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A test for the input noise type in the Fitzhugh-Nagumo neuronal model

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Abstract. A nonlinear system of differential equations, known as the Fitzhugh-Nagumo (FN) equations, is used to describe the physiological state of a nerve membrane. Several different kinds of noise are added to the FN model to investigate the effect of noise on the membrane. They are Gaussian white noise, Ornstein-Uhlenbeck process and Poisson noise. Gaussian white noise represents many small synaptic inputs and Poisson noise represents a few large synaptic inputs. The non-oscillatory region before and after the bifurcation region is used to distinguish between Wiener vs. Poisson inputs by using a hypothesis test about the mean number of level crossings. A sampled version of the process was used in order to make use of the level crossing results of [3]. The null hypothesis is the expected level crossings of the equilibrium state by a time sampled linearized FN set of differential equations with Wiener input. The test performs well in rejecting non Wiener inputs in simulation studies, both in the linearized and nonlinear FN model. A resonance type phenomenon was also observed. The eigenvalues of the linearization provide some guidance in choosing the sampling times. The similarity of the results for the linearized and the nonlinear FN models provides some support for using noisy two compartment models such as [11].

1. INTRODUCTION

The Fitzhugh-Nagumo (FN) model is a more realistic model compared to the leaky-integrate and fire model. The leaky-integrate and fire model does not explicitly describe the action potential feature when the threshold is not taken into consideration [15]. Differently, the formation of the action potential is provided in the FN model. This model originated from the Hodgkin-Huxley neural model. Hodgkin and Huxley conducted the patch clamp experiments on the giant squid axon and constructed the mathematical model with 4 state variables. In [8], the 4 variables of the Hodgkin-Huxley model are reduced to only 2 variables in order to simplify the mathematical framework, which still have the important feature of the neuronal activity. Here the FN model is examined aiming to characterize the input voltage using the information of the output voltage. The types of the input

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voltage are hardly confirmed from the output voltage recordings of the neuron and are basically interrelated with noise. We apply different types of the input noise on the model. Our goal is to be able to distinguish the types of the input noise using the information in the output voltages.

2. ANALYSIS OF FN MODEL

The FN model is described by the following equations:

$$\begin{cases} \frac{dx}{dt} = f(x, y) , \\ \frac{dy}{dt} = g(x, y) , \end{cases}$$

where $f(x, y) = c(y + x - (x^3/3) + z)$, and $g(x, y) = -(x - a + by)/c$. The variable z is an input voltage. We will use the same value for the constants as in the original paper by Fitzhugh [8], namely $a = 0.7$, $b = 0.8$, and $c = 3$.

Since our purpose here is to determine the type of the input voltage, we only focus on the subthreshold behavior of the FN model. Therefore we investigate the system with the input voltage $z = -3, 1$, and 3 . The reasoning for choosing these values of input voltage is based on the bifurcation diagram. When the input voltage z falls outside of the range between $(-1.403; -0.3465)$, the subthreshold behavior of the system is illustrated, namely a single steady state rather than oscillations. Figure 1 is the bifurcation diagram which shows the steady state as a function of input voltage z . The Hopf bifurcation occurs at the branches of the closed orbit and the curve when $z = -1.403$ and $z = -0.3465$. This diagram illustrates that there are 2 steady states when z is in the range of $(-1.403; -0.3465)$. This means that the system is undergoing the oscillatory state. For the region outside of the closed orbit only one steady state is observed.

One of the difficulties of investigating FN model is the nonlinearity of the system. As long as the voltage is around the equilibrium point, the linearized system locally well describes the nonlinear system [15]. Linearization of the system helps us to obtain information about the original system. Linearization of the system is given by

$$\begin{cases} \frac{dx}{dt} = c(1 - x^{*2})(x - x^*) + c(y - y^*) , \\ \frac{dy}{dt} = -\frac{1}{c}(x - x^*) - \frac{b}{c}(y - y^*) . \end{cases}$$

In Figure 2, we compare the non-linear system and linear system for the case $z = 1$. The left plot shows the nonlinear system and the right plot shows the linear system. Both of the systems eventually reach the steady state $x^* = 1.6382$ and $y^* = -1.1727$. The direction field for $z = 1$ is plotted in Figure 3 along with the nullclines and the voltage trajectory. The red lines are the nullclines and the black lines are the voltage trajectory for the initial conditions $x(0) = 0$ and $y(0) = 0$.

3. FN MODEL WITH NOISE

Now we will consider the model with the different types of the noise: White Gaussian noise, Poisson noise, and the Ornstein-Uhlenbeck process noise (OU noise).

3.1. White Gaussian noise. The input term for the FN model with White Gaussian noise is $z + k(dW/dt)$, where W is a standard Wiener process, z is the mean of the input voltage and k is the standard deviation or intensity of the input noise. Thus, the FN model with the White Gaussian noise is represented by

$$\begin{cases} \frac{dx}{dt} = c \left(y + x - \frac{x^3}{3} + z + k \frac{dW}{dt} \right), \\ \frac{dy}{dt} = -\frac{x - a + by}{c} \end{cases}$$

3.2. Poisson noise. To consider FN model with Poisson noise, we remove the input term z and add the Poisson noise term $a_\epsilon(dP/dt)$, where a_ϵ is a jump size, and P is the Poisson process, so that the FN model is the average process of the Poisson noise input model. The FN model with the Poisson noise is given by

$$\begin{cases} \frac{dx}{dt} = c \left(y + x - \frac{x^3}{3} + a_\epsilon \frac{dP}{dt} \right), \\ \frac{dy}{dt} = -\frac{x - a + by}{c} \end{cases}$$

3.3. Ornstein-Uhlenbeck noise. The third case of the noise type is given by the OU noise n . The mean input is z and the steady state variance is $\sigma^2\tau_{ou}/2$

$$\begin{cases} \frac{dx}{dt} = c \left(y + x - \frac{x^3}{3} + z + n \right), \\ \frac{dy}{dt} = -\frac{x - a + by}{c}, \\ \frac{dn}{dt} = -\frac{n}{\tau_{ou}} + \sigma \frac{dW}{dt} \end{cases}$$

4. LEVEL CROSSINGS THEORY

To distinguish the noise input types of the neuron, we will use level crossings theory (e.g. [1]). We expect the number of crossings at the equilibrium point is different among the different types of the noise even though the mean and the variance of the input or the output voltages are the same. First, the number of crossings at the equilibrium point obtained by simulation is compared with the theoretical mean number of crossings. We test if the voltage with the different types of the noise shows different mean number of crossings both in theory and in simulation. Second, the number of crossings is tested at a certain level different from the equilibrium point. This second scenario is for comparing differences between the non-linear FN model and the linearized FN model. As we will see below, our theoretical number of crossings is obtained using linearized FN models. Even

though the level crossings theory works well for both linear and non-linear FN model at the equilibrium point, there would be a clear distinction at a certain level far from equilibrium due to the nonlinear term. Finally we characterize when these criteria are applicable. Under certain conditions, the types of the noise are not distinguishable due to the same number of the theoretical crossings obtained among different noise types.

For the voltage at a certain level a , the number of crossings is given by Rice's formula [18]

$$\begin{aligned} & \text{E}[\# \text{ of crossings of } x \text{ at level } a \text{ per unit of time}] = \\ & = \frac{1}{\pi} \left[-\frac{\ddot{R}_{xx}(0)}{R_{xx}(0)} \right]^{1/2} \exp \left[-\frac{a^2}{2\ddot{R}_{xx}(0)} \right], \end{aligned}$$

where $R_{xx}(\tau)$ is the autocorrelation function of $x(t)$. However Rice's theorem can only be used when the second derivative of the system autocorrelation exists. The difficulties of applying the level crossings theory to the FN model are that the system is nonlinear and its autocorrelation is not differentiable in mean square. Thus we are not able to apply the Rice's theorem to the model. Instead of using this formula, we use the level crossings formula for the samples of the process [3]

$$\begin{aligned} & \text{E}[\# \text{ of } a\text{-crossings}] = \\ & = \frac{T}{\pi dt} \left\{ \arccos \frac{R_{xx}(dt)}{R_{xx}(0)} \right\} \left\{ \exp \left(-\frac{a_n^2}{1 + R_{xx}(dt)/R_{xx}(0)} \right) \right. \\ & \quad \cdot \frac{a_n \sqrt{\pi}}{\sqrt{1 + R_{xx}(dt)/R_{xx}(0)} \arccos(R_{xx}(dt)/R_{xx}(0))} \\ & \quad \cdot \int_{\sqrt{2(1+R_{xx}(dt)/R_{xx}(0))}}^2 \exp \left(\frac{-a_n^2 q^2}{2(2(1 + R_{xx}(dt)/R_{xx}(0)))} \right) \\ & \quad \left. \cdot \text{erf} \left(\frac{a_n \sqrt{4 - q^2}}{2\sqrt{1 + R_{xx}(dt)/R_{xx}(0)}} \right) dq \right\}, \end{aligned}$$

where $a_n = a/\sigma_x$. We call it Barbe's equation.

It is important to note that the sampling point should be less than the reciprocal of the smallest eigenvalue of the linearized system. In our simulations, the time step is set to $dt = 0.01$. This sampling time is also similar or smaller than that commonly used in the actual voltage neuronal recordings. We also examined the effect of the different sampling times. A thorough study of the effect of recording parameters, interfering signals, histograms bin width and duration of the recording signal, on post-stimulus time and interval histograms, was done by [10]. A recent review of spike response latency estimation examines a number of methods and their dependence on the recording and statistical tuning parameters ([13] see also references therein).

We use the linearized FN model to determine the autocorrelation of the system. Let the FN model with any noise be

$$\begin{cases} \frac{dx}{dt} = c((1 - x^2)x + y + n(t)), \\ \frac{dy}{dt} = -\frac{1}{c}x - \frac{b}{c}y, \end{cases}$$

where $n(t)$ is noise term and $x = x - x^*$, $y = y - y^*$ with x^* and y^* the equilibrium points.

We apply the Laplace transform to obtain the system transfer function

$$\begin{cases} sX(s) = c((1 - x^{*2})X(s) + Y(s) + N(s)) \\ sY(s) = -\frac{1}{c}X(s) - \frac{b}{c}Y(s) \end{cases}$$

Then the transfer function is

$$H(s) = \frac{X(s)}{N(s)} = \frac{c}{s - c(1 - x^{*2}) + (1/(s + b/c))}$$

The system autocorrelation is obtained by Fourier transform of the magnitude squared of $H(s)$, taking its partial fraction expansion and using the Fourier transform table.

4.1. Theoretical mean number of equilibrium crossings for White Gaussian noise. The Fourier transform of the magnitude squared of the $H(s)$ determines the variance of the output voltage at the steady state for the White noise input, since the autocorrelation of the output voltage for the White noise input is determined by (e.g. [9])

$$R_v(\tau) = \frac{1}{2\pi} \int_{-\infty}^{\infty} P_N(\omega) |H(j\omega)|^2 \exp(j\omega\tau) d\omega,$$

where $P_N(\omega) = k^2$ and k^2 is the input variance. Therefore $R_v(\tau) = k^2 F[|H(j\omega)|^2]$.

Here, $F[|H(j\omega)|^2]$ includes the Heaviside function, Heaviside(t), which is not defined at $t = 0$. Using the fact that the autocorrelation function is symmetric about $t = 0$, we take the right limit of $F[|H(j\omega)|^2]$ to obtain the variance of the output voltage. Using Barbe's formula, the theoretical mean number of equilibrium crossings is

$$E[\# \text{ of zero-crossings}] = \frac{T}{\pi dt} \left(\arccos \frac{R_v(dt)}{R_v(0)} \right).$$

Note that $a = 0$ is the level at the equilibrium since $x = x - x^*$ in our system. To determine the theoretical mean number of zero crossings, we need to evaluate the autocorrelation at $t = dt$, where $dt = 0.01$. The following table shows the expected number of crossings for $dt = 0.01$ and for White Gaussian noise.

$dt = 0.01$	$z = -3$	$z = 1$	$z = 3$
WG	108.9903	101.468	146.6378

TABLE 1. Theoretical mean number of equilibrium crossings for $dt = 0.01$

4.2. Simulation of the mean number of crossings. There are two possible cases to match the variance, which is the variance of the input process or the variance of the output process at equilibrium. For both cases, the null hypothesis is the expected mean number of zero crossings equal to the simulated mean number of zero crossings being tested.

5. HYPOTHESIS TEST AT EQUILIBRIUM LEVEL FOR MATCHED INPUT NOISE
VARIANCE

The tests are performed with the mean input values set to $z = -3, 1$ and 3 . Then the input noise standard deviation of the White Gaussian noise is

- a) $k = 0.547723, 1.7321$ and 3 for $z = -3$;
- b) $k = -0.3162, 1$ and 1.7321 for $z = 1$;
- c) $k = 0.5477, 1.7321$ and 3 for $z = 3$.

These choices arise from matching the mean input of the process with the White Gaussian noise to the one with Poisson noise. Indeed, since the mean input for the Poisson process is $a_\epsilon \lambda$, then we set the jump size $a_\epsilon = 0.1, 1$ and 3 . The parameter λ is automatically determined by the mean input z and the jump size a_ϵ , for example

- b) $\lambda = 10, 1$ and $1/3$ for $z = 1$;
- c) $\lambda = 30, 3$ and 1 for $z = 3$.

Since the standard deviation of the Poisson process is $a_\epsilon \sqrt{\lambda}$ then we set $k = a_\epsilon \sqrt{\lambda}$ in order to match the standard deviations of the two processes, the one with White Gaussian input noise and the other with Poisson input noise.

For the OU noise, the mean of the input noise is z . To match the input standard deviation of the White Gaussian and Poisson cases, we set the standard deviation $\sigma = k \sqrt{2/dt \tau_{ou}}$. This condition derives from the following considerations. Observe that the differential equations for the White Gaussian noise and the OU noise can be rewritten as

$$\begin{aligned} \frac{dx}{dt} &= c \left(y + x - \frac{x^3}{3} + z + k \frac{dW}{dt} \right) \Leftrightarrow dx = c \left(y + x - \frac{x^3}{3} \right) dt + cz dt + ck dW \\ \frac{dx}{dt} &= c \left(x + y - \frac{1}{3} x^3 + z + n \right) \Leftrightarrow dx = c \left(x + y - \frac{1}{3} x^3 \right) dt + c(z + n) dt. \end{aligned}$$

Then the input noise is $cz dt + ck dW$ for the first equation (White noise) and $c(z + n)dt$ for OU noise. Since the mean process is the same for both and equal to $cz dt$, we set $\text{Var}(ck dW) = \text{Var}(cn dt)$, to match the two noise variances. Then $c^2 k^2 \text{Var}(dW) = c^2 dt^2 \text{Var}(n)$ using the property of the variance. W is the Wiener process, so that $\text{Var}(dW) = dt$. The variance of the OU process is $\text{Var}(n) = \tau \sigma^2 / 2$. Therefore, we obtain

$$\text{Var}(ck dW) = \text{Var}(cn dt) \Leftrightarrow k^2 = dt \frac{\tau_{ou} \sigma^2}{2} \Leftrightarrow \sigma = k \sqrt{\frac{2}{dt \tau_{ou}}}$$

5.1. Hypothesis test. We simulated 100 voltage trajectories. We compare the theoretical mean number of level crossings with the average number of level crossings obtained by simulation. We count the number of the level crossings of the voltage trajectories in each simulation in two different ways to get the average number of level crossings.

The first setting is when 100 voltage recordings are available. In this scenario, we count the number of crossings per 10msec interval starting from 10msec up to 100msec for each voltage trajectory, and average the 100 numbers of crossings per 10msec interval. This gives us 9 numbers, one for the average number of crossings between 10msec and 20msec, the second for the average number of crossings between 20msec and 30msec, and up to the interval 90msec-100msec. Then a sample of size 9 of observed frequencies is constructed. Simulations are repeated for each different

type of input noise such as White Gaussian, Poisson, and OU noise. A Chi-square test is then executed in terms of linearized FN model. We test if there is a significant difference between the observed frequencies and the theoretical mean numbers of crossings in each time interval for the White Gaussian case in order to test if the input noise of the voltage recording is different from White Gaussian noise.

The second setting is the situation when there is only one available voltage recording. In this case, we cannot average over 100 trajectories. So we average the number of crossings per 10msec for each interval: 10msec-20msec, 20msec-30msec and so on, just for one simulation. The transient part is discarded, that is 0msec-10msec. Then we get only one number. We compare this number with the theoretical number of level crossings for the White Gaussian case. A T-test is used for this scenario with 9 degrees of freedom. We expect that the test accepts the null hypothesis only for the linear White Gaussian case and rejects in the other cases.

5.2. Chi-squared test for average number of crossings of 100 simulations.

$$H_0 : E [N(a = 0, T = 10, dt = 0.01)] =$$

= Mean # of zero-crossings per 10msec in simulation with 9 bins (10-100msec)

The Chi-square tests for different types of noise are executed and shown in Table 2. Except for one case, all the White Gaussian noise cases are accepted and the other processes are rejected. The exceptional case is the nonlinear system with White Gaussian where the theoretical mean number is determined based on the linear system. We will discuss the difference between the nonlinear and linear system in a later section using level crossings theory at a certain level instead of at the equilibrium.

Chi-squared test (< 16.92 := C) L=linearized, NL=nonlinear, W=white Gaussian, P= Poisson, OU(t) = Ornstein-Uhlenbeck with time constant t											
z	k(std)	NL-W	L-W	NL-P	L-P	NL-OU(1)	L-OU(1)	NL-OU(5)	L-OU(5)	NL-OU(30)	L-OU(30)
-3	0.5477	8.60<C	0.20<C	45.02>C	112.76>C	856.74>C	828.97>C	917.28>C	898.45>C	943.15>C	940.03>C
-3	1.7321	4.75<C	0.27<C	471.15>C	448.55>C	833.96>C	830.50>C	916.90>C	900.73>C	949.44>C	938.22>C
-3	3	8.18<C	0.47<C	711.94>C	740.37>C	819.22>C	833.28>C	910.21>C	897.04>C	952.98>C	941.99>C
1	0.3162	1.8<C	0.248<C	62.91>C	52.17>C	794.65>C	765.78>C	846.95>C	831.64>C	871.57>C	870.89>C
1	1	18.1>C	0.134<C	101.18>C	677.23>C	781.76>C	768.16>C	847.81>C	831.47>C	880.72>C	871.90>C
1	1.7321	3.13<C	0.307<C	809.83>C	813.9>C	765.91>C	766.5>C	849.02>C	832.75>C	880.17>C	867.88>C
3	0.5477	0.095<C	0.681<C	137.07>C	157.06>C	1150>C	1117>C	1226>C	1219>C	1262>C	1272>C
3	1.7321	14.67<C	0.59<C	673.27>C	707.64>C	1147>C	1117>C	1238>C	1218>C	1279>C	1273>C
3	3	6.66<C	0.863<C	1028.4>C	1046.7>C	1135>C	1117>C	1232>C	1215>C	1275>C	1284>C

TABLE 2. Chi-squared values testing the number of equilibrium crossings for different noise types

5.3. T-test for each simulation. A T-test is executed for each simulation, so that 100 t -values are obtained for each parameter set. The processes with non-White Gaussian noise are rejected almost 100% of the time. For the OU noise, $\tau = 1, 5$ and 30msec are tested.

5.4. Optimal variance to distinguish linearity. For the nonlinear White Gaussian case, we have observed that the chi-squared value assumes the largest or smallest value for $a_\epsilon = 1$, which is in the middle among $a_\epsilon = 0.1, 1$ and 3. Instead for the linear White Gaussian case, these values are almost the same for all variances. The result for the nonlinear White Gaussian case was quite surprisingly, since intuitively the chi-square value should increase as the variance increases. We executed

the Chi-squared test for different standard deviations from $a_\epsilon = 0.1$ to $a_\epsilon = 3$ and for $z = 1$. In particular we have chosen $a_\epsilon = 0.1, 0.2, 0.4, 0.8, 2, 2.2, 2.4, 2.8$ and 3 . The chi-squared values are shown in Table 3 and a plot of the chi-squared values versus standard deviations is shown in Figure 4. The critical value is 16.92. For values greater than 16.92, the simulated mean number of level crossings is significantly different from the linear White Gaussian process. The chi-squared value exceeds 16.92 when $a_\epsilon = 0.8$ and $a_\epsilon = 1$. In these two cases, the nonlinear and linear systems are distinguishable but not in the other cases. When the noise intensity is too small or too large, the test cannot distinguish the linearity of the system. To explain this, we have plotted the phase plane in Figure 5. As we can see from the phase plane, the area is divided into 4 regions by nullclines. With small noise intensity, the voltage trajectory stays mutually in the same region, and the voltage trajectory is dominated by the noise, when the noise is large for both nonlinear and linear systems. When the noise intensity is not too small or large, the voltage in the nonlinear system reaches the nonlinear nullcline, and is pushed to the upper part of the phase plane. This does not happen for the linear system. This is a special feature of the nonlinear system. There is an optimal standard deviation to distinguish between the linear and nonlinear models.

		Chi-squared test ($< 16.92 := C$)		
z	a_ϵ	$k(\text{std})$	NL-W	L-W
1	0.1	0.3162	1.803	0.248
1	0.2	0.4472	9.922	0.129
1	0.4	0.6325	16.59	0.403
1	0.8	0.8944	19.78	0.226
1	1	1	18.1	0.134
1	1.2	1.0954	14.25	0.392
1	1.4	1.1832	13.42	0.158
1	1.8	1.3416	7.241	0.625
1	2	1.4142	9.951	0.066
1	2.2	1.4832	6.483	0.412
1	2.4	1.5492	6.547	0.553
1	2.8	1.6733	3.395	0.189
1	3	1.7321	3.128	0.307

TABLE 3. Chi-squared values for the number of equilibrium crossings for different standard deviations

6. HYPOTHESIS TEST AT EQUILIBRIUM LEVEL FOR MATCHED OUTPUT NOISE VARIANCE

Matching the input variance not necessarily gives output voltages similar to the White Gaussian case, as it happens for the OU process. When output is similar, some mistakes could occur in labeling the type of input noise. Here, instead of matching the input variance, we investigate the case when the output variance of the OU process is the same as the White Gaussian case. This gives us voltage

trajectories of OU process with magnitude similar to the White Gaussian process. Then a suitable test helps in distinguishing the input noise types when the voltage trajectories are similar in magnitude.

First we need to match the output variance of the voltage between the process with White Gaussian noise and the one with OU noise. Using the autocorrelation function of the output voltage, we obtain,

$$\sigma^2 \left(\lim_{t \rightarrow +0} F \left[|H_{ou}(j\omega)|^2 |H(j\omega)|^2 \right] \right) = k^2 \left(\lim_{t \rightarrow +0} F \left[|H(j\omega)|^2 \right] \right)$$

where the left hand side corresponds to the OU noise and the right hand side corresponds to the White Gaussian noise. Therefore, σ represents the standard deviation of the White Gaussian noise for the process with OU noise and the OU process satisfies the following equation

$$\frac{dn}{dt} = -\frac{n}{\tau} + k \sqrt{\frac{\lim_{t \rightarrow +0} F \left[|H(j\omega)|^2 \right]}{\lim_{t \rightarrow +0} F \left[|H_{ou}(j\omega)|^2 |H(j\omega)|^2 \right]}} \frac{dW}{dt}$$

Then, we have tested if the processes simulated with OU noise give a number of crossings which is different from the theoretical mean number of equilibrium crossings. As before, the theoretical mean number for the White Gaussian process is used as null hypothesis. Since the mean number of equilibrium crossings does not depend on the variance, we expect to obtain chi-squared values similar in magnitude.

1. *Chi-squared test when the output variance is matched.* The chi-square values are quite similar to the case when the input variance is matched. All the cases for the White Gaussian noise are accepted, and the other cases are rejected.
2. *T-test when the output variance is matched.* For the T-test, the linear White Gaussian case is all accepted. More than 5% of the time the Nonlinear White Gaussian case is rejected for $a_\epsilon = 1$ and 3. When the variance is small, $a_\epsilon = 0.1$, the test accepts both. Other than White Gaussian noise, they are all significantly different from the White Gaussian noise.

7. HYPOTHESIS TESTING AT A CERTAIN LEVEL DIFFERENT FROM EQUILIBRIUM

The theoretical mean number of level crossings is the same for the level $-a$ and $+a$ and the linearization is used to determine the value. For the nonlinear FN model, the cubic term $-x^3/3$ pulls the voltage variable in the negative direction so that the number of level crossings at the level $-a$ is expected to be different from the one at the level $+a$. By using this property on symmetric levels, we distinguish linear model from nonlinear one. When the level is positive, the linearity of the model cannot be recognized differently from the negative level. We note that the theoretical mean number of level crossings depends on the variance of the input. For the level equal to (fixed point) -0.75 , all the nonlinear White Gaussian noise processes, except one, are statistically different from the theoretical value obtained by the linearization of the FN model. The excepted case for $z = 3$ and $a_\epsilon = 3$ is accepted but the computed chi-squared value 14.04 is not far from the critical value 16.92.

8. CRITERIA OF APPLICABILITY OF THE THEORY

When we apply the level crossings theory at the equilibrium point, the autocorrelations at $t = 0$ and at $t = dt$ are different. As long as the autocorrelation at $t = 0$ and $t = dt$ give different values, the level crossings theory for the sampled process is applicable. The level crossings theory cannot distinguish the input noise types when the autocorrelation at $t = 0$ and $t = dt$ are the same, or the ratio of the autocorrelation at $t = 0$ and $t = dt$ is the same, being

$$\frac{R_{v_WG}(\tau = 0.01)}{R_{v_WG}(\tau = 0)} = \frac{R_{v_OU}(\tau = 0.01)}{R_{v_OU}(\tau = 0)}$$

9. CONCLUSION AND DISCUSSION

In this paper, we have investigated different types of noise in the Fitzhugh-Nagumo neural model. In our study, we only focused on the subthreshold behavior, to examine the basic effect of the noise on the model. For this model, we have investigated three types of the noise: White Gaussian, Poisson, and Ornstein-Uhlenbeck process noise. We focused on if we can distinguish the input noise types by observing the output voltage. We showed that the number of level crossings of the output voltage is different depending on the noise types. The application of the level crossings theory is achieved by the linearization of the system, so that the limitation of the applicability of the theory is studied. Linearity rarely is distinguishable using the number of equilibrium crossings. However, the number of crossings at negative level (hyperpolarization) from the equilibrium point mostly distinguishes the linearity of the model. We also found that there is an optimal input variance to distinguish the linearity of the model. The lack of distinguishability of the FN model and the two compartment linearizations provide some additional support for using two compartment stochastic models such as in [11]. The oscillatory state of the model is also of interest for future work. For a recent review of stochastic resonance in nonlinear neural models, see [14] and [12]. Long memory noise was compared to Gaussian White noise in a linearized FN model and was found to shift the position of the peak in stochastic resonance [16, 17]. Poisson noise remains to be examined in the context of stochastic resonance. The issue of transition to chaos in the FN model [4] would also be of interest with Poisson noise, as well as the stability of FN coupled oscillators [7, 21] and the use of the stochastic sensitivity function technique [4]. The noise effects with a bichromatic signal for the FN model can also induce a type of resonance with White Gaussian noise and OU noise [6]. However Poisson noise in this scenario has not been examined. Finally a comparison with Poisson noise to the five equation moment approach of [20] for single and networks of FN neurons could shed insight on how some aspects beyond the first two moments of the fast and slow processes are involved.

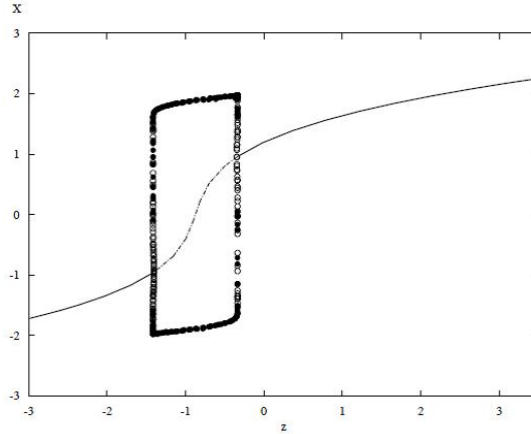


FIGURE 1. Bifurcation diagram for FN model (voltage vs. input): The parameters are $a = 0.7$, $b = 0.8$ and $c = 3$. The figure is showing the fixed points when z is changed from -3 to 3.5 . There are two bifurcation points at $z = -1.403$ and $z = -0.3465$. This bifurcation is a Hopf bifurcation (e.g. [19]). In the range of the orbits, there are two steady states since it is oscillating. There is only one fixed point if z is outside of the orbits

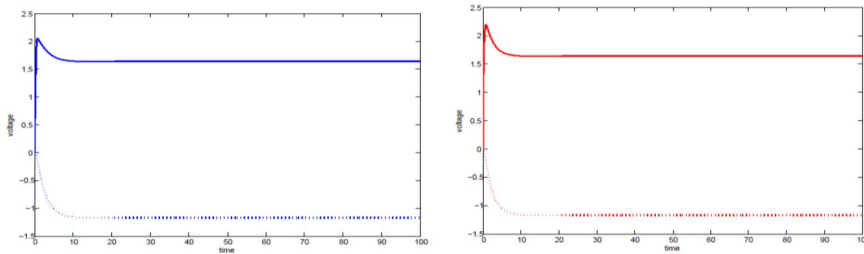


FIGURE 2. The steady state is $x = 1.6382$ and $y = -1.1727$. Solid curve is the fast variable x and the dotted plot is the slow variable y . LEFT : Nonlinear system RIGHT: Linear system. For the upper figure, negative nonlinear term of the differential equation for the fast variable makes the peak lower than the linear case. Voltage trajectory without noise (voltage vs. time): The voltage trajectory of the system is plotted for the mean input $z = 1$.

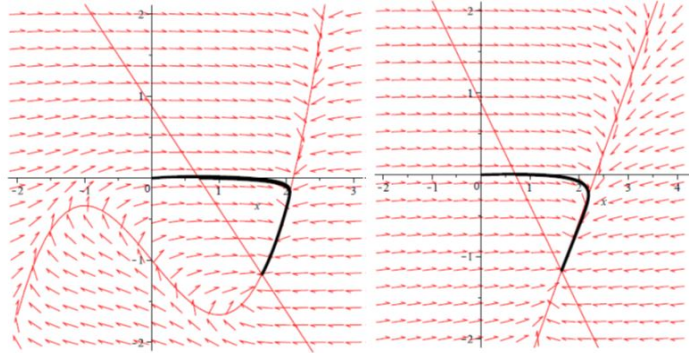


FIGURE 3. Voltage trajectory plotted on the direction field (y vs. x): The system with $z = 1$. LEFT: Nonlinear system, RIGHT: Linear system. Red solid lines are the nullclines and the black line is the voltage trajectory with initial conditions $x(0) = 0$ and $y(0) = 0$.

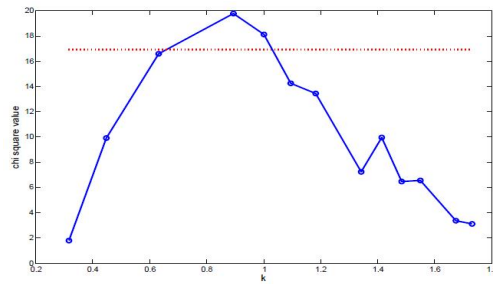


FIGURE 4. Chi-squared value vs. noise intensity k for nonlinear White Gaussian model: the number of equilibrium crossings for 100 simulations are obtained for $k = 0.3126, 0.4472, 0.6325, 0.8944, 1, 1.0945, 1.1832, 1.3416, 1.4142, 1.4832, 1.5492, 1.6733, \text{ and } 1.732$.

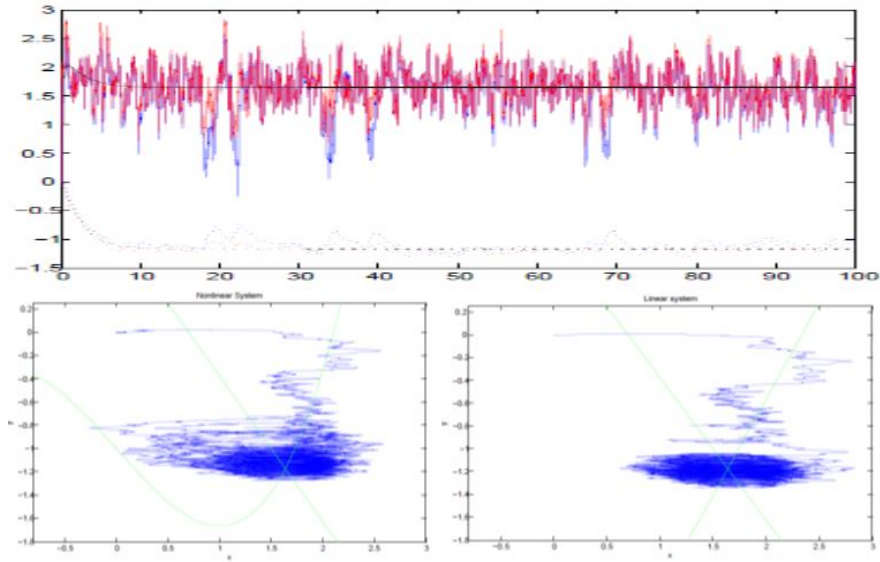


FIGURE 5. Voltage Trajectory and Phase plane for White Gaussian model with $z = 1$ and $a_e = 0.1$: Top: Voltage trajectory for linear (Red) and nonlinear (Blue) White Gaussian model. Left: Phase plane for the nonlinear system. Right: Phase plane for the linear system.

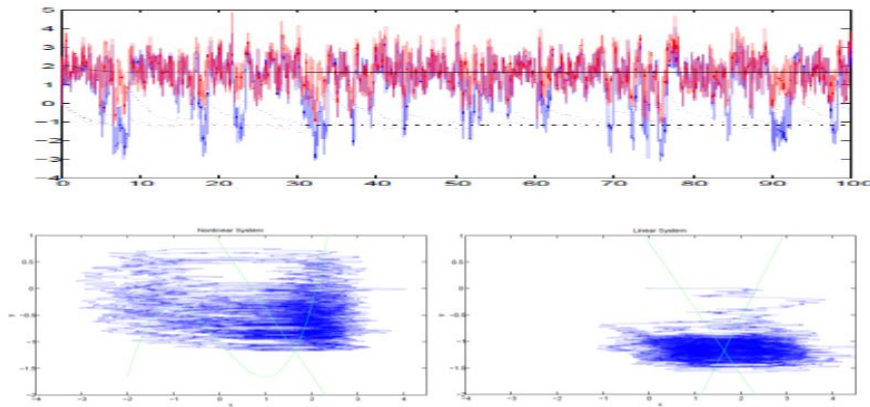


FIGURE 6. Voltage Trajectory and Phase Plane for White Gaussian model with $z = 1$ and $a_e = 0.8$: Top: Voltage trajectory for linear (Red) and nonlinear (Blue) White Gaussian model. Left: Phase plane for the nonlinear system. Right: Phase plane for the linear system.

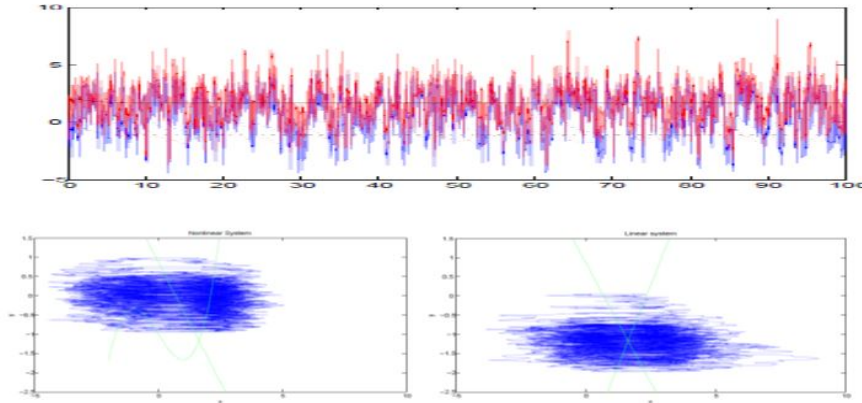


FIGURE 7. Voltage Trajectory and Phase plane for White Gaussian model with $z = 1$ and $a_e = 3$: Top: Voltage trajectory for linear (Red) and nonlinear (Blue) White Gaussian model. Left: Phase plane for the nonlinear system. Right: Phase plane for the linear system.

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