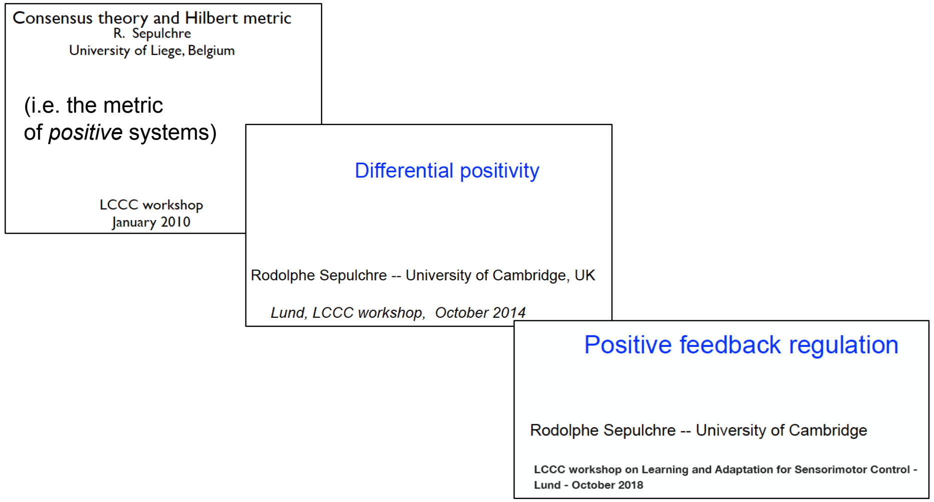
Positive feedback regulation

Rodolphe Sepulchre -- University of Cambridge

LCCC workshop on Learning and Adaptation for Sensorimotor Control - Lund - October 2018

LCCC is a positive environment



Consensus theory and Hilbert metric
R. Sepulchre
University of Liege, Belgium

(i.e. the metric
of *positive* systems)

LCCC workshop
January 2010

Differential positivity

Rodolphe Sepulchre -- University of Cambridge, UK

Lund, LCCC workshop, October 2014

Positive feedback regulation

Rodolphe Sepulchre -- University of Cambridge

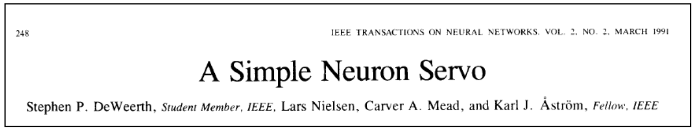
LCCC workshop on Learning and Adaptation for Sensorimotor Control - Lund - October 2018

Take-home message

Positive feedback is essential
to regulation *across scales*

Control across scales by positive and negative feedback,
R.S., Alessio Franci, Guillaume Drion.
Annual Reviews of Control, Robotics, and Autonomous Systems. In press.

Regulation across scales



248 IEEE TRANSACTIONS ON NEURAL NETWORKS, VOL. 2, NO. 2, MARCH 1991

A Simple Neuron Servo

Stephen P. DeWeerth, *Student Member, IEEE*, Lars Nielsen, Carver A. Mead, and Karl J. Åström, *Fellow, IEEE*

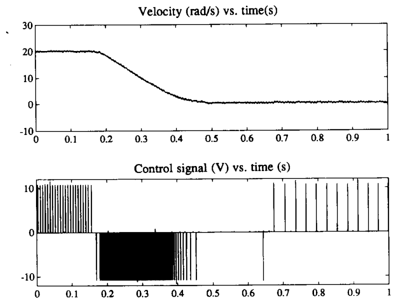


Fig. 4. Step response using neuron servo. The desired velocity is changed from a medium high speed, 20 rad/s, to 0.1 rad/s. The control is obtained by changing the pulse frequency, and the motion continues also at the low speed.

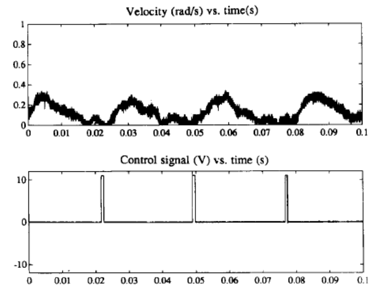


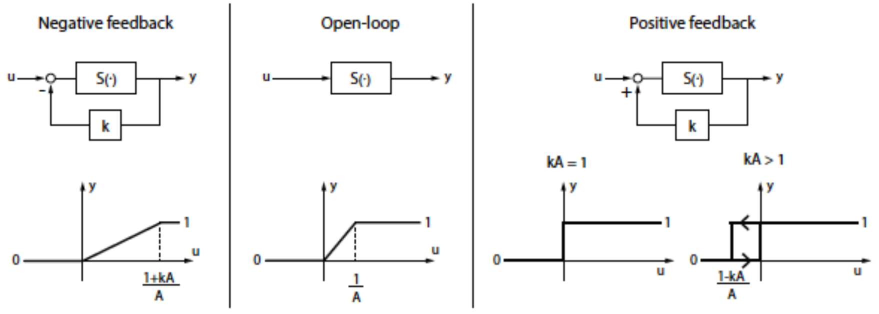
Fig. 5. Experiment with the neuron servo at a velocity 0.1 rad/s, for the dc servo. (The conventional servo does not move in the corresponding situation.) Each pulse moves the servo a bit to create a time-averaged velocity of the desired value.

At low speed, the regulation is *across scales*.

Contents

- Positive and negative feedback regulation
- Positive feedback regulation of bursting
- Positive feedback regulation of the half-center oscillator
- Positive feedback regulation of central pattern generators

A key concept



Infra-sensitive	S-behavior	Ultra-sensitive
(linear-like)	(localised gain)	(switch-like)
(continuous)		(discrete)

Excitability as mixed feedback amplification

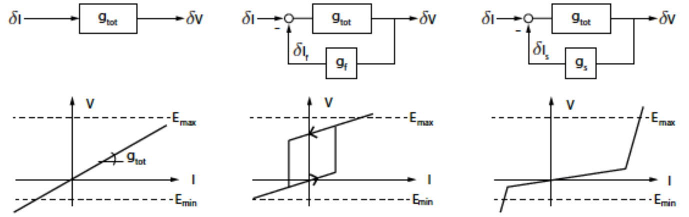
‘First’ positive feedback : ultra-sensitivity, threshold, fast switch.

‘Then’ negative feedback : infra-sensitivity, refractoriness, slow repolarization.

‘ = ’ spike : discrete event triggered by continuous input

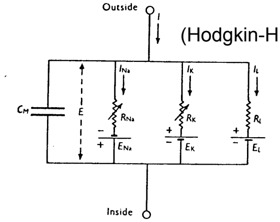
Excitability as mixed feedback amplification

‘instantaneous’ ‘fast’ ‘slow’



activation of
inward current

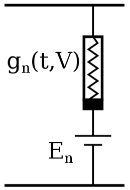
inactivation of
inward current
+
activation of
outward current



(Hodgkin-Huxley, 1952)

Fig. 1. Electrical circuit representing membrane. $R_{Na} = 1/g_{Na}$; $R_K = 1/g_K$; $R_l = 1/\bar{g}_l$. R_{Na} and R_K vary with time and membrane potential; the other components are constant.

Positive feedback = negative conductance



$$I = g(\cdot)(V - E)$$

local gain :

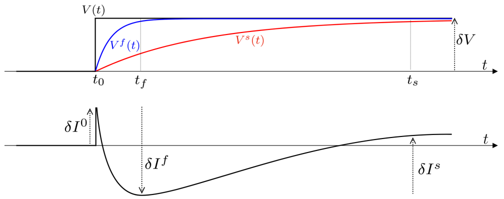
$$\delta I = g(\cdot)\delta V + \delta g(\cdot)(V - E)$$

dynamic !

the (variational) conductance can be transiently negative if

activation $(\delta g(\cdot) > 0)$ of an inward current $(V < E)$

or inactivation $(\delta g(\cdot) < 0)$ of an outward current $(V > E)$



A simplified model of excitability

(Nagumo circuit)

(Relay-feedback system)

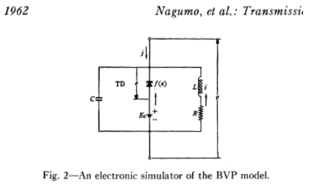
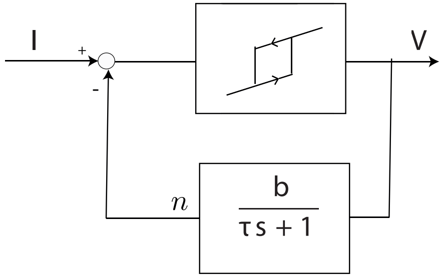

1962 Nagumo, et al.: Transmissi

Fig. 2—An electronic simulator of the BVP model.

$$0 = kV - \frac{V^3}{3} - n + I$$

$$\tau \dot{n} = -n + bV$$



The capacitor is neglected and the fast positive feedback is approximated as instantaneous

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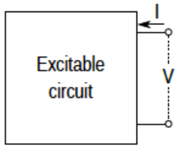
Excitability as mixed feedback amplification

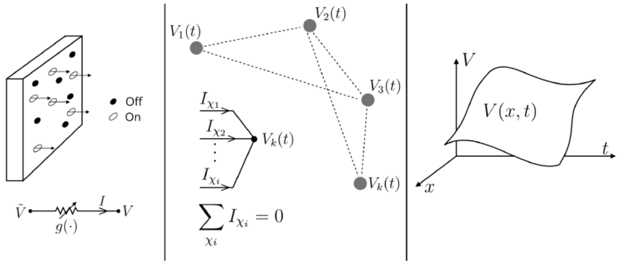


‘First’ positive ‘then’ negative feedback ‘ = ’ spike

No ultra-sensitivity without positive feedback

Does this scale up ?

An electrical model across scales



micro-scale

macro-scale

Current types	Nodal	Network
Passive	$\bar{g}\ (V_k - E)$	$\bar{g}\ (V_k - V_l)$
Active	$g(V_k^f, V_k^s)\ (V_k - E)$	$g(V_l^f, V_l^s)\ (V_k - E)$

Active nodal currents provide positive or negative feedback.

Active network currents are excitatory or inhibitory.

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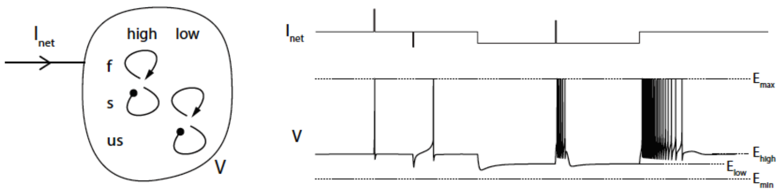
Bursting as two mode excitability

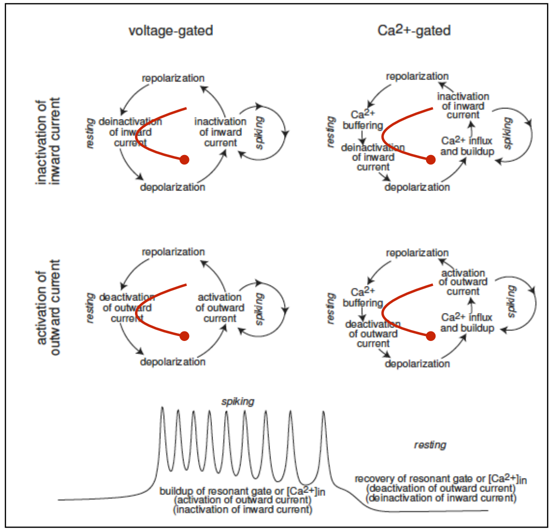


Two independent positive feedback loops mean two independent thresholds : high/fast and low/slow

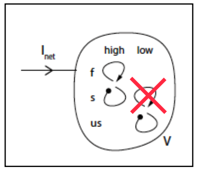
A burst is a spike of spikes. Two independent negative feedback loops mean independent regulation of intra-burst refractoriness and inter-burst refractoriness.

Input-output behavior is *spike* excitable or *burst* excitable depending on the neuron polarization.

A (widely accepted) textbook model of bursting



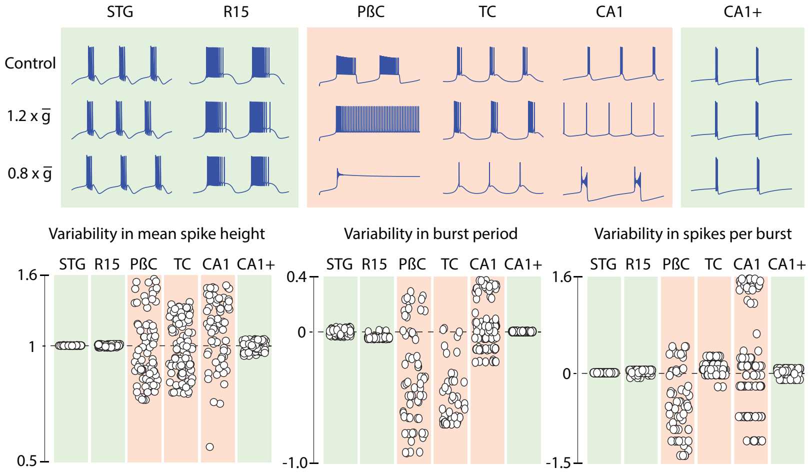
Izhikevich, Chapter 9
Terman and Ermentrout, Chapter 5
Keener and Sneyd, Chapter 9



(Izhikevich, 2008, p.330)

Bursting = negative feedback adaptation of spiking.

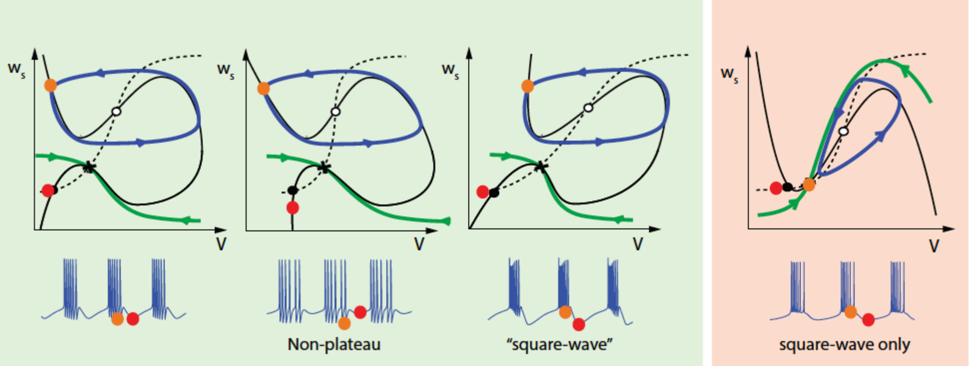
A burster is fragile without slow positive feedback



Five published models of bursting.
The red ones lack slow positive feedback.
The model CA1+ is the model CA1 with slower calcium activation.

(Franci, Drion, RS, 2018)

A burster is rigid without slow positive feedback

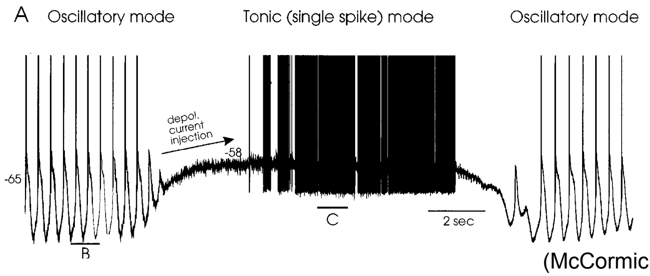


tunable

rigid

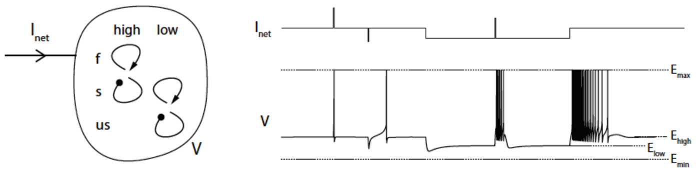
(Franci, Drion, RS, 2018)

The slow positive feedback is the key regulator of transitions between "on" and "off" modes

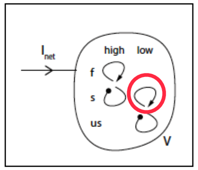


(McCormick & Bal, 1997)

A cellular regulation fundamental to brain 'states' (arousal, attention, …)
A key target for neuromodulation.



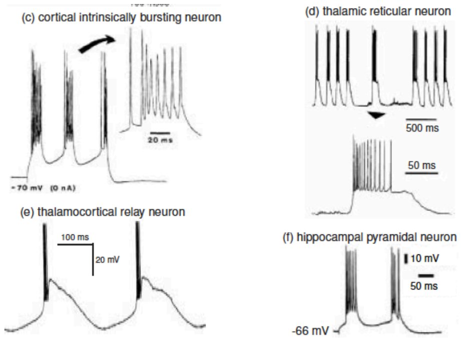
Positive feedback regulation of bursting



No distinction between high/fast and low/slow threshold without two independent positive feedback loops

The low/slow positive feedback is essential to make bursting

- *robust* (with respect to parameter uncertainty)
- *tunable* (many types of bursters)
- *neuromodulable* (transitions between spiking and bursting)
- *tractable* (three time-scale analysis)



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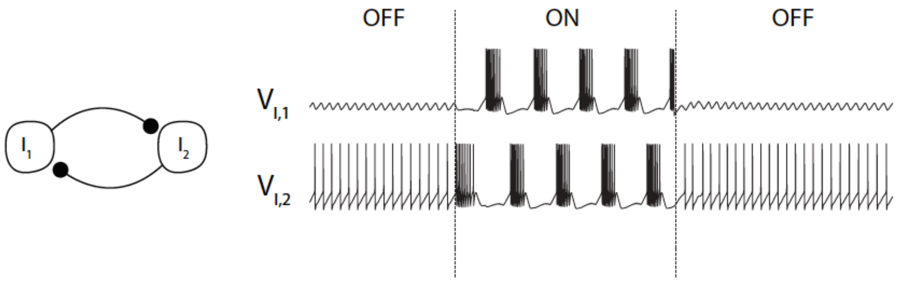
The half-center oscillator: a fundamental motif of clock control

(Brown, 1911 !)

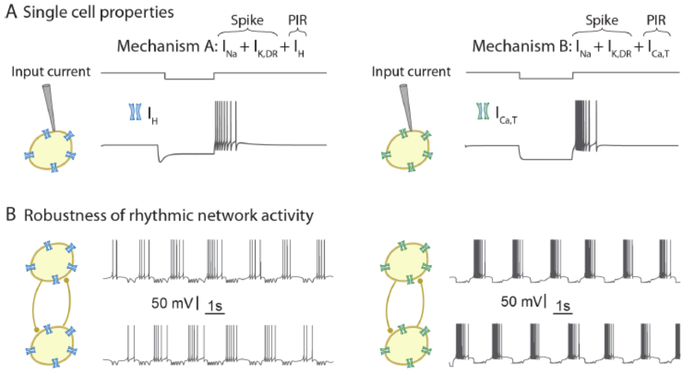


cellular behavior network behavior

The on-off control is through the maximal conductance of the slow positive feedback current *only*. No change in (synaptic) coupling parameters.

A long debated question

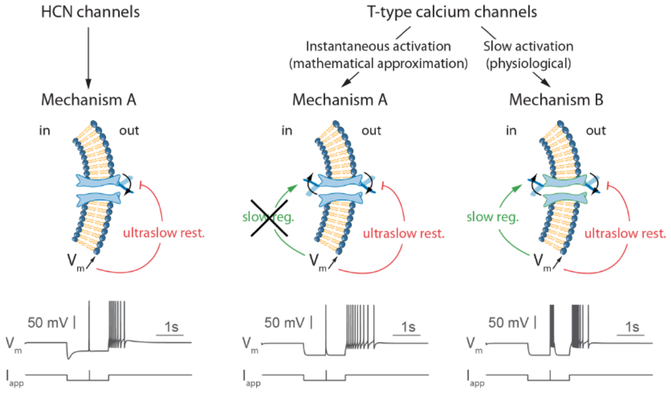
Which currents contribute to the post-inhibitory rebound ?
In particular, I_h versus $I_{Ca,T}$?



(Dethier, Drion, Franci, RS, 2015)

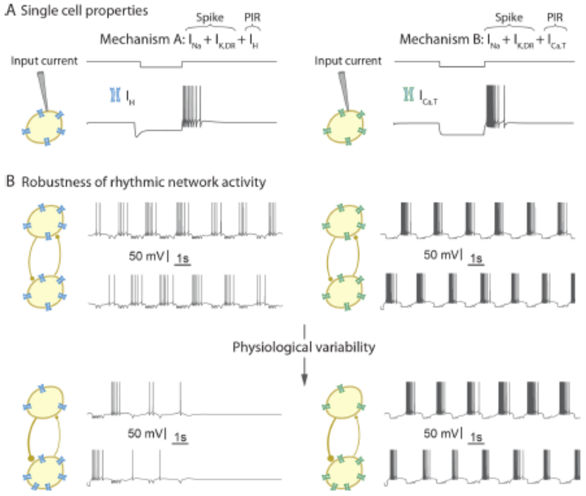
The feedback properties of the two currents differ strikingly

Only the *slow activation of* $I_{Ca,T}$ contributes to
the low/slow positive feedback regulation of the behavior



(Dethier, Drion, Franci, RS, 2015)

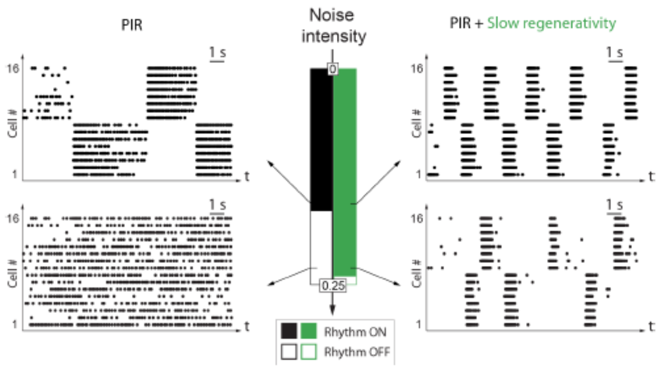
The PIR is fragile without positive feedback



A hidden example of positive feedback regulation

(Dethier, Drion, Franci, RS, 2015)

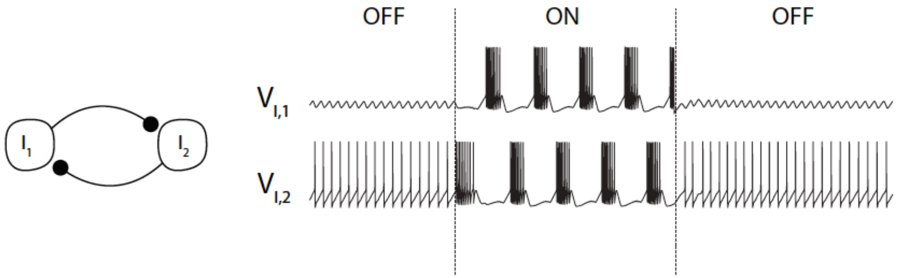
Cellular positive feedback is essential to network behavior



- robust to noise, parameter uncertainty, and network heterogeneity
- tunable by synaptic coupling (e.g. network frequency)

(Dethier, Drion, Franci, RS, 2015)

Positive feedback regulation of the half-center oscillator



A cellular mechanism for network control.

Fundamental to tunability, robustness, and control of the network behavior.

An example of regulation *across* scales.

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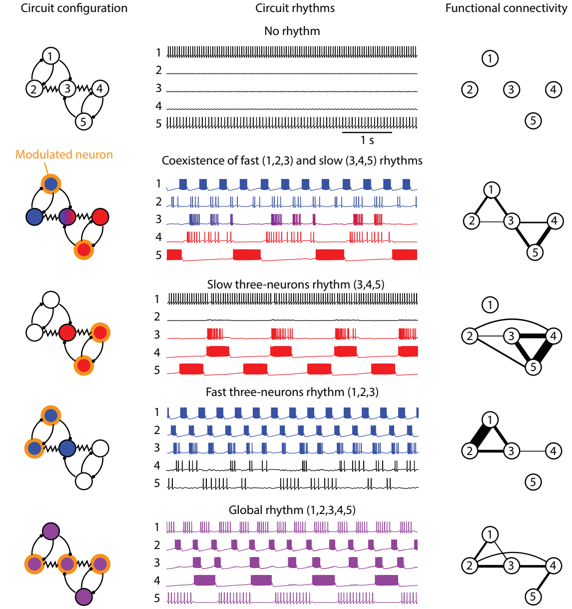
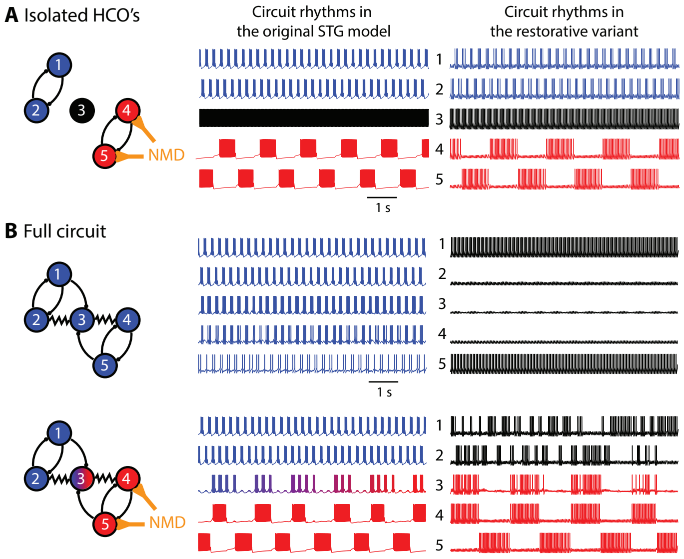
Central pattern generators as interconnected half-center oscillators



Cellular control of functional connectivity. No synaptic tuning involved.

(Drion, Franci, RS, 2018)

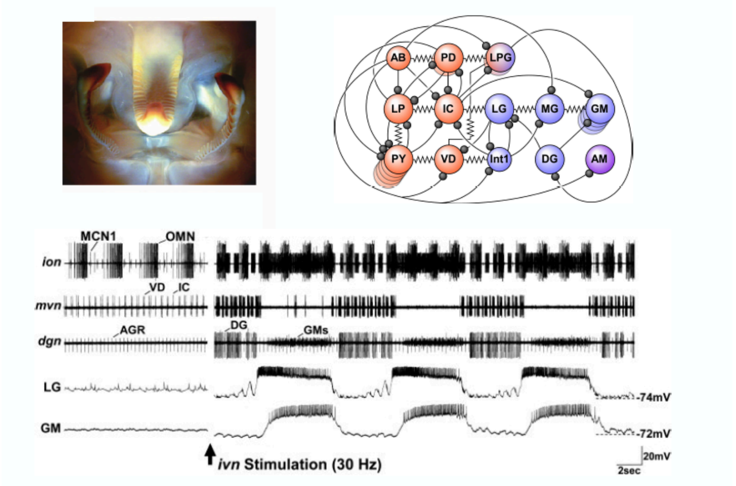
Regulation across scales is lost without the cellular positive feedback



(Drion, Franci, RS, 2019)

Positive feedback regulation of central pattern generators

One step closer to a tractable model of one of the most extensively studied central pattern generators : co-regulation of pyloric and gastric rhythms in the STG.



(Marder and Bucher, 2007) (Christie et al., 2004)

Conclusions

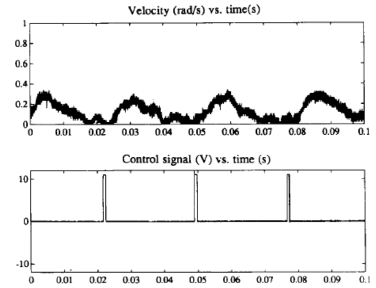


Fig. 5. Experiment with the neuron servo at a velocity 0.1 rad/s, for the dc servo. (The conventional servo does not move in the corresponding situation.) Each pulse moves the servo a bit to create a time-averaged velocity of the desired value.

- Positive feedback is essential to regulation across scales.
- Why? because it regulates ultra-sensitivity and thresholds.
- The role of positive feedback regulation is poorly understood and often neglected both in control and in neurophysiology.
- No *learning* across scales without positive feedback ?