



# A Brief History of the Cerebellum

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## Abstract

Cerebellar structure and function have intrigued investigators and clinicians for millennia. Major anatomic features were recognized early, and the role of the cerebellum in coordinating movements was established two centuries ago. Cerebellar involvement in nonmotor functions was described in clinical and experimental observations starting around the same time, but attention to their importance rose to the fore only recently. Functional localization was first derived from comparative morphology. Ablation degeneration and physiological studies in animals and neurological observations in patients with focal injury led to the lobular theory of organization. This was refined by delineation of the mediolateral parasagittal zonal organization of cerebellar connections. Histological studies date back to Cajal, with descriptions of additional neuronal elements and circuitry evolving over the years. Recognition of the cerebellar cognitive affective syndrome and the neuropsychiatry of the cerebellum, observations from connectional neuroanatomy, and advances in anatomic, task-based, and functional connectivity magnetic resonance neuroimaging provide contemporary support for the earliest notions that the cerebellum is engaged in a wide range of neurological functions. Together with new theories of cerebellar function, and elucidation of the genetic basis of inherited or sporadic ataxias and neurobehavioral disorders, the cerebellum has become increasingly relevant to contemporary clinical neurology and neuropsychiatry.

## Keywords

Historical background · Cerebellum · Ataxia · Dysmetria  
Cognition · Vestibular

The cerebellum has been recognized since antiquity. Notions regarding its functions included the belief that it imparted strength to the motor nerves (Galen A.D. 129/130–200/201), was a center for memory (Nemesius, c.A.D. 390, and Albert von Bollstädt/Albertus Magnus 1193–1280), controlled sensory functions including unconscious sensibility (Co(n) stanzo Varolio/Variolus 1543–1575), was involved with involuntary activity including the functions of the heart and respiration (Thomas Willis 1621–1675), and was the seat of amative love (Franz Joseph Gall 1758–1828) (Neuburger 1897/1981; Clarke and O'Malley 1996; Schmammann and Pandya 2006). As is apparent from the historical account below, the conclusions of these pioneers, although based on flimsy or fanciful evidence, were rather prescient.

## 2.1 Early and Evolving Views of Cerebellar Organization and Function

Rolando (1809) first demonstrated that ablation of the cerebellum results in disturbances of posture and voluntary movement. Fodéra (1823) showed the release of postural mechanisms, and extensor hypotonia following acute cerebellar injury in pigeons, guinea pigs, and rabbits. Flourens (1824) showed in pigeons that the cerebellum is responsible for the coordination, rather than generation, of voluntary movement and gait, a concept that has remained the guiding principle of cerebellar function. François Magendie's (1824) lesion studies led to the understanding that the cerebellum is essential for equilibrium. Disturbances of motor control following focal cerebellar lesions in monkeys were demonstrated by Luciani (1891), Ferrier and Turner (1893), and Russell (1894).

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Comparative anatomists such as Lodewijk “Louis” Bolk (Bolk 1902; Glickstein and Voogd 1995) derived structure–function correlations by comparing the size of a cerebellar region with the characteristics of the species to which it belonged. They concluded that the vermis coordinates bilateral symmetrical movements, the cerebellar hemispheres coordinate unilateral movements of the limbs, and the development of manual dexterity corresponded with the expansion of the lateral cerebellar hemispheres. The lobular theory (Fulton and Dow 1937; Larsell 1970; Brodal 1967; see Angevine et al. 1961) held that the cerebellum is functionally organized into lobes. The flocculonodular lobe, archicerebellum, and vestibulocerebellum became synonymous. The anterior lobe, pyramis, and uvula in the vermis of the posterior lobe, and the paraflocculus were termed the paleocerebellum or spinocerebellum. The lateral parts of the cerebellar hemispheres and the middle portion of the vermis were termed the neocerebellum or pontocerebellum.

Ablation-degeneration studies in animals (Jansen and Brodal 1940; Chambers and Sprague 1955a, b) introduced the concept of the organization of the cerebellum into three bilaterally symmetrical longitudinal corticonuclear zones. These studies (see Dow and Moruzzi 1958 for review) showed that the medial zone (vermis and fastigial nucleus) regulates vestibular function and the tone, posture, locomotion, and equilibrium of the body, with somatotopic localization in the vermal cortex – the head, neck, and eyes at the posterior vermis, the tail and lower limbs at the rostral aspect of the anterior vermis, and the upper limbs situated in between. The intermediate zone (paravermal cortex and nucleus interpositus) regulates spatially organized and skilled movements and the tone and posture associated with these movements of the ipsilateral limb, and lesions in the intermediate zone produced motor deficits including tremor, ataxia, and postural instability. The lateral zone (hemispherical cortex and dentate nucleus) was thought to be involved in skilled and spatially organized movements of the ipsilateral limbs, although lateral hemispheres or dentate nucleus lesions produced only minor impairments of the distal extremities, without clear somatotopic organization. Dow (1942, 1974) identified the dentate nucleus in man and anthropoid apes as consisting of two parts, a dorsomedial microgyric, magnocellular older part homologous to the dentate nucleus of lower forms, and an expanded new part comprising the bulk of the dentate nucleus, the ventrolateral macrogyric parvicellular part. He postulated that the newer “neodentate” expanded in concert with, and was connected to, the frontal, temporal, and parietal association areas of

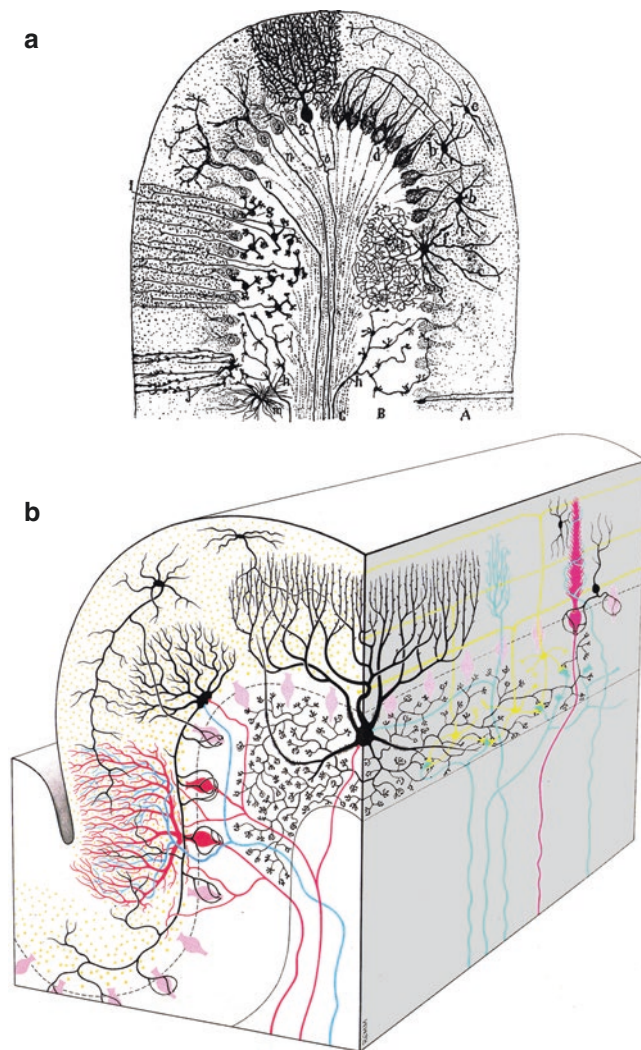
higher primates and man, an idea he later expanded upon with Leiner et al. (1986).

The study of the cerebellar role in nonmotor functions has a rich history (see Schmammann 1991, 1997a, b, 2010 for review and citations). Physiological and ablation studies demonstrated cerebellum to be engaged in autonomic functions such as pupil diameter, blood pressure, and sleep wake cycle. Cerebellar stimulation influenced the size of stroke following middle cerebral artery ligation in rats, produced generalized arousal of the electroencephalogram, evoked hyperactivity in monkeys and cats, and produced complex behaviors including grooming, predatory attack, aggression, and sham rage. Studies also showed the cerebellum to be essential for conditional associative learning including fear-conditioned bradycardia in the rat and the nictitating membrane response in rabbits, in addition to its role in spatial navigation and visual-spatial learning.

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## 2.2 Cerebellar Cortex

Jan Evangelista Purkyně (1787–1869) described the cell that would come to bear his name (Purkyně 1837), and Ramón y Cajal (1909) provided the first detailed description of the neuronal architecture of the cerebellar cortex, including mossy fibers, granule cell glomeruli, and parallel and climbing fibers (Eccles et al. 1967; Palay and Chan-Palay 1974; Brodal et al. 1975) (Fig. 2.1). Later investigators described Lugaro cells (Fox 1959; Palay and Chan-Palay 1974) and unipolar brush cells in the vestibulocerebellum (Mugnaini and Floris 1994). Using acetylcholinesterase, Voogd and colleagues (Voogd 1967, 1969; Marani and Voogd 1977) demonstrated parasagittal zonal organization in cerebellar white matter: zones A and B at the vermis, paravermal zones C1, 2, and 3, and zones D1 and 2 in the hemispheres. Hawkes and colleagues (Gravel and Hawkes 1990) demonstrated this zonal pattern in the cortex using monoclonal antibodies. Histochemical markers confirmed these parasagittal zones, each with topographically arranged connections with the deep cerebellar nuclei (Haines 1981) and inferior olive (Groenewegen and Voogd 1977; Hoddevik and Brodal 1977; Groenewegen et al. 1979). The demonstration of fractured somatotopy in sensory projections to cerebellum (Shambes et al. 1978; Bower and Kassel 1990) is consistent with the observation that Purkinje cells (PCs) can be activated by the ascending axons of granule cells (Llinas 1984; Cohen and Yarom 1998) as well as by beams of parallel fibers.



**Fig. 2.1** General organization of the cerebellar cortex. (a) Santiago Ramón y Cajal (1911/1995) diagram of the neurons in the cerebellar cortex-oriented perpendicular to the long axis of the folium, as well as fibers and glial cells. A molecular layer, a Purkinje cell, B granular layer, b basket cell, C white matter of the folium, d pericellular baskets around the PC soma formed by the basket cell axon, e superficial stellate cell, f Golgi cell, g granule cell, h mossy fiber, i ascending axon of granule cell, j Bergmann glial cell, m astroglial cell, n climbing fiber, o recurrent collateral branches of a PC. (b) Diagram redrawn from Eccles et al. (1967) in Gray's Anatomy (1995). A single cerebellar folium is shown sectioned in its longitudinal axis (diagram right) and transversely (left). Purkinje cells are red; superficial and deep stellate, basket and Golgi cells are black; granule cells and ascending axons and parallel fibers are yellow; mossy and climbing fibers are blue. Also shown are the glomeruli with mossy fiber rosettes, claw-like dendrites of granule cells, and Golgi axons. Lugaro and unipolar brush cells are not shown (Figures reproduced with permission)

## 2.3 Connectional Anatomy

Myelin and degeneration studies in the nineteenth and early twentieth centuries revealed that cerebellar connections with spinal cord, vestibular system, brainstem, and cerebral cortex are topographically arranged. Bechterew (1888) showed that the caudal pons is linked with the cerebellar anterior lobe, but rostral pons is linked with the cerebellar posterior lobe. Sherrington's (1906) physiological studies showed cerebellar afferents from the proprioceptive system (he viewed cerebellum as the “head ganglion of the proprioceptive system”), and others showed topographically arranged inputs to cerebellum following proprioceptive, cutaneous (Dow and Anderson 1942; Snider and Stowell 1942; Hampson et al. 1952) vagal, visual, and auditory stimulation (Snider and Stowell 1942; Dow and Moruzzi 1958).

Cerebellar somatotopy was subsequently confirmed in anatomical and physiological investigations of afferents to the cerebellum from the spinal cord (Chambers and Sprague 1955a, b; Grant 1962a, b; Oscarsson 1965), with spinocerebellar tracts terminating exclusively in the anterior lobe and lobule VIII (sensorimotor areas of cerebellum). Spinal-recipient olivary nuclei project to sensorimotor cerebellum (anterior lobe and lobule VIII), whereas most of the principal olive (devoid of spinal afferents) projects to the cerebellar posterior lobe (Oscarsson 1980; Ruigrok et al. 1992; Groenewegen et al. 1979).

Anatomical studies of the feedforward loop of the cerebrocerebellar system (Brodal 1978; Glickstein et al. 1985; see Schmähmann 2004), and electrophysiological experiments of the cerebrocerebellar system (Henneman et al. 1952; Sasaki et al. 1975; Allen and Tsukahara 1974) demonstrated predominantly motor connections of cerebellum in a topographically precise manner. Studies also linked cerebellum with limbic structures – hippocampus, septum, and amygdala (Maiti and Snider 1975; Heath and Harper 1974), the hypothalamus (Haines et al. 1997), and the ventral tegmental area (Snider and Maiti 1976) that gives rise to the mesolimbic dopaminergic system critical for behavioral modulation (Carta et al. 2019). Anterograde isotope studies of cortico-pontine pathways demonstrated precisely arranged inputs from motor and supplementary motor areas (Schmähmann et al. 2004), and also from associative and paralimbic regions of the prefrontal, posterior parietal, superior temporal, and parastriate cortices concerned with higher order functions (Schmähmann and Pandya 1997a, 1997b; see Schmähmann

2010). Trans-synaptic viral tracing studies revealed that cerebellar linkage with association areas is reciprocal – cerebral areas that project via pons to cerebellum in turn receive projections back via thalamus from the cerebellum (Middleton and Strick 1994). They also showed that cerebellar anterior lobe and dorsal dentate nucleus are linked with motor cortices, whereas cerebellar posterior lobe and ventral dentate nucleus are linked with prefrontal and posterior parietal regions (Clower et al. 2001; Dum and Strick 2003).

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## 2.4 The Cerebellar Motor Syndrome

Early studies in patients with Friedreich's ataxia, cerebellar cortical atrophy, and penetrating gunshot injuries of the cerebellum (Brown 1892; Marie 1893; Babinski 1899; Holmes 1907) established the critical role of cerebellum in coordination of extremity movement, gait, posture, equilibrium, and speech. Holmes (1939) later analyzed the motor and speech deficits resulting from focal cerebellar injury. Much of Holmes' terminology and neurologic examination remain in contemporary use (see Chap. 3). These clinical studies confirmed in human that the vestibular cerebellum was important for posture and equilibrium, the spinocerebellum for locomotion and extremity movement, and they suggested that the neocerebellum was important for manual dexterity. The anterior superior cerebellar vermis was particularly important for gait. Hypotonicity was a frequent accompaniment of bilateral cerebellar lesions. Lesions involving both cerebellar hemispheres produced characteristic cerebellar dysarthria. More than a century of clinical neurology has further refined the understanding of the cerebellar motor syndrome, and now clinical rating scales are helpful in defining the nature and severity of the motor incapacity.

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## 2.5 The Cerebellar Cognitive Affective Syndrome

From the earliest days of clinical case reporting, at least since 1831 (Combette 1831), instances of mental and intellectual dysfunction were described in the setting of cerebellar pathology (Schmahmann 1991). Sizable posterior lobe strokes may produce only nausea and vertigo at the onset, and gait impairment subsides once the vestibular syndrome improves (Duncan et al. 1975; Schmahmann et al. 2009). Surgically induced dentate nucleus lesions in humans do not produce motor disability (Zervas et al. 1967). Cerebellar abnormalities have been identified in autism (Bauman and Kemper 1985), schizophrenia (Moriguchi 1981; Snider 1982), and attention-deficit disorder (Berquin et al. 1998). Cognitive impairments were noted in patients with cerebellar stroke (Botez-Marquard et al. 1994; Silveri et al. 1994),

cerebellar cortical atrophy (Grafman et al. 1992), and in those with cerebellar developmental disorders (Joubert et al. 1969; see Schmahmann 1991, 1997a). The spinocerebellar ataxias have changes in cognition to varying degrees throughout the course of the illness (Manto 2014); and in children, mutism and subsequent dysarthria occur following excision of cerebellar tumors (Wisoff and Epstein 1984), often accompanied by regressive personality changes, emotional lability, and poor initiation of voluntary movement (Pollack et al. 1995; Levisohn et al. 2000; Gudrunardottir et al. 2016).

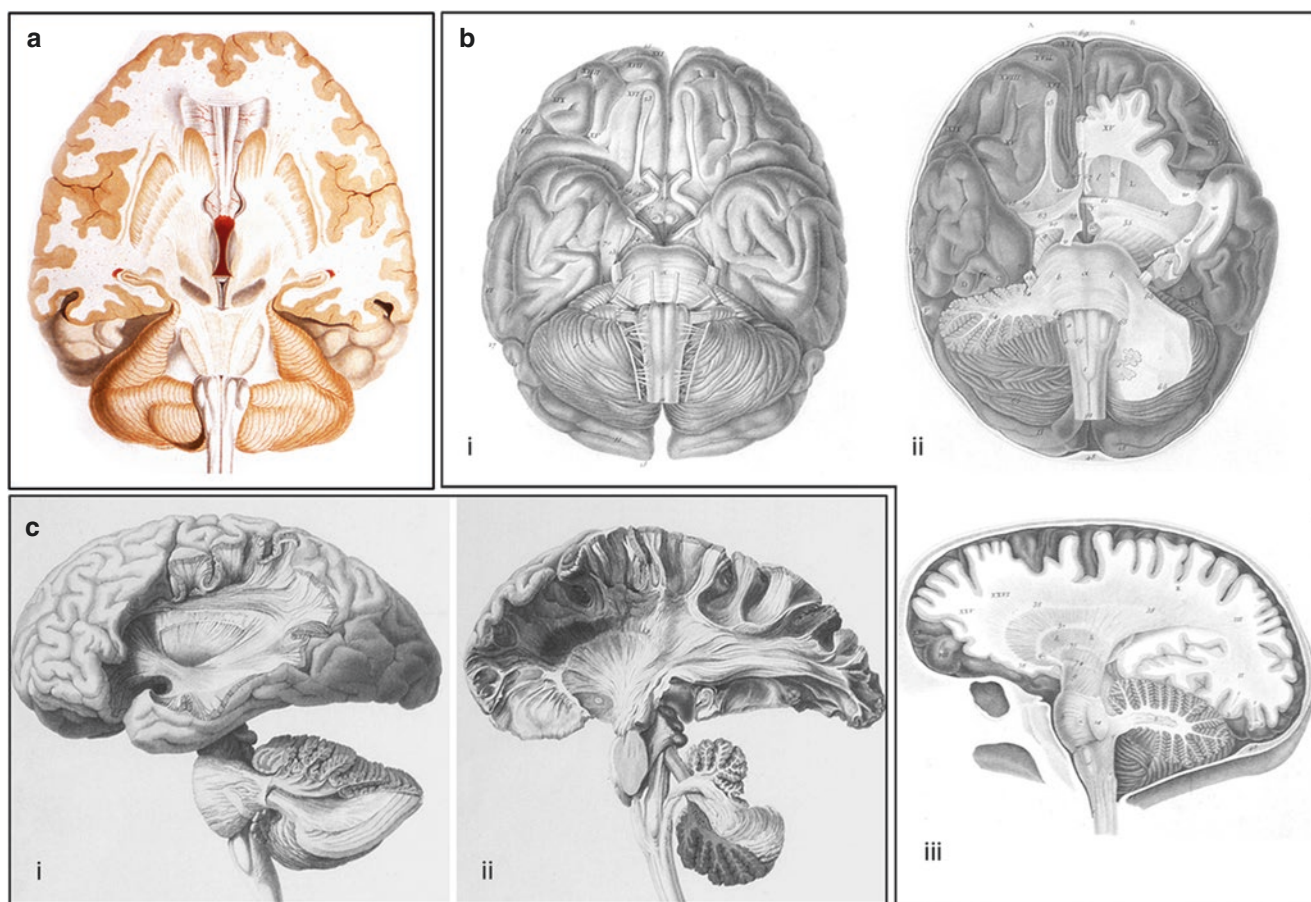
Schmahmann and Sherman (1998) described the cerebellar cognitive affective syndrome (CCAS) in patients with acquired cerebellar lesions characterized by impairment of executive functions such as planning, set-shifting, verbal fluency, abstract reasoning, and working memory; difficulties with spatial cognition including visual-spatial organization and memory; personality change with blunting of affect or disinhibited and inappropriate behavior; and language deficits including agrammatism and dysprosodia. The CCAS occurred following lesions of the cerebellar posterior lobe, and the vermis was usually involved when there was a prominent affective component. The CCAS was then described in children (Levisohn et al. 2000) with a similar pattern of cognitive deficits, the affective changes reflecting damage to the vermis, and it has been replicated widely (e.g., Neau et al. 2000; Riva and Giorgi 2000; Tedesco et al. 2011). Metalinguistic deficits (Guell et al. 2015) are related to impaired social cognition (Hoche et al. 2015), and neuropsychiatric symptoms occur in the domains of attention, mood, social cognition, autism, and psychosis spectrum behaviors (Schmahmann et al. 2007). It is now apparent that there is a double dissociation in the motor vs cognitive dichotomy of cerebellar clinical neurology. Holmes' (1917) cerebellar motor syndrome of ataxia, dysmetria, and dysarthria arises following lesions of the sensorimotor anterior lobe but not the posterior lobe; the CCAS/Schmahmann syndrome (Manto and Mariën 2015) arises from the cognitive – affective posterior lobe, but not the anterior lobe (Schmahmann and Sherman 1998; Levisohn et al. 2000; Schmahmann et al. 2009). The cognitive and limbic consequences of cerebellar injury and the underlying neurobiology and theory of the putative cerebellar role in cognition were crystallized in the 1997 monograph on this topic (Schmahmann 1997b).

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## 2.6 Atlases and Functional Neuroimaging

Vincenzo Malacarne provided the first detailed description of the cerebellum (Malacarne 1776), naming the vermis, lingula, and tonsil. The atlas of Vicq-d'Azur (1786) showed the structure of the cerebellum. Depictions of cerebellum and brainstem were included in drawings by Franz Joseph Gall (Gall and Spurzheim 1810) and Herbert Mayo (1827), and in





**Fig. 2.2** Depictions of the cerebellum by early anatomists. (a) Image from the atlas of Vicq-d’Azyr (1786). His Plate IV includes the cerebellum. The image is flipped vertically, as in the atlas the cerebellum is shown at the top. (b) Images from the atlas of Gall and Spurzheim (Gall and Spurzheim 1810). *i* Gall and Spurzheim’s Plate IV, shows the base of the brain with cerebral hemispheres, cerebellum and brainstem. *ii* Plate XIII, shows dissections of the cerebral hemisphere and cerebellum.

*iii* Plate X shows cerebral and cerebellar hemispheres partially dissected in the sagittal plane. (c) Depictions of white matter dissections of the cerebral hemisphere, cerebellum, and brainstem by Mayo (1827). *i* Plate III shows dissection of the middle cerebellar peduncle. In *ii* Plate IV, brainstem and cerebellar dissection with removal of the MCP reveals the inferior and superior cerebellar peduncles

numerous volumes on cerebellum (Bolk 1906; Edinger 1909; Ingvar 1918; Riley 1929; Ziehen 1934; Larsell and Jansen 1972) (Fig. 2.2). The most detailed human atlas available was that of Angevine et al. (1961), until the introduction of the three-dimensional MRI Atlas of the Human Cerebellum (Schmahmann et al. 2000) for use with anatomic and functional neuroimaging. It depicted cerebellum in the three cardinal planes in Montreal Neurologic Institute stereotaxic space, included histological specimens with cerebellar nuclei, and revised Larsell’s nomenclature. This atlas facilitated the development of the on-line SUIT atlas (Diedrichsen 2006) for functional neuroimaging.

Magnetic resonance imaging (MRI) revolutionized the ability to visualize posterior fossa structures and lesions. Task-based functional MRI reliably shows cerebellar activation by motor (Fox et al. 1985) and nonmotor tasks (Petersen et al. 1989; Gao et al. 1996). The topography of functions in

cerebellum is exemplified in fMRI meta-analyses and prospective studies showing areas of cerebellum dedicated to motor control, cognition, and emotion (Stoodley and Schmahmann 2009; Stoodley et al. 2012; Guell et al. 2018; King et al. 2019). Resting state functional connectivity MRI has added physiological connectivity evidence to the connective data from non-human primates, showing functionally and anatomically distinct cerebrocerebellar circuits (Buckner et al. 2011; Habas et al. 2009; O’Reilly et al. 2010).

## 2.7 Theories

Snider (1952) proposed that cerebellum is the great modulator of neurologic function, and Heath (1977) regarded it as an emotional pacemaker for the brain. Gilbert and Thach (1977) confirmed the hypothesis of Marr (1969) and Albus

(1971) that cerebellar climbing fibers and mossy fibers work in collaboration to facilitate a cerebellar role in motor learning. Ito used the model of the vestibular ocular reflex (Lisberger and Fuchs 1978) to suggest that the cerebellum engages in error correction in the realms both of movement (Ito 1984) and of thought (Ito 1993). Leiner et al. (1986) and Leiner and Leiner (1997) drew on evolutionary considerations of the dentate nucleus expanding in concert with cerebral association areas to propose that cerebellum serves as a multipurpose computer designed to smooth out performance of mental operations. Thach (1996) suggested that the cerebellum uses the mechanism of context-response linkage for motor adaptation, motor learning, and higher function. Llinas and Welsh (1993) highlighted the role of the olivocerebellar system in entraining cerebellar neuronal firing, focusing on the cerebellar role in movement. Other ideas include the view that the cerebellum is critical for timing (Ivry and Keele 1989), sensory perception (Bower 1995), anticipation and prediction (Courchesne and Allen 1997), and sequence learning (Molinari et al. 1997). Schmahmann's dysmetria of thought theory (Schmahmann 1991, 2000, 2010) holds that there is a universal cerebellar transform that maintains function around a homeostatic baseline according to context; information being modulated is determined by topographically arranged anatomical circuits; the universal cerebellar impairment is dysmetria – resulting in the motor ataxia syndrome when the motor cerebellum is damaged, the CCAS when the cognitive-limbic cerebellum is damaged.

## 2.8 Evolving Techniques and Therapies

Walker (1938) showed that stimulation of the cerebellum alters electrical activity of the motor cortex. Cerebellar stimulation in patients produced amelioration of aggression (Heath 1977) and reduced the frequency of seizures (Riklan et al. 1974). The recognition of the cerebellar incorporation into the distributed neural circuits subserving cognition and emotion as well as motor control has opened the way to brain modulation using transcranial magnetic stimulation and transcranial direct current stimulation of the cerebellum. These approaches have been used to study cerebrocerebellar interactions in health (Hashimoto and Ohtsuka 1995; Schutter and van Honk 2006; Halko et al. 2014) and disease (e.g., Wessel et al. 1996; Brady Jr et al. 2019). They have also been used to treat motor and cognitive/emotional manifestations in individuals with cerebellar disorders, and to improve motor learning, stroke recovery, speech and language functions, and non-ataxic neuropsychiatric and movement disorders (Demirtas-Tatlidede et al. 2010; Grimaldi et al. 2014;

Cattaneo et al. 2021; Manto et al. 2021). Magnetoencephalography (MEG) can record activity in the human cerebellum (Tesche and Karhu 1997) and provides a temporal dimension to the study of cerebellar circuitry and function.

Magnetic resonance spectroscopy (MRS) is sensitive to metabolic changes (Ross and Michaelis 1996), is abnormal in patients with cerebellar degeneration (Tedeschi et al. 1996), and together with morphometric studies of volumetric change may be useful as a biomarker of cerebellar dysfunction in the spinocerebellar and other ataxias (Öz et al. 2011, 2020). Diffusion tensor MRI (Takahashi et al. 2014) and optical coherence tomography (Liu et al. 2021) also now enable novel insights into cerebellar anatomy, connections, and disease.

Physical, occupational, and speech rehabilitation strategies have long been the mainstay of therapy for ataxia. Therapeutic nihilism has given way to the appreciation that many symptoms experienced by ataxia patients can be treated successfully with medications. Rest tremor, spasticity, camps, dystonia, neuropathic pain, dysphagia, urogenital symptoms, orthostasis, fatigue, mood and attention, among others symptoms, can all be effectively managed by repurposing medications from other neurological disorders, mandating that ataxia clinicians be more proactive in the care of these patients (Stephen et al. 2019; Perlman 2020). Medications are also being repurposed or newly developed for the treatment of kinetic ataxia that address the underlying molecular and physiological defects that produce cerebellar motor, cognitive, and other syndromes.

Since the discovery of the genetic basis of Friedreich's ataxia (Campuzano et al. 1996), the understanding of autosomal dominant spinocerebellar ataxias and recessive ataxias has produced a paradigm shift in the care of patients and families with heritable cerebellar disorders. Exome sequencing and genome analysis have catapulted this further forward. Advances in understanding the genetics of the ataxias and the development of novel approaches to gene-related therapies such as the introduction of antisense oligonucleotides, modulation of downstream common pathway mechanisms, and direct implantation of genes using viral vectors (Ashizawa et al. 2018) hold out real promise for amelioration, cessation, and perhaps even prevention of the phenotypic manifestations of the genetic ataxias.

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