

Suppression of noise in FitzHugh–Nagumo model driven by a strong periodic signal

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Abstract

The response time of a neuron in the presence of a strong periodic driving in the stochastic FitzHugh–Nagumo model is investigated. We analyze two cases: (i) the variable that corresponds to membrane potential is subjected to fluctuations, and (ii) the recovery variable associated with the refractory properties of a neuron is noisy. The influence of noise sources on the delay of the response of a neuron is analyzed. In both cases we observe a resonant activation-like phenomenon and suppression of noise: the negative effect of fluctuations on the process of spike generation is minimal near the resonance region. The phenomenon of noise enhanced stability is also observed in both cases. The role of the initial phase of the periodic driving is examined.

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1. Introduction

The investigation of influence of various external perturbations on the generation of electrical pulses in neurons has attracted great attention in the last ten

years [1–8,10,14,15]. The FitzHugh–Nagumo (FHN) model is one of the simplified modifications of widely known Hodgkin–Huxley model, that describes the neuron dynamics and in general the dynamics of excitable systems in different fields, such as kinetics of chemical reaction and solid state physics [2,3,9,10]. From a mathematical point of view the FHN model is easy to investigate, nevertheless many effects observed in neural cells are qualitatively contained in it. That is why this model is widely used in the literature. Most of

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the previous papers analyzed the influence of noise on FHN model in the absence of any periodic forcing (coherence resonance) [2,3], or in a subthreshold regime (stochastic resonance, etc.) [4–6]. For strong driving it was shown by several authors that the presence of noise has only a detrimental effect on the encoding process [7,8]. However, how to minimize the effect of fluctuations in a strongly driven FHN model, in order to decrease the delay of transmission of an external information in neuronal systems, is still an open question.

With the aim to answer this question we investigate the influence of noise on the appearance time of a first spike in the output of FHN model, subjected to periodic driving in suprathreshold regime. We call this time the response time. We show that the negative influence of noise on the spike generation can be significantly minimized. We analyze the behaviors of the mean response time (MRT) versus both the driving frequency and the noise intensity. We find that a resonant activation-like effect [11] and the noise enhanced stability (NES) phenomenon occur [12]. The role of these noise-induced effects on the response time of a neuron, in the presence of a strong periodic driving force, is investigated. Specifically the MRT and its standard deviation have a minimum as a function of the driving frequency, minimizing the transmission delay. The NES effect, however, increases the average response time of the neuron. We will also show here that the phase of the strong periodic driving plays a significant role in the process of spike generation.

2. Model

The dynamic equations of the FitzHugh–Nagumo model with additive periodic forcing are

$$\begin{aligned}\dot{x} &= F_1(x, y) + A \sin(\omega t + \varphi_0), \\ \dot{y} &= F_2(x, y),\end{aligned}\quad (1)$$

where x is the voltage, y is the recovery variable, $F_1(x, y) = x - x^3/3 - y$, and $F_2(x, y) = \epsilon(x + I)$. Here ϵ is a fixed small parameter ($\epsilon = 0.05$). In the absence of both external driving and noise, there is only one steady state of the system (1) corresponding to the point of intersection of curves $F_1(x, y) = 0$ and $F_2(x, y) = 0$, that is $x_0 = -I$; $y_0 = -I + I^3/3$.

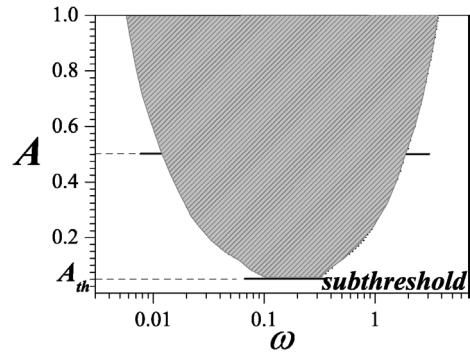


Fig. 1. The parameter plane (ω , A) for $D = 0$, $\varphi_0 = 0$. Suprathreshold signals are the signals with amplitudes and frequencies taken from the shaded region.

The choice of the constant I , therefore, fully specifies the location of the equilibrium state in the phase space (x, y) . In particular, if the rest point lies on the middle branch of the curve $F_1(x, y) = 0$, i.e., $|I| < 1$, the unique equilibrium point is unstable and there is a stable periodic solution. In this case the system fires periodically. For $|I| > 1$ the equilibrium point is stable and all trajectories of the system are attracted by this point. Here we consider $I = 1.1$ and assume that evolution of our system state under action of an external perturbation starts from the point (x_0, y_0) . In the present study we examine the case in which the system is subjected to periodic driving. Here, we would like to note that whereas we consider sinusoidal driving, we only investigate the appearance time of the first spike, that mainly occurs within the first quarter of sinusoidal driving. After generation of the first spike we break the realization off, and start a new one with the same initial conditions (x_0, y_0) . In our calculations we did not use the periodicity of the signal. We vary mainly the shape of the input signal because of different values of driving frequency. In this context, such signal can represent both an environmental stimulus and stimulus arising from other neurons. We have assumed that an external forcing is suprathreshold if the system starting from the point (x_0, y_0) exhibits spikes even in the deterministic dynamical regime (shaded region in Fig. 1). The threshold value of the driving amplitude required for spike generation is $A_{th} \sim 0.05$, as we can see from Fig. 1. Here we choose $A = 0.5$, although, we note that effects, observed in the present study, can also be founded for other values of driving amplitudes.

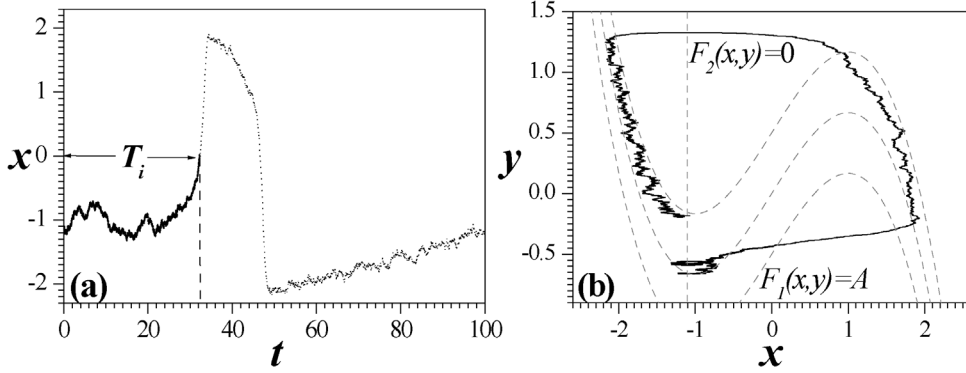


Fig. 2. (a) An example of a stochastic trajectory for case I. $A = 0.5$, $\omega = 0.01$, $D = 0.01$. The estimation of the response time as a first passage time at the boundary $x = 0$. (b) Corresponding stochastic trajectory in the phase space. Dashed lines are possible nullclines of the system (1) for the deterministic case. Upper cubic nullcline is $y = x - x^3/3 + A$, and lower is $y = x - x^3/3 - A$. These boundary nullclines bound the possible oscillations of real nullclines.

From Fig. 1 we can see in fact that alteration of this parameter leads to changing of the width of the characteristic ranges, such as the region of suprathreshold signal, for example. Moreover, the recent results obtained within the frame of Hodgkin–Huxley neuronal model [13], allow to say about generality of the effects described here that similar results are expected for other neuron models. In our simulation $A = 0.5$, therefore, the frequency range where the signal of such amplitude is suprathreshold is: $\omega \in (0.013–1.9)$ (see Fig. 1). Strictly spiking, within this range periodic responses of the system include $n : m$ phase locking patterns with m firings for n forcing cycles [5]. But, in the present study we consider the appearance time of the first spike, characterizing the delay of the systems response. In the absence of noise, within the range where signal is suprathreshold, this time has a non-monotonic behavior as a function of driving frequency with a minimum at $\omega \sim 1.2$.

From neurobiology we know that there are many factors that make the environment noisy. Among them there are the fluctuative opening and closure of the ion channels within the membrane of the cell, the noisy presynaptic currents, and so on [2,3]. We consider therefore two different cases in which the noise is added to the first or the second equation of the system (1). According to the experimental results, the Gaussian noise mimics well the signals received by the neurons from the environment [14]. So we consider Gaussian white noise with zero mean and correlation function $\langle \xi(t)\xi(t+\tau) \rangle = D\delta(\tau)$.

Case I The variable that corresponds to the membrane potential is subjected to fluctuations [5–7]. In this case, the first equation of the system (1) becomes the following stochastic differential equation

$$\dot{x} = x - x^3/3 + A \sin(\omega t + \varphi_0) - y + \xi(t); \quad (2)$$

Case II The recovery variable associated with the refractory properties of a neuron is noisy [2–4,15]. Here, the second equation of the system (1) becomes

$$\dot{y} = \epsilon(x + I) + \xi(t). \quad (3)$$

As a result of cooperative action of both strong periodic driving and noise, a stochastic evolution of our system state occurs. A typical voltage variable time behavior with the corresponding stochastic trajectory in the phase space (x, y) is shown in Fig. 2. The variable x , which is responsible for the membrane potential, changes rapidly during the action potential. Therefore it is possible to choose a certain value of this variable x as a boundary. When this value is reached the self-regenerative depolarization starts. Thus we obtain the mean response time (MRT) by averaging the first passage time [16] through the boundary $x = 0$ over the ensemble of N realizations: $\tau = \langle T \rangle = \frac{1}{N} \sum_{i=1}^N T_i$, where T_i is the response time for i th realization. To obtain smooth average for all the noise values investigated, we need different number of realizations N in the above considered cases. Namely, $N = 5000$ in case I, and $N = 15000$ in case II, specifically when the noise intensities are comparable with

the value of the parameter $\epsilon = 0.05$. For numerical simulations we use the modified midpoint method and the noise generator routine reported in Ref. [17].

Finally we note that the parameter T_i characterizes the delay of the systems response, and has a non-zero value even in the deterministic case, because of the non-instantaneous neuronal response. In our case of a strong driving, the noise increases the time of appearance of the first spike and lead to an additional delay of the signal detection. In the next section we show that a proper choice of driving force parameters can minimize this negative effect of the noise.

3. Results

Case I First we investigate the MRT dependence on driving frequency for some fixed values of noise intensity. We found, for $D \rightarrow 0$, a typical behavior (see Fig. 3) with perpendicular walls disposed at the frequencies corresponding to the boundaries of the shaded region in Fig. 1. These walls go down with increasing noise intensity. We observe a resonant activation-like phenomenon: The MRT exhibits a minimum as a function of the driving frequency, which is almost independent of the noise intensity. By increasing the noise level, in a narrow frequency range ($0.6 \lesssim \omega \lesssim 1.3$), we found a non-monotonic be-

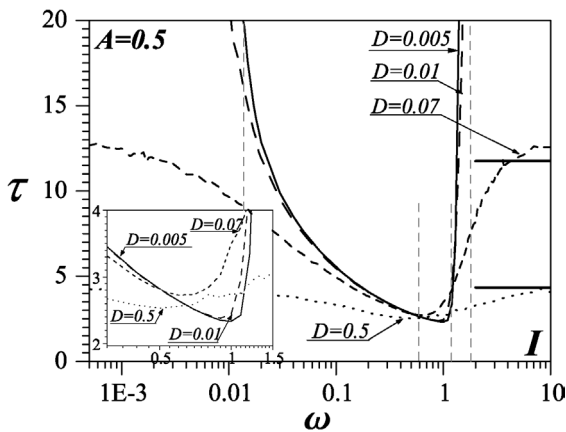


Fig. 3. The mean response time dependence versus frequency of periodic driving for case I for four values of noise intensity. Namely: $D = 0.5, 0.07, 0.01, 0.005$. The parameter setting is: $I = 1.1$, $\epsilon = 0.05$, $A = 0.5$, and $\varphi_0 = 0$. The right solid lines give the theoretical values of τ for fixed bistable potential. Inset: frequency range where the noise enhanced stability effect is observed.

havior of the MRT: the noise enhanced stability effect is observed. Out of this range the MRT monotonically decreases with increasing noise intensity. For large noise intensities the MRT dependence on driving frequency takes a constant-like behavior in the range of the investigated frequency values ($\omega \in [5 \times 10^{-4} - 10]$). The dynamics of the system is mainly controlled by the noise, and the frequency of periodic driving does not affect significantly the neuron response dynamics. By numerical simulations of our system we find that, for large noise intensities, the MRT coincides with that calculated by standard technique for a Brownian particle moving in a bistable fixed potential $\varphi(x)$ [18]: $\tau = 2/D \int_{x_0}^0 e^{2\varphi(x)/D} \int_{x_\infty}^x e^{-2\varphi(y)/D} dy dx$. The theoretical values $\tau = 11.75$, and $\tau = 4.33$ calculated for $D = 0.07$, and $D = 0.5$, respectively, reported in Fig. 3, agree with the limiting values of τ for $\omega \rightarrow 0$ and $\omega \rightarrow \infty$. For $\epsilon \ll 1$, in fact, x is a fast variable and y is a slow variable, so $\dot{y} \simeq 0$ and this case can be recast as an escape problem from one-dimensional double well potential.

Case II We found again a resonant activation-like phenomenon (see Fig. 4), which is independent of the noise intensity, as in case I, until D reaches the value of parameter ϵ . The minimum tends to disappear for greater noise intensities. We observe a frequency range ($0.019 \lesssim \omega \lesssim 1.6$), larger than in the previ-

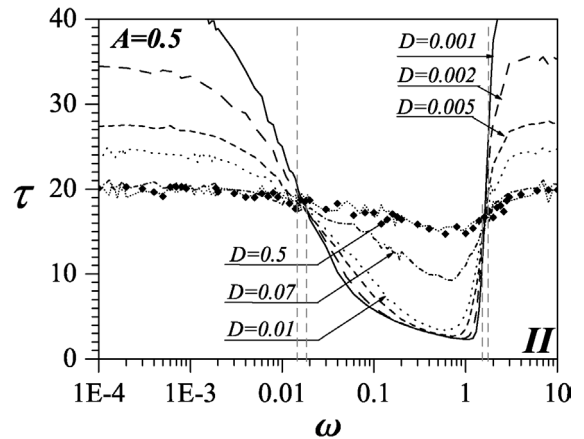


Fig. 4. The mean response time dependence vs frequency of periodic driving for case II, for six values of noise intensity. Namely: $D = 0.5, 0.07, 0.01, 0.005, 0.002, 0.001$. The other parameters are the same of Fig. 3. The curve with diamonds gives the values of τ for fixed bistable potential, when the noise source is a Wiener process.

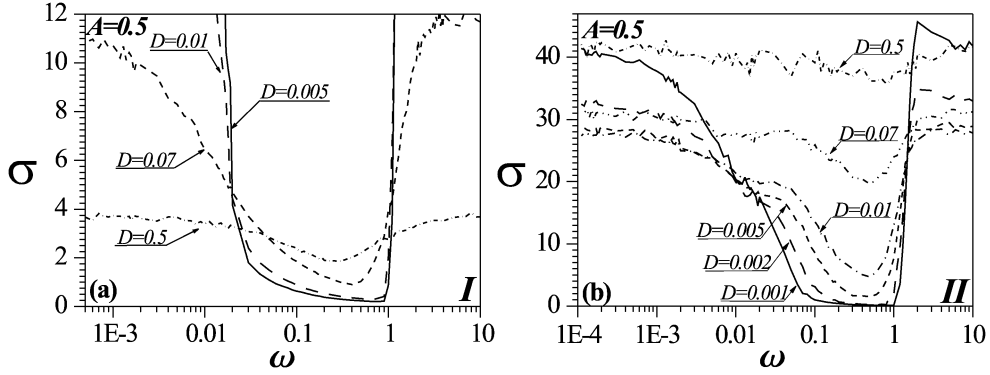


Fig. 5. The standard deviation of the response time dependence vs frequency of periodic driving for case I (a) and case II (b). The parameter values are respectively equal to those of Figs. 3 and 4.

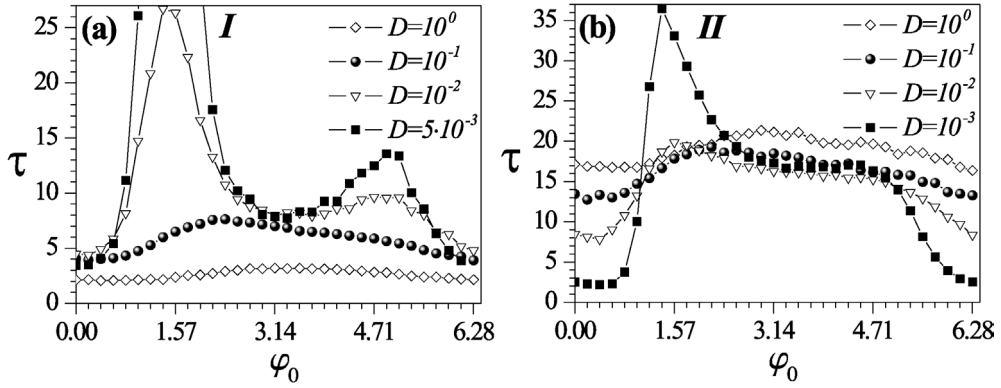


Fig. 6. The influence of the initial phase vs response time for four different values of noise intensity. (a) Noise is in the 1st equation; (b) noise is in the 2nd equation. The values of the parameter set are: $A = 0.5$, $\omega = 1.2$.

ous case, where an increasing noise intensity leads to monotonic growth of the MRT. Out of this range the MRT monotonically decreases with increasing noise intensity, as in case I. For noise intensity values greater than $\epsilon = 0.05$, the recover variable can be approximate by a Wiener process, which acts now as noise source in a double well potential. In Fig. 4 the curve with diamonds shows the good agreement between the results of this approximation for $D = 0.5$ and those obtained by Eq. (3). To get deeper understanding about noise influence on the considered system, we evaluate the mean-square deviation dependence of the response time on the frequency of periodic forcing (see Fig. 5): $\sigma = \sqrt{\langle T^2 \rangle - \langle T \rangle^2}$.

We found that σ has a minimum, in both cases, as a function of driving frequency. From Figs. 3, 4 and 5 we

see, therefore, that the noise has minimal effect in the same range of frequencies where we observe resonant activation-like phenomenon. We observe also that the saturation level reached in each case is different. Particularly in case II it is greater than in case I, because the MRT is calculated with respect to the membrane voltage x and with different noise source. In phase space, therefore, the variable x reaches, in case I, in a minor average time the boundary $x = 0$ according to Eq. (2). While in case II the variation of x depends on the dynamics of the y coordinate and takes much more time to reach the same boundary. Now we analyze the role of the initial phase of the periodic driving force in the process of spike generation. We consider uniform density for the phase. The MRT dependence on initial phase of the external forcing with $A = 0.5$ and $\omega = 1.2$, for different values of noise intensity, is

shown in Fig. 6: (a) case I, (b) case II. In both cases for large enough noise intensities ($D \sim 1$) initial phase weakly changes the MRT. However, some interesting behaviors appear when noise intensity decreases. As we can see from Fig. 6 an optimal range of initial phases around $\varphi_0 = 0$ exists where response time takes the minimal values regardless of noise level. The existence of such phase can be explained as follows. In this range ($\varphi_0 \approx 0$) the system is approximately driven by the periodic signal $A \sin(\omega t)$, that increases from time $t = 0$ until $t_0 = \pi/2\omega$. In this time interval the dynamical threshold decreases and the response time of the neuron decreases too. While for $\varphi_0 \neq 0$ and outside the range of optimal initial phases we can have two situations: (i) the time in which the dynamical threshold decreases is shorter than t_0 or (ii) the dynamical threshold increases, as, for example, for $\varphi_0 = \pi/2$. In both cases the response time is larger then for zero-phase case.

The decreasing of D in case I leads to monotonic increasing of the MRT almost for all phases except for two small regions, around $\varphi_0 \approx 0$, and $\varphi_0 \approx \pi$, where the MRT has non-monotonic behavior. While, the decreasing of D in case II leads to non-monotonic behavior of MRT for the majority of initial phases. But around $\varphi_0 = 0$ the MRT increases monotonically with the noise intensity [see Fig. 6(b)].

Finally, we calculate the phase average of the MRT τ_φ and we compare its behavior, as a function of noise intensity D , with the analogous behavior of τ . In case I the NES effect, with a non-monotonic behavior of MRT, is observed in a rather narrow fre-

quency range [$\omega \in (0.6–1.3)$, see Fig. 3]. Within this range for each value of the driving frequency the optimal noise strength for suppressing the first action potential exists. Thus, for $\varphi_0 = 0$ and $\omega = 1.2$, the MRT can be significantly increased by fluctuations at $D = 0.02$, in comparison with the deterministic case. This growth reaches $\approx 210\%$ [see Fig. 8(a), solid bold line]. Note, that the noise intensity giving the largest τ decreases with increasing driving frequency, as it is shown in Fig. 7. The phase-averaging procedure in this case leads to vanishing of NES effect: τ_φ monotonically decreases with increasing noise intensity, [Fig. 8(b), solid bold line]. Out of this region for suprathreshold signals [$\omega \in (0.013–0.6) \cup (1.3–1.9)$],

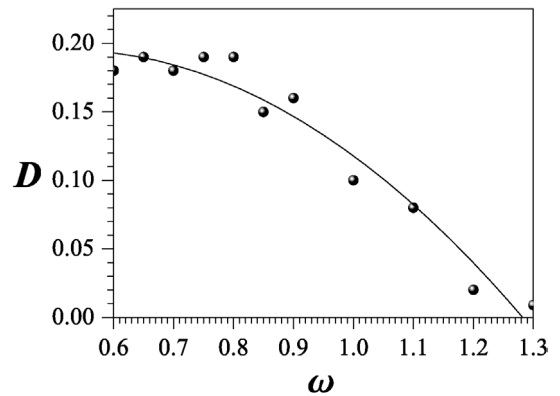


Fig. 7. The noise intensity D corresponding to the largest τ as a function of the driving frequency ω . This noise intensity causes the largest delay of the response time within the range where NES effect is observed in case I (circles). Quadratic approximation is shown by the solid line.

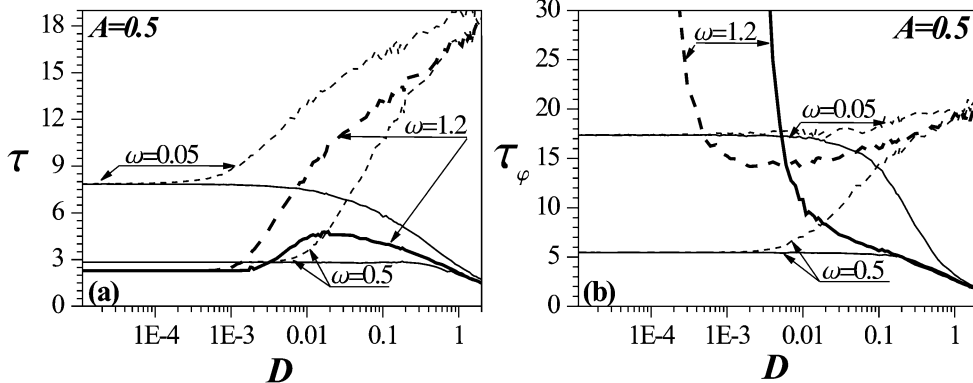


Fig. 8. (a) The mean response time as a function of noise intensity with zero phase; (b) the phase-averaged mean response time as a function of noise intensity. The values of parameter set are: $A = 0.5$, $\omega = 0.05, 0.5, 1.2$. Solid lines correspond to case I, dotted lines for case II.

the monotonic decreasing of the MRT from a deterministic response time is observed [Fig. 8(a)]. The phase-averaging procedure leads only to quantitative changing [Fig. 8(b)].

In case II the MRT monotonically grows in a wider frequency region than in previous case ($0.019 \lesssim \omega \lesssim 1.6$). This growing rate increases considerably, resulting to a giant NES effect (till up to $\approx 1000\%$ for $\omega = 1.2$). Here, the phase-averaging procedure strongly changes the behavior of MRT versus noise intensity. For some driving frequencies the non-monotonic behavior of τ_φ is observed, i.e., the optimal noise intensity exists where τ_φ is minimal ($\omega = 1.2$, $D \approx 0.002$) [Fig. 8(b), dotted bold line]. For other frequencies ($\omega = 0.05$, $\omega = 0.5$) τ_φ exhibits smaller NES effect than in Fig. 8(a), but it is still rather large (till $\approx 370\%$ for $\omega = 0.5$). The NES effect therefore strongly depends on the initial phase of the driving force. The averaging over the phase leads to decreasing, sometimes vanishing, of this effect. It is worthwhile to note that the resonant activation-like phenomenon, observed in Figs. 3–5, does not change significantly its behavior with the phase.

4. Conclusions

Two noise-induced effects are observed in the noisy FitzHugh–Nagumo model in the presence of a suprathreshold periodic driving. Namely the noise enhanced stability and the resonant activation-like phenomena. These effects play different role on the response time of a neuron. The NES effect increases the delay of the neuron response, while the resonant activation-like phenomenon minimizes this delay. In fact near the resonance region $0.03 \lesssim \omega \lesssim 1$, for all noise intensities in case I and for $D \leq 0.05$ in case II, the effect of noise suppression occurs: the noise-induced delay of the neuron response is minimal.

As a result there is an optimal frequency operating range where the response time and its standard deviation are minima and the NES effect is negligible.

In both cases the role of the initial phase of the periodic driving in the process of generation of a neuron's response is examined. An interesting non-monotonic behaviour of the averaged MRT, with a minimum, is found as a function of the noise intensity. The phase-

averaging procedure in any case leads to increase the response time, and, at the same time, to minimize the NES effect.

The investigation of these noise induced effects in the stochastic FitzHugh–Nagumo model is not only important for the response time of a neuron (to realize high rate signal transmission with the suppression of noise), but also in all excitable systems, ranging from chemistry to physics and biology, where this model can be used.

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