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AFFERENT FIBRES FROM THE ABDOMEN IN THE VAGUS NERVES.

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EVIDENCE has recently been advanced of the existence of afferent fibres from the abdomen in the splanchnic nerves [Bain, Irving and McSwiney, 1935]. It is also believed that afferent fibres from the abdomen are present in the vagus nerves, but the evidence in support of the presence of these fibres is unsatisfactory, and in many instances the experimental results reported are contradictory. Thus on the one hand it is stated that there is no evidence for the presence of sensory fibres in the abdominal vagus nerves [Müller, 1911]; while other investigators, working on dogs, have found that when all afferent pathways except the vagi have been eliminated, the abdominal viscera still remain sensitive [Lebedenko and Brjussowa, 1930].

Histological studies of the abdominal vagus nerves have been made by Edgeworth [1892], Müller [1911], van Gehuchten and Molhant [1911], and Chase and Ranson [1914]. Heinbecker and O'Leary [1933] have studied the time of conduction of impulses in the vagus nerve, and are of the opinion that all the afferent fibres of the nerve are medullated fibres of the somatic type. Edgeworth also describes large medullated fibres in the abdominal vagus nerves which he regards as sensory in function, but he considers it unlikely that these are the sole sensory fibres in the vagus.

Examination of the literature reveals the fact that while a number of investigators have obtained evidence of afferent fibres in the vagus trunks of the abdomen, few of these have set out definitely to investigate the course and pathway of these fibres. The study of afferent fibres in the vagus trunks of the abdomen in all instances has depended upon the elicitation of some reflex response in the animal.

Various reflexes have been used in these observations. Stimulation of the central end of a gastric vagus branch in the dogfish was found by Lutz [1930] to produce cardiac and respiratory inhibition. McWilliam [1885] obtained similar results in the eel on stimulating the vagus nerves on the œsophagus, but found that stimulation of the vagus nerves on the stomach was ineffective in producing inhibition. On the other hand, a rise of blood-pressure and acceleration of the heart were observed by Carlson and Luckhardt [1921] on stimulating the central end of the gastric vagus nerves in the turtle. Brodie and Russell [1900], working on cats and dogs, observed a slowing of the heart, after a preliminary slight increase in the blood-pressure and heart rate, on stimulating the central ends of the gastric vagus nerves. A comparison of the effect of stimulation of afferent fibres in the abdominal vagus upon the blood-pressure and respiratory movements in the rabbit and cat has been made by Miller [1911] and by Neumann [1914].

Contraction of the lung and of the stomach has also been used as an index of visceral afferent fibres from the abdomen. Carlson and Luckhardt [1920] obtained reflex lung contraction on stimulation of the central end of branches of the gastric vagus nerves in turtles. Rogers [1917], working on decerebrate dogs, found that stimulation of the central end of one abdominal vagus trunk or of the vagus in the neck produced spasmodic contraction of the entire stomach, if the other vagus was left intact.

As the dilatation of the pupil in the chloralosed cat is a more sensitive index of visceral afferent nerve activity than the reflex responses used by previous investigators, we have used this reaction to demonstrate the existence of visceral afferent fibres in the abdominal vagus nerves, and to work out the centripetal pathways of these fibres. Bain, Irving and McSwiney [1935] have recently published a series of observations in which they used the dilatation of the pupil as an index of afferent fibres in the splanchnic nerves. The mechanism of the dilatation of the pupil, which is fully discussed by Bain, Irving and McSwiney, appears to be the same for afferent fibres in both the vagus and the splanchnic nerves, that is, the dilatation is produced by inhibition of the nucleus of the third cranial nerve.

Anatomy of the abdominal vagus nerves in the cat.

Caudal to the roots of the lungs the right and left vagus nerves form the œsophageal plexus of the vagus round the lower part of the œsophagus. From the œsophageal plexus arise the ventral and the dorsal vagus trunks, which pass through the diaphragm on the ventral and dorsal aspects of the œsophagus respectively, and it is by these two nerve trunks that the vagus nerves reach the abdomen. The ventral vagus trunk is mainly distributed to the stomach, while the major portion of the dorsal trunk passes by its cœliac division to the cœliac ganglia.

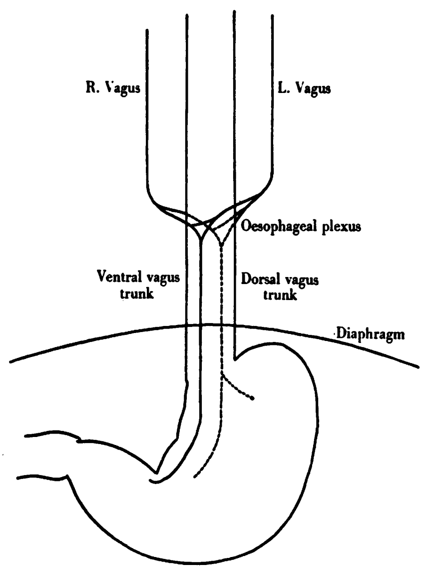

Fig. 1. The abdominal vagus nerves.

METHODS.

All the experiments were performed on cats. Anæsthesia was induced by ether and maintained by the intravenous injection of chloralose [Martindale], the dosage varying from 0·07 to 0·08 g. per kg. body weight. The pupil was illuminated by a small lamp, and the changes in diameter observed through a low-power microscope with a micrometer scale in the eyepiece.

The abdominal vagus nerves were approached transperitoneally through a mid-line incision, and the portion of nerve to be stimulated was dissected out and cut between ligatures. Stimulation was applied to the central end of the ventral or dorsal vagus trunks near the cardia, or to branches of these trunks on the lesser curvature of the stomach. In our earlier experiments we stimulated the central end of the cut nerve by faradic shocks, using either unipolar or bipolar electrodes. We subsequently observed that these nerves were more sensitive to pinching with a pair of artery forceps, and in our later experiments we have frequently used this type of stimulus.

EXPERIMENTAL RESULTS.

The afferent fibres from the upper abdomen may pass by the vagus nerves to the medulla; by the phrenic nerves to the fifth and sixth cervical dorsal roots; by the splanchnic nerves, which, as Bain, Irving and McSwiney have shown, contain afferent fibres which enter the spinal cord as high as the third thoracic dorsal roots; and by the intercostal nerves from the anterior abdominal wall as high as the sixth or seventh thoracic dorsal roots.

Afferent fibres in the cervical vagus nerves.

In the first series of experiments we eliminated all afferent pathways except the vagus nerves by transecting the spinal cord between the second and third cervical roots. Stimulation of the ventral or of the dorsal trunks in the abdomen produced dilatation of the pupil (Fig. 2A). On repeating the stimulation after section of either the right or the left vagus nerve in the neck dilatation of the pupil was still obtained (Fig. 2B). After subsequent section of the remaining vagus nerve in the neck no dilatation of the pupil was obtained on stimulating the ventral or dorsal vagus trunks (Fig. 2C), although the pupil still responded to stimulation of the pinna.

From these experiments we conclude that visceral afferent fibres in the ventral vagus trunk and in the dorsal vagus trunk pass to the medulla by both cervical vagus nerves.

Cell stations in the afferent cervical vagus nerves.

In another series of animals 1 p.c. nicotine was painted on the ganglion nodosum of the right and left vagus nerves, and on both superior cervical sympathetic ganglia after section of the cord between the second and third cervical roots. Thirty minutes later stimulation of the cervical sympathetic, which had previously caused a dilatation of the pupil, was without effect, showing that the nicotine had paralysed the synapses in the superior cervical sympathetic ganglion. The dilatation of the pupil on stimulating the ventral or dorsal vagus trunks was, however, quite unaffected. We therefore conclude that the visceral afferent fibres passing to the medulla by the vagus nerves have no synapses in the ganglia nodosa comparable to those in the sympathetic ganglia in the efferent sympathetic pathway.

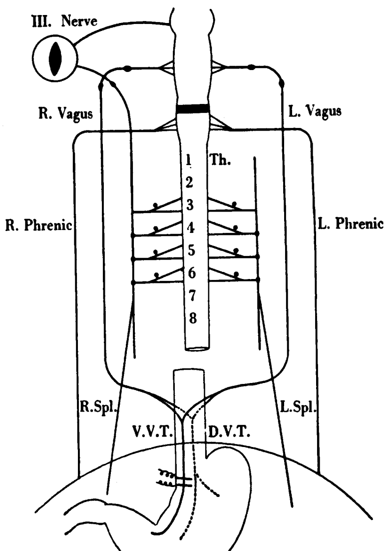

Fig. 2 A.

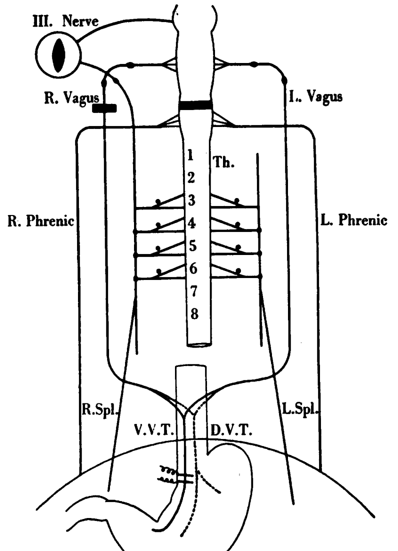

Fig. 2 B.

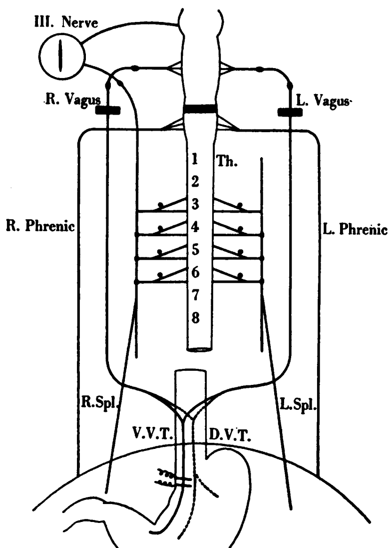

Fig. 2 C.

Fig. 2. Illustrating that afferent fibres from the abdominal vagus nerves reach the medulla by both cervical vagus nerves. A, stimulation of the abdominal vagus nerves, after transection of the spinal cord between the second and third cervical roots, causes dilatation of the pupil. B, dilatation of the pupil is still obtained on stimulation of the abdominal vagus nerves, after section of the right vagus nerve in the neck. C, after section of the left vagus nerve in the neck, no dilatation of the pupil is obtained on stimulating the abdominal vagus nerves.

R.Spl. = right splanchnic nerve; *L.Spl.* = left splanchnic nerve; *V.V.T.* = ventral vagus trunk; *D.V.T.* = dorsal vagus trunk.

Afferent fibres in the vagus nerves which enter the spinal cord.

We have also obtained evidence of a second group of afferent fibres which leave the vagus nerves in the thorax and enter the spinal cord by the dorsal spinal roots. To demonstrate the existence of this second pathway a series of experiments of the following type was carried out.

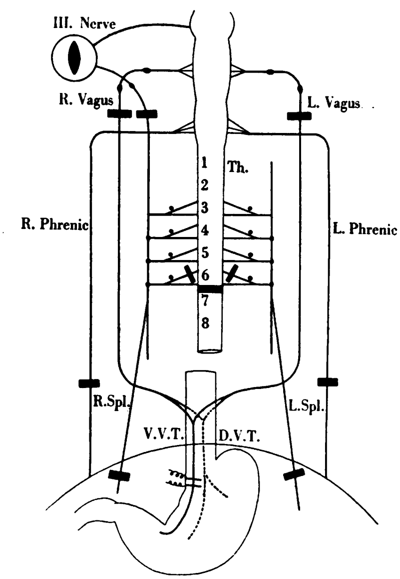

Fig. 3 A.

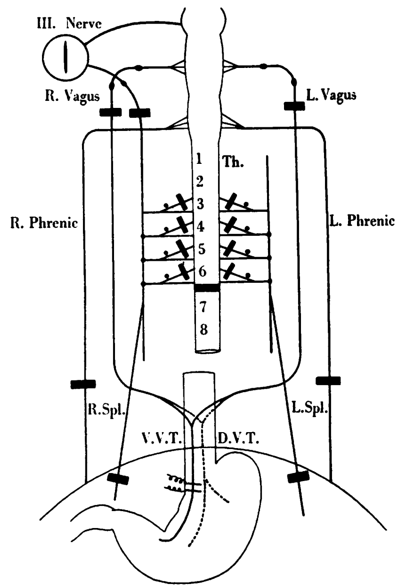

Fig. 3 B.

Fig. 3. Illustrating that afferent fibres from the abdominal vagus nerves enter the spinal cord by the thoracic dorsal roots. A, after elimination of all known afferent pathways from the upper abdomen, stimulation of the abdominal vagus nerves produces dilatation of the pupil. B, after section of the third, fourth and fifth thoracic dorsal roots on both sides, no dilatation of the pupil is obtained on stimulation of the abdominal vagus nerves. Lettering as Fig. 2.

All known afferent pathways from the upper abdomen were eliminated by the following procedures. The spinal cord was transected between the sixth and seventh thoracic roots and the sixth dorsal roots were cut, to eliminate afferent fibres in the intercostal nerves. The sympathetic pathway was interrupted by section either of the splanchnic nerves extraperitoneally on both sides, or of the sympathetic chains in the thorax below the level of section of the spinal cord. Both phrenic nerves were divided in the thorax, and both vagus nerves and both cervical sympathetics were cut in the neck.

Stimulation of the ventral or dorsal vagus trunks or of their branches on the lesser curvature of the stomach now produced dilatation of the pupil (Fig. 3 A), but after section of the third, fourth and fifth dorsal spinal roots on both sides stimulation of the trunks was ineffective and dilatation of the pupil was not obtained (Fig. 3 B).

As all known pathways from the upper abdomen were eliminated the dilatation of the pupil in this instance must have been due to conduction of impulses in afferent fibres of the abdominal vagus nerves which enter the spinal cord. In some experiments it was necessary to cut the second thoracic dorsal roots to abolish the dilatation. The impulses which enter the spinal cord by these fibres ascend in the central nervous system at least as high as the mid-brain, as dilatation is still obtained after section of the cervical sympathetics.

A further series of experiments was performed to obtain more precise information of the pathway of these fibres in the thorax. In the first series the preliminary operative procedures were similar to those just described, but in addition the third, fourth and fifth thoracic dorsal roots were divided on the right side. Any dilatation of the pupil on stimulating the abdominal vagus trunks could thus only be produced by afferent fibres reaching the spinal cord by the second right and the second, third, fourth and fifth left dorsal roots.

Stimulation of the ventral or dorsal vagus trunks produced dilatation of the pupil. The third, fourth and fifth left intercostal arteries were then cut between ligatures close to their origin from the aorta, and stimulation of the ventral and dorsal vagus trunks was repeated, but no dilatation of the pupil was obtained. The left sympathetic chain was then stimulated above the point of section and dilatation of the pupil was obtained. Stimulation of the third, fourth and fifth left intercostal nerves was also effective, indicating that section of the intercostal arteries had not affected the conduction of nervous impulses by the dorsal roots. From this we conclude that these afferent fibres in the abdominal vagus nerves which enter the spinal cord run in close relationship to the intercostal arteries, as they take origin from the aorta.

We occasionally failed, in animals where the abdominal vagus nerves were smaller than usual, to obtain dilatation of the pupil, when only the third, fourth and fifth left dorsal roots were conducting. The failure to obtain dilatation in these experiments may therefore be due to an insufficient number of fibres conducting impulses by these roots from the abdomen.

A second series of experiments was carried out to determine whether these fibres which entered the spinal cord by the upper thoracic roots left the thoracic vagal trunks in the region of the œsophageal plexus. In this series the same preliminary operative procedure was carried out. After dilatation of the pupil had been obtained on stimulating the ventral and dorsal vagus trunks, the œsophagus was tied and cut between ligatures at the level of the seventh to eighth thoracic vertebra, and the vagus nerves, lying on the wall of the œsophagus, were included in the ligature and cut. Stimulation of the abdominal vagus nerves now failed to elicit dilatation of the pupil. We conclude therefore that the fibres entering the spinal cord by the upper thoracic roots leave the thoracic vagal trunks above the level of the œsophageal plexus.

To determine the extent of the distribution of the afferent fibres in the abdominal vagus trunks which enter the spinal cord, a series of experiments of the following type was performed. The phrenic nerves and sympathetic chains were cut in the thorax and both vagus nerves and both cervical sympathetics were divided in the neck. The second, third, fourth and fifth thoracic dorsal roots on both sides were cut. Stimulation of the ventral or dorsal vagus trunks produced dilatation of the pupil. The dilatation of the pupil was still obtained after section of the sixth and seventh dorsal roots on both sides, but was not obtained after section of the eighth dorsal roots. By experiments of this type we have determined that fibres from the ventral and dorsal vagus trunks enter the spinal cord by the dorsal roots as low as the eighth thoracic roots. The upper level of entry was usually found to be the third thoracic dorsal roots, but in a number of experiments conducting fibres were present in the second thoracic dorsal roots.

Collating the results of these sets of experiments we conclude that a proportion of the visceral afferent fibres in the abdominal vagus nerves leave the thoracic vagal trunks, accompany the intercostal arteries from the aorta, join the intercostal nerves close to their exit from the intervertebral foramina, and enter the spinal cord by the dorsal roots from the third to the eighth thoracic roots inclusive. We have obtained no evidence that these fibres pass through the thoracic sympathetic chains in any part of their course, nor have we obtained any evidence that afferent fibres from the abdominal vagus nerves enter the spinal cord by the ventral roots. Removal of the adrenal glands did not appear to alter the reaction of the pupil to stimulation of the nerve fibres.

We have examined the first portions of the third to the sixth left intercostal arteries by Gairn's gold chloride method, and have found one or more bundles of nerve fibres accompanying the arteries in the extrapleural fat. These bundles contain both myelinated and non-myelinated fibres, but we have at present no evidence as to which of these fibres are afferent components from the abdominal vagus nerves.

Cell stations in the afferent spinal fibres of the abdominal vagus nerves.

In animals prepared so that only the third and fourth thoracic dorsal roots were conducting impulses from the abdominal vagus nerves, 1 p.c. nicotine was painted on the third and fourth thoracic dorsal root ganglia and on the right superior cervical sympathetic ganglion. Thirty minutes later stimulation of the right cervical sympathetic, which had previously produced dilatation of the pupil, was without effect. Stimulation of the ventral or dorsal vagus trunks, on the other hand, produced dilatation of the pupil. We conclude therefore that the visceral afferent fibres in the abdominal vagus nerves which enter the spinal cord by the thoracic dorsal roots have no synapses in the dorsal root ganglia comparable to those in the sympathetic ganglia in the efferent sympathetic pathway.

SUMMARY.

Using dilatation of the pupil in animals anæsthetized with chloralose as an index of afferent nerve activity we have obtained evidence of the existence of afferent fibres in the abdominal vagus nerves of the cat.

Two groups of visceral afferent fibres have been identified in the abdominal vagus nerves. Fibres of the first group pass from the ventral and from the dorsal vagus trunk directly to the medulla by both cervical vagus nerves. Fibres of the second group leave the thoracic vagal trunks, accompany the intercostal arteries from the aorta, join the intercostal nerves close to their exit from the intervertebral foramina, and enter the spinal cord by the dorsal roots from the second to the eighth thoracic roots inclusive.

The medullary fibres have no synapses in the ganglia nodosa, and the spinal fibres have no synapses in the dorsal root ganglia, comparable to those in the sympathetic ganglia in the efferent sympathetic pathway.

The impulses which pass to the central nervous system by the medullary and by the spinal fibres ascend at least as high as the mid-brain.

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