ARTICLES FROM
"THE REFERENCE HANDBOOK OF THE MEDICAL SCIENCES"
(WILLIAM WOOD & CO., NEW YORK, THIRD EDITION, 1914)

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I

CRANIAL NERVES

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II

EAR: ANATOMY OF THE AUDITORY (ACOUSTIC) NERVE AND ITS END-ORGANS

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END-ORGANS, NERVOUS

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Among these, one which I have found successful is tying a tape about each thigh just above the knee. This is done just before retiring. Raising the head of the bed by placing one or two bricks under the posts is a measure which I have not found to do any good. A dose of bromide with alkalies at night, or a mixture containing gr. v. each of lupulin and camphor, may be given. In severe cases, especially in pregnancy, codeine or opium may be added to these. Massage and faradization of the limbs will sometimes ward off attacks, and so will small doses of strychnine continuously administered.

When the attack comes on, the affected muscles must be vigorously rubbed and kneaded. If the patient jumps up at once and puts the muscles on the stretch, he can often break up the cramp. A little rubbing and exercise will then quiet the muscle. In the cramps of later life due to arterial sclerosis this condition must be treated. CHARLES L. DANA.

Cranial Nerves.—From the standpoint of the peripheral nervous system the organs of the body may be conveniently divided into three groups: (1) the organs of the trunk region, whose spinal nerves are evidently arranged in a segmental way; (2) a series of respiratory, gustatory, and other visceral organs, innervated from the medulla oblongata and in lower vertebrates intimately associated with the gills (branchial region); (3) the organs of the head, devoted largely to the higher senses and their central connections within the brain and to the higher cerebral association centers. The limits of these regions and their distinguishing characteristics are more evident in lower vertebrates than in higher.

The branchial region of some lower fishes is very extensive and it has a characteristic segmentation (branchiomerism) which is of quite different character from that of the trunk region, though the two segmental patterns may overlap. In the trunk the organs are partly of somatic type, being concerned mainly with locomotion and other similar reactions of the body musculature to external stimuli, and partly visceral systems whose nerve supply is much smaller and which receive their nerves in part from the branchial region. But the branchial region is dominated by the gills, which are visceral structures, while the somatic systems are here greatly reduced. In mammals the gills have disappeared, but the associated part of the brain, the medulla oblongata, preserves its character as a center devoted chiefly to respiratory and other visceral functions.

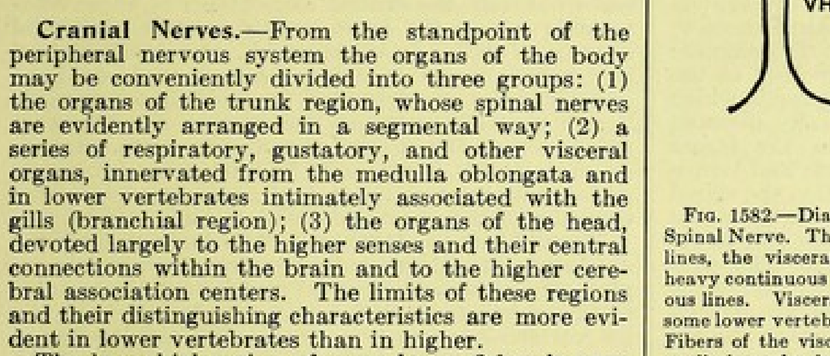

FIG. 1581.—Cross-section of Spinal Cord to Illustrate Gaskell's Views. (Hans Gadow.) *A*, Cells of dorsal horn; *B*, cells of Clarke's column; C, cells of lateral horn; *D*, cells of ventral horn; *E*, solitary cells at base of dorsal horn; *a*, somatic afferent fibers; *b*, splanchnic ganglionated efferent fibers; *c*, splanchnic non-ganglionated efferent fibers for visceral and enteric muscles; *d*, somatic efferent fibers; *e*, splanchnic afferent fibers.

Thus, the V., VII., IX., X., and XI. cerebral nerves are of branchiomeric type, with visceral functions predominating. The I., II., III., IV., VI., and VIII. nerves belong to the organs of special sense and their accessories, while the XII. cerebral nerve is a modified spinal nerve. Comparative anatomy and embryology show that most of these nerves (and perhaps all) are the descendants of more typical segmental nerves, but in all existing vertebrate types the original segmental pattern has been more or less highly modified and obscured. In the human body this modification has been carried much farther than in the lower vertebrates, and accordingly much valuable information regarding the significance and relationship of the cerebral nerves has been derived from the study of fishes and other more primitive vertebrate animals.

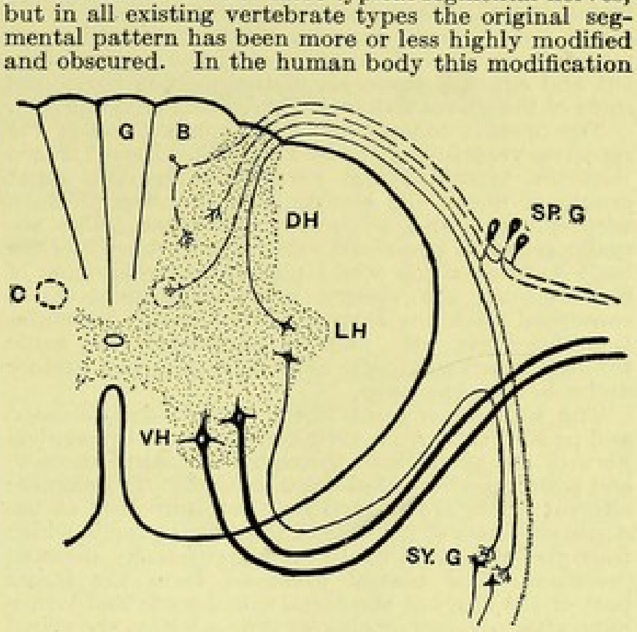

FIG. 1582.—Diagram Illustrating the Composition of the Typical Spinal Nerve. The somatic sensory fibers are represented by broken lines, the visceral sensory by dotted lines, the somatic motor by heavy continuous lines and the visceral efferent by lighter continuous lines. Visceral efferent fibers are found in the dorsal roots of some lower vertebrates; their presence in mammals is controverted. Fibers of the visceral efferent system arise chiefly from an intermedio-lateral column of cells which lie in or near the outer border of the lateral cornu. The central terminus of the visceral sensory fibers is uncertain, probably in the intermediate zone in the vicinity of the nucleus dorsalis of Clarke. *B*, Fasciculus cuneatus (of Burdach); *C*, nucleus dorsalis (of Clarke); *DH*, dorsal horn; *G*, fasciculus gracilis (of Goll); *LH*, lateral horn containing the intermedio-lateral column of cells; *SP.G*, spinal ganglion; *SY.G*, sympathetic ganglion; *VH*, ventral horn.

The Doctrine of Nerve Components.—The knowledge of the composition of the cranial nerves was long retarded by persistent attempts to analyze them in accordance with the analogy of a supposed simple spinal pattern. Sir Charles Bell in the early part of the nineteenth century made plain the difference between the sensory and motor roots of the cranial and spinal nerves. But the common statement of Bell's law, that the dorsal spinal roots are sensory and the ventral roots are motor, leaves out of consideration important parts of his scheme and ascribes to the spinal nerves a really artificial simplicity. The attempt to classify the still more complex cranial nerves in accordance with this simplified segmental scheme, thus treating all sensory roots as metamerically equivalent structures and all motor roots likewise as directly homologous with spinal motor roots, has resulted only in confusion.

Gaskell in 1886 and 1889 amplified Bell's analysis of the spinal nerves and elaborated a four-root theory which has been the point of departure for the best recent studies upon the composition of the peripheral nerves. The details of Gaskell's scheme have been greatly modified, but the fundamental distinction which he clearly drew between somatic and visceral systems of nerve components has been more and more evidently justified as time passed on. Fig. 1581 illustrates the chief features of Gaskell's analysis of the spinal nerves, each segmental nerve containing somatic afferent and efferent fibers and also visceral afferent and efferent fibers, all of the afferent fibers and some of the efferent visceral fibers being ganglionated.

The present conception of the composition of the spinal nerves is illustrated by Fig. 1582. Here it is seen that the typical spinal nerve contains two great groups of fibers, the somatic and the visceral, each with afferent and efferent subdivisions. The somatic group is concerned with the adjustments of the body to the outside world (exteroceptive systems of Sherrington); the visceral group (interoceptive) is concerned with the internal mechanisms of circulation, digestion, etc., and its connections are made through the sympathetic nervous system (see further under *Brain, Anatomy*).

The somatic efferent fibers are non-ganglionated and pass directly from their cell bodies in the ventral horn of the spinal cord through the ventral roots to end upon the fibers of skeletal muscles. The somatic afferent fibers are formed by the bifurcation of the single processes of the cells of the spinal ganglia which thus give rise to centrally and peripherally directed processes. The central processes form the larger part of the fibers of the dorsal spinal roots and terminate, after a longer or shorter course within the spinal cord, about cells of the dorsal horn or nuclei of the dorsal funiculi. The peripheral processes end in receptive organs in or immediately under the skin (exteroceptors) or else in deep sense organs among the muscles, tendons, joints, etc. The latter are termed by Sherrington proprioceptors and serve for the internal regulation of the somatic organs of response and not, like the interoceptors, for visceral reactions. The somatic motor and sensory roots of the cranial nerves are organized in essentially the same way as those of the spinal nerves just described.

The visceral fibers of the spinal nerves are less numerous than the somatic fibers and they are chiefly efferent in function. These visceral efferent fibers arise from the intermediate zone of the spinal cord between the dorsal and ventral horns and especially from an intermedio-lateral column of cells lying within and just external to the lateral horn (Bruce). They probably do not arise from the cells of Clarke's column, as suggested by Gaskell. They do not reach their terminal organs (smooth muscles, glands, etc.) directly, but always end in some sympathetic ganglion, with whose cells they effect functional connection. The impulse is then carried on to the peripheral organ by axones of these sympathetic cells. The neurone of the first order, whose cell body lies within the central nervous system, is termed the preganglionic neurone; the neurone of the second order is the postganglionic neurone (Langley).

The visceral sensory fibers of the spinal nerves are relatively very few in number. Some such fibers arise from cells of the spinal ganglia, whose peripheral processes distribute through the sympathetic nervous system to mucous surfaces, etc., and whose central processes enter the spinal cord through the dorsal roots to terminate probably in the intermediate zone of gray matter at the base of the dorsal horn. It is probable that some cells of the sympathetic ganglia also send sensory processes centripetally through the rami communicantes to enter the spinal ganglia and thus after a synapse in the ganglion to discharge into the dorsal roots of the spinal nerves. But our knowledge of these fibers is still very incomplete.

The cranial nerves exhibit a much more complex and diversified pattern than do the spinals. The primary segmentation is obscure and there is still some difference of opinion as to the segmental relations of the twelve pairs (of Sömmering) as now commonly enumerated. These twelve pairs are convenient anatomical units, but for physiological and clinical purposes a more useful unit is the *functional system*. Each system may be defined as the sum of all the nerve fibers in the body, which possess certain physiological and morphological characters in common, so that they may react in a common mode. Morphologically, each system is defined by the terminal relations of its fibers—by the organs to which they are related peripherally and by the centers in which the fibers arise or terminate. The fibers of a single system may appear in a large number of nerves, repeated more or less uniformly in a metameric way (as in the cutaneous nerves of the spinal cord), or they may all be concentrated into a single nerve (as in the olfactory nerve). On the other hand, a single nerve may contain several components; *i.e.* its fibers may belong to several of these systems. It becomes necessary, therefore, to analyze the root complex of each pair of cranial nerves into its components and to trace not only the central connections of these components within the brain, but also their peripheral courses as well. In other words, the description of any given ramus is not complete when we have given its point of origin from the nerve trunk or ganglion, the details of its devious courses and the exact points where the several ramuli terminate. In addition to this it is necessary to learn what functional systems are represented in the ramus and the precise central and peripheral relations of each system.

The difficulty in determining this latter point is the chief obstacle in the way of researches on the nerve components; for, while the central connections of any nerve can be determined by the microscopical method and by various experimental procedures, the peripheral courses are usually studied by gross methods which reveal nothing of the precise relations of the several components and hence do not permit a knowledge of each system as a whole. To trace the components of the more complex cranial nerves continuously from their central nuclei of origin or termination by means of serial sections to their ultimate peripheral connections has never been attempted in the human body. In some lower vertebrates, however, this has been accomplished with a fair measure of success. The pioneer work in this field was done by Dr. Oliver S. Strong in 1895 on the frog tadpole, and this has been followed by many similar studies. All of the types thus far examined in this way exhibit certain broad general resemblances and permit the establishment of a schematic type of cranial nerve components which is presumably applicable to the vertebrates as a whole. From anatomical, physiological, and pathological data already in hand it is possible to compare the human nerves with this scheme and to infer the composition of most of the peripheral rami with more or less of accuracy.

In the branchial region of the lowest fishes the gills are very numerous (as many as seventeen pairs in some cyclostomes) and each gill is supplied by a branchiomeric nerve. The segmentation of these gills does not coincide with that of the myomeres of the same region and it is a controverted point whether this diversity is primary or a secondary modification. But it is clear that in primitive vertebrates the entire branchial region contained greatly enlarged visceral structures, the gills, and also somewhat reduced somatic structures, the myomeres, or body musculature, and the sensory organs of cutaneous and muscular sensibility. The somatic motor roots in the branchial region of fishes are usually enumerated as spinal nerves. They all disappear in mammals, except one or more of the ventral roots which are represented in the hypoglossus nerve.

In primitive vertebrates (cyclostomes) the typical nerve of this region contains sensory and motor somatic fibers arranged in series of dorsal and ventral roots as

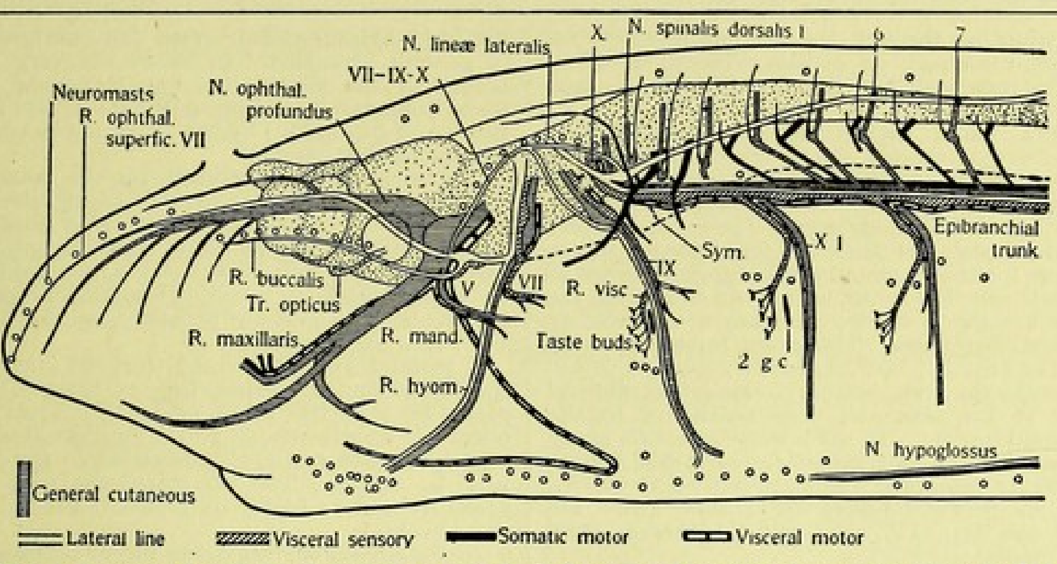

Fig. 1583.—A Reconstruction of the Cranial Nerves of a Cyclostome Fish, *Petromyzon dorsatus*, seen from the Left Side, to Show the Arrangement and Distribution of the Several Systems of Nerve Components. The general or unspecialized somatic sensory system (general cutaneous) is shaded with horizontal lines; the special somatic sensory system (lateral line) is drawn in outline without shading, the VIII nerve, which also belongs to this system, being omitted. Only three of the gill clefts are indicated in the drawing. 2 *g.c.* marks the second gill cleft; its branchiomeric nerve is the first division of the vagus (*XI.*). The sympathetic nervous system is indicated by a broken line (*Sym.*). (After Johnston.)

in the spinal nerves, and in addition an intermediate or lateral series of visceral sensory and motor roots for the branchial apparatus. During the course of vertebrate evolution the branchial region has been greatly shortened (chiefly by suppression of the more caudal branchiomeres), resulting in the loss of the more caudal lateral roots. The remaining branchiomeric nerves tend to be combined into a common vago-accessorius trunk. Meanwhile the myomeres and the corresponding somatic nerve roots were reduced in number from before backward. Fig. 1583 illustrates an early phase of this metamorphosis of the branchial region, as seen in cyclostome fishes. In some higher fishes a section through the region of the vagus nerve (Fig. 1584) shows that here the somatic motor component has entirely disappeared (though present at this level in some other teleosts), while the somatic sensory system is represented by a small cutaneous root and ganglion. The latter becomes in man the ramus auricularis vagi, while the somatic motor system is here represented by the hypoglossus nerve. In mammalian embryos, where gill clefts and gill arches are still preserved, the branchiomeric nerves are related in all fundamental respects as in fishes, and the data of comparative anatomy and comparative embryology are essential to a proper understanding of the adult relations.

A comparison of the composition of the nerves of the trunk and branchial regions reveals in both cases the fundamental distinction between the somatic and visceral divisions. In the trunk region each of the four primary components of a spinal nerve is further subdivided into functional systems (for various forms of cutaneous and deep sensibility, various functionally related groups of muscles, etc.), but all of these systems are relatively unspecialized. In the nerves of the branchial and cerebral regions, on the other hand, we have, in addition to unspecialized components like those of the spinal nerves, also highly specialized derivatives, each with a particular function and a more or less elaborately differentiated peripheral and central terminal apparatus. Thus the four primary divisions of the spinal nerves are represented by eight divisions in the cranial nerves, arranged in the human body as follows:

1. General somatic motor, supplying myomeres of the general bodily or skeletal musculature. This system is present in the branchial region of fishes, but is lost in mammals, except perhaps a part of the fibers of the XI. nerve for the trapezius muscle.

2. Special somatic motor, supplying specialized striated muscles derived from the myotomes; viz., the eye muscles and a part of the tongue muscles; III., IV., VI., and XII. nerves.

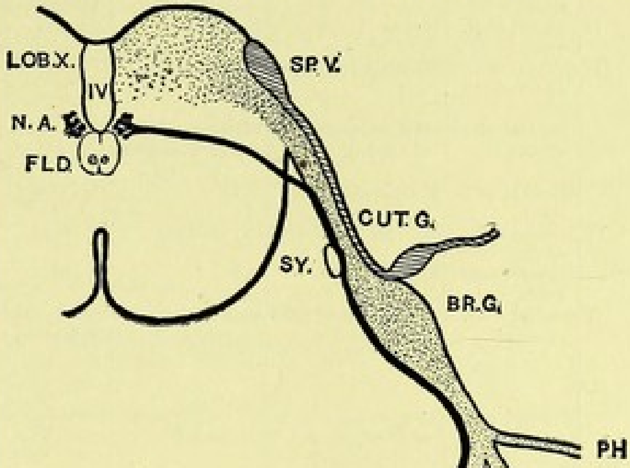

Fig. 1584.—Diagram of a Branchiomeric Nerve in the Vagus Region of a Teleostean Fish (*Menidia*). The visceral sensory component is stippled; the visceral efferent is drawn in black (these two constituting the branchiomeric nerve proper). The somatic sensory system is cross hatched. The somatic motor system is here absent, though in some other fishes fibers of this system arise at this level from cells lying ventrally of the nucleus ambiguus and form an independent ventral root. *B.C*, Branchial cleft; *BR.G*, branchial ganglion; *CUT.G*, general cutaneous or somatic sensory ganglion; *FLD*, fasciculus longitudinalis medialis; *IV*, fourth ventricle; *N.A*, nucleus ambiguus; *LOB.X*, lobus vagi, the terminal nucleus of the visceral sensory fibers; *PH*, ramus pharyngeus; *POST*, posttrematic ramus; *PRE*, pretrematic ramus; *SP.V.*, spinal V. tract, associated with the terminal nucleus of the somatic sensory fibers; *SY*, sympathetic ganglion.

3. General visceral motor, preganglionic nerve

fibers distributing through the sympathetic nervous system for unstriped or cardiac visceral muscles, glands, etc.; represented in the III., VII., IX., X., and XI. nerves.

4. Special visceral motor, supplying highly differentiated striated muscles which are connected with the gills or their derivatives and which are derived embryologically, not from the myotomes, but from the unsegmented ventral mesoderm. These nerve fibers in the adult resemble those of the somatic motor system save for their origin from a different series of motor nuclei in the brain. They do not enter the sympathetic nervous system and are not related to postganglionic neurones. This group is represented in the V., VII., IX., X., and XI. nerves.

5. General somatic sensory, supplying general sensibility to the skin and deep sensibility to the muscles, tendons, etc. In the lowest fishes this group is represented in all segments of the branchial region, but in man its cutaneous fibers are limited to the V., IX., and X. nerves. Fibers for muscle sense are found in the III., IV., V., and VI. nerves, and probably others.

6. Special somatic sensory, specialized nerves for the innervation of highly differentiated sense organs derived phylogenetically from the cutaneous organs of general sensation. In fishes the very extensive nerves of the lateral line organs belong here. In man this group is represented only by the VIII. nerve and (probably) by the visual organ related with the so-called II. nerve.

7. General visceral sensory, for the innervation of visceral mucous surfaces without highly differentiated sense organs. The relations of these fibers are not clearly understood, as they are mingled with the much more numerous fibers of the next group. They distribute chiefly or wholly through the sympathetic nervous system and are probably represented in the VII., IX., and X. nerves.

8. Special visceral sensory, for the innervation of specialized end-organs serving the sense of taste and probably also the sense of smell. The gustatory fibers are clearly related to the unspecialized visceral sensory system and are represented in the VII., IX., and X. nerves. The olfactory nerve (I. nerve) is probably a more highly differentiated member of the same group.

In the accompanying table the components of the twelve pairs of cerebral nerves as commonly enumerated are analyzed in accordance with the preceding scheme.

TABLE OF CRANIAL NERVE COMPONENTS.

Nerve.	Components.	Chief functions.	Cells of origin.	Nerve roots.	Primary nuclei and secondary connections.	Chief rami.
I	Special visc. sens.	Smell	In nasal muc. membrane	Fila olfactoria	Olf. bulb; lat. olf. area; med. olf. area; uncus; hippocampus	
II	Special som. sens.	Vision	In retina	. . . .	Retina; optic nerve and tract to thalamus and midbrain	Not a true nerve.
III	Special som. efferent	Movement of eyeball	III. nucleus	III. root	To III. nuc. from med. obl. by fasc. long. med.; from tectum opticum and cerebral cortex	Branches to mm. rectus sup., rectus inf., rectus int., obliquus inf., levator palpebræ sup.
	General visc. efferent	Intrinsic muscles of eyeball	Nucleus of Edinger-Westphal	III. root	Do.?	Preganglionic fibers to g. ciliare; postganglionic fibers in ciliary nerves
	General som. sens.	Muscle sense of eye muscles	?	III. root	?	Fibers mingled with motor fibers to four eye muscles
IV	Special som. efferent	Movement of eyeball	IV. nucleus	IV. root	To IV. nuc. same as III. nerve	Nerve of m. obliquus superior
	General som. sens.	Muscle sense	?	IV. root	?	Fibers mingled with motor fibers to m. obliquus superior
V	Special visc. efferent	Movement of jaws	Motor V. nucleus	Portio minor V.	To mot. V. nuc. from sens. V. nuc., mesenc. V. nuc., cerebellum and cerebral cortex	By n. mandibularis to temporal, masseter, ext. and int. pterygoid, tensor palati, tensor tympani, ant. belly of digastric and mylohyoid muscles
	General som. sens.	A. gen. sens. skin of head, nose, teeth, mouth, meninges	G. semilunare (Gasseri)	Portio major V.	From sens. V. nuc. and spinal V. nuc. to mot. nuclei of obl. and cord, to cerebellum, nuc. lat. thalami and cortex	N. ophthalmicus, n. maxillaris, n. mandibularis
		B. muscular sens. of jaw muscles	Nuc. mesencephalicus V.	Portio major V.	From root fibers and nuc. mesenc. to mot V. nuc. and other motor centers	Fibers distribute with muscular branches of V.
VI	Special som. efferent	Movement of eyeball	VI. nucleus	VI. root	To VI. nuc. from sup. olive; also same connections as III. nerve	Nerve of m. rectus lateralis
	General som. sens.	Muscle sense	?	VI. root	?	Fibers mingled with motor fibers to m. rectus lateralis
VII	General visc. efferent	Secretion of saliva	Nuc. salivatorius superior	Portio intermedia	To nuc. saliv. from nuc. of fasc. sol. and other sens. centers; cortex	Preganglionic fibers in chorda tympani; postgang. fibers from submax. gang. to submax. and sublingual glands
	Special visc. efferent	Hyoid and facial musculature	Motor VII. nucleus	Portio dura	To mot. VII. nuc. from sens. nuclei of oblongata and cortex	Stapedius, post. belly of digastric, stylohyoid, auricular and scalp muscles and superficial facial musculature
	General visc. sens.	Deep visc. sensibility	G. geniculatum	Portio intermedia	From nuc. of fasc. sol. to formatio reticularis	Probably in great superf. petrosal and chorda tympani and tympanic plexus
	Special visc. sens.	Taste on ant. part of tongue	G. geniculatum	Portio intermedia	From nuc. of fasc. sol. to mot. nuclei of oblongata and cortex	Chorda tympani
VIII	Special som. sens.	A. equilibration and stat c sense	G. vestibulare	Radix vestibularis	From vestibular nuclei and cerebellum to eye-muscle nerves, motor centers of obl. and cord	Nervus vestibuli
		B. hearing	G. spirale	Radix cochlearis	From dors. and vent. coch. nuc. and sup. olive to collic. sup., corp. genic. med., cortex	Nervus cochleæ

TABLE OF CRANIAL NERVE COMPONENTS.—*Continued*.

Nerve.	Components.	Chief functions.	Cells of origin.	Nerve roots.	Primary nuclei and secondary connections.	Chief rami.
IX	General visc. efferent	Secretion of saliva	Nuc. salivatorius inferior	Motor IX. root?	To nuc. saliv. from nuc. of fasc. sol. and other sens. centers; cortex	Preganglionic fibers in tympanic and small superf. petrosal nerves; postgang. from otic ganglion to parotid gland
	Special visc. efferent	Movement of pharynx	Nuc. ambiguus	Motor IX. root	To nuc. ambiguus from nuc. of fasc. sol. and other sens. centers.	Ramus stylopharyngeus IX.
	General visc. sens.	Sensation of pharynx, etc.	G. petrosum IX.	Sens. IX. root	From nuc. of fasc. sol. to visc. motor centers	Pharyngeal and tympanic branches of IX. and various sympathetic connectons?
	Special visc. sens.	Taste on post. part. of tongue	G. petrosum IX.	Sens. IX. root	From nuc. of fasc. sol. to visc. mot. centers and cortex	Ramus lingualis IX.
	General som. sens.	Tactile sense on post. part of tongue	G. superius IX.	Sens. IX. root	From nuc. of spinal V. tract to mot. centers	Ramus lingualis IX.
X	General visc. efferent	Unstriped muscles and glands of gut and other viscera	Dorsal mot. nuc. of X.	Motor X.	To mot. X. nuc. from nuc. of fasc. sol. and other sensory centers	Rami for pharynx, esophagus, stomach, heart, lungs, etc., via symp. system (preganglionic fibers)
	Special visc. efferent	Striated muscles of pharynx	Nuc. ambiguus	Motor X.	Do.; also from cerebral cortex	Superior and inferior laryngeal and pharyngeal nerves
	General visc. sens.	Visc. sens. of pharynx, thorax, and abdomen	G. nodosum	Sensory X.	From nuc. of fasc. sol. and dors. sens. nuc. to visc. mot. centers (and cortex?)	Rami from pharynx, esophagus, stomach, heart, lungs, etc., and various symp. connections
	Special visc. sens.	Taste in region of epiglottis?	G. nodosum?	Sensory X. ?	Do.?	Probably in internal laryngeal nerve
	General som. sens.	Cutaneous sens. behind ear	G. jugulare X.	Sensory X.	From nuc. of spinal V. tract to motor centers	Ramus auricularis vagi
XI	General visc. efferent	Same as in X. nerve	Dorsal mot. nuc. of X.	In cerebral roots of XI.	Same as in X. nerve	Preganglionic fibers distributed with the vagus
	Special visc. efferent	A. striated muscles of pharynx	Nuc. ambiguus	In cerebral roots of XI.	To nuc. ambiguus from visc. sens. centers	To striated muscles of the pharynx accompanying vagus branches
		B. movement of shoulder	Lateral horn of spinal cord	In spinal roots of XI.	To lat. horn from cord, oblongata, and cortex	Rami to trapezius and sternomastoid muscles
XII	Special som. efferent	Movement of tongue	XII. nucleus	XII. roots	To XII. nuc. from nuc. of fasc. sol. and other sens. centers and cortex	Hypoglossus nerve

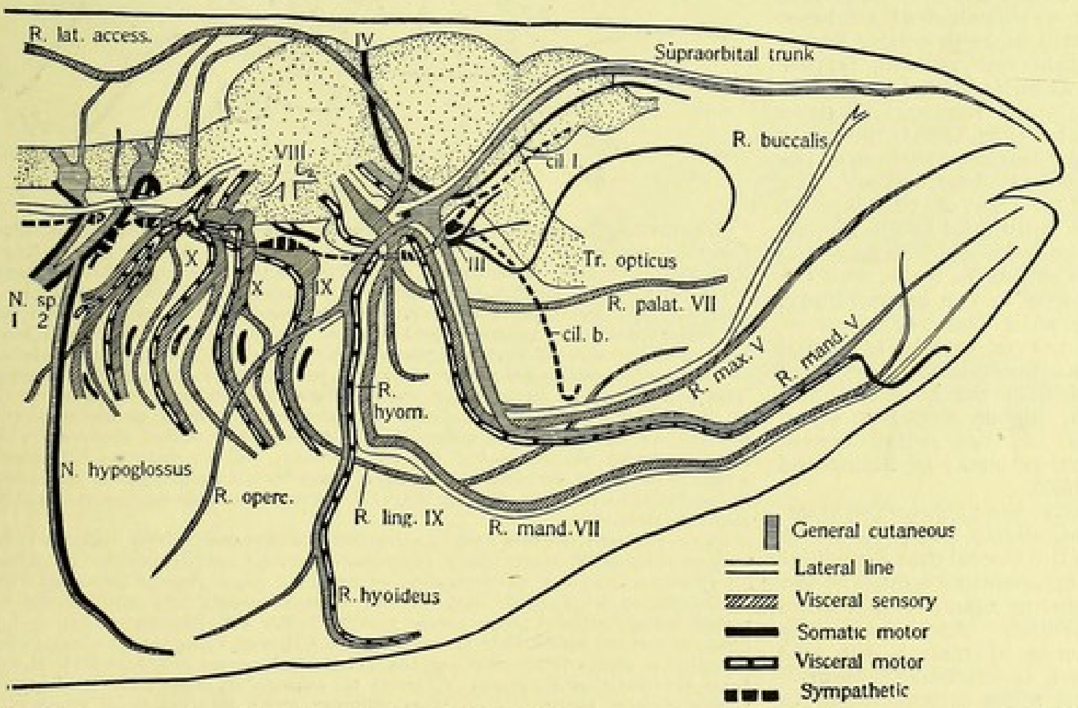

FIG. 1585.—A Reconstruction of the Chief Rami of the Cranial Nerves of a Bony Fish (*Menidia*), as seen from the Right Side, to Show the Arrangement of the Nerve Components. Compare Fig. 1583, of a lower type of fish. (After Herrick, from Johnston's Nervous System.)

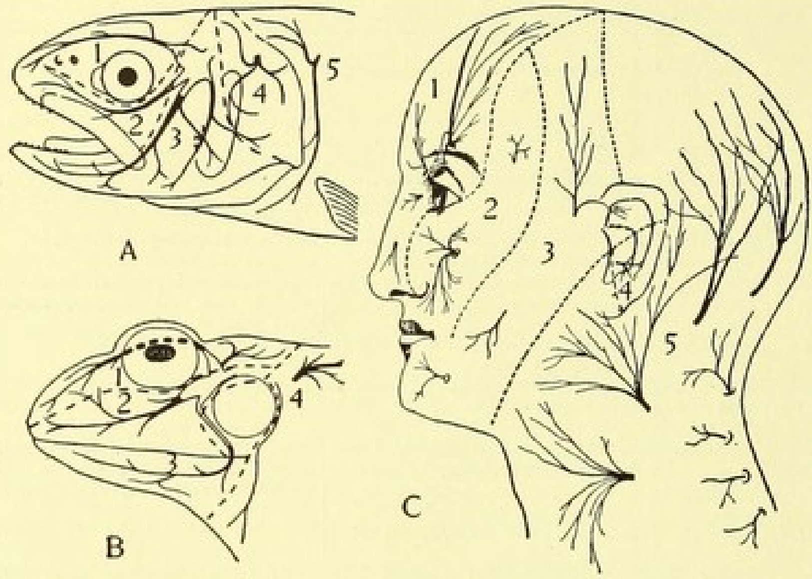

FIG. 1586.—Three Sketches to Illustrate the Distribution of the Cutaneous Nerves of the Head in a Fish, an Amphibian and Man. *A*, A teleostean fish; *B*, a frog; *C*, man, the figure being slightly modified from Cunningham's Anatomy by the addition of the ramus auricularis vagi. In all of the figures, area 1 is supplied by the ophthalmic division of the trigeminus; area 2 is supplied by the maxillary division; area 3 is supplied by the mandibular division; area 4 is supplied by the vagus; and area 5 is supplied by the spinal nerves. (After Johnston, Spengel's Ergebnisse und Fortschritte der Zoologie.)

An examination of the composition of the cerebral nerves in the different members of the vertebrate phylum shows that, as we pass from the lower to the higher members of the series, each functional system tends to become integrated from a diffuse segmental arrangement to a more compact form. For instance, the general cutaneous system in lower fishes (Fig. 1583) is represented in most of the cerebral nerves behind the IV. pair, and there is embryological evidence that in still more primitive forms this system was present farther forward as independent profundus and thalamic nerves. But in higher fishes (Fig. 1585) practically all of the cutaneous surface of the head is supplied from the V. pair and the vestige of this system which is still found in the X. pair terminates centrally in connection with the spinal V. tract; and the same is true in the human body. Parallel with the reduction of somatic nerves in the branchial region, an increasingly large part of the skin of the head is innervated, in higher vertebrates, by branches of true spinal nerves lying farther back, as illustrated in Fig. 1586.

Similarly, the gustatory system, which is widely distributed in fishes in the buccal and branchial region and sometimes even in the outer skin, in man is much more circumscribed. And again, the VIII. nerve of man is the sole survivor of an extensive system of cutaneous sense organs found in fishes (the acustico-lateralis system), whose nerve supply passes out in connection with several of the other cerebral nerves. There is some evidence that even the eyes were originally represented in several segments of the head (Locy).

The convergence of the fibers belonging to each functional system, no matter by what nerve roots they may enter the brain, so that all fibers of the same system terminate in a distinct cerebral center, is seen in Fig. 1587 which illustrates the composition of the nerve roots of the same animal as Fig. 1585, with a part of the central course of the several nerves sketched in. In the lower fishes the centers reached by these several systems of nerve fibers are clearly marked by eminences on the surface of the medulla oblongata or in the walls of the fourth ventricle (Fig. 1588). In the human medulla oblongata the same regions may be identified, though they are not so clearly seen from the surface (cf. *Brain, Anatomy*).

Development.—A brief account of some of the processes involved in the early embryology of the peripheral nerves will be found in the articles, *Brain, Anatomy*, and *Spinal Cord*. The entire dorsal ectoderm of the embryo may be regarded as potentially nervous. Along the mid-dorsal line this ectoderm is invaginated to form the central nervous system. Other cells are proliferated on each side of the body along the seam or line of separation between the neural

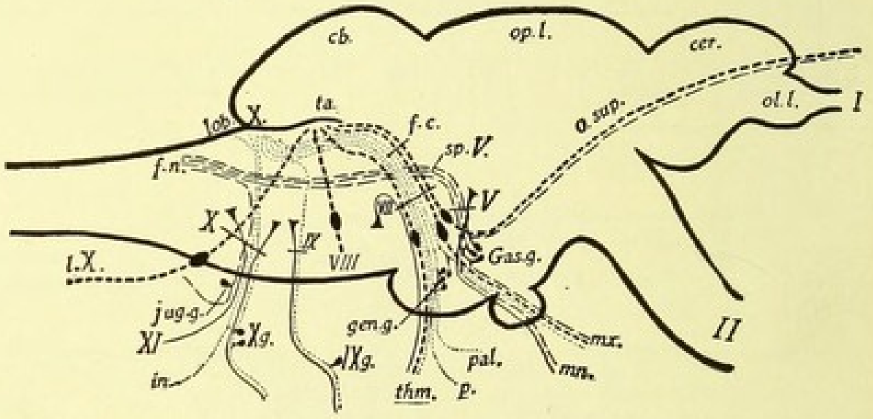

FIG. 1587.—The Cranial Nerves of *Menidia* as seen from the Right Side, Illustrating the Central Convergence of the Sensory Components of the Several Nerves into Functional Systems. The eye-muscle nerves have been omitted, the superficial origins of the others being indicated by the Roman numerals at the transverse lines drawn across their roots. The visceral motor roots are drawn as continuous lines, the general somatic sensory roots as broken lines, the acusticolateral (special somatic sensory) system as heavier broken lines, and the visceral sensory system as dotted lines. The positions of the auditory and of the four lateral line ganglia are indicated, though no special designations are given them. This scheme can be applied with but slight modification to all of the fishes. The student of comparative anatomy will notice that some rami peculiar to the teleosts nave been omitted, *e.g.* the r. lateralis accessorius. Compare the detailed plot from which this diagram is drawn off, *Journal of Comp. Neurology*, vol. ix., plate xvi. The scheme can be adapted to higher vertebrates (including man) by the suppression of the lateral line roots of the facialis and vagus, leaving the VIII. nerve as the only representative of the acustico-lateral system.

cb, Cerebellum; *cer*, cerebrum; *f.c*, fasciculus communis (=fasc. solitarius); *f.n*, terminal nucleus of spinal V. tract; *Gas. g*, Gasserian ganglion; *gen.g*, geniculate ganglion; *in*, ramus intestinalis vagi; *IX. g*, glossopharyngeal ganglion; *jug.g*, jugular (gen. cutaneous) ganglion of the vagus; *lob.X*, lobus vagi (sensory vagus nucleus); *l.X*, ramus lateralis vagi; *mn*, ramus mandibularis V; *mx*, ramus maxillaris V.; *ol.l*, olfactory lobe; *op.l*, optic lobe; *o.sup*, superficial ophthalmic branches of the VII. and V. nerves (the latter = frontal nerve of man); *p*, pretrematic branch of the facialis; *pal*, ramus palatinus VII. (= great superficial petrosal); *sp.V*, spinal V. tract; *ta*, tuberculum acusticum (terminal nucleus for acustico-lateral system); *thm*, hyomandibular trunk (= great facial trunk of man); *Xg*, visceral vagus ganglion; *XI*, motor fibers for trapezius muscle, supposed to represent the accessory nerve.

tube and the adjacent ectoderm to form the neural crest, from which a part of the cranial and spinal ganglia and of the sympathetic system are to be derived. And in the head region farther laterally patches of thickened sensory epithelium are differentiated to form ectodermal placodes. These lie in two rows, one more dorsal, the suprabranchial series, and one more ventral, the epibranchial series (Fig. 1589). The latter are formed in intimate relation with the external openings of the gill clefts.

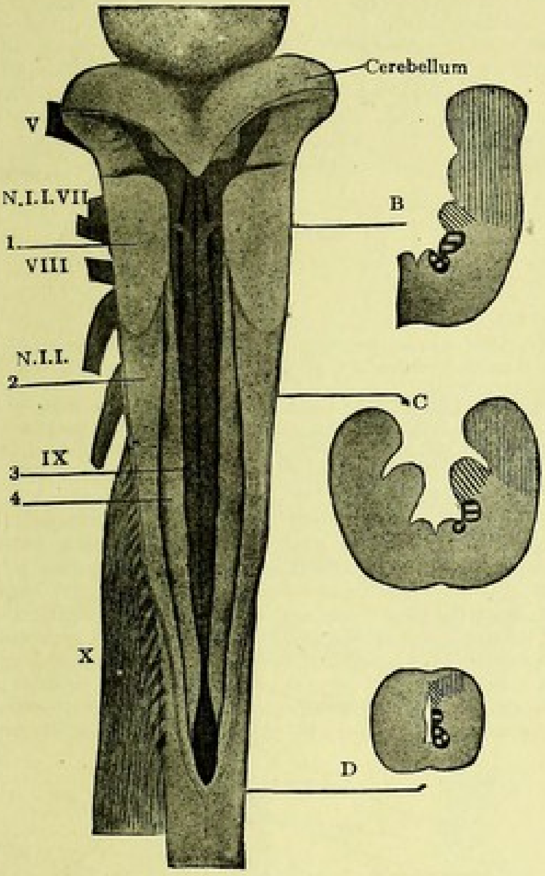

Fig. 1588.—The Medulla Oblongata and Cerebellum of the Lake Sturgeon (*Acipenser rubicundus*), to Show the Longitudinal Columns which are Developed as Centers for the Four fundamental Functional Systems of the Peripheral Nerves. A dorsal view with the chorioid plexus of the fourth ventricle removed. *B*, *C* and *D*, sketches of sections at the levels indicated by the reference lines. The dark area with the light circles is the somatic motor column, continuing the ventral horn of the spinal cord. The dark area with rectangular spaces is the visceral motor column, continuing the lateral horn of the spinal cord. The area with oblique cross hatching is the visceral sensory column, or lobus visceralis, containing both general visceral and gustatory centers. The area with vertical cross hatching is the somatic sensory column, containing below the general cutaneous centers and above the special somatic sensory nuclei (tuberculum acusticum and lobe of the lateral line). (After Johnston.) 1. Lobus lineæ lateralis; 2, tuberculum acusticum; 3, fasciculus longitudinalis medialis; 4, lobus visceralis.

In the trunk region the neural crests become segmented and their cells crowd together in each segment and migrate ventrally (Fig. 1592). Some cells are directly transformed into spinal ganglion cells, others migrate outward to form sheath cells of the peripheral nerves, while still others enter the sympathetic nervous system. In the head the development of the cranial nerve ganglia is much more complex. The neural crest, as in the trunk, becomes segmented and contributes important components to the cerebral ganglia. Rudiments of the neural crest extend forward beyond the trigeminus ganglion, probably representing vestiges of segmental nerves which have disappeared in the course of vertebrate evolution. Figs. 1590 and 1591 illustrate forms taken by the neural crest in two species of fishes, and Figs. 1592 and 1593 in human embryos.

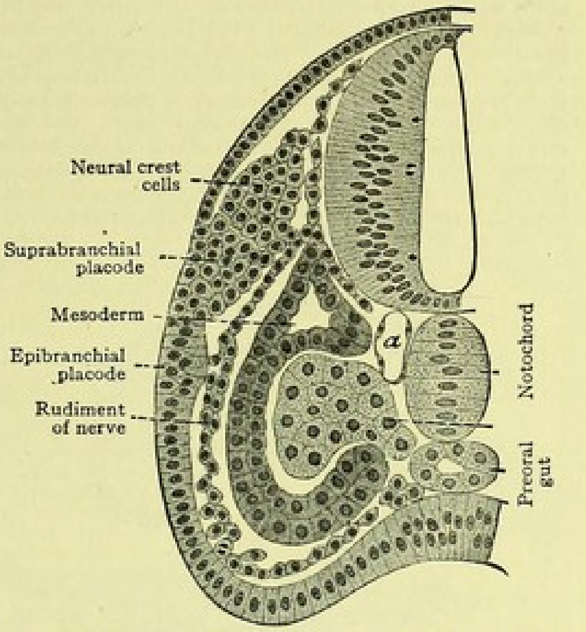

Fig. 1589.—Transverse Section Through the Head of a 7-day Embryo of *Petromyzon* in the Region of the Trigeminus Ganglion. (After von Kupffer.)

During the process of differentiation of cells of the cranial ganglia from the neural crest the suprabranchial and epibranchial placodes are undergoing an independent differentiation in the ectoderm, and finally cells are proliferated from the placodes which

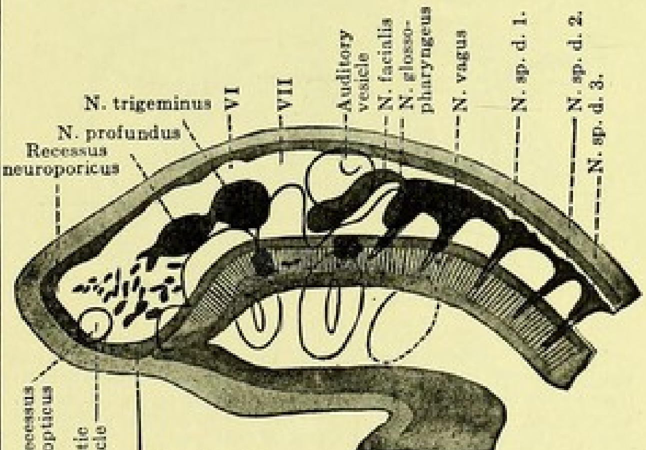

Fig. 1590.—A Diagram of the Head of the Embryo of *Petromyzon* at a Stage when Two Gill Clefts are Open and the Neural Crest is Segmented into the Rudiments of the Cranial Ganglia. From the left side. The suprabranchial (dorsolateral) placodes are indicated by vertical and horizontal cross lines, the epibranchial placodes by oblique lines. (After Koltzoff, from Johnston's Nervous System of Vertebrates, P. Blakiston's Son & Co.)

enter into the ganglia of some of the cranial nerves. The exact rôle played by placodal cells in the formation of the cerebral ganglia is not in all cases clear and it appears that there is considerable diversity among different species of vertebrates in this respect.

It is evident that in the head, as in the trunk, the systems of unspecialized components are derived from the neural crest. The researches of Landacre have further shown that the ganglion cells of the specialized visceral sensory system (gustatory neurones) are derived, apparently wholly, from the epibranchial series of placodes. In other words, the visceral sensory ganglia of the VII., IX., and X. cerebral nerves have a two-fold embryological origin which is correlated with their two-fold composition, the ganglion cells of the general or unspecialized visceral sensory component arising from the neural crest, while those of the specialized visceral sensory (gustatory) component come from the epibranchial placodes. After these placodes have thus contributed cells to the visceral ganglia they disappear.

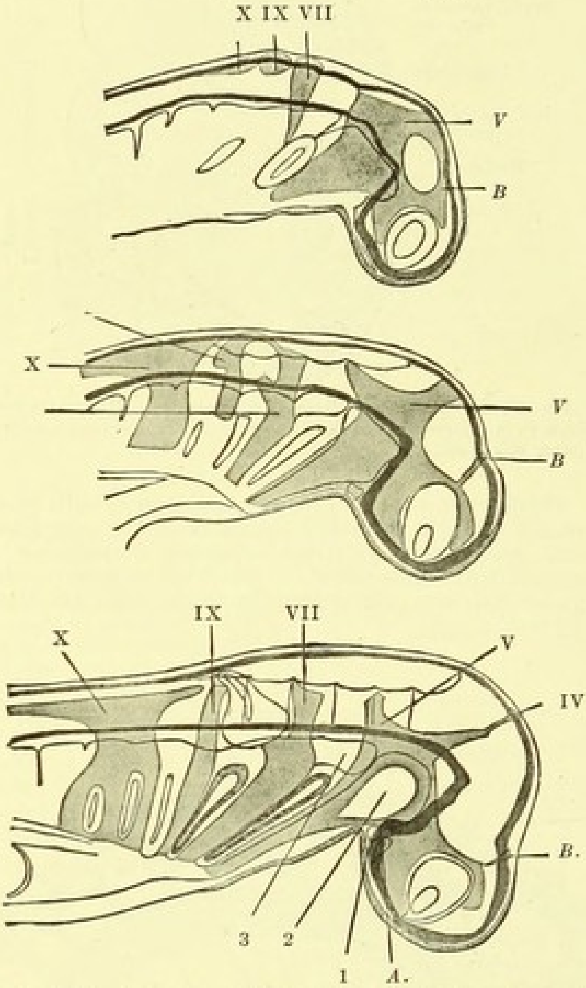

Fig. 1591.—Diagrams of Three Stages in the Development of the Head of the Embryo Shark, *Squalus acanthias*, to show the differentiation of the neural crest into the cranial ganglia; *A*, 1, 2, 3, somites; *B*, nervus thalamicus. (After Neal, from Johnston's Nervous System, P. Blakiston's Son & Co.)

The suprabranchial placodes are also transient structures with one exception. The auditory vesicle arises by the invagination of one member of this series. In the catfish (Ameiurus), where these relations have been most carefully studied, the ganglion of the VIII. nerve is proliferated from the auditory vesicle, the vesicle then differentiating into the membranous labyrinth with its contained areas of sensory epithelium, etc. The lateral line ganglia in the catfish arise partly from the auditory vesicle (lateralis IX. ganglion), partly from the suprabranchial placodes and partly from an undifferentiated lateral mass of cells which probably contains the representatives of the suprabranchial placode and neural crest. Further research is needed to determine the full significance of the suprabranchial series of placodes, but the special somatic sensory organs of the internal ear (and at least a part of the lateral line ganglia in fishes) take their origin from this source, while the general somatic sensory ganglia of the cutaneous systems are wholly derived from the neural crest, as in the case of the spinal nerves.

The olfactory organ arises as a sensory placode, from which neuroblasts migrate inward to form the

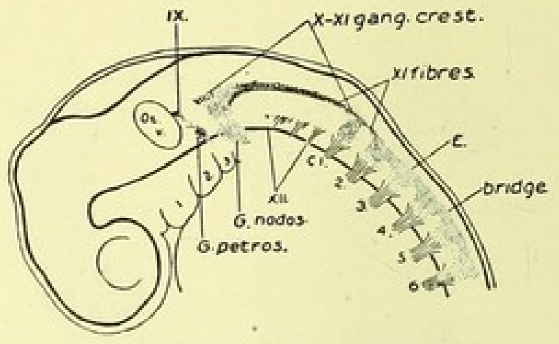

Fig. 1592.—Reconstruction of a Part of the Peripheral Nerves of a Human Embryo of 4 mm. (Hertwig's collection, No. 137.) × 16.7.

The neural crest in the trunk region has begun to segment into spinal ganglia (*E*). In the head region the cerebral ganglia of the IX., X., and XI. nerves are indicated. *Ot.v*, ear vesicle. (After Streeter, Am. Journal of Anatomy.)

ganglion of the nervus terminalis (Brookover), but the relations of this placode to those lying farther back are still undetermined. The cell bodies which give rise to the fibers of the olfactory nerve remain permanently at the surface in the olfactory epithelium.

The analysis of the cranial ganglia into general or unspecialized systems derived from the neural crest and special sensory systems derived from ectodermal placodes is most clearly evident in fishes, but similar placodes are known to occur in human embryos

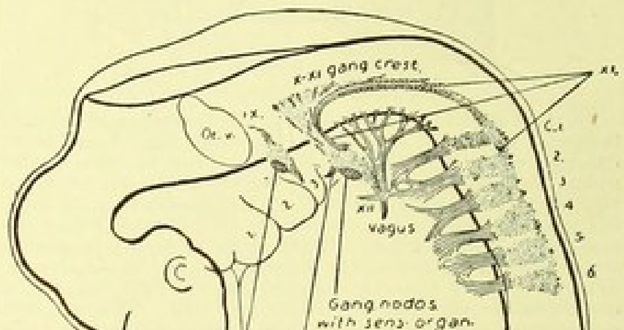

Fig 1593.—Reconstruction of the Nerves in the Occipital Region of a 7 mm. Human Embryo (Mall's collection, No. 2), which shows sensory placodes in connection with the ganglion petrosum and the ganglion nodosum. × 16.7. *Ot.v*, ear vesicle; *gang. crest*, neural crest. (After Streeter, Am. Journal of Anatomy.)

and the same fundamental relations probably prevail here. The interpretation of these data has been retarded by the failure of many investigators to take into account the diversity in the functional composition of some of the cranial ganglia. The recognition of the fact that the ganglia on some of the more complex cranial nerves contain two or more functional components clarifies the developmental history of the peripheral nerves in much the same way that the doctrine of nerve components has assisted in the analysis of the medulla oblongata into functionally defined columns.

In mammals the ganglion on the V. nerve will probably prove to be derived from the neural crest, these neurones belonging to the general or unspecialized somatic group and supplying chiefly the skin of the head. The semilunar or Gasserian ganglion represents at least two embryonic segments, which primitively contained respectively the profundus and the trigeminus nerves (cf. Fig. 1590). The VII. ganglion is probably derived partly from the neural crest (general visceral neurones) and partly from the epibranchial placode on the hyoid cleft (special visceral or gustatory neurones), these two components being indistinguishably fused in the geniculate ganglion on the portio intermedia of the VII. nerve, as found in the adult body. The ganglion cells on the IX. and X. nerves also have a two-fold origin, partly from the neural crest (general or unspecialized

In a four-millimeter human embryo (Fig. 1592) the neural crest is in process of differentiation into ganglia. In the cervical region of the spinal cord the segmental enlargements of the neural crest, which later become the spinal ganglia, are still connected by bridges of cells. The XII. nerve is here seen in its primitive relations as a series of motor rootlets which directly continue the ventral root series of the spinal nerves. The neural crest in this region is largely devoted to the formation of the XI. and X. ganglia. In a seven-millimeter embryo (Fig. 1593) all of the ganglia of the cranial nerves have been laid down and the epibranchial placodes connected with the IX. and X. ganglia are seen. Fig. 1594 illustrates a reconstruction of the roots and ganglia of a ten-millimeter human embryo, and Fig. 1595 shows the relations in a fourteen-millimeter embryo. In the latter figure the transitory ganglia on the XI. and XII. (Froriep's ganglion) nerves are clearly shown.

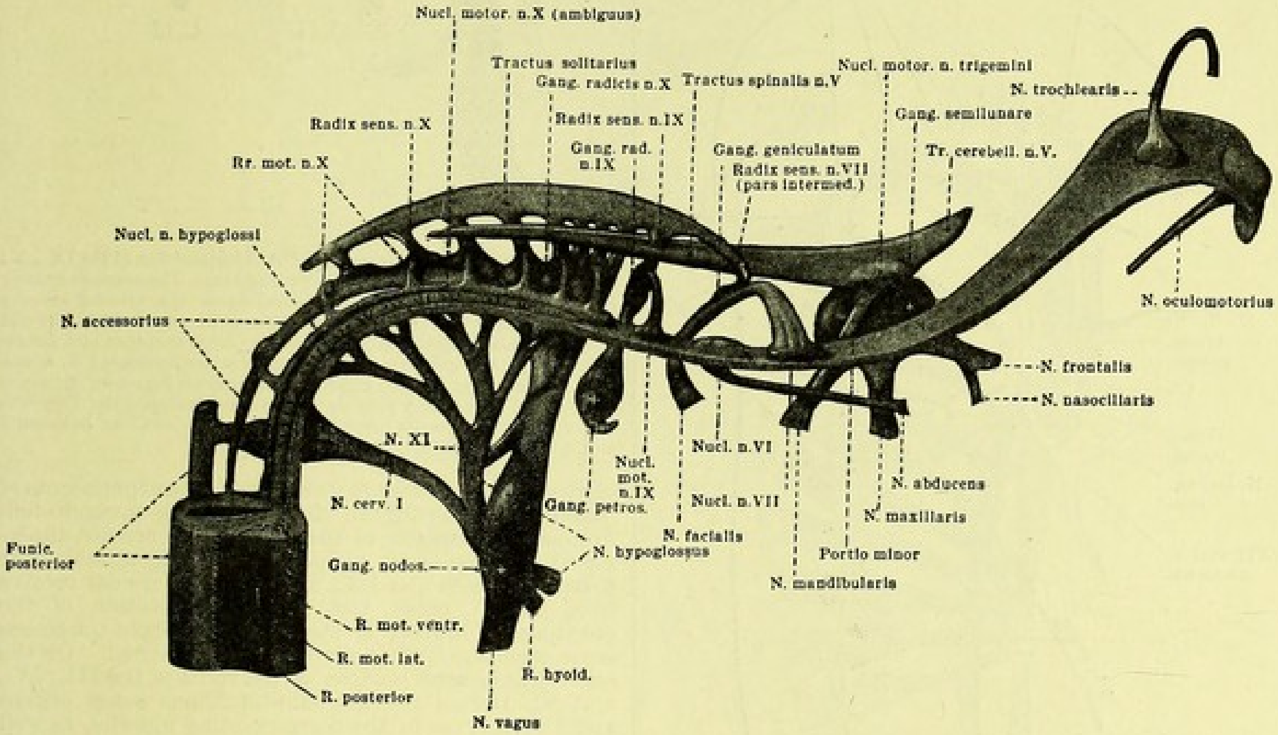

FIG. 1594.—Medial View of a Model of the Cranial Nerves of a 10 mm., Human Embryo (Huber collection, No. 3). A portion of the spinal cord is represented and above that everything is cut away excepting the sensory bundles and motor nuclei cf the different nerves, and that portion of the marginal zone which is to form the funiculus ventro-lateralis. The somatic motor nuclei are seen to form a column which is the continuation of the ventral horn of the spinal cord. (After Streeter, Am. Journal of Anatomy.)

group) and partly from epibranchial placodes (special visceral or gustatory). The unspecialized sensory neurones of these nerves belong to two components: (1) general visceral neurones which in the adult are mingled with the special visceral neurones to form the visceral or trunk ganglia (ganglion petrosum IX. and ganglion nodosum X.); (2) general somatic neurones which in the adult form the root ganglia (ganglion superius, or jugulare, IX. and ganglion jugulare X.). The ganglion cells on the XI. nerve are derived from the neural crest and probably belong to the general visceral system. These ganglion cells, however, have only a transient existence, most of them disappearing before adult life. A small transient ganglion is found in human and other mammalian embryos on the XII. nerve (Froriep's ganglion). This is derived from the neural crest and is probably a vestige of the general somatic sensory ganglia on the nerves of the spino-occipital group from which the XII. nerve is phylogenetically derived.

Fig. 1596 illustrates the relations beween the IX., X., and XI., cranial and the spinal nerves of man, as determined by embryological and comparative studies. The root ganglia of the IX. and X. nerves (superior and jugular ganglia) and the transitory ganglion of Froriep on the XII. nerve are in part, at least, of somatic sensory type, homologous with the chief component of the spinal ganglia. The ganglia on the spinal accessory rootlets, like the g. petrosum IX. and the g. nodosum X., are of visceral sensory type. The motor fibers of the spinal accessory rootlets are in part general visceral in function for distribution with the vagus branches and sympathetic system, and in larger part special visceral motor for the striated musculature of the larynx region and for the trapezius and sternomastoid muscles. The latter muscles appear to be of mixed origin, chiefly from the branchial musculature, but partly from the myotomes, and they have a double innervation—visceral motor from the XI. nerve and somatic motor from the cervical spinal nerves. By some anatomists the spinal portion of the accessorius is regarded as somatic motor in type.

The cells of the ganglia of the cranial nerves are at first bipolar, one process being directed centrally to form root fibers, the other peripherally. But in the course of further embryological development the two poles of the cell are gradually approximated and the processes finally coalesce, thus forming the T-shaped neurones which are characteristic of the cerebrospinal ganglia. Several stages in this process are illustrated in Fig. 1597. The ganglion cells of the VIII. cranial nerve, however, retain their bipolar character throughout life.

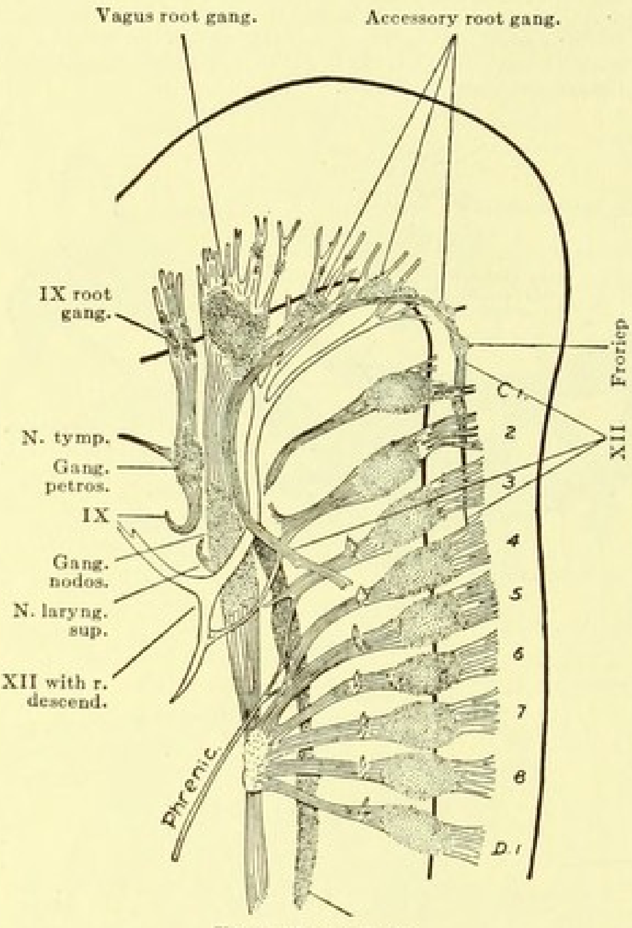

Fig. 1595.—Reconstruction of Some of the Peripheral Nerves of a 14 mm. Human Embryo (Mall collection, No. 144). × 16.7. (After Streeter.)

The nerves of special sense (I., II., and VIII. pairs) are described in special articles. In Fig. 1598 some of the general relations of the cranial and cervical spinal nerves are diagrammatically indicated, and in Fig. 1599 the details of the relations of their roots to the base of the skull. The central connections of the cranial nerves are briefly described in the article, *Brain, Anatomy*.

III. Nervus Oculomotorius.—The motor fibers of the third nerve arise from a group of nuclei in the floor of the aqueduct of Sylvius of the midbrain and emerge in several rootlets from the inner face of the crus cerebri. The somatic motor fibers supply the mm. rectus superior, inferior and internus, obliquus inferior and levator palpebræ superioris. The visceral motor fibers are of the preganglionic type and terminate in the ganglion ciliare, which they enter by the short root of this ganglion. The postganglionic neurones pass from the ciliary ganglion by way of the short ciliary nerves to the ciliary muscle and the constrictor muscle of the iris. The ciliary ganglion also receives a long root from the nasal branch of the V. nerve and sympathetic fibers from the cavernous plexus.

The eye muscles are provided with the usual muscular sense organs (muscle spindles and tendon organs), in addition to motor end plates, and these are supplied by sensory fibers which enter the brain with the III., IV., and VI. roots. These fibers constitute somatic sensory components of their respective nerves. Their

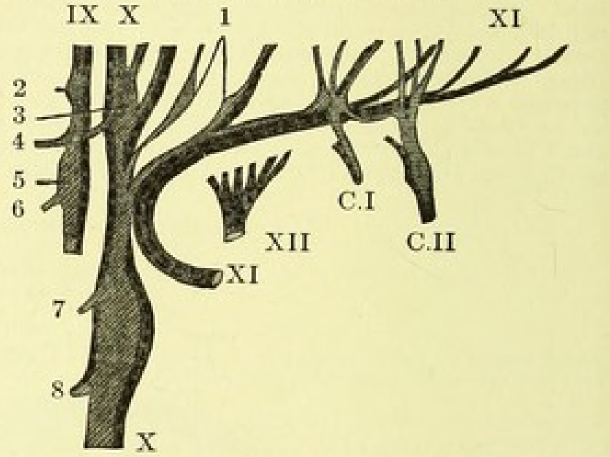

Fig. 1596.—Diagram Illustrating the Composition of the IX., X., XI., and XII. and First Spinal Nerves of Man. The somatic sensory component is shaded with horizontal lines, the visceral sensory with oblique lines, the somatic motor with round dots and the visceral efferent with dark rectangles. (After Streeter and Johnston, Spengel's Ergebnisse und Fortschritte der Zoologie.) 1, Accessory root ganglia; 2, root ganglion; 3, ganglion jugulare; 4, ramus auricularis; 5, ganglion petrosum; 6, ramus tympanicus; 7, ramus pharyngeus; 8, superior laryngeal nerve. The swelling between 7 and 8 in the ganglion nodosum.

central connections are unknown. The experiments of Tozer and Sherrington show that the musculo-tendinous sense organs of the eye muscles are not innervated, as formerly supposed, by the anastomotic filaments which the III., IV., and VI. nerves receive from the V. nerve, but that upon section of the ophthalmic branch of the V. the musculo-tendinous sense organs and their nerves are not affected. On the other hand, after section of the roots of the III., IV., and VI. nerves the musculo-tendinous sense organs and their nerves in the corresponding muscles, as well as the motor end plates, promptly degenerate.

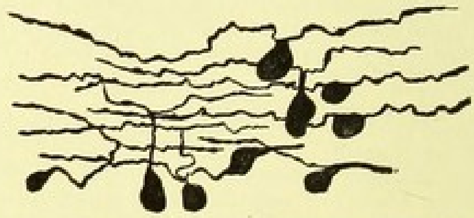

Fig. 1597.—Transformation of Bipolar into Unipolar Ganglion Cells in the Gasserian Ganglion of an Embryo Guinea-pig. (After Van Gehuchten.)

IV. Nervus Trochlearis.—The nucleus of the IV. nerve lies in the floor of the aqueduct of Sylvius just caudad to that of the III. nerve. The fibers curve outward, dorsally and backward to emerge from the dorsal surface of the brain behind the corpora quadrigemina, there to decussate completely in the valve of Vieussens, thence to run forward to supply the superior oblique muscle. It is joined by filaments from the sympathetic and from the ophthalmic branch of the trigeminus. Somatic sensory fibers are present in this nerve for muscular and tendinous sense organs of the superior oblique muscle.

VI. Nervus Abducens.—The VI. nerve arises from a nucleus in the floor of the fourth ventricle and pursues a direct course to the external rectus muscle of the eyeball. It receives minute filaments from the carotid plexus of the sympathetic and from the ophthalmic branch of the trigeminus. The VI. nerve also contains somatic sensory fibers for muscle and tendon sense organs in the external rectus muscle.

V. Nervus Trigeminus.—The composition and distribution of the V. nerve are remarkably constant throughout the vertebrate phylum. It supplies motor and sensory fibers to the muscles of mastication and mediates general sensibility of the face, nasal cavity, mouth, and teeth. It has two roots, the portio major, sensory, and the portio minor, motor. There is in addition the mesencephalic root, which in some lower vertebrates has a separate origin distinct from the other portions. In some animals this root appears to be combined with the portio major and in still others with the portio minor. In human embryos this root emerges from the brain with the portio major (Johnston), but most of its fibers are distributed peripherally with the motor branches of the trigeminus (Willems). The trigeminus ganglion (semilunar or Gasserian ganglion) is borne on the portio major, immediately distal to which the nerve breaks up into three divisions which give the nerve its name, the ophthalmic, maxillary, and mandibular nerves. The motor branches all arise from the nervus maxillaris.

(1) The ophthalmic nerve is wholly sensory (Fig. 1601). It communicates with the sympathetic, III., IV., VI., and VII. nerves. Its first branch is a recurrent meningeal twig for the tentorium, after which it divides into nasociliary, frontal and lacrymal branches. The nasociliary nerve furnishes the long root of the ciliary ganglion (a ganglion of the sympathetic system), the long ciliary nerves, twigs for the conjunctiva, lining of the nasal fossa and skin of the tip of the nose. The frontal nerve supplies the conjunctiva and skin of the upper eyelid and the forehead. The lacrymal branch innervates the lacrymal gland, conjunctiva and adjacent skin. (2) The maxillary nerve (Fig. 1602) is also wholly sensory, supplying the skin of the side of the face (cheek, temple, lower eyelid, nose, and upper lip), the mucous lining of the nose and upper part of the pharynx and the teeth of the upper jaw, and communicating with the sympathetic sphenopalatine ganglion. (3) The mandibular nerve (inferior maxillary) receives the remainder of the general cutaneous fibers and all of the motor fibers of the trigeminus roots. The motor fibers supply the following muscles: temporal, masseter, external and internal pterygoid, tensor palati, tensor tympani, mylohyoid, and the anterior belly of the digastric. The sensory fibers supply the skin of the lower jaw, side of the head, external ear, external auditory meatus (in part), teeth of the lower jaw, anterior part of the tongue (general sensation only), mucous lining of the mouth and other parts adjacent. It communicates with the facialis and with the otic and submaxillary ganglia of the sympathetic system. The lingual branch is joined by the chorda tympani from the facial nerve and there has been much discussion regarding the exact courses of the fibers of these two nerves. The weight of evidence is clearly in favor of relegating the gustatory fibers all to the chorda and excluding this system from the trigeminus entirely.

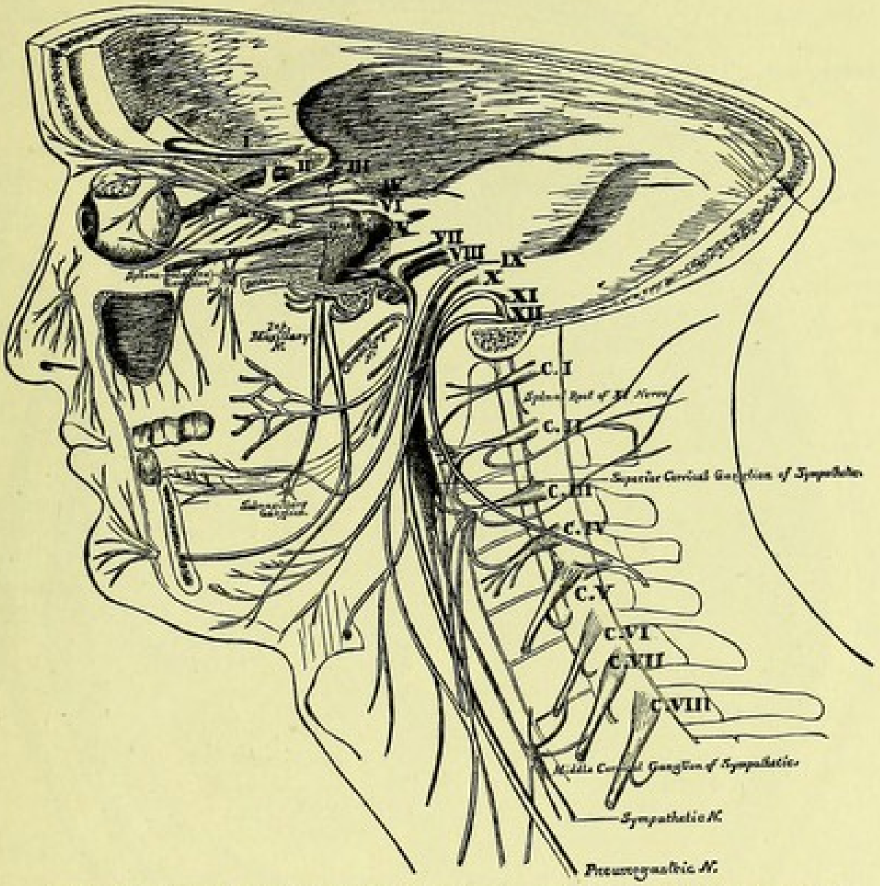

FIG. 1598.—General View of the Cranial Nerves. (Altered from Allen Thomson.)

The three divisions of the V. nerve supply sensory fibers to three well-defined areas of the skin of the head (cf. Fig. 1586). Fibers of musculo-tendinous sensibility go out with all of the motor branches and thus reach the trigeminus musculature. There are also numerous peripheral anastomoses with those branches of the VII. nerve which supply the superficial musculature, probably for the innervation from the trigeminus of the musculotendinous organs of these muscles (Fig. 1610).

The V. nerve in some respects resembles the typical branchiomeric nerves rather closely, since it forks around the mouth as they do around the gill clefts, the special visceral motor component enters the post-trematic (mandibular) ramus, etc. But the other visceral systems characteristic of the branchiomeric nerves are greatly reduced or absent. Few, if any, general visceral fibers occur in the V. roots, such of these fibers as are found in the peripheral branches being derived chiefly from various anastomoses with the sympathetic nervous system. The trigeminus is the great nerve of general cutaneous and muscular sensibility for the head, and with the enlargement of this system the other sensory components suffered reduction.

The motor fibers of the V. nerve are derived from the motor nucleus near the superficial origin of the root and probably also from the locus cœruleus farther forward. The fibers of musculo-tendinous sensibility are probably derived from the mesencephalic nucleus, whose cells represent elements of the neural crest permanently enclosed within the neural tube (Johnston, Willems, etc.). The cutaneous fibers terminate partly in the chief sensory nucleus at the level of the entrance of the root fibers and partly in the spinal V. nucleus, which extends from the chief sensory nucleus backward into the cervical region of the spinal cord. Clinical, experimental, and comparative data show that fibers which enter the spinal V. tract are so arranged that cutaneous fibers derived from the ophthalmic and maxillary nerves lie farther ventral in the tract, while the fibers from the mandibular nerve, especially those from the tongue and mouth cavity, lie farther dorsal (Fig. 1604). This brings the latter fibers into more intimate relation with the visceral sensory centers related to the fasciculus solitarius, and indeed some of the trigeminal root fibers pass directly into the fasciculus solitarius.

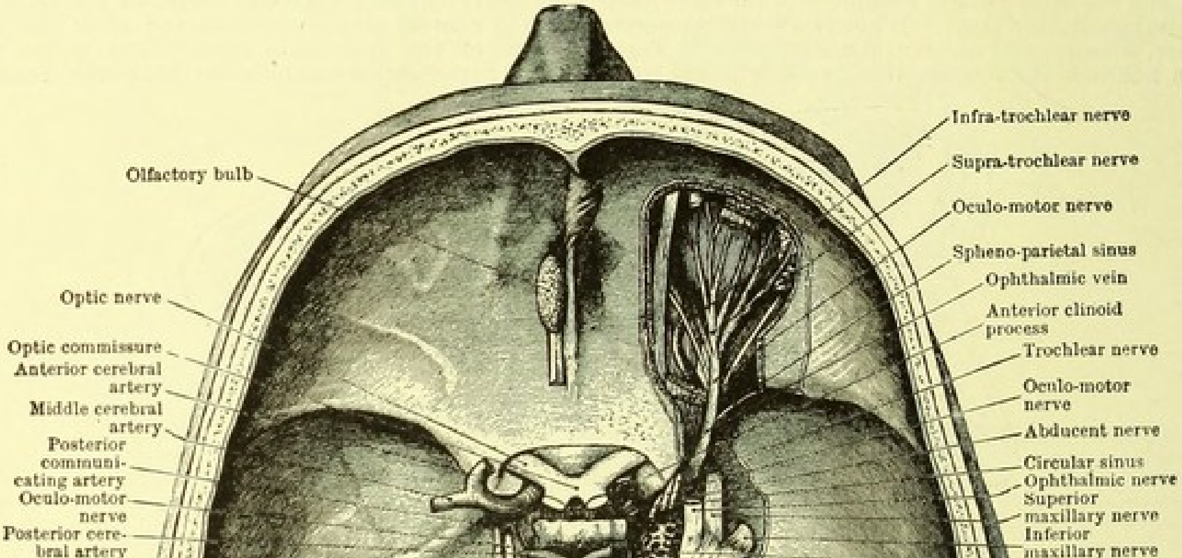

FIG. 1599.—The Base of the Skull, to Show the Dura Mater, Sinuses, Arteries, and Nerves. (From Cunningham's Anatomy.)

VII. Nervus Facialis.—In lower fishes the facialis is a typical branchial nerve. The hyoid arch is a modified gill arch, as shown 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 other branchial nerves fork around their respective gill clefts (Figs. 1584 and 1605). The visceral sensory and motor components are arranged in typical branchiomeric fashion. The VI. nerve probably represents the somatic motor root of this segment. In cyclostome fishes there is also a somatic sensory (general cutaneous) root in the VII. nerve, but this disappears in all higher forms.

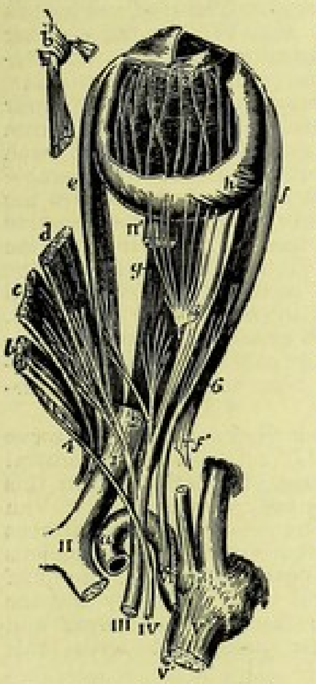

Fig. 1600.—View from Above of the Motor Nerves of the Eyeball and Its Muscles. (From Quain's "Anatomy.")

a, Upper part of the internal carotid artery emerging from the cavernous sinus; *b*, superior oblique muscle; *b'*, its anterior part passing through the pulley; *c*, levator palpebræ superioris; *d*, superior rectus; *e*, internal rectus; *f*, external rectus; *f'*, its upper tendon turned down; *g*, inferior rectus; *h*, insertion of inferior oblique muscle; II, optic commissure; II', part of the optic nerve entering the eyeball; III, common oculomotor; IV, trochlearis; V, large root of the trigeminus; V', small, or motor root; VI, abducens; 1, upper division of III. nerve, giving twigs to the levator palpebræ and superior rectus; 2, branches of the lower division supplying the internal and inferior recti muscles; 3, the long branch of the same nerve, proceeding forward to the inferior oblique muscle, and close to the number 3 the short root of the ciliary ganglion; this ganglion is also shown receiving from behind its long root, which has been cut short, and giving forward some of its ciliary nerves which pierce the sclerotic coat; 3', marks the termination of some of these nerves in the ciliary muscle and iris, after having passed between the sclerotic and choroid coats; 4, the trochlear nerve entering the upper surface ofh te superior oblique muscle; 6, the abducens nerve passing into the external rectus.

In the human facial nerve the portio dura is a special visceral motor root, while the portio intermedia contains the visceral sensory component (which is associated with the geniculate ganglion) and the unspecialized (preganglionic) visceral efferent fibers. The facial trunk and the chorda tympani represent the posttrematic branch, the Eustachian tube being the mammalian equivalent of the spiracular gill cleft of fishes. The facial trunk contains chiefly special visceral motor fibers for striated muscles, with a few visceral sensory fibers from the geniculate ganglion and probably some general visceral motor (preganglionic) fibers. The chorda tympani contains general visceral efferent fibers (chiefly preganglionic salivatory fibers for the submaxillary ganglion, whose postganglionic fibers supply the submaxillary and sublingual salivatory glands), and a larger number of special visceral (gustatory) fibers for taste buds on the anterior two-thirds of the tongue. Other visceral sensory fibers pass out from the geniculate ganglion by the great superficial petrosal nerve, which corresponds with the r. palatinus of fishes, and still other visceral connections are effected with the sympathetic system through the small superficial petrosal and other anastomotic twigs (Figs. 1606 and 1607).

The chorda tympani, accordingly, contains chiefly preganglionic salivatory fibers for the sublingual and submaxillary glands and special sensory fibers for the anterior part of the tongue. Its anastomosis with the V. nerve naturally follows from the fact that the facial and trigeminal fibers which combine to form the lingual nerve have the same area of distribution on the anterior two-thirds of the tongue, though different functions to perform there. The special visceral motor fibers of the facial trunk supply the hyoid musculature (stylohyoid, posterior belly of the digastric, and stapedius muscles) and an extensive system of superficial facial muscles.

The special visceral sensory, or gustatory, component of the VII. nerve is very large in fishes, whose

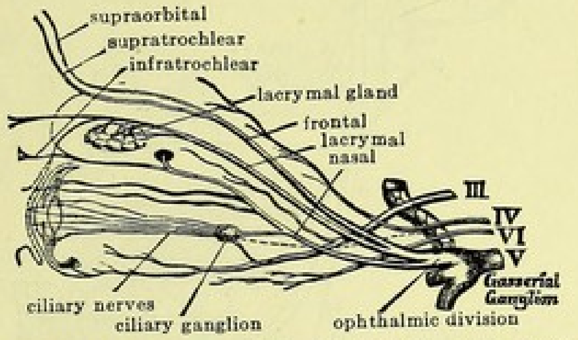

Fig. 1601.—The Nerves of the Left Orbit. (After Young, reduced.)

taste buds are very numerous and widely distributed. In some species, like the carp (Cyprinus) and catfish (Ameiurus), taste buds are found, not only very abundantly in the mucous membrane of the mouth, gills, and lips, but also distributed over the entire outer surface of the body. The cutaneous taste buds are always supplied by nerves arising from the geniculate ganglion (Fig. 1608), which here has important cutaneous branches reaching all parts of the body surface. These sense organs and nerves have nothing to do with the lateral line organs, which have an independent nerve supply belonging to the special somatic sensory (acustico-lateralis) system.

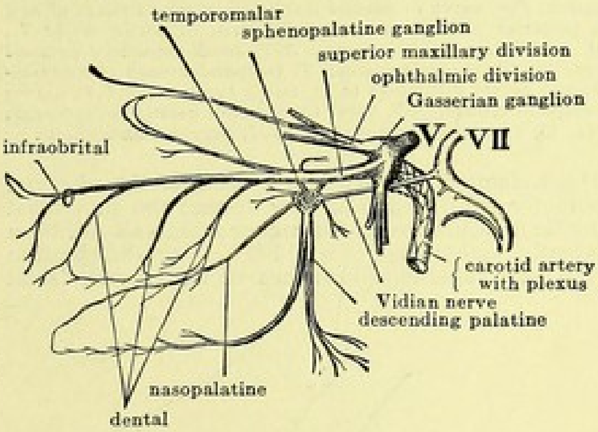

Fig. 1602. Plan of the Maxillary Division of the Trigeminus as seen from the Left Side. (Altered from Young.)

In fishes the motor root of the VII. nerve is relatively small and it supplies only the hyoid musculature, while the portio intermedia is often the largest nerve in the body. The course of evolution shows a remarkable metamorphosis of the facialis nerve (quite apart from the history of the lateral line nerves of fishes, some of which are associated with the facialis), from a branchiomeric nerve which is chiefly visceral sensory with a small motor component, to the human nerve which is chiefly motor and whose sensory component is so small that anatomists have often ignored it altogether. This metamorphosis is correlated with the reduction of the gustatory system of the mouth and lips and the great enlargement of a system of facial muscles derived from the hyoid musculature. These muscles originally included as their most important element a constrictor system of the pharynx (sphinctor colli) and from this system the superficial mimetic musculature of the higher mammals has been gradually elaborated (Fig. 1609). The distribution of the more superficial branches of the human facial nerve and its anastomoses with the trigeminus are illustrated in Fig. 1610.

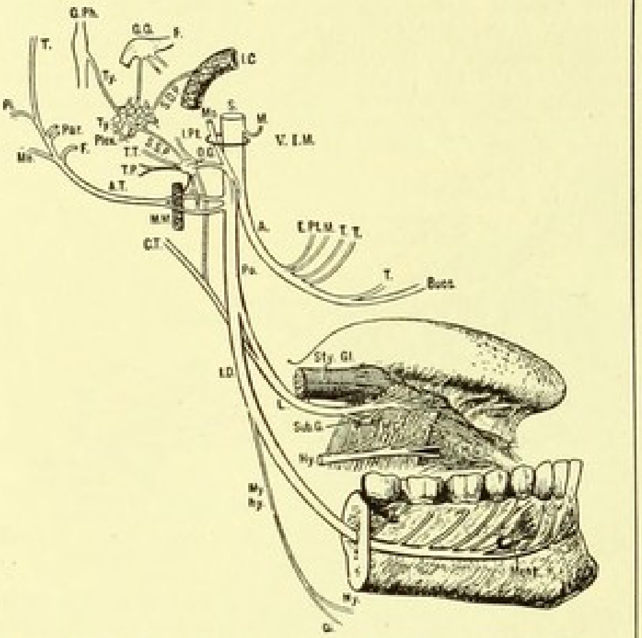

Fig. 1603.—Scheme of the Distribution of the Mandibular Nerve. (From Cunningham's Anatomy.) *A*, Anterior division of the n. mandibularis; *AT*, auriculotemporal nerve; *Bucc*, nerve to buccinator muscle; *CT*, chorda tympani; *Di*, nerve to anterior belly of digastric muscle; *EPt*, nerve to external pterygoid muscle; *F*, facial nerve; *F*, communication of auriculotemporal with facial nerve; *GG*, geniculate ganglion; *GHG*, m. genioglossus; *GPh*, IX. nerve; *HGl*, m. hyoglossus; *IC*, internal carotid artery; *ID*, inferior dental nerve; *IPt*, nerve to internal pterygoid muscle; L, lingual nerve; *M*, meningeal branch of *V*. nerve; *M*, nerve to m. masseter; *MM*, middle meningeal artery; *Me*, nerve to meatus of ear; *Ment*, mental nerve; *Mo*, portio minor V.; *My*, nerve to mylohyoid muscle; *My.hy*, mylohyoid nerve; *OG*, otic ganglion; *Par*, nerve to parotid gland; *Pi*, nerve to pinna of ear; *PO*, posterior division of n. mandibularis; *S*, portio major V.; *SDP*, small deep petrosal nerve; *SSP*, small superficial petrosal nerve; *Sty Gl*, m. styloglossus; *T*, temporal branch of auriculotemporal nerve; *TT*, nerve to m. tensor tympani; *T.T.T*, nerves to temporal muscles; *TP*, nerve to m. tensor palati; *Ty*, tympanic nerve; *Ty Plex*, tympanic plexus; *VIM*, nervus mandibularis.

The course of the fibers in the chorda tympani has given rise to much controversy. The study of lesions in the vicinity of the V. and VII. roots, whether experimentally or pathologically produced, has frequently yielded ambiguous results. In particular, many cases of surgical removal of the semilunar ganglion have resulted in disturbances of taste, from which it was inferred that gustatory fibers must reach the brain through the V. root. But a considerable number of carefully studied recent cases support the clear evidence from both embryology and comparative anatomy that the V. nerve has no connection with the specific gustatory organs, though its termini on the tongue may be sensitive to certain types of chemical stimulation not related with taste buds (Sheldon). Fig. 1601 illustrates the now generally accepted course of the specific gustatory fibers and some of the theoretical pathways which have been advocated by different neurologists.

The special visceral motor fibers of the VII. nerve arise from the motor VII. nucleus. The central localization of various groups of muscles within this nucleus has been experimentally determined by Van Gehuchten (Fig. 1612). The general visceral efferent fibers of the salivatory system arise from the nucleus salivatorius superior lying dorso-laterally of the chief motor nucleus. The general visceral sensory and the gustatory fibers enter the fasciculus solitarius and terminate in the nucleus associated with this tract.

IX. Nervus Glossopharyngeus.—In lower fishes this is the most typical branchiomeric nerve (Figs. 1583 and 1605), containing the characteristic visceral components, a general somatic sensory component for the overlying skin and sometimes a special somatic sensory component for lateral line organs, all distinct from other nerve roots. In Bdellostoma, Johnston is of the opinion that a somatic motor root is also present in the IX. segment, thus completing the typical segmental pattern, though this component is absent in all higher forms.

The human IX. nerve contains general and special visceral efferent fibers, general and special visceral sensory fibers and a general somatic sensory component. The general visceral efferent group are preganglionic fibers, chiefly for salivary secretion, passing through the tympanic and small superficial petrosal nerves and terminating in the otic ganglion, from which postganglionic fibers pass to the parotid salivary gland. Other preganglionic fibers may connect with the sympathetic system by other anastomosing twigs. The special visceral motor fibers innervate the stylo-pharyngeus muscle. The tympanic nerve corresponds to the palatine branch and

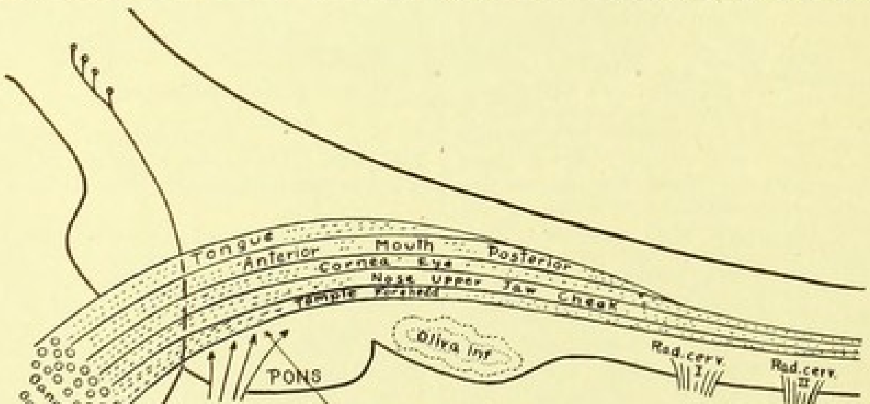

Fig. 1604.—Diagram of the Roots of the Nervus Trigeminus, to illustrate the arrangement of the sensory fibers, after the researches of Wallenberg and Marburg. (Modified from Edinger.)

the IX. trunk to the posttrematic branch of the nerve of the first gill cleft in fishes.

There are two ganglia on the IX. nerve, of which the larger (g. petrosum) belongs to the visceral sensory group. The smaller root ganglion (g. superius) probably, by analogy with lower forms, belongs, in part or wholly, to the somatic sensory component. The distribution of the general visceral sensory fibers is not clearly determined, probably to the mucous lining of the tympanum, Eustachian tube, and pharynx. The special visceral sensory, or gustatory, fibers supply taste buds on the posterior third of the tongue. The somatic sensory fibers supply general sensation to the posterior third of the tongue and, by an anastomosis with the vagus, probably share in the distribution of the r. auricularis vagi.

Centrally the special visceral motor fibers arise from the nucleus ambiguus. None of the preganglionic fibers arise from the dorsal motor IX. + X. nucleus, the salivatory fibers arising from a special nucleus salivatorius inferior which lies between the nucleus ambiguus and the dorsal motor nucleus. All visceral sensory fibers enter the fasciculus solitarius and terminate in the nucleus of cells which accompanies this tract, especially in an enlargement which extends dorsally to the ventricular surface under the lateral end of the trigonum vagi, the dorsal sensory nucleus. A portion of the IX. root fibers enter the spinal V. tract, here descending to form the most dorsal fibers of this tract (Ramón y Cajal). They probably terminate in the somatic sensory nucleus which accompanies the spinal V. tract (substantia gelatinosa Rolandi). These are probably fibers of the somatic sensory component.

X. Nervus Vagus.—This nerve represents a fusion of several branchiomeric units (cf. Figs. 1605, 1592, 1613, 1596). It has the same composition as the IX. nerve. The XII. nerve contains somatic motor fibers which belong to the vagus region.

The vagus communicates with the VII., IX., XI., XII., first and second 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 nervous system and it seems to share many of its functions with the latter. It controls, more or less directly, the more important auto-

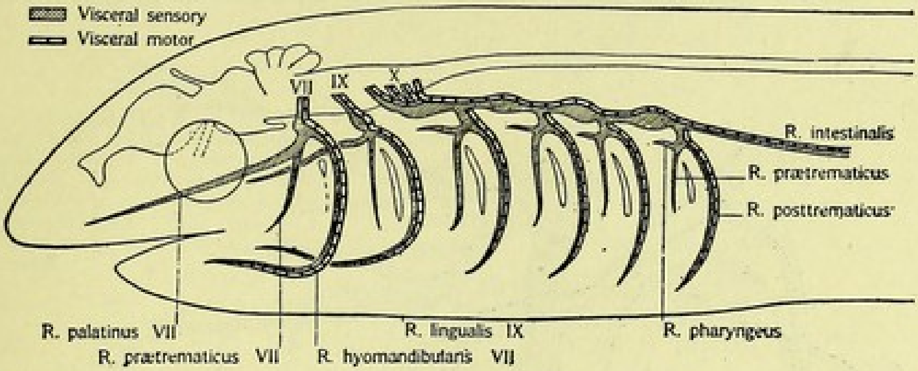

FIG. 1605.—Diagram of the Branchial Nerves of a Fish (*Selachian*). The V. nerve and the other somatic roots of the branchial region are omitted. (After Johnston, Spengel's Ergebnisse und Fortschritte der Zoologie.)

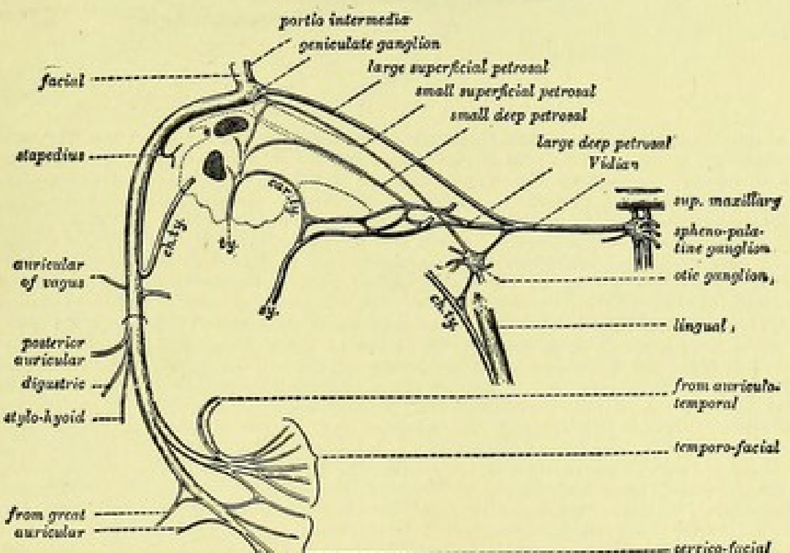

FIG. 1606.—Plan of the Facial Nerve. (After Thane, from Quain's "Anatomy.") *ch.ty.*, Chorda tympani, its middle part removed; *ty.*, tympanic branch of the glossopharyngeus; *sy.*, sympathetic on the internal carotid artery; *car.ty.*, caroticotympanic nerve, passing between the tympanic nerve and the sympathetic in the carotid canal.

matic and vegetative functions of the body, such as circulation and digestion, and is thus of the most profound physiological significance.

The general visceral efferent fibers take their origin from the dorsal motor nucleus and ultimately distribute through the sympathetic system. The special visceral motor fibers arise from the nucleus ambiguus and supply striated muscles of the pharynx and larynx. The visceral sensory fibers arise from the ganglion nodosum and for the most part distribute to the viscera through the sympathetic system. Centrally they enter the fasciculus solitarius and its nucleus. The special visceral sensory system is very extensively developed in the vagus of lower vertebrates, where taste buds are numerous in the branchial region. A few taste buds are found on the epiglottis and adjacent parts (J. G. Wilson), which are probably supplied by the vagus. The somatic sensory component has a separate ganglion (g. jugulare) and supplies most of the fibers of the ramus auricularis vagi for the skin of the external auditory meatus and back part of the pinna. As in the case of the IX. nerve, these somatic sensory fibers are probably the component of the root which enters the spinal V. tract, a condition which is known to prevail in several types of lower vertebrates.

XI. Nervus Accessorius.—The spinal accessory nerve consists of two parts, an accessory vagus part and a spinal part. The former contains general and special visceral efferent components and distributes with the vagus branches. The latter contains special visceral motor fibers from the lateral horn of the spinal cord for the trapezius and sternomastoid muscles. The comparative morphology of this nerve has been already considered.

XII. Nervus Hypoglossus.—This nerve in man corresponds to the ventral roots of several segmental nerves of the posterior part of the branchial region of fishes. A vestige of its transient ganglion (of Froriep) rarely persists in the adult. The hypoglossus fibers emerge in from ten to fifteen rootlets, pass through the

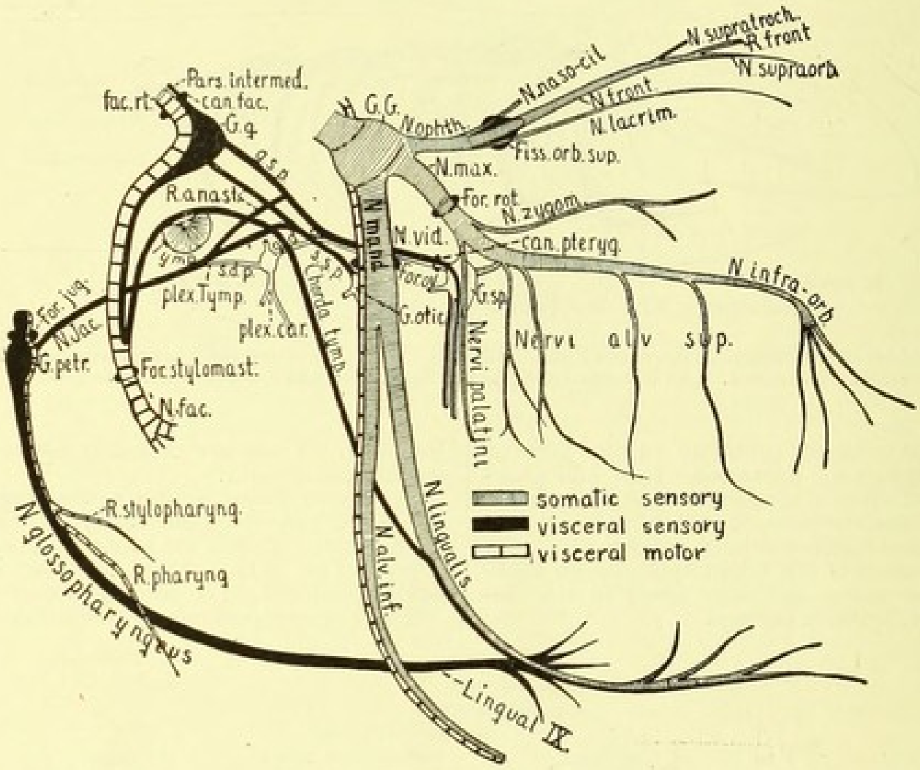

FIG. 1607.—Diagram of the Trigeminal, Facial, and Glossopharyngeal Nerves in Man, from the Right Side. The glossopharyngeal nerve, instead of appearing in its normal position in front of the facial, has been placed behind it. This is its true morphological position. This change necessitates the lengthening of Jacobson's nerve and a slight distortion of the tympanic plexus. The post-ganglionic sympathetic system is unshaded. It should be noted that the visceral nerves shown in black contain not only taste fibers but also several kinds of preganglionic sympathetic fibers of the efferent vasodilator and excito-glandular type. Many of these nerves undoubtedly contain also post-ganglionic fibers from the unshaded sympathetic ganglia. The somatic sensory fibers of the glossopharyngeal have not been indicated in the diagram. *Can fac*, canalis facialis; *can pteryg*, canalis pterygoideus; *chorda tymp*, chorda tympani; *fac rt*, motor facial root; *Fiss orb sup*, fissura orbitalis superior; *For jug*, foramen jugulare; *For os*, foramen ovale; *For rot*, foramen rotundum; *For stylomast*, foramen stylomastoideus; *GG*, ganglion Gasseri; *Gg*, ganglion geniculi; *G otic*, ganglion oticum; *G petr*, ganglion petrosum; *G sp*, ganglion sphenopalatinum; *gdp*, great deep petrosal, from the carotid plexus to the great superficial petrosal to form the Vidian nerve; *gsp*, great superficial petrosal, from the geniculate ganglion to the sphenopalatine ganglion, probably carrying taste fibers for the soft palate through the palatine nerves; *N alv inf*, nervus alveolaris inferior; *Nervi alv sup*, nervi alveolares superiores; *N front*, nervus frontalis; *N infra-orb*, nervus infra-orbitalis; *N Jac*, nerve of Jacobson or the tympanic nerve; *N lacrim*, nervus lacrimalis; *N lingualis*, nervus lingualis for the anterior part of the tongue; *N mand*, nervus mandibularis V.; *N max*, nervus maxillaris V.; *N nasocil*, nervus naso-ciliaris; *N ophth*, nervus ophthalmicus V., *Nervi palatini*, palatine nerves for the soft palate; *N supraorb*, nervus supraorbitalis; *N supratroch*, nervus supratrochlearis; *N. vid*, vidian nerve; *N zygom*, nervus zygomaticus; *Pars intermed*, pars intermedia of Wrisberg, the sensory root of the facial; *plex car*, plexus caroticus; *plex tymp*, plexus tympanicus; *R anast*, anastomotic rami between the geniculate ganglion and tympanic plexus and the small and great superficial petrosal nerves, respectively; *R front*, ramus frontalis; *R pharyng*, rami of the glossopharyngeal nerve for the pharyngeal plexus; *R stylopharyng*, ramus stylopharyngeus IX.; *sdp*, small deep petrosal nerve from the carotid plexus to the tympanic plexus; *ssp*, small superficial petrosal, formed by the junction of the Jacobson's nerve through the tympanic plexus and the anastomotic branch from the geniculate ganglion; *Tymp*, tympanum. (After Sheldon.)

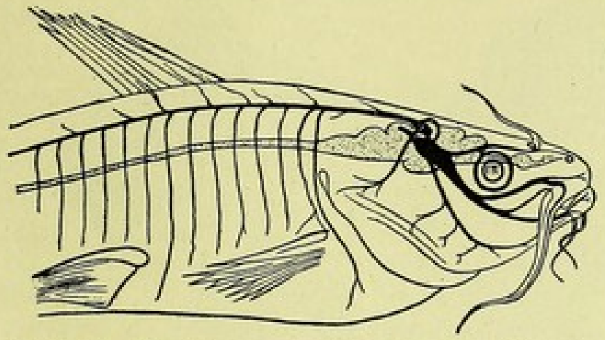

Fig. 1608.—The Cutaneous Gustatory Branches Arising from the Geniculate Ganglion of the Facial Nerve of the Catfish (*Ameiurus melas*). Projected upon the Right Side of the Body. Spinal cord and brain stippled. The geniculate ganglion, its roots and cutaneous branches are drawn in black; the branches of this nerve distributed to the mucous lining of the mouth cavity are omitted. Taste buds are found in all regions of the outer skin to which these branches are distributed.

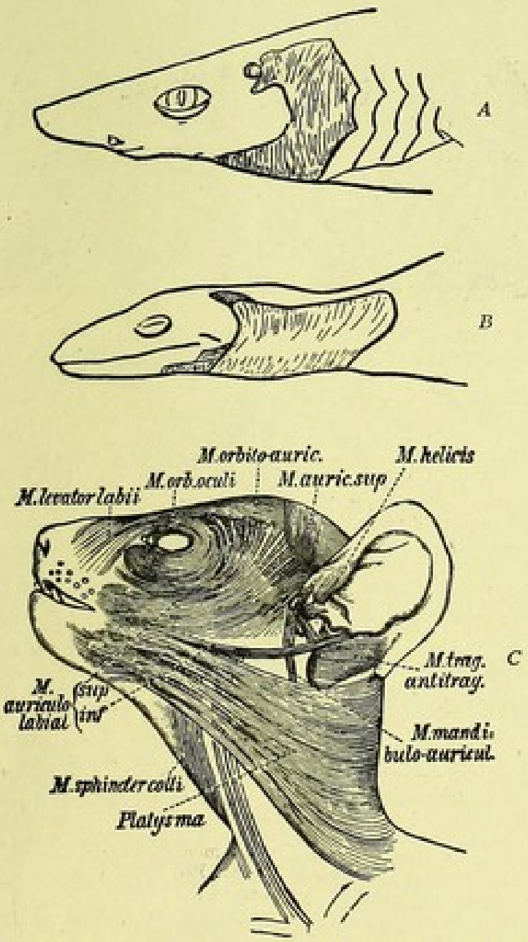

Fig. 1609.—Sketches Illustrating the Phylogeny of the Facialis Musculature. All of the muscles here indicated are innervated from the nervus facialis. The gradual expansion of this system from the branchial musculature of the hyoid arch (fishes) to a general constrictor system of the pharynx (reptiles), and finally the derivation of the superficial mimetic musculature from the latter system (mammals) are illustrated. (After Ruge.) *A*, Facialis musculature of a shark; *B*, of a lizard; *C*, of a generalized mammal (*Lepilemur*).

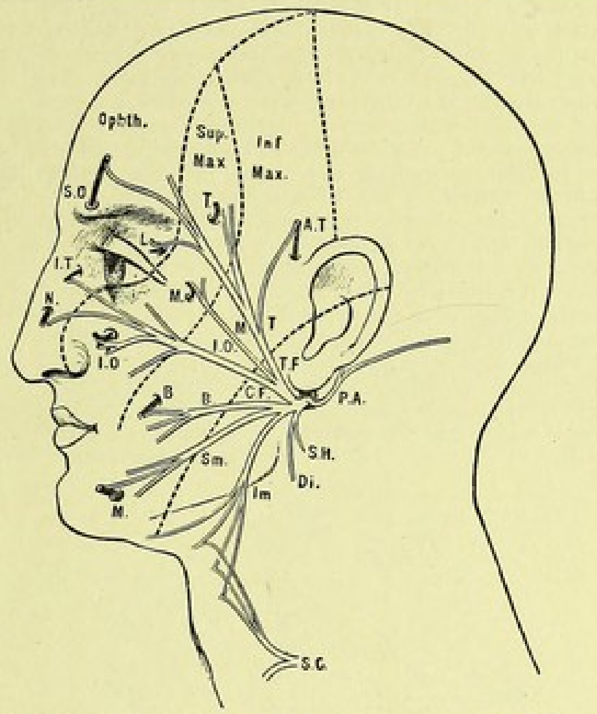

Fig. 1610.—Distribution of the Facial Nerve Outside the Skull, and its Communications with the Trigeminal Nerve On the Face. (From Cunningham's Anatomy.)

Facial Nerve.—*B*, Buccal; *CF*, cervicofacial division; *Di*, nerve to posterior belly of digastric muscle; *Im*, inframandibular branches; *IO*, infraorbital branches; *M*, malar; *PA*, posterior auricular nerve; *SH*, nerve to stylohyoid muscle; *Sm*, supramandibular; *T*, temporal; *TF*, temporofacial division.

Trigeminal Nerve.—*AT*, Auriculotemporal; *B*, buccal; *Inf Max*, inferior maxillary (mandibular) division; *IO*, infraorbital branches; *QT*, infratrochlear; *L*, lacrymal branches; *M*, malar; *M*, mental branches; *N*, external nasal; *Ophth*, ophthalmic division; *SC*, superficial cervical nerve; *SO*, supraorbital; *Sup Max*, superior maxillary division; *T*, temporal.

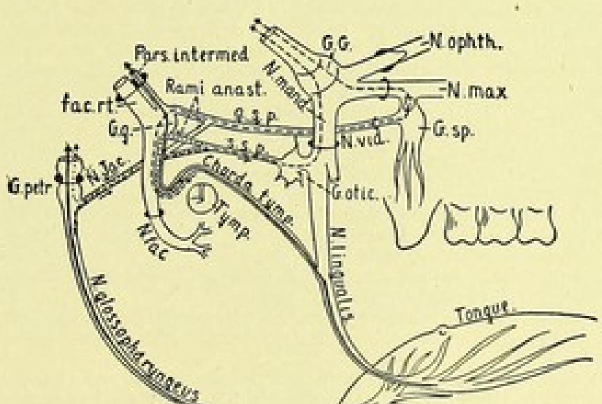

Fig. 1611.—Diagram Showing Some of the Various Courses Which have been Advocated for the Taste Fibers in Man. The courses advocated in this article are shown by heavy black lines; other suggested courses are indicated by broken or dotted lines. (After Cushing and Sheldon, Anatomical Record.) *fac.rt*, Motor facial root; *GG*, Gasserian ganglion; *Gg*, geniculate ganglion; *G.otic*, otic ganglion; *G petr*, ganglion petrosum; *G sp*, sphenopalatine ganglion; *g s p*, great superficial petrosal nerve; *N fac.*, facial trunk; *N Jac*, Jacobson's or the tympanic nerve; *N vid*, vidian nerve; *Rami anast*, anastomotic rami between the geniculate ganglion and tympanic plexus and the small and great superficial petrosal nerves respectively; *s s p*, small superficial petrosal nerve; *Tymp*, tympanum.

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. Its distribution is to the tongue musculature, a group of muscles which have migrated forward into their present position from the branchial region.

In the preceding discussion of the cranial nerves attention has been directed especially to their more general relations. The anatomical details are easily accessible in the standard text-books. A functional analysis is essential, not only for the clinical, but also for the anatomical interpretation of the cranial nerves; and for this we are to a large extent dependent upon experimental and comparative data. In no departments of anatomy have the comparative and genetic methods yielded more valuable results than in the study of the peripheral nervous system.

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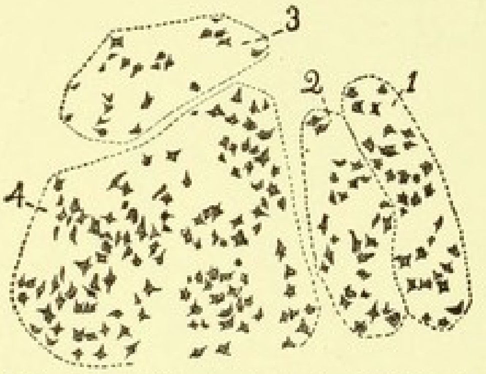

Fig. 1612.—Muscular Localization in the Facial Nucleus of the Rabbit. (After Van Gehuchten.) 1, Cells of the internal group related to the stapedius muscle; 2, cells of the internal group related to the muscles of the outer ear; 3, nucleus of origin of the fibers of the superior facial; 4, nucleus of origin of the fibers of the inferior facial, the inner portion related to the fibers of the inferior buccolabial branch, the outer portion to those of the superior buccolabial.

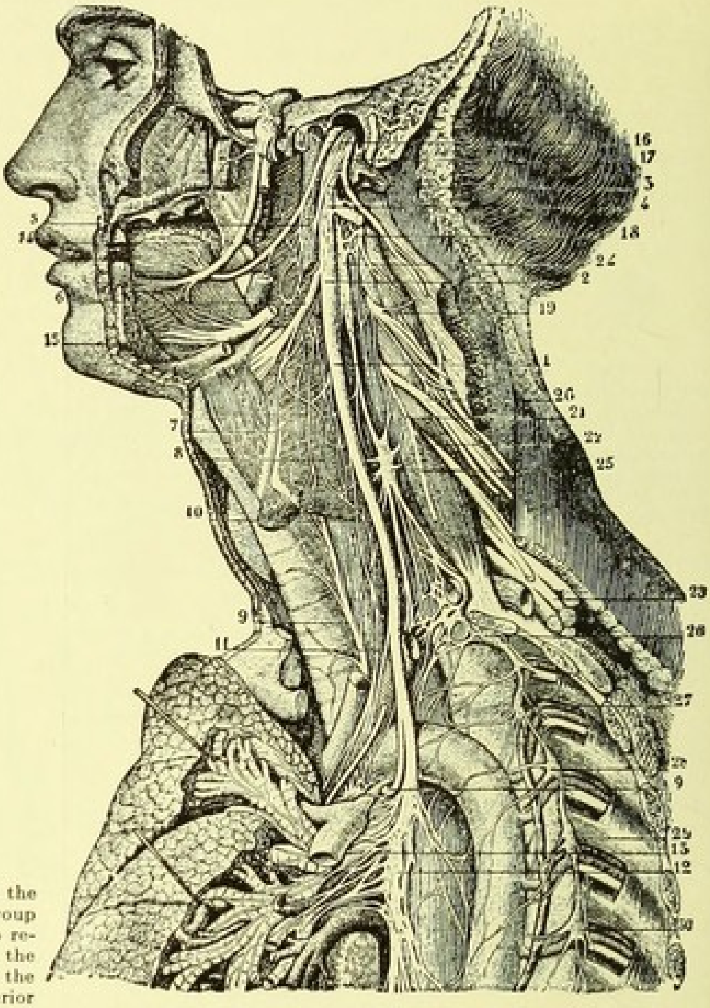

Fig. 1613.—The Distribution and Connections of the IX. and X. Nerves. (After Hirschfeld and Leveillé, from Quain's "Anatomy.") One-third. 1, Vagus nerve; 2, ganglion of its trunk; 3, accessory part of the spinal accessory; 4, union of the X. and XII. nerves; 5, pharyngeal branch of the vagus; 6, superior 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 sternomastoid 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.

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Craniocleidodysostosis.—In 1903 this term was applied by Marie and Sainton to the condition of congenital defect of the clavicle associated with imperfect ossification of the cranial bones. Although a typical example had been observed by Morand as early as 1766, only forty-five cases could be collected from the literature in 1905 by Villaret and Francoz. In 1910 this number was increased to fifty-eight by Fitzwilliams, who added two cases of his own, making in all, sixty undoubted cases of this striking and rare condition observed to date. Fitzwilliams gives in his paper an analysis of these cases with full bibliography, and to his paper the reader is referred for fuller data (*Lancet*, November 19, 1910, p. 1466).

The chief facts relating to this condition given here are taken for the greater part from Fitzwilliams' paper.

Craniocleidodysostosis is an hereditary condition affecting those bones that develop wholly or partly in membrane. Of the sixty cases collected by Fitzwilliams six showed complete absence of the clavicles; in two cases the left clavicle alone was present; in three cases the right; in twenty-three cases the sternal end of the left clavicle and in twenty-seven cases that of the right clavicle was alone represented; in one case the acromial end of the left and in two cases that of the right clavicle was alone represented; in fourteen cases the left, and in seventeen cases the right clavicle showed both portions present but not united; in five cases the left, and in two cases the right clavicle showed union of the two portions but revealing its formation from two parts by angling, arching, or notching; in thirteen cases the left and in eleven cases the right clavicle showed a ligament prolonging the inner end outward.

The skull changes consist in deficient and defective ossification of the cranial bones that develop in membrane, namely those of the cranial vault. During infancy a large portion of the vertex remains in a membranous state. The fontanelles are extremely large, or united into one large fontanelle. This membranous area is further increased by an open metopic suture in front and by the absence of the interparietal portion of the occipital bone. As age advances this membranous area diminishes in size until the metopic suture, sagittal suture, and posterior fontanelle are obliterated by bone. This is usually completed by the end of the twentieth year. The anterior fontanelle also gradually shrinks, until a few years later it is completely closed. Its closure is sometimes greatly delayed and in some cases it remains open through life; in one of the cases collected by Fitzwilliams it was as large as the palm of the hand at forty-seven, and in another case was still unossified at the age of fifty-six. The delay in ossification of the membranous bones is associated with an increased bone formation in those areas already ossified. Six prominent bosses develop on the vertex, arranged in three pairs, one behind the other, corresponding to the frontal, parietal, and occipital bones. On the one side the three bosses are separated from those of the opposite side by a broad median furrow, which is deepest in front, and gradually becomes shallower as it extends backward, while each symmetrical pair is separated from the other by a transverse furrow, one of which corresponds to the coronary and one to the lambdoidal suture; of these the anterior is the better marked, but is broader, shallower, and less marked than the median furrow. The appearances are similar to those of the "hot-cross bun head" seen in congenital syphilis; and such changes may be mistaken for those of syphilis or rachitis, but the frontal bosses are more prominent and the median furrow deeper than in those conditions. The diameters of the skull are greatly changed, circumference, length, and breadth being all increased, but not proportionally, the increase in breadth being greater than that in length, the skull becoming brachycephalic in character. A large number of Wormian bones may be formed.

In all cases in which there are well-marked skull changes there are also pronounced malformations of the facial bones, the face usually being much smaller than normal, so that the contrast between the small face and the large head becomes very striking. The supraorbital ridges are very prominent and overhang the orbits, while the other facial bones are small and appear flattened or depressed. The nose is short and badly formed, and usually deviates to one side. Narrowness of the upper jaws, high arching of the palate and imperfect dentition also characterize the condition. The changes in the facial bones are regarded as secondary to the lack of development, and are not of primary pathological significance (Fitzwilliams). Other writers regard the changes in facial and cranial bones as due to the same cause (fetal rickets).

The defective development of the clavicles is also responsible for various changes in the musculature of the shoulder girdle. The sternocleidomastoid varies with the state of development of the sternal end of the clavicle. The clavicular portion of the trapezius is frequently absent. The anterior fibers of the deltoid are frequently lacking or represented by only a few fasciculi. The infraspinatus may also be feebly developed. In some cases the posterior bundles of these muscles are well developed. The clavicular head of the pectoralis major is usually present, but is imperfectly developed when the sternal portion of the clavicle is small; it may be completely absent; the chondrosternal portion remains normal. Some writers doubt the existence of the subclavius, although Scheuthauer found it hypertrophied and inserted into the under surface of the ligamentous substitute of the clavicle. The deeper muscles are unaffected. In spite of these muscular changes ordinary movements are not usually disturbed, some patients not noticing any disability. Other patients easily become fatigued in arms and shoulders.

Associated with the defective development of the cranium and clavicle are other disturbances of development. In the sixty cases, peculiarities in the shape of the sternum were noted in ten cases, scoliosis, lordosis, or kyphosis in eleven cases, prominence of the transverse processes of the cervical vertebræ in six cases, genu valgum in four cases, peculiarities of the hands in four cases, curvatures of the long bones in three, and flat and pigeon breasts in two cases each. Many of the patients were undersized and of generally poor development, while in some the intelligence seemed diminished, although this was not the case in the majority.

Gegenbaur, in 1864, emphasized the hereditary nature of craniocleidodysostosis, and although later Gross opposed this view, its correctness is affirmed by recent studies. Of the sixty cases collected by Fitzwilliams thirty-one were furnished by eight families alone, and this writer believes that if the other cases had been carefully examined the hereditary tendency would have been even more clearly demonstrated. Transmission is possible from parents of either sex, for five mothers and three fathers transmitted it directly to twenty-three children. Fitzwilliams could find in the records no observation of its transmission to the third generation, but explains this by the difficulty in obtaining any information as to the grandparents from the ordinary hospital patient. The sexes seem equally affected, twenty-eight cases were seen in females, twenty-six in males, in six no mention was made of the sex.

Various opinions have been advanced as to the etiology. Alcoholism, tuberculosis, syphilis, and rachitis have all been put forth as etiological factors, but with little probability in any case. The relations of the affection to achondroplasia may be helpful in explaining both conditions; in craniocleidodysostosis the membranous bones are affected, while in achondroplasia there is defective development of those bones originating in cartilage. Fitzwilliams suggests that in both conditions the cause may be due to the presence or absence of certain chemical constituents that are necessary for the normal ossification of the membrane bones in the one case and the cartilage bones in the other, in much the same way that hemophilia must be due to an hereditary absence from or presence in the body of certain chemical constituents. Couvelaire advanced a similar view. He regarded hereditary craniocleidodysostosis as "the expression of a general taint with a predominance in certain osseous groups." Hart (*Lancet*, 1911, p. 124) believes the affection can be explained by Mendelian views, through the loss of the determinants of a Mendelian group of unit characters at the maturation of the ovum or found—"the sinus of Meyer"—in which foreign bodies lodge. The position of this concavity is such that it is often difficult to detect the presence of these foreign bodies and to remove them.

The posterior wall of the osseous meatus is of much surgical importance. It is formed by the union of the tympanic ring with the squama, and later with the anterior plate of the developed mastoid, this plate being quite thin and separating the canal from the cell spaces contained in the mastoid. Often the groove for the lateral sinus is in close proximity to this wall.

At the juncture of the upper and the posterior wall the scutum forms a portion of the outer wall of the mastoid antrum. In suppurative diseases of the tympanic cavity carious tracts (fistulæ) are often found in this region; they lead into either the tympanic attic or the antrum of the mastoid, and call for surgical interference. Just external to the upper posterior margin is often found a small bony spine—the suprameatal spine—which is of value as a surgical landmark in the operation for opening the mastoid antrum.

In the fully developed ear the drum is placed in an oblique position, the upper and back part forming an obtuse angle of about 135°, while the lower and anterior portion forms an acute angle of about 40°, with the canal wall.

The arterial supply to the auditory canal is quite abundant. The posterior auricular, a branch of the external carotid, sends a branch called the auricular. It passes in at the junction of the cartilaginous with the bony canal, and supplies the back wall of the canal, anastomosing with the anterior auricular, a branch of the temporal, which enters the anterior wall of the canal behind the condyle of the lower jaw. The tympanic branch of the internal maxillary enters the tympanic cavity through the Glaserian fissure, and sends a branch that supplies the skin of the canal adjacent to the membrana tympani. The veins take an irregular course. They empty their blood either directly (and this is the rule) into the external jugular or indirectly by way of the temporal or the internal maxillary vein.

The nerve supply is, first, from the auriculotemporal branch of the inferior maxillary division of the fifth nerve. Three small branches of this nerve supply the skin on the anterior wall and in the cartilaginous portion. Second, the auricular branch of the pneumogastric—"Arnold's nerve"—enters the back wall of the canal at its junction with the mastoid, and supplies the larger portion of the bony canal and a part of the back wall of the cartilaginous section. Irritation of this nerve by the accumulations of wax, by foreign bodies, or by the speculum when the ear is being examined or cleansed, produces the familiar reflex ear cough.

But little seems to be known regarding the lymphatic vessels contained in the walls of the external canal. Politzer states that they are probably connected with the lymphatic glands overlying the parotid, by way of the fissures of Santorini, since it is a matter of clinical observation that swelling of the lateral cervical glands often occurs in inflammatory conditions affecting the meatus.

The skin lining the auditory canal maintains all the histological characteristics of the skin in other parts of the body, although that part which lines the bony canal becomes very firmly united to the periosteum and altered in color. In its development there is a gradual growth outward of the skin, thus producing a constant tendency for the ear wax to move outward, this being further facilitated by the pressure of the condyle of the jaw, which in mastication constantly pushes the parotid gland against the anterior wall of the canal and somewhat influences its lumen.

The sinuous course of the canal is such that sound waves do not strike the membrana tympani directly, but are reflected from the walls of the canal and are thus modified in their intensity. Politzer states that the two most important points where this reflection takes place are on the back wall of the cartilaginous canal and on the anterior inferior portion of the bony canal.

The size of the canal plays no influence in the acuteness of hearing, although Burnett observes that large straight canals are more likely to be found in those possessing a so-called ear for music.

J. Morrison Ray.

Ear: Anatomy of the Auditory (Acoustic) Nerve and its End Organs.—Comparative Anatomy and Physiology.—The functions of audition and equilibration seem to be closely associated throughout the animal kingdom. The so-called auditory organs, or otocysts, of the invertebrates are in the majority of cases concerned largely, if not wholly, with equilibrium, though in some cases (notably among insects) true auditory organs undoubtedly exist. The structure of these organs is usually similar to that of the organs in the labyrinth of vertebrates.

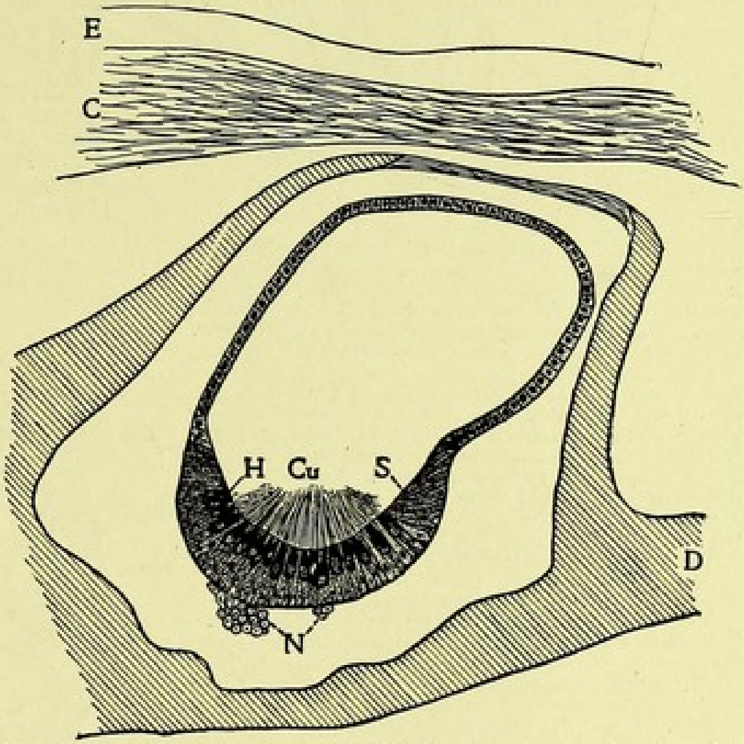

Fig. 1799.—Section through a Typical Lateral-line Organ of *Menidia* (the Fourth Canal Organ of the Mandibular Line of Fig. 1800). *C*, Corium; *Cu*, cupula, composed of hairs from the hair cells matted together and more or less gelatinized; *D*, dentary bone; *E*, epidermis; *H*, hair cells, or specific sensory cells; *N*, nerve fibers supplying the latter; *S*, supporting cells.

For the proper morphological comprehension of the eighth nerve and its terminal organs we must look far back to the early phylogenetic stages of its development in the vertebrates. The fishes possess a system of cutaneous and subcutaneous sense organs, the so-called lateral-line organs (Fig. 1799), widely distributed over the head and trunk. Part of these are in canals (the lateral line or "mucous" canals), and part are variously distributed over the skin, either naked or sunken in separate pits (the pit organs of ganoids and ampullæ of elasmobranchs); but all closely resemble structurally the maculæ and cristæ of the internal ear, and all are innervated by nerves which effect connections centrally, along with the auditory nerve in the area acustica. These lateral-line nerves go out with the vagus and facial roots and are conventionally associated with these nerves. They have, however, no physiological connection with them, but are more logically associated with the auditory nerve to comprise the "acustico-lateralis" or special somatic sensory system of nerves (*cf. Cranial Nerves*). The peripheral distribution of this component in a typical fish is expressed in the accompanying diagram (Fig. 1800).

The chief function of the lateral-line organs of fishes has been shown by Parker to be the recognition of water vibrations of low frequency, slower than the lowest sound waves audible to the human ear. They are probably also concerned with equilibration. The semicircular canals of the labyrinth as in the human body, are the chief organs of the equilibratory and static functions, while the sense organs of the sacculus of fishes are concerned with true hearing. There is no cochlea and the auditory sense is doubtless very simple with no capacity for tone analysis. All of these sense organs have the same fundamental structure and all are excited by movements in the fluid into which the hairs of the hair cells project. They are doubtless derived from a common type of simple cutaneous tactile sense organ.

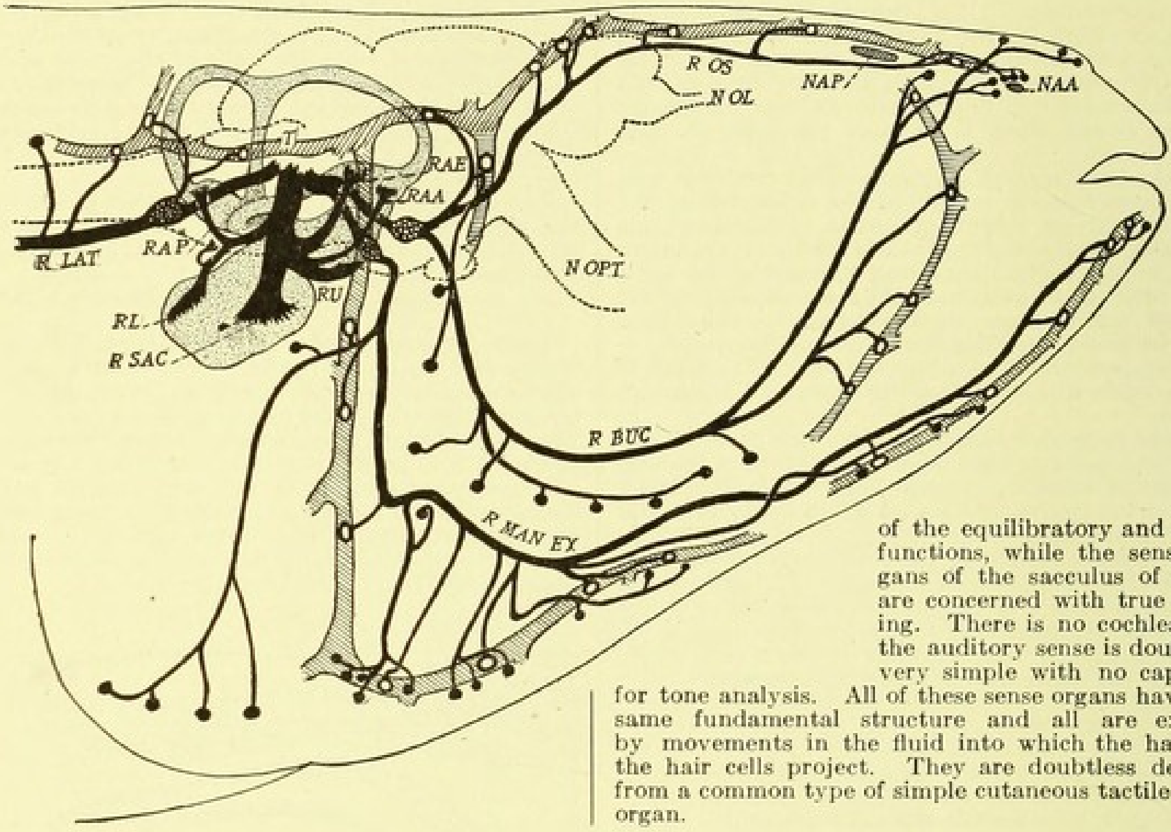

FIG. 1800.—The Acustico-lateral System of Nerves with Their Peripheral End Organs, as Seen from the Right Side, in the Silver Side, *Menidia*. Reconstructed from serial sections by projection upon the sagittal plane. ×12. The dotted outline represents the position of the brain, the lateral-line canals are shaded with cross-hatching, the auditory labyrinth is stippled, and the nerves are drawn in black. The organs of the lateral-line system are drawn as black discs when naked on the surface of the skin, and as black circles when lying in the canals. For the relation between the acustico-lateral nerves and the other systems of nerves in this fish, see the more detailed plot from which this was drawn off, in the *Journal of Comparative Neurology*, vol. ix., plate xv., or the *Archives of Neurology and Psychopath.*, vol. ii., plate ii. *NAA*, anterior nasal aperture; *NAP*, posterior nasal aperture; *NOL*, olfactory nerve; *N OPT*, optic nerve; *RAA*, ramulus acusticus ampullæ anterioris; *RAE*, ramulus acusticus ampullæ externæ; *RAP*, ramulus acusticus posterioris; *R BUC*, ramus buccalis facialis; *RL*, ramulus acusticus lagenæ; *R LAT*, ramus lateralis vagi; *R OS*, ramus ophthalmicus superficialis facialis; *R MAN EX*, ramus mandibularis externus facialis; *R SAC*, ramulus acusticus sacculi; *RU*, ramulus acusticus recessus utriculi; *T*, tuberculum acusticum.

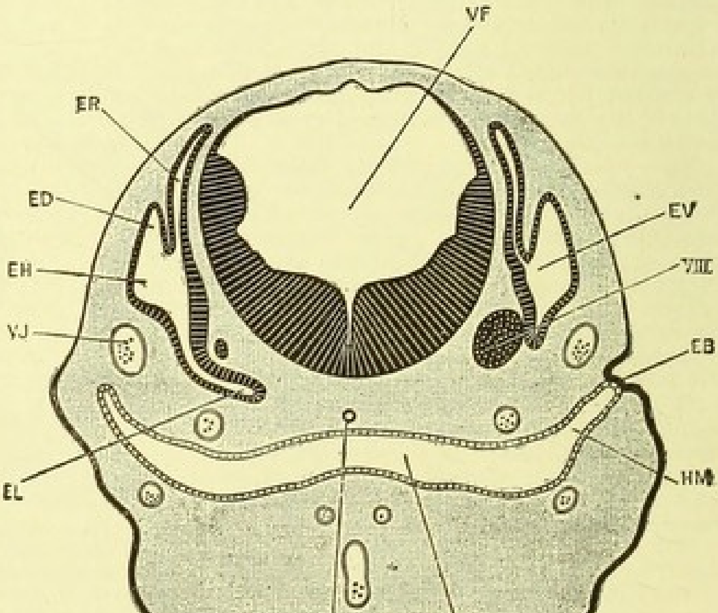

FIG. 1801.—A Transverse Section Across the Head of a Rabbit Embryo at the End of the Eleventh Day. The plane of the right half of the figure is slightly anterior to that of the left half. × 30. From Marshall's "Embryology." *CH*, notochord; *EB*, membrane closing the hyomandibular cleft; *ED*, common stem of the two vertical semicircular canals; *EH*, rudiment of the external semicircular canal; *EL*, cochlear canal; *ER*, recessus vestibuli; *EV*, auditory vesicle; *HM*, hyomandibular pouch; *TP*, pharynx; *VF*, fourth ventricle; *VJ*, jugular vein; *VIII*, auditory nerve.

The lateral-line organs are found in aquatic animals only (fishes and amphibians). The semicircular canals change very little, either in structure or function, from the lowest to the highest vertebrates, and the same is true of the large sensory spots in the sacculus and

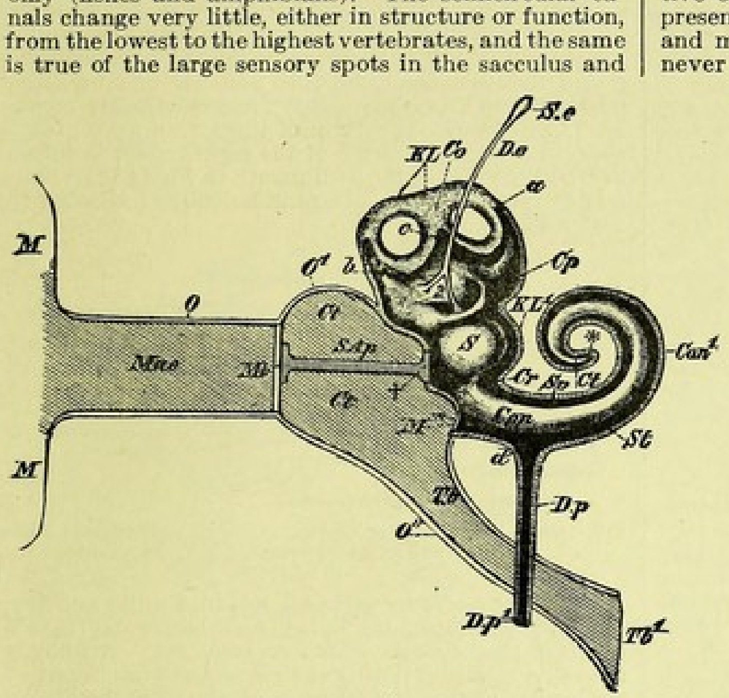

FIG. 1802.—Diagrammatic Representation of the Organ of Hearing of Man. (After Wiedersheim.) *Outer ear*—*M, M*, auricle; *Mae*, meatus auditorius externus; *O*, its wall; *Mt*, membrana tympani. *Middle ear*—*Ct, Ct*, cavum tympani; O^1, its wall; *SAp*, sound-conducting apparatus, which is drawn as a simple rod-like body instead of the auditory ossicles; the place † corresponds to the stapedial plate, which closes the fenestra ovalis; *Tb*, Eustachian tube; Tb^1, its opening into the pharynx; *O''*, its wall. *Inner ear*—The bony labyrinth, *KL*, KL^1, for the most part cut away; *S*, sacculus; *a*, *b*, the two vertical semicircular canals, of which one (*b*) is cut through; *S.e,D.e*, saccus and ductus endolymphatics, of which the latter is divided at 2 into two arms; *Cp*, cavum perilymphaticum; *Cr*, canalis reuniens, *Con*, membranous cochlea, which produces at * the vestibular cecum; Con^1, bony cochlea; *Sv* and *St*, scala vestibuli and scala tympani, which at * communicate with each other at the cupula terminalis (*Ct*); *D.p*, ductus perilymphaticus, which arises from the scala tympani at *d* and opens out at $D.p^1$. The horizontal semicircular canal is not especially designated.

utriculus. The fishes, however, possess a macula lagenæ in the sacculus which resembles the other sensory areas of the vestibule, but which in the course of further evolution undergoes a remarkable transformation, becoming the organ of Corti of the cochlea in mammals. Parallel with the evolution of the organ of Corti in land animals, for the analysis of tone, the sound-transmitting apparatus of the middle ear is elaborated.

Kappers is of the opinion that the cochlear system of mammals is more like the lateral line than the vestibular system of fishes, the central lateral-line path of fishes being comparable with the mammalian cochlear path. This is supported by Parker's experiments on the function the lateral-line organs cited above. But from this it does not follow that the cochlea is derived from the lateral-line organs, for the cochlea is known to be the derivative of the lagena already present in the fishes' labyrinth.

The middle and external ear do not appear in the fishes, the vibrations of the surrounding medium being transferred to the labyrinth through the tissues of the head. But air-breathing vertebrates require some intermediary mechanism to intensify the more feeble aërial vibrations. Accordingly, the middle ear, with its contained auditory ossicles, is seen for the first time in the Amphibia. The phylogeny of the auditory ossicles has been the subject of endless investigation, and there is still no agreement upon the details of this history. The internal ear in the lower fishes clearly lies in the hyoid segment of the head.

The Eustachian tube is now regarded as the derivative of the spiracular canal, a rudimentary gill cleft present in some of the lower fishes between the hyoid and mandibular arches. In the mammals this tube never quite reaches the surface of the head, but is cut off by an epithelial membrane composed of a layer of ectoderm and a layer of entoderm (*EB*, Fig. 1801), with an intervening layer of mesoderm appearing in later developmental stages. This membrane becomes the tympanic membrane, the portion of the tube within it the Eustachian tube, and the pit leading from it to the surface the external auditory meatus (Fig. 1802).

These alterations in the relative importance of the different members of the acustico-lateral complex are naturally reflected in the central nervous system. We therefore find that the size of the acustico-lateral centers (area acustica and cerebellum) in the fishes is directly proportional to that of the peripheral organs of this system. With the development of a cochlea in the mammals, an entirely new set of connections is effected in the oblongata, which are by no means so closely related to the cerebellum as are the end stations of the vestibular root. These are the ventral and dorsal cochlear nuclei. In connection with the fact that the secondary fibers connected with the cochlear root terminate very largely in the inferior member of the corpora quadrigemina (see below), it is interesting to note that this body appears upon the surface of the brain in the phylogeny contemporaneously with the cochlea. The cerebellum has been mentioned as a secondary end station for the acustico-lateral system of nerves. As the organ of equilibration (and of the static senses in general) for the body, this was probably its primary connection. But these static functions are served by all of the other senses as well (except, perhaps, the olfactory), so that the terminal nuclei of the other sensory nerves have also effected secondary connections with the cerebellum.

EMBRYOLOGY.—The auditory organ first appears in early embryos before the neural tube is closed, as a lateral ectodermal thickening. In animals in which the ectodermal epithelium at this stage is simple, the whole epithelium of the auditory plate invaginates to form the "auditory saucer," and later a vesicular sac which sinks down below the surface. But in other cases, in which the ectoderm becomes earlier two

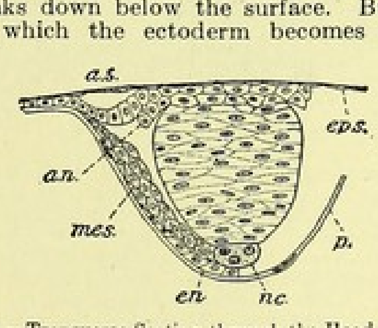

FIG. 1803.—Transverse Section through the Head of an Embryo of the Sea Bass of Thirty-five Hours. (After H. V. Wilson.) *a.n.*, Auditory nerve; *a.s.*, auditory saucer; *en*, entoderm; *ep.s.*, epidermic stratum of ectoderm; *mes.*, mesoderm; *nc.*, notochord; *p.*, periblast. The large oval mass of cells in the center of the figure is the medulla oblongata.

layered, it is only the inner, or nervous layer, which participates in this invagination, and the auditory vesicle never communicates with the surface of the body (Fig. 1803).

The auditory saucer, whether formed from the whole of the ectoderm or only from its inner layer, soon closes up and withdraws from the skin to form the auditory vesicle. In the elasmobranch fishes the vesicle retains its primary connection with the outer surface of the body to adult life by means of a slender tube, the ductus endolymphaticus, in this point

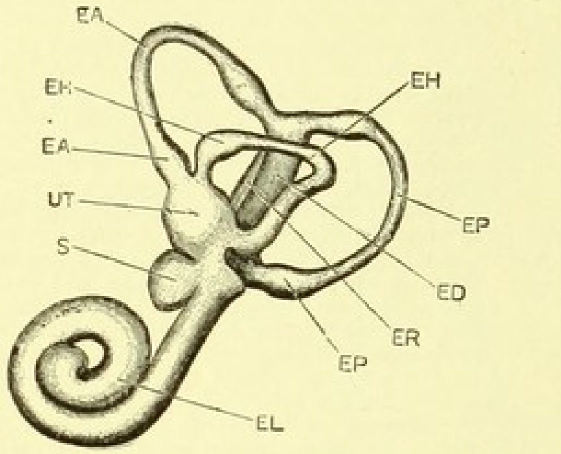

Fig. 1804.—The Left Auditory Vesicle of a Human Embryo of the Eighth Week, Seen from the Left Side. (After W. His, Jr., from Marshall's "Embryology." × 17. *EA*, Anterior vertical semicircular canal; *EA'*, ampulla of anterior vertical semicircular canal; *ED*, common stem of the two vertical semicircular canals; *EH*, horizontal semicircular canal; *EH'*, ampulla of horizontal semicircular canal; *EL*, cochlea; *EP*, posterior vertical semicircular canal; *EP'*, ampulla of posterior vertical semicircular canal. *ER*, recessus labyrinthi; *S*, sacculus; *UT*, utriculus.

resembling the lateral line canals, which open freely to the surface by means of a series of pores. But in all of the higher animals this connection is lost, though the tube persists as a blind pouch, the saccus and ductus endolymphaticus (Fig. 1802, *D.e.*, and

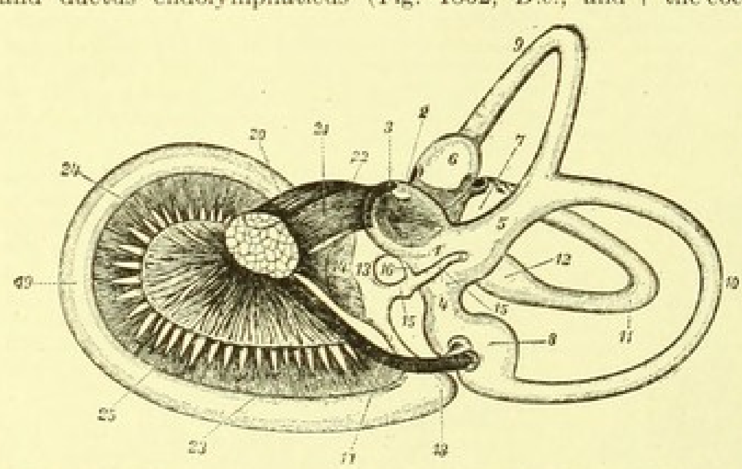

Fig. 1805.—The Membranous Labyrinth of the Right Internal Ear of a Human Embryo at the Fifth Month, Seen from the Medial Side. (After Retzius, from Barker's text-book.) 1–5, Utriculus; 2, recessus utriculi; 3, macula acustica utriculi; 4, sinus posterior; 5, sinus superior; 6, ampulla membranacea superior; 7, ampulla membranacea lateralis; 8, ampulla membranacea posterior; 9, ductus semicircularis superior; 10, ductus semicircularis posterior; 11, ductus semicircularis lateralis; 12, widened mouth of crus simplex of the lateral semicircular canal opening into the utriculus; 13, sacculus; 14, macula acustica sacculi; 15, ductus endolymphaticus; 16, ductus utriculo-saccularis; 17, ductus reuniens; 18, cecum vestibulare of ductus cochlearis; 19, ductus cochlearis; 20, nervus facialis; 21–24, N. acusticus; 21, N. vestibuli; 22, N. saccularis; 23, N. ampullaris inferior; 24, N. cochleæ; 25, distribution of N. cochleæ within the lamina spiralis ossea.

Fig. 1805, 15), which joins the membranous labyrinth at the ductus utriculosaccularis.

The auditory plate is the most highly differentiated member of the series of suprabranchial placodes (cf. *Cranial Nerves*). In fishes similar preauditory and postauditory placodes give rise to a part (sometimes to all?) of the ganglia of the lateral-line nerves (Landacre).

The primitive pear-shaped auditory vesicle in early human development is divided into a small vestibular pouch and a larger cochlear pouch. The vestibular pouch becomes separated into saccular and utricular portions and from the latter the semicircular canals are pinched off. The form of the membranous labyrinth in a human embryo of the eighth week is shown in Fig. 1804 and of the fifth month in Fig. 1805. The adult relations are diagrammatically indicated in Fig. 1806.

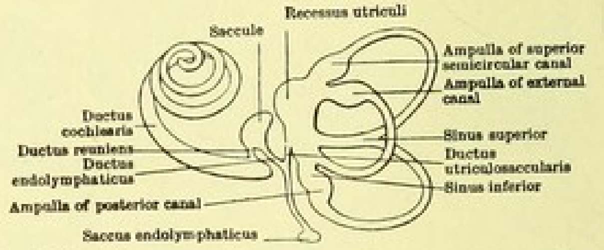

Fig. 1806.—Diagrammatic Representation of the Different Parts of the Membranous Labyrinth. (Cunningham.)

While the auditory vesicle is still in a quite undifferentiated condition, its lining epithelium develops a patch of sensory cells which enlarges very irregularly in such a way that during the subsequent plications of the walls of the vesicle each of the chambers thus evaginated (except the endolymphatic duct) receives a portion of this modified epithelium. These patches now become separated by non-sensory pavement epithelium and constitute the three cristæ in the ampullæ of the semi-circular canals, the maculæ of the utriculus and sacculus and the organ of Corti of the cochlea.

The auditory vesicle, which is primarily ectodermal, at first lies simply embedded in the surrounding mesoderm (Fig. 1801). A portion of this mesoderm is added to the vesicle, and thus the definitive membranous labyrinth is formed from both of these germ layers. The enveloping cartilages—which become, when ossified, the bony labyrinth—develop a short distance removed from the membranous labyrinth, and the intervening mesoderm is dissolved, leaving the perilymphatic spaces between the membranous and the bony labyrinth. The scala tympani and the scala vestibuli are the continuations of these spaces into the cochlea, while the scala media is the only part of the cochlea which is lined by a derivative from the original ectodermal auditory vesicle. Accordingly, the organ of Corti is developed in the floor (membrana basilaris) of the scala media.

The origin of the VIII ganglia has been variously described. Its cells probably are proliferated wholly or in part from the auditory vesicle at a very early stage. The ganglion is so on divided into two parts which retain their independence throughout life, the vestibular and the spiral or cochlear ganglion (Fig. 1807). In their further development these ganglia pursue very different courses, the cells of the vestibular ganglion being distributed along the course of their nerve, while those of the cochlear ganglion remain throughout life at the distal end of their nerve in the cochlea. The cochlear and vestibular nerves, moreover, remain distinct to a late developmental period. It has been customary, following Retzius and His, Jr., to describe the ramus vestibularis as supplying the utricle and the superior and lateral ampullæ, and the ramus cochlearis as supplying the saccule the posterior ampulla and the cochlea. More recent work (Cannieu, Alexander, Streeter) has emphasized the anatomical as well as the physiological independence of the cochlear nerve, the

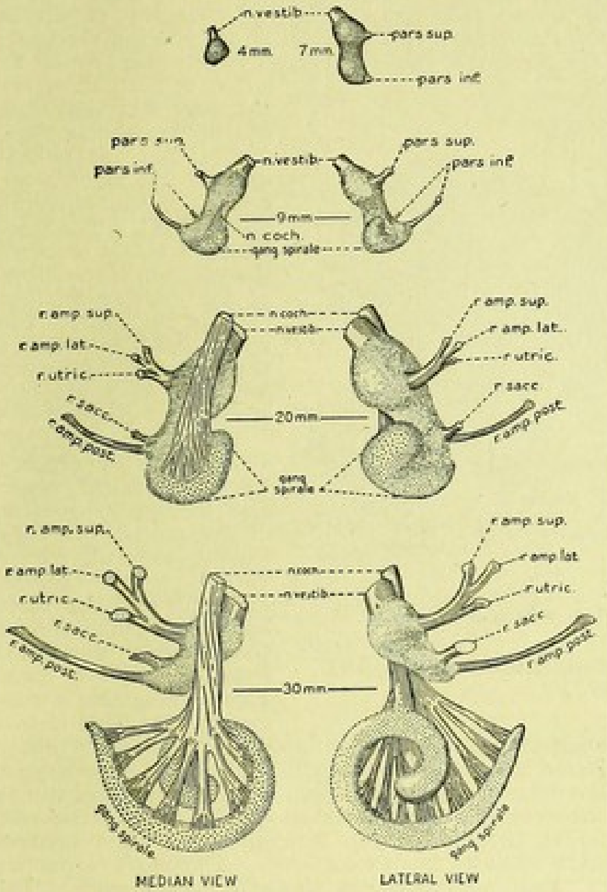

Fig. 1807.—Stages in the Differentiation of the Acoustic Nerve Complex. The vestibular ganglion is shown by fine dots, the spiral ganglion by large dots. (After Streeter.)

nerves of the saccule and posterior ampulla belonging to an inferior ramus of the vestibular nerve, as indicated below:

n. vestibularis	pars superior	r. ampul. sup. r. ampul. ext. r. recess. utric.
	pars inferior	r. saccularis r. ampul. post.
n. cochlearis. . .	ramuli spirali	

The Auditory or Acoustic Nerve.—The intimate association of nerves and end organs serving so diverse functions in the internal ear is explained, as above suggested, by their common phyletic origin from a much more generalized somatic sensory system. The physiological separateness of the sense of hearing, on the one hand, and the equilibratory and static reflexes, on the other hand, is very evident. Similarly, the peripheral receptive organs of the cochlea are in mammals quite distinct from those of the vestibule and labyrinth, and the central connections of the cochlear and vestibular nerves are fundamentally different. The vestibular nerve terminates in reflex centers of the oblongata and cerebellum with no important cortical connections, while the cochlear nerve has, in addition to important reflex connections in the oblongata, the much stronger ascending pathway in the lateral lemniscus to the inferior colliculus, medial geniculate body and cortex (cf. *Brain, Anatomy*). Nevertheless the fact that fishes undoubtedly hear, notwithstanding their lack of cochlea or any other receptors more complex than the sensory spots in the saccule, demonstrates the relatively late phylogenetic origin of the cochlear system from the vestibular, and has suggested to some physiologists that even in man these two systems are not wholly distinct. Support for the latter idea has been sought from the intimate relations existing between the cochlear nerve and the nerve of the saccule and posterior ampulla. But the demonstration of the complete anatomical independence of the cochlear nerve in development (Streeter) and in the adult leaves small basis for this contention.

The nervus vestibularis, in the wider sense in which this term is here employed, supplies the three ampullary sense organs and the sensory maculæ of the utriculus and sacculus. These sense organs are simple sensory epithelia, in fundamental structure resembling each other and also the sense organs of the lateral lines of fishes (Fig. 1799). The supporting cells of these organs constitute a simple columnar epithelium. Among these cells are the shorter hair cells, or specific sensory cells, extending only part of the distance through the thickness of the epithelium; their relations to the termini of the nerve are shown in Fig. 1808.

The hairs which arise from the free surfaces of the specific sensory cells do not float free in the endolymphatic fluid, but are embedded in a semi-gelatinous substance within which small particles of calcium carbonate, the otoliths, are also found (otolithic membrane, cupula).

The cupula of the ampullary sense organs (cristæ) is described by Shambaugh (1912) as a cap firmly fixed upon the crista, not as a movable structure as sometimes stated. The hair cells are stimulated by an interaction between the hairs and the cupula occasioned by the impact of the endolymphatic fluid against the sides of the cupula, different groups of hair cells being excited according to the direction of flow of the endolymph. The hair cells on one side of the cupula are more easily excited than are those on the opposite side, for the reaction which follows upon stimulation by one direction of endolymphatic flow is greater than that arising from the flow in the opposite direction. This peculiarity has an important bearing upon the interpretation of the phenomena of nystagmus of labyrinthine origin (for the details of which see the paper by Shambaugh cited).

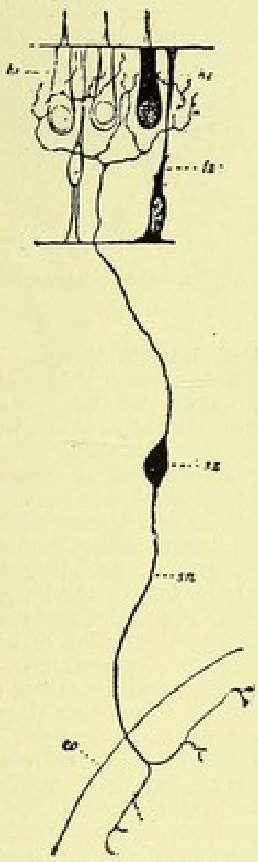

Fig. 1808.—Scheme of the Peripheral Termination of the Nervus Vestibuli. (After Retzius, from Barker's text-book.) *co*, Central nervous system; *fz*, supporting cell; *hz*, hair cells; *sn*, neurite of N. vestibuli; *sz*, cell body of vestibular neurone.

The fibers of the vestibular nerve arise from ganglion cells lying in the course of the nerve, the vestibular ganglion or ganglion of Scarpa. These cells, like all others connected with the nerves of the internal ear (and the lateral, line nerves of fishes as well), remain bipolar throughout life in all animals. The method of the termination of the peripheral processes about the specific cells of the sensory spots has already been illustrated. The central processes form the vestibular (medial or anterior) root of the eighth nerve. It enters the brain ventrally and cephalad of the cochlear root and passes dorsad between the fibers of the restiform body and the spinal V tract.

The central relations of the nervous pathways concerned in nystagmus of labyrinthine origin have been studied by Wilson and Pike (1912), who have shown that such nystagmus in the dog and cat consists of two phases—a slow deviation followed by a quick return—varying definitely in direction with the labyrinth which is stimulated or destroyed. These phases are distinct. The slow deviation is a function of the vestibulo-oculomotor apparatus in the medulla oblongata and mid-brain and is unmodified by removal of the cerebral hemispheres and thalamus. The quick phase of nystagmus, on the other hand, is a function of the cerebrum.

The cell bodies from which the fibers of the cochlear nerve arise lie chiefly (if not wholly) in the spiral ganglion, or ganglion of Corti, in the axis of the bony cochlea. The peripheral processes of these ganglion cells terminate in the organ of Corti. The central processes constitute the cochlear (lateral or dorsal) auditory root. In the embryological development they become medullated somewhat later than those of the vestibular root, a feature to be correlated with the fact that this nerve appears in the phylogeny at a later period than the vestibular nerve.

All of the fibers of the cochlear nerve appear to enter the ventral or the dorsal cochlear nucleus either to terminate in them or to pass through them. The ventral nucleus is often spoken of as accessory nucleus, and is thought by Sala and Onufrowics to contain some of the ganglion cells of the peripheral auditory neurones. The dorsal nucleus is the tuberculum acusticum of human anatomy.

The Organ of Corti.—The specific sensory area which develops in the embryonic cochlear pouch becomes much more complex than do the other sense organs of the internal ear. The generally accepted structure of this organ of Corti, as presented in the classical researches of Retzius, is shown in Fig. 1809. Upon a basement membrane of mesodermal origin is a very highly differentiated sensory epithelium, part of whose cells are supporting elements of diverse sorts and part (the hair cells) are specific receptors. The termini of the cochlear nerve arborize around the bodies of the hair cells in the same way that fibers of the vestibular nerve are related to the hair cells of the maculæ and cristæ of the labyrinth (Fig. 1808). The membrana tectoria occupies the position of the cupula of the crista ampullaris and is intimately connected with the hairs of the hair cells. Its shape has been very carefully studied by Hardesty.

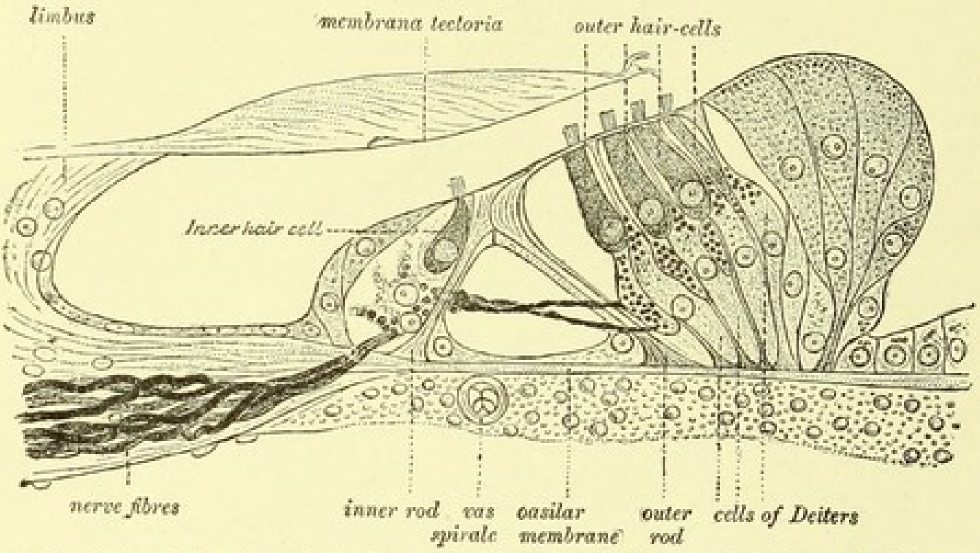

Fig. 1809.—Section through the Organ of Corti of the Middle Turn of the Human Cochlea. (After Retzius, from Quain's "Anatomy.")

Many details of the structure of the organ of Corti, or spiral organ, and the whole question of the mode of its functioning are still controverted. Our present knowledge of the histological organization of the basilar membrane shows that it is structurally incapable of serving the function of tone analysis in the way postulated by Helmholtz's theory. Based upon important additions to our knowledge of the minute structure of the organ of Corti and clinical observations upon diseased conditions, several different theories of the mechanism of tone analysis have recently been expressed. The most important of these researches are those of Shambaugh. This author has demonstrated that the hairs of the hair cells do not terminate freely in the endolymph, as commonly figured, but that they are firmly attached to the under surface of the tectorial membrane. This membrane has a semi-gelatinous texture and is capable of taking up sympathetically the vibrations of the endolymph within which it floats.

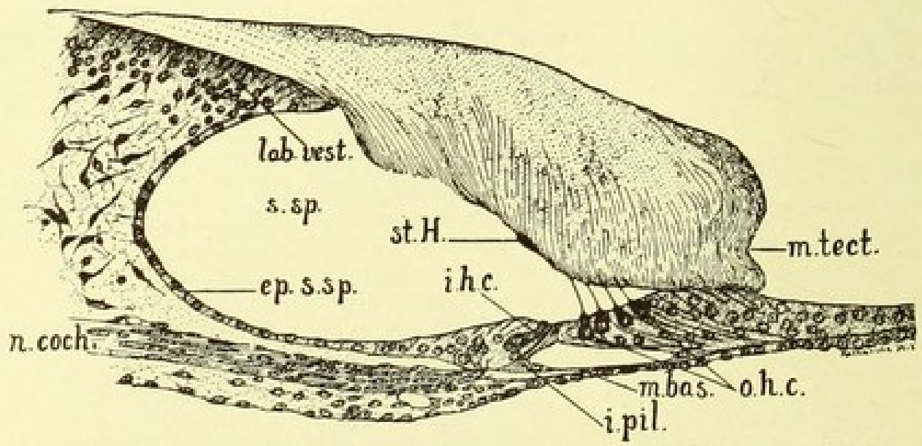

Fig. 1810.—Section through the Apical Turn of the Cochlea of the Pig at about Full Term, showing outer auditory hairs imbedded in the membrana tectoria. *ep.s.sp.*, Epithelium of spiral sulcus; *i.h.c.*, inner hair cells; *i.pil.*, inner pillar; *m.bas.*, basal membrane; *m.tect.*, membrana tectoria; *lab.vest.*, labium vestibulare; *n.coch.*, cochlear nerve; *o.h.c.*, outer hair cell; *s.sp.*, sulcus spiralis; *st.H.*, Hensen's stripe. (After C. W. Prentiss.)

The development of the tectorial membrane has recently been restudied by Prentiss, who finds that it first appears as a thin cuticular plate developed over the free ends of the columnar cells which form the inner epithelial thickening of the basal cochlear wall. Since it is present before the appearance of hair cells in the spiral organ, it cannot be regarded as developed from these hairs. The membrane grows in thickness by the secretion of a cuticulum formed between the ends of the epithelial cells, thus giving to the mature membrane a chambered or honeycomb structure. The attachment of the membrane to the spiral organ was confirmed, not only by sections but by dissections of fresh and fixed cochleæ (Fig. 1810). The membrana tectoria, then, is a delicate chambered cuticular structure, coextensive with the spiral organ. It is attached by its inner zone to the labium vestibulare, by its outer zone between the cells of the spiral organ, thus bridging over the spiral sulcus. Its sectional area at base and at apex is as 1:40 approximately. As the hairs of the auditory cells project directly into the chambers of the membrana, vibrations of the membrana would be directly transmitted to them.

Shambaugh concludes that the tectorial membrane takes the part of a physical resonator by responding in its various parts to tones of different pitch, depending on the size of the membrane, tones of higher pitch being taken up by the hair cells located near the beginning of the basal coil, those of lower pitch by the cells near the apex of the cochlea, where the tectorial membrane attains its maximum size. The stimulation of the hair cells is effected only through the medium of their projecting hairs, these being excited by vibrations of the tectorial membrane to which they are attached.

C. JUDSON HERRICK.

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Ear: Anatomy of the Auricle.—The auricle or pinna forms with the auditory canal or meatus the external ear. It is placed on the side of the head about midway between the external angle of the eye and the occipital protuberance; the upper border is about on a level with the eyebrow; the lower edge of the lobe is about on a level with the tip of the nose. Its vertical line is parallel to the ramus of the jaw and forms an angle of about 100 or 105 degrees with the horizontal plane of the head. Those ears in which this angle exceeds 112 degrees are called slanting ears. In height the auricle measures from 55 to 60 millimeters, and in width from 25 to 35 millimeters. The height of the auricle is generally found to be equal to the length of the nose. The true length of the auricle varies in man from 22 to 49 millimeters, the average being 35.9 millimeters; in woman it varies from 24 to 41 millimeters, the average being 33.7 millimeters. The true width* of the auricle varies in man from 33 to 58 millimeters, the average being 44.4 millimeters, while in woman it varies from 30 to 61 millimeters, the average being 40 millimeters. The anterior third of the auricle is firmly attached to the root of the zygoma and to the squamous and mastoid surfaces of the temporal bone by means of ligamentous, muscular, and cutaneous tissues. The posterior two-thirds is free and is placed so as to form with the lateral surface of the head the cephalo-auricular angle which, opening backward, measures on an average from 30 to 40 degrees, and may vary between 0 and 90 degrees; the angle decreasing in size as it passes upward and forward.

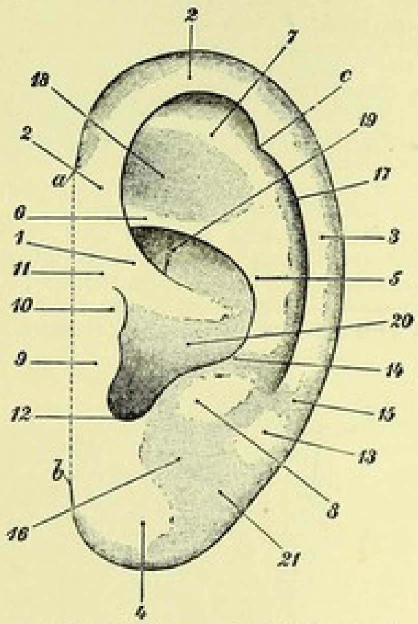

FIG. 1811.—Auricle of a Man. (After Schwalbe.) *ab*, Base of the auricle; *abc*, triangle of the auricle; *c*, Darwinian point or tubercle; 1, crus helicis; 2, 2, ascending (anterior upper) portion of the helix; 3, descending (posterior) portion of the helix; 4, lobule; 5, main portion of the antihelix; 6, crus inferius anthelicis; 7, crus superius anthelicis; 8, antitragus; 9, tragus; 10, tuberculum supratragicum; 11, sulcus auris anterior (incisura trago-helicina); 12, incisura intertragica; 13, tuberculum retrolobulare of His; 14, sulcus auris posterior (incisura anthelicis); 15, sulcus helicolobularis; 14+15, sulcus obliquus of His; 16, sulcus supralobularis; 17, fossa navicularis or scaphoidea; 18, fossa triangularis; 19, cymba conchæ; 20, cavitas conchæ; 21, sulcus retrolobularis.

The *framework* of the auricle consists of convoluted folds of yellow reticulated cartilage, from 1 to 2 millimeters in thickness, and is covered by its perichondrium. It supports the glandular, vascular, muscular, and cutaneous tissues of the auricle. The cartilage does not enter into the construction of the lobule and is deficient between the tragus and the spina helicis.

The auricle may be considered to be an expansion of the external auditory canal, which it surrounds, and especially so above and behind. It is oval in form, with the longest axis vertical and its broadest

* The terms "true length" and "true width" are explained further on.

extremity above. It has two surfaces—an external and an internal—and a circumferential border. The external surface looks obliquely outward, forward, and slightly downward. It is so folded upon itself that it presents a number of elevations and depressions, which give it a most irregular and characteristic appearance. The outer surface is as a whole concave, while the inner is convex, and the depressions and elevations of one surface correspond in a general way to the elevations and depressions of the other.

The border of the auricle—that is, the upper third of the anterior portion, all of the superior portion, and the upper two-thirds of the posterior portion—is rolled in upon itself and forms the most prominent elevation or crest on the external surface of the organ. It is called the *helix* (Fig. 1811, 1, 2, 3). It begins in a thin root, the *crus helicis* (Fig. 1811, 1), in the cavity of the concha, and passes obliquely upward and forward, and then in a semicircle upward, backward, and downward, to terminate in a free extremity, the *processus helicis caudatus* (Fig. 1812, 2), at the *sulcus helicolobularis* (Fig. 1811, 15). The *crista helicis* divides the concha into two parts—the upper and smaller, the *cymba conchæ* (Fig. 1811, 19), and the lower and larger, the *cavitas conchæ* (Fig. 1811, 20), which is continuous with the external auditory canal. By the incurving of the helix a groove is formed beneath it—the *fossa of the helix*. This groove is well marked in its ascending portion, and gradually becomes shallow as it passes backward and downward. A small spine, the *spina helicis* (Fig. 1812, 1), is given off from the ascending portion of the helix. It serves to give a firm attachment to the attrahens auriculum

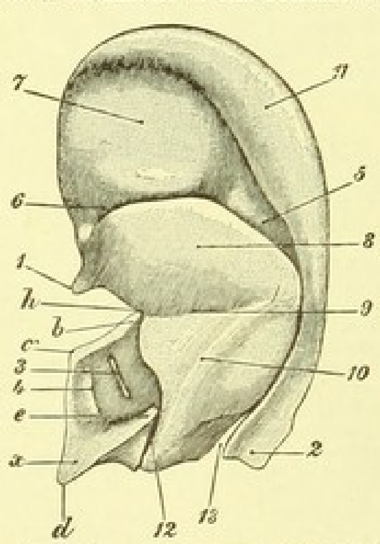

FIG. 1812.—Cartilaginous Framework of the Human Auricle (Inner Surface). (After Schwalbe.) *bc*, Upper border of the cartilaginous furrow for the blood-vessels; *cd*, anterior medial border; *de*, posterior medial border; *x*, processus triangularis; *h*, angle of the anterior margin of the concha; 1, spina helicis; 2, processus helicis caudatus; 3, lateral bipartite Santorinian incisura; 4, medial Santorinian incisura; 5, fossa anthelicis; 6, sulcus anthelicis transversus; 7, eminentia fossæ triangularis; 8, eminentia conchæ; 9, sulcus cruris helicis; 10, ponticulus; 11, eminentia fossæ navicularis; 12, incisura terminalis; 13, fissura antitrago-helicina.

muscle. This spine, as well as the *processus caudatus helicis*, is to be seen only when the cartilage is denuded of its coverings. At the junction of the horizontal portion of the helix with the descending portion we have a tubercle known as the *Darwinian point* or *tubercle* (Fig. 1811, *c*), which possesses much morphological importance, as will be shown below. It corresponds to the ear tip of animals.

A second eminence or crest, the *antihelix* (Fig. 1811, 5), begins, in the upper anterior portion of the fossa helicis, in two converging crests, the *crura furcata*, or the *crus inferius anthelicis* (Fig. 1811, 6) and the *crus*

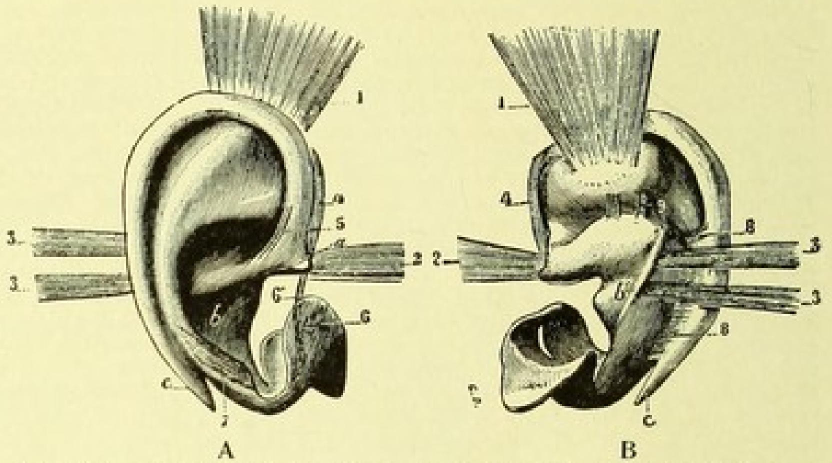

FIG. 1813.—Muscles of the Auricle: A, as Seen on the External Surface; B, as Seen on the Internal Surface. 1, The attolens auriculum or musculus auricularis superior; 2, the attrahens auriculum or musculus auricularis anterior; 3, 3, the retrahens auriculum, or musculus auricularis posterior; 4, the helicis major; 5, the helicis minor; 6, the tragicus, with 6′, its accessory fasciculus; 7, the antitragicus; 8, the transversus auricular; 9, the obliquus auriculæ; *a*, spina helicis; *b*, concha, with *b′* its posterior thickening or ponticule; *c*, spina caudatus helicis. (After Testut.)

superius anthelicis (Fig. 1811, 7). It passes downward and backward in front of the descending portion of the helix. The depression which is formed between the two crests is known as the *fossa navicularis* or *fossa scaphoidea* (Fig. 1811, 17). The depression between the crura furcata is called the *fossa intercruralis* or *triangularis* (Fig. 1811, 18). The antihelix is separated, by the sulcus auris posterior (incisura anthelicis, Fig. 1811, 14), from a rounded eminence—the *antitragus* (Fig. 1811, 8), and in front of this eminence, and separated from it by that portion of the cavity of the concha which is called the *incisura intertragica* (Fig. 1811, 12), is a lid-like covering to the auditory canal—the *tragus* (Fig. 1811, 9). It is separated from the root of the helix by the *sulcus auris anterior* or *incisura tragohelicina* (Fig. 1811, 11).

The most dependent part of the auricle, which is devoid of cartilage and is made up principally of connective and adipose tissues, is called the *lobe* (*lobulus auricularis*) (Fig. 1811, 4).

On the inner surface the elevations, as they correspond to the depressions on the outer surface, have received similar names, and are known consequently as the *eminentia fosssæ caphoideæ vel triangularis* (Fig. 1812, 7); the *eminentia fossæ navicularis* (Fig. 1812, 11); and the *eminentia conchæ* (Fig. 1812, 8). From the posterior inferior border of the latter eminence arises a crest, the *ponticulus* (Fig. 1812, 10), which passes obliquely downward and forward to the *incisura terminalis* (Fig. 1812, 12); and to this crest is attached the retrahens auriculum muscle.

In a like manner the following names have been given to the depressions on the inner aspect of the auricle: the *fossa anthelicis*, (Fig. 1812, 5); the *sulcus anthelicis transversus* (Fig. 1812, 6); the *sulcus cruris helicis* (Fig. 1812, 9); and the *fissura antitrago-helicina* (Fig. 1812, 13).

To aid in holding the cartilaginous folds in place and in uniting the auricle to the head, two sets of *ligaments* are provided—the intrinsic and the extrinsic.

The *intrinsic ligaments* are four in number: two are on the inner surface of the auricle and unite the emthe cases. The urine usually contains albumin and casts and often there is definite blood due to infarction of the kidney.

The typhoidal type is characterized by a more or less continuously high fever, delirium, dry tongue, distended abdomen, roseola, splenic enlargement, and possibly diarrhea, but no definite localizing symptoms. The differentiation from typhoid fever is often possible only by means of the blood culture.

In the cerebral type the symptoms due to embolism of the brain and usually of the left middle cerebral artery dominate the picture. There is a history of onset with chills and fever and then a sudden development of hemiplegia and perhaps unconsciousness. Purulent meningitis may develop.

There is a chronic form of malignant endocarditis which may last several months. It is characterized by asthenia, a moderate degree of remittent or intermittent fever, chills, petechiæ, and changing heart signs. There is progressive anemia with gradual loss of weight. The leucocytes are increased but usually not beyond 15,000. A positive blood culture may not be obtained until after several attempts. In this type of endocarditis the *Steptococcus viridans* has been found more frequently than any other organism.

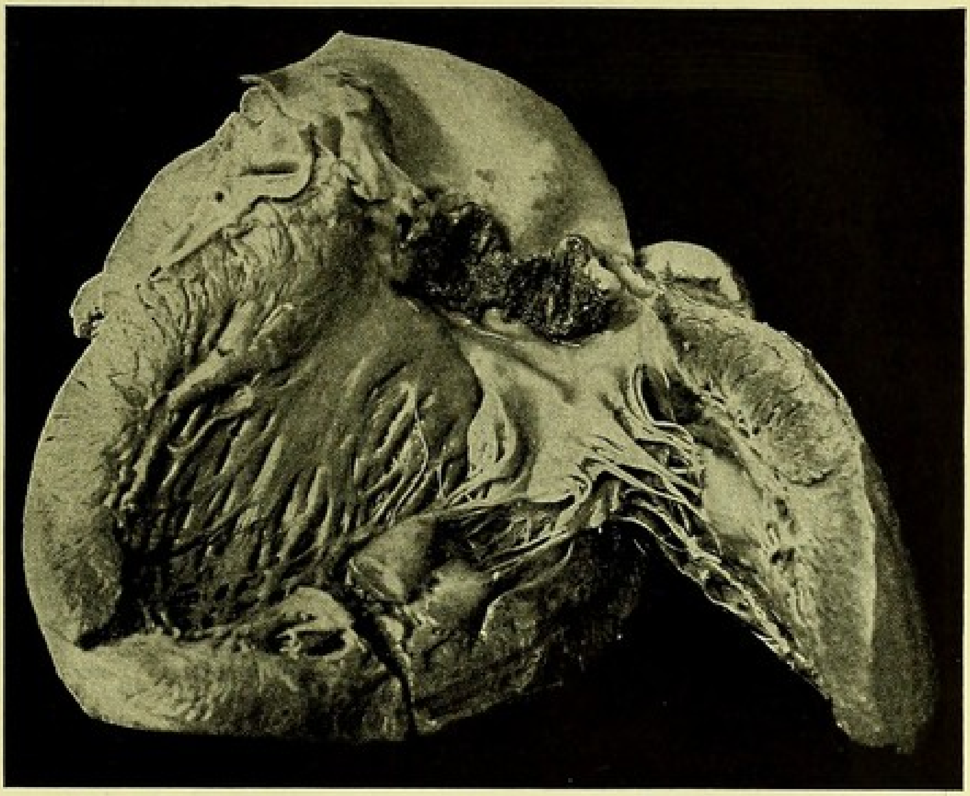

Fig. 2033.—Malignant Endocarditis; Ulceration of the Aortic Valves; Hole through One of the Valves; Old Atheroma. (Original.)

The symptoms of simple acute endocarditis are primarily those of the accompanying rheumatic disease. The onset of the cardiac complication may be marked by pain and collapse. The rise in fever may be very slight. The sudden appearance of a heart murmur or the symptoms of embolism may be the first evidence of implication of the heart. There is sometimes precordial bulging in children.

Differential Diagnosis.—In the simple acute type the associated disease should lead to expectation of cardiac involvement and the characteristic signs should be recognized as they appear. In the malignant type the blood culture is the most important single diagnostic measure. The differentiation from pneumonia and from typhoid fever may be very difficult and depend entirely upon the findings in the blood. If in the course of an acute disease a murmur develops under our observation, which cannot be accounted for by anemia or weakness of

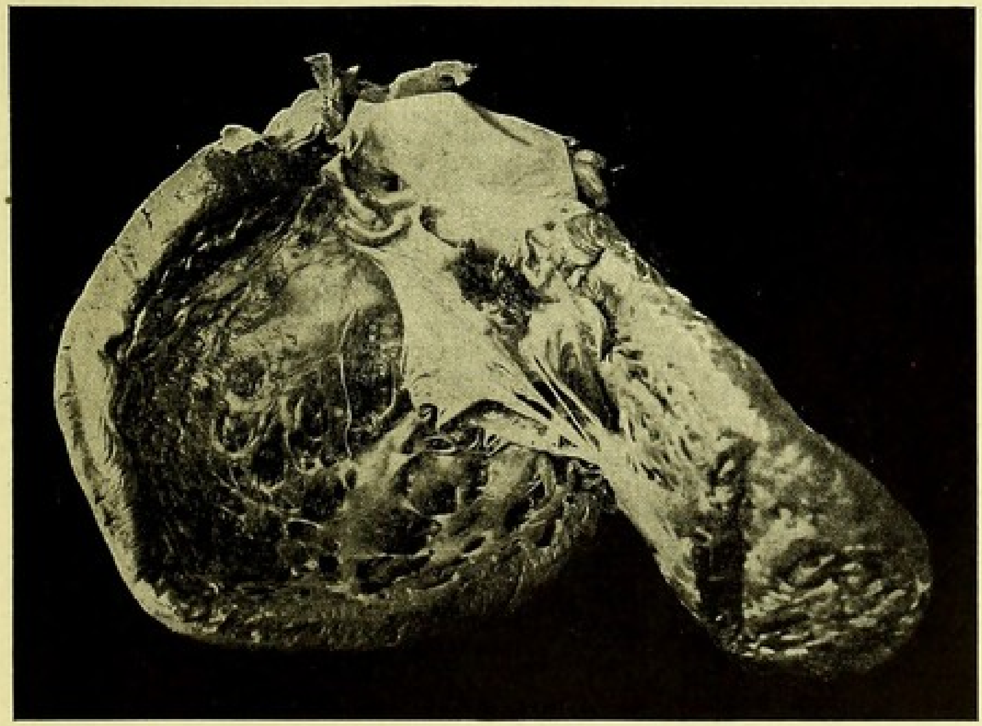

Fig. 2034.—Malignant Endocarditis; Destruction of Aortic Leaflet; Old Thickening of Aortic Valves; Dilatation of the Left Ventricle. (Original.)

the cardiac wall, and especially if it is accompanied by an increase in fever, we are justified in diagnosing endocarditis.

Prognosis.—In the vast majority of cases simple acute endocarditis entails no immediate danger. The lesions heal to a greater or lesser extent and the subsequent cicatricial contractures result in valvular defects which may prove fatal long afterward. In malignant endocarditis, death may take place in three days, or, as when due to *Str. viridans*, only after ten to fourteen months. The prognosis is always unfavorable but in some instances recovery does occur and the patient acquires a valvular disease of the heart.

Treatment.—The treatment of simple acute endocarditis is first of all the treatment of the associated disease. The salicylates should be given in doses sufficient to control the arthritic pain but they are said to have a certain amount of depressing effect upon the heart. Rest is all important. Digitalis is the most important single drug and strychnine may often be used to advantage. The diet should be especially nutritious and iron may be indicated in order to combat the anemia. Arsenic is also used for this purpose. One of the most important prophylactic measures consists in the removal of tonsils which are subject to recurrent inflammation. The removal should of course be done in the interval between attacks. It is sometimes very striking to see the improvement in a patient following the removal of susceptible tonsils. The care of the teeth in order to prevent caries and pyorrhea is also very important. The treatment of malignant endocarditis is that of any form of general septicemia; absolute rest, light diet, and an ice-bag over the precordium to quiet the action of the heart. Drugs are of little value and sometimes the heart is so damaged that attempts at stimulation are actually harmful. Intravenous infusions of collargol and other antiseptic solutions, and the administration of Marmorek's antistreptococcus serum have proven of no value. Inoculation with bacterial vaccines, more especially autogenous ones, has apparently resulted favorably in a small percentage of cases but the disappointments have been many. The administration of filtrates of cultures of one or more organisms, the so-called phylacogens, has little to recommend it theoretically and there has as yet been no convincing demonstration of beneficial results following their use.

The effects and treatment of chronic endocarditis are those of chronic valvular lesions and will be considered under that heading.

James Rae Arneill.
Revised by Ralph G. Stillman.

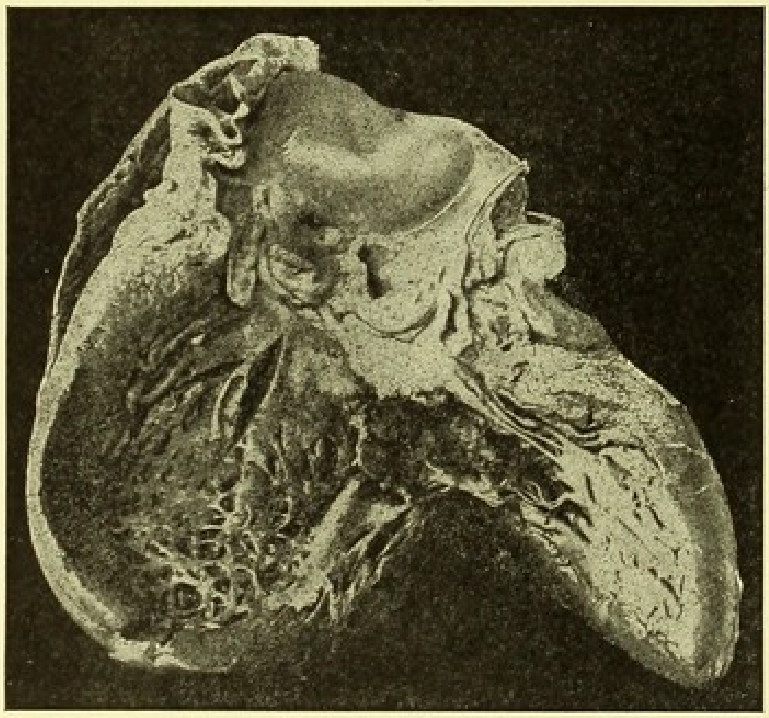

Fig. 2035.—Malignant Endocarditis on Top of Old Sclerosing Process. Marked involvement of the mitral valves. (Original.)

End-organs, Nervous.—The nervous end-organs fall into two groups which have very appropriately been termed by Sherrington the receptors and the effectors, the former being the nervous endings in the sense organs and the latter the endings within the organs of response—muscles, glands, etc.

The body is surrounded by a complex of manifestations of energy which impinge upon its surface, some of which are noxious, some beneficial, and others indifferent. Those sense organs which respond to the action of these external agents are termed exteroceptors, in distinction from the interoceptors which are stimulated by internal (chiefly visceral) processes.

We are surrounded by many forms of external energy to which our receptive end-organs are entirely insensitive, such as ultraviolet rays from the sun, Hertzian electric waves, etc. Receptors have been differentiated only for those forces of our natural environment which can either benefit or injure the body; to the rest we are entirely indifferent. The purpose of the receptors, then, is to analyze the environing energy complex in such a way as to facilitate the execution of the adaptive or useful modes of response to all significant environmental factors. This is accomplished, as Sherrington points out, by lowering the stimulus threshold of each receptor for some one kind of energy manifestation and raising it for all others; or, otherwise stated, each receptor is attuned to respond only within a definite range of energy manifestations and to remain silent to all others.

An acceptable classification of the receptors or sense organs of the body must take account of their anatomical relations, of the nature of the physical or chemical forces which serve as the adequate stimuli, of the subjective qualities which we experience upon their excitation, and of the character of the physiological responses which commonly follow their stimulation. The last point has been too much neglected.

In fact, the most fundamental division of the nervous system which we have, cutting down through the entire bodily organization, is based upon this physiological criterion. Sherrington, whose analysis with some modifications is here adopted, recognizes three types of sense organs, or receptors: (1) the interoceptors, or visceral receptive organs, which respond only to stimulation arising within the body, chiefly in connection with the processes of nutrition, excretion, etc.; (2) the exteroceptors, or somatic sense organs, which respond to stimulation arising from objects outside the body; (3) the proprioceptors, a system of sense organs found in the muscles, tendons, joints, etc., to regulate the movements called forth by stimulation of the exteroceptors. This third group is really subsidiary to the somatic system, or exteroceptors, and will be considered more in detail beyond. The important point to bear in mind here is that stimulation of the visceral sense organs typically calls forth visceral responses, *i.e.* adjustments wholly within the body, while stimulation of the somatic (exteroceptive) sense organs typically calls forth somatic responses, *i.e.* a readjustment of the body as a whole with reference to its environment. This is a very fundamental distinction.

From this standpoint the nervous system has a two-fold part to play in the vital economy. In the first place, the nervous system is the chief organ by which the correlation or "correspondence" (Herbert Spencer) of bodily and environmental forces is maintained. And in the second place, the nervous system has the important function of the internal regulation of the parts of the body *inter se*, to ensure their proper nutrition and continued well-being. These two functions are quite diverse and the organization of these two parts of the nervous system shows corresponding structural differences.

We divide the nervous organs, then, into two great groups, the exteroceptive or somatic group, and the interoceptive, visceral or splanchnic group. The latter group comprises the nerves and nerve centers concerned with digestion, respiration, circulation, excretion and reproduction. These are chiefly found within the sympathetic nervous system and those parts of the central nervous system directly connected therewith, though the more highly specialized members of this group are independent of the sympathetic system. The exteroceptive or somatic group comprises the greater part of the brain and spinal cord and the cerebral and spinal nerves, or briefly, the cerebrospinal nervous system, as distinguished from the sympathetic system. This is the mechanism by which the body is able to adjust its own activities directly in relation to those of the outside world—to procure food, avoid enemies, and engage in the pursuit of happiness.

Fig. 2036. — Tactile Nerve Endings in the Deep Layer of the Cutis from the Nose of a Cat. (After Botezat.)

The organs belonging to each of these two groups do much of their work independently of the other group; *i.e.* visceral stimuli call forth visceral responses and external or somatic stimuli call forth somatic responses. Nevertheless the two groups of organs are by no means entirely independent, for external excitations may produce strong visceral reactions, and conversely. Thus, the sight of luscious fruit (exteroceptive stimulus) naturally calls forth movements of the body (somatic responses) to go to the desired object and seize it. But if one is hungry, the mouth may water in anticipation, a purely visceral response. On the other hand, the strictly visceral (interoceptive) sensation of hunger is apt to set in motion the exteroceptive reactions necessary to find a dinner.

With these principles in mind, let us now undertake an analysis of the human sense organs and of their effectors. The following list is by no means complete and is in some parts merely provisional.

I. Somatic Senses.—These are senses concerned with the adjustment of the body to external or environmental relations.

A. Exteroceptors.—Stimulated by objects outside the body and typically evoking reactions of the whole body, such as locomotion, etc. This group includes a very complicated system of general cutaneous sense organs, some organs of deep sensibility, and some of the higher sense organs. The cutaneous exteroceptors comprise a complex system whose analysis has proven very difficult. The conclusions presented in the paragraphs which follow are based chiefly upon the observations of von Frey and Henry Head. The correlation of the data of physiological experiment with the anatomical structure of the cutaneous end-organs is still somewhat problematical and the structures assigned here to the various cutaneous senses should be regarded as provisional rather than as demonstrated.

1. End-organs of the pressure or tactile sense. These fall into three groups distinguished by Henry Head as epicritic, protopathic, and deep sensibility. Epicritic tactile sensibility is a highly refined type, regarded as of later evolutionary origin than the other two. It includes light touch on the hairless parts of the body particularly. Cutaneous localization ("spot-naming") and the discrimination between two points simultaneously stimulated ("the compass test") are functions of this system. The threshold for pressure stimuli is lower than in the case of direct stimulation of the protopathic and deep end-organs. The receptive organs are special tactile bodies, such as Meissner's corpuscles. They are generally found in the cutis and subcuticular tissues, either as free skein-like terminal arborizations of medullated cutaneous nerves or as similar more elaborate endings enclosed in connective-tissue capsules. Fig. 2036 illustrates a simple form of these endings in the cutis of the nose of a cat, and Fig. 2037 a more complex endings, partly within the perichondrium and partly within the cutis from the same region. The Meissner's corpuscles (Fig. 2038) are the most characteristic tactile endings of this system in the human body, consisting of a similar skein of nerve termini enclosed within a connective-tissue capsule.

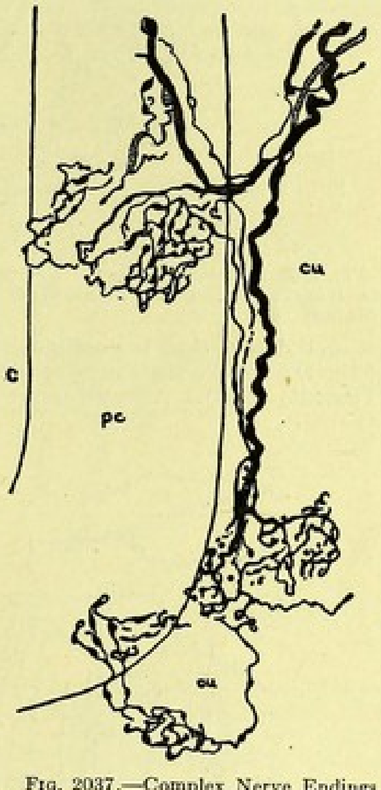

Fig. 2037.—Complex Nerve Endings, from the Nose of a Cat. (After Botezat.) The apparatus lies partly in the cutis *cu.* and partly in the perichondrium *pc.* above the nasal cartilage *c.*

Protopathic tactile sensibility is a more primitive type of general diffuse touch, especially well developed on the hairy parts of the skin. These sensations have no clearly defined local sign, and yet their end-organs are themselves definitely grouped about the hair bulbs. The hairs are the most important sources of excitation of these organs and the sensitiveness of hair-clad parts is greatly reduced after the hair is shaved. "The liminal stimulus for the touch spots about a short hair is three to twelve times greater than for the hair itself, *i.e.* the hair is three to twelve times more sensitive than the spots" (Sherrington).

The innervation of the hair bulbs is very complex and varies greatly for different animals and for the different kinds of hairs on the same body, so that no

FIG. 2038.—Meissner's Tactile Corpuscle from the Cutis of the Human Skin. (After Dogiel from Böhm-Davidoff-Huber's Histology.)

general description is possible. The large vibrissæ of the rat receive their nerve supply from two sources (Vincent, 1913). A large nerve bundle pierces the

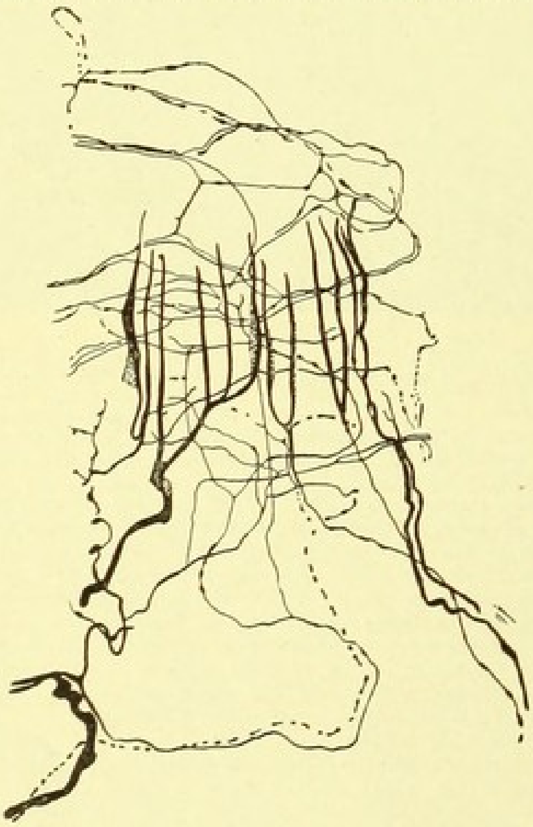

FIG. 2039.—Straight and Circular Nerve Endings on the Root of a Soft Hair from the Lower Lip of a Man 49 Years Old. (After Szymonowicz.) The coarser forked endings belong to the straight system and the finer fibers to the circular system.

dermal sheath in the lower part of the bulb, spreads out over the inner follicle in a heavy plexus, and terminates chiefly in a mantle of touch cells, resembling Merkel's corpuscles, in the outer root sheath all over the follicle. A second nerve supply comes from the dermal plexus of the skin, from which branches run down and form a nerve ring about the neck of the follicle. Experimental studies show that these hairs are very important not only as general tactile organs, but specifically as aids in locomotion and equilibration. The ordinary hairs of man and other mammals have three forms of specific nerve endings in addition to various forms of terminal arborizations in the surrounding tissues: (1) straight and often forked endings running parallel with the base of the hair;

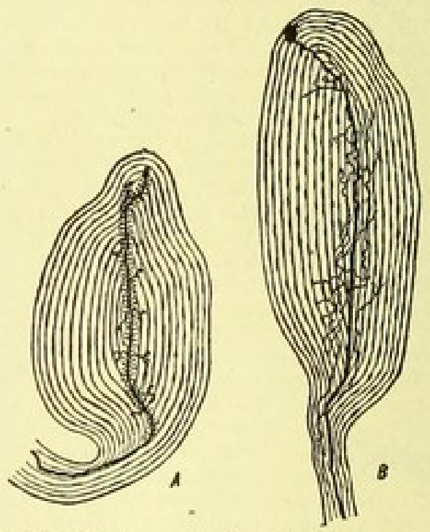

FIG. 2040.—Pacinian Corpuscles from the Mesorectum of a Cat. (After Sala from Böhm-Davidoff-Huber's Histology.)

(2) circular fibers forming a plexiform ring around the root of the hair external to the straight endings; and (3) leaf-like nerve endings associated with special cells resembling Merkel's corpuscles. Fig. 2039 illustrates the first and second types of these endings.

The deep pressure sense is served by special nerve endings throughout the tissues of the body and is preserved after loss of all cutaneous nerves. By these end-organs relatively coarse pressure may be discriminated and localized and movements of muscles and joints can be recognized. Most of the functions of the deep sensory nerves belong to the interoceptive and proprioceptive series (see beyond), but some

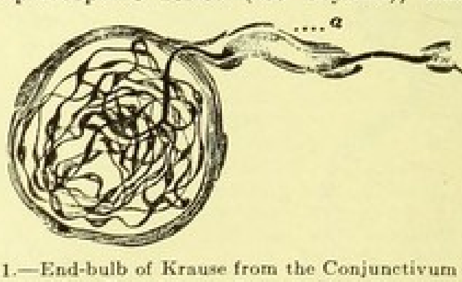

FIG. 2041.—End-bulb of Krause from the Conjunctivum of Man. (After Dogiel from Bailey's Histology.)

exteroceptive functions are here present also. The latter are probably related chiefly to the Pacinian corpuscles and similar encapsulated end-organs. The Pacinian corpuscle has a central nerve fiber enclosed in a firm lamellated connective-tissue sheath (Fig. 2040).

2. End-organs for sensibility to cold.

3. End-organs for sensibility to heat. Physiological experiment shows that heat and cold are sensed by different parts of the skin—the warm spots and the cold spots respectively—and that each of these may be present in an epicritic and a protopathic form. What end-organs are involved here is by no means certain. The margin of the cornea was found by

von Frey to be sensitive to pain and cold only. The free nerve endings found here he assumes to be pain receptors and the end-bulbs of Krause (Fig. 2041) to be cold receptors. By an analogous argument he assumes that the "genital corpuscles" of Dogiel

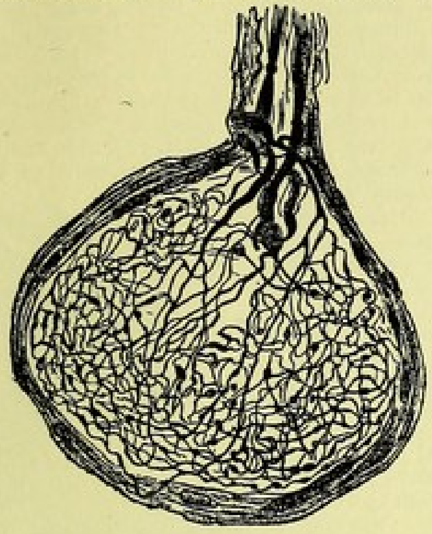

FIG. 2042.—Genital Corpuscle from the Glans Penis of Man. (After Dogiel from Böhm-Davidoff-Huber's Histology.)

(Fig. 2042) and some similar endings widely distributed in the skin are warmth receptors. By some other physiologists these two types of end-organs are regarded as belonging to the tactile system.

4. End-organs for pain. Some physiologists believe that there are separate nerve endings for pain;

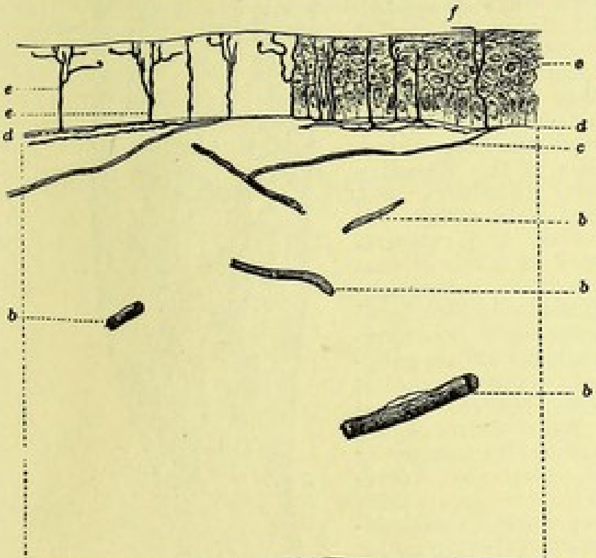

FIG. 2043.—Vertical Section Through the Cornea. (After Cohnheim from Barker's Nervous System.) The corneal corpuscles and the cells of Descemet's membrane are left out of the drawing; the anterior epithelium has been drawn only in part. *a*, Descemet's membrane; *b*, nerves from the plexuses; *c*, branches going to the epithelium, here ascending by accident very obliquely; *d*, fibers of the subepithelial layer; *e*, vertical cut threads with horizontal outrunners; end nodules can be seen; *f*, an undoubted precorneal horizontal fiber.

others regard pain as a quality which may be present in any sense, and not as itself a true sensation. The free intraepithelial nerve endings are regarded by von Frey as the pain receptors, because these endings alone are present in some parts of the body where susceptibility to pain is the only sense quality present, such as the dentine and pulp of the teeth and the cornea (Fig. 2043). Similar endings are found throughout the epidermis (Fig. 2044) and in many deep structures.

5. End-organs of general chemical sensibility. In man this is found only on moist epithelial surfaces, such as the mouth cavity; but in fishes it may be present over the entire bodily surface (Sheldon). The sense organ is probably the free nerve terminals among the cells of the epithelium, never special sense organs like taste buds, for these when present in the skin belong to a quite different system.

6. Organs of hearing. The stimulus is material vibrations whose frequency ranges between 16 and 40,000 per second. The receptor is the organ of Corti in the cochlea, perhaps also the sensory spots in the saccule and utricle. There are two forms, (1) noise, stimulated by sound concussions or irregular mixtures of aërial vibrations; (2) tone, stimulated by sound waves or periodical aërial vibrations.

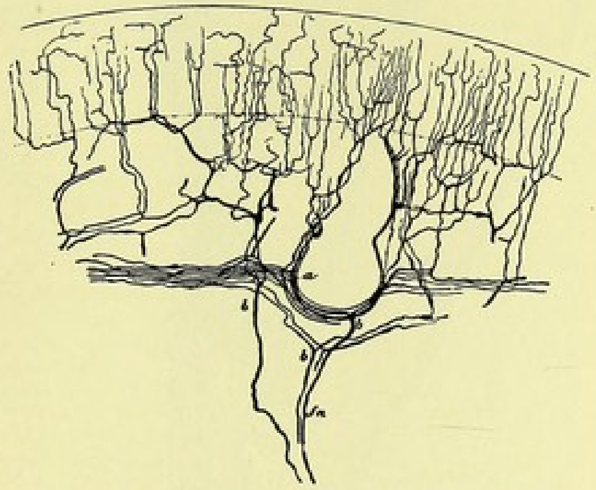

FIG. 2044.—Transverse Section Through the Skin of the Ear of a White Mouse Three Days Old. (After Van Gehuchten.) *a*, horizontal fibers; *b*, bifurcation; *fn*, nerve fibers.

7. End-organs of vision. The stimulus is ethereal vibrations ranging between 392 billions and 757 billions per second. Here also there are two forms: (1) brightness, stimulated by mixed ethereal vibrations; (2) color, stimulated by simple ethereal vibrations.

8. End-organs of smell. This sense has both exteroceptive and interoceptive qualities, the latter being apparently the more primitive. See the fuller discussion beyond under the Interoceptors (Visceral Senses) and in the article *Olfactory Nerve*.

B. Proprioceptors.—These sense organs are contained within the skeletal muscles, joints, etc., and are stimulated by the normal functioning of these organs, thus reporting back to the central nervous system the exact state of contraction of the muscle, flexion of the joint, tension on the tendon, etc. These reactions are generally unconsciously performed.

9. End-organs of muscular sensibility. The organ is a series of nerve endings among special groups of muscle fibers known as muscle spindles. These endings are usually spirally wound around their muscle fibers and are stimulated by the contraction of the muscle (Fig. 2045).

10. End-organs of tendon sensibility. Similar nerve endings are spread out over the surfaces of tendons and are stimulated by stretching the tendon during muscular contraction (Fig. 2046).

11. End-organs of joint sensibility. Nerve endings found in the joints and the surrounding tissues are stimulated by bending the joint and report back to the central nervous system the degree of flexion

of the joint. The chief end-organs are probably Pacinian corpuscles.

12. Static and equilibratory sensations arising from stimulation of the semicircular canals of the internal ear (Fig. 2047). This is the most highly specialized member of the proprioceptive group and acts in conjunction with all of the other somatic senses to maintain equilibrium, posture, and the tone of the muscular system. The eyes and most of the other exteroceptive sense organs, so far as they act in the way just suggested, serve as proprioceptors.

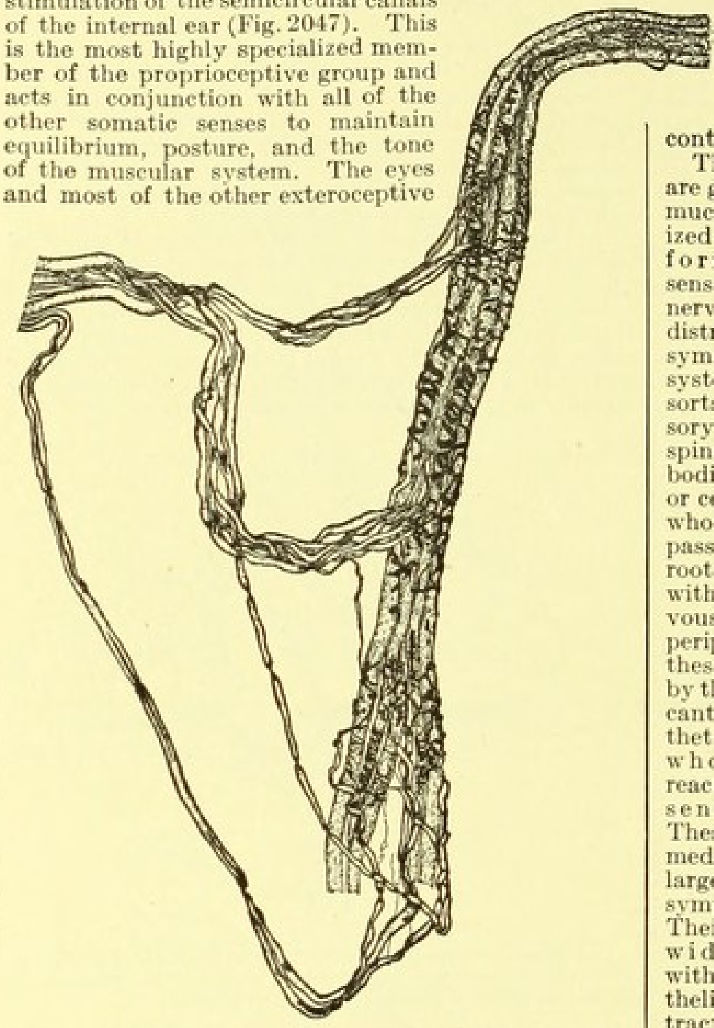

Fig. 2045.—Neuro-muscular Nerve End-organ from the Intrinsic Plantar Muscles of a Dog, from Teased Preparation Stained with Methylene Blue. The figure shows the intrafusal muscle fibers of the muscle spindle, the nerve fibers and their terminations; the capsule and the sheath of Henle are not shown. (After Huber and DeWitt.)

II. Visceral Senses.—The visceral or interoceptive senses fall into two well-defined groups. First, the general visceral senses are without highly specialized end-organs and are innervated through the sympathetic nervous system. Their reactions are chiefly unconsciously performed. Second, the special visceral senses are provided with highly developed end-organs which are innervated directly from the brain without any connection with the sympathetic system. The special visceral sense organs may in some cases serve as exteroceptors as well as interoceptors. Their reactions may be conscious and voluntary.

A. General Visceral Senses.—13. Hunger. Stimulus, strong contractions of the gastric muscle (Cannon, Carlson). This is a variety of muscle sense.

14. Thirst. Stimulus, dryness of the pharyngeal mucous membrane (?).

15. Nausea. Stimulus, antiperistaltic reflex.

16. Respiratory sensations, suffocation, etc.

17. Circulatory sensations, flushing, heart panics, etc.

18. Sexual sensations.

19. Sensations arising from distention of cavities, stomach, rectum, bladder, etc. (muscle sense).

20. Visceral pain.

21. Obscure abdominal sensations associated with strong emotions of fright, anger, affection, etc., characterized (probably correctly) by the ancients by such expressions as "yearning of the bowels," etc. The stimulus is probably a tonic contraction of the unstriped visceral musculature.

The nerve endings of the general visceral receptors are generally free arborizations in or under the various mucous surfaces, without the development of specialized accessory cells to form differentiated sense organs. These nerves in general are distributed through the sympathetic nervous system and are of two sorts: (1) Visceral sensory fibers of cerebrospinal origin, whose cell bodies lie in the spinal or cerebral ganglia and whose central processes pass through the dorsal roots to terminate within the central nervous system. The peripheral processes of these neurones pass out by the rami communicantes into the sympathetic system through whose nerves they reach their respective sensory surfaces. These fibers are usually medullated and are the largest fibers of the sympathetic nerves. Their endings spread widely below and within the mucous epithelia of the digestive tract, bladder, etc. (Figs. 2048, 2049). (2) Besides the visceral fibers of cerebrospinal type, there are throughout the body peripheral sympathetic neurones forming a diffuse ganglionic plexus pervading all the tissues. Some of these neurones are regarded by Langley as non-polarized and serving local reflexes; others are apparently differentiated as specific motor (postganglionic) or sensory elements. Many ciliated epithelial and glandular visceral surfaces are innervated by endings which either arborize freely around the epithelial cells or end upon them with trefoil expansions (Fig. 2050). These are probably endings of this type. Unmedullated fibers of this system enter the spinal ganglia through the rami communicantes and there effect functional connections with the spinal ganglion neurones (Dogiel).

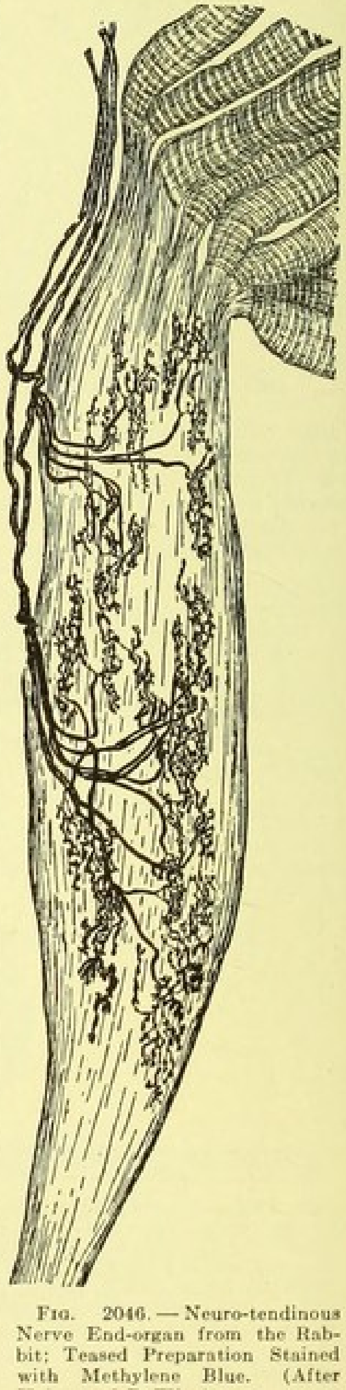

Fig. 2046. — Neuro-tendinous Nerve End-organ from the Rabbit; Teased Preparation Stained with Methylene Blue. (After Huber and DeWitt.)

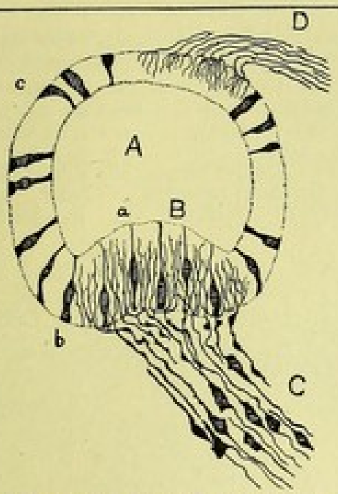

Fig. 2047.—Transverse Section of the Semicircular Canal of the Ear of a Mouse showing Terminals of the Vestibular Branch of the VIII. Nerve. (After Ramón y Cajal.) *A*, Lumen of the canal; *B*, crista acustica; *C*, bundle of nerve fibers containing bipolar ganglion cells; *D*, a similar bundle supplying the top of the canal; *a*, *b*, and *c*, varieties of bipolar epithelial cells.

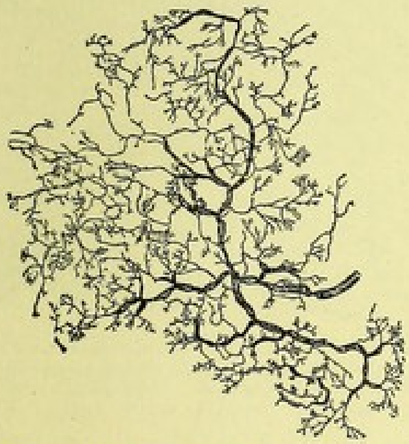

Fig. 2048.—Tangential Section of the Mucosa of the Esophagus of a Cat. (After DeWitt.)

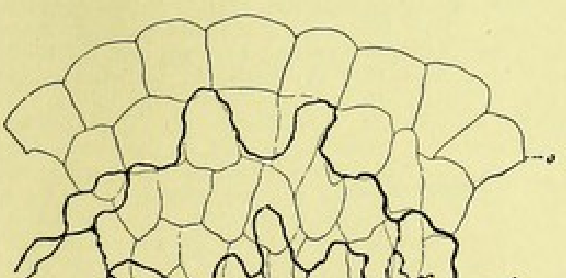

Fig. 2049.—Free Endings of Afferent Nerve Fibers in the Epithelium of a Rabbit's Bladder. (After Retzius.) *bg*, Subepithelial connective tissue; *n*, nerve fiber entering the epithelium where it breaks up into numerous terminals among the epithelial cells; *o*, surface epithelium of the bladder.

B. Special Visceral Senses.—22. Taste. Chemical stimulation of taste buds on the tongue and pharynx by sweet, sour, salty, or bitter substances. In man

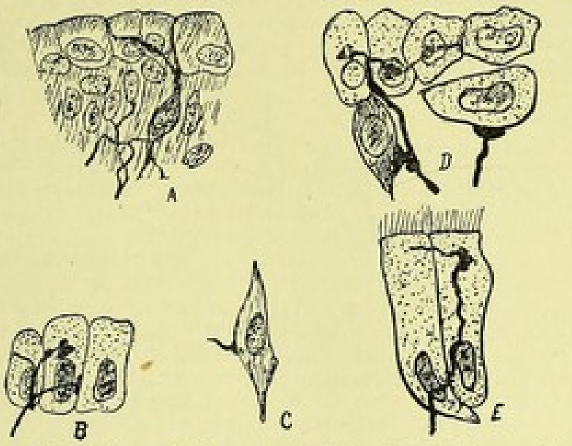

Fig. 2050.—Nerve Endings in the Mouth Epithelium of the Frog. (After Bethe.) *A*, "Gabezelle," from sensory papilla of the tongue; *B*, cylinder cells; *C*, isolated rod cell; *D*, upper part of papilla; *E*, ciliate cells of palate

this is a strictly interoceptive sense; but in some fishes taste buds are scattered over the outer body surface in addition to the mouth cavity, and thus serve as exteroceptors also.

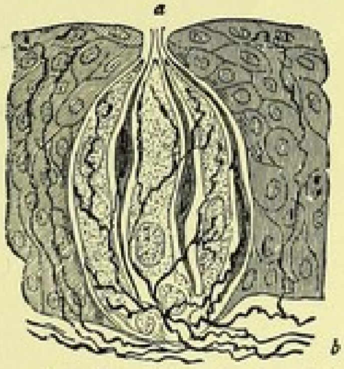

Fig. 2051.—Taste Bud from Side Wall of Circumvallate Papilla. (After Merkel-Henle.) *a*, Taste pore; *b*, nerve fibers, some of which enter the taste bud (intragemmal fibers), while others end freely in the surrounding epithelium (intergemmal fibers).

The organ is a specialized flask-shaped collection of epithelial cells of two sorts, supporting elements and specific sensory elements (Fig. 2051). There is a double innervation, partly by perigemmal fibers whose endings surround the bud, and partly by intragemmal fibers which penetrate the bud and arborize in intimate relation with the specific sensory cells (Figs. 2052, 2053).

23. Smell. Chemical stimulation of the specific olfactory mucous membrane of the nose. The number of substances which may act as stimuli is greater than in the case of taste buds, the number of subjective qualities is also greater, and the discrimination threshold is much lower. That this

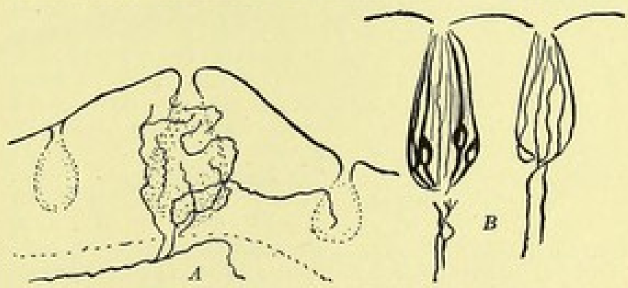

Fig. 2052.—*A*, Perigemmal Nerve Ending from Taste Buds of the Conger Eel; *B*, intragemmal nerve endings from taste buds of Barbus vulgaris. (After Lenhossék.)

system was originally an interoceptive sense seems clear; but in all vertebrates living at the present time the visceral responses to smell are quite subordinate to the somatic reactions. The sense of smell is the leading exteroceptor in most lower vertebrates, and this function has been secondarily derived from the primary visceral function. We have seen above that the sense of taste in some fishes has secondarily acquired exteroceptive functions; and in the case of smell this secondary change has been carried still further until the exteroceptive function has come to dominate the primitive interoceptive, though the latter has by no means been entirely eliminated (cf. *Olfactory Nerve*).

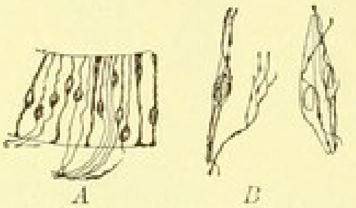

Fig. 2053.—*A*, Olfactory Nerve Endings in Jacobson's Organ (After Lenhossék.) *B*, Nerve endings in taste buds. (After Arnstein.)

The peripheral organ of smell is a specific sensory epithelium within the nose, whose sensory cells give rise directly to the fibers of the olfactory nerve, this being the only peripheral nerve of the human body whose fibers arise from superficially placed cell bodies. Jacobson's organ of many animals gives rise to a separate part of the olfactory nerve, the nervus vomero-nasalis (Fig. 2053).

III. Somatic Effectors.—24. End-organs on the striated skeletal muscles. These muscles are derived

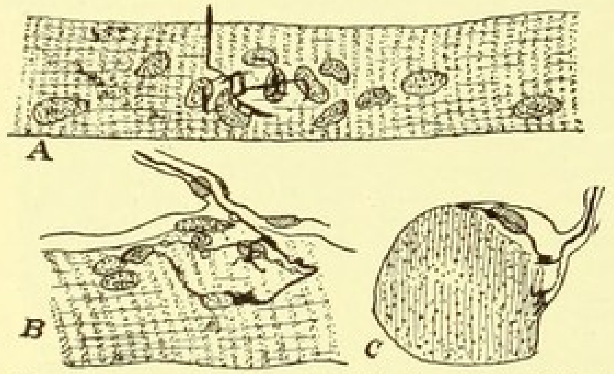

Fig. 2054.—*A* and *B*, Motor End-plates from Striated Muscle of the Rabbit; *C*, cross-section of a muscle fiber and motor end-plate of the frog. (After Huber and DeWitt.)

embryologically from the somites or primary mesodermal segments of the embryo. They are under the direct control of the will and are concerned chiefly with locomotion or other movements which change the relations of the body to its environment; they are typically stimulated to action through the exteroceptive sense organs. They are innervated by

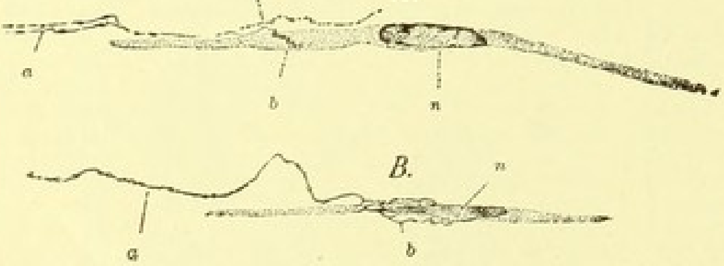

Fig. 2055.—Nerve Endings on Smooth Muscle Cells. (After Huber and DeWitt.) *a*, Axis cylinder; *b*, its termination; *n*, nucleus of the muscle cell.

a system of somatic motor nerves arising from a ventral motor column of nerve centers. The components of this system found in the cranial nerves (III., IV., VI., and XII. pairs) are sometimes distinguished as a special group, in contrast with the general somatic motor nerves of the trunk (cf. *Cranial Nerves*). The end-organ, or motor end-plate, is a complex terminal arborization of the motor nerve fiber, associated with an elevated granular mass of sarcoplasm and a collection of nuclei of the muscle fiber (Fig. 2054).

IV. Visceral Effectors.—25. End-organs on the involuntary visceral muscles. These muscles may be unstriated or striated (as in heart muscle).

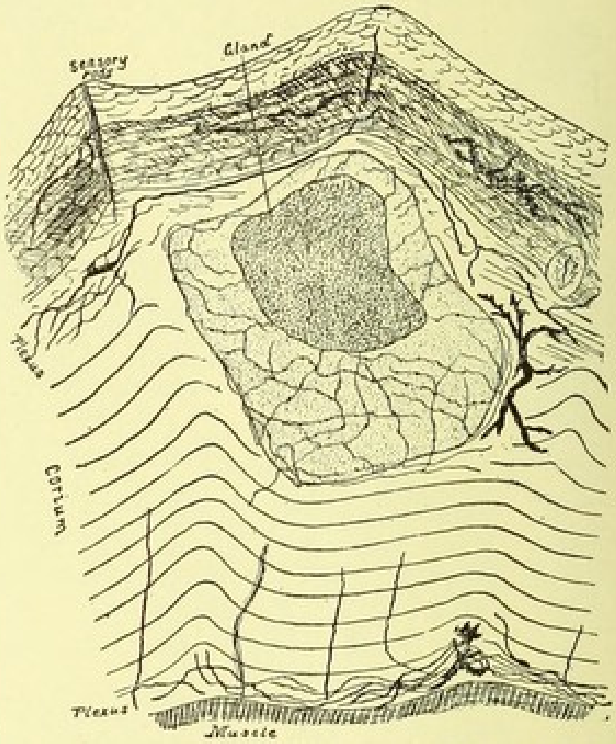

Fig. 2056.—Thick Section Through the Skin of a Toad (Bufo). Illustrating a network of fine unmedullated nerve fibers over the uncut surface of a cutaneous gland. The duct and part of the body of the gland are out of the plane of the section. (After C. L. Herrick.)

They are innervated through the sympathetic nervous system and typically by a chain of two neurones, the preganglionic and the postganglionic neurones. The body of the preganglionic neurone lies in the central nervous system and its neurite passes out into the sympathetic nervous system where it ends in a sympathetic ganglion. The efferent impulse is here taken up by a postganglionic neurone, whose body lies in the sympathetic ganglion in question and whose neurite passes onward through a sympathetic nerve to end in the appropriate effector. The nerve endings of this system are simple or branched free terminals ending on the surface of the muscle fiber (Fig. 2055); in the case of heart muscle the fibers usually have expanded trefoil tips.

26. End-organs on glands. The innervation of these organs is in most respects similar to that of the involuntary muscle last described. A fine plexus of non-medullated fibers of sympathetic origin envelops the smaller glands and pervades the larger ones (Fig. 2056); they are believed to be the excitoglandular fibers.

27. Special visceral motor end-organs. The nerves of this system have no connection with the sympathetic system. These effectors are striated muscles acting under the direct control of the will. They are derived phylogenetically from the branchial or gill muscles of lower vertebrate ancestors and they are

developed embryologically from the ventral unsegmented mesoderm and not from the primitive mesodermal segments which give rise to the somatic muscles. They are innervated directly from a ventrolateral column of motor neurones of the medulla oblongata, whose neurites form part of the motor roots of the V., VII., IX., X., and XI. cerebral nerves.

C. Judson Herrick.

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Endothelioma.—See *Sarcoma*.

Enema.—See *Enteroclysis*.

Enema, Nutritive.—See *Alimentation, Rectal*.

Energy.—This term may be roughly defined as the doing or the capacity for doing work; that which overcomes resistance; activity; the exertion of power; efficiency. It is purely a matter of one's intellectual temperament and philosophical opinions whether mental energies or energy be included for him or not in this definition. The word energy comes from the Greek adverb *energos* (meaning active), which in its turn was compounded of *en*, in, and *ergon*, work. The idea comprised in this expression "in working" is indeed very exactly the essence of the modern physical concept expressed by the word energy. One of the two great classes of energies, those of *position*, termed in physics potential energy, is of especial interest in organic energetics and therefore in medicine; the other class of energies, those of *motion*, kinetic energies, are far more obviously true energies, since they contain the root idea of activity. A man, for example, pulling upward on a ring-bolt firmly fixed in the curbstone, might exert a great amount of energy without exerting any "energy" at all on the purely physical definition of energy as "the capacity for doing work," where "work" means the overcoming of resistance through space. The nonsense of this old-time definition of work, then, as involving *space* of necessity, is at once apparent, for of all energies the energies of living organisms are the most obviously certain. If, then, such a notion of energy interferes with a definition in physics, we must give up the definition, for the expense of energy under the conditions suggested is quite undeniable.

The tendency, then, is to limit the term energies to those by physics termed kinetic, energies of motion. Potential energy, that imagined as inherent in position, is less obviously energy or even something else, in a sense, being a wholly relative matter, relative namely to space. On the other hand real or obvious energy may be, as we have seen by the illustration above, wholly independent of space, especially in organisms. The relations here are metaphysical and recondite to a degree, and taken together suggest how intimately derived from our own exertion is our concept of energy.

No definition of energy, for example "the capacity to do work," is satisfactory which is so utterly relative that it fits only a part of the instances. Suppose, for another instance, a stone carried to the summit of a granite mountain and thrown into a vertical hole drilled out of the rock there; the conventional physicist would say it had "acquired the (potential) energy required to lift it from its original place, and that if the mountain were removed this energy would show itself as kinetic energy and draw it toward the center of the earth." Certainly this stone in its new position has no velocity of its mass; on the other hand, to define its acquired (potential) energy as due to strains is to ascribe it not to itself but to the earth which somehow tends to attract it into its midst. The conventional physicist seems to be content with the old-time definitions of his science, however, although he cannot well help being puzzled at times by their inconsistencies. We may well rest with an opinion not unlike that of the well-known English philosopher, F. H. Bradley: "No one is bound to be intelligible outside his own science, I am quite convinced as to that." It is not any too pleasing, none the less, to see glaring inconsistencies (compare the conservation of energy doctrine taken as an absolute law!) concerning the one ultimate thing (energy) with which the science is properly concerned.

Not only in such respects, but in others, is the idea of energy commonly held by the world at large at present in a state of fusion not to say confusion—fusion with other concepts, confusion because of the discovery of radium and its emanations, together with the doctrine of the "electrons" and of the "structureless" ether between them. Yet even here we may not rest, because scientists and thinkers as valid as the learned world has produced do not hesitate to think of consciousness as a form of energy and indeed as the most pervasive of all its forms. We are at a loss for answers to all these indefinitenesses concerning the limitations of the energy-concept, and consequently can do no better, perhaps, in the entire absence of authority (because authorities conflict) than to attempt a brief discussion of the most obvious of the various phases of energy, so far, especially, as medicine is concerned with them.

Whether in part hereditary or (according to John Locke) entirely the result of personal experience during infancy (the former seems the more likely supposition), the human concept of energy must originate wholly, either at first-hand or at second-hand, from the direct expenditure of energy by our muscles under the stimulation of our coordinating cerebral (voluntary) nerve impulses. Here alone do we come in direct relationship with the expenditure of force—but here we experience this very thing continually. Our whole life is, in fact, a series of experiences of this phenomenon as a manifestation of irritability; in many respects it is most unfortunate that language has crystallized the concept unduly hard into what we think of as "cause and effect." At any rate, useful as is this idea in our common life as an indicator of a certain phase of empirical relationship, it is quite essential to remember that in pointing to an event or a condition as the "cause" of another event or condition we are using only a symbol of convenience for what is really a multiplicity of conditions each more or less concerned in the series of events. This obvious integrative and broadening trend in the thought, especially the biologic thought, of the day was so ably expressed by Max Verworn of Bonn in his Silliman Lectures at Yale in October, 1911, that we can do no better than to quote his remarks at some length, as follows:

"The interpretation of the unity of being and happenings in accordance with natural laws, which to-day is widely accepted in the scientific world as the only exact one, implies the assumption of a causation according to which things are explained by the law of 'cause and effect.' I have already on various occasions taken the opportunity to criticise this view and to show the error and confusion to which it leads. I should like here to enter somewhat more in detail into the reason for this criticism. It is particularly directed against the scientific use of the term 'cause' on the basis of our best known theoretical principles. It is clear that all scientific observations and explanations are founded on experience. Can it be said that the conception of 'cause' originates from experience?

"We can say with absolute certainty that the conception of cause dates from prehistoric times. Its beginning reaches back to the stone age, at least to neolithic, possibly to paleolithic culture. This is demonstrated by the careful reconstruction of these prehistoric races based on a critical comparison of the remains of their culture with that of primitive races living to-day. The ideas of these primitive races show an inclination to an extraordinary degree to explain all happenings in the world anthropomorphously. All happenings in surrounding nature are given the same origin as the activities of man himself. To man on this plane of fantastic religious speculation all events in nature appear as the acts of will of invisible powers, which, having originally proceeded from the souls of dead human beings, think, feel, and act exactly as *he does*. This anthropomorphic conception of the occurrences in the surrounding world is one of the many conclusions which ensue from the supposition of an invisible soul, which can be separated from the body. It was this conception which gave the impetus for the transition of human thought from the era of the naïvely practical to the era of the theoretical spirit in that far removed age. In this anthropomorphic transference of personal subjective impulses of will to the objectively observed events of the surrounding world, lies the origin of causal conception, which since then has been generally used as the explanation of the happenings in the world. One cannot assert that the formation of the conception of cause is purely a product of *experience* but rather a result of *naïve speculation*. Even if a later evolution of human thought shows a continued endeavor to dismantle the conception of cause of its primitive trappings, and to modernize, as it were, its outer appearance, we still find today many inner components clinging to it, which do not agree with the strict demands of critical scientific exactness, demands which must particularly be made concerning a conception which has been given such fundamental importance in theoretical knowledge.

"I wish to observe here, however, that the conception of cause, even though more or less unconsciously so, is still the remains of a part of the old anthropomorphic mysticism carried over into our own times. This shows itself especially in the conception of *force*, which is nothing more than a form of the conception of cause [and of energy]. Force is the cause of movement. One has here in anthropomorphic manner transferred the action of the *will* of man, which produces movement of the muscles, into lifeless nature. The force of the sun attracts the earth, that of the magnet attracts iron, etc. In short, one has introduced a mysterious unknown factor instead of being content with the simple description of facts such as G. Kirchhoff ('Vorlesungen über mathematische physik. Mechanik,' Leipzig, 1876) has advanced in the field of mechanics. Although of late natural science has also dispensed more and more with the conception of force as a means of explanation, it is still to-day not wholly done away with."

We might continue the history of this "naïve speculation" as to the notion of energy, force, and cause, and be still more sure at the end that our conception of these arose wholly in our own expenditure of energy in our organism, product of hundreds of thousands of years of quasi-human evolution. It will be better, however, to try to obtain a notion of the concept of energy as held by its actual employers in their scientific work.

As a chance example of the research which is tending to demonstrate the unity of the "different kinds of energy" described by the former conventional physicist (surer of his principles than of his own actual experience), we may quote part of the summary and conclusions from experimental work on the mechanical efficiency of muscle done by A. V. Hill of Cambridge University and reported in the *Journal of Physiology* for August, 1913 (xlvi., 6): "It is concluded that under certain conditions the initial process of contraction consists largely if not entirely of the liberation of free potential energy, manifested as tension energy in the excited muscle; that this potential energy can be used indifferently for the accomplishment of work or the production of heat; that, including the recovery process, the efficiency of the whole muscular process may be almost as high as fifty per cent.; that the muscular machine is one in which free energy, prospective mechanical or potential energy, is stored in certain unstable chemical compounds, under the influence of preliminary chemical processes carried out in the presence of oxygen with the evolution of heat; and that after activity these unstable chemical compounds are rebuilt; that the chemical body possessing this free energy is the lactic acid precursor; and that under some conditions, *e.g.* high initial tension and strong excitation, more or less of the free energy may be degraded into heat before appearing as mechanical potential energy in the muscle."

For our present purpose (as well as for other purposes) there is a whole lot of thought-food in a chance report like this, for it suggests how entirely arbitrary, as a matter of denotative and descriptive words only, the various concepts of varieties of energy at present are—how perfectly integrated and unified and almost identified they must be in fact in the actual nature. And even then the dominant aspect of bodily energy, namely, the actuating (or inhibiting?) kinetic strains in the motor neurones, are only alluded to casually (*e.g.* "strong excitation") although of the living normal neuromuscular mechanism they must constitute a most essential factor, and through them the whole volitional phase of energies is involved in the actual motor event.

In an appendix to this same article Hill discusses this germane topic of free energy in relation to physiologic problems. This goes so directly to the heart of our present topic that it is expedient to quote it almost entire, thus: J. Bäron and M. Polànyi (*Biochem. Ztschr.*, liii., p. 1, 1913), "assuming the truth of various hypotheses made by Nernst, find that the free energy of the oxidation of glucose at 37° C. is some fourteen per cent. greater than the total energy of that oxidation; in other words this reaction can conceivably be made to give up not only 100 per cent. of its energy as mechanical work, but actually to acquire some of the heat energy of the surroundings and turn this also into work. In the same way they show that the free energy developed in the oxidation of fat is 106 per cent. of the total energy, and in the oxidation of protein 107 per cent. Whether Nernst's assumptions and figures are exact or not it seems probable that the free energy of all food stuffs is at any rate very high, that the plant stores free energy from the sunlight in a very concentrated form and is