Floquet spectra of the splay states in pulse-coupled networks

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Introduction (I)

Splay States

These states represent collective modes emerging in networks of fully coupled nonlinear oscillators.

- all the oscillations have the same wave-form X ;
- their phases are "splayed" apart over the unit circle

The state x_k of the single oscillator can be written as

$$x_k(t) = X(t + kT/N) = Acos(\omega t + 2\pi k/N) \;\; ; \quad \omega = 2\pi/T \;\; ; \qquad k = 1, \ldots, N$$

- N = number of oscillators
- T = period of the collective oscillation
- X = common wave form

Introduction (II)

Splay states have been numerically and theoretically studied in

- Josephson junctions array (Strogatz-Mirollo, PRE , 1993)
- globally coupled Ginzburg-Landau equations (Hakim-Rappel, PRE, 1992)
- globally coupled laser model (Rappel, PRE, 1994)
- fully pulse-coupled neuronal networks (Abbott-van Vreesvijk, PRE, 1993)

Splay states have been observed experimentally in

- multimode laser systems (Wiesenfeld et al., PRL, 1990)
- electronic circuits (Ashwin et al., Nonlinearity, 1990)

Nowdays Relevance for Neural Networks

- LIF + Dynamic Synapses - Plasticity (Bressloff, PRE, 1999)
- More realistic neuronal models (Brunel-Hansel, Neural Comp., 2006)

Introduction (III)

Watanabe & Strogatz (Physica D - 1994) have demonstrated for a system of N identical phase oscillators with local force fields represented by single harmonic function

$$\dot{\theta}_j = f + g \ \cos\theta_j + h \ \sin\theta_j \qquad j = 1, \ldots, N \qquad ;$$

where $\theta_j \in [0:2\pi]$ and f,g and h are functions of $\{\theta_k\}$ periodic in each argument, that the splay states are characterized by $N-3$ neutrally stable directions. The functions f,g, h represent common fields determined by all the oscillators.

This result extends also to systems where the phase oscillators are coupled to some external dynamical variable Q, e.g this is the case of a Josephson junction arrays:

(1) $$\dot{\theta}_j + \sin\theta_j + \dot{Q} = I_b \qquad j = 1, \ldots, N \qquad ;$$

(2) $$L\ddot{Q} + R\dot{Q} + C^{-1}Q = \frac{1}{N}\sum_{k=1}^{N}\dot{\theta}_k$$

in this case the above N+2 set of equations can be reduced via a nonlinear transformation to a five-dimensional system.

Summary

- Network of pulse-coupled identical neurons with generic force field (Leaky Integrate-and-Fire (LIF) models representing a special case)
- stability properties of states with uniform spiking rate (Splay States)

LIF model $F(x) = a - x$

- The network dynamics can be rewritten as an Event Driven Map
- The stability of the Splay State reduces to a fixed point stability analysis
- The Floquet spectrum can be analyzed in two limiting case: Short (SWs) and Long Wavelengths (LWs) (analogy with Extended Systems)
- In finite networks, approximations $\mathcal{O}(1/N^4)$ are needed to reproduce the splay state Floquet spectrum, that scales as $1/N^2$

Generic force field $F(x)$

- For continuous F, the SW Floquet spectrum scales faster than $1/N^2$
- For discontinuous F, the stability/instability of the SW spectrum is determined by the sign of the difference $[F(1) - F(0)]$

The Model

The dynamics of the membrane potential $x_i(t)$ of the i–th neuron is given by

$$\dot{x}_i = F(x_i) + gE(t)\,,\ x_i \in (-\infty, 1), \quad \Theta = 1, \quad x_R = 0, \qquad i = 1, \dots, N$$

- $F(x)$ is periodic in $[0:1]$ - for LIF neurons $F(x) = a - x$
- single neurons are in the repetitive firing regime ($F(x) > 0$)
- g is the coupling - excitatory ($g > 0$) or inhibitory ($g < 0$)

Pulse Coupling Scheme

- each emitted pulse has the shape $E_s(t) = \frac{\alpha^2}{N} t e^{-\alpha t}$
- the field $E(t)$ is due to the (linear) super-position of all the past pulses
  - the field evolution (in between consecutive spikes) is given by

$$\ddot{E}(t) + 2\alpha\dot{E}(t) + \alpha^2 E(t) = 0$$

  - the effect of a pulse emitted at time t_0 is

$$\dot{E}(t_0^+) = \dot{E}(t_0^-) + \alpha^2/N$$

Event-driven map(I)

By integrating the field equations between successive pulses, one can rewrite the evolution of the field $E(t)$ as a discrete time map:

$$E(n+1) = E(n)e^{-\alpha\tau(n)} + NQ(n)\tau(n)e^{-\alpha\tau(n)}$$

$$Q(n+1) = Q(n)e^{-\alpha\tau(n)} + \frac{\alpha^2}{N^2}$$

where $\tau(n)$ is the interspike time interval (ISI) and $Q := (\alpha E + \dot{E})/N$.

For the LIF model also the differential equations for the membrane potentials can be exactly integrated

$$x_i(n+1) = [x_i(n) - a]\mathrm{e}^{-\tau(n)} + a + gF(n) = [x_i(n) - x_q(n)]\mathrm{e}^{-\tau(n)} + 1 \quad i = 1, \ldots, N$$

with $\tau(n) = \ln\left[\frac{x_q(n)-a}{1-gF(n)-a}\right]$ where $F(n) = F[E(n), Q(n), \tau(n)]$ and the index q labels

the neuron closest to threshold at time n.

Event-driven map(II)

In a networks of identical neurons the order of the potential x_i is preserved, therefore it is convenient :

- to order the variables x_i;
- to introduce a comoving frame $j(n) = i - n$ Mod N;
- in this framework the label of the closest-to-threshold neuron is always 1 and that of the firing neuron is N.

The dynamics of the membrane potentials for the LIF model becomes simply:

$$x_{j-1}(n+1) = [x_j(n) - x_1(n)]e^{-\tau(n)} + 1 \qquad j = 1, \dots, N-1 \;\; ,$$

with the boundary condition $x_N = 0$ and $\tau(n) = \ln \left[\frac{x_1(n) - a}{1 - gF(n) - a} \right]$.

A network of N identical neurons is described by $N + 1$ equations

Splay state - LIF

In this framework, the periodic splay state reduces to the following fixed point:

$$\tau(n) \equiv \frac{T}{N}$$

$$E(n) \equiv \tilde{E}\,,\;\; Q(n) \equiv \tilde{Q}$$

$$\tilde{x}_{j-1} = \tilde{x}_j e^{-T/N} + 1 - \tilde{x}_1 e^{-T/N}$$

where T is the time between two consecutive spike emissions of the same neuron.

A simple calculation yields,

$$\tilde{Q} = \frac{\alpha^2}{N^2}\left(1 - e^{-\alpha T/N}\right)^{-1}\,,\;\; \tilde{E} = T\tilde{Q}\left(e^{\alpha T/N} - 1\right)^{-1}\;.$$

and the period at the leading order ($N \gg 1$) is given by

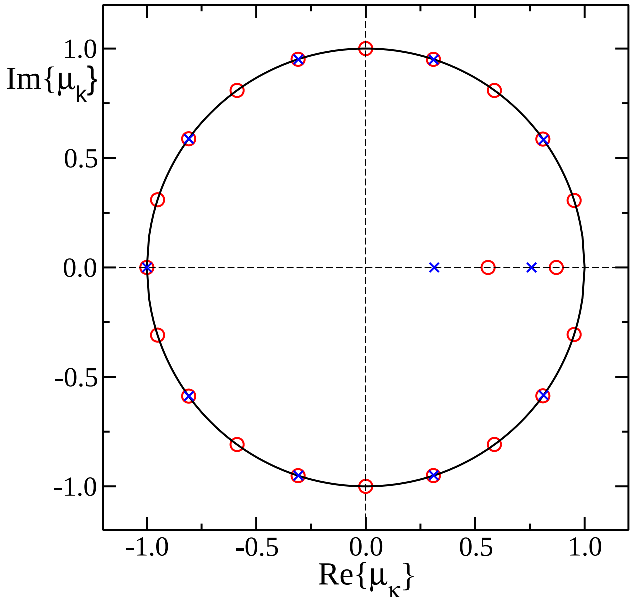
$$T = \ln\left[\frac{aT + g}{(a-1)T + g}\right]$$

Stability of the splay state

- In the limit of vanishing coupling $g \equiv 0$ the Floquet (multipliers) spectrum is composed of two parts:
  - $\mu_k = \exp(i\varphi_k)$, where $\varphi_k = \frac{2\pi k}{N}$, $k = 1, \ldots, N-1$
  - $\mu_N = \mu_{N+1} = \exp(-\alpha T/N)$.

  The last two exponents concern the dynamics of the coupling field $E(t)$, whose decay is ruled by the time scale α^{-1}
- As soon as the coupling is present the Floquet multipliers take the general form
  - $\mu_k = e^{i\varphi_k} e^{T(\lambda_k + i\omega_k)/N}$
    $\varphi_k = \frac{2\pi k}{N}$, $k = 1, \ldots, N-1$
  - $\mu_N = e^{T(\lambda_N + i\omega_N)/N}$
    $\mu_{N+1} = e^{T(\lambda_{N+1} + i\omega_{N+1})/N}$

  where, λ_k and ω_k are the real and imaginary parts of the Floquet exponents.



Analogy with extended systems

The "phase" $\varphi_k = \frac{2\pi k}{N}$ plays the same role as the wavenumber for the stability analysis of spatially extended systems: the Floquet exponent λ_k characterizes the stability of the $k-$th mode

- If at least one $\lambda_k > 0$ the splay state is unstable
- If all the $\lambda_k < 0$ the splay state is stable
- If the maximal $\lambda_k = 0$ the state is marginally stable

We can identify two relevant limits for the stability analysis:

- the modes with $\varphi_k \sim 0$ mod(2π) corresponding to $||\mu_k - 1|| \sim N^{-1}$ Long Wavelengths (LWs)
- the modes with finite φ_k corresponding to $||\mu_k - 1|| \sim \mathcal{O}(1)$ Short Wavelengths (SWs)

For the LIF model the implicit expression of the Floquet spectrum is

$$A(\mathrm{e}^T - 1)\mu_k^{N-1} = -\left(A(\mathrm{e}^T - 1) + \mathrm{e}^\tau\right) \frac{\mathrm{e}^{\tau - T} - \mu_k^{N-1}}{1 - \mu_k \mathrm{e}^\tau} + \mathrm{e}^\tau \frac{1 - \mu_k^{N-1}}{1 - \mu_k}$$

where $A = A(\tau, \bar{x}_1, \bar{E}, \bar{E})$

Infinite Network – LIF

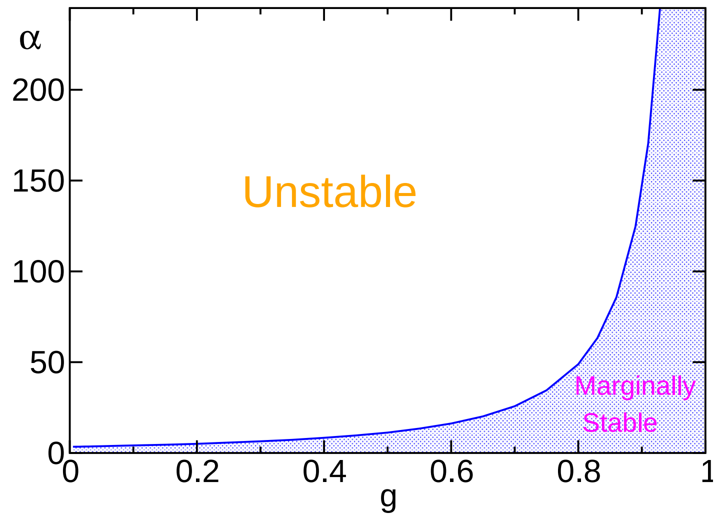
Post-synaptic potentials with finite pulse-width $1/\alpha$ and large network sizes (N)

$N \to \infty$ Limit

- The instabilities of the LW-modes determine the stability domain of the splay state, this corresponds to the Abbott-van Vreeswijk mean field analysis (PRE 1993)
- The spectrum associated to the SW-modes is fully degenerate

$$\omega_k \equiv 0 \qquad \lambda_k \equiv 0$$

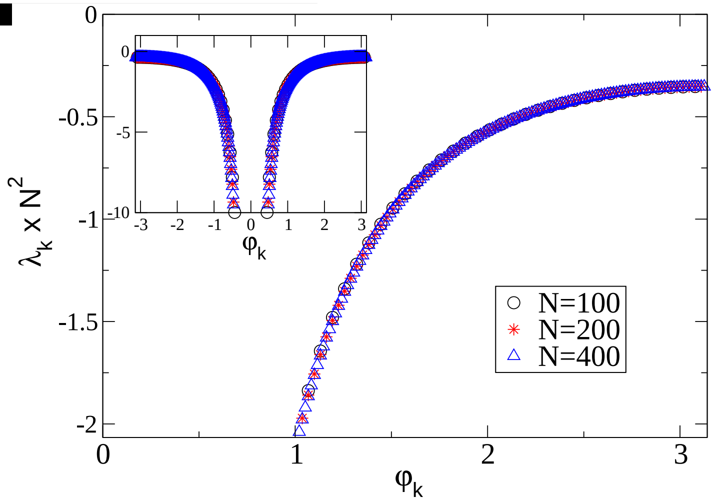
- The splay state is always unstable for inhibitory coupling
- For excitatory coupling there is a critical line in the (g, α)-plane dividing unstable from marginally stable regions



Finite Network – LIF

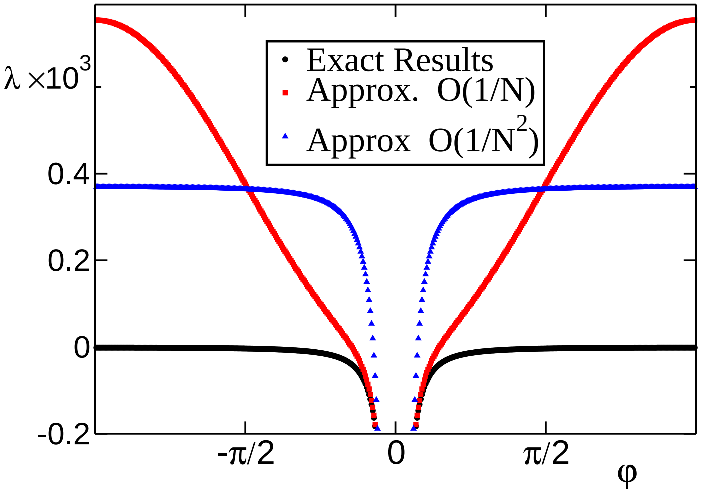
In finite networks,

- Splay state are strictly stable;
- the maximum Floquet exponent approaches zero from below as $1/N^2$



For the LIF model it is possible to write the exact event driven map, but for other neuronal models perturbative expansion are needed to derive the map evolution.

- A perturbative expansion correct to order $O(1/N)$ cannot account for such deviations
- In the present case, even approximations correct up to order $O(1/N^2)$ give wrong results
- First and second-order approximation schemes yeld an unstable splay state

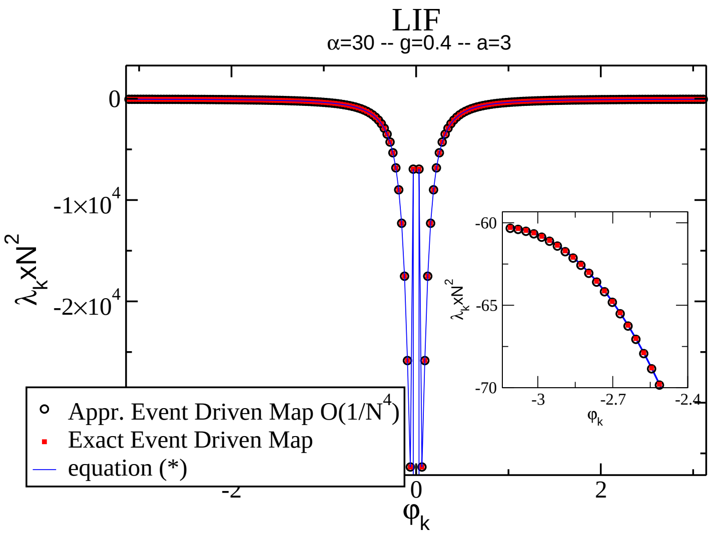


Finite Network – LIF

Since event-driven maps are usually employed to simulate pulse-coupled networks, extreme care should be employed in performing $1/N$ perturbative expansion of the original models

- A perturbative expansion $O(1/N^2)$ of the Floquet matrix is sufficient to well reproduce the Floquet spectrum

$$\lambda_k * N^2 = \frac{g\alpha^2}{12T^2}(e^T - 2 + e^{-T})\left[1 + \frac{6}{(\cos\phi_k - 1)}\right]$$



- Instead, in order to get the spectrum with the same accuracy event driven maps should include terms up to $O(1/N^4)$

Generic Force Field

For a generic force field $F(x)$, the dynamics of the membrane potential $x_i(t)$ of the i–th neuron is given by

$$\dot{x}_i = F(x_i) + gE(t)\,, \; x_i \in (-\infty, 1), \quad \Theta = 1, \quad x_R = 0, \qquad i = 1, \ldots, N$$

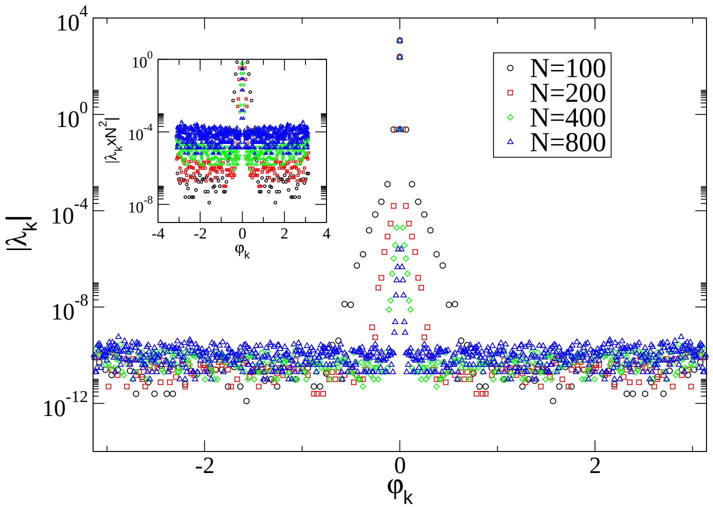
- For $F(x) = \sin(2\pi x + \alpha)$ the stability of the splay state is characterized by exactly $N-3$ zero Floquet exponents and 5 not zero exponents;
- For $F(x) = a - x$ the splay state is stable, but the Floquet exponents scale as $1/N^2$, this is in general true for the SWs modes
- What can we say about the splay state stability for generic $F(x)$?

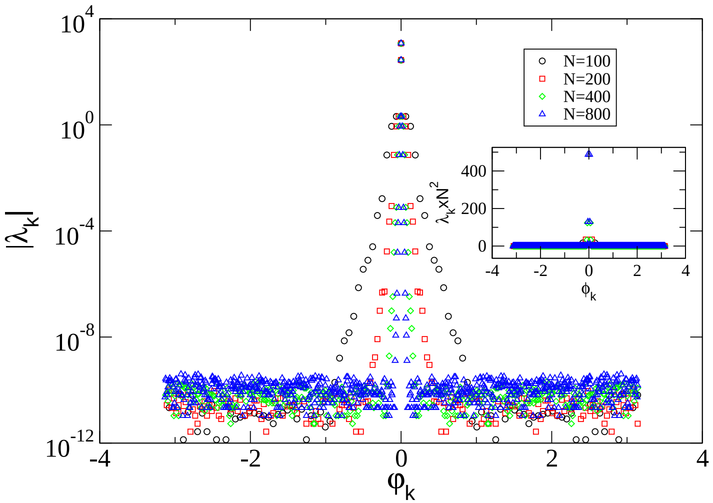
To numerically address this problem we consider event driven maps obtained via a $O(1/N^4)$ expansion of the original model.

This approximate approach allows us to determine the splay state and to evaluate its stability properties.

Harmonic Force Field

$F(x)$ are now $C^\infty[0:1]$

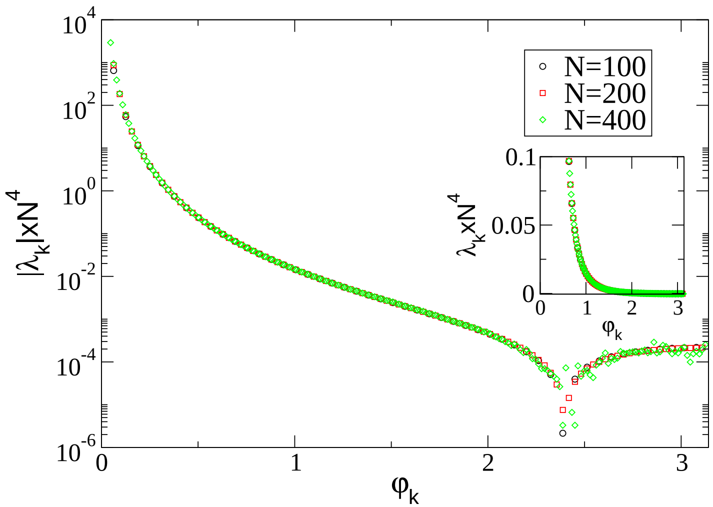




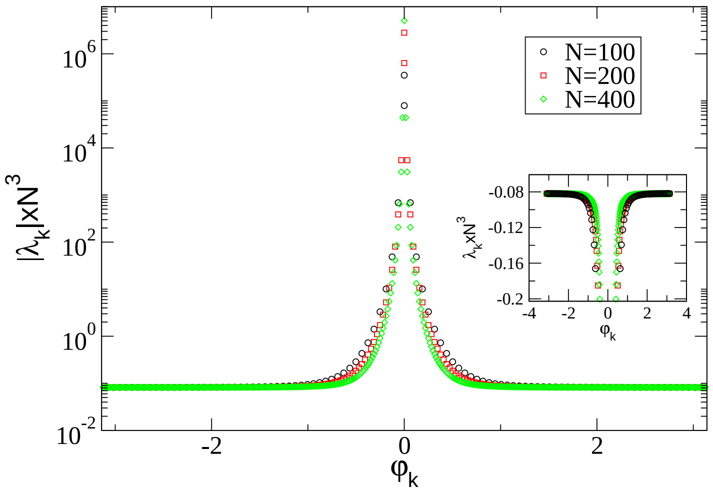
- $F(x) = a - sin(2\pi x)$, with $a = 3$, $g = 0.4$ and $\alpha = 30$
- Most of the Floquet exponents (corresponding to SW-modes) are zero within numerical accuracy;
- 4 negative exponents remains finite for $N \to \infty$:
- for finite N is unstable:
- No clear scaling with N is observable.
- $F(x) = 3 + 0.5 * sin(2\pi x) + 0.1 * sin(4\pi x) + 0.01 * sin(6\pi x)$
- 8 negative exponents remains finite for $N \to \infty$.

Continuous Force Field

$F(x)$ have discontinuous first derivative

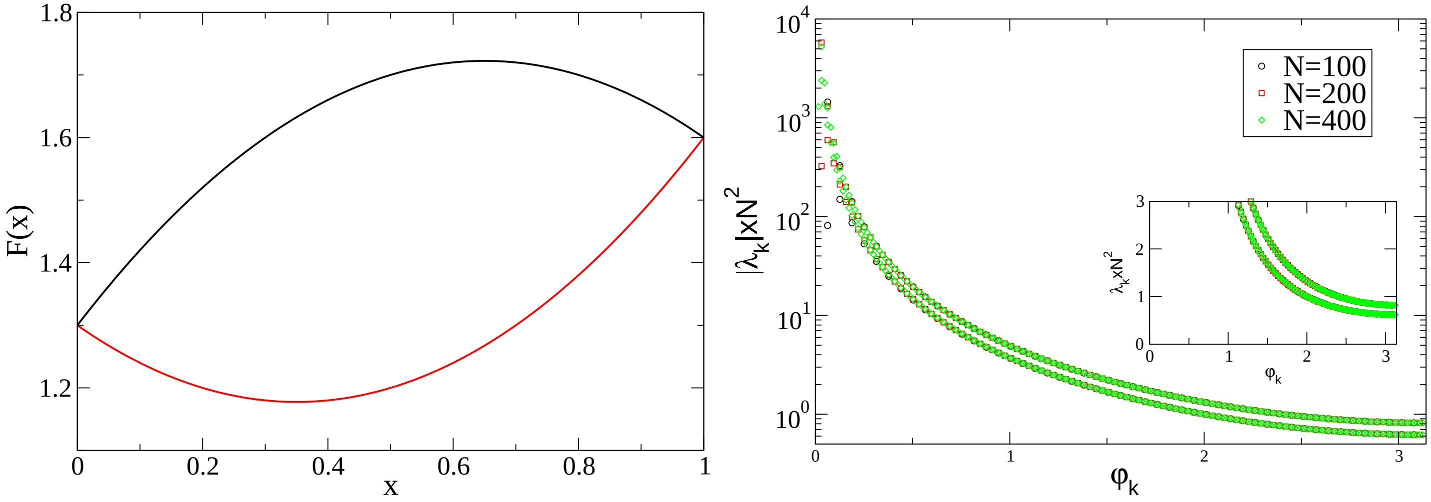


- $F(x) = 1.3 - x(x-1)$ with $g = 0.4$ and $\alpha = 6$
- The exponents associated to SW modes vanish faster than $1/N^2$ (apparently $1/N^4$)
- the splay state is unstable: the LW modes determine its stability



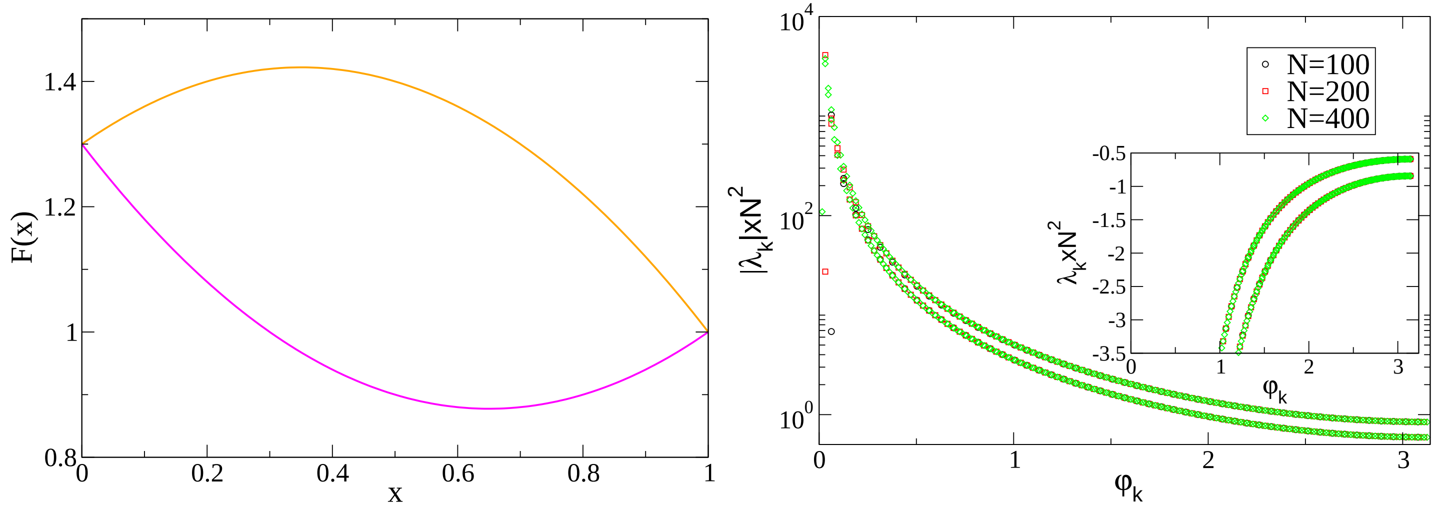
- $F(x) = 1.3 - 0.025 * \sin(\pi x)$ with $g = 0.4$ and $\alpha = 6$
- The exponents associated to SW modes vanish faster than $1/N^2$ (apparently $1/N^3$)
- for finite N the splay state is stable

Discontinuous Force Field (I)



- $[F(1) - F(0)] > 0$
- The part of the Floquet spectrum corresponding to SW modes scale as $1/N^2$
- The splay state is unstable for finite N due to SW instabilities
- The asymptotic stability is determined by the LWs modes

Discontinuous Force Field (II)



- $[F(1) - F(0)] < 0$
- The part of the Floquet spectrum corresponding to SW modes scale as $1/N^2$
- The SW modes are stable for finite N
- The asymptotic and finite N stability are determined by the LWs modes
- This situation is analogous to the leaky integrate-and-fire case

Conclusions (I)

- The stability of splay states for the leaky integrate-and-fire model can be addressed by reducing a globally coupled ODE model to event-driven maps;
- An analytical analysis of the Jacobian reveals that the eigenvalue spectrum is made of three components
  1. long wavelengths eigenmodes, which can be found also within a mean-field approach (Abbott - van Vreeswijk);
  2. short wavelengths eigenmodes;
  3. isolated eigenvalues, signaling the existence of strong instabilities
- The stability of large networks of neurons coupled via narrow pulses depends crucially on the ratio between the interspike interval and the pulse width, thus the dynamical stability of these models demands for more refined analysis than mean field.

[R. Zillmer, R.Livi, A. Politi & AT PRE **76** (2007) 046102]

Conclusions (II)

- The stability of splay states for a Generic Force Field $F(x)$ can be captured by writing event-driven maps correct at least up to order $\mathcal{O}(1/N^4)$.
- The stability of SW modes for FINITE pulse-coupled networks is determined by the force field $F(x)$ continuity properties:
  1. Continuous Force Fields :
     (a) harmonic $F(x)$: the SW exponents identically vanish (W-S)
     (b) discontinuous F': the SW exponents scale faster than $1/N^2$
  2. Discontinuous $F(x)$: the SW exponents scale as $1/N^2$
     (a) $[F(1) - F(0)] > 0$: Unstable SW modes
     (b) $[F(1) - F(0)] < 0$: Stable SW modes

In the mean-field approach the "spatial discreteness" of the network is neglected: no SW instabilities can occur.
However, the Abbott-Van Vreeswijk approach is still commonly employed :
Brunel - Hakim, Neural Comp. , 1999

[M. Calamai, A. Politi & AT, in preparation]

Open Problems

For the mathematicians

- Our numerical findings should be demonstrated in rigourous manner;
- The degree of continuity of the force field should be linked to the spectrum characteristics.

For the others

- How general is the finite N scaling observed for the splay states (namely $1/N^2$) and its origin ?
- Is this scaling observable also for other exact solutions of pulsed-coupled networks, like partially synchronized states ?
  [van Vreeswiijk, PRE (1996)]

Vanishing Pulse-Width (I)

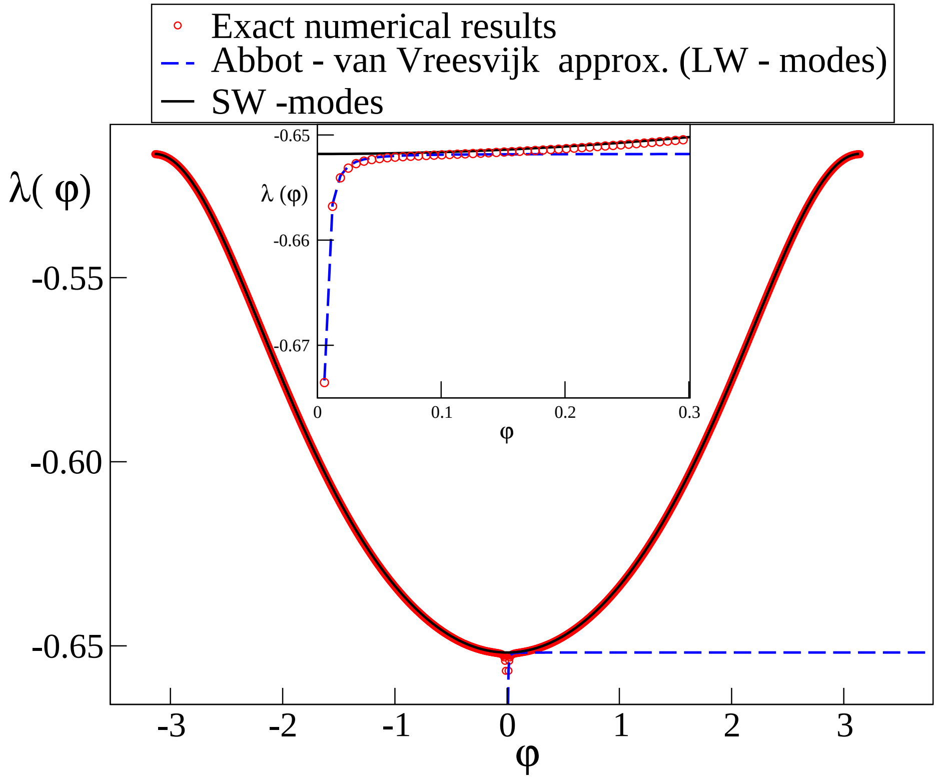
The Abbott - van Vreeswijk mean field analysis does not reproduce the stability properties of the splay state for δ-like pulses:

- The limit $N \to \infty$ and the zero pulse-width limit do not commute
- To clarify this issue we introduce a new framework where the pulse-width $1/\alpha$ is rescaled with the network size N:

$$\boxed{\alpha = \beta N}$$

- The relevant parameter is now $\boxed{\beta}$
- Now, we deal with two time scales :
  - a scale of order $\mathcal{O}(1)$ for the evolution of the membrane potential;
  - a scale of order $\alpha^{-1} \sim N^{-1}$ that corresponds to the field relaxation.
- For finite β-values
  - with excitatory coupling ($g > 0$) the splay state is always unstable
  - with inhibitory coupling ($g < 0$) the splay state can be stable for sufficiently large β

Vanishing Pulse-Width (II)



For inhibitory coupling ($g < 0$) the Floquet spectrum associated to the splay state is well reproduced by the stability analysis of the Short Wavelenght (SW) Modes.

Vanishing Pulse-Width (III)

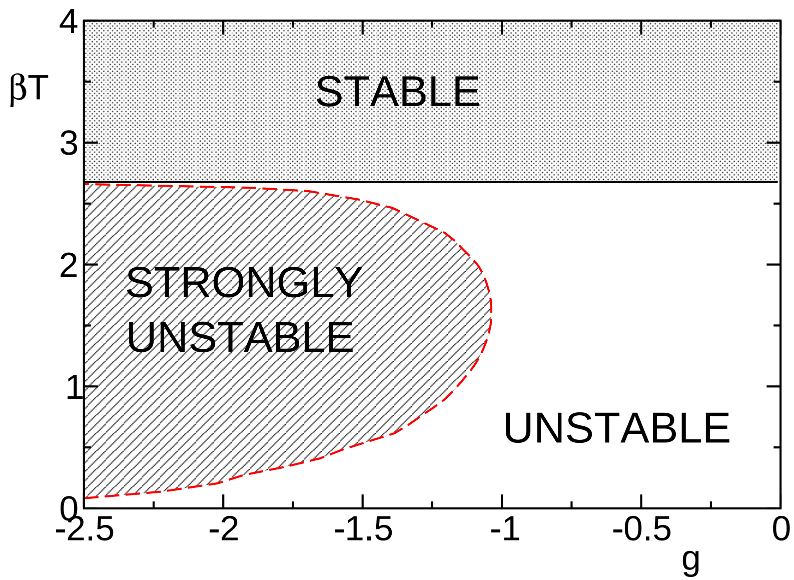
For inhibitory coupling ($g < 0$) the transition from stable to unstable splay states is well captured by the instabilities of the π-mode:

$$\lambda_\pi = -1 + \frac{1}{T} \ln \left[1 + \frac{1}{a - 1 + 2\beta^2 T g \left(1 + e^{2\beta T}\right) \left(e^{3\beta T} - 2e^{\beta T} + e^{-\beta T}\right)^{-1}} \right]$$

The relevant parameter for the transition is the ratio between the ISI and the pulse-width

$$\beta T = \frac{T/N}{1/\alpha}$$

Strongly Unstable Regime:
the isolated eigenvalues $\lambda_{N,N+1} \sim N$ crosses the zero axis



Failure of the mean field (I)

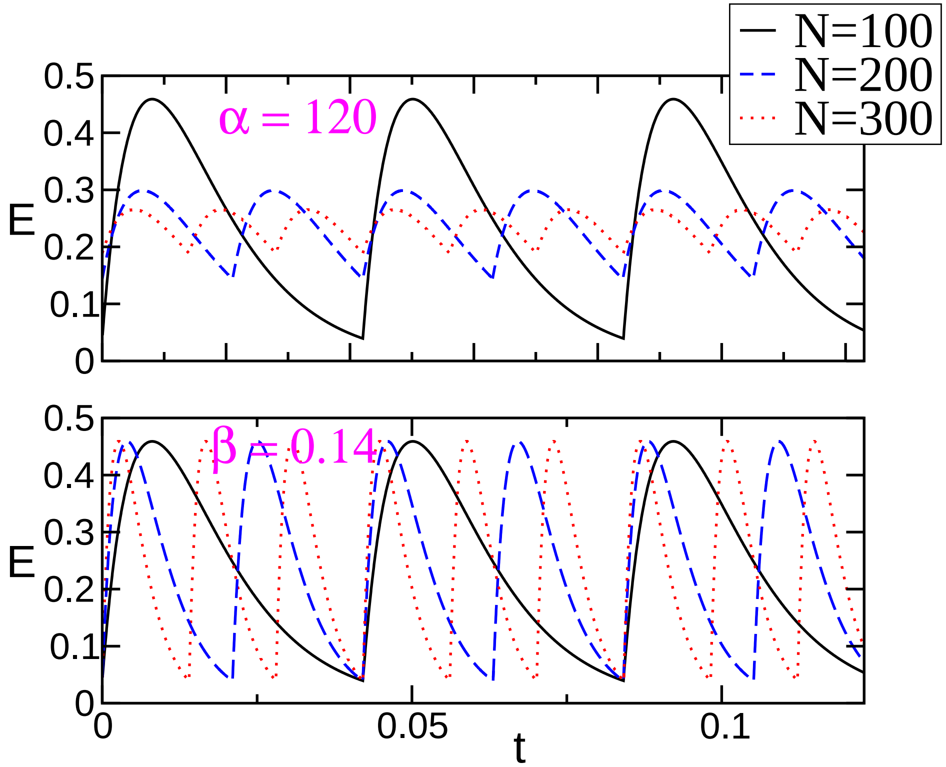
To derive the mean-field stability analysis for the splay state Abbott-Van Vreeswijk made the following hypothesis:

- the field $E(t) = E_0$ is constant, therefore the period is $T = 1/E_0$;
- to describe the state of the population of the oscillators they reformulate the dynamics as a continuity equation describing a flow of phases (of the oscillators);
- they neglect the "spatial discreteness" of the network, no SW instabilities can occur.

The Abbott-Van Vreeswijk approach is still commonly employed :

Brunel - Hakim, Neural Comp. , 1999
Brunel, J. Comput Neurosci, 2000

Failure of the mean field (II)



The reason for the failure of the mean field approach is related to the fact that for Finite Pulse-Width (constant α) the oscillations of $E(t)$ decreases with N, while for Vanishing Pulse-Width (constant β) the oscillations are independent of N.

Conclusions

- The stability of splay states can be addressed by reducing a globally coupled ODE model to event-driven maps, where the discrete time evolution corresponds to consecutive pulse emission;
- An analytical analysis of the Jacobian reveals that the eigenvalues spectrum is made of three components
  1. long wavelengths eigenmodes, which can be found also within a mean-field approach;
  2. short wavelengths eigenmodes;
  3. isolated eigenvalues, signaling the existence of strong instabilities
- The stability of large networks of neurons coupled via narrow pulses depends crucially on the ratio between the interspike interval and the pulse width, thus the dynamical stability of these models demands for more refined analysis than mean field.