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On the interspike-intervals of periodically-driven integrate-and-fire models

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ABSTRACT

We analyze properties of the firing map, which iterations give information about consecutive spikes, for periodically driven linear integrate-and-fire models. By considering locally integrable (thus in general not continuous) input functions, we generalize some results of other authors. In particular, we prove theorems concerning continuous dependence of the firing map on the input in suitable function spaces. Using mathematical study of the displacement sequence of an orientation preserving circle homeomorphism, we provide a complete description of regularity properties of the sequence of interspike-intervals and behaviour of the interspike-interval distribution. Our results allow to explain some facts concerning this distribution observed numerically by other authors. These theoretical findings are illustrated by computational examples.

1. Introduction

The scope of this paper are one-dimensional integrate-and-fire (IF) models

$$\dot{x} = F(t,x), \quad F: \mathbb{R}^2 \to \mathbb{R} \tag{1}$$

$$x(t) = x_T \quad \Longrightarrow \quad x(t^+) = x_r. \tag{2}$$

The dynamical variable $x(t)$ evolves according to the differential equation (1) as long as it reaches the threshold-value $x = x_T$, say at some time t_1. Next it is immediately reset to a resting value $x = x_\mathrm{r}$ and the system continues again from the new initial condition (x_r, t_1) until possibly next time t_2 when the threshold is reached again, etc. This resetting condition is written as (2). Hybrid dynamical systems of this kind are present in neuroscience, where the threshold-reset behaviour is supposed to mimic *spiking* (generation of action potential) in real neurons. Of course, x_r and x_T could be arbitrary constant values and, moreover,

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it is possible to consider varying (i.e. time-dependant) threshold and reset, which allows to introduce to these one-dimensional spiking models some other more biologically realistic phenomena (such as refractory periods and threshold modulation [9]). However, often analysis of models with varying threshold and the reset can be reduced to studying the case of constant x_{r} and x_T through the appropriate change of variables (see e.g. [3]).

Except for the models of neuron's activity IF systems (and circle mappings induced by them in case of periodic forcing) can also be used in modeling of cardiac rhythms and arrhythmias [1], in some engineering applications (e.g. electrical circuits of certain type, see [4]) or as models of many other phenomena, which involve accumulation and discharge processes that occur on significantly different time scales.

For simplicity set $x_r = 0$ and $x_T = 1$ and suppose that Eq. (1) has the property of existence and uniqueness of the solution for every initial condition $(t_0, x_0) \in \mathbb{R}^2$.

Definition 1.1. The firing map for the system (1)–(2) is defined as

$$\Phi(t) := \inf\{s > t\colon\ x(s; t, 0) \geq 1\}, \quad t \in \mathbb{R},$$

where $x_r = 0$, $x_T = 1$, and $x(\cdot\,; t, 0)$ denotes the solution of (1) satisfying the initial condition $(t, 0)$.

Of course, the firing map $\Phi(t)$ does not need to be well defined for every $t \in \mathbb{R}$ since for some t it might happen that the solution $x(\cdot; t, 0)$ never reaches the value $x = 1$. Thus the natural domain of Φ is the set (compare with [5]):

$$\mathrm{D}_\Phi = \{t \in \mathbb{R}\colon\ \text{there exists } s > t \text{ such that } x(s; t, 0) = 1\}.$$

Later on we will give necessary and sufficient conditions for the firing map $\Phi : \mathbb{R} \to \mathbb{R}$ of the models considered to be well-defined.

The consecutive firing times t_n can be recovered via the iterations of the firing map:

$$t_n = \Phi^n(t_0) = \Phi(t_{n-1}) = \inf\{s > \Phi^{n-1}(t_0)\colon\ x\big(s; \Phi^{n-1}(t_0), 0\big) = 1\}.$$

The sequence of interspike-intervals (time intervals between the consecutive resets) is given as

$$t_n - t_{n-1} = \Phi^n(t_0) - \Phi^{n-1}(t_0).$$

There are two basic quantities associated with the integrate-and-fire systems, the firing rate:

$$\mathrm{FR}(t_0) = \lim_{n\to\infty} \frac{n}{t_n} = \lim_{n\to\infty} \frac{n}{\Phi^n(t_0)},$$

and its multiplicative inverse, which is the average interspike-interval:

$$\mathrm{aISI}(t_0) = \lim_{n\to\infty} \frac{t_n}{n} = \lim_{n\to\infty} \frac{\Phi^n(t_0)}{n}.$$

Obviously, in general the limits above might not exist or depend on the initial condition $(t_0, 0)$.

In [14] the following observation for periodically driven models was made (the remark was not directly formulated in this way but it is a well-known fact):

Fact 1.2. *If the function F in (1) is periodic in t (that is, there exists $T > 0$ such that $F(t, x) = F(t + T, x)$ for all x and t), then the firing map Φ has periodic displacement $\Phi - \mathrm{Id}$. In particular for $T = 1$ we have $\Phi(t + 1) = \Phi(t) + 1$ and thus Φ is a lift of a degree one circle map under the standard projection $\mathfrak{p} : t \mapsto \exp(2\pi\imath t)$.*

In case of periodic forcing, the underlying circle map $\varphi : S^1 \to S^1$ such that Φ is a lift of φ, is referred to as the *firing phase map*.

In particular, we will take into account the Leaky Integrate-and-Fire model (LIF):

$$\dot{x} = -\sigma x + f(t) \tag{3}$$

and the Perfect Integrator (PI):

$$\dot{x} = f(t), \tag{4}$$

where $f : \mathbb{R} \to \mathbb{R}$ will be, usually, periodic and not necessary continuous but only locally-integrable.

Mathematical analysis of one-dimensional IF models was performed e.g. in [3,5,9]. Firing map was also investigated combining analytical and numerical approach ([6] – phase-locking and Arnold tongues, [14] – LIF model with sinusoidal input, [18] – LIF with periodic input, [23] – LIF with periodic input and noise, etc.). Analytical results concerning the firing map Φ were obtained assuming that $F(t, x)$ is regular enough (always at least continuous) and often periodic in t.

Allowing also not continuous functions might be important from the point of view of applications where the inputs are often not continuous. Moreover, although as for the firing map of systems with continuous and periodic drive some rigorous results have been proved (e.g. in [3,5,9]), the sequence of interspike-intervals even in such a case, according to our knowledge, has not been investigated in detail yet. However, sometimes the sequence of interspike-intervals might be of greater importance than the exact spiking times themselves [20]. Interspike-intervals are said to be used in information encoding by neurons (see [10] and references therein).

We will often use mathematical results proved by us in [16]. But the main problem of this paper is to study the properties of interspike-interval sequence in the models of integrate-and-fire type, i.e. defined by an equation of the form $\dot{x} = F(t, x)$ with the resetting mechanism, with emphasis placed on the analytical form of $F(t, x)$ stimulated by applications, whereas the work [16] concerns only with the displacement sequence of a circle homeomorphism.

In Section 2 we consider the LIF model and redefine the notion of the firing map so that it is well-defined for input functions $f \in L^1_{\mathrm{loc}}(\mathbb{R})$. Then we provide sufficient conditions for the continuity of the mapping $f \mapsto \Phi$ from $L^1_{\mathrm{loc}}(\mathbb{R})$ into $C^0(\mathbb{R})$. This enables us to use existing results for circle homeomorphisms in Section 3 where we consider locally integrable periodic inputs. In particular, we obtain results concerning regularity of the interspike-interval sequence $\mathrm{ISI}_n(t) := \Phi^n(t) - \Phi^{n-1}(t)$: unless the input f is constant, the sequence $\mathrm{ISI}_n(t)$ is (asymptotically) periodic or almost strongly recurrent (18), depending on the rotation number of the underlying circle homeomorphism $\varphi := \Phi \bmod 1$. Next, we prove theorems on distribution of interspike-intervals for case of irrational rotation number (continuity of the distribution with respect to the input in terms of weak convergence of measures and the existence of the density of this distribution, under further assumptions). In the end we show that this distribution is well approximated (in the Fortet–Mourier metric) by empirical distributions derived for arbitrary trajectories of the LIF model with every other input function $\tilde{f} \in L^1_{\mathrm{loc}}(\mathbb{R})$, sufficiently close to f, independently of whether the induced rotation number of the approximating system is irrational or not. This phenomenon is illustrated by the numerical example.

2. Locally integrable input functions for LIF and PI models: some general properties

In the section we do not make yet the assumption that f is periodic and that is why the results presented below have general character.

2.1. Preliminary definitions and facts

Unless stated otherwise, considering the LIF-model (3) we assume that $\sigma \geq 0$, admitting also $\sigma = 0$ to include Perfect Integrator (4) as well. As for the function f in (3) and (4), we assume that $f \in L^1_{\mathrm{loc}}(\mathbb{R})$, i.e. for every compact set $A \subset \mathbb{R}$ the Lebesgue integral $\int_A |f(u)|\,du$ exists and is finite. For such functions we redefine the notion of the firing map:

Definition 2.1. For systems (3) and (4) the firing map Φ is defined as

$$\Phi(t) := \inf\left\{ t_* > t:\ \mathrm{e}^{\sigma t} \leq \int_t^{t_*} [f(u) - \sigma]\mathrm{e}^{\sigma u}\,du \right\}. \tag{5}$$

The above definition is generalization of the "classical" firing map Φ for the differential equation (3) with f being continuous, since from Definition 1.1 Φ has to satisfy the implicit equation:

$$\mathrm{e}^{\sigma t} = \int_t^{\Phi(t)} [f(u) - \sigma]\mathrm{e}^{\sigma u}\,du. \tag{6}$$

Lemma 2.2. *The necessary and sufficient condition for the firing map (5) $\Phi : \mathbb{R} \to \mathbb{R}$ to be well-defined is that*

$$\limsup_{t\to\infty} \int_0^t [f(u) - \sigma]\mathrm{e}^{\sigma u}\,du = \infty. \tag{7}$$

Proof. Suppose that (7) is satisfied. Choose $t_0 \in \mathbb{R}$. Then $\limsup_{t\to\infty} \int_{t_0}^t [f(u) - \sigma]\mathrm{e}^{\sigma u}\,du = \infty$ and hence there exists t_* such that $\int_{t_0}^{t_*} [f(u) - \sigma]\mathrm{e}^{\sigma u}\,du \geq \mathrm{e}^{\sigma t_0}$. Consequently $\Phi(t_0)$ is defined.

Now assume that $\Phi : \mathbb{R} \to \mathbb{R}$ is defined, i.e. for every $t \in \mathbb{R}$ there exists $t_* = \Phi(t)$ such that $\mathrm{e}^{\sigma t} = \int_t^{\Phi(t)} [f(u)-\sigma]\mathrm{e}^{\sigma u}\,du$. In particular, by Definition 2.1, taking $t = 0$ we obtain that $n = \int_0^{\Phi^n(0)} [f(u)-\sigma]\mathrm{e}^{\sigma u}\,du$. Thus $\lim_{n\to\infty} \int_0^{t_n} [f(u) - \sigma]\mathrm{e}^{\sigma u}\,du = \infty$ for $t_n = \Phi^n(0)$, which proves the statement. □

Lemma 2.3. *In the model (3) with $\sigma \geq 0$ and $f \in L^1_{\mathrm{loc}}(\mathbb{R})$, suppose that there exists $\varsigma > 0$ such $f(t) - \sigma > \varsigma$ a.e. (i.e. for almost all $t \in \mathbb{R}$ in the sense of Lebesgue measure). Then the firing map $\Phi : \mathbb{R} \to \mathbb{R}$ is a homeomorphism.*

Proof. Notice that under the stated assumptions, $D_\Phi = \mathbb{R}$ on the ground of Lemma 2.2 because for every fixed t the integral $\int_t^{t_*} [f(u) - \sigma]\mathrm{e}^{\sigma u}\,du$ is a strictly increasing unbounded continuous function of t_*. It follows that Φ is also a continuous monotone function. From (5) we have $0 \leq \Phi(t) - t < 1/\varsigma$ which gives that $\lim_{t\to\infty} \Phi(t) = \infty$ and $\lim_{t\to-\infty} \Phi(t) = -\infty$ and ends the proof. □

We prove also the following simple lemma:

Lemma 2.4. *Suppose that $f \in L^1_{\mathrm{loc}}(\mathbb{R})$. Then every run of the model (3) has only finite number of firings in every bounded interval.*

Proof. Suppose that there is a firing at time t_0. Denote $t_n = \Phi^n(t_0)$ for $n \in \mathbb{N}$. If $\{t_n\} \subset [a, b]$ for some bounded interval $[a, b] \subset \mathbb{R}$ (i.e. $\lim_{n\to\infty} t_n = t_* \in (a, b]$ as sequence t_n is non-decreasing), then from Eq. (5)

(or equivalently from the solution $x(t;t_0,0) = \mathrm{e}^{-\sigma t}\int_{t_0}^{t_1} f(u)\mathrm{e}^{\sigma u}\,du$ of (3) and the condition $x(t_1;t_0,0) = 1$ for the firing at time t_1) we obtain that

$$\mathrm{e}^{\sigma t_1} = \int_{t_0}^{t_1} f(u)\mathrm{e}^{\sigma u}\,du \le \mathrm{e}^{\sigma t_1}\int_{t_0}^{t_1} \left|f(u)\right|du$$

and thus $1 \le \int_{t_0}^{t_1}|f(u)|\,du$ and in general $1 \le \int_{t_{n-1}}^{t_n}|f(u)|\,du$ for $n \in \mathbb{N}\cup\{0\}$. From this we estimate that

$$n \le \int_{t_0}^{t_n}\left|f(u)\right|du \le \int_a^b \left|f(u)\right|du.$$

As n is arbitrary, it results in $\int_a^b |f(u)|\,du = \infty$ which contradicts that $f \in L^1_{\mathrm{loc}}(\mathbb{R})$. □

2.2. Special properties of the Perfect Integrator

The simple model (4) has many distinct properties than other models. Here we list some of them (for the proofs we refer to [15]).

Fact 2.5. *Suppose that $f \in L^1_{\mathrm{loc}}(\mathbb{R})$ and let Φ be the firing map for the Perfect Integrator (4). Then:*

1. *The consecutive iterates of the firing map are equal to*

$$\Phi^n(t) = \min\{s > t\colon\ x(s;t,0) = n\} \tag{8}$$

and there is only a finite number of firings in every bounded interval.
2. *Φ is increasing, correspondingly, non-decreasing, iff $f(t) > 0$, or $f(t) \ge 0$ respectively, a.e. in $\mathbb{R}$.*
3. *If $f(t) \ge 0$ a.e., then*
   (i) Φ is left continuous,
   (ii) Φ is not right continuous at every point $\bar{a} \in \Phi^{-1}(a)$ for which there exists $\delta_0 > 0$ such that $f(t) = 0$ almost everywhere in $[a, a+\delta_0]$. Furthermore, such points are the only points of discontinuity of Φ.
4. *If $f(t) > 0$ a.e., then Φ is continuous.*

For the simplified model (4) we even have the analytical expression for the firing rate. Indeed, the following theorem was proved in [3] (originally for f continuous but the proof is valid for $f \in L^1_{\mathrm{loc}}(\mathbb{R})$ as well):

Theorem 2.6. *Suppose that for the model (4) there exists a finite limit*

$$r = \lim_{t\to\infty}\frac{1}{t}\int_0^t f(u)du. \tag{9}$$

Then for every point $t_0 \in \mathbb{R}$ the firing rate $r(t_0)$ exists and is given by the formula (9). In particular, the firing rate $r(t)$ does not depend on t.

The proof of the above theorem is immediate: It relies on the fact that $n = \int_{t_0}^{\Phi^n(t_0)} f(u)\,du$ for every t_0 by definition of the firing map and if the above limit exists and equals r, then also $\lim_{n\to\infty}\frac{1}{\Phi^n(t_0)}\int_{t_0}^{\Phi^n(t_0)} f(u)\,du = r$.

Example 1. Let

$$f(t) = \begin{cases} 2, & t \in [n, n+1/2],\ n \in \mathbb{Z}; \\ 0, & t \in (n+1/2, n+1). \end{cases}$$

We easily get that $\mathcal{M}(f) = \varrho = 1$ and that

$$\Phi(t) = \begin{cases} t+1, & t \in (k, k+1/2),\ k \in \mathbb{Z}; \\ k+1/2, & t = k; \\ k+3/2, & t \in [k+1/2, k+1). \end{cases}$$

In particular, Φ is left-continuous, non-decreasing and constant in the intervals $(k+1/2, k+1)$. However, it is not right-continuous at the points $t = k$. Note that at such points $\Phi(t) = k+1/2$ and $f = 0$ in the right neighbourhood $(k+1/2, k+1)$ of $\Phi(t)$ which agrees with Fact 2.5.

2.3. Continuous dependence on the input function

Definition 2.7. The essential supremum of the Lebesgue measurable function $f : \mathbb{R} \to \mathbb{R}$ is defined as

$$\operatorname{ess\,sup} f := \inf\bigl\{a \in \mathbb{R}:\ \Lambda\bigl(\{t:\ f(t) > a\}\bigr) = 0\bigr\}, \tag{10}$$

where Λ denotes the Lebesgue measure on $\mathbb{R}$. If $\{a \in \mathbb{R}:\ \Lambda(\{t:\ f(t) > a\}) = 0\} = \emptyset$, then we write that $\operatorname{ess\,sup} f = \infty$.

If $\operatorname{ess\,sup} |f| < \infty$, then we say that f is *essentially bounded*.

We also define the essential supremum of f over a compact subset $K \subset \mathbb{R}$ as

$$\operatorname*{ess\,sup}_K f := \inf\bigl\{a \in \mathbb{R}:\ \Lambda\bigl(\{t \in K:\ f(t) > a\}\bigr) = 0\bigr\}.$$

In particular, for the measurable functions f and g, $\operatorname{ess\,sup}_K |f - g| = a_*$ for some $a_* \geq 0$ implies that $|f(t) - g(t)| \leq a_*$ a.e. in K. In general an essentially bounded function does not need to be measurable, since equivalently we might say that a_* is an essential supremum of f if the set $\{t:\ f(t) > a\}$ is contained in some set of measure zero. However, we will consider only locally integrable functions, thus also measurable. Notice that when f is essentially bounded (and measurable), it is also locally integrable. However, a locally integrable function does not need to be essentially bounded: take for example $f(t) = \frac{1}{\sqrt{|t|}}$ (with arbitrary finite value at $t = 0$).

We consider the space $L^\infty_{\mathrm{loc}}(\mathbb{R})$ of all locally bounded functions (i.e. $f \in L^\infty_{\mathrm{loc}}(\mathbb{R})$ iff $\operatorname{ess\,sup}_K |f| < \infty$ for every compact $K \subset \mathbb{R}$) as the *Frechet space* with semi-norms and metric defined respectively as

$$\|f\|_{L^\infty([-k,k])} := \operatorname*{ess\,sup}_{[-k,k]} |f|$$

and

$$\mathrm{d}_{L^\infty_{\mathrm{loc}}}(f, g) := \sum_{k=1}^{\infty} \frac{1}{2^k} \frac{\|f-g\|_{L^\infty([-k,k])}}{1 + \|f-g\|_{L^\infty([-k,k])}}.$$

We will mainly consider measurable functions $f \in L^\infty_{\mathrm{loc}}(\mathbb{R})$. Note that such functions form a subspace of $L^1_{\mathrm{loc}}(\mathbb{R})$, which is again a Frechet space with the following semi-norms:

$$\|f\|_{L^1([-k,k])} := \int\limits_{[-k,k]} \bigl|f(u)\bigr|\,du, \quad k = 1, 2, 3, \ldots.$$

The metric on $L^1_{\mathrm{loc}}(\mathbb{R})$ can be defined as

$$\mathrm{d}_{L^1_{\mathrm{loc}}}(f,g) := \sum_{k=1}^{\infty} \frac{1}{2^k} \frac{\|f-g\|_{L^1([-k,k])}}{1+\|f-g\|_{L^1([-k,k])}}.$$

$L^1_{\mathrm{loc}}(\mathbb{R})$ with this metric is a complete metric space (see for instance [17, p. 2]).

Similarly in spaces $C^0(\mathbb{R})$ and $C^m(\mathbb{R})$ of, respectively, continuous and m-times continuously differentiable functions $f:\mathbb{R}\to\mathbb{R}$, we introduce the metrics $d_{C^0(\mathbb{R})}$ and $d_{C^m(\mathbb{R})}$ with the use of semi-norms:

$$\|f\|_{C^0([-k,k])} := \sup_{t\in[-k,k]} \big|f(t)\big|, \quad k=1,2,3,\dots$$

and

$$\|f\|_{C^m([-k,k])} := \max\Big\{ \sup_{t\in[-k,k]} \big|f(t)\big|, \sup_{t\in[-k,k]} \big|f^{(1)}(t)\big|, \dots, \sup_{t\in[-k,k]} \big|f^{(m)}(t)\big| \Big\}, \quad k=1,2,3,\dots$$

where $f^{(n)}(t)$ is the n-th derivative of f.

Proposition 2.8. *In the model (3) with $\sigma \ge 0$ and measurable $f \in L^\infty_{\mathrm{loc}}(\mathbb{R})$, the mapping $f \mapsto \Phi$ is continuous from the $L^\infty_{\mathrm{loc}}(\mathbb{R})$-topology into $C^0(\mathbb{R})$-topology at every point f satisfying $f(t)-\sigma > \varsigma$ a.e. for some $\varsigma > 0$.*

The above proposition says, in particular, that if we have a family of systems $\dot{x} = -\sigma x + f_\omega(t)$, where $\omega \in \Omega \subset \mathbb{R}^k$ parameterizes $\{f_\omega\}$ continuously in the $L^\infty_{\mathrm{loc}}(\mathbb{R})$-topology and $\inf\{\varsigma(\omega)\colon\ f_\omega(t)-\sigma > \varsigma(\omega) \text{ a.e.}\} > 0$, then the enough small change of parameter ω causes an arbitrary small change of the firing map Φ in the $C^0(\mathbb{R})$-topology (but, of course, even if the firing maps $\Phi_{\omega_1}(t)$ and $\Phi_{\omega_2}(t)$ are uniformly close, the firing times $t_n^{(1)} = \Phi^n_{\omega_1}(t_0)$ and $t_n^{(2)} = \Phi^n_{\omega_2}(t_0)$ with $n\to\infty$ might deviate a lot from each other).

Proof of Proposition 2.8. Let $f(t)-\sigma > \varsigma > 0$ a.e. Our aim is to prove

$$\forall_{\varepsilon>0}\ \exists_{\delta>0}\ \forall_{g:\mathbb{R}\to\mathbb{R}} \quad d_{L^\infty_{\mathrm{loc}}(\mathbb{R})}(f,g) < \delta \quad \Longrightarrow \quad d_{C^0(\mathbb{R})}(\Phi_f,\Phi_g) < \varepsilon, \tag{11}$$

where Φ_f and Φ_g are the firing maps induced by $\dot{x} = -\sigma x + f(t)$ and $\dot{x} = -\sigma x + g(t)$, respectively ($f$ and g satisfy requirements stated in Proposition 2.8). Firstly we prove that:

$$\forall_{\varepsilon>0}\ \forall_{K\in\mathbb{N}}\ \exists_{N\in\mathbb{N}}\ \exists_{\delta>0}\ \forall_{g:\mathbb{R}\to\mathbb{R}} \quad \operatorname*{ess\,sup}_{[-N,N]} \big|f(t)-g(t)\big| < \delta \quad \Longrightarrow \quad \sup_{t\in[-K,K]} \big|\Phi_f(t)-\Phi_g(t)\big| < \frac{\varepsilon}{2}. \tag{12}$$

Fix any positive integer K. Define $N := K + \lceil \frac{2}{\varsigma} \rceil$, where $\lceil \frac{2}{\varsigma} \rceil$ is the smallest integer greater than or equal to $2/\varsigma$. Let $\delta := \min\{\frac{\varsigma}{2}, \frac{\varsigma^2\varepsilon}{4}\}$. Choose the function g satisfying the assumptions and such that $\operatorname{ess\,sup}_{[-N,N]} |f(t)-g(t)| < \delta$. Then $g(u)-\sigma > \varsigma/2 > 0$ a.e. in $[-N,N]$. Let then $t \in [-K,K]$ be fixed and suppose that $\Phi_g(t) > \Phi_f(t)$. By definition of the firing map,

$$\mathrm{e}^{\sigma t} = \int_t^{\Phi_f(t)} \big[f(u)-\sigma\big]\mathrm{e}^{\sigma u}\,du = \int_t^{\Phi_f(t)} \big[g(u)-\sigma\big]\mathrm{e}^{\sigma u}\,du.$$

It follows that

$$\int_{\Phi_f(t)}^{\Phi_g(t)} \big[g(u)-\sigma\big]\mathrm{e}^{\sigma u}\,du = \int_t^{\Phi_f(t)} \big[f(u)-g(u)\big]\mathrm{e}^{\sigma u}\,du.$$

Since $0 \le \Phi_f(t) - t < 1/\varsigma$ by the assumption on f and $t, t + 1/\varsigma \in [-N, N]$ by our choice of N, we estimate

$$\int_{\Phi_f(t)}^{\Phi_g(t)} \big[g(u) - \sigma\big] e^{\sigma u}\, du = \int_t^{\Phi_f(t)} \big[f(u) - g(u)\big] e^{\sigma u}\, du < \delta\big(\Phi_f(t) - t\big) e^{\sigma \Phi_f(t)} < \frac{\delta}{\varsigma} e^{\sigma \Phi_f(t)}.$$

Simultaneously

$$\int_{\Phi_f(t)}^{\Phi_g(t)} \big[g(u) - \sigma\big] e^{\sigma u}\, du > \frac{\varsigma}{2} \big|\Phi_g(t) - \Phi_f(t)\big| e^{\sigma \Phi_f(t)},$$

provided that $\Phi_g(t) \le N$. However, suppose that $\Phi_g(t) > N$. Then $\int_t^N [g(u) - \sigma] e^{\sigma u}\, du < e^{\sigma t}$ by definition of the firing map. On the other hand, by our assumptions on N and g,

$$\int_t^N \big[g(u) - \sigma\big] e^{\sigma u}\, du > \frac{\varsigma}{2}(N - t) e^{\sigma t} > \frac{\varsigma}{2} \frac{2}{\varsigma} e^{\sigma t} = e^{\sigma t}$$

which contradicts our previous estimate. Thus always $\Phi_g(t) \le N$ and finally we obtain

$$\big|\Phi_g(t) - \Phi_f(t)\big| < \frac{2\delta}{\varsigma^2} \le \frac{\varepsilon}{2}.$$

If $\Phi_f(t) \ge \Phi_g(t)$, then immediately $\Phi_g(t) \le N$ (since $\Phi_f(t) \le N$ as $\Phi_f(t) - t < 1/\varsigma$) and we can perform similar calculations.

Now we show how (12) implies (11). Given $\varepsilon > 0$, there exists the smallest integer K_* such that $\sum_{k=K_*}^{\infty} \frac{1}{2^k} \le \varepsilon/2$ and thus

$$\sum_{k=K_*}^{\infty} \frac{1}{2^k} \frac{\|\Phi_f(t) - \Phi_g(t)\|_{C^0([-k,k])}}{1 + \|\Phi_f(t) - \Phi_g(t)\|_{C^0([-k,k])}} < \frac{\varepsilon}{2}.$$

Therefore if also $\sum_{k=1}^{K_*} \frac{1}{2^k} \frac{\|\Phi_f(t) - \Phi_g(t)\|_{C^0([-k,k])}}{1 + \|\Phi_f(t) - \Phi_g(t)\|_{C^0([-k,k])}} < \frac{\varepsilon}{2}$, then $d_{C^0(\mathbb{R})}(f,g) < \varepsilon$ (the metric in the Frechet space). But as the function $u \mapsto \frac{u}{1+u}$ is increasing (from $[0,\infty)$ onto $[0,1)$) and the norms $\|\Phi_f(t) - \Phi_g(t)\|_{C^0([-k,k])}$ are non-decreasing with k, it follows that

$$\begin{aligned}\sum_{k=1}^{K_*} \frac{1}{2^k} \frac{\|\Phi_f(t) - \Phi_g(t)\|_{C^0([-k,k])}}{(1 + \|\Phi_f(t) - \Phi_g(t)\|_{C^0([-k,k])})} &\le \sum_{k=1}^{K_*} \frac{1}{2^k} \frac{\|\Phi_f(t) - \Phi_g(t)\|_{C^0([-K_*,K_*])}}{(1 + \|\Phi_f(t) - \Phi_g(t)\|_{C^0([-K_*,K_*])})} \\ &\le \sum_{k=1}^{K_*} \frac{1}{2^k} \big\|\Phi_f(t) - \Phi_g(t)\big\|_{C^0([-K_*,K_*])} < \big\|\Phi_f(t) - \Phi_g(t)\big\|_{C^0([-K_*,K_*])}.\end{aligned}$$

Now from (12) we know that there exist $N_* = K_* + \lceil \frac{2}{\varsigma} \rceil$ and $\widetilde{\delta}$ such that $\|f - g\|_{L^\infty([-N_*,N_*])} < \widetilde{\delta}$ implies $\|\Phi_f(t) - \Phi_g(t)\|_{C^0([-K_*,K_*])} < \varepsilon/2$ and thus it also implies $d_{C^0(\mathbb{R})}(f,g) < \varepsilon$. But then

$$\|f - g\|_{L^\infty_{\mathrm{loc}}(\mathbb{R})} < \frac{1}{2^{N_*}} \frac{\|f - g\|_{L^\infty([-N_*,N_*])}}{1 + \|f - g\|_{L^\infty([-N_*,N_*])}} < \frac{1}{2^{N_*}} \frac{\widetilde{\delta}}{1 + \widetilde{\delta}}.$$

Therefore with $\delta := \frac{1}{2^{N_*}}\frac{\tilde{\delta}}{1+\tilde{\delta}}$ we have $d_{L^\infty_{\mathrm{loc}}(\mathbb{R})}(f,g) < \delta \Longrightarrow d_{C^0_{\mathrm{loc}}(\mathbb{R})}(\Phi_f,\Phi_g) < \varepsilon$, which proves the statement. □

Under stronger assumptions on f we prove the following:

Proposition 2.9. *If $f \in C^0(\mathbb{R})$, then the mapping $f \mapsto \Phi$ is continuous from the topology $C^0(\mathbb{R})$ into $C^1(\mathbb{R})$-topology at every point f satisfying the following condition: there exist $\varsigma > 0$ and M such that $\varsigma < f(t) - \sigma < M$ for all t.*

Proof. Eq. (6), equivalent to $e^{\sigma t} = H(\Phi(t),t)$ with $H(x,t) = \int_t^x [f(u)-\sigma]\mathrm{e}^{\sigma u}\,du$, differentiated with respect to t gives that

$$\Phi'(t) = \frac{f(t)}{f(\Phi(t)) - \sigma}\mathrm{e}^{-\sigma(\Phi(t)-t)}. \tag{13}$$

Note that this formula is well-defined for all t since by our assumption $f(\Phi(t)) - \sigma \neq 0$.

Suppose now that $\|f-g\|_{L^\infty([-N_*,N_*])} < \delta$ (notation as in the previous proof). Then for $t \in [-K_*,K_*]$ we have the following estimates: $\Phi_f(t) - t < 1/\varsigma$ and $\mathrm{e}^{-\sigma(\Phi_f(t)-t)} < M/\varsigma$, correspondingly $\Phi_g(t) - t < 2/\varsigma$ and $\mathrm{e}^{-\sigma(\Phi_g(t)-t)} < 4M/\varsigma$, which can be obtained from (6). Calculations allow us to estimate

$$\begin{aligned}\left|\Phi'_f(t) - \Phi'_g(t)\right| &= \left|\frac{f(t)}{f(\Phi_f(t)) - \sigma}\mathrm{e}^{-\sigma(\Phi_f(t)-t)} - \frac{g(t)}{g(\Phi_g(t)) - \sigma}\mathrm{e}^{-\sigma(\Phi_g(t)-t)}\right| \leq \dots \\ &< \frac{M\delta}{\varsigma^2} + \frac{2(2M+\sigma)}{\varsigma^2}\left(\frac{M\delta}{\varsigma} + \frac{4M^2\sigma}{\varsigma}\left|\Phi_f(t) - \Phi_g(t)\right|\right).\end{aligned}$$

As $\delta \to 0$ also $|\Phi_f(t) - \Phi_g(t)| \to 0$ uniformly in $t \in [-K_*,K_*]$ by the previous result. This proves the continuity of $f \mapsto \Phi$ from the Frechet space $C^0(\mathbb{R})$ to the Frechet space $C^1(\mathbb{R})$. □

Remark 2.10. For the Perfect Integrator (4) we obtain that

$$\Phi'(t) = \frac{f(t)}{f(\Phi(t))} \tag{14}$$

and thus we can prove the statement of Proposition 2.9 for the PI-model under the assumption that $f \in C^0(\mathbb{R})$ and $0 < \varsigma < f(t) < M$ even easier.

Lemma 2.11. *For the model $\dot{x} = -\sigma x + f(t)$, $\sigma \geq 0$*

(a) if $f \in C^k(\mathbb{R})$, where $k \in \mathbb{N} \cup \{0\}$, and $f(t) - \sigma > 0$ for all t, then $\Phi \in C^{k+1}(\mathbb{R})$,
(b) if $f \in L^1_{\mathrm{loc}}(\mathbb{R})$ and $f(t) - \sigma > 0$ a.e., then $\Phi \in C^0(\mathbb{R})$.

Proof. The first part is a direct consequence of the formula (13). As for the second part, choose $t_0 \in \mathbb{R}$ and let $t_n \searrow t_0$. By definition of the firing map (6) and the assumption that $f(t) - \sigma > 0$ a.e., $t_n > t_0$ implies $\Phi(t_n) > \Phi(t_0)$ and we can write the following equation, involving $\Phi(t_n)$ and $\Phi(t_0)$:

$$\mathrm{e}^{\sigma t_n} - \mathrm{e}^{\sigma t_0} + \int_{t_0}^{t_n}\left[f(u) - \sigma\right]\mathrm{e}^{\sigma u}\,du = \int_{\Phi(t_0)}^{\Phi(t_n)}\left[f(u) - \sigma\right]\mathrm{e}^{\sigma u}\,du.$$

Since $t_n \searrow t_0$, the left side of this equation decreases to 0 with $n \to \infty$. Hence also $\int_{\Phi(t_0)}^{\Phi(t_n)}[f(u)-\sigma]\mathrm{e}^{\sigma u}\,du \to 0$. But as the integrand is positive a.e., it must hold that $\Phi(t_n) \searrow \Phi(t_0)$. Thus Φ is right-continuous at t_0. Similarly, we prove that it is left-continuous. □

3. Periodic drive for LIF and PI models

In case of a periodic drive, we will frequently use results proved by us in [16] but we will also rely on what we have proved in previous part of the paper and on the special properties of the LIF system.

Definition 3.1. We say that a function $f \in L^1_{\mathrm{loc}}(\mathbb{R})$ is *periodic*, if there exists $T > 0$ such that $f(t+T) = f(t)$ a.e.

Remark 3.2. Notice that if $f \in C^0(\mathbb{R})$ is periodic, then the condition $f(t) - \sigma > \varsigma$ for some $\varsigma > 0$ reduces to $f(t) - \sigma > 0$. In this case $\Phi : \mathbb{R} \to \mathbb{R}$ is a lift of an orientation preserving circle homeomorphism by Fact 1.2.

However, for locally integrable periodic functions the requirement $f(t) - \sigma > \varsigma > 0$ a.e. is not equivalent to $f(t) - \sigma > 0$ a.e. (take, for example, $\sigma = 1$ and $f(t) = 1/n + 1$ for $t \in [k - \frac{1}{2^{n-1}}, k - \frac{1}{2^n})$, $k \in \mathbb{Z}$, $n \in \mathbb{N}$). Nevertheless, for $f \in L^1_{\mathrm{loc}}(\mathbb{R})$ periodic it is enough to assume that $f(t) - \sigma > 0$ a.e. in order to assure that the firing map Φ (in the generalized sense of Definition 2.1) has the desired property:

Lemma 3.3. *If $f \in L^1_{\mathrm{loc}}(\mathbb{R})$ is periodic with period $T = 1$ and $f(t)-\sigma > 0$ a.e., then the firing map Φ induced by (3) is a lift of an orientation preserving circle homeomorphism.*

Proof. From (6) and periodicity of f we have

$$\mathrm{e}^{\sigma(t+1)} = \int_{t+1}^{\Phi(t+1)} \big[f(u) - \sigma\big]\mathrm{e}^{\sigma u}\,du = \int_{t+1}^{\Phi(t+1)} \big[f(u-1) - \sigma\big]\mathrm{e}^{\sigma u}\,du = \mathrm{e}^{\sigma} \int_{t}^{\Phi(t+1)-1} \big[f(u) - \sigma\big]\mathrm{e}^{\sigma u}\,du$$

which is equivalent to

$$\int_{t}^{\Phi(t)} \big[f(u) - \sigma\big]\mathrm{e}^{\sigma u}\,du = \int_{t}^{\Phi(t+1)-1} \big[f(u) - \sigma\big]\mathrm{e}^{\sigma u}\,du.$$

Since for fixed t, $F(t_*) = \int_t^{t_*}[f(u) - \sigma]\mathrm{e}^{\sigma u}\,du$ is a continuous increasing function of t_* as the integrand is positive a.e., the above implies that $\Phi(t+1) = \Phi(t) + 1$ and thus Φ has the property of a degree one circle map. Then as Φ is continuous and increasing, it must be in fact a lift of an orientation preserving circle homeomorphism. □

Thus when $f \in L^1_{\mathrm{loc}}(\mathbb{R})$ is periodic and $f(t) - \sigma > 0$ a.e., the unique firing rate $\mathrm{FR}(t) = r$ always exists (independently of t), since it is the reciprocal of the unique rotation number $\varrho(\Phi) = \lim_{n\to\infty} \frac{\Phi^n(t)}{n}$, $t \in \mathbb{R}$.

For the simple model (4), where $f \in L^1_{\mathrm{loc}}(\mathbb{R})$, $f(t) > 0$ a.e. and f is periodic (with period 1), $\Phi : \mathbb{R} \to \mathbb{R}$ is a lift of an orientation preserving circle homeomorphism φ (which is then the firing phase map), as follows from the lemma above. Moreover, in [3] it was proved that in this case $\varphi : S^1 \to S^1$ is always conjugated with the rotation r_ϱ by ϱ via the homeomorphism γ with a lift Γ given as

$$\Gamma(t) := \frac{\int_0^t f(u)\,du}{\int_0^1 f(u)\,du}, \quad t \in \mathbb{R}. \tag{15}$$

Formula (9) for the firing rate when f is periodic with period $T = 1$ reduces to $r = \int_0^1 f(u)\,du$. Thus

$$\varrho = \frac{1}{\int_0^1 f(u)\,du} \tag{16}$$

is the analytical expression for the rotation number of φ. One can check by a short direct calculation that indeed we have $\Gamma(\Phi(t)) = \Gamma(t) + \varrho$, where Γ is continuous, increasing and satisfies $\Gamma(t+1) = \Gamma(t) + 1$, i.e. γ conjugates φ with r_ϱ.

Observe that an almost everywhere non-negative function $f : \mathbb{R} \to \mathbb{R}$, where $f \in L^1_{\mathrm{loc}}(\mathbb{R})$, defines a measure μ_f on $\mathbb{R}$ for which f is the density (the Radon–Nikodym derivative of μ_f), i.e.

$$\mu_f(A) := \int_A f(u)du, \tag{17}$$

where A is any measurable (Borel) subset of $\mathbb{R}$. From definition of the firing map and the fact that it is a homeomorphism we justify:

Proposition 3.4. *Let $f \in L^1_{\mathrm{loc}}(\mathbb{R})$, $f(t) > 0$ a.e. be periodic, $\Phi : \mathbb{R} \to \mathbb{R}$ be the firing map associated with (4), and μ_f the associated with f measure. Then μ_f is Φ-invariant, i.e. Φ preserves the measure μ_f.*

Compare the above result with Proposition 6 in [3] where the author considered the firing map cut to its image $\mathrm{Im}\,\Phi$ in order to show invariance of the measure $\tilde{\mu}_f$ defined as $\tilde{\mu}_f(A) := \int_{A\cap \mathrm{Im}\,\Phi} f(t)\,dt$ but this restriction is not necessary when we take $f > 0$ a.e. (and then of course $\tilde{\mu}_f = \mu_f$).

Throughout the rest of this section we assume that

(1) f is measurable and $f \in L^\infty_{\mathrm{loc}}(\mathbb{R})$ (thus in particular $f \in L^1_{\mathrm{loc}}(\mathbb{R})$)
(2) f is periodic (allowing also the case of f constant) in the sense of Definition 3.1 (with period $T = 1$, without the loss of generality)
(3) $f(t) - \sigma > 0$ a.e. in $\mathbb{R}$.

Under these assumptions the firing map Φ is a lift of a circle homeomorphism $\varphi \sim \Phi \bmod 1$. Note that in this case Φ satisfies $\Phi(t+1) = \Phi(t) + 1$ for every $t \in \mathbb{R}$ and thus the compact convergence in the Frechet space $C^0(\mathbb{R})$ ($C^m(\mathbb{R})$) is equivalent to the uniform convergence (uniform convergence up to m-th derivative) on $\mathbb{R}$ because it is enough to consider Φ and Φ_n cut to the interval $[0,1]$ (we say that Φ_n converges compactly to Φ if for every $K \subset \mathbb{R}$ compact $\lim_{n\to\infty} \sup_{t\in K} |\Phi_n(t) - \Phi(t)| = 0$). In other words, if we admit only 1-periodic inputs f and f_n, then $\sup_{t\in\mathbb{R}} |\Phi_n(t) - \Phi(t)| = \sup_{t\in[0,1]} |\Phi_n(t) - \Phi(t)| < \varepsilon$ whenever $d_{L^\infty_{\mathrm{loc}}(\mathbb{R})}(f_n, f) < \delta$ for sufficiently small δ.

Except for the continuity of the mapping $f \mapsto \Phi$ from the $L^\infty_{\mathrm{loc}}(\mathbb{R})$-topology into $C^0(\mathbb{R})$, we will also need the continuity $f \mapsto \Gamma$, where $\Gamma : \mathbb{R} \to \mathbb{R}$ is the lift of the map $\gamma : S^1 \to S^1$ (semi-)conjugating the firing phase map $\varphi : S^1 \to S^1$ with the rotation r_ϱ, where $\varrho = \varrho(\varphi) \in \mathbb{R} \setminus \mathbb{Q}$ is the rotation number of φ.

Lemma 3.5. *Suppose that $\varrho(\Phi) \in \mathbb{R} \setminus \mathbb{Q}$, where Φ is a firing map induced by Eq. (3) with $\sigma \geq 0$. Then the mapping $f \mapsto \Gamma$, where $\Gamma : \mathbb{R} \to \mathbb{R}$ is a lift of γ (semi-)conjugating φ with the rotation r_ϱ, is continuous from the $L^\infty_{\mathrm{loc}}(\mathbb{R})$-topology into $C^0(\mathbb{R})$ (with $\sup_{\mathbb{R}}$-norm) at every point f such that $f(t) - \sigma > \varsigma$ a.e. for some $\varsigma > 0$.*

By the continuity of $f \mapsto \Gamma$ we mean that when $\widetilde{f}$ is a small enough perturbation of f, with respect to L^∞_{loc}-topology, and $\widetilde{\varrho} = \varrho(\widetilde{\Phi}) \in \mathbb{R} \setminus \mathbb{Q}$, then $\widetilde{\Gamma}$ can be chosen such that Γ and $\widetilde{\Gamma}$ are uniformly close, where $\widetilde{\Phi}$ is a firing map induced by $\dot{x} = -\sigma x + \widetilde{f}(t)$ and $\widetilde{\Gamma}$ is a lift of $\widetilde{\gamma}$ where $\widetilde{\gamma} \circ \widetilde{\varphi} = r_{\widetilde{\varrho}} \circ \widetilde{\gamma}$.

Proof of Lemma 3.5. We have already proved the continuity of the mapping $\varphi \mapsto \gamma$ from $C^0(S^1) \to C^0(S^1)$ in Theorem 2.3 in [16]. From this it follows the continuity of $\Phi \to \Gamma$ from $C^0(\mathbb{R})$ into $C^0(\mathbb{R})$ (with $\sup_{\mathbb{R}}$-topologies). Since we also have the continuity of $f \to \Phi$ under the stated assumptions, the statement of the lemma holds. □

3.1. Regularity properties of the ISI_n *sequence*

We will formulate some detailed results concerning regularity of the sequence of interspike-intervals for PI and LIF models. By regularity properties we mean periodicity, asymptotic periodicity and the property of almost strong recurrence.

Due to Lemma 3.3 investigation of interspike-intervals $\mathrm{ISI}_n(t_0)$ for f periodic is covered by the analysis of the displacement sequence $\eta_n(z_0)$ of an orientation preserving circle homeomorphism, being the firing phase map φ. Thus $\mathrm{ISI}_n(t_0)$ equals $\eta_n(z_0)$ (where $z_0 = \mathrm{e}^{2\pi\imath t_0}$) up to some constant integer and the sequences $\mathrm{ISI}_n(t_0)$ and $\eta_n(z_0)$ have virtually the same properties.

Proposition 3.6. *Consider the Perfect Integrator model $\dot{x} = f(t)$. If $T = \int_0^1 f(u)\,du = q/p \in \mathbb{Q}$, then the sequence $\mathrm{ISI}_n(t)$ for every initial condition $(t, 0)$ is periodic with period q.*

Proof. The analytical expression for the firing rate (9) of PI model for f 1-periodic reduces to $\int_0^1 f(u)\,du$. This means that in our case the rotation number of the underlying firing phase map $\varphi : S^1 \to S^1$ equals to $\varrho = 1/\int_0^1 f(u)\,du$. Thus if $T = 1/\varrho = q/p$ is rational, φ is topologically conjugated to the rational rotation r_ϱ by ϱ and thus there are only periodic orbits with period q. As a result, the sequence of displacements of φ, and consequently the sequence $\mathrm{ISI}_n(t_0)$, is periodic with period q. □

Example 2. For the LIF model $\dot{x} = -x + \frac{1}{1-\mathrm{e}^{-q}}$, where $q \in \mathbb{N}$, the sequence of interspike-intervals is constant: $\mathrm{ISI}_n(t_0) = q$. Indeed, in [3] it was shown that the input current of such a form induces conjugacy with the rational rotation by $\varrho(\Phi) = q$. Consequently, the firing map Φ satisfies $\Phi(t) = t + q$ and is simply a translation by q. Thus for every $n \in \mathbb{N}$ and t we have $\Phi^n(t) - \Phi^{n-1}(t) = q$ and we observe 1 spike per every q periods of forcing.

Brette [3] also proved that $f(t) = \frac{1}{1-\mathrm{e}^{-q}}$ is the only one input current which induces conjugacy with a rotation by $q \in \mathbb{N}$ (for $\sigma = 1$). It is much harder to show what are all the input currents that induce conjugacy with $\varrho = q/p$ ($p \neq 1$) but this assumption implies some constraints on $f(t)$, which seem to be quite restrictive (for some values of p/q the conjugacy might not be possible at all, see discussion in [3]). Thus we might conclude that in "majority of cases" the firing phase map arising from the LIF model, which has rational firing rate, is not conjugated to the corresponding rotation and:

Remark 3.7. For the LIF model with a firing rate $\mathrm{FR} = q/p$, the sequence of interspike-intervals $\mathrm{ISI}_n(t_0)$ is "typically" not periodic but only asymptotically periodic (with the period equal to q in the limit $n \to \infty$). Precisely,

$$\forall_{\varepsilon>0}\ \exists_{N\in\mathbb{N}}\ \forall_{n\in\mathbb{N}}\ \forall_{k\in\mathbb{N}} \quad \left|\mathrm{ISI}_{n+kq}(t_0) - \mathrm{ISI}_n(t_0)\right| < \varepsilon.$$

Proof. This is a simple consequence of the fact that the firing phase map φ induced by LIF with $\varrho \in \mathbb{Q}$ is usually not conjugated to a rational rotation but it is a semi-periodic circle homeomorphism. Thus φ has also non-periodic orbits, being asymptotically attracted to periodic ones (cf. [21]). □

When the input function is periodic, the (asymptotically) periodic output of the system, in terms of interspike-intervals, is connected with the phenomena called phase-locking, see Fig. 1. Precisely, we say that

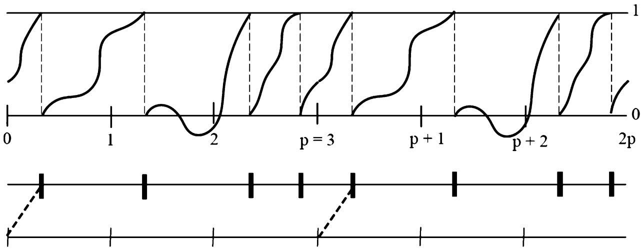


Fig. 1. An example of 4 : 3-phase locking.

the system exhibits $q : p$-phase locking (which corresponds to the rotation number equal to p/q), when it fires q spikes for every p cycles of forcing (the spikes occur in fixed phases of the forcing period) and this state is structurally stable, i.e. it persists under a small change of a parameter $\theta \in \Theta$. Types of phase-locking change with the change of the rotation number, but the mapping $\theta \mapsto \varrho$ is usually constant (under some conditions) on rational values of ϱ (look for such concepts as the Devil-staircase and Arnold-tongues).

In next we pass to the case of irrational firing rate. The same property as for the displacement sequence of a circle homeomorphism with the irrational rotation number can be shown for the sequence of interspike-intervals for the LIF model:

Theorem 3.8. *Consider the LIF model $\dot{x} = -\sigma x + f(t)$ ($\sigma \geq 0$) where $f \in L^1_{\mathrm{loc}}(\mathbb{R})$ is periodic, $f(t) - \sigma > 0$ a.e. and the rotation number $\varrho(\Phi)$ is irrational.*

Then the sequence $\{\mathrm{ISI}_n(t_0)\}$ is almost strongly recurrent *for all $t_0 \in \widetilde{\Delta}$, where $\widetilde{\Delta}$ is a lift to $\mathbb{R}$ of the underlying minimal set $\Delta \subset S^1$ (possibly $\Delta = S^1$), i.e.*

$$\forall_{\varepsilon>0}\ \exists_{N\in\mathbb{N}}\ \forall_{n\in N}\ \forall_{k\in\mathbb{N}\cup\{0\}}\ \exists_{i\in\{0,1,\ldots,N\}}\quad \left|\mathrm{ISI}_{n+k+i}(t_0) - \mathrm{ISI}_n(t_0)\right| < \varepsilon. \tag{18}$$

Moreover, if $f \in C^2(\mathbb{R})$, then the sequence $\{\mathrm{ISI}_n(t_0)\}$ is almost strongly recurrent for all $t_0 \in \mathbb{R}$ (in this case $\Delta = S^1$).

Proof. Under the stated assumptions the firing phase map $\varphi : S^1 \to S^1$ is a homeomorphism with irrational rotation number. For $t_0 \in \widetilde{\Delta}$ the underlying displacement sequence $\eta_n(z_0) = \Phi^n(t_0) - \Phi^{n-1}(t_0) \bmod 1$, $z_0 = e^{2\pi\imath t_0}$, is almost strongly recurrent as proved in [21] (the proof is based on the fact that all the orbits of points in the minimal set of a continuous transformation on a compact metric space are almost periodic, cf. [12]). But then the sequence of interest $\mathrm{ISI}_n(t_0) = \Phi^n(t_0) - \Phi^{n-1}(t_0)$ is almost strongly recurrent as well.

As for the second part of the statement, notice that if $f \in C^2(\mathbb{R})$, then $\varphi \in C^2(S^1)$ and thus on the ground of the Denjoy Theorem [8], φ is transitive and $\{\mathrm{ISI}_n(t_0)\}$ is almost strongly recurrent for all $t_0 \in \mathbb{R}$. □

Remark 3.9. Notice that Proposition 3.6, Remark 3.7 and Theorem 3.8 remain true when one replaces the "sequence of interspike-intervals" simply with the "sequence of firing times phases", i.e. the sequence $\Phi^n(t_0) \bmod 1$.

3.2. Distribution of interspike-intervals

In this part we consider IF models, for which the firing rate, and consequently the rotation number of the firing phase map φ, is irrational.

Proposition 3.10. *Consider the LIF model $\dot{x} = -\sigma x + f(t)$, where $f \in L^1_{\mathrm{loc}}(\mathbb{R})$ is 1-periodic, $f(t) - \sigma > 0$ a.e. and the rotation number $\varrho = \varrho(\Phi)$ is irrational. By Γ denote the lift of γ (semi-)conjugating φ with r_ϱ. Under these assumptions:*

(1) If φ is transitive (for example, when $f \in C^2(\mathbb{R})$), then the sequence $\mathrm{ISI}_n(t_0)$ for every $t_0 \in \mathbb{R}$ is dense in the interval

$$\mathcal{S} = \Psi\big([0,1]\big) = \Omega\big([0,1]\big), \tag{19}$$

where $\Psi(t) = \Phi(t) - t$ is a displacement function of Φ and $\Omega(t) := \Gamma^{-1}(t+\varrho) - \Gamma^{-1}(t)$.

(2) If φ is not transitive, then the sequence $\mathrm{ISI}_n(t_0)$ for $t_0 \in \widetilde{\Delta}$ (the total lift of Δ to $\mathbb{R}$) is dense in the set

$$\widehat{\mathcal{S}} = \Psi(\widetilde{\Delta}) = \widehat{\Omega}(\widehat{\Delta}_0),$$

where $\widehat{\Delta}_0$ is a lift to $[0,1]$ of a subset $\widehat{\Delta} \subset \Delta$, such that the semi-conjugacy γ is invertible on $\widehat{\Delta}$, and $\widehat{\Omega} := \widehat{\Gamma}^{-1}(t+\varrho) - \widehat{\Gamma}^{-1}(t)$, where $\widehat{\Gamma} := \Gamma \restriction \widehat{\Delta}_0$ is a lift of γ cut to the set $\widehat{\Delta}_0$.
Moreover, when one takes $t_0 \in \mathbb{R} \setminus \widetilde{\Delta}$, then for every $t \in \widetilde{\Delta}$ there exists an increasing sequence n_k, $k \in \mathbb{N}$, such that for every $l \in \mathbb{N}$ we have

$$\lim_{k\to\infty} \mathrm{ISI}_l\big(\Phi^{n_k}(t_0)\big) = \Phi^{n_k+l}(t_0) - \Phi^{n_k+l-1}(t_0) = \Phi^l(t) - \Phi^{l-1}(t) = \mathrm{ISI}_l(t).$$

Since usually we do not know the formula for the (semi-)conjugacy Γ (except for the Perfect Integrator), the equivalent formula for the concentration set of ISI involving Ω is not directly useful but it is used in proving statements concerning the distribution of interspike-intervals with respect to the unique invariant measure.

Proof of Proposition 3.10. The above proposition is a direct consequence of Proposition 2.1 in [16], the corresponding statement for the displacement sequence of an orientation preserving circle homeomorphism with irrational rotation number. □

Proposition 3.10 means that even if we are not able to compute directly the set of concentration of interspike-intervals, we know at least that interspike-intervals practically fill a whole interval (i.e. do not form for instance something in the type of a Cantor set), provided that f is smooth enough. This is also visible in numerical Example 5. However, note that in a special case, where φ is a strict rotation (as happens for example for LIF and PI with constant input), this interval degenerates to a single point $\{\varrho\}$ (since the rotation is an isometry).

We will discuss the distribution μ_{ISI} of interspike-intervals with respect to the unique (up to normalization), φ-invariant measure μ.

Definition 3.11. Suppose that the rotation number $\varrho(\Phi)$ is irrational. Let μ be the unique invariant probability measure for $\varphi \sim \Phi$ mod 1. The distribution of interspike-intervals is defined as

$$\mu_{\mathrm{ISI}}(A) := \mu\big(\big\{t \in [0,1]\colon\ \Phi(t) - t \in A\big\}\big) = \mu\big(\Psi^{-1}(A)\big), \quad A \subset \mathbb{R}$$

where $\Psi(t) = \Phi(t) - t$, $t \in [0,1]$, is a displacement function associated with Φ.

Note that since Φ mod 1 is periodic with period 1, we consider only $t \in [0,1]$. Moreover, although the measure μ has support contained in $[0,1]$, as it is the invariant measure for Φ mod $1 : [0,1] \to [0,1]$, the measure μ_{ISI} has support equal to $\Psi([0,1])$, which in general might not be contained in $[0,1]$ but it is always contained is some interval of length not greater than 1 because Φ maps intervals of length 1 onto intervals of length 1 due to the fact that $\Phi(t+1) = \Phi(t) + 1$ for every t (the resulting interval, containing $\mathrm{supp}(\mu_{\mathrm{ISI}})$, is shifted by a from its projection mod 1 into $[0,1]$, where $a > 0$ is such that $\Phi(0) = a$). We can consider

$\mu_{\mathrm{ISI}}(A)$, where A is an arbitrary subset of $\mathbb{R}$, if we adopt the convention that μ_{ISI} is defined on the whole $\mathbb{R}$ but it simply vanishes everywhere outside its support.

As a direct consequence of Proposition 3.10 we obtain

Corollary 3.12. *Under the assumptions of Proposition 3.10 the distribution μ_{ISI} is the transported Lebesgue Λ measure on $[0,1]$:*

1. *If φ is transitive, then*
$$\mu_{\mathrm{ISI}}(A) = \Lambda\big(\Omega^{-1}(A)\big), \quad A \subset \mathbb{R}$$
and the support of μ_{ISI} equals
$$\mathrm{supp}(\mu_{\mathrm{ISI}}) = \Psi\big([0,1]\big) = \Omega\big([0,1]\big).$$
2. *If φ is not transitive, then analogously*
$$\mu_{\mathrm{ISI}}(A) = \Lambda\big(\widehat{\Omega}^{-1}(A)\big), \quad A \subset \widehat{S},$$
and the support of μ_{ISI} equals
$$\mathrm{supp}(\mu_{\mathrm{ISI}}) = \Psi(\widetilde{\Delta}),$$
where Ω, $\widehat{\Omega}$, $\widetilde{\Delta}$ and $\widehat{S}$ are as in Proposition 3.10.

Obviously, the support $\mathrm{supp}(\mu_{\mathrm{ISI}})$ is just the set of concentration of the interspike-intervals sequence.

We are concerned with the distribution μ_{ISI} of interspike-intervals with respect to the natural invariant measure μ, since this theoretical distribution is a limiting distribution of interspike-intervals computed along an arbitrary trajectory:

Proposition 3.13. *Under the assumptions of Proposition 3.10 (regardless the transitivity of φ), for $A \subset \mathbb{R}$ we have*
$$\lim_{n\to\infty} \frac{\sharp\{0 \le i \le n-1\colon\ \mathrm{ISI}_i(t) \in A\}}{n} = \mu_{\mathrm{ISI}}(A),$$
where $\sharp$ denotes the number of elements of the set, and the above convergence is uniform (with respect to $t \in \mathbb{R}$).

The average interspike interval aISI *(which equals the rotation number $\varrho(\Phi)$) is the mean of the distribution μ_{ISI}:*
$$\mathrm{aISI} = \int_{\mathbb{R}} \Phi(t) - t\, d\mu(t) = \int_{\mathbb{R}} d\mu_{\mathrm{ISI}}.$$

Proof. The statements can be justified by the Birkhoff Ergodic Theorem applied to the observable $\Psi(t) = \Phi(t) - t$. The uniform convergence in the first part follows from the fact that the system $(\Phi \bmod 1, [0,1], \mu)$ is not only ergodic but uniquely ergodic (compare with Proposition 4.1.13 and Theorem 11.2.9 in [13] or Remark 2.5 in [16]). □

Our aim will be to consider parameter-dependant IF systems and to formulate results describing how the distribution μ_{ISI} varies with change of the parameter.

Definition 3.14. (See e.g. [2].) Let X be a complete separable metric space and $\mathcal{M}(X)$ the space of all finite measures defined on the Borel σ-field $\mathcal{B}(X)$ of subsets of X.

A sequence μ_n of elements of $\mathcal{M}(X)$ is called weakly convergent to $\mu \in \mathcal{M}(X)$ if for every bounded and continuous function f on X

$$\lim_{n\to\infty} \int_X f(x)\, d\mu_n(x) = \int_X f(x)\, d\mu(x).$$

We denote the weak convergence as $\mu_n \Longrightarrow \mu$.

Definition 3.15. A Borel set A is said to be a continuity set for μ if A has μ-null boundary, i.e.

$$\mu(\partial A) = 0.$$

One can show (cf. [19]) that $\mu_n \Longrightarrow \mu$ if and only if for each continuity set A of μ, $\lim \mu_n(A) = \mu(A)$.

Proposition 3.16. *Consider the systems $\dot{x} = -\sigma x + f(t)$ and $\dot{x} = -\sigma x + f_n(t)$, $n \in \mathbb{N}$, where the functions f_n, $f \in L^\infty_{\mathrm{loc}}(\mathbb{R})$ are measurable, periodic with period 1 and f satisfies $f(t) - \sigma > \varsigma > 0$ a.e. Suppose that all the induced firing maps Φ_n and Φ have irrational rotation numbers, ϱ_n and ϱ, respectively. By $\mu^{(n)}_{\mathrm{ISI}}$ and μ_{ISI} denote the interspike-interval distributions, correspondingly for Φ_n and Φ, with respect to the corresponding invariant measures $\mu^{(n)}$ and μ.*

If $f_n \to f$ in $L^\infty_{\mathrm{loc}}(\mathbb{R})$-topology, then

$$\mu^{(n)}_{\mathrm{ISI}} \Longrightarrow \mu_{\mathrm{ISI}}.$$

Proof. Recall that the invariant measures, $\mu^{(n)}$ and μ, are the Lebesgue measure transported by the maps Γ_n and Γ (semi-)conjugating corresponding firing maps Φ_n and Φ with the rotations. Since we already know that the mapping $f \mapsto \Gamma$ is continuous from the $L^\infty_{\mathrm{loc}}(\mathbb{R})$-topology into $C^0(\mathbb{R})$, it must hold that $\Gamma_n \to \Gamma$ in $C^0(\mathbb{R})$ (with $\sup_{\mathbb{R}}$-topologies). But then $\mu^{(n)} \Longrightarrow \mu$, i.e. we have the weak convergence of the invariant measures. Since the interspike-interval distributions are in turn the invariant measures transported by the corresponding displacement functions $\Psi_n \to \Psi$ in $\sup_{\mathbb{R}}$, by the same argument we get the statement on $\mu^{(n)}_{\mathrm{ISI}}$ and μ_{ISI}. □

Recall that the weak convergence of measures does not imply the point-wise convergence of the corresponding densities: in general the densities of $\mu^{(n)}_{\mathrm{ISI}}$ or μ_{ISI} might not exist, as in Example 3.

Notice that in the above proposition we needed the fact that all the rotation numbers ϱ_n and ϱ are irrational since this guarantees that the unique invariant measures $\mu^{(n)}$ and μ exist and we can define the distributions $\mu^{(n)}_{\mathrm{ISI}}$ and μ_{ISI}. Later on we will see what happens if the intermediate firing maps Φ_n may have rational rotation numbers as well.

However, now we want to formulate some more detailed theorems on convergence of interspike-interval distributions. This is quite simply achievable for the simplest model, the Perfect Integrator Model.

Proposition 3.17. *Consider the systems of Perfect Integrators $\dot{x} = f_n(t)$, $n \in \mathbb{R}$, and $\dot{x} = f(t)$, where the functions f_n, $f \in C^0(\mathbb{R})$ are periodic with period 1, $f_n(t)$, $f(t) > 0$, $f_n \to f$ in $C^0(\mathbb{R})$ and where all the rotation numbers of the firing maps are irrational, ϱ_n, $\varrho \in \mathbb{R} \setminus \mathbb{Q}$. Then the invariant measures $\mu^{(n)}$ and μ have densities, say g_n and g correspondingly, and*

$$g_n \to g \quad \text{in } C^0\big([0,1]\big).$$

As for the distributions of interspike intervals, if additionally the set of critical points of the displacement function $\Psi := \Phi - \mathrm{Id}$ *of the limiting firing map* Φ*, i.e. the set* $\mathcal{C}_\Psi := \{t \in [0,1]\colon\ \Psi'(t) = 0 \iff \Phi'(t) = 1\}$*, is of Lebesgue measure* 0*, then we have*

$$\sup\bigl[\bigl|\mu_{\mathrm{ISI}}^{(n)}(I) - \mu_{\mathrm{ISI}}(I)\bigr|,\ I \in \mathcal{J}\bigr] \to 0, \tag{20}$$

where $\mathcal{J}$ *denotes the class of all intervals* $I \subset [0,1]$ *(open, closed, half-closed).*

Proof. Proposition 3.4 provides the following formula for the unique invariant probability measure μ of the firing phase map for the Perfect Integrator:

$$\mu(A) = \frac{\int_A f(u)\,du}{\int_{[0,1]} f(u)\,du}, \quad A \subset [0,1] - \text{Borel subset}. \tag{21}$$

This formula is also consistent with the formula for the (semi-)conjugacy Γ, since by the standard result on circle homeomorphisms (see [7, p. 34]) it holds that $\Gamma(t) = \mu([0,t])$ (provided that $\Gamma(0) = 0$ which we can assume without the loss of generality as the conjugacy Γ is given up to the additive constant). Thus $g_n(t) = f_n(t)/\int_0^1 f_n(u)\,du = \Gamma_n'(t)$, $t \in [0,1]$, correspondingly $g(t) = f(t)/\int_0^1 f(u)\,du = \Gamma'(t)$, and the uniform convergence of densities follows. This in particular implies that

$$\sup\bigl[\bigl|\mu^{(n)}(A) - \mu(A)\bigr|;\ A - \text{Borel subset of } [0,1]\bigr] \to 0. \tag{22}$$

Indeed, by the existence and convergence of densities Γ_n' and Γ', $|\mu^{(n)}(A) - \mu(A)| = |\int_A \Gamma_n'(u) - \Gamma'(u)\,du| < \varepsilon\Lambda(A)$ for sufficiently large n, but since $\Lambda(A) \le 1$, the convergence is uniform with respect to the choice of $A \subset [0,1]$.

Unfortunately, without the assumption on the 0-measure of the set of critical points of the limiting displacement function Ψ, we cannot assure that the distribution μ_{ISI} of interspike-intervals has density (with respect to the Lebesgue measure), as we will see in Example 3. However, under this assumption by Proposition 2.10 in [16] we obtain (20), i.e. we know that convergence of interspike-intervals distributions is uniform on the collection of all the intervals (in this case the density of μ_{ISI} exists by Theorem 3.18 below, but the densities of $\mu_{\mathrm{ISI}}^{(n)}$ might still not exist and we cannot argue as above for (22)). □

In order to compute the set $\mathcal{C}_\Psi$ for Perfect Integrator one has to solve in t the implicit equation $f(t) = f(\Phi(t))$ by (14), which usually is difficult. But in the forthcoming example we will see that verifying the assumption on the zero Lebesgue measure of this set is sometimes not that challenging. We only remark that when, in particular, f is constant, this assumption is not satisfied. However, in this case the emerging firing map Φ is exactly the lift of the rotation by ϱ and the distribution of interspike intervals equals simply the Dirac delta δ_ϱ. Thus μ_{ISI} is not absolutely continuous with respect to Λ.

The theorem below provides sufficient conditions for the distribution μ_{ISI} to have the density with respect to the Lebesgue measure. We formulate it in the most general form:

Theorem 3.18. *Suppose that the firing map* Φ *arising from the system* $\dot{x} = F(t,x)$ *is a* C^1*-diffeomorphism with irrational rotation number* ϱ*, which is conjugated with the translation by* ϱ *via a* C^1*-diffeomorphism* Γ *and that the set* $\mathcal{C}_\Psi \subset [0,1]$ *of critical points of the displacement function* $\Psi\restriction_{[0,1]}$ *is of Lebesgue measure* 0*.*

Then the distribution μ_{ISI} *is absolutely continuous with respect to the Lebesgue measure* Λ *with the density* $\Delta(y)$ *equal to*

$$\Delta(y) = \begin{cases} 0 & \text{if } y \notin \operatorname{supp}(\mu_{\mathrm{ISI}}); \\ \sum_{t \in \Psi^{-1}(y)} \Gamma'(t)\frac{1}{|\Phi'(t) - 1|} & \text{if } y \in \operatorname{supp}(\mu_{\mathrm{ISI}}), \end{cases} \tag{23}$$

where the latter is well-defined almost everywhere in $\mathrm{supp}(\mu_{\mathrm{ISI}})$*, i.e. in* $\mathrm{supp}(\mu_{\mathrm{ISI}}) \setminus V(C_\Psi)$*, where* $V(C_\Psi)$ *denotes the set of critical values of* $\Psi \restriction [0,1]$.

Proof. The theorem is a mere tautology of Theorem 2.14 in [16]. □

In particular, for the Perfect Integrator we make use of the formulas (14) and (15) for the derivative $\Phi'(t)$ and the conjugacy Γ in order to obtain that (23) reduces to:

$$\Delta(y) = \begin{cases} 0 & \text{if } y \notin [\min_{u\in[0,1)} \Phi(u) - u, \max_{u\in[0,1)} \Phi(u) - u]; \\ \sum_{t\in\Psi^{-1}(y)} \frac{f(t)}{\int_0^1 f(u)\,du} \frac{f(\Phi(t))}{|f(t)-f(\Phi(t))|} & \text{if } y \in [\min_{u\in[0,1)} \Phi(u) - u, \max_{u\in[0,1)} \Phi(u) - u]. \end{cases}$$

Example 3. Consider the systems $\dot{x} = f_n(t)$, where

$$f_n(t) = A_n + B_n \cos(2\pi n t)$$

and

$$A_n \to A_0 > 0 \quad \text{and} \quad 0 < B_n \to 0.$$

Suppose that the constants A_n and B_n are such that $f_n(t) > 0$, at least for sufficiently large $n \in \mathbb{N}$. In particular, we have the convergence $f_n \to f_0$ in $C^1(\mathbb{R})$, where $f_0 \equiv A_0$. The firing maps Φ_n are then the lifts of circle diffeomorphisms with rotation numbers $\varrho_n = \frac{1}{A_n}$. Moreover, on the account of Proposition 2.9, $\Phi_n \to \Phi_0$ in $C^1(\mathbb{R})$, where $\Phi_0(t) = t + \varrho_0 = t + \frac{1}{A_0}$ is the firing map induced by the equation $\dot{x} = f_0(t)$ and simply a lift of the rotation by ϱ_0. The firing maps Φ_n and Φ_0 are conjugated to the corresponding rotations, respectively, via diffeomorphisms

$$\Gamma_n(t) = \varrho_n \int_0^t f_n(u)\,du = t + \frac{B_n}{2\pi n A_n} \sin(2\pi n t)$$

and

$$\Gamma_0(t) = t.$$

Assume that $\varrho_n, \varrho_0 \in \mathbb{R} \setminus \mathbb{Q}$, $n \in \mathbb{N}$. Obviously, $\Gamma_n \to \Gamma_0$ in $C^1(\mathbb{R})$. In particular, the densities $\Gamma_n'(t) = \frac{f_n(t)}{A_n}$ and $\Gamma_0'(t) = \frac{f_0(t)}{A_0}$ of invariant measures $\mu^{(n)}$ and $\mu^{(0)}$ converge uniformly. As for the interspike-interval distributions, we certainly have $\mu_{\mathrm{ISI}}^{(n)} \Longrightarrow \mu_{\mathrm{ISI}}^{(0)}$. However, the assumption on the zero measure set C_{Ψ_0} is not satisfied since Φ_0 is a lift of the rotation and its displacement $\Psi_0 = \varrho_0$ is a constant function. Thus the set of critical points of Ψ_0 has full measure and indeed the distribution $\mu_{\mathrm{ISI}}^{(0)}$ is degenerated to a point ϱ_0 (i.e. it is not absolutely continuous with respect to the Lebesgue measure). Nevertheless, the distributions $\mu_{\mathrm{ISI}}^{(n)}$ are absolutely continuous since the sets C_{Ψ_n} of critical points of displacement functions Ψ_n are countable (and the densities $\Delta^{(n)}(y)$ exist on the ground of Theorem 3.18). Indeed: Note that $t \in \mathbb{R}$ is a critical point of Ψ_n if and only if $\Phi_n'(t) = 1$. But $\Phi_n'(t) = \frac{f_n(t)}{f_n(\Phi_n(t))} = 1$ means that $\cos(2\pi n t) = \cos(2\pi n \Phi_n(t))$ which holds if and only if $\sin(\pi n(\Phi_n(t) + t)) = 0$ or $\sin(\pi n(\Phi_n(t) - t)) = 0$. Anyone of these two alternatives happens for at most countably many choices of t (as one justifies with a little effort).

Thus for each $n \in \mathbb{N}$ the displacement functions Ψ_n have countably many critical points. Now, by Theorem 3.18, the distributions $\mu_{\mathrm{ISI}}^{(n)}$ have densities $\Delta^{(n)}$ with respect to the Lebesgue measure. Nevertheless, the limiting (in terms of weak convergence of measures) distribution $\mu_{\mathrm{ISI}}^{(0)}$ is not absolutely continuous.

Example 4. Let us consider Perfect-Integrator Model: $\dot{x} = f_n(t)$, where

$$f_n(t) = A + B\cos(2\pi nt), \quad n \in \mathbb{N}.$$

If $A > B > 0$ then $f_n(t) > 0$ for every $n \in \mathbb{N}$ and $t \in \mathbb{R}$. In this case the firing maps $\Phi_n : \mathbb{R} \to \mathbb{R}$ induced by the equations $\dot{x} = f_n(t)$ are lifts of orientation preserving circle homeomorphisms $\varphi_n : S^1 \to S^1$. Moreover, each Φ_n is conjugated with the lift $R_{\varrho_n}(t) = t + \frac{1}{A}$ of the rotation by $\varrho_n = 1/\int_0^1 A + B\cos(2\pi nt)\mathrm{d}t = \frac{1}{A}$ via

$$\Gamma_n(t) = \frac{\int_0^t A + B\cos(2\pi nu)\mathrm{d}u}{A} = t + \frac{B}{2\pi nA}\sin(2\pi nt).$$

In particular, all the rotation numbers ϱ_n of Φ_n are the same and can be set rational or irrational with arbitrary Diophantine properties (it depends only on the choice of A).

Since $\Gamma_n \to \mathrm{Id}$ uniformly (i.e. in $C^0(\mathbb{R})$), also $\Gamma_n^{-1} \to \mathrm{Id}$ uniformly. Consequently,

$$\Phi_n(t) = \Gamma_n^{-1}\big(\Gamma_n(t) + \varrho_n\big) = \Gamma_n^{-1}\left(t + \frac{B\sin(2\pi nt)}{2\pi nA} + \frac{1}{A}\right) \to t + \frac{1}{A}$$

and thus also $\Phi_n \to \Phi_0$ uniformly with $\Phi_0(t) = t + \frac{1}{A}$ being simply a lift of the rotation by $\frac{1}{A}$. Note that $\Phi_0(t)$ can be seen as a firing map induced by the equation $\dot{x} = f_0(t)$ with $f_0(t) = A$. However, it is not true that $f_n \to f_0$ uniformly or even pointwise.

From the uniform convergence $\Phi_n \to \Phi_0$ we have the weak convergence $\mu^{(n)} \Longrightarrow \mu^{(0)}$ of the corresponding unique invariant probability measures:

$$\mu^{(n)}(V) = \frac{\int_V f_n(u)\mathrm{d}u}{A}, \quad V \subset [0,1],$$

where $\mu^{(0)} = \Lambda$ is the Lebesgue measure on $[0,1]$ (being the invariant measure of Φ_0). From the formula for $\mu^{(n)}$ we see that the invariant measures $\mu^{(n)}$ have densities

$$\widetilde{f_n} = \frac{f_n}{A}$$

and the measure $\mu^{(0)}$ has a density

$$\widetilde{f_0} = \frac{f_0}{A} \equiv 1.$$

However, $\widetilde{f_n} \nrightarrow \widetilde{f_0}$, similarly as $f_n \nrightarrow f_0$. In particular, this shows that the weak convergence of measures does not imply (even pointwise) convergence of the corresponding continuous density functions. Thus the sequence of conjugacies Γ_n does not converge in $C^1(\mathbb{R})$ but only in $C^0(\mathbb{R})$.

3.3. Empirical approximation of the interspike-interval distribution μ_{ISI}

Virtually we are able to calculate only the empirical interspike-interval distribution, i.e. the distribution derived by counting interspike-intervals along a particular trajectory (a run of a system). In case of the rational firing rate necessarily there are periodic orbits (and usually also non-periodic but these are attracted to the periodic ones) and although all the periodic orbits have the same period, the (finite) sequences $\mathrm{ISI}_n(t_0)$ derived along the orbit of each periodic point t_0 might consist of different elements unless the system induces a rigid rotation. However, in case of the irrational rotation number we have the unique invariant ergodic measure that gives the distribution of orbits phases. Thus μ_{ISI} is also well-defined and the empirical distribution of interspike-intervals derived for any trajectory will well approximate μ_{ISI}, provided that the trajectory is long enough. However, basically when we do numerical computations, we do not work with irrational rotation numbers, but the rational ones which are close to them. We will see in what meaning the empirically derived interspike-interval distribution for an arbitrarily chosen initial condition $(t, 0)$ of a system with rational firing rate, being "close" enough to our entire system with irrational firing rate, approximates the desired distribution μ_{ISI} of the "irrational" (ergodic) system.

We have to define the empirical interspike-interval distribution formally:

Definition 3.19. Let Φ be the firing map arising from the IF system $\dot{x} = F(t, x)$. Choose the initial condition $(t, 0)$ $(x_r = 0)$. Then the empirical interspike-interval distribution for the run of length n (i.e. having n-spikes) starting at $(t, 0)$ equals

$$\omega_{n,t} = \frac{1}{n}\sum_{i=0}^{n-1} \delta_{\mathrm{ISI}_i(t)},$$

where $\delta_{\mathrm{ISI}_i(t)}$ is a Dirac delta centred at the point $\mathrm{ISI}_i(t) = \Phi^{i+1}(t) - \Phi^i(t)$.

Thus $\omega_{n,t}(A) = \frac{1}{n}\sharp\{0 \le i \le n-1\colon\ \Phi^{i+1}(t) - \Phi^i(t) \in A\}$, $A \subset \mathbb{R}$.

Note that if $\widetilde{\varphi}$ with rotation number $\widetilde{\varrho}$ is close in $C^0(S^1)$-metric to φ with irrational rotation number ϱ, then the rotation numbers $\widetilde{\varrho}$ and ϱ are also close due to the continuity of the rotation number in $C^0(S^1)$ (cf. Proposition 11.1.6 in [13]).

In order to measure the distance between interspike-interval distribution we introduce the notion of the Fortet–Mourier metric (cf. [22]):

Definition 3.20. Let μ and ν be the two Borel probability measures on a measurable space $(\Omega, \mathcal{F})$, where Ω is a compact metric space. Then the distance between the measures μ and ν is defined as

$$d_F(\mu, \nu) := \sup\left\{\left|\int_\Omega f\, d\mu - \int_\Omega f\, d\nu\right|\colon\ f \text{ is 1-Lipschitz}\right\}.$$

We formulate the following:

Proposition 3.21. *Consider the integrate-and-fire systems $\dot{x} = -\sigma x + f_{\theta_1}(t)$ and $\dot{x} = -\sigma x + f_{\theta_2}(t)$, where $f_{\theta_i} \in L^\infty_{\mathrm{loc}}(\mathbb{R})$, periodic with period 1 and $f_{\theta_1}(t) - \sigma > \varsigma > 0$. By Φ_{θ_1} and Φ_{θ_2} denote the firing maps emerging from the corresponding systems. Suppose that the rotation number associated with Φ_{θ_1} is irrational.*

For any $\varepsilon > 0$ there exists a neighbourhood $\mathcal{U}$ of f_{θ_1} in $L^\infty_{\mathrm{loc}}(\mathbb{R})$-topology such that if $f_{\theta_2} \in \mathcal{U}$, then for every initial condition $(t, 0)$ we have:

$$d_F\Big(\lim_{n\to\infty} \omega^{(\theta_2)}_{n,t}, \mu^{(\theta_1)}_{\mathrm{ISI}}\Big) < \varepsilon, \tag{24}$$

where $\omega^{(\theta_2)}_{n,t}$ is the empirical interspike-interval distribution for the run of the system $\dot{x} = -\sigma x + f_{\theta_2}(t)$ starting from $(t, 0)$ and $\mu^{(\theta_1)}_{\mathrm{ISI}}$ is the interspike-interval distribution for $\dot{x} = -\sigma x + f_{\theta_1}(t)$ with respect to its invariant measure $\mu^{(\theta^1)}$.

Proof. The proof relies again of the fact that the mapping $f \mapsto \Phi$ is continuous from ess sup-topology into $C^0(\mathbb{R})$. Then the statement follows immediately from Theorem 2.17 in [16]. $\square$

As the convergence under Fortet–Mourier metric implies weak convergence of measures [11] we conclude:

Corollary 3.22. *Under the notation as in Proposition 3.21, for every $t \in \mathbb{R}$ we have*

$$\lim_{n\to\infty} \widetilde{\omega}_{n,t}^{(\theta_2)} \Longrightarrow \mu_{\mathrm{ISI}}^{(\theta_1)}.$$

The above result can be illustrated by the numerical example:

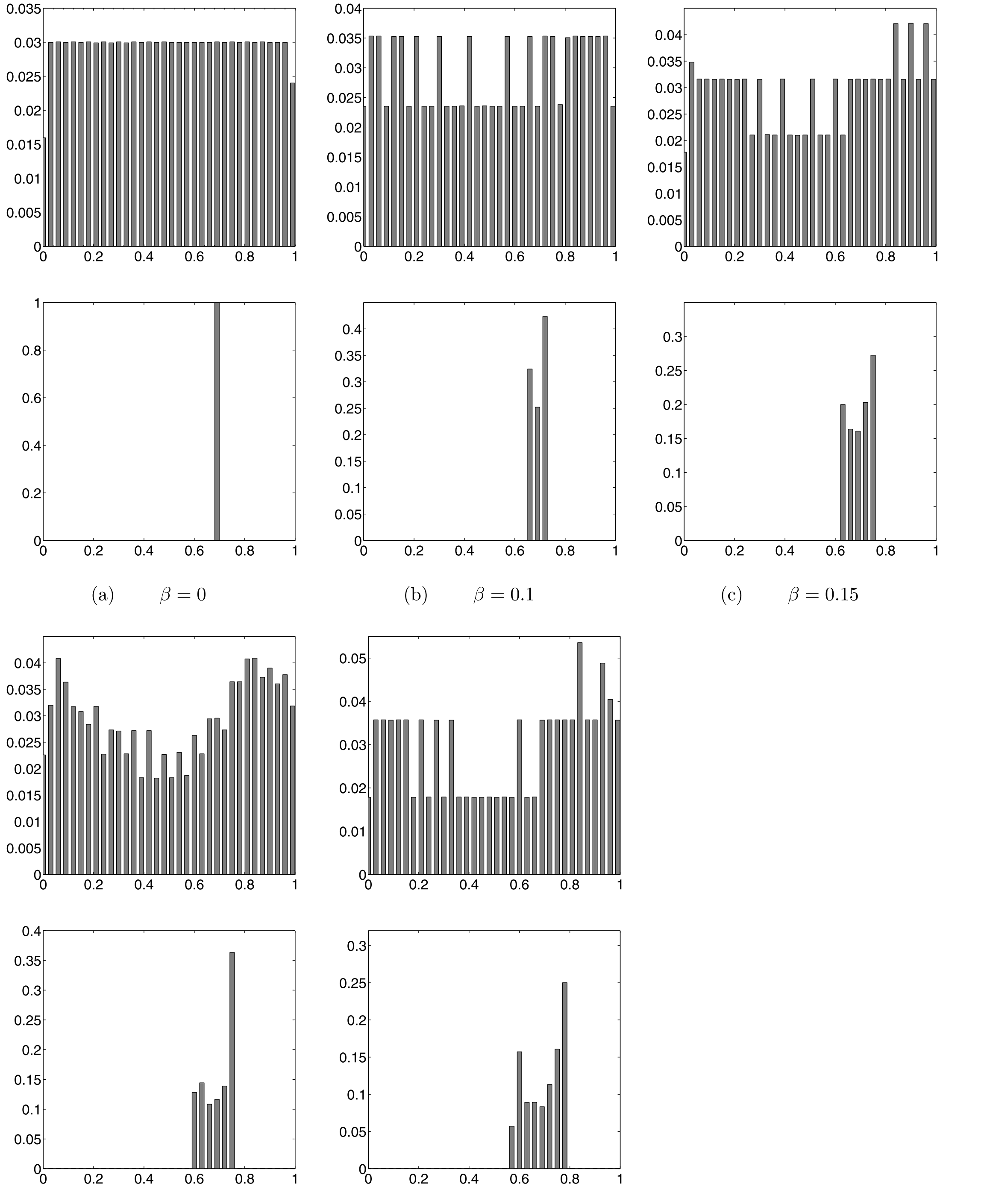
Example 5. We investigate the system $\dot{x} = -x + 2(1 + \beta\cos(2\pi t))$ (the computations were done in Matlab). Notice that the analogous example was considered in a classical paper [14], but the authors gave no rigorous explanation of the behaviour of interspike-intervals histograms under a small change of a parameter. Our results allow us to make theoretical predicates of what actually we can expect for the interspike-interval distribution when the parameter β varies. We easily obtain that for $0 \le \beta < 0.5$ the firing map $\Phi : \mathbb{R} \to \mathbb{R}$ is a lift of a circle homeomorphism. The results of numerical simulations for $\beta = 0, 0.1, 0.15, 0.2$ and 0.25 are presented in Fig. 2. All the simulations were started from the initial condition $(0, 0)$.

When $\beta = 0$ the system is forced by the constant input which induces the rotation by an irrational angle. Indeed, by solving the equation and direct computation we obtain that $\mathrm{ISI}_n(t) = \varrho = -\ln(0.5) \approx 0.6931$ for every n and $t \in \mathbb{R}$. This is reflected in Fig. 2(a): the firing phases are distributed uniformly in $[0, 1]$ and the interspike-interval distribution is simply a Dirac delta at $\mathrm{ISI}^{(0)} \approx 0.6931$. Thus for $\beta = 0$ we are dealing with the irrational rotation. When we slightly change the parameter β (Fig. 2b–2e), we observe that both the distribution of phases and of interspike-intervals change "continuously" as we anticipate from the fact that the corresponding distributions are close in d_F metric, since the firing maps are close in $C^0(\mathbb{R})$ metric. In particular the distribution of interspike-intervals is concentrated in the interval around the value of $\mathrm{ISI}^{(0)}$ and the distribution practically fills this whole interval, which is consistent with Proposition 3.10 as in our case the input function is smooth.

We also have checked what happens for greater values of β and the results are presented in Fig. 3. When $\beta = 0.4$, firing phases admit ten distinct values, which suggest that there is a periodic orbit of period 10 and indeed, the rotation number was computed as $\varrho = 7/10$. When the parameter changes to $\beta = 0.45$ it seems that there are no more periodic orbits (and the rotation number is irrational). Thus here the small change of the parameter by 0.05 causes the real qualitative change in the behaviour of the system. However, we must recall that usually (i.e. unless the firing phase map is conjugated to the rational rotation), having the rational rotation number of a particular value p/q is stable with respect to the small change of parameters and thus the system (in terms of periodic orbits) behaves in the same way, which is what we call *phase locking*. In fact the smaller the denominator of the rotation number, the more stable it is. Thus the small change of parameters within the neighbourhood of the firing map with rational rotation number, also does not cause a qualitative change of the behaviour of the system, as long as this change of parameters preserves the rotation number (recall that, under some constraints, the mapping $\Phi \mapsto \varrho$ is a Devil-staircase, strictly increasing at irrational values and constant at rational ones, cf. e.g. Proposition 11.1.11 in [13]).

In Fig. 3 we may see also what happens for values of β greater than 0.5, precisely for $\beta = 1$ and $\beta = 2$. However, for these parameter values the firing map is not a homeomorphism any more and thus in particular the results might depend on the initial condition $(t, 0)$. Therefore these cases are beyond the scope of this work.

Remark 3.23. Note that the analogous statements of Propositions 3.13, 3.16 and 3.21 hold for the distribution of the firing phases, which is simply the invariant measure μ.



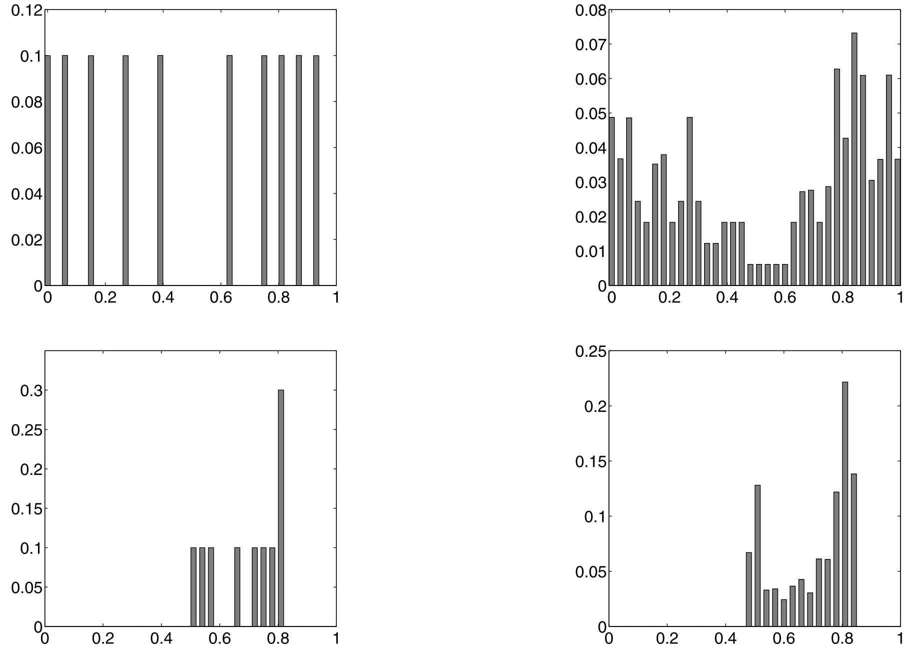
(a) $\beta = 0$ (b) $\beta = 0.1$ (c) $\beta = 0.15$

(d) $\beta = 0.2$ (e) $\beta = 0.25$

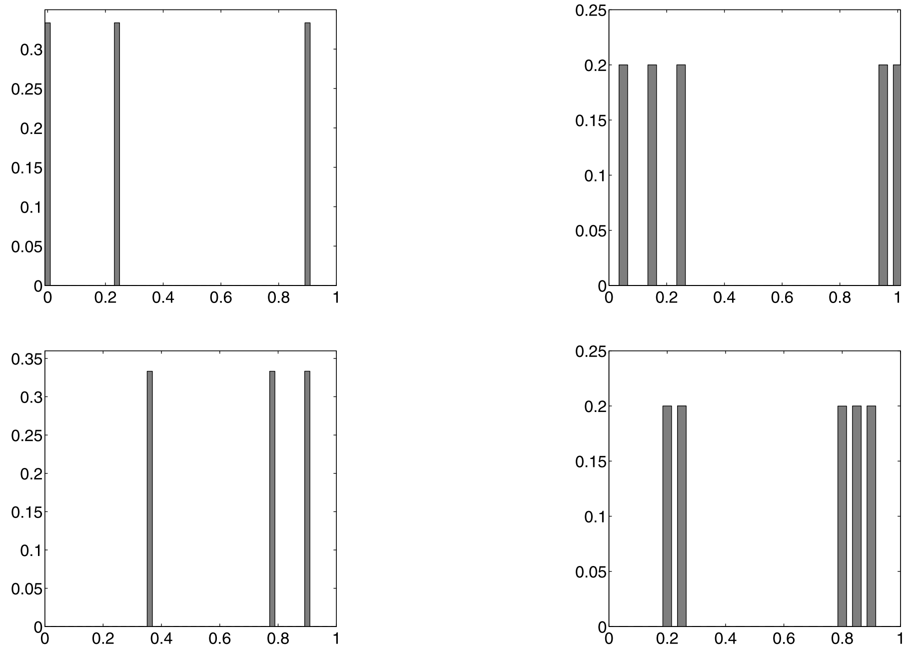
Fig. 2. Histograms of firing phases (at the top of each subfigure) and interspike-intervals (at the bottom of each subfigure) for the model $\dot{x} = -\sigma x + 2(1 + \beta \cos(2\pi t))$ and $\beta = 0, 0.1, 0.15, 0.2, 0.25$.

4. Discussion

We have shown many specific properties of the interspike-interval sequence arising from linear periodically driven integrate-and-fire models for which the emerging firing phase map is a circle homeomorphism.



(a) $\beta = 0.4$. (b) $\beta = 0.45$.



(c) $\beta = 1$. (d) $\beta = 2$.

Fig. 3. Histograms of firing phases (at the top of each subfigure) and interspike-intervals (at the bottom of each subfigure) for the model $\dot{x} = -\sigma x + 2(1 + \beta \cos(2\pi t))$ and $\beta = 0.4, 0.45, 1, 2$.

However, it would be interesting to have such rigorous results on interspike-intervals for periodically driven integrate-and-fire models with the firing phase map being not necessary a homeomorphism, but for instance just a continuous circle map. We predict that in such systems greater variety of phenomena may be observed, mainly due to the fact that in this case we have *rotation intervals* instead of the unique rotation number.

The natural extension of this research would be to provide a detailed description of the interspike-interval sequence for bidimensional IF models [24] or one-dimensional IF systems with an almost periodic input [15].

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