Modelos en neurociencia: sistemas dinámicos y más allá

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Sistemas dinámicos y neurociencia
Ddays 2021

Outline

1. Models of dynamical systems in neuroscience
    - The role of dynamical systems
2. Parameter estimation: At the edge of DS
    - Using the period function in spiking regimes
    - Estimation of synaptic inputs using sliding mode control
3. Empiric models: Beyond DS
    - Black-box models
    - Gray-box models: food for DS

1. Models of dynamical systems in neuroscience

Models of neurons/populations activity

- Based on biophysical principles (Hodgkin-Huxley type models)

$$\begin{cases} C\,\dfrac{dv}{dt} &= -g_L(v - V_L) - \sum\limits_{\iota\in\Upsilon} g_\iota\, w_\iota^{p_\iota}(v - V_\iota) + I_{app}, \\ \dfrac{dw_\iota}{dt} &= \dfrac{W_\iota(v) - w_\iota}{\tau_\iota(v)}, \qquad |\Upsilon| \approx\ \sharp \text{ ionic channels.} \end{cases}$$

$v \in [-100, 60]\,\mathrm{mV}$ approximately is the membrane potential of the neuron, and $w_\iota \in [0,1]$ are the gating variables.

Models of neurons/populations activity

- Based on biophysical principles (Hodgkin-Huxley type models), or (over)simplifications of them (Fitzhugh-Nagumo, integrate and fire,. . .).

$$\begin{cases} \dot{v} &= -f(v) + w + I_{app}, \\ \dot{w} &= \epsilon\,(-v - \gamma\, w), \end{cases} \qquad \begin{cases} \dot{v} &= -g_L(v - V_L) + I_{app}, \\ & v(t^-) = \theta \Rightarrow v(t^+) = v_{reset}. \end{cases}$$

Models of neurons/populations activity

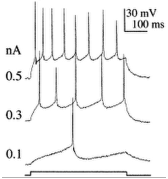
- Based on biophysical principles (Hodgkin-Huxley type models), or (over)simplifications of them (Fitzhugh-Nagumo, integrate and fire,. . .).
- Mean-field models derived *analytically* from the biophysical ones (firing rate models, population density models, neural mass models, neural field models,. . .).

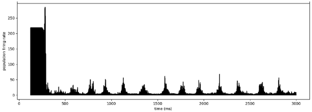
$$\begin{cases} \tau_E \dot{E} &= -E + (1 - r\,E) S_E[w_{EE}\,E - w_{EI}\,I + k\,P(t)], \\ \tau_I \dot{I} &= -I + (1 - r' I) S_I[w_{IE}\,E - w_{II}\,I + k'\,Q(t)], \end{cases}$$ [Wilson-Cowan, 1972]

$$\begin{cases} \dot{r} &= \delta/\pi + 2rv, \\ \dot{v} &= v^2 + \bar{\eta} - \pi^2\, r^2 - J\, r + I_{app}(t). \end{cases}$$ [Montbrió et al, PhysRevX 2015]

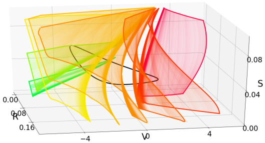
Models of neurons lead to dynamical systems

- Thanks to the underlying (bio)physical analogies, they are written as dynamical systems; so, from a biological point of view, we can benefit from the study of “familiar elements and features” like:
    - limit cycles (spikes, oscillations) and their bifurcations,
    - slow-fast systems,
    - invariant manifolds,
    - . . .





[N. Gutiérrez, TFM 2021]



[Pérez-Cervera et al, J Nonl Sci 2019]

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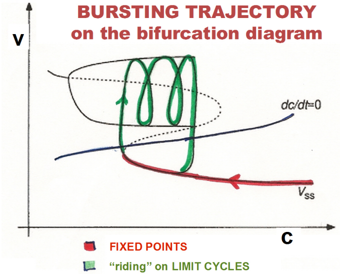
  - limit cycles (spikes, oscillations) and their bifurcations,
  - slow-fast systems,
  - invariant manifolds,
  - ...
- So, the connection between dynamical systems and neuroscience is clear.

How do dynamical systems help?

- Simplified models allow to inspect which mechanisms are involved in relevant neuroscience problems (bursting).

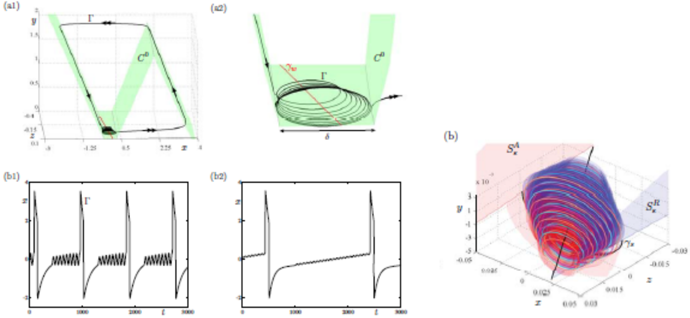
v, w fast, c slow:



[Rinzel, 1980's]

How do dynamical systems help?

- Simplified models allow to inspect which mechanisms are involved in relevant neuroscience problems (bursting, mix-mode oscillations).



[Desroches et al., SIAM Rev. 2016]

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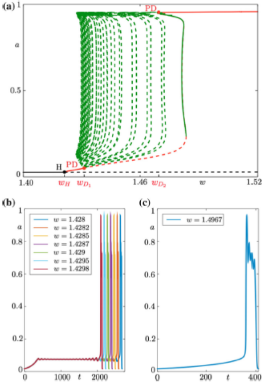

[Köksal-Ersöz et al., J Math Biol 2020]

How do dynamical systems help?

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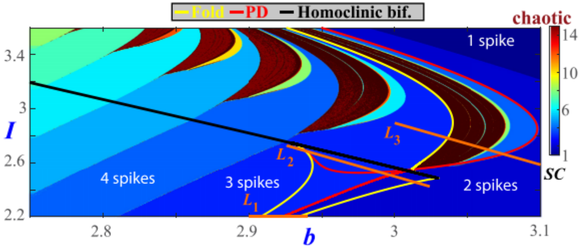
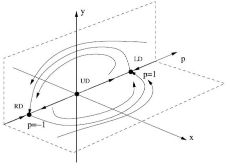


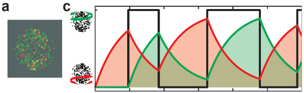
[Barrio et al., CNSNS 2020]

How do dynamical systems help?

- Simplified models allow to inspect which mechanisms are involved in relevant neuroscience problems (bursting, mix-mode oscillations, mix-mode bursting oscillations, spike-adding).
- What is necessary to rise complexity? Use of separatrix maps for quasi-periodic forcing in binocular rivalry systems.

$$\begin{cases} \dot{p} &= h(p) + x^2(1-p) + y^2(-1-p), \\ \dot{x} &= f(p,x,y) + I_x\, x + \varepsilon\eta_x(t), \\ \dot{y} &= f(-p,y,x) + I_y\, y + \varepsilon\eta_y(t). \end{cases}$$





[Pastukhov et al., Front. Comp. Neuro. 2013]

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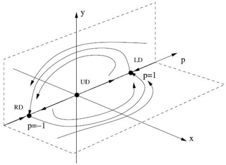
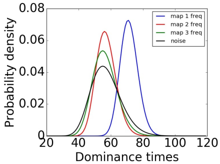




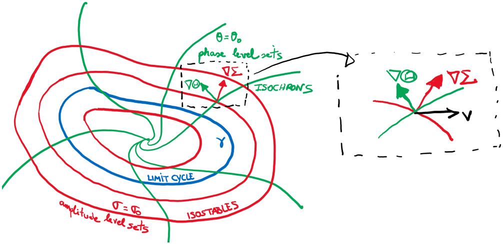
Comparison between fittings to log-normal distribution of the dominance times histograms.

[Delshams, G., Huguet, Chaos 2018]

How do dynamical systems help?

- Simplified models allow to inspect which mechanisms are involved in relevant neuroscience problems.
- What is necessary to rise complexity?
- DS tools allow to make accurate predictions (e.g., phase and response functions)...

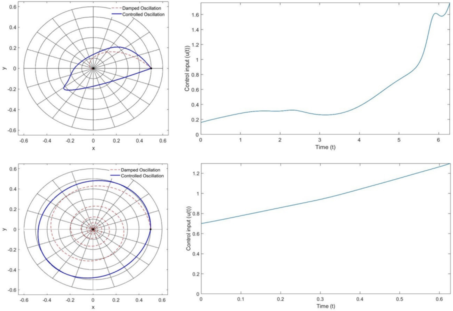
$$\boldsymbol{PRF}(x) = \nabla\Theta(x)\cdot \mathrm{v},$$
$$\boldsymbol{ARF}(x) = \nabla\Sigma(x)\cdot \mathrm{v}.$$



[Cabré et al, JDE 2003], [Freire, Gasull, G., BScMat 2007], [G., Huguet, SIADS 2009], [Castejón, G., Huguet, JMathNeuro 2013], [Pérez-Cervera et al, JNonSci 2019], [Castejón, G., CNSNS 2020],...

How do dynamical systems help?

- Simplified models allow to inspect which mechanisms are involved in relevant neuroscience problems.
- What is necessary to rise complexity?
- DS tools allow to make accurate predictions (e.g., phase and response functions) and exert control.



[Moreno, TFM 2019; Martínez-Añón, TFM 2020]

How do dynamical systems help?

- Simplified models allow to inspect which mechanisms are involved in relevant neuroscience problems (bursting, mix-mode oscillations, mix-mode bursting oscillations, spike-adding. . .).
- What is necessary to rise complexity?
- DS tools allow to make accurate predictions (e.g., phase and response functions) and exert control.
- Underlying models are a solid ground also for **parameter estimation**.

2. Parameter estimation: At the edge of DS

Parameter estimation: at the edge of DS

- Now, we start thinking on real data, where only v and few other outcomes are measurable.
- Electrophysiological experiments are crucial to know the set Υ (number and type of ionic channels) and estimate the parameters from data. . . but it is not always possible.

$$\begin{cases} C\,\dfrac{dv}{dt} &= -g_L(v - V_L) - \displaystyle\sum_{\iota\in\Upsilon} g_\iota\, w_\iota^{p_\iota}(v - V_\iota) + I_{app}, \\ \dfrac{dw_\iota}{dt} &= \dfrac{W_\iota(v) - w_\iota}{\tau_\iota(v)}, \qquad |\Upsilon| \approx \ \sharp \text{ ionic channels.} \end{cases}$$

Challenging questions arise:

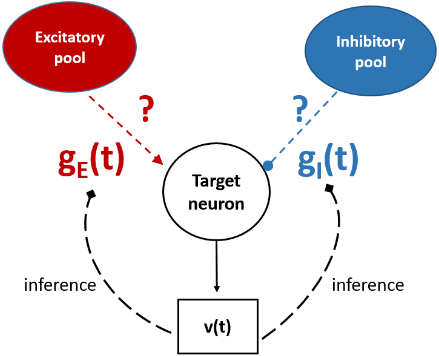
- How can we estimate inputs from partial observations?
- How can we disambiguate models from partial observations?
- How can we determine the underlying system,. . . when data sources are uncertain (so, not clear biophysics)?

Estimation of synaptic inputs

Inverse problem:

From a measurable (e.g., membrane potential) we aim at inferring the temporal contribution of the synaptic current and discerning global excitation from global inhibition.

- Note that we assume that other variables are not measurable (e.g., partial observations).
- The time course of synaptic conductances arriving at a single cell provides local information about its functional connectivity, often an indicator to validate more general theories (e.g., un/balanced networks).



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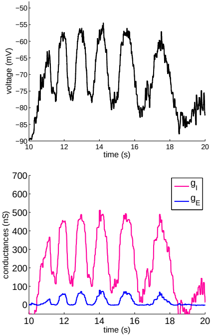
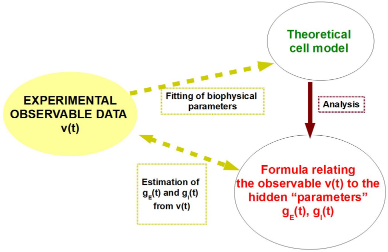


Estimation of synaptic inputs: mathematical formulation



Theoretical cell model

EXPERIMENTAL OBSERVABLE DATA v(t)

Fitting of biophysical parameters

Analysis

Formula relating the observable v(t) to the hidden “parameters” $g_E(t)$, $g_I(t)$

Estimation of $g_E(t)$ and $g_I(t)$ from v(t)

Theoretical cell model:

$$\begin{cases} C\dot{v} = f(v,\mathbf{w};\mu_1) + I_{app} - I_{syn}, \\ \dot{\mathbf{w}} = h(v,\mathbf{w};\mu_2) \\ \qquad \text{where } v \in \mathbb{R},\ \mathbf{w} \in \mathbb{R}^n,\ \mu_i \in \mathbb{R}^{p_i}. \end{cases}$$

- f, h nonlinear, ionic currents, ion channels' dynamics;
- I_{app}, externally applied current (control parameter);
- $I_{syn}(t) = \mathrm{g_E(t)}(v(t) - V_E) + \mathrm{g_I(t)}(v(t) - V_I)$, synaptic input.

Main goals:

1. How to estimate $I_{syn}(t)$ given $v(t)$?
2. How to estimate $g_E(t)$ and $g_I(t)$ given $v(t)$? (ill-posed)

Estimation of synaptic inputs in spiking regimes

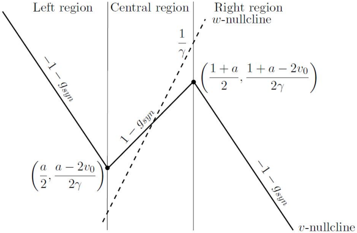
We consider a piecewise version of the Fitzhugh-Nagumo model, the McKean model, given by

$$\begin{cases} C\,\dot{v} = f(v) - w - w_0 + \boldsymbol{I_{app}} - I_{syn}(v), & C \ll 1, \\ \dot{w} = v - \gamma w - v_0, \end{cases} \tag{1}$$

where

$$I_{syn}(v) = g_{syn}(t)\,(v - V_{syn})$$

$$f(v) = \begin{cases} -v, & v < a/2; \\ v - a, & a/2 \leq v \leq (1+a)/2; \\ 1 - v, & v > (1+a)/2. \end{cases}$$



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where

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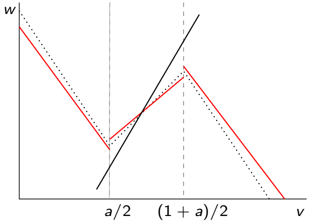
3 zones: $v-$ and $w-$nullclines

slow manifolds



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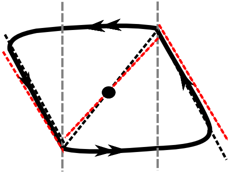
where $I_{syn}(v) = g_{syn}(t)\,(v - V_{syn})$.

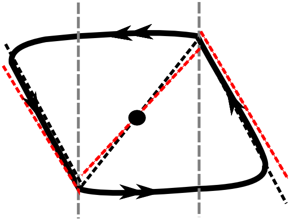


Main goal:

Express the period T of the periodic orbit as a function of g_{syn} and $\boldsymbol{I_{app}}$, i.e. $T(\boldsymbol{I_{app}}, g_{syn})$,

McKean w/ synaptic input: period of limit cycle

We approximate $T(I_{app}, g_{syn})$ by $\hat{T}(I_{app}, g_{syn})$ using analytical computations and slow-fast approximations.



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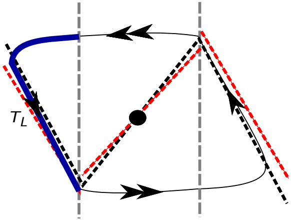

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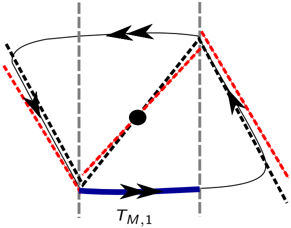

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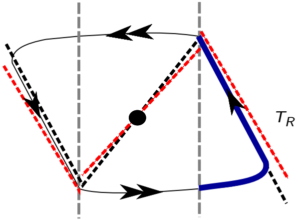

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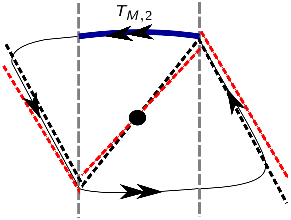
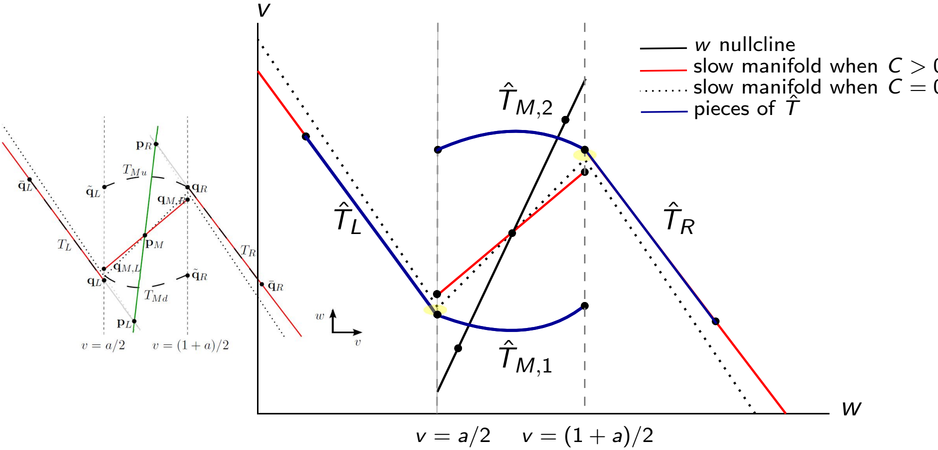


Analytical approximation $\hat{T}(I_{app}, g_{syn})$ of the period



[Fernández-García et al., SIADS 2015; G., Prohens, Teruel, Vich, SIADS 2017]

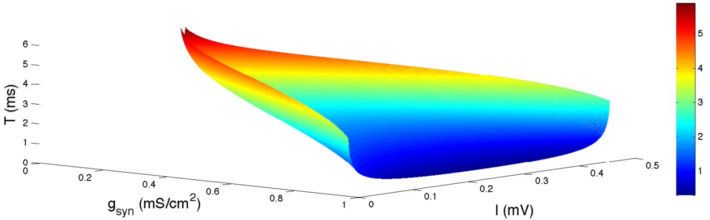
Analytical approximation of the period, $\hat{T}(g_{syn})$

$$\hat{T} = \hat{T}_L + \hat{T}_{M,2} + \hat{T}_R + \hat{T}_{M,1}. \text{ That is,}$$

$$\hat{T}(g_{syn}) = \sum_{i=1}^{2} \Bigg[\frac{1}{\lambda_{s,L}} \ln\left(\left| \frac{\gamma(I_{app} - I_i)}{\gamma(I_{app} - I_i) - K_L} \right| \right) + \frac{1}{\lambda_{q,M}} \ln\left(\left| \frac{\gamma(I_{app} - I_i) + K_M}{\gamma(I_{app} - I_i) + K_{M,i}} \right| \right)$$

- $\lambda_{\mathrm{s,L}}$ and $\lambda_{\mathrm{q,M}}$ are the slow lateral and the fast middle eigenvalues, respectively. They have a **nonlinear dependence on** g_{syn}
- $\mathrm{K_L}$, $\mathrm{K_M}$, $\mathrm{K_{M,1}}$ and $\mathrm{K_{M,2}}$ are given functions. They have a **nonlinear dependence on** g_{syn}
- $\mathrm{I_1}$ and $\mathrm{I_2}$ are the minimum and maximum values of external current. They **depend linearly on** g_{syn}

Use of the period expression

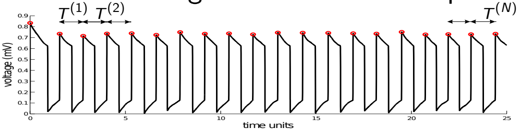


$\hat{T}$ is **"highly" nonlinear** but **monotone** with respect to g_{syn}.

Solving $\hat{T}(I^*, g_{syn}) = T^*$, given I^*,we estimate g_{syn}.

Procedure to estimate $g_{syn}(t)$

1. Record $v(t)$ for an specific I^* such that the neuron oscillates.
2. Extract a sequence of times $\{T^{(k)}\}_{k=1}^{N}$, where each $T^{(k)}$ corresponds to the time length of the k-th interspike interval.

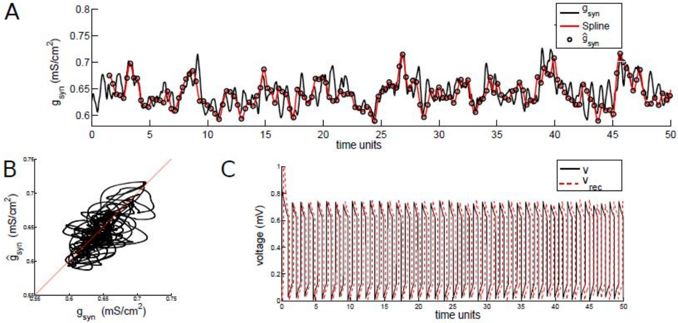


$$\{T^{(1)}, T^{(2)}, \ldots, T^{(N)}\}$$

3. Solve $\hat{T}(I^*, g_{syn}^{(k)}) = T^{(k)}$, for each $T^{(k)}$, to find $g_{syn}^{(k)}$.
4. Assign at each $g_{syn}^{(k)}$ the time $t^{(k)}$; the $(k+1)$-th peak.
5. Interpolate $(t^{(k)}, g_{syn}^{(k)})$ and obtain $\hat{g}_{syn}(t)$.

Refinement: use subperiods together with the partial approximations of $\hat{T}_L$, $\hat{T}_{M,2}$, $\hat{T}_R$ and $\hat{T}_{M,1}$.

Example: an estimation with realistic data



Actual and estimated synaptic input received by a cell from the computational model of the layer 4Cα of the primary visual cortex by [McLaughlin et al. (2000), Tao et al. (2004)].

Voltage reconstruction.

High frequency synaptic input hinders estimations, but still, there is a good approximation in mean!

[G., Prohens, Teruel, Vich, SIADS 2017; Vich at al., Mathematics 2020]

Estimation of synaptic inputs

Using sliding mode control

We consider the Morris-Lecar model:

$$\begin{cases} C_m \dot{v} & = -g_L\,(v - V_L) - g_K\,w\,(v - V_K) - g_{Ca}\,m_\infty(v)\,(v - V_{Ca}) + I_{app} - I_{syn}, \\ \dot{w} & = \phi \frac{w_\infty(v) - w}{\tau_w(v)}. \end{cases}$$

$$m_\infty(v) = \frac{1 + \tanh(\frac{v - V_1}{V_2})}{2},\ w_\infty(v) = \frac{1 + \tanh(\frac{v - V_3}{V_4})}{2},\ \tau_w(v) = \left(\cosh(\frac{v - V_3}{2V_4})\right)^{-1}.$$

- I_{app} : represents a constant externally applied current
- $I_{syn}(t) = g_E(t)(v - V_E) + g_I(t)(v - V_I)$ represents the synaptic input.

A state observer for w and synaptic input estimation

We consider a copy of the Morris-Lecar model with an extra input term instead of the synaptic input. Namely,

$$\begin{cases} C_m \dot{v} & = -g_L\,(v - V_L) - g_K\,\hat{w}\,(v - V_K) - g_{Ca}\,m_\infty(v)\,(v - V_{Ca}) + I_{app} + u, \\ \dot{\hat{w}} & = \phi \frac{w_\infty(v) - \hat{w}}{\tau_w(v)}. \end{cases}$$

Since v is the only measured output, it can be used in the $(\hat{v}, \hat{w})$ dynamics. Let us define $e_v = v - \hat{v}$ and $e_w = w - \hat{w}$. Combining the two systems:

$$\begin{aligned} C_m \frac{de_v}{dt} &= -g_K\,(v - V_K)\,e_w - I_{syn} - u, \\ \frac{de_w}{dt} &= -\tfrac{\phi}{\tau_w(v)}\,e_w. \end{aligned} \tag{4}$$

The control action

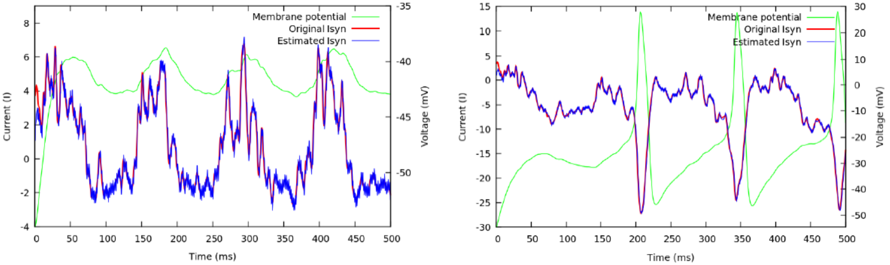
The control action $u = U \cdot \text{sign}(e_v)$ with

$$U \geq \left| -g_K \left(v - V_K \right) e_w - I_{syn} \right|, \quad \text{for all} t,$$

forces $e_v \dot{e_v} < 0$ and $e_v(t)$ to converge to zero in finite time, presumed that

- Filtering input $u(t)$ provides an approximation of $I_{app} - I_{syn}$ and so, I_{syn} (I_{app} is known).
- The error dynamics e_w, converges to zero since $e_w = 0$ is the unique equilibrium point and e_w^2 is a Lyapunov function
$$\frac{de_w^2}{dt} = -\frac{\phi}{\tau_w(v)}\, e_w^2 \leq -\phi e_w^2.$$
- It is an off-line procedure.

Estimation of synaptic inputs using sliding mode control; examples



Actual and estimated synaptic input for $I_{app} = 30$ (left) and $I_{app} = 45$ (right).

[L. Tresserras, TFM 2020; Fossas, G., Tresserras, in progress]

3. Empiric models: Beyond DS

Empiric models

Paradigm:

What to do when we do not have a model? Mainly, because of lack of knowledge about the biophysical structure of the *source* (neuron, population,. . .).

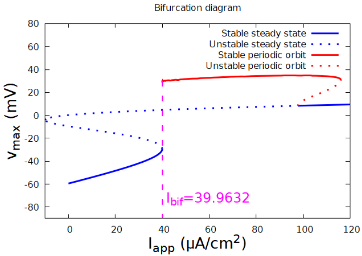
- We can do a statistical model fitting.
- Machine learning and other methods from AI can be helpful.

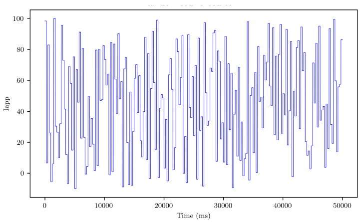
Black-box models: a proof-of-concept

Consider again the Morris-Lecar model:

$$\begin{cases} C_m \dot{v} &= -g_L\,(v - V_L) - g_K\, w\,(v - V_K) - g_{Ca}\, m_\infty(v)\,(v - V_{Ca}) + I_{app}(t), \\ \dot{w} &= \phi \frac{w_\infty(v) - w}{\tau_w(v)}. \end{cases}$$

- We integrate the system with external input $I_{app}(t)$. The design of $I_{app}(t)$ is important: we want it to *visit all the states* of the system.

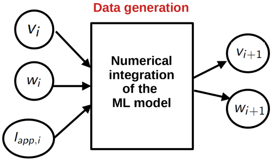




Black-box models: a proof-of-concept

- Let $x_i := \{(v_i, w_i, I_{app,i})\}_{i=0}^{M-1}$ the set of initial conditions and $y_i := \{(v_{i+1}, w_{i+1})\}_{i=0}^{M-1}$ the set of corresponding outputs. In the sequel, we ignore the model and imagine the paired vectors x and y as raw data from an experiment.

- Next, we use some method of machine learning (artificial neural networks, genetic algorithms,...) to learn the input-ouput relationship.



- We use a less sophisticated method: a regression method that does not require training: we construct a wavenets, a network based on Mallat's multiresolution analysis.

Black-box models: a proof-of-concept

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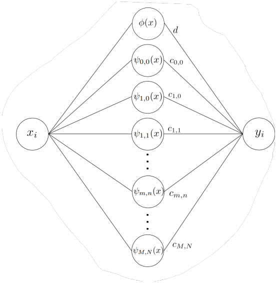


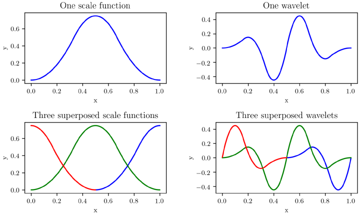
- We use a less sophisticated method: a regression method that does not require training: we construct a wavenets, a network based on Mallat's multiresolution analysis.

Black-box models. The wavenet

- The goal is to express approximate $y = \hat{f}(x)$, with

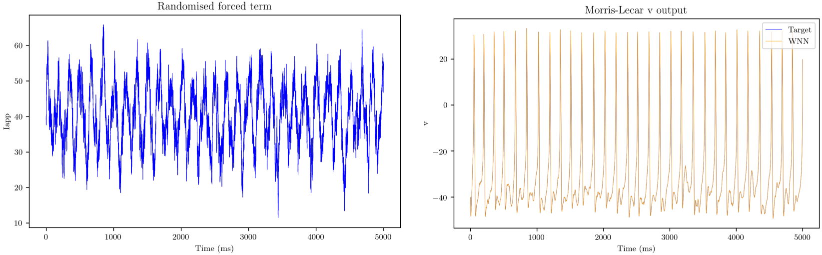
$$\hat{f}(x) = \sum_{k=1}^{K} d_k \phi_k(x) + \sum_{r=0}^{R} \sum_{s=0}^{S} c_{m,n} \psi_{s,r}(x),$$

where ϕ_0 is the so-called scale function and the $\psi_{s,r}$ are the resulting wavelets up to some resolution level R (see Mallat's theory).



- We have introduced modifications (not shown here) to gain computational efficiency (python packages), reduce the resolution levels (basis expanded to function frames),. . .

Black-box models. Results



Prediction versus actual voltage using a stochastic I_{app} input (different from the *training* (step-wise) $I_{app}(t)$.

Black-box models. Last comments

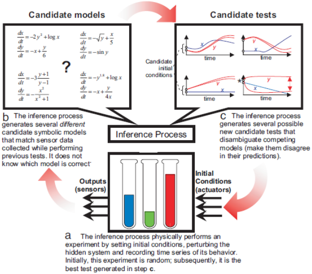
- Excellent approximation but . . . it is too ad hoc, we lose the possibility of analysis (mechanisms, control,...), are there experimental (timing) constraints?
- Is there any biophysical information encoded in the network? In general, when approximating input/output relationships in a dynamical system, do the coefficients contain information about the original parameters of the system?
- Preliminary explorations show some monotonic relationship between original parameters and groups of weights in the wavenet, but nothing conclusive. In fact, it seems a very naive question, we are *shooting in the dark*.
- Intermediate solution:

Black-box models: last comments

- Design AI schemes to identify parameters: $|\Upsilon|$, $\{g_\iota\}_{\iota\in\Upsilon}$, $\{V_\iota\}_{\iota\in\Upsilon}$, parameters involved in W_ι and τ_ι.

$$\begin{cases} C\,\dfrac{dv}{dt} &= -g_L(v - V_L) - \sum_{\iota\in\Upsilon} g_\iota\, w_\iota^{p_\iota}(v - V_\iota) + I_{app}, \\ \dfrac{dw_\iota}{dt} &= \dfrac{W_\iota(v) - w_\iota}{\tau_\iota(v)}, \qquad |\Upsilon| \approx \ \sharp \text{ ionic channels.} \end{cases}$$

Black-box models: last comments. Food for DS



b The inference process generates several *different* candidate symbolic models that match sensor data collected while performing previous tests. It does not know which model is correct

c The inference process generates several possible new candidate tests that disambiguate competing models (make them disagree in their predictions).

a The inference process physically performs an experiment by setting initial conditions, perturbing the hidden system and recording time series of its behavior. Initially, this experiment is random; subsequently, it is the best test generated in step **c**.

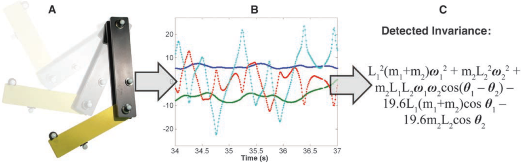


Fig. 1. Mining physical systems. We captured the angles and angular velocities of a chaotic double-pendulum (**A**) over time using motion tracking (**B**), then we automatically searched for equations that describe a single natural law relating these variables. Without any prior knowledge about physics or geometry, the algorithm found the conservation law (**C**), which turns out to be the double pendulum's Hamiltonian. Actual pendulum, data, and results are shown.

[Bongard, Lipson, PNAS 2007]

[Schmidt, Lipson, Science 2009]

⏩ Go to control-induced oscillations

Summary

1. Models of dynamical systems in neuroscience.
    - Simplified models and DS tools allow to inspect which mechanisms are involved in relevant neuroscience problems (bursting, mix-mode oscillations, mix-mode bursting oscillations, spike-adding. . .) or explain facts like what is necessary to rise complexity.
    - DS tools allow to make accurate predictions (e.g., phase and response functions) and exert control.
2. Parameter estimation: At the edge of DS.
    - Underlying DS models are a solid ground also for **parameter estimation**.
3. Empiric models: Beyond DS.
    - AI methods give excellent approximations but we lose the possibility of analysis (mechanisms, control,...).
    - Is there any biophysical information encoded in the network? In general, when approximating input/output relationships in a dynamical system, do the coefficients contain information about the original parameters of the system?
    - Future work: Design AI schemes to identify model parameters within a family of systems. New food for DS!

Collaborators

- Estimation of parameters using control and empiric models: David Aquilué (Master student, Univ. Paris-Saclay), Pau Fisco (Master student, UPC), Enric Fossas (IOC, UPC), Néstor Roqueiro (UFSC, Brazil), Lluc Tresserras (UPC).
- Phase and amplitude response functions: Oriol Castejón (former PhD student), Gemma Huguet (Dept. Mathematics, UPC), Kevin Martínez-Añón (PhD student, CRM), Román Moreno (PhD student, Dept. Mathematics, UPC).
- Estimation of synaptic inputs: Rafel Prohens (UIB), Antonio Teruel (UIB), Cati Vich (UIB).
- Slow-fast dynamics: Mathieu Desroches (INRIA), Elif Köksal-Ersöz (INRIA), John Rinzel (NYU), Joël Tabak (Exeter Univ.); M.D. (INRIA), Enrique Ponce (US), R.P. (UIB), Serafim Rodrigues (BCAM), A.T. (UIB).
- Separatrix map, bistable perception: Amadeu Delshams (Dept. Mathematics, UPC), Gemma Huguet (Dept. Mathematics, UPC).
- Parameter disambiguation (not in this talk): Susanne Ditlevsen (U. Copenhaguen), Horacio Rotstein (NJIT).
- Estimation of network parameters (genetic algorithms)(not in this talk): David Aquilué (TFG student, UPC), Antonio J. Pons (UPC).
- Topological data analysis (not in this talk): Nils Gutiérrez (Master student, UPC), Esther Ibáñez-Marcelo (ISI-Torino).

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