Firing map for periodically and almost-periodically driven integrate-and-fire models: a dynamical systems approach.

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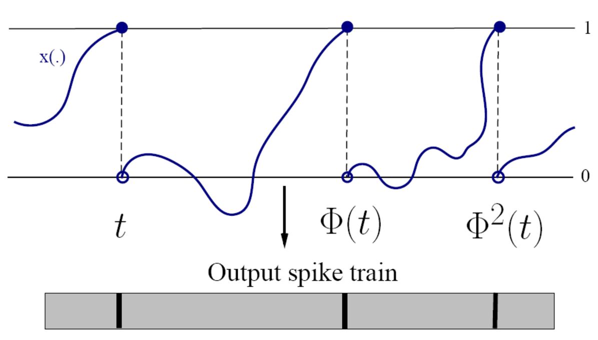
Introduction

The integrate-and-fire (IF) models are used mainly in neuroscience to describe nerve-membrane voltage response to a given input:

$$\dot{x} = F(t,x) \quad F:\mathbb{R}^2\to\mathbb{R} \qquad (1)$$
$$\lim_{t\to s^+} x(t) = 0, \quad \text{if} \quad x(s)=1$$



The question is to describe the sequence of consecutive resets $\{t_n\}$ as iterations of some map, called the *firing map*, and the sequence of interspike-intervals $\{t_{n+1}-t_n\}$ as a sequence of displacements along a trajectory of this map.

Let $x(\cdot;t,0)$ denote a solution of (1) satisfying the initial condition $(t,0)$ and $D_\Phi = \{t\in\mathbb{R}:\ \exists_{s>t}\ x(s;t,0)=1\}$. For equation (1) we define a map $\Phi: D_\Phi\to\mathbb{R}$:

Definition: Firing map

$$\Phi(t) := \inf\{s>t:\ x(s;t,0)=1\}$$

Consecutive spike-timings t_n are then given as:

$$t_n = \Phi^n(t) = \inf\{s>\Phi^{n-1}(t):\ x(s;\Phi^{n-1}(t),0)=1\}$$

The most popular model is the Leaky Integrate-and-Fire

$$\dot{x} = -\sigma x + f(t), \quad \sigma>0 \qquad (2)$$

which for $\sigma=0$ reduces to the Perfect Integrator $\dot{x}=f(t)$.

Fact ([4]). If the function F in (1) is continuous and periodic in t, then the firing map Φ is a lift of a degree-1 circle map $\varphi: S^1\to S^1$.

Definition: Firing rate & average interspike interval

1. firing rate $FR(t) := \lim_{n\to\infty}\frac{n}{\phi^n(t)}$
2. average interspike interval $\text{aISI}(t) := \lim_{n\to\infty}\frac{\phi^n(t)}{n}$

Periodic drive

When the function F is periodic in t, the problem of describing interspike intervals is covered by investigating displacement sequences of circle maps.

Displacement sequence of an orientation preserving circle homeomorphism

Let $\varphi: S^1\to S^1$ be an orientation preserving circle homeomorphism, $\Phi:\mathbb{R}\to\mathbb{R}$ its lift (where $\mathbb{R}$ covers S^1 by the covering projection $\mathfrak{p}: x\mapsto \exp(2\pi i x)$ and $\Psi(x) := \Phi(x)-x$ the displacement function of Φ. By $\varrho(\varphi)$ denote the rotation number of φ.

Definition: Displacement sequence of a point $z=\exp(2\pi i x)\in S^1$

$$\eta_n(z) := \Psi(\Phi^{n-1}(x)) \bmod 1 = \Phi^n(x)-\Phi^{n-1}(x) \bmod 1,\ n\in\mathbb{N}$$

A simple observation gives:
- If φ is a rotation by $2\pi\varrho$, where ϱ can be either rational or irrational, then the sequence $\eta_n(z)=\varrho$ is constant.
- If φ is conjugated to the rational rotation by $2\pi\varrho$, where $\varrho=\frac{p}{q}$, then the sequence $\eta_n(z)$ is q-periodic.

Homeomorphims with irrational rotation number:
Let $\varrho(\varphi)\in\mathbb{R}\setminus\mathbb{Q}$. If φ is not transitive, by $\Delta\subset S^1$ denote the unique minimal set of φ and by $\widetilde{\Delta}_0$ its lift to $[0,1)$.

Proposition. If φ is transitive, then for every $z\in S^1$ the sequence $\eta_n(z)$, $n\in\mathbb{N}$, is dense in the interval $\mathcal{S}=\Psi([0,1])=\Omega([0,1])$, where $\Omega(x) := \Gamma^{-1}(x+\varrho)-\Gamma^{-1}(x)$ and Γ is a lift of a homeomorphism γ conjugating φ with the rotation r_ϱ. $\mathcal{S}$ is the support of the distribution μ_Ψ of displacements with respect to the invariant measure μ:

$$\mu_\Psi(A) := \mu(\{x\in[0,1]:\ \Phi(x)-x\in A\}) = \Lambda(\Omega^{-1}(A)),\ A\subset\mathbb{R}$$

If φ is not transitive, then the distribution μ_Ψ is concentrated on $\widehat{\mathcal{S}}=\Psi(\widetilde{\Delta}_0)$. Moreover, for $z\in S^1\setminus\Delta$ and $w\in\Delta$ there exist increasing sequences $\{n_k\}$ and $\{\widehat{n}_k\}$ such that for every $l\in\mathbb{Z}$

$$\lim_{k\to\infty}\eta_l(\varphi^{n_k}(z))=\eta_l(w) \text{ and } \lim_{k\to\infty}\eta_l(\varphi^{-\widehat{n}_k}(z))=\eta_l(w)$$

The measure $\mu_\Psi(A)$ can be approximated by measuring the average frequency of points $\Phi^i(x)$ with values $\Psi(\Phi^i(x))$ in A along a trajectory $\{\Phi^i(x)\}$, $i\in\mathbb{N}$:

$$\frac{\sharp\{0\le i\le n-1:\ \Psi(\Phi^i(x))\in A\}}{n}\to\mu_\Psi(A),$$

where the convergence with $n\to\infty$ is uniform with respect to x.

Theorem. The mapping $\varphi\mapsto\gamma$ assigning to a homeomorphism φ with irrational rotation number ϱ a map $\gamma: S^1\to S^1$ semiconjugating (or conjugating, if φ is transitive) φ with the rotation r_ϱ, is a continuous mapping from $C^0(S^1)$ into $C^0(S^1)$-topology.

Proposition. Suppose that φ_n is a sequence of homeomorphisms with irrational rotation numbers ϱ_n which converges in the metric of $C^0(S^1)$ to the homeomorphism φ with irrational rotation number ϱ. Then the corresponding displacement distributions $\mu^{(n)}_{\Psi_n}$ with respect to the invariant measures $\mu^{(n)}$ converge weakly to μ_Ψ:

$$\mu^{(n)}_{\Psi_n}\Longrightarrow\mu_\Psi$$

Moreover, if the conjugacy $\gamma\in C^1(S^1)$ and the set of critical points of Ψ is of Lebesgue measure 0, the convergence of distributions is uniform on the class of all intervals $I\subset[0,1]$ ([7]).

For $n\in\mathbb{N}$ and $z=\exp(2\pi i x)\in S^1$ define a sample displacements distribution:

$$\omega_{n,x}=\frac{1}{n}\sum_{i=0}^{n-1}\delta_{\Psi(\Phi^i(x))}$$

Theorem. Let φ be a homeomorphism with irrational rotation number and the displacement distribution μ_Ψ with respect to the invariant measure μ. For every $\varepsilon>0$ there exists a neighborhood $\mathcal{U}\subset C^0(S^1)$ of φ such that for every homeomorphism $\widetilde{\varphi}\in\mathcal{U}$ and every $x_0\in[0,1]$ we have

$$d_F\Big(\lim_{n\to\infty}\frac{1}{n}\sum_{i=0}^{n-1}\delta_{\widetilde{\Psi}(\widetilde{\Phi}^i(x_0))},\mu_\Psi\Big)<\varepsilon,$$

where d_F is the Fortet-Mourier metric. Consequently,

$$\lim_{n\to\infty}\frac{1}{n}\sum_{i=0}^{n-1}\delta_{\widetilde{\Psi}(\widetilde{\Phi}^i(x))}\Longrightarrow\mu_\Psi \quad \text{as } \widetilde{\varphi}\to\varphi \text{ in } C^0(S^1)$$

Regularity of the displacement sequence
Some classical results in topological dynamics ([3]) allowed us to show that even in case of irrational rotation number the displacement sequence exhibits a kind of regularity:

Proposition. If φ is transitive, then for all $z\in S^1$ the displacement sequence $\{\eta_n(z)\}$ is *almost strongly recurrent*, i.e.

$$\forall_{\varepsilon>0}\,\exists_{N\in\mathbb{N}}\,\forall_{n\in N}\,\forall_{k\in\mathbb{N}\cup\{0\}}\,\exists_{i\in\{0,1,\dots,N\}}\,|\eta_{n+k+i}(z)-\eta_n(z)|<\varepsilon$$

If φ is not-transitive, then the sequence $\{\eta_n(z)\}$ is almost strongly recurrent for all $z\in\Delta$.

Semi-periodic circle homeomorphism:
A circle homeomorphism with rational rotation number which is not conjugated to a rotation is called *semi-periodic*.

Proposition. For a semi-periodic circle homeomorphism φ the sequence $\eta_n(z)$ is asymptotically periodic. Precisely, if $\varrho(\varphi)=p/q$ then for every $z\in S^1$:

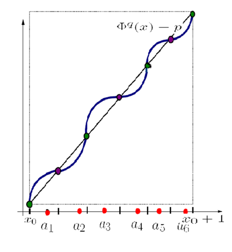
$$\forall_{\varepsilon>0}\,\exists_{N\in\mathbb{N}}\,\forall_{n>N}\,\forall_{k\in\mathbb{N}}\quad|\eta_{n+kq}(z)-\eta_n(z)|<\varepsilon$$

Theorem. Let $\varrho(\varphi)=\frac{p}{q}$. Then for every $\varepsilon>0$ there exists N such that for every $z\in S^1$ the sequence $\{\eta_n(z)\}_{n=-\infty}^{\infty}$ satisfies at least one of the following statements:
1) $\forall_{n>N}\,\forall_{l\in\mathbb{N}}\,|\eta_{n+lq}(z)-\eta_n(z)|<\varepsilon$
2) $\forall_{n>N}\,\forall_{l\in\mathbb{N}}\,|\eta_{-(n+lq)}(z)-\eta_n(z)|<\varepsilon$

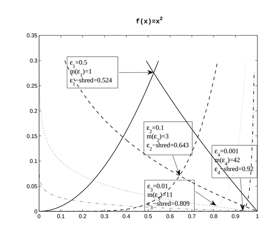
If $\varphi: S^1\to S^1$ has finitely many periodic points $\{z^1,z^2,\dots,z^r\}$, then given $\varepsilon>0$ for each interval (z^k,z^{k+1}) between the two consecutive periodic points we can define a point a_k called *ε-basins shred*, which is used to find the smallest number N satisfying the statement of the above theorem: Suppose that the points z^k and z^{k+1} are, respectively, backward and forward attracting under φ^q for $z\in(z^k,z^{k+1})$. For $m\in\mathbb{N}$ define the functions

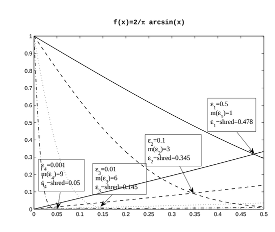
$$\tau^+_m(z) := \max_{0\le i\le q-1}|\varphi^{mq+i}(z)-\varphi^i(z^{k+1})|, \quad \tau^-_m(z) := \max_{0\le i\le q-1}|\varphi^{-mq-i}(z)-\varphi^{q-i}(z^k)|$$

and the subsets of $[z^k,z^{k+1}]$, $U^+_m := \{z:\ \tau^+_m(z)<\varepsilon\}$ and $U^-_m := \{z:\ \tau^-_m(z)<\varepsilon\}$. There exists the smallest natural number $m=m(\varepsilon)$ such that $U^+_{m(\varepsilon)}\cap U^-_{m(\varepsilon)}\neq\emptyset$. Then the ε-basins shred is defined as the unique point $a_k\in U^+_{m(\varepsilon)}\cap U^-_{m(\varepsilon)}$ such that $\tau^+_{m(\varepsilon)}(a_k)=\tau^-_{m(\varepsilon)}(a_k)$.



Example.





Interspike intervals for IF models

Interspike intervals are said to be used in information encoding by neurons. Consider the LIF model (2) and assume that f is continuous, periodic with period $T=1$ and $\underline{f(t)-\sigma>0}$ for all t. Then

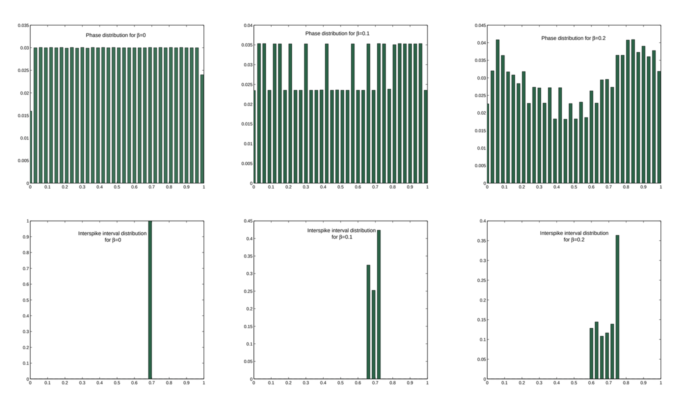
Proposition. The firing map Φ is a lift of an orientation preserving homeomorphism. Consequently, there exists a unique firing rate $FR(t)=1/\varrho(\Phi)$, independent of the initial condition $(t,0)$.

By $\text{ISI}_n(t)$ denote a sequence of interspike intervals for a spike train arising from an initial condition $(t,0)$.
Suppose that $FR(t)\in\mathbb{R}\setminus\mathbb{Q}$. Then:

- the sequence $\text{ISI}_n(t)$ is dense in a set $\mathcal{S}$ depending on the displacement map (which is simply the interval $\Psi([0,1])$ whenever $f\in C^2(S^1)$). Moreover, the interspike interval distribution μ_{ISI} with respect to the unique invariant ergodic measure μ changes continuously with parameters and is well approximated by sample interspike interval distributions (in d_F metric).

Example. $\dot{x}=-x+2(1+\beta\cos(2\pi t))$

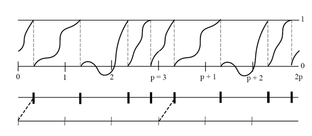
- $\beta=0 \implies \text{ISI}_n(t)=\varrho=\ln(0.5)\approx 0.6931$



Suppose that $FR(t)\in\mathbb{Q}$. Then:

- if the firing phase map $\varphi: S^1\to S^1$ is conjugated to the rational rotation then the sequence $\text{ISI}_n(t)$ is periodic. In particular
  1. For Perfect Integrator $\text{ISI}_n(t)$ is periodic whenever $T=\int_0^1 f(u)\,du\in\mathbb{Q}$.
  2. For Leaky Integrate-and-Fire $\dot{x}=-\sigma x+\frac{1}{1-e^{-q}}$ $\text{ISI}_n(t)$ is constant: $\text{ISI}_n(t)=q$.
- if φ is semi-periodic then $\text{ISI}_n(t)$ is asymptotically periodic.

This is a "typical" case for the LIF model. It is connected with a phenomenon called *phase-locking*.



Almost periodic drive

Assume now that f in (2) is not continuous but only locally integrable (which might be the case in some applications). For $f\in L^1_{\text{loc}}(\mathbb{R})$ we redefine the notion of the firing map as follows:

$$\Phi(t) := \inf\{s>t:\ s \text{ satisfies } e^{\sigma t}=\int_t^s[f(u)-\sigma]e^{\sigma u}\,du\}$$

Under the assumption that $\underline{f(t)-\sigma>\delta}$ a.e. for some $\delta>0$, $\Phi:\mathbb{R}\to\mathbb{R}$ is a homeomorphism.

Definition: Stepanov & Bohr almost periodic functions

- A function $f:\mathbb{R}\to\mathbb{R}$, $f\in L^p_{\text{loc}}(\mathbb{R})$, is Stepanov almost periodic, if for any $\varepsilon>0$ the set $\text{SE}\{\varepsilon,f(t)\}$ of all the numbers τ such that $\|f(t+\tau)-f(t)\|_{\text{St,r,p}}<\varepsilon$ is relatively dense, where

$$\|f\|_{\text{St.,r,p}} := \sup_{t\in\mathbb{R}}\Big[\frac{1}{r}\int_t^{t+r}|f(u)|^p\,du\Big]^{1/p}, \quad r>0,1\le p<\infty$$

- A continuous function $f:\mathbb{R}\to\mathbb{R}$ is Bohr (or uniformly) almost periodic, if for any $\varepsilon>0$ the set $\text{E}\{\varepsilon,f(t)\}$ of all the numbers τ such that for all $t\in\mathbb{R}$ $|f(t+\tau)-f(t)|<\varepsilon$ is relatively dense.

Theorem. Let $f:\mathbb{R}\to\mathbb{R}$ be a Stepanov almost periodic function. Then the firing map Φ induced by the model (2) has Bohr almost periodic displacement. In particular, Φ is then uniformly continuous.

This theorem is analogous to the fact that a continuous and periodic function f gives rise to a firing map with periodic displacement.

Corollary. Under the above assumptions, for the system $\dot{x}=-\sigma x+f_\lambda(t)$, $\lambda\in\Lambda\subset\mathbb{R}^n$, there exists a unique firing rate $FR(t)=r$, which is a continuous function of the input parameters λ.

In [6] we gave detailed description of the regularity of Φ for $f\in L^1_{\text{loc}}(\mathbb{R})$ under weaker assumptions and provided a formal framework for investigating the sequence of interspike intervals in case of almost periodic drive.

Outlooks:

- description of $\text{ISI}_n(t)$ for an almost periodic input function $f(t)$ using Bohr compactification of the reals $\mathbb{R}$:

$$\mathbb{R}\simeq G\subset\prod_{\xi\in\mathbb{R}}S^1_\xi, \quad \mathfrak{p}_\xi:\mathbb{R}\to S^1_\xi,\ \mathfrak{p}_\xi(t)=e^{i\xi t}$$

- including stochasticity in the analysis (e.g. random firing threshold; stochastic input)

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