

# The Cerebellum as a Predictor: Recent Insights Into Cognitive Control and Extension of Kalman Filter Theory to Cognition

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Traditionally viewed as a motor control center, the cerebellum is increasingly recognized as a crucial component of a neural network that enables adaptive behavior across various domains, including cognition, affect, emotion, and social interactions. Recent clinical studies have linked cerebellar dysfunction to impairments in mentalizing and narrative coherence in autism spectrum disorder (ASD). Given that narratives involve the temporal sequencing of causally related events and actions, these findings imply the potential role of the cerebellum in predictive sequence. The aim of this review is to dissect the neural circuitry and computational mechanisms underlying cerebellar predictive cognitive control. We propose that the Kalman filter model, which has been applied successfully to the motor cerebrocerebellum, can be extended to the non-motor (cognitive/affective/social) regions. In sharp contrast, the cerebral cortex employs a recurrent network architecture, as evidenced by intracortical connections, which underlies hierarchical processing in areas such as the visual and motor cortices. Surprisingly, the computational principles of the cerebrocerebellar loop have received relatively little attention in computational and theoretical neuroscience. We stress the need for a comprehensive theory on cerebrocerebellar connectivity that integrates the distinct neural mechanisms of the cerebrum and cerebellum, to help understand the role of this network in cognitive, affective, and social functions. Our theory provides a theoretical framework that explains how the cerebellum deals with motor and non-motor operations. The Kalman filter theory fits with two major requirements: sequencing and predictions. We propose a core operational mechanism for motor, cognitive, affective and social operations handled by the cerebellar circuitry.

**Keywords:** cerebellum; forward model; Kalman filter; motor control; higher brain functions; cognition; affection

## Introduction

The neural circuitry of the cerebellum is strikingly uniform. Theories on cerebellar function and signal processing have to explain how the cerebellar microcircuitry implements neural information processing and how the cerebellar connectivity achieves various operations. We reported previously that a variety of divergent cerebellar motor abnormalities, such as dysmetria, adiadochokinesis, and intention tremor, can be comprehensively explained through a unified framework of disturbance in the predictive function of the internal model inherent in the cerebellum [1]. On the other hand, the presence of reciprocal and parallel circuits between the cerebellum and the cerebral cortex, in addition to the clinical observations, strongly suggests a relationship between the cerebellum and cognitive functions [2]. Schmahmann and colleagues [3] described the association of various cognitive abnormalities with cerebellar disorders, collectively called cerebellar cognitive affective

syndrome/Schmahmann syndrome. The uniform neural circuit structure of the cerebellum suggests that abnormalities in both the motor and cognitive areas develop based on the same principles (e.g., Schmahmann's dysmetria of thought and emotion) [4]. This paper provides clinical, neurophysiological, and computational evidence that abnormalities in predictive control based on the cerebellar internal model can explain cerebellar cognitive symptoms. At the same time, we highlight the issues that need to be addressed in the predictive computational theory of cognitive function. We emphasize the importance of the Kalman filter as a common and genuine computational function of the cerebellar circuitry.

## Conceptual Frameworks Derived From Clinical Studies

This section reviews recent clinical studies on the role of the cerebellum in predictive cognitive control. We per-

formed a PubMed search using the keywords/terms “cognition” AND “cerebellum” AND “prediction” AND “2021–2024”. We checked the abstracts of the thirty-six identified articles and selected three relevant articles from these [5–7]. From the literature, we selected articles that focused on diseases associated with cognitive impairment or discussed the pathophysiology of these diseases.

Since the seminal Schmahmann’s studies, numerous meta-analyses have consistently highlighted the significant roles of the cerebellum in perception, language, emotion, social cognition, and higher cognitive functions [5–7]. In particular, studies that discussed the cognitive/affective contributions of the cerebellum have concluded that patients with cerebellar disorders exhibit deficits in executive functions, linguistic operations, spatial cognition and affect control, all being considered as clinical manifestations of dysmetria of thought [5–7]. Notably, strong associations have been established between the cerebellum and autism spectrum disorder (ASD), particularly with regard to social behaviors. Furthermore, neuromodulatory interventions in ASD mouse models have shown promising results in alleviation of social symptoms [5–7]. However, there is still no comprehensive mechanistic framework that can fully integrate these findings, despite the similar architecture of the cerebellar microcircuits in all cerebellar lobules and the closed loops between the cerebellum and cerebral cortex. The current literature search underscores the pathophysiological mechanisms underpinning the core symptoms associated with ASD. Likewise, the notions of adaptive expectation and external feedback have subserved to elucidate the pathophysiology of ASD. Specifically, a deficit in sequential prediction now appears in the mechanistic framework for the underlying physiological processes.

#### *Deficits in Mentalizing and Narrative Coherence in Autism*

Bylemans *et al.* [5] studied autistic adults and stressed the behavioral relationship between difficulties in mentalizing (understanding others’ mental states) and narrative coherence (structural storytelling) [5]. The authors argued that impairments in mentalizing and narrative coherence could explain the link between ASD symptoms and cerebellar disorders for the following reasons:

(1) Based on resting-state parcellation, there exists a bidirectional closed-loop between the default mode network (a network of cerebral areas activated when no specific cognitive tasks are being executed) [8,9] and the posterior cerebellar Crus I and II [10]. The cerebral mentalizing area constitutes a large part of the default network [11,12].

(2) Functional connectivity between the cerebral default mode/mentalizing area and the cerebellar Crus area is altered in autism [13–15].

(3) Based on task-based parcellation, there exists an overlap between the narrative function area and the default mode/mentalizing area in the posterior Crus [16].

At the same time, the authors noted that narratives present a temporal sequence of causally related events and actions by the self and others [5]. It has been pointed out that autistic individuals often do not present their stories in a logical order [17], do not process story onsets at the beginning of a narrative sequence, and do not use prior contextual information to form a sequentially coherent narrative [18].

#### *Impairments in Adaptive Prediction*

Frosch *et al.* [7] argued that impairment in cerebellar adaptive prediction is a key clinical feature of ASD, representing the process of creating expectations or predictions in advance in order to adapt quickly to changing stimuli or situations [7]. Adaptive prediction involves using experience to (1) infer intentions from the actions of others, (2) predict what others might say, and (3) infer the mental states of others, allowing us to quickly modify and adapt our own behavior to match the intentions of those around us [19]. Needless to say, autistic individuals have difficulties in adapting their past experiences to the social environment.

Language understanding is fundamentally predictive, meaning that we can understand a context based on previously acquired linguistic knowledge and context, even when the linguistic input is noisy and ambiguous [7]. An imaging study has shown increased activation of Crus I and II during a semantic prediction [20]. Accumulating evidence suggests the presence of impaired adaptive prediction in autistic individuals. When children with autism read ambiguous words (such as “read”) aloud, they cannot adapt their pronunciation to changes in the surrounding words [21].

Frosch *et al.* [7] also emphasized that motor control involves the ability of the cerebellar internal model to adapt to new environments by matching the efferent copy of the movement with the predicted sensory feedback. They proposed that such adaptation is the essence of predictive control of cognition [7].

#### *Impairments in External Feedback*

Berlijn *et al.* [6] conducted a systematic review to delineate the localization of the external feedback in the cerebellum that is used by the internal model [6]. The authors reviewed two neuroimaging studies. In the first, Balsters and Ramnani (2011) [22] showed that “high learning cues”, in which feedback information reflects the outcome of the current trial, significantly increased neural activity in Crus I compared to “low learning cues”, where feedback information did not reflect the outcome of the current trial. In their second reviewed study, Balsters *et al.* [23] showed increased activation of Crus I and II during higher-order rule learning but not during behavioral features [23]. Based on the results of these two studies, Berlijn *et al.* [6] suggested that the posterolateral region of the cerebellum plays a crucial role in monitoring performance, particularly in predicting or receiving external feedback in non-motor learning [6].

## Impairment in Prediction of Sequencing

The concept of “sequencing prediction” is essential in explaining cerebellar cognitive functions using forward models [5]. This concept stems from a theory by Leggio & Molinari [24] and Molinari & Masciullo [25]. They proposed that the cerebral cortex sends, via a closed loop, an efferent copy of cognitive processes to the cerebellum, which, in turn, identifies the temporal sequence of these events and encodes them in the internal model. Thus, the cerebellum compares any novel inputs from the cerebral cortex with the behavioral and sensory consequences. When discrepancies are detected, the cerebellum automatically fine-tunes the cerebral cortex.

Consistent with this theory, van Overwalle *et al.* [26] recorded higher neural activity in Crus I and II during sequential conditions, which was more pronounced during social sequences than non-social sequences. The same group hypothesized that the posterior cerebellum is responsible for learning, automating, and predictively regulating social action sequences and that damage to the postero-cerebellum results in loss of plasticity and flexibility in learning appropriate social behaviors in a given social context [27].

## Morphologic and Physiologic Basis for Cerebellar Prediction

### *An Enigmatic Corticonuclear Microcomplex in the Cerebrocerebellum Is the Hallmark of the Kalman Filter Model*

The Kalman filter is an optimal estimation method that integrates the prediction from a dynamical model and the observation from sensors [28]. The optimal estimate of the state balances the prediction and the observation in a Bayes optimal manner; when the observation is unreliable with a large variance, the Kalman filter emphasizes the prediction and suppresses the observation, or vice versa. The Kalman filter was applied originally to engineering problems such as the Apollo project and only recently to neuroscientific problems. The brain needs to compute an optimal estimate of the body at every moment for motor control, so it is natural that evolution has acquired the mechanism of the Kalman filtering in the cerebellum. One behavioral experiment demonstrated that the Kalman filter model reproduced the pattern of variance propagation in arm movements [29]. Although the Kalman filter model explains human psychological experiments, its anatomic and physiologic mechanisms have not yet been elucidated.

In our previous studies [30–32], we provided neural evidence that the cerebrocerebellum can predict future cortical activities from present cerebellar inputs (i.e., mossy fiber (MF) activities), the hallmark of a forward model. A forward model predicts the future state due to motor command. The forward model requires two distinct inputs to predict a future state: an efference copy from the controller and a sensory feedback signal from the periphery (Fig. 1A,

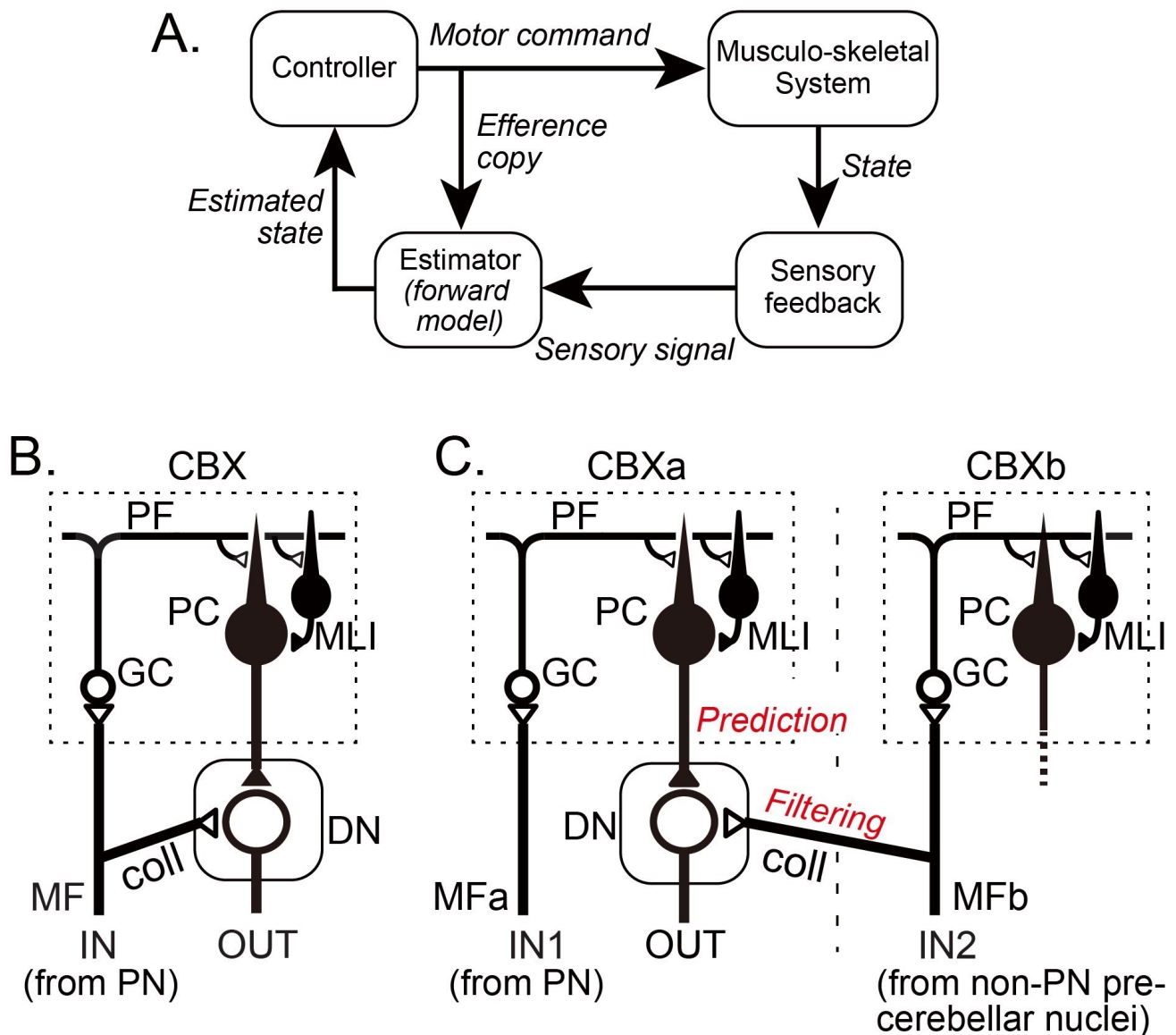
Ref. [31]). However, the importance of the dual inputs for prediction was not fully recognized among cerebellar researchers until recently. For instance, Fig. 1B depicts a typical corticonuclear microcomplex described in many textbooks. This diagram illustrates that a single mossy fiber (MF) projects to the cerebellar cortex (CBX) and dentate nucleus (DN) with collaterals, implying that the Purkinje cell (PC) and DN cell (DNC) receive a common input. The common input to the prediction step in CBX and the filtering step in DN (Fig. 1B) is inconsistent for the cerebellum to function as a forward model. Nevertheless, the cerebellum has long been the popular locus of a forward model.

Two enigmatic neuroanatomical reports about MF collaterals to DN initially received little attention but these two neural structures were later considered to be critical components of the forward model. First, Wu *et al.* (1999) [33] demonstrated that MFs from the lateral reticular nucleus (LRN), which conveys somatosensory inputs from the spinal cord, project to the vermis and the intermediate zone with an abundant collateral projection to DN and other cerebellar nuclei [33]. Second, Na *et al.* (2019) [34] demonstrated that a single MF from the pontine nucleus (PN) projects to the hemispheric part of the CBX without collaterals to DNC [34]. We consider the two findings to be complementary and provide morphologic support for the cerebellar forward model (Fig. 1C) [30,32]. In this diagram, the primary input (IN1, MFa) conveys an efference copy from the motor cortex and contributes to the prediction step in the CBXa. The secondary input to DN (IN2, MFb) conveys a sensory feedback signal and contributes to the filtering step in DN on its way to a distinct CBXb. Namely, MFa and MFb have different projection areas in CBX. It is also important to note that the two MF inputs exhibit a causal relationship. Each motor command brings a sensory consequence.

We tested this seemingly enigmatic cortico-nuclear microcomplex by analyzing the activities of these neuronal elements recorded in behaving monkeys [30,31]. We identified two distinct populations of MF activities in the cerebrocerebellum, which were compatible with the cerebellar forward model hypothesis (Fig. 1C) [30]. Activities of one MF population contributed to the PC activities in the prediction step. In contrast, activities of the other MF population contributed to the DNC activities in the filtering step [30]. The linear equations derived from the cerebellar neuron activities resembled those of a predictor known as the Kalman filter, composed of prediction and filtering steps [30].

### *Extending the Cerebellar Kalman Filter Model to the Non-Motor Cerebrocerebellum*

Prediction is not a monopoly of motor control. In fact, prediction is essential for cognitive/affective functions. For instance, when an individual plays soccer, successful passing depends on accurate prediction of the movements of both the teammates and opponents, in addition to



**Fig. 1. The forward model and its implementation to the cerebrocerebellum.** (A) Schema of closed-loop optimization. The Estimator (forward model) needs an Efference copy of concurrent Motor command and delayed Sensory feedback data (Sensory signal) to compensate for the sensory delay. It is important to note that the Estimator and the Controller form a loop. Thus, they can continue to generate time-varying motor commands even when sensory feedback becomes unavailable or unreliable. (B,C) Two types of cortico-nuclear organization. (B) The textbook scheme of cortico-nuclear organization is incompatible with the forward model in (A). In this scheme, the same mossy fibers (MF) project to the cerebellar cortex (CBX) and the dentate nucleus (DN) with collaterals (coll). (C) The cortico-nuclear organization compatible with the forward model in (A). In this scheme, MFs (MFa) from pontine nuclei (PN) project to the cerebro-cerebellum (CBXa) without collaterals to DN, whereas other MFs (MFb) project to DN with collaterals. Note that MFa and MFb have distinct projection areas in CBX. (C) is also consistent with the latest neuroanatomical data for the cerebrocerebellum. CBX, cerebellar cortex; coll, collateral; DN, dentate nucleus; GC, granule cell; IN, input; MLI, molecular layer interneuron; MF, mossy fiber; PC, Purkinje cell; PF, parallel fiber; PN, pontine nuclei. Modified from Tanaka H, Ishikawa T, Lee J, Kakei S. (2020) [31] under CC-BY license.

the player's own motion. Note that multiple forward models work in parallel in the player's brain. A critical ques-

tion arises: whether the Kalman filter model for the motor cerebrocerebellum can be extended to the non-motor (cog-

nitive/affective) parts. The vital key is the identification of the Kalman filter-specific corticonuclear microcomplex (Fig. 1C). There are two neuroanatomical criteria: (1) outputs from the non-motor cortical areas are relayed by MFs (MFa) originating from PN and terminate in the non-motor CBX (MFa in Fig. 1C), (2) MFs from non-PN precerebellar nuclei send collaterals to DN on their way to the outside of the non-motor CBX (MFb in Fig. 1C) [35]. First, most non-motor cortical areas send outputs to the non-motor cerebrocerebellum via the PN, including the prefrontal cortex [36], the parietal association cortex [37], the superior temporal cortex [38], the occipitotemporal cortex, and the parahippocampal cortex [39]. Second, there are at least two sources of MF collateral inputs to DN in the reticular formation: the nucleus reticularis tegmenti pontis (NRTP) [40] and the LRN [33]. The NRTP receives extensive inputs from the sensorimotor, prefrontal, and parietal association cortices [41]. The LRN receives primary inputs from the spinal cord [42] and additional inputs from the sensorimotor cortex and the red nucleus [43,44]. Therefore, it is highly likely that the non-motor cerebrocerebellum also satisfies the criteria of the Kalman filter model [35] (Fig. 2, Ref. [35,45–49]). In addition, the cerebellar circuitry is also connected to basal nuclei via disynaptic loops [45] (Fig. 2, Basal nuclei). Although the Basal loop may not satisfy the second criterion (i.e., filtering step), the first criterion is sufficient for the cerebrocerebellum to function as a predictor, even if its prediction without a filtering step (i.e., the second criterion) may be suboptimal for a faster event. In other words, the lack of filtering may not be critical for predicting slower events related to reward expectation, affection, or social interactions. Overall, unraveling the cerebellar circuitry's elemental computational principle will also clarify the respective roles of the major subcortical networks involved in motor, cognitive, affective, and social functions subserving human behavior. It should be noted that the Kalman filter theory may fit with the universal cerebellar transform (UCT) suggested by Schmahmann (2023) [50], in which the cerebellum handles both motor and non-motor operations similarly.

Is there neurophysiologic support for the adoption of the Kalman filter model in cognitive/affective functions? Recent studies [51–53] have suggested the contribution of the cerebellum in predicting periodic events, although their experiments were not designed to identify the Kalman filter model.

Extension of the Kalman filter model to the cognitive/affective functions may introduce a new viewpoint in evaluating cognitive prediction functions: filtering. We expect to apply this viewpoint to improve batteries for evaluating cognitive deficits in patients with cerebellar disorders or other cognitive disorders. It should also be noted that the output from the Kalman filter is helpful for the controller (Fig. 1A) only when there is some experience with current conditions. On the other hand, it is not helpful when there

is no knowledge or past experience with them. Moreover, the prediction may be misleading or useless if the cerebellar prediction mechanism is biased from “normal” or out of order.

## Computational Principle of the Cerebro-Cerebellar Circuit

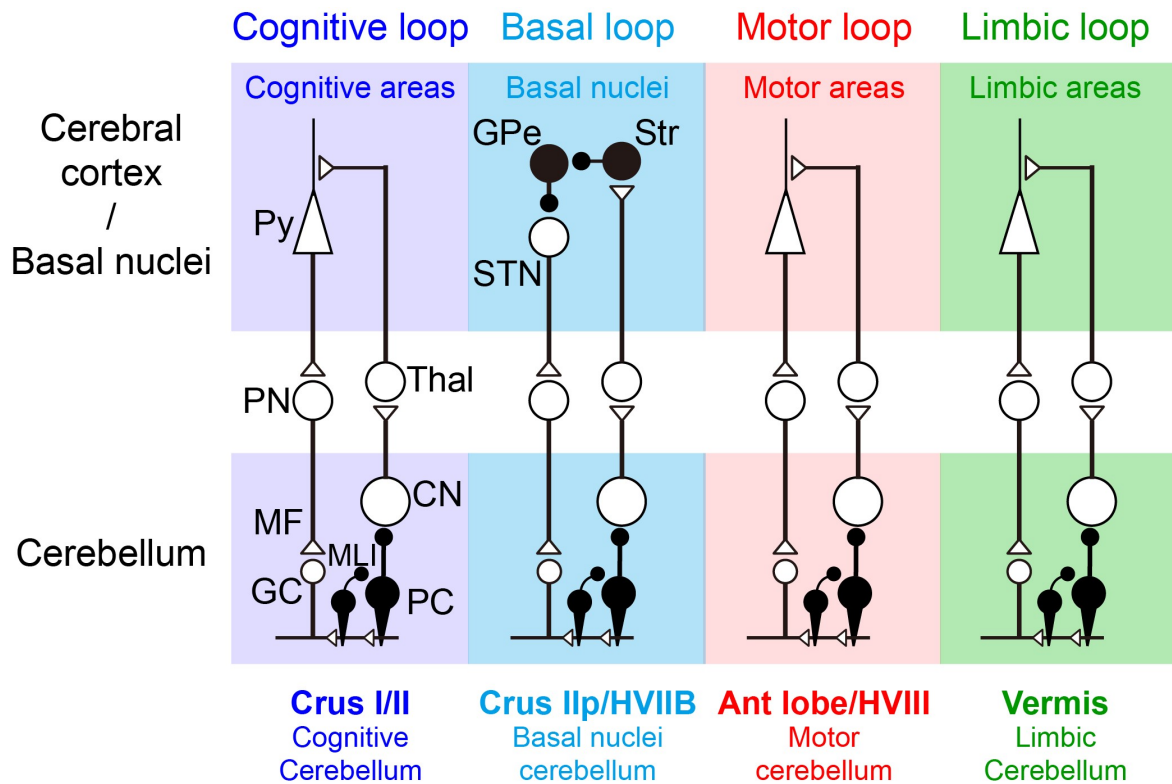
### *Neural Network Models of the Cerebral Cortex and the Cerebellum*

Traditionally, the cerebral cortex and the cerebellum have been modeled independently. Neural network modeling of brain functions dates to the seminal work of Marr (1969) [54] and Albus (1971) [55] on CBX and of Zipser and Andersen (1988) [56] on the posterior parietal cortex. For CBX, Marr and Albus postulated that the Purkinje cells operate as a perceptron, a single-layer neural network with adaptive weights. Each Purkinje cell receives two synaptic projections: parallel fibers from granule cells and a climbing fiber from the inferior olive. This anatomical structure inspired a Purkinje cell to adjust the synaptic weights of parallel fibers according to the supervised signal from the climbing fiber. The key prediction of the model was that the parallel-fiber-Purkinje-cell synapses adapt to the supervised signal from the climbing fiber. For the posterior parietal cortex, Zipser and Andersen [56] formulated a coordinate-transformation problem as a multilayer perceptron and demonstrated the gain-field responses in units in the hidden layer, the properties of Area 7a neurons reported previously.

The recent resurgence of interest in neural networks in the field of artificial intelligence since the 2010s rekindled neural network modeling of the cerebral cortex and the cerebellum [57]. The two main architectures of neural networks are feedforward neural networks (FNNs) and recurrent neural networks (RNNs). The anatomical structure of CBX allows a feedforward network modeling from mossy fibers to Purkinje cells. Various cerebellar models have been described that explain temporal processing [58], motor learning [59], and internal models of social interactions [60]. In comparison, the intracortical connections in the cerebral cortex favor a recurrent network modeling within the cortical layers. These models explain hierarchical visual processing in the visual cortex [61], motor control in the motor cortex [62], and cognitive processing in the frontal and association cortices [63]. Whereas these neural network models have successfully explained various neurophysiological and behavioral results, no computational framework exists for the cerebro-cerebellar loop. Surprisingly, the computational principle of the cerebrocerebellar loop has attracted little attention in computational and theoretical neuroscience.

### *Functional Role of the Cerebro-Cerebellar Loop*

The cerebro-cerebellar loop is a neuroanatomical structure through which specific areas of the cerebral cortex



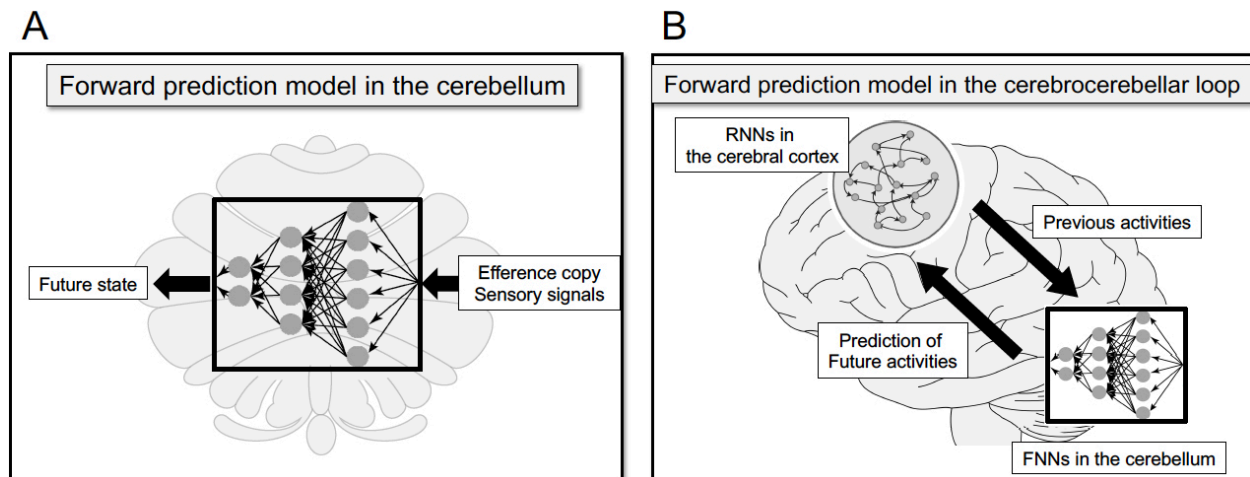
**Fig. 2. The parallel organization of the cerebro-cerebellar and the basal nuclei-cerebellar loops.** The cerebellum contains functionally distinct loops between the cerebral cortex and the basal nuclei. The Cognitive loop connects cognitive areas and Crus I/II. The Motor loop connects motor areas and the anterior lobe/the hemispheric part of lobule VIII. The Limbic loop connects limbic areas and the vermis. The Basal loop connects the basal nuclei and Crus IIp/the hemispheric part of lobule VIIIB. These loops overlap significantly in the CBX due to the divergent projection of single MFs and PFs, as discussed in [46]. In each loop, MF input facilitates PCs di-synaptically through the granule cells (GCs), while the same MF suppresses PCs tri-synaptically through GCs and MLI. It is critical to note that suppression precedes and dominates the facilitation, as demonstrated in behaving monkeys [47]. The complex spike induces long term depression (LTD) of the facilitation and long term potentiation (LTP) of the suppression [48], enabling a wide range of adaptive changes for the cerebellar neuron circuitry. This figure was prepared partly based on [35,45,49]. Ant lobe, anterior lobe; CN, cerebellar nuclei; GPe, Globus pallidus external segment; PN/P, pontine nuclei cells; PyV, layer V pyramidal cells; STN, subthalamic nucleus; Str, striatum; Thal/T, thalamus. We used Adobe Illustrator 2023 to prepare Fig. 2.

connect reciprocally to the cerebrocerebellum. Anatomical findings suggest that the cerebro-cerebellar loop has an essential functional role and has endured through evolution; the volume of the cerebellum and the cerebral cortex are proportional to each other in various mammalian species, the projection from the cerebral cortex to the cerebellum is approximately 500 times of that from the cerebellum to the cerebral cortex [64]. Neuroimaging findings of humans and animals suggest that a newly learned skill in the cerebral cortex transfers to the cerebellum as the learned skill consolidates [65,66]. From a neural network perspective, an FNN is functionally simple and easily trained but cannot handle complex temporal sequences; an FNN functions as pattern recognition of static features. On the other hand, an RNN can model temporal sequences, but it is not easy to train. Also, an RNN is prone to noisy perturbations [67]; the activity at a one-time step influences the activity at the next step, so the network might suffer a slight deviation over

time and fail to complete its computation. Here, we pose a problem: why has the brain acquired the FNNs in the cerebellum and the RNNs in the cerebral cortex, and what is the computational principle that governs the cerebro-cerebellar loop?

#### *Predictive Corrections of the Cerebral Cortex*

We postulate that in the cerebro-cerebellar loop, the cerebral cortex learns complex and time-varying task sequences and that the cerebellum predicts and corrects the activity of the cerebral cortex for reliable performance of a task. The RNNs in the cerebral cortex are powerful enough to represent temporal sequences such as language sentences and muscle activations but are slow in learning and prone to noisy perturbations. The internal model hypothesis posits that the cerebellum predicts future consequences of motor control, cognitive processing, and social interactions



**Fig. 3. Internal forward model prediction in the cerebellum.** (A) The cerebellum predicts future states of movements in motor control, possible outcomes in cognitive processing, and other minds in social interactions. (B) The cerebellum predicts the future activities of the cerebral cortex, enabling robust and flexible computation in the cerebrocerebellar loop. FNNs, feedforward neural networks; RNNs, recurrent neural networks. This figure was prepared with Microsoft PowerPoint Ver. 16.93.

(Fig. 3A). We propose that the cerebellum copies the cortical dynamics and predicts future cerebral cortex activity (Fig. 3B). In this framework, the cerebellum is an internal model of the cerebral cortex. By projecting the cerebellar prediction of the cortical activity, the cerebral cortex reliably stabilizes its activity. Our proposal extends our previous findings: (1) the predictive control is selectively impaired in patients with cerebellar disorders [68], and (2) the cerebellar output (the dentate-nucleus activity) at a one-time point is predictive of the cerebellar input (the mossy-fiber activity) at a future time point [30]. The internal-model mechanism in the cerebellum subserves initially motor control and motor learning and subsequently cognitive processing, such as language processing. Our proposal asserts that the cerebellum has evolved as a general state predictor for body states, language sequences, and cortical activities. Our tentative numerical simulations confirm that an RNN can generate temporal sequences reliably under noisy perturbations with the help of cerebellar corrections (not included). The brain can learn complex tasks and then perform the task reliably by integrating the learning computation of cortical RNNs and the predictive computation of the cerebellar FNNs.

### *Continual Learning and Cerebellar Reserve in the Cerebellum*

Finally, we speculate on the neurophysiological mechanism of cerebellar learning and cerebellar reserve (the ability of the cerebellum to recover from damage) [69]. Humans do not forget how to play the piano after their first training session and how to play the violin after a second training session. On the other hand, artificial neural networks could suffer catastrophic forgetfulness, in which subsequent learning of a new task requires wiping out the

memory of previously acquired tasks [70]. It is thus surprising that the cerebellum has continuing and unbounded abilities to develop new skills in a lifetime. Our proposed neurophysiological mechanism is the silent synapses in the parallel-fiber-Purkinje-cell projections [71]. A single Purkinje cell receives 100,000 synaptic inputs from granule cells through parallel fibers, but about 50% of these synapses are idle. Therefore, the silent synapses maintain the room for forthcoming learning of a new task or recovering skills after damage. We conclude that the cerebellum is a continuous learner of the inner workings of the cerebral cortex, enabling learning, relearning, and recovering from multiple complex skills.

### Conclusion

Based on anatomical and physiological evidence, we propose that the Kalman filter model for the feedforward network of the motor cerebrocerebellum can be extended to the cognitive and affective parts. In contrast, the intracortical connections of the cerebral cortex are characterized by recurrent networks. The distinct neural architectures of the cerebellum and the cerebral cortex raise a fundamental question: “What is the elemental computational principle governing the cerebro-cerebellar loop?” Furthermore, the cerebellum also forms a loop circuitry with the basal nuclei. Therefore, unraveling the computational principle of the cerebrocerebellar loop will also characterize the functional roles of the basal nuclei in various functional domains subserving human behavior.

We propose that the Kalman filter model fits well with the universal cerebellar transform (UCT) and further provides testable predictions at the level of the corticonuclear micro-complexes.

## Availability of Data and Materials

Not applicable.

## Author Contributions

Concept and preparation: SK, HT, HM, and MM. Draft: all authors. All authors contributed significantly to editorial changes of important content. All authors read and approved the final manuscript. All authors have participated sufficiently in the work and agreed to be accountable for all aspects of the work.

## Ethics Approval and Consent to Participate

Not applicable.

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## Conflict of Interest

The authors declare no conflict of interest. Mario Manto is serving as one of the Editorial Board members of this journal. We declare that Mario Manto had no involvement in the review of this article and has no access to information regarding its review.

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