Coherence resonance and polymodality in inhibitory coupled excitable oscillators

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We have analyzed the firing activity of two and three excitable FitzHugh-Nagumo oscillators, coupled via slow variable diffusion and under the action of an external noise. We find a different form of coherence resonance in this system, which is, in contrast to previous studies, intrinsically based on the antiphase behavior of coupled elements. Additionally, we show that an exchange, performed by this form of coupling, is remarkably rhythmogenic and results in polymodal interspike distributions without any external periodic stimuli. The dependence of these distributions on the noise amplitude and the coupling strength is studied.

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I. INTRODUCTION

Counterintuitively, the application of noise to nonlinear systems is sometimes able to induce ordering in the behavior of this system. One of such manifestations is the effect of coherence resonance (CR), in which noise shows the surprising ability to induce ordered periodicity in the output of the nonlinear nonequlibrium system. CR has been reported in different kinds of systems, in particular, it has been found that some noise amplitude exists at which the coherence of spiking in the output of the system can be significantly enhanced in an isolated FitzHugh-Nagumo (FHN) system [1], in the Hodgkin-Huxley [2] and Plant-Hindmarsh-Rose neuron models [3], and in dynamical systems close to the onset of bifurcations [4] (note also experimental verifications of CR in optical systems [5]). In addition, CR has been found in the behavior of a dynamical system, which shows jumps between several attractors [6].

In recent years, there has been a great interest in the CR behavior of spatially extended systems consisting of many interacting elements [7–9]. It has been shown that matching the noise-related characteristic time scales of the coupled excitable elements results in noise-induced synchronization regimes very similar to those for coupled limit cycles. Moreover, *array-enhanced* CR has been reported, in which constructing an array of coherence-resonance oscillators significantly improves the periodicity of the output [10]. To our knowledge, all these studies of the CR behavior have been performed in systems with coupling via fast variable exchange or pulsed coupling which activates the neighbors. These modes of coupling lead to many collective phenomena, including noise-induced spiral waves [11] and "clustering" of FHN stochastic oscillators [12]. As a consequence of this form of activatory coupling in spatially extended systems, CR may happen only if coupled oscillators move synchronously and *in phase*. However, other interactions between stochastic oscillators, for example, inhibitory coupling, are also very interesting and reported to be important in numerous physical [13], electronical [14], and chemical systems [15,16]. To be particular, the inhibitory form of coupling is used to explain morphogenesis in hydra regeneration and animal coat pattern formation [17], or to provide the understanding of pattern formation in an electron-hole plasma and low temperature plasma [13]. In chemistry, the effective increase of inhibitor diffusion by reducing of activator diffusivity via the complexation of iodide (activator) with the macromolecules of starch results in a turing structure formation [18]. It is interesting to note that systems with inhibitory coupling in its rhythmogenic activity resemble very much systems with time delay [19,20]. Noteworthy, although the rhythmogenesis in small neural networks is well known in the literature [21,22], its role in the real spiking behavior of *inhibitory* coupled excitable elements as a function of noise amplitude has not been studied.

Following this motivation, in this paper, we study a system of noise-driven FHN elements, which are coupled, in contrast to previous studies of CR, by the slow variable, i.e., by a diffusive inhibitory coupling. This delays the firing of an element, when its neighbors are firing. We show that a system of two coupled excitable elements demonstrates CR, which is intrinsically based on *the antiphase behavior* of the elements. This is a new mechanism of CR, which works via noise-induced synchronization in antiphase [23] of excitable elements. We demonstrate that this effect is connected to the fact, that such systems have very rich dynamics in the generation of rhythms, and, as a result, generate a polymodal interspike distribution. It is important to note that the generation of polyrythms is an important problem in the description of several natural processes, such as locomotion [24] or playing piano [25]. Recently, many model investigations have been motivated by experimental studies of the firing activity of neurons that revealed polymodality in the interspike interval histograms (ISIH) [26,27] or studies of locomotor behavior of halobacterium [28]. The most interesting feature of such systems is the appearance of polymodality even without additional forcing. In this study, we show that the application of an inhibitory coupling in a system of excitable oscillators is another possible mechanism for the generation of polymodality without any external periodic stimuli. We study this behavior in systems of two and three coupled elements and show how the degree of coherence can be controlled by the noise amplitude and the coupling strength. Such a nontrivial behavior can be expected from the possibility of noise-induced generation of coupling-dependent transient out-of-phase stochastic attractors in the phase space. For two-dimensional FHN limit cycles, inhibitory coupling results in the appearance of out-of-phase limit cycles that are stable in large areas of the parameter space if the stiffness is large. The overlapping of the in-phase and the antiphase limit cycles is typical for two or three coupled oscillators and depends on the stiffness [29].

II. POLYMODALITY IN INHIBITORY COUPLED OSCILLATORS

We begin with the study of two FHN systems, coupled via diffusive exchange of the recovery (slow) variable, which is a kind of mutual inhibition of motion of the phase points along the slow part of the FHN *N*-shaped nullcline. The equations of motion for identical bidirectionally coupled elements are

$$\frac{dx_{1,2}}{dt}=A-y_{1,2}+C(x_{2,1}-x_{1,2})+\xi_{1,2}, \tag{1}$$

$$\varepsilon\frac{dy_{1,2}}{dt}=x_{1,2}-y_{1,2}^3/3+y_{1,2}. \tag{2}$$

Here, $\varepsilon \ll 1$ is a small parameter, which determines that y_i are the fast variables and A is responsible for the excitatory properties of the isolated elements. It is well known that for $|A|>1$ the only attractor is a stable fixed point. For $|A|<1$, the limit cycle generates a periodic sequence of spikes. The choice of ranges for ε and A is crucial in this study. We fix A close to the bifurcation in the interval (1.01–1.05) in order not to use high-level noise (parameter D) to excite oscillations and thereby to avoid masking of the fine structure of the ISIHs. Here, ε is in the range (0.001–0.0001), which is significantly smaller compared to those that are commonly used [1,8]. To emphasize this specifically small value of ε, the term ''relaxator'' will be used instead of ''very relaxation oscillator.'' The stochastic forcing is represented by Gaussian white noise ξ_i with zero mean and intensity $2D$: $\langle \xi_i(t)\xi_j(t+\tau)\rangle = 2D\delta(\tau)\delta_{i,j}$.

For numerics, we take the standard constant-step Runge-Kutta fourth-order routine with the white noise added according to the algorithm [30]. In cases of any doubt, control runs have been done with smaller steps. The ISIH usually contains about 10 000 interspike intervals, ensuring a reasonable statistical accuracy. The numerical results are presented in Fig. 1. For weak noise [Fig. 1(a)] the distribution is polymodal with equidistant positions of the peaks and progressively decreasing peak amplitudes. Hence, the inhibitory coupling really provides a mechanism for polyrhythm generation in a system of FHN oscillators. A 2.5 fold increase of the noise amplitude shifts the peak positions and their relationships. The second peak becomes now the main one [Fig. 1(b)]; however, the polymodal structure of the ISIH is still preserved. A further increase in the noise amplitude results in the disappearance of polymodality because of the global dominance of the second peak [Fig. 1(c)]. The spiking behavior becomes highly regular. This simple ISIH shape is observed in a broad range of noise amplitudes (at least up to $D=10^{-3}$). For comparison, in a similar system but with an activatory coupling, the ISIH has always the same structure with one peak, as it is shown in the built-in plot in the Fig. 1.

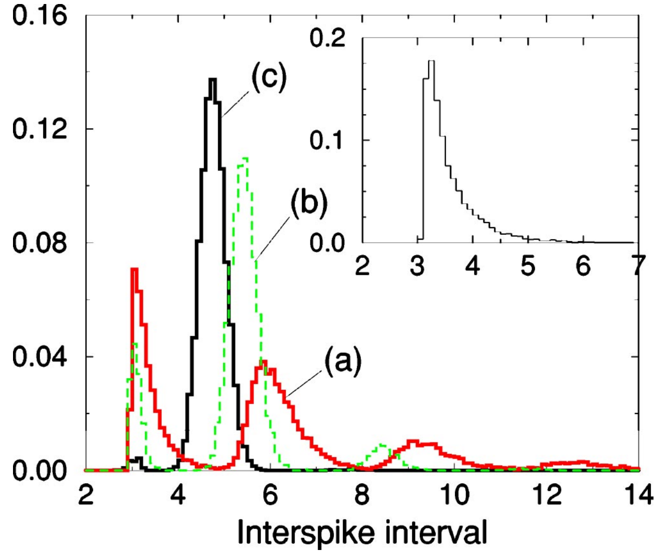

FIG. 1. Interspike interval histograms for two coupled very stiff ($\varepsilon=0.0001$) relaxators Eqs. (1) and (2) for $A=1.01$, $C=0.1$: (a) $D=10^{-6}$, (b) $D=2.5\times10^{-6}$, (c) $D=10^{-5}$. The built-in plot corresponds to the typical histogram for a system with activatory coupling ($C=1.5$).

These qualitative changes in the ISIH shape may be explained by analyzing the stochastic time series. As in Ref. [1], the characteristic time of isolated stochastic oscillations is the sum of the activation and excursion times. The former is the waiting time of the appropriate excitation and fluctuates in a broad range; the latter is almost constant ($T_{ex}\approx 3$ for our parameters). At low noise amplitudes and low coupling strengths, the shape and position of the first peak in Fig. 1(a) are very similar to those of the entire ISIH for each isolated element and for activatory coupled elements (built-in plot in Fig. 1). The origin of the ISIH polymodality is seen from the time dependences of the slow variables as presented in Fig. 2(a). At this particular noise amplitude, the average activation time is such that the order of spike generation by the two relaxators excited near the steady state does not depend on the coupling. However, as soon as one element fires, the phase point of the other element moves away from the excitation threshold due to a slow variable exchange [see Fig. 2(b)]. In other words, when the noise amplitude is low, the second element is unlikely to fire, while its neighbor makes an excursion. This simple consideration explains why the average interpeak interval equals nT_{ex}. Obviously, the probability of three consecutive firings of the same element is lower than that of two consecutive firings; therefore, the greater the number of the peaks, the lower the peak amplitude. If the noise amplitude increases at a fixed coupling strength, the activation time becomes shorter, and the antiphase noise-induced regime as well as the previously described random excitations begin to compete. Their competition enlarges the second peak in the ISIH and shifts it to the left [Fig. 1(b)], because the augmented noise may induce one element to fire slightly before the other finishes its excursion. A further increase in the noise amplitude leads to the

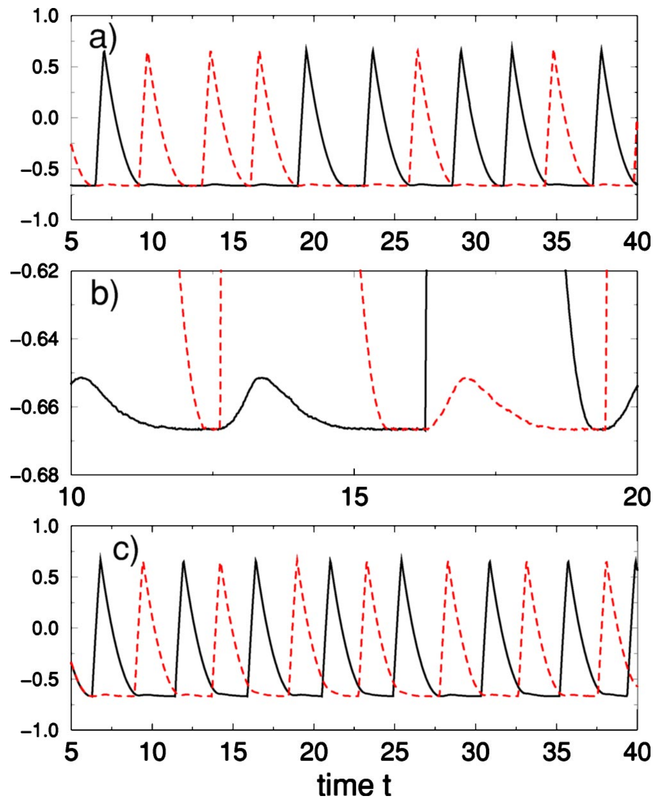

FIG. 2. Typical waveforms of the slow variables for the cases (a) and (c) in Fig. 1. (b)—an enlargement of (a) in the area near the firing point.

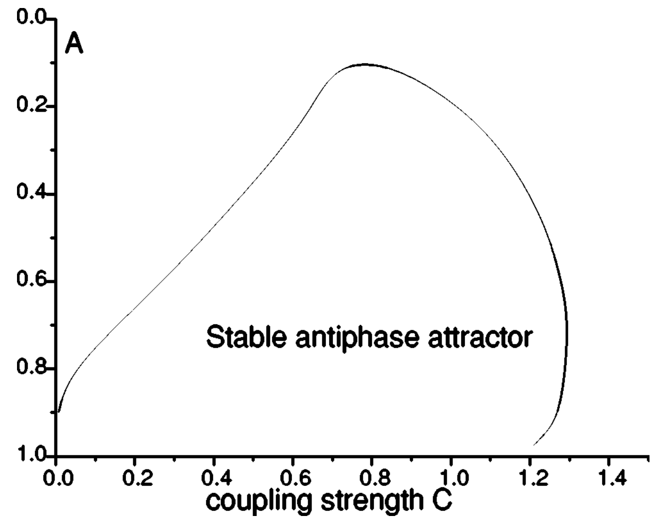

FIG. 3. The region of stability for the antiphase regime in the deterministic case of two coupled oscillators in the plane (C,A). The in-phase attractor is stable everywhere within this plot. For $A>1.0$, the attractor is only a point and the system becomes excitable.

full dominance of antiphase stochastic oscillations [Fig. 1(c)], as can be seen from the waveforms presented in Fig. 2(c).

Additional calculations (as in Ref. [29]) show that the dominance of the antiphase regime is not surprising because the basin of attraction of the antiphase deterministic limit cycle (e.g., for $A=0.98$) is significantly larger for coupling strengths $0.1<C<0.3$ than the in-phase regime basin. This is not the case for larger values of coupling, for which even strong noise is unable to induce coherency via antiphase motion. The stability region of the antiphase attractor for the deterministic case of two coupled oscillators is shown in Fig. 3. Noteworthy, the in-phase regime is stable everywhere within this plotting.

Figure 4 shows the ISIH for $C=0.6$ and for different noise levels. In the case of low-level noise, the ISIH shape is as in Fig. 1(a), because changes in the coupling strength are not significant for the mechanism of equidistant polymodality. The other two histograms, Figs. 4(b) and 4(c), are different from those in Fig. 1 in that (i) antiphase stochastic oscillations are not dominant in them and (ii) their peaks are split (especially the first peak of the histograms). The effect of peak splitting is a bright manifestation of the dual role of the coupling we consider: on the one hand, it causes the phase points to move more slowly when they are on different branches of the nullcline; on the other hand, it reduces the phase shift between them when they are on the same branch. Figure 5 shows the time series of slow variables in the presence of (a) moderate and (b) high-amplitude noise. Comparing Fig. 2(c) with Fig. 5(b), one can see that, if the coupling strength is high, the phase points strongly attract each other on the right slow part of the nullcline and remain closely spaced when approaching the excitation threshold. Obviously, strong coupling enhances the probability of successive firings of the same element and of in-phase excitation of the two elements. The interspike intervals that correspond to successive firings (two examples are marked $T1a$ in Fig. 5) have the shortest duration and contribute to the left split component of the first peak in the ISIH. If one of the element fires in phase with its neighbor, the interspike intervals are slightly longer (see markers $T1b$ in Fig. 5) because of the absence of coupling dependent attraction. When both noise and coupling are very strong [Fig. 5(b)], the probability for

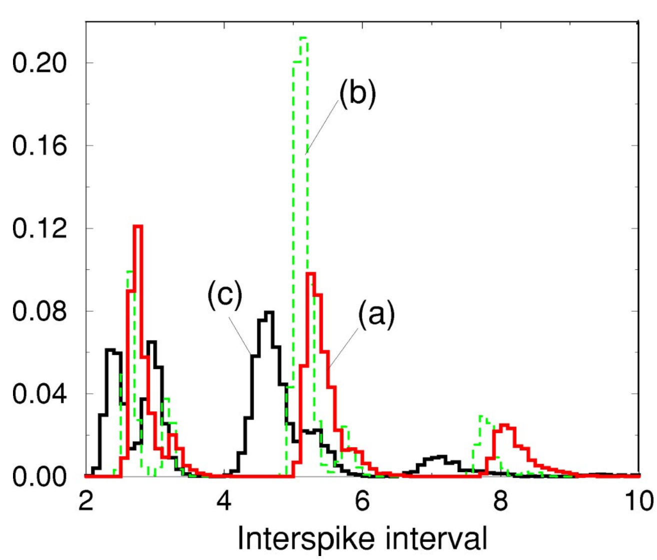

FIG. 4. Interspike interval histograms for a larger coupling $C=0.6$: (a) $D=10^{-6}$, (b) $D=10^{-5}$, (c) $D=10^{-3}$.

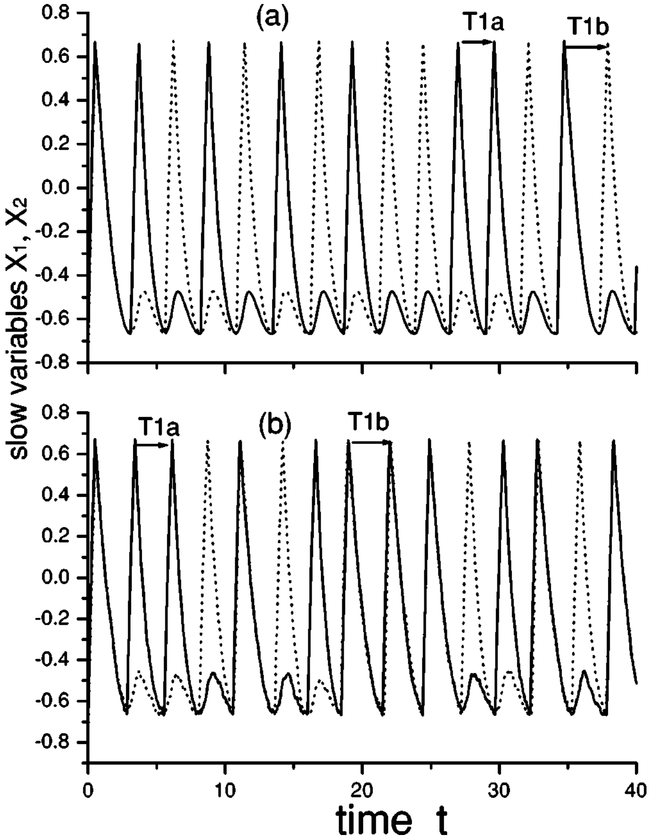

FIG. 5. Examples of waveforms of slow variables for the cases (b) and (c) in Fig. 4. It shows the correspondence of some intervals to the first ($T1a$) and to the second ($T1b$) parts of the first peak of histograms in Fig. 4.

the two phase points of moving in-phase increases, and their more or less regular antiphase motion becomes less likely.

This behavior can be also illustrated by the transition line between polymodality and unimodality with respect to the different noise intensities and coupling strengths (see Fig. 6). It can be clearly seen that in the whole interval of the noise amplitude, which is necessary for unimodality, an increase of the coupling strength will lead to the disappearance of the unimodal regime. On the other hand, for moderate values of the inhibitory coupling an increase of noise will result in the unimodal behavior, that will be again destroyed if we increase the noise intensity further. In the calculation of this diagram, we have defined the unimodal regime as a regime with ISIH, in which the main peak is at least ten times larger than other peaks. This has been made to avoid difficulties to determine exactly the unimodal regime in the presence of noise.

III. ANTIPHASE COHERENCE RESONANCE

At $A = 1.01$, we find two main scenarios (Figs. 1 and 4), how noise controls the evolution of ISIH polymodality. Both regimes, which differ in the value of coupling, demonstrate polymodality, but only for small values of coupling noise is able to suppress this behavior and inducing a coherent motion via antiphase oscillations. These observations hold not

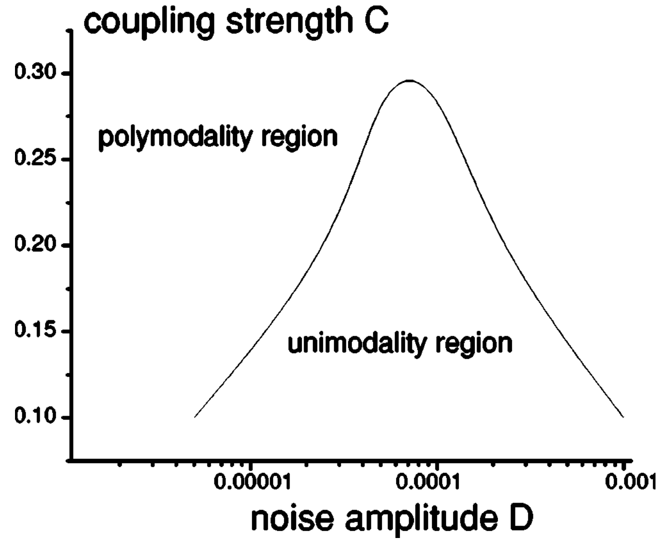

FIG. 6. The transition line between polymodality and unimodality depending on the noise intensity vs coupling. This plot illustrates that large values of coupling suppress unimodal regimes in a system of inhibitory coupled oscillators.

only if the system is very close to the bifurcation point. For example, for $A = 1.03$, the main steps of the ISIH evolution do not change, but a significantly stronger noise is required for overcoming the threshold.

The changes in the ISIH structure with the noise amplitude increasing in the range from 10^{-6} to 10^{-3} clearly indicate a growing coherence of ISIs, which is especially strong for small values of coupling. In order to characterize this effect quantitatively, we compute the normalized autocorrelation function of the slow variable: $C(\tau) = \langle x(t)x(t+\tau)\rangle / \langle x(t)^2\rangle$, $x(t) = x(t) - \langle x\rangle$. An important characteristic of the autocorrelation function is the correlation time $\tau_c = \int C(t)^2 dt$. Figure 7 shows τ_c as a function of the noise level for weak and strong coupling strengths. The coherence

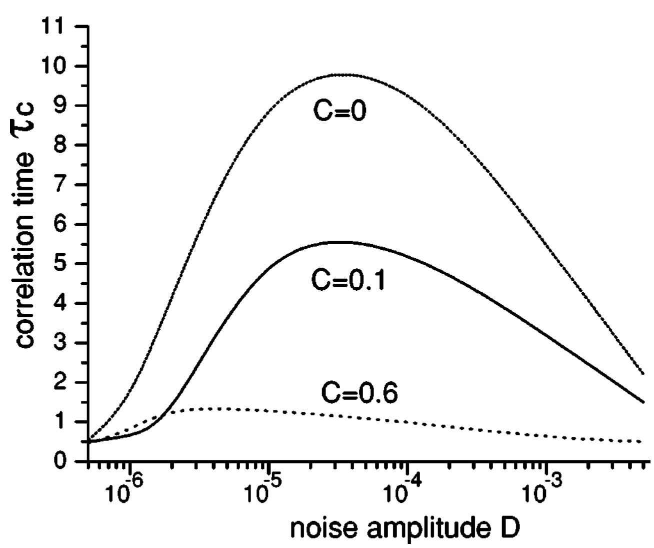

FIG. 7. Coherence resonance in inhibitory coupled noise-driven excitable oscillators. Correlation time τ_c vs the noise intensity for different coupling strengths C, $A = 1.01$.

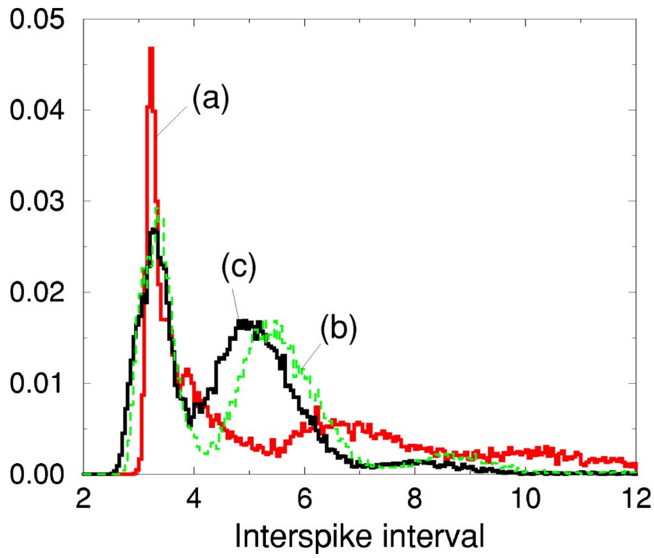

FIG. 8. Interspike interval histograms for two coupled not very stiff relaxators ($\varepsilon=0.01$) for $A=1.01$, $C=0.2$: (a) $D=10^{-4}$, (b) $D=8\times10^{-4}$, (c) $D=2\times10^{-3}$.

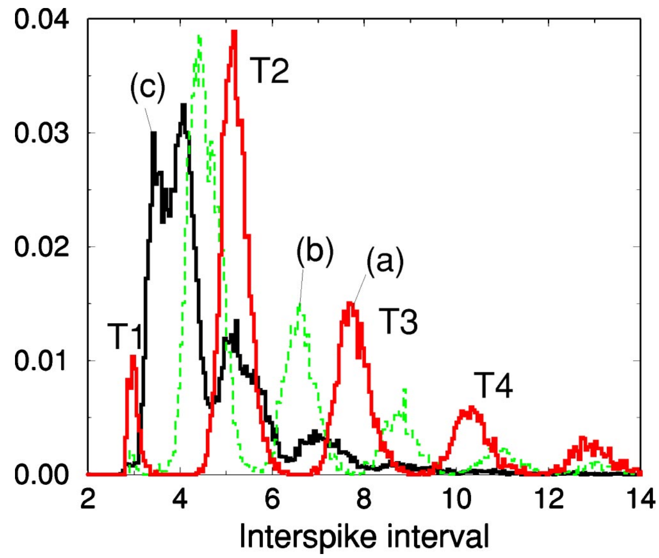

FIG. 9. Interspike interval histograms for a ring of three very stiff relaxators ($\varepsilon=0.0001$ for $C=0.1$, $A=1.01$). (a) $D=2\times10^{-6}$, (b) $D=10^{-5}$, (c) $D=10^{-4}$.

resonance is clearly seen from this figure; its significant dependence on the coupling strength is evident. The increase in τ_c with the noise level can be easily understood from the above considerations of the ISIH evolution. The reason for smaller τ_c at higher noise amplitudes is as in Ref. [1]: in this region, the ISIH dispersion grows up more rapidly with the noise level than does the average ISI value. Note, however, that two stochastic relaxators are running mainly in antiphase, hence the underlying mechanism of this new form of CR is significantly different from the CR effects reported till now in ensembles of excitable systems [7,8,10].

Now we discuss how the parameters of the system should be adjusted to reveal the observed behavior. Generally, we expect that any noisy excitable oscillators, coupled with inhibitory coupling, are able to demonstrate this new form of CR. However, sometimes this effect can be masked by too large noise or can compete with conventional mechanism of CR [1]. In our paradigmatic model the situation is as follows. Above we have discussed the situation with another coupling. Noteworthy, this ''antiphase'' CR can also be observed for other values of the bifurcation parameter *A*, including the value considered in Ref. [1]. Our calculations show that unimodal antiphase behavior is possible for the parameter *A* till value 1.1. For larger *A* one needs larger noise for firing, and this will lead to a masking of the effect due to spreading of peaks in the ISIH. Another parameter important in the regulation of spiking is ε. It controls not only the sizes of basins where coupling-dependent attractors coexist and are stable, but also the rates of transitions between them in the perturbed system. As ε increases up to about 0.01, the basins for the in-phase and antiphase stochastic motions become comparable in size. Therefore, in the broad range of noise levels (see Fig. 8), the noise-induced changes in the ISIH shape are not so sharp and dramatic as those for $\varepsilon=0.0001$, although the second peak position clearly depends on the noise level. Again an increase of the noise will lead to an increase of the second peak (Fig. 8), which is responsible for antiphase CR under consideration.

IV. POLYMODALITY IN A RING OF THREE ELEMENTS

The next important question is how the degree of ISIH polymodality depends on the number of interacting relaxators? We consider only the simplest extension, a system of three elements with cyclic boundary conditions. For this ring of three oscillators, large regions of the phase diagram are co-occupied mainly by the following attractors [29]: (i) in-phase oscillations and the antiphase regime in which two oscillators move in phase with each other and in antiphase with the third one; (ii) the in-phase limit cycle and different types of the rotating waves (all phase differences are equal to one-third of the period); and (iii) the antiphase regime and rotating waves [29]. It has been shown recently [14] that several additional attractors arise when three inhibitorily coupled relaxators are slightly detuned. It is natural to expect that the underlying attractors determine the richness of noise-induced behavior, although any particular attractor manifests itself only temporarily in the case of stochastic relaxators. The noise-dependent evolution of the ISIH in the ring with a low excitation threshold ($A=1.01$) and a low coupling strength ($C=0.1$) is presented in Fig. 9. The qualitative properties of the distributions are not sensitive to C if $C\in(0.05–0.3)$ and to A if $A\in(1.01–1.05)$. The main difference between the histograms in Figs. 9 and 1 is in the number of detectable peaks, which grows with the number of elements. However, even in this case, due to the mechanism of out-of-phase motion, provided by inhibitory coupling, the increase of noise leads to an increase of coherency. It manifests itself in the dominance of only one peak in the corresponding ISIH [see the evolution in Figs. 9(a)–9(c)] and is based on the transient out-of-phase motion of any two oscillators. Figure 10(a) shows the time series of the slow variables for a low-level noise.

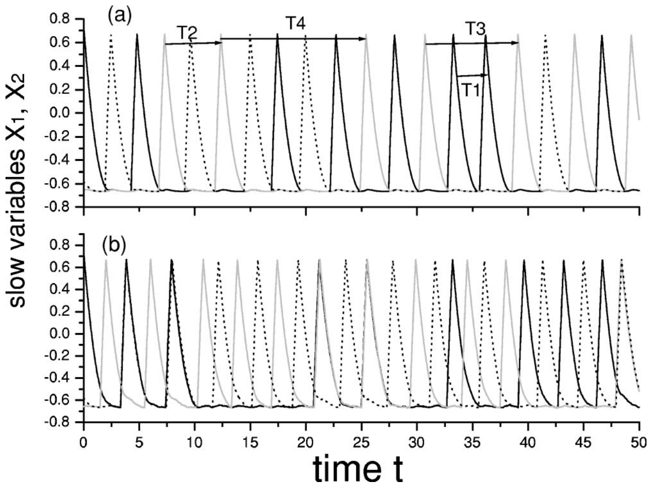

FIG. 10. The examples of waveforms of slow variables for the cases (a) and (c) in Fig. 9. It demonstrates the correspondence of some intervals to the peaks $T1$, $T2$, $T3$, $T4$ of histograms in Fig. 9.

After exciting one element, the other two elements become excited after a delay, which is accounted for slow variable exchange. When completing its excursion, the excited element has a very small chance of being excited again at this noise level. Therefore, noise excites one or both neighbors (the latter is less likely). Thus, the firing events of a given element may be separated by one excursion of its neighbors [peak $T2$ in Fig. 9, the most probable case marked $T2$ in Fig. 10(a)], two excursions (marked $T3$), etc. This consideration explains the ‘‘internal'' structure of the ISIH in the presence of weak noise. If the noise amplitude is large and the coupling strength is low, the internal structure [see Fig. 10(b)] is more heterogeneous mainly because the antiphase regime may arise over the short term when the two elements are excited during their in-phase motion. If the coupling is strong, it can split all peaks of the ISIH, but a detailed analysis of this phenomenon is beyond the scope of this paper.

V. CONCLUSIONS

In summary, we have demonstrated two related phenomena, induced by inhibitory coupling in a system of excitable oscillators.

(i) The first effect is the generation of nontrivial polymodal distributions of interspike intervals without any periodic stimuli. Instead of external characteristic times, the time delays of the motion caused by the inhibitor exchange modulate the probability of the firing. The values of these delays define the peak's positions in the ISIHs.

(ii) The second effect is the coherence resonance that appears for this polymodal regime if we increase the noise amplitude. This CR has in the background the noise-dependent dominance of some out-of-phase attractor (antiphase one for two coupled relaxators). This type of CR is slightly weaker than the classical CR; it is based on a completely different mechanism and seems to be quite perspective for the selective interactions of coupled relaxators with signals of different periods and forms. We have demonstrated these two effects on a simple model but in a general framework, and, therefore, we expect that these theoretical findings can be detected and used in different experimental systems with inhibitory coupling in physics [13], biology [17], electronics [14], or chemistry [15,16].

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