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Predicting Synchronization of Three Mutually Inhibiting Groups of Oscillators with Strong Resetting

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Abstract: Neural populations encode sensory information, memory and motor patterns through electro-chemical firings, which propagate throughout the nervous system via synapses, a structure that couples neurons together. A powerful tool to investigate synchronization issues in such systems are the Phase Resetting curves. However these are best suited for brief and small perturbations. Motivated by the observation of strong inhibition in some neural circuits, we investigate a resetting model with similar features to a known neural population called *striatum*, in which three groups of neurons inhibit themselves. The model is intrinsically based on Kuramoto oscillators, and is analytically treatable. We derive a synchronization threshold in this model, and show numerically an unexpected complex dynamics.

Keywords: Phase oscillators, phase resetting, synchronization, critical coupling

This paper is dedicated to the memory of Professor Josè Sousa-Ramos.

1 Introduction

The key mechanism underneath several complex phenomena and behaviors in biological systems is in the dynamics of well coordinated coupled units [1,2,3]. In special, large interacting populations of neurons can generate complex motor patterns [4,5] and behaviors [2, 6] that drive life. On the mainstream there are the Central Pattern Generators, representing core circuits, often with intricate information flow despite a relatively small number of neurons [7], responsible for the maintenance of vital functions such as circulatory rhythms [8,9].

These systems have been successfully studied using interdisciplinary techniques led by biology, physics and dynamical systems. They are usually described by a group of interacting (non-linear) oscillators [10,11], trapped in limit cycles with huge basins of attraction, resulting in robust closed trajectories that encode important patterns [12,13,6]. Powerful and elegant

Nevertheless a primary assumption in such formalisms is that the perturbation is brief and weak, as a very short and small amplitude pulse. Once it is established that this is the case, a lot of information can be derived from the PRCs itself using differential calculus [6]. Specifically, regardless of the phase in which a perturbation is presented the oscillator will always stay very close to the original limit cycle. Such systems are thus classified as type 1 [2].

This may be the case in several systems, but if the interaction between the oscillators does not fit into this class, then it is harder to properly estimate the PRCs,

methods have been proposed to deal with such often complex systems, and the main toolkit are the Phase Resetting curves (PRCs) [14,15], which assess how the trajectory of a system deviates when an external perturbation is prompted. With this technique, it is possible to derive informative dynamical variables, such as the Lyapunov exponent, and then understand synchronization and phase-locking effects [14,6]. This technique has been extensively applied to neuroscience [16], especially to experimental setups [17,18,19,20,21] and medical applications [22,23,24,25,26,27,28]

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which hinders further development [29, 14]. Depending on the system this may manifest drastically on the PRCs, for instance, in form of discontinuities. This defines a second class of PRCs, the type 0.

Even with a PRC properly estimated, further analytical results on strong perturbations may not hold as infinitesimal arguments are not valid anymore. Not surprisingly, in real systems interactions may be strong [30,18,31,32,33,34,35,13,55]. To fill this gap, we propose a simple model for synchronization in an inhibitory circuit, in which the interaction is short but not weak. As its elements are based on Kuramoto oscillators [36,37], it has the virtue of being analytically tractable and can be universally applied [38].

The connections are displayed in mutually inhibiting groups, as in the striatum, a subcortical region of the forebrain [39,40]. Although we do not intend to thoroughly study the striatum here, it is a central structure for generating time patterns and control complex motor behaviors [41,42,43]. Malfunction of the striatum may result in Parkinson's desease, Huntington's disease, and other movement disorders usually linked to synchronization issues [44,45,46]. Very recent models have dwelled with the mechanisms underlying endogenously firing patterns which sequentially switch cell assemblies [39] and how such systems are capable of timing control [47].

In this paper we use the striatum connectivity as a benchmark while developing a framework intended to predict synchronization of strongly coupled populations of neurons. We show that some simple initial configurations undergo a phase transition from an unordered phase (non-synchronized oscillators) to an ordered phase (fully synchronized oscillators) at a critical value of the coupling constant. This core result will be illustrated with numerical simulations using a similar model, closer to the dynamics of neuron cells, implying the possibility of new investigations and efforts targeted at rigorous results with strong inhibition.

This paper is organized as follows. We first define the model in Section 2 and in Section 3 we note details of the numerical simulations. In sections 4 and 5 we exploit the model and simulations to understand conditions under which synchronized states are possible. At the end, we find a necessary condition for full synchronization to take part in the dynamics. We finally conclude our findings in Section 7.

2 The mathematical model

The model consists of 3 groups \mathscr{G}_n of *N* phase oscillators $\phi_k^n(t)$ (n = 1, 2, 3, k = 1, ..., N) having an inhibitory coupling with all oscillators in the "previous" group, where we understand that the three groups are cyclically ordered. These phases evolve in time according to the

system of differential equations

$$\dot{\phi}_k^n(t) = \omega_k^n - \frac{\varepsilon}{N} F^{n-1}(t), \qquad (1)$$

 $t \ge 0$, where

- $-\phi_k^n(t)$ is a real-valued function to account for more than one complete turn in either direction. To locate a phase on the unit circle, we take $\phi_k^n(t) \mod 2\pi$ in the interval $[0, 2\pi)$, unless otherwise stated;
- $-\omega_k^n > 0$ is the *natural frequency* of oscillator $k \in \mathscr{G}_n$;
- $-\varepsilon > 0$ is the *coupling strength*, which is the same for all oscillators; and
- $-F^{n-1}(t)$ is the *interaction term* which, as indicated by the notation, depends on the oscillators of \mathscr{G}_{n-1} . Its precise expression will be given below. Let us only mention at this point that $0 \le F^{n-1}(t) \le N$ for any *n* and *t*.

Henceforth we stick to notation in (1), i.e., lower indices k, j, ... (possibly accompanied by other lower indices) label the phase oscillators belonging to the group indicated by the upper index (n, n - 1, ...). Note that the interaction term is the same for all oscillators in a group.

Since $0 \le F^{n-1}(t) \le N$ for any *n* and *t*, then

$$\omega_k^n - \varepsilon \le \omega_k^n - \frac{\varepsilon}{N} F^{n-1}(t) \le \omega_k^n, \tag{2}$$

that is

$$\omega_k^n - \varepsilon \le \phi_k^n(t) \le \omega_k^n. \tag{3}$$

Integration of (1) between 0 and t > 0 yields

$$\phi_k^n(t) = \phi_k^n(0) + \omega_k^n t - \frac{\varepsilon}{N} \int_0^t d\tau F^{n-1}(\tau).$$
(4)

According to (3),

(i) if $\varepsilon \leq \omega_k^n$ then $\phi_k^n(t)$ will grow forever (i.e., circle in positive direction), while

(ii)if $\varepsilon > \omega_k^n$ then $\dot{\phi}_k^n(t)$ may become negative.

We suppose for the time being that (ii) is the case.

Thus, let $\varepsilon > \omega_k^n$, $\dot{\phi}_k^n(0) > 0$, and $t_{k,1}^n$ be the first time that $\phi_k^n(t) \mod 2\pi$ reaches the value 0 with negative speed:

$$\phi_k^n(t_{k,1}^n) \mod 2\pi = 0, \ \dot{\phi}_k^n(t_{k,1}^n) < 0.$$
 (5)

Let now $t_{k,2}^n > t_{k,1}^n$ be the earliest time $(t_{k,2}^n = \infty$ otherwise) such that the speed $\dot{\phi}_k^n$ reverses sign (from a negative to a positive speed), i.e.,

$$\dot{\phi}_k^n(t_{k,2}^n) = 0, \ \ddot{\phi}_k^n(t_{k,2}^n) > 0,$$
 (6)

where $\ddot{\phi}_k^n(t) = -\frac{\varepsilon}{N} \dot{F}^{n-1}(t)$ according to (1).

In our model, the observable quantities (or the quantities with a possibly biological meaning) are not going to be the phases themselves but their *activity* $\Phi_k^n(t)$, defined by

$$\Phi_k^n(t) = \begin{cases} \phi_k^n(t) \mod 2\pi \text{ if } t \in [0, t_{k,1}^n] \\ 0 \qquad \text{if } t \in [t_{k,1}^n, t_{k,2}^n] \end{cases} .$$
(7)



Note that

$$\Phi_k^n(0) = \phi_k^n(0) \bmod 2\pi.$$

We say that the phase oscillator $k \in \mathcal{G}_n$ has been reset (to 0) at time $t_{k,1}^n$ to describe the fact that its activity $\Phi_k^n(t)$ vanishes in the time interval $[t_{k,1}^n, t_{k,2}^n]$. We anticipate that k (its activity proper) will be "reactivated" at time $t_{k,2}^n$.

If $t_{k,2}^n < \infty$, this procedure can be repeated. The final result is a finite sequence of ordered times

$$0 < t_{k,1}^n < t_{k,2}^n < \dots < t_{k,s_{\max}}^n, \tag{8}$$

or an infinite one,

$$0 < t_{k,1}^n < t_{k,2}^n < \dots < t_{k,2r}^n < t_{k,2r+1}^n < \dots$$
(9)

 $(s_{\max} = \infty)$, where $t_{k,2r+1}^n$, $r \ge 0$, are the *reset times*, i.e.,

$$\phi_k^n(t_{k,2r+1}^n) \mod 2\pi = 0, \ \dot{\phi}_k^n(t_{k,2r+1}^n) < 0,$$
 (10)

and $t_{k,2r}^n$, $r \ge 1$, are the *reactivation times*, i.e.,

$$\dot{\phi}_k^n(t_{k,2r}^n) = 0, \ \ddot{\phi}_k^n(t_{k,2r}^n) > 0.$$
 (11)

Formally we can set $t_{k,0}^n = 0$. Note that $t_{k,1}^n = 0$ if $\phi_k^n(0) \mod 2\pi = 0$ and $\dot{\phi}_k^n(0) < 0$. We come back to oscillators with zero initial phase below.

The definition of the activity $\Phi_k^n(t)$ in the intervals $[t_{k,2r}^n, t_{k,2r+2}^n]$ with $r \ge 1$ is formally the same as before. Specifically,

$$\boldsymbol{\Phi}_{k}^{n}(t) = \begin{cases} \boldsymbol{\phi}_{k}^{n}(t) \mod 2\pi \\ 0 \\ \left(\boldsymbol{\phi}_{k}^{n}(t) - \boldsymbol{\phi}_{k}^{n}(t_{k,2r}^{n})\right) \mod 2\pi \end{cases}$$
(12)

if

$$\begin{cases} \text{if } t \in [0, t_{k,1}^n] \\ \text{if } t \in [t_{k,2r-1}^n, t_{k,2r}^n] \text{ for } r = 1, 2, ..., \left\lfloor \frac{s_{\max} - 1}{2} \right\rfloor \\ \text{if } t \in [t_{k,2r}^n, t_{k,2r+1}^n] \text{ for } r = 1, 2, ..., \left\lfloor \frac{s_{\max} - 2}{2} \right\rfloor \end{cases}$$

respectively. If $s_{\max} < \infty$, then $t_{k,s_{\max}+1}^n := \infty$. As stated above, the activity function or 'actual' phase $\Phi_k^n(t)$ is the observable quantity, the phase $\phi_k^n(t)$ acting as a mathematical scaffolding. The reason why we need to deal with both phases is that $\phi_k^n(t)$ is the solution of the time evolution law (1), while $\Phi_k^n(t)$ results from $\phi_k^n(t)$ via ad hoc decision rules (reset and reactivation) on the values of $\phi_k^n(t)$, see (12).

We can summarize the above discussion by saying that the phase oscillator $k \in \mathscr{G}_n$ is reset at times $t_{k,2r-1}^n$ and reactivated at times $t_{k,2r}^n$, although it is properly its activity Φ_k^n which is reset and reactivated at those times. Sometimes we also say that the oscillator is 'active' if $\Phi_k^n(t) \neq 0$ (i.e., if $t \in (t_{k,2r}^n, t_{k,2r+1}^n)$), then otherwise $\Phi_k^n(t)$ is constantly equal to 0. In the latter case we say that the oscillator is inactive. If $t_{k,1}^n = 0$ then (12) holds also true if we dispense with the first "interval" $[0, t_{k,1}^n] = \{0\}$.

The geometrical meaning of the reset and reactivation times is the following. At $t = t_{k,2r+1}^n$ the curve $t \mapsto \phi_k^n(t)$ on the Cartesian plane (t,ϕ) crosses a level line axis $\phi = 2\pi v$ ($v \in \mathbb{Z}$) with a negative slope, while at $t = t_{k,2r+1}^n$ it has local minima. The resulting activity curve $t \mapsto \Phi_k^n(t)$ vanishes in the inactivity periods, $[t_{k,2r-1}^n, t_{k,2r}^n]$, and it is a translate of $\phi_k^n(t) \mod 2\pi$ in the activity periods, $[t_{k,2r}^n, t_{k,2r+1}^n]$. Reset and reactivation times alternate: an oscillator can only be reset if active, and it can only be reactivated if inactive.

For the interaction term $F^n(t)$ we use hereafter the *ansatz*

$$F^{n}(t) = \sum_{k=1}^{N} \chi_{[2\pi - \Delta, 2\pi)}(\Phi_{k}^{n}(t)), \qquad (13)$$

where $\chi_{[2\pi-\Delta,2\pi)}$ is the *indicator function* of the interval $[2\pi-\Delta,2\pi), 0 < \Delta < 2\pi$, i.e.

$$\chi_{[2\pi-\Delta,2\pi)}(\Phi) = \begin{cases} 0 \text{ if } \Phi \notin [2\pi-\Delta,2\pi), \\ 1 \text{ if } \Phi \in [2\pi-\Delta,2\pi). \end{cases}$$

Therefore, $F^n(t)$ counts the number of oscillators $k \in \mathcal{G}_n$ such that $2\pi - \Delta \leq \Phi_k^n(t) < 2\pi$.

From a mathematical point of view, $F^n(t)$ is a piecewise constant function. Therefore, its derivative is actually a generalized function. Nonetheless, we will consider below only the case of a continuous distribution of oscillators so as $F^n(t)$ will be a continuous function. This being the case, we assume henceforth that $F^n(t)$ is differentiable except possibly at a finite set of points. As a result, the auxiliary phases $\phi_k^n(t)$ are continuous and piecewise differentiable functions, while the actual phases $\Phi_k^n(t)$ are, in general, only piecewise continuous and differentiable.

For further reference we prove the following result.

Proposition 1. A necessary and sufficient condition for $\phi_k^n(t_{k,2r}^n) > \phi_k^n(t_{k,2r+2}^n)$, $r \ge 0$, to hold is

$$\int_{t_{k,2r}^n}^{t_{k,2r+2}^n} t dF^{n-1}(t) \equiv \int_{t_{k,2r}^n}^{t_{k,2r+2}^n} t \dot{F}^{n-1}(t) dt < 0.$$
(14)

Proof. From (see (11) and (1))

$$\dot{\phi}_k^n(t_{k,2r}^n) = 0 \iff \omega_k^n = \frac{\varepsilon}{N} F^{n-1}(t_{k,2r}^n),$$

we obtain (see (4))

$$\begin{split} \phi_k^n(t_{k,2r}^n) &= \phi_k^n(0) + \omega_k^n t_{k,2r}^n - \frac{\varepsilon}{N} \int_0^{t_{k,2r}^n} F^{n-1}(t) dt \\ &= \phi_k^n(0) + \frac{\varepsilon}{N} \left(F^{n-1}(t_{k,2r}^n) t_{k,2r}^n - \int_0^{t_{k,2r}^n} F^{n-1}(t) dt \right) \\ &= \phi_k^n(0) + \frac{\varepsilon}{N} \int_0^{t_{k,2r}^n} t dF^{n-1}(t). \end{split}$$

Therefore,

$$\phi_k^n(0) - \phi_k^n(t_{k,2r}^n) \equiv \phi_k^n(t_{k,0}^n) - \phi_k^n(t_{k,2r}^n)$$
$$= -\frac{\varepsilon}{N} \int_0^{t_{k,2r}^n} t dF^{n-1}(t)$$

and

$$\phi_k^n(t_{k,2r}^n) - \phi_k^n(t_{k,2r+2}^n) = -\frac{\varepsilon}{N} \int_{t_{k,2r}^n}^{t_{k,2r+2}^n} t dF^{n-1}(t),$$

for $r \ge 1$, which proves the proposition. \Box

The main scope of this paper is to study the possibility of synchronization in the above model. We say that two oscillators $j, k \in \mathscr{G}_n$ are synchronized (or activity synchronized) if there is a time t_0 such that $\Phi_j^n(t) = \Phi_k^n(t)$ for all $t \ge t_0$. In the remaining sections we are going to study the possibility of full synchronization, i.e., that all oscillators in a group are synchronized from a given finite time on. Owing to the complexity of the model, a theoretical analysis of this question will require some simplifying hypotheses. Further recourse to the auxiliary phases $\Phi_k^n(t)$ will be still needed to keep track of the activities $\Phi_k^n(t)$.

3 Numerical results in a similar model network

This study is motivated by the observations of strongly coupled phase oscillators present in biological systems, mostly in neuroscience [14,3,15]. Thus, we also show results from simulations of a slightly different model that represents pulse oscillators close to neurons coupled through inhibitory synapses, complementing the mathematical formulation. The connections are instantaneous. The only difference relies on the functional form (13): instead of the activity Φ_i^n , we use the phase itself - explicitly defined below. We show that, in this scenario, our mathematical conclusions still hold and this motivates new efforts targeted at new rigorous results with strong inhibition.

We have simulated three mutually inhibitory groups of phase oscillators, whose interaction term is

$$F^{n}(t) = \sum_{j=1}^{N} \chi_{[2\pi - \Delta, 2\pi)}(\phi_{j}^{n}(t)), \qquad (15)$$

which means that whenever the phase of an oscillator lies on the interval $[2\pi - \Delta, 2\pi)$, it is inhibiting the following group of oscillators. This is very common in excitable models, in which there are (at least) an excited state and a resting state. The differential equation (1) is then integrated during a time window *T* large enough so that the equilibrium is achieved. Also, the phases are restricted to the interval $[0, 2\pi)$. To assess synchronization, we have used the usual Kuramoto order parameter [37]. If not stated otherwise, $N = 3 \times 10^3$, $\omega_j^{(n)} = \omega^{(n)} = 1 \forall j, n, T = 10^5$ and the initial condition for all oscillators was drawn from a uniform distribution over the interval $[0, 2\pi)$. Finally, Δ will be set so that the oscillator is active only during 10% of the whole interval, i.e., $\Delta = 0.1 \times 2\pi$.

4 Study case I: $\varepsilon \leq \omega_k^n$

In this case, see (3), all oscillators circle counterclockwise with variable or constant angular speed, hence their phases are not reset. By (4)

$$\phi_k^n(t) - \phi_j^n(t) = \phi_k^n(0) - \phi_j^n(0) + (\omega_k^n - \omega_j^n)t$$

This shows that phase synchronization is not possible. By way of illustration, suppose that

$$\omega_k^n = \omega^n$$
,

for all $k \in \mathcal{G}_n$, i.e. all oscillators of Group *n* have the same natural frequency. Then all phases wind around the unit circle with a constant relative phase difference:

$$\phi_k^n(t) - \phi_j^n(t) = \phi_k^n(0) - \phi_j^n(0) = const$$
(16)

Any distribution of initial phases rotates around the circle as a rigid ring. We say that the phases are locked. In particular, the uniform distribution, $\rho^n(0,\phi) = \frac{N}{2\pi}$, is also stationary, i.e., $\rho^n(t,\phi) = \frac{N}{2\pi}$ for $t \ge 0$.

5 Study case II: $\varepsilon > \omega_k^n$

To illustrate the dynamics of this supposedly simple model and to gain some insight, we first show in Figures 1 and 2 the time evolution of some phases in each group run. We assume that $\omega_k^n = \omega^n$ for $1 \le n \le 3$ and all k, and $\rho(0, \phi) = \frac{N}{2\pi}$. Therefore, (16) holds also true in this case, i.e., the curve $t \mapsto \phi_k^n(t)$ is a vertical translate of the curve $t \mapsto \phi_j^n(t)$ on the (t, ϕ) plane for all k, j within each group (see Figure 1). Consequently, all oscillators $k \in \mathcal{G}_n$ are initially activity-locked and will become partially synchronized as some of them become reset and jointly reactivated.

Furthermore, note that a complete oscillation of 2π rad in positive direction does not change the activity of the phases, while it synchronizes the activity of them all if in negative direction; from then on the whole group remains synchronized. This being the case, we may restrict our attention to oscillations whose angle range is not greater than 2π rad. Specifically we assume hereafter that there is an angle $\phi = \alpha$,

$$\Delta < \alpha \le 2\pi, \tag{17}$$

such that

$$-\alpha \le \phi_{k_0}^n(t) \le 2\pi - \alpha \tag{18}$$



Fig. 1: Here we show the time evolution of two oscillators per group with $\varepsilon = 8$. Each curve is a randomly chosen oscillator within a same group, as labeled in the top right of each graph. We can not only see the phase synchronization after some transient time, but also clearly see that Equation (16) holds also true in this case: the curve $t \mapsto \phi_k^n(t)$ is a vertical translate of the curve $t \mapsto \phi_j^n(t)$ on the (t, ϕ) plane for all k, j within each group. Not all oscillators may synchronize for every value of ε though, and this is expected as for low values of ε the system itself is basically uncoupled.



Fig. 2: Same as in Figure 1, setting $\varepsilon = 10$. We see several complex behaviors throughout the time evolution: phase locking, overlapping of phases, intermittency and, finally, synchronization. At the end, we will see that in fact $\varepsilon = 10$ will play an important hole as the transition point to full synchronization.

for all $t \ge 0$, where $k_0 \in \mathscr{G}_n$ is (without restriction) the oscillator with initial phase $\phi_{k_0}^n(0) = 0$. The parameter Δ is the same that appears in the expression of $F^n(t)$, Eq. (13). Therefore, we are assuming that k_0 may take both positive and negative phases and it oscillates in such a

way that $2\pi - \alpha$ is its maximal amplitude in positive (counterclockwise) direction, and $-\alpha$ is its maximal amplitude in negative (clockwise) direction. We say then that the phases of Group *n* are performing *small* oscillations¹.

It is possible that some oscillators synchronize for small values of ε , but the system as a whole may not synchronize. In this section, the phase oscillators with zero initial phases will play an important role in the formal description of the activity synchronization.

5.1 Synchronization separatrices

Let

$$0 = t_{k_0,1}^n < t_{k_0,2}^n < \dots < t_{k_0,s_{\max}}^n$$

 $s_{\max} \ge 2$, be the finite $(t_{k_0,s_{\max}}^n < \infty)$ or infinite $(t_{k_0,s_{\max}}^n = \infty)$ sequence of reset times $(t_{k_0,2r-1}^n)$ and reactivation times $(t_{k_0,2r}^n)$ of the oscillator $k_0 \in \mathcal{G}_n$ with initial phase $\phi_{k_0}^n(0) = 0$. We call the curve $\phi_{k_0}^n(t)$ the 0th separatrix of synchronization.

By (16), if

$$\phi_{k_1}^n(0) = -\phi_{k_0}^n(t_{k_0,2}^n),$$

(as real-valued function), then $\phi_{k_1}^n(t_{k_0,2}^n) = 0$ in virtue of

$$\phi_{k_1}^n(t) = \phi_{k_0}^n(t) + \phi_{k_1}^n(0)$$

(see (16)). We call $\phi_{k_1}^n(t)$ the first separatrix of synchronization. All oscillators with initial phases

$$\phi_k^n(0) \in \left[0, \phi_{k_1}^n(0)\right] = \left[0, \left|\phi_{k_0}^n(t_{k_0,2}^n)\right|\right]$$

will be reset in the time interval $[t_{k_0,1}^n, t_{k_0,2}^n)$ and hence altogether will be reactivated at time t_2^n and remain activity synchronized with $\phi_{k_1}^n(t)$ for $t \ge t_{k_0,2}^n$. Therefore, by time $t = t_{k_0,2}^n$ there are at least $\frac{N}{2\pi}\phi_{k_1}^n(0)$ oscillators synchronized.

The construction of separatrices can be iteratively continued —there is one for each reactivation time. Thus, the *rth separatrix of synchronization* corresponds to the phase trajectory of the oscillator k_r ,

$$\phi_{k_r}^n(t) = \phi_{k_0}^n(t) + \phi_{k_r}^n(0) \tag{19}$$

(see (16)) such that

$$\phi_{k_r}^n(t_{k_{r-1},2}^n) = 0$$
, i.e., $\phi_{k_r}^n(0) = -\phi_{k_0}^n(t_{k_{r-1},2}^n)$.

By definition,

$$\phi_{k_{r-1}}^n(t_{k_{r-1},2}^n) < 0 = \phi_{k_r}^n(t_{k_{r-1},2}^n)$$

and thus,

$$\phi_{k_{r-1}}^n(t) < \phi_{k_r}^n(t) \text{ for all } t \ge 0$$
(20)

¹ In the simulations we use $\alpha_n = 0$ for n = 1, 2, 3 though.



because they are solutions of the same differential equation. Furthermore,

$$t_{k_r,2}^n = t_{k_0,2(r+1)}^n \tag{21}$$

as long as $2(r+1) \le \lfloor s_{\max}/2 \rfloor$, but the above construction of the *r*th separatrices can be done even if $s_{\max} = 2$.

Likewise as before, it follows that all oscillators such that

$$\phi_k^n(0) \in \left[\phi_{k_{r-1}}^n(0), \phi_{k_r}^n(0)\right) = \left[\left|\phi_{k_0}^n(t_{k_{r-2},2}^n)\right|, \left|\phi_{k_0}^n(t_{k_{r-1},2}^n)\right|\right)$$
(22)

will be reset for the first time in the time interval $[t_{k_{r-1},1}^n, t_{k_{r-1},2}^n)$. Note that the interval (22) is non-empty because of (20). We conclude that all oscillators $k \in \mathscr{G}_n$ with

$$\phi_k^n(0) \in \left[0, \phi_{k_r}^n(0)\right) = \left[0, \left|\phi_{k_0}^n(t_{k_{r-1},2}^n)\right|\right)$$
(23)

will be reset in the period $[t_{k_{r-1},1}^n, t_{k_{r-1},2}^n)$ and hence altogether will be reactivated at time $t_{k_{r-1},2}^n$ and synchronized with $\phi_{k_{r-1}}^n(t)$.

The activity synchronization in the whole period $[t_{k_{r-1},2}^n, t_{k_r,2}^n]$ for oscillators of \mathcal{G}_n with initial positive phase is the following:

$$\boldsymbol{\Phi}_{k}^{n}(t) = \begin{cases} \left[\phi_{k_{r}}^{n}(t) \right]_{+} \text{ if } \phi_{k}^{n}(0) \in \left[0, \phi_{k_{r}}^{n}(0) \right) \\ \left[\phi_{k}^{n}(t) \right]_{+} \text{ if } \phi_{k}^{n}(0) \in \left[\phi_{k_{r}}^{n}(0), \phi_{k_{r+1}}^{n}(0) \right) \\ \phi_{k}^{n}(t) \text{ otherwise} \end{cases}$$
(24)

where $\phi_{k_n}^n(t)$ is given by (19).

Till now we have considered only separatrices in the positive direction from the 0th separatrix. To introduce negative separatrices, call τ_r^n the *reversal time* of $\phi_{k_r}(t)$ immediately before the reset time $t_{k_r,1}^n$, $r \ge 1$. If $t_{k_0,1}^n = 0$ (i.e., $\phi_{k_0}^n(0) < 0$), then set $\tau_0^n = 0$. Thus,

$$\dot{\phi}_{k_r}^n(\tau_r^n) = 0, \, \ddot{\phi}_{k_r}^n(\tau_r^n) < 0,$$
 (25)

where $0 \le \tau_0^n \le t_1^n$, and $t_{k_{r-1},2}^n < \tau_r^n < t_{k_r,1}^n$ for $r \ge 1$. At the reversal times the functions $\phi_k^n(t)$ have local maxima.

Consider now oscillators with negative initial phase. Similarly to what we did above, if

$$\phi_{k_{-1}}^n(0) = -\phi_{k_0}(\tau_0^n), \tag{26}$$

then $\phi_{k-1}^n(\tau_0^n) = 0$. We call

$$\phi_{k_{-1}}^n(t) = \phi_{k_0}^n(t) + \phi_{k_{-1}}^n(0)$$

the separatrix of order -1. It follows that all oscillators $k \in \mathcal{G}_n$ with

$$\phi_k^n(0) \in \left(\phi_{k_{-1}}^n(0), 0\right] = \left(-\phi_{k_0}(\tau_0^n), 0\right]$$

© 2015 NSP Natural Sciences Publishing Cor. will be reset in the time interval $(\tau_0, t_{k_0,1})$ and reactivated at time $t_{k_0,2}$, provided $t_{k_0,1} > 0$. If $t_{k_0,1} = 0$ then $\phi_{k_{-1}}^n(t) = \phi_{k_0}^n(t)$.

Separatrices of order -r, $\phi_{k_{-r}}^n(t)$, are defined as follows:

$$\phi_{k_{-(r+1)}}(\tau_r^n) = 0$$
, i.e., $\phi_{k_{-(r+1)}}(0) = -\phi_{k_0}(\tau_r^n) < 0$,

see (19). As in the case of separatrices of positive order, we conclude that all oscillators $k \in \mathcal{G}_n$ such that

$$\phi_{k}^{n}(0) \in \left(\min_{0 \le i \le r} \phi_{k_{-(i+1)}}(0), 0\right] = \left(-\max_{0 \le i \le r} \phi_{k_{0}}(\tau_{i}^{n}), 0\right]$$
(27)

will be reset in the time interval $[\tau_r^n, t_{k_r,1})$, and reactivated at time $t_{k_r,2}$. Here we have to take the minimum $\min_{0 \le i \le r} \phi_{k_{-(i+1)}}(0)$ because, contrarily to (20), the separatrices $\phi_{k_{-1}}(t), ..., \phi_{k_{-(r+1)}}(t)$ need not be monotonically ordered. From then on, the phases (27) are synchronized with $\phi_{k_{r+1}}(t)$.

Proposition 2. A necessary and sufficient condition for $\phi_k^n(0) < \phi_k^n(\tau_0^n)$ (if $\tau_0^n > 0$), and $\phi_k^n(\tau_r^n) < \phi_k^n(\tau_{r+1}^n)$, $r \ge 0$, to hold is

$$\int_{0}^{\tau_{0}^{n}} t\dot{F}^{n-1}(t)dt > 0 \tag{28}$$

and

$$\int_{\tau_r^n}^{\tau_{r+1}^n} t \dot{F}^{n-1}(t) dt > 0$$
(29)

respectively.

Proof. For a given oscillator $k \in \mathscr{G}_n$,

$$\dot{\phi}_k^n(\tau_r^n)=0,$$

since the solution flow of (1) has local maxima at all separatrix reversal times. Replace then $\phi_k^n(t_{k,2r}^n)$ by $\phi_k^n(\tau_r^n)$ in the proof of Proposition 1 to obtain (29). \Box

In sum, if for
$$n = 1, 2, 3$$
,

$$\dots \cup (\phi_{k_{-2}}^{n}(0), \phi_{k_{-1}}^{n}(0)] \cup (\phi_{k_{-1}}^{n}(0), 0) \cup [0, \phi_{k_{1}}^{n}(0)) \cup [\phi_{k_{1}}^{n}(0), \phi_{k_{2}}^{n}(0)) \cup \dots = (-\alpha_{n}, 2\pi - \alpha_{n})$$

or, equivalently,

$$\begin{split} \dots \cup (-\phi_{k_0}^n(\tau_1^n), -\phi_{k_0}^n(\tau_0^n)] \cup (-\phi_{k_0}^n(\tau_0^n), 0) \cup \\ [0, \phi_{k_0}^n(t_{k_0,2}^n)) \cup [\phi_{k_0}^n(t_{k_0,2}^n), \phi_{k_0}^n(t_{k_1,2}^n)) \cup \dots \\ &= (-\alpha_n, 2\pi - \alpha_n), \end{split}$$

where some intervals with negative separatrices might be repeated, then all oscillators end up activity synchronized.



5.2 Evolution equations for small oscillations

Remember that all phases in a group move under the same force, and we are assuming a uniform initial distribution of the initial phases, $\rho^n(0, \phi) = N/2\pi$.

Consider the geometrical representation of a phase oscillator $\phi^n(t)$ as a point on the unit circle. If $\phi^n(0) = 0$ then its time evolution corresponds to the 0th separatrix of synchronization of the group \mathscr{G}_n . In the notation of the previous section, $\phi^n(t) = \phi_{k_0}^n(t)$; quantities like ϕ^n and t^n without the subscript k refer hereafter to the 0th separatrix, $k = k_0$, of \mathscr{G}_n . In a typical oscillation, the phase $\phi^n(t)$ changes from negative to positive speed at the first reactivation time t_2^n . It starts then moving in the positive direction till it stops at the first reversal time $t = \tau_1$ and bounces back in the negative direction, and stops again at $t = t_{k_1,2}$ before reversing direction once more, and so on.

According to (23) and (27), whether $\dot{\phi}^n(0) < 0$ (in which case $0 = \tau_0^n = t_1^n$, $\phi(\tau_0^n) = 0$) or $\dot{\phi}^n(0) > 0$ (in which case $0 < \tau_0^n < t_1^n$, $\phi(\tau_0^n) > 0$), all oscillators $k \in \mathscr{G}_n$ such that

$$\phi_{k}^{n}(0) \in \left(\min_{0 \le i \le r} \phi_{k_{-(i+1)}}(0), \phi_{k_{r+1}}^{n}(0)\right) = \left(-\max_{0 \le i \le r} \phi_{k_{0}}(\tau_{i}^{n}), \left|\phi^{n}(t_{k_{r},2}^{n})\right|\right) \quad (30)$$

will be synchronized at $t = t_{k_r,2}^n$ with $\phi_{k_{r+1}}(t)$, their common activity being

$$\Phi_k(t) = \phi_{k_{r+1}}(t) = \phi(t) + \phi_{k_{r+1}}(0)$$

for $t \in [t_{k_r,2}^n, t_{k_{r+1},1}^n]$. Thus, full synchronization is possible via the combination of two mechanisms:

- Mechanism 1. There is a sequence of separatrix reactivation times $t_{k_r,2}^n$ such that $\phi^n(t_{k_r,2}^n) \to -\alpha_n$.
- Mechanism 2. There is a sequence of separatrix reversal times τ_r^n such that $\phi^n(\tau_{r-1}^n) < \phi^n(\tau_r^n)$ for every *r*, and $\phi^n(\tau_r^n) \to 2\pi \alpha_n$.

Exceptionally, full synchronization might be also achieved via Mechanism 1 alone ($\alpha_n = 2\pi$).

Proposition 3. Let ϕ^n be the 0th synchronization separatrix of \mathcal{G}_n .

(i) A necessary and sufficient condition for the synchronization of the oscillators $k \in \mathscr{G}_n$ with $\phi_k^n(0) \in \left[0, \left|\phi(t_{k_{r_s},2}^n)\right|\right) \subset [0, 2\pi - \alpha_n], s \ge 0$, is

$$\int_{0}^{t_{k_{r_0},2}^{n}} t \dot{F}^{n-1}(t) dt < 0 \tag{31}$$

and, if $s \ge 1$,

$$\int_{t_{k_{r_i,2}}^{t_{k_{r_{i+1},2}}^{n}} t \dot{F}^{n-1}(t) dt < 0$$
(32)

for i = 0, 1, ..., s - 1.

(ii) A necessary and sufficient condition for the synchronization of the oscillators $k \in \mathscr{G}_n$ with $\phi_k^n(0) \in (-\phi(\tau_{r_h}^n), 0] \subset [-\alpha_n, 0]$ is the existence of a subsequence of separatrix reversal times $\tau_{r_1}^n, \tau_{r_2}^n, ..., \tau_{r_h}^n, h \ge 1$, such that

$$\int_{0}^{\tau_{r_{1}}^{n}} t \dot{F}^{n-1}(t) dt > 0$$

and, if $h \ge 2$,

$$\int_{\tau_{r_{i}}}^{\tau_{r_{i+1}}^{n}} t\dot{F}^{n-1}(t)dt > 0$$
(33)

for i = 1, ..., h - 1.

Proof. (i) For $t = t_{k_{r_i},2}^n$,

$$\dot{\phi}(t^n_{k_{r:},2}) = 0$$

since the solution flow of (1) has local minima at all the separatrix reactivation times. Replace then $\phi_k^n(t_{k,2r}^n)$ by $\phi(t_{k_{r_i},2}^n) \equiv \phi_{k_0}(t_{k_{r_i},2}^n)$ in the proof of Proposition 1 to obtain (32).

(ii) Replace $\phi_k^n(\tau_r^n)$ by $\phi^n(\tau_{r_i}^n)$ in Proposition 2. It follows then $\phi^n(0) < \phi^n(\tau_{r_i}^n) < ... < \phi^n(\tau_{r_k}^n)$. \Box

The bottom line is that the separatrix reactivation times $t_{k_0,2}^n$, $t_{k_1,2}^n$, ..., and reversal times τ_0^n , τ_1^n , ... (or a subsequence of them) describe the whole activity synchronization process in the setting considered in this section.

To extract further information out of Proposition 3, we are going to exploit the specific form (13) of the interaction term $F^n(t)$ in the regimen of small oscillations (17)-(18). According to (13), $F^n(t)$ counts the number of oscillators $k \in \mathscr{G}_n$ with $\Phi_k^n(t) \in [-\Delta, 0)$. Note that the proviso (17) guarantees that reactivated oscillators do not enter the angular sector $[-\Delta, 0)$ because $\Phi_k^n(t) \ge 0$ for them. In view of (30), the separatrices that inform about which other oscillators have their activities in $[-\Delta, 0)$ at time *t* are

$$\phi^{n}(t;\tau_{r}^{n}) := \min_{0 \le i \le r} \phi_{k_{-(i+1)}}(t) = \phi^{n}(t) - \max_{0 \le i \le r} \phi^{n}(\tau_{i}^{n}),$$
(34)

where *r* is fixed by the condition that τ_r^n is the greatest reversal time such that $\tau_r^n < t$. If $\tau_0^n > 0$ and $t < \tau_0^n$, set $\phi^n(t;\tau_0^n) := \phi^n(t)$, although we are interested in the asymptotic dynamic. The separatrices (34) divide the oscillators $k \in \mathcal{G}_n$ with $\phi_k^n(t) \in [-\Delta, 0)$ which have been reset, namely,

$$\phi^n(t;\tau_r^n) < \phi_k^n(t) \le 0$$

(and hence $\Phi_k^n(t) \ge 0$), from those which have not been reset yet, namely,

$$-\Delta \leq \phi_k^n(t) \leq \phi^n(t;\tau_r^n)$$

(and hence $\Phi_k^n(t) = \phi_k^n(t)$), for $\tau_r^n \le t < \tau_{r+1}^n$. This being the case, we find that, for $t_{k_{r-1},2}^n \le t < \tau_r^n$ $(t_{k_{r-1},2}^n = 0 \text{ for } r = 0),$

$$F^{n}(t) = \begin{cases} \frac{N\Delta}{2\pi} \\ \frac{N\Delta}{2\pi} + \frac{N}{2\pi} \phi^{n}(t; \tau_{r-1}^{n}) \\ 0 \end{cases}$$
(35)
if
$$\begin{cases} 0 \le \phi^{n}(t; \tau_{r-1}^{n}) \le 2\pi - \alpha_{n} \\ -\Delta \le \phi^{n}(t; \tau_{r-1}^{n}) \le 0 \\ -\alpha_{n} \le \phi^{n}(t; \tau_{r-1}^{n}) \le -\Delta \end{cases}$$

while for $\tau_r^n \leq t \leq t_{k_r,2}^n$,

$$F^{n}(t) = \begin{cases} \frac{N\Delta}{2\pi} + \frac{N}{2\pi} \phi^{n}(t;\tau_{r}^{n}) \text{ if } -\Delta \leq \phi^{n}(t;\tau_{r}^{n}) \leq 0\\ 0 & \text{ if } -\alpha_{n} \leq \phi^{n}(t;\tau_{r}^{n}) \leq -\Delta \end{cases}$$
(36)

since $\phi^n(t; \tau_r^n) \leq 0$ in the period $[\tau_r^n, t_{k_r,2}^n]$. From (1) it follows that for $t_{k_{r-1},2}^{n-1} \leq t < \tau_r^{n-1}$,

$$\dot{\phi}^{n}(t) = \begin{cases} \omega^{n} - \frac{\varepsilon \Delta}{2\pi} \\ \omega^{n} - \frac{\varepsilon \Delta}{2\pi} - \frac{\varepsilon}{2\pi} \phi^{n-1}(t; \tau_{r-1}^{n-1}) \\ \omega^{n} \end{cases}$$
(37)
if
$$\begin{cases} 0 \le \phi^{n-1}(t; \tau_{r-1}^{n-1}) \le 2\pi - \alpha_{n-1} \\ -\Delta \le \phi^{n-1}(t; \tau_{r-1}^{n-1}) \le 0 \\ -\alpha_{n-1} \le \phi^{n-1}(t; \tau_{r-1}^{n-1}) \le -\Delta \end{cases}$$

while for $\tau_r^{n-1} \leq t \leq t_{k_r,2}^{n-1}$,

$$\dot{\phi}^{n}(t) = \begin{cases} \omega^{n} - \frac{\varepsilon \Delta}{2\pi} - \frac{\varepsilon}{2\pi} \phi^{n-1}(t; \tau_{r}^{n-1}) \\ \omega^{n} \end{cases}$$
(38)
if
$$\begin{cases} -\Delta \leq \phi^{n-1}(t; \tau_{r}^{n-1}) \leq 0 \\ -\alpha_{n-1} \leq \phi^{n-1}(t; \tau_{r}^{n-1}) \leq -\Delta \end{cases}$$

Finally, upon differentiation of (35) and (36), we obtain for $t_{k_{r-1},2}^n \leq t < \tau_r^n,$

$$\dot{F}^{n}(t) = \begin{cases} 0 & \text{if } 0 < \phi^{n}(t; \tau_{r-1}^{n}) \le 2\pi - \alpha_{n} \\ \frac{N}{2\pi} \dot{\phi}^{n}(t) & \text{if } -\Delta < \phi^{n}(t; \tau_{r-1}^{n}) < 0 \\ 0 & \text{if } -\alpha_{n} \le \phi^{n}(t; \tau_{r-1}^{n}) < -\Delta \end{cases}$$
(39)

and for $\tau_r^n \leq t \leq t_{k_n,2}^n$,

$$\dot{F}^{n}(t) = \begin{cases} \frac{N}{2\pi} \dot{\phi}^{n}(t) & \text{if } -\Delta < \phi^{n}(t; \tau_{r}^{n}) < 0\\ 0 & \text{if } -\alpha_{n} \le \phi^{n}(t; \tau_{r}^{n}) < -\Delta \end{cases}$$
(40)

5.3 Full synchronization

Suppose that $\phi^n(t)$ is performing small oscillations, see (17) and (18).

Proposition 4. A necessary condition for the oscillators k to reach full synchronization in the three groups \mathcal{G}_n through a finite number of small oscillations is

$$\varepsilon > \frac{2\pi\omega^n}{\Delta} \tag{41}$$

for n = 1, 2, 3.

Proof. According to Proposition 3(i), a necessary condition for the synchronization in all $k \in \mathcal{G}_n$ with

$$\phi_k^n(0) \in [0, 2\pi - \alpha_n]$$

is that

$$\int_{0}^{t_{k_{0,2}}^{n}} t\dot{F}^{n-1}(t)dt < 0, \ \int_{t_{k_{r,2}}^{n}}^{t_{k_{r+1,2}}^{n}} t\dot{F}^{n-1}(t)dt < 0$$
(42)

for $r = 0, 1, ..., r_{\max}^n - 1$ (if $r_{\max}^n \ge 1$), with $\left| \phi^n(t_{k_{\max}^n}^n, 2) \right| =$ $2\pi - \alpha_n$, and n = 1, 2, 3. From (37) we obtain

$$\inf\left\{\dot{\phi}^n(t): t_{k_{r-1},2}^{n-1} \le t \le \tau_r^{n-1}\right\} = \omega^n - \frac{\varepsilon\Delta}{2\pi}$$

 $(t_{k_{r-1},2}^{n-1} = 0 \text{ for } r = 0)$ because $\phi^{n-1}(t; \tau_{r-1}^{n-1}) \leq 0$. Therefore, see (39),

$$\dot{F}^{n}(t) \begin{cases} \geq \frac{N}{2\pi} \left(\omega^{n} - \frac{\varepsilon \Delta}{2\pi} \right) \text{ if } -\Delta \leq \phi^{n-1}(t; \tau_{r-1}^{n-1}) \leq 0 \\ = 0 & \text{otherwise} \end{cases}$$
(43)

for $t_{k_{r-1},2}^{n-1} \le t \le \tau_r^{n-1}$ ($\phi^{n-1}(t; \tau_{r-1}^{n-1}) = \phi^{n-1}(t)$ if r = 0). Likewise, from (38) we obtain

$$\inf\left\{\dot{\phi}^n(t):\tau_r^{n-1}\leq t\leq t_{k_r,2}^{n-1}\right\}=\omega^n-\frac{\varepsilon\Delta}{2\pi}$$

because $\phi^{n-1}(t; \tau_r^{n-1}) \leq 0$. Hence, see (40),

$$\dot{F}^{n}(t) \begin{cases} \geq \frac{N}{2\pi} \left(\omega^{n} - \frac{\varepsilon \Delta}{2\pi} \right) \text{ if } -\Delta \leq \phi^{n-1}(t; \tau_{r}^{n-1}) \leq 0 \\ = 0 & \text{otherwise} \end{cases}$$
(44)

for $\tau_r^{n-1} \le t \le t_{k_r,2}^{n-1}$. Altogether, (43) and (44) amounts to

$$\dot{F}^{n}(t) \begin{cases} \geq \frac{N}{2\pi} \left(\omega^{n} - \frac{\varepsilon \Delta}{2\pi} \right) & \text{if } t^{n-1}_{k_{r-1},2} \leq t \leq t^{n-1}_{k_{r}}. \end{cases}$$
(45)

Therefore, if $T = \min\{t_{k_{r_{\max}^1,2}}^1, t_{k_{r_{\max}^2,2}}^2, t_{k_{r_{\max}^3,2}}^3\}$ we conclude that

$$\dot{F}^{n}(t) \begin{cases} \geq \frac{N}{2\pi} \left(\omega^{n} - \frac{\varepsilon \Lambda}{2\pi} \right) \\ = 0 \end{cases} \quad \text{if } 0 \leq t \leq T \tag{46}$$

for n = 1, 2, 3.

Assume now that

$$\omega^n \ge \frac{\varepsilon \Delta}{2\pi} \tag{47}$$

for n = 1, 2, 3. It follows then from (46) that

$$\int_{t_{k_{r},2}^{n+1}}^{t_{k_{r+1,2}}^{n+1}}t\dot{F}^{n}(t)dt\geq 0$$

for every $[t_{k_{r},2}^{n+1}, t_{k_{r+1},2}^{n+1}] \subset [0,T]$. This proves by contradiction with (42) the necessity of (41) for the



Fig. 3: Phase transition in the Kuramoto order parameter. The network achieve full synchronization only when conditions of equation (41) hold. We also note that precisely at the boundary of inequality (41) the convergence of the dynamics is considerably slower. In fact, this was depicted in Figure 2: transient dynamics is 10 times slower than for both smaller and larger coupling ε .

oscillators $k \in \mathscr{G}_n$ with $\phi_k^n(0) \in [0, 2\pi - \alpha_n]$ to synchronize, hence, for full synchronization. \Box

Proposition 4 is an important prediction about the dynamics of the system, as it defines a critical coupling value $\varepsilon_c = 2\pi\omega^n/\Delta$ under which there cannot be full synchronization. In Figure 3 we show the phase transition from an unsynchronized (unordered) phase to a synchronized (ordered) phase obtained by simulations varying ω . Since $\Delta = 0.1 \times 2\pi$, then the necessary condition (41) becomes

$$\varepsilon > 10\omega^n$$
. (48)

Not only Figure 3 complies with this result, showing that $\varepsilon_c = 10\omega$ is a threshold point to synchronization, but we also have tested several values of Δ as well to actually verify that this condition holds (not shown).

Additionally, we note that near the critical coupling ε_c the oscillators always tend to delay its synchronization, going through a transient dynamics that may last up to ten times more than with values larger or smaller than ε_c . For instance, in Figure 2 we have shown the network exactly at the critical point $\varepsilon = \varepsilon_c = 10$. For networks set up with $\varepsilon = 8$ (see Figure 1) or $\varepsilon = 12$, for all initial conditions tested the transient dynamics did not last more than 100 time units, which is a quarter of the transient period shown in Figure 2 for $\varepsilon = 10$. This is completely unexpected, since usually the transient dynamics tend to subside quickly as a stronger coupling/inhibition takes place. This resembles notwithstanding effects seen in statistical physics models, in which at the edge of a phase transition several thermodynamics potentials and variables may diverge, as the time scales defining correlations among the units [48].



Fig. 4: Phase transition curve for a initial configuration of phases drawn from a truncated gaussian distribution, with mean 3.0 and variable variance σ^2 . The necessary condition (41) for full synchronization does not hold anymore: full synchronization is achieved for a lower ε than expected, showing that the initial phases distribution plays an important role in the mechanism of synchronization. As σ grows, the gaussian becomes more scattered and thus become similar to an uniform distribution. As σ grows the same results from the uniform initial distribution is regained.

6 Final considerations on the model

Most of our results are derived for a specific initial phases distribution, namely, an uniform distribution. To check if those results are robust to changes in this distribution, we have performed simulations with a truncated Gaussian in the interval $[0, 2\pi)$ with different values of variance. As a result, the critical coupling ε_c may change with the variance: as the variance grows, ε_c also grows. We show this effect in Figure 4. Naïvely, one can expect that with a lower variance in the distribution of initial conditions the oscillator phases would be already grouped together, thus needing a smaller coupling to achieve a higher level of synchronization. For a larger enough variance, the same results with uniform distribution are retrieved.

Finally, we have also briefly tested how noise affects the system, as it is one of the most important ingredients in real natural systems [49,50,51], and its effects on PRCs have been investigated in the past [52]. To account for a simple source of noise, we turned the equation (1) into the stochastic differential equation

$$\dot{\phi}_k^n(t) = \omega_k^n - \frac{\varepsilon}{N} F^{n-1}(t) + \sigma dW, \qquad (49)$$

where σdW is a Wiener process. This adds a white noise with variance σ^2 and zero mean, as shown in Figure 5 top. A slightly more complicated case is to add a small phase dependence on the noise [52], but we shall stick to the this simpler and more illustrative case. As result, the phase transition seems more smooth, although the inequality seems to still hold (see Figure 5 bottom). Such changes in the phase transitions are expected and usual in the dynamics of Kuramoto oscillators or excitable units [53].



Fig. 5: Top: the time evolution of a phase oscillator, without interaction, following Equation (49) with increasing values of σ . A vertical splitting was added to each case for easy identification. **Bottom:** Phase transition curve when the oscillators are in presence of noise. It is clear that the transition has become smoother, although inequality 41 seems to still hold.

7 Concluding remarks

In this study we have investigated how synchrony emerges in a simple analytical resetting model based on Kuramoto oscillators driven by strong inhibition. In particular, the oscillators are divided into three mutually inhibiting groups, mimicking a common architecture found in forebrain subcortical region (striatum). For small oscillations, we have shown in Proposition 4 a necessary condition for the full synchronization of all oscillators in each of these groups, also verified by simulations of a very similar model, slightly closer to realistic neurons connected by fast and strong inhibitory connections. With this necessary condition, we can predict what is the minimum coupling strength ε_c capable of generating a synchronous state, apparently robust to noise. We have also shown that the initial phase distribution may break down this necessary condition.

Similar studies also investigated in the past the effects of strong couplings. In particular, strongly excitatory phase resetting models, with a dissipative contribution in their dynamics (*e.g.*, leaky integrate-and-fire models), present synchronous states independently of the initial conditions and/or strength of their connections [54].

We believe our findings motivate the search for further rigorous results on networks of non-linear oscillators with strong couplings. This is the case, for instance, of a network consisted of conduction-based model neurons, interacting through non-linear couplings. A better understanding of such mechanisms may lead to important developments on our understanding of how synchronization takes place in the brain.

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References

- J. Buck, "Synchronous Rhythmic Flashing of Firefliex. II.," *The Quarterly Review of Biology*, vol. 63, no. 3, pp. 265–289, 1988.
- [2] A. T. Winfree, "Biological rhythms and the behavior of populations of coupled oscillators," *Journal of Theoretical Biology*, vol. 16, pp. 15–42, July 1967.
- [3] R. F. Galán, N. Fourcaud-Trocmé, G. B. Ermentrout, and N. N. Urban, "Correlation-induced synchronization of oscillations in olfactory bulb neurons.," *The Journal of neuroscience*, vol. 26, pp. 3646–55, Apr. 2006.
- [4] R. Laje and D. V. Buonomano, "Robust timing and motor patterns by taming chaos in recurrent neural networks.," *Nature neuroscience*, vol. 16, pp. 925–33, July 2013.
- [5] R. Latorre, C. Aguirre, M. I. Rabinovich, and P. Varona, "Transient dynamics and rhythm coordination of inferior olive spatio-temporal patterns.," *Frontiers in neural circuits*, vol. 7, p. 138, Jan. 2013.
- [6] R. F. Galan, "Cellular Mechanisms Underlying Spike-Time Reliability and Stochastic Synchronization: Insights and Predictions from the Phase-Response Curve," in *Phase response curves in neuroscience: theory, experiment, and analysis* (N. W. Schultheiss, A. A. Prinz, and R. J. Butera, eds.), vol. 6, pp. 237–255, New York, NY: Springer New York, 2012.
- [7] L. Brochini, P. V. Carelli, and R. D. Pinto, "Single synapse information coding in intraburst spike patterns of central pattern generator motor neurons.," *The Journal of neuroscience*, vol. 31, pp. 12297–306, Aug. 2011.
- [8] S. L. Hooper, Encyclopedia of Life Sciences. Chichester: John Wiley & Sons, Ltd, May 2001.
- [9] A. I. Selverston, M. I. Rabinovich, H. D. Abarbanel, R. Elson, A. Szücs, R. D. Pinto, R. Huerta, and P. Varona, "Reliable circuits from irregular neurons: A dynamical approach to understanding central pattern generators," *Journal of Physiology-Paris*, vol. 94, pp. 357–374, Dec. 2000.
- [10] G. B. Ermentrout and N. Kopell, "Multiple pulse interactions and averaging in systems of coupled neural oscillators," *Journal of Mathematical Biology*, vol. 29, pp. 195–217, Jan. 1991.



- [11] R. F. Galan, "The Phase Oscillator Approximation in Neuroscience: An Analytical Framework to Study Coherent Activity in Neural Networks," in *Coordinated activity in the brain: measurements and relevance to brain function and behavior* (J. L. P. Velazquez and R. Wennberg, eds.), vol. 2, pp. 65–89, New York, NY: Springer New York, 2009.
- [12] P. Goel and B. Ermentrout, "Synchrony, stability, and firing patterns in pulse-coupled oscillators," *Physica D: Nonlinear Phenomena*, vol. 163, pp. 191–216, Mar. 2002.
- [13] T. Krogh-Madsen, R. Butera, G. B. Ermentrout, and L. Glass, "Phase Resetting Neural Oscillators: Topological Theory Versus the Real World," in *Phase response curves in neuroscience: theory, experiment, and analysis* (N. W. Schultheiss, A. A. Prinz, and R. J. Butera, eds.), vol. 6, pp. 33–51, New York, NY: Springer New York, 2012.
- [14] E. M. Izhikevich, Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting. The MIT Press, 2010.
- [15] C. Canavier, "Phase response curve," *Scholarpedia*, vol. 1, no. 12, p. 1332, 2006.
- [16] R. M. Smeal, G. B. Ermentrout, and J. A. White, "Phaseresponse curves and synchronized neural networks.," *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, vol. 365, pp. 2407–22, Aug. 2010.
- [17] C. Canavier, R. Butera, R. Dror, D. Baxter, J. Clark, and J. Byrne, "Phase response characteristics of model neurons determine which patterns are expressed in a ring circuit model of gait generation," *Biological Cybernetics*, vol. 77, pp. 367–380, Dec. 1997.
- [18] S. A. Oprisan, V. Thirumalai, and C. C. Canavier, "Dynamics from a time series: can we extract the phase resetting curve from a time series?," *Biophysical journal*, vol. 84, pp. 2919–28, May 2003.
- [19] S. a. Oprisan, a. a. Prinz, and C. C. Canavier, "Phase resetting and phase locking in hybrid circuits of one model and one biological neuron.," *Biophysical journal*, vol. 87, pp. 2283–98, Oct. 2004.
- [20] E. M. Izhikevich, "Phase Equations for Relaxation Oscillators," *SIAM Journal on Applied Mathematics*, vol. 60, pp. 1789–1804, Jan. 2000.
- [21] R. Galán, G. Ermentrout, and N. Urban, "Efficient Estimation of Phase-Resetting Curves in Real Neurons and its Significance for Neural-Network Modeling," *Physical Review Letters*, vol. 94, p. 158101, Apr. 2005.
- [22] A. Lewy, "Clinical implications of the melatonin phase response curve.," *The Journal of clinical endocrinology and metabolism*, vol. 95, pp. 3158–60, July 2010.
- [23] R. J. Elble, C. Higgins, and L. Hughes, "Phase resetting and frequency entrainment of essential tremor," *Experimental Neurology*, vol. 116, pp. 355–361, June 1992.
- [24] R. G. Lee and R. B. Stein, "Resetting of tremor by mechanical perturbations: a comparison of essential tremor and parkinsonian tremor.," *Annals of neurology*, vol. 10, pp. 523–31, Dec. 1981.
- [25] P. A. Tass, "Desynchronization of brain rhythms with soft phase-resetting techniques.," *Biological cybernetics*, vol. 87, pp. 102–15, Aug. 2002.
- [26] P. A. Tass, "Desynchronizing double-pulse phase resetting and application to deep brain stimulation," *Biological Cybernetics*, vol. 85, pp. 343–354, Nov. 2001.

- [27] R. W. Thatcher, D. M. North, J. Neubrander, C. J. Biver, S. Cutler, and P. Defina, "Autism and EEG phase reset: deficient GABA mediated inhibition in thalamocortical circuits.," *Developmental neuropsychology*, vol. 34, pp. 780–800, Jan. 2009.
- [28] W. R. Gruber, W. Klimesch, P. Sauseng, and M. Doppelmayr, "Alpha phase synchronization predicts P1 and N1 latency and amplitude size.," *Cerebral cortex (New York, N.Y. : 1991)*, vol. 15, pp. 371–7, Apr. 2005.
- [29] J. Lewis, M. Bachoo, C. Polosa, and L. Glass, "The effects of superior laryngeal nerve stimulation on the respiratory rhythm: phase-resetting and aftereffects," *Brain Research*, vol. 517, pp. 44–50, May 1990.
- [30] S. Demir, R. Butera, A. DeFranceschi, J. Clark, and J. Byrne, "Phase Sensitivity and Entrainment in a Modeled Bursting Neuron," *Biophysical Journal*, vol. 72, pp. 579– 594, Feb. 1997.
- [31] L. J. Borg-Graham, C. Monier, and Y. Frégnac, "Visual input evokes transient and strong shunting inhibition in visual cortical neurons.," *Nature*, vol. 393, pp. 369–73, May 1998.
- [32] C. M. Root, K. Masuyama, D. S. Green, L. E. Enell, D. R. Nässel, C.-H. Lee, and J. W. Wang, "A presynaptic gain control mechanism fine-tunes olfactory behavior.," *Neuron*, vol. 59, pp. 311–21, July 2008.
- [33] S. E. Folias, S. Yu, A. Snyder, D. Nikolić, and J. E. Rubin, "Synchronisation hubs in the visual cortex may arise from strong rhythmic inhibition during gamma oscillations.," *The European journal of neuroscience*, vol. 38, pp. 2864–83, Sept. 2013.
- [34] C. Czeisler, R. Kronauer, J. Allan, J. Duffy, M. Jewett, E. Brown, and J. Ronda, "Bright light induction of strong (type 0) resetting of the human circadian pacemaker," *Science*, vol. 244, pp. 1328–1333, June 1989.
- [35] P. L. Lakin-Thomas, "Commentary: Strong or Weak Phase Resetting by Light Pulses in Humans?," *Journal of Biological Rhythms*, vol. 8, pp. 348–350, Dec. 1993.
- [36] Y. Kuramoto, *Chemical Oscillations, Waves, and Turbulence*. Dover Publications, 2003.
- [37] S. H. Strogatz, "From Kuramoto to Crawford: exploring the onset of synchronization in populations of coupled oscillators," *Physica D: Nonlinear Phenomena*, vol. 143, no. 1-4, pp. 1–20, 2000.
- [38] F. Rozenblit and M. Copelli, "Collective oscillations of excitable elements: order parameters, bistability and the role of stochasticity," *Journal of Statistical Mechanics: Theory and Experiment*, vol. 2011, p. P01012, Jan. 2011.
- [39] A. Ponzi and J. Wickens, "Sequentially switching cell assemblies in random inhibitory networks of spiking neurons in the striatum," *The Journal of neuroscience : the official journal of the Society for Neuroscience*, vol. 30, pp. 5894–911, Apr. 2010.
- [40] M. D. Humphries, R. Wood, and K. Gurney, "Reconstructing the three-dimensional GABAergic microcircuit of the striatum.," *PLoS computational biology*, vol. 6, p. e1001011, Jan. 2010.
- [41] C. V. Buhusi and W. H. Meck, "What makes us tick? Functional and neural mechanisms of interval timing.," *Nature reviews. Neuroscience*, vol. 6, pp. 755–65, Oct. 2005.
- [42] W. H. Meck, T. B. Penney, and V. Pouthas, "Cortico-striatal representation of time in animals and humans.," *Current* opinion in neurobiology, vol. 18, pp. 145–52, Apr. 2008.



- [43] M. B. Reyes, R. Huerta, M. I. Rabinovich, and A. I. Selverston, "Artificial synaptic modification reveals a dynamical invariant in the pyloric CPG.," *European journal* of applied physiology, vol. 102, pp. 667–75, Apr. 2008.
- [44] J. S. Kish, K. Shannak, and O. Hornykiewicz, "Uneven pattern of dopamine loss in the striatum of patients with idiopathic Parkinson's disease," *New England Journal of Medicine*, vol. 318, no. 14, pp. 876—880, 1988.
- [45] F. O. Walker, "Huntington's disease.," *Lancet*, vol. 369, pp. 218–28, Jan. 2007.
- [46] V. Ghiglieri, C. Sgobio, C. Costa, B. Picconi, and P. Calabresi, "Striatum-hippocampus balance: from physiological behavior to interneuronal pathology," *Progress in neurobiology*, vol. 94, pp. 102–14, July 2011.
- [47] I. Tristan, N. F. Rulkov, R. Huerta, and M. Rabinovich, "Timing control by redundant inhibitory neuronal circuits," *Chaos: An Interdisciplinary Journal of Nonlinear Science*, vol. 24, p. 013124, Mar. 2014.
- [48] K. Christensen and N. R. Moloney, *Complexity and criticality*. Imperial College Press, 2005.
- [49] R. B. Stein, E. R. Gossen, and K. E. Jones, "Neuronal variability: noise or part of the signal?," *Nature reviews*. *Neuroscience*, vol. 6, pp. 389–97, May 2005.
- [50] J. P. Sethna, K. A. Dahmen, and C. R. Myers, "Crackling noise.," *Nature*, vol. 410, pp. 242–50, Mar. 2001.
- [51] L. S. Tsimring, "Noise in biology.," *Reports on progress in physics. Physical Society (Great Britain)*, vol. 77, p. 026601, Feb. 2014.
- [52] B. Ermentrout and D. Saunders, "Phase resetting and coupling of noisy neural oscillators.," *Journal of computational neuroscience*, vol. 20, pp. 179–90, Apr. 2006.
- [53] B. Bag, K. Petrosyan, and C.-K. Hu, "Influence of noise on the synchronization of the stochastic Kuramoto model," *Physical Review E*, vol. 76, p. 056210, Nov. 2007.
- [54] R. E. Mirollo and S. H. Strogatz, "Synchronization of Pulse-Coupled Biological Oscillators," *SIAM Journal on Applied Mathematics*, vol. 50, pp. 1645–1662, Dec. 1990.
- [55] T. S. Mosqueiro, L. de Lecea and R. Huerta, "Control of sleep-to-wake transitions via fast amino acid and slow neuropeptide transmission," *New Journal of Physics*, vol. 16, pp. 115010, Nov. 2014.



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