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Letters

Analytical determination of firing times in stochastic nonlinear neural models

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Abstract

We present for the first time an analytical approach for determining the time of firing of nonlinear stochastic neuronal models. The theory of Markov processes is applied to the Fitzhugh–Nagumo system with a constant mean, Gaussian white noise input, representing stochastic excitation and inhibition. An equation obtained for the mean of the time to first spike is solved by means of an accurate one-dimensional approximation. Verification of the method is obtained through the excellent agreement between the moments of the firing time found by numerical solution of differential equations and those obtained by simulation of the solutions of the model stochastic differential equations. We also find a maximum at small noise values which constitutes a form of stochastic resonance. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

It has been observed that the activity of individual neurons in the mammalian central nervous system is, for the most part, highly irregular and unpredictable [1,8]. Recently there has been strong interest in such aspects of neuronal spiking activity especially with regard to an understanding of "information processing" [2,5,7,9]. There have been many experimental studies of the spike trains emitted by cortical cells in response to natural and artificial stimulation [3] but it is still uncertain which models reproduce experimental details [6,8]. Early studies assumed there were two possible states for

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each element corresponding to a firing or nonfiring nerve cell, but models now include physiological details of neurons such as synaptic currents.

We have derived equations for the moments of random variables associated with the time to reach threshold in the Fitzhugh–Nagumo system, which is relatively simple and more directly amenable to analysis than that of Hodgkin and Huxley. We have used several methods to find mean firing times by solving associated ordinary or partial differential equations, including approximations suitable for small and large values of the noise parameter. Comparison is made with results obtained by numerical solution of the stochastic Fitzhugh–Nagumo system.

2. The stochastic Fitzhugh–Nagumo model

The Fitzhugh–Nagumo system has solitary waves (action potentials or spikes) as well as repetitive activity (periodic solutions) in certain ranges of stimuli. We consider the following corresponding stochastic version of this model [11] in which the components obey the following equations:

$$\mathrm{d}X = [f(X) - Y + I]\,\mathrm{d}t + \sigma\,\mathrm{d}W, \tag{1}$$

$$\mathrm{d}Y = b(X - \gamma Y)\,\mathrm{d}t, \tag{2}$$

where $X = X(t)$ is the "voltage" variable, $Y = Y(t)$ is the recovery variable, $\{W = W(t), t \geqslant 0\}$ is a standard (zero mean, variance t) Wiener process, σ is a constant determining the overall input noise level, $I = I(t)$ is a deterministic input current (stimulus) which may be constant or time-varying, and b and γ are positive constants. The function f is a cubic

$$f(x) = kx(x - a)(1 - x), \quad 0 < a < 1. \tag{3}$$

We let $T(x, y)$ be the first exit-time of (X, Y) from a set A in the phase space for a starting point (x, y). With a constant stimulus I, the process is in fact temporally homogeneous and the theory of Markov diffusion processes [10] yields the following partial differential equation for the first moment $F(x, y) = E[T(x, y)]$:

$$[f(x) - y + I]\,\frac{\partial F(x,y)}{\partial x} + b(x - \gamma y)\,\frac{\partial F(x,y)}{\partial y} + \frac{\sigma^2}{2}\,\frac{\partial^2 F(x,y)}{\partial x^2} = -1, \tag{4}$$

which is solved with suitable boundary conditions. The time to first threshold crossing or time to first spike, from an initial point $(0, y_0)$, which has first moment $F(0, y_0)$, is not the same as the interspike interval.

We have approached the solution of the moment equations in various ways. Approximate solutions can always be obtained by simulation [12]. However, accurate numerical solution of the moment equations is a useful and perhaps necessary check on simulation results which are subject to sampling error. We have pursued the following methods of solution: (a) a simplified approach which considers the single component process X;

(b) approximate solution of Eq. (4) when σ is small; and, (c) the solution of Eq. (4) when σ is large.

In the first approach, we reduce the problem to a one-dimensional one. For Eq. (4) this is tantamount to neglecting the F_y term. The justification for this approach is the observation that during the initial stages of the interspike interval, the recovery variable $Y(t)$ is practically unchanged and may therefore be set as a constant equal to the initial value $Y(0) = y_0$. We may then consider the diffusion process satisfying

$$dX = [f(X) - y_0 + I]\,dt + \sigma\,dW. \tag{5}$$

Letting $X(0) = x \in (-\infty, \theta)$, we consider the exit time $T_\theta(x)$ which is the time to first reach the level θ, identified as the threshold for an action potential, given that the voltage started below this value. The first moment $F(x)$ of this exit time satisfies the simple differential equation

$$\frac{\sigma^2}{2}\frac{d^2F(x)}{dx^2} + [f(x) - y_0 + I]\frac{dF(x)}{dx} = -1. \tag{6}$$

One boundary condition is $F(\theta) = 0$ and the other may be taken as $F_x(-\alpha) = 0$, where $\alpha > 0$. The quantity of interest is then the mean of the time to reach threshold from rest, $F(0)$. We have also developed parametric series solutions in σ valid when σ is small and when σ is large. When σ is small, Eq. (4) can be solved approximately using perturbation methods with the resulting first-order partial differential equation solved by the method of characteristics.

3. Results and discussion

We have determined the first two moments of $T(x, y)$ and simulated the processes described by the evolution Eqs. (1) and (2) using a standard Euler method. This was done principally with the set of parameter values $a = 0.1, b = 0.015, \gamma = 0.2, k = 0.5$ for various values of σ and I. The threshold value θ for spikes was estimated. The initial value of $X(t)$ was set at 0 and that of $Y(t)$ set at 1.0 in the results to be reported. When I is less than about 1.3, the (expected) value of $X(t)$ rarely attains the designated threshold value of $\theta = 0.6$. For the chosen parameters we therefore consider only values of $I \geqslant 1.3$. The values of the noise parameter σ are chosen from 0.05 to 5.0. For small values of σ the number of trials in simulations was 4500, whereas for larger values only 1500 trials were employed.

Plots of the mean of the time for $X(t)$ to reach θ for various I as a function of σ are shown in Fig. 1. For a given value of I, results obtained by numerical solution are shown in the same figure for comparison, the values of I being 1.3 and 1.5. The numerical results shown here were obtained using the simplified approach. There is excellent agreement between the two sets of results, especially allowing for sampling error in the simulation results. In general, the means from simulation are slightly larger than those obtained by solution of the differential equation. It can be clearly seen in the top part of Fig. 1, where $I = 1.3$, that as σ increases away from zero, the

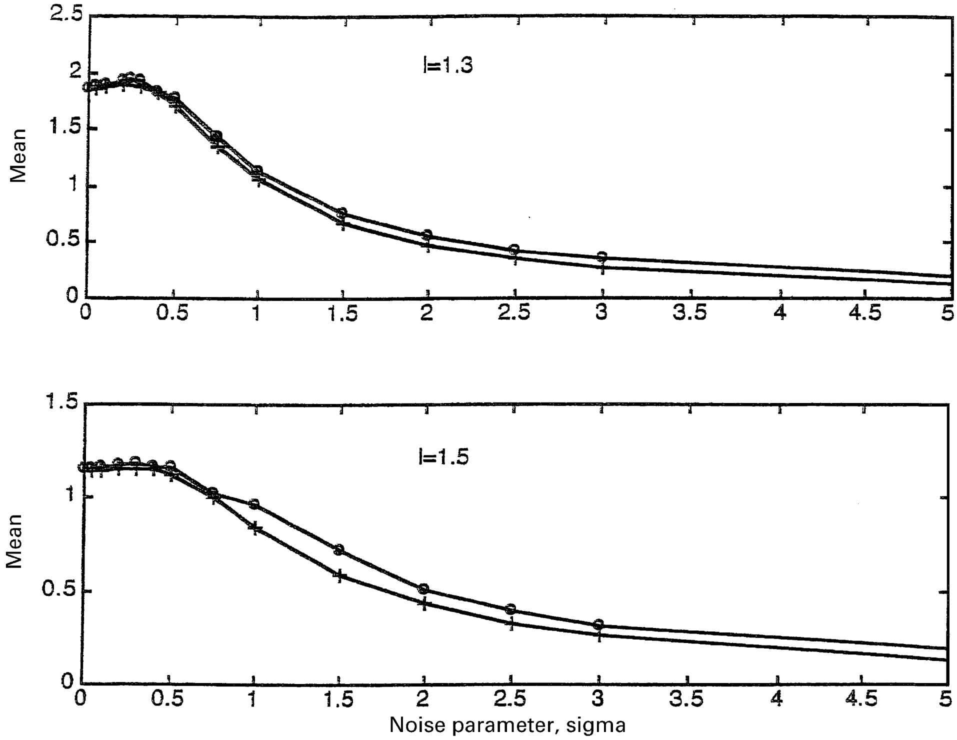

Fig. 1. Mean times to reach threshold versus noise parameter σ. Parameter values given in the text. Values determined by simulation (circles) and by numerical solution of the differential equation (4) (+).

mean first passage time actually increases. After reaching a maximum when σ is about equal to 0.25, the mean then declines as is expected with increased variability. Similar behaviour is observed for the larger values of the mean input current, except that the maximum of the mean interval occurs at larger values of σ. This phenomenon is akin to stochastic resonance, well documented in nonlinear systems with noise, including neural systems [4].

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