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# Coherence resonance and discharge time reliability in neurons and neuronal models

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## Abstract

Neurons are subject to internal and external noise that have been known to modify the way they process incoming signals. Recent studies have suggested that such alterations have functional roles and can also be used in biomedical applications. The present work goes over experimental and theoretical descriptions of the response of neurons to white noise stimulation. It examines various forms of noise related behavior in a standard neuronal model, namely the leaky integrate and fire. This clarifies the conditions under which specific noise induced changes occur in neurons, and consequently can help in determining whether nervous systems operate under similar circumstances. © 2001 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

Neurons are subject to various forms of internal and external noise (Holden, 1976). That these affect their response has long been known. For instance early experiments showed that only a fraction of widely spaced pulsatile stimuli of a given amplitude evoked a discharge from nerves (Pecher, 1939), and that whether a firing occurred or not probably depended on the influence of internal fluctuations. Many studies have been devoted to the description of the noise present in neuron membranes (Verveen & DeFelice, 1974) and (external) noise related changes in neuronal responses (reviewed in Segundo, Vibert, Pakdaman, Stiber & Diez-Martínez, 1994). These have shed light on phenomena such as linearization by noise whereby the nonlinear distortions in the input–output relation of neurons decrease in the presence of an auxiliary noisy signal.

In the past decades, a number of novel noise-induced changes in neuronal responses were observed. These include surprising and somewhat counter-intuitive effects such as coherence resonance—noise-increased discharge regularity—and stochastic resonance—noise-enhanced sensitivity to weak stimulation. The purpose of the present work is to review the experimental and theoretical

evidence for such noise related changes in neuronal behavior in the absence of any other input, and provide a description of each in the leaky integrate and fire model. In the process, we will also present novel analyses of some of these phenomena, which shed light on the underlying mechanisms.

One motivation behind our work is that it has been suggested that noise induced changes can be used in biomedical applications, for instance as a means to improve cochlear implants (Morse & Evans, 1996), or to compensate for a pathological decrease in sensory sensitivity (Cordo, Inglis, Verschueren, Collins, Merfeld, Rosenblum et al., 1996). Such potential usage, and recent evidence for the functional implication of noise and stochastic resonance (Braun, Wissing, Schäfer & Hirsch, 1994; Russell, Wilkens & Moss, 1999) highlight the necessity for an overview of the influence of noise on neuronal behavior. To this end, we examine the effect of noise alone, in the absence of any other inputs on neuronal behavior. While this topic is of interest by itself and numerous studies have been devoted to it (references are provided in the appropriate sections), it is also a prerequisite for clarifying the role of noise when used as an auxiliary signal such as in linearization by noise and stochastic resonance.

This paper is organized as follows. Section 2 presents a brief description of the leaky integrate and fire model. Sections 3–5 are, respectively, devoted to coherence

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resonance, discharge time reliability and noise-induced transition in neurons and neuronal models. Section 6 presents a discussion of the results.

## 2. The leaky integrate and fire model

The leaky integrate and fire (LIF) model is one of the earliest mathematical models for neurons which has been extensively studied (see Tuckwell, 1988, and two recent comprehensive reviews: Lansky & Sato, 1999 and Ricciardi, Di Crescenzo, Giorno & Nobile, 1999). The subthreshold dynamics of the membrane potential of this model is described as:

$$\frac{dV(t)}{dt} = -\frac{V}{\tau} + \mu + I(t) + n(t), \quad V(t) < S_0,$$

$$V(t^+) = V_0, \quad \text{if} \quad V(t) = S_0, \quad (1)$$

where  $V(t)$  is the membrane potential,  $S_0$  is the constant firing threshold,  $V_0 (< S_0)$  the post-discharge resetting potential,  $\tau$  the membrane time constant,  $\mu$  the resting potential,  $I(t)$  the input signal, and  $n(t)$  the noise. In the following, we mainly consider  $n(t)$  to be white Gaussian noise.

The LIF generates an action potential when  $V$  exceeds  $S$ , which is described by an impulse. After that,  $V$  is immediately reset to  $V_0$ . Subsequent inputs lead to repetition of the process. In this way, the LIF captures two key properties of neurons and other excitable membranes: (i) it displays an all-or-none response because of the threshold, and (ii) each firing is followed by a refractory period during which the LIF progressively recovers its excitability due to the post discharge resetting of the membrane potential to a value  $V_0$  which lies in general below the resting potential  $\mu\tau$ .

In the absence of noise i.e.  $n(t) = 0$ , one can distinguish between sub and suprathreshold forcing. If  $t \rightarrow \mu\tau + \int_{-\infty}^t e^{-(t-s)/\tau} I(s) ds$  remains below the threshold  $S_0$  for  $t$  large, then the LIF will fire at most a finite number of discharges and remain quiescent henceforth. This is a subthreshold input. If, conversely, the quantity defined above takes values larger than  $S_0$  on at least a sequence  $\{t_i\}$  tending to  $+\infty$ , then, the LIF generates sustained firing. The input is suprathreshold. When the injected input  $I = 0$ , then one finds the standard conditions  $\mu\tau < S_0$  and  $\mu\tau > S_0$  for sub and suprathreshold, respectively.

When  $I = 0$  and  $n(t)$  is a white Gaussian noise of intensity  $D$ , i.e. the formal derivative of  $DW(t)$  the standard Wiener process, the stochastic process satisfying Eq. (1) with  $S_0 = +\infty$  is called (the free running) Ornstein–Uhlenbeck (OU) process. In other words, the OU is solution to Eq. (1) with no threshold.

We refer to the first-passage-time (FPT) as the time interval  $u$  after which  $V$  reaches  $S_0$  for the first time given  $V(t') = V_0 < S_0$ , where  $t'$  is the previous firing time. In

other words,

$$\text{FPT} = \inf\{u : V(t' + u) > S_0 | V(t') = V_0 < S_0\} \quad (2)$$

The FPT is a random variable with probability density function (pdf)  $g(S_0, u | V(0) = V_0)$  satisfying the following integral equation (Ricciardi, 1978)

$$p(x, t | V_0, 0) = \int_0^t g(S_0, u | V_0) p(x, t | S_0, u) du \quad (3)$$

where  $x > S_0$ ,  $V(0) = V_0 < S_0$ , and  $p(x, t | y, s)$  is the transition pdf of the free running OU process (without any threshold):

$$p(x, t | y, s) = \frac{1}{\sqrt{2\pi D_{t,s}}} \exp\left[-\frac{(x - ye^{-(t-s)/\tau})^2}{2D_{t,s}^2}\right] \quad (4)$$

$$D_{t,s}^2 = \frac{D^2\tau}{2}(1 - e^{-2(t-s)/\tau}). \quad (5)$$

Thus,  $g(t)dt$  represents the probability for a discharge to occur after the interval  $(t, t + dt)$  from the previous firing.

## 3. Coherence resonance

When neurons are in the excitable regime, they remain quiescent unless a strong enough stimulation is applied which evokes an action potential followed by a return to the resting state. When the stimulation is white Gaussian noise, it leads to recurrent excursions of the membrane potential across the firing threshold, thereby producing repetitive firing. The main concern of this section is the regularity of such noise evoked spike trains.

At low noise intensities, the membrane potential fluctuates mainly around its resting value, with an occasional threshold crossing. In this regime, the discharge times can be well approximated by a Poisson process. Conversely, at large noise regimes, the membrane potential fluctuations are completely dominated by noise. The firing is fast and highly irregular. Coherence resonance (CR) refers to a phenomenon that occurs in the intermediate range of noise and whereby the firing becomes more regular than the low and high noise intensity regimes. While this term was first coined by Pikovsky and Kurths (1997) in their study of the FitzHugh–Nagumo model, various aspects of the phenomenon itself had been described in earlier papers and different models.

Sigeti and Horsthemke (1989) examined an elementary system evolving on a circle and at a saddle–node bifurcation. They reported that noise led to pseudo-regular oscillations in this system, thus providing evidence for CR. Gang, Ditzinger, Ning and Haken (1993) studied a similar system which could also be approximated by a point moving around a circle and which displayed two simultaneous saddle–node bifurcations. They systematically examined the influence of noise on the regularity of the behavior of the system in both the excitable regime (where the system possessed two stable

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