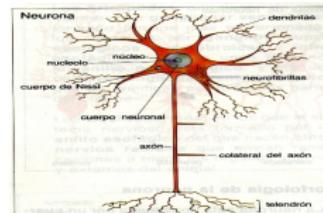
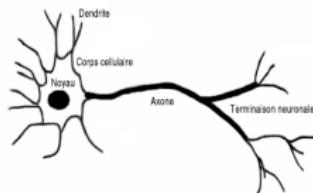
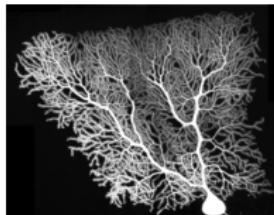


# PDEs for neural networks analysis and behaviour

Benoît Perthame

Course IV. Networks, time elapsed models



- I. The single neuron,
- II. Networks, examples
- III. Networks, Integrate & Fire
- IV. Networks, time elapsed models
  - IV. 1. time elapsed networks
  - IV. 2. Blow-up and spontaneous activity
  - IV. 3. Voltage vs time elapsed

# Elapsed time structured model



Based on K. Pakdaman, J. Champagnat, J.-F. Vibert

- $s$  represents the time elapsed since the last discharge
- $n(s, t)$  probability of finding a neuron in 'state'  $s$  at time  $t$
- $N(t) = \text{activity of the network}$

$$\frac{\partial n(s, t)}{\partial t} + \overbrace{\frac{\partial n(s, t)}{\partial s}}^{\text{elapsed time advances}} + \overbrace{r(s, bN(t)) n(s, t)}^{\text{firing neurons}} = 0,$$
$$N(t) := n(s=0, t) = \underbrace{\int_0^{+\infty} r(s, bN(t)) n(s, t) ds}_{\text{reset of firing neurons}},$$

# The renewal equation



$$\begin{cases} \frac{\partial n(s,t)}{\partial t} + \frac{\partial n(s,t)}{\partial s} + r(s) n(s, t) = 0, \\ N(t) := n(s=0, t) = \int_0^{+\infty} b(s) n(s, t) ds \end{cases}$$

We want a steady state (compute the growth rate)

Long standing equation (Feller, renewal process)

# The renewal equation



$$\begin{cases} \frac{\partial n(s,t)}{\partial t} + \frac{\partial n(s,t)}{\partial s} + [\lambda + r(s)] n(s,t) = 0, \\ N(t) := n(s=0, t) = \int_0^{+\infty} b(s) n(s, t) ds \end{cases}$$

We look for the first eigenfunction/eigenvalue

$$\begin{cases} \frac{\partial \bar{n}(s)}{\partial s} + [\lambda + r(s)] \bar{n}(s) = 0 \\ \bar{n}(s=0) = \int_0^{+\infty} b(s) \bar{n}(s) ds \end{cases}$$

$$\bar{n}(s) > 0$$

# The renewal equation



We look for the first eigenfunction/eigenvalue

$$\begin{cases} \frac{\partial \bar{n}(s)}{\partial s} + [\lambda + r(s)] \bar{n}(s) = 0, \\ \bar{n}(s=0) = \int_0^{+\infty} b(s) \bar{n}(s) ds \end{cases}$$

$$\bar{n}(s) = \bar{n}(0)e^{-R(s)-\lambda s}, \quad R(s) = \int_0^s r$$

In the boundary condition

$$\bar{n}(0) = \bar{n}(0) \int_0^{\infty} b(s)e^{-R(s)-\lambda s} ds$$

**Find  $\lambda$  such that**

$$\int_0^{\infty} b(s)e^{-R(s)-\lambda s} ds = 1$$

# The renewal equation



$$\begin{cases} \frac{\partial n(s,t)}{\partial t} + \frac{\partial n(s,t)}{\partial s} + [\lambda + r(s)] n(s,t) = 0, \\ N(t) := n(s=0, t) = \int_0^{+\infty} b(s) n(s, t) ds \end{cases}$$

$$\bar{n}(s) = \bar{n}(0)e^{-R(s)-\lambda s}, \quad R(s) = \int_0^s r$$

**Find  $\lambda$  such that**

$$\int_0^\infty b(s)e^{-R(s)-\lambda s} ds = 1$$

When  $b(\cdot) = r(\cdot)$  then  $\lambda = 0$

# The renewal equation



$$\begin{cases} \frac{\partial n(s,t)}{\partial t} + \frac{\partial n(s,t)}{\partial s} + [\lambda + r(s)] n(s,t) = 0, \\ N(t) := n(s=0, t) = \int_0^{+\infty} b(s) n(s, t) ds \\ \bar{n}(s) = \bar{n}(0) e^{-R(s)-\lambda s}, \quad \int_0^{\infty} b(s) e^{-R(s)-\lambda s} ds = 1 \end{cases}$$

Prove that

$$n(s, t) \rightarrow \bar{\rho} \bar{n}(s)$$

Use Generalized Relative Entropy

# The renewal equation



$$\begin{cases} \frac{\partial n(s,t)}{\partial t} + \frac{\partial n(s,t)}{\partial s} + [\lambda + r(s)] n(s,t) = 0, \\ N(t) := n(s=0,t) = \int_0^{+\infty} b(s) n(s,t) ds \\ n(s,t) \rightarrow \bar{\rho} \bar{n}(s) \end{cases}$$

Dual eigenfunction

$$\frac{\partial \phi(s)}{\partial s} - [\lambda + r(s)] \phi(s) = -\phi(0)b(s)$$

We have

$$\frac{d}{dt} \int n(s,t) \phi(s) ds = 0$$

$$\int n(s,t=0) \phi(s) ds = \bar{\rho} \int \bar{n}(s) \phi(s) ds$$

So the dual eigenfunction is important

# The renewal equation



$$\begin{cases} \frac{\partial n(s,t)}{\partial t} + \frac{\partial n(s,t)}{\partial s} + [\lambda + r(s)] n(s,t) = 0, \\ N(t) := n(s=0,t) = \int_0^{+\infty} b(s) n(s,t) ds \end{cases}$$

Dual eigenfunction

$$\frac{\partial \phi(s)}{\partial s} - [\lambda + r(s)] \phi(s) = -\phi(0)b(s)$$

Usually for a conservative equation  $\phi \equiv 1$

- For example, when  $b(\cdot) = r(\cdot)$ , then  $\lambda = 0$ .
- Then the relative entropy is  $\int_0^{\infty} \bar{n}(s) H\left(\frac{n(s,t)}{\bar{n}(s)}\right) ds$
- Other standard example is the Fokker-Planck equation

# The renewal equation



$$\begin{cases} \frac{\partial n(s,t)}{\partial t} + \frac{\partial n(s,t)}{\partial s} + [\lambda + r(s)] n(s,t) = 0, \\ N(t) := n(s=0, t) = \int_0^{+\infty} b(s) n(s, t) ds \\ \frac{\partial \phi(s)}{\partial s} - [\lambda + r(s)] \phi(s) = -\phi(0)b(s) \end{cases}$$

The Generalized Relative Entropy is, with  $u(s, t) = \frac{n(s, t)e^{-\lambda t}}{\bar{n}(s)}$

$$E(t) := \int_0^{\infty} \phi(s) \bar{n}(s) H(u(s, t)) ds$$

# The renewal equation



$$\begin{cases} \frac{\partial n(s,t)}{\partial t} + \frac{\partial n(s,t)}{\partial s} + [\lambda + r(s)] n(s,t) = 0, \\ N(t) := n(s=0,t) = \int_0^{+\infty} b(s) n(s,t) ds \end{cases}$$

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The Generalized Relative Entropy is, with  $u(s,t) = \frac{n(s,t)e^{-\lambda t}}{\bar{n}(s)}$

$$E(t) := \int_0^{\infty} \phi(s) \bar{n}(s) H(u(s,t)) ds$$

$$\frac{dE(t)}{dt} = -D_H(t)\phi(0)$$

$$\begin{aligned} D_H(t) &= \int b(s) \bar{n}(s) H\left(\frac{n(s,t)}{\bar{n}(s)}\right) ds - H\left(\int b(s) \bar{n}(s) \frac{n(s,t)}{\bar{n}(s)} ds\right) \\ &> 0 \quad \text{by Jensen inequality} \end{aligned}$$

# The renewal equation



And a Poincaré inequality?

$$\nu \int_0^\infty \phi(s) \bar{n}(s) |u(s)| ds \leq \int b(s) \bar{n}(s) |u(s)| ds - \left| \int_0^\infty b(s) \bar{n}(s) u(s) ds \right|$$

when

$$\int b(s) \bar{n}(s) = 1, \quad \int u(s) \bar{n}(s) \phi(s) ds = 0$$

## Theorem

If  $b(\cdot) \geq \nu\phi(s)$ , then the Poincaré inequality holds true.

Poincaré inequality

$$\nu \int_0^\infty \phi(s) \bar{n}(s) |u(s)| ds \leq \int b(s) \bar{n}(s) |u(s)| ds - \left| \int_0^\infty b(s) \bar{n}(s) u(s) ds \right|$$

when

$$\int b(s) \bar{n}(s) ds = 1, \quad \int u(s) \bar{n}(s) \phi(s) ds = 0$$

Proof of Poincaré inequality

$$\left| \int_0^\infty b(s) \bar{n}(s) u(s) ds \right| = \left| \int_0^\infty [b(s) - \nu \phi(s)] \bar{n}(s) u(s) ds \right|$$

## Poincaré inequality

$$\nu \int_0^\infty \phi(s) \bar{n}(s) |u(s)| ds \leq \int b(s) \bar{n}(s) |u(s)| ds - \left| \int_0^\infty b(s) \bar{n}(s) u(s) ds \right|$$

when

$$\int b(s) \bar{n}(s) = 1, \quad \int u(s) \bar{n}(s) \phi(s) ds = 0$$

## Proof of Poincaré inequality

$$\begin{aligned} \left| \int_0^\infty b(s) \bar{n}(s) u(s) ds \right| &= \left| \int_0^\infty [b(s) - \nu \phi(s)] \bar{n}(s) u(s) ds \right| \\ &\geq \int_0^\infty [b(s) - \nu \phi(s)] \bar{n}(s) |u(s)| ds \end{aligned}$$

# The renewal equation



Poincaré inequality

$$\nu \int_0^\infty \phi(s) \bar{n}(s) |u(s)| ds \leq \int b(s) \bar{n}(s) |u(s)| ds - \left| \int_0^\infty b(s) \bar{n}(s) u(s) ds \right|$$

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Proof of Poincaré inequality

$$\begin{aligned} \left| \int_0^\infty b(s) \bar{n}(s) u(s) ds \right| &= \left| \int_0^\infty [b(s) - \nu \phi(s)] \bar{n}(s) u(s) ds \right| \\ &\geq \int_0^\infty [b(s) - \nu \phi(s)] \bar{n}(s) |u(s)| ds \\ &= \int_0^\infty b(s) \bar{n}(s) |u(s)| ds - \int_0^\infty \nu \phi(s) \bar{n}(s) |u(s)| ds \end{aligned}$$

The GRE is robust

$$\begin{cases} \frac{\partial n(s,t)}{\partial t} + \frac{\partial n(s,t)}{\partial s} + r(s, t) n(s, t) = 0, \\ N(t) := n(s=0, t) = \int_0^{+\infty} b(s, t) n(s, t) ds \end{cases}$$

Assume that  $r(s, t)$ ,  $b(s, t)$  are time periodic

# Floquet case



$$\begin{cases} \frac{\partial n(s,t)}{\partial t} + \frac{\partial n(s,t)}{\partial s} + [\lambda_F + r(s,t)] n(s,t) = 0, \\ N(t) := n(s=0, t) = \int_0^{+\infty} b(s, t) n(s, t) ds \end{cases}$$

$r(s, t)$ ,  $b(s, t)$  are time periodic

$$\begin{cases} \frac{\partial n(s,t)}{\partial t} + \frac{\partial n(s,t)}{\partial s} + [\lambda_F + r(s,t)] n(s,t) = 0, \\ N(t) := n(s=0,t) = \int_0^{+\infty} b(s,t) n(s,t) ds \end{cases}$$

$r(s, t)$ ,  $b(s, t)$  are time periodic

$$\begin{cases} \frac{\partial \bar{n}(s,t)}{\partial t} + \frac{\partial \bar{n}(s,t)}{\partial s} + [\lambda_F + r(s,t)] \bar{n}(s,t) = 0, \\ \bar{N}(t) := \bar{n}(s=0,t) = \int_0^{+\infty} b(s,t) \bar{n}(s,t) ds \end{cases}$$

$$\frac{\partial \bar{\phi}(s,t)}{\partial t} + \frac{\partial \bar{\phi}(s,t)}{\partial s} - [\lambda_F + r(s,t)] \bar{\phi}(s,t) = \phi(0,t) b(s,t),$$

with

$$\bar{n}(s, t) > 0, \quad \bar{\phi}(s, t) > 0 \text{ time periodic}$$

$$\begin{cases} \frac{\partial n(s,t)}{\partial t} + \frac{\partial n(s,t)}{\partial s} + [\lambda_F + r(s,t)] n(s,t) = 0, \\ N(t) := n(s=0,t) = \int_0^{+\infty} b(s,t) n(s,t) ds \end{cases}$$

The Generalized Relative Entropy is

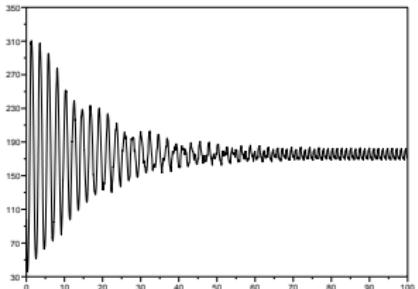
$$E(t) := \int_0^\infty \bar{\phi}(s,t) \bar{n}(s,t) H\left(\frac{n(s,t)}{\bar{n}(s,t)}\right) ds$$

$$\frac{dE(t)}{dt} = -D_H(t)\phi(0,t)$$

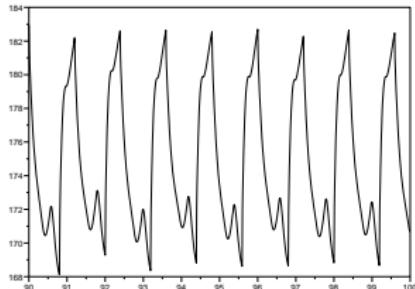
$$D_H(t) = \int b(s,t) \bar{n}(s,t) H\left(\frac{n(s,t)}{\bar{n}(s,t)}\right) ds - H\left(\int b(s,t) \bar{n}(s,t) \frac{n(s,t)}{\bar{n}(s,t)} ds\right)$$

> 0      by Jensen inequality

# Floquet case



global simulation



zoom on the last periods

Total cell density  $\int_0^\infty n(s, t) ds$  as a function of time

# Elapsed time structured model



$$\frac{\partial n(s,t)}{\partial t} + \overbrace{\frac{\partial n(s,t)}{\partial s}}^{\text{elapsed time advances}} + \overbrace{r(s, bN(t)) n(s,t)}^{\text{firing neurons}} = 0,$$
$$N(t) := n(s=0, t) = \underbrace{\int_0^{+\infty} r(s, bN(t)) n(s,t) ds}_{\text{reset of firing neurons}},$$

**Theorem** For small or large connectivity ( $b > 0$  small or large) then desynchronization still holds

$$n(s, t) \xrightarrow[t \rightarrow \infty]{} P_b(s)$$

$$\frac{\partial n(s,t)}{\partial t} + \overbrace{\frac{\partial n(s,t)}{\partial s}}^{\text{elapsed time advances}} + \overbrace{r(s, bN(t)) n(s,t)}^{\text{firing neurons}} = 0,$$

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**Theorem** For small or large connectivity ( $b > 0$  small or large) then desynchronization still holds

$$n(s, t) \xrightarrow[t \rightarrow \infty]{} P_b(s)$$

- In the middle range connectivity there are several periodic solutions (analytic forms of solutions),
- These are stable (observed numerically).

$$\frac{\partial n(s,t)}{\partial t} + \overbrace{\frac{\partial n(s,t)}{\partial s}}^{\text{elapsed time advances}} + \overbrace{r(s, bN(t)) n(s,t)}^{\text{firing neurons}} = 0,$$

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**Theorem** For small or large connectivity ( $b > 0$  small or large) then desynchronization still holds

$$n(s, t) \xrightarrow[t \rightarrow \infty]{} P_b(s)$$

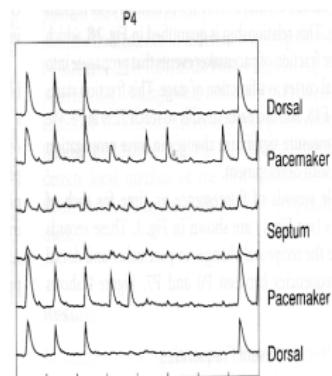
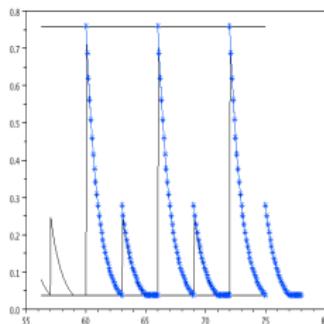
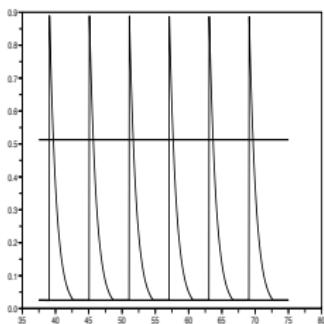
- Most accurate results today : Mischler, Cañizo-Yoldas

# Elapsed time structured model



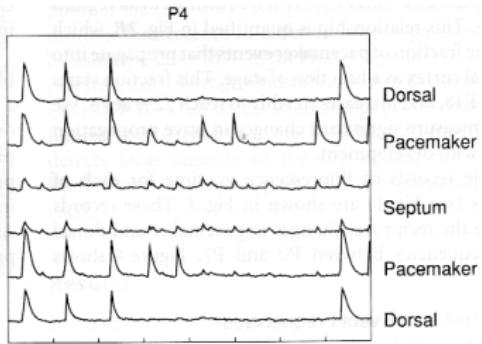
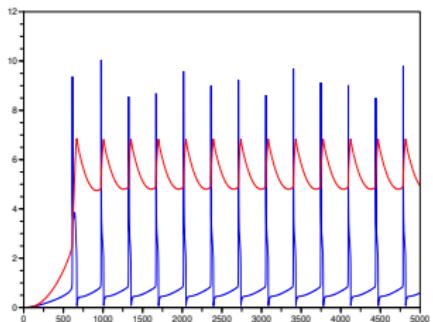
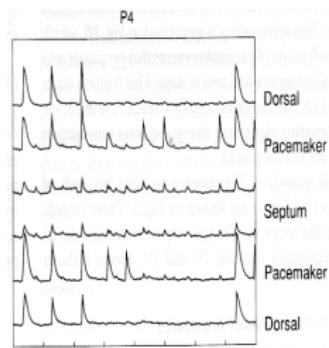
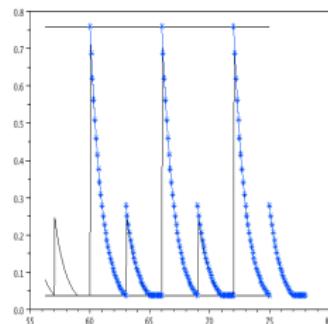
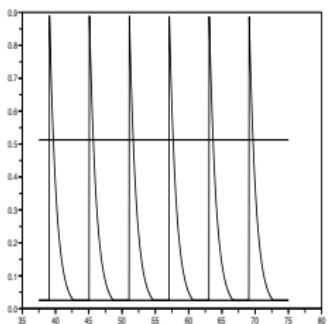
elapsed time advances

$$\frac{\partial n(s,t)}{\partial t} + \underbrace{\frac{\partial n(s,t)}{\partial s}}_{\text{firing neurons}} + \underbrace{r(s, bN(t))}_{\text{reset of firing neurons}} n(s,t) = 0,$$
$$N(t) := n(s=0, t) = \underbrace{\int_0^{+\infty} r(s, bN(t)) n(s, t) ds}_{\text{reset of firing neurons}},$$



Right : Conhaim et al (2011) J. of physiology 589(10) 2529-2541.

# Comparison with I&F



We encountered two equations

## Time elapsed

$$\begin{cases} \partial_t n + \partial_s n + r(s)n = 0, \\ n(s=0, t) = \int_0^\infty r(s)n(s, t)ds =: N(t), \\ n(s, 0) = n^0(s), \end{cases}$$

## LIF

$$\begin{cases} \partial_t \hat{n} + \partial_v [h(v)\hat{n}] - a\partial_{vv}^2 \hat{n} = N(t)\delta(v - V_R), \\ \hat{n}(V_F, t) = 0, \quad N(t) := -a\partial_v \hat{n}(V_F, t). \end{cases}$$

Is there a connection between these two equations?

From G. Dumont and J. Henry (linear equations)

Being given  $V_R$ ,  $V_F$ ,  $h(\cdot)$  and

$$\begin{cases} \partial_t \hat{n} + \partial_v [h(v) \hat{n}] - a \partial_{vv}^2 \hat{n} = N(t) \delta(v - V_R), \\ \hat{n}(V_F, t) = 0, \quad -a \partial_v \hat{n}(V_F, t) = N(t). \end{cases}$$

**Theorem** There are functions  $r(s)$ ,  $q(v, s)$  such that, for solutions of

$$\begin{cases} \partial_t n + \partial_s n + r(s)n = 0, \\ n(s=0, t) = \int_0^\infty r(s)n(s, t)ds =: N(t), \\ n(s, 0) = n^0(s), \end{cases}$$

then, with the same  $N(t)$ , we have

$$\hat{n}(v, t) = \int_0^\infty q(v, s)n(s, t)ds$$

$$\begin{cases} \partial_s q(v, s) + \partial_v [h(v)q] - \partial_{vv}^2 q = r(s)q \\ q(V_F, s) = 0 \\ q(v, s=0) = \delta(v - V_R) \\ r(s) := -\partial_v q(V_F, s) \quad (\text{implicit}) \end{cases}$$

We notice that  $\int_{-\infty}^{V_F} q(v, s)dv = 1, \quad \forall s \geq 0.$

Because

$$\frac{d}{ds} \int_{-\infty}^{V_F} q(v, s)dv + r(s) = r(s) \int_{-\infty}^{V_F} q(v, s)dv.$$

Next, let  $n(s, t)$  solve the age structure equation

$$\begin{cases} \partial_t n + \partial_s n + r(s)n = 0, \\ n(s=0, t) = \int_0^\infty r(s)n(s, t)ds =: N(t), \\ n(s, 0) = n^0(s), \quad \text{with } \int_0^\infty n^0(s)ds = 1. \end{cases}$$

# Elapsed time and IF



Is there a solution to

$$\begin{cases} \partial_s q(v, s) + \partial_v [h(v)q] - \partial_{vv}^2 q = r(s)q \\ q(V_F, s) = 0 \\ q(v, s=0) = \delta(v - V_R) \\ r(s) := -\partial_v q(V_F, s) \quad (\text{implicit}) \end{cases}$$

# Elapsed time and IF



Is there a solution to

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$$\begin{cases} \partial_s q_0(v, s) + \partial_v [h(v)q_0] - \partial_{vv}^2 q_0 = 0 \\ q_0(V_F, s) = 0 \\ q_0(v, s=0) = \delta(v - V_R) \end{cases}$$

and set

$$q(v, s) = \frac{q_0(v, s)}{\int q_0(v, s) dv}$$

$$\begin{cases} \partial_t n(s, x, t) + \partial_s n + r(s, S(t, x))n = 0, \\ N(x, t) := n(s=0, x, t) = \int_0^\infty r(s)n(s, x, t)ds \end{cases}$$

$$\frac{dS(t, x)}{dt} + S(t, x) = \int w(x, y)N(t, y)dy$$

$$\begin{cases} \partial_t n(s, x, t) + \partial_s n + r(s, S(t, x))n = 0, \\ N(x, t) := n(s=0, x, t) = \int_0^\infty r(s)n(s, x, t)ds \end{cases}$$

$$\frac{dS(t, x)}{dt} + S(t, x) = \int w(x, y)N(t, y)dy$$

Assume quasi-steady state

$$n(s, x) = n(0, x) \exp(R(s, x, \mathcal{N})), \quad \int n(s, x)ds = 1$$

$$N(x, t) = \left( \int \exp(-R(s, S(x, t)))ds \right)^{-1}$$

$$\begin{cases} \partial_t n(s, x, t) + \partial_s n + r(s, S(x, t))n = 0, \\ N(x, t) := n(s=0, x, t) = \int_0^\infty r(s)n(s, x, t)ds \end{cases}$$

$$\frac{dS(t, x)}{dt} + S(t, x) = \int w(x, y)N(y, t)dy$$

Assume quasi-steady state

$$n(s, x) = n(0, x) \exp(R(s, x, \mathcal{N})), \quad \int n(s, x)ds = 1$$

$$N(x, t) = \left( \int \exp(-R(s, S(x, t)))ds \right)^{-1}$$

One gets Wilson-Cowan type model

$$\frac{dS(x, t)}{dt} + S(x, t) = \int w(x, y)\sigma(S(y, t))dy$$

## THANKS TO MY COLLABORATORS



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D. Salort



K. Pakdaman



C. Wainrib

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# THANK YOU