Integration of Paired Spiking Cerebellar Models for Voluntary Movement Adaptation in a Closed-Loop Neuro-Robotic Experiment. A Simulation Study

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Integration of paired spiking cerebellar models for voluntary movement adaptation in a closed-loop neuro-robotic experiment. A simulation study

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Abstract— **Motor control is a very important feature in the human brain to achieve optimal performance in motor tasks. The biological basis of this feature can be better understood by emulating the cerebellar mechanisms of learning. The cerebellum plays a key role in implementing fine motor control, since it extracts the information about movements from sensory-motor signals, stores it by means of internal models and uses them to adapt to the environment. The hypothesis is that different internal models could work both independently and dependently. So far, there have been a few studies that aimed to prove their dependency; however, this hypothesis has not been widely used in robot control. The purpose of this work is to build paired spiking cerebellar models and to incorporate them into a biologically plausible composite robotic control architecture for movement adaptation. This is achieved by combining feedback error learning and cerebellar internal models theories. Thus the control architecture is composed of cerebellar feed-forward and recurrent loops for torque-based control of a robot. The spiking cerebellar models are able to correct and improve the performance of the two-degrees of freedom robot module Fable by providing both adaptive torque corrections and sensory corrections to the reference generated by the trajectory planner. Simulations are carried out in the Neurorobotics platform of the Human Brain Project. Results show that the contribution provided by cerebellar learning leads to an optimization of the performance with errors being reduced by 30% compared with the case where the cerebellar contribution is not applied.**

I. INTRODUCTION

Neuroscience and robotics play a conjoint role in building intelligent robotic systems (neurorobots) that mimic human behavior in performing complex, coordinated and precise movements [1]. The biological basis of this ability is still not completely understood [2], however, by emulating the cerebellar mechanisms of learning, new insights can be revealed. As a matter of fact, the cerebellum plays a key role in implementing fine motor control [3], allowing actions to be performed rapidly and precisely by reason of its predictive control. Neurorobots are built by combining robotic agents and biologically plausible neural systems and can be used to investigate how neural representations and control systems adapt to a dynamic environment.

It has been widely accepted that the cerebellum stores internal models to represent input-output properties of a body part [4], [5]: forward and inverse models. The existence of an internal model dependency has been suggested by [6], [7]. Considering the structure of the control system for voluntary movements, [8] depicted two different plausible control paths of the connections between the cerebral cortex and the cerebellum that have both anatomical and physiological bases: the feed-forward [9], [10], [11], and the recurrent control loops [12], [13], [14]; comparisons among the two schemes are also available in literature [15].

[16] proposed an architecture based on coupled inverse and forward models. Nevertheless, the pairing of internal models remains only partially investigated [13], [17] and they have not been used widely in robot control. In this work a novel composite bio-mimetic control architecture in which a feedback controller and paired spiking cerebellar inverse and forward models are implemented and combined together. The spiking cerebellar models provide adaptive torque corrections (inverse model/feed-forward loop) to the ones provided by the feedback controller, and sensory corrections to the reference generated by the trajectory planner (forward model/recurrent loop). The spiking cerebellar model was built and integrated in the Neurorobotics Platform (NRP) of the Human Brain Project (HBP) [18] to evaluate the sensory-motor cerebellar adaptation, mediated by a plasticity mechanism located at the cerebellar molecular layer, for voluntary control of hand movements. This simulation study adopts an experimental setup (eight-shape trajectory) widely used by computational neuroscientists to better understand the contribution of certain specific cerebellar properties (i.e., distributed plasticity, neural properties and coding, cerebellar topology, etc.) to fast adaptation. Finally, this work shows the proof of principle of an embodiment of paired spiking cerebellar models in the NRP for robot control.

II. METHODS

A. Voluntary Movement Adaptation

There is clear evidence that motor systems are organized in functional hierarchies where each level focuses on a different task level as presented in [19] and in Fig. 6.1 of [3].

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This research includes a few of the known pathways, seeking to establish a minimal setup for a closed-loop system with adaptive behavior:

- **Premotor and Sensory Cortex**: is where the motor plan is being generated by converting an abstract intention into a representation for how to achieve this through movement. This motor plan is passed on to both the Motor Cortex and the Inferior Olive.
- **Motor Cortex**: receives the abstract motor plan and transforms it into motor commands, sending these motor commands directly to the spinal cord (motor) as well as a to the cerebellum (efference copy).
- **Inferior Olive**: receives the motor plan from the Premotor and Sensory Cortex as well as the sensory information relating limb movement and positions. These signals are compared and converted into a teaching or error signal, which is sent to the cerebellum.
- **Cerebellum**: receives both the teaching signal from the Inferior Olive, sensory information about limb movement and positions, as well as the efference copy of motor commands. These inputs are then used to "emit corrective signals that can affect movement directly (through the spinal cord/brainstem - feed-forward loop) or change the motor plan itself (through the motor cortex - recurrent loop)" [3].
- **Spinal Cord (Motor)**: is where the initial motor commands from the Motor Cortex and the corrective signal from the cerebellum are combined into the final motor command. This stimulation is passed on to the body. Once the task is being performed, the internal sensory information is updated and used to adapt the movement.

In this paper, most of these elements are modeled in a simplified way in order to resemble their main function but yet having a comprehensive overview of the biological architecture.

B. Composite Control System Architecture

The role of the cerebellum has been widely mimicked in feed-forward control architectures by spiking neural networks. By means of the feedback error learning, the original commands from the motor cortex can be adjusted by feed-forward corrections [20]. This contribution corresponds to the red line in Fig. 1 that directly corrects torque values. Since the need of complex neural structures to estimate the motor error may be required [21], Porrill and Dean suggest the use of the recurrent control architecture. This is represented with the blue line in Fig. 1, where the cerebellar contribution provides sensory corrections. By having a certain knowledge of the signals used for the learning process this configuration avoids the distal error problem [21], [14]. In this paper we propose the combination of the feed-forward and recurrent approaches in a whole control system, the composite control architecture as shown in Fig. 1.

The trajectory planner, emulating the premotor and sensory cortex, provides the desired trajectory involving the desired state (position, velocity and torque values) to the
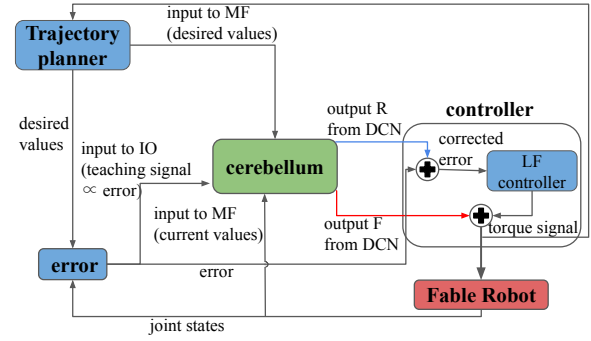

Fig. 1. The composite control system architecture. The spiking cerebellar model provides effective corrective position, and torque add-on terms from the error signal related to sensory-motor input to improve the performance of the desired robotic task. The output signals of the cerebellum are provided by the Deep cerebellar Nuclei (DCN) and are the result of the feed-forward model learning (F, red line) and the recurrent model learning (R, blue line). The desired values of the trajectory are transmitted through the mossy fibers (MF) and the teaching signal (error) is carried by the inferior olive (IO) through the cerebellar models.

cerebellum and to the motor cortex, which is represented as Learning Feedback (LF) controller (see details in [14]) in Fig. 1. The position information is shared by the feed-forward and recurrent models whereas the velocity is only used in the feed-forward and the desired torque in the recurrent.

The LF controller [14] is used to ensure the initial stability of the system before the cerebellar contribution is giving corrections. The LF controller produces the necessary joint torque values to obtain the robust, but not precise execution of the planned trajectory. The tuning of this controller was done in a non-optimal way in order to see the effects of the cerebellar contribution over time. The values used are $K_1 = [0.44, 1.0]$, $K_2 = [0.056, 0.04]$, $K_3 = [0.074, 0.5]$, where each gain is a vector containing the value of the gain for each joint (see description of the robot in Section II-E).

The error block in Fig. 1 compares the motor plan and the sensory information in order to calculate the joint error that will be used as the error signal. This block partially embodies the task of the inferior olive since the cerebellum uses it as the teaching signal that is going to guide it to correct wrongly performed movements. Additionally, the error value is used by the LF controller in order to produce the torque signal that is going to be sent to the Fable robot. In the case where the cerebellar contribution is not active, this error signal goes directly into the LF controller. However, when the cerebellum is active, there are two different outputs corresponding to the feed-forward and the recurrent contributions. The recurrent part provides a correction to the error in the input to the LF controller. On the other hand, the torque command computed by the LF controller is adapted by the feed-forward contribution. The combination of both will improve the performance of the controller as shown in results section.

C. Neurorobotics Platform

The Neurorobotics Platform (NRP) [18] was created and evolved in the framework of the HBP, a multidisciplinary

project integrating neuroscience scientists, computational neuroscientists, robotic engineers as well as software developers amongst others. One of the major goals of NRP lies in facilitating the implementation of simulated brain-body-environment experiments. Beyond providing access to robotic platforms to non-experts (such as the neuroscientific community), it also facilitates the reproducibility of the results by other research groups, since not only the experiment description but also the specific experimental setup can be shared and reproduced. The NRP integrates all the tools necessary for embedding artificial brain models to robotic systems. In particular, it facilitates the coordination between spiking neural networks and continuous time system. The implementation of the neural systems is done in NEST [22], which is connected to the virtual robot and its environment, that are implemented in Gazebo.

D. Cerebellar Model

The cerebellar brain region is widely regarded as an integral part of motor control [3]. Multiple hypotheses for its role have been proposed, though, at the current stage, this is not possible to have a unique answer [23]. The cerebellum contains more than half of the brain neurons condensed in 1/10th of the brain volume and has projections to several different places in the brain. The cellular structure of the cerebellum is highly uniform and organized in a repetitive structure of microcircuits, which suggests that it performs the same type of general computation on various different inputs [23].

This research employs a simplified version of the cerebellar microcircuit, also known as the computing unit of the cerebellum. This simplified circuit is an extension of the seminal theory by Marr, Albus and Ito [24], [25] and consists of two types of cells: Granule Cells (GR) and Purkinje cells (PC) with approximately 10-100 Billion GRs and 1.5 Million PCs in the human cerebellum. Further cerebellar elements included in this model are the Inferior Olive (IO) and Deep cerebellar Nuclei (DCN). These are connected by three types of fibers (neuronal axons). These fibers are mossy fiber (MFs), parallel fibers (PFs) and climbing fibers (CFs). A visual representation of the complete cerebellar microcircuit can be found in Fig. 6.3 of [3].

Overview of the cellular connections (based on [19]): MFs serve as the prime input to the cerebellar microcircuit. They are excitatory axons which branch several times and synapse with two types of cells: DCN and GR. Their connection to the DCN passes their signal directly from the input to the output. This signal can then be modulated by the GR-PC pathway. This happens through the MF-GR synapses. The GR then projects into the Molecular layer, referred to as PF. These PFs form excitatory synapses on about 100 PCs along the way. Each PC receives excitatory input from around 200.000 PF synapses. When a PCs spikes due to PF input it is called a Simple Spike (SS) [23]. SSs have been found to predicts kinematics [26], [19], the frequency of which has been found to encode amplitude [23]. Each PC furthermore receives excitatory input from a single CF,

which wraps around the PC, synapsing at multiple sites. When excited by a CF, a PC will exhibit a so-called Complex Spike (CS) which is found to be a key driver for plasticity of the GR-PC synapses. Each CF branches to about 10 different PCs and forming about excitatory 300 synapses on each. The PCs' axons project down into the white matter where they form inhibitory synapses on the DCNs. This closes the loop, allowing the PCs to modulate the DCN output [23].

Adaptive learning: The scientific literature is currently aware of 15 different types of plasticity in the cerebellum [27]. While studies have shown that the interaction between multiple plasticities can increase performance [28], the present study focuses only on the most well-known plasticity, the GR-PC Spike-timing-dependent plasticity (STDP).

The GR-PC STDP is classified in two types: Long Term Depression (LTD) and Long Term Potentiation (LTP). At the event of a CS, the CF synapses on the spiking PC that were active at a certain interval prior to the spike will experience depression (LTD) [26], [29].

One of the most important aspects to understand is the CF-PC adaptation. While it is not known what signals travel up the CFs from the IO, it is widely believed to form some kind of error or teaching signal. CFs fire at very low rates of about 1 Hz in their baseline, seemingly at random times [23]. Their spike rate can increase to a maximum of 5-10 Hz and each CF spike reliably induces a CS in the PC, causing adaptation [26], [23].

Composite topology and learning capabilities: A modified version of the cerebellar model introduced in [30] is presented in order to comply with the proposed composite architecture. In Fig. 2 a full description of the model is presented. It can be inspected that the circuit shown in Fig. 2.a of [30] has been duplicated. One of the loops is used to calculate the feed-forward contribution and the other one the recurrent. Even though they are independent, they share the error information coming from the IOs.

The sensory information is carried by the MFs. The feed-forward loop uses desired position and velocity values as well as the current state of the body. On the other hand, the recurrent MFs inputs consist of the desired position and torque value, and the current state. This sensory-motor information is going to be decorrelated by GRs [31], to then reach the CF-PC-DCN branch. This part of the circuit is where the learning is achieved. The approach implemented is the following for both feed-forward and recurrent learning: the CF-PC-DCN sub-neural populations are equally divided in positive and negative parts. Each of them is active depending on the sign of the error provided by the teaching signal. Finally there is a positive and a negative cerebellar contribution based on the deviation of the error. Before applying this value to the body, the average of the output is calculated to give the absolute contribution necessary to correct the ongoing performance (i.e., the motor torque, for the feed-forward loop or the sensory prediction, for the recurrent loop).

This new structure consists of a combination between the cerebellar microcircuit for the feed-forward case and the recurrent one. Each of them has its own close-loop with
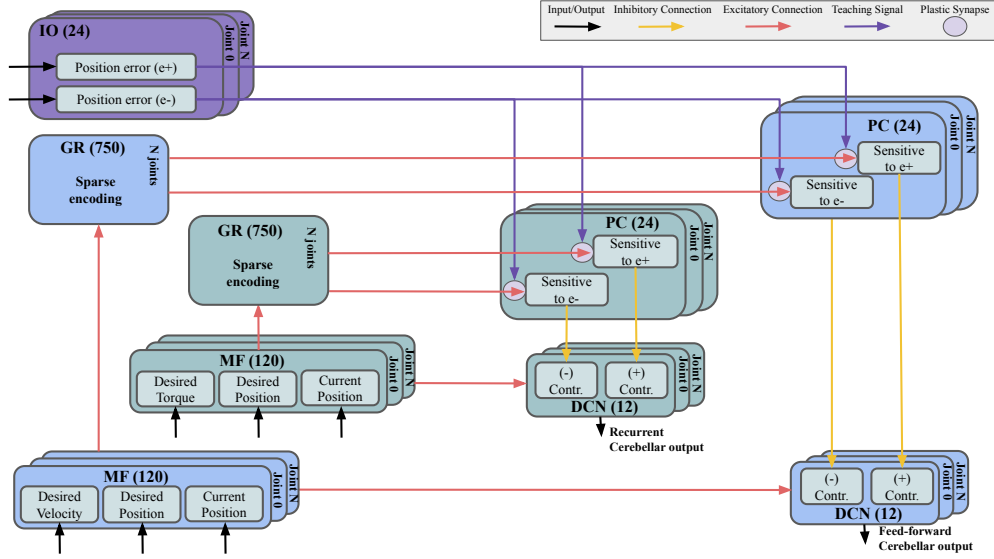
Fig. 2. Simplified composite cerebellar topology (adapted from [28]). The blue blocks form the feed-forward cerebellar loop and the green blocks form the recurrent cerebellar loop. The two loops share the IO block. However this teaching signal is going to guide two different learning processes, the torque command adaptation and the sensory information correction. In addition, the teaching signal is specialized in a positive and a negative part depending on the deviation of the error signal from the desired value. All the block are divided into N sub-blocks (N is the number of robot joints) with identical internal neural representation.

a common teaching signal that is based on the difference between the desired position values and the current ones. Finally, following the different pathways of the composite control architecture, it can be seen that the combination of both feed-forward and recurrent DCN contributions allows to have an ongoing adaptation of the movement.

It can be noticed that the number of joints of the robotic system does not imply a modification of the topology. This is due to the fact that the structure is modular, which allows a scalable system to be implemented in a straight forward way.

This cerebellar model was developed in NEST within the NRP where all neurons are implemented as Leaky Integrate and Fire models and all synapses are modeled as conductances.

E. Fable Robot

Fable is a modular robot system consisting of detachable modules [32]. This project uses its joint module SDF model to run the robot simulations in NRP. The module has 3 links and 2 actuated revolute joints. The two joints are rotating around different axes, with an offset of 90 degrees between the two. The robot model is configured with mass distribution and inertia equal to its physical counterpart. In this work, the torque is applied directly to the joints, whereas in a real robot, torque would be provided by an actuator with its own dynamics. Tests on a single active module with 2 degrees of freedom (DOFs) were conducted where the robot arm is attached to the ground by its base link, and is standing upright, able to move 90 degrees in both directions of both joints as seen in Fig. 3. The task performed in the different tests is an eight-shaped trajectory described in (1), where y_0 and y_1 are the angular positions of joint 0 and joint 1, which

depend on the time step t, the phase θ and the amplitude of the eight figure defined by A.

$$y_0 = Asin(\pi t), \quad y_1 = Asin(\pi t + \theta) \tag{1}$$

Fig. 3. Experimental set up. One module of the Fable robot arm is fixed to a table in order to avoid undesired dynamics.

F. Coding/Decoding integration

The Fable robot arm and the spiking cerebellar module work with different types of information. The robotics system simulated in Gazebo, provides sensory-motor data (inputs of the cerebellar model) such as current position, velocities, and torques of the joints. Furthermore, its motors are actuated by a torque command. The cerebellum simulated in NEST provides spiking activity (output of the cerebellar model). In order to be able to coordinate and translate analog signals coming from the robot to the cerebellum, and spiking activity coming from the cerebellum towards the robot, there is a need of some sort of transfer functions or interfaces. [30] proposes the use of three different interfaces.

The first one computes the input current for MFs with a radial basis function (RBF) method. RBF centers are uniformly spread along the dimensions of the sensory input, with their widths tuned to avoid the overlapping in the response of consecutive MF.

The second interface is needed to have the correct mapping from joint errors into the teaching signal computed by the IO activity. As previously mentioned in Section II-D, the CFs base firing rate is very low and it happens at random times. This irregular behavior could be approached in a statistical way by sampling the error signal over multiple steps [30]. The firing rate is modeled by a Poisson generator function provided by the NRP. As proved in [33], [34], the probability of having spikes in the IO can be seen as a proportional value to the error signal.

The last interface needed to translate the different data and to be able to close the control loop is the one that decodes the output of the cerebellum (DCN) from neural activity to an analog signal. The feed-forward and recurrent parts of the cerebellum are going to have their own contributions. Each of them is going to be specialized depending on the sign of the teaching signal. This will result in a cerebellar output with a positive and negative part. By computing the moving average of the firing rate of the positive and negative contribution, it is possible to calculate the mean DCN value that is going to be proportional to the desired analog signal [35].

III. RESULTS

The system performance, position error of the joints and the neural activity, is recorded and saved through the tools offered by the NRP. To measure the performance of the composite control architecture, the robot is given the desired trajectory, described in (1), that has to be repeated for 100 seconds. Once the task is finished, the moving average of the angular position error, which is one of the possible values used to verify the adaptive contribution of the cerebellum, is calculated. Results presented in Fig. 4 show that the composite control architecture allows the reduction of the position error in both joints when compared with the LF controller. At the beginning of the experiment the variance between the two joints with the cerebellar controller is bigger than the LF controller because of the initial online learning phase of the cerebellum. The first joint has to compensate the dynamics of the joint two due to the configuration of the robot. After less than 20 seconds of execution, the performance improves significantly reaching a stable overall decrease of over 30% after 60-65 seconds of simulation.

When analyzing the learning process of the cerebellum, Fig. 5 shows the evolution of the activity of the PC population (positive and negative part) for the feed-forward contribution on the first joint. Starting with a baseline of around 100 Hz [28] that inhibits the activity in the DCN, the frequency evolves to values between 80-90 Hz. This is due to the adaptation provided by the PF-PC plasticity that is modulated by the IO teaching signal. When the error signal increases, this is going to be translated in a reduction of the PC spiking frequency that will allow the increase of the DCN activity, which means an increment of the cerebellar contribution. Notice that the evolution of the PC is going to oscillate along with the execution of the task; when the robot needs to correct its position, the DCN is going to be

active due to a reduction of the PC activity. On the other hand, when the error has been reduced, the PC activity will increase again, and the DCN will stop giving corrections. This process is repeated during the moving task. Similar behavior can be observed for the other PCs, of both the feed-forward and the recurrent loops, and for the second joint. Of course, each PC population evolves differently, according to the correction (motor or sensory) that it has to generate.

The results prove that the composite control architecture implemented in the NRP helps in adapting the motor control of the Fable robot. The feed-forward and recurrent part of the extended cerebellum proposed in this paper receive different information in their respective input layers (MF), including an efference copy of the desired motor command [19]. This will help in having two different learning processes that are going to be specialized in a positive and negative part depending on the value of the teaching signal, resulting in two different cerebellar outputs (DCN).

Furthermore, the way the cerebellar module has been developed provides a scalability property that is needed in modular robotics and also in any other robotic systems with multiple DOFs, where a different number of joints can be simultaneously active.
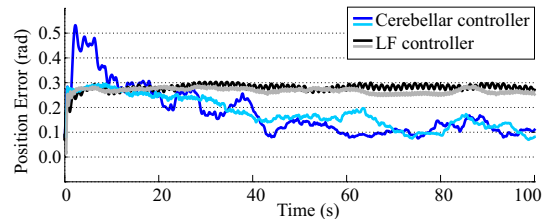

Fig. 4. Error evolution of the cerebellar composite control loop and the LF controller without cerebellar corrective terms acting on the loop. The plot shows the moving average of the angular position error in radians, darker and lighter lines represent the angular error of the first and the second joint, respectively.
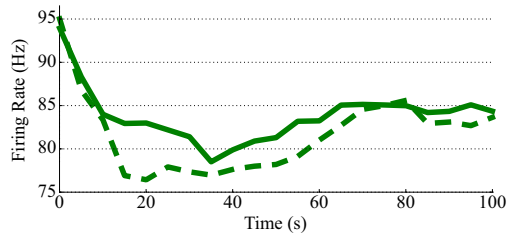

Fig. 5. The average Purkinje cell (PC) activity (Hz) related to the first joint of the Fable robot module, which was recorded during the learning of feed-forward cerebellar model. The solid line represents the positive contribution, while the dotted line represents the negative contribution.

IV. CONCLUSIONS

In this work, we present a case-of-study of cerebellar embodiment in a composite control system architecture for voluntary movement adaptation. Two spiking cerebellar internal models were paired to learn how to improve the performance of a desired task thanks to their STDP adaptive mechanisms that generate the activity in terms of both sensory and motor

output corrections. The STDP mechanisms adapt the synaptic weights of PFs-PCs according to the teaching signal coming from the CFs and the sensory information sensed by the vestibular system through MFs.

Results show that the cerebellar control learning leads to an optimization of the performance with errors being reduced by 30% compared with the case where the cerebellar contribution is not applied (black and grey lines in Fig. 4). We argue that the performance obtained within the composite control loop could be improved by implementing both an optimization method of internal parameters [30] and a learning mechanism of coupling [16] between cerebellar forward and inverse models. Besides, the coupling emulation could be beneficial for the control of robots in presence of singularities or under altered dynamics conditions [6]. Future work will address the extension of the current cerebellar model to provide more accurate details of neural units, connectivity properties, and plasticity mechanisms, and to better understand how the cerebellum processes the information. Finally, the performance of the control system may be increased by optimizing the adaptation speed and accuracy in the NRP.

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REFERENCES

[1] D. Floreano, A. J. Ijspeert, and S. Schaal, "Robotics and neuroscience," *Current Biology*, vol. 24, no. 18, pp. R910–R920, 2014.

[2] K. V. Byadarhaly, M. C. Perdoor, and A. A. Minai, "A modular neural model of motor synergies," *Neural Networks*, vol. 32, pp. 96–108, 2012.

[3] E. D'Angelo, "Physiology of the cerebellum," in *Handbook of clinical neurology*, vol. 154, pp. 85–108, Elsevier, 2018.

[4] T. J. Ebner, *Cerebellum and Internal Models*, pp. 1279–1295. Dordrecht: Springer Netherlands, 2013.

[5] T. Ishikawa, S. Tomatsu, J. Izawa, and S. Kakei, "The cerebro-cerebellum: Could it be loci of forward models?," *Neuroscience Research*, vol. 104, pp. 72 – 79, 2016.

[6] M. Kawato, "Internal models for motor control and trajectory planning," *Current Opinion in Neurobiology*, vol. 9, no. 6, pp. 718 – 727, 1999.

[7] M. Ito, "Control of mental activities by internal models in the cerebellum," *Nat Rev Neurosci*, vol. 9, no. 4, pp. 304 – 313, 2008.

[8] M. Ito, *The cerebellum : brain for an implicit self*. Upper Saddle River, N.J. : FT Press, 2012.

[9] T. Shibata and S. Schaal, "Biomimetic gaze stabilization based on feedback-error-learning with nonparametric regression networks," *Neural Networks*, vol. 14, no. 2, pp. 201–216, 2001.

[10] S. Tolu, M. Vanegas, N. R. Luque, J. A. Garrido, and E. Ros, "Bio-inspired adaptive feedback error learning architecture for motor control," *Biological cybernetics*, vol. 106, no. 8-9, pp. 507–522, 2012.

[11] L. Vannucci, E. Falotico, S. Tolu, V. Cacucciolo, P. Dario, H. H. Lund, and C. Laschi, "A comprehensive gaze stabilization controller based on cerebellar internal models," *Bioinspiration & Biomimetics*, 2017.

[12] P. Dean, J. Porrill, and J. V. Stone, "Decorrelation control by the cerebellum achieves oculomotor plant compensation in simulated vestibulo-ocular reflex," *Proceedings of the Royal Society of London B: Biological Sciences*, vol. 269, no. 1503, pp. 1895–1904, 2002.

[13] N. R. Luque, J. A. Garrido, R. R. Carrillo, S. Tolu, and E. Ros, "Adaptive cerebellar spiking model embedded in the control loop: Context switching and robustness against noise.," *Int. J. Neural Syst.*, vol. 21, no. 5, pp. 385–401, 2011.

[14] S. Tolu, M. Vanegas, J. A. Garrido, N. R. Luque, and E. Ros, "Adaptive and predictive control of a simulated robot arm," *International journal of neural systems*, vol. 23, no. 03, p. 1350010, 2013.

[15] E. Franchi, E. Falotico, D. Zambrano, G. Muscolo, L. Marazzato, P. Dario, and C. Laschi, "A comparison between two bio-inspired adaptive models of vestibulo-ocular reflex (VOR) implemented on the iCub robot," in *2010 10th IEEE-RAS International Conference on Humanoid Robots, Humanoids 2010*, pp. 251–256, 2010.

[16] D. M. Wolpert and M. Kawato, "Multiple paired forward and inverse models for motor control," *Neural Networks*, vol. 11, no. 7-8, pp. 1317–29, 1998.

[17] J.-B. Passot, N. Luque, and A. Arleo, "Coupling internal cerebellar models enhances online adaptation and supports offline consolidation in sensorimotor tasks," *Frontiers in Computational Neuroscience*, vol. 7, p. 95, 2013.

[18] E. Falotico, L. Vannucci, A. Ambrosano, U. Albanese, S. Ulbrich, J. C. Vasquez Tieck, G. Hinkel, J. Kaiser, I. Peric, O. Denninger, *et al.*, "Connecting artificial brains to robots in a comprehensive simulation framework: the neurorobotics platform," *Frontiers in neurorobotics*, vol. 11, p. 2, 2017.

[19] E. R. Kandel, J. H. Schwartz, T. M. Jessell, S. A. Siegelbaum, and A. Hudspeth, *Principles of Neural Science*, vol. 1. 5. ed., 2013.

[20] M. Kawato, "Feedback-error-learning neural network for supervised motor learning," in *Advanced neural computers*, pp. 365–372, Elsevier, 1990.

[21] P. J. Porrill and Dean, "Recurrent cerebellar loops simplify adaptive control of redundant and nonlinear motor systems.," *Neural Computation*, vol. 19, no. 1, pp. 170–193, 2007.

[22] S. Kunkel *et al.*, "Nest 2.12.0," Mar. 2017.

[23] C. R. Miall, "Cerebellum: Anatomy and Function," in *Neuroscience in the 21st Century: From Basic to Clinical*, pp. 1–3111, 2013.

[24] D. Marr, "A theory of cerebellar cortex," *The Journal of Physiology*, vol. 202, no. 2, pp. 437–470, 1969.

[25] J. S. Albus, "A theory of cerebellar function," *Mathematical Biosciences*, vol. 10, no. 1-2, pp. 25–61, 1971.

[26] D. J. Herzfeld, Y. Kojima, R. Soetedjo, and R. Shadmehr, "Encoding of error and learning to correct that error by the purkinje cells of the cerebellum," *Nature neuroscience*, vol. 21, no. 5, p. 736, 2018.

[27] E. D'Angelo, L. Mapelli, C. Casellato, J. A. Garrido, N. Luque, J. Monaco, F. Prestori, A. Pedrocchi, and E. Ros, "Distributed Circuit Plasticity: New Clues for the Cerebellar Mechanisms of Learning," *Cerebellum*, vol. 15, no. 2, pp. 139–151, 2016.

[28] A. Antonietti, C. Casellato, J. A. Garrido, N. R. Luque, F. Naveros, E. Ros, E. D'Angelo, and A. Pedrocchi, "Spiking neural network with distributed plasticity reproduces cerebellar learning in eye blink conditioning paradigms," *IEEE Transactions on Biomedical Engineering*, vol. 63, no. 1, pp. 210–219, 2016.

[29] J. F. Medina and S. G. Lisberger, "Links from complex spikes to local plasticity and motor learning in the cerebellum of awake-behaving monkeys," *Nature Neuroscience*, vol. 11, no. 10, pp. 1185–1192, 2008.

[30] A. Antonietti, D. Martina, C. Casellato, E. DAngelo, and A. Pedrocchi, "Control of a humanoid nao robot by an adaptive bioinspired cerebellar module in 3d motion tasks," *Computational intelligence and neuroscience*, vol. 2019, 2019.

[31] N. R. Luque, J. A. Garrido, R. R. Carrillo, E. D'Angelo, and E. Ros, "Fast convergence of learning requires plasticity between inferior olive and deep cerebellar nuclei in a manipulation task: a closed-loop robotic simulation," *Frontiers in Computational Neuroscience*, vol. 8, no. 97, 2014.

[32] M. Pacheco, R. Fogh, H. Lund, and D. Christensen, *Fable II: Design of a Modular Robot for Creative Learning*, pp. 6134–6139. IEEE, 2015.

[33] M. L. Streng, L. S. Popa, and T. J. Ebner, "Climbing fibers control purkinje cell representations of behavior," *Journal of Neuroscience*, vol. 37, no. 8, pp. 1997–2009, 2017.

[34] M. Junker, D. Endres, Z. P. Sun, P. W. Dicke, M. Giese, and P. Thier, "Learning from the past: A reverberation of past errors in the cerebellar climbing fiber signal," *PLoS biology*, vol. 16, no. 8, 2018.

[35] C. Casellato, A. Antonietti, J. A. Garrido, R. R. Carrillo, N. R. Luque, E. Ros, A. Pedrocchi, and E. D'Angelo, "Adaptive robotic control driven by a versatile spiking cerebellar network," *PLOS ONE*, vol. 9, pp. 1–17, 11 2014.