E-I Balanced Neural Network

Xiao Liu

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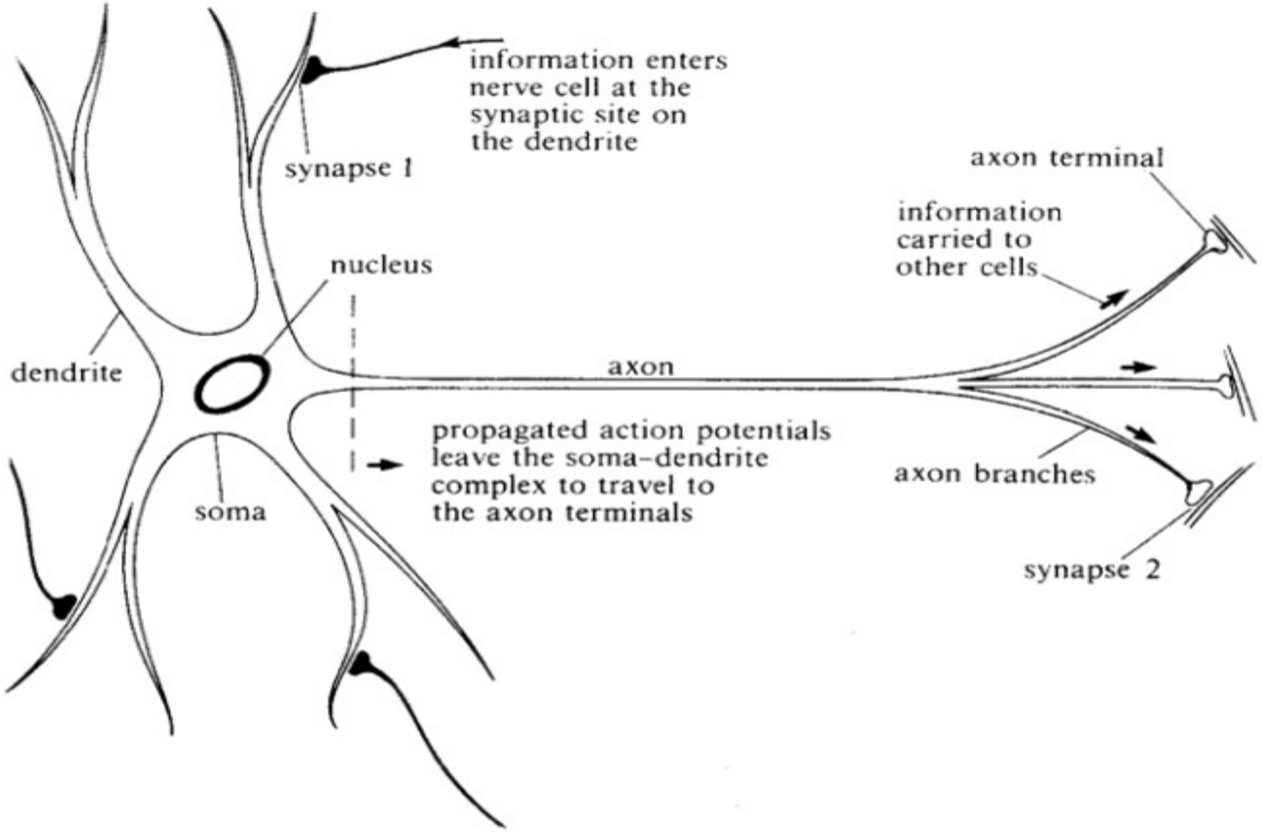
01

Irregular Spiking of Neurons

Signal process of single neuron

Neural Activity

External Stimulus →  → … → Perception or action

Signal process of single neuron

Signal neuron model

External Stimulus → → … → Perception or action

Signal process of single neuron

Signal neuron model

The LIF neuron model

External Stimulus →

$$\tau \frac{\mathrm{d}V}{\mathrm{d}t} = -(V - V_{\text{rest}}) + RI(t)$$

$$\text{if } V > V_{\text{th}}, \quad V \leftarrow V_{\text{reset}} \ \text{last } t_{\text{ref}}$$

→ … → Perception or action

Signal process of single neuron

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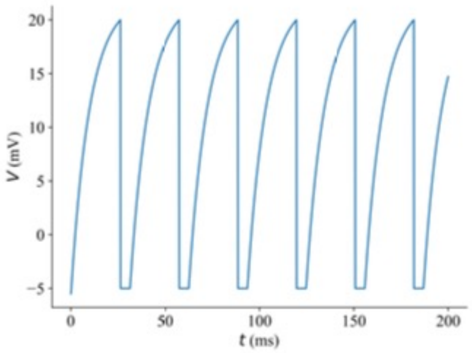

Signal process of single neuron

Signal neuron model

The LIF neuron model

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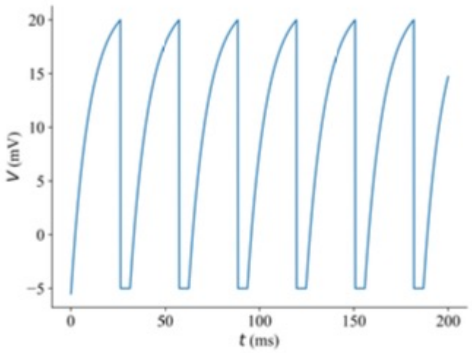
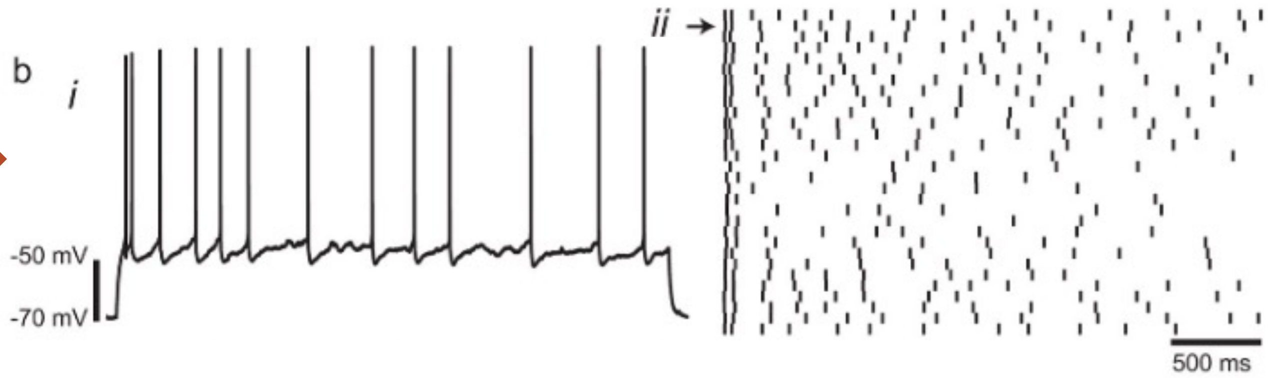


Simulation

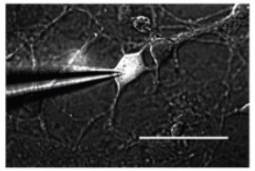
↔

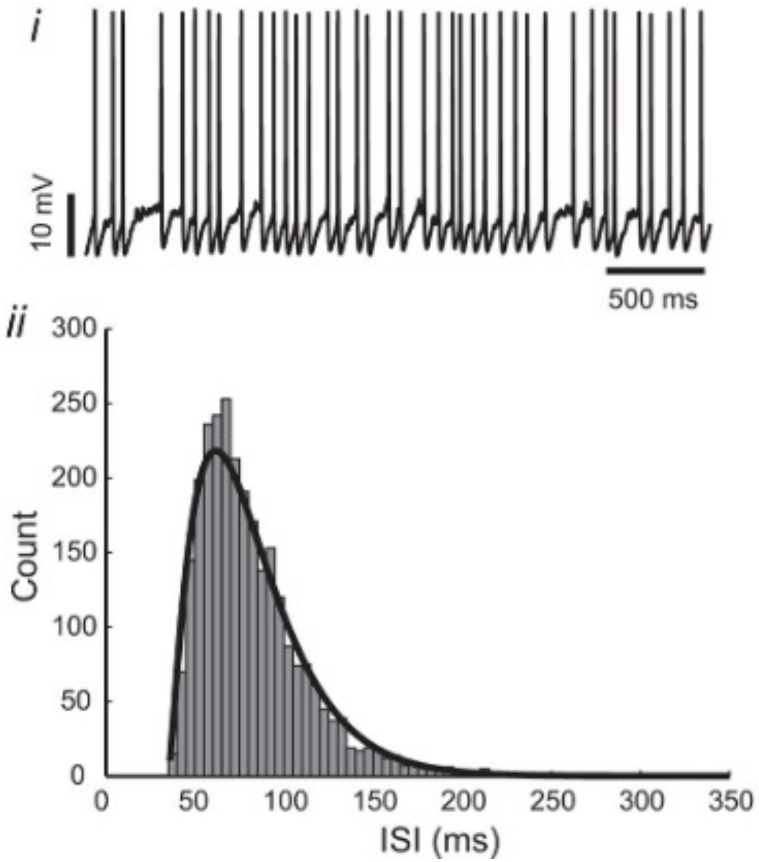


Neuron recorded in vivo

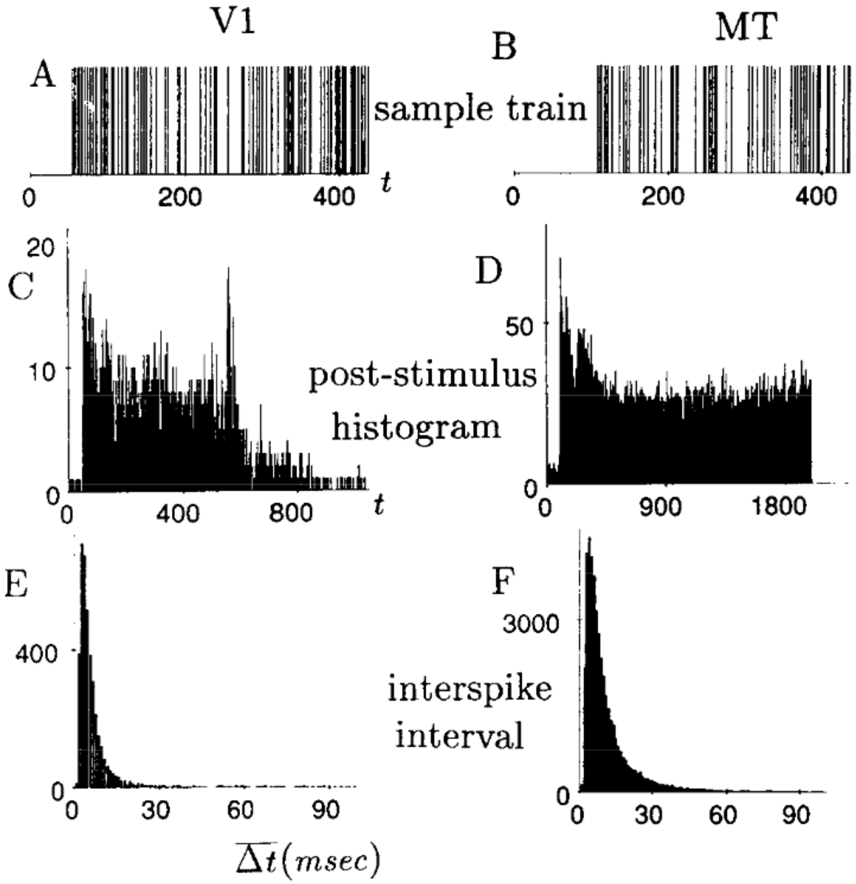
Mendonça et al., 2016

Irregular Spiking of Neurons





Mendonça et al., 2016



Knierim and Van Essen, 1992

Britten et al., 1992

ISI: Interspike interval

Statistical Description of Spikes

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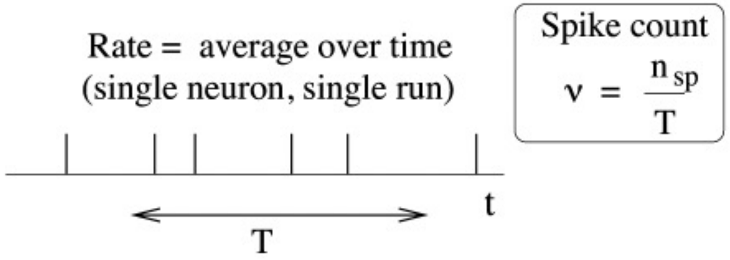
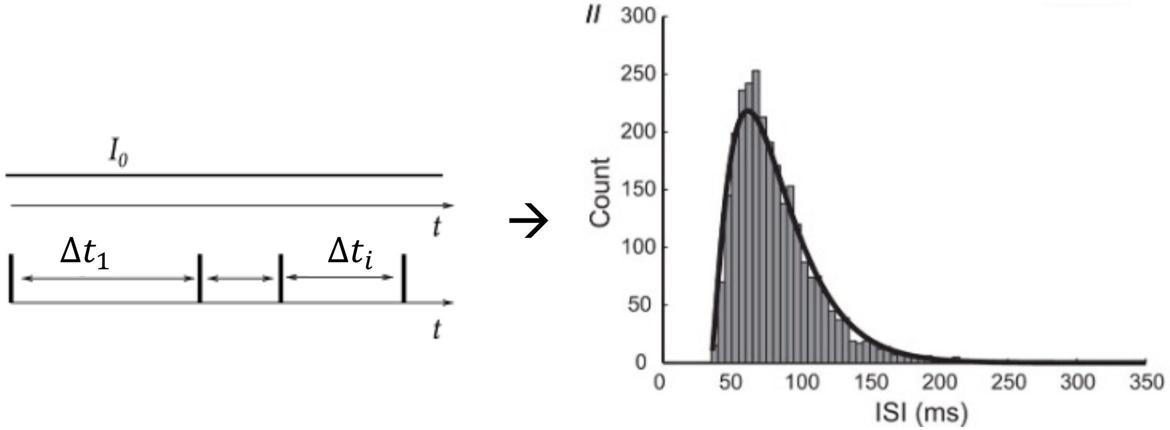
- Firing Rate



- ISI (Interspike interval distributions)

average ISI: $\overline{\Delta t} = \frac{1}{n_{sp}-1}\sum_{i=1}^{n_{sp}-1} \Delta t_i$



standard deviation ISI: $\sigma_{\Delta t}^2 = \sum_{i=1}^{n_{sp}-1}(\Delta t_i - \overline{\Delta t})^2$

Gerstner, W., et al., 2014.

- C_V (Coefficient of variation, Fano factor)

$$C_V = \sigma_{\Delta t}^2 / \overline{\Delta t}$$

Poisson Process

In probability theory and statistics, the Poisson distribution is a discrete probability distribution that expresses the probability of a given number of events occurring in a fixed interval of time or space if these events occur with a known **constant mean rate** and **independently** of the time since the last event。

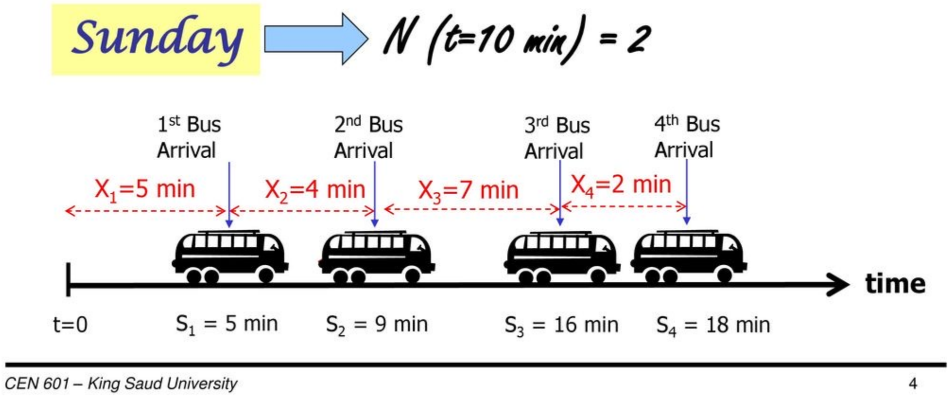
$$P(X = k \text{ events in interval } t) = e^{-rt}\frac{(rt)^k}{k!}$$

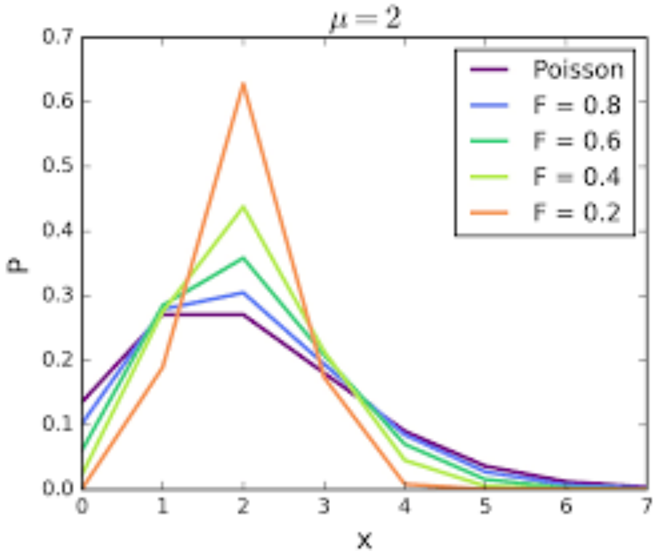
mean: $\bar{X} = rt$

variance: $\sigma^2 = rt$

Fano factor: $\frac{\sigma^2}{\bar{X}} = 1$

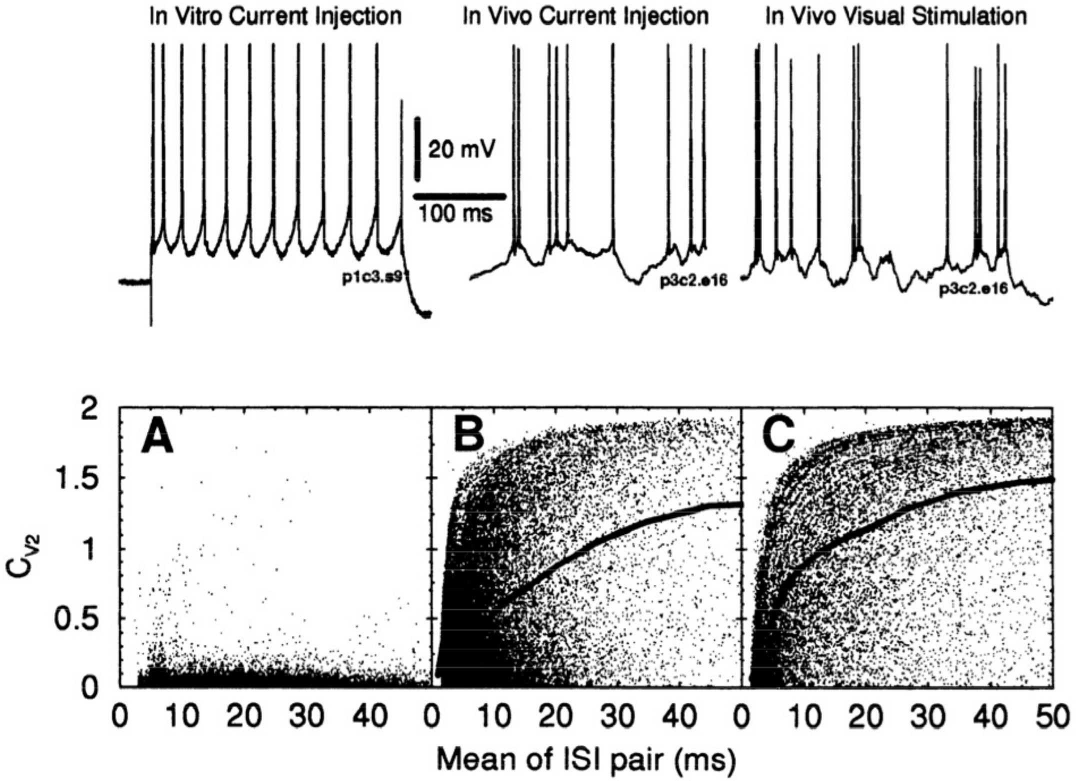
Fano factor → noise-to-signal ratio

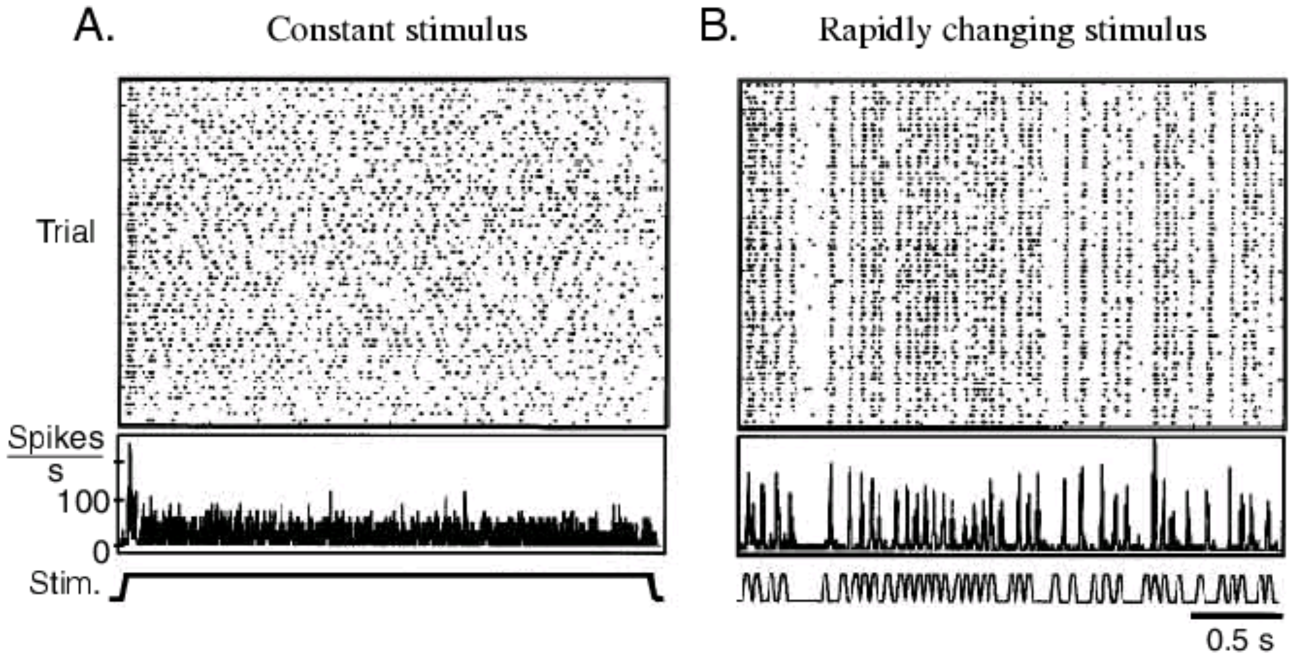




Poisson distribution. In *Wikipedia,* The Free Encyclopedia.

Irregular Spiking of Neurons



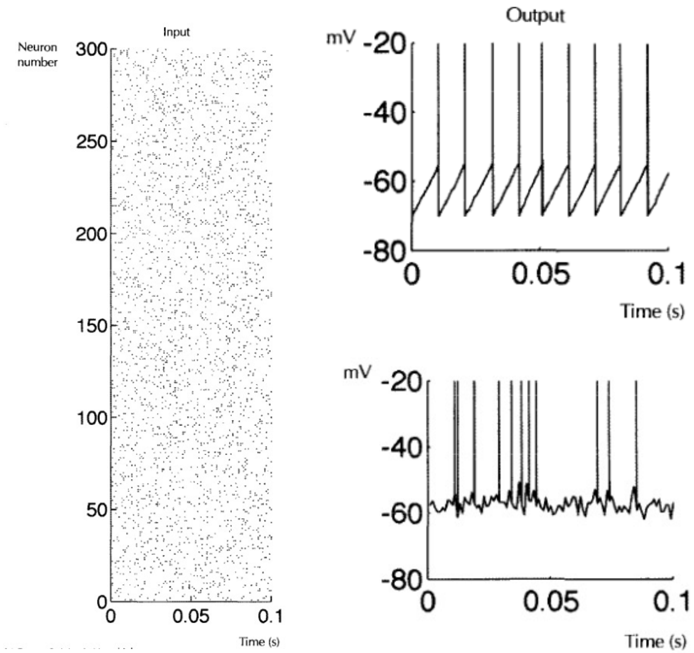


Fano factor >1!

Why Irregular ?

- Random input?
- Noise in the system?
- Coincidence detector?

On average, a cortical neuron receives inputs from 1000~10000 connected neurons. → averaged noise ~ 0



Counts of 300 EPSPs

Coincidence of 35 EPSPs in 1ms

The Journal of Neuroscience, January 1993, 13(1): 334–350

The Highly Irregular Firing of Cortical Cells Is Inconsistent with Temporal Integration of Random EPSPs

William R. Softky[1,2] and Christof Koch[2]

[1]Division of Physics, Mathematics, and Astronomy and [2]Computation and Neural Systems Program, California Institute of Technology, Pasadena, California 91125

Noise, neural codes and cortical organization

Michael N Shadlen and William T Newsome

Stanford University School of Medicine, Stanford, USA

02

E-I Balanced Network

E-I Balanced Network

$$\tau \frac{du_i^E}{dt} = -u_i^E + \sum_{j=1}^{K_E} J_{EE} r_j^E + \sum_{j=1}^{K_I} J_{EI} r_j^I + I_i^E$$

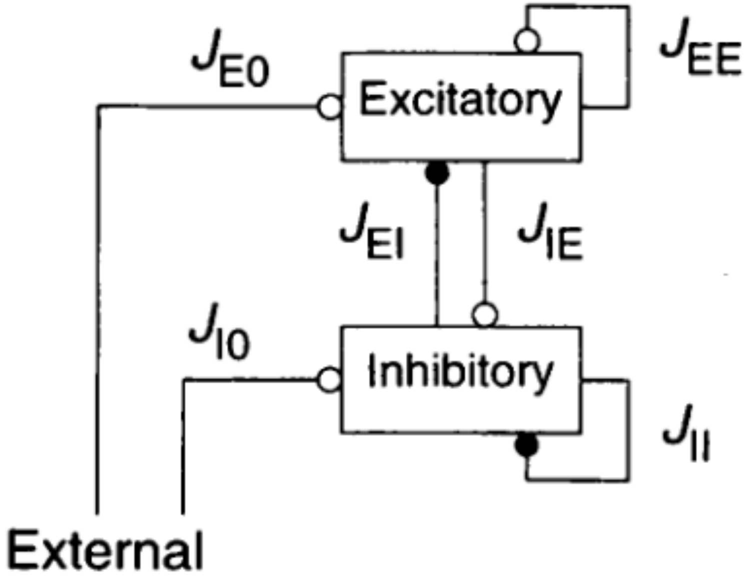
$$\tau \frac{du_i^I}{dt} = -u_i^I + \sum_{j=1}^{K_I} J_{II} r_j^E + \sum_{j=1}^{K_E} J_{IE} r_j^I + I_i^I$$

Sparse & random connections: $1 \ll K_E, K_I \ll N_E, N_I$

Neurons fire largely **independently** to each other.

Chaos in Neuronal Networks with Balanced Excitatory and Inhibitory Activity

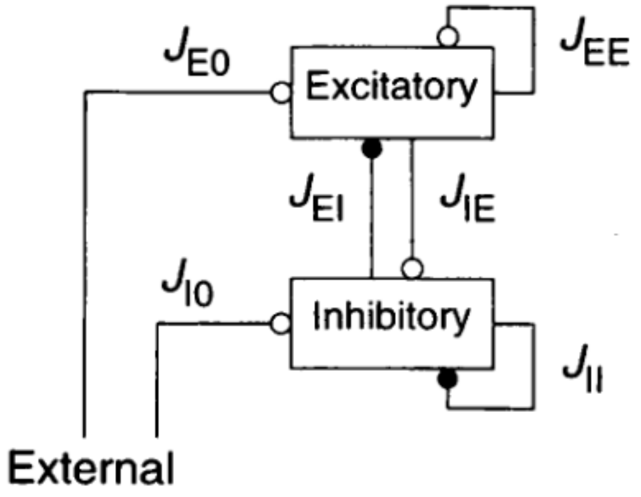
C. van Vreeswijk and H. Sompolinsky



Van Vreeswijk and Sompolinsky, 1996

E-I Balanced Network

$$\tau \frac{du_i^E}{dt} = -u_i^E + \sum_{j=1}^{K_E} J_{EE} r_j^E + \sum_{j=1}^{K_I} J_{EI} r_j^I + I_i^E$$
$$\tau \frac{du_i^I}{dt} = -u_i^I + \sum_{j=1}^{K_I} J_{II} r_j^E + \sum_{j=1}^{K_E} J_{IE} r_j^I + I_i^I$$



Van Vreeswijk and Sompolinsky, 1996

Single neuron fires irregularly r_j^E, r_j^I with mean rate μ and variance σ^2.

The mean of recurrent input received by E neuron:

$$\sim K_E J_{EE} \mu - K_I J_{EI} \mu$$

The variance of recurrent input received by E neuron:

$$\sim K_E (J_{EE})^2 \sigma^2 + K_I (J_{EI})^2 \sigma^2$$

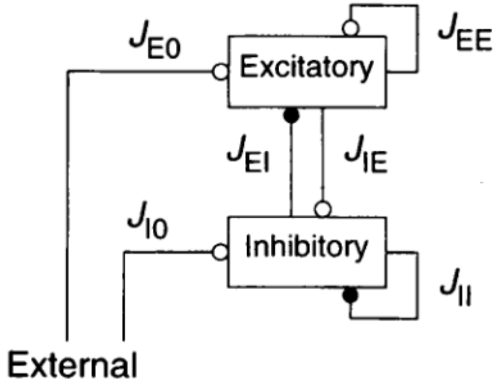
The balanced condition:

$$K_E J_{EE} - K_I J_{EI} \sim O(1)$$
$$J_{EE} = \frac{1}{\sqrt{K_E}}, J_{EI} = \frac{1}{\sqrt{K_I}}, K_E (J_{EE})^2 \sigma^2 + K_I (J_{EI})^2 \sigma^2 \sim O(1)$$

E-I Balanced Network

$$\tau\frac{du_i^E}{dt} = -u_i^E + \sum_{j=1}^{K_E} J_{EE} r_j^E + \sum_{j=1}^{K_I} J_{EI} r_j^I + I_i^E$$

$$\tau\frac{du_i^I}{dt} = -u_i^I + \sum_{j=1}^{K_I} J_{II} r_j^E + \sum_{j=1}^{K_E} J_{IE} r_j^I + I_i^I$$



$$\frac{I_E}{I_I} > \frac{J_E}{J_I} > 1$$

$$J_E > 1$$

τ not too big

Van Vreeswijk and Sompolinsky, 1998

$$\overline{I_a} = \overline{F_a} + \overline{R_a} = \sqrt{N}(f_a\mu_0 + w_{aE}r_E + w_{aI}r_I), \quad a = E, I,$$

$$w_{ab} = p_{ab}j_{ab}q_b$$

$$J_{ij}^{ab} = j_{ab}/\sqrt{N};$$

$$\frac{f_E}{f_I} > \frac{w_{EI}}{w_{II}} > \frac{w_{EE}}{w_{IE}}.$$

For more details, please refer to Tian et al., 2020

03

BrainPy Simulation

Simulation

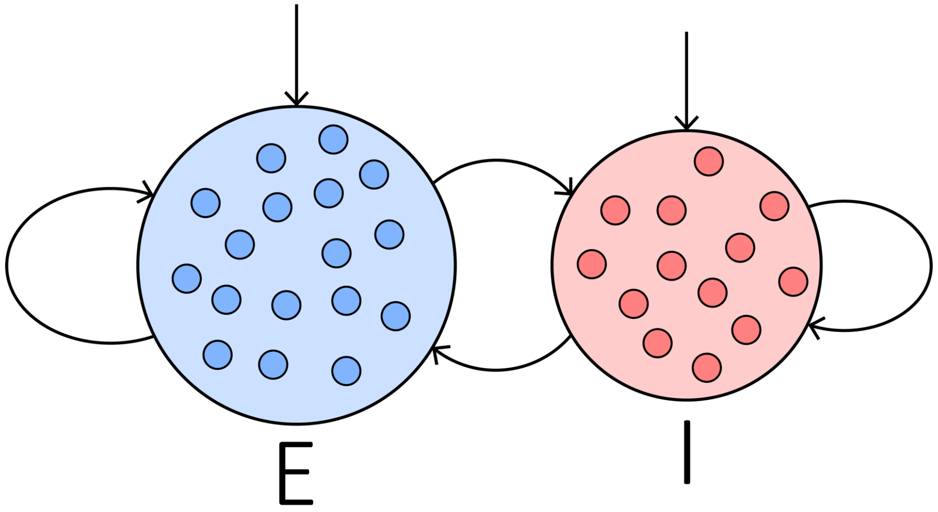
LIF neuron 4000 (E/I=4/1, P=0.02)

τ = 20 ms

V_{rest} = -60 mV

Spiking threshold: -50 mV

Refractory period: 5 ms



$$\tau \frac{dV}{dt} = (V_{\text{rest}} - V) + I$$

$$\tau_{exc} \frac{dg_{exc}}{dt} = -g_{exc}$$

$$\tau_{inh} \frac{dg_{inh}}{dt} = -g_{inh}$$

$$I = g_{exc}(E_{exc} - V) + g_{inh}(E_{inh} - V) + I_{\text{ext}}$$

$E_{\text{exc}} = 0\text{mV}$ and $E_{\text{inh}} = -80\text{mV}, I_{\text{ext}} = 20.$
$\tau_{\text{exc}} = 5$ ms, $\tau_{\text{inh}} = 10$ ms, $\Delta g_{\text{exc}} = 0.6$ and $\Delta g_{\text{inh}} = 6.7.$

Vogels and Abbott, 2005

Synaptic Computation

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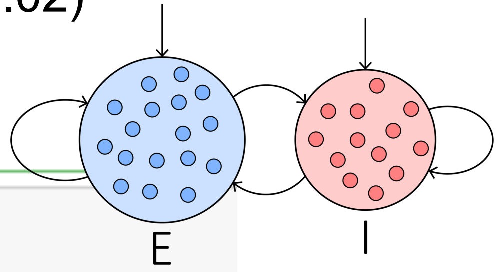
$$\tau_{exc}\frac{dg_{exc}}{dt} = -g_{exc}$$
$$\tau_{inh}\frac{dg_{inh}}{dt} = -g_{inh}$$
$$I = g_{exc}(E_{exc} - V) + g_{inh}(E_{inh} - V) + I_{\text{ext}}$$

```
import brainpy as bp
import numpy as np
import brainpy.math as bm
import matplotlib.pyplot as plt
```

```
# 基于 align post Exponential synaptic computation
class Exponential(bp.Projection):
  def __init__(self, pre, post, delay, prob, g_max, tau, E, label=None):
    super().__init__()
    self.pron = bp.dyn.ProjAlignPost2(
      pre=pre,
      delay=delay,
      comm=bp.dnn.EventCSRLinear(bp.conn.FixedProb(prob, pre=pre.num, post=post.num), g_max), # 随机连接
      syn=bp.dyn.Expon(size=post.num, tau=tau),# Exponential synapse
      out=bp.dyn.COBA(E=E), # COBA network
      post=post,
      out_label=label
    )
```

E-I Balanced Network

LIF neuron 4000 (E/I=4/1, P=0.02)
τ = 20 ms
V_{rest} = -60 mV
Spiking threshold: -50 mV
Refractory period: 5 ms



$E_{\text{exc}} = 0\text{mV}$ and $E_{\text{inh}} = -80\text{mV}, I_{\text{ext}} = 20.$

$\tau_{\text{exc}} = 5$ ms, $\tau_{\text{inh}} = 10$ ms, $\Delta g_{\text{exc}} = 0.6$ and $\Delta g_{\text{inh}} = 6.7.$

```python
# 构建 E-I Balanced Network

class EINet(bp.DynamicalSystem):
  def __init__(self, ne=3200, ni=800):
    super().__init__()

    # bp.neurons.LIF()
    self.E = bp.dyn.LifRef(ne, V_rest=-60., V_th=-50., V_reset=-60., tau=20., tau_ref=5.,
                           V_initializer=bp.init.Normal(-55., 2.))
    self.I = bp.dyn.LifRef(ni, V_rest=-60., V_th=-50., V_reset=-60., tau=20., tau_ref=5.,
                           V_initializer=bp.init.Normal(-55., 2.))

    #### E2E, E2I, I2E, I2I Exponential synaptic computation
    # delay=0,prob=0.02, g_max_E=0.6, g_max_I=6.7, tau_E=5, tua_I=10,
    # reversal potentials E_E=0, E_E=-80, label=EE,EI,IE,II
    self.E2E = Exponential(self.E, self.E, 0., 0.02, 0.6, 5., 0., 'EE')
    self.E2I = Exponential(self.E, self.I, 0., 0.02, 0.6, 5., 0., 'EI')
    self.I2E = Exponential(self.I, self.E, 0., 0.02, 6.7, 10., -80., 'IE')
    self.I2I = Exponential(self.I, self.I, 0., 0.02, 6.7, 10., -80., 'II')
```

E-I Balanced Network

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$$I = g_{exc}(E_{exc} - V) + g_{inh}(E_{inh} - V) + I_{\text{ext}}$$

$$\tau \frac{dV}{dt} = (V_{\text{rest}} - V) + I$$

```python
def update(self, inp=0.):
  #### 更新突触传入电流
  self.E2E()
  self.E2I()
  self.I2E()
  self.I2I()

  ### 更新神经元群体
  self.E(inp)
  self.I(inp)

  # 记录需要 monitor的变量
  E_E_inp = self.E.sum_inputs(self.E.V, label='EE')  # E2E的输入
  I_E_inp = self.E.sum_inputs(self.E.V, label='IE')  # I2E的输入
  return self.E.spike, self.I.spike, E_E_inp, I_E_inp
```

Simulation

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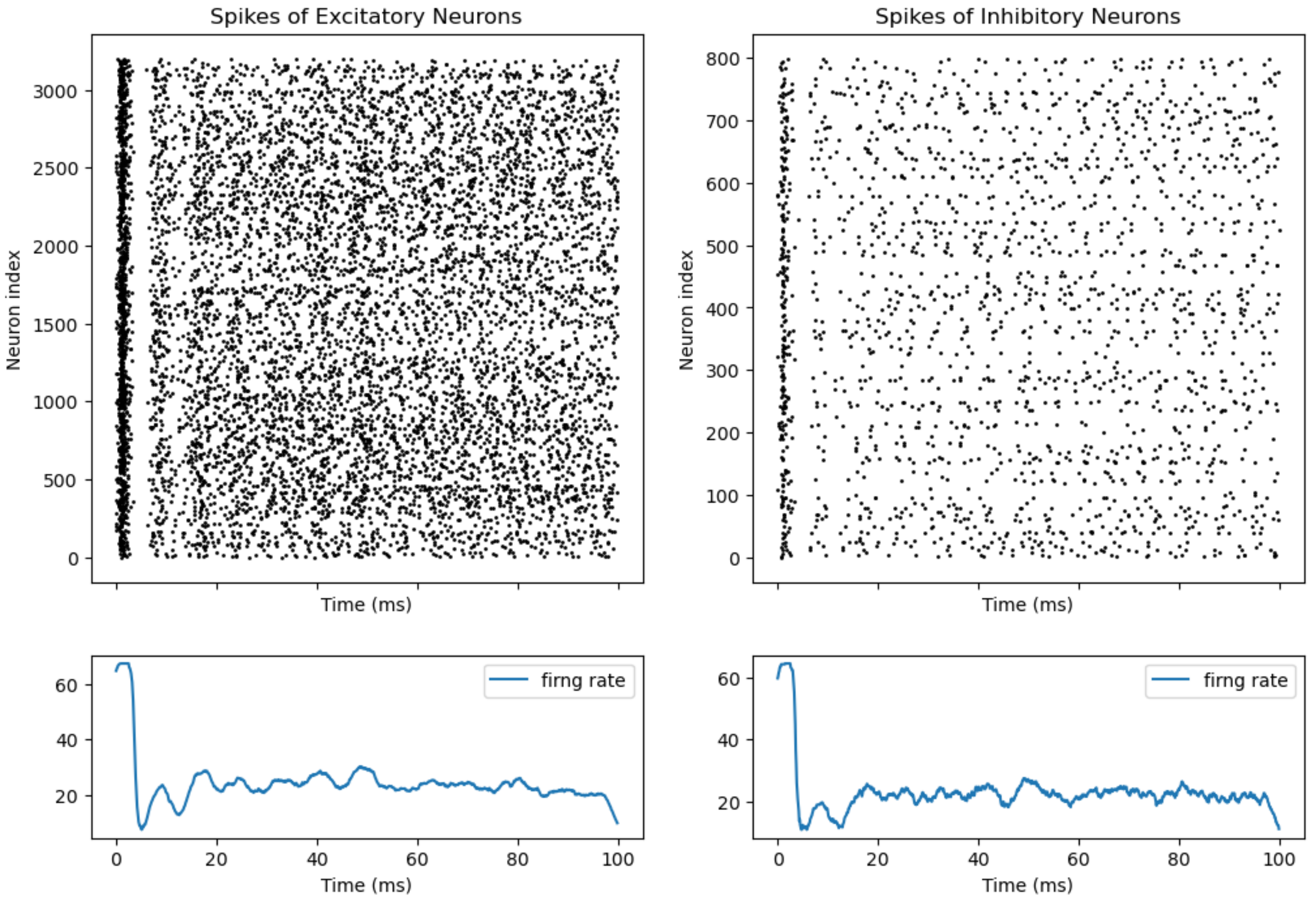
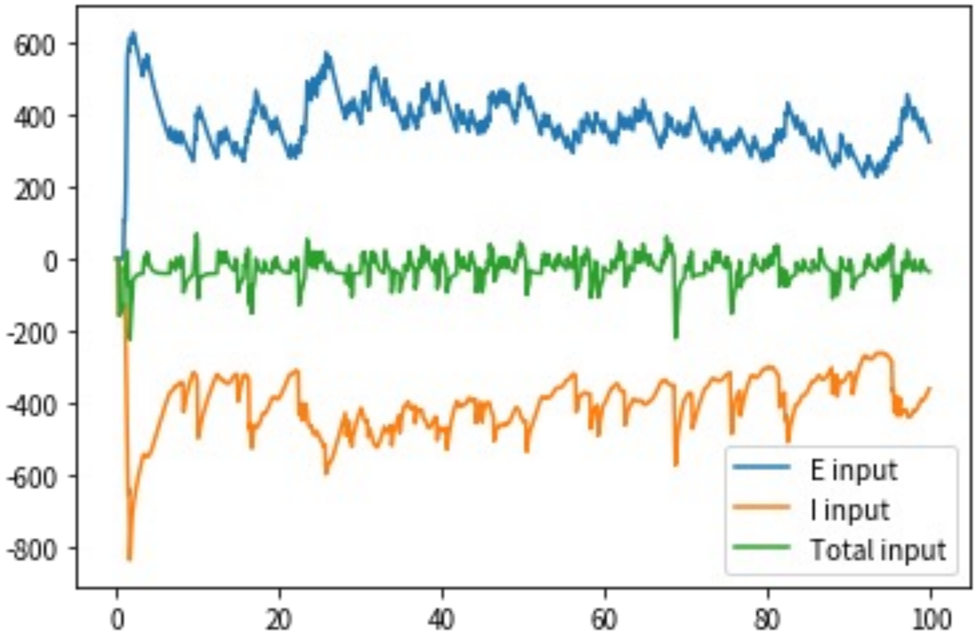
```
# 数值模拟
model = EINet(ne=3200, ni=800) #实现4000个神经元的E-I模型，其中E：I=4:1
runner = bp.DSRunner(model)
inputs = np.ones(1000) * 20.  # 100 ms
e_sps, i_sps, ee_inps, ie_inps = runner.run(inputs=inputs)

# 可视化
# 兴奋性脉冲发放
fig, gs = plt.subplots(2,2,gridspec_kw={'height_ratios': [3, 1]}, figsize=(12, 8), sharex='all')
plt.sca(gs[0,0])
bp.visualize.raster_plot(runner.mon['ts'], e_sps, title= 'Spikes of Excitatory Neurons')
plt.sca(gs[0,1])
bp.visualize.raster_plot(runner.mon['ts'], i_sps, title= 'Spikes of Inhibitory Neurons')

# 平均发放速率
plt.sca(gs[1,0])
rate_e = bp.measure.firing_rate(e_sps, 5.)
bp.visualize.line_plot(runner.mon['ts'], rate_e, legend='firng rate')
plt.sca(gs[1,1])
rate_i = bp.measure.firing_rate(i_sps, 5.)
bp.visualize.line_plot(runner.mon['ts'], rate_i, legend='firng rate',show=True)
```

Results





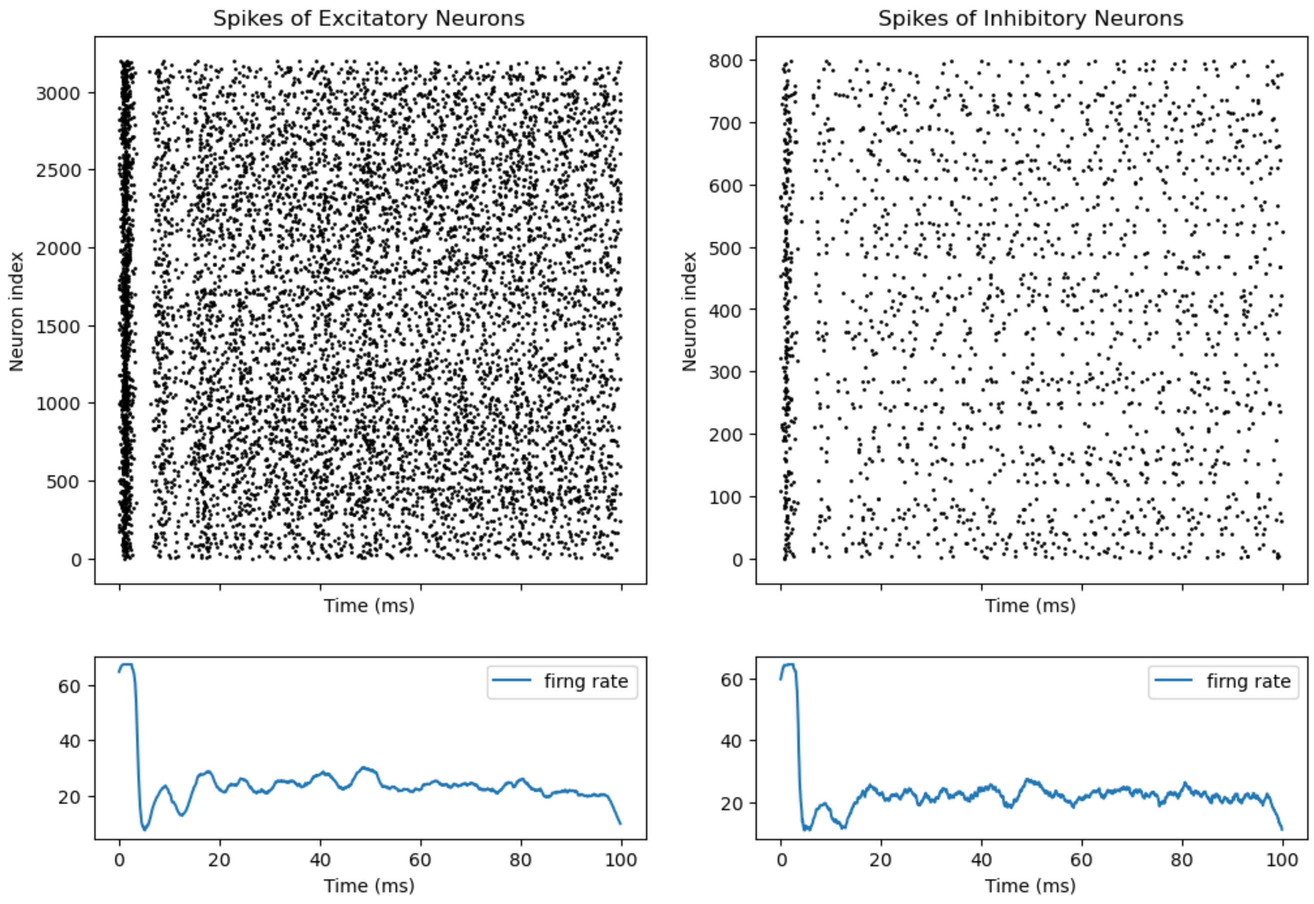
Inputs of Single Neuron

04

Properties of E-I Network

Properties of a E-I Balanced Network

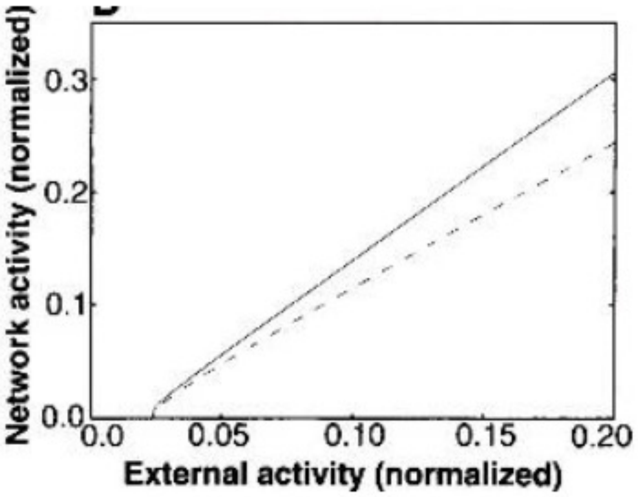
- Irregular firing (chaos) emerge from the network dynamics, without fine tuning parameters
- Neuronal firing is driven by input fluctuations

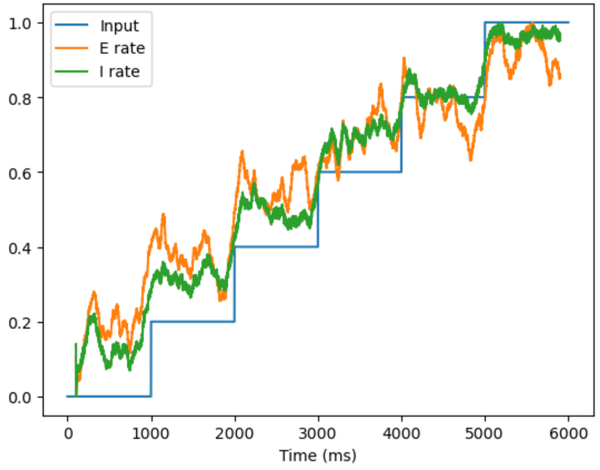


Properties of a E-I Balanced Network

- Linear encoding

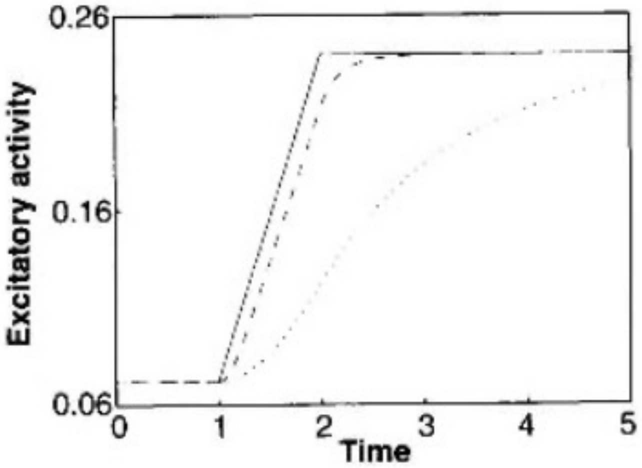
External input strength is "linearly" encoded by the mean firing rate of the neural population

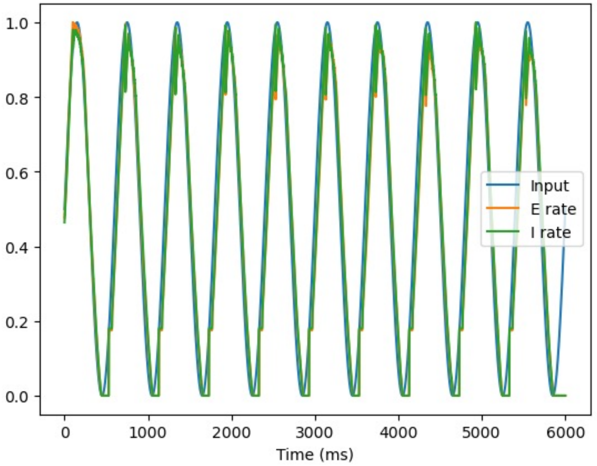




- Fast Response

The network responds rapidly to abrupt changes of the input





Van Vreeswijk and Sompolinsky, 1996

Noise speeds up computation

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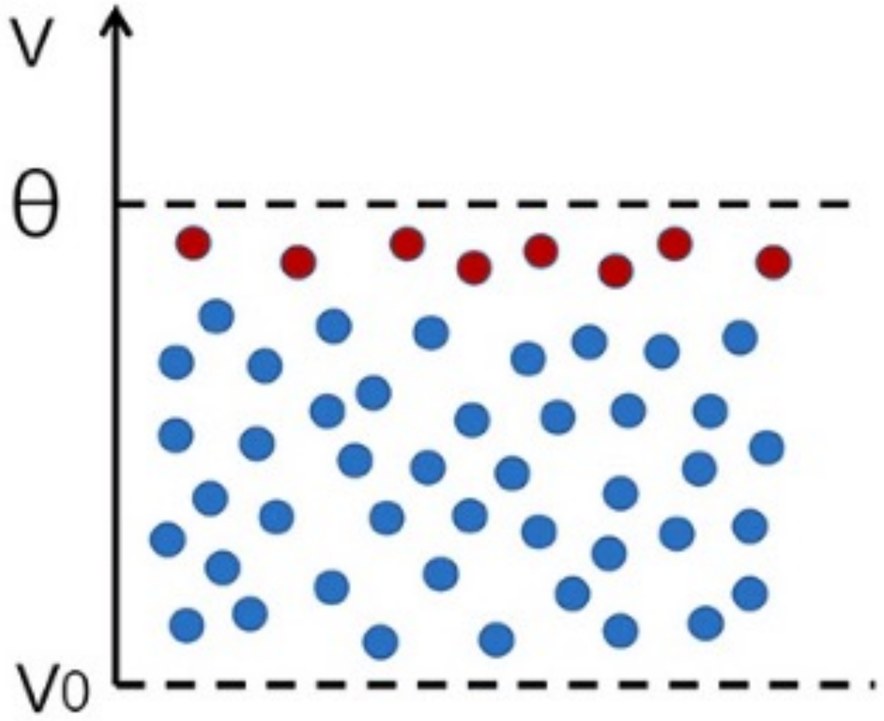
- A neural ensemble jointly encodes stimulus information;
- Noise randomizes the distribution of neuronal membrane potentials;
- Those neurons (red circle) whose potentials are close to the threshold will fire rapidly;
- If the noisy environment is proper, even for a small input, a certain number of neurons will fire instantly to report the presence of a stimulus.



Take-Home Message

Irregular spiking

Fano factor >1

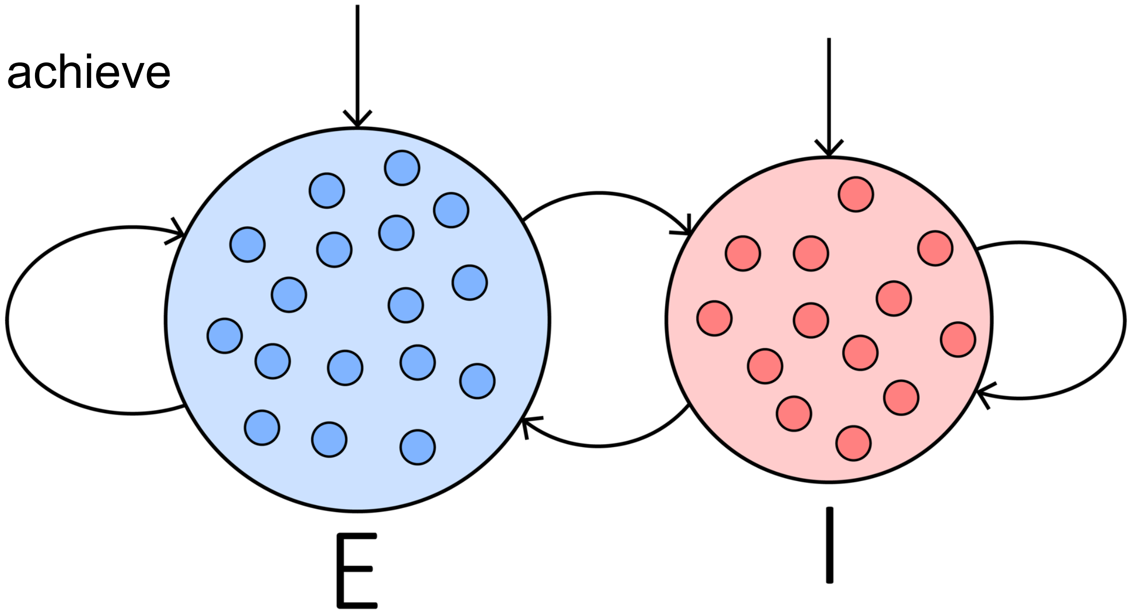
Single neuron cannot achieve

Balanced everywhere

Satisfying

$$J_{ij}^{ab} = j_{ab}/\sqrt{N};$$

$$\frac{f_E}{f_I} > \frac{w_{EI}}{w_{II}} > \frac{w_{EE}}{w_{IE}}.$$



E-I Balanced Network

Functions:

- Linear encoding
- Fast respond
- speeds up computation