

Integrative Mechanisms of The Cerebellum

Bon E. I*, Maksimovich N.Ye, Zimatkin S.M, Kiskevich P.V

Grodno State Medical University, Grodno, Belarus.

***Corresponding Author:** Elizaveta I Bon, Candidate of biological science, Assistant professor of pathophysiology department named D. A. Maslakov, Grodno State Medical University; Grodno State Medical University, 80 Gorky St, 230009, Grodno, Belarus.

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Abstract

The study of integrative mechanisms of cerebellar activity is currently of great interest. There are undoubtedly a number of reasons for this. These include, first of all, the idea that the cerebellum works like a calculating machine which is based on the following facts. On the other hand, on the basis of studies on animals with the cerebellum removed and observation of people with traumatic its damage, it is known that the cerebellum performs a number of motor functions: a) maintenance of posture and balance; b) maintenance of muscle tone and its redistribution; c) coordination of voluntary movements

Key Words: integrative mechanisms; cerebellum; neural structure; synaptic organization

Introduction

The study of integrative mechanisms of cerebellar activity is currently of great interest. There are undoubtedly a number of reasons for this. These include, first of all, the idea that the cerebellum works like a calculating machine which is based on the following facts [1-4].

1. The cerebellar cortex is relatively simple and is characterized by a relatively identical composition and stereotypical interrelationships of cellular elements in various vertebrate representatives; thus, it is adapted to fast and efficient processing of incoming information [4-8].

2. The cerebellar cortex has two afferent inputs, one of which has a mixed excitatory-inhibitory, and the other exclusively excitatory effect on the key element of the cerebellum, the Purkinje cell. The latter represents the only exit from the cerebellum and has an inhibitory effect on the cells of the intracerebellar nuclei [9-10].

3. The cerebellar cortex, like the cerebral cortex, perceives almost all types of afferent stimuli and, in turn, influences many parts of the CNS. In addition to the well-studied tactile, proprioceptive, and vestibular inputs, the cerebellum presents interoceptive afferents, as well as inputs of other modalities arriving in the cerebellum through the structures of the trunk and reticular formation [12].

4. Finally, the cerebellar output has a strong influence on the sensorimotor area of the cerebral cortex.

On the other hand, on the basis of studies on animals with the cerebellum removed and observation of people with traumatic its damage, it is known that the cerebellum performs a number of motor functions: a) maintenance of posture and balance; b) maintenance of muscle tone and its redistribution;

c) coordination of voluntary movements [13-15]. Although these functions are purely motor in themselves, they nevertheless require the participation of specific sensory inputs in their realization. Thus, setting the correct posture is associated with information coming from the spindles about the state of postural tone, making permanent corrections to balance is transmitted by signals from the vestibular apparatus, and adequate coordination of movements requires additional information from the visual, auditory and other analyzers. In this sense, the cerebellum must be considered as an organ of sensorimotor integration.

Afferent Systems of The Cerebellum

Given the complexity of the integrative mechanisms of the cerebellum, it is appropriate to dwell on a brief description of some features of its structure and synaptic organization.

Structure And Synaptic Organization Cerebellar Cortex

The mammalian cerebellar cortex is relatively simple: it has a 3-layer structure and consists of an outer - molecular layer (approximately 300 µm thick), a middle layer of Purkinje cells (70-100 µm thick) and a granular layer, which is 400-500 µm thick at the apex of the lobe, whereas in the depth of the sulcus it is about 100 µm thick. The cortex contains five cell types (granular, basket cells, stellate cells, Golgi cells, Purkinje cells), of which only the granular cells are excitatory and all others are inhibitory [16-18].

The cross section of Fig. 3.1 shows the branching dendrites of Purkinje cells, basket cells, and stellate cells. The key element of the cerebellum, Purkinje cells, represent a typical example of highly differentiated neurons with

extensive dendritic branching and various types of synaptic contacts. Their total number is estimated at 1.2 million [17].

There are three types of inhibitory insertion neurons in the molecular layer: basket, short-axon and long-axon stellate cells. The descending part of the basket cell axon ends in the form of a basket on the lower part of the Purkinje cell body. The axons of the stellate cells establish synaptic contact with the Purkinje cell in the ratio of 17: 1. The granular layer contains Golgi cells in addition to granular cells. The number of granular cells in 1 mm³ is 2.8 -106. The axons of the granular cells ascend to the surface, branch T-shaped[^] forming parallel fibers and extend from the branching point about 1.5 mm [19-22].

Over 100,000 parallel fibers form excitatory synapses on the dendrites of the Purkinje cell. Parallel fibers also form excitatory synapses with the dendrites of basket cells, stellate cells, and Golgi cells, on which, likewise, the as well as on neighboring Purkinje cells, collaterals of Purkinje cell axons form weak inhibitory synapses. The weak inhibitory action of Purkinje cell axon collaterals on an adjacent Purkinje cell is one of the essential mechanisms in the localization of cerebellar functions [23-25].

Afferent Fiber Systems

All afferent information reaches the cerebellar cortex by two systems of anatomically separate inputs that terminate on Purkinje cells in the form of mossy and climbing fibers, while the Purkinje cell itself is the only output element of the cerebellum. Recently, however, a third type of afferent endings in the cerebellar cortex, whose chemical transmitter is norepinephrine, has been detected by fluorescence. However, these data have not yet been confirmed [20].

The system of climbing fibers of the cerebellum, first described by Ramon Cahal, is a monosynaptic input that makes direct synaptic contact with the soma and dendrites of the Purkinje cell. Synaptic contact with Purkinje cell dendrites is made by means of spines, the number of which is close to 300 in the frog and 170 in the alligator; this number varies little in the higher classes of vertebrates. The multiplicity of synaptic contacts with the Purkinje cell in each climbing fiber is the main prerequisite for the exceptionally strong synaptic excitatory action of the climbing fiber input. The shapes of these synaptic contacts do not differ significantly in animals at different levels of phylogeny. It follows that the input of climbing fibers changes very little as the CNS evolves. Ontogenetically, the synapse between the climbing fiber and the Purkinje cell is initially established at the level of the soma in the form of a "hood," which gradually moves upward during postnatal development to the region of the Purkinje cell dendrite. The climbing fibers in their apical part are myelinated, the course of their branching almost repeats the pattern of arborization of the Purkinje cell dendritic tree [24-28].

The activity of climbing fibers, being one of the indicators of cerebellar maturity, is registered earlier in mature animals (guinea pigs) than in immature animals, and its functional maturation is slightly ahead of the maturation of afferent input of mossy fibers. Altman believes that the postnatal morphogenesis of Purkinje cells (dendritic branching, growth of spines) largely depends on the inducing action of satellite cells of the cortex (basket cells, stellate cells, and granular cells).

Climbing fibers establish synaptic contact with Purkinje cell dendrites in a 1: 1 ratio, although other data suggest that this contact is not restricted to a single Purkinje cell. The main source of origin of climbing fibers is considered to be the inferior olive. However, there are indications that even after chronic transection of the olivo-cerebellar pathway, activation of Purkinje cells along the input of climbing fibers in a significant percentage of cells persists [27].

Direct electrical stimulation of olive cells exerts a strong excitatory synaptic effect on the Purkinje cell via climbing fibers. A large VPSP appears, at the top of which there are three to five PDs of decreasing amplitude with a frequency of 300-500/s (it is commonly referred to in the literature as a "complex discharge" or "climbing fiber response")

Under the action of a basket cell discharge, the number of impulses in such a response can be reduced to one, but it is never possible to obtain complete blockade of additional discharges. This suggests that "basket" inhibition acts as a regulator of the degree of inhibitory suppression only within certain limits.

During the registration of focal activity of the cerebellar cortex layers in response to stimulation of the inferior olive, activation of the granular layer is expressed in the predominance of long-latency positive potentials, whereas in the molecular layer, in the region of dendrites, negativity prevails, reflecting the impulse activity of axons of granular cells and the subsequent discharge of Purkinje cells and other cells of the molecular layer. The comparatively long latent period (4-6 ms) of focal potentials during activation of the climbing input in response to stimulation of the cells of the lower olive is associated with a low conduction velocity (5-20 m/s) along climbing fibers. It has been found that discharge evoked through climbing inputs is accompanied by an inhibitory pause (from 100 to 800 ms) in Purkinje cell activity [26-29]. It is believed that inhibition of Purkinje cells after a complex discharge is associated with the action of basket cells, Golgi cells activated by collaterals of climbing fibers. An indication of this is the possibility of repeated activation of Purkinje cells only within 10-20 ms, whereas at longer intervals, the activation of climbing fibers is accompanied by VSPs of reduced amplitude due to the beginning of the inhibitory action of interneurons. Taking into account that the value of focal potential U3 is a measure of granule cell discharge, it can also serve as an indicator of the degree of inhibition of granule cells by Golgi cells. Thus, the input of climbing fibers has an excitatory-inhibitory effect on Purkinje cells, while basket and stellate cells have only an inhibitory effect on them.

Afferent mossy fibers are found in the cerebellum of all vertebrates. The ends of the mossy fibers form a synaptic contact with the dendrites of granule cells. This type of synapse is called glomerular because the terminal portion of the afferent mossy fiber forms approximately 10 rosettes, allowing contact with an order of magnitude greater number of granule cell dendrites [18]. The exiting axon of the granule cell, T-branching, forms parallel fibers that establish synaptic contact with Purkinje cell dendrites. The system of mossy fibers-granule cells-parallel fibers-Purkinje cell dendrites is basically similar in all vertebrates, but it undergoes significant quantitative growth in phylogeny. This is the reason for the strong development of the molecular layer in higher vertebrates, the sharp increase in the number of synaptic contacts of parallel fibers with Purkinje cells, and the development of the system of inhibitory interneurons (basket cells, stellate cells, and Golgi cells) in the vertebrate cerebellar cortex [20].

Along with the development of the system of inhibitory neurons, the system of collaterals of climbing fibers and axonal collaterals of Purkinje cells has developed greatly in phylogeny. It is interesting to note that synaptic contact between parallel fibers and Purkinje cells matures earlier than that between mossy fiber input and granular cells. Therefore, the maturation sequence of the ascending afferent pathway in ontogeny does not go in the direction from the periphery to Purkinje cells, but in the opposite direction. The sequence of maturation of synaptic contacts of afferent inputs of climbing and mossy fibers to Purkinje cells of the cerebellum in postnatal ontogenesis is also expressed in the fact that axodendritic contacts with spines of Purkinje cells mature later than deep axosomatic contacts [17-19].

Electrophysiological evidence of this is the fact of earlier appearance of Purkinje cell activity* caused by activation of mossy fibers in guinea pigs, kittens, rabbits, rats.

In order to identify the discharge of mossy fibers, a number of criteria are used, among which the most suitable are: a) the frequency of the background discharge of mossy fibers should be within the range of 5-70 imp/s; b) the response to muscle nerve stimulation should include two to five simple peaks with a frequency of 500-800 Hz (the polarity of the biphasic peak should be 3/4 negative) c) the time of occurrence of the evoked peak should precede the negative $_U2$ wave of the focal potential; d) the latency time of the response to stimulation of the forelimb nerve should not exceed 3-5 ms; e) the cell activity should be recorded at a microelectrode displacement of up to 100 μ m. Fig. 3.3 shows a schematic of Purkinje cell activation via afferent inputs of climbing and fascicular fibers, from which the temporal characteristics of Purkinje cell activation during intra- (a) and extracellular (b) recordings can be seen [15].

There is evidence that mossy fibers transmit to the cerebellum rapid changes in proprioceptive information from peripheral receptors, on the basis of which the Purkinje cell produces appropriate correction impulses.

Mossy fibers originate in many parts of the CNS and consequently transmit a variety of information to the cerebellum. However, the greatest proportion of afferent signaling enters the cerebellum to the cerebellum via the ventral and dorsal dorsal spinocerebellar tracts, lateral reticular and external cuneiform nuclei, vestibular nuclei, and the reticular formation. Irritation of these extracerebellar structures has a mixed excitatory-inhibitory effect on Purkinje cells. Direct activation of the last link of afferent input to the cerebellum - parallel fibers near Purkinje cells - has a predominantly inhibitory effect on Purkinje cells. However, this effect is extremely sensitive and very dependent on the functional state of the superficial layers of the cerebellar cortex, which usually begins to deteriorate 2-3 h after the onset of cortical work [14-16].

The main indicator of a background-active Purkinje cell is the presence of a pulse irregular discharge caused by activation through mossy fibers and registered at the level of dendrites and cell soma. Its frequency in awake animals (cats, monkeys) varies in rather wide ranges (from 3 to 125 and higher imp/s, and on average from 20 to 70 imp/s) depending on the functional state of the object of study, the type of animal, and the place of Purkinje cell registration in the cerebellum. At the same time, the frequency of Purkinje cell activation through climbing fibers or the frequency of complex discharges in awake cats and monkeys is extremely low and ranges on average from 0.33 to 2.5 imp/s. It has been shown that in intact pigeons the mean discharge frequency of simple Purkinje cell peaks averages 49.3 imp/s, ranging from 12.0 to 118.5 imp/s. The standard deviations of the discharge frequency of simple commissures in intact and decerebrated pigeons are 30.5 and 26.5 imp/s, respectively, while their coefficient of variation is close, 0.62 and 0.64. According to their data, the average frequency of complex peaks in Purkinje cells of intact pigeons is 2.61 imp/s, varying from 1.27 to 4.35 imp/s. The same values in decerebrated pigeons are: average 1.96 imp/s, and fluctuate from 0.58 to 3.51 imp/s [9-13].

Thus, under the influence of decerebration the activity of Purkinje cells in both pigeons and cats is somewhat reduced. At the same time, the appearance of simple peaks under decerebration conditions in response to peripheral stimulation is facilitated, whereas the generation of complex discharges to the same type of afferent influence is hampered. The frequency of the background discharge of Purkinje cells increases with age in both mature and immature births, but mainly due to an increase in the frequency of simple peaks.

Nembutalol anesthesia depresses both the background activity of Purkinje cells and that caused by irritation of superficial parallel fibers and bridge structures, but it has almost no effect on the generation of complex peaks caused by direct irritation of the inferior olive. Thiopental anesthesia has a somewhat weaker effect on the background activity of Purkinje cells [5].

The activity of Purkinje cells in the anterior lobe of the cerebellum changes markedly during sleep. The activity arriving via mossy fibers is particularly enhanced during the paradoxical phase of sleep compared to the phase of synchronized sleep, and it is the stronger the more pronounced the REM phase. The activity of the climbing input of Purkinje cells also changes during paradoxical sleep, but in different ways: in some cells it increases and in others it decreases; however, since the frequency of simple peaks is many times higher than the frequency of complex peaks, the total flux of Purkinje cell activity always increases during paradoxical sleep. The increased activity of Purkinje cells of the inhibitory area of the cerebellum during paradoxical sleep is attributed to the change in tone that occurs during this stage of sleep [8-11].

Reactions Of Purkinje Cells to Afferent Stimuli

For a long time, many physiologists believed that the successful work of the cerebellum as an organ of regulation and coordination of motor activity should be combined with its performance of sensory functions. Numerous physiological experiments of recent years, conducted on representatives of all classes of animals, convince us of this. This is expressed in the reactions of Purkinje cells and cerebellar cortex in response to the arrival of afferent waves of various modalities and in different species of animals: in fish, amphibians, reptiles, birds and mammals [14].

One of the important features of afferent input to the cerebellum is the more pronounced spatial and temporal efficiency of the synaptic action of cutaneous as compared to the action of muscle afferents. These differences are most clearly manifested during suprathreshold stimulation of cutaneous-muscular afferents and registration of total discharge frequency distribution curves. On the entire path of the afferent wave to the Purkinje cell, the greatest difficulties for the passage of the wave are created at the place of synaptic contact of afferent endings of mossy fibers with dendrites of granular cells. The obstacle in this place is best overcome not by single, but by a short series of impulses, which causes discharge of granular cells [20-22].

The study of the nature of convergence of the mossy afferent input to Purkinje cells revealed great diversity in the reactions of the latter to stimulation of the nerves of the limbs. On one Purkinje cell can converge the influences coming through the mossy fibers from the anterior and posterior limbs, and sometimes two Purkinje cells, which are in close proximity, give opposite reactions - one is inhibited and the other is excited under the influence of the same modality of stimulation. It has also been shown that there is overlap and convergence of climbing fibers to the same Purkinje cell activated from different nerves of the fore and hind limbs [26].

If we assume that a stimulus of one modality can activate the inputs of both fascicular and climbing fibers, it seems interesting to investigate the mechanism of the relationship between these two inputs on the same Purkinje cell. It is known that irritation of limb nerves, muscle tendons, or activation of vestibular, visual receptors can change the frequency of discharge of inputs of both mossy and climbing fibers. The highest discharge frequency of complex peaks was recorded in response to caloric stimulation of the labyrinth and was 9 imp/s. This high frequency had a strong inhibitory effect on the frequency of discharge evoked through mossy fibers. It is known, however, that the number of discharges in the 'complex peak can be varied by changing the level of polarization of Purkinje cells, in which case it appears that this may influence the degree of inhibitory effect of the complex

peak on the discharge evoked through the mossy fibers, which may be as high as 800 ms. The mechanisms of such depression are considered to be: a) inactivation - mechanisms of electrical excitability; b) "basket" inhibition as a result of activation of basket cells by axon collaterals of climbing fibers and subsequent hyperpolarization of Purkinje cell - mechanism of direct inhibition; c) finally, activation of Golgi cells by axon collaterals of climbing fibers, as a result of which the effect of mossy fiber input on granular cells is inhibited and the excitability of Purkinje cells to afferent stimuli is reduced (the phenomenon of dysfacilitation) [18-21].

At the same time, it is known that in certain areas of the cerebellum, in response to electrical or natural stimulation of a number of afferent inputs of visual, muscle receptors, and cutaneous mechanoreceptors, activation of the same Purkinje cell via both mossy and climbing fibers is observed. This led to the conclusion that the functional organization of the cerebellar cortex is such as to require some correspondence between the inputs of the climbing and mossy fibers when impulses of the same modality converge to the Purkinje cell. However, according to Llinas et al., in response to direct irritation of the vestibular nerve, activation of Purkinje cells of the vestibulo-cerebellum is carried out only through mossy fibers [26]. This gave rise to the viewpoint that the afferent inputs of mossy and climbing fibers represent two independent channels of information. At the same time, it was shown that mossy and climbing fibers, which are not activated from visual and vestibular receptors, can converge on the same Purkinje cell of the vestibulocerebellum. However, it was later found that if natural maze stimulation was used, the same Purkinje cell of the rabbit cerebellum could be activated via both mossy and climbing fibers.

It has been found that there is a connection between Purkinje cell activity and saccadic eye movements, with the discharge of Purkinje cells of the worm part of the cerebellum (VI-VII) preceding the onset of eye movements by 11-24 ms, and the maximum of Purkinje cell activity corresponding to the time of eye movement onset [14].

Somatotopic Organization of The of Mossy and Climbing Fiber Entrances

A complete review of the somatotopic representation in the cerebellum can be found in the extensive monograph by Dau and Moruzzi. At present, the greatest interest is in identifying the somatotopic distribution of mossy and climbing fiber inputs in the cerebellar cortex. Unfortunately, data on this subject (extracellular and total registration) are limited mainly to the anterior lobes of the cerebellum. There are a number of summaries and papers dealing with somatotopic representation in the cerebellum. Mossy fiber terminations in the form of sagittal bands 1 mm wide are grouped in the anterior lobe of the cerebellum and belong to four main tracts: proprioceptive and exteroceptive components of the cuneo-cerebellar and dorsal dorsal spinocerebellar tracts; rostral and ventral spinocerebellar tracts; and two spinocerebellar pathways with a break in the lateral reticular nucleus [23-25].

A number of functional features of synaptic transmission in neurons of spinal cerebellar tracts were considered in the works of Kostyuk and Zadorozhny and Pyatigorsky and Vasilenko. The endings of climbing fibers in the form of sagittal bands are also concentrated in the anterior lobes and include 17 pathways of climbing fibers (dorsal-olive-brain) passing through the inferior olive. The hind limbs project into the rostral part of the anterior lobe of the cerebellum and the anterior limbs into the caudal part, and in the wormlike part, of the three sagittal bands, two represent the hind limbs and one (medial) represents the anterior limbs. In the intermediate part of the anterior lobe, in addition, there is one mixed area in which all limbs are represented. A similar type of distribution in the cerebellum has been shown when the anterior and posterior limb areas of the sensorimotor cortex are irritated. Each narrow sagittal stripe represents a functional center integrating activity

that represents motor function, which is different for different zones. It has been shown that each sagittal stripe of the mossy fiber input is strictly connected to the climbing fiber input, and both of these inputs can report to the Purkinje cell changes in the periphery of the motor apparatus [16].

Efferent Systems of The Cerebellum

Of the five types of neurons in the cerebellar cortex, four are inhibitory, including the only efferent neurons, the Purkinje cells. Therefore, at the output of the cerebellar cortex, the mechanism of restraining its activity, the mechanism of inhibition, rather than the mechanism of triggering the next neuron in the reflex chain acts as the active beginning. This peculiarity imposes its imprint on the construction of the efferent system of the cerebellum; its first two links are in coo-

The inhibitory influence of Purkinje cells is opposed to the tonic excitation of cerebellar nuclei neurons [25-27].

Cortical-Nuclear Projections

Anatomically, the entire mammalian cerebellar cortex is subdivided into three symmetrical longitudinal cortical-nuclear zones: the medial (worm) zone projecting to the medial (fastigial) nucleus and the lateral vestibular nucleus; the intermediate (near-worm) zone projecting to the intermediate nucleus; and the lateral zone projecting to the lateral (dentate) nucleus. The topical principle of the projection of the cerebellar cortex to its nuclei was also revealed in the rostro-caudal direction. The efferent zonal organization of the cerebellar cortex has been shown in embryogenesis and confirmed in the form of homologous zones in the lower standing representatives of the phylogenetic series. Recently, overlap between neighboring projection zones has been found and the projection of one zone to two or three cerebellar nuclei has been shown, which is especially pronounced in the lateral cerebellar zone [17-19]. It is concluded that a gradient of overlap rather than strict boundaries between adjacent longitudinal zones is a general property of the organization of cortical-nuclear projections of the cerebellum. The principle of "multilateral" organization has been put forward, according to which there is a large fractionalization of longitudinal zone projections in the cerebellar cortex. This is consistent with the data on the fine topical distribution of Purkinje cell axons in cerebellar nuclei.

Quantitative analysis of morphological data has shown that each of the two or three terminal branching axons of Purkinje cells has 160-200 terminals. Their total number in all cerebellar nuclei reaches 5.7×10^7 and they form 11600 terminals on each nuclear neuron. Purkinje cell axons account for approximately 60% of the primary terminals terminating on nuclear neurons. It is shown that about 860 Purkinje cells take part in innervation of one nuclear neuron, and axon branches of one Purkinje cell cover 26-39 nuclear neurons [11].

Electrophysiological study of the effects of cerebellar cortex irritation on the impulse activity of nuclear neurons has in principle confirmed the existence of a longitudinal zonal organization of the cerebellum. The fan-shaped character of the organization of cortical-nuclear connections in both rostro-caudal and medio-lateral directions and the absence of a strict boundary between separate longitudinal aeons were shown, which is in agreement with morphological data. Along with this, an extraordinary fractionality and mosaicism of cortical-nuclear influences, the presence of zones of maximum density of projection to an individual nuclear neuron, and convergent-divergent influences of Purkinje cells of the cerebellar cortex were found [30].

Recently, anatomical and electrophysiological methods in cats and monkeys have shown a cerebellar nucleo-cortical projection. This projection is represented by collateral branching of axons of efferent neurons of cerebellar nuclei projecting to extramotile structures. The projection from the nuclei

to the cerebellar cortex is organized according to the topographic principle and is similar in this respect to the cortico-nuclear projection. There is reason to believe that the nucleo-cortical projections end in the granular layer of the cerebellar cortex, as do the mossy fibers. Functionally, this projection may represent an intracerebellar feedback system by which cerebellar output can influence integration in the cerebellar cortex not only through its action on neurons in the trunk nuclei containing cells giving rise to cerebellar afferent fibers, but also directly through afferent nuclear neurons. In this respect it should represent an important complement to the inhibitory cortical-nuclear influence exerted by Purkinje cells [25-27].

The medio-lateral principle of cerebellar organization was confirmed and developed in physiological experiments, which showed that the medial zone is associated mainly with the maintenance of body equilibrium, the intermediate zone with locomotion and the lateral zone with arbitrary movements, i.e., each longitudinal zone acts as a coordinator for a particular type of motor act.

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