Cerebellar Classic

Commentary on “The Significance of the Granular Layer of the Cerebellum: A Communication by Heinrich Obersteiner (1847–1922) Before the 81st Meeting of the Society of German Natural Scientists and Physicians in Salzburg, September 1909”

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Abstract

This commentary highlights a “cerebellar classic” by Heinrich Obersteiner (1847–1922), the founder of Vienna’s Neurological Institute. Obersteiner had a long-standing interest in the cerebellar cortex, its development and pathology, having provided one of the early accurate descriptions of the external germinal layer (sometimes called the “marginal zone of Obersteiner” or “Obersteiner layer”). In his communication before the 81st Meeting of the Society of German Natural Scientists and Physicians in Salzburg in September 1909, Obersteiner placed special emphasis on the histophysiology of the granule cell layer of the cerebellum, and covered most of the fundamental elements of the cerebellar circuitry, on the basis of Ramón y Cajal’s neuronism. Those elements are discussed in a historic and a modern perspective, including some recent ideas about the role of granule cells, beyond the mere relay of sensorimotor information from mossy fibers to the Purkinje cells, in learning and cognition.

Keywords Cerebellar histophysiology · External germinal layer · Granule cell · Purkinje cell · History of Neuroscience

A pioneer of European neuroanatomy and neuropathology, Heinrich Obersteiner (1847–1922) was also the founder, in 1882, of Vienna’s Neurological Institute (Fig. 1), one of the first interdisciplinary centers for brain research in the world [1–3].

Obersteiner was born in Vienna into a family of physicians. He studied medicine at the University of Vienna from 1865 to 1870. His research career began during his student years in the neurohistological laboratory of the Physiological Institute, headed by Ernst Wilhelm von Brücke (1819–1892). Obersteiner became *Dozent* (Lecturer) in 1873, *Extraordinarius* (Associate Professor) in 1880, *Ordinarius* (Full Professor) in 1898 and *Hofrat* (Court Councillor) in 1906 [4].

Obersteiner studied the histology of the cerebellar cortex and its development [5–7]. Already in 1869, he had likened the dendritic arbors of Purkinje cells to espalier trees, or trellises, as opposed to free-standing trees like the oak [5, 8]. He gave one of the early accurate descriptions of the external germinal layer of the cerebellum—sometimes referred to by later authors as the “marginal zone of Obersteiner” [9] or “Obersteiner layer” [10]—and further noted the migration of granule cells from the external germinal layer, through the molecular layer, and their final settling in the internal granule cell layer [6].

Historically, the first description of the external germinal layer, as well as its fate in adults, is credited to Nicolaus Hess [11], who, in his doctoral thesis at the University of Dorpat (then in the Governorate of Livonia, today University of Tartu in Estonia), showed that the cerebellar anlage was covered by a so-called “stratum granulosum periphericum” (Fig. 2g) [12, 13]. Obersteiner’s contribution [5] was that, with Carmine staining, he distinguished in the external germinal layer a superficial, tightly-packed sublayer, and a deeper sublayer with rounded, loosely-arranged cells. In agreement with Hess [11], Obersteiner [5] described in the molecular layer radial processes emanating from external granule cells [13]. The histogenesis of the cerebellum was subsequently clarified owing to the detailed studies of Ramón y Cajal [14] in several vertebrate species.

In his *Introduction to the Study of the Structure of the Central Nervous Organs in Health and Disease* [7, 15], he summarized the state-of-the-art knowledge on the normal and pathological anatomy of the human nervous system. While Toeplitz and Deuticke, the publishers, printed 1888 on the title page [15], Obersteiner’s preface is actually dated October 1887. This textbook went through four additional German editions over the following 25 years, and it was translated into English, Russian, French, and Italian. Obersteiner integrated many of his original research findings into the book. Otto Marburg (1874–1948), his successor at the Institute, remarked that “it is always the disadvantage of a textbook, whereby the author’s own research can become lost, and one might hardly appreciate how many of his own new findings that book contains…that would be difficult to list singly” [16].

In reviewing Obersteiner’s textbook [15], the young neurologist Sigmund Freud [4] noticed the fact that the section on the cerebellum was particularly rich (Fig. 2). This part of the brain had been essentially neglected since the time of Benedikt Stilling (1810–1879). In his day, Obersteiner was considered a distinguished scholar of the cerebellum [17]. The particular lecture at the Salzburg meeting [18] is presented as a cerebellar classic in order to serve as a gateway to his other work.

In the textbook, Obersteiner [15] devoted two sections on the macroscopy, connections, ontogeny, and pathology of the cerebellum. Regarding the fate of distal Purkinje dendritic branches in the molecular layer (“the finest twigs”), he commented that the views whereby these ended freely on the surface or a portion of them bent round and turned inwards at the surface or deeply in the molecular layer, “must be regarded as hypothetical and intended to help us out of the embarrassment in which our inability to discover such a termination of these twigs as will satisfy the physiological necessities of the case places us.” And added: “Not only are coarse anastomosing branches between the Purkinje cells wanting, but even the very finest processes of the cells fail to unite with one another, no proper network, in the strict sense of the work, is present in the molecular layer” [7]. A clear stance against reticularism is evident in these words.

Furthermore, Obersteiner noticed certain small (ectopic) clumps of grey matter in the midst of the white matter (Fig. 4h) that contained club-shaped neurons similar to Purkinje cells, granule cells, and a close capillary network [6, 15]. In the subheading on pathological changes, he briefly went over congenital atrophies, tumors, vascular, and inflammatory diseases [7], including chronic encephalitis, where the spaces in which Purkinje cells used to lie were still recognizable (Fig. 4i).

In an earlier paper on “The finer structure of the cerebellar cortex in humans and animals” [6], Obersteiner attributed the slow progress on the histological structure of the cerebellar cortex in part to the optical limitations of microscopes available at the time. An early echo of neuronism can be found in his phrase, “I must note that there are no major anastomoses between Purkinje cells and that even the finest processes do not unite with others, i.e., there is actually no nerve fiber network in the strict sense of the word in the molecular layer” [6].

The structural organization of the cerebellar circuitry was deciphered by Santiago Ramón y Cajal (1852–1934) after three years of intense research [19–21]. Using the Golgi method, he discovered the mossy and climbing fibers [22, 23], and went further, by describing the articulation between mossy fibers and granule cell dendrites at the level of the cerebellar glomerulus, as well as the participation of the Golgi neuron axonal ramifications in it [24]. Those observations led him to postulate the concept of a synapse by "gearing" [25].

The original German edition of Obersteiner's textbook [15] came out just before Ramón y Cajal began publishing his first studies with the Golgi method. Nonetheless, Obersteiner made insightful comments on contiguity versus continuity. In the second edition, Obersteiner [26] cited Ramón y Cajal's new discoveries on the embryonic spinal cord, which provided evidence for the autonomy of the nerve cells [27]. In the subsequent editions, Obersteiner [28–30] expanded the section on the histology of the nerve cell with repeated references to Ramón y Cajal's findings [19–21], and even used the latter's classic drawing of the cerebellar circuitry. He certainly relied on Ramón y Cajal's observations in the lecture of 1909 [18], and the refutation of the reticular theory pleads in his favor.

The 81st Meeting of the Society of German Natural Scientists and Physicians was held on 19–25 September 1909 in Salzburg, Austria. Several prominent faculty members of the School of Medicine of Vienna University spoke in the Session on Neurology and Psychiatry, including Emil Redlich (1866–1930) on epilepsy, Julius Wagner von Jauregg (1857–1940) on progressive paralysis, Alfred Fuchs (1870–1927) on myelohyperplasia, and Obersteiner on the cerebellum (Fig. 3). In a historic context, at the same conference, in the Session on Physics, Albert Einstein developed his views on the nature and constitution of radiation [31]; he showed that photons must carry momentum and should be treated as particles, and thus introduced the wave-particle duality of electromagnetic radiation [32].

In his talk, Obersteiner focused on the histology and physiology of the granule cell layer of the cerebellum [18, 33]. An English translation of the communication is provided in the companion cerebellar classic [34]. He covered most of the fundamental elements of the cerebellar circuit, namely, the unique morphology of the soma and the processes of granule cells; the monoplanar disposition of Purkinje cell dendrites; the arrangement of parallel fibers and their contacts with Purkinje dendritic spines; the mossy fiber input and the formation of the cerebellar glomeruli; the climbing fiber and basket cell axonal investment of Purkinje cells; the Purkinje axonal projection to the cerebellar nuclei; the Golgi neurons inside the granule cell layer, and the Golgi epithelial cells (the cells of origin of Bergmann glia). Concerning the latter, he reiterated that he had previously described, in 1895, what the French researchers Maurice Lannois (1856–1942) and Jean Paviot (1866–1944) of Lyon termed a "new layer" (i.e., the Golgi epithelial cells) in the vicinity of the Purkinje cell layer. Finally, he made some functional correlations, especially regarding the interaction of the vestibular and the cerebellar systems in maintaining body balance, and rebutted the “reticularist” stance of the Hungarian histologist Stephan (István) von Apáthy (1863–1922) of Kolozsvár (today Cluj-Napoca, Romania), who had attacked the neuron theory by insisting that nervous conduction took place through small fibers passing from one nerve cell into another [35].

Subsequently, Obersteiner’s interest in the comparative morphology of the cerebellum was extended to include the Indian elephant (Elephas indicus) and the fin whale (Balaenoptera physalus) [36]. In an one-year old elephant, he depicted the outer granular layer comprising 2–3 rows of cells, similar to the neonatal avian and mammalian cerebellum. Compared to humans, but even more to small mammals, Purkinje cells were arranged in very loose rows, occasionally leaving rather wide cell-free spaces. Obersteiner also described the presence of Golgi neurons in the granular layer of the elephant cerebellum (Fig. 4a). In the whale cerebellum, the molecular layer showed nothing remarkable; as in the elephant, Purkinje cells were also quite scattered. The larger neurons of the granular layer which were seen in the elephant appeared to be present only in very small numbers in the whale, with large neurons found in considerable numbers in the subcortical white matter, underneath the granular layer (Fig. 4b).

The general plan of the connections in the cerebellar cortex remains constant in all vertebrates and serves as a basis for understanding its function [6, 15, 37]. Furthermore, the cerebellum of all animals is closely tied to the brain centers that receive fibers from the receptors for linear and rotational acceleration in the vestibular nuclei, although the connections of the vestibular nuclei with the cerebellum are not so extensive, limited to the flocculus and parts of the vermis [38]. In its rudimentary form in Cyclostomes, the cerebellum is merely a “bridge” of nerve tissue with parallel fibers and Purkinje cells between the left and the right vestibular nuclei [37].

The convergence of separate sensory (upper body proprioceptive) and basilar pontine pathways onto individual granule cells informs us about the multimodality of mammalian granule cells and substantiate their associative capacity; further, the convergent basilar pontine pathways carry corollary discharges from upper body motor cortical areas. The merging of related corollary and sensory streams is a critical component of circuit models of predictive motor control [39].

It is currently understood that granule cells do more than just relay the signals of mossy fibers to the Purkinje cells. They actually perform complex and diverse transformations in space and time, being subjected to feedback and feedforward inhibition alike [40]. Moreover, there is an excitatory feedback projection between the cerebellar nuclei and the granule cell layer, which terminates in mossy fiber-like endings [41].

The cornerstone of the emerging models of cerebellar function is the implication of the cerebellum in behaviors beyond purely sensorimotor. The traditional dichotomy of motor and cognitive processes is outdone [42–44].

A pertinent foresight by Obersteiner becomes evident in the following statement: “Impressions of muscle-sense and of equilibrium…continually exert an influence on the threshold of consciousness and so modify the movements of the body without needing the interventions of the cerebral cortex” [7].

Marr [45] first proposed that the cerebellar cortex might act as a learning device for performing motor skills. Marr [45] and Albus [46] suggested that granule cells acted as combinatorial expanders, sparsely encoding ongoing sensorimotor information to allow associative learning at the Purkinje cells, their postsynaptic targets [42]. Modern studies with in vivo calcium-imaging show that, compared to what was predicted by the models of Marr [45] and Albus [46], the actual density of active granule cells during simple tasks is even higher [44].

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Compliance with Ethical Standards

Conflict of Interest The author declares that he has no conflict of interest.

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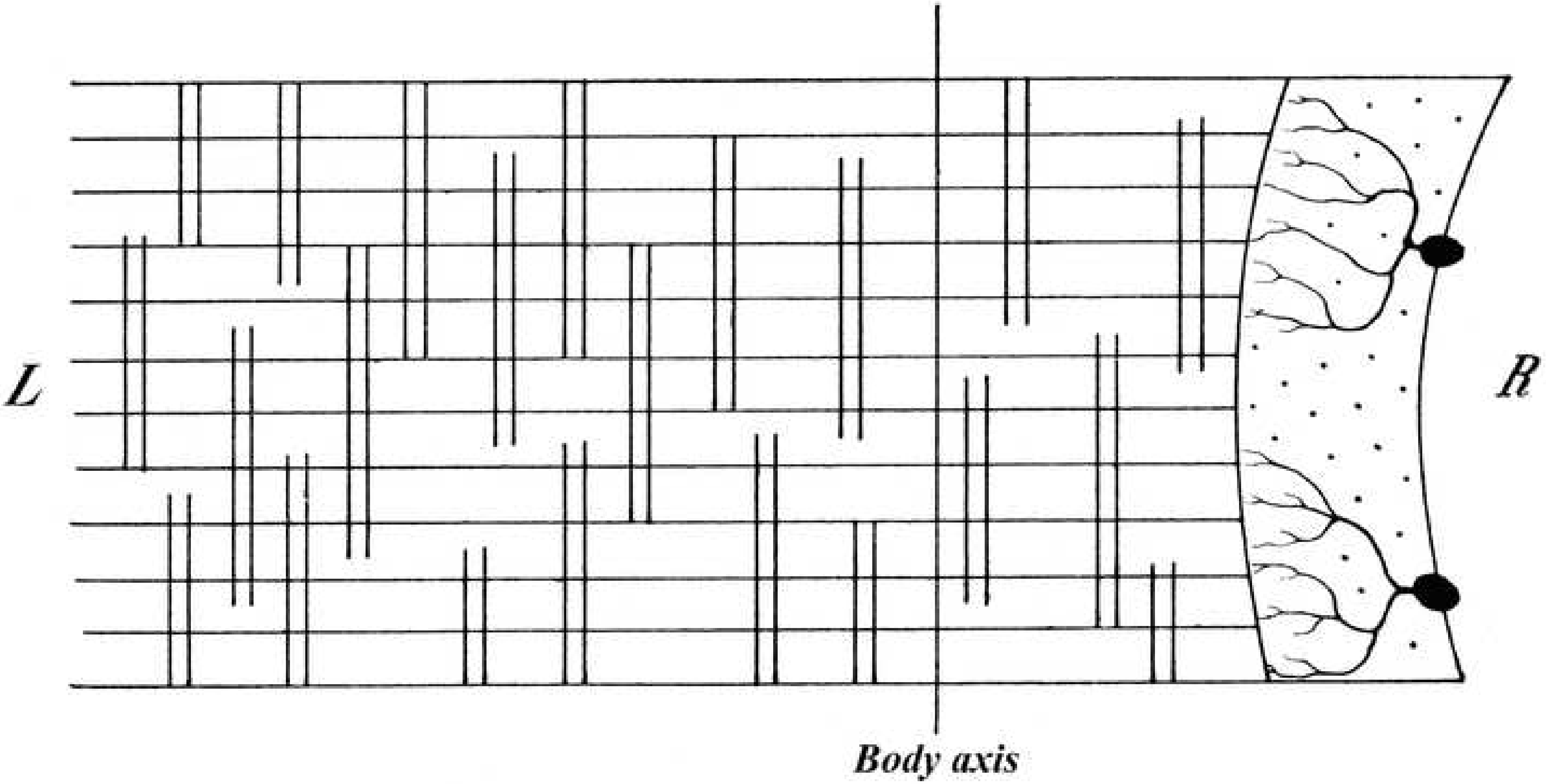
Figure captions

Fig 1 The Laboratory of the Neurological Institute in Vienna. The "University Institute for the Anatomy and Physiology of the CNS" was renamed "Neurological Institute" in 1900. Heinrich Obersteiner is seen seated, third from the left. Photo by Elfriede Hanak-Broneder [1]

Fig 2 Cerebellar histological illustrations from Obersteiner's textbook [7], except **g**, which is from the thesis of Hess [11]. **a** A frontal section through the cerebellum and medulla of an ape. **b** Cross-section through a cerebellar folium, stained with Carmine. **c** Cross-section through a cerebellar lobule stained with the Weigert method. **d** Vertical section of normal cerebellar cortex from the lateral surface of a folium, stained with Carmine. **e**, **f** The biplanar disposition of Purkinje cell dendrites as seen with the Golgi method in a sagittal and a coronal section. **g** Section of calf cerebellum. *A*, white matter; *a*, prominent axon; *b*, denuded axon; *c*, bifurcated axon; *d*, bifurcated white matter fibers; *e*, scattered granules in the white matter; *B*, internal granular layer ("stratum granulosum centrale"); *C*, cellular layer; *f*, Purkinje cell axon ("centralis cellulae nerveae processus"); *g*, Purkinje cell dendrite ("periphericus cellulae nerveae processus"); *D*, molecular layer; *h, h´*, grains in the molecular layer; *E*, external granular layer ("stratum granulosum periphericum"); *F*, pia mater; *i*, prominent processes of pia mater [11]. **h** Section through a small heterotopic gray patch *(b)* within the cerebellar white matter *(a)*. **i** Weigert stain of the human cerebellum in a case of encephalitis with the radial fibers of the molecular layer being distinct, and so are the holes out of which the Purkinje cells have disappeared

Fig 3 Abstract of Obersteiner's communication from the Proceedings of the Salzburg Meeting [33]. The Session on Neurology and Psychiatry was chaired by Guido Weber (1837–1914) of the Sonnenstein Mental Asylum in Pirna, near Dresden

Fig 4 Histological drawings of **a** the elephant and **b** the whale cerebellar cortex [36]


L
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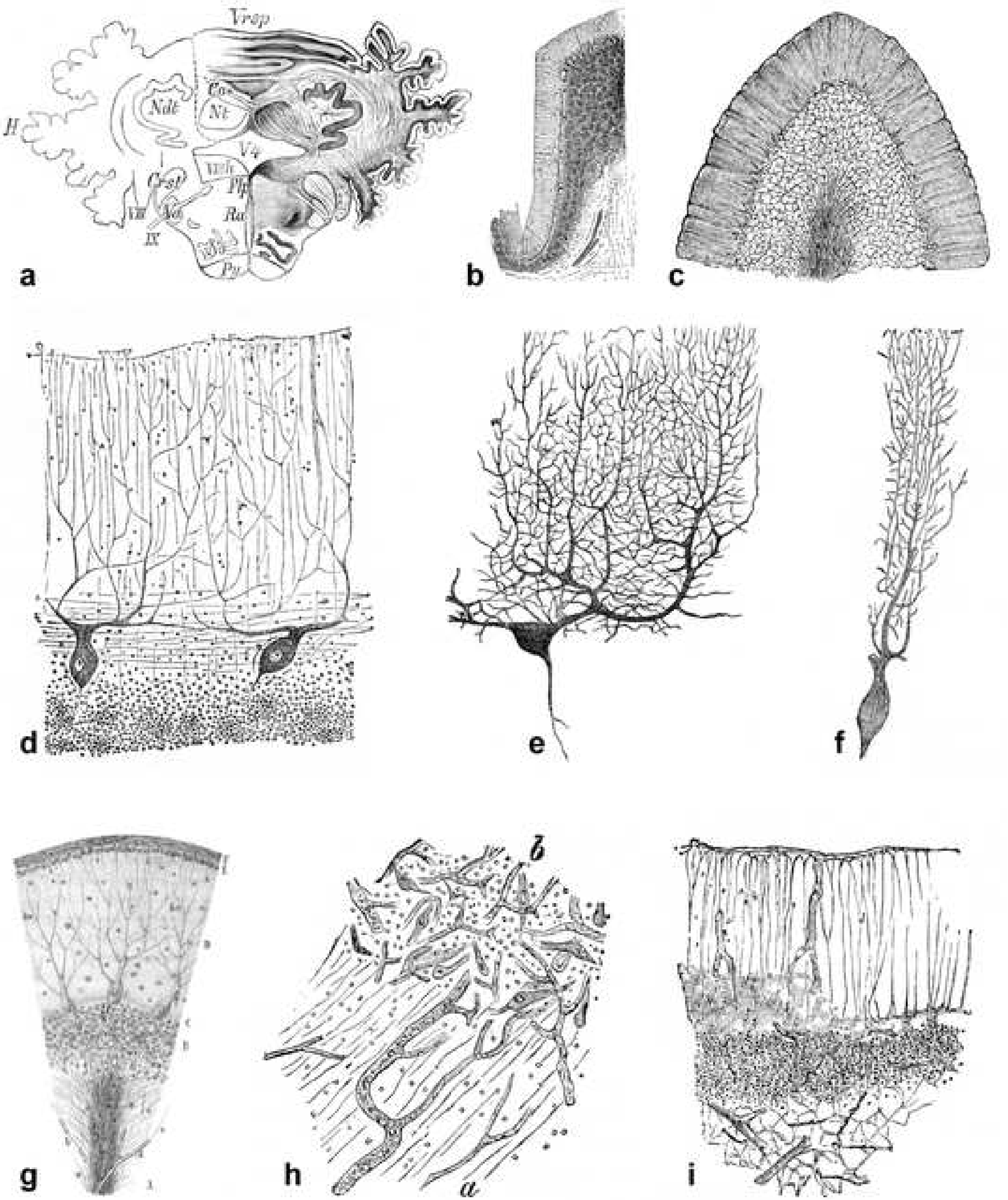
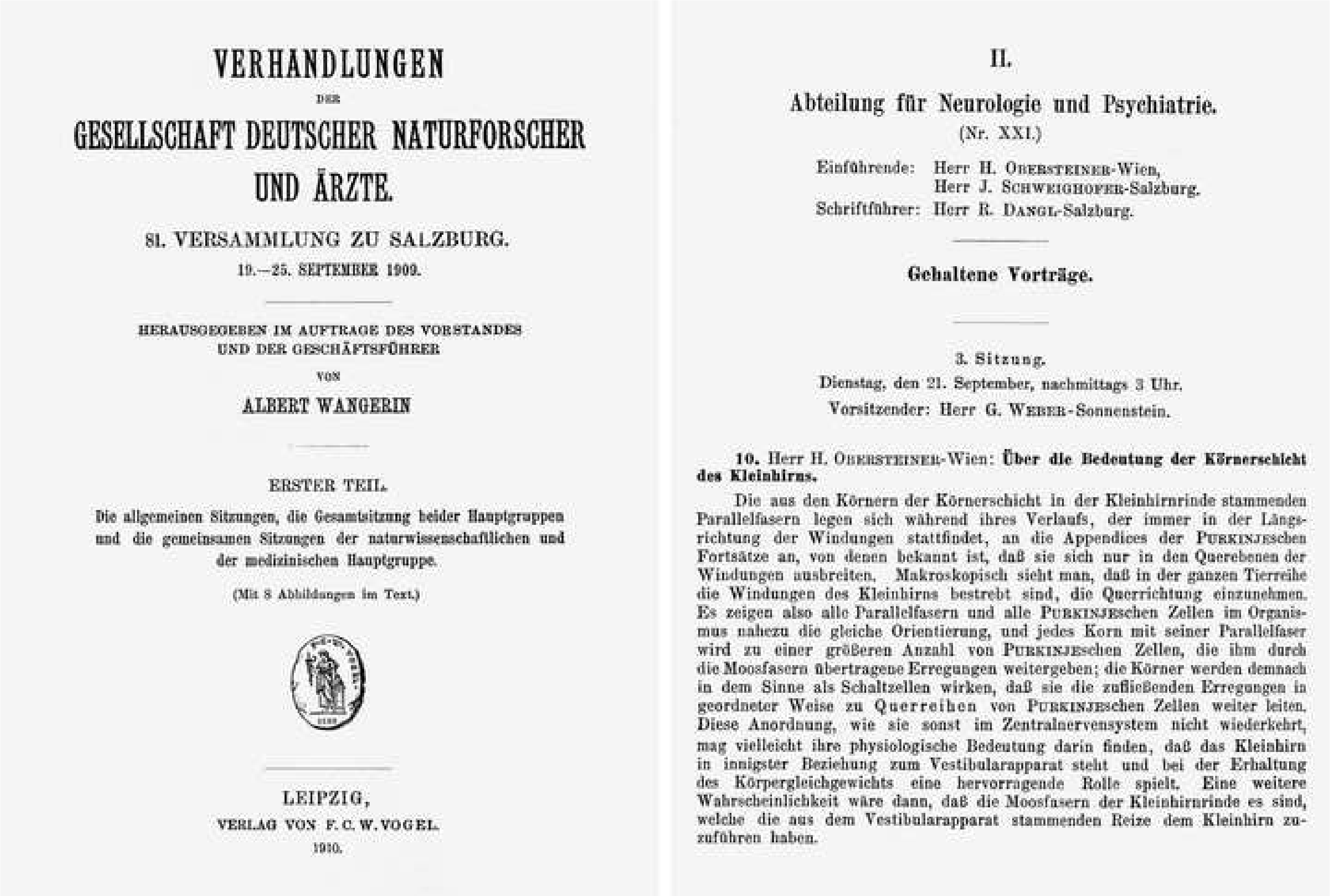
Body axis

Commentary Figure 2



Commentary Figure 3



VERHANDLUNGEN
DER
GESELLSCHAFT DEUTSCHER NATURFORSCHER
UND ÄRZTE.

81. VERSAMMLUNG ZU SALZBURG.
19.—25. SEPTEMBER 1909.

HERAUSGEGEBEN IM AUFTRAGE DES VORSTANDES
UND DER GESCHÄFTSFÜHRER
VON
ALBERT WANGERIN

ERSTER TEIL.
Die allgemeinen Sitzungen, die Gesamtsitzung beider Hauptgruppen und die gemeinsamen Sitzungen der naturwissenschaftlichen und der medizinischen Hauptgruppe.

(Mit 8 Abbildungen im Text.)

LEIPZIG,
VERLAG VON F. C. W. VOGEL.
1910.

II.

Abteilung für Neurologie und Psychiatrie.
(Nr. XXI.)

Einführende: Herr H. Obersteiner-Wien,
Herr J. Schweighofer-Salzburg.
Schriftführer: Herr R. Dangl-Salzburg.

Gehaltene Vorträge.

3. Sitzung.
Dienstag, den 21. September, nachmittags 3 Uhr.
Vorsitzender: Herr G. Weber-Sonnenstein.

10. Herr H. Obersteiner-Wien: **Über die Bedeutung der Körnerschicht des Kleinhirns.**

Die aus den Körnern der Körnerschicht in der Kleinhirnrinde stammenden Parallelfasern legen sich während ihres Verlaufs, der immer in der Längsrichtung der Windungen stattfindet, an die Appendices der Purkinjeschen Fortsätze an, von denen bekannt ist, daß sie sich nur in den Querebenen der Windungen ausbreiten. Makroskopisch sieht man, daß in der ganzen Tierreihe die Windungen des Kleinhirns bestrebt sind, die Querrichtung einzunehmen. Es zeigen also alle Parallelfasern und alle Purkinjeschen Zellen im Organismus nahezu die gleiche Orientierung, und jedes Korn mit seiner Parallelfaser wird zu einer größeren Anzahl von Purkinjeschen Zellen, die ihm durch die Moosfasern übertragene Erregungen weitergeben; die Körner werden demnach in dem Sinne als Schaltzellen wirken, daß sie die zufließenden Erregungen in geordneter Weise zu Querreihen von Purkinjeschen Zellen weiter leiten. Diese Anordnung, wie sie sonst im Zentralnervensystem nicht wiederkehrt, mag vielleicht ihre physiologische Bedeutung darin finden, daß das Kleinhirn in innigster Beziehung zum Vestibularapparat steht und bei der Erhaltung des Körpergleichgewichts eine hervorragende Rolle spielt. Eine weitere Wahrscheinlichkeit wäre dann, daß die Moosfasern der Kleinhirnrinde es sind, welche die aus dem Vestibularapparat stammenden Reize dem Kleinhirn zuzuführen haben.

Commentary Figure 4