Multifractal distribution of spike intervals for two oscillators coupled by unreliable pulses

LETTER TO THE EDITOR

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Johannes Kestler and Wolfgang Kinzel

Institute for Theoretical Physics, University of Würzburg, Am Hubland, 97074 Würzburg, Germany

E-mail: jkestler@physik.uni-wuerzburg.de

Abstract
Two neurons coupled by unreliable synapses are modelled by leaky integrate-and-fire neurons and stochastic on–off synapses. The dynamics is mapped to an iterated function system. Numerical calculations yield a multifractal distribution of interspike intervals. The covering, information and correlation dimensions are calculated as a function of synaptic strength and transmission probability.

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Networks of pulse-coupled oscillators are simple models which have been investigated in the context of synchronization and dynamical clustering [1, 2]. In particular, the dynamics of neurons interacting by synaptic transmission has been described by pulse-coupled oscillators, for instance, networks of leaky integrate-and-fire neurons [3, 4]. These models consist of oscillators sending spikes to other oscillators which either excite or inhibit the phase of the receiving units.

So far, only deterministic interactions between oscillating units have been considered. Synaptic transmission, however, seems to be a stochastic process. In the cortex, transmission probabilities between 10% and 90% are reported [5, 6]. Hence, it is important to understand the dynamics of oscillators coupled by unreliable transmission of pulses.

A quantitative measure of the activity of neurons is the distribution of their interspike intervals. Typically, one observes broad distributions which may be described by a simple mathematical approach: each neuron is modelled by a stochastic process which is driven by random uncorrelated synaptic inputs. Hence, usually the effect of unreliable synapses is modelled by an external uncorrelated noise [3, 4].

In this letter we investigate the dynamics of two integrate-and-fire units coupled by unreliable synapses. The transmission of pulses is explicitly modelled by a Bernoulli process: any synapse transmits the incoming spike with some probability p which is independent of the state of the system. We show how to calculate the spike intervals from an iterated-function system (IFS). Our main result is a multifractal distribution of interspike intervals. The
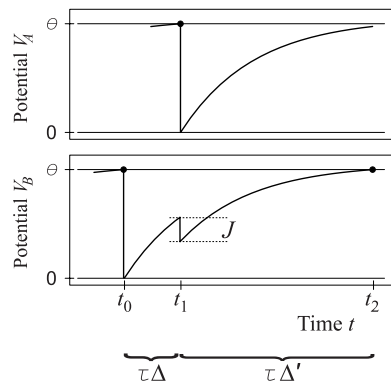
Figure 1. Membrane potential of the two neurons. The spike of neuron A at time t_1 is transmitted to neuron B.

covering, information and correlation dimensions are calculated as a function of the synaptic strength and the probability of synaptic transmission. We find a transition between connected and multifractal support of the distribution of spike intervals.

Our model neurons are leaky integrate-and-fire units working above threshold. In a more general framework, our model is a system of two identical pulse-coupled oscillators [1]. Without synaptic contacts the neurons are deterministic and oscillate periodically, one obtains two intervals between the firing times of the two neurons. With reliable inhibitory synaptic contact, and without any delay of the synaptic transmission, the two neurons relax into a state of anti-phase oscillations with a single spike interval. With unreliable synapses, however, the system has a broad distribution of spike intervals which becomes multifractal in some range of the model parameters.

In our model, each neuron is described by the following differential equation for the time-dependent membrane potential $V(t)$:

$$\tau \frac{dV}{dt} = \mu - V(t). \tag{1}$$

As soon as the potential crosses a threshold value θ it is reset to a value $V_r < \theta$. In addition it fires, i.e. it sends a spike to its neighbour which is transmitted with a probability p. If a spike is transmitted, it reduces the potential of the receiving neuron by an amount J. For simplicity, we consider only inhibitory synapses to avoid an introduction of a refractory time.

The neurons are working above threshold, $\theta < \mu$, otherwise they would not fire at all. Hence, the parameter μ controls the effect of any mechanism which forces the neurons to fire. Without synaptic couplings each neuron fires periodically with the period

$$T = \tau \ln \frac{\mu - V_r}{\mu - \theta}. \tag{2}$$

Without loss of generality we set $V_r = 0$, $\mu = 1$ and $\tau = 1$, and in the following we use the parameter $\theta = 0.95$ which gives a period of $T \simeq 2.996\tau$.

Figure 1 shows the potential of the two neurons for a typical situation. At time t_1 the neuron A fires and the spike is transmitted to neuron B resulting in a decrease of the potential by an amount J. The next firing event occurs at time t_2. The time interval between firing events is denoted by Δ. Using the analytic solution of the differential equation (1), one obtains an iteration of the spike intervals Δ. For the quantity $x = \exp(-\Delta)$ the iteration has the form

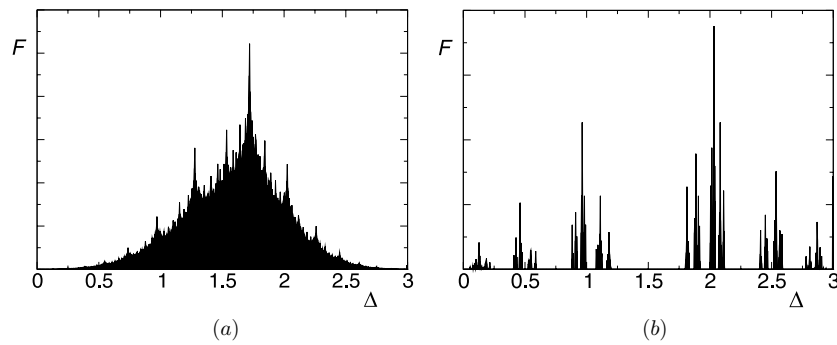$$x' = f_i(x), \qquad i \in \{1, 2, 3, 4, 5\}, \tag{3}$$

Figure 2. Histogram of the spike intervals for the transmission probability $p = 0.5$ and the strength of the synaptic pulse $J = 0.1$ (a) and $J = 0.25$ (b).

where the five functions f_i are selected according to the transmission probability p and the previous value of x. For the situation of figure 1, which occurs with probability p (transmission), one finds

$$x' = \frac{1 - \theta}{x + J} =: f_1(x). \tag{4}$$

With probability $1 - p$ (no transmission) the sum $\Delta + \Delta' = T$ is identical to the period of unperturbed oscillations which gives

$$x' = \frac{1 - \theta}{x} =: f_2(x). \tag{5}$$

Hence, two simple functions are iterated according to probability p of synaptic transmission. The situation becomes slightly more complicated when neuron A overtakes neuron B, i.e. when one neuron fires twice before the other one is firing again. This occurs when the potential $V_B(t_1+)$ becomes negative after neuron A has fired, that is when $x > 1 - J$. In this case one has $\Delta' = T$ or

$$x' = 1 - \theta =: f_3(x). \tag{6}$$

But now Δ'' depends on Δ and one finds with probability p

$$x'' = \frac{1}{x + J + \frac{J}{1-\theta}} =: f_4(x) \tag{7}$$

and with probability $1 - p$

$$x'' = \frac{1}{x + J} =: f_5(x). \tag{8}$$

If the synaptic pulse J is larger than $\theta/(2 - \theta)$ the same neuron can even fire more than twice in a row, but we do not consider such large unphysiological values of J.

In summary, only five simple functions are iterated to calculate the distribution of spike intervals Δ. It is well known that such a system (IFS) may lead to a fractal structure of the set of iterated values [7]. In our numerical simulations of equations (4) to (8) we have generated about 10^{11} spike intervals for each set of parameters. Figure 2 shows two histograms of the spike intervals for small and large values of J. Obviously, the distribution of spike intervals has a complex structure which we quantify by the Rényi dimensions [8]

$$D(\beta) = \lim_{\varepsilon \to 0} \frac{1}{\ln \varepsilon} I(\beta), \qquad I(\beta) = \frac{1}{\beta - 1} \ln \sum_{i=1}^{r} p_i{}^{\beta}. \tag{9}$$
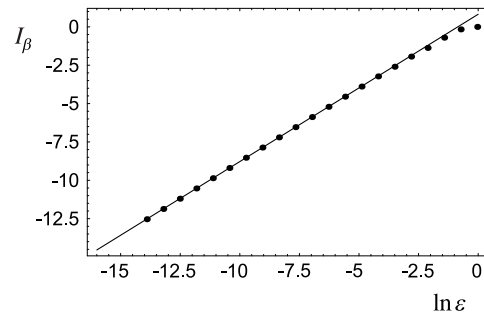
Figure 3. The quantity I_β as a function of the size ε of the covering boxes (here for $\beta = 1$, $p = 0.5$ and $J = 0.15$). The slope of the figure is an estimate of the Rényi dimensions $D(\beta)$ which are shown in figure 4.
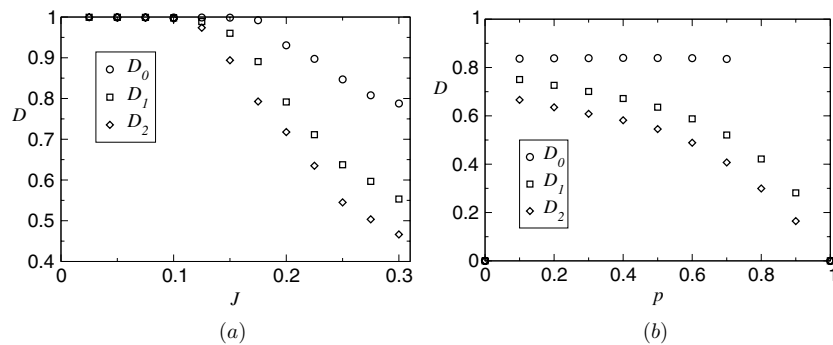

Figure 4. Rényi dimensions (*a*) as a function of the strength J of the synaptic pulse (for $p = 0.5$) and (*b*) as a function of the transmission probability p (for $J = 0.25$)

Here, ε is the size of the boxes of the histogram and p_i is the normalized number of data points in the box i. The sum runs over all nonempty boxes. For $\beta = 1$, the entropy $I(1) = \sum_{i=1}^{r} p_i \ln p_i$ is calculated.

We consider three Rényi dimensions: the covering or box dimension $D(0)$, the information or entropy dimension $D(1)$ and the correlation dimension $D(2)$. Figure 3 shows that a plot of $I(\beta)$ versus $\ln \varepsilon$ yields a straight line over several orders of magnitude; hence, the corresponding dimension can reliably be estimated from the slope of this line. In addition, we checked our results for the correlation dimension by applying the software package TISEAN to our data [9].

The results for the three different Rényi dimensions are shown in figure 4. Of course, our results obey the exact relations $D(2) \leqslant D(1) \leqslant D(0)$. With increasing coupling strength J and transmission probability p the three dimensions decrease. For small values of J the distribution of spike intervals is smooth; hence, one observes $D(0) \simeq D(1) \simeq D(2) \simeq 1$. For large values of J the three dimensions are different, which means that the distribution of spike intervals is multifractal [8]. While the covering dimension $D(0)$, i.e. the structure of the support of the distribution, is insensitive to the value of p, the information dimension as well as the correlation dimension decrease to the value zero in the deterministic limit $p \to 1$. In fact, for $p = 1$, the distribution of spike intervals is a delta peak at the fixed point of f_1 which
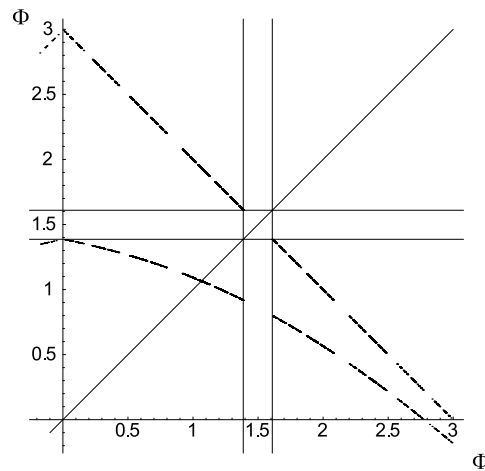
Figure 5. The phases ϕ of the neurons are iterated by the two functions F_1 (bottom) and F_2 (top) shown by the dashed lines. The openings of the two functions show the empty intervals in the distribution of iterated phases.

gives $\Delta = -\ln\left(-J + \sqrt{4 + J^2 - 4\theta}\,\right)\big/2$. Surprisingly, even for $p < 1$ the distribution has its maximum at this value, a sharp peak, as can be seen from figure 2.

The results of figure 4(a) do not rule out a sharp transition between a smooth and multifractal distribution of spike intervals. In fact, for the covering dimension $D(0)$, the transition point can be found analytically. It is convenient to transform equation (1) to $\mathrm{d}\phi/\mathrm{d}t = 1$, where the phase ϕ is defined as

$$\phi(V) = -\ln(1 - V). \tag{10}$$

Now we consider the phase which one neuron occupies after the other one has fired. After the neuron A has fired it has the phase $\phi = 0$, whereas the other neuron B has a nonzero phase ϕ_i. If ϕ_i is positive it will be neuron B which fires next, namely, after the time $T - \phi_i$. However, if ϕ_i is negative then neuron A will fire again after the time T. Regardless of which neuron fires, in both cases we record the phase ϕ_{i+1} of the neuron which has not fired. Given a phase ϕ_i, the next phase ϕ_{i+1} results by applying one of the two mappings depending on whether a spike has been transmitted at time t_{i+1} or not. These two mappings $\phi_{i+1} = F_1(\phi_i)$ and $\phi_{i+1} = F_2(\phi_i)$ which describe the transformation of phases are as follows (see figure 5):

$$F_1(\phi) = -\ln[\exp(|\phi| - T) + J] \text{ (transmission)} \tag{11}$$

$$F_2(\phi) = T - |\phi| \text{ (no transmission).} \tag{12}$$

The function F_2 just flips the lower interval $[0, T/2]$ to the upper one $[T/2, T]$. The function F_1 maps the complete interval $[0, T]$ to the interval $[-\ln(1 + J), -\ln(1 - \theta + J)]$. If the maximum of F_1 is smaller than $T/2$, then there exists an interval in the vicinity of $T/2$ which cannot be reached from outside. In figure 5 this interval is indicated by the small square in the centre of the figure. This interval in the centre is either flipped by F_2 or mapped to an interval outside it by F_1. This means that finally any point inside the square will leave it. In addition, no other point can enter this interval. Hence, the distribution of phases has an opening on this interval. By consecutive iterations of F_1 and F_2 this opening is distributed on the complete range of phases, as depicted in figure 5 by the openings in the functions F_1 and F_2. This indicates—but does not prove it—that the support of the distribution of spike intervals has a

fractal structure, leading to $D(0) < 1$. By these arguments the support of the distribution has a fractal structure if the maximum of F_1 is smaller than $T/2$, which gives a critical point

$$J_* = \sqrt{1 - \theta} - (1 - \theta). \tag{13}$$

For $J < J_*$ the distribution fills the complete range of ϕ values, while for large values of J the distribution has empty intervals. Indeed, this value is consistent with the data of figure 4(a) where the covering dimension $D(0)$ deviates from the value $D(0) = 1$ at about $J_* = 0.1736$. Note, however, that even below J_* the distribution is multifractal because the values of $D(1)$ and $D(2)$ are still smaller than 1. We do not know whether there is a sharp transition to a smooth structure for small J values or whether the fractal dimensions $D(1)$ and $D(2)$ just come very close to the value 1. The data of figure 4 do not allow to distinguish between these two possibilities.

This letter reports a new phenomenon which may be related to the dynamics of real neurons. On one side, our system of two identical pulse-coupled oscillators with random on–off synapses is a very simplified model of two coupled neurons. For instance, synaptic transmission may be multi-valued [10, 11] and time delayed [2], and a much better model would include the dynamics of ion channels [12]. In addition, it is clear that any kind of noise will smear out the distribution of spike intervals. On the other side, in any model, a random uncorrelated process which opens and closes synaptic transmission always yields an iterated function system which can produce fractal distributions of spike intervals depending on the model parameters. Up to now, a fractal structure of spike intervals has not yet been observed. But, to our knowledge, experiments on two interacting neurons under controlled conditions have not yet been reported, either. Our model makes predictions for such an experiment which may help to clarify the stochastic nature of synaptic transmission.

Acknowledgment

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