

# Athermal dynamics of strongly coupled stochastic three-state oscillators

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We study the collective behavior of a globally coupled ensemble of cyclic stochastic three-state systems with transition rates from state  $i - 1$  to state  $i$  proportional to the number of systems already in state  $i$ . While the mean field theory predicts only decaying oscillations in this system, direct numerical simulations indicate that the mean field exhibits stochastic oscillations even in the limit of large number of oscillators. We characterize the regularity of oscillations by the coherence parameter which has a well-defined maximum at the coupling constant of order 1. In contrast, the order parameter characterizing the level of synchrony among oscillators, increases monotonously with the coupling strength. We derive the exact solution of the full master equation for the stationary probability distribution and find the analytical expression for the order parameter.

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Interacting stochastic systems emerge in a variety of physical and biological contexts, from arrays of Josephson junctions [1] and laser arrays [2] to neural networks [3, 4] and gene regulatory networks [5, 6]. While the dynamics of individual elements can be rather complicated and non-generic, the dynamics of a large ensemble of coupled units often exhibits universal behavior. Therefore, studies of canonical models with simple individual dynamics and interaction rules have proven very useful for understanding the behavior of specific systems. Well-known examples of such canonical systems are the Desai-Zwanzig model [7] of coupled bistable systems and the Kuramoto model [8] of coupled phase oscillators. The Kuramoto model and its many variations and generalizations (see [9]) have been very successful in describing the transition to coherent oscillations in ensembles of coupled phase oscillators. Stochastic dynamics of individual elements in such models are described by coupled nonlinear Langevin equations. In the thermodynamic limit, they can be reduced to low-dimensional deterministic equations for the mean field or the order parameter characterizing global behavior of large systems.

A simpler way of describing interacting stochastic systems incorporates stochastic elements with a discrete set of states with certain transition rates. It is most often done for bistable systems which are replaced by two-state stochastic systems with suitably chosen transition rates. For example, array-enhanced stochastic resonance has been studied in a system of globally coupled two-state systems [10]. A transition to regular oscillations in an ensemble of two-state systems coupled through a delayed mean field was studied in [11].

Recently, Prager *et al.* [12] introduced a globally coupled three-state stochastic “oscillators” with unidirectional ( $1 \rightarrow 2 \rightarrow 3 \rightarrow 1$ ) transitions as a paradigmatic model of noise-driven excitable systems. This model is simple enough to make analytical and large-scale numerical studies of large systems feasible [12, 13].

An important property is their behavior in the thermodynamic limit, when the number of units approaches infinity. Prager *et al.* [12] considered Markovian systems with transition rates depending on the suitably defined mean field and found no Hopf bifurcation in the thermodynamic limit. Instead, they found oscillations in this limit if the transitions between states are characterized by non-exponential waiting time distributions which imply non-Markovian dynamics. Later, Wood *et al.* [13] studied the dynamics of both globally and locally coupled Markovian three-state systems in the thermodynamic limit and did find a supercritical Hopf bifurcation to coherent periodic oscillations for strong enough coupling. While the individual systems considered in [12] and [13] were essentially identical, the difference between the models was in the way the coupling between the systems was introduced.

In this Letter we focus on the seemingly “less interesting” situation when a globally coupled ensemble of three-state systems *does not* exhibit a Hopf bifurcation in the thermodynamic limit. However, we find that in any finite-size system, quasi-regular oscillations of the mean field are present. We introduce the *coherence parameter* which characterizes regularity of mean field oscillations, and the *order parameter* which characterizes the degree of synchrony among the oscillators. We show that while the order parameter increases monotonously with the coupling strength, the coherence parameter has a maximum at a certain intermediate coupling strength. The simplicity and a high degree of symmetry in the system under study allow us to find the statistical properties of the finite ensemble analytically, however we expect similar behavior in ensembles of more general cyclic stochastic systems at strong enough coupling which do not exhibit Hopf bifurcation in the thermodynamic limit.

A *single stochastic three-state unit* with unidirectional transitions is schematically shown in the inset to Fig. 1b. We assume that in an isolated unit all three transitions from state  $i$  ( $i = 1, 2, 3$ ) to state  $i + 1 \pmod{3}$  are Marko-

vian with identical rate  $a$  [14]. Without loss of generality we take  $a = 1$ . Statistical properties of this system have been investigated in Ref. [12]. The cyclic behavior of a single oscillator is characterized by the mean time  $T$  of an oscillator to return to the initial state after an excursion through the other two states. Since the mean time of switching from state  $i$  to state  $i + 1$  is  $T_s = 1$ , we get  $T = 3T_s = 3$ . The probability for a system to be in state  $i = 1, 2, 3$  at time  $t$  is given by the continuous-time master equation

$$\dot{P}_i = -P_i + P_{i-1}, i = 1, 2, 3 \quad (1)$$

This master equation has a fixed point  $P_1^s = P_2^s = P_3^s = 1/3$  corresponding to equipartition among the three states, and three eigenvalues  $\lambda_k = -1 + e^{2i\pi k/3}$ ,  $k = 0, 1, 2$ . The first eigenvalue ( $k = 0$ ) corresponds to the conservation of the total probability, and the other two describe equilibration of the probability distribution among the three states. Imaginary part of these eigenvalues implies that there are decaying periodic oscillations of deviations from equipartition with the mean frequency  $\omega = \sqrt{3}/2$ .

*Globally coupled three-state oscillators.* Now let us consider an ensemble of  $N$  identical three-state oscillators. The specific mechanism of coupling is the following. We assume that the probability  $\pi_{i,i+1}$  of switching of an oscillator from a state  $i$  to state  $i + 1$  at time  $t$  is linearly proportional to the number of oscillators  $n_{i+1}(t)$  already at state  $i + 1$  at time  $t$ , with the proportionality constant  $b$  (which we call *coupling coefficient*),  $\pi_{i,i+1}(t) = 1 + b n_{i+1}(t)$ . This type of coupling is reminiscent of the auto-catalytic transitions in gene regulatory circuits when multiple copies of a single gene are present in the cell.

Since this model is Markovian, it can be efficiently simulated using Gillespie algorithm [15]. Figure 1 shows sample stochastic trajectories for the occupation number of oscillators in states 1, 2, and 3 as a function of time for different values of coupling parameter  $b$  for  $N = 1000$ . The initial condition for all cases is  $n_1(0) = N, n_{2,3}(0) = 0$ . For  $b = 0$ , the population slowly drifts toward an equilibrium state with  $n_1 = n_2 = n_3 = N/3$  with  $O(N^{1/2})$  stochastic fluctuations. For even very small non-zero  $b \ll 1$ , noisy oscillations around the mean become visible. As  $b$  grows, the period becomes shorter, and the amplitude of oscillations grows until for  $b \sim 1$  it approaches  $N$ , i.e. almost all oscillators are simultaneously in the same state. At large  $b \gg 1$ , the system exhibits switching behavior resembling the dynamics of a single oscillator. It is easy to understand: at very large  $b$ , once a single oscillator makes a transition from state  $i$  to state  $i + 1$  (which occurs with rate  $N$ ), all other oscillators quickly follow. So indeed in the limit  $b \gg 1$  the dynamics of the ensemble becomes equivalent to the dynamics of a single oscillator with a rescaled transition rate  $N$ , a result confirmed by analytical calculations [20].

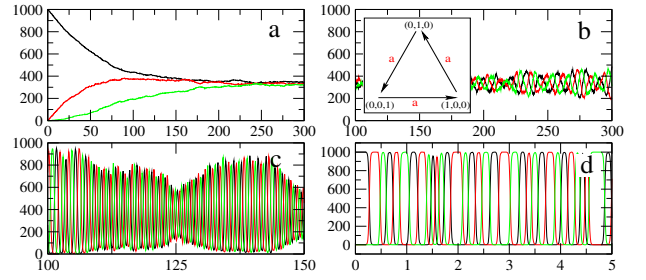


FIG. 1: Time series of the instantaneous occupation numbers oscillators  $n_1, n_2, n_3$  in states 1, 2, 3 respectively for  $N = 1000$ , and different values of the coupling parameter: (a)  $b = 0$ , (b)  $b = 0.1$  (Inset: Transition diagram in a single unit); (c)  $b = 1$ , (d)  $b = 10$ .

We computed the power spectrum of the time series of the occupation numbers and determined the central frequency  $\omega$  and the half-width  $\Delta\omega$  of the spectral peak. We call the ratio  $CP = \omega/\Delta\omega$  the *coherence parameter*. Figure 2a shows  $\omega, \Delta\omega$ , and  $CP$  as functions of the coupling parameter  $b$ . Both  $\omega$  and  $\Delta\omega$  increase with  $b$ , however the coherence parameter has a distinct maximum at a certain  $b$  which decreases with  $N$ , see Fig. 2a. Thus, we observe a manifestation of the *coherence resonance* [16], however the difference is that the maximum appears not at a certain noise strength but a certain value of the coupling.

This coherence resonance should not be confused with *synchronization* among the oscillators. The degree of synchronization can be characterized by the order parameter

$$R = \left\langle N^{-1} \left| \sum_{j=1}^N e^{i\phi_j} \right|^2 \right\rangle \quad (2)$$

with discrete phases of oscillators  $\phi_j = 2\pi k/3, k = 1, 2, 3$ . This order parameter was introduced by [13] by analogy with coupled continuum phase oscillators in the Kuramoto model [8]. The order parameter is zero when all oscillators are equally distributed among the three states ( $n_1 = n_2 = n_3 = N/3$ ), and it approaches unity if all oscillators are perfectly synchronized, so all of them are simultaneously in the same state. As expected, the order parameter increases monotonously with  $b$ , see Fig. 2b. As Figure 2b shows, the order parameter for a given  $b$  is *independent* of the number of oscillators in population  $N$ .

*Mean-field approximation.* In the thermodynamic limit  $N \rightarrow \infty$  of globally coupled oscillators, the mean-field equations for the deterministic “concentrations” of oscillators  $x_i = n_i/N$  are given by

$$\dot{x}_i = x_{i-1}(1 + bNx_i) - x_i(1 + bNx_{i+1}), i = 1, 2, 3(\text{mod}3) \quad (3)$$

From the symmetry of the underlying dynamics it immediately follows that the fixed point of this system is

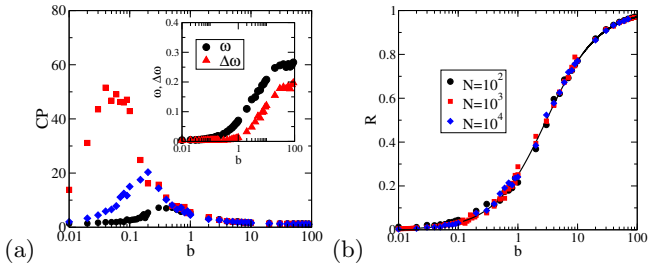


FIG. 2: Gillespie simulations of coupled stochastic oscillators: coherence parameter  $CP = \Delta\omega/\omega$  (a) and order parameter  $R$  (b) vs.  $b$  for  $N = 10^2, 10^3, 10^4$ . Solid line in (b) is (8). Inset: frequency  $\omega$  and bandwidth  $\Delta\omega$  vs.  $b$ .

$x_1 = x_2 = x_3 = 1/3$ . The associated two complex eigenvalues (the first eigenvalue is 0 as before because of the conservation law)  $\lambda_{2,3} = -\frac{3}{2} \pm i\sqrt{3}\left(\frac{1}{2} + \frac{bN}{3}\right)$  always have negative real part, which indicates the absence of Hopf bifurcation at any coupling  $b$ . This is in contrast with the model by Wood *et al.* [13], in which a different form of coupling was proposed (the transition rate from  $i$  to  $i+1$  was an exponential function of the linear combination of  $n_{i\pm 1}, n_i$ ), for which the mean field had a Hopf bifurcation at large enough coupling strength [17].

*Stochastic description.* The full description of the stochastic properties of the system is given by the master equation for the probability  $p(n_1, n_2, n_3)$  that at time  $t$  there are  $n_1$  oscillators at state 1,  $n_2$  at state 2, and  $n_3$  at state 3 (obviously,  $n_1 + n_2 + n_3 = N$ ),

$$\begin{aligned} \dot{p}(n_1, n_2, n_3) = & (n_1 + 1)[1 + b(n_2 - 1)]p(n_1 + 1, n_2 - 1, n_3) \\ & + (n_2 + 1)[1 + b(n_3 - 1)]p(n_1, n_2 + 1, n_3 - 1) \\ & + (n_3 + 1)[1 + b(n_1 - 1)]p(n_1 - 1, n_2, n_3 + 1) \\ & - [N + b(n_1 n_2 + n_2 n_3 + n_3 n_1)]p(n_1, n_2, n_3) \end{aligned} \quad (4)$$

The total number of states  $(n_1, n_2, n_3)$  in this system is  $(N + 2)(N + 1)/2$ . It is convenient to depict the state space as a triangular grid, see Figure 3a.

According to the Frobenius-Perron Theorem, the master equation has a unique stationary solution. We were able to find the exact solution in a closed form,

$$p_s(n_1, n_2, n_3) = C_b \frac{G(b, n_1)G(b, n_2)G(b, n_3)}{n_1!n_2!n_3!} \quad (5)$$

where  $G(x, n) = \prod_{k=0}^{n-1} (1 + kx)$  and  $C_b$  is the normalization constant, which can be verified by direct substitution. Expression (5) shows that the stationary solution is not only invariant with respect to cyclic permutations but also with respect to any permutation of coordinates  $(n_1, n_2, n_3)$ . This property is remarkable because the equation itself does not possess this symmetry.

It is easy to check by direct substitution that (5) satisfies the relation

$$(n_3 + 1)[1 + b(n_1 - 1)]p_s(n_1 - 1, n_2, n_3 + 1)$$

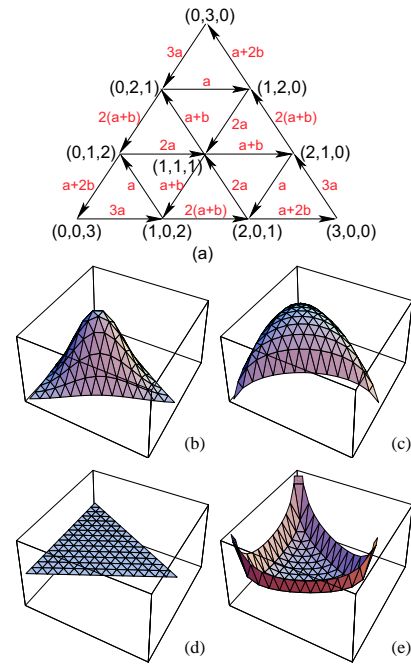


FIG. 3: (a) State space of the three-oscillator system  $N = 3$ ; correspond to distinct states  $(n_1, n_2, n_3)$  of the system, and arrows indicate transitions among the states. Expressions at the arrows show the corresponding transition rates. (b-e) Stationary probability distributions for  $N = 14$  and  $b = 0.2$  (b),  $b = 0.8$  (c),  $b = 1$  (d),  $b = 2$  (e).

$$= n_1(1 + bn_3)p_s(n_1, n_2, n_3) \quad (6)$$

and two other relations obtained from (6) by cyclic permutations (adding these 3 relations and using the rotation symmetry gives the stationary master equation (4) without l.h.s.).

It is straightforward to obtain convexity properties of the stationary solution (5). Indeed, according to (6), we have  $p_s(n_1 - 1, n_2, n_3 + 1) < p_s(n_1, n_2, n_3)$  iff  $0 < (n_3 + 1 - n_1)(1 - b)$ . If  $b < 1$  (resp.  $b > 1$ ) the probability increases (resp. decreases) when one moves one step to the right in the left part of the triangular lattice and vice versa [18]. Combining it with the rotation symmetry, we conclude that the distribution is convex with a maximum in the center when  $b < 1$  and concave with a maximum in the corners for  $b > 1$ ; for  $b = 1$  the distribution is flat.

For zero coupling ( $b = 0$ ), the stationary distribution is trinomial

$$p_s(n_1, n_2, n_3) = \frac{N!}{3^N n_1!n_2!n_3!}$$

which of course could be deduced directly since oscillators are independent and in the long term limit they become uniformly distributed among the three states. The most probable state is in the middle of the triangle ( $n_1 = n_2 = n_3 = N/3$ ) and the least probable states are in the corners  $(N, 0, 0), (0, N, 0), (0, 0, N)$ .

For large  $b$ , the stationary distribution is highly localized at the corners. However there is a small ( $O(1/b)$ ) probability flux in and out of the corners. In the first order of  $1/b$ , the stationary probability distribution is

$$p_s(n, 0, N - n) = \frac{N}{3bn(N - n)} + O(1/b^2), \quad n = 1, N - 1$$

$$p_s(0, 0, N) = \frac{1}{3} - \frac{2}{3b} \sum_{k=1}^{N-1} \frac{1}{k} + O(1/b^2)$$

(the remaining state probabilities follow from cyclic permutation) and  $p_s(n_1, n_2, n_3) = O(1/b^2)$  for  $n_1 n_2 n_3 \neq 0$ . Thus the probability distribution has a deep minimum at the center of the triangle, and sharp peaks in the corners (Fig. 3e). The dynamics close to equilibrium can be approximated by the probability flow around the edges of the triangle, ignoring the influence of the inner nodes. This simplification allows us to compute the non-zero eigenvalues of the full system in the first order in  $1/b$  [20]. As expected, for large  $b$  these eigenvalues are  $\lambda_k N + O(1/b^2)$ ,  $k = 1, 2$ , where  $\lambda_k$  are the eigenvalues of the single oscillator. It is interesting to note that the equilibration rate  $\text{Re}(-\lambda_{1,2}N)$  is independent of  $b$ .

For large  $n_1, n_2$  and  $n_3$  one can use Stirling formula to find an asymptotic expression for the distribution (5),

$$p_s(n_1, n_2, n_3) = C_b \frac{b^N}{\Gamma^3(1/b)} (n_1 n_2 n_3)^{1/b-1} \quad (7)$$

with  $C_b = b^{-N} \Gamma(3/b) \Gamma^{-2}(1/b) N^{1-2/b}$ . We can use this expression, replace summation by integration and compute the order parameter for large  $N$  explicitly [19]. This straightforward calculation results in a surprisingly simple formula

$$R = \frac{b}{b+3} \quad (8)$$

This formula agrees very well with direct Gillespie simulations (Fig. 2b). Note that the order parameter is independent of  $N$  (at least for large  $N$ ). For arbitrary  $N$ , the order parameter can be computed from the stationary distributions at zero coupling and large coupling respectively. For zero coupling, we get  $R = 1/N$  and for large coupling, we have  $R = 1 - \frac{3}{b}(1 - \frac{1}{N}) + O(1/b^2)$ .

*Discussion.* Our analysis indicates that the large systems of globally coupled three-state units exhibit significant stochastic oscillations, and while the frequency of these oscillations scales as  $N$ , their temporal coherence reaches maximum at a finite  $b \sim 1$  independent of the number of oscillators. This result is counterintuitive, since the mean-field theory predicts no sustained oscillations in the thermodynamic limit  $N \rightarrow \infty$ . The origin of this apparent contradiction is that for large coupling strength, nearly all oscillators are clustered in a single state, and other states are nearly empty, thus giving rise to strong stochasticity. For large  $b$ , *all* oscillators are strongly correlated: as soon as the first one makes a transition, others very quickly follow. This leads to the noisy

but correlated and thus athermal behavior of the globally coupled system at large  $b$ . Of course, in any real system the transition rate should saturate as  $N \rightarrow \infty$ . Then eventually the thermal behavior of the system would be recovered, however in the intermediate scaling regime of finite  $N$  the dynamics described here can be observed.

Our analytical results are easily generalizable to the case of arbitrary  $d$ -state oscillators with any  $d > 1$ . The order parameter for  $d$ -oscillators is simply  $R_d = b/(b+d)$ . For all  $d > 2$ , the coherence parameter reaches maximum at  $b \sim 1$ . However, two-state systems ( $d = 2$ ) are qualitatively different since for those the detailed balance condition is satisfied, and the probability current is zero. In this case, the quasi-regular oscillations are completely absent, and the coherence parameter remains small  $O(1)$  for any  $b$  (see [20] for more details).

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$[\Pi'(1/3) - 3\Pi(1/3)]/2$ , so the the Hopf bifurcation occurs only if the relative slope of the coupling function  $\Pi'(1/3)/\Pi(1/3)$  can exceed 3.

[18] The left part of the lattice corresponds to points for which  $n_1 \leq n_3 - 1$ .

[19] When  $N$  is large, the states  $(n_1, n_2, n_3)$  close to the edges, where the expression (7) is not valid, give a little contribution to the order parameter.

[20] See EPAPS Document No. [XX].