Neuroanatomy

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J. Voogd

The history of neuroanatomy in the Netherlands, like that of other scientific disciplines, is the history of people and their ideas. Only a few gifted scientists occupy the centre of the stage; their scientific progeniture occupies many of today's chairs of Neurology and Anatomy. Their ideas and interests, which inspired their contemporaries, have often lost some of their glamour. In some cases, however, there has been a continuity of the topics of the research throughout the generations. This continuity, and the emergence of completely new initiatives, is the subject of this review. Dutch neuroanatomy is not an isolated affair; it participates in the international development of concepts and techniques. Achievements of Dutch neuroanatomists, therefore, should be viewed against the background of events elsewhere in the world. The first section of this review is a rough sketch of these international developments from the early s onwards. It begins with the introduction of the compound microscope and the use of achromatic objectives by Lister, in . Indeed, neuroanatomy is a science of microscopy, just as astronomy is non-existent without the telescope. The description of the gross anatomy of the central nervous system, which was almost complete around that time, accordingly, will not be considered in this chapter. Dutch contributions to this field were reviewed in the monograph of Schulte and Endtz ( ). Publications on neuroanatomy and related subjects from the period of approximately up to are listed in the bibliographies of Mesdag ( ) and Bouman ( ). The main international developments in neuroanatomy are summarised in Table I. Table II depicts the genealogy of Dutch neuroanatomists.

International developments

The emergence of new methods to study the microscopical anatomy and the histology of the brain, the development of ideas about the histology of nervous tissue, and the growing interest in the microscopical topography of the central nervous system have been summarised in the three, more or less synchronous time-columns of Table I. More complete reviews and the references to these topics can be found in the monographs of Clarke and O'Malley ( ), Haymaker and Schiller ( ), Bracegirdle ( ), Shepherd ( ) and Jacobson ( ). The early history of the histology of the nerve cell is copied from Van der Loos ( ).

With a few exceptions, there are no Dutch among the scientists who developed the field in the th century. It is almost exclusively an affair of the German-speaking world. Most of the techniques for ethanol and chromic acid fixation, which remained in

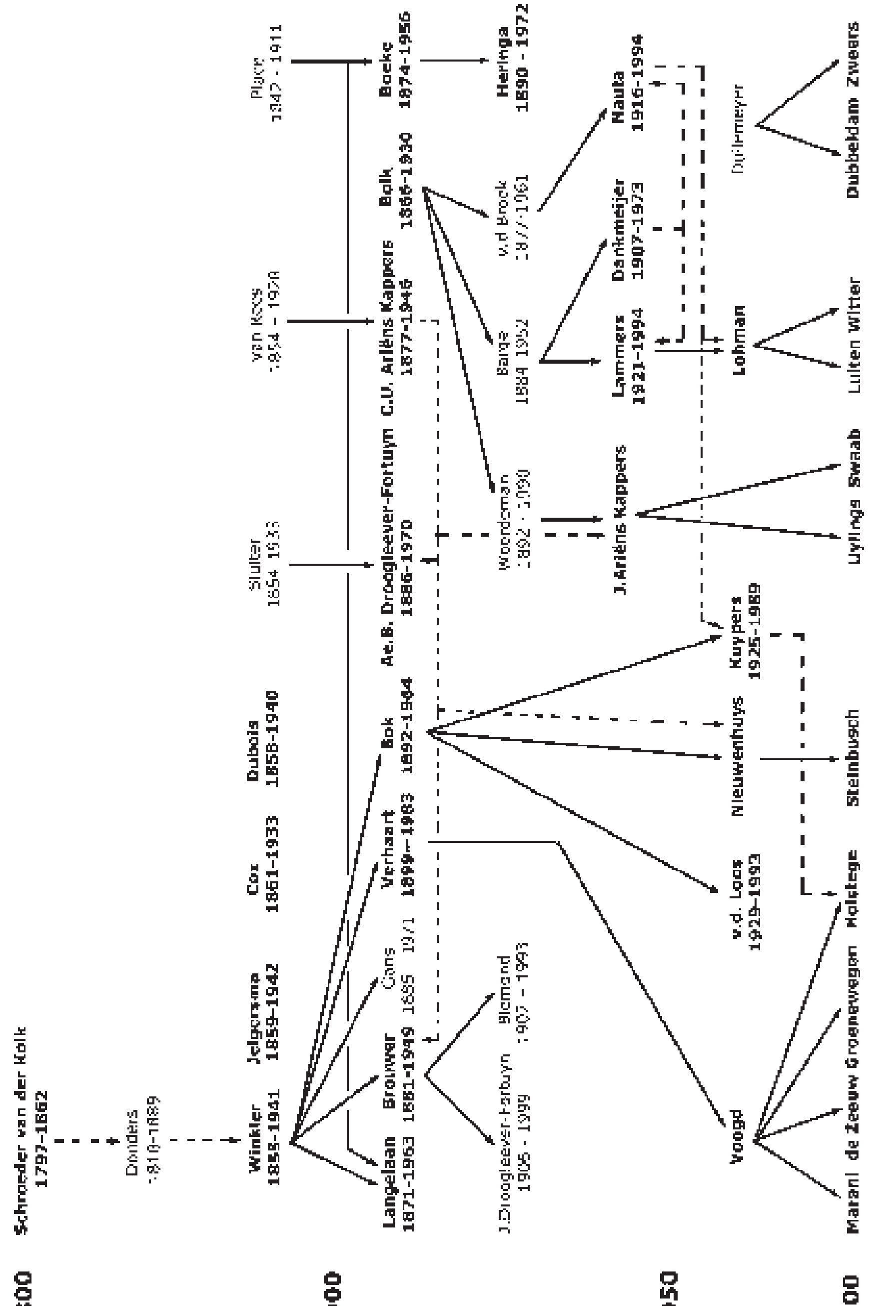

Table II. The genealogy of Dutch neuroanatomy.
Only scientists who occupied academic chairs or lectureships are included, with the exception of Cox. Those who found one of their main occupations in neuroanatomy are in bold print.

common use till Blum introduced formalin as a fixative in , serial sectioning, the staining of nervous tissue with carmine and with Ehrlich methylene blue, as in the Nissl method, the introduction of the aniline–dye 'Perkin's mauve" by Beneke ( ), Weigert's myelin stain, embedding in paraffin and celloidin (introduced by Duval in , and improved by Schiefferdecker in), were discovered in German laboratories. These improvements in histological techniques favoured studies on the microscopical topography and the comparative anatomy of the brain and the spinal cord, starting with the beautiful volumes of Stilling (b, , , -) illustrating unstained, serial sections of the cord, the medulla oblongata, the pons and the cerebellum in unsurpassed detail, followed by the textbooks of Meynert (/ , "Erst seit Meynert ist das Gehirn beseelt" [Meynert blew the breathe of mind into the brain]) , his pupil Flechsig ( ) and his second-generation student von Bechterew ( ). Meynert, Flechsig and von Bechterew, like other authors of texts on the topography of the central nervous system such as Obersteiner, von Monakow and Dejerine, were clinicians, who fostered the hope that the advances in neuroanatomy would explain nervous and mental diseases. The comparative anatomical studies of the nervous system of Judson Herrick who, together with his brother Clarence, founded the *Journal of Comparative Neurology* in , and Edinger were also facilitated by these techniques.

Türck's (, a,b) observation of granule cells in degenerating pyramidal tract and some ascending spinal fiber systems of the cord, and Waller's discovery in the same year of his method of secondary degeneration (a "New method for studying the nervous system which can be applied to research of the distribution of the nerve columns"), paved the way for the tracing of nervous connections. Von Gudden's ( ) method of secondary atrophy of tracts and nuclei, upon removal of parts of the brain in young animals, introduced the experimental approach in neuroanatomy. Most influential, however, was the myelogenetic method, introduced by Flechsig and extensively used by von Bechterew and Edinger, which allowed the tracing of pathways in the central nervous system of human feotuses, neonates and young children, who acquire their myelin sheaths at different dates. The discovery by Marchi and Algieri ( ) that degenerating myelin, mordanted with potassium dichromate, could be stained with osmium, was the birth of modern tract tracing. Retrograde changes in nerve cells were observed with the Nissl method, published in the same year. As Gowers (-) remarked "We may learn as much of the course of fibres by studying them in their birth as in their death – in their development as in their decay" (cited by Haymaker and Schiller).

The anterograde and retrograde tracing of fibre connections, implies knowledge of the origin of nerve fibres from nerve cells. This notion took a long time to become established knowledge. Van der Loos's ( ) account of the ideogenesis of the nerve cell has been used for the early part of the time-column in Table ; references on this period can be found in his paper. Starting from van Leeuwenhoek ( ), ideas about nerve fibres and nerve cell bodies follow a separate course. Observations on the origin of the nerve fibre from the cell body culminated in Deiters' ( ) description of the essential differences in the morphology of the axon and the dendrites as prolongations of the nerve cell. Van der Loos ( ) noticed that Deiters found a second system of small axons that took their origin from the dendrites. These small axons probably represent terminals on the dendrites, but, at the time, they were considered rather as part of a reticulum, connecting all neurons. The neuron theory, “the enlightened idea that the expansions of nerve cells end freely in the grey substance just as they do in the peripheral sense organs” (Cajal), was formulated by Forel ( ) and His ( ) and epitomised by Waldeyer ( ). Forel based his concept on experimental studies with the von Gudden method of secondary atrophy; the ideas of His were derived from embryological studies. Cajal, in monumental studies, substantiated and extended the neuron theory for most systems in the brain.

Remarkably, the advances in histological techniques scarcely contributed to the development of ideas on the morphology of the nerve cell in the early th century. Most of its students used free hand dissection to isolate nerve fibres and nerve cells. The change was made by Golgi’s discovery in of the ‘reazzione nera’, the intravital methylene blue stain by Ehrlich ( ), and their adoption by Cajal.

The - surge in the development of neuroanatomy ended with the discovery and the application of the reduced silver methods by Bielschowsky ( ), Cajal ( ), del Rio Hortega ( ) and with the publication of *Histologie du système nerveux* by Cajal (/).

The long period of relative neuroanatomical silence, which lasted throughout the interbellum and the the Second World War, saw spectacular developments in the electrophysiological techniques and the ideas about nervous transmission. It followed Sherrington’s discovery (,) that the synapse conducts in one direction only, refuting Cajal’s hypothesis that the direction of conduction (the dynamic polarisation) is a property of the neuron. In the Netherlands, however, neuroanatomy flourished in this period, and saw the production of Winkler’s *Textbook of Neurology* (-) as well as the codification of comparative neuroanatomy by Ariëns Kappers, Huber and Crosby ( ).

The second half of the th century observed a ‘second flowering’ (Nauta) of neuroanatomical research, where the focus moved from Europe to the United States. With improved methods for tissue preparation, electron microscopy of nervous tissue became possible, which confirmed the neuron theory and clarified the structure of the synapse (Palade and Palay). Tract-tracing methods made it possible to analyse connections with increasing detail. In this field, Nauta, Kuypers and other Dutch scientists made notable contributions. The demonstration by Eccles ( ) of separate classes of inhibitory and excitatory neurons, in combination with enzyme histochemistry, fluorescent microscopy, immunocytochemistry and in-situ hybridisation, made it possible to approach nervous transmission with combinations of electrophysiological and morphological techniques. Dutch descriptive and comparative neuroanatomy flourished in these years, culminating in the recent monumental publication by Nieuwenhuys, ten Donkelaar and Nicholson of the *Central Nervous System of Vertebrates* in .

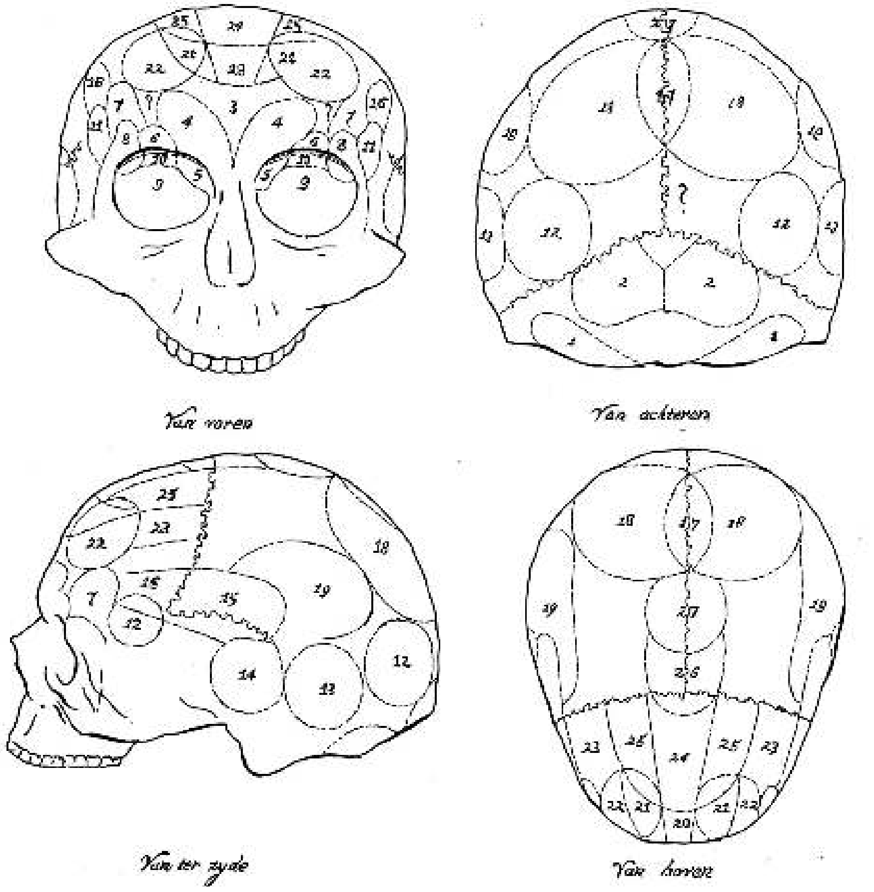

Figure .
Localisation on the skull of the different mental organs distinguished in the lectures by Gall. From Stuart ( ), retouched. The location of the sense of art ( ) and music ( ), the sense of murder ( ), and the sexual drive ( ) are indicated. Higher mental functions, such as comparative intelligence ( ) and benevolence ( ) are located frontally and dorsally.

The early years: Schroeder van der Kolk

Between the th and the th of April , Frans Joseph Gall lectured in Amsterdam on the brain as a collection of the various organs of the mind, in the auction room of an inn, ‘the Amsterdam Arms’. In his anatomy of the brain, special faculties of the mind are localised at special sites. The surface of the skull makes it possible to decide about the state of these different organs. Most of them are present in the brains of both animals and humans. The senses of art and music, located in the lower frontal region, are strongly developed in beavers and singing birds respectively (Fig.). Sexual drive is located in the cerebellum; the broad neck of Turkish men is related to

Figure .
Skull of a murderer. From the collection of Brugman at the Anatomical Museum in Leiden. Reproduced from "Het vergeten fenomeen Sebald J. Brugman," Museum Boerhaave, Leiden, / .

their polygamous inclinations. Higher mental functions are located in the upper and frontal regions of the brain, which are lacking in animals. These early public lectures on neuroanatomy were noted down and illustrated by Stuart ( ).

Interest in phrenology was widespread, also among Dutch academic anatomists. Skulls used by S.J. Brugmans (-), the Leiden professor of natural history in his phrenological studies, can still be found in the Leiden Museum of Anatomy (Brugmans ; Fig.). Gall's ideas took a long time to die out. Schroeder van der Kolk, the first Dutch microscopist of the brain, of the th century, still mentions the possible involvement of the cerebellum in sexual functions in his publications of and .

Some idea of the state of the knowledge of neuroanatomy in the Netherlands in the early th century can be gained from the Dutch translation of Bock's textbook of anatomy ( ). The extensive account of the gross anatomy of the brain and the spinal cord does not differ essentially from today's textbooks. The sections on the histology of nervous tissue are fairly up to date. Valentin's ( ) description of the globular bodies in the grey matter and the ganglia, with their vesicular nucleus and their nucleolus, is cited. Their continuity with the nerve fibres is not mentioned, with the exception of the origin of the grey, 'organic' (unmyelinated) fibres of Remak ( ) from the globules in the sympathetic ganglia. Bell's ( ) discovery of the sensory function of the dorsal and the motor function of the ventral roots is discussed and extended to van Deen's ( ) suggestion that sensory and motor functions can be attributed to the dorsal and ventral white columns of the cord, respectively. Observations on central connections are rare, with the exception of a remark on the decussation of the ventral white columns of the spinal cord, just below the corpora pyramidalia.

J.L.C. Schroeder van der Kolk (-) was appointed professor of anatomy and physiology at the University of Utrecht in as the successor to J. Bleuland (-). He is best known for his institutional reform of psychiatric care in the Netherlands, but he also published and lectured extensively on subjects of general biology, pathological anatomy, philosophy and neurology. His biography and a complete and annotated bibliography are included in van der Esch's thesis ( ). Schroeder van der Kolk published two long papers on the anatomy and the physiology of the spinal cord ( ) and the medulla oblongata (, a,b). His ideas on the structure and the function of the central nervous system were published in .

Schroeder van der Kolk's anatomical studies were clearly influenced by van Deen's observations on the physiology of the spinal cord. Van Deen (-), as his sur-

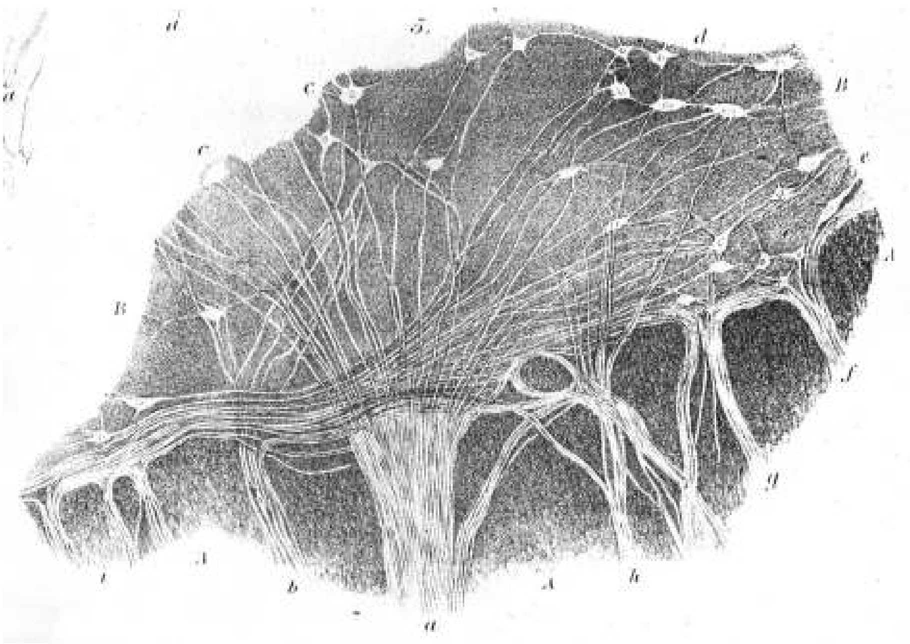

Figure .

Section through the anterior horn. Note origin of the ventral root fibres from the anterior horn cells, and anastomosing network of fibres connecting these cells. From Schroeder van der Kolk ( ). Abbreviations: A, white matter; B, grey matter; a,b, two nerve roots for motility, which extend into the grey matter; ccc, multpolar cells, giving origin to nerve roots; d,e, interconnected cells, which receive fibres from the white matter; f,g,h,i, grey ramifications from the horn and the white matter, which continue in cells as in f or constitute a marginal plexus as in i.

name suggests, was of Danish descent. His father was the chief rabbi in Groningen. He studied medicine in Denmark, and later in Leiden, where he received his doctorate in . He practiced medicine in Zwolle, and was appointed professor of physiology at the University of Groningen in . He was a careful observer and a skilled experimenter. He studied the 'nervous circulation', the distribution of reflex movements and strychnine-induced convulsions after partial transections in the cord in eviscerated frogs (van Deen ,). He concluded that sensory impressions from the dorsal roots are received by the substantia gelatinosa, and conducted by the posterior white substance to the brain. The anterior white substance subserves voluntary movement. Some of the impressions received by the posterior white columns are not conducted to the brain, but to the substantia spongiosa, the grey matter of the cord. This 'reflex sensation' causes 'reflex movement', conducted by the ventral roots. The substantia spongiosa distributes the reflex-sensation bilaterally. He suggested that the ventral roots take their origin from the substantia spongiosa. His ideas were severely, but unjustly, criticised by Stilling (a).

Schroeder van der Kolk used Stilling's method of serial sectioning of ethanol-hardened material, cleared in calcium chlorate. In his papers of and , Schroeder discusses the origin of the dorsal and ventral roots and the cranial nerves

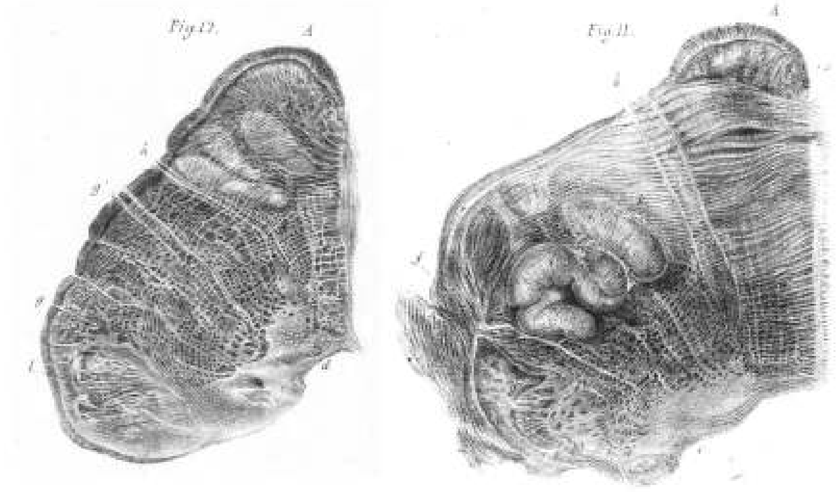

Figure .
Sections of the medulla oblongata of the cat, reproduced from Schroeder van der Kolk ( ). Left section taken at the level of the inferior olive, right section at the level of the superior olive. Abbreviations: A, corpora pyramidalia; d, facial nerve nucleus; d, nucleus of the hypoglossal nerve; f, fibrae arciformis; g, root of the trigeminal nerve; h, abducens nerve; h, hypoglossa; nerve; i, corpora olivaria superiores; k, corpora olivaria inferiores (left), superiores (right); l, restiform body.

from the grey matter. He found that the primitive fibres of the ventral root originate from groups of multipolar ganglion cells in the ventral horn, and that similar fibres interconnect these cells (Fig.). Dorsal root fibres either pass through the substantia gelatinosa of the dorsal horn as transverse bundles or ascend in the dorsal columns. In the dorsal horn they originate from ganglion cells. The transverse bundles disperse in the grey matter or may continue into the ganglion cells of the ventral horn. The sensory stimuli ultimately reach the thalamus through the dorsal white columns. He observed what later became known as Lissauer's tract (Lissauer), as a layer of small fibres surrounding the dorsal horn, and described and illustrated the marginal cells in this region, later called after Waldeyer ( ).

Originally, Schroeder considered his transverse bundles as reflex fibres that conduct the stimulus to the ganglion cells of the ventral horn, and the ascending fibres as the conductors of sensibility. After he had become acquainted with Brown-Séquard's ( ) observations on hemisection of the cord, he changed his mind and attributed the crossing of sensory impulses at the level of their entrance in the cord to the fibres in the transverse bundles. Longitudinally running fibres in the dorsal horm subserve the coordination of movement; this function, therefore, should not be attributed to the cerebellum.

His account of the decussation of the corpora pyramidalia and their continuity with the ventral columns of the cord, is the same as in Bock's Handbook. These fibres subserve movement of the extremities, and transmit impressions of our volition to the ganglion cells. He does not seem to have been aware of Türck's (, a,b) description of the course of the degenerated pyramidal tract in the cerebral peduncle, its partial decussation, and the crossed and uncrossed spinal pyramids. The first complete account of Türck's findings in the Dutch language can be found in Leubuscher ( ). In Schroeder's paper of the description of descending motor systems is still vague and incomplete. Fibres, descending mainly from the corpora striata, the centres of movement, enter the medulla oblongata, cross in the raphe and carry impressions of our volition to the nuclei of the cranial nerves. The occurrence of a crossed paralysis of the cranial nerves, therefore, is due to the decussation of these descending fibres, and not to a crossed origin of the cranial nerves.

Schroeder van der Kolk was the first to distinguish and to report on the comparative anatomy of the superior and inferior olives (Fig.). He considered these nuclei as adjuncts to the cranial nerves passing through them. The inferior olive is concerned with movements of the tongue by the hypoglossal and accessory nerves; in man, where it is extremely large, it is involved in speech.

Cornelis Winkler and his contemporaries: the late 1800s

W. Koster (-) succeeded Schroeder van der Kolk as professor of Anatomy, but his neuroanatomical studies lacked unequivocal follow-up. No publications by Dutch authors on neuroanatomical subjects appeared between and and I have been unable to find any Dutch textbooks discussing the great developments in neuroanatomy in this period.

Cornelis Winkler (-) acknowledged Donders' brilliant lectures on physiology and Donders' influence on his own later career (Winkler). It was in the lab of Donders' son-in-law, Professor Th.W. Engelmann (-), who had taken over Donders' lectures in histology in , that Winkler, still a student, started his research. His interest in neuroanatomy was awakened some years later when, as an assistant in internal medicine, he spent his free time repeating Fritsch and Hitzig's ( ) demonstration that electrical stimulation of the cerebral cortex induced motor responses in C.A. Pekelharing's laboratory(-). During tours of German psychiatric institutes, which he made at Donders' suggestion before his appointment as a lecturer in psychiatry in , he met von Gudden, Meynert, Obersteiner, Edinger and Weigert. On his return to Utrecht, he started experiments on rabbits, using von Gudden's method of secondary atrophy, but he did not publish on this subject at that time.

During his lectureship and his later professorship of Neurology and Psychiatry in Utrecht (-) he published only a few anatomical papers on the origin of the pyramidal tract (, Winkler and Wellenbergh), which he (mistakenly) located in posterior central gyrus and the lobulus paracentralis, and on the localisation of fibres from more posterior parietal and temporal regions in the lateral portion of the cerebral peduncle ( ). After his appointment as professor of neurology and psychiatry in Amsterdam (-), most of his publications were still concerned with

Figure .
Winkler's lab in Utrecht in the early s: Verhaart ( ), Freule van As van Wijck ( ), mevr. Winkler-Junius ( ), Ada Potter ( ), Winkler ( ), Stenvers ( ), de Ruiter ( ), C.G.M. de Vos ( ), ? ( ), Koopmans ( ), mej. Hoogland ( ). Courtesy of ir. P. Verhaart.

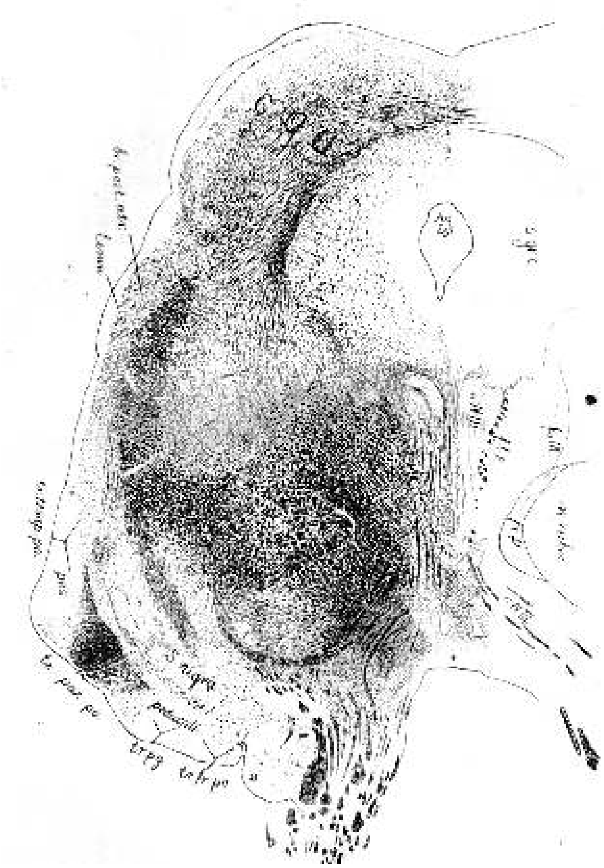

Figure .
Weigert-stained section through the mesencephalon, of a case with a large softening of the cerebral hemisphere. Drawing by Ada Potter, legends in Winkler's handwriting. Winkler, Handbook ( ).

clinical or forensic subjects and matters of organisation. One of his main anatomical interests during this period was the anatomy of the eighth nerve. In a lengthy treatise ( ) he described the partial overlap in the distribution of the vestibular and cochlear nerves, and was able to follow their fibres, across the midline, in what was already known at the time as the secondary vestibular and cochlear pathways (Fig.). These observations were confirmed in the thesis of Valeton ( ) on the myelination of the vestibulo-cochlear nerve and in the second volume of Winkler's *Handbook of Neurology* (-). The observations by Cajal ( ) and others on the absence of overlap and the more limited termination of these nerves were apparently not taken into consideration by Winkler.

Experimental anatomical and physiological studies on the vestibular system were also conducted by L.J.J. Muskens (-), another of Winkler's pupils, who received his doctorate shortly after Winkler had left Utrecht in . Muskens practiced neurology and neurosurgery in Amsterdam. He is best known for his demonstration of the 'ascending tract of Deiters' ( ), the uncrossed ascending connection of the vestibular nuclei, which has nothing to do with Deiters' nucleus, and which still plays a controversial role in conjugated horizontal eye movements (Baker and Highstein). His scientific life's work was summarised in a monograph of .

The numerous students who obtained a doctorate under Winkler's guidance are listed in his Opera Omnia ( ). During this period he also started his collaboration with Ada Potter, whose anatomical atlas of the rabbit brain (Potter) was published as her thesis. Her skill in drawing produced the *Anatomical guide to experimental researches on the cat's brain* (Winkler and Potter **),** the unfinished atlas of the human brain (Winkler and Potter), and many of the illustrations in Winkler's later publications. The cat atlas was the first publication to be supported by the Remmert Adriaan Laan Foundation, one of Winkler's creations, which still supports the publication of neuroanatomical research. The human atlas was part of an international project, inspired by the Brain Commission, of which only some of the large-scale drawings of Fuse and von Monakow (-) were realised in the Zürich Brain institute.

Winkler moved back to the Utrecht in (Fig.). In the period up to his retirement in he wrote the last three volumes of his *Textbook on Neurology* (-) and supervised the theses of Bok ( ), Hoeneveld ( ), Verhaart ( ) and others. His textbook is an impressive monument to his knowledge of neuroanatomy, but as a reference book it is almost useless. Winkler acknowledged the contributions of others, but without dates or references. Descriptions and Ada Potter's illustrations of histological preparations of the brain of man or animals, unpublished experiments of unknown provenance and diagrams, all labelled in his own handwriting, are combined into a very personal, five volume account of neuroanatomy (Fig.). I doubt whether many of the neurologists and psychiatrists, to whom these volumes were addressed, ever read them.

Winkler, who spent much of his time behind the microscope, according to his own testimony and to that of his biographers (Brouwer), was foremost a teacher, a clinician and an influential and well-connected organiser. He started, together with L. Bolk, the short-lived Dutch journal for anatomy *Petrus Camper* (-), he founded the Society of Amsterdam Neurologists together with C.T. van Valkenburg, K.H. Bouman and J.K.A. Wertheim-Salomonson in , and was one of the three initiators of the foundation of the Central Institute of Brain Research in Amsterdam in the same year. Through his students, Verhaart and Bok, most of today's neuroanatomists are his second or third generation successors (Table II). Winkler's collection of histological slides is kept at the Netherlands Institute of Brain Research in Amsterdam.

During the last decades of the th century, three other Dutch anatomists, Eugène (M.E.F.T) Dubois (-), G. Jelgersma (-) and W.H. Cox (-) started their research: Dubois in the Department of Anatomy in Amsterdam; Jelgersma and Cox as house doctors in asylums for the insane. None of them had had a gymnasium education when they entered medical school and, as a consequence of the legislation of the time, they were not admitted to a doctorate. This was remedied by the conferral of honorary doctorates to Dubois by the University of Amsterdam in , and to Jelgersma and Cox by the University of Utrecht in . L. Bolk, the future professor of Amsterdam, who did not even finish the gymnasium, received an honorary degree from Leiden in .

Eugene Dubois is best known for his discovery of the fossiled remains of the Pithecanthropus erectus in Trinil on the Indonesian island of Java between and . Before that time, he started publishing on the relationship of brain weight to body size (Dubois a,b; for later publication see Brummelkamp). He distinguished two exponents that determine this relationship. The somatic exponent determines the relationship of brain size with body weight in a group of animals whose brains are of a similar organisational level. Dubois found that the value of this exponent of / was very similar for mammals of quite different orders. The cephalisation factor determines the 'psychic', i.e., organisational level of the brain. For the human brain the cephalisation factor was calculated at . , for the antropoid apes at . , for the mouse at . , and for the shrew at . . These studies were pursued later by several of C.U. Ariëns Kappers' students. Brummelkamp's thesis ( ) applied the theory of cephalisation to anthropological problems, which interested Ariëns Kappers during the later part of his career. Dubois and Brummelkamp concluded that the increase of the encephalisation factor from more primitive orders to the primates is a saltatory one, following an arithmatic progression. More recently the subject was reviewed, and Dubois' and Brummelkamp's ideas were criticised by Hofman ( ) and van Dongen ( ). Dubois' approach can be recognised in Bok's mathematical description of the structure and the progressive development of the cerebral cortex , which will be considered in the next section of this chapter.

Jelgersma was still a student when he was appointed prosector at Meerenberg (Carp). Jelgersma was a prolific author: he published more than papers, many of them on neuroanatomy before his appointment as a professor of Psychiatry in Leiden, in . His writings were occasionally lacking on carefully researched anatomical detail, but they often contained interesting analogies and original ideas on functional correlations. From circa onwards his main interest went out to psychoanalysis. After his retirement in , he published his well-known *Atlas anatomicum cerebri humani* ( ), which later appeared in Ranson and Clarke's ( ). His original research on the internal structure of the brain of aquatic mammals was published as a monograph in . His collection of histological preparations is still kept at the Department of Physiology of Leiden University (Marani et al.).

Jelgersma made important contributions to the functional anatomy of the cerebellum, the first time in , in a series of publications in international journals (see Carp for references) and in two monographs (,). He conceived the cerebellum as reciprocally connected with the cerebral cortex through the cerebello-thalamic and cortico-ponto-cerebellar systems, and with the periphery, through the spinocerebellar tracts and the descending limb of the superior cerebellar peduncle, which he, mistakenly, supposed to terminate in the spinal cord. Afferent fibres from the pons terminate as mossy fibres in the cerebellar cortex and influence Purkinje cells through the parallel fibres, the axons of the granule cells. Climbing fibres, therefore, are the terminals of another pathway, i.e., of the spinocerebellar tracts that relay peripheral stimuli to the Purkinje cells. The cerebellum coordinates simple reflex movements or automatisms (low-level coordination) and learned, compound movements such as locomotion and speech, which involve the cerebral cortex (high-level coordination). Coordination is achieved by the Purkinje cells, the central elements of the cerebellar cortex, which project to the cerebellar nuclei, the source of the efferent pathways of the cerebellum. When a movement is initiated by the cerebral cortex, the

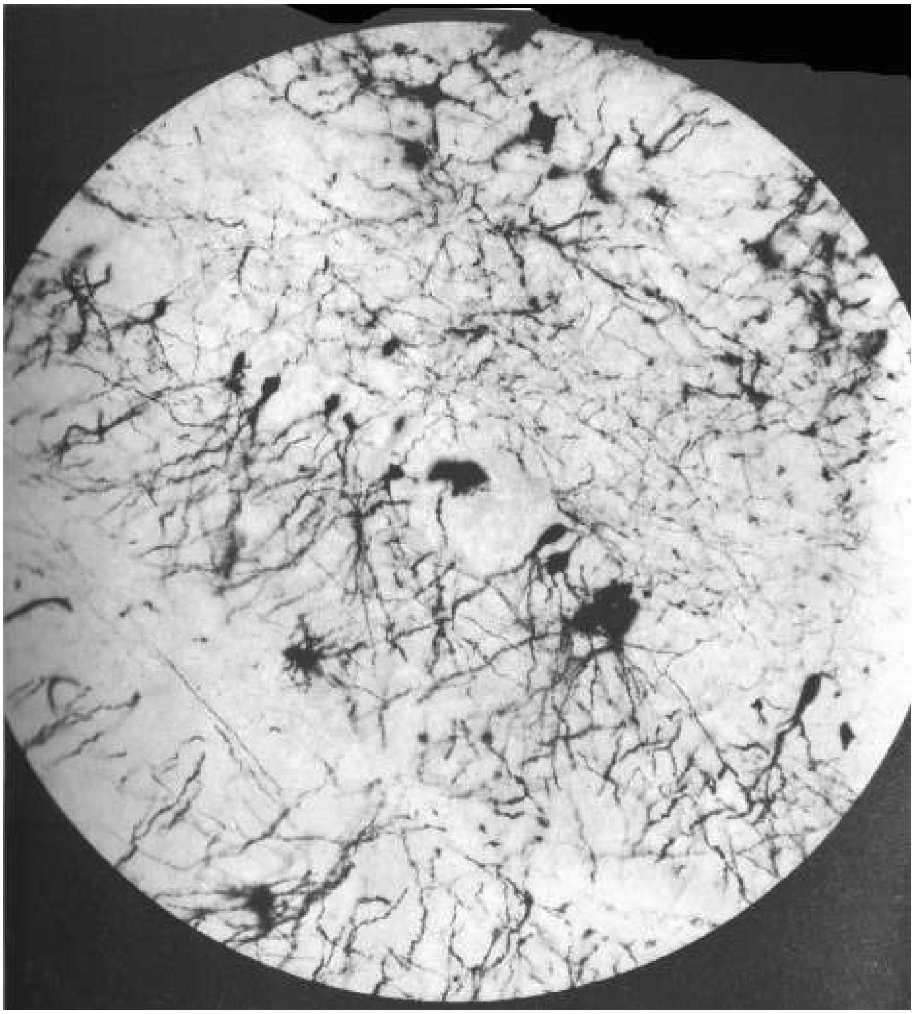

Figure .
Golgi-Cox section of the fascia dentata. From Cox ( ).

Purkinje cells receive a representation of the movement from the cerebral cortex, through the mossy fibre-parallel fibre pathway and an image of the actual movement through the climbing fibres from the periphery. When the two images match, the movement is correct, when there is a mismatch the Purkinje cells send a corrective stimulus to the periphery.

Recently, my attention was drawn to Jelgersma's publication on *Connections* (*Schakelingen*) from , where he postulates the formation of new, temporary connections in the brain in the learning process involved in higher forms of coordination. Jelgersma's ideas on the function of the Purkinje cells and the role of plasticity in cerebellar coordination, therefore, predate the modern, and very similar concepts on long-term adaptation of movement by the Purkinje cells of the cerebellum (Marr , Ito).

From , W.H. Cox worked in Brinkgreve, a psychiatric hospital in Deventer. In a short paper (Cox) he published the protocol for his well-known modification of the Golgi method (Fig.). Although the 'Golgi-Cox' method has been and still is used by many others, I have been unable to find any publications showing Cox using it himself. His interest in neuroanatomy was apparently short-lived. After he only published on clinical, organisational and moral matters.

Anatomy reborn: the early decades of the 20th century and the interbellum

Winkler, Dubois and Jelgersma continued their studies during this period, but new trends were set by Louis Bolk, who was appointed professor of anatomy at the University of Amsterdam in . The Central Institute for Brain research in Amsterdam was opened in , with C.U. Ariëns Kappers as its first director, and the careers of the self-made neurohistologist J. Boeke and of four of Winkler's pupils, J.W. Langelaan, B. Brouwer, W.J.C. Verhaart and S.T. Bok developed during this period.

The ascent of Louis (Lodewijk) Bolk (-) to the chair of Anatomy in Amsterdam

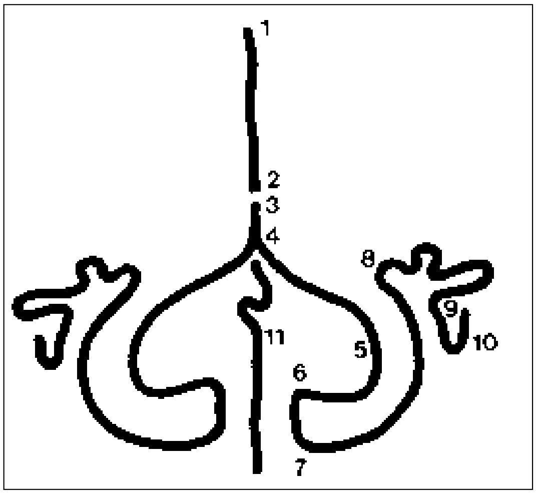

Figure .
Wire diagram of the subdivision of the mammalian cerebellum by Bolk ( ). Behind the undivided anterior lobe (-) and the lobulus simplex (-), the cerebellum divides into the folial chains of the vermis ( ) and the hemisphere. The hemisphere can be subdivided into the ansiform lobule ( ), the paramedian lobule (-), the crus circumcludens (- : the present paraflocculus) and the uncus terminalis (, the flocculus).

in was as rapid – he had received his medical degree just two years before – as it was unexpected. The board of the University had recommended the appointment of the residing lecturer, the German Seidel, and had named Eugène Dubois as a second, but the city council of Amsterdam decided otherwise (Baljet). Bolk was a typical gross anatomist, using observation and dissection as the only tools in his research (reviewed in van Limborgh and Nieuwenhuys). What distinguished Bolk was the innovative, sometimes provocative quality of his concepts and generalisations. This is well illustrated in his address on 'Brain and Culture' on the occasion of the anniversary of the University of Amsterdam in , published in . According to Bolk, the superior weight of the human brain cannot be explained as a consequence of functional adaptation or selection, but should be understood as the fixation of the high fetal brain/body ratio in the human species. This was the first mention of his well-known retardation or fetalisation theory (reviewed by Dullemeijer).

Bolk acquired a well-deserved place in neuroanatomy through his studies of the comparative anatomy of the mammalian cerebellum (Bolk ; reviewed by Voogd , and Glickstein and Voogd). Bolk applied his generalized 'blueprint' of the mammalian cerebellum in his theory on functional localisation (, ,). The fact that later investigations failed to substantiate this theory did much to discredit Bolk's work. His nomenclature, however, has survived (Fig.) and his ideas on the morphology of the cerebellum have proved to be of fundamental importance in the understanding of the basic longitudinal subdivision of this organ in more recent times (Voogd and Glickstein).

In , Bolk started up annual meetings of Dutch anatomists in his new department at the Mauritskade in Amsterdam. In , these meetings led to the foundation of the Dutch Association of Anatomists. His students later occupied most of the chairs of anatomy in Holland (Fig. : A.J.P. van den Broek, Utrecht; J.A. Barge, Leiden; M.W. Woerdeman, Amsterdam) and the Dutch East Indies (W.A. Mijsberg, Batavia).

Together with Winkler, Bolk was instrumental in the foundation of the Central Institute for Brain Research. In the German anatomist and neuroembryologist Wilhelm His took the initiative for a proposal of the 'Königlich Sächsische Gesellschaft der Wissenschaften' to the recently founded International Association of Scientific Academies at their meeting in Paris, to stimulate international collaboration in neuroscience. This resulted in the formation of the 'Brain Commission', with representatives from existing brain institutes in the U.S.A, Spain, Switzerland, Russia and Germany. The Brain Commission made plans for an international division of labour in neuroscience, and stimulated the foundation of brain research institutes in other countries. Winkler and Bolk, in an official report accepted by the Royal Academy of Science, proposed the foundation of a Brain Institute in Amsterdam, although Jelgersma informed the Academy that a Brain Institute could be accommodated in his quarters in Oegstgeest, and that, in his opinion, addition of a single technician would suffice (Ariëns Kappers). Winkler and Bolk's plans were adopted. The city of Amsterdam built a new accommodation for the Brain Institute, next to the new Department of Anatomy on the Mauritskade and on Tuesday June , the new institute was opened by Professor J.D. van der Waals on behalf of the Royal Academy, in the presence of Golgi, von Monakow and other members of the Brain Commission with addresses by Winkler, Waldeyer and the newly appointed director, C.U. Ariëns Kappers (van der Waals). It turned out to be the last act of the Brain Commission, it fell apart with the outbreak of the Great War, and its good intentions were left to slumber until the foundation of the IBRO (International Brain Organisation) by the UNESCO in .

As a medical student C.U. Ariëns Kappers (-) worked on neuranatomical subjects in the laboratories of Winkler and of J. van Rees, the professor of histology in Amsterdam, and the supervisor of his thesis (Ariëns Kappers ,), which was based on studies of the brain of fishes and started in the Zoological Station in Napels in . In he joined Edinger in the Senckenbergisches Institute in

Figure .

Painting by Martin Monnickendam of the 'Anatomical lesson of professor Louis Bolk'. Bolk is sitting in the middle, dissecting an orang-utan. Barge is looking over his shoulder; Boeke is depicted on the left and van den Broek on the right. The painting probably commemorates the publication of the Dutch textbook Anatomy by van den Broek, Boeke and Barge in (Baljet). From the collection of the University Museum Amsterdam. Photography: Gert Jan van Rooy.

Frankfurt. The collaboration with Edinger probably decided his future career in comparative neuroanatomy (Ariëns Kappers). It was here that he first published on the possible explanation of phylogenetic differences in position of the cranial motor nuclei, as yet without using the term ‘neurobiotaxis’ (Ariëns Kappers).

The Central Institute for Brain Research, where he was appointed as director in , counted two neurologists among its staff: C.T. van Valkenburg (see the chapter in this book) as assistant-director and E. de Vries (-). Although anatomical and neuropathological studies on the human brain appeared from their hands, the main theme of the Brain Institute remained the comparative anatomy of the central nervous system until Ariëns Kappers’ retirement and death in . Ariëns Kappers only became an Extraordinarius of Neuroanatomy at the University of Amsterdam in . Before that time the students he supervised obtained their Ph.D. from his professorial colleagues (i.e., van der Horst , and Schepman , both with professor Sluiter in Amsterdam, Kooy with van Wijhe in Groningen)

The career and the personality of C.U. Ariëns Kappers are discussed in chapter . His autobiographical notes, which have been published recently (Ariëns Kappers), give some interesting sidelights about his life. Van Valkenburg’s and de Vries’s anatomical contributions are considered in chapters and , respectively. The interesting career of Ae.B. Droogleever Fortuyn, one of Ariëns Kappers early collaborators, started with a thesis on the cytoarchitecture of the mouse ( ). Droogleever wrote the first volume on the central nervous system of non-vertebrates (Ariëns Kappers and Droogleever Fortuyn). He became a lecturer in Histology in Leiden, and later took on a professorship at Peking Union College. His last anatomical publications date from this period ( ). At the outbreak of the war he moved to the Americas, to become connected to the medical school in Paramaribo (Surinam). In later years he only published on genetics.

According to Nieuwenhuys (Nieuwenhuys et al.) “The research of Ariëns Kappers and his numerous associates was almost exclusively based on non-experimental material, stained with the Weigert-Pal method to stain myelinated fibres and counterstained with paracarmine for cell bodies. [...] The works by Ariëns Kappers and his allies (/ , ,) may be (considered as) attempts at reconstructing the phylogenetic history of the central nervous system of vertebrates. It is important that in these works this history is presented as a progressive process, thought to be driven by an undetermined, intrinsic force .... The results of this entelechic tendency [...] are seen in the progressive development of the brain in accordance with a general plan, in the progressive differentiation and adjustment of its constituents, and in their mutual general relations” (Ariëns Kappers et al.). Ariëns Kappers’ theory of neurobiotaxis is an attempt at inferring generalisations from observed differences between the brains of vertebrates (Ariëns Kappers , , , ,). According to this theory, simultaneous and successive stimulations from a certain source extert a neurotropic action on neurons, and are responsible for their position near the source of these stimuli. Nieuwenhuys ( ) points out how this theory was extrapolated into a law of association, which governed the presumed migrations of neuronal populations in many parts of the brain. Such an ordering principle, certainly, was needed to bring some order in the enormous number of observations on the central nervous system of vertebrates, documented in the publications from the Central Institute of Brain Research.

J.W. Langelaan (-) completed his thesis on muscle tone with Winkler, in . He became a professor of Anatomy in Leiden in , but left again in (Fig.). Heringa ( ) recorded his remark "I came to Leiden to learn about the anatomy of the nervous system; once I knew it, I left." He published on the development of the cerebral commissures (a) and the human cerebellum (b,). He wrote one of the finest Dutch textbooks on neuroanatomy ( ). It contains an extensive, introductory review of the development of the brain, and is superbly illustrated by the medical artist, G. Koster (Fig.). In his later career, Langelaan returned to his neurological practice and to his physiological and microscopic studies of striated muscle in the labs of Boeke and Heringa. He became a member of the Royal Academy in . His model of muscle contraction and his studies on the innervation of striated muscle have been disproved by later developments.


Figure . Portrait of J.W. Langelaan (-), probably taken around . Courtesy of the Department of Anatomy and Embryology, University of Leiden.

After a fairly undistinguished thesis on the acoustic system in a case of congenital deafness, supervised by Winkler (Brouwer), which surprisingly earned him a Cum Laude (with honours) (see chapter), B. Brouwer (-) developed into one of the first Dutch experimental neuroanatomists. He became acquainted with the use of secondary degeneration in the tracing of neural pathways, through the studies on the topical projection of the retina on the tectum opticum in fish by P.C. Zeeman, the Amsterdam professor of Opthalmology, and J. Lubsen (Lubsen) in the Central Institute of Brain Research. Although Ariëns Kappers was opposed to the use of animals in experimental research, he did not impose this conviction on his students.

Brouwer succeeded van Valkenburg as assistant-director of the Brain Institute and later was appointed as a professor of Neurology in Amsterdam in . He was invited to deliver the Herter lectures in Johns Hopkins in Baltimore in (Brouwer). His tours of the United States, and his ensuing correspondence with John Fulton, were the subject of recent papers by Koehler and Bruyn ( ) and Koehler (in press). During the years of the Second World War, Brouwer acted as Rector of the University of Amsterdam. He succeeded Ariëns Kappers as director of the Central Institute of Brain Research in and died in .

In his first Herter lecture, Brouwer summarised his experimental studies of the connections of the optic nerve in rabbits, cats and primates (, ; Brouwer and Zeeman ; Overbosch ; Fig.). Brouwer took off where K.H. Bouman had left off, studying the anatomy of the visual system in one of the first studies using the Marchi method in this country (Bouman). Thalamo-cortical connections were studied by two of Brouwer's students, F.E. Posthumus Meyjes ( ) and J. Droogleever Fortuyn ( ). Droogleever Fortuyn's thesis, especially, remains a readable, authoritative account, which discusses his experiments on the thalamo-cortical projection in the rabbit, against the background of the new contributions of Le Gros Clark, Mc Rioch and Walker on the subdivision and connections of the thalamus of that period. Droogleever Fortuyn (-) became a professor of Neurology in Groningen in . Centrifugal connections of the visual cortex were charted in the thesis of Biemond ( ). A. Biemond (-) succeeded Brouwer on the chair of Neurology in Amsterdam.

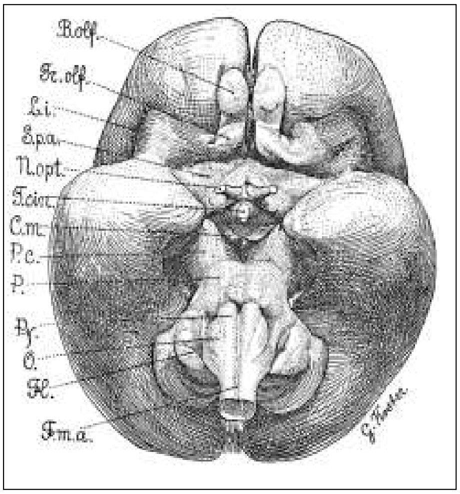

Figure .
Ventral view of the brain of a human fetus at the end of the fifth month of gestation. Drawing by G. Koster. From Langelaan ( ).

Another subject raised by Brouwer in his Herter lectures (Brouwer) was the subdivision of the cerebellum. This was a hot topic at the time, debated among the proponents of Edinger's ( ) original distinction of a palaeo- and neocerebellum, adepts of Bolks's ideas on functional localisation in the cerebellum, and the adherents of van Hoeneveld's ( ) intussusception of 'neocerebellar', afferents in palaeocerebellar territory. Van Valkenburg ( ) studied corticogenesis in human fetus. He found that Purkinje cells, between the fourth and seventh month of gestation, replace the outer layer of the internal granular lamina. This change occurs earlier in Edinger's palaeocerebellum, than in the neocerebellum. In more recent publications on this subject it was shown that Purkinje cells are already present in the cortex, long before granule cells settle in the internal granular layer, and that regional differences in corticogenesis occur between multiple, longitudinal zones in vermis and hemisphere, rather than between palaeo- and neo-cerebellar subdivisions (Korneliussen). Hoeneveld described a case of olivo-ponto-cerebellar atrophy. His concept of 'intussusception' is based on the premise that the neo-cerebellar nuclei of the pons and the inferior olive are a source of mossy fibres. From the partial preservation of the myelinated mossy fibre plexus in the granular layer in the vermis and portions of the hemisphere, he concluded that neocerebellar territory has become intercalated in the palaeocerebellum. For the distribution of mossy fibres Hoeneveld's conclusion is correct, although his methods are questionable. For the inferior olive, which turned out to be the exclusive source of the climbing fibres only much later (Desclin), Brouwer showed that it incorporates both neo- and palaeocerebellar parts, confirming earlier observations of Holmes and Stewart ( ).

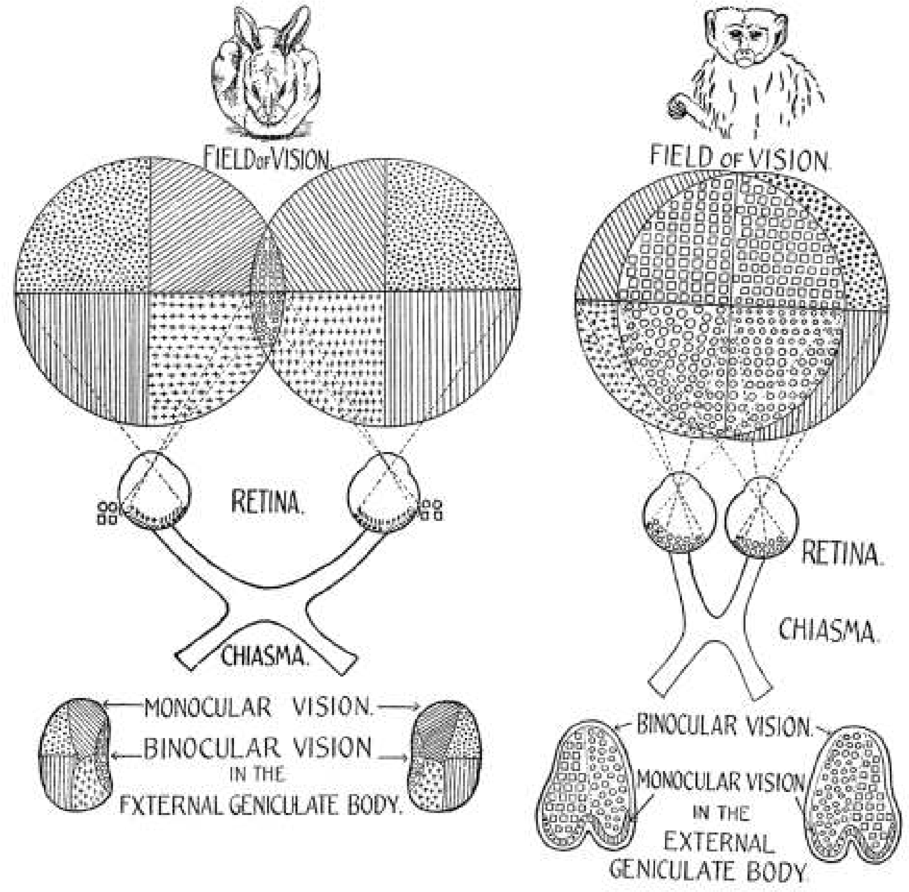

Figure .
Projection of the visual fields in mammals with laterally-positioned and with frontal eyes. From Brouwer's Herter Lectures ( ).

In human cases of 'neocerebellar' atrophy, which spared the vermis and the flocculus, Brouwer found an intact rostromedial dentate, with the medial and interposed nuclei, and demyelination of the caudolateral dentate, which, apparently, received a projection from the atrophied neocerebellum (, , , ; Brouwer and Coenen ,). Some years later Gans ( ) discovered a similar division of the human dentate nucleus, on the basis of its iron content. A. Gans (-) was another of Winkler's students, who became a lecturer in Neurology at the University of Leiden.

S.T. Bok (-) wrote a thesis supervised by Winkler (Bok), worked for some time as a neuropathologist in the Valerius clinic with professor L. Bouman, and was appointed as a professor of Histology and Microscopical Anatomy in Leiden in . From till his retirement in he was director of the Central Institute for Brain Research in Amsterdam.

His thesis is a systematic analysis of the early development of the neuronal connections in the spinal cord in the chicken embryo, culminating in a general blueprint of the cord. Bok devised the theory of stimulogenic fibrillation to explain the position of the different elements in his blueprint (Bok a,b; Fig.). This blueprint also served as the basis for his chapter on the spinal cord in Von Möllendorff's *Handbook* ( ). One element of this blueprint, the localisation in the dorsal columns, was elaborated in the important thesis of Lietaert Peerbolte ( ). Bok later applied this plan to higher levels of the central nervous system (Bok). Although these generalisations, combined with Bok's selective use of the literature, sometimes lead to absurd conclusions, his approach had a great didactic value. His lectures, which I attended in the early s (Bok et al. ; Fig.), were superb.

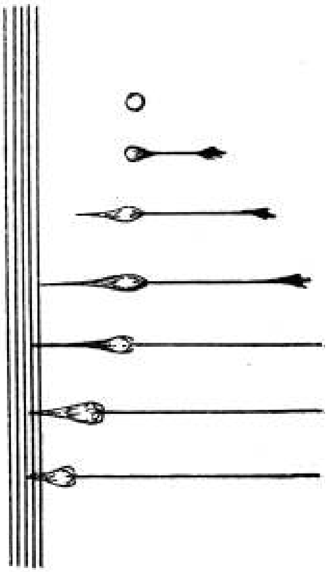

Figure .
Diagram of the outgrowth of axon and dendrites, perpendicular to the fibre system from which the neuron receives its stimuli. From the paper of Bok (a,b) on the theory of stimulogenic stimulation.

Bok's interest in the quantification of the nervous system, started with his paper on the influence of the gyration of the hemisphere on cortical thickness (a,b). Together with his student van Erp Taalman Kip, Bok resumed Dubois' approach in his studies on factors determinating thickness and area of the cerebral cortex (Bok , van Erp Taalman Kip). Renes ( ) found a constant density of fibres in the cortex, and stated that they are separated by a constant distance, determined by the vacuolisation of the cortical protoplasm. In , Bok reported that these vacuoles may be identified as the site of memory. Although Bok's research was handicapped by his strong convictions and generalisations, his introduction of statistical and stereological methods in neuroanatomy has been of lasting significance (J. Ariëns Kappers a,b). In the Central Institute of Brain Research his approach to the quantification of the cortex was followed by Colon ( ), G.J. Smit ( ) and H.B.M. Uylings ( ), who initiated new studies on the quantitative histology, the ontogenesis and the areal subdivision of the cerebral cortex.

The saddest story of this period is that of the fate of the neuron theory on the Dutch scene. C.A. Pekelharing, the successor of Edelmann as professor of Histology in Utrecht, gave a lucid account of the history and the status of this theory at the outset of the th century, in his *Lectures on Histology* ( ). He emphasised the indisputable support for the neuron theory drawn from observations with the Golgi and the Ehrlich methylene method, which never revealed anything like Gerlach's (or Schroeder van der Kolk's) anastomosing dendritic network, or Golgi's axonal reticu-

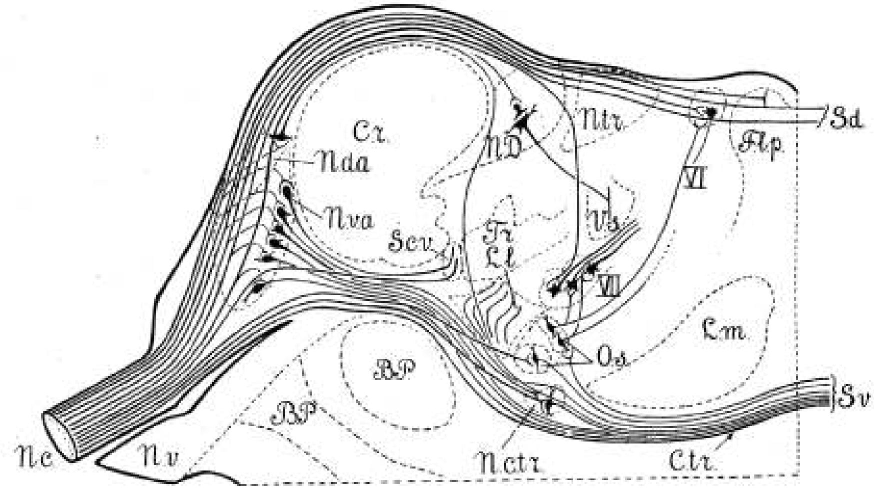

Figure .
Diagram of the termination of the cochlear nerve, redrawn by G. Koster for Langelaan's ( ) textbook, from Winkler's ( ) experimental study of the vestibulo-cochlear nerve. In addition to the terminations in the dorsal (N.d.a.) and ventral cochlear nucleus (N.d.v.), Winkler found cochlear root fibres in the dorsal acoustic striae, dorsal to the restiform body (C.r.) and in the corpus trapezoides (Ctr). Although it was well known at the time that these connections do not exist, the Figure was still reproduced by Bok in .

lum of anastomosing axons. He pointed out that the arguments against the neuron theory stemmed from the observations of Apathy and Bethe of a neurofibrillar network, extending uninterruptedly from one neuron to the next. Cajal negated these observations with his own, new reduced silver methods, which showed that neurofibrils always remain confined within a single neuron. However, his opponents, using gold-toning, were able to demonstrate the continuity of the neurofibrils with an intercellular network.

In the Netherlands, J. Boeke (-) and his student G.C. Heringa (–) were among the most vehement opponents of the neuron theory. Boeke completed a thesis on a pharmacological subject with the Amsterdam physiologist Laplace in . On a visit to the marine biological institute in Naples in the same year, Boeke met Apathy, with whom he spent four months working in his lab in Kolasvar, Hungary (Heringa). In he became lecturer in Histology, and in professor of Anatomy in Leiden, as the successor of Langelaan. From till he occupied the chair of Histologyand Embryology in Utrecht, as the successor of Pekelharing. During his long academic career, Boeke received numerous scientific honours, medals, memberships of learned societies and four honorary degrees.

Using his own modifications of the Bielschowsky method, Boeke showed the continuity of the neurofibrils in the motor end plate with a periterminal net extending into the sarcoplasm (Boeke). Similar observations were made by Heringa in his thesis of (Fig.) on the developing sensory corpuscles of Grandry and Herbst in the duck bill, where neurofibrils of the nerve fibre could be followed into a lighter-stained proplasmatic neural network extending into the entire corpuscle,. Heringa later occupied the chair of Histology in Amsterdam from until . Akkeringa, another of Boeke's students, observed the presence of a periterminal network in the retina (Akkeringa). In the theses of Boeke's students van Esveld ( ) and Leeuwe ( ), the periterminal net was described as a neural syncytium connecting the ganglion cells and the interstitial cells of the gut. Boeke discovered a double innervation of striated muscle by motor endplates and sympathetic fibres (Boeke ,), for which he received the Wilhelm Roux medal in . In his studies on the development or the regeneration of peripheral nerves, Boeke again denied the developmental unity of the nerve cell. Growing axons incorporate protoplasm of a syncitium, consisting of epithelial, mesodermic and muscle cells. Anastomosing neurofibrils from different nerve cells populate the resulting neural network (Boeke).

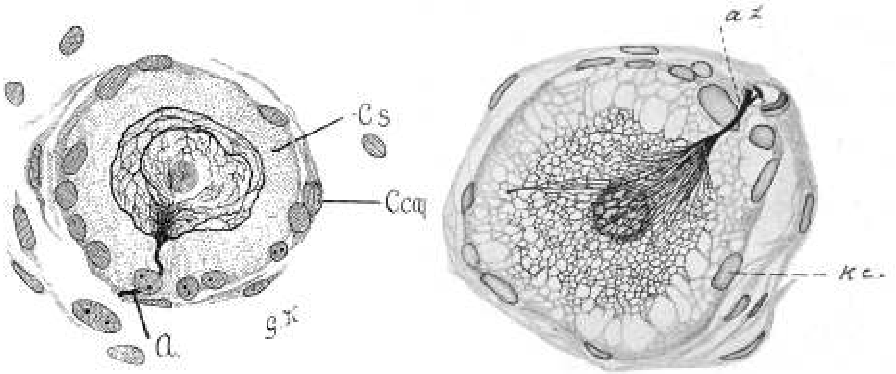

Figure .
Drawings of sensory corpuscles of Grandry in the duck bill. The left-hand drawing is by G. Koster from Langelaan ( ), based on a Cajal silver preparation from E. van der Velde ( ), showing a well-demarcated fibre plexus in the centre of the corpuscle. The right-hand drawing is from Heringa ( ). It shows how the central, neurofibrillar plexus merges with the lighter-stained 'terminal net' of Boeke, which permeates the entire corpuscle.

In their textbook (Boeke, de Groodt and Heringa) and their publications, Boeke and Heringa clearly and repeatedly stated their position: "It is well known … how rapidly the first enthusiasm (for the concept of strictly individual cell units) cooled. The Golgi-forms of the central nervous system appeared to offer – in the long term – no true foundation of the neuron theory" (Heringa); and "Only we feel every time more strongly, how far and irretrievably we are separated nowadays from the old simplistic conceptions of the neuron theory of the former century…" (Boeke). Cajal honoured them with a sharp reprieve in his last monograph, *Neurinismo o reticularismo*, which appeared shortly after his death, in . Cajal convincingly showed that observations on a periterminal net depend on the vagaries of the staining methods, and remarks how “The discovery of the Dutch authors has been welcomed by Held,” one of Cajal’s chief opponents, “who reproduced the figures of these authors with belated delight.” Held was not the only one, Langelaan ( ), Winkler ( ) and Ariëns Kappers ( ) all shared some of Boeke’s convictions.

Heringa and Boeke were men of principles. Boeke resigned from the (then no longer Royal) Dutch Academy of Sciences when all Jewish members were expelled in . Heringa was removed from his chair and interned by the German occupants (Ariëns Kappers). In a publication of Boeke took his stand for the last time. He died in , two years after the demonstration by Palade and Palay ( ) of the discontinuity of nerve cells in the synapse under the electron microscope. When Heringa evaluated Boeke’s scientific work in , he still hesitated to answer the question whether Boeke’s life’s work had become worthless, in the affirmative. Strangely, Heringa never mentioned his own responsibility for the lost battle against the neuron theory.

The apogee: the post-war era

Figure .
Walle J.H. Nauta.
- .Courtesy of the M.I.T. Museum, Cambridge, Massachusetts, USA.

On November , W.J.H. Nauta (-) defended his thesis on the role of the hypothalamus in sleep-regulation, in Utrecht, a few months after the Dutch universities had reopened and tried to overcome the ravages of the war. Nauta had started his research on the anatomy of the hypothalamus in as a medical student, shortly before the outbreak of the Second World War, with a group of scientists, led by J. Dankmeyer (-), the future professor of Anatomy in Leiden (Dankmeijer and Nauta , Nauta). His first paper on his quest for silver impregnation of degenerating axoplasm dates from this period (Dankmeyer and Nauta). After the University of Leiden had been closed by the Nazi authorities in (for being a “hornet’s nest of ideological subversion”), Nauta moved to Utrecht, where he received his medical degree, and where he worked at the anatomical laboratory of A.J.P van den Broek (Schmitt). He returned to Leiden, but soon accepted a position in Anatomy with Professor G. Töndury in Zürich in . In collaboration with the Swiss chemist P.A. Gygax he published on silver impregnation of degenerated axons with a modification of the Bielschowsky silver method (Nauta , Nauta and Gygax). The suppression of normal axons with oxidation by permanganate, at the favour of the silverimpregnation of the degenerated axons, was discovered in collaboration with another scientist, L. Ryan, and the ‘suppressive method’ was published in its final form with Gygax (Nauta and Ryan , Nauta and Gygax , Nauta). The Nauta method revolutionised tract tracing, and fomented numerous papers on connections within the central nervous system, from every part of the world for the next two decennia. In Nauta moved to the newly founded Division of Neuropsychiatry at the Walter Reed Army Institute of Research in Washington. In he was appointed to a professorship at the University of Maryland and in he joined the Department of Brain and Cognitive Sciences at the Massachusetts Institute of Technology (M.I.T.) in Cambridge as a professor of Neuroanatomy, where he received the title of Institute Professor, the highest professorial rank given by the M.I.T., in (Fig.).

In the Walter Reed and the M.I.T. he founded an influential school of neuroanatomists, which included W.R.H. Mehler, H.G.J.M. Kuypers, L. Heimer, H.J. Karten, Ann Graybiel and Patricia S. Goldman-Rakic. He never returned to the Netherlands, but the postdocs of the Dutch neuroanatomists H.T.M. Lohman and H.J. Groenewegen, who spent some time with Nauta in the M.I.T., created a lasting bond. Nauta published extensively on the hypothalamus and limbic system (, /), the connections of the frontal lobe ( ), striatum and cerebellum (Mehler and Nauta), and on comparative anatomical topics (Nauta and Karten). His Friday lectures on neuroanatomy were an institution attended by students and local Nobel Prize winners alike.

Dankmeijer's group of students of the hypothalamus fostered other neuroscientists. One of them was H.J. Lammers (-). Lammers completed his Ph.D. with Barge and became the first professor of Anatomy at the new medical school of the Catholic University of Nijmegen in . Here he was joined by A.H.M. Lohman, a lecturer in Anatomy in Nijmegen, and a professor of Anatomy of the Vrije Universiteit in Amsterdam from until (Smeets and Groenewegen). Studies of the hypothalamus and the limbic system were pursued by Lammers (Gastaut and Lammers). Lohman mainly published on the olfactory system (Lohman). In the group founded by Lohman in Amsterdam, the limbic system has remained one of the main research topics, in the investigations of the 'limbic' striatum of professor H.J. Groenewegen (Groenewegen et al.), and the combined anatomical, electrophysiological and imaging studies of professor M.P. Witter (Room and Witter , Rombouts et al.). P.G.M. Luiten, another of Lohman's students (Luiten), became a professor of Zoology at the University of Groningen, where he founded a research group that made important contributions to the anatomy of memory (van der Zee and Luiten).

H.G.J.M. Kuypers (-) wrote his Ph.D. thesis with Bok in Leiden, on the connections of the central grey, where he used Nauta's , non-suppressive silver technique (Kuypers). He aborted his residency in Neurology, with J. Droogleever Fortuyn in Groningen, when Nauta invited him in to join his group at the University of Maryland at Baltimore (see Moll's chapter and Lemon). In he moved to a full professorship at Western Reserve University, Cleveland, Ohio. Kuypers applied the suppressive Nauta method in his classical studies of the medial and lateral components of the motor system in cats and primates, where he combined anatomy with observations on motor behaviour (Kuypers). In he returned to the Netherlands as the founding professor of Anatomy at the Erasmus

University Rotterdam. Here he continued his interdisciplinary studies, with the neurologists and physiologists D. Lawrence, S. Miller and R. Lemon, who received appointments as lecturers or professors in his department (Godschalk et al. , Holstege and Kuypers , Lawrence and Kuypers). It was here that he developed new retrograde double labelling techniques, using fluorescent tracers (Huisman et al.). In Kuypers moved to Cambridge, where he studied the use of viruses as transneuronal tracers, together with Gabriella Ugolini and P. Strick (Kuypers et al. ; Kuypers and Ugolini). He became a Fellow of the Royal Society in . He died, suddenly, in . In the Netherlands, G. Holstege continued Kuypers' anatomical approach, as a professor of Anatomy in Groningen, adding a third, 'emotional motor system' to Kuypers' earlier medial and lateral systems (Holstege).

Dankmeijer's hand can also be seen in the appointment of W.J.C. Verhaart (-) as the successor of Bok in the chair of MicroscopicalAnatomy in Leiden in . Verhaart's scientific career, as a student of Winkler, is told in another chapter of this book. In the case of Verhaart, the introduction of another histological method, the Häggqvist-modification of the Alzheimer-Mann method, changed the face of the microscopical topography of the brain. In his lab, the apportioning of different parts of the brain to different students, left the cerebellum as my research object on my arrival as a student. These cerebellar studies were continued during my appointment as a lecturer in Leiden ( ) and as the successor of Kuypers in the chair of Anatomy at the Erasmus University Rotterdam (-). Electron microscopy of the nervous system was introduced in Leiden by G.F.J.M. Vrensen in the Anatomical Laboratory of 'Endegeest' in Oegstgeest, under the directorship of J. Stotijn. Vrensen made important contributions to the stereology of synapses (Vrensen and de Groot , Vrensen et al.). In the Department of Zoology in Leiden, J.L. Dubbeldam ( ) and G.A. Zweers ( ) initiated neuroanatomical and behavioral studies in birds, in close collaboration with Verhaart. Verhaart's neuroanatomical laboatory was incorporated later in the Neuroregulation group, in the Department of Neurosurgery, under E. Marani. In Rotterdam the borders between the disciplines became erased, when the old Departments of Anatomy and Physiology merged in the new Department of Neuroscience, under Voogd's successor, professor Chr. de Zeeuw, in .

Under the directorship of Bok, from till his retirement in , the Central Institute of Brain Research moved from its cramped quarters at the Mauritskade, to the more spacious, but still temporary, barracks at the Ydijk in Amsterdam. Electrophysiology, ethology and neurochemistry made their entrance. Comparative neuroanatomy was resumed by R. Nieuwenhuys; the Golgi method was re-introduced in the research of H. van der Loos. J. Ariëns Kappers succeeded Bok as director of the Brain Institute in . His interest in the autonomic nervous system was fostered by his uncle, C.U. Ariëns Kappers, but J. Ariëns Kappers focussed his research on the epiphysis cerebri. In Kappers' student, the neuroendocrinologist D.F. Swaab, took over his directorship. He supervised the move of the Institute to a new building, an annex of the Amsterdam Medical Centre. Swaab's studies of gender-related specialisations in the hypothalamus (Swaab et al.), and of sustained activity on the fate of neurons ("use it or lose it," Swaab) received considerable interest. Under his directorship the scope of neuro-morphology was considerably broadened.

R. Nieuwenhuys left the Brain Institute to take up a position as professor of Morphology of the Nervous System in Nijmegen, in (Nicholson and Smeets). Like C.U. Ariëns Kappers, most of his studies were done on normal material, but in his case the scope of these studies was broadened by the introduction of histochemical and immunohistochemical techniques (Nieuwenhuys). His student H. Steinbusch was the first to prepare antibodies against catecholamines (Steinbusch et al.). Steinbusch was appointed later as a professor of Neuroscience in Maastricht. Extensive experimental studies on lower vertebrates were undertaken by Nieuwenhuys's student, H.J. ten Donkelaar. The comparative studies on the morphogenesis and anatomy of the nervous system by Nieuwenhuys and his students have been collected recently in the three volumes *Central Nervous System of Vertebrates* (Nieuwenhuys et al.). Nieuwenhuys retired in . His vacant chair was never reoccupied, and reorganisation by the Medical Faculty in Nijmegen decimated his former research group, putting an end to almost one hundred years of research in the comparative neuroanatomy in The Netherlands.

The re-introduction by H. van der Loos (- ; Fig.) of the Golgi method in Dutch research and his appreciation of the historical roots of the neuron theory (van der Loos) restored some of the harm done by Boeke and Heringa during the first half of the th century. His thesis on dendro-dendritic relations from , based on observations with the Golgi-Cox method, as yet without electron-microscopy, traces the history of these connections and attempts to quantify these 'ephapses' in the cerebral cortex of the rabbit. In , van der Loos joined David Bodian's group at the Johns Hopkins Medical School in Baltimore, where he was appointed full professor in . He became a Senior Research Scholar of the Kennedy Foundation after his knowledge of brain development was brought to the attention of the family of John F. Kennedy (Molliver and Welker). In he became director of the Institut d'Anatomie of the University of Lausanne. From the large body of his publications, his paper on the discovery, with Tom Woolsey, of the representation of the facial whiskers in the barrel-area in the sensory cortex of the mouse (Woolsey and van der Loos) stands out as the beginning of a new and productive line of research in neuroscience. Van der Loos was a gifted and charismatic speaker, his lectures were carefully rehearsed acts, presented with the skill of a born actor. The sudden death of this great Dutch neuroanatomist in shocked the neuroscience community throughout the world.

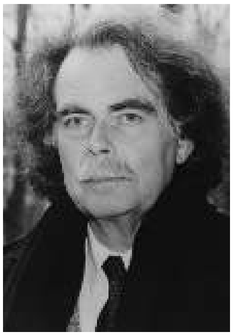

Figure . H. van der Loos. - .Courtesy of Prof. E. Welker, Department of Anatomy, University of Lausanne, Switzerland.

Neuroanatomists are dependent on their technicians for most of their material. A few of their names have been provided: Kouw, Jelgersma's technician, Winkler's technicians, Mrs. E. Winkler- Junius, Winkler's second wife, and Miss Hoogland (Fig.), and J. Langhout, T. Brouwer and C. Roosemeyer (Brouwer et al.) from the crew of C.U. Ariëns Kappers. More than anything, neuroanatomical publications are dependent on the quality of their illustrations. C. Koster, Langelaan's illustrator, Ada Potter, Winkler's alter ego, Chr. Vlassopoullos. Ariëns Kappers illustrator from until , Jan Tinkelenberg, the versatile Leiden medical artist and Chr. Van Huijzen, who illustrated much of Nieuwenhuys's work, deserve much of the credit for their patrons' publications.

Today's position of neuroanatomy in neuroscience research and in the medical curriculum has changed. Neuroscience research has become an interdisciplinary effort, where molecular biology and physiology, and clinical applied imaging of the brain, play the upper hand. Classical neuroanatomy and the study of the chemoarchitecture and the ultrastructure of the brain remain indispensable, but as an independent (and predominantly male) discipline neuroanatomy is about to become part of the history of science.

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