PERSPECTIVES

A century of cerebellar somatotopy: a debated representation

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The existence of functional localization within the cerebellum was advanced exactly one century ago by both comparative anatomical and physiological studies. Here, we will discuss how models of cerebellar localization have evolved over the last 100 years. Like the somatotopic representation in neocortical sensorimotor areas, the representation size of different body parts in the cerebellum does not reflect their peripheral extent, but rather the different demands on the sensory inputs for different movements.

Few fields in the neurosciences have integrated different approaches as beautifully as investigations into cerebellar localization. Morphology (comparative anatomy, embryology, hodology), physiology (ablation and stimulation experiments, electrophysiology), pathology (morbid anatomy, clinical neurology), and neuroimaging studies have contributed in different and complementary ways to the development of the present concepts of cerebellar localization.

At the beginning of the twentieth century, it was widely believed that the cerebellum was essential for smoothness and effectiveness of movement, with a diffuse cerebellar influence on all motor activities. This stemmed from the work of Luigi Rolando[1] and Pierre Flourens[2] at the beginning of the nineteenth century. After lesioning the cerebellum, they observed severe impairments in motor functions, but no evident alteration in vital or intellectual functions, and they both advanced the principle of the cerebellum 'working as a whole'. In this article, we will discuss how this view has changed over the last 100 years (TIMELINE), but first we will take a step back and consider how cerebellar function was perceived in the nineteenth century.

Cerebellar localization

In the nineteenth century. In a monumental study[3], Luigi Luciani approached the topic of cerebellar function by analysing the effects of total or partial cerebellectomy[4]. On the basis of his experimental findings, Luciani described a triad of symptoms — atonia (loss of muscle resistance), asthenia (diminished strength of muscles) and astasia (defective stability of muscular contraction) — as being comprehensive of all dysfunctions of cerebellar origin. As he failed to observe focal symptoms after circumscribed ablations of the cerebellar cortex, Luciani denied that there was any somatotopic organization in the cerebellar cortex, and he vigorously rejected the idea of localization either of single body parts or specific functions. He believed only that each cerebellar hemisphere controlled the corresponding half of the body, whereas the vermis controlled the trunk: "We cannot regard the cerebellum as a collection of functionally distinct or different centres, as if each of its segments is in more or less intimate or direct relation with a special group of muscles or is designed for functions of different character."[3]

At the end of the nineteenth century, Charles S. Sherrington[5], and Max Loewenthal and Victor Horsley[6] observed, almost simultaneously, that electrical stimulation of the anterior lobe of the cerebellum provoked inhibition 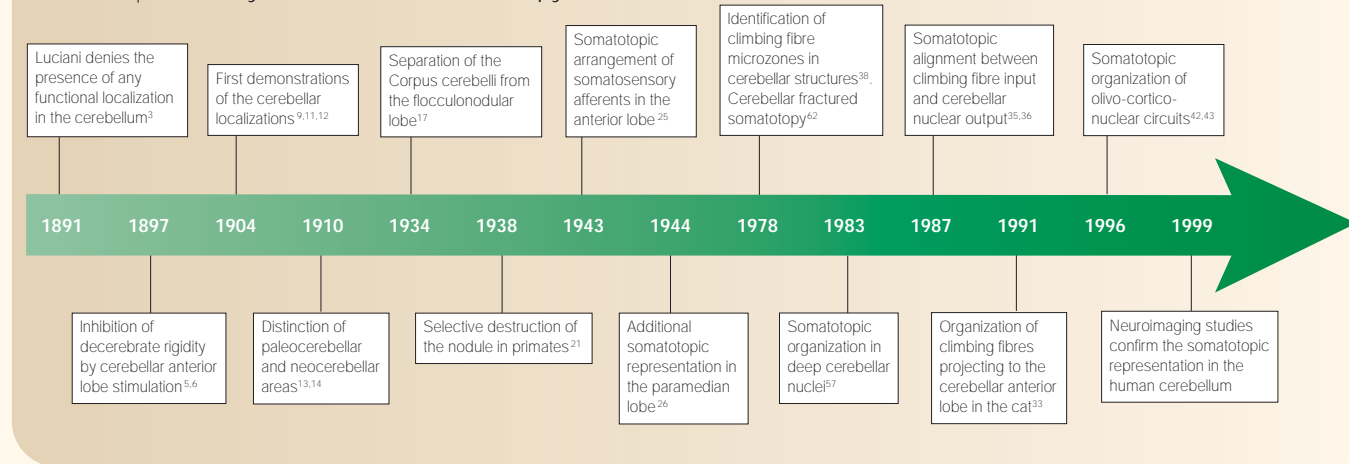of decerebrate rigidity (a condition that is characterized by a spontaneous rigid extension of the limbs). Sherrington reported that, in the monkey, when a faradic current was applied to the surface of the anterior portion of the cerebellar cortex from the midline far out towards the lateral borders, the resulting inhibition affected the muscles of the ipsilateral limbs, neck and tail[5]. Loewenthal and Horsley[6] obtained similar effects by stimulating the underlying white matter and the cerebellar peduncles.

Although these reports might represent the first rough indication of functional localization within the cerebellar cortex, they did not arouse noticeable interest in the scientific world. In fact, they were completely neglected in Luciani's *Handbook of Physiology*[7], and were barely recalled by Sherrington himself in the account of cerebellar physiology that he prepared for Schäfer's *Textbook of Physiology*[8].

At the end of the nineteenth century, however, several comparative anatomists paved the way for the formulation of a doctrine of functional localization in the cerebellar cortex. Impressed by the graceful patterns of folia and fissures, lobes and lobules, they asked whether it was possible to recognize a common principle underlying the architectural plan of the cerebellum in different mammals. They noticed the constancy of some easily identifiable transverse grooves, permitting cerebellar subdivisions that were more reliable and rational than the mere distinction between vermis and hemispheres. In spite of this, the issue of functional localization within the cerebellum was still disregarded.

Early localization attempts. The beginning of the twentieth century saw a change in thinking about the diffuse cerebellar influence. 1904 was the pivotal year in which different authors with different approaches simultaneously reported that there were functional localizations within the cerebellum. In this year, Lodewijk Bolk[9] introduced his original scheme of the anatomo-functional organization of the cerebellum and advanced a pioneering interpretation of cerebellar

Timeline | A century of cerebellar somatotopy

Luciani denies the presence of any functional localization in the cerebellum[3]

First demonstrations of the cerebellar localizations [9,11,12]

Separation of the Corpus cerebelli from the flocculonodular lobe[17]

Somatotopic arrangement of somatosensory afferents in the anterior lobe [25]

Identification of climbing fibre microzones in cerebellar structures[38]. Cerebellar fractured somatotopy[62]

Somatotopic alignment between climbing fibre input and cerebellar nuclear output[35,36]

Somatotopic organization of olivo-cortico-nuclear circuits[42,43]

| 1891 | 1897 | 1904 | 1910 | 1934 | 1938 | 1943 | 1944 | 1978 | 1983 | 1987 | 1991 | 1996 | 1999 |

Inhibition of decerebrate rigidity by cerebellar anterior lobe stimulation[5,6]

Distinction of paleocerebellar and neocerebellar areas[13,14]

Selective destruction of the nodule in primates[21]

Additional somatotopic representation in the paramedian lobe[26]

Somatotopic organization in deep cerebellar nuclei[57]

Organization of climbing fibres projecting to the cerebellar anterior lobe in the cat[33]

Neuroimaging studies confirm the somatotopic representation in the human cerebellum

functions on the basis of careful phylogenetic comparisons.

Bolk examined the cerebella of more than 60 different mammalian species, and he concluded that the transverse division was the most important partition of the cerebellar regions, rather than the sagittal division, as had previously been believed. According to his subdivision, the sulcus primarius anterior or fissura prima splits the cerebellum into an anterior and a posterior lobe (FIGS 1,2a). The anterior lobe is a single, unpaired structure, whereas the posterior lobe consists of several parts, some that are located on the midline and others that are located laterally and symmetrically. In some ways, this mirrored the old cerebellar subdivision into vermis and hemispheres. The key elements of Bolk's plan are a sagittal continuity of the cerebellar cortex within the folia chains of the vermis and hemispheres, and a transverse continuity between vermis and hemispheres that is maintained by the parallel fibres.

To provide a functional interpretation of these anatomical subdivisions, Bolk carefully compared the habits and behaviour of specific animal species with their different movements. Starting from the indication that the cerebellum is involved in the control of movement, he established for the first time that specific cerebellar lobules control specific muscle groups, and that each movement has to be represented in a definable area of the cerebellar cortex. Bolk proposed that the unpaired, bilaterally symmetrical anterior lobe and lobulus simplex, which lack a clear division into vermis and hemispheres, would coordinate bilateral symmetrical movements of the head and neck, such as turning of the head. Coordination of the unilateral independent movements of the extremities, such as

grasping objects, would be located in the paired independent folial chains of the posterior hemispheres. According to Bolk, crus I and II were responsible for the coordination of forelimb and hindlimb muscles, respectively (FIGS 1,2a). The portion of vermis that is located between the ansiform lobules (Larsell's lobule VII) would be responsible for the coordination of synergic movements of the limbs. Interestingly, this part of the vermis is excessively developed in mammals that use their limbs in a synergistic, stereotyped fashion, such as the ungulates. The anterior lobe would contain the coordination centre

for the group of head muscles (eyes, tongue, masticatory and facial muscles) and, in addition, muscles of the larynx and pharynx. The lobulus simplex would contain the coordination centre of the cervical muscles, whereas the tail muscles would be represented in the formatio vermicularis (which is now conventionally subdivided into paraflocculus and flocculus).

This tentative relationship between structure and function was based on precise comparative anatomical observations. In a rather funny anecdote, Bolk realized that the simplex lobule was related to the neck muscles
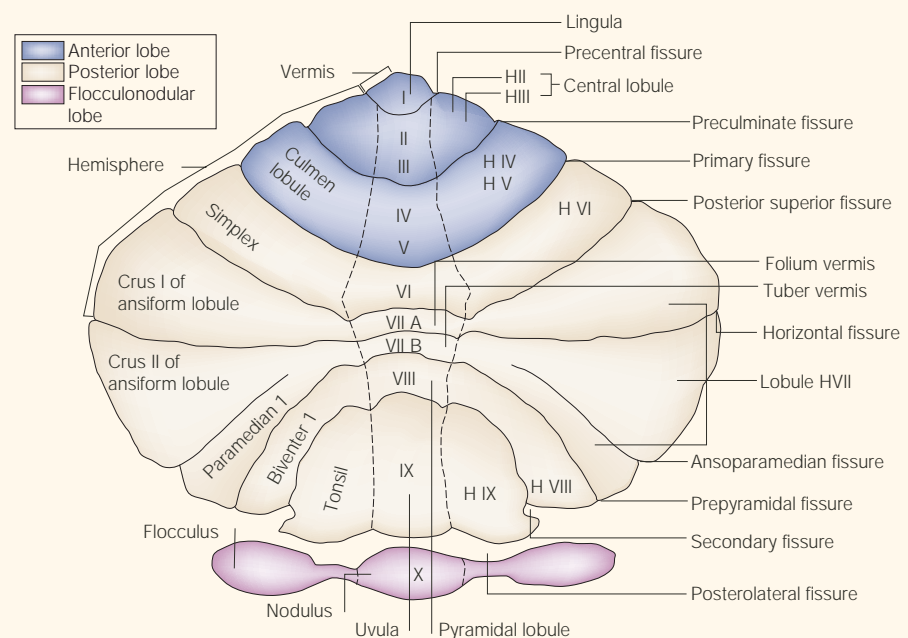

Figure 1 | **Unfolded view of the cerebellar cortex showing lobes, lobules (by name and number) and main fissures.** The lobules of the hemispheres are designed by the prefix 'H', according to Larsell's classification.

by observing its huge development in the giraffe. For the first time, Bolk's schema vividly asserted that the cerebellar representation of a given body part was related to its functional importance and to the accuracy of its movements. At odds with preceding research, this new functional approach had a remarkable impact on experimental research on the cerebellum and became a landmark in the development of the doctrine of cerebellar somatotopic organization. For example, see Jansen's comparative studies on the early development and morphology of the cerebellar structures in cetacea and humans[10].

Simultaneously, and probably unaware of Bolk's research, the Italian physiologist Guiseppe Pagano obtained experimental findings that supported the existence of cerebellar somatotopy. By injecting small doses of curare in the lobulus simplex or in crus I and II, Pagano observed localized contractions of the ipsilateral forelimb or hindlimb, respectively. He advanced the presence of 'motor points', the stimulation of which induced finely localized movements. He concluded his paper on cerebellar localization[11] by stating that the cerebellum was not functionally homogeneous and that its different activities were related to specific areas, as occurs in other brain regions.

In the same year, the Dutch physiologist Giovanni van Rijnberk[12] carried out circumscribed ablation of the lobulus simplex in the dog, and he observed a selective cervical astasia with continuous head weaving in the transverse plane, without motor impairment in other body parts. He also performed unilateral lesions of crus I. Immediately after ablation, any acoustic or mechanical stimulus induced sudden lifting of the ipsilateral forelimb, so that the paw was brought near the ear — a symptom that pantomimed the military salute. The cervical astasia progressively disappeared and the dog began to show marked locomotor dysmetria of the ipsilateral forelimb, a symptom defined as 'cock gait' or 'goose step'. Interestingly, unilateral ablation of crus II provoked similar symptomatology in the ipsilateral hindlimb. Van Rijnberk's findings provided physiological support for Bolk's anatomical interpretation of cerebellar somatotopy, at least as far as neck and limb muscles were concerned.

Edinger and Comolli's subdivision. In 1910, Antonio Comolli, working in Ludwig Edinger's lab, developed an important new approach to the problem of cerebellar localization. He introduced the concept of paleocerebellum and neocerebellum to indicate the oldest and youngest cerebellar regions, respectively — a concept that has been of tremendous importance for our subsequent understanding of cerebellar physiology. However, whereas Bolk's cerebellar subdivision immediately captured the interest of researchers, Edinger and Comolli's cerebellar organization had less impact at the time, in spite of its originality.

According to the new conception[13,14], the vermis and the flocculus represent the paleocerebellum, and the hemispheres the neocerebellum (FIGS 1,2b). The cerebellar hemispheres are prominent in mammals, but are barely discernable in birds. Furthermore, in the superior mammals, the vermis is progressively reduced in size, whereas the cerebellar hemispheres are markedly enlarged. As the hemispheres are widely connected with the cerebral cortex through the pontine nuclei, their progressive development is related to the concurrent development of the pons. Interestingly, in cats and primates, destruction of neocerebellar regions[15] induces the same symptoms (hypotonia, asthenia and astasia) that were described by Luciani after hemicerebellectomy, indicating that the syndrome of cerebellar origin is mainly linked to the neocerebellar regions. It is of crucial importance that, whereas Bolk's scheme was particularly concerned with the localization of efferent projections, Edinger and Comolli's model emphasized the role of cerebellar afferents.

The distinction between paleocerebellum and neocerebellum, with the suggestion that the paleocerebellum was concerned with regulating postural tone, and the neocerebellum with influencing neocortical activities, meant, as Frédéric Bremer pointed out in 1935, that "the localization is no longer muscle-related, but is a localization of functions."[16]

Larsell's subdivision. In 1934, Olof Larsell proposed a further subdivision of the cerebellar areas[17]. His research was expanded over more than 30 years, and the results were posthumously published in 1970 in a book by Jan Jansen[18]. Larsell's work was a further attempt to provide a comparative anatomical basis for the theory of cerebellar localization, and he developed our present concepts of cerebellar morphology. He started from the observation that the fissure that emerges most precociously in ontogeny, as well as in phylogeny, is the sulcus posterolateralis. This fissure splits the cerebellum into two lobes — the flocculonodular
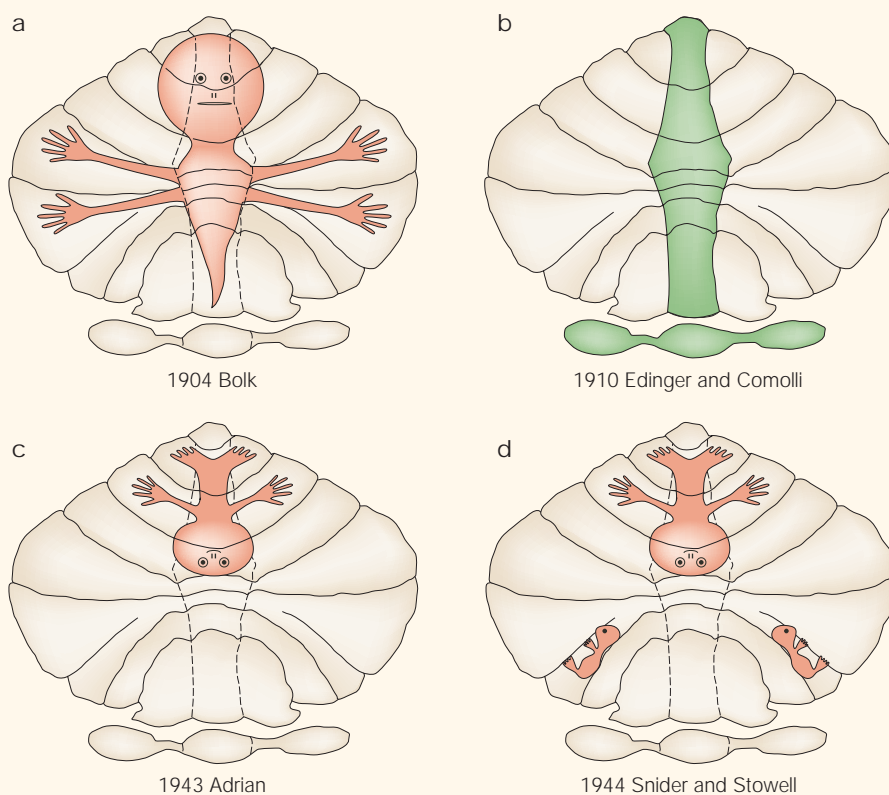

Figure 2 | **The evolution of cerebellar somatotopy from Bolk to Snider and Stowell. a** | The somatotopic organization proposed by Bolk[9]. **b** | The subdivision in paleocerebellar (green) and neocerebellar (white) areas proposed by Edinger and Comolli[13,14]. **c** | The somatotopic organization proposed by Adrian[25]. **d** | The somatotopic organizations proposed by Snider and Stowell[26]. Acoustic and visual inputs are not depicted.

Sub-figure labels: a — 1904 Bolk; b — 1910 Edinger and Comolli; c — 1943 Adrian; d — 1944 Snider and Stowell

lobe, which was included in the posterior lobe described by Edinger and Comolli, and the corpus cerebelli, which encompasses the whole remaining cerebellum. The corpus cerebelli is further subdivided into two lobes, anterior and posterior, by the fissura prima. According to Larsell, the vermis can be further subdivided into ten lobules, labelled I–X from lingula to nodulus. The flocculonodular lobe and the lingula, with their wide vestibular connections, represent the archicerebellum. The anterior lobe and the pyramis, with their spinal projections, are considered paleocerebellar areas, and the remaining areas (the hemispheres) represent the neocerebellar regions.

Paradoxically, although the flocculonodular lobe is the earliest structure phylogenetically, it was the last cerebellar region to be studied in detail. Nodular lesions had traditionally been concurrent with those of other non-vestibular parts of the posterior vermis[19,20], and even today, studies on the effects of its ablation are rare. Robert S. Dow (1938) was the first to demonstrate that, in primates, ablation of the nodulus and the lower part of the uvula results in a disequilibrium syndrome with wide head oscillations, side falls and ataxic gait[21]. In the guinea pig[22,23], unilateral destruction of the nodulus induces compulsive circling and rolling movements, ocular nystagmus, and head and trunk postural asymmetries.

Degeneration studies on cerebellovestibular efferents also supported Larsell's scheme, indicating that fibres from the flocculus selectively terminate in lateral and superior vestibular nuclei, whereas fibres from the nodulus project to all four vestibular nuclei[24].

Localization of cerebellar afferents
At the beginning of the 1940s, important new findings on cerebellar somatotopy emerged from electrophysiological investigations. The task of separately mapping out the afferent and efferent connections in the cerebellum was successfully achieved through the work of several researchers, using the technique of evoked potentials. These new data provoked a revolutionary modification of the theory of cerebellar localization, and constituted the definitive rejection of the scheme that Bolk had proposed 40 years earlier.

Edgare D. Adrian[25] recorded cerebellar unitary discharges during joint displacements, muscle stretching or tactile stimulation in anaesthetized cats and monkeys, as well as in decerebrate cats. He demonstrated that proprioceptive and exteroceptive information is somatotopically arranged in the anterior lobe of the cerebellum. Specifically, hindlimb afferents project to vermian and hemispherical regions of the lobulus centralis (Larsell's lobules III and HIII), forelimb afferents project to the culmen (lobules IV, V and HIV and HV), and face afferents project to the lobulus simplex (lobules VI and HVI) (FIGS 1, 2c).

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In deeply anaesthetized cats and monkeys[26], Ray S. Snider and A. Stowell (1944) revealed two inverted somatotopic maps in the anterior lobe and in the paramedian lobule (FIGS 1,2d), where exteroceptive information from hair or vibrissae is received. This early mapping was based on recordings of surface potentials, which reflect the predominant input and provide a coarse representation of somatotopic connections. The body map in the anterior lobe has the hindlimbs orientated forwards, whereas the face extends backwards into the first lobule of the posterior lobe. The map in the paramedian lobule has the head forward and the limbs represented on either side of the midline. Arms and legs are represented adjacent to the vermis over the intermediate cortex of the hemispheres. The projections to the anterior lobe are strictly ipsilateral, whereas the afferents to the paramedian lobule are bilateral, although with a slight bias towards the ipsilateral projection. This body mapping is similar in cats and monkeys.

As already suggested by others[27], in addition to somatosensory projections, Snider and Stowell described the presence of auditory and visual inputs that probably reach the cerebellum through the colliculi and the tectocerebellar tract. These slightly overlapping inputs were identified in the vermian area — more specifically, the lobulus simplex, folium and tuber vermis (Larsell's lobules VI and VII). The somatotopic representation that was demonstrated for exteroceptive and proprioceptive inputs that are mediated by spinocerebellar pathways was valid also for the neocortical afferents that reach cerebellar regions by way of the pontine nuclei. Subdivisions of the primary motor cortex that represent the face, arms and legs project within the cerebellum into the same areas as the spinocerebellar projection from face, arms and legs, respectively, demonstrating an elegant somatotopic arrangement of inputs, regardless of the site of origin[25].

It is worth noting that the somatotopic arrangement of afferent projections was recognizable in anaesthetized animals, whereas in non-anaesthetized animals it was entirely missing, or was at least characterized by considerable overlap[28,29].

This intriguing result seems to indicate the presence of a double sensory representation in the cerebellar cortex. The more extensive one is made up of sensory fibres intermingling and terminating primarily in the culmen, simplex and in the posterior folia of the centralis (lobules III–VI). These are bilaterally represented with a slight preponderance for the ipsilateral projection. The second projection seems to be arranged in a definite somatotopic manner, with specific areas receiving a localized afferent supply, in addition to a diffuse projection[29]. The first representation is bilateral and diffuse, and it seems to be dominant in physiological conditions. The other is somatotopically arranged, latent in normal conditions and detectable only under anaesthesia. This indicates that the difficulties encountered by previous researchers in detecting the somatotopic representation in the cerebellum might be due to the masking effect of the spread of activity in non-anaesthetized animals. Later studies in awake cats showed that climbing fibre inputs (see next section) in forelimb-receiving areas of the anterior lobe are similar to those that were mapped in the anaesthetized animals[30].

Olivocorticonuclear complexes
Afferent information reaches the cerebellum through two systems — mossy fibres, which originate from various central nervous system regions, and climbing fibres, which arise from the inferior olive. New findings on the organization of the climbing fibre projection have recently been reported[31–33]. It is now widely accepted that one functionally significant feature of the neuronal circuitry of the mammalian cerebellum is its parasagittal division into several 'olivocorticonuclear complexes'[34–37] (FIG. 3). Each of these modules includes a long narrow strip of cerebellar cortex, a localized subpopulation of contralateral inferior olivary neurons that provide climbing fibres to the cortical zone, and a group of deep cerebellar nuclear neurons. The olivocerebellar climbing fibre zones that are innervated by the dorsal accessory olive (the only olivary part in which a clear-cut somatotopic pattern has been described) can be further subdivided into
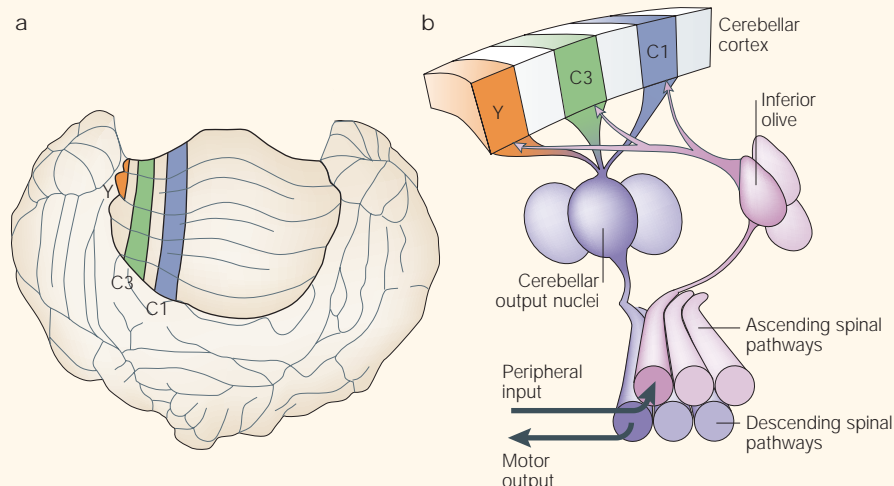
Figure 3 | Zonal organization of olivocorticonuclear connections. a | Dorsal view of the cat cerebellum. Thick lines demarcate the extent of the anterior lobe and the borders of some sagittal zones (C1, C3 and y). **b** | A schematic representation of the input and output connections (pink and purple shading, respectively) of sagittal zones C1, C3 and y. Modified, with permission, from REF. 41 © (1998) The American Physiological Society.

microzones — groups of climbing fibres that share the same peripheral receptive field and innervate a narrow strip of Purkinje cells that project in turn to distinct subgroups of deep nuclear neurons[35,38]. In some of these zones (B zone, C1 and C3 zone, zone y), the microzones are arranged in a somatotopic pattern, and they control skilled movements by means of the rubrospinal and corticospinal tracts[38]. Multiple representations of the body surface are present in the climbing projection to the anterior lobe, and the C3 zone contains two mirrored representations of the forelimbs[31,40,41].

Electrophysiological studies in unanaesthetized cats have shown that many microzones of C1 and C3 are stimulated during locomotion. The highest excitability of climbing fibres was observed during the swing phase, whereas the lowest activity was observed during the stance phase. In other regions of the rostral paramedian lobule, the opposite pattern was recorded[42,43]. So, the excitability of climbing fibres to the C1/C3 zones is not uniformly controlled during locomotion. These contrasting patterns of movement-related gating indicate that although cortical zones within somatotopically 'corresponding' regions of the cerebellar cortex (that is, zones that receive inputs from the same peripheral portions) share some olivary inputs, they also have 'private' lines of climbing input, enabling distinct information to be forwarded to different parts of the same zone. This arrangement could permit integration with specific combinations of mossy fibre afferents at different rostrocaudal levels within a zone[44].

As the receptive fields of climbing fibres differ at different levels, the gating of climbing fibres could provide a means of facilitating responses to inputs that occur when no peripheral input is expected. For example, climbing fibres that are easily activated by stimuli in a passive animal are not activated

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when similar stimuli result from active movement, for example during locomotion, but they again discharge in response to unexpected stimuli, such as a sudden obstacle that is encountered during stepping[42,43]. By combining electrophysiological mapping with axonal tracing methods, cortical zones that are functionally different in terms of their climbing input have been demonstrated[45]. It has been suggested that climbing fibres signal sensory 'errors' whenever a mismatch occurs between the intended and the actual movement. This signal for performance error could

lead to remodelling of the cerebellar circuits through synaptic plasticity processes[44]. As the motor output regulated by Purkinje cells is specific to their climbing fibre receptive fields, the activation of an interneuron through skin contact with an external object results in a muscle activation to withdraw that skin area from the object, through a reduction in Purkinje cell inhibition in the deep cerebellar nucleus[46,47].

Most mossy fibre systems seem to terminate in bilaterally symmetrical, ill-demarcated longitudinal aggregates of mossy fibre terminals[48]. Recent reports[49] revealed a similarity in the peripheral receptive field organization of Purkinje cell complex spikes (generated by climbing fibre activity) and granule cells (which receive input from mossy fibres), indicating that the somatotopic distribution of the mossy fibres could correspond to that of the climbing fibres. The presence of two cerebellar regions, in the anterior and posterior lobe, with similarly organized input from climbing and mossy inputs, with a corresponding biochemical pattern, and with projections to the same deep nuclei, seems to be a redundant feature of cerebellar circuitry, whose functional importance requires further investigation[48]. Furthermore, inhibitory interneurons (stellate and basket cells) have well-defined parallel fibre receptive fields that are specific for the local climbing fibre input[46,50].

Cerebellar afferents versus efferents
For a full understanding of the contribution of different cerebellar components to regional function, it is necessary to analyse cerebellar efferents, which, it transpires, are also somatotopically arranged. Stimulation of the cerebellar cortex evokes localized movements (for a review, see REF. 51). As for the anterior lobe, stimulation of the lobule simplex evokes head movements comprising the face and jaw, stimulation of the culmen evokes forelimb movements, stimulation of the centralis evokes hindlimb movements, and stimulation of the lingula evokes tail movements. Trunk muscles are represented medially, whereas limb muscles are represented laterally. This scheme, which was first recorded in the decerebrate animal, was confirmed in intact animals by means of chronically implanted electrodes. In 1952, J. Hampson, C. Harrison and C. Woolsey reported that in the decerebrate cat, dog and monkey, electrical stimulation of the medial three-fifths of the anterior lobe provoked an ipsilateral decrease in extensor rigidity, whereas electrical stimulation of the lateral two-fifths gave the opposite result[52]. Conversely, an ipsilateral increase and a contralateral inhibition of hypertonus occurred when

paravermian or hemispherical portions were stimulated. Inhibition of decerebrate rigidity ipsilaterally to a unilateral fastigial lesion has also been described[53]. Further experiments on cats by W. W. Chambers and James Sprague revealed striking differences between the effects of ablation of the vermian and the intermediate portion of the anterior lobe. Although discrete lesions of the vermian cortex affect the entire body, somatotopic localization can still be recognized. Conversely, the intermediate zone controls individual movements of the ipsilateral limb, reaching the most discrete somatotopic mapping[54]. Other research demonstrated that motor activity elicited by neocortical areas was inhibited or facilitated by stimulation of the anterior lobe[55]. So, output points in the cerebellar cortex (recall the 'motor points' described by Pagano 50 years earlier) are somatotopically arranged, like the output points in the neocortex.

As demonstrated for the cerebellar afferents, a double symmetrical representation of cerebellar efferents is present in part of the posterior lobe. Movements of face, forelimbs and hindlimbs are ipsilaterally evoked by stimulating the superior, median and inferior folia of the paramedian lobule, respectively. Movements of the arms and tail are also evoked by stimulating the pyramis. However, movements evoked by stimulation of the paramedian lobe are less localized than those evoked by anterior lobe stimulation.

More recent studies using retrograde/ anterograde transport of tracers or electrophysiological recordings have shown that in the mammalian cerebellum, the main afferent and efferent projections have a parasagittal band-like topographical organization. This somatotopic organization was demonstrated for climbing and mossy fibre afferents, as well as for the efferent Purkinje cell projection to cerebellar deep nuclei and the lateral vestibular nucleus. In the pars intermedia of the anterior lobe, as far as the climbing fibres are concerned, the hindlimb is represented in the lobus centralis (lobules II and III) and the forelimb in the culmen (lobules IV and V). Conversely, in the vermian portion of the anterior lobe, a sagittal organization was found, with the forelimb and hindlimb represented medially and laterally, respectively[31,56]. This somatotopic arrangement, first revealed by studies on cerebellar afferents and then extended to the cerebellar efferents, once more refuted Bolk's assumption. In particular, the physiological role of crus I and crus II in controlling forelimb and hindlimb muscles could no longer be maintained. Only the functional role of the lobulus simplex, as a centre controlling the neck muscles, was upheld.

Anatomical studies of primates show that the deep cerebellar nuclei are also somatotopically organized[57,58]. They are arranged to receive projections from the two maps on the dorsal and ventral surfaces of the intermediate and lateral zones of the cerebellar cortex, and they project to the magnocellular red nucleus and primary motor cortex through the thalamus.

Physiological studies have indicated that the cerebellum is involved in the learning
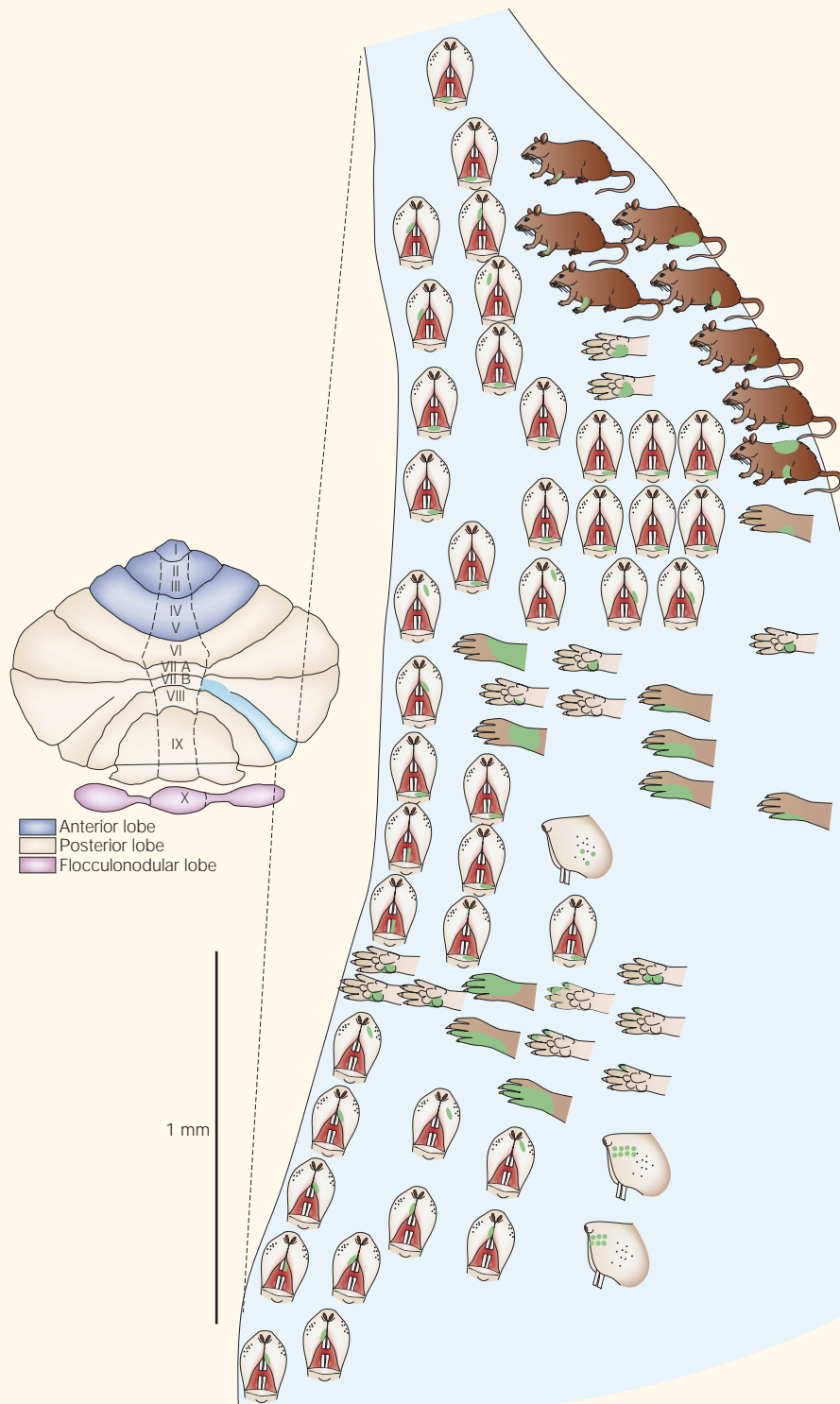

Figure 4 | **The fractured somatotopy of the cerebellar cortex.** Recordings of the receptive fields of granule cells in the rat cerebellar cortex (paramedian lobule) reveal multiple representations of the same body parts in different locations. Modified, with permission, from REF. 62 © (1978) S. Karger AG, Basel.

The ipsilateral relationship between the lateral portions of the cerebellum and the corresponding extremities is commonly accepted in clinical neurology[67]. However, it is difficult to locate specific topographical regions or parts of the body in specific areas or subdivisions of the cerebellum on the basis of clinical symptoms. The clinical neurologist T. H. Weisenburg (1927) hypothesized the functional parcellation of the cerebellum as follows[68]:

"In the vermis are represented the synergistic activities of the trunk: in the superior vermis the movements of the shoulder girdle or the upper trunk; in the inferior vermis the pelvic girdle or the lower trunk. Synergistic activities concerned in talking and movements of the eyes are located in the vermis, in all probability the superior vermis. Synergistic control of the limbs is in the lateral hemispheres, for the upper limbs in the superior portions, for the lower in the inferior."

Despite this optimistic view, symptoms of cerebellar deficiency in humans defy limitation to any one division of the cerebellum. For example, gait disturbances result from lesions of the flocculonodular lobe that cause equilibrium dysfunction. Lesions of the anterior lobe cause loss of cerebellar control of the spinal and brain stem reflexes that are involved in standing, and lesions of the posterior lobe of the corpus cerebelli disturb the tone and voluntary movement of the lower extremities.

Other symptoms are more closely related to specific cerebellar areas. For example, ataxia of voluntary movement of the upper extremities is probably chiefly related to lesions of the posterior lobe or the lateral part of the cerebellum. However, even for these symptoms, it is not possible to map out a precise somatotopic representation by relating a regional cerebellar area to a disturbance in specific muscle districts. It must be kept in mind that folia related to a particular body part have been found in at least three different areas — one contralateral, and the others ipsilateral in the anterior and posterior lobes. It is inconceivable that a pathological process could destroy all three areas and fail to affect other areas that are thought to be responsible for cerebellar control of the movements of other body parts.

and/or performance of the classically conditioned eyeblink response. Such responses are under strong cerebellar control from areas in the C1 and C3 zones that receive climbing fibre input from the periorbital area, implying that the conditioned responses depend on the cerebellum in a different way to unconditioned responses. The cortical component of the olivocorticonuclear loop is essential for acquisition of the classically conditioned eyeblink response, and eyeblink control areas in the HVI region are crucial. These findings are consistent with cerebellar learning models that assign essential plasticity to the cortex or to a distribution between levels in olivocorticonuclear modules[59–61].

The fractured somatotopy
At a finer level of resolution, experimental studies based on multiple unit recordings in mammals have shown that body parts are not represented continuously over a large area of the cerebellar cortex, but are broken into smaller, discontinuous patches. A small area of the cortex that receives sensory input from the arm (by way of mossy fibre–granule cell connections) might be located adjacent to an area that receives input from a non-contiguous region of the same upper extremity. In addition, each body part is represented in several locations (FIG. 4). This pattern of spatial representation is referred to as fractured somatotopy[62].

This discontinuous map probably reflects the mossy and climbing fibre distribution. Before any definite conclusions can be drawn, the fractured somatotopy needs to be re-investigated in light of the knowledge of the somatotopic arrangement of climbing (and mossy) fibre projections. The fractured character of patches might resolve into an orderly somatotopic pattern, like the microzonal organization.

The human cerebellum
Neuroimaging studies. Early attempts to address the issue of somatotopy in the human brain relied on clinical evidence (BOX 1). Detailed functional mapping of the human cerebellum only became possible with the advent of positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). These new neuroimaging techniques allowed investigation of the broad topic of somatotopic representation by detecting cerebellar activation during natural movements. However, it is important to keep in mind that maps of individual subjects show considerable differences in location and extent for each of the performed movements, so an ordered relationship among different activations in the cerebellum is barely detectable, and tends to be concealed by additional continuous or fragmented bands of activation, which are spread over the cerebellar cortex. In spite of this, activated areas that

are consistently observed between subjects indicate regions that are essentially involved in a given movement.

In general, neuroimaging studies have confirmed the classical view of representation in the cerebellum, characterized by the existence of two homunculi, one in the anterior lobe and one in the posterior lobe (FIG. 5). In the anterior lobe, the craniocaudal alignment reveals an upside-down order of body parts. Movements of arm, elbow joint, wrist and all fingers are separately represented in vermian lobule V, in intermediate lobules HIV and HV, and in hemispherical lobules HVI and HVIII, respectively, whereas the foot is represented in hemispherical lobules HII–HIV. Tongue and lip representation is located in lobule HVIA, mostly at the posterior border of the anterior lobe (FIG. 5). In the posterior lobe, representation of fingers and toes is around the pre-pyramidal fissure between lobules HVIII and HIX, with the peak of the toe representation in HIX, posterior and lateral to the finger representation[63–65]. The arm and face fall into HVIII (FIG. 5). Furthermore, segregated peaks of activation are found in the pyramis, implying a third representation[63]. It has been proposed that the predominance of fractured representations for one limb in a region, as found with micromapping, leads to the large-scale somatotopy in imaging studies.

Concurrently with physiological and clinical observations, the fMRI activation for right- or left-sided movements is also predominantly ipsilateral. If bilateral structures are involved in motion, such as in lip and tongue movements, hemispheric activation is bilateral and symmetrical, with a lower activation of the vermis in between. Conversely, hand movements show an ipsilateral activation in V–VIII, HV and HVIII.

So, although activation foci for upper and lower limbs are distinct and non-overlapping, the cerebellar somatotopic component does not seem to be as precise as in the primary sensorimotor cortex. This is shown by the lack of within-limb topic segregation. However, even with formally equivalent tasks for upper and lower limbs, it must be noted that motor functions, such as reaching and grasping, or posture and gait, are embedded in different contexts.

In conclusion, for the upper cerebellum, the craniocaudal and mediolateral alignment adds up to an upside-down somatotopy. Although no clear differentiation is recognizable within the face area, there are separate representations within the upper limbs, revealing a differentiation not only of proximal and distal joints, but also a strip along the primary fissure, where single fingers are
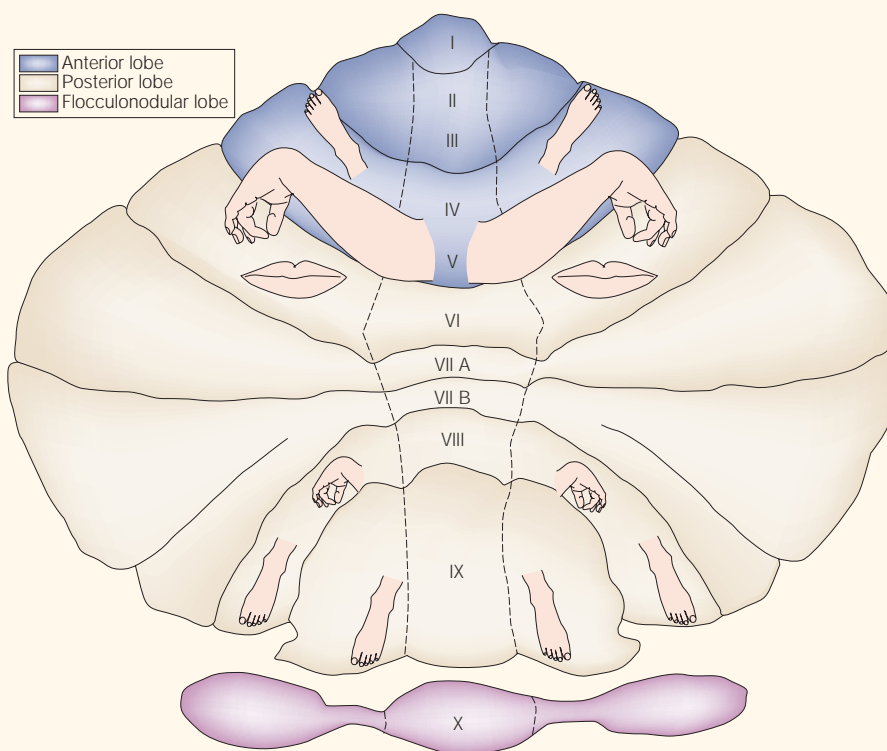
Figure 5 | **Functional somatotopy of the cerebellum.** Sketched representation of the arms, feet and lips in the human cerebellum (following the sensorimotor mapping of the cerebellum proposed by Grodd et al.[64]). Face representation is not indicated.

Legend:
- Anterior lobe
- Posterior lobe
- Flocculonodular lobe

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aligned. Like the somatotopic representation in telencephalic sensorimotor areas, the representation size of different body parts in the cerebellum does not reflect their peripheral extent, but rather the different demands on the sensory inputs for different movements.

Conclusions
The debate over cerebellar somatotopic representation that has been going on for more than a century is still not completely settled. By collecting neuroimaging data in more 'functional' contexts, such as during voluntary performance of motor acts, it has been possible to confirm the presence of a somatotopic organization in the human cerebellum. However, cerebellar coding of motor behaviour of different body parts is more complex than simple topic representation, containing local, modular repeats of small segments of receptor locations, with a global topography that includes splits, disproportions and other transformations.

Given that topographical organization of maps is a general solution arrived at by all mammals in various parts of the brain, what functional benefits are gained through this type of organization? Maps allow the nervous system to efficiently extract features, aspects and dimensions of external events, and to quickly guide an appropriate behavioural action, thereby providing the structural framework for neural plasticity. Topographical maps effectively cluster highly interconnected neurons for most types of neuronal computation, decreasing requirements for long, slow and metabolically expensive connections. Topography provides an economical algorithm for wiring of the brain, requiring less genetic information than other wiring arrangements. Furthermore, topographical mapping might facilitate the identification of inputs from items that are adjacent in space, recognizing them as separate units. Topographically arranged structures also facilitate the sharpening of diffuse receptive fields through lateral inhibition. As H. B. Barlow pointed out[66], maps allow the occurrence of local neural circuits that average or interpolate over space and time.

The fundamental advantage of multiple mapping is the specialization to preferentially address different stimulus attributes by having specialized sets of modules. Somatotopic mapping does not seem to be incidental, but is essential to many aspects of brain function in sensory as well as in motor systems. The cerebellum, which provides an interface between motor and sensory events, obeys this general law. A century of studies has resulted in notable findings on the principles that guide somatosensory mapping in cerebellar circuitry, but the debate is by no means resolved.

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