SIMILAR NONLEAKY INTEGRATE-AND-FIRE NEURONS WITH INSTANTANEOUS COUPLINGS ALWAYS SYNCHRONIZE[*]

WALTER SENN[†] AND ROBERT URBANCZIK[‡]

Abstract. We reconsider the dynamics of pulse-coupled integrate-and-fire neurons analyzed by Mirollo and Strogatz [*SIAM J. Appl. Math.*, 50 (1990), pp. 1645–1662]. Lifting their restriction to identical oscillators, we study the case of different intrinsic frequencies and thresholds of the neurons as well as different but positive couplings. For nonleaky neurons, we prove that generically the dynamics becomes fully synchronous for any initial conditions if the intrinsic frequencies, the thresholds, and the couplings are not too different. For the case of linear evolution functions, this confirms Peskin's conjecture (1975) according to which nearly identical pulse-coupled oscillators, in general, synchronize. It also shows that the requirement of concave evolution functions imposed by Mirollo and Strogatz to ensure global synchronization is not necessary.

Key words. synchronization, pulse-coupled biological oscillators, integrate-and-fire, pacemaker

AMS subject classifications. 92A09, 34C15, 58F40

PII. S0036139998346038

1. Introduction. Synchronization phenomena are widespread in nature. They occur in the rhythmic flashing of fireflies [7], in models of earthquake cycles [23], in arrays of Josephson junctions [16] or semiconductor lasers [32], in neuronal networks generating the circadian rhythm [11] or the pace of the heart [25], and in collective high frequency oscillations of cortical cells [28, 10, 21]. A rich collection of examples of biological oscillators and their synchronization is the book by Winfree [31]. For a review on synchronization phenomena of pulse-coupled oscillators, see Perez et al. [24], or the popular work of Strogatz and Stewart [26].

An adequate description of synchronization phenomena is often given by a population of mutually coupled oscillators which interact by short pulses. Pulse-coupling is contrasted to phase-coupling, where the oscillators smoothly interact during the whole oscillation cycle (see, e.g., [19]). In 1975 Peskin introduced a model of pulse-coupled oscillators for cardiac pacemaker cells and proved synchronization for two coupled oscillators [25]. The research activity was revived 15 years later when Mirollo and Strogatz succeeded to demonstrate global synchronization for this model with any number of oscillators [22]. Their analysis, however, is restricted to identical oscillators with equal weights, equal frequencies, and strictly concave evolution functions. We show that in fact none of these assumptions are necessary.

Peskin's model assumes N integrate-and-fire neurons of the form

$$(1.1) \qquad \frac{dx_i}{dt} = -\gamma x_i + I_i, \quad 0 \le x_i \le \theta_i \quad (i = 1, \ldots, N)$$

with input $I_i > 0$, threshold θ_i, and leakiness $\gamma \ge 0$. Whenever the activation of jth oscillator reaches or exceeds its threshold, $x_j \ge \theta_j$, the oscillator fires. As a

[†]Mathematical Institute, University of Bern, and Physiological Institute, University of Bern, Bühlplatz 5, CH-3012 Bern, Switzerland (wsenn@cns.unibe.ch).

[‡]Physiological Institute, University of Bern. Current address: Institute of Theoretical Physics, University of Würzburg (urbanczik@physik.uni-wuerzburg.de).

consequence of the firing of j, the activation of any other oscillator i is incremented by the coupling w_{ij} and immediately after firing the oscillator j is reset to zero. Moreover, the firing of j may have caused other oscillators to fire at the same instant as well, and subtleties arise in the definition of such an "instantaneous" interaction, especially if the couplings can be negative. The main feature of this class of models is that all oscillators which have fired synchronously have zero activation immediately after firing. In what follows, all couplings are assumed positive, $w_{ij} > 0$ for $i \neq j$, and for this case a simple characterization of the spike dynamics can be given (cf. (2.1) below).

Peskin conjectured that, first, for identical oscillators and almost all initial conditions "the system approaches a state in which all oscillators are firing synchronously" and that, second, "this remains true even when the oscillators are not quite identical" [25, p. 274]. While the first part of the conjecture was proven by Peskin for $N = 2$, Mirollo and Strogatz proved it for an arbitrary size by induction over N, as suggested by Peskin. Specifically, they proved global synchronization for a class of identical oscillators with strictly concave evolution functions which includes the above model under the restriction $\gamma > 0$ (strict concavity), $w_{ij} = \omega$, $I_i = I_0$, and $\theta_i = 1$. While their proof seems to be generalizable to small variations of the input I_i, the induction argument does not work anymore for small variations of the weights.

In trying to tackle the second part of Peskin's conjecture Kuramoto was able to show global synchronization in the limit of large populations and small couplings with identical oscillators subject to small noise [20]. We shall show that small variations in the input, weights, and thresholds can be treated rigorously for any size of population and any size of coupling if one considers the linear oscillator model with $\gamma = 0$ in (1.1). Specifically, for almost all inputs I_i, thresholds θ_i and weights w_{ij} which differ only slightly, the dynamics converges to synchronous firing for any initial conditions x. This is rather astonishing since the concavity is a key element in both of the cited works. Indeed, our method of proof is completely different from that of Mirollo and Strogatz as well as of Kuramoto. Our result differs from the findings of Mirollo and Strogatz in that for nonleaky neurons *almost all* networks with weak homogeneity converge for *all* initial conditions to synchronous firing, while in their work with identical neurons and concavity assumption the dynamics synchronizes for *all* parameter values only for *almost all* initial conditions. Interestingly, for nonleaky neurons the case of exactly identical oscillators and weights is exceptional in that it does not ensure full synchronization.

Numerical investigations of the model with slightly perturbed parameters performed by Bottani [3] actually show that often populations with strictly convex evolution function ($\gamma < 0$) of the neurons synchronize as well. In this case the neurons initially drift apart until they again come closely together, but now shifted by one cycle, and then synchronize. Once two neurons synchronize they stay together, form a "condensation point," and induce an avalanche of further synchronizations. Bottani also argues that networks of identical linear neurons should become fully synchronous for generic initial conditions in a suitably constructed thermodynamic limit. However, it seems very difficult to treat the two above cases rigorously.

A generalization of Peskin's model with $\gamma > 0$, equal weights, inputs, and threshold but with constant delays in the propagation of the pulses is numerically investigated in [12] and the case $N = 2$ is treated analytically. For positive delays and positive weights the synchronous state is found to be unstable while it is stable for positive delays and negative weights. Another model of pulse-coupled linear oscillators with a slightly different update rule which does not provide for synchronization is

investigated in [18] and [13]. For this type of model global convergence to a periodic state was shown under the severe homogeneity restriction that the sum of the weight onto each oscillator must be constant. The restriction is technically necessary in order to define a Liapunov function for the dynamics. Both the Liapunov function and the complete identity of the neurons in the case of Mirollo and Strogatz allow us to define a synchronization measure which monotonically decreases during the evolution of the dynamics. As soon as the homogeneity assumptions are violated, however, these standard techniques fail. The present work shows that global synchronization can nevertheless be proven by combinatorial arguments for a weakly heterogeneous ensemble of nonleaky neurons.

When considering more realistic biophysical models with a finite duration of the synaptic response the conditions for synchronization become even more intriguing [17]. In this case only local stability analysis of the synchronous [14, 8] or asynchronous state [2] can be performed. The local stability of the synchronous state turns out to be dependent on the rise and decay times of the synaptic responses. For two mutually coupled neurons with slow synaptic raise time it turns out that it is inhibition rather than excitation which leads to perfect synchronization [30, 27]. Different local stability criteria are known for weakly heterogeneous networks where the neurons and the connections might slightly vary [8]. In general, analytical work only seems feasible in the case of either two mutually connected neurons [4, 30, 27, 5] or in the case of an infinite number of weakly coupled neurons [19, 29], and often only local stability results have been obtained. In view of these difficulties and the wide range of different synchronization phenomena it is important to analytically study networks in the limit of instantaneous coupling and nonleaky integrate-and-fire neurons. As far as we know this is the only example where global convergence to a fully synchronized state can strictly be proven for weak network heterogeneities with an arbitrary finite number of neurons.

2. Dynamics and main theorem. Before discussing two illustrative examples we give an alternative, discrete definition of the dynamics. The formulation of the main theorem will be followed by an outline of the proof and an explanation of the inherent difficulties we have to cope with.

The dynamics. Since the dynamics in between spike events is of little interest, we shall consider a discrete description of the model (1.1) where a discrete time increment takes us from one instance when at least one neuron fires to the next such instance. For simplicity, we consider only the case of linear neurons ($\gamma = 0$). Given an $x \in \mathbb{R}^N$ with $0 \le x_i < \theta_i$, let $t(x)$ be the next time point when a neuron reaches threshold and let $V(x)$ be the set of neurons reaching threshold simultaneously with this neuron. Thus $x_i + I_i t(x) \le \theta_i$ for all neurons, and $i \in V(x)$ iff $x_i + I_i t(x) = \theta_i$ (and since at least one neuron has reached threshold $V(x) \ne \emptyset$). We shall call $V(x)$ the *trigger set*. The neurons in $V(x)$ spike at time $t(x)$, add some weights to the other neurons, and this may cause these to spike as well, perhaps leading to a chain reaction. Assuming the interaction to be instantaneous, we denote by $U(x)$ the set of all neurons which spike at time $t(x)$ and call this set the *spike set*. Immediately after time $t(x)$ the dynamics is in the state $\phi(x)$ given by

$$(2.1) \qquad \phi(x)_i = \begin{cases} 0 & , \ i \in U(x), \\ x_i + I_i t(x) + \sum_{j \in U(x)} w_{ij} & , \ i \notin U(x) . \end{cases}$$

Since all of the weights are positive, it is possible to define $U(x)$ without considering step by step the chain reaction. Let U be a set of neurons and assuming that the

neurons in U spike, we would immediately after time $t(x)$ have the state $\phi_U(x)$ given by $\phi_U(x)_i = 0$ for $i \in U$ and $\phi_U(x)_i = x_i + I_i\,t(x) + \sum_{j \in U} w_{ij}$ for $i \notin U$. For U to be an acceptable set, we require that for all indices $\phi_U(x)_i \in [0, \theta_i)$. Since the w_{ij} are positive, the intersection of acceptable sets is acceptable, and there is thus a unique minimal acceptable set and this is the spike set $U(x)$. Hence we have $\phi = \phi_{U(x)}$.

Since we are interested in the dynamics which results from iterating ϕ, we shall use the shorthand notation x^k for $\phi^k(x)$. Note that in particular $x^0 = x$ and x_i^k denotes the ith component of $\phi^k(x)$ with $k \in \mathbb{N}_0$. By the *trajectory* of x we refer to the sequence x^k $(k = 0, 1, \dots)$. We shall say that the *trajectory becomes periodic* if $x^k = x^{k+n}$ for a suitable n and all $k > k_0$ and that the trajectory of the point x becomes *fully synchronous* if $x_i^k = 0$ for all $i = 1, \dots, N$ and all $k > k_0$.

Two examples. To gain some insight into the possible behavior, let us first discuss the case of two neurons, $N = 2$. For simplicity assume that $\theta_i = I_i = 1$, for $i = 1, 2$; thus the fully synchronous state is stable under the dynamics. Considering an initial condition, $x_1 = 0$ and $0 < x_2 < 1$, neuron 2 will be the trigger. Further we either have $U(x) = \{1, 2\}$, and $\phi(x)$ is fully synchronous, or $\phi(x)_1 = 1 - x_2 + w_{12} < \theta_1 = 1$. In the latter case, for the next step we obtain that either x^2 is fully synchronous or $x_2^2 = x_2 - w_{12} + w_{21} < \theta_2$ and $x_1^2 = 0$. Therefore if $w_{12} = w_{21}$ we have that either already $\phi(x)$ is fully synchronous or $x^2 = x$, and the trajectory is periodic and asynchronous. However, if $w_{12} \neq w_{21}$ the distance between the neurons changes by $w_{12} - w_{21}$ until the trajectory eventually becomes fully synchronous. For two neurons with the above assumption the dynamics therefore becomes always fully synchronous unless the neurons have identical parameter values and the dynamics may be asynchronous with period 2. If the thresholds are unequal, say, $\theta_1 \leq \theta_2$, the fully synchronous state is locally stable iff $w_{21} \geq \theta_2 - \theta_1$. With the same arguments as above one shows that under this restriction the dynamics may be asynchronous and 2-periodic if $\theta_2 - \theta_1 = w_{21} - w_{12}$ while it becomes always fully synchronous otherwise.

For $N = 3$ much more complicated dynamics is possible. While our simulations indicate that for many choices of the parameters the fully synchronous state is globally attractive if it is locally stable, one can construct nontrivial examples where this is not true and complex periodic behavior arises. We again assume $\theta_i = I_i = 1$ (therefore the fully synchronous state is always stable) but construct a weight matrix with the property that if just two neurons are synchronous they will no longer spike synchronously when one of them spikes the next time unless full synchrony sets in. Let i, j, k be three different indices and consider the initial conditions $0 = x_i = x_j < x_k$. Therefore neuron k will spike and if another neuron spikes together with k, either the synchronization between i and j is broken or we have full synchrony. Therefore we need only consider the case $U(x) = \{k\}$ and then obtain $\phi(x)_i = 1 - x_k + w_{ik}$ and $\phi(x)_j = 1 - x_k + w_{jk}$. Assuming that $w_{ik} > w_{jk}$ we have that $V(\phi(x)) = \{i\}$. Now $j \notin U(\phi(x))$ is equivalent to $x_j^2 = 1 + w_{jk} - w_{ik} + w_{ji} < 1$. Consequently, if

$$w_{ik} > w_{jk} \Rightarrow w_{ji} < w_{ik} - w_{jk}$$

holds for any triple of different indices, any partial synchronization of just two neurons will be broken on the first or second iteration of the dynamics unless full synchrony is achieved.

A weight matrix satisfying the above conditions is given by

$$(2.2) \qquad 150\,w = \begin{pmatrix} 0 & 0 & 0 \\ 4 & 0 & 1 \\ 6 & 1 & 0 \end{pmatrix} + \tilde{w},$$
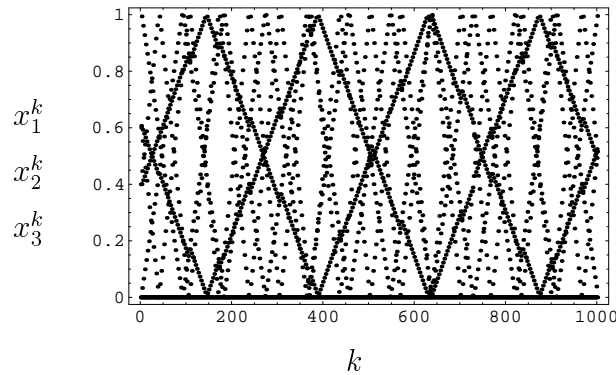
FIG. 2.1. *Superposition of the trajectories x_i^k of the 3 neurons $i = 1, 2, 3$ with weight matrix given by (2.2) and initial condition $x^0 = (0, 0, 0.4)$. The full trajectory of x^0 quickly becomes periodic but the period n is very long, $n = 729$ (see also Figure 2.2).*

where $\tilde{w}_{ij} = \sin^2(3i + j)/10$. Of course the choice of $\bar{w}$ is rather arbitrary. On the one hand, by including it in the definition of w, all w_{ij} are positive. More importantly, the choice ensures that the weights of w are rationally independent. This is motivated by the fact that our subsequent analysis yields that rational dependencies between the weights can give rise to exceptional behavior. Note that the first column of the weight matrix represents the weights from neuron 1 onto the others.

As a consequence of the construction of w the asymptotic behavior can be much more complicated than fully synchronous spiking. The trajectory, however, always seems to become periodic although the period can be quite long (cf. the conjecture in section 4). An example of this behavior for a specific choice of initial conditions is shown in Figure 2.1. The fact that such a nontrivial periodic behavior exists, even though the weights have no rational dependencies, is rather remarkable. The stabilizing mechanism which accounts for this is that information about the initial condition of a neuron is lost when it gets synchronized by another neuron. This is considered in more detail in Figure 2.2.

The main theorem. Since networks with more than just two neurons can exhibit complex behavior, our main goal is to give a condition on the parameters of the network which guarantees that the dynamics becomes fully synchronous. We shall show that in a fully connected network this is generically the case if the spiking of any neuron has a similar effect on the other neurons. To make this precise we require that for suitable parameters ω_j, ϵ_{ij} and u the following holds for any two different indices i, j:

$$(2.3) \qquad 0 < w_{ij} = \omega_j(1 + \epsilon_{ij}) \quad \text{with} \quad |\epsilon_{ij}| \le u.$$

Note that for small u the weights from one specific presynaptic neuron to all others are similar while they may be different form those from another presynaptic neuron. Abbreviating $\omega = \min_j \frac{\omega_j}{I_j}$, $\theta = \max_i \frac{\theta_i}{I_i}$, and $\triangle\theta = \max_i \frac{\theta_i}{I_i} - \min_i \frac{\theta_i}{I_i}$ we require $\triangle\theta \le \omega$ and u to be small in the sense that

$$(2.4) \qquad 0 \le 2\,u\,(\omega + \theta) + \triangle\theta \le \omega$$

must be satisfied. The condition roughly says that the fluctuation in the thresholds together with the fluctuations in the weights (of one neuron onto the others) must be
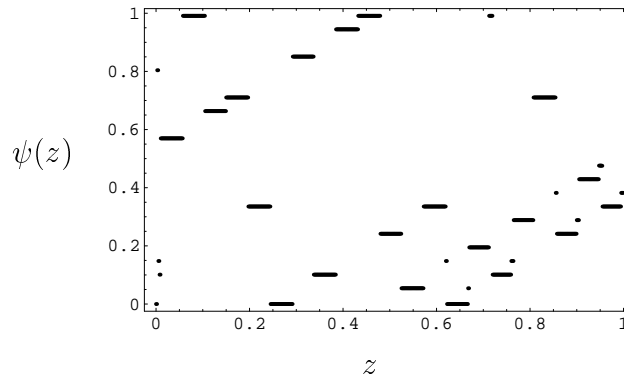
$\psi(z)$

FIG. 2.2. *For any initial condition with weight matrix given by* (2.2) *there seem to be infinitely many times at which neurons* 1 *and* 2 *spike synchronously. Thus setting* $x = (0, 0, z)$ *and* $x^k = (0, 0, \psi(z))$, *where* k *is the minimal natural number such that* $x_1^k = x_2^k = 0$, *yields the return map* ψ *plotted above. When a neuron is synchronized by another one, some information about its initial condition is lost and the return map* ψ *is piecewise constant. This stabilizing mechanism allows for complex periodic behavior.*

smaller than the weights themselves. Our main result then characterizes the generic dynamics of such networks.

Main theorem. *For almost all weights* w_{ij}, *thresholds* θ_i *and inputs* I_i *satisfying* (2.3) *and* (2.4), *the trajectory of any point* $x \in \mathbb{R}^N$ *with* $0 \le x_i \le \theta_i$ *becomes fully synchronous.*

Strategy of the proof. We will show that conditions (2.3) and (2.4) imply that any two neurons which spike synchronously at some point will do so in the future. The conditions ensure that the differences in the states of the neurons which build up due to fluctuations in the weights are absorbed when one of the two neurons spikes. The synchronization of two neurons constitutes irreversible progress towards full synchronization and we shall show that sufficiently many partial synchronizations must occur, except in cases where rational dependencies exist between the parameters of the network. That the weights of the network are different, however, has an important consequence for the techniques which may be used in the proof. Even if a pair of neurons i, j always spikes synchronously, it cannot be treated as a single particle. The reason for this is that, depending on what the remaining neurons do, the trigger of this particle may at some time be i and at other times be j and the "weight" onto this particle cannot be defined uniquely. This implies that induction over the number N of neurons as in the case of identical oscillators is no longer possible.

However, the fact that any two neurons which spike synchronously once continue to do so has an important consequence for the long term behavior of the trajectory: the set of neurons is partitioned into groups of neurons which always spike synchronously. A basic observation underlying our proof is that for such a trajectory, which we shall call a partition, the interaction between neurons which never spike simultaneously is largely unaffected by the complicated nonlinear synchronization effects. Hence the findings of the $N = 2$ case carry over to larger systems in the following sense: For generic parameters of the network a periodic partition is fully synchronous.

However, we still need to know that the trajectory does indeed become periodic. The main idea here is that since the state space is bounded, we can on any trajectory

find two different points x and y which are arbitrarily close. Since the points are close one can hope that $U(x) = U(y)$ and by analyzing the mapping ϕ one sees that then the iterates will be close as well. For partitions, we are thus able to show that $U(x^k) = U(y^k)$ for all k and sufficiently close points x,y on the trajectory. This yields that the sequence $U(x^k)$ is periodic, but we need to demonstrate that the sequence x^k becomes periodic. In fact it is possible to relate periodicity in the spike sets to periodicity in the firings.

The line of the proof leads backwards through these steps. In Lemma 3.1 we show that the periodicity of the spike trains leads to periodicity in the trajectory. Lemmas 3.2–3.4 show by means of a Lipschitz property for ϕ that, if the spike sets define a partition, the periodicity of the spike trains is implied. This allows us to directly conclude that a trajectory defining a partition will become periodic. Lemma 3.5 now shows that for almost all parameter values such a trajectory actually must become fully synchronous. It remains to show in Lemma 3.6 that the trajectory will eventually define a partition if the variation of the parameter values across the neurons is small.

3. Proof of the main theorem. From (2.1) one easily sees that by applying the rescaling

$$\hat{x}_i = x_i/I_i \,, \;\; \hat{\theta}_i = \theta_i/I_i \,, \;\; \hat{w}_{ij} = w_{ij}/I_i \,, \;\; \hat{I}_i = 1 \,,$$

one arrives at an equivalent dynamical system, and thus we henceforth assume $I_i = 1$. Using this convention the spike dynamics (2.1) may be written in the more explicit form as

$$(3.1) \qquad \phi(x)_i = x_i + \theta_{\alpha_x} - x_{\alpha_x} + \sum_{j \in U(x)} w_{ij}$$

for $i \notin U(x)$ and α_x in the trigger set $V(x)$. Setting $w_{ii} = 0$, we further have that the right-hand side (RHS) of (3.1) is greater or equal to θ_i iff $i \in U(x)$.

We shall say that the pair $(V(x), U(x))$ defines a *spike event* $S(x)$. To $S(x)$ we may associate a remapping S_x of the index set by defining

$$S_x(i) = \left\{ \begin{array}{ll} \alpha_x & , \; i \in U(x), \\ i & , \; i \notin U(x), \end{array} \right.$$

where α_x is an element of $V(x)$, e.g., the smallest one. In terms of this mapping, we can relate the values of ϕ on two points x and y which lead to the same spike event $(S(x) = S(y))$ by

$$\phi(x)_i - \phi(y)_i = \Delta_{S_x(i)} - \Delta_{\alpha_x}$$

for $\Delta = x - y$.

To analyze the dynamics in general, we need to introduce some further terminology. We call the sequence $S(x^k)$ $(k = 0, 1, \dots)$ the *spike train* of x and say that x and y have the *same spike train up to time n* if $S(x^k) = S(y^k)$ for $k = 0, \dots, n-1$. Assuming this and setting $\Delta = x - y$, by induction the iterates of x and y are related via

$$(3.2) \qquad x_i^n - y_i^n = \Delta_{\iota_{x,n}(i)} - \Delta_{\iota_{x,n}(\alpha_{x^{n-1}})},$$

where $\iota_{x,n} = S_x \circ S_{x^1} \circ \cdots \circ S_{x^{n-1}}$. In particular, independently of n we have the Lipschitz condition $|x^n - y^n| \le 2|\Delta|$, where $|.|$ denotes the maximum norm.

Further note that if an index i is not an image of $\iota_{x,n}$, the value of x^n will not be changed by fluctuations in the ith coordinate of x as long as these fluctuations do not alter the spike train. Therefore information about the initial condition x may be lost during the dynamics, and such a loss is of course irreversible: the number of images of $\iota_{x,n}$ cannot increase with n.

As a first step in analyzing the dynamics, we show that some properties of the trajectory can be inferred from the knowledge of its spike train. We shall say that a point x becomes *spike periodic* if $S(x^k) = S(x^{k+n})$ for a suitable period n and all $k > k_0$. An even weaker notion of periodicity will be useful in what follows as well. If only $U(x^k) = U(x^{k+n})$, for a suitable n and all $k > k_0$, we say that x becomes *weakly spike periodic*.

LEMMA 3.1. *If a point x is spike periodic, then its trajectory becomes periodic.*

Proof. Let the spike period of x be n. Setting $\iota = \iota_{x,n}$, due to spike periodicity we have $\iota_{x,kn} = \iota^k$ for any positive integer k, where ι^k is the k-fold composition of ι with itself. Since there are only finitely many mappings of the index set into itself, the sequence ι^k must become periodic. That is for suitable k_0 and m, $\iota^{k_0+lm} = \iota^{k_0}$ holds for any nonnegative integer l. Setting $\Delta = x^{mn} - x$ (3.2) yields that for any integer $l \ge 0$

$$x_i^{(k_0+(l+1)m)n} - x_i^{(k_0+lm)n} = \Delta_{\iota^{k_0}(i)} - \Delta_{\iota^{k_0}(\alpha_{x^{n-1}})}.$$

Since the above RHS is independent of l and the state space is bounded, this RHS must in fact vanish and the trajectory of x^{nk_0} is periodic. □

In the following we shall be interested in situations where certain groups of neurons always spike synchronously. We shall say that the trajectory of a point x is a *partition* if $U(x^k)$ and $U(x^n)$ are either identical or disjoint for any n and k in $\mathbb{N}_0$. For partitions a weaker version of the above lemma is available.

LEMMA 3.2. *If the trajectory of x is a partition and weakly spike periodic, then x becomes spike periodic.*

Proof. Let n be the period of the spike sets $U(x^k)$. Since the trajectory is a partition, the index mapping $\iota_{x,m}$ is constant on each set $U(x^l)$ with $l < m$. Due to the weak periodicity one may in fact lift the restriction on l when $m \ge n$, and in this case for any l and k there is a suitable α such that $\iota_{x^k,m}(i) = \alpha \in U(x^l)$ for all $i \in U(x^l)$.

As the number of spike trains of a given length is finite, we can find two different exponents k and k' such that x^k and $x^{k'}$ have the same spike train up to time n (and $k - k'$ will then be a multiple of n). We shall show that the spike trains of x^k and $x^{k'}$ must be the same for all times. Assume them to be the same up to some time $m \ge n$. By weak periodicity $U(x^{k+m}) = U(x^{k'+m})$, and now the remark in the preceding paragraph together with (3.2) yields that for a suitable α and any $i \in U(x^{k+m})$

$$x_i^{k+m} - x_i^{k'+m} = (x^k - x^{k'})_\alpha - (x^k - x^{k'})_{\iota_{x^k,m}(\alpha_{x^{k+m-1}})}.$$

The RHS is independent of i, and abbreviating it with δ, we have $x_i^{k+m} = x_i^{k'+m} + \delta$ for all $i \in U(x^{k+m})$. But this implies that the trigger sets of x^{k+m} and $x^{k'+m}$ are identical, $V(x^{k+m}) = V(x^{k'+m})$. Therefore the spike trains are the same up to time $m + 1$ and thus for all times. This means that the trajectory of x^k is spike periodic, with a period which may perhaps be larger than n. □

The following simple observation will repeatedly be useful in what follows. Let x and y be two points in $\mathbb{R}^2$ and assume that $x_1 \leq x_2$ but $y_1 \geq y_2$. Then $|x_1 - y_2| \leq |x - y|$ by the following case distinction:

$$
(3.3) \qquad \text{If } \begin{array}{ccc} x_1 & \geq & y_2, \\ x_1 & \leq & y_2, \end{array} \text{ then } \begin{array}{ccccc} 0 & \leq & x_1 - y_2 & \leq & x_2 - y_2 \\ 0 & \leq & y_2 - x_1 & \leq & y_1 - x_1. \end{array}
$$

LEMMA 3.3. *If the points x and y have the same spike sets up to time n, i.e., $U(x^l) = U(y^l)$ for $l = 0, \ldots, n-1$, then the Lipschitz condition $|x^n - y^n| \leq 2|x - y|$ holds.*

Proof. For $l = 0, \ldots, n$ we shall construct N dimensional vectors $\Delta^{(l)}$ and real numbers $\delta^{(l)}$ such that the differences between the two trajectories satisfy $x_i^l - y_i^l = \Delta_i^{(l)} + \delta^{(l)}$ and such that further the following relations hold:

$$
(3.4) \qquad x - y = \Delta^{(0)}, \quad |\Delta^{(l+1)}| \leq |\Delta^{(l)}|, \quad \text{and} \quad |\delta^{(l+1)}| \leq |\Delta^{(l)}|.
$$

For $l = n$ this immediately yields the lemma.

We proceed by induction and for the base case $l = 0$ we get $\delta^{(0)} = 0$. Fixing some $l > 0$ with $l < n$, we set $\alpha = \alpha_{x^l}$ and $\beta = \alpha_{y^l}$. If $i \notin U(x^l)$, since $U(x^l) = U(y^l)$ we have by (3.1)

$$
\begin{aligned}
x_i^{l+1} - y_i^{l+1} &= x_i^l - y_i^l + ((\theta_\alpha - x_\alpha^l) - (\theta_\beta - y_\beta^l)) \\
&= x_i^l - y_i^l - \delta^{(l)} + ((\theta_\alpha - x_\alpha^l + \delta^{(l)}) - (\theta_\beta - y_\beta^l))
\end{aligned}
$$

and thus set $\delta^{(l+1)} = (\theta_\alpha - x_\alpha^l + \delta^{(l)}) - (\theta_\beta - y_\beta^l)$ and $\Delta_i^{(l+1)} = \Delta_i^{(l)}$. If $i \in U(x^l)$, we set $\Delta_i^{(l+1)} = -\delta^{(l+1)}$ since $x_i^{l+1} - y_i^{l+1} = 0$. Thus the second inequality in (3.4) implies the first one.

To prove the second inequality, note that $(\theta_\alpha - x_\alpha^l + \delta^{(l)}) \leq (\theta_\beta - x_\beta^l + \delta^{(l)})$ since α is a trigger for x^l and $(\theta_\alpha - y_\alpha^l) \geq (\theta_\beta - y_\beta^l)$ since β is a trigger for y^l. Applying the observation (3.3) to the two inequalities then yields

$$
\begin{aligned}
|\delta^{(l+1)}| &\leq \max\{|-x_\alpha^l + \delta^l + y_\alpha^l|, |-x_\beta^l + \delta^l + y_\beta^l|\} \\
&= \max\{|\Delta_\alpha^{(l)}|, |\Delta_\beta^{(l)}|\} \leq |\Delta^{(l)}|. \qquad \square
\end{aligned}
$$

LEMMA 3.4. *If the trajectory of a point x is a partition, then x becomes weakly spike periodic.*

Proof. Set $w_{\min} = \min\{w_{ij} | i \neq j\}$. By boundedness of the state space, we can find two different exponents m and n such that $4|x^n - x^m| < w_{\min}$. We claim that $U(x^{n+k}) = U(x^{m+k})$ for all nonnegative integers k, i.e., that x becomes weakly spike periodic. Otherwise let $k \geq 0$ be minimal such that $U(x^{n+k}) \neq U(x^{m+k})$. We just need to show that $U(x^{n+k})$ and $U(x^{m+k})$ are not disjoint, thus violating the assumption that the trajectory is a partition. To lighten the notation set $y = x^{n+k}, \alpha = \alpha_y, z = x^{m+k}$, and $\beta = \alpha_z$. Further note that by the minimality of k we may apply Lemma 3.3 and obtain $2|y - z| < w_{\min}$. Since $\alpha \in U(y)$, we need only to prove that also $\beta \in U(y)$. Conversely, assume that $\beta \notin U(y)$; then from (3.1) we get $\theta_\beta > y_\beta + \theta_\alpha - y_\alpha + w_{\beta\alpha}$, and thus $w_{\min} < \theta_\beta - y_\beta - (\theta_\alpha - y_\alpha)$. Now

$$
\begin{aligned}
\theta_\beta - y_\beta - (\theta_\alpha - y_\alpha) &= z_\beta - y_\beta - ((\theta_\alpha - y_\alpha) - (\theta_\beta - z_\beta)) \\
&\leq |y - z| + |(\theta_\alpha - y_\alpha) - (\theta_\beta - z_\beta)|.
\end{aligned}
$$

To bound the second summand, note that the pairs $(\theta_\alpha - y_\alpha, \theta_\beta - y_\beta)$ and $(\theta_\alpha - z_\alpha, \theta_\beta - z_\beta)$ satisfy the preconditions of (3.3) since α is a trigger for y and β a trigger for z. Applying (3.3) yields that also $|(\theta_\alpha - y_\alpha) - (\theta_\beta - z_\beta)| \leq |y - z|$. Hence $\beta \notin U(y)$ implies $w_{\min} < 2|y - z|$ and this is impossible by the construction of y and z. □

LEMMA 3.5. *For almost all weights w_{ij}, any trajectory which is a partition and is periodic has period 1.*

Proof. First note that since the trajectory is a partition, for any index i there is a unique set $U(x^l)$ such that $i \in U(x^l)$ and we denote this set by U_i. One then has that $\iota_{x,l}(i) \in U_i$ and $\iota_{x,l}(\alpha_x) = \alpha_x$ for any $l \geq 0$.

The next step will be to show that for $l > 0$ the activation x_i^l can be written as

$$(3.5) \qquad x_i^l = x_{\iota_{x,l}(i)} - x_{\iota_{x,l}(\alpha_{x^{l-1}})} + W_i^{(l)} - W_{\alpha_{x^{l-1}}}^{(l)} + \Theta_i^{(l)}$$

with suitable $W_i^{(l)}$ and $\Theta_i^{(l)}$ from the following sets:

$$W_i^{(l)} \in \left\{ \sum_{j \in U_i} \sum_{k=1}^N m_{jk} w_{jk} \mid m_{jk} \in \mathbb{N}_0 \right\},$$

$$\Theta_i^{(l)} \in \left\{ \sum_{k=1}^N z_k \theta_k \mid z_k \text{ integer} \right\}.$$

In addition, if $i \notin U(x^{l-1})$, then $W_i^{(l)}$ can be chosen to be positive. For $l = 1$ the statements are an immediate consequence of (3.1). For the induction step first assume that $i \in U(x^l)$ and thus $\iota_{x,l+1}(i) = \iota_{x,l+1}(\alpha_{x^l})$. So $x_i^{l+1} = 0$ can be written in the form (3.5) by setting $W_i^{(l+1)} = W_{\alpha_{x^l}}^{(l+1)} = W_{\alpha_{x^l}}^{(l)}$ and $\Theta_i^{(l+1)} = 0$. For the case $i \notin U(x^l)$ we have $\iota_{x,l+1}(i) = \iota_{x,l}(i)$. Further $\iota_{x,l+1}(\alpha_{x^l}) = \iota_{x,l}(\alpha_{x^l})$, and by using (3.1) as well as (3.5) for x_i^l and $x_{\alpha_{x^l}}^l$ we obtain

$$x_i^{l+1} = x_{\iota_{x,l+1}(i)} - x_{\iota_{x,l+1}(\alpha_{x^l})} + W_i^{(l)} + \sum_{j \in U(x^l)} w_{ij} - W_{\alpha_{x^l}}^{(l)} + \Theta_i^{(l)} - \Theta_{\alpha_{x^l}}^{(l)} + \theta_{\alpha_{x^l}}.$$

We have already set $W_{\alpha_{x^l}}^{(l+1)} = W_{\alpha_{x^l}}^{(l)}$ and thus the induction step is completed by the assignments

$$W_i^{l+1} = W_i^{(l)} + \sum_{j \in U(x^l)} w_{ij} \quad \text{and} \quad \Theta_i^{(l+1)} = \Theta_i^{(l)} - \Theta_{\alpha_{x^l}}^{(l)} + \theta_{\alpha_{x^l}}.$$

Now assume that the period n of the trajectory is greater than 1. Then we can find an l such that $U(x^{l-1})$ and $U(x^l)$ are disjoint and we may assume that this is true for $l = n$. Further $\iota_{x,n}(\alpha_x) = \alpha_x$ and using $x_{\alpha_x}^n = x_{\alpha_x}$ (3.5) yields

$$0 = -x_{\iota_{x,n}(\alpha_{x^{n-1}})} + W_{\alpha_x}^{(n)} - W_{\alpha_{x^{n-1}}}^{(n)} + \Theta_{\alpha_x}^{(n)}.$$

Further since $U(x^{n-1})$ and $U(x^n)$ are disjoint, $\alpha_x \notin U(x^{n-1})$, and so we may assume that $W_{\alpha_x}^{(n)} > 0$. Now $\iota_{x,n}(\alpha_{x^{n-1}}) \in U_{\alpha_{x^{n-1}}} = U(x^{n-1})$, and thus by periodicity we have $x_{\iota_{x,n}(\alpha_{x^{n-1}})} = 0$. Therefore the above equation means that the numbers $\{w_{jk} \mid j \in U(x), k = 1, \ldots, N\}$ are rationally dependent on $\{w_{jk} \mid j \in U(x^{n-1}), k = 1, \ldots, N\} \cup \{\theta_k \mid k = 1, \ldots, N\}$. □

LEMMA 3.6. *The conditions* (2.3) *and* (2.4) *imply that any neurons which spike synchronously at some time will always spike synchronously in the future, i.e., for all* $p, l_0 \geq 0$ *the relation* $x_i^{l_0} = x_j^{l_0} = 0$ *implies that* $x_i^{l_0+p} = 0 \Leftrightarrow x_j^{l_0+p} = 0$.

Proof. Assuming $l_0 = 0$ and $x_i = x_j = 0$, let p_i (p_j) be the smallest natural number such that $x_i^{p_i} = 0$ ($x_j^{p_j} = 0$).

If $p_i > p_j$, using (3.1) to compute x^{p_j}, we obtain that for a suitable nonnegative t

$$\theta_j \leq t + W_j \qquad \text{where } W_j = \sum_{n=0}^{p_j-1} \sum_{m \in U(x^n)} w_{jm},$$

$$(3.6) \qquad \theta_i > t + w_{ij} + W_i \text{ where } W_i = -w_{ij} + \sum_{n=0}^{p_j-1} \sum_{m \in U(x^n)} w_{im}.$$

In particular, since $w_{jj} = 0$, for suitable $m_k \geq 0$ we have $W_j = \sum_k m_k w_{jk}$ and $W_i = \sum_k m_k w_{ik}$. As p_j is the smallest number such that $j \in U(x^{p_j-1})$ we may assume that $m_j = 0$, and we may further assume $m_i = 0$ since $p_i > p_j$. Using the representation of the weights given in (2.3) this means that $W_i, W_j \in [\lambda(1 - u), \lambda(1 + u)]$ for some nonnegative λ. The second inequality in (3.6) allows us to upper bound λ by $\lambda < \theta_i/(1 - u)$. Combining the two inequalities in (3.6) yields $t + w_{ij} + W_i - \theta_i < t + W_j - \theta_j$ and thus $w_{ij} < |W_i - W_j| + |\theta_i - \theta_j| \leq 2u\lambda + |\theta_i - \theta_j|$. Using that $\omega_j(1 - u) < w_{ij}$ and the upper bound on λ we obtain that $p_i > p_j$ implies $\omega_j(1 - u) < 2u(\max_k \theta_k)/(1 - u) + \max_k \theta_k - \min_k \theta_k$.

Conversely

$$(3.7) \qquad \omega_j \geq \frac{\max_k \theta_k - \min_k \theta_k}{1 - u} + \frac{2u \max_k \theta_k}{(1 - u)^2} \quad \text{for } j = 1, \dots, N$$

implies that $p_i \geq p_j$ and since this holds for all indices, it implies $p_i = p_j$. Condition (2.4) is just a more readable and more restrictive form of condition (3.7). □

We may now prove the following version of our main theorem.

THEOREM 3.7. *For almost all weights satisfying* (2.3) *and one of the conditions* (2.4) *or* (3.7), *the trajectory of any point x becomes fully synchronous.*

Proof. According to Lemma 3.6 the conditions imply that two neurons which spike synchronously once will do so in the future, and thus for any positive integer k either $U(x^l) \cap U(x^{l+k}) = \emptyset$ or $U(x^l) \subseteq U(x^{l+k})$. Since there are finitely many neurons, from some l_0 onward all such inclusions must be equalities; that is, the trajectory of x^{l_0} is a partition. By Lemma 3.4 such a trajectory becomes weakly spike periodic, by Lemma 3.2 it becomes spike periodic, and by Lemma 3.1 it actually becomes periodic. Given the thresholds, for almost all weights this period now has length 1 according to Lemma 3.5 and this means that all neurons will eventually spike synchronously. □

4. Discussion. One motivation of the present work was Peskin's second conjecture according to which nearly identical pulse-coupled oscillators become fully synchronous. It turns out that, although somewhat unexpected after the work of Mirollo and Strogatz, this conjecture is correct for linear neurons ($\gamma = 0$ in (1.1)). The conjecture still remains to be proven, however, for leaky integrate-and-fire neurons ($\gamma > 0$). Although the concavity has an additional synchronizing effect it changes the situation for a proof drastically. This is reflected in the structure of the exceptional set: while with $\gamma > 0$ and identical oscillators the population synchronizes for all parameters but

only for almost all initial conditions [22], it synchronizes with $\gamma = 0$ only for almost all similar parameters but for all initial conditions. Nevertheless, by using perturbative arguments, it might be possible to extend our results to leaky neurons in the case that the magnitude of γ is small compared to the fluctuations of the network parameters.

An interesting question is whether for some other values of the parameters the dynamics can be chaotic. For $\gamma = 0$, our analysis suggests that this is not the case and that the trajectory of any point x will eventually become periodic. Note that the number of images of $\iota_{x,n}$ cannot increase with n and it is reasonable to assume that the cases where this number does not shrink to 1 correspond to periodic behavior and rational dependencies of the parameters. If it does shrink to 1, however, x is contained in a region in which all points have identical long term behavior. If there are only finitely many such regions, the dynamics must again become periodic. Thus we conjecture that *a network of nonleaky pulse-coupled integrate-and-fire neurons with arbitrary positive weights, thresholds, and inputs will always converge to periodic firing for any initial conditions*; neither chaos nor quasiperiodicity is possible. This is certainly true for a network of two neurons but remains to be proven for $N \geq 3$. The corresponding conjecture for *leaky* integrate-and-fire neurons is shown to be true for a pair of neurons with identical positive weights and identical thresholds but different speeds [4].

In view of the different synchronization and phase-locking phenomena encountered in cortical measurements (see [10, 9] for references) it would be challenging to characterize such periodic states and to focus onto patterns of partial synchrony. For leaky integrate-and-fire neurons first steps in this direction are done by identifying parameter regimes with partially synchronized, periodic, or quasi-periodic firing patterns [1, 29, 15, 6]. The current model which may be prototypical for excitatory networks with fast synaptic responses and weak leakiness suggests that these networks have a tendency to periodic firing and, in particular, to full synchrony if the network heterogeneity is weak.

<div align="center">REFERENCES</div>

[1] L. F. ABBOTT, *A network of oscillators*, J. Phys. A, 23 (1990), pp. 3835–3859.
[2] L. F. ABBOTT AND C. VAN VREESWIJK, *Asynchronous states in networks of pulse-coupled oscillators*, Phys. Rev. E (3), 48 (1993), pp. 1483–1490.
[3] S. BOTTANI, *Pulse-coupled relaxation oscillators: From biological synchronization to self-organized criticality*, Phys. Rev. Lett., 74 (21) (1995), pp. 4189–4192.
[4] A. BRAILOVE, *The dynamics of two pulse-coupled relaxation oscillators*, Int. J. of Bifurcation and Chaos, 2 (1992), pp. 341–352.
[5] P. BRESSLOFF AND S. COOMBES, *Desynchronization, Mode Locking, and Bursting in Strongly Coupled Integrate-and-Fire Oscillators*, Phys. Rev. Lett., 81 (1998), pp. 2168–2171.
[6] P. BRESSLOFF AND S. COOMBES, *Spike train dynamics underlying pattern formation in integrate-and-fire oscillator networks*, Phys. Rev. Lett., 81 (1998), pp. 2384–2387.
[7] J. BUCK, *Synchronous rhythmic flashing of fireflies. II*, Quart. Rev. Biol., 63 (1988), pp. 265–289.
[8] C. CHOW, *Phase-locking in weakly heterogeneous neuronal networks*, Phys. D, 118 (1998), pp. 343–370.
[9] E. DOMANY, J. L. VAN HEMMEN, AND K. SCHULTEN, EDS., *Models of Neural Networks II, Temporal Aspects of Coding and Information Processing in Biological Systems*, Springer-Verlag, Berlin, 1994.
[10] A. K. ENGEL, P. KÖNIG, A. K. KREITER, T. B. SCHILLEN, AND W. SINGER, *Temporal coding in the visual cortex: New vistas on integration in the nervous system*, Trends in Neurosci., (1992), pp. 218–226.
[11] J. T. ENRIGHT, *Temporal precision in circadian systems: A reliable neuronal clock from unreliable components?*, Science, 209 (1980), pp. 1542–1545.
[12] U. ERNST, K. PAWELZIK, AND T. GEISEL, *Delay-induced multistable synchronization of biolog-*

ical oscillators, Phys. Rev. E (3), 57 (1998), pp. 2150–2162.

[13] W. Gerstner, *Rapid phase locking in systems of pulse-coupled oscillators with delays*, Phys. Rev. Lett., 76 (1996), pp. 1755–1758.

[14] W. Gerstner, J. L. van Hemmen, and J. D. Cowan, *What matters in neuronal locking*, Neural Computation, 8 (1996), pp. 1653–1676.

[15] D. Golomb and J. Rinzel, *Dynamics of globally coupled inhibitory neurons with heterogeneity*, Phys. Rev. E (3), 60 (1999), pp. 4810–4811.

[16] P. Hadley, M. Beasly, and K. Wiesenfeld, *Phase-locking of Josephson-junction series arrays*, Phys. Rev. B, 38 (1988), pp. 8712–8719.

[17] D. Hansel, G. Mato, and C. Meunier, *Synchrony in excitatory neural networks*, Neural Computation, 7 (1995), pp. 307–337.

[18] A. V. M. Herz and J. J. Hopfield, *Earthquake cycles and neural reverberations: Collective oscillations in systems with pulse-coupled threshold elements*, Phys. Rev. Lett., 75 (1995), pp. 1222–1225.

[19] Y. Kuramoto, *Chemical Oscillations, Waves and Turbulence*, Springer-Verlag, New York, 1984.

[20] Y. Kuramoto, *Collective synchronization of pulse-coupled oscillators and excitable units*, Phys. D, 50 (1991), pp. 15–30.

[21] K. MacLeod and G. Laurent, *Distinct mechanisms for synchronization and temporal patterning of odor-encoding neural assemblies*, Science, 274 (1996), pp. 976–979.

[22] R. E. Mirollo and S. H. Strogatz, *Synchronization of pulse-coupled biological oscillators*, SIAM J. Appl. Math., 50 (1990), pp. 1645–1662.

[23] Z. Olami, *Self-organized criticality in a continuous, nonconservative cellular automaton modeling earthquakes*, Phys. Rev. Lett., 68 (1992), pp. 1244–1247.

[24] C. Pérez, A. Corral, A. Díaz-Guilera, and K. C. and A. Arenas, *On self-organized criticality and synchronization in lattice models of coupled dynamical systems*, Int. J. of Modern Physics B, 10 (1996), pp. 1111–1151.

[25] C. S. Peskin, *Mathematical Aspects of Heart Physiology*, Courant Institute of Mathematical Science, New York University, New York, 1975.

[26] S. H. Strogatz and I. Stewart, *Coupled oscillators and biological synchronization*, Scientific American, 269 (1993), pp. 102–109.

[27] D. Terman, N. Kopell, and A. Bose, *Dynamics of two mutually inhibitory neurons*, Phys. D, 117 (1998), pp. 241–275.

[28] R. D. Traub, R. Miles, and R. K. S. Wong, *Model of the origin of rhythmic population oscillations in the hippocampal slice*, Science, 243 (1989), pp. 1319–1325.

[29] M. Tsodyks, I. Mitkov, and H. Sompolinsky, *Pattern of synchrony in inhomogeneous networks of oscillators with pulse interactions*, Phys. Rev. Lett., 71 (1993), pp. 1280–1283.

[30] C. van Vreeswijk, L. Abbott, and G. Ermentrout, *When inhibition not excitation synchronizes neural firing.*, J. Comp. Neurosci, 1 (1994), pp. 313–322.

[31] A. T. Winfree, *The Geometry of Biological Time*, Springer-Verlag, New York, 1980.

[32] H. Winful and S. Wang, *Stability of phase locking in coupled semiconductor laser arrays*, Appl. Phys. Lett., 53 (1988), pp. 1894–1896.