Noise-Induced Coherence in Neural Networks

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We investigate numerically the dynamics of large networks of N globally pulse-coupled integrate and fire neutrons in a noise-induced synchronized state. The power spectrum of an individual element within the network is shown to exhibit in the thermodynamic limit ($N \to \infty$) a broadband peak and an additional delta-function peak that is absent from the power spectrum of an isolated element. The power spectrum of the mean output signal exhibits only the delta-function peak. These results are explained analytically in an exactly soluble oscillator model with global phase coupling. [S0031-9007(96)01163-5]

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The response of dynamical system to noise has received considerable attention recently. Most of the work has focused on cases where the noise was found to increase the coherence of the system. One such case is stochastic resonance [1], where a particle in a bistable potential is subject to noise, in conjunction with a weak periodic force. The inclusion of noise facilitates the switching of the particle between the two wells and leads to an increase in the signal-to-noise ratio of the output signal. The signal-to-noise ratio is further increased in the case of a chain of oscillators with a bistable potential [2]. It has been shown that stochastic resonance is not limited to systems with a bistable potential but can occur also in a single excitable element [3] and in spatially extended excitable systems [4]. Furthermore, studies on the effect of noise in globally coupled maps [5], in mathematical models that display stable and unstable fixed points [6,7], and in globally coupled oscillators [8] showed that noise can induce a coherent response even in the absence of an external periodic force.

Excitable elements underlie many biological functions and are often subject to complex external stimuli which can be aperiodic in time and/or exhibit random variations in amplitude. Neurons in the brain are excitable units that are connected to a large number of other neutrons (typically 1000–10 000 [9]). They can be stimulated by signals from the external world or other parts of the brain. These signals are subject to synaptic noise. In a number of situations, including seizures [10] and signal processing in the visual cortex [11], large collections of neurons fire synchronously and generate a coherent output signal.

In this Letter, we investigate the dynamics of large networks of N globally coupled excitable elements that exhibit a globally synchronized state above a critical noise threshold [12]. We focus on understanding how the dynamical behavior of an individual element within the network differs from that of an isolated element (i.e., not coupled to any other elements), as well as on the mean output signal of all the elements. The main result of interest is drawn schematically in Fig. 1. The power spectrum of the individual element within the network exhibits both a broadband peak and, in the thermodynamic limit, a delta-function peak that is absent from the power spectrum of an isolated element. The power spectrum of the mean output signal, in contrast, exhibits only a delta-function peak in that limit. We show that these results can be qualitatively understood analytically in a noisy oscillator model with global phase coupling. It is important to emphasize that the coherence in our neural network is induced *solely* by noise in conjunction with the global coupling, and not by a periodic external driving force as in standard stochastic resonance. It also does not depend, as in earlier work in neural networks, on a constant dc drive [13], the oscillatory nature of the elements [14], special initial conditions [15], or an additional cellular mechanism [16].

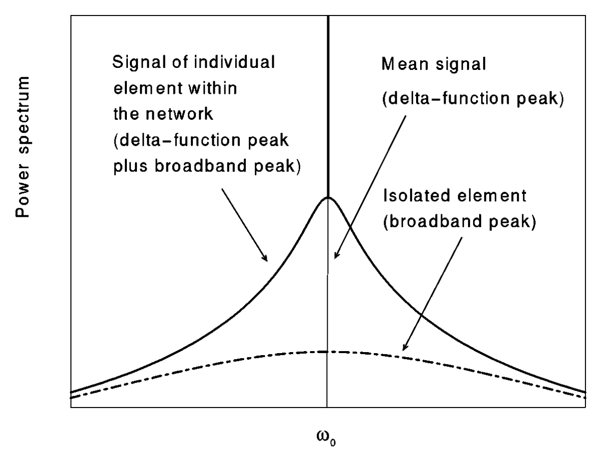

FIG. 1. Schematic drawing of the power spectra of the mean output signal of an infinite noise-driven network (a delta function at ω_0, the intrinsic frequency of the elements), the signal of an individual element within this network (a delta function at ω_0 plus a broadband peak at ω_0) and of the signal of an isolated element (a broadband peak at ω_0).

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The model we study numerically is the globally pulse-coupled integrate-and-fire model (IF) [17] modified to include a relative refractory period:

$$\tau_1 \frac{dh_i}{dt} = -h_i + \frac{R}{N} I_i^{\text{syn}}(t) + R\eta_i(t), \tag{1}$$

where τ_1 is the membrane time constant and where I_i^{syn} describes the synaptic input current that decays with a time constant τ_2:

$$I_i^{\text{syn}} = \int_0^\infty ds' \frac{1}{\tau_2} e^{-s'/\tau_2} \sum_{j=1}^{N} K_{ij} \sum_{f=1}^{F} \delta(t - t_j^f - s'). \tag{2}$$

Here, t_j^f denotes the firing time of the jth neuron, K_{ij} the coupling constant, and R the resistance. If the membrane potential h_i reaches a threshold value $\theta(t)$, the element fires a delta-function pulse after which h_i is immediately reset to zero. The threshold value for every element is a function of the time chosen as

$$\theta(t) = \begin{cases} \infty & t - t_f \leq T_{\text{ref}}, \quad (3) \\ \tau_3/(t - t_f - T_{\text{ref}}) + \theta_0 & t - t_f > T_{\text{ref}}. \quad (4) \end{cases}$$

This models an *absolute* refractory period T_{ref} during which an element cannot fire followed by a *relative* refractory period. The relevant time scale during the relative refractory period is τ_3/θ_0 and is chosen here to be of the same order as T_{ref}. Finally, the noise term η_i is uncorrelated and taken to be Gaussian with mean $\langle \eta_i(t) \rangle = 0$ and $\langle \eta_i(t)\eta_j(t') \rangle = 2D\delta(t - t')\delta_{ij}$.

We have integrated Eqs. (1) and (2) numerically using a second order stochastic Runge-Kutta method. We have calculated the power spectra of (i) an isolated element, $P_{\text{iso}}(\omega)$, (ii) an individual element within the network $P_i(\omega)$, and (iii) the mean $\overline{h} = \sum_i \frac{1}{N} h_i$ of all the elements, $P_{\text{mean}}(\omega)$. The resulting signal of an individual element consists of a series of delta-function pulses at the firing times $0 \leq t_{i,j}^f \leq T$: $h_i(t) = \sum_j \delta(t - t_{i,j}^f)$. The Fourier components of h_i are then given by $h_i(\omega) = \sum_j \exp[-i\omega t_{i,k}^f]$ from which we can compute the power spectrum defined as $P_i(\omega) = T^{-1}\langle |h_i(\omega)h_i^*(\omega)| \rangle$. $P_i(\omega)$ is averaged over different numerical runs and the normalization factor is introduced to ensure that it is independent of T in the limit of large T. The power spectra $P_{\text{iso}}(\omega)$ and $P_{\text{mean}}(\omega)$ are calculated in the same way.

Simulations reveal that noise can induce a dramatic increase in the coherence of the global output signal. The increase is achieved when the N elements are completely or nearly completely synchronized which leads to a coherent firing state. The noise-induced state is sandwiched between two incoherent states at small and large noise levels. This is in agreement with recent work on a model of stochastic rotator neurons [12]. To illustrate the transitions to the incoherent states we have plotted in Fig. 2 the height H of the peak in P_{mean} normalized to the maximum height, H_{max}, as a function of the noise (solid circles). The first transition, for small noise levels, corresponds to the onset of synchronization and occurs on very short time scales, typically less than 1–2 refractory periods. The second transition, for large noise levels, corresponds to the destruction of synchronization due to noise and occurs because some elements are far from their rest state and cannot be entrained on the time scales τ_1 and τ_2 of the coupling and membrane potential. In between the two transitions H has a clear maximum for a nonzero noise level.

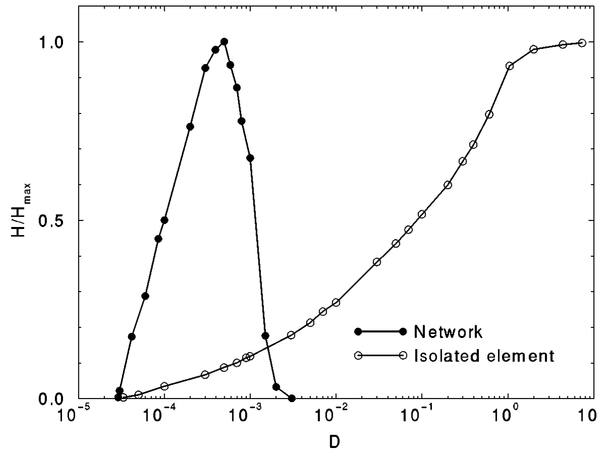

FIG. 2. The normalized height of the peak of the power spectrum as a function of the noise level D for the mean output signal of a network of IF neurons (solid circles) and for an isolated element (open circles). The parameter values are $\tau_1 = 1$, $\tau_2 = 0.1$, $\tau_3 = 0.004$, $T_{\text{ref}} = 0.3$, $\theta_0 = 0.01$, $F = 5$ (for both the isolated element and the network) and $K_{ij} = 1$, $R = 1$, $N = 100$ (for the network). We have checked that different parameter values give similar results.

It is interesting to note that a single isolated IF element exhibits also a transition from incoherent behavior to a more periodic behavior as the noise level is increased. In Fig. 2 we show H corresponding to P_{iso}, again normalized by H_{max}, as a function of D (open circles). For weak noise, the rate of escape over the threshold is very small and the resulting time series for h can be effectively described as shot noise: the pulses are independent and have a Poisson distribution [18]. For larger noise levels escape events are more frequent and the mean time between two firing events approaches T_{ref} which leads to a coherence and an increase in H. However, since T_{ref} is fixed the coherence for an isolated element is, in contrast to networks, not destroyed by large noise.

In Fig. 3 we plot for a fixed noise level the power spectra P_{mean}, P_i, and P_{iso}. The noise level is chosen such that the network is in the noise-induced coherent state. Consequently, P_{mean} displays a sharp peak at a frequency that is the inverse of the refractory period. This refractory period and hence the frequency of the peak are functions of the noise level. It can be clearly seen in the figure that the peak of the global output signal is much higher and sharper than the peak for an *isolated* element at the same noise level. We have found that the height

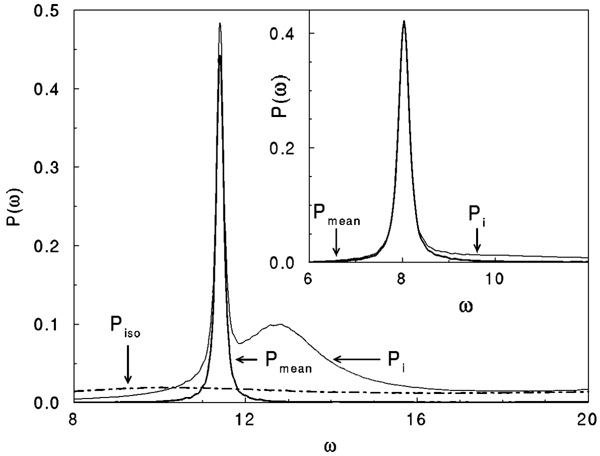

FIG. 3. Comparison of the power spectra of the signal of the mean (P_{mean}), of a individual element in the network (P_i) and of an isolate element (P_{iso}). The parameter values are as in Fig. 2 with $D = 10^{-3}$ and $D = 10^{-4}$ (inset).

of the sharp peak scales as N while the width scales as $1/N$. This indicates that in the thermodynamic limit this peak becomes a delta function. The power spectrum for an individual element within the network displays a nearly identical sharp peak at the same frequency but has also a broadband peak at a different frequency than the sharp peak. In contrast to the latter, the broadband peak for the individual element within the network remains unchanged in the thermodynamic limit. Moreover, this peak is much higher than that for an isolated element which is still in a shot noise regime for this noise level as shown in Fig. 2.

In the entire noise induced coherent region P_{mean} displays a sharp peak that will approach a delta function for infinite N. The broadband peak of P_i, however, depends on the noise level. It is maximal near the high noise level transition and minimal near the low noise level transition (see Fig. 2). This can be seen in the inset of Fig. 3 where we have shown P_{mean} and P_i for a smaller noise level.

Our findings can be qualitatively understood as follows: the noise induces the elements to exceed the threshold value and to fire. For sufficiently strong coupling, this results in a coherent synchronous state in the network which produces a sharp peak in the power spectrum. As we increase N, the average noise decreases as $1/N$ which leads to a delta-function peak in the thermodynamic limit. An individual element within the network is driven by the mean which results in a sharp peak that becomes a delta-function peak for infinite networks. Each element, however, experiences its own nonzero noise that produces a broadband peak. The broadband peak is independent of N and decreases for decreasing noise levels.

An analytical understanding of these spectra can be obtained in a model of globally coupled oscillators, $q_i = e^{i\phi_i}$, of constant amplitude but varying phase whose dynamics is defined by

$$\dot{\phi}_i = \omega_0 + J(\overline{\phi} + \phi_i) + \eta_i \,, \tag{5}$$

where ω_0 is the intrinsic frequency of the oscillator, J is the coupling strength, $\overline{\phi}$ is the mean phase, $\overline{\phi} = \frac{1}{N}\sum\phi_i$, and $\langle\eta_i(t)\eta_j(t')\rangle = 2D\delta(t - t')\delta_{ij}$. There are two motivations for studying this model. First, the fact that the elements are excitable does not seem essential once they have escaped and are entrained on the global limit cycle. Second, the amplification of the output signal with increasing N is due to phase coherence of the oscillators, which is captured by the coupling term in Eq. (5). We are interested in calculating the average power spectrum of the order parameter $q_N = \frac{1}{N}\sum q_i$:

$$P_{\text{mean}}(\omega) = \int_{-\infty}^{\infty}\langle q_N(t)q_N^*(t + \tau)\rangle e^{-i\omega\tau}\,d\tau \tag{6}$$

with

$$\langle q_N(t)q_N^*(t + \tau)\rangle = \frac{1}{N^2}\sum_{j,k}\langle e^{i[\phi_j(t) - \phi_k(t+\tau)]}\rangle \,. \tag{7}$$

In addition, we calculate the average power spectrum of an individual element within the network:

$$P_i(\omega) = \int_{-\infty}^{\infty}\langle q_i(t)q_t^*(t + \tau)\rangle e^{-i\omega\tau}\,d\tau \,. \tag{8}$$

Exact expressions for these spectra can be derived by first rewriting (5) in the form

$$\dot{u}_i = -Ju_i + \eta_i + J\int^t \mu\,dt' \,, \tag{9}$$

where we have defined $u_i = \phi_i - \omega_0 t$ and where μ is the average noise: $\mu = \frac{1}{N}\sum\eta_i$ with correlation $\langle\mu_i(t)\mu_j(t')\rangle = 2\,\frac{D}{N}\,\delta(t - t')\delta_{ij}$. Integrating this equation then gives

$$u_i(t) = e^{-Jt}\int_0^t dt_1 e^{Jt_i}\left[\eta_i(t_1) + J\int_0^{t_1}\mu\,d\tau\right]. \tag{10}$$

Finally, using the identity

$$\langle e^{i[u_j(t) - u_k(t+\tau)]}\rangle = e^{-\frac{1}{2}\langle[u_j(t) - u_k(t+\tau)]\rangle} \,, \tag{11}$$

we obtain after lengthy but straightforward algebra that in the limit of large N the power spectrum for the mean is a Lorentzian of the form

$$P_{\text{mean}}(\omega) = e^{-\frac{D}{2J}}\,\frac{\frac{D}{N}}{(\frac{D}{2N})^2 + (\omega_0 - \omega)^2} \,. \tag{12}$$

As in our simulations, the peak height of P_{mean} scales as N, the width scales as $1/N$, and P_{mean} approaches a delta function $2\pi\exp[-D/2J]\delta(\omega - \omega_0)$ as $N \to \infty$.

The power spectrum for an individual element within the network in the limit of large, but finite, N is given by $P_i(\omega) = P_{\text{mean}}(\omega) + I(\omega)$, where

$$I(\omega) = e^{-\frac{D}{2J}}\int_{-\infty}^{\infty}d\tau\,\cos[(\omega_0 - \omega)\tau]e^{-\alpha J|\tau|} \times \{\exp[-\alpha(e^{-\alpha J|\tau|} - 1) + N\alpha e^{-J|\tau|}] - 1\} \tag{13}$$

and $\alpha = D/2JN$. Thus, P_i consists of two distinct parts: P_{mean} and a peak centered around ω_0 that remains broadband and that can be written in the thermodynamic limit as

$$I(\omega) = e^{-\frac{D}{2J}} \int_{-\infty}^{\infty} d\tau \cos[(\omega_0 - \omega)\tau] \times \left(\exp\left[\frac{D}{2J} e^{-J|\tau|}\right] - 1\right). \tag{14}$$

These results show that this simple model can capture the dependence on N of these power spectra in the noise-induced synchronized state: (1) P_{mean} becomes a delta function in the thermodynamic limit and (2) P_i has the same delta-function peak plus a broadband peak in this limit. This model, however, does not reproduce the dependence on noise of these power spectra because it is oscillatory and not excitable as the IF model. First, this oscillator model does not exhibit the two transitions present in our excitable networks as shown in Fig. 2. Instead, both $P_{\text{mean}}(\omega)$ and $P_i(\omega)$ decrease exponentially with D and reduce to a delta function in the limit of vanishing D. Secondly, the broadband peak of an isolated element [obtained by taking the limit $J \to 0$ in Eq. (14)] is higher than the peak of an individual element within the network, while the opposite occurs in the IF model because isolated elements exhibit shot noise. Finally, we note that in the oscillator model the broadband peak is symmetrically centered around the delta function. In our simulations, however, the broadband peak is not symmetric and occurs at a different frequency than the sharp peak. This is simply due to the asymmetry in the function describing the refractory period [Eqs. (3) and (4)].

In summary, we have investigated the noise-induced coherent state in a globally coupled neutral network. The power spectrum of the global output signal exhibits a sharp peak with a height that scales as N and that becomes a delta function in the thermodynamic limit. The power spectrum of an individual element within this network displays the same sharp peak and an additional broadband peak. Identical qualitative power spectra are reproduced by a simple oscillator model with global phase coupling, demonstrating that the excitable nature of the elements is not crucial. Thus, these spectra should be present in any excitable and oscillatory stochastic system with a coherent state. We have checked that a globally coupled FitzHugh-Nagumo model [19] produces similar results. The observed gain in coherence and synchronization in the network is achieved nearly instantaneously. This suggests the interesting possibility that neurons use noise to produce coherent signals. The global output signal in that case should be markedly different from the output signal of an individual element. This behavior could potentially be investigated experimentally. Future work should also focus on the degree of excitability of the network as well as the degree of connectivity.

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