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THE CEREBELLUM OF THE FROG

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SEVENTEEN FIGURES

INTRODUCTION

The cerebellum of the frog is of considerable morphological importance because of its relatively simple structure. The further fact that here in the same species there are present in larval stages both lateral line and vestibular systems, while in the adult the latter alone remains, adds interest to a detailed study of this part of the brain in this animal. In view of the close relationship of these two sensory systems to the development of the cerebellum, it is of importance to observe the results of nature's experiment, which has eliminated the lateral line apparatus and its connections in the adult frog.

The frog's cerebellum was studied in considerable detail, particularly as regards its connections, by Wlassak ('87) chiefly with the aid of the Weigert technique. Subsequently it was described by Gaupp ('99), who however relied largely on Wlassak's work for details. Banchi ('03) has given an account of the organ in the toad (Bufo). Kappers and Hammer ('18) describe the cerebellum of the bull-frog briefly, and more recently Kappers ('21) has summarized the studies on amphibian cerebella, making use of a manuscript by Röthig, in addition to the observations just cited, for a description of the anuran cerebellum. Röthig's account has not been accessible to me, and has only come to my attention since my own observations were completed through the reference by Kappers. A more detailed comparison of the results obtained by Röthig with my own would be highly desirable, but is not possible at the present time. No formal review of the literature will be attempted in this paper.

The plan of the investigation included a study of the cerebellum of a series of larval stages, as well as of the adult frog, by the various methods of neurological technique. The Golgi method is indispensable for many phases of a detailed study, but up to the present time I have been unsuccessful in securing a sufficient number of satisfactory silver-bichromatic preparations of larval stages below 36 to 40 mm. in length to complete the work as originally contemplated. It appears desirable, however, to present the results obtained with especial reference to the adult cerebellum and such observations on larval stages as have a direct bearing on adult structure, at the present time. It is hoped to supplement the account at some future date with a detailed study of the larval cerebellum, from its earliest inception.

MATERIAL AND METHODS

The material included ninety-four series of larval and adult stages of several species of frogs, prepared by various methods, as indicated below. Thirty-eight of these series, including a number prepared by the Golgi and the Weigert methods by Dr. Paul S. McKibben, were kindly placed at my disposal through the courtesy of Dr. C. Judson Herrick. I am greatly indebted to these gentlemen for the opportunity to make use of this valuable material.

Rana pipiens, adult:
  24 series by Golgi method in transverse, horizontal and sagittal planes.
  10 series by method of Ramón y Cajal, transverse, horizontal and sagittal.
  6 series by Weigert method, transverse, horizontal, and sagittal.
  3 series by Marchi method, transverse.
  5 series stained with toluidin blue and erythrosin, transverse.
  8 series, stained with hematoxylin and eosin, transverse, horizontal and sagittal.
Rana catesbiana, adult and larval:
  5 series by Golgi method, horizontal and sagittal.
Hyla regilla larvae
  16 series by Golgi method, from 32 mm. to 40 mm. in length, transverse, horizontal and sagittal.
  6 series stained with hematoxylin and eosin or hematoxylin and orange G, varying from 18 to 32 mm. in length and cut transversely.

8 series fixed and stained in vom Rath's fluid, varying from 25 to 36 mm. in length, transverse, horizontal, and sagittal.

Acris gryllus, adult:

3 series by Golgi method, horizontal.

In addition to the study of the histological preparations, models were constructed of the cerebellum in larval stages of 18, 25, and 36 mm., and of the organ in the adult frog. The blotting-paper and paraffine method of Mrs. Gage was utilized in making the reconstructions.

GENERAL MORPHOLOGY

The cerebellum of the frog, as of other vertebrates, has its origin from the rhomboidal lip by an upward and medial growth of the area acustica or area statica of Kappers. In the earlier stages of its development the amount of massive tissue is very small. There is a wide recessus lateralis of the rhomboid fossa (fig. 1, A and B), but the roof of this recess is entirely membranous in the 18 mm. larva. The floor of the rostral portion of the lateral recess inclines upward so as to form a swelling which represents the eminentia ventralis cerebelli of Herrick, medially, and the rudiment of the auricular lobe, laterally. A slight forward continuation (fig. 1 A, *d. a.*) of the recessus lateralis is regarded as corresponding with the anterior diverticulum of Herrick. This is covered with a membranous structure, but its rostral and medial walls are massive. They are continuous ventrally with the ventral cerebellar eminence, and represent the anlage of the corpus cerebelli. The massive structure is connected medially with the anterior medullary velum, which is entirely membranous at this stage. There is, accordingly, only the small eminence on either side, immediately rostral and medial to the anterior diverticulum, to represent the corpus cerebelli.

In the larva of 25 mm. (fig. 1 B) a considerable advance in development is apparent. The corpus cerebelli extends medially almost to the mid-line. The connection between the two corpora cerebelli contains fibers, but no nerve cells. The body of the cerebellum is encroaching upon this still membranous portion from either side. The anterior diverticulum of the recessus lateralis is reduced to a small pit. Lateral to this is the prominent auricular lobe.

The tadpole of 36 mm. (fig. 1 C) approaches the adult condition in the development of the cerebellum. At this stage the hind-legs, as well as the fore-legs, are well developed, and the animal uses them considerably. The cerebellum is massive throughout, except at the dorso-caudal margin close to either side of the mid-line. The auricular lobe persists, but in somewhat reduced form. A well defined ridge, the eminentia granularis, continues caudally from this lobe toward the VIII nerve.

In all of the larval stages studied the ventral cerebellar eminence (fig. 1, *em. v.*) is pronounced, but is more laterally placed than in urodeles. It is continuous dorsally and rostrally with the corpus cerebelli. In the 36 mm. larva there is a medial continuation of the eminence which forms a projecting mass into the rhomboid fossa just below the corpus cerebelli. This prominence is bounded

ABBREVIATIONS

aq. S., aqueductus Sylvii
br. conj., brachium conjunctivum
cb., cerebellum
c. cb., corpus cerebelli
c. n. mgc., cell of nucleus magnocellularis
com. cb., commissura cerebelli ventralis
com. lat., commissura cerebelli lateralis
d. a., diverticulum anterior
dec. v., decussatio veli
em. gr., eminentia granularis
em. v., eminentia cerebelli ventralis
f. arc. ex. d., fibrae arcuatae externae dorsalis
f. ex. arc., fibrae arcuatae externae
gr. c., granule cell
l. aur., lobus auricularis
l. inf., lobus inferior
med. obl., medulla oblongata
mes., mesencephalon
n. IV, nervus trochlearis
n. V, nervus trigeminus
n. VII, nervus facialis
n. VIII, nervus acusticus
n. IX, nervus glossopharyngeus
n. X, nervus vagus
nuc. cb., nucleus cerebelli
nuc. isth., nucleus isthmi
nuc. pr. is., nucleus pre-isthmi
nuc. tr. sol., nucleus tractus solitarii
nuc. vest., nucleus vestibuli
nuc. vis. sec., nucleus visceralis secundus
Pur. c., Purkinje cell
r. mot. V, radix motorius trigemini
s. l., sulcus limitans
s. v. cb., sulcus ventralis cerebelli
str. gr., stratum granulosum
str. mol., stratum moleculare
tr. bu. cb., tractus bulbo-cerebellaris
tr. cb. teg., tractus cerebello-tegmentalis
tr. mes. V, tractus mesencephalico-trigemini
tr. sol., tractus solitarius
tr. sp. cb., tractus spino-cerebellaris
tr. sp. t., tractus spino-tectalis
tr. t. cb., tractus tecto-cerebellaris
tr. t. isth., tractus tecto-isthmi
tr. V-cb., tractus trigemino-cerebellaris
tr. V-sp., tractus trigemino-spinalis
tr. vest. cb., tractus vestibulo-cerebellaris
tr. vest. d., tractus vestibulo-cerebellaris direct
tr. vis. as., tractus visceralis ascendens
tr. vis. tert., tractus visceralis tertius
tr. t. isth., tractus tecto-isthmi
vent. IV, ventriculus quartus
v. m. a., velum medullare anterius

dorsally and separated from the medial portion of the body of the cerebellum by a groove which will be designated the sulcus ventralis cerebelli (fig. 1, *s. v. cb.*). This sulcus continues rostrally and medially to a point beneath the anterior medullary velum. The ventral boundary of the eminence under consideration is the sulcus limitans. It is difficult to account for the prominence of this medial portion of the ventral cerebellar eminence at this

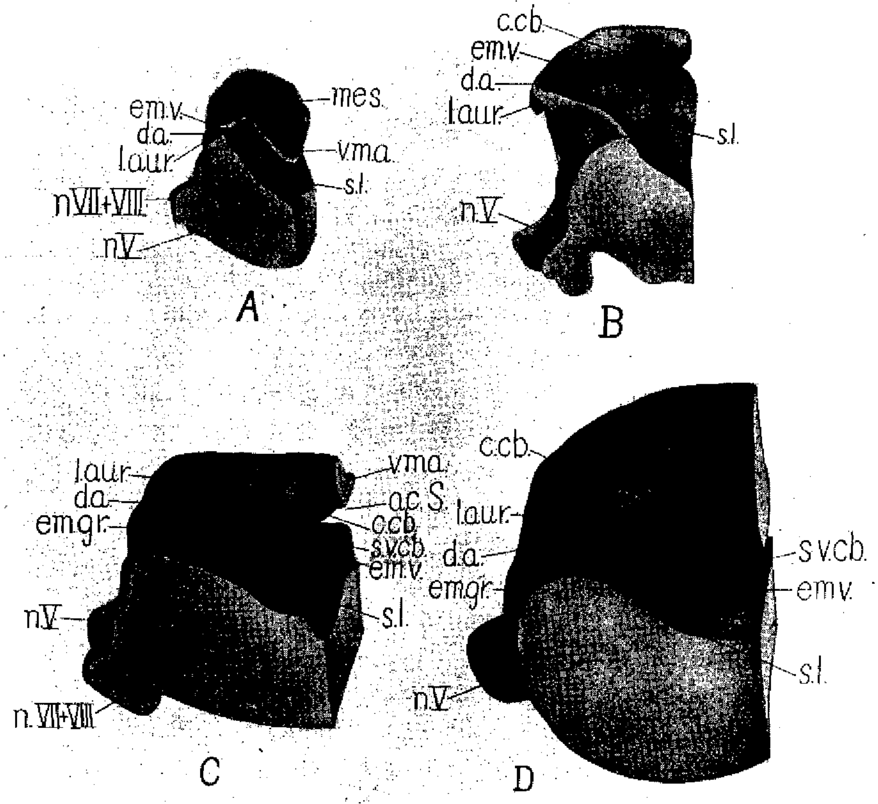


Fig. 1 Views of models of the left side of frog's cerebellum from behind and slightly from above, showing relations of cerebellar structures to recessus lateralis. A. Larval frog of 18 mm., with no legs visible externally. Hyla regilla. × 40. B. Larval frog of 25 mm., with hind-legs just appearing. Hyla regilla. × 40. C. Larval frog of 36 mm., with well-developed legs. Hyla regilla. × 40. D. Adult frog, Rana pipiens. × 20.

stage except on the ground that the nucleus isthmi, which in the 36 mm. tadpole is of large size, has crowded the structures below the corpus cerebelli, caudally and medially. The caudal boundary of the nucleus isthmi itself at this stage is at a level with the rostral boundary of the corpus cerebelli.

In the adult frog the ventral cerebellar eminence has so fused with the body of the cerebellum as to be indistinguishable from the latter except for a small area just lateral to the sulcus limitans and directly ventral to the main portion of the corpus cerebelli. Here a triangular area (fig. 1 D, *em. v.*) appears to correspond with the ventral cerebellar eminence of urodeles and of frog larvae. The ventral cerebellar sulcus remains as a shallow groove.

The cerebellum of the adult frog is massive throughout (fig. 1 D). The medial portion extends rostrally, and the corpus cerebelli on either side is developed caudally in such a manner as to give the entire cerebellum, as viewed from above, a somewhat curved outline, with the convex side directed forward. Cerebellar tissue encroaches upon the anterior medullary velum to such a degree as to greatly reduce the extent of this structure. A slight pit (*d. a.*, fig. 1 D) continues forward from near the extremity of the lateral recess into the massive structure rostrad. This appears to correspond with the anterior diverticulum of urodeles, as Kappers ('21) also has stated in describing the cerebellum of the bull-frog. The auricular lobe, which lies lateral to this pit, is much reduced in the adult frog. This is evidently due to the fact that the lateral line system, present in larvae, disappears at metamorphosis. There remain therefore only vestibular connections with this part of the structure which has developed from the area acustica. The eminentia granularis, which was noted in the 36 mm. larva, continues, also in the adult frog, from the auricular lobe toward the VIII nerve. As shown in figure 16 cellular structure may be recognized as far caudally as about the level of the middle of the mass of the trigeminal roots. There is formed by this mass a ridge on the dorso-lateral aspect of the rostral portion of the medulla oblongata.

NUCLEI OF THE CEREBELLAR REGION

The tegmentum of the bulb continues dorsally on either side as an eminence which appears to correspond with the eminentia ventralis cerebelli of Herrick, already noted. As compared with urodeles, the ventral eminence in the frog is more definitely a part of the cerebellum. The nucleus cerebelli contained within it is marked off from the secondary visceral nucleus, to be described below, which lies rostrally, and in part, ventral to it (figs. 2 and 4) by a mass of fibers. A similar boundary, but not so pronounced, separates it caudally (fig. 3) from the vestibular nucleus and the eminentia V. Ventro-medially it is continuous with the tegmentum. The cells in the region thus bounded are larger and the nerve fibers are less numerous than are those in the tegmental region. Golgi sections show multipolar cells (figs. 2 and 4) whose axones pass rostrally and medially, in part, to form the brachium conjunctivum. This nucleus appears to correspond to the combined nuclei lateralis and medialis of van Hoëvell ('16). Allen ('23) has recently shown by experimental methods that there are no visceral connections with any of the deep cerebellar nuclei in mammals, and results obtained by Doctor Allen, which are as yet unpublished, indicate that the globose and emboliform nuclei, at least, are related in the guinea-pig to the nucleus dentatus. These facts, together with the comparative studies of van Hoëvell, just cited, and of Brunner ('19), would seem to indicate that the nuclear mass in question probably represents all of the deep cerebellar nuclei in a primitive condition. It will therefore be designated nucleus cerebelli, rather than nucleus dentatus. The latter name was used by Herrick ('14) in describing the cerebellum of Necturus, and by myself ('20) in connection with the cerebellum of Amblystoma, but I now consider it inadequate.

Nucleus visceralis secundus. Just caudal to the nucleus isthmi, which is the most prominent landmark in this region of the frog's brain (fig. 2), there is found both in adult frogs and in larvae, a group of cells (*nuc. vis. sec.*, figs. 2, 4, 5, and 6) which in position and connections corresponds with the secondary gustatory nucleus of fishes (Herrick, '05; Johnston, '06). The nucleus has fairly sharp outlines. The concave rostral border, as shown in the figures, lies against the caudal side of the nucleus isthmi. The growth of the nucleus isthmi and of the nucleus cerebelli, which is contained within the ventral cerebellar eminence dorsocaudad to the secondary visceral nucleus, appears to have crowded the latter between the two in such a manner that the medial portion has become attenuated, while the lateral portion remains rounded. The relation of the secondary visceral nucleus to the cerebellum can best be understood by reference to figures 2 and 4. As illustrated, it lies just ventral to the rostral part of the nucleus cerebelli and rostral to the upward sweep of the spino-cerebellar tract. The latter tract, together with other fibers, separates the nucleus in question from the nucleus cerebelli. In its dorso-ventral relations it lies just dorsal to the level of the sulcus limitans. Larval stages (fig. 2) show clearly that it is located caudal to the sulcus which bounds the isthmus from the midbrain.

Herrick ('14 a) describes and figures a nucleus in larval Amblystoma which corresponds to the one above described. In a more recent paper (Herrick, '17) he describes also in Necturus the secondary visceral nucleus "as a lateral extension of the central gray in the angle between the body of the cerebellum and the midbrain." In the same paper this nucleus is referred to the midbrain in larval Amblystoma. This is obviously an error of statement, which Doctor Herrick has corrected elsewhere, and also in a personal communication to the writer. Kappers ('21) does not regard the secondary visceral nucleus as a part of the cerebellum, but considers its relationship to that organ as merely topographical. The fiber tract connections will be considered below.

Nucleus vestibularis or ventral VIII nucleus. This nucleus, while not a part of the cerebellum proper, may be considered briefly because of its close relationship in development and in its connections. It is present in differentiated form in frog larvae of 40 mm., and perhaps earlier. The ventral bundle of the VIII nerve passes in part to this nucleus (fig. 3), and axones from its

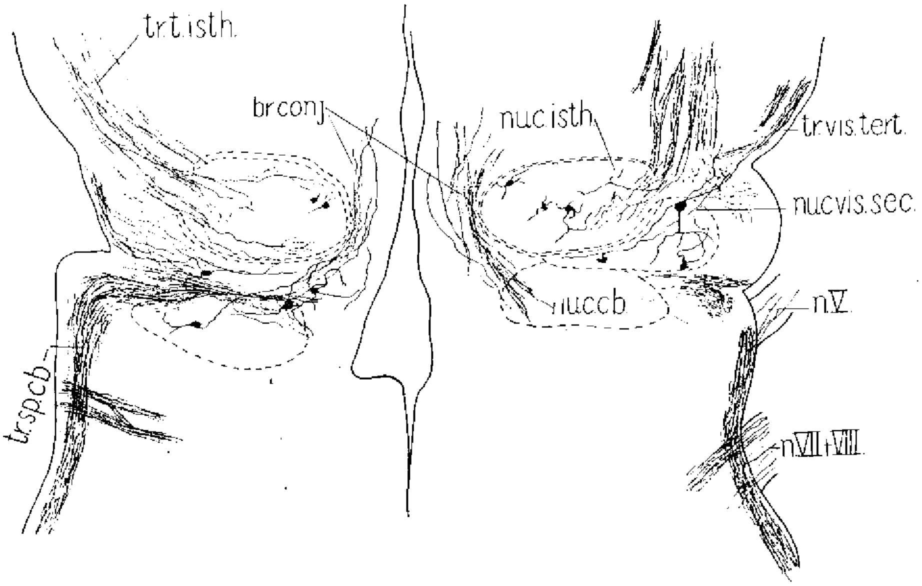
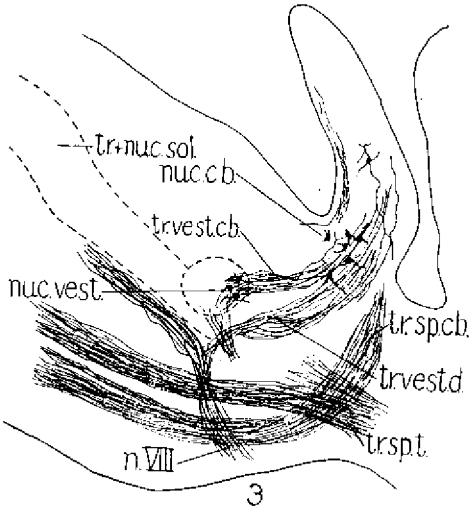


Fig. 2 Horizontal sections through the ventral part of cerebellar region of a larval frog of 32 mm., with well-developed legs. Hyla regilla, Golgi method. Leitz projection apparatus. × 60.



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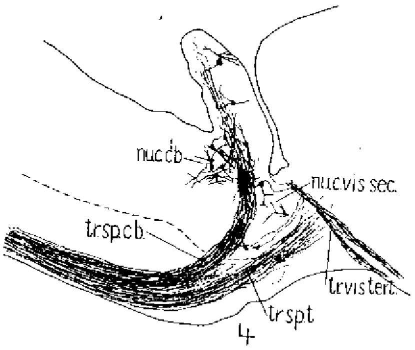


Fig. 3 Section in parasagittal plane, through cerebellum and vestibular region of larval frog of 40 mm., with well-developed legs. Hyla regilla, Golgi method. Cam. luc. × 54.

Fig. 4 Section through cerebellar region in parasagittal plane, of larval frog of 40 mm. Hyla regilla, Golgi method. Cam. luc. × 32.

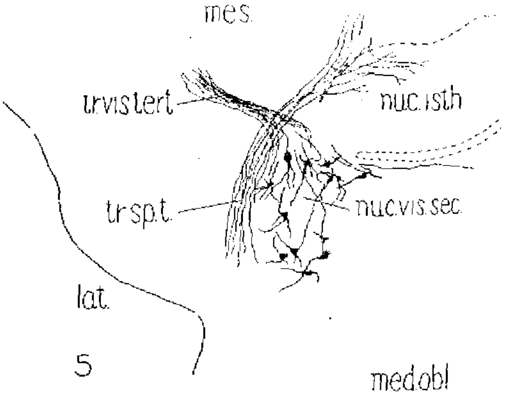
cells continue to the cerebellum as the vestibulo-cerebellar tract. Kappers ('21) regards this nucleus in Amphibia as in part homologous with Deiters' nucleus of higher forms. I have not studied it in the frog except in its relation to the cerebellum, but in this respect it corresponds to Bechterew's nucleus also, in so far as the latter sends fibers to the cerebellum.

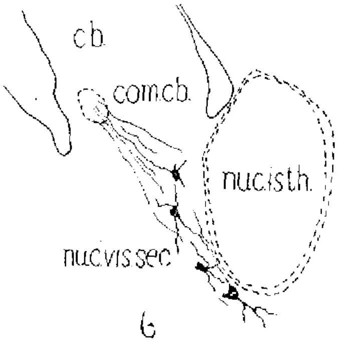
In the border zone of the ventral cerebellar eminence between the nucleus cerebelli and the tegmentum there occur in the adult frog, as shown in Golgi sections, cells of large size (fig. 7) which suggest Purkinje cells, but are much less differentiated than the Purkinje cells in the corpus cerebelli of the same individual. Some of the dendritic processes extend laterally, to end among the fibers of the spino-cerebellar tract, others extend medially and ventrally into the tegmentum. The axones could not be followed beyond the stratum griseum, and are regarded as cerebello-tegmental fibers. As shown in figure 11, the direct vestibulo-cerebellar tract sends numerous collaterals into the region occupied by these cells. They thus receive, not only impulses from the cord, but also vestibular stimuli, as well as others by means of the dendrites which pass into the gray substance. They may be regarded as a more primitive cerebellar correlating apparatus than is found in the corpus cerebelli.

Herrick ('14) found cells in both the medial and the lateral walls of the recessus lateralis of Necturus, which he regards as greatly reduced Purkinje cells, whose connections are essentially the same as described above for the frog. I have seen these cells only in the region of the ventral cerebellar eminence, adjacent to the nucleus cerebelli, but they appear to be of the same type as Herrick's, somewhat more elaborated. They have a striking resemblance to some of the Purkinje cells described by the writer ('20) in Amblystoma.

GENERAL HISTOLOGY

Histologically the frog's cerebellum may be divided into three zones, corresponding with those found in the cortex of the mammalian cerebellum, namely, a molecular layer, a layer of Purkinje cells, and a granular layer (figs. 8 and 9). All the elements characteristic of the mammalian cortex except basket cells, Golgi cells, and the superficial stellate cells, have been found, but in less specialized form than in mammals. Cajal and Weigert sections show a considerable number of cells in the molecular layer, but in none of our Golgi preparations were these well impregnated, so that it was not possible to determine clearly their structural type.





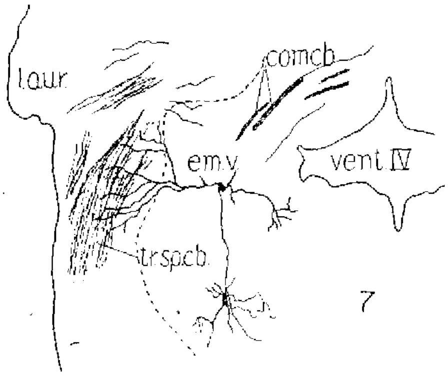


Fig. 5 The secondary visceral nucleus, and the tertiary visceral tract. Horizontal series of adult R. pipiens. Golgi method. Cam. luc. × 60.

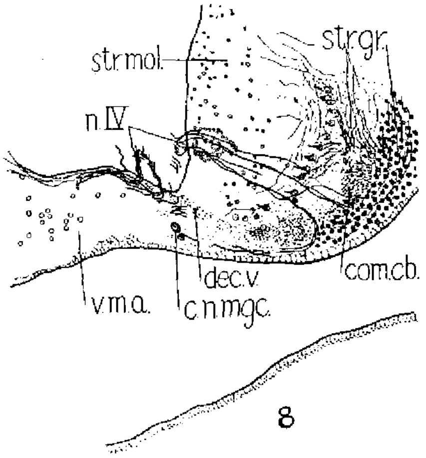
Fig. 6 Secondary visceral nucleus, showing fibers from it to the cerebellar commissure. Parasagittal section of 40 mm. larva. Hyla regilla, Golgi method. Cam. luc. × 73.

Fig. 7 Cell in ventral cerebellar eminence. Transverse section adult R. pipiens. Golgi method. Cam. luc. × 32.

The granular layer is made up of characteristic small and rounded cells, with a number of short dendritic processes. Many of the processes terminate in typical claws. As compared with mammalian granules, those in the frog are relatively simple in structure. As is shown in figure 9, which was drawn from a specimen of Acris gryllus, the axones pass to the molecular layer where they bifurcate. The two resulting branches pass laterally toward either side of the cerebellum, parallel with its surface. Rana shows the same structure. In the ventral portion of the corpus cerebelli, as illustrated in figure 8, the granules do not reach to the layer of Purkinje cells, but are separated from them by a considerable stratum of fibers. Numerous fibers are also scattered throughout the granular layer and represent the terminal processes of the various entering tracts. Clear evidence of mossy fibers was not found in the material available, although Banchi ('03) found fibers which resemble them in the toad.

As shown in figures 15 and 16, the granular layer extends laterally into the lobus auricularis. From the region of the lobe the cellular mass continues caudally as far as the middle of the trigeminal roots, in the adult frog. It gives rise to the ridge already noted as the eminentia granularis.

The layer of Purkinje cells occupies a well-defined position between the granular and molecular layers. There is considerable variation in its thickness. In many places but one layer of cells may be found, but two, three, or four layers are common. The Purkinje cells of the corpus cerebelli are well differentiated. They have a rounded or ovoid cell body, with a single large dendritic branch (figs. 9 and 10). The dendrite quickly subdivides into secondary and tertiary processes, which are studded with the characteristic gemmules. The dendritic processes are distributed so that their greatest spread, as the figure shows, is rostro-caudally. They thus resemble mammalian Purkinje cells in their relation to the fibers from the granules. The axones pass for a short distance into the granular layer, where they are deflected ventrally. A careful study of their distribution in Golgi sections leaves one with the strong impression that many end in the nucleus cerebelli, while others continue without interruption into the brachium conjunctivum, as described below. Banchi ('03) describes the Purkinje cells in the toad as sending axones into the midbrain, and shows figures of Golgi impregnations in which continuous processes are depicted from the cells to the midbrain region. Our preparations were not so fortunate



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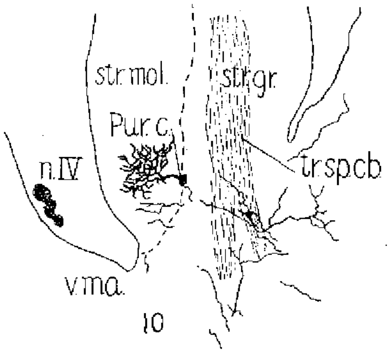

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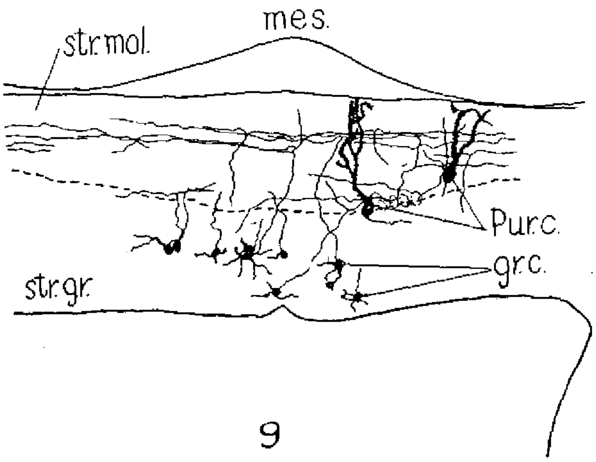

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Fig. 8 Ventral portion of cerebellum and part of anterior medullary velum, near mid-sagittal plane of adult R. pipiens. Sagittal series. Method of Ramón y Cajal. Cam. luc. × 73.

Fig. 9 Horizontal section through cerebellum of Acris gryllus, showing principal histological elements. Golgi method. Cam. luc. × 73.

Fig. 10 Parasagittal section through ventral portion of cerebellum, showing a Purkinje cell. Adult R. pipiens, Golgi method. Cam. luc. × 43.

in this respect, but Weigert and Cajal material, together with the Golgi preparations, give sufficient warrant for the interpretation offered above.

The molecular layer is composed almost entirely of fibers from the granules and from the vestibular tracts. As already stated, numerous small cells (fig. 15) are scattered rather evenly throughout this layer. It is probable that the majority, if not all, represent neuroglia cells. In well-impregnated Golgi series, cut parallel with the sagittal plane, the spread of the Purkinje cell dendritic processes fill the entire area of the molecular layer in portions of many sections. Climbing fibers are present in typical relation to the Purkinje cell dendrites. They ascend from the fibrous zone of the granular layer.

FIBER TRACTS AND CONNECTIONS

Tractus spino-cerebellaris. This is the most prominent bundle connected with the cerebellum. It accompanies the spino-tectal tract through the bulb as far as the level of the trigeminal roots. The combined bundles up to this point lie ventral to the spinal V tract. Here, however, the spino-cerebellar fibers arch dorsalward and medially, many passing through the V root bundles, and enter the body of the cerebellum. The fibers terminate, crossed and uncrossed, in the granular layer. As shown in figures 2 and 4, the bundle passes rostrally to the nucleus cerebelli. It appears from this fact, as well as from other considerations, to correspond to the ventral spino-cerebellar tract of other forms. It is doubtful if any dorsal spino-cerebellar fibers are contained within it.

The dorsal spino-cerebellar tract does not appear to me to be clearly evident as such in the frog. Wlassak ('87), from Weigert preparations, describes a dorsal tract as terminating in the cerebellar cortex, homolaterally. He subdivides it into three parts, namely, 1) a bundle which forms a large bow from below, and which Stieda ('70) believed to be composed of fibers from the gasserian ganglion; 2) fibers which penetrate the dorsal column and pass to the acoustic (vestibular?) nucleus; 3) fibers which bend around the dorsal column. Banchi ('03) describes a 'cordoni posteriori' derived in part from the V, VIII, IX, and X nerves, and in part from the spinal nerves, which appears to correspond in the toad, in many respects with Wlassak's dorsal tract. I have found the various elements given by Wlassak, by other methods of technique, as well as in Weigert preparations, and will describe them more fully in their proper place. All authors are agreed on the ventral tract, but there is considerable variation in the descriptions of the dorsal. None of the components of the bundle described by Wlassak and by Banchi, so far as I can determine, continue into the cord, and cannot therefore be regarded as spino-cerebellar. Marchi preparations of frogs, whose cords were hemisected just caudal to the medulla oblongata, show degeneration along the course of the spino-cerebellar tract (ventral) as described above, but none which could be followed into the cerebellum appeared more dorsally.

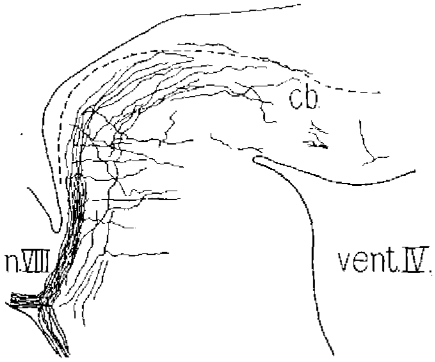


Fig. 11 Horizontal section, showing bifurcation of vestibular fibers to form the direct vestibulo-cerebellar tract. Adult R. pipiens, Golgi method. Cam. luc. × 17.

Tractus vestibulo-cerebellaris. There are two vestibular tracts to the frog's cerebellum, a direct tract, and one arising from the vestibular nucleus, as previously noted. The direct vestibulo-cerebellar tract (figs. 3, 11, and 17) is formed by bifurcation of the primary vestibular fibers. The finer ascending branches, as shown in the figures, pass directly into the cerebellum. In their course these fibers give off collaterals (fig. 11) already noted, toward the ventral cerebellar eminence.

The remaining fibers of the ventral branch of the VIII nerve also bifurcate, but their ascending branches reach only to the vestibular (ventral VIII) nucleus (fig. 3). As previously noted, axones from this nucleus pass to the cerebellum as the vestibulo-cerebellar tract. Both tracts under consideration continue primarily into the auricular lobe (figs. 15 and 16). From this region numerous fibers pass medially into the granular layer. Others extend dorsally into the molecular layer, some to terminate on the same side, but many cross to the opposite side. The crossing fibers form a fine fibered commissure which lies directly beneath the dorsal surface of the cerebellum, within the molecular layer. It appears to correspond with the commissura lateralis of lower forms.

Tractus mesencephalicus trigemini. This tract may be followed from the region of the motor V nucleus to the cerebellar commissure. On emerging from the commissure it passes through the velum and into the midbrain. The fibers are of large size and so closely resemble trochlearis fibers, described below, as to be indistinguishable from the latter within the commissure. One gains the impression that the mesencephalic V fibers are related in some manner in the frog to cerebellar structures, but I have no clear evidence in support of this statement.

Nervus trochlearis. The trochlear nerve in R. pipiens splits into three roots before entering the brain. Two of the roots enter the anterior medullary velum, one to pass rostral to the nucleus isthmi, the second to pass through this nucleus, after which it joins the first. The united bundle then continues to the trochlear nucleus. The third root, which concerns us more directly, enters the cerebellum proper. As shown in figure 8, many of the fibers, which are scattered, pass through the molecular and Purkinje cell layers to enter the cerebellar commissure. Here they become intermingled with the other fibers to such an extent that, in spite of their large size, it is extremely difficult to follow them. In sagittal sections, especially those prepared by the Cajal method, however, many of the fibers may be traced individually for considerable distances. It is clear that many are uncrossed and pass with the mesencephalic V root toward the region of the motor V nucleus, but the number appears to diminish as the nucleus is approached. A few, as shown in the figure, pass toward the tectum. In this region an occasional large, rounded nerve cell is encountered (fig. 8, *c. n. mgc.*) which in appearance and in size resembles the cells of the nucleus magnocellularis tecti of urodeles. Johnston ('09) states that in the frog the cells of the mesencephalic V root, as compared with Necturus and Cryptobranchus, "are fewer in number, and, so far as I have seen, are placed far laterally in the dome-shaped tectum." This is undoubtedly true, and the few cells which I have seen in the region of the velum which correspond to this type are probably aberrant in position. They are, however, suggestive in accounting for the fibers of the caudal root of the IV nerve.

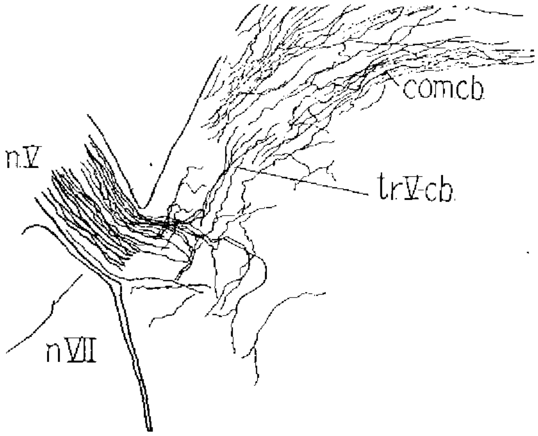


Fig. 12 Horizontal section, showing bifurcation of trigeminal fibers, with formation of a trigemino-cerebellar tract. Neighboring sections show more numerous fibers, but not so many which enter the cerebellar commissure. Adult R. pipiens, Golgi method. Cam. luc. × 73.

McKibben ('13) states that in Necturus there appear to be a few uncrossed fibers which enter the IV nerve, and "which seem to be larger fibers than those which make up the trochlear nerve and to belong to the mesencephalic root of the trigeminal nerve which lies here beneath the trochlear nerve." Davidson Black ('17) makes the statement concerning R. catesbiana: "It is possible that some of the fibers entering the trochlear nerve at their emergence are uncrossed and are derived, as McKibben ('13) has suggested in Necturus, from the mesencephalic nucleus of the trigeminal nerve."

These suggestions, together with the clue presented by such relations as illustrated in figure 8, point to the interpretation that the most caudal of the three roots in Rana pipiens contains muscle sense fibers, whose distribution is evidently to the trochlearis muscle.

Tractus trigemino-cerebellaris. The frog has a definite tract from the V roots to the cerebellum which is quite distinct from the mesencephalic V bundle. It arises (fig. 12) from a group of small fibers in the trigeminus which bifurcate on entering the medulla oblongata, and send the smaller branches which result rostrally and medially into the cerebellum and the cerebellar commissure. The larger rami of the bifurcated fibers pass caudally with the spinal V tract. Herrick ('14 a) describes trigeminal fibers in Amblystoma which continue to the rostral end of the auricular lobe, but apparently none of these enter the cerebellar commissure or the corpus cerebelli. This tract in the frog corresponds to Stieda's fibers which pass to the cerebellum from the gasserian ganglion, to which reference has been made. Banchi ('03) clearly illustrates these fibers in the toad.

Tractus tecto-cerebellaris. A small group of cells which are located immediately rostral to the medial portion of the nucleus isthmi (fig. 13), gives rise to a tract which passes around the margins of the nucleus isthmi caudally, and then continues laterally into the cerebellum. The fibers are small in size and few in number, as revealed in Golgi preparations. The tract is present in both larval and adult stages.

Kappers ('21) states that the tecto-cerebellar tract in the frog may be distinguished from that of fishes by its more limited extent and by its more caudal origin in the midbrain. He publishes a figure by Röthig which shows a portion of the tract arching beneath the nucleus isthmi, rather more ventrally than my preparations indicate. Kappers appears to be somewhat uncertain if this should not be regarded as a cerebello-tectal tract, but my Golgi preparations leave no room for doubt as to the presence of tecto-cerebellar fibers. Cerebello-tectal fibers could not be found in any of our preparations.

The presumption is that the tract as above described corresponds to the anterior mesencephalico-cerebellar tract of Gadus and other fishes with well-developed optic apparatus, but this question must be left until the homologies of the midbrain structures in the frog are better understood. Dendritic processes, as shown in the figure, extend from the cells of this pre-isthmial nucleus toward the spino-tectal tract. Some of our preparations show a synaptic relationship, as represented in diagram in figure 17.

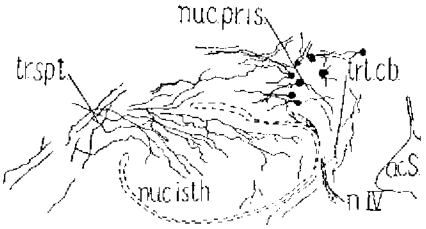


Fig. 13 Section showing nucleus isthmi and the pre-isthmial nucleus, from which the tecto-cerebellar fibers have their origin. Adult R. pipiens. Horizontal series Golgi method. Cam. luc. × 32.

Fibrae arcuatae externae arise from various nuclei of the medulla oblongata along its entire length, but particularly from its caudal portion. The cell masses here located appear to foreshadow the nuclei gracilis and cuneatus, although Kappers states that these nuclei are not differentiated in the frog. The fibers in question pass forward, just below the floor of the rhomboid fossa, and laterally around the dorsal cochlear nucleus and dorsal to it, to enter the cerebellum at its caudalmost contact with the medulla oblongata. Many scattered fibers, apparently of this category, lie quite medially also. All of these fibers are coarse and in sagittal and horizontal sections appear 'crinkly.' They are designated collectively (fig. 17) as the bulbo-cerebellar tract.

Tractus visceralis secundus. Cells from the nucleus of the solitary tract give rise to delicate fibers which pass rostrally in small bundles, which because of their unmyelinated condition can only be recognized in silver preparations, and which terminate in the secondary visceral nucleus above described. As shown in figure 14 A, processes from these cells of origin pass into the solitary tract to form synaptic relations with fibers from the IX nerve and presumably also with the VII and X, although actual synapses have not been observed in the case of the last two nerves named. The entire tract, which is best followed in transverse Cajal sections (figs. 15 and 16, *tr. vis. as.*), is much reduced and at times is very difficult to trace. The principal bundle of the fibers is located just dorsal to the spinal V tract for the greater part of its course. Some of the fibers, after passing through the secondary visceral nucleus, where the greater number terminate, probably cross to the opposite side through the cerebellar commissure (fig. 6).

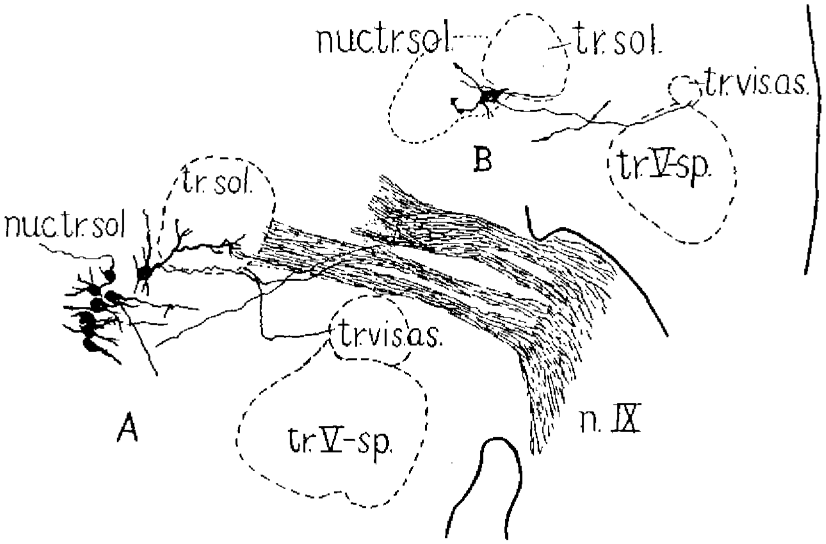


Fig. 14, A and B From transverse sections at different levels of same specimen of adult R. pipiens, showing relation of cells in the nucleus of the solitary tract to the ascending visceral tract. Golgi method. Cam. luc. × 30.

Brachium conjunctivum. This tract has already been noted in connection with the nucleus cerebelli. Its fibers have their origin in part from this nucleus (fig. 2) and apparently in part from more dorsal regions of the cerebellum, probably as direct axones of some of the Purkinje cells. The bundles pass rostrally and ventrally into the midbrain. They decussate in the ansulate commissure, and continue forward in the stratum griseum. Their final termination could not be determined.

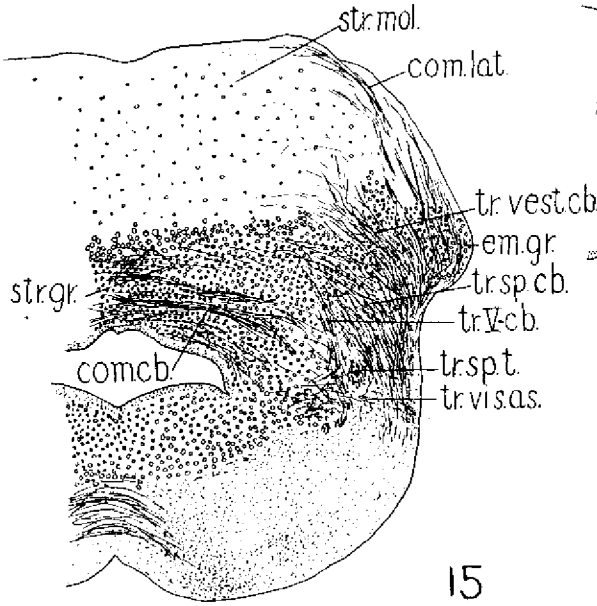
Tractus cerebello-tegmentalis. In addition to the brachium conjunctivum there are efferent fibers from the ventral cerebellar eminence and apparently from other parts of the cerebellum, which pass into the tegmentum as cerebello-tegmental fibers (figs. 7 and 17).

Tractus visceralis tertius. In many of our Golgi series, both larval and adult, the cells of the secondary visceral nucleus are well impregnated, and their axones may be seen to extend rostrally and medially, with a considerable ventral dip (figs. 2, 4, and 5), to form a well-defined tract. On approaching the spino-tectal bundle the tract divides into two main fasciculi, which pass on either side of the spino-tectal tract, to reunite rostrally to the latter. The reunited bundle then continues to the hypothalamus. No fibers from the hypothalamus to the cerebellum were observed, although they might be expected to be present in the frog, in view of the fact that they have been found in urodeles.

Other fibers (fig. 17) from the secondary visceral nucleus pass laterally and ventrally, with a slight rostral direction, to become lost in the great mass of fibers which constitute the ventral portion of the isthmial region. They appear to include both axones and dendrites.

Commissura cerebelli. The ventral cerebellar commissure (figs. 6, 8 and 15) is prominent. It is made up of several components which include mesencephalic V fibers, spino-cerebellar fibers, commissural fibers between the secondary visceral nuclei, and chiefly, fibers which connect the two masses of the nuclei cerebelli.

Decussatio veli. The decussation of the velum proper is quite distinct from the commissure above described in the frog. As shown in figure 8, it occupies the thin portion of the velum immediately rostral to the cerebellum. It is composed of trochlearis fibers of the two more anterior roots, fibers of the mesencephalic V root, and a number of finer fibers which include the tecto-cerebellar tract, and others which appear to have no relation to the cerebellum.



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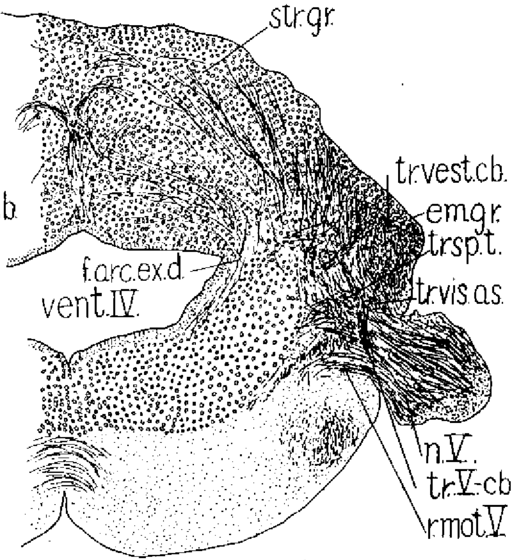

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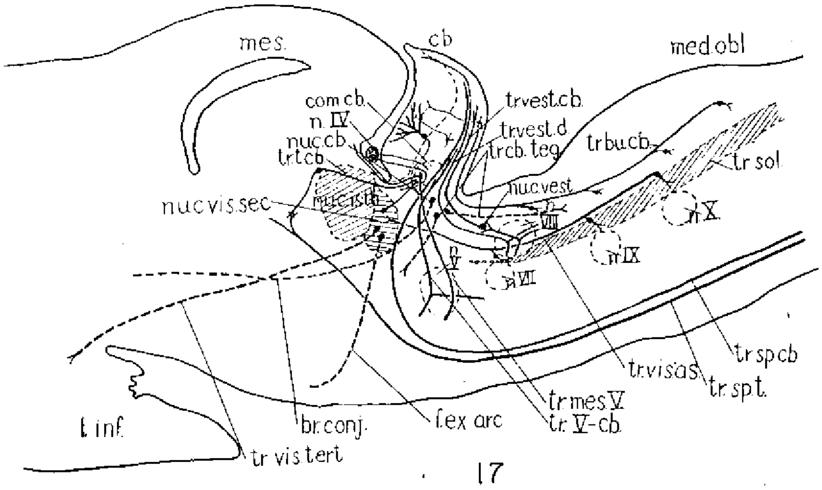

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Fig. 15 Transverse section through middle region of cerebellum of adult R. pipiens. Method of Ramón y Cajal. Cam. luc. × 30.

Fig. 16 Transverse section through caudal region of cerebellum of adult R. pipiens. Method of Ramón y Cajal. Cam. luc. × 30.

Fig. 17 Diagram of the cerebellum and its connections in the frog, represented as projected on a plane about midway between the mid-sagittal plane and the lateral surface of the cerebellum.

SUMMARY

The cerebellum of the frog shows considerable advance over that of urodele amphibia. Well-developed Purkinje cells and granule cells are present, but basket cells and other elements of higher cerebella have not been found. A ventral nuclear mass, which is called the nucleus cerebelli, foreshadows the deep cerebellar nuclei of higher forms. A well-developed nucleus, which is placed laterally in the cerebellar segment, just dorsal to the level of the sulcus limitans, appears from its position and connections to be homologous to the secondary visceral nucleus of fishes.

The fiber tract connections with the cerebellum include a direct trigemino-cerebellar tract, vestibulo-cerebellar and direct vestibular tracts, spino-cerebellar, tecto-cerebellar and bulbo-cerebellar tracts, besides brachium conjunctivum and cerebello-tegmental fibers.

The trochlear nerve sends some uncrossed fibers directly into the cerebellum. These appear to become related to the mesencephalic V tract which also passes through the organ.

The secondary visceral nucleus gives origin to a tract which passes to the hypothalamic region. Other fibers from this nucleus, apparently both axones and dendrites, extend toward the interpeduncular region. An ascending visceral tract from the nucleus tractus solitarii terminates in the secondary visceral nucleus.

The lateral line system, which in the frog disappears at metamorphosis, appears to be compensated for by a greater development of the vestibular system, and seemingly, to some extent, by inclusion within the cerebellum of muscle-sense fibers. The auricular lobe, which receives vestibular fibers only in the frog, is present in relatively reduced form.

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