



ELSEVIER

Neurocomputing 32–33 (2000) 147–154

NEUROCOMPUTING

www.elsevier.com/locate/neucom

Effect of noise on neuron transient response

Alix Herrmann*, Wulfram Gerstner

*Center for Neuromimetic Systems, Swiss Federal Institute of Technology, Lausanne, EPFL-DI,
CH-1015 Lausanne EPFL, Switzerland*

Accepted 13 January 2000

Abstract

A good approximation to the integrate-and-fire model with diffusive noise can be obtained using a noisy threshold model. This allows the response of a population of noisy neurons to a current transient to be described using a linear filter. Here we apply these analytical results to the peristimulus time histogram (PSTH) of a single neuron. The effect of the noise on the PSTH in our model is similar to that seen in experimental findings of Poliakov et al. (*J. Physiol.*, Part 1, 495 (1996) 143–157) on hypoglossal and cat lumbar motoneurons and could help in interpreting their results. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Noise; Integrate-and-fire; PSTH; Motoneuron

1. Introduction

Random synaptic inputs to a neuron causes its membrane potential to fluctuate. These random inputs are commonly modeled using diffusive noise. Diffusive noise added to an integrate-and-fire model can elicit ‘spontaneous’ activity even when the neuron is nominally operating below threshold. Intuitively, we expect this noise to affect the ability of a neuron to transmit a pulse — but how? This question has been studied experimentally in motoneurons and in this paper we attempt to provide a theoretical explanation for the observed results.

Motoneurons receive convergent input and are thus subject to synaptic “noise” due to the large number of (stochastically) arriving spikes. Measurements have been made in motoneurons of the effect of synaptic noise on the membrane potential, showing a roughly Gaussian distribution of the synaptic potential [1]. Input–output

* Corresponding author. Tel.: + 41-21-693-3910; fax: + 41-21-693-5263.
E-mail address: alix.herrmann@epfl.ch (A. Herrmann).

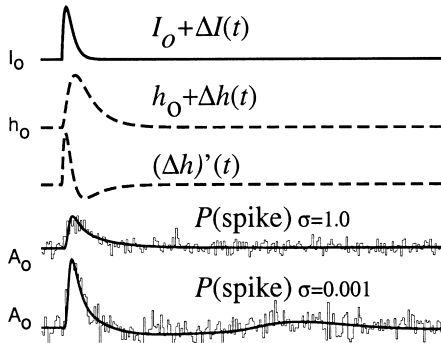


Fig. 1. In the absence of a signal, a neuron exhibits a constant level of activity A_0 due to synaptic noise. When a current transient, $I(t) = I_0 + \Delta I(t)$ (top row) is applied, the neuron responds with an increased spiking probability. The theoretical probability density $P(\text{spike})$, shown in the third and fourth traces (thick lines), is related to the postsynaptic potential (PSP) $\Delta h(t)$ (second trace), its derivative $\Delta h'(t)$ (bottom trace), and the noise level, σ . (Traces are not shown to scale.) In experiments, $P(\text{spike})$ would be estimated by way of the peristimulus time histogram (PSTH) (stepped lines, bottom two rows).

measurements have been performed experimentally on motoneurons by a number of researchers and it has long been established that the PSTH profile is clearly related to the PSP profile, its derivative, or both [9,2,14,15]. Gustafsson et al. [7] suggested that the PSTH response of a motoneuron to smaller PSPs also depends on the level of noise. Poliakov et al. [15] extensively studied the effect of noise on PSTH responses of rat hypoglossal and cat lumbar motoneurons to small PSP-like current transients injected into the soma. In another comprehensive study [14], they showed that linear combination of the PSP profile and its derivative can generally be used to approximate a given PSTH profile, but the coefficients are not constant for different current inputs and it is not clear how they might be determined by the noise except in certain restrictive cases [12,10]. They also used white-noise analysis to derive Wiener kernels up to second order [14]. Unfortunately, the Wiener-kernel description is difficult to interpret in terms of underlying mechanisms and does not allow predictions to be made about how noise controls the shape of the PSTH profile.

Fig. 1 schematically summarizes the situation. A model neuron is subjected to a constant level of background synaptic noise and fires stochastically at some baseline rate A_0 . The neuron may now be tested with a ‘signal’, a small pulse that generates a PSP. In the figure, a current pulse $I(t)$ applied to the neuron results in the PSP $\Delta h(t)$, which may or may not in turn elicit a spike. By repeatedly applying the same pulse and measuring spike times, a PSTH is accumulated, giving an estimate of the probability of a spike following the input pulse. The profile may be compared to the PSP and its derivative, $\Delta h'(t)$. The analytical approach we present here aims to show how the relative influences of the PSP and its derivative are controlled by the noise level σ .

Consider a homogeneous population of N noisy neurons initialized with random initial conditions, all receiving the same input. If the neurons are not connected to

each other, the activity of the population as a whole in response to a given stimulus is equivalent to the PSTH compiled from the response of a single noisy neuron to N repeated presentations of the same stimulus. Hence, we can apply theoretical results for homogeneous populations to the PSTH of an individual neuron. The next section summarizes the theory.

2. Theory

Our analytical approach will consist of two steps. First, we need a model of an individual neuron that explicitly describes noise, presented next in Section 2.1. The second step will be to derive the expected PSTH response of the model neuron in Section 2.2.

2.1. Spike response model and noise model

The spike response model [5] for the case of connectionless neurons describes the response of a neuron in terms of a threshold, θ ; a response kernel $\varepsilon(t)$ that gives the input potential $h(t)$ generated in response to current input; and a refractory function, $\eta(t)$. The net input potential

$$h(t) = \int_0^\infty \varepsilon(s)I(t-s) ds \quad (1)$$

is the sum of the postsynaptic potentials caused by current input $I(t)$. The membrane potential $u(t)$ is the sum of the refractory potential and the net input potential:

$$u(t) = \eta(t - \hat{t}) + h(t). \quad (2)$$

We will use the exponentially decaying kernels $\varepsilon(s) = (1/\tau) \exp[-(s/\tau)]H(s)$ and $\eta(s) = -\exp(-s/\tau)H(s)$, where τ is the membrane time constant and $H(s)$ is the Heaviside function. In this case, between firings, the deterministic membrane potential evolves according to

$$\tau \frac{du}{dt} = -u(t) + J_{\text{ext}}I(t), \quad (3)$$

where $I(t)$ is the external current, J_{ext} is a scalar coupling factor which we will set to 1, and \hat{t} is the last firing time of the neuron. This model is very similar to the well-known integrate-and-fire model (for details, see [4]).

We now consider a model of noise in the spike generation process in which noise is added to the thresholding process [6]. Here we specifically address only the below-threshold regime. The probability of a spike at time t , $\rho_h(t)$, is determined by an escape rate $f[u]$ which is simply a function of the membrane potential u . f could be a normal distribution for example, which would be consistent with a fluctuating,

Gaussian-distributed threshold:

$$f[u] = \frac{1}{\tau} \exp\left[-\frac{(u - \theta)^2}{2\sigma^2}\right], \quad (4)$$

where τ is the membrane time constant, and σ is the amplitude of the noise. The above escape rate function was studied in [8]. The escape rate function we will use here, known as the Arrhenius and Current model [13] (see also the paper by Plesser and Gerstner in this proceedings volume) contains an additional term proportional to the membrane potential derivative, u' :

$$f[u] = \left(\frac{c}{\tau} + \frac{u'}{\sigma\sqrt{2\pi}}\right) \exp\left[-\frac{(u - \theta)^2}{2\sigma^2}\right]. \quad (5)$$

The constant c is a parameter whose optimal value is 0.72 [13]. This modification gives an improved description of the response in case of strong transients. In the below-threshold regime, this function corresponds to the intuitive idea that the chance of a spike should decrease with increasing distance from threshold. The probability of firing depends implicitly on the time of a previous spike because of the refractory function $\eta(t)$ and the input potential $h(t)$ inside $u(t)$. The probability density for a spike at time t , given a spike at time s , is

$$\begin{aligned} P_h(t|\hat{t}) &= P(\text{spike at } t)P(\text{no firing after } \hat{t} \text{ until } t) \\ &= \rho_h(t) \exp\left(-\int_{\hat{t}}^t \rho_h(s) ds\right), \end{aligned} \quad (6)$$

where $\rho_h = f[u(t)] = f[\eta(t - \hat{t}) + h(t)]$. We contrast this model with the more standard integrate-and-fire neuron with diffusive noise [16,17], for which an analytic expression for the above distribution is not known. Note that a number of different escape rate functions are possible; see [13] and the article by Plesser and Gerstner in this proceedings volume for a comprehensive comparison.

2.2. Population activity

So far we have a description of an individual neuron subjected to noise. In order to obtain a proper prediction of the shape of the PSTH, we need a way to represent the activity of an ensemble of such neurons (equivalent to the PSTH as outlined in Section 1). We will use the theory developed by Gerstner [3,6] describing the activity $A(t)$ of a homogeneous population of neurons in terms of (a) the net input potential $h(t)$ applied to the entire population, and (b) the previous activity of the population, in the following integral equation:

$$A(t) = \int_{-\infty}^t P_h(t|\hat{t})A(\hat{t}) d\hat{t}, \quad (7)$$

where

$$A(t) = \lim_{\Delta t \rightarrow 0} \frac{1}{\Delta t} \frac{n_{\text{act}}(t; t + \Delta t)}{N} \tag{8}$$

is the proportion of active neurons in a population of size N ; $P_h(t|\hat{t})$ is the probability density describing the probability of firing for each neuron at time t , given a spike in the network at a previous time \hat{t} and resulting from the net input potential $h(t)$. $A(t)$ thus corresponds to the PSTH expressed as a firing rate.

By using the interval distribution $P_h(t|\hat{t})$ obtained in the previous section for the spike response model with escape noise, we can perform a linear expansion of the above integral equation to obtain the response to a small fluctuation. The first step is to consider a population receiving a constant input potential h_0 . The mean activity A_0 of the population is just the inverse of the mean interval, calculated from the interval distribution $P_h(t|\hat{t})$.

Suppose now that we add a fluctuation to the input, a small synaptic current pulse reflected in the input potential as $h(t) = h_0 + \Delta h(t)$. (Thus the PSP is $\Delta h(t)$.) The population activity will respond by undergoing a fluctuation reflected in a peak in the PSTH, i.e. $A(t) = A_0 + \Delta A(t)$; the shape of the peak $\Delta A(t)$ depends on the size (and duration) of the pulse, the particular noise model, and the population activity itself:

$$\begin{aligned} \text{change in activity} &= (\text{influence of past perturbations}) \\ &+ \frac{d}{dt}(\text{a filtered version of the potential}) \end{aligned}$$

or, after linear expansion of the population integral equation,

$$\Delta A(t) = \int_{-\infty}^0 d\hat{t} P_h(t|\hat{t}) \Delta A(\hat{t}) + A_0 \frac{d}{dt} \left[\int_0^{\infty} dx L(x) h_1(t-x) \right], \tag{9}$$

where the filter for our specific noise model is $L(x) = \int_x^{\infty} f'[u(\hat{x}-x)] S_0(\hat{x}) d\hat{x}$, where $S_0(t-\hat{t}) = \exp(-\int_{\hat{t}}^t \rho(t') dt')$ is the survivor function in the unsynchronized state prior to the pulse.

3. Results

We numerically calculated L for various levels of noise and used these to predict the responses to brief pulses of external input. The shape of L varies according to the level of noise; for low noise, it resembles a δ -function while for high noise it becomes a low-pass filter. We simulated the responses of populations of spike-response neurons using the exponential kernels and escape noise model described above, for various levels of noise. Fig. 2 shows the responses to brief pulses for two different noise levels, together with the numerically calculated theoretical responses.

Next, we simulated the response of the same neurons but with diffusion noise (Fig. 3). Remarkably, the theoretical results calculated for the noisy threshold are

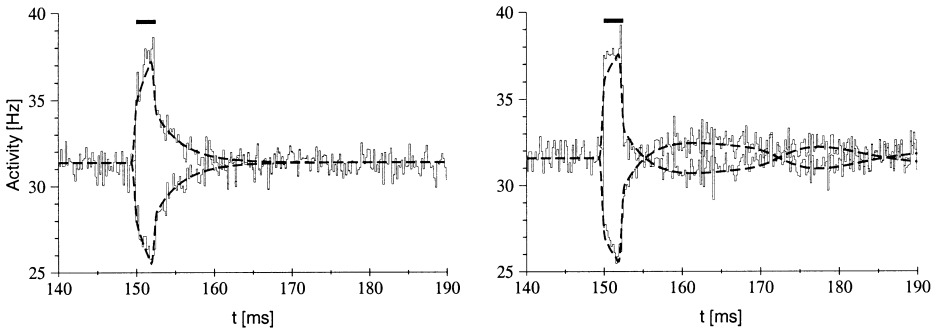


Fig. 2. Simulation results for a noisy threshold population responding to positive and negative square pulses of duration 2.5 ms for two different noise levels (solid line), and the theoretical responses (dashed). Left: High noise, $\sigma = 1$. Right: Low noise, $\sigma = 0.005$. Parameters: time constant $\tau = 4$ ms; thresholds chosen to produce the same mean activity $A_0 \approx 31$ Hz for both noise levels; input step size chosen to produce peaks of comparable size, $\Delta A \approx 6$ Hz. Simulation step size 0.2 ms.

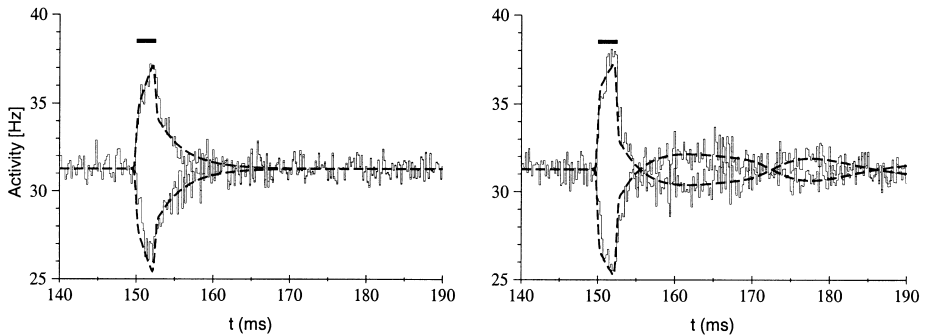


Fig. 3. Simulation results for a population of noisy integration neurons responding to positive and negative square pulses of duration 2.5 ms for two different noise levels (solid, stepped lines), compared with the theoretical responses (dashed) calculated for the noisy threshold model. Left: Noisy integration, high noise, $\sigma = 1$. Right: Noisy integration, low noise, $\sigma = 0.005$. The theory curve shown is the one calculated for the noisy threshold model. Parameters: number of neurons, time constant, and input step size identical to the ones used in Fig. 2; thresholds adjusted to produce the same mean activity $A_0 \approx 31$ Hz; time step 0.1 ms (averaged to 0.2 ms).

quite similar to the simulations with noisy integration, despite the fact that there are no free parameters in the model (given that we use the value of c from Plesser and Gerstner [13]).

4. Discussion

We have seen how the shape of the PSTH response $A(t)$ to a pulse $\Delta h(t)$ may be calculated analytically using population theory provided the interval distribution

$P_h(t|\hat{t})$ is known. This distribution can be calculated using a spike-response neuron with an escape-noise model. This gives us a way to analyze the effect of noise on the form of a PSTH in response to a pulse. Here we have shown that a simple integrate-and-fire-type model together with an intuitively appealing noise model (for the subthreshold regime) can reproduce the effect of noise found experimentally in motoneurons, usually modeled using the computationally inconvenient noisy integration model (integrate-and-fire with diffusive noise). Because the spike-response model on which this approach is based is a very general model, the effect could also be explored for more realistic neuron models (such as Hodgkin–Huxley) simply by utilising the appropriate kernels [11].

In the simulations of the noisy threshold model and of the noisy integration model, the shape of the PSTH response to a pulse depends on the noise level, as in the motoneuron experiments. Both simulated responses are in good agreement with the analytical prediction made using the noisy threshold (Arrhenius and Current) model in the below-threshold regime: for low noise levels, the PSTH response is strongly influenced by the derivative of the input pulse, while for higher noise levels, the PSTH resembles the input pulse itself. Thus, for low noise and given a mean input h_0 that is just below threshold, the effect of applying a pulse to a neuron is to force a spike resulting in the main peak of the PSTH. Due to the noise it will again be possible for the neuron to spike one typical period later, resulting in a secondary peak. In high noise, synchrony between membrane trajectories is rapidly lost following the primary peak and a secondary peak is not observed. The duration of this synchrony is related to the length of time it takes for the survivor function $S(t|\hat{t}) = 1 - \int_0^t P_h(s|\hat{t}) ds$ to decay towards 0 following \hat{t} .

The noisy threshold model predictions compare remarkably well to the observed behavior of the noisy integration model. The only free parameter in the model is not even really free, given that we use the optimized value from Plesser and Gerstner [13]. This shows how a population-based model can accurately incorporate the effect of synaptic noise and provides a good basis for interpreting the results of the motoneuron experiments of Poliakov et al.

References

- [1] W.H. Calvin, C.F. Stevens, Synaptic noise and other sources of randomness in motoneurone interspike intervals, *J. Neurophysiol.* 31 (1968) 574–587.
- [2] E.E. Fetz, B. Gustafsson, Relation between shapes of post-synaptic potentials and changes in firing probability of cat motoneurons, *J. Physiol.* 341 (1983) 387–410.
- [3] W. Gerstner, Time structure of the activity in neural network models, *Phys. Rev. E* 51 (1) (1995) 738–758.
- [4] W. Gerstner, A framework for spiking neuron models – the spike response method, in: J. Leo van Hemmen (Ed.), *Models of Neural Networks*, Vol. 4, Springer, New York, 1999.
- [5] W. Gerstner, J.L. van Hemmen, J.D. Cowan, What matters in neuronal locking, *Neural Comput.* 8 (1996) 1689–1712.
- [6] W. Gerstner, Population dynamics of spiking neurons: fast transients, asynchronous states and locking, *Neural Comput.* 12 (2000) 43–89.
- [7] B. Gustafsson, D. McCrea, Influence of stretch-evoked synaptic potentials on firing probability of cat spinal motoneurons, *J. Physiol.* 347 (1984) 431–451.

- [8] A. Herrmann, W. Gerstner, Understanding the PSTH response to synaptic input, in: D. Willshaw and A. Murray (Eds.), ICANN'99, Ninth International Conference on Artificial Neural Networks, Vol. 2, The Institution of Electrical Engineers, London, 1999, pp. 1012–1016.
- [9] P.A. Kirkwood, T.A. Sears, The synaptic connexions to intercostal motoneurons as revealed by the average common excitation potential, *J. Physiol.* 275 (1978) 103–134.
- [10] P.A. Kirkwood, T.A. Sears, Cross-correlation analysis of motoneurone inputs in a co-ordinated motor act, in: J. Krüger (Ed.), *Neuronal co-operativity*, Springer, Berlin, 1991, pp. 225–248.
- [11] W.M. Kistler, W. Gerstner, J. Leo van Hemmen, Reduction of Hodgkin–Huxley equations to a single-variable threshold model, *Neural Comput.* 9 (1997) 1015–1045.
- [12] C.K. Knox, Cross-correlation functions for a neuronal model, *Biophys. J.* 14 (1974) 567–582.
- [13] H.E. Plesser, W. Gerstner, Noise in integrate-and-fire neurons: from stochastic input to escape rates, *Neural Comput.* 12 (2000) 367–384.
- [14] A.V. Poliakov, R.K. Powers, M.D. Binder, Functional identification of the input–output transforms of motoneurons in the rat and cat, *J. Physiol.*, Part 2, 504 (1997) 401–424.
- [15] A.V. Poliakov, R.K. Powers, A. Sawczuk, M.D. Binder, Effects of background noise on the response of rat and cat motoneurons to excitatory current transients, *J. Physiol.*, Part 1, 495 (1996) 143–157.
- [16] H.C. Tuckwell, *Introduction to Theoretic Neurobiology*, Vol. 1, Cambridge University Press, Cambridge, 1988.
- [17] H.C. Tuckwell, *Stochastic Processes in the Neurosciences*, SIAM, Philadelphia, 1989.



Alix Herrmann is a doctoral student at the Center for Neuromimetic Systems MANTRA at the Swiss Federal Institute of Technology Lausanne (EPFL). Her undergraduate degrees are in Physics/Astronomy (Pomona College, Claremont, California) and Engineering (California Institute of Technology, Pasadena, California). Her research interests are in temporal coding using spiking neurons in sensory systems, and in the processing of transient sounds in the auditory system.



Wulfram Gerstner is an Assistant Professor and Director of the Center of Neuromimetic Systems MANTRA at the EPFL. His research interests are in the theory of neural network with a special emphasis on models of spiking neurons, on the problem of temporal coding, and on the role of spatial representation for navigation and path planning of autonomous agents. He teaches courses on Neural Networks for Computer Scientists, Electrical Engineers, and Physicists at the EPFL.