Predictions by Cerebellar Internal Models

Mitsuo Kawato

ATR Computational Neuroscience Labs

Discovery Channel

Topics

1. Understanding brain by creating brain
2. Basics of cerebellum
3. Internal models are necessary
4. Feedback-error-learning model
5. Cerebellar STDP
6. Neurophysiology of ocular following responses
7. Chaotic resonance in inferior olive
8. Human cerebellum and MOSAIC

Japanese Humanoids

Understanding Brain by Creating Brain

- Robots and computers are much inferior to humans.
- This demonstrates that we do not understand brain functions.
- Only if we try to create a brain, we can understand information processing in the brain.
- Creating only a brain does not make sense, and a body and its environment are essential.

Computational Neuroscience

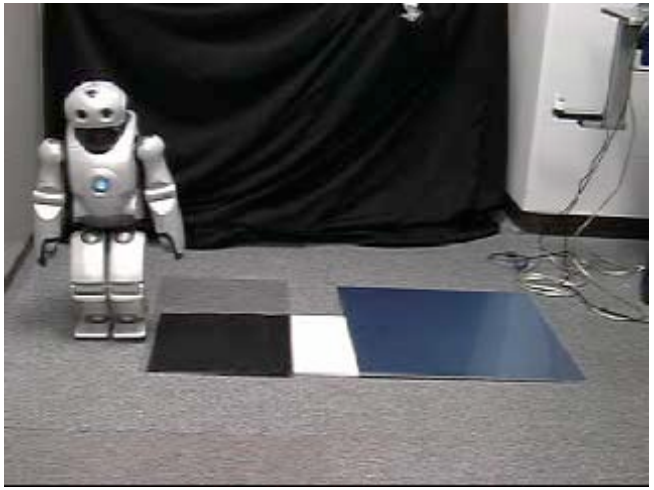
We elucidate information processing of the brain to the extent that artificial machines, either computer programs or robots, can be built to solve the same computational problems that are solved by the brain, essentially in the same principle.

Biped

Neuroscience

Schaal S, Sternad D, Osu R, Kawato M: Rhythmic arm movement is not discrete. *Nature Neuroscience*, **7**, 1137-1144 (2004).
Nakanishi J, Morimoto J, Endo G, Cheng G, Schaal S, Kawato M: Learning from demonstration and adaptation of biped locomotion, *J. Robotics and Autonomous Systems*, **47**, 79-91 (2004).

Endo G, Nakanishi J, Morimoto J, Cheng G: Experimental studies of a neural oscillator for biped locomotion with QRIO. *IEEE International Conference on Robotics and Automation*, 598-604 (2005)



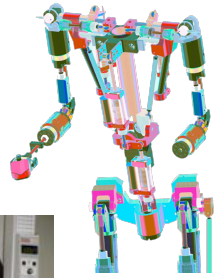
By SONY IDL and ATR Collaborative Research

Humanoid "DB" (Dynamic Brain)

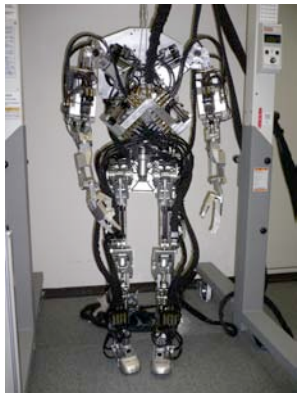
- 30 DOFs
- 190 cm height
- 80 kg weight
- Compliant
- Biomimetic oculomotor system
- Co-designed by SRC and KDB

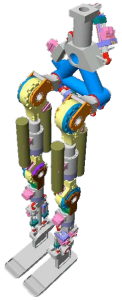
Shibata, T. and Vijayakumar, S. and Conradt, J. and Schaal, S.: Biomimetic Oculomotor Control. *Adaptive Behavior*, **9**, 189-208 (2001).

New Humanoid "CB" with SARCOS



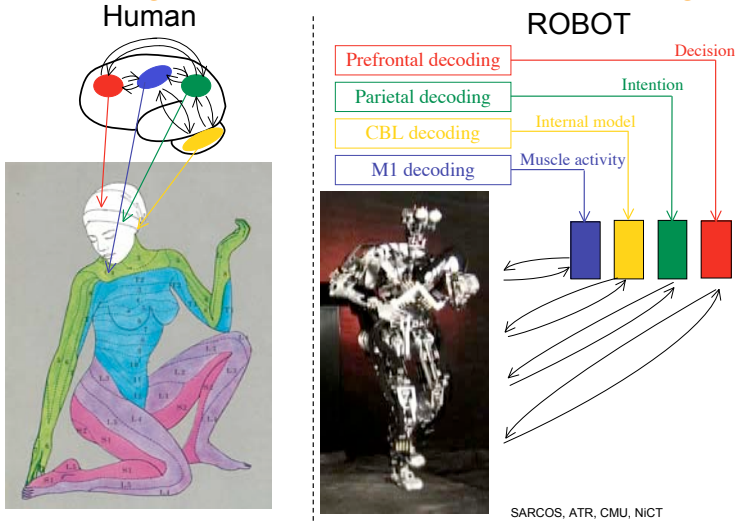
An ATR/SARCOS development





- Closer to human (speed and power)
- Fully autonomous
- 160cm and 60 Kg
- Mechanically compliant

Understanding Hierarchical Sensory-Motor Control by the Brain through Robot Control with Neural Decoding



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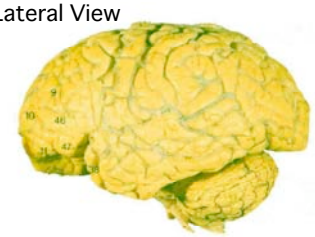
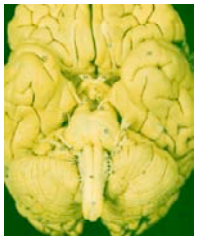
Cerebellum and Cerebral Cortex

Lateral View



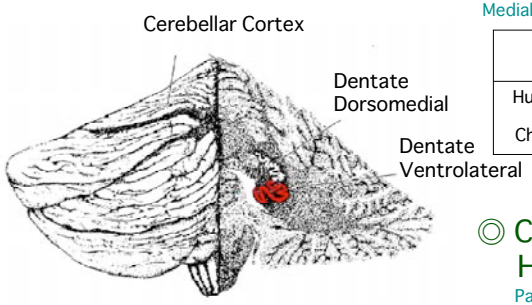
Medial View

Bottom View



	Cerebellum		Cerebral Cortex
Weight	130g	1to10	1,300g
Surface Area	50,000mm^2	1to2	80,000mm^2
Number of Neurons	10^{11}	>	10^{11}
Expansion from Average Primates	2.8	~	3.2

Cerebellum and Human Intelligence



◎ Cerebellar Nuclei

Medial 0.8, Dentate 4.5 relative to prosimian

	Body Weight	Dentate Nucleus Volume	W & H	Leng.
Human	65kg	1,167mm^3	same	twice
Chimp	45kg	456mm^3	same	half

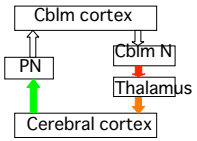
◎ Cerebellar Size and Human Intelligence

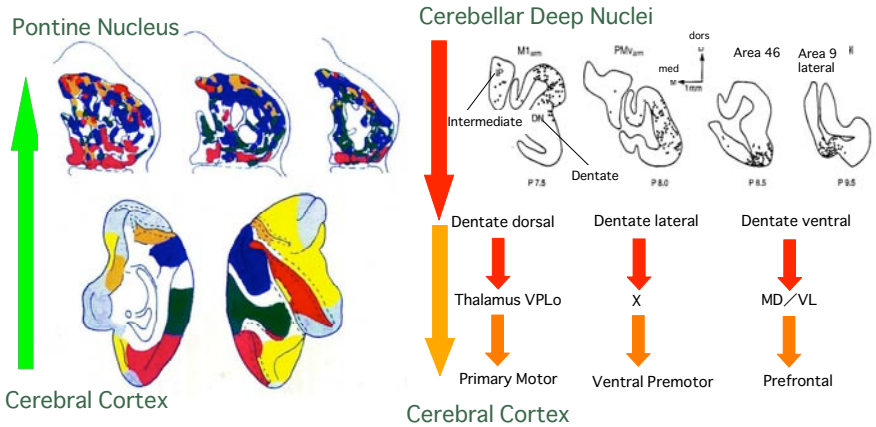
Paradiso (1997)

Finger tapping	r=0.22	p<0.05
Verbal memory	r=0.27	p<0.02
General IQ (WAIS-R)	r=0.19	p<0.07

No correlation for left temporal lobe

Cerebro-Cerebellar Communication Loop





Private Communication between Cerebrum and Cerebellum with Closed-loop Circuits

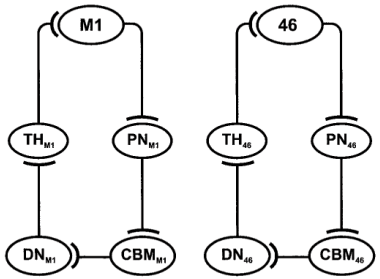
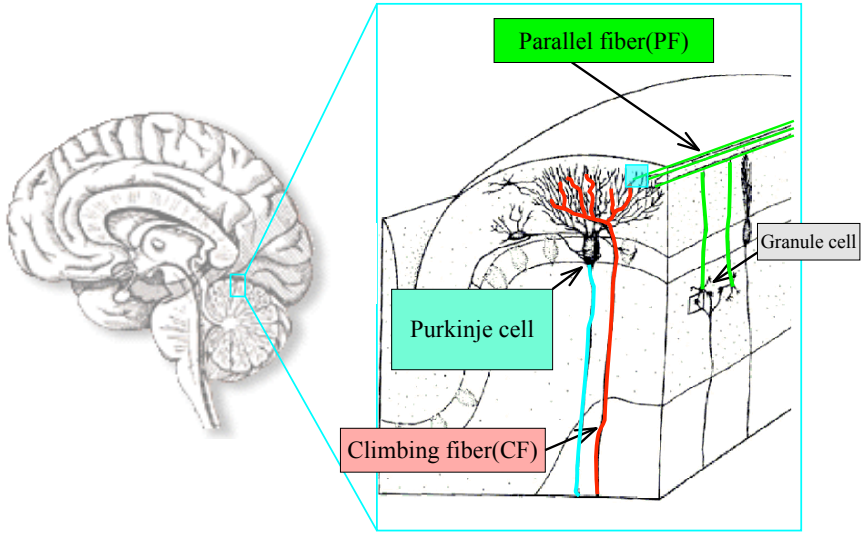
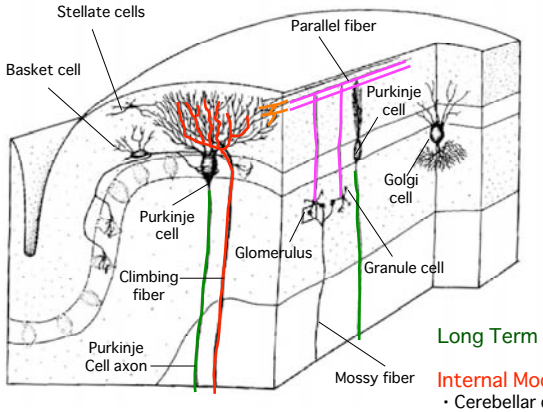


Figure 14. Summary diagrams of the closed-loop circuits that link the cerebellum with M1 and area 46. Note that the cortical area, which is the major source of input to a circuit, is the major target of output from the circuit. See Discussion for complete details. CBM, Cerebellar cortex; DN, dentate nucleus; PN, pontine nuclei; TH, subdivisions of the thalamus.

Neural Circuit of Cerebellar Cortex

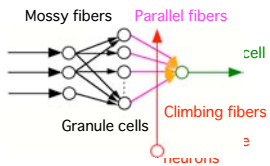


Neural Circuit, Synaptic Plasticity and Models of Cerebellum



Marr-Albus-Ito (~1970)

- Climbing fiber inputs as teacher (error signal)
- Parallel-fiber-Purkinje-cell synapse changes its efficacy

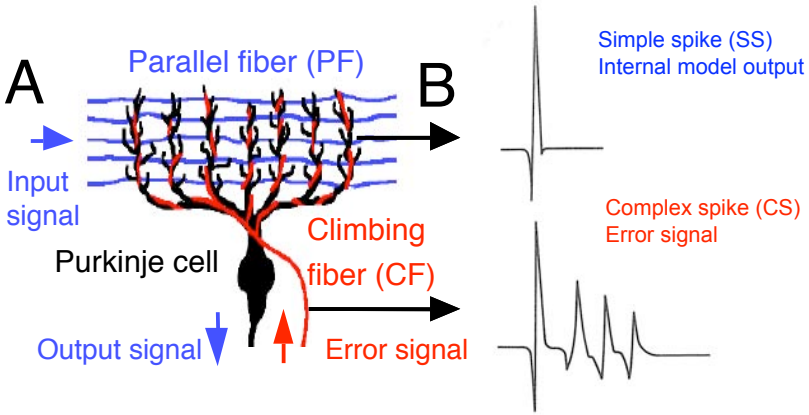


Long Term Depression, LTP, RP (~1982)

Internal Model Theory (~1984)

- Cerebellar cortex acquires internal models by learning
- Climbing fiber represents motor command error

Parallel Fiber and Climbing Fiber Inputs to Purkinje cells: Simple Spikes and Complex Spikes



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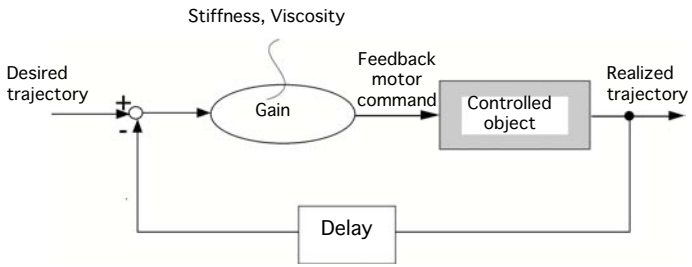
Cerebellar Internal Model Theory

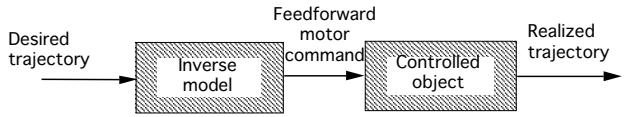
- The cerebellum consists of many modules (micro-zones) which perform different input-output transformations.
- Synaptic weights change and different transformations can be learned.
- Supervised learning guided by an error signal
- Different modules acquire internal models of controlled objects, tools, other brains, etc.

Pole and CBLM

A Feedback control



B Feedforward control



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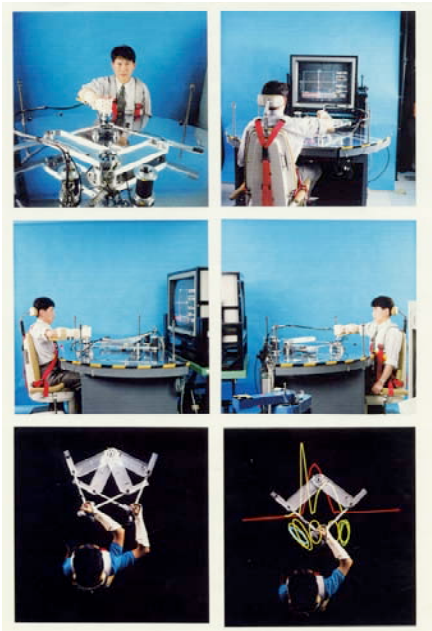
Neuroscience: Tilting Against a Major Theory of Movement Control

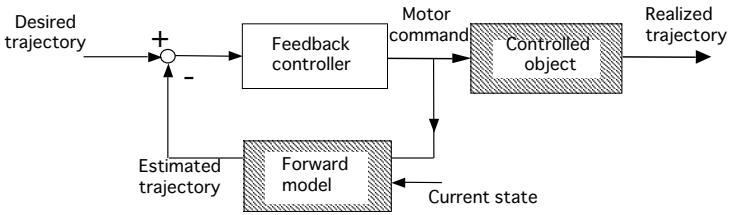


Stiffness Measurement by PFM

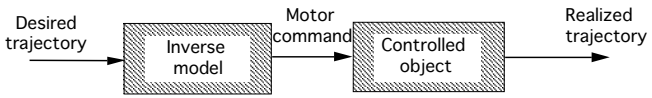
Hiroaki Gomi

Mechanical perturbations in 8 directions were given during point-to-point movement and reaction forces were measured. Then stiffness and viscosity were estimated.

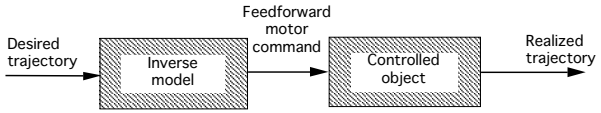
A Internal feedback control by forward model



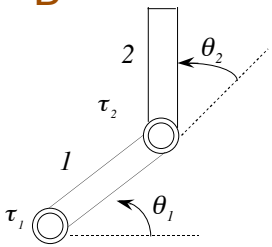
B Feedforward control by inverse model



A



B

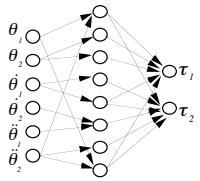


C

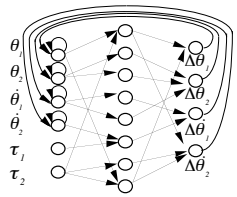
$$\tau_1 = (M_2L_1^2 + 2M_2L_1S_2\cos\theta_2 + I_1 + I_2)\ddot{\theta}_1 + (M_2L_1S_2\cos\theta_2 + I_2)\ddot{\theta}_2 - M_2L_1S_2(2\dot{\theta}_1 + \dot{\theta}_2)\dot{\theta}_2\sin\theta_2 + B_1\dot{\theta}_1$$

$$\tau_2 = (M_2L_1S_2\cos\theta_2 + I_2)\ddot{\theta}_1 + I_2\ddot{\theta}_2 + M_2L_1S_2\dot{\theta}_1^2\sin\theta_2 + B_2\dot{\theta}_2$$

Inverse Dynamics Model



Forward Dynamics Model



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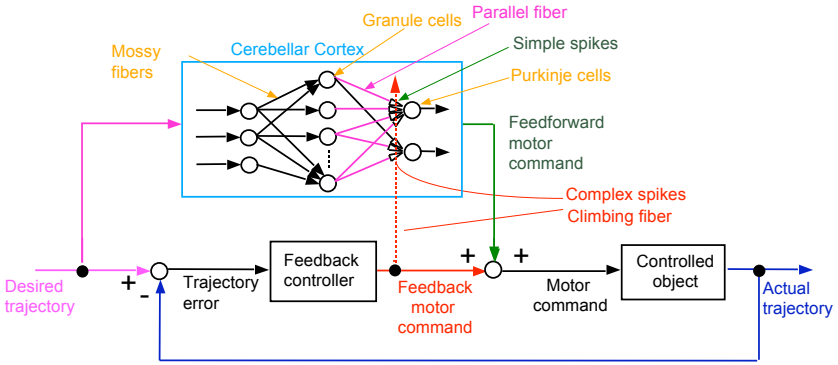
Feedback Error Learning in Cerebellum



(1) Parallel-fiber inputs represent desired trajectory
(2) Simple spike represents feedforward motor command
(3) Cerebellar cortex constitutes inverse model
(4) Complex spike represents error in motor-command coordinate
(5) LTD time window (optimal if PF leads CF)

Jun Nakanishi and Stefan Schaal : Feedback error learning and nonlinear adaptive control. *Neural Networks*, **17**, 1453-1451 (2004)

Comparison of Feedback Error Learning with Supervised Learning for Motor Command

Feedback error learning

$$d\omega/dt = \varepsilon(\partial\tau_{\mathrm{ff}}/\partial\omega)^T\tau_{\mathrm{fb}} \qquad (1)$$

Supervised learning

If teaching signal for motor command is given as τ_{desired}, then the steepest descent direction of ω for the following squared error, $E = \frac{1}{2}(\tau_{\mathrm{desired}} - \tau_{\mathrm{ff}})^T \cdot (\tau_{\mathrm{desired}} - \tau_{\mathrm{ff}})$ is given as follows.

$$d\omega/dt = \varepsilon(\partial\tau_{\mathrm{ff}}/\partial\omega)^T(\tau_{\mathrm{desired}} - \tau_{\mathrm{ff}}) \qquad (2)$$

Comparing equations (1) and (2), τ_{fb} approximates $(\tau_{\mathrm{desired}} - \tau_{\mathrm{ff}})$ in the feedback error learning scheme. That is, the feedback motor command plays a role of the error signal for the motor command. This works only when the feedback controller is an approximate inverse model of the controlled object. The following two conditions should be satisfied.

The common coordinate frame for τ_{fb} and τ_{desired}.
The two temporal waveforms τ_{fb} and $\tau_{\mathrm{desired}} - \tau_{\mathrm{ff}}$ are similar.

LTD and LTP as Synaptic Plasticity for the Feedback Error Learning Scheme

Simple linear input–output model of Purkinje cell

Output: y Firing of i–th parallel fiber input: x_i
i–th synaptic weight: ω_i Number of inputs: n

$$y = \sum_n \omega_i x_i \qquad (1)$$

Model of LTD and LTP

$$d\omega_i/dt = -\varepsilon x_i (C - C_{\text{spont}}) \qquad (2)$$

Interpretation by feedback error learning

The difference of climbing fiber inputs from its spontaneous level $C - C_{\text{spont}}$ encodes the feedback motor command.

$$\begin{aligned} d\omega_i/dt &= \varepsilon(\partial\tau_{\text{ff}}/\partial\omega_i)\tau_{\text{fb}} \\ &= \varepsilon(\partial(-y)/\partial\omega_i)\tau_{\text{fb}} \\ &= -\varepsilon x_i (C - C_{\text{spont}}) \end{aligned} \qquad (3)$$

Approximate Mirror-Image Relationship Between CS and SS

$$SS(t) = \sum_n w_i(t) x_i(t) \qquad (1)$$

$$\tau \mathrm{d}w_i(t)/\mathrm{d}t = -\varepsilon x_i(t)\{CS(t) - CS_{\text{spont}}\} - w_i(t) \qquad (2)$$

$$w_i(t) \sim -\varepsilon \overline{x_i(t)\{CS(t) - CS_{\text{spont}}\}} \qquad (3)$$

$$\begin{aligned} SS(t) &= -\varepsilon \sum_n \overline{x_i(t)\{CS(t) - CS_{\text{spont}}\}} x_i(t) \\ &\sim -\delta\{CS(t) - CS_{\text{spont}}\} \end{aligned} \qquad (4)$$

Prediction

Feedback, After Learning : mirror image
Feedback, Before Learning : no relation
Feedforward, Delay, After Learning : CS at beginning
Feedforward, No Delay, After Learning: CS vanishes

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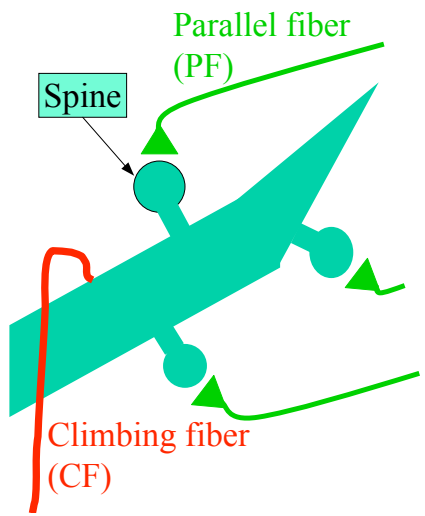
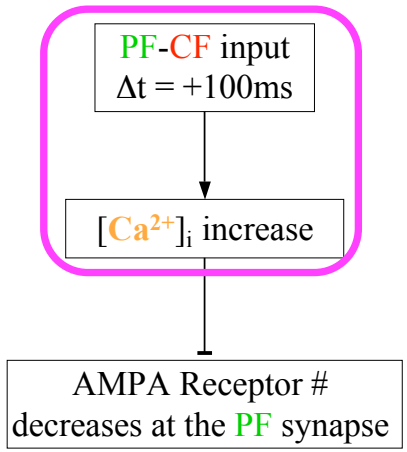
Spike Timing, Ca^{2+}, and LTD



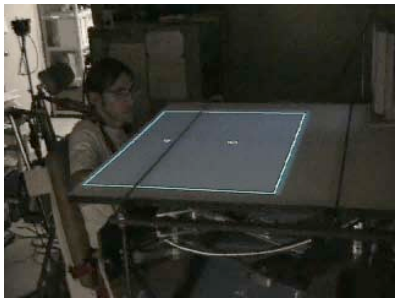


Computational Theory of Cerebellar STDP

- Computational theory requires that the temporal window should exist in cerebellar LTD
- Behavioral learning experiments suggest the temporal window in cerebellar LTD
- Computational model of Ca^{2+} dynamics within spine coherently reproduces LTD data.
- Signal transduction pathway model of LTD

Adaptation to Various Force Fields

- Forward reaching with 25 cm and 600 msec
- Two force fields VF and DF suddenly changed from NF
- Hand path, joint angle, joint torque measured and estimated
- Stiffness ellipse measured



Burdet E, Osu R, Franklin D, Milner T, Kawato M: The central nervous system stabilizes unstable dynamics by learning optimal impedance. *Nature,* **414** 446-449 (2001).

Osu R, Burdet E, Franklin DW, Milner TE , Kawato M: Different mechanisms involved in adaptation to stable and unstable dynamics. *Journal of Neurophysiology*, **90**, 3255-3269 (2003).

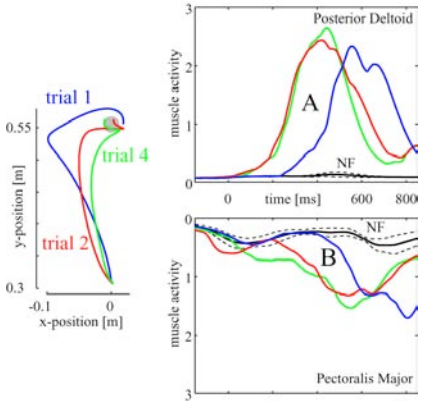
Franklin DW, Osu R, Burdet E, Kawato M, Milner TE: Adaptation to stable and unstable environments achieved by combined impedance control and inverse dynamics model. *Journal of Neurophysiology*, **90**, 3270-3282 (2003).

Franklin DW, Burdet E, Osu R, Kawato M, Milner TE: Functional significance of stiffness in adaptation of multijoint arm movements to stable and unstable dynamics. *Experimental Brain Research,* **151** 145-157 (2003).

Osu R, Hirai S, Yoshioka T, Kawato M: Random presentation enables subjects to adapt to two opposing forces on the hand. *Nature Neuroscience,* **7**, 111-112 (2004).

Data supporting FEL with Time Advance and Cross-Muscle Reflex

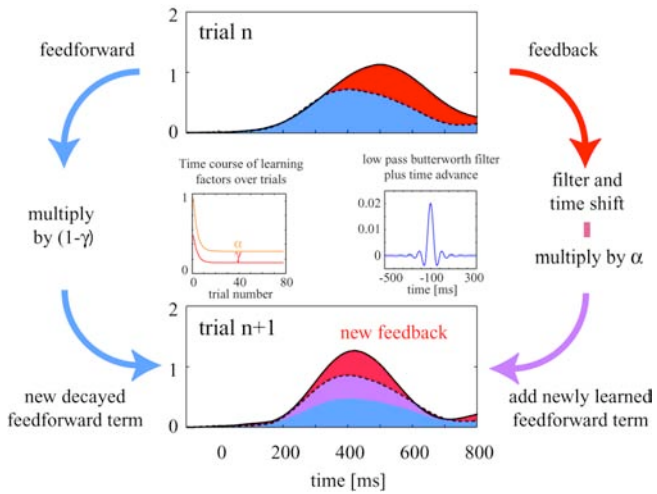
◆Hand path and EMG of the first few movements



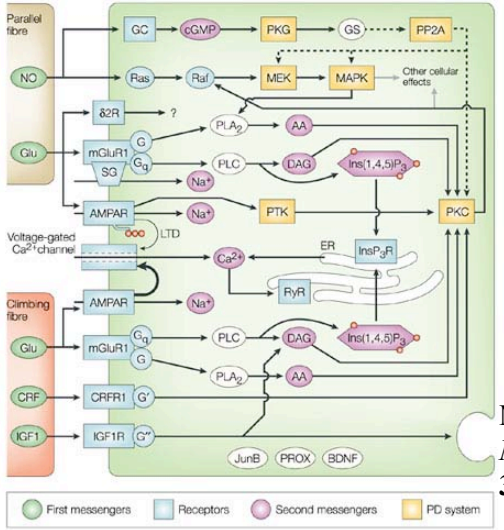
A: incorporation of feedback command into feedforward command in next trial with phase advance for the stretched and main muscle compensating VF

B: delayed feedback in un-stretched antagonist muscle, incorporated into feedforward command in next trial.

EMG Temporal Waveforms Reconstruction by the Model

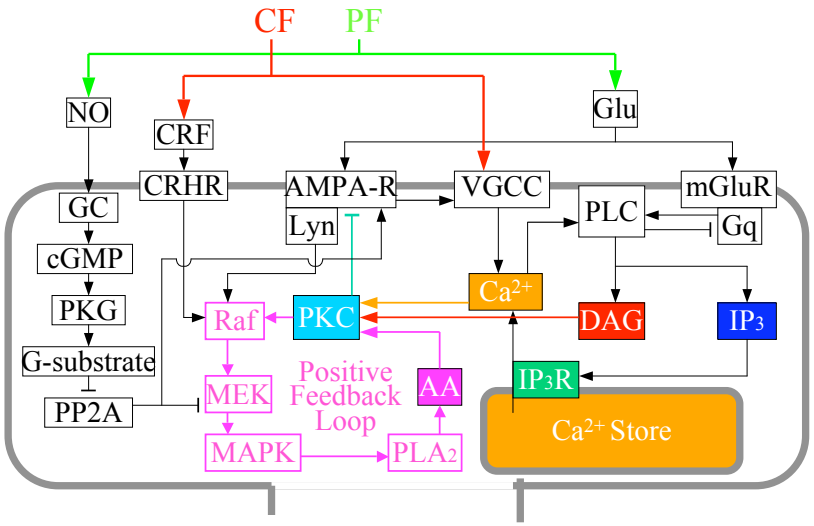


Signaling Networks in Cerebellar LTD



Masao Ito,
Nat Rev Neurosci
3, 896-902 (2002)

Simulation of Cerebellar LTD

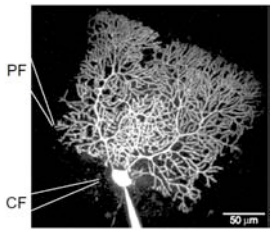


Doi T, Kuroda S, Michikawa T, Kawato M: IP3-dependent Ca2+ threshold dynamics detect spike-timing in cerebellar Purkinje Cells. *Journal of Neuroscience*, **25**, 950-961 (2005).

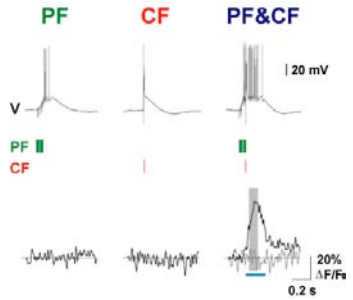
Ca^{2+} Dynamics Model for Coherent Understanding of Diverse and Confusing Experimental Data on LTD Time Window

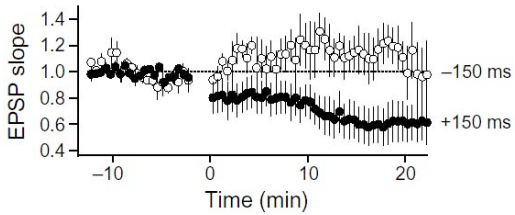
- Cerebellar learning theories require LTD time window where CF is delayed with respect to PF for 100-200 msec.
- Several experimental supports to this prediction
- Strong bundle stimulation to PF alone, uncaging of Ca^{2+} or IP_3 can induce LTD without PF-CF conjunction or time delay.
- Some experiments even reported CF preceding PF is optimal.
- Serious doubts and criticisms on LTD as a cellular basis of cerebellar supervised learning

Ca^{2+} Imaging in Purkinje-cell Spines

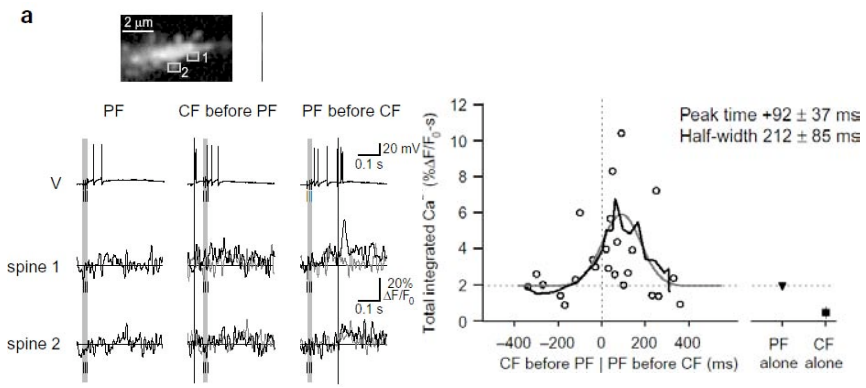


Wang *et al.*, *Nat Neurosci*
3, 1266-1273 (2000)

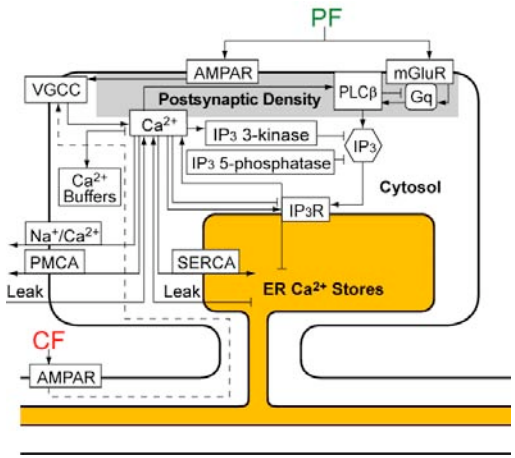




Signal-Transduction Pathways detect Input Spike Timing within a Spine



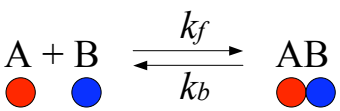
Block Diagram of Ca^{2+} Signaling



PF input ◊ Ca^{2+} influx & IP_3 production
CF input ◊ Ca^{2+} influx

Formulation of Biochemical Reaction

(1) Binding Reaction

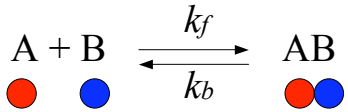


$$d[AB]/dt = + k_f[A][B] - k_b[AB]$$

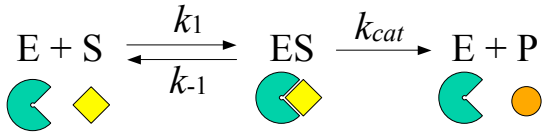
Dissociation Constant, $K_d = k_b / k_f$: equilibrium point
Time Constant, $\tau = 1/(k_f + k_b)$: speed for convergence

Formulation of Biochemical Reaction

(1) Binding Reaction



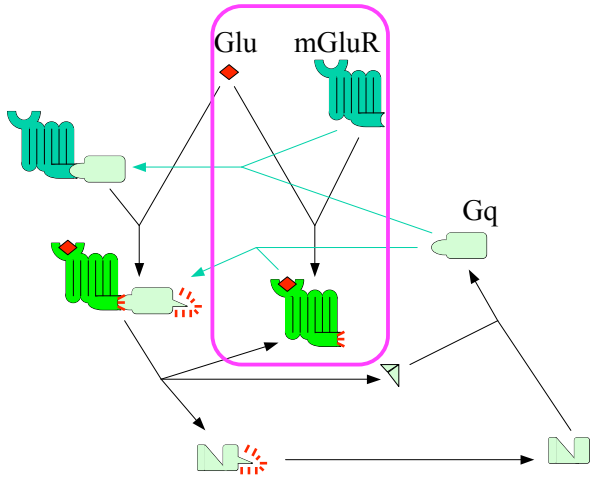
(2) Enzymatic Reaction (Michaelis-Menten)



$$K_m = \frac{k_{-1} + k_{cat}}{k_1}$$

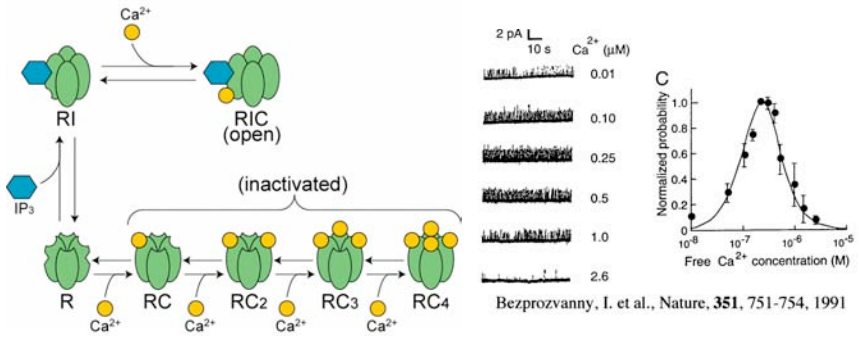
E: Enzyme, S: Substrate, P: Product

Example: Glu→mGluR→Gq



IP_3 Receptor Kinetic Model

based on Adkins and Taylor (1999)



- IP_3R-opening requires binding to both IP_3 and Ca^{2+}
- Excessive Ca^{2+} inactivates IP_3R
- Ca^{2+}-dependent activation is assumed faster than Ca^{2+}-dependent inactivation

Variables and Parameters

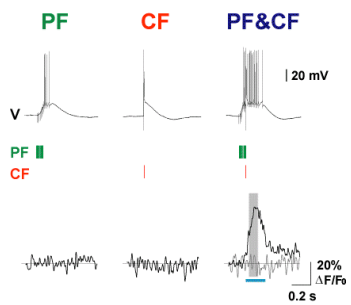
	Unknown/Total
Time Constant, τ	31 / 34
Dissociation Constant, K_d Michaelis Constant, K_m	3 / 29
Enzyme Turnover, V_{max}	3 / 12
Concentration, [A]	3 / 21

- 53 ordinary differential equations and 96 parameters
- None of the unknown parameters has significant effects on peak-time or width of the temporal window.
- Four unknown parameters (time constants and maximum enzyme velocity regarding mGluR-Gq & IP_3-Ca^{2+}) were determined from peak-height of the temporal window.

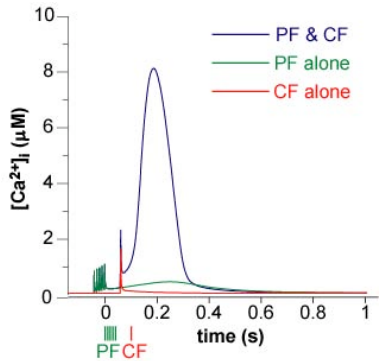
Supralinear Ca^{2+} signal appears when PF is followed by CF

Ca^{2+} Imaging

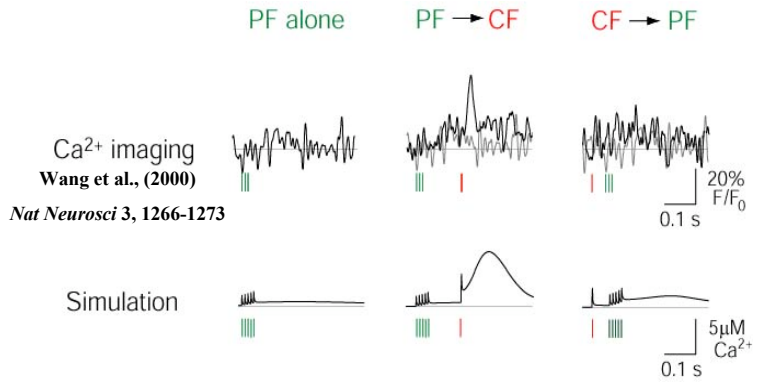
Wang *et al.*, (2000) *Nat Neurosci*



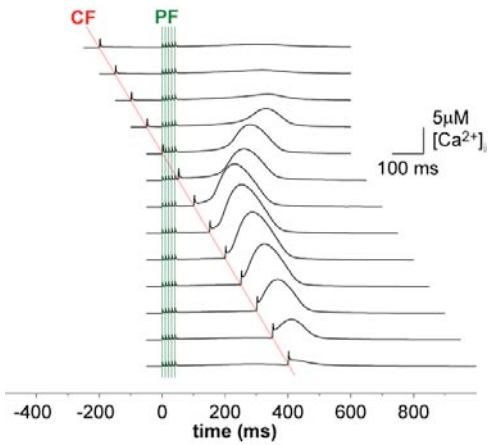
Simulation



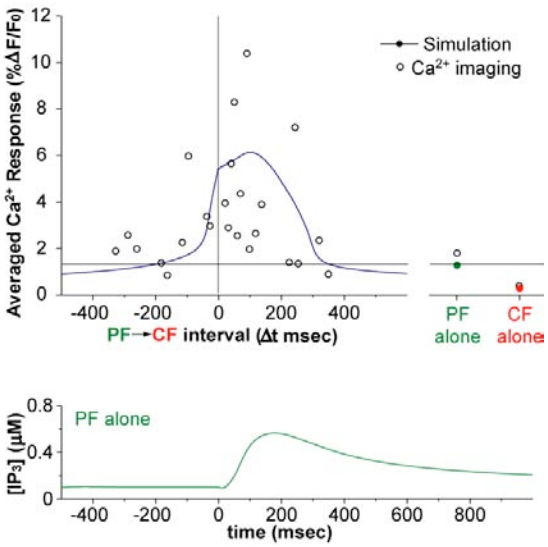
Temporal Window of PF and CF Inputs for Ca^{2+} Signaling and LTD



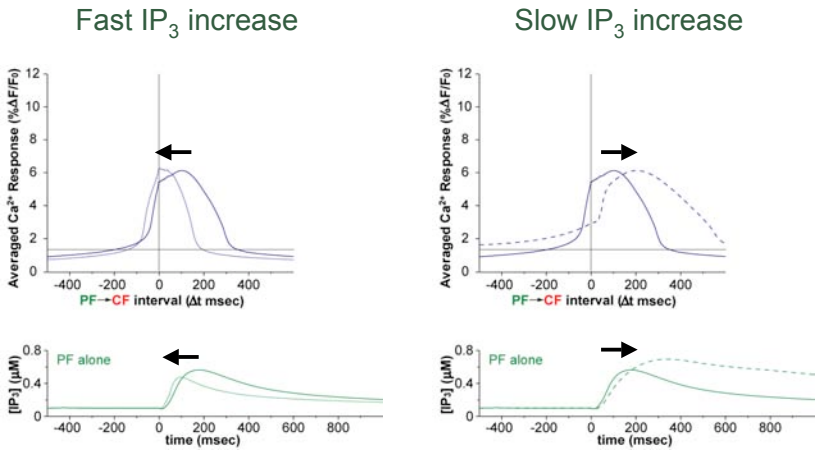
Ca^{2+} Signaling is determined by Timing of PF and CF Inputs



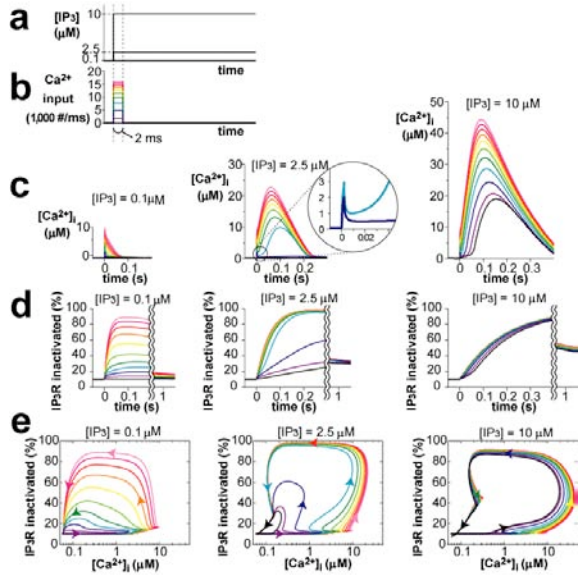
Time Window of Ca^{2+} Response



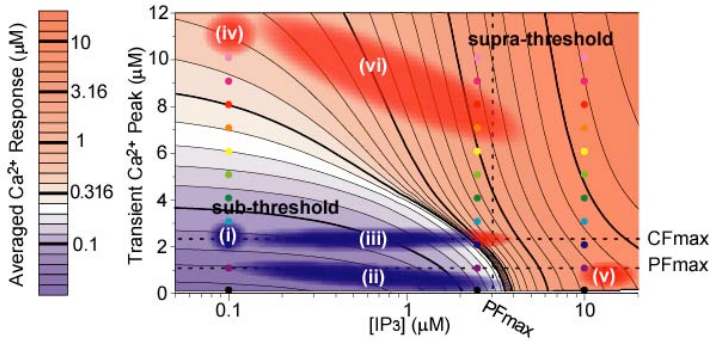
IP_3-Increase Time Course determines LTD Time Window



IP_3-dependent Ca^{2+} Dynamics

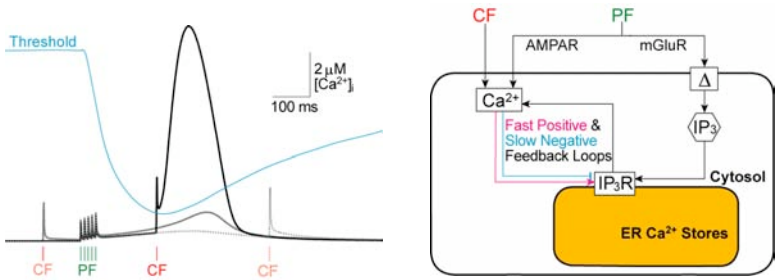


Ca^{2+} Dynamics and LTD Experiments



(i) CF alone does not induce LTD
(ii) PF alone does not induce LTD
(iii) Conjunctive PF-CF induces LTD
(iv) Ca^{2+} uncaging induces LTD
(v) IP_3 uncaging induces LTD
(vi) Massive PF stimulus induces LTD

Schematic Model of Timing-detection



- Delay in slow PF metabotropic pathway compared with fast CF electrical pathway as a mechanism for timing-detection
- Fast positive feedback loop generates large Ca^{2+} signals.
- Slow negative feedback loop shuts down the Ca^{2+} increase.

Summary of Ca^{2+} Dynamics Model

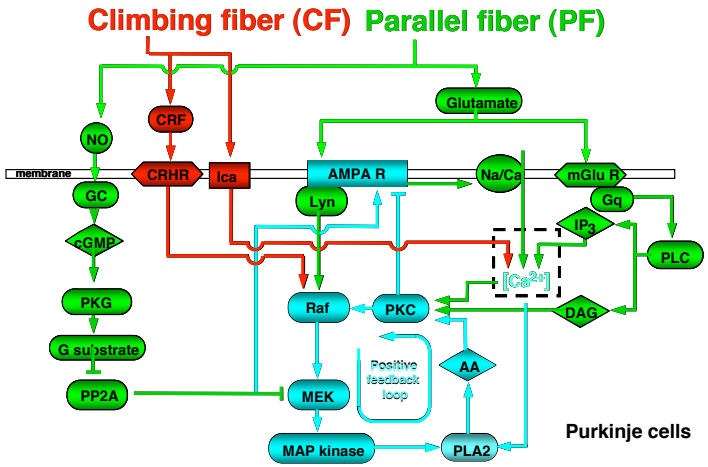
- LTD temporal window reproduced by Ca^{2+} dynamics
- Under physiological conditions, only the input order PF◊CF generates large Ca^{2+} increase.
- Ca^{2+} threshold dynamics dependent on IP_3
- Qualitatively different Ca^{2+} dynamics dependent on different IP_3 concentrations can coherently reproduce diverse data.
- Several experiments to test model predictions
- Only heterosynaptic (PF-CF) conjunctive LTD can implement supervised learning. Homosynatic (PF alone, or CF alone) LTD may implement meta-learning or hyper-parameter tuning.
- Chemical plasticity of temporal window itself is possible.

Computational Theory of Cerebellar STDP

- Computational theory requires that the temporal window should exist in cerebellar LTD
- Behavioral learning experiments suggest the temporal window in cerebellar LTD
- Computational model of Ca^{2+} dynamics within spine coherently reproduces LTD data.
- Signal transduction pathway model of LTD

Kuroda S, Schweighofer N, Kawato M: Exploration of signal transduction pathways in cerebellar long-term depression by kinetic simulation. *Journal of Neuroscience*, **21** 5693-5702 (2001).

LTD Signal Transduction Pathways
AMPAR Phosphorylation



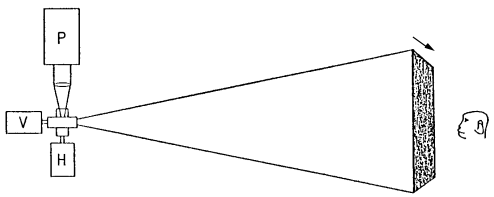
Topics

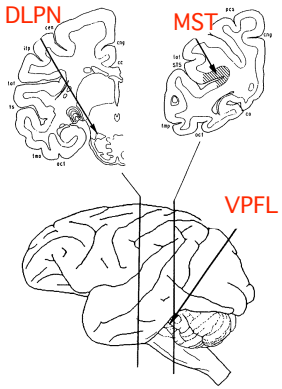
1. Understanding brain by creating brain
2. Basics of cerebellum
3. Internal models are necessary
4. Feedback-error-learning model
5. Cerebellar STDP
6. Neurophysiology of ocular following responses
7. Chaotic resonance in inferior olive
8. Human cerebellum and MOSAIC

Ocular Following Responses and Related Brain Regions

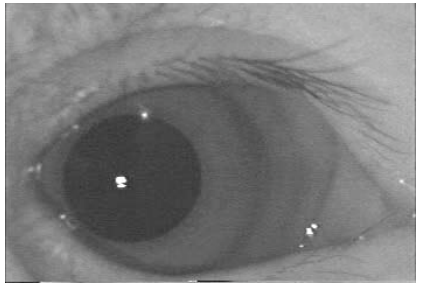
Experiments by Kawano, Shidara, Takemura, Kobayashi et al. (ETL at Tsukuba)

Reflex eye movements induced by visual motion of large field

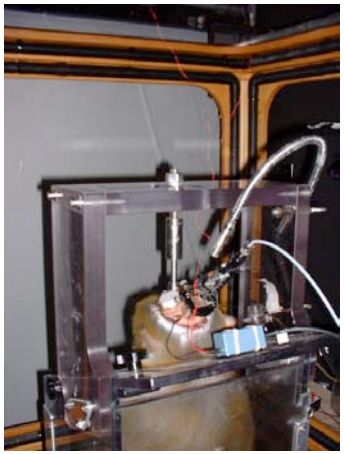




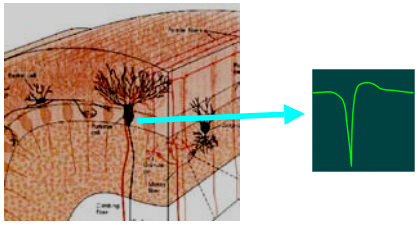
Purkinje Cell Activity of Awake Monkeys during Eye Movement Tasks



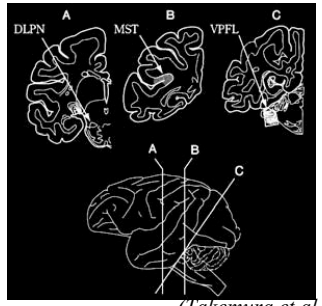
Eye movements are recorded by implanted search coil.



Simple and Complex Spikes of Purkinje Cells in Monkeys during Ocular Following Responses

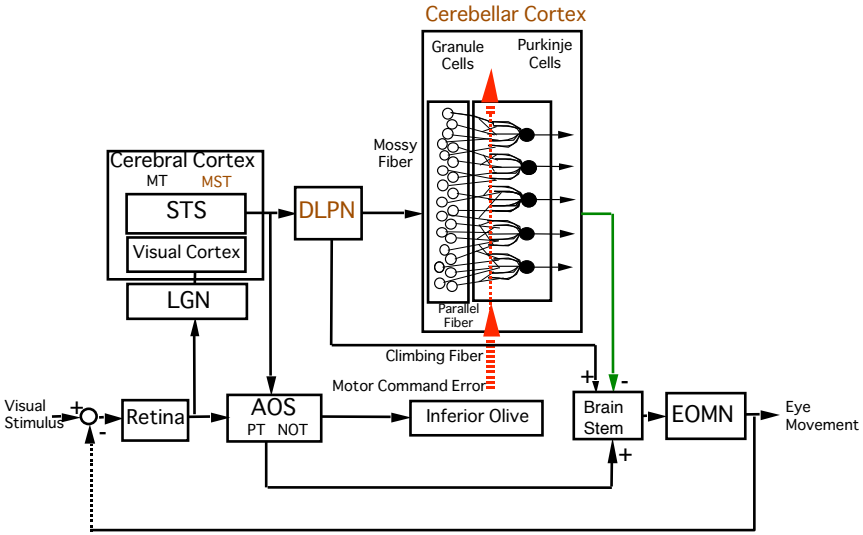


(Kandel 1989)

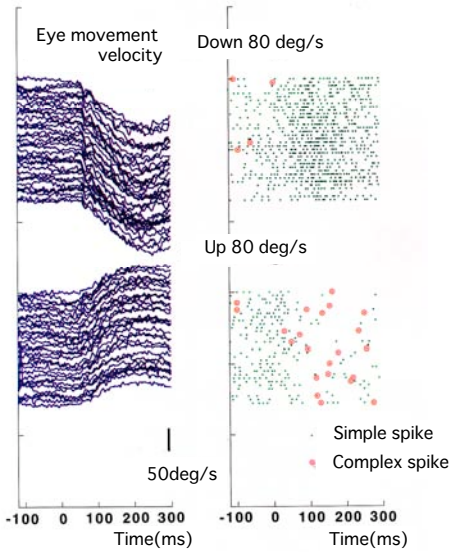


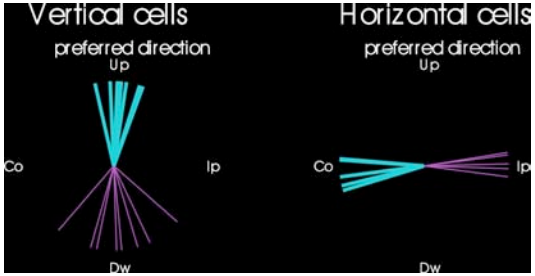
(Takemura et al, 2001)

Ocular Following Responses: (Reflex eye movement induced by movement of large visual field)

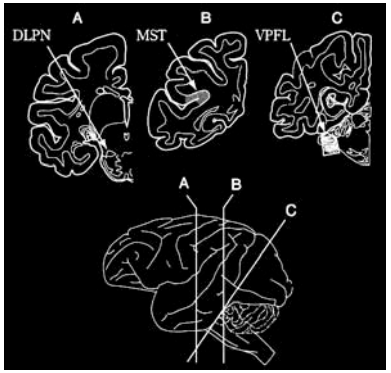


Direction Selectivity of Simple and Complex Spikes

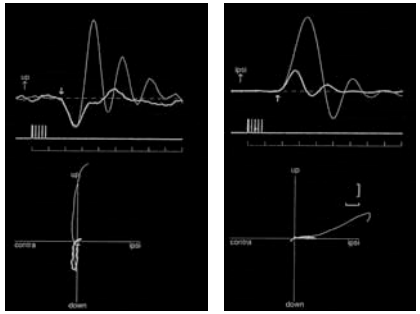




Simple spikes (purple) are maximally induced by ipsiversive or downward stimulus movement.
Complex spikes (blue) are opposite.

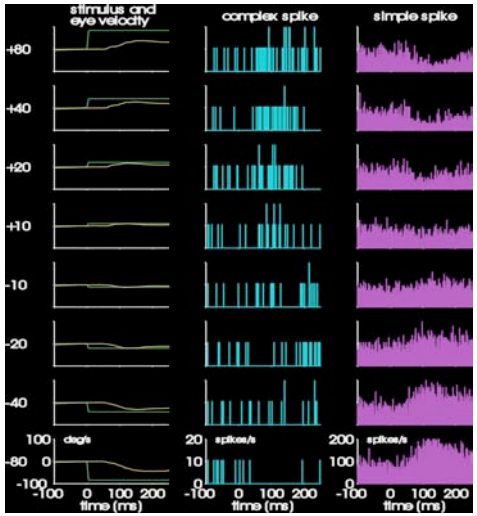


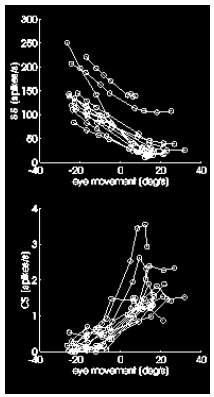
(Takemura 2001)



(Kawano and Shidara1993)

Electrical stimulation evokes ipsiversive or downward movement.



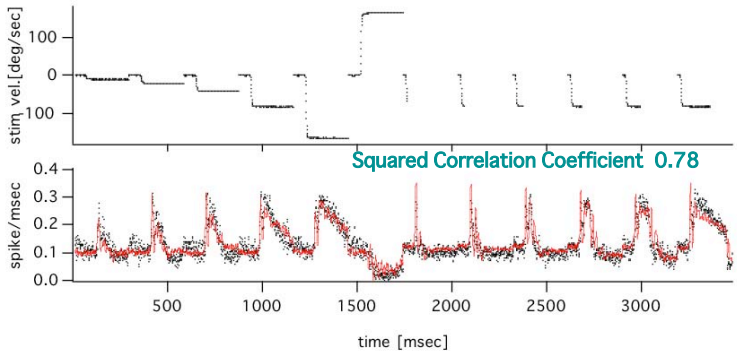


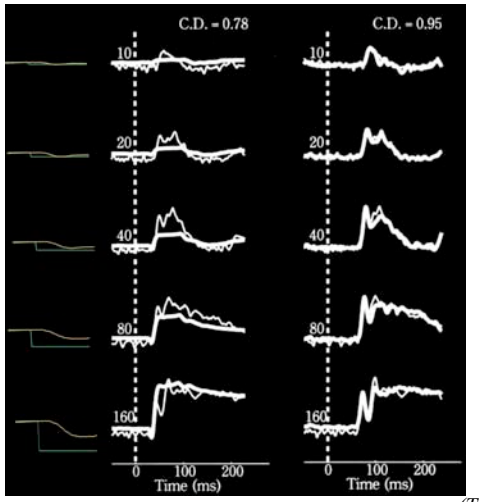
Firing rate is related to magnitude of eye movement.

Reconstruction of Firing Frequency for Different Stimulus Speeds and Duration

f(t): firing frequency *θ(t)*: eye movement

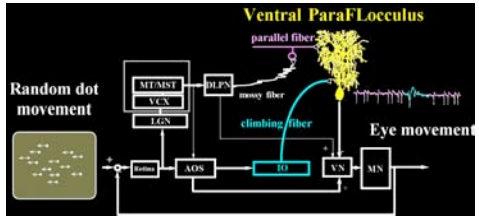
$$f(t) = M\ddot{\theta}(t+\delta) + B\dot{\theta}(t+\delta) + K\theta(t+\delta) + f_{bias}$$

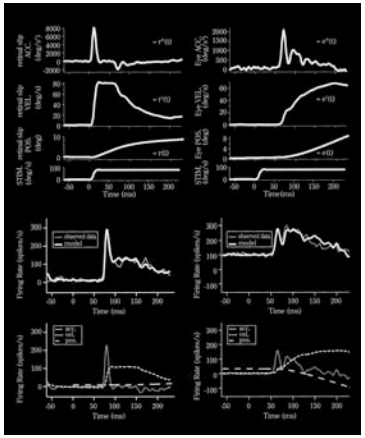




(Takemura et al, 2001)

Simple spike encodes eye movement rather than image motion.

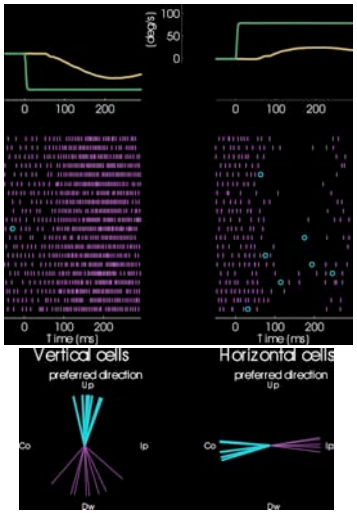


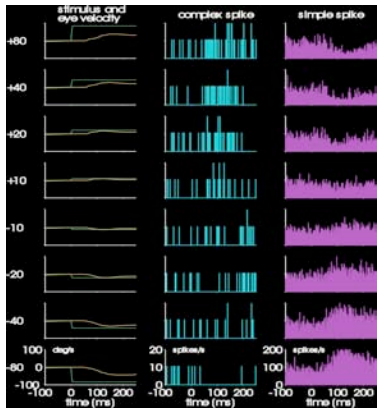


(Takemura et al, 2001)

Simple spike encodes eye movement, but MST/DLPN neurons encode image motion.

Comparing simple spike and complex spike, temporal pattern is opposite, and firing rate is very different (100 spikes/sec vs. 1 spike/sec)





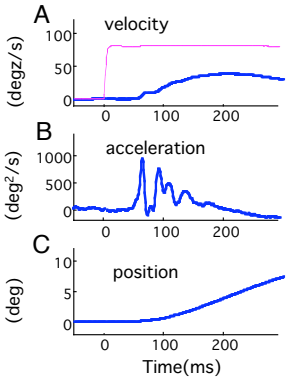
Do climbing fiber inputs carry poor or rich information?

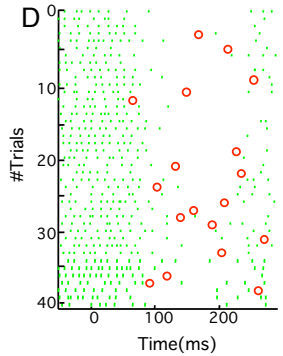
1～2 spikes per second

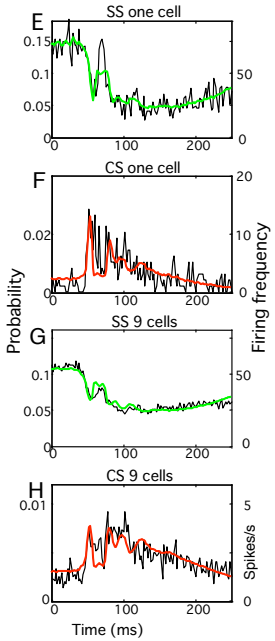
Poor
- Unexpected event detector
- 0/1
- Reinforcement learning

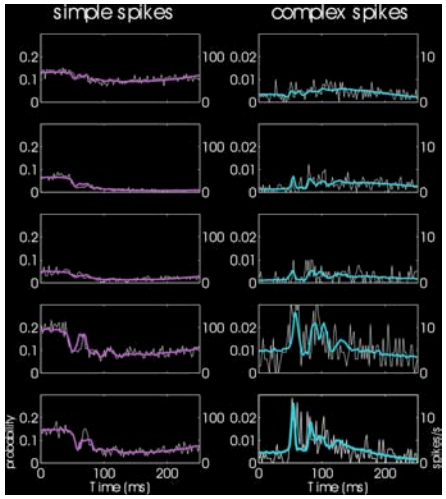
Rich
- Error signal with magnitude and direction
- Firing probability profile (high-frequency temporal pattern)
- feedback-error-learning

Instantaneous firing frequency is information carrier for complex spikes (CS) and simple spikes (SS).

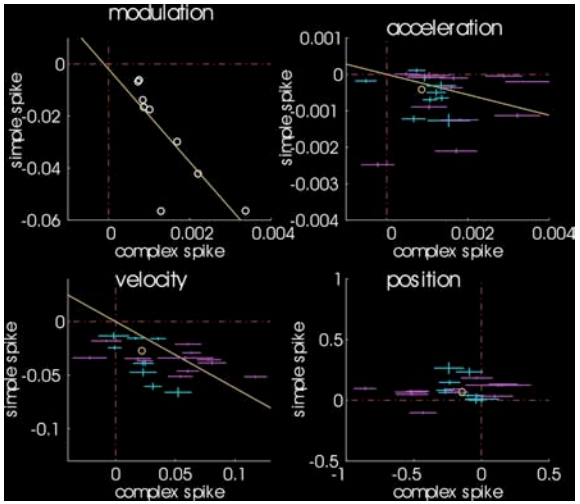






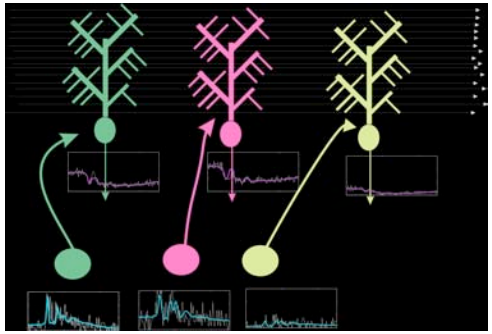


- **Temporal profile of simple spike firing and complex spike firing for each neuron is very similar (just opposite in sign and firing rate is different).**
  - **Complex spike firing may be a template for simple spike firing.**
  - Simple spike of individual cell is prescribed by complex spike.

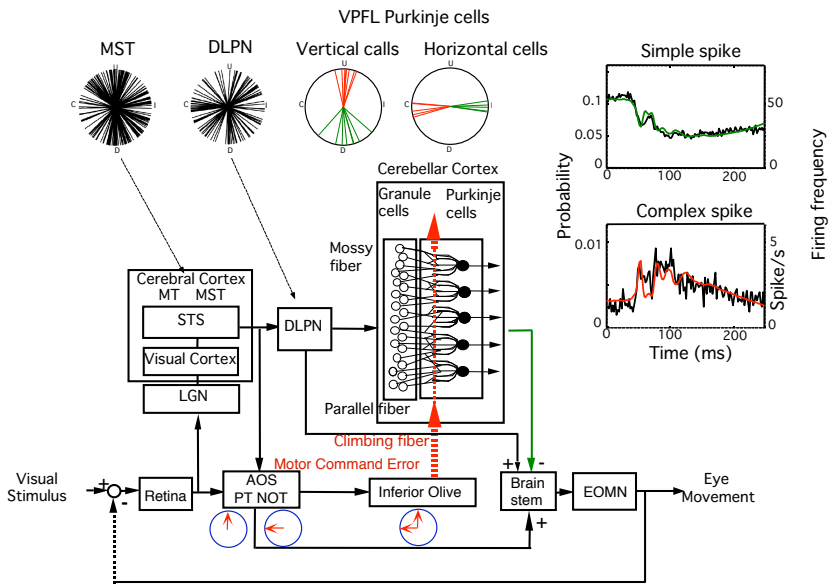


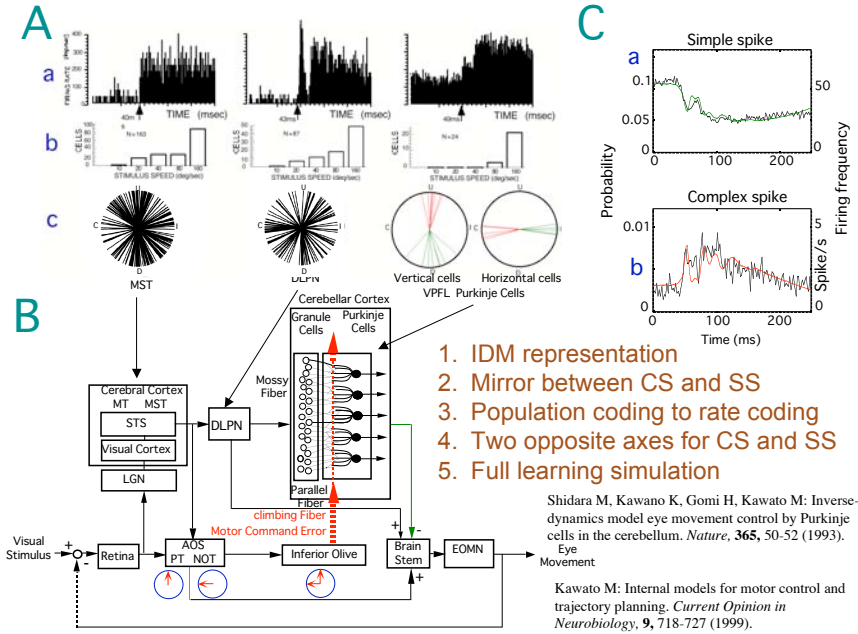
Mirror Image Relationships between CS and SS

Complex Spike as Individual Error Signal for Simple Spike



Teacher shapes student's action by hetero-synaptic plasticity (Long-term depression/potentiation of parallel fiber synapse by climbing fiber activation).





1. IDM representation
2. Mirror between CS and SS
3. Population coding to rate coding
4. Two opposite axes for CS and SS
5. Full learning simulation

Shidara M, Kawano K, Gomi H, Kawato M: Inverse-dynamics model eye movement control by Purkinje cells in the cerebellum. *Nature*, **365,** 50-52 (1993).

Kawato M: Internal models for motor control and trajectory planning. *Current Opinion in Neurobiology*, **9,** 718-727 (1999).

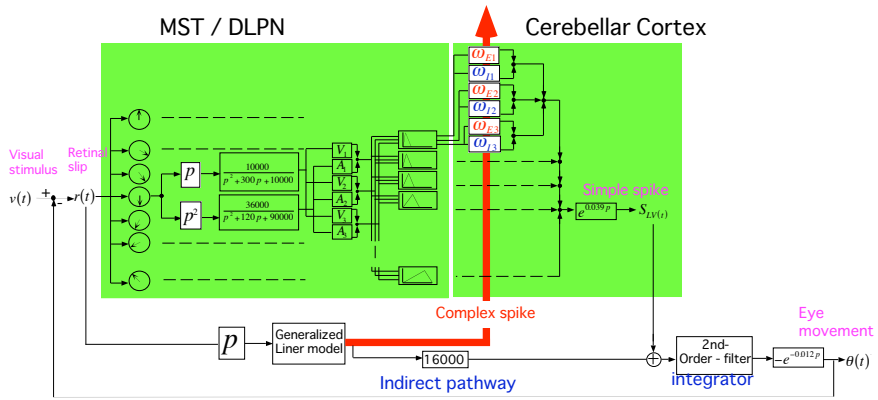
Data Supporting Internal Model Theory and Feedback-Error-Learning

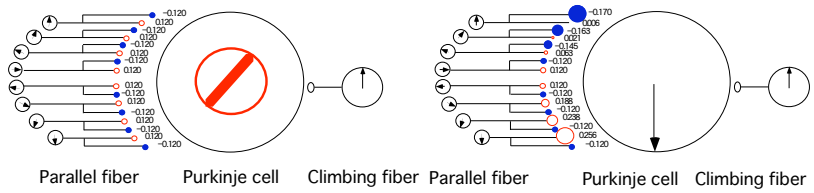
(1) Simple spikes (cerebellar output) are well reconstructed by an inverse dynamics model.

(2) Visual inputs to the cerebellum (MST and DLPN) are not well reconstructed by an inverse dynamics model, but well reconstructed by retinal slips.

(3) Climbing fiber inputs (complex spikes) of ultra-low firing rates convey high-frequency motor command errors.

(4) Drastic change of neural codes from population coding to firing rate coding at parallel-fiber-Purkinje-cell synapses (direction, speed, waveform) is supervised by climbing fiber inputs (accessory optic system).





Cerebral Cortex	Cerebellar Cortex
population coding	firing rate coding
probabilistic internal model	deterministic internal model
cortical dynamics	input-output transformation
probability density	moments
multiple peaks	competing modules
unsupervised learning	supervised learning

	Cerebral Cortex	Cerebellum	Basal Ganglia
Neural circuit	Horizontal and reciprocal	feedforward	loop
Synaptic plasticity	Hebbian, anti-Hebbian	Hetero-synaptic (LTD)	Hebbian and Dopamine
Learning algorithm	Un-supervised, statistical	Supervised learning	Reinforcement learning
Artificial NN	Associatron, Cognitron	Perceptron, MADALIN	Actor-critique architecture
Modularity	Areas, column	Microzone	Dorso-ventral channels
Function: old view	Everything	Movement coordination	Behavior selection
Function: new view	Everything	Everything	Everything
Computational principle	Learning statistical model filter: neighborhood Gaussian horizontal: distant coincidence	Learning of predictive and control model of dynamical systems	Learning of value funciton, reward function
Input, output, and internal representation	Efficient representation based on statistics of the external-world data	Modeling of dynamics based on efficient representations acquired in cerebral cortex	Modeling of value based on emotion and efficient cerebral representation
Computation done	Compress to low-dimension	Learning cause-and-effect	Learning behavior-reward link
Essence	Stocahsticity	Regularity	Adaptive significance
Language analogue	Lexicon	Syntax	Semantics

Adapted, modified and expanded from Doya (1999)

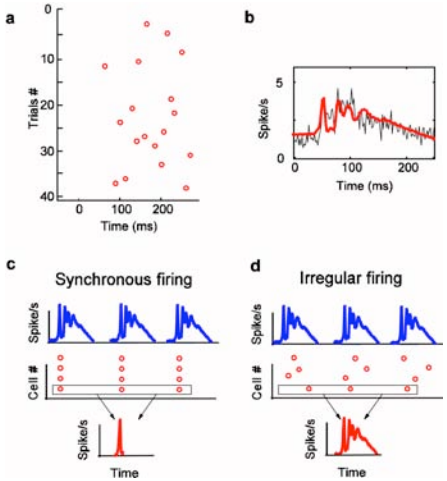
Topics

1. Understanding brain by creating brain
2. Basics of cerebellum
3. Internal models are necessary
4. Feedback-error-learning model
5. Cerebellar STDP
6. Neurophysiology of ocular following responses
7. Chaotic resonance in inferior olive
8. Human cerebellum and MOSAIC

Controversies of Inferior Olive Functions: Rhythmicity and Synchrony versus Learning Signals

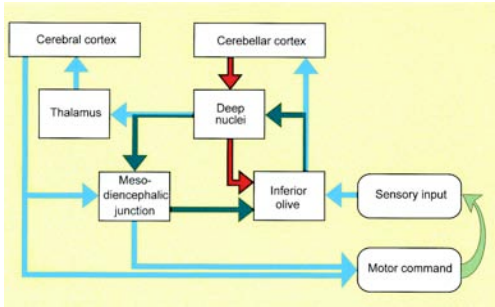
1. Most intensive gap junctions (electrical coupling) between IO neurons
2. Strong rhythmicity and synchrony under anesthetized rodents with blockades of synaptic inputs to IO (Llinas)
3. No rhythmicity and little synchrony for awake monkeys (Thach)
4. Leaning theory should explain gap junctions and low firing rates

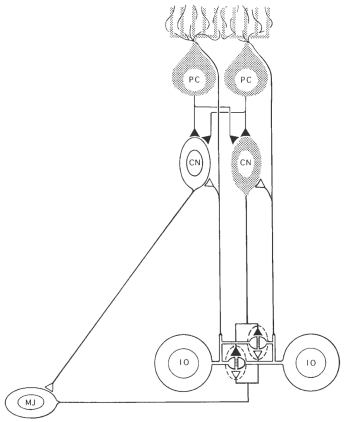
Chaotic Resonance in Inferior Olive



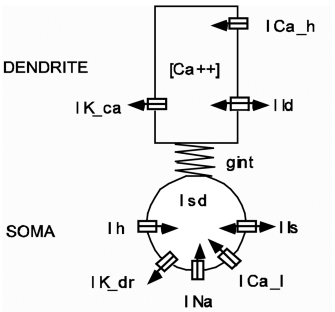
Schweighofer N, Doya K, H. Fukai, Chiron JV, Furukawa T, Kawato. M: Chaos may enhance information transmission in the inferior olive. *Proc Natl Acad Sci USA*., **101**, 4655-4660 (2004).

Microcircuitry of Cerebello-IO Network



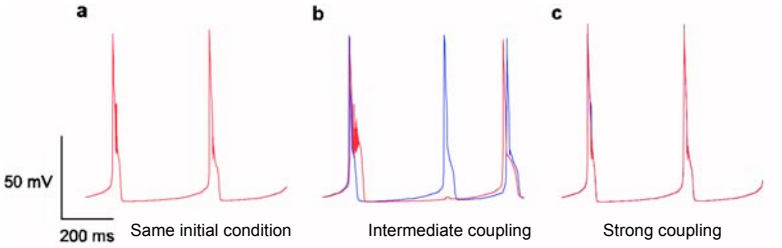


De Zeeuw CI, Simpson JI, Hoogenraad CC, Galjart N, Koekkoek SKE, Ruigrok TJH: Microcircuitry and function of the inferior olive. *Trends in Neurosciences*., **21**, 391-400 (1998).

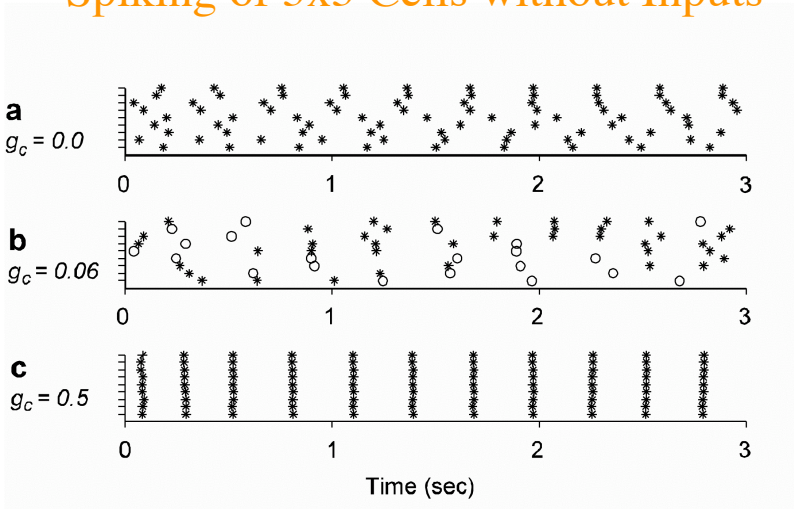


Biophysical model of IO neuron

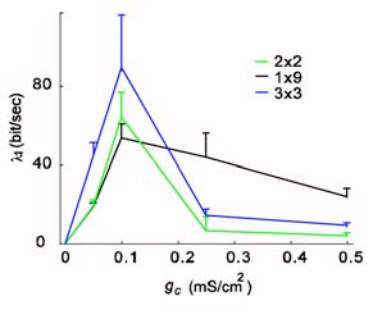
Schweighofer N, Doya K, Kawato M: Electrophysiological propersties of infereor olive neurons: a compartmental model. *Journal of Neurophysiology* **82,** 804-817 (1999).



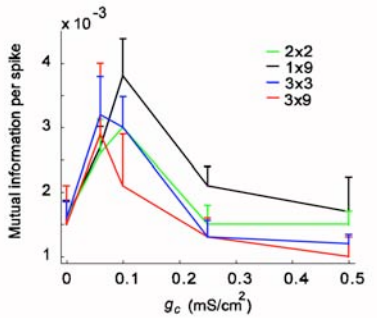
Spiking of 3x3 Cells without Inputs



Largest Lyapunov Exponent



Network Mutual Information per Spike



Conclusions of IO Chaotic Resonance

1. Chaotic resonance can enhance information transmission with low firing frequency.
2. Chaos is more efficient than synaptic noise in information transmission.
3. IO network model can explain decrease of rhythmicity and synchrony with decrease in coupling under physiological synaptic inputs.
4. Partial synchrony of a small subset of IO cells was reproduced.

Topics

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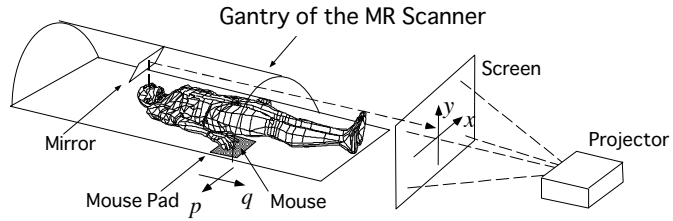
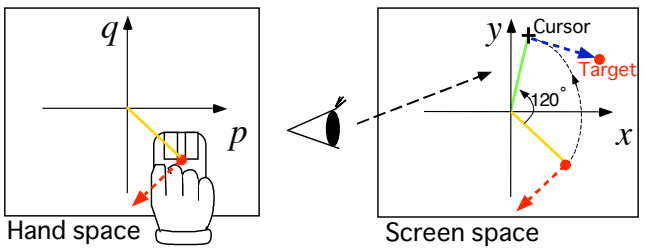


Tracking Task

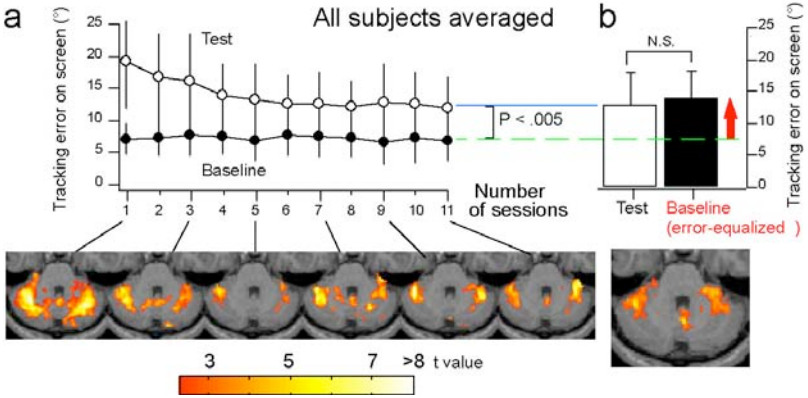
Rotational transformation $\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \cos\alpha & \sin\alpha \\ \sin\alpha & \cos\alpha \end{pmatrix} \begin{pmatrix} p \\ q \end{pmatrix}$



Integral transformation

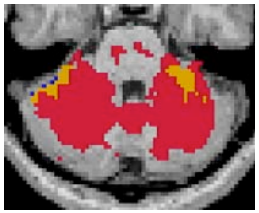
$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} p \\ q \end{pmatrix}$

Behavioral and Imaging Data for Learning Sessions: All Subjects Averaged



Imamizu H, Miyauchi S, Tamada T, Sasaki Y, Takino R, Puetz B, Yoshioka T, Kawato M: Human cerebellar activity reflecting an acquired internal model of a new tool. ***Nature* 403** 192-195(2000)

Two types of activity were observed

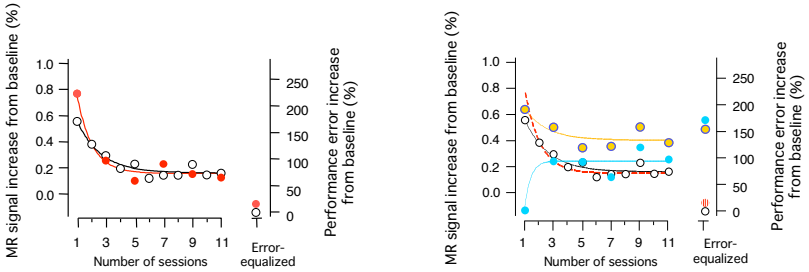


1. Error signals that guide learning
2. Acquired internal models

Correlated with performance error

Correlated with the rotation after learning while the errors were equalized

Conjunctions of and



Switching Modules by Responsibility Signal λ_i (Goodness of Prediction)

Responsibility signal: relative goodness of Prediction by forward models

$$\lambda_i(t) = \frac{\exp\left\{-\left\|x_A(t) - x_i(t)\right\|^2\right\}}{\sum_{j=1}^{n} \exp\left\{-\left\|x_A(t) - x_j(t)\right\|^2\right\}} \quad (1)$$

Weighting of motor commands from Inverse models

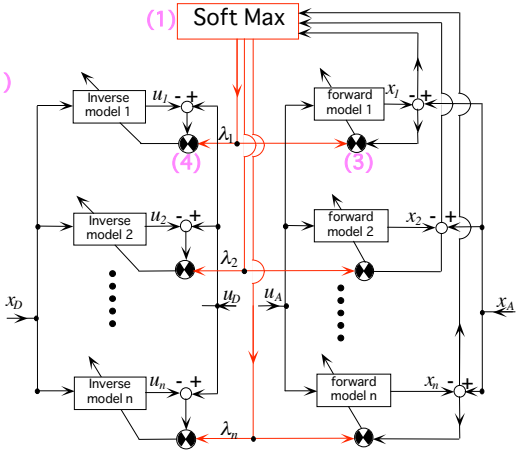
$$u_E(t) = \sum_{i=1}^{n} \lambda_i(t)\, u_i(t) \quad (2)$$

Gating of forward model learning

$$\frac{dw_i}{dt} = \varepsilon\, \lambda_i(t) \frac{d\phi_i}{dw_i}\left(x_A(t) - x_i(t)\right) \quad (3)$$

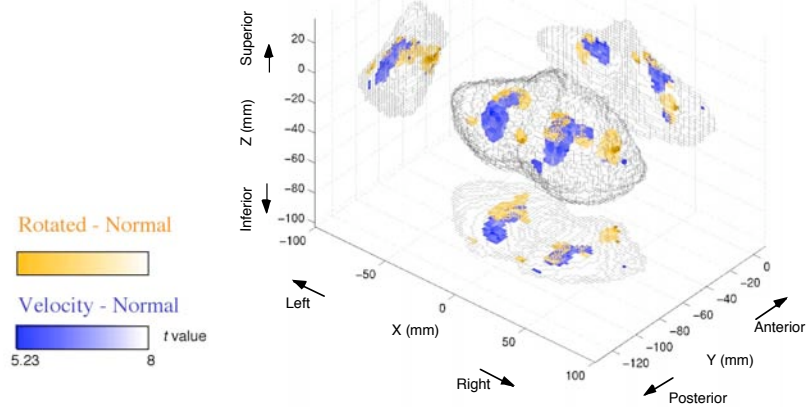
Gating of inverse model learning

$$\frac{d\alpha_i}{dt} = \varepsilon\, \lambda_i(t) \frac{d\psi_i}{d\alpha_i}\left(u_D(t) - u_i(t)\right) \quad (4)$$



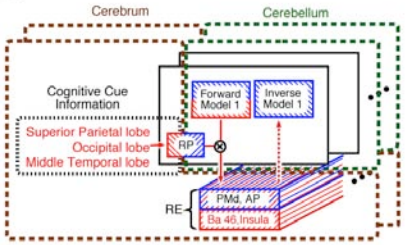
Wolpert D, Kawato M: Multiple paired forward and inverse models for motor control. *Neural Networks* **11,** 1317-1329 (1998).

Multiple Internal Models

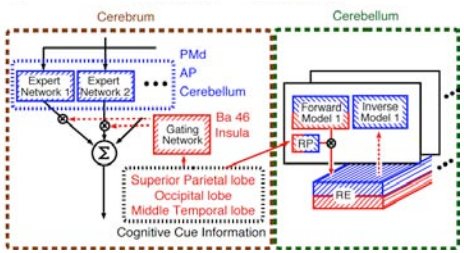


Imamizu H, Kuroda T, Miyauchi S, Yoshioka T, Kawato M: Modular organization of internal models of tools in the human cerebellum. *Proc Natl Acad Sci USA.*, **100**, 5461-5466 (2003).

Major part of MOSAIC is in cerebellum



Prefrontal cortex; gating and MOSAIC cerebellum



Imamizu H, Kuroda T, Yoshioka T, Kawato M: Functional magnetic resonance imaging examination of two modular architectures for switching multiple internal models. *Journal of Neuroscience* **24**, 1173-1181(2004)