Pulse-Coupled Relaxation Oscillators: From Biological Synchronization to Self-Organized Criticality

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It is shown that globally coupled oscillators with pulse interaction can synchronize under broader conditions than widely believed from a theorem of Mirollo and Strogatz. This behavior is stable against frozen disorder. Beside the relevance to biology, it is argued that synchronization in relaxation oscillator models is related to self-organized criticality in stick-slip-like models.

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Large assemblies of oscillator units can spontaneously evolve to a state of large scale organization. Collective synchronization is the best known phenomenon of this kind, where after some transient regime a coherent oscillatory activity of the set of oscillators emerges. This effect has attracted much interest in biology for the study of large scale rhythms in populations of interacting elements [1]. The southeastern fireflies, where thousands of individuals gathered on trees flash in unison, is the most cited example [2]. Other examples are the rhythmic activity of cells of the heart pacemaker, of cells of the pancreas, and of neural networks [2–4]. Most of the works on synchronization have used models in which the interaction between the oscillators is smooth and continuous in time (see, e.g., [5]). Comparatively, few analytical results are known on models where the interactions are episodic and pulselike [1,3,6,7], although they are relevant to several biological situations as fireflies and neural networks. This Letter deals with the emergence of synchronization in a very simple model of globally coupled integrate and fire (IF) oscillators; see Eq. (1) for the definition and [2]. It is shown that synchronization occurs under broad conditions on the properties of the oscillators, thus generalizing a theorem of Mirollo and Strogatz [1], the usual interpretation of which restricted the synchronization conditions in a too drastic way. Furthermore, I show that the synchronized state is stable against a frozen disorder of the oscillator properties, a subject much studied in models with continuous interaction [5]. This result is different from that of a previous study [7] on a closely related model.

Besides synchronization, another form of collective organized behavior is known to occur in large assemblies of elements with pulse interaction, that is, self-organized criticality (SOC). This concept has been proposed in [8] to describe out of equilibrium systems that are generically critical, i.e., that organize into a scale invariant critical state spontaneously, without tuning of a control parameter. Systems displaying SOC are externally driven with a drive slower than any other characteristic time. These models are made critical by the choice of a threshold dynamics that forbids them to follow adiabatically the exter-

nal drive. They can be modeled as coupled map lattices and can be divided into two subclasses based on the concept of oscillators. In subclass (a) the external drive acts globally and continuously on all the lattice sites of the coupled map, until one of them reaches the threshold, in which case it relaxes to zero: Each site is therefore a *relaxation oscillator*. These are the stick-slip-like models [9]. They are deterministically [9] or not [10,11] driven systems, for which no conserved quantity is known, and can exhibit SOC even when they are dissipative [9]. The systems of subclass (b) are driven at each time step by the increment of a unique site, so that sites are *not* oscillators. These are the sandpilelike models [8,12]. The model studied in this Letter is a simple model of fireflies flashing and is a mean field version of class (a) models. As this mean field approach suggests, we argue in the following that there is a close relationship between SOC and synchronization [10,11,13].

The biological mechanisms controlling the fireflies flashing have been extensively studied (see [2] for a review) by testing the response of an isolated insect to single or periodic flashes of light. It appears that there are several mechanisms for synchronization and entrainment among the different species, so that no general conclusion can be drawn about both the mechanism and the biological function of synchronized flashing. It is therefore interesting in this context to study under which general conditions a synchronization may emerge in relaxation oscillator models. Experiments indicate that the rhythmic spontaneous flashing of the fireflies is, in general, governed by a flash-control pacemaker in the brain, cycling as an oscillator with a given intrinsic rhythm between a basal level of excitation (state variable of the oscillator) and a fully excited flash-triggering level [2]. After each flash the state variable resets quickly to the basal level. Light-flash stimuli on a single firefly have different effects depending on the species. This has motivated the introduction of essentially two models, the phase advance and phase delay models [2]. In the phase advance model, the effect of a pulse of light is to advance the flashing of each insect pushing the state

variable towards the threshold. Flashing delay relative to the intrinsic rhythm is impossible in this case. This accounts for the behavior of at least two species, *Photinus Pyralis* and *Photinus concisus*, which, however, display only transient synchrony, possibly because these species are rover [2]. On other species, as *P. cribellata*, a pulse of light inhibits the oscillator, thus delaying the next flash. This is interpreted in the phase delay model as the resetting of the state variable to the basal level. In this model, advance or delay of flashing is possible. Let us mention that other firefly species have behaviors that cannot be described by any of these two models. The model we study in the following [1,10] is equivalent to the phase advance model.

The mean field model.— It consists of N relaxation oscillators O_i represented when they evolve freely by a state variable $E_i = E(t) \in [0, E_c = 1]$, monotonically increasing in time with period 1. The interaction is so defined that when $E_i \geq 1$ it relaxes to zero and increments all the other oscillators by a pulse α/N:

$$E_i \geq 1 \Rightarrow \begin{cases} E_i & \to & 0, \\ E_{i \neq j} & \to & E_j + \alpha N, \end{cases} \qquad (1)$$

where $\alpha \in [0,1]$ is a dissipation parameter. The model is taken into the slow drive limit by assuming that any avalanche of firings, i.e., any succession of firings triggered by the relaxation of one oscillator, is instantaneous. We assume a supplementary rule that in most circumstances does not change the behavior of the system but simplifies the discussion. This is the so-called absorption rule of [1], which is equivalent to a reaction death time of the oscillators immediately after their relaxation. This is taken into account by assuming that oscillators within the same avalanche are not incremented by the pulses resulting from the following relaxations in the avalanche.

The theorem of Mirollo and Strogatz [1] that applies to this model states that for a convex function $E_i = E(t)$ the system synchronizes completely but for a set of initial conditions of Lebesgue measure null. Although the validity of this theorem cannot be questioned, we will see in the following that for all the physically interesting situations the system synchronizes even for a linear and a range of concave functions $E(t)$.

Let us call a configuration as the set of ordered distinct values $E_1^{(j)} < E_2^{(j)} < \cdots < E_{m_j}^{(j)} = 1$ of the state variables present in the system just before the $(j + 1)$th avalanche. To each $E_i^{(j)}$ corresponds a group of $N_i^{(j)}$ oscillators at this value ($\sum_{i=1}^{m_j} N_i^{(j)} = N$). Let us call a cycle as the time necessary for all the m_j groups to avalanche exactly once. To trace the evolution of the system, it is useful to follow, cycle after cycle, the gaps $s_i^{(j)} = E_{i+1}^{(j)} - E_i^{(j)}$ between the values of successive groups. If one of these gaps $s_i^{(j)}$ becomes smaller than the value $\alpha N_{i+1}^{(j)}/N$ of the pulse of the $(i + 1)$th group, then the ith group gets absorbed by the $(i + 1)$th group. For a

linear $E(t)$, an elementary calculation shows that the gap between a group $i + 1$ and a smaller one i is reduced during one cycle by $\delta s_i = |\alpha(N_i - N_{i+1})/N|$. Therefore large groups unavoidably absorb the smaller ones that follow them and become larger and larger [14]: It is this positive feedback that leads to synchronization. The only way to stop this mechanism and therefore the evolution towards synchronization is to get a configuration where all groups are of equal size. Apart from the random initial conditions, where all the groups are of size 1, it is exceptional for large N to be stuck during the evolution in such a state. It is, in fact, a difficult task to calculate in general the probability for this situation to occur, but, first, extensive numerical calculations show that this is indeed exceptional even for small N; second, it is even a physically ill-defined question, since it depends on the factorization of N; and, third, if one imagines that the oscillators are not exactly identical, the slightest splitting between their pulse intensities forbids any δs_i to vanish. Therefore to see if the system does not get stuck in the initial configuration, the only relevant question is whether it is possible with random initial conditions to get groups larger than one during the first cycle. The probability for pair formation may easily be computed from the Poissonian distribution $P(s)ds = Ne^{-Ns}ds$ ($N \gg 1$) of gaps s between the N random numbers $E_i^{(1)}$ in $[0,1]$. The number of oscillator pairs in the random initial values satisfying the synchronizing conditions $s < \alpha/N$ is then

$$N \int_0^{\alpha/N} P(s)ds = N(1 - e^{-\alpha}), \qquad N \gg 1. \qquad (2)$$

The absorption process of oscillators into groups takes place as long as there is at least one such gap. It follows directly from (2) that this is typically the case when $\alpha \geq 1/N$ [10]. Initial configurations of values where no gap is smaller than α/N are, in principle, possible, but for large systems with an $O(e^{-\alpha N})$ probability of occurrence. In conclusion, the set of linear oscillators completely synchronizes almost always, when α is of order 1 compared to N. The reason why this is not in contradiction with the theorem of Mirollo and Strogatz is that their recursive demonstration requires that two single oscillators synchronize. While this is the case for convex oscillators, it is not so for linear and concave ones. However, I disagree with the ususal interpretation of the theorem of Mirollo and Strogatz as the impossibility of synchronization for nonconvex oscillators: In fact, this theorem tells nothing in this case. In [6], it was noted that convexity is not necessary for synchronization in the case of a model with transmission delays. We see here that this condition is not even necessary. Moreover, even concave oscillators can synchronize, provided that the concavity is not too large. In this case, positive feedback is in competition with concavity that has, for effect, to increase the gap between groups as they approach the threshold.

For small concavities positive feedback prevails, whereas for larger concavity groups are not able to grow. This process can be seen on the class of concave functions $E(t) = t^a$, $a > 1$. Let us call $x_c = 1 - (1 - n\alpha/N)^{1/a}$ the value of the phase difference between two successive groups of n and m oscillators ($n > m$) below which the first group absorbs the second one. The first return map of the phase difference x_i between these two groups when the largest one gets to the threshold [i.e., the state value of the second group is $(1 - x_i)^a$] has an attractive fixed point x_0. The condition for synchronization is $x_0 < x_c$. For a fixed pulse α/N there is an upper value for the concavity $a_{max} = 1 - \log(1 - \alpha/N)/\log 2$ below which the preceding condition is fulfilled for all group sizes $n > m$. In this case the system synchronizes as with linear oscillators. Since a_{max} is the most stringent bound, we expect that synchronization almost always occurs for a larger range of values of a. This has been extensively verified numerically [11].

Up to now, all the oscillators were identical. However, it is known that firefly populations have a spread of individual frequencies [2]. Therefore it is necessary to show that the phase delay model accounts for synchronization even in this case.

Frequency distribution.—Different frequencies may be allowed in IF models by keeping an identical threshold for the oscillators, but letting them have different slopes $E_i(t) = a_i t$, $E_i \in [0, 1]$, so that the a_i's are the internal frequencies. Positive feedback here is also the effective mechanism leading to synchronization for small disorder of frequencies. For larger frequency dispersion the formation of large groups is not always possible, since two oscillators relaxing together at one moment do not necessarily relax again together at the next cycle. In fact, two questions must be answered: First, can stable groups exist, and, second, can such groups be formed during the evolution? As we will see, this second point is not problematic and stability is the most stringent condition for the emergence of synchronization. Let us first notice that a necessary condition for the stability of a group of n oscillators is that the relaxation of the fastest one triggers the avalanche of all the others. Therefore stable groups must fire at the rhythm of the elements with highest frequency. Let us now study the stability of a group of $n + 1$ elements in the background of the other $N - (n + 1)$ oscillators, assuming that the subset of the n first ones, $O_1, \ldots, O_n$ of frequencies $a_1 > \cdots > a_n$ is stable, and that the $(n + 1)$th oscillator O_{n+1} has the lowest frequency a_{n+1}. Assuming that $O_1, \ldots, O_n, O_{n+1}$ have just relaxed together, the condition for again relaxing together after a cycle is

$$1 - a_{n+1}\left(\frac{1}{a_1} + \Delta\frac{a_1 - a_{n+1}}{a_1 a_{n+1}}\right) \leq n\frac{\alpha}{N}, \qquad (3)$$

where Δ is the summed strength of the pulses of all the other oscillators. Therefore the most stringent condition

of stability for a group of $n + 1$ oscillators is

$$\frac{a_1 - a_i}{a_1} \leq (i - 1)\frac{\alpha}{N}, \quad \forall i = 1, \ldots, n + 1. \qquad (4)$$

Therefore, given a system of N oscillators with a random uniform distribution of frequencies centered on a with width $D = a_{max} - a_{min}$, the probability that the whole system remains stable is

$$P_N(D/a, \alpha) = \rho^N \int_0^\delta da_1' \int_{a_1'}^{2\delta} da_2' \cdots \int_{a_{N-1}'}^{N\delta} da_N' \, e^{-\rho a_N'}$$

$$= 1 - e^{-\rho\delta} - \rho\delta e^{-2\rho\delta}$$

$$- e^{-\rho\delta} \sum_{j=2}^{N-1} \frac{(j + 1)^{j-1}}{j!}(\rho\delta e^{-\rho\delta})^j, \qquad (5)$$

where $\rho = N/D$ and $\delta = \alpha a_{max}/N$. One can see in Fig. 1 that even for large D/a there is a relatively high probability to have a realization of frequencies allowing complete synchronization as long as α is not too small, in which case the system decouples and synchronization is less probable. One can verify that when the probability P_N is not vanishingly small it is almost independent of N for large N (~ 100). Now we will see that any two stable groups of oscillators will, at some moment, relax together. Although positive feedback is still acting as in the case of identical oscillators, it is in competition with disorder that tends to desynchronize groups. However, contrary to the case of identical linear oscillators, it is easy to show that the dispersion of frequencies implies that the relative positions of any two groups change monotically in time. Therefore at some moment the two groups must relax together. If their union is itself stable, it forms a unique stable group. This proves that if the distribution of frequencies fulfills the stability conditions, Eq. (4), the system completely synchronizes. If this condition is not satisfied, there is partial synchronization: the subsystems that individually fulfill Eq. (4) synchronize. Extensive numerical simulations confirm all these conclusions [11].
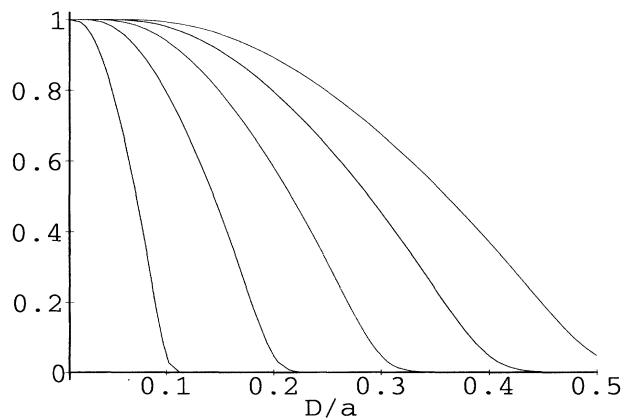

FIG. 1. Plot of the probability P_N, Eq. (6), for different dissipation levels. From top to bottom $\alpha = 0.5, 0.4, 0.3, 0.2, 0.1$.

It is natural to think of other kinds of frozen disorder. For instance, the pulses do not necessarily need to be of the same strength, and also the oscillators may have different threshold values. As expected, and for similar reasons as those previously explained for the case of a spread of frequencies, synchronization occurs also in this case and even for strong disorder. These results are different from the conclusions in [7], where for a similar but different model the completely synchronized state is unstable even against weak disorder.

Lattice models.—Besides synchronization or quasisynchronization, lattice models of pulse-coupled oscillators may display SOC. This is the case for the models of class (a), for which, however, SOC seems to be related to a tendency to synchronization [10,13]. SOC also appears when a system is perturbed, which otherwise should synchronize totally or partially [10,11], or which should be periodic [15]. The most striking example of class (a) models is the Olami-Feder-Christensen (OFC) model [9] that consists of oscillators E_i on a square lattice that relax to zero when they exceed a given threshold E_c, thus incrementing their nearest neighbors by a pulse which is α ($\alpha \leq 1/4$) times their value:

$$E_i \geq E_c \Rightarrow \begin{cases} E_i & \rightarrow & 0, \\ E_{nn} & \rightarrow & E_{nn} + \alpha E_i . \end{cases} \quad (6)$$

With open boundary conditions this model shows SOC, while the Feder-Feder (FF) model [16], which is identical but for the increment, which is a constant that can be seen as the mean of αE_i (pulse of the FF model $= \Delta = \overline{\alpha E_i}$), shows partial synchronization [10,11] (not SOC as claimed in [16]). This clearly means that the randomness of the initial conditions, which is dyamically eliminated in the FF model while it is mantained via the increment in the OFC model, changes the behavior of the system from partial synchronization to SOC. Furthermore, different kinds of perturbations incompatible with a periodic behavior change periodically ordered states for SOC. If, for instance, a random noise is added to the increment in the FF model, synchronization disappears and the system becomes SOC [10]. On the other hand, if, instead of open boundary conditions, periodic conditions are used, SOC disappears in favor of a periodic state, the period being the number of sites of the lattice [15]. It reappears if one inhomogeneity is introduced on the lattice [15]. Extensive numerical simulations [11] show that large avalanches are spatially quasistable. This means that during activation cycles of the oscillators sites participating in large avalanches are synchronized. Thus the system finds a compromise between synchronization and SOC, although

this seems contradictory since SOC is incompatible with complete synchronization [11,13].

In this Letter I have shown that in the mean field relaxation oscillator models such as the IF phase advance model synchronize under not as constrained conditions as suggested by the usual (erroneous) interpretation of the Mirollo and Strogatz theorem. Moreover, disorder, which is a constant of the real world, does not spoil synchronization in this model, opening the prospect of a larger applicability of IF oscillator models and of variants.

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