PHYSICAL REVIEW E **93**, 032202 (2016)

Marginal chimera state at cross-frequency locking of pulse-coupled neural networks

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(Received 27 November 2015; published 2 March 2016)

We consider two coupled populations of leaky integrate-and-fire neurons. Depending on the coupling strength, mean fields generated by these populations can have incommensurate frequencies or become frequency locked. In the observed 2:1 locking state of the mean fields, individual neurons in one population are asynchronous with the mean fields, while in another population they have the same frequency as the mean field. These synchronous neurons form a chimera state, where part of them build a fully synchronized cluster, while other remain scattered. We explain this chimera as a marginal one, caused by a self-organized neutral dynamics of the effective circle map.

DOI: 10.1103/PhysRevE.93.032202

I. INTRODUCTION

Studies of the dynamics of globally coupled populations of oscillators, pioneered more than 40 years ago by Winfree and Kuramoto [1], are the focus of current research due to numerous applications in diverse fields from physics to neuroscience, but also due to striking effects such as synchronization, collective chaos, and chimera states [2].

While typically ensembles of identical oscillators either fully synchronize or desynchronize, depending on whether the coupling is attractive or not, there are situations where oscillators produce a macroscopic mean field without full synchrony; such a regime is called partial synchronization [3,4] (see Ref. [5] for its experimental observation). Remarkably, partial synchronization can be explained within a simplest setup of one-dimensional oscillators, described either by their phase dynamics [4] or as integrate-and-fire units [3].

Quite recently, chimera states in populations of coupled oscillators attracted large interest. In the pioneering work by Kuramoto and Battogtokh [6] a coexistence of coherent and incoherent states in a lattice of nonlocally coupled oscillators has been reported, which can be understood as a symmetry breaking (where coherent, synchronized state is the symmetric one). A simpler setup for such a symmetry breaking has been suggested by Abrams *et al.* [7], who reported on chimera states in two coupled populations of identical units, where coupling inside and between populations was different. Generally, in this model quasiperiodic chimera states are observed [8], where one subpopulation is partially synchronized and another is completely synchronous. In Refs. [7,8] one-dimensional phase oscillators have been considered, similar to the original Kuramoto-Battogtokh example. In Ref. [9], two identical populations of one-dimensional leaky integrate-and-fire units, very similar to that introduced in Ref. [3], have been studied, and chimera states very similar to that in Ref. [7] have been observed: one population was fully synchronized while the other one was partially synchronous. For a recent review of the subject see Ref. [10]. Chimera states can be observed also in globally coupled, identical and identically driven units (however, not for one-dimensional phase models but in oscillators described by equation having order higher than one) [11].

It is instructive to compare symmetry properties of different setups where chimera states have been observed. The model of Kuramoto and Battogtokh [6] is formulated as a homogeneous one-dimensional lattice, symmetric with respect to spatial shifts $\theta_k \to \theta_{k+l}$. It possesses a spatially homogeneous synchronous state, and the chimera state can be considered as breaking of the spatial homogeneity. In setups treated in Refs. [7,9], one considers two subpopulations $\theta_k^{(1)}, \theta_k^{(2)}$ with different internal and mutual couplings. The system possesses symmetry with respect to exchange of subpopulations $1 \leftrightarrow 2$; it is also symmetric with respect to exchange of any two units inside each subpopulation $\theta_k^{(1,2)} \leftrightarrow \theta_j^{(1,2)}$. There is, however, no symmetry with respect to exchange of units between subpopulations. The chimera state here corresponds to breaking the symmetry between subpopulations $1 \leftrightarrow 2$, while the symmetry inside each subpopulation is unbroken (all the units in one subpopulation are synchronous, all the units in the other subpopulation are asynchronous and have the same properties). The driving forces acting on two subpopulations are different in the chimera state. The situation considered in Refs. [11] is a setup of globally coupled identical units. It is symmetric with respect to exchange of any two units $x_k \leftrightarrow x_j$. Here in the chimera state, one part of a unique, single population of identical oscillators synchronize and form a cluster, while the other remains asynchronous. Because of common driving, this regime requires self-induced bistability in the ensemble of identical, identically coupled oscillators. To the best of our knowledge, symmetry breaking within one single population of identical, identically coupled one-dimensional units (like phase oscillators and integrate-and-fire units) has not been reported.

In this paper we study mutual coupling of two populations of partially synchronous integrate-and-fire oscillators and find a surprising chimera state in this system: at mutual 2:1 locking of two macroscopic mean fields, elements of one ensemble form a cluster and a marginally stable scattered group. This means that nontrivial chimeras can happen in populations of identical, identically forced one-dimensional units (in previously observed chimeras [7,9] units where not identically forced). The main objective of our paper is to show this state and to explain how the mean field dynamics, yielding effective bistability in such ensembles, appears in a self-consistent way.

Before proceeding to description of the model, we mention that mutual influence of two or several populations of oscillators, generating macroscopic mean fields at significantly different frequencies, has been studied recently in the context of phase dynamics of Kuramoto model type [12]. Here we extend these studies to realistic neural models of integrate-and-fire neurons, which is applicable for explanation of cross-relations between brain waves. Indeed, in the brain one observes macroscopic oscillations in different frequency ranges [13], and these relatively regular mean fields are not related to exact synchrony of individual neurons, but rather to a temporal organization of their firing events. Thus, the model of partial synchronization we consider below appears more adequate for the neural dynamics than the Kuramoto model of phase oscillators.

II. THE MODEL

Our consideration of two neural populations is based on the model of globally coupled leaky integrate-and-fire oscillations, a prototypical example of generation of nontrivial mean fields due to partial synchronization [3]. One such population has been thoroughly studied in Refs. [3,14,15]. The potential x_k of each neuron (here $1 \leqslant k \leqslant N$, N is the size of the population) is described by the following equation:

$$\dot{x}_k = a - x_k + gE, \tag{1}$$

where the mean field E is composed by contributions from all the neurons,

$$\ddot{E} + 2\alpha\dot{E} + \alpha^2 E = \frac{\alpha^2}{N}\sum_{k,j}\delta(t - t_{k,j}). \tag{2}$$

The potential of neuron k grows from 0 to the threshold value 1, governed by the suprathreshold input current $a > 1$ and the excitatory action from the field E [Eq. (1)]. When this potential reaches 1 at a time instant $t_{k,n}$, the neuron fires, contributing a δ-function pulse to the field E [Eq. (2)], and is reset to 0. Linear Eq. (2) describes thus sequences of so-called α pulses created by the spiking neurons. As the analysis of system Eqs. (1) and (2) has shown (see Refs. [3,14,15] for details), for large values of the coupling parameter g (at given α) the neurons are desynchronized: the time intervals $t_{k,n} - t_{k-1,n}$ between successive firing events of two neurons are constant (do not depend on k), and the field E is nearly a constant (with small variations $\sim N^{-1}$). At some critical value of coupling g this regime becomes unstable, and the neurons start to form a group with a smaller interval between firings, as a result the mean field $E(t)$ demonstrates macroscopic nearly periodic variations [3,14]. This state is called partial synchronization because neurons never synchronize fully (never fire simultaneously). In fact, in this state the dynamics is, strictly speaking, quasiperiodic, because frequency of spiking of a neuron ω (it is the same for all neurons because they are identical) is incommensurate to the frequency of the macroscopic mean-field oscillations Ω.

In this paper we consider two interacting populations of neurons of the described type. Contrary to Ref. [9], where two identical populations have been considered, we study two different populations (while inside each population all the neurons are identical), therefore we use slightly changed notations: membrane potentials of the neurons in the populations will be denoted as x_k and y_k, while the mean fields generated by them as X and Y, respectively. Interaction is due to a mixture of the mean fields: on neurons x acts the field $E_x = (1-\varepsilon)X + \varepsilon Y$, while on neurons y acts the field $E_y = (1-\varepsilon)Y + \varepsilon X$. Parameter ε describes the coupling between populations. Equivalently, one can consider this setup as one with two acting mean fields (E_x, E_y), which are fed by spikes from two populations: each spike of a neuron x contributes a δ kick with amplitude $(1-\varepsilon)$ to the field E_x, and a δ kick with amplitude ε to the field E_y, and similarly for neurons y. The physical interpretation behind introducing parameter ε and considering two fields acting on two populations, is that the two populations of neurons are spatially separated, thus action inside each of them differs from the mutual action (for $\varepsilon < 1/2$ interpopulation action is weaker than the intrapopulation one). We will assume that both populations have equal number of neurons N. The equations of the model thus read

$$\dot{x}_k = a_x - x_k + g_x[(1-\varepsilon)X + \varepsilon Y], \tag{3}$$

$$\dot{y}_k = a_y - y_k + g_y[(1-\varepsilon)Y + \varepsilon X], \tag{4}$$

$$\ddot{X} + 2\alpha_x\dot{X} + \alpha_x^2 X = \frac{\alpha_x^2}{N}\sum_{k,n_x}\delta\big(t - t_{k,n_x}\big), \tag{5}$$

$$\ddot{Y} + 2\alpha_y\dot{Y} + \alpha_y^2 Y = \frac{\alpha_y^2}{N}\sum_{k,n_y}\delta\big(t - t_{k,n_y}\big). \tag{6}$$

Integration of these equations can be performed semianalytically (cf. Ref. [15]). Between the firings, equations for X, Y are linear and the solution can be written explicitly; substitution of these solutions to Eqs. (3) and (4) allows also for an analytic representation of $x_k(t)$, $y_k(t)$. This results in transcendent equations for determining the next firing time, which is solved numerically using the Newton's method.

III. CROSS-FREQUENCY LOCKING

In this section we focus on the effect of cross-frequency locking in two interacting populations. As has been already mentioned, one neural population demonstrates macroscopic mean-field oscillations with frequency Ω; two noninteracting populations will have generally different macroscopic frequencies Ω_x, Ω_y. We demonstrate now that the interaction can lead to a rather nontrivial regime of locking of these macroscopic oscillations (regimes of 1:1 locking of two symmetric populations of leaky integrate-and-fire units have been reported in Ref. [9]). In Fig. 1 we report on the frequencies of two neural populations for $a_x = 1.5$, $g_x = 0.35$, $a_y = 1.21$, $g_y = 0.09$, $\alpha_x = \alpha_y = 10$, $N = 50$. The figure shows the ratio of two macroscopic frequencies Ω_x/Ω_y as a function of the coupling constant ε. One clearly sees an interval of cross-frequency 2:1 locking for $\varepsilon \in [0.25; 0.33]$, here $\Omega_x = 2\Omega_y$. Outside of the resonant (locking) zone, a macroscopic quasiperiodic regime with an irrational ratio Ω_x/Ω_y is observed as illustrated by the phase portraits projections on plane (X, Y) in Fig. 2. One clearly distinguishes the locked state at $\varepsilon = 0.3$ from the quasiperiodic states at $\varepsilon = 0.2$ and $\varepsilon = 0.4$ on these Lissajous-type curves. Furthermore, outside of the resonant zone both populations x and y are partially synchronized: the states of all neurons are different, but distributed nonuniformly,

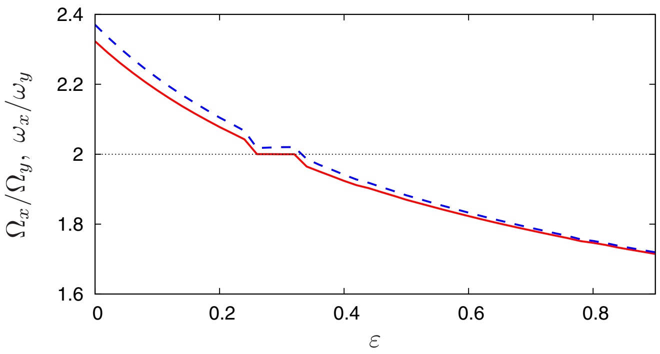

FIG. 1. Frequency ratios Ω_x/Ω_y(solid line) and ω_x/ω_y (dashed line). The 2:1 locking is observed for $\varepsilon \in [0.25; 0.33]$, but in this case ω_x/ω_y is not equal to 2.

producing macroscopic mean fields. Noteworthy, the state at $\varepsilon = 0.5$, where the same fields acts on two subpopulations, is also quasiperiodic.

The frequency locking of the mean fields X, Y does not mean that the individual neurons in two populations are also mutually locked. We illustrate the dynamics of individual neurons in Fig. 3 for $\varepsilon = 0.3$. Here we plot stroboscopic observations of one neuron from the population, at moments of time when $X = 1.5$ and $\dot{X} > 0$. One can easily compare the locking properties of two populations. In population x the states of the neuron are different, what indicates that its firing frequency ω_x is incommensurate with the frequency Ω_x of the mean field $X(t)$. In contradistinction to this, in population y all the states are the same (they take two values because, due to 2:1 locking, the mean-field X demonstrates two oscillations within one oscillation of the mean field Y) what means that neurons in this population are locked by the mean field $Y(t)$ and fire with the same period as the period of $Y(t)$, i.e., $\Omega_y = \omega_y$. This property explains the behavior of the ratio of firing rates of neurons plotted in Fig. 1: in the whole region where one observes locking 2:1 of the mean fields X, Y, the ratio ω_x/ω_y of the firing rates of the neurons remains also a constant, although not equal to 2, but slightly exceeds this value due to a small difference between ω_x and Ω_x.

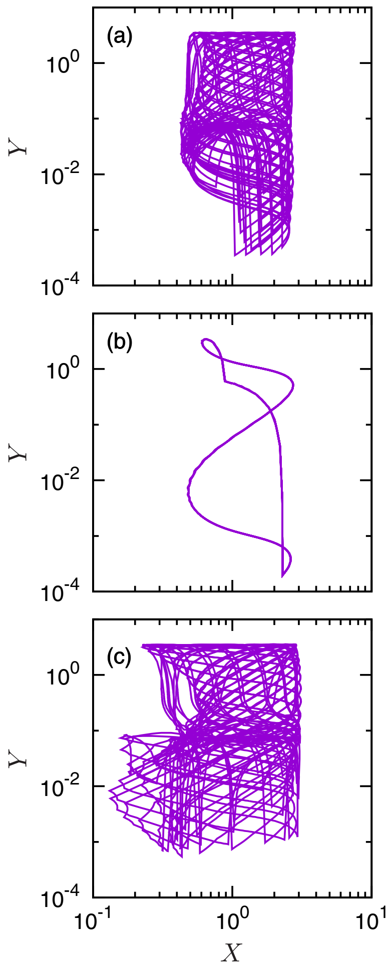

FIG. 2. Projections of the phase portraits on plane (X, Y) for $\varepsilon = 0.2$ (a), $\varepsilon = 0.3$ (b), and $\varepsilon = 0.4$ (c).

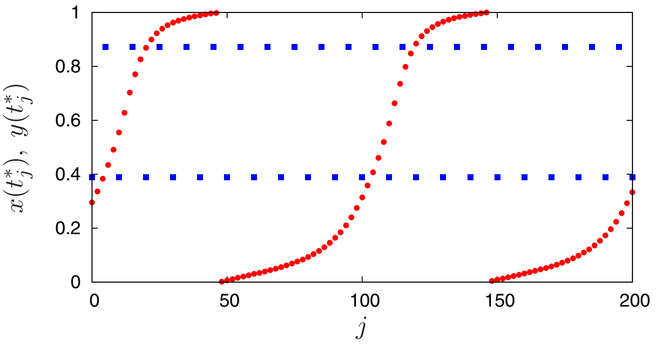

FIG. 3. Stroboscopic observations of the states of two oscillators in two populations, taken at $X(t_j^*) = 1.5$, $\dot{X} > 0$. Red circles, values $x(t_j^*)$; blue squares, values $y(t_j^*)$. Not all points are depicted for better visibility.

IV. MARGINAL CHIMERA STATE

Locking of the neuron states in ensemble y by the mean field acting on these neurons, at $\varepsilon = 0.3$, allows one to expect that these neurons form a fully synchronized cluster. Surprisingly, this is not the case. In Fig. 4(a) we plot the states of all neurons in two populations at a certain moment of time, in the locked regime $\varepsilon = 0.3$. In population x all the states are different, what corresponds to the fact that they are in a quasiperiodic mode of partial synchronization. Neurons in population y are in a chimera state: a part of them build a fully synchronized cluster $y_1 = y_2 = \ldots = y_m$, while all the neurons y_k, $k > m$, are distributed in some range.

Existence of a cluster manifests itself in a specific pattern of firing events in two populations. We illustrate it in Fig. 5, where we compare the situation with chimera [Fig. 5(b)] with the usual partial synchronization [Fig. 5(a)]. One can see that population y in the chimera state produces a "burst" of firing events, at the end of which all units in the cluster fire simultaneously (this happens at times $t \approx 1.44$ and ≈ 2.98; because the spikes overlap one cannot distinguish them on the figure). It is worth noting that here an ensemble of firing neurons operates as a "burster," contrary to the usual bursting

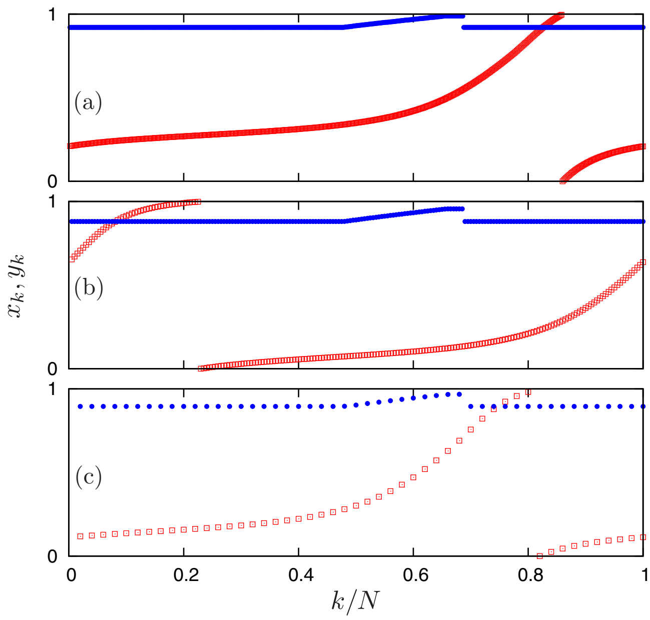

FIG. 4. Snapshots of states x_k (red open squares) and y_k (blue filled circles) in the 2:1 locked state for $\varepsilon = 0.3$ and different population sizes and transient times T_{tr}: (a) $N = 500$, $T_{\text{tr}} = 4.19\times10^8$; (b) $N = 200$, $T_{\text{tr}} = 1.67\times10^9$; (c) $N = 50$, $T_{\text{tr}} = 1.67\times10^9$. While all values of x_k are different, in population y part of the population forms a cluster.

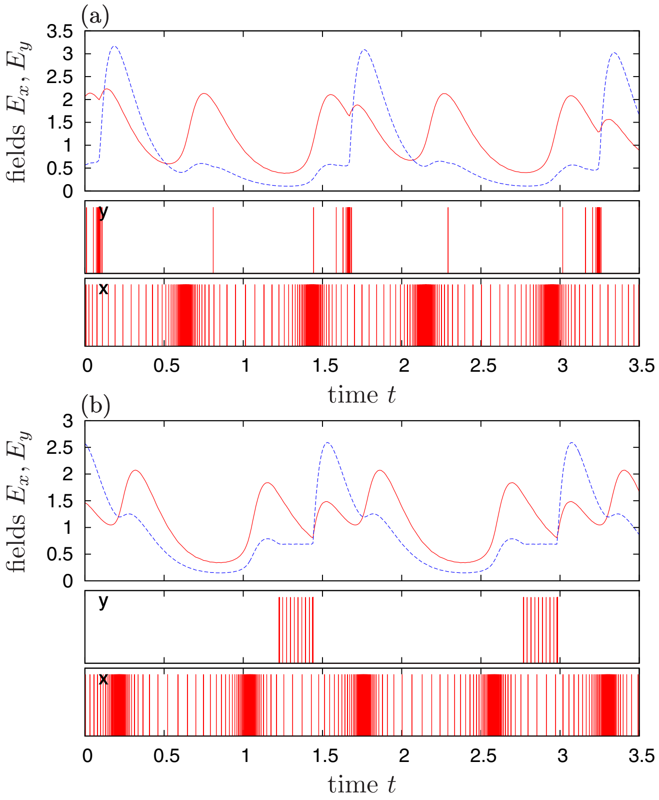

FIG. 5. Fields E_x (full line) and E_y (dashed line) and the firing events in both populations, for $N = 50$ and two values of coupling ε: (a) $\varepsilon = 0.2$, quasiperiodic nonlocked state without chimera; (b) $\varepsilon = 0.3$ locked state with chimera.

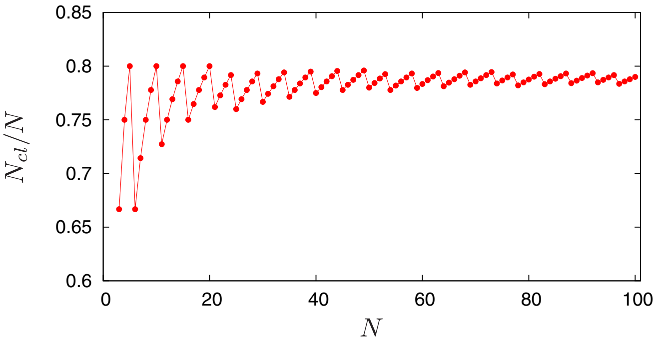

FIG. 6. Relative cluster size N_{cl}/N vs. the ensemble size N, for the same parameters as described in the caption of Fig. 4. The oscillators have been attributed to a cluster, if their states after transient time 5×10^6 were closer than 10^{-10} to each other.

where one neuron operating in a mixed-mode state produces patches of spikes interrupted by silent stages.

To check that this state is robust and not a transient, we have performed simulations with different ensemble sizes (from 50 to 500) and different integration times (up to 1.67×10^9), and in all cases observed the marginal chimera state. Two examples for $N = 200$ and $N = 500$ are presented in Figs. 4(b) and 4(a). Moreover, the same regime is observed if the sizes of populations x and y are different. Remarkably, the chimera state can be observed also for very small population sizes, starting from $N = 3$. For this minimal size for which chimera can be defined, in population y there are two units with equal states $y_1 = y_2$, and one unit different from them $y_3 \neq y_{1,2}$; in population x all three units are different. In Fig. 6 we show that the chimera states occur for all $3 \leqslant N \leqslant 100$, and the size of the synchronized cluster N_{cl} varies in the range $2/3 \lesssim N_{\text{cl}}/N \lesssim 4/5$. Furthermore, we have observed such a chimera state in the regime of 3:1 locking, at parameter values $a_x = 1.5$, $g_x = 0.36$, $a_y = 1.07$, $g_y = 0.05$, $\alpha_x = \alpha_y = 10$, $\varepsilon = 0.35$.

At first glance, a chimera state in a population of identical oscillators described by first-order equations [like Eqs. (3) and (4) of our model] is impossible. Indeed, in the case of a periodic forcing by mean fields $(X(t), Y(t))$, Eq. (4) for a neuron in population y reduces to a one-dimensional circle map, if a stroboscopic map is constructed from this first-order equation. This map is the same for all neurons in population y. According to general theory of one-dimensional circle maps, all neurons have the same frequency (because the rotation number of one-dimensional maps does not depend on initial conditions). Moreover, for general one-dimensional maps one has a dichotomy [16]: (i) either there is an equal number of unstable and stable periodic orbits, the latter attract all the points of the circle except for those lying exactly on unstable orbits; (ii) or the dynamics is quasiperiodic and reduces according to Denjoy's theorem to a shift on the circle, here all initially different states remain different. This dichotomy allows for quasiperiodic (partial synchronization) and fully synchronized regimes, but seemingly excludes chimera states.

In the dynamics of our two coupled populations we see, that the population y violates the dichotomy above. To clarify this point, we constructed a stroboscopic map $y(t_0) \to y(t_0 + T)$,

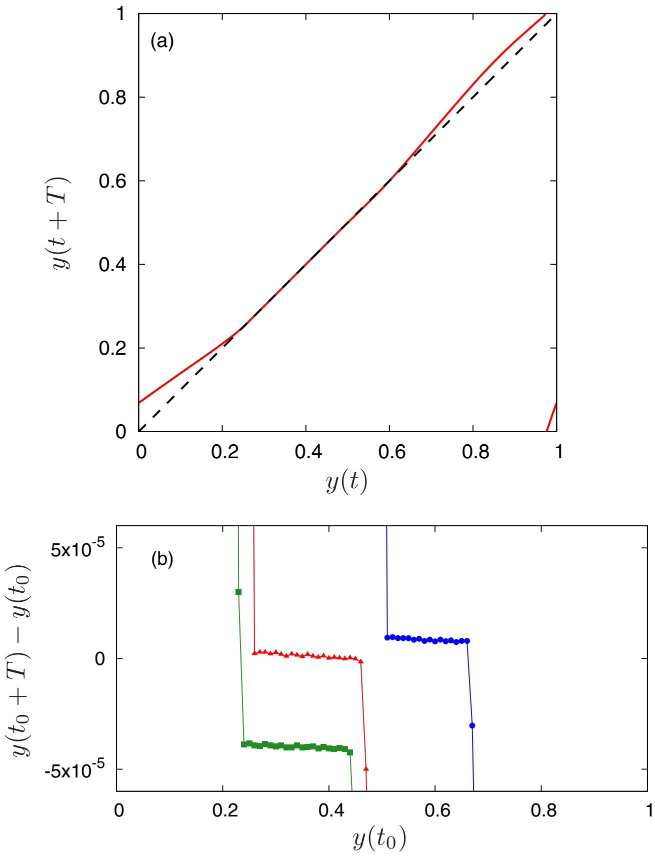

FIG. 7. (a) The stroboscopic map $y(t) \to y(t+T)$ for neurons in population y in the 2:1 locked regime for $\varepsilon = 0.3$. For the chosen phase of the mean field, in the region $0.25 \lesssim y \lesssim 0.45$ the map is nearly identity. This region is resolved in panel (b), where we plot values $y(t_0+T) - y(t_0)$ vs. $y(t_0)$ for different choices of t_0. Small vertical shifts are due to a tiny degree of qusiperiodicity in the fields $X(t)$, $Y(t)$.

where T is period of the field $Y(t)$ (Fig. 7) and $0 \leqslant y(t_0) < 1$. One can see that this map is not of general smooth type, as it has an interval (we call it marginal domain) where $y(t_0+T) \approx y(t_0)$ with high accuracy. This can be seen in Fig. 7(b), where the marginal domain is enlarged. Here the deviations $y(t+T) - y(t)$ are of order 10^{-5}. Moreover, these deviations fluctuate in sign, if the stroboscopic map is built at different phases t_0 of the mean fields $X(t_0)$, $Y(t_0)$. These fluctuations are due to the fact, that the fields $Y(t)$ is, strictly speaking, not exactly periodic. Indeed, due to quasiperiodicity of the population x, the fields $X(t)$, $Y(t)$ are quasiperiodic, although deviations from the pure periodicity are extremely small and are not seen in Fig. 2. This quasiperiodicity can, e.g., be seen if one at a given value of Y plots values of $\dot{Y}$, these are spread in a small interval. Due to this small spreading, the deviations from identity map fluctuate in the marginal domain.

Existence of the marginal domain, together with a complementary interval where $y(t_0+T) \neq y(t_0)$, explains the observed chimera state: those neurons that have initial conditions in the nonmarginal domain are attracted to one state and form a cluster, while those in the marginal domain remain scattered and form a "cloud." Noteworthy, the described nongeneral properties of the dynamics are not prebuilt to the system, but appear in a self-consistent manner, because the fields X, Y are composed from the contributions from individual neurons. Quite unexpectedly, these mean fields are self-organized in such a manner that one population is purely quasiperiodic, while another one combines properties of stable and marginal dynamics that results in a chimera.

V. CONCLUSION

In this paper we considered two populations of integrate-and-fire oscillators having definitely different frequencies of the generated mean fields. First we showed that due to mutual coupling, a 2:1 locking of the mean fields can be observed, without synchronization between the individual neurons. Noteworthy, neurons in two populations behave differently in the locked state: while in one population they are not synchronized by the mean field and have a different frequency, in another population the period of firings is the same as the basic period of the mean field. However, this synchronous state is rather nontrivial, and this is our second main result: identical neurons in the synchronous population build a chimera; one part of them forms an identical cluster, while other oscillators do not join this cluster and remain scattered. We explain this regime as a self-sustained marginal dynamics of the driven neurons: the corresponding stroboscopic one-dimensional map has a domain where this map is practically an identity. This marginality is possibly the only way to achieve a bistability in a one-dimensional map, as the period here must be independent of initial conditions. This is another peculiarity of the marginal chimera: in other cases where chimera has been observed in identical units, the frequencies of a cluster and a scattered populations were different [11].

ACKNOWLEDGMENTS

We acknowledge discussions with S. Olmi, A. Politi, and A. Torcini. M.B. was supported by ITN COSMOS (funded by the European Unions Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie Grant Agreement No. 642563). This work was supported by the Russian Science Foundation (Project No. 14-12-00811).

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