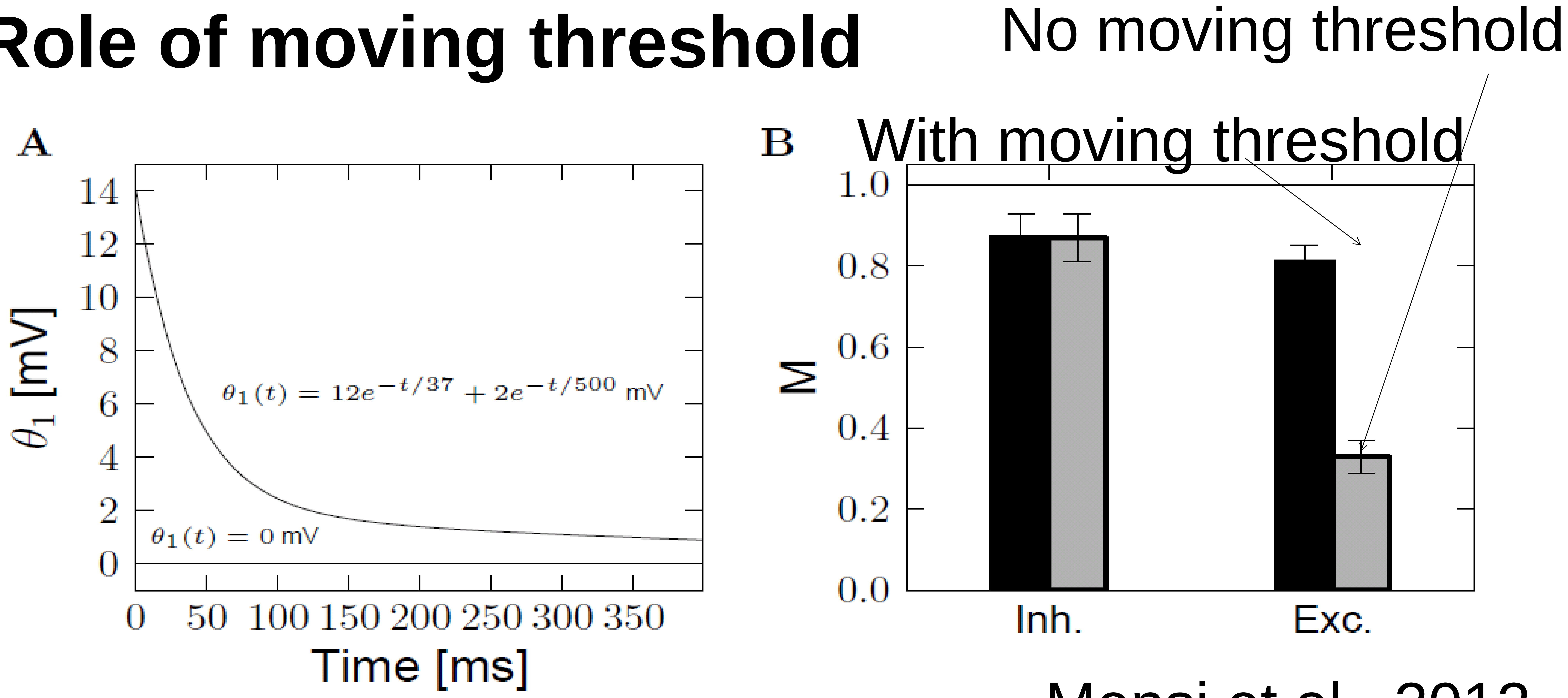


Image:Mensi et al.

Role of moving threshold



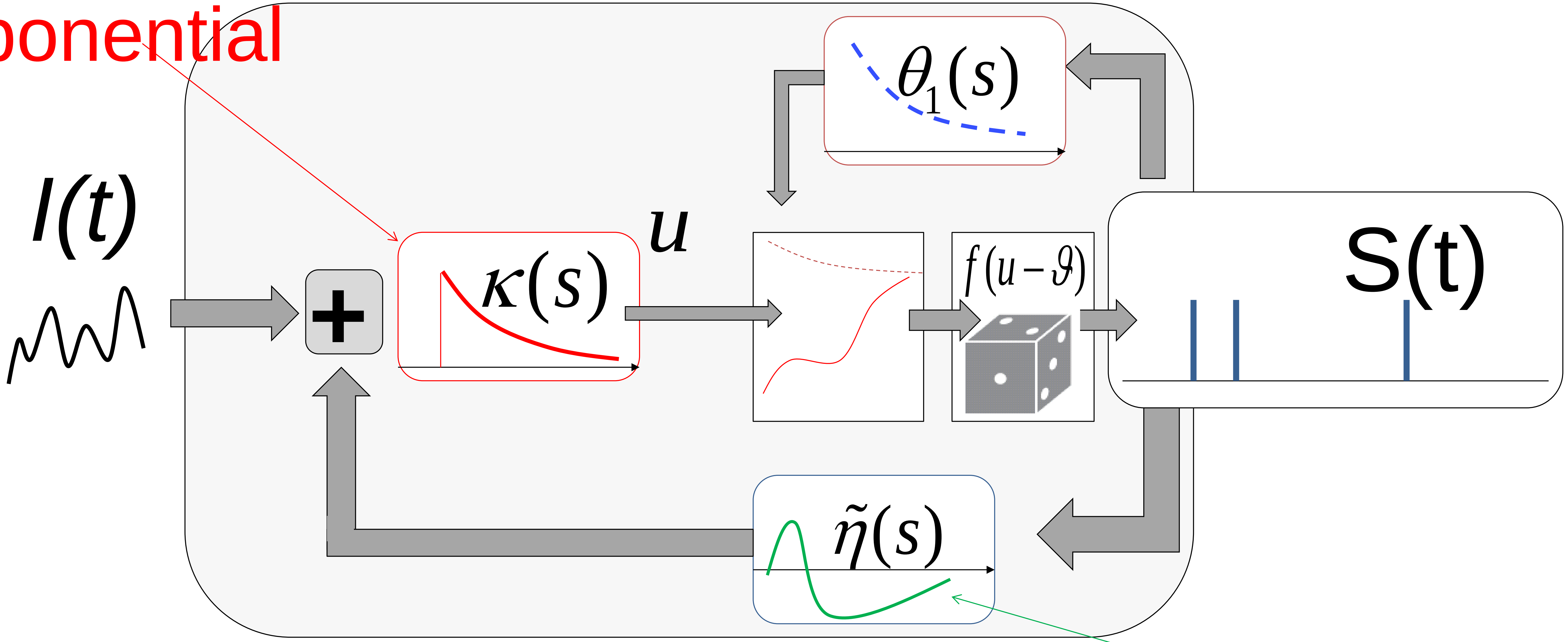
Mensi et al., 2012

Change in model formulation:

What are the units of .... ?

'soft-threshold adaptive IF model'

exponential



adaptation current

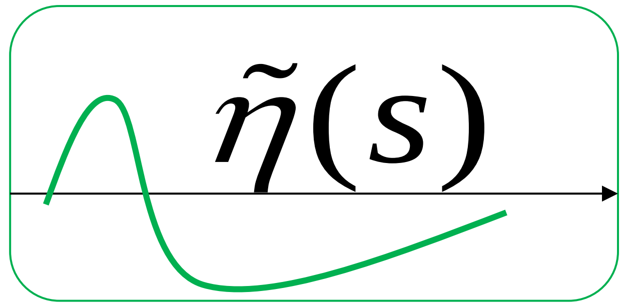
potential $$C\frac{d}{dt}u(t) = \int \tilde{\eta}(s)S(t-s)ds \quad +I(t)$$

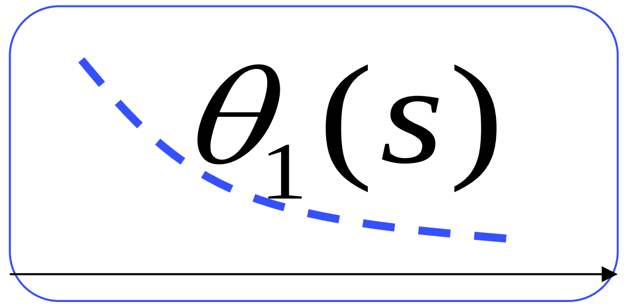
threshold $$\vartheta(t) = \theta_0 + \int \theta_1(s)S(t-s)ds$$

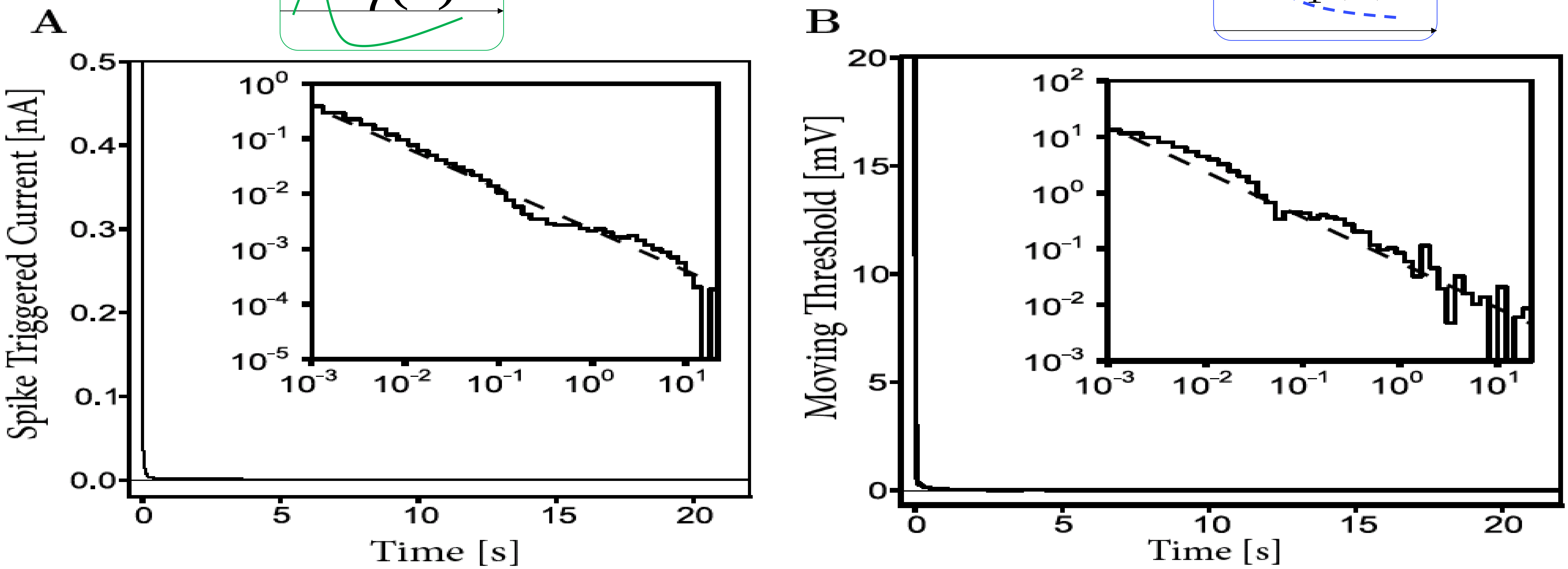
firing intensity $$\rho(t) = f(u(t) - \vartheta(t))$$

Time scale of filters?

→ **Power law**

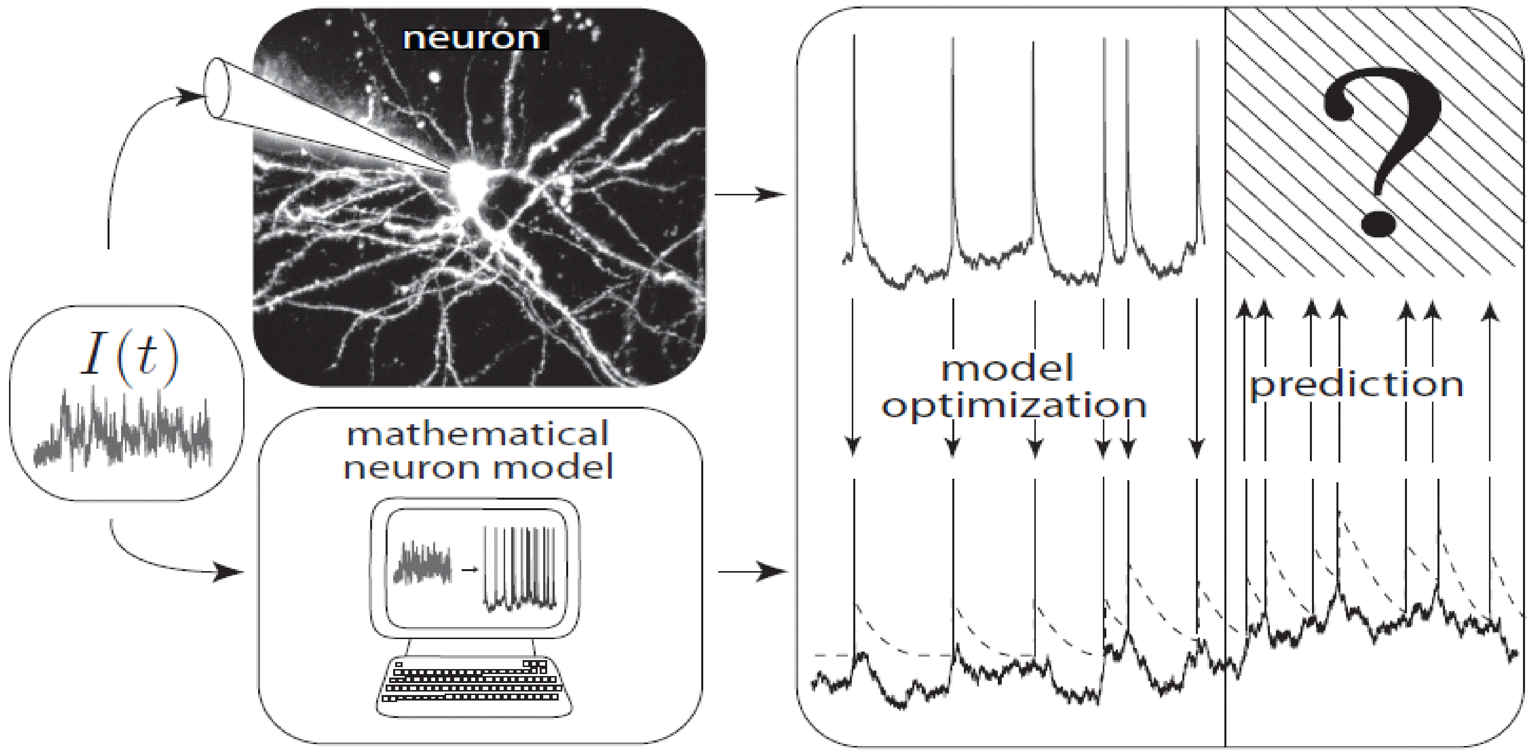






Pozzorini et al. 2013

A single spike has a measurable effect more than 10 seconds later!



-Predict spike times
-Predict subthreshold voltage
-Easy to interpret (not a ‘black box’)
-Variety of phenomena
-Systematic: ‘optimize’ parameters

BUT so far limited to in vitro

Week 7 – part 7: Helping Humans

ÉCOLE POLYTECHNIQUE
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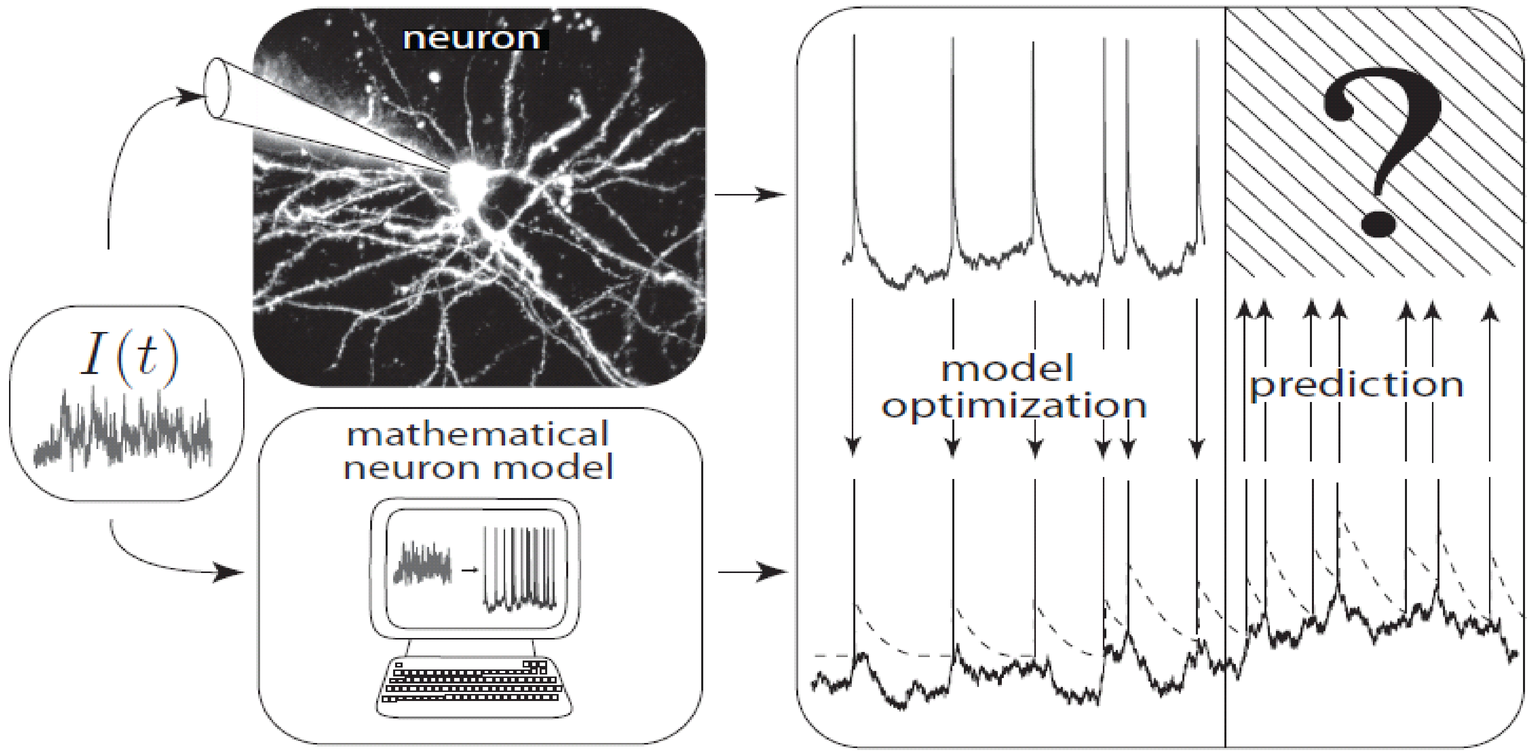
Neuronal Dynamics:
Computational Neuroscience of Single Neurons

Week 7 – Optimizing Neuron Models For Coding and Decoding

Wulfram Gerstner

EPFL, Lausanne, Switzerland

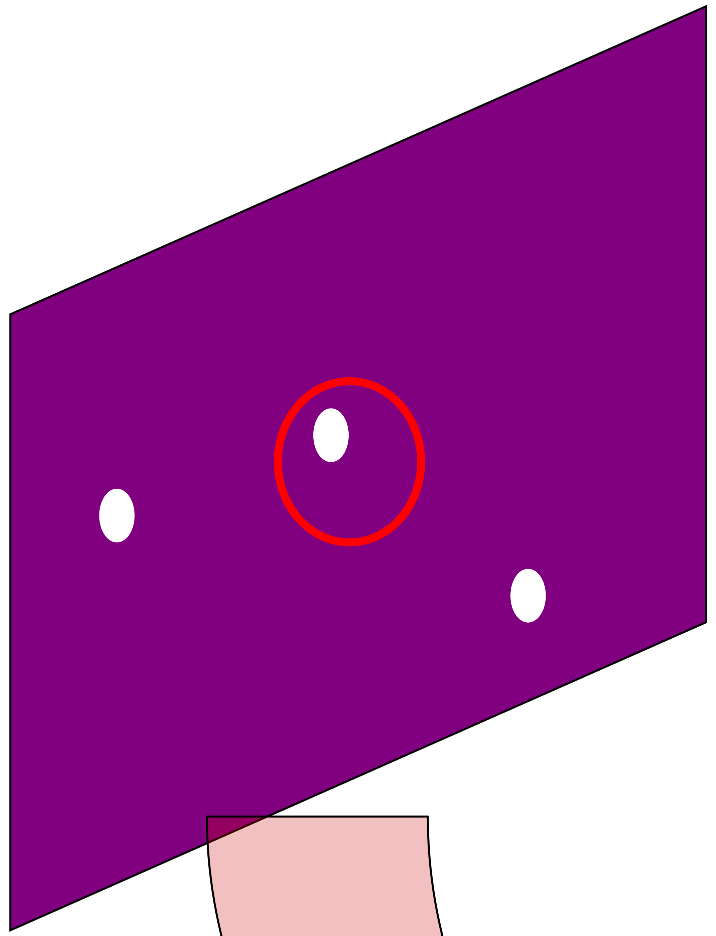
Neuronal Dynamics – Review: Models and Data

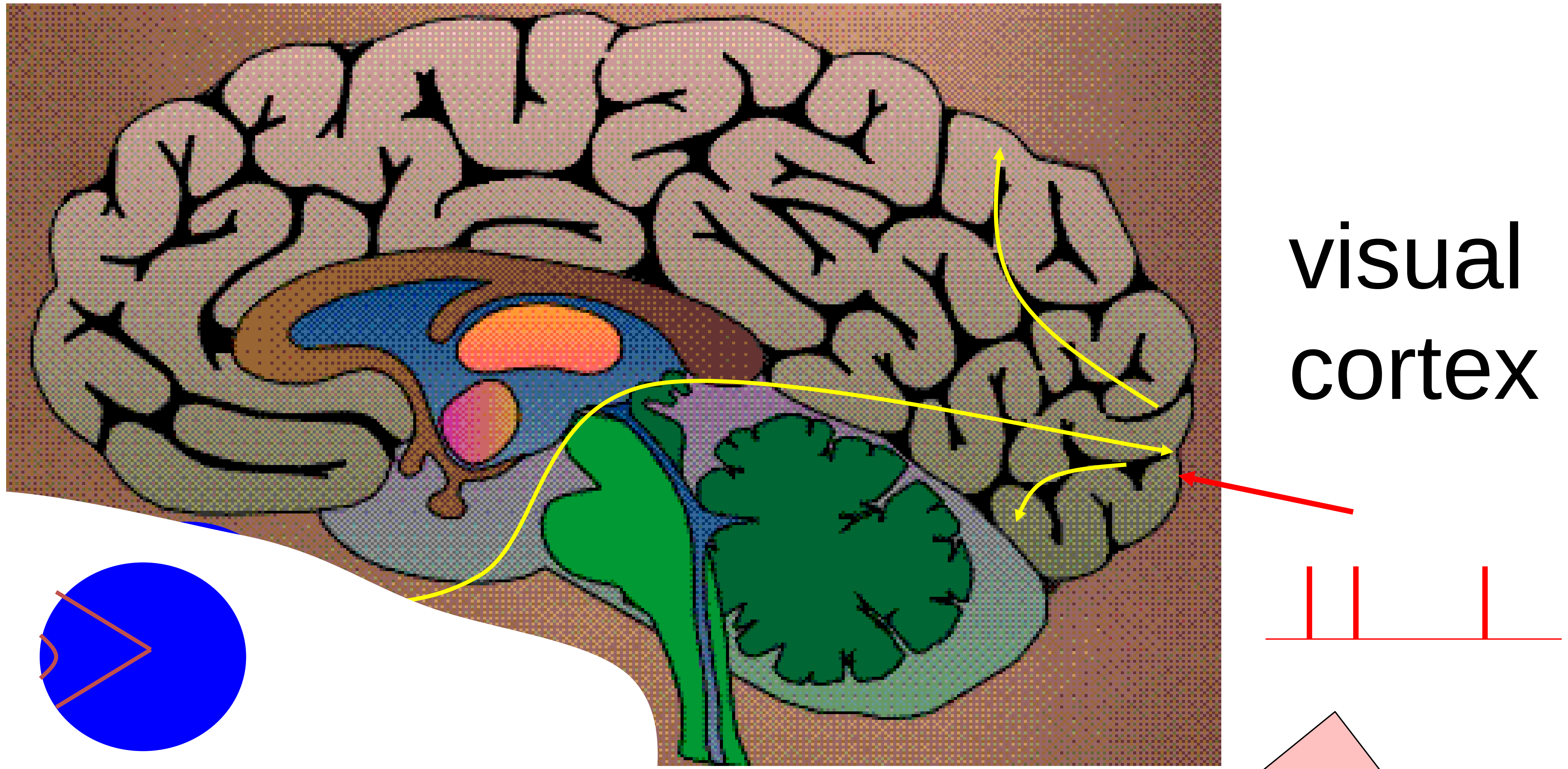


-Predict spike times
-Predict subthreshold voltage
-Easy to interpret (not a 'black box')
-Variety of phenomena
-Systematic: 'optimize' parameters

BUT so far limited to in vitro

Now: extracellular recordings





A) Predict spike times, given stimulus
~~B) Predict subthreshold voltage~~
C) Easy to interpret (not a 'black box')
D) Flexible enough to account for a variety of phenomena
E) Systematic procedure to 'optimize' parameters

Model of 'Encoding'

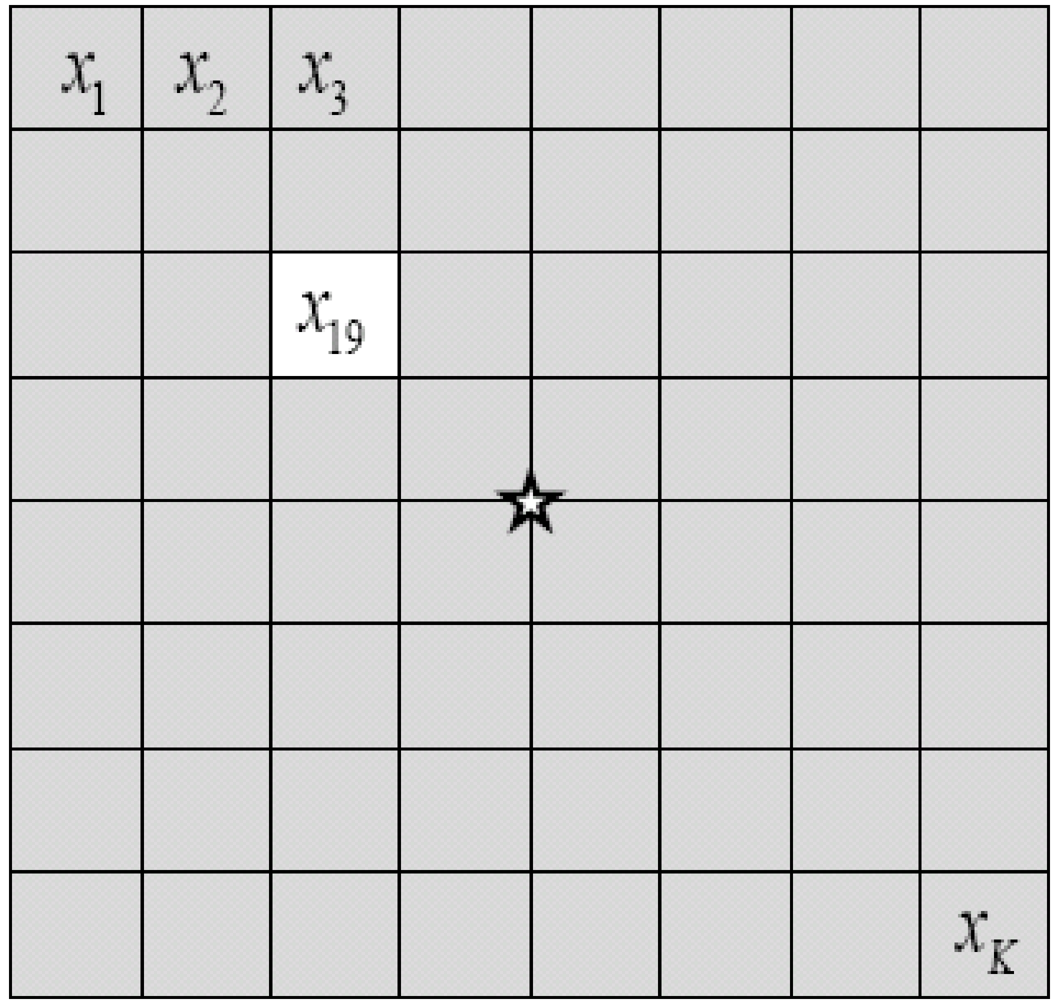
Estimation of spatial (and temporal) receptive fields

$$u(t) = \sum k_k \, I_{K-k} + u_{rest}$$

LNP

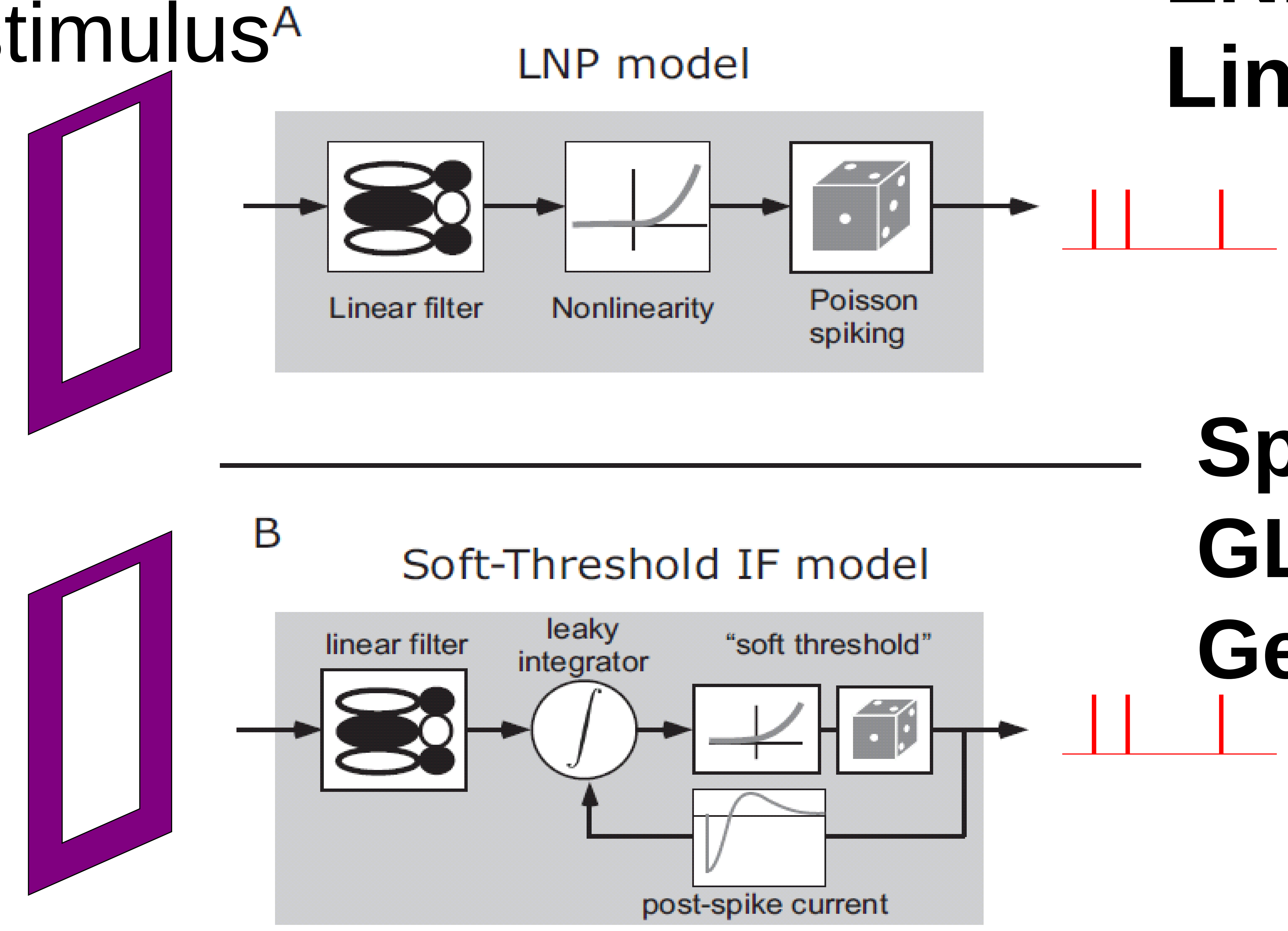
firing intensity $\rho(t) = f\,(u(t) - \vartheta(t))$

$\vec{x}_t = (x_1, \quad x_2, \quad x_3, \quad \ldots, \qquad x_K)$



$$
\begin{array}{c|cccccc}
\text{time} \diagdown \text{input } \vec{\mathbf{x}} & x_1 & x_2 & x_3 & \ldots & & x_K \\
\hline
t=1 & 0 & 1 & 0 & 0 & & 0 \\
t=2 & 0 & 0 & 1 & 0 & & 0 \\
t=3 & 0 & 0 & 0 & 0 & & 1 \\
. & & & & & & \\
. & & & & & & \\
. & & & & & & \\
t=T & 0 & 0 & 0 & 0 & 1 & 0
\end{array}
\quad \mathrm{d}t
$$

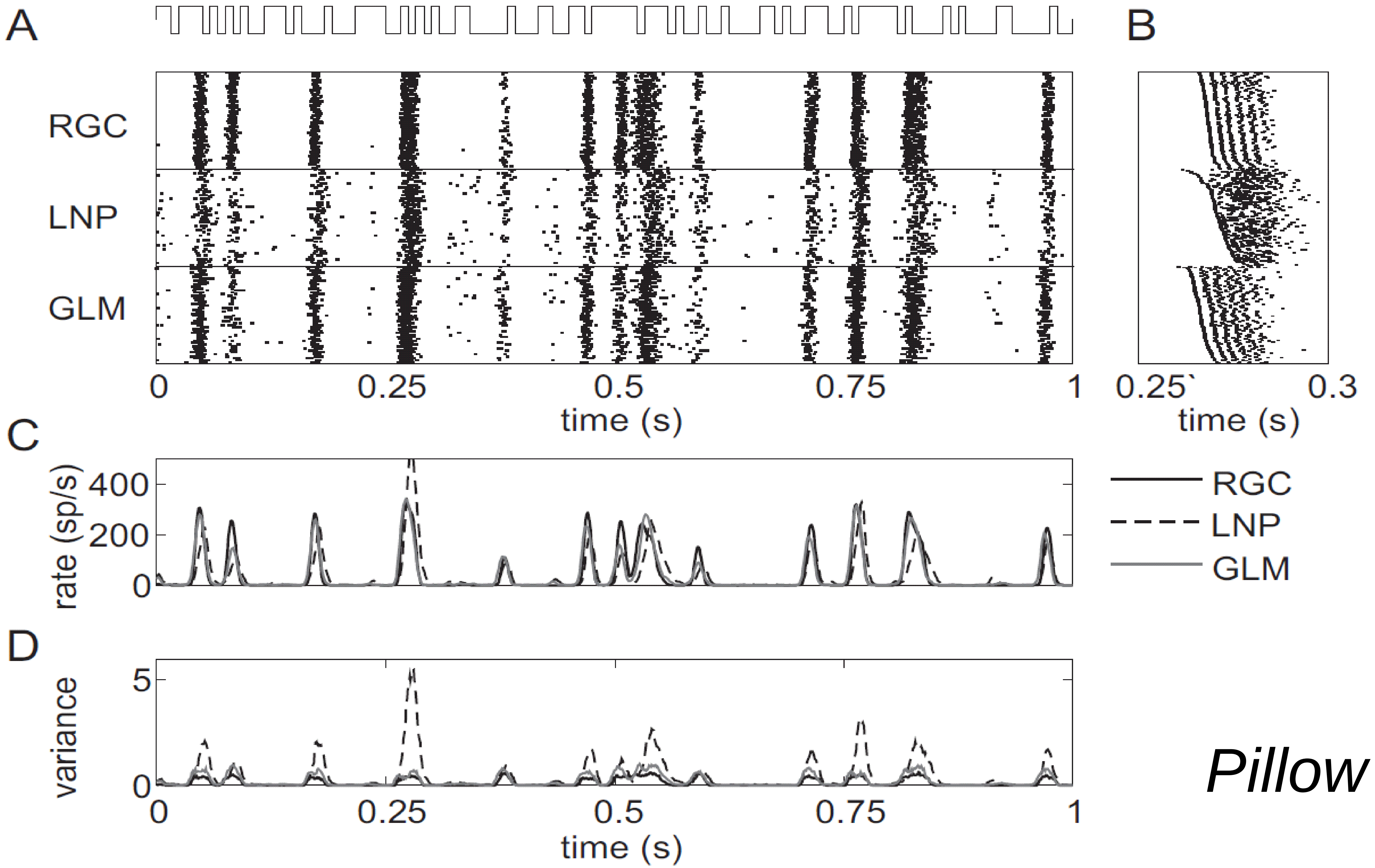
visual stimulus



LNP = Linear-Nonlinear-Poisson

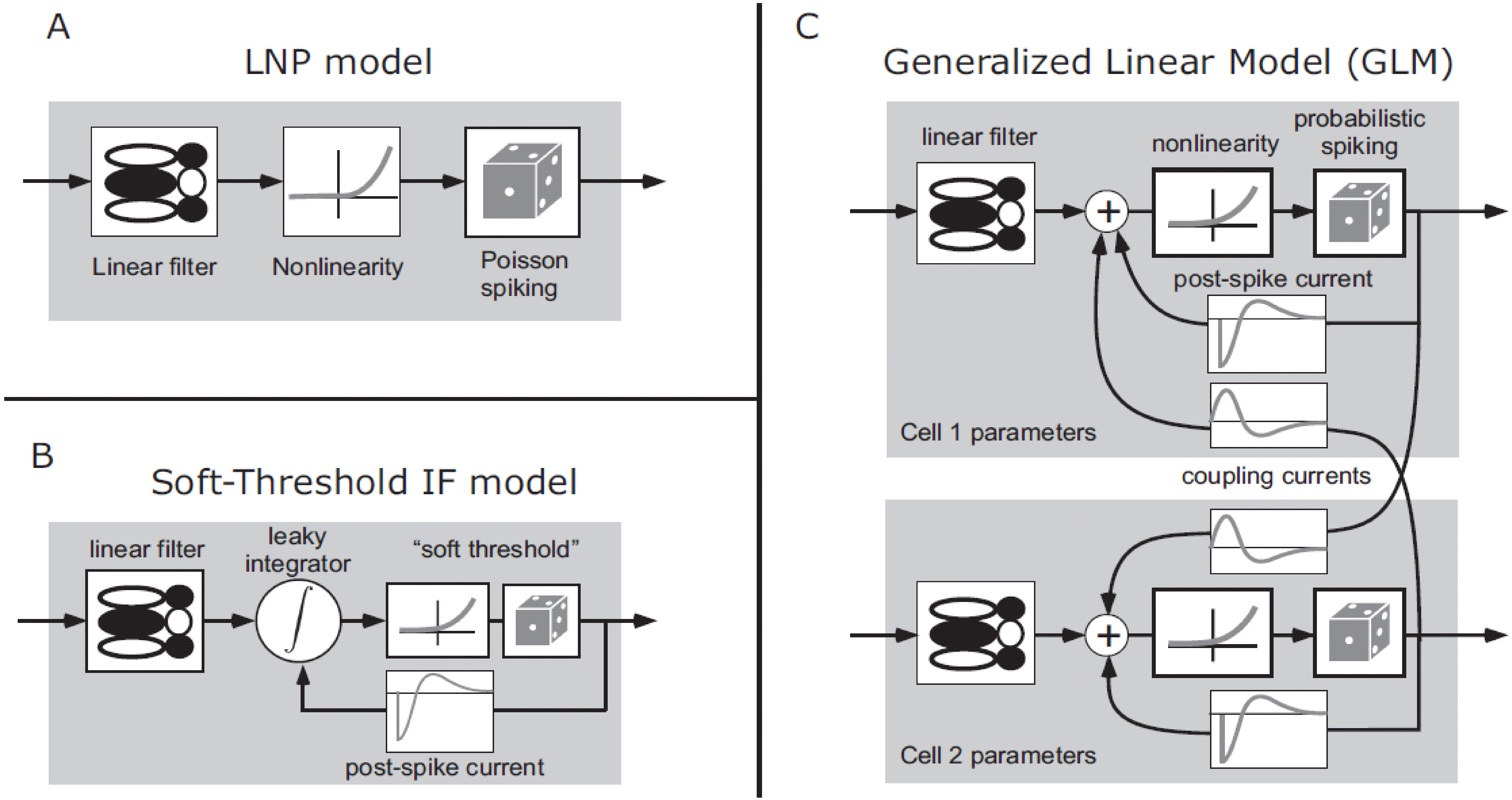
Special case of GLM= Generalized Linear Model

GLM for prediction of retinal ganglion ON cell activity

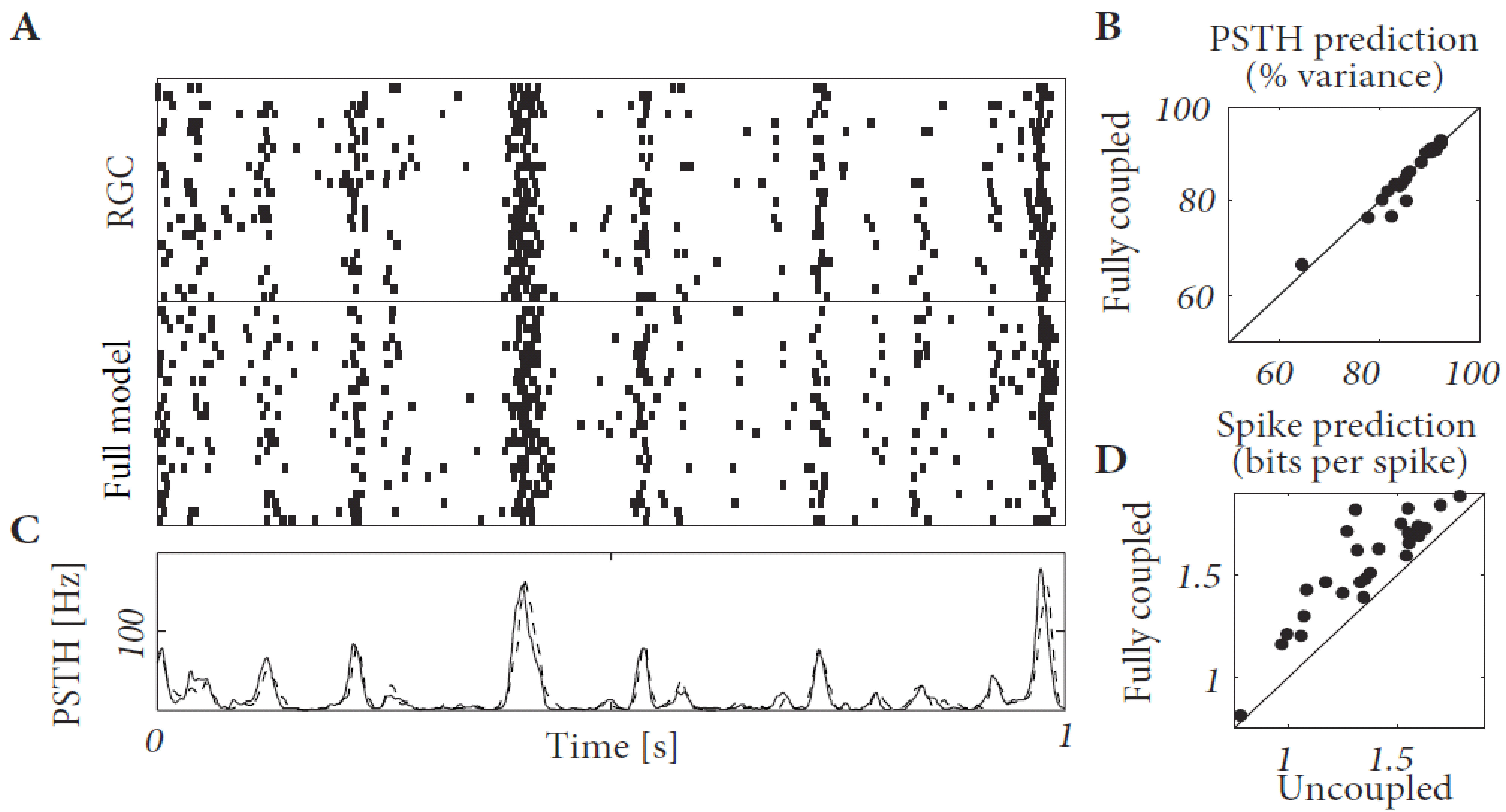


Pillow et al. 2008

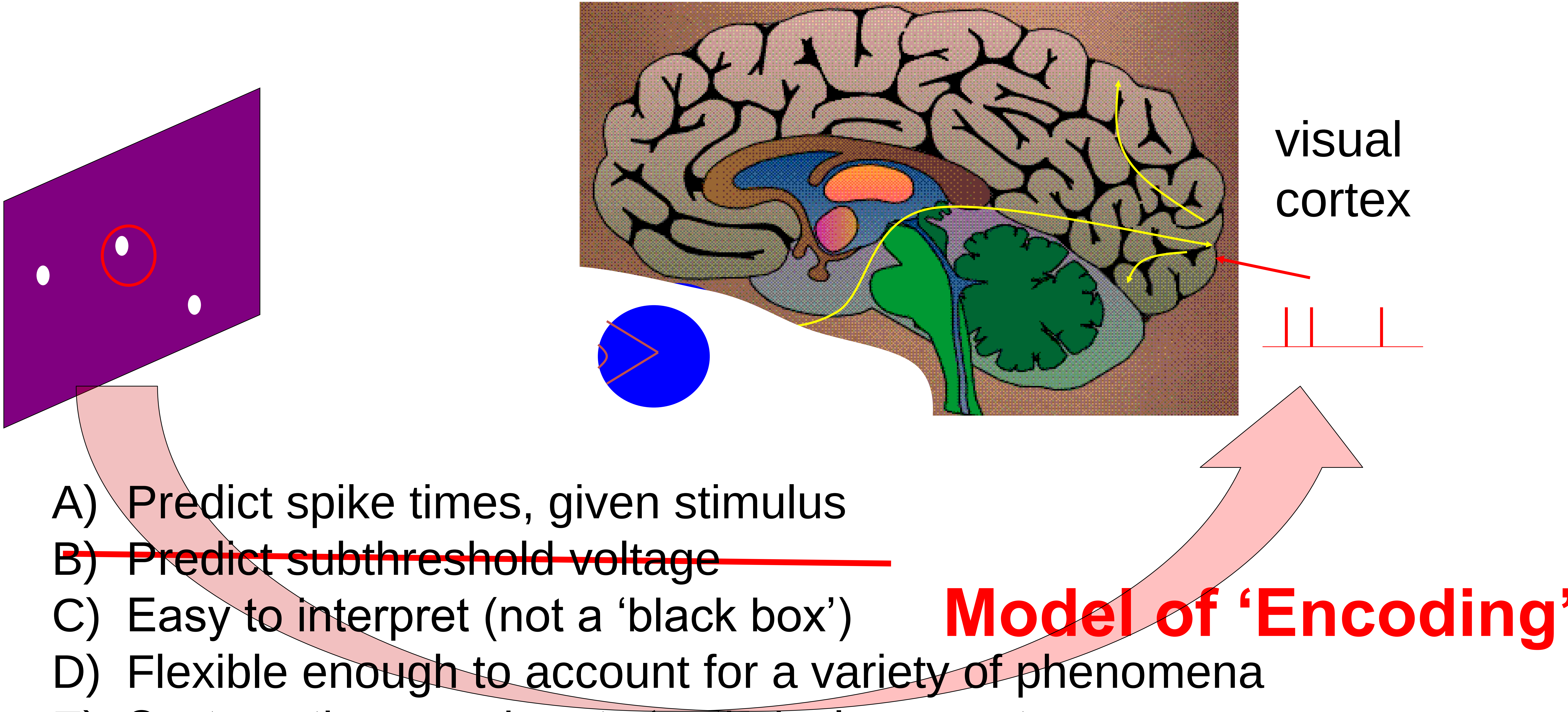
Neuronal Dynamics – 7.7 GLM with lateral coupling



One cell in a Network of Ganglion cells



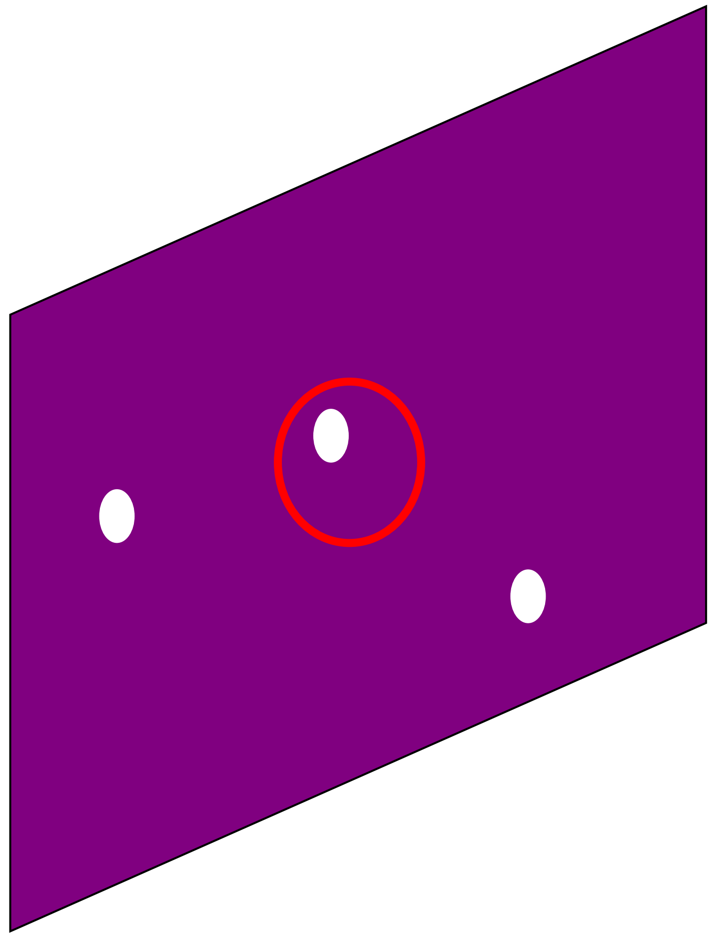
Pillow et al. 2008

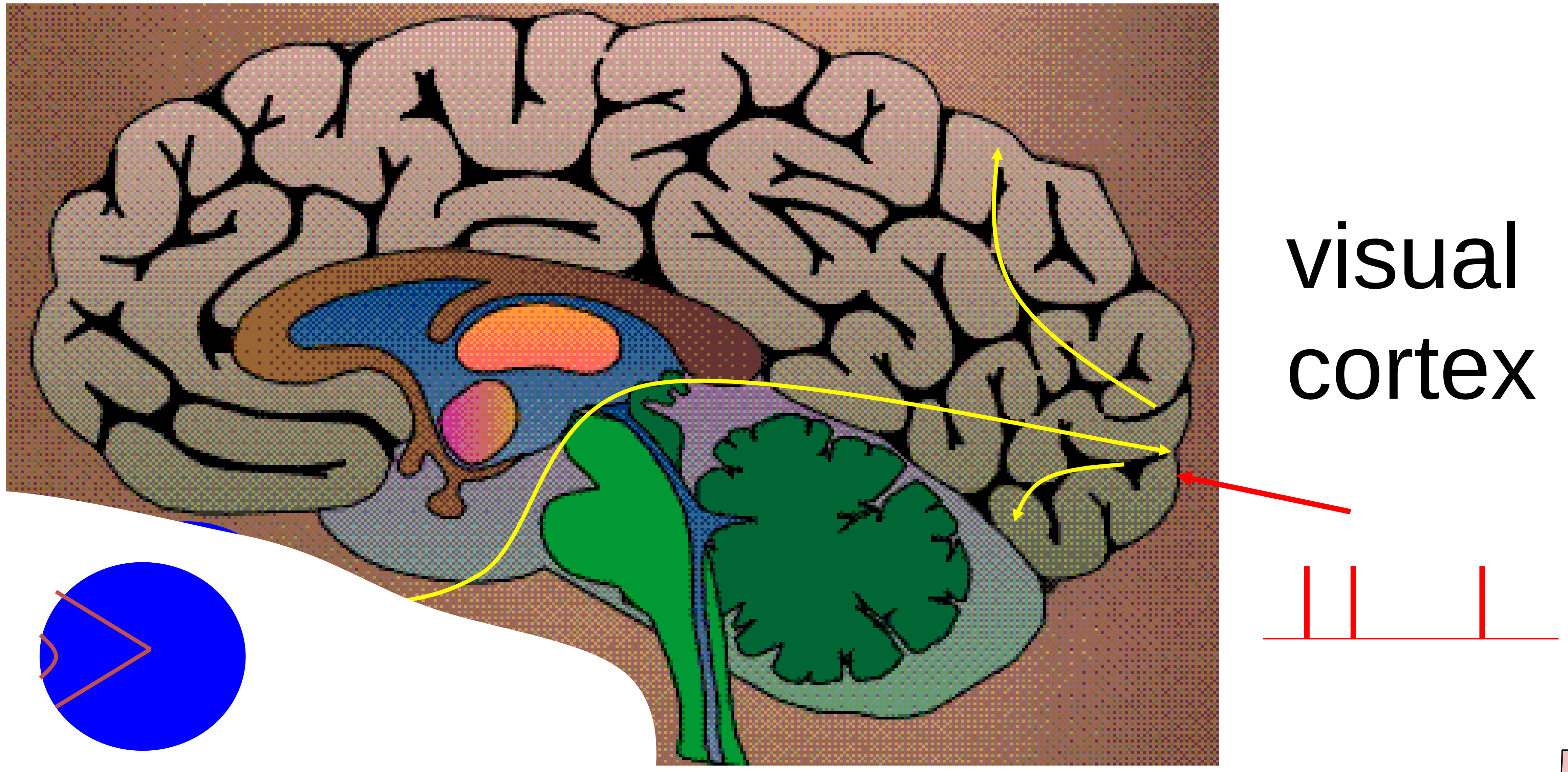


A) Predict spike times, given stimulus
B) ~~Predict subthreshold voltage~~
C) Easy to interpret (not a 'black box')
D) Flexible enough to account for a variety of phenomena
E) Systematic procedure to 'optimize' parameters

Neuronal Dynamics – 7.7 Model of DECODING

Predict stimulus!

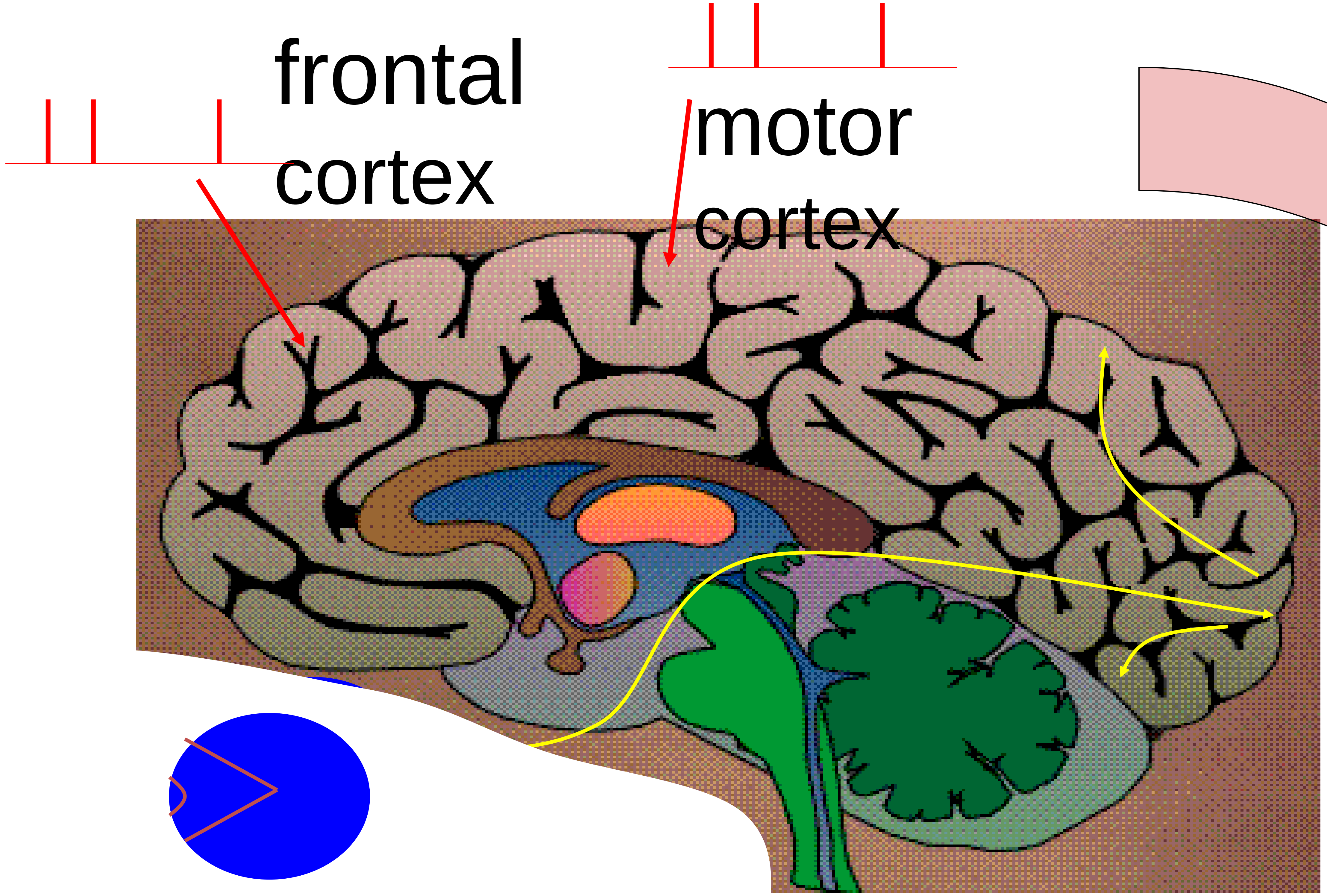




Model of ‘Decoding’:

predict stimulus, given spike times

Application: Neuroprosthetics



Many groups world wide work on this problem!

Model of ‘Decoding’

Predict intended arm movement, given Spike Times

Application: Neuroprosthetics

Decode the intended arm movement

Hand velocity

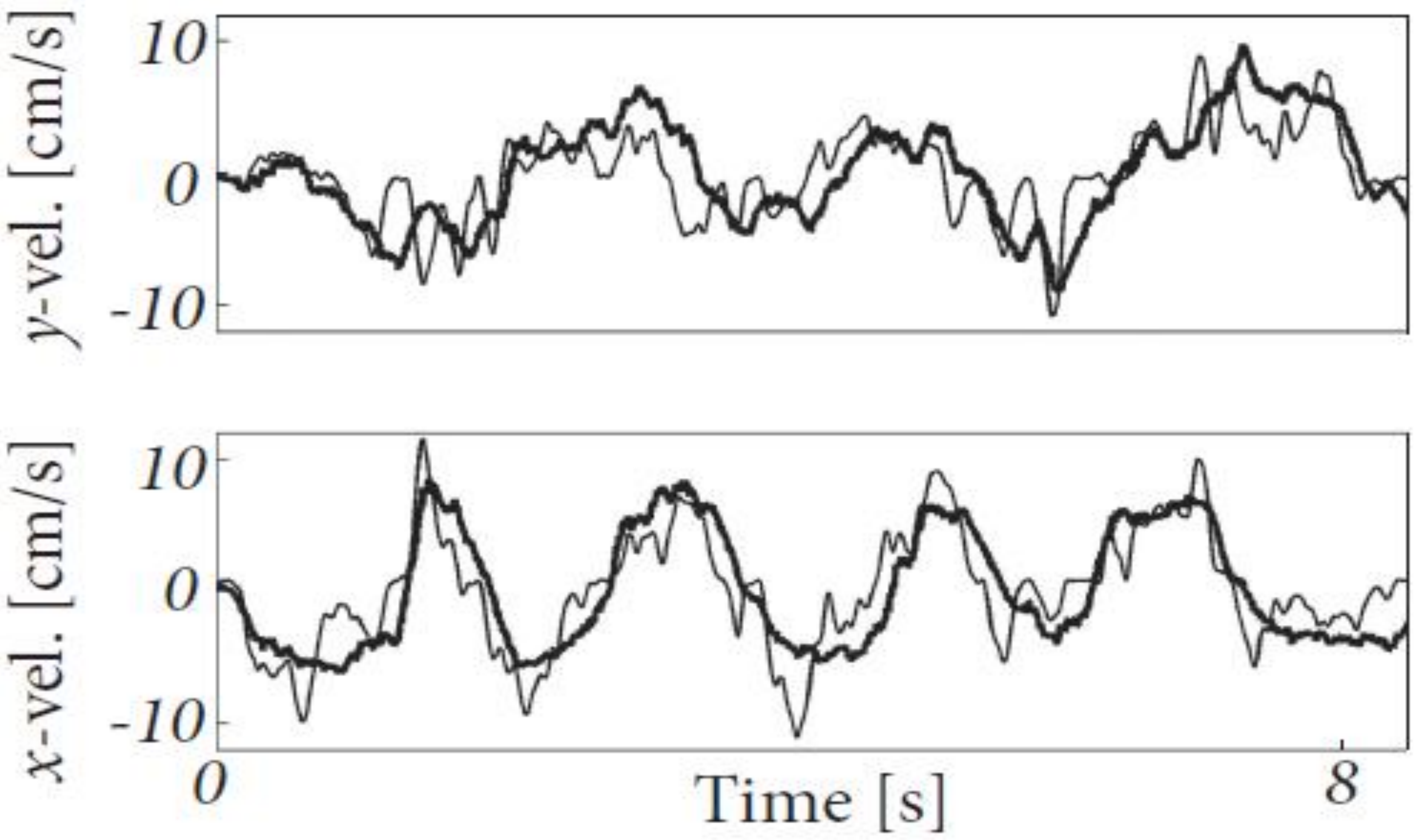


Fig. 11.12: Decoding had velocity from spiking activity in area MI of cortex. The real hand velocity (thin black line) is compared to the decoded velocity (thick black line) for the $x-$ (top) and the $y-$components (bottom). Modified from Truccolo et al. (2005).

Mathematical models for neuroscience

help humans

The end

Exercise 3: AdEx model – phase plane analysis

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

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

What firing pattern do you expect?

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