

The distal vagal ganglion of the hen (*Gallus domesticus*). A histological and physiological study*

G. K. WAKLEY† AND A. J. BOWER

*Department of Human Biology and Anatomy, University of Sheffield,
Sheffield S10 2TN*

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INTRODUCTION

In 1975 Bower, Molony & Brown published details of an autoradiographic method to demonstrate selectively afferent nerves in the respiratory tract of the domestic hen. Their method relied on the assumption that the distal vagal ganglion of the hen contains only sensory neurons. This implies that the ganglion is the avian homologue of the inferior vagal (nodose) ganglion of the mammal. Although there is a general agreement that the nodose ganglion is a sensory ganglion, doubts have been expressed. Gaskell (1886), Holzmann & Dogiel (1910), Möllgaard (1912), Kidd (1914), Köreisa (1931), Kiss (1931, 1932), Morgan & Goland (1932), Jones (1932, 1937) and Heinbecker & O'Leary (1933*a, b*) all suggested that the nodose ganglion contains multipolar efferent cells and that it should be considered a mixed autonomic ganglion. However, no convincing histological evidence for the presence of either multipolar cells or synapses has been found. Köreisa (1931), Morgan & Goland (1932) and Heinbecker & O'Leary (1933*a, b*) claimed to have physiological evidence which pointed indirectly to the presence of efferent cells in the nodose ganglion but this evidence has not been confirmed by the majority of workers. Very little work has been performed on the avian distal vagal ganglion but there are three main points in favour of its homology with the nodose ganglion: (1) the (unsatisfactory) histological evidence available suggests that the cell types of the two ganglia are similar. (2) In the bird, branches to the aorta are said to leave the vagus at the ganglion (Nonidez, 1935) which is analogous to the situation in some mammals (Douglas & Ritchie, 1956). (3) The unusual thoracic position of the distal vagal ganglion may be explained by the elongation of the neck of the hen. Other structures normally cervical in position in mammals (e.g. bifurcation of the common carotid artery, position of the thyroid gland) in the hen are also found in the thoracic inlet.

The present work was undertaken to (*a*) provide a morphological description of the types of neuron present in the avian ganglion, (*b*) show whether there is evidence for an efferent function in this ganglion and (*c*) thereby determine whether the distal vagal ganglion is homologous with the nodose ganglion.

* Reprint requests to A. J. Bower.

† Present address: University Department of Orthopaedics and Accident Surgery, Royal Liverpool Hospital, Prescot Street, Liverpool L7 8XP.

MATERIALS AND METHODS

Histological survey

Thirteen birds (Shaver Starcross 585 hybrids) were used for this part of the study. Four were used for cell counts of the distal vagal ganglion and nine for cell counts combined with morphological studies of the cells present. After the birds had been killed, lengths of the right and left vagi extending about 2 cm cranial and caudal to the thyroid gland were removed and mounted under light tension on pieces of cardboard. Material for cell counts was fixed in 10 % formol saline and the material for morphological studies immersed in Susa fixative (Drury & Wallington, 1967). The nerves were embedded in paraffin wax, and were cut transversely at 15 μm for cell counts and longitudinally at 25 μm for morphological studies.

For cell counts the ganglia were serially sectioned. To determine the extent of the ganglion every tenth section was mounted on a slide, stained with toluidine blue and examined under the microscope. When the ganglion was located every other section was mounted, stained and examined at a magnification of 600 diameters. All neuron profiles with nuclei were counted and the totals multiplied by 2 to give the final totals (Konigsmark, 1970). In this way four left and two right ganglia were examined. In addition five of the ganglia (two right, three left), longitudinally sectioned for morphological studies, were used for cell counts.

To study the morphology of the neurons, serial sections were mounted on slides and impregnated using Holmes' (1947) silver nitrate method. Sections from the lowest cervical sympathetic ganglia of one bird were also stained, using this method, to test the ability of the stain to detect the presence of multipolar cells. The cell diameters were measured by examining cells at a magnification of 1500 and using an eyepiece graticule. The search for multipolar cells was carried out by examining the sections at $\times 600$ and using an eyepiece graticule to ensure that every section of the field was looked at. Any neuron which looked as if it might be multipolar was re-examined at $\times 1500$. A total of eleven ganglia was so examined.

Physiological studies

Twelve hens were used for this part of the study. A chronic vagotomy cranial to the distal vagal ganglion will cause the efferent fibres originating from the brain stem to degenerate but leave the cell bodies in the ganglion and their distal fibres intact. Thus if any efferent effects are seen when the vagus nerve is stimulated at the level of the distal vagal ganglion, in the presence of a chronic vagotomy proximal to the ganglion, this may be due to the presence of efferent cells in the ganglion. The hens were anaesthetised with intravenous pentobarbitone sodium, the right vagus (six cases) or the left vagus (six cases) exposed in the neck and at least a 1.0 cm section of nerve removed. The cut ends of the nerve were ligatured, the wound sutured and the animal allowed to survive for periods ranging from 12–38 days. At the end of the survival period the animal was anaesthetised with intravenous 70 % urethane and the intact and operated nerves exposed either in the cervical region (six cases) or at the level of the distal vagal ganglion (six cases). In the latter cases the operative approach demonstrated by Bower & Parry (1978) was used. To prevent effects due to vago-vagal reflexes (Harper, Kidd & Scratcherd, 1959), all animals had the operated and intact vagus nerves severed high in the cervical region and the stimuli were applied distal to the cut. The nerves were placed over a pair of silver

Table 1. Showing the number of neurons in the left and right distal vagal ganglia

Animal No.	Right	Mean	Animal No.	Left	Mean	Total mean
*6	6244		*10	6334		
15	5343	6165	*11	6590		
18	6192	± 365	14	6657	7020	6710
*20	6882		*15	8235	± 268	± 227
			17	7557		
			18	6904		
			*21	6864		

The asterisk indicates that the animal had a vagotomy proximal to the distal vagal ganglion.

stimulating electrodes connected to a Devices digitimer stimulator. The nerves were stimulated with square wave pulses of 1 or $\frac{1}{2}$ millisecond width at 20-40 volts at a frequency between 5-50 Hz. The site of stimulation was either: (1) cranial to the distal vagal ganglion, to test the hypothesis by Heinbecker & O'Leary (1933*b*) that there are efferent pseudo-unipolar cells; (2) on the ganglion, to check if there were any efferent cells present; (3) caudal to the ganglion, to check that there were no efferent cells in its vicinity. Blood pressure was monitored by exposing a common carotid artery in the thoracic inlet and inserting a cannula connected to a pressure transducer (S.E.M. 4/88, S.E. Labs). The impulse was amplified by an E.M.M.A. amplifier (S.E. Labs) and displayed on a chart recorder (Bryans 28000). Gastro-intestinal motility was monitored by inserting a Foley catheter into the gastro-intestinal tract and filling the balloon with 15-20 ml of saline at 30 °C. The pressure was recorded by connecting the catheter to the apparatus described above. The precise location of the tip of the catheter was determined by post mortem examination immediately after the experiment.

RESULTS

Histology

It has previously been reported that the distal vagal ganglion is not always obvious as a distinct swelling (Choudray, 1953; Parker, 1975). We can confirm that observation. Occasionally it has to be located by noting a slight increase in vascularity of the nerve and by the relationship of the ganglion to other thoracic viscera such as the thyroid gland. The lengths of the ganglia varied considerably, ranging from 3.25 to 8.75 mm with a mean of 5.5 mm (\pm S.E. 0.28, $n = 17$). The difference in length was found to be due to the packing density of the cells rather than differences in the numbers of neurons present. The total number of neurons was found not to vary significantly between left or right ganglia, or between ganglia taken from operated or unoperated nerves. These numbers have been pooled to give a grand mean of 6710 ± 227 ($n = 11$). The full results are shown in Table 1.

Morphology of the cells

In determining the types of neurons present in the distal vagal ganglion five categories were used. (1) Apolar. These were any nucleated profile with no visible processes. These were the result of the plane of section being such that the processes were missed. They formed 13% of the population of neurons and had a mean diameter of 30 μ m (\pm S.E. 1.21, $n = 23$) (Fig. 1A). (2) Pseudo-unipolar. These were the

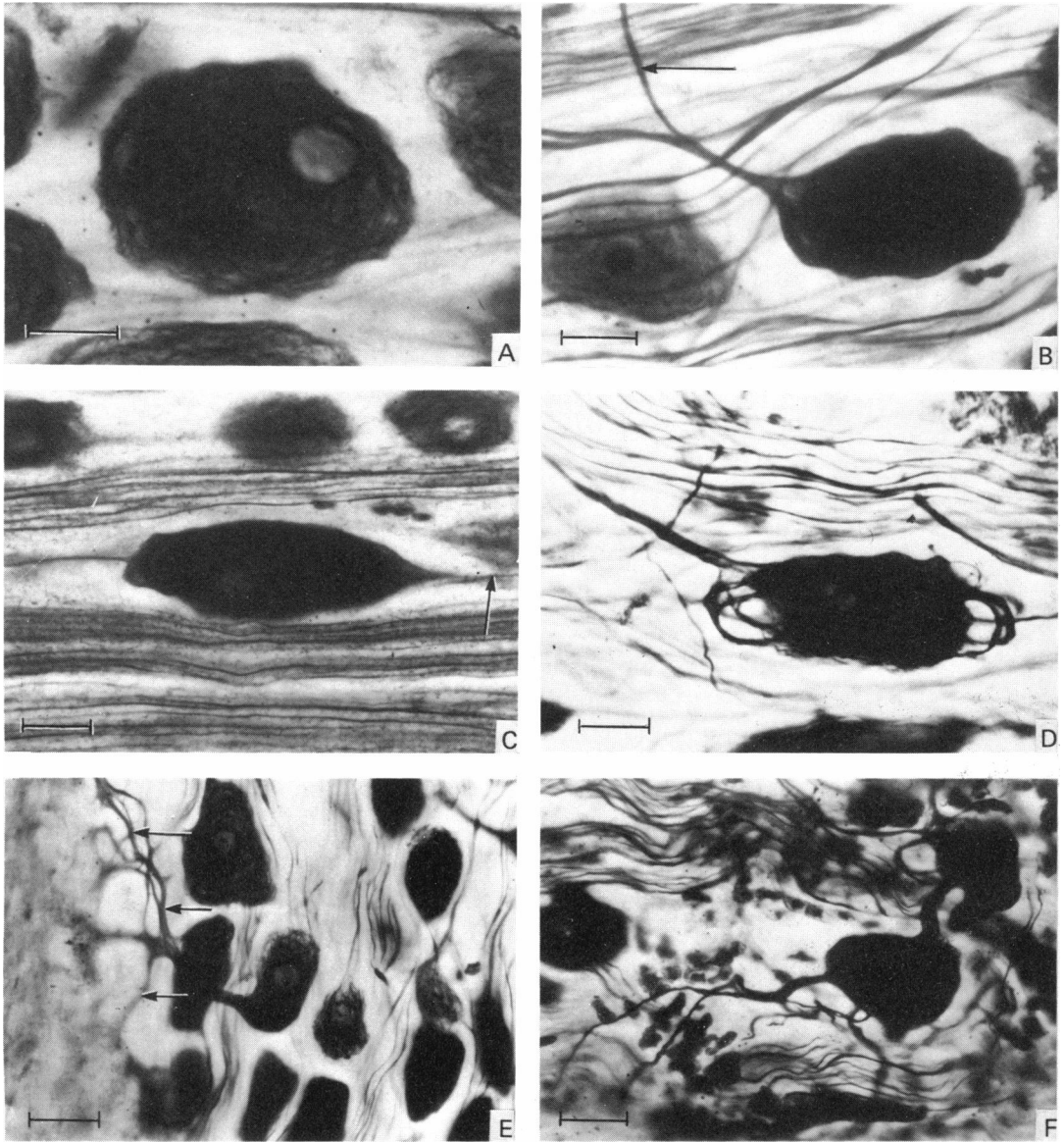


Fig. 1. Showing the different cell types that were seen in the distal vagal ganglion. A. Apolar. B. Pseudo-unipolar. The arrow indicates the thinner, centrally directed process. C. Elongated bipolar. The arrow indicates the thinner centrally directed process. D. Bipolar fenestrated. E and F. Examples of multipolar cells. E. shows processes (arrowed) directed towards the capsule of the ganglion. F. shows an example of the bicellular glomerular structure. Holmes' silver nitrate method. The bar in each case indicates 10 μ m.

classical pseudo-unipolar type of nerve cell. When the single process could be followed until it split into two, it could be seen that the centrally directed process was thinner than the peripherally directed one. Unlike pseudo-unipolar cells of spinal ganglia the initial process was never visibly coiled on itself but left the perikaryon in a straight course (Fig. 1 B). These cells formed 41.2% of the total and the perikaryon

Table 2. The percentage of each category of neuronal profile in the distal vagal ganglia of normal and operated vagi. Note the change in percentages found in the ganglia from the operated side, and particularly the bipolar cells

Profile	Normal (all left) %	After supraganglion vagotomy	
		L	R
Apolar	13.0	17.1	14.9
Unipolar	41.2	49.0	53.5
Bipolar	44.8	28.7	28.2
Fenestrated	0.8	5.0	3.4
Others	0.2	0.2	0.1
	100.0	100.0	100.0

had a mean diameter of $30 \mu\text{m}$ (± 1.21 , $n = 23$). The nucleus was usually large and centrally placed. (3) Bipolar. These were the classical type of bipolar cell with two processes arising from the perikaryon, the central process being thinner than the peripheral one (Fig. 1 C). They formed 44.81 % of the neuronal population of the ganglion. The cell profile was either elongated, measuring $48.0 \mu\text{m} \pm 0.54$ and $26.5 \mu\text{m} \pm 0.64$, $n = 63$, with the processes arising at 180° from each other in the polar regions of the cell, or they were rounded, measuring $31 \mu\text{m} \pm 1.23$, $n = 29$ with the processes arising at less than 180° from each other. (4) Fenestrated. These tended to occur in small groups in the ganglion rather than as scattered individuals. They possessed a number of fine processes which were sometimes confined to the polar regions of the perikaryon (Fig. 1 D) or arose from the whole of one side. The fine processes eventually merged to form the process that leaves the perikaryon. The merger always occurred within the pericellular capsule. They formed 0.82 % of the neuronal population and had a mean diameter of $25.4 \mu\text{m}$. At least 13 sub-types of fenestrated cells have been described (Hoffman, 1958) but for the purposes of this study they were all classed as one group. (5) Other. This group consisted of cells possessing thickened processes, processes with swellings, vacuolated cells and cells with features that prevented them from being included in other groups. It is estimated that 100 000 neuronal profiles were examined and of these only nine (0.009 %) had three or more large processes or had apparently typical dendrites arising from the perikaryon (Figs. 1 E, F). In addition to these nine, two others were seen to have short processes, those of one cell apparently intermingling with those of the other. They resemble the bicellular glomerular nerve cell described in sympathetic ganglia by Ranson & Billingsley (1918), but may represent two closely adjacent fenestrated cells (see Fig. 1 F).

There were indications that while the total numbers of neurons in the distal vagal ganglion were not changed by a vagotomy proximal to the ganglion, the proportions of the different types of neuron were affected (see Table 2).

Physiological experiments

Site of stimulation

The results were the same if the stimulus was cranial to, on, or caudal to the distal vagal ganglion.

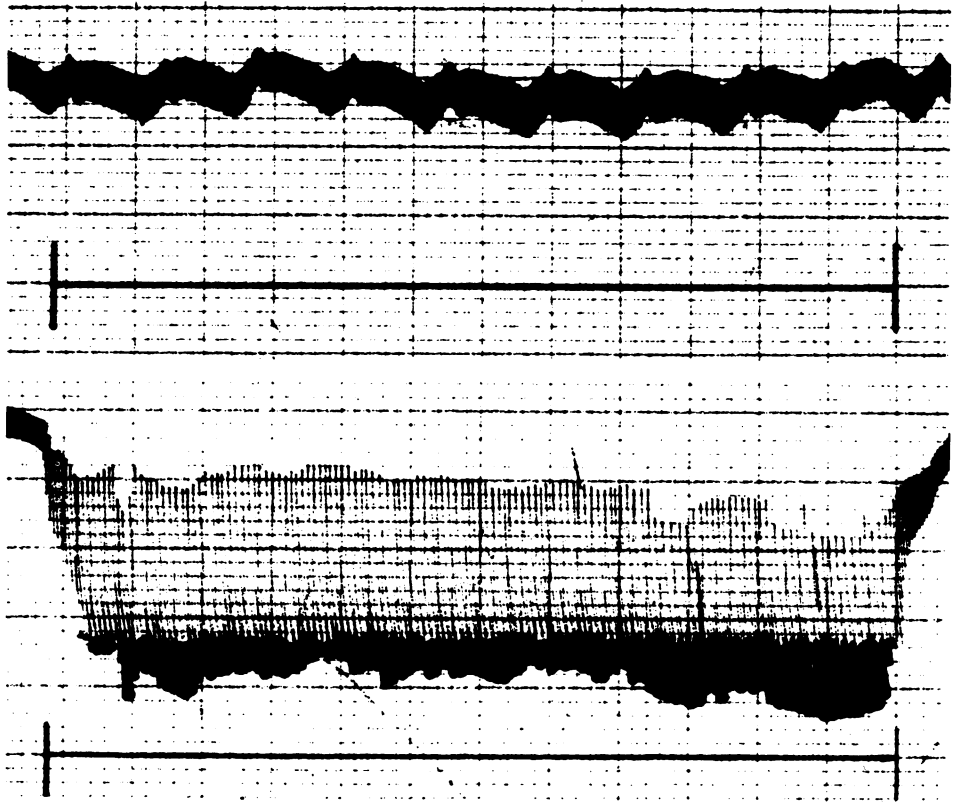


Fig. 2. Photographs of tracings of the heart rate and blood pressure during stimulation of the chronically severed vagus (top trace) and the acutely severed vagus (bottom trace). The bar indicates the period of stimulation. It can be seen that stimulation of the chronically operated nerve has no effect; stimulation of the acutely operated nerve has a profound effect. 1 small square = 1 sec.

Effects on blood pressure

When the acutely sectioned nerve was stimulated there was a dramatic fall in both blood pressure and the pulse rate with an increase in pulse pressure. The precise degree of drop depended on the frequency and intensity of stimulation. For example, at 20 Hz the blood pressure fell from 150/130 mmHg to 130/50 mmHg. There was a drop in pulse rate from approximately 224 beats/minute to 24 beats/minute. There was no drop in either the blood pressure or the heart rate when the chronically sectioned nerve was stimulated. Typical results are shown in Figure 2.

Effects on motility of gastrointestinal tract

Results were recorded from three different regions of the tract: (a) the crop, (b) the proventriculus and (c) the gizzard. Four animals were used for each region.

(a) *The crop.* Spontaneous activity was typically in the form of a single isolated contraction which lasted for 15 seconds. It was the only contraction seen in a 15 minute period. When the acutely sectioned vagus was stimulated complex waves were seen which started with and lasted as long as the stimulus (Fig. 3).

(b) *The proventriculus.* The spontaneous activity was high amplitude rhythmic

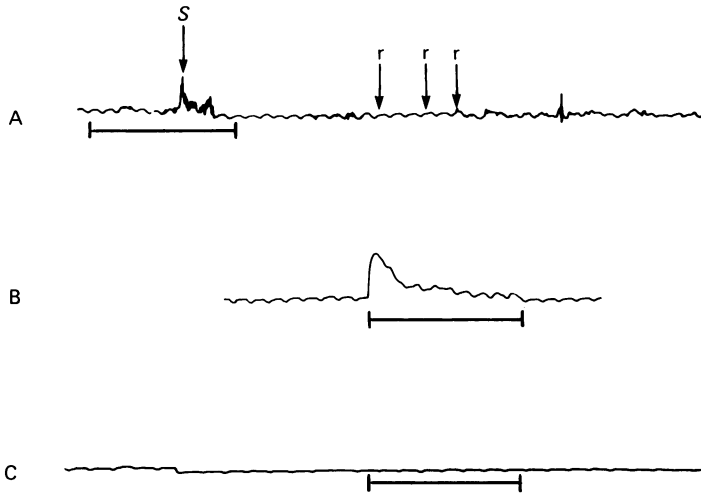


Fig. 3. Photographs of tracings made of the crop pressure during stimulation of the acutely and chronically operated nerves. Line A shows the spontaneous activity (S) and the changes in pressure brought about by the respiratory movements of the hen (r). B. shows the response to 10 Hz stimulation. C. shows the lack of response in the chronically operated nerve to a 10 Hz stimulation. The bar in all tracings indicates 1 minute and in lines B and C also indicates the duration of the stimulation.

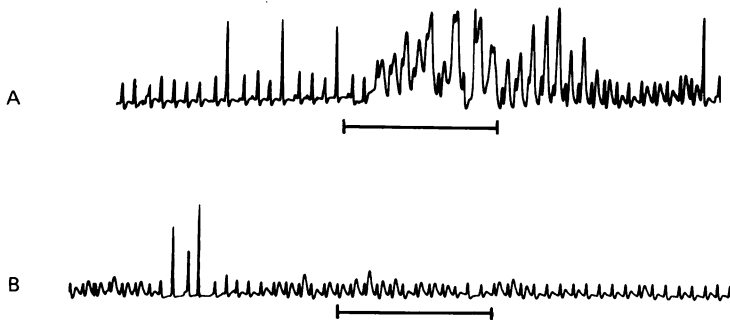


Fig. 4. Photographs of tracings of proventricular pressure during stimulation of the acutely and chronically operated nerves. Line A shows the response in the acute nerve to a 5 Hz stimulation for 1 minute shown by the bar. Line B shows no response in the chronic nerve to a 20 Hz stimulation also for one minute shown by the bar.

waves. Six such contractions were typically observed in a 12 minute period. On stimulating the acutely sectioned vagus either high amplitude, high frequency monophasic or complex waves were seen, depending on the frequency of the stimulus. The latency of onset of the evoked contractions was 20 seconds and they continued for one to two minutes after the stimulation was stopped (Fig. 4).

(c) *The gizzard.* The spontaneous activity was high amplitude complex waves. Five such waves were typically recorded in a 10 minute period. The response to stimulation of the acutely sectioned nerves was very high amplitude, high frequency complex waves. They did not start until the end of the stimulation and persisted for up to 10 minutes after the stimulation had finished (Fig. 5).

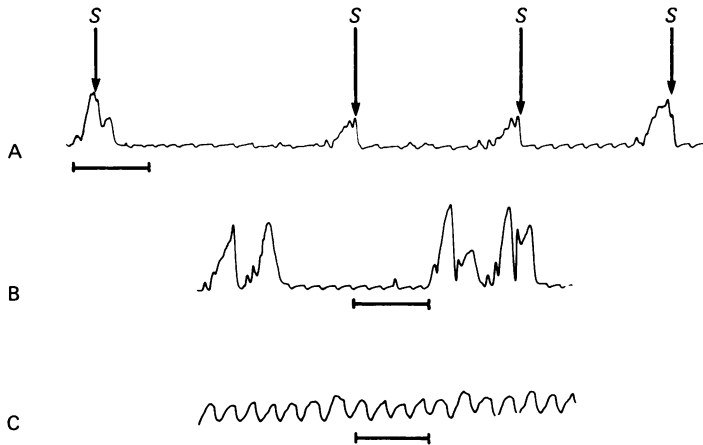


Fig. 5. Photographs of tracings of the gizzard pressure during stimulation of the acutely and chronically operated nerve. Line A shows the spontaneous activity (S). Line B shows the response in the acute nerve to a 10 Hz stimulation. Line C shows no response to a 10 Hz stimulation of the chronic nerve. The bar in all lines indicates 1 minute and in lines B and C also indicates the period of stimulation.

No responses were observed in the gastrointestinal tract when the chronic nerve was stimulated at any parameter or at any site cranial to, on, or caudal to the distal vagal ganglion.

DISCUSSION

Morphology

The most striking feature of the distal vagal ganglion of the hen is the very low number of neurons present. This study reports a mean of 6710 neurons which is in marked contrast to (for example) the cat which has between 26000 neurons (Foley & Dubois, 1937) and 29600 neurons (Jones, 1937) in its nodose ganglion. The proportion of afferent fibres in the cervical vagus of the hen is also very different from the cat. Agostoni, Chinnock, Daly & Murray (1957) showed that at least 86% of the fibres in the cervical vagus nerve of the cat are afferent. However Brown (1970) showed that the cervical vagus nerve of the hen contains about 15000 fibres which, with the distal vagal ganglion containing only 6170 neurons, means that only about 45% of the cervical vagus nerve fibres in the hen are afferent. In 1979 Abdalla & King reported that the hen had about 3700 myelinated afferent fibres in the right cervical vagus nerve and about 4100 myelinated afferent fibres in the left cervical vagus nerve, with their cell bodies in the distal vagal ganglia. Those results and the results reported here indicate that about 2400 right distal vagal ganglion neurons (6100 from Table 1 minus 3700) and about 2900 left distal vagal ganglion neurons (7000-4100) give rise to unmyelinated neurons. This means that approximately only 40% of the distal vagal ganglion neurons give rise to unmyelinated fibres, which is in contrast to the high proportion of nodose ganglionic neurons reported by Daly & Evans (1953), and Mohiuddin (1953) for the cat and by Evans & Murray (1954) for the rabbit. If the number of unmyelinated fibres arising from the distal vagal ganglion is added to the total number of myelinated fibres in the cervical vagus nerve (about 9100 on the right and about 8500 on the left, reported by Abdalla

& King, 1979) then a count of about 11 500 for the right cervical vagus nerve and a count of about 11 400 for the left vagus nerve is obtained. This means that 3500 (15000 from Brown minus 11 500) unmyelinated fibres on the right and about 3600 unmyelinated fibres on the left (15000–11 400) have arisen from the brain stem or elsewhere. If, as argued above, 55 % of the fibres in the cervical vagus nerve are efferent, then of 8250 efferent fibres 3600 on the left and 3500 on the right, i.e. about 42 %, are unmyelinated. The possibility that 42 % of the fibres arising from the brain stem are unmyelinated is in contrast to the results reported in the cat by Mohiuddin (1953) who could not find any degeneration of unmyelinated fibres following supranodose vagotomy.

Another difference between the distal vagal ganglion of the hen and the nodose ganglion of the mammal is the proportion of bipolar neurons. This study indicates that about 45 % of the neurons in the distal vagal ganglion were bipolar, whereas Cajal (1909) found only unipolar neurons in the nodose ganglion of the mammal. A small percentage of the neurons in the bird was fenestrated, which is similar to the nodose ganglion, and only 9 of the 100000 cell profiles examined had processes that could be classed as belonging to multipolar cells. A careful search of the perikaryon failed to reveal any boutons which would indicate that these cells were efferent. A receptor function has been postulated for the nodose ganglion (Chai & Wang, 1966; Chai, Wang, Hoffman & Wang, 1967), and these multipolar cells may have had such a role.

When the central processes of the neurons in the distal vagal ganglion were cut there was no evidence of chromatolysis, which agrees with the finding of Lieberman (1969), who found no evidence of chromatolysis following supranodose vagotomy. However, our results did indicate that the proportion of the different types of neuron in the distal vagal ganglion changed following vagotomy proximal to the ganglion, though whether this is a permanent or temporary change is not yet known.

Physiology

The results of stimulating the acutely sectioned vagus nerve were the same regardless of whether the stimulus was applied cranial to, on, or caudal to the distal vagal ganglion. The lack of response on stimulating the chronically operated nerve was also the same regardless of the site of stimulation. This would indicate that the ganglion does not contain any efferent neurons, either of the multipolar type or efferent pseudo-unipolar as suggested by Heinbecker & O'Leary (1933*b*). It would also indicate that there are no efferent neurons in the vicinity of the distal vagal ganglion.

This study therefore presents no evidence that the distal vagal ganglion contains any efferent neurons and the conclusion is that the ganglion is entirely sensory in nature.

The morphology of the neurons, the lack of chromatolysis and the lack of evoked responses following vagotomy proximal to the distal vagal ganglion, together with the fact that the hen is not unique in having a distally placed vagal ganglion (reptiles also have a distal vagal ganglion; Ranson, 1915) indicates that the distal vagal ganglion of the hen is homologous with the nodose (inferior vagal) ganglion of the mammal. However, there are differences between the distal vagal ganglion of the hen and the nodose ganglion of the mammal, i.e. the proportion of bipolar cells, the number of neurons giving rise to unmyelinated fibres and the ratio of afferent to efferent fibres in the cervical vagus. Therefore a final decision about the possible

homology between the two ganglia must await the appropriate embryological studies.

SUMMARY

The distal vagal ganglion of the hen was examined histologically and physiologically. The numbers of neurons in the right and left distal vagal ganglia were counted and a mean figure of 6710 neurons obtained. The proportions of the different types of neuron present were determined and their size measured. No multipolar cells with boutons on them were found. Morphologically the ganglion is sensory.

Following chronic vagotomy proximal to the distal vagal ganglion the vagus nerves were stimulated and the effect on the heart and gastrointestinal tract monitored. It was found that stimulation of the acutely sectioned nerve caused a drop in heart rate and an increase in gastrointestinal activity. There was no cardiac or gastrointestinal response when the chronically operated nerve was stimulated.

Physiologically the ganglion is sensory. The evidence is reviewed for homology between inferior vagal ganglion of the mammal and the distal vagal ganglion of the hen.

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REFERENCES

- ABDALLA, A. B. & KING, A. S. (1979). The afferent and efferent myelinated fibres of the avian cervical vagus. *Journal of Anatomy* **128**, 135-142.
- AGOSTONI, E., CHINNOCK, J. E., DALY, M. D. B. & MURRAY, J. G. (1957). Functional and histological studies on the vagus nerve and its branches to the heart, lungs and abdominal viscera in the cat. *Journal of Physiology* **135**, 182-205.
- BOWER, A. J. & PARRY, K. (1978). A demonstration of the use of autoradiography as a method of exploring the afferent autonomic innervation of the respiratory tract. *Journal of Physiology* **281**, 3-4P.
- BOWER, A. J., MOLONY, V. & BROWN, C. M. (1975). An autoradiographic method for the demonstration of vagal afferent nerve fibres in the lower respiratory tract of the chicken (*Gallus gallus domesticus*). *Experientia* **31**, 620-622.
- BROWN, C. M. (1970). Observations on the fibre sizes and their conduction velocities in the vagus of *Gallus domesticus* and some of its branches. B.Sc. thesis, University of Liverpool.
- CAJAL, S. RAMON, Y. (1909). *Histologie du Système Nerveux de l'Homme et des Vertébrés*. Paris: Maloine.
- CHAI, C. Y. & WANG, S. C. (1966). Mechanisms of sinus bradycardia induced by veratrum alkaloids-proveratrine A. *Journal of Pharmacology and Experimental Therapeutics*, **154**, 546-557.
- CHAI, C. Y., WANG, H. H., HOFFMAN, B. F. & WANG, S. C. (1967). Mechanisms of bradycardia induced by digitalis substances. *American Journal of Physiology* **212**, 26-34.
- CHOUDRAY, D. S. (1953). A comparative study of the carotid body and the carotid sinus of vertebrates. II. The carotid body and the carotid sinus of the fowl (*Gallus domesticus*). Ph.D. thesis, University of Edinburgh.
- DALY, M. DE BURGH & EVANS, D. H. L. (1953). Functional and histological changes in the vagus nerve of the cat after degenerative section at various levels. *Journal of Physiology* **120**, 579-595.
- DOUGLAS, W. W. & RITCHIE, J. M. (1956). Cardiovascular reflexes produced by electric stimulation of non-medullated afferents in the vagus, carotid sinus and aortic nerves. *Journal of Physiology* **134**, 167-178.
- DRURY, R. A. & WALLINGTON, E. A. (1967). *Carleton's Histological Technique*, 4th ed. London: Oxford University Press.
- EVANS, D. H. L. & MURRAY, J. G. (1954). Histological and functional studies on the fibre composition of the vagus nerve of the rabbit. *Journal of Anatomy* **88**, 320-337.
- FOLEY, J. O. & DUBOIS, F. S. (1937). Quantitative studies of the vagus nerve in the cat. 1. The ratio of sensory to motor fibres. *Journal of Comparative Neurology* **67**, 49-67.
- GASKELL, W. H. (1886). On the structure and function of the nerves which innervate the visceral and vascular systems. *Journal of Physiology* **7**, 1-80.
- HARPER, A. A., KIDD, C. & SCRATCHERD, T. (1959). Vago-vagal reflex effects on gastric and pancreatic secretion and gastrointestinal motility. *Journal of Physiology* **148**, 417-436.

- HEINBECKER, P. & O'LEARY, J. O. (1933*a*). Nature and function of certain fibres of the vagus—a new concept in peripheral nerve organisation. *Proceedings of the Society for Experimental Biology New York* **30**, 506–508.
- HEINBECKER, P. & O'LEARY, J. O. (1933*b*). The mammalian vagus nerve—a functional and histological study. *American Journal of Physiology* **106**, 623–646.
- HOFFMAN, G. (1958). Beiträge zur Histopathologie des Vegetativen Nervensystems bei Viruskrankheiten der Haustiere. I. Mitteilung des Verhalten peripherer vegetativer Ganglien Schweinepest. *Archiv für experimentelle Veterinärmedizin* **XII**, 451–501.
- HOLMES, W. (1947). Silver staining of nerve axons in paraffin sections. *Anatomical Record* **86**, 157–158.
- HOLZMANN, K. & DOGIEL, J. (1910). Ueber die Lage und den Bau des Ganglion nodosum nervi bei einigen Säugetieren. *Archiv für Anatomie und Physiologie* 33–41.
- JONES, R. L. (1932). Components of the vagus nerve. *Proceedings of the Society for Experimental Biology and Medicine* **29**, 1138–1141.
- JONES, R. L. (1937). Cell fibre ratios in the vagus nerve. *Journal of Comparative Neurology* **67**, 469–482.
- KIDD, L. J. (1914). The nucleus intercalatus of Ständerini. *Review of Neurology and Psychiatry* **12**, 1–21.
- KISS, F. (1931). Le rapport entre le pneumogastrique et la grande sympathique. *Archives du Muséum d'histoire naturelle* **7**, 147–172.
- KISS, F. (1932). Sympathetic elements in the cranial and spinal ganglia. *Journal of Anatomy* **66**, 488–498.
- KONIGSMARK, B. W. (1970). Methods for the counting of neurons. In *Contemporary Research Methods in Neuroanatomy* (ed. W. J. H. Nauta & S. O. E. Ebbesson), Berlin: Springer.
- KÖREISA, L. (1931). Vagus und Sympathicus. IV. Funktion der Anastomosen zwischen dem Ganglion nodosum und dem oberen sympathischen Halsganglion. *Zeitschrift für die gesamte Neurologie und Psychiatrie* **59**, 208.
- LIEBERMAN, A. R. (1969). Absence of ultrastructural changes in ganglionic neurons after supranodose vagotomy. *Journal of Anatomy* **104**, 49–54.
- MOHIUDDIN, A. (1953). Vagal preganglionic fibres to the alimentary canal. *Journal of Comparative Neurology* **99**, 289–318.
- MÖLLGAARD, H. (1912). Studien über das respiratorische Nervensystem bei den Wirbeltieren. *Skandinavisches Archiv für Physiologie* **26**, 315–383.
- MORGAN, L. O. & GOLAND, P. P. (1932). Demonstration of the accelerator nerve and of the postganglionic parasympathetic fibres in the vago-sympathetic trunk of the dog. *American Journal of Physiology* **101**, 274–281.
- NONIDIZ, J. F. (1935). The presence of depressor nerves in the aorta and carotid body of birds. *Anatomical Record* **62**, 47–73.
- PARKER, S. A. (1975). Autoradiography and the afferent innervation of the trachea, syrinx and extrapulmonary bronchus of *Gallus domesticus*. B.Sc. thesis, University of Liverpool.
- RANSON, S. W. (1915). The vagus nerve of the snapping turtle (*Chelydra serpentina*). *Journal of Comparative Neurology* **25**, 301–316.
- RANSON, S. W. & BILLINGSLEY, P. R. (1918). The superior cervical ganglion and the cervical portion of the sympathetic trunk. *Journal of Comparative Neurology* **29**, 313–358.