Multiscale organization and modeling of cerebellum

insights and perspectives for motor learning and control

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High performance in skilled movements requires the cerebellum

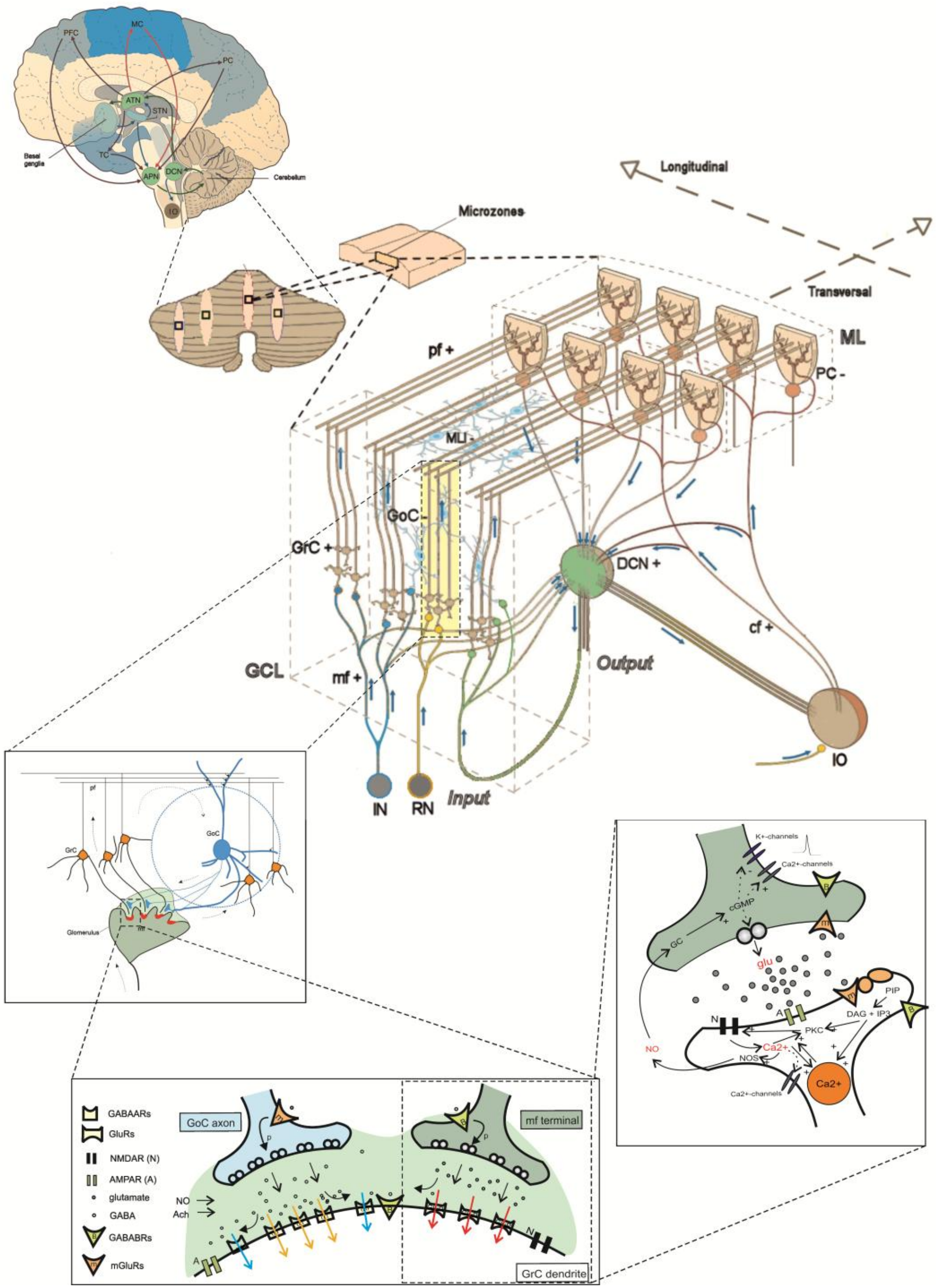
→*Real -time high-speed control of movement requires special circuit properties. In the brain this control is performed in circuit loops involving the* ***cerebellum***

→*The* ***cerebellum*** *learns to predict the sensory consequences of a motor action*

→*The* ***cerebellum*** *performs high-order correlations among spatio-temporally organized activity patterns*

In the example of the pianist, the over 600 mucles of the body are corrdinated in highly ordered sequences under multisenorail control. The sequences have been learned and optimized through a trial-and-error process. The system is highly automatized and make s the pianist free to concentrate on the interpretation .

The when, what and how of cerebellum



…….

*While the cerebellum has been classically associated to the control of movement and its pathological counterpart, **ataxia**, it has recently been related also to **cognitive processing** and supposed to be involved in **autism, dyslexia, multiple sclerosis and Alzheimer disease** just to mention some. And it could also be specifically involved in epilepsy !*

…….

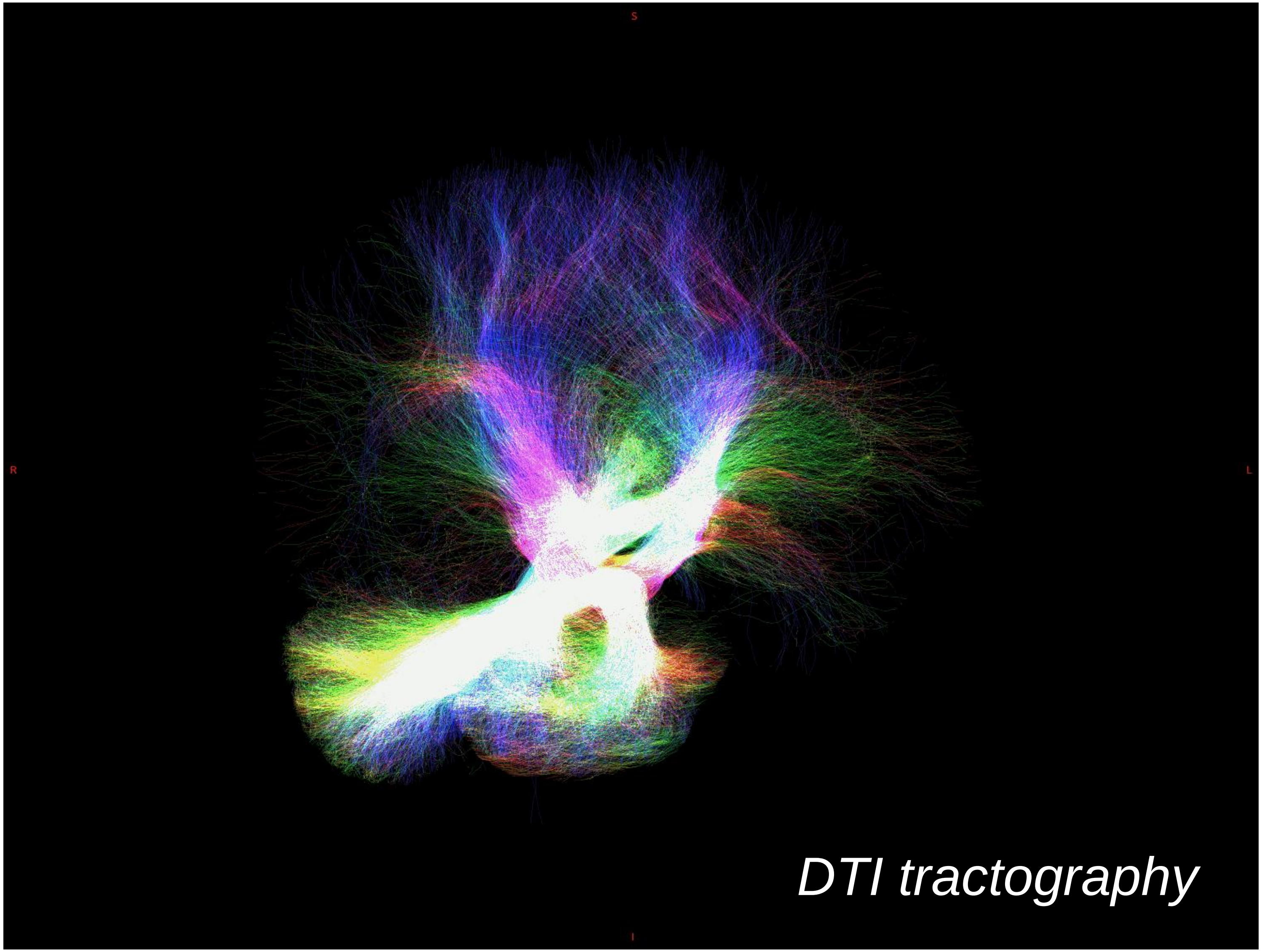
*The way of understanding the **when, what and how** of cerebellum is changing ! Not just a motor structure but one that integrates in major brain loops involved in a variety of functions and pathologies.*

……..

→There is a urge to represent the cerebellum at different levels and to integrate it into large-scale brain models !!

The cerebellum is deeply interconnected to cerebral cortex

>80% tracts to/from associative areas
<20% tracts to/from motor areas



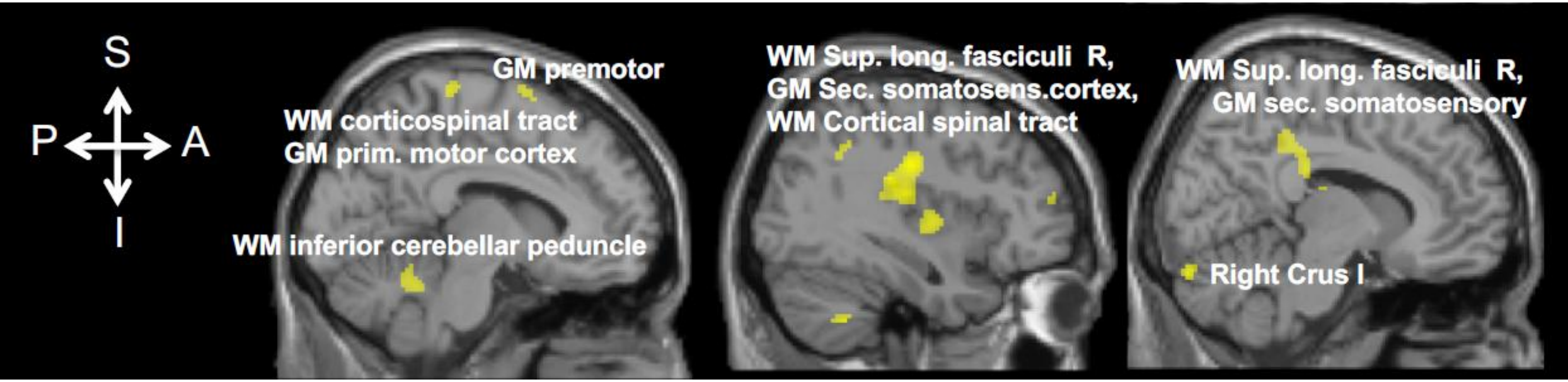
Graphical elaboration - Courtesy of Nick Rolandi

Palesi F, De Rinaldis A, Castellazzi G, Calamante F, Muhlert N, Chard D, Tournier JD, Magenes G, D'Angelo E, Gandini Wheeler-Kingshott CAM. **Sci Rep. 2017**

The cerebellum is engaged in sensori-motor tasks (finger tapping)

WHEN

*The task employed in this initial experiment was indeed demanding: 1 min of **self-paced finger taping** requires motor planning and concentration.*
***GM - M1 (BA4) ... BA2 … BA6… anterior cerebellum … Crus I/II**, **lobule VI**, and **lobule VIIIa**,*
***WM**, - **CST … superior longitudinal fasciculus … CC**.*



frontiers in Neuroscience

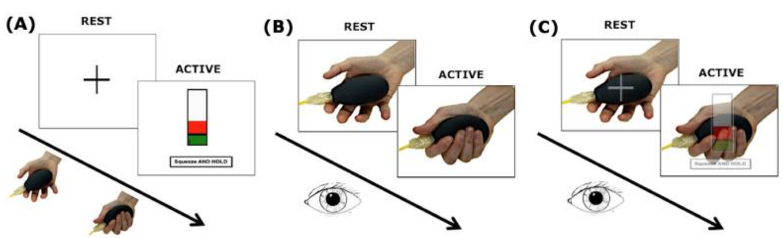
PERSPECTIVE
published: 09 November 2018
doi: 10.3389/fnins.2018.00810

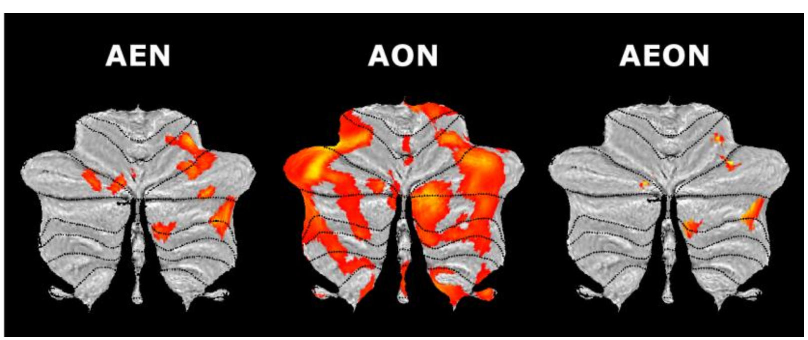
Challenges and Perspectives of Quantitative Functional Sodium Imaging (fNaI)

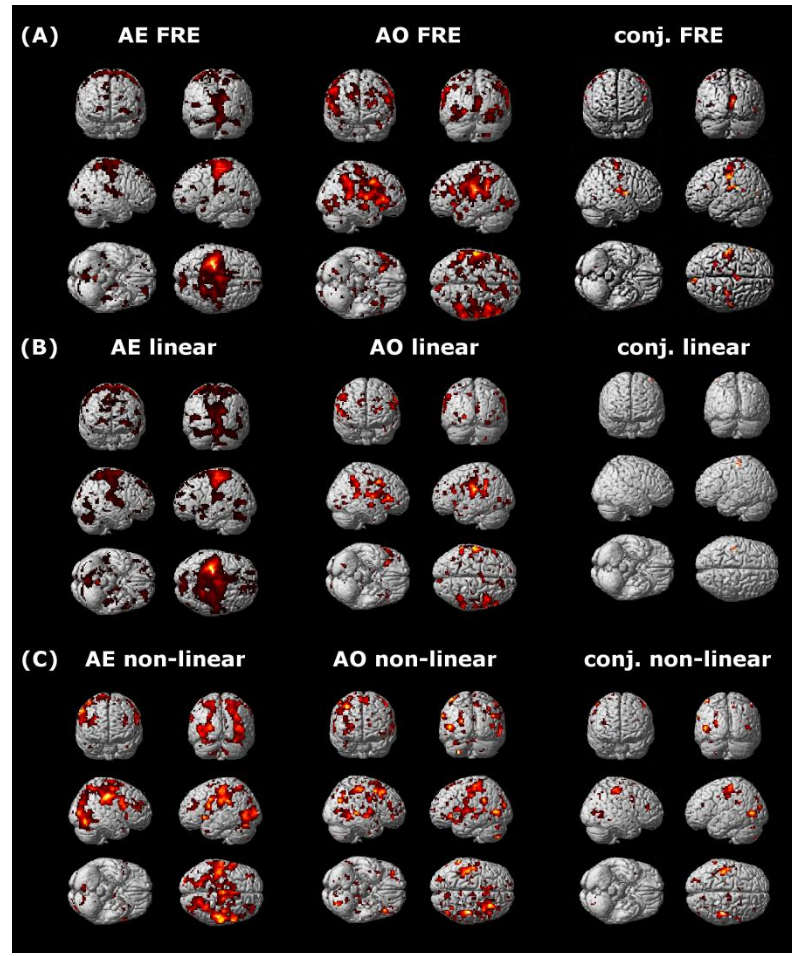
Claudia A. M. Gandini Wheeler-Kingshott[1,2,3*†], Frank Riemer[1,4†], Fulvia Palesi[5], Antonio Ricciardi[1,6], Gloria Castellazzi[1,7], Xavier Golay[8], Ferran Prados[1,6,9], Bhavana Solanky[1] and Egidio U. D'Angelo[2,10]

The cerebellum is engaged in both sensori-motor and cognitive tasks

task-dependent fMRI (AEON "mirror" network)





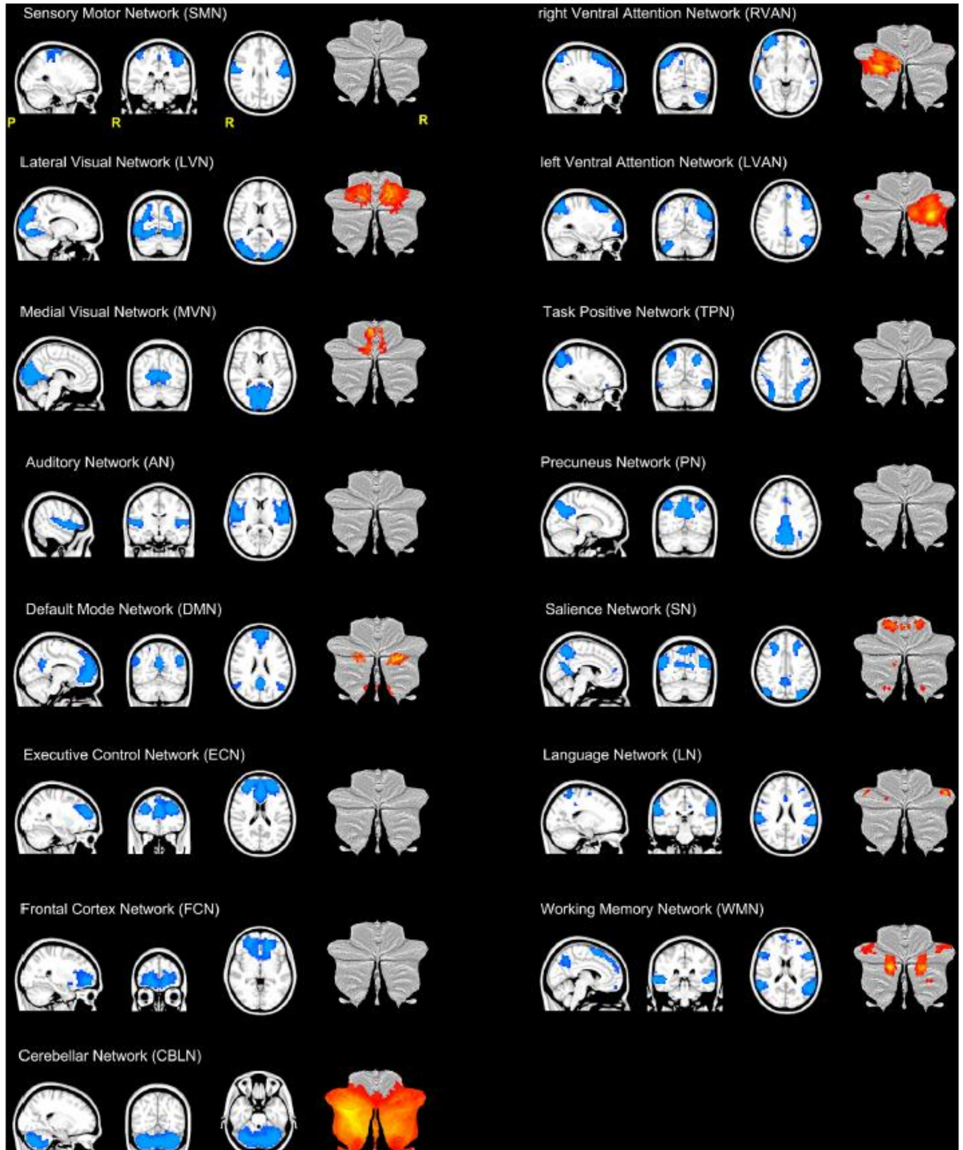


Letizia Casiraghi , Adnan AS Alahmadi, Anita Monteverdi, Fulvia Palesi , Gloria Castellazzi, Giovanni Savini, Karl Friston, Claudia AM Gandini WheelerKingshott , Egidio D'Angelo. **Cerebral Cortex, 2018**,.

The cerebellum is engaged in both sensori-motor and cognitive resting-state networks

Resting-state fMRI – Very-low frequency coherent oscillations

SMN
LVN
MVN
AN
DMN
ECN
FCN
CBLN

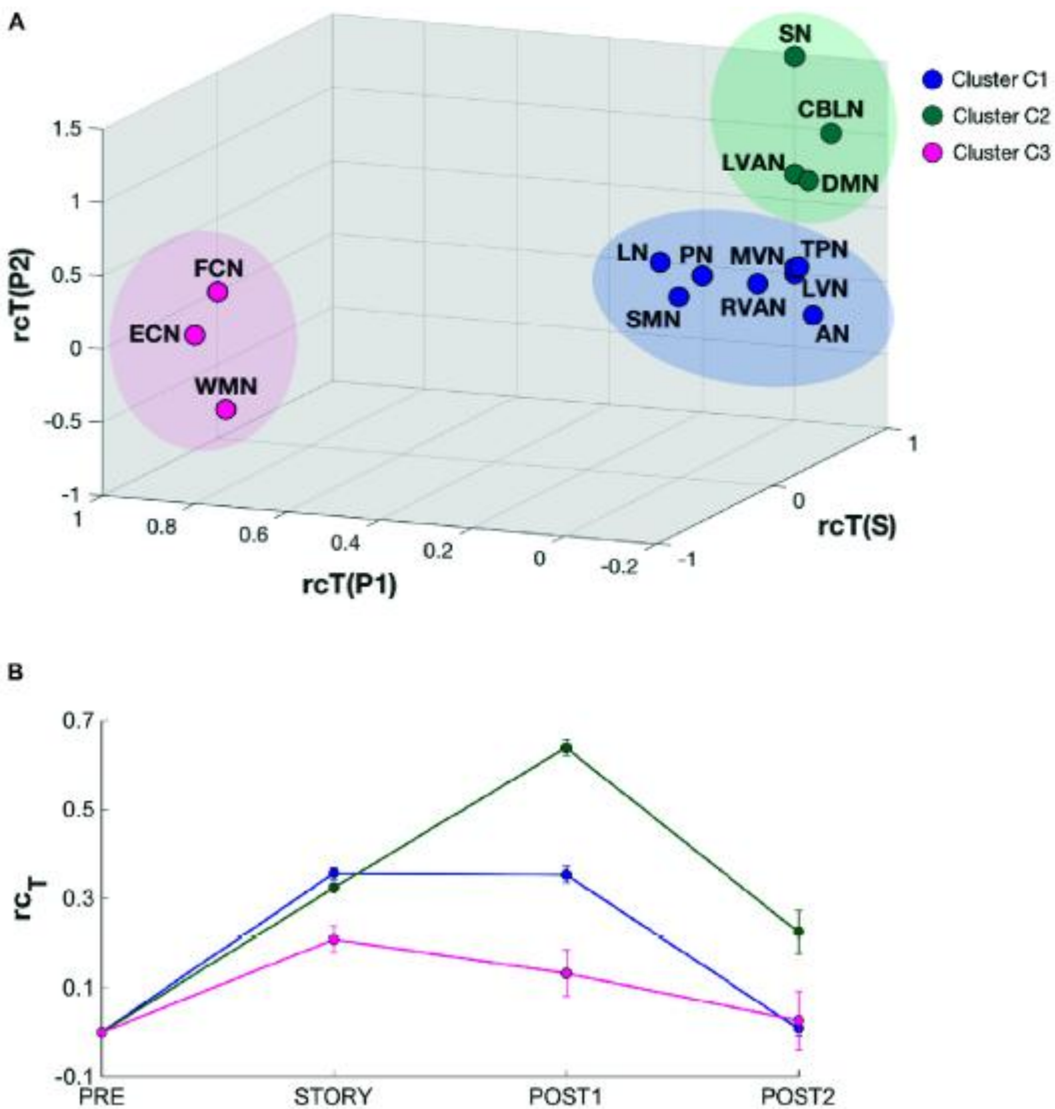


rVAN
lVAN
TPN
AN
SN
LN
WMN

Gloria Castellazzi[1,2,3], Stefania D. Bruno[4], Ahmed T. Toosy[5], Letizia Casiraghi[3,6], Fulvia Palesi[7], Giovanni Savini[3,8], Egidio D'Angelo[3,6†] and Claudia Angela Michela Gandini Wheeler-Kingshott[1,6,9†]*

Front Cell Neurosci, 2018

The cerebellum is engaged in continuous cognitive processing

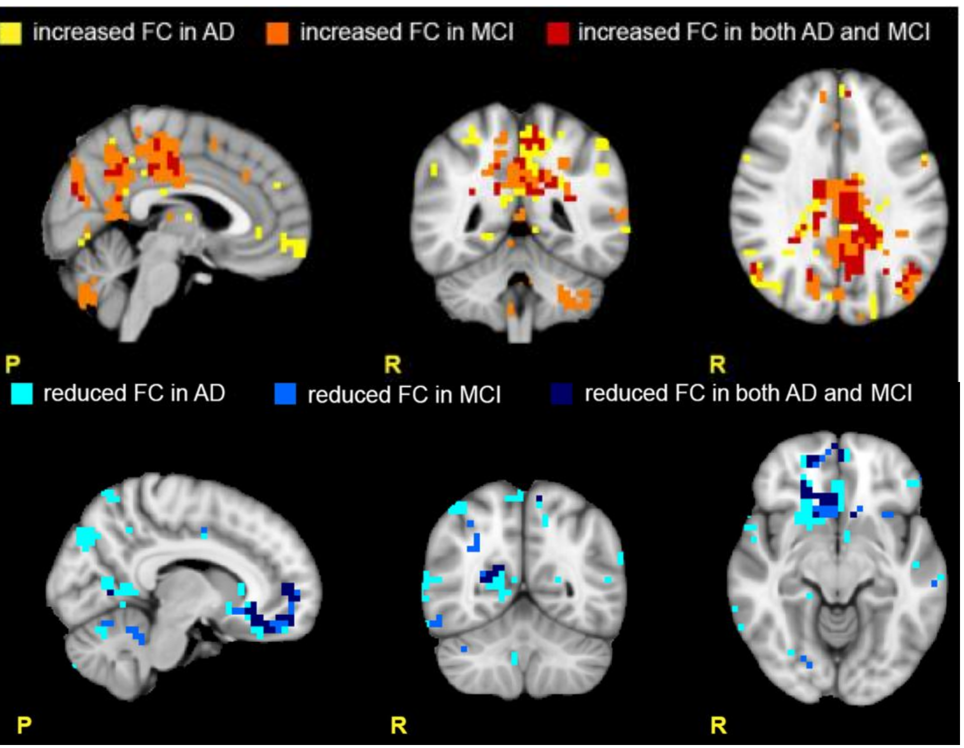


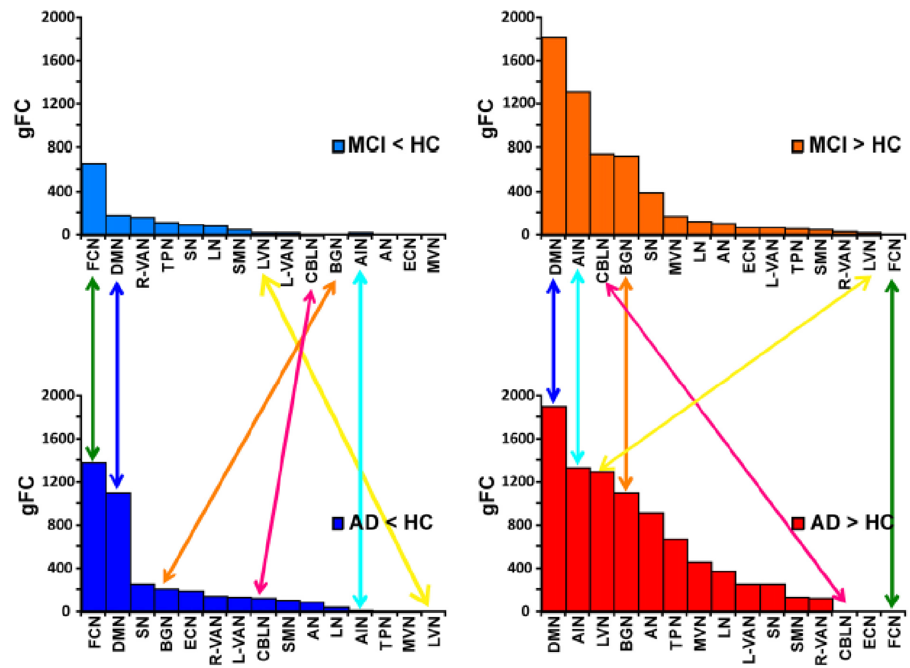
Gloria Castellazzi[1,2,3], Stefania D. Bruno[4], Ahmed T. Toosy[5], Letizia Casiraghi[3,6], Fulvia Palesi[7], Giovanni Savini[3,8], Egidio D'Angelo[3,6†] and Claudia Angela Michela Gandini Wheeler-Kingshott[1,6,9†]*

Front Neurosci, 2018

In MCI and AD, relevant alterations occur in cerebellum functional connectivity

WHEN





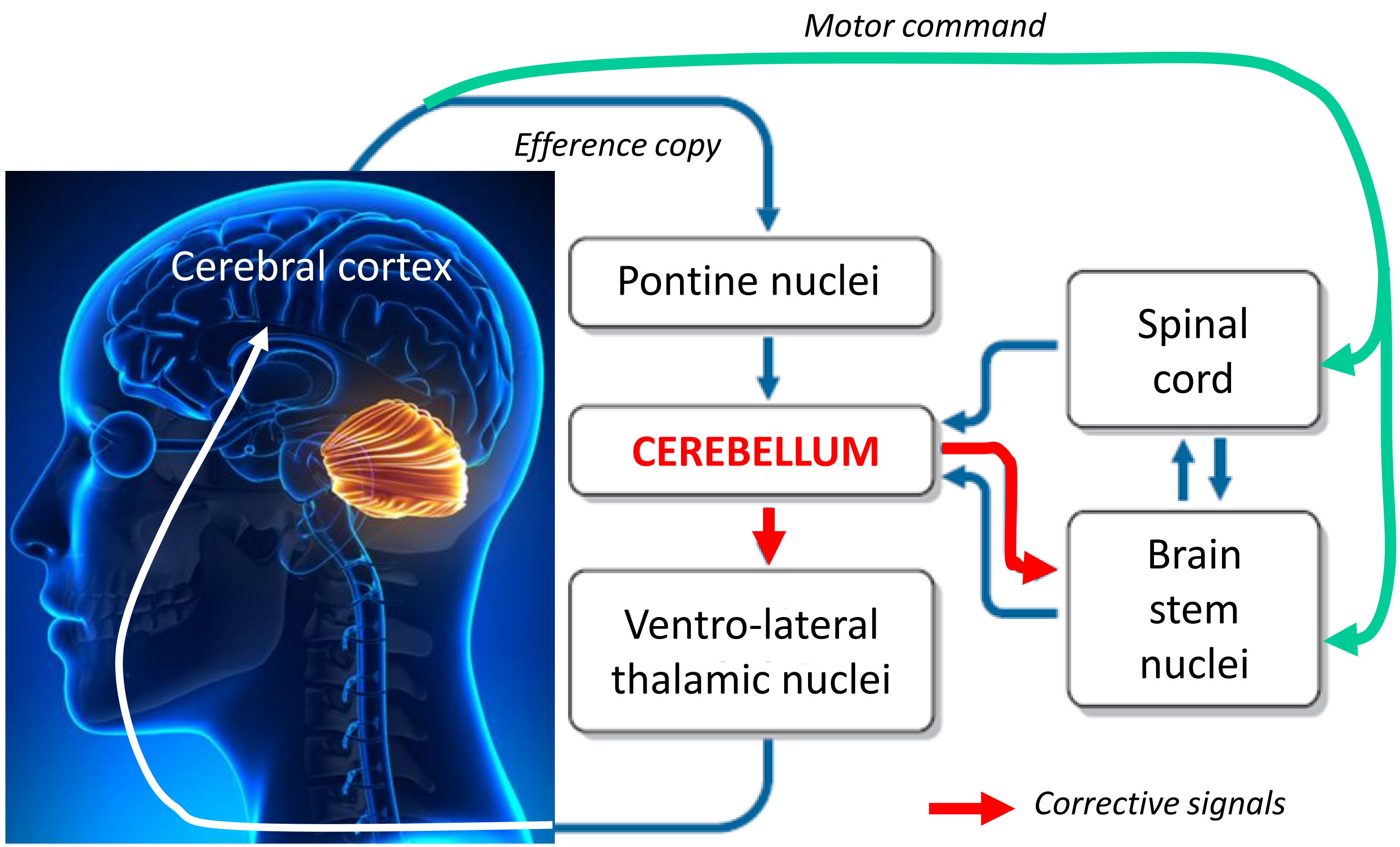
Gloria Castellazzi[1,2], Fulvia Palesi[2,3], Stefano Casali[2,4], Paolo Vitali[5], Elena Sinforiani[6], Claudia A. M. Wheeler-Kingshott[7]* and Egidio D'Angelo[2,4]**

Front Neurosci, 2014

The cerebellum operates both as an inverse and a forward controller

WHAT

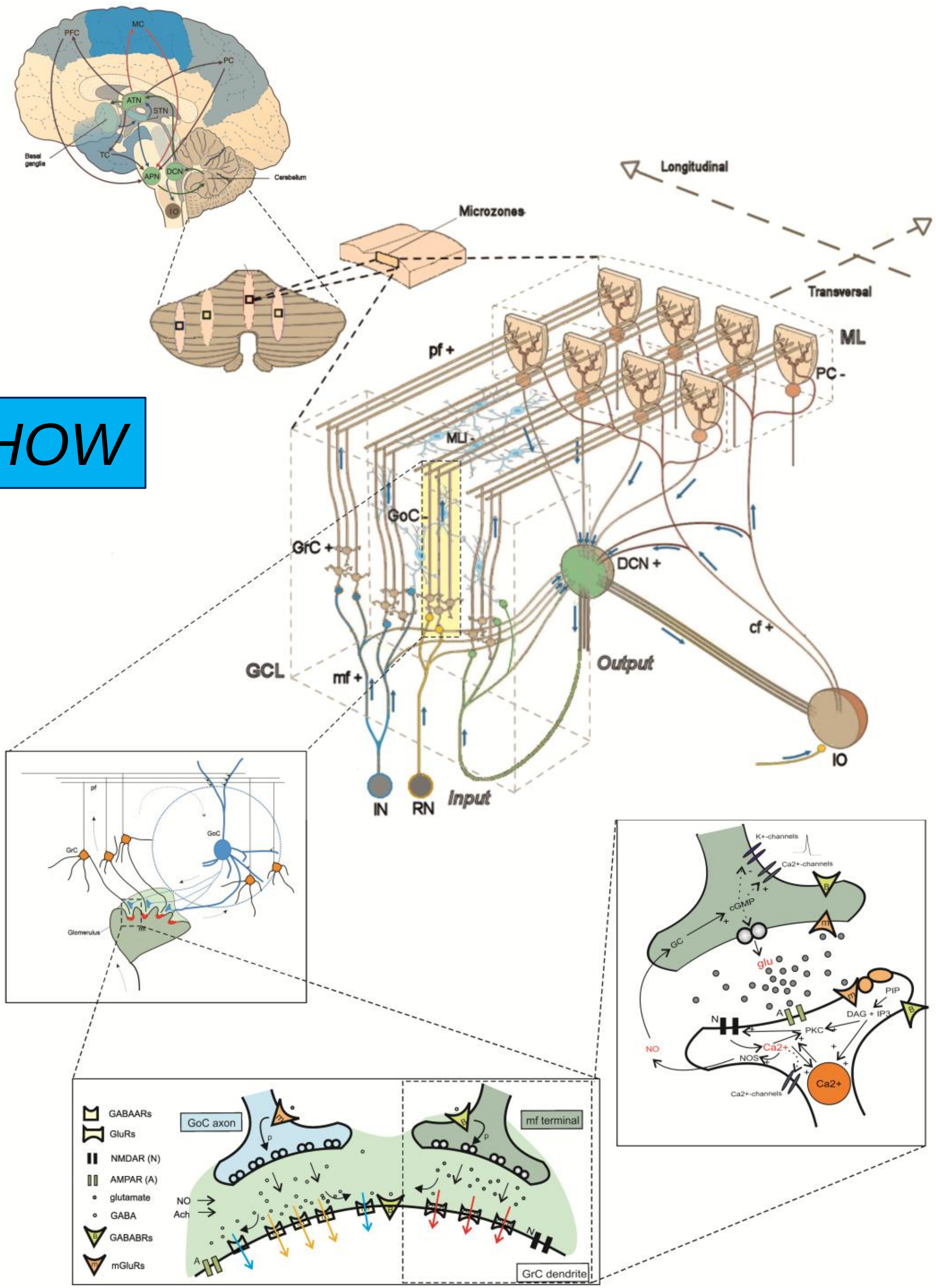
D'Angelo, Hndbooks of Neurology 2018



The cerebellar forward controller is thought *to learn to predict the precise timing of correlated events*. <u>How</u> does the cerebellum do it ?

The cerebellum is organized in modules operating through a generalized computational algorithm

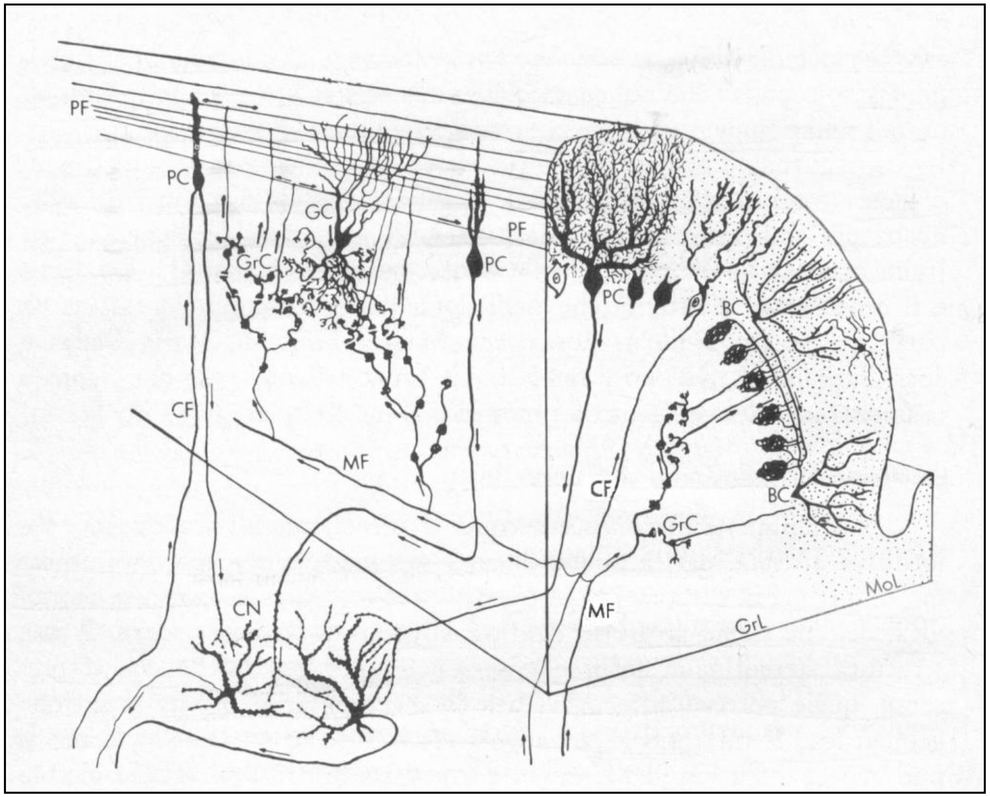
HOW



The generalized algorithm, depending on the brain regions to which a given module is connected, can lead to different behavioral consequences.

D'Angelo et al., 2013, 2016 – **Frontiers in Cellular Neuroscience**

Marr-Albus-Ito develop the Motor Learning Theory predicting that cerebellar learning occurs through plasticity at the PF-PC synapses under CF control



*"For me the most significant property of the cerebellar circuitry would be its plastic ability, whereby it can participate in motor learning, that is the acquisition of skills. This immense neuronal machine with the double innervation of Purkinje cells begins to make sense if it plays a key role in motor learning… **it could be optimistically predicted that the manner of operation of the cerebellum in movement and posture would soon be known in principle"*** **(J.C. Eccles, from the foreword to Ito, 1984).**

But Marr: (D'Angelo, in Ito and Vaina 2016)

!!) does not consider other forms of plasticity

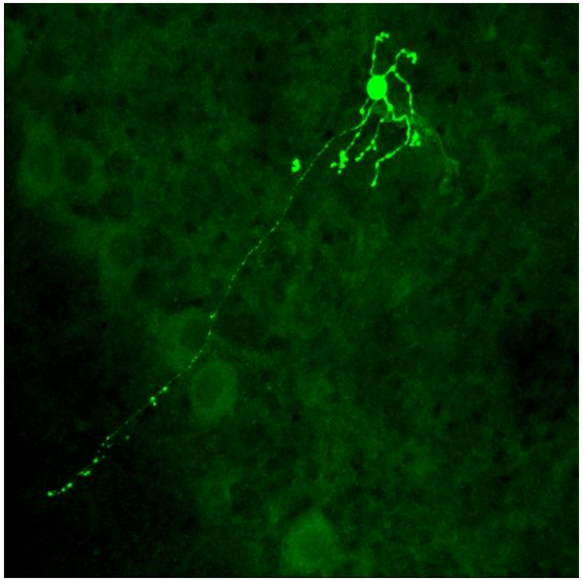
!!) does not consider neuronal firing dynamics and molceular complexity

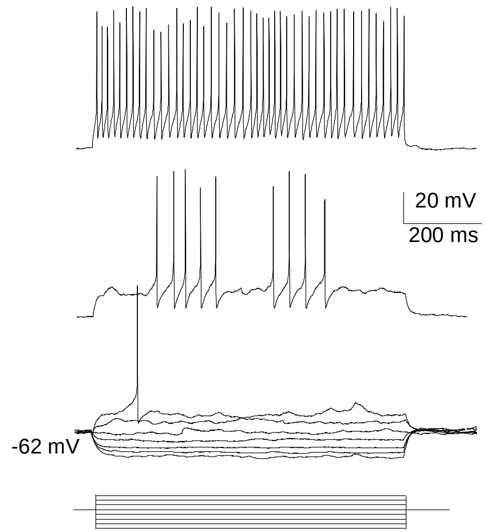
!!) does not consider geometry (only topology and statistics)

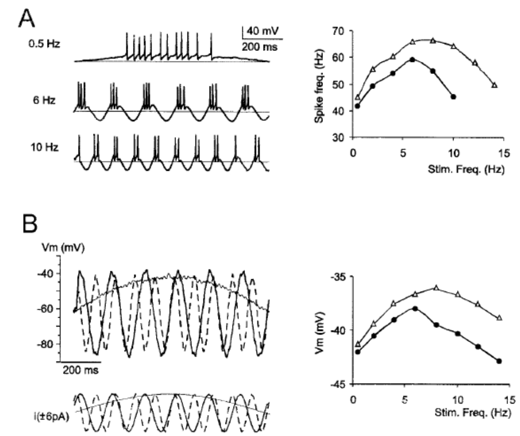
Non-linear neuron properties in the granular layer

D'Angelo et al., 1995, 1998, 2001

Granule cell

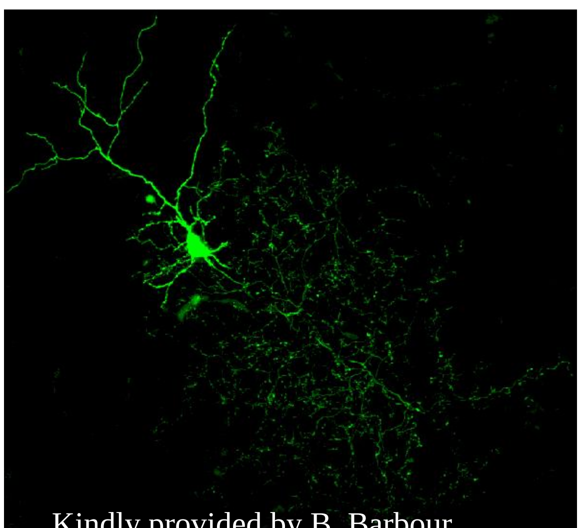


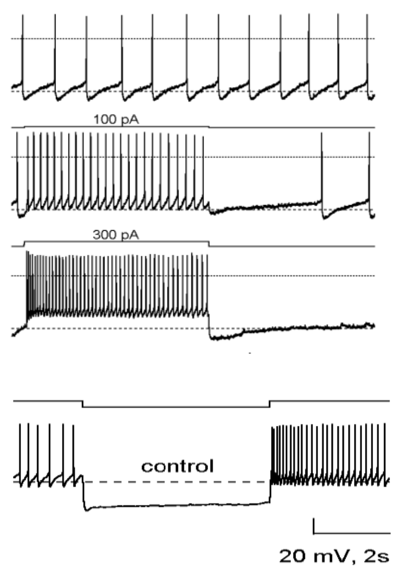


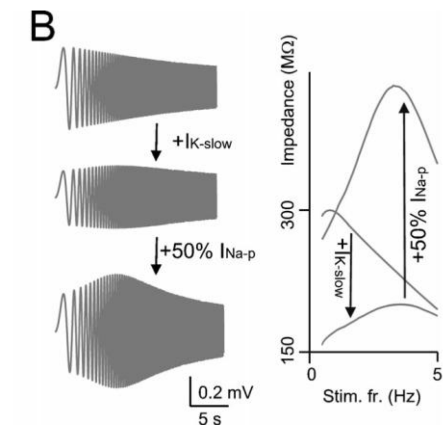


Forti et al., 2006.

Golgi cell

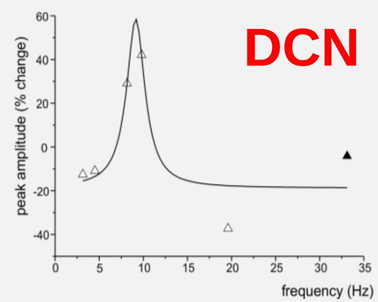




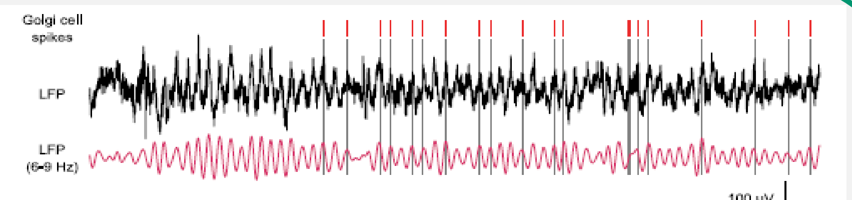


Gandolfi et al, 2013; Solinas et al., 2007; D'Angelo et al., 2001

Theta-band oscillation - resonance - plasticity hypothesis

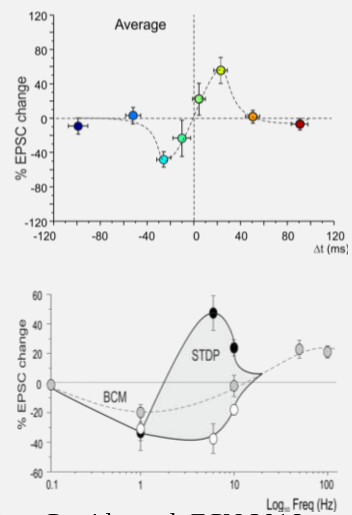


Montagma Mapelli, D'Angelo - submitted



Pellerin & Lamarre, 1997; Hartmann & Bower, 1998; Courtemance et al., 2009).

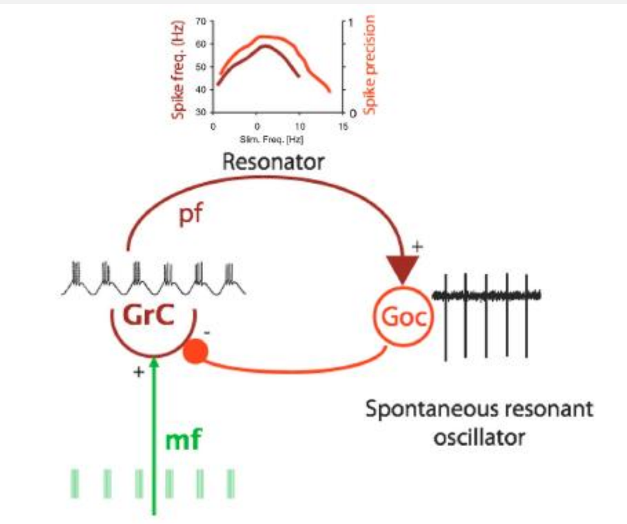
HEBBIAN STDP



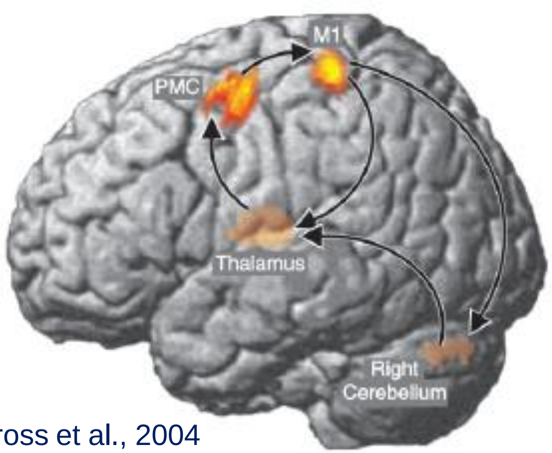
Garrido et al, FCN 2016

Prestori et al., J Neuroci 2017

Granular layer

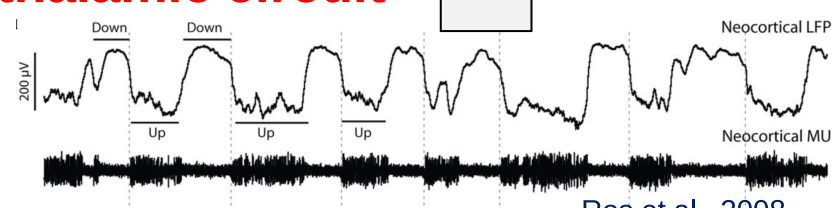


-Theta-band oscillating transmitter: cortico-thalamic system
-Theta-band resonant receiver: granular layer
- Theta-band plasticity encoder



Gross et al., 2004

Cortico-thalamic circuit



Ros et al., 2008

This example shows complex and multiple properties of neurons, whose understanding requires integration into realistic <u>models</u> considering:

1) ***Detailed description of microscopic properties***
2) ***Connection of neurons into large-scale networks***

and eventually

3) ***Simplification of models***
4) ***Embedding into large-scale circuits***
5) ***Reconstruciton and analysis of integrated brain signals and functions***

From the lab to models, simulations and back again

REALISTIC MODEL

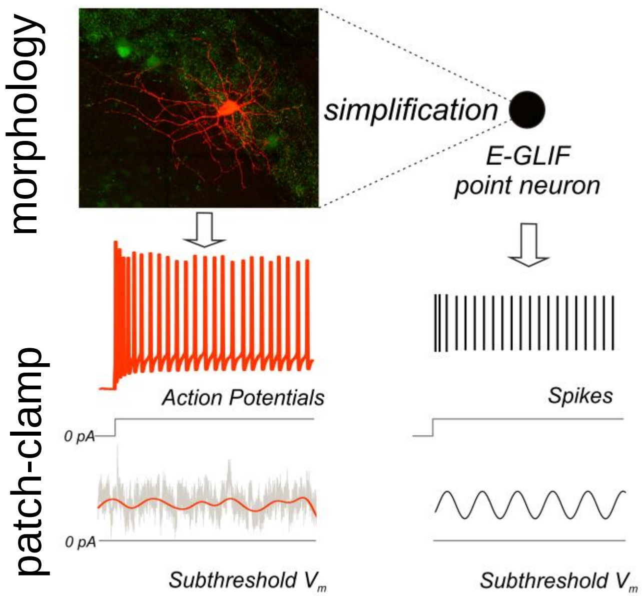
~10^3 compartments
~10^4 ODEs

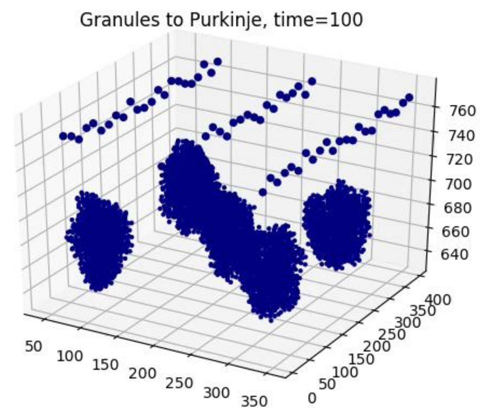
SIMPLIFIED MODEL
EGLIF
1 compartment
3 ODEs

Propagation

NETWORK SIMULATIONS

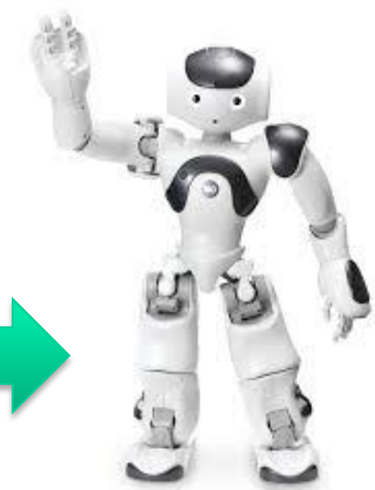
10^6 neurons
10^9 synapses





SCAFFOLD models of microcircuits
pyNEST
pyNEURON

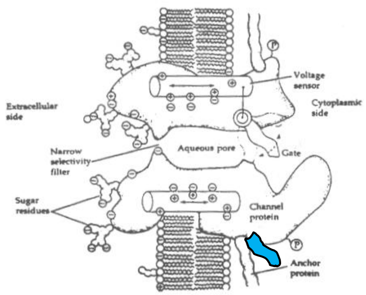
Geminiani et al., 2018; Casellato et al., submitted



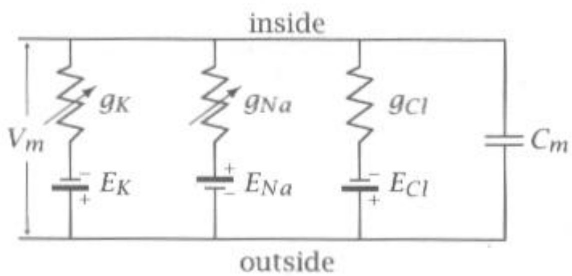
Incorporation into large-scale networks and brain models and robots

EXPERIMENTS

Emergence of elementary properties in ensemble signals and closed-loop behaviors



Realistic neuron models are based on mathematical representations of molecular mechansims (e.g. ionic ionic chanlles and receptors) and neuronal morphology



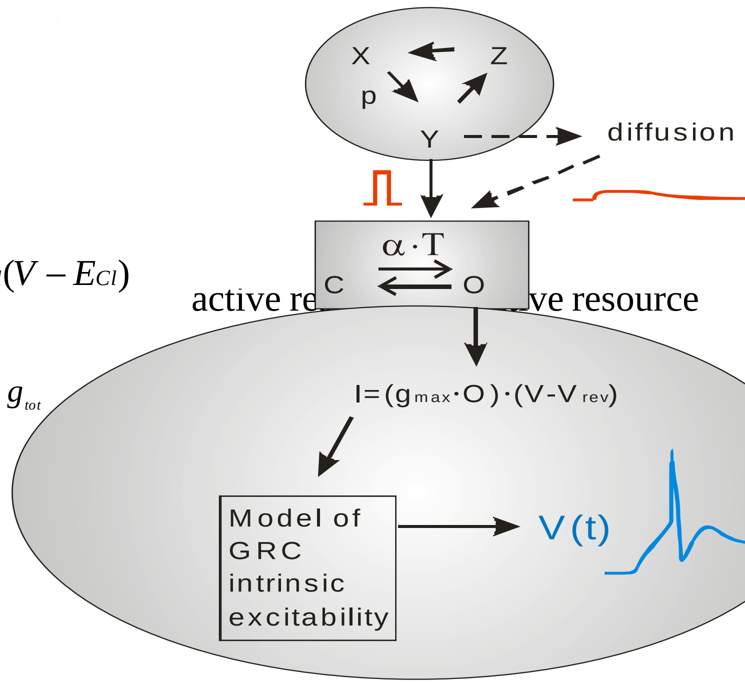
$$I = I_c + I_K + I_{Na} + I_{Cl}$$

$$I = C\frac{dV}{dt} + g_K(V - E_K) + g_{Na}(V - E_{Na}) + g_{Cl}(V - E_{Cl})$$

$$\begin{cases} \dfrac{dV}{dt} = \dfrac{1}{\tau_m}\left(V - \dfrac{\sum_i g_i(V - E_i)}{g_{tot}}\right) \quad \text{dove } \tau_m = R_m / g_{tot} \\ \dfrac{dy_i}{dt} = \alpha_i - (\alpha_i + \beta_i) y_i \end{cases}$$

$$g_i = g_i^{\max} y_{i-att}^{n} y_{i-inatt}^{m}$$

$$\alpha_i, \beta_i = f(V, t)$$



$$\frac{dx}{dt} = \frac{z}{\tau_{REC}} - u \cdot x \cdot \delta(t - t_{SPIKE})$$

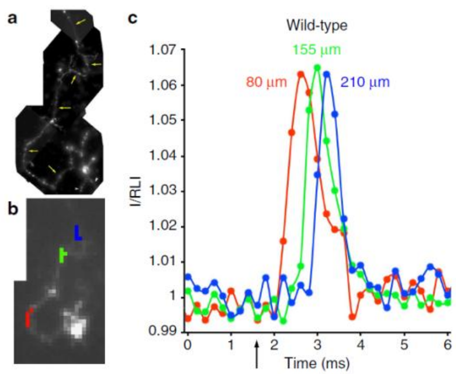
$$\frac{dy}{dt} = -\frac{y}{\tau_1} + u \cdot x \cdot \delta(t - t_{SPIKE})$$

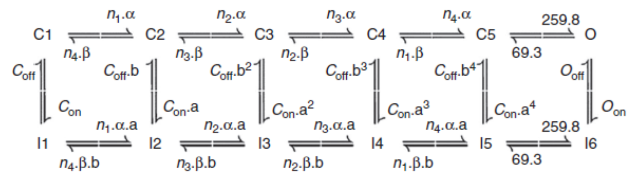
$$\frac{dz}{dt} = \frac{y}{\tau_1} - \frac{z}{\tau_{REC}}$$

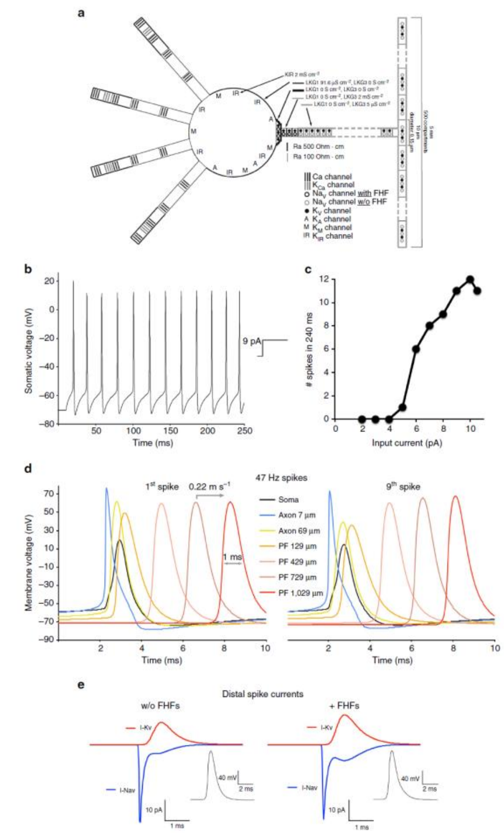
$$\frac{du}{dt} = -\frac{u}{\tau_{FACIL}} + U \cdot (1 - u) \cdot \delta(t - t_{SPIKE})$$

D'Angelo et al., J Neurosci 2001, 2013

Spike initiation and propagation in granule cell axon







Detailed description and hypothesis on ionic current dynamics . D'Angelo e al. (1998) **J Neurophys**

BUT: One channel is missing !

FIRST granuel cell models in NEURON . D'Angelo e al. (2001) **J Neurosci**

BUT: AP amplitude does not match !!

Na channel kinetics, localization, modulation. Magistretti et al. (2006) J Physiol; Goldfarb et al., (2007) **Neuron**

BUT: AP propagation does not match !!

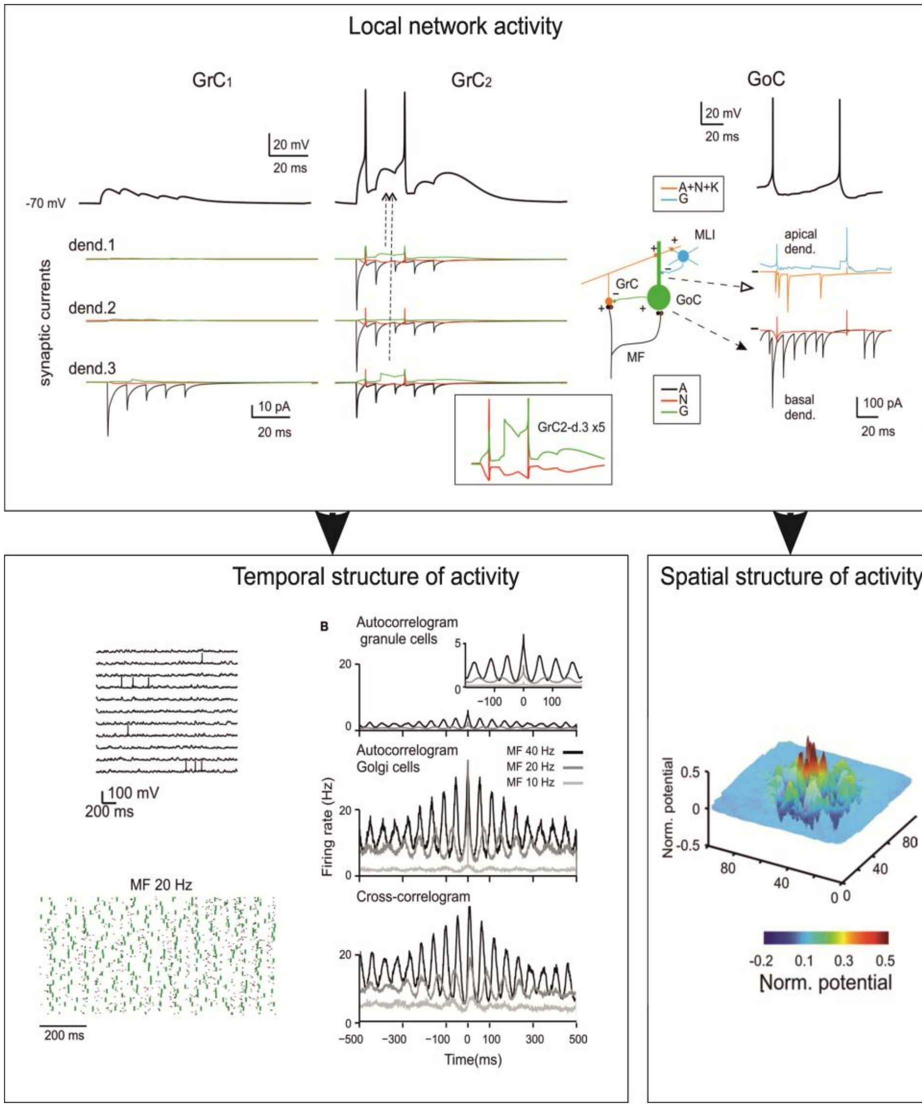
Na channel modulation by FHF in the axon Dover et al. (2016) **Nature**

BUT: Granule cell discharge shows a richness of patterns

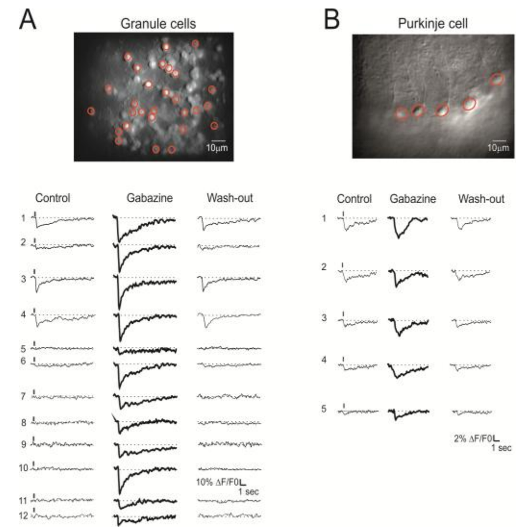
Another channel is missing !!!

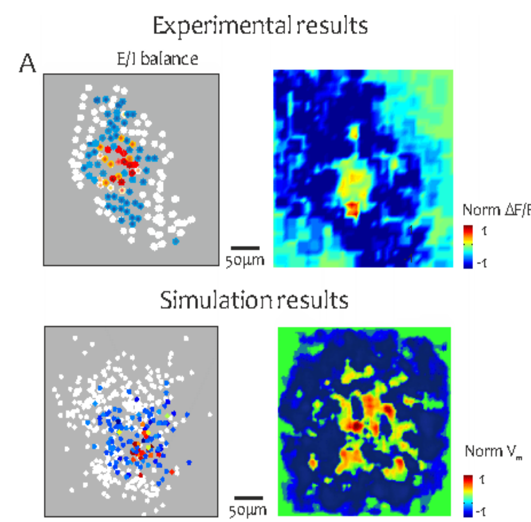
See poster !!

→ *Spatio-temporal dynamics in the granular layer microcircuit*



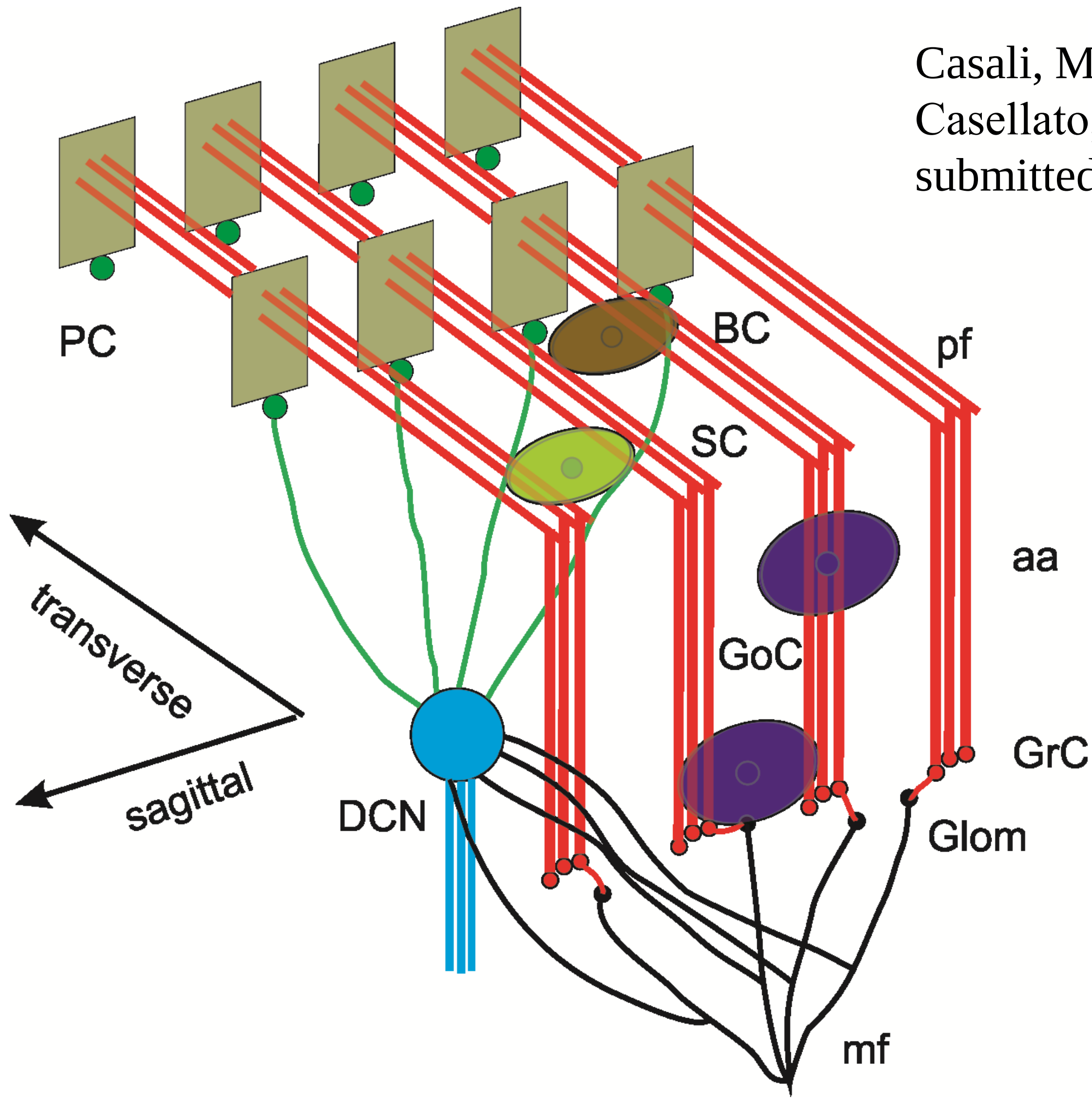
Validation against complex output space



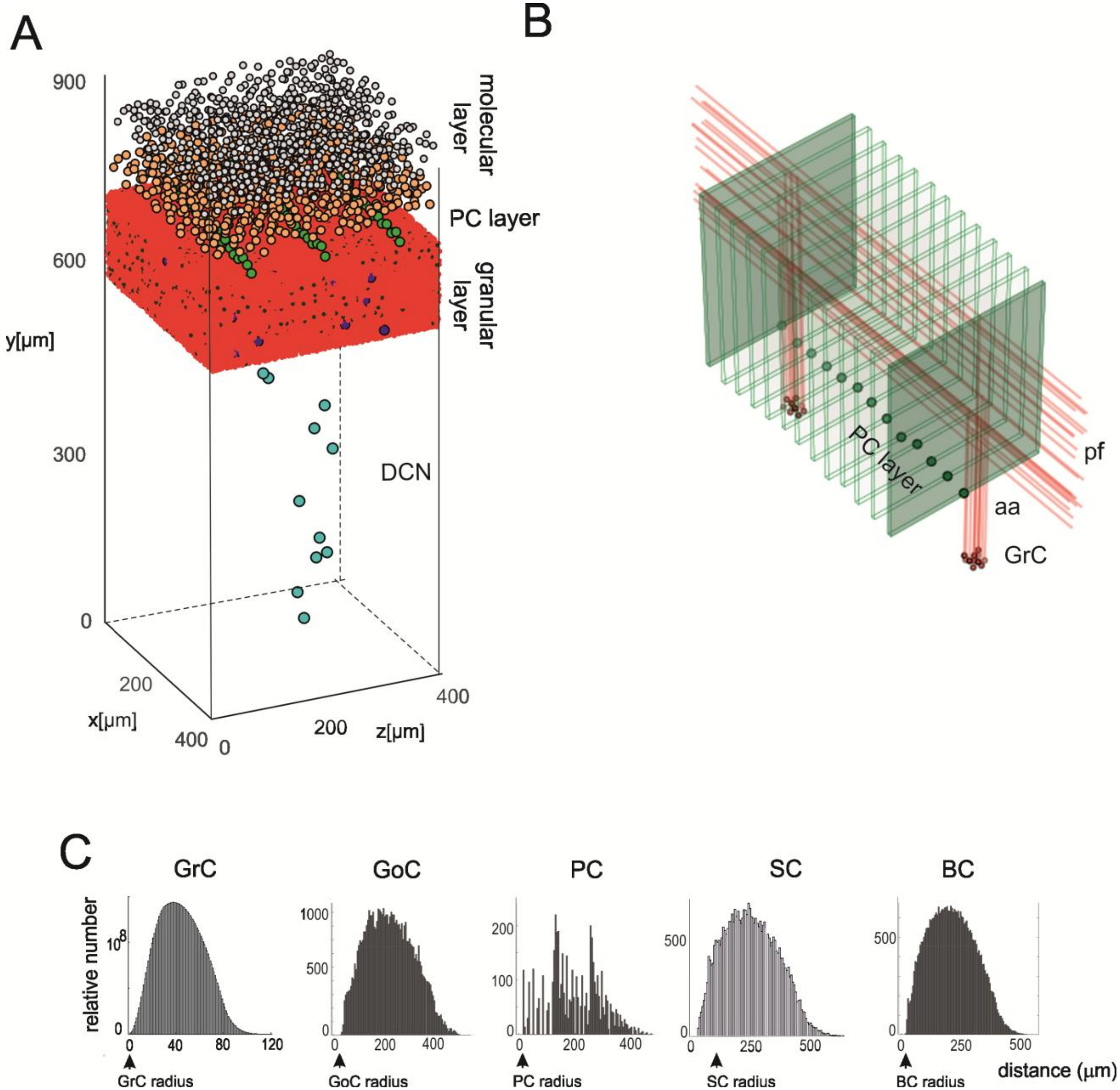


THE CEREBELLUM SCAFFOLD MODEL

Casali, Marenzi, Medini, Casellato, D'Angelo – to be submitted

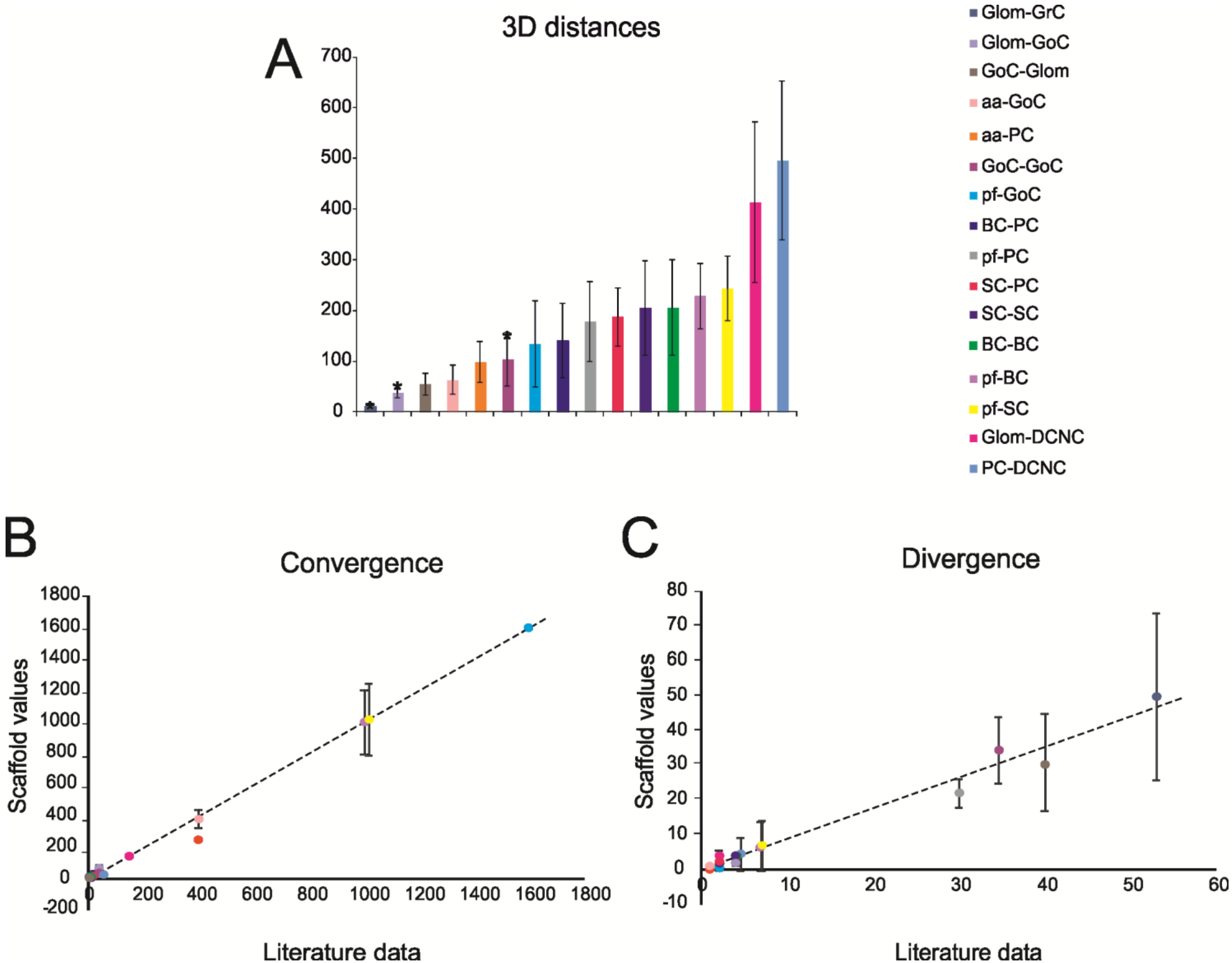


THE CEREBELLUM SCAFFOLD MODEL
Cell placement

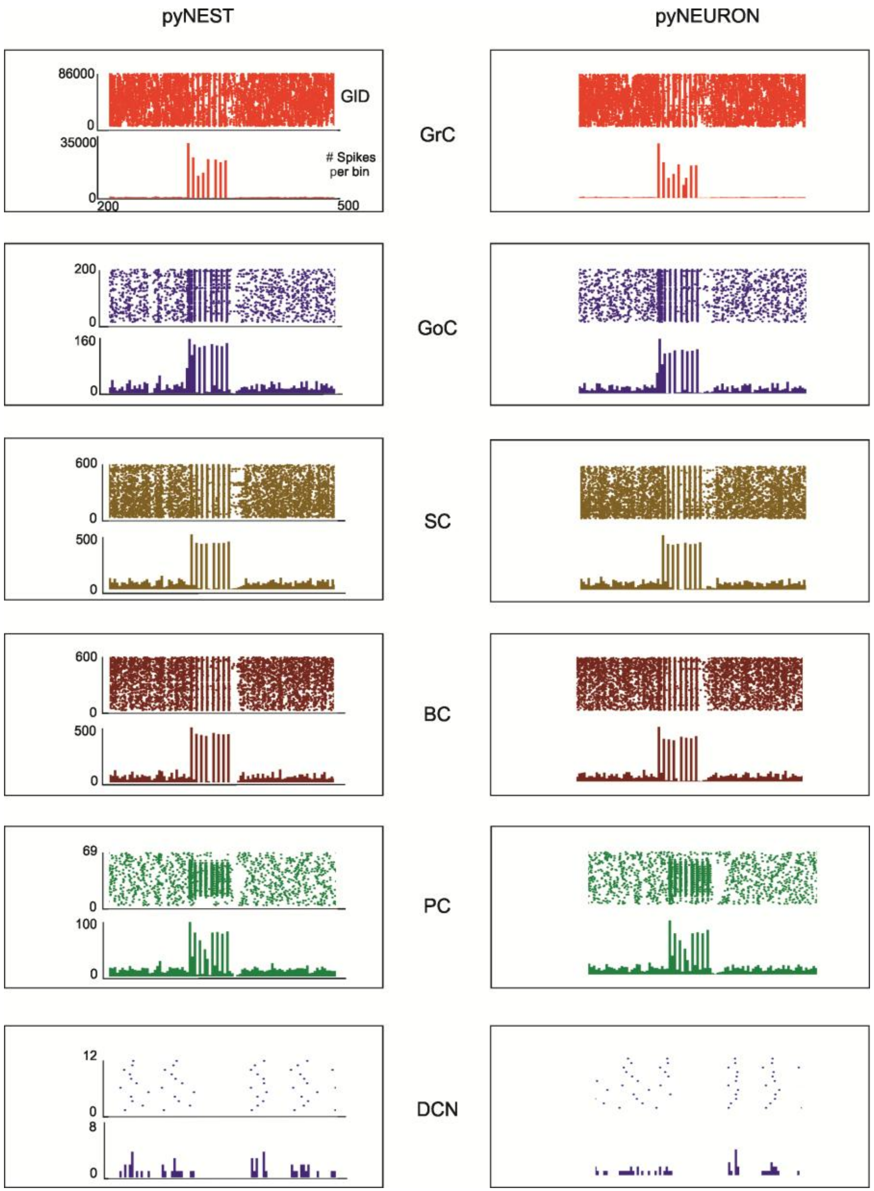


About 100000 neurons

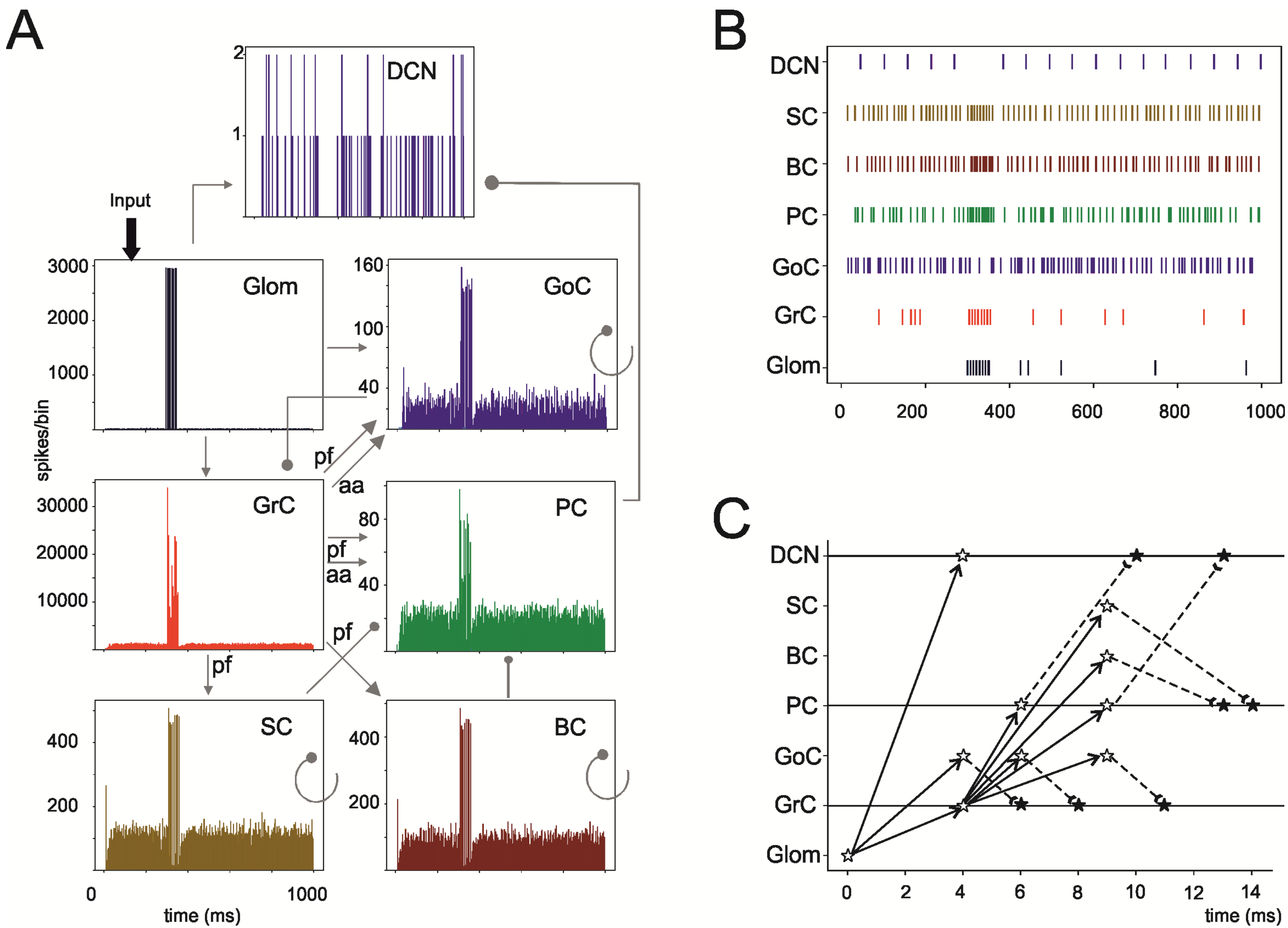
THE CEREBELLUM SCAFFOLD MODEL
Cell connectivity



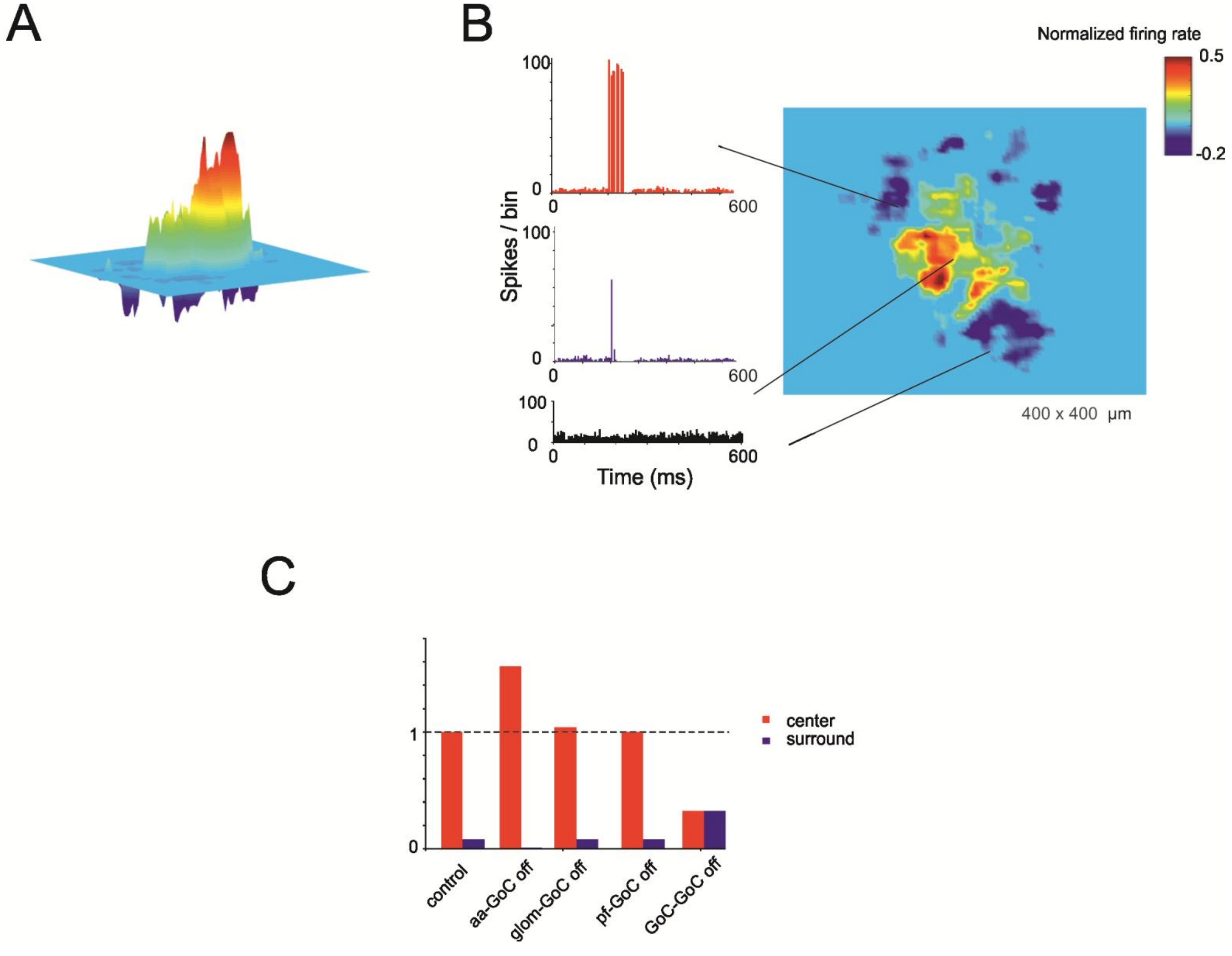
THE CEREBELLUM SCAFFOLD MODEL
Cell activity



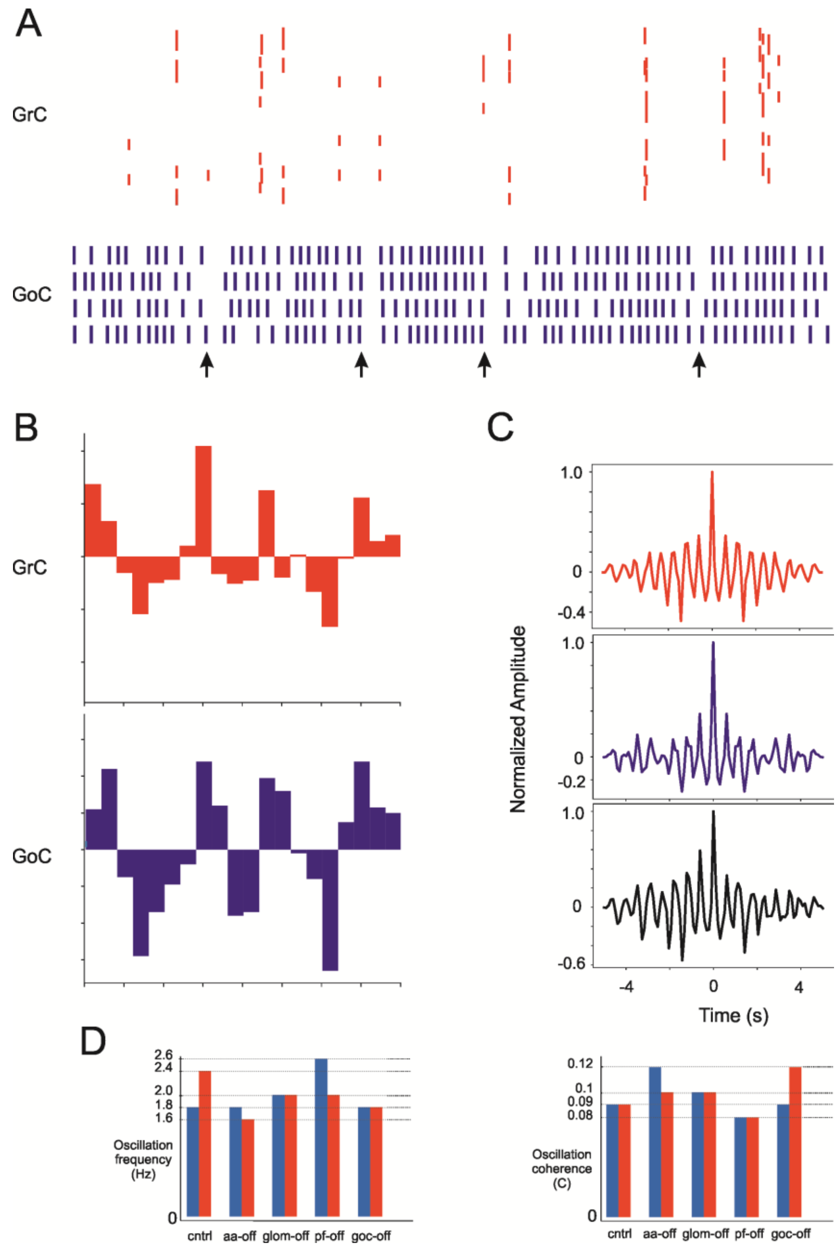
THE CEREBELLUM SCAFFOLD MODEL
Activity propagation



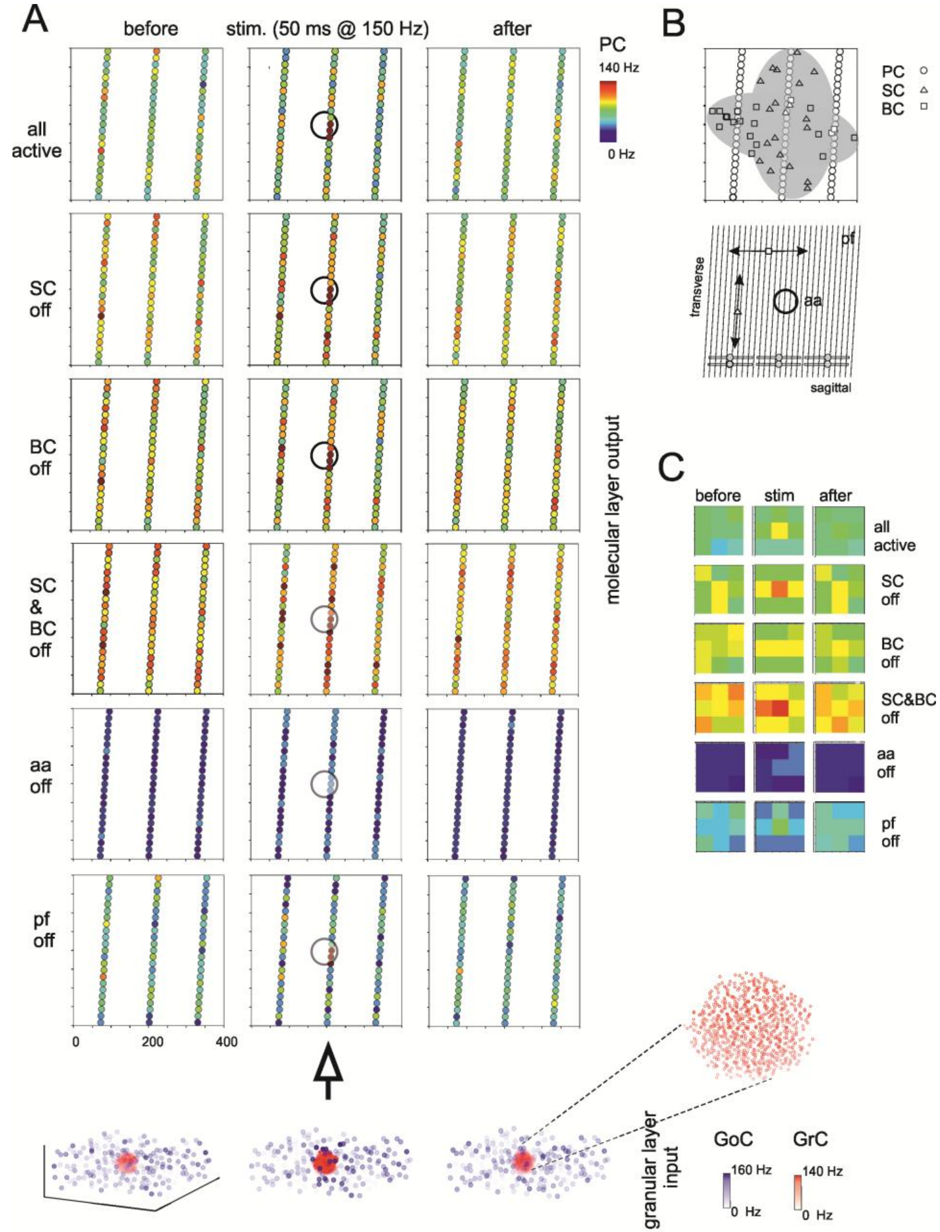
THE CEREBELLUM SCAFFOLD MODEL
Spatial organization of responses in the granular layer



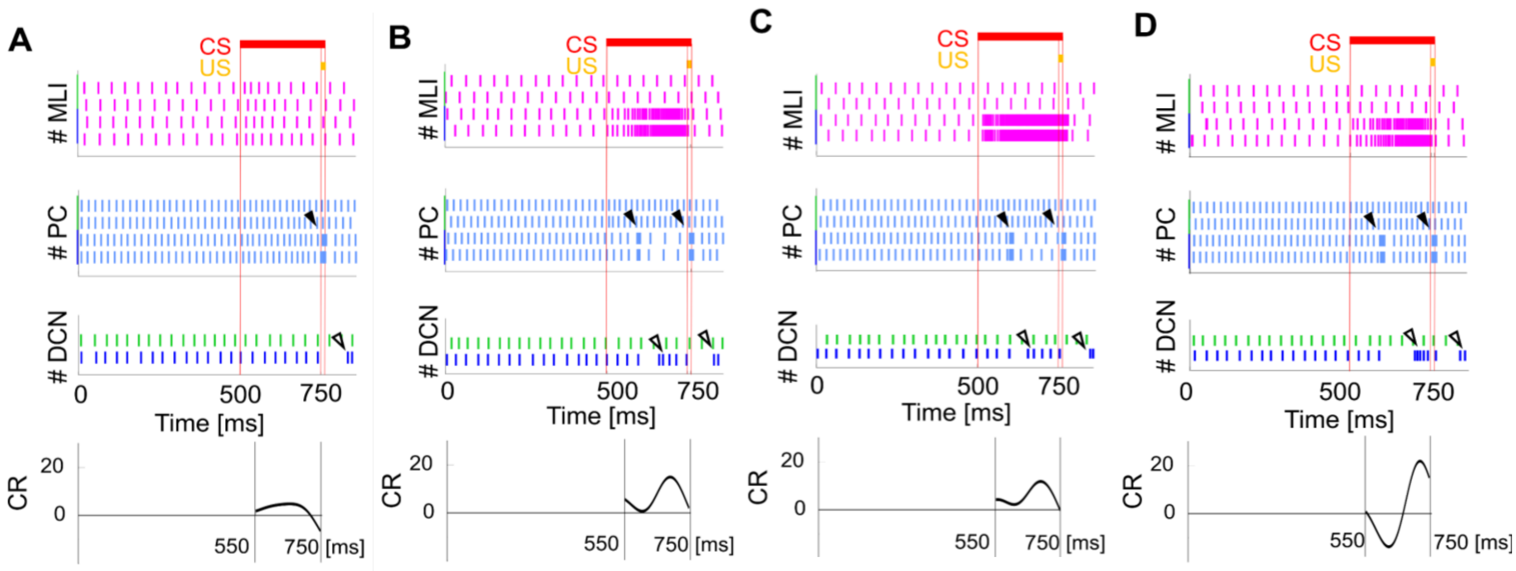
THE CEREBELLUM SCAFFOLD MODEL
Temporal organization of responses in the granular layer



THE CEREBELLUM SCAFFOLD MODEL
Propagation of responses to the molecular layer



THE CEREBELLUM SCAFFOLD MODEL
Implementation with E-GLIF neurons and plasticities (in progress)



Start learning

End learning – control

End learning – no PF-PC plasticity

End learning – no MLI inhibition

EBC learning results from the interaction of multiple mechanisms at different scales

A. Geminiani, C. Casellato, H.-J. Boele, C.I. De Zeeuw, A. Pedrocchi, E. D'Angelo – in preparation

-The scaffold can account for flexible handling of cell positioning connectivity and learning rules accouning for the data provided by experiments

-The scaffold implemented with LIF neurons already shows the emergence of local network dynamics revealed experimentally

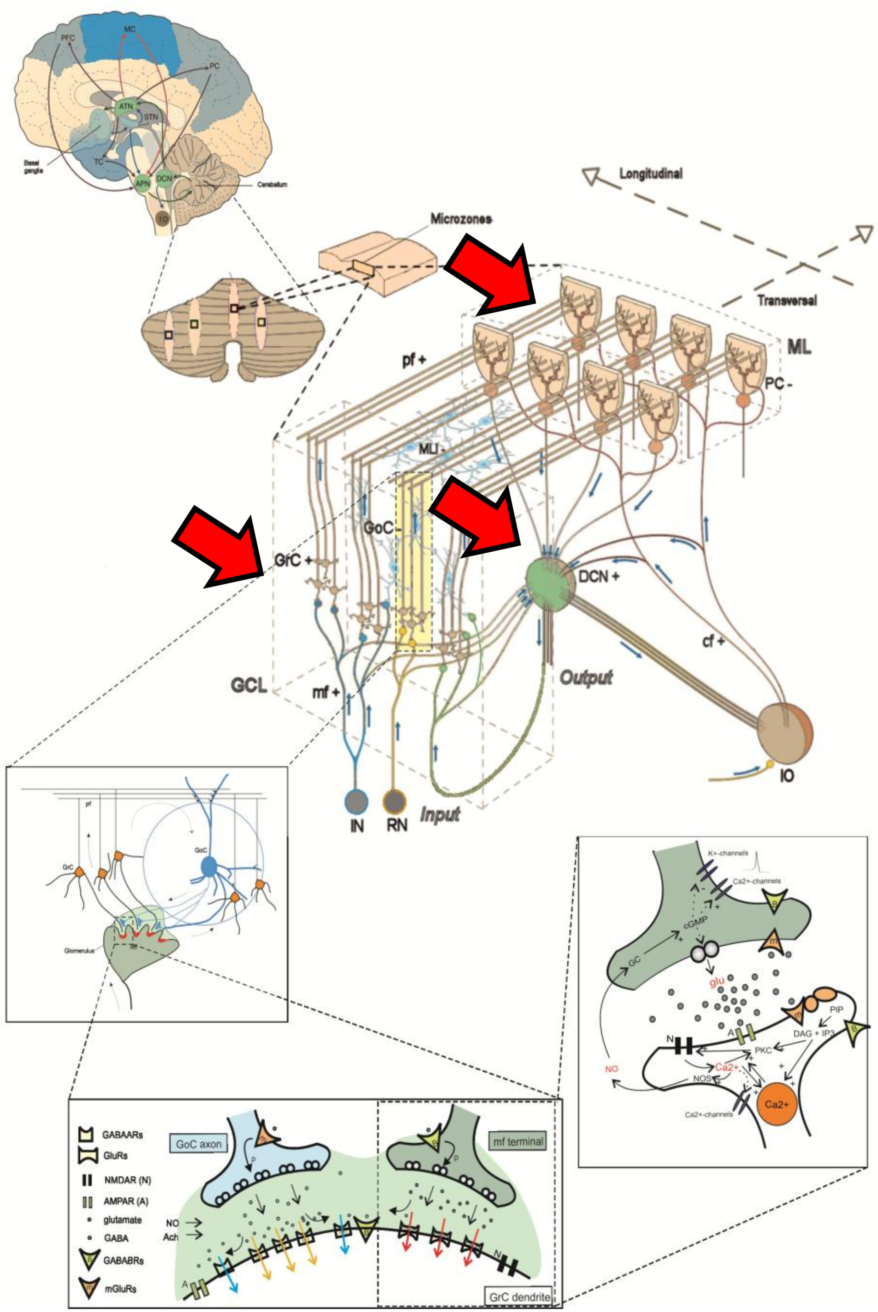
-The further implementation with E-GLIF neurons and REALISTIC NEURONS is needed to investigiate non-linear spatio-temporal dynamics during continuous signal processing

Synaptic plasticity and dynamic network processing in robots

Plasticity occurs at 3 main sites in the cerebellar network:

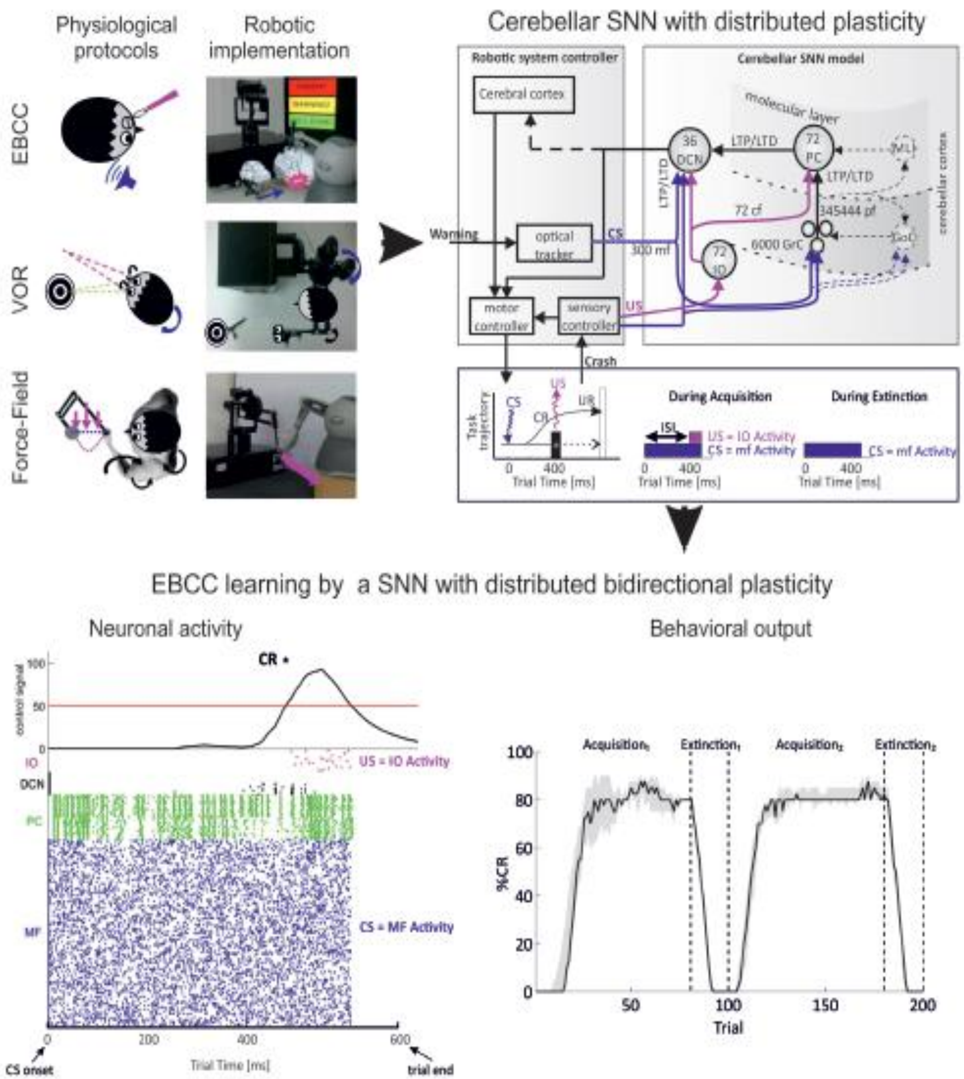
1) granular layer
2) molecular layer
3) DCN

These plasticities are bidirectional and depend on spike timing



Hansel, Linden, D’angelo, Nature Neurosci, 2001
D’Angelo nd DeZeeuw, TINS 2010
D’Errico et al., J Physiol, 2008
Sgritta et al., J Neuosci, 2017

A plastic SNN of the cerebellum in the control system of a neuro-robot



- Simplified network (1 small module, 10000 neurons)
- Simplified neurons (LIF)
- Simplified learning rules (3 bidirectional STDP)

Prediction of Purkinje cells and DCN cell dynamics during EBCC learning

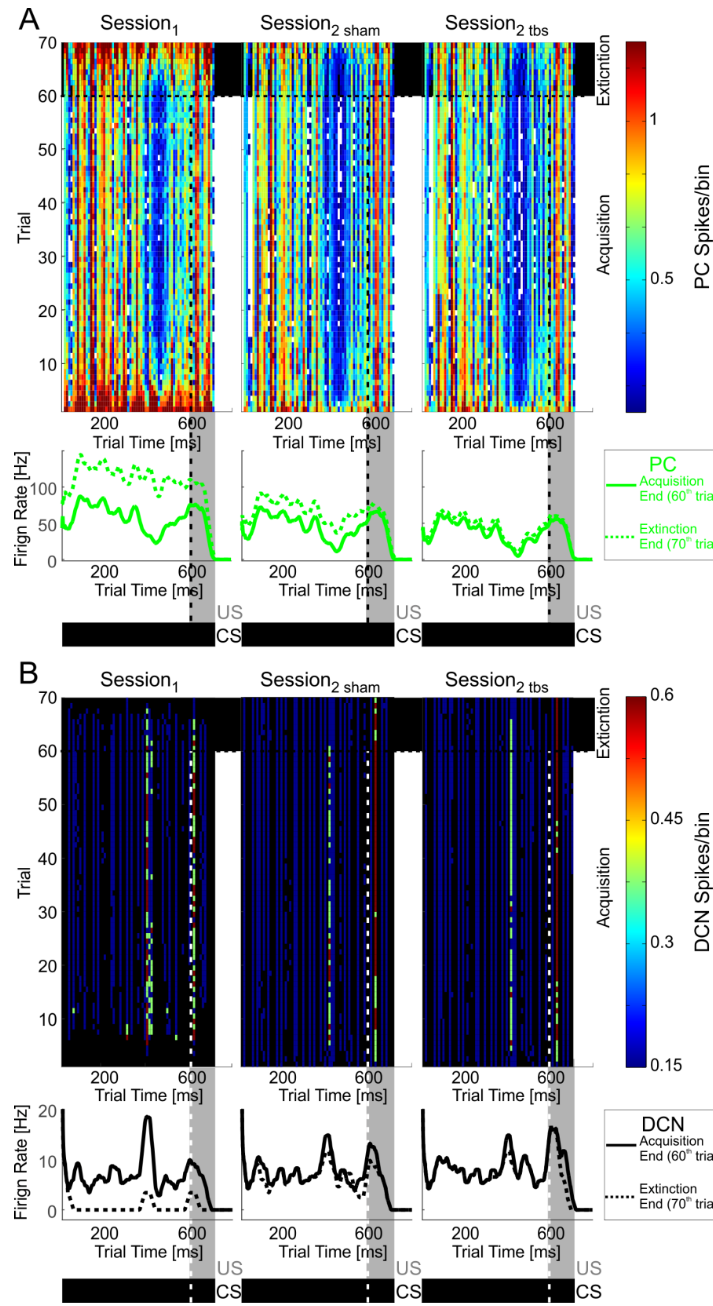
-The cerebellum opeates as an inverse controller correcting movement coordination through the identification and earning of correlated sensory events.

-the cereblelum uses distributed bidirectional synatic plasticity to control learning in a biologically meaningful manner

-Plasticity is managed dynamically with faster time constnat in the cerebellar cortex that in the DCN

PC

DCN



Fallout and planning for 2019-2021

Implementaiton in REAL ROBOTS - NAO NAO

Test the oscillation/resonance/plasticity hypothesis and other moelcular/cellular hypotheses with the network with enhanced dynamics and robotic models.

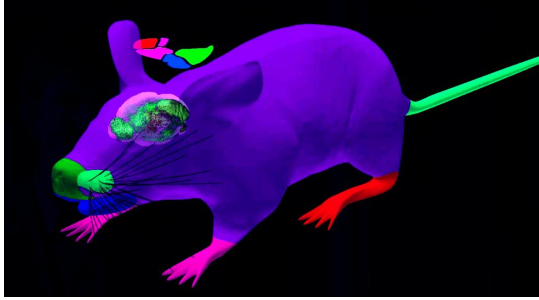
But, for further understanding of the brain-cerebelum system, 3 operations are being developed in parallel :

A) fully develop bottom-up modeling toward whole-brain (doable for robotic implementations in mice)

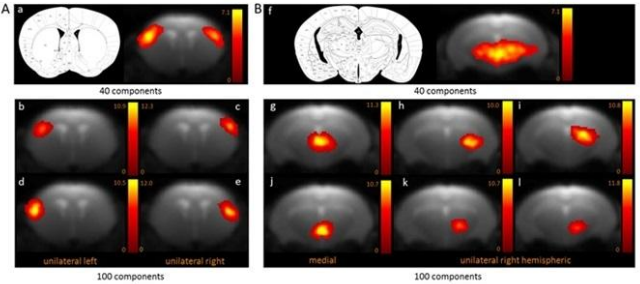
B) integrate bottom-up with top-down modeling (typically needed to interpret human data)

C) Instruct bottom-up models at different scales using bioophisically meanngful featires (BMF) from MRI to predict microcircuit alterations in pathology

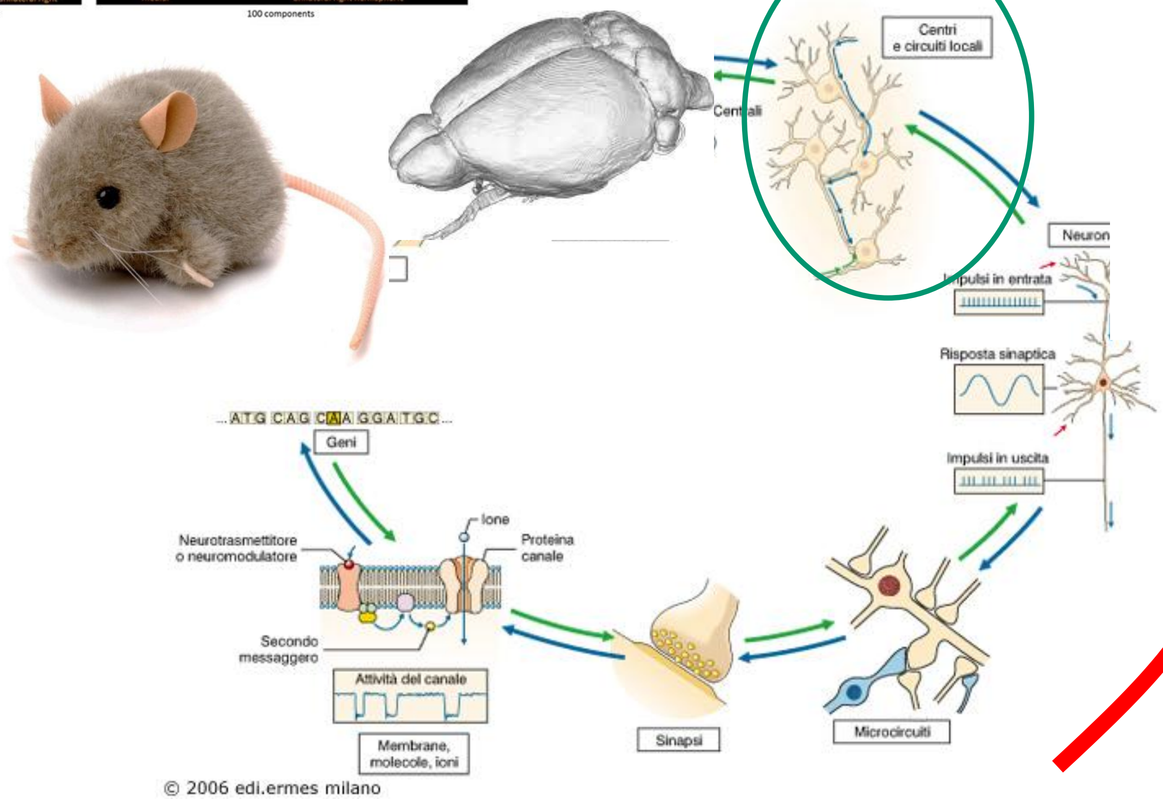
(A) BOTTOM-UP INFERENCE of fMRI signals

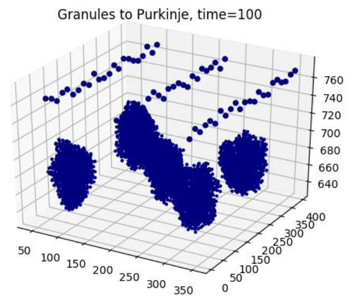


Implement the scaffold into the virtual mouse brain model with full bottom-up reconstruction of the ensemble signals through the development of a novel “NA-NVC module”



“NVC module”



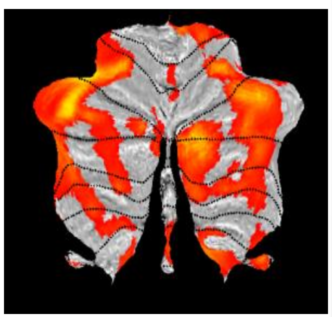


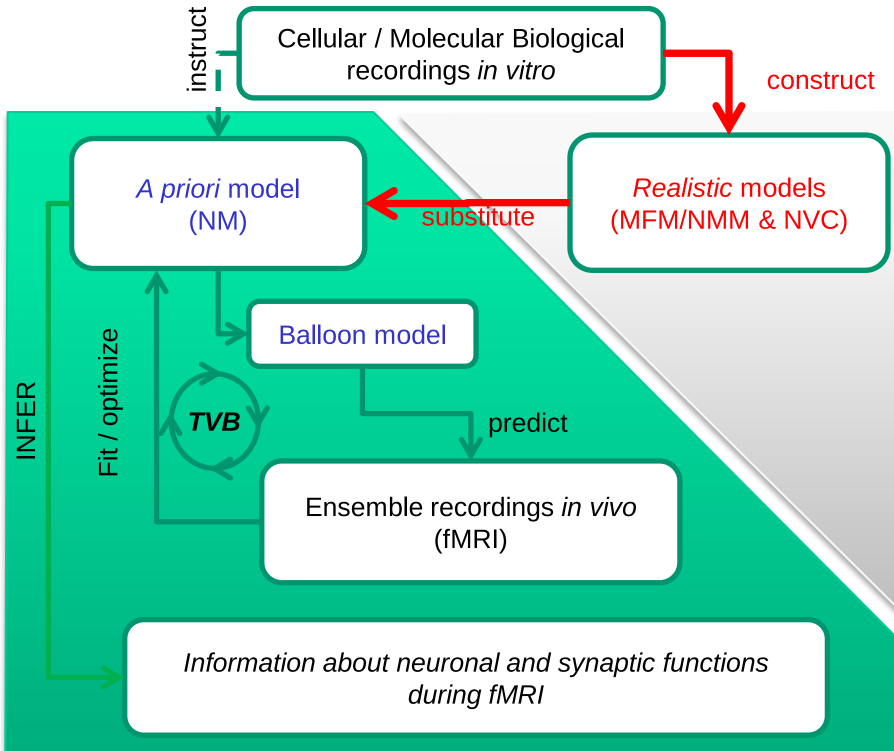
“NA module”

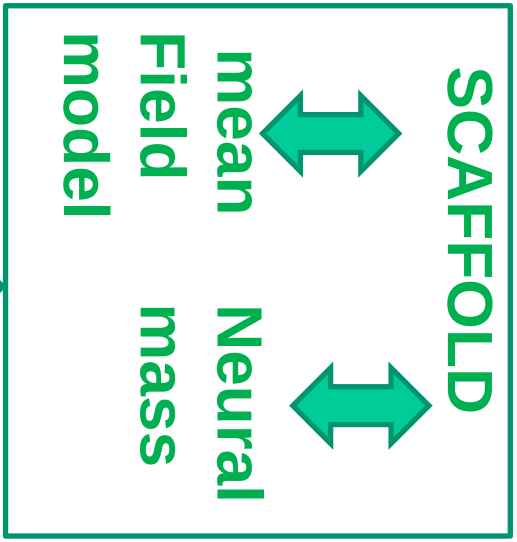
Bottom-up

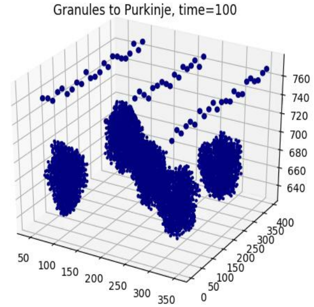
(B) MODEL INVERSION in the Virtual Brain - humans

Implement novel neural masses or mean-field equations keeping an explicit connection to data-driven models and Integrate them into The Virtual Brain to simulate the contributions of elementary mechanisms to ensemble brain signals (e.g. fMRI, EEG).



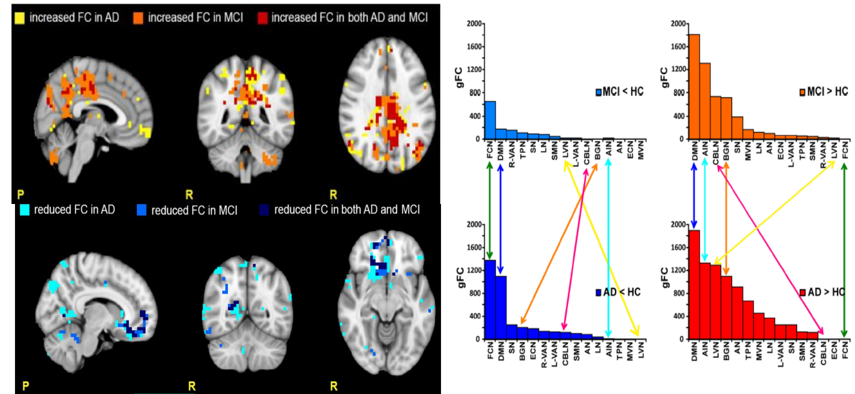






(C) INSTRUCTION/PREDICTION – human pathology

Information derived from MIP classification is used in data-driven models to predict neuronal and network parameter changes in human brain pathologies.

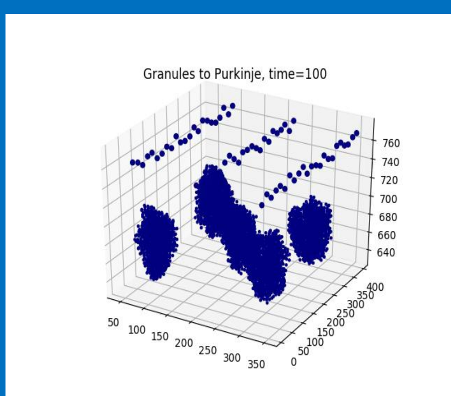


biophysical meaningful features

specific biolgical information: gene mutations (ionic channels, recepotrs ...), neuronal loss, condicion velocity etc ...

LITERATURE, MIP

Scaffold modification



Pediction of pathogenetic mechasnims,e.g. :

- circuit dynamics
- Neuronal activity
- Connection strength
- Synaptic weights

MILESTONES

2018

1) Definition of methods for NVC investigation

Achieved at end of 2017 – paper published on J Neuoscience (Mapelli et al., 2017)

2) Definition of mechasims of NVC in the cerebelum

Achieved – new data sampling concluded and paper in preparation on the comparison of differnt cerebellar regions – Abstracts at FENS, Berlin, July 2018; Abstrct and poster at Erice School “Camillo Golgi”, December 12-15, 2018.

3) Initial models of NVC

Achieved - First model version generated – advanced module for pyNEURON under development .

2019-2021

1) Definition of the NA / NVC relationship in the cerebellum
2) “fMRI module " of cerebellum to reconstruct the fMRI-BOLD signal.
3) "Neural mass and mean-field models" of cerebellum to analyze the fMRI-BOLD signal.

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