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CORTICO-NUCLEAR PROJECTIONS FROM THE PARAMEDIAN LOBULE AND CRUS II OF THE CAT CEREBELLUM: AN EXPERIMENTAL STUDY WITH SILVER IMPREGNATION METHODS

The exact site of termination of fibers from the paramedian lobule and Crus II was investigated by making lesions in these regions and mapping terminal degeneration with the Nauta-Laidlaw method.

The paramedian lobule sends three, non-overlapping, ipsilateral projections upon the cerebellar nuclei. The first projection is located in the ventral part of the lateral nucleus (NL), the second in the caudal part of the posterior interposed nucleus (NIP), and the third projection is found in the dorsal portion of the anterior interposed nucleus (NIA) continuing through the NL-NIA transition zone.

Crus II sends two ipsilateral projections upon the cerebellar nuclei: the first is located in the anterior half of the NIP, and the second in the dorsal part of the NL continuing through the NL-NIA transition zone.

Within each zone of projection of the paramedian lobule and Crus II, an orderly distribution of cortico-nuclear fibers is revealed by differences in localization of degenerated fibers after lesions in different regions of the paramedian lobule and Crus II. Since both of these lobules receive an afferent input which is organized somatotopically, the topographical distribution of cortico-nuclear fibers from the paramedian lobule and Crus II means a somatotopy.

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Submitted to
the Faculty of Graduate Studies and Research
of McGill University
in partial fulfillment of the requirements
for the degree of Master of Science

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August 1971

This study was conducted in the neuro-anatomy laboratories
at the Montreal Neurological Institute
and in the Department of Physiology
of the Université de Montréal

Cette étude sur les connections cortico-nucléaires n'aurait pu être ni conçue, ni achevée sans l'aide de mon directeur de recherche, le Dr Jacques Courville.

Par ses constants conseils et sa patiente direction, il a essayé de m'initier non seulement aux techniques de la neuro-anatomie expérimentale, mais aussi à la rigueur de la pensée scientifique. Je tiens à lui exprimer une vive admiration ainsi qu'une immense gratitude.

La qualité des dessins ainsi que le travail histologique de cette étude sont dus à Monsieur G. Filosi. Je lui dois de sincères remerciements.

Je tiens aussi à remercier Monsieur Edward Rupnik qui est responsable de la photographie.

Des remerciements sont dus à Madame Ruth Duchesne pour son assistance dans la salle opératoire, et à Madame Suzanne Dufresne pour son travail de dactylographie.

TABLE OF CONTENTS

I

INTRODUCTION

SURVEY OF EARLY LITERATURE

In this introduction, there will be an attempt to review the historical development of the subject of cerebellar cortico-nuclear projections. The literature of the nomenclature and subdivisions of the cerebellar cortex and nuclei will also be reviewed since it is pertinent to the understanding of cortico-nuclear connections. Finally, studies dealing specifically with the projections of Crus II and the paramedian lobule will be discussed in detail.

In the early investigations of the cerebellar efferent projections it was attempted to establish the main relationship of the cerebellum with the spinal cord and brain stem. To this end, extensive lesions were produced and they usually involved the cortex as well as the nuclei of the cerebellum. Among the investigators who were interested in this field in the last decades of the 19th century, one must mention Thomas who published in 1897 one of the first monographs on the cerebellum, Marchi (1891), the inventor of a staining technique bearing his name, and others such as Ferrier and Turner (1894), and Klimoff (1899). In publications of that time, the connections of the cerebellum with the pontine and vestibular nuclei, the spinal cord and the thalamus were described as if all regions of the cerebellum were related to all these sites.

An important contribution concerning the existence of an orderly distribution of the cerebellar connections was the discovery that the efferent projection of the cerebellar cortex consists solely of the Purkinje cell axons. The merit of this discovery belongs to Ramon y Cajal, who worked with the methods of Golgi and Ehrlich's methylene blue. This author also observed that any collateral given off by the Purkinje cell axons returns to the vicinity of the cortical cells.

This first evidence was soon confirmed by Clarke and Horsley (1905) in an experimental study of the cortico-fugal connections using cats, dogs and monkeys and done with the Marchi technique. While Cajal described the efferent projections of the cortex on normal material, Clarke and Horsley described them on the basis of the distribution of degenerated cortico-nuclear fibers following cortical lesions. In their conclusions, they emphasized Ramon y Cajal's ideas, stating that: "... no fiber issuing from the cortex leaves the cerebellum by way of the peduncles," and that "all fibers leaving the cerebellum originate in one or other of the cerebellar nuclei." Their original contribution also covered other aspects of the cerebellar projections. In contrast to older publications they reported that there is a precise organization of cerebellar projections. Among other things, they mentioned that the cortical efferent fibers project to the cerebellar nucleus closest to the site of origin of the fiber.

Allen (1924) working with the guinea-pig and using the Marchi technique gave the first indication of a medio-lateral division of the cerebellar cortico-nuclear projections. From his results, he concluded that the cortex can be divided into two longitudinal zones of projection. The medial zone sends its projection upon the "medial nucleus", and the lateral zone to the "lateral nucleus" which in our terms includes the lateral and interposed nuclei of the present nomenclature. Furthermore, in contrast to Clarke and Horsley whose conclusions implied that the cerebellar projection upon the nuclei is homolateral, Allen stated that the lateral zone also projects upon the contralateral medial nucleus. This question of the existence of crossed cortico-nuclear connections has been the subject of a long controversy to which we will return further.

A few years later, Hohman (1929) gave a fairly detailed account of a medio-lateral arrangement of the cortico-nuclear projections in the cat. He described in the anterior lobe, three longitudinal bundles connecting the medial, intermediate and lateral parts of the vermis to the "roof nucleus, Deiter's nucleus and an intermediate cell group" respectively. He also described a similar arrangement in the caudal cortex where the "inferior vermis" projects upon the posterior half of the "roof nucleus", whereas the hemispheres are connected with the "roof and intermediate nuclei". Hohman's concept that portions of cortex in the form of vertical strips project upon different nuclei was the first demonstration of a principle of organization which was later advocated by many authors (Jansen and Brodal, 1940, 1942, Voogd, 1964).

Dow's work (1936) added a new dimension to the knowledge on the arrangement of cortico-fugal fibers. In his results in the cat and monkey (Marchi technique), he demonstrated that the uvula (lobule IX of Larsell) projects mainly to the fastigial nucleus, whereas the nodulus (lobule X) projects mainly to the vestibular nuclei. As mentioned above there is evidence that the projection of medial portions of the cortex differs from that of lateral parts, but Dow's results suggested that, at least for the posterior vermis, there is in addition a rostro-caudal organization.

It appears from this short review, that in the late thirties, the knowledge on cerebellar cortico-nuclear organization was rather sketchy. Results were often contradictory owing to the fact that different authors used different nomenclatures and subdivisions for the cerebellar nuclei. However, indications of a topographical arrangement of cortico-nuclear fibers were already available and prompted further investigations.

MORPHOLOGY OF THE NUCLEI AND CORTEX OF THE CEREBELLUM

It is appropriate to recall the evolution of ideas on the morphology of the cerebellar nuclei since this is one of the critical aspects for the description of cortico-nuclear connections.

It was as early as 1899 that Weidenreich distinguished four cerebellar cell groups. His nomenclature however, includes two principal nuclei only: the nucleus medialis and the nucleus lateralis. He further subdivides the latter into nucleus lateralis proper, situated most laterally and nuclei lateralis anterior and lateralis posterior located between the medialis and lateralis proper. He pointed out that the entity which he calls nucleus lateralis posterior is connected to the nucleus medialis, whereas the nucleus lateralis anterior is connected to the nucleus lateralis proper. Some of Weidenreich's terms have not been retained but his subdivision of the nuclei is still applicable to the cerebellar nuclei of the cat as will be seen further.

Another nomenclature of the cerebellar nuclei proposed by Brunner in 1919 was even more widely utilized. In a comparative anatomical investigation, Brunner described three major subdivisions of the intracerebellar cells in higher mammals: the nucleus medialis, the nucleus interpositus and the nucleus lateralis. Brunner did not subdivide the nucleus interpositus into anterior and posterior portions. He stressed the fact that although the three nuclei are recognizable entities, they are not entirely separate but form a more or less continuous cell mass.

Recently Flood and Jansen (1961) reinvestigated the cerebellar nuclei of the cat. In their conclusions, they supported Weidenreich's original proposal that the cytoarchitecture of the nuclei warrants the distinction of four cerebellar nuclei which they called medialis, interpositus anterior, interpositus posterior and lateralis. They also pointed out that the nuclei interpositus anterior and interpositus posterior are clearly distinct one from the other, but that the nucleus interpositus anterior fuses with the nucleus lateralis at one point and that some cell strands interconnect the medialis and interpositus posterior.

Another aspect of cerebellar morphology which is of fundamental importance for the analysis of the cortico-nuclear relationship is the nomenclature and subdivision of the cerebellar cortex. Many authors have been interested in this aspect and nomenclatures and subdivisions have been proposed by Elliott Smith (1902), Bradley (1904), Bolk (1906), Edinger (1910), Langelaan (1919), Jakob (1928) and Larsell (1937, 1947). Good reviews of these studies are available (Jansen 1954, Jansen and Brodal 1958) and this point need not be commented further here. Larsell's work in the cat and monkey (1953) and his monumental comparative study (1947, 1967, 1970) deserve special attention. This author described the cerebellum as composed of a series of transversely arranged lobules each comprising a vermian and a hemispheral part. The lobules are ten in number and arranged consecutively along a rostro-caudal axis and simply numbered with Roman numerals. The first five lobules correspond to the anterior lobe, lobules VI to IX form the posterior lobe, and the single lobule X corresponds to the flocculo-nodular lobe. In the posterior lobe, Larsell also used various names to designate the hemispheral regions of the lobules.

The principle of Larsell's description rests on the fact that the cerebellar cortex during embryonic life, develops according to a regular sequence which is the same for a large number of species. The fissures forming between cerebellar regions because of the growth and folding are therefore appearing in the same sequence and are constant in number. They serve as useful landmarks to outline the various lobules in spite of their great variation in shape and size among the species. Fig. 3 illustrates the cerebellum of the cat shown unfolded with the lobules labelled according to Larsell (1953).

REVIEW OF LITERATURE OF THE CORTICO-NUCLEAR CONNECTIONS

An important contribution to the knowledge on the cerebellar corticofugal organization was made by Jansen and Brodal in 1940-42. Using the Marchi technique, these authors experimented with the rabbit, cat and macaque. They concluded to the existence of two main principles of organization: in the first place they showed that each half of the cerebellar cortex can be divided into medial, intermediate and lateral zones projecting on the medial, interposed and lateral nuclei respectively. Secondly, they described a topography of the cortical projections in the rostro-caudal direction, the rostral cortex of a zone sending fibers to the rostral parts of the corresponding nucleus, and caudal areas of that cortex projecting to caudal parts of the nuclei.

The authors used Bolk's (1906) nomenclature for the cerebellar lobes in which no border is described between the vermis and the hemispheres of the cortex of the anterior lobe. However, Jansen and Brodal recognized the vermis as a distinct part both in the anterior and posterior lobes because it projects to the medial and vestibular nuclei. They included in their intermediate zone the paravermian parts of the anterior lobe cortex, the ansiform lobe, simple lobule, parts of the paraflocculus and the entire paramedian lobule. The hemispheres which include Crus I, Crus II and certain parts of the paraflocculus were shown to project to the lateral nucleus and formed the lateral zone. In the monkey, the lateralmost part of the anterior lobe also projects upon the lateral nucleus and therefore also belongs to the lateral zone.

Jansen and Brodal used Brunner's division of the nuclear masses. However they mentioned that their division of the nuclear complex into separate nuclei is, in many instances, arbitrary because of the difficulty of identifying exact nuclear borders.

Their arrangement of the cortico-nuclear connections in a number of vertical strips has served as an anatomical reference in nearly all subsequent publications on this subject. However recent studies reveal that the organization is somewhat more complex that what Jansen and Brodal have shown.

Goodman, Hallett and Welch (1960) did an extensive study on the cortico-nuclear projections in the rat with the silver-impregnetion method of Nauta. They proposed a modified principle of vertical strips for the cortico-nuclear projection whereby each of three longitudinal zones of cortex that they distinguished is related to several nuclei. The area of termination within the nuclei differs however for each zone.

Eager's (1963) work on the cortico-nuclear projections in the cat and the monkey with the Nauta method provided additional evidence of exceptions to Jansen and Brodal's concept of three longitudinal projection zones. Eager described a medio-lateral fanning out the cortical projections upon the cerebellar nuclear complex for which he adopted Brunner's subdivisions. In his experiments, he showed that even a restricted lesion of the cortex is followed by degeneration in several cerebellar nuclei. According to this author, the lateral part of the anterior lobe, the medial portion of the ansiform lobule, the paramedian lobule and the caudal part of the dorsal paraflocculus all project upon all three ipsilateral cerebellar nuclei. Except for the lateral portion of the anterior lobe, these same regions were also found to send fibers to the contralateral fastigial nucleus. Furthermore, Eager stated that he has traced cortico-vestibular projections not only from the vermis but also from the paravermal cortex. Another one of his findings which challenges Jansen and Brodal's rostro-caudal topography, is that the projection from any cortical region covers nearly the entire rostro-caudal length of the nuclei to which it projects.

Another study with the Nauta technique was done by Walberg and Jansen (1964). These authors supported the original idea of longitudinal zones but emphasized the lack of sharpness between the boudaries of different zones. According to their results, the medial cortical zone projects exclusively on the ipsilateral fastigial nucleus. However, the projections from the paravermal and lateral zones rather than being related to the nucleus interpositus and nucleus lateralis respectively spread out medio-laterally throughout the two nuclei. Walberg and Jansen also reported that a localized region of the cortex projects upon the entire rostro-caudal length of a nucleus.

Voogd (1964) has proposed a pattern of longitudinal zones of projection between the cortex and the nuclei which in some ways resembles the pattern of Jansen and Brodal but otherwise differs significantly from it. He also recognized four cerebellar nuclei: the medial, the interposed anterior and posterior and finally the lateral nucleus. However of the basis of the distribution of the cortico-nuclear projections, he subdivided the lateral nucleus into a ventro-rostral part which he calls "pars rotunda", and a dorso-caudal part, "the pars convexa". He also pointed out that the pars convexa is fused with the lateral portion of the anterior interposed nucleus. The posterior interposed nucleus, according to Voogd, is connected to the medial nucleus by narrow cellular bridges.

In his experimental cases, Voogd showed that a number of lobules project to more than one cerebellar nucleus. Because of this fact, he proposed the hypothesis that the cortex of each lobule can be divided into longitudinal strips, each strip projecting upon a single nucleus. Voogd's summarizing diagram of the projections of the cortex (Fig. 13) shows four cortical zones A, B, C and D connected by separate fibre bundles to the medial nucleus, the posterior interposed nucleus, the anterior interposed nucleus including the pars convexa, and finally to the pars rotunda of the lateral nucleus. Voogd's zones of projection correspond to those of Jansen and Brodal apart from the fact that he distinguished different origins for the fibers to the medial and lateral vestibular nuclei. In the posterior lobe, Voogd's zones can be called longitudinal only when one imagines the hemispheral cortex unfolded and the lobules forming a chain which they are arranged consecutively in the following order: lobulus simplex, Crus I, Crus II, the paramedian lobule, the dorsal and ventral paraflocculus, and finally the flocculus. Each of the hemispheral lobule enumerated above sends a fibre bundle to one of the nuclear subdivisions. Van Rossum (1969) studied the cortico-nuclear projection of the vermis of the anterior lobe in the rabbit with the Nauta technique. He utilized Voogd's multizonal subdivision but in addition he could distinguish a fifth vertical zone corresponding to the projection to the "pars convexa" of the lateral nucleus in lobules I, III and IV. Apart from this arrangement in five vertical strips rather than three, his results essentially agree with those of Jansen and Brodal (1942).

Finally, it may be mentioned that the existence of a longitudinal principle in the organization of the cerebellar cortex is not derived from studies of the cortico-fugal fiber system only. Olivo-cerebellar (Brodal 1940), ponto-cerebellar (Brodal and Jansen 1946), spino-cerebellar (Voogd 1967), reticulo-cerebellar (Brodal 1943) fiber systems were described as terminating in the cortex of the cerebellum as longitudinally organized strips. A longitudinal division of the cortex basedon the distribution of enzymatic activity was also described by Scott (1964). He demonstrated a concentration of the enzyme 5-nucleotidase in antero-posterior bands located in the molecular layer of the cerebellar cortex.

Another line of evidence favoring the longitudinal division of the cerebellum and specifically that of the paramedian lobule comes from the work of Maffei and Pompeiano (1962). Their experiments involving localized stimulations of the paramedian lobule in decerebrate animals have shown the existence of two cortical strips: a paravermal one facilitating extensor and inhibiting flexor motoneurons of the ipsilateral limbs, and a lateral cortical strip facilitating flexor motoneurons.

All these lines of evidence favor the existence of a longitudinal organization, especially evident in the anterior lobe. It must be stressed however that the organizations proposed by various authors differ in many respects and that a clear definition of this pattern and on the number of zones remains an open question.

PROJECTIONS OF THE PARAMEDIAN LOBULE AND CRUS II

Early workers in the field of cerebellar cortico-nuclear connections concerned themselves with a general description of the projection from large cortical regions and therefore the projection of the paramedian lobule as such, was not described.

In the work of Clarke and Horsley (1905) and Hohman (1929), lesions which covered the paramedian lobule also encroached on large areas of the adjacent cortex: the subsequent degeneration which the authors described in the "globose" or interposed nucleus was not related to the paramedian lobule only.

The specific projection of the paramedian lobule in the monkey and cat was first described by Jansen and Brodal (1940-42). From their results they concluded that the paramedian lobule is mainly related to the nucleus interpositus and therefore the paramedian lobule belongs to the intermediate cortical zone. It is to be underlined, however, that besides a heavy degeneration in the caudo-medial parts of the interposed nucleus, they also observed a slight projection upon the lateral as well as the medial nucleus. The authors explained the divergence of the paramedian projection of the cat upon the medial nucleus and the lateral nucleus, by slight encroachments of the vermis and Crus II, especially since the area of projection of the paramedian lobule in the lateral nucleus overlapped with the area of projection of Crus II.

In the rabbit, Jansen and Brodal observed that the paramedian lobule is related to the interposed nucleus in its entire rostro-caudal length. The projection of the paramedian lobule upon the lateral nucleus and ventrolateral parts of the medial nucleus was again explained by the undercutting of the fibers of the ansiform lobule and pressure upon the vermis.

Eager's results in the cat (1963) showed a widespread projection of the paramedian lobule upon the nuclear mass. After lesions of that lobule he described degeneration in the rostral and caudal poles of the lateral nucleus, leaving the central portions of that nucleus clear, in the central and caudal parts of the interposed nucleus and in the caudal parts of both the homolateral and contralateral medial nuclei.

A similar wide projection of the paramedian lobule was described by Ford and Russell (1964, Nauta method) in the cat. They found that lesions in the paramedian lobule produce degeneration in the entire lateral nucleus, in the interposed and perhaps in the medial nucleus.

Goodman, Hallett and Welch (1963, Nauta) described a highly organized cortico-nuclear projection of the paramedian lobule in the albino rat. They planned their lesions of the cortex in accordance with a subdivision into three longitudinal zones determined electrophysiologically by Goodman and Simpson (1961): the lateral, the paravermal and the vermal zones. The cortex of the paramedian lobule is part of the paravermal and lateral zones and therefore lateral and medial regions of this lobule were expected to be different in their efferent projections.

The part of the paramedian lobule contained in the lateral zone projects upon the dorsal half of the lateral nucleus, the lateral third of the interposed nucleus, the dorso-lateral "hump" region of the interposed nucleus, and on the dorso-lateral protuberance of the medial nucleus.

The medial portion of the paramedian lobule sends fibers upon the central part of the interposed nucleus, and on the "crest" region of this nucleus, and upon the protuberance of the medial nucleus.

Despite same overlap, the lateral and the medial regions of the paramedian lobule differ for the most part as to the exact site of termination of the projections (the fibers from the lateral paramedian lobule terminate more laterally within each of the nuclei) and also in the number of nuclear projections (the lateral portions of the paramedian lobule project to four sites, the medial region to three only).

Still another pattern of projection for the paramedian lobule of the cat was described by Voogd. According to this author, the cortex of the paramedian lobule can be divided into three longitudinal bands, B, C and D, each band being related to a single subdivision of the cerebellar nuclei. To support his hypothesis, Voogd presented two lesions: the first one restricted to the two medial bands of projection of the paramedian produced degenerations in the posterior interposed nucleus, and in the anterior interposed and lateral nuclei (LC-IA). Degeneration resulting from the second lesion which encroached on the lateral as well as the other two bands of projection showed degeneration in the ventral part of the lateral nucleus along with the projection to the other two sites. It is obvious from the description of these results that the exact area of termination of fibers from the paramedian lobule is far from being definitively established. The projection of this cortical region would be limited to the interposed nucleus according to Jansen and Brodal, and on the other hand, workers such as Eager, Goodman et al. have shown that the paramedian lobule projection fans out to all ipsilateral nuclei.

There are similar discrepancies concerning the exact distribution of the projection of Crus II. Early investigators such as Clarke and Horsley (05, cat and monkey), Hohman (29, cat), Dow (36, cat) all agreed that this lobule and the adjacent cortex project on the lateral nucleus only. In their publications of 1940 and 1942, Jansen and Brodal also stated that Crus II projects exclusively upon the caudal part of the lateral nucleus in both cat and monkey.

On the other hand, a wider zone of termination for Crus II was reported by Eager (1963) in the cat. According to him, this region of the cortex sends fibers to the medial part of lateral nucleus, to the lateral portion of the NIP and to the caudal poles of both fastigial nuclei.

Ford and Russel (1964) reported that Crus II projects upon two nuclei only in the cat: the caudo-lateral portion of the interposed nucleus and the central and lateral parts of the lateral nucleus.

Voogd's experiments on the cortico-nuclear projection of Crus II in the cat showed that this lobule has a triple projection: a lesion of this part of the cortex gives degeneration in the posterior interposed nucleus, in the anterior interposed nucleus and in the dorsal part of the lateral nucleus "Lc-IA", and in the ventral part of the lateral nucleus. He also suggested, in accordance with his zonal principle, that the medial part of Crus II is responsible for the projection to the NIP and the lateral portion of Crus II on the lateral nucleus.

As in the case of the paramedian lobule, there are numerous discrepancies concerning the site of projection between various authors. According to the traditional partitioning of the cortex into three longitudinal zones of projection (Jansen and Brodal), the paramedian lobule would be located in the intermediate zone and Crus II in the lateral one. Hence the paramedian lobule and Crus II should project to the interposed and lateral nuclei respectively. On the other hand, more recent experiments (Eager, 1963, Goodman et al., 1963, Ford and Russell, 1964, Voogd, 1964, van Rossum, 1969) seem to indicate that both Crus II and the paramedian lobule project to two or more of the cerebellar nuclei.

PRINCIPAL AIMS OF THE STUDY

In the present series of experiments, it was undertaken:

1. to determine as precisely as possible the total area of termination of cortico-nuclear fibers from the paramedian lobule and Crus II of the cat,

2. to determine whether the area of termination of the cortico-nuclear fibers of Crus II overlaps with that of the paramedian lobule,

3. to uncover a possible topographical arrangement of the cortico-nuclear fibers from these two lobules,

4. to test Voogd's hypothesis concerning a division of the paramedian lobule and Crus II in three longitudinal bands, with each band projecting to a single subdivision of the cerebellar nuclei.

In order to attain the above mentioned objectives, we planned a series of experiments consisting of lesions and subsequent mapping of the degeneration shown with the silver impregnation method of Nauta.

To find out the total area of termination of the paramedian lobule and Crus II, we made a number of lesions which, when added together, covered their entire surface. The combination of zones of degeneration in the nuclei in all these cases on standard diagrams showed the total extent of the projection.

Having plotted the degeneration produced by lesions of Crus II on one hand, and the terminal areas of fibers from the paramedian lobule, we were able to compare the sites of terminations of the fibers from these two lobules and to determine the exact extent of overlap.

The problem of a possible topographical organization of the fibers of Crus II and the paramedian lobule is suggested in the results of anatomical and physiological investigations showing that these two lobules receive somatotopically organized afferent fiber systems.

Grant (1962, cat) demonstrated with silver impregnation methods that the dorsal spino-cerebellar tract which contains fibers entering the cord below mid-thoracic levels ends in the caudal folia of the paramedian lobule. This author also showed that the fibers from the external cuneate nucleus (cervical cord equivalent of the column of Clarke) containing fibers entering at cervical and upper thoracic levels terminate in the rostral folia of the paramedian lobule. Electro-physiological studies support this pattern of representation of body regions in the paramedian lobule (Snider and Stowell, 1942, 1944, Oscarsson, 1965).

There is also evidence brought forward by Snider and Eldred (1948, '51, '52) that the paramedian lobule receives a somatotopically organized projection from the primary motor and primary sensory cortices which follows the same distribution as the spinal afferent fibers.

Jansen Jr. (1957) described a similar cortico-cerebellar somatotopic relationship in the Crus II. The antero-lateral part of Crus II is related to the leg area, and the postero-medial part to the arm area. This localization in the Crus II is not as easily revealed as that of the paramedian lobule.

Sousa-Pinto and Brodal (1969) showed a somatotopical pattern in the projection from the brain cortex to three regions of the inferior olive. One of these, in the rostral part of the principal olive, coincides with an area shown to send an orderly projection to the cortex of Crus II (Brodal 1940). The pattern which emerges from these studies reveals, that in Crus II the upper portions of the body are represented in the medial folia, while the lower one are situated laterally.

In order to test the existence of a somatotopical projection, we made lesions which were located either in the rostral folia or in the caudal folia of the paramedian lobule, and in the medial and lateral folia of Crus II, and compared the distributions of cortico-nuclear fibers in the nuclei.

Voogd's idea of longitudinal strips was tested in the paramedian lobule. The nearly vertical distribution of folia in this lobule lends itself well to narrow longitudinal lesions. Such vertical lesions can be expected to destroy only one or another of the zones of projection, and would determine whether or not each zone projects exclusively to one nucleus.

II

METHOD AND MATERIAL

Altogether 39 cats were used for this study of an average weight of 3.2 kg.. For the surgery, the animals were anesthetized by an intravenous injection of sodium nembutal, 30 mg/kg body weight. They were then placed in a stereotaxic apparatus and the cranium overlying the cerebellum was exposed. A small hole was drilled over the region of cortex to be destroyed. A number of our lesions were made through the dura with a heated glass or metal rod. This method has the advantage of avoiding exposure of the cortex and prevents any accidental accroachment. It does not permit precise identification of the folial pattern, however. In order to localize specific parts of the cortex, it was necessary to cut open the dura in a number of other cases. The lesions were then made with a heated ophthalmic knife or needle scraped along the surface of the cortex. Lesions of the caudal folia of the paramedian lobule were made by opening the great cistern, and approaching by way of the fourth ventricle. Except for vermian lesions and a few control cases, bilateral lesions were made in every animal. The cortex was then covered with strips of muscles soaked in physiological saline, and a thin cap of dental plaster was applied over the dura hole and held in position by screws drilled into the cranium.

The animals were sacrificed under deep nembutal anesthesia on the sixth post-operative day by intra-cardiac perfusion, first with a physiological saline solution, and then with 10% formalin. Survival times of five to eight days were used and the optimal time was found to be six days. Before removing the cerebellum, the animal was left standing for about an hour, and then the brain was placed in a large volume of 10% formalin for a minimum of ten days.

When sufficiently hardened, the cerebellum was quickly frozen with dry ice and then cut at fifteen μ with a freezing microtome. Every fifteenth section was stained with the method of Nauta-Laidlaw (1954). Series of thionine stained and paraffin mounted sections in each of the three conventional planes were available for the investigation of the normal morphology of the nuclei.

Most of the experimental series were cut in the sagittal plane. The latter plane as well as the horizontal plane which was also used in certain cases are advantageous because the cortex and the nuclei are kept in continuity by the white matter in most of the sections.

The sections were drawn under a projector at a magnification of about 10X. The lesions and the degenerated fibers en passage were verified under the microscope (40X) and entered in the drawings. The nuclei were then outlined and the terminal degeneration mapped on a microscope pantograph. The diagrams of the cortex used for representing the lesions are modifications of those used by Jansen and Brodal (1940, 1942). The nomenclature of Larsell (1953) is followed for the cortex, and that of Flood and Jansen (1961) for the nuclei. A standard series of diagrams of the nuclei has been utilized for comparing various cases. This series corresponds to one of the experimental cases representative of the majority.

The evaluation of degeneration was based on the criteria utilized by other authors using the same technique, and is described in papers by Nauta and Gygax (1954) and Glees and Nauta (1955).

III

RESULTS

EVALUATION OF THE LESIONS AND OF THE COURSE OF CORTICO-NUCLEAR FIBERS

An ideal requirement for the analysis of the cortico-nuclear projection is to obtain lesions located in well defined regions of the cortex without encroaching on adjacent regions. Many technical difficulties prevent one from attaining this goal regularly. Therefore, a precise assessment of any lesion obtained, and a thorough verification of the surrounding regions of the cortex is necessary. In this way, truly restricted lesions are identified and encroachments can be taken into account in the interpretation of data.

For each case, the lesion was outlined on a diagram of the cerebellar cortex according to its macroscopic aspect and then corrected according to the microscopic findings. The degenerating fibers coursing to the nuclei from the lesion were followed in serial sections in order to establish the distribution of the cortico-nuclear fibers. All folia of the sections were searched for the presence of degenerating fibers descending towards the white matter, and in this way unwanted extents of our lesions and inadvertent damage were detected. When one considers the extent of the cortical damage found in most cases in spite of our planning of small circumscribed lesions, it becomes evident that the cerebellar cortex is extremely sensitive to any kind of trauma. Such factors as a slight contact with the instruments of even the exposure to air during the surgical procedure and any degree of edema or vascular impairment in the post-operative period seem sufficient to cause the death of some neurons and the ensuing degeneration of their axon. In numerous cases, degenerated axons were traced from cortical regions which looked intact on macroscopic examination.

Coursing fibers encountered in folia outside the region of the lesion present a problem of interpretation since they could be association fibers rather than cortical efferent fibers. Regarding fibers encountered in folia outside the immediate vicinity of the lesion, it was possible in the great majority of cases to discover a small cortical lesion and to follow these fibers in the white matter towards the nuclei. In addition, the distribution of terminal degeneration in the nuclei also differed from that of cases which did not show degenerated coursing fibers in that cortical region. In the case of the folia adjacent to the site of a lesion, it has been observed that they regularly show a fair amount of degeneration. Some of it may come from the lesion and because of an oblique course appear to belong to the medullary stem of adjacent intact folia. But it was also felt that some of these fibers were association fibers because one could observe simultaneously some terminal degeneration in the granular layer of the cortex and around the Purkinje cells. It is evident that the experimental silver impregnation methods are ill suited for the distinction of association or cortical efferent fibers since the relationships of axons with their parent structures and their terminal sites are not seen. Indirect evidence reported above however, seems compatible with the existence of short association fibers as demonstrated by the Golgi method (Cajal, 1909), but casts some doubt on the existence of long association fibers demonstrated with experimental silver methods (Eager, 1963).

In order to localize the lesions precisely, identification of the limits of various lobules in our histological sections is necessary. Larsell (1953) described morphological landmarks, characterizing the various lobules of the cerebellum. Thus the paramedian lobule and Crus II are easily recognizable by their location and appearance. The paramedian lobule is bordered by the posterior vermis medially, lobule VI rostrally, Crus II and the dorsal paraflocculus laterally. It is delimited from adjacent lobules by the paramedian sulcus medially, posterior superior fissure rostrally and the ansoparamedian sulcus laterally. The most caudal folia of the paramedian lobule curve ventrally and rostrally and are resting on the dorsal portion of the pons. In the adult cat, the number of folia in the paramedian lobule varies: there are as few as seven folia in some animals, and as many as eleven or twelve in others. The paramedian lobule is not oriented exactly in the sagittal plane. The rostral folia are more laterally situated than the caudal ones. Thus, a true sagittal plane passing medially through the paramedian lobule shows only the caudal two third of this lobule (Fig. 3, section 26), while lateral sections (Fig. 3, section 17) contain only the rostral folia of the paramedian lobule. The long axis of each folium of the paramedian lobule is approximately in the transverse plane, while the long axis of the folia of Crus II is longitudinal medially, and transverse laterally. Ventrally Crus II is bordered by the dorsal paraflocculus, rostrally by Crus I.

These macroscopic features of the various lobules helped to identify them in our experimental sagittal and horizontal series. Furthermore, our histological sections offered additional criteria for setting more exact limits between various lobules. Voogd has called attention to a number of interruptions of the cerebellar cortex in the depth of some fissures. In our own material we observed a discontinuity of the cortex at the bottom of certain fissures. In these places, there is an abrupt interruption of the cortex and the white matter comes to the surface. Thus on its medial side, the paramedian lobule is delimited from the posterior vermis by a strip of white matter coming to the surface except most rostrally, where the paramedian cortex fuses with the cortex of the posterior vermis. This interruption of the cortex on the medial aspect of the paramedian lobule is found in the depth of the paramedian sulcus.

Another constant interruption of the cortex is present at the bottom of the posterior superior fissure (Fig. 10, Larsell, 1953) which marks the limit between the paramedian lobule and lobule VI. There is a narrow bridge of cortex which unites the first folium of the paramedian lobule to the most-medial folium of Crus II. More caudally, where the central folia of the paramedian lobule are adjacent to the second and third folium of Crus II, there is a gap of the cortex at the bottom of the fissure separating the two lobules.

When there is an interruption of the cortex, it is relatively easy to delimit the borders of a lobule. However, when two lobules are continuous at one point, the exact limit is more difficult to establish. For instance, the paramedian lobule is continuous rostrally with Crus II and caudally with the dorsal paraflocculus. It is possible however in serial sections to recognize the development of new folia as one moves away from the transition zone. The limit is therefore set at the level of the bridging folium. Some of these details can be seen in the sagittal sections of Fig. 3. The transversely cut folia of the paramedian lobule are recognizable in levels 28, 20 and 17. In these levels, a discontinuity between the cortex of the paramedian and lobule VI can be observed. This discontinuity is indicated by the disappearance of the inner line which indicates the limit between the cortex and the white substance. In level 17, in the depth of the posterior superior fissure which separates the paramedian lobule from lobule VI, the rostral portion of the paramedian cortex begins to expand. Laterally, this part of the cortex continues to grow and constitutes the most medial folium of Crus II as can be seen in level 15.

CEREBELLAR NUCLEI

For precise mapping of the degeneration in the cerebellar nuclei, it was deemed necessary to clarify the division of these nuclei in the cat.

For our experimental series, the sagittal plane of cutting proved to be most advantageous. However, the main features of the nuclei are best understood in the horizontal plane. The latter plane will be described first.

Figure 1 illustrates horizontal sections through the cerebellar nuclei. The medial nucleus (NM) (in vertical lines) is situated nearest to the midline. It is characterized by a dorso-posterior prolongation (sections 70, 74, 76). In more ventral levels (66, 62), the medial nucleus is separated form the posterior interposed nucleus by a few cell strands.

Lateral to the medial nucleus, one sees the anterior (NIA) and posterior (NIP) interposed nuclei. These two nuclei are separated by a thin fiber bundle running between them. Even in sections where they are in close apposition to each other as in section 62, they never present a fusion.

At the lateral extremity in each section, is the lateral nucleus (NL). In ventral levels (50, 54, 58), this nucleus is separate from adjacent structures; dorsally (sections 62, 66) the lateral nucleus fuses with the anterior interposed nucleus. This zone of fusion which we call "transition zone" (NL-NIA) is indicated with cross-hatched lines in these levels. At this point, the cyto-architecture does not permit to draw a limit between

FIGURE 1

THE CEREBELLAR NUCLEI OF THE CAT IN HORIZONTAL SECTIONS

This series of equally spaced sections shows the shape and the relative positions of the four cerebellar nuclei. Different symbols correspond to each of the nuclei. The right-hand side of each rectangle corresponds to the midline. Note the area of fusion between the anterior interposed and lateral nuclei (NL-NIA, corss-hatchings). The vertical line A, B and C corresponds to different sagittal planes (see text). Abbreviations listed on page 101 and 102.

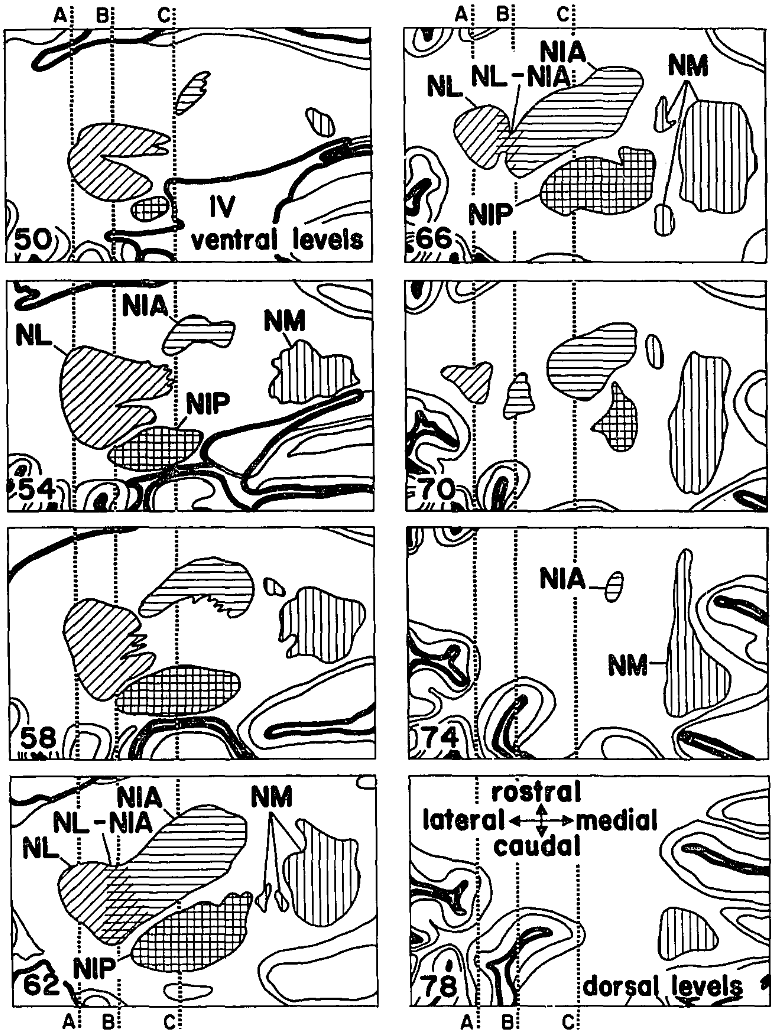
A
B
C
IV
ventral levels
50
NIA
NL
NL-NIA
NM
NIP
66
NIA
NL
NM
NIP
54
70
58
NIA
NM
74
NIA
NL-NIA
NM
NL
NIP
62
rostral
lateral
medial
caudal
78
dorsal levels

FIGURE 1

the two nuclei: there are no clear fibre bundles running between the two nuclei, and the cell populations closely resemble each other.

The sagittal sections of the cerebellar nuclei can be well understood with these horizontal sections. A sagittal line A (Fig. 1) passing through the lateral nucleus shows level 4 or 5 in Figure 2 where only the lateral nuclei is present.

A line medial to this will pass through the lateral nucleus ventrally, but dorsally would cut through the transition zone, as can seen at the level of line B. Such sections also show the posterior interposed nucleus. Nuclei cut in a sagittal plane at levels corresponding approximately to line B would be seen in section 7, 8 or 9 in Figure 2.

Finally, a sagittal section even further medially (line C) passes through both the anterior and the posterior interposed nuclei. In Figure 2, sections 15 or 16 would correspond to that situation.

TOTAL PROJECTION OF CRUS II

Altogether nine partial lesions of Crus II were combined in order to obtain the total area of projection of this lobule (Fig. 2). We used such a combination of lesions because they cover nearly all of the surface area of the cortex of Crus II; only the most lateral folium is not entirely damaged. For the determination of the total projection, this proved to be more precise than using large lesions which on the one hand leave large parts of the cortex undamaged and on the other, usually encroach heavily on surrounding structures. Nevertheless, the degeneration following a large lesion such as that of cat CN-38R (Fig. 4) corresponds essentially to the degeneration resulting from the addition of a number of smaller lesions.

Of the nine lesions we used for the determination of the total projection of Crus II, none encroach on the cortex of the paramedian lobule or of Crus I. However, lesions of cat CN-9L and CN-39R damage a portion of the cortex of the dorsal paraflocculus. The projection of the latter lobule was determined (see later in the text) and is not included in the diagrams representing the total projection of Crus II.

The degeneration resulting from these nine lesions covering the greater part of the surface cortex of Crus II is located in two distinct, non overlapping zones in the cerebellar nuclei. The first of these two zones of projection begins in the lateral nucleus and continues uninterrupted throughout the transition zone in the lateral portion of the anterior interposed nucleus. This medio-laterally oriented strip of degeneration has a slight dorso-ventral

FIGURE 2

TOTAL DESTRUCTION OF CRUS II AND CORRESPONDING AREAS OF PROJECTION

The extent of nine lesions of the cortex of Crus II is plotted on a diagram of the left half of the cerebellar posterior lobe. Lesions originally on the left side are labelled with a L, those done on the right side have a R. Together these lesions cover nearly all the surface area of Crus II (lateral limit of the lobule indicated by a whicker line between the folia, and the medial limit marked by a vertical fissure between this lobule and the paramedian lobule). A number of equally spaced standart diagrams of the nuclei in the sagittal plane show the area of termination of the projection of Crus II. The latter extend mediolaterally through the NL, NL-NIA, and NIA on the one hand, and through the NIP on the other. Abbreviations listed on page 101 and 102.

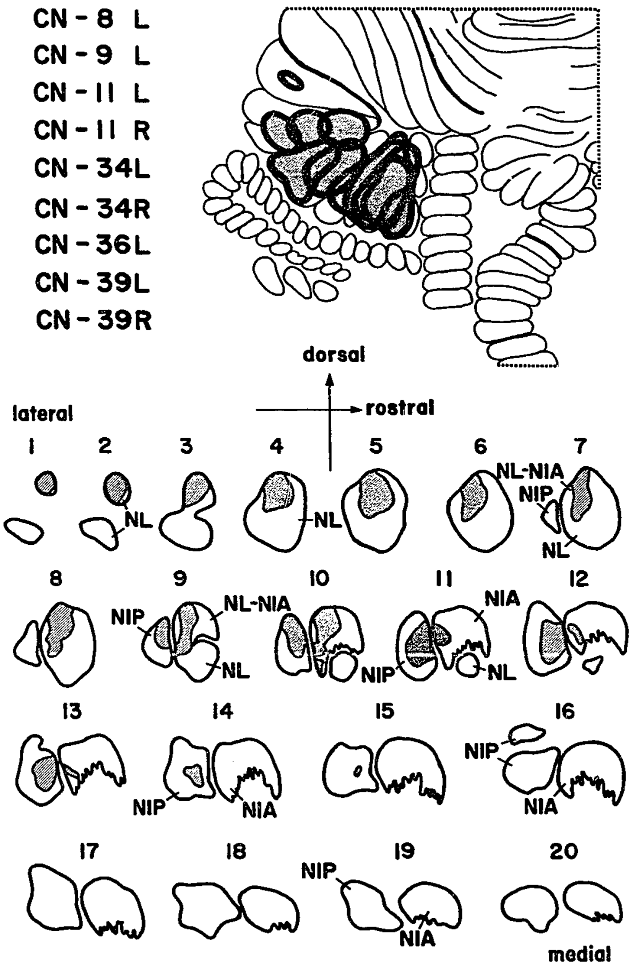
CN - 8 L
CN - 9 L
CN - 11 L
CN - 11 R
CN - 34L
CN - 34R
CN - 36L
CN - 39L
CN - 39R
dorsal
rostral
lateral
1
2
3
4
5
6
7
NL
NL
NL-NIA
NIP
NL
8
9
10
11
12
NIP
NL-NIA
NL
NIA
NIP
NL
13
14
15
16
NIP
NIA
NIP
NIA
17
18
19
20
NIP
NIA
medial

FIGURE 2

slant. Laterally the projection is entirely dorsal, medially it shifts into ventral position. In the lateral nucleus, the degeneration is located in a central and somewhat caudal position, but in the anterior interposed nucleus, it extends along the posterior border of the nucleus. It is to be noticed that the area of terminal degeneration is greatest in the lateral nucleus, diminishes slightly in the transition zone and tapers out medially in the anterior interposed nucleus.

The second zone of degeneration, about half as large in area as the first, is found entirely within the lateral half of the posterior interposed nucleus. As in the case of the first zone of projection, this strip of degeneration has an oblique orientation. Leaving a thin lateral portion of the posterior interposed nucleus clear, the degeneration begins dorsally and rostrally, medially it shifts into a more ventral position. This second zone of projection in the posterior interposed nucleus, ends a few levels more medially than the other one described above.

TOPOGRAPHY OF THE PROJECTION OF CRUS II

Since the indications in the literature are that the somatotopical representation in the cortex of Crus II is from medial to lateral, we will describe in detail two lesions located at both extremities of this lobule.

Figure 3 illustrates cat CN-8L, in which a medial lesion of Crus II was produced. The lesion, as indicated on the diagrams of the sagittal sections of the cerebellum, begins in level 15 and ends in level 13. However, degenerated fibers are present in levels which are more lateral than that. The cortex of the paramedian lobule is intact, as well as that of the dorsal paraflocculus.

Heavy degeneration is represented in the nuclei with horizontal lines, scanty degeneration with dots. As in the case of the total lesion of Crus II, the terminal degeneration in cat CN-8L is located in two zones. The first zone of projection, begins in the transition zone (level 13, 14). Its position here is dorsal and somewhat central. Medially, the degeneration becomes progressively ventral and caudal.

The second zone of projection in the posterior interposed nucleus, also appears as a medio-laterally extending strip. From a dorsal position laterally, it moves to a ventral one medially. It is to be noticed that the lateral part of the posterior interposed nucleus (section 14 to 17) is free from heavy degeneration.

The lesions in cats CN-33R, CN-33L, CN-34R, CN-34L and CN-39L illustrated in Figure 4, resemble case CN-8L since they all damage only the medial folia

FIGURE 3

LESION OF THE MEDIAL REGION OF CRUS II AND AREAS OF PROJECTION

In the upper left hand corner, a diagram of the unfolded cerebellar cortex is shown and labelled according to Larsell. The lesion appears in solid black and hatched lines surrounding it illustrate the exact extent of cortical damage as revealed by the sections. To the right, a series of sagittal sections through the left posterior lobe of cat CN-8L illustrates the lesion and the course of cortico-nuclear fibers. Numbers underneath the sections indicate their relative spacing (consecutive numbers indicating a spacing of 225μ). In the series of equally spaced sagittal nuclear outlines from this case, the distribution of area of terminal degeneration is seen. One of these areas is in the NL-NIA transition zone and in the NIA; the other in the NIP. Solid horizontal lines indicate intense terminal degeneration, dots represent scattered degeneration. Abbreviations listed on page 101 and 102.

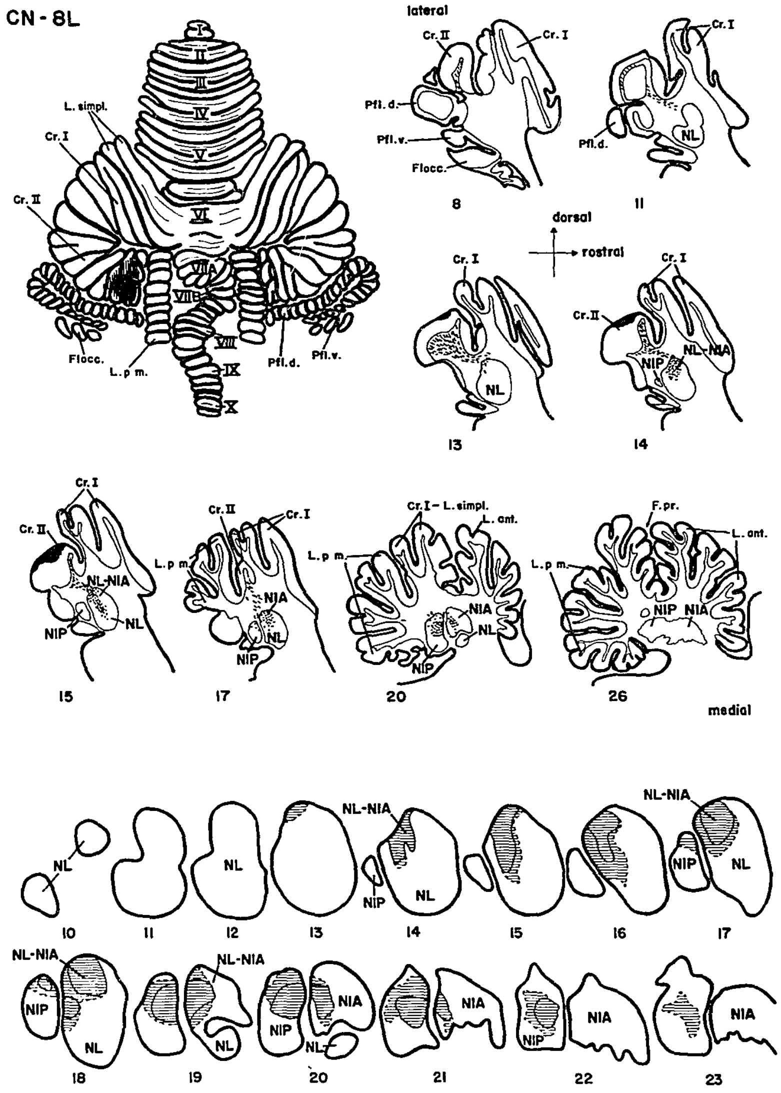
CN - 8L
I
II
III
IV
V
VI
VIIA
VIIB
VIII
IX
X
L. simpl.
Cr. I
Cr. II
Flocc.
L. p m.
Pfl. d.
Pfl. v.
lateral
8
11
13
14
dorsal
rostral
NL
NIP
NL-NIA
15
17
20
26
medial
NIA
L. ant.
F. pr.
Cr. I - L. simpl.
10
12
16
18
19
21
22
23

FIGURE 3

Leaf 43 omitted

in page numbering.

FIGURE 4

LESIONS OF CRUS II

On these four diagrams of the unfolded cortex of the cerebellar posterior lobe are illustrated eleven lesions of various portions of Crus II, including in some cases, encroachments of adjacent lobules. Black regions indicate cortical destruction, hatched regions indicate extensions of the lesions as determined by the presence of degenerated efferent fibers observed in the histological sections.

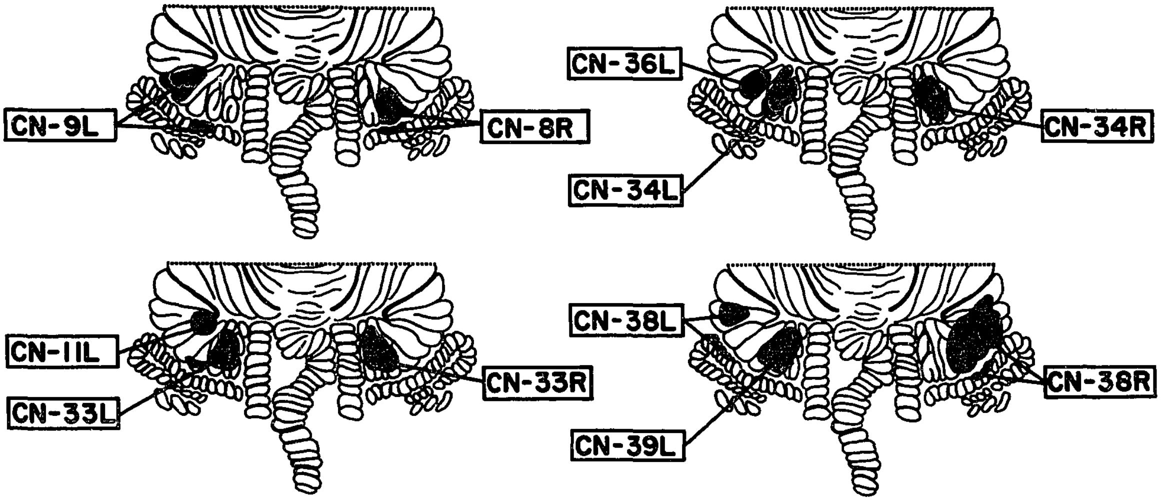
CN-9L
CN-8R
CN-36L
CN-34R
CN-34L
CN-11L
CN-33R
CN-33L
CN-38L
CN-38R
CN-39L

FIGURE 4

of Crus II. They are all restricted to Crus II since none of them encroach on the cortex of either the paramedian lobule or on the dorsal paraflocculus. The degeneration corresponds to what was found for case CN-8L.

Cat CN-39R in Figure 5 has a small lesion situated in the lateral half of the three rostralmost folia of Crus II and extending to the adjacent folia of the dorsal paraflocculus. The lesion can not be verified histologically because lateral folia of Crus II and of the paraflocculus were detached in the frozen sections. However, the absence of a lesion and of degenerated fibers in the medial folia of Crus II can be seen in levels 19-16 and 13. The course of degenerated fibers reveals that the projection originates in lateral folia of Crus II. Similar criteria apply for the determination of the lesion in the dorsal paraflocculus. In addition, the approximate size and the site of the lesion had been previously assessed by a careful macroscopic examination of the cerebellar cortex.

The degeneration illustrated in the cerebellar nuclei in cat CN-39R is the result of a lesion of Crus II as well as the dorsal paraflocculus. A brief survey on the projections of the dorsal paraflocculus makes it possible to recognize the degeneration due to a lesion of this lobule. Cats CN-39R, CN-9L, CN-8R, CN-38L and CN-38R all have in common an accessory lesion of the dorsal paraflocculus in addition to a principal lesion in Crus II. By analyzing the degeneration following such lesions, a common region of projection which was not present in cases where there was no encroachment on the cortex of the dorsal paraflocculus was identified. All the lesions which have an encroach-

FIGURE 5

LESIONS OF THE LATERAL REGION OF CRUS II AND AREAS OF PROJECTION

In the upper left hand corner, the lesion is displayed on a diagram of the unfolded cerebellar cortex. It is located in the lateralmost three folia of Crus II which are incompletely damaged and it also encroaches on three folia of the dorsal paraflocculus. The sagittal sections to the right show the two streams of degenerated coursing fibers from the lateral portion of Crus II and from the paraflocculus (more ventral). The medial portion of Crus II is intact. In the nuclear outlines below, two areas of terminal degeneration are identified: one in the dorsolateral part NL and extending in the NL-NIA transition zone, and the other in the NIP. Solid horizontal lines indicate heavy terminal degeneration, dots correspond to scanty degeneration. The degeneration seen in the ventral half of the NL is related to the fibers from the paraflocculus (level 19, see text). Abbreviations listed on page 101 and 102.

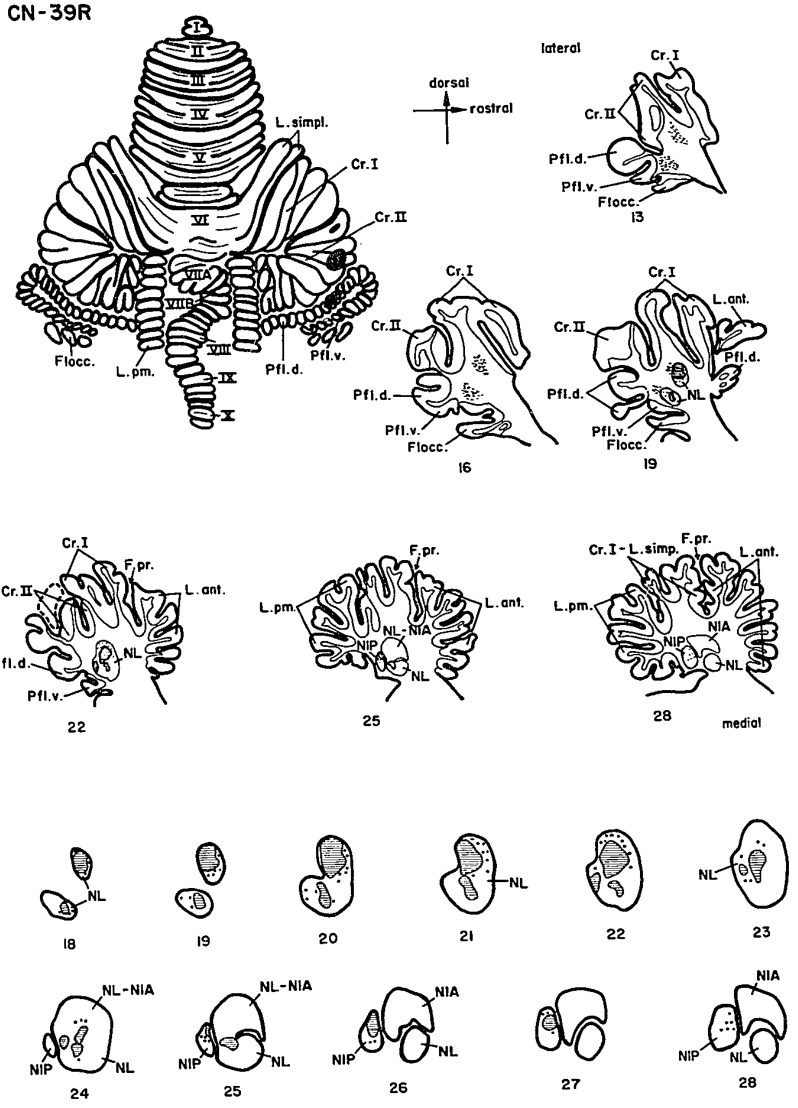
CN-39R
I
II
III
IV
V
VI
VIIA
VIIB
VIII
IX
X
L.simpl.
Cr.I
Cr.II
Flocc.
L.pm.
Pfl.d.
Pfl.v.
dorsal
rostral
lateral
Cr.I
Cr.II
Pfl.d.
Pfl.v.
Flocc.
13
Cr.I
Cr.II
Pfl.d.
Pfl.v.
Flocc.
16
Cr.I
L.ant.
Cr.II
Pfl.d.
Pfl.d.
NL
Pfl.v.
Flocc.
19
Cr.I
F.pr.
Cr.II
L.ant.
Pfl.d.
NL
Pfl.v.
22
F.pr.
L.pm.
L.ant.
NL-NIA
NIP
NL
25
F.pr.
Cr.I - L.simp.
L.ant.
L.pm.
NIA
NIP
NL
28
medial
NL
18
19
20
NL
21
22
NL
23
NL-NIA
NIP
NL
24
NL-NIA
NIP
NL
25
NIA
NIP
NL
26
27
NIA
NIP
NL
28

FIGURE 5

ment on the dorsal paraflocculus present degeneration within the ventral half of the lateral nucleus. This patch of degeneration occupies a central position. It did not appear probable from our material that the dorsal paraflocculus projects upon the posterior interposed nucleus. Our lesions of Crus II which encroach on the dorsal paraflocculus did not show a projection in the posterior interposed nucleus which differed from that shown in cases with pure lesions of Crus II. If the dorsal paraflocculus does project upon the posterior interposed nucleus, this projection certainly overlaps in great part with the projection of Crus II in this nucleus.

Therefore in case CN-39R, it is interpreted that the degeneration found in the ventral half of the lateral nucleus is due to the paraflocculus lesion. The projection of the lateral folia of Crus II therefore covers the rest of the distribution. The first zone of projection begins in the most lateral section of the lateral nucleus (level 18) and ends in the transition zone. From a dorsal position in the lateral nucleus, the degeneration becomes progressively ventral in the transition zone.

The second zone of projection from the lateral folia of Crus II is found in the dorsal and caudal parts of the posterior interposed nucleus. Quantitatively, this projection appears less important than the one found in the lateral nucleus.

There is only one of our cases which is comparable to CN-39R. Lesion CN-11R is restricted to the lateral folia of Crus II without encroaching on the paraflocculus and the degeneration following this lesions is similar to that obtained in case CN-39R (Fig. 6, stippled) apart from the zones already attributed to the projection of the paraflocculus.

The distributions of degeneration in two cases having lesions in the medial and lateral extremities of Crus II have been plotted together on a series of standard diagrams of the nuclei with different symbols for each case. Figure 6 shows the degeneration following a medial (cat CN-8L) and a lateral (cat CN-11R) lesion of Crus II. In the first zone of projection (NL and NL-NIA), there is some overlap in the transition area (levels 7-8-9). In these levels, the projection from the lateral folia of Crus II is slightly more ventral that from the medial parts of this lobule. Otherwise, there is no overlap, cat CN-11R sending its projection to the dorsal parts of the lateral nucleus (levels 2 to 6, stippled areas), and cat CN-8L to the caudal part of the anterior interposed nucleus (levels 10 to 13, vertical lines).

The topography is less clear in the second zone of projection which is located in the posterior interposed nucleus. Here, the degeneration from the two extreme lesions of Crus II present more overlap (levels 11 to 14). Nevertheless, there is again, a tendency of the projection from the lateral part of Crus II to be more ventral than the projection from CN-8L in most levels.

Four of our lesions (cats CN-8R, CN-9L, CN-36L, CN-38L, Figure 4) were located in the intermediate folia of Crus II. The degeneration produced by such lesions overlaps partly with the projection from the medial portion and partly with that of the lateral part of Crus II which were illustrated in Figure 3, 5 and 6. In these cases, the projection in the NL-transition-zone-NIA is neither as lateral as the one from CN-11R, nor as medial as that

FIGURE 6

MEDIAL AND LATERAL LESIONS OF CRUS II AND COMPARISON OF THEIR PROJECTIONS

Two lesions are indicated on the diagram of the unfolded cortex of the posterior lobe of the cerebellum. The medial lesion (CN-8L) is located in the most medial part of Crus II and does not encroach upon the surrounding cortex; the lateral lesion (CN-11R) damages the central part of the lateral folia, leaving the most rostrolateral folium intact. Degeneration following these two lesions is plotted on a standart series of cerebellar nuclei with different symbols. Only heavy degeneration has been marked on this series of nuclei. In the case of the medial lesion (represented with vertical lines), the degeneration is located in the NL-NIA transition zone extending into the NIA, and in the NIP. Degeneration following a lateral lesion of Crus II is situated in the NL and NL-NIA transition zone and also in the NIP. The overlap between the projections from these two lesions is indicated.

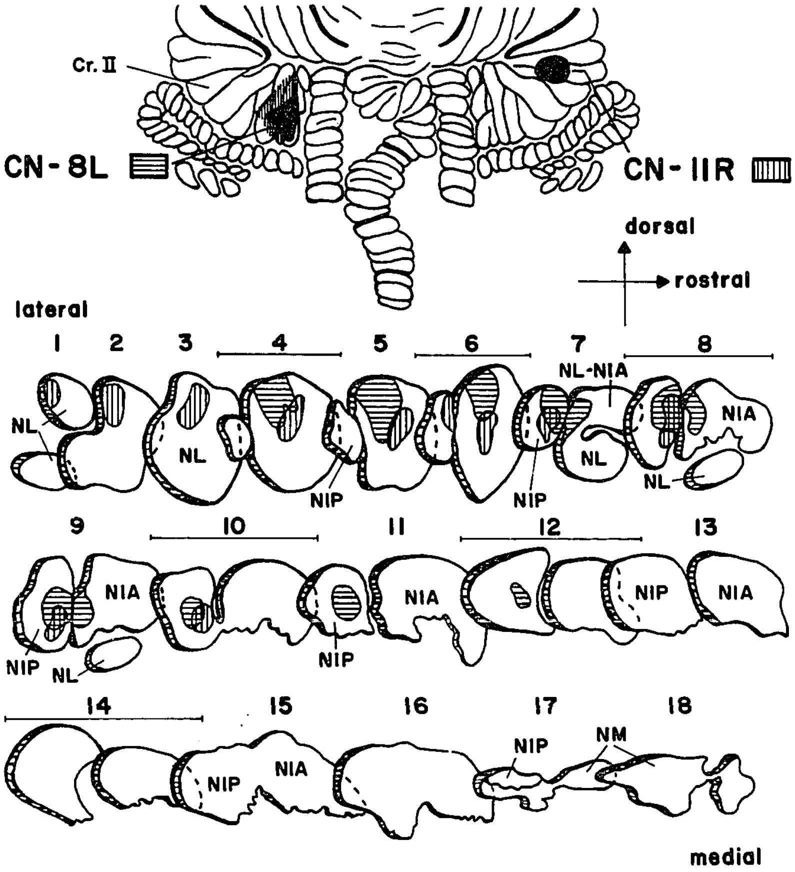
Cr. II
CN-8L
CN-11R
dorsal
rostral
lateral
1
2
3
4
5
6
7
8
NL
NL
NIP
NIP
NL-NIA
NL
NIA
NL
9
10
11
12
13
NIA
NIA
NIP
NIA
NIP
NL
NIP
14
15
16
17
18
NIP
NIA
NIP
NM
medial

FIGURE 6

of CN-8L. Similarly in the posterior interposed nucleus, the degeneration ensuing lesions of intermediate folia of Crus II overlaps with the distribution from the extreme lesions without being so extensive.

In the following Figure 7, the degeneration from two medial lesions (cats CN-8L, CN-34L) was combined and represented upon a standard series of nuclei (oblique lines). This part of the cortex of Crus II corresponds to the representation of superior parts of the body (schematically indicated as forelimb). Lesions in cat CN-11R and CN-39R injuring lateral folia of Crus II are represented with stipples. This is referred to as the hindlimb representation. The two zones of projection from these lesions are illustrated on two separate series of nuclei, one for the projection to NL and NL-NIA and the other to the NIP. In this way, the differences in the projections from lateral and medial parts of Crus II as well as the continuity of the terminal areas from section to section are more apparent.

In the top row, dotted lines help to visualize the two strips of degeneration. In this way, the oblique orientation of the two strips becomes obvious. The lateral strip (hindlimb) presents very little overlap with the medial strip (forelimb). Only in levels 5,6,7,8 is there an overlap between them, otherwise the two projections are distinct.

Therefore, in the NL and NL-NIA, the somatotopical representation takes the shape of oblique, medio-laterally oriented strips with little overlap.

In the NIP, the cortico-nuclear projection shows a topographical

FIGURE 7

SOMATOTOPICAL PATTERN IN THE PROJECTION OF CRUS II

The two rows of sections of this figure represent series of standart sagittal planes of section through the cerebellar nuclei. Interrupted lines with figures between the two rows indicate the extent of the nuclei at every other level.

The nuclear degeneration following two medial lesions of Crus II (CN-8L, CN-34L) was combined. The two projections (one in the NL and NL-NIA, the other in the NIP) were plotted on two separate series of standart cerebellar nuclei in order to make the mediolateral continuity more apparent. This part of the cortex of Crus II receives input from the anterior parts of the body abbreviated to "forelimb" in this diagram and represented with oblique lines. Lateral lesions of Crus II (CN-11R, CN-39R) representing that part of the cortex of Crus II which receives input from posterior parts of the body abbreviated as "hindlimb", produce degeneration which is plotted with stippled symbols.

In the upper series of nuclei where the projection to the NL and NL-NIA is plotted for both the medial and the lateral lesions of Crus II, dotted lines help to visualize the oblique orientation of the strips of degeneration. The second projection, in the NIP, represented on the lower series of nuclei shows a greater overlap between the projections from "forelimb" and "hindlimb" regions of Crus II.

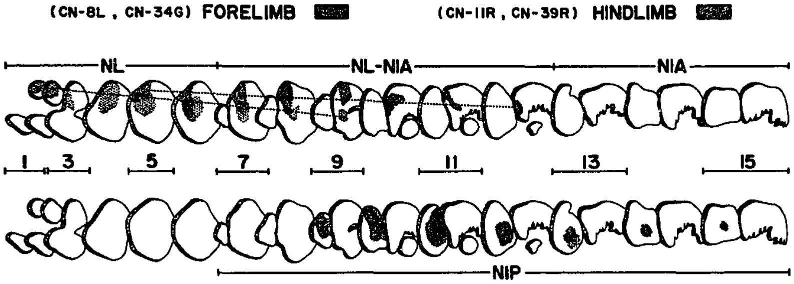
(CN-8L , CN-34G) FORELIMB ▨
(CN-11R , CN-39R) HINDLIMB ▨
NL
NL-NIA
NIA
1
3
5
7
9
11
13
15
NIP

FIGURE 7

pattern which is less clear than the one in the NL-transition zone NIA. The representation of regions corresponding to superior portions of the body is slightly dorsal compared to the representation of inferior regions but there is a large overlap between the two projection areas.

TOTAL PROJECTION OF THE PARAMEDIAN LOBULE AND COMPARISON WITH THE PROJECTION OF CRUS II

Altogether 14 cats were used for the experiments on the cortico-nuclear projection of the paramedian lobule. Only ten cases were selected for presentation, because their lesions cover every region of the cortex of the paramedian lobule. The other cases were rejected because they had misplaced lesions or important encroachments on unwanted regions of the cortex. Two cases were not used because of unsuccessful fixation or staining.

In order to obtain the projection of the entire paramedian lobule, two separate lesions were combined. The lesion in cat CN-19L covers approximately the rostral 3/5 of the paramedian lobule and extends from the lateral to the medial borders of this lobule with slight encroachments on Crus II and lobule VIII of the posterior vermis. The lesion in cat CN-13R covers the medial part of the caudalmost three folia of the paramedian lobule and encroaches upon lobule VIII. Together, these two lesions cover almost entirely the surface area of the cortex of the paramedian lobule.

In Figure 8, the two lesions described above are illustrated on the upper left. The projection of the paramedian lobule is represented with vertical lines on a standart series of cerebellar nuclei. On this same series, the projection of Crus II is also plotted (in horizontal lines). The degeneration resulting from a total lesion of the paramedian lobule is located in three regions: the ventral part of the NL, the dorsal part of the NL-NIA transition zone extending to the NIA, and in the NIP.

FIGURE 8

PROJECTIONS OF THE PARAMEDIAN LOBULE AND CRUS II

The degeneration from two lesions (CN-19L, CN-13R) was combined in order to obtain the total projection of the paramedian lobule. The degeneration resulting from these lesions is represented on a standart series of cerebellar nuclei with vertical lines. The total projection of Crus II represented with horizontal lines was obtained by combining the degeneration obtained in three lesions of this lobule: lateral lesions CN-11R and CN-11L, and a medial lesions CN-8L.

Only heavy degeneration has been plotted. The three projectionsof the paramedian lobule can be seen in the ventral part of the NL, the caudal part of the NL-NIA transition zone and NIA, and in the NIP. The degeneration resulting from the lesions of Crus II is located in the dorsal part of the NL and NL-NIA transition zone, and in the anterior part of the NIP. The sagittal series of nuclei stops before the lateral appearance of the medial nucleus. This nucleus is not represented in any of our series because neither Crus II nor the paramedian lobule project upon it.

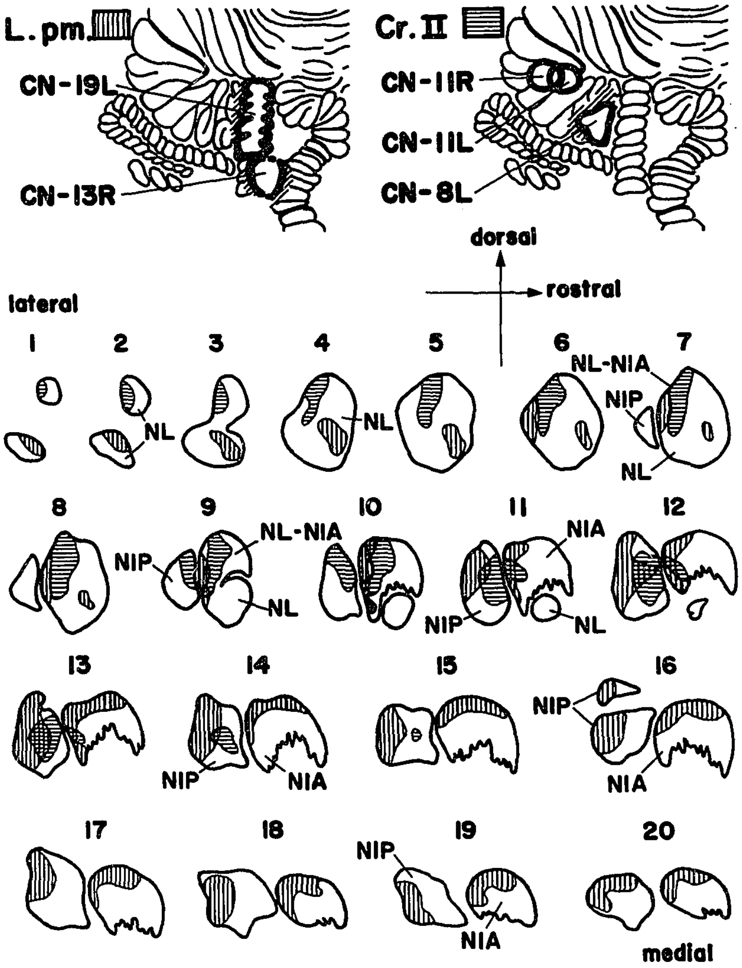
L. pm. ▥
Cr. II ▤
CN-19L
CN-13R
CN-11R
CN-11L
CN-8L
dorsal
rostral
lateral
1
2
3
4
5
6
7
NL
NL
NL-NIA
NIP
NL
8
9
10
11
12
NIP
NL-NIA
NL
NIA
NIP
NL
13
14
15
16
NIP
NIA
NIP
NIA
17
18
19
20
NIP
NIA
medial

FIGURE 8

The first one of these projections is situated in the ventral part of the lateral nucleus. The terminal degeneration is well circumscribed and covers relatively less area than the other two projections.

The second projection of the paramedian lobule is more extensive. It begins laterally at the level of the transition zone and ends in the most medial sections of the NIA (levels 6 to 20). In the transition zone, the degeneration is located at the posterior border of the nucleus, medially it migrates to a more dorsal and anterior position.

The third projection of the paramedian lobule is found in the caudal half of the posterior interposed nucleus: it extends for the entire width of this nucleus except most laterally.

The medial nucleus does not receive a projection from the paramedian lobule. Although in case CN-19L and CN-13R there is degeneration present in the medial nucleus, this is due to the injury of the cortex of the posterior vermis. In all our cases where there is an encroachment of lobule VII or VIII degenerated fibers can be traced from this part of the cortex to the medial nucleus. On the other hand, case CN-12L where the lesion is restricted entirely to the paramedian lobule (Figure 9), the medial nucleus is free of degeneration. Furthermore in cats CN-23 and CN-24R where the lesion is restricted to lobules VII and VIII, a projection is found in the medial nucleus only, the other cerebellar nuclei showing no degeneration. These results indicated that the intermediate and lateral parts of the cortex of the posterior cerebellum do not project to the NM, while the vermis proper projects exclusively to the NM.

In Figure 8, the projection of Crus II is illustrated with three cases of lesions situated at the two extremities of the lobule, and the distribution of which approximates closely the extent of the total projection of Crus II. The comparison shows a minimal overlap in the projections from these two lobules. In sections 6,7 and 8 they are adjacent but not overlapping. In sections 9 to 13, the projections in the medial part of the transition zone and lateral part of the NIA exhibit some overlap which is relatively small compared to the total areas of the two projections.

TOPOGRAPHY OF THE PROJECTION OF THE PARAMEDIAN LOBULE

Since physiological as well as anatomical evidence indicates that the somatotopical arrangement in the paramedian lobule is distributed rostrocaudally, lesions at both extremities of this lobule were used to determine a topographical pattern in the cortico-nuclear projections.

Cat CN-12L has a lesion of the first three rostral folia of the paramedian lobule. Medially, it leaves approximatively one fourth of the surface cortex undamaged, and it extends laterally to encroach very slightly upon Crus II. In Figure 9, in the cerebellar sagittal section 10 and 14, degenerated fibers can be seen coursing from Crus II, although no lesion of this lobule can be detected at these or more lateral levels. The lesion of the paramedian lobule is seen in two of the three sections where the rostral folia are present (level 17 and 21).

Three regions receive a projection from the rostral folia of the paramedian lobule. In the ventral part of the NL, the projection is situated ventrally and anteriorly and in contained entirely within the lateral half of this nucleus. The second projection begins in the NL-NIA transition zone and extends up to the medial levels of the NIA. This projection is found near the caudal limit of the nucleus and somewhat dorsally.

Intense terminal degeneration in the NIP is also seen in the lateral two thirds of this nucleus, but some degenerated fibers are also observed more medially (levels 27 and 28). The patch of degeneration in the NIP is

FIGURE 9

ROSTRAL LESION OF THE PARAMEDIAN LOBULE

On the diagram of the cortex in the upper left corner, the lesion has been represented in solid black, and the light encroachment upon Crus II as revealed by the histological sections with lines. To the right, are shown sagittal sections of the cerebellum on which the lesion (section 17, 21) has been marked with a thick black line, and the coursing degenerated fibers have also been plotted (section 10 to 25). Such degenerated fibers are seen coming not only from the rostral folia of the paramedian, but also from Crus II (section 10, 14). Heavy degeneration following this lesion has been plotted on the original outlines of the nuclei of this case with lines, scanty degeneration with dots. The projection of the rostral folia of the paramedian is located in the central part of the NL, in the caudal part of the NL-NIA transition zone and NIA, and in the dorsal half of the NIP.

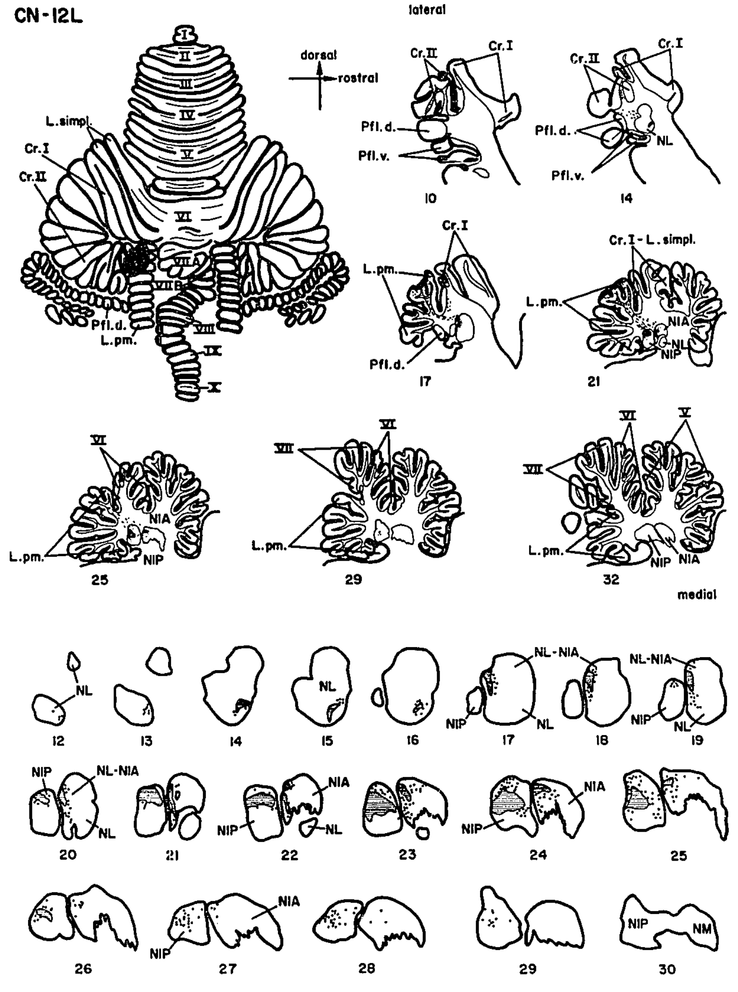
CN-12L
lateral
dorsal
rostral
I
II
III
IV
V
VI
VII A
VII B
VIII
IX
X
L.simpl.
Cr.I
Cr.II
Pfl.d.
L.pm.
Pfl.v.
NL
NIA
NIP
Cr.I-L.simpl.
NL-NIA
NM
medial
10
14
17
21
25
29
32
12
13
15
16
18
19
20
22
23
24
26
27
28
30

FIGURE 9

mostly in the dorsal half of the nucleus.

In Figure 10, the degeneration from cat CN-12L was transposed on a standard series of cerebellar nuclei and compared with the degeneration resulting from caudal lesions of the paramedian lobule.

Two partial lesions were combined in order to obtain the total projections of the caudal extremity of the paramedian lobule. Cat CN-24L has a minute lesion confined to the lateral half of the third from the last folium. Cat CN-13R has a small lesion made with a knife: it undercuts the fibers of the medial half of the three caudalmost folia of the paramedian lobule.

The caudal folia of the paramedian lobule send a triple projection on the cerebellar nuclei, indicated in this diagram with vertical lines. The first projection is in its usual position, in the ventral and anterior portion of the NL, but is contained in the medial half of this nucleus. The second projection is located entirely within the NIA (section 13 to 20) where it occupies a rostral and dorsal position. There are no degenerated fibers in the NL-NIA transition zone or even in the lateral sections of the NIA (section 11 and 12). The third projection from the caudal folia of the paramedian lobule is found approximatively in the medial half of the NIP. This degeneration is circumscribed and located caudally.

When the degeneration resulting from the caudal lesions (in vertical lines) is compared with the degeneration after a rostral lesion (in horizontal lines), the small extent of overlap between these becomes evident. In the

FIGURE 10

COMPARISON OF DEGENERATION AFTER A ROSTRAL AND A CAUDAL LESION OF THE PARAMEDIAN LOBULE

On the diagram of the left half of the cerebellar cortex, a rostral lesion (CN-12L) and two caudal ones (CN-24L and CN-13R) have been outlined with a black line. The encroachments of adjacent lobules are shown in oblique lines. The degeneration following these extreme lesions of the paramedian lobule are plotted on a standart sagittal series of the cerebellar nuclei. The three projections from the rostral lesion (in horizontal lines) are seen in the ventral part of the NL, the transition zone and the lateral half of the NIA, and in the lateral 2/3 of the NIP. The cortico-nuclear projection of the caudal folia of the paramedian lobule (in vertical lines) is shown in the medial half of the ventral part of the NL, in the dorsal part of the NIA and medial half of the NIP.

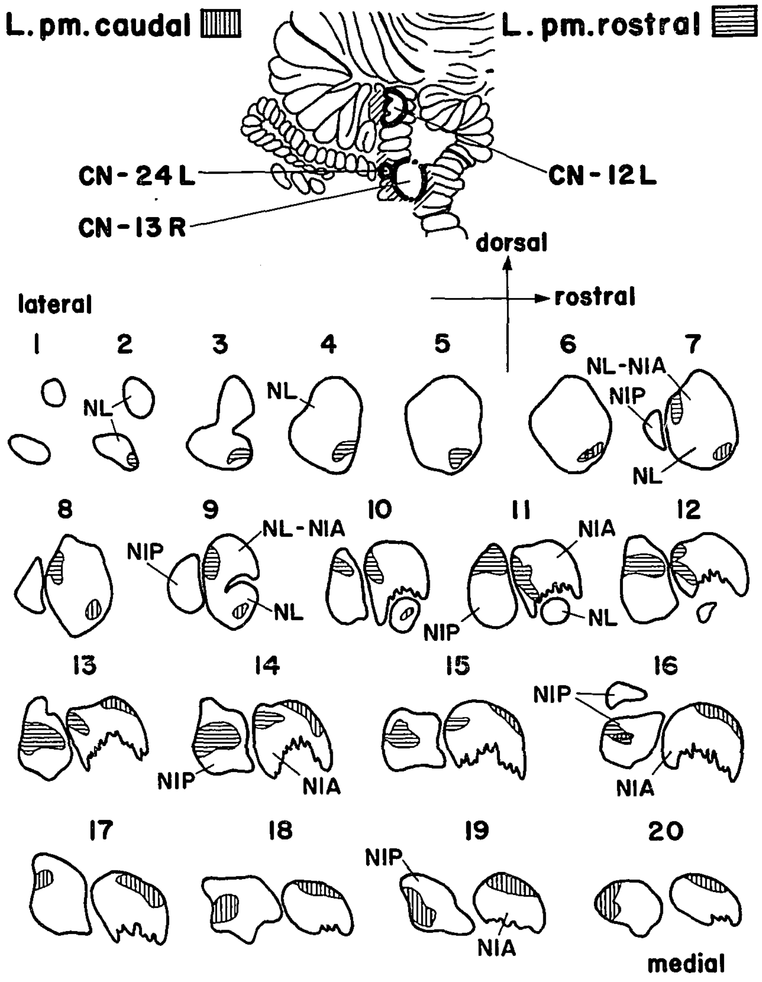
L.pm.caudal ▥
L.pm.rostral ▤
CN-24L
CN-13R
CN-12L
dorsal
rostral
lateral
1
2
3
4
5
6
7
NL
NL
NL-NIA
NIP
NL
8
9
10
11
12
NIP
NL-NIA
NL
NIA
NIP
NL
13
14
15
16
NIP
NIP
NIA
NIA
17
18
19
20
NIP
NIA
medial

FIGURE 10

NL, the two projections show an overlap only in section 6, in the NIP only in section 16. In both these nuclei, the caudal folia of the paramedian lobule send a projection which is more medial. This is also true for the projection in the NL-NIA transition zone and NIA: the rostral folia send a projection to the NL-NIA transition zone and lateral parts of the NIA, the caudal folia to the medial portions of the NIA. In sections 13, 14 and 15 where both projections are present, there is no overlap at all, the two patches of degeneration being separated by a wide zone free of any degenerated fibers. This empty zone in this nucleus would contain the projection from intermediate folia of the paramedian lobule. The comparison of these two distributions therefore, indicates a clear topographical organization in all three regions of the projection of the paramedian lobule. The projection in the NL-NIA and NIA however, shows a much clearer topography than the other two projections.

There were also four lesions (cats CN-7L, CN-15R, CN-15L and CN-9R) which injured the indermediate folia of the paramedian lobule.

Cats CN-7L and CN-15R both had lesions of the rostral half of the paramedian lobule, yet are not as rostral as in cat CN-12L. Both lesions leave a narrow medial strip of the surface cortex of this lobule undamaged. In both cases, there is degeneration in the ventral part of the NL, the NL-NIA transition zone and the NIA and finally in the NIP. These three projections resemble very closely the ones obtained after a lesion of the rostral folia of the paramedian lobule (cat CN-12L) which has been described.

Cats CN-15L and CN-9R have lesions which are located in the caudal half on the paramedian lobule without injuring the three caudalmost folia of this lobule. CN-15L is a medial lesion, whereas CN-9R covers the entire mediolateral extent of the surface cortex of the lobule.

The degeneration in these two cases overlaps partly with the projections from both the rostral (CN-12L) and the caudal (CN-13R, CN-24L) lesions. Thus in levels 13, 14 and 15 (Figure 10), the projection of the intermediate lesions fills the gap between the projections from the extreme lesions of the paramedian lobule and overlaps partly with both of them.

COMPARISON OF VERTICAL LINEAR LESIONS OF THE PARAMEDIAN LOBULE

To test Voogd's hypothesis that each of three vertical strips of the cortex of the paramedian lobule projects upon a single subdivision of the nuclei, we attempted to obtain restricted longitudinal lesions of the cortex.

In cat CN-17R, a thin vertical lesion was made on the medial side of the paramedian lobule. The lesion extends from the most rostral to the caudalmost folia. The lesion enlarges somewhat in places, but the lateral half of the paramedian lobule is entirely spared. Crus II is intact, but the vermis is injured at the level of lobules VII and VIII.

From such a lesion which for its greater part is located in the medial half of the surface cortex of the paramedian lobule, the degeneration is found in three zones in the cerebellar nuclei (Figure 11) corresponding to the one described previously. The degeneration in the NL is localized in the anterior and ventral part of this nucleus. This projection does not extend from the lateral to the medialmost sections of the NL but is present only in a few central sections (horizontal lines, levels 5 and 6). The second projection is found in the transition zone and in the NIA. The degeneration in the lateral part of the transition zone is sparse: in the medial part of the transition zone and in the NIA the projection is intense. This second projection is located near the caudal border of the NIA. The third projection is in the NIP. The projection begins near the lateral border of the nucleus and ends in the most medial sections of this nucleus. It is located

FIGURE 11

COMPARISON OF DEGENERATION AFTER A LATERAL AND MEDIAL LESION OF THE PARAMEDIAN LOBULE

Two lesions of the paramedian lobule are represented on the diagram of the cerebellar cortex. CN-17L is a lesion of the lateral part of the paramedian lobule which encroaches slightly on the medial aspect of this lobule as well as on Crus II. CN-17R is a lesion which in restricted to the medial half of the paramedian lobule and damages the posterior vermis at the level of lobule VII and VIII. The degeneration is plotted on a standart series of sagittal nuclei with different symbols for each lesion. In each case there are three projections: on the ventral part of the NL, in the NL-NIA transition zone and NIA, and in the NIP.

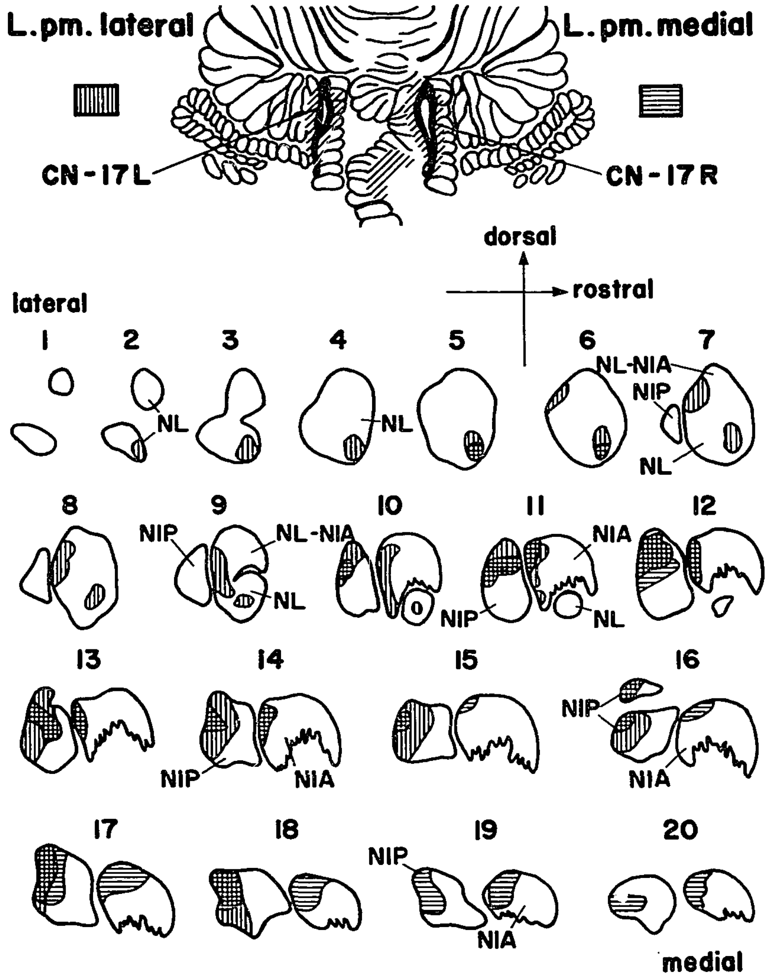
L. pm. lateral
L. pm. medial
CN - 17L
CN - 17R
dorsal
rostral
lateral
1
2
3
4
5
6
7
NL
NL
NL-NIA
NIP
NL
8
9
10
11
12
NIP
NL-NIA
NL
NIP
NIA
NL
13
14
15
16
NIP
NIA
NIP
NIA
17
18
19
20
NIP
NIA
medial

FIGURE 11

dorso-caudally. The medial nucleus receives a projection due to the encroachment of the vermis (not illustrated).

Cat CN-17L has a vertical lesion of the lateral portion of the paramedian lobule. All folia except the last two are injured. The lesion is restricted to the lateral third of the paramedian cortex except in the second and third folia where it extends somewhat medially. The vermis is intact but there is a minimal encroachment of Crus II as a few fibers could be seen coursing from there.

Again as in the case of the medial vertical lesion, there are three different projections in the central nuclei. The first projection located in the NL is extensive. The ventral part of the NL shows degeneration almost throughout its medio-lateral extent. The second projection begins in the dorsal part of the NL, extends through the transition zone and ends in the central region of the NIA. The third projection is in the caudal half of the NIP. The degeneration in this nucleus begins laterally and goes further medially than the degeneration in the NIA. Nevertheless, the medialmost sections of this nucleus are free from degeneration.

We have other lesions which are restricted to either the medial or the lateral side of the paramedian lobule. These lesions are small and injure only a few folia at a time. The pattern of cortico-nuclear projection after these lesions corresponds in most respects to either CN-17R of CN-17L depending on whether the lesions are medial or lateral. Thus lesions in cats

CN-12L, CN-7L, CN-15R and CN-24L which leave the medial side of the paramedian lobule intact, produce heavier degeneration in the NL than lesions which are restricted to the medial side of this lobule (CN-13R, CN-15L). In the transition zone and the NIA, and in the NIP the projections from the lateral lesions are situated laterally in these nuclei, and medially after medial lesions.

It is clear from the analysis of the lesions of cat CN-17L and CN-17R that medial as well as lateral portions of the paramedian lobule project to all three sites. Differences however in the distribution from one or another cortical region are apparent in the case of two of the projections and will be commented upon in the discussion.

SUMMARY

Figure 12 summarizes schematically the topographical distribution of the projections from Crus II and from the paramedian lobule. The projections from these lobules are represented on a diagram of a horizontal section through the cerebellar nuclei where all the sections have been superimposed. Circles represent Crus II, triangles represent the paramedian lobule. Black symbols stand for the superior part of the body, empty ones for the inferior parts of the body.

In the somatotopical distributions which have been demonstrated for these portions of the cerebellar cortex, the medial part of Crus II and the rostral part of the paramedian lobule (adjacent regions) are the sites of representation of upper portions of the body while the lateral part of Crus II and the caudal portion of the paramedian lobule correspond to lower body regions.

This arrangement seems to be reflected in the cortico-nuclear projections of these lobules. In the NL-NIA transition zone, the regions corresponding to the upper regions are next to each other, whereas the representation of the lower body regions are distant from each other. A similar pattern is also present in the NIP. The small projection of the paramedian lobule in the ventral part of the NL has no counterpart from Crus II.

FIGURE 12

SOMATOTOPICAL PROJECTION OF THE PARAMEDIAN LOBULE AND CRUS II

The somatotopical projections of the paramedian lobule and Crus II are represented on a schematic outline of a horizontal section of the cerebellar nuclei. The triangles represent the projections of the paramedian lobule and circles that of Crus II. The black symbols represent that part of the cerebellar cortex (and corresponding projections) which receives input from anterior parts of the body, empty triangles and circles symbolize the cortex (and the cortico-nuclear projections) which receives input from posterior parts of the body. The three projections from the paramedian lobule can be seen in the anterior part of the NL, the NL-NIA transition zone and NIA, and in the NIP. The two projections of Crus II are located in the NL and NL-NIA transition zone and in the NIP. (See text).

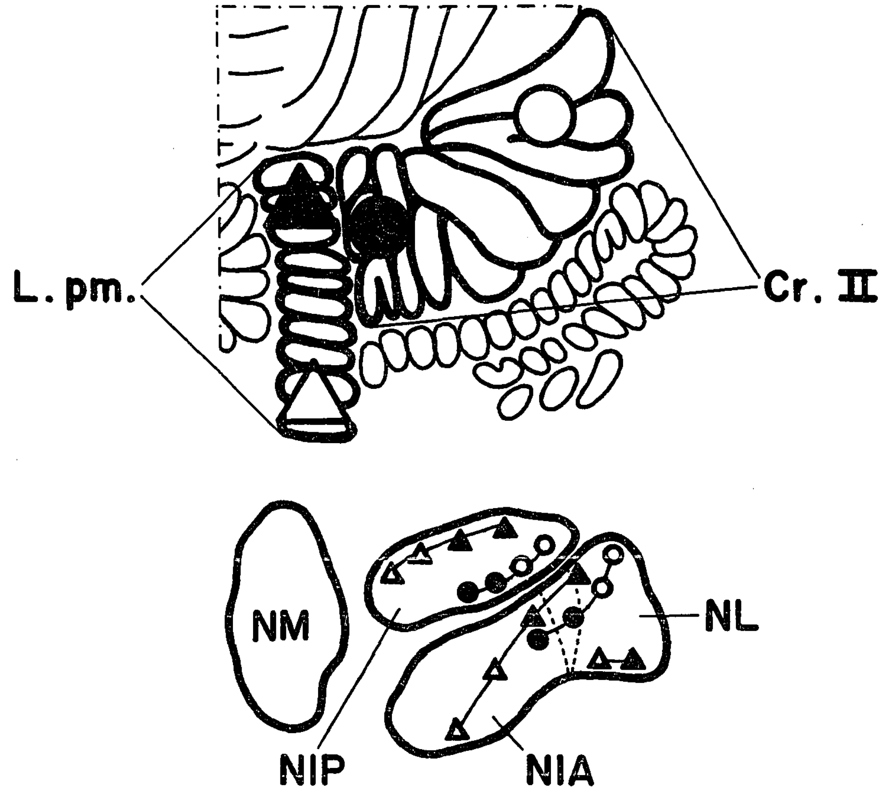

FIGURE 12

FIGURE 13

DIAGRAM ILLUSTRATING VOOGD'D ZONAL ORGANIZATION OF THE CORTICO-NUCLEAR PROJECTIONS

On this diagram of the unfolded lobules of the cerebellar cortex, the zones of cortico-nuclear projection are indicated with different symbols. In the diagram of a horizontal section of the cerebellar nuclei, the termination of the cortico-nuclear fibres from different projection zones is indicated with the same symbol. See text. Abbreviations listed on page 101 and 102.

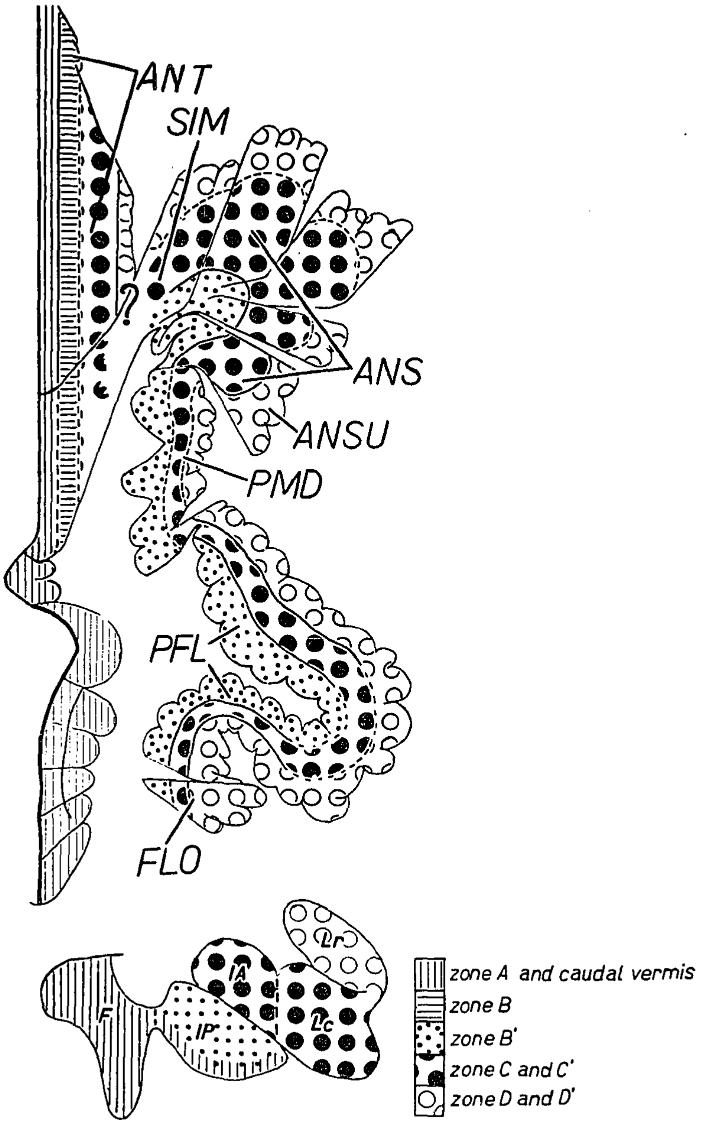
ANT
SIM
ANS
ANSU
PMD
PFL
FLO
F
IP
IA
Lr
Lc
zone A and caudal vermis
zone B
zone B'
zone C and C'
zone D and D'

FIGURE 13

IV

DISCUSSION

CORTICO-NUCLEAR PROJECTIONS OF CRUS II AND THE PARAMEDIAN LOBULE

Our results indicate that the cortico-nuclear projection of Crus II is distributed to two distinct, non-overlapping regions in the cerebellar nuclei: the first region of projection in the NL and NL-NIA transition zone, and the second, in the NIP.

In the case of the projection in the NIP, the borders of this nucleus being well defined, it is possible to see that the degenetation is contained within the limits of the nucleus. However, in the case of the other projection, the projection begins in the dorsal part of the NL and extends medially without interruption into the NIA, these two nuclei presenting a fusion in their dorsal part. Even though, this zone of projection is not limited to one nucleus, the degeneration can be followed from section to section and its continuity from one nucleus to the next can be established.

Even when the two projections of Crus II happen to be adjacent (Figure 3, sections 19 and 20), it is clear that they are distinct because the two fields of degeneration are discontinuous and are separated by fibre bundles. Sometimes the two projections can be further distinguished by different densities of terminal degeneration in each of the zones of projection.

Most authors who observed degeneration after a lesion of Crus II, agree that this lobule sends efferent fibers to the lateral nucleus. Jansen and Brodal concluded from their experiments that Crus II projects only upon the lateral nucleus. However, in their study of 1940, they present a lesion of Crus II (cat no. 18) following which it is possible to distinguish a large zone of distribution comprised in the NL and NIP as defined in the present study. The one distribution in the dorsal part of the lateral nucleus was attributed by the authors to the lesion of Crus II. The rest of the degeneration in the ventral part of the lateral nucleus and in the interposed nucleus, was interpreted as coming from the paraflocculus and the paramedian lobule which were inadvertently injured. By subtracting the degeneration due to inadvertent lesions, Jansen and Brodal drew the conclusion that the projection of Crus II covers practically the entire lateral nucleus, leaving only the ventro-lateral and caudo-medial portions of this nucleus free. As they followed Brunner's nomenclature and subdivisions for the cerebellar nuclei (1919), Jansen and Brodal did not draw a border between the lateral and the interposed nucleus. Applying to their results the subdivisions of the nuclei proposed here, it is seen that their distribution of degeneration coincides remarkably well with what has been observed in this study. However, a point of importance which these authors did not mention is the discontinuity between the two fields of degeneration. It is probable that the Marchi technique did not allow to recognize this distinction.

The results of Walberg and Jansen (1964) demonstrate that Crus II sends fibers upon the lateral and the posterior interposed nuclei. Their cats B.St.L244, 192, and 194 with inadvertent lesions of the posterior part of the ansiform lobule and minor encroachments upon the dorsal paraflocculus and Crus I, show degeneration within the lateral and the posterior interposed nucleus. In their cat C.St.L237R, where the lesion is restricted to Crus II (the encroachment upon the posterior vermis not being considered, since this lobule projects to the medial nucleus), Walberg and Jansen find a projection upon the lateral portion of the anterior interposed nucleus, in addition to a projection upon the lateral and posterior interposed nucleus. Since these authors used Flood and Jansen's (1961) subdivisions of the cerebellar nuclei, they drew a border between the NL and the NIA. This lateral region of the NIA which receives a projection from Crus II corresponds to our transition zone. Except for the fact that Walberg and Jansen show an interruption between the degenerations in the NL and NIA at a point where we have not seen any, our results on the projection of Crus II are in agreement with those of these authors. It is necessary to point out that these authors did not report the discontinuity in the distribution of the degeneration but indicated a limit there because of the presence of a nuclear border.

Eager (1963) reported that lesions of Crus II produce degeneration in the medial part of the lateral nucleus, and lateral part of the interposed nucleus as well as the caudal poles of both fastigial nuclei. The transverse plane of cutting which Eager used exclusively did not permit him to retain the injured folia on the sections and he could not verify histologically the exact site and extent of his cortical lesions. It is strongly suspected that his lesions were much more extensive than what he describes, since in most of his cases, degenerated coursing fibers can be observed underneath many other lobules than the ones which are presumably injured. Thus in the case of his lesion of Crus II which is shown on the diagram of the cortex to be restricted to a single folium of this lobule, degenerated coursing fibers can be observed coming from the dorsal paraflocculus, lobule simplex and Crus I.

These numerous encroachments can account for the wide projections that Eager observes. However, the degeneration in the poles of both fastigial nuclei is not in continuity with the degenerated fibers coming from Crus II or from the other lobules damaged inadvertently. Most probably this degeneration results form an encroachment of the posterior vermis; this cannot be verified since the caudalmost sections are lost in the transverse sections and the continuity between the fibers from the posterior vermis and the degeneration in the fastigial nuclei cannot be established.

Voogd has no lesions which are restricted only to the cortex of Crus II. His lesions of this lobule in cat B-17R and B-17L are complicated by encroachments upon the paramedian lobule and the posterior vermis. His cat B-19, in addition to a lesion of Crus II, bears an injury to the dorsal and ventral paraflocculus. In all three cases, Voogd reports degeneration in the pars rotunda, in the pars convexa-anterior interposed nucleus and in the posterior interposed nucleus. Disregarding the fact that in these cats there were important encroachments on adjacent lobules, Voogd concludes that the ansula and the ansiform lobule (our Crus I and Crus II) project on the three subdivisions mentioned above. By comparing these projections to those from other lobules, Voogd states that when there is a lesion of Crus II, the degeneration is more caudal in the pars convexa, more lateral in the pars rotunda, and more ventro-lateral in the posterior interposed nucleus than in cases where this lobule is undamaged.

Our results agree with those of Voogd in that we find a projection in the NIP and in the NIA throughout its fusion with the dorsal part of the NL. However, in none of our cases is there a projection of Crus II upon the ventral portion of the NL. This projection that Voogd reports can be accounted for by the large encroachments of the adjacent paramedian lobule in his cases with lesions of Crus II.

Our results on the projection of the paramedian lobule demonstrate that this lobule sends fibers to three different regions in the nuclei. This seems to be in apparent disagreement with the conclusions of Jansen and Brodal (1940) which state that the paramedian lobule projects upon the caudo-medial parts of the "fused lateral and interposed nuclei". However, on closer inspection of their cases with lesions of the paramedian lobule, it becomes evident that they also noticed degeneration in other regions of the nuclei as well. In their cat 13, there is a small patch of degeneration in the central and anterior part of the lateral nucleus as well as in the anterior part of the interposed nucleus. The latter projection is attributed by the authors to an inadvertent lesion of lobule VI, while the small projection in the ventral part of the lateral nucleus is presumably considered as an artefact, since it is not mentioned in the results or in the discussion. In their other lesion of the paramedian lobule (cat 3), there is damage to the adjacent cortex of Crus II, and again the degeneration in the anterior portions of the interposed nucleus and in the lateral nucleus is attributed to this lobule. Although the conclusions of Jansen and Brodal do not agree with ours, their results on the projection of the paramedian lobule resemble the ones obtained in our experiments.

Walberg and Jansen (1964) have only one case where there is a restricted lesion of the paramedian lobule with a posterior vermis encroachment the projection of which is related to the fastigial nucleus. In this cat (B.St.L237), heavy degeneration is reported in the medial and ventral part of the NIP and in the central part of the NL. The authors also speak of a projection of the paramedian lobule upon the ventral part of the NIA. However, in their illustration of this case (Figure 11), this projection in the ventral part of the NIA seems continuous with that in the NIP. It is probable that these authors drew the limit between the anterior and posterior interposed nuclei for too caudally, a mistake easily made in the transverse plane. In this way, if one attributes the degeneration in the ventral part of the NIA to the NIP, the discrepancy between our results and theirs is lessened. The main difference consists in the fact that they do not find degenerated fibers in the dorsal part of the NIA as we do. No explanation can be offered for this discrepancy.

Eager's lesions of the paramedian lobule (cat 2 and 21), supposedly restricted to this lobule, certainly encroach upon lobule simplex, the caudal vermis, Crus II and Crus I, since massive numbers of degenerated fibers are seen coursing from all these lobules. It is not surprising to find degeneration in the entire lateral, interposed and medial nuclei.

Voogd illustrated three cases (B-17R, B-17L, B-18), where among other structures the paramedian lobule is also injured. A triple projection upon the nuclei is found in these cases: one in the pars rotunda, in the pars convexa-anterior interposed nucleus, and in the dorsal part of the posterior interposed nucleus. Taking into consideration the fact that in Voogd's cases there are important encroachments of adjacent lobules, our results on the projection of the paramedian lobule essentially agree with his.

It becomes clear from this review of results of different authors that, although their interpretation and conclusions differed, their results on the projections of Crus II and of the paramedian lobule often agree, for the greater part, with ours.

One of the conclusions which can be extrapolated from our results is that, although the cortex of Crus II is adjacent to that of the paramedian lobule and even continuous with it at one point by a narrow cortical bridge (Voogd 1964, our own observations), the respective cortico-nuclear projections of Crus II and of the paramedian lobule, are for the greater part, different.

First of all, these two lobules differ in the number of projections that they send upon the nuclei. Every region of Crus II sends only two projections, while every region of the paramedian lobule, be it rostral or caudal, sends a triple projection upon the cerebellar nuclei. The small projection of the paramedian lobule upon the ventral part of the lateral nucleus has no counterpart from Crus II.

Secondly, in the two nuclear regions upon which both Crus II and the paramedian lobule project, the two projections are distinct one from the other despite some overlap. Crus II projects upon the NL and the NL-NIA transition zone; the paramedian lobule sends fibers upon the NL-NIA transition zone and the NIA. In the transition zone, where the two projections are present, the paramedian projection is located caudally, that from Crus II more rostrally. This is the region where the two projections present a small overlap.

In the second common region of projection, the NIP, the projection from the paramedian lobule is again more caudal than the one from Crus II. This is the second region in the nuclei where the projections from the paramedian lobule and Crus II present an overlap.

All these differences in the cortico-nuclear projections of Crus II and of the paramedian lobule indicate that the two regions probably represent different functional entities. The present evidence adds to the embryological and morphological criteria that Larsell (1953) used for distinguishing these two lobules in the cat.

SOMATOTOPICAL ORGANIZATION IN THE CORTICO-NUCLEAR PROJECTIONS OF CRUS II AND THE PARAMEDIAN LOBULE

There are no direct references in the literature to a topographical organization in the cortico-nuclear fibers of Crus II or of the paramedian lobule. Walberg and Jansen (1963) did state, without formulating any conclusions as to the significance of their findings, that in the case of the paramedian lobule and of Crus II, "..the more lateral the lesion extends, the less is the nucleus interpositus and the more is the dentate nucleus involved in the projection." Voogd gave indications of the existence of a medio-lateral topography: the lateral part of Crus II and of the paramedian lobule projects upon the pars rotunda, the intermediate, upon the pars convexa-anterior interposed nucleus, and the medial portion upon the posterior interposed nucleus.

It is in the results of this author that one can uncover one of the first indications of a rostro-caudal difference of projection in the paramedian lobule: degeneration in the medial part of the anterior interposed nucleus is reported only when the lesion affects the caudal part of the paramedian lobule. Voogd did not reach any conclusions as to the presence of a topography in the cortico-nuclear projections of the paramedian lobule, presumably because of an insufficient number of experiments involving this lobule.

Our series of experiments show that the cortico-nuclear fibers of Crus II and of the paramedian lobule are arranged in a topographical manner. Since the cortices of these two lobules receive a somatotopical organized input, one can draw the conclusion that the topographical arrangements of the cortical efferent fibers corresponds to a somatotopy.

It must be remarked, however, that the cortico-nuclear topography is not equally clear in all the zones of projection. In the case of the cortico-nuclear fibres of Crus II, the first projection in the NL and NL-NIA transition zone, shows a distinct topographical pattern. Areas of termination of cortico-nuclear fibers in this region following a medial or a lateral lesion of Crus II show very little overlap (see Figure 7). On the other hand, fibres from the medial and lateral regions of Crus II show a marked degree of overlap in the NIP and the projection to that nucleus is perhaps nor organized in a somatotopical manner. More data on the afferent and efferent connections of the NIP are needed before our results can be interpreted.

Each of the three projections of the paramedian lobule, exhibits a different degree of overlap in the termination of fibres from rostral and caudal regions of this lobule. In the NIP and in the central part of the NL, the fibres from the rostral and the caudal regions of the paramedian lobule present a good deal of overlap. However, in the third area of projection, the NL-NIA transition zone and NIA, the difference in the site of termination between fibers coming from rostral and caudal parts of the paramedian lobule is so great, that not only is there no overlap between them, but they are separated by a wide space (Figure 10, section 13, 14 and 15). This space corresponds to the area of projection from intermediate folia of the paramedian lobule, this projection overlapping partly with those from the rostral and the caudal folia of this lobule.

Since both the paramedian lobule and Crus II send somatotopically organized fibers upon the nuclei, it can be asked whether the representations from these two lobules follow a similar orientation. Figure 12, illustrating very schematically the somatotopical cortico-nuclear projections of Crus II and of the paramedian lobule clarifies this point. It must be underlined that the somatotopical pattern of projection in this figure is represented in an oversimplified manner, the overlap of projections from different regions of the cortex not being indicated. Keeping this shortcoming in mind, it is possible to see that both Crus II and the paramedian lobule have distinct body representations in the nuclei. It is interesting to note that, in the NL-NIA transition zone and in the NIP where the projections from these two lobules are adjacent, it is the fibers from the rostral part of the paramedian lobule and the medial part of Crus II that show a small degree of overlap in their termination. (Both these parts of the cortex receive input from the upper part of the body).

VOOGD'S HYPOTHESIS

Voogd (1964) formulated the hypothesis that the lobules of the posterior lobe are divided into three longitudinal bands along their main axis, each band projecting to a different subdivision of the central cerebellar nuclei.

The obvious criticism to be levelled at his work is the lack of experimental cases to prove his hypothesis. The only experiments using anterograde degeneration which he uses to argument the existence of longitudinal bands of projection are his cases B-22 and B-23.

Cat B-22 has a lesion of the medial part of the paramedian lobule and lobule VII. In this case, no degeneration is found in the ventral portion of the lateral nucleus; only the posterior interposed and the anterior interposed nuclei receive a projection.

In cat B-23, there is a lesion of the lateral aspect of the paramedian lobule and lobule VI. Degeneration is found in the anterior and posterior interposed nuclei as well as in the ventral part of the lateral nucleus.

In these two cases, where the lesions are restricted to one, or at most two of his zones of projection, Voogd still finds degeneration in two nuclei in cat B-22, and in three nuclei in cat B-23.

Voogd's other cortical lesions involve not only more than one of his hypothetical bands of projections but also more than one lobule.

Our results do not support the hypothesis of Voogd. Fine vertical lesions placed in the lateral and medial portions of the paramedian lobule do demonstrate medio-lateral differences in the projection of this lobule, but not in the sense that a region of this lobule projects exclusively upon one nucleus.

In medial lesions of the paramedian cortex, there is markedly less degeneration in the ventral part of the NL, and the degeneration in the NIA and the NIP is located in the medial aspects of these nuclei. On the other hand, after a lateral lesion, the ventral part of the NL contains more degenerated fibers and the medial sections of the NIA and NIP are relatively free of degeneration. However, in neither case is any of the three zones of projection entirely absent. Small partial lesions injuring a few folia of the paramedian lobule at a time, are consistent with these results.

All our lesions of Crus II are followed by degeneration in two different regions in the nuclei. It is to be remarked however, that in cat CN-39R (with a lateral lesion), there is relatively more degeneration in the NL and NL-NIA than in the NIP as can be seen in Figure 5. On the other hand, lesions which injure the medial part of the cortex of Crus II (CN-8L, CN-11R) show a heavier projection in the NIP than lesions which are restricted to the lateral aspect of this lobule.

Thus, there seems to be a quantitative difference in the number of fibers going to a particular projection zone as one moves from the lateral to the medial side of a lobule. It seems as if the medial part of the cortex of the two lobules in question has few Purkinje cells which project upon the lateral nucleus, and numerous Purkinje cells which send their axon to the NIP. As one moves from medial to lateral, the number of Purkinje cells connected with the NL increases, while the number of Purkinje cells projecting upon the NIP decreases.

There are several technical difficulties impeeding a more definite demonstration of the absence of the three bands of projection in the lobules of the hemispheres. It is extremely difficult to localise a lesion to one of the three longitudinal zones of projection. Our surgical technique allows us only to make lesions which are relatively more in one zone than in another. Furthermore, the cortex which is visible on the surface and accessible to surgery, may constitute only a fraction of the total surface of the cortex of the lobules studied.

Perhaps the most convincing argument in defence of our hypothesis that any point of the cortex of the paramedian lobule projects to three nuclei is the following: the lateral part of the cortex of the paramedian lobule projects upon the transition zone and on the lateral portion of the NIA whereas a medial part of this lobule projects upon the medial half of the NIA. There is a medio-lateral topography in the projection of the paramedian lobule upon the transition zone-NIA. The presence of a medio-lateral topography of the paramedian lobule in one nucleus, excludes the presence of one zone of projection exclusively connected to a single nucleus.

Another argument which Voogd advances to support his hypothesis of three longitudinal bands of projection in the lobules of the hemispheres is the fact that degeneration from a single lobule is found in three separate regions in the nuclei without any overlap, whereas degeneration from different lobules but from the same band of projection (B, C or D) does overlap. This has not been substantiated in our results. The projection of the paramedian lobule to the ventral part of the NL is clearly separate from the projection of Crus II which is located in the dorsal portion of this nucleus.

To support further his hypothesis, Voogd presents experiments of retrograde degeneration. According to this author, each of the hemispheral lobules is connected to three different subdivisions of the nuclei by three different fibre bundles which are separated by "raphes" (discussed later). Therefore after a lesion of a particular subdivision of the nuclei, retrograde degeneration is found only in the medullary zone which is connected to that nuclear subdivision. Thus, after a lesion of the posterior interposed nucleus, only the medial third of the white matter in the hemispheral lobule (when unfolded parallel to a midsagittal line) should show degenerated fibers. In the original configuration of the cortex, this would correspond to the medial third of the paramedian lobule, the ventral part of the dorsal paraflocculus and the dorsal part of the ventral paraflocculus.

In his case D8, where there is a restricted lesion of the caudal part of the posterior interposed nucleus, Voogd illustrates degenerated fibers in these parts: the ventral third of the dorsal paraflocculus and the dorsal third of the ventral paraflocculus. In contradiction to this scheme, where the posterior interposed nucleus is connected only to the medial parts of the unfolded hemispheral lobules, the white matter of the lateral portion of the paramedian lobule in case D8 also shows degenerated fibers.

Voogd's other two cases (D3 and D9) using retrograde degeneration involve more than one subdivision of the cerebellar nuclei and the subsequent degeneration is located in more than one of Voogd's hypothesis medullary bands.

Voogd's hypothesis that each of the hemispheral lobules projects to a single nuclear subdivision by means of a separate fibre bundle is partly based upon the difference of calibre of fibers projecting from different areas of the cortex. According to this author, the axons of Purkinje cells from a band of cortex projecting to one subdivision of the nuclei form a bundle of characteristic calibre and orientation. Such bundles of Purkinje cell axons are separated by "raphes" which Voogd observed with the Haggqvist technique. The term "raphe" is used by the author to denote the accumulation of small calibre fibers between compartments of large calibre fibres (the Purkinje cell axons). Voogd reports that the "raphes" can be traced to the subdivisions of the central cerebellar nuclei. If that is the case it would seem improbable that the "raphes" represent the afferent fibre system of the cerebellum as Voogd suggest in a later publication (1969) where he states that the spino-cerebellar fibres collect at the sites of the "raphes". Furthermore, he describes that fibres from different zones of projection B and C for example, are of different calibre. If these fibers are the axons of Purkinje cells, the difference of calibre of fibers from a band of projection to the next is difficult to account for.

V

SUMMARY AND CONCLUSION

In this study, the site of termination of cortico-nuclear fibers arising from Crus II and from the paramedian lobule of the feline cerebellum was described. Our experimental data allow us to formulate the following conclusions:

1. The cortex of the paramedian lobule sends three, distinct, non-overlapping ipsilateral projections upon the cerebellar nuclei. These are found in the lateral nucleus, and finally in the transition zone and the anterior interposed nucleus.

   Crus II, on the other hand, sends only two ipsilateral projections upon the cerebellar nuclei. The first zone of projection begins in the lateral nucleus, continues through the transition zone and ends in the anterior interposed nucleus. The posterior nucleus receives the second projection from this lobule.

2. The cerebellar cortico-nuclear projections of the paramedian lobule and Crus II, are distributed to distinct regions of the nuclei and present very little overlap when they become adjacent. The projection of the paramedian lobule to the ventral part of the lateral nucleus does not come anywhere near the Crus II projection. The second projection of the paramedian lobule which begins in the transition zone is situated near the posterior border of the nucleus, whereas the projection of Crus II in this region is distributed more anteriorly. Furthermore, the latter projection of Crus II ends in the most lateral sections of the anterior

interposed nucleus, while that of the paramedian lobule continues to the most medial sections of this nucleus.

In the posterior interposed nucleus, the projection of the paramedian lobule is situated caudally and extends throughout the medio-lateral extent of this nucleus, while the projection from Crus II is found anteriorly and is restricted to the lateral half of this nucleus.

3. Both the paramedian lobule and Crus II send topographically organized fibers to the cerebellar nuclei. Since both of these lobules are known to receive a somatotopically organized afferent input from the brain cortex, the topographical arrangement of the efferent fibers of these lobules can be interpreted as a somatotopical representation.

4. Voogd's hypothesis that the cortex of the paramedian lobule and Crus II is arranged in longitudinal strips projecting to different nuclei was disproved. Both medial and lateral aspects of the paramedian lobule and Crus II project upon all the sites of termination of cortico-nuclear fibers from these lobules.

VI

ABBREVIATIONS

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ans.	ansiform lobule
ansu.	ansula
CN-8R	cat number 8, lesion on the right side of the cerebellum
CN-9L	cat number 9, lesion on the left side of the cerebellum
Cr.I	Crus I
Cr.II	Crus II
F.pr.	primary fissure
flocc.	flocculus
forelimb	rostral parts of the body
Hindlimb	caudal parts of the body
IA	Anterior interposed nucleus
IP	Posterior interposed nucleus
L.ant.	anterior lobe
L.pm.	paramedian lobule
L.simpl.	lobule simplex
Lc	pars convexa of the lateral cerebellar nucleus
Lr	pars rotunda of the lateral cerebellar nucleus
NIA	anterior interposed nucleus
NIP	posterior interposed nucleus
NL	lateral nucleus
NL-NIA	transition zone between the lateral and the anterior interposed nucleus

NM	medial nucleus
Pfl.d.	dorsal paraflocculus
Pfl.v......................	ventral paraflocculus
IV	fourth ventricle
I, II, III, IV .... X	Roman numeral indicating the cerebellar lobules I to X according to Larsell

VII

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