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SEGMENTAL DISTRIBUTION OF CERTAIN VISCERAL AFFERENT NEURONES OF THE PUPILLO-DILATOR REFLEX IN THE CAT

By B. A. McSWINEY and S. F. SUFFOLK
From the Sherrington School of Physiology,
St Thomas's Hospital, London

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In a previous paper [Irving *et al.* 1937] it was shown that impulses are conducted to the central nervous system from the stomach and small intestine by visceral afferent fibres contained in the right and left splanchnic and the right and left vagus nerves.

Little information is available of the segmental distribution of the visceral afferent neurones in the splanchnic nerves. Among the earliest references are those of Head [1893] and Thorburn [1893], who noted the skin areas to which pain from a particular viscus was referred, and from the nerve supply of these skin areas they deduced the segmental supply. Similar methods have been used by more recent workers; in particular by Gaza [1924], Miller & Simpson [1924], and Bloomfield & Polland [1931].

Kappis [1913] working with dogs used pain reactions as indices of afferent impulses, and found the whole abdominal cavity insensitive to any kind of stimulus after transection of the spinal cord above the level of the 6th thoracic roots. A similar method has been used by Fröhlich & Meyer [1922], who found that in dogs pain fibres from the small intestine did not enter the spinal cord above the 4th thoracic segment. In 1930 Lebedenko & Brjussowa observed changes in pulse rate, blood pressure and respiration on stimulating the gut, and were able to show that afferent neurones from any one part entered a large number of segments of the spinal cord.

By the use of histological methods Ranson & Billingsley [1918] showed that in the cat afferent fibres are most numerous from the 7th to the 10th thoracic white rami. Lebedenko & Brjussowa [1930] removed various viscera and allowed nerve degeneration to take place. They claim to have observed histological changes occurring in the cells of the sympathetic ganglia. Their results by this method suggest a much narrower distribution than was indicated by their other observations.

A table is given (Table I) summarizing the results of previous investigators. It will be seen that the widest segmental distribution has been described by Lebedenko & Brjussowa.

TABLE I. Segmental distribution as described by previous workers

	Cardia	Stomach	Pylorus	Duodenum	Small intestine	Cæcum
Bloomfield & Polland (man)	T 7–T 9	—	—	—	—	—
Fröhlich & Meyer (dogs)	—	—	—	—	Not above T 4	—
Gaza (man)	T 6–T 7	T 6–T 9	—	—	T 9–T 10	—
Head (man)	T 6–T 7	T 6–T 9	T 9	—	T 9–T 12	T 9–T 12
Kappis (dogs)	—	T 6–T 9	—	—	T 7–T 13	—
Lebedenko & Brjussowa (dogs):						
By stimulation	—	T 5–L 4	—	T 5–T 12	—	—
Histologically	—	T 7–T 9	—	T 8–T 11	T 6–T 11	T 11–T 12

We report in this paper the result of our studies on the segmental distribution of the visceral afferent neurones of the pupillo-dilator reflex found in the splanchnic nerves.

METHODS

Our observations have been made on cats. Anæsthesia was induced with ether and maintained with intravenous chloralose (0·08 g./kg.). Dilatation of the pupil was the reflex response generally used as an index of afferent fibres, but in some experiments reflex changes of blood pressure resulting from distension of the stomach and intestine were also recorded. The experimental technique was similar to that previously described [Irving & McSwiney, 1935; Irving *et al.* 1937]. Large balloons previously calibrated were used to distend the body and fundus of the stomach. Smaller balloons were inserted into the small intestine and pylorus. A calibration curve of the pyloric and intestinal balloons is given in Fig. 1. Using the calibration curve it was possible to ascertain approximately the pressure exerted by the wall of the viscus. Total pressures recorded and cubic centimetres of air used in the experiments are given in the tables. The vagus and cervical sympathetic nerves were cut in the neck in all experiments, and in some instances the phrenic nerves were cut in the thorax to abolish the afferent pathway from the diaphragm. Transection of the spinal cord, spinal root section or section of the sympathetic chains in the thorax was carried out if required. Details of procedure are described later in this paper.

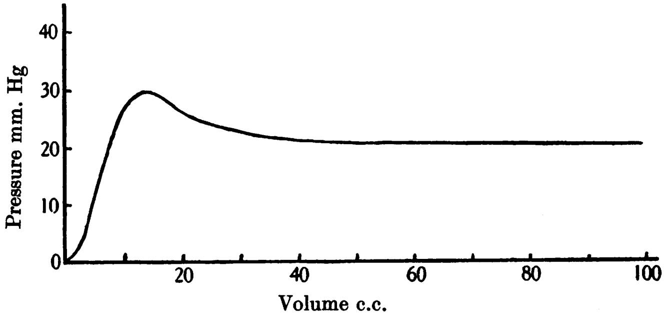

Fig. 1. Calibration curve of typical balloon.

EXPERIMENTAL RESULTS

The experiments were divided into three main groups:

(*a*) Experiments to find the upper limit of entry of afferent neurones into the spinal cord from different parts of the stomach and small intestine.

(*b*) Experiments to find the lowest level of entry into the cord.

(*c*) Experiments to show that afferent neurones enter the spinal cord between the extremes found in (*a*) and (*b*).

(*a*) *Upper limit of entry of afferent neurones into the spinal cord*

Bain *et al.* [1935] have shown that afferent fibres in the splanchnic nerves enter the spinal cord *via* the dorsal roots from the 3rd thoracic to the 1st lumbar segment inclusive. In those experiments no evidence was obtained that afferent neurones in the splanchnic nerves from the abdominal viscera enter the spinal cord above the 3rd thoracic segment.

In the first series of experiments we attempted to find the upper level of entry of afferent neurones into the spinal cord from different regions of the stomach and small intestine. Balloons were inserted, the vagus nerves were cut in the neck, and the spinal cord transected in the middle or lower thoracic region. The balloons were inflated and the pressures required to produce a dilatation of the pupil (the threshold pressures) were observed. The lowest conducting spinal root on each side was then cut and the cat was allowed to rest until the pupil constricted, when new threshold pressures were established. Spinal roots were cut until the upper conducting roots were identified. When the cord had been cut between T 6 and T 7 and three or four afferent roots were conducting impulses into the cord, the section of the 6th dorsal roots was not found to alter appreciably the threshold pressures. As further conducting roots were cut the effect on the threshold became more marked until, finally, section of one pair of roots, either raised the threshold from below 100 to over 200 mm. Hg, or abolished the pupil response completely. We therefore concluded that this last pair of roots was the upper limit of entry of afferent fibres for that particular part of the gut (Fig. 2).

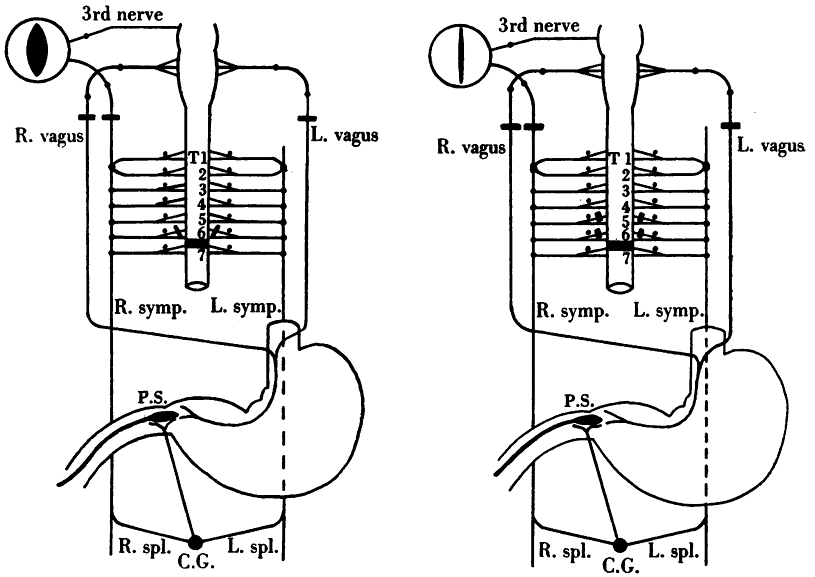

Fig. 2 A.

Fig. 2 B.

Fig. 2. A. Cord transected between 6th and 7th thoracic segments. Right and left vagus, and right and left cervical sympathetic nerves cut in the neck. 6th thoracic dorsal roots cut on both sides. Dilatation of the pupil on distension of the pyloric sphincter. B. Dilatation abolished after section of the right and left 5th thoracic dorsal roots.

The consistency of the results obtained from a large number of similar experiments supports this view, and we consider that few, if any, afferent neurones enter the spinal cord above this level from the particular area of the gut.

It has been shown previously [Irving *et al.* 1937] that dilatation of the pupil obtained on distension of the gut with pressures of less than 100 mm. Hg is due to stimulation of nerve endings in the muscle wall. Reflex responses obtained with pressures above 100 mm. Hg are possibly due to traction on nerve trunks. In these experiments, therefore, we have only used pressures up to 100 mm. Hg. The results of a typical experiment are given in Table II:

TABLE II. After section of spinal cord below T 6, section of 6th thoracic roots and section of vagus in neck

	Fundus Threshold stimulus	Pyloric sphincter Threshold stimulus	Jejunum Threshold stimulus
3.20 p.m.	30 mm. Hg (9 c.c.)	100 mm. Hg (11 c.c.)	No response
3.40	5th thoracic roots cut both sides	—	—
4.30	40 mm. Hg (9 c.c.)	No response	No response
4.35	4th thoracic roots cut both sides	—	—
5.00	No response	No response	No response

From this and similar experiments it was found that the upper limit of entry into the spinal cord of afferent neurones from any one part of the gut was almost constant in all the animals used. Indeed, the limit was never found to vary by more than one root. The results obtained are tabulated in Table III:

TABLE III. Upper limit of entry into spinal cord

Fundus and body of stomach	T 3 or T 4
Pyloric antrum	T 5
Pyloric sphincter	T 5
Duodenum	T 6
Jejunum	T 7

(b) *Lowest levels of entry of afferent neurones into the spinal cord*

In a second series of experiments, we attempted to determine the lowest levels of entry of afferent fibres from different regions of the stomach and small intestine. Balloons were inserted into the gut and the vagus nerves cut in the neck. In our preliminary experiments the sympathetic chains were cut on both sides in the thorax above the level of the 9th thoracic rami. After the threshold pressures for the different balloons had been obtained the 9th roots on each side were cut and a new threshold obtained. The process of root section was continued caudally. It was found that when the 12th thoracic roots were the highest roots conducting impulses, a positive pupil response was still obtained from all parts of the viscera under examination. We therefore concluded that afferent neurones from the stomach and small intestine entered the cord below the 11th dorsal roots.

In subsequent experiments the sympathetic chains were cut in the thorax between the 11th and 12th thoracic rami and the threshold pressure obtained. The thorax was then reopened, the sympathetic chains were cut between the 12th and 13th thoracic rami, and the 12th thoracic segments of the chains removed; new thresholds were then established. Successive segments of the sympathetic chains were removed caudally until the pupil response was abolished or a marked increase in the threshold pressure was required to elicit the reflex.

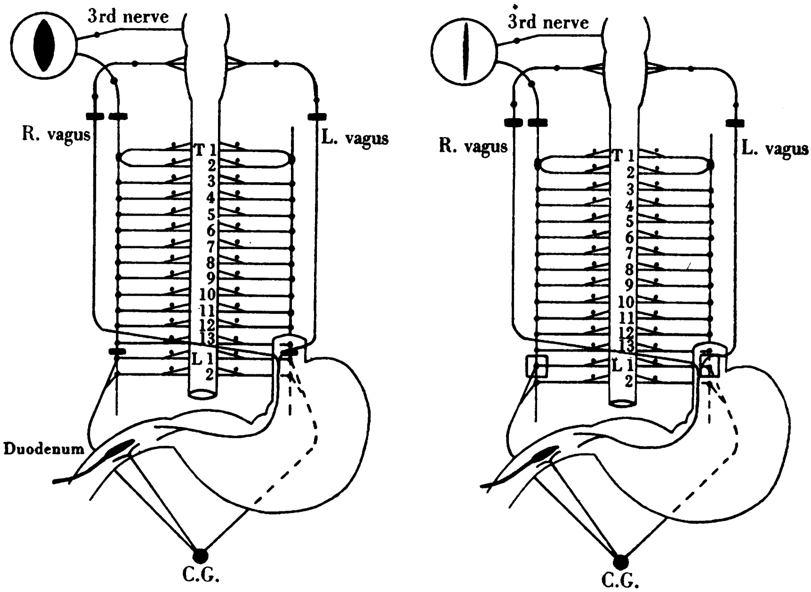

Fig. 3A.

Fig. 3B.

Fig. 3. A. Right and left vagus and right and left cervical sympathetic nerves cut in the neck. Right and left sympathetic chains cut between T 13 and L 1. Dilatation of the pupil on distension of the duodenum. B. Dilatation abolished after removal of segment of right and left sympathetic chains at level of 1st lumbar roots.

Table IV. After section of the sympathetic chains between T 13 and L 1

	Pyloric sphincter Threshold stimulus	Duodenum Threshold stimulus
3.45 p.m.	75 mm. Hg (6 c.c.)	95 mm. Hg (3 c.c.)
4.00	Sympathetic chains cut between L 1 and L 2	—
4.45	95 mm. Hg (9 c.c.)	No response

In a certain number of experiments no response was obtained on distension of the pyloric sphincter after section of the sympathetic chains between L 1 and L 2. From this and similar experiments the lower limits given in Table V were obtained.

TABLE V. Lowest dorsal roots conducting

Fundus and body of stomach	T 13
Pyloric antrum	T 13
Pyloric sphincter	L 1 or L 2
Duodenum	L 1
Jejunum	T 12 or T 13

It will be observed that the lowest afferent neurones from the jejunum enter the spinal cord through the 12th or 13th thoracic roots at least one root higher than the lowest afferent fibres from the duodenum. As the jejunum is much less sensitive to distension than the duodenum, the results obtained might have been due to stimulation of too small an area; for it is possible that the jejunum receives fewer and more widely dispersed afferent fibres than the duodenum. Consequently experiments were made using long balloons so that approximately 3 in. of the jejunum were stimulated. The results agreed with those previously described. We therefore conclude that afferent fibres from the jejunum do not enter the spinal cord below the 12th or 13th thoracic roots.

(c) *Intermediate roots*

The experiments previously described show that afferent neurones from any one part of the stomach and small intestine enter the spinal cord through the upper thoracic roots and through the lower thoracic and upper lumbar roots. Experiments were next carried out to show that afferent neurones also reached the cord *via* the intermediated roots.

A separate experiment was performed for each pair of roots from the 6th thoracic to the 12th thoracic segment inclusive. For example, when it was intended to leave the 7th thoracic roots as the sole afferent conducting pathway the preliminary procedure was the same as that used in the earlier experiments. In a cat anæsthetized with chloralose, balloons were inserted into the pyloric antrum, the duodenum and the jejunum and the vagus and cervical sympathetic nerves were cut in the neck. The spinal cord was transected at the level of the 8th thoracic segment to exclude impulses reaching the mid-brain *via* roots below T 7. The sympathetic chains were cut in the thorax between the 5th and 6th thoracic rami. By this procedure the 6th and 7th thoracic roots were the only pathways conveying impulses from the gut to the spinal cord.

After the threshold pressures required to elicit dilatation of the pupil were obtained, the sympathetic chains were cut between the 6th and 7th thoracic rami, leaving only the 7th thoracic roots conducting.

Distension of the gut still elicited dilatation. Section of the 7th thoracic dorsal roots, however, abolished the pupil response. The threshold pressures obtained in this experiment are given in Table VI.

Table VI. With 6th and 7th thoracic roots conducting

	Pyloric antrum Threshold stimulus	Duodenum Threshold stimulus	Jejunum Threshold stimulus
4.15 p.m.	60 mm. Hg (5 c.c.)	70 mm. Hg (4 c.c.)	70 mm. Hg (7 c.c.)
4.25	After section of 6th thoracic roots	—	—
5.15	100 mm. Hg (7 c.c.)	95 mm. Hg (6 c.c.)	80 mm. Hg (8 c.c.)

Similar experiments were carried out for the other thoracic roots from T 6 to T 12 inclusive, the positions of the balloons being varied in different experiments. Without exception it was found that each pair of roots formed part of the afferent pathway. Section of the single conducting pair of roots in each experiment abolished the pupil response to distension of the viscera.

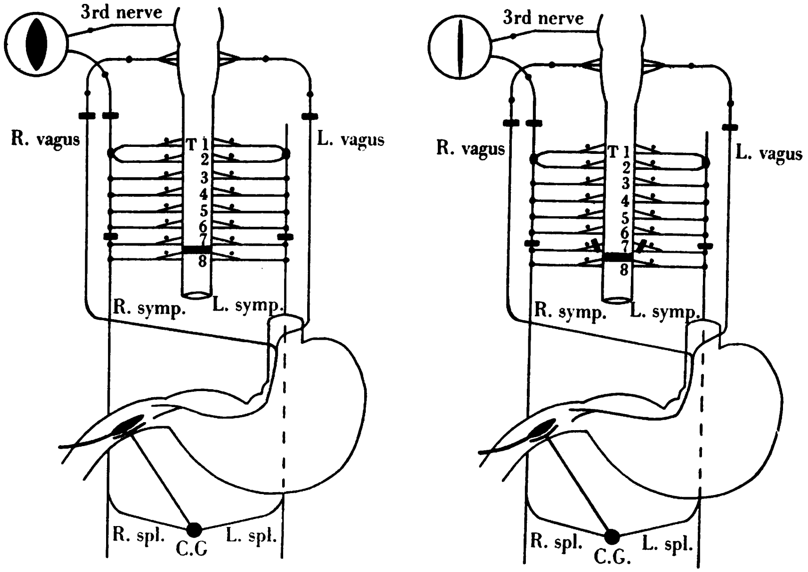

Fig. 4 A.

Fig. 4 B.

Fig. 4. A. Cord transected between 7th and 8th thoracic segments. Right and left vagus and right and left cervical sympathetic nerves cut in the neck. Right and left sympathetic chains cut between 6th and 7th thoracic roots. Dilatation of the pupil on distension of the duodenum. B. Dilatation abolished after section of the right and left 7th thoracic dorsal roots.

Thus our experiments show that different parts of the viscera receive their afferent innervation from all the dorsal roots between the limits given in Table VII, and shown in Fig. 5.

TABLE VII. Summary of highest and lowest levels of entry into the spinal cord of afferent neurones of the pupillo-dilator reflex from the stomach and small intestine

Area stimulated	Upper limit	Lower limit
Fundus and body of stomach	T 3 or T 4	T 13
Pyloric antrum	T 5	T 13
Pyloric sphincter	T 5	L 1 or L 2
Duodenum	T 6	L 1
Jejunum	T 7	T 12 or T 13

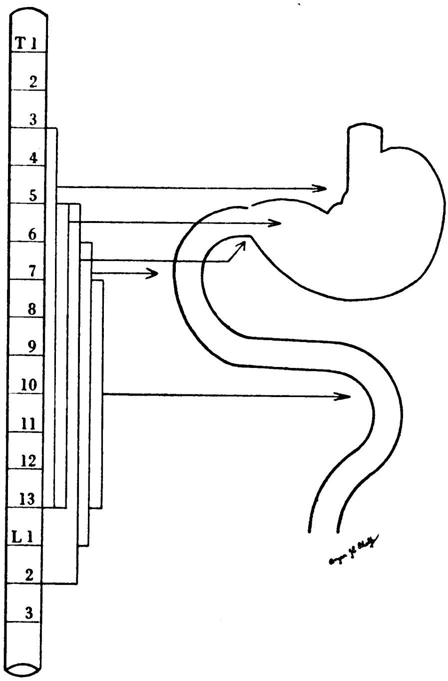

Fig. 5. Diagram to show innervation of different regions of the gastro-intestinal tract.

The experiments already described suggest that there is a wide segmental distribution of afferent neurones of the pupillo-dilator reflex from the stomach or small intestine. Fibres from the stomach and pyloric sphincter apparently enter the spinal cord through no less than ten dorsal roots. Such a wide distribution is contrary to the results of many earlier investigators.

There appeared to be two possible sources of error in our experiments which had not so far been controlled. It was possible that distension of a balloon in any part of the stomach or small intestine might produce stretching of the muscle in adjoining portions not in contact with the balloon. Or again there might be a spread of nerve impulses through the myenteric plexus to adjacent parts of the gut. Thus distension of the duodenum might produce an effect upon the pyloric sphincter sufficient to stimulate this region, and impulses might be propagated to the spinal cord *via* afferent neurones which had no connexion with the duodenum. Incorrect levels would, therefore, be obtained for the upper and lower limits of entry of afferent neurones into the cord.

Some of the earlier experiments described in this paper on the upper and lower limits were repeated with one variation in experimental procedure. The gut was divided between ligatures above and below a balloon inserted into the duodenum, and purse-string sutures were used, if required, to prevent hæmorrhage from the cut surfaces. In this way all connexion between the duodenum and the adjacent sphincter and jejunum was abolished. Nerve fibres passing up or down the gut wall would also be severed. Subsequent cord and nerve sections were carried out as previously described.

From experiments of this type we have confirmed the results given in Table VII. Isolation of the area of the gut under observation did not effect the results. We conclude, therefore, that there is no reason to believe that mechanical effects or spread of nerve impulses to adjacent parts of the alimentary canal in any way invalidate our previous observations.

A further possibility of error concerning the highest point of entry of fibres into the spinal cord was then considered. It seemed possible that in those experiments in which the spinal cord was transected at about the mid-thoracic level, that impulses entering the cord below the transection might interfere with the results. Thus on stimulating, say, the duodenum, an impulse might enter the spinal cord below the level of section and set up a reflex disturbance in some organ, from which a second impulse might enter the cord above the level of section to produce dilatation of the pupil or alteration of blood pressure (Fig. 6).

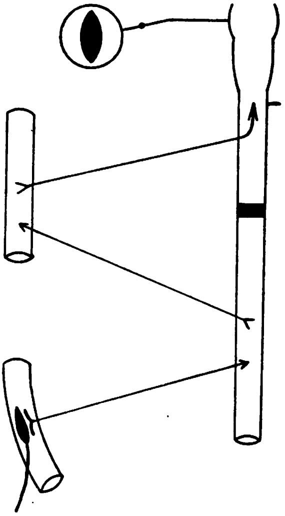
Fig. 6. Diagram to show possible pathway of impulses from isolated segment of gut to upper part of spinal cord.

Experiments were accordingly carried out in which balloons were inserted into the pyloric sphincter and the isolated duodenum. The vagus nerves were cut in the neck, and the spinal cord transected between the 8th and 9th thoracic segments. The threshold pressures required to elicit dilatation of the pupil were then obtained. In addition a blood-pressure record was then taken from the right carotid artery, showing the rise of blood pressure on distension of the gut. The spinal cord was then exposed from the level of transection to the 3rd lumbar segment, and completely removed between these two limits after section of all the ventral and dorsal roots on both sides (Fig. 7).

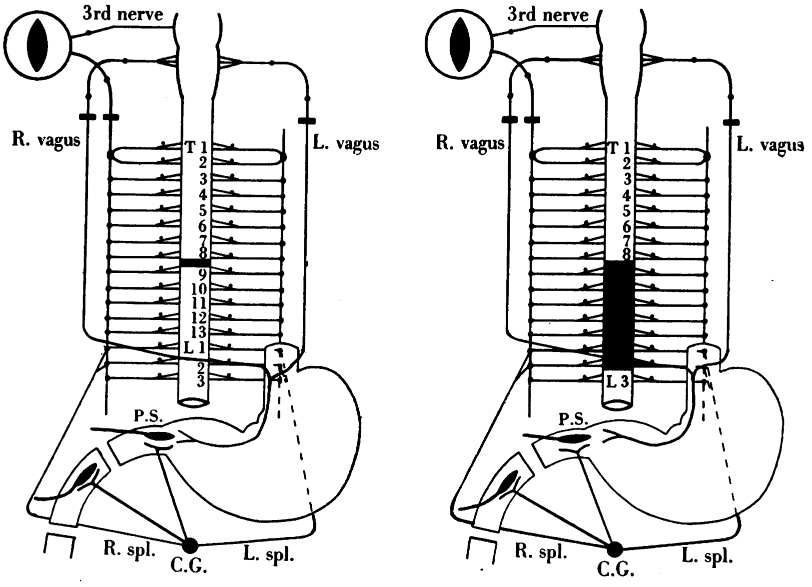

Fig. 7 A.

Fig. 7 B.

Fig. 7. A. Cord transected between 8th and 9th thoracic segments. Right and left vagus and right and left cervical sympathetic nerves cut in the neck. Dilatation of the pupil obtained on distension of the pyloric sphincter and the duodenum. B. Cord removed from level of transection to 3rd lumbar segment. Dilatation of pupil on distension of pyloric sphincter and the duodenum.

The pupil reactions and blood-pressure changes were then observed. The threshold pressures for pupil dilatation are given in Table VIII. It will be seen that removal of this portion of the spinal cord did not produce significant effects. Inflation of either the pyloric or intestinal balloon produced a rise of blood pressure (Fig. 8).

The purpose of taking blood-pressure records in these experiments was to be able to record that the animals were still in a satisfactory condition, despite the considerable vaso-motor disturbance which must necessarily be expected after such a drastic experimental procedure.

Subsequent section of the 7th and 8th thoracic dorsal roots abolished the pupil and blood-pressure responses from the duodenum, but distension of the pyloric sphincter still elicited a dilatation of the pupil (Table VIII), and produced a very slight rise of blood pressure (Fig. 8).

Table VIII. Spinal cord transected between the 8th and 9th thoracic segments

Pyloric sphincter Threshold stimulus	Duodenum Threshold stimulus
20 mm. Hg (2 c.c.)	60 mm. Hg (4 c.c.)
After removal of spinal cord below transection to 3rd lumbar segment	
30 mm. Hg (2 c.c.)	70 mm. Hg (4 c.c.)
After section of 7th and 8th dorsal thoracic roots	
100 mm. Hg (4 c.c.)	No response

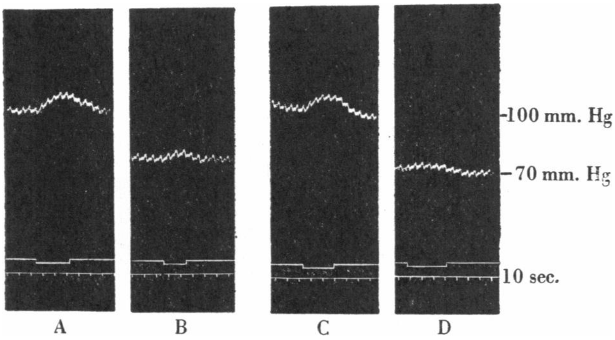

Fig. 8. Tracings to show rise of blood pressure on distension of pyloric sphincter and duodenum after removal of spinal cord from 9th thoracic to 3rd lumbar segment: A. Distension of pyloric sphincter 50 mm. Hg, 2·5 c.c. air. C. Distension of duodenum 75 mm. Hg, 3·0 c.c. air. After section of 7th and 8th thoracic dorsal roots: B. Distension of pyloric sphincter 100 mm. Hg, 4 c.c. air. D. Distension of duodenum 180 mm. Hg, 8 c.c. air.

Thus the highest pair of roots conducting afferent impulses from the duodenum in this experiment was the 7th thoracic, one root lower than that previously obtained. However, we consider that this slight difference lies within the limits of experimental error.

Repetition of these results in subsequent similar experiments show that the conception of a reflex connexion between the upper and lower halves of the transected cord in the manner suggested is not tenable. The evidence shows that our results are not liable to such source of error.

DISCUSSION

In the chloralosed cat it has been shown that the segmental distribution of the afferent neurones of the pupillo-dilator reflex from the stomach and small intestine is extensive. Previous views of the arrangement of these fibres appear to be based mainly on clinical evidence. If pain fibres from the stomach and intestine have a segmental distribution similar to the pupillo-dilator fibres, then an explanation is afforded for the diffuse character of visceral abdominal pain.

SUMMARY

Dilatation of the pupil and reflex changes of blood pressure in the cat anæsthetized with chloralose have been used as indices of afferent impulses, and evidence has been obtained of the segmental distribution of the afferent neurones of the pupillo-dilator reflex in the right and left splanchnic nerves from the stomach and small intestine.

The highest and lowest levels of entry into the spinal cord of the afferent neurones is shown in Table IX.

TABLE IX

Area stimulated	Upper limit	Lower limit
Fundus and body of stomach	T 3 or T 4	T 13
Pyloric antrum	T 5	T 13
Pyloric sphincter	T 5	L 1 or L 2
Duodenum	T 6	L 1
Jejunum	T 7	T 12 or T 13

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