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Different Types of Noise in Leaky Integrate-and-Fire Model of Neuronal Dynamics with Discrete Periodical Input

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Abstract. Different variants of stochastic leaky integrate-and-fire model for the membrane depolarisation of neurons are investigated. The model is driven by a constant input and equidistant pulses of fixed amplitude. These two types of signal are considered under the influence of three types of noise: white noise, jitter on interpulse distance, and noise in the amplitude of pulses. The results of computational experiments demonstrate the enhancement of the signal by noise in subthreshold regime and deterioration of the signal if it is sufficiently strong to carry the information in absence of noise. Our study holds mainly to central neurons that process discrete pulses although an application in sensory system is also available.

Introduction

Generation of spikes and the spatio-temporal patterns they form represent the basic mechanism by which information is exchanged by neurons. Spike sequences, recorded from neurons located in very different structures and under different experimental conditions, suggest the presence of stochastic forces influencing neuronal activity. This random component, generally considered as a noise, can be contained either in the input signal or generated in the target neurons themselves. In communication theories, the term noise usually denotes something negative and blurring the signal. In living systems, the noise can be a message by itself (Cecchi et al. 2000; Lánský and Sacerdote 2001) or its highly desirable part, as shown in articles on stochastic resonance (Moss et al. 1993; Longtin et al. 1994; Bulsara et al. 1996 and many others).

A typical model of single neuron mimics the voltage of its membrane by using an equivalent electrical circuit described by a system of differential equations. The

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integrate-and-fire model is obtained by reducing these differential equations (Abbot and Kepler 1990). The most important simplification implies that the shape of the action potentials is neglected and every spike is considered as an uniform event defined only by the time of its appearance. The description of experimental data in terms of stochastic point processes is the most common method for modeling of spiking data (Johnson 1996). The integrate-and-fire models, despite being considered oversimplified, play their important role in computational neuroscience since they are used as templates for the results obtained in more complex models.

Two general levels of signals can be recognised in the nervous system and consequently in the neuronal models. The strong signals which evoke responses are defined as suprathreshold. The weak signals, which are insufficient to evoke any response, are called subthreshold signals. This classification of the two types of signal is valid only in absence of noise. In this paper we assume that the ideal result is achieved for the suprathreshold signals in absence of noise. It means that the neuron fires only when driven by the signal. The generated spike train is completely reproducible once the initial conditions are known. Introduction of noise in the case of suprathreshold signal destroys this reproducibility and it is an open question up to which extent. Conversely, in absence of noise, the subthreshold signals evoke no response and is a matter of question what are the conditions on the noise which permit the neuron to fire.

The positive effect of the noise on information transfer in nervous system was usually analysed for weakly subthreshold signals. This effort was separated from the situation when the signal is sufficiently strong by itself and the noise has only a negative effect on its transfer. Here we investigate this problem from both sides. It means that we study if the same level of noise which is able to enhance the subthreshold signal has a destroying effect in suprathreshold conditions. To quantify the results we selected a method, independent of the model, which is easy to use in the data obtained in the experiments, and the results of which are easily interpretable.

Deterministic leaky integrate-and-fire model

The simplest realistic model which has been used for describing the voltage, $v(t)$, of neuronal membrane is the deterministic leaky integrate-and-fire (LIF) model,

$$C\frac{\mathrm{d}v(t)}{\mathrm{d}t} = -\frac{(v(t)-v_0)}{R} + i(t), \qquad v(0) = v_0 \tag{1}$$

where $i(t)$ is an input current, C is the membrane capacitance, R is its resistance and v_0 is the membrane resting level, and the initial time corresponds to the instant of the last spike generation. Dividing equation (1) by C and studying instead of the voltage its difference, $x(t)$, with respect to the resting level, we obtain the equation in the form investigated in this paper,

$$\frac{\mathrm{d}x(t)}{\mathrm{d}t} = -\frac{x(t)}{\tau} + \mu(t), \qquad x(0) = 0 \tag{2}$$

where $\mu(t) = i(t)/C$ and $\tau > 0$ is a time constant governing the decay of the voltage back to the resting level according the the membrane capacitance and resistance ($\tau = RC$). Equation (2) has often been used for modeling sensory neurons under constant or a sinusoidal stimulation (e.g., Knight 1972; Scharstein 1979; Bugmann 1991, 1992; Christodoulou and Bugmann 2000; and for a review see Tuckwell 1986). The term $\mu(t)$, appearing in (2), is a representation of an external signal (e.g., light, sound, odorant or input from other neurons) transformed into an internal generator with dimension of voltage *per* time.

Due to the simplicity of equation (2), the action potential generation is not an inherent part of the model (like in more complex models) and for this purpose it is necessary to impose firing threshold S, such that $S > 0$. The LIF model fires whenever the depolarisation $x(t)$ reaches the threshold S. The depolarisation $x(t)$ is then instantaneously reset to zero and its time-evolution starts anew in accordance with equation (2). The time elapsed between two consecutive crossings of the threshold (spikes) defines an interspikes interval (ISI). If the signal $\mu(t)$ is also reset following the depolarisation, we call such a signal endogenous whereas if it continues independently in its evolution after the spike generation, it is called exogenous (Lánský 1997).

For constant signal, $\mu(t) = \mu$, the relation between the intensity of stimulation and the output frequency (defined as the inverse of the ISI), is

$$f(\mu) = \begin{cases} \dfrac{1}{\tau \ln\left(\dfrac{\mu\tau - S}{\mu\tau}\right)} & \text{for} \quad \mu > S/\tau \\ 0 & \text{for} \quad \mu \leq S/\tau \end{cases} \tag{3}$$

and assuming for simplicity that there is no refractory period after spike generation, the firing frequency tends to infinity for $\mu \to \infty$. An important feature of relation (3) between firing frequency and input intensity is discontinuity of the derivative of $f(\mu)$ at point S/τ. Location of this discontinuity separates sub- and suprathreshold stimulation in this model. For

$$\mu\tau > S \tag{4}$$

neuron fires regularly while in the opposite case it remains silent.

For signal consisting of regularly appearing pulses (for example, short stimulation pulses or a sequence of spikes on excitatory synapse connected to the neuron, if a higher order neuron is concerned) $\mu(t) = a\sum_{i=1}^{\infty} \delta(t - id)$ where $d > 0$ represents inter-pulse duration, $a > 0$ pulse amplitude and δ is the Dirac delta function, model (2) behaves as follows. The voltage has a sequence of depolarising steps of size a. Steps are separated by intervals of constant length, d, and the depolarisation decays to the resting level between two jumps. For consistency with other papers on this topic, we identify the jumps with the excitatory postsynaptic potentials (EPSPs), although they could be caused, as mentioned, by the external stimulation in sensory neurons. Also the model with EPSPs operates in two distinct regimes, firing or silence. A condition analogous to condition (4) for suprathreshold behavior is

$$\frac{a}{1-\exp(-d/\tau)} > S \tag{5}$$

In the model with jumps, $\mu(t) = a\sum_{i=1}^{\infty}\delta(t-id)$, the crossing of the threshold can arise only at a moment of EPSP generation because the potential decays elsewhere. As a consequence, the ISI can only be an integer multiple of d. There is no simple analytical counterpart of relation (3), (Tuckwell 1986). In contrast to model (2), here two input parameters, a and d, determine the output frequency. If simultaneously $a \to 0$ and $d \to 0$ in such a way that $a/d \to \mu$, then both models coincide. In Fig. 1 is illustrated a sample path (dashed line) under the conditions $a = 2.5$ mV, $d = 5$ ms and $\mu = 0$.

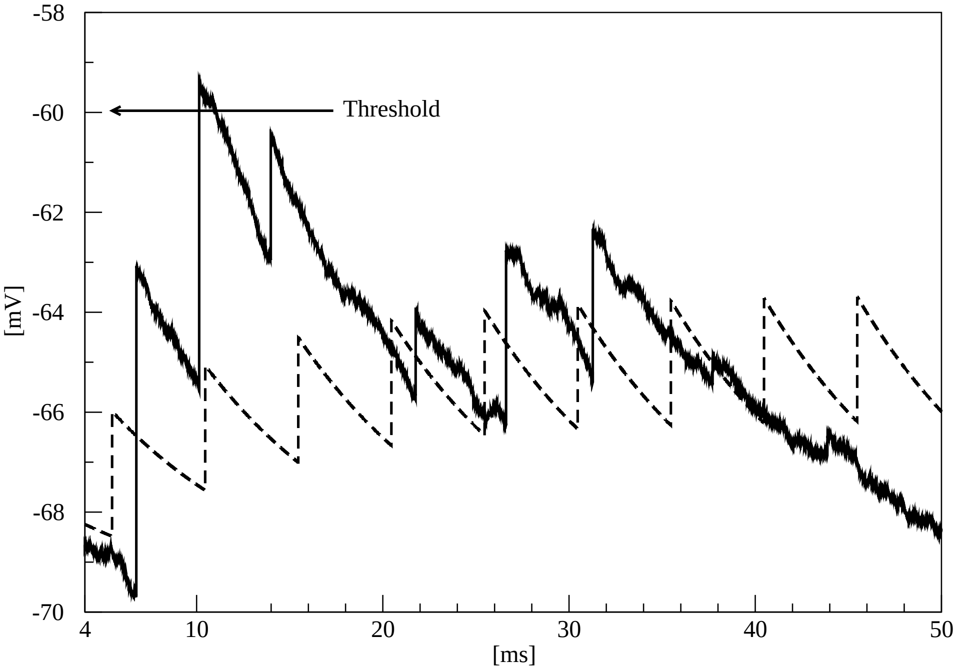

Figure 1. Example of the effect of noise on membrane potential in absence of threshold. The voltage time course in absence of noise (i.e., $\sigma_a = 0$, $\sigma_d = 0$ and $\sigma_\mu = 0$) is shown by dashed line. The stimulus applied here is composed of voltage jumps (EPSPs) with constant amplitude ($a = 2.5$ mV) and constant inter-jumps intervals ($d = 5$ ms). The continous line is the voltage time course if stimulation has variable amplitude ($\sigma_a = 3$), the inter-jumps interval is jittered ($\sigma_d = 2$) and $\sigma_\mu = 0.2$. The arrow shows a point of possible crossing of the threshold if it would be imposed. Such crossing would apear only due to the application of the noise. In both the examples $\tau = 10$ ms and simulation time step is 0.001 ms.

For a mixture of the two signals (continuous and pulses), $\mu(t) = a\sum_{i=1}^{\infty}\delta(t - id) + \mu$, there are again EPSPs of size a appearing at constant intervals d but in the interpulse period the membrane depolarisation tends exponentially, with the time constant τ, to the level $\mu\tau$. Under this condition, the component creating discontinuities in the membrane depolarisation can be interpreted as the activation of synapses close to the trigger zone of the neuron and the continuous component as the contribution of integrated activity of synapses located on the neuronal dendrite. Analogously to the previous versions, this model also operates in two distinct regimes. Combining inequalities (4) and (5), it is defined by the triplet of input parameters $\{\mu, d, a\}$, for which

$$\mu\tau + \frac{a}{1 - \exp(-d/\tau)} > S \tag{6}$$

Now depolarisation can cross the threshold either by the EPSP or by the continuous force μ. There is no general rule to determine which of these two situations will produce the firing event and only a special case can be distinguished when the threshold is above asymptotic depolarisation corresponding to the constant input, $\mu\tau < S < a[1 - \exp(-d/\tau)]^{-1}$. Of course, in this case the firings are caused by the EPSPs only.

The ISIs are constant in model (2) only under special conditions on the input function $\mu(t)$. Fortunately, in three above considered cases ISIs are not constant only in presence of EPSPs and if simultaneously the threshold crossing is due to the constant component μ. In this case, the waiting time to the first EPSP after the spike is not equal to d but to the remaining part of d which is the difference between an integer multiple of d and the previous ISI (for example, if ISI equals to 31 and $d = 7$, then the time to the next EPSP is 4). The ISIs are constant in all other cases and there is no difference between endogenous and exogenous stimulation.

Stochastic model

A simple phenomenological way to introduce stochasticity into the deterministic LIF model is by adding noise terms in equation (2). For memoryless stochastic inputs, it is to combine the original Stein's model (Stein 1965) with the Ornstein–Uhlenbeck model which is Stein's model diffusion approximation. The model is described by a stochastic differential equation,

$$\frac{\mathrm{d}X(t)}{\mathrm{d}t} = -\frac{X(t)}{\tau} + \mu\,(t) + \sigma\xi(t) + G(t), \qquad X(0) = 0 \tag{7}$$

where $\xi(t)$ represents a δ-correlated Gaussian noise with zero mean and strength 2σ, and $G(t)$ is a stream of delta pulses of size A the occurrence of which follows a Poisson process with intensity ω, $\mu(t)$ is any deterministic signal.

In contrast to the previous Section, the membrane depolarisation X undergoes random excursions to the firing threshold S. Again, as soon as the threshold is reached, a firing event occurs and the membrane depolarisation is reset to the resting level. The ISIs are identified with the first-passage time of X across S,

$$T = \inf \{ t \geq 0,\ X(t) > S,\ X(0) = 0 < S \} \tag{8}$$

The properties of the random variable T can be compared with properties of experimentally observed ISIs. If the evolution of the membrane depolarisation is influenced by the state of the input prior the reset, then the length of the current ISI is influenced by the length of the previous one (inputs with memory – temporally correlated) and ISIs are correlated variables. Therefore the Gaussian white noise $\xi(t)$ and the stream of Poissonian pulses are the only suitable for achieving a renewal process on the output of the model neuron.

In general, the distribution of T represented (for example) by the probability density function is investigated. When the distribution is too difficult to obtain, the analysis is usually restricted to its moments, M_n, primarily the mean $E(T) = M_1$ and the variance $\mathrm{Var}(T) = M_2 - M_1^2$. The reciprocal relationship between the firing frequency on one hand and the mean ISI on the other leads to plotting of reciprocal value of $E(T)$ *versus* the intensity of stimulation μ as a stochastic counterpart of relation (3).

The diffusion model, equation (7) with $\omega = 0$, is probably the most commonly used neuronal model. In the case of constant input, $\mu(t) = \mu$, it is called the Ornstein–Uhlenbeck model and its output is a renewal process (for the results on this model see Ricciardi and Sacerdote 1979; Lánský and Rospars 1995). The shot noise model, equation (7) with $\sigma = 0$, is used in the neuronal context without any restriction on size of A (can be both negative and positive mimicking excitatory and inhibitory postsynaptic potentials). Model (7) combining diffusion and randomly distributed EPSPs, was introduced by Tuckwell (1986), further studied by Musila and Lánský (1992) and by Deco and Schurmann (1998) in the context of stochastic resonance.

In this paper, we focus on equation (7) assuming the absence of the Poissonian input $G(t)$ which means that formally we put $\omega = 0$. There are three reasons for this assumption. At first, the model with Poissonian input was studied in Chapeau-Blondeau et al. (1996). At second, while there are clear evidences how and why Gaussian white noise can be present in membrane fluctuations, Poissonian noise is based only on the assumption that some of the input sites are not relevant for the signal. Serious doubts can be raised against this assumption. At third, this input changes directly the input frequency, which is the basic parameter under investigation.

Periodic input

We assume that the signal contains a periodic component of discrete form and that this periodic component is subject to two types of random disturbances. Stochastic

LIF has been studied on many occasions not only for constant input μ but, first of all, under the influence of periodic input composed of a constant and a sinusoidal component (Bulsara et al. 1996; Shimokawa et al. 1999, 2000; Plesser and Geissel 2001 and many others). Recently a detailed comparison of the effect of noise for subthreshold stimulation in dependency on exogenous *versus* endogenous with sinusoidal input in LIF model has been presented (Shimokawa et al. 1999; Plesser and Geissel 2001). Other results on periodically stimulated LIF can be found in (Barbi et al. 2003). The studies considering the periodic part composed of equidistant pulses are less frequent (Chapeau-Blondeau et al. 1996). In this paper we consider only the cases in which ISIs are constant and form renewal processes in absence of noise (intervals between threshold crossing are independent and identically distributed random variables) and the cases when the noise is present.

In the sequel we investigate equation

$$\frac{\mathrm{d}X(t)}{\mathrm{d}t} = -\frac{X(t)}{\tau} + \mu + A\sum_{i=1}^{\infty}\delta(t-iD) + \sigma_\mu\xi(t), \quad X(0)=0 \tag{9}$$

where the input signal has constant level μ, A represents random amplitudes of input pulses, D is random inter-pulse interval. A sample path of the depolarisation given by equation (9) is illustrated in Fig. 1 in absence of the firing threshold. We can see that if the noise is applied (continuous line) the regular behaviour of membrane potential is altered and the applied noise can drive the membrane potential above the threshold (see the arrow in Fig. 1). The statistics of threshold crossing (spikes) have been analysed in terms of interspike intervals (ISI) for each type of noise and for the simultaneous application of all the three types of noise. The signal in model (9) is represented by frequency of pulses, $1/E(D)$, and by μ. It is assumed that A is normally distributed with mean a and variance σ_A^2, $A \sim N(a, \sigma_A^2)$. The constant interval between the pulses is jittered in a similar way, $D \sim N(d, \sigma_D^2)$. We assume that $\sigma_D \ll d$, to ensure that realisations of D are positive. Model (9) differs from the scenario investigated by Chapeau-Blondeau and Godivier (1996) where the noise was Poissonian and therefore changed systematically the input frequency. The jitter into timing of the incoming EPSPs was introduced in a study by Marsalek et al. (1997). If the noise is only on A or D then the output process is a renewal process and crossings appear only in times of EPSP generation. It means that the ISIs are multiples of d or its jitter. With positive μ and white noise the situation is different. However, if amplitude of white noise is small, it can be neglected, otherwise we would have to distinguish between endogenous and exogenous stimulation.

Numerical simulation

Simulation was carried by using a C++ program. The resting potential was fixed at −70 mV, which is a resting level common to several types of pyramidal neurons, the threshold was set to −60 mV and the membrane decay time constant τ was taken equal to 10 ms. These parameters, although biologically reasonable, are not of great importance for the general form of the model. Their values can affect the absolute values of ISIs (and hence the scale in which results can be observed) but not the form of their distribution.

Three supra and three subthreshold conditions were considered for each of the above parameters. The program computed the mean value of EPSP by solving the following equation

$$\mu\tau + \frac{a}{1 - \exp(-d/\tau)} = S + b \tag{10}$$

for unknown a, ($b = -0.1, -1, -2, +0.1, +1, +2$), and thus the maximum value of the membrane voltage would be $S + 0.1$ mV, $S + 1$ mV and $S + 2$ mV in the suprathreshold experiments, and $S - 0.1$ mV, $S - 1$ mV and $S - 2$ mV for the subthreshold experiments (in the following denoted respectively as $S_{+0.1}$, S_{+1}, S_{+2}, $S_{-0.1}$, S_{-1} and S_{-2} experiments). The value of d was fixed to 5 ms while the constant input μ was fixed to 0.0 mV, or 0.1 mV. All statistics were made on 10,000 ISIs for each type of noise tested and for each of the above conditions. Simulation time step was 0.001 ms. The noise amplitude were respectively $\sigma_A \in (0, 5)$, $\sigma_\mu \in (0, 5)$ and $\sigma_D \in (0, 2)$. For each of these intervals, σ was tested with increments 0.1. We are aware that simulation of the first-passage-time density for stochastic diffusion processes may be unreliable as, at least for some parameters (rare crossings are produced by low noise), it overestimates the exact first-passage time (Lánský and Lánská 1994). Therefore, the simulation procedure was checked using the shorter step and very low noise cases were excluded.

Measure of the input-output reliability

Before going into the comparison of the effect of noise in the different computational experiments, we selected a suitable method for this purpose. The method, introduced in Rodriguez and Lánský (2000), checks the effect of noise in both sub- and suprathreshold conditions. It is based on the comparison of firing pattern in absence of noise with that which is induced by noise. There is no output in the absence of noise for the subthreshold conditions. The ideal result can be achieved by increasing the signal by adjusting the parameters in such a way that the signal is at least minimally suprathreshold. Then, we can return to our noisy subthreshold signal and measure the distance between the ideal output and that produced under the effect of the noise. If for suprathreshold stimulation in absence of noise ISI = const. = θ, a measure of noise-induced cooperative effect, or noise-induced distortion, can be taken as

$$\Delta_m = \int_0^\infty \left| x - \theta \right|^m f(x)\mathrm{d}x \tag{11}$$

where $m > 0$ and f is the ISI probability density. The minimum of Δ_m equal to zero is achieved for regular firing at period θ, $f(x) = \delta(x - \theta)$.

For $m = 2$, relation (11) defines the mean squared distance, however, other values of m can also be considered. It is obvious that Δ_m is less sensitive (especially for large m) to double firings within one period than to missing one or, even worse, several periods in a row without a spike. If the mean ISI is θ, $E(T) = \theta$, and $m = 2$, then Δ_2 gives the variance of the ISI, otherwise

$$\Delta_2 = \mathrm{Var}(\mathrm{ISI}) + \Big(E(T) - \theta\Big)^2 \tag{12}$$

which has an intuitive interpretation (the distance is given by the variability of ISIs and the squared distance between mean ISI and θ). To estimate Δ_m from simulated ISIs, $x_i (i = 1, \dots, n)$,

$$\widehat{\Delta}_m = \frac{1}{n} \sum_{i=1}^{n} \big| x_i - \theta \big|^m \tag{13}$$

is evaluated. The value $m = 1$ was chosen and the quantity denoted by Δ. The results for $m = 2$ were very similar and this suggests that there are no extremal values among ISIs. The value of θ for the suprathreshold conditions was the constant ISI obtained for $S_{+0.1}, S_{+1}$ and S_{+2} experiments in absence of noise. For the subthreshold condition, the value of θ was the constant ISI obtained for $S_{+0.1}$ condition.

In addition to the measure introduced above we also studied the behavior of the mean ISI and its coefficient of variation CV, defined as ratio $\sqrt{\mathrm{Var}(T)}/E(T)$. If the output is characterised by constant ISIs for suprathreshold stimulation, then any deviation from this constant length and any increase in the variability of ISI suggests that the output signal is corrupted by noise.

Results

Three sources of noise are present in the model given by equation (9); the Gaussian white noise with amplitude σ_μ, the jitter in timing of the EPSPs with standard deviation σ_D and the fluctuation of the amplitudes of the EPSPs with standard deviation σ_A. These three types of noise were analysed separately taking into account noise on one of the signal components and showing the effect on mean ISI, its CV and Δ. The results outline different effect of noise when the sub- or suprathreshold conditions are tested.

For the timing of pulses, D, in all cases the mean ISI decreases while σ_D increases (Fig. 2A). For $S_{-0.1}$ condition, a small value of noise ($\sigma_D = 0.2$) is sufficient to gain the firing. For the conditions S_{-1} and S_{-2} to gain the same effect larger values of σ_D are necessary (respectively $\sigma_D = 1$ and $\sigma_D = 1.7$). For the suprathreshold conditions (Fig. 2B) the decrease in the mean ISI is apparent only for $S_{+0.1}$ case, while for S_{+1} and S_{+2} the effect of noise on D does not substantially affect the spiking frequency. The other statistical measures also show different behavior for sub- and suprathreshold conditions. The mean absolute difference Δ

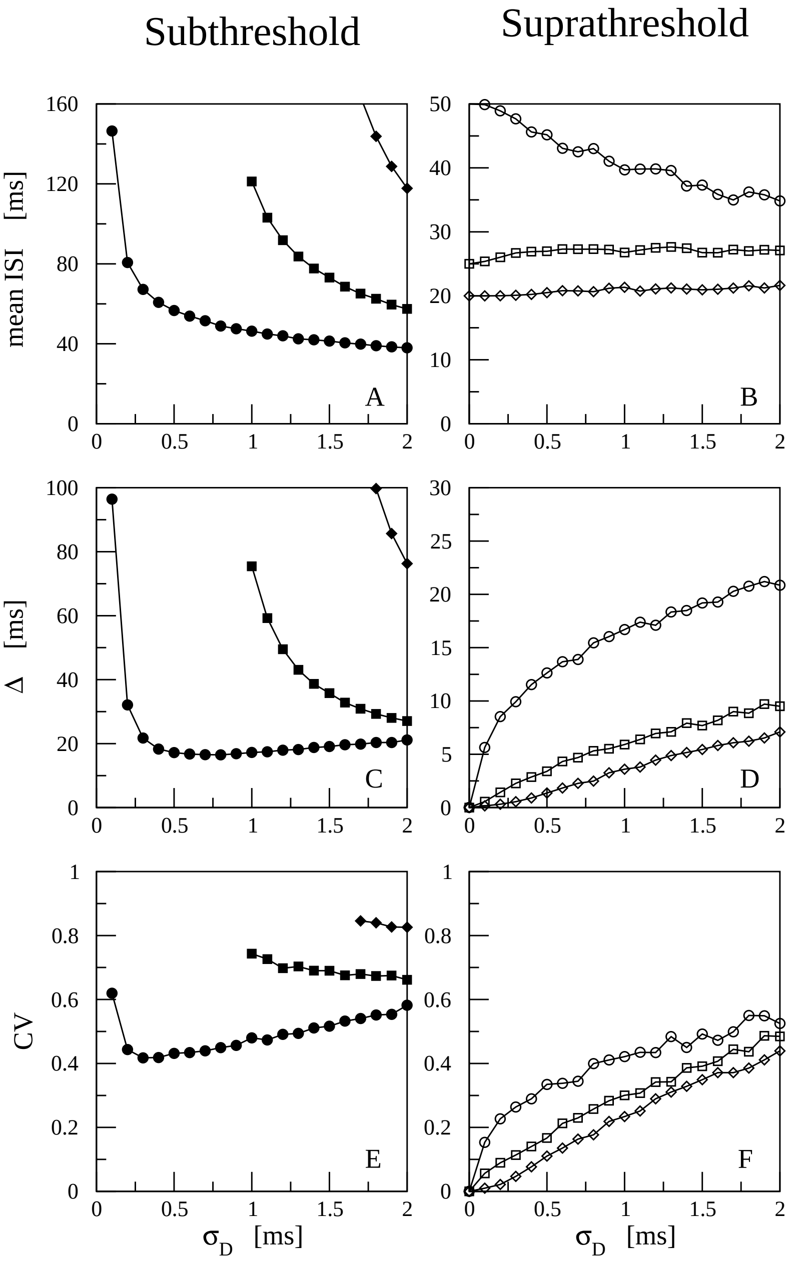

Figure 2. Effect of noise applied on time intervals separating EPSPs under different conditions. Left column (filled symbols) shows subthreshold experiments and the right column (empty symbols) the suprathreshold experiments. Circles denotes ($S_{-0.1}$, $S_{+0.1}$), squares (S_{-1}, S_{+1}) and diamonds (S_{-2}, S_{+2}) conditions. Top row, mean ISI in dependence on σ_D; middle row, Δ in dependence on σ_D; bottom row, CV in dependence on σ_D.

always increases for suprathreshold conditions as well as the CV (Figs. 2D and 2F), indicating that the noise increases variability of ISIs. Of course, most sensitive to the noise is the case $S_{+0.1}$ where the largest variability with respect to other conditions is observed (see Fig. 2D). In subthreshold conditions, the noise at first quickly decreases the variability while with larger noise it starts to grow again. This effect is apparent for $S_{-0.1}$ experiment but cannot be well observed in other two cases.

If compared with noise on D, the noise on A produces a sharper reduction of the mean ISI in both sub- and suprathreshold conditions (Fig. 3A,B). For the suprathreshold conditions, the variability quantified by Δ and CV seems to be similar to that produced by noise on D. For the subthreshold condition $S_{-0.1}$, a minimal level of variability is apparent in the range by $\sigma_A \in (0.2, 0.4)$. In this interval the mean ISI is comparable with the constant ISI obtained for the $S_{+0.1}$ condition without noise ($\sim$50). No minimal level of variability is clearly visible for the conditions S_{-1} and S_{-2}.

Fig. 4 shows the results when applying white noise in absence of a constant input ($\mu = 0$). Similar results are obtained for $\mu = 0.1$ (results not shown). For both values of μ and for both sub- and suprathreshold conditions, the curves giving dependency of mean ISI on σ_μ are steeper than those obtained for other types of noise. In all cases, for large values of noise there is a high spiking frequency with mean ISI comparable and even shorter than the constant ISI obtained for S_{+1} and S_{+2} conditions in absence of noise. The measure Δ behaves differently in dependence of the value of μ. For $\mu = 0.0$, for all the subthreshold conditions there is an interval of σ_μ, for which a minimal variability can be observed and its location depends on the experimental condition (i.e., if $S_{-0.1}, S_{-1}$ or S_{-2}; see Fig. 4C). This effect is not apparent for $S_{-0.1}$ condition if the CV is considered but is still evident for the S_{-1} and S_{-2} conditions (Fig. 4E). It can be considered as a stochastic resonance effect strongest among these three noise situations. For $\mu = 0.1$, this effect is less apparent. There still remains a minimal value for the CV in the case of S_{-1} and S_{-2}, while it is strongly reduced if Δ is considered (figures not shown). In both cases (i.e., for $\mu = 0.0$ and $\mu = 0.1$) for suprathreshold experiments noise increases variability depending on the experimental conditions being most sensitive for $S_{+0.1}$. For large values of σ_μ, in the subthreshold conditions the mean ISIs decreases and becomes comparable with those obtained in suprathreshold conditions S_{+1} and S_{+2}.

From the above results we confirmed that the most sensitive conditions for the effect of noise are those very close to the threshold. For these conditions (i.e., $S_{+0.1}$, and $S_{-0.1}$) we performed additional computational experiments where different types of noise were applied simultaneously. An example is given in Fig. 5, where the results of using noise on A and then adding also noise on D and/or on μ, are shown. A clear evidence of these experiments is that noise decreases consistently the mean ISI both in sub- and suprathreshold cases. The effect of adding two or three different types of noise is additive (although not proportionally) in reducing the mean ISI. The addition of different types of noise does not change the position of minimal variability for the subthreshold condition which always corresponds to

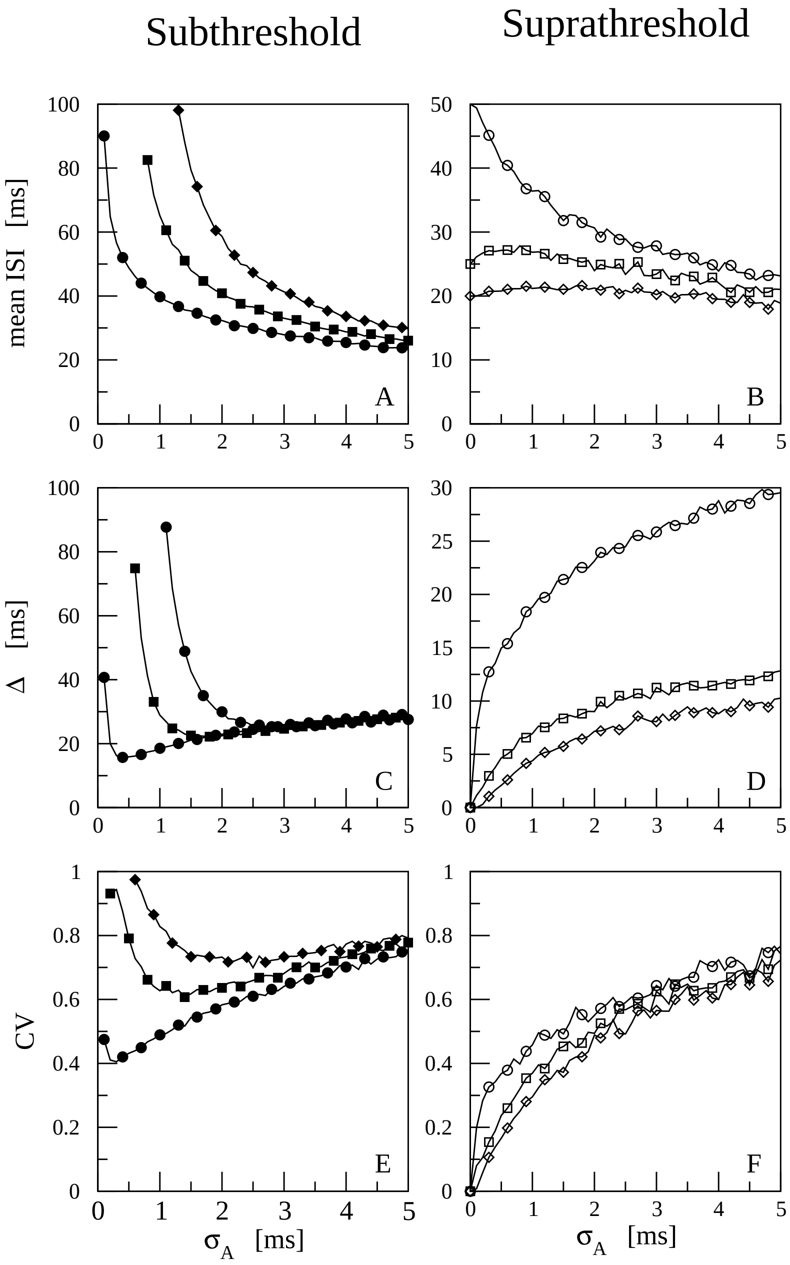

Figure 3. Effect of noise applied on EPSP amplitude under different noise conditions. Left column (filled symbols) shows subthreshold experiments and the right column (empty symbols) the suprathreshold experiments. Circles denotes ($S_{-0.1}$, $S_{+0.1}$), squares (S_{-1}, S_{+1}) and diamonds (S_{-2}, S_{+2}) conditions. Top row, mean ISI in dependence on σ_A; middle row, Δ in dependence on σ_A; bottom row, CV in dependence on σ_A.

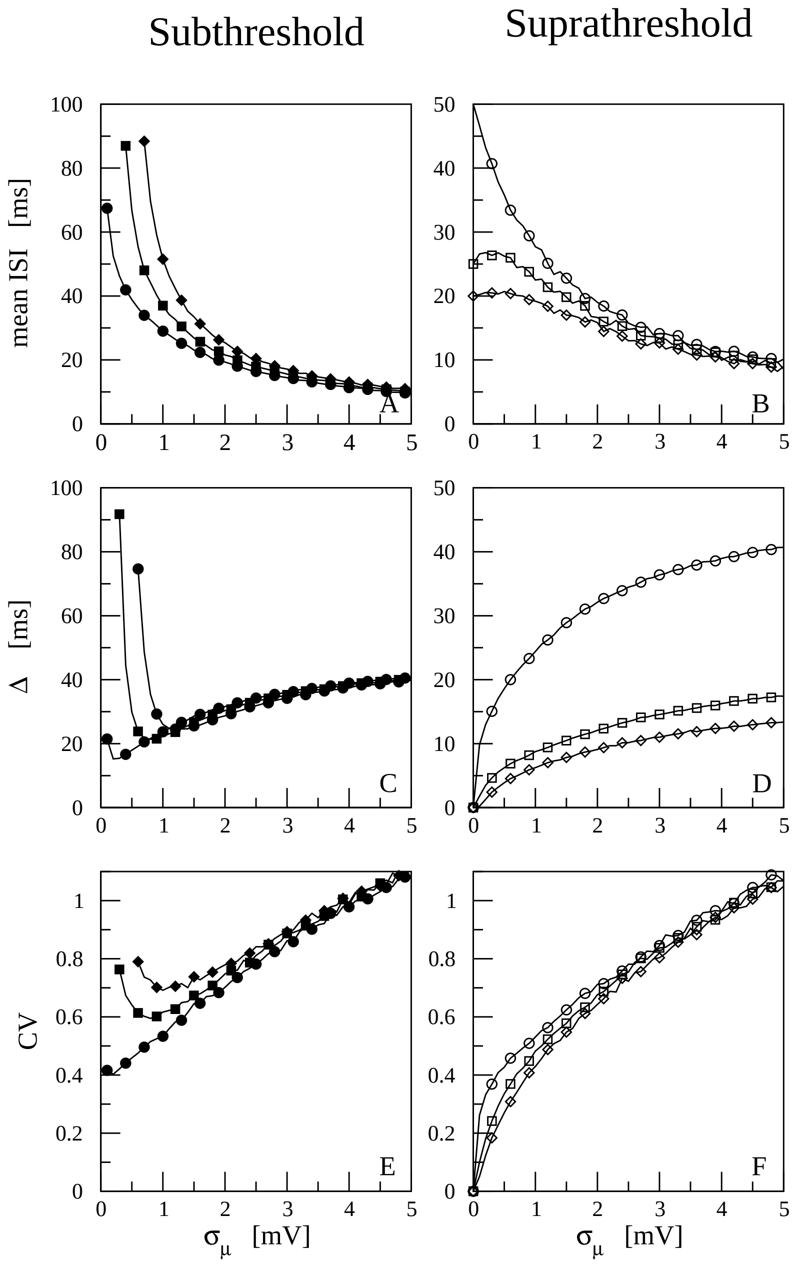

Figure 4. Effect of white noise. Left column (filled symbols) shows subthreshold experiments and the right column (empty symbols) the suprathreshold experiments. Circles denotes ($S_{-0.1}$, $S_{+0.1}$), squares (S_{-1}, S_{+1}) and diamonds (S_{-2}, S_{+2}) conditions. Top row, mean ISI in dependence on σ_μ; middle row, Δ in dependence on σ_μ; bottom row, CV in dependence on σ_μ.

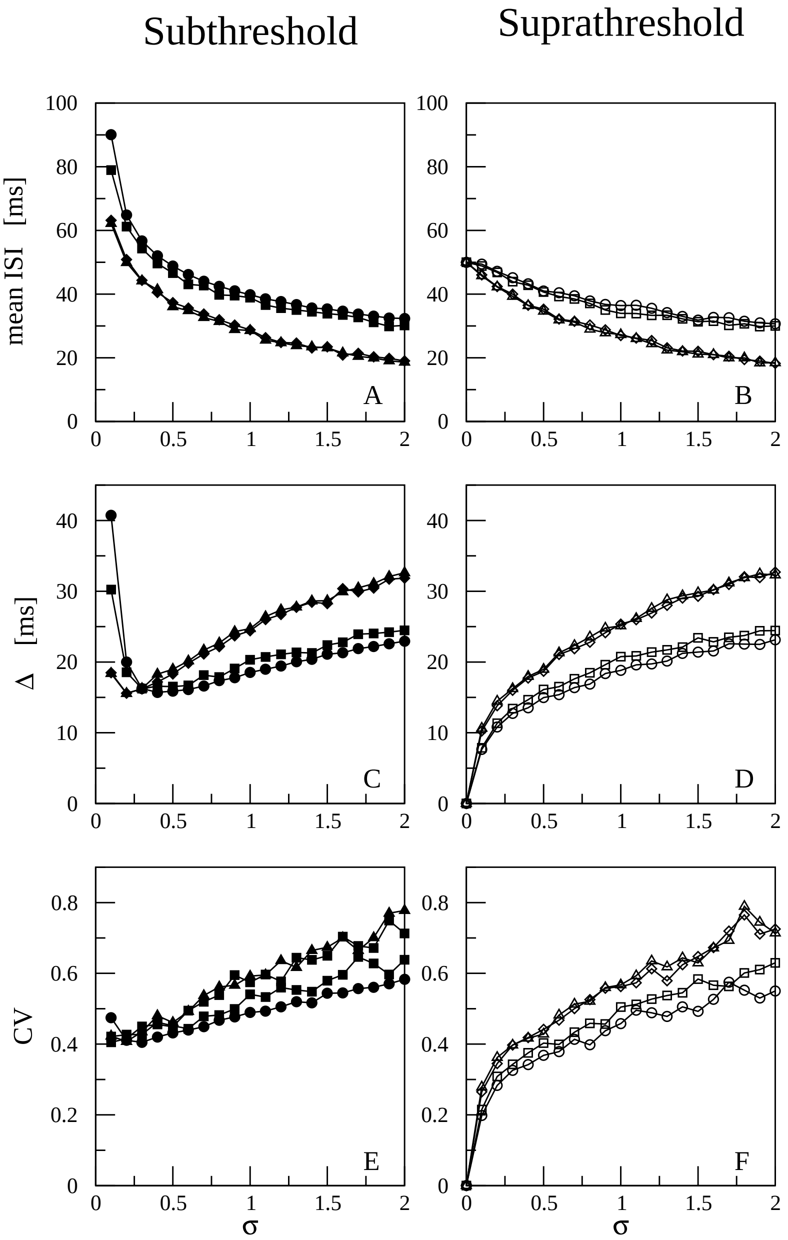

Figure 5. Effect of combined noise for near threshold conditions. $S_{-0.1}$ (left column, filled symbols) and $S_{+0.1}$ (right column, empty symbols). Circles denote noise on EPSP, squares noise on EPSP combined with noise on time interval between EPSPs, diamonds noise on EPSP combined with white noise, triangles denote noise on EPSP combined with noise on time interval between EPSPs and white noise. Top row, mean ISI in dependence on σ; middle row, Δ in dependence on σ; bottom row, CV in dependence of σ.

the level of noise which produces the same mean ISI obtained in S_{+1} condition with no noise (∼50).

In Fig. 5 the same scales for sub- and suprathreshold conditions are used to outline that for large values of σ, the means ISI tend to the same values which depend only on the type of noise and are independent from the condition (sub- and suprathreshold; compare Figs. 5A and 5B). Also the parameters used to test the variability (Figs. 5C and 5D for Δ and Figs. 5E and 5F for CV) show that the system, for large values of σ, tends to the same level of variability which depends only on the type of noise applied.

Discussion

We investigated three realistic types of noise. Their effect has been studied in sub- and suprathreshold conditions. Our results can be partly compared with the results of Deco and Schurmann (1998) who studied model (7) in absence of constant input, $\mu = 0.0$, and for a constant EPSP size, $a = 1$. In their Fig. 1 they plot, for $\tau = 1$ and $\tau = 10$, dependencies of input frequency $(1/d)$ for which the enhancement of the signal by noise is the largest. It follows from their figure that for $\tau = 1$ holds $(1/d)_{\rm opt} = S/\tau - 0.5$, while for $\tau = 10$, it is almost $(1/d)_{\rm opt} = S/\tau$ (equation (1) gives these relations in the first approximation). In other words, increasing τ, the position of the effect moves close to the threshold. Further, in both cases this dependency is linear.

Chapeau-Blondeau and Godivier (1996) considered periodic train of input pulses corrupted by a white noise. They illustrate the results on LIF model with periodical EPSP input and Gaussian white noise. In addition, they assume reset of the input in the moment of spike generation, on other words endogenous periodicity of the signal, and show the stochastic resonance effect. Similarly Chapeau-Blondeau et al. (1996) studied LIF model but with Poissonian noise. Marsalek et al. (1997) investigated the effect of jitter in the timing of the input on the variability of the neuronal output. In contrast to present study, they considered only suprathreshold situation and did not investigate possible enhancement of the signal by noise.

Standard methods for quantifying synchronisation of the output with input is based on the cycle histograms presenting the spikes with respect to the phase of the driving force. This method, suitable mostly for sinusoidal stimulation, stresses the synchronisation but neglects missing periods of firing. In other words, a spike fired after a long period of silence has the same effect, if well synchronized with the signal, as the spike fired during the first period after the reset. For this reason we have not applied this method.

Another method to check the role of noise is based on the comparison of values of the ISI probability density, g, at the value d (the period of stimulation) in dependency of the amplitude of the noise and the critical noise was declared that reaching the maxima at $g(d)$. This method was applied previously for LIF model with sinusoidal input by Bulsara et al. (1996) and by Shimokawa et al. (1999) and

Barbi et al. (2003). This method is computationally demanding since the density of ISIs needs to be evaluated.

The most common measure of stochastic resonance – the signal-to-noise ratio – was used by Chapeau-Blondeau et al. (1996). The method is not suitable for the exogenous periodicity which violates the renewal character of the output. The method following from the framework of information theory was used by Deco and Schurmann (1998). It is based on the estimation of the transmitted information which is given by the mutual information between input and output signals. This method is also suitable for the renewal processes at the output. A measure based on Fisher information was also proposed and another criteria can be based on correlation or coherence between the input and output. Apparently, there is a complete range of methods for quantification of the noise effect in signal transmission and the choice must depend on the purpose, conditions and interpretability of the results. The main advance of the methods applied here is its simplicity and transparency.

Conclusions

A general conclusion is that for the small amplitudes of noise, different effects on neural firing in sub- and suprathreshold conditions are observed. This holds for all types of tested noise. The effects are different both quantitatively and qualitatively. For weakly subthreshold condition, the noise sometimes increase the robustness of the system. In contrast, in the suprathreshold conditions, the noise always destroys regularity of the firing pattern. Further one can easily determine if the stimulation is sub- or suprathreshold. For strongly subthreshold conditions (far below the threshold) the effect of a weak noise is negligible otherwise it produces sufficient firing activity. For suprathreshold stimulations the noise reduces firing regularity proportionally (nonlinear) to the stimulation level.

For large values of noise, the effects become independent from the system condition and depend only on the type of noise. This result is strongly related to the fact that increasing noise always increases frequency of spikes (see Figs. 1 and 3A,B). Then for a high frequency one cannot distinguish a neuron which receives a subthreshold or suprathreshold input.

Minimal values of variability, as measured by Δ or CV, can be observed for the conditions which produce relatively low frequency of spikes. The same is not so evident for those conditions which produce high frequency of spikes for the low levels of σ. When the frequency increases after a limiting point, the increase become a linear function of σ and then minimal values disappear. Being μ proportional to the dendritic input in the LIF model, the results ofthe present experiments show that this can be very powerful on the spike emission when a large number of desynchronised (noise) synapses act on the neuron. This is even more evident if we consider the cases of single type of noise application with $\mu = 0.0$ (balanced excitation and inhibition). If this input is applied to several neurons in a neural network, then the outcome effect can also be to synchronise the network (Rodriguez et al. 2003).

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