Stochasticity in Neurocomputing: Some Simple Stochastic Models

Neuroinformatics / Neuroscience

Introduction

- In modern electro-physiological experiments on real neurons to measure their responses to certain stimuli, the neuro-scientist **repeats** several times the presentation of the same **stimulus** and then **averages** over all the times that the stimulus has been repeated.

- But before averaging, the neurophysiologist realizes that the **neuronal response is not the same** every time the same stimulus is presented.

Introduction

- This is one of the many proves that demonstrate the certain **randomness present** in **neurons** and their way of acting.

- Other significant proves of the stochastic nature in neurobiology are the **electroencephalogram** records that were correctly **approximated** by zero-average **Gaussian processes**.

- **Fluctuations in excitability** have also been observed when, with identical electrical discharges in inputs, action potentials in the axons of neurons are caused in a random way.

Introduction

- Another important example of neuronal stochasticity is the **variability in the inter-firing intervals** of the action potentials generated in neurons.

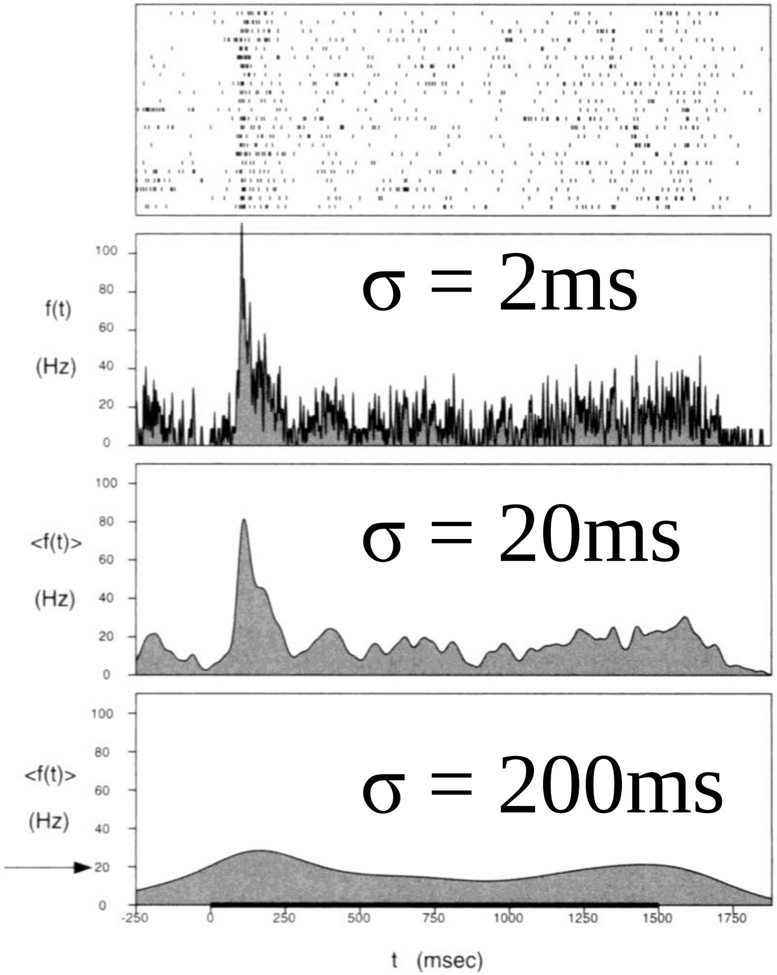


Fig. 14.1 What Is the Firing Rate Definition of the *firing rate*. The starting point is numerous trials in which the same stimulus is repeatedly presented to the animal and the spikes generated by some cell are recorded. These are shown in the *raster diagram* at the top, taken from a cell in cortical area V4 in the awake monkey. The stimulus—a grating—is flashed on at 0 and lasts until 1500 msec. Twenty-three of these trials are averaged, smoothed with a Gaussian of 2-msec standard deviation σ and normalized. This averaging window is so small that it effectively defines the instantaneous firing rate $f(t)$. These plots are known as *poststimulus time histograms* (PSTHs). The two lower plots illustrate an *average firing rate* $\langle f(t) \rangle$ obtained from the raster diagrams using Gaussian smoothing with σ set to 20 and 200 msec. In many experiments, only the average number of spikes triggered during each trial, corresponding to a very large value of σ (see arrow at 19.5 Hz), is used to relate the cellular response to the behavior of the animal. It is important to realize that a single neuron only sees spike trains and not a smoothly varying firing rate. Unpublished data from D. Leopold and N. Logothetis, printed with permission.

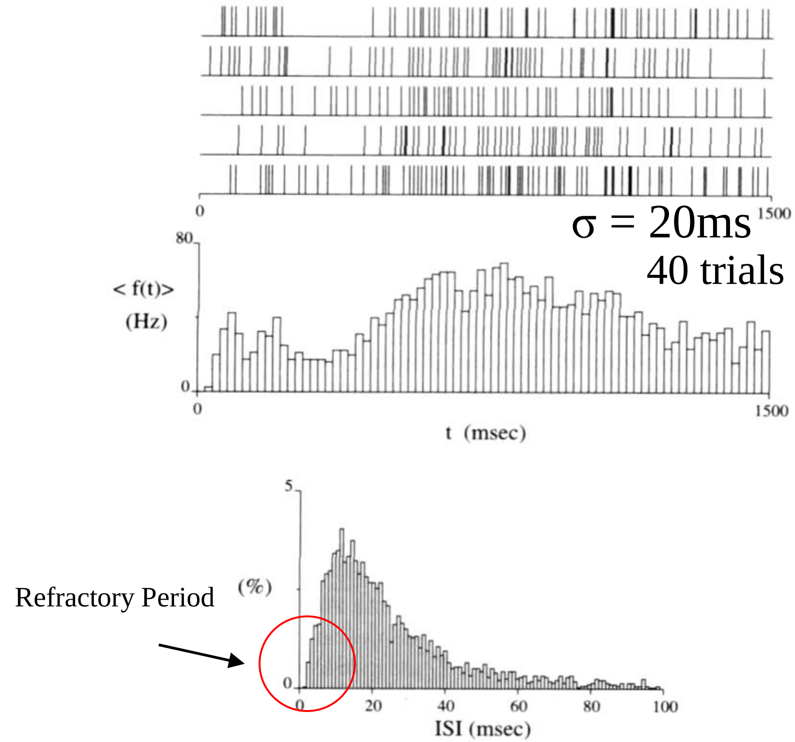


Fig. 15.1 Variability of Neuronal Spiking A high-contrast bar is swept repeatedly over the receptive field of a cortical cell in the awake macaque monkey. Much variability in the microstructure of spiking is evident from trial to trial. The poststimulus time histogram in the middle corresponds to the averaged firing rate $\langle f(t) \rangle$ (using 20 msec bins) taken over 40 trials. The lower plot illustrates the associated interspike interval (ISI) histogram. It shows a lack of very short intervals, indicative of a refractory period, and an exponentially decreasing likelihood of finding very large gaps between spikes. The lack of reproducibility of the detailed spike pattern is the primary reason arguing for the idea of a mean rate code (Eq. 14.1). Yet neurons deep within the cortex can faithfully reproduce the microstructure of spiking over several hours (Fig. 15.11). From W. Newsome, K. Britten, personal communication.

Stochastic Modeling

- Because there is sufficient **evidence**, as we have seen so far, that **biological systems** are based on **certain stochastic or noise** components, it is necessary to **incorporate them** into the possible neuronal **models** that are formulated.

- Various **authors** have **devised several ways** to **include** this **stochastic** character of neuronal machinery in their **models**.

Stochastic Modeling

- One of the **first stochastic** models was the work of **Landahl et at. (1943)** derived directly from the pioneering work of McCulloch and Pitts (1943) on the classical logical neuron model.

- Landahl and collaborators devised this model for motor neurons that **received excitation of elastic receptors**. In this model it was assumed that a neuron generated an action potential, when at least a certain threshold number of **excitation inputs** activated it, in a certain **time interval** (in that same interval no **inhibitory input** arrived).

Stochastic Modeling

- The activation of each synaptic input to the neuron was supposed to be governed by a **stochastic Poisson process**, each with a constant firing frequency.

- If the number of neuron receptors is assumed to be large enough, then the **central limit theorem** can be applied so that this process is approximated by a **normal distribution**.

- As regards the synaptic receptors of a neuron, **the idea of Poisson's distribution** in their activation **was not so misleading**.

Stochastic Modeling

- In fact, one of the best studied phenomena, which is governed by a **Poisson process**, are the **neurotransmitter release times** in the frog's neuromuscular junction (Fatt and Katz, 1952).

- Because the **release of vesicles** from these neurotransmitters can **generate the potential for firing in the postsynaptic neuron**, it would be reasonable to think that **the generation of neural spikes** in this neuron is **also** somewhat **stochastic**.

Stochastic Modeling

- In fact, in **recent neuron records** *in vivo* **irregular neural spikes have been obtained** with great variability in the intervals between spikes (Holt et al., 1996).

- We can say, in a first approximation, that in some neurons, particularly **in cortical** ones, it is observed that the **firing intervals are independent**.

- That is, the **width of each firing interval** is **independent** of whether it was **equal, larger, or smaller before**.

Stochastic Modeling

- Thus, the process to model this behavior is a process in which the **random variables** are **independent** and **identically distributed**.
- Therefore, the simplest stochastic process for modeling this behavior is again the **Poisson** process.
- This process is characterized by a **single parameter**, which is the **average of the random variable**.

Stochastic Modeling

- In computational neuroscience, the **statistical approach** is usually **used to incorporate all the irregularities** that we have already mentioned.
- Irregularities are included as noise.
- Thus, noise could be described by a random variable, which can take different values.
- **The nature of the process generating** and the particular value of the variable **is not known**.
- In fact, we will **consider noise to those variables that cannot be predicted**.

Stochastic Modeling

- Probability reminder (see appendix A).

- Although **we cannot predict the precise value of the random variable**, we are able to **give some statistical measure** (or any other measure) that somehow characterizes the underlying stochastic process in the biological system.

- One of the best ways to do this is to draw the **histograms of periods between neuronal spikes**.

Stochastic Modeling

https://en.wikipedia.org/wiki/Brodmann_area_46 (Brodmann area 46, or BA46: sustaining **attention** and managing **working memory**)

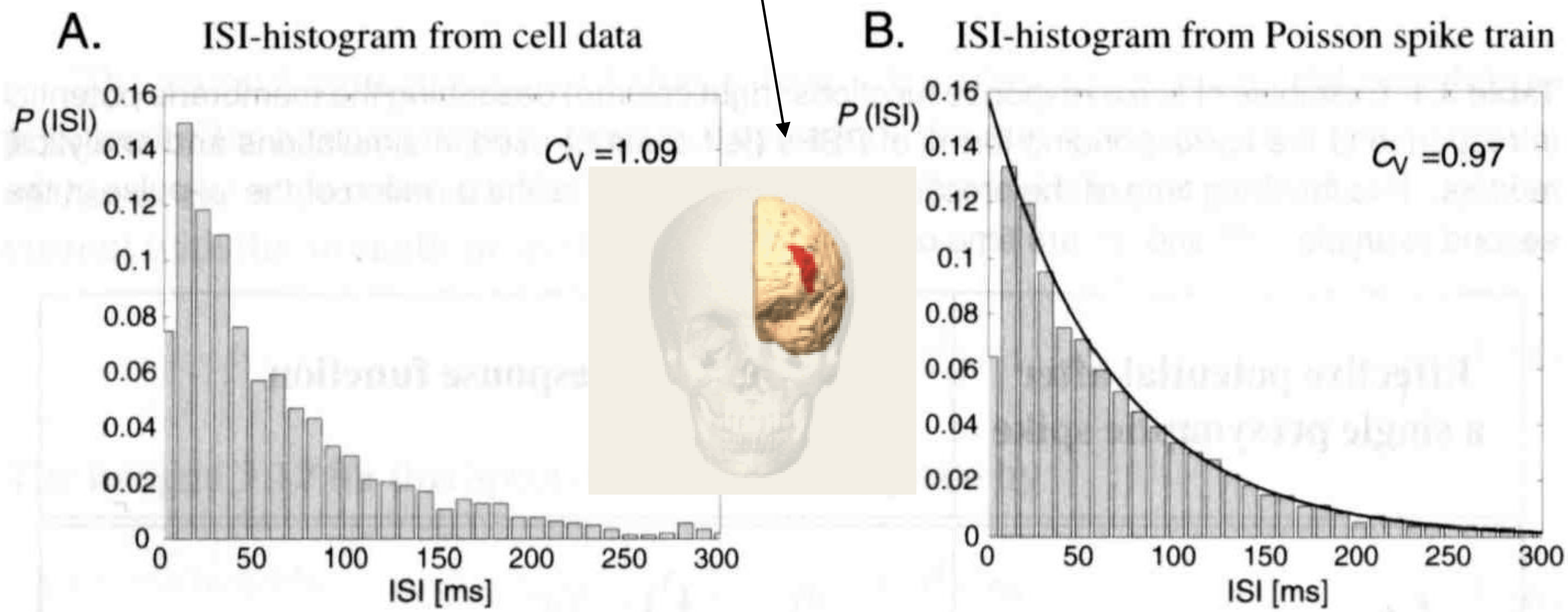


Fig. 3.4 Normalized histogram of interspike intervals (ISIs). (A) Data from recordings of one cortical cell (Brodmann's area 46) that fired without task-relevant characteristics with an average firing rate of about 15 spikes/s. The coefficient of variation of the spike trains is $C_V \approx 1.09$ [data courtesy of Stefan Everling]. (B) Simulated data from a Poisson distributed spike trains in which a Gaussian refractory time has been included. The solid line represents the probability density function of the exponential distribution when scaled to fit the normalized histogram of the spike train. Note that the discrepancy for small interspike intervals is due to the inclusion of a refractory time.

$$C_V = \frac{\sigma}{\bar{x}}$$

Stochastic Modeling

- If you had an **infinite amount of data**, you could use the **bin size as small as you would like** (continuous distribution).
- The normalized version of the **histogram** is what we call **probability distribution** of the random variable we are measuring (ISI), or the probability density function.
- This distribution **defines all statistical measures**, mean, variance and other high order moments.

Stochastic Modeling

- In nature all the typical probability distribution functions (PDFs) of the book are possible, and many others too.

- However**, many random processes observed in nature** can be approximated quite well by a **Gaussian curve**.

- The distribution is given by:

$$f^{\text{gaussiana}}(x;\mu,\sigma) = \frac{1}{\sigma\sqrt{2\pi}} e^{(x-\mu)^2/2\sigma^2}$$

Stochastic Modeling

- As an illustrative example, upon examining about 200 ISI histograms from various neurons in different animals, at least 10 different types of distribution have been distinguished:

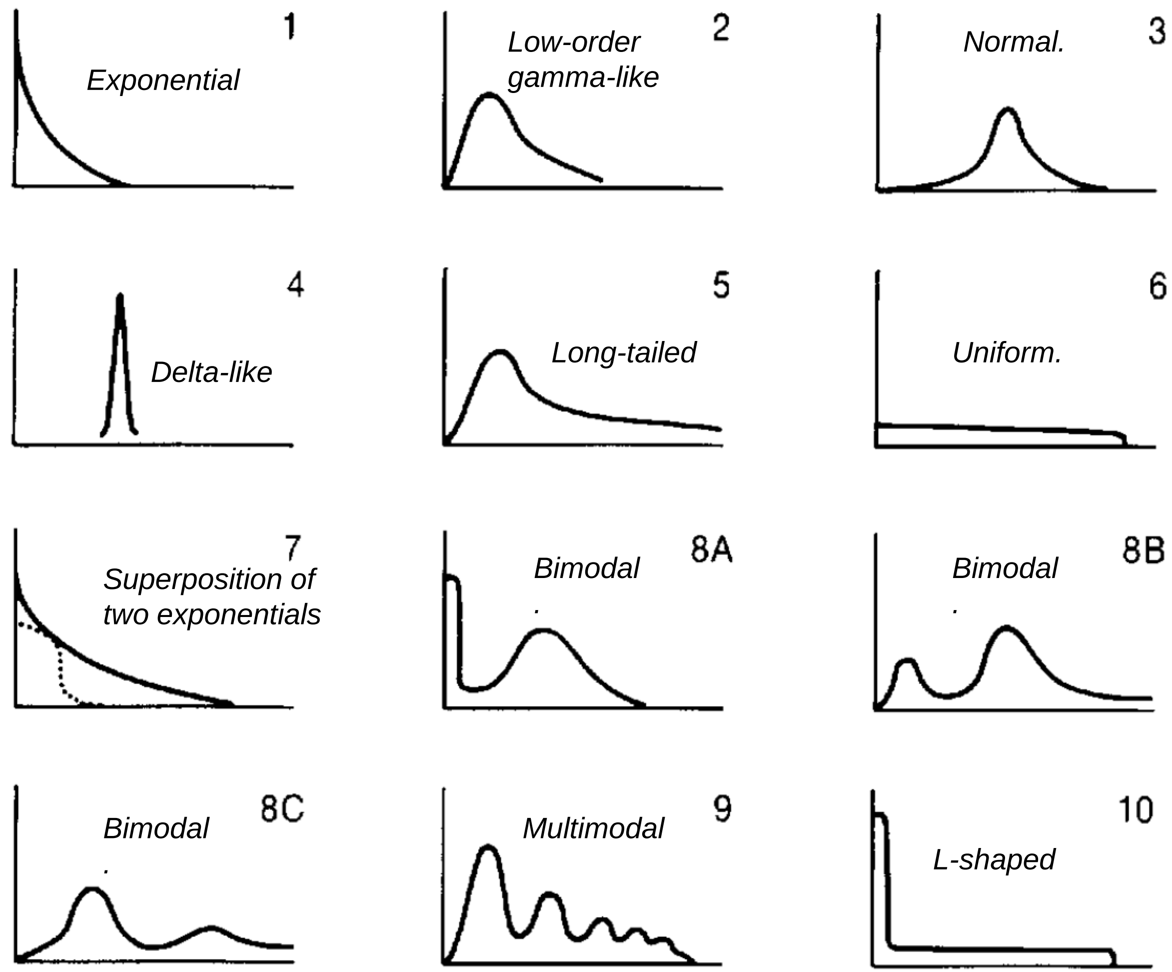


Figure adapted from the book:Stochastic processes in the neurosciences. Tuckwell, Henry C.,Philadelphia: Society for Industrial and Applied Mathematics, 1989.

Stochastic Modeling

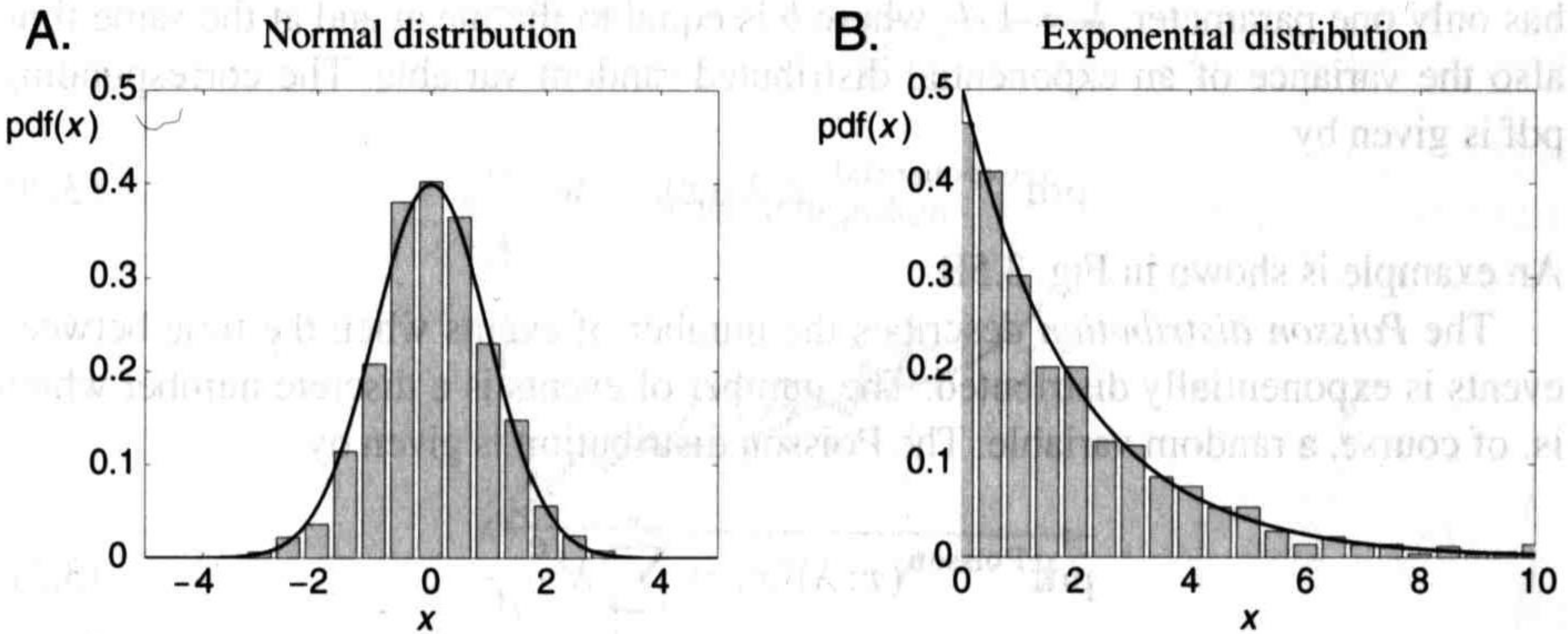


Fig. 3.5 A normalized histogram of 1000 random numbers and the functional form of the corresponding probability distribution functions (pdfs). (A) Random variables from a normal distribution (Gaussian distribution with mean $\mu = 0$ and variance $\sigma = 1$). The solid line represents the corresponding pdf (eqn 3.19). (B) Exponential distribution with mean $b = 2$ (eqn 3.20).

Stochastic Modeling

- **A Gaussian or normal distribution** with the mean equal to zero is called the standard normal distribution or white noise.

- The **importance of this probability is due to the central limit theorem**, which roughly says: a random variable that is obtained as the sum of infinite random variables, whose probability distribution for all of them is the same and also arbitrary, results in a distribution of Gaussian probability.

Stochastic Modeling

- The CLT, of course, is applied as an approximation, since obviously not all variables have to be governed by the same probability distribution.
- In practice, this white noise approach to explain irregular fluctuations around a known average value is often used frequently.
- However, one must keep in mind that the normal distribution is not the only distribution in nature.

Stochastic Modeling

- It is clear that the **distribution of intervals between spikes** that we have seen before, **cannot be approximated to a normal** distribution (see figure).
- In this case, we observe a rapid **exponential** decay, after a rapid raise, which coincides with the refractory period (see Appendix B).

Stochastic Modeling

- An **exponential distribution** has a single parameter λ, with $E[x]=1/\lambda$ y $V[x]=1/\lambda^2$ (see figure).

$$f^{\text{exponential}}(x;\lambda) = \lambda e^{-\lambda x}$$

Stochastic Modeling

- In general, the **Poisson distribution describes the number of events when the time between them is exponentially distributed**.

- This number of events is a discrete number that is represented by a random variable.

- The Poisson distribution is given by, with the parameter λ as the mean and variance:

$$f^{\text{Poisson}}(x;\lambda) = \lambda^x \frac{e^{-\lambda}}{x!}$$

Stochastic Modeling

- Thus, **we characterize the Poisson distribution as the number of events with time between events exponentially distributed.**

- The exponential distribution and the Poisson distribution are based on the same process (a Poisson process) and only measure **different things from this process: number of events or time intervals between events** (see appendix C).

Stochastic Modeling

- A **Poisson process** is frequently used to artificially generate **firing trains**, because of the distribution of the intervals between firings correctly approximates an exponential probability distribution.

- In contrast, **white noise** is frequently assumed for **processes internal to neurons**.

Stochastic Modeling

- How can we include noise in neural models?
- There are many possibilities. Let's assume, for simplicity, that we have an integration and fire model (we will see more in detail later).
- Similar procedures can be used with other models.
- The objective is to determine the stochastic firing times of the neurons.

Stochastic Modeling

- In general, there are **three ways** to include stochasticity in the model.
  - **Stochastic threshold**: replace the firing threshold of the neuron with a stochastic threshold.

$$\vartheta \rightarrow \vartheta + \eta^{(1)}(t)$$

Stochastic Modeling

– **Stochastic reset**: When we return to the resting potential, it can be stochastic.

$$\upsilon^{res} \rightarrow \upsilon^{res} + \eta^{(2)}(t)$$

Stochastic Modeling

– **Noisy integration**: The mechanisms of integration in the neuron can be noisy, describing them using a stochastic differential equation:

$$\tau_m \frac{du}{dt} = -u + RI_{ext} + \eta^{(3)}(t)$$

Stochastic Modeling

- With the appropriate choices of the **random variables $\eta^{(1)}$, $\eta^{(2)}$ and $\eta^{(3)}$ equivalent results** can be produced for the stochastic processes of a neuron.

- Although the same probability distribution for each model, it can produce different results for each of the proposed noisy models.

- In practice, we will choose the appropriate distributions to capture the same behavior of the experimental data

Stochastic Modeling

- For **analytical treatments it is better to use the random threshold model**.

- Although there is **less evidence** that actual neural thresholds change over time, this model is equivalent to other noisy models, and therefore it is correct to model in this way.

- **Numerical studies use noisy inputs to model stochastic processes in the brain**.

Stochastic Modeling

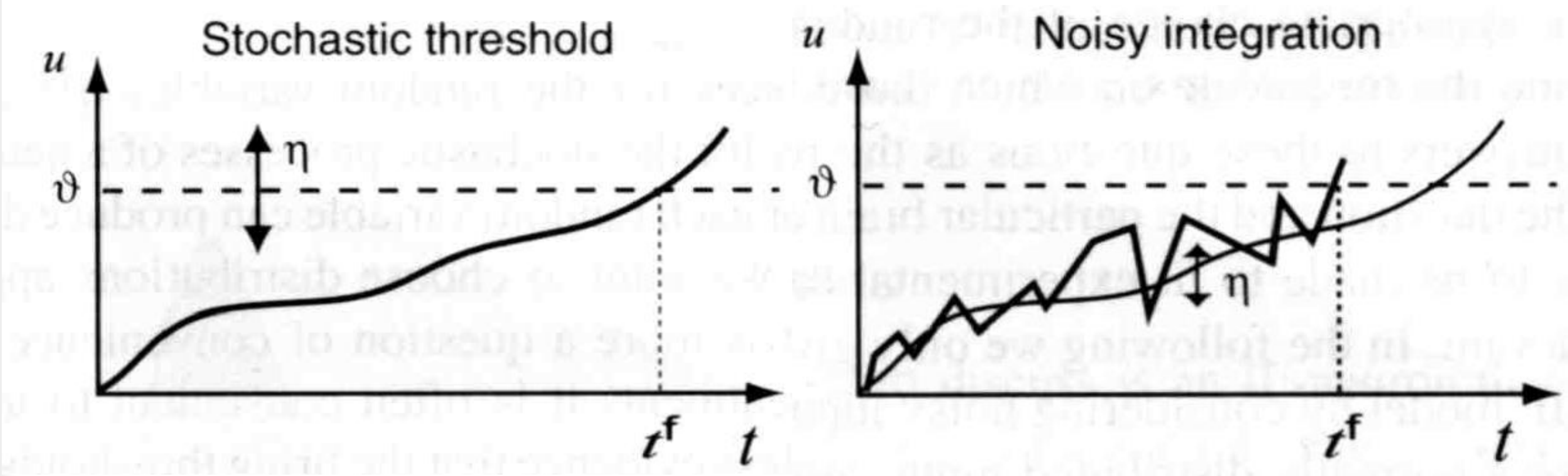
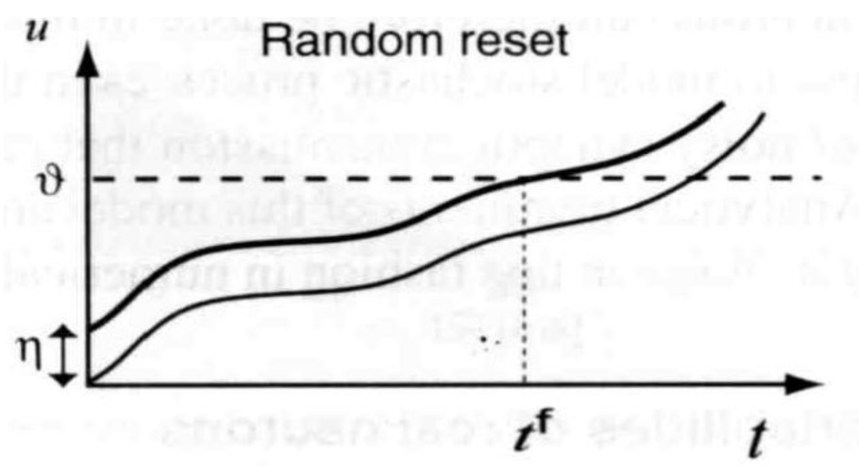


Fig. 3.6 Three different noise models of integrate-and-fire neurons. (A) Stochastic threshold, (B) random reset, and (C) noisy integration [adapted from W. Gerstner, in *Pulsed neural networks*, Maass and Bishop (eds), MIT Press, 1998].



Stochastic Modeling: Example 1

Neural Inferior Olive

- We will now present a **stochastic mod**el where neurons show **subthreshold oscillations** and **spike activity**.
- We will build a network with **electrical coupling** between the first neighbors.
- We are inspired by the architecture and characteristics observed in the **inferior mammal olive**.
- We will show the wide variety of coherent **spatio-temporal patterns of neural activity**.

Stochastic Modeling: Example 1

Neural Inferior Olive: Introduction

- There are **several animal neural systems** that exhibit **subthreshold oscillations** in combination with spike activity.
- An example is the **shark's Lorenzini ampullae**, where subthreshold oscillations determine the basic rate of impulse generation.
  - Braun H.A., Wissing H., Schäfer k. and Hirsch, M.C. 1994. Oscillation and noise determine signal transduction in shark multimodal sensory cells. Nature 367, 270–273.
- Another example is the **mammalian inferior olive**, which is made up of electrically coupled networks.
- The inferior olive (IO) generates subthreshold oscillations and spike activity.

Stochastic Modeling: Example 1

Neural Inferior Olive: Introduction

- Many other examples of **subthreshold oscillations:**
  - Temporal Neuronal Oscillations can Produce Spatial Phase Codes. Christopher Burgess, et. al, in Space, Time and Number in the Brain, 2011.
  - Olivocerebellar System. R.R. Llinas and K.D. Walton in Encyclopedia of Neuroscience 2009, Pages 217-224.
  - 4.37 - Physiology of the Main Olfactory Bulb. M. Ennis, in The Senses: A Comprehensive Reference Volume 4, 2008, Pages 641-686.
  - V-GHAFFARI B; KOUHNAVARD M; KITAJIMA T (2016). "Biophysical Properties of Subthreshold Resonance Oscillations and Subthreshold Membrane Oscillations in Neurons". Journal of Biological Systems. 24 (4): 561–575. doi:10.1142/S0218339016500285.
  - Lampl, Ilan (November 1993). "Subthreshold Oscillations of the Membrane Potential: A Functional Synchronizing and Timing Device" (PDF). Journal of Neurophysiology. 70 (5): 2181–6. doi:10.1152/jn.1993.70.5.2181.

Stochastic Modeling: Example 1

Neural Inferior Olive: Introduction

- In vivo records using thin IO slices have shown the presence of characteristic **spatio-temporal activity patterns**.
  - Leznik E., Makarenko V. and Llinas R. 2002. Electrotonically Mediated Oscillatory Patterns in Neuronal Ensembles: An In Vitro Voltage-Dependent Dye-Imaging Study in the Inferior Olive. Journal of Neurocience 22(7):2804–2815.
- Another example of spatio-temporal activity: spatio-temporal patterns of neuronal activity in the brain of a resting mouse (https://youtu.be/g2t-DK4HHc0).
- The cerebellum and olive have been studied with great intensity, but **their role in the brain remains uncertain**.
- There are several IO **hypotheses that are related to motor rhythm coordination control and learning**.
- Computer models, through the computer, can give us great information about this function and the role of the IO that is not yet clear.

Stochastic Modeling: Example 1

Neural Inferior Olive: Introduction

- Thus, **a stochastic model is proposed for the study of electrically coupled systems with subthreshold dynamics** in combination with spike activity.
- The **stochastic model can qualitatively reproduce these phenomena** and considerably reduce the computing time required to implement large networks with more realistic approaches.
- **Individual neuron activity is implemented by a random walker** with absorbent barriers.
- We will verify that these networks of stochastic neurons with subthreshold oscillations can show coherent spatial-temporal patterns, which are similar to those obtained with models of detailed dynamics of conductances.

Stochastic Modeling: Example 1

Neural Inferior Olive: Introduction

- The **spontaneous evolution** of the neuronal activity of an isolated neuron follows a random path.
- **Neural activity is considered discrete** and is characterized by the variable a(t).
- The stochastic dynamics of the isolated unit i is governed by

$$a_i(t+1) = \begin{cases} a_i(t) + C & \text{with probability } p \\ a_i(t) & \text{otherwise,} \end{cases}$$

where p is the probability of transit of the internal state per unit of time.

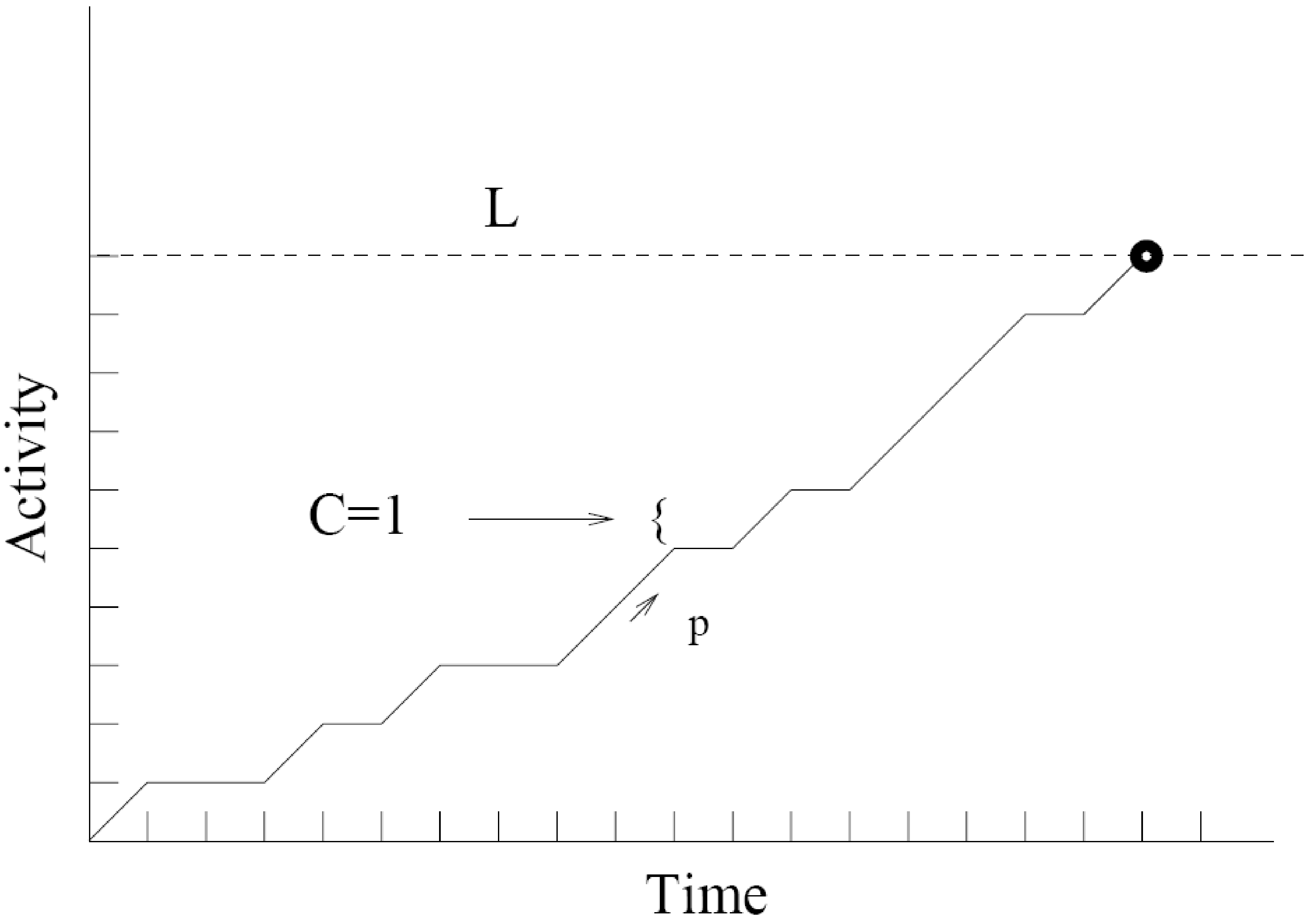
Stochastic Modeling: Example 1

Neural Inferior Olive: Isolated Neuron

- Thus, 1-p is the probability of remaining in the current state.
- **C is a parameter** that depends on the temporal evolution of the activity of the unit.
- This parameter can take **three different values** in our model.
- The neuron begins to increase its activity from an initial state of resting potential, with probability p, using C=1.

Stochastic Modeling: Example 1

Neural Inferior Olive: Isolated Neuron



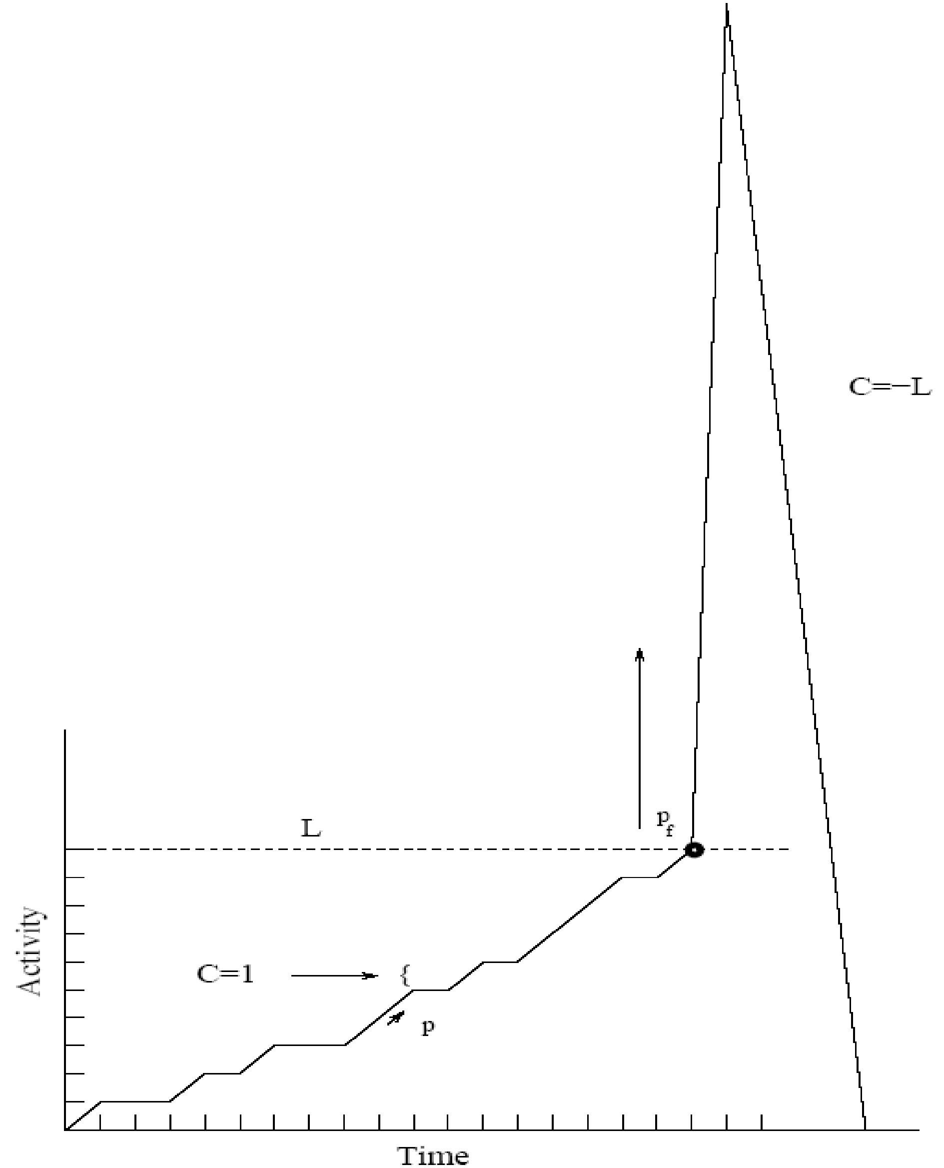
Stochastic Modeling: Example 1

Neural Inferior Olive: Isolated Neuron

- When the neuron reaches the activation **threshold L, a firing occurs according to a firing probability p_f.**
- **Activity is increased by 3L** to generate the trigger event (It is a parameter that can change).
- **Then, the activity begins to decrease** to the initial state following the previous equation, but with **C=-L**, until it reaches the lowest activity.

Stochastic Modeling: Example 1

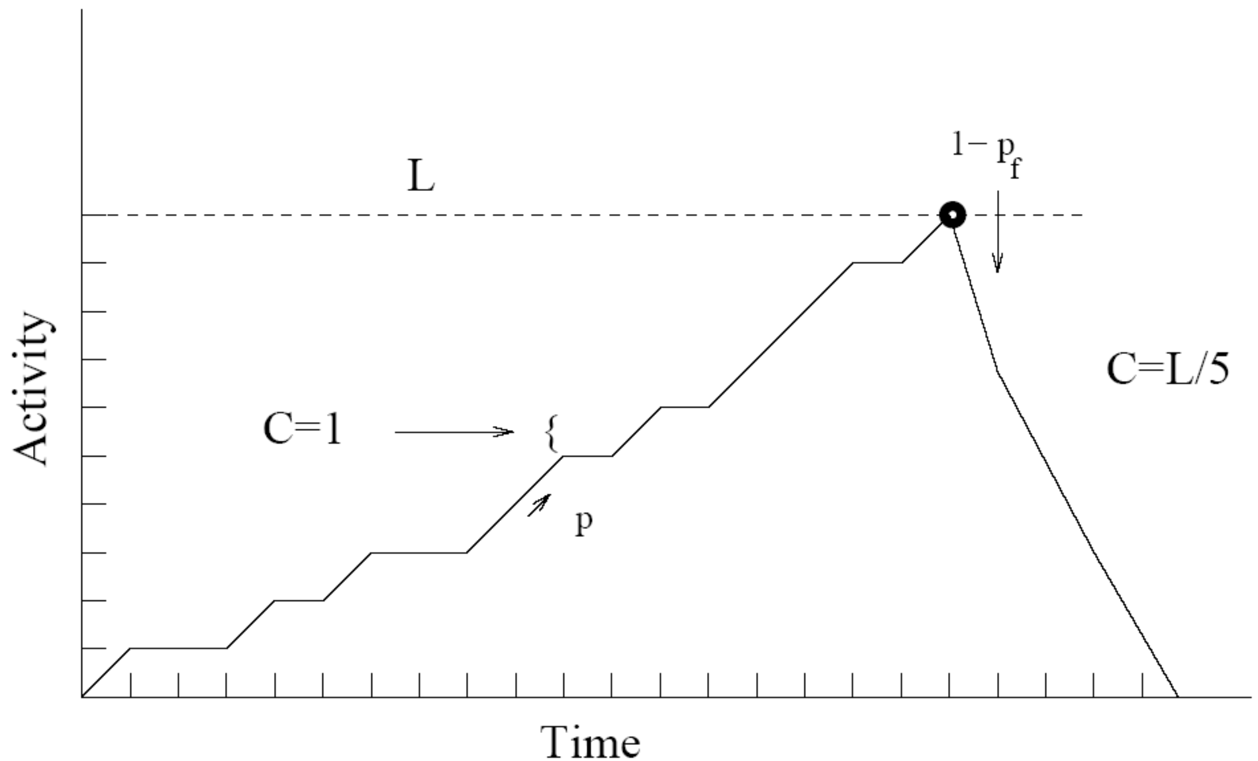
Neural Inferior Olive: Isolated Neuron



Stochastic Modeling: Example 1

Neural Inferior Olive: Isolated Neuron

- When the neuron reaches the activation threshold L, and **does not fire with probability 1-p_f**, its activity begins to decrease again, but now with **C=-L/5** (It is a parameter that can change).



Stochastic Modeling: Example 1

Neural Inferior Olive: Isolated Neuron

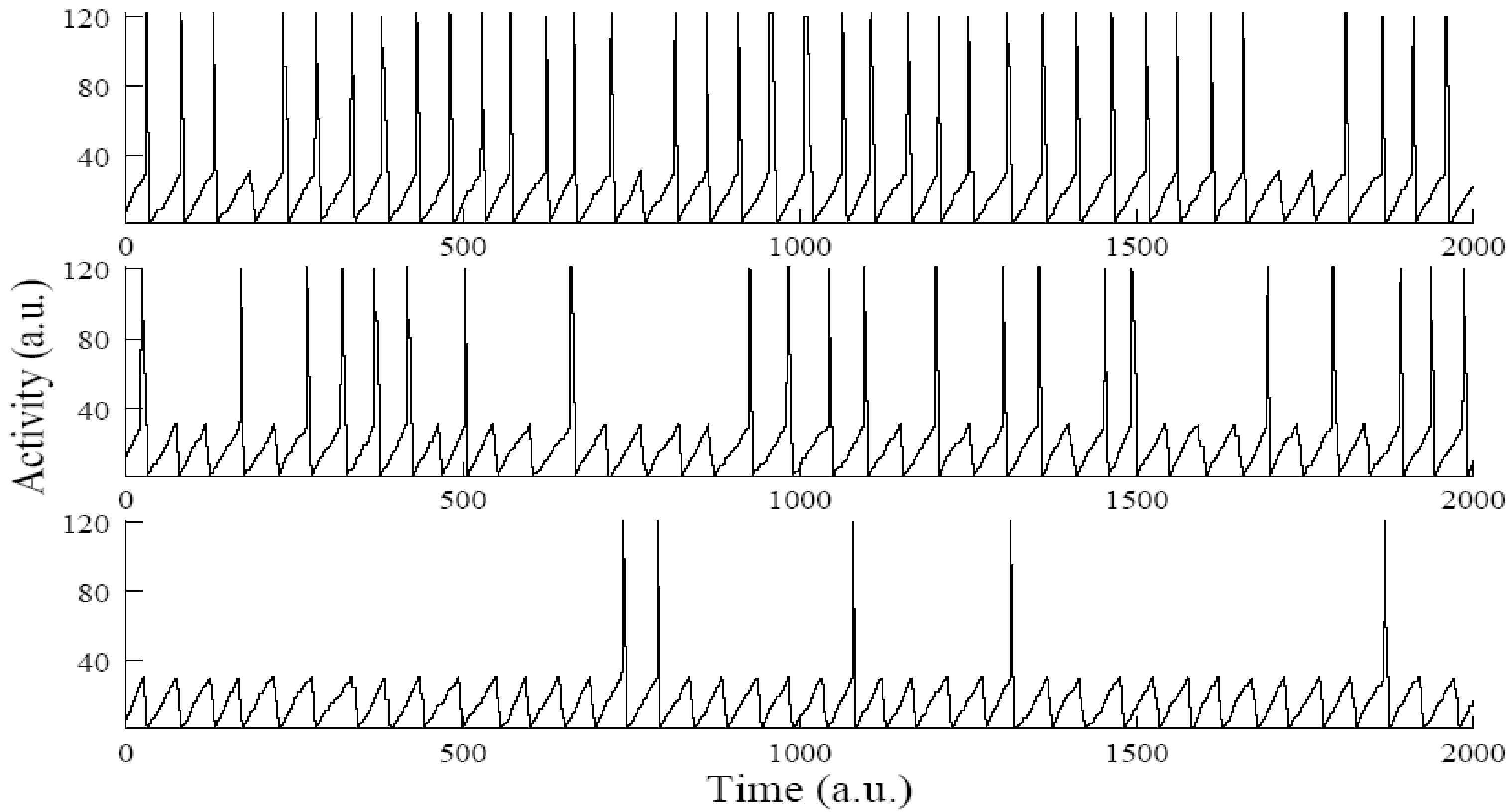


Figure 1: Activity of an isolated neuron for three different values of p_f. From top to bottom: $p_f = 0.9, 0.5, 0.1$ (p=0.7 and L=30 in all simulations).

Stochastic Modeling: Example 1

Neural Inferior Olive: Interaction between Neurons

- To build networks we use **diffusive coupling** between neighboring neurons. Thus, we build two-dimensional networks with periodic boundary conditions to avoid edge effects.

- Neurons connect by emulating electrical coupling, and the rule of exchange between unit i and its neighbors j is defined by

$$a_i(t) = a_i(t) + g \sum_{j=neighbors} [a_j(t-1) - a_i(t-1)],$$

Stochastic Modeling: Example 1

Neural Inferior Olive: Interaction between Neurons

- Parameter **g is the electrical coupling** or conductance.
- We have assumed that the parameter **g is the same for each connection** (homogeneous network).
- It should be noted that in this stochastic model we not only care about the precise moment of the fire, but also the generation of the subthreshold wave.
- So the model includes a more detailed form of neural activity and we are not left with just the firing neural times.

Stochastic Modeling: Example 1

Neural Inferior Olive: Interaction between Neurons

- The evolution of the activity of each neuron in the network is given by two contributions:
  - The spontaneous random path

$$a_i(t+1) = \begin{cases} a_i(t) + C & \text{with probability } p \\ a_i(t) & \text{otherwise,} \end{cases}$$

  - And the interaction between neighboring neurons

$$a_i(t) = a_i(t) + g \sum_{j=neighbors} [a_j(t-1) - a_i(t-1)]$$

Stochastic Modeling: Example 1

Neural Inferior Olive: Results

- We have studied the generation of coherent spatial-temporal patterns in two-dimensional networks of 50x50 identical stochastic neurons.
- In all the networks described here, each neuron was connected to its 4 closest neighbors by means of electrical connectivity.
- The formation of these patterns depends on g.
- We first study the model in extreme cases: g=0.001 (uncoupled oscillators) and g = 0.17 (synchronized oscillators).

Stochastic Modeling: Example 1

Neural Inferior Olive: Results

- **Spatial-temporal patterns emerge** for moderate values of electrical conductance, g.
- **When neurons fire they increase the firing probability of their neighbors.**
- **Nearby neighbors tend to fire with a small phase shift**. This generates a wavefront propagating through the network creating the pattern.
- It should be noted that t**he width of the spike depends on the coupling value**.
- Remember that **when C=-L and g is high**, the **activity** of the **neighbors** accelerate the **descent**, and therefore there is a narrowing of the spike.

Stochastic Modeling: Example 1

Neural Inferior Olive: Results

- Because we are interested in studying the ability of these networks to **encode different rhythms**, **we then introduce stimuli into two separate clusters of the 2D network**.
- Each cluster is made up of **6x6 neighboring neurons**.
- **All network** neurons, except stimulus clusters, have $\mathbf{p_f=0.4}$.
- When the stimulus has a high probability of firing, $\mathbf{p_f=0.8}$, the propagated wave always emerges from the **stimulus clusters**.

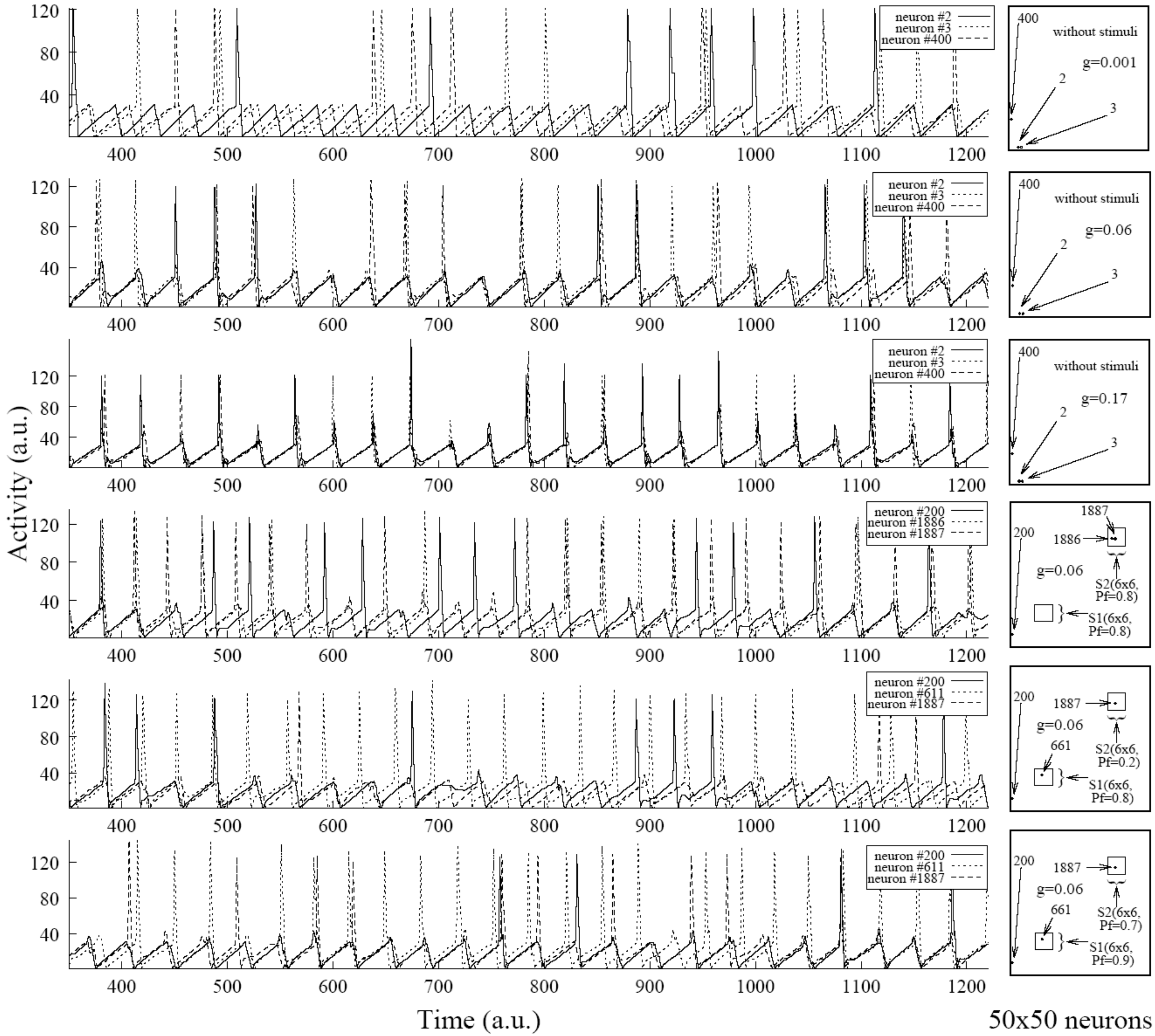
Stochastic Modeling: Example 1

Neural Inferior Olive: Results

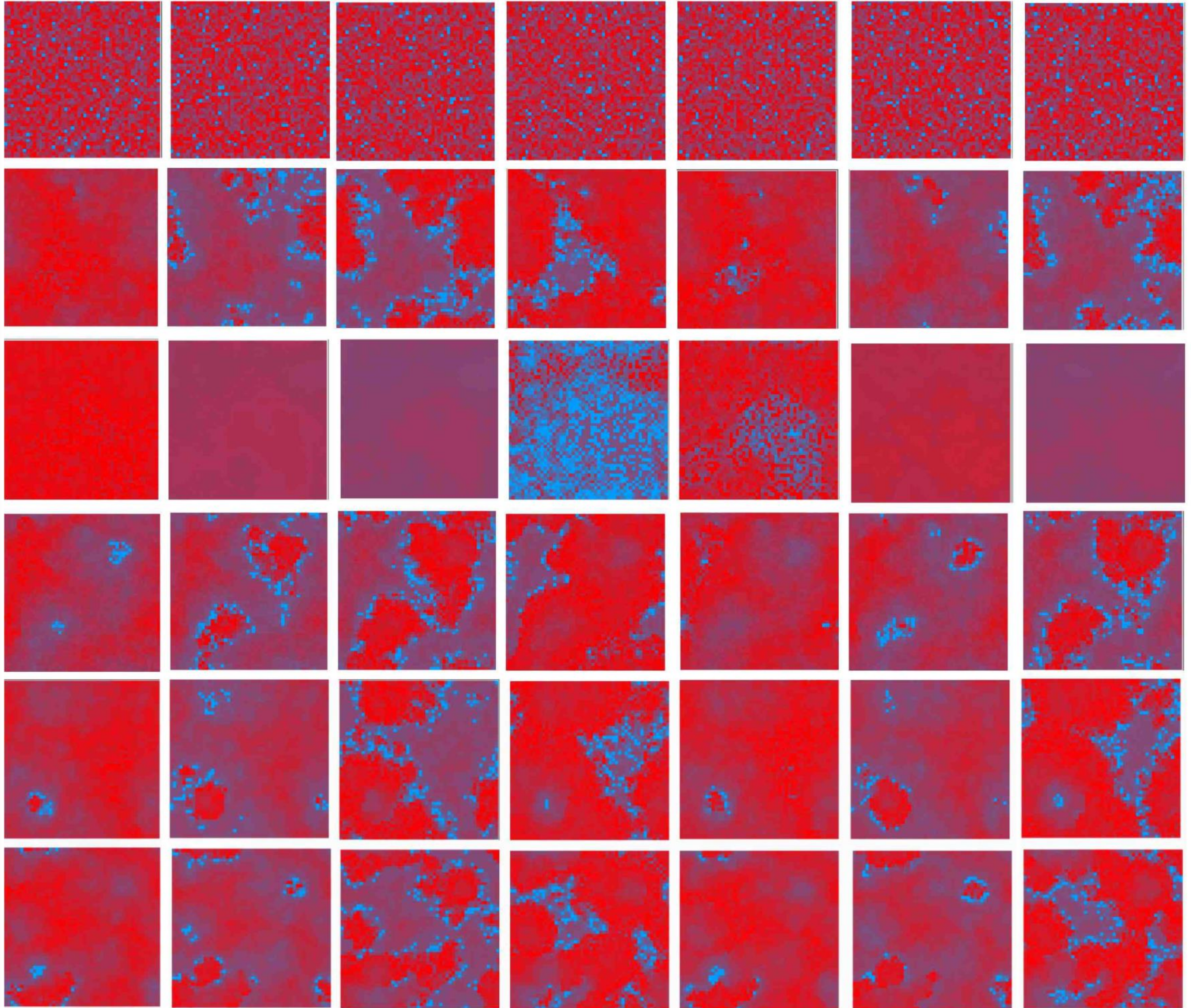
- When the stimulus has a low probability of triggering in **one cluster, p_f = 0.2**, and high in **another, p_f = 0.8**, the low frequency of a cluster acts as a sink for the propagated activity (it was discovered in the stochastic model and extended to the model more detailed based on conductance channels).

- Finally, when both stimulus clusters have a high but different firing probability (**p_f = 0.7, p_f = 0.9**), **the propagated wave emerges from the clusters at different time phases.**

- There is **coexistence of regions in the temporal-spatial pattern** with different regions in the network.



Activity (a.u.)
Time (a.u.)
50x50 neurons
neuron #2
neuron #3
neuron #400
without stimuli
g=0.001
g=0.06
g=0.17
neuron #200
neuron #1886
neuron #1887
neuron #611
S2(6x6, Pf=0.8)
S1(6x6, Pf=0.8)
S2(6x6, Pf=0.2)
S2(6x6, Pf=0.7)
S1(6x6, Pf=0.9)



Stochastic Modeling: Example 1

Neural Inferior Olive: Results

Sin estímulos y con g pequeña.

2 estímulos de alta frecuencia.

Sumidero (un estímulo de alta frecuencia y otro de baja).

Stochastic Modelling: Example 2 Introduction

- All these models are paradigms to try to simulate the stochastic activity of a single neuron.
- The model to be presented below is somewhat similar to the lossless random walker model, but in this case the distribution that controls the evolution of the neuron's membrane potential is determined by the negative binomial distribution and not by the distribution of Poisson that we will see in the following example.

Stochastic Modelling: Example 2 Introduction

- We are going to use this stochastic model to study the synchronization paradigm for neural coding.
- The brain is a complex machine capable of processing a multitude of information in a very precise way.
- Neurons are the fundamental units. How are information processes carried out in the brain?
- How is the information that comes from the outside represented internally in the brain?

Stochastic Modelling: Example 2
Introduction

- Action potentials generated by neurons are used to encode information.
- How is all this neural firing code organized to carry out this information processing?

Stochastic Modelling: Example 2 Introduction

- What main paradigms exist for neural coding?
  - Rate coding: frequency coding, more classic.
  - Timing coding: opens up a wide range of possibilities for the internal representation of information.
- Synchronization is one of the most interesting forms of timing coding.

Stochastic Modelling: Example 2 Introduction

- Other information coding mechanisms are not ruled out, but these two aspects are the most studied.
- There are experiments that show both types of coding.

Stochastic Modelling: Example 2
Introduction

- As we have already introduced, due to the intrinsic nature of biological systems, noise is a factor present in all of them.
- There is a large body of evidence supporting stochastic phenomena in neurobiology.
- Intuitively, this stochastic character would cloud and disturb the timing coding paradigm.
- But experimentally this coding paradigm has been corroborated.

Stochastic Modelling: Example 2 Introduction

- This motivates trying to know why and what is the basis for natural systems to maintain their functionality under significant amounts of noise.
- The stochastic nature of biological systems cannot be forgotten in the possible neuronal models that are designed.

Stochastic Modelling: Example 2

Hypothesis for the Stochastic Neural Model

- As we already know, there are different ways to model neural dynamic systems, depending on the level of detail with which we want to simulate the process.
  - Advantages and disadvantages?
- We want a model whose fundamental ingredients are the spikes, and which incorporates the stochastic character inherent in nature.
- We understand the nervous system as a population of units that send and receive messages.

Stochastic Modelling: Example 2

Hypothesis for the Stochastic Neural Model

- Neurons are the basic units for understanding information processing in the brain.
- Action potentials are responsible for carrying that information.
- The dendrites receive signals from the surroundings through synaptic connections.
- Neuronal morphology integrates action potentials.

Stochastic Modelling: Example 2

Hypothesis for the Stochastic Neural Model

- For adequate membrane potentials, if a certain threshold is exceeded, a new action potential is generated.
- In general, an isolated neuron will also fire from time to time (spontaneous activity).
- With all these hypotheses, we are ready to formulate our model of integration and stochastic firing.

Stochastic Modelling: Example 2

Isolated neuron

- The activity of unit i at time t is represented by the state $a_i(t)$, and its dynamics is given by:

$$a(t+1) = \begin{cases} a_i(t)+1 & \text{with } p \\ a_i(t) & \text{with } 1-p \end{cases}$$

$$\text{for } a_i(t) \in \{1,\ldots,L_i - 1\}.$$

- Spike: transition from state $a_i(t) \geq L_i$ to state 1 with probability 1.

Stochastic Modelling: Example 2

Isolated neuron

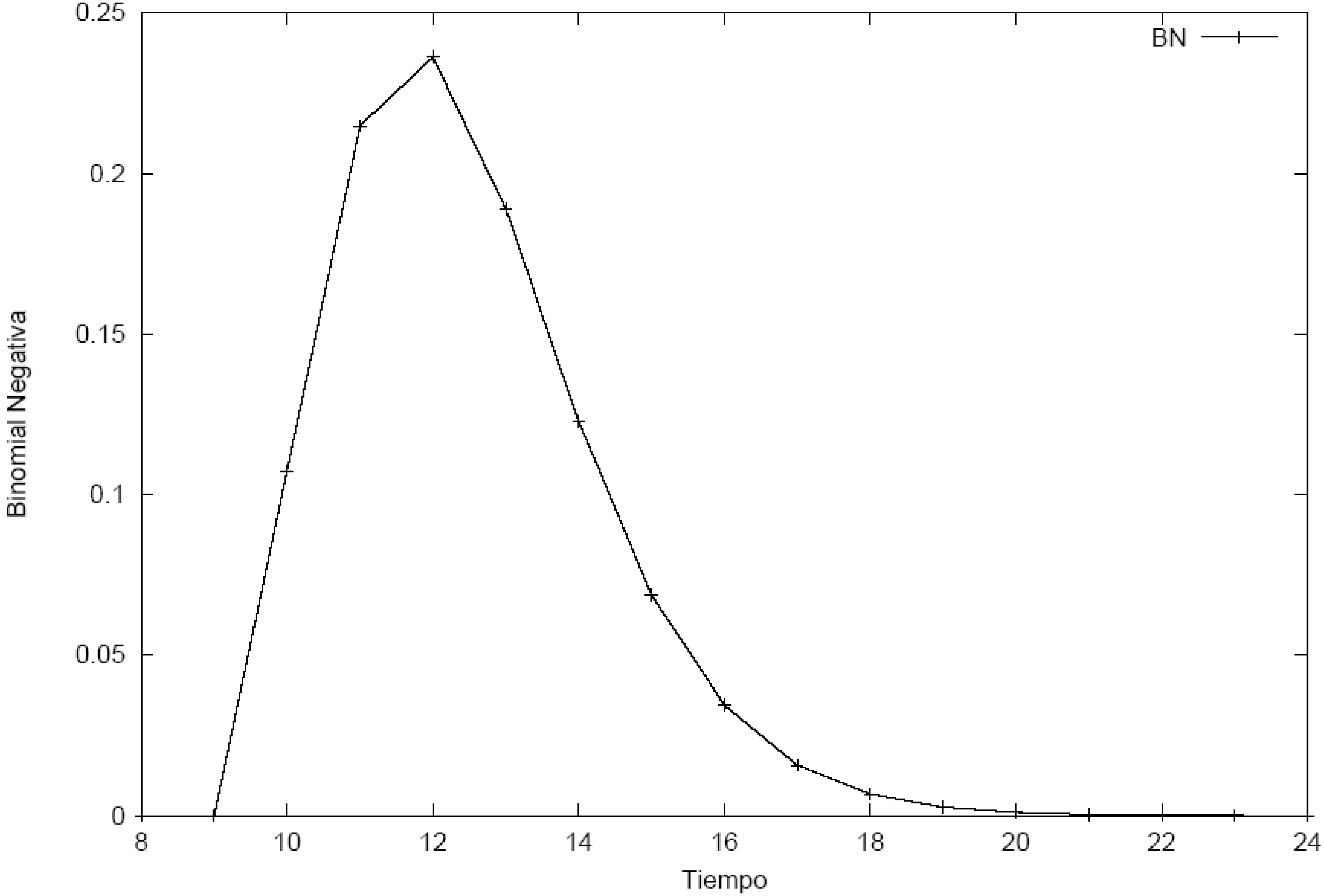
- The time that elapses between two consecutive shots (T_i) for unit i with probability p of advancing, and 1-p of staying, has a probability distribution:

$$P_{L_i,p_i}(T_i) = \binom{T_i - 1}{T_i - L_i} p_i^{L_i} (1 - p_i)^{T_i - L_i}$$

Para L=10 y p=0.9 tenemos la siguiente distribución binomial negativa.

Stochastic Modelling: Example 2

Isolated neuron



Stochastic Modelling: Example 2

Isolated neuron

- The average firing period τ and its standard deviation σ y are derived from the negative binomial probability distribution:

$$\tau_i = 1 + \frac{L_i - 1}{p}, \quad \sigma_i = \frac{\sqrt{(L_i - 1)(1 - p)}}{p}$$

Stochastic Modelling: Example 2

Interaction between Neurons

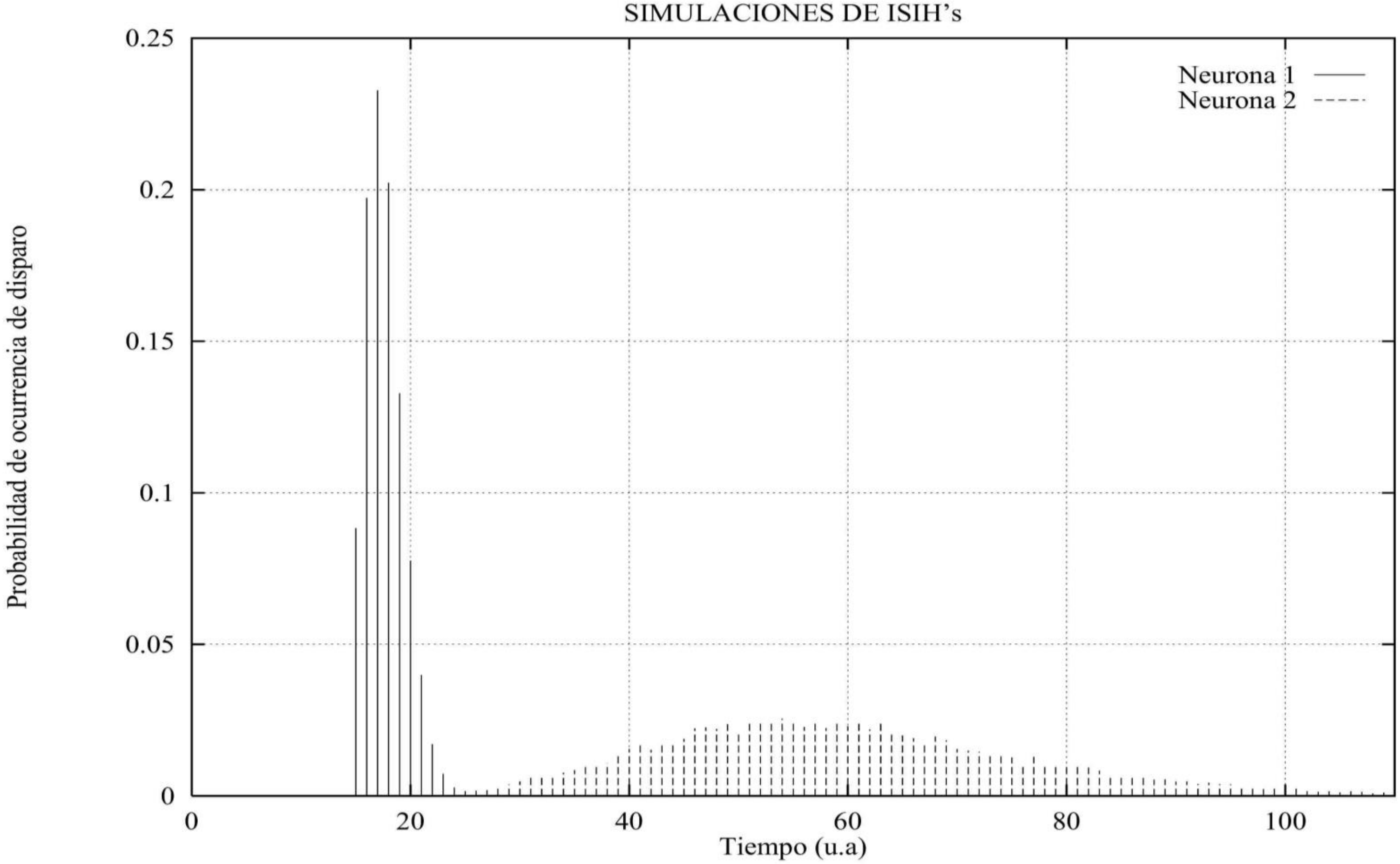
- Unit j at time t will be affected by the fire of unit i at time t_i^d by:

$$a_j(t) = a_j(t) + \delta((t - t^r) - t_i^d)\varepsilon_{ij}$$

- According to this rule, an isolated unit behaves like an integrate and shoot stochastic oscillator:
  - Instantaneous or delayed interaction, $t^r=0$ o $t^r=1$.
  - Discrete.
  - Stochasticity depending on p.
  - Absorption.

Stochastic Modelling: Example 2

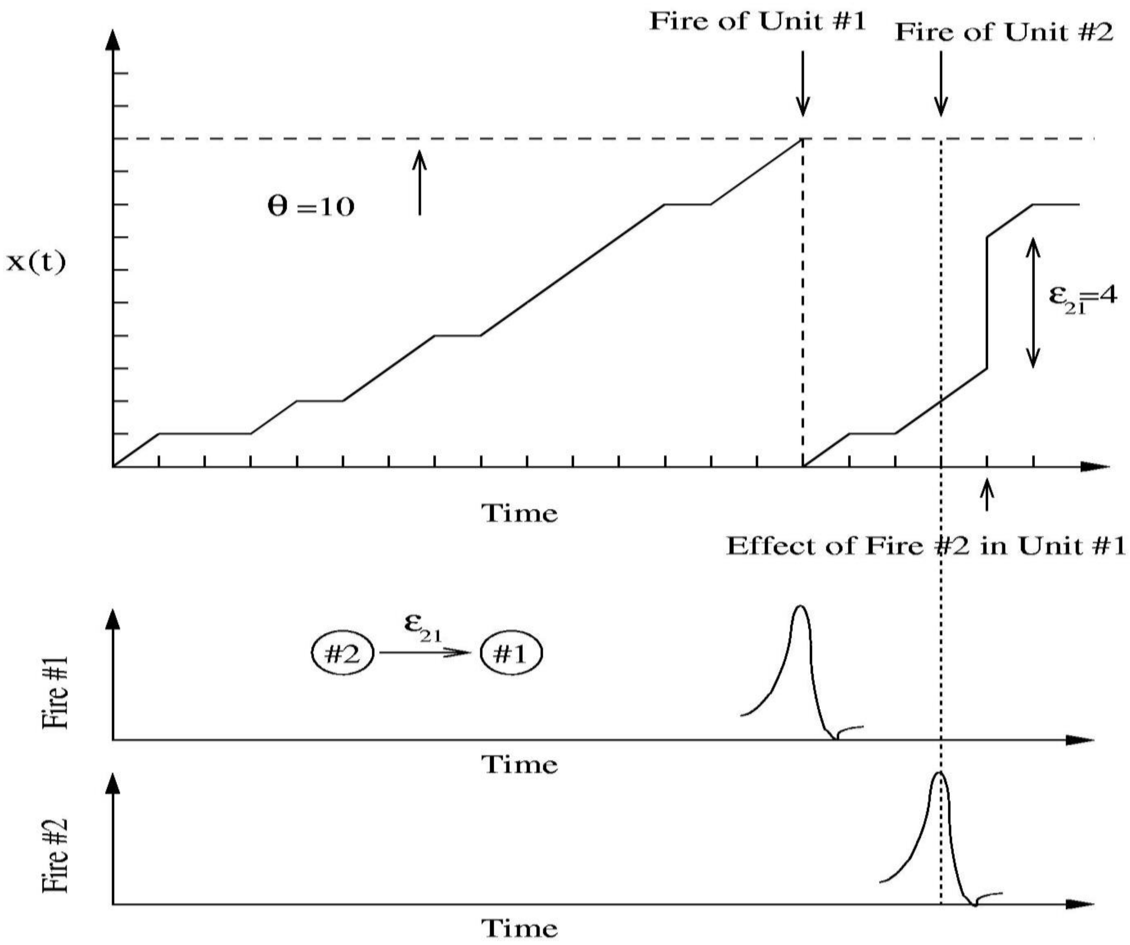
Example of two isolated neurons



Simulation of two isolated neurons with parameters: L_1=15, p_1 = 0.85, L_2=10, p_2 =0.17. Neuron 1 fires quickly and regularly, while neuron 2 is slow and noisy.

Stochastic Modelling: Example 2

Example of two neurons interacting



Example of how the fire is instantly transmitted ($t^r=0$) from one unit to another. We have assumed that there is only one connection from unit 2 to unit 1.

Stochastic Modelling: Example 2

Two Neurons, Some Questions

- The simplest problem is two units interacting.
- What happens if the two units are the same?
- And if they are different?
- How will the synchronization depend on the parameters?
- What role does the intrinsic noise that the units have incorporated play?
- Will the behavior of the system depend on the initial state in which the neurons start?

Stochastic Modelling: Example 2

Relevant Magnitudes

- τ_0 : Represents the average time of the first synchronization, when starting in a random state. It gives a measure of the elapsed time for the synchronization of a group of neurons.

- σ_0 : Represents the standard deviation of τ_0. This value will indicate the dependency of the initial state of the system.

Stochastic Modelling: Example 2

Relevant Magnitudes

- τ : This magnitude represents the time elapsed between synchronous shots, starting from the first synchronization.

- σ : Similarly, this quantity represents the standard deviation of the synchronization period τ . Again, this magnitude gives an estimate of the stability of the synchronization between units, after reaching the first synchronization.

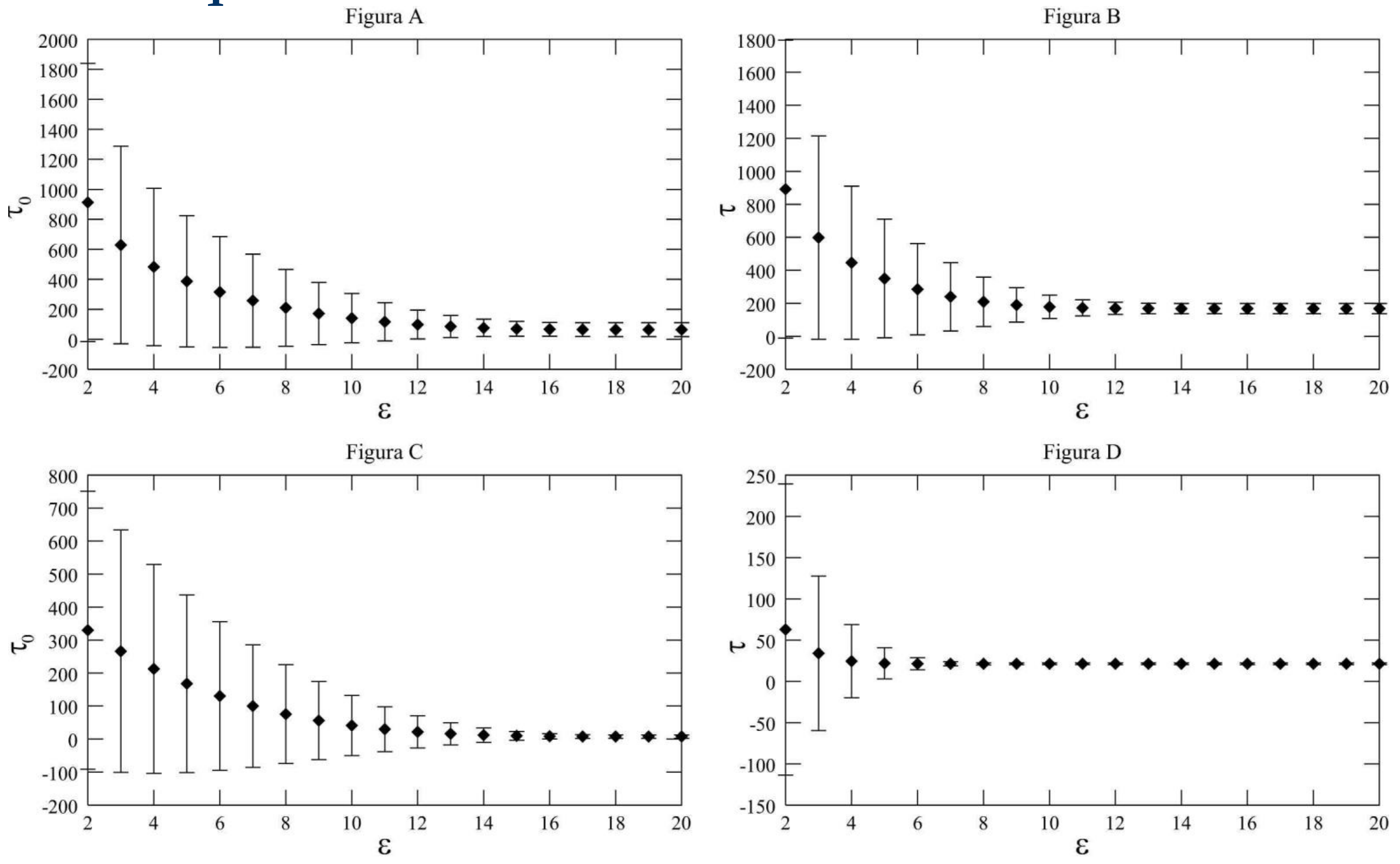
Stochastic Modelling: Example 2

Relevant Magnitudes

- The mathematical formalism of Markov chains allows us the numerical calculations of the synchronization parameters, τ and σ.
- In the Markov formalism, the starting point is the matrix of all transition probabilities between the possible accessible states of the system.
- τ and σ can be calculated by algebraic operations of the transition probability matrix of the system.
- Obviously it can also be done by simulations with different initialization seeds.

Stochastic Modelling: Example 2

Two Equal Neurons



Simulation using Markov chains for two stochastic neurons with identical parameters. A and B: $p=p_1=p_2=0.1$, $L=L_1=L_2=20$, $\varepsilon_{12}=\varepsilon_{21}=0 - 20$. C and D: $p=p_1=p_2=0.9$, $L=L_1=L_2=20$, $\varepsilon_{12}=\varepsilon_{21}=0 - 20$.

Stochastic Modelling: Example 2

Two Equal Neurons

- The synchronization error increases as the stochasticity parameter decreases.
- No abrupt change is observed.
- The most interesting case is the decay of synchronization dispersion as a function of increased synaptic efficiency.

Stochastic Modelling: Example 2

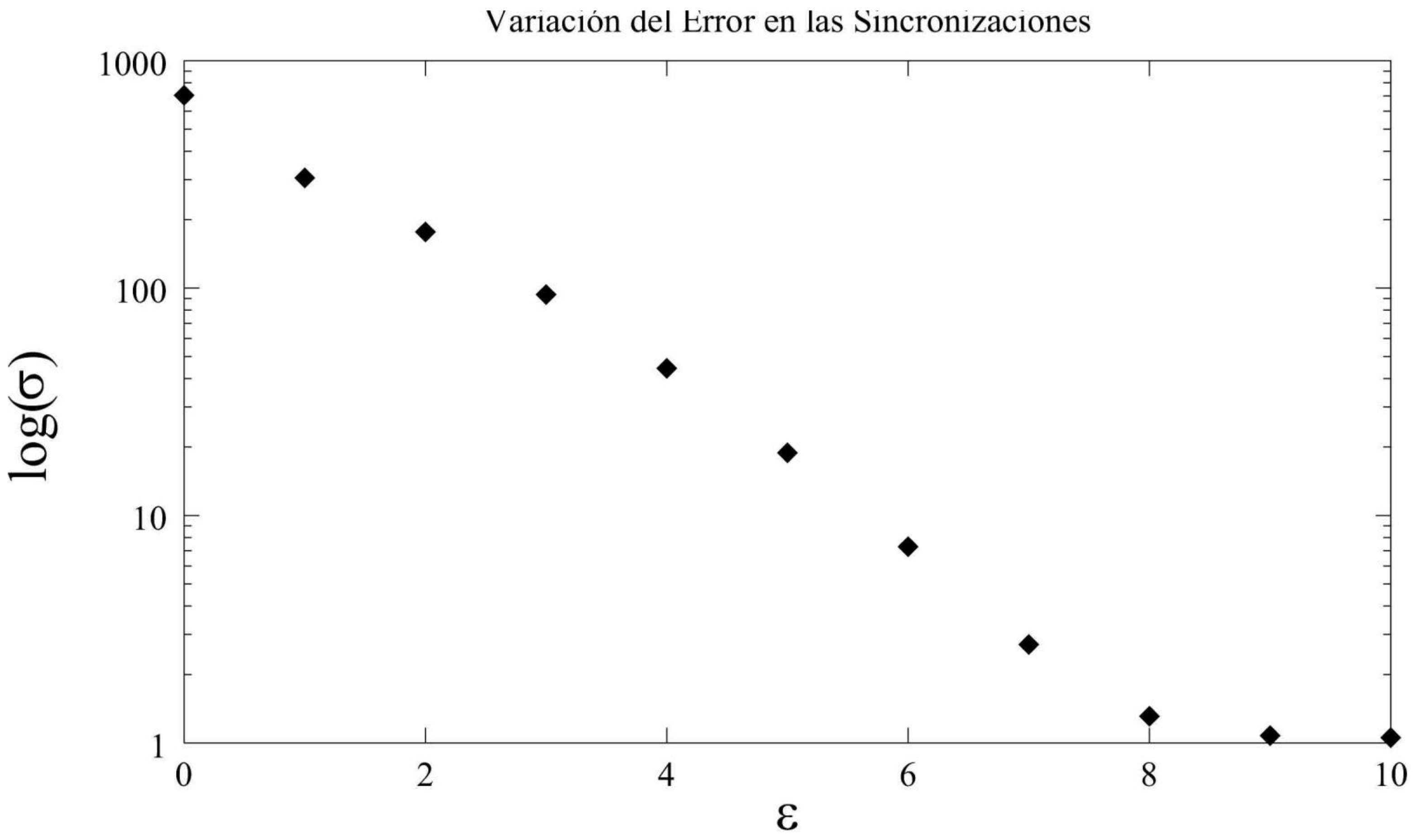
Two Equal Neurons

- This result is interesting since the synchronous firing of two neurons, for appropriate values of synaptic connection ($\varepsilon_{12} = \varepsilon_{21} = 10$), can be a more periodic system and with more regular behavior than the neurons alone.
- The separate dispersion for the units is $\sigma_1 = \sigma_2 = 1.531$.
- The dispersion $\sigma = 1.054$ is consistent with p=0.9 and L=10.

ϵ_{12}	ϵ_{21}	τ_0	σ_0	τ	σ
0	0	752.536442	790.547251	488.901235	704.430929
1	1	416.609727	489.749031	138.390308	305.307134
2	2	329.937590	421.190096	62.797588	176.515790
3	3	266.275277	367.259298	33.939418	93.691831
4	4	212.771627	316.615689	24.430170	44.373690
5	5	167.878150	269.186050	21.918961	18.875202
6	6	130.651136	225.394287	21.384574	7.292721
7	7	100.201845	185.549672	21.292163	2.708359
8	8	75.687294	149.845742	21.279103	1.309936
9	9	56.311993	118.373895	21.277590	1.075668
10	10	41.329435	91.135036	21.277447	$\boxed{1.054543}$

Stochastic Modelling: Example 2

Two Equal Neurons



Variation of σ against the synaptic weight of example C and D of the previous Figure. The abscissa axis is on a logarithmic scale.

Stochastic Modelling: Example 2

Two Different Neurons

- We consider the case of a neuron with a regular rhythm and rapid firing (Unit 1), and another with a slow firing and irregular rhythm (Unit 2).
- We measure the synchronization of the system based on the variation of the synaptic weight and the thresholds.
- **Regions of specificity** are formed where synchronization is relatively stable.

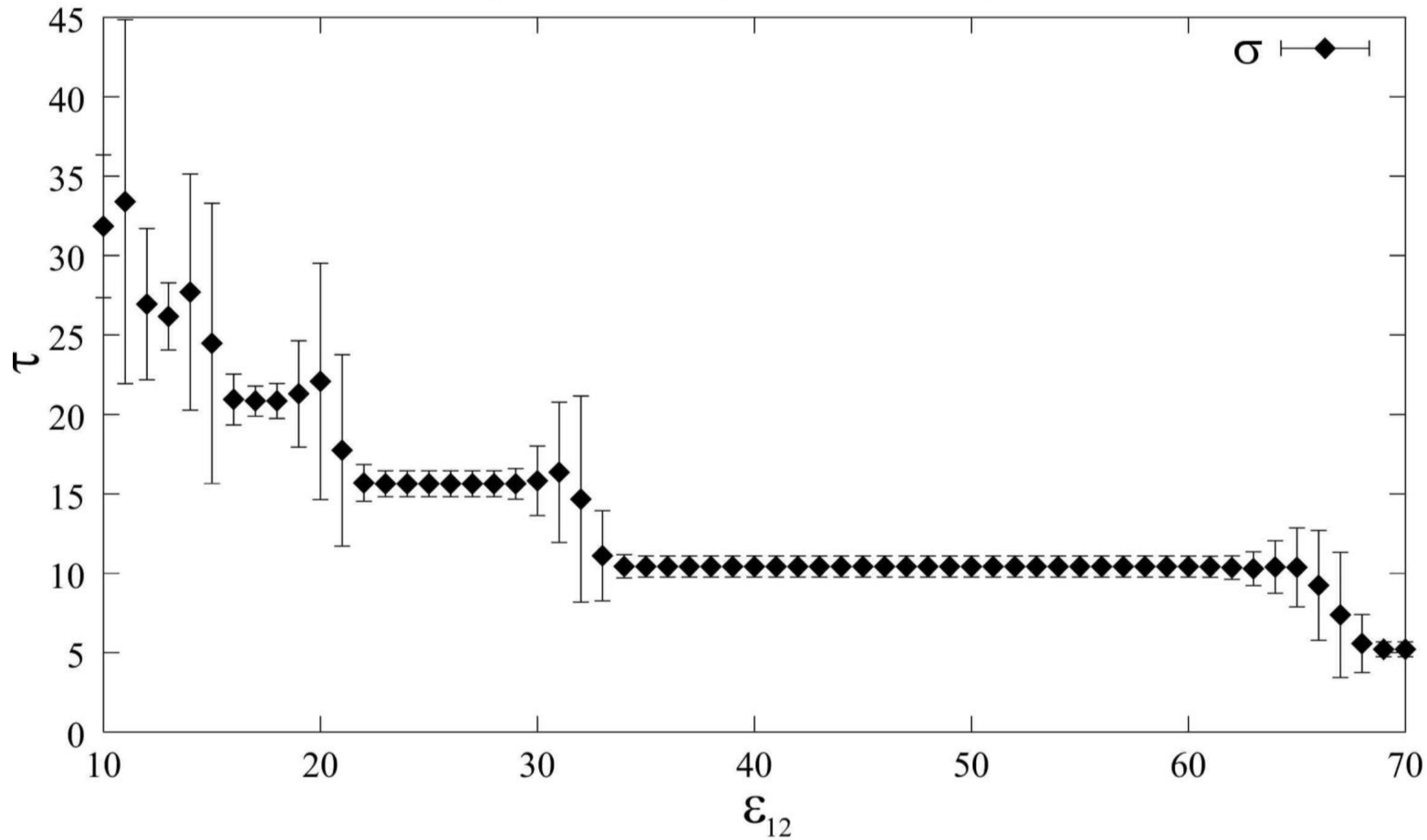
Stochastic Modelling: Example 2

Two Different Neurons

unit	ϵ	p_i	L_i	τ_i	σ_i
1	$\epsilon_{12} = 0 - 70$	0.95	5	5.21	0.47
2	$\epsilon_{21} = 2$	0.5	70	139	11.747

Stochastic Modelling: Example 2

Two Different Neurons



Specificity regarding synaptic weight: Variation of the mean synchronization time versus ε_{12}, for the configuration of above Table. The error bars in the figure refer to the deviation from the mean of the synchronization time. This simulation is calculated using the Markov chain mathematical formalism.

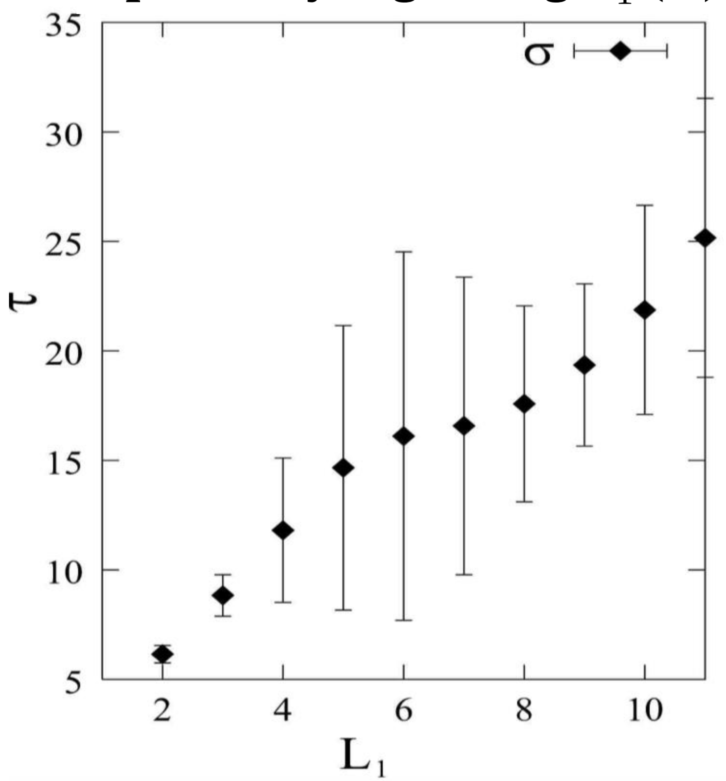
Stochastic Modelling: Example 2

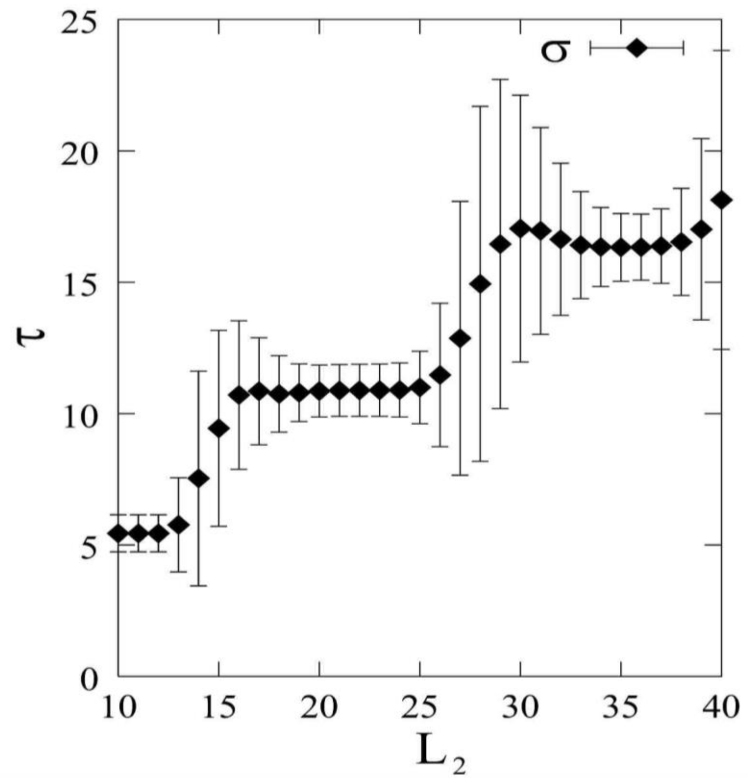
Two Different Neurons

- For restricted values of ε_{12} unit 2 is driven to fire regularly by unit 1, the period being a multiple of unit 1's period.
  - For ε_{12} =13 there is regular firing at τ=26.2.
  - For $\varepsilon_{12} \in$ (16, 18) there is regular firing at τ~21.
  - For $\varepsilon_{12} \in$ (22, 29) there is regular firing at τ~15.
  - For $\varepsilon_{12} \in$ (35, 61) there is regular firing at τ~10.4.
  - For $\varepsilon_{12} \in$ (69, 70) there is regular triggering at τ~5.2.
- For $\tau \sim mL_1$ with m=1,2,3,..., the dispersion σ is consistent with the dispersion of a neuron of p=0.95 and threshold $L=mL_1-(m-1)$.

Stochastic Modelling: Example 2

Two Different Neurons





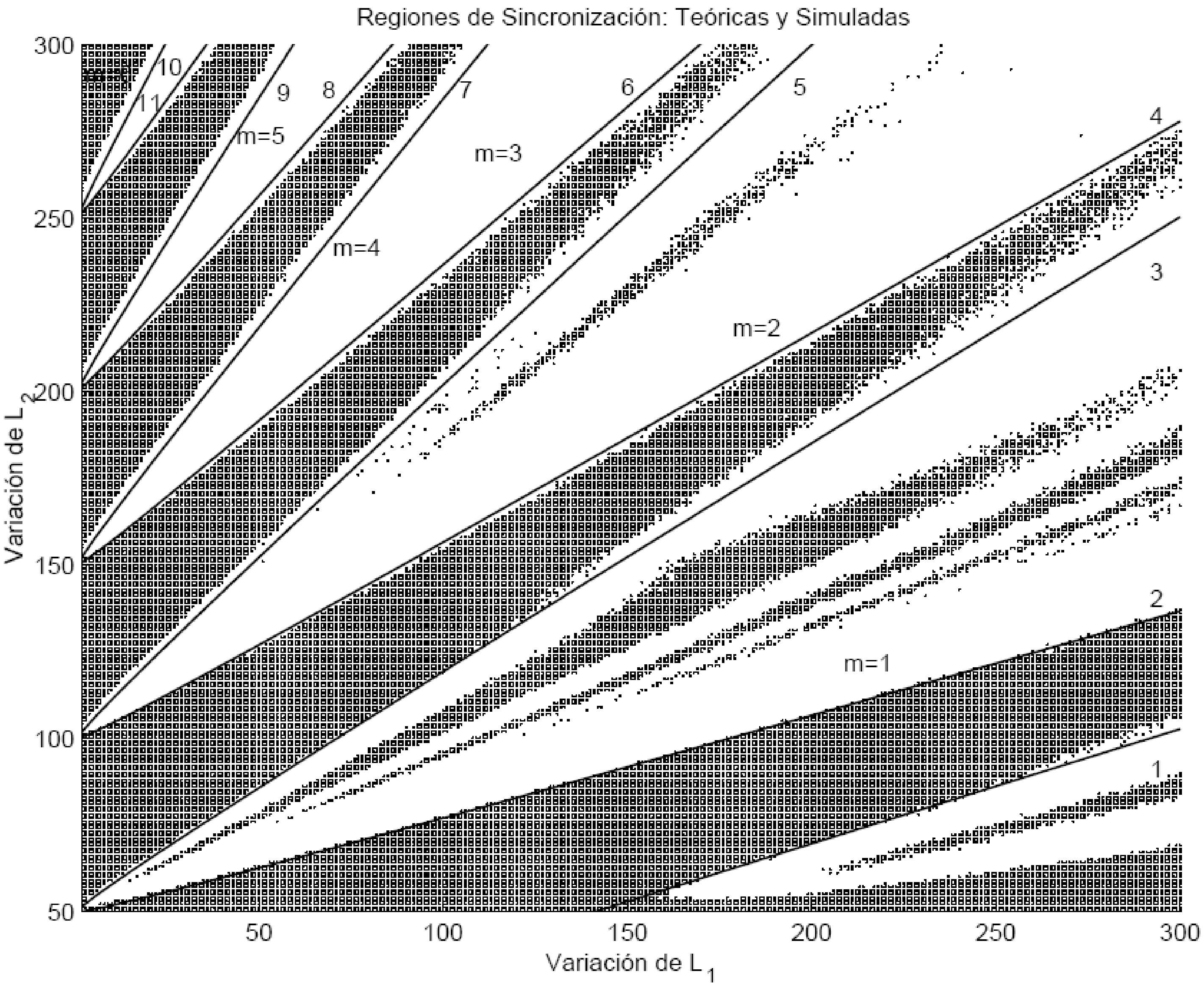
i	ϵ_{ij}	p_i	L_i	τ_i	σ_i
1	7	0.95	$2-12$	var	var
2	2	0.5	20	39	6.16

i	ϵ_{ij}	p_i	L_i	τ_i	σ_i
1	2	0.9	5	5.44	0.703
2	11	0.5	$10-40$	var	var

Specificity regarding firing thresholds

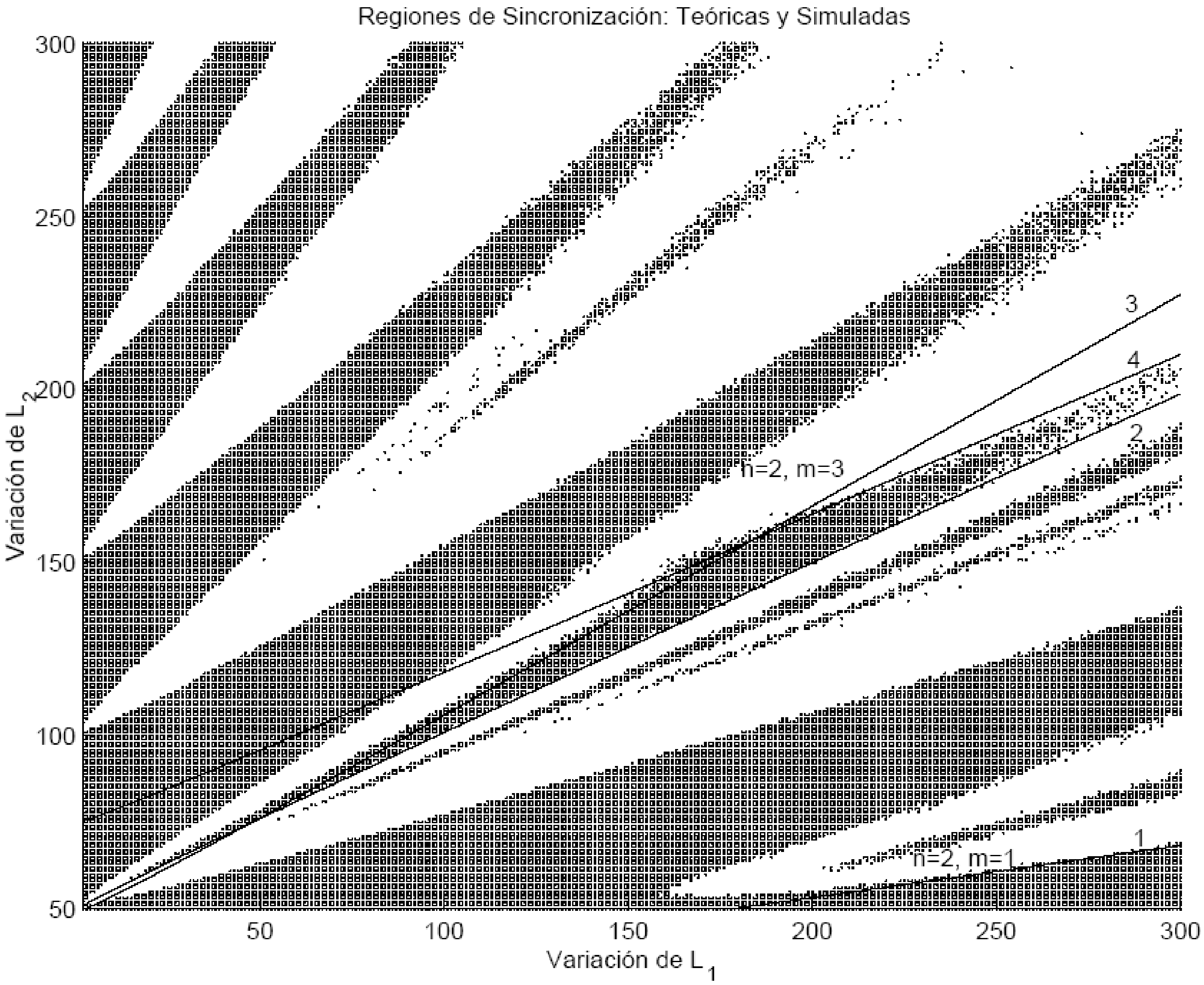
Stochastic Modelling: Example 2

Regions of Synchrony



Stochastic Modelling: Example 2

Regions of Synchrony



Stochastic Modelling: Example 2

Some final conclusions

- Despite the intrinsic noise of the system, the synchronization phenomenon can occur adequately.
- The stochastic character that is included in our neural model clearly acts as a stabilizer, allowing a robust and precise synchronization between the activities of a network composed of two neurons.
- These synchronizations are independent of the initial state with which the units start.

Stochastic Modeling: Example 3

- Now suppose **a firing and integrating neuron that is bombarded by stochastic synaptic inputs**. The bombardment is distributed according to a Poisson distribution.

- We are going to **disregard** the **leaky term** that the membrane may have, as well as the **refractory period**.

- We also assume that the integrating cell receives **excitatory synaptic inputs** that follow **a Poisson process** with a **mean λ_e and a synaptic weight a_e.**

Stochastic Modeling: Example 3

- Conceptually, **each synaptic input** can increase the charge of capacitance C by an amount proportional to a_e, **increasing** the membrane potential by an amount $\mathbf{a_e/C}$ toward the threshold potential V_{th}.

- Thus, the membrane potential V(t) is given by the following evolution:

$$V(t) = a_e N_e(t)$$

Stochastic Modeling: Example 3

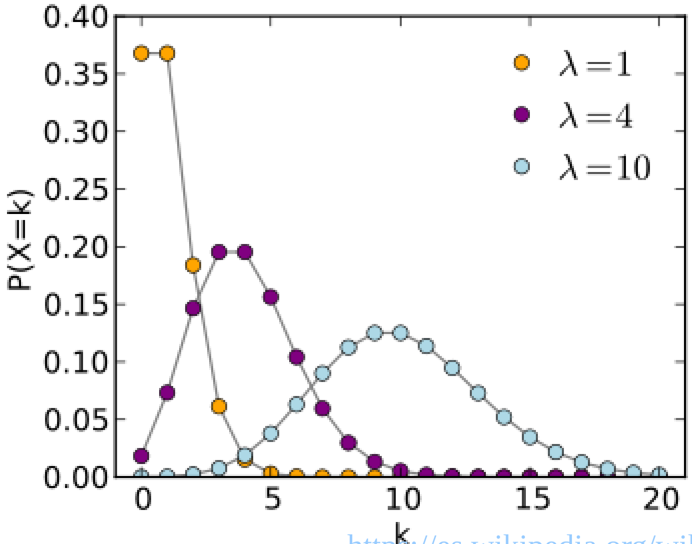
- Where **$N_e(t)$ is a random variable distributed according to a Poisson distribution** that takes a discrete value at time t.

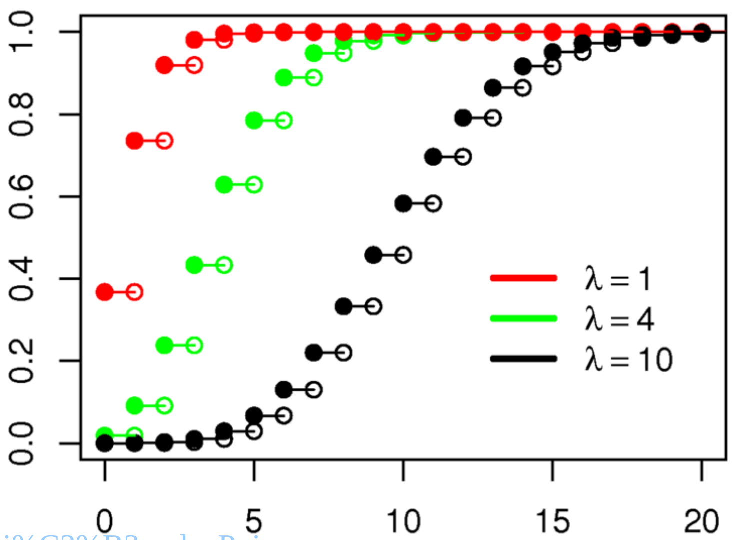
- When the **potential reaches the V_{th}** threshold, a **pulse is generated** and the **membrane potential returns to zero**.

- This random process for the membrane potential shows random jumps of amplitude a_e.

Stochastic Modeling: Example 3

How to generate Ne (t) with Poisson





https://es.wikipedia.org/wiki/Distribuci%C3%B3n_de_Poisson

- Poisson distribution
  - Matlab example (each unit t a lambda average)
  - t=1;lamda=1;hist(random('poisson',t*lamda,[1,10000]),500)

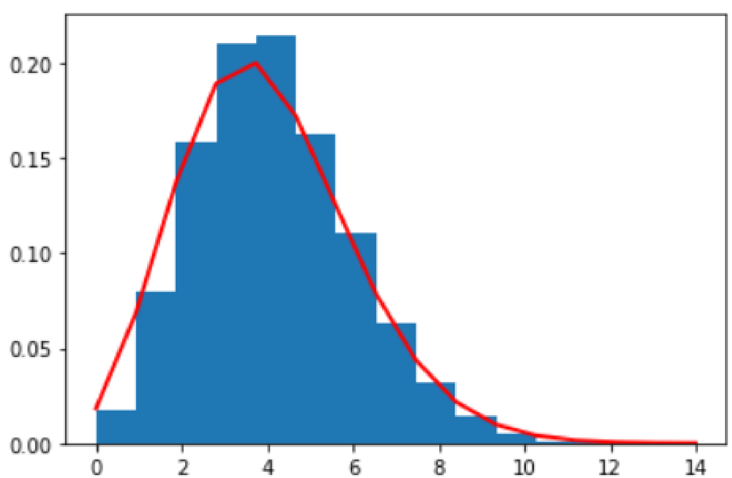
$$P(x) = e^{-\lambda t} \frac{(\lambda t)^x}{x!}$$

Stochastic Modeling: Example 3

How to generate Ne (t) with Poisson

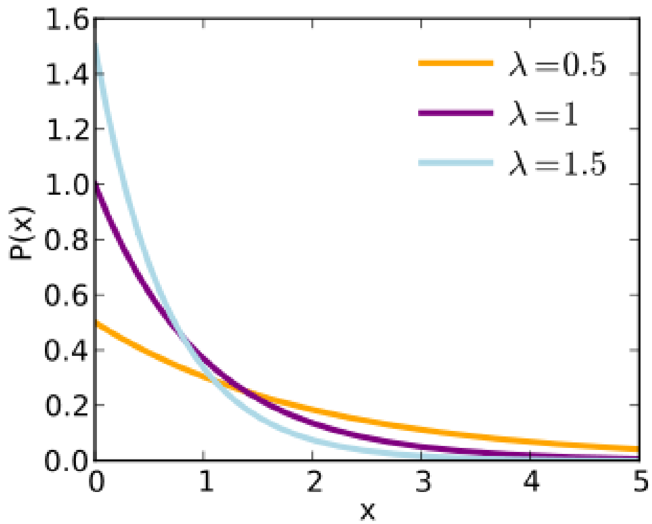
In [11]:

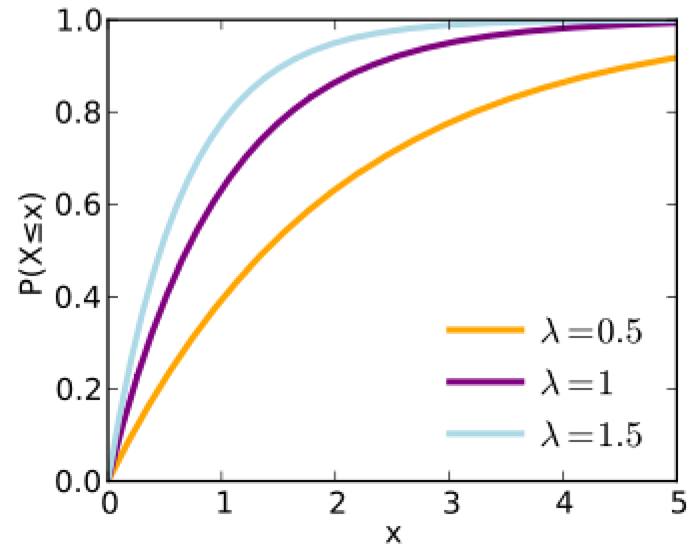
```
# Poisson distribution calculation, see convergence as a function of samples.
%matplotlib inline  # Muy importante, que los gráficos salgan embebidos en la página.
import matplotlib.pyplot as plt
import numpy as np
from scipy.special import factorial
# Poisson parameters
t, la, muestras =1, 4, 10000
# creating the data sample
p = np.random.poisson(t*la,muestras)
# Experimental poisson
neventos, bins, basura = plt.hist(p, 15, density=True)
# Theoretical poisson
_ =plt.plot(bins, (np.exp( - (t*la)) * ((t*la) ** bins)) / factorial(bins), linewidth=2, color='r')
```



Stochastic Modeling: Example 3

How to generate Ne (t) with Exponential





https://es.wikipedia.org/wiki/Distribuci%C3%B3n_exponencial

- Exponential Distribution (times between spikes)
  - Matlab example (each unit t a lambda average)
  - t=1;lamda=1;hist(random('Exponential',t*lamda,[1,10000]),500)

$$f^{\text{exponential}}(x;\lambda) = \lambda e^{-\lambda x}$$

Stochastic Modeling: Example 3

- Now **we can do the same with inhibitory synapses**, if we assume the inhibitory inputs modeled **by a Poisson process with a mean λ_i and a synaptic weight a_i**.

- Now the random process of V(t) can also go down in amplitude jumps a_i:

$$V(t) = a_e N_e(t) - a_i N_i(t)$$

$$V(0) = 0$$

$$V < V_{th}$$

Stochastic Modeling: Example 3

- This model is an example of the **random walker**, with Stein (1965) being one of the first to propose a similar Gerstein model.
- Previously, **Gerstein and Mandelbrot (1964)** proposed their random walker model toward an absorbent barrier, to describe different ranges of neural activity for a single neuron.
- We can consider a leaky integrator, and what we get by analogy to the previous problem is a **leaky random walker**. It was Stein who first incorporated the term leaky in random walkers.

Stochastic Modeling: Example 3

- The expected value of this process (random walker) is:

$$\langle V(t)\rangle = a_e\langle N_e(t)\rangle - a_i\langle N_i(t)\rangle =$$

$$a_e\lambda_e t - a_i\lambda_i t =$$

$$\lambda t$$

$$\lambda = a_e\lambda_e - a_i\lambda_i$$

- Being λ **the trend of the random walker**. This parameter corresponds to the input current to the unit.

Stochastic Modeling: Example 3

- The variance of the voltage over time is:

$$Var[V(t)] = a_e^{\,2} Var[N_e(t)] - a_i^{\,2} Var[N_i(t)] =$$

$$a_e^{\,2} \lambda_e t - a_i^{\,2} \lambda_i t = \sigma^2 t$$

$$\sigma^2 = a_e^{\,2} \lambda_e - a_i^{\,2} \lambda_i$$

- Variance property: $V(aX+b)=a^2V(X)$.
- The variance of a constant is zero ($V(b)=0$).
- Being σ^2 the variance parameter of the random walker.

Stochastic Modeling: Example 3

- **When will the membrane potential reach the V_{th} threshold and generate a pulse?**

- This amount is known as the time of the **first passage to the threshold**.

- This time of the first passage has a non-trivial but well-characterized probability distribution, $f_{th}(t)$.

- Suppose T_{th} is the random time needed for the potential V to go from state V=0 to $V=V_{th}$.

Stochastic Modeling: Example 3

- Thus, we can say that (Tuckwell 1988)

$$P(T_{th} < \infty) = \int_0^{\infty} f_{th}(t)dt$$

$$P(T_{th} < \infty) = \begin{cases} 1 & \text{si } \lambda \geq 0 \\ (a_e \lambda_e / a_i \lambda_i)^{V_{th}} & \text{si } \lambda < 0 \end{cases}$$

- From this we can deduce that if the trend of the random walker is positive then it will fire with probability 1.

Stochastic Modeling: Example 3

- If the **trend** or input to the neuron is **negative**, then a **fluctuation** in input must be expected to **raise V to the threshold**.

- This will become less and **less likely as effective inhibition exceeds excitation more**.

- In the first case, when $a_e \lambda_e > a_i \lambda_i$, the first and second moments for T_{th} can be easily calculated.

Stochastic Modeling: Example 3

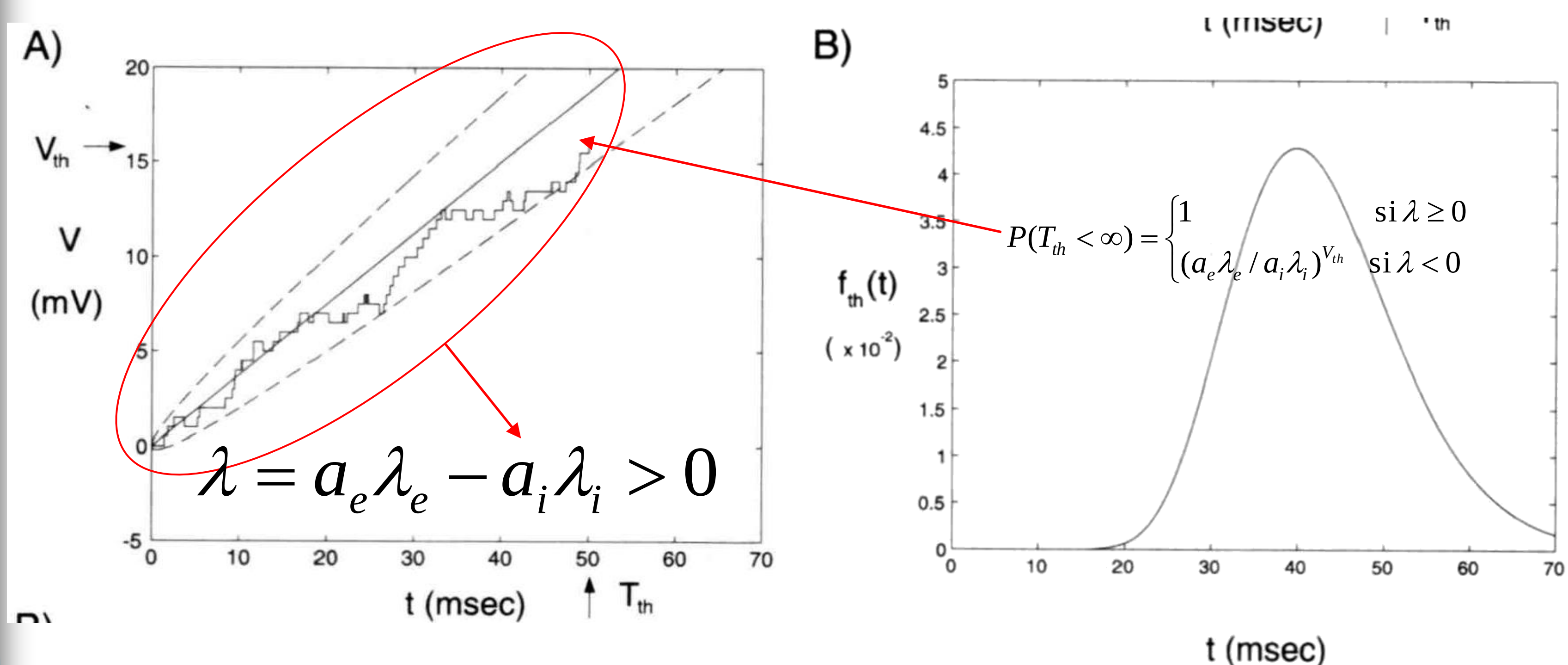
- Specifically, the mean firing time and its variance are (< T_{th} > actually corresponds to the average of intervals between adjacent spikes):

$$\langle T_{th} \rangle = \frac{V_{th}}{\lambda}$$

$$Var[T_{th}] = V_{th} \frac{a_e \lambda_e + a_i \lambda_i}{\lambda^3}$$

- A **Vienner** process, or **Browian** movement, is the continuous version of the random walker. To arrive at this continuous model, the amplitude of each synapse is allowed to be infinitesimally small, while the speed at which the signals arrive is increasingly faster.

Stochastic Modeling: Example 3



$$\lambda = a_e\lambda_e - a_i\lambda_i > 0$$

$$P(T_{th} < \infty) = \begin{cases} 1 & \text{si } \lambda \geq 0 \\ (a_e\lambda_e / a_i\lambda_i)^{V_{th}} & \text{si } \lambda < 0 \end{cases}$$

Fig. 15.7 Random Walk of the Membrane Potential Illustration of the random walk model of excitatory and inhibitory synaptic input into a nonleaky integrate-and-fire unit as pioneered in this form by Stein (1965). The cell receives Poisson distributed excitatory input (with rate $\mu_e = 1000$ Hz), each increasing the voltage by 0.5 mV, and Poisson distributed inhibitory input (at a rate of 250 Hz), each input decreasing the potential by 0.5 mV. Threshold is reached at 16 mV. (**A**) One instantiation of such a random walk, together with the expected mean potential and its standard deviation. The unit generates a spike at around $T_{\text{th}} = 50$ msec. (**B**) Probability density $f_{\text{th}}(t)$ for the first passage to threshold, that is, for the time it takes before the voltage threshold is reached for the first time.

Stochastic Modeling: Example 4

- We are going to simulate the **variabilities of real neurons**.
- Considering **inputs to a neuron distributed according to a normal** is a good approximation when we consider many independent synaptic inputs.
- Thus the central limit theorem can be applied.
- If we assume this, the coefficient of variation of the result approaches the lower end of the coefficient of variation of some cortical neurons (see figure 3.7 slides later).

Stochastic Modeling: Example 4

- Suppose a noisy integration and fire model

$$\tau_m \frac{du}{dt} = -u + RI_{ext} + \eta\ (t)$$

- In this case, η **is a random variable that is distributed according to a standard normal**.

- Thus, in this model, we use a resulting external current whose distribution is determined by white noise.

Stochastic Modeling: Example 4

- Remember that by the central limit theorem, this approximation is good when we consider that our neuron has many independent synaptic inputs with the same distribution.

- **The ISI distribution of this model can be perfectly adjusted by a normal-log distribution**:

$$f^{\text{normal-log}}(x;\mu,\sigma)=\frac{1}{x\sigma\sqrt{2\pi}}e^{\frac{-(\log(x)-\mu)^2}{2\sigma^2}}$$

Stochastic Modeling: Example 4

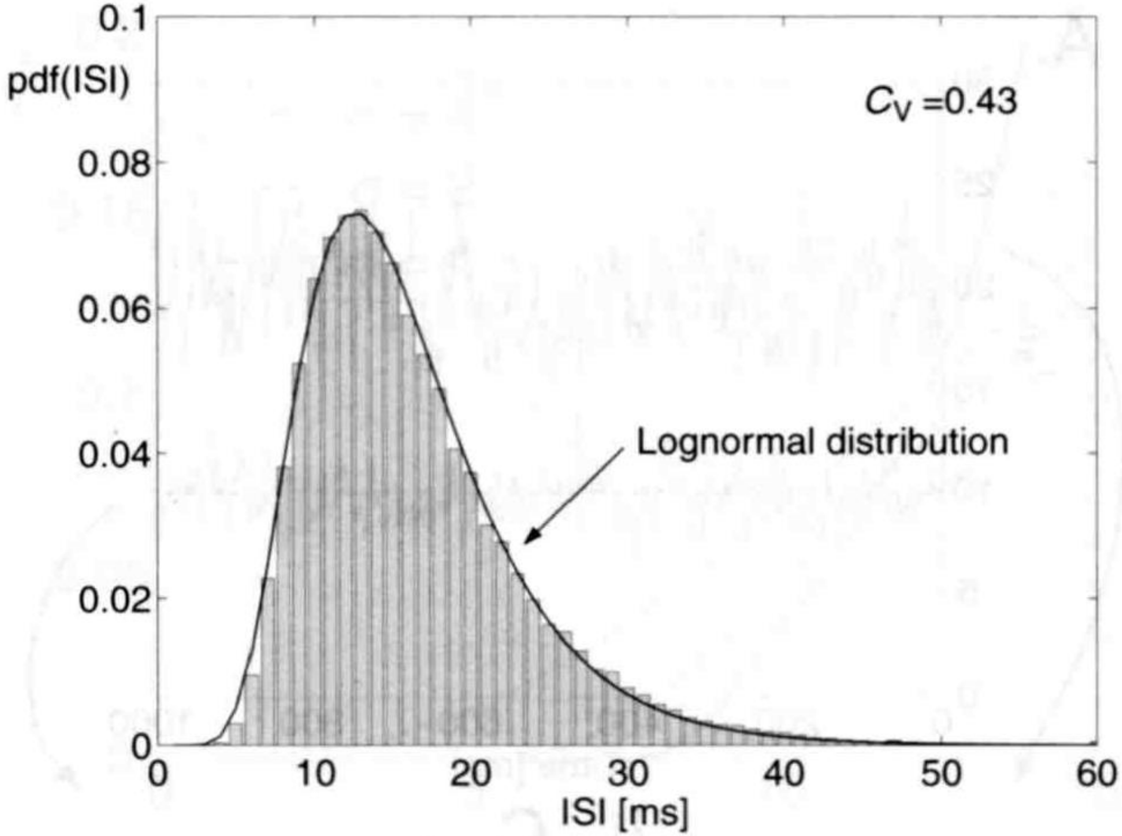


Fig. 3.7 Simulated interspike interval (ISI) distribution of a leaky IF-neuron with the threshold $\vartheta = 10$ and time constant $\tau_{\mathrm{m}} = 10$. The underlying spike train was generated with noisy input around the mean value $RI = 12$. The fluctuation were therefore distributed with a standard normal distribution. The resulting ISI histogram is well approximated by a lognormal distribution (solid line). The coefficient of variation of the simulated spike train is $C_{\mathrm{V}} \approx 0.43$.

Appendix A: Basic Theory of Probability

- A **random variable**, X, is a variable that can take different values at each time. We are not completely sure of the value of that variable for a given moment, but it depends on a probability.
- We assign values to that variable through a process or an experiment.
- **Discrete** and **continuous** random variables.
- The mathematical formulation varies for the two types of variables: **summation** or **integral**.

Appendix A: Basic Theory of Probability

- For example, the **probability function** $P_X(x)=P_X(X=x)$ describes the frequency at which each possible x value of the discrete variable of X occurs.

- **Normalization** of the probability function :

$$\sum_{x} P_X(x) = 1$$

- In the case of **continuous variables**, we have **infinite values** of x. Thus, these values can be infinitesimally very small.

Appendix A: Basic Theory of Probability

- Therefore, it is more convenient to write the probability distribution function (P.f.) $P_X(x)=p_X(x)dx$, where $p_X(x)$ is the **probability density function** (P.d.f.). Is fulfilled

$$\int_X p_X(x)dx = 1$$

- The probability density $p_X(x)$ measures the probability of an event for the interval ($x \leq X < x+dx$).

Appendix A: Basic Theory of Probability: Bernoulli

- A **Bernoulli random variable** is one that has only two possible events: success with probability p and failure with probability 1-p:

Probability function:

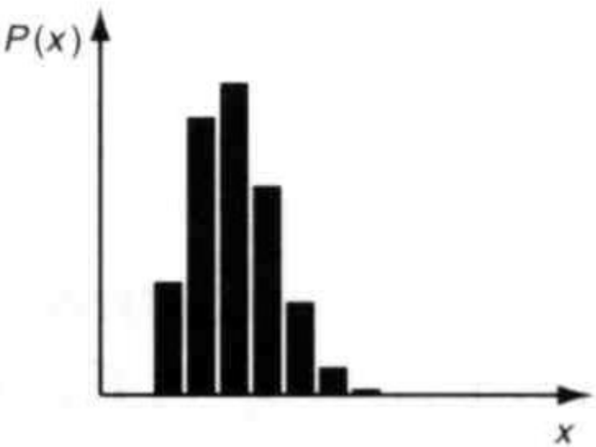
$$P(\text{success}) = p; P(\text{failure}) = 1 - p$$

mean: p

variance: $p(1 - p)$

Appendix A: Basic Theory of Probability: Binomial

- The number of successes in n Bernoulli events with probability p:



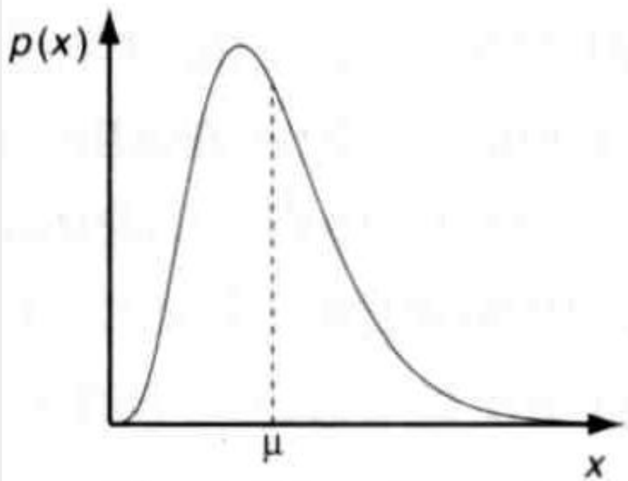
Probability function:

$$P(x) = \binom{n}{x} p^x (1-p)^{n-x}$$

mean: np

variance: $np(1-p)$

Appendix A: Basic Theory of Probability: χ^2



Probability density function:

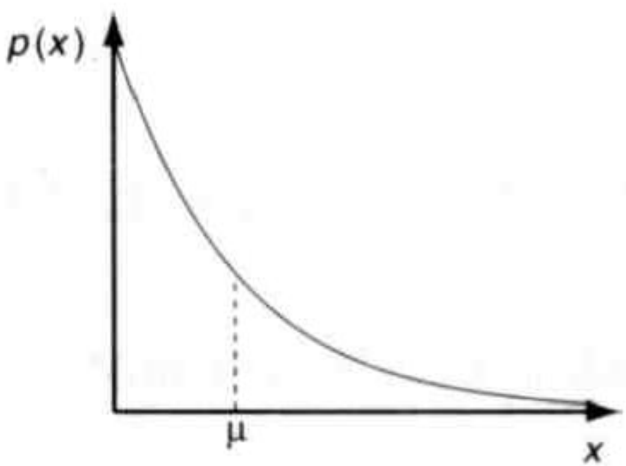
$$p(x) = \frac{x^{(\nu-2)/2} e^{-x/2}}{2^{\nu/2}\Gamma(\nu/2)}$$

mean: ν

variance: 2ν

Appendix A: Basic Theory of Probability: Exponential

- Represents the distribution of times between events that are distributed according to a Poisson distribution. It depends on a single parameter λ.



Probability density function:

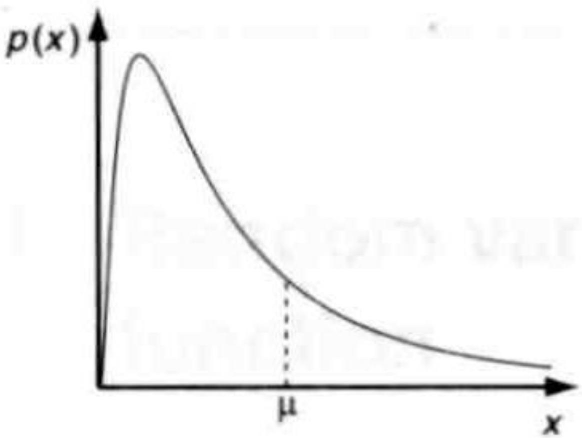
$$p(x) = \lambda e^{-\lambda x}$$

mean: $1/\lambda$

variance: $1/\lambda^2$

Appendix A: Basic Theory of Probability: Log-Normal

- Distribution that is restricted to value 0 when x is 0. It depends on two parameters: the **scale parameter** m (median), and the **shape parameter σ.**



Probability density function:

$$p(x) = \frac{1}{x\sigma\sqrt{2\pi}} e^{\frac{-[log(x/m)]^2}{2\sigma^2}}$$

mean: $m e^{\frac{1}{2}\sigma^2}$

variance: $m^2 e^{\sigma^2}(1 - e^{\sigma^2})$

Appendix A: Basic Theory of Probability: Multinomial

- Generalization of the binomial distribution, with k possible events, each with probability p_i.

Probability function:

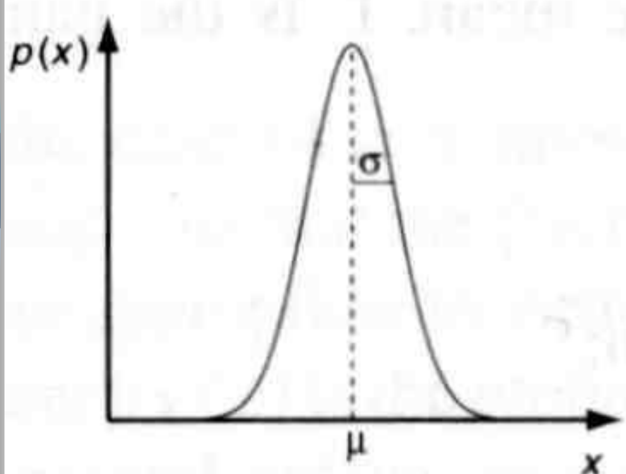
$$P(x_i) = n! \prod_{i=1}^{k} (p_i^{x_i} / x_i!)$$

mean: np_i

variance: $np_i(1 - p_i)$

Appendix A: Basic Theory of Probability: Normal

- Limit of the binomial distribution when the number of events is very large (this distribution is important for the central limit theorem, TCL).



Probability density function:

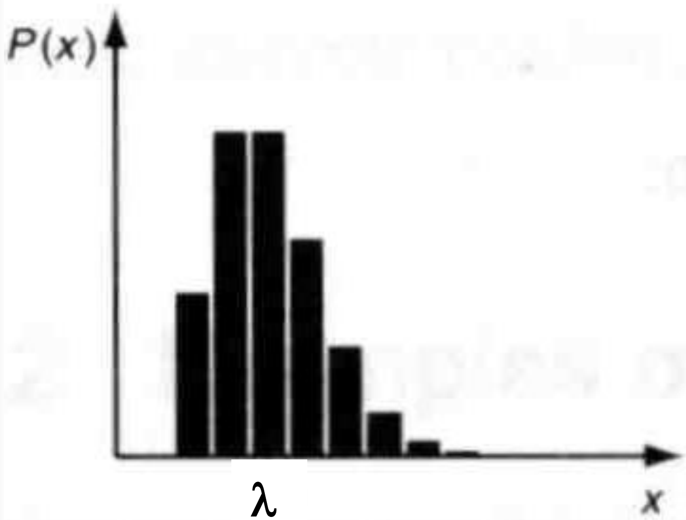
$$p(x) = \frac{1}{\sigma\sqrt{2\pi}} e^{\frac{-(x-\mu)^2}{2\sigma^2}}$$

mean: μ

variance: σ^2

Appendix A: Basic Theory of Probability: Poisson

- This discrete distribution is frequently used to model the firing trains of cortical neurons. The only parameter λ is equal to the mean and the variance.



Probability function:

$$P(x) = \frac{\lambda^x}{x!} e^{-\lambda}$$

mean: λ

variance: λ

Appendix A: Basic Theory of Probability: Poisson

- In certain applications it is necessary to replace the unit time interval with an interval of arbitrary length t.
- Thus, in this case, λ is replaced by λt

$$P(x) = e^{-\lambda t} \frac{(\lambda t)^x}{x!}$$

- This expression calculates the probability of finding exactly x events in the fixed interval of length t.

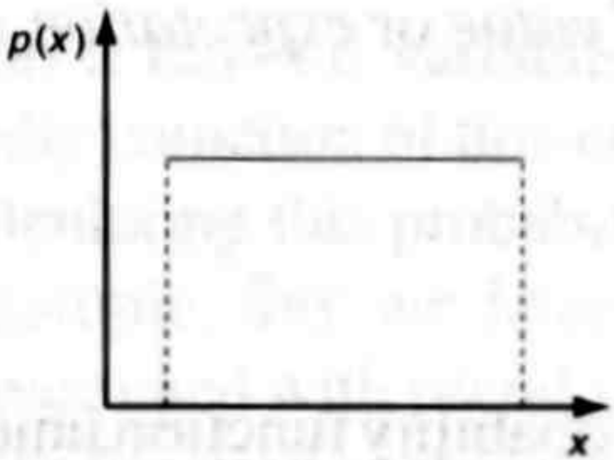
Appendix A: Basic Theory of Probability: Poisson

- In particular, the probability of not finding any event in the interval of length t is given by

$$P(0) = e^{-\lambda t}$$

Appendix A: Basic Probability Theory: Uniform Probability Function

- Distribution of random numbers in the interval a and b. Pseudo-random variables with this distribution are frequently generated by routines in many programming languages.



Probability density function:

$$p(x) = \frac{1}{b-a}$$

mean: $(a+b)/2$

variance: $(b-a)^2/12$

Appendix A: Basic Theory of Probability: cumulative probability function

- The probability of having the value x for a random variable X in the range x_1 and x_2 is given by

$$P(x_1 \le X \le x_2) = \int_{x_1}^{x_2} p(x)dx$$

$$P^{acum}(x < y) = \int_{-\infty}^{y} p(x)dx$$

Appendix A: Basic Theory of Probability (Moments)

- Random variables are entirely specified by probability.
- Sometimes we don't know exactly the shape of the probability distributions, and we are only able to measure certain characteristics of the random variable.
- A characteristic is the mean or expected value of the random variable, defined by

$$\mu = \int_{-\infty}^{\infty} x f(x) dx$$

Appendix A: Basic Theory of Probability (Moments)

- This quantity is not enough to characterize the probability function in a unique way.

- To do this, we must know all the moments of a probability distribution, where the n-th moment around the mean is defined as

$$m^n = \int_{-\infty}^{\infty} (x-\mu)^n f(x) dx$$

Appendix A: Basic Theory of Probability (Moments)

- Thus, the second moment around the mean is called the **variance**.

$$\sigma^2 = \int_{-\infty}^{\infty} (x-\mu)^2 f(x) dx$$

- This measures the variation of the random variable around the mean value.

- The square root of the variance is what is called the **standard deviation**.

Appendix A: Basic Theory of Probability (Moments)

- The mean and variance can be estimated from a set of samples as

$$\bar{x} = \frac{1}{n}\sum_{i=1}^{n} x_i \text{ (estimator of the mean)}$$

$$s_1^2 = \frac{1}{n}\sum_{i=1}^{n} (\bar{x} - x_i)^2 \text{(estimator of the variance)}$$

$$s_2^2 = \frac{1}{n-1}\sum_{i=1}^{n} (\bar{x} - x_i)^2 \text{(estimator of the variance unbiased)}$$

Appendix A: Basic Probability Theory: Functions of Random Variables

- A function of a random variable X is also a random variable Y.

$$Y = f(X)$$

- Frequently, we are also interested in the probability of the new random variable Y.
- However, you have to be more careful in calculating this new probability function.

Appendix A: Basic Probability Theory: Functions of Random Variables

- Suppose we have a variable X with a uniform distribution, so the probability density is given by

$$p_X(x) = \begin{cases} 1 & \text{for } 0 \le x \le 1 \\ 0 & \text{in otherwise} \end{cases}$$

- And for instance, we are interested in the probability density $P_Y(y)$ of the random variable

$$Y = e^{-X^2}$$

Appendix A: Basic Probability Theory: Functions of Random Variables

- At any given time, you might think that the random variable Y is distributed according to a Gaussian, but it is not.

- To calculate the probability density function we can use the cumulative density function, noting that

$$P(Y \le y) = P(e^{-X^2} \le y) = P(X \ge \sqrt{-\ln y})$$

Appendix A: Basic Probability Theory: Functions of Random Variables

- This probability can be calculated from the uniform probability density function $p_X(x)$

$$P(X \geq \sqrt{-\ln y}) = \begin{cases} \displaystyle\int_{\sqrt{-\ln y}}^{1} 1 dx = 1 - \sqrt{-\ln y} & \text{para } e^{-1} \leq y \leq 1 \\ 0 & \text{in otherwise} \end{cases}$$

- In fact, this probability density is quite different from a normal distribution.

Appendix A: Basic Probability Theory: Functions of Random Variables

- A special function of random variables, which is of particular interest, is the one given by the sum of many random variables.

- For example, such a sum occurs when we calculate the averages of certain measured quantities.

$$\overline{X} = \frac{1}{n}\sum_{i=1}^{n} X_i$$

- We are interested in the probability density of such a resulting random variable.

Appendix A: Basic Probability Theory: Functions of Random Variables

- The central limit theorem says that the mean (normalized sum) of n random variables, which are drawn from a probability distribution with mean μ and variance σ, approximates a normal mean μ and variance σ/n, when n is big enough.

- This approach in practice works for small samples. For example, the random variable that is the normalized sum of only 7 variables, with a uniform distribution, behaves like a normal distribution.

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Appendix B: Refractory Period

- There is a maximum number of spikes with which a neuron can respond.
- Absolute refractory period: the inactivation of the sodium channel makes it impossible to initiate another action potential until a certain time has passed (around 1 ms, although it depends on the cell type).
- This characteristic limits the neuron to fire with a maximum of 1000 Hz (assuming 1 ms of absolute refractory period).

Appendix B: Refractory Period

- On the other hand, due to the hyperpolarization of the action potential, it is relatively difficult to initiate another spike during this period.
- This is what is called a relative refractory period.
- This other period further reduces the neural firing frequency.
- Very fast neurons have been measured in nature, down to even more than 600 Hz.

Appendix B: Refractory Period

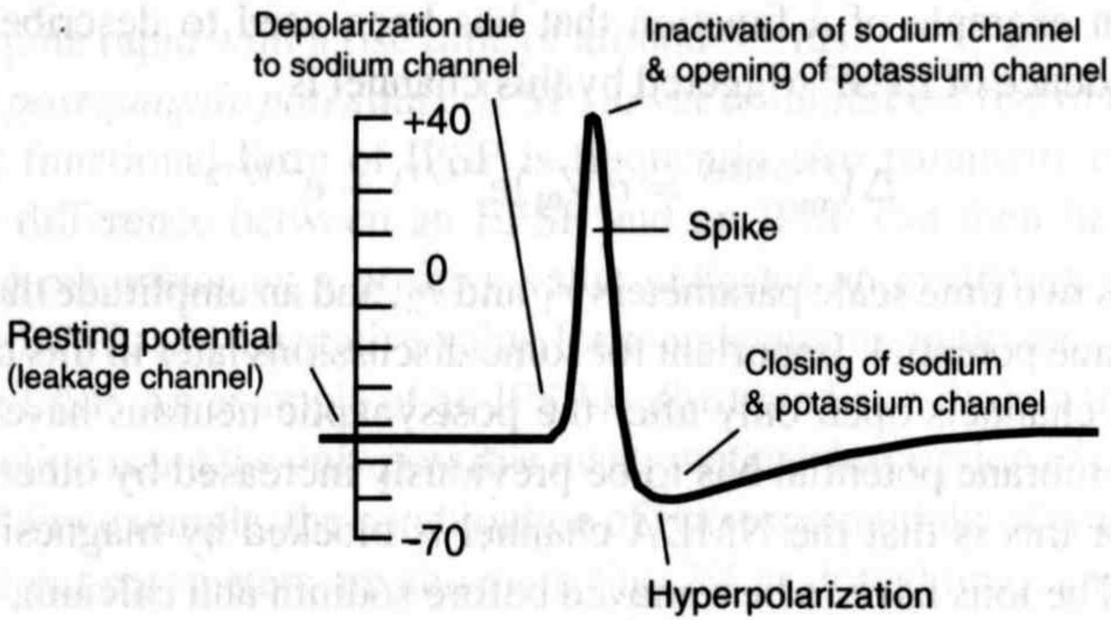

Fig. 2.5 Typical form of an action potential, redrawn from an oscilloscope picture of Hodgkin and Huxley.

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Appendix C: ISI distribution

- Suppose we have a sequence of spikes that follow a Poisson distribution, where the parameter λ represents the average number of spikes per unit time.

$$f^{\text{Poisson}}(x;\lambda) = \lambda^x \frac{e^{-\lambda}}{x!}$$

- We ask ourselves the following question: How long do we have to wait until another fire is generated?

Appendix C: ISI distribution

- We assume that at $t = 0$, a fire occurred, and we want to know at which time the next spike will occur.

- This function can be calculated if we know what is the probability that no spike will occur between 0 and t, and then we subtract it from 1. The average of events between 0 and t is λt.

Apéndice C: ISI distribution

- The probability that in a Poisson process of mean λt no event will occur at time t is :

$$e^{-\lambda t}$$

- Thus, the distribution function of the next spike is one minus the previous value:

$$P(t) = 1 - e^{-\lambda t}$$

Apéndice C: ISI distribution

- The probability density of that distribution function is the derivative with respect to time (exponential distribution):

$$p(t) = dP(t)/dt = \lambda e^{-\lambda t}$$

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