

Received 24 June 2024, accepted 24 July 2024, date of publication 29 July 2024, date of current version 26 November 2024.

Digital Object Identifier 10.1109/ACCESS.2024.3435141

TOPICAL REVIEW

Advancements in Cerebellar Modeling and Its Practical Applications: A Comprehensive Review

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This work was supported by Shantou University (STU) Scientific Research Initiation Grant, No. NTF24003T.

ABSTRACT The cerebellum plays a crucial role in motor learning and memory, and recent studies have proposed various cerebellar models to investigate these functions. This review examines the literature on different levels of cerebellar modeling, including animal models, neuronal and synaptic plasticity models, relevant artificial intelligence (AI) paradigms, and real-time applications. The development of cerebellar models is discussed, from simple to complex and from theory to application. Optimization methods used in AI for optimizing cerebellar neuronal electrophysiology parameters are also highlighted, allowing for the prediction of difficult-to-observe neuronal features. Combining neuroscience and computer science-oriented neural networks, such as the spiking neural network (SNN) and the artificial neural network (ANN), can enable the cerebellar model to adapt to various applications, including robotic control, neurological disease simulation, and drug delivery simulation. This review provides a useful guide for future research on cerebellar modeling.


INDEX TERMS Cerebellar modeling, motor learning, synaptic plasticity, robotic control, artificial intelligence.

I. INTRODUCTION

The cerebellum, located at the base of the brain where the spinal cord meets the brain, is a critical structure in the central nervous system. Anatomically, it consists of two hemispheres connected by the vermis. Internally, it features a complex arrangement of gray and white matter, including the cerebellar cortex and deep cerebellar nuclei. The cerebellar cortex has a simple structure with three layers: the molecular layer, the Purkinje layer, and the granular layer, from the outermost to the innermost. Interestingly, the Purkinje cell (PC), the sole output of the cerebellum, has a large dendritic

tree like a fan in the sagittal plane. Physiologically, the cerebellum plays a pivotal role in coordinating voluntary movements, maintaining balance and posture, and fine-tuning motor activities. It receives sensory input from the spinal cord and other parts of the brain, processes this information to detect errors in movement, and sends corrective signals to motor centers. This ensures smooth, precise, and coordinated muscular activity, crucial for everyday tasks such as walking, writing, and speaking.

The cerebellum has a crucial role in motor learning behaviors, and its exploration has led to the development of cerebellar modeling. Although the cerebellum has a wide range of functions [1], [2], [3], [4], it can naturally demonstrate motor learning and consolidation abilities better

The associate editor coordinating the review of this manuscript and approving it for publication was Zheng H. Zhu .

than the advanced microcontroller-equipped robot system controller, despite significant progress in AI [5]. The study of the cerebellum goes beyond animal behavior, anatomical structure analysis, electrophysiology recording, behavior-neural circuit analysis, and simple/complicated neural circuit simulation to a more refined analysis and application [6], [7], [8], [9], [10], [11], [12], [13]. In essence, cerebellar simulation has undergone two major changes in two directions: from simplicity to complexity, and from theory to application, which have mutually benefited each other.

A. FROM SIMPLICITY TO COMPLEXITY

The modeling of the cerebellum initially focused on exploring its function through anatomy and physiology, resulting in the conceptualization of the cerebellum as a perceptron pattern classification device based on its network structure, resembling a top-down modeling approach [14], [15]. Top-down modeling primarily emphasized the influence of network structure on animal behavior, simplifying neuronal structure and cellular properties for efficient signal transmission between neurons (Fig. 1) and thus inspiring ANNs [16].

Over time, with the advancement of electrophysiology and increased knowledge about neuronal ion channels and receptors, cerebellar modeling has shifted towards a bottom-up approach. This approach involves modeling the intricate electrical features of individual neurons and considering the connectivity between neurons with different rules [21], [22], [23], [24], [25]. Various types of cerebellar neurons, such as granule cells (GrCs), Golgi cells (GoCs), PCs, deep cerebellar nuclei (DCN), inferior olive (IO), basket cells (BS), stellate cells (SC), and unipolar brush cells (UBC), have been modeled with greater subtlety (Fig. 1B) [12], [26], [27], [28], [29], [30], [31], [32]. Furthermore, several neuronal and network models of the cerebellum have been proposed, taking into account the compartmental properties of neurons and their interactions within the network (Fig. 2A) [12], [33].

Advancements in supercomputing have allowed for the simulation of cerebellar networks with a larger number of neurons and synapses, enabling the modeling of human-scale neurons [34], [35]. Drawing inspiration from the reconstruction and simulation of neocortical microcircuitry, considering cell density and morphology [36], a brain scaffold builder (BSB) approach has been proposed, which takes into account the network volume, cell types, cell placement, and cell connectivity [37] (Fig. 2B). This has led to a shift in cerebellar modeling from simplicity to complexity, encompassing both neuronal and network levels.

B. FROM THEORY TO APPLICATION

The modeling of the cerebellum is based on its unique properties, such as its neuronal structure, network arrangement, and electrophysiology, as well as animal responses to neuronal activity.

It is important to note that as our theoretical knowledge and simulation techniques improve, we can create more realistic and complex models of the cerebellum.

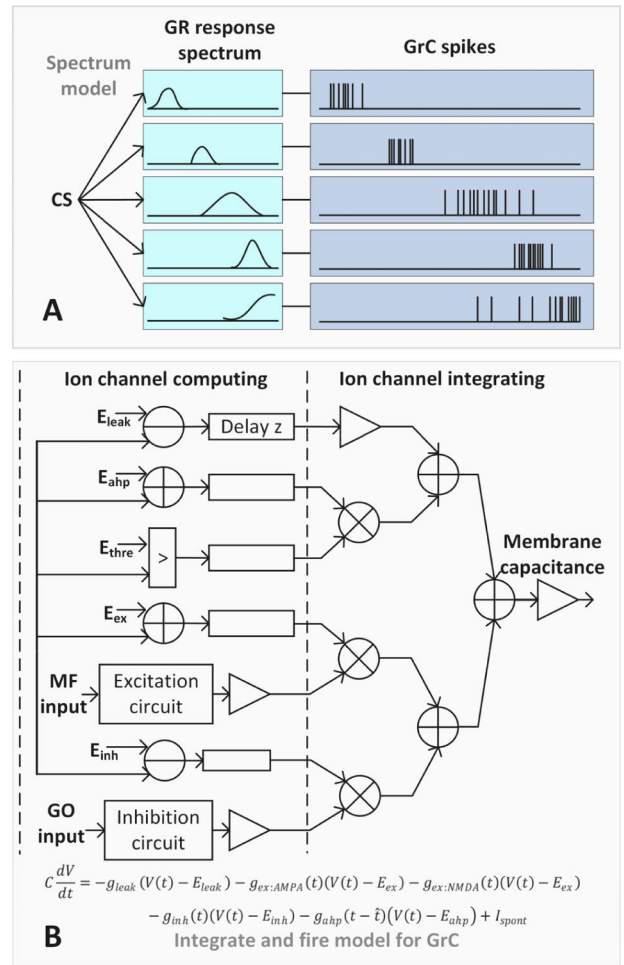


FIGURE 1. The neuronal modeling for GrC evolves from a simple spectrum model to an integrate and fire (IF) model. **A**, spectrum model [17], [18]. **B**, IF model for GrC with hardware implementation via FPGA [19], [20].

Practical applications of cerebellar modeling take advantage of the structural properties of the cerebellar network. For example, in SNN models for the cerebellum used in multi-joint robotic control, the number of neurons and connections depend on the variables being controlled (such as joint position or velocity) (Fig. 3) [13], [40]. Neuronal properties are often simplified to adapt them to specific applications, such as neglecting pontine nuclei (PN) and granular layers (GLs) in some cases, and replacing PF-PC plasticity with CS-PC modality in a cerebellar neuroprosthetic system (Fig. 4A) [41], [42], [43], [44].

Encoding and decoding methods differ from those of neurons themselves. In more realistic modeling of GL, the GrCs have various properties such as center-surround organization, time-window matching, long-time constant of NMDAR and high-pass filtering [33], [45], [46], [47]. However, such properties may be aversive to practical modeling, where GrCs are used to convey spatial/temporal information for afferents. Thus, the encoding of afferent signals is transformed as ordered and similar GrC activities, and the decoding of yield

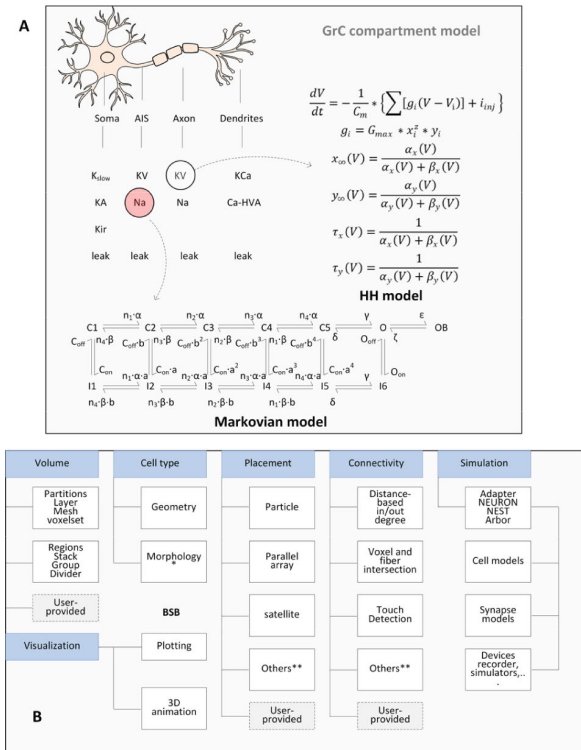


FIGURE 2. Complicated neuronal model. A, GrC compartment model [31], [38], [39]. B, BSB approach for neurons [37].

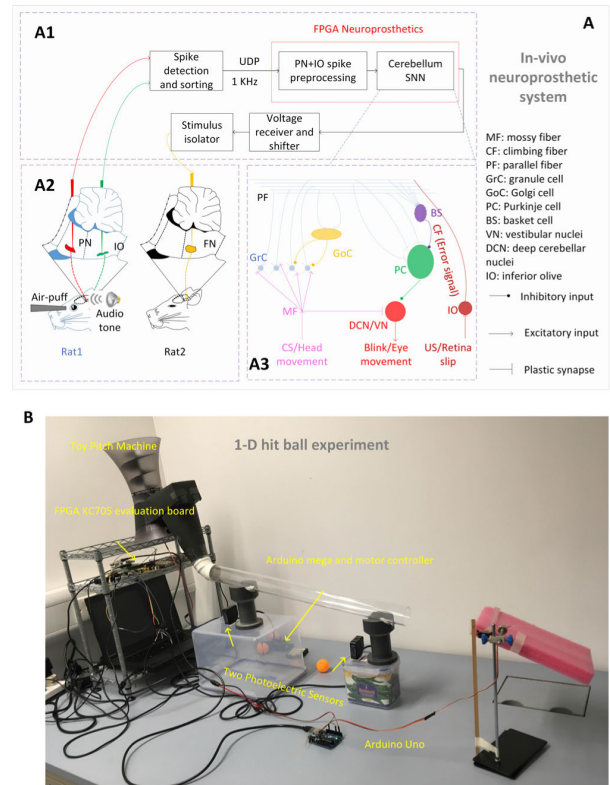


FIGURE 4. Cerebellar model related applications. A, in-vivo neuroprosthetic system [19]. B, 1-D hit ball experiment [42], [55].

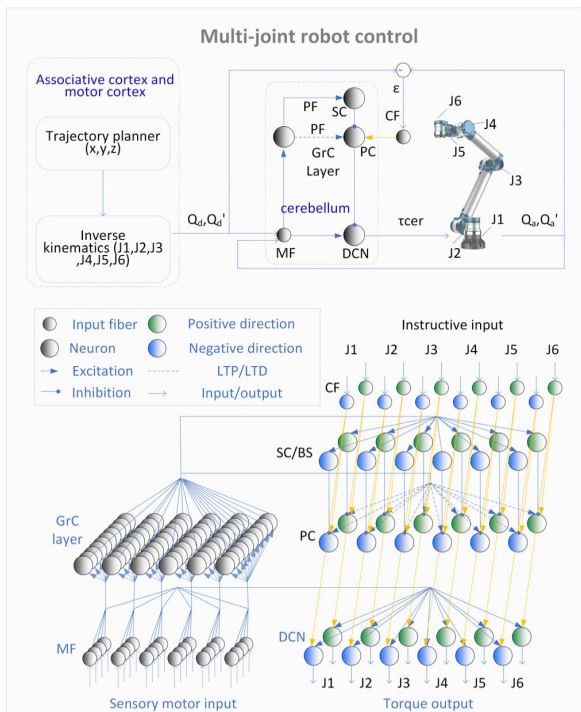


FIGURE 3. Multi-joint robot control [13], [40].

spikes is transformed with a uniform rule for recognition by lower devices [13], [40], [41], [48], [49]. Additionally, biophysical models like Hodgkin-Huxley (HH) and Markovian models have been proposed, and the implemen-

tation of cerebellar models for real-time applications has adopted more complex neuronal structures to exploit high-performance computing technologies [50].

In real-time applications, timeliness, model size, hardware platform, and computational method are important considerations [19]. There is still debate over whether the cerebellum operates in sparse coding mode [51], [52]. And thus, the number of neurons used for practical studies depends on specific applications, and researchers try to accommodate more neurons with smaller chips to ensure the authenticity of the simulation. Moreover, real-time performance also varies based on the application in which behavioral simulations should be based on factual evidence whereas signaling between devices may drive the model to work in a faster speed (Fig. 4A and B) [19], [20], [53].

The interplay between cerebellar models and AI is an intriguing research topic [54]. The cerebellum's vast number of small GrCs enables high-dimensional computation, which bears similarities to AI's deep learning. Researchers have employed various optimal algorithms to fine-tune cerebellar model parameters. These findings beg the question of whether neuronal modeling in the cerebellar model can be supplanted and to what degree artificial models can capture motor learning.

This study reviews literature on cerebellar modeling from animal models to the modelling of neuronal and structural of the cerebellum as well as its applications in AI and real-time

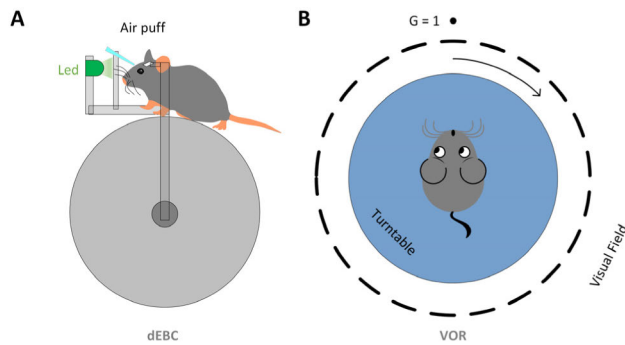


FIGURE 5. Two kinds of animal models (dEBC and VOR) for the cerebellar related studies.

scenarios. We will draw conclusions based on our findings and propose future directions for research.

II. ANIMAL MODELS FOR CEREBELLAR MODELING

Animal models for cerebellar modeling are mainly derived from the models used for cerebellar motor learning, including delay eyeblink conditioning (dEBC), vestibular ocular reflex (VOR), optokinetic response (OKR), and the saccade. The common feature of these models is simplicity, a single and pure mode of motion, and usually a relatively passive motion. These models provide insights into the cellular and molecular mechanisms underlying cerebellar processes.

A. dEBC

The cerebellar neural circuits are widely recognized for their role in cerebellar motor learning, due to the simplicity of the cerebellar circuit and the straightforward paradigm of motor learning behavior, such as dEBC in mice [6], [17], [46], [56], [57], [58], [59], [60], [61]. The micro-complex responsible for dEBC is the zebrin-negative area of lobule IV (lobule simplex) in the cerebellum's two hemispheres [5], [7]. In dEBC, mice learn a timed response to a neutral stimulus that would not normally trigger an eyeblink (Fig. 5). The conditioned stimulus (CS) and unconditioned stimulus (US) are conveyed by the mossy fiber (MF) and climbing fiber (CF), respectively. Repeated paired stimuli to the relayed parallel fiber (PF) and CF diminish the simple spikes of PCs in response to the US, making the modeling of dEBC centered around balancing the timing of reducing PC simple spikes [56], [57], [59], [62]. However, traditional PC models, such as time derivative models, resemble models used in cybernetic theories and lack biological plausibility [18], [63]. To address this, a PC model with metabotropic glutamate receptor activation was proposed and the learning in this model is based on population voltage changes induced by $\text{Na}^+/\text{Ca}^{2+}$ exchange currents [58], [64]. To incorporate more biological evidence [65] while simplifying the molecular and cellular machinery, SNN models accompanied by conductance-based leaky integrate and fire (CLIF) models for each neuron were proposed [46], [60], [61]. These models strike a good balance between biological plausibility, the scale of the neural network, and running speed [19], [20], [42]. Furthermore, SNN models allow for the design of

learning rules to validate the impact of synaptic changes on dEBC motor learning and memory consolidation [66], [67], and can even be pruned to model deficient cerebellum in gene knockout mice or cerebellar pathologies [61], [68], [69]. With the ongoing research on the structure, function, and dynamics of cerebellar circuits, the development of BSBs has enabled the reconstruction of cerebellar dEBC neural networks, taking into account the morphology of neurons within the network, including their anisotropy and regular geometry [37], [70], [71]. Recently, the understanding of bidirectional plasticity in different microzones has become crucial for motor learning. This has led to more refined simulations of delay eyeblink conditioning (dEBC), where synergetic downbound and upbound areas of the cerebellar nuclei are modeled. These simulations contribute to a finely tuned associative motor learning behavior [72].

B. VOR AND OKR

Animal models for the VOR and OKR are often used to demonstrate how the cerebellum functions as a controller for motor learning, regulating both gain and timing (Fig. 5) [9], [73], [74]. These two paradigms have distinct neural circuits but are mediated by the same controller: the cerebellum. The zebrin-positive area of the floccules in the cerebellum's two hemispheres mediates rate coding for VOR or OKR [9]. In a feedforward system, the afferent signal to the cerebellum for VOR is derived from head movement conveyed by the semicircular canal and floccular projection neurons. Conversely, the afferent signal for OKR comes from the accessory optic system, which supports a feedback neural circuit [75]. Unlike dEBC, VOR and OKR require a continuous experimental protocol, making a rate-based scheme more suitable for simulation since it can omit the transformation between neural spikes and firing rates [73], [76], [77]. However, simulating VOR/OKR with SNNs has drawbacks, such as determining the baseline firing rate of PC, requiring an additional item of current to be added into CLIF equations [78]. Another example is modeling phase reversal learning (PRL) of VOR [73], [79] with a SNN model (Fig. 6A) where the phase reversal is rapid because the subtle retina slip induced by learning cannot be accurately translated by neural spikes innervating PC through climbing fiber leading to large variations in gain and phase (Fig. 6B and C) [55], [80]. Furthermore, the phase cannot be completely reversed to 180° due to a lack of delay of error feedback [77], [81], [82].

C. SACCADIC

Saccadic eye movements are crucial for efficient visuo-motor control, allowing for rapid focusing on new targets [83], [84]. The cerebellum is also involved in saccades, controlling eye movement amplitude, peak speed, and duration [85], [86], [87]. The cerebellar control of saccades is a feedforward system, with errors induced by the difference between the shifting target on the retina and the shifting eye position input to PCs via CF afferents in the posterior

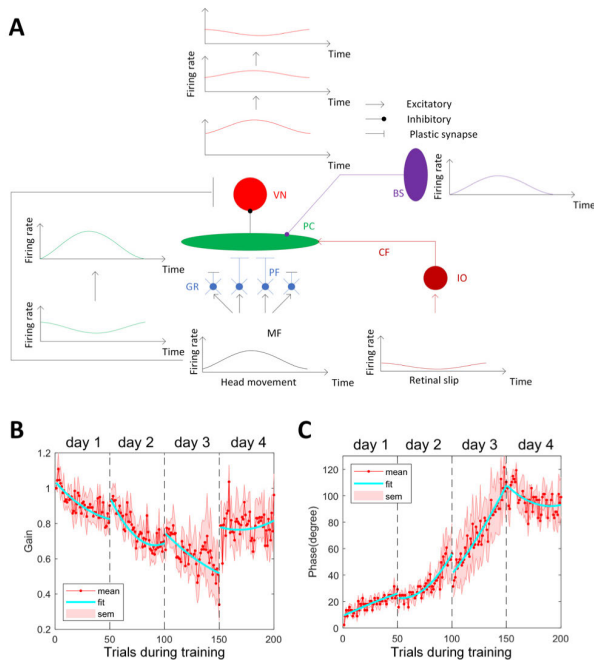


FIGURE 6. PRL. A, the principle of PRL. B and C, the gain and phase changes in the PRL with a SNN model according to A.

vermis of the cerebellum. Several models have been proposed for the cerebellar control of saccades [88]. The midbrain superior colliculus (SC) is also involved in saccadic eye movement control, and pure SC component models have been proposed [89], [90]. Synergistic models considering the interaction of the SC and cerebellum have also been proposed [91], [92], [93]. A feedforward and feedback loop model considering the cascade of retina, cortex, SC, cerebellum, brain stem, and the eye has been suggested [94], [95]. However, these models lack the influence of SNNs on saccadic behavior. Gad et al. proposed integrated models of PC and fastigial oculomotor region cells with neural plasticity and a parallel pathway of SC and cerebellum shifting to a cascade one, where the cerebellum relays information from the SC [75], [96]. More recently, Fruzzetti et al. proposed a cerebellar SNN with LIF model considering the joint influence of neural plasticity to the eye movement speed [97]. The PF-PC plasticity mechanisms are similar to that in the VOR adaptation and dEBC, indicating that the cerebellar neural circuit implements general computational algorithm but with different cerebellar regions and diverse plasticity constituting high dimensional representation.

III. NEURONS AND STRUCTURES FOR MODELING

The cerebellum has a relatively simple structure, consisting of the deep cerebellar nuclei and the cerebellar cortex, which is composed of three layers: the ML, the PC layer, and the GL from outermost to innermost. Modeling of the cerebellum primarily focuses on the GL and the PC layer due to the numerous but tiny GrCs and the complex morphology of PCs. This complexity contributes to the intricate electrophysiology of the cerebellum, leading to its various motor functions.

A. GL

The Marr-Albus computational cerebellar model suggests that the GL processes afferent information from the MFs as sparse coding although it contains small but dense GrCs [98]. However, the small size of GrCs makes it challenging to record in in-vivo experiments and thus, the modeling of the GL has evolved from a simple hypothesis to a fine inference based on electrophysiology recordings [8].

Prior to structuring a specific GrC model, Moore et al. proposed tapped-delay-line models in which the input afferent to PC is sequentially conveyed by different elements [57], [59]. This method is an embryonic form of a liquid-state generator for the GL, which was proposed by Yamazaki and Tanaka [99]. Although the tapped-delay-line model lacks biological plausibility, its evolutionary version, labeled-line coding (LLC), can be well adapted to various cerebellar-related robotic applications due to its simplicity and well-timed properties [41], [48], [49].

The core idea behind these modelings for the GL is to transform the afferent signal via MF into the sequential activation of GrCs, known as the passage-of-time. The passage-of-time within the GL is attributed to the high-dimension representation of GrCs, so that computations of representative behavior states are distributed into orthogonal subspaces [100]. With the breakthrough of electrophysiology recording, the modeling of the GL considers more about the electrophysiological characteristics of neurons, the spatiotemporal property, the influence of neural plasticity, and even realistic morphological features of the neurons. Table 1 shows a comparison of different models [101], [102], [103], [104] for the GL with various types of neurons [30], [33], [38], [105], [106].

B. PC

The PC plays a crucial role in motor learning, acting as the sole output of the cerebellum and determining the activity of downstream nuclei and the whole network property through its integrator-like function [107], [108]. For example, the PC spike burst-pause dynamics are critical for sensorimotor adaptation: gating the vestibular-motor response association during VOR acquisition, mediating the LTD/LTP balance for VOR, and reshaping synaptic efficacy distributions for the PRL of VOR [109]. Another example shows that the PC dynamics like PC firing rate, firing phase, and temporal spike pattern can be modulated by the integration of PF-PC and MLI-PC pathway together with short-term plasticity at both single neuronal level and network level [107].

Due to its intricate neuronal morphology and multiple ion channels, modeling PC requires assembling different parts of a neuron. A PC compartment model called R-DB model which contains more than 1600 compartments was proposed by De Schutter and Bower based on the extended work of Rapp et al. [12], [110], [111], [112]. The complicated model endows the PC modeling to replicate physiological responses under multiple possibilities [113], [114]. Furthermore, various dynamic properties of PC [115], [116], [117], [118],

[119] which are derived from experimental methods can be revealed with models [120], [121], [122], [123], [124], [125] to imply the capability of strong computation of PC at both single neuronal level and network level (Table 2) [108], [122], [123], [126]. Moreover, the compartment model is more suitable for studying local characteristic subcellular mechanisms of PC in terms of connectivity and discharge instead of merely yielding somatic properties of PCs within a large-scale network [127], [128], [129], [130]. Such a modeling can augment our recognition of the fine-tuning of PC during motor learning as well as the functional organization of cerebellar cortical circuitry. Further studies have extended the model compartment to include axon initial segments (AIS), paraAIS, nodes of Ranvier (RN), and non-myelinated collateral to study the localization and gating of PC ionic channels [131].

Although the complicated compartment model can well describe the input and output transformation of the PC, the information processing of the cerebellar may not merely depend on PC complex structure [73], [132]. As a result, a simplified model may well illustrate the essence of PC dynamics. For example, an adaptive exponential IF model was adopted to explain the relationship between the intrinsic property of PC bistability and inverse stochastic resonance (ISR) which is a possible mechanism for information processing in the cerebellar cortex [126]. Furthermore, only a few studies use a full compartment model to build network level simulation [133], [134]. Instead, researchers have used simplified models for specific application scenarios [135]. When studying PC at the network level or network-based applications, the modeling will be further simplified to adapt to real-time requirements and corresponding firing patterns [13], [17], [41], [46], [56], [60], [62], [66].

C. CEREBELLUM WITH OTHER NEURAL CIRCUITS

Although different modules within the cerebellum are responsible for the execution of various motor tasks [136], [137], [138], [139], the motor planning proceeding the movements or the movements initiation are maintained by neural circuits that span multiple brain regions [140], [141], [142]. The connectivity between the cerebellum and cerebral cortex is organized in parallel loops [143], [144], [145], [146], [147], [148], one of which is the cerebello-thalamo-cortical circuit that facilitates goal-directed action initiation [140], [149]. This circuit can simulate cerebellar ataxia [150] and be modeled with refined neuronal models to integrate with other neurological disorders for more refined treatment methods [151], [152]. The cerebellum works as a motion execution unit, receiving information from the visual cortex network and yielding output together with prefrontal cortex planned signals as the control signal for a collision-free robot task, highlighting the synergy of different brain regions in motor tasks [11]. Other circuitry, such as cortico-spino-cerebellum, is also applied in cerebellar learning of arm control [153].

In addition, there are local circuits within the cerebellum that enhance the performance of cerebellar associative learning by providing feedback [154]. The nucleo-cortical circuit involves the DCN providing feedback to key components like GoCs [155], MFs [156] and PN [157], which can also be measured through network simulations. The convergence of input signals from three different similar cortical regions with different inputs, including external afferents and internal feedback, amplifies cerebellar motor learning through the DCN [158]. However, current modeling techniques tend to oversimplify this process by focusing solely on linear summation, ignoring the critical balance and feedback mechanisms within the cerebellar circuit [159], [160].

Another way to model the cerebellum is by creating a brain functional connectome (FC) using non-invasive data such as electroencephalography (EEG), magnetoencephalography (MEG), or functional magnetic resonance imaging (fMRI). This involves representing different brain regions as nodes and connecting them with wires based on their correlation values during a specific task [161], [162], [163], [164]. This type of modeling goes beyond simple motor learning tasks and can also be used for cognitive tasks such as working memory, [165], driving fatigue [166], and even disease detection [167]. However, it is important to note that there are differences between the neural circuit scale of the cerebellum and other circuits (macroscale) and the microscale of cerebellar motor learning function. Integrating data from both scales can be challenging due to differences in spatio-temporal resolution and bridging gaps between AI and neuronal modeling. Nonetheless, understanding how different brain regions coordinate in terms of both macroscale and microscale during a task is crucial for advancing our knowledge of the brain.

IV. SYNAPTIC PLASTICITY IN CEREBELLAR MODELING

There are various types of synaptic plasticity within the cerebellum which play important role in cerebellar motor learning. Two reviews expound the neural plasticity within the cerebellum with both in-vivo and in-vitro experiments according to the neuron type and network structure [67], [169]. As mentioned in the review [45], both short-term and long-term plastic change exist at almost all synapses within the cerebellum but may be adaptive to different circumstances [45], [67], [170]. In the modeling of these synaptic plasticity, the function of LTD at PF-PC sites is the most explicit which manifests the acquisition of a motor learning behavior. On the other hand, the acquisition of motor learning also needs to be stored as memory consolidation which behaves as long-term plastic change at MF-nuclear outside the cerebellum in the neuronal level. The learning process and the memory process is linked by PC spike pattern [41], [48], [53], [55], [60], [76]. Moreover, the direction of plasticity at MF-nuclear sites is variable according to different tasks. For example, in the OKR adaptation, LTP at MF-VN strength the memory consolidation of such adaptation. However, in the simulation of PRL of VOR, the gain alteration of MF-VN

TABLE 1. Different models for the GL.

Contributor	Neuron type and model, network structure model	Behavior	Influence	Ref
Fujita	CrC, Golgi cell (GoC), rate-based scheme, oscillator model	VOR	An individual GrC is an oscillator with a frequency specified by a MF signal representing the head velocity and with a different time lag	[63]
Moore et al	PN, GoC, time derivative model, delay line model	dEBC	This model can perform learning of conditioned response	[57, 59]
Bullock et al	CrC, GoC, rate-based scheme, spectral timing model	nictitating membrane response	The model is based on the widely distributed membrane time constant of different GrCs	[18]
Yamazaki	GrC, GoC, rate-coded scheme, random projection model	dEBC	Time passage from the trigger of an external signal could be represented by the sequence of activity patterns	[99]
Yamazaki	GrC, GoC, conductance-based integrate and fire model, random projection model	dEBC, VOR	Passage of time (POT) was represented by GrC spikes and a long time constant of NMDA receptor contributes to GrCs' POT	[46, 78]
Sudhakar et al	MF, GrC [33, 38, 105], GoC [30, 106], leaky integrate-and-fire model for MF, HH model for GrC, HH and Markovian model for GoC, random projection model	No	A large-scale 3D network model is constructed so that GrCs and GoCs oscillates with mossy fiber inputs of a wide variety of firing patterns	[101]
Rössert et al	one-population and two-population model [99]	No	A random projection network can generate the necessary signal transformation as long as it operates in a state close to chaotic behavior	[102]
Mapelli et al	GrC [33, 38, 105], GoC [30, 106], HH model for GrC, HH and Markovian model for GoC, random projection model	No	the effect of LTD and LTP in modulating MF input converged to output GrC that regulates the gain and timing of output firing	[103]
Schepper et al	GrC, GoC, Markovian and HH model, random projection model	PC firing pattern for dEBC and VOR	They proposed a structure-function network model for the cerebellar cortical microcircuit which focuses on studying the impact of realistic morphologies as well as multi-compartment neurons with cell-specific membrane and neurotransmitter release mechanisms on cerebellar motor behaviors	[37]
Solinas et al	GrC [33, 38, 105], GoC [30, 106], HH model for GrC, HH and Markovian model for GoC, random projection model	No	A modeled GL possesses various properties	[33]
Barri et al	MF, GrC, rate-based scheme, similar to spectral timing model	dEBC	The short-term plasticity of MF-GrC is sufficient to enable GrCs to reproduce various temporal sequences supporting PC to learn precisely timed pauses without the help of GoC inhibition	[104]

TABLE 2. Modeling of various PC dynamic properties.

Author	Dynamic property	Implication	Model type
Phoka et al [108]	Phase response curve (PRC)	PC shows different dynamic behavior depending on their firing rate. at high firing rates PCs can transmit information via a temporal code whereas at low firing rates they are well-suited for rate coding	single compartment model/ Morris-Lecar model [120]
Buchin et al [126]	Inverse stochastic resonance	Synaptic noise allows PCs to quickly switch between functional regimes, so that the synaptic noise in particular amplitude can significantly enhance the transmission of information across the PCs to downstream neurons	adaptive exponential IF model [121]/R-DB model
Luque et al [109]	Spike burst-pause	PC spike burst-pause is important to normal VOR adaptation and phase reversal version	Compartment model/IF model
Roth and Häusser [115]	Steady-state electrotonic structure of PCs	Synapses located in close proximity to the soma have a privileged position to exert a precise temporal influence on the membrane potential of the soma	single compartment and two-compartment model
Khaliq et al [122]	High frequency firing with resurgent Na ⁺ current	Na ⁺ currents with a resurgent kinetics boost and accelerate PC firing	single compartment model
Akemann and Knöpfel [123]	Spontaneous firing rate of PC	K _{v3.3} can increase the spontaneous firing rate via cooperation with resurgent sodium currents.	single compartment model
Fernandez et al [116]	Saddle-node bifurcation/homoclinic bifurcation	PC firing dynamics are consistent with a system undergoing a saddle-node bifurcation in the transition from rest to firing and a saddle homoclinic bifurcation from firing to rest and thus PC firing is related to the underlying bifurcation structure	HH model
Loewenstein et al [117]	Bistability of PC	PC bistability may have a key role in the short-term processing and storage of sensory information in the cerebellar cortex	Single compartment model
Ostojic et al [118]	Morphology-induced resonance of PC	Cellular morphology induces high frequency resonance	Single/multi-compartment model [122], [123], adaptive exponential IF model [124]
Couto et al [132]	PRC	PC phase response curve depends on PC firing rate which influence the transition of phase independent integrator to a phase dependent mode of a PC	Single compartment model
Zang et al [119]	PRC	PRC changes lead to oscillations and spike correlations mainly at high firing rates. The rate adaptation of PRCs can help organize the spatio-temporal input from PCs to the DCN	Watts-Strogatz model [125]
Zang et al [168]	PC response from voltage and branch specific CF	PC voltage can mediate both the amplitude and the spatial range of CF-evoked Ca ²⁺ influx by the availability of K ⁺ currents	Compartment model

decrease followed by an increase which resembles an erase of VOR memory and then adding an OKR adaptation [77]. The synaptic plasticity at other sites within the cerebellum is

still indispensable [41], [73], [77], [171] especially in the area where extracerebellar signals import as the plasticity involves signal coding. For instance, the MF-GrC synapse together

with GoC inhibition regulates GrC activities. It generates bidirectional synaptic change at MF-GrC sites to fine-tuning the spike timing of GrC in/beyond a window set by GoCs in response to specific motor behavior [33], [47]. Due to the variability of GrC firing pattern, the plasticity at MF-GrC sites is a short-term one which can be donated as small value of time constant of presynaptic facilitation and vesicle inactivation [33]. On the other hand, DiGregorio et al validated short-term synaptic property of MF-GrC sites with both experimental and numerical methods. The short-term plasticity of MF-GrC is sufficient to enable GrCs to reproduce various temporal sequences supporting PC to learn precisely timed pauses without the help of GoC inhibition [104], [172]. However, there still remains long-term plastic change at MF-GrC sites which are confirmed to influence the burst initiation and frequency of GrCs in terms of both experimental observation and theoretical analysis [105].

V. NON-MAINSTREAM MECHANISMS FOR CEREBELLAR MOTOR LEARNING

The mainstream theory of cerebellar motor learning proposes that the synaptic plasticity between PF and PC is responsible for this process, while the GL provides POT representation. However, there is a non-mainstream theory that suggests that motor learning comes from an internal timing mechanism within the PC itself, rather than through traditional synaptic changes. This is supported by evidence showing that PC can learn well-timed pause responses to different inter-stimulus intervals even with direct stimulation to PF and CF [173], [174]. Additionally, interrupted CS still generates CRs at the same learned interval, and changing the stimulation frequency does not affect the timing of the CR [174], [175] whereas blocking GABAergic interneurons and glutamatergic AMPAR in the molecular layer did not affect PC pause responses to unpaired CS [173], [176]. If the PF-PC plasticity were the only mechanism for cerebellar motor learning, then the timing of the CR would be affected by the duration and frequency of the stimulation. Therefore, it is likely that mechanisms located within the PC complement this main machinery [177] (Fig. 7B).

Nevertheless, the well-trained PC response to CS can be abolished by antagonists of the specific metabotropic glutamate-based receptor type 7 (mGluR7) manifesting that mGluR7 mediates an adaptively timed learned response. And thus, a model of PC that can encode time interval was proposed where the temporal memory is embedded within the dynamics of a set of proteins like mGluR7, G-protein, protein kinase A (PKA), etc. [178] (Fig. 7A).

Another biochemical model of PC has been presented as a complementary mechanism of motor learning with the modification of synaptic weights, where five elements, a decoupling mechanism, a “clock”, a coincidence detector, and a positive and a negative feedback loop are in accordance with interactive biochemical candidates like Ca^{2+} , IP_3 , adenylyl cyclase, PKA, regulators of G protein signaling (RGS) [177].

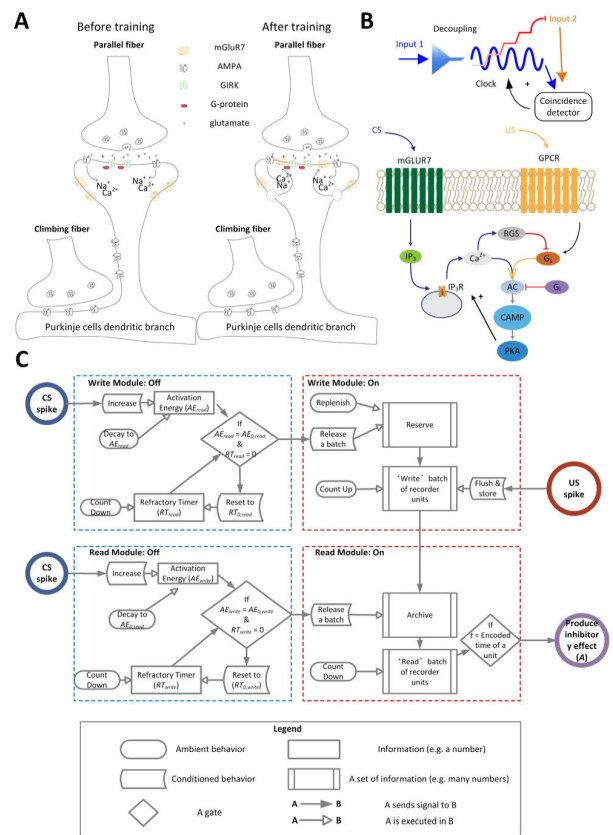


FIGURE 7. Non-mainstream theory and model for cerebellar motor learning. A, mGluR7 receptor distribution before and after conditional training in the PC [178]. B, model scheme and molecular interactions in the PC modeled for time representation [177]. C, the cerebellar response in the modeled PC with write and read modules [179]. One thing that these models.

Furthermore, a proof-of-principle model of POT for PC has been proposed. When CS onset occurs, the PC releases a batch of evolving “recorder units”, which contribute to the inhibition of the cell at the interval it has coded. The strength of inhibition is decided by the repetition of CS-US pairs [179] (Fig. 7C).

VI. DIFFERENT NEURONAL MODELING

The neuronal modeling for cerebellar model varies from simple algebraic summation to ionic simulation for different neuronal compartments depending on its complexity [26], [31], [37], [46], [57], [180], [181]. Usually, the neuronal modeling can be classified into rate-based one and SNN according to model tasks. The advantage of SNN is not limited to its biological plausibility but the ability to handle continuous afferent streams from outside world which is the major problem for the robot control that it should confront a time series evolution of dynamics [111], [182], [183]. The LIF model is a basic neuronal modeling that can make a trade-off between neuronal/network complexity and biological plausibility. To better understand the property of neuronal network, the LIF has derived many variants such as CLIF and extended-generalized LIF, which can be well integrated

into SNNs saleably to mimic motor behavior and close-loop applications [19], [41], [46], [184].

A. HH MODEL

The HH model is a conductance-based model functioning on the gating of various ionic channels with different conductance state and numbers of subunit so that the biophysical mechanism of a cell can be represented in details (Fig. 2A). The membrane voltage of a compartment can be obtained with the time integral of different ionic currents which depend on the gating variables (Fig. 2A, Eq. 1-6). In this way, the neuronal modeling can be represented by the assemble of ionic channel opening and closing. In the cerebellar neuronal modeling, the PC, GrC, GoC and even SC/BC are simulated with HH model so that the electrophysiological property and the neural network characteristics can be well presented [26], [30], [33], [38], [106], [131], [181].

B. MARKOVIAN MODEL

While ion channels can basically switch in two states: open and closed, ligand-gated receptors can switch between multiple states. Markov chains, a type of Markovian model, can be used to model the complex state transitions of synaptic receptors (Fig. 2A). The complexity of a Markov chain depends on the type and subtype of synaptic receptors like AMPARs, NMDARs and GABA_A [185]. In cerebellar neurons which contain various postsynaptic receptors, Markov chains are used to model the state transitions of aforementioned receptors in complex neuronal models [26], [33], [37], [39], [105], [181], [186]. In addition, regenerative Ca²⁺ signaling in IP₃ pathway, a critical procedure for cerebellar LTD, can also be simulated with Markov chain [187]. However, to simplify computing, the presynaptic vesicle cycle and the neurotransmitter diffusions are often replaced with presumptive parameters [26], [39], [187], unless the presynaptic dynamics need to be explicitly modeled [101], [103], [105]. Moreover, Markov chains are also applied in modeling the ionic channels with multiple states such as K_{AHP} current in GoCs [30], [106] and Nav1.6, Kca1.1, 2.2 in PCs [131]. This enables a more comprehensive understanding of neuronal signaling and neuronal modeling.

VII. CEREBELLAR MODELING AND AI

AI and neuroscience have a long history of collaboration which has led to advancement in the field of AI visual processing [188], [189], motor control [190], behavior and its neural correlates [191], [192] and even the development of AI and brain theory [193]. Here we mainly focus on the reviewing cases of application of AI in cerebellar models.

A. CEREBELLAR MODEL FOR AI BASED APPLICATION

Because of the excellent control ability of cerebellum for motor behavior, a series of cerebellum-related controller were proposed based on cybernetics and algebraic methods [14], [194], [195], [196], [197], [198], [199], [200], [201]. However, in this review, we do not aim to review control theory based cerebellar model as it only adapts a similar structure

of the cerebellum while neglects the property of a biological neuron such as the neural plasticity thus lacks biological plausibility [202]. Due to that the cerebellum possess large numbers of tiny GrCs which resembles the neural scale of an ANN, it is rewarding to study the link of cerebellar neural network to an artificial one. Medini et al. proposed a spike encoding model inspired from the cerebellum GL which can be decoded by various classification algorithms [203]. The LTD at the PF-PC site together with large numbers of PF is easy to be evolve into an artificial one as it is an adjustable feedforward convergence from a large scale of neurons to a single one [204]. Additionally, a systems-level computational model of cerebro-cerebellar interactions was proposed where the biological circuits were mapped into deep learning model such as cerebral area simplified with long short-term memory recurrent neural network (LSTM) and cerebro-cerebellar interaction modeled with recurrent neural network (RNN) [205]. The most commonly used AI scenario for cerebellar models is the control of robotic arms as the model can overcome drawbacks of the nonlinear property of elastic joints and owns a predictive motor control ability confronting uncertain time delay [13], [40], [206], [207], [208], [209]. Specifically, the cerebellum cooperates with other brain regions like visual cortex and prefrontal cortex together to complete collision-free movement planning in which the visual information processing, movement coordination and decision making can be tackle smoothly [11]. Although such a model adopts a SNN, the training process uses supervised learning and reinforcement learning [210] for different modules, which is a combination of AI and brain-inspired structure. In addition, due to the cerebellum work as a liquid state machine, it works inherently as a sequential supervised learner and thus the cerebellar model can be used for limited static pattern recognition (Boolean function and MNIST digits recognition) and limited temporal pattern recognition [209], [211]. Compared with well-tuned ANNs, the cerebellar network did not outperform in terms of signal to noise ratio and accuracy [204], [209]. However, the advantage of biological cerebellar model lies in the good coordination capability in multi-joint robotic control. Furthermore, the structure of the cerebellar neural network is simple so that tuning of parameters becomes easy and can be adaptive to various tasks behaving a good learning ability for different tasks.

B. OPTIMIZE CEREBELLAR MODEL

Moreover, the application of AI techniques can aid in deepening our understanding of the cerebellum's structure and electrophysiology. Neuronal modeling involves various ionic channels that contribute to the final output of different compartments of a neuron. To match the firing pattern with electrophysiology recordings, maximum ionic conductance values for different channels must be adjusted. Optimization algorithms like genetic algorithm and particle swarm optimization algorithm, commonly employed in AI classification problems, can be utilized for neuronal parameter optimization

of neurons within the cerebellum [31], [212]. This provokes inquiry into whether an artificial model can substitute the neuronal one when modeling cerebellar motor learning. Furthermore, an ANN can be established by recorded data with transformation to analyze the correlation between neural electrophysiology and animal behavior. This method directly finds the relationship between corresponding neurons in a network structure without considering the dynamics of relay neurons between them [213]. In terms of neuronal connectivity, neuroimaging techniques like transmission electron microscopy (TEM) and serial-sectioning scanning electron microscopy (ssSEM) together with convolutional neural network (CNN) can benefit the structural cognition of cerebellar neurons [214], [215]. By simple modeling with recognized neuronal connectivity, researchers found that the redundant, non-random cerebellar connectivity motifs increase the signal to noise ratio at a negligible cost to the overall encoding capacity. The application of AI focuses on the neuronal structural recognition and such exploration for cerebellar connectivity [214], [215] can also benefit motor learning related modeling of the cerebellum in a network level simulation. In addition, the combination of AI modeling and neuroscience-inspired modeling is a new trend for the solution of complex dynamic problems [216]

VIII. REAL-TIME APPLICATIONS WITH CEREBELLAR MODEL

Due to the motor regulatory role of the cerebellum itself, the application of cerebellar models mainly emphasizes their real-time and adaptability and thus the accuracy of the cerebellar model is relatively low. Here, we mainly introduce the real-time applications of the cerebellar model from the perspectives of implementation, control theory with applications, and the potential applications for future work.

A. IMPLEMENTATION OF CEREBELLAR MODEL

In order to test how well the cerebellar model performs in real-time applications, researchers have been exploring different hardware implementations such as graphic process units (GPUs), very-large-scale-integration (VLSI), FPGAs, supercomputers, and event-driven lookup tables (EDLUTs). There are five main areas (Table 3) where the cerebellar model has been applied: humanoid robot simulation (red), obstacle avoidance or tracking cars (orange), robot arm control (cyan), network level simulations with large scale neurons (aquamarine), and cerebellar neuroprosthetic system development (no background color) [217], [218], [219], [220], [221], [222], [223], [224].

One thing that these models have in common is that they tend to use simplified neuronal models, except for the PC representation for humanoid eye movement [53], [56], [225]. To encode temporal information more effectively with GrCs for robot arm control, researchers have implemented the labeled-line model so that the time cost and accuracy of the GrCs can benefit each other [49], [206] and the

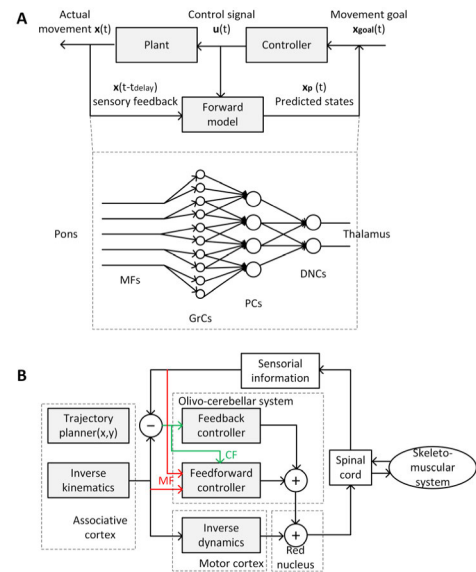


FIGURE 8. Cerebellar control in both theory and application. A, schematics of motor movement control and the cerebellar circuit [148]. B, schematics of cerebellar control in real-time application [49].

number of GrCs used depends on the degree of freedom of the robot [13], [40]. However, to test the performance of architecture design for a cerebellar network, neuronal models with more complex structures should be designed to ensure the flexibility and scalability of the platform [20], [34], [70], [226]. Additionally, the complexity of the cerebellar model used in a neuroprosthetic system depends on whether the research is focused on engineering or scientific issues [43], [44], [156].

B. FEEDFORWARD CONTROL AND FEEDBACK CONTROL FOR REAL-TIME APPLICATIONS

Previous studies believe the cerebellum functions as the loci of internal-forward-models [227], [228], [229], [230]. Neuroanatomically, the cerebellum receives input from the cerebral cortex and processes sensory feedback from peripheral systems [147]. This positioning allows the cerebellum, particularly the PC, to integrate motor commands from the motor cortex and sensory feedback from movement. The internal-forward-model for motor control within the cerebellum suggests that MF relays the delayed state and control signal, while the predicted state corresponds to the output of the dentate nucleus cells (错误!未找到引用源。A) [148]. However, the cerebellum is known to perform both feedforward and feedback control functions. Examples of cerebellar feedforward and feedback control include the VOR and OKR. Although both error signals in VOR and OKR afferent into PC through the dorsal cap, their sources are different.

Nevertheless, in real-time applications using cerebellar models, due to the lack of necessary neural modules, most works adopt cerebellar feedforward control. The control method depends on whether there is a comparison for the afferents at the input terminal of the cerebellar model.

For example, in torque control for a multi-joint robot, the afferents to the cerebellar model are both the desired trajectory and velocity of the joint, together with the current ones, whereas the control strategy transmitted to the IO of the cerebellar model is the difference between the desired (trajectory and velocity) and current one (Fig. 3) [13], [40], [49]. Due to the trial-and-error learning process for the feedforward control of the cerebellar model, a feedback controller can be added to stabilize the plant influenced by perturbations (Fig. 8B) [45], [49], [231]. Additionally, the cerebellar feedforward control strategy or feedback control strategy acts as a learning or refining process of the skeletal-muscular system. Therefore, a coarse inverse dynamic model derived from the motor cortex can be added to the control loop to increase convenience in dealing with changeable environmental features, as several different corrections can easily be accomplished by the adaptable forward controller (Fig. 8B). In contrast, switching or interpolating between different inverse models to deal with these changes would require a large amount of storage capacity [49], [232], [233], [234], [235], [236].

C. POTENTIAL APPLICATIONS FOR THE CEREBELLAR MODEL

The cerebellar model has been used in a wide range of real-time applications, particularly those that involve control systems and robotics. And thus, we suppose that the cerebellar model can be applied in the following aspects:

Autonomous vehicles: The cerebellar model can be used to develop control systems for autonomous vehicles that enable them to navigate through complex environments and avoid obstacles. As mentioned before, the cerebellar model-based obstacle avoidance car have been developed with camera. Likewise, the electric vehicle equipped with multi-camera or multi-radar can provide environmental information for the decision make of the cerebellar modeled control system.

Humanoid robot: in the present study, the cerebellar model can support the VOR based eye movement tracking and the perturbed reaching tasks [206]. And the multi-joint robotic arm controlled by the cerebellar model implies that the cerebellar model is able to provide control for synergistic motion which can be applied on humanoid robots [40]. Therefore, researchers can create more sophisticated robots that can perform complex movements and interact with humans more effectively.

Sports training: The cerebellum is heavily involved in motor learning and coordination, making it an ideal target for sports training. By developing cerebellar models that simulate specific sporting movements, coaches and athletes can use these models to improve their technique and performance. In addition, the sports training like hurdle refers to both rate coding and temporal coding which belong to different regions of the cerebellum [9]. Therefore, such a modeling will be challenging in that brain regional electrophysiology feature as well as the interaction between these regions should be considered.

IX. FUTURE WORK FOR CEREBELLAR MODELING

There are some new challenges that may be faced by cerebellar modeling which will be summarized here.

Modeling the cerebellum is a complex task due to the intricate cellular division and migration events that occur during its development. For instance, during postnatal development [237], [238], [239], [240], GrC progenitors undergo significant changes while located in the germinal external GL, which affect the 3D structure and electrophysiology of cerebellar neurons.

While both immature and mature neurons play critical roles in motor learning, their differences make modeling challenging. Currently, researchers have figured out the 3D ultrastructure of GrCs in the cerebellar cortex during early stages of postnatal development [214], and GrC migration model and PC growth model was proposed for the modeling of the cerebellum during early cerebellar development [241], but compartment modeling is still lacking. Additionally, there is a lack of electrophysiological modeling for cerebellar neuronal development at both the neuronal and network levels, which is essential for understanding the motor learning process [242].

Although a refined model for most types of neurons within the cerebellum, such as GrC, GoC, PC, SC, and IO, has been established, along with an understanding of the structure-function-dynamics of the cerebellar cortical microcircuit, there still exists a weak link between neuronal dynamics, network characteristics, and animal behavior. For example, rate-based modeling schemes for PRL of VOR emphasize the plastic changes of various synapses and the gain and phase changes of neurons for motor learning while neglecting neuronal electrophysiological properties [77]. In contrast, cerebellar modeling with accurate HH and Markovian models can accurately replicate neuronal electrophysiology, such as irregular firing of PCs induced by ablated GABA_A inhibition from molecular layer interneurons (MLIs), but it is challenging to balance such properties in network-level modeling for PRL of VOR [37], [171].

Furthermore, recent discoveries have raised significant issues that require more attention, such as MLIs suppressing CF-evoked dendritic Ca²⁺ spiking in PCs and graded climbing fiber Ca²⁺ signaling by MLIs expanding error coding in the cerebellum [243], synaptic AMPA receptor endocytosis in LTD of VOR motor learning [244], intrinsic excitability increases after dEBC [245], bidirectional plasticity of PCs in dEBC [82], intact VOR but impaired dEBC for the mice with PC-specific knockout of calcium-activated K⁺ channel SK2 [246], presynaptic NMDAR within GrC to cerebellar PC in motor learning [247]. These issues are concerned with subtle cellular machineries at both the neuronal and network levels, which require more realistic models [45]. All in all, the experimental progress is ahead of the computational model of the cerebellum [248].

With the development of realistic models for most cerebellar neurons and their successful application in various automation tasks such as SNN for multi-joint robotic

TABLE 3. Hardware implementation of cerebellar model with its applications.

Contributor	Platform, applications	Scale, Function, Neural model	Speed	Main contribution	Ref
Yamazaki and Igarashi	GPU, 1D robotic control	10 ⁶ , dEBC, CLIF	0.98s/1s	Real-time cerebellum can provide supervised learning towards engineering application	[42]
Luo et al	FPGA, simulation of passage-of-time	10 ⁶ , GL, CLIF	0.256s/1s	An efficient FPGA-based network on chip architecture was proposed for a large-scale cerebellar GL	[20]
Xu et al	FPGA, neuroprosthesis	10 ⁵ , dEBC, CLIF	64us/1s	An in-vivo experiment of dEBC was implemented so that rat cerebellum can be replaced by a silicon one	[19]
Yamazaki et al	PEZY-SC processors, model simulation	10 ⁹ , OKR, CLIF	1s/1s	The cerebellar network which contains more than 1 billion neurons can work in real time	[226]
Yamaura et al	K computer, model simulation	6.8*10 ¹⁰ , OKR, CLIF	425+s/1s	The cerebellar network can work with human-scale neurons	[34], [35]
Kuriyama et al	Scaffolding model simulation	96000, OKR, CLIF	375ms/1s	Scaffolding model was implemented with GPU so that the running time was accelerated 100 times	[70]
Bogdan et al	SpINNaker, scaffolding model	97000, CLIF	N.M.	Real-time execution of large-scale, bio-physically constrained cerebellum model run on SpINNaker	[217]
Yang et al	FPGA, neuromorphic model	3.5*10 ⁷ , dEBC and OKR, CLIF	~0.7s/1s	Mapping the cerebellar anatomical structure into the large-scale integrate and fire model	[218]
Verschure	IQR421, robot learning task	N.M.	N.M.	A real-time model of the cerebellar circuitry underlying dEBC with both simulation and robotic studies	[219]
Hofstötter	IQR421, robot learning task	500, dEBC, IF/rebound	N.M.	A computational model was proposed for cerebellar associative learning with both simulation and robotic studies	[56]
Hofstötter	VLSI, robot learning task	500, dEBC, IF/rebound	N.M.	An analog VLSI implementation of a cerebellar model of dEBC	[225]
Herreros et al	VLSI, neuroprosthesis	500, dEBC, IF/rebound	N.M.	A simple cerebellum model was interfaced with anesthetized rat to perform acquisition, retention, and extinction of the dEBC	[220]
Hogri et al	VLSI, neuroprosthesis	500, dEBC, IF/rebound	N.M.	A VLSI chip was designed to implement essential cerebellar synaptic plasticity rules and was interfaced with cerebellar input and output nuclei in real time	[43]
Kumar et al	FPGA, neuroprosthesis	DCN-deep brain stimulation (DBS)	N.M.	A real-time FPGA based closed-loop DBS targeting the DCN for cerebellar ataxia rescue	[224]
Carrillo et al	EDLUT, robot arm control	2000, dEBC, IF	N.M.	The cerebellar model in a robot control system can complete a target-reaching task	[221]
Casellato et al	C++ controller, robotic arm control	N.M., 8-like trajectory tracking Non-spiking model	N.M.	A feedforward block, a feedback controller and a cerebellum-like learning module have been integrated and tested with an anthropometric robotic arm	[222]
Garrido	C++ based Simulink S function, simulated robot arm control	N.M., dEBC, Non-spiking model, LLC for GL	N.M.	Multiple plasticity within the cerebellum contribute to gain control in robotic simulation	[48]
Luque et al	N.M., simulated light-weight robot	N.M., dEBC, Non-spiking model, LLC for GL	N.M.	IO-DCN plasticity accelerates convergence of learning	[49]
Casellato et al	EDLUT, robot arm control	1580, dEBC and VOR, spiking model	N.M.	A spiking neural network can reproduce dEBC and VOR with a robotic system	[206]
Casellato et al	C++ controller, robot arm control	2000, dEBC and VOR, Non-spiking model, LLC for GL	N.M.	The cerebellar controller can reproduce human-like behavior in real-robot sensorimotor task	[41]
Abadía, et al	EDLUT, robot arm control	61440, dEBC, IF	N.M.	A novel biological approach for the compliant control of a robotic arm in real time	[40]
Abadía, et al	CPU and GPU, robot arm control	61440, dEBC, IF	N.M.	They propose a cerebellar-like spiking neural network controller which is adaptive, compliant, and robust to variable sensorimotor delays	[13]
Naveros et al	EDLUT, humanoid eye movements	2700, VOR, PC, HH model; GrC, state generator; others, LIF	<85ms	A real-time SNN dominates the VOR adaptation of the humanoid eye movements mimicking a human being	[53]
Kalidindi et al	N.M. saccade adaptation	300, saccade, leaky-integrator units for rate-based model	100 Hz	The saccade can be implemented with cerebellar model which learns to compensate for the missing sensory feedback, while also maintaining the movement optimality	[223]
Torti et al	GPU, PC model with complex morphology	1-10980, PC, compartment model	107.73s/1s	They designed a complex PC model considering morphological detail with different ionic channels	[50]
McKinstry	Segway robotic, Traverse S shape courses	27688, similar to dEBC, rate-based scheme	40ms/cycle	The reflex control of cerebellum can be replaced by the predictive control	[208]

control [13], [40], [49], [53], [206], it is now possible to create a hardware-in-the-loop system that can test ion channel influence or cellular/synaptic mechanisms related to cerebellar behaviors. Using consistent neural spike decoding methods, we can simulate a series of drug tests on cerebellar function with this system. For instance, Yamazaki and Tanaka have simulated dEBC by ablating NMDAR within GrCs and GoCs to mimic receptor blockade influence [46]. With a refined model, we can intuitively observe the impact of NMDARs within the cerebellum in real-time using such a robotic system. When it comes to recording neural activity, there are two main methods: invasive and non-invasive.

Non-invasive methods like EEG and fMRI are used for complex tasks in which different regions of the brain are activated together. To analyze these signals, researchers commonly use functional and structural brain network connectivity methods. Researchers have also found that non-invasive electrodes placed on the scalp of the inferior parietal lobule (which includes CP1) can improve auditory-verbal working memory in aging individuals [165], [249]. These macro-level analyses can also be extended to the cerebellum using fMRI/MRI data [250]. It is important to understand how micro-level neuronal computation within a local brain region contributes to macro-level brain activity. A prime

way to explore this relationship is to model with shared data between these two levels. Recently, transcranial direct current stimulation (tDCS) under MRI-based segmentation are imposed on human cerebellar neurons throughout the region and then the resulted parameters like extracellular potential can be applied on 3D multicompartiment cerebellar model with quantitative analysis [250]. Such a combined methodology protrudes the important of 3D model in real applications and such a modeling can deepen our understanding of mechanisms of the tDCS for neuromodulation therapy in clinical applications [251], [252]. Furthermore, understanding the relationship between micro-level neuronal computation and macro-level brain activity could lead to more dynamic brain simulations, which would help us better understand the workings of the brain and the pathogenesis of neurological diseases.

Here we give some suggestions to different groups. Firstly, for the neuroscientists who have been engaging in computational neuroscience, as more and more subtle regulatory mechanisms are being discovered [253], [254], computational models need to be enriched to become useful tools for predicting phenomena that cannot be observed experimentally. Additionally, simplified aspects in previous simulations should be re-evaluated, as some seemingly reasonable practices have been shown to be poorly considered. For example, in cerebellar modeling for motor learning, the CF inputs to PCs are often modeled as binary (0 or 1) upon IO firing. The mechanism involved is complex, and whether CF can serve as the sole instructive signal for all motor learning processes has not yet been determined [254], [255], [256]. Secondly, for robotic engineers, cerebellar modeling can be applied to robots with complex or non-rigid structures. Cerebellar control excels in flexibility rather than precision. Neuroprosthetics using cerebellar modeling and control are particularly worth studying. Additionally, humanoid robots may benefit from cerebellar control, as this could enhance emotional acceptance. Thirdly, for theoreticians, cerebellar modeling may be combined with deep learning theory, especially with large models. Similar to the large models used in deep learning, the cerebellum contains an extremely large number of neurons, with each neuron considered a dimension. However, it is still unknown how the cerebellum utilizes numerous neurons for fine regulation. For instance, a person can write beautifully with a pencil, and after some practice, can also write beautifully with a pen. Except for the PF-PC regulation, how this adaptation occurs for numerous GrCs, and whether there is a paradigm for neuronal coordination within the cerebellum, requires theoretical validation.

X. CONCLUSION

In this study, we have focused on reviewing literature related to cerebellar modeling. Our review covers a range of topics including animal models, neuron types, network structures for modeling, neuronal modeling, and the application of cerebellar modeling in AI and real-time settings. Over the

past 40 years, there has been extensive development in cerebellar cortex theory, leading to more complex mechanisms being explored and an increased focus on practical applications. The emergence of AI has further propelled the exploration of refined network structures and electrophysiology characteristics in cerebellar modeling. This progress holds significant promise for various areas such as cerebellar-related neurological disorders, precision robotic arm control, and computational processes involved in drug metabolism within the cerebellum. Our research aims to promote the development of cerebellar modeling by summarizing the current state of research and identifying key areas for future investigation.

ACKNOWLEDGMENT

(Shaojia Huang and Tao Xu contributed equally to this work.)

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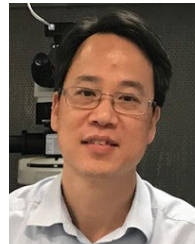


functions and the emergence of emotions-related behaviors that could be impaired in different brain disorders including neurodegenerative diseases. To meet these challenges, a multi-disciplinary approach employing different neuroscience research tools like molecular biology, virus-based circuit mapping, opto/chemo-genetics, in vivo/in vitro electrophysiological recording, brain imaging and novel behavioral paradigms is adopted.

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