Frequency-dependent stochastic resonance in inhibitory coupled excitable systems

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We study frequency selectivity in noise-induced subthreshold signal processing in a system with many noise-supported stochastic attractors which are created due to slow variable diffusion between identical excitable elements. Such a coupling provides coexisting of several average periods distinct from that of an isolated oscillator and several phase relations between elements. We show that the response of the coupled elements under different noise levels can be significantly enhanced or reduced by forcing some elements in resonance with these new frequencies which correspond to appropriate phase relations.

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I. INTRODUCTION

The signal processing in an excitable system of oscillators or networks is a key element of information exchange in neural networks. By the investigation of such processes several unexpected phenomena have been found. One of the most interesting and counterintuitive effect is stochastic resonance (SR) [1], initially found in bistable systems [2], and later studied in a large variety of physical [1] or biological systems [3], including also noise-induced structures [4] or excitable systems [5,6]. SR consists in an improvement of the system response to an input signal due to an optimal noise intensity acting upon the system. In SR a part of the noise energy is used for constructive purposes, to cause a form of synchronization between input and output signals [7]. Several investigations have been performed to find possibilities for the amplification of this SR effect. Array-enhanced SR has been considered in Refs. [8,9], where it has been shown that embedding of the processing element in a network of elements with optimal coupling and noisy strength [10] can improve the signal. This effect is closely connected and sometimes conceptually indistinguishable from spatiotemporal SR [11] or SR in extended bistable systems [12]. Another possibility to amplify the SR effect has been exploited in Ref. [9] by application of noninvasive control of SR. In this case, the external feedback has enhanced the response of a noisy system to a monochromatic signal. Finally, there were investigations, which have shown that with internal colored noise the SR effect can be enhanced in systems with a large memory time [13].

In isolated excitable systems, SR has been usually investigated for the paradigmatic FitzHugh Nagumo (FHN) model [5,6,14,15], as well as array-enhanced SR has been considered for FHN oscillators coupled via diffusion of their fast variables. Recently it has been shown that a frequency and phase locking in an ensemble of noise stimulated excitable oscillators can be enhanced by an optimal number of coupled elements [16,17]. Typically, studies of SR do not demonstrate a sensitive dependence on the frequency of the forcing. Partially this is caused by using an adiabatic approximation which is applied to get analytic results about SR. There are only some investigations in which the frequency of the signal is the essential parameter. Gang *et al.* [18] have shown that SR in specifically globally coupled large bistable systems with two series of cells demonstrates the bell-shaped dependence on the signal frequency. Lindner *et al.* [19] have shown the amplification of the spectral power at particular frequencies in small arrays of underdamped monostable oscillators. To our knowledge, the role of the signal frequency for *excitable* systems has been studied in Refs. [15,17,20–23] for isolated FHN, when the characteristic time of the system, defined by an external period providing the maximal level of synchronization, practically coincides with the excursion time of an excitable element, and this time is the single natural reference point for time scale. Such a form of frequency selectivity can be also important for biological membranes in enzymatic systems [24]. In other studies the frequency sensitivity in weak signal processing results from a resonance between small oscillations around steady state and a signal [25–28]. Hence, despite different excitation mechanisms, the oscillation frequency is defined by the parameters of isolated elements. On the other hand, our mechanism is based on the appearing of new resonance frequencies due to special phase relations in an inhibitor coupled array.

In this paper we investigate the influence of a signal frequency in SR effects in a system of excitable oscillators, coupled via the inhibitory variable. This form of coupling between oscillators may provide a broad spectrum of additional frequencies in the system's behavior. Oscillatory media with inhibitory coupling have very rich dynamics and have been reported to be important in numerous physical [29], electronical [30], and chemical systems [31,32]. To be particular, the inhibitory form of coupling is used to explain morphogenesis in Hydra regeneration and animal coat pattern formation [33], or to provide the understanding of pattern formation in an electron-hole plasma and low-temperature plasma [29]. 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 [34]. It has been shown that the dominance of such a coupling between identical oscillators results in the generation of many stable limit cycles with different periods and phase relations [35,36]. This type of diffusion is referred to the class of "dephasing" interaction because there is a large area of the phase space where the phase points repel each other due to this interaction. Dephasing is a source of multirhythmicity, which was observed in different systems [37–40]. For excitable noisy elements the dephasing interaction of stochastic limit cycles (instead of deterministic ones) may provide coexistence of spatiotemporal regimes which are selectively sensitive with respect to the period of external signals. In these systems noise plays two roles, at least: (i) it stimulates firings of stable elements and, consequently, their interaction during return excursion and (ii) it stimulates transitions between coupling-dependent attractors if they occur and have visible lifetimes.

The paper is structured as follows. After the explanation of the model equations and the method, used to estimate signal processing, we review the classical SR effect in an isolated excitable oscillator to emphasize the difference with the selective SR in a coupled system. Then we study a chain of two identical inhibitory coupled excitable oscillators. In this situation the phase relation becomes important for the resonance frequency and the antiphase motion exhibits another resonance frequency than that of an isolated oscillator. In contrast to an isolated oscillator, the ensemble reacts very sensitively upon the new resonance frequency of the antiphase attractor. This new frequency selectivity can be used for an enhancement of the signal processing and information transport in the SR effect at this new resonance frequency. After that, we study a chain of three coupled elements with a richer spectrum of the phase relations and the frequencies. Beside the antiphase motion (two in-phase oscillators are in antiphase with the third one), this system demonstrates the so-called dynamic trap regime in which the middle element does not produce spikes because of antiphase motion of neighbors. This additional resonance frequency of the ensemble enables to demonstrate a frequency selective modifications of the signal processing.

II. MODEL

We study several rather simple small arrays of inhibitory diffusively coupled stationary but very strongly excitable FitzHugh Nagumo models (FHN) under the action of white additive noise and subthreshold periodic signal which is applied to one of the elements. The FHN model is a paradigmatic model describing the behavior of firing spikes in neural activity [41], and in general the activator-inhibitor dynamics of excitable media [42]. We show that for some values of the signal period the dependence of SR measures on the noise level has a second maximum and the dependence of SR on the values of the signal period under some fixed noise resembles the conventional resonance.

In order to get the reference frame for further comparisons, we begin with the study of the dependence of classical SR on the signal period in the simplest version of FHN model. The previous investigation [21] was very limited in relation to the value of the periods studied. The model is given by the following equations:

$$\frac{dx}{dt}=A-y+\xi+A_s\sin\left(\frac{2\pi}{T_s}t\right), \tag{1}$$

$$\varepsilon\frac{dy}{dt}=x-\frac{y^3}{3}+y, \tag{2}$$

where, in a neural context, $y(t)$ represents the membrane potential of the neuron and $x(t)$ is related to the time-dependent conductance of the potassium channels in the membrane [41]. The dynamics of the activator variable y is much faster than that of the inhibitor x, as indicated by the small time-scale-ratio parameter ε. 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. We fix A close to the bifurcation in the interval $[1.01,1.03]$ in order not to use high-level noise to excite oscillations and thereby to avoid masking of the fine structure of the interspike intervals histograms. Here ε is in the range $[0.0001,0.001]$, which is significantly smaller compared to those that are commonly used. Such a stiff excitation is needed to provide a fast jumping between the attractors. The stochastic forcing is represented by Gaussian white noise ξ with zero mean and intensity σ_a^2, $\langle\xi(t)\xi(t+\tau)\rangle=\sigma_a^2\delta(\tau)$. The harmonic signal is subthreshold, $A_s<A-1.0$. To evaluate the amplitude of the input frequency in the output signal, we calculated the linear response at the input frequency $\omega=2\pi/T_s$ [1],

$$Q_{\sin}=\frac{\omega}{2n\pi}\int_0^{2\pi n/\omega}2y(t)\sin(\omega t)dt,$$

$$Q_{\cos}=\frac{\omega}{2n\pi}\int_0^{2\pi n/\omega}2y(t)\cos(\omega t)dt,$$

$$Q=\sqrt{Q_{\sin}^2+Q_{\cos}^2},$$

when n is the number of periods T_s, covered by the integration time.

III. CLASSIC SR IN AN ISOLATED FHN

Figure 1 shows the dependence of the linear response Q on the noise amplitude for different values of the signal period. For the numerical integration of the model we have used here and below the Heun's algorithm [43]. All curves demonstrate standard SR behavior, but the influence of the period is not weak especially for $T_s=3.2$ which corresponds to the duration of excursion time after firing $T_{\rm exc}$. For this period the optimal signal amplification takes place in a broad range of noise amplitude. Furtheron, the resonance frequency depends on the noise intensity σ_a^2 and hence the driving period T_s can be in resonance only at a suitable range of σ_a^2 and not overall [Fig. 1(b)]. This explains the appearance of the additional maximum in the dependence for $T_s=3.2$. A detailed investigation of the resonant forcing of an isolated FHN can be found in Ref. [21]. Under strong noise, the realizations of stochastic cycles are very similar to corresponding noisy limit cycle (e.g., with $A=0.99$) and the de-

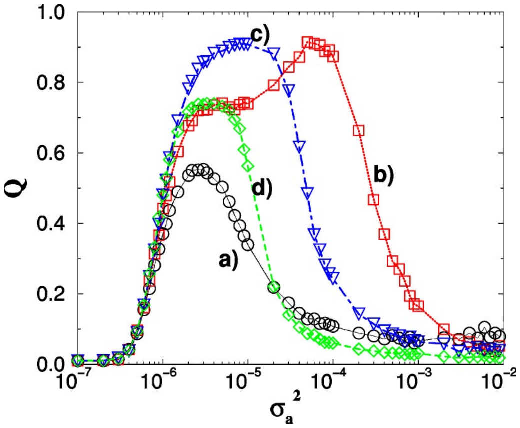

FIG. 1. The linear response Q for an isolated FHN [Eqs. (1) and (2)] as function of the noise intensity σ_a^2 for different signal periods $T_s=2.8$ (a), 3.2 (b), 3.4 (c), and 4.0 (d). Other parameters are $A=1.02$, $\varepsilon=0.0001$, $A_s=0.01$.

pendence of Q on the period under fixed large noise contains the conventional main resonance and secondary resonances at $T=1.6$, 1.08, at least (Fig. 2). A conventional resonance occurs when the time moments of the end of phase point excursions coincide with "negative" phase of the signal which significantly facilitates the next firing (A is shifted closer to 1.0). Figure 2 illustrates that if the signal period is one half or one third of the excursion time T_{exc} then the secondary resonances occur.

IV. FREQUENCY-DEPENDENT SR IN TWO COUPLED OSCILLATORS

Now we consider two identical and coupled elements and introduce the diffusion of the inhibitory variables,

$$\frac{dx_{1,2}}{dt}=A-y_{1,2}+\xi_{1,2}+A_{s\,1,2}\sin\left(\frac{2\pi}{T_s}t\right)+C(x_{2,1}-x_{1,2}), \tag{3}$$

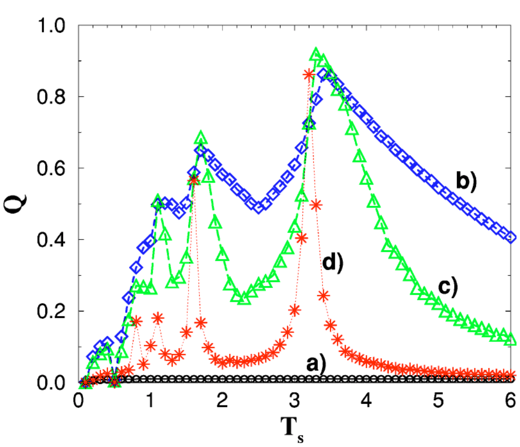

FIG. 2. The dependence of the linear response Q for an isolated FHN [Eqs. (1) and (2)] on the signal period T_s for several values of the noise level $\sigma_a^2=0.0$ (a), 3×10^{-6} (b), 1×10^{-5} (c), 1×10^{-4} (d).

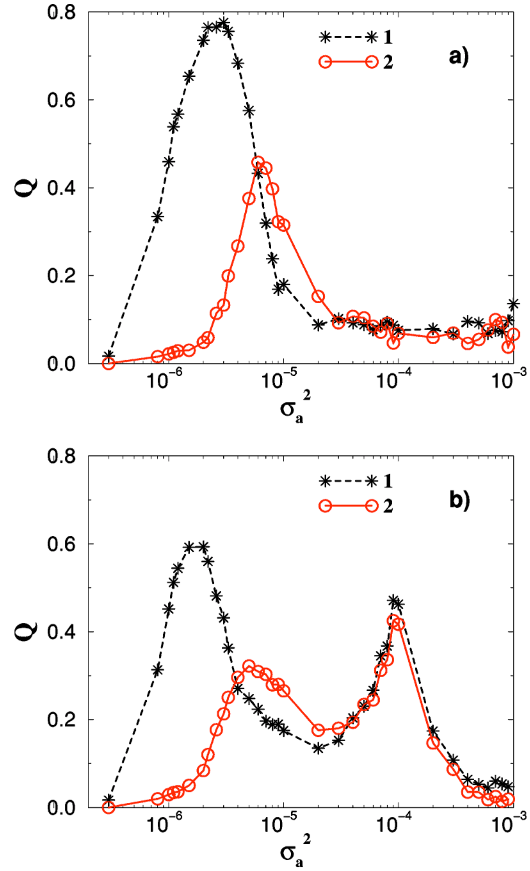

FIG. 3. The linear response Q for two inhibitor coupled FHN's [Eqs. (3) and (4)] as function of the noise intensity for signal periods $T_s=3.2$ (a) and $T_s=4.2$ (b). $A=1.02$, $\varepsilon=0.0001$, $A_{s\,1}=0.01$, $A_{s\,2}=0.0$, $C=0.1$.

$$\varepsilon\frac{dy_{1,2}}{dt}=x_{1,2}-\frac{y_{1,2}^3}{3}+y_{1,2}, \tag{4}$$

where the signal is applied only to the first element ($A_{s\,1}=0.01$ and $A_{s\,2}=0.0$), and $\langle\xi_i(t)\xi_j(t+\tau)\rangle=\sigma_a^2\delta(\tau)\delta_{i,j}$.

We investigate the dynamics of Eqs. (3) and (4) in the same region of the signal periods and noise levels as in Figs. 1 and 2 and select the most typical results. Figure 3 presents the dependence of Q on the noise intensity for (a) $T_s=3.2$ and (b) $T_s=4.2$.

Under the action of weak noise the first element shows SR at any T_s and the transmission of the signal to the second element is observed starting from the SR-optimal noise. For standard SR a further evolution of Q with noise for both element should be a continuous decreasing of Q. The same is true for the elements coupled via their fast variables, but the inhibitory coupled relaxation excitable elements demonstrate a large second peak [Fig. 3(b)] for some interval of $T_s=4.2$–4.5. The nature of this peak is the noise-induced antiphase stochastic cycle in the presence of the coupling. It has been shown recently that in a broad interval of noise amplitudes the antiphase cycle dominates and results in a new type of coherence resonance [44]. The period of this cycle depends on the coupling strength and the noise amplitude which define the position of the second peak on the curve $Q(\sigma_a^2)$ in Fig. 3(b). The influence of the stiffness is also essential because for $\varepsilon > 0.001$ the second peak cannot be clearly observed (data not shown), but the rate of $Q(\sigma_a^2)$ decreasing is less than that for standard SR (Fig. 1). A similar double maximum in the power spectral amplitude at the forcing frequency as a function of the noise intensity has been found recently but for an underdamped bistable system where two maxima are linked with two noise-induced motions: intrawell and interwell [45]. These results show that we can use inhibitory coupled oscillators for frequency selection in stochastic resonance. Notably, a multipeak *coherence* resonance also has been observed in coupled FHN models [46].

V. FREQUENCY-DEPENDENT SR IN A CHAIN OF THREE OSCILLATORS

Three identical coupled elements can demonstrate a richer set of regimes which depend on the configuration

$$\frac{dx_1}{dt}=A-y_1+\xi_1+A_{s\,1}\sin\left(\frac{2\pi}{T_s}t\right)+C(x_2-x_1), \quad (5)$$

$$\frac{dx_2}{dt}=A-y_2+\xi_2+A_{s\,2}\sin\left(\frac{2\pi}{T_s}t\right)+C(x_1-x_2)+C(x_3-x_2), \quad (6)$$

$$\frac{dx_3}{dt}=A-y_3+\xi_3+C(x_2-x_3), \quad (7)$$

$$\varepsilon\frac{dy_{1,2,3}}{dt}=x_{1,2,3}-\frac{y_{1,2,3}^3}{3}+y_{1,2,3}, \quad (8)$$

where $\langle \xi_i(t)\xi_j(t+\tau)\rangle=\sigma_a^2\delta(\tau)\delta_{i,j}$.

Let us analyze possible attractors in the autonomous system of three inhibitory coupled identical oscillators. For a linear chain of oscillators whose bifurcation parameters are close to Hopf bifurcation, three main types of stable attractors occur [47]. The first is in antiphase regime in which oscillators at the ends move in antiphase with the middle one. The second type was called ''dynamic trap'' because the antiphase motion of the end's oscillators does not permit the firing of the middle one. The third type is not a single attractor but a family of attractors which may be designated as $n/2/n$, where $n=3,5,7,\ldots$. The value of n depends on the coupling strength and the distance of A from the bifurcation value. The closer the A to 1.0 (for FHN model) the larger is the value n and the stronger is the crowding of attractors. If the elements do not oscillate deterministically but are excited by noise, then the observed stochastic collective modes only partially resemble these types of regimes due to noise-dependent perturbations of trajectories. The attractors $n/2/n$ will be practically corrupted by noise. This type of multimodal distributions is not model specific and was observed for autooscillating [48] and excitable [49] electronic arrays with dephasing (inhibitory) interactions.

Figure 4 shows the distribution of interspike intervals (ISIs) for three coupled excitable elements without an exter-

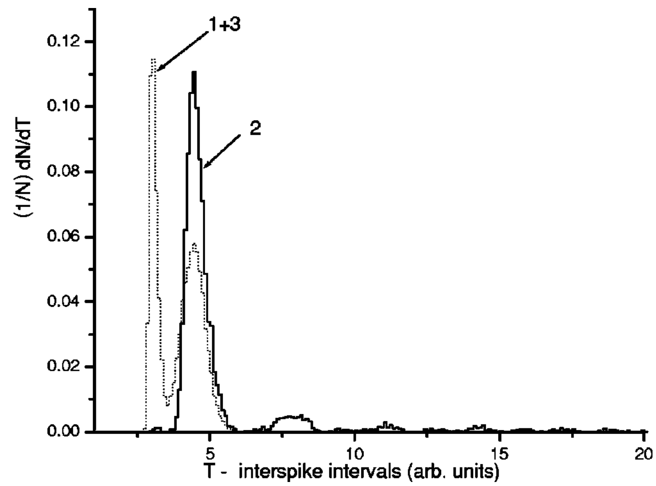

FIG. 4. The ISI distributions for a chain of three coupled excitable elements [Eqs. (5)–(8)] and no signal ($A_s=0.0$). The ISI distributions of first and the third (1+3) oscillators are denoted by a dashed line and the second one (2) by a solid line. The other parameters are $A=1.02$, $C=0.1$, $\sigma_a^2=10^{-4}$, and $\varepsilon=0.0001$.

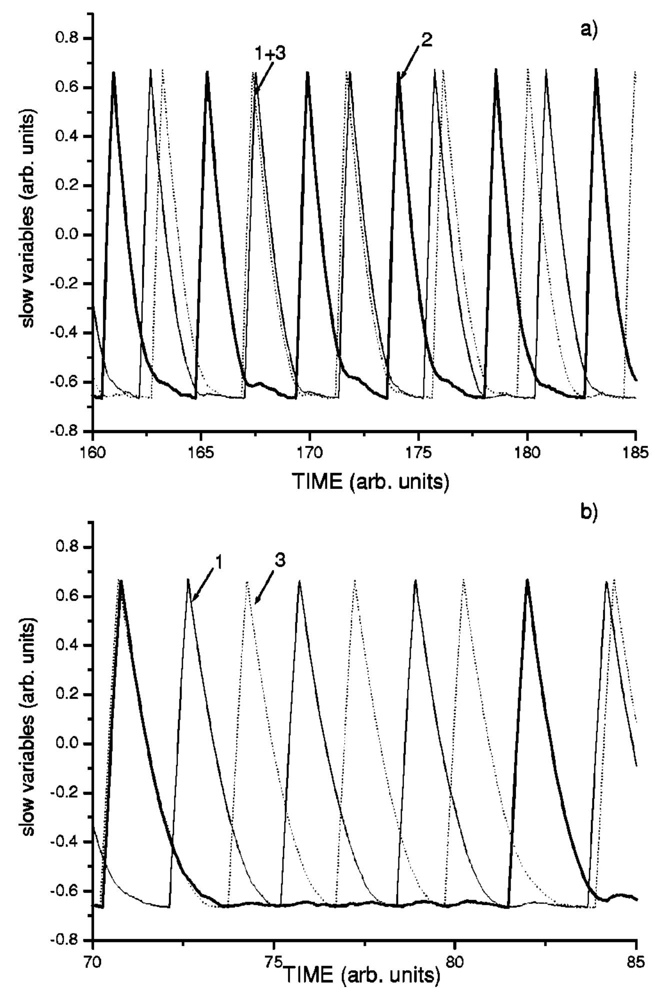

FIG. 5. The time-series intervals selected from trajectory giving ISI distribution of Fig. 4. They present the antiphase regime (a) and dynamic trap (b).

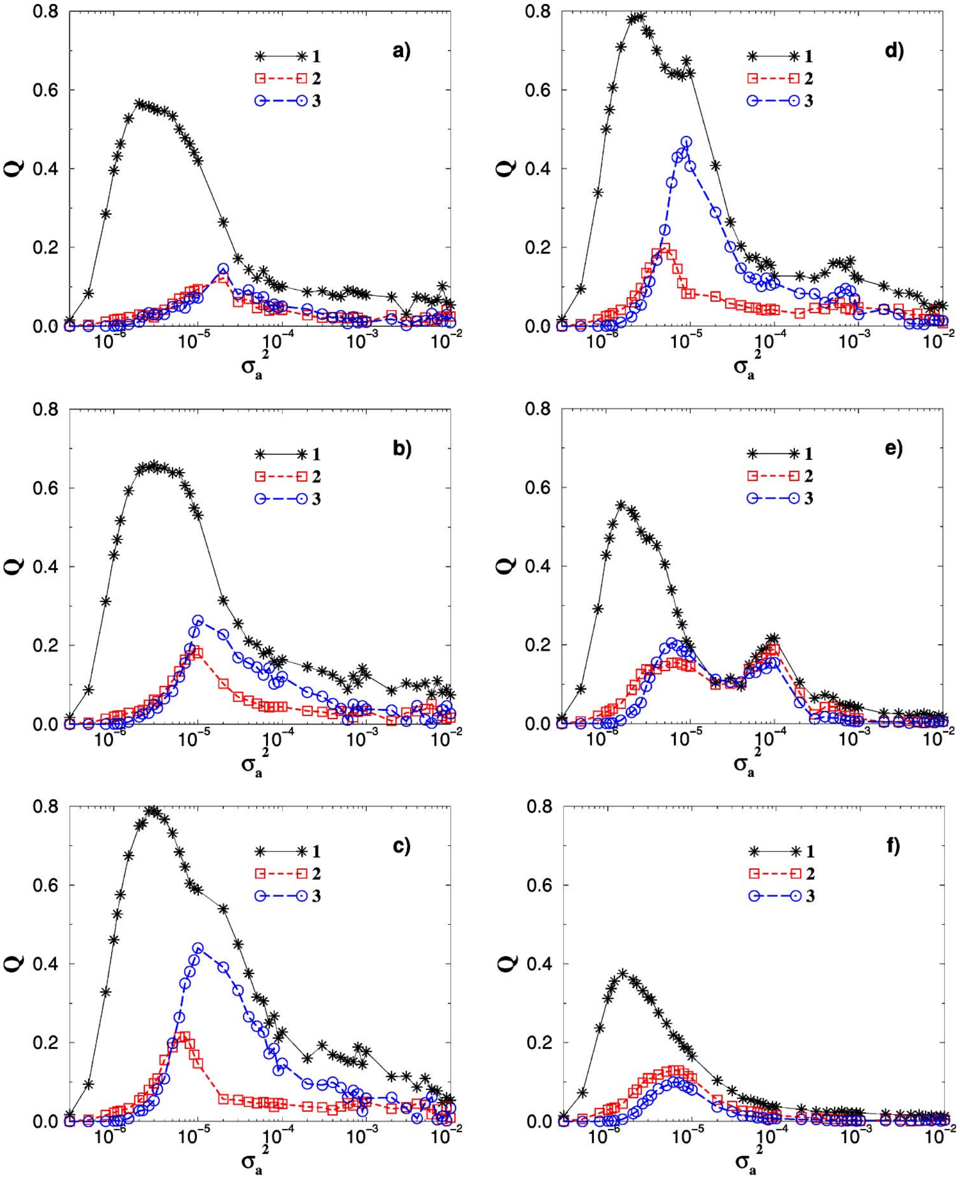

FIG. 6. The dependencies of the linear response Q for a chain of three elements [Eqs. (5)–(8)] as a function of the noise intensity for different signal periods: $T_s = 2.8$ (a), 3.0 (b), 3.2 (c), 3.4 (d), 4.5 (e), 6.0 (f); $A = 1.02$, $\varepsilon = 0.0001$, $C = 0.1$. The signal of the amplitude $A_{s1} = 0.01$ is applied to the first oscillator only ($A_{s2} = 0.0$).

nal signal. It can be clearly seen that only two stochastic attractors are really manifested in the ISI distributions. In the dynamic trap, in which the first and the third oscillators are moved in average in antiphase, their interspike intervals are around $T \approx 3.0$ that is very close to $T_{\mathrm{exc}} = 3.2$. Since the system is symmetric, the ISI histograms of the first and third elements are identical. In this regime the ISI distribution for the middle element is very broad and polymodal. There are only infrequent realizations with very large ISI for the second element. In the antiphase regime, in which the first and the third oscillators are moving in average in-phase but in antiphase with middle oscillators, they all have the same average period about $T_{anti} \approx 4.2$ under the given set of the other parameters. Figure 5 shows typical selected time series of the inhibitor variables $x(t)$ of the three coupled oscillators related to the two main phase regimes antiphase motion Fig. 5(a) and of dynamic trap Fig. 5(b).

The lifetimes and periods of attractors depend on the coupling strength and noise values, which may be adjusted to enhance (or to inhibit) the acceptance of a sinusoidal signal of a given period. To check this possibility, we calculate $Q(\sigma_a^2)$ for different signal periods and present results which clearly reflect the specific modification of signal acceptance. We consider two cases.

Case 1. The harmonic signal with $A_{s\,1} = 0.01$ is applied only to the first oscillator ($A_{s2} = 0.0$). The corresponding dependencies of the linear response, measured for all three oscillators are shown in Fig. 6 for different periods of the external signal T_s. As discussed above, we have in this system two noise-supported attractors: a dynamical trap ($T = 3.0$–3.6) and an antiphase attractor ($T \approx 4.2$). These two time scales demonstrate itself also in the frequency selectivity by signal processing. If the signal period $T_s < 3.0$ (e.g., $T_s = 2.8$) or $T_s > 5.5$, the behavior of $Q_1(\sigma_a^2)$ is quite similar to that of isolated FHN and $Q_2 \approx Q_3$ have only one peak as in the classical SR [Figs. 6(a) and 6(f)]. If the signal period is in the interval $T_s = [3.0, 3.4]$ then Q_1 sharply declines in comparison with Fig. 1 but Q_3 dramatically increases for noise amplitudes in the interval $[10^{-5}, 5\times 10^{-5}]$ [Figs. 6(b)–6(d)], i.e., the signals with these periods easily penetrate through the middle element and are selectively manifested in the time series of the third oscillator. For $T_s > 3.6$ Q_3 decreases again [Fig. 6(e)]. The reason for this phenomenon is the coincidence of the signal period with the average values of the interspike intervals of the stochastic dynamic trap [Fig. 5(b)]. In this regime the average ISI of the first and the third elements are equal and their interspike distributions are significantly narrower than that of the second element. Therefore, the signal manifestation in the behavior of the second oscillator is small enough for this interval of the signal period.

If the noise amplitude is larger than 5×10^{-6}, the average activation time of excitation is small and several stochastic attractors may occur, but the harmonic signal supports those which has a similar value of average period. The next stochastic attractor which has a noticeable lifetime (not very sensitive to noise) under stronger noise is the antiphase oscillation with the average period $T_{anti} \approx 4.2$. The second peak on the curves $Q_i(\sigma_a^2)$ at $T_s = 4.0$–4.5 at about $\sigma_a^2 \approx 2\times 10^{-4}$ is realized for all oscillators [Fig. 6(e)], because the average ISIs are the same for all elements in this regime [Fig. 5(a)]. All the three oscillators generate a similar spike sequences and hence perform with nearly the same linear response Q. For the current model and the given set of other parameters, the distance between ISIs is not large (Fig. 4) and the selectivity of signal enhancement is limited by noise-induced transitions between these regimes.

Case 2. The harmonic signal is applied only to the middle element ($A_{s1} = 0.0$ and $A_{s2} = 0.015$). This example of the selective enlargement of $Q(\sigma_a^2)$ is presented in Fig. 7(a) and 7(b). For $T_s = 3.2$, which corresponds to the maximal manifestation of the signal in the behavior of an isolated oscillator up to noise amplitude 10^{-4} (see Fig. 1), the function Q_2 dramatically decreases if the noise is around 10^{-5}. Such a behavior reflects the absence of small ISIs in the time series of the second element after this noise value. The increase of signal period up to $T_s = 4.0$ results in the appearance of the second peak on all curves $Q_{1,2,3}(\sigma_a^2)$ and that is similar to Fig. 6(e) except for here Q_2 is larger than $Q_{1,3}$ because the signal is applied to the middle element of the chain.

Thus, the presence of a double resonant peak structure of $Q(\sigma_a^2)$ is caused by the coexistence of two stochastic limit cycles which share the phase space due to the inhibitor exchange. In our model the distances between average periods of attractors are not large and therefore the amplitudes of the second peaks in Figs. 3, 6, and 7 are noticeable but not so pronounced as compared with the standard SR peak which, however, is almost the same for any values of the external periods.

The attractors not only differ by the periods but by the phase relations as well, which means (opens) the possibility for additional checking of our explanation by the simultaneous applications of two harmonic subthreshold signals with appropriate phase shift. For instance, the second peak on the $Q_{1,2,3}$ has a larger height if two signals are applied to the end's oscillators in phase but $Q_{1,2,3}$ is almost negligible if the same signals are in antiphase each other (data not shown).

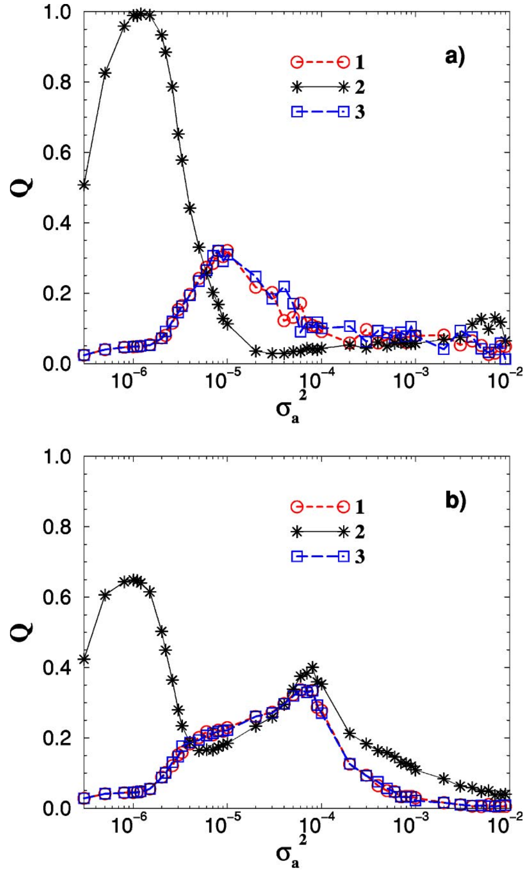

FIG. 7. The linear response Q as a function of the noise intensity for signal periods $T_s = 3.2$ (a) and $T_s = 4.5$ (b). $A = 1.02$, $\varepsilon = 0.0001$, $C = 0.1$. The periodic signal $A_{s2} = 0.015$ is applied only to the middle oscillator ($A_{s1} = 0.0$).

The manifestation of the described effects depends not only on the stiffness but on the other model parameters too: the coupling strength and the proximity of A to the bifurcation value. Our studies have shown that the results are retained under a two-fold changing of coupling and the difference $(A - 1.0)$.

VI. CONCLUSION

In summary, we have demonstrated the frequency selective response and information propagation in a noisy system which consists of inhibitory coupled excitable units and is driven by a subthreshold harmonic signal. The signals with periods from some intervals (e.g., $T_s = 4.0$–4.2) may be enhanced not only for small but also for larger noise which are typically ineffective for standard SR. The signals with shorter periods (e.g., $T_s = 3.0$–3.2), which are the most effective for SR, may be strongly inhibited under some noise levels in comparison with Fig. 1. The background of the selectivity is the multirhythmicity generated by the inhibitory coupling in combination with the high stiffness of elements which provides the fast transitions between stochastic attractors.

The mechanism of this selectivity can be explained by the appearance of new resonance frequencies of the coupled system which are caused by different phase relations of the oscillators and differ from the resonance frequency of an isolated FHN. Especially the resonance frequencies of the antiphase and dynamic trap regime exhibit stable attractors in a noisy environment. By forcing one element of the network in resonance with these coupling-dependent resonance frequencies, we observe an additional resonance peak in the SR curve besides the typical bell-shaped curve of standard SR. Another interesting phenomenon, which we have explained, is the masking of the information flow in the dynamic trap regime. In this effect, the last oscillator in the row shows a much better response at the signal frequency, which was fed at the first oscillator of the row, than the middle one. We believe that the study of the frequency selective SR and the masking of information flow in an array due to inhibitory coupling can be useful for understanding of multifrequency information exchange mechanisms in neural networks. Because of the generality of these effects for diffusive coupled activator-inhibitor oscillator arrays and not only to FHN systems, we expect that the findings can be applied also in other fields, e.g., in chemistry or biology.

It is important to note that these results contribute also to the study of fundamental synchronization phenomena [50]. In frames of this study SR can be considered as a synchronizationlike phenomenon, in which optimal noise induces phase synchronization between output and input signals. In Ref. [51] it has been shown that in deterministic systems of coupled elements, synchronization can happen through the asynchronized region. The effect, considered here, demonstrates a synchronizationlike behavior through the dynamical trap, and can be considered as a stochastic analog of this kind of a phase synchronization in deterministic systems.

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