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Review

Linking cellular-level phenomena to brain architecture: the case of spiking cerebellar controllers

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ABSTRACT

Linking cellular-level phenomena to brain architecture and behavior is a holy grail for theoretical and computational neuroscience. Advances in neuroinformatics have recently allowed scientists to embed spiking neural networks of the cerebellum with realistic neuron models and multiple synaptic plasticity rules into sensorimotor controllers. By minimizing the distance (error) between the desired and the actual sensory state, and exploiting the sensory prediction, the cerebellar network acquires knowledge about the body-environment interaction and generates corrective signals. In doing so, the cerebellum implements a generalized computational algorithm, allowing it "*to learn to predict the timing between correlated events*" in a rich set of behavioral contexts. Plastic changes evolve trial by trial and are distributed over multiple synapses, regulating the timing of neuronal discharge and fine-tuning high-speed movements on the millisecond timescale. Thus, spiking cerebellar built-in controllers, among various computational approaches to studying cerebellar function, are helping to reveal the cellular-level substrates of network learning and signal coding, opening new frontiers for predictive computing and autonomous learning in robots.

1. Introduction

The brain is composed of multiple interconnected networks, each one playing a specific role and at the same time contributing to ensemble functions and dynamics (Parr et al., 2022). The cerebral cortex and the cerebellum are the main cortical brain structures, and although the cerebellum is volumetrically smaller than the cerebral cortex, it contains, on average across species, 3.6 times more neurons because of its higher neuronal density (Herculano-Houzel, 2010). The two brain structures show remarkable functional differences, though. While the cerebral cortex is organized in multiple internal recurrent loops (Bellec et al., 2020), the cerebellar network features a predominantly forward architecture from the granular to molecular layer and then into deep cerebellar nuclei, with additional recurrent pathways including the nucleo-cortical loop and inhibitory circuits (Ghez & Fahn, 1985). Moreover, several synaptic and excitable mechanisms are ultrarapid (e.g., see Refs in D'Angelo and De Zeeuw (2009), De Zeeuw et al. (2011)), allowing faster network processing in the cerebellar than in the cerebral cortex. This makes the cerebellum suitable for controlling brain timing on the millisecond scale (Ivry et al., 2002). Moreover, while the cerebral cortex learns on the basis of unsupervised learning schemes, the cerebellum performs mostly supervised error-based learning and, more recently, it has also been recognized to control reinforcement learning in other brain circuits like the basal ganglia (Doya, 2000; Ros et al., 2006; Kostadinov & Häusser, 2022), contributing to the integration of learning across the main brain structures (super-learning hypothesis: (Caligiore et al., 2019)).

Historically, the cerebellum was the first (and probably is still the most advanced) brain region for which the structure-function-dynamics-behavior relationship has been clarified comprehensively. This

What I cannot create, I do not understand (R. Feynman)

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knowledge has been cast in solid theories guiding experiments and models, which brought into light the learning and timing properties of the cerebellum (Eccles et al., 1967; Marr, 1969; Albus, 1971; Ito et al., 1982, 2006). This led J.C. Eccles to say that "*…it could be optimistically predicted that the manner of operation of the cerebellum in movement and posture would soon be known in principle" (in Ito (1984))*.

Starting from the '70 s, numerous models of the cerebellar circuit have been developed across multiple labs worldwide to explain behavioral features in motor learning and control (Fujita, 1982; Kawato et al., 1987; Kawato & Gomi, 1992; Tyrrell & Willshaw, 1992; Wolpert & Kawato, 1998; Wolpert et al., 1998; Dean et al., 2002; Ito, 2006, 2013). These models have evolved from relatively simple abstractions to increasingly complex implementations, including rate-based neural networks, mean-field models, point neuron networks, and detailed multicompartmental simulations. Nonetheless, in light of recent developments in neurophysiology, neuroimaging, and modeling, the mechanisms and role of the cerebellum need now to be considered further. The multiscale modeling, i.e., data-driven models using biological information at multiple scales to simulate brain activity (De Schutter et al., 2005; D'Angelo & Jirsa, 2022), has brought into the foreground the need to combine advanced neuroscientific theories and neuroinformatic approaches (Ascoli et al., 2003) with a large and diverse set of experimental observations (D'Angelo et al., 2016; D'Angelo & Jirsa, 2022). Within the broader landscape of cerebellar modeling, two complementary pathways have emerged:

The development of biologically plausible computational models of the cerebellar microcircuits in terms of cellular and network properties focused on spiking neural networks. These models simulate the way neurons communicate through discrete electrical impulses (or "spikes") and capture both the cellular dynamics and the network properties of the cerebellum (Yamazaki & Tanaka 2007a; Yamazaki & Igarashi 2013; Lennon et al., 2014; De Schepper et al. 2022; Geminiani et al. 2024).

The design and validation of cerebellar computational models applied to neurorobotic controllers, creating what we refer to as spiking cerebellar built-in controllers, in which the biologically inspired microcircuits have been used to control behavioral tasks in perception-action loops (Medina et al. 2000a; Medina & Mauk 2000; Honda et al. 2018; Antonietti et al. 2019; Fruzzetti et al. 2022).

Among the many cerebellar spiking network models developed in recent years, in this Review, we particularly focus on the design and performance of spiking cerebellar built-in controllers to link neural mechanisms with sensorimotor behavior. While acknowledging the broader landscape of computational cerebellar research, we have chosen to highlight this specific approach as it allows for direct testing of how cellular-level properties translate to functional outcomes in closed-loop systems. By embedding biologically plausible cerebellar spiking neural networks into sensorimotor loops, these controllers provide a unique window into the structure-function-dynamics relationship central to understanding cerebellar computation.

In parallel with the recognition of its central role in motor learning and control, the cerebellum is now recognized to play a critical role in cognition and emotion (Ito, 2008; De Zeeuw et al., 2021; Ciapponi et al., 2023; Faris et al., 2024). Consistently, cerebellum dysfunction is emerging as a core element not just in ataxia, with which it has been associated early on, but also in other major neurological disorders affecting the sensorimotor domain (including dystonia, paroxysmal dyskinesia, Parkinson's disease) (Morigaki et al., 2021; Ekmen et al., 2022; Li et al., 2023), in neurodegenerative and inflammatory brain diseases (multiple sclerosis, dementia) (Parmar et al., 2018; Toniolo et al., 2023; Wenger et al., 2024), and psychiatric disorders (dyslexia, autism, depression, schizophrenia) (Ashburn et al., 2020; Brady et al., 2019). As well as motor dysmetria is the manifestation of cerebellar alterations in the motor domain, cognitive dysmetria appears in various brain pathologies, causing the so-called cognitive-affective cerebellar syndrome (Schmahmann & Sherman, 1998; Andreasen et al., 1998; Schmahmann, 2004; Schmahmann & Caplan, 2006; Schmahmann, Weilburg, & Sherman, 2007; Ito, 2008; Argyropoulos et al., 2020).

1.1. The cerebellum in the predictive brain

The brain can be conceived as a predictive machine operating as an autonomous system modulated by senses (Llinas et al., 1997; Llinás & Roy, 2009) that generates inferences about the body/environment interaction (Parr et al., 2022). This operation is needed to move and behave, but it equally well applies to abstract/symbolic reasoning and cognition. The brain generates an internal representation of reality that allows us to interact with the world (Churchland & Sejnowski, 1992; Llinas et al., 1997) (Fig. 1). To our best understanding, the brain is a complex adaptive system that continuously generates, stores, and enacts a large set of behavioral schemes. The schemes may represent, e.g., the ability to speak, write, move, and reason. Thus, a scheme may be used to manipulate abstract symbols, semantic or not semantic, as much as a hand manipulates a physical object. Importantly, the scheme includes a representation of the sensory consequences of an action, and therefore, it is predictive. These predictive mechanisms are referred to as internal models—cognitive constructs that the brain develops to forecast the outcomes of actions and sensory inputs based on prior experience and current sensory information. Internal models enable the brain to anticipate future states of the world, adjust behavior accordingly, and refine its predictions over time (Ito, 1970, 1972; Wolpert et al., 1995). Once a predictive scheme is enacted, it generates consequences on the world, which are sensed and brought back to the brain through afferent pathways (again, the same applies to immaterial symbols when the brain operates fully in its virtual space). At this point, the sensed and predicted schemes are compared, and differences are detected. This allows brain circuits to continuously correct errors, detect novelty, minimize unwanted consequences of upcoming stimuli, and eventually modify the schemes through learning if the differences occur repeatedly (Blakemore et al., 1998).

The brain's predictive capabilities emerge from the coordinated action of multiple neural systems. While the exact anatomical mapping is complex, three key brain regions make distinct contributions to this predictive framework. The cerebellum implements internal models that predict the sensory consequences of actions and refines these predictions through error-based learning. Beyond the classical view of error-driven supervised learning, the cerebellar circuit generates and tests predictions about movement, reward, and other non-motor operations (Hull, 2020). Its unique circuit architecture supports both motor and non-motor anticipatory responses, enabling rapid, automated prediction of temporal relationships between events (Narain et al., 2018). Basal ganglia evaluate and select different possible actions using reward signals to reinforce successful behaviors (Humphries et al., 2006). Through this process, it helps optimize behavior by favoring internal models that lead to better outcomes. This reward-based evaluation complements the cerebellum's error-based learning, creating an integrated learning system. The cerebral cortex processes complex sensory information through pattern recognition and feature extraction while maintaining attention and determining behavioral relevance. It makes high-level decisions and provides contextual information. These systems work together in a coordinated manner: the cerebellum provides rapid predictions, the basal ganglia evaluate outcomes and selects actions, and the cortex provides high-level control and context. These functions that make the brain a complex adaptive system, mapped onto specific brain centers and operations (Ito, 2008), suggest the design of a biomimetic controller (Fig. 2). Typically, a sensorimotor controller includes a motor planner, a motor commander and other centers connected to the cerebellum, which can thus take part in operations of both planning and execution (Inagaki et al., 2022).

In summary, the brain embeds three levels that successfully interplay

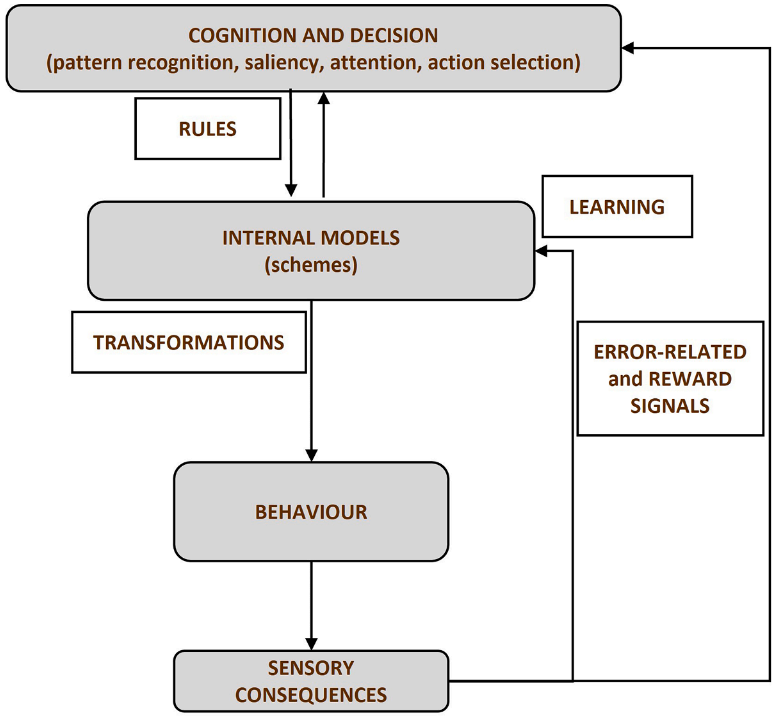

Fig. 1. The brain as a predictive adaptive system.
This functional scheme shows the brain as a system making predictions about the consequences of the interaction of the body with the world. These predictions are based on internal models (or schemes) that are learned and transformed into actions. The consequences are revealed by the senses and fed back to the brain. The general plant requires closed-loop control and learning deriving from errors generated by the comparison of predicted and actual sensory states. These functions, that make the brain a complex adaptive system, are remapped onto operations and specific brain centers in Fig. 2.

to adapt schemes and optimize behavior: (1) closed loop circuits compensating for errors in real-time, (2) predictive circuits learning by trial and error and modulating schemes over time, and (3) rewarding processes to reinforce learning. Eventually, once a scheme is validated, behavior can move from controlled to automatic, accelerating brain processing and making it effortless (Ramnani, 2014). Interestingly, this process can be explained by circuits centered on the cerebellum, which is, therefore, supposed to play an essential role in the predictive brain.

1.2. The cerebellum as a generalized forward model

The cerebellum is made of several regions that are extensively interconnected with multiple brain areas, allowing it to take part not just in the motor but also in cognitive and emotional control (Schmahmann & Sherman, 1998; Andreasen et al., 1998; Schmahmann, 2004; Schmahmann & Caplan, 2006; Schmahmann et al., 2007; Ito, 2008; Argyropoulos et al., 2020). Nonetheless, this multiplicity of functions is based on a common microcircuit design, leading to the concepts of generalized computation algorithm and universal cerebellar transform (Schmahmann, 1996). This organization is best understood from a phylogenetic perspective, in which the cerebellum is already present in the lowest vertebrates and then co-evolves with the cerebral cortex (Magielse et al., 2023). Extensive rewiring allowed reusing the same cerebellar circuit module for different functional purposes in multiple cerebello-cerebrocortical loops (Ciapponi et al., 2023; Faris et al., 2024).

The main function attributed to the cerebellum is to learn to predict the precise timing of correlated events (Eccles, Ito & Szentágothai, 1967; Marr, 1969; Ivry et al., 2002). While this principle is elegantly demonstrated in simple associative learning tasks like eyeblink conditioning, where the cerebellum learns to predict the timing between a neutral stimulus and an aversive one, it extends far beyond such basic paradigms. The cerebellum applies this predictive timing capability across a spectrum of behaviors, from coordinating multi-joint movements by predicting the temporal relationships between motor commands and their sensory consequences, to regulating eye movements by predicting visual target trajectories, to anticipating the timing of sensory events in cognitive tasks. This ability to extract and learn temporal relationships between correlated events allows the cerebellum to compare predictions (or expectations) with the effect (or consequence) of their actuation across motor, sensory, and cognitive domains. The main fallout of this principle is that learning of timing sets the basis for motor coordination (Mauk et al., 2000; Medina et al., 2000b). It processes both short and long intervals while monitoring discrepancies between expected and actual timings to correct errors. As it develops these timing patterns, the cerebellum enhances its predictive capabilities, facilitating smoother and more coordinated responses. Through appropriate wiring, this computational paradigm would apply to cognitive control as well as to motor control. Therefore, the main hypothesis is that the cerebellum operates as a generalized forward model (Shadmehr & Krakauer, 2008).

1.3. The mechanisms of cerebellar functioning

The first attempt to reconnect when, what, and how of the cerebellum came in the 60s-80 s, when Marr-Albus-Ito developed the Motor Learning Theory, from which the Adaptive Filter Model derives (Marr, 1969; Albus, 1971; Ito, 1984; Dean et al., 2010; Porrill et al., 2013). The Motor Learning Theory suggests that the cerebellum refines motor skills by adjusting neural pathways through error correction, with the Adaptive Filter Model extending this idea by conceptualizing the cerebellum as a dynamic system that continuously fine-tunes motor commands based on sensory feedback. Directly from this definition, the Adaptive Filter Model is understood as a forward model, predicting the sensory consequences of motor actions to optimize performance. In his foreword to (Ito, 1984), Eccles wrote: "*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*

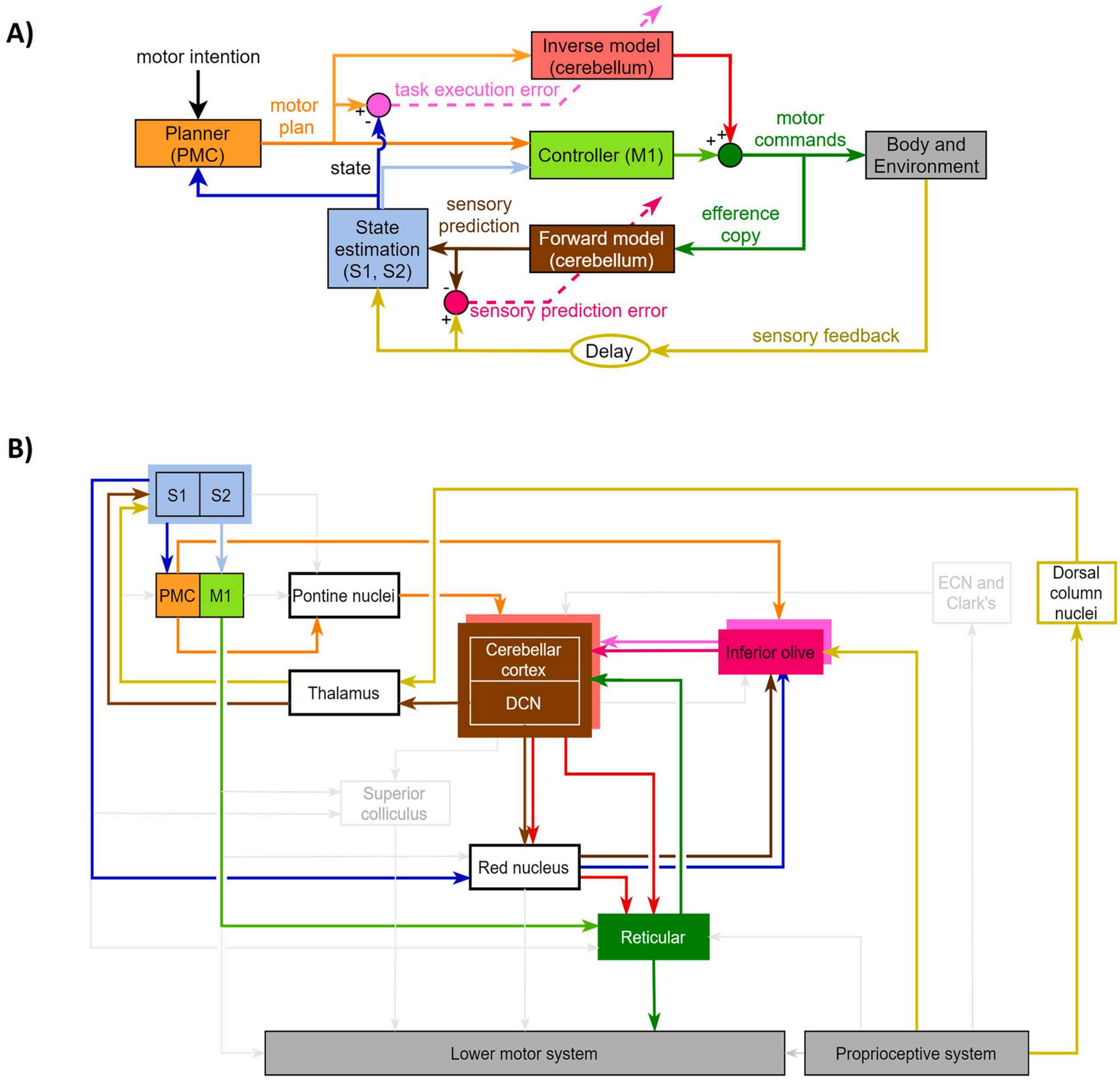

Fig. 2. Architecture of cerebellar controllers.
(A) The forward model receives an efference copy of the motor commands through mossy fibers, and predicts their sensory consequences (Shadmehr & Krakauer, 2008).As such, this module provides a fast feedback that could be used: (i) by the controller (motor cortices M1) to quickly update the motor commands according to the desired motor plan, providing a stable control even if the actual sensory feedback is delayed; and (ii) by the planner (premotor cortices PMC) to define an appropriate motor plan given the desired movement intention even before movement initiation, when there is no sensory feedback. Learning in the forward model (brown) is guided by the error in predicting the sensory information (sensory prediction error), which is encoded in one section of the inferior olive (pink) to drive plasticity. The inverse model (red) receives the desired motor plan via mossy fibers and computes the corresponding motor commands in feedforward (Ito, 2013). As such, this mechanism allows to adjust motor commands computed by motor cortices even before obtaining the sensory information (whether predicted or actual). Learning in the inverse model is driven by the error in executing the desired plan, fed to the cerebellar microcircuit via another section of the inferior olive (purple). Predicted and actual sensory signals are integrated by the state estimator (somatosensory cortices S1 and S2, which process sensory signals). Using Bayesian integration, the state estimator computes a weighted average of the two sensory signals (predicted and actual) based on their estimated reliability (Körding & Wolpert, 2004). (B) The operations are mapped on brain regions considering current knowledge on brain connectivity. No-color blocks and connections are not yet mapped in the control scheme in A.

machine with the double innervation of Purkinje cells begins to make sense if it plays a key role in motor learning".

The Motor Learning Theory and Adaptive Filter Model brought about several fundamental predictions about the way the cerebellar network should work (Fig. 2A). Along the mossy fibers (mf) pathway, the granular layer would perform a sparse representation of input patterns generating combinatorial expansion, spatiotemporal re-coding and pattern separation. The Purkinje cells (PC) should act as a perceptron of granule cell patterns, while the synapses between parallel fibers (pf) and PCs should learn under control of the error signal conveyed through the climbing fibers (cf), which encodes temporal difference prediction error (Ohmae & Medina, 2015). The whole circuit would then operate as an adaptive filter (Dean et al., 2010; Porrill et al., 2013). In another interpretation, the functional roles of the granular layer and Purkinje cells are regarded as a liquid state generator and readout neurons, respectively, suggesting that the whole circuit would operate as a liquid state machine (Yamazaki & Tanaka, 2007b). However, recent experimental and theoretical work reveals that granule cells encode a much richer representation of the system state. Beyond pure temporal coding, they integrate diverse contextual information including multimodal sensory inputs, motor commands, and feedback signals (Giovannucci et al., 2017; Wagner et al., 2017). Through their diverse synaptic properties, granule cells perform sophisticated pattern separation and combine multiple streams of information about the animal's movement, sensory environment, and task context (Cayco-Gajic et al., 2017; Lanore et al., 2021). This expanded view suggests that granule cells create high-dimensional representations that capture both temporal relationships and broader contextual states, enabling the cerebellum to generate predictions based on the full state of the system rather than just temporal sequences.

Although the original theories provide the guideline, now we know much more about the cerebellum, so a complex biological reality must be accounted for (Bower, 2002; D'Angelo, 2016). For example, the Motor Learning Theory did not consider (1) multiple forms of plasticity, (2) molecular complexity, (3) neuronal non-linear and time-dependent properties, (4) circuit geometry (only topology and statistics), (4) mesoscale and macroscale connectivity, (5) and cognitive and emotional control in addition to motor control. Nowadays, anatomo-physiological observations can be integrated into powerful computational models (D'Angelo & Jirsa, 2022). These models can be applied in neurorobotic systems to explore cerebellar physiology and pathology in closed-loop integrated systems, as well as to evaluate the validity of foundational theories, leading to the development of what we will refer to as cerebellar controllers.

A pivotal concept for understanding cerebellar physiology concerns the signals entering the circuit. The *cf* pathway is thought to convey the error (or novelty) with respect to a template. There has been a long (and not ended yet) discussion about whether the *cf*s convey such a teaching signal or rather a timing signal for movement initiation (Kitazawa et al., 1998; Jacobson et al., 2008; De Zeeuw et al., 2011; Herzfeld et al., 2020). Conversely, the *mf* pathway conveys contextual information consisting of both sensory information and the efference copy of cortical commands (Hesslow et al., 1999; Giovannucci et al., 2017). This biological insight informed the development of cerebellar controllers, even if most implementations focused on processing efference copy signals through the *mf* pathway, while using *cf* signals for error-based learning. Expanding these models to process both types of *mf* inputs (i.e., sensory information and efference copy of motor commands) remains an important direction for future work.

Another pivotal concept concerns the transformations operated by neurons and synapses of the cerebellar circuit on the incoming signals. Neurons and synapses express complex filtering properties that can regulate the gain, bandwidth, timing, and phase of the signals. Moreover, neurons and synapses express a complex set of short-term and long-term plasticity mechanisms that are thought to modulate signal transmission and store information in the cerebellar circuit at multiple sites (Masoli et al., 2022). By embedding specific constructive and functional mechanisms by design, we can investigate different hypotheses about the wiring and computational impact of afferent signals, neurons, synapses, and learning rules. The cerebellar controllers have not yet fully exploited their complex networks and neuronal mechanisms, whose impact on the network input-output relationship remains to be carefully investigated.

1.4. What the cerebellar circuit is physically doing

The cerebellar network is thought to extract, through learning, fundamental parameters about the body-environment (or body-object) interaction (Schweighofer et al., 2001). This configures an inverse mathematical problem. At the same time, a direct model predicts the effects knowing the causes, and an inverse model hints about the causes given the effects. More formally, if one knows the model $F(p)$ along with its parameters p, one can directly predict the observable signals $d_{obs}=F(p)$. Inversely, one can determine p based on d_{obs}: $p = F^{-1}(d_{obs})$. This is the case that the cerebellum must face by inferring the hidden causes of the empirical sensory observation. Mathematically, the challenge is the non-invertibility of the problem, which is typically addressed by minimizing some cost functions (D'Angelo & Jirsa, 2022). A cerebellar controller can cope with this problem naturally, converging toward an optimal solution. In a closed-loop motor controller, e.g., one including a cerebellar adaptive circuit, the problem of finding model parameters translates into that of adapting synaptic weights in the embedded cerebellar Spiking Neural Network (SNN). Now, synaptic weights, p, and properties of the external world, d_{obs}, are free model parameters so that the controller works as the agent that extracts the parameter values, implementing an internal model of the world.

Let us examine how forward and inverse models operate in robotic control using examples from object manipulation under gravitational forces.

A forward model is exemplified in anticipatory grip force adjustments during object manipulation. When moving an object, the cerebellum predicts the sensory consequences (object slip, changing loads, d_{obs}) that will result from the motor actions (p). This prediction allows anticipatory adjustment of grip force before sensory feedback arrives, preventing object slip. Here, the cerebellum uses an internal model to transform motor commands into predicted sensory outcomes, solving the forward problem: $d = F(p)$.

An inverse model is illustrated when a robot must lift an object of unknown mass. Here, the cerebellum must determine appropriate motor commands (forces, p) needed to achieve a desired outcome (stable object position, d_{obs}). The controller implicitly solves the inverse problem of extracting $p = F^{-1}(d_{obs})$ (without requiring an artificial comparison with a template, as is the case with machine learning procedures). It should be noted that weight adaptation at circuit synapses generates an implicit and distributed representation of p. Through experience, the cerebellar SNN generates an internal model of the body-object system, learning the physical rules governing object manipulation and acquiring the physical rules governing kinematics and dynamics of masses in the gravitational field along with apparent (centrifugal and Coriolis) forces and frictions (Schweighofer et al., 2001).

Akin to the concept of a generalized computation algorithm (Doya, 2000) and universal cerebellar transform (Schmahmann, 1996), this example may be generalized to many different cases extending from the sensorimotor to the cognitive domain Ito (2008).

2. Cerebellum models in robotic controllers

In computational models, the main issue is the multiscale problem, i.e., connecting cellular mechanisms to system functions. This means moving from structure to function to dynamics to behavior (Arbib et al., 1997; Arbib & Érdi, 2000). The challenge can be faced by generating neurorobotic controllers. Nonetheless, data plays a critical role in model construction, as well as in the case of robotic controllers generating hybrid architectures that embed biological SNNs into task-driven architectures (D'Angelo & Jirsa, 2022).

Robotic controllers are inspired by neural properties encompassing neurons, circuit architecture, and brain connectivity. Unlike more abstract brain models that attempt to capture high-level cognitive processes, these controllers focus on implementing specific sensorimotor functions with clear input-output relationships. Moreover, they can interact with the environment by exploiting feedback sensory loops and incorporate plasticity rules for learning and memory allowing them to generate adaptive behaviors through their interaction with the environment.

Cerebellar SNNs have been effectively embedded into sensorimotor controllers to create spiking cerebellar built-in controllers. The architecture is composed of (1) a planner, (2) a motor commander, (3) body actuators, (4) sensory feedback, (5) error calculation modules, (6) cerebellar SNNs connected as an inverse model and as a forward model, (7) a state estimator (Fig. 2A). The state estimator weights the sensory feedback and the predictive sensory consequence; if sensory feedback is unavailable (e.g. in ballistic movement), the state is estimated using only the predictions generated by the cerebellum (delay higher than movement duration). Overall, the cerebellar predictions stabilize the controller, otherwise unstable due to the delay in the sensory feedback.

2.1. Spiking neural networks in cerebellar controllers

To account for the multiscale modeling issue, a cerebellar SNN has been developed, derived from a data-driven reconstruction and validation process at multiple scales so that biological features are effectively brought into the artificial system (Solinas et al., 2010; De Schepper et al., 2022). Following anatomical constraints, these SNNs usually contain the cerebellar cortex, deep cerebellar nuclei (DCN), and inferior olive (IO) modules, with $\sim 10^4$–10^5 neurons as a whole (Vijayan & Diwakar, 2022). The cerebellar cortex module contains the main cerebellar neuronal populations, i.e., Purkinje cells (PC), Golgi cells (GoC), granule cells (GrC), basket cells (BC), and stellate cells (SC) collectively called molecular layer interneurons (MLI), *mf*s, *cf*s, and *pf*s wired as in Fig. 3. Granule cell layer processing is expected to promote spatial group selection of granule cell activity as a function of timing of mossy fiber input (Berends et al., 2004; Sudhakar et al., 2017), therefore the cerebellar spiking granular layer represents the passage-of-time (Yamazaki et al., 2007a). Recent experimental work has further validated this concept through simultaneous recordings of GrC and *cf*s, demonstrating how these cells learn to track temporal intervals in behaviorally relevant tasks (Garcia-Garcia et al., 2024). While the main signal flow is forward through these components, there is also an important recurrent nucleo-cortical pathway from DCN back to the granular layer. This pathway provides predictive feedback signals about ongoing movements to granule cells, either through direct excitation via nuclear collaterals or through disinhibition via nuclear projections to Golgi cells (Giovannucci et al., 2017). Such recurrent signaling allows the cerebellum to participate in closed feedback loops that can regulate and adjust ongoing predictive responses in real time, effectively implementing forward models that overcome delays in sensory feedback. This pathway has been recently implemented in the cerebellar models to investigate its role in learning calibration and multiple timescales of plasticity. At the level of single neurons, leaky integrate-and-fire (LIF) is, in general, the most common neuron model for SNN, representing neuron membrane dynamics as a "leaky" capacitor and the firing behavior as a threshold-based mechanism. While the first versions of cerebellar SNN employed LIF neurons, more recent implementations use more complex models, such as extended-generalized LIF (E-GLIF), to account for the diverse electroresponsive phenotypes of cerebellar neurons. E-GLIF models for the different neuronal populations are parametrized based on the biological data of the corresponding neuron type and reproduce non-linear neuronal dynamics (De Schepper et al., 2022). With these advanced neuron models, for example, the burst-pause effect typical of PC emerges, improving the control of spike timing at the output. (Fig. 3 and Box 1). To model the transient increase of synaptic conductance following a pre-synaptic spike, in most of the cerebellar SNNs the synapses are conductance-based and their dynamics is modeled as an alpha function. Long-term synaptic plasticity rules have been progressively updated to include spike-timing dependent plasticity (STDP) at *pf*-PC synapses, PC-DCN synapses, mf-DCN synapses, IO-DCN synapses, and *pf*-MLI synapses. Initially, learning in the cerebellar SNNs was driven by *pf*-PC bidirectional plasticity only, following the Motor Learning Theory (Tang et al., 2021; Welniarz et al., 2021). Then, the original *pf*-PC plasticity rule (Mauk & Donegan, 1997) was refined based on more recent experimental observations (Yamazaki & Tanaka, 2007a). Following experimental (Ohyama et al., 2006) and theoretical studies suggesting that bidirectional synaptic plasticity also occurs in the cerebellar nuclei and plays a crucial role in learning and consolidation, *mf*-DCN learning rules have been introduced in cerebellar SNNs and complemented with PC-DCN plasticity rules (Zheng & Raman, 2010; Nagao, 2021). To model learning stabilization and convergence, IO-DCN synaptic plasticity was also introduced. More recently, additional

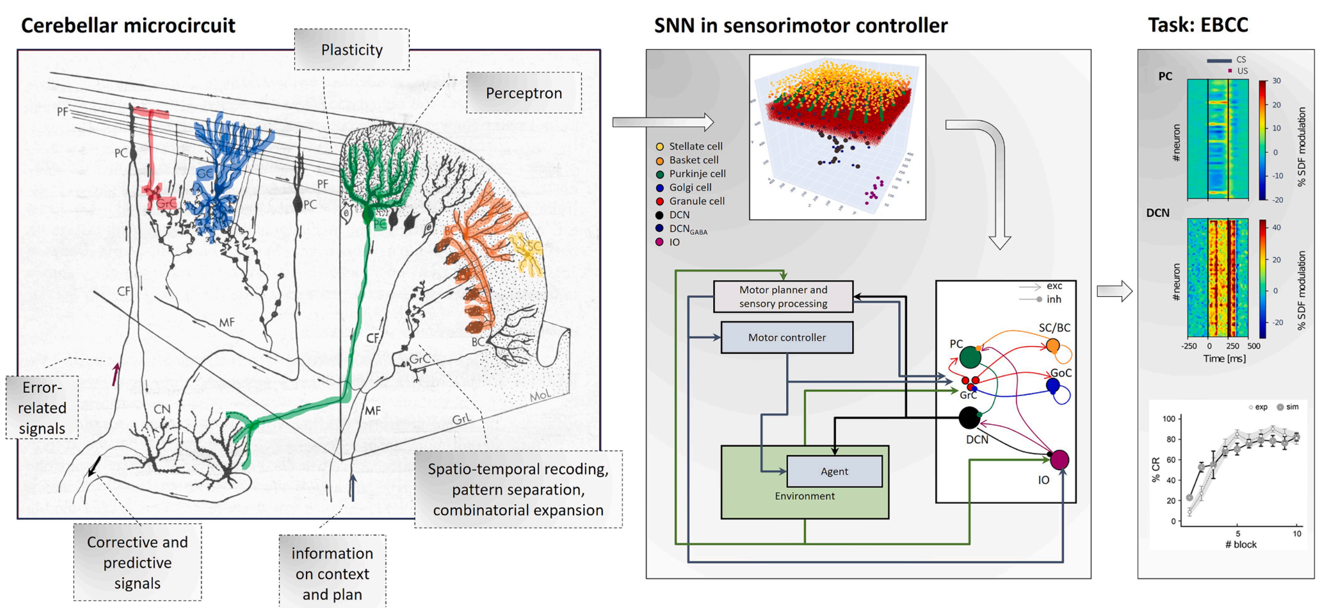

Fig. 3. From the cerebellar circuit to an SNN integrated into a sensorimotor controller.
The cerebellar microcircuit is shown with its fundamental elements. The gray labels reflect the terminology adopted in the Motor Learning Theory (Marr, 1969; Ito, 2006). According to the Motor Learning Theory and the subsequent Adaptive Filter Model, the GrL performs spatiotemporal recoding, pattern separation, and combinatorial expansion of mf signals, which convey information on context and plans. The PC operates as a perceptron. The pf-PC synapses are one of the main sites of learning. The cf conveys teaching error-related signals. The cerebellar microcircuit is then transformed into an SNN and wired into a sensorimotor controller. The spike-to-analog and the analog-to-spike conversions are governed by encoding/decoding rules in appropriate interfaces (Mathis et al., 2024). It should be noted that cerebellar SNNs are made of point neurons and allow fast mesoscale simulations exploiting spike timing and synaptic plasticity. The plots on the right show an example of spike frequency modulation (using Spike Density Function, SDF) in PC and DCN cells during a robotic simulation of eye-blink classical conditioning (EBCC). Note that, after learning PCs learn to pause, and DCN cells learn to fire at a specific time (x-axis) with millisecond precision. Model simulations of EBCC yield a learning curve of conditioned responses (%CR) superimposed to the experimental one recorded in mice. Adapted from Eccles et al. (1967), D'Angelo and Jirsa (2022), Geminiani et al. (2024). PC, Purkinje cell; GoC, Golgi cell; GrC, granule cell; BC, basket cell; SC, stellate cell; DCN, deep cerebellar nucleus; MF, mossy fiber, CF, climbing fiber; MoL, molecular layer; GcL, granular cell layer. CS, Conditioned Stimulus; US, Unconditioned Stimulus.

plasticity sites in the cerebellar cortex have been considered in the molecular and granular layer. Based on in vitro experimental observation, a *pf*-MLI bidirectional plasticity model was proposed (Lennon et al., 2015) and based on experimental observations in mice during classical eyeblink conditioning (ten Brinke et al., 2015), a version for SNN simulations of in vivo tasks was implemented and used to investigate the contribution of different plasticities in the cerebellar cortex, at pf-PC and MLI, during eyeblink conditioning (Geminiani et al., 2024). In the granular layer, a frequency-dependent STDP learning rule has been implemented to reproduce the theta-band specific synaptic plasticity at *mf*-GrC connections that is supposedly responsible for filtering and amplifying cerebellar input signals.

These forms of plasticity have been modeled taking into account different induction and expression rules and different time constants, as revealed by biological experiments. The elevated number of types and the distributed nature of cerebellar plasticity embedded in the cerebellar SNN has allowed us to demonstrate a series of biological properties, including (1) double acquisition time constant, (2) self-rescaling over a large range of inputs, (3) learning acceleration toward biological rates. Following the different plasticity rules, the synaptic weights change progressively during learning, transferring memory from the cerebellar regions that acquire information more rapidly, e.g., the cerebellar cortex, to the slower ones (consolidation), e.g., the cerebellar nuclei. Then, the weight is redistributed due to sensory and internal feedback. A synapse can change its plasticity several times during a learning cycle, and several combinations of weights on different synapses may be equally effective (Bhasin et al., 2024).

Some synaptic properties remain to be embedded into the cerebellar SNN, including (1) short-term synaptic plasticity to improve local circuit dynamics (D'Angelo et al., 2016; Masoli et al., 2022), (2) postsynaptic receptors with specific properties, like the NMDA receptor, (3) neuromodulation to gate the learning process and to avoid destructive interference (Schweighofer et al., 2001), (4) memory transfer and consolidation across brain regions (Kellett et al., 2010). The accumulation of multiple patterns remains to be tested.

2.2. Control circuits and simulated behaviors

Cerebellar SNNs have been embedded into different control loops to cope with specific behaviors, of different complexities, derived from biological experiments and clinical tests, including eye-blink classical conditioning (EBCC), vestibulo-ocular reflex (VOR), saccadic eye movements, whisking, arm reaching tasks, and force field compensation (Casellato et al., 2014; Luque et al., 2016; Honda et al., 2018; Xu et al., 2018; Antonietti et al., 2019; Fruzzetti et al., 2022; Liu et al., 2023; Shinji et al., 2024). While EBCC was traditionally viewed as a simple associative task, recent work has shown it involves coordinated motor synergies across multiple degrees of freedom, including precisely orchestrated movements of the eyelid, surrounding facial muscles, and deeper protective structures (Heiney et al., 2021). Similarly, arm-reaching movements require coordination across multiple joints in 3D space. Both tasks involve learning temporal relationships between sensory cues and motor outputs but differ in their spatial complexity and the number of muscles and joints that need to be coordinated. The cerebellar network architecture remains consistent across these tasks, supporting the concept of a universal computational algorithm. This can happen by exploiting a common learning strategy: the teaching signal provided by the IO drives synaptic weight adaptation at *pf*-PC synapses, as predicted by the Motor Learning Theory. These computational models thus provide critical support to the Motor Learning Theory and allow the connection of cerebellar circuit mechanisms to behavior through specific brain architectures and error-driven learning. While these cerebellar models have successfully reproduced various motor learning tasks using a similar circuit architecture, it's important to note that these tasks (EBCC, VOR, reaching movements) all involve sensorimotor learning and adaptation. The cerebellum's role extends far beyond motor control to cognitive and emotional functions (Van Overwalle, 2024; Schmahmann, 2019; De Zeeuw et al., 2021), and whether the same computational principles apply to these broader domains remains an open question. Testing if this framework generalizes to non-motor functions, such as cognitive prediction, language processing, or emotional regulation, represents an important challenge for future computational work (Ohmae & Ohmae, 2024).

EBCC proves quite useful since it is supported by extended experimental evidence that can be used for model construction, tuning, and validation. EBCC is well understood in its neuronal mechanisms and is, therefore, the workbench for any further cerebellar physiological investigation (Fig. 3). For example, a cerebellar SNN has been extended to include up-bound and down-bound microzones, and this new architecture has been tested in EBCC simulations (Geminiani et al., 2024); EBCC has also been used as the reference task to investigate *in silico* the impact of cerebellar circuit lesions associated to several cerebellar-related pathologies (Radell & Mercado, 2014; Geminiani et al., 2018; Trimarco et al., 2021).

2.3. Simulation of pathological states

The simulation of pathological states with spiking cerebellar built-in controllers involves understanding how various neurological diseases impact the cerebellum. The cerebellum can exhibit resistance to certain neurodegenerative mechanisms, yet it can also be highly vulnerable in cases of accelerated neurodegeneration (Liang & Carlson, 2020) and cerebellar degeneration significantly contributes to symptoms like impaired motor skills and ataxia (Rüb et al., 2013).

To understand diseases such as ataxia, Parkinson's disease, and dystonia, researchers have utilized computational models focusing on the cerebellum and its interactions with other brain regions like the basal ganglia and thalamocortical circuits (Geminiani et al., 2018, 2022 Shaheen & Melnik, 2022; Kumar & Ma, 2023; Gambosi et al., 2024). These models aim to elucidate the impact of changes in the cerebellar controller (e.g., dopamine depletion, altered connection strengths, and changes in neural activity) on disease progression and motor symptom manifestation.

The cerebellum's role in Parkinson's disease is highlighted by PCs' cellular apoptosis and reduced cerebellar activity in animal models of Parkinsonism, suggesting its involvement in the disease process, historically more studied for the basal ganglia disruption. Additionally, the cerebellum is implicated in reinforcing aberrant neural activity through the cerebello-thalamocortical loop in Parkinson's disease, affecting motor learning and performance (Gambosi et al., 2024). Spiking cerebellar built-in controllers have been enhanced with simulated dopamine depletion mechanisms to study their effects on cerebellar function. These models capture the shifts in cellular and network properties associated with changes in brain rhythms, providing insights into the pathophysiology of Parkinson's disease.

Other studies have explored the impact of cerebellar pathologies on neural network dynamics using spiking controllers to predict how changes at the neuronal level, such as loss of PCs, lesions to *mfs*, and damages to synaptic plasticity, affect motor learning processes (Geminiani et al., 2018). Different olivocerebellar lesions were correlated to different dystonic EBCC phenotypes in simulations (Geminiani et al., 2022). By applying region-specific lesions in a full-scale cerebellar model, it will be possible to explore the contribution of different cerebellar lobules to various forms of dystonia. EBCC was also used to investigate abnormal learning in autism spectrum disorder, highlighting the role of cortico-cerebellar hyper-connections and reduced PC in explaining the neural mechanisms underlying atypical behaviors in this disorder (Trimarco et al., 2021). (Solouki et al., 2022) focused on localizing long-term synaptic plasticity defects to study deficits in optokinetic reflexes.

These studies collectively underscore the significance of spiking controllers in elucidating the pathophysiology of various cerebellar-related diseases, providing a platform to explore neural mechanisms, circuit alterations, and potential therapeutic interventions.

2.4. Knowledge gained and open issues

The development and simulation of spiking cerebellar built-in controllers unveil the nature of the internal models of the cerebellum and the underpinnings of learning at the microcircuit level, providing important cues to understand the mechanisms of cerebellar functioning (Wolpert et al., 1998). These models, embedded into cortico-cerebellar-spinal loops, perform well in inverse and forward mode, confirming previous Motor Learning Theory-based theoretical predictions (Kawato et al., 1987; Kawato & Gomi, 1992; Jordan, 1992; Wolpert & Kawato, 1998; Wolpert & Ghahramani, 2000). Is the cerebellum crucial for learning to associate motor commands with novel sensory consequences (forward model) or is the cerebellum important for learning to associate sensory goals with novel motor commands (inverse model) (Izawa et al., 2012)? The inverse and forward models can also work in tandem (Honda et al., 2018; Wolpert & Kawato, 1998; Kawato, 1999), an issue that needs further development and investigation in spiking systems. This dual cerebellar controller brings about the issue of the operations carried out by the IO and its subsections, which should decode multiple error types.

The cerebellar SNN learns about the body-environment or body-object interaction and emits signals able to minimize errors between planning and execution. Simulations performed with a variety of tasks support the concept that the cerebellum implements a generalized computational algorithm, allowing it to learn the timing between correlated events independent of the task being performed. The spiking cerebellar built-in controllers, in principle, are implementing a universal cerebellar transform applicable to multiple sensorimotor domains (Schmahmann, 1996). The extension to cognitive domains and variants to circuit architecture and function (Ciapponi et al., 2023) remains to be investigated.

According to Motor Learning Theory, the error signal is part of the design in spiking cerebellar built-in controllers and proves essential to allow error-based predictive learning. No other ways to control cerebellar learning have been investigated so far. State-dependent neuromodulation may gate the learning process in specific behavioral contexts (like attention or sleep) under the control of neuromodulators (like dopamine, serotonin, acetylcholine, and noradrenaline) (Schweighofer et al., 2001). There are indeed indications that the cerebellum may also take part in reward-based learning in close interaction with the ventral tegmental area and the striatum (Carta et al., 2019; Kostadinov & Häusser, 2022). Recent work by Hoang et al. (2025) has further demonstrated how climbing fiber inputs encoding predictive reward-prediction errors can integrate modular reinforcement learning with supervised learning in the cerebellum, providing a mechanism for context-specific motor commands during discrimination tasks. The investigation of this double error-based and reward-based learning scheme may benefit large-scale multi-area spiking models, including the cerebellum and basal ganglia, that are currently under development (Kuniyoshi et al., 2023; Gambosi et al., 2024).

Beyond Motor Learning Theory, there are multiple mechanisms of timing and plasticity in the cerebellar circuit (D'Angelo & De Zeeuw, 2009) that await to be correlated with phenomenological aspects of sensorimotor learning. A critical observation is that motor learning occurs on two main, fast and slow, time scales (Smith, Ghazizadeh & Shadmehr, 2006; Herzfeld et al., 2014). Indeed, the cerebellum may hold at least two separate Smith Predictors responsible for different learning time scales (Miall et al., 1993). Spiking cerebellar built-in controllers have substantially contributed to understanding how distributed circuit plasticity supports the mechanisms of cerebellar learning. Indeed, *pf*-PC plasticity turns out to allow fast acquisition of information, while DCN plasticity operates on a slower timescale. Moreover, simulations have revealed that learning is dynamically redistributed over multiple synapses. Learning in the cerebellar circuit involves two major input pathways processing different types of information (Garcia-Garcia et al., 2024):

- The *cf* pathway carries sensory error signals that reflect the difference between predicted or desired and actual sensory states. These error signals evolve across learning trials as performance improves and predictions become more accurate.
- The *mf* pathway carries both efference copy (internal copy of motor commands) and sensory feedback signals. However, current computational implementations have primarily focused on the efference copy component, limiting their ability to fully capture the richness of cerebellar processing.

The dynamic redistribution of synaptic weights during learning reflects how these error signals, conveyed by *cf*s, gradually shape network connectivity to improve performance. Future models incorporating both efference copy and sensory feedback through the *mf* pathway could provide a more complete picture of how the cerebellum integrates different information streams during learning. Multiple synapses and recurrent loops (e.g., IO-PC-DCN-IO) allow to accelerate learning to biological speed and to self-rescale learning, avoiding saturation when the size of the input signals change. The persistence of plasticity is still an open issue, as it would require structural and genomic changes in the cerebellar SNN (e.g., (Gao et al., 2016)) that have not been modeled yet.

Spiking cerebellar built-in controllers embed realistic cerebellar SNNs, allowing an almost direct comparison of simulated neural activity with experimental data. The effects of discontinuous computing with spikes have been considered elsewhere and include enhanced timing capabilities, the possibility of implementing digital logic, and to generate energy-efficient codes (Mo & Wang, 2021; Yamazaki et al., 2022). In spiking cerebellar built-in controllers, the use of SNNs bears specific implications. First, spikes can be generated using E-GLIF models (Geminiani et al., 2018) that can bring non-linearity in the system. Secondly, spikes instantiate timing on the millisecond scale, akin to the predicted role of the cerebellum as a timing device. Thirdly, spikes are used to implement learning rules based on spike-timing dependent plasticity (STDP), which is indeed present at several (if not all) cerebellar synapses. Finally, spike coding can be implemented using look-up tables generating event-driven schemes that allow accelerated computing to real-time and driving real physical robots (Antonietti et al., 2019).

While spiking cerebellar controllers have emphasized the molecular layer sub-circuit, they have not resolved the granular layer sub-circuit (mostly the mossy fiber-GrC-GoC system) yet. This is at odds with the extensive knowledge that has been recently gained about the granular layer of the cerebellum. Cerebellar granule cells acquire a widespread predictive feedback signal during motor learning (Giovannucci et al., 2017) and can adaptively regulate the bandpass, gain, and phase of signal transmission along the *mf*-GrC pathway. *mf*s convey contextual information from multimodal sensory, cognitive, and emotional systems so that the granular layer would be required to multiplex and decorrelate signal components conveyed by numerous and diverse input pathways (Cayco-Gajic et al., 2017; Lanore et al., 2021; Xie et al., 2023). The GoC circuits are fundamental for inhibition-mediated adaptive gain control and spatiotemporal patterning of the downstream GrCs (Gurnani & Silver, 2021). However, in their current configuration, spiking cerebellar built-in controllers are dealing with simple tasks so that the elaboration of contextual information in the granular layer may not be critical. Therefore, addressing the issue would involve not just extending the wiring of the cerebellar network but also increasing the dimensionality of the task. A main issue concerning the granular layer is synaptic plasticity. Initially, it was represented as a gating process controlled by neuromodulators (Schweighofer et al., 2001). Although gating is relevant to control the induction of plasticity, different mechanisms have recently been reported, including STDP at *mf*-GrC and *mf*-

GoC (Masoli et al., 2022; Sgritta et al., 2017). A preliminary implementation of STDP has not been integrated into the full cerebellar SNN and has not been tested in task simulations yet. It should be noted that *mf*-GoC STDP is induced under *pf* guidance and could, in turn, impact *mf*-GrC STDP, generating a complex process regulating information flow through the cerebellar input stage and engaging multiple cerebellar modules and intermodular communication. Since now spiking cerebellar built-in controllers are made of a single module, they should be expanded to multidimensional modules. Therefore, implementing granular layer functionalities would imply a profound restructuring of the controller and its SNNs.

An expansion of the spiking cerebellar built-in controllers in this direction would eventually instantiate an Adaptive Filter Model (Dean et al., 2010; Porrill et al., 2013), with differential filtering of *mf* signals on the GrC lines that should be able to instantiate the spatio-temporal reconfiguration of the input predicted by Sudhakar et al. (2017). This would not be very useful with simple tasks like EBCC, but it would become a key factor in handling complex behaviors in a multiparametric parameter space.

Finally, considering the granular layer would bring about large-scale network dynamics based on theta-frequency oscillations and resonance (D'Angelo & De Zeeuw, 2009; Solinas et al., 2010), which are not currently considered since the rest of the controller does not have intrinsic oscillatory dynamics. This consideration leads to contemplating the confluence of spiking controllers into virtual brain models that are indeed capable of generating intrinsic space-time dynamics (D'Angelo & Jirsa, 2022).

2.5. Challenges and conclusions

By implementing a reverse engineering approach, robotic controllers can help face issues about cerebellar functioning that can be coarsely divided into those concerning theory, architecture, and circuit mechanisms.

The recognition that the cerebellum is not just sensorimotor but also cognitive (De Zeeuw et al., 2021) requires an extension of its wiring inside the controller loops. Future research needs, therefore, to address these core issues that are intimately bound together, i.e., modeling and simulating a dual spiking cerebellar built-in controller (inverse and forward) connected not just with motor but also with cognitive brain centers, to shed light on the neural basis of cognitive processing and mental experience (Nichols & Newsome, 1999) and how the conserved circuit architecture of the cerebellum contributes to more abstract brain functions (Carey, 2024). This would imply wiring the cerebellar SNNs with cognitive layers resorting to artificial intelligence, since an implicit coding (e.g., with a spiking neural network) of mental representations is still impractical (Nichols & Newsome, 1999).

In front of experimental progress in characterizing cerebellar functioning, circuit mechanisms should be extended along several lines. First, while learning is now based on *cf* error signals, reward mechanisms and gating signals (e.g., state-dependent neuromodulation that can enhance or suppress cerebellar learning based on behavioral context) should also be considered. Secondly, while the cerebellum has evolved to cope with complex multidimensional tasks, it is now often being tested with a limited number of dimensional tasks (e.g., 1 in EBCC or 3 in arm movement tasks). Thirdly, while the cerebellum is multimodular, it is now modeled with a single module. As a whole, these issues challenge the functions of the granular layer, which are currently underrepresented, along with sensory signals conveying contextual information developed across multiple modules intercommunicating through *pfs*.

Some technical challenges also emerge about the development and use of spiking cerebellar built-in controllers. First, learning requires very long-term simulations, bringing about intensive computations and high-performance computing (HPC). There are indeed examples of very large-scale simulations using cerebellar SNN running on HPC, making use of GPUs (Kuriyama et al., 2021; Yamazaki et al., 2021). Secondly, the embodiment in physical robots requires that computations are accelerated to quasi-real-time. HPC could be best obtained using neuromorphic cerebellar models, e.g. on SpiNNaker (Bogdan et al., 2021). Real-time has been achieved with event-driven look-up table technology (EDLUT: (Ros et al., 2006; Antonietti et al., 2019)), but translating SNNs into this format is laborious and not all the relevant biological properties can be maintained, and the system efficiency is limited by network size, synapse density and firing rates. Alternatively, the embodiment can be tested in silico, such as by using the Virtual Neurorobotic Platform (Falotico et al., 2017).

The spiking cerebellar built-in controllers, by recreating the fundamental components of a biological system by reverse engineering, are helping us understanding what the role of the cerebellum in the brain is and, at the same time, clarifying the neural architecture supporting predictive brain capabilities. These investigations are opening new perspectives for the generation of autonomous robots.

BOX 1 – Technology of cerebellar robotic controllers

Interface with the environment and spikes/analog interconversions

One significant challenge in implementing controllers that integrate spiking (cerebellar) models is the communication between the spiking controller and the environment, e.g., in the sensorimotor controller scheme outlined in Fig. 2.

The signal from the cortical system serving as the movement target is analog and requires digitization, processing into trajectory commands, and conversion into spikes to be fed to the cerebellar controller. Similarly, the error calculation module, responsible for comparing sensory feedback obtained from the movement effector following the motor commands with the cerebellar prediction, must handle spikes and transmit them to the cerebellar module. Lastly, the opposite transformation is performed to interface with the effector. Indeed, it receives spikes encoding a command, which represent torques or muscle strength to be applied, necessitating decoding into analog signals for each degree of freedom (DoF).

Specific interfaces are needed to convert analog signals into spikes. These conversions can be accomplished through encoding mechanisms based on *population rate coding*, which involves creating two pools of spiking neuronal populations (one for the positive ("agonist") and one for the negative ("antagonist") part of the signal) (Herzfeld et al., 2018; Ito, 2013). These populations encode the time course of the analog signal within their population rate. To perform the opposite transformations, the decoding of a spike into an analog signal, the average population rate of these two pools is calculated, and two signals (positive and negative ones) are extracted and combined through a simple summation. In this context, the cerebellar controllers can be useful to tackle issues that have been difficult to study experimentally, such as the neural coding of the DCN.

Testing protocols

Cerebellar controllers can be challenged across a range of sensorimotor tasks to assess their functionality and efficiency, comparing their performance with biological and behavioral data. These tasks encompass diverse paradigms such as associative Pavlovian tasks, which involve learning a timing association between stimuli, vestibulo-ocular tasks focusing on maintaining visual stability during head movements, and perturbed arm reaching tasks designed to evaluate motor adaptation and coordination in response to external disturbances. These testing protocols have different degrees of complexity, ranging from simple timing association to multi-DoF control of a limb, and therefore allow researchers to comprehensively examine the performance and adaptability of cerebellar controllers, testing also different hypotheses of cerebellar functioning.

Robotic embodiment

To execute these tasks effectively, a robotic embodiment of the controller becomes essential. A critical component of the embodiment is the movement effector, tasked with translating movement commands into actions, executing the desired movements, and generating sensory feedback. This effector can manifest as either a physical robot or its virtual avatar, depending on the specific experimental setup and requirements. If the cerebellar controller simulates slowly because of the high complexity of the model, real-time control of the robot becomes unfeasible, prompting the preference for a simulated robotic environment such as PyBullet (https://pybullet.org/) or the NeuroRobotics Platform (Falotico et al., 2017). Conversely, if the simulation is accelerated, e.g., by reducing spiking components, utilizing lookup tables to minimize solving differential equations, or leveraging neuromorphic architectures, a real physical robot may be the choice (Zahra et al., 2021, 2022; Yang et al., 2022; Mompó Alepuz, Papageorgiou, & Tolu, 2024). Simulations offer controlled testing but cannot replicate real-world complexity, even if introducing noise can prove robustness. Real robots face uncertainties, providing the ultimate test. Therefore, since the cerebellum's role in noise rejection is crucial, a mix of simulations and real-robot experiments is likely to be necessary: simulations are used for initial development and testing, and real robots are used for final validation and refinement.

Another crucial aspect is the complexity of the movement to be simulated, directly linked to the number of DoFs one intends to control in the robot and, consequently, the number of neurons required in the simulations. This consideration also prompts another decision: while the simplest approach involves treating each DoF independently and scaling up the entire controller for the number of DoFs, it is important to acknowledge that the cerebellum and other brain regions do not function in this isolated manner. Instead, they operate with interconnected and synergistic modules, necessitating thoughtful decisions in this regard. Multi-area models encompassing not only the cerebellum but also the sensorimotor cerebral cortex, basal ganglia, thalamus, brainstem, and spinal cord are needed to have a holistic model of sensorimotor control and learning.

Cerebellar neurons and circuits

While cerebellar neuronal populations have been quite well characterized, their role in behavior has not been clarified yet. Therefore, cerebellar SNNs need to embed realistic properties of neuron physiology to resolve the link between neuronal dynamics and behavior through simulations. Neurons can be modeled as point neurons to allow limited computational load while keeping biological plausibility (Izhikevich, 2004). Specifically, models from the Leaky Integrate and Fire (LIF) family have been used, with additional state variabl es to reproduce more complex spiking properties like adaptation or bursting. The Izhikevich model, for example, represents neuron dynamics through a two-dimensional system that can simulate various patterns of cortical and thalamic neurons based on parameter value combinations (Izhikevich, 2003). The Adaptive Exponential Integrate-and-Fire (AdEx) model introduces an exponential term and adaptive current to represent realistic spike initiation and adaptation (Brette & Gerstner, 2005). Finally, Generalized LIF (GLIF) models extend LIF by adding multiple dimensions and features like dynamic spike threshold and spike-triggered currents, to capture fast and slow subcellular properties, while keeping the system linear (Pozzorini et al., 2015; Teeter et al., 2018). For cerebellar SNNs, LIF, AdEx, and GLIF models have been applied (Lennon et al., 2014; Marín et al., 2020). For instance, the E-GLIF model has been developed and tuned to reproduce the main electroresponsive properties, e.g., spike-frequency adaptation, bursting, rebound, sub-threshold oscillations, and resonance, different for each neuronal population in the cerebellum. This is achieved through 3 state variables: the membrane potential and two intrinsic currents, one accounting for fast depolarization mechanisms like bursting, and the other, coupled with the membrane potential, accounting for slower hyperpolarization mechanisms like spike-frequency adaptation (Geminiani et al., 2018). Each neural population parameter model is tuned to obtain cell-specific electroresponsive phenotypes.

Thanks to the modular and stereotyped architecture of the cerebellar microcircuit, the topology of cerebellar SNNs can be derived from anatomical data. In the biological-grounded cerebellar SNNs, the main cerebellar neuronal populations (see Fig. 3 and the corresponding paragraphs in the text) are connected following morphology intersection connectivity rules or statistical rules based on connection-specific convergence/divergence values (De Schepper et al., 2022).

Recently, the nucleo-cortical recurrent loop has been introduced, since it plays a demonstrated role in cerebellar predictive functions and learning. Studies have shown its importance in amplifying associative learning signals (Gao et al., 2016), modulating the timing and amplitude of learned responses (Ohmae, Ohmae, Heiney, Subramanian, & Medina, 2021), and contributing to prediction-error computations (Xiao et al., 2023). While these behavioral links are established, their computational implementation in spiking cerebellar built-in controllers offers opportunities to further investigate the mechanisms underlying these functions.

Cerebellar learning rules

To assess learning capabilities, the synapses within the cerebellar controller require plasticity. One approach is to represent them as conductance-based alpha functions. Over time, long-term synaptic plasticity rules have evolved to incorporate spike-timing dependent plasticity (STDP) at various synapses, including pf-PC synapses, pf-MLI synapses, PC-DCN synapses, mossy fibre-DCN synapses, IO-DCN synapses.

The general rule for the changes in synaptic strength can be defined as follows:

$$\mathrm{W}(\mathrm{t}+1) = \mathrm{W}(\mathrm{t}) + \Delta\mathrm{W}(\mathrm{t})$$

Where (t) is the synaptic weight at time t and $\Delta\mathrm{W}(\mathrm{t})$ is the weight change. It can be defined as the combination of two different processes: a strengthening of the synapse (*LTP*) and a weakening of the synapse (*LTD*).

$$\Delta\mathrm{W}(\mathrm{t}) = \mathrm{LTP}(\mathrm{t}) - \mathrm{LTD}(\mathrm{t})$$

Each synapse follows a specific rule for the weight change. At the pf-PC synapses, the predominant type of LTD is induced heterosynaptically by *cf* (from IO) activity, through induced complex spikes in PCs. Conversely, the primary form of LTP does not rely on *cf* activity and is instead associated with the simple spikes produced by pf activity. This is based on the observation that a co-activation of a *cf* and a *pf* induces LTD in the corresponding *pf*-PC synapse, whereas *pf* activation without *cf* synchronous activity results in LTP as shown in Coesmans et al. (2004). The latter is weaker and slower than the former, as demonstrated by in vivo experiments (Yang & Lisberger, 2014).

The pf-MLI plasticity was constructed following the same principle of pf-PC plasticity but with reversed effects. When a specific signal (teaching signal) is received from the IO, it strengthens connections (LTP). The amount of strengthening depends on how frequently these pathways were active before receiving the teaching signal. The LTP process is based on experimental data about the timing of neuron activity change during learning, as measured in (ten Brinke et al., 2015). If a pathway is active without receiving the teaching signal, it weakens instead (LTD) (Geminiani et al., 2024).

For the cerebellar nuclei, experimental findings provide evidence of synaptic and intrinsic plasticity during learning (Ohyama, Nores & Mauk, 2003; Ohyama et al., 2006; Uusisaari & de Schutter, 2011). This occurs at a slower time scale than in the cerebellar cortex, consistent with the hypothesis that nuclear plasticity may be under PC control (Zheng & Raman, 2010). In cerebellar SNNs, for *mf*-DCN plasticity, LTP happens when the driving inhibition from PCs decreases in strength. Conversely, LTD occurs when PCs are strongly active, so that it potentiates the silencing of DCN. For PC-DCN synapses, a standard unsupervised STDP learning is used, depending only on the difference between the pre- and post-synaptic firing times (Caporale & Dan, 2008). Furthermore, another plasticity site at DCN level has been introduced in some cerebellar models, the IO-DCN plasticity, which adjusts the strength of connections based on the current error signal from *cfs*; this mechanism would allow for quick adaptation to changes in the environment and would ensure that adjustments are made promptly but can also be forgotten when they are no longer necessary. The biological validation of IO-DCN plasticity is still missing (Uusisaari & Knöpfel, 2011).

CRediT authorship contribution statement

Egidio D'Angelo: Writing – review & editing, Writing – original draft, Conceptualization. **Alberto Antonietti:** Writing – review & editing, Writing – original draft, Supervision. **Alice Geminiani:** Writing – review & editing, Writing – original draft. **Benedetta Gambosi:** Writing – review & editing, Writing – original draft. **Cristiano Alessandro:** Writing – review & editing. **Emiliano Buttarazzi:** Writing – review & editing, Writing – original draft. **Alessandra Pedrocchi:** Writing – review & editing, Supervision, Conceptualization. **Claudia Casellato:** Writing – review & editing, Writing – original draft, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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No data was used for the research described in the article.

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