ON THE RELATIONS
BETWEEN THE
FUNCTION, STRUCTURE, ORIGIN, AND DISTRIBUTION
OF THE NERVE-FIBRES
WHICH COMPOSE THE
SPINAL AND CRANIAL NERVES.
BEING THE
MARSHALL HALL PRIZE ORATION.

BY
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IN order to comply with the request of the Royal Medical and Chirurgical Society to give some account of those researches for which they have awarded me the Marshall Hall Prize, I have, after consideration, determined to sketch out as rapidly as possible the work which I have done in the order of my investigations, thinking it might interest you to see the manner in which one research led to another.

In 1881 I was enabled, by the use of a new method, to show that the vagus nerve not only inhibited the rate and force of the contractions of the heart in the frog, but also was able to accelerate the rate, and to augment in the most marked manner the strength, of the contractions of the heart.

These observations led to the discovery that the vagus nerve of the frog was in reality the vago-sympathetic, that the vagus fibres proper were inhibitory, and that the sympathetic fibres not only caused the acceleration and augmentation observed but also that they reached the heart by way of the annulus of Vieussens in precisely the same manner as in the case of the mammal. I was enabled further to show that in the cold-blooded tortoise and crocodile the heart is also supplied by two nerves of opposite function, having the same course as in the mammal.

Further, my investigations convinced me that the inhibitory fibres as well as the augmentor fibres retain the same function up to their termination in the cardiac muscle, and that therefore inhibition is something taking place in the muscle itself and cannot be explained by any theories of interference of nerve action outside the muscle.

Again, taking into account not only the primary effect but also the more lasting after-effect of the stimulation of these two opposing kinds of nerve fibres, I came to the conclusion that the process of inhibition was bound up with changes in the muscle of a beneficial nature to the further action of that muscle, while the action of the augmentor nerve resembled rather the action of a motor nerve and caused an exhaustion of the muscular activity. I concluded therefore that inhibition of contraction is a symptom of the action of an anabolic nerve, *i. e.* a nerve which brings about constructive metabolism just as much as contraction or augmentation of a contraction is a symptom of the action of a katabolic nerve, *i. e.* a nerve which causes a destructive metabolism.

In connection with this conclusion the consideration of the nerve supply of the rest of the vascular system, of the muscular tissue of the alimentary tract, and of the glands, led me to suggest that all tissues are supplied with anabolic and katabolic nerves, so that the efferent nerves and their centres of origin in the central nervous system are divisible into two great anabolic and katabolic nerve systems.

With this suggestion present in my mind I was investi-

gating under a dissecting lens the course of the sympathetic cardiac fibres in the tortoise and was much struck with the difference of appearance between them and the vagus fibres going to the heart. I promptly, therefore, looked at osmic preparations of the same nerves in the dog and rabbit, and found, to my delight, that invariably the augmentor fibres between the annulus of Vieussens and the heart were entirely composed of non-medullated nerve fibres, while the vagus cardiac fibres were all small strongly medullated fibres.

Here, then, was an anatomical difference between anabolic and katabolic nerves which immediately led to the question,—Does this distinction hold good along the whole length of their course?—thus leading to the investigation of the structure of the rami communicantes and of the roots of the spinal nerves.

Now, it was known that the accelerator fibres for the heart passed out of the spinal cord in the anterior roots, and, indeed, I myself had proved that they passed out in the anterior root of the third spinal nerve of the frog. I therefore examined the structure of the anterior roots of the dog in the upper dorsal and lower cervical region and found that they were absolutely free from non-medullated fibres, so that these accelerator nerves did not leave the spinal cord as non-medullated but as medullated fibres. At the same time I was struck with the difference in structure between the anterior roots of the thoracic and cervical region, the former, as pointed out by Reissner, containing groups of very fine medullated nerve fibres, varying in size from one $1.8\ \mu$ — $3.6\ \mu$, which were absent in the latter roots.

Further investigation showed that these fine, medullated fibres of the anterior roots formed the bulk of the fibres contained in the white rami communicantes, so that the course of the accelerator nerves was now evident; clearly they left the central nervous system as fine medullated fibres, passed to the ganglia of the sympathetic chain, along the white rami communicantes as fine medullated fibres,

lost their medullary sheath in the sympathetic ganglia, and passed to the heart as non-medullated fibres. The anatomical difference, therefore, between the anabolic and katabolic nerves of the heart consists simply in the place where the medullary sheath is lost; they both leave the central nervous system as nerve fibres of very similar histological character.

This connection between the structure of the anterior root and of the white ramus communicans led me to a detailed investigation of the anterior roots and rami communicantes along the whole length of the nervous system, and I was enabled to show that, throughout, the presence of white rami communicantes was associated with the presence of these groups of very fine, medullated fibres in the corresponding anterior roots, so that where they were absent the rami communicantes were grey, *i. e.* composed almost entirely of non-medullated fibres, and therefore peripheral in direction, going, in fact, to supply the blood-vessels of the district supplied by the spinal nerves in question and of the membranes of the cord; while, on the other hand, where they were present both a white and a grey ramus existed.

The simultaneous existence of white rami communicantes and of these groups of fine, medullated fibres in the anterior roots was found to be limited to the region of the cord comprised between the second thoracic and the second lumbar nerves inclusive.

Further, I argued, that if in other parts of the central nervous system groups of fine, medullated fibres appeared in the anterior roots, then, even although no evident white rami communicantes were present in connection with such roots, we might expect to find something formed strictly homologous to such white rami communicantes. Such I found to be the case. The anterior roots of the second and third sacral nerves contain numbers of these smaller visceral nerve fibres which pass out to form the *nervi erigentes* and pass into the ganglia of the hypogastric plexus; and in the upper cervical region another similar group is found in the

upper roots of the spinal accessory nerve, which pass out to help form the internal branch of the spinal accessory and enter into the *ganglion trunci vagi*.

I came therefore to the conclusion that it was better no longer to speak of rami communicantes, and of the sympathetic system, but rather to use the term of the morphologist and to speak only of rami viscerales, and it was evident that such visceral nerves did not pass equally from all parts of the spinal cord of the dog, but that they formed three marked outflows :

1. A cervico-cranial outflow in connection with the vagus and spinal accessory nerves ;
2. A thoracic outflow ; and
3. A sacral outflow.

This marked and striking inequality in the origin of the visceral nerves led immediately to a number of other considerations.

In the first place, the inequality appeared to be clearly due to the interposition of the plexuses for the anterior and posterior extremities ; for these plexuses fill up the gaps between the three visceral outflows.

In the second place, the limits of the outflows correspond so closely with the limits of Clarke's column of cells as to force one irresistibly to the conclusion that this group of cells is connected with visceral nerves.

In the third place, an explanation is at once given of the extraordinary round-about course which the constrictor nerves of the blood-vessels and the so-called sympathetic glandular nerves take to reach their destination in the various parts of the body ; for such nerves are apparently confined to the thoracic outflow, and losing their medullary sheath in the ganglia of the so-called main sympathetic chain, pass in all directions to their destination as non-medullated fibres.

Further, I was able to point out how this appearance and distribution of small medullated fibres corresponded to known facts as to the distribution of the nerves governing the muscles of the alimentary tract, how the known cases

of vaso-dilator nerves and the secretory nerves of the glands were all characterised by the fineness of the calibre of their fibres and the presence of ganglion-cells on their course; that in fact a large class of nerves existed of various functions which might all be called visceral or splanchnic nerves, all characterised by the fineness of their fibres, and by the peculiarity that although efferent in function they were in connection with ganglia in some part of their course.

The result of the investigation therefore up to this point led me directly to regard the sympathetic and homologous ganglia as the motor or efferent ganglia of these visceral fibres, so that instead of the old conception of two nervous systems which interchanged fibres with each other I would substitute the following definition of the nerves belonging to a spinal segment:—

A spinal nerve is composed of an anterior and posterior root, both of which are ganglionated, the difference between the two roots being that the ganglion of the afferent root is always stationary in position, being situated near the exit of the nerves from the central nervous system, while that of the efferent root is vagrant and has travelled away to various distances from the central nervous system. Moreover, these vagrant efferent ganglia are connected with the specially fine-fibred visceral efferent nerves.

This conception that fully-formed spinal nerves possessed motor ganglia as well as sensory ganglia appeared at once to throw light upon the vexed question of the relationship of the cranial to the spinal nerves, and to suggest the removal of the difficulty, so frequently noticed in morphological works, that a nerve which corresponded apparently to a posterior root should contain fibres which were clearly motor in function.

I determined therefore to compare the structure of the cranial with the spinal nerves and see how far they corresponded.

The first point which struck me was that these fine ganglionated efferent visceral nerve fibres appeared to have a more or less special relationship to a group of large-

fibred motor nerves, which were especially concerned with the function of respiration and deglutition, such as the external branch of the spinal accessory, the pharyngeal and laryngeal motor nerves of the vagus group, the nerves of the muscles of expression and deglutition; for in close connection with all these nerves are found groups of small medullated fibres, which are efferent in function and pass to various ganglia. It was possible therefore, that some close connection existed between these small-fibred efferent nerves and these large motor nerves which corresponded closely with Bell's group of respiratory nerves.

The connection appeared to me to be clearly pointed out by van Wijhe's researches on the mesoderm segments in the head of Selachians. For he has pointed out that a double segmentation is plainly visible in the head. On the one hand, a dorsal segmentation into somites from which are formed a series of muscle-plates which give rise to the muscles innervated by the third, fourth, sixth, and twelfth nerves, and, on the other hand, a ventral segmentation in connection with the formation of visceral and branchial clefts forming the lateral plates of mesoblast, *i. e.* the mesoblast surrounding the walls of the clefts, which give rise to the muscles of mastication, the facial muscles, and the muscles of deglutition and respiration; muscles supplied by the fifth, seventh, ninth, and tenth nerves.

In other words, if we use the terms somatic and splanchnic to denote the dorsal and ventral segments respectively, we can look upon the nerves of the body as divisible into two corresponding groups, viz. somatic and splanchnic groups, and can therefore define a spinal nerve as composed of:

1. A posterior root with a stationary ganglion, into which both somatic and splanchnic afferent fibres pass.

2. An anterior root, composed of (a) a large-fibred somatic and splanchnic non-ganglionated portion, and (b) a small-fibred ganglionated splanchnic portion, of which the ganglion is vagrant.

By somatic meaning that the nerves supply parts derived

from the epiblast and from the mesoblastic somites; by splanchnic meaning nerves which supply parts derived from the hypoblast and from the rest of the mesoblast.

The examination of the evidence as to the origin of the cranial and spinal nerves in the central nervous system which is given in the text-books of human anatomy, fully confirmed the existence of such a division of the nervous system, for the arrangement of the nerve cell groups in the spinal cord appear naturally to fall into two groups, one of which is in connection with somatic and the other with splanchnic nerve fibres, and it appears to me that the nerve cells of the somatic nerves are situated in the outlying horns of the grey matter, while the nerve cells of the splanchnic nerves form a group in the neighbourhood of the central canal.

Taking into consideration the corresponding groups in connection with the cranial nerves, we have five groups for investigation :

Firstly, the cells of the anterior horn (A in Fig.), which are known to give origin to the large motor nerves, and which are continued cranial-wards as the nuclei of the twelfth, sixth, fourth, and third nerves. These are clearly connected with efferent somatic nerves.

Secondly, three separate groups of cells (c, d, e, in Fig.), viz. Clarke's column, the solitary cells of Schwalbe, and the cells of the intermedio-lateral tract, which all appear to be connected with splanchnic nerves, for the cells of Clarke's column coincide with the outflow of visceral nerves in the spinal cord, form parts of the vagus nucleus, and apparently are continued upwards as the cells of the *locus caeruleus*. The solitary cells of Schwalbe appear to increase largely in number as the vagus nucleus is approached, for which reason they also must be looked on as splanchnic.

The cells of the intermediate lateral tract as pictured by Schwalbe are well defined only in the thoracic region corresponding to the outflow of vaso-motor nerves, and if they exist in the cranial region they may perhaps constitute that group of cells known as the antero-lateral

nucleus in the medulla oblongata which is defined by the observations of Ludwig and his pupils as the vaso-motor centre.

Section of spinal cord in the dorsal region
(slightly modified from Schwalbe).

Thirdly, it is significant that the centres of origin for the motor nerves of the muscles of mastication, deglutition, of expression, of the pharynx and the larynx, should, as is well known, form a well-defined consecutive series in the central nervous system separate from the groups which give origin to the somatic motor nerves; in fact, separate centres of origin for the non-ganglionated efferent nerves of the splanchnic system corresponding to the separate origin of the muscles which these nerves supply.

In the spinal cord this group of nerve cells forms a part of the lateral group of motor cells in the cervical region, and it is doubtless connected with some at all events of the motor fibres of the spinal accessory and with the phrenic nerves.

It is not apparently the same as the smaller cells of the

tractus intermedio-lateralis, and it appears to me suggestive in consideration of the embryonic position of the muscles supplied by this group that in the thoracic region a few larger cells (B in Fig.) should be found connecting the cells of the *tractus intermedio-lateralis* with the cells of the anterior horn proper.

Without speculating further into the functions of the nerves which are probably connected with these different groups of nerve cells, enough has been said to show that not only the nerves themselves but the central nervous system itself is divided, in accordance with the natural division of the body, into somatic and splanchnic segments, and seeing that such segments are only well defined in the head, it was natural to endeavour to see how far the structure of the cranial nerves threw light upon their segmental arrangement.

In connection with this question I had previously noticed a fact which is of importance in estimating the spinal character of the cranial nerves, viz. that the anterior root of a spinal nerve does not necessarily pass free from the posterior root-ganglion. In most of the nerves of such an animal as the tortoise, in the two first cervical nerves of the dog, the fibres of the anterior root pass into the root-ganglion and are mixed up with its cells, so that it is not necessary for a spinal nerve to possess an anterior root, which runs free from the root-ganglion.

We may therefore look on a cranial nerve as built up on the same plan as a spinal nerve, if it possesses a large-fibred splanchnic and somatic efferent portion, a small-fibred splanchnic efferent portion in connection with a vagrant ganglion, and a splanchnic and somatic afferent part in connection with a stationary ganglion, even although the efferent nerves do not run separately from the stationary afferent ganglion.

As yet I have not finished the investigation of the structure of the cranial nerves, but have seen enough to satisfy myself that they were originally built up on the same plan as the spinal nerves.

If we leave out of consideration the nerves of special sense, viz. the optic, olfactory, and auditory, we find that the remaining nerves fall naturally into two groups :

1. A foremost group, which in man are almost entirely efferent, viz. oculo-motor, trochlearis, abducens, motor part of trigeminal, and facial.

2. A hindmost group of nerves of mixed character, viz. glosso-pharyngeal, vagus, spinal accessory, hypoglossal, and sensory part of trigeminal.

The nerves of the first group resemble spinal nerves in their anterior roots, for they contain a large-fibred efferent portion which supplies voluntary muscles, both of the splanchnic and somatic systems, and a small-fibred efferent portion connected with vagrant ganglia. In the oculo-motor nerve these bundles of small fibres are especially well seen, for they separate out from the large fibres supplying the striated muscles of the eye, and pass into the oculo-motor ganglion, from whence they pass along the short ciliary nerves to supply the sphincter and ciliary muscles. In the trochlearis nerve groups of small fibres are also found, but as yet I have not traced them to any vagrant ganglion. In the motor part of the trigeminal the small fibres are probably in connection with the *ganglion nasale*, while in the abducens nerve it is doubtful whether such groups of small fibres exist, this nerve being probably the somatic portion of the motor part of the trigeminal. In the facial the groups of small fibres compose the main part of the *nervus intermedius*, and pass into the *ganglion geniculatum*.

They resemble them also in their posterior roots, inso-much as they possess a ganglion near the place of exit of the nerves from the central nervous system. There is, however, a great difference between the root-ganglion of these nerves and that of an ordinary spinal nerve, for in their case neither the ganglion cells nor the nerve-fibres in connection with them are any longer functional ; both nerve fibres and nerve cells are phylogenetically degenerated, so that a characteristic arrangement of connective-

tissue elements is all that is left to show where the nerve-structures have formerly been (see Pl. II).

This foremost group, then, of cranial nerves is composed of at least four complete segmental nerves built up on the same type as the segmental spinal nerves, and all characterised by the peculiarity that the afferent roots with their root-ganglia have undergone degeneration. These four segmental nerves are oculo-motor, trochlearis, motor part of trigeminal together with abducens, and facial.

The nerves of the second group are also formed on the same plan as a spinal nerve; here, however, no loss of any component has occurred, but rather there is good evidence that a group of at least five segmental nerves has been split up, so that the various components which characterise fully-formed segmental nerves have become separated from each other in their exit from the central nervous system, though still arising each from its appropriate group of nerve cells in the central nervous system; a scattering which is associated with an extensive origin and an extensive distribution. The nerves of this group in fact arise partly from spinal and partly from cranial regions, and are distributed over a wide area in connection especially with the alimentary canal. The different components of the group are arranged somewhat as follows:

1. The ascending root of the trigeminal, together with the auricular branch of the vagus, contains the somatic afferent nerves. The ganglion of these nerves is mainly the Gasserian ganglion.

2. The ascending root of the glosso-pharyngeal and vagus nerves contains the splanchnic afferent fibres with the *ganglion jugulare* for its stationary root ganglion.

3. The hypoglossal and probably part of the spinal accessory form the somatic efferent portion.

4. The large motor nerves of the glosso-pharyngeal (?), vagus, and spinal accessory (in part) form the splanchnic, non-ganglionated, efferent fibres.

5. The small fibres of the glosso-pharyngeal, vagus, and spinal accessory with the *ganglion petrosum glosso-*

pharyngei, and *ganglion trunci vagi* for their motor ganglia form the splanchnic ganglionated efferent fibres.

Thus we see that this second group is characterised not by a loss of any component but by a splitting up of the group into its separate components, a splitting up which, in all probability, is associated with the making good of the loss of those parts which was the cause of the phylogenetic degeneration so characteristic of the first group of cranial nerves.

We see then clearly that the cranial nerves, with the exception of the nerves of special sense, are built up on the same plan as the spinal nerves, but are divisible into two groups, the meaning of which remains yet to be seen.

When we have a clear conception of the change which has occurred in the past history of the vertebrate animal by which the peculiarities of these two great groups of cranial nerves have been brought about, then we shall be able to speak clearly and definitely about the number of cranial segments; at present I can only say that I hope before long to offer an explanation of the meaning of these lost parts, which I sincerely trust will receive the same kind consideration as you have given to-night to the somewhat speculative views which I have had the honour of laying before you.

(For report of the discussion on this paper, see 'Proceedings of the Royal Medical and Chirurgical Society,' New Series, vol. ii, p. 402.)

DESCRIPTION OF PLATE II

On the Relations between the Function, Structure, Origin, and Distribution of the Nerve-Fibres which compose the Spinal and Cranial Nerves (WALTER HOLBROOK GASKELL, M.D., F.R.S.).

The sections are all carefully drawn from osmic acid preparations of the nerves of man.

FIG. 1.—Transverse section of rootlet of third cranial nerve to show degenerated ganglion. (Zeiss A, Oc. 4.)

FIG. 2.—Three transverse sections of fourth cranial nerve (Zeiss A, Oc. 2):

- a. Section near exit of nerve from valve of Vieussens, showing degenerated tissue arranged so as to form a sheath around the functional medullated nerve-fibres.
- b. Section of nerve farther away from point of exit, showing the formation of the degenerated ganglion.
- c. Section of nerve peripheral to the ganglion. The degenerated tissue has almost entirely disappeared.

FIG. 3.—Transverse section of seventh cranial nerve to show degenerated ganglion. (Zeiss A, Oc. 2.)

FIG. 4.—Longitudinal section of a rootlet of third cranial nerve to show the structure of the degenerated material. (Zeiss D, Oc. 2.)

Fig. 1.

Fig. 2. a.

Fig. 2. b.

Fig. 3.

Fig. 2. c.

Fig. 4.