PHYSICAL REVIEW E, VOLUME 64, 030901(R)

External noise synchronizes forced oscillators

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(Received 15 May 2001; published 13 August 2001)

Periodic pulsatile perturbation of nonlinear oscillators generates phase-locking, quasiperiodic, and chaotic responses. This work shows that the application of external noise to ensembles of such forced systems can synchronize oscillations, even in regimes where neither the noise nor the periodic forcing, when applied alone, would lead to such a phenomenon.

DOI: 10.1103/PhysRevE.64.030901 PACS number(s): 87.19.La, 87.17.Aa

Periodic stimulation can entrain nonlinear systems such as neurons and heart cells into phase locked, quasiperiodic, and chaotic discharge patterns [1]. In systems such as sensory neurons, these patterns are altered by noise [2,3]. Such perturbations can have opposite effects on input-output phase synchronization depending on signal and system characteristics. For instance, noise induced phase skips can reduce phase synchronization between the driving periodic input and an oscillator's response [4], or on the contrary, noise induced stochastic phase locking can regularize the response when the entry signal alone is too weak to entrain an excitable system [5].

In systems where information processing and transmission relies on arrays of units operating in parallel, besides phase synchrony to input, another issue of importance is that of synchronization between the components of the ensemble [6]. The present work addresses this topic. We show that the addition of external noise to a periodic stimulation affecting all units within the ensemble can synchronize the units with one another. Such interunit synchronization takes place even without phase synchrony to the input. Figure 1 illustrates this phenomenon in an ensemble of periodically forced FitzHugh-Nagumo model (FHN) [7] without (upper panels) and with noise (lower panels). The former evokes a chaotic firing with sensitive dependence on initial conditions being responsible for driving the units out of synchrony [8]. This situation is drastically changed when the same external noise is applied to all units. After a transient time, the units discharge synchronously, despite the fact that the firing remains irregular. This stabilizing effect of noise is also confirmed through the computation of the leading Lyapunov exponent of the system, which is positive in the absence of noise, and progressively becomes negative when the noise intensity is increased (not shown).

In the following, we first present an analysis of this phenomenon in an oscillator, namely, the radial isochronic clock (RIC), also referred to as Poincaré oscillator, which is one of the canonical models of oscillating biological systems (see references in [9–11]), and then discuss the generalization of the results.

In polar coordinates, the dynamics of the RIC are governed by

$$\dot{r}=kr(1-r), \tag{1}$$

$$\dot{\alpha}=2\pi, \tag{2}$$

where k is a positive constant. The unit circle (i.e., $r=1$) is a stable limit cycle of Eqs. (1) and (2) that attracts trajectories of all initial points except the origin. Pulses of amplitude A result in a horizontal translation from a point X in the plane to $X'=X+(A,0)$.

We assume that $k\gg 0$, so that, essentially, the dynamics take place on the unit circle. In this way, a pulsatile perturbation produces a phase shift from α to $\beta=f(\alpha)$, where f is the phase transition function:

$$\begin{aligned} f(\alpha)&=\arccos\left[\frac{A+\cos(\alpha)}{\sqrt{A^2+2A\cos(\alpha)+1}}\right] \quad \text{if } \sin\alpha\geq 0\\ &=2\pi-\arccos\left[\frac{A+\cos(\alpha)}{\sqrt{A^2+2A\cos(\alpha)+1}}\right] \quad \text{if } \sin\alpha<0. \end{aligned} \tag{3}$$

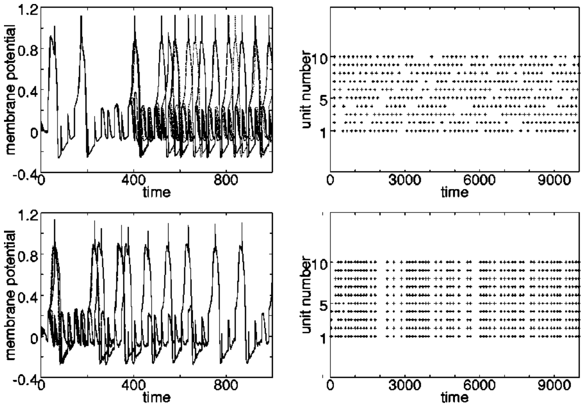

FIG. 1. Left panels: time (in arbitrary units) against superimposed membrane potentials (in arbitrary units) of ten FHN units. Right panels: each line represents the discharge times of one of the ten units (raster plot), without noise (upper panels), and with a white Gaussian noise with amplitude $\sigma=0.01$ (lower panels). Abscissa, time in arbitrary units, ordinates, unit number (dimensionless). Model equations are the same as in Ref. [8] with parameters: $a=0.139$, $b=2.54$, $c=0.008$, stimulation period $\tau=29$, and amplitude $A=0.27$. Numerical simulation was done using the Euler method with a step of 0.01. The initial conditions of the two variables v and w of the ten units were $v=k\times 0.01$ for $k=0,\ldots,9$ and $w=0$.

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Thus, defining $F(\alpha,2\pi\tau)=f(\alpha)+2\pi\tau$ modulo 2π, the response of the RIC to a pacemaker pulse train with period τ is captured by [9]

$$\alpha_{n+1}=F(\alpha_n,2\pi\tau). \tag{4}$$

References to analyses of Eq. (4) and variants are given in Refs. [9,10].

We model the effect of external noise on an ensemble of RICs by adding $\xi(t)$, white Gaussian noise of intensity σ, to Eq. (2). Thus, the phase α^i of the ith unit within an ensemble of RICs satisfies

$$\dot{\alpha}^i=2\pi+\xi(t). \tag{5}$$

We modify Eq. (4) to take the noise into account. More precisely, given a phase α_n at the time of the nth pulse delivery, the system is almost instantaneously shifted to the phase $f(\alpha_n)$. From this point, it moves along the circle according to Eq. (5) for a time τ, when the next pulse is applied. Thus, the phase at the time of the $(n+1)$th stimulus satisfies $\alpha_{n+1}=f(\alpha_n)+2\pi\tau+\zeta_n$, where ζ_n are independent identically distributed centered Gaussian random variables with standard deviation $\sigma\sqrt{\tau}$. We can rewrite this relation for the ith unit within the ensemble as

$$\alpha^i_{n+1}=F(\alpha^i_n,2\pi\tau+\zeta_n). \tag{6}$$

Synchrony within the ensemble is ensured when the differences between α^i_n, for different values of i, tend to zero as $n\rightarrow\infty$.

In some systems, the application of a fluctuating input can induce interunit synchrony [12,13]. In phase models, this situation occurs when the movement along the unit circle is nonuniform [14]. Here, we analyze a situation less favorable for synchrony, because in the RIC, noise alone, without periodic pulses, cannot produce such an effect. Indeed, direct examination of Eq. (5) shows that starting from two RICs with initial phases $\alpha^1(0)$ and $\alpha^2(0)$, the corresponding phase difference $\Delta\alpha(t)=\alpha^1(t)-\alpha^2(t)=\Delta\alpha(0)$ remains constant throughout time so that the discharge times of the units do not synchronize.

It is the combination of noise and periodic stimulation that ensures synchrony. Figure 2 illustrates this point. Taking an ensemble of N RICs with initial phases $\alpha^i_0=2i\pi/N$, $i=1\cdots N$, the figure represents α^i_1 (right panels), α^i_{51} (middle panels), and α^i_{101} (left panels) against α^i_0, for ensembles without (upper row) and with noise (lower row), in a regime where the noise-free periodically forced RIC displays chaos. The lower row shows that, in contrast with noise-free RICs, those receiving external noise fully synchronize with one another, as the phases of the units take on the same value. The following paragraphs are devoted to the analysis of this phenomenon. We examine, successively, the response of a single RIC, and ensembles of such units to both noise and periodic forcing.

For a single unit, the probability to reach a phase β at the time of a pulse delivery provided that it was at a phase α prior to the previous pulsatile perturbation is

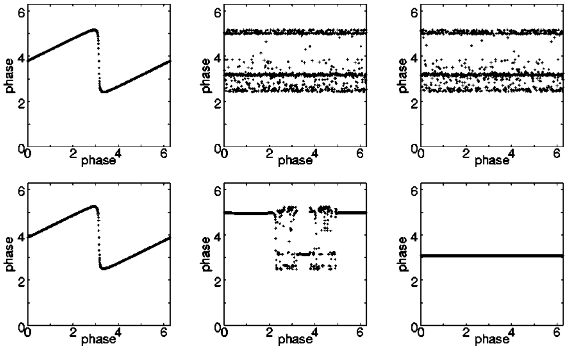

FIG. 2. First, fifty first, and hundred first iterates of the phase transition function (from left to right) without (upper row) and with noise (lower row). Abscissa and ordinate in all panels represent the phase in radians. Model parameters: $\tau=0.602$, $A=1.02$, and $\sigma=0$ and 0.1 (upper and lower rows)

$$K(\beta,\alpha)=\sum_{p=-\infty}^{p=+\infty} g[\beta+2p\pi,\tau|f(\alpha)], \tag{7}$$

where the summation takes into account the possibility of multiple rotations around the unit circle, and g is the transition probability density function associated with Eq. (5):

$$g(u,t|x)=\frac{1}{\sqrt{2\pi t}\sigma}\exp\left[-\frac{1}{2}\frac{(u-x-2\pi t)^2}{\sigma^2 t}\right]. \tag{8}$$

If the phase α_0 prior to the first pulse has a density $h_0(\alpha)$, the phase distribution h_n prior to the $(n+1)$th pulse is determined by iterating the Markov operator P with stochastic kernel K:

$$Ph(\beta)=\int_0^{2\pi}K(\beta,\alpha)h(\alpha)d\alpha. \tag{9}$$

Given that K is strictly positive, the Markov operator P is ergodic [15]. Therefore, even for small noise intensities σ and in regimes where the deterministic RIC may display multistability, the operator P has a unique invariant probability density function h^*, and iterates of all initial densities eventually converge to it [15,16]. This results from the fact that for Gaussian noise, regardless of how small the intensity can be, the support of the density g is unbounded. For other forms of perturbations leading to densities with bounded support, P may not be ergodic (see examples in Ref. [17] and p. 322 of Ref. [15]).

The Markov approach depicts the "one point motion" of the system. To analyze synchronization within the ensemble, we consider the "n point motion," that is the joint dynamics of several RICs to the same input consisting of pacemaker pulse train and noise. We denote by $\omega=\{\ldots,\zeta_{-n},\ldots,\zeta_{-1},\zeta_0,\zeta_1,\ldots,\zeta_n,\ldots\}$ one specific sequence of ζ_i. The question we need to address is whether sequences $\alpha^i_n(\omega)$ and $\alpha^j_n(\omega)$ of the stimuli phases of two units within the ensemble, initiated at different phases, and receiving the same external noise ω and pacemaker stimulation, tend to one another as $n\rightarrow\infty$. To examine this, we evaluate the local stability of a sequence $\alpha_n(\omega)$ through the computation of the Lyapunov exponent:

$$\lambda(\alpha_0,\omega)=\lim_{n\to\infty}\frac{1}{n}\sum_{p=0}^{n}\ln\left|\frac{dF}{d\alpha}(\alpha_p)\right|, \tag{10}$$

where the arguments of λ indicate that *a priori*, this quantity depends on both the initial phase α_0 and the specific noise realization ω. Traditionally, the sign of the leading Lyapunov exponent is an indicator of sensitive dependence on initial conditions (or lack of thereof) in deterministic systems. This work presents a different interpretation for it: we show that a negative Lyapunov exponent is the indicator of synchrony within the ensemble, because in ergodic random dynamical systems, negative Lyapunov exponents imply that trajectories cluster at at finite number of stochastic equilibria [19]. This is explained in the following.

Ergodicity ensures that λ depends on neither α_0 nor ω and can be evaluated as [18]

$$\lambda=\int_0^{2\pi}h^*(\alpha)\ln\left|\frac{dF}{d\alpha}(\alpha)\right|d\alpha=\int_0^{2\pi}h^*(\alpha)\ln\left|\frac{df}{d\alpha}(\alpha)\right|d\alpha. \tag{11}$$

In other words, the Lyapunov exponent for all units within the ensemble, regardless of their initial state, and for almost all external noise sample paths ω, takes on the same value given by Eq. (11). Consequently, $\lambda<0$ means, not only that a specific phase sequence α_n^i of a single unit within the ensemble is locally stable, but also, more generally, that this is the case for all units. In other words, $\lambda<0$ implies that sequences α_n^i are mutually attracted one to another, and, in fact, that they eventually cluster at a finite number m of sequences, denoted by $\gamma_n^1(\omega),\ldots,\gamma_n^m(\omega)$ [19]. Furthermore, when $\lambda<0$, we have $m=1$ for Eq. (6). This is a consequence of the fact that starting from arbitrary initial phases α_0^1 and α_0^2, it is possible to find a sequence ω such that for some $n>0$, $\alpha_n^1(\omega)$ and $\alpha_n^2(\omega)$ become arbitrarily close to one another [20]. Heuristically, this means that each γ^i attracts all neighboring sequences, and the previous condition ensures that, at some point, γ^i comes arbitrarily close to any other sequence, and therefore attracts it, so that eventually sequences merge into a single one.

The consequence of the above arguments for synchronization within the ensemble is that $\lambda<0$ ensures that for almost any external noise sample path ω, there exists a unique sequence $\gamma_n(\omega)$ which attracts the $\alpha_n^i(\omega)$. In other words, when $\lambda<0$, units within the ensemble synchronize one with another, and we need only evaluate λ to determine the regimes of synchrony.

Systematic numerical evaluations of λ revealed the following (see illustrations in Fig. 3): (i) When f (and consequently F) is invertible (so that the noise-free RIC can either phase lock or display quasiperiodic responses), $\lambda<0$, even for small noise. (ii) Similar results were found when f is not invertible, and the noise-free system stabilizes in a periodic response. (iii) When f is not invertible and the noise-free response is chaotic, for small noise $\lambda>0$, but λ becomes negative when noise is increased.

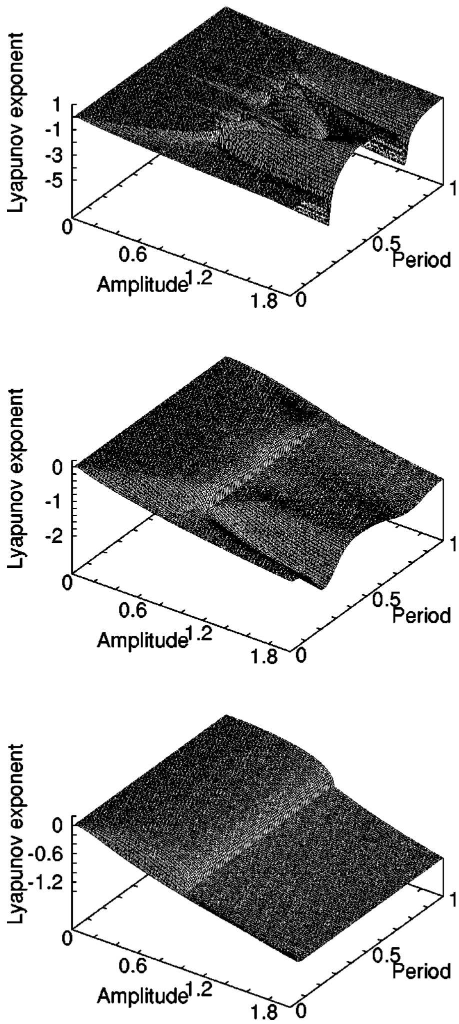

FIG. 3. Lyapunov exponent of the noisy RIC with pacemaker pulsatile forcing, against stimulation period and amplitude for $\sigma=0.05$ (top), 1 (middle), and 5 (bottom). Abscissa, ordinate, and vertical axes are in arbitrary units.

In summary, the main influence of noise is to make the Lyapunov exponent negative. Two separate mechanisms account for this. One holds for invertible circle maps in general, at all noise levels, and the other for the noise induced stabilization of chaotic regimes when f is noninvertible. We describe these successively.

In a given $\omega=\{\zeta_n\}$, even with low σ, one almost surely encounters subsequences of arbitrary length in which $2\pi\tau+\zeta_n$ are close to one. In fact, such subsequences occur recurrently, and at arbitrarily large times. When f is invertible, passage through such a subsequence leads rapidly to a regime of 1:1 alternation independently from initial phases [11]. This phenomenon is responsible for the contraction that wipes out dependence on initial conditions when f is invertible. This phenomenon bears consequences for both phase locking and quasiperiodic regimes. For instance, in a noise-free $1:q$ phase locking (one rotation of the RIC per q input cycles) with $q\geqslant 2$, units within an ensemble can cluster into

q synchronous groups, with groups being $2p\pi/q$-shifted ($p=1,2,\ldots,q-1$) one with respect to another. With the addition of noise, even of low intensity, all q clusters eventually merge into a single one.

One consequence of the above analysis is that the asymptotic (random) dynamics of the periodically forced noisy RIC sharply differ from those of the deterministic case. Namely, the latter can display multistability due to the coexistence of stable fixed points or stable periodic orbits. However, this situation is not possible in the corresponding random dynamical system, where almost all orbits cluster into a single one. In this sense, noise destroys multistability. A similar phenomenon occurs in scalar bistable systems perturbed by additive noise [21].

While the above mechanism holds for arbitrary invertible circle maps f, and is not a special property of the system considered here, the stabilizing effect of large noise when f is noninvertible depends on the particular geometrical properties of this map. More precisely, h^* flattens at large σ because there are no preferential phases in this regime. Consequently, λ tends to the average of $\ln|f'|$ [Eq. (11)], which is negative for models such as the RIC. This itself is due to the fact that f, even for parameter ranges where pacemaker stimulation evokes chaotic responses, presents long stretches with slopes lower than 1.

The above considerations provide the setup for discussing the generality of the results. In our approach, we described the behavior of the forced system through the iterates of phase transition maps. This is well-documented in forced biological oscillators such as neurons and heart cell aggregates, and it also applies to a wide variety of physical systems [1]. Furthermore, besides oscillators, the response of other classes of systems, notably excitable ones, can also be captured by iterates of maps [22]. Thus, our approach is not limited to pacemakers or oscillators, but holds for a wider class of systems. Figure 1, which showed the stabilizing effect of noise on the chaotic response of an excitable FHN to periodic pulse train, confirms this point.

We have argued that when the map approximating the response of the units is an invertible circle map, even small noise can synchronize the ensemble, and that this result is independent from the particular shape of the map. When the map is not invertible, whether synchronization takes place or not depends on whether the contracting regions in the map dominate. Remarkably, this is the case not only in the RIC and its variants (e.g., Ref. [11]), but is actually observed in experimental records of pacemaker cells (e.g., Ref. [10]), and appears also in the maps approximating the response of excitable systems [22].

In conclusion, the present work shows that external noise can synchronize an ensemble of periodically stimulated units such as oscillators or excitable systems, and that this phenomenon is independent from phase synchrony to the input. This constitutes an alternative effect of noise in the sense that (i) it does not concern synchrony with respect to the periodic input, but instead interunit synchronization, (ii) it results from external rather than internal noise applied to the units, representing situations where, for instance, the noise is delivered through an external biomedical device, and (iii) unlike phenomena such as stochastic resonance, is not confined to a specific bounded range of noise intensities.

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