

A STUDY BY EMBRYOLOGICAL, EXPERIMENTAL ANATOMICAL AND
NEUROPHYSIOLOGICAL METHODS OF THE AFFERENT FIBER
TRACTS AND THE RECEPTIVE AREAS OF THE
AVIAN CEREBELLUM

by

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I INTRODUCTION

The avian cerebellum has been the subject of numerous anatomical and experimental investigations, beginning with the physiological studies of Rolando, in 1809, up to the present time. It has long been recognized that the greater part of the cerebellum of birds corresponds, in general, to the vermis of the organ in mammals, but homologies between the subdivisions of the avian cerebellum and the lobules of the vermis have been difficult to establish. So far as they have been pointed out their foundations have been far from secure. The presence of a paraflocculus in the avian cerebellum has been another question concerning which widely divergent views have been expressed by various investigators. Also interpretations regarding the presence of any structure homologous to the cerebellar hemispheres of mammals and of a pons or of pontine connections have differed greatly.

Recent morphological re-interpretations of the avian cerebellum (Larsell, '48) have demonstrated a fundamental pattern of flocculonodular lobe and corpus cerebelli in common with all other classes of vertebrates. It was also shown that the two primary subdivisions have a secondary pattern of folia in which homologies with the subdivisions of the mammalian vermis were established in detail.

A re-study of the afferent fiber tracts of the bird cerebellum, by standard neuro-anatomical methods was undertaken by the present writer to determine more precisely the pathways to the various subdivisions of the organ. This was followed by exploration by oscillographic methods to determine zones of localization, if they exist as in mammals.

The investigation was suggested by Dr. O. Larsell, under whose direction it has been conducted. The oscillographic experiments were planned and carried out with the guidance and help of Dr. John M. Brookhart. I wish to express my sincere appreciation to these two men for their invaluable advice and supervision, and to Mary Whitlock for her generous assistance in technique.

II REVIEW OF LITERATURE

Present concepts of the morphology of the avian cerebellum have been slowly attained and have followed a more thorough understanding of the organ in other vertebrate classes and especially in mammals. A brief review of the principal contributions leading to present interpretations of the cerebellum in mammals, and a more extensive review of the literature on the anatomy of the avian cerebellum is therefore desirable. This will be followed by a review of the chief contributions to cerebellar physiology in the two vertebrate classes. Since study of the organ with the aid of the cathode-ray oscillograph hitherto has been limited to mammals, it is necessary to review the results obtained by this method on the mammalian cerebellum for comparison with those to be described in birds.

MORPHOLOGY OF MAMMALIAN CEREBELLUM

Kuithan (1895) described a transverse fissure which divides the mammalian cerebellum into anterior and posterior lobes. This fissure was called by Kuithan the sulcus primarius and was regarded to be the

first fissure to appear in the cerebellum of the human embryo. Stroud (1895) called the corresponding fissures in human and cat embryos the furcal sulcus, and also regarded it as the first to appear. This investigator differentiated and named the paraflocculus, as this term has since been used in the mammalian cerebellum, in the cat; he also identified the flocculus in cat and human embryos. Evidently, however, he homologized the paraflocculus of the cat with the accessory flocculus (Nebenfloek of Henle) of human descriptive anatomy.

Elliot Smith ('02, '03a, '03b) studied the adult brains of many animals and concluded that certain fissures were consistently present in all mammals. These he designated as fissura floccularis, fissura parafloccularis, fissura postnodularis, fissura prima (sulcus primarius of Kuitman), and fissura secunda. Smith described and named the fissura floccularis and postnodularis, but he failed to recognize their continuity or their significance in the fundamental division of the cerebellum. He described the fissura prima as the first to appear in the mammalian embryo and as the most important morphologically. The cerebellum, according to Smith, is composed of four basic lobes, which he called anterior, middle, posterior, and floccular. The anterior lobe is delimited from the median lobe by the fissura prima, while the median lobe is divided from the posterior lobe by his fissura secunda. The uvula and nodulus together he called the posterior lobe, and the flocculus and the paraflocculus were grouped into a floccular lobe.

Bradley ('03, '03a, '04) studied the development of the cerebellum in various mammals. He described the cerebellar folia and fissures by a scheme of letters and numbers, designating the folia by the letters

a to e, starting anteriorly, and the major fissures by the numbers I to IV. He recognized the close relationship between the flocculus and the nodulus. Bradley observed that his fissure II, which corresponds to the fissura prima of Elliot Smith, was the second fissure to develop in the rabbit and in the pig. This is in agreement with the more detailed studies of the embryology of the cerebellum by Larsell and Dow ('35) and Larsell ('35, '36, and studies as yet unpublished).

Bolk ('06) made a comprehensive survey of the comparative anatomy of the mammalian cerebellum and divided it into anterior and posterior lobes, which were separated by the fissura prima. He further subdivided the posterior lobe into a lobulus simplex and a lobulus complicatus. The median part of the latter was designated by Bolk as the lobulus medianus posterior, while the lateral part was called lobulus lateralis posterior. He subdivided this into the ansiform lobule, which included crus I and crus II; the paramedian lobule, and the lobulus vermicularis. From his comparative studies, Bolk suggested a topographical localization within the cerebellum. Such localization has been established by neurophysiological methods in recent years, although the arrangement of the functional areas differs considerably from the pattern predicted by Bolk.

Edinger ('10) subdivided the cerebellum into the "palaeocerebellum" or vermis and flocculus, and "neocerebellum", which comprises the rest of the cerebellum and which was regarded by him as the newer portion of the organ from the standpoint of phylogeny.

Ingvar ('16) attempted to subdivide the cerebellum from a functional point of view. He eventually included the terminations of the afferent fiber systems as part of the basis for his subdivisions.

According to his analysis, the cerebellum is composed of three main divisions, which he designated anterior, medial, and posterior lobes, subdivided by the sulcus primarius and the sulcus prepyramidalis respectively. Ingvar thus deviated from the fundamental subdivision of the cerebellum proposed by Elliot Smith. Both of these investigators recognized a medial lobe but Smith defined it as lying between fissura prima and fissura secunda, while Ingvar placed this lobe between fissura prima and the prepyramidal sulcus. The three cerebellar lobes were compared by Ingvar ('18, '28), on the basis of the afferent fiber connections, to a three story house composed of vestibular, spinal, and cerebral floors. This concept included not only the evolution of the cerebellum from the functional point of view, but also functional localization within the organ.

Langelaan ('19) described the development of the lobules of the cerebellum in the human embryo and pointed out the continuity between the vermian segments and the hemispherical lobules. He designated Elliot Smith's fissura prima by the term superior anterior fissure of descriptive human anatomy. This investigator divided the human cerebellum into 10 lobes each of which included a medial, or vermian, and a lateral portion.

Riley ('29) made an extensive study of a large series of adult mammals and in general agreed with Bolk in the classification of cerebellar lobes, lobules and fissures. Following Bolk he divided the organ into two lobes, the anterior and the posterior, delimited from each other by the fissura prima. He noted a definite relationship between the degree of development of the cerebellar hemispheres and that of the cerebral cortex. Dow ('42) has published a comprehensive review of the

evolutionary development of the cerebellum. It is only necessary, therefore, in this summary of the literature on cerebellar morphology to point out the principal steps leading to our present concepts of its structural pattern.

The fundamental pattern was set forth in Larsell's penetrating review and interpretation of this organ which appeared in 1937. This interpretation was based on an extensive background of meticulous study of the comparative anatomy of the cerebellum of lower vertebrates and primitive mammals (Larsell, '20, '26, '31, '32, '32a, '35, '36, '36a; Larsell and Dow, '35) and clearly defined for the first time its fundamental subdivisions. These had been designated by Larsell ('34) as the flocculonodular lobe and the corpus cerebelli, the boundary between them being the posterolateral fissure. In the same interpretative paper, Larsell also pointed out that the floccular lobe of Elliot Smith, consisting of paraflocculus and flocculus, is not a morphological entity, the paraflocculus belonging to the corpus cerebelli and the flocculus to the flocculonodular lobe. On the grounds of the development of these two lobules, phylogenetically and ontogenetically, it was shown that they are unrelated, save topographically. Their close juxtaposition in most adult mammals, and their apparently common peduncle in many species are the result of secondary growth factors. In his 1937 paper Larsell pointed out that the posterolateral fissure is the first to appear phylogenetically and that the flocculonodular lobe is intimately related to the vestibular apparatus and is phylogenetically the oldest portion of the cerebellum. The corpus cerebelli is the portion of the cerebellum developing rostrally and medially to the posterolateral fissure. It is subdivided by Larsell into an anterior and a posterior lobe, which are

separated by the fissura prima of Elliot Smith. While the anterior lobe and the pyramis and uvula of the posterior lobe undergo little change in most vertebrate species, the anterior folia of Larsell's posterior lobe, which correspond to Ingvar's median lobe, undergo a marked increase in size in the higher vertebrates. This is particularly true of the lateral extension of this part of the cerebellum. These lateral parts or hemispheres constitute the phylogenetically youngest divisions of the cerebellum, and were therefore designated by Edinger ('04) as the neocerebellum. In the developing human cerebellum the patterns found in the lower vertebrates and in the more primitive mammals are repeated (Larsell, '47). Edinger's concept of paleocerebellum and neocerebellum has been modified as a result of Larsell's investigations. According to his most recent definition of these divisions the latter author ('51) holds that the flocculonodular lobe, receiving the primary vestibulo-cerebellar fibers, as was conclusively demonstrated by Dow ('36, '38a, '39), is the archicerebellum. The paleocerebellum is confined to the vermal part of the anterior lobe, the pyramis, the uvula, and the paraflocculus. This latter part receives the spino-cerebellar system (McNally and Horsley, '09) and the dorsal column systems (Brodal, '41) and probably the tecto-cerebellar and trigemino-cerebellar systems. The neocerebellum is that part of the cerebellum which receives the preponderance of ponto-cerebellar projections. The structural plan of the cerebellum, which was laid down by Larsell, favored localization and pointed the way for later physiological experiments.

MORPHOLOGY OF AVIAN CEREBELLUM

The anlage of the bird cerebellum was identified by Mesdag ('09) in the 4-1/2 day chick embryo. Bilateral swellings of the forward part of the rhombencephalon were observed by Ingvar ('18) in the 5 day chick. He considered these enlargements, which had not yet fused across the midline, as an early stage of the cerebellum. Mihalkovics (1877) previously had recognized a similar bilateral origin in human embryos. Ingvar noted in the chick embryo of 9 days 12 hours incubation that the two lateral swellings had fused across the midline, in the roof of the ventricle, to form a flattened helmet.

Larsell ('48) described the paired swellings in the 8 day chick and noted that they fuse at about 9 days. He found a similar sequence in the duck embryo of corresponding stages and in the cormorant embryo of 27 mm. C.R. length. This investigator identified two commissural bands of fibers which cross the midline through the tela choroidea even before fusion of the more massive lateral swellings takes place. One of these bands lies in the rostral part of the cerebellar primordia and is regarded as corresponding to the commissura cerebelli of lower vertebrates. It is composed of ventral spino-cerebellar and trigeminal fibers. A second band of fibers lies along the caudal margin of the cerebellum and occupies a position corresponding to that of the lateral commissure. Thus the two commissures, which are found in the cerebella of lower vertebrates and of mammals, are also present in the avian cerebellum. In 8 day chick embryos, and in the duck at a corresponding stage, the corpus cerebelli, which forms along the commissura cerebelli, is recognizable as two rounded masses, one on either side, which are fused across the midplane, but the plane of fusion is still visible as

a shallow sagittal groove. At this same stage of development the flocculus is clearly recognizable as a lateral projection on each side. The posterolateral fissure, delimiting the flocculus from the corpus cerebelli, is bilaterally represented but has not yet fused medially. At 9-1/2 days, in the chick, this fissure is continuous from side to side so that the two fundamental morphological divisions of the cerebellum, namely the corpus cerebelli and the flocculonodular lobe, are established. The duck embryo shows a similar development (Larsell, '46). The parafloccular component of the suricle of later embryonic stages and of adult birds is not yet present. It is present, however, in the duck embryo of 13 days incubation, having been formed by a lateral extension, on either side, of the caudal portion of the corpus cerebelli.

According to Brouwer ('13), Murphy ('00) found no cerebellar fissures in the 9 day chick embryo, but described as the sulcus primarius a furrow which appears in the posterior area of the cerebellum of the duck embryo of 14-1/2 days, corresponding to the 10-1/2 day chick embryo. He noted the subsequent development of cerebellar furrows during the later growth of the embryo; however he did not attempt to homologize the cerebellar furrows, which he described, with those of the mammalian cerebellum. Brouwer ('13) studied the development of the cerebellum in a series of chick embryos. He also described the absence of transverse fissures in the 10 day embryo but stated that numerous sulci appear on the upper surface of the cerebellum of the 11 day chick. One of the most prominent of these sulci, according to this investigator, extends transversely across the posterior part of the cerebellum between the flocculi. This sulcus, he states, delimits the more poster-

ior lobules and does not correspond to his fissura y of adult birds. Brouwer was unable to homologize any of these fissures in the avian embryo with those of mammals.

Ingvar ('18) described a slight depression in the 9 day chick on each side of the cerebellum as separating the floccular portion of what he called the auricle from the remainder of the cerebellum. This furrow, the medial part of which he designated fissure un in the later embryonic stages, corresponds in part to the posterolateral fissure of Larsell's ('48) terminology. Ingvar confirmed Murphy's finding that no other fissures are present in the cerebellum of the 9 day chick. He noted, however, that in the chick of 9 days and 12 hours incubation three transverse furrows were present. Following the terminology of Brouwer, Ingvar designated these fissures as x, y, and un. Fissura x separated his anterior lobe from his median lobe, and his median and posterior lobes were separated by fissura y. These two furrows were regarded by this author as the principal fissures of the avian cerebellum. Ingvar studied developmental stages of the chick up to 21 days incubation, and described the anterior lobe as becoming eventually subdivided into 4 lobules. In the posterior lobe a fourth transverse fissure appears at 9-1/2 days, according to this author, which he designated as fissura n. It lies between fissura y and fissura un. These fissures subdivide the posterior lobe into three lobules which he called p, n, and n. The portion of the cerebellum lying between fissures x and y, designated by Ingvar as the medial lobe, he described as divided by transverse furrows into 2 lobules.

Larsell ('48) studied the development of the chick cerebellum in 5 to 10 day embryos, thus including the stages of early fissure formation, and compared its development with that of duck and cormorant embryos.

In general his observations confirm those of Ingvar. As already noted, he described the posterolateral fissure between the rounded swellings of the corpus cerebelli and the flocculus, which forms the lateral tip of the cerebellum in the embryo. This fissure is continuous into the lateral surface of the medulla oblongata in the 9 day chick and the 10 day duck. The median portion of Larsell's posterolateral fissure is regarded by this author as corresponding to Ingvar's fissure un.

Shortly after the appearance of the posterolateral fissure a second fissure develops on the surface of the anterior part of the cerebellum. This furrow Larsell designates as fissura prima and regards as corresponding to fissure x of Brouwer and of Ingvar. In the 11 day duck embryo, and in the corresponding stage of the chick embryo, two grooves appear in the posterior lobe between the fissura prima and the posterolateral fissure. These are regarded as corresponding to Ingvar's fissures y and z, and Larsell labels them prepyramidal fissure and fissura secunda, respectively. In the duck embryo of 11-1/2 days and in the 65 mm cormorant embryo two more furrows are present. One of these, located caudal to fissura secunda, Larsell designates as uvular sulcus 1, and regards as corresponding to Ingvar's fissure z, as labelled in the figures of the latter author representing the adult bird cerebellum, but not to his fissure z in the embryonic chick. The second furrow appears in the duck embryo at about 18 days, between the fissura secunda and uvular sulcus 1. This is called by Larsell uvular sulcus 2. A third furrow between uvular sulcus 1 and the posterolateral fissure appears at 20 days incubation in the duck and is designated by Larsell as uvular sulcus 3. In addition to fissura secunda, prepyramidal fissure, and uvular sulci 1, 2, and 3, a shallow furrow appears anterior to the

prepyramidal fissure. This is designated as the posterior superior fissure. In the later stages the portion of the cerebellum between the fissura prima and the posterior superior fissure is subdivided into three secondary folia. The anterior lobe of the 13 day duck embryo shows three transverse grooves which divide it into four main folia. The second furrow below the fissura prima is labelled by this investigator as the preculminate fissure. He states that the cerebellar fissures subdivide the organ in the embryo into 10 primary folia. For convenience of description, he labels these I to X, beginning anteriorly. Thus the pattern of the adult cerebellum is definitely established in the later stages of the development of the bird embryo.

The cerebellum of the adult bird was described by Turner (1891), who dealt primarily with the external form of the organ and touched only briefly on the sulci and folia. He noted the flocculus, describing it as an extension projecting laterally from the basal portion of the cerebellum, and that it is almost completely imbedded in a special cavity of the skull. Brandis (1894) studied the cerebella of 209 species of birds. He described the deep nuclei, the fiber tract connections, and the arbor vitae. For descriptive purposes he divided the folia into ventral and dorsal groups and numbered the folia anteriorly and posteriorly from a centrally placed dorsal folium, which he called the "spitzen ast." The number of folia, according to Brandis, increases in relation to the size of the species. Following the grouping of Brandis, Friedländer (1898) partitioned the bird cerebellum into an upper and ^alower vermis. Conolly (1910), according to Edinger (1910), noted that the superior surface is subdivided into lobules by numerous transverse furrows. Edinger stated that the two most caudal lobules extend laterally to form a projection

which he calls eminentia lateralis. This corresponds to the auricle of other students of the bird cerebellum. Edinger further described absence of pontocerebellar fibers and concluded that the avian cerebellum corresponds to the paleocerebellum of mammals.

Subdivision of the cerebellum of the adult bird into lobes was first attempted by Murphy ('00). He divided it into three lobes, the lingula and the four principal folia dorsal to it constituting the anterior lobe; the next 4 major folia forming the dorsal lobe; and the 3 caudal folia, including the nodulus, composing the posterior lobe. Frenkel ('09) considered the cerebellum of the pigeon to be subdivided by fissures into nine folia. The 4 folia anterior to fissure x of Brouwer and of Ingvar were designated as the anterior lobe and the remaining 5 were grouped together as the posterior vermis.

Shimazono ('12) described the cerebellum of the bird as divided into a large middle portion, the vermis, and two lateral extensions which he designated the lateral lobules. He further subdivided the vermis into posterior and anterior halves, according to their position with reference to the cerebellar ventricle. He called the caudal half the vermis posterior, and the anterior half the vermis anterior.

Brouwer ('13), after studying the cerebella of 25 species of birds in the adult stage, noted that the larger birds have more folia than the smaller species and, further, that birds which fly well have a larger cerebellum than the poor flyers. He subdivided the cerebellum into three parts which he called pars anterior, pars media, and pars posterior, and designated the boundaries between these divisions as fissures x and y respectively. The pars anterior, in 16 of the 25 species, was described by him as composed of four lobules. Brouwer's

figures indicate that his pars posterior consists of 3 constant lobules. The pars media, lying between fissures x and y, shows considerable variation from species to species. This investigator did not attempt to designate specific lobules of the avian cerebellum as associated with the muscle groups of various parts of the body, as Bolk ('06) had done in mammals.

Ingvar ('18) after study of the cerebellum of 43 species of adult birds divided the organ into three lobes which he called the lobulus anterior, lobulus medius, and lobulus posterior. Following Brouwer's terminology for the furrows, Ingvar separated the anterior and the medial lobe by fissura x, and the medial from the posterior lobe by fissura y. He agreed with Brouwer's observation that his anterior lobe, which corresponds to the pars anterior of Brouwer, is the most constant in its structure. Both of these authors recognized four lamellas in the anterior lobe of the adult bird. The medial lobe of Ingvar was described as composed of three principal lobules, the anterior and the posterior of these being divided into two subfolia. Similarly, the posterior lobe is composed of three primary lobules, which are more strongly developed than those of either the anterior or medial lobes. He describes lateral extensions of these three lobules as forming the flocculi. According to Ingvar his anterior and posterior lobes remain relatively constant but the medial lobe varies considerably with the size of the animal's body.

The interpretations of Brouwer and of Ingvar were accepted, in general, by Ariens Kappers ('21), who added his own observations of the cerebellum of a newly hatched ostrich. Kappers, Huber and Crosby ('36) also describe the adult avian cerebellum in terms of Ingvar's and Brouwer's interpretations and note that a deep branched fissure separates

the pyramidal portion of Ingvar's posterior lobe from the remainder of the cerebellum. In his latest book Ariens Kappers ('47) reviews the development and subdivision of the avian cerebellum and here also bases his description on Brouwer and Ingvar.

A small lateral hemisphere in the bird cerebellum was described by Jelgersma (1889). Brouwer ('13), as well as Turner (1891) and Brandis (1894), was unable to demonstrate this structure. A rudimentary lateral hemisphere also was described by S. Ramon Cajal ('11) but, as Larsell ('48) points out, Cajal's figure 86 indicates that he was describing the flocculus. Larsell noted that the anterior basal aspect of the avian cerebellum consists of unfoliated cortex which he considered as corresponding to the substrate from which the lateral hemispheres develop in mammals.

As already stated Larsell ('48) divides the avian cerebellum into flocculonodular lobe and corpus cerebelli, these 2 fundamental divisions corresponding to those similarly named in all other classes of vertebrates. The corpus cerebelli is further subdivided into anterior and posterior lobes by the fissura prima. This fissure frequently is difficult to identify in the adult bird, but on the basis of embryonic development of the cerebellum in several species he established it and its relations with certainty. The fissura prima, as a result, can be identified with assurance in the adult cerebellum. The medial portion of the bird cerebellum, which corresponds to the vermis of mammals, consists, according to this author, of 10 primary folia, including the nodulus of the flocculonodular lobe. These folia he numbers I to X, beginning anteriorly. Each receives a primary medullary ray. Folia I to V constitute the anterior lobe and folia VI to IX form the posterior lobe of

the corpus cerebelli. Folium X is the nodulus of the flocculonodular lobe. Larsell regards folium I as corresponding to the lingua of mammals and, accordingly, names the furrow between it and folium II the precentral fissure. Folia II and III correspond to the mammalian central lobule, and folia IV and V he regards as corresponding to the culmen. Folium IV, according to this author, is subdivided into two secondary folia in some avian species, which he labels folia IVa and IVb, while folium V shows a secondary subdivision in many species. Folium VI he regards as corresponding to the declive of the mammalian cerebellum. It may show two or three subfolia which he designates folia VIa, VIb and VIc. Folium VII which is delimited from folium VI by the posterior superior fissure, may also be subdivided in some birds into secondary folia ^{VIIc} VIIa and ^{VIIb} VIIb. It corresponds to the combined folium-vermis and tuber vermis of mammals. Folium VIII, which is separated from VII by the prepyramidal fissure, is considered as the homologue of the pyramis. It is subdivided in some species. Posterior to this lies folium IX, the uvula, the fissura secunda delimiting it from folium VIII. Uvular sulci 1 and 2 subdivide folium IX into subfolia IXa, IXb, and IXc. Folium X, separated from folium IX by the posterolateral fissure, is the nodulus as already indicated.

Larsell studied in detail the subdivisions of the cerebellum of the duck, chicken, grouse, pigeon, humming bird, and eagle. The pigeon cerebellum was selected by him as typical of the avian cerebellum because it is well developed in respect to its primary folia and fissures, it has prominent auricles, and yet retains a relatively simple form and pattern. The 10 primary folia and many of the above mentioned secondary folia can be readily identified in this species.

The cerebella of certain species of adult birds that exhibit specialized functional activity were also closely compared by this investigator. The humming bird and the eagle were selected as examples of strong fliers, although their methods of flying vary from the swift darting and hovering ability of the humming bird, to the strong, soaring flight of the eagle. He also noted that the humming bird has very small legs, while the eagle has very powerful talons. In comparing the cerebella of these two birds, Larsell noted that both the humming bird and the eagle have a well developed folium I. Considering this in the light of the studies of Nulsen, Black and Drake ('48) on mammals, he suggests that this lobule is concerned with the muscles of the tail feathers, which are extremely important in flight. Folia II and III are almost lacking in the humming bird while they are very large and subfoliated in the eagle. Larsell regards these facts as suggesting that the two lobules named are concerned with the functions of the legs. Folia IV, V, and VI vary with the flying ability of the species. These folia are well developed in the eagle and the humming bird. The large size of folium VI, the declive, in the duck, which has a large trigeminal nerve as compared with that of the gallinaceous bird, suggested to Larsell that this folium may receive trigeminal nerve fibers also. Folium VII was suggested as concerned with auditory function, as has been demonstrated for the corresponding region in mammals (Snider and Stowell, '44). Folium VIII is subdivided in the duck and the eagle, whose relatively large body surfaces must receive a considerable amount of stimulation. Although the paramedian lobule of mammals is not represented as such in birds, it is possible that the enlargement of folium VIII, which results in subfoliation in these and other species, is in part related to increased

somatic stimulation. Unpublished investigations by Larsell on the development of the paramedian lobule in mammalian embryos demonstrate that part of it is derived from the corresponding lobule of the vermis. Since Snider and Stowell ('44) have shown that visual and auditory stimuli also activate the corresponding cerebellar region of mammals, enlargement of folium VIII in some species of birds may represent increased importance of these systems. Lobulus IX was observed by Larsell to be relatively large in all birds. He suggests that this lobule, which receives spino-cerebellar, secondary vestibular and probably other fibers plays a role in coordinating the impulses carried by these tracts in such a manner that maintenance of equilibrium is served in flight, walking or swimming. Lobulus X, because of its connections, is considered entirely vestibular.

The auricle of birds has been interpreted in various ways by different investigators. Edinger ('10), who regarded this structure as formed by the lateral extensions of the two caudal cerebellar folia, called it the eminentia lateralis. Ingvar ('18) described the auricle and stated that all three folia of his posterior lobe extend laterally to take part in its formation. He recognized the avian paraflocculus as part of the auricle and held that it is morphologically related to the flocculus. Scholten ('46) considers the paraflocculus of mammals as part of the phylogenetically newer lobules of the cerebellum. Since he regards these as absent in birds he concludes that the bird has no paraflocculus, but notes that the pyramis and the uvula may extend into part of the auricle. In discussing the auricle of the avian cerebellum, Larsell, after study of closely graded embryos of the duck and chick, and detailed comparison with the adult cerebellum, states that the avian

auricle is composed of the lateral extensions of folia IXc and X. He considers the lateral extension of IXc as paraflocculus and that of X as flocculus, the two being separated by a faint lateral continuation of the posterolateral fissure.

With reference to the fissures of the avian cerebellum, Brouwer ('13), as already pointed out, designated as fissure x the furrow between his pars anterior and pars medialis, and as fissure y that between pars medialis and pars posterior. Ingvar ('18) considered Brouwer's fissura x as corresponding to the fissura prima of Elliot Smith ('02) in mammals, although he did not so label it in his figures, using instead Brouwer's designation, fissure x. In his text Ingvar also constantly refers to it as fissure x, pointing out the homology with the mammalian fissura prima in a footnote. Kappers, Huber and Crosby⁽¹³⁶⁾ agree with Ingvar with respect to this homology, as does Larsell. According to the latter author, as already pointed out, this fissure divides the corpus cerebelli into anterior and posterior lobes, while Ingvar regards it as the boundary between his anterior lobe, which corresponds to that of Larsell, and his medial lobe. Larsell does not recognize a medial lobe, his posterior lobe of the corpus cerebelli constituting all of the cerebellum between fissura prima and posterolateral fissure, previously described. Brouwer's fissura y was referred to by Ingvar as homologous to the fissura secunda of mammals, although in many of his figures he designated the prepyramidal fissure as y, and fissura z as fissura secunda. Larsell agrees that the fissures designated y and z in Ingvar's figure 16 and 17 are homologous with the prepyramidal fissure and fissura secunda, respectively, of mammals.

The remaining fissures of the bird cerebellum had not been

designated by name prior to Larsell's investigation. He labels the fissure separating his folium I, the lingula, from folium II, the lower part of the central lobule, as the precentral fissure, as in the mammalian cerebellum. His preculminate fissure, between folia III and IV, is also homologous to the fissure of the same name in mammals. He regards the fissure between folium VI, the declive, and folium VII, the tuber folium, as homologous to the posterior superior fissure of mammals, using the same name in the bird cerebellum. Folium VII, the folium-tuber vermis lobule, and VIII, the pyramis, are separated by fissura prepyramidalis. Between the pyramis, VIII, and the uvula, IX, lies the fissura secunda, and between IX and X, the nodulus, lies the posterolateral fissure. The furrows between the subfolia of VI and IX are named declival sulcus 1, declival sulcus 2, uvular sulcus 1, uvular sulcus 2, and uvular sulcus 3, respectively, according to the order in which they make their appearance in chick and duck embryos.

SUMMARY OF CEREBELLAR MORPHOLOGY

In summary, Larsell's analysis of the avian cerebellum demonstrates that the flocculonodular lobe and the corpus cerebelli are homologous to the divisions so designated by him in all other classes of vertebrates in which the cerebellum is sufficiently elaborated to show this fundamental subdivision. These include all of the major divisions of the vertebrate phylum except the myxinooids, in which the cerebellum is very rudimentary (Larsell, '47a).

The flocculonodular lobe has the same fundamental relations as the auricular lobe in lower vertebrates. Expansion of cerebellar

cortex along the medial region of the lateral commissure has resulted in birds in folium X, the nodulus, not found in lower vertebrates. The change in designation of the auricular lobe of lower vertebrates to the flocculonodular lobe, therefore, is appropriate in the avian cerebellum.

The so-called auricle of birds includes not only the flocculus, which is the homologue of the auricle of amphibians, fishes and reptiles, but also a lateral growth of folium IX of the corpus cerebelli, the avian paraflocculus.

The corpus cerebelli, divided into anterior and posterior lobes, is homologous to that of reptiles and of mammals, in which class the lateral hemispheres are added. The substrate of the hemispheres is present in birds as the unfoliated cortex, described by Larsell, at the basal margin of the corpus cerebelli.

The folia and fissures of the avian cerebellum have been shown to be homologous, in detail, to the lobules and fissures of the mammalian vermis. A basis for close comparison of the results of experimentation on the avian cerebellum with those obtained from mammalian experimental work is thus established.

HISTOLOGICAL STRUCTURE AND FIBER TRACTS

Histology of bird cerebellum

In his discussion of the histology of the cerebellum of the bird S. Ramon y Cajal ('11) noted that the cortex of the avian cerebellum exhibits the three classical layers which are characteristically found in all but the lowest forms of vertebrates, namely, molecular, Purkinje cell, and the granular. He described the branching character of the Purkinje

cells in the bird and recognized the numerous collaterals which arise from the axons of these cells. P. Ramon y Cajal (1890) compared the number of collaterals of axons of the Purkinje cells in various animals, including the bird. The basket cells of the avian cerebellum, according to S. Ramon y Cajal, are very numerous and are arranged in a fashion similar to that found in the mammalian cerebellum. The granular layer is thick in the bird and, according to Cajal, the stellate cells are similar in number and disposition to those of mammals. The terminal branches of the granule cell dendrites, however, are formed by finer, shorter and fewer fibers than in mammals. The number, form and connections of the mossy fibers also are similar in general to those of mammals, but they are less complex and less numerous. Climbing fibers were also observed by Cajal in birds. Craigie ('26) described the claw-like terminations along the mossy fiber and noted that each one may synapse with the dendrites of several granule cells. Kappers, Huber and Crosby ('36) describe the great prominence of the granular layer, and the especially rich branching of dendrites of the Purkinje cells. Löwenberg ('38, '39) described "synarmotique" cells and Golgi cells in this layer.

The neuroglia of the bird cerebellum was described by S. Ramon y Cajal ('11) as similar to that of mammals.

In general the histology of the avian cerebellum is not unlike that of mammals, the principal points of difference consisting in thicker terminal dendrites and less numerous collaterals of the Purkinje cell axons; a greater development of the terminations of the basket cells; shorter, finer dendrites of the granule cell; and less complicated and fewer mossy fibers in birds.

Cerebellar nuclei

The deep nuclei of the bird cerebellum have been described in detail by Ramon y Cajal ('11). He recognized four major nuclear groups within the cerebellum, namely, the nucleus tecti, or internal nucleus; the nucleus intercalatus; the nucleus intermedius; and the nucleus lateralis. Van Hoëvell ('16) studied the cerebellar nuclei in birds and noted that the medial nucleus is composed of a large celled portion which he called the pars magnocellularis, and a small celled portion, the pars parvocellularis. Bartels ('25) attempted to classify the cerebellar nuclei of birds in relation to the singing activity of various species. Craigie ('28) observed similar nuclear groups in the cerebellum of the humming bird; however, he was unable to identify the superior part of Cajal's lateral nucleus in this species. Sanders ('29) adopted the terminology of Cajal. She described a lateral cerebellar nucleus, which is ordinarily divided into a superior and an inferior part; an internal nucleus, or nucleus fastigii of Craigie; and an intercalary nucleus. Kappers, Huber and Crosby ('36) state that in the sparrow the cerebellar gray is one continuous mass which shows regional thickenings and undulations. This regional variation serves to increase the surface area of the nuclear mass and permits more definite localization of the afferent and the efferent paths. They noted, as did Van Hoëvell ('16), that this common nuclear mass connects with the brain stem. Doty ('46) describes various subdivisions of the four nuclei and concludes that they are continuous, and that their development is related to some extent to that of the inferior olive. Kappers ('47) restated his conclusions that these nuclei are

divided into a median and a lateral group, which are the homologues of the nucleus fastigii and of the nucleus dentatus of mammals, respectively.

Fiber tracts

The afferent fiber systems of the avian cerebellum have been the subject of considerable investigation. The spino-cerebellar tracts were first described in the bird by Friedländer (1898). Since this original observation many investigators have confirmed their presence (Frenkel, '09; Shimazono, '12; Ingvar, '13; Sanders, '29). The spino-cerebellar system is extremely large in birds and, according to the investigations of Friedländer (1898) and Ingvar ('13), arises from the upper lumbar region of the spinal cord. It is divided into a dorsal spino-cerebellar tract and a ventral spino-cerebellar tract. Both tracts were described as carrying crossed and uncrossed fibers, the decussation of the anterior tract occurring at the cerebellar commissure (Kappers, Huber and Crosby, '36), and around the cerebellar nuclei (Sanders, '29). Ingvar ('13) studied intensively the terminations of this system in the avian cerebellum. He observed, as did Shimazono ('12) and Kuhn and Trendelenburg ('11), that the major proportion of the fibers end in the anterior part of the cerebellum. A small contribution extends into the anterior folia of Ingvar's medial lobe, and into the pyramis and uvula of his posterior lobe. The termination of these tracts was considered to be in the Purkinje cell layer of the cerebellar cortex. Some fibers, according to Sanders, pass to the central nuclei of the cerebellum.

The vestibulo-cerebellar connections are summarized by Wallenberg ('00). He noted the presence of direct vestibulo-cerebellar fibers

to the cortex and to the central nuclei of both sides. These fibers probably correspond to Edinger's "directe sensorische Kleinhirnbahn des acusticus". Ramon y Cajal ('08a) described similar direct vestibular fibers, as did Sanders ('29). Ariëns Kappers ('47), following the descriptions of these authors and of Ingvar ('18) and Schepman ('18), states that these fibers terminate in the medial cerebellar nucleus and, probably, in the uvula, the nodulus, and the flocculus.

The secondary connections between the vestibular nuclei have been described by many authors. Shimazono ('12) described fibers from the internal vestibular nucleus to the flocculus. Sanders ('29) observed connections between the ventrolateral vestibular nucleus and the cerebellum, and traced fibers from the superior vestibular nucleus to the inferior cerebellar nucleus. Ramon y Cajal ('08) and Groebbels ('27) described similar connections.

A few investigators have described connections between the cochlear nuclei and the cerebellum. Bok ('15) indicated a cochleo-cerebellar tract to the lateral cerebellar nucleus. Mesdag ('09) considered as present connections from the cerebellum to the laminar nucleus. Sanders ('29) described both lamino-cerebellar (or cerebello-laminar) and cerebello-cochlear tracts. Stotler ('51) demonstrated that the laminar nucleus of birds corresponds in morphology and in its connections to the medial accessory olive. This suggests that if the distribution of the secondary auditory pathways of birds corresponds to mammals no such condition should be present.

Trigemino-cerebellar connections in the avian cerebellum were described by Biondi ('13), who, according to Craigie ('28), observed fibers extending from the superior sensory nucleus of V to the homolat-

eral aspect of the cerebellum. Craigie describes a homologous pathway in the humming bird. The degeneration experiments of Wallenberg ('04) indicated that some fibers of the mesencephalic root of V, in the dove, enter the cerebellum and end in the medial cerebellar nucleus. Sanders ('29) and Woodburne ('36) described direct sensory root fibers of the trigeminus in the bird cerebellum and also a large secondary trigemino-cerebellar component, crossed and uncrossed, which arises from the superior sensory trigeminal nucleus. Woodburne noted, in addition, that some commissural fibers from the superior sensory nucleus pass across the cerebellum in the region of the lingula. Larzell ('48) mentioned similar fibers in the duck embryo. Ariens Kappers ('47) stated that fibers arise from a trigemino-cerebellar nucleus in birds which is separated from the superior sensory nucleus, and are distributed to the anterior lobe. A group of cells lying dorsomedial to the main mass of the superior sensory Vth nucleus was also described in the opossum by Larzell ('35) as contributing fibers to the commissura cerebelli. In his paper of 1937 this author designates this cell group as the nucleus commissura cerebelli.

The tecto-cerebellar tract has been observed in birds by Munzer and Wiener (1898). It was later described by Wallenberg ('00). Frenkel ('09) observed that this tract degenerates after injury to the medial wall of the optic tectum. Sanders ('29) noted that some of these fibers enter the anterior medullary velum and decussate, while others pass to the cerebellum of the same side. Kappers, Huber and Crosby ('36) agree with Sanders and suggest that these fibers terminate in the medial and caudal portion of the cerebellum, an observation previously made by Shimazono ('12). Ariens Kappers ('47) indicates a similar course for

this tract, as shown in his figure 116. Craigie ('28) noted fibers which arise from the semilunar nucleus of the tectum which he designated the semilunar-cerebellar tract. According to Sanders ('29) these accompany the tecto-cerebellar tract.

The olivo-cerebellar connections were first demonstrated by Yoshimura ('10), who extirpated part of the cerebellum and noted degeneration in the contralateral olive. Kooy ('16) described the structure of this nucleus in birds and confirmed its connection with the cerebellum. Ariens Kappers ('47) states that this tract passes to all parts of the vermis.

Ponto-cerebellar fibers have been the subject of considerable debate. Most authors state that ponto-cerebellar connections, as such, do not exist in the bird. Shimazono ('12), however, believed that an afferent tract from a primitive pons to the cerebellum is present. Papez ('29) also considered such a possibility, as did Craigie ('30). Recently, Brodal, Kristiansen and Jansen ('50) have conclusively demonstrated a primitive ponto-cerebellar connection in birds and emphasize the morphological similarity of the cell masses in which the fibers arise to the external arcuate nucleus of mammals. They note that the majority of fibers from these nuclei pass to the lateral parts of folia VI-VIII of Larsell's ('48) terminology, as well as to the unfoliated cortex and the paraflocculus. These authors conclude that the unfoliated cortex and, in addition, the lateral parts of folium V, VI, VII, and VIII, represent the avian homologue of the mammalian cerebellar hemispheres.

An afferent tract to the cerebellum from the striatal region of the fore-brain of birds has been described by Schroeder ('11), Craigie ('28), and Huber and Crosby ('29). This strio-cerebellar tract

arises, according to these authors, from the paleostriatum and enters the cerebellum.

The efferent tracts of the cerebellum include the cerebello-bulbar and spinal tracts, which according to Ramon y Cajal ('08a), Shimazono ('12) and others, arise in the medial cerebellar nucleus. Kappers, Huber and Crosby ('36) noted, as did the aforementioned authors, that these fibers pass to the medulla oblongata and to the spinal cord. They consider them comparable to the bundle of Russell of the mammalian cerebellum. These tracts are closely associated with the inferior cerebello-reticular tract of Sanders ('29).

The cerebello-motor tract has been described by many investigators (Frenkel, '09; Wallenberg, '00; Kappers, '21; Groebbels, '27, '28). The efferent tracts arise from all the cerebellar nuclei. Kappers, Huber and Crosby ('36) have suggested that the largest contribution is from the medial nucleus of the cerebellum. The fibers from this nucleus have been described as distributed to the Vth nucleus, the vestibular nuclei, the motor Vth nucleus, the homolateral and contralateral medial longitudinal fasciculus, and to the motor centers of the spinal cord.

The brachium conjunctum arises solely from the lateral nucleus of the cerebellum, according to Kappers, Huber and Crosby ('36). Ariens Kappers ('47), however, noted that this tract arises from both the medial and the lateral cerebellar nuclei. Wallenberg (1898) and Frenkel ('09) described some of the fibers of this system as extending to the nucleus of the ^{IIIrd} nerve. In general, however, most authors agree that the tract ends, after decussating, in the red nucleus. Frenkel, according to Ariens Kappers ('47), described some of the fibers as ending in the lateral tegmental nucleus.

FUNCTIONAL LOCALIZATION IN THE CEREBELLUM

Mammals

Sherrington ('06) in his discussion of the physiological dominance of the brain describes the cerebellum as "the head ganglion of the proprioceptive system." This unitarian concept of cerebellar function dominated theories of cerebellar physiology for a generation.

In 1939 Dow, while studying the afferent fiber connections to the cerebellum by electrophysiological techniques, noted that stimulation of a purely cutaneous nerve, the saphenous, induced action potentials in the anterior lobe of the cerebellum. This was the first demonstration of an exteroceptive sensory representation in the organ. Dow and Anderson ('42) and Snider and Stowell ('42), working independently, presented preliminary reports of evidence of sensation other than proprioceptive in the cerebellum. In a more extensive paper ('42a) Dow and Anderson noted activity in the culmen and the pyramis of the cerebellum of the rat in response to stimulation of various proprioceptors and exteroceptors, while Snider and Stowell^{had} described the occurrence of responses in the cerebellum induced by tactile stimuli to vibrissae and foot-pads. The latter investigators noted that these responses were maximal in the anterior lobe and in the paramedian lobule, and that there was evidence of somatotopic arrangement of these action potentials within these cerebellar areas. Adrian ('43) mapped similar areas in the cerebellum by stimulation of tactile end-organs. These findings were considerably amplified in 1944 by Snider and Stowell. They noted not only evidence of tactile representation, but also demonstrated the presence of auditory and visual receiving areas in the cerebellum. Snider and Stowell concluded that cerebellar function must

therefore be influenced by tactile, auditory, and visual stimuli, as well as by impulses from the proprioceptors and the cerebral cortex. These papers served to point out, as had been predicted by Bolk ('06), Van Rijnberk ('26) and by Larsell ('37), that localization existed within the cerebellum, and broadened the concept of cerebellar function.

In an attempt to determine specific functional areas of the cerebellum re-investigations of the relationships between the cerebellum and cerebrum were undertaken. An excellent anatomical study by Brodal and Jansen ('46) on ponto-cerebellar connections appeared to confirm the experimental anatomical finding of Sunderland ('40) that no point to point relationship between cerebellum and cerebral cortex exists. These observations were in harmony with the physiological results of Dow ('39, '42) and Curtis ('40). Curtis, using cats, concluded from oscillographic studies that no region of the neocerebellum can be said to be related to any specific region of the cerebral cortex. Dow, in the cat and in the monkey, found no point to point relationship between the subdivisions of the cerebral cortex and the cerebellum, but demonstrated that a higher percentage of responses was obtained in certain areas of the cerebellum by stimulation of cerebral area 4.

Adrian ('43) described a pattern of ponto-cerebellar projections, as a result of electrical stimulation of area 4 of the cortex, which corresponds to areas that he and others had earlier considered as responding to peripheral stimulation. Snider and Eldred ('48) and Hampson ('49) have demonstrated that similar connections exist between the primary tactile, auditory and visual sensory areas of the cerebrum and the areas

of the cerebellum which had previously been demonstrated as associated with these modalities of sensation. As Snider ('50) points out, it is tempting to speculate on the function of these dual systems. They probably act as a "check and balance" mechanism between the cerebellum and the cerebrum.

The efferent systems of the cerebellum have also been subjected to considerable study by physiological methods in the past two decades. Denny-Brown, Eccles and Liddell ('28) noted that stimulation of the anterior lobe excites or inhibits muscle tone. Moruzzi ('36, '41) analyzed intensively the action of the anterior lobe on postural tone and on movements induced by stimulation of the cerebral cortex. Jansen and Brodal ('42) demonstrated projection of specific areas of the cerebellar cortex to discrete portions of the deep nuclei. Nilsen and Nilsen ('47), Nilsen, Black and Drake ('48), and Snider, McCulloch and Magoun ('49) mapped these "motor" areas of the cerebellum and found that they were almost identical in their location to those described for tactile, auditory, and visual reception.

Hampson, Harrison, and Woolsey ('46) stimulated the anterior lobe, the lobulus simplex, and the paramedian lobules in decerebrated animals. Overt movements resulting from stimulation of the cerebellar areas, were produced in the various parts of the body. These cerebellar areas were found to be somatotopically arranged and co-extensive with the areas described by Snider and Stowell for exteroceptive reception.

Hare, Magoun and Ranson ('36), Clark ('39), and Chambers ('47) studied the cerebellar cortex and the deep cerebellar nuclei and their effect on facilitation and inhibition, and analyzed the mechanisms of cerebellar rebound phenomena. Walker ('38) noted changes in the elec-

trical activity of area 4 after stimulation of the lateral aspects of the rostral lobules of the posterior lobe of the corpus cerebelli. Henneman, Cooke and Snider ('46) demonstrated that, in general, the anterior lobe, the lobulus simplex and the paramedian lobules project to sensory-motor areas of the cerebral cortex. Likewise, the "audio-visual" area of the cerebellar cortex projects to the primary auditory and to most of the visual cerebral cortex.

Thus there is a cerebro-cerebello-cerebral circuit between functionally related areas of these 2 divisions of the brain. As Snider ('50) has pointed out this can act as a self-regulating feed-back mechanism that can add or subtract from the total effect of incoming afferent volleys from different functional areas. According to Snider, the cerebellum is the "great modulator of neurologic function".

The concepts of cerebellar autonomic function are still very vague. Moruzzi ('40, '50) has shown that stimulation of the anterior lobe of the cerebellum will inhibit vasomotor and respiratory reflexes mediated by the carotid sinus. Hampson ('49) has noted reflex inhibition of pupillary dilatation induced by stimulation of the sciatic nerve when the lateral hemispheres of the cerebellum were activated. He noted, also, that the eye-fields in the rostral part of the cingulate gyrus of the cerebral hemispheres project to the lateral hemispheres of the cerebellum.

Birds

The function of the avian cerebellum has occupied various investigators since Rolando, in 1809, published the results of his pioneer experiments. Until the last two decades the problem has^{been} attacked

by two principal methods, namely comparative anatomy and extirpation of portions or all of the cerebellum. The method of comparative anatomy of the cerebellum attempted to correlate the degree of development of the organ or its subdivisions, in different species or types of birds with their capacity to perform various functions. The other utilized the experimental method of extirpating portions or all of the cerebellum and observing the effects upon the animal.

Flourens (1824) noted that no sensory loss occurred after damage to the superficial cortex. Magendie (1825) observed postural dysfunction following lesions of the avian cerebellum, as recorded in his "Precis Elementaire de Physiologie." Longet (1842) confirmed the findings of Flourens. Brown-Sequard (1859-61), however, questioned the theories of Flourens. Wagner (1853-60) and Dalton (1861) studied the effect of partial or total cerebellectomy on pigeons. Renzi (1864) noted nystagmus following cerebellar injury. Weir-Mitchell (1869) did a series of extirpations and excitations of the avian cerebellum. He described the disturbances of coordination and balance, resulting from extensive cerebellar destruction and noted that these signs disappeared in time. Lange (1891) obtained similar results in birds. Luciani (1893) described postural disturbances resulting from cerebellar lesions in birds as being homolateral. Brandis (1894) noted, on purely anatomical grounds, that the size of the cerebellum of the bird was related to the functional activity of the species. Shimazono ('12) noted circling movements of pigeons following superficial lesions.

Ten Cate ('27) concluded, on experimental grounds, that control of the tail muscles and limbs is localized in part in Ingvar's posterior lobe, and proposed a principle of localization according to the direction

of the movements. Bremer ('24) discovered that the anterior lobe of a decerebrate pigeon was excitable with a weak electrical current. The response was an inhibition of tonus of the homolateral extensors, with an increase of tonus of the contralateral extensors of all parts of the body. The medial lobe of Ingvar did not show any such effect and was unexcitable. Ingvar ('28) noted, as did Bremer, that the inhibitory areas correspond to the terminations of the spino-cerebellar pathways. Bremer and Ley ('27) stimulated the cerebellar cortex of the anterior lobe of birds and noted modifications of tonus in the musculature. The homolateral extensor muscles exhibited a decrease of tonus, while the contralateral extensor muscles shows increased resistance. The reverse was true when the stimulus was removed. No effect on muscle tone was observed by these investigators when the medial lobe of Ingvar was stimulated. They noted no evidence of segmental localization of this response.

The physiology of the cerebellum, as well as ^{of} the rest of the central nervous system of birds, was reviewed by Ten Cate ('36). His analysis of the function of this organ was based largely upon the results of extirpation and stimulation experiments. Bremer, Dow and Moruzzi ('39), in their physiological analysis of the general cortex in reptiles and birds, noted that movements of the head and eyes could be evoked by stimulation of the forebrain of the pigeon. They did not attempt, however, to determine the effect of cerebellar stimulation on these cortically induced movements. According to these workers the cerebral cortex of the pigeon reacts to illumination of the contralateral eye. This finding is similar to the results obtained from the cerebellum presented in this investigation. Moruzzi ('36, '47) described similar movements induced by electrical or strychnine stimulation of the optic lobe

in the thalamic pigeon. He mentions the relation of the tectal eye field to the cerebral hemispheres and the "bulbopontine" centers, but does not elaborate on this area and its connections with the cerebellum. Zanchetti ('49) described facilitation of movements induced by tectal stimulation in the first three lobules of the median lobe of Ingvar. This effect is less constant than similar results described for stimulation of the anterior lobe in mammals.

In summarizing the earlier studies of the function of the avian cerebellum it should be noted that some of the ablation experiments indicated localization of function within the cerebellum (Ten Gate, '36). However, the pattern suggested by these workers is difficult to compare with present concepts of cerebellar localization and function.

The recent morphological and developmental study of the avian cerebellum by Larsell ('48) indicates that it exhibits a certain pattern of localization which fits into modern concepts of physiological localization in the organ. Larsell suggests that the lingula is associated with the tail muscles. Hulsén, Black and Drake ('48) have noted similar localization in mammals. The central lobule in the bird is apparently related, according to Larsell, to the lower extremity, and the culmen to the upper extremities. This pattern was also found in mammals by Hampson, Harrison, and Woolsey ('46). Larsell suggests that the declive of birds is related in part to the Vth nerve. Tactile responses from the face, which must be mediated by way of this nerve, have been described by several authors in mammals (Adrian, '43; Snider and Stowell, '44). Larsell indicated that the tuber veralis of the bird may be associated with auditory functions and, following Hampson's ('48) demonstration that the mammalian pyramis is associated with the cerebral somatic

sensory area II, that the pyramids of birds may be associated with somatic stimulation. He also suggests that the uvula and the nodulus, together with the paraflocculus and flocculus, function in the control of balance. Since the relation of the flocculonodular lobe of mammals to vestibular centers has been demonstrated electrophysiologically by Dow ('39), Larsell's suggestion regarding the function of this lobe in birds is supported by its fiber tract connections.

III. ANATOMICAL STUDIES OF AFFERENT FIBER TRACTS

A restudy of the afferent fiber systems of the bird cerebellum was undertaken in the hope of augmenting the excellent contributions of Shimazono ('12) and Ingvar ('18) regarding the origins and terminations of the fibers. The intracerebellar distribution of most of the tracts has been obscure, as Brodal, Kristiansen and Jansen ('50) have pointed out. The present investigation places the chief emphasis on the folia of termination of the afferent systems within the cerebellum, and attempts to correlate the terminal distribution with the newer concepts of morphology of the avian cerebellum which have been proposed by Larsell ('48). This author's anatomical investigations formed the fundamental background upon which the physiological aspects of the cerebellum of birds were studied.

MATERIALS AND METHODS

The afferent fiber tracts of the avian cerebellum were studied initially in normal embryonic and adult brains. Observations were made

- 1 sagittal series, young adult bantam, Weigert method
- Humming Bird: 1 transverse series, Cyanolacmus elemanciae, toluidine
blue stain
- 1 transverse series, Cyanolacmus elemanciae, Weil method
- 1 sagittal series, Lampornis sp., cresyl violet stain
- 1 transverse series, Cyanolacmus elemanciae, Weil method
- 1 transverse series, Cyanolacmus elemanciae, cresyl
violet stain
- 1 transverse series, Cyanolacmus elemanciae, cresyl
violet stain
- Pigeon: 1 transverse series, adult, Weigert and neutral red stain
- 1 sagittal series, adult, Weigert and neutral red stain
- 1 sagittal series, adult, pyridine-silver method
- 1 transverse series, adult, Nissl method
- Short-eared owl:
1 transverse series, adult, Weigert method
- 1 transverse series, adult, Nissl method
- Dusky horned owl:
1 transverse series, adult, Weigert method
- 1 transverse series, adult, Nissl method

The afferent fiber tracts were also studied by experimental methods. Lesions were made in various afferent systems. After 7 to 14 days for degeneration of affected fibers, the cerebellum was treated by the Marchi method and serially sectioned for investigation of distribution within it of the respective fiber tracts. A total of 19 adult pigeon's brains were studied by this method. In 8 of this series, lesions of the spinal cord as far caudally as the lower lumbar segments produced

degeneration of the spino-cerebellar tracts. In the 11 remaining pigeons, degeneration of the trigemino-cerebellar, vestibulo-cerebellar, tecto-cerebellar, and olivo-cerebellar tracts was produced after appropriate lesions in the brain stem, and distribution of these tracts into the cerebellar folia was followed. Confirmation of the distribution of the afferent fiber tracts was obtained from cerebella of adult pigeons in which lesions of various folia had been made. Eight of these cerebella were sectioned serially after allowing 7 to 14 days for chromatolysis and were stained with thionin.

Larsell's ('48) terminology is employed in describing the various folia and fissures of the avian cerebellum. The mammalian homologues, as interpreted by him for the various folia, are placed in parenthesis immediately following the numerical designations of the folia.

OBSERVATIONS

Cerebellar commissures

The commissura cerebelli crosses the midplane in the rostral part of the cerebellum. It is easily recognized in 8 to 15 day chick embryos and 10 to 15 day duck embryos. The commissure is composed of a trigeminal bundle and a ventral spino-cerebellar bundle (fig. 1 and 2). The trigeminal contribution comes directly from the trigeminal root and from cells in the region of the trigeminal sensory nuclei. These fibers pass rostrally into the region of the junction of the anterior medullary velum with the cerebellum. Here the trigeminal and ventral spino-cerebellar fibers intermingle and cross the midplane. This observation of a commissura cerebelli in birds confirms the earlier des-

cription of this structure in the avian cerebellum by Larsell ('48). The decussation of spino-cerebellar fibers also was observed in Marchi preparations of the adult pigeon following lesions of the spino-cerebellar system. In the adult animal the decussation occurs in the medullary substance just caudal to folium II and folium III (central lobule) (fig. 5), as also shown in Larsell's figure 5. The ultimate distribution of the fibers of the 2 components of the commissura cerebelli is described under the tracts of which they represent the decussation.

The lateral commissure in duck and chick embryos consists of small, scattered bundles of fibers that cross the midline near the caudal margin of the cerebellum (fig. 1). The fibers composing these bundles arise for the most part from cells of the vestibular nuclei. A small number of fibers also passes into the caudal region of the cerebellum directly from the vestibular root of VIII. The direct and secondary vestibular fibers can be traced into the flocculus and toward the midline, running parallel to the posterolateral fissure. The fibers become less numerous as they approach the midline and appear to terminate in the region bordering on the posterolateral fissure. This commissure was originally described in the cerebellum of birds by Larsell ('48).

Distribution of afferent fiber tracts

The spino-cerebellar tracts are plainly visible in the superficial portion of the lateral white funiculus in the spinal cord of 15 and 20 day duck embryos stained by the silver-gelatin method. The fibers of this system can be traced rostrally in these embryos along the lateral

surface of the medulla oblongata. The dorsal spino-cerebellar tract passes through the rootlets of the VIIIth nerve and curves abruptly upward to enter the cerebellum. The ventral spino-cerebellar tract continues rostrally to the level of the roots of the Vth nerve and then curves upward under the surface of the medulla oblongata to enter the cerebellar peduncle and the cerebellar commissure (fig. 1).

In brains of the adult pigeon, the chicken, the humming bird, the short-eared owl and the dusky horned owl, stained by a variety of silver methods as well as by the Weigert or Weil techniques, a similar course was observed.

The effects of experimental lesions of the spino-cerebellar system in the spinal cords of 8 adult pigeons were studied by means of the standard Marchi technique. Degenerating fibers were found in the superficial zone of the posterior part of the lateral funiculus (fig. 3). They were followed rostrally through the medulla oblongata and into the cerebellar peduncle. From the peduncle the dorsal spino-cerebellar tract passes upward into the cerebellum somewhat caudally to the ventral spino-cerebellar tract (fig. 4). A similar course of the spino-cerebellar system has been described by Ingvar ('18), although he did not subdivide it into dorsal and ventral tracts. This division, however, was recognized previously by Friedländer (1898). In the cerebellum degenerating fibers were found in folia II and III (central lobule), folia IV and V (culmen), and in folium VIa and b (rostral declive), as shown in figure 5. A lesser concentration of degenerating fibers was found in all parts of folium IX (uvula). A few scattered bundles appear in folium VIII (pyramis) (fig. 5). None of the fibers could be followed to the deep nuclei in the preparations studied in the present investigation, although

Sanders ('28) described spino-cerebellar fibers into these structures. It appears from our investigations that the majority of the spino-cerebellar fibers, if not all, terminate in the cortex of the cerebellum.

The trigemino-cerebellar tract in 10 to 15 day duck embryos, and in corresponding stages of the chick embryo, appears as a direct connection of the Vth root with the cerebellar commissure from which it continues into the corpus cerebelli (fig. 1). A similar connection also has been noted in birds by Woodburne ('36). Furthermore, fibers arising from the dorsal region of the superior sensory nucleus of V can be followed into the commissure and into the medullary portion of the cerebellum (fig. 1). This group of fibers corresponds to Sander's ('28) tractus trigemino-cerebellaris dorsalis. The trigeminal connections with the cerebellum were also visible in later embryonic stages (fig. 2) and in adult material which had been stained with silver.

The distribution of the trigemino-cerebellar connections within the cerebellum was investigated by experimental anatomical methods. In three adult pigeons, the superior sensory Vth nucleus, or the region just dorsal to it, was destroyed. In producing these lesions other overlying fiber systems of the cerebellum were unavoidably interrupted and resulting degeneration of these additional fibers partially obscured the exact terminal distribution of the trigemino-cerebellar tract. In all of the lesions, however, degenerating fibers could be traced from the region of the sensory Vth nuclei to folium V (upper culmen), folium VI (declive), and occasionally to folium VII (the folium-tuber vermis lobule). Figures 6 and 7 illustrate the results of typical experiments in which not only were the trigemino-cerebellar pathways cut, but also

the adjacent vestibular connections of the cerebellum were interrupted.

The terminal distribution of the trigeminal tracts, as observed in Marchi material, was confirmed in Nissl preparations of the trigeminal nuclei. Following removal of the dorsal surface of folium VI (declive) and of folium VII (the folium-tuber vermis lobule) in two adult pigeons, cells in the dorsolateral part of the superior sensory nucleus of the trigeminus showed chromatolytic degeneration as illustrated in figure 8. The trigemino-cerebellar tract has been described in reptiles (Larsell, '32). The part of the Vth nucleus which gives rise to fibers to the commissura cerebelli has been designated the nucleus of the commissura cerebelli (Larsell, '37).

Vestibulo-cerebellar tracts were found both in developmental and adult stages. In cerebella of 10 to 15 day old duck embryos and in corresponding stages of chick embryos, stained by the silver-gelatin and Bodian methods, these pathways were followed into the caudal portions of the cerebellum (fig. 1). The fibers arise from the VIIIth nerve root and from the vestibular nuclei. Direct and secondary vestibular fibers form the lateral commissure already described. Most of the fibers end in the cerebellar cortex adjacent to the posterolateral fissure but both direct and secondary vestibular fibers appear to enter the deep cerebellar nuclei in the embryonic material.

The adult avian cerebellum has similar vestibular pathways. They are sometimes difficult to differentiate from other tracts in the mature bird because of increased concentration of other fibers that also pass through the region of the vestibular nuclei.

In an attempt to clarify the intracerebellar distribution of the vestibulo-cerebellar tracts, lesions of the VIIIth nerve and the

vestibular nuclei were made in 3 adult pigeons and the Marchi method was applied. The results, as illustrated in figures 9 and 10, indicate that the vestibulo-cerebellar system arises both directly from the VIIIth nerve and from the vestibular nuclei, as has been demonstrated by Wallenberg ('00). In our preparations direct vestibular fibers could be traced into the auricle and into folium X (nodulus). Some possibly reach folium IX (uvula). Secondary vestibular fibers also are distributed to the auricle, representing lateral extensions of folia IX and X.

Shimazono ('12) has indicated in his figure 19 that the distribution of the secondary vestibulo-cerebellar fibers is in the auricle. Vestibular fibers from the VIIIth root and from the vestibular nuclei appear to pass to the deep cerebellar nuclei as described in normal avian material by Sanders ('29). In 2 adult pigeon brains stained by the Nissl method, I found chromatolytic cells in the superior vestibular nucleus, following removal of the homolateral auricle (fig. 11). It was not possible to ascertain if the fibers involved terminate in the flocculus alone, or in both elements of the avian auricle, namely flocculus and paraflocculus.

Cochlear connections with the cerebellum have been described by Bok ('15), Sanders ('29), and others. The possible pathways between the cochlear nuclei and the cerebellum were studied in one adult pigeon in which the cochlear region, in addition to the vestibular region, was destroyed. No connections between any part of the cochlear group of nuclei and the cerebellar cortex were found in the Marchi preparations, nor was there evidence of any connection between auditory nuclei and deep cerebellar nuclei, as described by Bok ('15). Lesions of the cortex of the part, or ^{of} all folia of the posterior lobe of the corpus cereb-

elli in 3 adult pigeons resulted in no retrograde chromatolysis in the laminar or the magnocellular nuclei of the cochlear nuclear complex.

The tecto-cerebellar tracts could be distinguished, in silver preparation, in the anterior medullary velum of chick and duck embryos (fig. 1), as Larsell ('48) illustrates in his figure 2. In the embryonic as in the adult cerebellum the fibers of this bundle extend from the superior and medial regions of the tectum through the anterior medullary velum and into the cerebellum, as also shown by Shimazono ('12).

In 2 adult pigeons these tracts were interrupted by destruction of the medial part of the tectal gray substance around the ventricle, or of the anterior medullary velum. The resulting Marchi degeneration extended into the posterior lobe of the corpus cerebelli (fig. 10). Since other fiber connections to and from the cerebellum were interrupted by the lesions, the exact folia in which the tecto-cerebellar tract terminates could not be ascertained. The projection in pigeons, as determined by the Marchi method, however, appears to be principally to folia VI (declive), folium VII (the folium-tuber vermis lobule), folium VIII (pyramis), and possibly folium IX (uvula).

Removal of the cortex of folium VI (declive) and folium VII (the folium-tuber vermis lobule) resulted in chromatolytic changes in the cells of the nucleus isthmi and in the tectal region (fig. 12), further indicating that these folia are associated with the tectum.

The olivo-cerebellar tract is well shown in silver preparations of late embryonic stages and in Weigert series of normal adult birds. In one adult pigeon the inferior olivary complex was destroyed unilaterally. The Marchi degeneration resulting from this lesion crossed the midline and extended upward into the cerebellar peduncle.

The fibers terminate in all folia of the cerebellum (figs. 13 and 14). The degeneration of the cells of the inferior olive following lesions of the cerebellum in birds described by Yoshimura ('10), may be similarly interpreted. The fact that these fibers are distributed primarily to the contralateral cerebellar cortex was demonstrated by retrograde degeneration studies in 2 adult pigeons in which half of the cerebellar cortex was removed. Resulting chromatolysis was found only in the inferior olive of the opposite side (fig. 15). This experiment confirms the interpretation reached from study of silver and Weigert preparations of unoperated brains, namely, that the olivo-cerebellar system is entirely crossed in birds.

Ponto-cerebellar fibers are present in both embryonic and adult stages of the bird cerebellum, as shown by Brodal, Kristiansen and Jansen ('50) whose observations I confirm. Fibers of this system arise from the rudimentary pons nuclei in the ventral portion of the medulla oblongata and extend upwards along its superficial margin into the cerebellar peduncle. No intracerebellar localization of these fibers was attempted in the present investigation. Removal of the cortex of the rostral folia of the posterior lobe of the corpus ^{cerebelli} / produced chromatolysis of cells in the homolateral and contralateral pontine nuclei (fig. 16).

IV NEUROPHYSIOLOGICAL STUDIES OF RECEPTIVE AREAS

Neurophysiological methods were employed in the investigation of the receptive areas because they permit demonstration of functionally continuous but anatomically discontinuous and complex pathways. The techniques employed confirm the connections of specific fiber tracts with various subdivisions of the cerebellum and clarify the terminal

distribution of the afferent system.

As considerations in selecting a suitable physiological method, ablation experiments and stimulation procedures by other means were discarded because these techniques do not permit discrete localization of the fiber systems or of functional activity, as Bremer ('24) has pointed out. Further, the results of these methods are produced primarily through the effector mechanisms of the cerebellum. The method of recording neuronal activity from fairly circumscribed cerebellar regions, however, fulfills the requirements of localization (Woolsey, Marshall and Bard, '42). Since stimulation of afferent pathways to the cerebellum activates the organ, as is well known to be true in mammals, the methods of stimulation and oscillography so successfully used by a number of investigators of the mammalian cerebellum, were adapted to the study of the organ in birds.

If somatotopic localization exists in the avian cerebellum, as it does in mammals (Snider and Stowell, '44), the assumption that the distribution of the electrical fields should reveal the pattern was the starting point of the neurophysiological phase of the investigation.

MATERIAL AND METHODS

The animals used were the pigeon (Columba livia, Gmelin), the dusky horned owl (Bubo virginianus saturatus, Ridgeway) and the domestic mallard duck (Anas platyrhynchos platyrhynchos, Linnaeus). The pigeon was used in the majority of the experiments because its cerebellum represents an intermediate morphological type which has a

relatively simple structure, yet shows the primary folia and fissures common to the cerebella of all birds (Larsell, '48). The unique visual powers (Walls, '42) and well developed auditory system (personal observation) of the owl made this bird especially valuable for the examination of the relationship between the optic and auditory systems and the cerebellum. Owls therefore were chiefly used in the study of cerebellar visual and auditory areas. Experiments on the tactile system were carried out on all three species of birds. The large exteroceptive component of the trigeminal nerve in the duck appears to be correlated with the large size of the declive in this species (Larsell, '48). Therefore, the duck was selected for the study of projections from the sensory receptors of the face and bill to the cerebellum. A total number of 50 birds was examined, of which 33 were pigeons, 13 owls, and 4 ducks.

For anesthesia sodium pentobarbital (35 mg. per Kg.) was administered intraperitoneally. The action of this barbiturate is intermediate in duration (Goodman and Gilman, '41), and the depth of anesthesia is more easily controlled than with the briefly acting pentathol or with Dial, whose action is more prolonged. Sodium pentobarbital, in addition, does not have the irritating effect on the tracheobronchial tree, with resulting excessive mucus secretion and obstruction of the airway that occurs in prolonged inhalation ether anesthesia (Goodman and Gilman, '41). It has the disadvantage, however, of depressing cerebellar responses from stimulation of auditory and visual receptors. A similar effect has been noted in mammals (Snider and Stowell, '44). To circumvent this difficulty, acute decerebrate preparations were also utilized, the brain-stem being

cut above the level of the colliculi with the animal under ether anesthesia and atropine. This procedure does not depress spontaneous activity or evoked potentials (Adrian, '43) in the mammalian cerebellum and the animal may be maintained in a relatively constant state for long periods. The supracollicular level was selected as the optimum level of section because the tecto-cerebellar tract, which has been demonstrated in mammals to be an essential link in the transmission of auditory and visual impulses to the cerebellum (Snider, '45), and also the optic tracts, would be spared by transection at this level.

The following table summarizes the use of the two anesthetics in the species of birds studied:

	Sodium pentobarbital	Decerebration
Pigeon	20	13
Owl	8	5
Duck	1	3

Exploration of the avian cerebellum required the development of a surgical procedure which would permit adequate surface exposure and yet maintain a viable cerebellum. To meet these requirements, a tracheotomy was first performed to assure maintenance of a constant air way. The exposure originally used was accomplished by rongeur-ing away the bone and incising the dura overlying the dorsal aspect of the cerebellum. The single advantage of this approach is that it permits access to the cerebellum when the forebrain is still in place but it allows only a small portion of the dorsolateral surface of the cerebellum to be exposed. Because of the large dural sinuses that surround much of the avian cerebellum, and which are easily penetrated, this method of exposure frequently resulted in massive hemor-

rhages. The dural sinuses were injected with India ink in two animals in order to determine an approach to the cerebellum which would produce the least circulatory interference, since it has been emphasized that an adequate blood supply to the cerebellum is essential during study of its activity (Brookhart, Moruzzi and Snider, '51). The results of this study of the dural sinuses indicated ^{that} a far better approach consisted of exposure of the anterior surface of the organ through the forebrain cavity of the skull, following supracollicular decerebration. This procedure allowed a large surface exposure with few intervening dural sinuses. The surface of the cerebellum could be kept moist easily by covering it with mineral oil instilled into the skull cavity. The chief limitation of this method was the difficulty encountered in paralleling the anterior cerebellar surface with the penetrating electrodes.

In activating the afferent pathways to the cerebellum, it is necessary to utilize a stimulus which can be repeated at any desired interval. The stimulus must be sufficiently localized to permit its application to individual parts of the body. The method of stimulation must produce a synchronous volley of afferent impulses capable of evoking cerebellar responses.

In the first 16 experiments the stimulus was applied directly to a peripheral nerve in one of the major subdivisions of the body. The afferent volley so produced represents all types of impulses carried in a mixed motor-sensory nerve. The responses recorded in the cerebellum during stimulation of a nerve were used to map out the receiving zones of the cerebellum. The nerve was exposed by incising and retracting the overlying skin and muscle. A pair of silver wire electrodes

were placed 2 mm. apart, on the nerve and single electrical thyatron-controlled condenser discharges were applied directly to the nerve. These shocks were repeated at regular intervals and maintained at an intensity just below the visible reflex threshold of the part.

In the remaining $3\frac{1}{4}$ birds, physiological stimuli were employed exclusively. This method of stimulation permits an examination of the relationship between individual modalities of sensation and the cerebellum, as pointed out by Dow and Anderson ('42). Discrete parts of the body may be activated in rapid succession and the responses, recorded from the cerebellum during stimulation of these parts, may be compared and localized. The trauma inflicted on the experimental animal also is minimized so that it can be maintained in good condition for a much longer period.

Tactile stimulation was produced by movement of individual feathers with a stylus attached to an electromagnetic device. The tip of the stylus moving through a distance of approximately 3 mm. produced a sudden displacement of the feather which could be repeated at regular intervals. The validity of this method of tactile stimulation of hairs or vibrissae has been demonstrated in mammals (Snider and Stowell, '44). Four of these stimulating devices were used synchronously, the stylus of one being placed on a feather of the face, another on a wing feather, a third on a leg feather, and the fourth on a tail feather. A multipolar selector-switch which controlled the four electromagnets that energized the individual stimulators permitted stimulation in rapid succession of the feathers of the body regions indicated without disturbing the animal between tests of individual regions. The resulting patterns of response could then be compared

for evidence of somatotopic specificity. Activation in the cerebellum was accepted as a true tactile response if it occurred only when a feather was displaced. If activation persisted after removal of the stylus from the surface of the feather, it was regarded as resulting from the click of the stimulator and therefore^{as}/cochlear in origin. These responses to the tactile stimulator's click, however, were not considered in the results of activation of the auditory system. The same criterion was used by Snider and Stowell ('44) in their investigation of the tactile areas of the mammalian cerebellum.

Stimulation of the visual receptors was produced by a flash of light from a Strobotron (Sylvania SA309) placed 10 cm. from the dark-adapted eye. This instrument produces a white light with a discharge spectrum ranging between 4,000 and 7,000 Angstrom units. The duration of the wave front of the light, which is 0.6 msec., was determined by impressing the output from a photoelectric cell activated by the discharge of the flash tube on the 1 msec. time-base of a cathode-ray oscilloscope. A thyatron-controlled condensory discharge triggered the light and permitted repetition at any desired interval. A similar method of stimulation has been successfully used in the investigation of the visual receiving areas of the mammalian cerebellum (Snider and Stowell, '44).

Papez ('29) states that the avian optic tracts are completely crossed at the optic chiasma. In accord with this anatomical fact, we found in preliminary experiments on 2 pigeons that activation of the optic tectum induced by a flash of light to the eye was produced only in the tectum contralateral to the retina stimulated. In the experiments involving visual activation the cerebellar electrodes were

on the side opposite to the eye stimulated. In birds, as in mammals (Snider and Stowell, '44), the optic tectum (superior colliculus) must be intact for activation of the cerebellum by visual impulses.

In order to eliminate any afferent impulses which might arise from movement of the eyelids, the surfaces of the cornea and the eyelids were anesthetized with 1% pontocaine, instilled into the conjunctival sac. The extraocular muscles were left intact because they produce little movement of the globus oculi (Walls, '42), and they are difficult to excise without damaging adjacent nervous structures.

Activity recorded from the cerebellum after a flash of light to the contralateral eye was regarded as a true visual response if present only when the light was permitted to enter the eye but disappeared when the eye was covered. In most of the experiments a unipolar recording electrode was placed on the activated optic tectum. The complex tectal responses to retinal stimulation, recorded through this electrode, were used as controls in predicting the approximate latency of the cerebellar responses.

The stimulus used in studying the relationship between the auditory system and the cerebellum consisted of a simple "click" of undetermined pitch and volume. The click was produced by a hearing-aid ear-phone which was placed 5 cm. from the homolateral ear. The ear-phone was activated by the thyatron-controlled condenser discharges. The click could be repeated at regular intervals. This type of stimulus has been used successfully in the examination of the auditory receiving areas of the cerebellum of mammals (Snider and Stowell, '44). The responses in the cerebellum were regarded as auditory in origin if they disappeared when the click stimulus was eliminated, but reappeared when

it was again raised to threshold level. True auditory responses have a constant latent period and may be masked by appropriate continuous sounds. Care was taken to insure that the ear-~~phone~~ did not contact the skin or feathers of the head, thus avoiding cutaneous stimulation.

The recording technique necessary for the experiments described must meet certain requirements. It must be capable of registering the small and rapid fluctuations of potential which characterize the spontaneous activity of the cerebellum, as pointed out by Adrian ('35). It also must be capable of representing the temporal course of the fluctuations of potential produced by an afferent volley in such a manner as to permit observation of latency, duration and contour. In addition, the method must permit localization of responses arising in the cerebellum and of representing localized activity in such a manner that permanent records can be made when desired.

Difficulties in recording the small and rapid changes of potential were minimized by use of low-level differential recording amplifiers. The output of the amplifier was led to the ^{binding post} 'input' of a dual cathode-ray oscilloscope, which permitted visualization of this activity. An adequate time-base was assured by synchronizing the linear sweep of the oscilloscope with the stimulus.

Localization of evoked activity in the cerebellum required the use of a recording method which would register only differences of potential. The gradients of these differences due to local activity are maximal in the immediate vicinity of an active zone and undergo a sharp spatial decrement (Lorente de No, '47). Since the differential input stage of the preamplifier rejects all fluctuations except those produced by differences in potential, the action potentials recorded from

closely approximated bipolar electrodes were regarded as localized near the recording electrodes.

Bipolar recording electrodes were employed exclusively in this investigation. These were composed of insulated copper wire 75 μ in diameter. Four of the wires were cemented together by a suitable adhesive, such as glyptal enamel, to form a cable. The cable was threaded through a plexiglass support which contained four binding posts, each of which received one of the wires of the cable (fig. 17). The end of the cable was cut diagonally so that the exposed tip of each wire was separated from its neighbor by an interval of approximately 0.5 mm. The most distal tip was designated number 1, the next tip was number 2, the next number 3, and the most proximal tip was number 4. The cut end of the cable was immersed in normal saline. By applying a potential of 1.5 - 3.0 ^{volts direct current} / to each binding post, a visible bubble of hydrogen was generated at the corresponding exposed tip. In this way, the relationship of the arrangement of the uninsulated tips to their proximal attachments could be established.

The leads of two separate differential amplifiers having similar characteristics were attached to the binding posts in such a way that electrode pairs 1 and 2 could be compared with 3 and 4. The output of the amplifiers was visualized on a dual cathode-ray oscilloscope (fig. 17).

In determining the approach in exploring the cerebellum for evidence of activation by peripheral stimulation, certain factors had to be considered. As has been previously noted, the amount of cerebellar surface area which can be exposed is restricted. This eliminated the possibility of obtaining adequate surface records. Penetrating

electrodes, however, can be passed through the small surface area exposed into any deep part of the cerebellum. Bipolar differential recording electrodes permit localization of the response. By use of the electrode cable and comparison of the simultaneous records derived from each of the paired electrodes, the boundaries of the activated areas could be established (figs. 21, 22, 23). Any overlapping of the borders of these areas could also be demonstrated.

This method of exploration, however, has certain limitations. Only a few penetrations can be made in each animal. Also there is difficulty in accurately locating the electrode tips and in projecting their exact position onto a standard diagram. Localization of the electrode tips was accomplished by the following method: after each exploration the penetrating electrode was cut and was left in situ. At the end of the experiment, the entire brain, in situ in the skull, with all electrodes in place, was submerged in 15% formalin for hardening. When sufficiently hardened, remaining bone and dura that had not been dissected away for exposure of the cerebellum were carefully removed, without disturbing the electrodes, and the cerebellum was taken from the skull cavity. It was then rapidly dehydrated in graded alcohols and finally cleared in methyl salicylate. The cleared cerebellum (fig. 17) was examined with the aid of a dissecting microscope and the exact location of individual tips of the electrode cable was plotted on standard diagrams of the midsagittal plane and the anterior or posterior surface views of the organ. As a check on possible displacement of electrodes by post-experimental handling of the preparations, as described, similar electrodes were implanted in the cerebella of 3

control birds. These electrodes were cut at the cerebellar surface and each brain, with electrodes in place, was then subjected to the same hardening, dehydrating and clearing procedures used on the experimental cerebella. No demonstrable displacement of electrodes in these controls was observed. Further, it has been noted in experiments performed prior to the present series, that even when the cerebellum underwent shrinkage, the original positions of the uninsulated tips of the copper wire electrodes which were buried at various levels in the organ could be localized by a greenish discoloration which they produced in the tissue surrounding them. In the shrunken brains there was little evidence of displacement of the tip of the electrodes from the folia in which they were embedded.

For permanent records of the results of the experiment the electrode placements were plotted on standard diagrams of the cerebellum of each species examined. The transposition of this placement to the diagram constituted one of the most difficult features of the record and should be recognized as a possible source of error. To aid in comparison, the points localized in the cerebellum were projected to the surface of the folia. This was considered to be a valid procedure because of the small distances involved and the extent of overlap between the various areas.

The potentials produced by cerebellar activity, shown as "spikes" on the dual cathode-ray oscilloscope, were photographed.

Regions stimulated and number of electrode placements from which cerebellar activity was recorded following stimulation of each region.

Animal	Type of stimulation	Tail	Leg	Wing	Face	Auditory	Visual	Total
Pigeon	Electrical stimulation of nerve	2	3	7	2			14
	Physiological stimulation of receptor	5	8	18	4	6	5	46
Owl	Electrical stimulation of nerve	1	6	7		1 tectal stimulation	1 tectal stimulation	16
	Physiological stimulation of receptor	4	3	5	3	7	6	28
Duck	Electrical stimulation of nerve				1			1
	Physiological stimulation of receptor	1	3	3		3	2	12
Totals		13	23	40	10	17	14	117

Table 1

Regions stimulated and location of responses									
Animal	No.	Tail	Leg	Wing	Face	Auditory	Visual		
Pigeon	33	Tail							
Electrical stimulation of nerve	10	IV	IV-V	IV-V-VIa	VIabc VIabc or				
Physiological stimulation of receptor	23	III-IV-Va	IV-V-VIa	V-VIa	VIabc	VII-VIII	VII-VIII		
Owl	13	Tail	Leg	Wing	Face	Auditory	Visual		
Electrical stimulation of nerve	5	III	III-IV-Va	IV-V					
Electrical stimulation of tectal region						VII	VII		
Physiological stimulation of receptor	6	III-IV	IV-V	IV-V-VIa	VIabc	VII-VIII	VII-VIII		
Duck	4	Tail	Leg	Wing	Face	Auditory	Visual		
Electrical stimulation of nerve	1				VIabc				
Physiological stimulation of receptor	3	IV	V-VI ₁	V-VI _{1,2}		VII-VIII	VII-VIII		

Table 2

EXPERIMENTAL RESULTS

A summary of the regions to which stimuli were applied is given in table 1. The number of individual electrode placements is also indicated for all of the animals used from which responses were recorded within the cerebellum as a result of excitation of the receptors of these regions. Table 2 indicates the regions stimulated and the folia in which the resulting activity was obtained in each of the 3 species. The two types of stimulation employed, as described in the section on physiological methods, are indicated to permit comparison of the results of the excitatory techniques. The results of exploration following stimulation of peripheral nerves are also summarized in the 2 tables.

The positions of cerebellar loci responding to peripheral stimulation are represented on composite diagrams of midsagittal anterior and posterior views of the cerebellum of each species of bird studied (figs. 18, 19, 20). In the anterior and posterior views each responding site is projected to the surface of the folium from which it was recorded. Many more recording electrodes were inserted to other parts of the cerebellum but the placement points which were not activated by stimulation of peripheral receptors are not shown in the diagrams. Figures 21, 22, and 23 ^{depict} examples of the types of cerebellar responses that were obtained and illustrate how boundaries between the active areas could be established in some cases.

Electrical stimulation of peripheral nerves

The portions of the cerebellum which respond to electrical

stimulation of a large mixed peripheral nerve of a body part are first described. The tactile receiving regions are then considered, and finally the auditory and visual receiving parts of the cerebellum of the bird are discussed. Larsell's (1948) terminology is employed with reference to the folia of the avian cerebellum. The name of the mammalian lobule corresponding to the folia, or of which individual folia are a part, is given in parenthesis next to Larsell's numerical designation to facilitate the recognition of the various responding sites.

The regions of the cerebellum responding to electrical stimulation of a mixed motor and sensory peripheral nerve of each body part were located primarily in the anterior portions of the cerebellum. In one pigeon and one owl electrical stimulation of a mixed motor and sensory nerve in the tail region produced responses, the latency of which ranged between 14 and 20 msec. The responding sites were located on the ipsilateral sides of folium III (upper central lobule) and folium IV (lower culmen). Electrical stimulation of a nerve of the tail region evoked activity in 3 separate electrode placements in the folia named, as indicated in table 1. Stimulation of the sciatic nerve resulted in responses in 2 experiments on pigeons and in 4 experiments on owls. The latent period of these responses ranged from 16 to 22 msec. The cleared cerebella revealed that the responding sites were located in the ipsilateral side of folium III (upper central lobule), folium IV and folium V (culmen), and were represented in 9 electrode placements. Stimulation of the radial nerve of the wing produced responses in 6 pigeons and in 5 owls, the latency ranging from 10 to 16 msec. The responding loci were found to be located ipsilaterally in folium IV and folium V (culmen) as well as in folium VIa (rostral declive) and were represented in 14

electrode placements. Stimulation of the infraorbital branch of the trigeminal nerve in 2 experiments on pigeons and in one experiment on a duck produced responses after a latent period of 6 to 10 msec. The locations of the sites responding to stimulation of the trigeminus were found in the ipsilateral side of folia VIa, VIb and VIc (declive). The responses were recorded from 3 electrode placements. Direct electrical stimulation of the surface of the optic tectum in one experiment on an owl produced a response in folium VII, which had a latency of only 2 to 4 msec.

The cerebellar activity evoked by stimulation of peripheral nerves with a single electrical shock and recorded from the depths of the cerebellum was diphasic, triphasic or complex in wave form.

In summarizing the findings with respect to cerebellar response to electrical stimulation of regional nerves, it is to be noted that the responding loci are distributed ipsilaterally in folium III (upper central lobule), folium IV and folium V (culmen), and folium VIa, VIb, and VIc (declive), according to the nerve involved. There is a definite somatotopic arrangement of the responding sites into areas. The borders of these areas overlap each other. The tail region area is located most rostrally, the leg area, the wing area and the face area following in sequence caudal to it. In one bird electrical stimulation of the optic tectum, as above noted, produced a response in folium VII (the folium-taber veralis lobuli).

Tactile stimulation

Responses to tactile stimulation, resulting from movements

of feathers of the various regions, occur in several folia. Stimulation of a tail feather in 4 experiments on pigeons, 4 experiments on owls, and 1 experiment on a duck, resulted in activation, after a latent period of 22 to 36 msec., in folium III (upper central lobule) and folium IV (lower culmen) on the same side of the body, as was subsequently determined by the electrode placements in the cleared brains. Stimulation of leg feathers evoked activity in 6 experiments on pigeons, 2 experiments on owls, and 1 experiment on a duck. The latency of these tactile responses ranged from 22 to 30 msec. The points of response were located ipsilaterally in folium IV and folium V (culmen), and in one instance, in folium VIa (rostral declive). Tactile responses from the leg were recorded from 14 electrode placements in the folia indicated.

Movements of a feather of the wing evoked responses in 15 pigeons, 5 owls, and 1 duck. The latent period ranged from 16 to 22 msec. The activated sites were located ipsilaterally in folium IV and V (culmen), and in folium VIa (rostral declive). Twenty electrode placements were found in the cleared brains from which responses were recorded following wing stimulation. In 2 pigeons and 2 owls movements of the feathers of the face resulted in responses, with a latency of 10 to 16 msec. The responding areas were located ipsilaterally in folium VI (declive), as shown by 7 electrode placements.

In summary tactile impulses reach folium III (upper central lobule), folium IV and folium V (culmen), as well as folium VI (declive). The responding zones are located on the ipsilateral side of the cerebellum. There is a definite somatotopic arrangement of the activated loci into tail, leg, wing, and face tactile areas. These are co-extensive with those described as responding after electrical stimulation

of the nerves to the corresponding parts of the body. The borders of the tactile areas overlap extensively.

Auditory and visual stimulation

Stimulation of the bird's cochlea with a simple "click" from a hearing-aid ear-phones, as described, also evoked cerebellar responses, as shown in 5 experimental pigeons, 5 experimental owls, and 2 experimental ducks. The regions activated were located in folium VIc (caudal declive), folium VII (the folium-tuber vermis lobule), and folium VIII (pyramis). The latency of the auditory responses ranged from 4 to 10 msec. Activity was recorded as a result of auditory stimulation from 16 electrode placements.

Stimulation of the retina with a flash of white light, as described, resulted in cerebellar response in 4 pigeons, 5 owls, and 2 ducks. The responses were localized, contralaterally, in folium VIc (caudal declive), folium VII (the folium-tuber vermis lobuli), and folium VIII (pyramis). The latency of the visual responses ranged from 24-26 msec. A total of 13 electrode placements in these folia indicated activity. The evoked potentials were more easily obtained if the stimulated eye was first allowed to adapt itself to darkness.

In summarizing the zones of response to auditory and visual stimulation, it is to be noted that they are approximately co-extensive. Responses to both types of stimuli were recorded from folium VIc (caudal declive), folium VII (the folium-tuber vermis lobuli) and folium VIII (pyramis). On the basis of the results of the present investigation it seems justifiable to designate this region of the cerebellum of birds as the audio-visual area.

V DISCUSSION

The present investigation demonstrates in duck and chick embryos, the existence of a commissura cerebelli and a lateral commissure as the earliest fiber bundles to appear in the cerebellum of birds. This observation confirms the interpretation of Larsell ('48), and also his description that the commissura cerebelli is composed of ventral spino-cerebellar and trigeminal fibers. The spino-cerebellar and trigeminal components of this commissure in birds had previously been noted by Sanders ('29), and Woodburne ('36). The lateral commissure consists of vestibular root fibers and secondary vestibular fibers. These commissures have been described in lower vertebrates and in mammals (Larsell, '20, '25, '26, '31, '32a, '32b, '35, '37, '47, '48, '50; Larsell and Dow, '35; Kappers, Huber and Crosby, '36). Larsell regards them as the fundamental commissural systems of the corpus cerebelli and the flocculonodular lobe, respectively.

The restudy of the afferent fiber tracts of the avian cerebellum confirms most of the results of previous investigators, but there are important exceptions as noted in the descriptive section of the text. The strico-cerebellar and semilunar-cerebellar tracts were not, however, examined in this investigation. The Marchi and chromatolytic methods, as well as the animals employed in this study, were similar to those which have been satisfactorily used by previous workers (Wallenberg, '00; Shimazono, '12; Ingvar, '18; and others). Brodal, Kristiansen and Jansen ('50), using a modified von Gudden method applicable to very young animals, in which cells affected by destruction of various regions of the nervous system are stained to bring out possible chromatolytic changes, have demonstrated ponto-cerebellar connections

that have previously been regarded as dubious.

The dorsal and ventral spino-cerebellar tracts were observed in normal embryonic and adult avian brains and in suitable experimental preparations. The division of this system into dorsal and ventral tracts, which was first noted in reptiles by Larsell ('32b), has also been described in birds (Kappers, Huber and Crosby, '36). This spino-cerebellar system has been identified by many authors (Friedländer, 1898; Shimazono, '12; Ingvar, '18; and others). In the present investigation the spino-cerebellar system has been followed as far caudally as the lower lumbar region of the cord, in agreement with the descriptions of Friedländer (1898) and Ingvar ('18). The cerebellar distribution of fibers is shown by the Marchi technique to folia II and III (central lobule), folia IV and V (culmen), and folia VIa and VIb (rostral declive) of the anterior lobe. This distribution in the anterior lobe confirms Ingvar's observations as he pictures them in his figure 75, although Ingvar's designations of the cerebellar lobules of this region are different. Lobuli IXa, IXb and IXc (uvula) also receive spino-cerebellar contributions, while lobulus VIII (pyramis) receives a few scattered fibers from this system. No spino-cerebellar fibers could be traced to folium I (lingula), folium VIb (caudal declive), folium VII (the folium-tuber vermis lobule) and folium X (nodulus). Ingvar ('18) described spino-cerebellar fibers in his posterior lobe as reaching only into his pyramis and uvula of birds, which correspond to Larsell's ('48) folium IXa, IXb, and IXc (uvula). Shimazono ('12) described such fibers as passing into the region that he designates as the two ventral lobuli of the posterior lobe. In the preparations used in the present investigation no connections between the spino-cerebellar

system and the deep cerebellar nuclei could be identified. Sanders ('26), however, described some fibers to these structures.

The two spino-cerebellar tracts of the bird, therefore, terminate approximately in the parts of the vermis that are homologous to those in which the corresponding tracts end in mammals, as described by MacNalty and Horsley ('09), Ingvar ('18), Janson ('31) and others. In mammals the dorsal tract of this system of fibers is also distributed to parts of the lateral hemispheres adjacent to the vermis. Using oscillographic methods, Dow ('39) has confirmed the distribution of these tracts in mammals as determined by the earlier investigators cited, who employed the Marchi technique. He found that the spino-cerebellar tracts were associated with the anterior lobe, lobulus simplex, pyramis, uvula and the paramedian lobules.

Root fibers and secondary trigeminal fibers from the superior sensory nucleus clearly pass into the cerebellum in our silver preparations of chick and duck embryos. Similar connections have been described by Sanders ('29), Woodburne ('36) and others, in birds. The present investigator observed, as did these authors, that part of trigemino-cerebellar tracts in the adult animal enters the region of the anterior nodillary velum ^{and} decussates as part of the commissura cerebelli. In reptiles similar trigemino-cerebellar pathways have been described by Larsell ('32). In a more recent contribution, Larsell ('37) designates the part of the Vth nuclear complex which gives rise to the secondary trigeminal fibers that reach the commissure as the nucleus of the cerebellar commissure. Pearson ('49) describes cells of the mesencephalic nucleus of the trigeminus in human fetuses, as extending into the base of the cerebellar vermis and hemispheres.

As described, experimental lesions of the superior sensory Vth nucleus result in degeneration of fibers which extend into folium V (upper culmen), folium VI (declive) and perhaps to folium VII (the folium-tuber vermis lobule) of the cerebellum of birds. Because other fiber systems were also involved by the lesions, a more exact localization was not possible by these anatomical methods. Removal of the cerebellar cortex of the latter two folia, however, produced chromatolytic changes in the dorsal part of the superior sensory nucleus of the trigeminal nerve. The results here recorded appear to represent the first demonstration by anatomical experimental methods of the trigemino-cerebellar tract and its connections in any vertebrate type. Larsell ('51) summarizes the trigemino-cerebellar connections and indicates diagrammatically in his figure 270 that these fibers terminate in the vermician region of the mammalian cerebellum around the fissura prima. The findings of the present investigation appear to agree well with this distribution.

Vestibulo-cerebellar connections were followed from the vestibular root and the vestibular nuclei into the lateral commissure of the duck and chick embryos, as has been previously shown by Larsell ('48). Experimental lesions of the VIIIth nerve and the vestibular nuclei permit degenerating fibers to be traced into the region of the auricle and into folium IX (uvula) and folium X (nodulus). The direct root fibers appear to be related to both portions of the auricle (lateral extensions of folium IXc and folium X). Vestibulo-cerebellar connections to the auricle of birds have been described by Wallenberg ('00), Shimazono ('12), Groebels ('27, '28) and others. S. Ramon y Cajal ('08a) and Sanders ('29) have traced direct and secondary vesti-

bular connections to the deep cerebellar nuclei. Frenkel ('09) was unable, however, to demonstrate these direct connections in the bird.

The mammalian cerebellum exhibits homologous vestibulo-cerebellar connections. Ingvar ('18) and Dow ('36) observed direct vestibular root fibers to the uvula and nodulus as well as to the lingula and the fastigial nucleus. Secondary vestibular connections with the cerebellum have been described also by these authors and by Larsell ('51) as arising from the vestibular nuclei in mammals. Dow ('39) observed that stimulation of the VIIIth nerve with single electrical shocks resulted in cerebellar action potentials in both flocculi, the nodulus, uvula, lingula, and the fastigial nuclei in mammals. In comparing the areas of the bird cerebellum which receive vestibular fibers with the corresponding areas in the mammalian cerebellum, it is to be noted that no vestibular connections have been described in birds to folium I (lingula), although vestibular connections to this folium have been described in mammals.

Cochleo-cerebellar (lamino-cerebellar) connections of birds have been described by Bok ('15), Sanders ('29), and others. No evidence of connections could be demonstrated from the cochlear nuclei to the cerebellar cortex in the present investigation. The existence of such a connection has been questioned on the basis of comparative studies of the auditory complex in birds and mammals (Stotler, '51). In mammals no cochleo-cerebellar tract has been demonstrated.

Tecto-cerebellar fibers were observed extending from the tectal region through the lateral margins of the anterior medullary velum to folium VI (declive), folium VII (the folium-tuber vermis lobule), folium VIII (pyramis), and doubtfully to folium IX (uvula).

This tract has been observed previously in birds by many investigators (Länzer and Wiener, 1898; Wallenberg, '00; Frenkel, '09; Shimazono, '12; and others). A similar origin in birds was described by Frenkel. Shimazono ('12) and Kappers, Huber and Crosby ('36) described the tecto-cerebellar fibers as distributed to the caudal and nodial vermis in birds. The difficulty of producing a lesion confined to this tract alone makes the exact termination of the fibers hard to delimit. Removal of the cortex of folium VI (declive) and folium VII (the folium-tuber vermis lobula) produced chromatolytic changes in the tectal gray from which the tract takes its origin, as already described. This demonstrated by an experimental anatomical method the source of these fibers.

The tecto-cerebellar tract has been demonstrated by neuro-histological methods in mammals and man by Hines ('25), Larsell ('36, '36a, '47) and Riley ('43), as well as in lower vertebrates (Larsell, '23, '26, '32a, '32b, and others). Oscillographic evidence of such a connection was demonstrated in mammals by Snider and Stowell ('44) and Snider ('45), who indicate that the projection of this tract to the cerebellar cortex is principally to the lobulus simplex and tuber vermis region.

The olivo-cerebellar fibers of birds were found in the present investigation to be distributed to all parts of the cerebellar cortex. These tracts have been described in birds previously by Yoshimura ('10), Sanders ('29) and others. Chromatolytic studies as well as normal Weigert preparations used in the present study suggest that this tract is mostly crossed. This is in agreement with the conclusions of the authors cited. In mammals, many investigators have demonstrated a similar wide distribution of olivo-cerebellar fibers

(Holmes and Stewart, '08; Brodal, '40; and others). Dow ('39) confirmed this in mammals electrophysiologically.

The ponto-cerebellar tracts of birds have been studied extensively by Brodal, Kristiansen and Jansen ('50). Their work indicates that the rudimentary pons nuclei project to both sides of the cerebellum. The fibers terminate principally in the lateral aspects of folium VI (declive), folium VII (the folium-tuber vermis lobule) and folium VIII (pyramis), as well as in the adjacent unfoliated cortex. The present investigation confirms the presence of these ponto-cerebellar connections in birds. Sunderland, ('40) and Brodal and Jansen ('46) have described the diffuse projection of ponto-cerebellar fibers in mammals. Dow's ('39) electrophysiological studies verified the connections between the pons and the cerebellum in mammals. Adrian ('43), Hampson ('49), and Snider ('50) have depicted a somatotopic relationship through this system between the cerebral cortex and the cerebellum.

The early studies of the physiological activity and the subdivisions of the avian cerebellum (Weir-Mitchell, 1869; Lange, 1891; Ten Cate, '27, '36; Zanchetti, '49) are difficult to relate to the results of the present investigation. These previous investigations primarily were studies of the effector activity of the organ and were based upon the results of ablation experiments (Ten Cate) or upon electrical or chemical excitation of the cerebellar cortex (Shimazono, Bremer, Zanchetti). No study of the avian cerebellum employing the method of recording neuronal activity in response to afferent stimulation, such as was used in this investigation has appeared. In mammals, however, similar studies of the cerebellum have been numerous (Dow, '39;

Dow and Anderson, '42; Snider and Stowell, '42, '44; Adrian, '43).

The recent study of the development and subdivisions of the cerebellum of birds by Larsell ('48) suggests a functional arrangement of the subdivisions of the avian cerebellum which may now be compared with the results described in the present investigations. After comparing the morphology of the cerebellum of various adult birds with the action of the wing, tail, and leg feathers, as recorded by Allen ('48) by means of high-speed flash photography, Larsell suggests that folium I (lingula) is associated with the tail muscles, and folium II and folium III (central lobule) with the degree of development of the legs. Folium IV and folium V (culmen), as well as folium VIa, are associated with the degree of development of the muscles of the wing. This author further pointed out the possibility that folium VI (declive) of the avian cerebellum might be associated with the exteroceptive component of the Vth nerve. It should be noted that the receiving areas of the tail and leg of the avian cerebellum, described in the present study are located somewhat posterior to the folia suggested by Larsell as being concerned with these body parts. This may possibly be explained by the fact that the pygostyle, which lies several vertebral segments caudal to the segments giving rise to the nerves of the tail stimulated in the present investigation, probably more nearly represents the homologue of the tail of other vertebrates. This author considered folium VII (the folium-tuber vermis lobale) as associated with auditory function in birds. The present study, as well as corresponding investigations in mammals (Snider and Stowell, '44), support and amplify this opinion.

There is no doubt that afferent receiving areas which respond

to nerve stimulation exist in the avian cerebellum. The areas concerned with the tail region, limbs, and face are somatotopically arranged in the anterior lobe. The tail receiving area is represented ipsilaterally principally in folium XIII (upper central lobule) and folium IV (lower culmen). The leg area may be delineated in folium III (upper central lobule), folium IV and folium V (culmen); the wing area in folium IV and folium V (culmen) as well as folium VIa (rostral declive); while the face area is found in folia VIa, b, and c (declive). In the posterior lobe of the cerebellum of one bird a cerebellar receiving area, representing the termination of a relay path from the tectum, was demonstrated in folium VII (the folium-tuber vermis lobule). The tail and upper and lower limb areas, as well as the face area, overlap extensively.

The distribution of the afferent fiber terminations of the avian cerebellum supports a somatotopic arrangement. The spino-cerebellar system is distributed primarily to the parts of the anterior lobe in which the tactile areas of the limbs and tail are located. The terminations of the corresponding tracts of mammals have been demonstrated to have a similar somatotopic arrangement (Adrian, '43). According to this author the spino-cerebellar receiving area for the hindlimb of mammals is located in the central lobule and lower culmen; the area for the forelimb is found in the culmen, and the rostral lobulus simplex. The trigemino-cerebellar tract has been described in the present investigation as distributed, at least in part, to the folium in the area in which responses followed stimulation of a nerve of the face. This tract from the exteroceptive parts of the trigeminal complex should be the pathway by which impulses from the face pass to the cerebellum.

Adrian ('43), however, describes a spino-cerebellar receiving area of the face in mammals, stating that it is located in the lobulus simplex. Larsell ('48, '51) calls attention to the relationship between the trigeminal nerve and the upper culmen-declive region of the cerebellum of birds and mammals.

The tecto-cerebellar tracts, which Snider and Stowell ('44) and Snider ('45) describe as being the link by which impulses are mediated from the colliculi to the lobulus simplex tuber veralis regions of the mammalian cerebellum, terminate generally in the corresponding folia of the avian cerebellum.

The responses recorded from the cerebellum following application of a tactile stimulus to a part of the body of birds, were found to exhibit a somatotopic arrangement closely paralleling that of the areas which respond to nerve stimulation. The tactile tail area was found to lie principally in folium III (upper central lobule) and folium IV (lower culmen); the tactile leg area in folium IV and folium V (culmen); the tactile wing area in folium IV and folium V (culmen); as well as folium VIa, folium VI-1 and folium VI-2 (rostral declive), and the tactile face area in folium VIabc (declive). These tactile areas are apparently co-extensive with the cerebellar areas responding to nerve stimulation and show the same tendency to overlap one another.

Since it is still not known whether spino-cerebellar fibers carry tactile impulses (Snider, '50), although the function of these tracts has been so described (Adrian, '43), the correlation between the termination of this system and these tactile areas in the cerebellum of birds has yet to be definitely established. Brodal ('41) has analyzed the connections between the posterior funiculi and the cerebellum

of mammals. This investigator established a definite relationship between the spino-cerebellar receiving areas and the lateral cuneate nucleus. Similar connections have been described by Shimazono ('12), Frenkel ('09) and others in birds even though the posterior column system in the avian brain is poorly developed (Ariens Kappers '47). The present investigation did not include a study of the cuneate cerebellar fibers. The possibility, however, exists as has been suggested in mammals, that tactile impulses may reach the cerebellum by way of the posterior funiculi as well as by the spino-cerebellar tracts.

In comparing the tactile areas of the avian cerebellum with those described in the cerebellum of mammals (Snider and Stowell, '42, '44; Adrian '43), it is at once to be noted that these areas in mammals, in addition to being represented ipsilaterally in the anterior lobe, are also present bilaterally in the paraxial lobules. No comparable posterior tactile representation could be demonstrated in the avian cerebellum. Since the paraxial lobules are absent in birds (Ingvar, '18; Larsell, '48), it seems logical that the posterior tactile areas which they contain also have not yet developed.

The tactile areas are somatotopically arranged in the anterior lobe of the mammalian cerebellum (Snider and Stowell, '42, '44; Adrian, '43) as they are in the bird. The mammalian hindlimb tactile area is located in the ^{central lobule & lower} culmen, the forelimb tactile area in the culmen and the lobulus simplex, while the face area in mammals is located primarily in the lobulus simplex. These areas overlap each other considerably in both birds and mammals. Although folium III (upper central lobule) responds to stimulation of the sciatic nerve, as previously indicated, no tactile responses could be recorded from this region. The tactile

leg area, however, as in the case of the other tactile areas, is probably co-extensive with the receiving area which responds to sciatic nerve stimulation and probably extends into folium III.

Comparison of the latency of response of the tactile areas in birds and mammals also indicated correspondence of position in the two classes. Snider and Stowell ('44) state that the latency of the hind-paw tactile area of the anterior lobe ranges from 28 to 34 msec. The latency of the corresponding area in the cerebellum of birds ranges from 22 to 30 msec. The tactile forepaw area of mammals responds after 14 to 17 msec., while the tactile wing area of birds is activated 16 to 22 msec. after stimulation of a feather of the wing. The latencies of response of the tactile face area in mammals is 10 to 14 msec. while in birds it is 10 to 16 msec.

The auditory and visual receiving areas of the cerebellum of birds are co-extensive and may overlap the tactile face area. These areas are located in folium VIII (pyramis), folium VII (the folium-tuber vermis lobale) and occasionally folium VIc (the caudal declive). In mammals, the corresponding areas have been identified by Snider and Stowell ('44) in the lobulus simplex, ^{and} folium/tuber vermis ^{and} pyramis complex.

The tecto-cerebellar tracts as has been previously discussed, have been shown in the present investigation to project into the corresponding region of the ^{and mammalian} avian cerebellum. Snider and Stowell ('44) and Snider ('45) consider that auditory and visual impulses are relayed to the cerebellum of mammals from the tectal region over these tracts. An intact optic tectum which gives origin to this tract is essential for the production of responses in the visual receiving areas of the cerebellum. The superior colliculus, the homologous mammalian structure, is

likewise an essential link in the production of the corresponding responses in the mammalian visual receiving areas (Snider and Stowell, '44). The relationship of the homologue of the inferior colliculus in birds, namely, the lateral mesencephalic nucleus, to the conduction of impulses to the auditory receiving areas of the avian cerebellum, was not studied in this investigation. In mammals the inferior colliculus is an essential relay for the impulses which pass to the auditory receiving areas of the cerebellum (Snider and Stowell, '44).

In comparing the latencies of the auditory and visual responses in birds to those of mammals it is to be noted that the auditory receiving area of the avian cerebellum responds to the click stimulus after a latency ranging from 4 to 10 msec. This is to be compared with the latency of 6 to 14 msec. for similar responses in mammals in the corresponding area. The visual areas of the bird respond after a latent period of 24 to 26 msec. In mammals, the visual area responds after a latency of approximately 20 msec. (Snider, '50).

VI SUMMARY AND CONCLUSIONS

1. The lateral and cerebellar commissure in birds, as described by Larsell ('48), is confirmed in this investigation.
2. The spino-cerebellar system originates at least as far caudally as the lower lumbar level of the spinal cord. The system is composed of a dorsal spino-cerebellar tract and a ventral spino-cerebellar tract. The latter contributes to the formation of the cerebellar commissure. These tracts project to folium II and folium III (central lobule), folium IV and folium V (culman), as well as to folia VIa and b

(rostral declive) of the avian cerebellum. A less concentrated contribution passes to folium VIII (pyramis) and folium IX (uvula).

3. The trigemino-cerebellar fibers can be identified as arising directly from the Vth root in the embryo as well as from the dorsolateral portion of the superior sensory nucleus of V in the adult. This tract terminates for the most part in folium V (upper culmen), folium VI (declive) and folium VII (the folium-tuber vermis lobule) of the avian cerebellum.

4. Vestibulo-cerebellar fibers arise from the VIIIth root and from the vestibular nuclei, whence they can be traced to the auricle and to folium IX (uvula) and folium X (nodulus).

5. Tecto-cerebellar fibers, arising in the medial tectal gray, pass into the avian cerebellum through the lateral aspects of the anterior medullary velum and terminate principally in folium VI (declive), folium VII (the folium-tuber vermis lobule), folium VIII (pyramis) and perhaps folium IX (uvula).

6. The olivo-cerebellar fibers pass to all parts of the cerebellar cortex in birds.

7. The presence of a ponto-cerebellar system in birds, described by Brodal, Kristiansen and Jansen (1950), is confirmed.

8. Receiving areas which respond following stimulation of a large nerve in the tail, leg, wing and face are identified in the cerebellum of birds. The tail area is located in ipsilateral folium III (upper central lobule) and folium IV (lower culmen), the leg area in folium IV and folium V (culmen) and probably in folium III (upper central lobule), the wing area in folium IV and folium V (culmen) as well as folium VIa (the rostral declive). Direct stimulation of the

optic tectum in one owl demonstrated a connection of this portion of the midbrain with folium VII.

9. Tactile receiving areas are present in the avian cerebellum. These are co-extensive with the areas responding to nerve stimulation and show a similar somatotopic arrangement. The latencies of response occurring in these tactile areas correspond rather closely with those described by other authors in mammals.

10. Auditory and visual receiving areas are present and are co-extensive in the avian cerebellum. These areas are found in folium VIc (caudal declive), folium VII (the folium-tuber vermis lobule), and folium VIII (pyramis). The latent period of the auditory and visual responses are comparable to those of similar responses described in the mammalian cerebellum.

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ABBREVIATIONS FOR ALL FIGURES

aur., auricle
br. conj., brachium conjunctivum
c. cb., corpus cerebelli
cb., cerebellum
co. cb., cerebellar commissure
co. lat., lateral commissure
c. p., cerebellar peduncle
sp., spongy
f. sec., fissura secunda
fl., flocculus
f. p. l., posterolateral fissure
f. pyd., prepyramidal fissure
f. pr., fissura prima
gn. V., ganglion of Vth nerve
gn. VIII., ganglion of VIIIth nerve
med. obl., medulla oblongata
n. V., trigeminal nerve
nu. cb. m., medial cerebellar nucleus
nu. s. s. V., *superior* sensory nucleus of the Vth nerve
nu. VIII. v., vestibular nucleus of VIIIth nerve
r. l., lateral recess of the 4th nerve
r. IV., root of IVth nerve
r. V., root of Vth nerve
r. V. cb., fibers from the trigeminal root
r. VIII., root of the VIIIth nerve

r. VIII. v., fibers from vestibular root of the VIIIth nerve

tr. o. c., olivo-cerebellar tract

tr. sp. cb., spino-cerebellar tract

tr. sp. cb. d., dorsal spino-cerebellar tract

tr. sp. cb. v., ventral spino-cerebellar tract

tr. t. cb., tecto-cerebellar tract

tr. V. cb., secondary trigemino-cerebellar tract

tr. VIII. cb., secondary vestibulo-cerebellar tract

V. 4, fourth ventricle

v. c., cerebellar ventricle

v. n. a., anterior nuchalary valva

Figure 1. Outline tracings of sagittal sections through the cerebellum of duck embryo incubated 12 days. Silver gelatin method. Projection apparatus X 34. Section 1 is through the auricle. Sections 2, 3, 4, and 5 are from successive medial sagittal planes. The positions of the commissura cerebelli and the lateral commissure are indicated. The fiber pathways contributing to the formation of the commissures are also denoted.

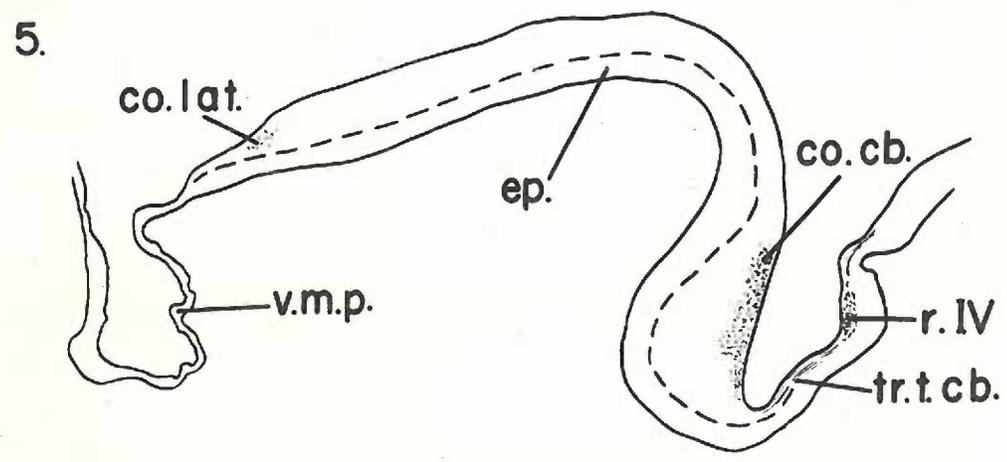
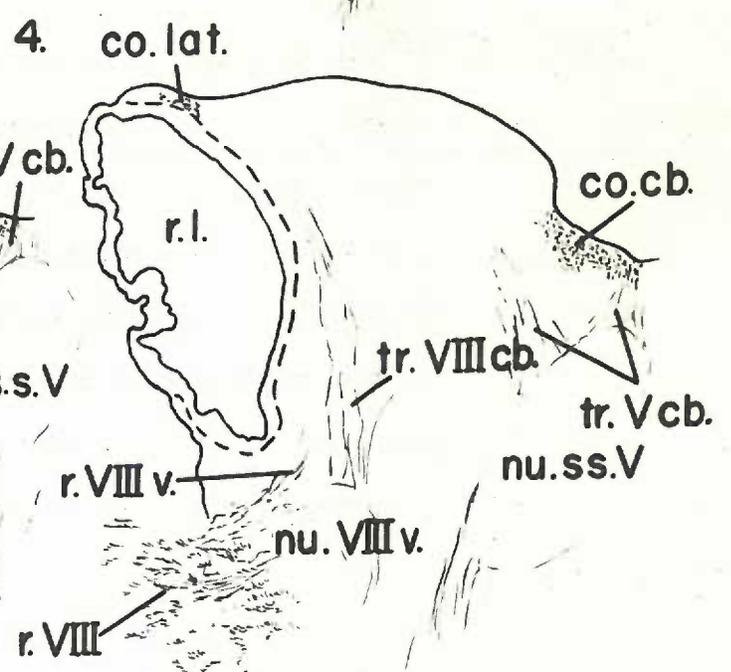
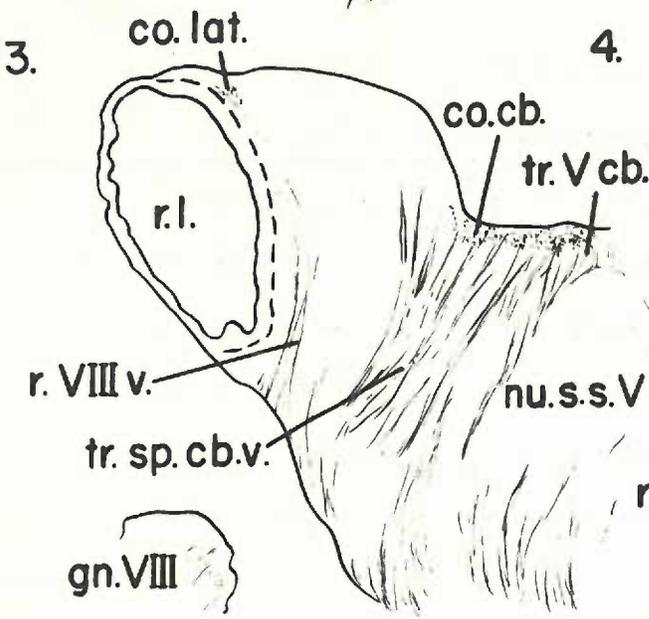
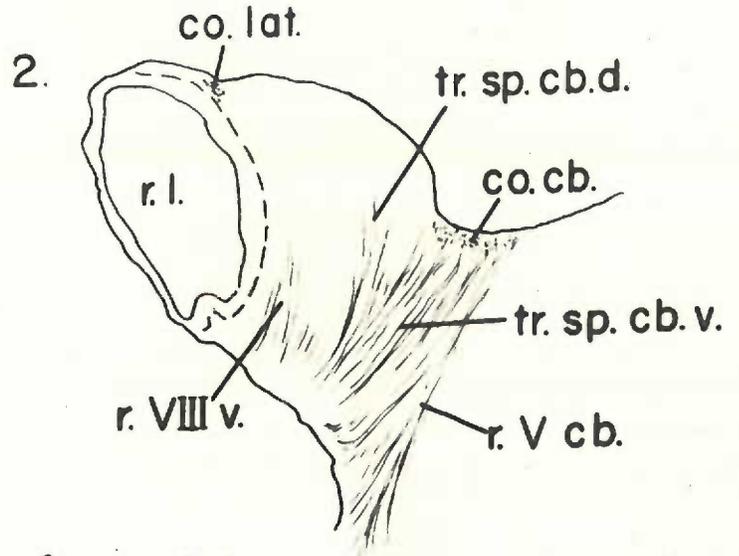
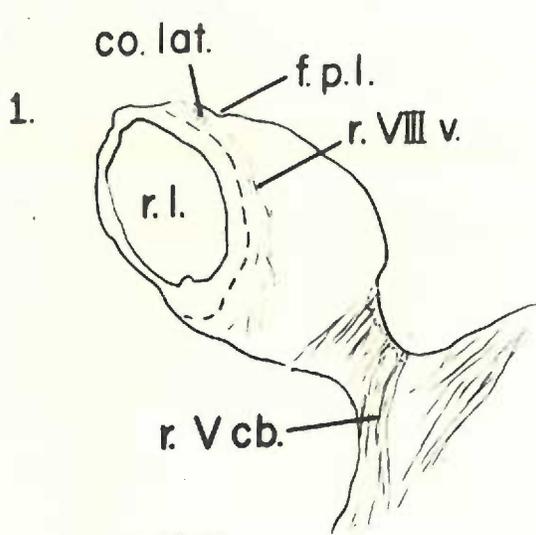


Figure 2. Outline tracings of transverse sections of cerebellum of duck embryo incubated 15 days. Silver gelatin method. Projection apparatus X 12. The origin and course of the fibers contributing to the commissure cerebelli are indicated.

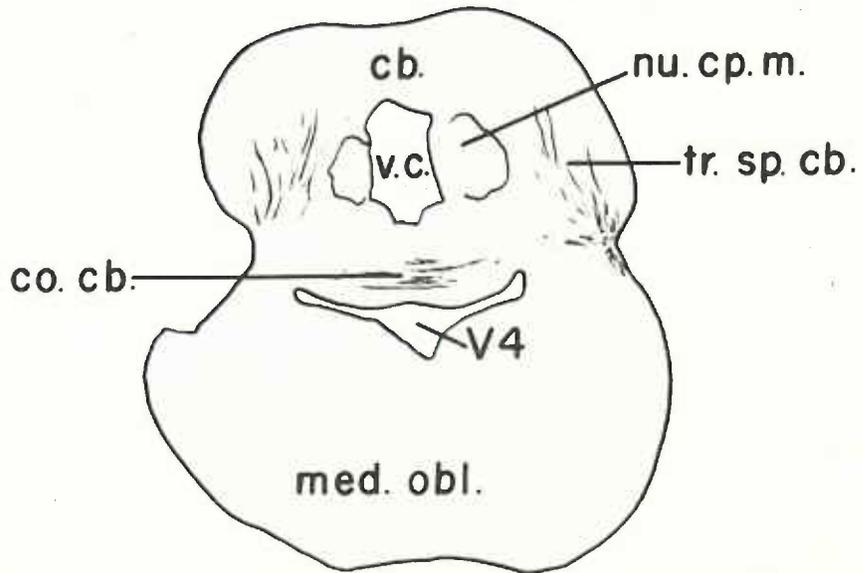
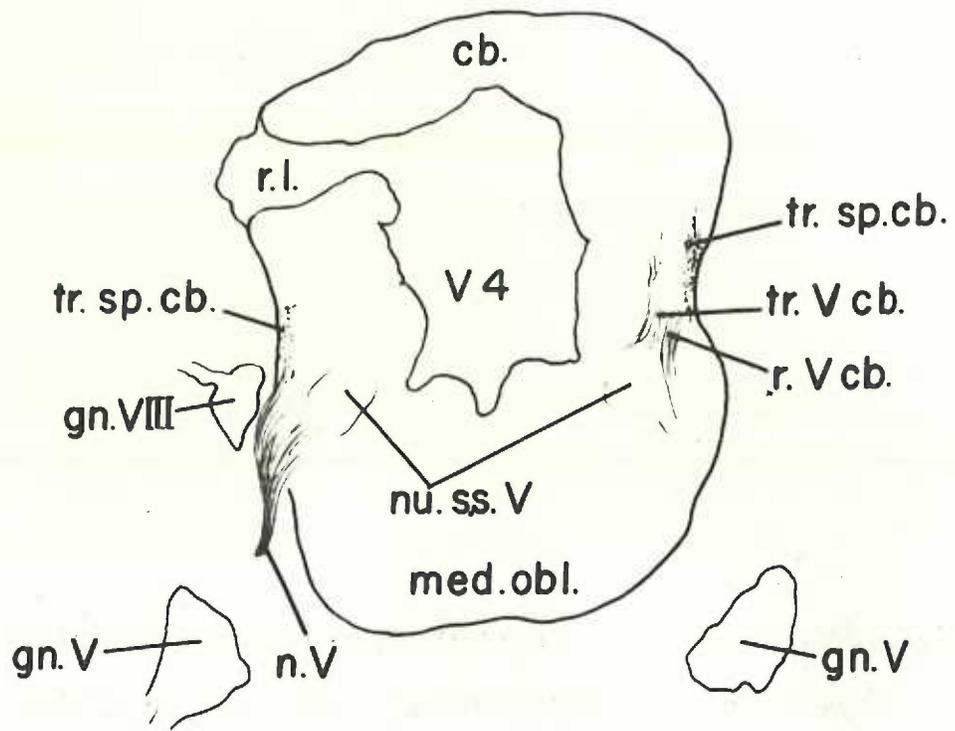


Figure 3. Outline tracing of a transverse section of lower cervical spinal cord of adult pigeon #16, showing degenerated spino-cerebellar tracts following a lesion of the ipsilateral side of lower thoracic level of spinal cord. Stained by the Marchi method. Projection apparatus X 18.

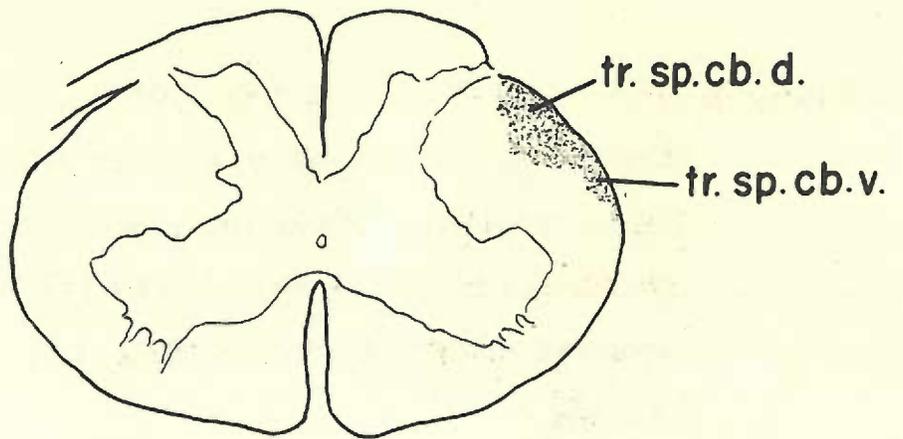
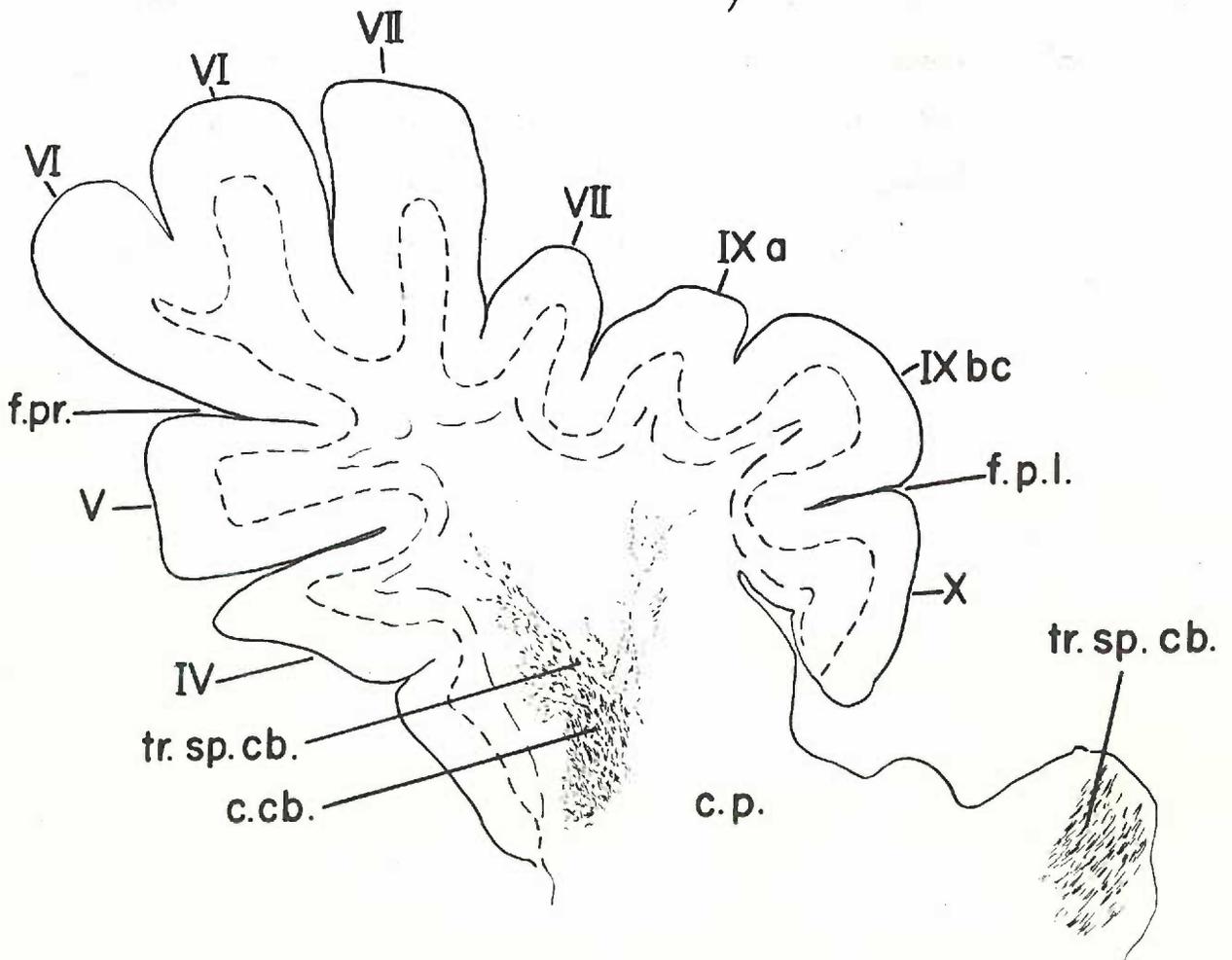
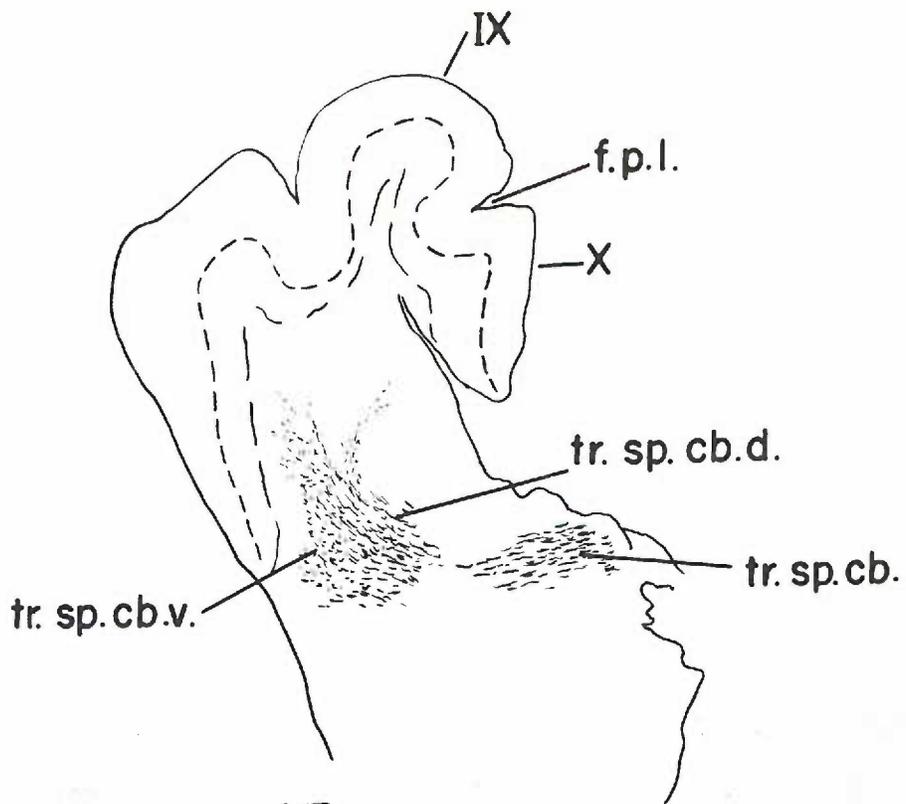


Figure 4. Outline tracings of sagittal sections of the cerebellum of adult pigeon #16, following a lesion of the ipsilateral spino-cerebellar tracts in the spinal cord. Stained by the Marchi method. Projection apparatus X 18. The positions of the dorsal and ventral spino-cerebellar tracts as they enter the cerebellar peduncle are shown.



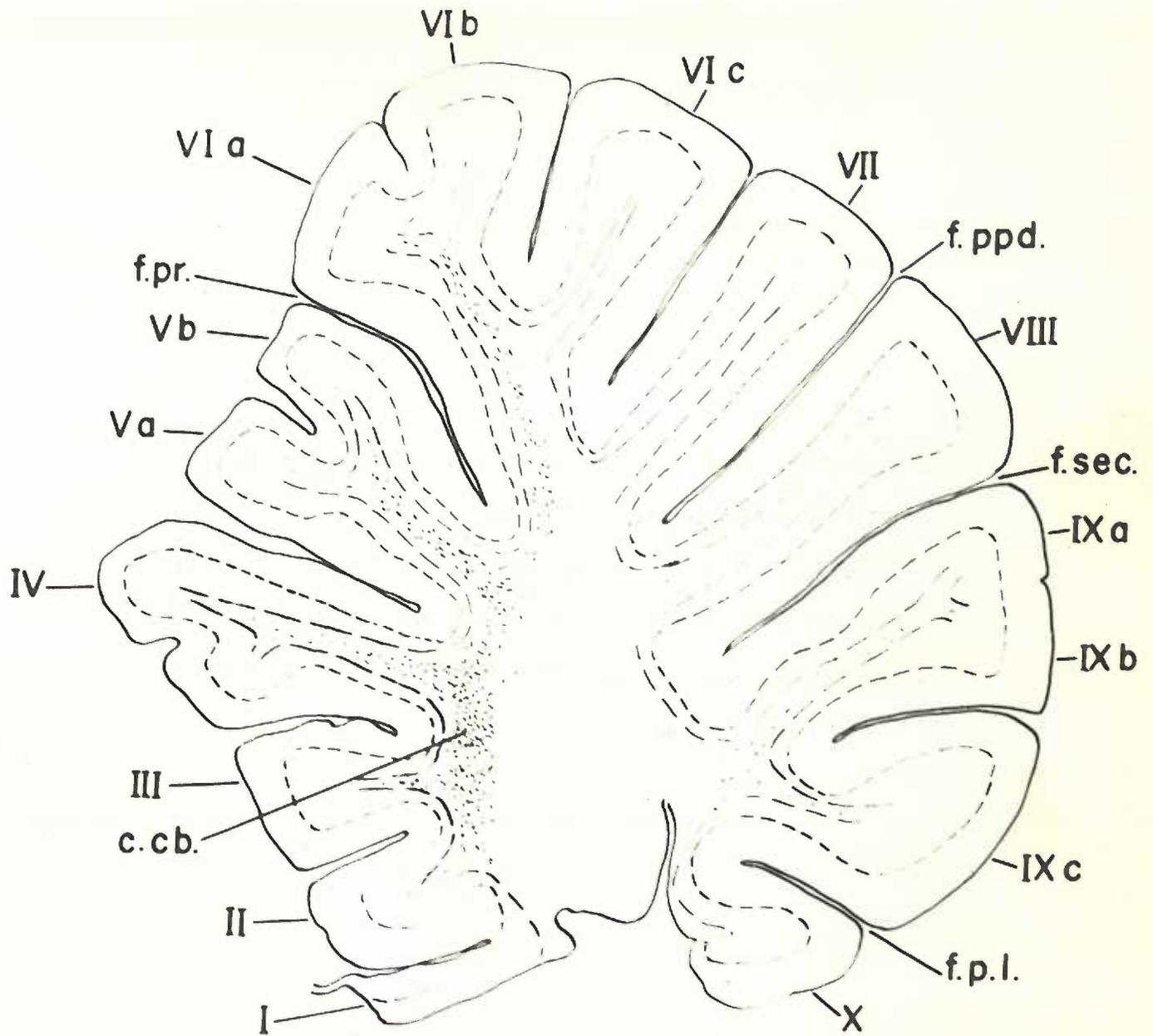


Figure 6. Outline tracings of sagittal sections of the brain of adult pigeon #10 following a lesion of the vestibular and trigeminal regions. Stained by the Marchi method. Projection apparatus, X 10. The course and distribution of the trigemino-cerebellar and vestibulo-cerebellar tracts are indicated.

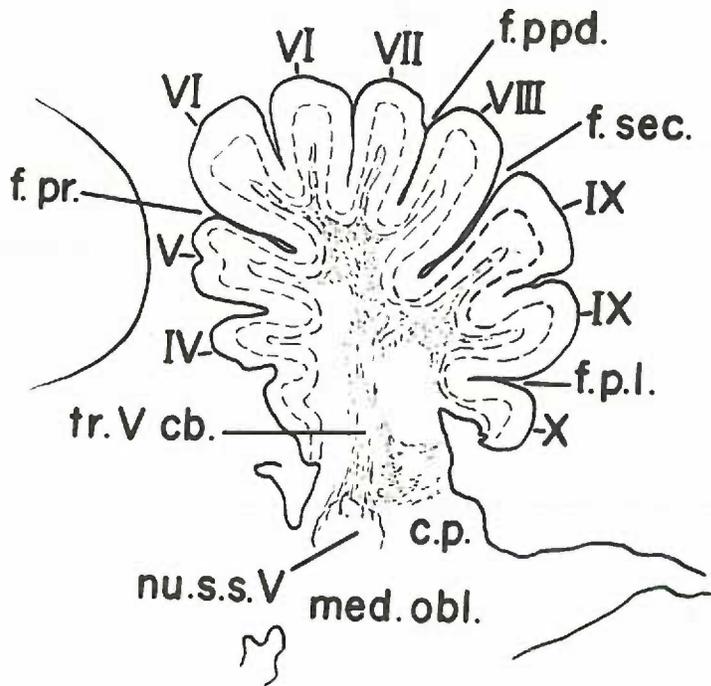
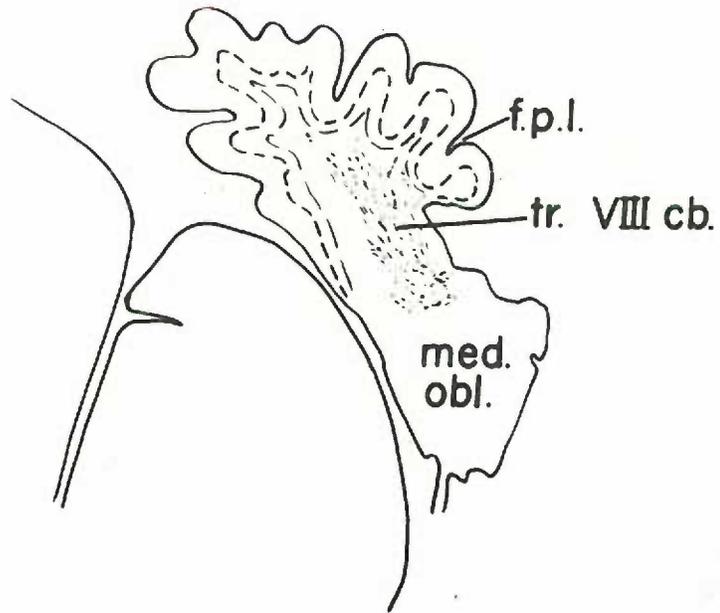


Figure 7. Outline tracings of sagittal section of the same brain.

The terminal distribution of the trigemino-cerebellar tracts to folia V, VI, and VII is indicated by the black lines and dots. The termination vestibulo-cerebellar tract is also indicated in folia IX and X.

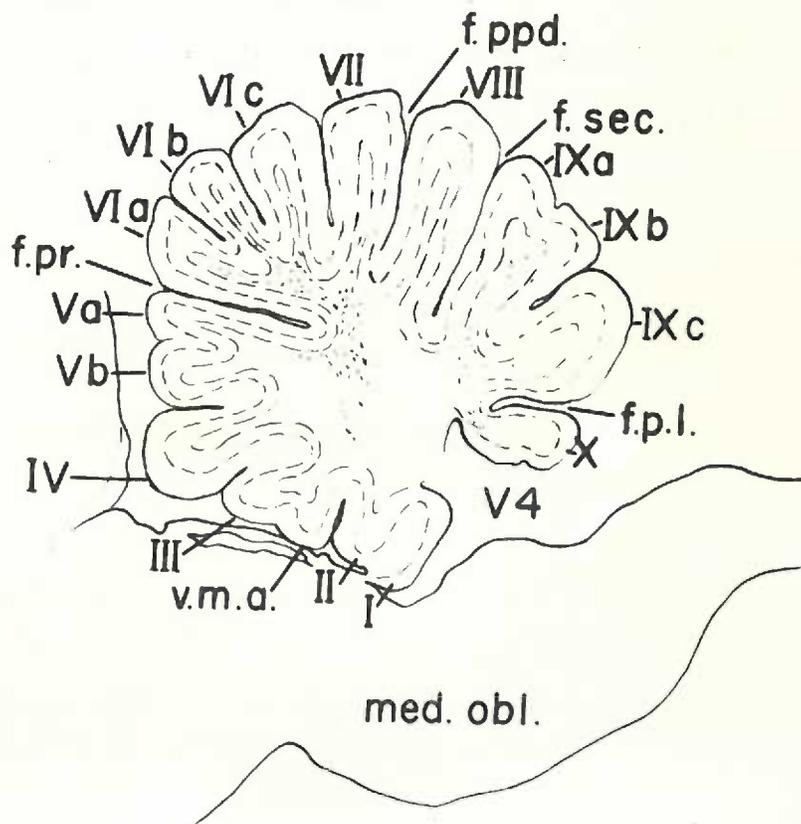
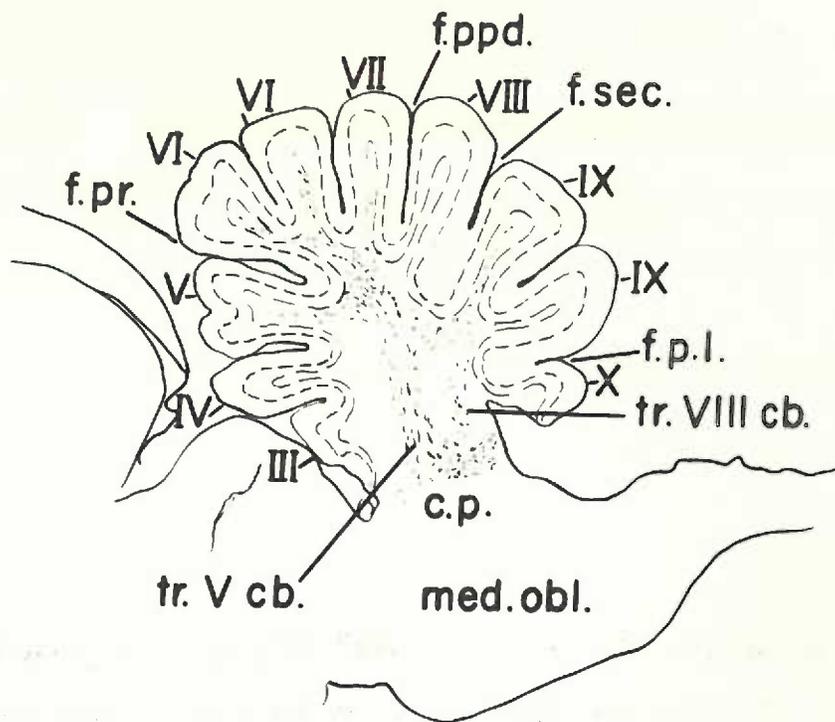


Figure 8. Photomicrographs taken of a transverse section of the brain of adult pigeon #7K, stained by the Nissl method. The location of low power photomicrograph no. 1 (X 20) is represented by square no. 1 on the line drawing. The location of high power photomicrograph no. 2 (X 450) is indicated within square no. 1 by square no. 2. Chromatolytic changes of the cells of the superior sensory nucleus of V 12 days after destruction of the dorsal surface of folia V, VI, and VII are shown in the photomicrograph no 2.

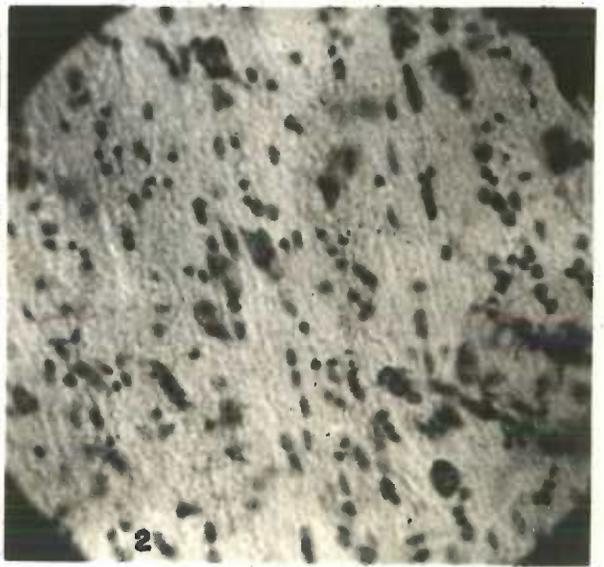
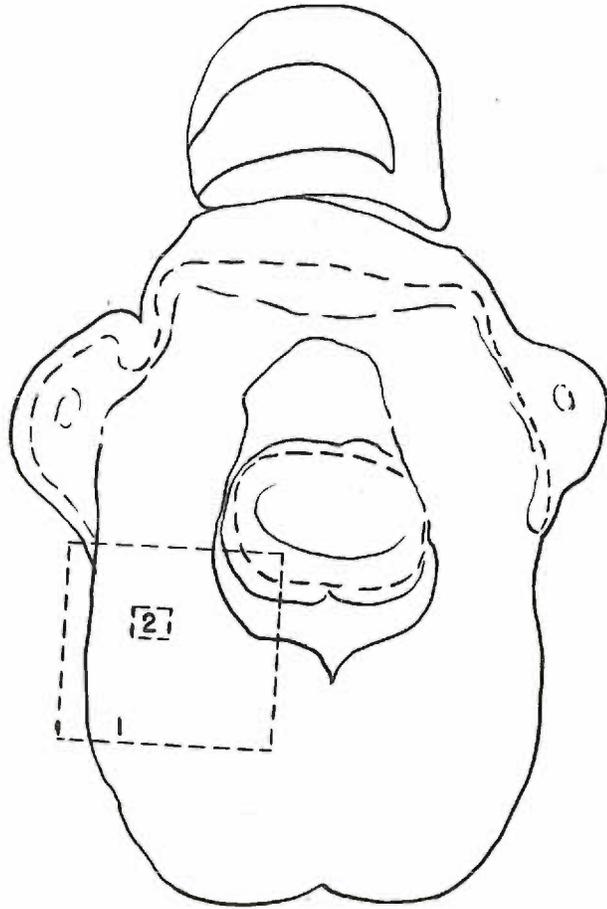


Figure 9. Outline tracings of sagittal sections of cerebellum of adult pigeon #10, following a lesion in the medulla oblongata. Stained by the Marchi method. Projection apparatus, X 10. The course and distribution of the degenerating vestibulo-cerebellar fibers is indicated by the black lines and dots.

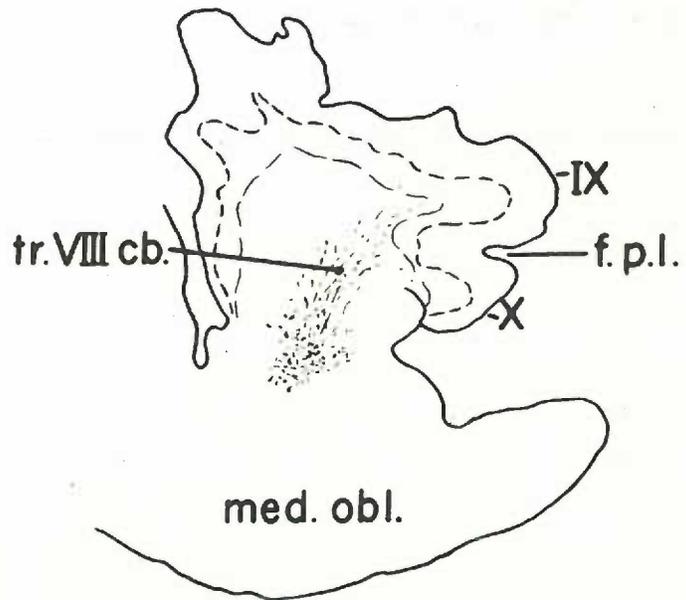
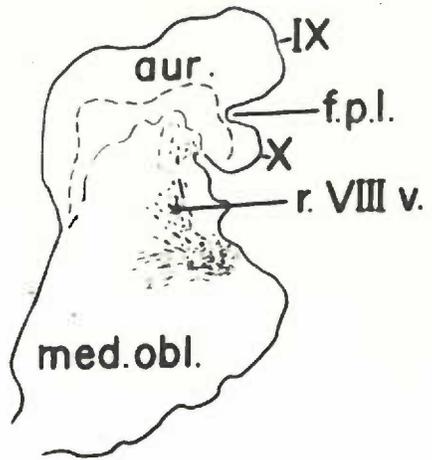


Figure 10. Outline tracings of sagittal sections of brain of adult pigeon #7, following a lesion in the medulla oblongata. Marchi stain. Projection apparatus, X 10. The terminal distribution of the tecto-cerebellar tracts and the vestibulo-cerebellar tracts, both of which were involved by this lesion, are indicated by the black lines and dots.

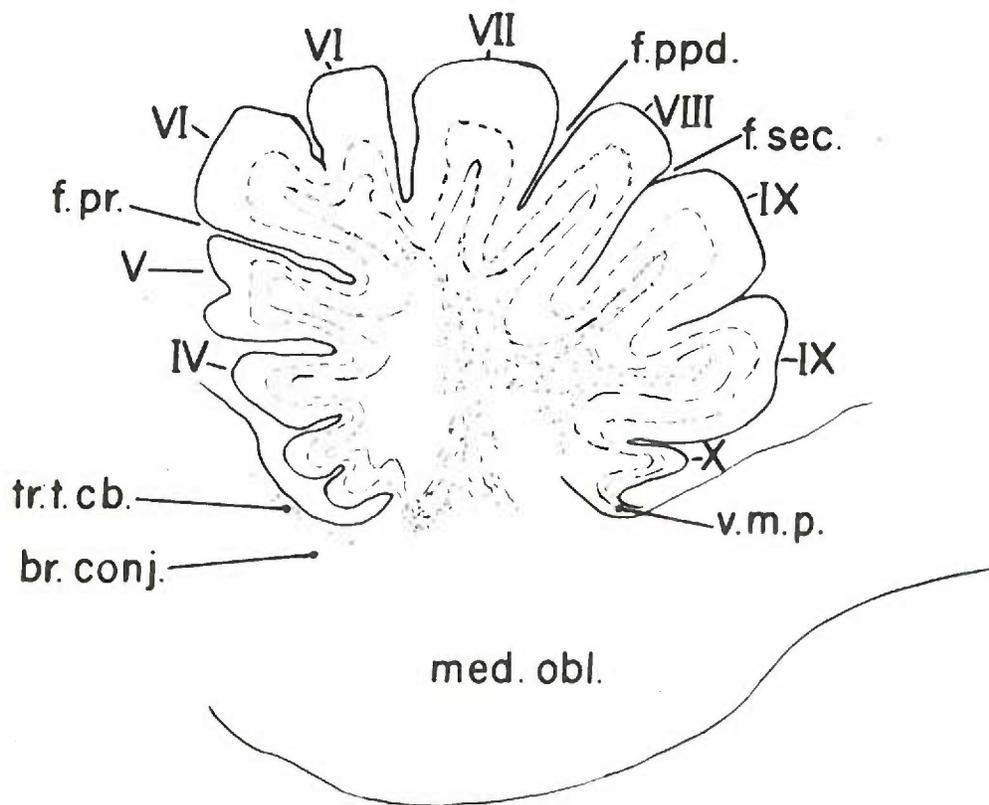
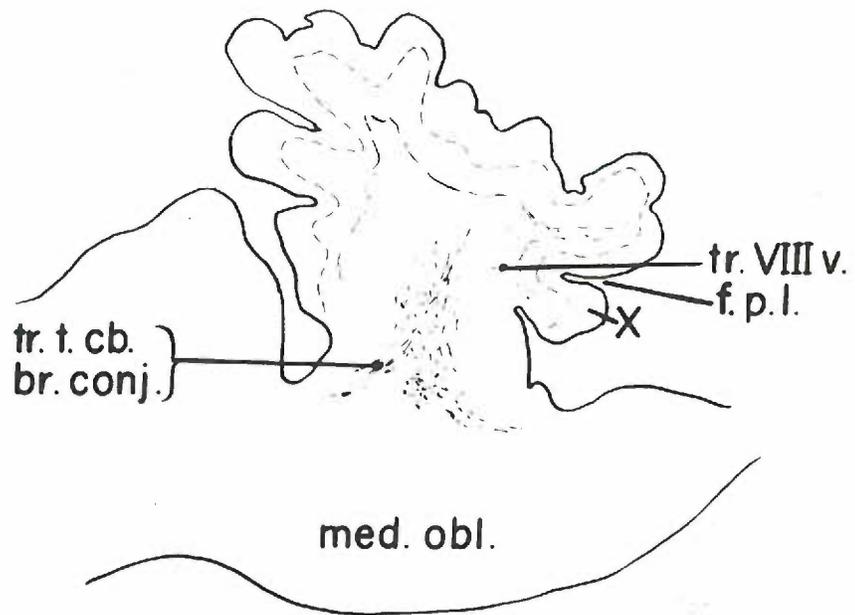


Figure 11. Photomicrographs of a transverse section of the brain of adult pigeon #5X, stained by the Nissl method. The approximate area of photograph no. 1 (X 20) is indicated by square no. 1 and the area of photograph no. 2 (X 450) by square no. 2 on the line drawing of the section. Degeneration of cells of the superior vestibular nucleus 14 days after destruction of the auricle is shown in photograph no. 2.

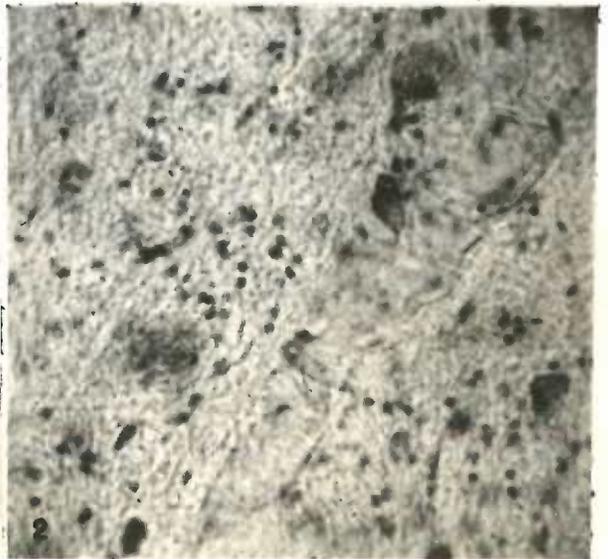
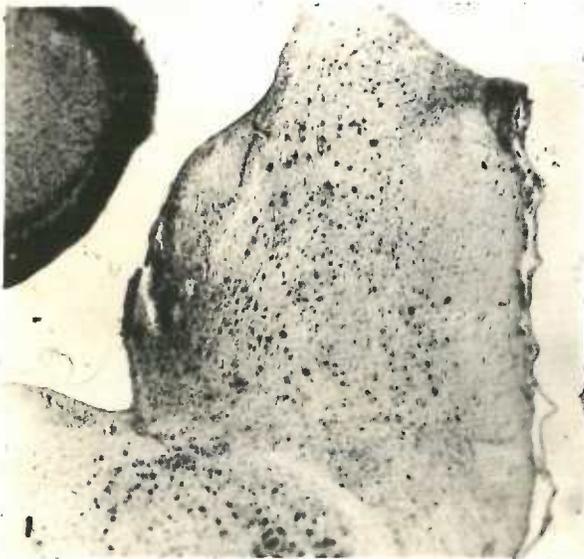
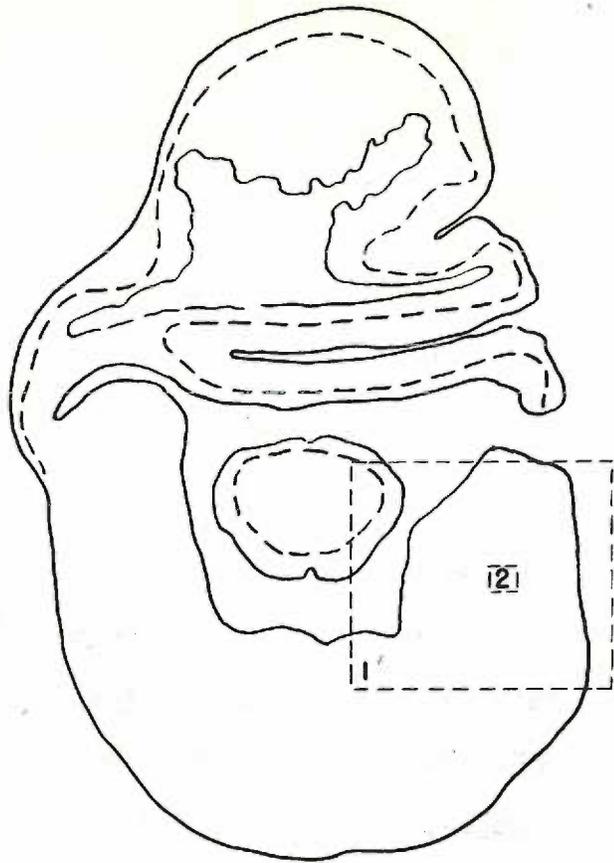


Figure 12. Photomicrographs of a transverse section of the brain of adult pigeon #73, stained by the Nissl method. The approximate area of the low (X 20) and high power (X 450) magnifications is indicated by square no. 1 and square no. 2, respectively. Photomicrograph no. 2 shows degenerating cells 14 days after destruction of dorsal surfaces of folia V, IV and VII.

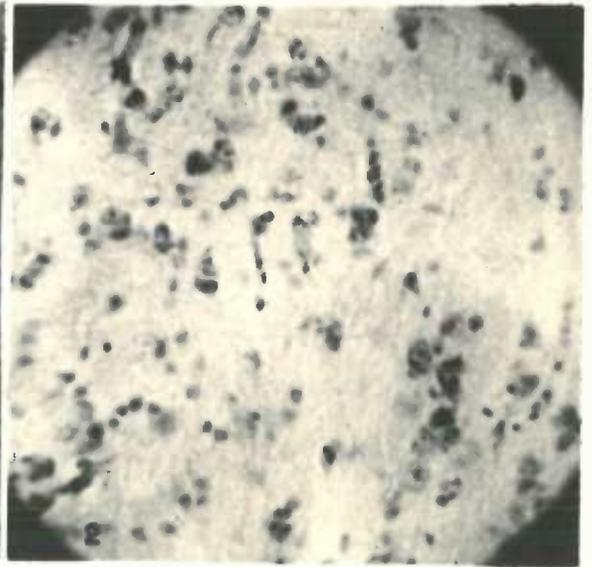
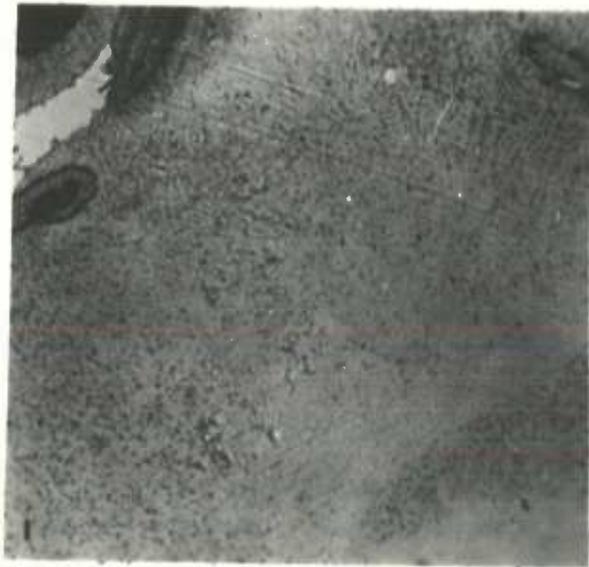
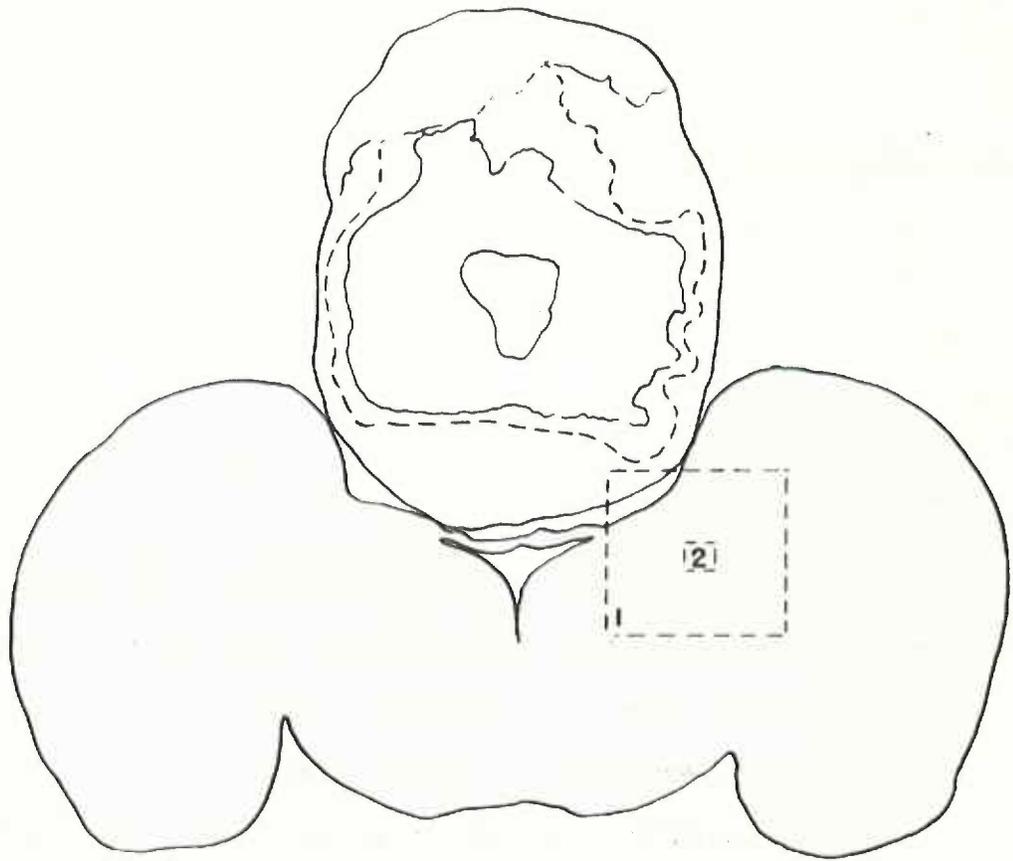


Figure 13. Outline tracings of sagittal sections of the brain of adult pigeon #8, following a lesion of the inferior olivary complex in the medulla oblongata. Stained by the Marchi method. Projection apparatus, X 10. The course and terminal distribution of the olivo-cerebellar fibers are indicated by the black dots.

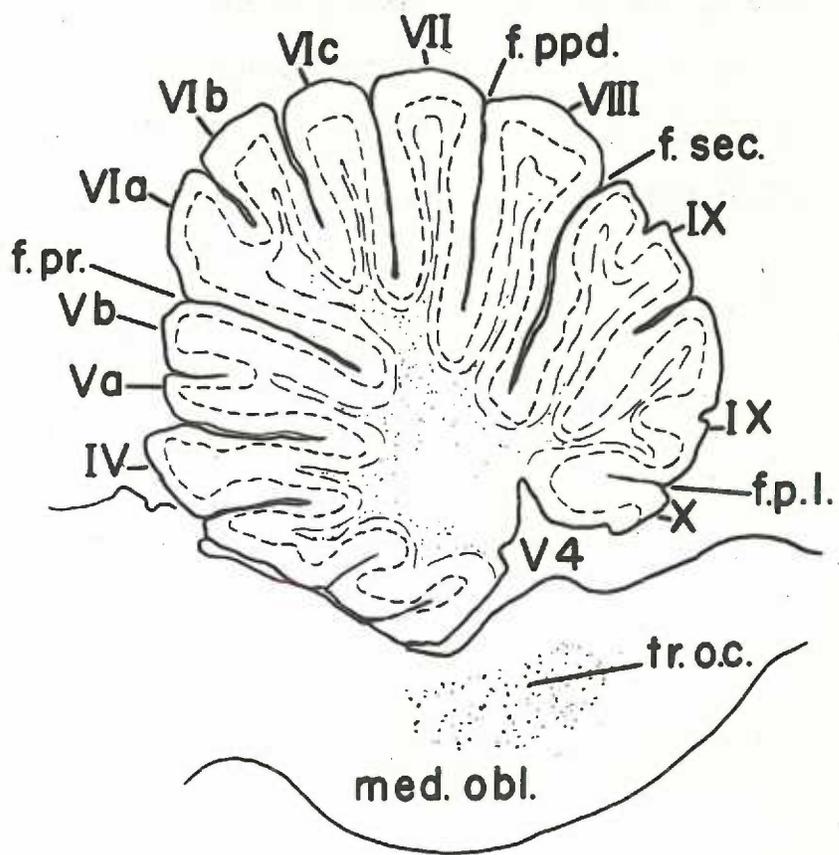
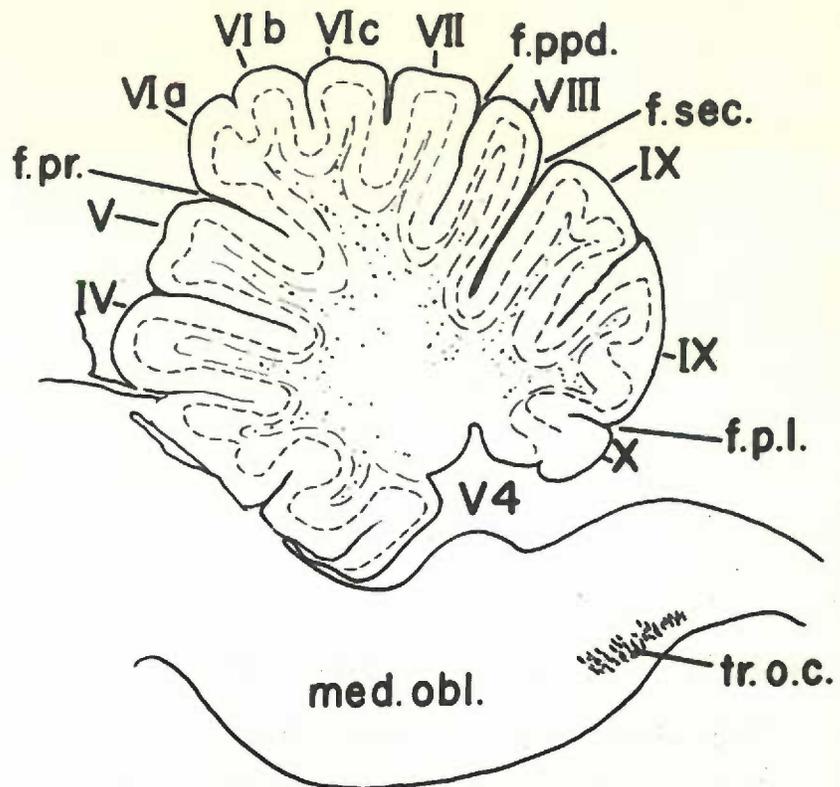


Figure 14. Outline tracings of sagittal sections of the same brain.

The course and distribution of the olivo-cerebellar tracts
are indicated.

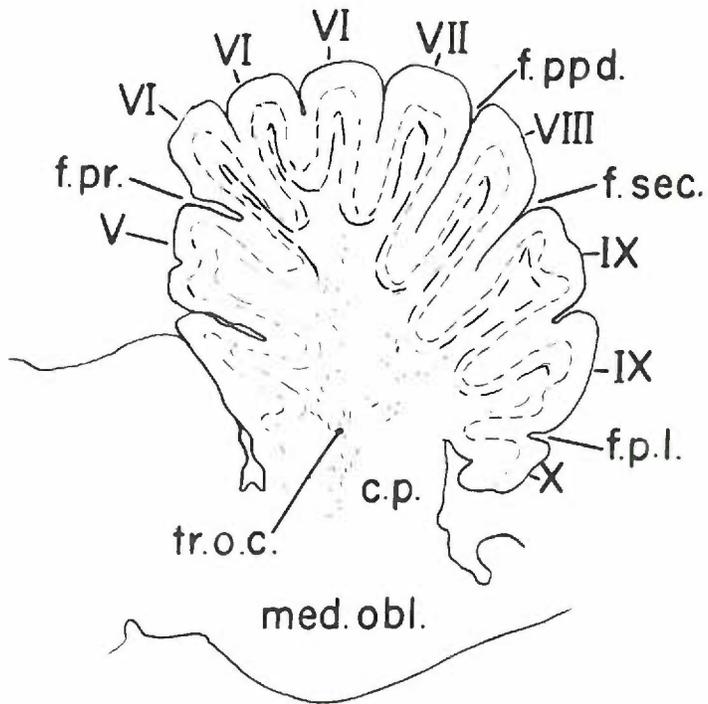
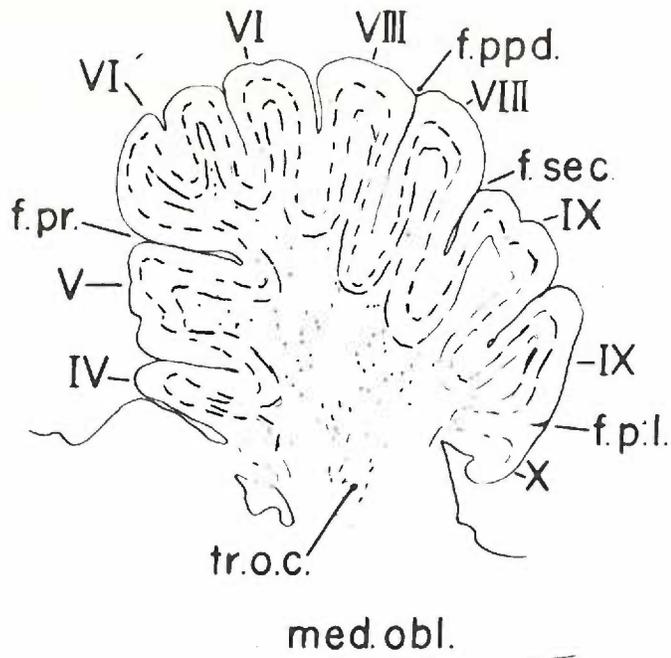


Figure 15. Photomicrographs of a transverse section of the brain of adult pigeon #8N, stained by the Nissl method. The low (X 20) and high power (X 450) magnifications represented approximately the area by square no. 1 and no. 2, respectively. Chromatolysis and degeneration of cells in the inferior olivary complex 10 days after destruction of the dorsal surface of folia V, VI, VII, and VIII are shown in photomicrograph no. 2.

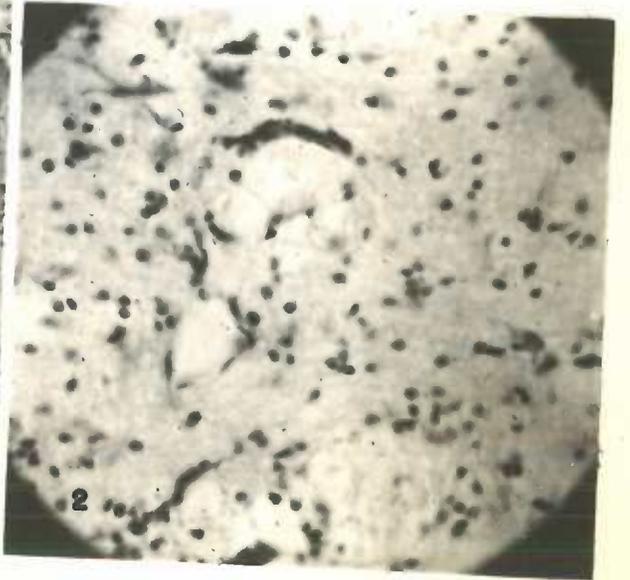
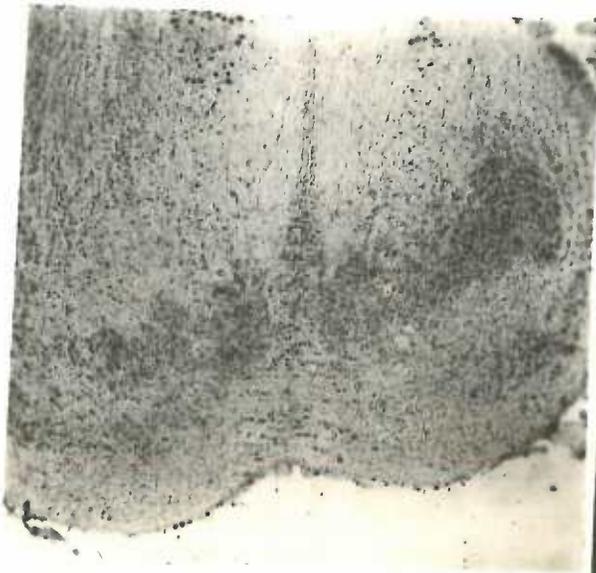
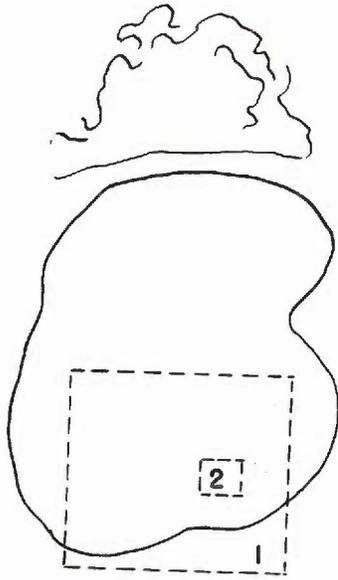


Figure 16. Photomicrographs of the brain of the same adult pigeon at the same magnifications as noted in figure 15. The approximate areas of photographs are indicated by squares 1 and 2 on the line drawing. Chromatolysis and degeneration of the cells of the pontine nuclei are shown in photomicrograph no. 2.

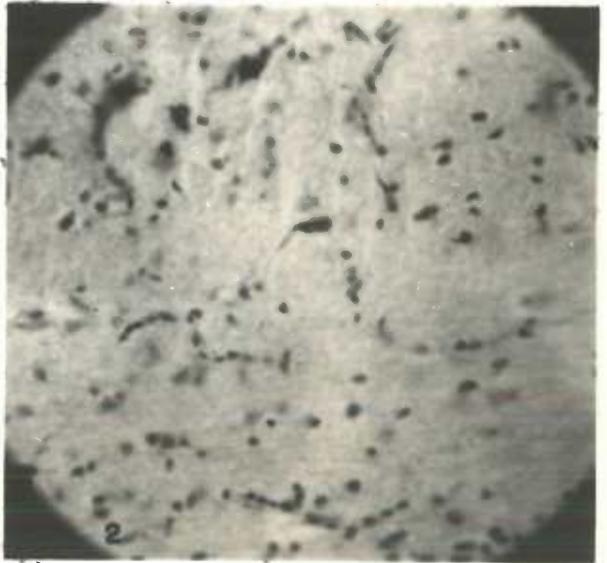
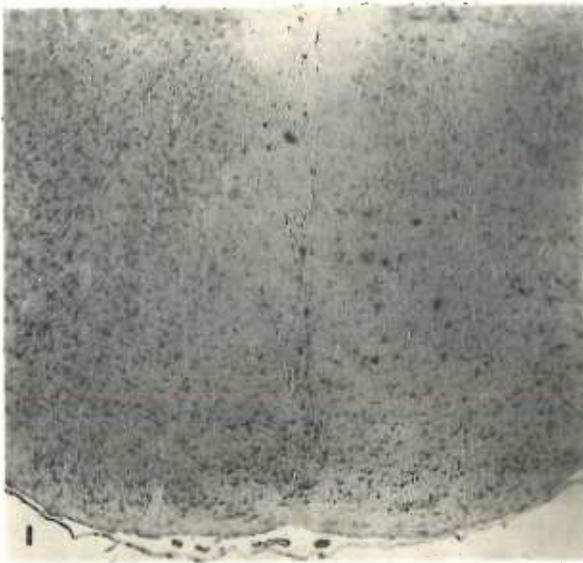
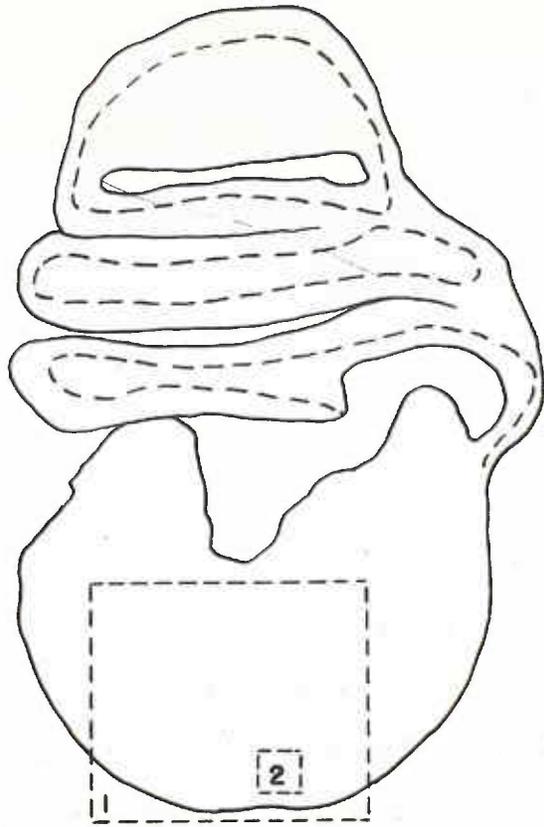


Figure 17. An illustration of the method employed in recording evoked potentials from the depths of the cerebellum. The responses were picked up between members of a pair of electrodes. Two pairs of electrodes comprise the electrode cable. The responses were first amplified (Amp.), then visualized or photographed as desired on a matched dual cathode-ray oscilloscope (C.R.O.). The photograph of the electrode cable in situ in adult pigeon cerebellum indicates its appearance in the cleared brain.

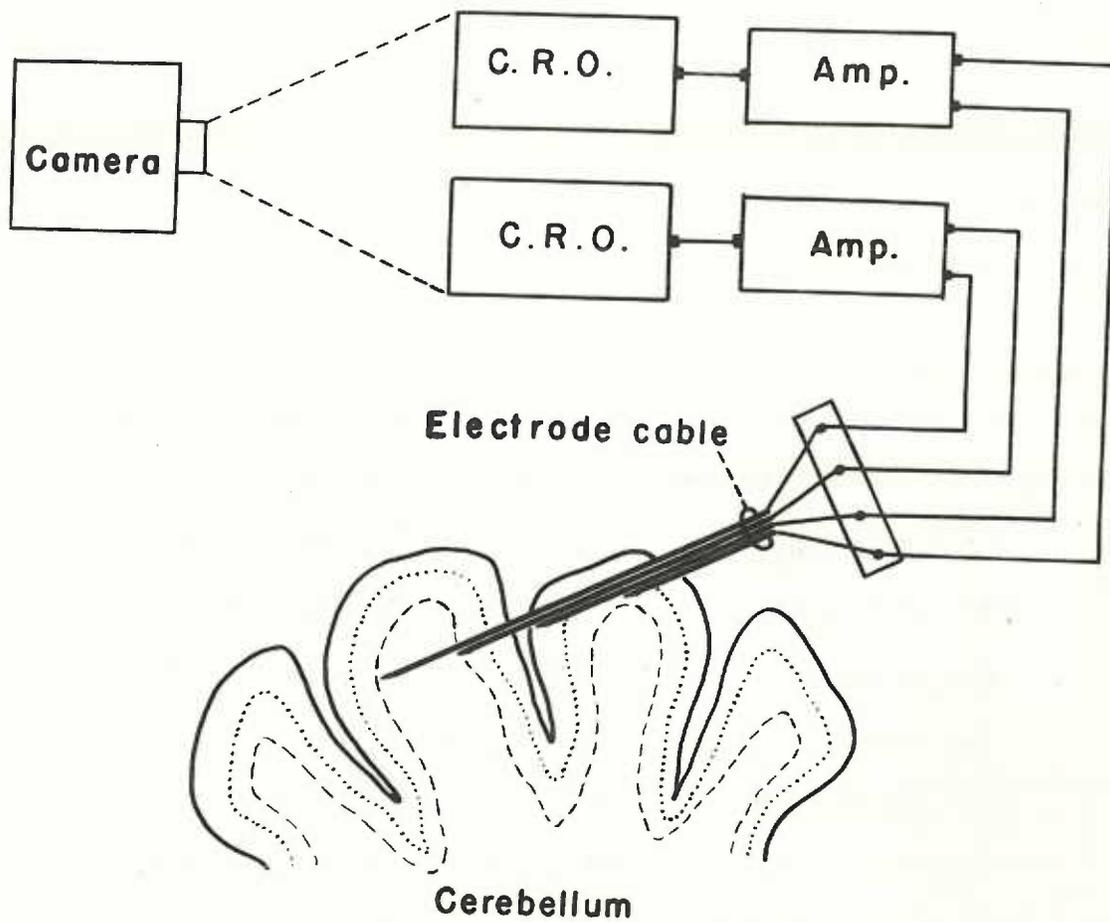


Figure 13. Composite diagrams of total number of active points located in the cerebellum of pigeon as plotted on mid-sagittal (A), anterior (C) and posterior (B) views. The stimulation of a peripheral nerve or of a tactile receptor or of various parts of the body, as well as auditory or visual receptors, are indicated as follows:

	Nerve Stimulation	Physiological Stimulation
Tail	◇	◆
Leg	○	●
Wing	△	▲
Face	□	■
Auditory		+
Visual		×
Tectal	T	

The active points are projected to the surface of the folium from which they were recorded in the anterior and posterior views.

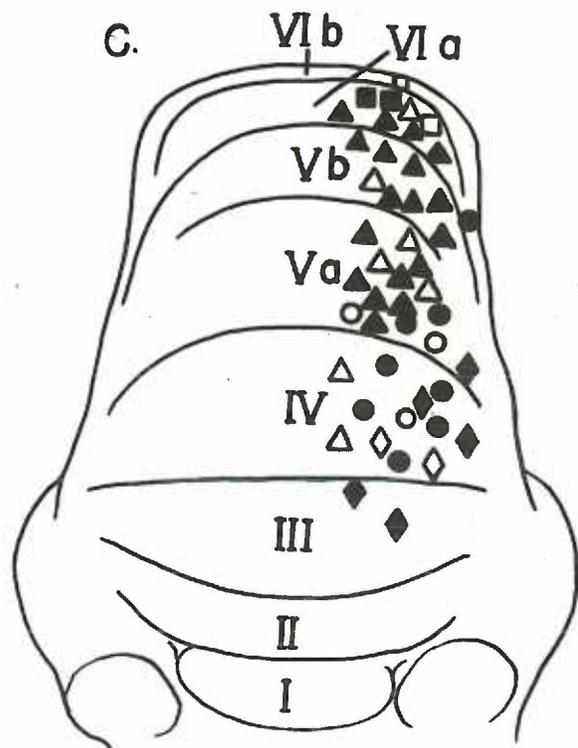
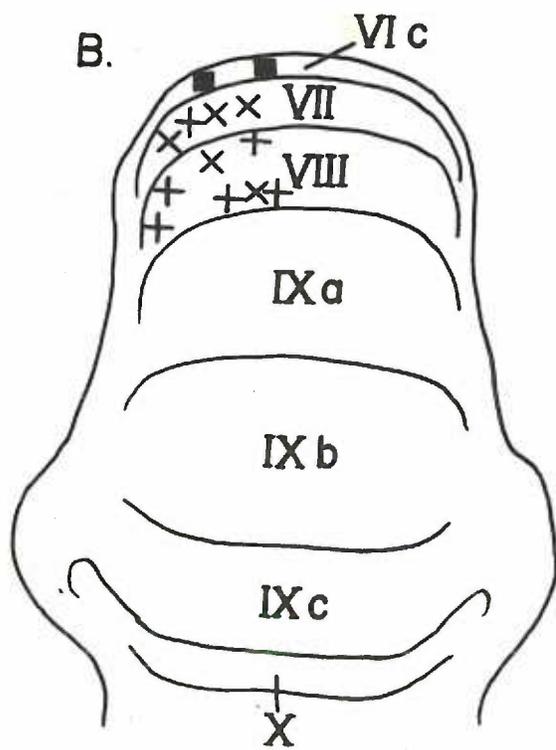
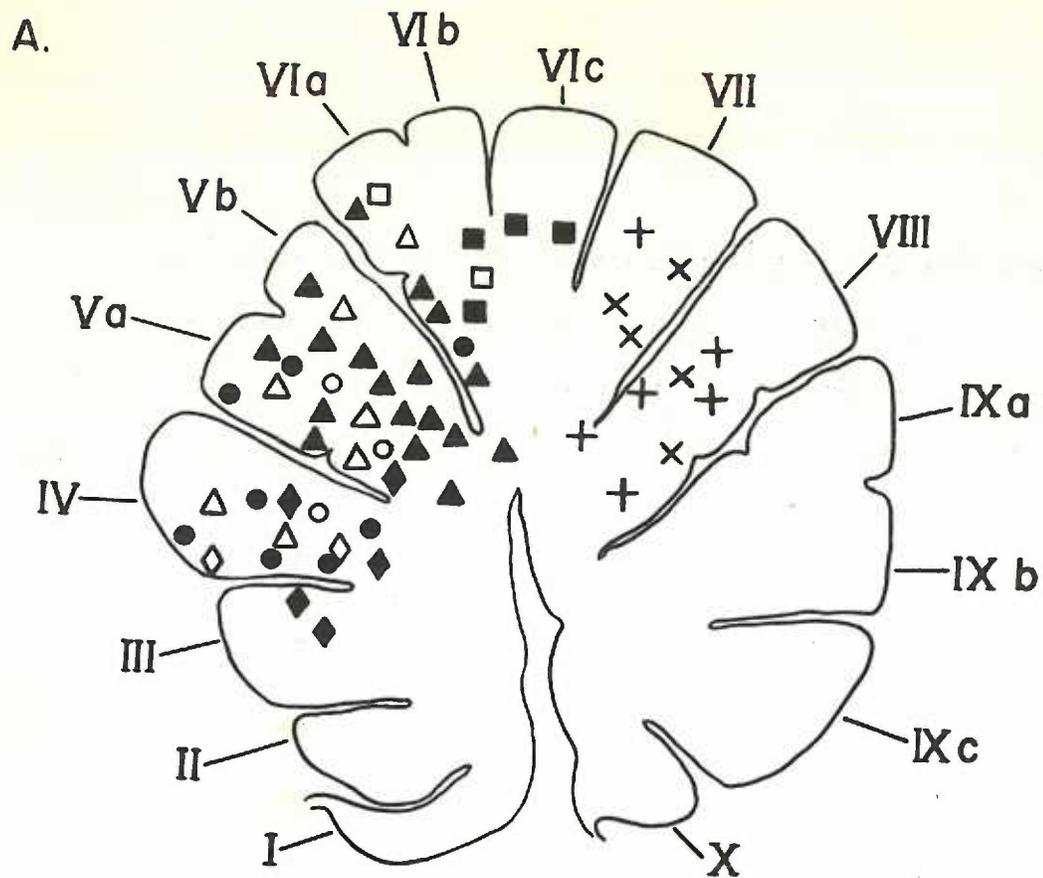
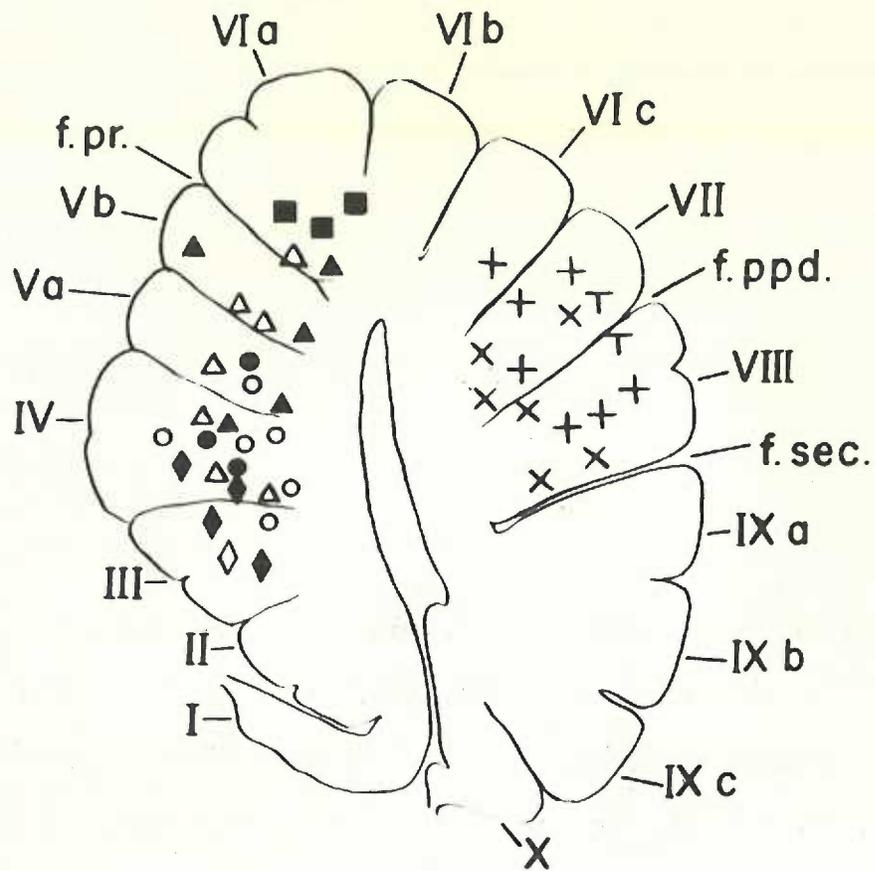
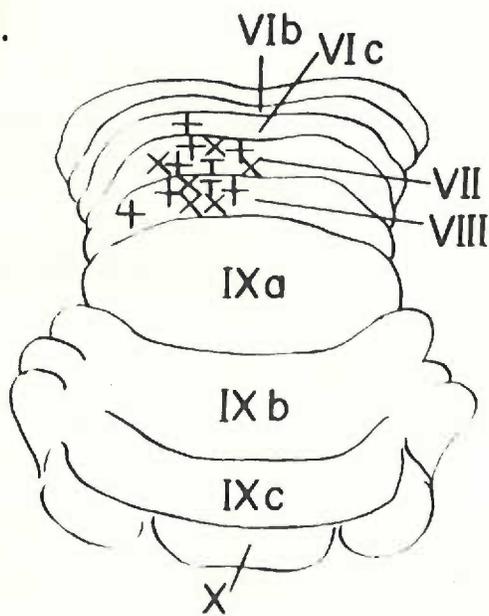


Figure 19. Composite diagrams indicating total number of active points located in the cerebellum of the adult owl as plotted on midsagittal (A), anterior (C) and posterior (B) views. The type of stimulation and region of the body is represented by the same symbols employed in figure 18.

A.



B.



C.

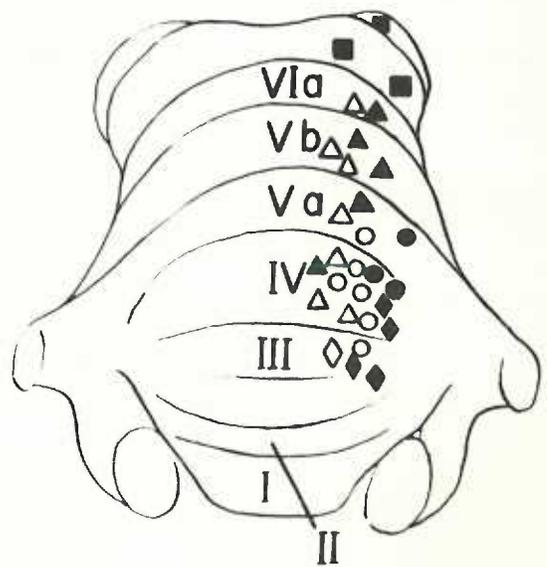
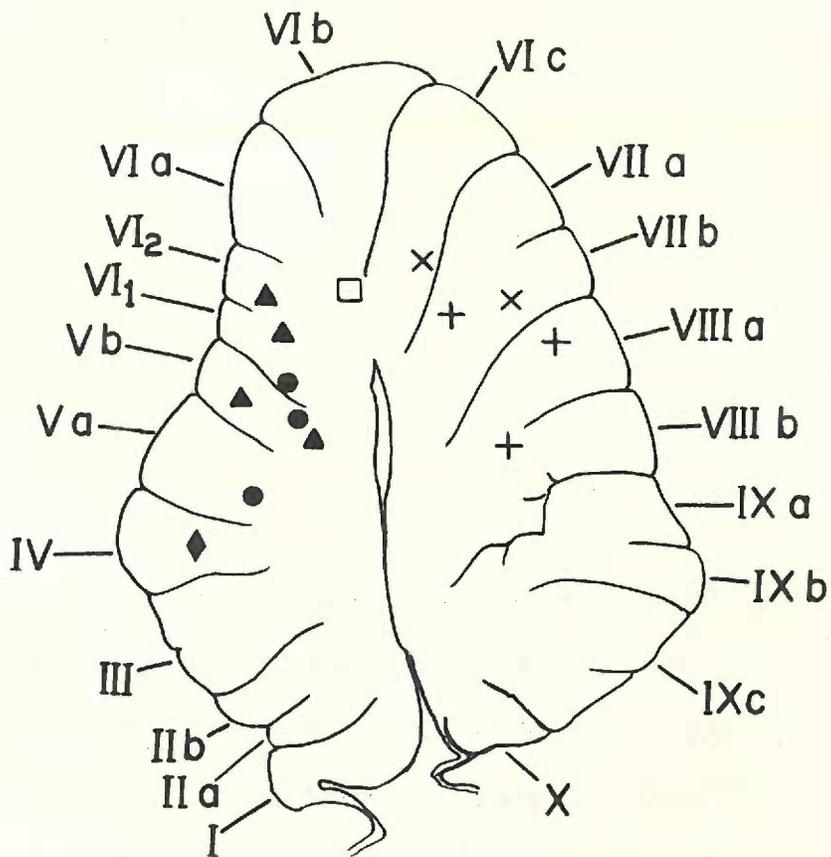
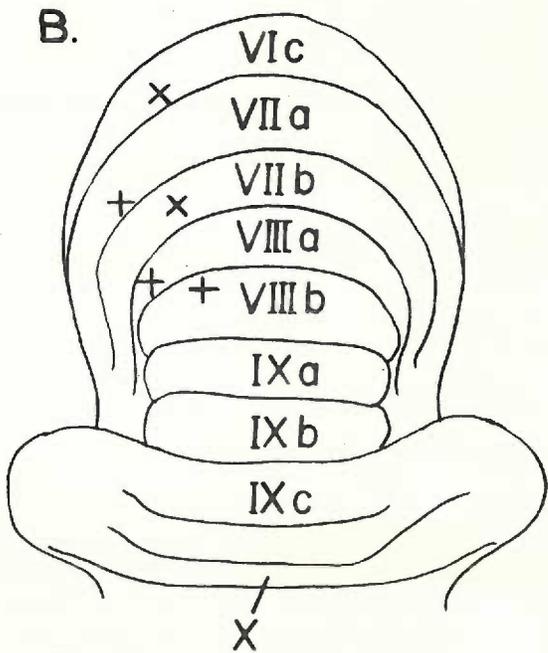


Figure 20. Composite diagrams indicating total number of active points located in the cerebellum of adult duck as plotted on midsagittal (A), anterior (C) and posterior (B) views. The types of stimulation and regions denoted by the symbols are described in figure 18.

A.



B.



C.

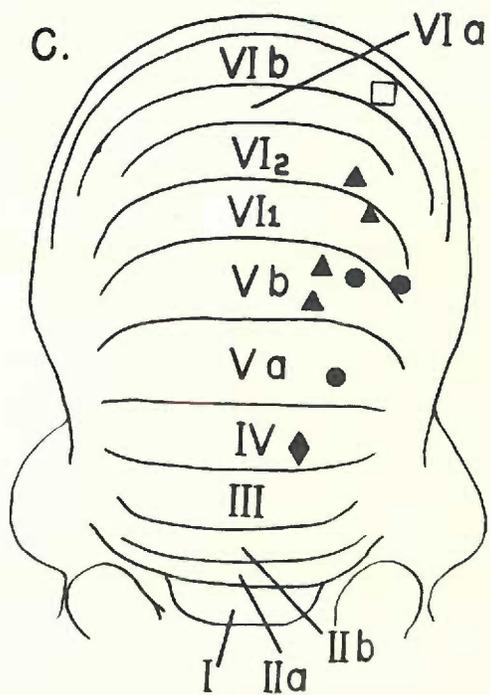


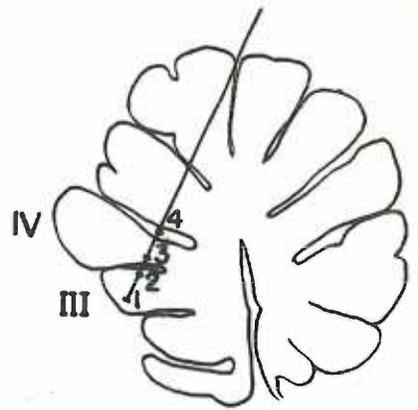
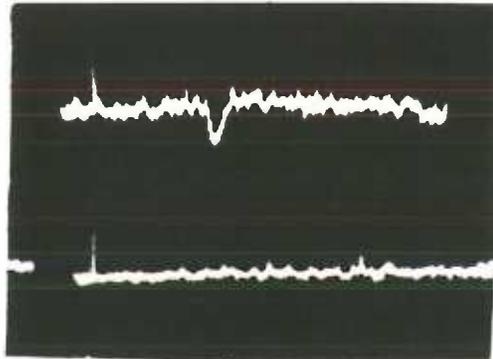
Figure 21. Photographs of groups of oscillograms recorded from the pigeon cerebellum following tactile stimulation of tail, leg and wing. The location of the recording electrode and its exposed tips is indicated in each case on the midsagittal and anterior views at the right. The upper two groups (A) of traces represent responses recorded from a single electrode placement in experiment #20 following stimulation of the tail feathers and then of the leg feathers. The tactile tail response is present only between electrode 1 and 2 while the tactile leg response is to be noted only between electrodes 3 and 4. The lower two groups (B) also represent a single electrode placement in experiment #35. The tactile leg response in this case is located between electrodes 1 and 2, while the tactile wing response is present only between electrodes 3 and 4.

A.

1-2

TAIL

3-4

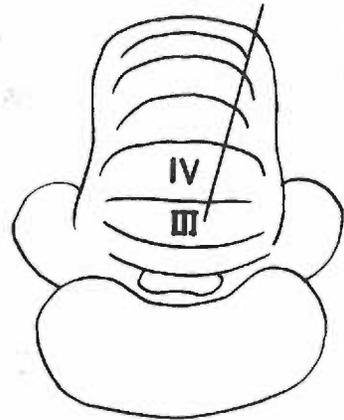


1-2

LEG

3-4

10 msec.

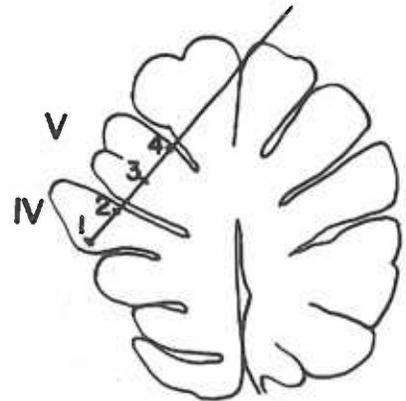
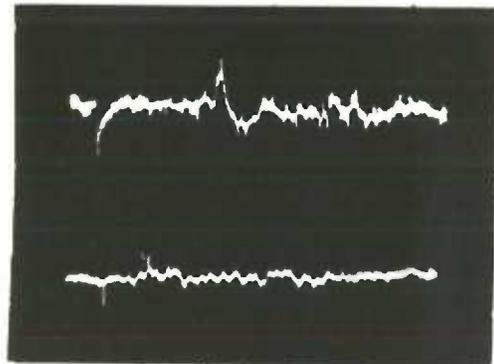


B.

1-2

LEG

3-4



1-2

WING

3-4

10 msec.

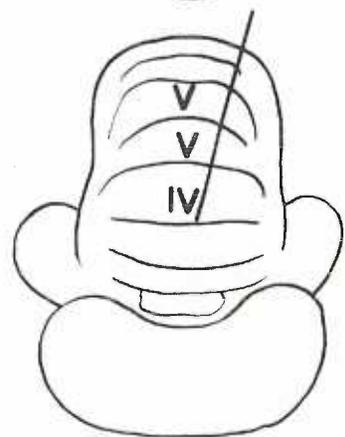
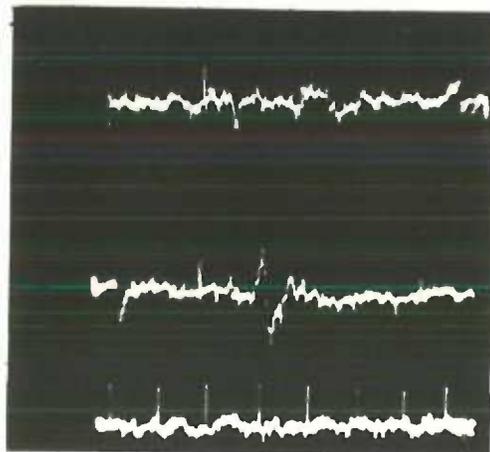


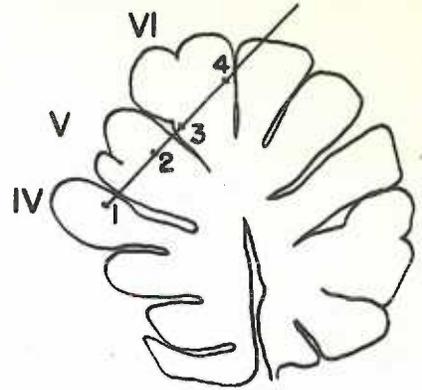
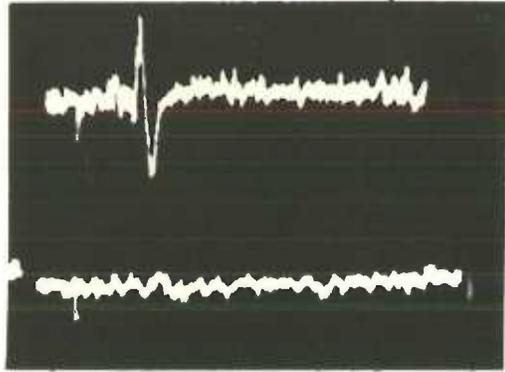
Figure 22. Photographs of oscillograms recorded from the cerebellum of a pigeon following tactile stimulation of the wing, face and tail. The position of the recording electrodes is indicated in each case in the diagrams on the right. The upper two groups of traces (A) demonstrate responses recorded from a single electrode placement in experiment #13 following tactile activation of the feathers of the wing and of the face. The tactile wing response is present only between electrodes 1 and 2 while the tactile face response is apparent only between electrodes 3 and 4. The lower two groups of traces (B) show responses recorded from an electrode placement in experiment #16 showing tactile wing responses only between electrode 3 and 4 while tactile tail responses are noted only between electrodes 1 and 2.

A.

1-2

WING

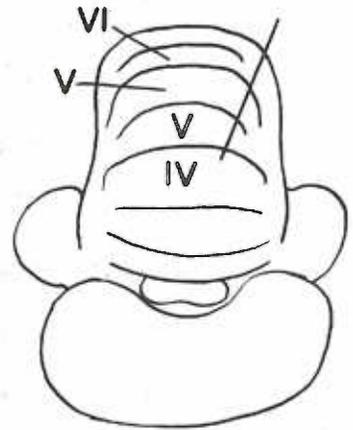
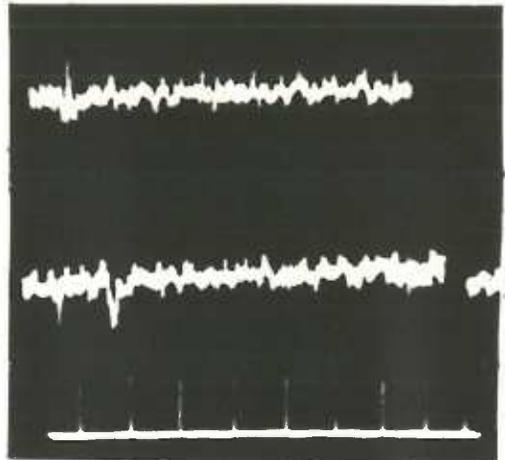
3-4



1-2

FACE

3-4



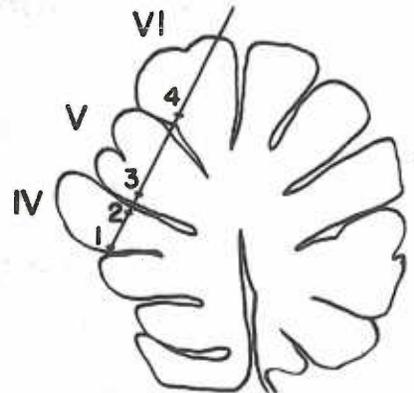
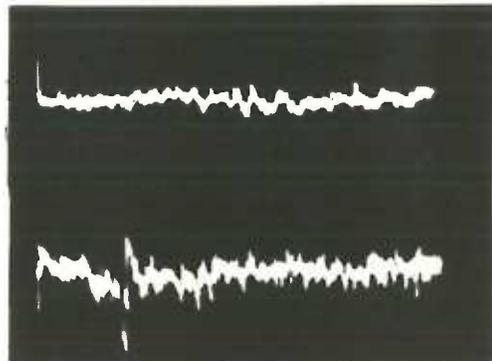
10 msec.

B.

1-2

WING

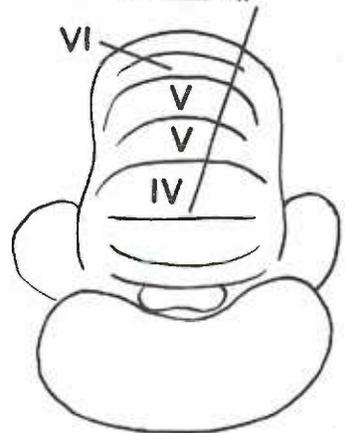
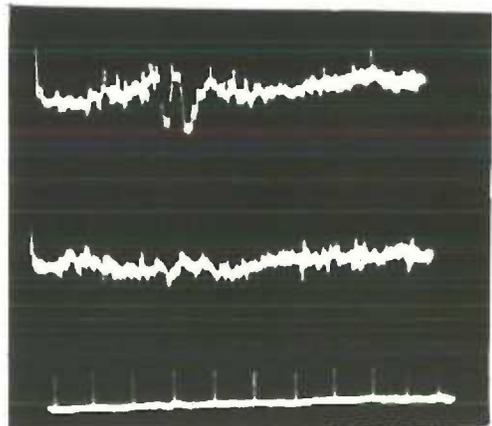
3-4



1-2

TAIL

3-4



10 msec.

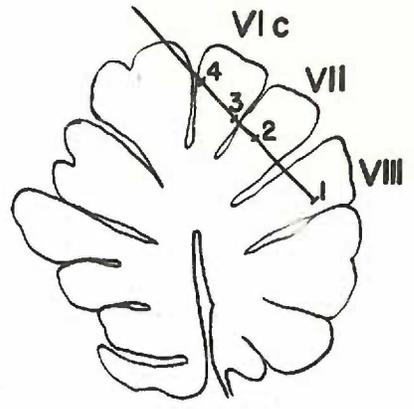
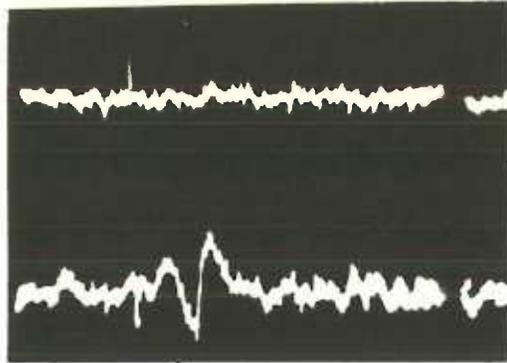
Figure 23. Photographs of oscillograms recorded from the pigeon cerebellum following tactile stimulation of the face as well as stimulation of the auditory and visual receptors. The position of the recording electrodes is indicated on the diagrams at the right. The upper two groups of traces (A) represent responses recorded from a single electrode placement in experiment #26 following firstly tactile stimulation of the face and secondly auditory stimulation. The tactile face response is recorded only between electrodes 3 and 4; the auditory response only between electrodes 1 and 2. The lower two groups of traces (B) represent a cerebellar response to stimulation of the visual receptors of the contralateral dark adapted eye which occurred only between electrodes 3 and 4 in experiment #31. The complex response of the tectum, which was recorded during visual stimulation, is also indicated.

A.

1-2

FACE

3-4

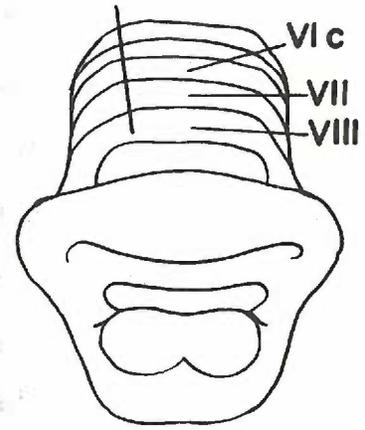
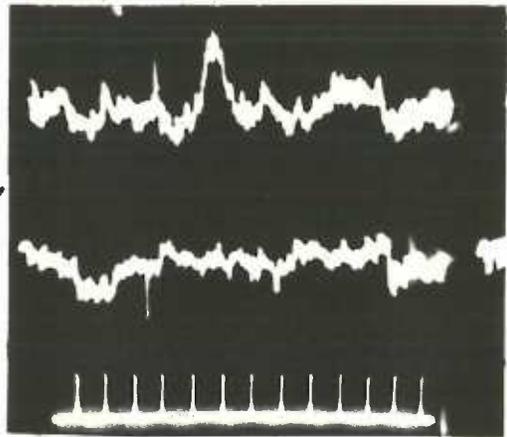


1-2

AUDITORY

3-4

10 msec.

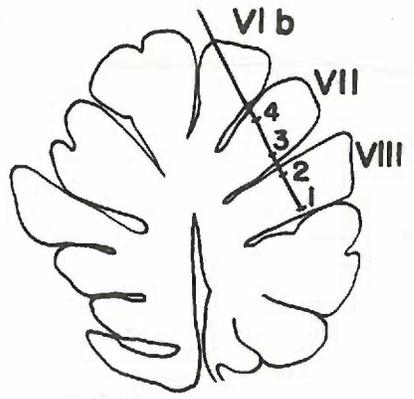
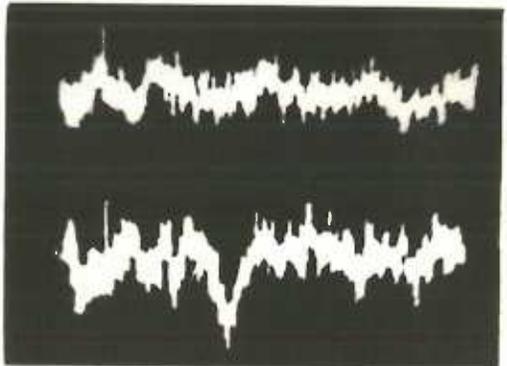


B.

1-2

VISUAL

3-4



TECTUM

10 msec.

