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Coherence Resonance: On the Use and Abuse of the Fano Factor

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Coherence resonance describes a phenomenon in excitable systems in which a suitable dose of noise generates excitation-events that maximizes its periodicity or coherence. The Fano-factor, defined as the ratio of the standard deviation of the time-intervals between successive events and the average time interval, exhibits a minimum at this optimal noise level. It is shown here that a decreasing Fano factor is a necessary but *not a sufficient* criterion to indicate enhanced coherence of a signal.

Keywords: Stochastic point processes; coherence resonance; neuroscience.

1. Introduction

To characterize temporal coherence of a signal is an important task when studying phenomena such as stochastic resonance (for a review, see [1]) or coherence resonance [2–8]. In periodically driven system such as the driven double-well dynamics most measures of coherence are based on the power spectrum of the signal (signal-to-noise ratio, signal-amplification, cross-correlations between driver and system) or on escape-time distributions [9]. In excitable systems, where the system's signal consists of a train of spiking events, used measures of coherence are based on the interval distribution between successive spikes (for a review see [1]). One of the measures used for the description of coherence resonance is the Fano-factor, i.e. the ratio of the standard deviation of the intervals from their mean value and the mean interval length. A decreasing Fano-factor is a necessary condition for increasing coherence since then all intervals have to be more narrowly distributed around a mean value. In this paper, we show that a decreasing Fano-factor, however, is not a sufficient criterion to indicate increased coherence although it is used as such in several studies [2–8]. This paper is organized into two major parts. In the first part we consider a cluster of potassium and sodium ion channels embedded in a cell-membrane. Such a system generates spontaneous action potentials at a rate that depends on the size of the cluster [10]. The temporal coherence of the spontaneously generated action potentials exhibits coherence resonance as a function of the cluster size ([10] and [11]). The occurrence of an optimal cluster size is verified by a peak in the power spectrum of the spike train and a simultaneous minimum of the Fano-factor. In the second part of this paper, we discuss a simple, action potential generating stochastic toy model which has the feature that the Fano factor *decreases* with increasing noise level, but yet the power spectrum does not indicate any coherence. We thus show that a decreasing Fano-factor is not a sufficient criterion for increasing temporal coherence.

2. Clustered ion channel system

Neuronal K^+ and Na^+ ion channels often occur in clusters. Since each channel is subject to open-closed fluctuations, a cluster of a finite size will generate spontaneous action potentials. We are interested in the coherence of the generated spike train as a function of the cluster size. Each potassium channel has four identical subunits (gates) that are either closed or open. The opening and closing rates $\alpha_K(v)$ and $\beta_K(v)$, respectively, for each subunit are given by [12]

$$\alpha_K(v) = \frac{0.01(10-v)}{\exp\left((10-v)/10\right)-1}, \quad \beta_K(v) = 0.125\exp\left(-\frac{v}{80}\right), \tag{1}$$

where v refers to the trans-membrane potential. The opening and closing processes of the subunits are assumed to be Markovian and described by the two-state master equation for the open-probability of a subunit

$$\dot{p}_n(t) = -\left(\alpha_K(v)+\beta_K(v)\right)p_n(t) + \alpha_K(v), \tag{2}$$

with $n = 1, 2, 3, 4$. The entire channel is open when all four subunits are open.

The sodium channel is composed of three identical (fast) subunits that – similar to the potassium channel subunits – tend to open when the trans-membrane voltage is increasing, i.e.

$$\alpha^f_{Na}(v) = \frac{0.1(25-v)}{\exp\left((25-v)/10\right)-1}, \quad \beta^f_{Na}(v) = 4.0\exp\left(-\frac{v}{18}\right), \tag{3}$$

with the corresponding two state master equations for the state of the gates

$$\dot{q}_n(t) = -\left(\alpha^f_{Na}(v)+\beta^f_{Na}(v)\right)q_n(t) + \alpha^f_{Na}(v), \tag{4}$$

with $n = 1, 2, 3$. The sodium channel also comprises a (slow) deactivation gate that tends to close with increasing trans-membrane voltage. The opening and closing rates of the deactivation gates are given by

$$\alpha^s_{Na}(v) = 0.07\exp\left(-\frac{v}{20}\right), \quad \beta^s_{Na}(v) = \frac{1}{\exp\left((30-v)/10\right)+1}, \tag{5}$$

with the associated two-state master equation describing the state of the deactivation gate

$$\dot{q}_4(t) = -\left(\alpha^s_{Na}(v)+\beta^s_{Na}(v)\right)q_4(t) + \alpha^s_{Na}(v). \tag{6}$$

A sodium channel is open when all three fast gates are open and the deactivation gate is open. In all equations above, the trans-membrane potential is measured in millivolts (mV), and the time is measured in milliseconds (ms). The small size of the ion channel cluster allows us to set the membrane potentials at each channel equal. The equations above are supplemented by an equation for the membrane potential

$$C\frac{dv}{dt} = -g_K(v - v_K) - g_{Na}(v - v_{Na}) - g_L(v - v_L)\,, \tag{7}$$

with the conductance of the sodium system, potassium system and leakage system given by g_K, g_{Na}, g_L, respectively. C denotes the membrane capacitance and v_K, v_{Na} and v_L the Nernst potentials of the ionic systems. Assuming that the densities of the potassium channels ρ_K and sodium channels ρ_{Na} are homogeneous throughout the cluster of area A, we can express g_K and g_{Na} in terms of the conductance of single open channels γ_K, γ_{Na}, i.e.

$$\begin{aligned} \frac{g_K}{A} &= \frac{N_K^{\text{open}}\gamma_K}{A} = \frac{N_K^{\text{open}}}{N_K}\rho_K\gamma_K\,, \\ \frac{g_{Na}}{A} &= \frac{N_{Na}^{\text{open}}\gamma_{Na}}{A} = \frac{N_{Na}^{\text{open}}}{N_{Na}}\rho_{Na}\gamma_{Na}\,. \end{aligned} \tag{8}$$

Dividing (7) by the cluster area, one finds

$$\begin{aligned} \frac{C}{A}\frac{dv}{dt} &= -\frac{N_K^{\text{open}}}{N_K}\rho_K\gamma_K(v - v_K) \\ &\quad -\frac{N_{Na}^{\text{open}}}{N_{Na}}\rho_{Na}\gamma_{Na}(v - v_{Na}) - g_L(v - v_L). \end{aligned} \tag{9}$$

For the following computations we use the characteristic values for the giant squid axon, $\rho_K = 18/\mu m^2, \rho_{Na} = 66/\mu m^2, \gamma_K = 20pS, \gamma_{Na} = 20pS, C/A = 1\mu F/cm^2$, and $g_L = 0.3mS/cm^2$. The fraction of open channels can be obtained at each time step by using a Markov-Monte-Carlo type technique put forward in [13]. Combining this Markov-Monte-Carlo scheme with a (linear) solver for Eq.9, one obtains a spike train of N action potentials at times T_n with the interspike intervals $\Delta T_n \equiv T_{n+1} - T_n$ where $n = 1, ..., N$.

In Fig.1 we show the average interspike interval $< T >$, and the Fano-factor η as a function of the cluster size N, with

$$\begin{aligned} < T > &\equiv \frac{T_l}{N}, \\ \sigma^2 &\equiv \langle \Delta T_n - \langle \Delta T \rangle \rangle^2, \\ \eta &\equiv \frac{\sigma}{\langle \Delta T \rangle}, \end{aligned} \tag{10}$$

where T_l is the length of the spike train.

The average interspike interval, as well as the variance and the Fano factor exhibit a minimum at a cluster size of about $2\mu m^2$. The largest firing rate goes parallel with a minimum in the variance and Fano-Factor, suggesting maximum coherence at the cluster size of about $1\mu m^2$. The power spectra in Fig.2 verify this hypothesis. The power spectrum of the spike train exhibits the largest maximum where the Fano Factor assumes a minimum.

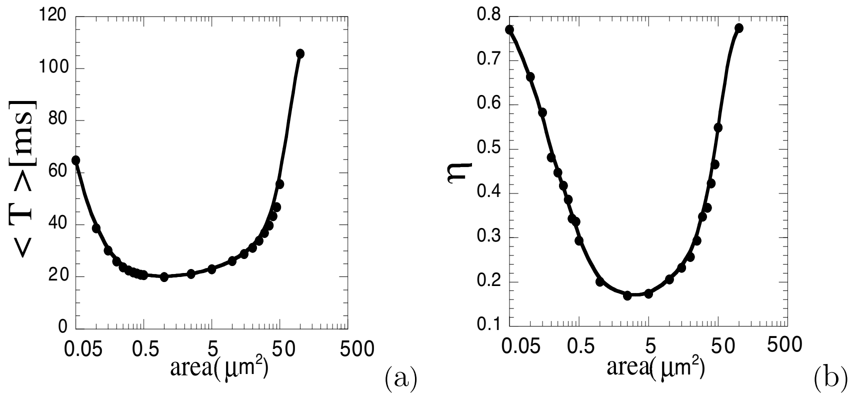

Fig 1. The average interval between two consecutive spontaneous spikes (a) and the Fano factor (b) are shown as a function of the area of the ion channel cluster.

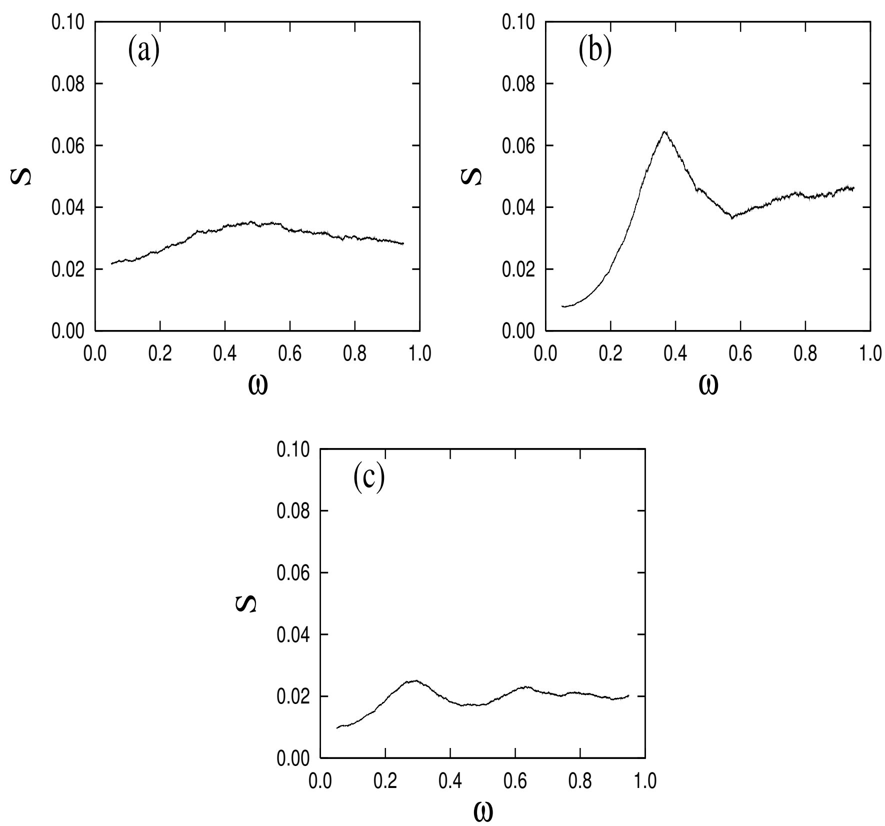

Fig 2. Power spectrum of spike train generated by a cluster of sodium and potassium channels of (a) 0.1 μm^2, (b) 2.0 μm^2 and (c) 50.0 μm^2. The angular frequency ω is measured in units of $2\pi/ms$. The peak occurs at a frequency that corresponds to an interspike interval of about 18ms which is a few millisceonds larger that the refractory time of the deterministic Hodgkin-Huxley model.

3. Spike coherence in a stochastic toy model

We now consider the linear, second order, stochastic differential equation,

$$\begin{aligned}\frac{dx}{dt} &= v,\\ \frac{dv}{dt} &= -\left(\frac{1}{\tau_1}+\frac{1}{\tau_2}\right)v-\frac{1}{\tau_1\tau_2}x+\frac{\sqrt{D}}{\tau_1\tau_2}\xi(t),\end{aligned} \tag{11}$$

with arbitrary, non-zero characteristic times τ_1 and τ_2 and noise strength D, describing the motion of an overdamped Brownian particle (in dimensionless units) in a parabolic potential with white, Gaussian noise $\xi(t)$, i.e.

$$\begin{aligned}\langle\xi(t)\rangle &= 0,\\ \langle\xi(t)\xi(t')\rangle &= 2\delta(t-t').\end{aligned} \tag{12}$$

Whenever the stochastic variable x is crosses the threshold x_0 from below, the system responds with a spike [14]. Denoting the times when the system crosses the threshold from below by t_n, the output $s(t)$ of the threshold system is the train of pulses $\delta(t)$

$$s(t)=s_0\sum_n\delta(t-t_n). \tag{13}$$

The correlation function $K(\tau)$ of the spike train can be expressed in terms of the threshold crossing rate r_{cr} as [14]

$$K(\tau)=\langle s(t+\tau)s(t)\rangle=s_o^2r_{cr}\delta(t-t\prime)+s_0^2g(\tau) \tag{14}$$

where $g(\tau)$ describes spike-spike correlation function and

$$r_{cr}=\frac{1}{2\pi}\exp\left(-\frac{x_0^2}{2\sigma}\right), \tag{15}$$

the threshold crossing rate. The first term on the right hand side of Eq.14 describes white shot noise with a spectral density [14]

$$S(\omega)=s_0^2r_{cr}. \tag{16}$$

Neglecting spike-spike correlations, the power spectrum is predicted flat. It has been shown in Ref. [14] that small corrections due to spike-spike correlations do not generate a peak in the power spectrum.

Our computer simulations confirm this prediction in Fig.3 with $\tau_1=\tau_2=1$. In Fig.3, we show the power spectra of the spike trains obtained by evaluating [10]

$$S(\omega)=\frac{1}{T_l}\left|\sum_n\exp\left(-2\pi i\omega T_n\right)\right|^2 \tag{17}$$

at various values of the noise strength D. The mean interspike interval $\langle T\rangle$, and the Fano factor η are shown in Fig.4 as a function of the noise strength. The variance σ^2 (not shown) decreases faster than the mean interval $\langle T\rangle$ and thus the Fano factor η *decreases with increasing noise strength* D. Thus a decreasing Fano factor in this example does not characterize increased coherence.

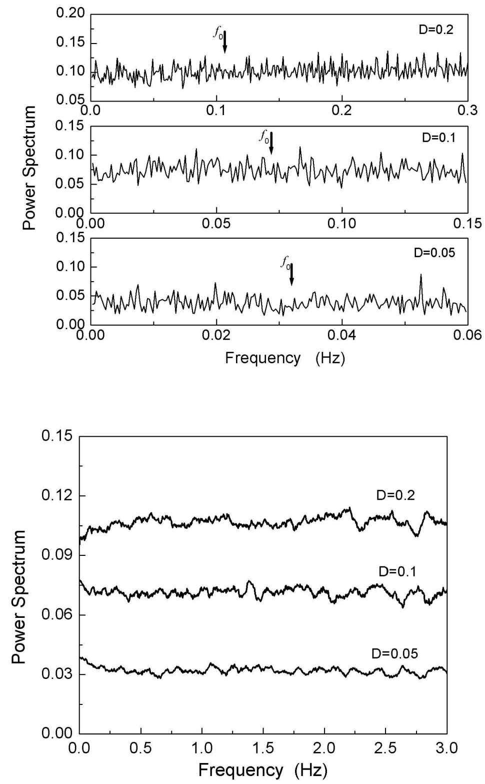

Fig 3. Power spectrum of spike train generated by the stochastic toy model at $D = 0.05, D = 0.1$, and $D = 0.2$ at a threshold of $x_0 = 0.2$. The frequency is measured in inverse units of the time. The fluctuations of the power spectra are due to finite length of the spike trains. The upper panel is focussed on a frequency range which includes the frequencies f_0 that correspond to the inverse average interspike intervals (arrows).

4. Conclusion

In this paper, we have shown that a decreasing Fano factor is not a sufficient indicator of increasing temporal coherence of a spike train. It is therefore necessary to consult the power spectrum in addition to the Fano factor to quantify coherence of spike trains.

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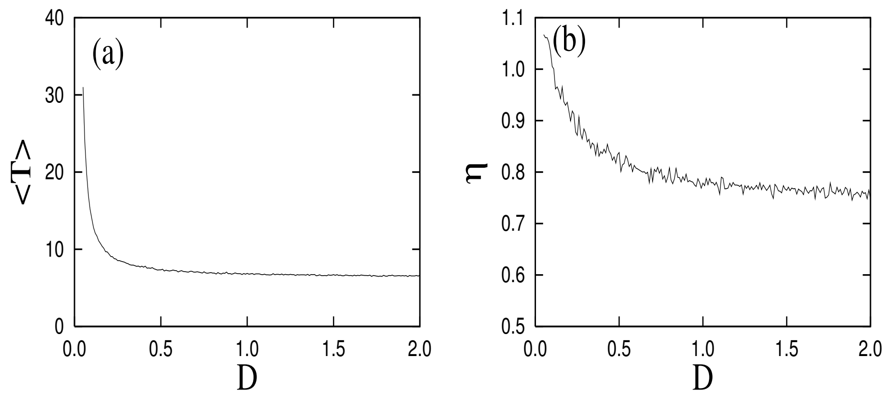

Fig 4. The average interval between two consecutive spontaneous spikes (b) and the Fano factor (b) generated by the stochastic toy model are shown as a function of the noise level D at a threshold of $x_0 = 0.2$.

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