Stability of the splay state in pulse-coupled neuronal networks

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Main Issues

- Network of globally coupled identical LIF neurons
- Stability of states with uniform spiking rate (Splay States)

The stability of the steady states for networks of globally coupled leaky integrate-and-fire (LIF) neurons is still a debated problem

Results in literature

- The splay state is stable only for excitatory coupling [Abbott - van Vreeswijk Phys Rev E 48, 1483 (1993)]
- Stable splay states have been found in networks with inhibitory coupling [Zillmer et al. Phys Rev E 74, 036203 (2006)]

Summary

- Stability of the splay states depends on the ratio between pulse-width $1/\alpha$ and inter-spike interval (ISI)
- Stability can depend crucially on the number of neurons in the network
- Splay states can be stable even for inhibitory coupling

The Model

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

$$\dot{x}_i = a - \eta x_i + gE(t)\,,\ x_i \in (-\infty, 1)$$

where

- the single neurons are in the repetitive firing regime ($a > 1$)
- g is the coupling - excitatory ($g > 0$) or inhibitory ($g < 0$)
- each post-synaptic potential (PSP) has the shape $E_s(t) = \alpha^2 t e^{-\alpha t}$
- the field $E(t)$ is due to the (linear) sovrapposition of all the past PSPs
  - 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

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

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

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

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

Once the the membrane potentials are ordered their dynamics becomes simply:

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

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

Splay state

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

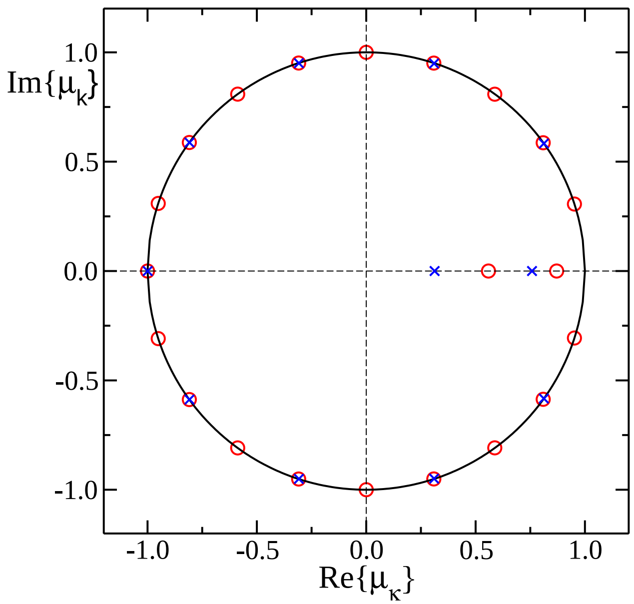
- In the limit of vanishing coupling $g \equiv 0$ the Floquet (multipliers) spectrum is composed of two parts:
  - $\mu_k = \exp(i\varphi_k)$, where $\varphi_k = \frac{2\pi k}{N}$, $k = 1, \ldots, N-1$
  - $\mu_N = \mu_{N+1} = \exp(-\alpha T/N)$.

  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" $\varphi_k = \frac{2\pi k}{N}$ play 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)

Finite Pulse-Width (I)

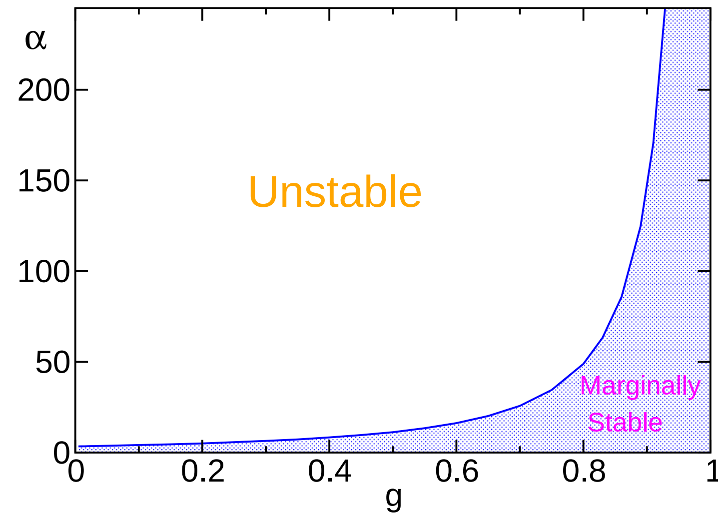
Post-synaptic potentials with finite pulse-width $1/\alpha$ and large network sizes (N)

$N \to \infty$ 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

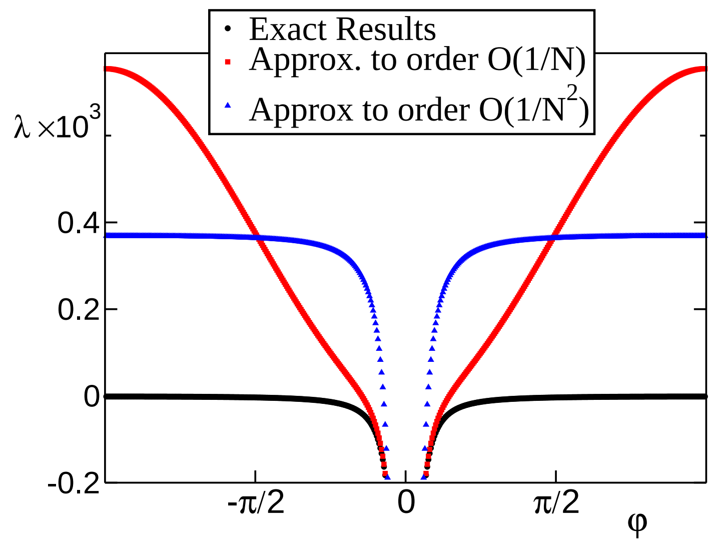


Finite Pulse-Width (II)

Finite N situation

In finite networks, the maximum Floquet exponent approaches zero from below as $1/N^2$

- Splay state are strictly stable in finite lattice
- A perturbation theory 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 reults
- First and second-order approximation schemes yeld an unstable splay state



Since event-driven maps are usually employed to simulate this type of networks, one should be extremely carefull in doing approximate expansion $1/N$ of continuous models.

Vanishing Pulse-Width (I)

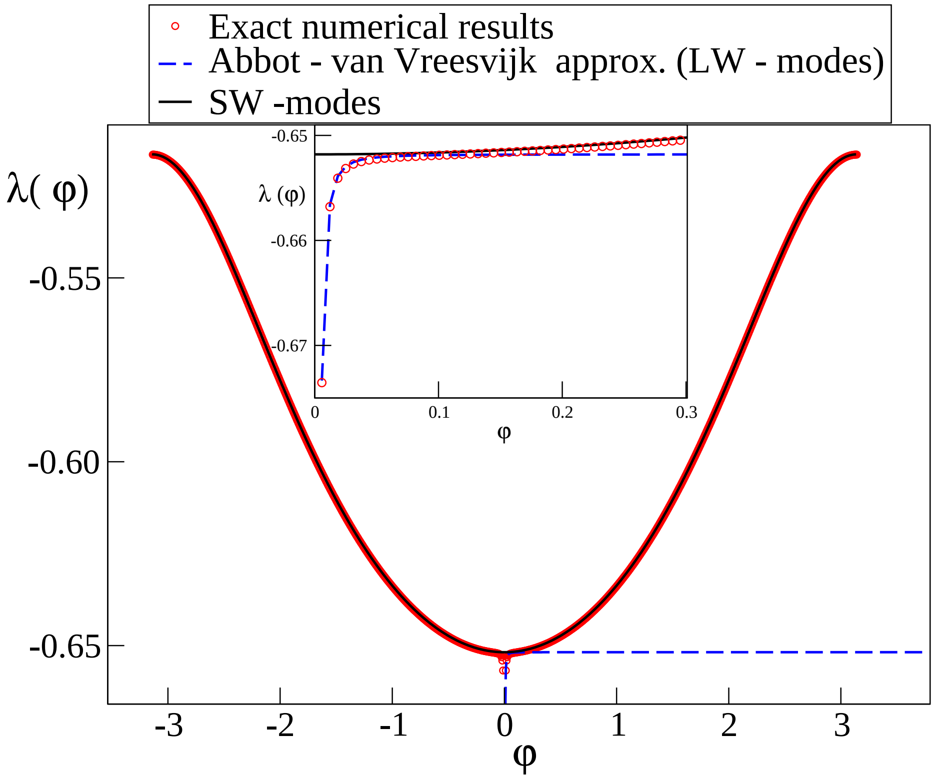
The Abbott - van Vreeswijk mean field analysis does not reproduce the stability properties of the splay state for δ-like pulses (PSPs):

- 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 Fourier spectrum associated to the splay state is well reproduced by the stability analysisi of the Short Wavelenght (SW) Modes.

Vanishing Pulse-Width (III)

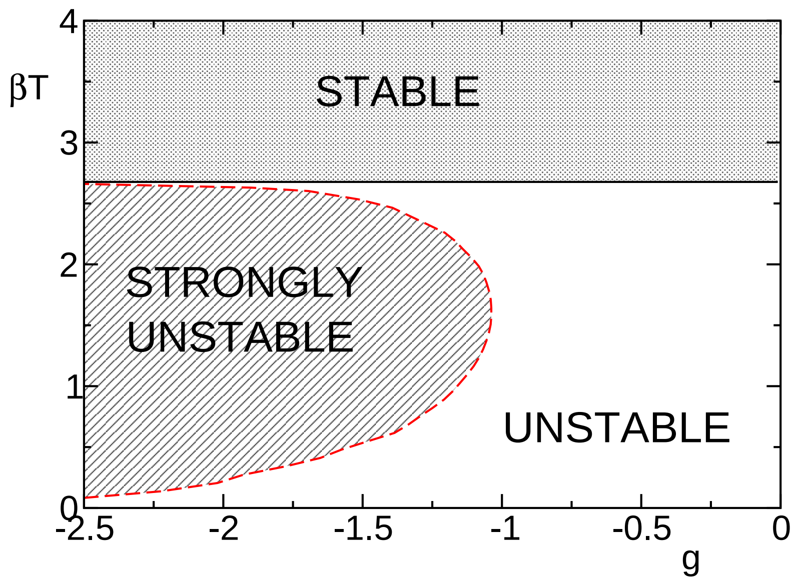
For inhibitory coupling ($g < 0$) the transition from stable to unstable splay states is well captured by the instabilities of the π-mode:

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

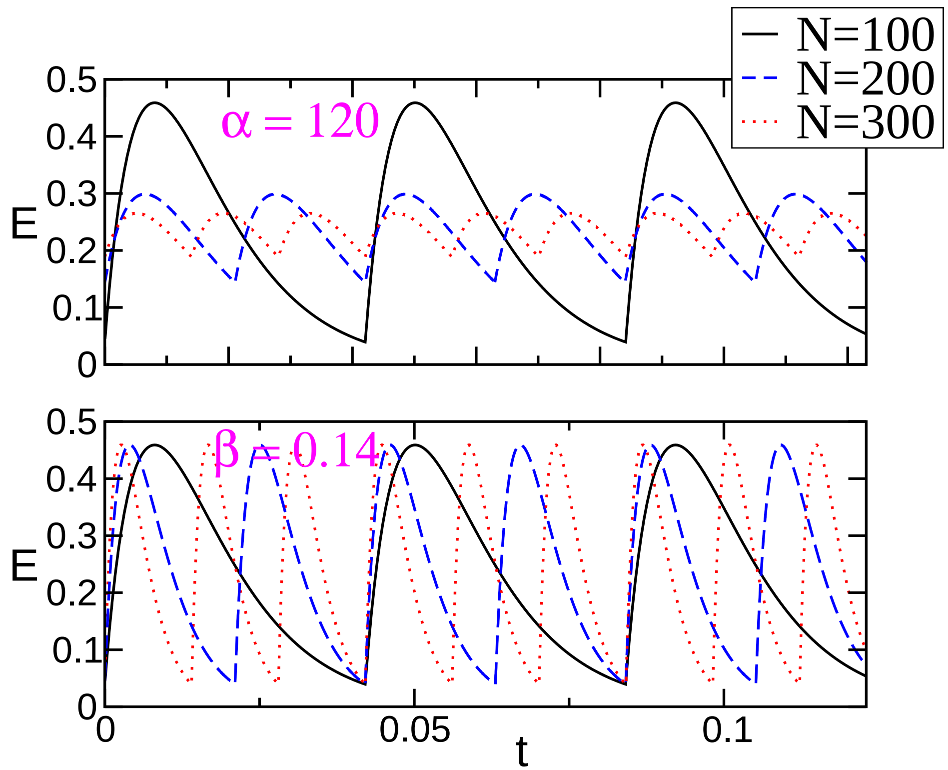
The relevant parameter for the transition is the ratio between the ISI and the pulse-width

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

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



Failure of the Mean Field



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.