The Embryology and Anatomy of the Cerebellum

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Abstract The cerebellum, an important structure in the central nervous system (CNS), controls and regulates motor and non-motor functions. It is located beneath the occipital lobe and dorsal to the brainstem. The cerebellum has a well-defined and highly organized structure which folds in lobes and lobules. The cortex of the cerebellum contains different glial cells and eight neuronal cell types and receives inputs from a variety of regions within the CNS and processes the information in a uniform manner. The cerebellar nuclei projects to a variety of different sites within the CNS to regulate motor and non-motor functions. Although much has been discovered regarding the complex architecture of the cerebellum and circuitry, there are significant gaps in our understanding of the broader role of the cerebellum in brain function. This chapter will briefly review the cerebellar embryology and provide an overview of anatomy of the cerebellum.

Keywords Cerebellum · Embryology · Anatomy · Histology · Function

Introduction

Recently, the cerebellum (Latin: “little brain”) has drawn the attention of more neuroscientists because not only does the cerebellum involve in motor functions (the regulation of posture, motor coordination, balance, and motor learning) but it also plays a role in non-motor functions such as emotion and cognition. In addition, the

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cerebellum is considered as an outstanding model in the research of neurogenesis and circuit assembly because of its well-organized structure. The cerebellum is a complex organ which makes it difficult to understand its functions and disorders.

First, this chapter briefly reviews the embryological development of this important organ in the posterior cranial fossa. Then, the subdivision of the cerebellum will be elaborated in which the anatomical description subdivides it into lobes, lobules, folia, and zones. There are many different cerebellar subdivisions, as the cerebellum has a unique anatomical organization. On the superior aspect, the cerebellum consists of the midline region referred to as the vermis, a narrow paravermal area immediately adjacent to the vermis, and large hemispheres on either side. Well-defined fissures divide the cerebellum in a rostrocaudal direction into an anterior lobe, posterior lobe, and flocculonodular lobe. The anterior and posterior lobes are divided further, into lobules and folia (in human), which greatly increases the surface area of the cerebellum (Fig. 1a, b). Next, the phylogenetic description subdivides the cerebellum into three functional divisions: the vestibulocerebellum, spinocerebellum, and cerebrocerebellum. The cerebellum consists of a uniform layer of cortical gray matter overlying white matter that surrounds four pairs of cerebellar nuclei (CN). The cerebellar cortex consists of three layers from outer to inner: molecular layer, Purkinje cell layer, and granular layer, and CN will be explained in more detail. Finally, connection of the cerebellum to the brainstem via three peduncles (superior, middle, and inferior) and blood supply of the cerebellum will be explained.

Embryology of the Cerebellum

During prenatal development of the nervous system, the central nervous system originates from the area of the ectoderm known as the neural plate. The neural plate thickens as a result of cell proliferation, and then begins to invaginate and thus forms the neural groove. The invagination of the neural groove continues until the lateral edges of the neural groove (neural fold) fuse to form the neural tube through a process referred to as neurulation. As the edges of the neural groove fuse to form the neural tube, which detaches from the ectoderm, a population of the neuroectodermal cells dissociate from the neural fold named neural crest cells [1]. During the third week of embryogenesis, the rostral extent of the neural tube develops into the prosencephalon, mesencephalon, and rhombencephalon. The prosencephalon

Fig. 1 (continued) (**c**) Schematic representation of the cerebellum showing the mossy fibers and climbing fibers convey information to the cerebellar cortex. The mossy fibers synapse on the granule cells and send collaterals to the cerebellar nuclei while the climbing fibers terminate on the dendrites of the Purkinje cells and may also send projections to the cerebellar nuclei. The granule cells project to the molecular layer and bifurcate to form the parallel fibers that contact the Purkinje cell dendrites as well as the basket cells and stellate cells. The Golgi cells receive input from mossy fibers and also project into the molecular layer of the cortex

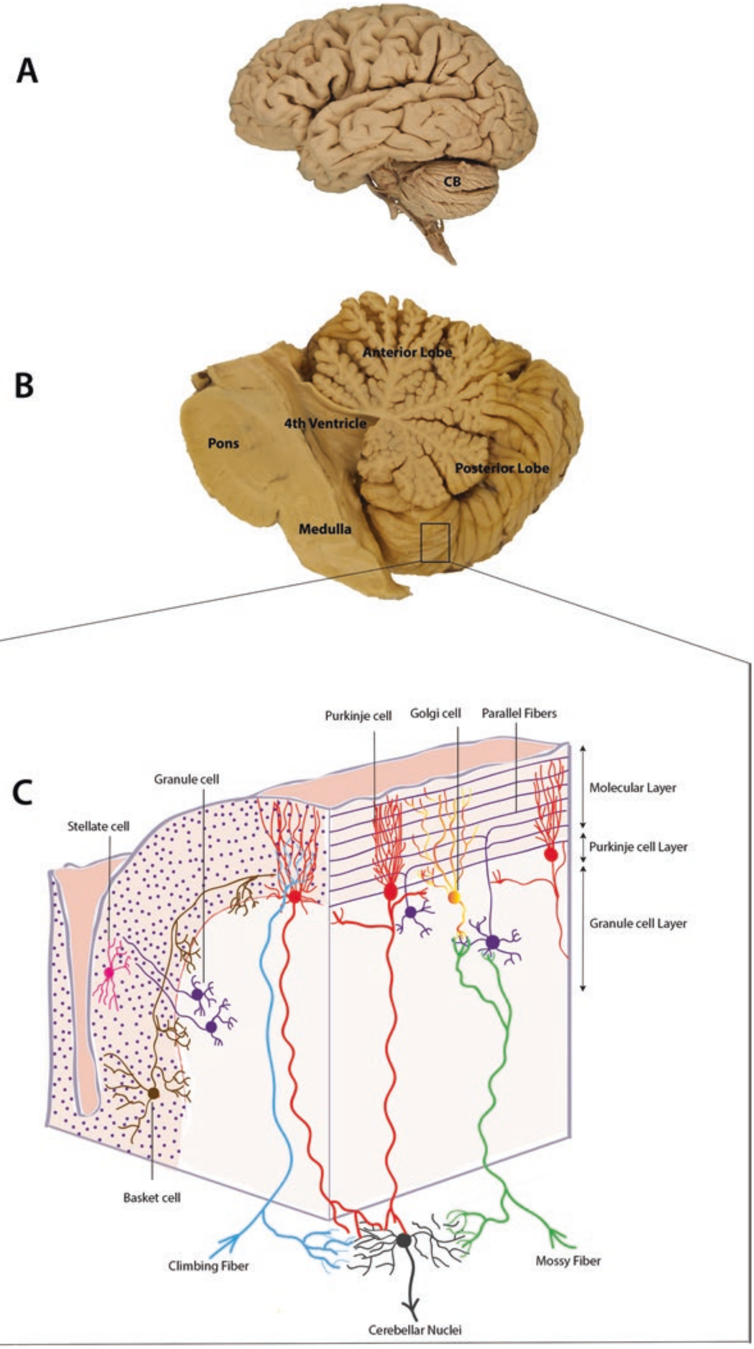

Fig. 1 (**a**) Location of the cerebellum *in situ*. (**b**) Hemisected view of the cerebellum showing the vermis, the locations of the anterior and posterior lobes, and its anatomical relationship to the brainstem.

(continued)

undergoes further development to form the telencephalon and diencephalon. The mesencephalon does not undergo further division while the rhombencephalon is divided into the metencephalon and myelencephalon. Caudal to the rhombencephalon, the neural tube develops into the spinal cord.

The cerebellum develops from the dorsal portions (i.e., the alar plate) of the metencephalon and the neural folds, the latter referred to as the rhombic lips. The alar plate of the rostral metencephalon undergoes bilateral expansion in the dorsolateral region to form the rhombomere 1 (r1). These rostral extensions of alar plate eventually join in the midline to form the vermis of the cerebellum. As the cerebellum begins to form, initially from the dorsal r1, it rotates 90° before fusing at the midline as the vermis. This rotation of dorsal r1 results in the conversion of rostrocaudal axis seen in the early neural tube, into the mediolateral axis seen in the mature cerebellum (the wing-like bilateral cerebellar primordia) [2]. As the bilateral cerebellar primordia fuse, the midline vermis is derived from the rostromedial ends while the cerebellar hemispheres are derived from the more caudolateral components of the rhombencephalon [3].

The neurons that reside within the cerebellum are derived from two distinct germinal zones: the ventricular zone and the rhombic lip. The ventricular zone is the neuroepithelium of the alar plate of the rhombencephalon that eventually forms the roof of the fourth ventricle. The neurons derived from the ventricular zone includes the Purkinje cells, candelabrum cells, Golgi cells, Lugaro cells, stellate cells, and basket cells. All of these neurons produce gamma-aminobutyric acid (GABA) neurotransmitter and reside in the two outer layers of the cerebellar cortex, Lugaro cells locate between the molecular layer and the granular layer, and Golgi cells within the granular layer. The neurons derived from the rhombic lip produce glutamate neurotransmitter, which includes the large excitatory neurons of the CN (projecting to the diencephalon and brainstem), unipolar brush cells and granule cells (the most numerous cells in the brain) [4, 5].

Anatomy and Histology of the Human Cerebellum

Gross Anatomy and Internal Structure of the Cerebellum

Cerebellum in the posterior cranial fossa, anteriorly separated from the pons and the medulla by the fourth ventricle, and superiorly separated from the occipital lobe by the Tentorium Cerebelli (Fig. 1a, b). Anatomically, cerebellum consists of two large bilateral hemispheres which are merged together by a median part called vermis. Morphologic and phylogenetic descriptions subdivide cerebellum differently.

Cerebellum consists of outer grey matter (cerebellar cortex) and inner grey matter (CN) which is embedded in white matter. The white matter consists of afferent and efferent fibers has branched to form a tree-like appearance, so-called the arbor vitae (tree of life). Afferent and efferent fibers pass through three cerebellar peduncles that emerge in the hilum of the cerebellum. All the aforementioned structures have been elaborated under following titles [6–8].

Subdivisions of the Cerebellum

The morphological description subdivides the cerebellum into lobes, lobules, folia, and zones. Fissures divide the cerebellum into three lobes in the rostrocaudal plane. The primary fissure, seen on the superior surface of the cerebellum, separates the anterior lobe from the posterior lobe, while the posterolateral fissure, seen on the inferior surface of the cerebellum, separates large posterior lobe from narrow and much smaller flocculonodular lobe. The flocculonodular lobe consists of bilateral extensions of cerebellar cortex called flocculi that are connected to the inferior portion of the vermis called the nodulus. During development, once the anterior and posterior lobes form, smaller "lobules" begin to form. Several anatomical fissures divide the cerebellar lobes into 10 smaller lobules (lobule I to X) in which enumeration is based on the Schmahmann classification. Lobular subdivisions of cerebellum are described in Table 1 [9, 10]. The lobules undergo further in folding and leads to the formation of "folia," which are particularly prominent in human cerebellum. It seems that folia of human cerebellum are not uniform in size and shape [11]. The structure of the folia is consistent throughout the cerebellum, with a three-layered cortex overlying the white matter consisting of the axons projecting to and from the cortex. It is noteworthy that some folia have their own white matter (core of the folium). Cerebellar folium has crown (apex) and walls (lateral surfaces) separating from the neighbor folia by fissures (interfolial) called "fundi" [11]. Zones are distinct: (i) medial or vermal zone, (ii) intermediate or paravermal zones on either side of vermal zone, and (iii) hemispherical zones on either side lateral to the paravermal zones.

As mentioned before, the phylogenetic description subdivides the cerebellum into three functional divisions: the vestibulocerebellum (archicerebellum), spinocerebellum (paleocerebellum), and pontocerebellum or cerebrocerebellum

Table 1 Lobular subdivisions of cerebellum. Enumeration is per the Schmahmann classification

Lobes	Subdivisions of vermis	Lateral extensions in hemispheres
Anterior lobe	I (Lingula)	Frenulum
	II–III (Central lobule)	Ala
	IV–V (Culmen)	Quadrangular lobule
Posterior lobe	VI (Declive)	Lobule Simplex
	VIIA (Folium)	Superior semilunar lobule (Crus I)
	VIIB (Tuber)	Inferior semilunar lobule (Crus II)
	VIII (Pyramid)	Biventral lobule
	IX (Uvula)	Tonsil
Flocculonodular lobe	X (Nodule)	Flocculus

(neocerebellum) [12–16]. This subdivision is based on connections to other brain sites and their respective roles in regulating movement and other non-motor functions.

Vestibulocerebellum is the oldest component of the cerebellum which includes the flocculonodular lobe. The cortex of this lobe receives input via mossy fibers from the vestibular ganglia on the ipsilateral side as well as input from the vestibular nuclei of the brainstem. The connections of the vestibulocerebellar cortex to the vestibular nuclei are reciprocal and the cortex of the vestibulocerebellum is the only component of the cerebellar cortex that sends projections directly to regions outside of the cerebellum. Briefly, the Purkinje cells of the cortex send inhibitory projections to the fastigial nucleus as well as the ipsilateral vestibular nuclei of the brainstem. The fastigial nucleus, which serves as the principal cerebellar nucleus of the vestibulocerebellum, sends excitatory bilateral projections to the vestibular nuclei through the inferior cerebellar peduncle. These projections play an important role in coordinating the vestibular ocular reflex to control eye movement. The vestibular nuclei also send descending fibers within the vestibulospinal tract which play a critical role in maintaining balance through activation of the antigravity muscles of the lower body. The fastigial nucleus also sends ascending projections via the superior cerebellar peduncle to the ventrolateral nucleus of the contralateral thalamus. This information is subsequently relayed to the corticospinal neurons of the anterior corticospinal tract (medial motor system) involved in maintaining posture and balance through activation of the axial musculature. Therefore, the vestibulocerebellum participates in the control of eye movements and maintains posture and balance.

Spinocerebellum is the second functional component of the cerebellum which consists of the midline vermis and a narrow portion of cortex on either side of the vermis referred to as the paravermis. This component is referred to as the spinocerebellum which is bulk of the input provided by ascending tracts in the spinal cord. The spinocerebellum receives some major inputs: (i) the dorsal spinocerebellar tract that transmits proprioceptive, cutaneous, and pressure information from the lower trunk and lower extremity (on the ipsilateral side); (ii) input from the cuneocerebellar tract, which carries somatosensory information from the upper trunk and upper extremity; (iii) input from the ventral spinocerebellar tract that transmits information regarding the activity of circuits within the spinal cord involved in regulating motor activity; and (iv) inputs from a number of brainstem nuclei including the reticular formation. The Purkinje cell axons of the paravermis project to the interposed nuclei which in turn project to both cerebral cortex and the brainstem are involved in regulating the limb musculature and the activity of the spinal cord motor neurons projecting to the upper and lower limbs, respectively. The vermis project to fastigial nuclei are primarily involved in regulating axial musculature. Thus, the spinocerebellum participates in regulating both axial and limbs musculature to control balance, posture, and locomotion.

Pontocerebellum (cerebrocerebellum or neocerebellum) is the largest and phylogenetically newest component of the cerebellum which consists of the large hemispheres immediately lateral to the spinocerebellum. The pontocerebellar cortex receives input principally from the contralateral cerebral cortex, particularly frontal and parietal lobes, via the pontine nuclei forming cortico-ponto-cerebellar pathways. The axons of Purkinje cells in the pontocerebellar cortex project to the dentate nuclei. Some fibers of pontocerebellum project to the cerebral cortex (premotor and primary motor cortices) via ventrolateral thalamus, and the descending neurons from the cerebral cortex form a large component of the lateral motor system. Some other fibers project to the inferior olivary nucleus of the medulla, via the red nucleus which projects back to the pontocerebellum and dentate nucleus forming a feedback loop to the cerebellum. The neocerebellum is particularly well developed in higher mammals and play a critical role in coordinating the muscle activation required for performing fine motor skills of the distal extremities (particularly upper limb), planning of motor activity, and cognitive functions.

Cerebellar Cortex

The cortex of the cerebellum is remarkable in its uniformity and segregates into three layers: the outer molecular layer, the Purkinje cell layer, and the inner granule cell layer [14, 15].

The Molecular Layer This layer contains of stellate cells and basket cells but is dominated by the dendrites and axons of other neurons. It receives input from neurons of the inferior olivary nucleus of the medulla, and these fibers are referred to as climbing fibers. The climbing fibers make abundant excitatory synaptic connections with the proximal dendritic tree of Purkinje cells (Fig. 1c) [8]. The molecular layer also receives abundant excitatory input from the granule cells of the cerebellar cortex. Granule cells send their axonal projections to the molecular layer cortex where the axons bifurcate and form parallel fibers that run parallel to the cortical surface and make synaptic connections with the dendritic tree of numerous Purkinje cells (Fig. 1c). The stellate cells of the molecular layer are inhibitory interneurons that produce GABA neurotransmitter and these cells are located primarily in the outer part of the molecular layer. These cells also receive input from parallel fibers and make synaptic contacts with the dendritic tree of Purkinje cells. Finally, the basket cells of the molecular layer are also GABAergic neurons and are located in the inner portion of the molecular layer. Basket cells receive excitatory input from the parallel fibers of the granule cells and make abundant inhibitory connections on the cell bodies of Purkinje cells in a basket-like manner.

The Purkinje Cell Layer This layer consists of the large cell bodies of the Purkinje cells and candelabrum cells [17]. Purkinje cells send an extensive dendritic tree into the molecular layer. The dendritic tree of a single Purkinje cell receives excitatory inputs from a single climbing fiber of the inferior olivary nucleus and numerous inputs from parallel fibers of the granule cells. The Purkinje cell is of particular importance because it represents the sole output of the cerebellar cortex. They are GABAergic and projects almost solely to the CN [18]. The exception to this rule is the Purkinje cells of the vestibulocerebellum that also project to the vestibular nuclei of the brain stem. Interspersed between the Purkinje cells within this layer are candelabrum cells that are also GABA-ergic neurons that send their dendritic projections into the molecular layer. The functional significance of these cells is poorly understood.

The Granule Cell Layer This layer is the innermost layer of the cortex and consists of granule cells, Golgi cells, unipolar brush cells, and Lugaro cells. The granule cells, developed from upper rhombic lip, are the most abundant neurons (99% of cerebellar neurons) in the human nervous system and are packed tightly within the granule cell layer [4]. They receive excitatory input from mossy fibers, which are the principal input into the cerebellum (Fig. 1c). Mossy fibers originate from numerous sites within the nervous system, including pontine nuclei, nuclei of the reticular formation, vestibular nuclei, and the fibers of the spinocerebellar tracts of the spinal cord. The granule cells, which produce glutamate neurotransmitter, extend their axons into the molecular layer where they bifurcate into the aforementioned parallel fibers and connect with the dendritic tree of up to hundreds of Purkinje cells. The activity of the granule cells plays a critical role in determining the activity of the Purkinje cells. Additionally, the parallel fibers of the granule cells also shape the activity of other cell types of the cerebellar cortex, including Golgi, stellate, and basket cells. The Golgi cells are relatively large cells that are more abundant in the superficial portion of the granule cell layer, nearer to the Purkinje cell layer. These are also GABA-ergic neurons that extend their dendrites into the molecular layer where they receive synaptic input from the parallel fibers of the granule cells. The Golgi cells also make synaptic connections to the granule cell dendrites, thereby providing a source of inhibition to the granule cells (Fig. 1c). Unipolar brush cells are neurons within the superficial part of the granule cell layer, and like granule cells are glutamatergic neurons. These cells are more abundant in the vestibulocerebellum than other parts of the cerebellum, and are closely associated with mossy fibers project to granule cells and other unipolar brush cells. The final cell intrinsic to the cerebellar cortex is the Lugaro cell. These are GABA-ergic neurons found primarily in the superficial portion of the granule cell layer. Their dendrites may extend into the molecular layer while their axon is restricted to the granule cell layer where they make connections with Golgi cells.

The cerebellar cortex also receives projections from a variety of areas of the brain including the locus coeruleus (noradrenergic fibers), raphe nuclei (serotonergic fibers), mesencephalic tegmentum (dopaminergic fibers), and the hypothalamus (histaminergic fibers) [16]. These inputs to the cerebellum terminate in all three layers of the cerebellar cortex as well as the CN. These projections to the cerebellum are commonly referred to as neuromodulatory cerebellar afferents and are thought to decrease the activity of Purkinje cells. The precise distribution and development of these afferents' projection to the cerebellum is not well understood. Within the cerebellar cortex, the connections and links between the parallel fibers of granule cells and the dendrites of inhibitory cells such as Purkinje cells, and also connections between the mossy fibers, Purkinje cells, and other neurons, makes a unique and uniform microcircuitry observed with great consistency in all parts of the cerebellar cortex.

Cerebellar Nuclei (CN)

There are four pairs of CN embedded within the white matter of the cerebellum (fastigial, interposed (consists of emboliform and globose nuclei), and dentate nuclei) that receive input from the cerebellar cortex as well as the collaterals of all fibers projecting to the cerebellar cortex [16]. The first generated cerebellar neurons are neurons of the CN. These cells originate from the rhombic lip and migrate tangentially to the nuclear transitory zone (NTZ). The CN constitute the sole output of the cerebellum (excepting some of the Purkinje cells of the vestibulocerebellum) and they receive the output of the cerebellar cortex from the inhibitory Purkinje cells. In addition to the inhibitory inputs from the Purkinje cells, the CN receive the collateral excitatory inputs from mossy fibers and climbing fibers projecting to the cortex. The majority of CN neurons are excitatory neurons that project to sites outside the cerebellum, including the thalamus, red nucleus, reticular formation, and vestibular nuclei. However, a small population of CN neurons are GABA-ergic and these neurons project to the inferior olivary nucleus.

The Fastigial Nucleus This nucleus is the smallest and most medial CN. The neurons of this nucleus receive input from the Purkinje cells of the vestibulocerebellum. (i.e., flocculonodular lobe). In addition, it receives input from Purkinje cells of the vermis that receive input from the vestibular ganglion directly or indirectly via the vestibular nuclei. The neurons of the fastigial nucleus project to the vestibular and reticular nuclei in the brainstem. As mentioned previously, some of the Purkinje cells of the flocculonodular lobe also send direct (inhibitory) projections to vestibular nuclei of brainstem.

The Interposed Nucleus It is located lateral to the fastigial nuclei in the paravermis, and composed of the globose nucleus (located medially) and the emboliform nucleus (located laterally), also referred to collectively as the interposed nuclei. These nuclei receive input from the Purkinje cells of the vermis and paravermal areas of the anterior lobe of the cerebellum, which in turn receive input from the cuneate nucleus (via the cuneocerebellar tract), the accessory cuneate nucleus, and Clarke’s nuclei (via the dorsal spinocerebellar tract). The interposed nuclei send projections primarily to the red nucleus of the midbrain and the ventrolateral nucleus of the thalamus. The latter nucleus relays this information to the primary motor, supplementary motor, and premotor cortices of the frontal lobe.

The Dentate Nucleus It is the largest and most lateral of the CN. It receives inhibitory input from the Purkinje neurons of the large lateral hemispheres and excitatory input from the collaterals of the climbing fibers and mossy fibers projecting to the lateral hemispheres that have their origin in the inferior olivary and basilar pontine nuclei, respectively. The neurons of the dentate nucleus project to the red nucleus and the ventrolateral nucleus of the thalamus, which relays the information to the motor cortices of the frontal lobe.

Cerebellar Peduncles

The cerebellum connects to the midbrain, pons, and medulla via three peduncles: the superior, middle, and inferior cerebellar peduncles, respectively [16].

The Superior Cerebellar Peduncle It consists primarily of efferent fibers from the dentate and interposed nuclei projecting to the contralateral red nucleus and ventral lateral nucleus of the thalamus. The cerebellar efferents of the spinocerebellum that project to nuclei of the reticular formation also pass through this peduncle. The cerebellar afferent contained within this peduncle are primarily fibers of the ventral spinocerebellar tract that project as mossy fibers to the granular layer of the spinocerebellum and send collateral branches to the interposed nuclei.

The Middle Cerebellar Peduncle It is a massive bundle of afferent fibers connecting nuclei in the basilar pons to the contralateral cerebellar cortex. These fibers project as the mossy fibers to the granular layer of the large lateral hemispheres and send collateral branches to the dentate nucleus.

The Inferior Cerebellar Peduncle It contains of fibers connecting the cerebellum to the medulla and consists of the restiform body and the juxtarestiform body. The juxtarestiform body primarily consists of the reciprocal connections of the cerebellum and the vestibular nuclei. The afferent fibers within the juxtarestiform body form the mossy fibers projecting to the granular layer of the vestibulocerebellum. The efferent fibers of the juxtarestiform body include Purkinje cell axons of the vestibulocerebellum and the projections of the fastigial nucleus to vestibular and reticular nuclei of the brainstem. The restiform body contains fibers that project from the brainstem and spinal cord to widespread areas of the cerebellum. This includes fibers of the dorsal spinocerebellar tract and cuneocerebellar tract projecting to the spinocerebellar cortex as mossy fibers with collateral projections to the interposed nuclei. In addition, fibers originating from the inferior olivary nucleus projecting to the molecular layer of the cerebellar cortex known as climbing fibers (with collateral projections to the dentate nucleus) are also contained within the restiform body. The inferior olivary nucleus receives inputs from spinal, vestibular, cranial, and cortical descending signals. The neurons of the inferior olivary nucleus relay somatosensory and noxious stimuli. A single climbing fiber of the inferior olivary nucleus projects to a few Purkinje cells, while each Purkinje cell makes synaptic connections with only one climbing fiber.

Blood Supply of the Cerebellum

The cerebellum is supplied with arterial blood via three cerebellar arteries: the posterior inferior cerebellar artery (PICA), the anterior inferior cerebellar artery (AICA), and the superior cerebellar artery (SCA) [15, 16]. These arteries are derived from the vertebral-basilar arterial system that supplies the posterior circulation of the brain.

Posterior Inferior Cerebellar Artery (PICA) The bilateral vertebral arteries pass through the foramen magnum and shortly after entering the cranium the PICA branches off the vertebral artery. The PICA supplies the cortex of the posterior portion of the inferior cerebellum, and the inferior portion of the underlying white matter. It also supplies the fibers of the inferior cerebellar peduncle.

Anterior Inferior Cerebellar Artery (AICA) The vertebral arteries fuse in the midline, near the junction of the pons and the medulla, to form the basilar artery and the AICA branches off the basilar artery immediately anterior to this junction. The AICA supplies the cortex of the anterior portion of the inferior cerebellum and the underlying white matter. Distal branches of the AICA may extend into the lateral portion of the dentate nucleus. The AICA also supplies the posterior part of the middle cerebellar peduncle while circumferential branches of the basilar artery supply the anterior portion of the middle cerebellar peduncle. The most lateral edge of the inferior surface of the cerebellum is generally the watershed area of the PICA and the AICA.

Superior Cerebellar Artery (SCA) The SCA branches off the basilar artery immediately posterior to the bifurcation of the basilar artery into the paired posterior cerebral arteries. The SCA supplies the superior surface of the cerebellum and the bulk of the white matter of the cerebellum. It also supplies the CN except for the lateral portion of the dentate nucleus that may be supplied by the AICA. The SCA also supplies the superior cerebellar peduncle together with branches of the posterior cerebral artery.

Conflicts of Interest The authors confirm there is no conflict of interest.

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