Ana Amador

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Professor at the Physics Dept. – Universidad de Buenos Aires

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ARGENTINA

Ana Amador

Interdisciplinary work in neuroscience

Masters in Physics, PhD in Physics (interdisciplinary) @ Univ. of Buenos Aires

Postdoc in Neuroscience (Organismal Biol & Anatomy) @ University of Chicago

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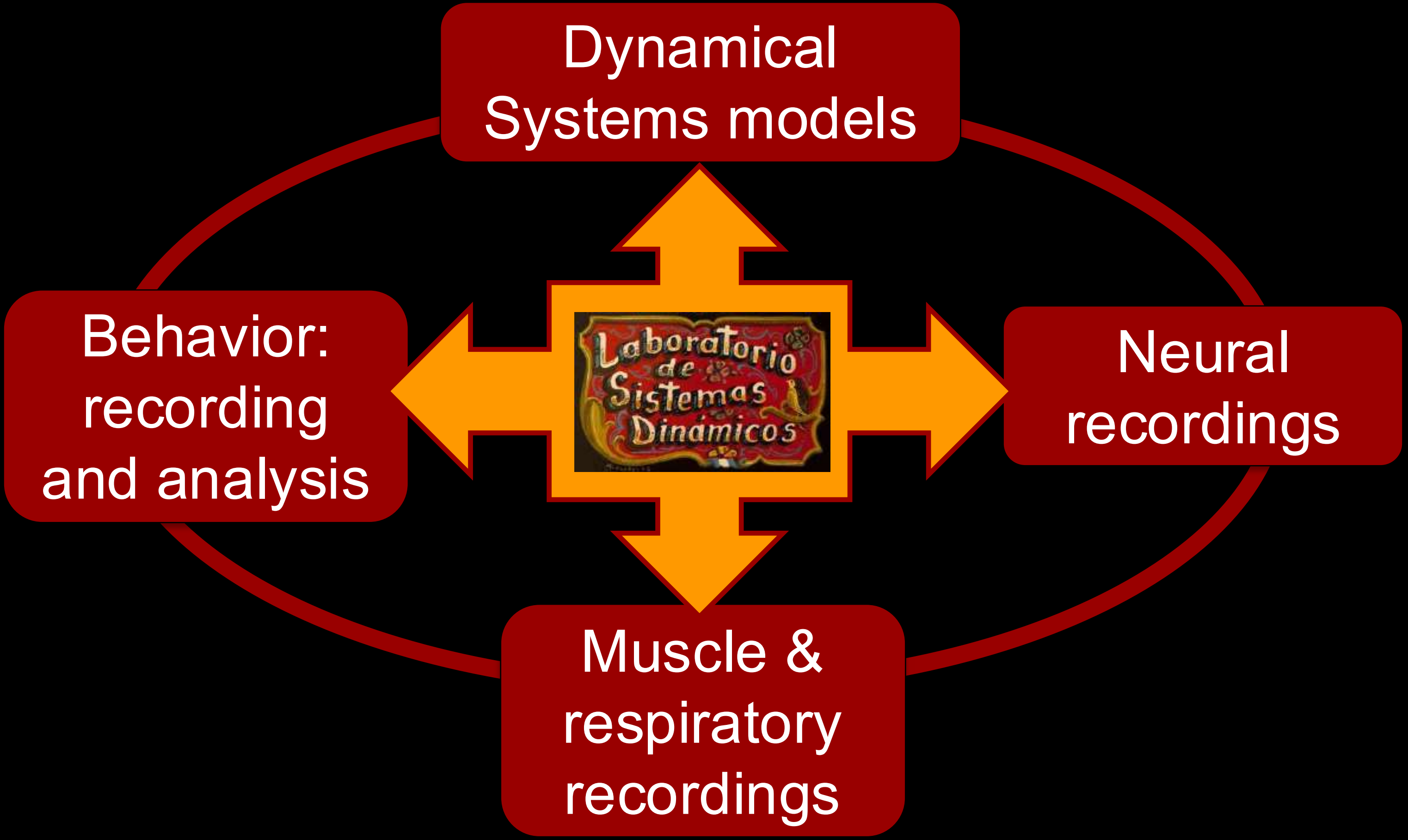
The goal of our research is to shed light on the **dynamical mechanisms involved in the perception and the generation of complex sounds** and to study the brain and the peripheral system in this process.



Lecture 1

Complex Systems in the modern era.

Nonlinear dynamics and excitable systems: from neurons to birdsong.

Lecture 2

Dynamical models, neurons and experimental data.

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Lecture 1

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Lab. Sistemas Dinámicos – Universidad de Buenos Aires
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One of the crucial intellectual decisions facing young scientists today is determining the balance between **interpretable** and **data-driven** approaches when addressing a scientific problem.

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Interpretable science

Variables have meaning

The relationship between the variables are interpretable mechanisms

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Interpretable science

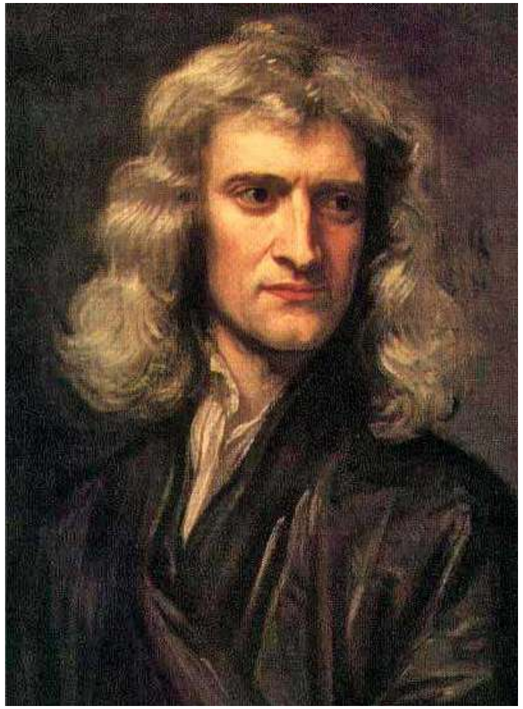
Variables have meaning

The relationship between the variables are interpretable mechanisms

Data driven science

A complex ”non interpretable” model (as a neural network) is trained with examples, and the model does not share with us the rationale behind its success

Counterpoint with history



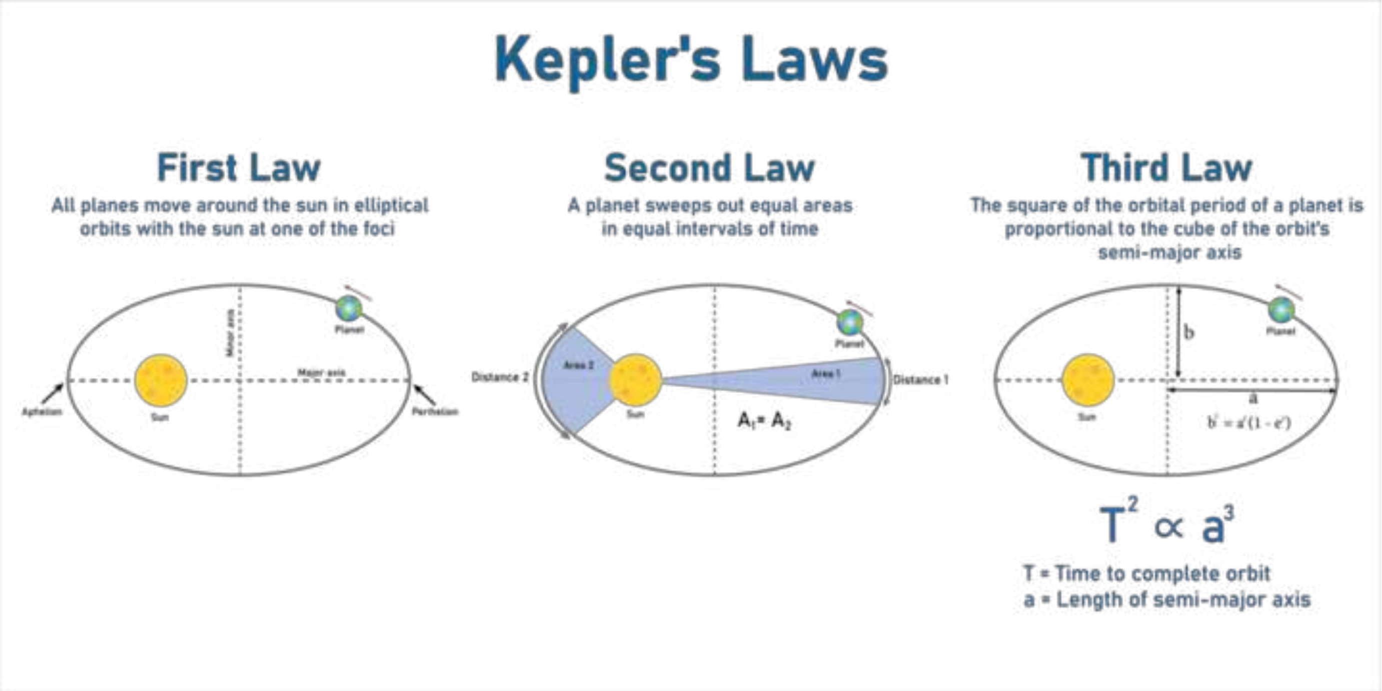
Kepler (1571-1630)

Newton (1643-1727))

Laplace (1749-1827): this is the “world’s system”
All we have to do is to compute “f”, and the initial conditions

Why should we try to describe a problem with differential equations? Should we? Can we?

One of the biggest revolutions in science was data driven.
And the "conversation" between Kepler and Newton is
the first battle between data science and interpretable science



The variables in Kepler's laws are interpretable, but we have no interpretable mechanism relating them.

Newton's approach gave us more

We define the velocity.ɪ: $$\frac{dx}{dt} = v$$

$$\frac{dv}{dt} = \begin{cases} 0 \\ \frac{1}{m} \end{cases}$$

In the absence of interctions with the universe (Galileo)

Multiplied by a functional form describing the interaction

Some functions, fundamental ones $$\boldsymbol{F} = \frac{-G\,m\,M}{{r_{12}}^2}\boldsymbol{e_{12}}$$

Others, phenomenological $$F = -kx$$

To perform a prediction,
we have to have a model relating the variables

$$\frac{dx}{dt} = y$$

$$\frac{dy}{dt} = f(x, y)$$

More than a law, it is a program of how to do science

1. Measure a finite set of initial conditions.
2. Elucidate the law that prescribes the rate of variation of these variables (assuming that the law involves the values of the variables **at that moment**).
3. Integrate an ODE

It does NOT describe

1. Systems of equations with delays
2. Partial differential equations (although…)

$$\frac{dx(t)}{dt} = x(t) - \sigma x(t-\tau)^2$$

Even electromagnetism is excluded…

Dynamical Systems

Definition : set of **variables** that describe state of the system and a **law** that describes the evolution of the state variables with time

how the state of the system in the next moment of time depends on the input and its state in the previous moment of time

Example:
The Hodgkin-Huxley model
(4-dimensional dynamical system)
Its state is uniquely determined by the membrane potential, V , and the "gating variables" n, m, and h for persistent K+ and transient Na+ currents.
The evolution law is given by a **4-dimensional system of ordinary differential equations.**

$$
\begin{aligned}
C\dot{V} &= I - \overbrace{\bar{g}_{\mathrm{K}} n^4 (V - E_{\mathrm{K}})}^{I_{\mathrm{K}}} - \overbrace{\bar{g}_{\mathrm{Na}} m^3 h (V - E_{\mathrm{Na}})}^{I_{\mathrm{Na}}} - \overbrace{g_{\mathrm{L}}(V - E_{\mathrm{L}})}^{I_{\mathrm{L}}} \\
\dot{n} &= \alpha_n(V)(1-n) - \beta_n(V)n \\
\dot{m} &= \alpha_m(V)(1-m) - \beta_m(V)m \\
\dot{h} &= \alpha_h(V)(1-h) - \beta_h(V)h\,,
\end{aligned}
$$

Is this dynamical system nonlinear?

Nonlinear Dynamics

Nonlinear rules

Mechanisms responsible for governing the temporal evolution of a system

Let´s see…

$$
\begin{aligned}
C\dot{V} &= I - \overbrace{\bar{g}_{\mathrm{K}} n^4 (V - E_{\mathrm{K}})}^{I_{\mathrm{K}}} - \overbrace{\bar{g}_{\mathrm{Na}} m^3 h (V - E_{\mathrm{Na}})}^{I_{\mathrm{Na}}} - \overbrace{g_{\mathrm{L}}(V - E_{\mathrm{L}})}^{I_{\mathrm{L}}} \\
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\begin{aligned}
\alpha_n(V) &= 0.01\frac{10-V}{\exp(\frac{10-V}{10})-1}\,, \\
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\beta_h(V) &= \frac{1}{\exp(\frac{30-V}{10})+1}\,.
\end{aligned}
$$

Dynamical Systems

Types of dynamical systems:

Differential equations

$$
\begin{aligned}
C\dot{V} &= I - \overbrace{\bar{g}_{\mathrm{K}} n^4 (V - E_{\mathrm{K}})}^{I_{\mathrm{K}}} - \overbrace{\bar{g}_{\mathrm{Na}} m^3 h (V - E_{\mathrm{Na}})}^{I_{\mathrm{Na}}} - \overbrace{g_{\mathrm{L}} (V - E_{\mathrm{L}})}^{I_{\mathrm{L}}} \\
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\end{aligned}
$$

Logistic map

Maps

$$x_{n+1} = r x_n (1 - x_n)$$

where x_n is a number between 0 and 1, which represents the ratio of existing population to the maximum possible population

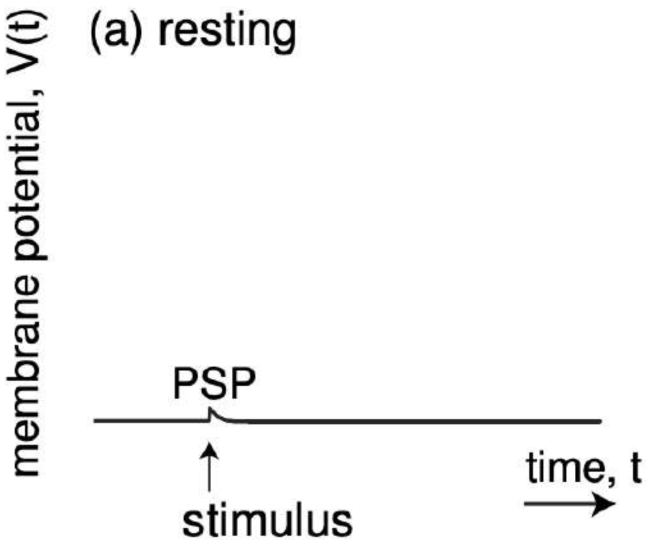
Chaos!

Phase portraits

The power of the dynamical systems approach to neuroscience (and to many other sciences) is that we can tell many things about a system without knowing all the details that govern the system evolution.

Phase portraits

Quiescent neuron whose membrane potential is resting



Isn´t it amazing that we can reach such a conclusion without knowing the equations that describe the neuron's dynamics?

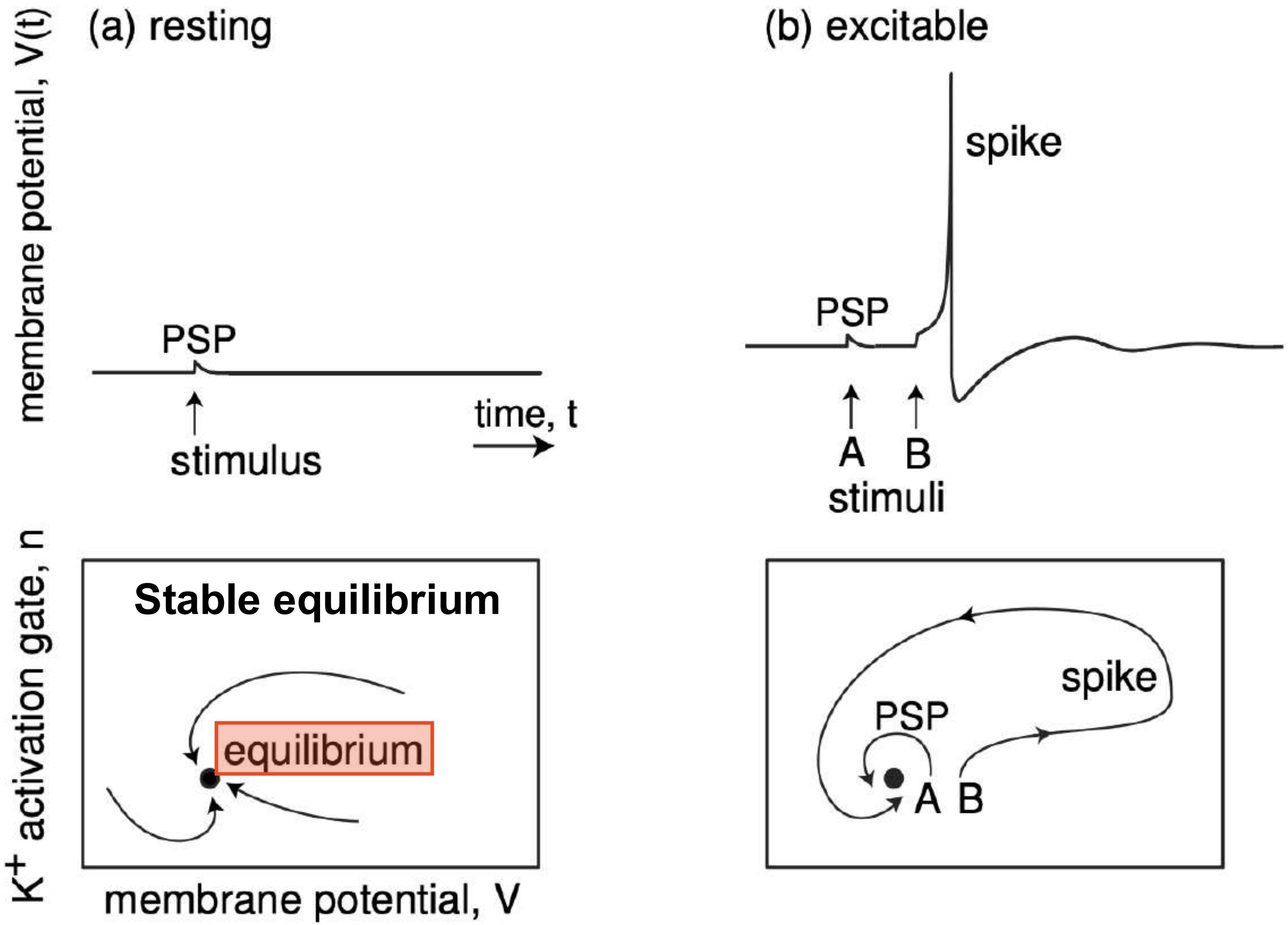
We do not even know the number of variables needed to describe the neuron

Phase portraits

Quiescent neuron whose membrane potential is resting

Neuron in an excitable mode

Phase portrait



Small perturbations **(A)** result in small excursions from the equilibrium (**PSP**, postsynaptic potential).

Larger perturbations **(B)**, are amplified by the neuron's intrinsic dynamics and result in the **spike response.**

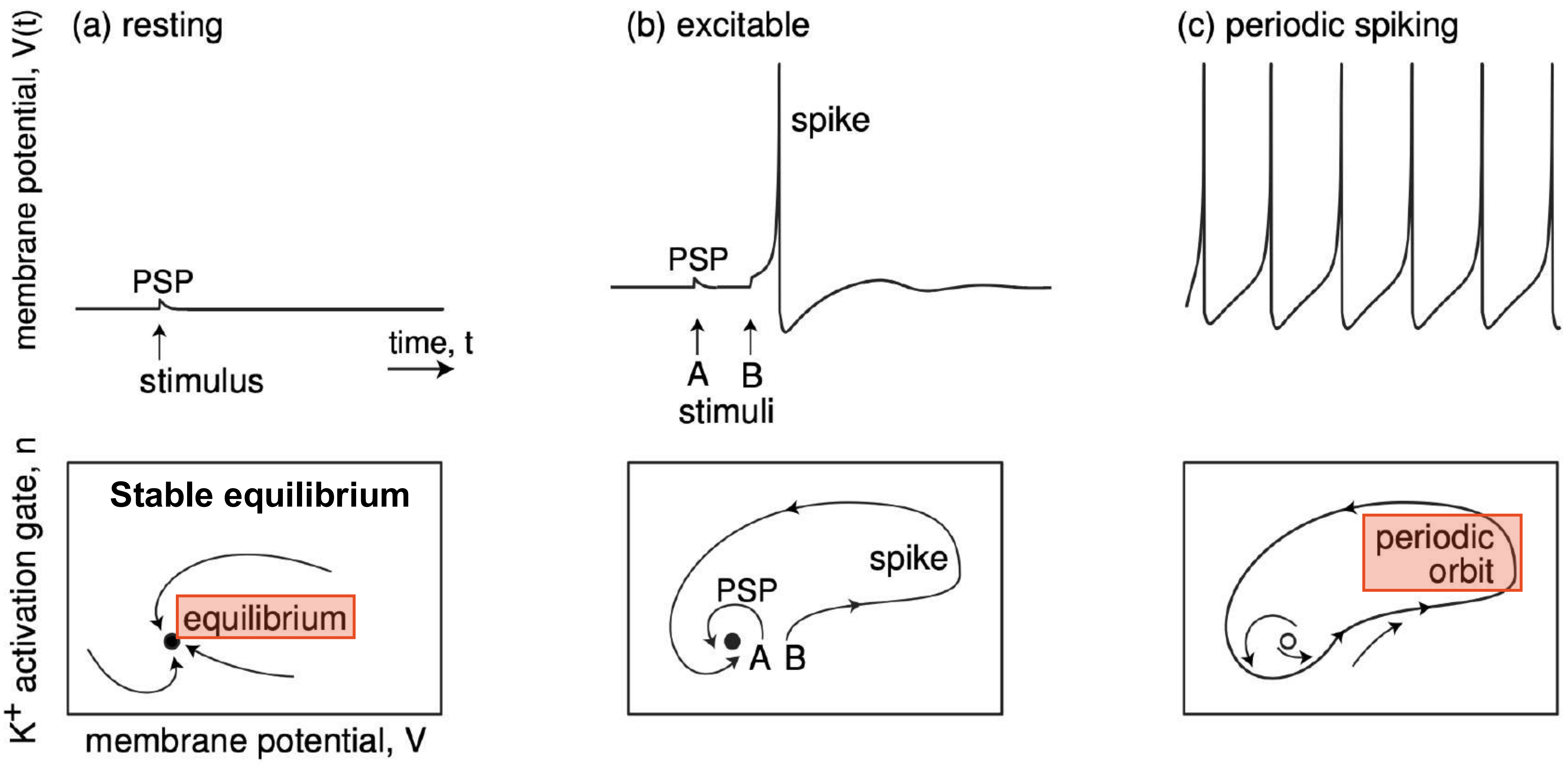
Excitable system

Phase portraits

Quiescent neuron whose membrane potential is resting

Neuron in an excitable mode

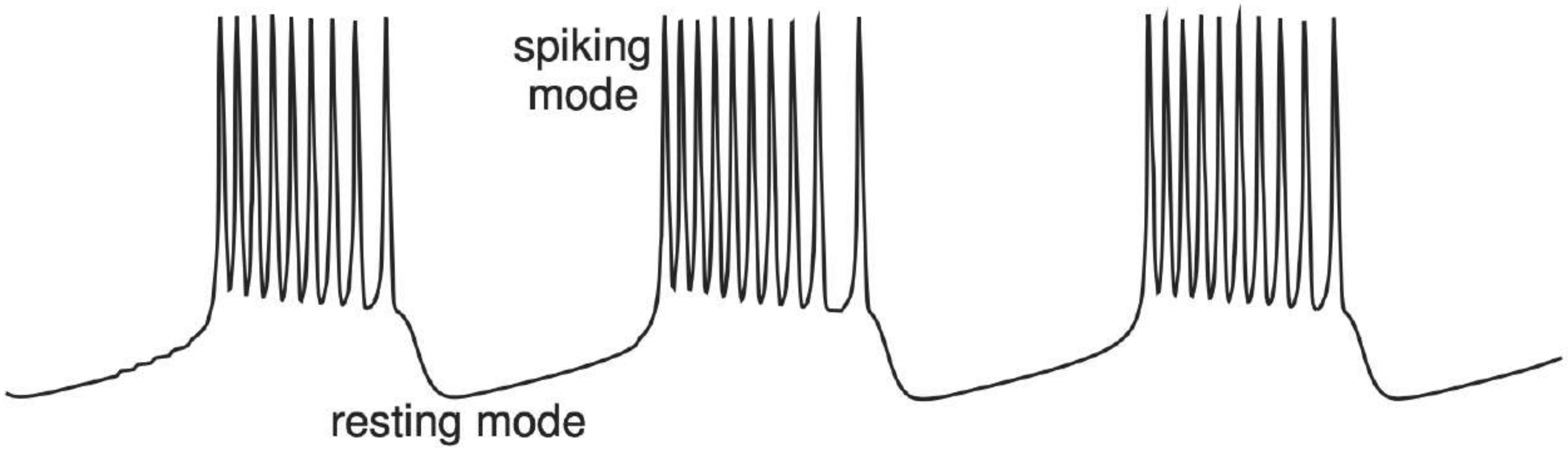
Pacemaker neuron



Phase portrait

Phase portraits

Equilibria and **limit cycles** can coexist, so a neuron can be switched from one mode to another by a transient input



Bifurcations

Qualitative changes

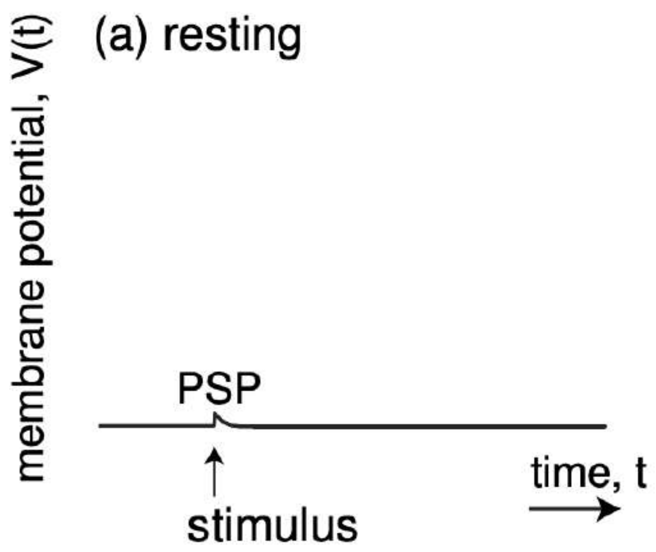
What is a bifurcation?

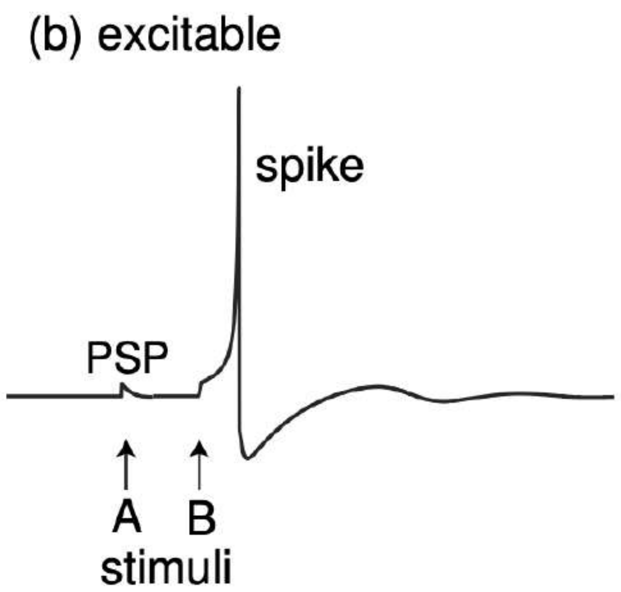
Bifurcations

Quiescent neuron whose membrane potential is resting

Neuron in an excitable mode

Qualitative changes





If the dynamical system goes from **(a)** to **(b)**, is it going through a bifurcation?

No bifurcation!

→ This dynamical system contains (a)

The differences between **(A)** and **(B)** are the initial conditions.

There is not a **qualitative change**

Bifurcations

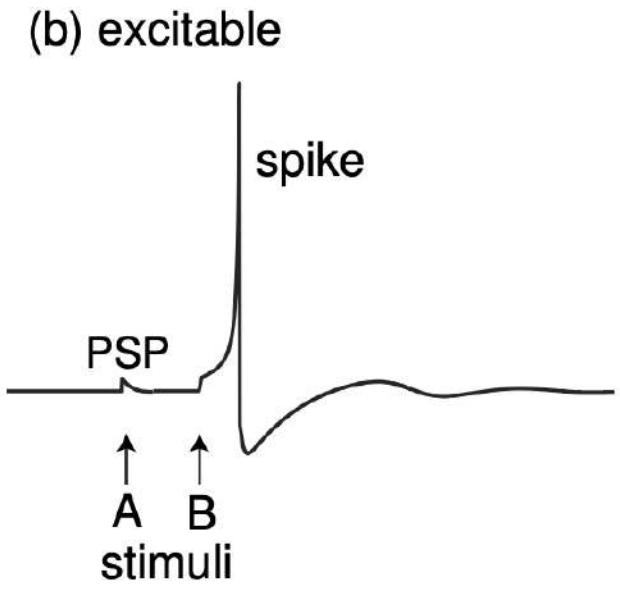
If the dynamical system goes from **(b)** to **(c)**, is it going through a bifurcation?

Let´s see…
(b) : stable fix point
(c) : unstable fix point and a limit cycle.

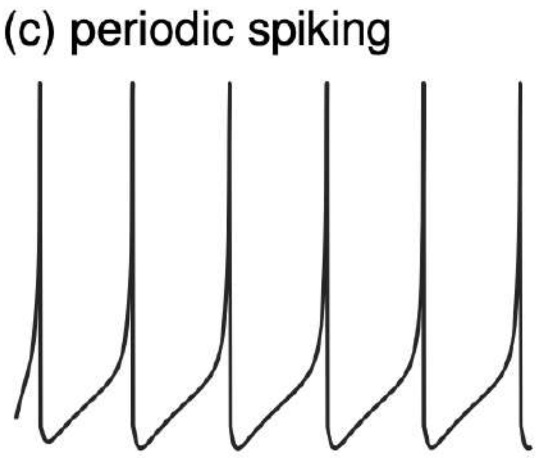
There is a **qualitative change**

Bifurcation!

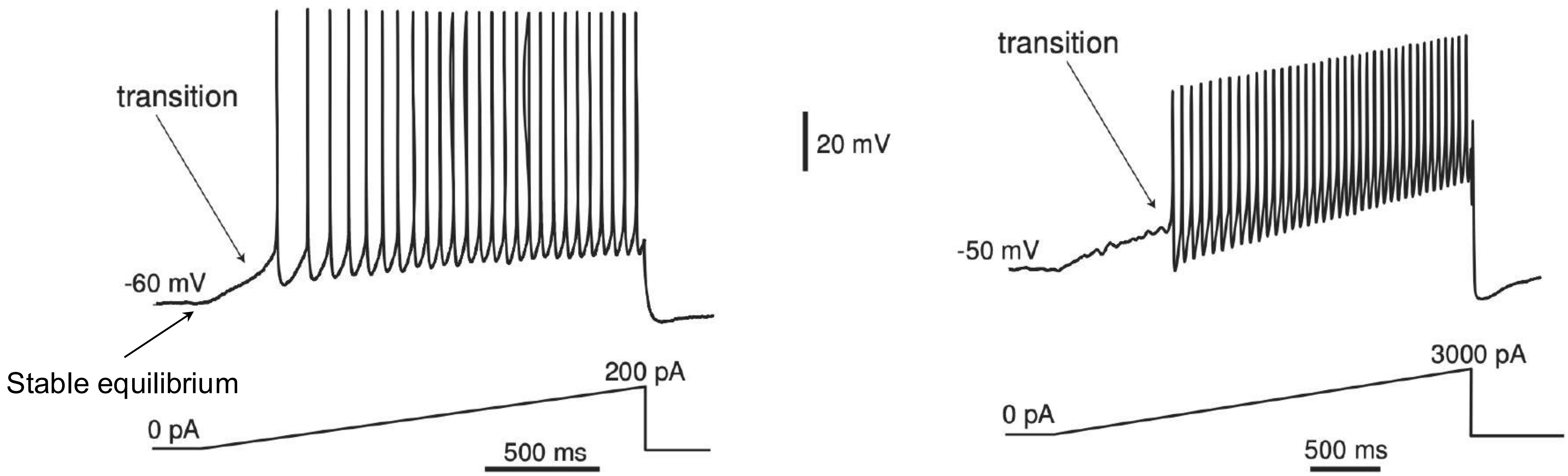
Neuron in an excitable mode



Pacemaker neuron



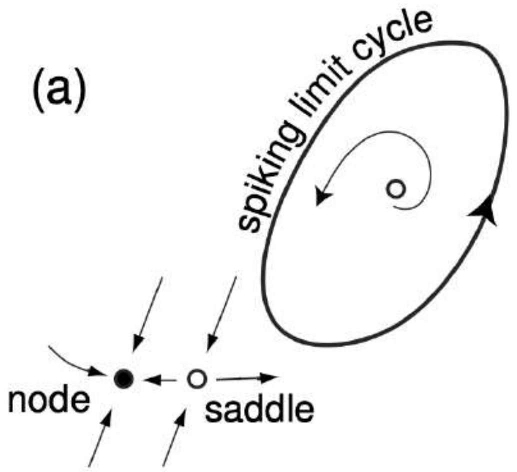
Bifurcations



As the magnitude of the injected current slowly increases, the neurons bifurcate from resting (equilibrium) mode to tonic spiking (limit cycle) mode.

Bifurcations

Equilibrium state leading to the transition from **resting** to **periodic spiking** behavior in neurons.
(codimension-1, i.e., 1 control parameter)



Saddle-node bifurcation

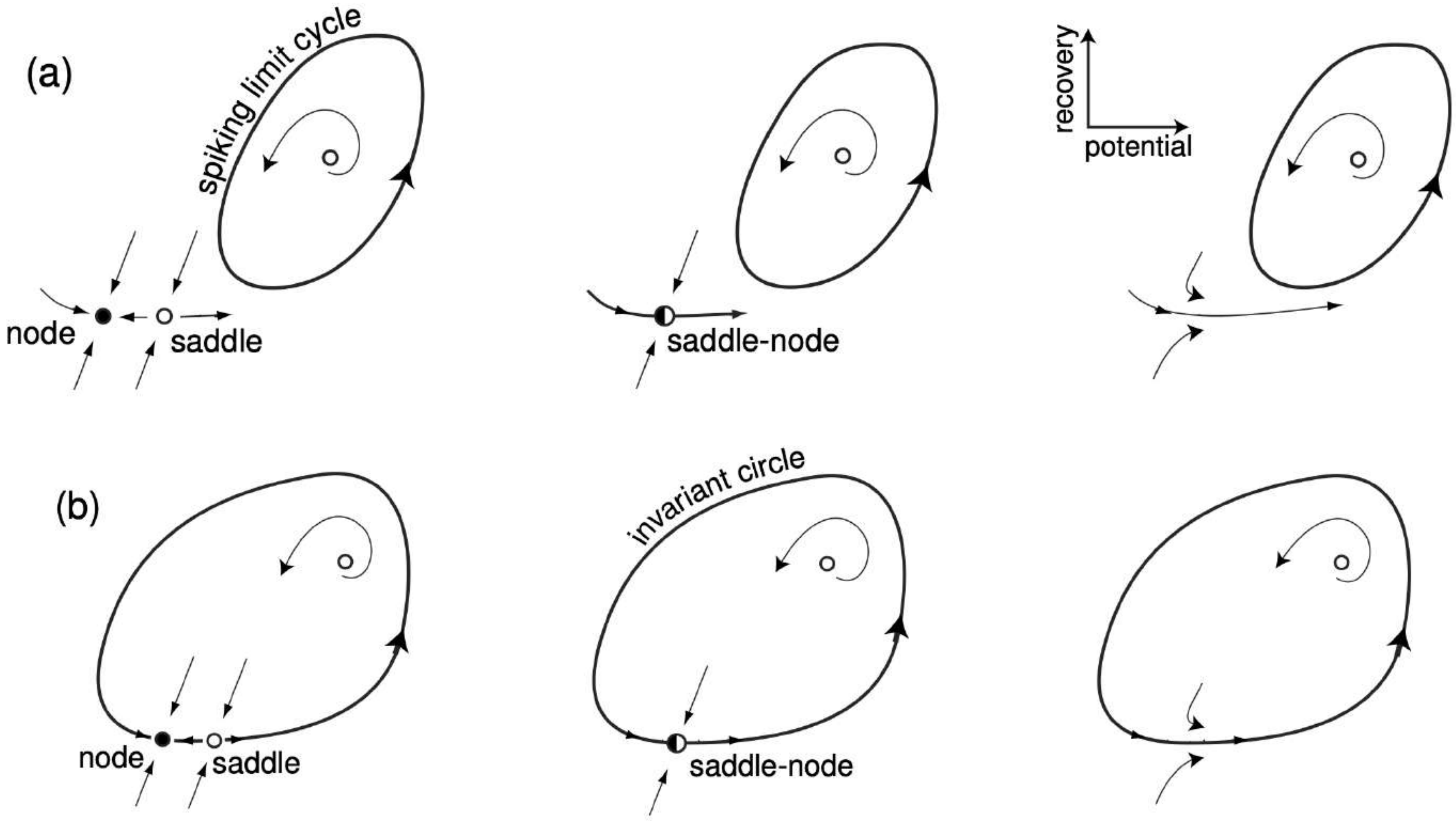
Depending on the initial conditions, the neuron may spike (or decay to the stable resting position) or burst

Bifurcation point

The saddle and node colapse and annihilate each other.
Only the limit cycle survives

Bifurcations

Equilibrium state leading to the transition from **resting** to **periodic spiking** behavior in neurons.
(codimension-1, i.e., 1 control parameter)

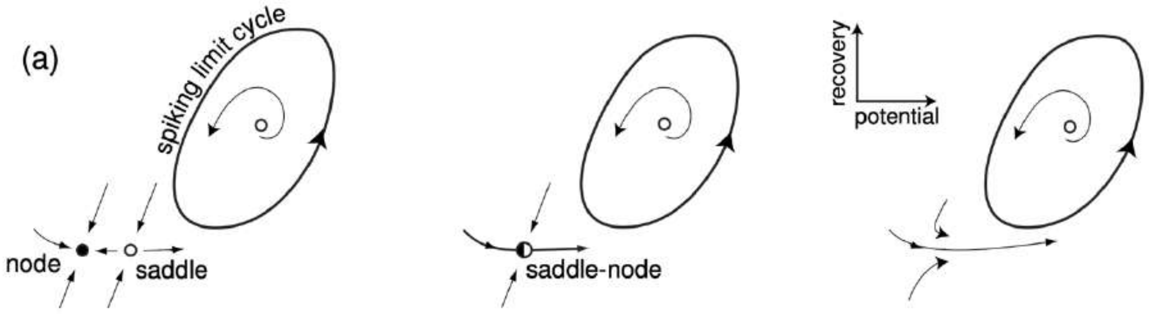


Saddle-node bifurcation

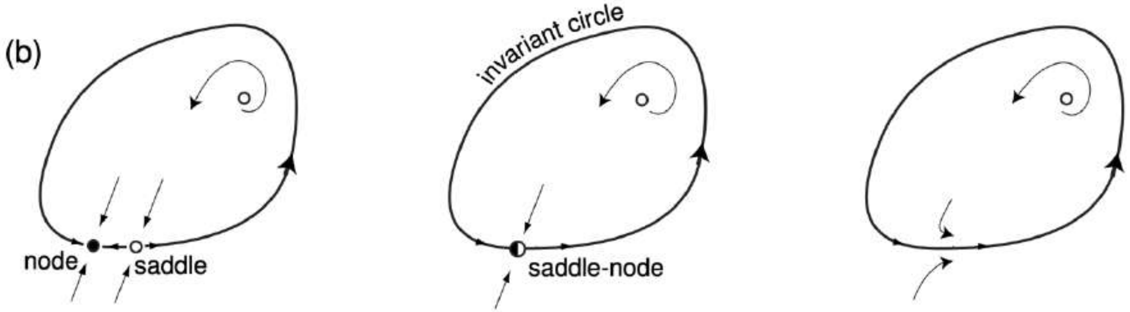
Saddle-node on invariant circle bifurcation

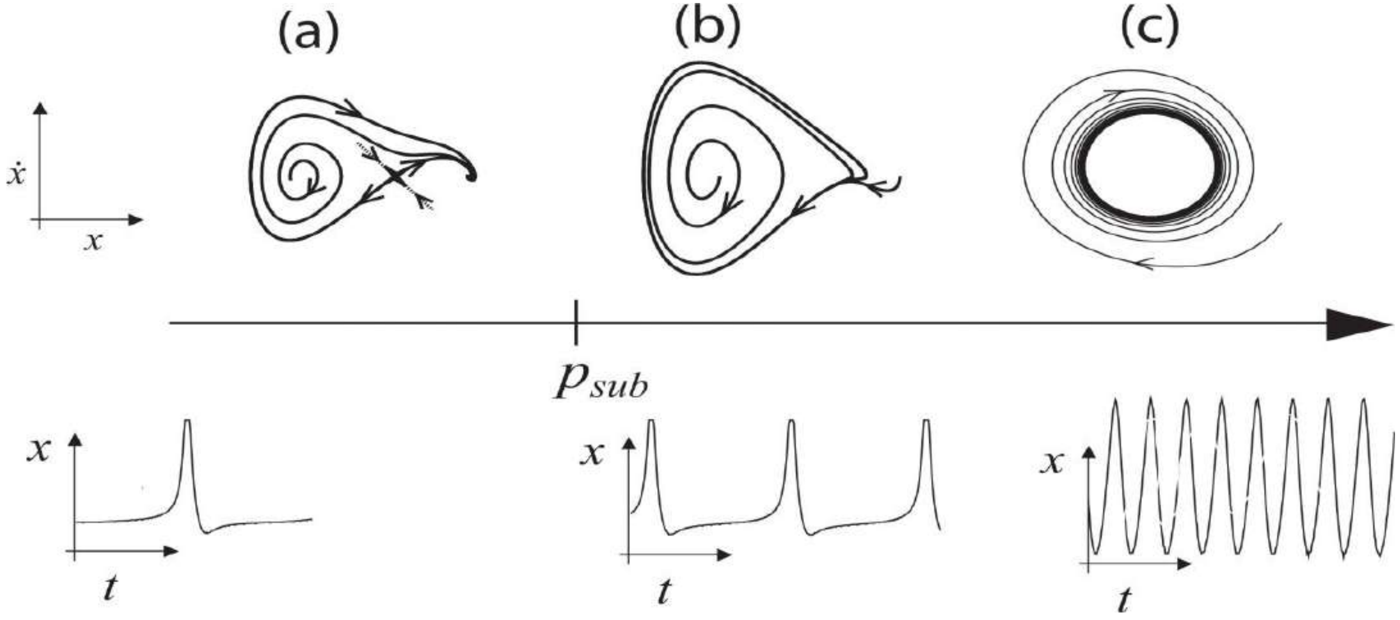
Bifurcations

Saddle-node bifurcation



Saddle-node on invariant circle bifurcation





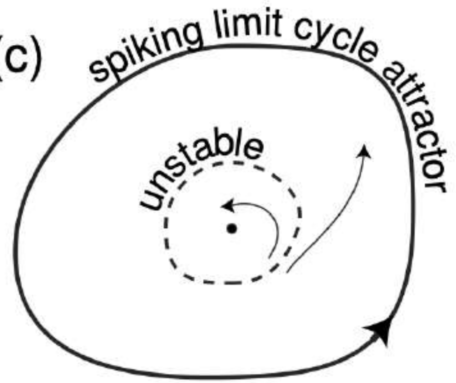
Saddle-node on invariant circle bifurcation

Saddle-node ghost

Bifurcations

Equilibrium state leading to the transition from **resting** to **periodic spiking** behavior in neurons.
(codimension-1, i.e., 1 control parameter)

(c)



Subcritical Andronov-Hopf bifurcation

A small unstable limit cycle shrinks to a stable equilibrium and makes it lose stability

The only stable state is the limit cycle

(d)

Supercritical Andronov-Hopf bifurcation

The stable equilibrium loses stability and gives birth to a small-amplitude limit cycle attractor

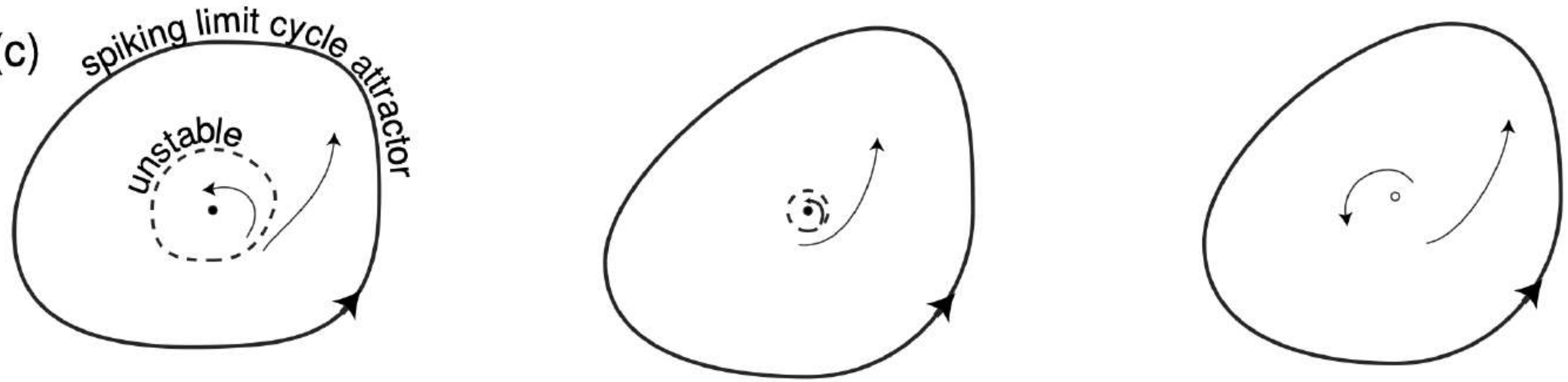
As the magnitude of the injected current increases, the amplitude of the limit cycle increases, and it becomes a full-size spiking limit cycle

Bifurcations

Equilibrium state leading to the transition from **resting** to **periodic spiking** behavior in neurons.
(codimension-1, i.e., 1 control parameter)

Bi-stable

(c)



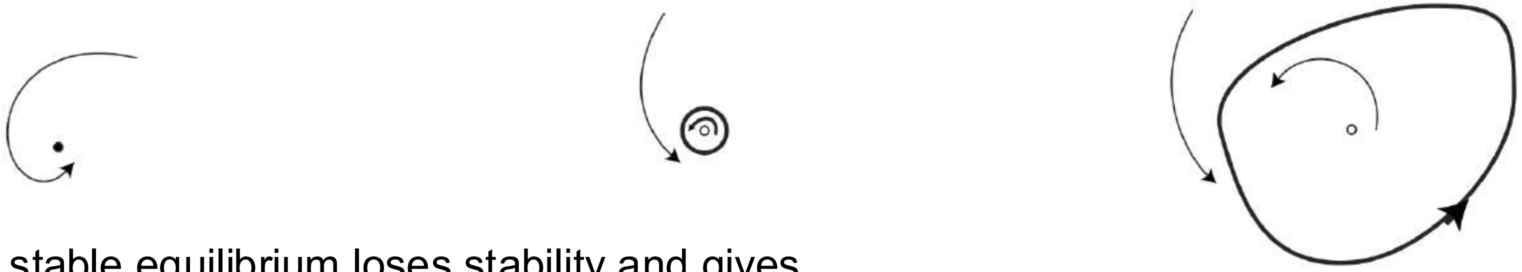
Subcritical Andronov-Hopf bifurcation

A small unstable limit cycle shrinks to a stable equilibrium and makes it lose stability

The only stable state is the limit cycle

(d)

Mono-stable



Supercritical Andronov-Hopf bifurcation

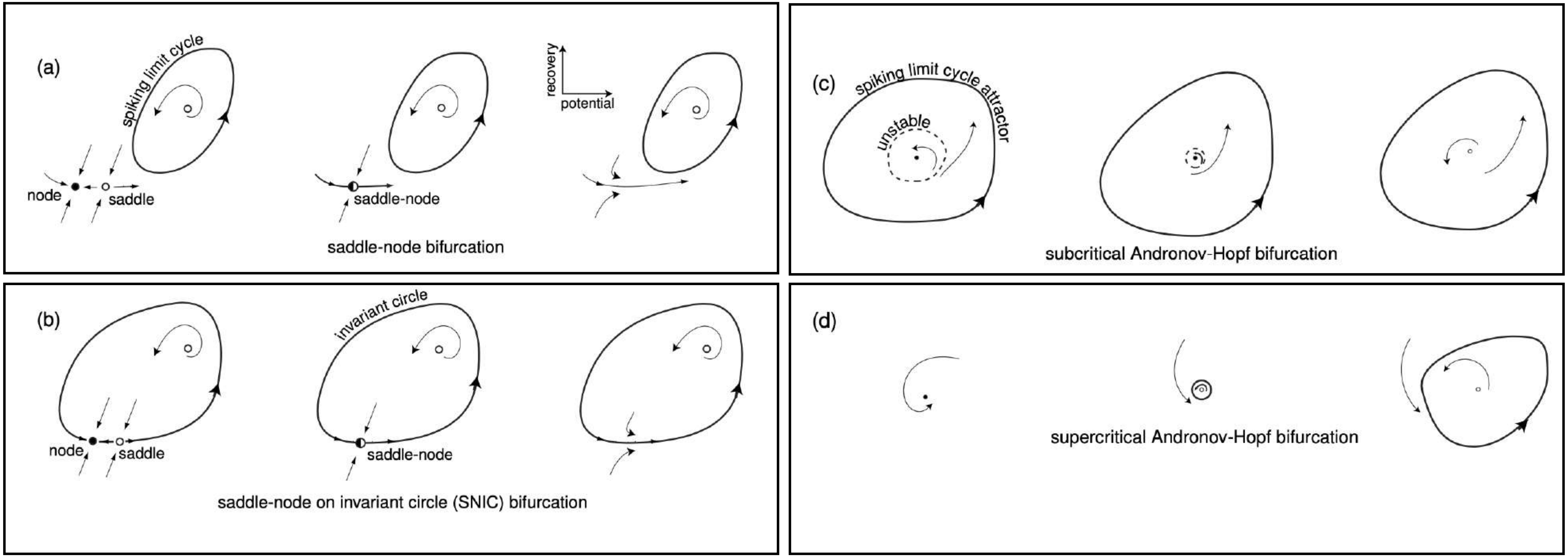
The stable equilibrium loses stability and gives birth to a small-amplitude limit cycle attractor

Bifurcations

coexistence of resting and spiking states

subthreshold oscillations	YES (bistable)	NO (monostable)
NO (integrator)	saddle-node	saddle-node on invariant circle
YES (resonator)	subcritical Andronov-Hopf	supercritical Andronov-Hopf

Bifurcations



Building models

First of all: you need neural recordings!
(from your own experiments or from a collaborator)

To make a model of a neuron: put the right kind of currents together and tune the parameters so that the model can fire spikes like the ones recorded.

Another way is to determine what kind of bifurcations the neuron undergoes and how the bifurcations depend on neuromodulators and pharmacological blockers.

These approaches can be complementary.

Interdisciplinary work

Respect the different “ideologies”

The Hodgkin – Huxley model

Using **pioneering experimental techniques** of that time, Hodgkin and Huxley (1952) determined that the squid axon carries three major currents:

- Voltage-gated persistent K^+ current with four activation gates (resulting in the term n^4 in the equation below, where n is the activation variable for K^+);
- Voltage-gated transient Na^+ current with three activation gates and one inactivation gate (the term m^3h below)
- Ohmic leak current, I_L, which is carried mostly by Cl^- ions.

$$\begin{aligned}
C\dot{V} &= I - \overbrace{\bar{g}_{\mathrm{K}} n^4 (V - E_{\mathrm{K}})}^{I_{\mathrm{K}}} - \overbrace{\bar{g}_{\mathrm{Na}} m^3 h (V - E_{\mathrm{Na}})}^{I_{\mathrm{Na}}} - \overbrace{g_{\mathrm{L}} (V - E_{\mathrm{L}})}^{I_{\mathrm{L}}} \\
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\end{aligned}$$

$$\begin{aligned}
\alpha_n(V) &= 0.01 \frac{10 - V}{\exp(\frac{10-V}{10}) - 1}\,, \\
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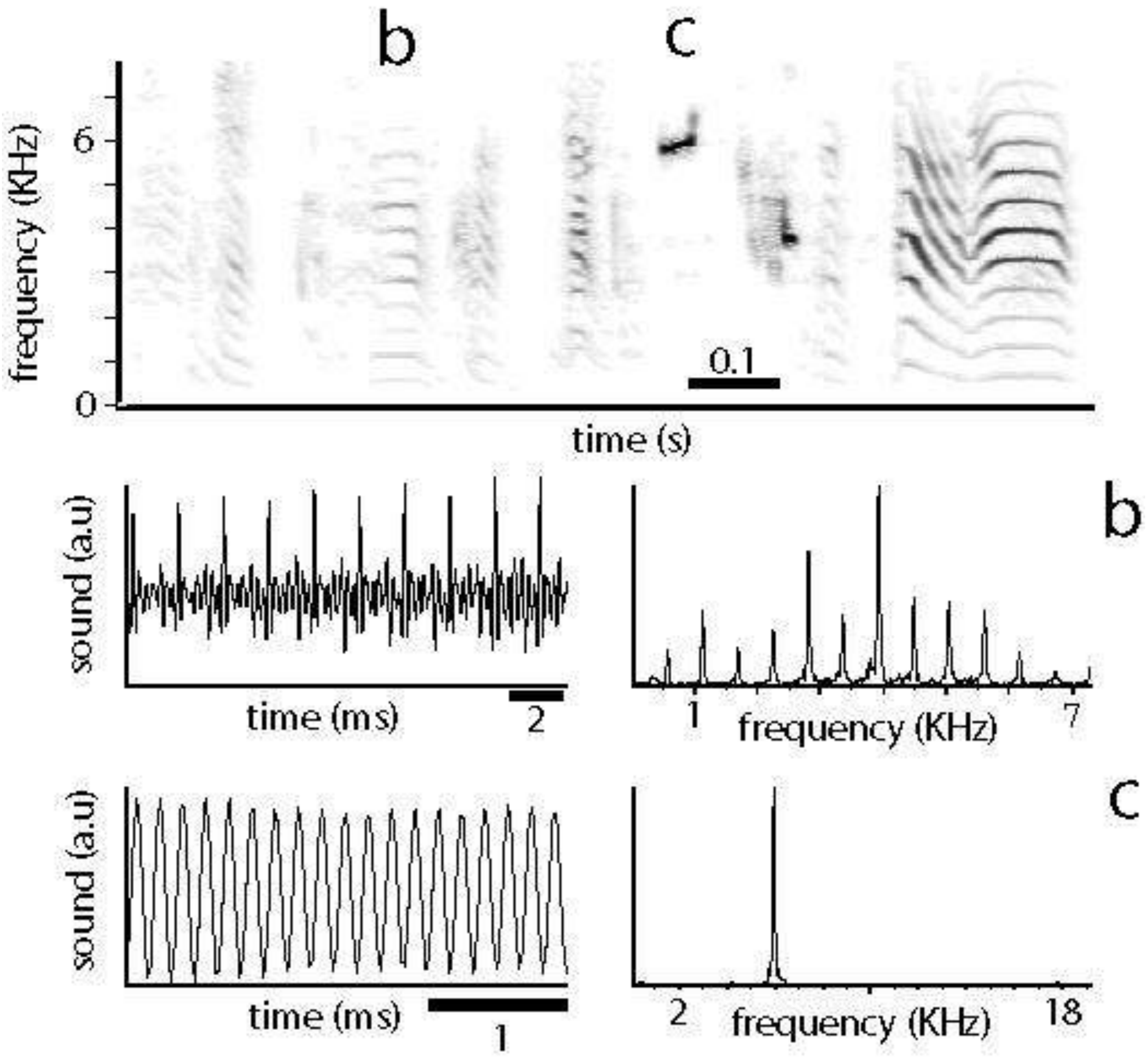
\alpha_h(V) &= 0.07 \exp\left(\frac{-V}{20}\right)\,, \\
\beta_h(V) &= \frac{1}{\exp(\frac{30-V}{10}) + 1}\,.
\end{aligned}$$

This model predicted the existence of ion channels!

Let´s see the power of physics and nonlinear dynamics!

Birdsong as a complex mechanism



Temporal trace: excitable system

Spectrally rich

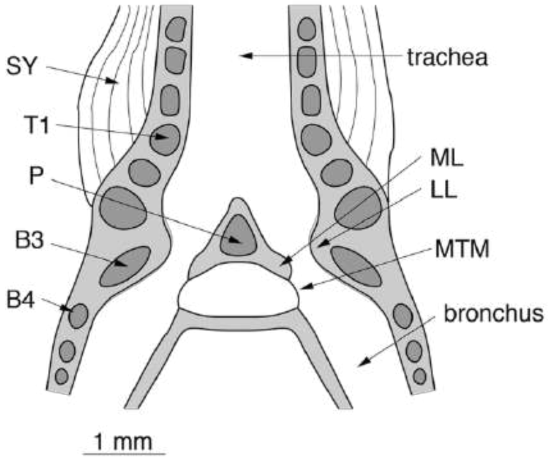
Almost tonal

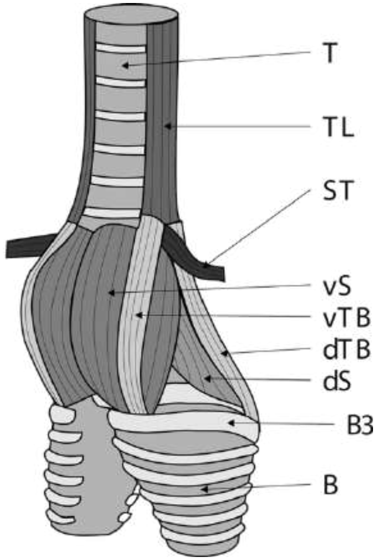
Birdsong as a complex mechanism

When physics and biology meet…

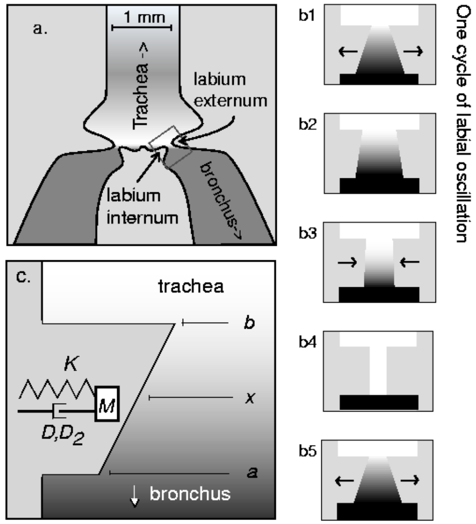
Different views of the syrinx

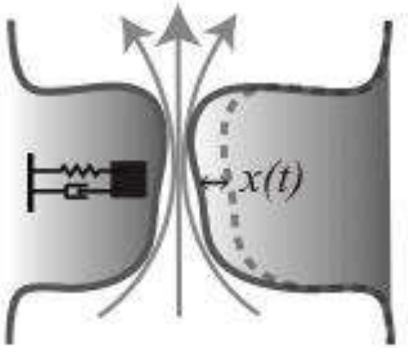
- Biology is used to complexity





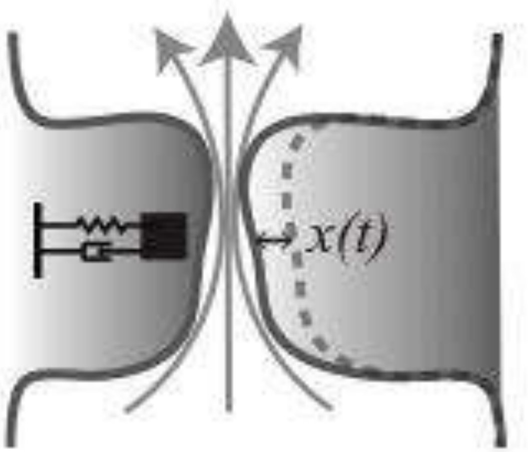
- Physics is obsessed with simplicity





The program of physics (or interpretable science)

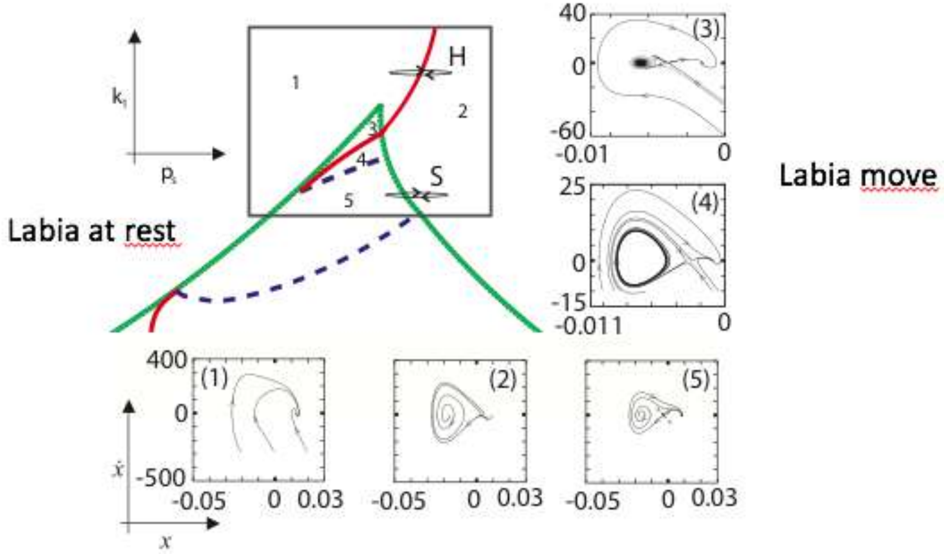
1. To identify the pertinent variables
And how to relate them through a model



$$
\begin{cases}
\dfrac{dx}{dt} = y, \\[2ex]
\dfrac{dy}{dt} = (1/m)\left[-k(x)x - b(y)y - cx^2 y + a_{lab} p_s \left(\dfrac{\Delta a + 2\tau y}{a_{01} + x + \tau y} \right) \right].
\end{cases}
$$

2. To study the solutions for different parameters

Bifurcation diagram



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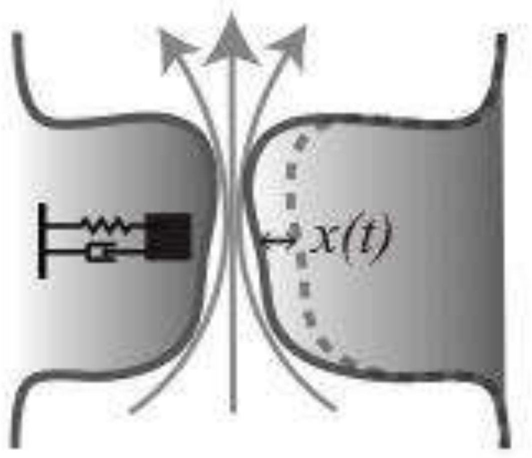
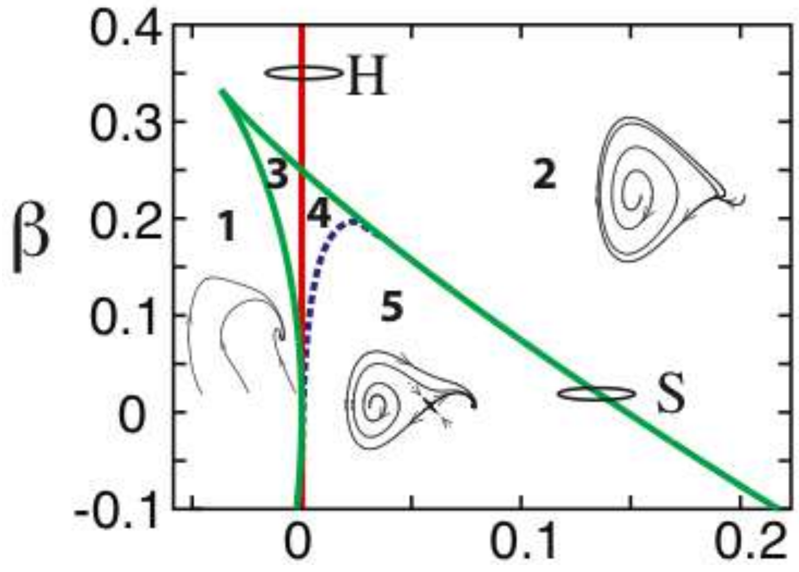


Normal form

$$\begin{cases} \frac{dx}{dt} = y \\ \frac{dy}{dt} = -\alpha(t)\gamma^2 - \beta(t)\gamma^2 x - \gamma^2 x^3 - \gamma x^2 y + \gamma^2 x^2 - \gamma x y \end{cases}$$

2. To study the solutions for different parameters

Bifurcation diagram



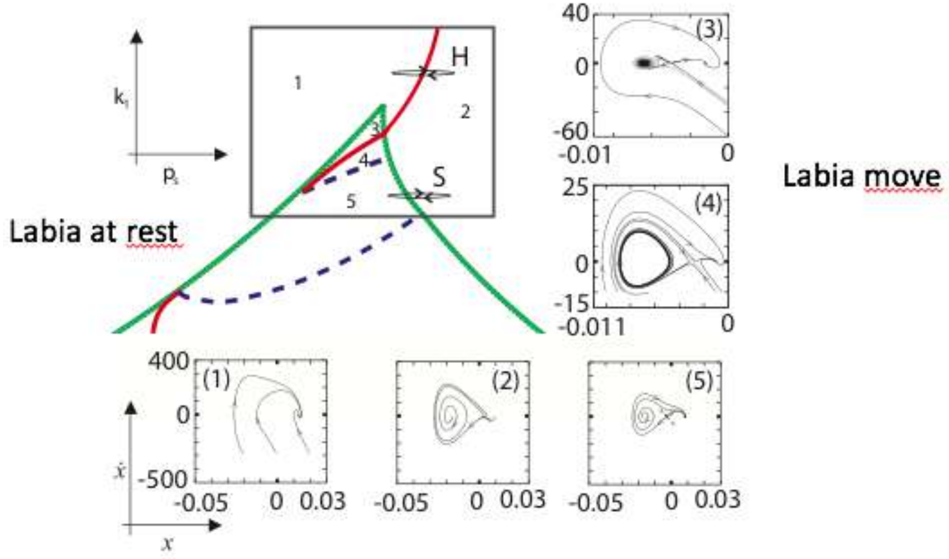
Normal form reduction

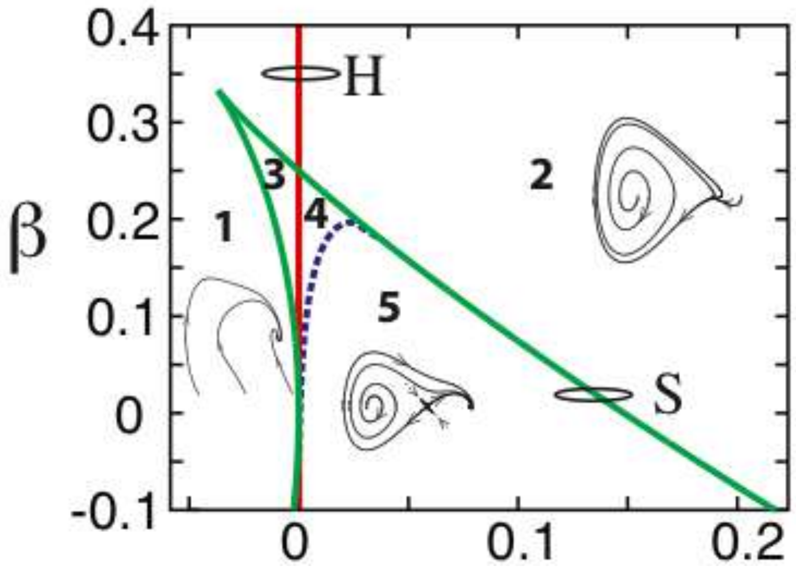
$$\begin{cases} \dfrac{dx}{dt} = y, \\ \dfrac{dy}{dt} = (1/m)\left[-k(x)x - b(y)y - cx^2y + a_{lab}p_s\left(\dfrac{\Delta a + 2\tau\tau}{a_{01} + x + \tau y}\right)\right]. \end{cases}$$

$$\begin{cases} \dfrac{dx}{dt} = y \\ \dfrac{dy}{dt} = -\alpha(t)\gamma^2 - \beta(t)\gamma^2 x - \gamma^2 x^3 - \gamma x^2 y + \gamma^2 x^2 - \gamma x y \end{cases}$$

Algorithmic procedure that allows you to reduce your nonlinear problem to a simpler one, close to a linear singularity. This simpler model will have less parameters, and **has been probably studied**

Normal form reduction





Dynamical analysis of the model

Parameters ***k1*** y ***Ps*** are related to physiological variables:
k1 ∝ activity of vS syringeal muscle
Ps ∝ subsyringeal pressure

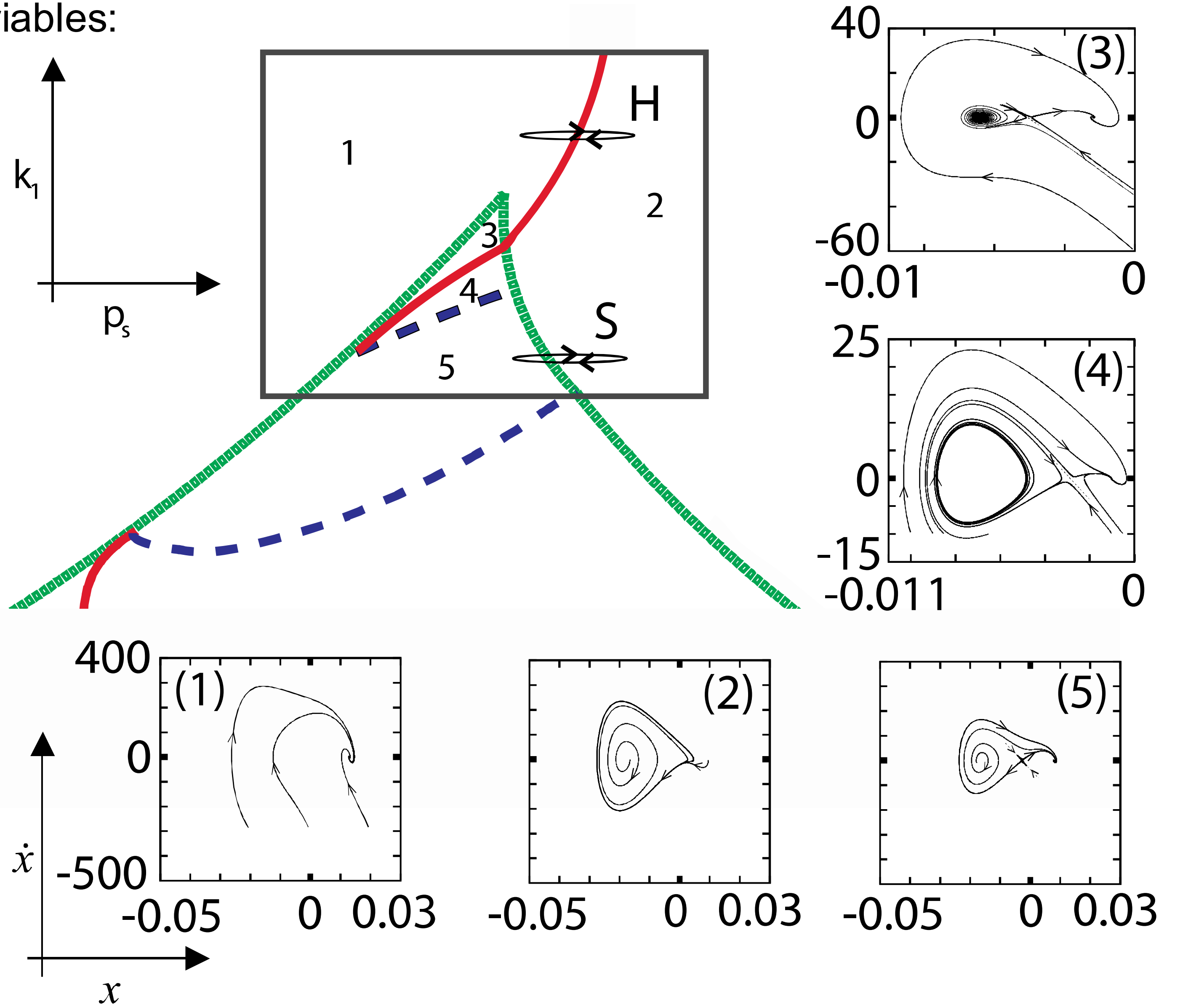
Bifurcations:

H: Hopf:

✓almost tonal
✓**frequency defined by k_1**

S: SNILC:

✓ spectrally rich
✓**fundamental frequency defined by pressure**



Numbers indicate regions of the parameter space with qualitative similar outputs

Dynamical analysis of the model

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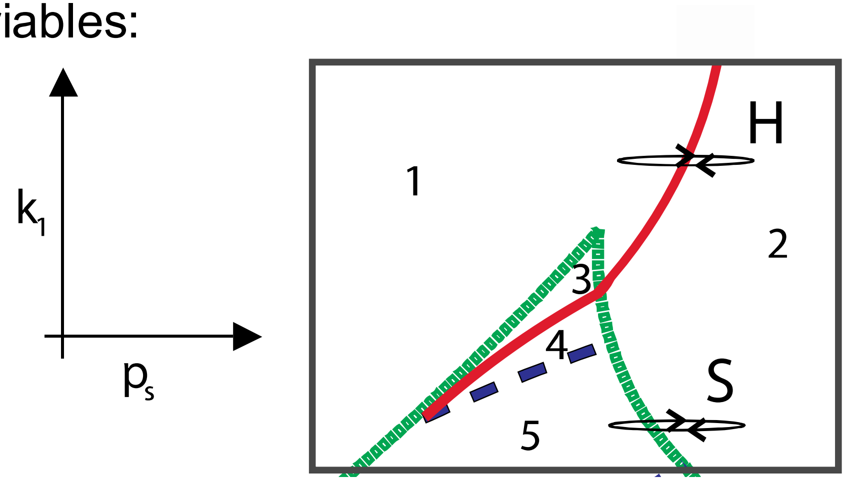

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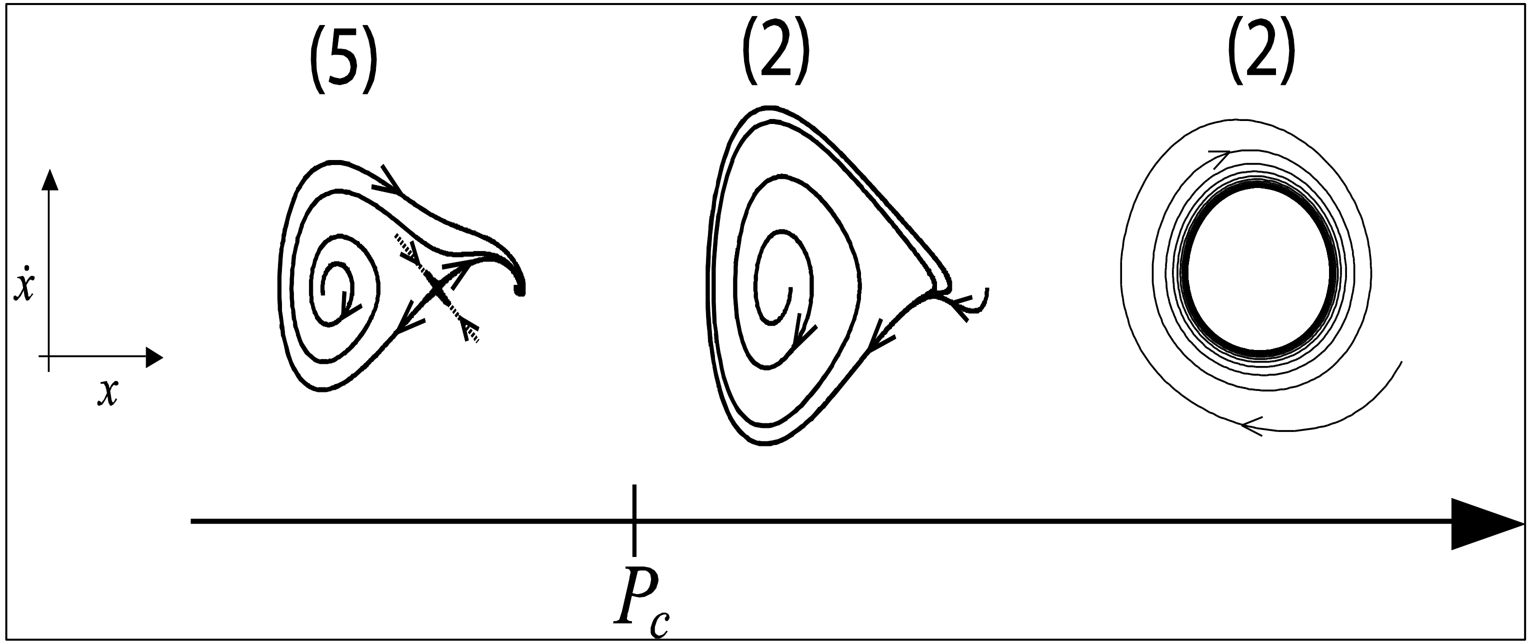
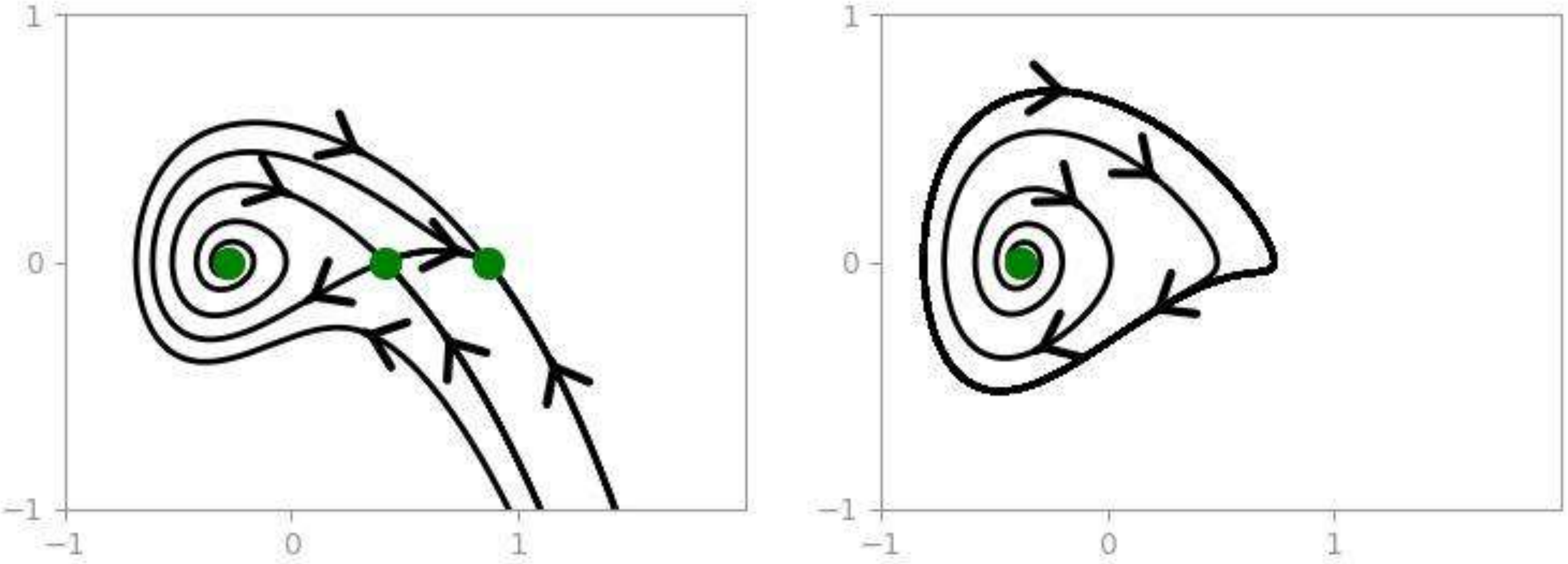
✓ spectrally rich
✓**fundamental frequency defined by pressure**

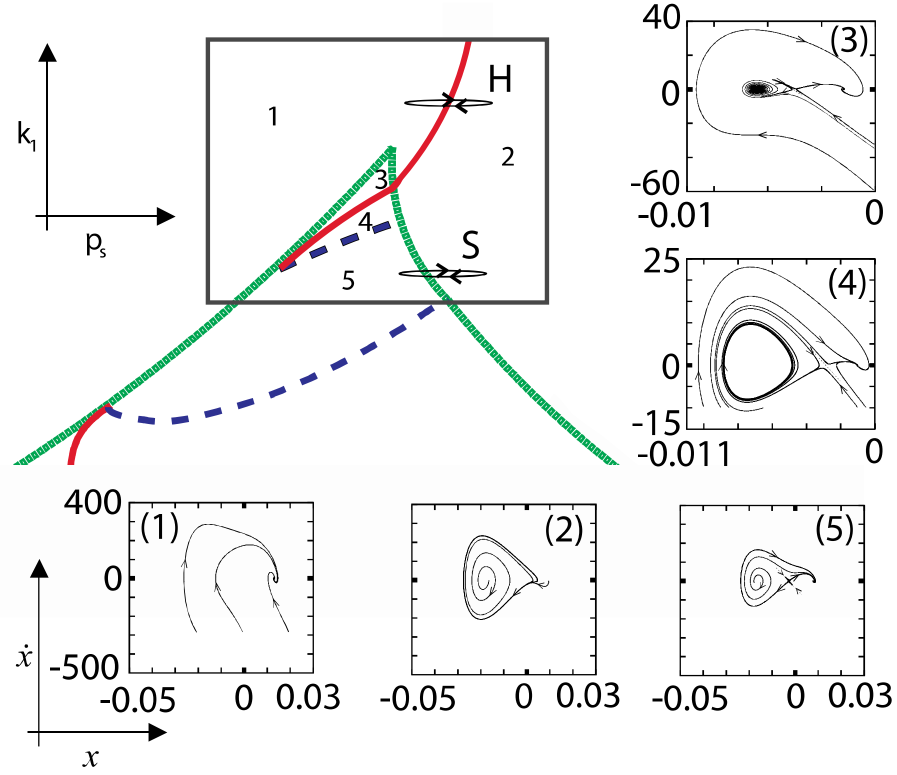




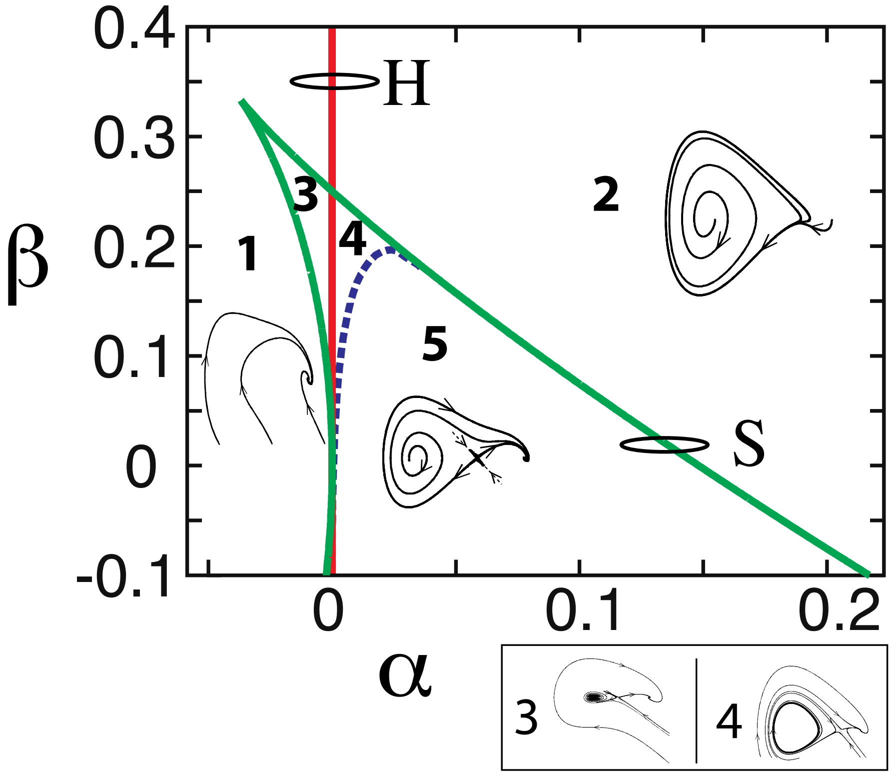
SNILC: one of the ways oscillations arise in 2d systems

Normal form reduction

Complete model



Normal form



$$\frac{dx}{dt} = y$$

$$\frac{dy}{dt} = -\alpha(t)\gamma^2 - \beta(t)\gamma^2 x - \gamma^2 x^3 - \gamma x^2 y + \gamma^2 x^2 - \gamma x y$$

Generating synthetic songs: source

Dynamical system model of the sound source

$$\frac{dx}{dt} = y$$

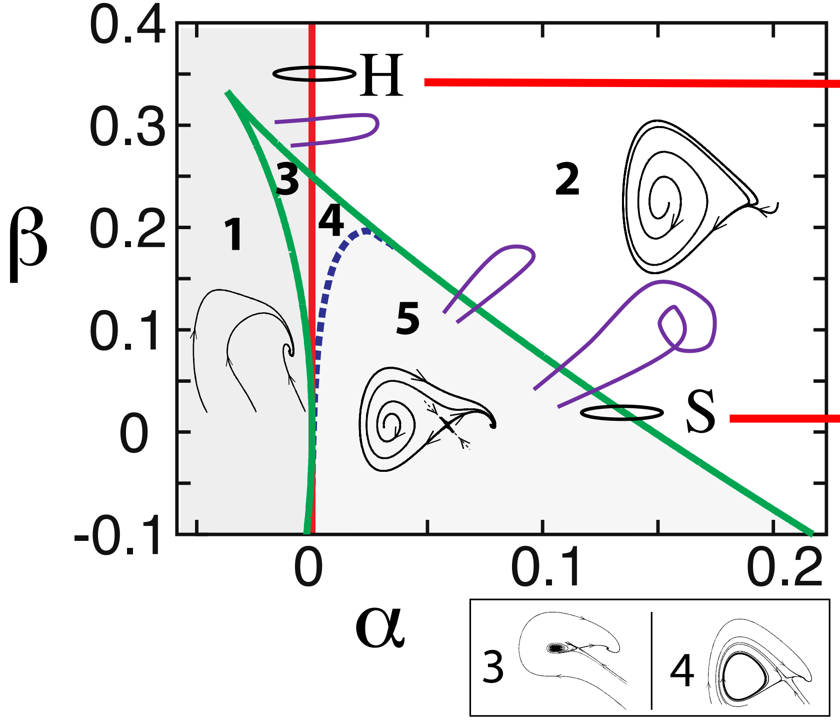
$$\frac{dy}{dt} = -\alpha(t)\gamma^2 - \beta(t)\gamma^2 x - \gamma^2 x^3 - \gamma x^2 y + \gamma^2 x^2 - \gamma x y$$

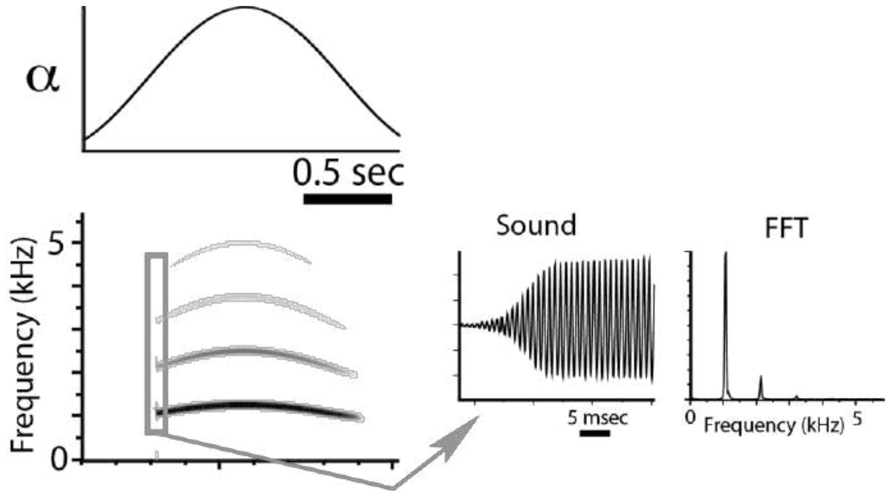
x: medial position of a labium

α: **pressure** of the air sac system, β: **tension** of the syringeal labia

Dynamical analysis of the sound source

Numbers indicate regions of the parameter space with qualitative similar outputs





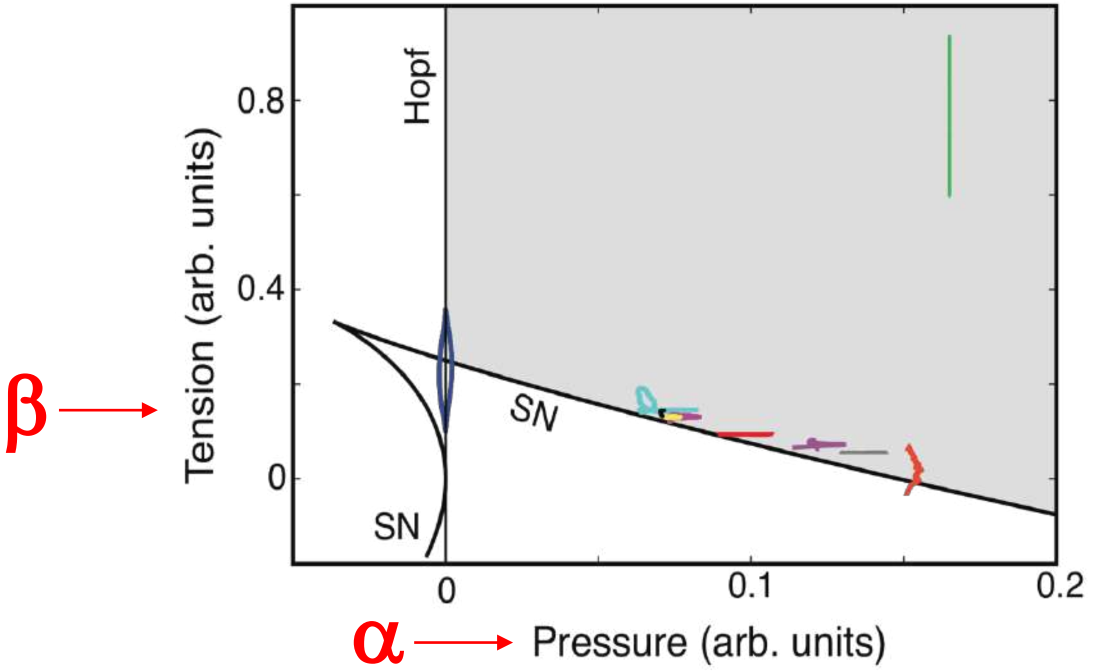
Generating synthetic zebra finch songs

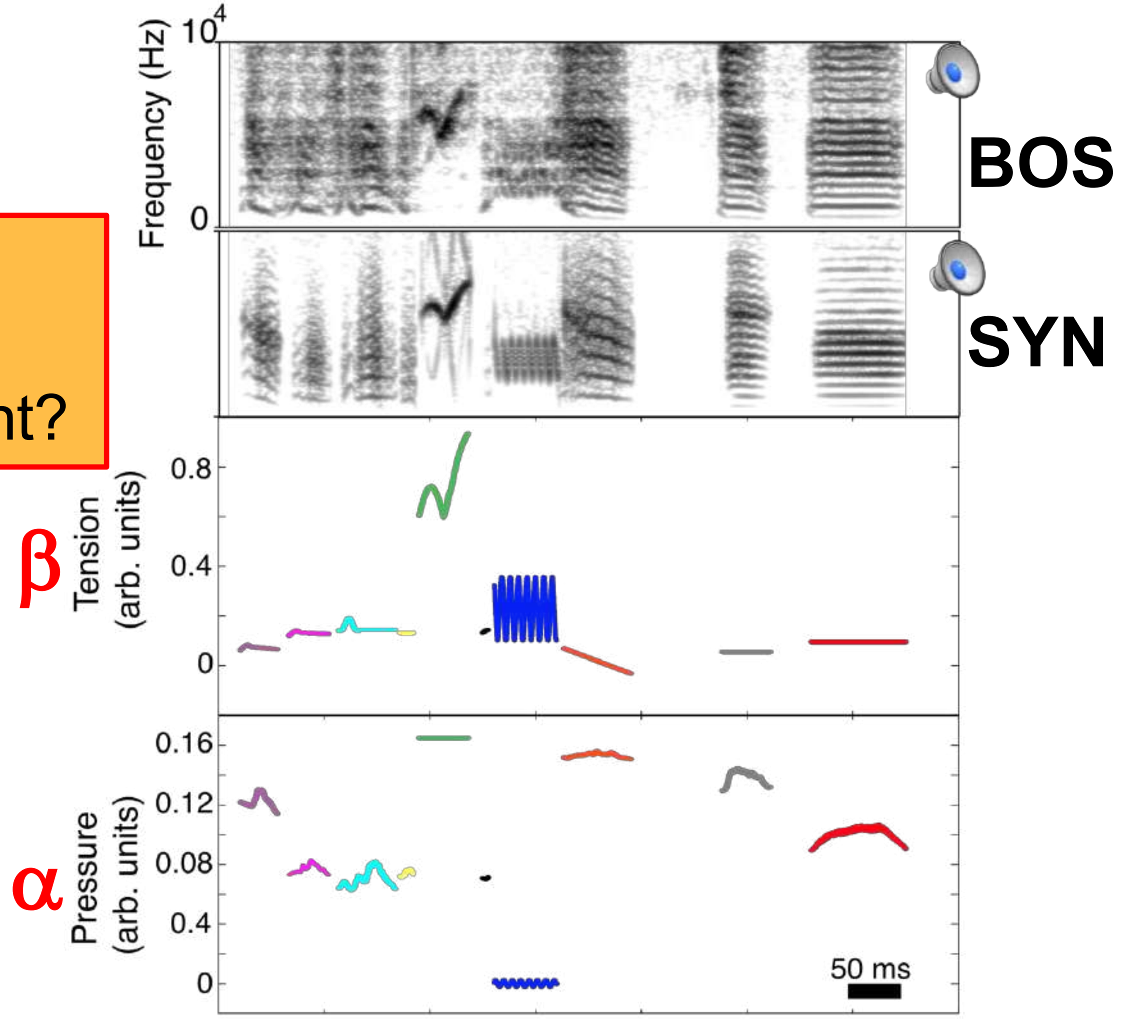
$$\frac{dx}{dt} = y$$

$$\frac{dy}{dt} = -\alpha(t)\gamma^2 - \beta(t)\gamma^2 x - \gamma^2 x^3 - \gamma x^2 y + \gamma^2 x^2 - \gamma x y$$

x: medial position of a labium
α : **pressure** of the air sac system
β : **tension** of the syringeal labia
γ : scale factor

Looks good!
Sounds good!
But is this relevant?



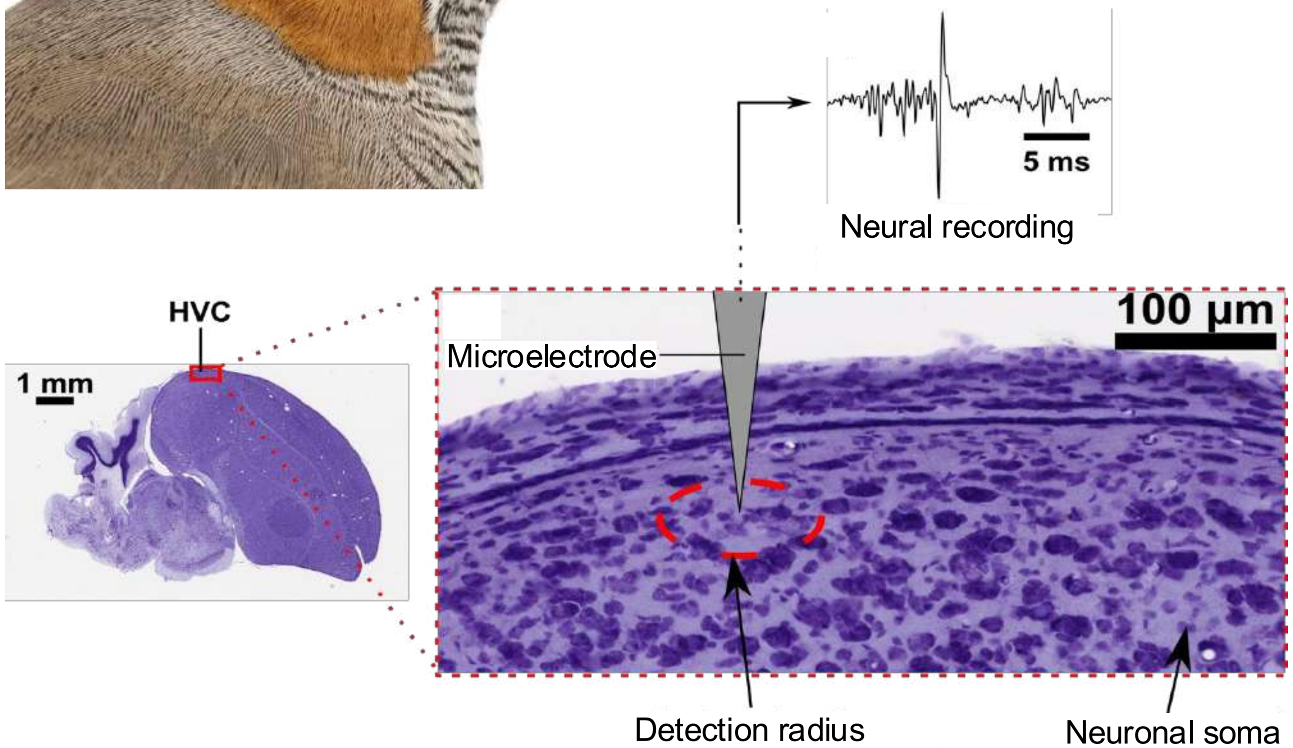


Synthetic copies of zebra finch song

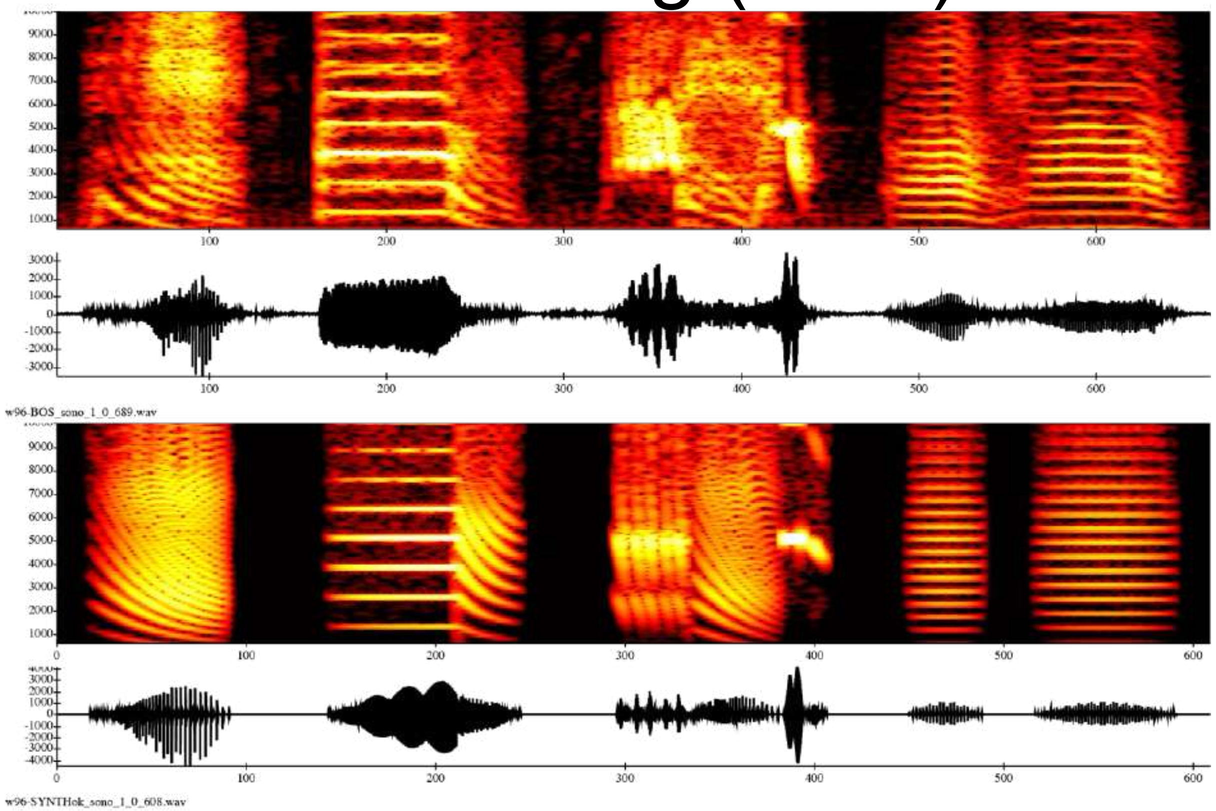
Neural recordings to validate the model

Ask the bird!

Extracellular recordings



Bird´s Own Song (BOS)

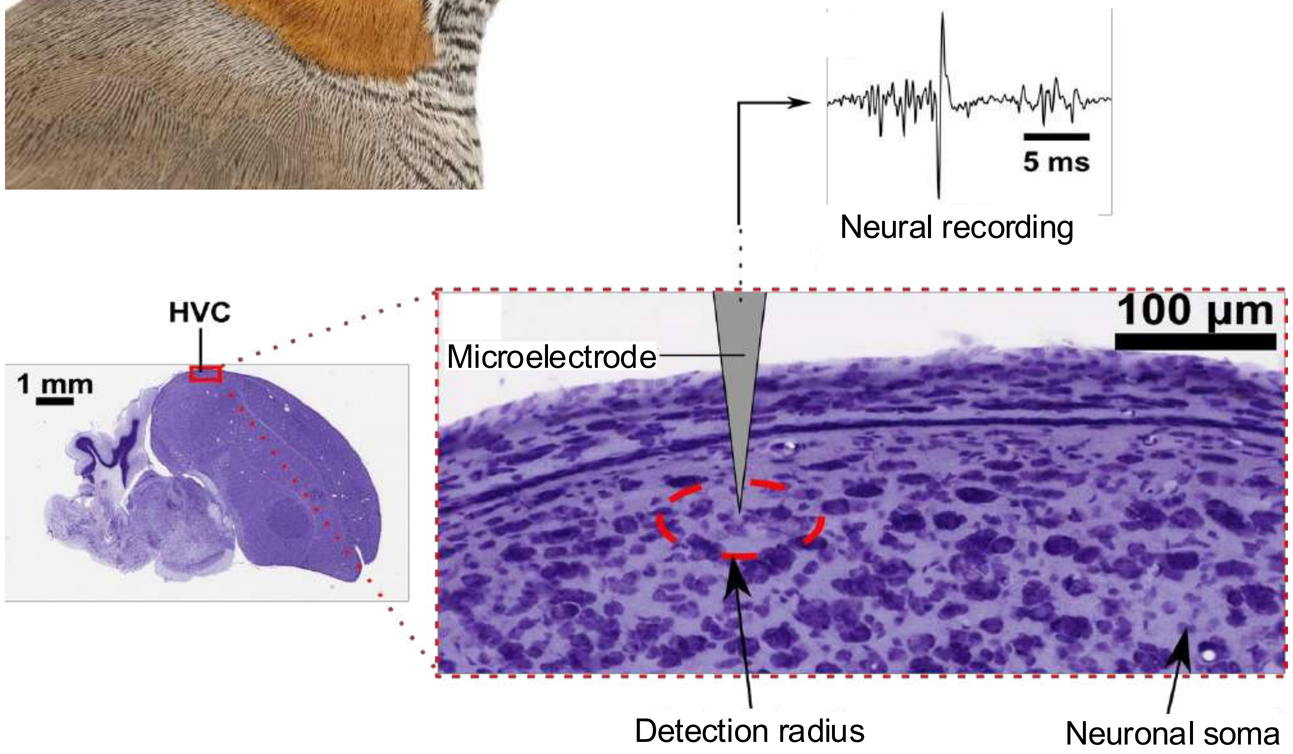


Synthetic copy (SYN)

Testing the model

Neural recordings to validate the model

Extracellular recordings



Neural selectivity in the song system

Neurons respond to the bird's own song (BOS) with a **distinctive pattern**.

Testing the model

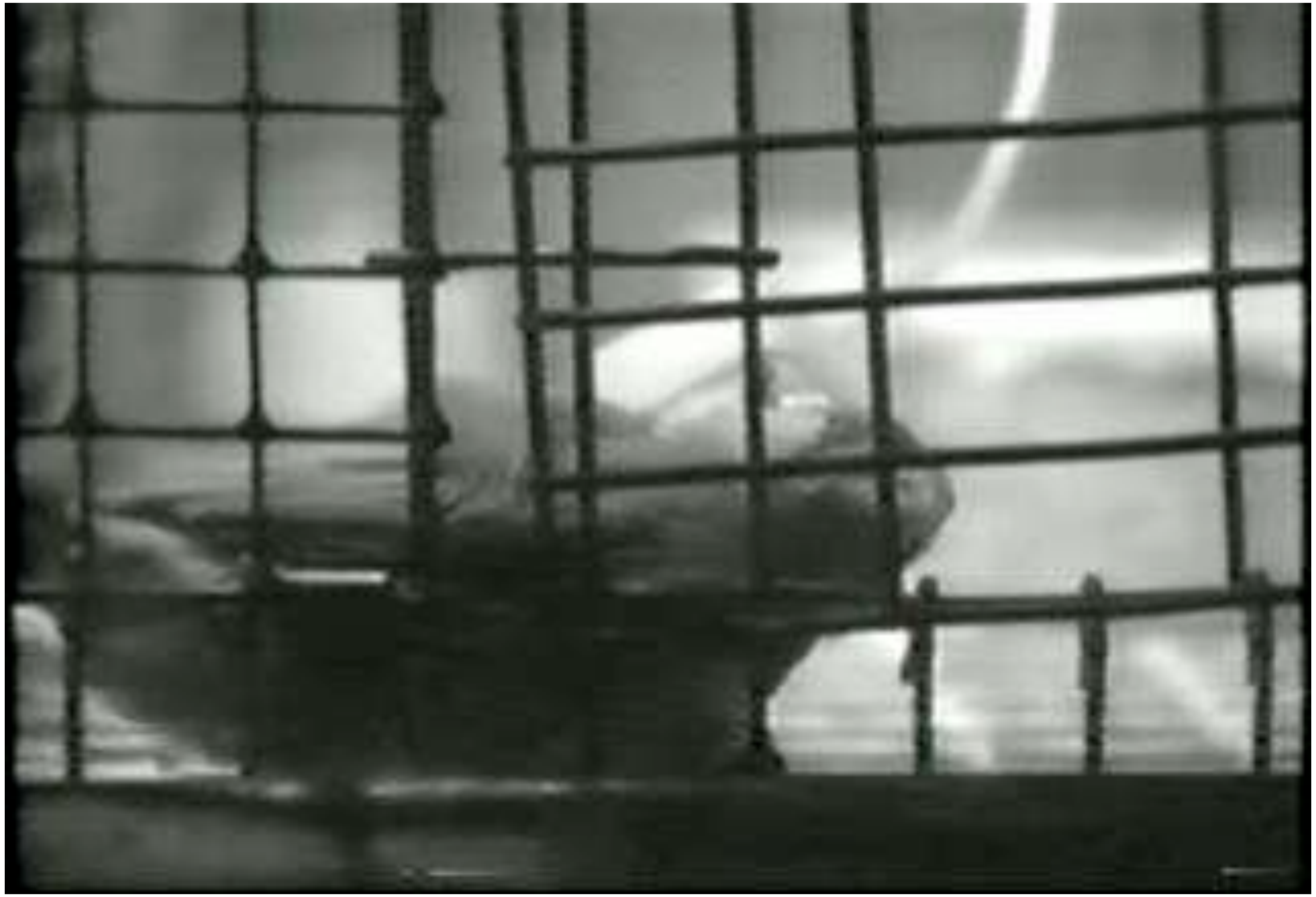
Selective neurons to the bird's own song (BOS)

Margoliash lab

Neurons code for the bird's own song (BOS) when singing

Testing the model

Selective neurons to the bird's own song (BOS)



Margoliash lab

The auditory presentation during sleep elicits the same pattern of response than during singing.

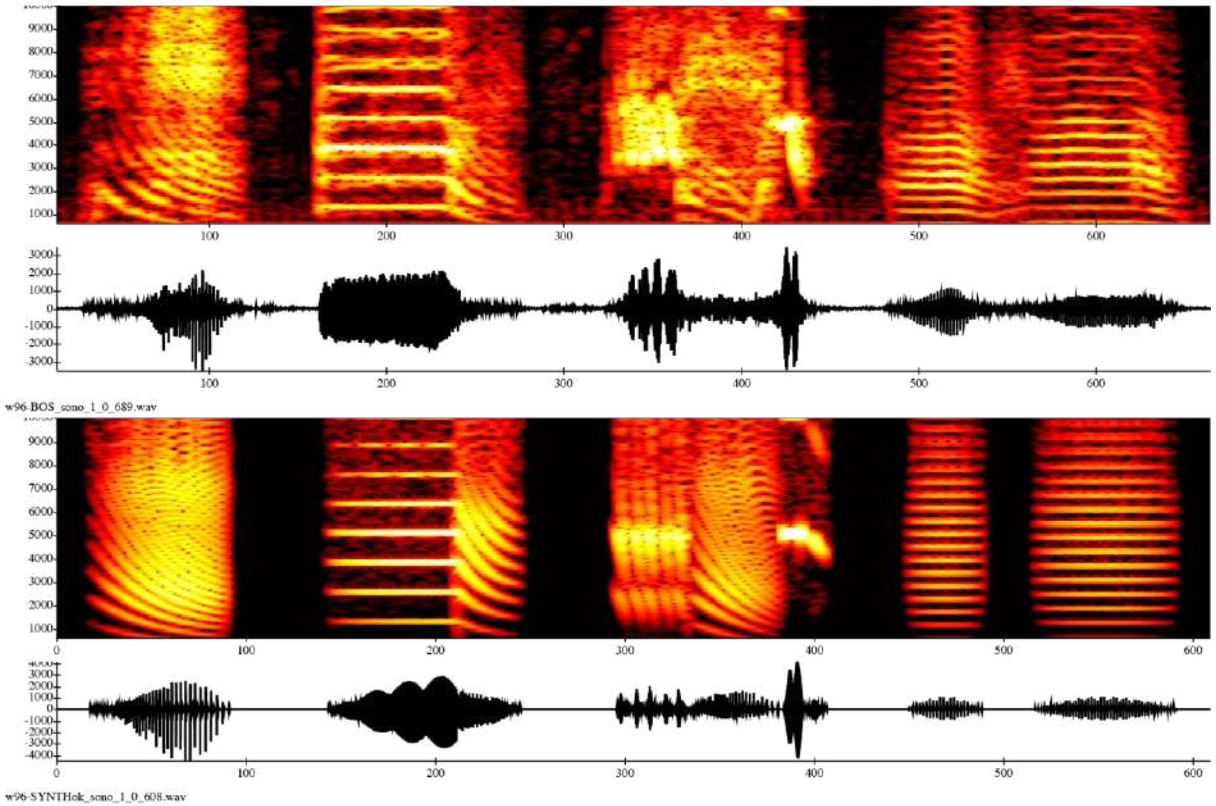
The response is state dependent (nothing if the bird wakes up)

Synthetic copies of zebra finch song

$$\frac{dx}{dt} = y$$

$$\frac{dy}{dt} = -\alpha(t)\gamma^2 - \beta(t)\gamma^2 x - \gamma^2 x^3 - \gamma x^2 y + \gamma^2 x^2 - \gamma x y$$

x: medial position of a labium
α : pressure of the air sac system
β : tension of the syringeal labia
γ : scale factor



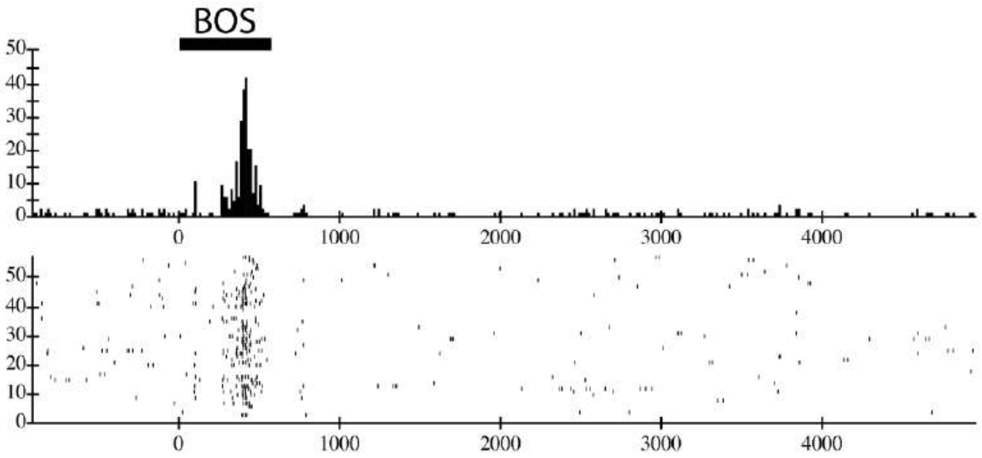
Zebra finch song

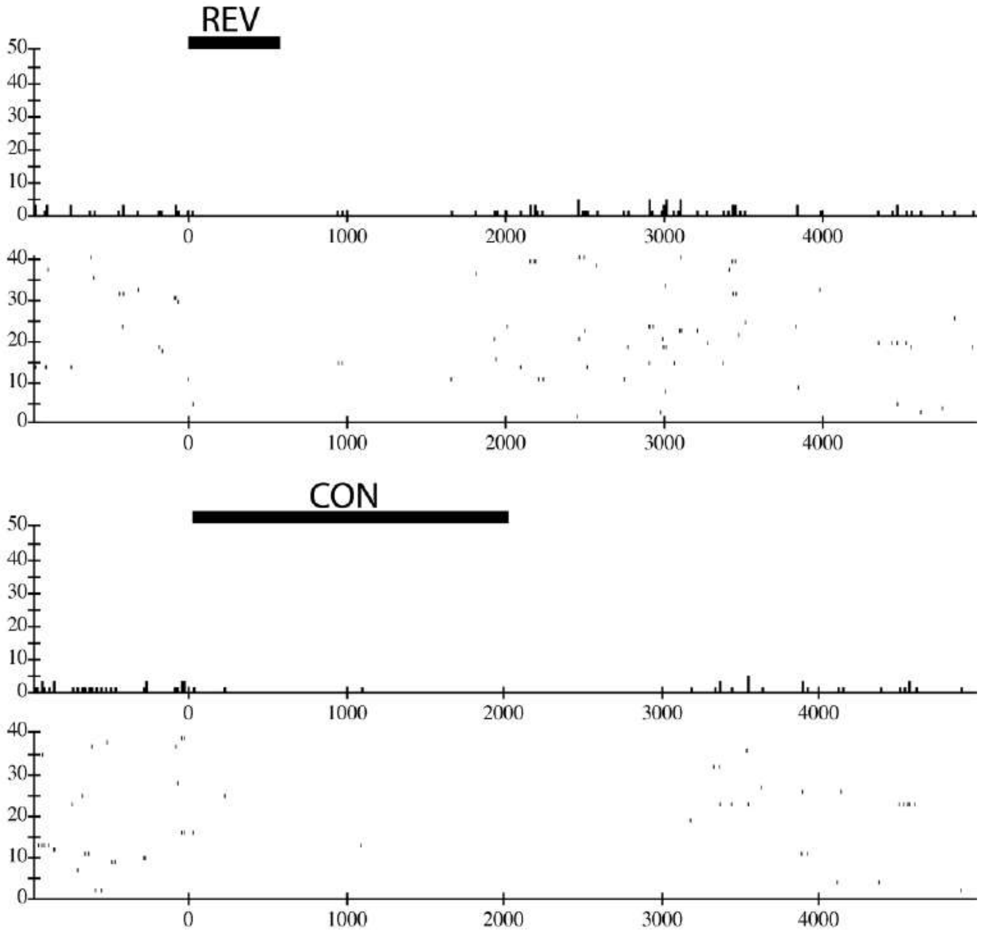
BOS

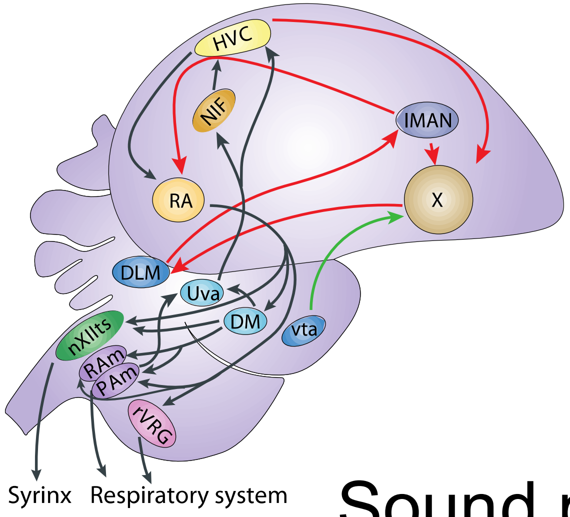
SYN

Testing the model

Neurons in HVC respond selectively to the Bird's Own Song (BOS)

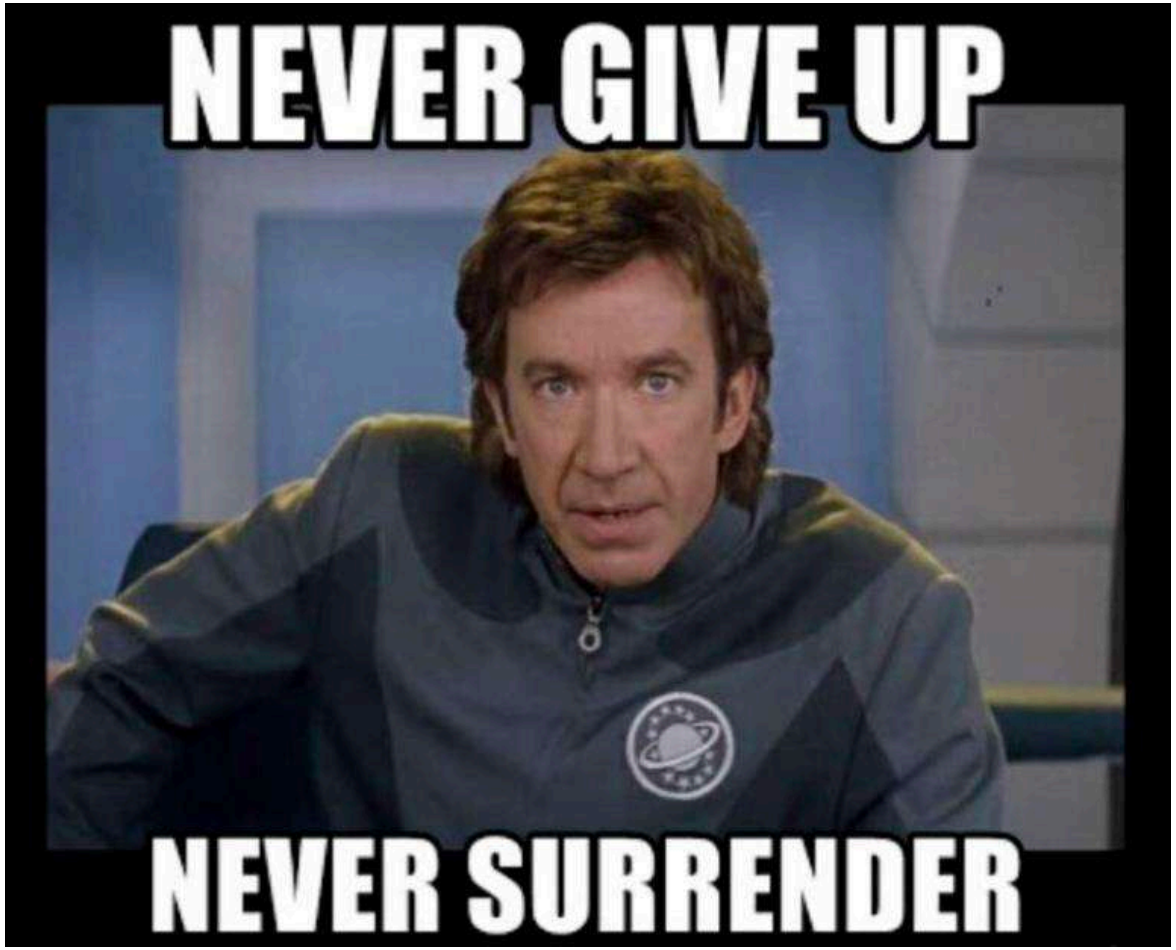


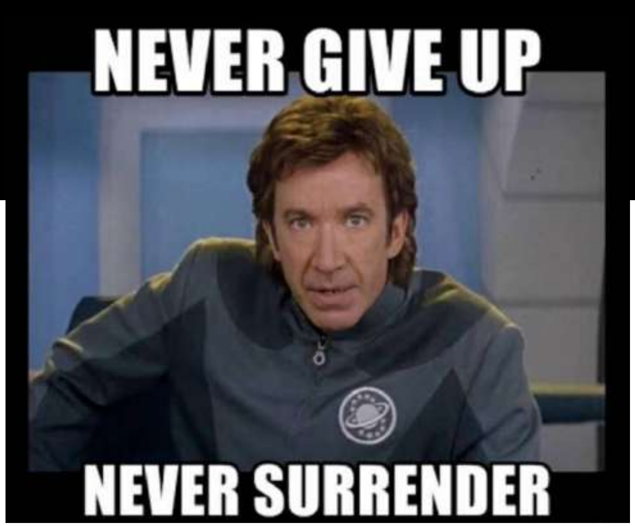




Sound presentation during sleep

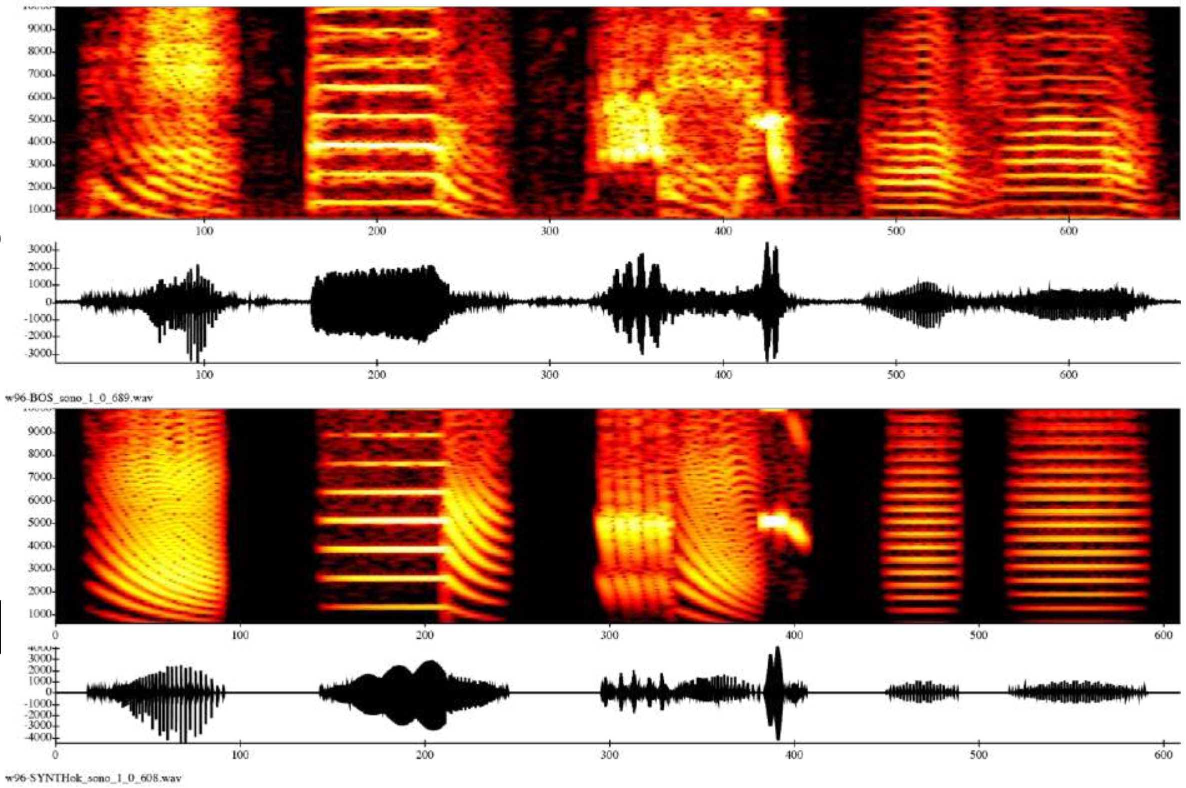
What do we do now ???





BOS

SYN



The challenge is
to remain simple!

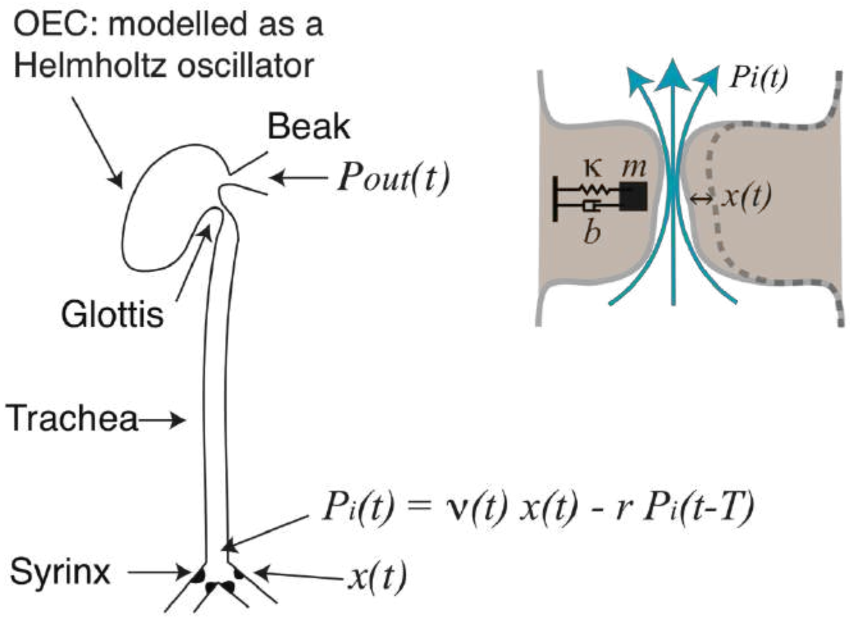
This is not working

A more detailed modeling

- ✓ More detailed modeling of the vocal tract (before: 3 tubes).

Oropharyngeal cavity as a resonator

- ✓ Noise in the labial tension (controlled by syringeal muscles)



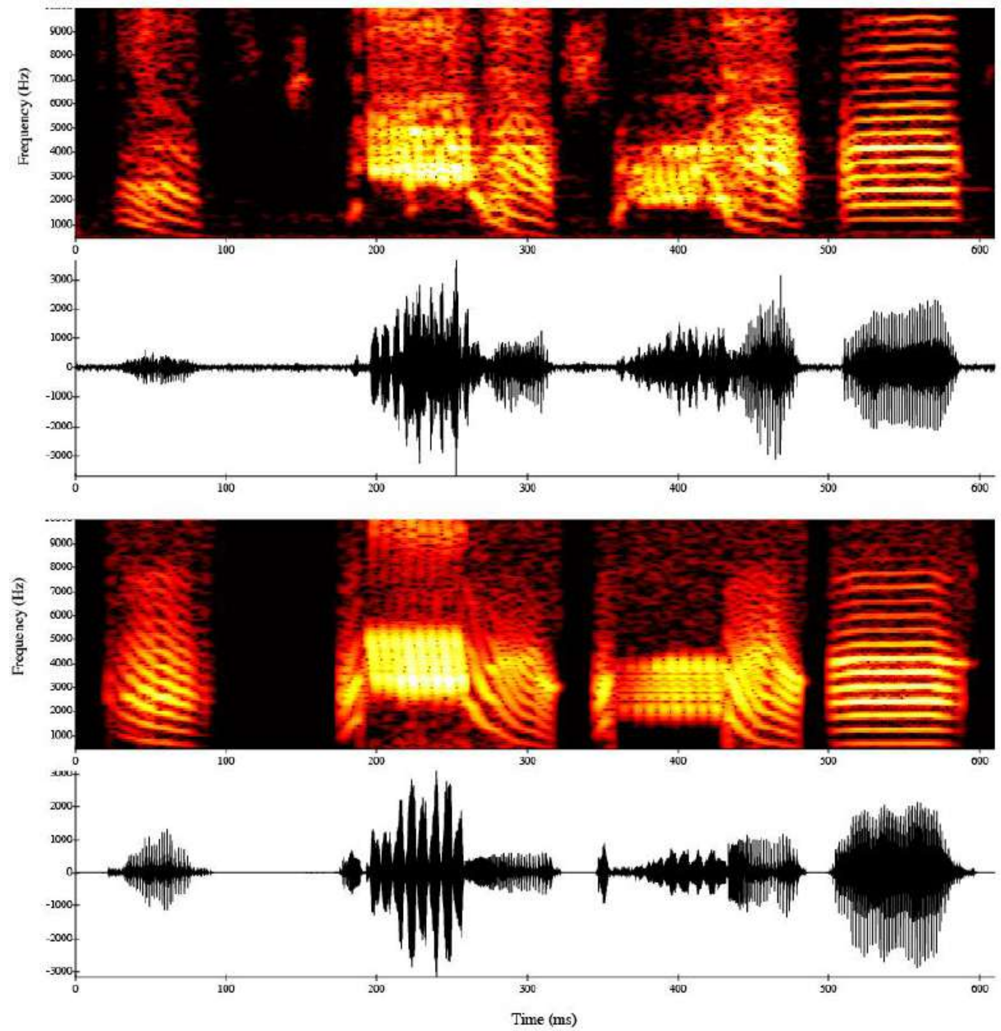
Same source

$$\frac{dx}{dt} = y$$

$$\frac{dy}{dt} = -\alpha(t)\gamma^2 - \beta(t)\gamma^2 x - \gamma^2 x^3 - \gamma x^2 y + \gamma^2 x^2 - \gamma x y$$

Amador et al, Nature 2013

A more detailed modeling



BOS

SYN

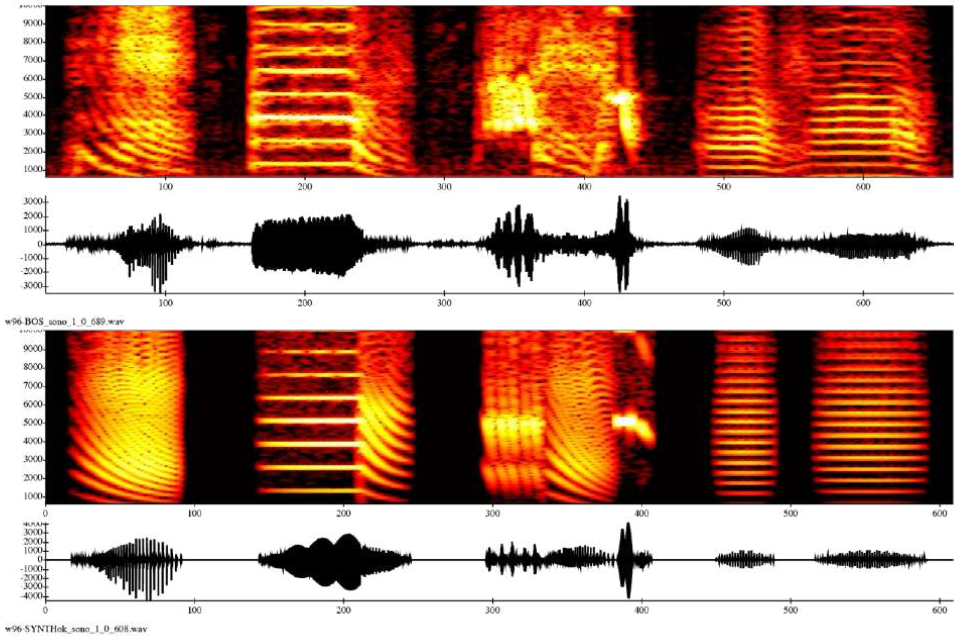
Amador et al., Nature 2013

A more detailed modeling

Before

BOS

SYN

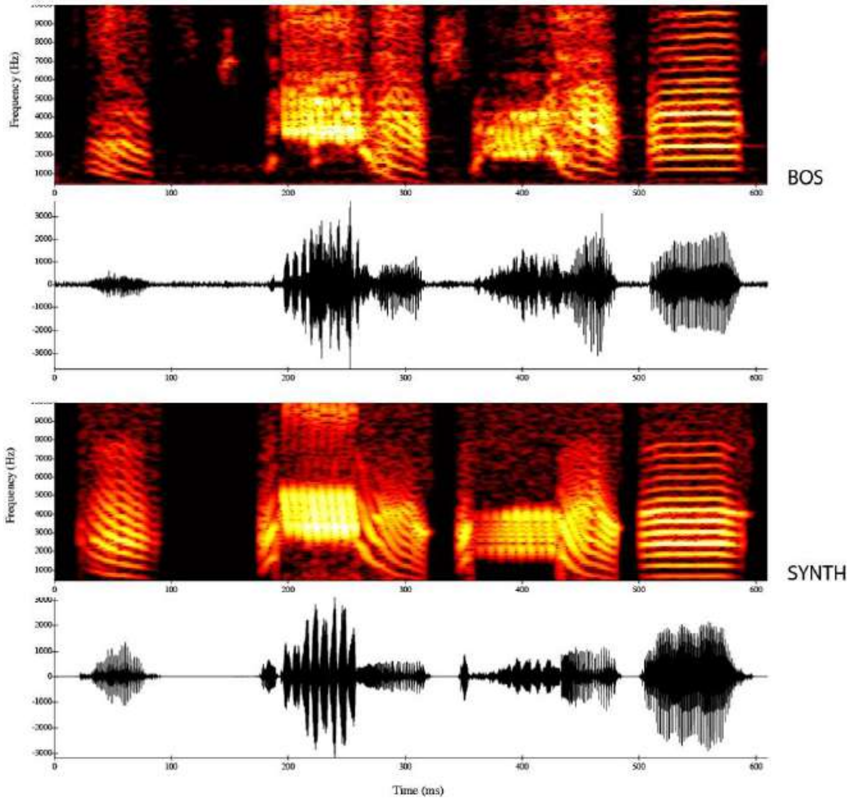


- No noise in Vs activity
- No oropharingeal cavity

After

BOS

SYN

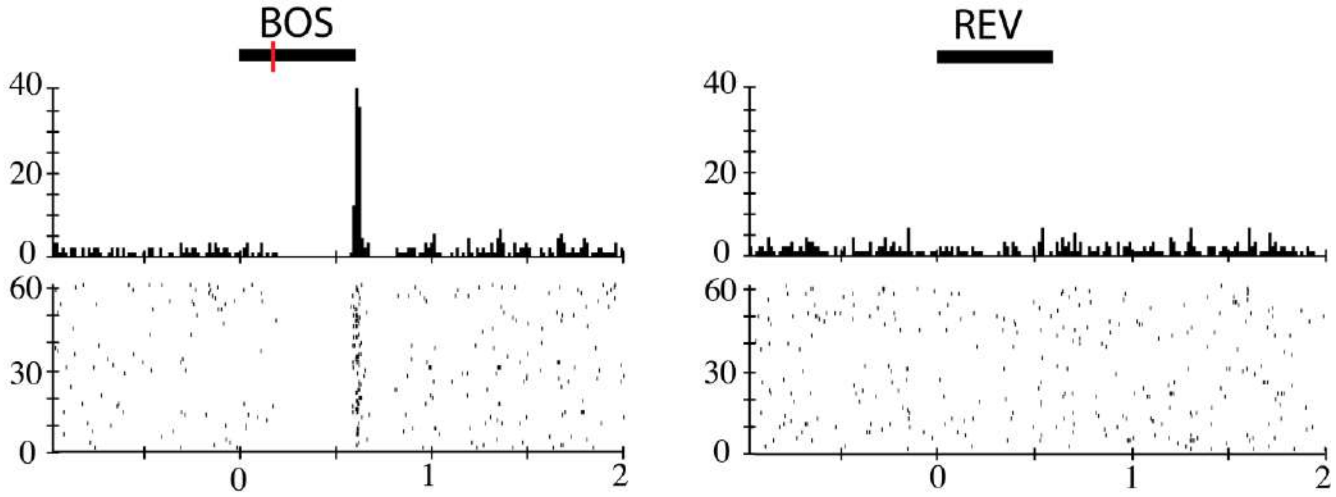


- ✓ Noise in Vs activity
- ✓ Oropharingeal cavity

Synthetic copies of zebra finch song

Neural selectivity in the song system

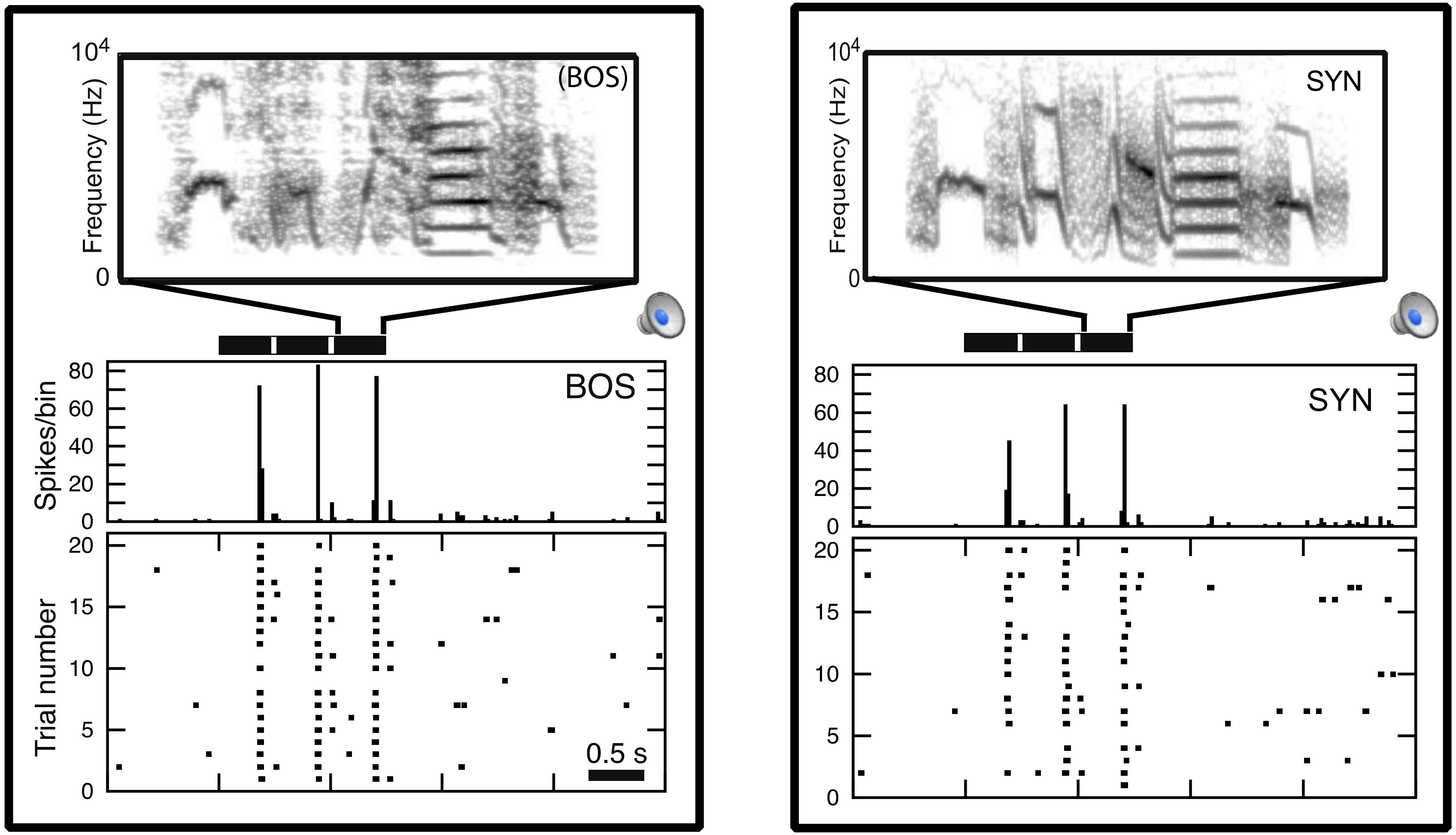
Extracellular recordings in HVC (sensorimotor nucleus)



The synthetic song elicits the same neural response than the bird's own song

Amador et al.(2013)Nature

A more detailed modeling

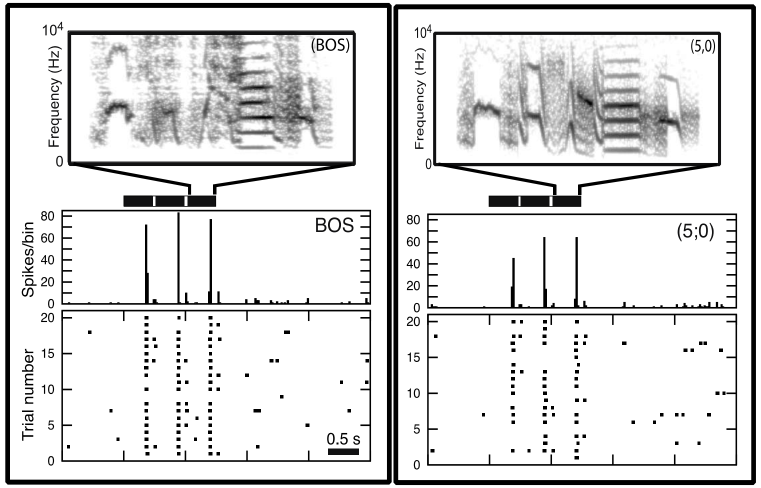


The synthetic song elicits the same neural response than the bird's own song

Amador et al, Nature 2013

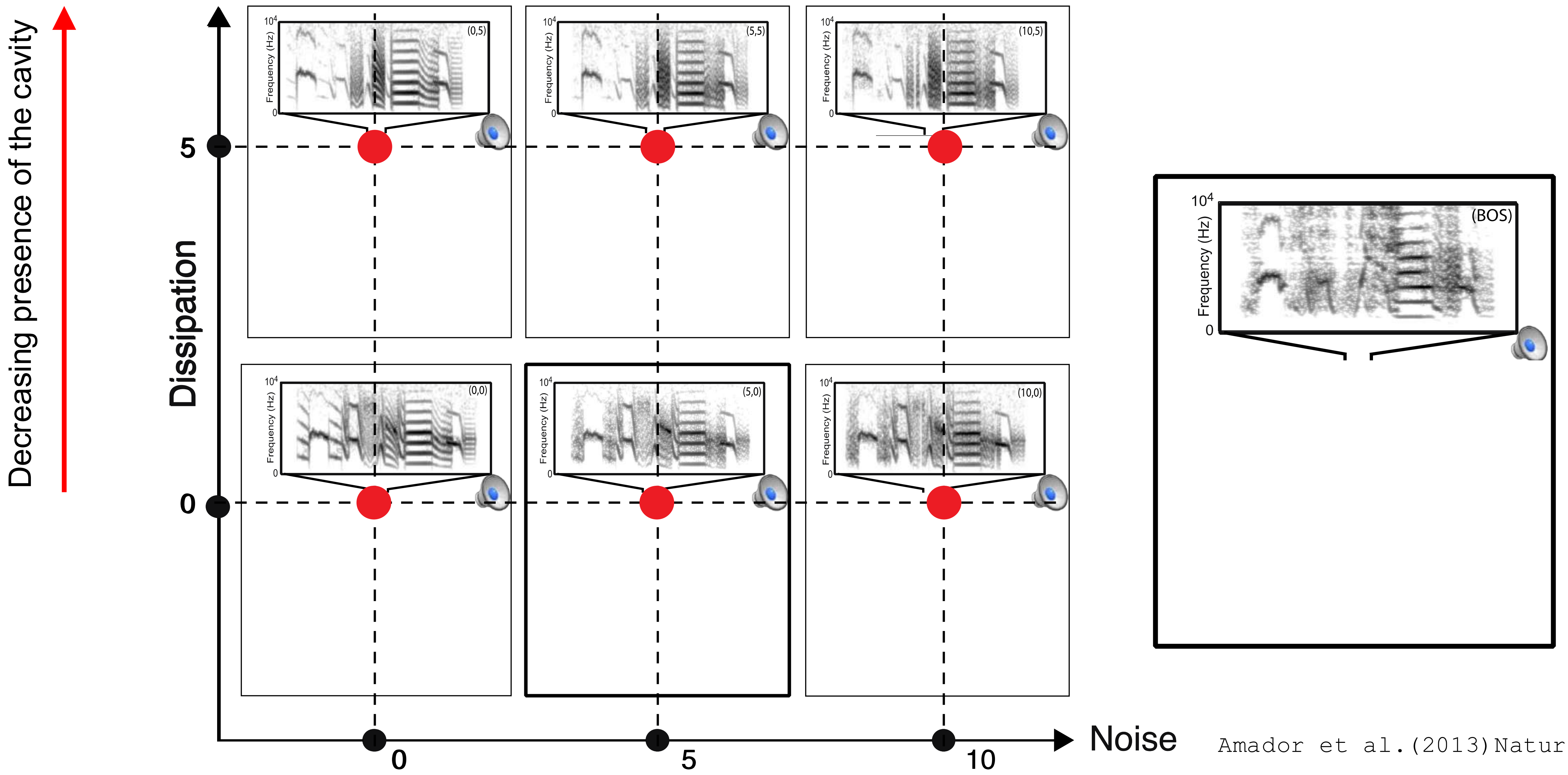
Partial summary

- A **minimal model** is able to generate **complex behavior** that is coded by neurons in the same way as natural behavior.



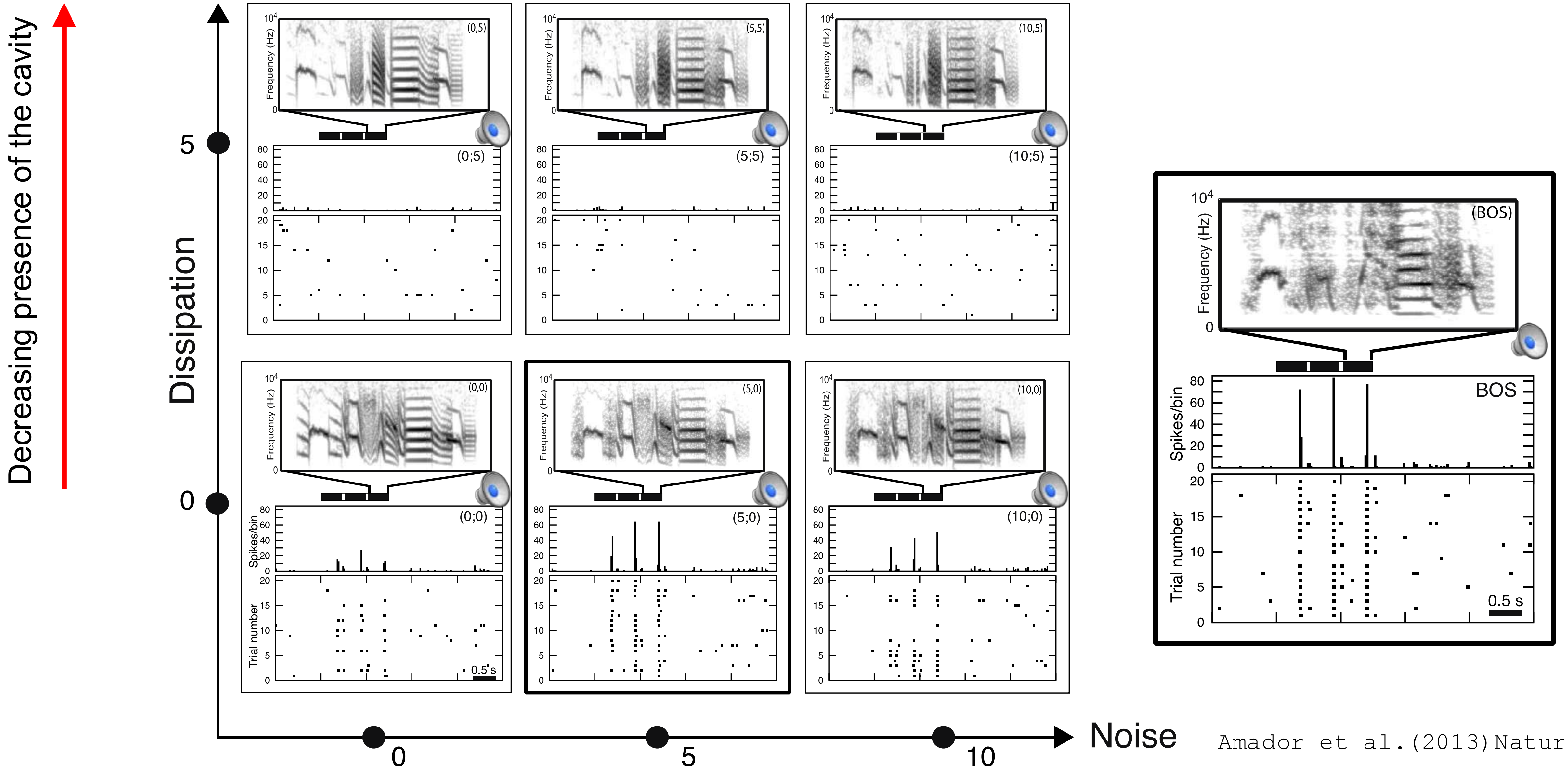
- We can now use the mathematical model as a **tool** to **study motor control**, **auditory perception** and **neural coding in songbirds**.

Studying relevance of static parameters



Amador et al.(2013)Nature

Studying relevance of static parameters



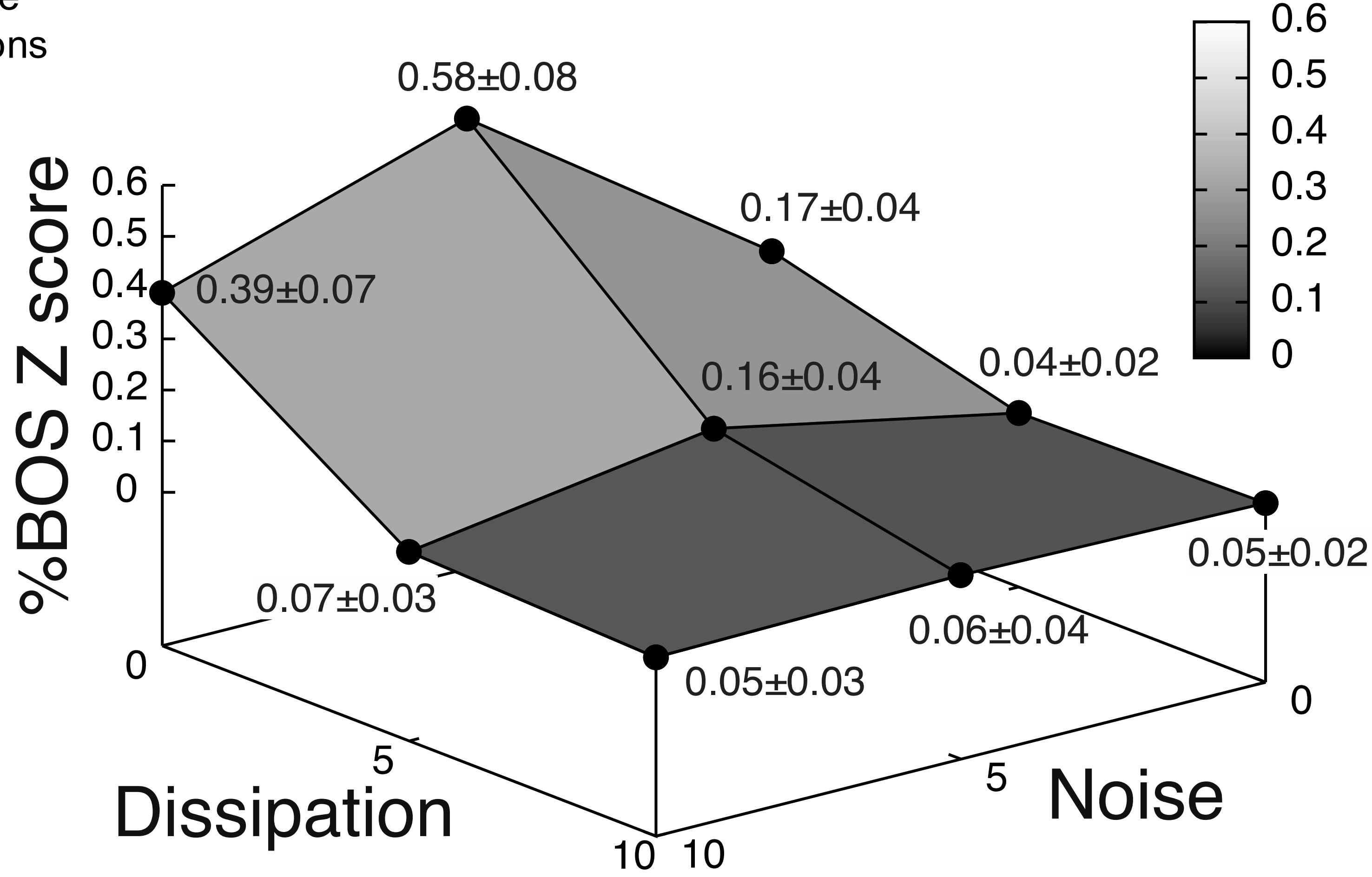
Amador et al.(2013)Nature

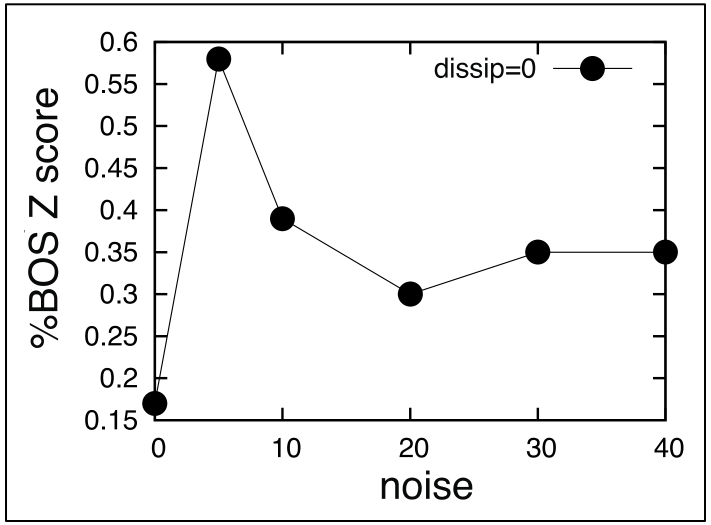
Hierarchy of static parameter relevance

Grouped data:

- 4 birds
- 30 selective HVC neurons

The resonant cavity is a relevant feature (can be controlled by the birds while singing)





The noise has a specific value that maximizes the neural responses.

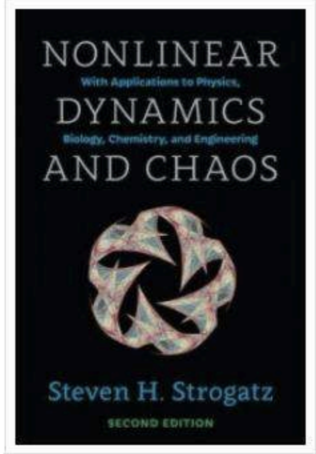
Amador et al.(2013)Nature

Bibliography

Bibliografía **dinamica**

- Mindlin G. B. Dinámica no lineal. Editorial Universidad Nacional de Quilmes (2018)

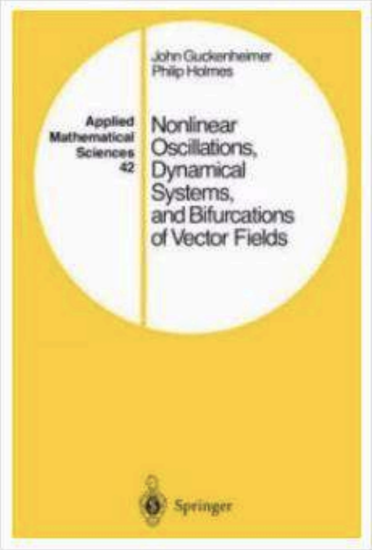
- Strogatz, S. Nonlinear Dynamics and Chaos, Westview (fácil, muy fácil… e ideal para



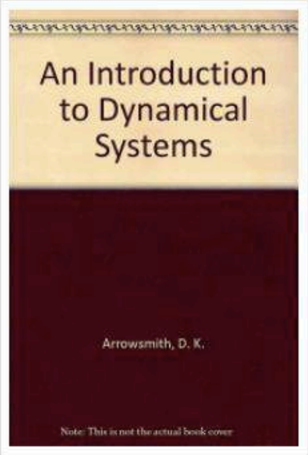
las primeras dos partes del curso)

Bibliography

- Guckenheimer J. and Holmes P. Nonlinear Oscillations, Dynamical Sistems and Bifurcations of vector fields. (y… es la biblia del tema. Para el que se anime…)



- Arrowsmith D and Place C. An introduction to dynamical systems, Cambridge (duro, pero lo que se aprende aquí, sirve siempre. Ideal para la parte 3 del curso) Aperitivos para curiosos de fin de semana



Detalles técnicos para el que esté interesado

The Hodgkin – Huxley model

Using **pioneering experimental techniques** of that time, Hodgkin and Huxley (1952) determined not only the equations but **measured all the parameters values** :

$$
\begin{aligned}
C\dot{V} &= I - \overbrace{\bar{g}_{\mathrm{K}} n^4 (V - E_{\mathrm{K}})}^{I_{\mathrm{K}}} - \overbrace{\bar{g}_{\mathrm{Na}} m^3 h (V - E_{\mathrm{Na}})}^{I_{\mathrm{Na}}} - \overbrace{g_{\mathrm{L}} (V - E_{\mathrm{L}})}^{I_{\mathrm{L}}} \\
\dot{n} &= \alpha_n(V)(1-n) - \beta_n(V)n \\
\dot{m} &= \alpha_m(V)(1-m) - \beta_m(V)m \\
\dot{h} &= \alpha_h(V)(1-h) - \beta_h(V)h \,,
\end{aligned}
$$

$$
\begin{aligned}
\alpha_n(V) &= 0.01 \frac{10 - V}{\exp(\frac{10-V}{10}) - 1} \,, \\
\beta_n(V) &= 0.125 \exp\left(\frac{-V}{80}\right) \,, \\
\alpha_m(V) &= 0.1 \frac{25 - V}{\exp(\frac{25-V}{10}) - 1} \,, \\
\beta_m(V) &= 4 \exp\left(\frac{-V}{18}\right) \,, \\
\alpha_h(V) &= 0.07 \exp\left(\frac{-V}{20}\right) \,, \\
\beta_h(V) &= \frac{1}{\exp(\frac{30-V}{10}) + 1} \,.
\end{aligned}
$$

Values of shifted Nernst equilibrium potentials (so that $V_{rest} = 0$) :

$$E_{\mathrm{K}} = -12 \text{ mV} \,, \qquad E_{\mathrm{Na}} = 120 \text{ mV} \,, \qquad E_{\mathrm{L}} = 10.6 \text{ mV};$$

Values of maximal conductances:

$$\bar{g}_{\mathrm{K}} = 36 \text{ mS/cm}^2 \,, \qquad \bar{g}_{\mathrm{Na}} = 120 \text{ mS/cm}^2 \,, \qquad g_{\mathrm{L}} = 0.3 \text{ mS/cm}^2.$$

Value of membrane capacitance:

$$C = 1\,\mu\text{F/cm}^2$$

The Hodgkin – Huxley model

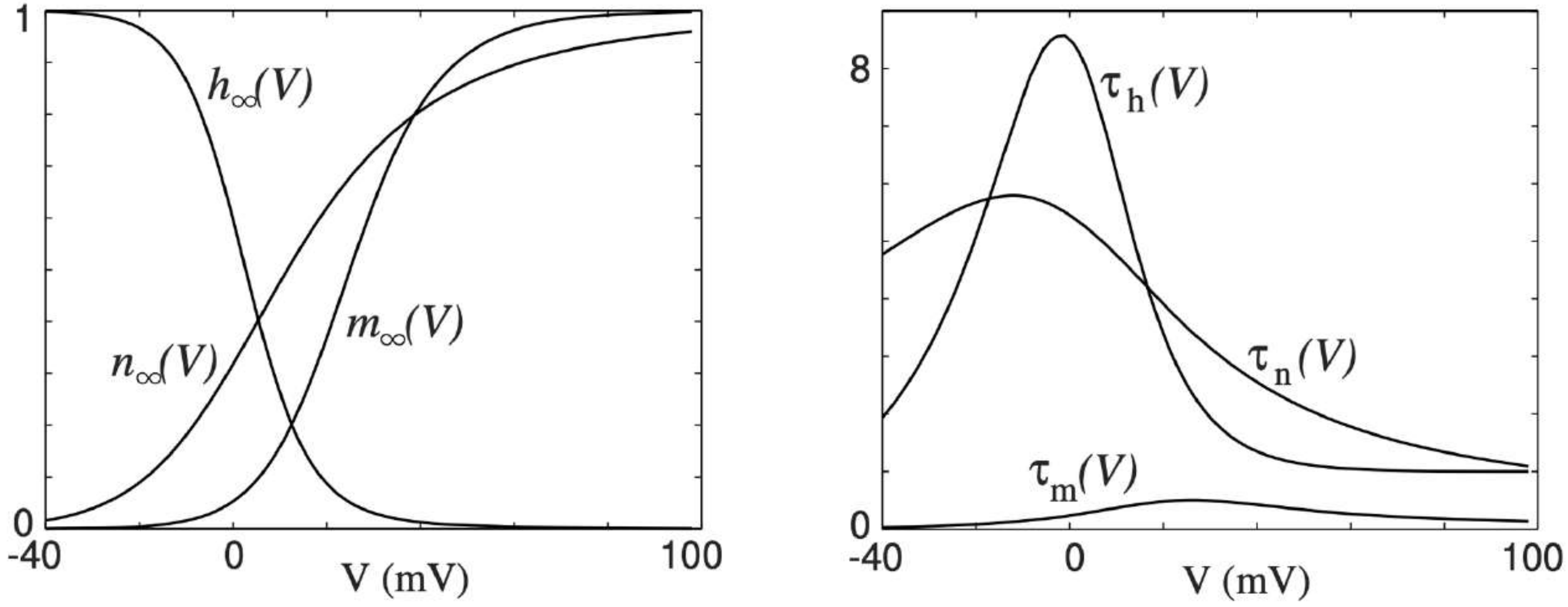
The functions α(V) and β(V) describe the transition rates between open and closed states of the channels

The notation presented before was used only for historical reasons.
It is more convenient to use:

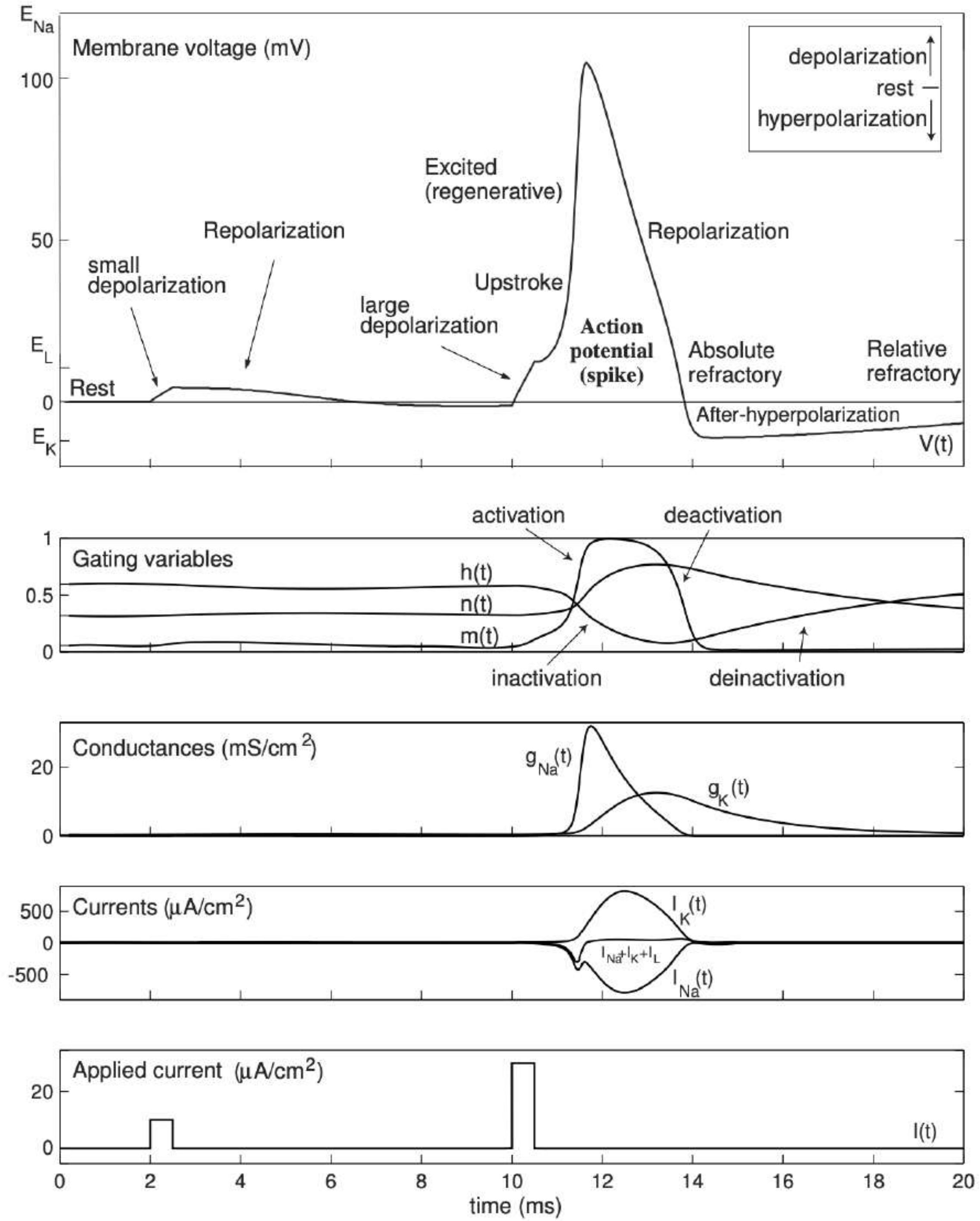
$$\dot{n} = (n_\infty(V) - n)/\tau_n(V) ,$$
$$\dot{m} = (m_\infty(V) - m)/\tau_m(V) ,$$
$$\dot{h} = (h_\infty(V) - h)/\tau_h(V) ,$$

where

$$n_\infty = \alpha_n/(\alpha_n + \beta_n) , \qquad \tau_n = 1/(\alpha_n + \beta_n) ,$$
$$m_\infty = \alpha_m/(\alpha_m + \beta_m) , \qquad \tau_m = 1/(\alpha_m + \beta_m) ,$$
$$h_\infty = \alpha_h/(\alpha_h + \beta_h) , \qquad \tau_h = 1/(\alpha_h + \beta_h)$$



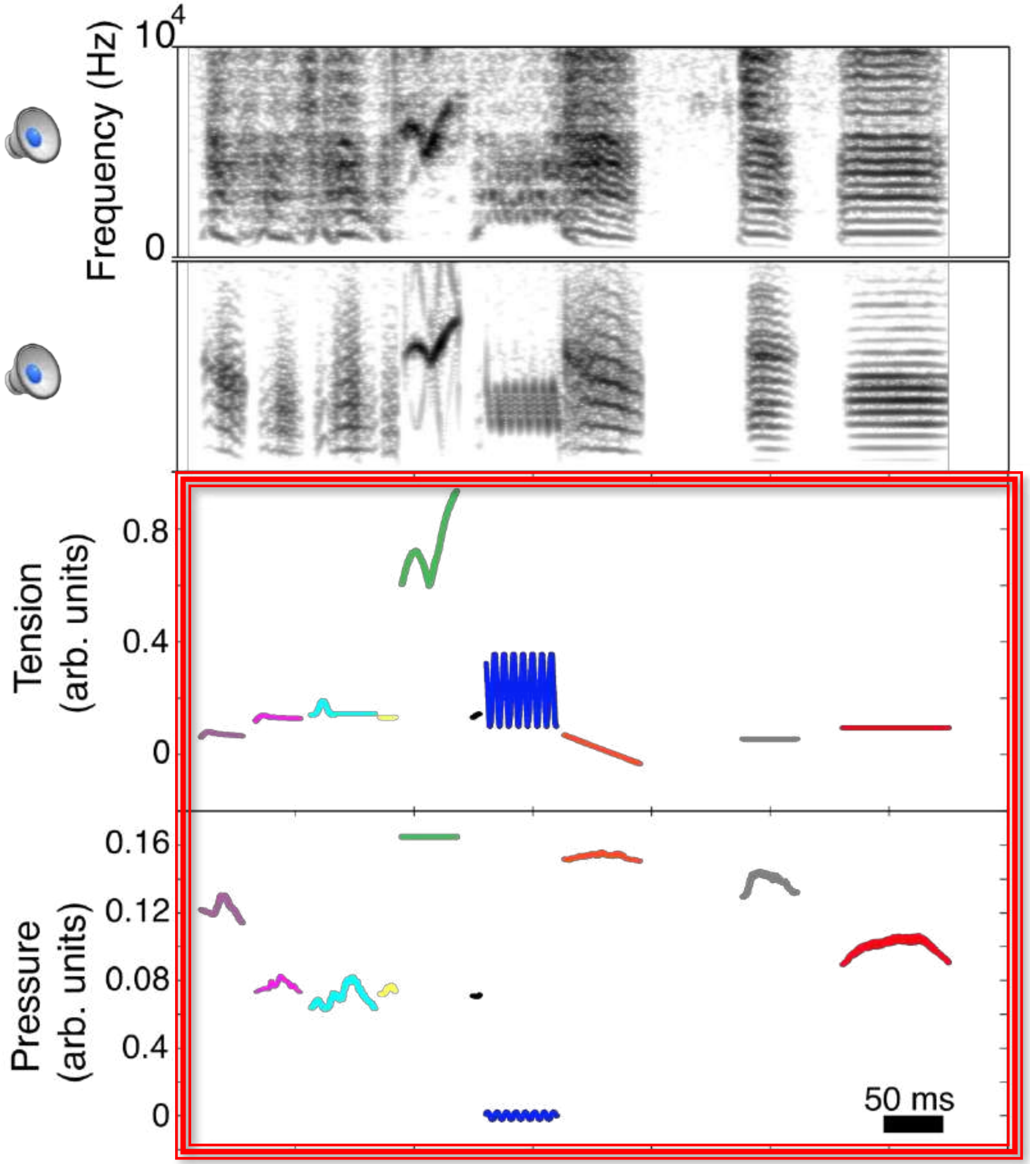
The Hodgkin – Huxley model



Our approach to biomechanics

BOS

SYN



The birdsong model provides a code in terms of α (pressure) and β (tension) . We fit these parameters so that BOS and SYN have:

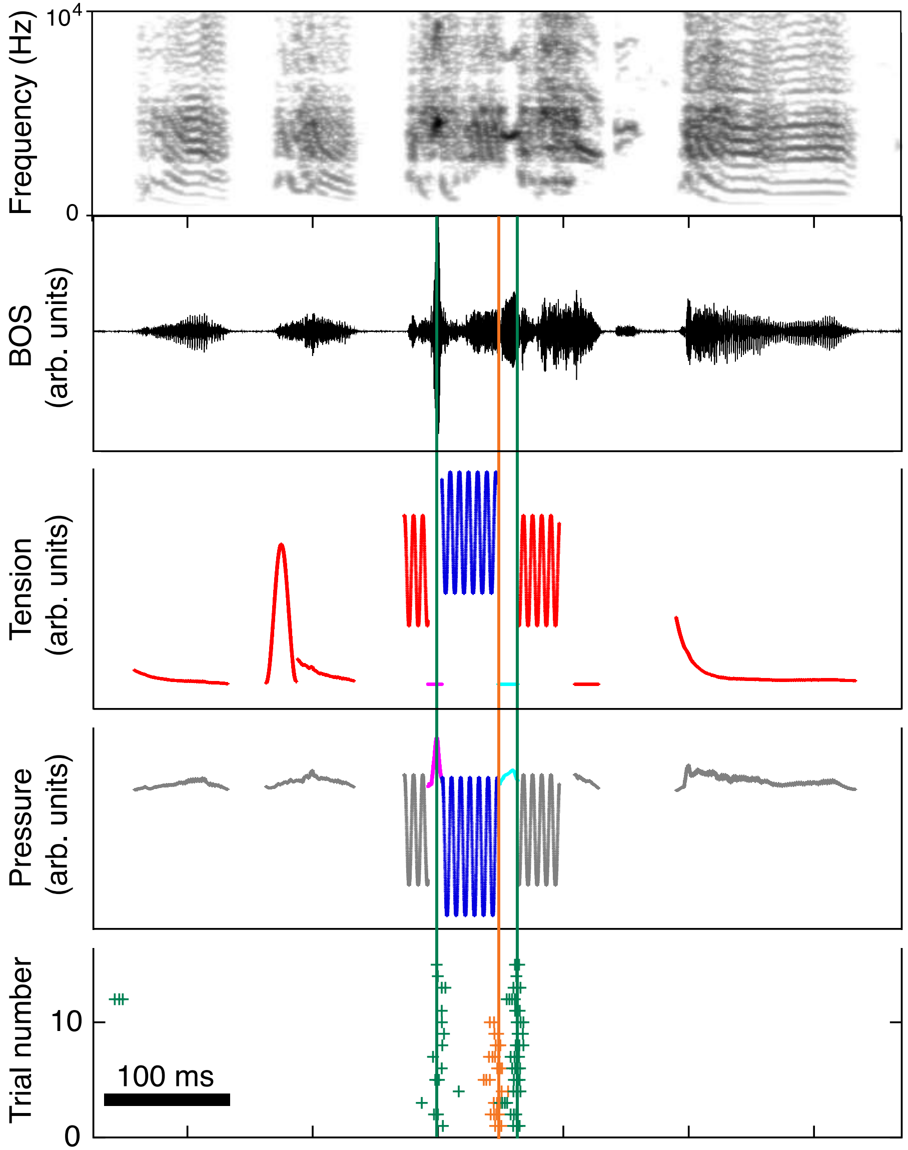
- ✓ Same fundamental frequency
- ✓ Same spectral content

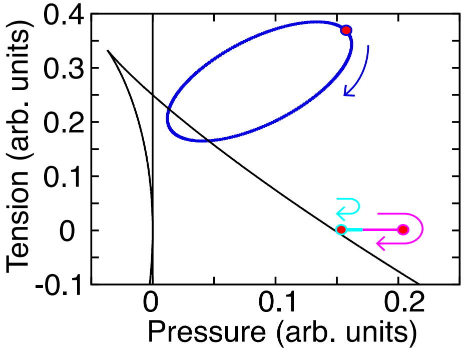
Emergence of "motor gestures"

Amador et al, Nature 2013

Using the model to unveil the neural code

Sleeping birds



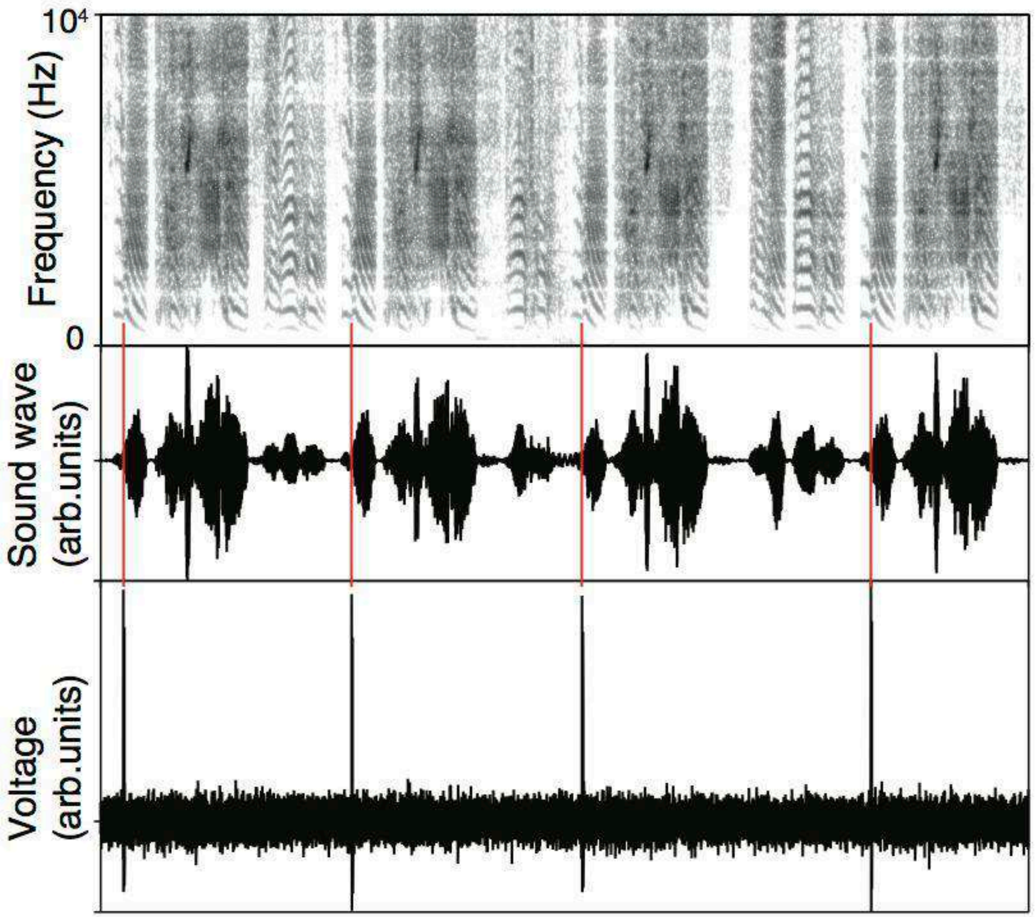


GTE Gesture Trajectory Extrema

Amador et al, Nature 2013

Using the model to unveil the neural code

Singing birds



Song

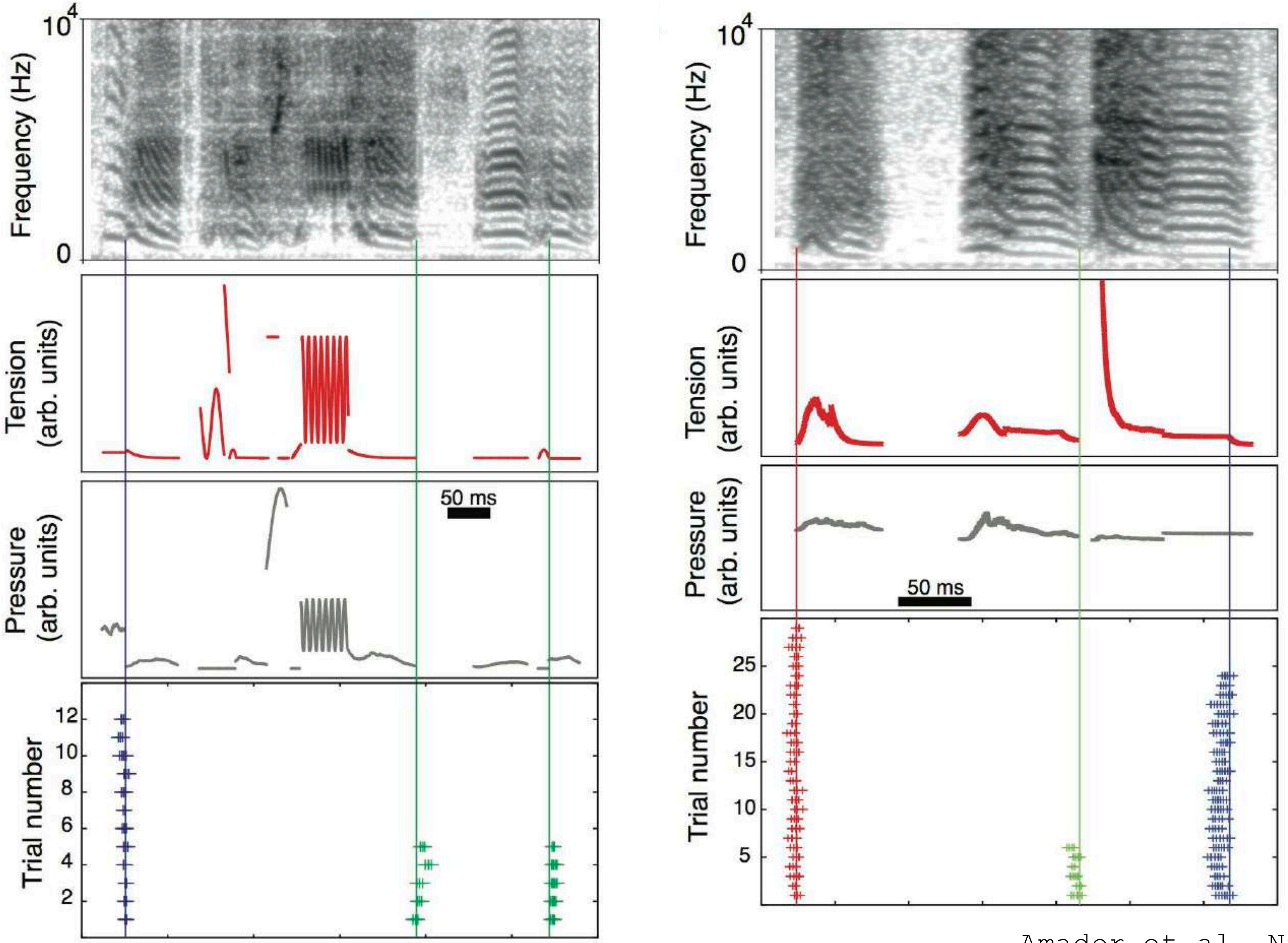
Neural activity

Amador et al, Nature 2013

Using the model to unveil the neural code

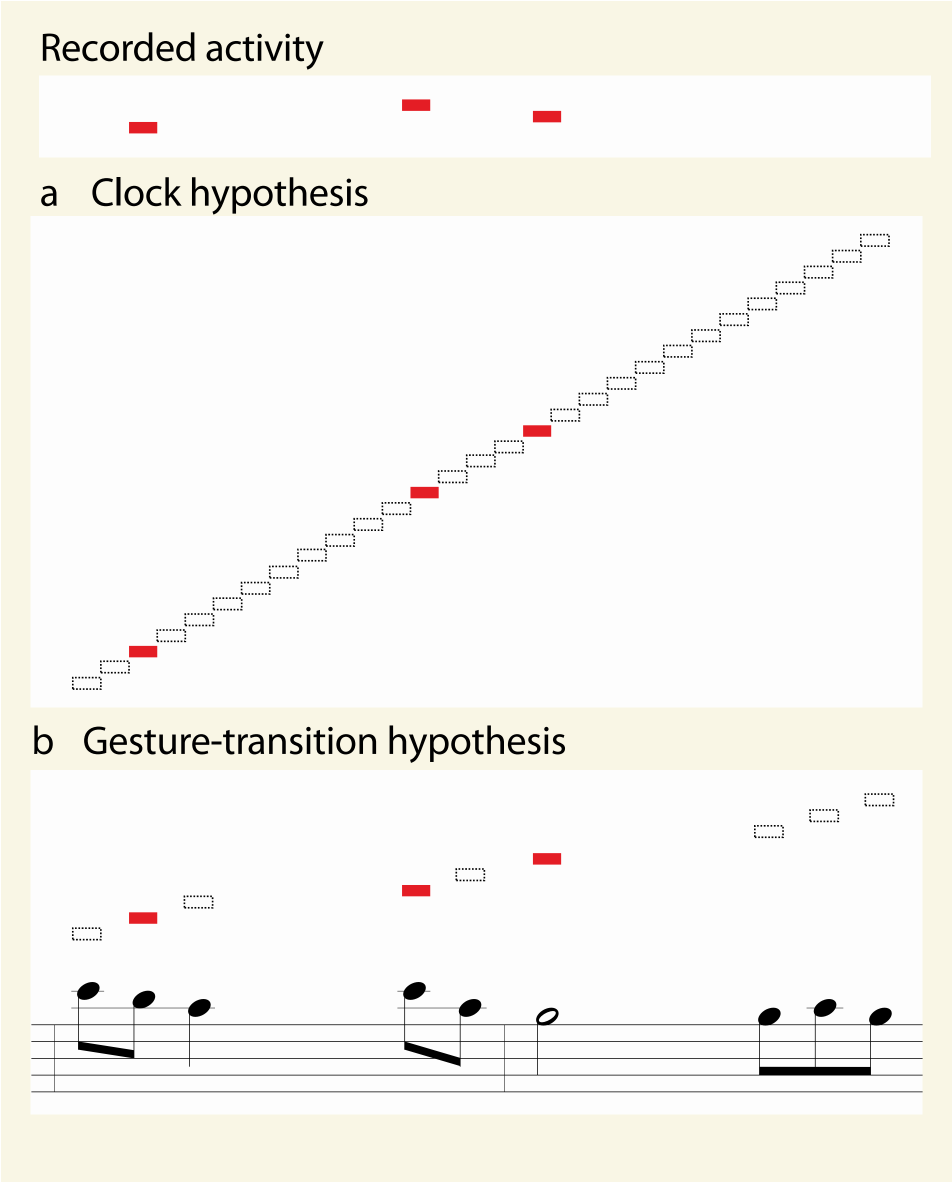
Singing birds

Neurons fire at significant motor instances



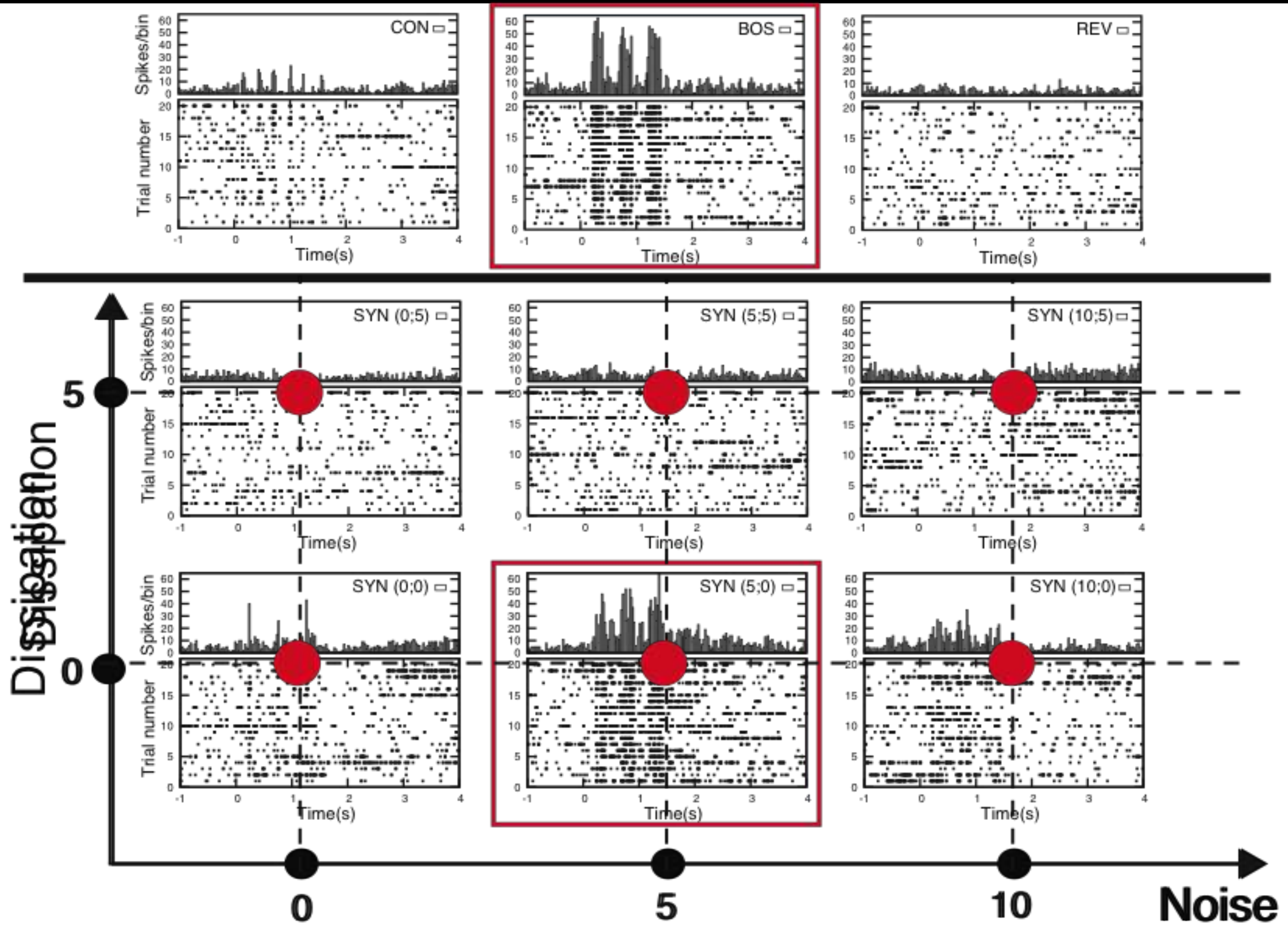
Amador et al, Nature 2013

Two hypothesis



Modified from Troyer, Nature 2013

Tonic neurons



Also, in a singing bird

• Neurons code for significant motor instances.

• Predictive model