Coherence resonance with multiple peaks in a coupled FitzHugh-Nagumo model

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Coherence resonance in a coupled excitable system is studied, through both a computer simulation and a circuit experiment, using a piecewise linear version of the FitzHugh-Nagumo model. White noise is added to the first element and spikes are accordingly generated and transmitted to the second element. The mean, standard deviation, and coefficient of variation of the interspike intervals in the second element have multiple peaks as the noise strengthens, when the coupling strength is small. This results from the phase locking to the spikes that the noise generates.

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I. INTRODUCTION

Coherence resonance (stochastic resonance without input signals), i.e., the phenomenon in which the regularity of oscillation is optimal at an intermediate noise strength, has recently received considerable attention. Coherence resonance was first found in some limit cycle models [1], and was shown to occur in excitable media, e.g., the FitzHugh-Nagumo model [2], the Plant model [3], the Hodgkin-Huxley model [4], monovibrator circuits [5], and a semiconductor laser with optical feedback [6].

The single element models in [2–4] are, however, too simple to allow the activity of an actual neuron to be studied. Most neurons have complicated shapes, particularly bifurcation patterns in dendrites and axon terminals. Furthermore, the properties of the nerve membrane, e.g., the density and kind of ion channels, depend on regions in a single cell. In this study, coherence resonance in a coupled FitzHugh-Nagumo model [7], incorporating the spatial distributions of a nerve cell, is studied through both a computer simulation and a circuit experiment. White noise is added to the first element so that spikes generate in the first element and transmit to the second element. When the strength of the coupling between the two elements is small, the spikes may fail to transmit from the first element to the second, as a result of a refractory period. This is a simplified model of the propagation failures of spikes observed in regions of low safety factor in a nerve fiber, e.g., due to branching or increasing diameter. Although coupled excitable systems were studied in [5], spike transmission failures were not considered. The irregularity of spiking in the second element may depend on such transmission failures as well as on the coherence resonance in the first element.

This paper is organized as follows. In Sec. II, the method and results of the computer simulation are shown. Three kinds of noise are added to the first element in a coupled piecewise linear FitzHugh-Nagumo model, and the spikes in the second element are observed. It is shown that the irregularity of spiking in the second element changes depending on the kind of noise and the strength of the coupling. It is of particular interest that the mean and standard deviation (SD), as well as the coefficient of variation (CV), of the interspike intervals in the second element have multiple peaks as the noise strengthens, when noise is added to the fast variable and the coupling strength is small. Section III shows the results of an experiment on an analog circuit for the coupled FitzHugh-Nagumo model. Two peaks in the mean, SD, and CV of the interspike intervals in the second element are also observed. Finally, the relevance of these results to neural signal processing, the mechanism that causes the multiple coherence resonance, and the effects of the noise properties and the form of the nonlinear function in the FitzHugh-Nagumo model are discussed in Sec. IV.

II. COMPUTER SIMULATION

In our computer simulation, two piecewise linear versions of the FitzHugh-Nagumo model with noise are used:

$$
\begin{aligned}
dv_1(t)/dt &= D(v_2(t)-v_1(t)) + f(v_1(t)-\sigma_f n(t)) \\
&\quad - w_1(t) + \sigma_v n(t), \\
dw_1(t)/dt &= \varepsilon v_1(t) + \sigma_w n(t), \\
dv_2(t)/dt &= D(v_1(t)-v_2(t)) + f(v_2(t)) - w_2(t), \\
dw_2(t)/dt &= \varepsilon v_2(t), \quad (\varepsilon = 0.01),
\end{aligned}
\tag{1}
$$

where D is the strength of coupling, $f(v)$ is a piecewise linear function,

$$
f(v) = \begin{cases} -v & [v \leq a/2] \\ v-a & [a/2 < v \leq (a+1)/2] \\ -v+1 & [v > (a+1)/2] \end{cases} \quad (a=0.02),
\tag{2}
$$

and $n(t)$ is Gaussian white noise with zero mean,

$$
\langle n(t) \rangle = 0,
$$
$$
\langle n(t_1) n(t_2) \rangle = \delta(t_1 - t_2).
\tag{3}
$$

Three kinds of noise are added to the first element: multiplicative noise on the fast variable v_1 through the nonlinear function f with strength σ_f (a), additive noise on the fast variable v_1 with strength σ_v (b), and additive noise on the slow variable w_1 with strength σ_w (c). [Note that the multiplicative noise (a) is realized as fluctuations in bias voltage

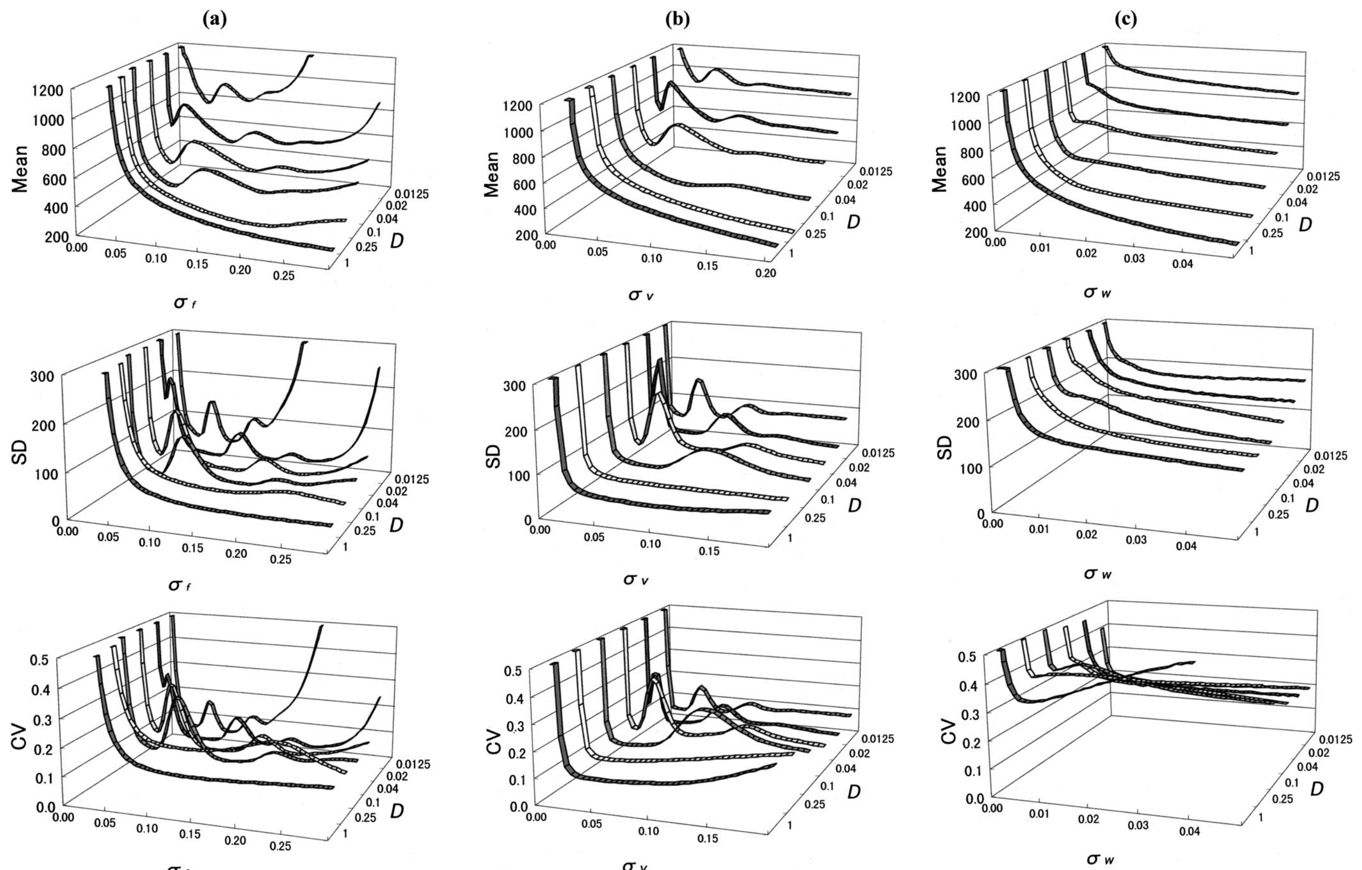

FIG. 1. Mean, SD, and CV of the interspike intervals in the second element vs noise strength σ_f (a), σ_v (b), and σ_w (c) with coupling strength $D=1.0$, 0.25, 0.1, 0.04, 0.02, and 0.0125; the multiplicative noise on v_1 (a), the additive noise on v_1 (b), and the additive noise on w_1 (b). (Note that the axes of the mean, SD, and CV are truncated at 1200, 300, and 0.5, respectively.)

in the analog circuit, although it may seem to be artificial.] Equation (1) is numerically calculated by the simple Euler method with $\Delta t=0.2$.

Spikes are generated in the first element by the noise and are transmitted to the second element. Figure 1 shows the mean, standard deviation, and coefficient of variation (standard deviation divided by the mean) of the interspike intervals in the second element plotted against the noise strength σ_f (a), σ_v (b), and σ_w (c). In each case the strength of the other noise is set to be 0 and 10^5 interspike intervals are used for estimation. The values of the coupling strength are $D=1.0$, 0.25, 0.1, 0.04, 0.02, and 0.0125.

When the coupling strength is large ($D=1.0$), the usual coherence resonance is obtained, i.e., the CV of the interspike intervals takes a minimum value at an intermediate noise strength. [Note that the CV increases to 1 (Poisson process) as the noise weakens to zero, which cannot be seen since the axes of the CV are truncated at 0.5 in Fig. 1. The axes of the mean and SD are also truncated, at 1200 and 300, respectively.] As the coupling strength decreases, however, minimal points appear in the graphs of the mean and SD (as well as the CV) of the interspike intervals against the noise strength on v_1 (a) and (b). There are, for instance, one minimal point for $D=0.25$, two points for $D=0.1$, three points for $D=0.04$, and four points for $D=0.02$ in the mean for the multiplicative noise on v_1 (a). (The spikes in the first element do not generate spikes in the second element for $D=0.01$.)

Two features are of interest. One is that not only the CV but also the mean and SD of the interspike intervals take minimal values. (This absolute coherence resonance was found in propagating spikes in [8].) The other is that they have multiple minimal points as the coupling strength becomes small. Note that these multiple peaks are clear only for the noises on v_1 (a) and (b), not for the noise on w_1 (c).

Figure 2 shows the time series v_1 and v_2 with $D=0.04$ for the multiplicative noise on v_1. The spikes in the second element are generated in the ratio 1:1 to those in the first element at the first minimal point $\sigma_f=0.04$ (a) and 1:2 at the second minimal point $\sigma_f=0.15$ (c). The ratio of the spikes in the second element to those in the first element is less than 1 between the minimal points [$\sigma_f=0.07$ (b)]. This decrease in the transmission ratio causes increases in the mean and SD of the interspike intervals in the second element. The situation is similar to the well-known phase locking that is observed in the firing of actual and model neurons with periodic stimulus pulses [9]. That is, the noise generates spikes in the first element, the mean of the interspike intervals of which decreases monotonically as the noise strengthens. The spikes in the first element play the role of stimulus pulses for the second element. The mean of the interspike intervals in the second element decreases as the noise strengthens when the spikes are phase locked to those in the first element. The mean of the interspike intervals increases, however, when the locking ratio drops, e.g., from 1:1 to 1:2.

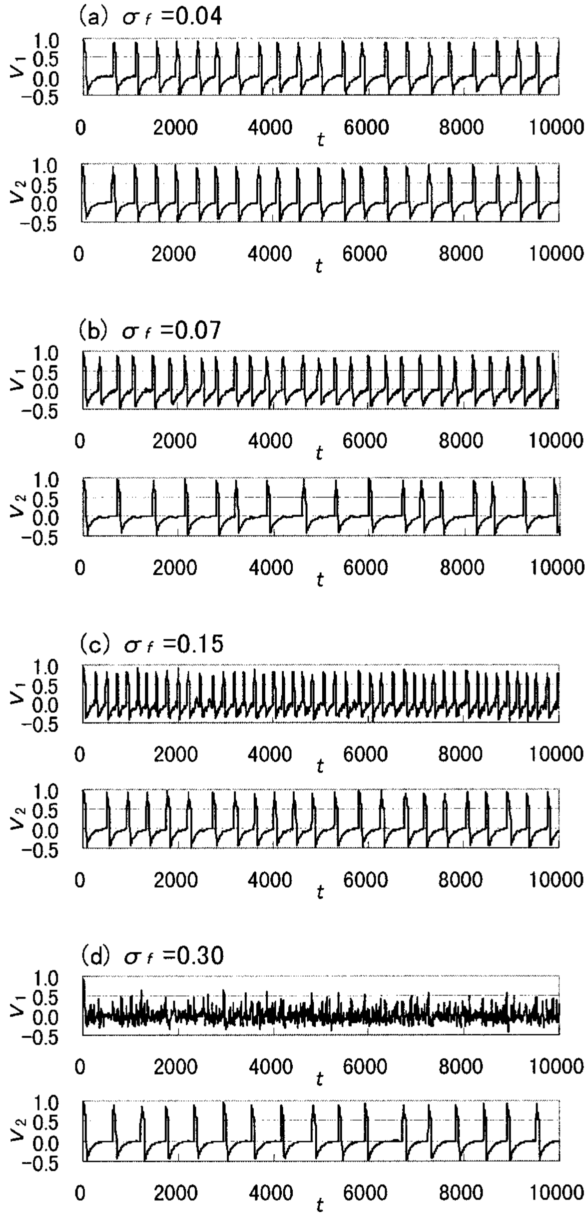

FIG. 2. Time series v_1 and v_2 with $D=0.04$ for the multiplicative noise on v_1 with $\sigma_f=0.04$ (a), 0.07 (b), 0.15 (c), and 0.3 (d).

The multiple peaks in the mean, SD, and CV of the interspike intervals occur within the range of noise strengths of biological interest. Fluctuations in the time series v_1 due to the noise increase and the proper forms of the spikes in the first element are unclear at $\sigma_f=0.3$, as shown in Fig. 2(d). As the noise strengthens further, the first element stops working as an excitable element and merely transmits to the second element fluctuations due to the noise, resulting in a single element with additive noise. (The irregularity of spiking in the second element then increases at this strong noise level.) This high noise strength at which the first element loses its excitable properties is meaningless in an actual nervous system. Multiple coherence resonance occurs at an appropriate noise level where the first element retains its excitable properties.

It is noted that the coupling has little effect on the properties of the spikes of the first element. Those properties are similar to the properties in a single element with noise. Further, when the noise is added to the second element also, the properties of the spikes in both elements are similar to those in a single element with noise. In both cases, the usual coherence resonance is observed. The multiple coherence resonance is caused by phase locking and transmission failures of the spikes between the two elements.

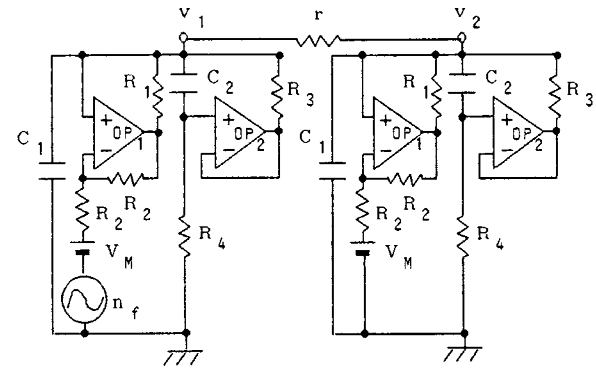

FIG. 3. Analog circuit for the coupled FitzHugh-Nagumo model.

III. CIRCUIT EXPERIMENT

Coherence resonance with multiple peaks was observed also in an experiment on an analog circuit for the coupled FitzHugh-Nagumo model. The circuit was made with operational amplifiers as shown in Fig. 3 [10]. The model equations are

$$C_1 dv_1/dt=(v_2-v_1)/r+f(v_1;V_c,V_M+\sigma n) -v_1/R_4-(1-R_3/R_4)w_1,$$

$$L\,dw_1/dt=v_1-R_3w_1,$$

$$C_1 dv_2/dt=(v_1-v_2)/r+f(v_2;V_c,V_M) -v_2/R_4-(1-R_3/R_4)w_2,$$

$$L\,dw_2/dt=v_2-R_3w_2 \quad (L=C_2R_3R_4), \tag{4}$$

where $f(v;V_c,V_M)$ is a piecewise linear function:

$$f(v;V_c,V_M) = \begin{cases} (-V_c-v)/R_1 & [v\leqslant(-V_c+V_M)/2] \\ (v-V_M)/R_1 & [(-V_c+V_M)/2<v<(V_c+V_M)/2] \\ (V_c-v)/R_1 & [v\geqslant(V_c+V_M)/2]. \end{cases} \tag{5}$$

The values of the parameters are as follows: $OP_{1,2}$ (Operational Amplifier RC4558), $V_c=10$ V (voltage of power supply to OP_1), $V_M=3.85$ V, $C_1=0.1\,\mu$F, $C_2=1\,\mu$F, $R_1=2.2\,\mathrm{k}\Omega$, $R_2=100\,\mathrm{k}\Omega$, $R_3=1\,\mathrm{k}\Omega$, $R_4=10\,\mathrm{k}\Omega$, and $r=100\,\mathrm{k}\Omega$. The white noise source n is added to the bias voltage V_M in the first element, which corresponds to the multiplicative noise n on v_1 (a) in the simulation. The results are shown in Fig. 4,

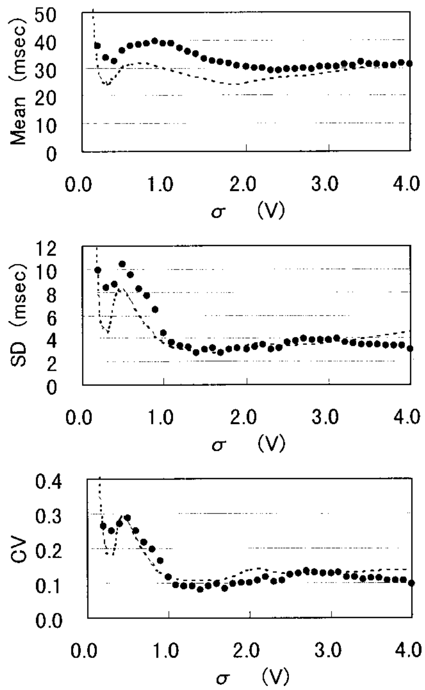

FIG. 4. Mean, SD, and CV of the interspike intervals in the second element vs the noise strength σ in the experiment on the analog circuit (dots) and in the numerical calculation of Eqs. (4) and (5) (dashed lines).

in which the mean, SD, and CV of the interspike intervals in the second element are plotted against the noise strength σ (dots). The recording time is 100 sec for each σ. There are two minimal points in the graph of the mean, at $\sigma=0.4$ and 2.4 V, which correspond to 1:1 and 1:2 locking, respectively.

The results of the numerical calculation of Eqs. (4) and (5) are also plotted in Fig. 4 (dashed lines). Although the qualitative features of the experimental results, e.g., two minimal points in the mean of the interspike intervals, are reproduced, the mean and SD of the interspike intervals in the experiment are larger than those obtained in the simulation, particularly for small σ. This difference is due to the fact that variations in the interspike intervals in the first element are larger in the experiment than in the simulation. The mean and SD of the interspike intervals in the second element, which are generated by the spikes in the first element, consequently become large in the experiment. By comparing the time series v_1 of the first elements in the experiment and simulation, it can be shown that most spikes in the first element in the experiment are generated as regularly as those in the simulation, but there are several spike generation failures in the experiment. (The corresponding interspike intervals are approximately doubled because of these spike failures.) The reason for the spike failures in the first element in the experiment is unclear.

IV. DISCUSSION

Multiple coherence resonance in the coupled FitzHugh-Nagumo model was studied; spatial distributions of an actual neuron were taken into account. Most neurons have complicated shapes, and the properties of the membrane vary according to region. There are regions in which the safety factor of spike propagation is reduced because of a change in the diameter of an axon or because of the branching of an axon, as well as regions in which decreases in channel density lower the excitability of the membrane. The low safety factor and low excitability weaken the coupling in the coupled FitzHugh-Nagumo model; this weakening can, in turn, prevent spikes from being transmitted. In computer simulations on spatially distributed and inhomogeneous models, such transmission and propagation failures have caused interesting properties: for example, nonmonotonicity in the firing rate in a coupled FitzHugh-Nagumo model [11], differential propagation due to noise at a branching point of a nerve fiber [12], and bifurcation and chaos in the decremental propagation in a nerve fiber of low excitability [13]. [It is noted that a single unit model is called the Bonhoeffer–van der Pol model and that a spatially extended model with a diffusion term is called the FitzHugh-Nagumo (FHN) model, as there has been confusion in their recent use.] The multiple peaks in the mean of the interspike intervals in the coupled FitzHugh-Nagumo model due to small coupling strength cause nonmonotonic relations in the response of a neuron to the variations in input. The second element can code the variance of the input to the mean of the interspike intervals (the mean firing frequency) nonmonotonically, which a single element can never do. It is known that nonmonotonicity in the response of a neuron improves the performance of multilayer networks [14] and the capacity of associative memory [15]. Although the significance of the multiple coherence resonance in signal processing in nervous systems is not clear, it can contribute to the formation of the complicated nonlinear functions of a single neuron.

The multiple peaks in the coherence of the coupled FHN model are due to phase locking and to changes in the response ratio of the second element to the first element. It is known that, when periodic stimulus pulses are added to a single element, the spikes are generated phase locked to the stimulus pulses. Spikes are not generated when the period of the stimulus pulses decreases to the refractory period, however. Consequently, a 1:2 response occurs after the 1:1 response, usually through $(n-1):n$ responses [9]. The spikes in the first element play the role of stimulus pulses to the second element in the coupled model with noise. When the spikes in the first element are rather regular (i.e., when the CV of the interspike intervals is small), the mean of the interspike intervals in the first element is considered to be the period of the stimulus pulses, which decreases as the noise strengthens. The transitions from the 1:1 through the $(n-1):n$ to the 1:2 response in the spikes in the second element are not clear, owing to the small variations in the interspike intervals in the first element. But an increase in the mean of the interspike intervals is observed in the second element during the changes in the response from 1:1 to 1:2. Increases in the mean of the interspike intervals in the second element can be observed at the changes from the 1:2 to 1:3 response and from the 1:3 to the 1:4 response, causing the multiple peaks.

Figure 5 shows a schematic diagram of the firing rate

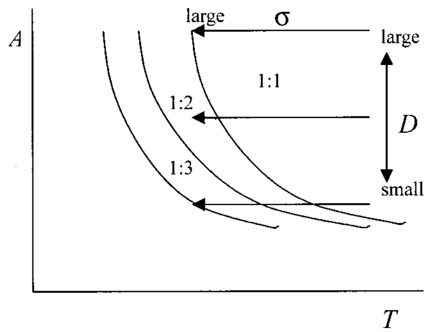

FIG. 5. Schematic diagram of the firing rate (response ratio) of a single element responding to periodic stimulus pulses in the plane of the amplitude A and period T of the stimulus pulses.

(response ratio) of a single element responding to periodic stimulus pulses in the plane of the amplitude A and period T of the stimulus pulses. In the coupled model with noise considered here, the period T corresponds to the mean of the interspike intervals in the first element, and the amplitude A corresponds to the coupling strength. As the noise strengthens, the mean of the interspike intervals in the first element decreases and the point in the diagram moves to the left. When the coupling strength of the two elements is large (A is large), the point moves in the upper regions upward and stays in the region of 1:1 response, i.e., each spike in the first element causes a spike in the second element. (The noise further strengthens, the proper forms of the spikes in the first element disappear, and the phase locking becomes unclear.) When the coupling strength is small, however, the point moves in the lower regions and enters the region of a 1:2 (and $1:n$) response when the spikes in the first element still retain their proper forms.

Therefore, in order to reach multiple coherence resonance due to phase locking it is crucial that variations in the interspike intervals in the first element are small. This is the reason that coherence resonance with multiple peaks does not clearly appear in the noise on w_1 (c). It can be seen from Fig. 1 that the CV of the interspike intervals for the noise on w_1 (c) is larger than that for the noise on v_1 (a) and (b). For example, the minimum values of CV are about 0.1 in (a) and (b), and about 0.3 in (c), when $D=1.0$.

Further, coherence resonance with multiple peaks is not obtained when a cubic function is used as $f(v)$ in Eq. (1) instead of the piecewise linear function [Eq. (2)]. The use of a cubic function increases the size of variations in the interspike intervals in the first element. The results of computer simulation in which we change the form of the nonlinear function f show that the variations in the interspike intervals in the first element are small enough to cause multiple coherence resonance when the maximal point of $w=f(v)$ is so large that the trajectory after the spike jumps to a point on the left branch of $w=f(v)$, far from the resting point (0,0). The recovery process from the jump end point to the resting point on the branch is expressed by the Wiener process with drift or by the Ornstein-Uhlenbeck process [16]. The mean and variance of the sojourn time on the branch until the next spike generation are approximately proportional to the distance between the jump end point and the resting point. The CV of the sojourn time then decreases inversely to the square root of the distance. The sojourn time occupies most of the interspike interval, and thus the variations in the interspike intervals decrease.

Finally, it is noted that there is a difference between the mean of the interspike intervals for the multiplicative noise (a) and that for the additive noise (b) and (c). It is expected that the mean of the interspike intervals tends to zero in the limit of large noise strength. In fact, the mean of the interspike intervals gradually decreases as the additive noise (b), (c) strengthens. The mean of the interspike intervals increases and fewer spikes are generated as the noise strengthens, however, when the coupling strength is small for the multiplicative noise (a). For instance, the mean of the interspike intervals tends to infinity and no spikes are generated as σ_f increases over 0.25 for $D=0.0125$ in Fig. 1(a). This is because the amplitude of the spikes in the first element decreases as the multiplicative noise strengthens, as can be seen in Fig. 2(d). Consequently, the first element cannot generate spikes in the second element at intermediate noise strength. The multiplicative noise changes the form of the nonlinear function f and reduces the excitability of the first element, while the additive noise only gives larger fluctuations.

In summary, it was shown by computer simulation and a circuit experiment that coherence resonance with multiple peaks occurs in the coupled FitzHugh-Nagumo model. The mean and SD, as well as the CV, of the interspike intervals in the second element take one or more minimum values at intermediate noise strengths when the coupling strength is small. These multiple peaks appear when the variations in the interspike intervals in the first element generated by the noise are small (only in the piecewise linear model with the noise on the fast variable). Multiple coherence resonance is caused by the phase locking (generated by the noise) of the spikes in the second element to those in the first element, the noise-induced phase locking.

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