Stability of the splay state in pulse-coupled neuronal networks

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Introduction (I)

Splay States

These states are 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

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

- 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 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)

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

$$\dot{x}_i = a - x_i + gE(t)\,,\ x_i \in (-\infty, 1), \quad \Theta = 1, \quad x_R = 0$$

where

- the single neurons are in the repetitive firing regime ($a > 1$)
- g is the coupling - excitatory ($g > 0$) or inhibitory ($g < 0$)
- 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 $Q := (\alpha E + \dot{E})/N$.

Then also the differential equations for the membrane potentials can be integrated giving

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

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 closest to threshold neuron 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 become 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

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

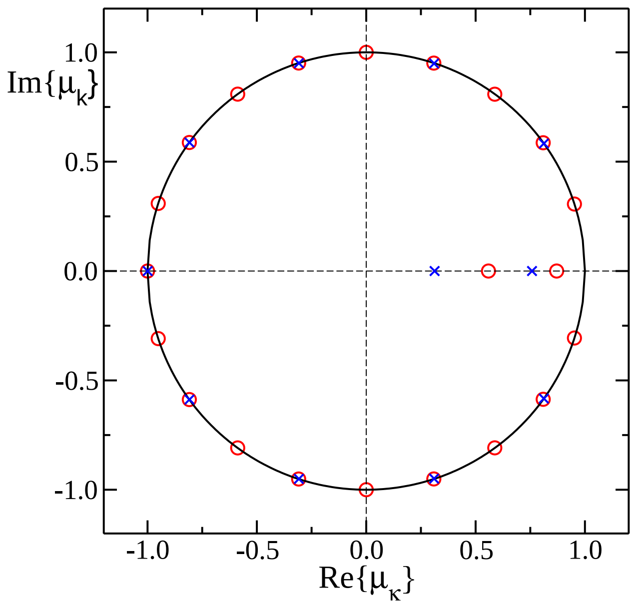
$$T = \ln\left[\frac{aT + g}{(a-1)T + g}\right]$$

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 $\varphi_k = \frac{2\pi k}{N}$, $k = 1, \dots, N-1$
  - $\mu_N = \mu_{N+1} = \exp(-\alpha T/N)$.

  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
  - $\mu_k = e^{i\varphi_k} e^{T(\lambda_k + i\omega_k)/N}$
    $\varphi_k = \frac{2\pi k}{N}$, $k = 1, \dots, N-1$
  - $\mu_N = e^{T(\lambda_N + i\omega_N)/N}$
    $\mu_{N+1} = e^{T(\lambda_{N+1} + i\omega_{N+1})/N}$

  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)

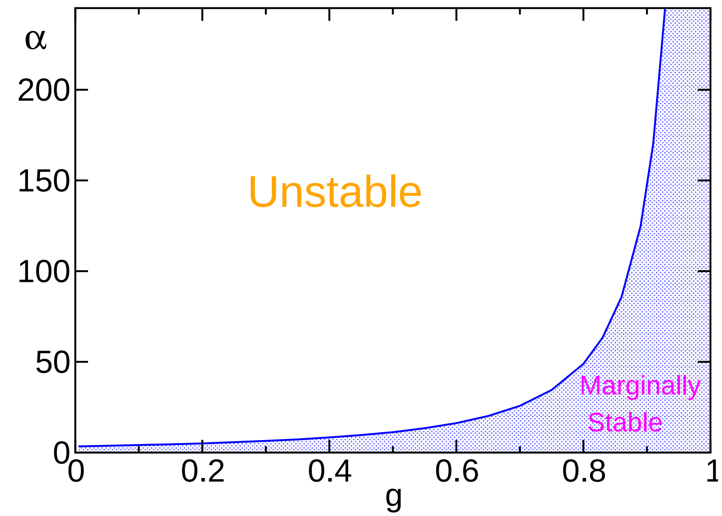
Post-synaptic potentials with finite pulse-width $1/\alpha$ and large network sizes (N)

$N \to \infty$ 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

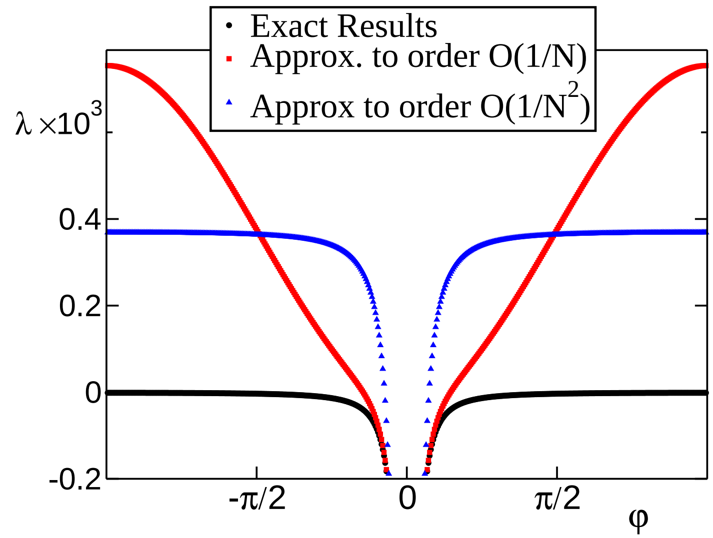


Finite Pulse-Width (II)

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)

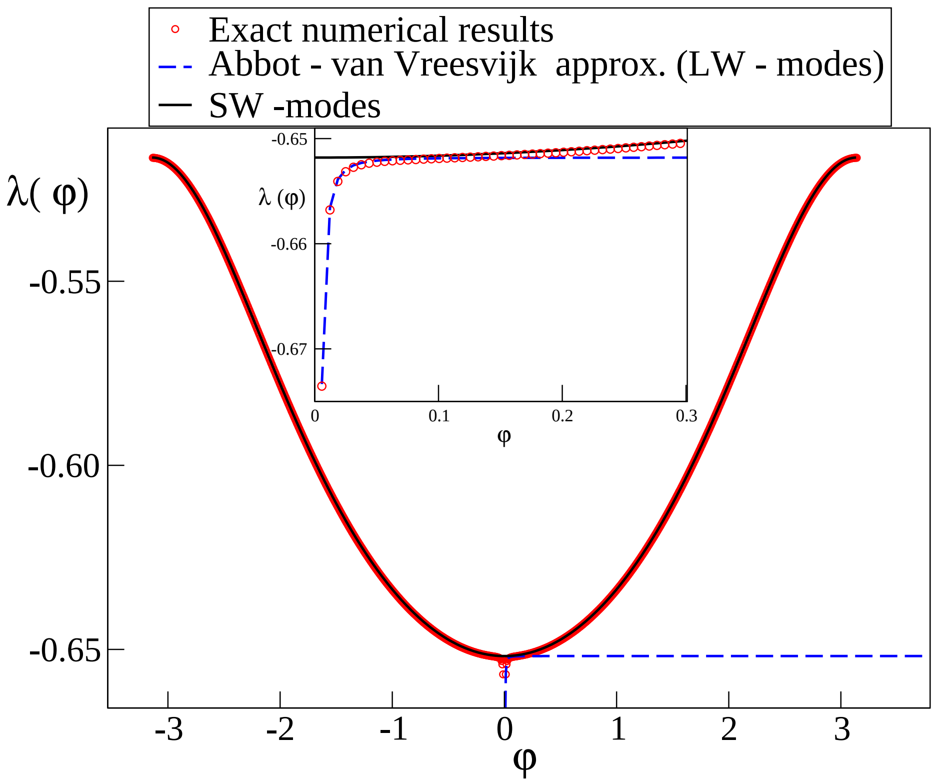
The Abbott - van Vreeswijk mean field analysis does not reproduce the stability properties of the splay state for δ-like pulses:

- 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)

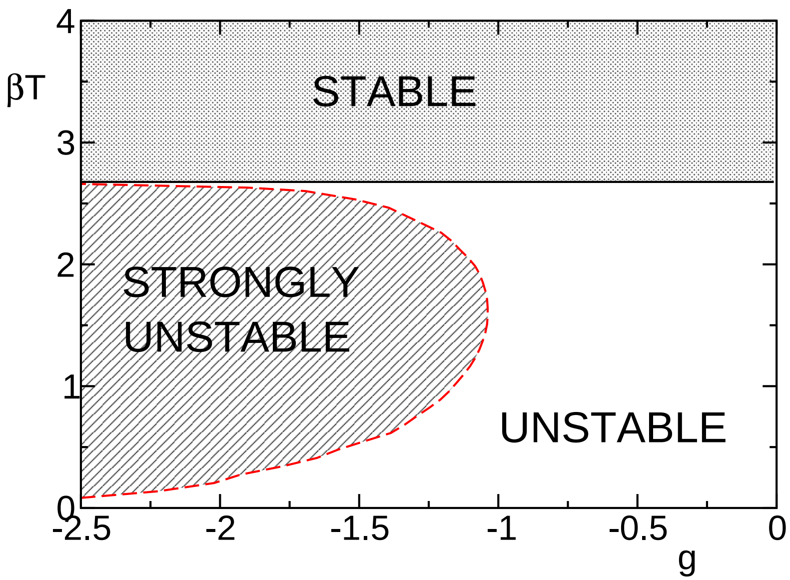
For inhibitory coupling ($g < 0$) the transition from stable to unstable splay states is well captured by the instabilities of the π-mode:

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

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)

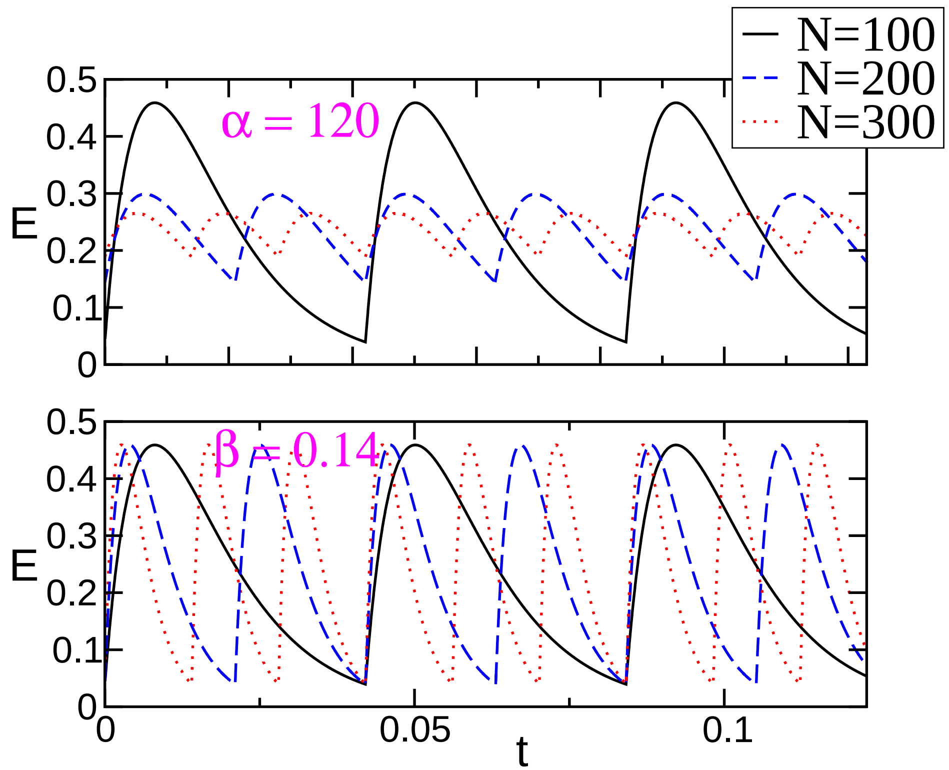
To derive the mean-field stability analysis for the splay state Abbott-Van Vreeswijk made the following hypothesis:

- 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.