

# Week 3 – Reducing detail: **Two-dimensional neuron models**

Wulfram Gerstner EPFL, Lausanne, Switzerland

Reading for week 3: **NEURONAL DYNAMICS** - Ch. 4.1- 4.3

Cambridge Univ. Press



# 3.1 From Hodgkin-Huxley to 2D

- Overview: From 4 to 2 dimensions
- MathDetour 1: Exploiting similarities
- MathDetour 2: Separation of time scales

### 3.2 **Phase Plane Analysis**

- Role of nullclines

# 3.3 Analysis of a 2D Neuron Model

- constant input vs pulse input
- MathDetour 3: Stability of fixed points



# **3.1. Review of week 2 :Hodgkin-Huxley Model**



→Hodgkin-Huxley model
→Compartmental models

# **3.1 Review of week 2 : Hodgkin-Huxley Model**

-70mV

lons/proteins

# Week 2:

### Cell membrane contains

 $\bigcirc$ 

- ion channels
- ion pumpsa

# Dendrites (week x:video): Active processes?



# **3.1. Review of week 2 :Hodgkin-Huxley Model**

#### $n_1$ (inside)



#### n<sub>2</sub> (outside)

#### ion pumps →concentration difference ⇔ voltage difference







$\underline{dm}$	$\underline{ m-m_0(u)}$
dt	$\tau_m(u)$

# Week 3 – 3.1. Overview and aims

# Can we understand the dynamics of the HH model? - mathematical principle of Action Potential generation? - constant input current vs pulse input? - Types of neuron model (type I and II)? (next week)

- threshold behavior? (next week)





# Week 3 – 3.1. Overview and aims

# Can we understand the dynamics of the HH model?

# → Reduce from 4 to 2 equations



# **Week 3 – Quiz 3.1.**

# A - A biophysical point neuron model with 3 ion channels, each with activation and inactivation, has a total number of equations equal to [] 3 or [] 4 or [] 6 or [] 7 or [] 8 or more



# Week 3 – 3.1. Overview and aims Toward a

# two-dimensional neuron model -Reduction of Hodgkin-Huxley to 2 dimension -step 1: separation of time scales

-step 2: exploit similarities/correlations



$C\frac{du}{dt} =$	$= -g_{Na}m^{3}h(u-E_{I})$	$(N_a) - g_K n$
$\underline{dm}$	$\underline{m-m_0(u)}$	
dt	$\tau_m(u)$	
dh	$h - h_0(u)$	
dt	$\tau_h(u)$	
dn =	$-\frac{n-n_0(u)}{2}$	
dt	$\tau_n(u)$	

1) dynamics of *m* are fast





#### **Reduction of dimensionality: Separation of time scales**

$$\tau_1 \frac{dx}{dt} = -x + c(t)$$

### Exercise 1 (week 3) at beginning of lecture 2 !

Two coupled differential equations

$$\tau_1 \frac{dx}{dt} = -x + h(y)$$
  
$$\tau_2 \frac{dy}{dt} = f(y) + g(x)$$

Separation of time scales

$$\tau_1 \ll \tau_2 \rightarrow x = h(y)$$

Reduced 1-dimensional system  $\tau_2 \frac{dy}{dt} = f(y) + g(h(y))$ 



1) dynamics of *m* are fast 2) dynamics of *h* and *n* are similar

#### $m(t) = m_0(u(t))$



# **Reduction of Hodgkin-Huxley** Model to 2 Dimension -step 1: separation of time scales

-step 2:



### exploit similarities/correlations

Now

$$C\frac{du}{dt} = -g_{Na}m^{3}h(u-E_{Na}) - g_{I}$$





# **3.1 Detour 1. Exploit similarities/correlations**



# dynamics of *h* and *n* are similar

# **3.1 Detour 1. Exploit similarities/correlations**



# dynamics of *h* and *n* are similar

#### 1 - h(t) = a n(t)

at rest

 $\frac{dh}{dt} = -\frac{h - h_0(u)}{\tau_h(u)}$  $\frac{dn}{dt} = -\frac{n - n_0(u)}{\tau_n(u)}$ 

# **3.1 Detour 1. Exploit similarities/correlations**



#### dynamics of h and n are similar

(i) Rotate coordinate system
(ii) Suppress one coordinate
(iii) Express dynamics in new variable

$$1 - h(t) = a n(t) = w(t)$$

<u> </u>	$\frac{h-h_0(u)}{(u)}$	dw	$w - w_0(u)$
	$\tau_h(u)$	=	$-\tau_{cff}(u)$
l	$\underline{n-n_0(u)}$		ejj < 7
	$\tau_n(u)$		

**3.1. Reduction of Hodgkin-Huxley model**  

$$I_{Na} \qquad I_{K} \qquad I_{leak}$$

$$C \frac{du}{dt} = -g_{Na}[m(t)]^{3}h(t)(u(t) - E_{Na}) - g_{K}[n(t)]^{4}(u(t) - E_{K}) - g_{l}(u(t) - E_{l}) + I(t)$$

$$C\frac{du}{dt} = -g_{Na} m_0(u)^3 (1-w)(u-E_{Na}) - g_K [\frac{w}{a}]^4 (u-E_K) - g_l(u-E_l) + I(t)$$

# 1) dynamics of *m* are fast 2) dynamics of *h* and *n* are similar

$$\frac{dh}{dt} = -\frac{h - h_0(u)}{\tau_h(u)} \longrightarrow \frac{dw}{dt} = -\frac{w - w_0(u)}{\tau_{eff}(u)}$$

$$\longrightarrow m(t) = m_0(u(t))$$

$$\longrightarrow 1 - h(t) = a n(t)$$

$$w(t) w(t)$$





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

# **3.1. Reduction to 2 dimensions**

#### 2-dimensional equation 111

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

$$\frac{dw}{dt} = g(u(t), w(t))$$

Enables graphical analysis!

- -Discussion of threshold
- Constant input current vs pulse input
- -Type I and II
- Repetitive firing



#### Phase plane analysis

# **Week 3 – Quiz 3.2-similar dynamics**

# Exploiting similarities:

A sufficient condition to replace two gating variables r,s by a single gating variable w is [] Both r and s have the same time constant (as a function of u) [] Both r and s have the same activation function [] Both r and s have the same time constant (as a function of u) AND the same activation function [] Both r and s have the same time constant (as a function of u) AND activation functions that are identical after some additive rescaling [] Both r and s have the same time constant (as a function of u) AND activation functions that are identical after some multiplicative rescaling



# Week 3 – Reducing detail: **Two-dimensional neuron models**

#### Wulfram Gerstner EPFL, Lausanne, Switzerland

# **√** 3.1 From Hodgkin-Huxley to 2D

- Overview: From 4 to 2 dimensions
- MathDetour 1: Exploiting similarities
- MathDetour 2: Separation of time scales

### 3.2 Phase Plane Analysis

- Role of nullclines

# 3.3 Analysis of a 2D Neuron Model

- constant input vs pulse input
- MathDetour 3: Stability of fixed points

#### **Discuss Exercise 1 – MathDetour 3.1: Separation of time scales**

#### Exercise 1 (week 3)

#### even more general

#### Two coupled differential equations

$$\tau_1 \frac{dx}{dt} = -x + h(y)$$
  
$$\tau_2 \frac{dy}{dt} = f(y) + g(x)$$

Separation of time scales

$$\tau_1 \ll \tau_2 \rightarrow x = h(y)$$
  
Reduced 1-dimensional system  
 $\tau_2 \frac{dy}{dt} = f(y) + g(h(y))$ 

# Discuss exercise 1 – Reduction of Hodgkin-Huxley model



#### dynamics of *m* is fast



stimulus

 $m(t) = m_0(u(t))$ 

Fast compared to what?

Neuronal Dynamics – Quiz 3.3.

A-Separation of time scales:

We start with two equations

$$\tau_1 \frac{dx}{dt} = -x + y + I(t)$$
  
$$\tau_2 \frac{dy}{dt} = -y + x^2 + A$$

[ ] If  $\tau_1 \ll \tau_2$  then the system can be reduced to

$$\tau_2 \frac{dy}{dt} = -y + [y + I(t)]^2 + A$$

[ ] If  $\tau_2 \ll \tau_1$  then the system can be reduced to

$$\tau_1 \frac{dx}{dt} = -x + x^2 + A + I(t)$$
[] None of the above is correct.

Pay attention to *I(t): We assume that I(t) is slow compared to both time constants.* 

# **Week 3 – Summary 3.1**

In order to reduce the HH model from 4 to 2 equations we have to simplify. We use two different mathematical methods.

1. Separation of time scale.

If the time scale of two variables is different by a factor 10 or a hundred, we can assume that the faster one of the two variables has already converged to its 'momentary stable state' on the slow time scale. Thus, we can remove the fast variable. We use the separation of time scale to remove the variable m. 2. Exploit similarities.

If two variables evolve on the same time scale, they have, if we are lucky, some similar temporal evolution. We can reduce the two variables to one dimension by turning the coordinate system such that the first dimension is the one where the two variables evolve 'together'. The simplification consists in suppressing the second variable. This is similar to PCA where you would also only keep the first component. However, we need to do this such that also the DYNAMICS stays approximately correct, after reduction to 1 dimension. We use this trick to compress h and n into a single variable w.



# Week 3 – Reducing detail: **Two-dimensional neuron models**

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#### 3.2 **Phase Plane Analysis**

- Role of nullclines

### 3.3 Analysis of a 2D Neuron Model

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#### **3.2. Reduced Hodgkin-Huxley model**



$\frac{dw}{dw}$	$\underline{w-w_0(u)}$
dt	$\tau_w(u)$

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



#### **3.2. Phase Plane Analysis/nullclines**

### First step:

#### *u*-nullcline: all points with *du/dt=0*

*w*-nullcline: all points with *dw/dt=0* 



#### 2-dimensional equation stimulus

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

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

### Enables graphical analysis! -Discussion of threshold -Type I and II

# **3.2. FitzHugh-Nagumo Model**

$$\tau \frac{du}{dt} = F(u, w) + RI(t)$$
$$= u - \frac{1}{3}u^3 - w + RI(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w) = b_0 + b_1 u - w$$

u-nullcline

w-nullcline

#### MathAnalysis, blackboard

# **3.2. flow arrows**

$$\tau \frac{du}{dt} = F(u, w) + RI(t)$$
 Stimulus I=0  
$$dw$$

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

# Consider change in small time step

### Flow on nullcline

# Flow in regions between nullclines





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# 3.1 From Hodgkin-Huxley to 2D

#### - Overview: From 4 to 2 dimensions

- MathDetour 1: Exploiting similarities
- MathDetour 2: Separation of time scales

#### 3.2 **Phase Plane Analysis**

- Role of nullclines

### 3.3 Analysis of a 2D Neuron Model

- constant input vs pulse input
- MathDetour 3: Stability of fixed points

# Neuronal Dynamics – 3.2. flow arrows

$$\tau \frac{du}{dt} = F(u, w) + RI(t)$$
 Stimulus I=0

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

### Consider change in small time step

#### Flow on nullcline

# Flow in regions between nullclines



# **Week 3 – Quiz 3.4**

#### A. u-Nullclines

[] On the u-nullcline, arrows are always vertical [] On the u-nullcline, arrows point always vertically upward [] On the u-nullcline, arrows are always horizontal

#### **B. w-Nullclines**

[] On the w-nullcline, arrows are always vertical [] On the w-nullcline, arrows are always horizontal [] On the w-nullcline, arrows point always to the left

### Take 1 minute

#### Exercise 1: Separation of time scales

#### **A.** One-dimensional system

Consider the following differential equation

$$\tau \frac{dx}{dt} = -x + c \,. \tag{1}$$

**1.1** Find the fixed point  $x_0$  of this system. Hint: a fixed point is a stationary solution  $\Rightarrow \frac{dx}{dt} = 0$ .

1.2 Show that the fixed point is a stable one, and that the solution of (1) converges exponentially towards the fixed point with a time constant  $\tau$ . Hint: write down the solution assuming an initial condition  $x(t=0) \neq x_0$ .

**1.3** Consider the case where *c* is time-dependent, namely,

$$c \equiv c(t) = \left\{ egin{array}{cc} 0 & {
m for} \ t < 0 \ c_0 \ {
m for} \ 0 \leq t < 1 \ 0 \ {
m for} \ t > 1 \,. \end{array} 
ight.$$

Calculate the solution x(t) with initial condition x(t = -10) = 0.

1.4 Take the expression x(t) you have found in the previous question. Consider  $\tau = 0.5$  and  $\tau = 0.01$  and sketch the function graph.

**B.** Separation of time scales

Consider the following system of equations:

$$\frac{du}{dt} = f(u) - m$$
$$\epsilon \frac{dm}{dt} = -m + c(u)$$

with  $\epsilon = 0.01$ .

1.5 Exploit the fact that  $\epsilon \ll 1$  and reduce the system to one equation (note the similarity between the m-equation and Eq.(1)).

**1.6** Set f(u) = -au + b where  $a > 0, b \in \mathbb{R}$  and  $c(u) = \tanh(u)$ . Discuss the stability of the fixed points with respect to a and b. Hint: use the graphical analysis for one dimensional equations from week 1: when plotting f(u) and c(u) against u, you can read off the fixed point from that graph.

#### 2.1 Linear system

Consider the following linear system:

$$\begin{bmatrix} \frac{du}{dt} &= \alpha u - w \\ \frac{dw}{dt} &= \beta u - w \\ -Ar \text{ where } r - \begin{pmatrix} v \\ \end{pmatrix} \text{ and } A - \begin{pmatrix} \alpha & -1 \\ \end{pmatrix} \text{ Determine}$$

These equations can be written in matrix form as  $\frac{d}{dt}x = Ax$  where  $x = \begin{pmatrix} c \\ w \end{pmatrix}$  and  $A = \begin{pmatrix} \alpha & -1 \\ \beta & -1 \end{pmatrix}$ . Determine the conditions for stability of the point (u = 0, w = 0) in the case  $\beta > \alpha$  by studying the eigenvalues of the

above matrix. (Hint: Distinguish the cases of real and complex eigenvalues.)

2.2 Piecewise linear Fitzhugh-Nagumo model

The Fitzhugh-Nagumo model is defined by the equations

$$\left[ egin{array}{cc} \displaystyle rac{du}{dt} &= F(u,w) = f(u) - w + I \ \displaystyle rac{dw}{dt} &= G(u,w) = bu - w \end{array} 
ight.$$

Here, u(t) is the membrane potential and w(t) is a second, time-dependent variable. I stands for the injected current. A simplified model is obtained by considering a piecewise linear f(u):

$$f(u) = \begin{cases} -u & \text{if } u < 1\\ \frac{u-1}{a} - 1 & \text{if } 1 \le u < 1 + 2a\\ 2(1+a) - u & \text{if } u > 1 + 2a \end{cases}$$

with a < 1, b > 1/a.

(i) Sketch the "nullclines" du/dt = 0 and dw/dt = 0 in a (u, v)-plot. Consider the case I = 0. How does the fixed point move as I is varied? Sketch the form of the flow (i.e., the vector (du/dt, dw/dt)) along the nullclines and deduce qualitatively the shape of the trajectories.

(ii) Calculate the Jacobian matrix evaluated at the fixed point,

$$J = \left( \begin{array}{cc} \frac{\partial F}{\partial u} & \frac{\partial F}{\partial w} \\ \frac{\partial G}{\partial u} & \frac{\partial G}{\partial w} \end{array} \right).$$

Determine, by studying the eigenvalues of J, the linear stability of the fixed point as a function of I. What happens when the fixed point destabilizes?

#### **3.2. FitzHugh-Nagumo Model**

$$\tau \frac{du}{dt} = F(u, w) + RI(t)$$
$$= u - \frac{1}{3}u^3 + RI(t) - w$$

≥

$$\tau_{w} \frac{dw}{dt} = G(u, w) = b_{0} + b_{1}u - w$$

$$/ / /$$
change bo, b1



Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014)

# **3.2. Nullclines of reduced HH model**

stimulus

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

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

u-nullcline

w-nullcline



Gerstner et al., Cambridge Univ. Press (2014)

### **3.2. Phase Plane Analysis**

2-dimensional equation stimulus

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

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

Enables graphical analysis! Important role of

- nullclines
- flow arrows

Application to neuron models

# **Week 3 – Summary 3.2**

Once we are in two dimensions we can use phase plane analysis. Two important concepts are the 'nullclines'; and the local direction of the 'flow'.

Intersections of the two nullclines correspond to fixed points. It is a bit of work to decide whether a fixed point is stable or not. However, in some cases (such as a saddle point) stability is visible directly from the graph.

Stability of a fixed point is determined by linearizing around the fixed point. Since we are in 2 dimensions, linearization yields a 2x2 matrix. The eigenvalues determine the stability (See exercise 2.1).

The FitzHuhg Nagumo model is a particularly simple 2-dimensional model. The reduction of the full Hodgkin-Huxley model yields a more complicated picture in the phase plane.

### **3.3. Analysis of a 2D neuron model**

# 2 important input scenarios

- Pulse input
- Constant input

# 2-dimensional equation

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

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

Enables graphical analysis!

# **3.3. 2D neuron model : Pulse input**



#### pulse input

$$\frac{d}{dt}u = F(u, w) + RI$$
$$\frac{d}{dt}w = G(u, w)$$

### **3.3. FitzHugh-Nagumo Model : Pulse input**

$$\tau \frac{du}{dt} = F(u, w) + RI(t) = u - \frac{1}{3}u^3 - w + RI$$



# **3.3. FitzHugh-Nagumo Model : Pulse input**



# 3.3. FitzHugh-Nagumo Model – 2 different inputs

Now

#### DONE! **Pulse input:**

- jump of voltage
- 'new initial condition'
- spike generation for large input pulses

#### 2 important input scenarios

#### constant input:

- graphics?
- spikes?
- repetitive firing?



#### **3.3. FitzHugh-Nagumo Model: Constant input**

$$\tau \frac{du}{dt} = F(u, w) + RI_0$$
$$= u - \frac{1}{3}u^3 - w + RI_0$$

$$\tau_w \frac{dw}{dt} = G(u, w) = b_0 + b_1 u - w$$

#### Intersection point (fixed point) -moves -changes Stability





*u*-nullcline

#### Week 3 – part 3: Analysis of a 2D neuron model





# **3.1 From Hodgkin-Huxley to 2D**

# **3.2 Phase Plane Analysis**

- Role of nullcline

### 3.3 Analysis of a 2D Neuron Model

- pulse input
- constant input

-MathDetour 3: Stability of fixed points

# Discussion of exercise 2 Detour. Stability of fixed points

2-dimensional equation stimulus

$$\tau \frac{du}{dt} = F(u, w) + RI_0$$

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

# How to determine stability of fixed point?

# Discussion of exercise 2 - Detour: Stability of fixed points.



# **Discussion of Exercise 2: Detour - Stability of fixed points**

#### stimulus

$$\tau \frac{du}{dt} = au - w + I_0$$

$$\tau_w \frac{dw}{dt} = c \, u - w$$





# **Discussion of Exercise 2: Detour.** Stability of fixed points

$$\tau \frac{du}{dt} = F(u, w) + RI_0$$

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

#### zoom in:



stable saddle



# **3.3. Neuron models and Stability of fixed points**

#### Now Back:

Application to our neuron model

#### 2-dimensional equation

$$\tau \frac{du}{dt} = F(u, w) + RI_0$$

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

# Stability characterized by Eigenvalues of linearized equations

 $\frac{\mathrm{d}}{\mathrm{d}t} \boldsymbol{x} = \begin{pmatrix} F_u & F_w \\ G_u & G_w \end{pmatrix} \boldsymbol{x}$ 

#### **3.3. FitzHugh-Nagumo Model: Constant input**

$$\tau \frac{du}{dt} = F(u, w) + RI_0$$
$$= u - \frac{1}{3}u^3 - w + RI_0$$

$$\tau_w \frac{dw}{dt} = G(u, w) = b_0 + b_1 u - w$$

#### Intersection point (fixed point) -moves -changes Stability



u-nullcline

#### **3.3. FitzHugh-Nagumo Model: Constant input**

$$\tau \frac{du}{dt} = F(u, w) + RI_0$$
$$= u - \frac{1}{3}u^3 - w + RI_0$$

$$\tau_w \frac{dw}{dt} = G(u, w) = b_0 + b_1 u - w$$

#### Intersection point (fixed point) -moves -changes Stability

 $\frac{dw}{dw} = 0$  w-nullcline W dt  $I(t)=I_0$ du dt

*u*-nullcline

#### **3.3. FitzHugh-Nagumo Model : Constant input**



FN model with  $b_0 = 0.9; b_1 = 1.0; RI_0 = 2$ constant input: u-nullcline moves

0

# Neuronal Dynamics – Quiz 3.5.

A. Short current pulses. In a 2-dimensional neuron model, the effect of a delta

current pulse can be analyzed [] By moving the u-nullcline vertically upward [] By moving the w-nullcline vertically upward [] As a potential change in the stability or number of the fixed point(s) [] As a new initial condition [] By following the flow of arrows in the appropriate phase plane diagram

**B.** Constant current. In a 2-dimensional neuron model, the effect of a constant current can be analyzed

[] By moving the u-nullcline vertically upward [] By moving the w-nullcline vertically upward [] As a potential change in the stability or number of the fixed point(s) [] By following the flow of arrows in the appropriate phase plane diagram

# NOW Exercise 2.1: Stability of Fixed Point in 2D

$$\frac{du}{dt} = \alpha u - w$$
$$\frac{dw}{dt} = \beta u - w$$

Exercises: 2.1**now!** 2.2 homework - calculate stability

 $\frac{dx}{dx} = -\frac{x}{dx}$ 

dt au

- compare



# Week 3 – Summary 3.3

Phase plane analysis of neuron models is particularly interesting because the input I only enters into the first variable (voltage u).

As a consequence of this observation, we can discuss two important input scenarios as follows:

- 1. Constant input. In this case the u-nullcline is shifted vertically.
- 2. Pulse input. In this case the u-nullcline is not shifted, but the pulse causes a horizontal shift of the initial condition.

# **Computer exercise now** Can we understand the dynamics of the 2D model?



#### **Now: computer exercises**

ramp input/ constant input

f-l curve



# NOW Exercise 2.1: Stability of Fixed Point in 2D

$$\frac{du}{dt} = \alpha u - w$$
$$\frac{dw}{dt} = \beta u - w$$

*Exercises:* - compare **2.1 start now!** 2.2 homework (you may start if you have time)



# Discussion of Exercise 2 Detour. Stability of fixed points

$$\tau \frac{du}{dt} = F(u, w) + RI_0$$

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

#### zoom in:

$$x = u - u_0$$

$$y = w - w_0$$

Fixed point at  $(u_0, w_0)$ At fixed point

$$0 = F(u_0, w_0) + RI_0$$
$$0 = G(u_0, w_0)$$

# Discussion of Exercise 2 - Detour. Stability of fixed points

$$\tau \frac{du}{dt} = F(u, w) + RI_0$$

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

#### zoom in:

$$x = u - u_0$$
  

$$y = w - w_0$$
  

$$\tau \frac{dx}{dt} = F_u x + F_w y$$
  

$$\tau_w \frac{dy}{dt} = G_u x + G_w y$$

# Fixed point at $(u_0, w_0)$ At fixed point

$$0 = F(u_0, w_0) + RI_0$$
$$0 = G(u_0, w_0)$$



# **Discussion of Exercise 2 Detour.** Stability of fixed points

Linear matrix equation

 $\frac{\mathrm{d}}{\mathrm{d}t}\boldsymbol{x} = \begin{pmatrix} F_u & F_w \\ G_u & G_w \end{pmatrix} \boldsymbol{x}_{\mathrm{f}}$ Search for solution  $\dot{x}(t) = e \exp(\lambda t)$ 

Two solution with Eigenvalues  $\lambda_{\perp}, \lambda_{\perp}$ 

$$\lambda_{+} + \lambda_{-} = F_{u} + G_{w}$$
$$\lambda_{+} \lambda_{-} = F_{u} G_{w} - F_{w} G_{u}$$

# Discussion of Exercise 2: Detour. Stability of fixed points

Linear matrix equation



Search for solution  $\dot{x}(t) = e \exp(\lambda t)$ 

Two solution with Eigenvalues  $\lambda_{+}, \lambda_{-}$ 

$$\lambda_{+} + \lambda_{-} = F_{u} + G_{w}$$
$$\lambda_{+} \lambda_{-} = F_{u} G_{w} - F_{w} G_{u}$$

# Stability requires: $\lambda_{+} < 0$ and $\lambda_{-} < 0$ $F_{\mu} + G_{w} < 0$ and $F_{\mu}G_{\mu} - F_{\mu}G_{\mu} > 0$

# Discussion of exercise 2: Detour. Stability of fixed points

stimulus

$$\tau \frac{du}{dt} = au - w + I_0$$

$$\tau_w \frac{dw}{dt} = c \, u - w$$





