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*The Spike-and-reset dynamics for non-linear
integrate-and-fire neuron models.*

Jonathan Touboul — Romain Brette

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The Spike-and-reset dynamics for non-linear integrate-and-fire neuron models.

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Key-words: No keywords

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The Spike-and-reset dynamics for non-linear integrate-and-fire neuron models

Résumé : Non-linear integrate and fire neuron models introduced in [22], such as Izhikevich and Brette-Gerstner neuron models, are hybrid dynamical systems, defined both by a continuous dynamics, the subthreshold behavior, and a discrete dynamics, the spike and reset process. Interestingly enough, the reset induces in bidimensional models behaviors only observed in higher dimensional continuous systems (bursting, chaos, ...). The subthreshold behavior (continuous system) has been studied in previous papers. Here we study the discrete dynamics of spikes. To this purpose, we introduce and study a Poincaré map which characterizes the dynamics of the model. We find that the behavior of the model (regular spiking, bursting, spike frequency adaptation, bistability, ...) can be explained by the dynamical properties of that map (fixed point, cycles...). In particular, the system can exhibit a transition to chaos via period doubling, which was previously observed in Hodgkin-Huxley models and in Purkinje cells.

Mots-clés : Pas de motclef

Introduction

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During the past few years, the neuro-computing community has made a huge effort to find a computationally simple and biologically realistic model of neuron. Indeed, there is more and more need to compare experimental recordings with numerical simulations of large-scale brain models. The key problem is to find a model of neuron realizing a compromise between its simulation efficiency and its ability to reproduce what is observed at the cell level, often considering in-vitro experiments [12, 16, 20].

Among the numerous neuron models, from the detailed Hodgkin-Huxley model [9] still considered as the reference, but unfortunately computationally intractable when considering neuronal networks, down to the simplest integrate and fire model [7] very effective computationally, but unrealistically simple and unable to reproduce many behaviors observed, two models seem to stand out [12]: the adaptive quadratic (Izhikevich, [11], and related models such as the theta model with adaptation [4, 8]) and exponential (Brette and Gerstner, [1]) neuron models. These models are based on the viewpoint that neurons are excitable systems and that the main effect to model is the transition from silence to spike. These models all fit in a general class of nonlinear bidimensional neuron models sharing common properties, introduced in [22]. Models of this class are computationally almost as efficient as the linear integrate and fire model. They are also biologically plausible, and reproduce several important neuronal regimes with a good adequacy with biological data, especially in high-conductance states, typical of cortical in-vivo activity. One of these models has recently been used in order to simulate a large scale brain model (see [13]).

These models are spiking models. They are defined by a subthreshold dynamics defined by a continuous dynamical system, which has been studied in [22]. It is also defined by a spiking process, which defines the spike emission and adaptation in the neuron. As observed in [11, 1, 22], these systems show very interesting dynamics which cannot exist in two dimensional continuous dynamical systems, such as bursting and chaos. These effects are directly linked with the spiking process.

The aim of this paper is to study this spiking process, to get a grasp on the different observed behaviors, and to get insights on the ranges of parameters to obtain a given behavior. In the first section of this paper, we introduce the model we study and basic definitions which will be useful in the rest of the paper. We then introduce a Poincaré function describing this spiking dynamics, and characterize some of its principal features, in the general case. We then find some simple conditions on Φ to get regular spiking, spike frequency adaptation and mixed mode. We then describe some simple features on this function directly linked with bursting solutions. Transient behaviors such as phasic spiking or bursting are not studied here. We then give an interpretation of the different kinds of excitability observed in the model. The third section is linked with results which had been not yet observed so far as we know: these models present chaotic spiking activity. The route to this chaotic activity is a period doubling cascade, as previously observed in Hodgkin-Huxley model and in intracellular recordings of the Pukinje cell.

1 Basic definitions

In this paper we consider a nonlinear integrate neuron model of the class of models introduced in [22]. This class includes for instance the adaptive exponential integrate-and-fire model [1], the quadratic adaptive model [11], and the quartic adaptive model [22]. This model is described by a nonlinear subthreshold dynamics of type:

$$\begin{cases} \frac{dv}{dt} = F(v) - w + I \\ \frac{dw}{dt} = a(bv - w) \end{cases} \quad (1.1)$$

where a, b and I are real parameters and F is a real function satisfying the following assumptions (see [22]):

Assumption (A1). *F is at least three times continuously differentiable.*

Assumption (A2). *The function F is strictly convex.*

Assumption (A3).

$$\begin{cases} \lim_{x \rightarrow -\infty} F'(x) < 0 \\ \lim_{x \rightarrow +\infty} F'(x) = +\infty \end{cases}$$

In this equation, v represents the membrane potential of the neuron, w is the adaptation variable, I represents the input intensity of the neuron, $1/a$ the characteristic time of the adaptation variable and b accounts for the interaction between the membrane potential and the adaptation variable¹.

We also assume there exists $\varepsilon > 0$ such that F grows faster than $v^{1+\varepsilon}$ when $v \rightarrow \infty$. In this case, the solution of first equation (with a constant w) can blow up in finite time. If the solution of the two-dimensional equation blows up at time t^* , we consider that a spike is emitted, and subsequently we have the following reset process:

$$\begin{cases} v(t^*) = v_r \\ w(t^*) = w(t^{*-}) + d \end{cases} \quad (1.2)$$

where v_r is the constant value of the reset of the membrane potential and $d > 0$ a real parameter accounting for the adaptation.

Proposition 1.1. The equations (1.1) and (1.2), together with initial conditions (v_0, w_0) give us the existence and uniqueness of a forward solution on \mathbb{R}^+ .

Proof. Because of the regularity condition (A1), Cauchy-Lipschitz theorem of existence and uniqueness of solution applies until the solution blows up. If the solution keeps bounded, then we have existence and uniqueness of solution. If the solution blows up at time t^* , then we are reset to a unique point, defined by the reset condition 1.2, and we are again in the case we already treated, hence we have existence and uniqueness of forward solution. \square

¹Brette and Gerstner [1] made a great effort in relating these constant to known biological constants, and obtain a good fit with biological recordings.

This system is an *hybrid dynamical system*: it is defined by both a continuous time dynamical system given by the equations (1.1) and a discrete dynamical system called the spike and reset mechanism, given by the equations (1.2), with five real parameters (a, b, I, v_r, d) . The parameters (a, b, I) govern the subthreshold dynamics, while the parameters v_r and d govern the spike and reset mechanism. In the article [22], the author studies the bifurcations of the subthreshold dynamics with respect to these three parameters. It appears that a is not a bifurcation parameter, and that the system undergoes a subcritical Bogdanov-Takens bifurcation. He also shows that under a simple condition on F the model can undergo a Bautin bifurcation. This analysis accounts for the subthreshold behavior of the neuron, and for instance explains the existence for self-sustained subthreshold oscillations when the model undergoes a Bautin bifurcation.

Nevertheless, this former study does not explain the spiking behaviors of the neuron, which are governed by the spike and reset mechanism. One of the greatest computational property is contained in the spike sequence. In the present paper we adress the question of characterizing these behaviors.

Because of existence and uniqueness of solution obtained in proposition 1.1, we conclude that the whole dynamics between two spikes depends only on the initial condition of the neuron, (v_r, w_0) . The differences in the spikes emitted is hence governed by the sequence of reset positions of the adaptation variable w . If there is a finite number of spikes, this means that the neuron stops firing after a while, which means that the trajectory of the neuron remains bounded in finite time. This behavior can be thus explained by the subthreshold dynamics after a spiking transient, and this is why it will not be our first interest in this paper.

We will be in this paper mainly interested in the case when there are infinitely many spikes emitted by the neuron. In this case, one of our main tool to qualify the dynamics will be the Poincaré map governing the evolution of the adaptation reset point.

Let us defined by \mathcal{D} the domain of w such that the solution of (1.1) with initial condition (v_r, w_0) blows up in finite time.

Definition 1.1. Let $w_0 \in \mathcal{D}$, and denote $(v(t), w(t))$ the solution of (1.1) with initial condition (v_r, w_0) and t^* the blowing time of v . The Poincaré map Φ is the unique function such that

$$\Phi(w_0) = w(t^*) + d$$

Remark 1. Assume that in the dynamical system defined by (1.1) have a repetitive firing (i.e. it fires after any given time T). Then let $(t_n)_{n \geq 0}$ be the sequence of spike times, and We define the sequence of adaptation reset points by $w_n := w(t_n) = w(t_n^-) + d$. The Poincare map of this dynamical system is the function Φ such that

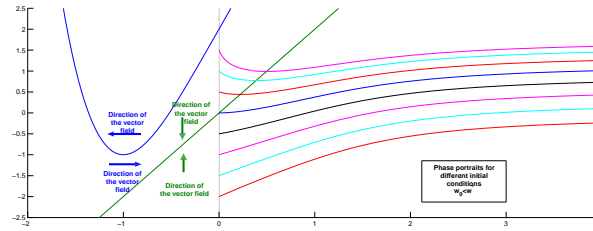
$$\Phi(w_n) = w_{n+1}$$

Hence we will be able to apply techniques of nonlinear analysis of iterations of maps to study the spiking location sequences and the spiking times.

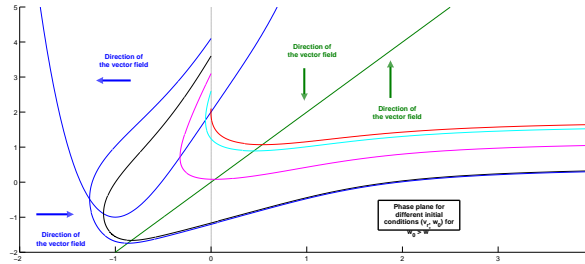
Remark 2. The Poincaré map is only defined in \mathcal{D} . It will be particularly interesting to study cases when \mathcal{D} is the greatest possible. This will be the case for instance when there is neither stable fixed point nor attracting limit cycle, for instance when the two nullclines do not cross or when after the Hopf bifurcation. In other cases, there will be bounded solutions, and return to “rest”, rest meaning there that the solution converges either to a fixed point or to a limit cycle (Poincaré Bendixon theorem).

2 Repetitive spiking behaviors

In this section we assume that the subthreshold dynamical system do not have any fixed point, i.e. $I > -m(b)$ where $m(b)$ is the unique minimum of function $G(b) = F(v) - bv$ (see [22]), and that there is no attractive limit cycle (for instance for Izhikevich or Brette-Gerstner models or for the quartic model before the Bautin bifurcation). In this case, the nullclines are of the form presented in figure Fig.1 and the neuron will spike for any initial condition.



(a) Phase plane for $w_0 < w^*$



(b) Phase plane for $w_0 > w^*$

Figure 1: Phase plane and trajectories in the case $I > -m(b)$.

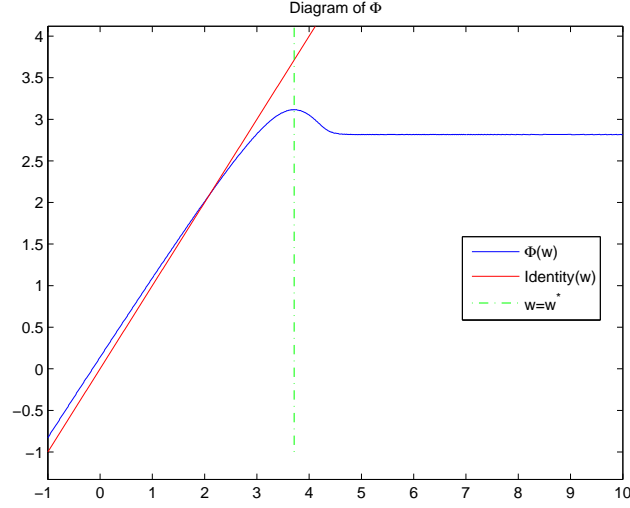


Figure 2: An example of Φ function in the quartic model. We can see the continuity, the monotony and the convergence for $w \rightarrow \infty$.

Theorem 2.1. *Let us define the intersections of the curve $\{v = v_r\}$ and the nullclines:*

$$\begin{cases} w^* &= F(v_r) + I \\ w^{**} &= bv_r \end{cases} \quad (2.1)$$

The Poincaré map satisfies the following properties:

- *It is increasing on $(-\infty, w^*]$ and decreasing on $[w^*, \infty)$,*
- *For all $w < w^{**}$ then $\Phi(w) \geq w + d > w$,*
- *The map Φ is regular,*
- *It has a unique fixed point in \mathbb{R} ,*
- *It converges to a fixed point when $w \rightarrow \infty$*

This theorem is quite important to understand the main properties of the reset sequence. These properties are straightforwardly proved if we had a spiking threshold, the only technical intricacy is the fact that the spike occurs when the membrane potential blows up. For this reason, we put the proof of theorem 2.1 in the appendix A

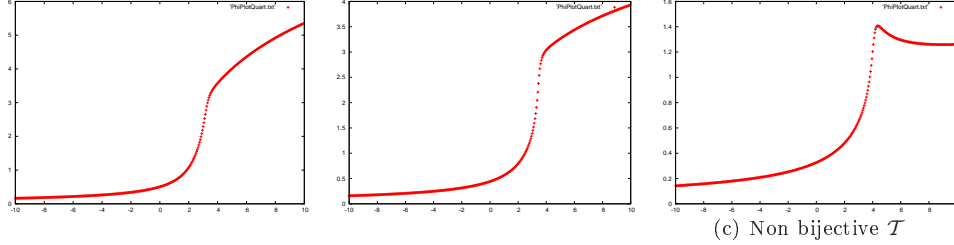


Figure 3: Spike times \mathcal{T} function for the quartic model for different values of a and b . We can see that the function is not always increasing as we suggested in the text, even if it is always increasing until w^* . We also observe that for reasonable values of the parameters the function \mathcal{T} is monotonous

Another important function to study is the map $\mathcal{T} : w \mapsto t^*(w)$ where $t^*(w)$ is the spike time if the membrane potential starts at (v_r, w) at time $t = 0$. If this map was one-to-one, then the reset location would be directly linked with the interspike interval (ISI). Nevertheless, this is not always the case in this type of models, as we can see in Fig. 3(c), even if in most of the cases for a reasonable range of parameters, we will see that the map \mathcal{T} will be one-to-one.

A description of the shape of the application \mathcal{T} is also given in appendix A. Figure Fig.3 represents the map \mathcal{T} in the case of the quartic model.

In the case where the map \mathcal{T} is increasing, the interspike interval and the spike times are directly linked with the reset location. The case where the neuron has cycles of period two with two points having the same spike time is nevertheless still considered as bursting, hence the study of the properties of the map Φ is the most important.

Now that we have showed some properties of the map Φ , we relate dynamical properties of the iteration of this map to the neurocomputational behaviors observed.

2.1 Regular spiking behaviors

In the original paper [22], the author describes the existence of a generalized limit cycle, which he called spiking limit cycle, virtually containing a point at infinity (see Fig. 4). The regular spiking behavior, whatever the phasic behavior, is linked with the presence of such a cycle. This cycle described is exactly a fixed point of the Poincaré application Φ , and the convergence to a regular spiking behavior is simply linked with the convergence of the reset location sequence to this fixed point.

These two properties imply a simple sufficient condition for regular spiking we make explicit in the following theorem.

Theorem 2.2. *Assume that $\Phi(w^*) \leq w^*$. Then the sequence of reset positions $(w_n)_{n \geq 0}$ will converge whatever the initial condition.*

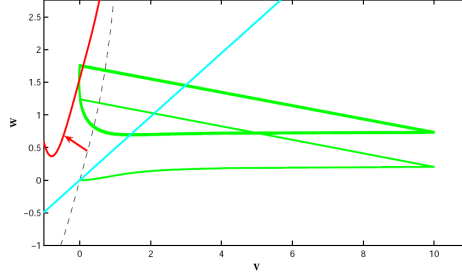


Figure 4: Spiking generalized limit cycle. In the simulation, we have cut the trajectories to a given threshold. At this threshold, we are sure that the solution will blow up, and the trajectory is almost horizontal, hence the real picture is very similar

Proof. First of all, we deal with the case $w_0 \leq w^*$. The sequence $(w_n)_{n \geq 0}$ is monotonous since we have Φ increasing on $(-\infty, w^*]$. Indeed, assume that $\Phi(w) \leq w$, then by induction on n we have

$$\Phi^{n+1}(w) \leq \Phi^n(w)$$

and hence the sequence is non-increasing. If $\Phi(w) \geq w$, the same argument gives us that the sequence $(w_n)_n$ is non-decreasing.

Note that in this case, we necessarily have $w^{**} < w^*$. Indeed, if it was not the case, then proposition A.2 would imply that $\Phi(w) > w$ which contradicts the hypothesis of the theorem.

If $w \in [w^{**}, w^*]$, then we know by the hypothesis of the theorem and by the result of the proposition A.2 that this interval is invariant under Φ , and hence $(w_n)_n$ is a monotonous sequence in a compact set, and hence will necessarily converge to a fixed point in $[w^{**}, w^*]$.

If $w < w^{**}$ then $\Phi(w) \geq w + d$ and hence there exists an index N such that $w_N \geq w^{**}$. We apply the result previously proved to obtain that $(w_n)_n$ converges to a fixed point in $[w^{**}, w^*]$.

If $w > w^*$, then Φ is decreasing on this interval, and hence $\Phi(w) \leq \Phi(w^*) \leq w^*$, hence we can use the previous analysis to prove that the system will converge to a fixed point in $[w^{**}, w^*]$. \square

Remark 3. This result implies the property of regular spiking we observed in numerical simulations. This would corresponds by analogy to the conductance based models to a *generalized attracting spiking limit cycle*, generalized because containing a spike in the class of model of interest means containing a point $(v = \infty, w)$ for some w .

This result implies a sufficient condition for having a regular spiking behavior. Note that the regular spiking behavior is linked with the convergence of the sequence $(w_n)_{n \geq 0}$. Indeed, if this sequence converges, then the frequency of the spikes will converge also. If it

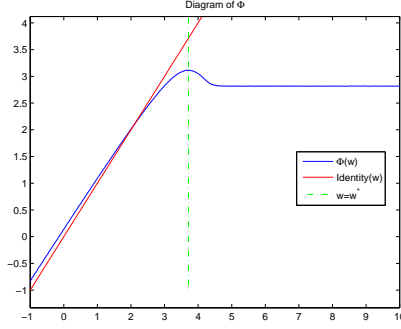
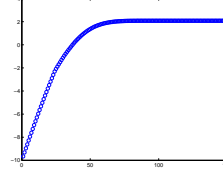
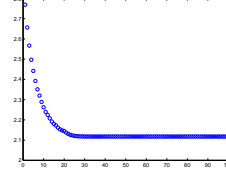
(a) plot of $\Phi(w)$ (b) Sample path of (w_n) with $w_0 < w^*$ (c) Sample path of (w_n) with $w_0 > w^*$

Figure 5: Convergence towards fixed point.

does not, the only way to have regular spiking is to have a cycle and each point of the cycle corresponds to the same spike time in the case where the map \mathcal{T} is not one-to-one. This case can occur, but it is clearly not generic.

Theorem 2.3. *Assume that $\Phi(w^*) > w^*$ and $\Phi^2(w^*) > w^*$. Then the sequence of reset positions will converge to a fixed point whatever the initial condition.*

Proof. First of all, we already noted that there exists a unique fixed point for the map Φ and that this fixed point is in $[w^*, \Phi(w^*)]$. If we have

$$w^* < \Phi^2(w^*) < \Phi(w^*)$$

Then because of the monotony of Φ on (w^*, ∞) , we have (by induction) for all $n \geq 1$:

$$\begin{aligned} \Phi^{2n}(w^*) &< \Phi^{2n+1}(w^*) < \Phi^{2n-1}(w^*) \\ \Phi^{2n}(w^*) &< \Phi^{2n+2}(w^*) < \Phi^{2n+1}(w^*) \end{aligned}$$

Hence the sequence $(w_{2n})_{n \geq 0}$ is an increasing sequence and $(w_{2n+1})_{n \geq 1}$ is decreasing, and for all n , we have $w_{2n} < w_{2n+1}$. Hence the two sequences converge.

We know that because of the monotony conditions on Φ and the plateau that Φ^2 has either a unique fixed point (the same as Φ) or three fixed points. Let $w_1 := \min\{\Phi^{-1}(w^*)\}$. Then Φ^2 is increasing on $(-\infty, w_1)$, decreasing on (w_1, w^*) and increasing again on (w^*, ∞) , and converges to a finite limit when $w \rightarrow \infty$. On $(-\infty, w^*)$, $\Phi^2(w) > w$ because it is clearly the case on $(-\infty, w_1)$ and the minimum of Φ^2 is reached at w^* where $\Phi^2(w^*) > w^*$, hence Φ^2 has a unique fixed point, which is the same as Φ .

Thus the two sequences converge to this same fixed point.

Let now w_0 be an initial condition. Then necesarilly the sequence w_n will be in the invariant interval $[w^*, \Phi(w^*)]$. Indeed, assume that $w_0 < w^*$. Then we know that the sequence will not be bounded by w^* , since there is no fixed point in $(-\infty, w^*)$. Hence there will be an integer p such that $\Phi^p(w_0) \leq w^*$ and $\Phi^{p+1}(w_0) \geq w^*$. Then because of the monotony of Φ we have $\Phi^{p+1}(w_0) \leq \Phi(w^*)$. \square

Interestingly enough, the input current has a stabilizing effect on the behavior of the neuron. We can even prove that for I large enough the sequence will always converge to a fixed point. Nevertheless, the complexity we described in the previous sections will clearly affect the dynamics when we vary I .

Proposition 2.4. Let a, b, v_r, d be fixed parameters. There exists I_s such that for all $I > I_s$ the sequence of iterates of Φ converges.

Proof. Indeed, consider the point $w^*(I)$ and let I increase. From this point $w^*(I)$, the vector field in the direction of v does not change, and in the direction of the adaptation variable w , it decreases linearly (i.e. increasing I by δI amounts adding $-\delta I$ to the vector field in the direction of w). This new dynamical system can be deduced from the original one changing w in $\tilde{w} = w - I$.

The trajectories are ordered and the order decreases with I . Indeed, let $I_1 < I_2$. The equation of the trajectory reads:

$$\frac{d\tilde{w}}{dv} = \frac{a(bv - w) - aI}{F(v) - w}$$

and hence is decreasing with I . Furthermore, at the point $\tilde{w}^* = F(v_r)$, the vector field is vertical and the amplitude of the vector field increases with I . Hence all the trajectories are ordered, and $\Phi(w^*) - I$ is decreasing with I . Moreover, the trajectories are diverging, i.e. the distance between two trajectories increase with time.

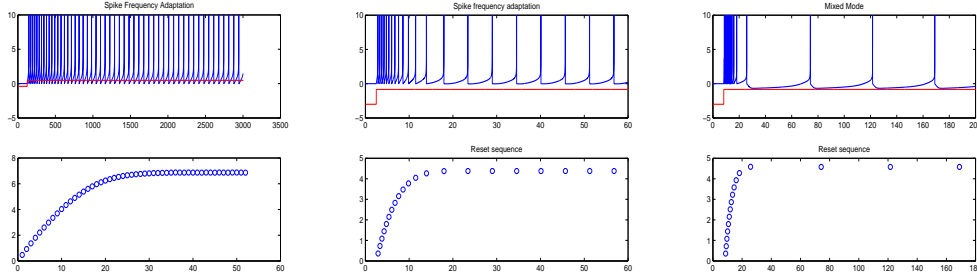
Finally, it is clear that the trajectory in w is not bounded at the beginning of the evolution. Indeed, the vector field at the initial instant is vertical and its amplitude tends to $-\infty$ when $I \rightarrow \infty$.

This can be proved easily by a reductio ad absurdum proof. Assume that \tilde{w} had a lower bound w_{\inf} for any I . Then in this case, we would have:

$$\dot{v} = F(v) - \tilde{w} \leq F(v) - w_1 \tag{2.2}$$

and hence $v(t) \leq v_1(t)$ the solution of this equation. This equation do not depend on I . Let dt be a finite time smaller than the explosion time of the equation (2.2) such that for $t \in [0, dt]$, $v(t) \leq v_1$ a given value $\geq v_r$. Then we have for I large enough:

$$\begin{cases} a(bv - w) - aI \leq a(bv_1 - w_1) - aI \leq 0 \\ 0 \leq F(v) - w \leq F(v) - w_1 \\ -\frac{dw}{dv} = -\frac{a(bv-w)-aI}{F(v)-w} \geq \frac{-a(bv_1-w_1)+aI}{F(v)-w_1} \end{cases}$$



(a) Spike Frequency Adaptation (multiplier 0.355) (b) Intermediate case (multiplier 0.068) (c) Mixed Mode (multiplier 10^{-4})

Figure 6: Different types of convergence for the quartic model, when all the parameters are fixed but the time scale of the adaptation variable a . The faster the adaptation is, the slower the convergence is.

This is not possible since for $v \in [v_r, v_1]$, when I increases, w will be as small as one wants. \square

Hence we have to simple criteria for regular spiking. Moreover, we have proved that for an input current large enough, the neuron will spike regularly. Nevertheless, this analysis doesn't distinguishes the simple tonic spiking from the mixed mode or the spike frequency adaptation. The differences between these behaviors is only the transient phase of spiking, which corresponds from a mathematical point of view to the convergence of the sequence of iterates towards the fixed point (see Fig.6). From the biological point of view, the distinction between these behaviors is not so clear either. In our framework, we can quantifiante the convergence speed, which is directly linked with the multiplier of the fixed point. If the modulus of this multiplier is very small (close to 0), then the convergence will be very fast, and we will see a short transient before the regular spiking, and hence we will have a mixed mode (see Fig. 6(c)). If the multiplier modulus is close to 1, then the convergence will be very slow, and we will have spike frequency adaptation (see Fig. 6(a)).

2.2 Bursting

In the original paper [22] again, the author observed that bursting activity was linked with the existence of an attracting generalized limit cycle, which he called bursting limit cycle, virtually containing many points having an infinite membrane potential (see Fig. 7). The regular bursting behavior, whatever the transient behavior, is linked with the presence of such a cycle, and this cycle corresponds exactly to periodic points for the the Poincaré map Φ .

We can prove that there exists cycles of any period. Indeed, one of the simplest application of Sarkovskii's theorem (see e.g. [2]) is that if there exist a periodic point of period

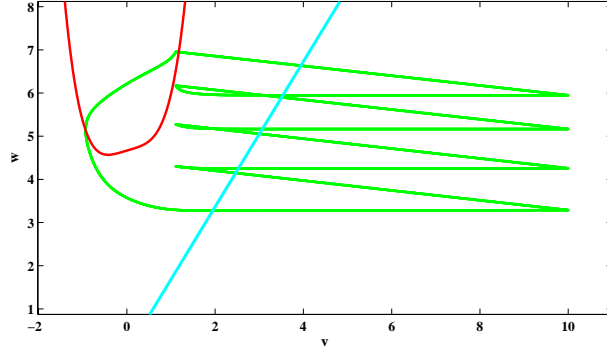


Figure 7: Bursting generalized limit cycle. In the simulation, we have cut the trajectories to a given threshold. At this threshold, we are sure that the solution will blow up, and the trajectory is almost horizontal, hence the real picture is very similar

3, then there exist periodic points of any period, hence bursts of any period. Theorem 2.5 gives us a simple criterion on the dynamics of Φ to have a period 3 cycle.

Theorem 2.5 (Cycles of any period). *Let $w_1 := \min\{\Phi^{-1}(w^*)\}$. Assume that:*

$$\begin{cases} \Phi(w^*) > w^* \\ \Phi^2(w^*) < w_1 \\ \Phi^3(w^*) > w^* \end{cases} \quad (2.3)$$

Then there exists a non-trivial period 3 cycle, hence the reset process has cycles of any period.

Proof. The only thing to prove is that there exist a real T such that

$$\begin{cases} \Phi^3(T) = T \\ \Phi(T) \neq T \end{cases}$$

We know that there exists a unique fixed point of Φ , which we denote w_∞ and which lies in the interval $[w^*, \Phi(w^*)]$. Here we prove that there exists another solution of $\Phi^3(x) = x$. Indeed, let us describe the function Φ^3 :

- It is increasing on $(-\infty, w_2)$ where $w_2 = \min\{\Phi^{-2}(w^*)\}$, and above the curve $y = x$ on this interval.
- decreasing on (w_2, w_1) and $\Phi^3(w_1) = \Phi^2(w^*) < w_1$ hence the curve crosses once the curve $y = x$, at a point strictly inferior to w^* .

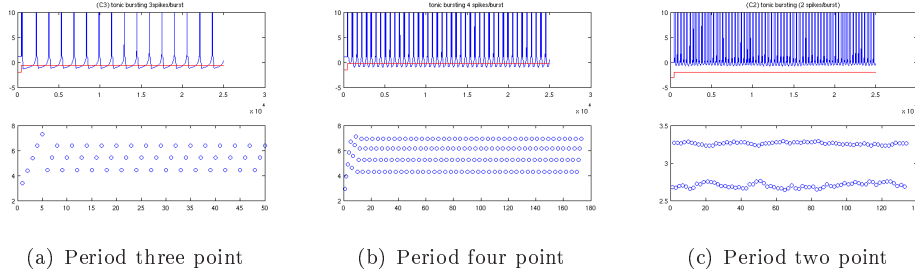


Figure 8: Different types of bursts and the periodic orbits of Φ associated. The last example of a point of period two shows that the system is quite excitable. Indeed, the precision of our integration scheme is very high in this case. This irregularity we observe is linked with numerical errors associated with the excitability of the system: we are very close of the disappearance of this cycle.

Hence we have proved that there exists a period 3 cycle. Sarkovskii's theorem (see e.g. [2]) ensures us that there are cycles of any period for the map Φ . \square

Remark 4. This theorem gives us a quite simple condition on Φ to get period 3 cycles. This implies that the system is chaotic, as shown in the excellent paper of Li and Yorke [17]. We will talk a little bit more of this point in the section dedicated to chaos.

We can easily find in our applications periodic points of period 3, when v_r varies. We can also find experimentally periodic points of different periods, as shown in figure 8.

2.3 Bifurcations and Chaos

Now we have seen that varying parameters can change the behavior of the sequence of iterates, from the convergence to a single point to the convergence towards cycles. Hence a natural question arises: how does the behavior of the sequence of iterates depend upon the parameters.

To understand better the transition between these different types of behaviors, it is important to understand better the dependency of the Poincaré map Φ in function of the parameters. The parameter having the simplest effect on the dynamics is the adaptation parameter d which only shifts the Poincaré map. Hence when d is very small, the fixed point will be attractive with a positive multiplier. When d will be very large, then the fixed point will be attractive with a negative multiplier, close to 0 (the fixed point will be on the flat region corresponding to the horizontal asymptote).

As we have already seen, when I increases, after a certain value of I , the sequence will converge towards a fixed point. Increasing I has the effect of linearly translating the point $w^* = F(v_r) + I$, inducing a smooth change of the curve Φ (see figure Fig.9).

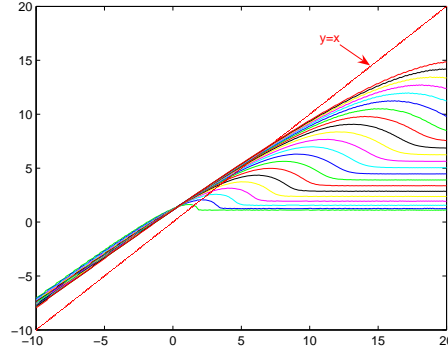


Figure 9: Poincaré application for the quartic model with $a = 1$, $b = 0.5$, $v_r = 3$, $d = 1$ and I ranging from 1 to 20.

The behaviors with respect to these two parameters are hence quite regular. When d is big or I is big, then we have regular spiking.

The dependency in the parameters a and b are also very smooth and monotonous. The map Φ hardly depends on b and the dependency in a is similar to the dependency in I .

A very interesting parameter would be the reset location v_r . As we will see in the simulations, the behavior of the system with respect to this parameter is very interesting and complex. The behavior of the set of curves Φ when varying v_r is not monotonous, and cannot be described very easily. First of all, the maximum of Φ , the point $w^* = F(v_r) + I$, will first decrease with v_r when v_r is inferior to the point where F takes its minimum, and then will increase again. The convexity of F makes the behavior of Φ quite sharp in function of v_r . Figure Fig.10 represents many curves when v_r varies. As we can see, for reasonable values of the parameter v_r , the curve Φ gets very sharp very fast and keeps sharper and sharper. As we see, the fixed point has a multiplier of absolute value strictly greater than 1 in the case presented for v_r large. It is also interesting to see that for very small values of v_r the Poincaré map is very flat.

If we study the fixed point and the stability of this map, we observe a very interesting behavior. The only fixed point loses quite fast its stability via a period doubling bifurcation. We numerically observe a cascade of period doubling bifurcations with some chaotic regions where we observe the period 3 (see figure Fig.11). It is quite interesting to observe chaos in this model. Indeed, the firing patterns observed in the nervous system are often chaotic. For instance in the Purkinje cell, it has been observed that as the temperature increases for a given input current, the calcium spiking presented a consecutive period doublings during *in vitro* experiments (see [19, 5, 18, 10]). The appearance of doublets was also observed *in vivo* on recordings done by Jaeger and Bower on the ketamine-anesthetized guinea pig when the

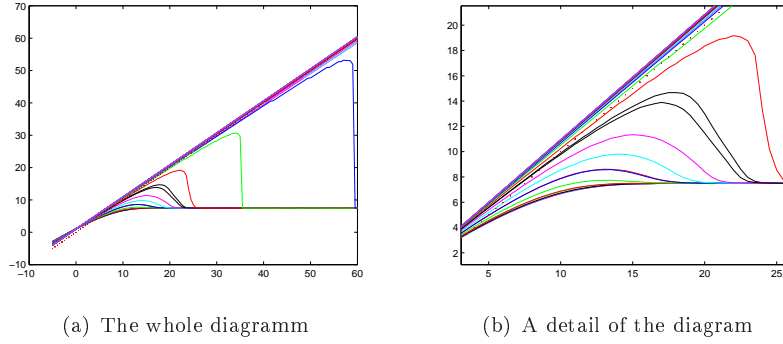


Figure 10: Poincaré application for the quartic model with $a = 1$, $b = 0.5$, $d = 1$, $I = 7$ and v_r ranging from -5 to 20 . The transition is very sharp, and the zoom let us see a little bit more precisely what happens before the fast change of Φ .

inhibition is blocked [14]. This type of route to chaos has also been shown in classical neuron models. For instance Rinzel and Miller in [21] located a period doubling on the interspike interval in the Hodgkin-Huxley model by computing eigenvalues along a family of periodic orbits. It has then been shown in other neuronal models, for instance in a version of the Hodgkin-Huxley model taking into account the temperature [6]. In this case, the system undergoes a period doubling cascade when varying the temperature.

In the figure Fig.11 we provide a diagram in the case of the adaptive exponential integrate-and-fire model. Indeed, this model has the advantage to be based on a biological analysis and has been fitted cautiously (see [1, 15]). For this reason we chose to instantiate the adaptive exponential neuron to be sure that the phenomenon occurs in a plausible range of values.

It is clear that this behavior influences the dependency in the other parameters, as we show in Figure fig.12.

3 Phasic behaviors

In this section, we consider that there exist bounded trajectories, i.e. fixed points or attracting limit cycles. As shown in [22], there always exist fixed point when the input current I is small enough. This is the set of parameters where the two types of dynamics really interact.

The aim of this section is to prove qualitatively some of the behaviors observed in the papers [1, 11, 22] in the framework we introduce in the present paper. We will be particularly interested in the type I and type II excitability observed in these models and the bistability and the phasic behaviors as phasic spiking and phasic bursting.

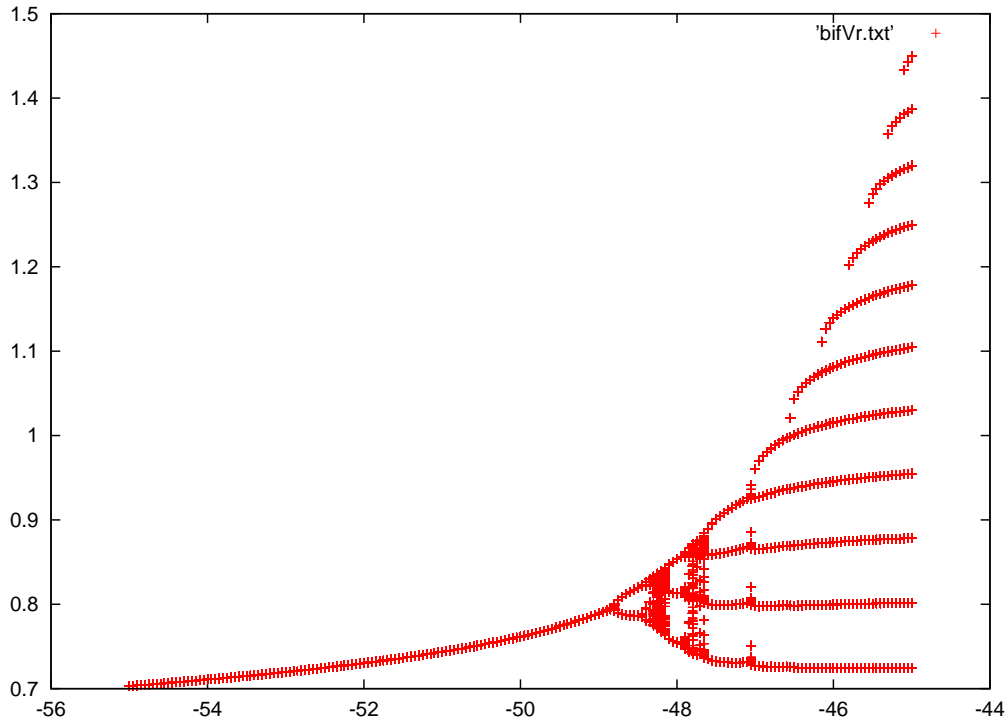


Figure 11: The period doubling route to chaos in the reset sequence for the adaptive exponential integrate-and-fire neuron, for the original parameters (see [1]), with $a = 0.01$, and V_r ranging from $-55mV$ which is the original value, to $-43mV$. We can clearly see the period three and the chaos it generates around, before the next period doubling bifurcation.

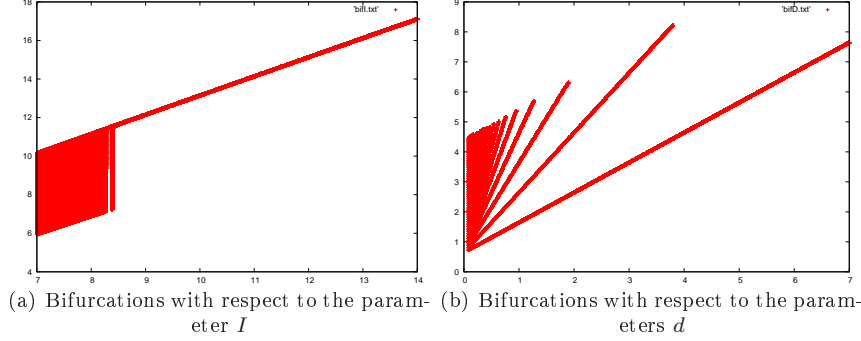


Figure 12: Fixed points and fixed cycles in function of the adaptation parameter I and d . The period doubling observed generated strange behaviors which are stabilized when the parameters increase

A Characterization of the Poincaré map

In this section we assume that the subthreshold dynamical system do not have any fixed point, i.e. $I > -m(b)$ where $m(b)$ is the unique minimum of function $G(b) = F(v) - bv$ (see [22]), and that there is no attractive limit cycle (for instance for Izhikevich or Brette-Gerstner models or for the quartic model before the Bautin bifurcation). In this case, the nullclines are of the form presented in figure Fig.1 and the neuron will spike for any initial condition.

First of all, we will state and prove some general properties on the Poincaré map. In the next section, we will instantiate a model and prove that the systems indeed has the expected behaviors we propose here.

We recall that the intersections of the curve $\{v = v_r\}$ and the nullclines are denoted (see equation (2.1)):

$$\begin{cases} w^* &= F(v_r) + I \\ w^{**} &= bv_r \end{cases} \quad (\text{A.1})$$

As already stated, between two spike times, subthreshold dynamics of the neuron satisfies the Cauchy Lipschitz conditions on the definition interval of the solution. Hence two orbits cannot cross between two spikes, since we have uniqueness of the solution for a given initial condition.

Let us consider the Jordan section defined by the curve $\{v = v_r\}$. By application of Jordan's theorem (see for instance [3, Chap. 9, appendix, p. 246]), the solutions are always ordered on this section. It means that if $w_1^0 < w_2^0$ and the two solutions cross again the

Jordan section, then the order of the new crossing positions w_1^1 and w_2^1 is changed, i.e. $w_2^1 < w_1^1$.

Theorem A.1 (Monotony of Φ). *The Poincaré map Φ is increasing on $(-\infty, w^*]$ and decreasing on $[w^*, \infty)$.*

Proof. Let $w_1(0) < w_2(0) \leq w^*$ two points in \mathcal{D} . Let $v_1(t)$ and $v_2(t)$ be the solutions of the equations (1.1) with initial conditions $\{v_1(0) = v_r, w_1(0)\}$ and $\{v_2(0) = v_r, w_2(0)\}$ respectively. Then we just have to show that the monotony of the solutions is conserved asymptotically when $v \rightarrow \infty$. Indeed, the solutions will not cross the v -nullcline and hence will spike directly. Since the solutions will not cross and v is always increasing, then the solutions are ordered the same way as the initial condition all along the trajectory and hence $w_1(t_s) \leq w_2(t_s)$ where t_s is the spike time. Hence Φ is increasing on $(-\infty, w^*]$.

Let now $w^* \leq w_1(0) < w_2(0)$. Then the related solutions will decrease in v at the beginning of the trajectory, will cross the v nullcline, and then increase. Hence those solutions will cross the Jordan section v_r an odd times, and thus the order of the solutions will be inverted, so $w_1(t_s) > w_2(t_s)$ and Φ is decreasing on $[w^*, \infty)$. □

Let us now describe the influence of the relative position of w with respect to w^{**} on Φ .

Proposition A.2. *If $w < w^{**}$ then $\Phi(w) \geq w + d > w$.*

Proof. Indeed, if $w < w^{**}$, then w will increase along the trajectory, and hence $w(t_s) \geq w$ and hence $\Phi(w) \geq w + d$. □

Theorem A.3 (Continuity of Φ). *The map Φ is continuous.*

Proof. First of all, the continuity of Φ for $w < w^*$ is clear. Indeed, we recall that the orbits form a partition of the phase plane. All the orbits are all oriented the same way for $w < w^*$, and the orbits are have vertical asymptotes (the equation of the orbit reads: $\frac{dw}{dv} = \frac{a(bv-w)}{F(v)-w+I}$ for v large enough) and that the orbits do not cross, then the map is continuous.

For $w > w^*$, the orbit will turn around the point (v_r, w^*) . Hence Φ is the composition of the application giving the first crossing location of the orbit with the curve $\{v = v_r\}$ and Φ for $w < w^*$. The second is continuous because of the latter argument, and the first one is clearly continuous. Indeed, we know that at the initial time both w and v will decrease. Fix $w_1 > w_2 > w^*$. Here again, the partition argument and the direction of the vector field ensures us that the position of the new crossing point is continuous with respect to the initial condition.

At the point $w = w^*$, the same argument is still valid, hence our theorem is proved. □

Theorem A.4 (Existence and uniqueness of the fixed point). *Assume that $I > -m(b)$. Then there is no fixed point in the system and the v -nullcline is everywhere greater than the w nullcline (see [22]). Then the Φ function has a unique fixed point in \mathbb{R} .*

Proof. Let $w_0 < w^*$.

The solution of equation (1.1) will never cross the v nullcline. Let us write the solution of the orbit curves:

$$\frac{dw}{dv} = g(v, w) := \frac{a(bv - w)}{F(v) - w + I} \quad (\text{A.2})$$

We consider the flow of the dynamical system (A.2) which we denote $\varphi(w_0, v_0, v)$ and we prove the convexity condition on φ :

$$\frac{\partial^2 \varphi}{\partial w_0^2} < 0 \quad \forall (w, v)$$

Indeed, we have:

$$\begin{cases} \frac{\partial g}{\partial w} &= -a \frac{F(v) - bv + I}{(F(v) - w + I)^2} \\ \frac{\partial^2 g}{\partial w^2} &= 2 \frac{bv - F(v) - I}{(F(v) - w + I)^3} \end{cases}$$

and we know that on the trajectory $F(v) - w + I > 0$ and that because of the nullclines positions $bv - F(v) - I < 0$. Hence we have

$$\begin{cases} \frac{\partial g}{\partial w} < 0 \\ \frac{\partial^2 g}{\partial w^2} < 0 \end{cases}$$

Now let us compute the second derivative of φ with respect to w_0 . We have $\varphi(w_0, v_0, v) = w_0 + \int_{v_0}^v g(u, \varphi(w_0, v_0, u)) du$ and hence:

$$\frac{\partial^2 \varphi}{\partial w_0^2} = \int_{v_0}^v \frac{\partial^2 g}{\partial w^2} \left(\frac{\partial \varphi}{\partial w_0} \right)^2 + \frac{\partial g}{\partial w} \frac{\partial^2 \varphi}{\partial w_0^2},$$

and hence we have $\frac{\partial^2 \varphi}{\partial w_0^2} \leq \int_{v_0}^v \frac{\partial g}{\partial w} \frac{\partial^2 \varphi}{\partial w_0^2}$. On the other hand, we can see using this equation that $\frac{\partial^2 \varphi}{\partial w_0^2}(w_0, v_0, v_0) = 0$. Thus using Gronwall's theorem we obtain the convexity of the function $\varphi(\cdot, v_0, v)$ for all v_0 and all v .

The Poincaré application Φ is defined by

$$\Phi(\cdot) = \lim_{v \rightarrow \infty} \varphi(\cdot, v_r, v)$$

and hence Φ has the same convexity property for $w < w^*$.

Since we have for all $x < w^{**}$ the property: $\Phi(x) \geq x + d$ and for $x > w^*$, $\Phi(x)$ is a non-increasing function, we have existence of at least one fixed point. The uniqueness is given by the concavity of Φ when it increases and the decrease after. \square

Theorem A.5 (Limit of Φ at ∞). *Then the Poincaré map Φ converges to a constant when $w \rightarrow \infty$.*

Proof. The only thing to prove is the existence of a solution diverging to $-\infty$ when $t \rightarrow -\infty$. To do so, we search for an invariant subspace of the phase plane for the inverse dynamics (i.e. for the dynamical system $(v(-t), w(-t))$ which does not cross the v nullcline : $\mathcal{N} := \{w = F(v) + I\}$.

For instance, we search for a domain bounded by two lines:

$$\mathcal{B} := \{(v, w) \mid v \leq v_0, w \leq w_0 + \alpha(v - v_0)\}$$

We show that we can find real parameters (v_0, w_0, α) such that this domain is invariant by the dynamics and does not cross \mathcal{N} .

First of all, for the boundary $\{v = v_0, w \leq w_0\}$, we want $\dot{v} \geq 0$, which only means $w \leq w^*(v_0) = F(v_0) + I$.

Now we have to characterize both v_0 , w_0 and α such that the vector field is flowing out of this affine boundary. This simply means that $\langle \begin{pmatrix} \dot{v} \\ \dot{w} \end{pmatrix} | \begin{pmatrix} \alpha \\ -1 \end{pmatrix} \rangle \leq 0$, i.e.: $\alpha \dot{v} - \dot{w} \leq 0$, on each point of the boundary, which is equivalent to:

$$a(bv - w_0 - \alpha(v - v_0)) \geq \alpha(F(v) - w_0 - \alpha(v - v_0) + I) \quad (\text{A.3})$$

Using the assumption $\lim_{v \rightarrow -\infty} F'(v) < 0$, hence there exists an affine function such that for all $v \in \mathbb{R}$ $F(v) + I \geq uv + \beta$.

We consider now $\alpha < 0$. Then condition (A.3) implies that

$$(ab - \alpha(u - \alpha) - a\alpha)v + (-aw_0 + \alpha av_0 + \alpha w_0 - \alpha^2 v_0) \geq 0$$

Hence the only thing to ensure is that $(ab - \alpha(u - \alpha) - a\alpha) < 0$. This condition is achieved when the discriminant of this equation is strictly positive, i.e. for all $u > 2\sqrt{ab} - a$ or $u < -2\sqrt{ab} - a$.

The initial condition on u was to be greater than the minimum of F' , hence any $u > \max(2\sqrt{ab} - a, \min_{v \in \mathbb{R}} F'(v))$ will be convenient, and $\alpha = \frac{a+u}{2}$.

In this case, for all $v < v_m$ and $w_0 < w_u$ the intersection of $\{v = v_m\}$ and the tangent at F at the point x_u solution of $F'(x_u) = u$, the vector field is flowing out \mathcal{D} and hence when we invert the time direction, the vector field is flowing in this zone, hence \mathcal{D} is flow invariant, hence every solution in this zone does not cross the nullcline, hence goes to infinity with a speed minored by the minimal distance between the nullcline and \mathcal{D} .

Hence we have proved that there is a solution going to $-\infty$, and which will spike by assumption. This solution crosses necessarily the line $\{v = v_r\}$, and denote w_L the w associated to this intersection. This solution cuts the phase space in two subspaces which do not communicate: every orbit starting in one of the two subspaces will stay in this subspace. Hence for all $w > w^*$, $\Phi(w) \geq \Phi(w_L)$, hence Φ is decreasing and minored, hence converges to a certain value. \square

Another important function to study is the map $\mathcal{T} : w \mapsto t^*(w)$ where $t^*(w)$ is the spike time if the membrane potential starts at (v_r, w) at time $t = 0$. It would be quite interesting

to be able to show that this map is one-to-one. If it was the case, then the reset location would be directly linked with the ISI. Nevertheless, as we can see in Fig. 3(c), it will not be always the case. Nevertheless, we can state some simple results on the function \mathcal{T} , and we will see that in the situations where the parameters are reasonable, the map \mathcal{T} will be one-to-one.

Proposition A.6. The map \mathcal{T} is increasing for $w \leq w^*$.

Proof. This is a straightforward application of the monotony of the modulus of the vector field with respect to w and the shape of the phase diagram partition in trajectories. \square

For $w > w^*$, the trajectory turns around the point (v_r, w^*) and crosses again the curve $v = v_r$. Here again, it is clear that the time it takes for crossing again the curve $v = v_r$ increases with w . This time increase is compensated by the fact that when w increases, the second crossing position of the curve $v = v_r$ decreases. Figures Fig.3 displays different \mathcal{T} functions and illustrates the fact that the function can be one-to-one or not.

Nevertheless, as we have seen, the second crossing location of the curve $v = v_r$ converges, hence after a given time, the map \mathcal{T} increases again, hence the composed application $\mathcal{T} \circ \Phi$ will also have a unique maximum, and will converge to a fixed value.

In the case where the map \mathcal{T} is increasing, the interspike interval and the spike times are directly linked with the reset location.

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