Stochastic Resonance Driven by Time-Modulated Neurotransmitter Random Point Trains

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Information transmitting by temporally modulated random point trains, such as neurotransmitter quanta and spikes, which are neither additive signal and noise nor diffusion approximated additive signal and noise, is studied. We demonstrate that tuning the input train's average rate can optimize the response of an integrate-and-fire model neuron to a signal modulated point train. The characteristics of this phenomenon and its biological significance are discussed.

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Stochastic resonance (SR), which was first proposed by Benzi *et al.* to explain the possible mechanism of the periodic ice ages, is a phenomenon that signal expression can be surprisingly optimized by tuning noise level [1]. Since the concept of SR was introduced, extensive attention has been paid to the response of a nonlinear system to signal with additive noise [2–7]. For neurons communicating with pulse trains, only similar situations were studied in which the drivings are either periodic pulses plus noise such as Poissonian pulse train [8] or trains of excitatory and inhibitory pulses with infinitesimal amplitude which can be approximated as analogous additive signal and noise [9,10].

However, a general situation is that a driving pulse train is a stochastic excitatory point train with rates modulated by the information it conveyed, wherein a stochastic point train is not only an information conveying medium but also a noise source at the same time and cannot be divided into additive signal and noise. Consider, for instance, the neurotransmitter trains which are released in quantum from inner hair cells and drive the auditory neurons, and the auditory neuron produced spike trains summed in the cochlear nucleus in the auditory system. Both the neurotransmitter trains and the auditory spike trains are random point drivings with rates modulated indirectly by stimulating sound [11]. Modulated stochastic point trains like these, also known as all-or-none event trains, are general information expressing form in the brain. How the random neural signal expresses deterministic information and how the random point expressed information is transmitted and processed are intriguing, and attract increasing attention [12–16]. Rate code and temporal code are focuses concerned. Point train coded temporal information's optimal transmission by tuning independent additive noise has been shown before [8,17]. By tuning the average point rate instead here, random points coded temporal information's optimal transmission is demonstrated.

In the present study, we propose a concept of random point process driven stochastic resonance, and show numerically in an integrate-and-fire neuron model that a random point train expressed signal can be transmitted optimally by means of stochastic resonance.

We consider the classic integrate-and-fire neuron model. Under the threshold V_{thr}, the neuron membrane potential $V(t)$ is controlled by

$$\frac{dV(t)}{dt} = -\frac{V(t)}{\tau_m} + S(t), \tag{1}$$

where τ_m is the time constant of a neuron, and $S(t)$ is the driving. When the membrane potential $V(t)$ reaches the threshold V_{thr}, a spike is fired by the neuron and the membrane potential resets to zero, from where the membrane potential resumes varying under the control of Eq. (1). The output of the neuron $y(t)$ is

$$y(t) = \begin{cases} 1, & V = V_{\mathrm{thr}} \\ 0, & V \neq V_{\mathrm{thr}} \end{cases} \tag{2}$$

and can be expressed as $y(t) = \sum_{t_n} \delta(t - t_n)$, where t_n is the moment the neuron is spiking.

The driving $S(t)$, contrary to the traditional additive signal and noise, is an inhomogeneous Poissonian point train with modulated intensity $\lambda(t)$, and can be expressed by the δ function as $S(t) = V_0 \sum_{t_m} \delta(t - t_m)$, where V_0, less than threshold V_{thr}, is the amplitude of the point driving and t_m is the stochastic instant when a driving neurotransmitter or spike is arriving. Figure 1

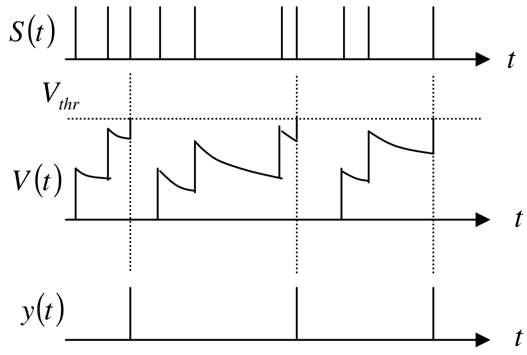

FIG. 1. Potential variation $V(t)$ and spike output $y(t)$ of a spike train $S(t)$ driven integrate-and-fire model.

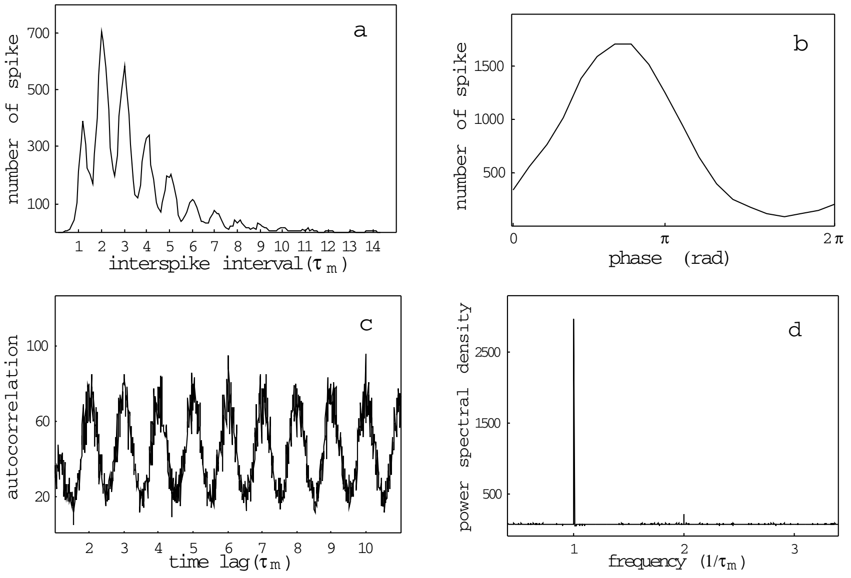

FIG. 2. Example of calculated (a) interspike interval histogram, (b) period histogram, (c) autocorrelation, and (d) power spectral density. $\lambda(t) = A + B\cos(2\pi f t)$, $A = 7$, $B = 5$, $T = \tau_m$, $f = 1/\tau_m$, and $V_0 = 0.1V_{\text{thr}}$. Time is scaled in τ_m. Amplitude is scaled in V_{thr}. The number of phase bins in a period is 20 in the period histogram.

demonstrates the processes of the membrane potential varying and the spike producing under the driving of $S(t)$. When a point stimulus arrives, the potential increases in a step of V_0. When the potential reaches the threshold V_{thr}, a spike is produced and the potential resets to zero, otherwise, the potential decreases in an exponential way until the next stimulus arrives.

In general, the intensity of a random point process, $\lambda(t)$, can be expressed as $\lambda(t) = a + \sum_n a_n \sin(n2\pi f t) + b_n \cos(n2\pi f t)$, where f is the frequency of the signal to be conveyed. For the reason of convenience, consider a simple situation $\lambda(t) = A + B\cos(2\pi f t)$, where $A \geq B$. This point process has a noise level AV_0^2 determined by its average rate A and a signal level $\frac{1}{2}B^2V_0^2$ determined by modulating amplitude B [18,19].

For Eq. (1), diffusion approximation [9,10] is not suitable because V_0 is not infinitesimal, but, for example, in auditory neuron, is one of a few parts of V_{thr} [20]. Up to now, to our knowledge, there is no analytical solution to probability density of the first passage time of the integrate-and-fire model driven by random point process even with a constant intensity λ. We demonstrate the response property of the integrate-and-fire neuron to random point stimuli with intensity $\lambda(t) = A + B\cos(2\pi f t)$ by numerical simulation. An Euler discretization with time step $\Delta t = 10^{-2}\tau_m$ is used in Eq. (1) to get the output instant t_n during a period of $5 \times 10^6 \Delta t$. Then the interspike interval histograms, the period histograms (distribution of a spike number in a phase bin, reflecting probability in which a spike outputs at a different phase [21]), and the autocorrelation functions $R_{yy} = \langle y(t)y(t+\tau)\rangle$ of output spike trains are computed. Fourier transforming the autocorrelation $R_{yy} = \langle y(t)y(t+\tau)\rangle$ gets the power spectral density $S_{yy}(f)$ of an output spike train. Figure 2 is an example of the calculation. The output spike interval histogram shows, in Fig. 2(a), that the output spike intervals are stochastic but tend to be a multiple of the period T of the conveyed signal. The period histogram shows, in Fig. 2(b), that the spikes are produced at a random time but tend to appear at a certain phase; that is, the output spikes are phase locked. Figures 2(c) and 2(d) show that the output spike train is temporal correlated and has a main component with the same frequency of the conveyed signal. Components with multiple frequencies of the conveyed signal have much smaller amplitudes than the main component. The height of background around the main component in Fig. 2(d) is the noise level of the output spike train. The output spike

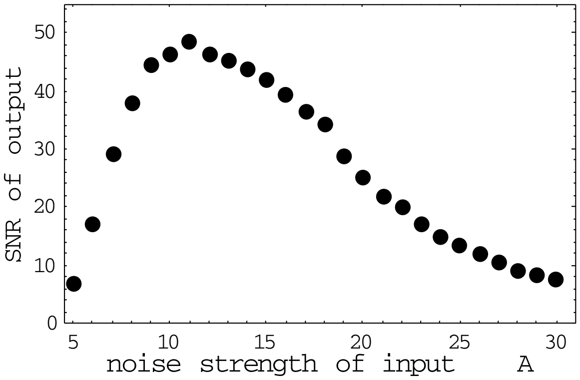

FIG. 3. Signal to noise ratio of output spike train. $\lambda(t) = A + B\cos(2\pi f t)$, $B = 5$, $T = \tau_m$, $f = 1/\tau_m$, and $V_0 = 0.1V_{\text{thr}}$.

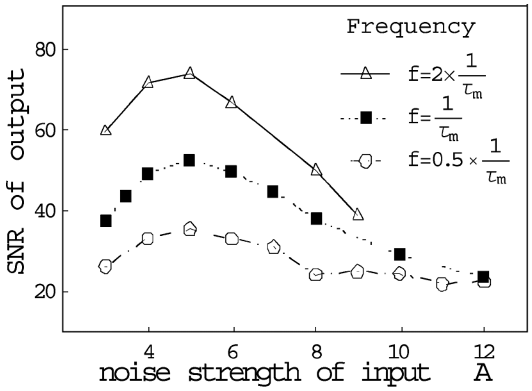

FIG. 4. Resonance curves of signals with different frequencies. $\lambda(t) = A + B\cos(2\pi f t)$, $B = 3$, and $V_0 = 0.2V_{\mathrm{thr}}$.

train's SNR (signal-to-noise ratio) is the level ratio of signal to background noise in the power spectral density of the output spike train.

In a certain range of parameters, there is an optimal average point rate, A_{optimal}, that is, an optimal input noise level, which produces the largest output SNR. Figure 3 shows an example of this phenomenon similar to the traditional stochastic resonance, which we call random point driven stochastic resonance.

It seems that this kind of optimal signal transmission should occur when the most possible interspike interval is equal to the period of transmitted signal, and that the random point driven stochastic resonance should be a bona fide resonance because of the most possible interspike interval's dependence on the average rate A. However, our results show, in Fig. 4, that signals with different frequencies have an identical optimal A independent of signal frequency. Our results show optimal A depends on the ratio of spike amplitude V_0 to firing threshold V_{thr} instead.

Figure 5 shows that with increasing V_0, the optimal A decreases. The larger V_0 is, the smaller the optimal A is. As an inhomogeneous Poissonian process, $\lambda(t) \geq 0$, and $B \leq A$. For a certain value of V_0, only when modulating amplitude B is smaller than a certain value, the neural signal transmitting performance can be improved by increasing A. So the optimal signal transmission is also limited to a weak signal, in addition to the limit $V_0 < V_{\mathrm{thr}}$, which the traditional stochastic resonance driven by the additive signal and noise is subject to [8].

The present study shows that random points expressed temporal information can be transmitted optimally through a nonlinear system by tuning the average rate, that is, the noise strength of the random point train medium. This is heuristic for understanding the information coding and processing mechanism in the neural system. For example, our results mean that the efficient transmission of the random point train coded information needs a point train with an optimal average rate, which does not express information, but just plays a role of information transmission media. The spontaneous neural activities may provide the optimal media point trains. One of the supporting factors is that the auditory neurons' responses to near threshold sound stimuli tend to be phase-locked fires instead of an increase in the average spike rates, and the sound intensity threshold for the change of the spiking temporal pattern is far below the intensity resulting in an increase of average rate [22]. Point trains bearing no information, such as the spontaneously released neurotransmitter trains of inner hair cells and the spontaneous auditory spike trains which exist when no sound stimuli are applied, may not be noise sources limiting our perception, but optimal point trains sensitizing our perception.

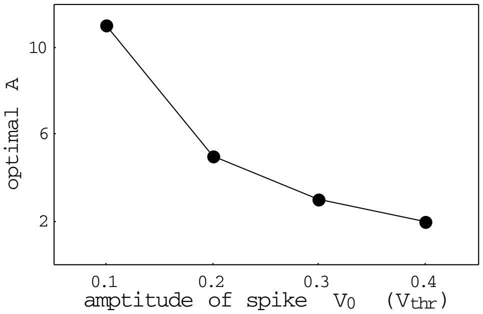

FIG. 5. Optimal rate A_{optimal}'s dependence on spike amplitude V_0. Because $\lambda(t) \geq 0$, $B \leq A$. The dependence of A_{optimal} on spike amplitude V_0 means that, for a certain value of V_0, the modulating amplitude A is needed to be small enough to observe increase of output SNR with an input noise level increase. V_0 is scaled in V_{thr}. Modulating frequency $f = 1/\tau_m$.

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