

the neural crest of the chick are illustrated in Figs. 1545 and 1546. The development of the neural crest of man is somewhat different, as may be seen in the three stages illustrated in Fig. 1547.

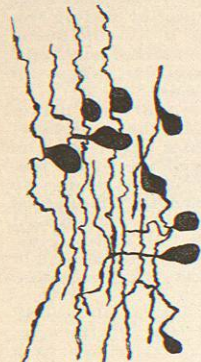


FIG. 1549.—Transformation of Bipolar into Unipolar Ganglion Cells in the Gasserian Ganglion of an Embryo Guinea-pig. (After Van Gehuchten.)

The two poles of these cells are at first opposite (Fig. 1548), but become gradually approximated until finally the cellulifugal and the cellulipetal fibres unite for a short distance and the cell becomes unipolar. Several stages in this process are shown in the accompanying figure of the Gasserian ganglion (Fig. 1549).

The motor roots, as is well known, grow out from cells lying in the ventro-lateral zone of the neural tube (Figs. 1550 and 1551). The general arrangement of the cranial nerves of the adult man are indicated in Fig. 1552, while their origins from the medulla oblongata are shown more in detail in Figs. 1553 and 1554, and their foramina in Fig. 1555.

NERVES OF THE SPINAL TYPE.—The composition of the typical spinal nerve we have already given. The distribution of the chief branches of such a nerve in the thoracic region is indicated in the accompanying figure (Fig. 1556).

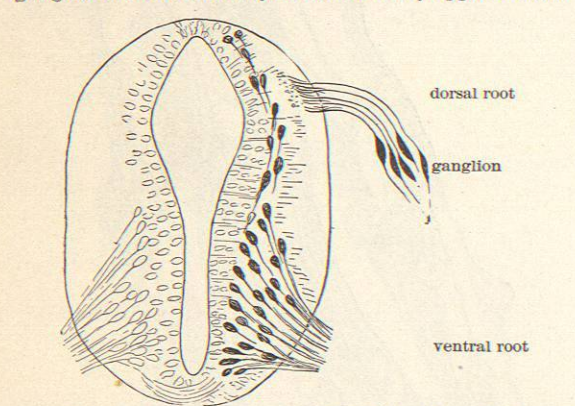


FIG. 1550.—Section through the Spinal Cord of a Human Embryo of four to four and one-half weeks. (After Edinger.)

connection with one or more of these roots, and rarely in the adult the last one bears a small vestige of the ganglion.

The nucleus of origin of the XII. nerve lies ventrolaterally of the tip of the fourth ventricle and is the continuation of the ventral horn of the cervical cord. The root fibres arise chiefly (and according to most authorities

wholly) from the nucleus of the same side. The nucleus receives from its lateral and ventral sides a very large number of delicate terminal fibres, including doubtless reflex fibres from the sensory nerves and motor fibres from the cortex. The latter are chiefly collaterals from the pyramids, but partly, according to Hoche, terminals of fibres running down mingled with the fibres of the mesial fillet. The hypoglossus fibres emerge in from ten to fifteen rootlets, pass through the anterior condylar foramen, effect connections with the superior cervical ganglion of the sympathetic, the vagus, the first three cervical nerves, and the lingual branch of the trigeminus. They distribute mainly to the muscles of the tongue, viz., the styloglossus, hyoglossus, genio-hyoid, genio-glossus, and the intrinsic muscles of the tongue.

NERVES OF THE BRANCHIOMERIC TYPE.—XI. The accessory nerve consists of two parts: (1) the accessorius vagi is really a bundle of detached filaments of the vagus, containing inhibitory fibres for the heart, motor fibres

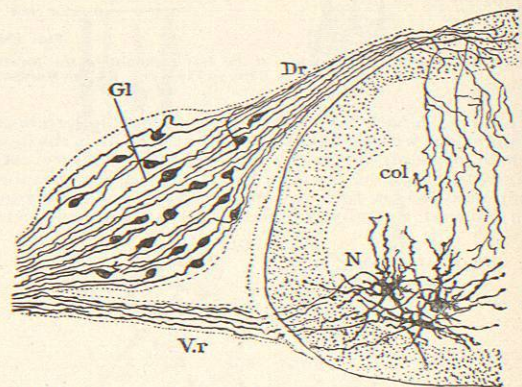


FIG. 1551.—Transverse Section of the Spinal Cord of a Chick at the ninth day of incubation. (After Ramón y Cajal.) Vr, Ventral root fibres, arising from ventral horn cells; N, Dr, dorsal root fibres, arising from ganglion cells; Gl; col, collaterals, from the latter fibres.

for the pharynx, etc.; (2) the accessorius spinalis arises from the lateral aspect of the spinal cord as far back as the fifth or sixth cervical vertebra in numerous separate strands. These fibres are motor and arise from the lateral cornu of the cord. They turn cephalad and are collected into a single trunk and emerge through the same foramen as the vagus. They supply the sterno-mastoid and trapezius muscles.

The morphology of the accessorius spinalis is still rather obscure. Its nucleus is a strand of cells lying in the lateral cornu and extending as far forward as the level of the lower third of the olive. In some fishes and amphibians, though a distinct accessorius is absent, yet certain fibres of the motor root of the vagus arise farther caudally than the others and supply the trapezius muscle. These are regarded as the representatives of the accessory nerve. As we pass upward in the animal series, the accessorius nucleus is extended farther caudad into the lateral horn region and this nerve is more clearly separable from the vagus. The distinction between the vagal and the spinal portions of the accessorius in any case is not of profound morphological significance, since both the accessorius and the motor vagus belong to the same component, the visceromotor, and both are differentiated from the lateral horn zone.

IX. and X. The vagus, or pneumogastric, and the glossopharyngeus are concerned primarily with the respiratory and nutritive mechanisms. In lower vertebrates they are typical branchial nerves, or rather, the vagus is a fusion of several such, the number of branchiomeres represented corresponding to the number of gill clefts minus one, the first cleft being supplied by the IX. pair. In the lowest

fishes these branchial nerves are quite separate from each other and each forks around a single gill cleft. In higher

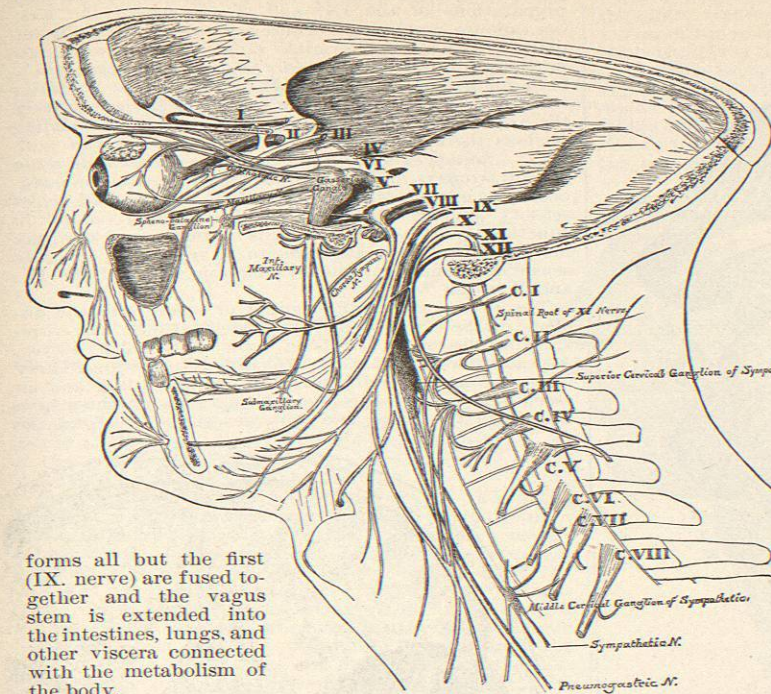


FIG. 1552.—General View of the Cranial Nerves. (Altered from Allen Thomson.)

forms all but the first (IX. nerve) are fused together and the vagus stem is extended into the intestines, lungs, and other viscera connected with the metabolism of the body.

The gill arches and their appendages are essentially visceral structures, and this has influenced the composition of these nerves. Except in some lower vertebrates, the vagus region contains no somatic muscles. When such muscles are present, they seem to be innervated from post-vagal spino-occipital nerves. Accordingly neither the vagus nor any of the other branchiomeric nerves contain somatic motor components. The general cutaneous component, too, has been greatly reduced in the post-trigeminal members of the series, the skin of this region being for the most part supplied either from behind by the spinals or from in front by the trigeminus. The vagus and glossopharyngeus, accordingly, have the following composition: (1) a small number of general cutaneous fibres, (2) visceral sensory fibres, (3) visceral motor fibres. In the fishes a large root of the lateral line system of nerves goes out through the vagus foramen and is conventionally associated with the vagus, though it has no morphological connection with it and is not represented at all in the higher animals. Compare the diagram of the acustico-lateral system, Fig. 417, Vol. I.; article *Auditory Nerve*.

1. In the fishes and amphibians the relations of the general cutaneous fibres are accurately known. Arising in a special ganglion on the root of the vagus (the jugular ganglion of Shore and Strong), they enter the spinal V. tract, to terminate about the cells associated with this tract. Peripherally they comprise dorsal branches of the nerve which supply the skin of the occipital region above and external to the gill chamber. In man most authorities describe the vagus root as simply passing through the spinal V. tract. Since, however, there is a general cutaneous twig supplying the corresponding region of the periphery (the ramus auricularis vagi, innervating the skin behind the ear),

it is probably true that in man also some vagal fibres terminate in the spinal V. tract, as the gray matter associated with this tract is the only terminal nucleus in the oblongata known for general cutaneous fibres. Cajal, moreover, has demonstrated fibres entering the spinal V. tract from the IX. root.

2. The remaining sensory fibres belong to the visceral system. Their peripheral distribution in the case of the vagus is very wide, viz., to the mucous surfaces of the pharynx and to the thoracic and abdominal viscera. The presence of these latter fibres is the probable explanation of the small number of the visceral sensory fibres in the spinal nerves. They spring mainly from the ganglion of the trunk (g. nodosum). Proximally of the ganglion these sensory fibres cannot easily be distinguished from the smaller motor fibres. Together they enter the oblongata in a series of twelve or more filaments in the groove between the olive and the restiform body. In lower vertebrate types the visceral sensory (communis) component of both the IX. and X. nerves contributes fibres for the general sensory innervation of the mucosa of the pharynx and adjacent regions, and in addition a still larger number

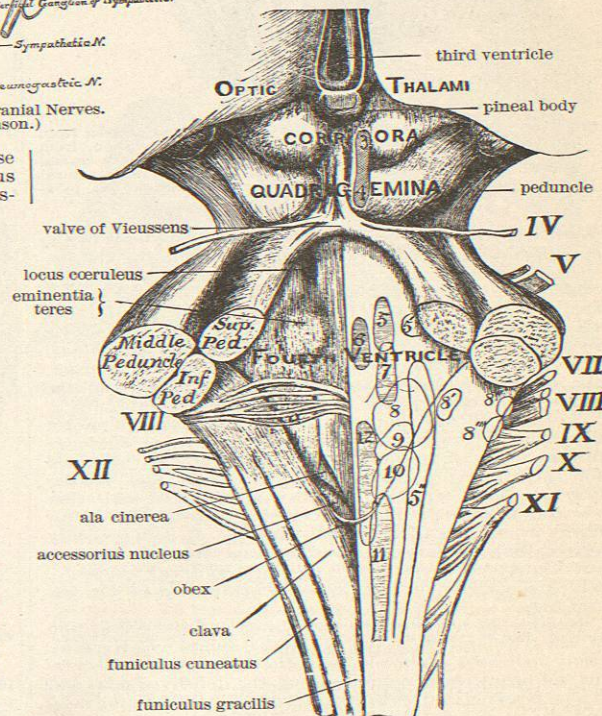


FIG. 1553.—The Medulla Oblongata as Seen from the Dorsal Side, slightly enlarged. (Adapted from Landois.) The Roman numerals indicate the superficial origins of the cranial nerves, the Arabic numerals their deep origins.

of fibres to the large taste buds plentifully scattered over the gills. In all cases the IX. sends a branch forward on to the dorsal surface of the hyoid (rudimentary tongue).

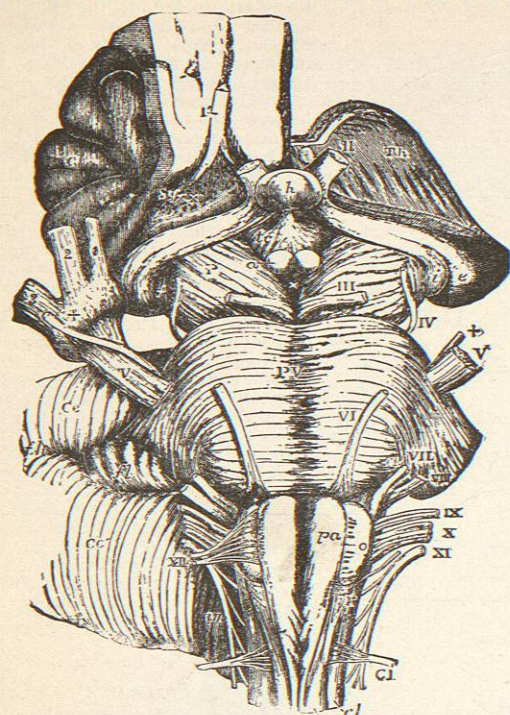


Fig. 1554.—The Medulla Oblongata and Parts Adjacent as seen from the Ventral Side. Natural size. (After Allen Thomson, from Quain's "Anatomy.") The Roman numerals refer to the cranial nerves; ca, ventral column of cord; cl, lateral column; ventral median fissure of cord; o, olive; P, cerebral peduncle; pa, pyramid; PV, pons Varolii.

With the disappearance of the gills, the taste buds of the corresponding regions vanish, and, accordingly, the lingual branch of the IX. is the only nerve of this complex which serves the function of taste in man, though, as we shall see beyond, the VII. nerve also participates. The IX. nerve of man enters the brain by some five or six rootlets in a line directly continuous with the vagus roots. The general cutaneous fibres enter the spinal V. tract, the communis fibres the fasciculus solitarius, and the motor fibres the cephalic end of the nucleus ambiguus.

3. In the fishes there are clearly two kinds of motor fibres in the vagus and glossopharyngeus, viz., large fibres arising from the nucleus ambiguus and destined for the striated musculature of the gills, and smaller fibres destined for the unstriated oesophageal and other visceral muscles of uncertain origin. Most of the motor fibres in man are of the small variety. It is universally agreed that they arise, in part at least, from the nucleus ambiguus (accessory vago-glossopharyngeal nucleus), which is a highly differentiated continuation of the lateral horn.

Besides the nucleus last mentioned and the connection of the IX. and X. roots with the spinal V. tract already indicated, there are two other centres, the fasciculus solitarius (fasc. communis of the Ichthyopsida) and the cells associated with it to form the "spinal nucleus," and the so-called "chief nucleus," the latter lying dorsomedially of the fasciculus between it and the IV. ventricle. It has been commonly held that the sensory vagus terminates mainly in the chief vago-glossopharyn-

geus nucleus, but partly in the fasciculus solitarius, while the IX. terminates chiefly in the fasciculus, but partly in the chief nucleus. Cajal from a study of Golgi preparations of the IX. and X. nerves of the newborn mouse concludes: "There are, therefore, in this animal not two sensory terminal clusters, nor two separate portions for the two nerves. A single root common to both nerves passes over into the fasciculus solitarius without loss of any fibres, in such a way that between the upper or chief nucleus and the lower or descending nucleus there is no distinction aside from that of position." Some years ago Forel, and since him several other careful workers, by a variety of the degeneration methods, have come to the conclusion that the so-called "chief sensory nucleus" is either wholly or largely motor in function, and that the fasciculus solitarius and the gray matter immediately adjacent to it represent the only sensory terminus for these communis fibres of the IX. and X. roots.

The presence of a descending or spinal root and nucleus in these nerves may be correlated with the corresponding feature of the dorsal roots of the spinal nerves. As each dorsal root fibre typically divides immediately upon entrance into the cord into a descending and an ascending limb, so here the entering sensory fibres have been seen to divide, one limb descending to form the

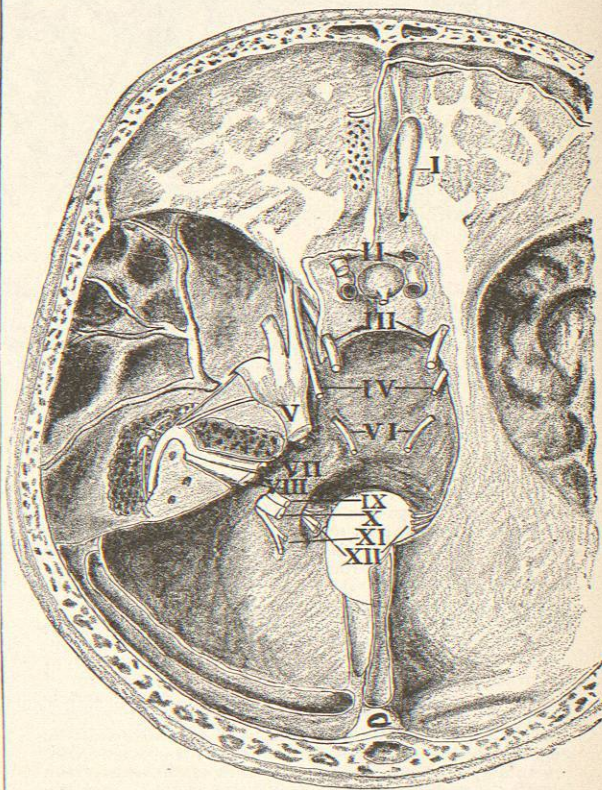


Fig. 1555.—The Base of the Skull, showing the Exits of the Cranial Nerves.

fasciculus solitarius and enter the spinal nucleus. The sensory roots of the VIII., VII., and V. nerves exhibit the same peculiarity.

The peripheral relations of the vagus and glossopharyngeus are illustrated in the accompanying figure (Fig. 1557). The lingual branch of the IX. supplies the

mucous membrane and circumvallate papillae of the back part of the tongue, the pharyngeal branches supply the stylo-pharyngeus muscle, and perhaps some of the con-

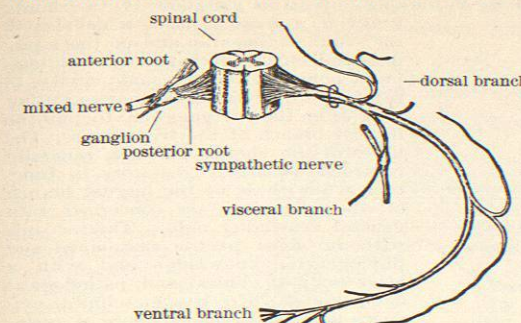


Fig. 1556.—Diagram of a Spinal Nerve of the Thoracic Region.

strictors of the pharynx, together with the mucous membrane adjacent. By its tympanic branch (nerve of Jacobson) it supplies the mucous lining of the middle ear. It communicates with the V., VII., and X. and sympathetic nerves.

The vagus communicates with the VII., IX., XI., XII., I. and II. spinals, and the sympathetic. Its distribution is extensive, comprising branches to the dura mater, external ear, pharynx, larynx, heart, lungs, stomach, and other viscera. Throughout its entire extent the vagus is in frequent communication with the sympathetic, and it seems to share many of its functions with the latter. It controls, more or less directly, the more important automatic and vegetative functions of the body, such as circulation and digestion, and is thus of the most profound physiological significance. Its vaso-motor function is of the most far-reaching significance. It carries three types of cardiac fibres, viz., accelerator, inhibitory, and depressor, the latter acting centripetally to produce reflexly a slowing of the heart. Trophic fibres have frequently been described in the vagus, though the weight of evidence now points to the belief that such fibres have no separate existence.

VII. Facialis.—In the lower fishes the facialis is a typical branchiomeric nerve. The hyoid arch is a modified gill arch, as evidenced by perfect gills on its posterior face, and it is separated from the mandibular arch by the spiracular cleft, around which the facialis forks in just the same way as the branchial nerves fork around their respective gill clefts (cf. Fig. 1537). The facialis, too, has the typical roots, viz., visceral motor and visceral sensory (communis), the latter very large in lower vertebrates but small in man and known as the portio intermedia of Wrisberg. It always has a ganglion, the geniculate ganglion. Moreover, the facial branches have the typical composition, the post-trematic nerve being motor and sensory, the pre-trematic and the palatine exclusively sensory. The post-trematic ramus corresponds to the main facial trunk in man, the pre-trematic, or a portion of it, probably to the chorda tympani, and the palatine is unquestionably the great superficial petrosal of human anatomy, the spiracular cleft being represented by the Eustachian tube. In none of the lower vertebrates do general cutaneous fibres emerge from the brain with the facial roots, though they may enter the facial trunk peripherally, running back into it from the Gasserian ganglion. In the Ichthyopsida a very large root of the acustico-lateral system joins the facialis, passing out with the post-trematic ramus to supply the lateral line organs of the mandible (see *Auditory Nerve*, Fig. 417, Vol. I.).

Between these lower vertebrates and man the facial nerve undergoes a striking metamorphosis. There it is a large nerve, chiefly sensory, whose sensory fibres have

a very wide distribution to specialized sense organs of the inside of the buccal cavity and also to varying extents all over the outer skin of the head and trunk, while the motor component is small and confined to the innervation of the muscles of the hyoid arch. In man, on the other hand, the sensory portion has dwindled to so small proportions as to have been quite ignored by many anatomists, while the peripheral distribution area of the motor portion has been enlarged to include almost the whole of the superficial facial musculature. The reduction of the sensory component is explained by the loss of the corresponding sense organs in air-breathing verte-

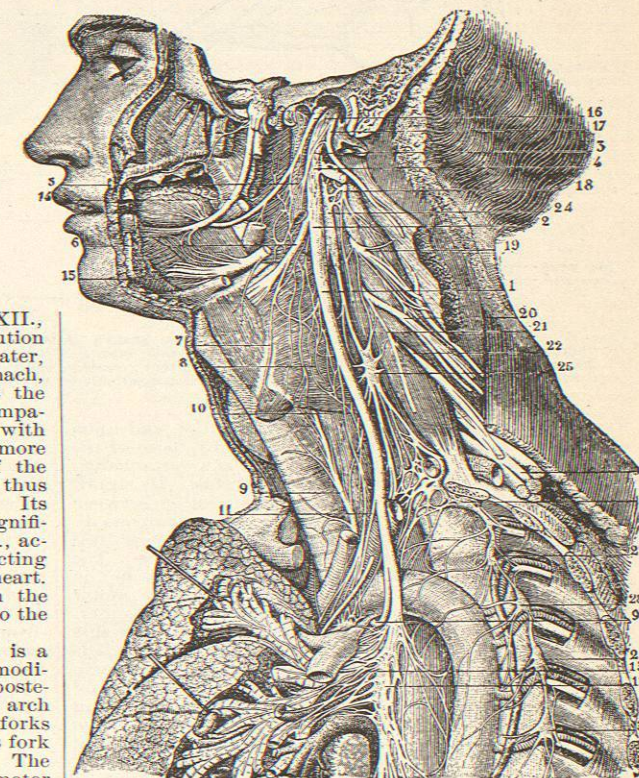


Fig. 1557.—The Distribution and Connections of the IX. and X. Nerves. (After Hirschfeld and Levellé, from Quain's "Anatomy.") One-third.

1, Vagus nerve; 2, ganglion of its trunk; 3, accessory part of the spinal accessory; 4, union of the X. and XII. nerves; 5, pharyngeal branch of the vagus; 6, superior laryngeal nerve; 7, exterior laryngeal; 8, communication of the latter with the superior cardiac branch of the sympathetic; 9, inferior or recurrent laryngeal; 10, superior, and 11, inferior cervical cardiac branches of the vagus; 12, 13, posterior pulmonary plexus; 14, lingual branch of the mandibular branch of the V.; 15, distal part of the hypoglossal nerve; 16, glossopharyngeus; 17, spinal accessory nerve, uniting by its inner branch with the vagus, and by its outer passing into the sterno-mastoid muscle; 18, II. cervical nerve; 19, III.; 20, IV.; 21, origin of the phrenic nerve; 22, 23, V., VI., VII., and VIII. cervical nerves, forming with the first thoracic the brachial plexus; 24, superior cervical ganglion of the sympathetic; 25, middle cervical ganglion; 26, inferior cervical ganglion, united with the first thoracic ganglion; 27, 28, 29, 30, second, third, fourth, and fifth thoracic ganglia.

brates, while the muscles of expression of the face are said to be derived phylogenetically from the hyoidean musculature.

In man the two roots emerge from the brain in close contact at the lower border of the pons and in intimate relations with the auditory nerve. The motor root arises

in a nucleus lying ventrally and slightly caudally of that of the VI. nerve. Its fibres are uncrossed, according to Van Gehuchten, though several earlier authors describe a crossed bundle also. They curve around the VI.

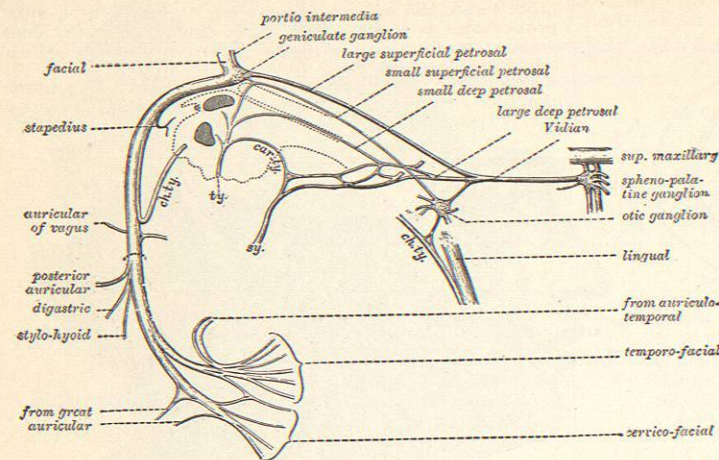


Fig. 1558.—Plan of the Facial Nerve. (After Thane, from Quain's "Anatomy.") *ch.ty.*, Chorda tympani, its middle part removed; *ty.*, tympanic branch of the glossopharyngeus; *sy.*, sympathetic on the internal carotid artery; *car.ty.*, carotico-tympanic nerve, passing between the tympanic nerve and the sympathetic in the carotid canal.

nucleus, forming the inner genu of the root, and upon emergence from the oblongata are joined by those of the portio intermedia. The internal genu is a very characteristic feature of this root in all vertebrates. Its significance is perhaps to be explained by a relation between the facialis root and the fasciculus longitudinalis medialis. Connections of different kinds have been described between this fasciculus and the motor cranial roots. The writer has observed these connections in the fishes and, in two of the cases (*viz.*, the IX. and VII.), the motor roots depart far from the shortest courses to their superficial origins to run for some distance along the outer side of the fasciculus. The bundle from the IX. nucleus divides before leaving the fasciculus into two nearly equal portions, of which one forms the root bundle and the other remains with the fasciculus. The ascending limb of the facial root in the same way runs along the outer side of the fasciculus for some distance immediately ventrally of the glossopharyngeal bundle, with which it finally fuses. The root portion, or descending limb of the facial root, soon separates, presumably leaving some fibres in contact with the IX. bundle, which soon fuses, a little farther cephalad, with the rest of the fasciculus longitudinalis medialis. In human anatomy, too, the facial genu passes along the outer side of this fasciculus, and there may be some relation between them, by means of collaterals or otherwise.

The sensory facialis fibres arise in the geniculate ganglion and terminate in the fasciculus solitarius (= fasc. communis) and the associated gray matter, thus reaching the same terminal nucleus as the other members of the communis system. The two roots run outward, accompanying the auditory nerve to the internal auditory meatus. Separating from the latter nerve they enter the aqueduct of Fallopius, within which a sharp turn is made, the external genu of the nerve. At this point is the geniculate ganglion, which is the root ganglion of the sensory portion. Within the aqueduct the following branches are given off from the trunk: (1) twigs communicating with the auditory nerve, (2) with the small superficial petrosal, and (3) with the auricular branch of the vagus; (4) a motor twig for the stapedius muscle; (5) the external superficial petrosal nerve; (6) the great su-

perforial petrosal nerve, wholly sensory and corresponding to the palatine of lower vertebrates, which is joined by the large deep petrosal to form the vidian nerve, terminating in the sphenopalatine ganglion; (7) the chorda tympani, a sensory nerve which leaves the trunk at the outer end of the aqueduct and curves back through the temporal bone and the tympanic cavity, to run forward, receiving a communicating twig from the otic ganglion, to join the lingual branch of the trigeminus. The fibres of the chorda are now generally regarded as largely gustatory in function, while those of the lingual branch of the trigeminus are concerned with general sensibility only. This accords with our most precise anatomical and phylogenetic knowledge and with a large body of clinical and pathological data, though there is some clinical evidence pointing to the existence of gustatory fibres in the trigeminus.

The facial trunk, upon emergence from the Fallopius aqueduct, is generally described as purely motor, but Van Gehuchten has very recently demonstrated a few sensory fibres in it from the geniculate ganglion. The motor fibres are distributed to the stylo-hyoid and posterior belly of the digastric muscles, to the muscles of the ear, scalp, and eyelids, and to the superficial facial musculature in general. The facial fibres for the frontalis, orbicularis palpebrarum, and corrugator supercilii muscles are said by some authorities to arise in the oculomotor nucleus and to descend to the facial root through the fasciculus longitudinalis medialis, and by others to arise in the VI. nucleus. Van Gehuchten has shown by Nissl's degeneration method that both of these suppositions are incorrect. He has analyzed the VII. nucleus of the rabbit as shown in Fig. 1559. Some authors have also described fibres passing from the facial root into the terminal nucleus of the spinal V. tract, presumably of general cutaneous nature; but this remains unconfirmed. The motor VII. nucleus receives terminal fibres (1) from the pyramidal tracts of the same and the opposite side; (2) from another tract of motor fibres which de-

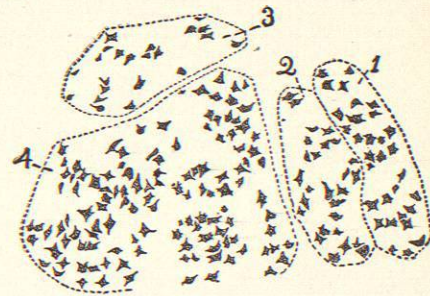
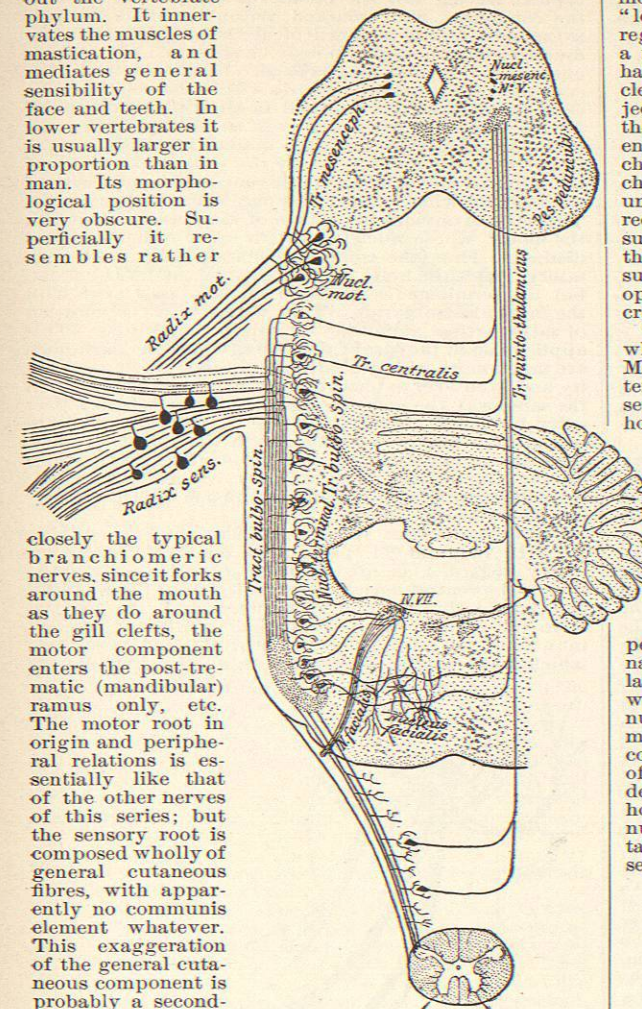


Fig. 1559.—Muscular Localization in the Facial Nucleus of the Rabbit. (After Van Gehuchten.)
1, Cells of the internal group related to the stapedius muscle; 2, cells of the internal group related to the muscles of the outer ear; 3, nucleus of origin of the fibres of the superior facial; 4, nucleus of origin of the fibres of the inferior facial, the inner portion related to the fibres of the inferior bucco-labial branch, the outer portion to those of the superior bucco-labial.

scends from the cortex in the region of the medial fillet, and hence quite independently of the pyramids (Hoche)—this tract also effects connections with the XII. nucleus, as already mentioned; (3) from the sensory V. root; (4) from the opposite nervus cochleae via the corpus trapezoides; (5) from the fundamental lateral column.

The secondary connections of the sensory root are not so well known, but are doubtless made in the general complex of the lateral fillet.

V. *The Trigeminus.*—The composition and distribution of the trigeminus are remarkably constant throughout the vertebrate phylum. It innervates the muscles of mastication, and mediates general sensibility of the face and teeth. In lower vertebrates it is usually larger in proportion than in man. Its morphological position is very obscure. Superficially it resembles rather



closely the typical branchiomic nerves, since it forks around the mouth as they do around the gill clefts, the motor component enters the post-trigeminal (mandibular) ramus only, etc. The motor root is composed wholly of general cutaneous fibres, with apparently no communis element whatever. This exaggeration of the general cutaneous component is probably a secondary arrangement, due to the reduction of general cutaneous fibres in the following nerves of the gill region of lower vertebrates and to a similar reduction in the pre-trigeminal region on account of the differentiation of the organs of higher sense. There is evidence that the general cutaneous component of at least one pre-trigeminal segmental nerve has fused with the trigeminus; for in lower sharks there is a distinct "profundus" nerve in front of the trigeminus and similar to it, a nerve which may be represented by the nasal branch of human anatomy.

The trigeminus arises by two roots. The portio minor, or motor root, whose fibres are commonly regarded as belonging to the visceromotor system, springs from two groups of cells. (1) The "chief motor nucleus" lies dorsally of the exit of the nerve from the medulla oblongata,

and is the morphological continuation of the facial nucleus. (2) A smaller number of fibres arises in an elongated cluster of large cells arranged sparsely along the side of the aqueduct, and constitutes the mesencephalic, or "descending" root. The cells of its lower portion are more crowded and are rich in pigment, constituting the "locus caeruleus." The mesencephalic nucleus has been regarded as trophic and as vaso-motor in function. As a matter of fact, its function is quite unknown. Cajal has shown that collaterals from the fibres from this nucleus envelop the cells of the chief nucleus, and he conjectures that this is a sort of relay mechanism by which the cells of the mesencephalic and chief nucleus (*i.e.*, the entire masticatory apparatus) can be simultaneously discharged by the same stimulus. The fibres from the chief motor nucleus are commonly described as mainly uncrossed, but partly crossed; but Van Gehuchten has recently found upon section of the trigeminus roots and subsequent examination by Nissl's method that all of the cells of both the chief and the mesencephalic nucleus suffer chromatolysis on the same side, but none on the opposite side. This leads him to the conclusion that crossed fibres do not arise from either nucleus.

The portio major is a complex structure, chiefly, if not wholly, sensory. Two roots can be distinguished: (1) Most of the fibres go to the spinal trigeminal tract and terminate in cells lying in its path (including the "chief sensory nucleus" of the trigeminus), and are therefore homologous with those of the dorsal roots of the spinal nerves, and like them belong to the general cutaneous system. This *spinal root*, often incorrectly called the "ascending root," runs down near the lateral aspect of the oblongata and can be traced, diminishing caudad, as far as the first or second cervical nerve. It is accompanied for its entire length along the inner aspect by a sparse collection of cells, the spinal nucleus of the trigeminus, which are enveloped by a dense mesh of fine terminal fibrils derived from the root fibres, the whole when stained by ordinary methods presenting a peculiar appearance which has given rise to its designation, "substantia gelatinosa." Vast numbers of collaterals from the root fibres participate in this meshwork. Others of these collaterals terminate in the motor nuclei of the V. and VII., and probably in the other motor cranial nuclei also. The homology and direct continuity of the spinal nucleus with the dorsal cornu of the spinal cord give us an important landmark for the determination of homologies in the oblongata. The homologies in the spinal cord of the other cranial nerve nuclei, both sensory and motor, are much more uncertain. (2) The second root of the portio major is the sensory cerebellar root of Edinger (indicated by dotted

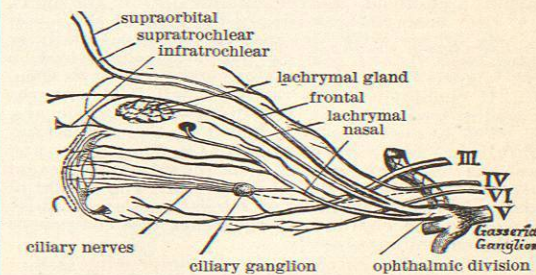


Fig. 1561.—The Nerves of the Left Orbit. (After Young, reduced.)

lines in Fig. 1560), which enters the cerebellum by way of the prepuduncle. The existence of this root is denied by some authors.

The central connections of the motor V. nuclei are doubtless made from the pyramidal tracts, though they are not very precisely known. The chief motor nucleus also receives collaterals from the sensory nuclei of the