Contractive piecewise continuous maps modelling networks of inhibitory neurons.

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Abstract

We consider piecewise continuous maps on a compact region of a finite dimensional manifold, that separates the distances between the different continuity pieces but are locally contractive. We prove that generically those maps are assympthotically periodic, having a finite number of persistent limit cycles. We apply this result to prove that a generic network of more than two inhibitory neurons phase lock to a periodic behaviour that persists under small perturbations of the set of parameter values.

1 Introduction

We study the mathematical model of a network composed with $n \geq 3$ inhibitory neurons. We consider each neuron's dynamic modelled as an integrate and fire cell [SFH 1972]. The neuron acts as a relaxation oscillator in which the internal variable $V = V(t)$ describing its potential evolves linearly, increasing on time t with a constant slope. This means that $V(t)$ is linear with positive first derivative $V'(t) > 0$ that is constant. When the potential reaches a given threshold value, fixed as 1, the neuron produces an action potential which, through inhibitory synapses, acts on the other $n-1$ neurons producing sudden negative changes of their respective potentials. The amplitude s of each change is an increasing function of the phase f of the respective neuron on which it acts.

In [BCRG 1996] we reduced networks of n inhibitory neuron cells, modelled as relaxation oscillators of the integrate and fire type [SFH 1972], to the dynamic of its Poncaré map, a contractive piecewise continuous map in a compact set of $n-1$ dimensions. For a seek of completeness we include an overview of the steps of this reduction in section 2 of this paper.

The dynamical system modelling the network is translated mathematically to a system of iterates of a map F in a compact connected set B of $\mathbb{R}^n$. This map F is discontinuous but *piecewise continuous*, i.e. the phase space can be partitioned into a finite number of pieces such that the map F restricted to each piece is continuous (and differentiable, if desired, of class C^r). The map F is also *locally contractive*, i.e. when restricted to each continuous piece F contracts

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distances in the space. If besides the n neurons of the network are not very different, then F verifies the *separation property*, i.e. the images of the compact pieces are pairwise separated by a positive minimum distance. In the last section of this paper we prove the main abstract mathematical result (Theorem 3.7) in which is based the rest of the paper:

Contractive piecewise continuous maps with the separation property generically exhibit an asymptotic periodic behavior with limit cycles that are persistent under small perturbations of the map.

As a consequence we obtain the following applied result:

Generic neuron networks composed by $n \geq 3$ inhibitory cells of the integrate and fire type, which are not very different each from the others, phase lock to a periodic behavior that is persistent under small perturbations of the set of parameter values.

This is a result generalizing the conclusions obtained for two neurons networks in [BTCE 1991] and [CB 1992].

2 The mathematical model of the inhibitory neurons network.

We include here an overview of the mathematical reduction of the model of the n inhibitory neurons network to a piecewise continuous contractive map $F : B \mapsto B$ with the separation property, as shown in [BCRG 1996].

The state of the system at time t is described as a point

$$v(t) = (V_1(t), \ldots, V_n(t)) \in Q$$

depending on t, where $V_i(t)$ is the potential level at time t of the i-th. neuron, and $Q = [0,1]^n$ is the n-dimensional cube.

Let B be the set of points in the n faces of the cube Q where at least one of the potentials V_i is zero. Analogously, let us call A the set of points in the n faces of the cube Q where at least one of the potentials V_i is one. Each of the sets A and B are compact and described with $n-1$ variables, so are $n-1$ dimensional sets in Q.

From an initial state $v(0) = v_0$ in B the system evolves linearly through trajectories inside Q that are parallel lines, until they reach (may be each trajectory at a different time) the set A. We define the transformation

$$\rho : B \mapsto A, \quad \rho(v_0) = v_1 : v(0) = v_0 \in B, \; v(t_1) = v_1 \in A,$$

where t_1 is the first non negative time such that $v(t_1) \in A$.

Definition 2.1 We define the metric (i.e. distance) $d(v_0, w_0), d(v_1, w_1)$ between points v_0, w_0 in B, or v_1, w_1 in A, as the distance between the parallel line trajectories $v(t)$ and $w(t)$ such that $v(0) = v_0$ and $w(0) = w_0$.

For three neurons this distance is the usual distance in the proyection of the three dimensional cube along a fixed direction. This projection is the hexagon of figure 1. In other words the distance is the usual one in the hexagon.

With this definition we have

Remark 2.2 The transformation $\rho : B \mapsto A$ is an isometry, i.e.

$$d(\rho(v_0), \rho(w_0)) = d(\rho(v_0, w_0))$$

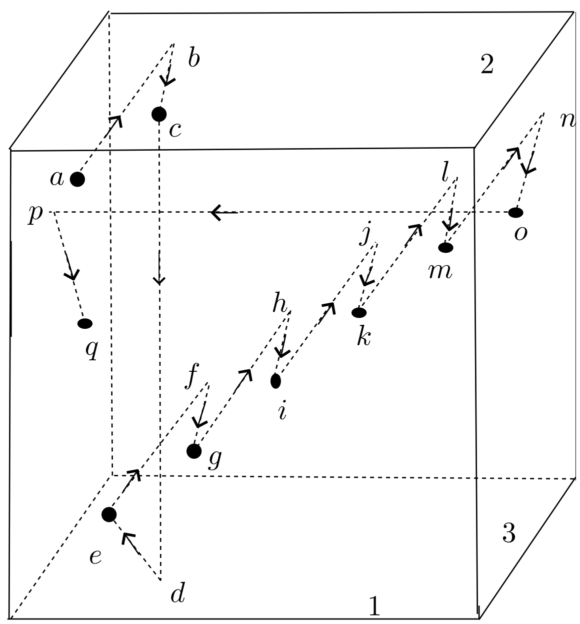
Definition 2.3 The set B is partitioned in n subsets $B_1, \dots, B_n$ where

$$B_j = \rho^{-1}(\{v_1 = (V_1, \dots, V_n) \in A : V_j = 1\})$$

In other words, the subset $B_j \subset B$ is the set of initial states in the faces B of the cube Q, such that the first neuron to reach the threshold level 1 (when the trajectory evolves to reach the faces A) will be the j-th. neuron.

In figure 1 the three sets B_1, B_2 and B_3 are the three backward faces of the cube (the faces that could not be seen if the cube were not transparent).

Figure 1: Model of a 3 neurons network in the 3-dimensional cube: Reaching the threshold level of neurons 1,2 and 3 corresponds to the front faces 1, 2 and 3 respectively of the cube. Points marked in black correspond to the linear evolution from backward faces to the front faces. This is the evolution of the system between two consecutive fires of the neurons. It is a line seen, due to perspective, as a black point. Firing of neurons 1, 2 or 3 correspond to the return lines from the respective front face to its parallel backwards face; for instance $a \mapsto b, c \mapsto d, e \mapsto f, \dots, o \mapsto p$. Due to the negative synapses the firing of each neuron produces a reduction of the voltage of the others. The synapses effect corresponds to segments along the same backward face; for instance $b \mapsto c, d \mapsto e, f \mapsto g, \dots, p \mapsto q$. The figure shows the evolution after 8 fires of the neurons 1,2,1,1,1,1,1 and 3.



We observe that the subsets B_j have pairwise disjoint interiors but their frontiers may intersect.

Due to synapses, when $v_0 \in B_j$, the state $v(t)$ reaches A because the j-th. neuron reaches the threshold level 1, it then suddenly changes to 0 and produces a negative change s_i in the other $n-1$ neurons potentials V_i $(i \neq j)$, being s_i larger when the potential V_i is larger.

Definition 2.4 We define the map

$$\gamma : A \mapsto B : \gamma(v_1) = v_2, \quad \text{where} \ \ v_1 = (V_1, \ldots, V_{j-1}, 1, V_{j+1}, \ldots, V_n) \in \rho(B_j) \subset A,$$

and

$$v_2 = (V_1 - s_1, \ldots, V_{j-1} - s_{j-1}, \ldots, 0, V_{j+1} - s_{j+1}, \ldots, V_n - s_n)$$

where $s_j = s_j(V_j)$ is increasing.

We note that γ is discontinuous in the frontier of each subset $\rho(B_j)$ but is continuous in each piece $\rho(B_j)$.

For two different points v_1, w_1 in $\rho(B_j) \subset A$ we have:

$$v_1 = (V_1, \ldots, V_{j-1}, 1, V_{j+1}, \ldots, V_n), \quad w_1 = (W_1, \ldots, W_{j-1}, 1, W_{j+1}, \ldots, W_n)$$

To $v_1 \neq w_1$ correspond two different points $v_2 \neq w_2$ in B through the map γ as follows:

$$v_2 = \gamma(v_1) = (V_1 - s_1, \ldots, V_{j-1} - s_{j-1}, 0, V_{j+1} - s_{j+1}, \ldots, V_n - s_n)$$

$$w_2 = \gamma(w_1) = (W_1 - u_1, \ldots, W_{j-1} - u_{j-1}, 0, W_{j+1} - u_{j+1}, \ldots, W_n - u_n)$$

where $(s_1, \ldots, s_n)$ and $(u_1, \ldots, u_n)$ are the sudden changes in the $n-1$ neurons potentials $V_i, \ i \neq j$, produced by the threshold level 1 changing to 0 of the firing neuron j.

Without no loose of generality we take $W_i > V_i$. Then $u_i > s_i$ and

$$0 < (W_i - u_i) - (V_i - s_i) = (W_i - V_i) - (u_i - s_i) < W_i - V_i$$

Then $d(\gamma(v_1), \gamma(w_1)) < d(v_1, w_1)$ and therefore:

Remark 2.5 The map $\gamma : A \mapsto B$ is piecewise continuous, and in each continuity piece $\rho(B_j) \subset A$ it is contractive, i.e.

$$d(\gamma(v_1), \gamma(w_1)) < d(v_1, w_1), \quad \forall v_1, w_1 \in \rho(B_j)$$

Definition 2.6 The Poincaré map is the first return map from B to B defined as follows:

$$G : B \mapsto B : \ G = \gamma \circ \rho$$

The second return map from B to B is

$$F = G \circ G$$

From 2.2 and 2.5 we deduce the following result:

Remark 2.7 The Poincaré map $G : B \mapsto B$ is a contractive piecewise continuous map. The second return map $F : B \mapsto B$ is a contractive piecewise continuous map.

The reason for considering the second return map F instead the first one G is that it may occur that $G(B_i) \cap G(B_j) \neq \emptyset$ for some $i \neq j$ and so G does not necessarily verify the separation property. Let us show that, if the neurons are not very different each from others (i.e. the synapsis $s_i, i = 1, 2, \ldots, n$ are in a neighborhood of the diagonal $s_1 = s_2 = s_3 = \ldots = s_n$), then $F = G \circ G$ is injective and so it verifies the separation property. As the separation property is an open condition, it is enough to prove it when $s_1 = s_2 = \ldots = s_n$.

Consider B_i and B_j with $i \neq j$, two continuity pieces of G such that $G(B_i) \cap G(B_j) \neq \emptyset$. This fact can occur only if, from some initial state v_0 the neuron j reaches the threshold level 1 when other neuron i has a potential level V_i too low (smaller than the negative change s_i that the negative synapses will produce on its level). Then, immediatly after change, the neuron i will exhibit a negative potential $V_i - s_i < 0$. One should wait until it reaches potential 0 to see a point $G(v_0) \in B$ with $V_i = 0$ and $V_j > 0$. On the other hand there could be some other initial state $w_0 \in B_i$ (the first neuron to fire is the i-th.) such that $G(v_0) = G(w_0)$ with $V_i = 0$ and $V_j > 0$.

The situation described above occurs only if we start with an initial state

$$v_0 = (V_1, \ldots, V_{i-1}, 0, V_{i+1}, \ldots, V_j, \ldots, V_n) \in B_j$$

such that $1 - V_j$ is small, say

$$0 \leq 1 - V_j \leq \epsilon = \min\{s_i(V_i) : 0 \leq V_i \leq 1\} \quad \text{for some } i \neq j \qquad [1]$$

Therefore neuron j will reach its threshold level 1 without giving enough time to neuron i potential increase more than ϵ. As the negative change in neuron i potential is s_i, greater in absolute value than ϵ, its potential will be negative immediately after the firing of neuron j. In resume

Remark 2.8 G is non injective only for the initial states $v_0 \in B_j$ verifying [1].

On the other hand, the state $v_1 = G(v_0)$ after the first return map to B verifies

$$v_1 = (V_1 - s_1, \ldots, V_{j-1} - s_{j-1}, 0, V_{j+1} - s_{j+1}, \ldots, V_n - s_n) \in G(B_j)$$

So for all $i \neq j$:

$$V_i^+ = V_i - s_i, \qquad 1 - V_i^+ = (1 - V_i) + s_i > \min\{s_i(V_i) : 0 \leq V_i \leq 1\} = \epsilon$$

Therefore, the first return point $v_1 = G(v_0)$ is not an initial position verifying [1]. Using 2.8 we obtain that $F = G \circ G$ is injective, so it verifies the separation property.

We conclude:

The second return map $F : B \mapsto B$ is a contractive piecewise continuous map with the separation property.

We shall study abstract contractive piecewise continuous maps with the separation property in $n-1$ dimensions, to apply the general results obtained in the next section to the model of n inhibitory neurons networks.

3 The abstract dynamical system.

Let M be a C^∞ Riemannian n-dimensional manifold. We call B a *compact region* of M if $B \subset M$ is compact, connected and $B = \overline{\text{int } B}$ (i.e. B is the closure of its interior in M).

We say that $\mathcal{P}$ is a *finite partition* of B if $\mathcal{P} = \{B_i\}_{1 \le i \le m}$ is a finite collection of compact regions B_i of B, such that $\bigcup_{1 \le i \le m} B_i = B$ and $\text{int } B_i \cap \text{int } B_j = \emptyset$, for $i \neq j$. We denote $S = \delta\mathcal{P} = \bigcup_{i \neq j} B_i \cap B_j$.

Definition 3.1 Given a finite partition $\mathcal{P} = \{B_i\}_{1 \le i \le m}$ of B, we call F a C^r $(r \ge 0)$ *piecewise continuous map on* $(B, \mathcal{P})$ *with the separation property* if F is a finite family $F = \{f_i\}_{1 \le i \le m}$ of C^r maps $f_i : B_i \mapsto B$, such that $f_i(B_i) \cap f_j(B_j) = \emptyset$ if $i \neq j$. We note that F is multidefined on $\delta\mathcal{P}$.

Definition 3.2 We say that F is *locally contractive* if $\text{dist}\,(f_i(P), f_i(Q)) < \text{dist}\,(P, Q)$, for all P and Q in the same B_i, for all $1 \le i \le m$. We note that, due to compacity, there exists a positive real number $\lambda < 1$, independent of i, such that $\text{dist}\,(f_i(P), f_i(Q)) \le \lambda\, \text{dist}\,(P, Q)$, for all P and Q in the same B_i.

Given a point $P \in B$, take its image set $F(P) = \{f_i(P) : P \in B_i\}$. If $H \subset B$, its image set is $F(H) = \bigcup_{P \in H} F(P)$. We have that $B \supset F(B) \supset \ldots F^k(B) \supset \ldots$.

Definition 3.3 For any natural number k, we call *atom of generation* k to the image of B_{i_1} by $f_{i_k} \circ \ldots \circ f_{i_2} \circ f_{i_1}$ where $(i_1, i_2, \ldots, i_k) \in \{1, 2, \ldots, m\}^k$.

We note that each atom of generation k is a compact, not necessarily connected set, whose diameter is smaller than $\lambda^k \text{diam} B$. The set $F^k(B)$ is a compact set, formed by the union of all (at most m^k) atoms of generation k.

A point Q is in the limit set of a point $P \in B$ if there exists $n_j \to \infty$ and $Q_j \in F^{n_j}(P)$ such that $Q_j \to Q$. The *limit set* $L^+(F)$ is the union of the limit sets of all points $P \in B$.

We say that a point P is *periodic of period* p if there exists a first natural number $p \ge 1$ such that $F^p(P) = \{P\}$. In this case we call the orbit of P (i.e. $\bigcup F^j(P), j = 1, \ldots, p$) a periodic orbit with period p.

The limit set $L^+(F)$ is contained in the compact, totally disconnected set $K = \bigcap_{k \ge 1} F^k(B)$. It could be a Cantor set. But generically K shall be the union of a finite number of periodic orbits, as asserted in Theorem 3.7.

Definition 3.4 We say that F is *finally periodic* with period p if the limit set $L^+(F)$ is formed by a finite number of periodic orbits with minimum common multiple of their periods equal to p. In this case we call *limit cycles* to the periodic orbits of F.

Let $\mathcal{P} = \{B_i\}_{1 \le i \le m}$ and $\mathcal{Q} = \{A_i\}_{1 \le i \le m}$ be finite partitions of the compact region B with the same number m of subsets. We define the distance between $\mathcal{P}$ and $\mathcal{Q}$ as

$$d(\mathcal{P}, \mathcal{Q}) = \max_{1 \le i \le m} \max_{x \in A_i, y \in B_i} \{d(x, B_i), d(y, A_i)\}$$

where $d(z, C)$ denotes the usual distance from a point $z \in B$ to a compact subset $C \subset B$: $d(z, C) = \min_{c \in C} d(z, c)$.

Definition 3.5 Let $F = \{f_i : B_i \mapsto B\}_{1 \leq i \leq m}$ and $G = \{g_i : A_i \mapsto B\}_{1 \leq i \leq m}$ be C^r $(r \geq 0)$ piecewise continuous maps on $(B, \mathcal{P})$ and $(B, \mathcal{Q})$ respectively. For a given positive real number ϵ we say that G is a $\epsilon - C^r$ *perturbation of* F if

$$\max_{1 \leq i \leq m} \|g_i - f_i\|_{C^r(B_i \cap A_i)} < \epsilon, \quad \text{and} \quad d(\mathcal{P}, \mathcal{Q}) < \epsilon$$

Definition 3.6 We say that the limit cycles of a finally periodic map F of period p are *persistent* if there exists $\epsilon > 0$ such that all $\epsilon - C^0$ perturbations of F are finally periodic with period p and the same finite number of periodic orbits than F.

Theorem 3.7 *Let F be a locally contractive C^r $(r \geq 0)$ piecewise continuous map with the separation property. Given $\epsilon > 0$ there exists a $C^r - \epsilon$ perturbation G of F that is finally periodic with persistent limit cycles.*

Lemma 3.8 *If there exists an integer $k \geq 1$ such that the compact set $K = \bigcap_{k \geq 1} F^k(B)$ does not intersect S, then F is finally periodic and its limit cycles are persistent.*

Proof: The distance from K to S is positive. As the maximum diameter of the finite number of atoms of generation k converges to zero when k goes to infinite, there exists sufficiently large k such that none of the atoms of generation larger or equal to k intersect S. So their successive images by F are single atoms. There is at least one atom of generation k that contains its whole image, by say F^p with $p \leq M^k$. As distances are contracted, all points of this atom converge to a periodic point of period p. The iterates of all the atoms of generation k are eventually in some atom of generation k having the last property, so also converge to a periodic point. The condition of the hypothesis and the itinerary of each atom of generation k remain unchanged with C^0 small perturbations. So the finite number of periodic orbits and their periods are persistent. $\square$

Proof of Theorem 3.7. Let us take F being not necessarily finally periodic.

The contractive diffeomorphisms f_i of the finite family $F = \{f_i : B_i \mapsto B\}_i$ can be C^r extended, being still contractive diffeomorphisms, to small compact neighborhoods $U_i \supset B_i$, in such a way that the extended map F_ϵ, now multidefined on $\bigcup_{i \neq j} U_i \cap U_j \supset S$, still verifies $f_i(U_i) \cap f_j(U_j) = \emptyset$ if $i \neq j$. We shall be given an arbitrarily sufficiently small $\epsilon > 0$, and take U_i such that the distance from B_i to the closure of the complement of U_i is larger than ϵ, for all $i = 1, 2, \ldots m$.

For a fixed $\epsilon > 0$, consider the compact, totally disconnected set

$$K^+ = \bigcap_{k \geq 1} \bigcup_{(i_1, \ldots, i_k) \in \{1,2 \ldots m\}^k} f_{i_k} \circ \ldots \circ f_{i_1}(U_{i_1}) \quad \supset \quad K$$

Observe that if there exists a point in $K \cap S$ then there exist a point $P \in K^+ \cap S$.

The diameters of the atoms of generations k that form K^+ are all smaller that $D\lambda^k$, where D is the maximum diameter of the open sets U_i. Therefore for sufficiently large k all the atoms' diameters are smaller that $\epsilon/2$. If some of these atoms intersect S, consider a new finite partition $\mathcal{Q} = \{A_i\}_{1 \leq i \leq m}$ of B such that the distance between $\mathcal{Q}$ and the given partition $\mathcal{P}$ is smaller than ϵ, and in such a way that $S_{\mathcal{Q}} = \bigcup_{i \neq j}(A_i \cap A_j)$ does not intersect the atoms of generation k of K^+. The first condition implies that $A_i \subset U_i$ and therefore the extension F_ϵ can be restricted to A_i.

Take $G = \{g_i : A_i \mapsto B\}_{1 \leq im}$ where $g_i = f_i|_{A_i}$. By construction G is a $\epsilon - C^r$ perturbation of the given F. Consider the limit set K_G of G as follows:

$$K_G = \bigcap_{k \geq 1} \bigcup_{(i_1,\ldots,i_k) \in \{1,2\ldots m\}^k} g_{i_k} \circ \ldots \circ g_{i_1}(A_{i_1})$$

As G is a restriction of F_ϵ to the sets A_i, we have that $K_G \subset K^+$, and therefore $K_G \cap S_Q = \emptyset$. Then, applying lemma 3.8, G is finally periodic with persistent limit cycles. $\Box$

References

[BCRG 1996] Budelli R., Catsigeras E., Rovella A., Gómez L.: *Dynamical behavior of pacemaker neurons networks.* Proc. of the Second Congress of Nonlinear Analists, WCNA 96, Elsevier Science. (1996)

[BTCE 1991] Budelli R., Torres J., Catsigeras E., Enrich H.: *Two neurons network, I: Integrate and fire pacemaker models.* Biol. Cybern. 66, 95-110.(1991)

[CB 1992] Catsigeras E., Budelli R.: *Limit cycles of a bineuronal network model.* Physica D, 56, 235-252. (1992)

[SFH 1972] Stein R., French A., Holden A.: *The frequency response, coherence and information capacity of two neuronal models.* Biophys. J., 12, 295-322. (1972)