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Frequency and phase locking of noise-sustained oscillations in coupled excitable systems: Array-enhanced resonances

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We study the interplay among noise, weak driving signal and coupling in excitable FitzHugh-Nagumo neurons. Due to coupling, noise-sustained oscillations become locked to the signal as functions of both signal frequency and noise intensity. Higher order $m{:}n$ locking tongues and various array-enhanced resonance features are demonstrated. This resonance and locking behavior due to a time scale matching between noise-sustained oscillations and the signal is fundamentally different from stochastic resonance in usual noisy threshold elements.

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I. INTRODUCTION

The response of a nonlinear system to a weak signal has been investigated in various contexts. In a self-sustained periodic oscillator with a natural frequency ω_0, the system adjusts its time scale, achieving frequency and phase locking to the signal. This conventional resonance of phase locking (PL) due to time scale matching is characterized by an Arnold tongue locking region with respect to the amplitude A and frequency Ω of the signal; locking can be achieved with almost vanishing A when the frequencies match, i.e., $m\Omega \approx n\omega_0$. It is of fundamental importance in various fields [1], and has been extended recently to chaotic oscillators [2–4].

Noise can induce oscillations in threshold systems. Stochastic resonance (SR) [5] occurs when the noise-controlled mean switching interval $\langle T\rangle$ is close to the period T_e of the signal and the response becomes optimal [6–8]. An effective, stochastic frequency and phase locking (SPL) occurs in an Arnold tonguelike parameter region of the noise intensity D and the signal amplitude A, for A rather close to the threshold [8]. SR and SPL, however, are fundamentally different from conventional resonance and PL in self-sustained oscillators, because the noise-induced oscillations in overdamped bistable systems have no deterministic natural frequency [8]. In fact, the optimal D of signal-to-noise ratio is independent of the signal frequency Ω for a slow enough signal, and SR can also occur for *aperiodic* signals, both in excitable [9] and bistable [10,11] systems. While SPL exhibits a resonance behavior with a change of D, it does not simply obey a time scale matching condition and does not display a locking and a resonance behavior with respect to Ω [8,11] in terms of synchronization measures. Consequently, a higher order $m{:}n$ locking (i.e., m switching events for every n periods of the signal) does not occur when the signal frequency moves to approximately $(n/m)\Omega$ [8]. In fact, effective SPL can also be achieved for close-to-threshold stochastic signals [9,11], such as dichotomic noise.

In excitable systems, noise alone can generate the most regular spike trains separated by a fluctuating interval T close to the refractory time T_r of the spikes. Due to this coherence resonance (CR) [12,13] behavior, SR of an excitable system shows a sensitivity to higher signal frequencies: the optimal noise intensity depends on Ω [14,15]. However, it has not yet been shown whether the frequency of the noise-sustained spike train can be *locked* to Ω, similar to PL of self-sustained oscillations, especially for signals well below the threshold.

Recently, the interest in SR and CR has been shifted to spatiotemporal systems [16–19]. Array-enhanced SR [17], array-enhanced CR [20,21], noise-enhanced synchronization [18,21,22] and clustering [23] have been demonstrated in coupled bistable or excitable elements. Although it has been shown that global coupling of bistable elements makes SR sensitive to Ω [19], still, it is not known whether there is a *locking* of the frequency and the phase to a very weak signal.

In this Rapid Communication, we demonstrate that, due to coupling, the noise-sustained oscillations in excitable systems achieve frequency and phase locking to weak signals as a result of time scale matching. Our model is a chain of N locally coupled FitzHugh-Nagumo (FHN) neurons [13,18],

$$\epsilon\dot{x}_i = x_i - (x_i^3/3) - y_i + A\cos\Omega t + g(x_{i+1} + x_{i-1} - 2x_i),$$
$$\dot{y}_i = x_i + a + D\xi_i, \qquad (1)$$

with a periodic boundary condition. When $\epsilon = 0.01$ and $a = 1.05$, the neurons are in an excitable regime [13]. We take $g = 0.05$ for the coupling strength and D is the intensity of Gaussian noise ξ_i, $\langle \xi_i(t)\xi_j(t-\tau)\rangle = \delta_{ij}\delta(\tau)$. To demonstrate the significant role of the coupling, we compare the chain to a single uncoupled neuron ($N=1$).

To characterize the locking behavior, we introduce a phase in each cell $\phi_i(t) = 2\pi[(t-\tau_k^i)/(\tau_{k+1}^i - \tau_k^i)] + 2\pi k(\tau_k \leqslant t < \tau_{k+1})$, where τ_k^i is the time of the kth firing in the ith cell. The mean firing frequency $\omega = 2\pi/\langle T\rangle$ is computed from the mean value $\langle T\rangle$ of the pulse interval $T_k^i = \tau_{k+1}^i - \tau_k^i$, by averaging over time and space. At $A=0$, the noise-induced mean spontaneous frequency (NIMF) $\omega_0(D)$ increases with the noise intensity D.

II. CR AND ARRAY-ENHANCED CR

Here we describe briefly the behavior without signal, i.e., $A=0$. In uncoupled neurons subjected to noise, the firing activity becomes the most coherent at a certain optimal noise

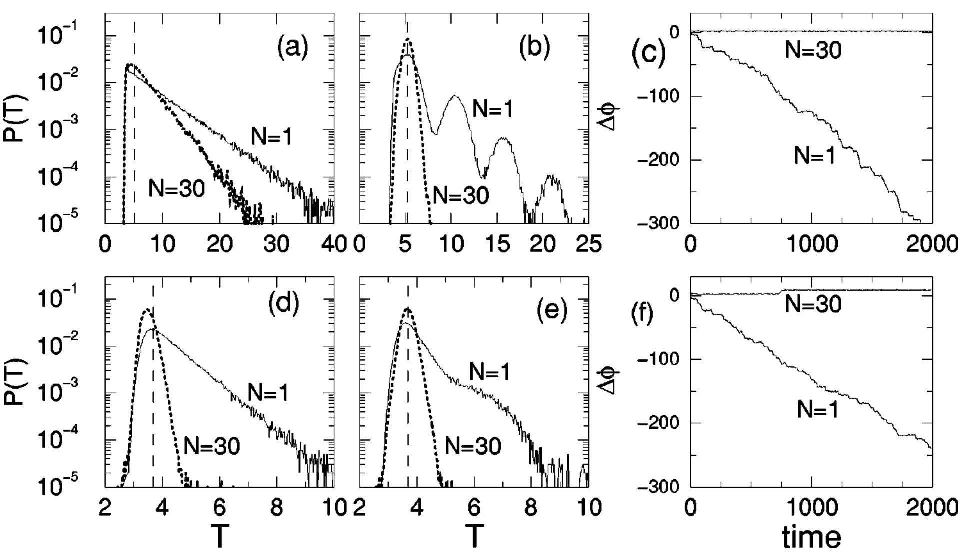

FIG. 1. Different responses of a single ($N=1$) and an array ($N=30$) of coupled FHN neurons to noise and signal. Upper panel: $D=10^{-1.75}$; lower panel: $D=10^{-1.3}$. Distribution of interspike interval at $A=0$ (a),(d) and $A=0.03$ (b),(e). Phase difference between the spike train (randomly selected neuron in the array) and the signal (c), (f) corresponding to (b),(e). The signal period T_e is indicated by the dashed lines in (a),(b),(d),(e).

intensity [13]. When coupled to an array, the spike of a neuron may propagate in the chain to excite its neighboring neurons. This mutual excitation may induce some neurons to fire in a synchronized fashion [18,21,22] and enhance coherence in the noise-induced spike trains [21].

We measure the temporal coherence of the spike trains based on the distribution $P(T)$ of the pulse interval T_k^i. For a weak noise [$D=10^{-1.75}$, Fig. 1(a)], both systems of a single ($N=1$) uncoupled neuron and an array ($N=30$) of coupled FHN neurons show a broad distribution, although the coupling has reduced the probability of long intervals. For a stronger noise [$D=10^{-1.30}$, Fig. 1(d)], the single neuron fires more coherently with more narrowly distributed T, but it still has some long intervals. In contrast, in the array, the distribution becomes very narrow and long intervals have been eliminated due to the coupling. The interplay between the noise and the coupling generates oscillations in the neurons very similar to a noisy periodic one. We measure the coherence by $R_{CR}=\langle T\rangle/\sigma_T$, where σ_T is the standard deviation of $P(T)$. An array-enhanced CR [21] can be seen clearly by a much larger maximal R_{CR} in the array with a smaller optimal noise intensity (Fig. 2). The behavior is similar for N as large as thousands.

The two systems also have quite different responses to the same subthreshold signal with a period T_e close to the peak of $P(T)$ (Fig. 1, dashed lines). For weak noise, an uncoupled neuron may fail to fire a spike at some periods of the signal, and a few peaks at nT_e show up in $P(T)$ [Fig. 1(b)], as is typical of usual SR systems at weak noise levels. The phases are not locked due to this occasional skipping of spikes [Fig. 1(c)]. In contrast, in the array, $P(T)$ becomes sharply peaked around the signal period T_e [Fig. 1(b)] and the phase is locked to the signal [Fig. 1(c)]. For a stronger noise, skipping of spikes still occurs for $N=1$, and $P(T)$ displays a shoulder at $2T_e$ [Fig. 1(e)] and the phase is not locked [Fig. 1(f)], while in the array, the originally sharp distribution is moved to a peak around T_e [Fig. 1(e)] and phase slips occur very rarely [Fig. 1(f)].

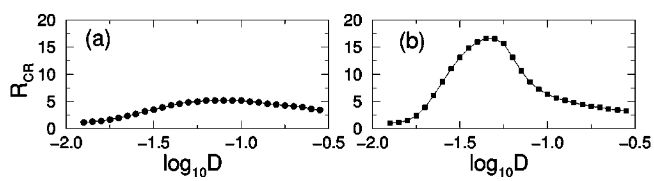

FIG. 2. Coherence resonance (CR) in the single neuron, with optimal noise intensity $D=10^{-1.1}$ (a), and array-enhanced CR in the array ($N=30$), with optimal noise intensity $D=10^{-1.3}$ (b).

III. SR AND ARRAY-ENHANCED SR

Now we study the response properties with respect to the noise intensity D for fixed signal frequencies. The mean frequency difference $\Delta\omega=\omega-\Omega$ is computed for $N=1$ and $N=30$.

We measure the response coherence by R_{SR} [15],

$$R_{SR}=\frac{T_e}{\sigma_T}\int_{(1-\alpha)T_e}^{(1+\alpha)T_e}P(T)dT. \tag{2}$$

This quantity takes into account both the fraction of spikes with an interval roughly equal to the forcing period $T_e=2\pi/\Omega$ and the jitter between spikes [15].

In both systems we depict the results of these measures for Ω equal to or smaller than the NIMF $\omega_0(D)$ when R_{CR} (Fig. 2) is maximal ($\omega_0=1.6$ for $N=1$ and $\omega_0=1.75$ for $N=30$). For $N=1$, the mean frequency difference $\Delta\omega$ changes monotonously with D, crossing zero at the noise intensity D_Ω (dotted line) which generates a matching of the NIMF to the signal frequency Ω, i.e., $\omega_0(D_\Omega)=\Omega$. Thus the spiking frequency ω is not locked by the signal [Fig. 3(a)], although the coherence factor R_{SR} exhibits a maximum and the optimal noise intensity D_{opt} of R_{SR} depends on Ω and is close to D_Ω [Fig. 3(b)], as observed in Ref. [14]. An effective SPL similar to Refs. [8,11] can be observed for A rather close to the threshold in the presence of weak noise. In the array, there exists a locking region around D_Ω, where the spiking frequency is independent of D and is locked to the signal frequency Ω [Fig. 3(c)]. R_{SR} increases, and importantly, the maximal value in the array is much larger than that

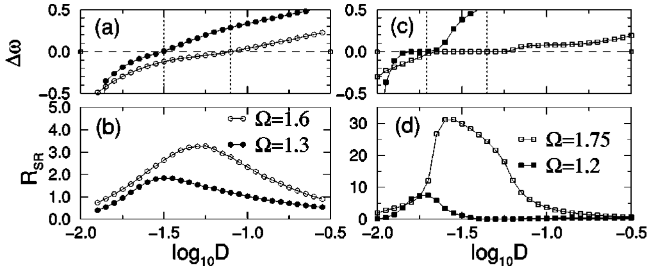

FIG. 3. Mean frequency difference $\Delta\omega$ (a),(c) and response coherence R_{SR} (b),(d) versus noise intensity D for $A=0.03$. Left panel (a),(b): $N=1$; right panel (c),(d): $N=30$. The vertical dotted lines in (a) and (c) denote the noise intensities D_{Ω} generating the NIMF $\omega_0(D_{\Omega})=\Omega$.

in uncoupled neurons. Thus we demonstrate an array-enhanced SR [17] similar to coupled bistable systems.

IV. CONVENTIONAL RESONANCE AND ARRAY-ENHANCED PL

For a fixed noise intensity D, we now consider a range of the driving frequency Ω close to $\omega_0(D)$. In Fig. 4, $\Delta\omega$ and R_{SR} are shown for two noise levels, smaller and equal to the optimal noise intensity of R_{CR} in Fig. 2. The corresponding NIMF $\omega_0(D)$ is shown by the vertical dotted lines [Figs. 4(a),4(c)]. For $N=1$, $\Delta\omega$ crosses zero at $\omega_0(D)$, but it does not show any plateaus of locking [Fig. 4(a)], although R_{SR} exhibits a weak resonance with respect to Ω [Fig. 4(b)]. For $N=30$ the behavior is quite different. At a weak noise, the spike train is locked to the signal in a large range of $\Omega > \omega_0(D)$. R_{SR} increases with Ω, reaches its maximal value when $T_e=2\pi/\Omega$ is very close to the peak value of $P(T)$ at $A=0$ [Fig. 1(a)], and decreases quickly at larger Ω when the system is not quick enough to generate 1:1 response when $T_e<T_r$, the refractory time of the spikes. At $D=10^{-1.3}$ which optimizes R_{CR} (Fig. 2), the locking region becomes quite symmetric around NIMF $\omega_0(D)$, and R_{SR} attains the maximum very close to $\omega_0(D)$. Compared to $N=1$, R_{SR} is much larger for $N=30$. We thus demonstrate an array-enhanced PL in the sense of a strongly enhanced response to a weak signal by frequency and phase locking.

Now we study systematically the locking behavior in the space (Ω, A). In a noise-free excitable system, a sustained

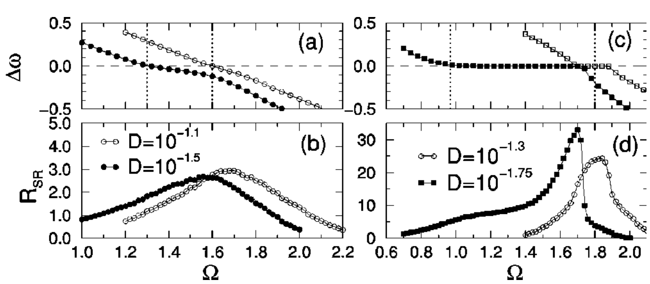

FIG. 4. Mean frequency difference $\Delta\omega$ (a),(c) and response coherence R_{SR} (b),(d) versus signal frequency Ω for $A=0.03$. Left panel (a),(b): $N=1$; right panel (c),(d): $N=30$. The dotted lines in (a) and (c) denote the NIMF $\omega_0(D)$.

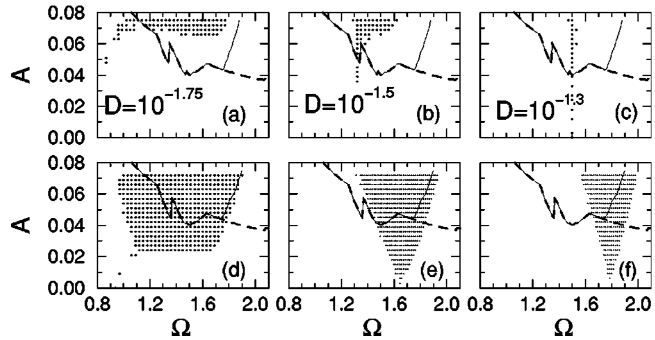

FIG. 5. Comparison of the locking behavior of $N=1$ (upper panel) and $N=30$ (lower panel) neurons at various noise intensities $D=10^{-1.75}$ (a),(d), $D=10^{-1.5}$ (b),(e), and $D=10^{-1.3}$ (c),(f). Filled dots, effective locking region ($|\Delta\omega|<0.002$) of the noisy systems. Dashed line, the threshold beyond which the noise-free systems generate sustained spike trains. Above the solid lines is the 1:1 superthreshold locking region of the noise-free systems.

and synchronized response only occurs when the signal exceeds a threshold. We find that uncoupled neurons and an array of coupled neurons display almost the same Ω-dependent firing threshold [Fig. 5, dashed lines] and the same 1:1 superthreshold response region [Fig. 5, above the solid lines]. A small noise $D=10^{-1.75}$ can induce an occasional skipping of spikes in an uncoupled neuron, thus the 1:1 superthreshold response is no longer perfect. An effective locking region ($|\Delta\omega|\leq 0.002$) is found only at a quite large superthreshold amplitude A [Fig. 5(a)], including a small subthreshold region for small Ω. At $D=10^{-1.5}$, such an effective locking region shrinks considerably and it only appears in the superthreshold region [Fig. 5(b)], and it disappears effectively at an even stronger noise level $D=10^{-1.3}$ [Fig. 5(c)] even though the noise-induced spontaneous spike trains are more coherent here.

An coupled array, in contrast, displays a much more prominent locking behavior. At $D=10^{-1.75}$, the superthreshold locking region of the noise-free system remains intact, while a large subthreshold locking region at $\Omega>\omega_0(D)$ emerges. At $D=10^{-1.5}$, *locking can be achieved with almost vanishing* A when Ω and $\omega_0(D)$ match [Fig. 5(e)]. At $D=10^{-1.3}$, the locking region shrinks a bit [Fig. 5(f)], and it shrinks further for even larger D. This is similar to shrinking Arnold tongue of self-sustained oscillators with increasing noise [24].

Higher order $m:n$ locking regimes, have also been observed (Fig. 6). It is seen again that a $m:n$ locking can be achieved with almost vanishing A when $m\Omega \approx n\omega_0(D)$. The locking regions are no longer confined by the borderlines of the superthreshold locking regions of the noise-free system; in contrast, they become centered around $(n/m)\omega_0(D)$ which moves with D. We emphasize that an $m:1$ $(m>1)$ superthreshold locking region does not exist in the noise-free system, while in the noisy array, a 2:1 region is observable.

The results in the above sections have shown that, the interplay between noise and coupling has generated oscillations in excitable media very similar to self-sustained oscillators. The system achieves resonant response really due to a matching between the noise-induced time scales and Ω, as

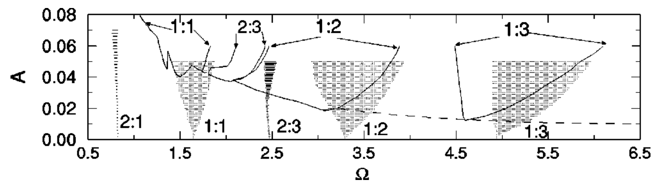

FIG. 6. $m:n$ Arnold tongues for an array ($N=30$) with $D=10^{-1.5}$. The dashed line shows the spiking threshold and the solid lines are borderlines of the $m:n$ superthreshold locking region at $D=0$.

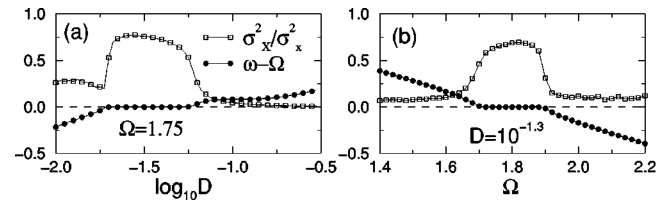

FIG. 7. Collective response in a larger array with $N=500$ versus noise intensity D (a) and signal frequency Ω (b). Signal amplitude $A=0.03$.

conventional resonance and PL in self-sustained periodic oscillators. In this way, the coupling has enhanced significantly the response sensitivity of the neurons to very weak subthreshold signals compared to uncoupled ones.

V. RESONANCE OF COLLECTIVE RESPONSE

Next we study the collective response of an array, which is closely related to spatial synchronization (see Fig. 7). We consider a larger array with $N=500$ neurons and focus on the mean field $X(t)=1/N\Sigma_{i=1}^{N}x_i(t)$. We compute the variance of $X(t)$, normalized by that of $x_i(t)$, i.e., σ_X^2/σ_x^2, as an indicator of the collective coherence. At $A=0$, this larger array shows a very similar CR behavior as $N=30$ in Fig. 2, and σ_X^2/σ_x^2 exhibits a small maximal value (~ 0.1) at the optimal R_{CR}. With a weak signal, we observe locking of the spike trains of the neurons to the signal as functions of both D and Ω (Fig. 6), as in the smaller array $N=30$. When D or Ω moves into the locking region, the mean response $X(t)$ consists of a spike train with the phase locked to the signal. σ_X^2/σ_x^2 increases quickly and reaches a maximal value of about 0.75. The locking and resonance behavior demonstrated in homogeneous arrays are similar for arrays with the randomly distributed parameter a_i in the excitable regime for different neurons.

VI. SUMMARY

In summary, we have shown that the interplay between coupling and noise can have a significant role in enhancing the resonant response of excitable systems, as manifested in the locking of the frequency and the phase with respect to both D and Ω. Resonances and locking occur really due to a matching between the noise-controlled time scale and that of the signal. Higher order $m:n$ locking has been observed in noise-induced oscillations. Various array-enhanced resonances may be important in neural systems, since coupling and noise together can establish a much higher sensitivity to both the frequency and the amplitude of signals by a synchronized collective response.

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