"Spikes alone do not behavior make: why neuroscience needs biomechanics" (II)

> Title borrowed from **Phil Holmes**, ED Tytell and AH Cohen

Gabriel Mindlin, covering P.H.







How complex, those instructions? The canary example. Candidate for simpler gestures...





Air sac dynamics

Inspiration is Inhibited by the inflated air sacs







Air sac dynamics

Inspiration is Inhibited by the inflated air sacs







# The additive model

$$\frac{dx}{dt} = -x + S(\rho + cx)$$

$$s(x) = \frac{1}{1 + e^{-x}}$$



### An ICTP initciative

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How the page works







From Nottebohm et al.









### When do the bursts occur in HVC?







Is it possible to build a model such that

1. its variables are the activities of different areas of the song system,

2. With an expiratory related area whose activity fits the recorded pressure patterns,

3. With sparse, bursting activity at a distant area (necessary for motor control) at significant motor instances?



### 

# A circular model





Canary pressure patterns Additive model (variables: rates; Average activities)

$$\frac{dx_i}{dt} = -x_i + S\left(\rho_i + \sum_j a_{ij}x_j\right),$$
  
$$S(x) = \frac{1}{1 + e^{-x}}$$



$$\begin{aligned} \frac{de_{er}}{dt} &= 149.5 \left(-e_{er} + S \left(-7.5 + \alpha_{eer,ra}e_{ra} + \alpha_{eer,F}F + 10e_{er} - 10i_{er}\right)\right) \\ \frac{di_{er}}{dt} &= 149.5 \left(-i_{er} + S \left(-11.5 + \alpha_{ier,ra}e_{ra} + 10e_{er} + 2i_{er}\right)\right) \\ \frac{de_{ra}}{dt} &= 20 \left(-e_{ra} + S \left(\rho_{e,ra} + \alpha_{era,Fd}F_{delayed} + \alpha_{era,Fd2}F_{delayed2} + \alpha_{era,ra}e_{ra} + \beta_{era,ra}i_{ra}\right)\right) \\ \frac{di_{ra}}{dt} &= 20 \left(-i_{ra} + S \left(\rho_{i,ra} + \alpha_{ira,Fd}F_{delayed} + \alpha_{ira,Fd2}F_{delayed2} + \alpha_{ira,ra}e_{ra} + \beta_{ira,ra}i_{ra}\right)\right) \end{aligned}$$

# preliminary data

- 1. For PO solutions, after the first pressure peak
- 2. At transitions





Gogui Alonso



Troyer

A continuous representation of time at the telencephalon:





Consistent with one Time scale...

Long & Fee



Mati's thesis





### How do we introduce the cooling into the model?



Voltage (mV) Voltage (mV)

1ms

spikes ax count

spikes ax count

ms)

normal

Time (ms)

Some things to take home:

1. CNS alone does not determine behavior (example to remember: The oscillations of labia depend on the biomechanical interaction of Tissue and the airflow; nothing spikes at 3 kHz controlling labial motion)

2. Nonlinear dynamics is an appropriate language to describe qualitative Behavior, regardless of details. Super important in biology, where details Can take a lifetime to be understood.

 Most sensory neurons are really picky, and won't respond to "noise", "pure tones" or anything a physicist would consider fair, complete or Representative. They evolve to interpret the pertinence through evolution.

# Material suplementario:

- Calculo de actividad media para poblaciones de theta neurons.
- Ponemos a prueba la hipotesis de que la actividad promedio muestra los mismos comportamientos dinamicos que las actividades en los modelos de Wilson Cowan
- Derivamos expresiones analiticas para la actividad, a partir de los parametros de orden.

# Hacia una teoria de campo medio



$$egin{aligned} \dot{ heta}_i(t) &= \omega_i - \cos heta_i(t) + rac{k_E}{N} \sum_{j=0}^N (1 - \cos heta_j(t)) - rac{k_I}{ ilde N} \sum_{j=1}^{ ilde N} (1 - \cos ilde heta_j(t)), \ \dot{ heta}_i(t) &= ilde u_i - \cos ilde heta_i(t) + rac{ ilde k_E}{N} \sum_{j=0}^N (1 - \cos heta_j(t)) - rac{ ilde k_I}{ ilde N} \sum_{j=1}^{ ilde N} (1 - \cos heta_j(t)), \end{aligned}$$



$$egin{split} \dot{ heta}_i(t) &= \omega_i - \cos heta_i(t) + k_Eig(1 - \operatorname{Re} z(t)ig) - k_Iig(1 - \operatorname{Re} ilde z(t)ig), \ \dot{ heta}_i(t) &= ilde u_i - \cos heta_i(t) + ilde k_Eig(1 - \operatorname{Re} z(t)ig) - ilde k_Iig(1 - \operatorname{Re} ilde z(t)ig). \end{split}$$

$$\begin{split} &\int_{-\infty}^{\infty} \int_{0}^{2\pi} f(\theta, \omega, t) d\theta d\omega = 1, \\ &\int_{-\infty}^{\infty} \int_{0}^{2\pi} \tilde{f}(\theta, \omega, t) d\theta d\omega = 1. \end{split} \qquad \qquad \int_{0}^{2\pi} f(\theta, \omega, t) d\theta = g(\omega). \end{split}$$

$$v( heta,\omega,t)=\omega-rac{e^{i heta}+e^{-i heta}}{2}+k_Eig(1-\operatorname{Re} z(t)ig)-k_Iig(1-\operatorname{Re} ilde z(t)ig),$$

$$\begin{split} z(t) &= \int_{-\infty}^{\infty} \int_{0}^{2\pi} f(\theta, \omega, t) e^{i\theta} d\theta d\omega, \\ \tilde{z}(t) &= \int_{-\infty}^{\infty} \int_{0}^{2\pi} \tilde{f}(\theta, \omega, t) e^{i\theta} d\theta d\omega. \end{split}$$



$$f( heta, \omega, t) = \sum_{n=-\infty}^{\infty} a_n(\omega, t) rac{e^{in heta}}{\sqrt{2\pi}},$$
 $a_n(\omega, t) = \int_{-\infty}^{\infty} f( heta, \omega, t) rac{e^{-in heta}}{\sqrt{2\pi}} d heta.$ 

$$\begin{split} 0 &= \frac{\partial f}{\partial t} + v \frac{\partial f}{\partial \theta} + \frac{\partial v}{\partial \theta} f \\ &= \sum_{n=-\infty}^{\infty} \frac{\partial a_n}{\partial t} \frac{e^{in\theta}}{\sqrt{2\pi}} + \left(\omega - \frac{e^{i\theta}}{2} + \frac{e^{-i\theta}}{2} + k_E(1 - \operatorname{Re} z) - k_I(1 - \operatorname{Re} \tilde{z})\right) ina_n \frac{e^{in\theta}}{\sqrt{2\pi}} + \\ &+ \left(\frac{-i}{2}e^{i\theta} + \frac{i}{2}e^{-i\theta}\right) a_n \frac{e^{in\theta}}{\sqrt{2\pi}} \end{split}$$

$$=\sum_{n=-\infty}^{\infty} \left(\frac{\partial a_n}{\partial t} + in\left(\omega + k_E(1 - \operatorname{Re} z) - k_I(1 - \operatorname{Re} \tilde{z})\right)a_n\right) \frac{e^{in\theta}}{\sqrt{2\pi}} + \frac{i}{2}(n+1)a_n \frac{e^{i(n+1)\theta}}{\sqrt{2\pi}} - \frac{i}{2}(n-1)a_n \frac{e^{i(n-1)\theta}}{\sqrt{2\pi}}$$

$$=\sum_{n=-\infty}^{\infty} \left[ \frac{\partial a_n}{\partial t} + in \Big( \omega + k_E (1 - \operatorname{Re} z) - k_I (1 - \operatorname{Re} \tilde{z}) \Big) a_n - \frac{i}{2} n a_{n-1} - \frac{i}{2} n a_{n+1} \right] \frac{e^{in\theta}}{\sqrt{2\pi}}.$$

$$egin{aligned} &rac{\partial a_n}{\partial t}(\omega,t) = &-in\Big(\omega+k_Eig(1-\operatorname{Re}z(t)ig)-k_Iig(1-\operatorname{Re} ilde z(t)ig)\Big)a_n(\omega,t)+ \ &+rac{i}{2}nig(a_{n-1}(\omega,t)+a_{n+1}(\omega,t)ig). \end{aligned}$$

$$\begin{split} f(\theta,\omega,t) &= \frac{g(\omega)}{2\pi} \Biggl( 1 + \sum_{n \geqslant 1} \frac{\sqrt{2\pi}}{g(\omega)} a_n(\omega,t) e^{in\theta} + \frac{\sqrt{2\pi}}{g(\omega)} a_n^*(\omega,t) e^{-in\theta} \Biggr) \\ &= \frac{g(\omega)}{2\pi} \Biggl( 1 + \sum_{n \geqslant 1} \alpha_n(\omega,t) e^{in\theta} + \alpha_n^*(\omega,t) e^{-in\theta} \Biggr), \end{split}$$

$$lpha_n(\omega,t)=rac{\sqrt{2\pi}}{g(\omega)}a_n(\omega,t).$$

$$egin{aligned} &rac{\partial lpha_n}{\partial t}(\omega,t) = &- in \Big( \omega + k_E ig(1 - \operatorname{Re} z(t)ig) - k_I ig(1 - \operatorname{Re} ilde z(t)ig) \Big) lpha_n(\omega,t) + \ &+ rac{i}{2} nig(lpha_{n-1}(\omega,t) + lpha_{n+1}(\omega,t)ig). \end{aligned}$$

$$egin{aligned} &lpha_n(\omega,t) = ig[lpha(\omega,t)ig]^n, \ &lpha(\omega,t) = lpha_1(\omega,t) \ &= rac{1}{g(\omega)}\int_0^{2\pi}f( heta,\omega,t)e^{-i heta}d heta. \end{aligned}$$

$$egin{aligned} &rac{\partiallpha^n}{\partial t} = nlpha^{n-1}rac{\partiallpha}{\partial t} = -in\Big(\omega+k_E(1-\operatorname{Re} z)-k_I(1-\operatorname{Re} ilde z)\Big)lpha^n+rac{i}{2}nig(lpha^{n-1}+lpha^{n+1}ig)\ &rac{\partiallpha}{\partial t}(\omega,t) = -i\Big(\omega+k_Eig(1-\operatorname{Re} z(t)ig)-k_Iig(1-\operatorname{Re} ilde z(t)ig)\Big)lpha(\omega,t)+rac{i}{2}ig(1+lpha^2(\omega,t)ig). \end{aligned}$$

$$\int_{-\infty}^{\infty} g(\omega)\alpha(\omega,t)d\omega = \int_{-\infty}^{\infty} \int_{0}^{2\pi} f(\theta,\omega,t)e^{-i\theta}d\theta d\omega$$
$$= z^{*}(t).$$

$$g(\omega) = rac{\Delta}{\pi} rac{1}{(\omega - \omega_0)^2 + \Delta^2} = rac{\Delta}{\pi} rac{1}{(\omega - \omega_0 + i\Delta)(\omega - \omega_0 - i\Delta)}$$



$$\begin{split} z^*(t) = & \int_{-\infty}^{\infty} \frac{\Delta}{\pi} \frac{1}{(\omega - \omega_0 + i\Delta)(\omega - \omega_0 - i\Delta)} \alpha(\omega, t) d\omega \\ = & -2i\pi \operatorname{Res} \left[ \frac{\Delta}{\pi} \frac{\alpha(\omega, t)}{(\omega - \omega_0 + i\Delta)(\omega - \omega_0 - i\Delta)} \right]_{\omega = \omega_0 - i\Delta} \\ & - \lim_{R \to \infty} \int_{0}^{-\pi} \frac{\Delta}{\pi} \frac{\alpha(Re^{i\varphi}, t)}{R^2 e^{2i\varphi} \left(1 + \mathcal{O}\left(\frac{1}{R}\right)\right)} iRe^{i\varphi} d\varphi \end{split}$$

$$=-2i\pi \left[rac{\Delta}{\pi}rac{lpha(\omega_0-i\Delta,t)}{(-2i\Delta)}
ight]+0$$
  
 $=lpha(\omega_0-i\Delta,t).$ 

$$egin{aligned} \dot{z} &= iig(\omega_0 + i\Delta + k_E(1-\operatorname{Re}z) - k_I(1-\operatorname{Re} ilde{z})ig)z - rac{i}{2}ig(1+z^2ig),\ \dot{ ilde{z}} &= iig( ilde{\omega}_0 + i ilde{\Delta} + ilde{k}_E(1-\operatorname{Re}z) - ilde{k}_I(1-\operatorname{Re} ilde{z})ig) ilde{z} - rac{i}{2}ig(1+ ilde{z}^2ig). \end{aligned}$$

 $\lim_{\mathrm{Im}\,\omega\to-\infty}\alpha(\omega,t)=0$ 

$$\frac{\partial |\alpha|}{\partial t}(\omega,t) = \operatorname{Im} \omega \cdot \left| \alpha(\omega,t) \right| - \frac{1 - |\alpha(\omega,t)|^2}{2} \operatorname{sen} \psi(\omega,t),$$

$$egin{aligned} \phi(t) &= \int_{-\infty}^{\infty} f( heta, \omega, t) v( heta, \omega, t) \Big|_{ heta = \pi} d\omega, \ ilde{\phi}(t) &= \int_{-\infty}^{\infty} \widetilde{f}( heta, \omega, t) \widetilde{v}( heta, \omega, t) \Big|_{ heta = \pi} d\omega. \end{aligned}$$





How did we get interested In sleeping birds...

It was the ultimate validation tool: To use the selectivity of the auditory responses to BOS, in order to compare it with the responses to SYN



Amish S. Dave, and Daniel Margoliash Science 2000;290:812-816



Unexpected by-product: Neuronal replay during Undisturbed sleep



The similarity induced to think in terms of "consolidation" (learning and maintenance)

The problem though: How to interpret The patterns which Are not "identical" to the ones used to sing

Amish S. Dave, and Daniel Margoliash Science 2000;290:812-816



### Can we use the activity controlling the periphery to inspect the CNS?



"song" ·••



Once at the level of Activity patterns controlling the Avian vocal organ, we can transduce Activity to behaviour.

The question is: Does the replay reach the muscles?



Patterns controlling The periphery During **song** 



Patterns controlling The periphery During **song** 

The patterns during **sleep** 

We can read the replay From the muscles!



The respiratory patterns Stay at regular rates with No significant fluctuations: (That is the reason there is no sound) Patterns controlling The perisphery During **song: tension** 





We can read the replay In the syringeal muscles!



### Identifying the patterns





High correlation

— Low correlation

### Distribution of the patterns during one night











<sup>0.2</sup> s



Time (s)

With Juan Doppler And Agustin Sanchez

# A technical issue before listening to dreams...



Two time dependent parameters Control many features of the vocalizations: air sac pressure and s.v. tension

# A technical issue before listening to dreams...



Only one parameter participates of the replay: the tension.

Is it a problem?



Instead of adjusting both parameters, We can fit only tension and synthesize Realistic songs

0.04

0.04

J. Neurophys. Boari et al. 2015









This is how a song sounds



This is how a song sounds



This is how a dream "sounds"







Syllables (or gestures) as natural units, altered order... And many practices that do not correlate well with patterns used during song production



And how do these non so well correlated sound like? ... Work in progress !



#### Conclusions

 Periphery as a tool to unveil what happens At the CNS.

2. Variability questions Replaying as a tool for Consolidation.

3. Existence of minimal Natural units. Gestures?

What are they? What Are they for?