Period incrementing and chaos in a hybrid neuron model

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joint work with
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Rosa (Rose, pl. Róża)

Neurons and Dynamical Systems

The main excitability properties of neurons can be linked with bifurcations of dynamical systems for

- Continuous dynamical systems: detailed neuron models and their reductions (Rinzel, Ermentrout, Guckenheimer, . . .).
- Discrete dynamical systems: map-based models (Caselles, Rulkov, . . .)

Hybrid dynamical systems

Integrate-and-fire neuron models combine:

- A continuous dynamical system (ordinary differential equations) accounting for input integration
- A discrete dynamical system (map iteration) accounting for spike emission.

$$\begin{cases} \frac{\mathrm{d}v}{\mathrm{d}t} = F(v) - w + I; \\ \frac{\mathrm{d}w}{\mathrm{d}t} = \varepsilon(bv - w); \end{cases} \qquad v(t) \xrightarrow[t \to t_*^-]{} \infty \implies \begin{cases} v(t_*) = v_R \\ w(t_*) = w(t_*^-) + d \end{cases}$$

- ε, b, $I \in \mathbb{R}$; v_R, $d > 0$ - parameters of the vector field and the reset

Assumption (A1)

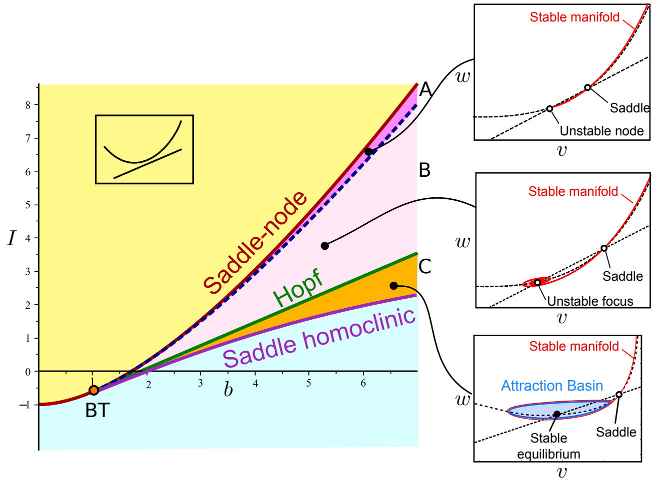
The map $F : \mathbb{R} \to \mathbb{R}$ has the following properties:

- it is regular (at least three times continuously differentiable);
- it is strictly convex;
- its derivative diverges at $+\infty$, i.e. $\lim_{v \to \infty} F'(v) = \infty$, and has a negative limit at $-\infty$ (possibly also negative infinite) satisfying:

$$\lim_{v \to -\infty} F'(v) < -\varepsilon(b + \sqrt{2});$$

- there exist $\eta, \alpha, \hat{v} > 0$ such that $F(v)/v^{2+\eta} \geq \alpha$ for all $v \geq \hat{v}$.

E.g. $F(v) = v^4 + 2av$, $F(v) = \mathrm{e}^v - v$



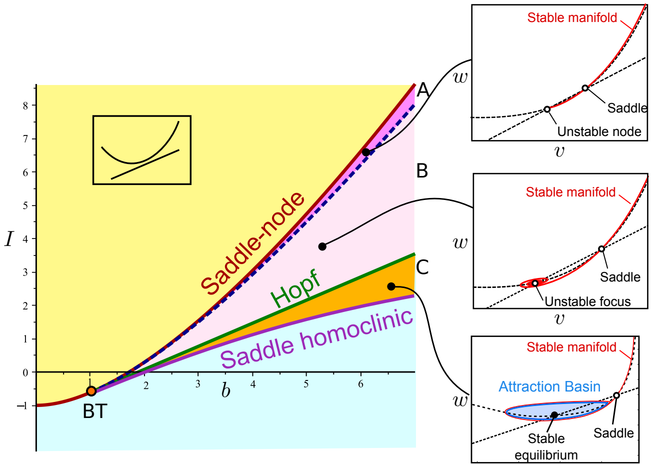
- Bifurcation analysis [Touboul, Brette, 2009]
- Other works on the model [Brunel, Latham, 2003; Brette, Gerstner, 2005; Foxall *et.al.*, 2012; Jimenez *et.al.*, 2003; Jolivet *et.al.*, 2008; Naud *et.al.*, 2008; ...]

In regions **B** and **C** the system can support stable **MM(B)Os** (**mixed-mode (bursting) oscillations**), whose signatures can be linked with rotation numbers of discontinuous interval maps:

- non-overlapping maps ([Keener 1980; Rhodes, Thompson 1986, 1991])
- overlapping maps (*old heavy maps* by [Misiurewicz 1986])

More: [J.R., J.S.-R., J.T., A.V. *Wild oscillations in a nonlinear neuron model with resets: (II) Mixed-mode oscillations.* DCDS-B 22 (2017), no. 10, 4003–4039.]

In some parameters regimes the induced adaptation map is a **Lorenz-like map**.
The work [Geller, Misiurewicz, *Farey-Lorenz permutations for interval maps.* Internat. J. Bifur. Chaos Appl. Sci. Engrg. 28 (2018), no. 2, 1850021] provides an effective algorithm allowing to decode *many* MMO signatures in this case.



• In Yellow region, with the increase of v_R, the system passes from regular tonic spiking to **bursting with spike-adding structure** (and **chaos** at the transitions)

[J.R., J.S.-R., J.T., A.V. *Wild oscillations in a nonlinear neuron model with resets: (I) Bursting, spike adding and chaos*, DCDS-B 22 (2017), 3967–4002]

Assumption (A2)

The w-nullcline lies entirely below the v-nullcline, i.e.

$$\forall_{v\in\mathbb{R}} \qquad F(v) + I > bv$$

The spike train of the spiking solution $(V(t; v_R, w), W(t; v_R, w))$ with initial condition (v_R, w) can be qualitatively described via the dynamics of the *adaptation map* Φ, with fixed points of Φ corresponding to tonic, regular spiking and periodic orbits to bursts.

Definition [Adaptation map]

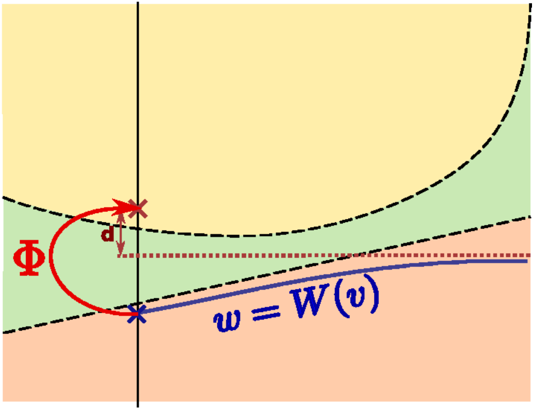
The adaptation map Φ associates to the value of the adaptation variable w the value of the adaptation variable after reset, i.e.

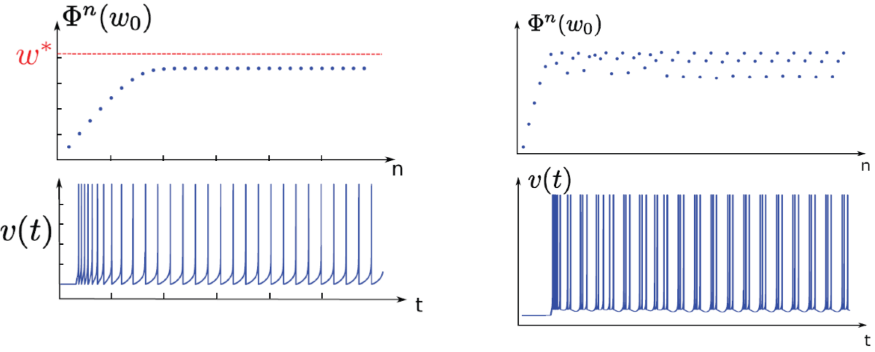
$$\Phi(w) := W(t_*; v_R, w) + d$$

Adaptation map

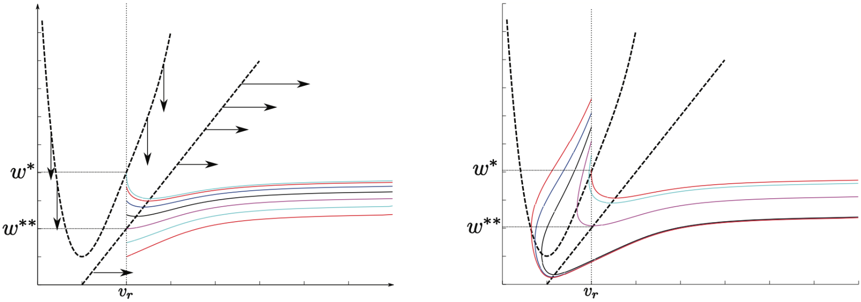
We define:

- $\mathcal{D}$ the set of w s.t. the solution starting from (v_R, w) spikes.
- $\Phi : \mathcal{D} \mapsto \mathbb{R}$ the function such that $\Phi(w)$ is the after-spike adaptation value.



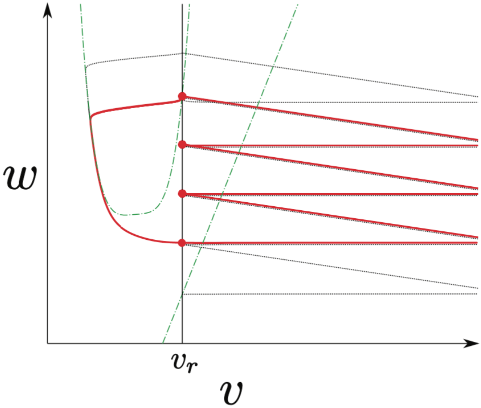


[Touboul, Brette, 2009]



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

[Touboul, Brette, 2009]



[Touboul, Brette, 2009]

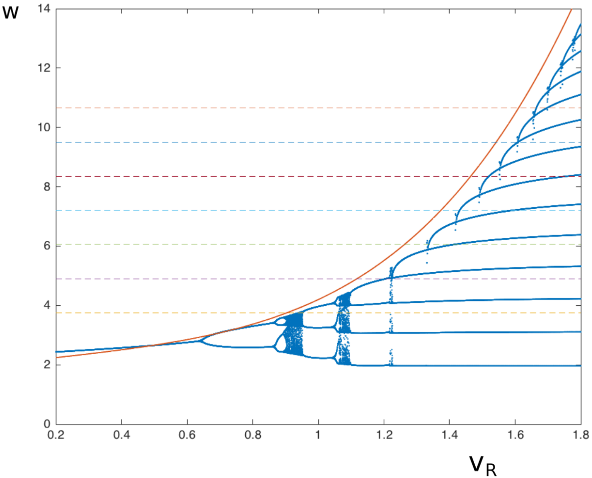
- $w^* = F(v_R) + I$ and $w^{**} = bv_R$ - intersections of the reset line $\{v = v_R\}$ with v- and w-nullclines, respectively

Theorem ([Touboul, Brette, 2009])

The adaptation map has the following properties

- $\Phi(w)$ *is defined for all* $w \in \mathbb{R}$
- Φ *is increasing and concave on* $(-\infty, w^*)$ *(with* $\Phi''(w) < 0$ *for* $w < w^*$*)*
- Φ *is decreasing and bounded below on* $[w^*, \infty)$ *and thus has an horizontal asymptote (plateau) at infinity*
- Φ *is at least* C^3 *(more generally,* C^k *if* F *is as well)*
- Φ *has a unique fixed point in* $\mathbb{R}$
- *For all* $w < w^{**}$*, we have* $\Phi(w) \geq w + d \geq w$

➡ Φ can be seen as a **unimodal interval map**



Period-incrementing (**spike-adding**) structure of Φ as v_R is varied for the quartic model with $F(v) = v^4 + 2av$, $a = 0.2$, $b = 0.7$, $I = 2$, $d = 1$, $\varepsilon = 0.4$.

Assumption (A3)

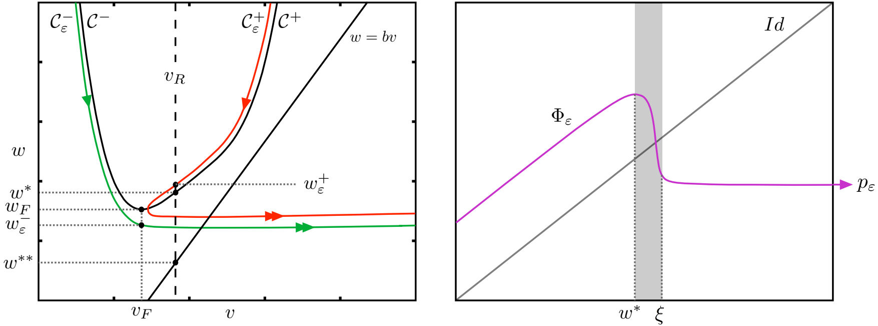
The reset line is placed to the right of the fold (v_F, w_F), i.e.

$$v_R > v_F$$

Idea: Consider firstly the dynamics in the limit of perfect time-scale separation ($\varepsilon \to 0$) and show that desired properties persist for $\varepsilon > 0$ small / approximate by piece-wise linear map Φ_0

Similar ideas:

- Belousov-Zhabotinsky reaction [Rinzel, Troy 1983]
- neon tubes [Levi 1990]
- map-based neuron models [Avrutin, Granados, Schanz 2011; Jia *et. al.* 2012; Juan *et. al.* 2010; Manica, Medvedev, Rubin 2010; Rulkov *et. al.* 2004]



- (v_F, w_F) - the fold ($(v_F, w_F - I)$ is the unique minimum of F)
- $\mathcal{C}$ - critical manifold $\{(v, F(v) + I)\}$, split into two parts $\mathcal{C}^-$ and $\mathcal{C}^+$
- $\mathcal{C}_\varepsilon^-$ and $\mathcal{C}_\varepsilon^+$ - attractive and repulsive slow manifolds (for ε small)

- $p_\varepsilon := \lim_{w\to\infty} \Phi_\varepsilon(w)$ - the plateau of Φ_ε
- $\xi := \sup\{w \in [w^*, \Phi(w^*)] : \; \Phi_\varepsilon'(w) < -1\}$

In the limit $\varepsilon \to 0$ Φ_ε can be approximated by

$$\Phi_0 : w \mapsto \begin{cases} w + d & w \leq w^* \\ p_0 := w_F + d & w > w^* \end{cases}$$

Let $d_{\mathrm{H}}(G(\Phi_\varepsilon), G(\Phi_0))$ denote the Hausdorff distance between the graphs of Φ_ε and Φ_0.

Proposition

For any fixed $v_R > v_F$, we have $d_{\mathrm{H}}(G(\Phi_\varepsilon), G(\Phi_0)) \to 0$ as $\varepsilon \to 0$. Moreover, given $\nu > 0$, with $\varepsilon \to 0$

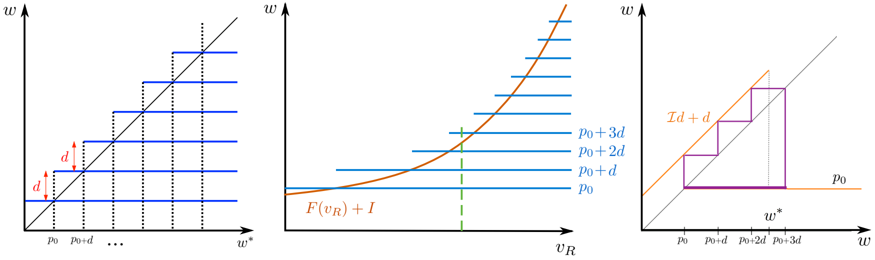
- $d_{C^0}(\Phi_\varepsilon, \Phi_0) \to 0$ *on* $(-\infty, w^*] \cup [w^* + \nu, +\infty)$
- $d_{C^1}(\Phi_\varepsilon, \Phi_0) \to 0$ *on* $(-\infty, w^* - \nu] \cup [w^* + \nu, +\infty)$

Proposition

For any v_R, the map Φ_0 has a unique periodic orbit, which is globally attractive and has period p given by:

$$p := \min\{k \in \mathbb{N} : \ p_0 + (k-1)d > w^*\}.$$

With the increase of v_R and hence w^*, the period of this orbit is incremented by 1 at each point $w^* = p_0 + (k-1)d$, $k \in \mathbb{N}$. **The map thus displays a period-incrementing structure with instantaneous transitions.**



w
d
d
p_0
$p_0{+}d$
...
w^*
w
p_0+3d
p_0+2d
p_0+d
p_0
$F(v_R)+I$
v_R
w
$\mathcal{I}d+d$
p_0
w^*
p_0
$p_0{+}d$
$p_0{+}2d$
$p_0{+}3d$
w

Proposition

Assume that $\Phi^2(w^*) < w^* < w^f < \xi < \Phi(w^*)$, *where* w^f *is the fixed point of* Φ *and* $\xi := \sup\{w \in [w^*, \Phi(w^*)] : \ \Phi'(w) < -1\}$. *If, moreover,* $\Phi^3(w^*) < w^*$, *then let* $k \in \mathbb{N}$ *be defined as*

$$k := \min\{i \geq 3 : \Phi^{i+1}(w^*) > w^*\}.$$

If there exists $\tilde{w} \geq \xi$ *such that*

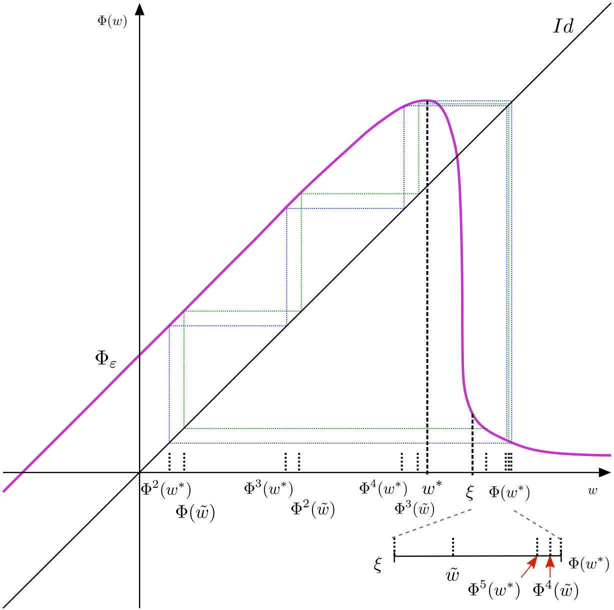
$$\Phi^i(w^*) < \Phi^{i-1}(\tilde{w}) < w^*, \ \ i \in \{2, 3, ..., k\}, \quad and \ \Phi^{k+1}(w^*) > \tilde{w},$$

then **Φ admits an asymptotically stable k-periodic orbit**, *with itinerary* $\mathcal{L}^{k-1}\mathcal{R}^1$, *attracting the orbit of* w^*.

Moreover, there is no other periodic orbit fully contained in the set $(-\infty, w^*] \cup (\tilde{w}, \infty)$ *and all points* $w \in [\Phi^2(w^*), \Phi(w^*)] \setminus H$ *are attracted by this k-periodic orbit, where*

$$H := A_1 \cup A_2 \cup ... \cup A_{k-1},$$

with $A_1 := (\gamma, \tilde{w})$, $\gamma := \Phi^{-1}(\tilde{w}) \cap (w^*, \Phi^*(w))$ *and* $A_i := \Phi^{-1}(A_{i-1}) \cap (\Phi^2(w^*), w^*)$, $i = 2, ..., k-1$.



$\Phi(w)$
Id
Φ_ε
$\Phi^2(w^*)$
$\Phi(\tilde{w})$
$\Phi^3(w^*)$
$\Phi^2(\tilde{w})$
$\Phi^4(w^*)$
$\Phi^3(\tilde{w})$
w^*
ξ
$\Phi(w^*)$
w
ξ
$\tilde{w}$
$\Phi^5(w^*)$
$\Phi^4(\tilde{w})$
$\Phi(w^*)$

Theorem (Period incrementing)

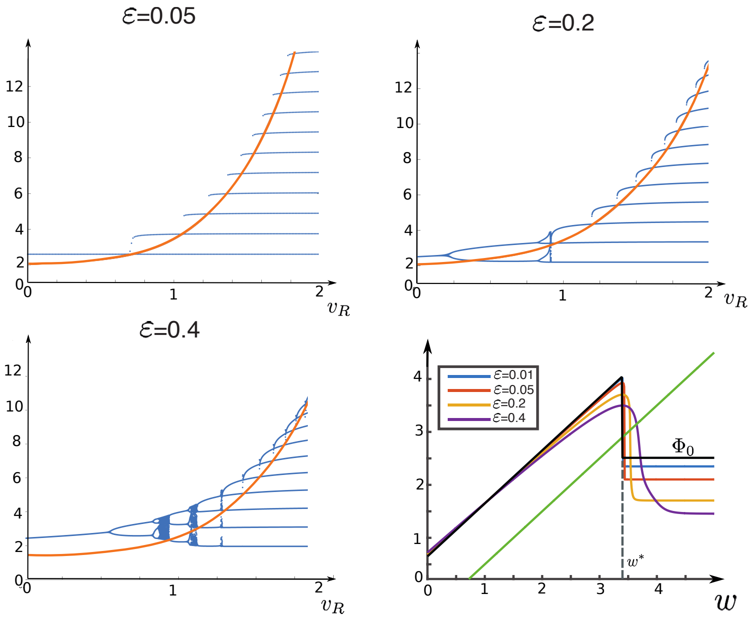
For any integer $N > 3$, there exist $\tilde{\varepsilon} > 0$ and a sequence $\{J_k\}_{k=3}^{N}$ of **intervals J_k of reset values v_R** *such that for any $\varepsilon \leq \tilde{\varepsilon}$ and $v_R \in J_k$, $k = 3, \ldots, N$, the adaptation map Φ_ε has an* **asymptotically stable k-periodic orbit** *with itinerary $\mathcal{L}^{k-1}\mathcal{R}$. Furthermore, for any $\zeta > 0$, we can pick $\tilde{\varepsilon}$ small enough so that for every $\varepsilon \leq \tilde{\varepsilon}$ and any $v_R \in J_k$ with $k \in \{3, \cdots, N\}$, the set H_ε of initial conditions w that might not be attracted by the k-periodic orbit of Φ_ε has Lebesgue measure smaller than ζ.*

Corollary

If for given $\varepsilon < \tilde{\varepsilon}$, we have $\mathrm{S}\Phi_\varepsilon < 0$, where $\mathrm{S}\Phi$ denotes the Schwarzian derivative of Φ, i.e.

$$(\mathrm{S}\Phi)(w) := \frac{\Phi'''(w)}{\Phi'(w)} - \frac{3}{2}\left(\frac{\Phi''(w)}{\Phi'(w)}\right)^2 < 0 \quad \text{for } w \neq w^*,$$

then the above k-periodic orbit is the unique attracting periodic orbit of Φ.



ε=0.05
ε=0.2
ε=0.4
v_R
ε=0.01
ε=0.05
ε=0.2
ε=0.4
Φ_0
w^*
w

Any given condition of the form

$$\Phi^2(w^*) < \Phi^3(w^*) < \ldots < \Phi^k(w^*) < w^* < \Phi(w^*)$$

is guaranteed to hold for v_R sufficiently large and ε sufficiently small.

Theorem

For every v_R the point w^* is the **unique critical point** *of Φ (i.e. $\Phi'(w) \neq 0$ for $w \neq w^*$). Moreover, if $F'(v_R) > \varepsilon$, then the critical point w^* is* **non-degenerate***:*

$$\Phi''(w^*) \neq 0$$

Theorem (Topological chaos)

Suppose that $\Phi^2(w^*) < \Phi^3(w^*) < w^* < \Phi(w^*)$. *Then*

1. *the map* Φ *has periodic orbits of all periods*
2. Φ^m *has a 'horseshoe' for some* $m \in \mathbb{N}$, *i.e. there exist two closed-subintervals* A_1 *and* A_2, *with disjoint interiors, such that*
$$(A_1 \cup A_2) \subseteq (\Phi^m(A_1) \cap \Phi^m(A_2))$$
3. Φ *has positive topological entropy*
4. Φ *is chaotic in the sense of Li-Yorke, Block and Coppel and Devaney (with some D-chaotic set* $Y \subset [\Phi^2(w^*), \Phi(w^*)]$*).*

[Li, Misiurewicz, Pianigiani and Yorke, *No division implies chaos*, Trans. Amer. Math. Soc. 273 (1982); Aulbach, Kieninger 2001; Block, Coppel 1991; Collet, Eckmann 2006; Misiurewicz 2011; ...]

➡ Topological chaos occurs for most of the parameter values v_R and ε

Definition [Metric chaos]

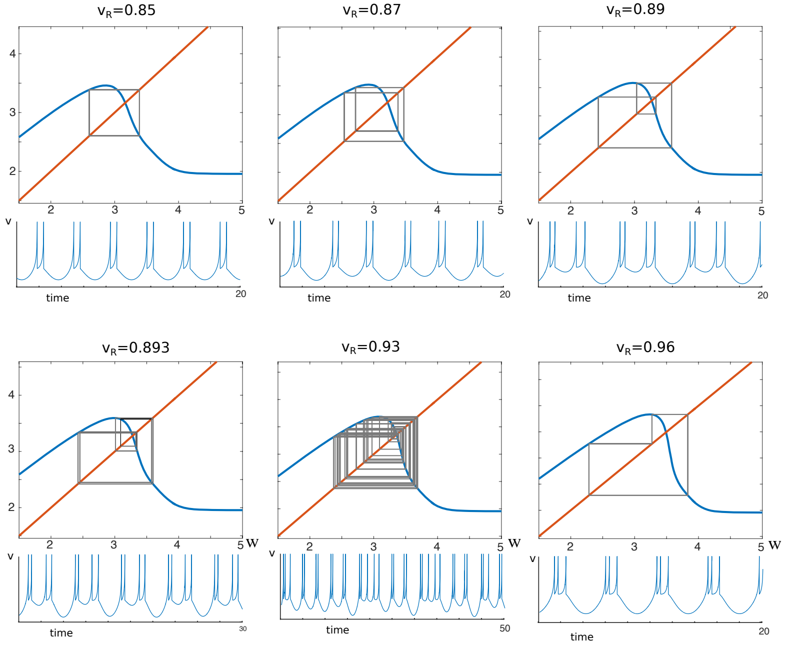
We say that Φ is chaotic if it admits absolutely continuous invariant probability measure (*acip*) μ, i.e. the invariant measure which is finite, normalised and has density with respect to the Lebesgue measure Λ, and when it has positive Lyapunov exponent almost everywhere.

Proposition

Let $\mathcal{V}$ be some bounded interval of parameter values $v_R > v_F$. For sufficiently small ε the corresponding family $\{\Phi_{v_R}\}$ of adaptation maps undergoes period incrementing transitions such that **between any two intervals $J_k = [a_k, b_k]$ and $J_{k+1} = [a_{k+1}, b_{k+1}]$ of v_R values**, *corresponding, respectively, to k and $k+1$ periodic orbits, there* **exists a parameter value $\bar{v}_R \in (b_k, a_{k+1})$** *such that*

$$(\Phi_{\bar{v}_R})^{k+1}(w^*_{\bar{v}_R}) = w^f_{\bar{v}_R},$$

i.e. **the critical point is mapped into a few steps onto a fixed point**.


v_R=0.85
v_R=0.87
v_R=0.89
v_R=0.893
v_R=0.93
v_R=0.96
W
v
time
20
30
50

Corollary (E.g. [de Melo, van Strien 1993; Thieullen, Tresser, Young 1994, Thunberg 2001; ...])

Suppose further that the fixed point $w^f_{\bar{v}_R}$ is unstable and that the map $\Phi_{\bar{v}_R}$ **does not have periodic attractors**. *Then there exist constants $\gamma > 0$ and $C > 0$ and a positive measure set $E \subset \mathcal{V}$ with $\bar{v}_R \in E$ as a Lebesgue density point, such that the* **Lyapunov exponent is positive along the orbit of the critical point***:*

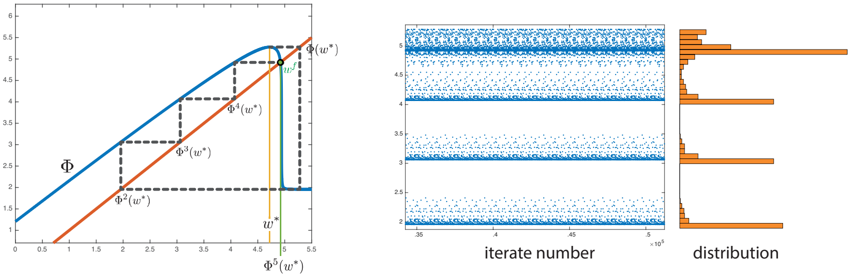
$$|(\Phi^n_{v_R})'(\Phi_{v_R}(w^*))| \geq Ce^{\gamma n} \quad \textit{for all } v_R \in E \textit{ and all } n \geq 1.$$

Moreover, if $S\Phi_{v_R} < 0$ for all $v_R \in E$, then the maps Φ_{v_R}, $v_R \in E$, **exhibit metric chaos** *with an acip μ_{v_R}, describing asymptotics for almost all orbits and with* **positive Lyapunov exponent almost everywhere**, *i.e.*

$$\lim_{n\to\infty} \frac{1}{n} \log |(\Phi^n_{v_R})'(w)| = \kappa > 0 \quad \textit{for a.a. } w \in \mathbb{R}$$

After e.g. [van Strien 1990] it follows that even if we cannot assure that $\Phi_{\bar{v}_R}$ does not have periodic attractors, then, at least, the periods of periodic attractors and non-hyperbolic periodic orbits of $\Phi_{\bar{v}_R}$ are uniformly bounded.

(A) (B)



(A) Adaptation map in the case where $\Phi^5(w^*) = w^f$ (fine-tuning of v_R value)

(B) Iterates of Φ in the same setting and the obtained distribution of orbits

Conclusions

- Rigorous explanation of period-incrementing transitions and regions of chaotic behaviour in non-linear IF models
- Versatility of 2D IF models: the system can support bursts of any period as a function of model parameters
- Slow-fast approach and establishing a deep relationship of IF dynamics with unimodal maps allow to explain results observed numerically
- Some results (e.g. uniqueness and non-degeneracy of the critical point) are independent of the slow-fast analysis

Thank you!

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