Coherence resonance due to transient thresholds in excitable systems

Ramana Dodla and Charles J. Wilson

Department of Biology, University of Texas at San Antonio, San Antonio, Texas 78249, USA
(Received 21 June 2010; published 6 August 2010)

Excitable systems can have more than one response threshold, but accessing each of these is only facilitated by preferential choice of the appropriate components in the input noise. The coherence resonance phenomenon discovered by Pikovsky and Kurths [Phys. Rev. Lett. **78**, 775 (1997)] utilizes only one response threshold, thus leaving the nature of the dynamics of a possible second threshold unspecified. Here we show using a FitzHugh-Nagumo excitable system that the second response threshold can be reached transiently by brief pulses in the negative noise component, leading to a coherence resonance phenomenon of its own. The resonance can occur both as a function of input amplitude and frequency. The phenomenon is also illustrated in more realistic Hodgkin-Huxley model equations, and analytical predictions are made using probabilistic considerations of the input. This phenomenon attributes more complex role noise can play in excitable systems.

I. INTRODUCTION

Noise is ubiquitous in dynamical systems [1] and has been shown to play a constructive role in signal detection and enhancement tasks. A number of noise-dependent dynamic phenomena have been discovered in the recent past [2–6]. Excitable systems in particular exhibit a novel coherence resonance phenomenon as a function of input noise level [3,7]. Coherence resonance is displayed by a wide variety of systems such as different formulations of FitzHugh-Nagumo model [7–13], Belousov-Zhabotinsky reaction equations [14,15], coupled Morris-Lecar models [16], and stochastic, and chaotic systems [17,18]. Experimental evidence of coherence resonance phenomenon is found in optical systems [19], electrochemical systems [20,21], chaotic diode lasers [22], and semiconductor lasers [23].

The universal premise of an excitable system is that there is an internal threshold surface that must be crossed by the system in response to a stimulus so that it may be excited from its equilibrium. To the best of our knowledge, all previous studies simplified this assumption to mean that there is a single planar threshold that must be crossed in order to exhibit coherence resonance phenomenon; The excitable systems are usually studied in parameter regimes that are close to a bifurcation point that signifies the birth of a periodic or a spiking solution, and thus ensuring that the system is near a response threshold. Though not necessary, this practice underlines the current understanding of how coherence resonance may appear in excitable systems.

The consequence of this assumption is that though noise can push the system above (i.e., positive or toward) or below (i.e., negative or away from) the equilibrium level, the component of the noise that can take the system toward the threshold is of central importance, and the other component is thought to have no meaningful role to play in coherence resonance. This is in contrast to the stochastic resonance phenomenon [6] where both components of noise can play a role in causing the resonance.

In this paper we show that both components of noise can play a role in causing coherence resonance, in particular, the component that takes the system farther from its threshold can itself cause coherence resonance. This does not contradict the definition of excitable system, but makes use of the phenomenon by which transient threshold events can be induced in response to brief pulses of input. Such phenomena were studied earlier in specific models of synchrony [24–26] and excitability [27], but an attempt to study its consequence to coherence resonance was never made. We show the phenomenon in FitzHugh-Nagumo (FHN) model that shows the phenomenon without decrease of the firing rate, as well as the original model from which it is derived, the Hodgkin-Huxley (HH) that shows the phenomenon with decrease in the firing rate. Our result emphasizes a greater role for noise in excitable systems. It reveals the similarity between stochastic response of excitable systems and that of stochastic resonant systems in which both components of noise can play active role in the underlying mechanisms. The reason why this mechanism was not recognized earlier is also clear: it uses a transient threshold mechanism for noise that lowers the equilibrium away from threshold, and the strength of input for eliciting a response for negative input is usually larger than that required for a positive input.

II. TWO-THRESHOLD SYSTEM

We consider the FitzHugh-Nagumo (FHN) equations [7,28] in the following formulation.

$$\epsilon \dot{x} = x - x^3 - y + I_{app} + \eta(t),$$

$$\dot{y} = \gamma x - y, \tag{1}$$

where $\epsilon = 0.01$, and $\gamma = 1.0$. $\eta(t)$ is the noise term. In the absence of noise, and for large ϵ, rest state $[(x^*, y^*) = (f, f)$ where $f = I_{app}^{1/3}]$ is stable for $I_{app} < -I^*$ or $I_{app} > I^*$, where $I^* = 1/3^{3/2}$. We set $I_{app} = -0.2$ such that the component of the noise $\eta(t) > 0$ would take the membrane closer to the bifurcation point, and the other component $\eta(t) < 0$ would take it away from it.

Model Eqs. (1) are excitable. A positive step of steady input current [Fig. 1(a)] can result in periodic oscillations of spikes with a nonzero frequency because the system is

(a) Response to positive step stimulus

(b) Response to negative step stimulus

(c) Response to brief negative pulse

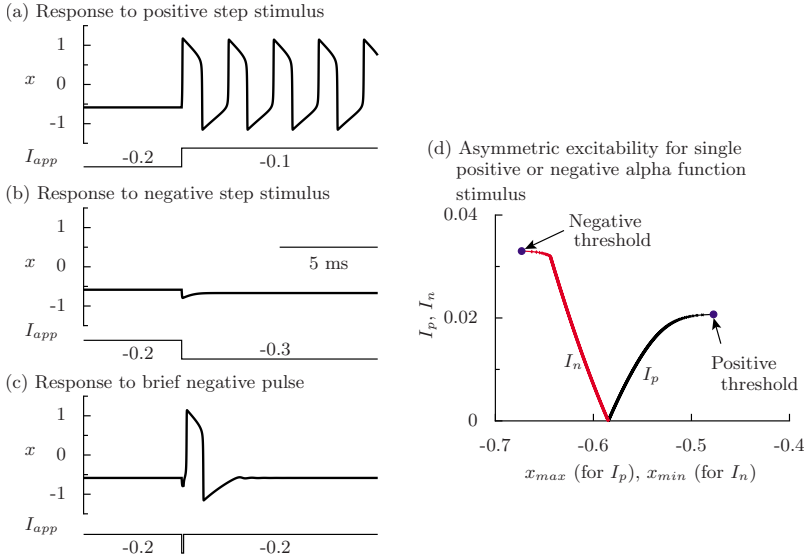(d) Asymmetric excitability for single positive or negative alpha function stimulus

FIG. 1. (Color online) Demonstration of transient threshold and asymmetry in excitability. Response of Eqs. (1) to a step of positive (a) and negative (b) steady applied currents, and to a 0.1 ms brief pulse of negative current of amplitude 0.1 (c). (d) The maximum deflection away from equilibrium caused by a single brief (alpha function) stimulus is plotted as a function of the strength of the stimulus. Increasing the strength of I_p or I_n beyond the indicated dots elicits a spike response in either case.

pushed past its subcritical Hopf bifurcation point into the periodic regime. A negative step of current with the same amplitude evokes another steady state and no spike response [Fig. 1(b)] because no bifurcation point is crossed in this regime, and in fact the system is pushed farther from the bifurcation point. But reducing the negative pulse width to last only a brief period of time, a spike response may be elicited [Fig. 1(c)]. This behavior is also termed postinhibitory rebound or anodal break excitation. Variations of this behavior include eliciting more than one spike for a brief negative pulse, or a response at the cessation of the negative pulse of even longer duration. In any of these cases, a continuous train of spikes is never elicited. And evoking a response is principally due to a reduction of spike threshold caused by the negative input, and the subsequent recovery of the x variable past the lowered threshold. The response however depends on the amplitude and duration of the negative stimulus. At a fixed pulse duration, a spike can be elicited with either positive or negative current if the amplitude is increased beyond a threshold level. The thresholds are not identical for positive and negative inputs [Fig. 1(d)], making it very likely for the negative threshold spikes that need larger input strength to be hidden from observation when noise of smaller amplitude is used.

Noise with sufficient amplitude can thus induce spike responses for both positive component in the noise, and the negative component as described above. The effect of negative component may be masked because of the offsetting effect of the positive component, or because of continuous barrage of negative inputs which again yield no response [the effect is similar to Fig. 1(b)]. But discrete inputs, if windowed appropriately, could summate to result in a super-threshold stimulus resulting in a spike. To have full control over the positive and the negative components of the noise, we set η to a Poisson arrival train with positive and negative deflections,

$$\eta(t) = \sum_{i=1}^{N_p} I_p g(t - t_i) - \sum_{j=1}^{N_n} I_n g(t - t_j), \qquad (2)$$

where t_i and t_j are two independent Poisson random arrival times with rate λ, and N_p and N_n are the number of

such arrivals during the entire integration time window. $g(t) = t/\tau \times e^{1-t/\tau} \delta(t)$ is an alpha function pulse that essentially acts like a very short impulse at the arrival of each Poisson input with a time constant τ (=0.005). I_p and I_n are, respectively, the strengths of positive and negative stimuli.

III. COHERENCE RESONANCE

A regular firing pattern [as the response in Fig. 1(a)] would have no variability among its spike times, and the coefficient of variation (R) of its spike times is zero. A random spike train pattern with the spike times determined by a Poisson process will have a R of unity. Setting $I_p = I_n$ and increasing the amplitude would take the model from an irregular firing pattern (R of 1) through a region of increased coherence (i.e., decreased R) and finally to an incoherent firing pattern at strong amplitude [Fig. 2(a)]. This is the original coherence resonance result reported by Pikovsky and Kurths [7]. Turning off the negative input pulses, and retaining only the positive input pulses, altered the profile of the resonance curve very little. Particularly, the maximum coherence attained (i.e., lowest R) is not altered significantly. Thus the negative pulses have slightly irregularizing effect at smaller amplitudes (by lowering the R), and regularizing effect at larger amplitudes.

But retaining the negative pulses alone produced a separate coherence resonance curve of its own with maximum coherence at a different amplitude level. Resonance phenomena can also be seen as a function of input frequency of the negative input [Fig. 2(b)] with the maximum coherence and its position dependent on the amplitude of the input. The increase in coherence is accompanied by an increase in the firing rate of the model, and the position of the maximum coherence is dependent on the quasithreshold offered by the refractory period of the model [3]. Such is still the case in the FHN model under the presence of pure negative inputs. But in models where the quasithreshold is stiffer (requiring stronger input), the recovery of the incoherence in the resonance curve is dominated by the reduction of the firing rate. The maximum coherence occurs when the firing rate is maxi-
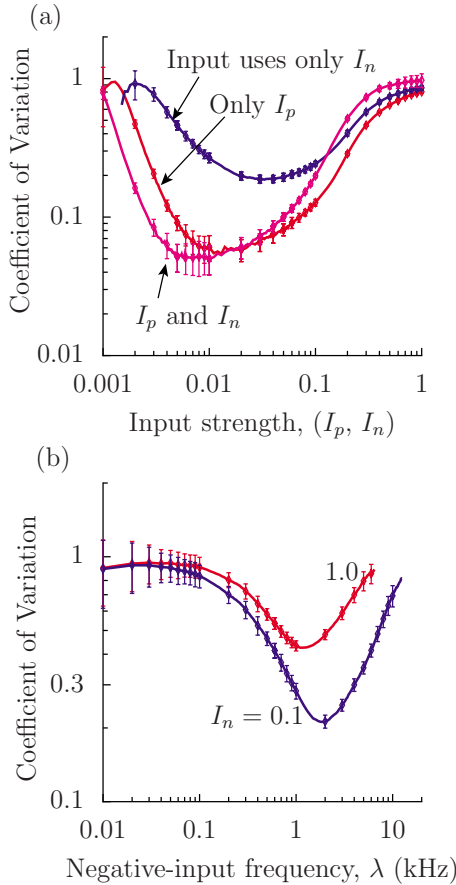
(a)

(b)

FIG. 2. (Color online) Coherence resonance due to brief negative inputs shown by Eqs. (1) as a function of strength and frequency. (a) Coefficient of variation (R) of interspike intervals as a function of the alpha function input amplitude when only negative input (I_n), positive input (I_p), or both negative and positive inputs (I_p and I_n) are present. The input frequency of each input is 10 kHz. (b) R as a function of negative input frequency at two values of input strength. A fourth-order Runge-Kutta algorithm with a time step of 0.001 ms and $\tau = 0.01$ ms is used. Averaging was done over 100 realizations with each integration lasting 1 s duration. The length the error bars (shown at selected parameters) is twice the standard deviation across the realizations.

mum. The Hodgkin-Huxley model [30] offers such a mechanism under the effect of random but pure negative or inhibitory input (Fig. 3). We now provide a probabilistic explanation for the resonant curve profile.

IV. ANALYTICAL ESTIMATE

If each arriving inhibitory input evokes a rebound spike, then the output interspike interval density follows the input interarrival density. Since the input is Poisson and the arrivals are independent, the waiting time for any arrival following any given pattern of arrivals will also follow exponential distribution. So if we disregard the input arrivals within the refractory period, t_R, then the interspike interval density is expected to be

$$f(t) = \lambda e^{-\lambda(t - t_R)} H(t - t_R),$$

where H is the Heaviside function, and λ is the rate of Poisson arrivals. From the density distribution function, we can
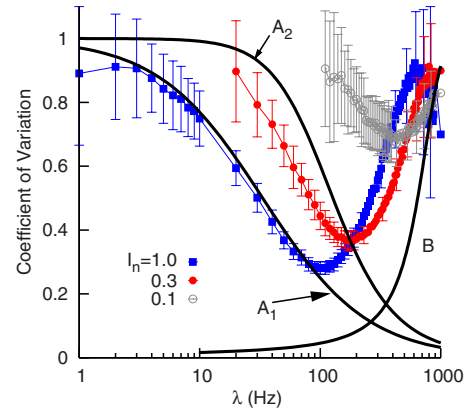

FIG. 3. (Color online) Computational and analytical profiles of coefficient of variation (R) of interspike intervals of the four variable Hodgkin-Huxley model as a function of inhibitory input rate λ at three different levels of input strength, I_n. A_1, A_2, and B are analytical predictions. Ten realizations of 1000 s each are used to compute the error bars (shown at selected points) whose length is twice the standard deviation over the realizations. $\tau = 1$ ms, and the integration time step of the fourth-order Runge-Kutta was 0.002 ms.

compute the mean and variance of the waiting times,

$$\langle t \rangle = \frac{1}{\lambda} + t_R,$$

$$\langle t^2 \rangle - \langle t \rangle^2 = 1/\lambda^2.$$

Hence, the coefficient of variation is

$$R = \frac{1}{1 + \lambda t_R}.$$

This is the curve A_1 shown in Fig. 3. From this formula we clearly see that the refractory period is crucial in causing the R to decrease from unity, similar to the coherence resonance mechanism that occurs for excitatory events [7]. In the limit of $t_R \to 0$, the output statistics follow that of the input, and the R becomes unity.

As the input strength I_n is decreased (see the curve for $I_n = 0.3$ in Fig. 3), one needs more than one input conductance to cooperatively summate to result in a rebound spike. We seek a density function for the distribution of such waiting times. The waiting time for an output spike is the time for obtaining two arriving inputs in a window smaller than t_w. Let us assume that the waiting time is t, and let us split this into time windows of width t_w, and hence there are $N \equiv t/t_w$ number of windows. Each window is allowed to have at most one input. So the combined probability that there is no event (of two inputs in any given window t_w) is

$$P(N_{(0,t]} = 0) = [e^{-\lambda t_w} + (\lambda t_w)^1 e^{-\lambda t_w}]^{t/t_w} = e^{-\lambda t}(1 + \lambda t_w)^{t/t_w}.$$

Hence, the probability function is

$$F = 1 - P(N_{(0,t]} = 0) = 1 - e^{-\lambda t}(1 + \lambda t_w)^{t/t_w}.$$

The probability density is

$$f = \frac{dF}{dt} = e^{-\lambda t}(1 + \lambda t_w)^{t/t_w}\left[\lambda - \frac{\ln(1 + \lambda t_w)}{t_w}\right].$$

From this the mean and the standard deviation can be derived. We note that we'll have to add t_R to the value of the mean to take into account the refractory period. We will do this while computing R. Since our input is Poisson timed, our statistics do not change if we had conditioned our probabilities on the arrivals in the refractory period. Thus

$$\langle t \rangle = \frac{t_w}{\lambda t_w - \ln(1 + \lambda t_w)},$$

$$\langle t^2 \rangle = \frac{2t_w^2}{[\lambda t_w - \ln(1 + \lambda t_w)]^2}.$$

The coefficient of variation is written as

$$R = \frac{(\langle t^2 \rangle - \langle t \rangle^2)^{1/2}}{\langle t \rangle + t_R} = \frac{1}{1 + \frac{t_R}{t_w}[\lambda t_w - \ln(1 + \lambda t_w)]}.$$

The expression for R is shown in Fig. 3 as A_2 for the parameters $t_R = 30$ ms and $t_w = 6.14$ ms. This predicts that decreasing the input strength has the effect of maintaining the high randomness among spike times for higher levels of input rate, but R nevertheless decreases with input rate.

Now we estimate R in the high input nonlinear regime. A number of spike evoking and suppressing mechanisms take place in this regime. But we set out to predict the profile of R based on simpler assumptions. In the high input regime, inhibition occurring in close succession keeps the membrane hyperpolarized, and a spike results only when there is a pause in such successive input sequence. We seek waiting time distribution of such pauses. Our simplifying assumption is that we do not impose any further conditions on how long this pause must be. Such conditions may be imposed, but the analysis will become more complicated, and it may not necessarily capture all the complex processes that take place at such input rates. We split the waiting time t into t/t_w windows, and require that each window should have $N+1$ or more number of arrivals to prevent a rebound spike (and keep the membrane in the hyperpolarized regime). So, the probability of waiting for not more than N spikes in successive windows of width t_w is

$$P = \left[1 - \sum_{k=0}^{N}\frac{(\lambda t_w)^k}{k!}e^{-\lambda t_w}\right]^{t/t_w} = \left[1 - \frac{\Gamma(N+1, \lambda t_w)}{\Gamma(N+1)}\right]^{t/t_w},$$

where we have used the definitions of both complete and incomplete gamma functions. The probability density function is

$$f = \frac{d}{dt}(1 - P) = -\frac{1}{t_w}\left[1 - \frac{\Gamma(N+1, \lambda t_w)}{\Gamma(N+1)}\right]^{t/t_w}$$
$$\times \ln\left[1 - \frac{\Gamma(N+1, \lambda t_w)}{\Gamma(N+1)}\right].$$

The first and second moments can be evaluated from the density function as follows:

$$\langle t \rangle = \frac{t_w}{\left|\ln\left[1 - \frac{\Gamma(N+1, \lambda t_w)}{\Gamma(N+1)}\right]\right|},$$

$$\langle t^2 \rangle = \frac{2t_w^2}{\ln\left[1 - \frac{\Gamma(N+1, \lambda t_w)}{\Gamma(N+1)}\right]^2}.$$

Then the coefficient of variation is calculated, by adding the refractory period to the first moment, as

$$R = \frac{\sqrt{\langle t^2 \rangle - \langle t \rangle^2}}{\langle t \rangle + t_R} = \frac{1}{1 + \frac{t_R}{t_w}\left|\ln\left[1 - \frac{\Gamma(N+1, \lambda t_w)}{\Gamma(N+1)}\right]\right|}.$$

This curve as a function of λ is plotted in Fig. 3 as B for $t_w = 13.5$ ms and $N = 7$. The value of N is chosen such that an alpha function conductance with 1 ms time constant which decays in 2 ms would not release the membrane from hyperpolarization if the inputs are spread equally in time in t_w window. The spike latency is taken as the value of t_w. The curve B_2 predicts the growth profile of R. Systematic corrections to our assumptions could be made to derive more specific curves corresponding to a given I_n value, but it is a daunting task.

V. CONCLUSION

We have shown that negative component in the noise (i.e., inhibitory input) could by itself show coherence resonance phenomenon, thus imparting more significance to the intrinsic components of noise in dynamical systems. In models of excitable systems, simplified, or conductance based neuron models, negative or inhibitory input can be seen to play more coherence-enhancing role just as positive input does. With an interplay between the components of the noise, desired coherence may be achieved in experimental systems where independent control of the noise components is feasible.

[1] *Noise in Nonlinear Dynamical Systems*, Theory of Noise Induced Processes in Special Applications, edited by F. Moss and P. V. E. McClintock (Cambridge University Press, New York, NY, 1989), Vol. 2.

[2] R. Benzi, A. Sutera, and A. Vulpiani, J. Phys. A **14**, L453 (1981).

[3] J. G.-O. B. Lindner, A. Neiman, and L. Schimansky-Geier, Phys. Rep. **392**, 321 (2004).

[4] Hu Gang, T. Ditzinger, C. Z. Ning, and H. Haken, Phys. Rev. Lett. **71**, 807 (1993).

[5] K. Wiesenfeld and F. Moss, Nature (London) **373**, 33 (1995).

[6] L. Gammaitoni, P. Hänggi, P. Jung, and F. Marchesoni, Rev. Mod. Phys. **70**, 223 (1998).

[7] A. S. Pikovsky and J. Kurths, Phys. Rev. Lett. **78**, 775 (1997).

[8] A. Longtin and D. R. Chialvo, Phys. Rev. Lett. **81**, 4012 (1998).

[9] A. Neiman, L. Schimansky-Geier, A. Cornell-Bell, and F. Moss, Phys. Rev. Lett. **83**, 4896 (1999).

[10] A. M. Lacasta, F. Sagués, and J. M. Sancho, Phys. Rev. E **66**, 045105(R) (2002).

[11] A. Zaikin, J. García-Ojalvo, R. Báscones, E. Ullner, and J. Kurths, Phys. Rev. Lett. **90**, 030601 (2003).

[12] E. Ullner, A. Zaikin, J. García-Ojalvo, and J. Kurths, Phys. Rev. Lett. **91**, 180601 (2003).

[13] T. Kreuz, S. Luccioli, and A. Torcini, Phys. Rev. Lett. **97**, 238101 (2006).

[14] P. Parmananda, H. Mahara, T. Amemiya, and T. Yamaguchi, Phys. Rev. Lett. **87**, 238302 (2001).

[15] L. Q. Zhou, X. Jia, and Q. Ouyang, Phys. Rev. Lett. **88**, 138301 (2002).

[16] S. K. Han, T. G. Yim, D. E. Postnov, and O. V. Sosnovtseva, Phys. Rev. Lett. **83**, 1771 (1999).

[17] A. Nikitin, Z. Néda, and T. Vicsek, Phys. Rev. Lett. **87**, 024101 (2001).

[18] Z. Liu and Y.-C. Lai, Phys. Rev. Lett. **86**, 4737 (2001).

[19] G. Giacomelli, M. Giudici, S. Balle, and J. R. Tredicce, Phys. Rev. Lett. **84**, 3298 (2000).

[20] Gerardo J. Escalera Santos, M. Rivera, and P. Parmananda, Phys. Rev. Lett. **92**, 230601 (2004).

[21] I. Z. Kiss, J. L. Hudson, G. J. Escalera Santos, and P. Parmananda, Phys. Rev. E **67**, 035201 (2003).

[22] J. F. Martinez Avila, H. L. D. de S. Cavalcante, and J. R. Rios Leite, Phys. Rev. Lett. **93**, 144101 (2004).

[23] O. V. Ushakov, H.-J. Wünsche, F. Henneberger, I. A. Khovanov, L. Schimansky-Geier, and M. A. Zaks, Phys. Rev. Lett. **95**, 123903 (2005).

[24] D. T. W. Chik and Z. D. Wang, Phys. Rev. E **68**, 031907 (2003).

[25] D. T. W. Chik, S. Coombes, and Z. D. Wang, Phys. Rev. E **70**, 011908 (2004).

[26] E. I. Volkov, E. Ullner, A. A. Zaikin, and J. Kurths, Phys. Rev. E **68**, 061112 (2003).

[27] R. Dodla and J. Rinzel, Phys. Rev. E **73**, 010903(R) (2006).

[28] C. Rocşoreanu, A. Georgescu, and N. Giurgiţeanu, *The FitzHugh-Nagumo Model—Bifurcation and Dynamics* (Kluwer Academic Publishers, Dordrecht, The Netherlands, 2000).

[29] A. L. Hodgkin and A. F. Huxley, J. Physiol. (London) **117**, 500 (1952).

[30] The original model [29] with the voltage transformation $V \rightarrow -V-60$ is used. The input is $\eta(t) = -\Sigma_{j=1}^{N_n} I_n g(t-t_j)(V-E_{inh})$, where $g(t)$ is as defined in the text, and $E_{inh} = -85$ mV.