

THE GENERAL VISCERAL EFFERENT COLUMN OF THE BRAIN STEM

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I. INTRODUCTION

It is generally accepted that the preganglionic fibres of the cranial autonomic outflow arise from cells in a series of nuclei, starting orally with the *Edinger—Westphal* nucleus and ending caudally with the dorsal motor vagal nucleus, which constitute the general visceral efferent column in the brain stem. Still there is some uncertainty concerning identification of the preganglionic nerve cells, as different kinds of cells are lying close together in the same area, and especially concerning the representation of different functions in diverse parts of this column. These difficulties are mainly due to the inadequacy of the technique applied. Most of the data concerning this column are gained from chromidial changes after sectioning of peripheric branches of the respective nerves or extirpation of vegetative cranial ganglia. But if we consider the difficulties in recognizing early retrograde changes in nerve cells, we may understand the diametral contradictions in the reports of different authors.

Some years ago we introduced a new technique [12, 14, 15, 16] in order to determine more exactly the functional representation in motor nuclei. After small lesions had been placed by means of the *Horsley—Clarke* stereotaxic method into different parts of the motor nuclei, subsequent secondary degeneration was investigated in several branches of the respective nerve and the muscles supplied by the nucleus. This method has furnished more clearcut results than even the method of elective stimulation, which is, however, superior to the method of retrograde degeneration, though errors caused by stimulation of supranuclear pathways instead of the nuclei may occur.

We therefore decided to investigate the exact location of the nerve cells giving origin to preganglionic fibres of the cranial nerves by placing small electrolytic lesions into different parts of the assumed general visceral efferent column of the brain stem. Secondary degeneration was very thoroughly investigated in the branches of cranial nerves with autonomic functions and in the cranial autonomic ganglia.

II. MATERIAL AND METHODS

Our investigations were carried out on adult cats. Lesions were set with the aid of a modified *Horsley—Clarke* apparatus. Ear plugs were not inserted into the external auditory meatus because of the danger of injuring the postganglionic branches of the superior sympathetic cervical ganglion, which are known to traverse on cats in great number the tympanic cavity, as well as the chorda tympani and the lesser superficial petrosal nerve. Instead a small hole was prepared with a dentist drill on both sides directly above the root of the arcus zygomaticus in a vertical line erected on the center of the auditory porus. Ear plugs were replaced by sharply pointed conical pieces, which were inserted into the prepared holes.

The operated animals were sacrificed after 4—5 days, and the material fixed in a 1 : 4 solution of neutral formol. The exact site of the lesions was determined on serial sections, the secondary degeneration of the preganglionic fibers and pericellular apparatuses was investigated on frozen sections after silver impregnation with the *Bielschowsky—Gros* method.

III. THE EDINGER-WESTPHAL NUCLEUS

Several years ago we [13] investigated the exact origin of the preganglionic fibers supplying the ciliary ganglion by the same method. We herewith summarize our main results.

The *Edinger—Westphal* nucleus is generally described to be situated in the rostral portion of the oculomotor nucleus. Two groups of cells are distinguished: the medial group is lying wedge-like between the divergent oral poles of the motor nucleus; the other one consists of two dorsolateral groups situated above and in front of the oral poles. It is presumed that the dorsolateral group gives rise to preganglionic fibers innervating the sphincter of the iris and the medial to those innervating the ciliary muscle. According to other authors the reverse holds true, and again to others no such functional localization exists in the *Edinger—Westphal* nucleus.

The first striking fact noticed in the course of our investigations mentioned above was the discordance between the number of nerve cells in the so called *Edinger—Westphal* nucleus and of the preganglionic fibers within the radix brevis of the ciliary ganglion. The number of the preganglionic fibers of the ciliary ganglion has been determined by *Wolf* [18] and ourselves (unpublished) several times and found to be on cats about 2000 on each side. The cell number of the medial group only of the *Edinger—Westphal* nucleus (count of the nucleoli on *Nissl* series) of the same animal is over 10 000 if the limits of the group are drawn rather narrowly. The cell number of the two dorsolateral groups together is about the same. Thus the so called *Edinger—Westphal* nucleus has at least five times as many nerve cells, as there are preganglionic fibers to the ciliary ganglion. From these facts the conclusion must be drawn, that most of the cells in the territory of the *Edinger—Westphal* nucleus do not give rise to preganglionic fibers.

In complete accordance with this conclusion stereotaxic lesions of the medial group do not cause any signs of secondary degeneration within the radix brevis of the ciliary ganglion. Secondary degeneration was only seen when the lesions destroyed the close dorsolateral neighbourhood of the rostral part of the oculomotor nucleus and a small region immediately rostrally to its rostral pole. — After lesion of the basal laminae of the lateral geniculate body, the pretectal region, or the posterior commissure, degeneration of synapses was found to be confined strictly to the same region. Since by these lesions the second neuron of the reflectoric pupillomotor pathway had been destroyed (intrinsic neurons of the retina not considered), these degenerated synapses were thought to belong to this path, which is another strong evidence in favour of our assumption, that only the dorsolateral and anterior part of the so called *Edinger—Westphal* nucleus can be considered as preganglionic center of the intraocular muscles. Even the number of cells within this restricted region is more than about two times larger than the number of preganglionic fibers. We therefore made a careful investigation of the cytoarchitectonics of this region on *Nissl* preparations. Two types of nerve cells were found (fig. 8. b. 1 and 2 of our paper referred to above); the small type is characterized by its chromidial substance, which is aggregated into two semilunar clods near the surface, the other type is very similar to the motoneurons though somewhat smaller with largely granulated chromidial bodies. Since the medial cell group, which had been found to have nothing to do with preganglionic fibers, is built up exclusively by the small type, it is inferred, that only the larger type should be considered as cells of preganglionic fibers. In accordance with this degenerated synapses were found only around these larger cells after lesions of the posterior commissure or the lateral geniculate body. We must refer to our original paper for further details.

IV. THE LACRIMO-SALIVARY COLUMN

The second part of the general visceral efferent column is the so-called salivary nucleus (*Kohnstamm* [5], *Yagita* [19]), which is generally described as lying in the reticular formation at the junction of the pons and the medulla. As determined earlier by the chromatolytic method and later by stimulation in the monkey (*Magoun* and *Beaton* [9]), it extends from the genu of the facial nerve to the nucleus of the hypoglossus. According to the above mentioned authors it lies just lateralward from the medial plane. More recently the stimulation experiments of *Wang* [17] have revealed a more lateral and more cranial localization. The efferent fibers arising from the more caudal portion — the so-called inferior salivary nucleus — join the glossopharyngeal nerve and are running to the otic ganglion. Those originating in the rostral portion — the superior salivary nucleus — are conveyed via the chorda tympani to the submaxillary ganglion.

In our own experiments degeneration within the different preganglionic branches of the »lacrimo-salivary« ganglia was investigated and the following relationship with the sites of the lesions was experienced.

1. *Greater superficial petrosal nerve*

Clear signs of degeneration were detected in this nerve, whenever the lesion was situated laterally and behind the motor trigeminal nucleus and medio-dorsally from the rostral part of the spinal tract of the trigeminus. Some degeneration was also found in case the lesion had been placed between and somewhat dorsad to the motor and principal sensory trigeminal nucleus (fig. 1. [1]). Signs of degeneration gradually disappear if the lesion had been situated in the level of, or more caudad than the genu of the facial nerve.

The same region was also explored with electric stimulation. The amount of lacrimal secretion was determined by small strips of filter-paper inserted into the conjunctival sack. The weight of the paper was determined by a torsion balance before and after stimulation. Stimulation of the region mentioned above yielded 12–15 mg/min lacrimal fluid in comparison to 3–4 mg/min on the other side. Hypersecretion of the nasal mucous membranes was also noticed during these experiments, but the amount of it could not be determined. The field from which a significant rise of lacrimal and nasal secretion can be elicited by stimulation slightly above threshold (measured on the threshold of the motor trigeminal nucleus) with faradic current is much larger than the one from which degeneration can be evoked by placing lesions. This clearly shows that also prenuclear systems (and perhaps longer dendrites) of the visceral efferent neurons are stimulated, which makes difficult to determine the exact limits of the nuclei.

2. *Chorda tympani*

Degeneration of myelinated fibres of smaller diameter is found in the chorda, whenever the lesion situated dorsomedial from the nucleus of the trigeminal spinal tract lies between the level rather rostral to that of the facial genu (fig. 1. [2]) and the level of the rostral pole of the facial nucleus. This is about the same region the stimulation of which yielded maximum submaxillary secretion in the experiments of Wang [17]. — The medium-sized myelinated fibres of the chorda, being sensory fibres with their cells of origin in the geniculate ganglion, do not at all degenerate after lesions in the brain stem.

3. *Lesser superficial petrosal nerve*

Degeneration of small myelinated fibres was found in this nerve, when the lesion situated medially of the nucleus of the trigeminal spinal tract lies between the level rather caudad from the facial genu and the level somewhat cranial from the caudal pole of the facial nucleus. Thus the cells of origin of the preganglionic fibres of the otic ganglion are situated dorsolaterally and somewhat cranially from the facial nucleus within the lateral reticular formation. This is approximately the same, though a little more limited region, the stimulation of which yielded a maximum of parotid secretion in the experiments of Wang.

4. *Lingual and pharyngeal branches of the glossopharyngeal nerve*

Some myelinated fibres of small diameter are showing subsequent secondary degeneration after lesions dorsolaterally from the posterior half of the facial nucleus (fig. 1. [4]). These degenerated fibres can be traced to multipolar ganglion cells, which are scattered in the tongue, mostly in close neighbourhood of the lingual branches of the IX nerve, and to some upper ganglion cells of the pharyngeal plexuses. These degenerated fibres must be considered as secretory fibres for the smaller salivary glands in the posterior parts of the tongue and the upper pharyngeal mucosa.

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* *

These results enable a localization of the secretory preganglionic neurons of the lacrimal gland and the nasal mucous membranes, and lend for the salivary nuclei a more exact localization than hitherto known. We may gather all these nuclei into a common »lacrimo-salivary« column which begins with its oral pole dorsally wedged between the principal sensory and motor trigeminal nuclei and extends to the level of the caudal half of the facial nucleus (Fig. 1). On cross

sections of the brain stem the column is situated cranially dorsomedial, more caudally medial from the spinal tract of the trigeminus. — On *Nissl* preparations it is difficult to identify the preganglionic nerve cells among the scattered cells of different character. From the fact that the total cell number in this region is much larger than that of the preganglionic fibres in the above mentioned branches of the VII and IX nerve, we must infer that different kinds of cells

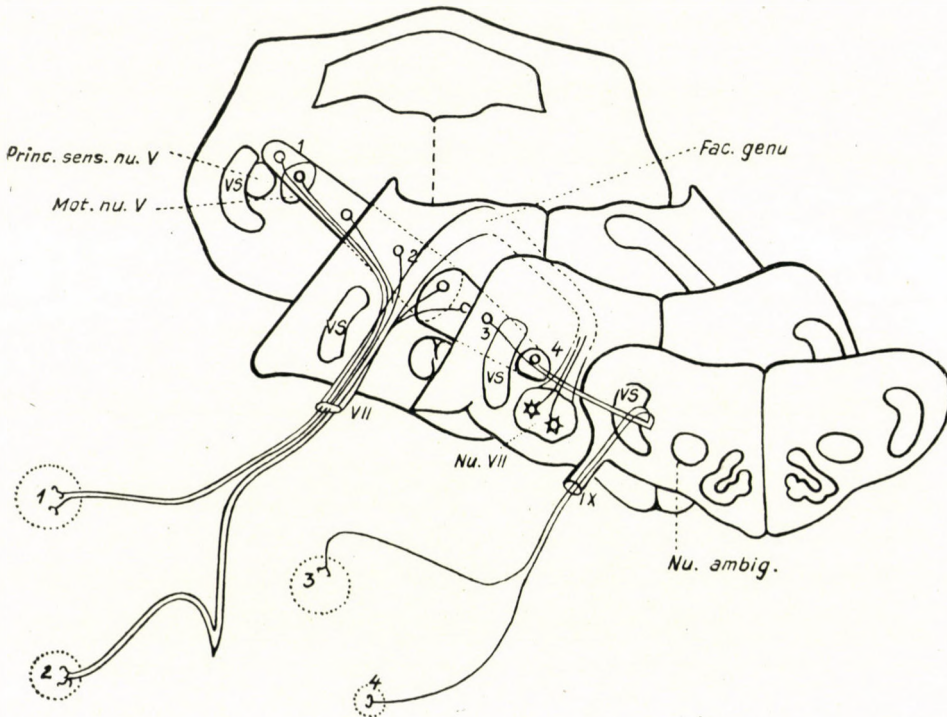


Fig. 1

The »lacrimo-salivary« column of the brain stem. 1. Cells supplying the lacrimal gland and the nasal and palatal mucous membranes via greater superficial petrosal nerve and sphenopalatine ganglion. 2. Nerve cells supplying the submandibular and sublingual glands via chorda tympany. 3. Preganglionic neurons to the otic ganglion conveyed by the lesser superficial petrosal nerve. 4. Preganglionic neurons for smaller ganglion cell groups attached to branches of the glossopharyngeal nerve

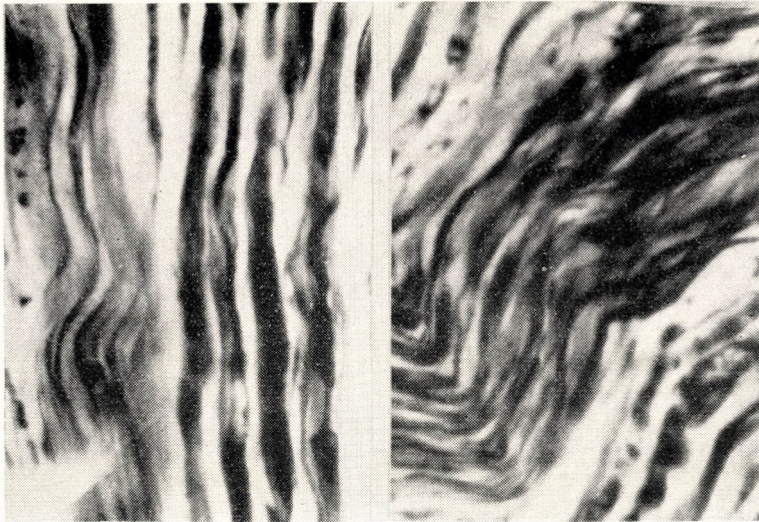
are intermingled. The roots of the column do not participate in the internal facial genu, since after its lesion no degeneration in the vegetative branches is found.

The lacrimo-salivary column has fairly clear functional subdivisions, though there exists a considerable overlap between the cells which give origin to preganglionic fibres for the different ganglia. The secretory cells for the lacrimal gland, the nasal and palatal mucosa are localized in its most rostral part. Behind them the secretory cells for the sublingual and submandibular

gland, and in its caudal part those for the parotid gland and posterior lingual and upper pharyngeal glands are situated. The salivatory nuclei are situated more cranially as thought by earlier authors and generally described also in recent hand-books of neuro-anatomy.

V. THE EFFERENT NUCLEUS FOR INNERVATION OF PHARYNGEAL AND ESOPHAGEAL STRIATED MUSCLES

The function and nerve supply of pharynx and esophagus stands between somatic and true vegetative innervation. This is partly due to the fact, that



A.

B

Fig. 2

Recurrent laryngeal nerve after lesion of the retrofacial nucleus (A) with large diameter fibres (to laryngeal muscles) intact, some fibres of small diameter (to the left) degenerated. (B) The same nerve after lesion of the caudal portion of the nucleus ambiguus. Fibres of large diameter degenerated (both sides), small fibres (center) intact

their musculature is partly striated and partly smooth. But even the function of the striated muscles has certain features resembling those of autonomically innervated organs. The motor end-plates of these striated muscle fibres belong

to the lower differentiated grape-like type, the motor fibres, though being myelinated, are exclusively of small diameter. The preterminal part of these fibres loses its myelin sheath and forms rich plexuses which are very similar to the well known vegetative preterminal plexuses.

The nerve cells supplying the different kinds of oesophageal musculature are not sufficiently localized. It is generally believed that the striated muscles are innervated directly by nerve cells lying in the nucleus ambiguus, whereas smooth muscle fibres, — relayed by peripheric ganglion cells —, by cells situated in the dorsal vagal nucleus.

In our experiments abundant degeneration of nerve fibres and motor endplates was encountered if lesions had been set immediately caudal to the facial nucleus. Regardless whether the fibres are leaving the brain stem through the IX nerve (those supplying the upper two third of the pharynx), or through the X (those supplying the lower third of the pharynx and the oesophagus) these fibres are arising from a small region, which is often referred to as *nucleus retrofacialis* (*Jacobsohn*), the relation of which to the IX and X nerves has often been denied (*Ziehen* [20]). The difficulty of identification of these cells with the motor radicular cells is due to the fact that they are much smaller. But this harmonizes with the small diameter of the fibres supplying the striated muscle fibres of the pharynx and esophagus. It is widely known that there is a relation between the size of the motor radicular cells and diameter (also length) of their fibres. In all cases when the lesion was localized directly behind the facial nucleus, in the recurrent laryngeal nerve almost all large fibres (supplying the laryngeal muscles) are intact, whereas thin fibres are degenerated (Fig. 2). If one traces this nerve upward it can clearly be seen that the degenerated smaller fibres are leaving the nerve trunk through thin branches to the oesophagus. The intact fibres with large diameter are remaining in the trunk and reaching the laryngeal muscles. — In cats and dogs, where the striated muscles are reaching the level of the diaphragm, even the lowest situated muscle fibres are supplied by the same nucleus.

VI. THE DORSAL MOTOR VAGAL NUCLEUS

The dorsal motor vagal nucleus (*nucleus alae cinereae medialis*) is generally considered to be the lower and most important part of the general visceral efferent column of the brain stem. In the older literature there was much controversy about the localization of functions in both the dorsal and the nucleus ambiguus [for reference: *Ziehen* 1. c]. There were many excellent investigators as *Bunzl—Federn* [2], *Hudovernig* [3], *Kosaka* and *Yagita* [7] and several others, who on the basis of chromatolytic findings localized the origin of preganglionic fibres especially for the lung and the heart into the nucleus ambiguus or

its immediate neighbourhood. Strangely enough in the modern literature everybody takes it for granted that all preganglionic fibres are arising from the so called dorsal nucleus. We cannot exactly understand this change of opinion, since all, earlier and modern, authors, have been using the same chromatolytic method.

In a number of experiments we placed small lesions with the aid of the *Horsley—Clarke* technique into this nucleus in order to determine the exact origin of the preganglionic fibres for different thoracic and abdominal organs. To our surprise we could not detect even one degenerated fibre in the stem, or in one of the branches of the vagus nerve. Later the whole ala cinerea was extirpated with the same completely negative result. At first we did not believe our own eyes, but at last the facts led us to the conclusion that no preganglionic fibers at all originate from the so called »dorsal motor vagal nucleus«, i. e. at least they show no degenerative changes after destruction of their cells of origin, which does not seem to be very probable.

VII. THE NUCLEUS AMBIGUUS

In the course of our further inquiries about the cells of origin of the preganglionic fibres in the vagus nerve, the nucleus ambiguus and its immediate neighbourhood was investigated with the same method. After having placed small lesions into the oral half of this nucleus, as well as between this nucleus and the nucleus of the trigeminal spinal tract, signs of degeneration were found in the oesophageal and in the cardiac and pulmonary branches. In the oesophagus evaluation of the findings meets with some difficulties. As in the lower regions of the oesophagus striated and smooth muscles are interwoven to a certain extent and supplied by the same intermuscular plexus, it is difficult to decide whether degenerated fibers are really terminating on ganglion cells, or are only passing by and finally ending on striated muscles. In some cases degenerated fibres were found in the submucosa (Fig. 3, b) and around nerve cells which were fairly isolated (Fig. 3, c) from which we may draw the conclusion that preganglionic fibres supplying the oesophagus are originating in the oral part of the nucleus ambiguus. Signs of degeneration were much more clearcut in the cardiac and especially in the pulmonary branches (Fig. 4). The degenerated fibres could be traced to vegetative nerve cells, where they terminate as pericellular synapses. Signs of degeneration were always scarce, since only small lesions could be placed in order to keep the animals alive. From a large number of experiments the impression is gained that preganglionic fibers arise especially from dorsolateral parts of the nucleus ambiguus, but exclusively from the oral half.

Very unfortunately we were unable to get clearcut results with this method concerning the origin of the preganglionic fibres in the abdominal branches.

This fact seems to be connected with the failure of the degeneration method in this part of nerve, though besides the *Bielschowsky—Gros* method the *Bodian*

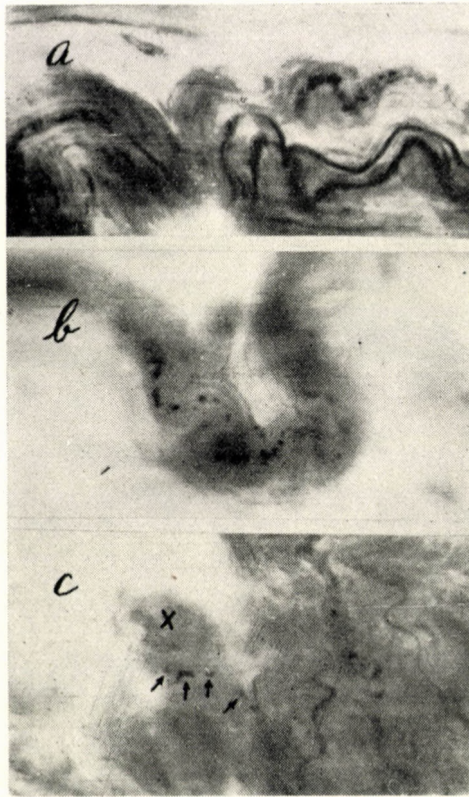


Fig. 3

Lesion in the oral part of the nucleus ambiguus. Photomicrographs taken from the oesophagus in the level of the diaphragm. *a*) Degenerated fibres in the intramuscular nerve plexus. *b*) Degenerated fiber in the plexus submucosus. *c*) Degenerated pericellular apparatus around a ganglion cell (x). Arrows are pointing to the degenerated fragments

method was also tried. We cannot explain this failure, but shortly some facts and inferences should be mentioned:

1. In the abdominal part of the vagus nerve of cats the majority of fibres is unmyelinated, some fibres of larger diameter are myelinated.

2. The myelinated fibres never show signs of degeneration if the nuclei of the vagus, or its roots, are injured, or even the nerve itself is transected above the ganglion nodosum. But subsequent secondary degeneration of these fibres is always seen, if the nerve is cut below the ganglion. From these facts it is obvious that the myelinated fibres of larger diameter and to some extent those of small diameter and even some unmyelinated fibres, which are also degenerating, are originating from cells of this ganglion and hence may be considered as sensory fibres.

3. The large majority of the unmyelinated fibres in the abdominal vagus does not degenerate after complete transection of the roots of the IX, X and XI nerves nor do these degenerate after transection of the vagus nerve below the ganglion nodosum. — With regard to this fact we should conclude, that the majority of unmyelinated fibres of the abdominal vagus are post-ganglionic. But then where are their cells of origin? Two possibilities must be considered.

a) The cells of origin are those scattered cells frequently described in the trunk of the vagus nerve.

b) The cells of origin may be situated in the cervical sympathetic ganglia, as Kiss [4] presumes and they join the vagus by anastomoses between the superior cervical and nodose ganglion.

Both possibilities must be tested by careful experimental analysis. We have already attempted to clear this question by transecting the vagus nerve in the thoracic cavity below the level of the hilus of the lung. On account of results of these experiments, — the number of which however is small, — we had the impression that the main difficulty is due to the strang

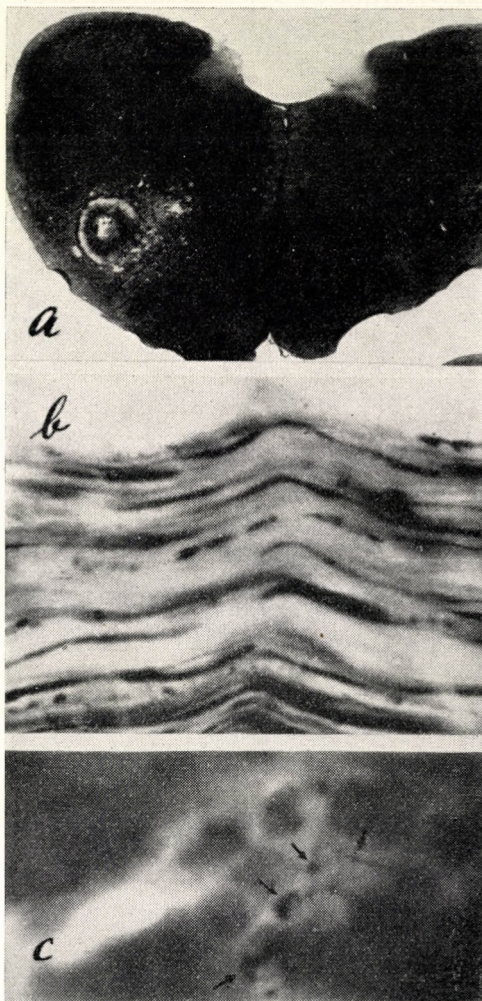


Fig. 4

Lesion in the oral half of the nucleus ambiguus (a), degenerated preganglionic fibres in a pulmonary branch (b), degenerating pericellular apparatus in a pulmonary ganglion (c)

fact that secondary degeneration within the lower thoracic and abdominal vagus (concerning unmyelinated fibres) does not follow the principles determined in peripheral and central nerve fibres and not even those determined in the sympathetic system and in other parts of the cranial autonomic outflow especially by Lavrentyev and his co-workers [8, 6, 10]. The method of secon-

dary degeneration has proved itself very useful in tracing fibres of different origin within the most intricate peripheric plexuses in our own investigations [11] and in those of other workers [1]. It has proved to be useful in this investigation to determine the central origin of the preganglionic fibres of the cranial vegetative outflow, but in the abdominal vagus this method seems to fail. An extensive experimental analysis of this striking question is being presently pursued in this department.

We are not the first to fail in the experimental-morphologic analysis of the abdominal part of the vagus nerve and the connection of its fibres with the enteric plexuses. Many authors claim to have found signs of degeneration in the enteric plexuses after transection of the vagus. But there is not one report showing positive signs of axonic fragmentation (except those of sensory fibers), which is the only acceptable conclusive sign of axonal degeneration. Authors are basing their conclusions on loss of nerve fibres in the enteric plexuses, which — taking into consideration the fallacies of the impregnation methods — naturally proves nothing. — Because of these difficulties the question of the central origin of preganglionic vagal fibers to the enteric plexuses must be postponed until the constitution and mode of degeneration of fibres in the abdominal vagus can be elucidated. The same applies also to the question whether any preganglionic fibres arise from the so-called dorsal motor vagal nucleus. It appears from our results that preganglionic fibers for oesophagus, heart and lungs do not come forth from this nucleus but originate in oral parts of the nucleus ambiguus. On account of the difficulties in tracing fibres to the abdominal branches with the aid of the secondary degeneration method it is nevertheless possible, — though as we shall see in the discussion it is not very probable, — that the nucleus alae cinereae medialis gives origin to the preganglionic vagal fibers of the abdominal organs.

Returning to the nucleus ambiguus, the question which cells of this nucleus give rise to preganglionic fibres of the vagus nerve must be discussed. From this point of view it is important to know, that *Bunzl—Federn* [2] and many other authors long ago described two cellular groups within this nucleus. The oral part, which is called »dense formation« contains smaller cells, the form and chromidial structure of which is not exactly the same as the form of ordinary radicular motor cells. More caudad the so called »loose formation« is built up partly of true large motor radicular cells, partly especially on its dorsolateral side, but exclusively in the oral half of the nucleus, of smaller cells. Referring to these facts *Ziehen* (1. c. pg. 262) says: »Es wird dadurch der Gedanke nahegelegt, ob der Nucleus ambiguus nicht doch in zwei Teile zerlegt werden muss, einen kleinzelligen und einen grosszelligen, von denen nur der letztere als Äquivalent einer Vorderwurzelzellengruppe zu betrachten wäre, während der erstere als eine abweichende Formation zu gelten hätte.« This seems to be in accord with our findings. The retrofacial region supplies the pharyngeal musculature as well as the striated muscles of the oesophagus, i.e. the same as the most rostral part of the so called dense formation of the nucleus ambiguus. From the lower

part of this dense formation and from scattered smaller cells dorsolaterally from the loose formation, preganglionic fibres for oesophagus, heart and lungs arise. For the heart a similar assumption was made already by *Kosaka* and *Yagita* [7]. The motor radicular cells in the nucleus ambiguus are supplying the laryngeal muscles; the exact localization of these in the nucleus ambiguus has already been described by us several years ago [14].

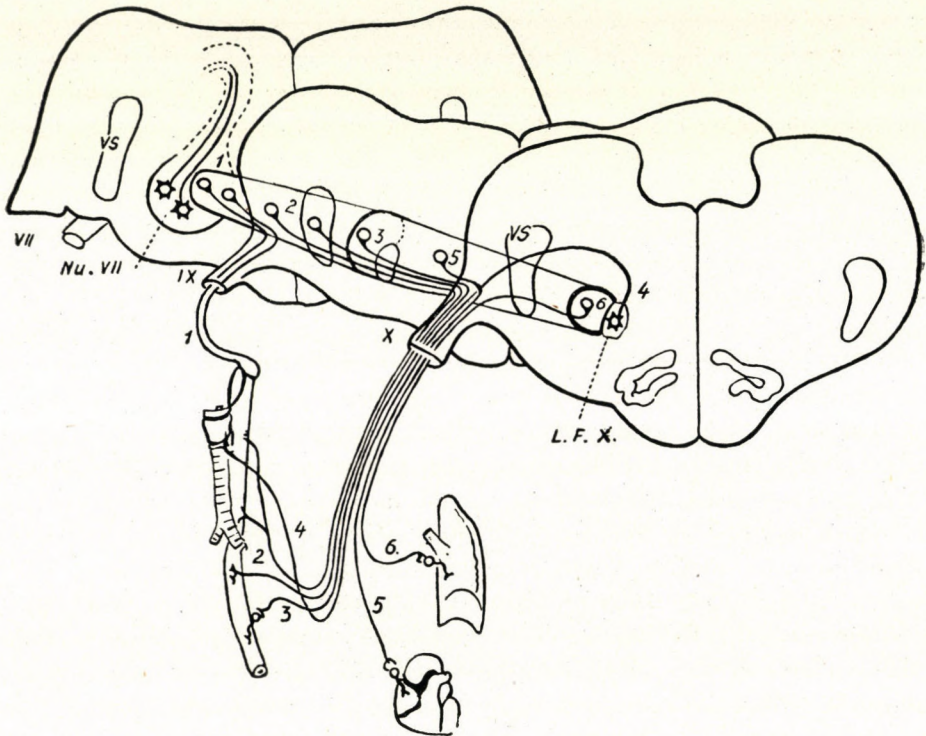


Fig. 5

Localization of the general visceral efferent neurons in the medulla. 1. Retrofacial nucleus and oral pole of nucleus ambiguus with neurons supplying striated muscles of pharynx and oesophagus (2); preganglionic neurons for lower part of oesophagus (3), heart (5) and lungs (6). LFX loose formation of nucleus ambiguus with motor radicular cells (4) for the laryngeal muscles

This view is also supported by the fact, that the diameter of nerve fibres supplying the laryngeal muscles, is exceedingly large ($12-16 \mu$), whereas the diameter of the motor fibres supplying the striated muscles of the esophagus is rather small ($3-6 \mu$), similar to that of the preganglionic fibres (Fig. 2). It is obvious, that from the smaller cells within the retrofacial nucleus and the oral half of the ambiguous nucleus thin motor and preganglionic fibres and from the large motor radicular cells large fibres are taking their origin.

VIII. COMMENT

On the basis of these findings the general visceral efferent column of the brain stem may be much better identified than before. The visceral efferent cells in the brain stem are situated medially to the sensory and dorsolaterally to the motor column. This is a completely analogous position to that of the lateral column of the spinal cord. Homologizing the architecture of the brain stem with that of the spinal cord two important facts must be considered. Firstly, in the region of pons and medulla all derivatives of the alar laminae are lying laterally from those of the basal laminae, whereas in the midbrain the situation is essentially the same as in the spinal cord. Secondly, the motor column in the brain stem is divided into two columns, the dorsomedial special somatic motor column from which nerves III, IV, VI and XII arise and the ventrolateral (special) visceral motor column from which the motor fibres of the branchial nerves V/3, VII, IX, X and partly XI are originating. (The remaining [lower] part of the accessory nerve supplying the sternocleidomastoid and trapezius muscles, originate from the caudal fusion of this column with the spinal motor column.)

It appears from our investigations, that the general visceral efferent column in the hind brain is attached — dorsomedially and to some extent intermingled, — to the visceral motor column of the branchial nerves, and not as presumed hitherto to the special somatic motor column of the brain stem. The latter must be considered as a cranial prolongation of the medial motor column of the spinal cord. Considering this it appears improbable that the so called dorsal motor vagal nucleus is in any connection with general visceral efferent functions. — Our investigations are giving clear evidence for the fact that pharynx, oesophagus, heart and lungs are supplied by the retrofacial nucleus and the oral half of the nucleus ambiguus, i. e. by smaller nerve cells lying in the dorsolateral part of this nucleus or immediately dorsolaterally to the true motor radicular cells. Concerning vegetative fibres supplying the abdominal organs, no information was gained from these investigations. — The preganglionic neurons for secretory supply of all noncutaneous exocrine glands of the head (salivary and lacrimal glands) have been localized in an uninterrupted column, which extends from the region between and above the principal sensory and motor trigeminal nuclei to the region dorsolaterally from the facial nucleus. This nuclear column may therefore be called »lacrimo-salivary column«; with functions localized as indicated in Fig. 1. This column is the direct cranial prolongation of the vagal vegetative column.

In the midbrain the situation changes. There is no special visceral motor column, and the original gray matter of the spinal cord is reduced to the central gray matter around the aqueduct. In this, the last remnant of the motor column, the trochlear and oculomotor nucleus remains a part of the dorsomedial

special somatic motor column. The mesencephalic tract of the trigeminal nerve is the most cranial part of the ordinary sensitive system. The *Edinger—Westphal* nucleus, as the most cranial part of the general visceral motor column, lies as much as possible laterad between the remnants of the motor and sensory columns. As clearly shown in our earlier experiments, the smaller nerve cells dorsomedially from the motor radicular cells do not belong to the general visceral motor column at all.

Summary

Location of preganglionic general visceral efferent (parasympathetic) neurons has been determined with the method of secondary degeneration after small electrolytic lesions placed in different parts of the brain stem with the aid of the *Horsley—Clarke* stereotaxic technique.

The exact site of the *Edinger—Westphal* nucleus has already previously been localized with the same method. The so called »dorso-medial« cell group of this nucleus has no relation to the preganglionic fibres of the ciliary ganglion at all.

The »lacrimo-salivary« column has been determined as an uninterrupted cellular group extending from the region between and dorsal the principal sensory and the motor trigeminal nuclei to an area dorsolaterally from the facial nucleus. Data concerning the preganglionic neurons for the salivary glands accord with the sites determined by *Wang* in stimulation experiments, but the region revealed by the degeneration method is a little more restricted.

The origin of nerve fibres supplying the striated muscles of pharynx and oesophagus was found in the retrofacial nucleus (*Jacobsohn*) and the oral pole of the nucleus ambiguus.

The preganglionic fibres for ganglion cells of the oesophagus, heart and lungs were localized in the oral half of the nucleus ambiguus (very probably cells localized dorsolaterally to the motor radicular cells).

No evidence for origin of preganglionic fibres in the so called »dorsal vagal nucleus« (nucleus alae cinereae medialis) was found with the aid of the secondary degeneration method, which is in strong contradiction with information attained through retrograde chromidial changes. This problem is obscured by the fact, that preganglionic fibres of the abdominal branch and their connections with the enteric plexuses cannot be traced by secondary axonic degeneration method. The possible causes of failure of this method in the abdominal branches are discussed.

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ОБЩИЙ ВИСЦЕРАЛЬНЫЙ ЭФФЕРЕНТНЫЙ (ПАРАСИМПАТИЧЕСКИЙ) ЯДЕРНЫЙ СТОЛБ СТВОЛА МОЗГА

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Резюме

Автор установил, на основе вторичной дегенерации волокон вегетативных нервных ветвей, точную локализацию парасимпатических ядер ствола мозга путем электрических очагов, помещенных по методу Гослей-Кларка.

Автор уже раньше установил этим же способом точную локализацию ядра Эдингера-Вестфала. Так называемый «дорсомедиальный» клеточный столб этого ядра совершенно не играет роли по вегетативной иннервации глаза.

Ядерный столб ствола мозга, регулирующий отделение слез и слюны, был точно определен как клеточный столб, тянущийся от области, расположенной посреди и выше двигательного и главного чувствительного ядер тройничного нерва, к области, расположенной на дорсолатеральной стороне ядра лицевого нерва.

Местом исхождения нервов поперечнополосатых мышц зева и пищевода является *nucleus retrofacialis* Якобсона, который переходит в конец *nucleus ambiguus cranialis*.

Вегетативные преганглионарные волокна пищевода, сердца и легких исходят из оральной половины *nucleus ambiguus*, из мелких нервных клеток, расположенных в дорсолатеральной части поперечного разреза данного ядра.

Примененным нами методом не удалось подтвердить общепринятый взгляд, согласно которому преганглионарные автономные волокна блуждающего нерва исходят из дорсального двигательного ядра блуждающего нерва (*nucleus alae cinereae medialis*), а даже является сомнительным, принадлежит ли вообще его ядро к системе блуждающего нерва. Установление происхождения вегетативных преганглионарных волокон брюшное части блуждающего нерва, и связи его с висцеральными сплетениями, до сих пор не оказалось возможным, из-за своеобразного и трудно объяснимого факта, что пока еще не удалось доказать Валлеровскую дегенерацию волокон.