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LETTER TO THE EDITOR

Synchronization of coupled oscillations: an analysis of the comparator model

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Abstract. We present a model for the study of the synchronization between coupled limit-cycle oscillators. This model is motivated by the recent observations that revealed the existence of synchronization in the firing patterns of neural cells. Our study is based on a particular coupling architecture where all the oscillators are coupled to a comparator unit that feeds back to each oscillator the mean value of the total phase. The various regimes of this model are analysed in the presence of non-uniform external driving.

The comparator model has been recently proposed as a synchronization mechanism for limit-cycle oscillators [1]. The main motivation is neurobiological. Indeed, detailed experiments have shown the existence of signal synchronization in various sensory systems submitted to an external stimulus. In the mammalian visual cortex, for example, strong stimulus-dependent oscillations of neural activities (35–80 Hz) have been recorded by several authors [2, 3]. The neurons fire in synchrony provided common stimulus features drive the assembly simultaneously. A striking fact is that this type of synchronization occurs also in other sensory systems under very different spatio-temporal shapes of the external stimulus: from well-timed signals in the auditory system to weak and sluggish signals in the olfactory one [4]. Eckhorn *et al* [5] propose an explanation by introducing two, complementary, types of synchronization: stimulus-forced synchronizations are directly driven by stimulus transients and establish fast but crude sketches of association in the visual cortex, while stimulus-induced synchronizations are internally generated by some coupling effect between stimulus-activated oscillators which allows the formation of more refined shapes.

Several theoretical models have appeared aiming at the description of the synchronization phenomenon [1, 6, 7]. An approach favoured by several authors combines two ingredients. First, a description of the activity of the basic unit is provided [8]: this unit can be a single neuron or a collection of neurons (such as the cortical columns). Second, an architecture for the coupling between the oscillatory units is chosen. Thus the model consists, in fact, of a collection of coupled oscillators. Following the results of Koppel and Ermentrout [9], we will make the assumption that it is possible to describe the system by the evolution of the oscillator phases once they have relaxed to their limit cycles. A single oscillator can then be described by a unique parameter: its phase θ_i along the limit cycle. Thus the behaviour of a population of N interacting oscillators can be approximated by the system:

$$\frac{\mathrm{d}\theta_i}{\mathrm{d}t}=\omega_i+f(\theta_1,\theta_2,\ldots). \qquad (1)$$

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Let us now give a biological interpretation of (1). The quantity θ_i can be related to the time at which a given cell i generates an action potential. The quantity ω_i plays the role of an external (rhythmic) stimulus, while the phase variation $\dot{\theta}_i$ is related to the firing frequency of the neuron and depends crucially on the stimulus ω_i. Following general arguments, the function f must be odd. This implies that, in the absence of external input ω_i, the phase relaxes to zero and the neuron becomes quiescent.

This letter is devoted to the detailed analysis of the comparator model of coupling between the different oscillatory units. In this model each neuron of the system is coupled to a single, comparator, cell which feeds back to every cell the average phase of the neurons of the system. Equation (1) takes, then, the following form:

$$\frac{\mathrm{d}\theta_i}{\mathrm{d}t}=\omega_i+f(\theta_i-\theta_0) \qquad i=1,\ldots,N \qquad \theta_0=\frac{1}{N}\sum\theta_i. \tag{2}$$

Let us point out an important characteristic of the model: it does not possess any intrinsic geometry and the only thing that distinguishes between the various sites is the external stimulus ω_i.

In [10] we have studied the comparator model under the influence of a uniform excitation, i.e. $\omega_i=\omega_0$ for $i\leqslant k(<N)$ and zero elsewhere. Our principal findings can be simply summarized.

For all values of ω_0 lower than some critical value ω_{cr}, depending on the excited-sites fraction k/N, the phases tend to separate to two perfectly synchronized classes corresponding to the excited and the non-excited sites. Beyond the critical value of ω_0 no synchronization occurs although there exists a net phase-separation of excited and non-excited oscillators. Thus the response of the system follows roughly the external stimulus but no fine-tuned synchronization appears possible for $\omega_0>\omega_{\mathrm{cr}}$.

Still, in view of the results for $\omega_0<\omega_{\mathrm{cr}}$ one would tend to consider the comparator model as a good synchronizer. However this assertion, based on the results of uniform excitations alone, would be unjustified. Thus a complete study, considering non-uniform excitations, seems in order at this point.

Starting from (2) and summing over all the sites we obtain:

$$\frac{\mathrm{d}\theta(t)}{\mathrm{d}t}=\bar{\omega}+\phi(t) \tag{3}$$

where

$$\bar{\omega}=\frac{1}{N}\sum\omega_i \qquad \phi(t)=\frac{1}{N}\sum f(\theta_i-\bar{\theta}). \tag{4}$$

Subtracting the two equations we have:

$$\frac{\mathrm{d}(\theta_i-\bar{\theta})}{\mathrm{d}t}=\omega_i-\bar{\omega}+f(\theta_i-\bar{\theta})-\phi. \tag{5}$$

We can now introduce a new variable

$$\eta_i=\theta_i-\bar{\theta} \tag{6}$$

in terms of which the equations read:

$$\frac{\mathrm{d}\eta_i}{\mathrm{d}t}=\omega_i-\bar{\omega}+f(\eta_i)-\phi. \tag{7}$$

Thus, by a suitable redefinition of the dynamical variable the system decouples formally. As a matter of fact, the only coupling between the different sites comes from $\phi(t)$: the latter must be computed self-consistently at each time step from the solution η_i

itself through $\phi(t)=(1/N)\sum f(\theta_i-\bar{\theta})$. Once the η_i (and $\phi(t)$) are obtained one can go back to the θ_i's. It suffices to integrate equation (3):

$$\bar{\theta}(t)=\bar{\omega}t+\int\phi(t)\,\mathrm{d}t+\bar{\theta}(0). \tag{8}$$

As in the case of uniform excitations we can distinguish two different regimes depending on the magnitude of ω. For ω sufficiently small there exists a stationary state for η_i, i.e. $\mathrm{d}\eta_i/\mathrm{d}t=0$. In that case we have:

$$f(\eta_i)=\phi-\omega_i+\bar{\omega} \tag{9}$$

where ϕ is the value of $\phi(t)$ to which the evolution is attracted and which depends on the initial conditions. The condition for stationarity is that the magnitude of the RHS of (9) be smaller than the range of f. If this holds then (9) can be inverted to give η_i:

$$\eta_i=f^{-1}[\phi-\omega_i+\bar{\omega}]. \tag{10}$$

We remark that the attractor here is a solution that transforms nonlinearly the excitation ω_i. The details depend, of course, on the precise nature of f; however this should not become apparent unless we are very near to the critical value of ω. Beyond this value no stationarity appears possible and η grows unboundedly.

To illustrate these considerations we have performed a numerical simulation using an array of 100 coupled oscillators and a simple Euler integration scheme. The choice of the latter was dictated by its extreme simplicity. However we were able to repeat the whole theoretical analysis at the level of the mapping resulting from the discretized Euler integration scheme, reaching exactly the same qualitative conclusions as for the continuous equations. For the coupling function we have chosen $f(u)=\tanh(u)$. The reason for this choice is that we wish to have phase attraction to not more than one fixed point. In fact if one draws schematically the RHS of (7) for some site i one obtains figure 1. Thus if $\omega_i<\omega_{\mathrm{cr}}$ the single fixed point is stable while for $\omega_i>\omega_{\mathrm{cr}}$ no fixed points exist. The external stimulus used in the stimulation was chosen in the following way: $\omega_i=\omega_0$ for $i\leqslant N/4$ and $\omega_i=0$ for $i\geqslant 3N/4$ while for $N/4\leqslant i\leqslant 3N/4$ ω_i was chosen randomly with uniform probability in the interval $(0,\omega_0)$. Now, due to the absence of intrinsic geometry in the comparator model, this choice is tantamount to choosing ω_i decreasing with a constant slope from ω_0 to 0 when i goes from $N/4$ to $3N/4$. It turns out that with this choice of ω_i the basin of attraction of $\phi=0$ is

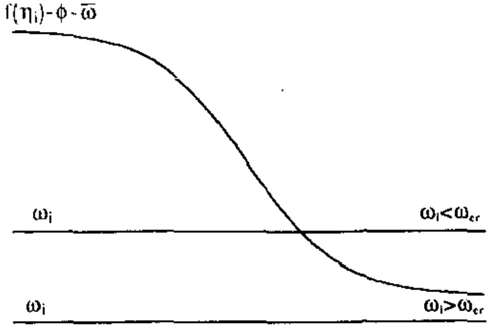

Figure 1. *Schematic representation of the* RHS *of* (7). One stable fixed point exists for $\omega_i<\omega_{\mathrm{cr}}$ while no fixed point can exist for $\omega_i>\omega_{\mathrm{cr}}$.

sufficiently large so as to attract all initial conditions starting with random θ_i's. Figures 2 and 3 present two different simulations. In the former we have $\omega_0 < \omega_{cr}$. We remark readily that the solution is qualitatively what one would expect from (10), a fact that is also quantitatively verified. Figure 3 corresponds to a case $\omega_0 > \omega_{cr}$, in which case the excitation becomes supercritical at least for some θ_i's. In this case no attraction of the phases to the external stimulus is possible and the detailed response of the system depends crucially on the precise form of the coupling function f. This is clear in figure 3 where we can distinguish a central subcritical region, described by (10). The response of the system follows the inverse hyperbolic tangent roughly up to ω_{cr} but beyond the critical value of ω_i the synchronization breaks down completely.

We can now summarize our findings on the comparator model. This model is an efficient synchronizing mechanism in the presence of uniform excitations. However, this is no longer true when the excitation becomes non-uniform. Moreover in the latter

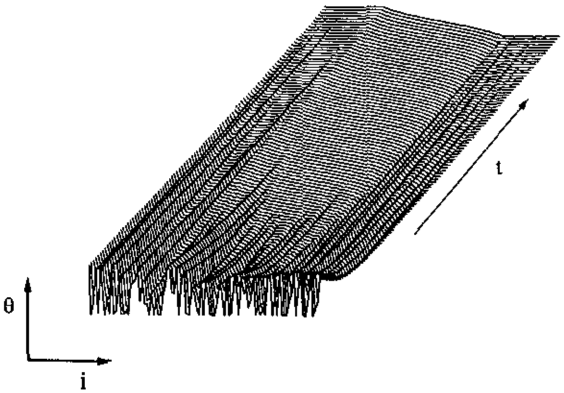

Figure 2. Evolution in time of the phases of an array of 100 coupled oscillators under the influence of a subcritical non-uniform excitation with $\omega_0 = 1.6$ (see text). The oscillators are disposed along the i-axis and their phases are given by the ordinate θ. Time evolution of the phases (for fixed stimulus) is represented by successive snapshots displayed in perspective.

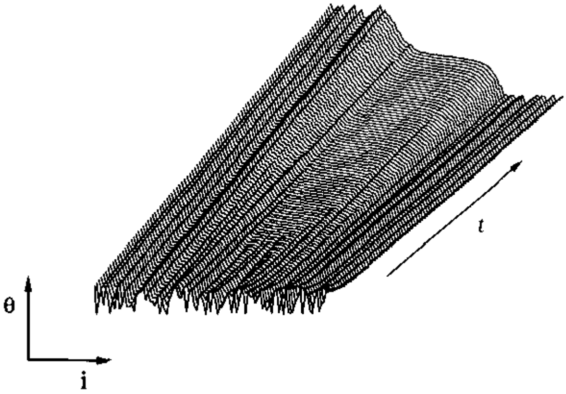

Figure 3. Evolution in time of the phases of an array of 100 coupled oscillators under the influence of a supracritical non-uniform excitation with $\omega_0 = 3$ ($\omega_{cr} = 2$). The same conventions as for figure 2 are used here.

case the detailed response of the system depends on the coupling function f. In all cases we can distinguish two regimes, a subcritical one where we have a stimulus-induced synchronization (in the terminology of [5]) and a supercritical one where we observe a 'stimulus-forced' separation of the phases without fine synchronization. In the case of non-uniform excitations a further complication is introduced by the fact that the two regimes may coexist. In view of the above remarks we do not believe that the comparator coupling can be an efficient mechanism for the synchronization of neural oscillations. Still, it remains a model of considerable physical interest, and we feel that the present study may serve as a starting point for further refinements.

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