Exam:

- written exam Wedn. 21. 06. 2017 from 8:15-11:15
- sample exams of previous years online
- miniproject counts 33 percent towards final grade

For written exam:

-bring 1 sheet A5 of own notes/summary
-HANDWRITTEN!
-no calculator, no textbook

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
•Predict outcome of dynamics
•Describe neuronal phenomena
•Apply model concepts in simulations

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

Your Questions for Exam?

LEARNING OUTCOMES (in red: repeated today)

- 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
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miniproject

Biological Modeling of Neural Networks

Week XX

Optimizing Neuron Models

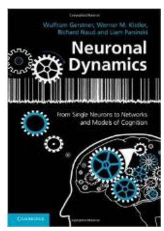
For Coding and Decoding

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for this week:
NEURONAL DYNAMICS
- Ch. 4.6, 6.1,6.2,6.4, 9.2
- Ch. 10.2.3, 11.1. 11.3.3

Cambridge Univ. Press



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

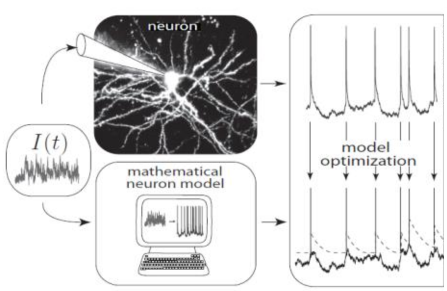
9.4 Generalized Linear Model
- Adding noise to the SRM
- Likelihood of a spike train

(9.5 Parameter Estimation)
(- Quadratic and convex optimization)

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

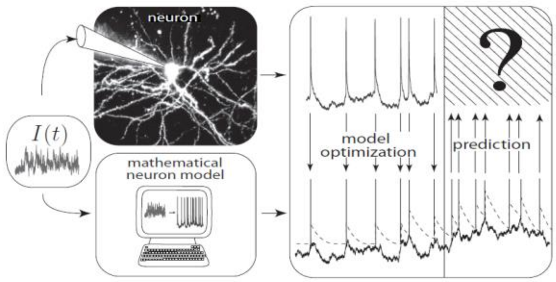
9.7. Helping humans – in vivo data

Neuronal Dynamics – 9.1 Neuron Models and Data



-What is a good neuron model?
-Estimate parameters of models?

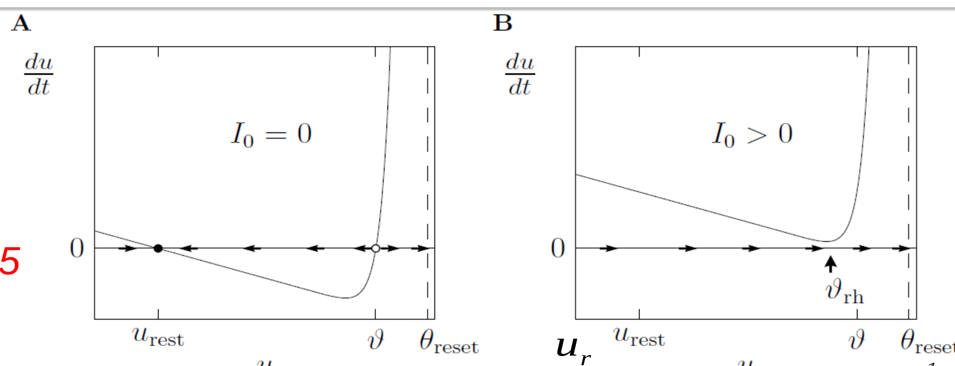
Neuronal Dynamics – 9.1 What is a good neuron model?



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



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

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

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

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

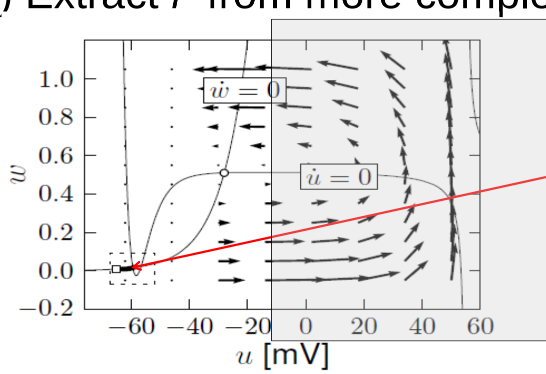
(i) Extract *f* from more complex models

(ii) Extract *f* from data

Neuronal Dynamics – Review: 2-dim neuron models

(i) Extract *f* from more complex models

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



A. detect spike and reset

resting state

Separation of time scales:
Arrows are nearly horizontal

Spike initiation, from rest

$w \approx w_{rest}$

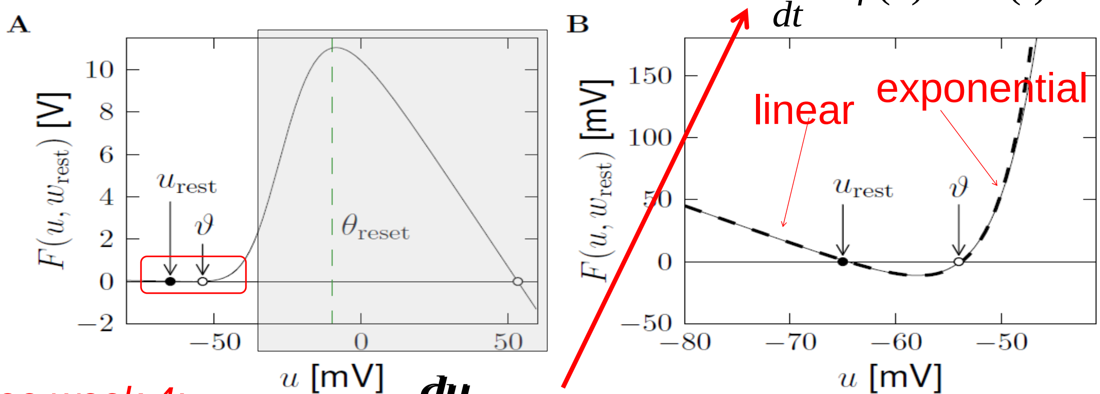
$$\tau \frac{du}{dt} = F(u,w) + RI(t)$$

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

B. Assume $w = w_{rest}$

Neuronal Dynamics – Review: Nonlinear Integrate-and-fire

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



See week 4: 2dim version of Hodgkin-Huxley

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

Separation of time scales

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

Neuronal Dynamics – Review: Nonlinear Integrate-and-fire

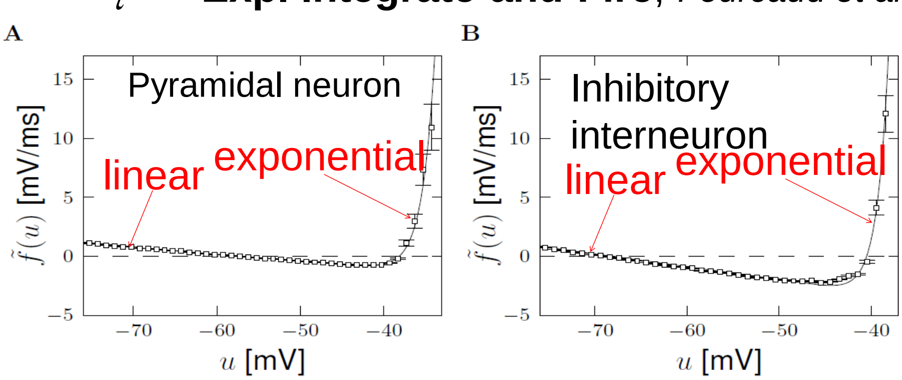
(ii) Extract *f* from data *Badel et al. (2008)*

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

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

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

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



Badel et al. (2008)

Neuronal Dynamics – Review: Nonlinear Integrate-and-fire

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

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

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

Week 9 – part 2 : Adaptive Expontential Integrate-and-Fire Model

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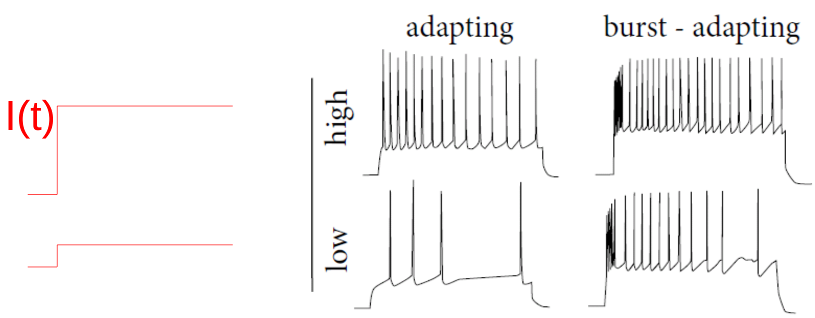
Biological Modeling of Neural Networks:

Week 9 – Optimizing Neuron Models For Coding and Decoding

Wulfram Gerstner
EPFL, Lausanne, Switzerland

Neuronal Dynamics – 9.2 Adaptation

Step current input – neurons show adaptation



Data: Markram et al. (2004)

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

Neuronal Dynamics – 9.2 Adaptive Exponential I&F

Add adaptation variables:

Blackboard !

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

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

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

SPIKE AND RESET

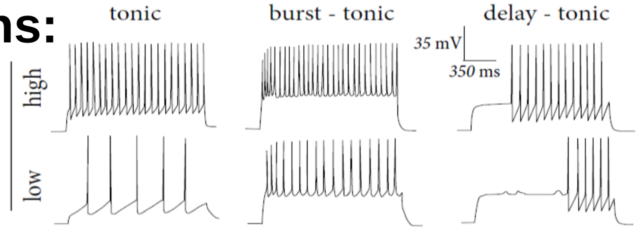
after each spike w_k jumps by an amount b_k

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

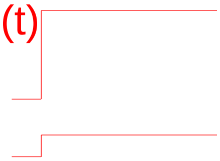
AdEx model, Brette&Gerstner (2005):

Firing patterns:

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

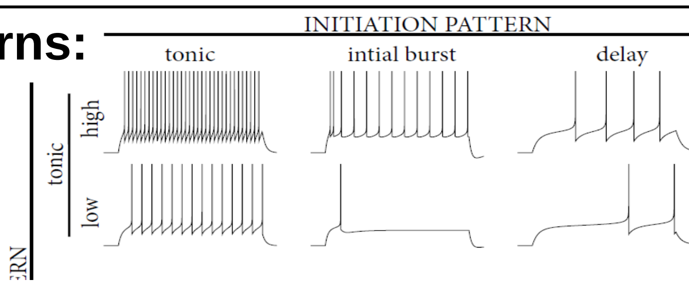


I(t)



Firing patterns:

Response to
Step currents,
AdEx Model,
Naud&Gerstner



I(t)

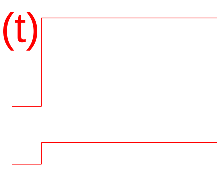


Image:
Neuronal Dynamics,
Gerstner et al.
Cambridge (2002)

Neuronal Dynamics – 9.2 Adaptive Exponential I&F

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

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

AdEx model

Phase plane analysis!

Can we understand the different firing patterns?

Neuronal Dynamics – Quiz 9.1. Nullclines of AdEx

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

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

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 u-nullcline?

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

3 minutes
Restart at 9:40

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

AdEx model

after each spike
u is reset to u_r

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

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

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

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

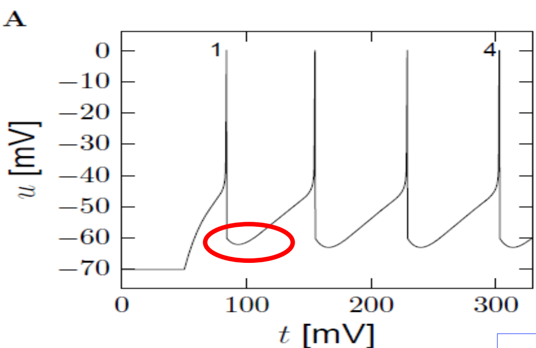
Can we understand the different firing patterns?

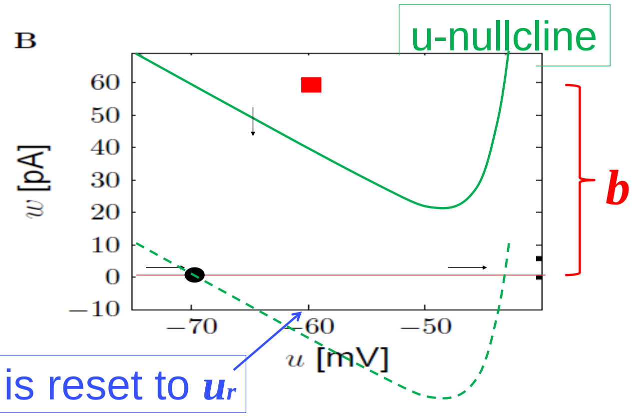
AdEx model – phase plane analysis: large *b*

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

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

a=0



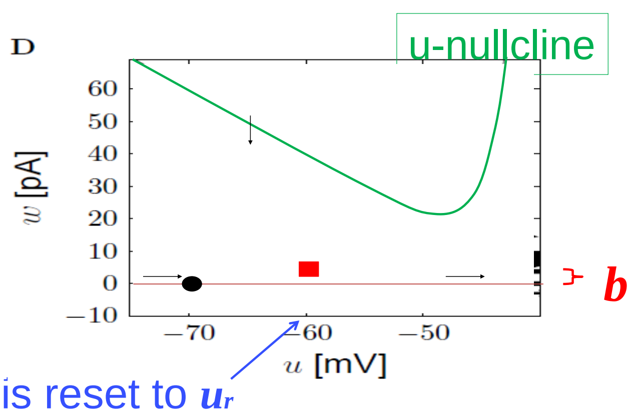


AdEx model – phase plane analysis: small *b*

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

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

adaptation



Quiz 9.2: AdEx model – phase plane analysis

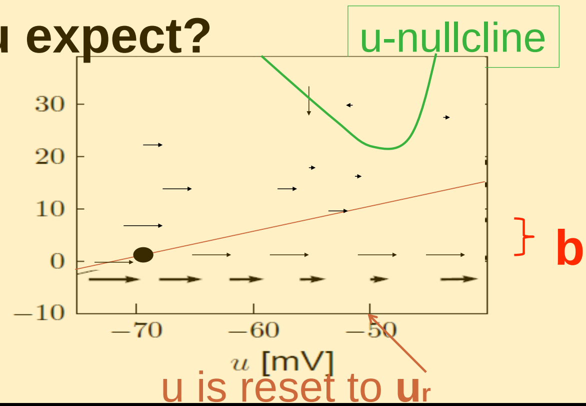
$\tau_w >> \tau$

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

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

What firing pattern do you expect?

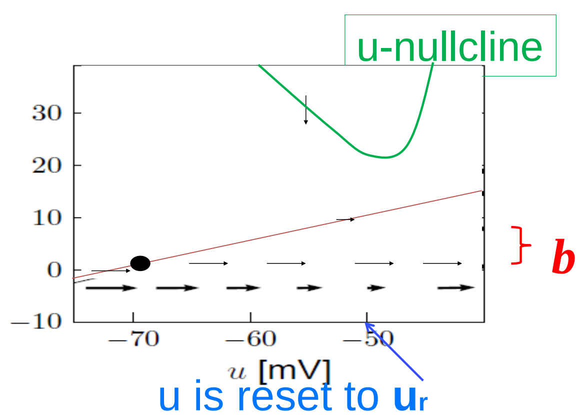
(i) Adapting
(ii) Bursting
(iii) Initial burst
(iv)Non-adapting



AdEx model – phase plane analysis: a>0

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

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



Neuronal Dynamics – 9.2 AdEx model and firing patterns

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

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

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

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

Blackboard:
Copy equations

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

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

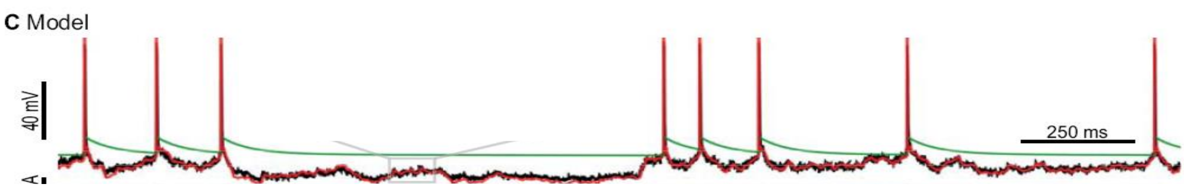
Neuronal Dynamics – 9.2 AdEx with dynamic threshold

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

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



Neuronal Dynamics – 9.2 Generalized Integrate-and-fire

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

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

add

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

Use 'escape noise'
(see earlier lecture)

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

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Biological Modeling of Neural Networks:

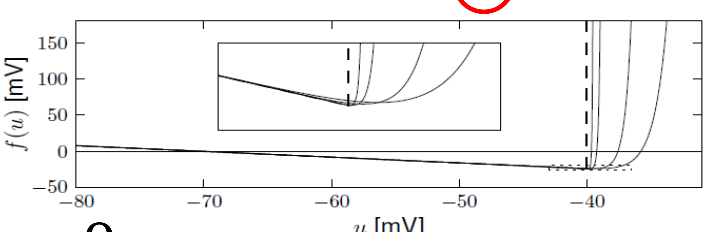
Week 9 – Optimizing Neuron Models For Coding and Decoding

Wulfram Gerstner

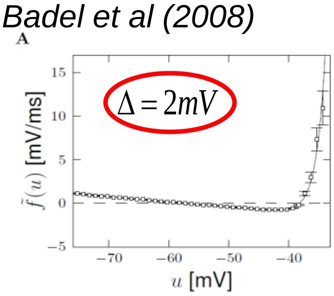
EPFL, Lausanne, Switzerland

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)



$$\Delta \rightarrow 0$$

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

Reset if u= ϑ

Leaky Integrate-and-Fire

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

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

Dynamic threshold

Exercise 1: from adaptive IF to SRM

$$\tau \frac{du}{dt} = -(u - u_{rest}) - R\,\alpha\, w + RI(t), \qquad \alpha = \{0,1\}$$

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

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

Start before break
Next lecture at 10:20

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

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

Hint: voltage reset equivalent to short current pulse

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

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!

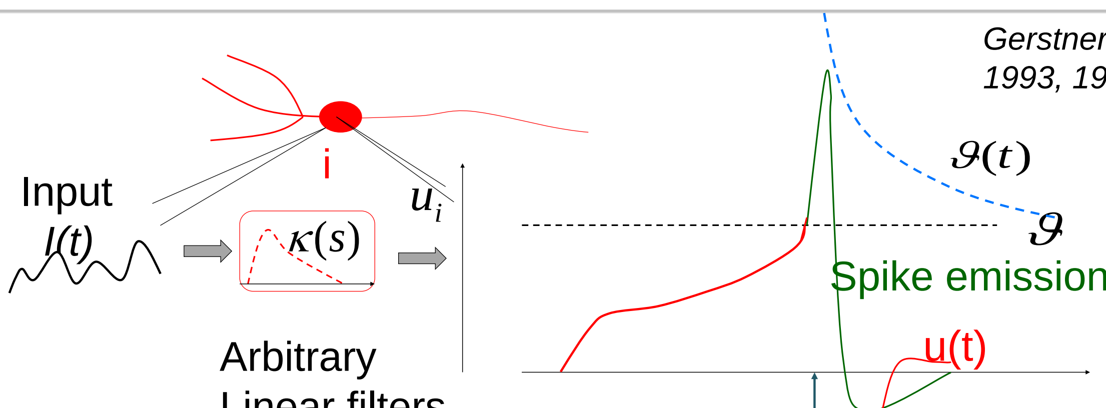
$$u(t) = \sum_f \eta\,(t - t^f) + \int_0^\infty ds\,\kappa(s) I(t - s)$$

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

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

Neuronal Dynamics – 9.3 Spike Response Model (SRM)

Gerstner et al., 1993, 1996



potential

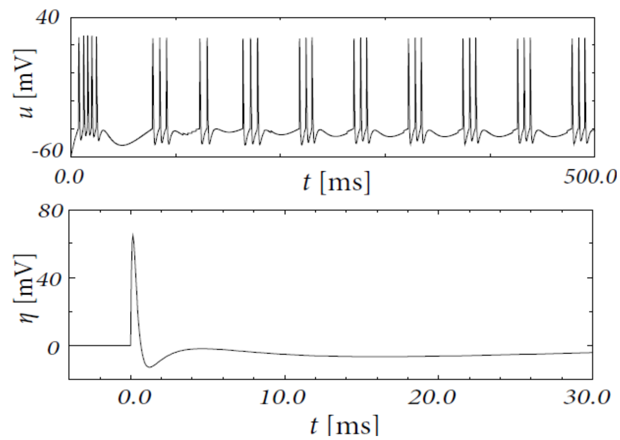
$$u(t) = \sum_{t'} \eta\left(t - t'\right) + \int_0^\infty \kappa(s) I(t - s) ds + u_{rest}$$

threshold

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

Neuronal Dynamics – 9.3 Bursting in the SRM

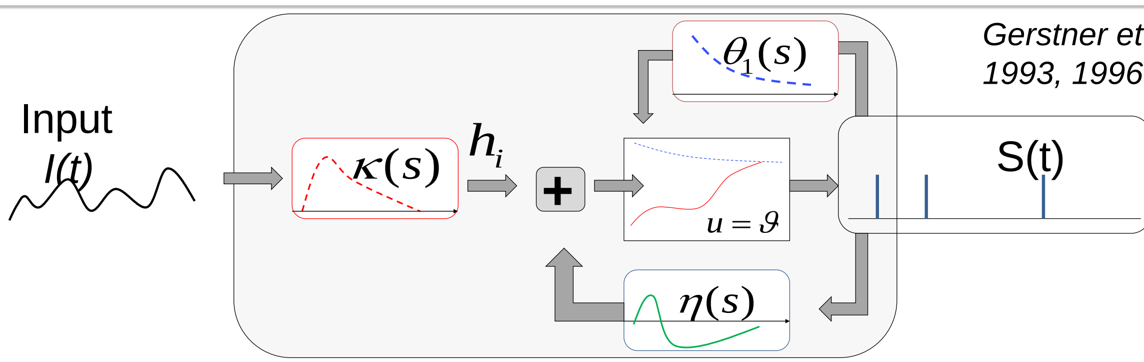
SRM with appropriate η leads to bursting



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

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

Neuronal Dynamics – 9.3 Spike Response Model (SRM)



Gerstner et al., 1993, 1996

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

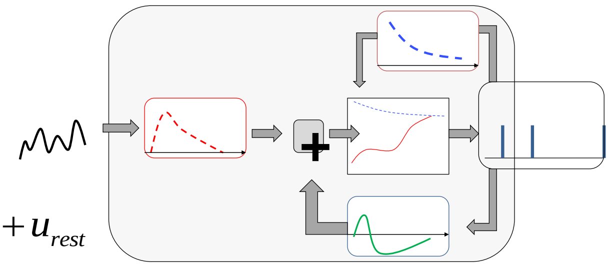
threshold $\vartheta(t) = \theta_0 + \sum_{t'} \theta_1(t - t')$

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

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

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

Linear filters for
- input
- threshold
- refractoriness

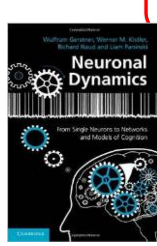
Biological Modeling of Neural Networks:

Week 9 – Optimizing Neuron Models For Coding and Decoding

Wulfram Gerstner
EPFL, Lausanne, Switzerland

Reading for this week:
NEURONAL DYNAMICS
- Ch. 4.6, 6.1,6.2,6.4, 9.2
- Ch. 10.2.3, 11.1. 11.3.3

Cambridge Univ. Press



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

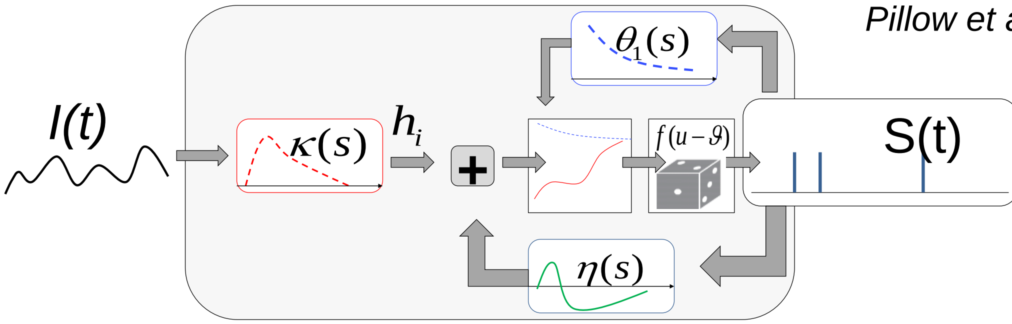
9.4 Generalized Linear Model
- Adding noise to the SRM
- Likelihood of a spike train

9.5 Parameter Estimation
- Quadratic and convex optimization

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

Spike Response Model (SRM)
Generalized Linear Model GLM

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



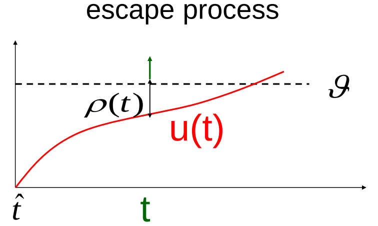
potential $u(t) = \int \eta(s) S(t-s) ds + \int_0^\infty \kappa(s) I(t-s) ds + u_{rest}$

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

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

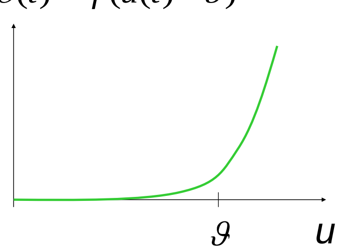
Neuronal Dynamics – review: Escape noise

escape process



escape rate

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



escape rate $\rho(t) = \rho_0 \exp(\frac{u(t)-\vartheta}{\Delta})$

Example: leaky integrate-and-fire model

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

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

Exerc. 2.1: Non-leaky IF with escape rates

$$\frac{du}{dt} = \frac{R}{\tau} I(t) = \frac{1}{C} I(t)$$ nonleaky

$reset\ to\ u_r = 0$

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

$reset\ to\ u_{rest} = u_r = 0$

Integrate for constant input (repetitive firing)

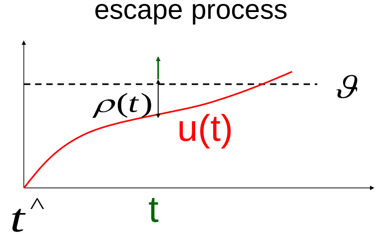
12 minutes, Next lecture at 10:55

Calculate

- potential $u(t-\hat{t})$
- hazard $\rho(t-\hat{t}) = \beta \cdot [u(t-\hat{t}) - \vartheta]_+$
- survivor function $S(t-\hat{t})$
- interval distrib. $P_0(t-\hat{t})$

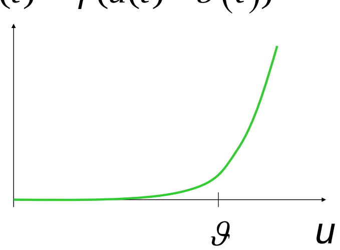
Neuronal Dynamics – review: Escape noise

escape process



escape rate

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



Survivor function

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

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

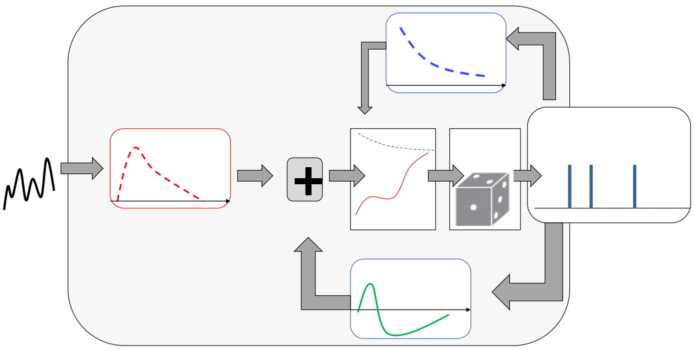
Interval distribution

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

Good choice

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

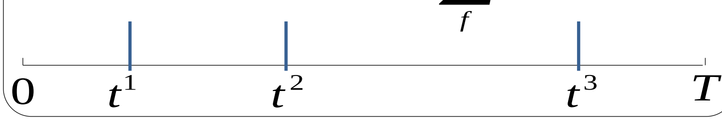
Neuronal Dynamics – Likelihood of spike train



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

Neuronal Dynamics – 9.4 Likelihood of a spike train in GLMs

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



→Blackboard

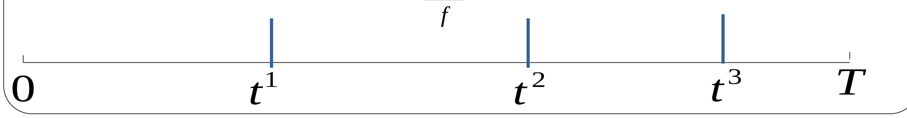
Measured spike train with spike times $t^1, t^2, \ldots t^N$

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

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

Neuronal Dynamics – 9.4 Likelihood of a spike train

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

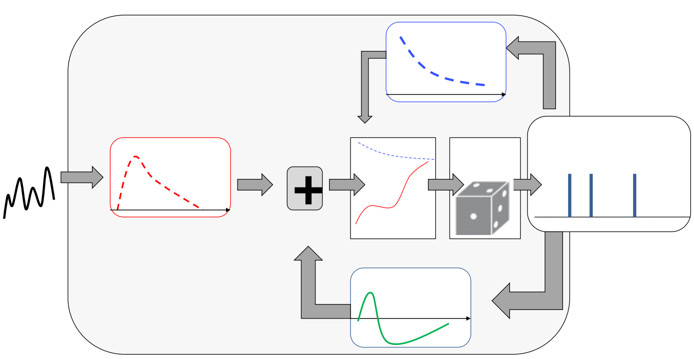


$$L(t^1,\ldots,t^N)=\exp\left(-\int_0^{t^1}\rho(t')dt'\right)\rho(t^1)\cdot\exp\left(-\int_{t^1}^{t^2}\rho(t')dt'\right)\rho(t^2)\ldots\cdot\exp\left(-\int_{t^N}^{T}\rho(t')dt'\right)$$

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

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

Neuronal Dynamics – 9.4 SRM with escape noise = GLM



-linear filters

-escape rate

→likelihood of observed spike train

→parameter optimization of neuron model

Week 9 – part 5: Parameter Estimation

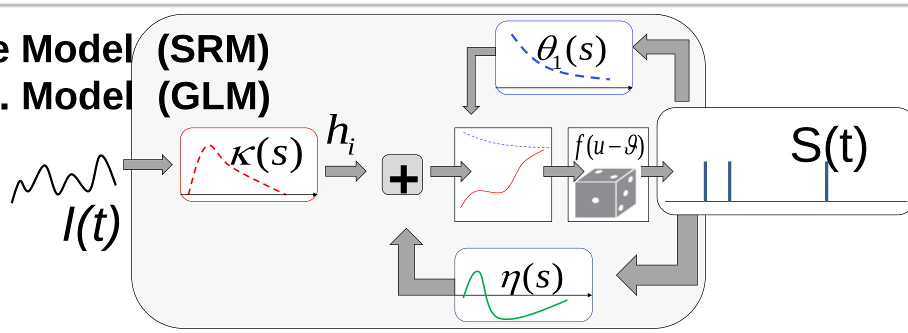
Biological Modeling of Neural Networks:

Week 9 – Optimizing Neuron Models For Coding and Decoding

Wulfram Gerstner
EPFL, Lausanne, Switzerland

Neuronal Dynamics – 9.5 Parameter estimation: voltage

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



Subthreshold potential

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

known spike train known input

Linear filters/linear in parameters

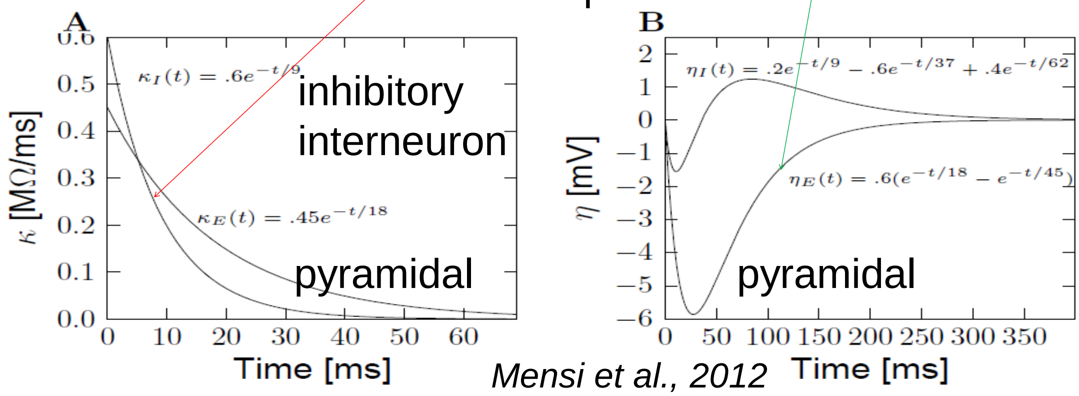
Neuronal Dynamics – 9.5 Extracted parameters: voltage

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

Week 9 – part 5b: Quadratic and Convex Optimization

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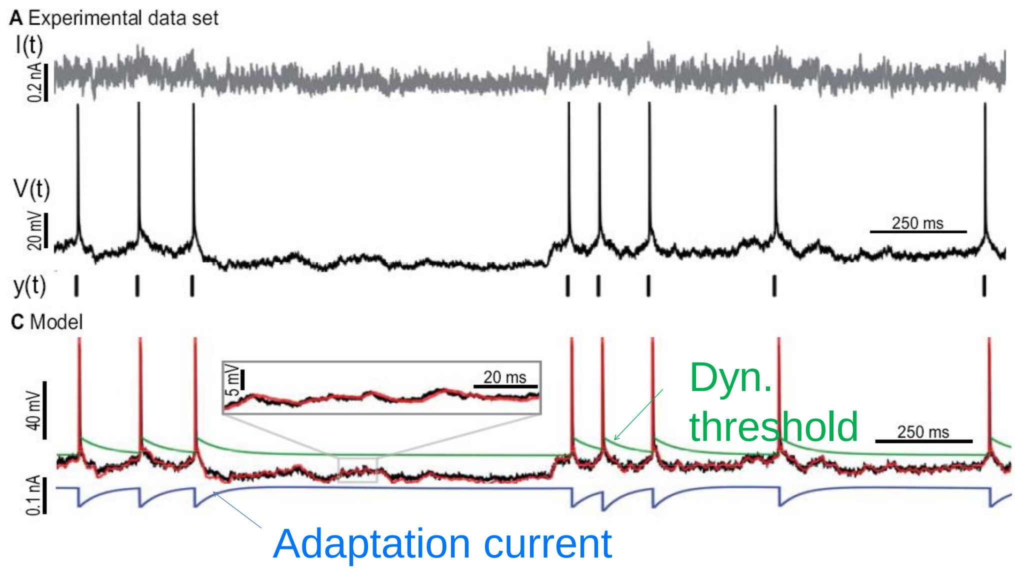
Biological Modeling of Neural Networks:

Week 9 – Optimizing Neuron Models For Coding and Decoding

Wulfram Gerstner

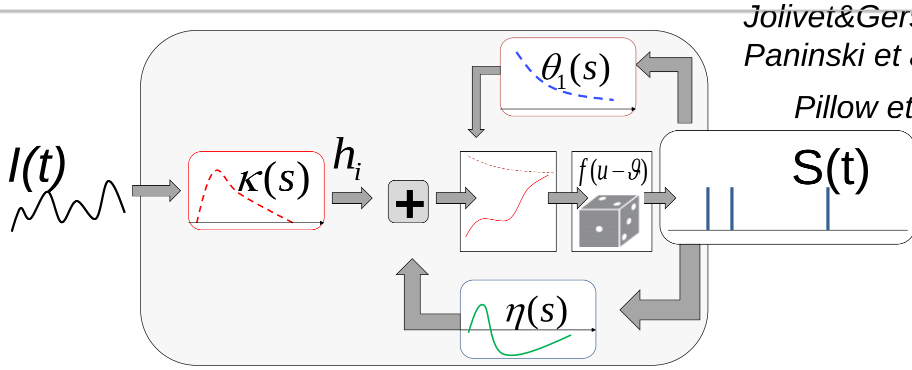
EPFL, Lausanne, Switzerland

Fitting models to data: so far ‘subthreshold’



Neuronal Dynamics – 9.5 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 $$\rho(t) = f(u(t) - \vartheta(t))$$

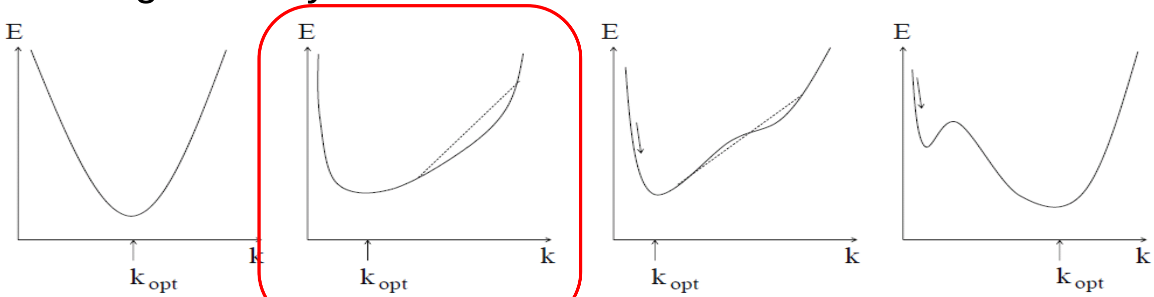
Neuronal Dynamics – 9.5 Generalized Linear Model (GLM)

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

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

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

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



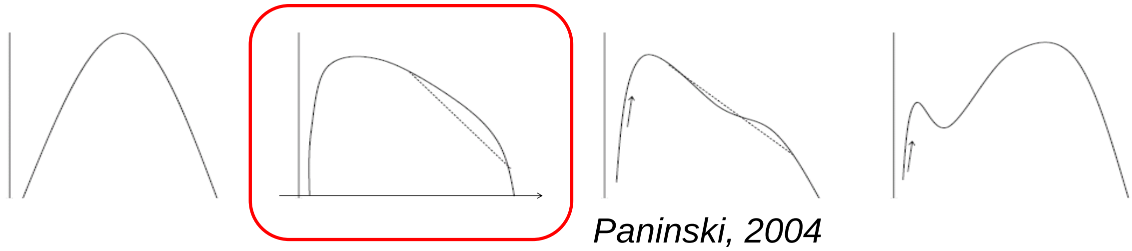
Neuronal Dynamics – 9.5 GLM: concave error function

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

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

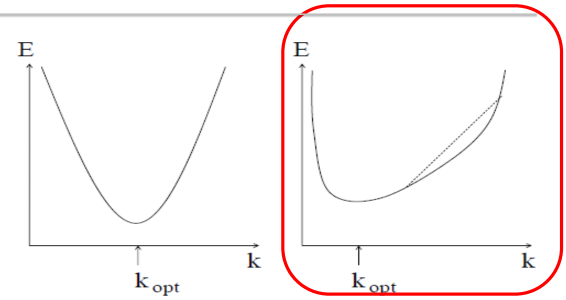
firing intensity $\rho(t) = f(u(t) - \vartheta(t))$

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



Paninski, 2004

Neuronal Dynamics – 9.5 quadratic and convex/concave optimization



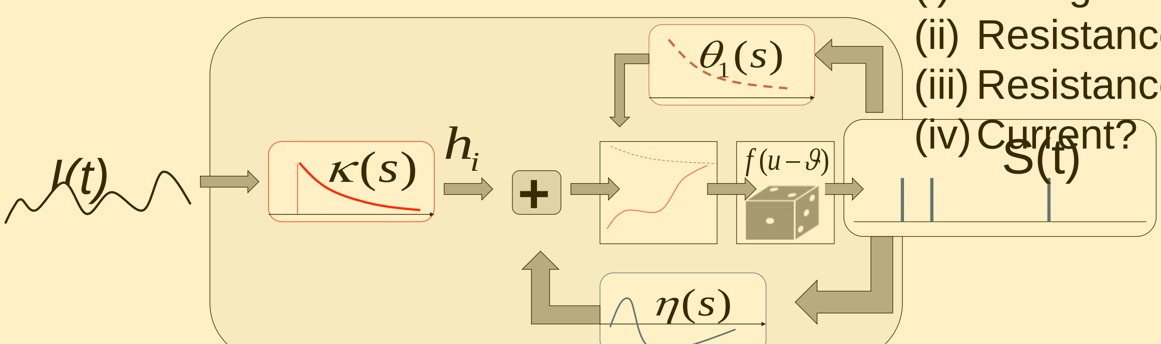
Voltage/subthreshold
- linear in parameters
  → quadratic error function

Spike times
- nonlinear, but GLM
  → convex error function

Quiz NOW :

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

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



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

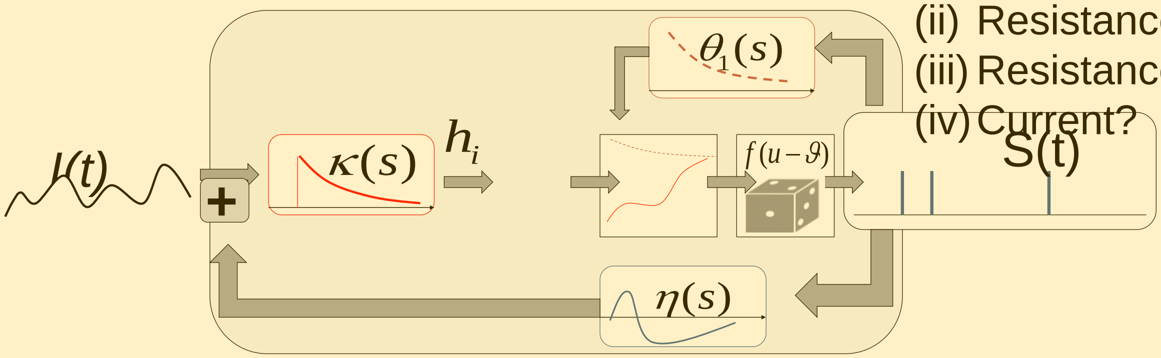
threshold $\vartheta(t) = \theta_0 + \int \theta_1(s) S(t-s) ds$

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

Quiz NOW:

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

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



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

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

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

Week 9 – part 6: Modeling in vitro data

Biological Modeling of Neural Networks:

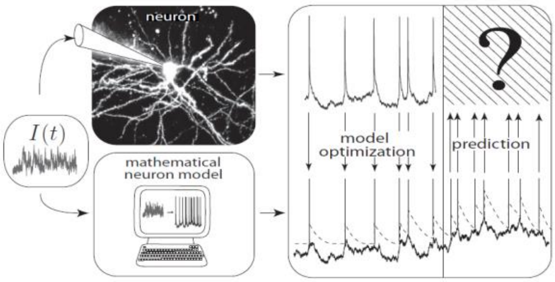
Week 9 – Optimizing Neuron Models For Coding and Decoding

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?
- **9.7. Helping Humans**

Neuronal Dynamics – 9.6 Models and Data

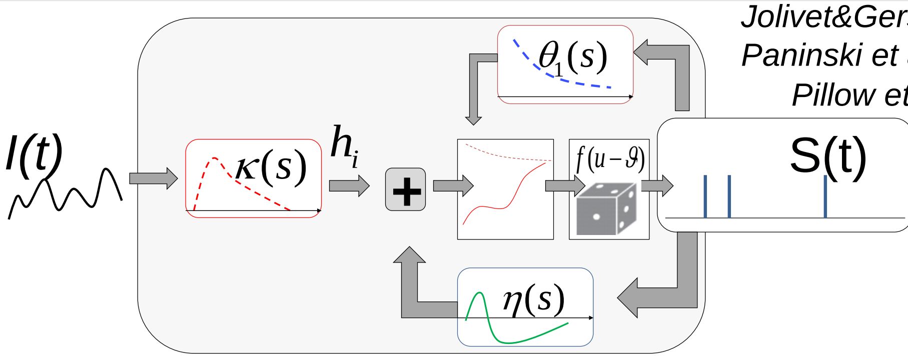
comparison model-data



Predict
-Subthreshold voltage
-Spike times

Neuronal Dynamics – 9.6 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 – 9.6 GLM/SRM predict subthreshold voltage

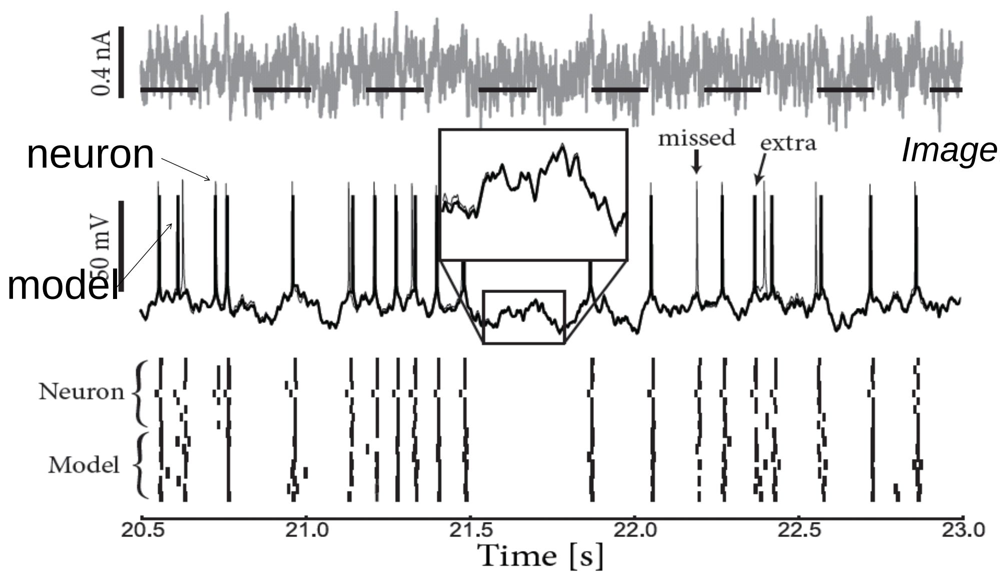


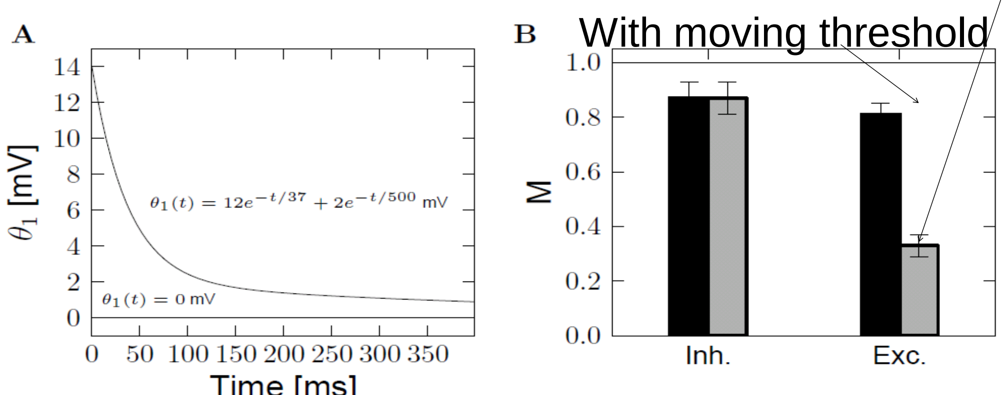
Image:Mensi et al.

Neuronal Dynamics – 9.6 GLM/SRM predict spike times

Role of moving threshold

No moving threshold

With moving threshold

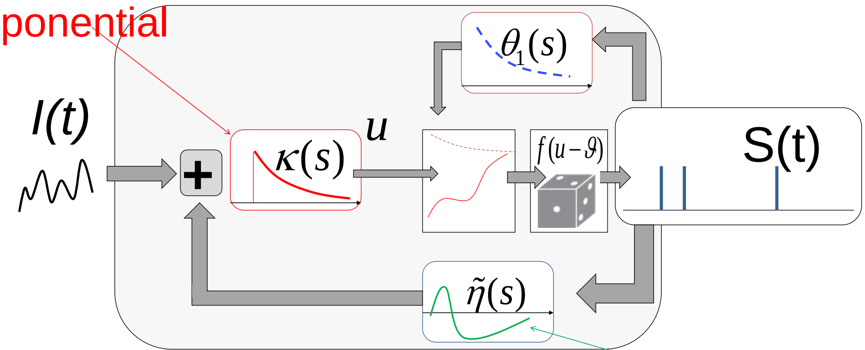


Mensi et al., 2012

Change in model formulation:

What are the units of …. ?

'soft-threshold adaptive IF model'



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

adaptation current

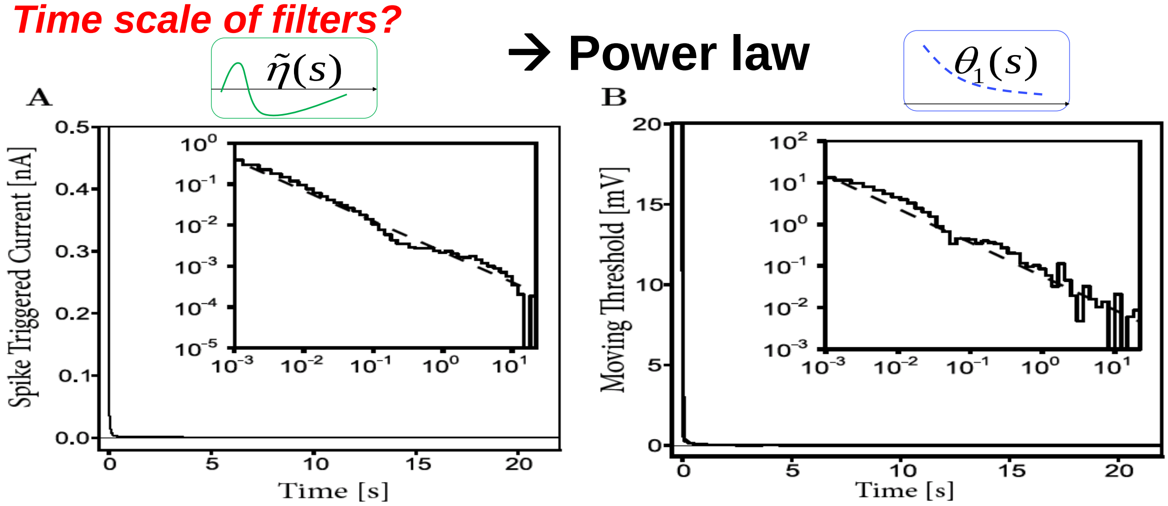
threshold $$\vartheta(t) = \theta_0 + \int \theta_1(s) S(t-s)ds$$

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

Neuronal Dynamics – 9.6 How long does the effect of a spike last?

Time scale of filters?

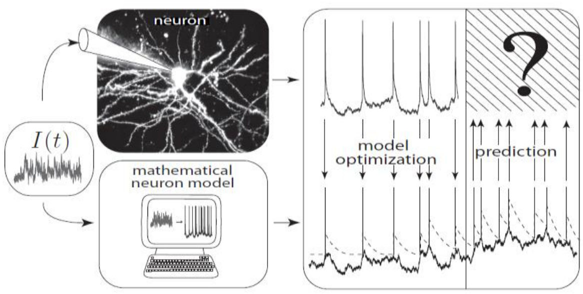
→ **Power law**



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

Pozzorini et al. 2013

Neuronal Dynamics – 9.6 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

Week 9 – part 6: Modeling in vitro data

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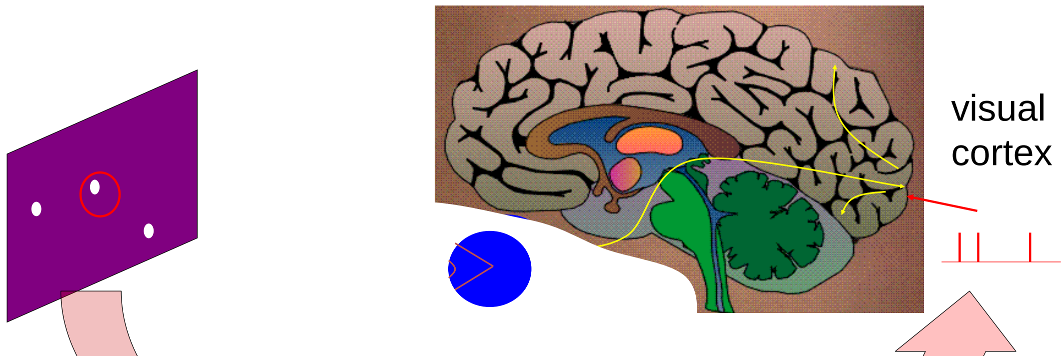
Biological Modeling of Neural Networks:

Week 9 – Optimizing Neuron Models For Coding and Decoding

Wulfram Gerstner
EPFL, Lausanne, Switzerland

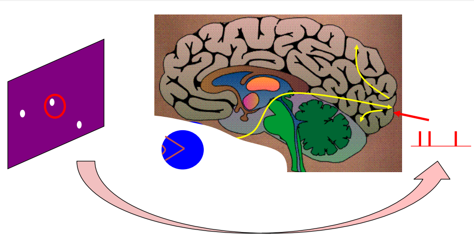
Neuronal Dynamics – 9.7 Model of ENCODING



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

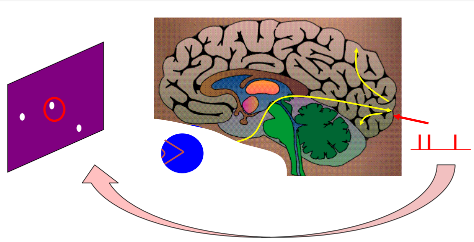
Model of 'Encoding'

Neuronal Dynamics – 9.7 ENCODING and Decoding



Model of 'Encoding'

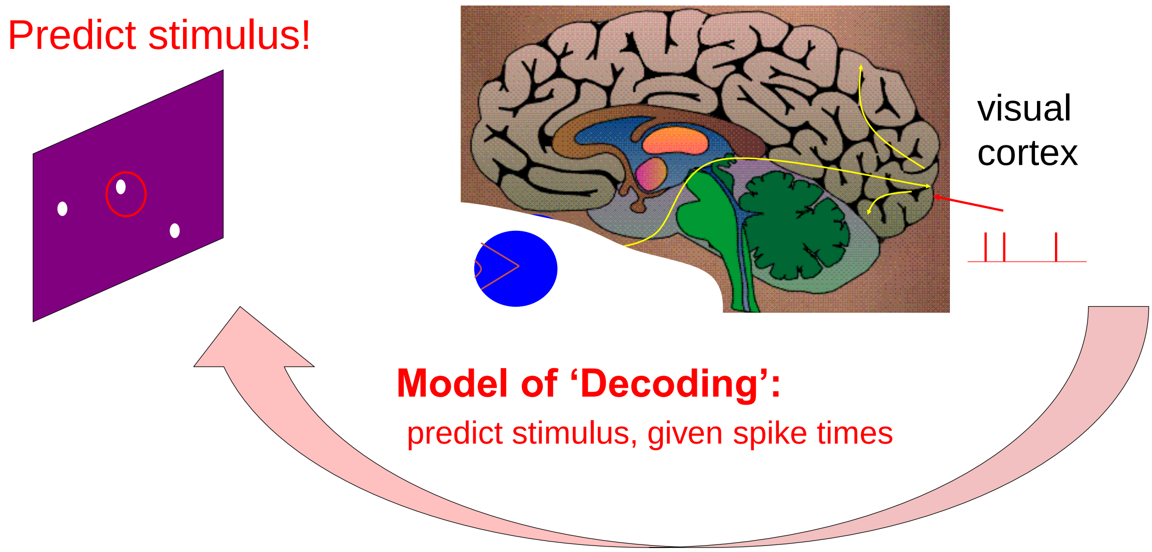
Generalized Linear Model (GLM)
- flexible model
- systematic optimization of parameters



Model of 'Decoding'

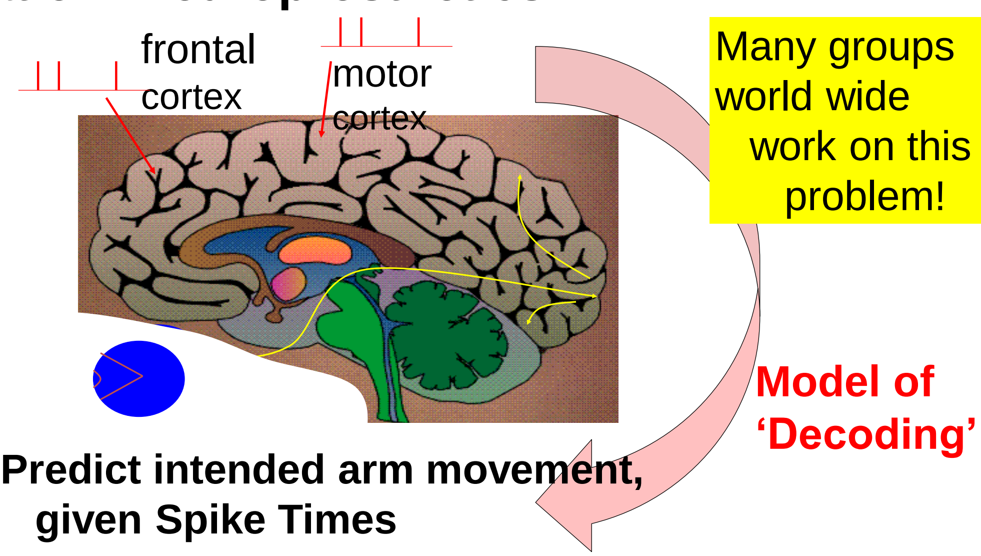
The same GLM works!
- flexible model
- systematic optimization of parameters

Neuronal Dynamics – 9.7 Model of DECODING



Neuronal Dynamics – 9.7 Helping Humans

Application: Neuroprosthetics



Neuronal Dynamics – 9.7 Basic neuroprosthetics

Application: Neuroprosthetics

Figure:
Neuronal Dynamics,
Cambridge Univ. Press;
See Truccolo et al. 2005

Decode the intended arm movement

Hand velocity

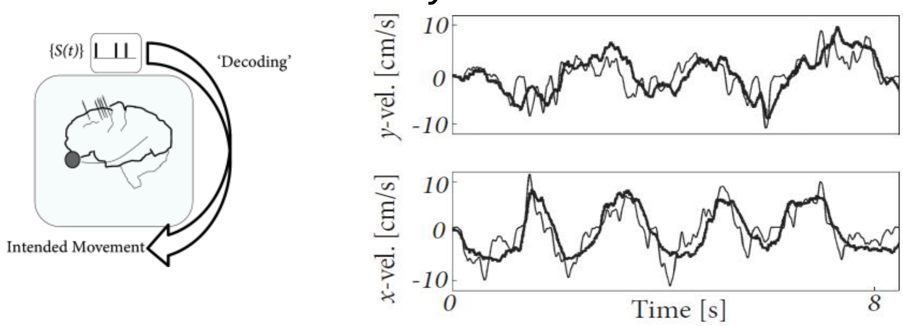


Fig. 11.12: Decoding had velocity from spiking activity in area MI of cortex. The real hand velocity (thin black line) is compared to the decoded velocity (thick black line) for the $x-$ (top) and the $y-$components (bottom). Modified from Truccolo et al. (2005).

Neuronal Dynamics week 7– Suggested Reading/selected references

Reading: W. Gerstner, W.M. Kistler, R. Naud and L. Paninski,
Neuronal Dynamics: from single neurons to networks and models of cognition. Ch. 6,10,11*:* Cambridge, 2014

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Fourcaud-Trocme, N., Hansel, D., van Vreeswijk, C., and Brunel, N. (2003). How spike …. *J. Neuroscience*, 23:11628-11640.
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-Brillinger, D. R. (1988). Maximum likelihood analysis of spike trains of interacting nerve cells. *Biol. Cybern*., 59:189-200.
-Truccolo, et al. (2005). A point process framework for relating neural spiking activity to spiking history, neural ensemble, and extrinsic covariate effects. Journal of Neurophysiology, 93:1074-1089.
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Encoding and Decoding
Rieke, F., Warland, D., de Ruyter van Steveninck, R., and Bialek, W. (1997). Spikes - Exploring the neural code. MIT Press,
Keat, J., Reinagel, P., Reid, R., and Meister, M. (2001). Predicting every spike … *Neuron*, 30:803-817.
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Donoghue, J. (2002). Connecting cortex to machines: recent advances in brain interfaces. Nat. Neurosci., 5:1085-1088.