Stability of the splay state 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)

Splay States in Neural Networks

- LIF + Plasticity (Bressloff, PRE 1999)
- LIF + Gap Junctions (Coombes, SIADS , 2008)
- More realistic neuronal models (Brunel-Hansel, Neural Comp., 2006)
- Quadratic Integrate Fire (Dipoppa et al, SIADS, 2012)

Summary

- Finite networks of pulse-coupled identical neurons with generic force field (Leaky Integrate-and-Fire (LIF) is a special case)
- Stability properties of states with uniform spiking rate (Splay States)

Generic model $F(x)$

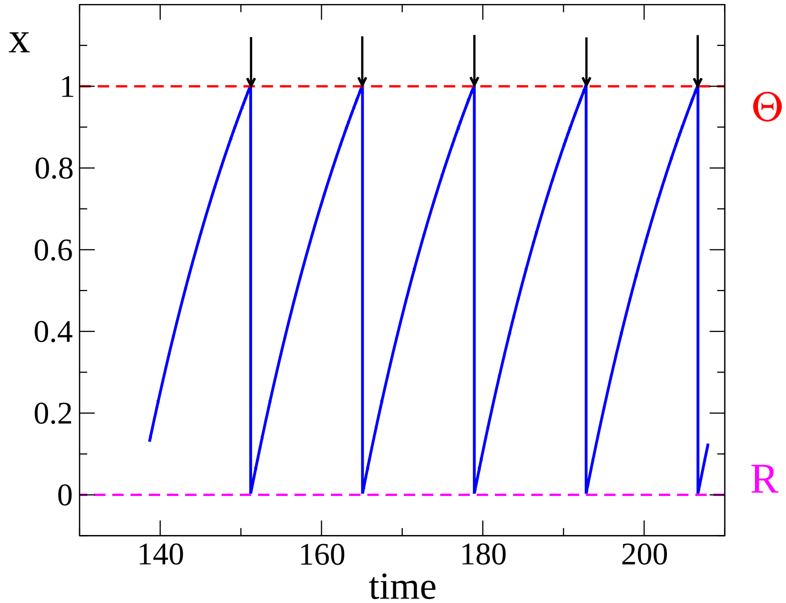
- The network dynamics can be rewritten as an approximate Event Driven Map
- The stability of the Splay State reduces to a fixed point stability analysis
- The Floquet spectrum can be analyzed in two limiting case:
  Short (SWs) and Long Wavelengths (LWs) (analogy with Extended Systems)
- In finite networks, the SW Floquet spectrum has an universal form and scales as $1/N^2$ for discontinuous force fields $F(0) \neq F(1)$, (analytical result)
- For continuous force fields $F(0) = F(1)$, the SW spectrum scales as $1/N^4$

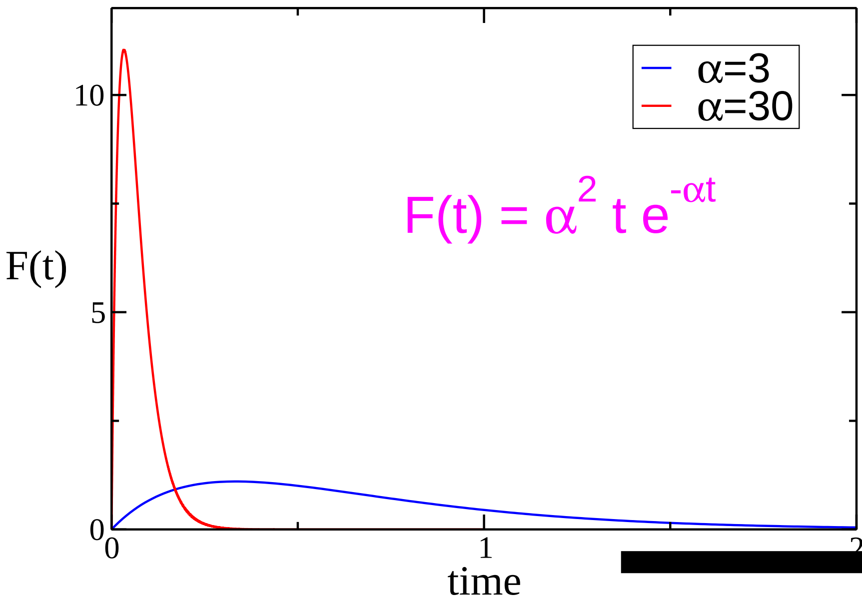
Leaky integrate-and-fire model

- Linear integration combined with **reset** = formal spike event
- Equation for the membrane potential x , with threshold $\Theta = 0$ and reset $R = 0$:

$$\dot{x} = a - x \qquad x = a(1 - e^{-t}) + x_0 e^{-t}$$

  - If $a > \Theta$ Repetitive Firing, Supra-Threshold
  - If $a < \Theta$ Silent Neuron, Below Threshold
- In networks: at reset a pulse is sent to connected neurons





The Model

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

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

- $F(x)$ 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 $E_s(t) = \frac{\alpha^2}{N} t \mathrm{e}^{-\alpha t}$
- the collective field $E(t)$ is due to the (linear) super-position of all the past pulses
  - the collective 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

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

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

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

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

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

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

with

$$\tau(n) = \ln\left[\frac{x_q(n) - a}{1 - gH(n) - a}\right]$$

where $H(n) = H[E(n), P(n), \tau(n)]$ and the index q labels the neuron closest to threshold at time n.

Splay state - LIF

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

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

$$E(n) \equiv \tilde{E}\,,\ P(n) \equiv \tilde{P}$$

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

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

A simple calculation yields,

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

Now we perform a $1/N$ expansion for finite networks.

Finite Network - LIF

The zeroth order approximation ($N \to \infty$) of the period is

$$T^{(0)} = \ln\left[\frac{aT^{(0)} + g}{(a-1)T^{(0)} + g}\right]$$

The first correction for the period is of the fourth order in $1/N$

$$\delta T = \frac{K(\alpha) - 6}{720} \frac{\left[a(1 - \mathrm{e}^{-T^{(0)}}) - 1\right]}{g e^{-T^{(0)}} + a\left(T^{(0)} + 1 - \mathrm{e}^{-T^{(0)}}\right) - 1} \frac{(T^{(0)})^5}{N^4}$$

The zeroth order approximation for the membrane potential is

$$\tilde{x}_j^{(0)} = \left(a + \frac{g}{T^{(0)}}\right)\left[1 - \mathrm{e}^{T^{(0)}(j/N-1)}\right] + \mathcal{O}(1/N^4)$$

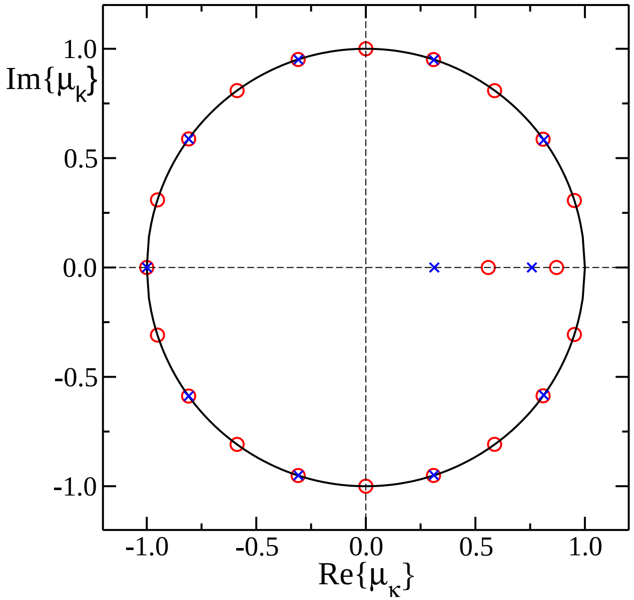
The linear stability analysis of the splay state can be performed by perturbing the zeroth order solution and by solving the associated eigenvalue problem in terms of the Floquet multipliers $\{\mu_k\}$

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

Generic Force Field

For a generic force field $F(x)$, the dynamics of the membrane potential $x_j(t)$ of the i–th neuron can be rewritten as an Event Driven Map by integrating the ODEs

$$x_{j-1}(t_{n+1}^-) - x_j(t_n) = \int_{t_n}^{t_{n+1}^-} dt F(x_j(t)) + g \int_{t_n}^{t_{n+1}^-} dt \Big[E_n + P_n(t-t_n)\Big] \mathrm{e}^{-\alpha t}$$

and by passing in the comoving reference frame

$$x_{n+1,j-1} = x_j(t_{n+1}^-)$$

The analytical solution for the membrane potential and the period T is found for finite N

- by performing a fourth order expansion in $1/N$ of the terms entering in the integrals appearing on the rhs in order to solve them
- by expanding the expression of the membrane potentials and of the period T up to the fourth order
- by introducing a continuous spatial coordinate $s = i/N$ (large N limit) and by solving the ODEs ruling the spatial evolution of the terms of different order

We show that the corrections to the infinite size limit solution for the period and the membrane potential are zero up to the third order (included)

Linear Stability Analysis SW

Linear stability analysis can be safely performed around the infinite size solutions $T^{(0)}$ and $\tilde{x}_j^{(0)}$, since corrections $o(1/N^3)$ do not affect the leading term of the linear analysis. The linear stability can be performed

- by differentiating the map around the fixed point, one obtains the linear equations for $\delta x_{n,j}$, δP_n and δE_n;
- the eigenvalue problem is resolved introducing the Floquet multiplier μ_k

$$\delta x_{n,j} = \mu_k^n \delta x_j \qquad \delta P_n = \mu_k^n \delta P \qquad \delta E_n = \mu_k^n \delta E \qquad \delta \tau_n = \mu_k^n \delta \tau$$

- by separating slowly and rapidly oscillating terms in the eigenvectors

$$\delta x_j = \pi_j + \vartheta_j e^{i\phi_k j}$$

$$\pi_j = \sum_{h=0,3} \frac{\pi_j^{(h)}}{N^h} + O\left(\frac{1}{N^4}\right) \quad , \quad \vartheta_j = \sum_{h=0,3} \frac{\vartheta_j^{(h)}}{N^h} + O\left(\frac{1}{N^4}\right)$$

- by introducing a spatial continuous variable

$$\Pi^{(h)}(s = \frac{j}{N}) = \pi_j^{(h)}, \ \Theta^{(h)}(s = \frac{j}{N}) = \vartheta_j^{(h)}$$

- Finally, we separate terms of different order and we solve the associated ODEs for $\Pi^{(h)}$ and $\Theta^{(h)}$

Main Result

$$\dot{x}_i = F(x_i) + gE(t) = \mathcal{F}(x_i) \qquad \mu_k = e^{i\varphi_k} e^{T(\lambda_k + i\omega_k)/N} \simeq e^{i\varphi_k} \left(1 + \sum_{h=1,3} \frac{\Gamma^{(h)}}{N^h}\right)$$

The leading term for the real Floquet SW component is

$$\lambda_k = \frac{\Gamma^{(3)}}{N^2 T} = \frac{g\alpha^2}{12} \frac{F(1) - F(0)}{\mathcal{F}(1)\mathcal{F}(0)} \left(\frac{6}{1 - \cos\phi_k} - 1\right) \frac{1}{N^2} \qquad \Gamma^{(1)} = \Gamma^{(2)} = 0$$

- Universal shape of SW spectra for discontinuous force fields $\boxed{F(0) \neq F(1)}$
- For $g > 0$ (resp. $g < 0$) the state is stable for $F(0) > F(1)$ (resp. $F(0) < F(1)$)

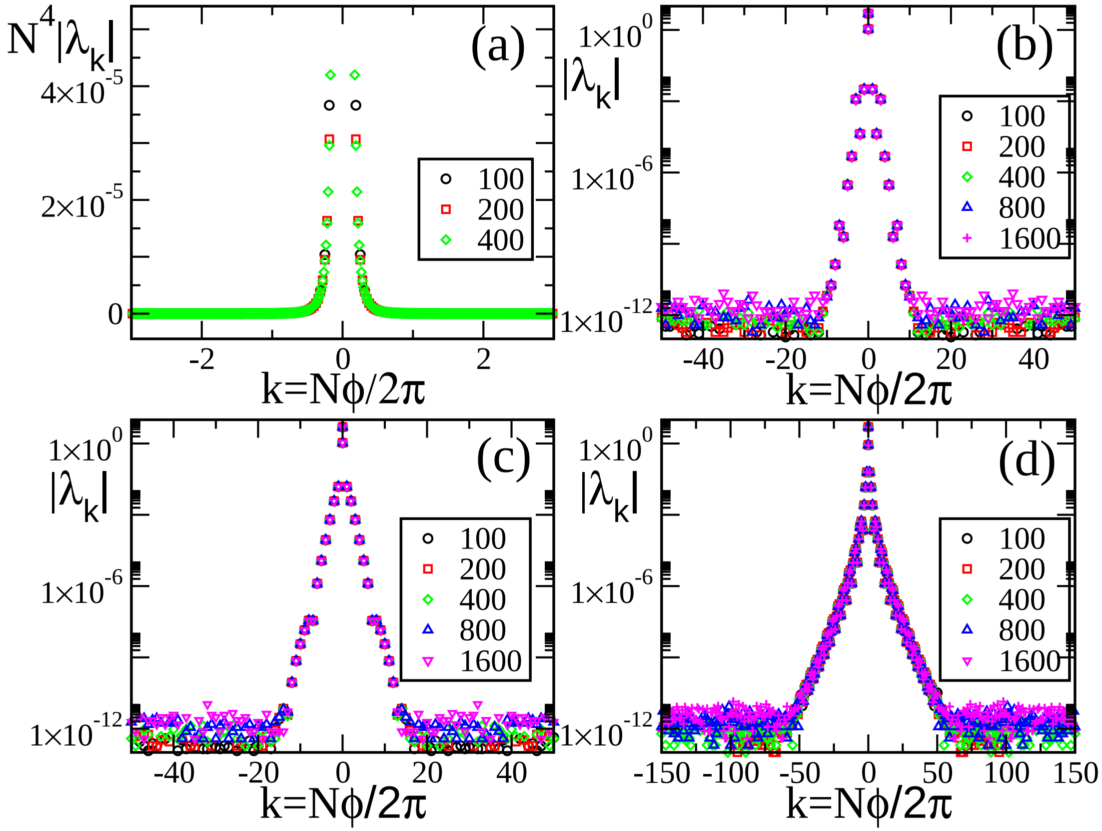
For the LW component, Abbott & Van Vreeswijk have shown that

- For sufficiently small coupling $|g| << 1$ and sufficiently broad pulses $\alpha < \alpha_c$ the splay state is stable whenever $F(0) > F(1)$

[S. Olmi, A. Politi & A. Torcini, The Journal of Mathematical Neuroscience 2, 12 (2012).]

Continuous Force Field

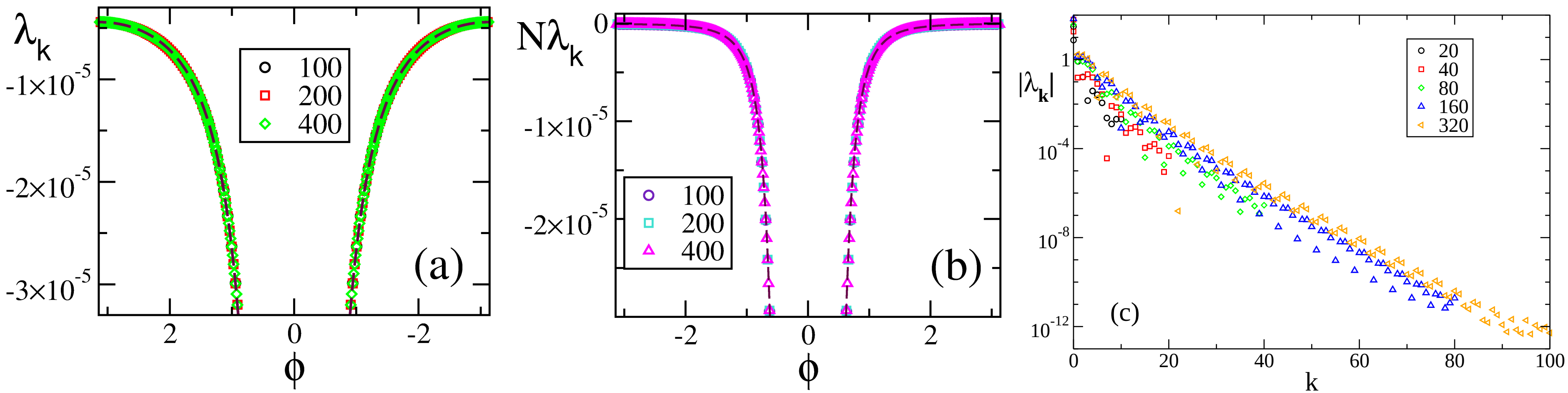
Finite pulse width



- (a) $F(x) = a - 0.25\sin(\pi x)\cos^2(\pi x)$ (b) $F(x) = a - 0.25\sin(\pi x)\cos^2(2\pi x)$
- (c) $F(x) = a - 0.25\sin(\pi x)e^{\cos^2(2\pi x)}$ (d) $F(x) = a - 1 + e^{\sin(2\pi x)}$

Vanishing pulse width

β-model $\quad E_s = (\beta^2 t)e^{\beta N t} \qquad \beta = \dfrac{\alpha}{N}$



- (a) $F(x) = a - x(x - 0.7)$, $\quad F(0) \neq F(1)$ discontinuous
- (b) $F(x) = a - 0.25\sin(\pi x)$, $\quad F(0) = F(1)$ continuous
- (c) $F(x) = a - 1 + e^{2\sin(2\pi x)}$, $\quad \mathcal{C}^\infty$ analytical
- The results found for δ spikes are consistent with the β-model ones: the SW spectra remains finite for $N \to \infty$

[S. Olmi, A. Politi & A. Torcini, *in preparation*]

Conclusions

- The Floquet spectrum of splay states for a Generic Force Field $F(x)$ can be obtained analytically, for finite N and discontinuous fields, in the Short-Wavelenght limit by expanding the solution at least up to order $\mathcal{O}(1/N^4)$, since the SW spectrum vanishes for $N \to \infty$
- For F differentiable at least four times the leading corrections to the infinite size results are of order $1/N^4$ for the period and the membrane potential
- 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 Theorem)
     (b) $F \in C^\infty$: the SW exponents scale exponentially fast with N
     (c) discontinuous F': the SW exponents scale as $1/N^4$
  2. Discontinuous $F(x)$: the SW spectra are universal and scale as $1/N^2$
     (a) $[F(1) - F(0)] > 0$: Unstable SW modes
     (b) $[F(1) - F(0)] < 0$: Stable SW modes
- β-pulses (δ-pulses) give rise to a completely different scenario

Event-driven map

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:

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

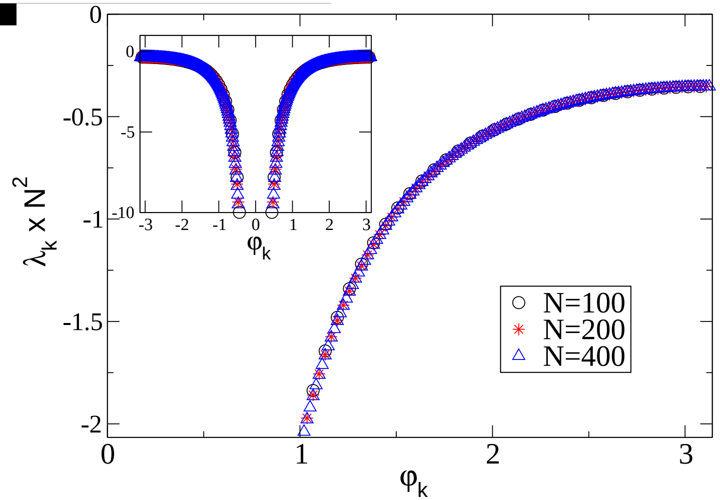
with the boundary condition $x_N = 0$ and $\tau(n) = \ln\left[\frac{x_1(n)-a}{1-gF(n)-a}\right]$.

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

Finite Network – LIF

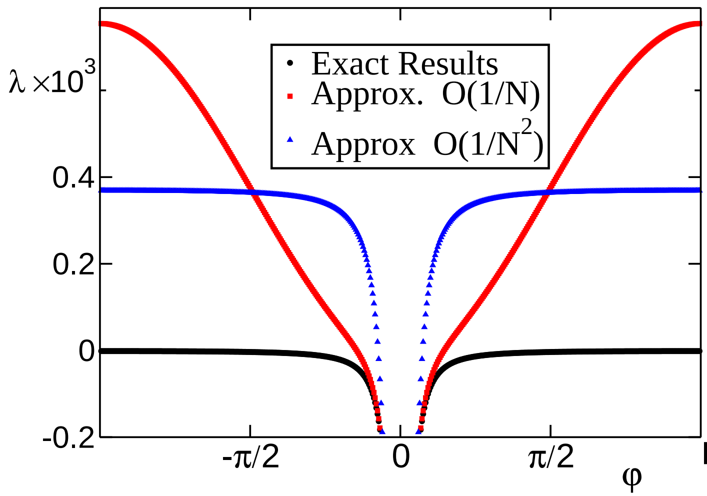
In finite networks,

- 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

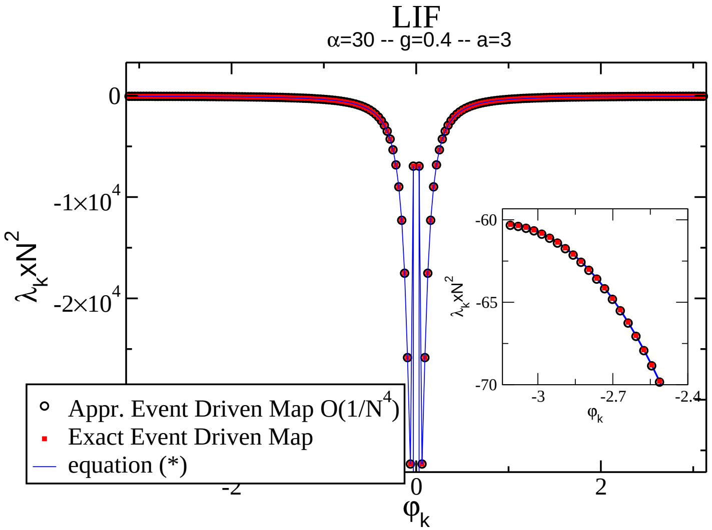


Perturbative expansion of the original models should be done with care

Finite Network – LIF

$$\mu_k = e^{i\varphi_k} e^{T(\lambda_k + i\omega_k)/N} = e^{i\varphi_k}\left(1 + \sum_{h=1,3} \frac{\Gamma^{(h)}}{N^h} + \mathcal{O}(1/N^4)\right)$$

A perturbative expansion $O(1/N^3)$ of the Floquet matrix is sufficient to well reproduce the SW Floquet spectrum



$$\lambda_k * N^2 = \frac{\Gamma^{(3)}}{T} = \frac{g\alpha^2}{12}(e^T + e^{-T} - 2)\left(\frac{6}{1-\cos\varphi_k} - 1\right) < 0$$

The approximation breaks down for $\varphi_k \sim 0$ corresponding to the LW limit

Infinite Network – LIF

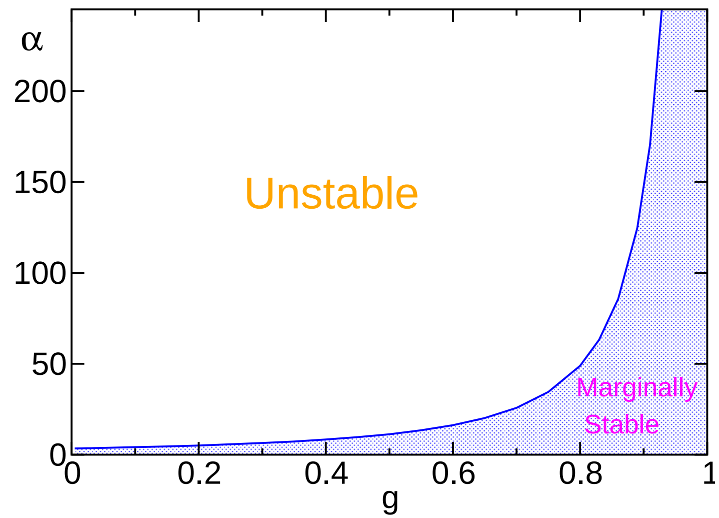
Post-synaptic potentials with finite pulse-width $1/\alpha$ and large network sizes (N)

$N \to \infty$ Limit

- The spectrum associated to the SW-modes is fully degenerate

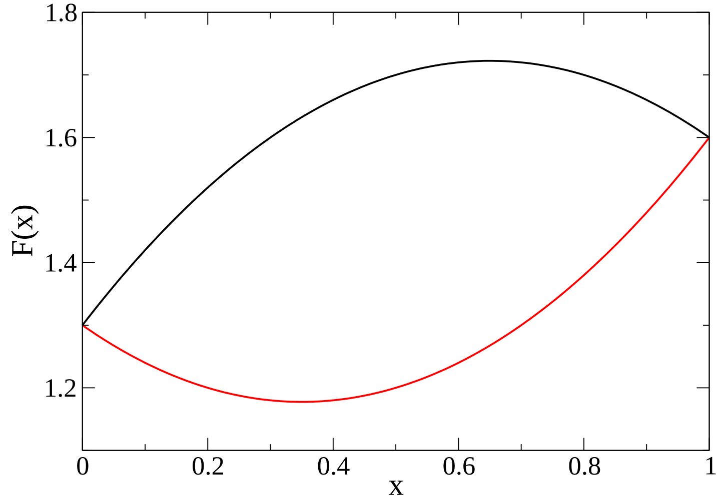
$$\omega_k \equiv 0 \qquad \lambda_k \equiv 0$$

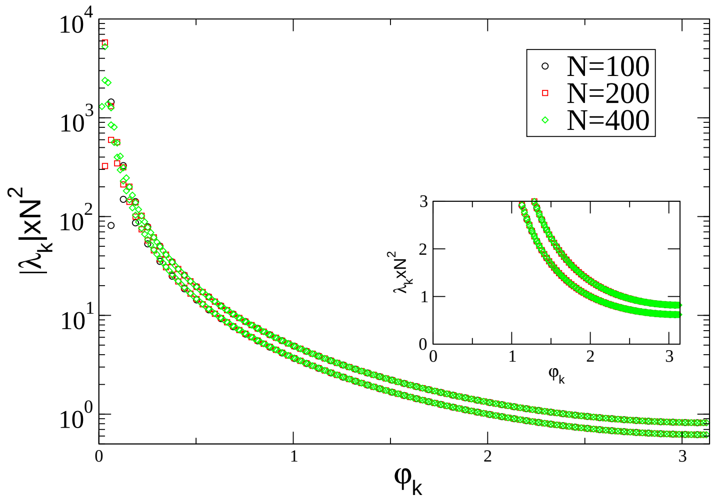
- The LW-modes determine the stability domain of the splay state, this corresponds to the Abbott-van Vreeswijk mean field analysis (PRE 1993)
- For excitatory coupling there is a critical line in the (g, α)-plane dividing unstable from marginally stable regions
- The splay state is always unstable for inhibitory coupling (numerical evidences by van Vreeswijk, 1996)



[R. Zillmer, R.Livi, A. Politi & A. Torcini PRE (2007)]

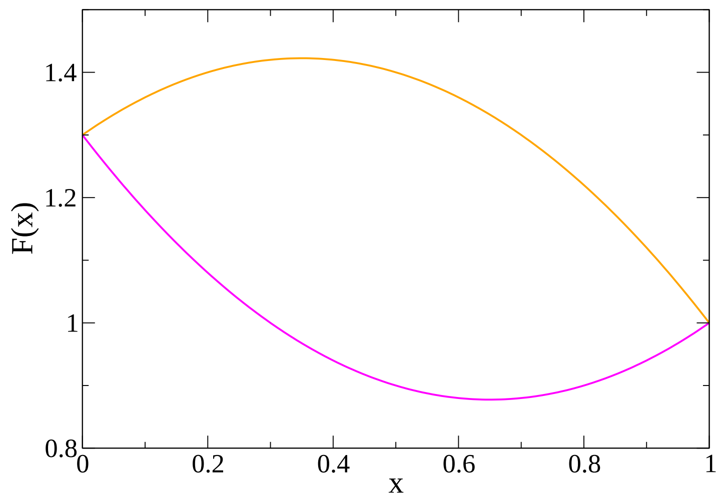
Discontinuous Force Field (I)

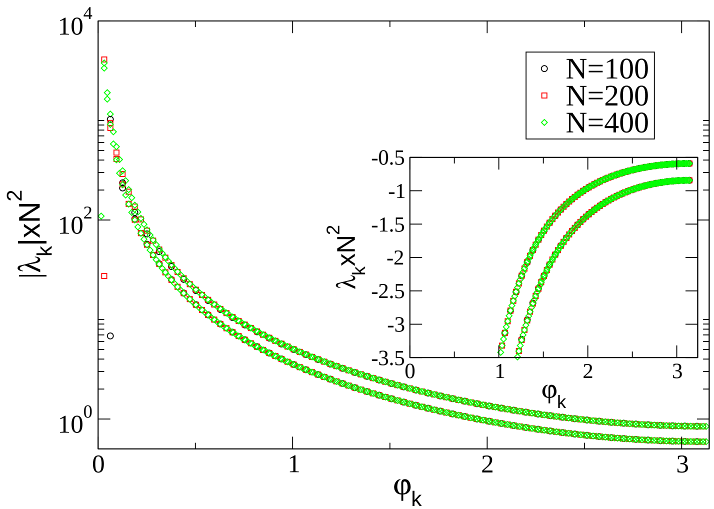




- $[F(1) - F(0)] > 0$
- The part of the Floquet spectrum corresponding to SW modes scale as $1/N^2$
- The splay state is unstable for finite N due to SW instabilities
- The asymptotic stability is determined by the LWs modes

Discontinuous Force Field (II)





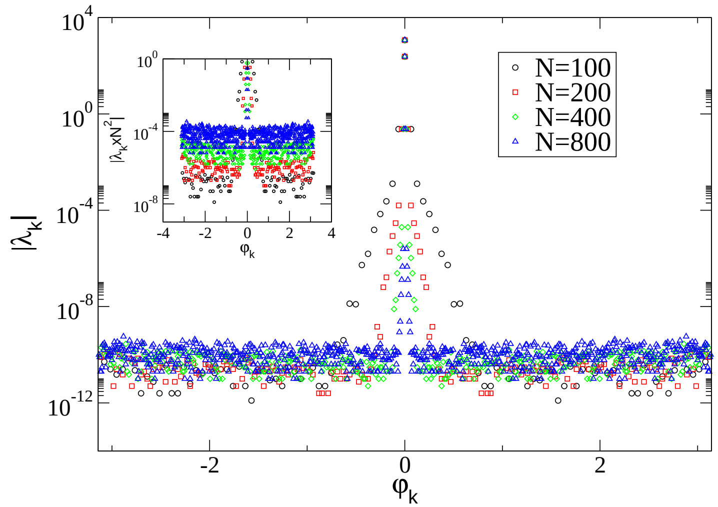
- $[F(1) - F(0)] < 0$
- The part of the Floquet spectrum corresponding to SW modes scale as $1/N^2$
- The SW modes are stable for finite N
- The asymptotic and finite N stability are determined by the LWs modes
- This situation is analogous to the leaky integrate-and-fire case
- LIF – EIF (exponential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

Harmonic Force Fields

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 collective fields determined by all the oscillators.



- $F(x) = a - sin(2\pi x)$, 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 $N \to \infty$.

These results applies also to the excitable Θ-neuron (QIF) model, [M. Dipoppa, M. Krupa, A Torcini, B. Gutkin, to appear in SIADS (2012)]

Open Problems

- It would be nice to extend the analysis for the LW modes to finite coupling g, but the LW exponents remain finite for $N \to \infty$: no smallness parameter for an expansion
- Our analysis for SW spectra should be extended beyond the leading $1/N^2$ term to demonstrate rigorously the other scaling observed only numerically (quite hard)
- The finite N scaling of the SW spectra observed for the splay states (namely $1/N^2$) seems quite general, we have numerical evidence that it applies to
  - Different pulse shapes, namely exponentially decaying pulses (LIF)
  - For other exact solutions of pulsed-coupled networks, like partially synchronized states (LIF) [van Vreeswijk, 1996]
- δ-pulses give rise to a completely different scenario, the SW spectra remains finite for $N \to \infty$

[R. Zillmer, R.Livi, A. Politi & A. Torcini PRE (2007)]
[M. Calamai, A. Politi & A. Torcini, PRE (2009)]
[S. Olmi, A. Politi & A. Torcini, submitted to JMNS (2012)]