Coherence and Incoherence in a Globally Coupled Ensemble of Pulse-Emitting Units

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(Received 29 March 1993)

A general theory of coherent behavior ("locking") in a globally coupled ensemble of pulse-emitting units is presented. Each unit is modeled as a dynamic threshold device with arbitrary excitability function and noise. The interaction is described by a general linear-response kernel that includes a transmission delay. In the bulk limit, the dynamics is solved exactly. Two types of solutions are studied, viz., coherent states with synchronous activity of all units and incoherent stationary states, and their stability is analyzed in the low-noise limit.

PACS numbers: 05.20.-y

Large ensembles of simple dynamic units can spontaneously switch into a state of collective synchronized activity. This "locking" effect [1] is known in fields as different as statistical physics [2–9], chemistry [10], and biology [11]. More recently the synchronized blinking of fireflies [12,13] and the coherent activity of neurons in the brain [14,15] have attracted an increased amount of theoretical interest [16–19]. Here, we present and analyze a general model of these phenomena with several new aspects. First, in contrast to most other models of ensemble locking, a single unit of the network is not described by a phase variable or nonlinear oscillator, but rather by a stochastic threshold element with a recovery cycle. Such a pulse-emitting element is similar to, but different from, the integrate-and-fire units which have recently been studied in the context of collective synchronization [8,9,13]. Second, the interaction between units is given by a general linear-response kernel $\epsilon(s)$ which includes transmission delays and can be adapted to describe various model systems. Third, a new stability criterion for locked oscillations is given which is different from the one discussed by Mirollo and Strogatz [13]. Finally, the stability analysis yields a regime of bistability in which fast and slow oscillations coexist. This result is illustrated by simulations.

We start by considering a network of N linearly coupled threshold elements. Each unit $1 \leq i \leq N$ is described by an internal variable $h_i(t)$. If, at time t_i^f, the field h_i reaches the threshold θ, a short signaling pulse is transmitted to all other elements of the network. At the same time a predominantly negative contribution $\eta(s)$ is added to h_i that resets the internal variable

$$h_i(t) = h_i^{\text{ext}}(t) + \eta(t - t_i^f), \tag{1}$$

where $h_i^{\text{ext}}(t)$ describes the external field due to the signals from other units $j \neq i$.

The *excitability* function $\eta(s)$ describes the (usually reduced) excitability immediately after signal emission at $s = 0$. In other words, it represents a refractory behavior. Typically, it is given by a dead time Δ^d with $\eta(s) = -\infty$ for $0 \leq s \leq \Delta^d$, followed by a period of reduced excitability, described by, e.g., $\eta(s) = -|\eta_0|/(s - \Delta^d)$. On the other hand, it may also include one or more periods of *increased* excitability, e.g., $\eta(s) = -|\eta_0| \exp(-s/s_0) \cos s$, favoring bursts of pulses [20]. In case of a constant external field, $h_i^{\text{ext}}(t) \equiv h_0 > 0$, the behavior of a single unit can be described as a cyclic process of signal emission and recovery with a period T_p given by the threshold condition $T_p = \inf[s|h_0 + \eta(s) = \theta]$.

Noise is included by the introduction of the probability P_E of signal emission

$$P_E(h; \delta t) = \delta t/\tau(h), \tag{2}$$

where δt is an infinitesimal time interval. The time constant $\tau(h)$ depends on the variable h and a noise parameter β, i.e., $\tau(h) = \tau_0 \exp[-\beta(h - \theta)]$. In the noiseless case ($\beta \to \infty$), we recover the strict threshold condition: The unit does not emit a signal if $h < \theta$ ($\tau \to \infty$), but it does so immediately if $h > \theta$.

After a transmission delay, a signal emitted by unit i is received by all other elements $j \neq i$ of the ensemble where it evokes some excitatory or inhibitory response. The time dependence of the response is described by the *response function* $\epsilon(s)$ which vanishes for $s \leq \Delta^{\text{tr}}$ where Δ^{tr} is the signal transmission time. The actual shape of $\epsilon(s)$ depends on the specific model of a physical system under consideration. The simplest case is a delayed δ pulse $\epsilon(s) = \delta(s - \Delta^{\text{tr}})$. In their model of firefly activity, Mirollo and Strogatz [13] consider the Heaviside function $\epsilon(s) = \Theta(s)$. If a sinusoidal function is chosen, e.g., $\epsilon(s) = \sin(2\pi s/T_p)$, the model becomes similar to but is not identical with the Kuramoto model [2]. In the context of neural nets, a delayed α function [21] $\epsilon(s) = [(s - \Delta^{\text{tr}})/\tau_s^2] \exp[-(s - \Delta^{\text{tr}})/\tau_s]$ for $s > \Delta^{\text{tr}}$ can describe the time course of a neuron's response to a presynaptic signal. For the sake of simplicity we assume throughout the paper that $\epsilon(s)$ is the same function for all units. Using the concept of sublattice (see below) it is straightforward to introduce a finite number of different response functions by assigning a specific characteristic to each neuron.

Apart from the time course $\epsilon(s)$, we also include

0031-9007/93/71(3)/312(4)$06.00

weights J_{ij} which model the amplitude of the response. Here we assume that the J_{ij} depend only on *local* properties of the sender j and the receiver i and not on topological distance. Then all elements with identical local properties $\mathbf{x}$ can be gathered into a common class, the sublattice $L(\mathbf{x})$ [22]. The number of elements in a given sublattice will be denoted by $Np(\mathbf{x})$. Thus, if $i \in L(\mathbf{x})$ and $j \in L(\mathbf{y})$, then J_{ij} can be written as $J_{ij} = N^{-1}J(\mathbf{x},\mathbf{y})$. With these abbreviations, the total external field on a receiving element $i \in L(\mathbf{x})$ is

$$h_i^{\text{ext}}(t) = \sum_{j=1}^{N} J_{ij} \sum_{f=1}^{\infty} \epsilon(t - t_j^f)$$
$$= \sum_{\mathbf{y}} N^{-1} J(\mathbf{x},\mathbf{y}) \sum_{j \in L(\mathbf{y})} \sum_{f=1}^{\infty} \epsilon(t - t_j^f). \quad (3)$$

Connection weights of the form $N^{-1}J(\mathbf{x},\mathbf{y})$ are widely used in the context of neural nets [23,24]. The simplest case, $J(\mathbf{x},\mathbf{y}) \equiv J_0$, describes a uniform coupling of all elements in the ensemble.

Analytic solution.—Equations (1)–(3) describe the dynamics of signal emission and reception in an ensemble of stochastic threshold elements. Using the concept of sublattice magnetization [22], one can obtain the general solution which describes the macroscopic dynamics of the ensemble. Let $A(\mathbf{x},t)\Delta t$ denote the mean number of signals emitted in a time interval Δt by the units in sublattice $L(\mathbf{x})$. In the limit of $N \to \infty$, the activity $A(\mathbf{x})$ is given by

$$A(\mathbf{x},t) = \int_0^\infty p(\mathbf{x},s,t)\tau^{-1}[h(\mathbf{x},s,t)]ds, \quad (4)$$

where $p(\mathbf{x},s,t)$ is the probability to find a unit $i \in L(\mathbf{x})$ which has been quiescent during a time s after the last firing and $\tau^{-1}[h(\mathbf{x},s,t)]\delta t = P_E[h(\mathbf{x},s,t)]$ is the probability of signal emission. It is determined by the field

$$h(\mathbf{x},s,t) = \sum_{\mathbf{y}} J(\mathbf{x},\mathbf{y}) \int_0^\infty \epsilon(s')p(\mathbf{y})A(\mathbf{y},t-s')ds' + \eta^{\text{ref}}(s). \quad (5)$$

The first term on the right is the external field (3) and the second term represents the excitability of a unit that has spent a time s without firing.

The time evolution of units which have been quiescent during a time $s > 0$ is governed by

$$\frac{d}{dt}p(\mathbf{x},s,t) = -\left(\tau^{-1}[h(\mathbf{x},s,t)] + \frac{d}{ds}\right)p(\mathbf{x},s,t). \quad (6)$$

The factor $\tau^{-1}[h(\mathbf{x},s,t)]$ describes the decay due to signal emission and d/ds is a drift term. Integration of (6) combined with (4) allows us to derive a solution to the global dynamics of the system in terms of the activity $A(\mathbf{x},t)$,

$$A(\mathbf{x},t) = \int_0^\infty ds\, A(\mathbf{x},t-s)\tau^{-1}[h(\mathbf{x},s,t)] \times \exp\left(-\int_0^s \tau^{-1}[h(\mathbf{x},s',t-s+s')]ds'\right), \quad (7)$$

with h given by (5).

Note the dependence of A upon the history of the system which is represented by three integrations over time. To discuss the nature of the solutions we consider two special cases, synchronous (coherent) and asynchronous (incoherent) signaling.

Stationary states; incoherent signal emission.—Incoherent signal emission can be defined by the condition $A(\mathbf{x},t) \equiv A(\mathbf{x})$. In this case, the integrals in (7) and (5) can be done exactly. What remains is a normalization condition which states that the acitivity $A(\mathbf{x})$ of a sublattice $L(\mathbf{x})$ is equal to the *mean rate of signal emission* f of a unit with field $h^{\text{ext}}(\mathbf{x})$, i.e.,

$$A(\mathbf{x}) = f[h^{\text{ext}}(\mathbf{x})] = f\left(\sum_{\mathbf{y}} p(\mathbf{y})||\epsilon||J(\mathbf{x},\mathbf{y})A(\mathbf{y})\right) \quad (8)$$

with $||\epsilon|| = \int_0^\infty \epsilon(s)ds$. Expression (8) is a fixed-point equation. Its solutions describe the stationary states of *incoherent* signal emission. Though Eq. (8) is equivalent to a *naive* mean-field solution of the network, it is derived here from a genuinely dynamical approach. Note that neither the response $\epsilon(s)$ nor the excitability $\eta(s)$ enter (8) explicitly. The function $f(h)$ is the *gain function* of a single unit and summarizes the effects of signal emission and recovery in terms of a single output parameter f. For a given set of model parameters, f is given by

$$f(h^{\text{ext}}) = \left[\int_0^\infty ds \exp\left(-\int_0^s \tau^{-1}[\eta(s') + h^{\text{ext}}]ds'\right)\right]^{-1}. \quad (9)$$

That is, the rate f is the inverse of the mean interval between two subsequent signals. In the noiseless case, one finds $f(h^{\text{ext}}) = T_p^{-1}$ where $T_p = \inf[s|h^{\text{ext}} + \eta(s) = \theta]$ is the period of signal emission of a single unit driven by the field h^{ext}.

We now turn to a stability analysis for the incoherent state. Since we have delays we must consider dynamic fluctuations. We restrict ourselves to the noiseless case and $J(\mathbf{x},\mathbf{y}) = J_0$. Linearization of (7) in the neighborhood of the fixed point $\overline{A}$ yields the continuity equation

$$A(t) - A(t-T_p) = -\frac{d}{dt}[A(t-T_p)v(t)], \quad (10)$$

where the "velocity" v is given by the perturbation $\Delta h(t)$ and the excitability, viz., $v(t) = \Delta h(t)[(d/ds)\eta|_{T_p}]^{-1}$. As before, T_p is the period of signal emission in a stationary state. A standard ansatz $A(t) = \overline{A} + A_1 \exp(i\omega t)$ yields the bifurcation points

$$2|\sin(\omega T_p/2)| = \frac{J_0|\tilde{\epsilon}(\omega)|}{\frac{d}{ds}\eta|_{T_p}}\overline{A}\omega, \qquad (11)$$

with the phase condition

$$\omega T_p/2 = \alpha \quad \text{for} \quad 2k\pi \leq \omega T_p/2 \leq (2k+1)\pi, \qquad (12)$$

and $\omega T_p/2 = \alpha - \pi$ otherwise. Here $|\tilde{\epsilon}(\omega)|\exp(-i\alpha) = \int_0^\infty \epsilon(s)\exp(-i\omega s)ds$ denotes the Fourier transform of the response function. In a weakly coupled system the right-hand side of (11) is small. Thus, dynamic instabilities may occur at a frequency $\omega_n = n(2\pi/T_p)(1+\kappa_n)$ with $\kappa_n \ll 1$ and n a positive integer.

For a given shape of the response function, i.e., fixed $|\tilde{\epsilon}(\omega)|$, the phase equation (12) can be used to derive conditions on the transmission delay Δ^{tr} that guarantee the dynamic stability of an incoherent state. It turns out that for all delays Δ^{tr} the incoherent state is unstable with respect to at least one of the oscillatory modes ω_n; see Fig. 1. Since, however, in realistic systems higher harmonics are suppressed by noise, only the modes with low frequencies need to be considered. By increasing the noise one destabilizes even these and the incoherent state becomes stable.

Locked oscillations; coherent signal emission.—The above stability analysis does not predict the form of oscillatory solutions beyond the linear regime. It is, however, possible to start at the other end, guess a coherent solution, verify its stability, and find that it is a completely different state. As above, we restrict ourselves to the noiseless case ($\beta \to \infty$) and a uniform network $J(\mathbf{x},\mathbf{y}) = J_0$. Coherent activity can be defined by the condition that all units emit signals at the same time. We assume that synchronous signaling is repeated with a period T_{osc}, i.e., the solution is of the form $A(t) = \sum_{n=0}^{\infty}\delta(t + nT_{\mathrm{osc}})$ for $t \leq 0$. T_{osc} is then obtained self-consistently and determined by the threshold condition

$$T_{\mathrm{osc}} = \inf\left[s \,\middle|\, \left(J_0\sum_{n=1}^{\infty}\epsilon(ns)\right) + \eta(s) = \theta\right]. \qquad (13)$$

If $\epsilon(s)$ is a fast decreasing function so that $|\sum_{n=2}^{\infty}\epsilon(nT_{\mathrm{osc}})| \ll |\epsilon(T_{\mathrm{osc}})|$, then (13) allows a simple graphical interpretation. The first crossing point of $\epsilon(s)$ with $-\eta(s)$ (shifted by θ) yields the period of the coherent oscillations (Fig. 1). Higher harmonics can be found by a similar argument.

To study the stability of coherent oscillations we assume that all units have fired synchronously at times $t = -nT_{\mathrm{osc}}$, with $n = 0, 1, 2, \ldots$, *except* unit j which did not fire at $t = 0$ but has been late by a time Δt. This is a local fluctuation. Stability then requires that the delay be reduced during the next period; i.e., if j emits the next signal at time t_j^f, we should have $t_j^f - T_{\mathrm{osc}} < \Delta t$. From the threshold condition (13) we find to first order in Δt

$$\frac{t_j^f - T_{\mathrm{osc}}}{\Delta t} = \frac{d}{ds}\eta\bigg|_{T_{\mathrm{osc}}}\left(J_0\sum_{n=1}^{\infty}\frac{d}{ds}\epsilon\bigg|_{nT_{\mathrm{osc}}} + \frac{d}{ds}\eta\bigg|_{T_{\mathrm{osc}}}\right)^{-1}, \qquad (14)$$

which should be less than 1. For a typical excitability function we have $(d/ds)\eta(s) \geq 0$ for all $s \geq 0$. In case of a quickly decaying response function, the locking condition is thus simply $\frac{d}{ds}\epsilon|_{T_{\mathrm{osc}}} > 0$, that is, at T_{osc} the response function ϵ should have an *upward* slope. A graphical interpretation of this result is given in Fig. 1.

We note that, in contrast to the argument of Mirollo and Strogatz [13], concavity of the excitability function is not required. The elegant reasoning of these authors is limited to the case of a Heaviside response function, i.e., $\epsilon(s) = \Theta(s)$. In this case $(d/ds)\epsilon(s) = 0$ holds for all $s > 0$ and, to first order, no locking occurs. A *second-order* expansion in Δt then yields the concavity requirement.

Summarizing, we have presented an analytical solution for the macroscopic states in a globally coupled network of stochastic pulse-emitting elements. Both the internal excitability $\eta(s)$ and the response to external signals $\epsilon(s)$ are modeled by arbitrary functions which can be adjusted to fit specific requirements. The shape of these functions, the delay Δ^{tr}, and the initial conditions determine whether the system will end up in an incoherent state of asynchronous activity or rather in a coherent state of periodic, synchronous firing. As an example we consider the response function $\epsilon(s) = [(s - \Delta^{\mathrm{tr}})/8]\exp[-(s - \Delta^{\mathrm{tr}})/2]$ for $s > \Delta^{\mathrm{tr}}$ (and 0 for $s < \Delta^{\mathrm{tr}}$) combined with an excitability $\eta(s) = (4 - s)^{-1}$ for $s > 4$ (and $-\infty$ for

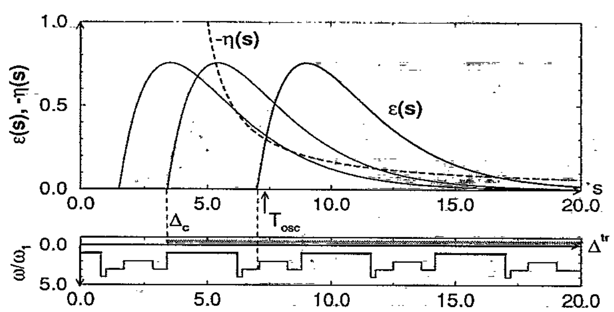

FIG. 1. Top: The negative of the excitability function $-\eta(s)$ (dashed line) and the response function $\epsilon(s)$ (solid line) for various transmission delays (left: $\Delta^{\mathrm{tr}} = 2.0$; middle: $\Delta^{\mathrm{tr}} = 3.4$; right $\Delta^{\mathrm{tr}} = 7.0$). We assume $\Theta = 0$. In this case, the crossing point $\epsilon(s_0) = -\eta(s_0)$ yields the period of coherent oscillatory activity, $T_{\mathrm{osc}} = s_0$. The oscillation is stable only if $(d/ds)\epsilon(s_0) > 0$ as for the right curve (arrow). It is unstable for the left curve and critical for $\Delta^{\mathrm{tr}} = \Delta_c = 3.4$. Bottom: Stability in the noiseless case as a function of Δ^{tr}. Locking is stable for $\Delta^{\mathrm{tr}} > \Delta_c$ (locking regime, grey). Whatever Δ^{tr}, the incoherent state is always unstable. The frequency ω_n of the dominant oscillatory mode is indicated ($\omega_1 = 2\pi/T_p$).

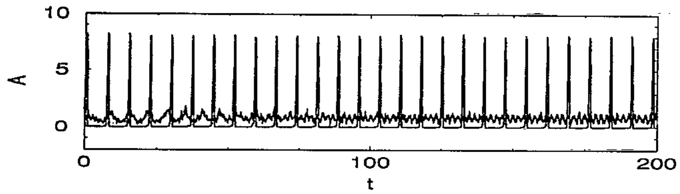

FIG. 2. Simulation of an ensemble of 1000 units (parameters as in Fig. 1 with $\Delta^{tr} = 7.0$; noise $\beta = 20$). Depending on the initial conditions, the system either relaxes into a locked coherent oscillation ($T_{osc} = 7.3$) or into a fast small-amplitude oscillation ($n = 3$) around the incoherent state.

$0 < s < 4$); see Fig. 1. The results of a stability analysis as a function of Δ^{tr} have been plotted in the lower part of Fig. 1. Given a delay of $\Delta^{tr} = 7.0$, locking into a coherent oscillation is possible. The stationary state, however, is unstable with respect to the $n = 3$ oscillatory mode, and we expect a much faster oscillation. This type of *bistability* is shown in two simulation runs with an identical set of parameters but different initial conditions (Fig. 2). If the system is prepared suitably, locking occurs despite the noise ($\beta = 20$) and the system oscillates coherently. On the other hand, the $n = 3$ instability shows up as a fast small-amplitude oscillation around the incoherent stationary state.

The general approach of our theory allows a description of locking phenomena in various ensembles of pulse-emitting units—independent of the type of signaling, be it optical, acoustical, electrical, or biochemical. All parameters of the model are, in principle, susceptible to experimental measurement. The theory can also be adapted to include a distribution of transmission delays and internal parameters. Thus a whole range of phenomena can be described from a unifying point of view.

This work has been supported by the Deutsche Forschungsgemeinschaft (DFG) under Grant No. He 1729/2-1.

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