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ON THE NERVOUS SUPPLY OF THE DOG'S HEART. By LIM BOON KENG, M.B. (Pl. XXV.)

(From the Cambridge Pathological Laboratory.)

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I. Introductory.

The anatomy of the cardiac nerves of the dog is perhaps of more interest to the physiologist than to the morphologist. At all events it was with that belief that I made the dissections on which the following communication is based. It appeared to me that with the improved methods of investigation applicable to the study of the mammalian heart which are being gradually introduced, a fairly complete account of the macroscopic anatomy of the cardiac nerves of the dog ought to be at the disposal of physiologists. This at the present time does not exist. While the functions of these nerves have been more or less fully investigated, their anatomy has been comparatively neglected. All the important cardiac nerves have been described long ago but as a rule only as a side issue to other subjects. Of recent papers that of Schmiedeberg¹ on the innervation of the heart is the most important, but he only described in detail the trunks of the cardiac nerves on the right side.

Scattered through the literature of the physiology of the heart, partial descriptions of the anatomy of the cardiac nerves in the dog are to be found, but nowhere as far as I can learn, is there available a tolerably complete account of the origin and course of the various nerves, which bind together, so to speak, the heart and the rest of the organism. Much of what I have to say must be known to those investigators of the physiology of the heart, who have taken the trouble to dissect out with sufficient care the cardiac nerves in a dozen or more dogs, and in my attempt to give a coherent account of the subject I am well aware that I must necessarily make statements which will be wanting in novelty to some physiologists. As, however, it is my object to describe the cardiac nerves as a whole, a certain amount of repetition cannot well be avoided.

Where it appeared desirable I have indicated how far the cardiac nerves of the dog correspond morphologically to those of man, of the rabbit and of the cat, and I have sought to keep in mind what is known of the function of the various nerves that enter or leave the heart.

The dissections were made chiefly on fresh specimens, though for the display of the delicate nerve filaments that form the plexuses, a special mode of preservation was adopted. The trunk of the animal was severed just below the diaphragm and the anterior half was allowed to bleed. The diaphragm was then removed and the aorta was injected with spirit or Müller's fluid. After a day or two, a rough dissection was made; and by means of a sponge, the part was wetted with some fat solvent such as benzole. By this method, it is comparatively easy to trace the delicate nerve fibres to their ultimate distribution; and if

¹ Ber. d. sächs. Ges. d. Wiss. 1871, p. 148.

Müller's fluid has been used, the nerves have an olive green tint that distinguishes them from connective tissues.

II. The Vagus and Sympathetic.

We do not propose here to deal elaborately with the anatomy of the vagus and the sympathetic, but will merely allude to such well-known facts or criticise such accepted opinions as concern the cardiac nerves. In the dog, the vagus and sympathetic nerves are united within one common sheath along nearly the whole length of the neck, and constitute the vago-sympathetic trunk; but they undoubtedly can be separated both anatomically and physiologically: shewing that the nerve fibres do not intermix to any extent.

The Vague. (Pl. XXV. Fig. 1., vag, vago. S.) Arising by about a 1. dozen fine roots from the ventro-lateral aspect of the medulla, the vagus passes outwards accompanied by the spinal accessory nerve to the iugular foramen. We do not seem to possess any experimental knowledge of the functions of these roots though they are not beyond reach in the living animal. If the lower jaw of one side be dislocated and removed, and the muscles attached to the skull on that side be cut away,-vessels being carefully ligatured-the base of the skull will be exposed and the large tympanic bulla will be our guide. With bone forceps or trephine remove the cranial bones above the bulla, and then cautiously clip off bit by bit the bony wall of the jugular canal. In such a dissection the roots may just be visible and for experimental purposes it may be advisable to remove the basi-occipital bone; and in doing this the easiest plan is to cut the nerve roots on one side. When the dissection is completed, the nerve roots on the intact side are It need scarcely be said that the operation is readily accessible. laborious and extremely apt to be fatal.

In the jugular canal, the vagus develops a swelling—the jugular ganglion (Pl. XXV. Fig. 1, J. G.), at which the spinal accessory nerve joins it. Immediately after emerging from the skull, the vagus presents another ganglion, which is fusiform in shape and in a fairly large dog about 1 cm. in length (Fig. 1, T. G.). The last mentioned ganglion is usually known as the ganglion of the trunk, and lies immediately internal to the huge tympanic bulla. From the caudal end or sometimes from the middle of the trunk ganglion, the vagus gives off the superior laryngeal nerve, slightly behind which a large nerve is seen passing from the trunk of the vagus to the superior sympathetic ganglion. This nerve is in reality the main cord of the cervical sympathetic chain. If it be desired to stimulate the vagus proper apart altogether from the sympathetic, then it is obviously necessary to expose the region which we have just referred to. The operation is not difficult and in our experience always successful. The way which is probably easiest in the end is to remove the lower jaw of one side and to expose as before the tympanic bulla-and pulling outwards the sternomastoid, the vagus, which contains fibres received from the spinal accessory, can be separated for 1 inch or more from the sympathetic cord, and can thus be stimulated without difficulty. Posterior to the trunk ganglion of the vagus, the vago-sympathetic runs caudalwards as a large nerve dorsal to the common carotid artery. Slightly above the level of the first rib or opposite it, there is a ganglion (Fig. 1, M. S. G.) on the vagosympathetic; and this is usually called the "inferior cervical ganglion." It is hardly necessary to say that the ganglion belongs to the sympathetic system and not to the vagus. It is not, however, the inferior cervical sympathetic ganglion for, from a morphological point of view, it is obviously the middle ganglion of the sympathetic. We shall reserve what we have further to say on this point when we come to discuss the sympathetic system. The vagus lies on the dorsal aspect of the common carotid artery and is in contact with the prevertebral muscles of the neck. With the artery, it is therefore under cover of the sterno-mastoid muscle. At the root of the neck the right vague is nearer to the cosophagus than the left and posterior to the middle ganglion of the sympathetic (i.e. the so-called inferior cervical ganglion) the relative position of the two vagi differing as in man. The left nerve is in a plane more ventral than that in which the other nerve lies. Tt is distributed partly to the ventral and partly to the dorsal aspect of the heart, whilst the right vagus is entirely destined for the deep cardiac plexus which is connected with the dorsum of the heart.

Both vagi however pass caudalwards in their course dorsal to the roots of the lungs on which they give off branches to form the pulmonary plexuses.

At the base of the skull, the vagus on each side receives various communications, but of these, the most important is that from the spinal accessory nerve, to which we have referred (Fig. 1, XI). The medullary portion of the spinal accessory passes to the heart through the trunk ganglion and thereafter in the substance of the vagus. The spinal part of the nerve leaves the vagus almost at the point of junction of the two nerves, and is distributed to certain muscles in the neck.

From the middle, or sometimes, caudal end of the ganglion of the trunk, proceeds the superior larvngeal nerve, which crosses the side of the pharvnx to reach the anterior border of the thyroid where it divides into an anterior and a posterior half (Fig. 1, S. L.). The latter (Fig. 1, C.), runs caudalwards under cover of the ala of the thyroid cartilage, and emerging posteriorly, it runs on the cricoid cartilage external to the recurrent laryngeal nerve. It is often lost in the last mentioned nerve, but sometimes can be distinctly traced to the deep cardiac plexus. Tt will be convenient to speak of all the nerve filaments except one which is posterior to this branch as off-shoots of the vago-sympathetic. The single exception is the recurrent laryngeal nerve. The origin of this branch from the vagus differs on the two sides-on the right it arises close to the middle sympathetic ganglion, whilst on the left, it does so when near the aortic arch, that is, a considerable distance behind the corresponding ganglion of its side (Figs. 3 and 4, R.). From the recurrent nerves, fibres are given off to the cardiac plexuses and are more numerous on the left; but the branches from the right nerve are larger. Usually one of these off-shoots leaves the recurrent in such a manner as to suggest that it is coming from before backwards (Fig. 1, C(?)). And in all probability this represents the backward continuation of the nerve coming from the superior laryngeal¹.

It is impossible to say definitely of the other cardiac fibres whether they belong entirely to the vagus or entirely to the sympathetic. But whilst we call them branches of the vago-sympathetic, we distinctly recognise that occasionally a cardiac nerve may appear to consist entirely of the vagus or of the sympathetic fibres. As a rule, these nerves consist partly of vagal and partly of sympathetic elements. The branches of the vago-sympathetic that came off at or near the middle cervical sympathetic ganglion contain vagal fibres that are the homologues of the superior cardiac branches of the vagus in man, which leave the nerve in the neck. The nerves that arise from the trunk of the vagus posterior to above-mentioned branches represent the inferior cardiac branches in the human subject. Thus in the dog we may say that the vagus has a couple of anterior cardiac and as many posterior cardiac branches of the vagus, but they are usually intermixed with sympathetic fibres.

2. The sympathetic (Fig. 1). We have to consider here only the cervical sympathetic chain. There are theoretically three ganglia, though the inferior cervical sympathetic ganglion is fused with the first

¹ Cf. Howell and Huber. This Journal, Vol. XII. p. 5.

one or two thoracic ganglia to form the ganglion stellatum. The superior cervical ganglion is situated close to the trunk ganglion of the vagus and sends a cardiac branch to the heart. The middle cervical ganglion is called by physiologists "the inferior cervical ganglion"; as it is placed on a level with or slightly above the first rib. It is however undoubtedly the homologue of the middle cervical sympathetic ganglion. It receives a communicating branch from the phrenic or from its roots (Fig. 1, p.); and gives off usually two cardiac branches which also contain-as before mentioned-fibres from the vagus. We purposely omit all mention of topographical details and of other branches. That the inferior cervical ganglion is contained in the ganglion stellatum, is proved by the fact that the last mentioned ganglion (often termed first thoracic) receives roots from the 7th and 8th cervical spinal nerves as well as from the first, second, and third dorsal nerves (Fig. 1, G. St. 1, 2, 3, 4, 5). When, as in man, three cervical sympathetic ganglia are present, the middle receives rami communicantes from the fifth and sixth cervical spinal nerves, whilst the inferior ganglion receives from the seventh and eighth nerves. The roots of the ganglion stellatum vary The ganglion itself is situated opposite the first intercostal in length. space and the shortest root is that from the first dorsal nerve; in front and behind of which the roots successively increase in length (Fig. 1).

The cord of the sympathetic is bound up with the vagus in the greater part of its course in the neck, although near the base of the skull, it may be got at as a separate trunk. Posterior to the middle sympathetic ganglion, it splits in two portions, which embrace the subclavian artery, forming the annulus (or ansa) of Vieussens and constituting the bond of union between the middle cervical sympathetic and stellate ganglia. The shape of the annulus is variable and very frequently the right annulus assumes the form of a triangle whilst the left that of an ellipse (Figs. 1 and 2). The difference is due to the superior intercostal artery on the right arising some distance further caudalwards than the corresponding artery on the other side; and this causes the ventral limb of the right annulus to be connected with the vagus behind the middle sympathetic ganglion, a varying length of the vagus, which forms the base of the triangle intervening (Fig. 3). In the relation of these ganglia to the annulus, we see another morphological evidence in favour of the view that the so-called "inferior cervical ganglion" is really the middle cervical sympathetic ganglion.

Each cervical ganglion may be said to send a branch to the heart (Fig. 1, S.S.G., M.S.G., G.St.); but as before stated the cardiac branches

arising from the vago-sympathetic contain vagal and sympathetic fibres, so that it is undesirable to attempt to assign any individual nerve either to the one or to the other main trunk. One may however prove by dissections that in these cardiac branches, filaments may be traced to the sympathetic ganglia. The largest offshoot comes off from the middle cervical ganglion and represents the ramus cardiacus magnus as seen in man. The cardiac branch of the inferior ganglion is found in the occasional cardiac branch from the ganglion stellatum or from the more constant branch leaving the ventral limb of the annulus; although often enough this nerve has an apparent origin from the vagus and may in this case contain other fibres (Fig. 3, b_i).

Physiological summary. The vagus contains afferent and 3. efferent fibres passing between the heart and the central nervous system. Through the fibres derived from the medullary portion of the spinal accessory nerve, centrifugal impulses pass to the heart affecting primarily the auricles so as to cause a slowing of the heart's action. A depressor nerve probably exists either in the vagus trunk or in the communicating branch of the superior larvngeal. Accelerating fibres reach the heart from the spinal cord through the anterior roots of the second and third (and possibly also the third and fourth) spinal nerves and through the annulus; but it is important to remember that the cardiac branches from the sympathetic arising from the vago-sympathetic trunk close to the middle cervical ganglion are not all "rami accelerantes" because the annulus undoubtedly also contains fibres which have an inhibitory action on the ventricles. The individual cardiac nerves vary somewhat in their physiological character owing to the inconstancy of the distribution of vagus and sympathetic fibres among them; and their functions are as yet imperfectly known.

III. The Cardiac Nerves.

We have already indicated the names and points of origin of the several cardiac nerves and shall now proceed to discuss them in detail beginning first with those which are best known.

1. Cardiac branches of the vago-sympathetic. The reason for not distinguishing the branches of the vagus and of the sympathetic (behind the middle cervical ganglion) has been given. Here it is only necessary to add that the proportions of vagus and sympathetic elements in each nerve vary in different dogs; and that even behind the middle cervical ganglion, it is impossible to say that nerves having an apparent origin from the vagus consist solely of vagus fibres since it is very common to find the ganglion united to the trunk of the vagus by three or four communicating branches (Fig. 2, C.S.). Possibly these fibres may pass to the heart along the posterior branches of the vago-sympathetic. As the cardiac branches on the two sides differ in their course and distribution it is necessary to describe them separately.

Branches of the right vago-sympathetic. Usually two large (a)nerves arise from the right vago-sympathetic at the site of the ganglion or close to it (Figs. 1 and 6, V.S., V.S.); though sometimes three are These represent cardiac branches from the middle cervical present. ganglion and the anterior branches of the vagus. It must be added that often they represent also the cardiac branch of the inferior cervical ganglion (fused in the ganglion stellatum). In some cases only one branch arises from the trunk of the vago-sympathetic whilst the other takes origin from the ventral limb of the annulus. These nerves are usually called "the rami accelerantes," but they may contain fibres which have other functions. They are easily found external and ventral to the subclavian artery in the interval between the innominate vein in front and superior intercostal vein behind (Fig. 3). They run parallel with one another backwards and inwards, lying ventrally to the subclavian and innominate arteries in succession. They then pass to the dorsal region of the aorta. In the greater part of their course they lie dorsal to the superior vena cava and close to or actually on the trachea. Thev come nearer each other as they approach the heart and each gives off one or more communicating branches. The two main nerves soon unite at an acute angle close to the bifurcation of the trachea (Fig. 6). The communicating twig from the anterior of these two nerves joins the cardiac branches coming from the recurrent nerve. The probable nature of these nerves has already been dealt with. The communicating branch of the posterior nerve unites with offshoots from the posterior branches of the vago-sympathetic. If the recurrent nerve is given off from the vagus behind the middle ganglion, its branches unite with both of the nerves in the anterior group of vago-sympathetic branches. Bv this rearrangement and fusion of the nerves, usually two nerves are the result (Figs. 5 and 6, α , β). These form a plexus on the right division of the pulmonary artery and distribute branches to its dorsal and ventral surfaces. At this region the plexus is reinforced by nerves coming from the left vago-sympathetic. The nerves which go to form this plexus send communicating filaments to a plexus on the auricles. From the ventral aspect of the plexus on the pulmonary artery a stout branch passes to the dorsum of the undivided pulmonary trunk, lying in its course in the interval between the aorta and pulmonary artery. On the dorsum of the main pulmonary artery, it unites with one of the ventral branches of the left vago-sympathetic.

The posterior branches of the right vago-sympathetic are two or three in number and contain fibres that are homologous with the inferior cardiac nerves of the vagus and of the inferior cervical sympathetic ganglion in man. That these nerves which have an apparent origin from the vagus do contain sympathetic elements is made probable by the fact that they are sometimes partly represented by a large nerve which arises from the ventral limb of the annulus (Fig. 6, an.). The posterior branches of the vago-sympathetic are usually small nerves and from their distribution may be divided into three groups. The first set supply the dorsum of the pulmonary artery and communicate with the plexus on the auricles. The second are distributed to the vena cava superior and the adjacent parts of the auricle, whilst the remaining nerves can be followed to the root of the right lung, and here they will be found closely investing the pulmonary veins. The nerve twigs of the different sets communicate with one another and with the pulmonary plexus (Fig. 6, $V.S_s$, an.).

(b) Branches of the left vago-sympathetic. The anterior branches of the vago-sympathetic are distributed partly to the dorsal and partly to the ventral aspect of the heart (Figs. 4 and 6, V.I., V.E.). Those that are situated ventrally are quite superficial, when the ventral thoracic wall has been removed and the animal placed on its back. They are usually two in number, although there are sometimes three and more rarely these branches arise by a short common trunk. We shall describe the most frequent arrangement. The two nerves lie internal to the vagus, with which they are at first parallel. They are situated in the interval between the left subclavian and left common carotid arteries. They reach the pericardium after crossing the aortic arch and then continue their course in the substance of the parietal pericardium inclining outwards to reach their destination and at the same time distributing branches to the pericardium. These two branches may therefore be spoken of as internal and external, and the internal nerve is also anterior in regard to its origin. The internal branch reaches the left division of the pulmonary artery at the line of reflection of the pericardium, whilst the external one runs farther caudalwards, arriving on the front of the auricle at the point where the pericardium passes on to the surface of the heart. The internal nerve continues its course on the ventral surface of the left division of the pulmonary

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artery just outside the portion usually enveloped in fat. It then runs round the posterior margin of the vessel to reach the dorsum of the main trunk of the pulmonary artery on which it forms a plexus with nerves from the right side (Fig. 6). This plexus may be called the central plexus for convenience. The internal nerve supplies the aorta and pulmonary artery as well as the auricles. The offshoots that go to the auricles pass dorsally through the interval between the aorta and the pulmonary artery.

The external branch, as we have seen, reaches the front of the auricle close to the entrance of the pulmonary veins. It gives off branches while in the pericardium not only to that membrane but also to the ventral surface of the pulmonary artery and aorta as well as to the dorsum of the auricles. The deep branches, which reach the auricles are the largest and penetrate the areolar tissue lying between the pulmonary artery and the anterior pulmonary veins. The branches on the pulmonary artery break up into fine twigs which communicate with the pulmonary plexus and other nerves ramifying on the vessel. The continuation of the external nerve lies embedded in a prominent but narrow streak of fat, and, following the direction of the coronary vein, reaches the auriculo-ventricular sulcus on the left margin of the heart. It then accompanies the terminal portion of the left coronary artery and is distributed to the dorsal aspects of the left auricle and ventricle reaching ultimately the posterior interventricular sulcus. This nerve therefore supplies the outer half of the ventral and dorsal surfaces of the left auricle and left ventricle as well as the parts of the two ventricles adjacent to the posterior interventricular sulcus.

As already indicated, there is sometimes a third ventral branch; which is a delicate filament distributed to the pericardium, aorta and pulmonary artery. The two usual nerves have the general arrangement above described except that their branches to the last mentioned parts may be fewer in number, smaller in size or altogether wanting. Occasionally the third nerve sends a branch to the dorsal aspect of the pulmonary artery. Sometimes the third branch or when it does not exist, the external nerve may take its origin directly from the ventral limb of the annulus (Fig. 2, C. V.).

The branches of the left vago-sympathetic that are distributed to the dorsum of the heart are two in number, though sometimes only one is present (Fig. 6, D.). When two are to be found, one generally arises directly from the middle cervical sympathetic ganglion and runs towards the middle line on the cosphagus and trachea. It fuses with cardiac nerves coming from the neck (branches of the superior sympathetic ganglion and superior laryngeal nerve) and being thus augmented, continues in its course, until it is joined by its companion, which arises from the trunk of the ganglion near the origin of the recurrent nerve. The nerves of the dorsal set are thus collected in one bundle, which either communicates with the plexus on the front of the right division of the pulmonary artery or contributes to the formation of the central plexus. Either individually or conjointly after their fusion these dorsal nerves of the vago-sympathetic give off deep branches that go to the auricles.

2. Cardiac branches from the Annulus of Vieussens. These have already been noticed partially and therefore may be briefly dealt with. They contain accelerator fibres and also fibres having other functions. They represent at least in part the cardiac branch of the inferior cervical ganglion (Figs. 2 and 3, C. V., b_{4} .).

(a) Branch of right annulus. This nerve is more frequently present than its companion on the other side, and is distributed to the deep cardiac plexus, right auricle and root of right lung (see Section III. 1, a.).

(b) Branch of left annulus. This is only occasionally met with and supplies the ventral aspect of the left side of the heart, taking the place of some of the branches of the vago-sympathetics, which represent it in its absence (see above Section III. 1, b.).

3. Cardiac branches of the Recurrent nerve. Each recurrent nerve is provided with cardiac branches. Those on the right are usually grouped into a large trunk, but those on the left proceed individually to the heart. Thus it appears that the left recurrent has more numerous off-shoots. The greater number of twigs from the left nerve pass to the auricle, while some go to the dorsum of the aorta, to the pulmonary artery, and possibly also to the nerve plexus between the aorta and pulmonary artery (Figs. 1, C. R. L., 2, b_1 , 5 and 6, C. R. L.).

4. Cardiac branches having an apparent origin from the vagus behind the Middle Cervical Sympathetic ganglion. These have been described (see Section III. 1.) as posterior branches of the vago-sympathetic.

5. Cardiac branches of the Cervical Sympathetic ganglia. These nerves have been fully treated and it need only be said that the superior cervical ganglion alone possesses a cardiac branch which is apparently unmixed with any vagus fibres. This nerve runs with the sympathetic fibres that accompany the superior laryngeal nerve to the larynx, and lies alongside the recurrent nerve by the side of the

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trachea, being ultimately lost in union with branches of the vagosympathetic (see above Section III. 1, a, b.).

6. Cardiac branch from Superior Laryngeal (see Section II. 1.).

IV. The Cardiac Plexuses.

The cardiac plexuses in the dog as in mammalia generally arrange themselves in two groups—(1) the ventral or superficial cardiac plexus formed by the vago-sympathetic of the left side; (2) the dorsal or deep cardiac plexus, deriving its nerves from the vago-sympathetic nerves of the right and the left.

1. The Superficial Cardiac Plexus (Fig. 4, Pl. XXV.). The ventral branches of the left vago-sympathetic form a sort of plexus on the ventral aspect of the aorta and the front of the right auricle. The nerve filaments communicate with the left pulmonary, the coronary and deep cardiac plexuses.

2. The deep Cardiac Plexus (Figs. 5 and 6). All the cardiac branches of the right side, and the dorsal cardiac twigs of the left vago-sympathetic are united in a plexus on the dorsum of the heart, opposite the bifurcation of the trachea and the concavity of the aortic arch. This plexus has ramifications surrounding the divisions of the pulmonary artery and may be described as consisting of two portions, (a) the central plexus and (b) the dorsal auricular plexus (Fig. 6).

(a) The Central Plexus. This network of nerve fibres is situated on the dorsal aspect of the main trunk of the pulmonary artery and is formed by the communicating branch of the plexus lying on the right division of the pulmonary artery, and by the ventro-internal branch of the anterior set of cardiac nerves, arising from the left vago-sympathetic. It gives off numerous branches but one of these-by far the largest,runs caudalwards in apparent continuation of the course of the cardiac nerve of the left side. This nerve runs along the dorsum of the pulmonary artery and passing gradually to its left side, runs on the surface of the auricle to reach the anterior interventricular sulcus. It distributes branches therefore to the median half of the ventral surface of the left auricle and of both ventricles. The smaller branches of the plexus supply the auricle and ventricle of the right side. Some of these pass between the aorta and pulmonary artery, supplying the region between these and then emerge on the right side, accompanying the small right coronary artery and running in the right auriculo-ventricular groove. The fibres supplying the median portion of the right auricle reach as

far as the entrance of the superior vena cava. Other smaller branches of the central plexus surround the large left coronary artery and follow it as far as the left margin of the heart. Thus it is obvious that almost all the cardiac nerves converge towards the position of this plexus and from it radiate in all directions nerves of the greatest functional significance—hence I feel justified in calling this plexus by the name "Central" for convenience of reference as well as for the sake of brevity.

(b) The auricular portion of the deep cardiac plexus (Fig. 5) lies on the auricles close to the trachea, between the pulmonary veins of the two sides, having connections with nerves on the auricles beyond this region. It is a direct continuation of the plexus on the dorsum of the pulmonary artery and its branches. The plexus is a very complicated one and consists of very fine filaments derived from cardiac nerves on both sides.

3. The Coronary Plexuses. These are largely composed of branches of the deep cardiac plexus but also contain fibres from the ventroexternal branch of the left vago-sympathetic. These plexuses surround the coronary arteries, and as the nerves have already been described, it is not necessary to repeat the description. It may be noted however that the left coronary artery is accompanied by nerves partly from the superficial and partly from the deep cardiac plexus. The right plexus is entirely a derivative of the central plexus. The importance of these plexuses is undoubtedly very great, but unfortunately we as yet have no knowledge of their functions.

4. Nerve Ganglia. The cardiac plexuses are well provided with ganglia especially on the auricles and in the region between the aorta . and the pulmonary artery. The nerves on the superior vena cava also present ganglionic enlargements. The distribution of the cardiac ganglia is probably similar to that in the heart of other mammals such as the horse or ox; and I made no attempt to study their exact distribution in the dog.

V. The distribution of Nerves on the heart.

1. Nerve supply of the Auricles. From the foregoing details, it must have been obvious that there is some sort of symmetry in the distribution of the cardiac branches of the two sides. Each auricle has its outer portion supplied by the vago-sympathetic of its own side. On the right the nerves are derived from the vagus behind the middle cervical sympathetic ganglion while on the left, they are filaments from the ventro-external branch of the left vago-sympathetic. The mesial half of each auricle on its ventral aspect receives its nerve supply from the central plexus, which, as we have seen, is a part of the deep cardiac The remaining portion of the auricles is that in the dorsal plexus. region between the pulmonary veins of the two sides. This area is covered by the auricular plexus, which has been described. Thus it is clear that the mesial half of each auricle is supplied by nerves derived from plexuses formed by the cardiac nerves of both sides. The interauricular septum probably receives fibres from the auricular and central divisions of the deep cardiac plexus-at least it is quite easy to trace fibres from the latter to it.

2. Nerve supply of the Ventricles. The left ventricle receives its nerves chiefly from the vago-sympathetic of the same side through the ventro-external cardiac branch; and partly also from the left coronary plexus and other branches of the central plexus. The right ventricle is supplied almost entirely by the deep cardiac plexus; but this is what one would expect inasmuch as the central plexus receives all the nerves of the right side. The right ventricle obtains its nerves from the right coronary plexus and the big branch of the central plexus in the anterior inter-ventricular groove. On the dorsal aspect, both ventricles are supplied by the continuation of the ventro-external branch of the left vago-sympathetic, and by off-shoots from the auricular plexus.

Nerve supply of the heart as a whole (Figs. 5 and 6). Each half 3. of the heart is supplied therefore by nerves derived from nerve trunks on both sides of the body. A careful study of the formation of the , central plexus brings home to one the importance of this fact, which doubtless accounts for the power of either vago-sympathetic to influence the action of the heart. The outer side of each half of the heart may be represented as supplied mainly by nerves of the corresponding side, but in the mesial region, it is necessary to separate the auricles from the ventricles. In the case of the auricles, the mesial half of both is supplied by the nerves of both sides of the body; but the ventricles have a slightly different arrangement. The mesial half of both ventricles is supplied in the ventral region by filaments derived from the nerves of both sides, but on the dorsal aspect the ventricles receive their supply mainly from the left vago-sympathetic, through its ventroexternal branch.

VI. Conclusion.

We may now briefly state a few of the results of our studies. Some of the following conclusions are of general application.

(1) The cardiac nerves on each side supply partly the auricle and ventricle of the corresponding side, and partly the median half of the auricle and ventricle of the opposite side.

(2) Afferent impulses may reach the central nervous system by various paths, and it does not appear that a separate depressor nerve such as that in the rabbit and cat, exists in the dog. Its analogue may be present in the vagus trunk.

(3) The cardiac nerves in different dogs differ in significance in different animals owing to the varying proportions of sympathetic and vagus fibres they contain.

(4) The blending of the various nerves becomes more and more intimate the nearer we approach the heart, and hence to obtain pure vagus or pure "augmentor" action, it is desirable to stimulate the nerves as near their origin as possible or even to stimulate the nerve roots through which they leave the brain and spinal cord. It may be said therefore that the nerve roots and rootlets are functionally simple, although from each may proceed fibres to parts which are anatomically at some distance from one another. As the nerves approach the periphery they become more complex in function and more simple in their anatomical distribution.

(5) Though individual cardiac nerves in the dog may have no apparent resemblance with those of other animals, it is obvious from the foregoing account, that there is a close similarity between them when the nerves are considered as a whole from a morphological point of view.

EXPLANATION OF FIGURES.

Fig. 1. The Vagus and Sympathetic nerves of the Right side. An, Annulus of Vieussens; C. communicating branch of Inferior Laryngeal nerve; C(i) probably continuation of C; C.br. Cardiac branch of Superior Sympathetic ganglion; C.R.L. Cardiac branch of Recurrent nerve; $C_V C_{VI} C_{VII} C_{VIII}$ Cervical spinal nerves; $D_1 D_2 D_3$ dorsal spinal nerves; d dorsal limb of annulus; G.St. ganglion stellatum; J.G. Jugular ganglion; M.S.G. Middle Cervical Sympathetic ganglion; M. Medullary portion of XI. nerve; Ph. Phrenic nerve. p. communicating branch of the same. R.L. Recurrent Laryngeal nerve. S.L. Sup. Laryngeal nerve; Sp. Spinal portion of XI. nerve; T.G. Trunk ganglion; $V.S_1$, $V.S_2$, $V.S_3$, $V.S_4$ Cardiac branches of Vago-Sympathetic; v. ventral limb of annulus; X. vagus XI, Spinal accessory; 1, 2, 3, 4, 5, roots of ganglion stellatum.

Fig. 2. Left Vago-Sympathetic and Annulus. C.S. Communicating branches of Middle Sympathetic ganglion. $C.V_1$, C.V. Ventral branches of Vago-Sympathetic.

Fig. 3. Right Vago-sympathetic and annulus. A.I. Innominate artery, $b_1b_2b_3b_4$ Cardiac branches. C.D. Right Carotid, C.S. Left Carotid. I.M. Intern. Mamm. art. I.T. Inferior Thyroid art. S.I. Superior intercostal. Sub. Subclavian artery.

Fig. 4. Ventral branches of Left vago-sympathetic and Superficial Cardiac plexus. Ao. Aorta, App. Appendix auriculæ, A.V.S. Auriculo-Ventric. sulcus. C.E. Central Plexus. C.S. Left Carotid artery. *i.v.* inter-ventricular sulcus. P.A. Pulmonary artery, P.C.S. Left Coronary Plexus. R. Recurrent nerve. V.E. Ventro-External branch. V.I. Ventro-internal.

Fig. 5. Auricular portion of deep Cardiac plexus seen from the back. L.A. Left auricle. L.V. Left ventricle. R.A. Right auricle. R.V. Right ventricle. a. continuation of $V.S_1$ to front of Pulmonary artery. β . ventral branch of $V.S_2$. Co. Communicating branch passing to the ventral surface between pulmonary artery and veins. For other letters see Fig. 1; * indicate that branches pass to the ventral aspect. V.E.S. Ventro-external branch of Left Vago-sympathetic.

Fig. 6. Central Plexus. an. Cardiac branch from Right annulus. D. dorsal branch of Left vago-sympathetic. D.I.S. Dorsal interventricular sulcus. P.Cor.D. Right Coronary, P.Cor.S. Left Coronary Plexus. P.V. branch of an. to pulmonary vein. V.C.S. branches of $an = V.S_4$ in Fig. 1, also compare $V.S_3$ in Figs. 1 and 6. R^1 branch of the middle sympathetic ganglion to join the Recurrent nerve. *.ex.* branches of the same to Innominate artery. Other letters are same as Figs. 1 and 4. Dotted lines indicate that the nerves are behind the Pulmonary artery (P.A.).

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