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Dynamics of one-dimensional spiking neuron models

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Abstract. In this paper we make a rigorous mathematical analysis of one-dimensional spiking neuron models in a unified framework. We find that, under conditions satisfied in particular by the periodically and aperiodically driven leaky integrator as well as some of its variants, the spike map is increasing on its range, which leaves no room for chaotic behavior. A rigorous expression of the Lyapunov exponent is derived. Finally, we analyse the periodically driven perfect integrator and show that the restriction of the phase map to its range is always conjugated to a rotation, and we provide an explicit expression of the invariant measure.

1. Introduction

The Leaky Integrate-and-Fire model (LIF), as introduced by Lapicque [23,20] is widely used in computational neuroscience for its relative simplicity compared to the more realistic Hodgkin-Huxley model [16]. It is also more amenable to theoretical analysis [20,18]. However, most theoretical studies deal with sinusoidally driven models [18,13,17,1], and not many mathematical results have been rigorously proven. Moreover, the many variants of the Integrate-and-Fire model [20,12, 1,31] would benefit from a unified framework. Here we study the general case of a spiking neuron model driven by a one-dimensional differential equation:

$$\frac{dV}{dt} = f(V,t) \tag{1}$$

where V is the membrane potential. We assume equation (1) to have a unique solution starting from any initial condition. Spiking is modelled as follows: when $V(t)$ reaches a threshold V_t, it is reset to V_r. We do not restrict ourselves to periodic stimulations. Time-varying threshold and reset can also be included in this framework (change of variables), as we will see in section 2.5. Besides, we assume that equation (1) satisfies at least one of the two following hypotheses:

(H1) equation (1) is leaky: $V \mapsto f(V,t)$ is decreasing for all t (i.e., $\frac{\partial f}{\partial V} < 0$ if f is $\mathcal{C}^1$).

(H2) $f(V_r, t) > 0$ for all t.

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Hypothesis (H1) implies that the difference between any two solutions of equation (1) decreases and tends to 0 as t tends to $+\infty$; hypothesis (H2) ensures that all trajectories remain between reset and threshold.

This framework was introduced in the context of spike timing reliability in [5]. It includes in particular the standard LIF model [23, 20]:

$$\tau \frac{dV}{dt} = -V + RI(t) \tag{2}$$

where $I(t)$ is the input current, τ is the membrane time constant, and R is the membrane resistance (see e.g. [35] for physiological values of the constants). Many models used in computational neuroscience [29, 2, 31, 30] can be written as follows:

$$\frac{dV}{dt} = A(t) + B(t)V \tag{3}$$

where $B(t)$ is negative. Equations (2) and (3) satisfy hypothesis (H1). Another popular model is the quadratic integrate-and-fire model[11, 10, 24], described by the following equation:

$$\frac{dV}{dt} = V^2 + I(t)$$

which has the particularity of blowing up in finite time. The time when V goes to infinity is the spike time, and the potential is then reset to $-\infty$. However, practically, we would set the threshold V_t at a high, but finite, value, and the reset potential V_r at a low value. Provided V_r is low enough, hypothesis (H2) will be satisfied (precisely, we must have $I(t) > -V_r^2$ for all t). The proofs based on hypothesis (H2) do not require the existence of solutions above the threshold, so that the results we present in this paper apply to the quadratic model with reset.

In section 2, we present and prove general results, and show how they apply to the case of periodic inputs in section 3. Finally, in section 4, we study the special case of the perfect integrator [20], defined by:

$$\frac{dV}{dt} = s(t) \tag{4}$$

where $s(t)$ is the input stimulus.

In the subsequent study, we shall call *solution* a solution of equation (1) (with no spikes), and *run* a solution of the system with spikes. To avoid confusion, we shall write $x(\cdot)$ for a solution and $V(\cdot)$ for a run.

2. General results

We assume that equation (1) satisfies either hypothesis (H1) or (H2). Up to a change of variables (which does not affect the hypotheses), we may assume $V_t = 1$ and $V_r = 0$.

2.1. Condition for sustained firing

We first prove that sustained firing does not depend on the initial condition.

Theorem 1. *All runs have infinitely many spikes or all runs have finitely many spikes.*

The theorem is easier to prove for hypothesis (H2).

Proof (hypothesis (H2)). Suppose a run stops firing after time t. Then from this time, the run is a (continuous) solution $x(\cdot)$ of equation (1) and is strictly contained between the lines $V = 0$ (reset) and $V = 1$ (threshold). Therefore, because solutions of the differential equation cannot cross, any solution starting at reset after time t is below $x(\cdot)$ and thus cannot reach the threshold. Thus no other run can have infinitely many spikes. □

If only hypothesis (H1) is assumed, we cannot claim that runs remain above reset, and we need the following lemma:

Lemma 1. *Consider equation (1) (no hypothesis required). Let $x(\cdot)$ be a solution such that $x(t_0) = x_0$ and $V(\cdot)$ a run such that $V(t_0) = x_0$. Then for every spike of the run at time $t_n > t_0$, $x(t_n) \geq 1$.*

Proof. The lemma follows from the observation that the solution $x(\cdot)$ is above the run $V(\cdot)$ from time t_0. Indeed, the difference $x(t) - V(t)$ does not change sign when there is no spike (solutions cannot cross), and increases by 1 every time there is a spike. Since $V(t_n) = 1$, we have $x(t_n) \geq 1$ for every spike time $t_n > t_0$. □

The theorem follows from this lemma and the leak hypothesis (H1).

Proof (theorem 1, hypothesis (H1)). Consider a run $V(\cdot)$ with infinitely many spikes at times t_n, and let $x(\cdot)$ be a solution such that $x(t_0) = 0$. According to lemma 1, we have $x(t_n) \geq 1$. Suppose there is another run that stops firing after time s, which means there is a solution $y(\cdot)$ of (1) such that $y(t) < 1$ for all $t > s$. It follows from the leak hypothesis that $x(t) - y(t)$ tends to 0 as t tends to $+\infty$, thus it is smaller than 1 after a certain time, which implies there is an n such that $y(t_n) > 0$. Therefore, $y(\cdot)$ is above $V(\cdot)$ between t_n and t_{n+1}, but this is a contradiction, since $V(t_{n+1}) = 1$. Thus there cannot be a run with finitely many spikes, which proves theorem 1. □

2.2. The spike map

In this section we suppose all runs have infinitely many spikes.

The spike map φ is defined as the map that gives the time $\varphi(t)$ of a spike following one at time t. Thus the sequence of spike times of a run starting from reset at time t is $t, \varphi(t), \varphi^2(t), \ldots$ This map was first introduced by [26] for the periodically driven LIF model and studied further in [18]. Formally, we can define it as follows: let Φ be the flow corresponding to equation (1), i.e., the map:

$$\Phi : \mathbb{R}^2 \times \mathbb{R} \rightarrow \mathbb{R}$$

which maps an initial condition (x, t) and a time s to the value $\Phi(x, t, s)$ at time s of the solution starting from x at time t. Then the spike map is defined as follows:

$$\varphi(t) = \inf\{s \geq t | \Phi(0, t, s) = 1\}$$

We first study the regularity of the spike map.

Theorem 2. *For all t, $f(1, \varphi(t)) \geq 0$. If f is C^r, φ is C^r in the neighborhood of any t such that $f(1, \varphi(t)) > 0$.*

Proof. The first assertion is straightforward and does not require any hypothesis about equation (1): if $f(1, \varphi(t))$ were negative, then $\Phi(0, t, s)$ would be greater than 1 on the left of $\varphi(t)$, which contradicts the definition of φ.

The second assertion follows from the implicit function theorem. If f is C^r, then the flow Φ is also C^r. The spike map φ is such that $\Phi(0, t, \varphi(t)) = 1$. If the condition

$$\frac{\partial \Phi}{\partial s}(0, t, \varphi(t)) \neq 0$$

is satisfied, then, by the implicit function theorem, the equation $\Phi(0, t, s) = 1$ defines φ in the neighbourhood of t as an implicit C^r function. We can see that

$$\frac{\partial \Phi}{\partial s}(0, t, \varphi(t)) = f(1, \varphi(t))$$

Thus the implicit function theorem applies when $f(1, \varphi(t)) \neq 0$. Since this quantity is never negative, the condition is: $f(1, \varphi(t)) > 0$. □

The following crucial result was first stated in [18] for the sinusoidally driven LIF [1]:

Theorem 3. *φ is strictly increasing on its range.*

Figure 1 shows the spike map of a periodically driven LIF, which is neither continuous nor increasing. The restriction to its range is increasing, but not continuous. Theorem 3 implies in particular that there can be no chaotic behavior when either hypothesis (H1) or (H2) is satisfied. Chaotic dynamics can arise for other systems, when φ cannot be restricted to an increasing map [19].

Proof. First, φ is locally (strictly) increasing at every point t where $f(0, t) > 0$. Indeed, in this case $f(0, u) > 0$ in a neighborhood of t, so that a solution starting at reset on the left of t goes above the solution starting from 0 at time t. It follows that, if hypothesis (H2) is satisfied, φ is locally increasing at every $t \in \mathbb{R}$, thus it is increasing on $\mathbb{R}$.

If only hypothesis (H1) is satisfied, φ is not locally increasing at every $t \in \mathbb{R}$, but, by theorem 2 and hypothesis (H1), it is locally increasing on its range. However, because the range is not necessarily connected, we cannot conclude that the spike map is increasing on it. The range of φ is a union of disjoint intervals. On each

[1] However, the argument in this paper contained only the proof that φ is locally increasing on its range.

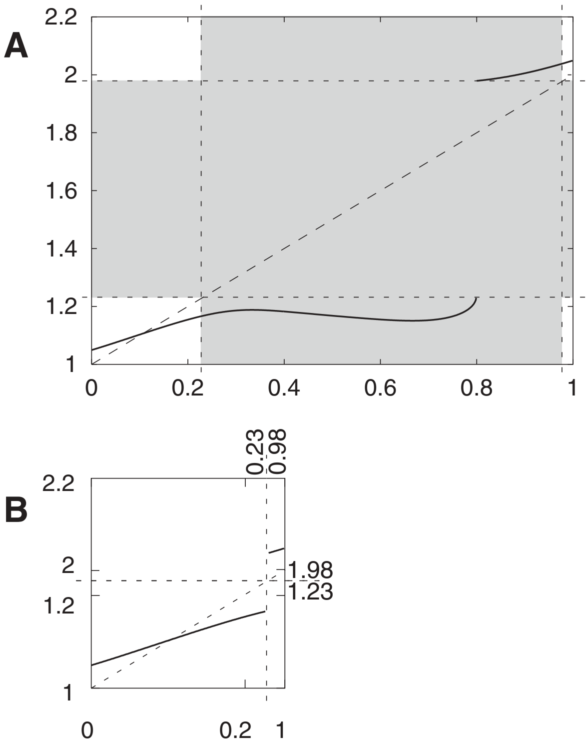

Fig. 1. *The spike map is increasing on its range.* (A) Graph of the function φ for the LIF described by equation $\frac{dV}{dt} = -V + 1.3 + 2.1\cos(2\pi t) + 0.5\cos(4\pi t)$. The spike map is discontinuous at 0.8 and is not increasing. Areas not belonging to the range of φ are depicted in grey. (B) Restriction of φ to its range, obtained by removing the shaded areas in (A). The resulting function is increasing but not continuous.

of these intervals φ is increasing. Consider two successive intervals of the range and let t be the right endpoint of the first one and s the left endpoint of the second one. We need to show that $\varphi(t) < \varphi(s)$. Let $x(\cdot)$ be the solution starting from 1 at time t. Then we have $x(u) < 1$ for all $u \in]t, s[$ and $x(s) = 1$ (otherwise we could lengthen one of the two intervals). Let $y(\cdot)$ be the solution starting from 0 at time t. Because of the leak hypothesis (H1), the distance between $x(\cdot)$ and $y(\cdot)$ decreases, so that $y(s) > 0$. It follows that the run starting from 0 at time t spikes before the one starting from 0 at time s, i.e., $\varphi(t) < \varphi(s)$. Thus, φ is (strictly) increasing on its range. □

2.3. The firing rate

The firing rate is defined for any initial condition $(0, t)$ as

$$F(t) = \lim_{n \to +\infty} \frac{n}{\varphi^n(t)}$$

(if the limit exists).

Proposition 1. *The firing rate, if it exists, does not depend on the initial condition.*

Proof. If there is no sustained firing, then for all initial conditions the firing rate is 0. Otherwise, the sequence $(\varphi^n(t))_{n\in\mathbb{N}}$ is increasing and tends to infinity for all t. Let t_1 and t_2 in $\mathbb{R}$ such that $\varphi(t_1) < \varphi(t_2)$. There is $m \in \mathbb{N}^*$ such that

$$\varphi^m(t_1) < \varphi(t_2) < \varphi^{m+1}(t_1)$$

Since φ is increasing on its range (theorem 3), it follows that for all integer n:

$$\varphi^{m+n}(t_1) < \varphi^n(t_2) < \varphi^{m+n+1}(t_1)$$

and therefore:

$$\frac{n}{\varphi^{m+n+1}(t_1)} < \frac{n}{\varphi^n(t_2)} < \frac{n}{\varphi^{m+n}(t_1)}$$

We can rewrite this inequality as follows:

$$\frac{n}{m+n+1}\frac{m+n+1}{\varphi^{m+n+1}(t_1)} < \frac{n}{\varphi^n(t_2)} < \frac{n}{m+n}\frac{m+n}{\varphi^{m+n}(t_1)}$$

Thus, if the firing rate $F(t_1)$ is well-defined, then the left and right sides of this inequality tend to $F(t_1)$ as n tends to infinity, so that $F(t_2)$ exists and equals $F(t_1)$, which proves the proposition. □

In particular, the firing rate is well-defined and is a continuous function of the parameters of the input (when the input is smoothly parameterized) for periodic [25, 7, 27, 28] and almost-periodic [22] inputs (which includes sums of periodic inputs, as in [34]).

2.4. Lyapunov exponent

The Lyapunov exponent for an orbit under φ starting at time t_0 is defined by:

$$\lambda(t_0) = \lim_{n\to+\infty}\frac{1}{n}\sum_{k=0}^{n}\log|\dot{\varphi}(\varphi^k(t_0))|$$

In this section we propose a more explicit expression of the Lyapunov exponent. The following proposition holds for the general case of equation (1) (no specific hypothesis required).

Proposition 2. *If $f \in \mathcal{C}^1$, then $\dot{\varphi}$ satisfies:*

$$\dot{\varphi}(t) = \frac{f(0,t)}{f(1,\varphi(t))}\exp\int_t^{\varphi(t)}\frac{\partial f}{\partial V}(x(s),s)ds$$

where $x(\cdot)$ is the solution starting from reset at time t ($x(s) = \Phi(0,t,s)$). In particular, for the standard LIF (equation (2)):

$$\dot{\varphi}(t) = \frac{RI(t)}{RI(\varphi(t))-1}\exp(-\frac{\varphi(t)-t}{\tau})$$

And for the perfect integrator:

$$\dot{\varphi}(t) = \frac{s(t)}{s(\varphi(t))}$$

Note that the last two equations are separable.

Proof. To express $\dot{\varphi}$, we observe that the flow satisfies, for all x, u, v:

$$\Phi(\Phi(x, v, u), u, v) = x$$

Partial differentiation with respect to u gives:

$$\frac{\partial \Phi}{\partial x}(\Phi(x, v, u), u, v) \times \frac{\partial \Phi}{\partial s}(x, v, u) + \frac{\partial \Phi}{\partial t}(\Phi(x, v, u), u, v) = 0$$

We choose $x = 1, u = t, v = \varphi(t)$. Using $\frac{\partial \Phi}{\partial s}(1, \varphi(t), t) = f(0, t)$, we obtain:

$$\frac{\partial \Phi}{\partial x}(0, t, \varphi(t)) \times f(0, t) + \frac{\partial \Phi}{\partial t}(0, t, \varphi(t)) = 0 \tag{5}$$

By definition, φ is such that $\Phi(0, t, \varphi(t)) = 1$. Deriving this equation, we get:

$$\frac{\partial \Phi}{\partial t}(0, t, \varphi(t)) + \frac{\partial \Phi}{\partial s}(0, t, \varphi(t)) \times \dot{\varphi}(t) = 0$$

We observe that $\frac{\partial \Phi}{\partial s}(0, t, \varphi(t)) = f(1, t)$ and use equation (5):

$$\dot{\varphi}(t) = \frac{f(0, t)}{f(1, \varphi(t))} \frac{\partial \Phi}{\partial x}(0, t, \varphi(t))$$

which can be expressed as follows (linearization):

$$\dot{\varphi}(t) = \frac{f(0, t)}{f(1, \varphi(t))} \exp \int_t^{\varphi(t)} \frac{\partial f}{\partial V}(x(s), s) ds$$

and the proposition is proved. □

This result leads to the following expression for the Lyapunov exponent of the LIF:

Proposition 3. *For the standard LIF, the Lyapunov exponent can be expressed as follows:*

$$\lambda(t_0) = -\frac{1}{\tau F} + \lim_{n \to +\infty} \frac{1}{n} \sum_{k=1}^{n} \log \frac{RI(\varphi^k(t_0))}{RI(\varphi^k(t_0)) - 1}$$

where F the firing rate (independent of t_0).

For the perfect integrator, if $s(\cdot)$ is bounded by positive numbers, then $\lambda = 0$ (indepently of t_0).

Proof. First, for the perfect integrator, we obtain:

$$\lambda(t_0) = \lim_{n \to +\infty} \frac{1}{n} \log \frac{s(t_0)}{s(\varphi^{n+1}(t_0))}$$

which equals 0 if $s(\cdot)$ is bounded by positive numbers.

For the LIF, we obtain:

$$\lambda(t_0) = \lim_{n\to+\infty} \frac{1}{n}\left[\frac{t_0 - \varphi^{n+1}(t_0)}{\tau} + \sum_{k=1}^{n} \log \frac{RI(\varphi^k(t_0))}{RI(\varphi^k(t_0))) - 1} - \log(RI(\varphi^{n+1}(t_0)) - 1)\right]$$

If the last term does not cancel out, then $\lambda(t_0) = +\infty$, otherwise we obtain the formula in proposition 3. Note that the absolute value in the Lyapunov exponent is not necessary, because we always have $RI(\varphi^k(t_0)) \geq 1$, by theorem 2. □

The Lyapunov exponent we derived is $1/F$ times the one worked out in [6], where the author considered the exponent of the flow (on the potential axis), instead of the discrete dynamical system (on the time axis).

Application:

We use proposition 3 to prove in a restricted case that the Lyapunov exponent is negative.

Proposition 4. *The Lyapunov exponent of a LIF driven by an input $I(\cdot)$ taking two values 0 and I^* (and with isolated discontinuity points) is strictly negative if the proportion of time during which $I(t) = 0$ is positive.*

Proof. In this setting the input current is not continuous, but the flow is continuous, and differentiable almost everywhere, which is enough for the definition of the Lyapunov exponent. For simplicity, we set $\tau = 1$ (a change of variables). Here the model can spike only when $I(t) = I^*$. Thus the Lyapunov exponent equals

$$\lambda = -\frac{1}{F} + \log \frac{RI^*}{RI^* - 1}$$

The second term of the sum is the interspike interval for a LIF driven by a constant current I^*. Consider two successive spike times $\varphi^n(t_0)$ and $\varphi^{n+1}(t_0)$. If the set $I^{-1}(\{0\}) \cap [\varphi^n(t_0), \varphi^{n+1}(t_0)]$ has measure Δ_n, then we have:

$$\varphi^{n+1}(t_0) - \varphi^n(t_0) \geq \Delta_n + \log \frac{RI^*}{RI^* - 1}$$

because the potential cannot increase when $I(t) = 0$. It follows that

$$\frac{1}{F} \geq \lim_{n\to+\infty} \frac{1}{n} \sum_{k=0}^{n} \Delta_k + \log \frac{RI^*}{RI^* - 1}$$

The first term of this sum is the proportion of time during which $I(t) = 0$, which is positive by hypothesis. It follows that $\lambda < 0$. □

Proposition 4 can be extended with little work to the case when $I(t) \in \{I_0, I_1\}$ with $RI_0 < 1$ (below threshold) and $RI_1 > 1$ (above threshold).

2.5. Varying threshold and reset

Some Integrate-And-Fire models include a varying threshold $V_t(t)$ and/or reset $V_r(t)$ [12,1,6]. We can transform these variants into equivalent models of the type we study. By *equivalent models*, we mean that the models have the same spike map. Define the following change of variables:

$$U(t) = \frac{V(t) - V_r(t)}{V_t(t) - V_r(t)}$$

$U(t)$ equals 1 when $V(t) = V_t(t)$ and 0 when $V(t) = V_r(t)$, and satisfies the following differential equation:

$$\frac{dU}{dt} = g(U, t)$$

with

$$g(U, t) = \frac{f(V_r + (V_t - V_r)U, t) - \dot{V}_r}{V_t - V_r} - \frac{U(\dot{V}_t - \dot{V}_r)}{V_t - V_r}$$

With threshold $U_t = 1$ and reset $U_r = 0$, this new system is of the type defined in the introduction and is equivalent to the original system (same spike map). Hypothesis (H1) translates into:

$$(H1) \qquad \frac{\partial f}{\partial V} < \frac{\dot{V}_t - \dot{V}_r}{V_t - V_r}$$

and (H2) translates into:

$$(H2) \qquad f(V_r, t) > \dot{V}_r$$

When one of these hypotheses is satisfied, the results we have presented apply. The resulting spike map is invertible and continuous when $g(1, t) > 0$ for all t, i.e., $f(V_t, t) > \dot{V}_t$.

We will discuss several models of this type below.

LIF with modulation of the firing threshold

Hypothesis (H2) does not depend on the threshold value. Thus, for a positive input current, the LIF with any modulation of the firing threshold satisfies (H2). For the sinusoidal case $V_t(t) = 1 + K \sin \omega t$ and constant input I (with normalized constants $R = 1$ and $\tau = 1$), as studied in [1,6], the spike map is invertible if $f(V_t, t) > \dot{V}_t$ for all t, i.e., for $I > K\omega$. When φ is not invertible, it is still increasing on its range (theorem 3), and thus no chaotic behavior arises, and results in section 3 apply.

LIF with modulation of the reset potential

For the LIF with constant threshold and modulation of the reset potential, hypothesis (H1) means (with normalized constants) $\dot{V}_r < V_t - V_r$ (for all t) and (H2) means $I > V_r + \dot{V}_r$ (for all t). For a constant input, we have $I > V_t$ for all t (otherwise there is no spike), and thus (H1) implies (H2). When (H2) is satisfied, the resulting spike map is invertible and continuous. For the sinusoidal case $V_r(t) = K \sin \omega t$ and $V_t = 1$, (H2) means $K < I/\sqrt{1 + \omega^2}$, as derived in [1,6].

LIF with sinusoidal modulation of the firing threshold and the reset potential

Let us analyse the case of the LIF (with unit constants) driven by a (constant or time-varying) current $I(t)$, with threshold $V_t = 1 + A\sin\omega t$ and reset $V_r = B\sin\omega t$. Hypothesis (H1) means $I(t) > B\omega$ for all t. (H2) translates into

$$-1 < \frac{A\omega\cos\omega t - B\omega\cos\omega t}{1 + (A - B)\sin\omega t}$$

for all t. The denominator is always positive, since otherwise we would have $V_t < V_r$ for some t. Thus we obtain

$$(A\omega - B\omega)\cos\omega t + (A - B)\sin\omega t > -1$$

which means

$$|A - B|\sqrt{1 + \omega^2} < 1$$

Note that the condition is independent of the input current. In particular, hypothesis (H1) is satisfied if the modulation is identical on threshold and reset.

Perfect integrator with modulation of the firing threshold and the reset potential

Let us consider the perfect integrator, described by equation (4), with threshold $V_t(t)$ and reset $V_r(t)$. Hypothesis (H1) means $\dot{V}_t - \dot{V}_r > 0$ for all t, and thus is never satisfied for a periodic modulation. Hypothesis (H2) means $s(t) > \dot{V}_r$ for all t. For example, for a constant input A and a sinusoidal reset potential $V_r(t) = B\sin\omega t$, (H2) is satisfied if and only if $A > B\omega$, and in this case the spike map is increasing, although it may not be continuous. In fact, a perfect integrator with varying threshold and reset potential is equivalent to a model of the type

$$f(V, t) = A(t) + B(t)V$$

with fixed threshold and reset potential, where $B(t)$ changes sign.

3. Periodic input

In this section we focus on the case of periodic input, i.e., we assume that $t \mapsto f(V, t)$ is periodic. For simplicity, we assume the period is 1 (up to a change of variables).

3.1. Condition for sustained firing

Theorem 1 can be refined in the following way:

Proposition 5. *Suppose (H1). There are infinitely many spikes if and only if* $\sup x^*(\cdot) > 1$, *where* $x^*(\cdot)$ *is the unique periodic solution of equation (1).*

Proof. The existence and uniqueness of $x^*(\cdot)$ follows from the leak hypothesis (H1) and can be defined as:

$$x^*(t) = \lim_{s \to -\infty} \Phi(0, s, t)$$

For the LIF, it can be expressed explicitly:

$$x^*(t) = \frac{1}{\tau(e^{T/\tau} - 1)} \int_0^T RI(t+u)e^{u/\tau} du$$

where T is the period.

If $\sup x^*(\cdot) \leq 1$, then the periodic solution is below threshold, so that any run starting below threshold cannot reach it (since it cannot cross the trajectory of $x^*(\cdot)$). It follows from theorem 1 that all runs have finitely many spikes. Conversely, suppose $\sup x^*(\cdot) > 1$, so that there is t^* such that $x^*(t^*) > 1$. Suppose there is a run that stops firing after time t_0, which implies that there is a solution $x(\cdot)$ such that $x(t) < 1$ for all $t > t_0$. Hypothesis (H1) implies that

$$\lim_{t \to +\infty} (x^*(t) - x(t)) = 0$$

which is impossible, because $x^*(t^* + n) = x^*(t^*) > 1$ for all integer n. Therefore all runs have infinitely many spikes. □

3.2. Phase-locking

When the model is periodically driven, the responses are said to be phase-locked to the stimulus if the input induces a stable periodic pattern of spikes, where the period is a multiple of the input period. This phenomenon has been observed experimentally [26,3,14,21,33] and studied mathematically in various models [18,13, 17,12,1].

The periodicity of the input implies that $\varphi(t+1) = \varphi(t) + 1$ for all t. By theorem 3, φ is always increasing on its range. If φ is a continuous invertible map (when $f(1,t) > 0$ for all t), it is the lift of a homeomorphism of the circle. If it is only increasing (but not continuous), it is the lift of an orientation-preserving circle map. Both are well-known mathematical objects [4,25,9,7,27,32,36,28,8], whose dynamics are determined by their *rotation number* α, which is the inverse of the firing rate, as defined in section 2.3. We briefly recall and comment the basic results:

1. The rotation number exists and does not depend on the initial condition. It is continuous with respect to the spike map [25,27,28]. Thus if the input is smoothly parameterized, the rotation number is a continuous function of the parameters.
2. If $\alpha \in \mathbb{Q}$, then all orbits under φ tend to a periodic orbit with the same period [25,7,27,28]. There may be several periodic orbits.

3. If $\alpha \in \mathbb{R} \setminus \mathbb{Q}$, then φ is uniquely ergodic and the sequence $\varphi^n(t)$ modulo the period is dense in either the circle or a Cantor set. Thus it is a Cantor set if φ is discontinuous ($f(1,t) < 0$ for some t). If the circle map induced by φ is a $\mathcal{C}^2$ diffeomorphism of the circle, which is the case if $f \in \mathcal{C}^2$ and $f(1,t) > 0$ for all t (by theorem 2), it is the circle, and moreover φ is topologically equivalent to a translation [9].

The unique ergodicity (when the rotation number is irrational) implies in particular that the distribution of inter-spike intervals does not depend on the initial condition. The property that φ is topologically equivalent to a translation implies that spike times depend on the initial condition (no convergence) and the dynamics are unstable, whether under noise or deterministic perturbations.

Suppose the input depends smoothly ($\mathcal{C}^1$) on a parameter λ. Then the following results apply:

1. if the circle maps induced by φ_λ are $\mathcal{C}^2$ diffeomorphisms ($f \in \mathcal{C}^2$ and $f_\lambda(1,t) > 0$ for all t), then unless the rotation number is the same for all parameters, the set of parameter values for which the rotation number is irrational has positive measure [15].
2. if the φ_λ are discontinuous, the set of parameter values for which the rotation number is irrational has null measure [19,36].

We illustrated these results in Figure 2, which shows the phase density of the orbit of 0 for a parameterized sinusoidally driven LIF. The spike map is continuous in the upper half of Figure 2.A and on the left of Figure 2.B, and is discontinuous in the lower half of Figure 2.A and on the right of Figure 2.B.

In the second case (discontinuous spike map), when φ_λ increases with λ (e.g., for the LIF, if the input current decreases), every rational rotation number between the two endpoints is reached in a closed interval of parameters, and there is phase-locking in the interior of this interval. Thus there is phase-locking almost everywhere. However, in the first case (continuous spike map), some or all rational rotation numbers may be reached for only one parameter value, which implies no phase-locking. This can happen if the circle map induced by φ_λ is conjugated with a rational rotation, i.e., if for some integers p and q, $\varphi^p(t) = t + q$ for all t. This problem was not addressed in previous studies, but it is an important point, since it actually happens for the perfect integrator, which is never phase-locked (see section 4). We shall show below that, although this is not impossible for the LIF, the leak imposes severe constraints on the inputs that would induce such a situation.

Conjugacy with a rational rotation for the LIF

We consider the LIF model with $\tau = 1$. When the rotation number is q/p, then the conjugacy with a rational rotation means:

$$\varphi^p(t) = t + q$$

and thus:

$$\frac{d}{dt}(\varphi^p) = 1$$

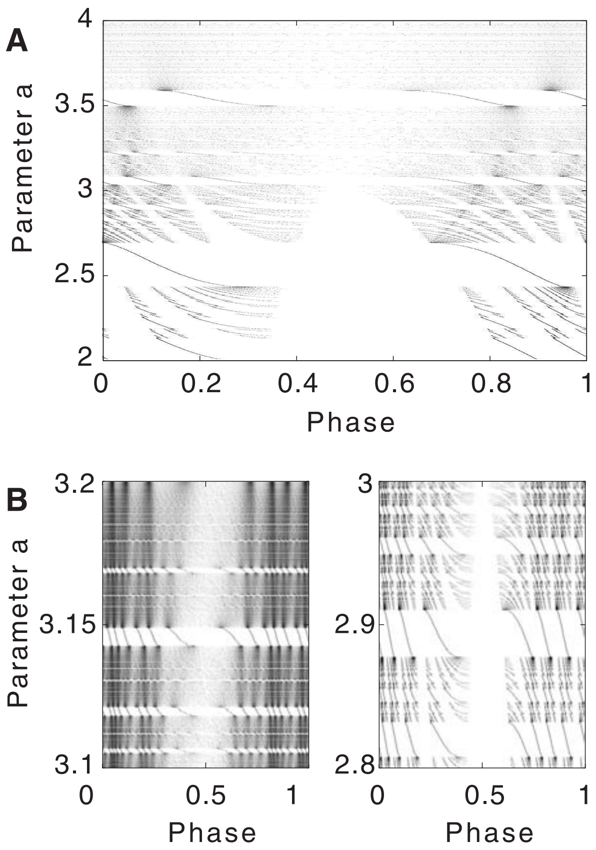

Fig. 2. *Orbit of* 0 *under* φ *for a parameterized family of periodic inputs to the LIF*. The model was a LIF described by $\frac{dV}{dt} = -V + a + 2\sin 2\pi t$, where a is a parameter. For each parameter value, the orbit of 0 under the spike map φ (modulo 1) is displayed horizontally as black dots; the first 20000 iterations of φ were discarded and the next 20000 were displayed. Light areas correspond to low phase densities. The spike map is continuous for $a > 3$ and discontinuous for $a < 3$. (A) Orbit of 0 for 2000 parameter values between 2 and 4. (B, left) Orbit of 0 for 2000 parameter values between 3.1 and 3.2, an interval where φ is continuous. (B, right) Orbit of 0 for 2000 parameter values between 2.8 and 3., an interval where φ is discontinuous.

First, if the rotation number is an integer q ($p = 1$), then, using proposition 3, we have for all t:

$$1 = \frac{RI(t)}{RI(t) - 1} e^{-q}$$

which implies that $I(\cdot)$ is constant, determined by q. Therefore, for each integer rotation number, there is only one input current that induces a conjugacy with a rotation. In contrast, for the perfect integrator, this is the case for all stimuli $s(\cdot)$ such that $\int_0^1 s \in \mathbb{N}^*$(hyperplanes).

The calculation is more complex when $p \neq 1$ and leads to the following constraint:

$$e^q = \prod_{n=0}^{p-1} \frac{RI(\varphi^n(t))}{RI(\varphi^n(t)) - 1} = \prod_{n=0}^{p-1} \left(1 + \frac{1}{RI(\varphi^n(t)) - 1}\right)$$

for all t. This functional equation is harder to deal with, because φ is an implicit function of I. To give an idea of how restrictive this functional constraint is, let us study the special case $I(t) = A + B\sin(2\pi t)$ and show that it can never be conjugated to a rotation with angle 1/2 ($p = 2$, $q = 1$). Define

$$F : x \mapsto 1 + \frac{1}{Rx - 1}$$

which is a decreasing function. The maximum of $F \circ I$ is $F(A - B)$, the minimum is $F(A + B)$. We have

$$F(I) \times F(I \circ \varphi) = e^q$$

It follows that $F(I)$ reaches its minimum when $F(I \circ \varphi)$ reaches its maximum, and conversely. Thus, for the input we considered, we must have $\varphi(1/4) = 3/4$, and $\varphi(3/4) = 1 + 1/4$. Integrating the differential equation shows that these two equalities are contradictory.

4. The perfect integrator

Up to a change of variables, we assume $V_r = 0$ and $V_t = 1$. We start with a simple, but useful, observation:

Lemma 2. *The difference between any two runs is constant modulo* 1.

Proof. Indeed, the difference between two runs remains constant when there is no spike (the derivative is 0), and increases or decreases by 1 when there is a spike. It follows that all trajectories are unstable. □

4.1. Condition for sustained firing

Theorem 4. *There are infinitely many spikes if, and only if,*

$$\lim_{t \to +\infty} \int_0^t s = +\infty$$

If $s(\cdot)$ is 1-periodic, this means $\int_0^1 s > 0$.

The firing rate is

$$\lim_{t \to +\infty} \frac{1}{t} \int_0^t s$$

(if well-defined).

Proof. Consider a solution $x(\cdot)$ starting from x at time 0 and the corresponding run $V(\cdot)$, with $V(0) = x$. For any t, the difference $x(t) - V(t)$ is the number of spikes between 0 and t. Thus, there are infinitely many spikes if and only if $x(t)$, which equals $\int_0^t s$, tends to $+\infty$. At time $\varphi^n(0)$, there have been n spikes and the potential is 0 (after reset), thus $x(\varphi^n(0)) = n$, i.e.:

$$\frac{1}{\varphi^n(0)} \int_0^{\varphi^n(0)} s = \frac{n}{\varphi^n(0)}$$

which gives the expression of the firing rate. □

4.2. Conjugacy with a rotation

We restrict ourselves to the case when $s(\cdot)$ is 1-periodic and the firing rate is positive, i.e., $\int_0^1 s > 0$. Since $\varphi(t+1) = \varphi(t) + 1$, the spike map induces a circle map ϕ, i.e., $\phi(t)$ is $\varphi(t)$ modulo 1.

Theorem 5. *The restriction of ϕ to its range is topologically equivalent to a rotation of angle $\frac{1}{\int_0^1 s}$.*

Proof. Define $h : \mathbb{R} \to \mathbb{R}$ by:

$$h(t) = \frac{\int_0^t s}{\int_0^1 s}$$

We have $h(t+1) = h(t) + 1$ and h is continuous. By definition of φ, we have

$$\int_t^{\varphi(t)} s = 1$$

and thus

$$\int_0^{\varphi(t)} s = \int_0^t s + 1$$

It follows that $h \circ \varphi = t_\alpha \circ h$, where t_α is the translation $t_\alpha : t \mapsto t + \alpha$, with

$$\alpha = \frac{1}{\int_0^1 s}$$

The spike map φ is not continuous if $s(t) < 0$ for some t. Let t_1 be the right endpoint of an interval of the range of φ and consider the solution $x(\cdot)$ starting from 1 (threshold) at time t_1. Then, if $t_2 > t_1$ is the first time such that $x(t_2) = 1$, t_2 is the left endpoint of the next interval. Since $\int_{t_1}^{t_2} s = 0$, $\varphi(t_1) = \varphi(t_2)$ and $h(t_1) = h(t_2)$. It follows that the restrictions of φ and h to $Im\,\varphi$ (range of φ) are both continuous, and they are also increasing. Therefore, they induce homeomorphisms of the circle and the equality $h \circ \varphi = t_\alpha \circ h$ implies that $\phi_{|\,Im\,\phi}$ is conjugated with a rotation of angle α. This is illustrated in Figure 3, which shows the spike map of a periodically driven perfect integrator and the restriction to its range. The spike map is discontinuous and not increasing, but its restriction is both continuous and increasing. □

Thus, when $\int_0^1 s \in \mathbb{Q}$, all trajectories are periodic, and when $\int_0^1 s \in \mathbb{R} \setminus \mathbb{Q}$, the system is uniquely ergodic with the invariant measure given below.

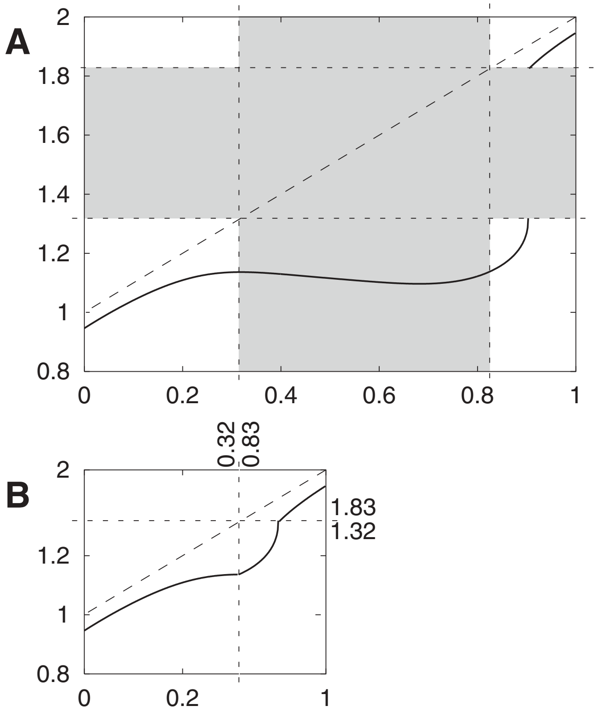

Fig. 3. *The spike map of the periodically driven perfect integrator, restricted to its range, is the lift of a homeomorphism of the circle*. (A) Graph of the function φ for the perfect integrator described by equation $\frac{dV}{dt} = 1.2 + 2.1\cos(2\pi t) + 0.5\cos(4\pi t)$. The spike map is discontinuous at 0.9 and is not increasing (it is actually decreasing in intervals not belonging to the range of φ). Areas not belonging to the range of φ are depicted in grey. (B) Restriction of φ to its range, obtained by removing the shaded areas in (A). The resulting function is increasing and continuous.

4.3. Invariant measure

Here we also restrict ourselves to the case when $s(\cdot)$ is 1-periodic and the firing rate is positive.

Proposition 6. *The measure μ_s defined by:*

$$\mu_f(A) = \int_{A \cap Im\,\varphi} s$$

for all borelian sets $A \subset \mathbb{R}$ is an invariant measure for φ.

Thus, when $\int_0^1 s \in \mathbb{R} \setminus \mathbb{Q}$, the measure μ_f (modulo 1) gives the distribution of phases of any orbit.

Proof. We need to show that

$$\mu_f(\varphi^{-1}(A)) = \mu_f(A)$$

Since $\varphi^{-1}(A) = \varphi^{-1}(A \cap Im\,\varphi)$ and $\mu_f(A) = \mu_f(A \cap Im\,\varphi)$, it is enough to prove the equality for $A \subset Im\,\varphi$, and thus it is equivalent to prove:

$$\mu_f(A) = \mu_f(\varphi(A))$$

Because μ_f is regular, we only need to prove the equality for segments $[a, b] \subset Im\,\varphi$. We have:

$$\begin{aligned}
\mu_f([a,b]) &= \int_a^b s \\
&= \int_a^{\varphi(a)} s + \int_{\varphi(a)}^{\varphi(b)} s + \int_{\varphi(b)}^{b} s \\
&= 1 + \int_{\varphi(a)}^{\varphi(b)} s - 1 \\
&= \mu_f(\varphi([a,b]))
\end{aligned}$$

which proves the proposition. □

5. Conclusion

We have proved general mathematical results about a broad class of one-dimensional spiking neuron models, that includes many variants of the LIF used in numerical simulations, where the input can be inserted multiplicatively in the equation through conductances, or additively as an input current. It also includes the quadratic integrate and fire model with reset, provided the reset value V_r is low enough.

Models satisfying hypothesis (H1) (leak) or (H2) (trajectories above reset) share the following properties:

- Sustained firing and the firing rate are independent of the initial condition.
- There is no chaotic behavior.
- Phase-locking to a periodic input always occurs if the vector field does not always point upward at threshold (i.e., for the standard LIF, if the current crosses the threshold), and occurs sometimes if the vector field always points upward at threshold (i.e., for the LIF, if the current is above threshold). When the model is not phase-locked, the dynamics are unstable, whether under noise or deterministic perturbation. Multiple phase-locked solutions can coexist, but the rotation number is unique.

Models with modulations of the firing threshold and reset potential can be transformed into equivalent models with constant threshold and reset, but do not always satisfy hypotheses (H1) and (H2), and thus chaotic behavior may arise. The perfect integrator is a very special spiking model that never phase-locks to a periodic input. Because of its structural unstability, which makes precise spike timing irrelevant, it can be seen as a spiking implementation of a frequency model.

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