Noise-induced multimode behavior in excitable systems

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Based on experiments with electronic circuits, we show how a system of coupled excitable units can possess several noise-induced oscillatory modes. We characterize the multimode organization in terms of the coherence resonance effect. Multiple gain of regularity is found to be related to different frequency entrainments and to the appearance of additional time scales.

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Noise can have quite different effects when acting on oscillatory or on excitable systems. In the deterministic case the oscillatory system already possesses an eigenfrequency that can be modified by the random forcing [1,2]. In contrast, the influence of noise on an excitable system is more surprising. Without any perturbation there is no response of the system at all, while too large fluctuations just result in a noisy output. For an appropriate noise intensity, however, the behavior of the excitable system becomes quite regular, a phenomenon known as coherence resonance [3–5]. In some cases coherence resonance can be understood as the response of a nonlinear dynamical system to noise excitation near the bifurcation of periodic orbit [5]. The basis of such an effect is that the power spectrum displayed by a system after a bifurcation may be visible even before the bifurcation if noise is applied [2]. Thus, a noisy precursor of the bifurcation, i.e., a *noise-activated* time scale, is observed. However, the effect of coherence resonance can be observed even if the excitable system does not possess any kind of oscillatory behavior. The corresponding mechanism is explained by means of different noise sensitivities for the excitation and relaxation times [4]. The trajectory in this case may be considered as a motion on a stochastic limit cycle [6] with a corresponding *noise-induced* eigenfrequency. These oscillations are controlled by noise and significantly depend on the noise intensity and statistics.

While generation and entrainment of single-mode deterministic or stochastic oscillations are well understood, the dynamics of systems with many oscillatory modes is less studied. Many living systems perform oscillations with different modes. The thalamocortical relay neurons can generate either spindle or δ oscillations [7]. Recently, Neiman and Russell [8] have found that the electroreceptors in paddlefish possess the property of being biperiodic. The functional units of the kidney, the nephrons, demonstrate adjustment of intrinsic slow and fast oscillations [9]. Two-mode stochastic dynamics was studied in the context of rhythmic applause [10].

In contrast to previous studies we focus on *noise-induced* rather then noise-activated oscillatory modes, i.e., we focus on time scales that are delivered and controlled by noise and that did not exist in the deterministic case. We provide experimental observation of such multimode behavior and investigate the conditions of generation and entrainment of the specified modes. With this aim, we examine different implementations of coupled *identical* excitable units with different types of coupling that are relevant to typical problems in physics and neuroscience. Namely, we consider (i) direct coupling when the output signal from one excitable unit is delivered to the input of another unit together with external noise [Figs. 1(b) and 1(c)], and (ii) an electronic version of synaptic coupling [Fig. 6(a)].

For real information-processing systems the external noise is considered as more accessible for control and measurement than the internal noise that is generally assumed to be negligible. However, Gailey *et al.* [13] have demonstrated that internal noise can play a constructive role in the operation of stochastic systems. In our case, we assume that the system is influenced by a weak fluctuating field of intensity B that causes rare spontaneous firings even with vanishing external force.

In the present paper, we describe results of experiments on coupled monovibrator circuits. This electronic model [11] captures well the essential aspects of excitable systems. A single monovibrator [Fig. 1(a)] generates a single electric impulse whenever the input voltage exceeds the threshold level V_{th}. The circuit employs an operational amplifier that supplies a nonlinear response to the voltage difference between two inputs together with an RC chain involved in the positive feedback that provides a time locking of the output circuit in an excited state via a gradual voltage change at the "+" input. The recharging time constant is $\tau_0 = -RC \ln\frac{1}{2}(V_{th}/U+1)$, where $V_{th} \leq U$ and U is the voltage of power supply. Being excited by white Gaussian noise $\xi(t)$ of an appropriate intensity D, the circuit reaches the regime of coherence resonance (CR) [11]. The noise-induced oscillations become quite regular and the whole system (excitable unit and noise) can be considered as a CR oscillator whose behavior is described by a peak frequency governed by the

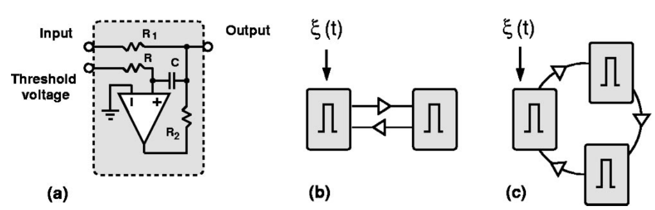

FIG. 1. Different implementations of coupled excitable units. (a) Electronic circuit of a single monovibrator; (b) mutually coupled units; (c) circle configuration.

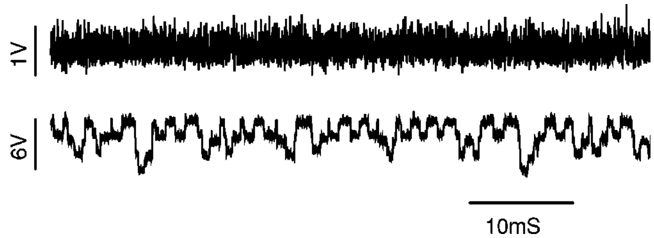

FIG. 2. Examples of time series for noise input (upper panel) and collective response from three coupled excitable units (lower panel).

noise and a phase introduced as the position on a stochastic limit cycle. For such coupled functional units, we have previously investigated synchronization phenomena by means of numerical simulations of a Morris-Lecar neuron model and by electronic experiments with a monovibrator circuit [12]. To characterize the collective response of the system [Figs. 1(b) and 1(c)] we use the summarized output from all functional units. Figure 2 compares the time series from the noise source $\xi(t)$ with the more regular response of the excitable system in Fig. 1(c). To characterize spectral properties of such signal we consider its power spectrum $S(f)$ calculated over a set of L sampled realizations

$$S(f)=\frac{1}{L}\sum_{i=1}^{L}|P_i(f)|^2, \tag{1}$$

where $P_i(f)$ is the fast Fourier transform calculated for ith realization from system's output. With large enough L (we use it about 200) the well-developed and smooth peaks can be detected for excitable units in the regime of coherence resonance. When $S(f)$ is calculated from summarized output signal of coupled units, all noise-induced time scales and their mutual entrainment can be observed.

Figure 3(a) demonstrates different collective behaviors when the coupling strength g of two symmetrically coupled excitable units is varied. Without coupling, the second unit can generate only randomly appearing impulses due to the presence of weak internal noise with an intensity $B \cong 0.0005V^2$. At the same time the first unit generates a pronounced peak in the power spectrum. With increasing g, a second peak appears. Within a wide range of g, the *peak frequencies* are found to keep ratio of 1:2 and 1:1. This means that the frequency locking takes place. However, within some ranges of parameter g, the resonance ratio between the noise-induced frequencies is broken down, and two peaks at incommensurate frequencies are clearly distinguished in the power spectrum. Corresponding regions are clearly distinguished in the three-dimensional plot. Hence, two-mode behavior is observed through the resonant and nonresonant ratio between the noise-induced frequencies. Such behavior is analogous to quasiperiodic motion in the deterministic case. Note, that (i) the multimode dynamics is induced by noise since with vanishing random excitation none of the systems exhibit oscillations, and (ii) there is no a priory introduced detuning between the time scale of the systems.

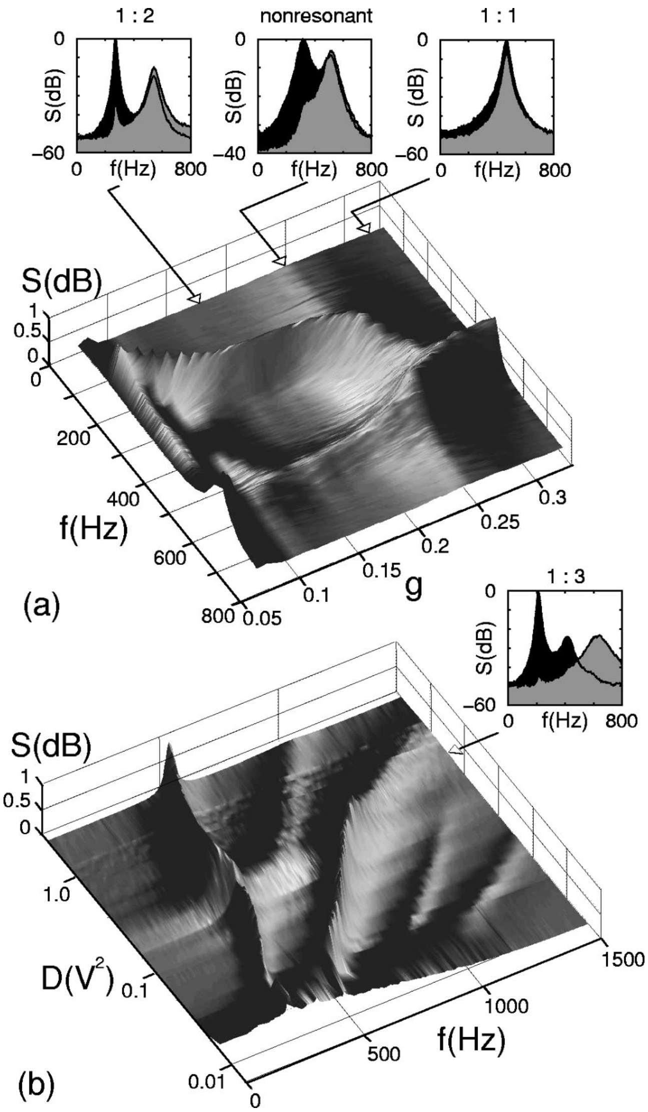

FIG. 3. Two-mode collective response in the system of two mutually coupled monovibrators [Fig. 1(b)]. (a) Three-dimensional plot illustrating frequency entrainment with varying coupling strength at $D=0.475V^2$. The evolution of the power spectrum clearly shows the transitions from 1:2 frequency locking ($g=0.18$) to nonresonant two-mode behavior ($g=0.25$) and, finally, to 1:1 mode locking ($g=0.325$). (b) With varying noise intensity D the power spectrum diagnoses the transitions from 1:3 mode locking (see inset for $D=0.77V^2$) to nonresonant two-mode behavior and, finally, to 1:2 mode locking. Coupling strength is fixed at $g=0.1$.

Coherence entrapments between interacting systems are also governed by noise. Figure 3(b) illustrates how distinct phase patterns appear for a coupling strength $g=0.1$. With varying noise intensity D, the frequencies of the noise-induced oscillations in the coupled systems move with respect to one another to give rise to oscillatory modes with two well-pronounced independent peaks in the power spectrum. For D ranging from $0.037V^2$ to $0.152V^2$, the 1:2 resonance behavior is observed. For $D\in[0.788V^2,1.07V^2]$, frequencies are locked in a 1:3 ratio [see inset in Fig. 3(b)].

In order to quantitatively characterize the effect of coher-

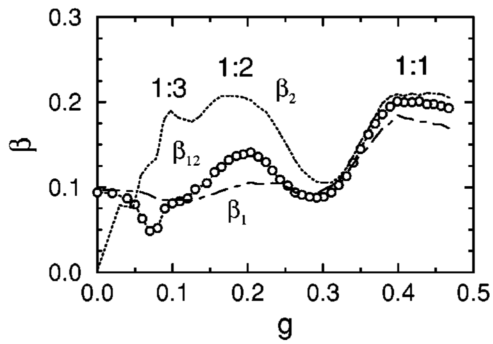

FIG. 4. Measures of regularity as a function of coupling strength ($D=0.475V^2$) for the first (β_1) and second (β_2) units, and for their collective response (β_{12}).

ence resonance, various researchers described the inhomogeneity of the spectrum by different methods, including calculation of the signal-to-noise ratio [5,6] and the autocorrelation function [4]. We choose a more universal method for characterizing the regularity of oscillations using their spectrum:

$$S_n(f_i)=\frac{S(f_i)}{\sum_{i=1}^{i=m} S(f_i)}. \tag{2}$$

Our approach is based on the formula of Shannon entropy applied for the normalized power spectrum S_n containing m components (2):

$$E=-\sum_{i=1}^{i=m} S_n(f_i)\ln(S_n(f_i)). \tag{3}$$

E takes zero value for harmonic signal being the most regular. White noise is considered to be completely irregular with homogeneous spectrum. In this case, E reaches the maximal value

$$E_{max}=-\sum_{i=1}^{i=m} \frac{1}{m}\ln\left(\frac{1}{m}\right)=\ln m. \tag{4}$$

The measure of regularity is calculating as

$$\beta=1-\frac{E}{E_{max}}. \tag{5}$$

Defined in this way, the β value reflects essentially the nonuniformity of the spectrum, varying from 1 for the purely harmonic oscillations to 0 for white noise.

For a single monovibrator the plot of β vs the noise intensity D has a single pronounced maximum, i.e., the system exhibits coherence resonance [11]. In the present work, we are particularly interested in establishing a relation between the regularity of the noise-induced oscillations and the strength of interaction. Figure 4 shows the behavior of β with increasing g both for the collective response of our system and for the individual units. It is clearly seen, that the second unit produces the most regular output. It is remarkable that the local maxima of regularity β_2 correspond to the regions of 1:3, 1:2, and 1:1 mode locking, where the relative width of the peaks in the power spectrum is considerably lower. The first unit is the subject of external random force $D\xi(t)$. Hence, its reaction to variations in g is insignificant, untill the coupling becomes strong ($g>0.3$). The collective response regularity β_{12} depends on g in a nonmonotonic way. For very weak coupling, $\beta_{12}\approx\beta_1$ since the second system receives a weak input and produces no firing. For $g \in (0.05,0.1)$, the β_{12} graph displays a considerable fall due to a rather irregular spike generation in the second unit. When g is further increased, both units enter the regime of coherence resonance and β_{12} generally follows the behavior of β_1 and β_2, displaying maxima in the mode locking regions and being small in the nonresonant regimes.

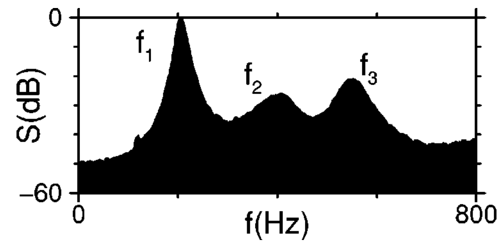

FIG. 5. Power spectrum illustrating three-mode collective behavior in a system of three interacting excitable units [Fig. 1(c)] at $D=0.35V^2$ and $g=0.03$. Peak frequencies are estimated as $f_1=205.3$ Hz, $f_2=403.5$ Hz, and $f_3=549.1$ Hz.

The main result of the above experiments is that symmetrically coupled identical excitable units can produce a few-mode stochastic oscillations. To confirm this proposition we consider a circle configuration that contains three functional excitable units [Fig. 1(c)]. For a certain range of control parameters, a regime with three different frequencies is observed. It manifests itself as mode locked states and as nonresonant behavior (Fig. 5). Thus, we can state that the three-unit system is able to generate three-mode stochastic behavior.

The coupling we considered above belongs to one of the simplest types. For neuronal excitable systems, a synaptic

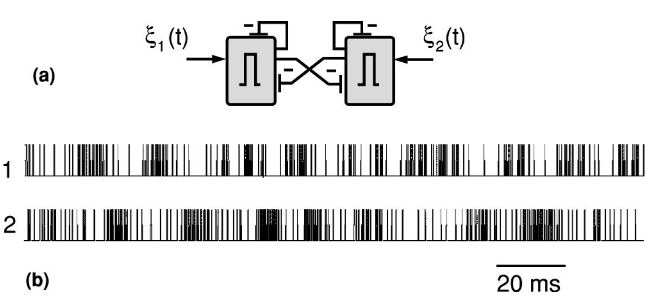

FIG. 6. (a) Two monovibrators with delayed inhibitory couplings imitate the simple neural circuit. (b) Stochastic spike trains generated by the first and second excitable units. Antiphase behavior is indicated on average.

(i.e., delayed inhibitory or excitatory) interaction is more realistic. Below we describe the two-mode stochastic behavior of system [Fig. 6(a)] that is actually the electronic model of the simplest breathing rhythm generator for a snail [14]. The circuit contains self-inhibitory and mutually inhibitory coupling chains that can increase the threshold voltages of the first (V_{th1}) and second (V_{th2}) units. Each coupling chain contains a rectifier and a low-pass filter with coupling strength g_{ij} and time constant τ_{ij}, where i,j are the unit numbers. Note, the self-inhibitory time constant were chosen to be equal and greater than the mutual-inhibitory time constants, i.e., $\tau_{11}=\tau_{22}>\tau_{12}=\tau_{21}$.

For small noise intensity D (which is the same for the two units), both excitable units keep silent most of the time, and their threshold voltages remain equal ($V_{th1}\approx V_{th2}$). For intermediate noise, the coupling influence on threshold voltages becomes significant. With this, one of two units gets an ''advantage'' to suppress the firings in the other unit since mutual inhibition makes the in-phase regime unstable. However, with intensive firing, the slow self-inhibitory chain with rate τ_{11} (or τ_{22}) comes into operation and suppresses the activity of the corresponding unit. This creates the best conditions for the excitation of the other unit. The process continues in a similar way, producing a behavior with time-varying firing rates for the two excitable units [Fig. 6(b)].

In this operating regime, two peaks in the power spectrum are clearly distinguished [Fig. 7(a)]. The high-frequency peak corresponds to noise-induced oscillations in the single system while the low-frequency peak reveals a new noise-induced oscillatory mode. Hence, the system of coupled excitable units generates an oscillatory mode that is characterized by the values of τ_{ij} and by the relation between the noise intensity and the initial threshold voltages (V_{th1}, V_{th2}). Figure 7(b) shows how the frequency of these oscillations (open circles) depends on the noise intensity. It is clearly seen that with increasing noise strength, both frequencies grow (i.e., they are noise controlled) but the growth rates are different (i.e., they are independent enough from each other). For strong noise, an excitable system can be immediately pushed out from the equilibrium state in spite of the threshold voltage. The low-frequency peak in the power spectrum disappears, and the additional time scale no longer exists.

The regularity of the low-frequency stochastic oscillations is related to the process of pulse generation in each excitable unit. Hence it is determined by the effect of coherence resonance. Figure 7(b) illustrates that the output regularity β (black circles) is suddenly increased when low-frequency oscillations appear but the peak at the noise-induced eigenfrequency f_2 becomes washed out because of the threshold modulation.

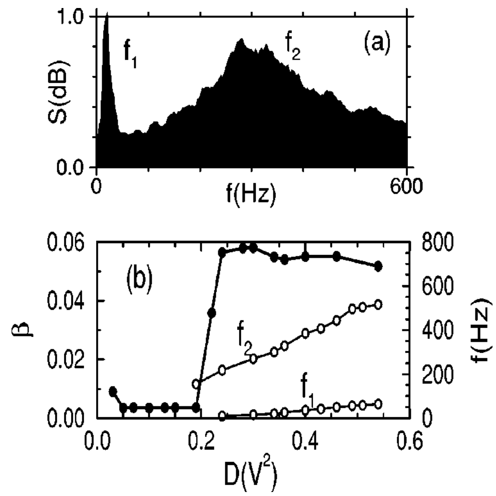

FIG. 7. Two-mode dynamics in the excitable system presented in Fig. 6(a). (a) Power spectrum with well-pronounced peaks ($D=0.34V^2$) and (b) peak frequencies (open circles) and measure of regularity β (black circles) vs noise intensity D.

In summary, we have shown that a simple system of coupled excitable functional units can generate a few oscillatory modes that are induced and controlled by noise. Possible advantages of multimode dynamics may include the following: (i) Increased sensitivity via coherence resonance. We have found the multiple coherence resonance related to different frequency entrainments and to the appearance of additional time scale. (ii) Expanded flexibility. The presence and interaction of two distinct oscillatory modes enrich the dynamical patterns. The building up approach involved excitable stochastic units with self-inhibitory and mutually inhibitory couplings can be applied to simulate neuron systems with distinct phase relations given a priory. We consider the presented results useful for understanding and modeling the origin of rhythmic biological phenomena.

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