



# Underlying interactive neural mechanism of motor learning governed by the cerebellum, the basal ganglia, and motor/sensory cortex: a review from theoretical perspective

Armin Hakkak Moghadam Torbati<sup>1</sup> · Shahab Jami<sup>2</sup> · Hamidreza Kobravi<sup>3</sup> · Narges Davoudi<sup>4</sup> · Mohammad Amin Gholibeigi<sup>3</sup> · Asal Ashkzari<sup>3</sup>

Received: 18 December 2023 / Accepted: 7 March 2024 / Published online: 5 April 2024  
© The Author(s), under exclusive licence to Springer Nature Switzerland AG 2024, corrected publication 2024

## Abstract

The pursuit of effective motion rehabilitation devices has been a prominent focus of research in recent decades. However, the efficacy of such devices relies heavily on their ability to induce motor learning. Thus, understanding the neuroscientific principles underlying motor learning is crucial. This paper highlights a significant number of studies investigating the roles of various brain regions such as the basal ganglia, cerebellum, and motor cortex in motor learning, either individually or in interactive processes. However, due to the theoretical nature of many proposed ideas, definitive conclusions about acceptable brain interactive mechanisms facilitating motor learning are challenging. Addressing the lack of a comprehensive review paper to scrutinize and compare these hypotheses, identify weaknesses, and offer new directions for researchers, this study provides a theoretical perspective review. Excluding works solely focused on neurophysiological connections or computational models, it categorizes selected papers into topics related to the contributions of basal ganglia, cerebellum, motor/sensory cortex, and super-learning mechanisms in motor learning. The analysis suggests that concepts emphasizing super-learning hypotheses and information

---

✉ Armin Hakkak Moghadam Torbati  
armin.hakkakmoghadamtorbati@unina.it

Shahab Jami  
Shahab.jami@uottawa.ca

Hamidreza Kobravi  
hrkobravi@iau.ac.ir

Narges Davoudi  
N.davoudi@studenti.unina.it

Mohammad Amin Gholibeigi  
min.gholibeigi@gmail.com

Asal Ashkzari  
asalztb@gmail.com

<sup>1</sup> Department of Advanced Biomedical Sciences, University of Naples “Federico II”, Via Sergio Pansini 5, 80131 Naples, Italy

<sup>2</sup> School of Human Kinetics, University of Ottawa, Ottawa, Canada

<sup>3</sup> Research Center of Biomedical Engineering, Mashhad Branch, Islamic Azad University, Mashhad, Iran

<sup>4</sup> Department of Physics “Ettore Pancini”, University of Naples Federico II, 80126 Naples, Italy

transmission mechanisms offer valuable insights into the processes underlying motor learning, warranting greater attention for designing rehabilitation interventions. Nonetheless, further experimental evidence is necessary to validate these hypotheses.

**Keywords** Basal Ganglia · Cerebellum · Cortex · Motor learning · Rehabilitation

## Introduction

Clinicians, neuroscientists, and the general public have been trying to understand the intricate processes by which the human brain learns and produces a vast spectrum of intricate motor behaviors that are indispensable in activities like dance, music, martial arts, and surgery. Developing efficient motion rehabilitation devices with high efficacy has been the goal of many types of research published during recent decades. Nevertheless, a movement rehabilitation device could not have high efficacy unless it could elicit motor learning. Therefore, focusing on the underlying neuroscientific concepts of motor learning makes sense. Motor learning is a process of acquiring skills to perform an appropriate motor task in response to a sensory cue, e.g. precise reaching with a mouse pointer to a target spot shown on the screen. This paper shows that the number of published papers that have addressed the contribution of different parts of the brain to motor learning is significant. Some of them investigated the contribution of the basal ganglia, Cerebellum, and motor cortex distinctly, while others focused on the interactive processes that emerged among them during motor learning. Since many of the posed ideas are purely theoretical issues, commenting decisively regarding acceptable brain interactive mechanisms that end up with motor learning is difficult. Nevertheless, according to the literature, the motor cortex plays a crucial role in the acquisition of motor skills, especially the precise and intricate abilities required for our preferred sports and professional pursuits. It was shown by Andrew E. Papale and his colleagues that the plasticity of the motor cortex, as well as certain descending pathways, plays a crucial role in the execution of skillful movements [1].

## The evolution of primary motor cortex engagement and disengagement in motor learning

The process of motor learning also entails the restructuring of the primary motor cortex (M1). To investigate the evolving role of the primary motor cortex (M1) in movement control during extended periods of learning, Eun Jung Hwang and his research team trained mice in a forelimb-based motor task over several months. They employed optogenetic inactivation and two-photon calcium imaging techniques in M1 during the course of long-term training. According to their findings, the researchers observed that disabling M1 had a detrimental effect on forelimb movements during the initial and intermediate stages of learning. However, in the later stage, this impairment was not evident, suggesting that the movements which initially relied on M1 became less reliant on it and could be executed independently. During the progression from the early to the middle stage of learning, the population activity in M1 exhibited a greater level of consistency across multiple trials, coinciding with the rapid improvement in task performance. However, in the transition from the middle to the late stage, the population activity in M1 once again exhibited variability, even though the expert behaviors remained consistent. The subsequent decrease in activity consistency implies a dissociation between M1 and the actual movements being performed. These findings indicate that extended motor learning can result in the disengagement of the primary motor cortex (M1) from the control of movements [2].

## Pivotal role of premotor cortex (M2) in motor learning

Apart from the role of M1 in movement control, some studies reveal novel properties of macroscopic cortical dynamics during motor learning, emphasizing the significance of premotor Cortex (M2) in the regulation of acquired movements. As the learning process progressed, the temporal compression of sequential activity across cortical modules increased, and the variability of this activity from one trial to another decreased. Moreover, during the learning process, a novel pattern of activity emerged from the premotor Cortex (M2), and M2 demonstrated predictive capabilities in relation to the activity of numerous other modules. Experiments involving inactivation demonstrated the crucial role of M2 in the post-learning dynamics of cortex-wide activity. Furthermore, the use of two-photon calcium imaging revealed that the

ensemble activity in M2 exhibited an earlier onset of activity and reduced variability during learning. These changes were found to be associated with modifications in the relationship between activity and movements [3].

### **Motor adaption for movement perturbations**

Some studies have focused on the specific aspects of motor learning. Motor adaptation is a form of motor learning to overcome movement perturbations caused by a novel environment or altered sensory feedback. During motor adaptation, future movements are corrected using error information acquired in previous trials [4]. So each part of the brain is studied in several works to investigate its performance in motor learning and motor adaption [5]. As we know, humans acquire and retain motor skills in order to adapt to a constantly evolving environment. However, the mechanisms through which the brain learns new internal models (IM) and converts them into long-term memory are not fully comprehended, as previous research has predominantly concentrated on the learning phase. Patrick Be'dard and his colleague showed that the basal ganglia are not actively involved in the dynamic formation of an internal model (IM). However, they do play a crucial role in the conversion of the initial memory into a long-term representation. They conducted a series of tests with the aim of gaining a deeper understanding of the possible role of frontostriatal networks in the development of long-term memory for an internal model (IM) associated with sensory-motor adaptation. For example, it has been shown that individuals with Parkinson's disease (PD) appear to develop compensatory mechanisms that effectively engage other brain regions, including the Cerebellum and parietal Cortex. These regions are recognized for their involvement in the process of adaptation [6].

### **Dynamics of Spatial Working Memory (SWM) through neural interplay in motor learning**

In addition to motor adaptation, spatial working memory (SWM) which has a determinant role in the transient process during motor learning has been addressed by some researchers. Spatial working memory (SWM) is a transient cognitive system that enables the manipulation of spatial information on a temporary basis, relying on the coordination of multiple brain regions. During spatial working memory (SWM) tasks, the simultaneous recording of local field potentials (LFPs) from the rat ventral hippocampus (HPC) and medial prefrontal Cortex (PFC) was conducted to examine the interaction between these brain regions in the context of SWM. The experimental findings demonstrate that the power of local field potentials (LFPs) in both the prefrontal Cortex (PFC) and hippocampus (HPC) decreased during the learning phase and reached its peak point prior to the rats' behavioral selection in spatial working memory (SWM) tasks. Moreover, the LFPs' power is mainly distributed in theta and gamma, which are related to SWM. Regarding functional connectivity, the PFC and HPC exhibit a similar effect of activity transmission during spatial working memory (SWM). The phase-amplitude coupling (PAC) between gamma oscillations in the PFC and theta oscillations in the HPC is positively correlated with the establishment of SWM and facilitates simultaneous interactions between the PFC and HPC. In terms of effective connectivity, the directed transmission of activity during spatial working memory (SWM) is more pronounced in the hippocampus (HPC) compared to the prefrontal Cortex (PFC), suggesting the flow of activity from the HPC to the PFC [7]. Despite of the attractive published studies, the lack of a review paper for scrutinizing and comparing the posed hypotheses, bolding the weaknesses, and opening new horizons in front of the involved researchers is sensible. The current study aims to fulfill this critical issue by investigating the role of basal ganglia, Cortex, and Cerebellum in isolation and their interactions during motor learning.

### **Learning paradigms in the brain**

According to a widely accepted perspective on brain learning processes, it is commonly believed that the three traditional learning paradigms—unsupervised, reinforcement, and supervised—occur in distinct brain regions, including the Cortex, basal ganglia, and Cerebellum respectively. In order to enhance movements based on the predicted sensory consequences of action, the Cerebellum faces the challenge of solving a credit assignment problem. The disparities between the actual and expected sensorimotor feedback are resolved through a supervised learning mechanism guided by climbing fibers (the cerebellar cortex inputs). The application of this supervised learning rule effectively characterizes cerebellar activity in both the CF and MF pathways across various behaviors. This model offers a convincing

explanation for how the Cerebellum can make modifications to specific movements. However, in intricate motor behaviors lacking a predetermined stimulus-action association, as well as numerous non-motor behaviors, comprehending how this supervised learning rule could serve as an effective mechanism for learning has proven to be a challenging task. Specifically, when the sensory information crucial for learning lacks a direct connection to the movement that needs adjustment or when the necessary sensory information is relevant only within a particular behavioral context, it remains uncertain how CFs could generate a supervised instructional signal in such cases. Indeed, there have been observations from behaviors that fulfill these criteria, suggesting that the existing supervised learning models of the Cerebellum are inadequate to fully describe the activity of CFs. As an illustration, in arbitrary visuomotor reaching tasks, it has been demonstrated that CF-driven Cspks (large dendritic calcium spikes (so-called complex spikes)) in Purkinje cells convey predictive signals that deviate from the patterns expected of motor errors [8, 9]. Instead, these studies have revealed that Cspks can exhibit predictability with regard to task parameters, including reach destination, forthcoming movement kinematics, or anticipated position errors. Notably, even in the context of eyelid conditioning, recent findings suggest that the Cerebellum may possess the ability to employ a broader spectrum of distinct learning rules in order to modify behavior [10].

Recent findings from novel studies have substantiated that the cortex not only plays a crucial role in unsupervised learning but also makes a substantial contribution to reinforcement learning. The frontopolar Cortex (FPC) plays a role in monitoring the reward associated with different choices during the decision-making process, along with evaluating their level of reliability. It is currently uncertain whether the function of the frontopolar Cortex (FPC) also encompasses the tracking of reward gradients related to continuous movements in the context of motor learning. In this regard, M. Herrojo Ruiz and his colleagues used anodal transcranial direct current stimulation (tDCS) over the right FPC to investigate its role in reward-based motor learning. The objective of their study was to utilize reward feedback on a trial-by-trial basis in order to uncover a concealed performance objective along a continuous dimension: timing. By regulating motor variability, Right FPC-tDCS facilitated accelerated learning when compared to the left M1-tDCS and the sham condition. Analysis using Bayesian computational modeling demonstrated that across all stimulation protocols, an augmentation in the trial-based expectation of reward resulted in a higher tendency toward exploitation. However, the strength of this association in the left M1-tDCS was weak, indicating a less effective learning strategy. The impact of frontopolar stimulation differed from that induced by left M1-tDCS and the sham, as motor exploration demonstrated greater sensitivity to inferred variations in the reward tendency (volatility). The results imply that rFPC-tDCS enhances the responsiveness of motor exploration to changes in reward volatility, leading to an acceleration in reward-based motor learning [11]. Another study that reveals the role of the cortex in this type of learning was conducted by Jane X. Wang and his colleagues. They drew on recent advances in artificial intelligence to introduce a new theory of reward-based learning. In this scenario, the dopamine system instructs the prefrontal cortex to function as an independent learning system. This novel perspective not only encompasses the findings that led to the development of the standard model but also adeptly addresses a broader array of observations, offering a renewed basis for future research [12]. Furthermore, the mounting evidence indicates that the neural network of the cerebral cortex and basal ganglia plays a crucial role in the process of reinforcement learning. We reviewed computational issues and possible algorithms for decision-making and reinforcement learning and recent findings on the neural correlates of the variables in those algorithms. Then we proposed a working hypothesis: The dorsolateral, dorsomedial, and ventral striatum forms distinct parallel and hierarchical modules for reinforcement learning, each responsible for actions occurring at various physical and temporal scales. The influential role of Reinforcement Learning (RL) models in comprehending diverse facets of basal ganglia function, including reward prediction and action selection, is evident [13]. The key point is the time that basal ganglia play an important role, but there remains a lack of theoretical consensus regarding the specific type of temporal representation employed by the basal ganglia. A unified computational system could potentially be responsible for both reinforcement learning (RL) and interval timing, which involves perceiving durations ranging from seconds to hours. This hypothesis, which extends upon previous models by integrating a time-sensitive action selection mechanism, could have significant implications for comprehending disorders such as Parkinson's disease, where both decision-making and timing abilities are compromised [14].

Overall, it seems that achieving optimal performance requires a well-balanced combination of unsupervised and reinforcement learning processes. In fact, excessive reliance on unsupervised learning tends to inadequately represent task-relevant features, while excessive reliance on reinforcement learning initially results in slow learning and subsequent susceptibility to getting trapped in local minima. These findings encourage further empirical investigations into category learning, with a focus on exploring similar effects in the extrastriate visual cortices [5].

## Basal ganglia, Cerebellum, and cortex interconnections

Before addressing the learning mechanisms involving the main parts of the brain, scrutinizing the existing evidence regarding the determinant neural interconnections could widen our insight into the likely role of the involved parts in motor learning. The motor system consists of various structures dispersed throughout the central nervous system, and understanding their collaboration in action control is important [15]. Accordingly, the Interaction of basal ganglia, Cerebellum, and cortex has been widely investigated through many methods in several works. Newly available information indicates that there is a connection between the basal ganglia and the Cerebellum at a subcortical level. A dense disynaptic connection to the cerebellar cortex originates from the subthalamic nucleus within the basal ganglia. Likewise, the dentate nucleus located in the Cerebellum serves as the origin for a concentrated disynaptic pathway that extends to the striatum. Based on these findings, a novel functional viewpoint emerges, suggesting that the basal ganglia, Cerebellum, and cerebral cortex collectively constitute an interconnected network [16]. Furthermore, recent anatomical findings have revealed the presence of two- and three-synaptic networks that connect the Cerebellum and basal ganglia. These discoveries have also provided evidence of more efficient communication with reduced latency. Moreover, following unilateral stimulation of the dentate nucleus in cats, it was observed that dopamine was released in the caudate nucleus, and its levels were elevated in the substantia nigra. These findings suggest that direct connections originating from the deep cerebellar nuclei may possess the capability to influence the dopaminergic activity in the basal ganglia [17]. For example, the connectivity between the Cerebellum and the primary motor cortex (M1) is crucial for executing everyday tasks, and any disruptions in these pathways can lead to impaired movement. Hence, it is imperative to develop and comprehend innovative techniques for investigating this pathway to enhance our knowledge in this area [18] due to limited knowledge regarding the interaction between the Cerebellum and cerebral cortical dynamics [19]. Using a combination of cerebellar stimulation and directional transcranial magnetic stimulation (TMS) over the primary motor cortex (M1), evidence has been provided for two distinct interactions between the Cerebellum and the cerebral cortex. These unique cerebellar–cerebral interactions exhibit varying responses to physiological plasticity and distinct motor learning tasks, indicating that they represent separate inputs from the Cerebellum to the premotor Cortex and M1. Overall, these findings indicate the existence of two separate CB-M1 networks that make distinct contributions to various motor behaviors [18]. The prevailing perspective on the role of the Cerebellum has traditionally emphasized its primary involvement in motor control and coordination. The current understanding of the Cerebellum has been significantly reshaped by recent discoveries from neuroanatomical, behavioral, and imaging investigations. Through the utilization of virus transneuronal tracers in neuroanatomical investigations, it has been revealed that the cerebellar output extends to expansive regions of the neocortex, encompassing both the prefrontal and posterior parietal cortex. Additionally, there exists reciprocal connectivity between the Cerebellum and the basal ganglia [20]. According to Alberto Cacciola and colleagues' findings, there is an anatomical basis for the interaction between cerebellar and basal ganglia activities in terms of control, indicating the functional integration of these systems in both motor and non-motor domains. Indeed, the potential direct pathways connecting cerebellum-pallidal and cerebellum-nigral may offer humans a rapid means of communication between the Cerebellum and basal ganglia through a short latency route, enabling them to swiftly synchronize their outputs in real time. The existence of substantial connections between the Cerebellum and basal ganglia at the subcortical level may have important implications in human disorders, specifically in Parkinson's disease and dystonia [21]. Fumika Mori and his colleagues also suggested the pedunculo-pontine tegmental nucleus (PPTg) may also act as an interface device between the basal ganglia and Cerebellum. Specifically, the pedunculo-pontine tegmental nucleus (PPTg) exhibits extensive connections with various regions of the basal ganglia, and one of its primary roles is to regulate and transmit activity within the basal ganglia network. Together, these components have been involved in the regulation of the motor control system, including functions like initiating or inhibiting voluntary movements, as well as influencing aspects of executive function, such as motivation [22]. Besides its close association with the basal ganglia, recent studies have revealed that the projections from the PPTg to the Cerebellum also activate the deep cerebellar nuclei through synaptic connections. In addition to PPTg, the thalamus is another place of interaction between basal ganglia and Cerebellum, which is proven by Andreas Hintzen and his colleagues by compiling data from electrophysiological and anatomical studies in rats, cats, dogs, and non-human primates [23]. On the other hand, the basal ganglia and the Cerebellum exhibit contrasting functionality in some cases. Firstly, among patients with cerebellar conditions, this effect was limited to the rhythm performed at a rapid pace, which imposes significant requirements on the accurate temporal representation of events. In contrast, patients with basal ganglia disorders exhibited a varied range of responses at a beat frequency, particularly for the more intricate rhythm that necessitates, the greater internal



generation of the beat. These findings present electrophysiological evidence indicating that these subcortical structures play a selective role in shaping the neural representation of rhythm. Furthermore, the findings propose that the analysis of rhythmic auditory stimuli depends on a complex functional network encompassing cortico-subcortico-cortical, which contributes to precise timing and entrainment sensitivities [24]. Secondly, motor adaptation to perturbations is achieved through the utilization of learning mechanisms within the Cerebellum and basal ganglia. Furthermore, the basal ganglia regulate cortical activity by driving a specific cortical network towards a different attractor state, effectively favoring certain attractors over others. The concepts of temporal difference learning and the convergence of corticostriatal fibers from various cortical regions within the striatum are integrated within a modular learning system that has the ability to acquire behavior with sequential organization [25]. Furthermore, the basal ganglia have a significant function in facilitating the development of connections between posterior cortical areas and frontal cortical regions, which are accountable for the execution of automatic behavior following extensive training [26]. David Gaffan and his colleagues designed and implemented a test on Macaque monkeys that proved interaction between these two regions is done by multi-synaptic corticocortical routes in strategy implementation [27].

## Motor learning-related interactive mechanisms

According to the evidence, different regions of the brain were activated to varying degrees at different stages of motor learning. Throughout the pre-conditioning phase, there was a progressive rise in activity within the cerebellar hemisphere crus, indicating an augmentation in attentional and cognitive processes. In the post-measurement phase, heightened activation was observed in the anterior cerebellar hemisphere and the putamen, suggesting an enhancement in sensorimotor feedforward processing and the development of automatized movements. A high initial anterior cerebellar and putamen activation predicted a better training effect. A.D. Walz and his colleagues' study clarified this issue. In their study, the researchers employed extensive training of the non-dominant hand in healthy individuals, leading to notable enhancements in motor performance. Moreover, they observed that the transfer of learning between the hands varied in magnitude depending on the specific type of movement being tested. While activation in the cortical motor areas declined over time, there was evidence of growing utilization of resources in the anterior cerebellar hemisphere and striatum following extended motor training [28]. However, the results of some works suggested that some parts of the brain have more impact on learning [29] and movement [30]. To gain insights into the process of learning, the study conducted by Hayley Ash and colleagues indicates that there are expanded sub-regions within the orbitofrontal cortex and ventromedial prefrontal cortex, as well as more intricate connectivity patterns between the prefrontal cortex and other brain regions associated with learning [29]. Supplementary motor area and pre-supplementary motor area, which were studied by Dalila Akkal and his colleagues, showed even though both the basal ganglia and the Cerebellum send outputs to these two cortical areas, it appears that these areas, which are involved in the internal generation and sequencing of movement, predominantly controlled by input from the basal ganglia [30]. In addition, it has been hypothesized that the excitability change in the sensorimotor cortex serves as the anatomical basis, indicating an initial alteration in cortical network function prior to the occurrence of structural plasticity. Recent experimental studies emphasize the significant involvement of the Cerebellum, particularly the interpositus nucleus, in facilitating the motor cortex's adaptation to repetitive stimulation trains. Interpositus neurons, receiving inputs from both the sensorimotor cortex and the spinal cord, contribute to somesthetic reflex behaviors and support the cerebral cortex in converting sensory signals into motor-oriented commands through the cerebello-thalamo-cortical projections. Moreover, climbing fibers that originate from the inferior olivary complex and innervate the nucleus interpositus facilitate the integration of comprehensive sensorimotor information derived from spinal modules. It appears that the interpositus nucleus serves as a primary subcortical regulator of the excitability modifications observed in the motor cortex, potentially serving as a foundation for early plasticity mechanisms involved in motor learning and the restoration of function following injuries or lesions [31]. Furthermore, as movement rates increased, the occurrence of movement errors also increased. Decreasing movement rates led to increased activation of the left Cerebellum (CB), while increasing movement rates resulted in increased activation of the (right) ipsilateral premotor Cortex (PMC). Furthermore, meaningful associations were found between individual movement errors and activation of the left Cerebellum (CB) at both movement rates, whereas similar relationships were not observed in the ipsilateral premotor Cortex (PMC). When considering the evidence as a whole, it is proposed that in the execution of precise and regulated tasks involving slow force production, the coordination between the cortical motor circuit (right PMC) and subcortical

motor circuit (left CB), i.e., a functional dissociation between PMC and CB, plays a distinct role in governing movement rate and correcting errors [32].

The aforementioned evidence proves the functional interaction among the cortex, basal ganglia, and cerebellum during a motor learning process. Although there is abundant evidence indicating anatomical and functional interactions among the Cortex, Cerebellum, and basal ganglia, the learning processes that occur within these regions, often categorized as unsupervised, supervised, and reinforcement learning, are typically studied independently [33]. For example, Gerraty and his colleagues used functional magnetic resonance imaging (fMRI) in conjunction with dynamic network neuroscience methodologies to acquire detailed, time-dependent descriptions of network coordination during the process of reinforcement learning in humans [34]. Although these types of information could be helpful, they sometimes lead to misunderstanding. An example of this is the research conducted by Aspen H and his colleagues, which demonstrated the potential risk of incorrectly attributing individual differences solely to the reinforcement learning process without considering other factors, such as working memory [35]. On the other hand, by examining the interaction between unsupervised learning (UL) and reinforcement learning (RL) during the development of categorical perception, we have gained a deeper understanding of how a balanced mix of these two learning processes gives rise to the emergence of an appropriate categorical perception [36]. Supervised learning for motor adaptation is supported by reinforcement learning. During the acquisition of motor sequences, both supervised and unsupervised learning mechanisms facilitate the process of reinforcement learning. The function of the cerebellum is the other elucidating example. Typically, the Cerebellum engages in motor adaptation by employing supervised learning and utilizing visual feedback to obtain information about movement errors. Nonetheless, in cases where visual feedback is severely distorted, the system may cease cerebellar error-based learning and instead transition to reinforcement learning mechanisms mediated by the basal ganglia. To ensure efficient learning, only one of these mechanisms should be operational at any given time. The switching between these mechanisms is facilitated by a specific circuit that effectively inhibits the learning process in one structure while enabling it in the other. In order to accomplish this, the circuit adjusts the learning rate in the Cerebellum and regulates dopamine release in the basal ganglia based on the efficiency of error-based learning [37]. As a result, when studying the aforementioned learning methods in isolation, their significant interdependence tends to be overlooked [33]. Accordingly, the super-learning concept is introduced. Undoubtedly, the brain regions form a highly interconnected system that integrates various learning mechanisms to create a powerful super-learning process, promoting the acquisition of adaptable motor behavior. Current research studying the reciprocal interactions between the three learning provides support for the concept of super-learning and indicates in which brain areas they interact (1-Cerebellum and basal ganglia: Supervised and reinforced learning interactions 2- Basal ganglia and Cortex: interactions between unsupervised and reinforcement learning 3- Cerebellum and Cortex: interactions between supervised and unsupervised learning). The second piece of evidence for proving interactions between the three learning methods is neuromodulators. Neuromodulators, primarily dopamine, noradrenaline, serotonin, and acetylcholine, work diffusely across the cortex, basal ganglia, and Cerebellum to control the reciprocal interplay of learning signals. Dopamine and serotonin, for instance, are crucial for both driving reinforcement learning and regulating the interaction between supervised and reinforcement learning processes. By controlling the exploration/exploitation aspects of trial-and-error behavior, noradrenaline facilitates this relationship even more, while acetylcholine helps to strengthen the interplay between unsupervised and reinforced learning processes [38]. The trial-and-error learning mechanism of the basal ganglia leads to the timely activation of appropriate frontal areas following the activation of the posterior associative cortex. This enables the Hebbian learning process for robust, rapid, and effective cortico-cortical information processing. This proposed mechanism is applicable in general, and the specific associations formed depend on the particular areas engaged. For instance, associations involving premotor areas would have a closer connection to behavior compared to associations involving the prefrontal Cortex [26].

## Conclusions and future perspectives

In this study, we investigated the role of the motor cortex, Basal ganglia, and Cerebellum in motor learning and motor adaption independently and in relationships with each other. In this way, we advanced the understanding of the performance of these brain regions during learning in order to pave the way for designing practical rehabilitation methods and equipment that need to elicit specific brain areas. Overall, the anatomical connection between the Cerebellum and basal ganglia suggests that these systems interact and work together in controlling various functions, including

both motor and non-motor processes. Different types of learning require specific parameters, indicating the need for distinct conditions depending on the type of learning being pursued. This emphasizes the participation of different brain regions in motor learning, indicating their unique contributions to attention, cognitive processes, sensorimotor processing, and the generation and organization of movements. New research has presented findings indicating the significant involvement of the cortex in both unsupervised and reinforcement learning processes. Nevertheless, it remains uncertain whether the frontal polar Cortex (FPC) plays a role in tracking reward gradients, specifically within the realm of motor learning. A novel hypothesis regarding reward-based learning proposes that the dopamine system guides the prefrontal cortex to operate as a distinct learning system, providing a broader perspective and serving as a foundation for further exploration and investigation in this area of study. Reinforcement learning models have played a significant role in enhancing our understanding of reward prediction and action selection mechanisms within the basal ganglia. However, there is currently a lack of consensus concerning the precise temporal representation utilized by the basal ganglia. Furthermore, although M1 and M2 have a significant role in motor learning, the relationship between cortical activity and movements needs to be studied more due to the fact that as motor learning progresses, the reliance on M1 decreases, and movements become more independent. In addition, the contribution of fronto-striatal networks and compensatory mechanisms in the Cerebellum and parietal Cortex appears to play a role in the development of long-term memories related to sensory-motor adaptation. However, the specific mechanisms involved in the learning and storage of internal models (IM) are not yet fully comprehended and require further research. Moreover, dynamical causal modeling, the Cerebellum interacting uniformly with the cerebral cortex, showed a universal cerebellar transform and provided a foundation for further exploration of this interaction.

In the subcortical regions, the interpositus nucleus seems to play a crucial role as a subcortical regulator in modifying excitability within the motor cortex. It is believed to serve as a fundamental component in the initial stages of plasticity mechanisms related to motor learning and the restoration of function after injuries or lesions. An instance of this is observed in stroke recovery, where somatosensory stimulation has demonstrated the ability to improve impaired arm function. This improvement is attributed to the positive effects of transcranial magnetic stimulation (TMS) on motor system plasticity, physiological plasticity, and motor behaviors.

The final point is regarding the learning paradigms attributed to the brain. Studying unsupervised, supervised, and reinforcement learning independently also sometimes leads to misunderstanding. For example, the potential risk of incorrectly attributing individual differences solely to the reinforcement learning process without considering other factors such as working memory [35]. Consequently, the interdependence between the different learning methods mentioned above is often disregarded when they are studied independently [38]. Therefore, the concept of super-learning emerges, highlighting the highly interconnected nature of brain regions that integrate various learning mechanisms. This super-learning process is crucial for the acquisition of adaptable motor behavior. However, further research is needed to thoroughly examine and understand this concept.

Overall, while studying the individual performance of each brain region yields valuable insights, it can sometimes lead to misleading conclusions. Therefore, it is crucial to take into account the interactions between different brain areas during the learning process when designing rehabilitation systems. Future research should focus on investigating these interplays in greater detail, with the aim of practical implementation. Figuring out how the brain network connectivity dynamics and information flow interrelate in the thalamocortical loop is crucial. It can help to design a model that describes not only normal interactive learning dynamics but also disordered learning dynamics. This is an important aspect of motor learning issues because the main goal of a rehabilitation device is to enhance the normal interactive learning process. One proposed idea is to utilize these findings in biofeedback intervention protocols to enhance the ability of motor control patients.

**Author contributions** Conceptualization, A.H.M.T, S.H, and H.K.; writing—original draft preparation, A.H.M.T, S.H, N.D, M.G, A.A, and H.K.; writing—review and editing, A.H.M.T and H.K.; supervision, A.H.M.T and H.K. All authors have read and agreed to the published version of the manuscript.

**Funding** No funding was received for conducting this study.

**Data availability** My manuscript has no associated data.

## Declarations

**Conflicts of interest** The authors declare no conflict of interest.



**Ethics approval** The authors declare that this review article adheres to ethical standards and guidelines, including proper citation and attribution of sources. As this is just a review of other papers does not need other regulations regarding human and animal subjects.

## REFERENCES

- Papale AE, Hooks BM. Circuit changes in motor cortex during motor skill learning. *Neuroscience*. 2018;368:283-97.
- Hwang EJ, Dahlen JE, Hu YY, Aguilar K, Yu B, Mukundan M, et al. Disengagement of motor cortex from movement control during long-term learning. *Science advances*. 2019;5(10):eaay0001.
- Makino H, Ren C, Liu H, Kim AN, Kondapaneni N, Liu X, et al. Transformation of cortex-wide emergent properties during motor learning. *Neuron*. 2017;94(4):880-90. e8.
- Leisman G, Braun-Benjamin O, Melillo R. Cognitive-motor interactions of the basal ganglia in development. *Frontiers in systems neuroscience*. 2014;8:16.
- Granato G, Cartoni E, Da Rold F, Mattera A, Baldassarre G. A Computational Model of Representation Learning in the Brain Cortex, Integrating Unsupervised and Reinforcement Learning. *arXiv preprint arXiv:210603688*. 2021.
- Bédard P, Sanes JN. Basal ganglia-dependent processes in recalling learned visual-motor adaptations. *Experimental brain research*. 2011;209:385-93.
- Zhang W, Guo L, Liu D. Concurrent interactions between prefrontal cortex and hippocampus during a spatial working memory task. *Brain Structure and Function*. 2022;227(5):1735-55.
- Kitazawa S, Kimura T, Yin P-B. Cerebellar complex spikes encode both destinations and errors in arm movements. *Nature*. 1998;392(6675):494-7.
- Streng ML, Popa LS, Ebner TJ. Climbing fibers control Purkinje cell representations of behavior. *Journal of Neuroscience*. 2017;37(8):1997-2009.
- Hull C. Prediction signals in the cerebellum: beyond supervised motor learning. *elife*. 2020;9:e54073.
- Herrojo Ruiz M, Maudrich T, Kalloch B, Sammler D, Kenville R, Villringer A, et al. Modulation of neural activity in frontopolar cortex drives reward-based motor learning. *Scientific reports*. 2021;11(1):20303.
- Wang JX, Kurth-Nelson Z, Kumaran D, Tirumala D, Soyer H, Leibo JZ, et al. Prefrontal cortex as a meta-reinforcement learning system. *Nature neuroscience*. 2018;21(6):860-8.
- Ito M, Doya K. Multiple representations and algorithms for reinforcement learning in the cortico-basal ganglia circuit. *Current opinion in neurobiology*. 2011;21(3):368-73.
- Gershman SJ, Moustafa AA, Ludvig EA. Time representation in reinforcement learning models of the basal ganglia. *Frontiers in computational neuroscience*. 2014;7:194.
- Rosahl SK, Knight RT. Role of prefrontal cortex in generation of the contingent negative variation. *Cerebral Cortex*. 1995;5(2):123-34.
- Bostan AC, Strick PL. The basal ganglia and the cerebellum: nodes in an integrated network. *Nature Reviews Neuroscience*. 2018;19(6):338-50.
- Milardi D, Quartarone A, Bramanti A, Anastasi G, Bertino S, Basile GA, et al. The cortico-basal ganglia-cerebellar network: past, present and future perspectives. *Frontiers in systems neuroscience*. 2019;13:61.
- Spampinato DA, Celnik PA, Rothwell JC. Cerebellar–motor cortex connectivity: one or two different networks? *Journal of Neuroscience*. 2020;40(21):4230-9.
- Bukhari Q, Ruf SF, Guell X, Whitfield-Gabrieli S, Anteraper S. Interaction between cerebellum and cerebral cortex, evidence from dynamic causal modeling. *The Cerebellum*. 2022;21(2):225-33.
- O’Doherty JP, Dayan P, Friston K, Critchley H, Dolan RJ. Temporal difference models and reward-related learning in the human brain. *Neuron*. 2003;38(2):329-37.
- Cacciola A, Milardi D, Livrea P, Place P, Anastasi G, Quartarone A. The known and missing links between the cerebellum, basal ganglia, and cerebral cortex. *The Cerebellum*. 2017;16:753-5.
- Mori F, Okada K-i, Nomura T, Kobayashi Y. The pedunculopontine tegmental nucleus as a motor and cognitive interface between the cerebellum and basal ganglia. *Frontiers in neuroanatomy*. 2016;10:109.
- Hintzen A, Pelzer EA, Tittgemeyer M. Thalamic interactions of cerebellum and basal ganglia. *Brain Structure and Function*. 2018;223:569-87.
- Nozaradan S, Schwartze M, Obermeier C, Kotz SA. Specific contributions of basal ganglia and cerebellum to the neural tracking of rhythm. *Cortex*. 2017;95:156-68.
- Djurfeldt M, Ekeberg Ö, Graybiel AM. Cortex–basal ganglia interaction and attractor states. *Neurocomputing*. 2001;38:573-9.
- Hélie S, Ell SW, Ashby FG. Learning robust cortico-cortical associations with the basal ganglia: an integrative review. *Cortex*. 2015;64:123-35.
- Gaffan D, Easton A, Parker A. Interaction of inferior temporal cortex with frontal cortex and basal forebrain: double dissociation in strategy implementation and associative learning. *Journal of Neuroscience*. 2002;22(16):7288-96.
- Walz A, Doppl K, Kaza E, Roschka S, Platz T, Lotze M. Changes in cortical, cerebellar and basal ganglia representation after comprehensive long term unilateral hand motor training. *Behavioural brain research*. 2015;278:393-403.
- Ash H, Chang A, Ortiz RJ, Kulkarni P, Rauch B, Colman R, et al. Structural and functional variations in the prefrontal cortex are associated with learning in pre-adolescent common marmosets (*Callithrix jacchus*). *Behavioural Brain Research*. 2022;430:113920.
- Akkal D, Dum RP, Strick PL. Supplementary motor area and presupplementary motor area: targets of basal ganglia and cerebellar output. *Journal of Neuroscience*. 2007;27(40):10659-73.

31. Luft AR, Manto M-U, Oulad Ben Taib N. Modulation of motor cortex excitability by sustained peripheral stimulation: the interaction between the motor cortex and the cerebellum. *The Cerebellum*. 2005;4:90-6.
32. Tanaka Y, Fujimura N, Tsuji T, Maruishi M, Muranaka H, Kasai T. Functional interactions between the cerebellum and the premotor cortex for error correction during the slow rate force production task: an fMRI study. *Experimental brain research*. 2009;193:143-50.
33. Kelly AC, Uddin LQ, Biswal BB, Castellanos FX, Milham MP. Competition between functional brain networks mediates behavioral variability. *Neuroimage*. 2008;39(1):527-37.
34. Gerraty RT, Davidow JY, Foerde K, Galvan A, Bassett DS, Shohamy D. Dynamic flexibility in striatal-cortical circuits supports reinforcement learning. *Journal of Neuroscience*. 2018;38(10):2442-53.
35. Yoo AH, Collins AG. How working memory and reinforcement learning are intertwined: A cognitive, neural, and computational perspective. *Journal of cognitive neuroscience*. 2022;34(4):551-68.
36. Granato G, Cartoni E, Da Rold F, Mattera A, Baldassarre G. Integrating unsupervised and reinforcement learning in human categorical perception: A computational model. *Plos one*. 2022;17(5):e0267838.
37. Todorov DI, Capps RA, Barnett WH, Latash EM, Kim T, Hamade KC, et al. The interplay between cerebellum and basal ganglia in motor adaptation: A modeling study. *PLoS One*. 2019;14(4):e0214926.
38. Caligiore D, Arbib MA, Miall RC, Baldassarre G. The super-learning hypothesis: Integrating learning processes across cortex, cerebellum and basal ganglia. *Neuroscience & Biobehavioral Reviews*. 2019;100:19-34.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.