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A comparative study of the vagal innervation of the stomach in man and the ferret*

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INTRODUCTION

The anatomy of the gastro-intestinal tract of the ferret is quite well known. Recent reports include work on the stomach (Stephens & Pfeiffer, 1968; Pfeiffer & Peters, 1969; Pfeiffer, 1970), biliary system (Poddar, 1977) and intestine (Bueno, Fioramonti & More, 1981). However, there is no description available of the innervation of the gut of the ferret.

Due to the interest in the ferret as an animal for gastro-intestinal research, the main objective of this study was to describe the parasympathetic innervation of the upper digestive tract, to complement previous physiological studies on the vagal control of the stomach.

An opportunity was also taken to re-examine the vagal innervation of the human stomach as a basis for a comparative study of the innervation of the human and ferret stomachs, which is of particular importance because the ferret has been shown to be a suitable model for man in terms of the gross gastric anatomy (Pfeiffer, 1970; Poddar & Murgatroyd, 1977), gastric acid secretion in response to various stimuli (Pfeiffer & Peters, 1969; Basso *et al.* 1971; Basso & Passaro, 1972) and the vagal regulation of gastric motility (Andrews & Scratcherd, 1980). An anatomical study of the gastric innervation in the ferret is also important if this animal is to be of use, as an alternative to cats and dogs, as a model for various gastric surgical procedures, e.g. superficial seromyotomy (Taylor, 1979).

This study of the ferret and human vagus nerves was carried out at several levels: gross dissections of whole specimens were used to elucidate the general distribution of the nerves; the fibre composition was examined using both light and electron microscopy and the electrophysiological characteristics of the major nerve trunks were investigated by recording the compound action potentials in fresh excised nerves. In the ferret, the distribution of the vagus nerve was also investigated by nerve stimulation and the recording of motility in various parts of the gut.

MATERIALS AND METHODS

Gross anatomical dissection

Human material

Thirty one formalin-fixed dissecting room cadavers and ten autopsy room specimens were examined. The mean age of the cadavers was 71 years (range 45–95) with a sex distribution of 20 males and 21 females. The autopsy specimens consisted of

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the subdiaphragmatic portion of the oesophagus, the stomach and the first part of the duodenum. All relevant nerves and vessels were left attached. The autopsy specimens were used only for histology.

Ferret material

Twenty three formalin-fixed ferrets (*Mustela putorius furo*) were dissected. The population consisted of 10 male fitches (mean 816 g, range 400–1230 g); three female fitches (mean 543 g, range 380–730 g), seven male albinos (mean 991 g, range 500–1240 g); three female albinos (mean 570 g, range 480–620 g). The average nose to base of tail length for the male animals was 477 mm (range 369–611 mm) and for the females 398 mm (range 312–460 mm).

Dissection of the autonomic innervation of the viscera

The human and ferret material was subjected to an extensive dissection beginning where the right and left vagus nerves re-formed from the posterior pulmonary plexus immediately caudal to the bifurcation of the trachea. The subsequent course and distribution of these nerves were examined.

The lengths of nerve trunks were measured *in situ* by laying a piece of cotton along the course of the trunk, and the number of branches and their points of branching from the main trunk were noted.

Nerve trunk diameters and lengths are expressed in the text as mean ± S.E. (number of observations).

Histological studies

Light microscopy

Segments of the nerves listed below were removed from ferrets immediately after death induced by anaesthetic overdose or a blow on the head. The nerves were fixed in 10% formol saline and 10 μm sections were cut after embedding in paraffin wax. (i) Parasympathetic nerves: dorsal and ventral vagal trunks; dorsal and ventral nerves of Latarjet; hepatic and coeliac divisions of the vagus. (ii) Peri-arterial nerves: left and right gastric nerves; splenic nerves; short gastric nerves; common hepatic nerves.

The following human tissue was removed from autopsy specimens and treated in a similar way to the ferret tissue. (i) Parasympathetic nerves: anterior and posterior vagal trunks; anterior and posterior nerves of Latarjet; hepatic and coeliac vagal divisions. (ii) Peri-arterial nerves: as above.

In addition four posterior vagal trunks were removed from patients undergoing elective anterior lesser curve superficial seromyotomy coupled with posterior truncal vagotomy (performed by Mr T. V. Taylor, Manchester Royal Infirmary). The trunks were fixed by immediate immersion in 10% formol saline.

All the tissue was stained with Peters' silver proteinate (Peters, 1958) and Holmes' silver nitrate (Margolis & Pickett, 1956) to demonstrate axons, solochrome cyanin (Page, 1970) and luxol fast blue (Margolis & Pickett, 1956) to demonstrate myelin; 10 μm sections of human ulnar nerve were used throughout as a positive control for the presence of myelin. Mallory and Masson's trichrome stain for connective tissue was used on double-embedded tissue (Culling, 1957).

Electron microscopy

Three posterior vagal trunks were removed from patients undergoing elective gastric surgery. Ventral and dorsal vagal trunks, ventral and dorsal nerves of Latarjet, hepatic and coeliac divisions and left greater splanchnic nerves were removed from ferrets (three animals). All these nerves were immediately immersed in chilled 2·0 % glutaraldehyde in Pipes buffer (pH 7·2) for 1 hour. The material was post-fixed in 1 % osmium tetroxide (in Pipes buffer) for 1 hour. The tissue was infiltrated and embedded with low viscosity epoxy resin (Spurr, 1969). Thin and ultrathin sections were cut on a Porter–Blum (MT-2) ultramicrotome. The thin sections were stained with toluidine blue to allow a suitable field to be chosen, and the remaining ultrathin sections were treated with uranyl acetate and lead citrate. These sections were viewed with an electron microscope (AE1-EM6B) and photographed.

Physiological studies

Compound action potentials

The compound action potential was recorded in the abdominal vagus nerves of urethane-anaesthetised (1·5 g/kg i.p.) ferrets in response to electrical stimulation (up to 30 V, 0·1–1 msec, 0·5–1 Hz) of the peripheral cut end of either cervical vagus nerve (Andrews & Scratcherd, 1980). The activity in the nerve was amplified (Neurolog NL104), filtered (Neurolog NL125) and recorded on a cassette (T.E.A.C. R-61 data recorder). The latency of each component was measured from an averaged record (Neurolog NL750 Averager) and the conduction velocity was calculated from the latency and the measured conduction distance.

Gastric motility

Intragastric pressure was monitored in urethane-anaesthetised (1·5 g/kg i.p.) ferrets (Andrews & Scratcherd, 1980). Recording the intragastric pressure during stimulation of vagal nerve trunks and their divisions allowed a functional classification of these nerves and delineation of several pathways not readily accessible by dissection.

RESULTS

(I) *Gross anatomical description – Ferret*

(1) *Peri-oesophageal arrangement of nerve trunks*

After reforming from the dorsal pulmonary plexus both vagal elements coursed caudally against the ventral or dorsal surfaces of the thoracic oesophagus as single left and right vagal trunks. A communicating branch was consistently present, and linked the vagal trunks by coursing supero-inferiorly from the left to the right trunk on the dorsal surface of the oesophagus (Fig. 1). A corresponding nerve which passed from left to right ventral to the oesophagus was present in only two animals. Thus, the oesophageal plexus in the ferret was extremely simple in appearance.

The presence of a communicating nerve linking the left and right vagal trunks and of a mid-line pulmonary plexus around the tracheal bifurcation from which the trunks arose, made it clear that either trunk may contain fibres from both cervical vagus nerves.

Single ventral and dorsal vagal trunks were present at the diaphragmatic level.

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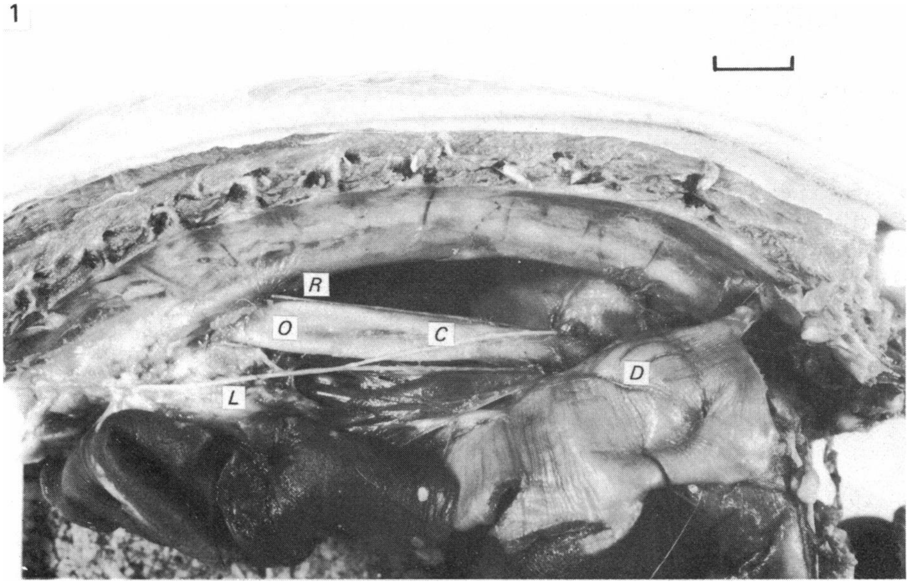

Fig. 1. Left lateral view of the thorax of a ferret showing left (*L*) and right (*R*) vagal trunks and communicating branch (*C*), diaphragm (*D*), oesophagus (*O*). Scale bar = 1 cm.

The mean diameter of the dorsal trunk (0·87 ± 0·06 mm ($n = 6$)) was significantly greater ($P > 0·05$) than that of the ventral trunk (0·64 mm ± 0·06 mm ($n = 6$)).

(2) *Ventral vagal trunk*

The ventral vagal trunk lay initially on the left lateral margin of the thoracic oesophagus but passed gradually medially to lie centrally or slightly to the left of centre of the lower thoracic oesophagus.

The ventral trunk gave off small branches to the oesophagus (to which it was always closely applied) and divided at a distance of 1·1 ± 0·1 cm ($n = 23$) caudal to the diaphragm on the intra-abdominal portion of the oesophagus into its two constant divisions, namely *hepatic* and *gastric*.

Hepatic division of the ventral vagal trunk (Figs. 2, 3)

This division was constantly present and the number of nerve bundles it contained is shown in Table 1A. No supradiaphragmatic hepatic division was present in any of the animals dissected.

The nerves of the hepatic division were visible against the caudate lobe of the liver as they passed between the two layers of the upper part of the gastrohepatic ligament towards the fissure for the ligamentum venosum. After a distance of 16 mm ± 3 mm ($n = 20$) it divided into:

(i) A branch to the porta hepatis, with a length of 12 ± 1·0 mm ($n = 22$).

(ii) A pyloric branch which descended in the free edge of the lesser omentum (following the proper hepatic artery) and divided to pass along both the right gastric and gastroduodenal arteries to the anterior and posterior surfaces of the antrum and pylorus of the stomach, to the first part of the duodenum and to the pancreas. The mean length of this branch was 17·5 ± 1·40 mm ($n = 19$).

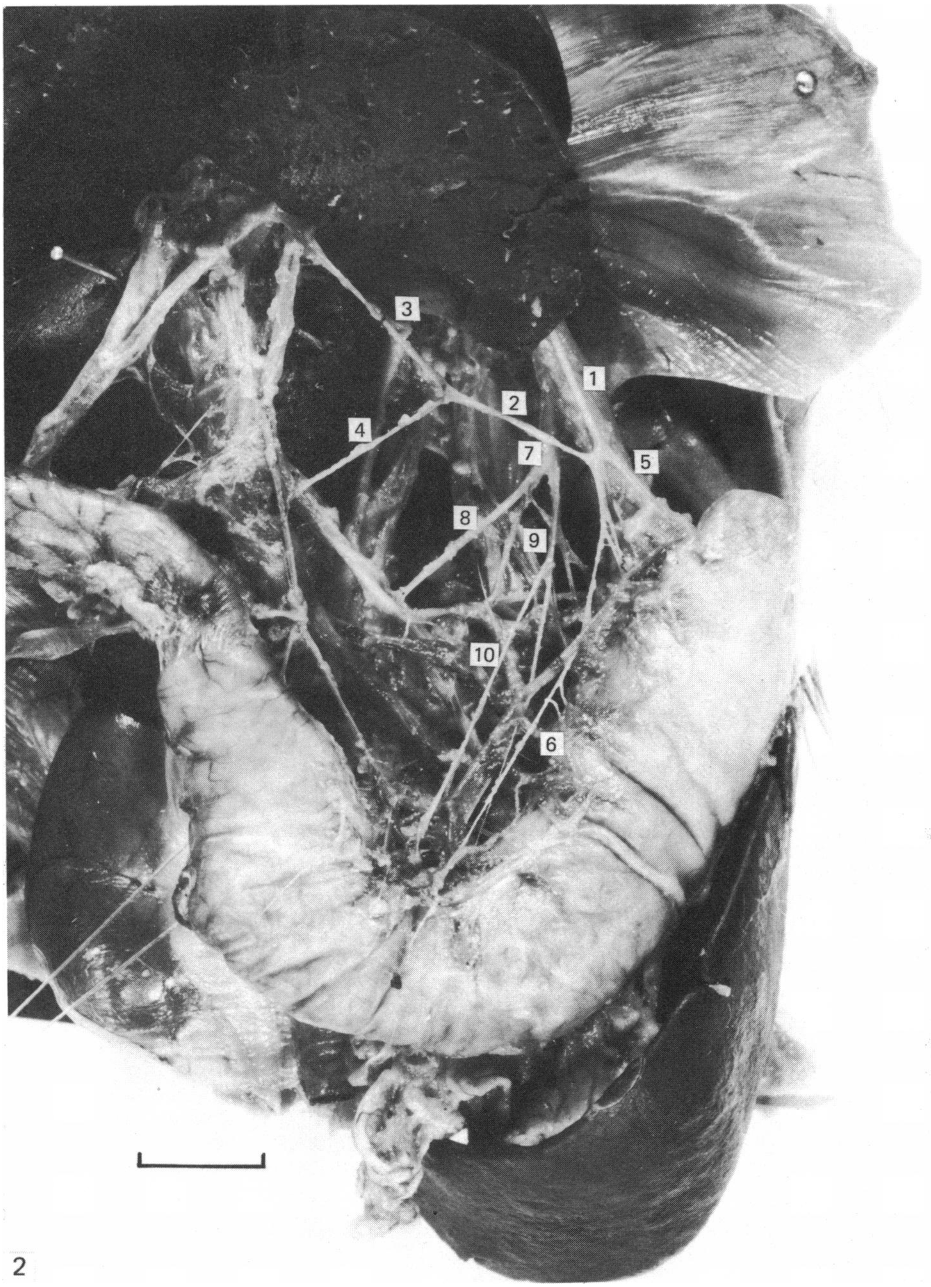

Fig. 2. The distribution of the ventral vagal trunk in the ferret. Scale bar = 1 cm. 1, ventral vagal trunk; 2, hepatic division of ventral vagal trunk; 3, hepatic branch of hepatic division; 4, pyloric branch of hepatic division; 5, gastric division of ventral vagal trunk; 6, ventral nerve of Latarjet; 7, dorsal vagal trunk; 8, coeliac division of dorsal vagal trunk; 9, gastric division of dorsal vagal trunk; 10, dorsal nerve of Latarjet.

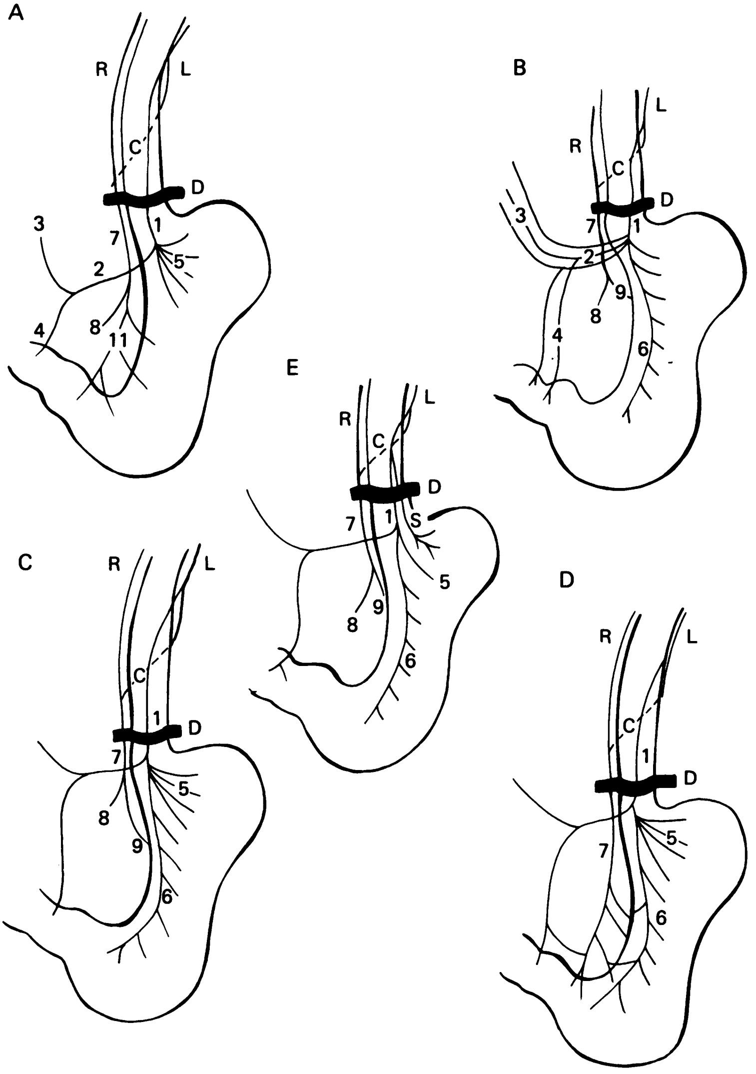

Fig. 3. (A–D). Diagram showing the major variations in the distribution of the ventral vagal trunk (ferret). (A) Ventral nerve of Latarjet arising from dorsal vagal trunk. (B) Multiple hepatic divisions. (C) Ventral nerve of Latarjet arising from ventral vagal trunk. (D) Double ventral nerve of Latarjet. (E) Supradiaphragmatic gastric division. Numbering as in Figs. 1 and 2; in addition, 11, ventral nerve of Latarjet arising from dorsal vagal trunk; S, supradiaphragmatic gastric division.

In ten of the specimens there were additional branches to the liver from the hepatic division, these being single in six and double in four cases. A double pyloric branch was present in one specimen which also showed two auxiliary hepatic branches (Fig. 3B).

Gastric division of the ventral vagal trunk (Fig. 2)

This division was the direct caudal continuation of the ventral vagal trunk along the lesser curvature of the stomach and was always present. It consisted of a number of discrete nerves which innervated the ventral surface of the stomach (Table 1B).

Table 1 A–B. *Composition of divisions of ventral vagal trunk in the ferret*

(A) Hepatic division		(B) Ventral division	
Number of nerves in the division	Number of specimens	Number of nerves passing to ventral surface of cardia and fundus	Number of specimens
0	1	0	0
1	20	1	0
2	1	2	0
3	1	3	1
—	—	4	4
—	—	5	3
—	—	6	9
—	—	7	3
—	—	8	2
—	—	9	0
—	—	10	1
Total	23		23

Table 1 C–D. *Composition of divisions of dorsal vagal trunk in the ferret*

(C) Coeliac division		(D) Dorsal gastric division	
Number of nerves in the division	Number of specimens	Number of nerves passing to dorsal surface of cardia and fundus	Number of specimens
0	0	0	0
1	6	1	0
2	4	2	0
3	5	3	1
4	2	4	0
5	1	5	2
6	4	6	5
7	0	7	6
8	1	8	4
—	—	9	2
—	—	10	2
—	—	11	0
—	—	12	0
—	—	13	1
Total	23		23

In 8 of the 23 specimens, the most medial of the branches of this division was the principal ventral nerve of the lesser curvature: the ventral nerve of Latarjet. This nerve passed parallel to the lesser curvature of the stomach between the two layers of the gastrohepatic ligament and crossed ventral to the main stem of the left gastric artery. It gave off an average of six branches to the ventral aspect of the body of the stomach before it divided into three to six terminal branches in the region of the incisura angularis to supply the ventral aspect of the pyloric antrum (Fig. 3C).

The ventral nerve of Latarjet was also seen to communicate with the corresponding dorsal nerve of Latarjet as both passed through the gastrohepatic ligament. Indeed, in the remaining fifteen specimens dissected, the ventral nerve of Latarjet actually took origin from the dorsal gastric division (Fig. 3A). In all but two of these animals the ventral gastric division innervated only the ventral aspects of the cardia, fundus and proximal portion of the body of the stomach, while the ventral nerve of Latarjet supplied the distal area of the body and the pyloric antrum. In two of these animals, however, this nerve was effectively duplicated because the ventral gastric division itself also gave rise to a corresponding nerve (Fig. 3D).

The ventral nerve of Latarjet never continued directly on to the ventral aspect of the pylorus although a communicating branch was present between this nerve and the perivascular nerves along the right gastric vessels in two specimens.

The nerve supply to the ventral aspects of the cardia and fundus of the stomach was derived from a number of sources:

(i) As the gastric division of the ventral vagal trunk passed over the intra-abdominal portion of the oesophagus proximal to the point of origin of the ventral nerve of Latarjet, it divided into several discrete branches which never formed a ventral gastric plexus (Table 1B).

(ii) In one animal a supradiaphragmatic division was present. This passed to the left of centre on the intra-abdominal oesophagus before dividing into six branches to the ventral aspects of the cardia and fundus of the stomach (Fig. 3E). This division communicated with the normal subdiaphragmatic gastric branches of the ventral vagal trunk which passed to this area of the stomach.

(iii) Proximal branches that were given off from the ventral nerve of Latarjet passed to the distal part of the cardia and the proximal portion of the body of the stomach.

No (ventral) coeliac division arose from the ventral vagal trunk in any of the 23 dissections.

(3) *Dorsal vagal trunk*

The dorsal vagal trunk crossed gradually from the right lateral margin of the oesophagus to lie to the right of centre on the dorsal surface of the subdiaphragmatic portion of the oesophagus (Fig. 4). Like the ventral vagal trunk, it was closely applied to the oesophagus.

The dorsal trunk gave off numerous small branches of supply to the oesophagus and ended by dividing into its two constant *coeliac* and *gastric* divisions at a distance of 1·77 ± 0·08 cm caudal to the diaphragm.

Coeliac division of the dorsal vagal trunk (Figs. 4, 5)

This division was constantly present, had a length of 20 ± 0·68 mm ($n = 23$), and was larger than any other division given off from either the ventral or dorsal vagal trunks. No supradiaphragmatic coeliac division was present in any of the 23 dissections.

The coeliac division consisted of a variable number of peri-arterial nerves (Table 1C) which passed along the stem of the left gastric vessels to reach and contribute to the coeliac plexus. Macroscopically it was impossible to trace these nerves through the plexus with any degree of certainty because of the preponderance of connective tissue and because of the dual autonomic input to this plexus. Gross anatomical preparations could not clarify which of the nerves that surrounded the left gastric vessels passed into or arose from the coeliac plexus. Moreover, it was impossible to determine macroscopically whether those nerves that could be positively identified as passing from the coeliac plexus to the stomach were sympathetic

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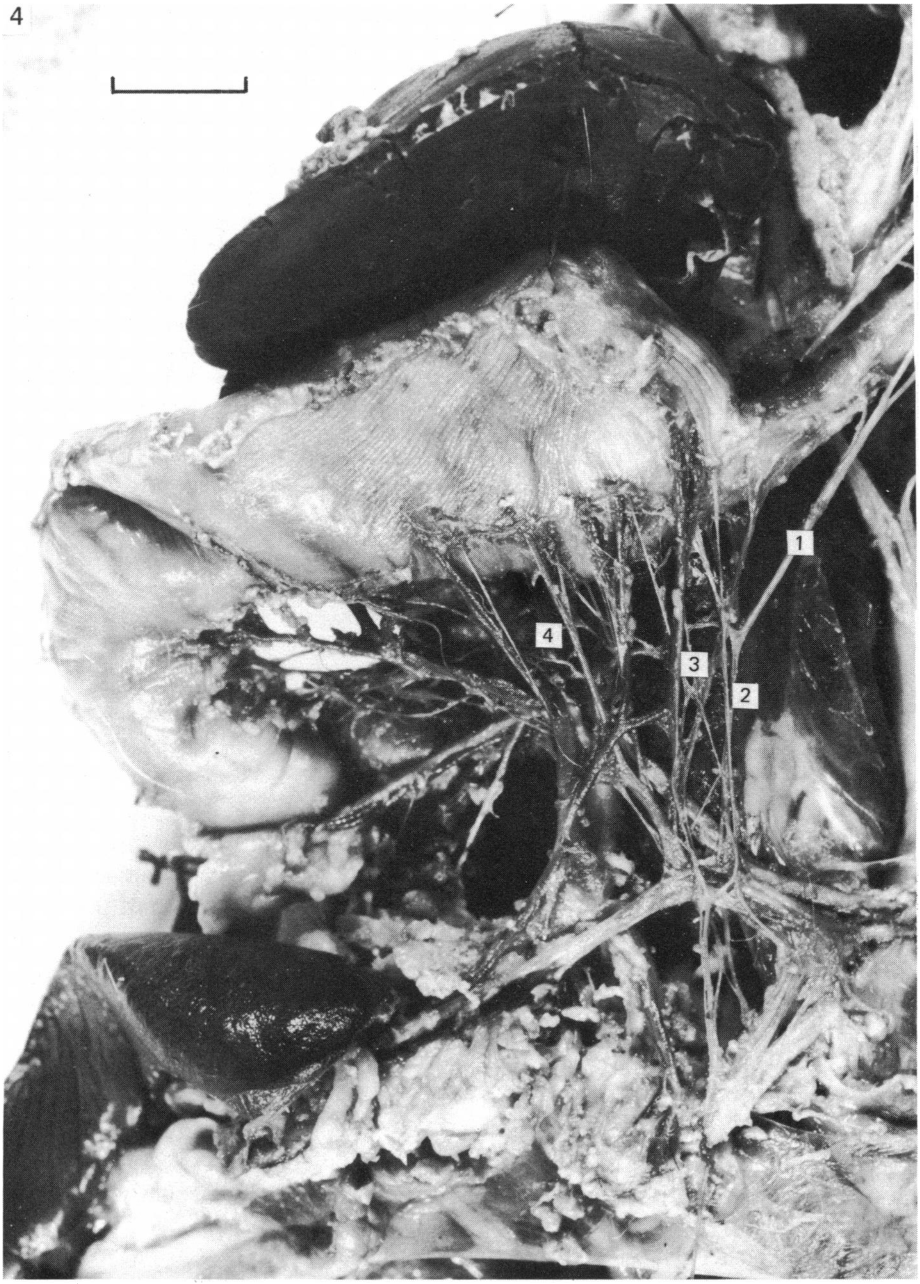

Fig. 4. The distribution of the dorsal vagal trunk in the ferret. Scale bar = 1 cm. 1, dorsal vagal trunk; 2, coeliac division of dorsal vagal trunk; 3, gastric division of dorsal vagal trunk; 4, dorsal nerve of Latarjet.

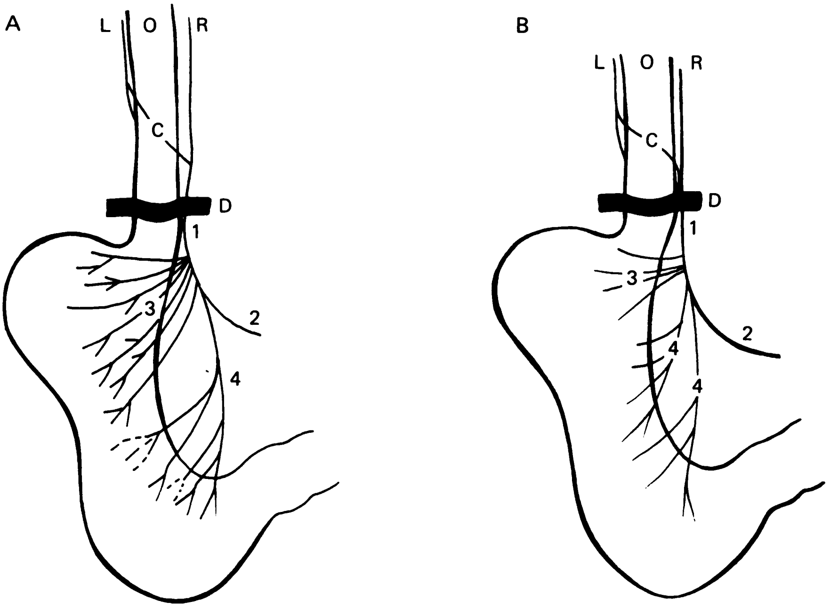

Fig. 5 (A–B). Diagram showing the major variations in the distribution of the dorsal vagal trunk (ferret). (A) Single dorsal nerve of Latarjet. (B) Double dorsal nerve of Latarjet. Numbering as in Figs. 1 and 4.

or parasympathetic in nature. Unquestionably, however, this provided a subsidiary route for innervation of the stomach, thus augmenting that from the gastric divisions of both the ventral and dorsal vagal trunks.

All the vessels which arose from the coeliac axis (splenic, common hepatic and left gastric) and their branches were surrounded by a leash of fine nerves. Thus, the greater curvature of the stomach received innervation via the plexuses on the right and left gastro-epiploic arteries, while the innervation of the lesser curvature from the ventral and dorsal vagal trunks was supplemented by nerves which passed along the right and left gastric vessels: the nerves to the stomach which surrounded the left gastric vessels came directly from the coeliac plexus while those associated with the right gastric vessels originated from two principal sources:

(i) The descending rami from the hepatic division of the ventral trunk which ran in the free edge of the lesser omentum and passed along the right gastric vessels.

(ii) Nerves which passed from the coeliac plexus along the common hepatic and then the proper hepatic arteries reached the liver by following the proper hepatic artery in the free edge of the lesser omentum or, alternatively, followed the right gastric artery to the stomach.

These two groups of nerves which followed the right gastric vessels to the first part of the duodenum and the pylorus were seen to communicate with the terminal branches of the ventral and dorsal gastric divisions in the region of the incisura angularis of the stomach in two animals.

As with the nerves on the left gastric vessels, it was impossible to tell macroscopically whether those nerves associated with the other branches of the coeliac axis were sympathetic or parasympathetic due to the dual autonomic input to the coeliac plexus. It was clear, however, that they provided an important source of innervation to both the lesser and greater curvatures of the stomach.

Gastric division of the dorsal vagal trunk (Fig. 4)

The dorsal gastric division was the direct caudal continuation of the dorsal vagal trunk along the lesser curvature and was invariably present. It consisted of a number of discrete nerves to the dorsal surface of the stomach (Table 1D; Fig. 5A).

In all dissections the most medial of its branches was the principal dorsal nerve of the lesser curvature: the dorsal nerve of Latarjet. This nerve passed amongst the dorsal gastric branches and tributaries of the left gastric vessels and ran parallel to the lesser curvature of the stomach in the gastrohepatic ligament. It gave off approximately six branches to the dorsal aspect of the body of the stomach and ended by dividing on the dorsal surface of the incisura angularis into four to six branches which passed to the dorsal aspect of the pyloric antrum. The dorsal nerve of Latarjet did not send any branches to the pylorus in any of the dissections.

Double and quadruple dorsal nerves of Latarjet were found in six and one specimens, respectively. In each case the nerve that lay furthest from the lesser curvature supplied a more distal segment of the body of the stomach (Fig. 5B).

In 15 animals the dorsal gastric division gave origin to the ventral nerve of Latarjet and this nerve supplied both the ventral and dorsal aspects of the body and pyloric antrum.

The innervation of the dorsal aspects of the cardia and fundus was derived from a number of sources:

(i) Separate branches of the dorsal gastric division that originated as this division passed distally over the intra-abdominal portion of the oesophagus, proximal to the point of origin of the dorsal nerve of Latarjet (Fig. 5A). These branches were always discrete and were never seen to form a dorsal gastric plexus (Table 1D).

(ii) Proximal branches that were given off from the dorsal nerve of Latarjet passed to the distal part of the cardia and the proximal portion of the body of the stomach..

No hepatic or supradiaphragmatic gastric divisions arose from the dorsal vagal trunk in any of the 23 dissections.

(II) *Gross anatomical description – human*

The results obtained from the human dissections were essentially similar to those outlined previously for the ferret.

(1) *Peri-oesophageal arrangement of nerves*

The right and left vagus nerves coursed caudally along the lateral borders of the oesophagus, as a variable but almost symmetrically constant number of branches (Table 2), for a distance of approximately 2·5–5·0 cm prior to forming a plexus around the circumference of the oesophagus. This peri-oesophageal plexus was usually more complicated than that present in the ferret, although it varied considerably from a fairly simple arrangement of nerves that constituted almost a direct caudal continuation of the right and left vagus nerves with very few intercommunicating branches, to an extremely complicated and truly peri-oesophageal network of intercommunicating nerves. In the main, however, the caudal continuation of the left vagus nerve from the posterior pulmonary plexus tended to be distributed to the anterior surface of the oesophagus as the anterior oesophageal plexus, while the right vagus was distributed mainly to the posterior aspect of the oesophagus thus forming the posterior oesophageal plexus. Because some fibres from the right and

Table 2. *Total number of branches derived from posterior pulmonary plexus and passing caudally along oesophagus in man*

Number of branches	Number of cadavers Right vagus	 Left vagus
0	0	0
1	1	1
2	8	8
3	10	7
4	11	10
5	1	4
6	0	1
7	0	0

Table 3 A. *Composition of anterior oesophageal plexus in man*

Number of branches	Number of cadavers Right vagus	 Left vagus
0	11	0
1	15	11
2	5	10
3	0	7
4	0	3
5	0	0

Table 3 B. *Composition of posterior oesophageal plexus in man*

Number of branches	Number of cadavers Right vagus	 Left vagus
0	0	5
1	9	16
2	10	7
3	9	2
4	3	1
5	0	0

Table 4. *Number of vagal trunks present at oesophageal hiatus in man*

Number of trunks	Number of cadavers Anterior vagal trunk	 Posterior vagal trunk
0	0	0
1	30	29
2	0	2
3	0	0
4	1	0
5	0	0

left vagus nerves passed to the anterior and posterior oesophageal plexuses, respectively, and communicating nerves passed around the borders of the oesophagus, both the anterior and posterior oesophageal plexuses contained nerve fibres from the right and left vagal nerves. The contributions made from the right and left vagus nerves to the peri-oesophageal plexuses are plotted in Table 3 A and B.

A variable number of anterior and posterior vagal trunks (Table 4) originated from the peri-oesophageal plexus on the distal one third of the thoracic oesophagus, but from the Table it is apparent that a single trunk was the most common arrangement.

The level at which these vagal trunks formed is shown in Table 5A and B.

Table 5A. *Levels of formation of vagal trunks with respect to diaphragm in man*

CMS	Number of cadavers Anterior vagal trunk	 Posterior vagal trunk
	Subdiaphragmatic	
1·1–2·0	0	0
0·1–1·0	2	1
At hiatus	7	7
	Supradiaphragmatic	
0·1–1·0	5	9
1·1–2·0	7	10
2·1–3·0	3	2
3·1–4·0	7	1
4·1–5·0	0	1
5·1–6·0	0	0

Table 5B. *Mean values*

	CMS supradiaphragmatically ± S.E.M.
Anterior vagal trunk	1·62 ± 0·31
Posterior vagal trunk	1·30 ± 0·21

Table 6A. *Diameter of vagal trunks at the level of the oesophageal hiatus in man*

MMS	Number of cadavers Anterior vagal trunk	 Posterior vagal trunk
0·1–1·0	3	0
1·1–2·0	10	3
2·1–3·0	15	8
3·1–4·0	2	9
4·1–5·0	1	8
5·1–6·0	0	2
6·1–7·0	0	1

Table 6B. *Mean values*

	Diameter (mm ± S.E.M.)
Anterior vagal trunk	2·60 ± 0·15
Posterior vagal trunk	4·00 ± 0·20

Short nerves that pierced the oesophageal musculature were seen to arise from the right and left vagus nerves as they emerged from the [posterior] pulmonary plexus, and others arose from both the peri-oesophageal plexus and the vagal trunks. Some of the branches which originated from the vagal trunks appeared to pass in a cephalic direction into the oesophageal musculature.

In one of the cadavers, a communicating branch passed from the upper part of the left thoracic ganglionated paravertebral sympathetic trunk to the posterior oesophageal and aortic plexuses.

(2) *Anterior vagal trunk*

Analysis of the number of anterior vagal trunks present (Table 4) and their diameters (Table 6A and B) at the diaphragmatic level (oesophageal hiatus in the diaphragm) revealed that a single anterior vagal trunk was usually present at this level and had a mean diameter of 2·6 ± 0·15 mm, although on one occasion four trunks were found and each of these trunks gave rise to supradiaphragmatic gastric and hepatic divisions.

Having arisen from the anterior oesophageal plexus at an average distance of

Table 7A–B. *Classification of vagal divisions in man*

Division	(A) Number of cadavers with this division from anterior vagal trunk	(B) Number of cadavers with this division from posterior vagal trunk
Coeliac	6	31
Gastric	31	31
Hepatic	31	1

Table 8. *Composition of hepatic division in man*

Number of branches	Number of cadavers
0	0
1	10
2	13
3	0
4	3
5	3
6	2
7	0

1·62 ± 0·31 cm above the diaphragm (Table 5B), the anterior vagal trunk ran caudally on the anterior surface of the oesophagus to lie either on the centre or slightly to the right of centre of the subdiaphragmatic portion of the oesophagus.

As in the ferret, the trunk was closely applied to the oesophagus, and the peri-oesophageal connective tissue had to be dissected away to expose the anterior vagal trunk and its oesophageal branches.

The trunk divided on the subdiaphragmatic oesophagus into the *hepatic* and *gastric* divisions. A *coeliac* division was occasionally present (Table 7A).

Hepatic division of the anterior vagal trunk

This division usually arose from the anterior vagal trunk as it passed over the intra-abdominal portion of the oesophagus, although a supradiaphragmatic hepatic division was present in three of the 31 dissections.

One of these cadavers had four anterior vagal trunks and each gave origin to a separate hepatic division. In the remaining two cadavers, the supradiaphragmatic hepatic divisions arose as single stems directly from the anterior oesophageal plexus. Each of these supradiaphragmatic divisions subsequently followed the normal distribution of their subdiaphragmatic counterparts.

The hepatic division consisted of a number of discrete nerves (Table 8) and its course was identical to that encountered in the ferret. It followed the hepatic branch of the left gastric artery through the gastrohepatic ligament when this branch was present (nine cadavers). This particular artery was not present in any of the ferret dissections.

Gastric division of the anterior vagal trunk

The nerves in this division were almost identical in their distribution to those in the ferret. Thus, the anterior gastric division was the direct caudal continuation of the

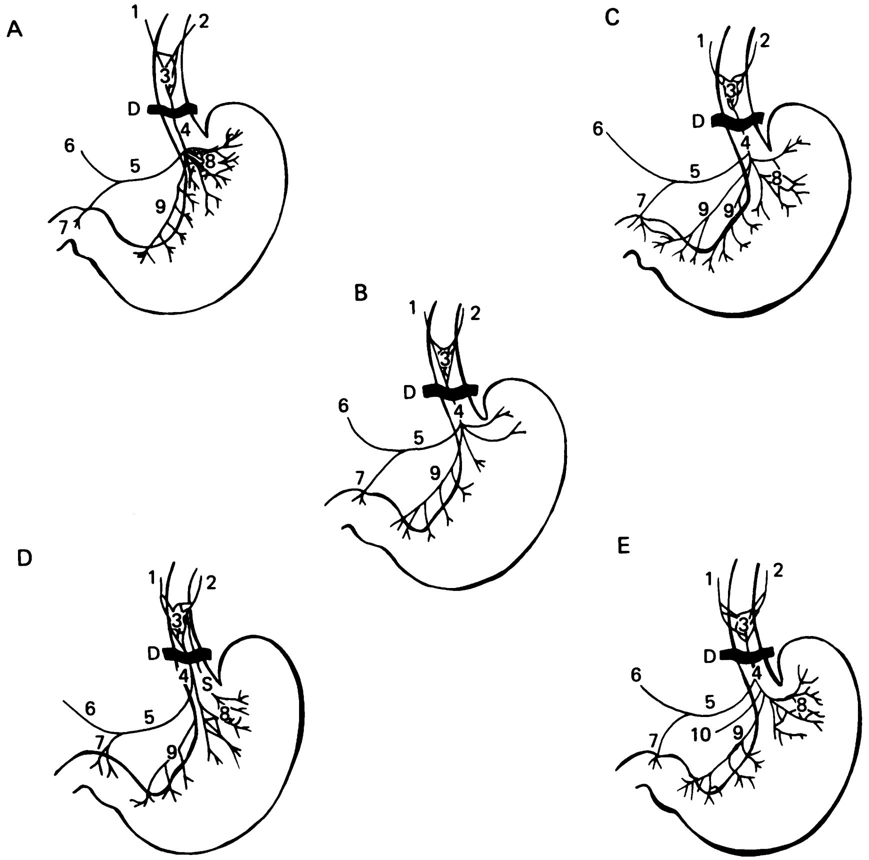

Fig. 6 (A–E). Diagram showing the major variations in the distribution of the anterior vagal trunk (human). (A) Anterior gastric plexus present (normal pattern). (B) Anterior gastric plexus not present. (C) Double anterior nerve of Latarjet arising from anterior vagal trunk. (D) Supradiaphragmatic gastric division. (E) Anterior coeliac division of anterior vagal trunk. 1, right vagus nerve; 2, left vagus nerve; 3, anterior oesophageal plexus; 4, anterior vagal trunk; 5, anterior hepatic division; 6, ascending ramus to liver; 7, pyloric branch of hepatic division; 8, anterior gastric plexus (discrete branches in Fig. 6B); 9, anterior nerve of Latarjet; 10, anterior coeliac division; D, diaphragm; S, supradiaphragmatic gastric division.

anterior vagal trunk along the lesser curvature of the stomach. It consisted of a series of branches arranged either in the form of a plexus situated on the anterior aspect of the cardia, fundus and proximal portion of the body of the stomach (18 cadavers; Fig. 6A) or formed a group of discrete nerves on the anterior aspect of the stomach (13 cadavers; Fig. 6B).

Similarly, the anterior nerve of Latarjet was present and passed parallel to, but approximately 1 cm from, the lesser curvature of the stomach and ran anterior to the main stem of the left gastric artery. It gave off 1–7 branches to the anterior aspect of the body of the stomach before it ended in 4–6 terminal branches as a 'crow's foot' (Hedenstedt & Moberg, 1971) arrangement of nerves in the region of the incisura angularis. The branches from this division passed anterior to, and obliquely across, the vessels of the lesser curvature but showed no tendency to run directly with these vessels.

Occasional communicating nerves passed from these terminal branches of the

Table 9A. *Composition of anterior gastric division in man*

Number of nerves present	Number of cadavers: gastric branches to anterior aspects of cardia and fundus*
0	0
1	1
2	9
3	5
4	1
5	3
6	10
7	1
8	0
9	1

* Only branches arising *directly* from the anterior gastric division are included. This does *not* include branches arising from the anterior nerve of Latarjet.

Table 9B. *Composition of posterior gastric division in man*

Number of nerves present	Number of cadavers: gastric branches to posterior aspects of cardia and fundus*
0	0
1	0
2	4
3	7
4	3
5	0
6	10
7	1
8	3
9	3

* Only branches arising *directly* from the posterior gastric division are included. This does *not* include branches arising from the posterior nerve of Latarjet.

anterior nerve of Latarjet to the peri-arterial nerves of the right gastric artery and indeed the anterior nerve of Latarjet itself continued to the anterior surface of the pyloric canal and sphincter in five cadavers.

Double anterior nerves of Latarjet were present in seven cadavers. In these, it was usual for the nerve that was furthest from the lesser curvature to supply the more distal segment of the stomach (Fig. 6C).

The anterior nerve of Latarjet communicated with the corresponding posterior nerve of Latarjet as both nerves passed through the gastrohepatic ligament. Indeed, in one body with two posterior nerves of Latarjet, one passed to the anterior surface of the distal part of the body of the stomach to augment the normal innervation from the anterior nerve of Latarjet which innervated a more proximal segment of the body.

The nerve supply to the anterior aspects of the cardia and fundus of the stomach was similar to the three sources encountered in the ferret:

(i) In 18 dissections, 1–9 branches (Table 9A) which originated from the anterior gastric division formed an anterior gastric plexus on the anterior surface of the cardia, fundus and proximal portion of the body of the stomach. In the remaining 13 cadavers a series of 1–9 discrete subdiaphragmatic branches (Table 9A) could be traced from this division to the same area of the stomach without any plexus formation (Fig. 6B).

(ii) In five cadavers with supradiaphragmatic gastric divisions, four were single nerves which originated from the anterior oesophageal plexus while the fifth was quadruple and originated from each of four separate anterior vagal trunks. In all five cases, however, the divisions passed distally and to left of centre on the subdiaphragmatic portion of the oesophagus and supplied a segment of the stomach as far distal as the proximal part of the body (Fig. 6D). All the supradiaphragmatic gastric nerves communicated with the normal subdiaphragmatic gastric branches of the anterior gastric division which passed to this area of the stomach.

(iii) As in the ferret, branches were given off from the anterior nerve of Latarjet

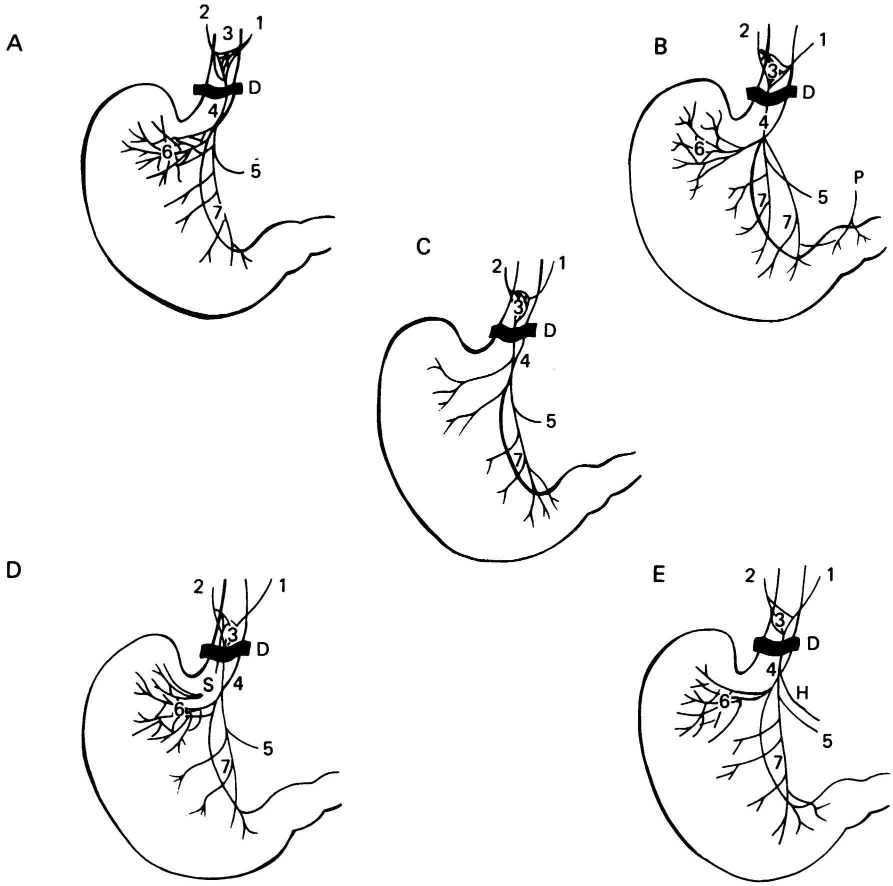

Fig. 7 (A–E). Diagram showing the major variations in the distribution of the posterior vagal trunk (human). (A) Posterior gastric plexus present (normal pattern). (B) Double posterior nerves of Latarjet. (C) No posterior gastric plexus. (D) Supradiaphragmatic gastric division. (E) Posterior hepatic division. 1, right vagus nerve; 2, left vagus nerve; 3, posterior oesophageal plexus; 4, posterior vagal trunk; 5, posterior coeliac division; 6, posterior gastric plexus; 7, posterior nerve of Latarjet; S, supradiaphragmatic gastric division; H, posterior hepatic division; P, pyloric branch of anterior hepatic division.

and passed to the distal area of the cardia and the proximal portion of the body of the stomach.

Coeliac division of the anterior vagal trunk (Fig. 6E)

This division was a minor offshoot of the anterior vagal trunk and was present in only six dissections. It was represented by a single ramus which passed along the stem of the left gastric artery towards the coeliac plexus.

(3) *Posterior vagal trunk* (Fig. 7)

The number and diameter of the posterior vagal trunks present at the level of the oesophageal hiatus in the diaphragm are shown in Tables 4 and 6. A single posterior vagal trunk was usually present at this level, with a mean diameter of 4·0 ± 0·2 mm. It arose from the posterior oesophageal plexus at an average distance of 1·3 ± 0·21 cm (Table 5B) above the diaphragm and inclined to the right to lie lateral to the right margin of the subdiaphragmatic oesophagus. This posterior vagal trunk was never as closely applied to the peri-oesophageal connective tissue as was the anterior trunk. Indeed, it was quite usual to find the subdiaphragmatic portion of the posterior vagal trunk very closely related to the abdominal aorta.

All the posterior trunks lay to the right of centre on the posterior aspect of the oesophagus at the diaphragm.

The posterior vagal trunk gave off numerous small branches to the distal third of the thoracic oesophagus and, as with the anterior vagal trunk, some of these nerves appeared to pierce the oesophageal musculature in a cephalic direction.

The posterior vagal trunk usually divided into *coeliac* and *gastric* divisions on the abdominal portion of the oesophagus, although a *hepatic* division was occasionally present (Table 7B).

Coeliac division of the posterior vagal trunk (Fig. 7A)

This division was identical morphologically to that present in the ferret. No supradiaphragmatic coeliac division was present in any of the 31 dissections. It was composed of a bundle of peri-arterial nerves that passed along the stem of the left gastric artery towards the coeliac plexus. This plexus had extensions along each of the vessels arising from the coeliac axis, and along their branches. Thus, the lesser and greater curvatures of the stomach received an innervation via the gastric (right and left) and gastro-epiploic (right and left) arteries to augment that from the anterior and posterior vagal trunks.

In addition, in one of the subjects, a branch from the coeliac division passed along the left gastric artery and communicated with nerves present around the common hepatic artery. This branch could then be traced further on the gastroduodenal artery until eventually it reached the posterior aspect of the pylorus, the first part of the duodenum and the head of the pancreas. It must be stressed, however, that this nerve was present in only one cadaver.

Gastric division of the posterior vagal trunk

The nerves in this division were almost identical in their distribution to those in the ferret. The posterior gastric division was the direct caudal continuation of the posterior vagal trunk along the lesser curvature of the stomach. The most medial of its branches was the posterior nerve of Latarjet and this nerve was almost identical in its distribution to its anterior counterparts. It lay parallel to, but approximately 1 cm from, the margin of the lesser curvature, passed posterior to the main stem of the left gastric artery and was recognisable with ease even in the more obese cadavers.

The posterior nerve of Latarjet gave off 3–6 branches along the lesser curvature and ended by dividing into 3–6 terminal branches on the posterior surface of the angular incisure as the 'crow's foot' arrangement of Hedenstedt & Moberg (1971). The main nerve continued distally as a discrete branch to the posterior aspect of the pyloric canal and sphincter in one cadaver only, although it communicated with the peri-arterial nerves of the right gastric artery in a further three specimens.

As with the anterior gastric division, it was possible to find double posterior nerves of Latarjet, but on only two occasions. On one of these occasions the posterior nerve of Latarjet actually crossed onto the anterior surface of the body of the stomach to augment the normal innervation from the anterior nerve of Latarjet which innervated a more proximal segment of the body. Again it was usual for the nerve which lay furthest from the lesser curvature to supply a more distal area of the stomach (Fig. 7B).

Similarly, the branches from the posterior gastric division showed no tendency to run directly with the vessels of the lesser curvature but lay posterior to these vessels and crossed them obliquely, before entering the musculature of the stomach.

The nerve supply to the posterior aspect of the cardia and fundus of the stomach was practically identical to that present on the anterior surface. Again, the nerves were derived from three sources:

(i) Separate branches of the posterior gastric division originated as the division passed distally over the intra-abdominal portion of the oesophagus, proximal to the point of origin of the posterior nerve of Latarjet (Fig. 7A). These branches assumed the form of a posterior gastric plexus on the surface of the cardia, fundus and proximal portion of the body in 20 dissections (Fig. 7A) and, as such, consisted of a network of communicating nerves linking the 1–9 main branches to this area (Table 9B). In the remaining 11 cadavers a series of 1–9 discrete subdiaphragmatic branches could be traced from the posterior gastric division to this area of the stomach without any clear indication of the existence of a plexus (Fig. 7C; Table 9B).

(ii) In two cadavers there were single supradiaphragmatic gastric divisions. One arose from the posterior oesophageal plexus and the other from the posterior vagal trunk, but both nerves coursed distally to lie to the right of centre on the posterior aspect of the subdiaphragmatic oesophagus before reaching the posterior aspect of the cardia and fundus where they communicated with the normal subdiaphragmatic gastric branches from the posterior vagal trunk which passed to this area (Fig. 7D).

(iii) Proximal branches that were given off from the posterior nerve of Latarjet passed to the distal part of the cardia and the proximal portion of the body of the stomach.

Hepatic division of the posterior vagal trunk (Fig. 7E)

This particular division was seen in only one cadaver and consisted of a slender single nerve that passed from the posterior gastric division to the fissure for the ligamentum venosum along the hepatic branch of the left gastric artery. It communicated with the lowest of three branches of the hepatic division of the anterior vagal trunk in the upper part of the gastrohepatic ligament. It could not be traced any further than to the fissure for ligamentum venosum due to the presence of the hepatic plexus.

(III) *Histological studies*

Under the light microscope the abdominal vagal trunks in man and the ferret were seen to be surrounded by a considerable layer of connective tissue. In man, the posterior vagal trunks had appeared to be single on gross dissection but were found to contain a number of discrete fasciculi intimately surrounded by connective tissue when examined histologically.

In fourteen human specimens (from surgery or autopsy), the mean number of fasciculi present in the posterior vagal trunks was 15 (range 5–32). No figures for human anterior vagal trunks were obtained because the only specimens available were from autopsy or cadavers and had suffered from post mortem autolysis.

In the ferret, however, single fasciculi were present in all ten of the ventral vagal trunks examined and in all but one of the ten dorsal vagal trunks. The one remaining dorsal vagal trunk was composed of three discrete fasciculi. The dorsal communicating branch was also composed of a single fasciculus in all ten specimens examined.

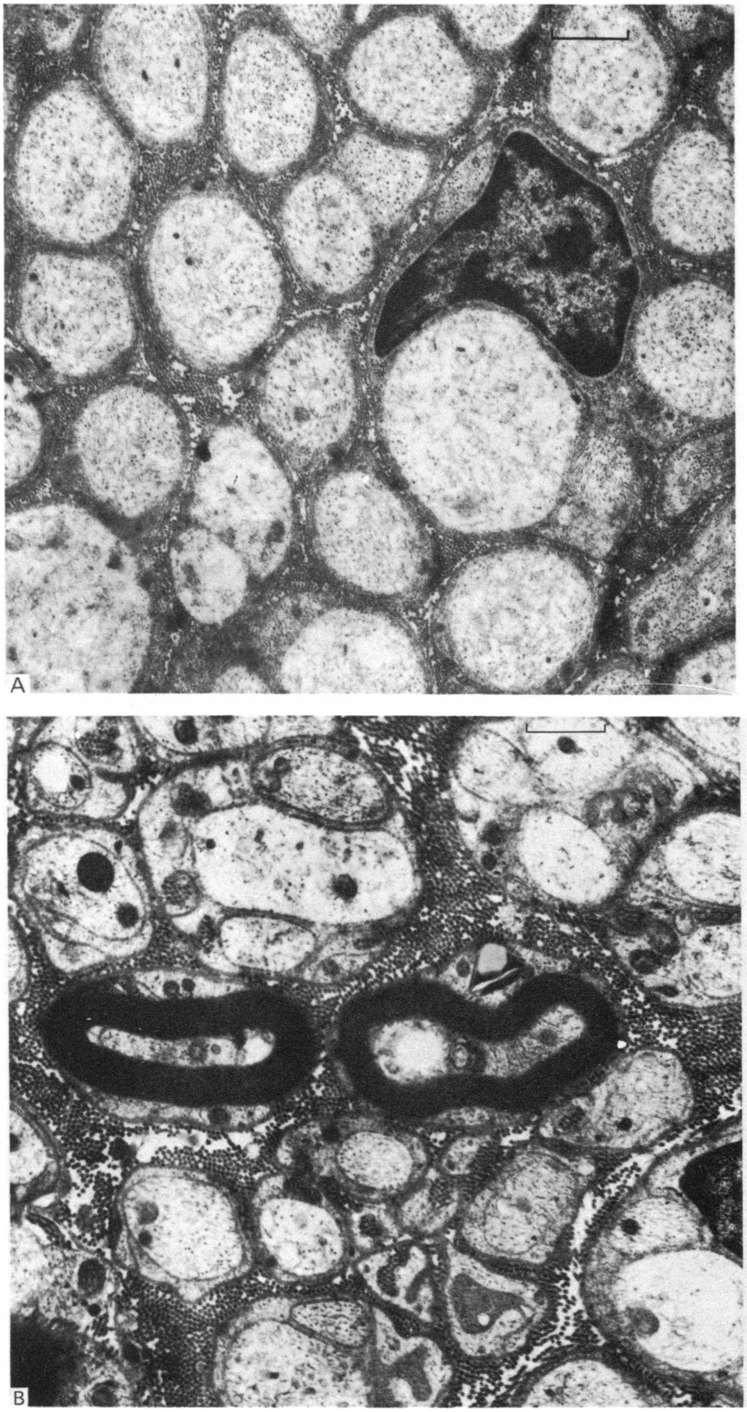

Fig. 8. Electron micrographs of transverse sections of the ventral abdominal vagus in the ferret (A) and the posterior abdominal vagus in man (B). Scale bar = 1 μm.

In both the human and ferret material all the fasciculi were composed mainly of fibres which did not show a positive reaction to a stain for myelin. A few positively-stained small diameter fibres were present in all the branches of ferret and human vagus nerves that were examined. These observations on the distribution of myelinated and unmyelinated nerve fibres were confirmed with the electron microscope (Fig. 8).

The presence in the nerve trunks of large amounts of connective tissue, formed mainly from collagen, was confirmed by electron microscopy.

Total nerve fibre counts have not yet been performed on human tissue due to the difficulty of obtaining a large enough sample of fresh vagal trunks removed under consistent conditions. In the ferret, an analysis of the fibre numbers, types and afferent: efferent ratio is in progress, but difficulty has been encountered in localising the extent of the nodose ganglion prior to performing chronic supra-nodose vagotomy.

(IV) *Physiological studies*

(1) *Compound action potentials*

In vivo recording of the compound action potential in anaesthetised ferrets confirmed the presence of a large component with a latency appropriate to conduction in C-fibres. This confirms the previous demonstration that the abdominal vagus nerve in the ferret contained efferent fibres with a conduction velocity of 1·20 ± 0·29 m/sec (Andrews, Fussey & Scratcherd, 1980), and also confirms the presence in the abdominal vagus nerves of afferent fibres (originating from the stomach) with a conduction velocity of 0·91 ± 0·21 m/sec (Andrews, Grundy & Scratcherd, 1980).

Stimulation of either cervical vagus nerve evoked a compound action potential in both the dorsal and ventral abdominal vagal branches, thus confirming the anatomical observations that both cervical vagus nerves contribute fibres to both abdominal vagus nerves. These studies also show that stimulation of the left cervical vagus nerve evoked a large response in the crossing branch and the dorsal trunk, but a smaller response in the ventral vagal trunk, thus confirming the observation that the left cervical vagus nerve makes a large contribution to the dorsal trunk via the communicating branch. It should be remembered that compound action potentials provide no evidence as to the absolute number of nerve fibres involved, and, with the technique used here, it is not possible to distinguish between the contribution of afferent and efferent nerve fibres.

Recordings of compound action potentials from human abdominal vagal branches *in vitro* show that the nerve contained components with conduction velocities ranging between 0·15 m/sec and 3·9 m/sec. The majority of potentials had latencies appropriate to C-fibre conduction (Andrews & Taylor, 1982).

(2) *Gastric motility*

Changes in intragastric pressure in anaesthetised ferrets were used to assess the functional nature of the visceral nerves described in (1) above. Stimulation of the peripheral cut end of the abdominal vagal trunk and divisions always produced an increase in intragastric pressure and stimulation of gastric contractions. These responses were blocked by atropine (1 mg/kg i.v.). In the presence of atropine, stimulation of the abdominal vagal trunk nerves produced a prompt fall in intragastric pressure followed by a rebound contraction when stimulation was stopped. The intragastric pressure took several minutes to return to control levels even after 10

Table 10. *Summary of studies on the vagal innervation of the human stomach*

Authors	Number of nerve stems passing through the diaphragm	Presence of plexuses on the stomach	Innervation of pylorus	Distribution of posterior trunk to stomach
Swan (1834; 1864)	1 anterior 2 posterior	Anterior present, no posterior	From hepatic plexus	To cardia and posterior aspect of stomach
Bourgery (1844)	3 anterior numerous posterior	Anterior present, no posterior	From hepatic plexus	Posterior aspect cardia, fundus and body along lesser curvature
Kollmann (1860)	1 anterior 1 posterior	Anterior and posterior may be present	From anterior trunk along lesser curvature	Only to proximal portion of stomach
Perman (1916)	—	None	From anterior trunk along lesser curvature	—
Latarjet (1921)	1 anterior 1 posterior	None	From hepatic plexus (supra-pyloric nerves)	Posterior aspect of stomach along lesser curvature
McCrea (1924; 1926)	1–2 anterior 1–2 posterior	Anterior and posterior may be present	(1) From hepatic plexus (2) Separate pyloric nerve through lesser omentum (direct branch from anterior vagal trunk)	As far distally as pyloric antrum
Mitchell (1938; 1940; 1953)	No constant number but it is unusual to find more than *two* on each aspect of the oesophagus	No anterior or posterior	Direct pyloric branch of anterior vagal trunk	To cardia, fundus and body of stomach along posterior aspect of lesser curvature
Jackson (1948; 1949)	1–3 anterior 1–3 posterior	Anterior and posterior plexus found in only 2% of cadavers	From hepatic plexus	Posterior aspect of stomach as far distally as 2·5 cm from pyloric sphincter
Griffith (1964)	1 anterior 1 posterior	None	From anterior and posterior gastric divisions along lesser curvature	Posterior aspect of stomach as far distally as pylorus
Ruckley (1964; (1970)	1–2 anterior 1–3 posterior	No anterior but posterior was present	(1) From hepatic plexus (2) Direct pyloric branch of anterior vagal trunk	Posterior aspect of stomach as far distally as antrum
Loeweneck *et al.* (1967)	1–4 anterior 1 posterior	Anterior was present but no posterior	(1) From hepatic plexus (2) From anterior and posterior gastric divisions (3) Direct pyloric branches from anterior vagal trunk	Usually only as far distally as posterior aspect of antrum but occasionally as far distally as pylorus

Table 10—*continued.*

Authors	Number of nerve stems passing through the diaphragm	Presence of plexuses on the stomach	Innervation of pylorus	Distribution of posterior trunk to stomach
Brizzi *et al.* (1973)	1–5 anterior 1–3 posterior	Anterior present in 20% of cases; no posterior	(1) From hepatic plexus (2) From anterior or posterior gastric divisions (3) Direct pyloric branches from anterior or posterior vagal trunks (4) From coeliac plexus	Usually only as far distally as posterior aspect of antrum but occasionally as far distally as pylorus
Skandalakis *et al.* (1974; 1980)	1–4 anterior 1–4 posterior	None	(1) From hepatic plexus (2) From anterior gastric division (3) Direct pyloric branches from anterior vagal trunk	Usually (97%) as far distally as posterior aspect of angula incisura but in 3% as far distally as posterior aspect of pylorus
Civalero (1979)	1 anterior 1 posterior	None	(1) From hepatic plexus (2) From anterior gastric division	As far distally as posterior aspect of antrum
Mackay (1981)	Usually 1 anterior although 4 were found on one occasion 1–2 posterior	Anterior in 58% of cadavers posterior in 65% of cadavers	(1) From hepatic plexus (2) Terminal branches of anterior and posterior gastric divisions (3) From coeliac plexus	Usually only as far distally as posterior aspect of antrum; posterior gastric division extended as far distally as pylorus in one cadaver

seconds stimulation. This response is said to be due to the activation by preganglionic vagal fibres of postganglionic neurons in the gastric wall whose transmitter is neither acetylcholine nor noradrenaline (Andrews & Scratcherd, 1980). It has been suggested that the transmitter responsible for this relaxation may be dopamine (Valenzuela, 1976), vasoactive intestinal polypeptide (Fahrenkrüg, Galbo, Holst & Schaffalitzky de Muckadell, 1978) or adenosine triphosphate (Burnstock, Campbell, Satchell & Smythe, 1970). Studies by Andrews & Scratcherd (1980) have shown that both the corpus and antral regions of the ferret stomach contain these non-cholinergic, non-adrenergic inhibitory fibres.

DISCUSSION

The results from the gross anatomical, histological and physiological studies will be discussed separately and, in the final section of the discussion, the suitability of the ferret stomach as a model for man will be assessed.

(1) *Innervation of the viscera*

The vagus nerves, and in particular their truncal divisions, represent the principal pathways for the distribution of parasympathetic innervation to the upper abdominal viscera in both man and the ferret.

The vagal distribution of both animals is similar although differences are evident and will be outlined below.

Many detailed anatomical descriptions of vagal distribution in man have been published and these are summarised in Table 10. There are four main points of disagreement between different authors and these are discussed in the light of the present study.

(i) *The number of nerve stems passing through the diaphragm*

(*a*) *Human*

This topic ceases to cause confusion if the vagus nerve, at the level of the oesophageal hiatus, is considered to occur in any one of the following three variants: the oesophageal plexus, the vagal trunks or the truncal divisions (Griffith, 1964).

Two discrete vagal trunks at the oesophageal hiatus is the most common arrangement found in the present study (Table 4). The anterior trunk lies either on the mid-line or slightly to the right of the mid-line of the oesophagus; the posterior trunk always lies to the right of the mid-line of the oesophagus.

This shift to the right is explained by Griffith (1964) on the basis of the embryological rotation of the stomach, so that the left and right trunks assume anterior and posterior positions respectively. However, this does not adequately explain the shift to the right present in both vagal trunks.

Whatever the method of formation of the vagal trunks and their subsequent divisions, each contains fibres from both cervical vagus nerves (Jackson, 1948), the anterior trunk containing more fibres from the left vagus nerve and the posterior trunk proportionately more fibres from the right vagus nerve.

Consequently, both the anterior and posterior surfaces of the stomach are innervated by fibres originally present in both cervical vagus nerves. This is evident both from the structure of the pulmonary and peri-oesophageal plexuses and from the observation that stimulation of a single vagus nerve in the neck will cause movements of the whole stomach (Duccheschi, 1911; Jackson, 1948), and also from degeneration studies carried out on animals (McCrea, 1924, 1926; Evans & Murray, 1954; Kemp, 1973*a*, *b*). Physiological studies in the dog show that mainly preganglionic axons cross over from the anterior to the posterior gastric surfaces but both pre- and postganglionic axons cross from the posterior gastric surface (Daniel & Sarna, 1976).

The presence of only two vagal trunks at the diaphragmatic level agrees with the findings of many previous workers including McCrea (1924, 1926); Mitchell (1940, 1953); Jackson (1948, 1949) and Skandalakis, Rowe, Gray & Androulakis (1974) (See Table 10).

Mitchell (1940) notes that in one of 34 dissections the vagal truncal disposition is reversed, with the left vagus nerve passing mainly to the posterior aspect of the oesophagus and the right vagus nerve passing onto the anterior surface where they formed plexuses in the usual manner. This arrangement was not present in any of the 31 cases dissected for this study.

When more than two nerve structures were present at the diaphragm in this study it was due to the following causes:

(1) *Multiple vagal trunks*

In one cadaver, four anterior vagal trunks were noted and in two other cadavers two posterior vagal trunks were found at this level (Table 4).

(2) *Trunks and divisions*

In ten cadavers, the trunks gave supradiaphragmatic divisions: three anterior hepatic; five anterior gastric and two posterior gastric; arising from either the oesophageal plexus (seven cadavers) or the vagal trunks (three cadavers). No supradiaphragmatic coeliac divisions were evident in any of the dissections.

(3) *Caudally displaced oesophageal plexus*

In two cadavers, the oesophageal plexus extended on to the abdominal portion of the oesophagus before forming its terminal vagal trunks. This arrangement was also noted in three cadavers from a total of 88 by Skandalakis *et al.* (1974).

In the present study, all 31 cadavers exhibited a gradation distally from oesophageal plexus to vagal trunks and finally to vagal divisions. Thus, it is only with reference to the diaphragm that variability in the level of formation of each component appears to occur, with the exception of the occurrence in seven bodies of a gastric or hepatic division arising directly from the oesophageal plexus, and the total absence of this plexus noted by Mitchell (1940) in one dissection. There was, however, always some form of oesophageal plexus present in our study.

The organisation of the oesophageal plexus in the ferret is described below.

(*b*) *Ferret*

Because the ferret is a quadruped, the terms ventral and dorsal will be considered to be synonymous with the terms anterior and posterior in the human.

Single ventral and dorsal vagal trunks were invariably present at the level of the diaphragm although the shift of the ventral trunk to the right on the caudal oesophagus was not as marked as that seen in man.

Although the oesophageal plexus was extremely simple in the ferret, the presence of both the pulmonary plexus around the tracheal bifurcation and the communicating branch linking the left and right vagal trunks served to illustrate that, as in man, both vagal trunks may contain fibres originally present in both cervical vagi.

Only one ferret had more than two nerve stems at the diaphragmatic level due to the addition of a supradiaphragmatic ventral gastric division.

(ii) *Anterior and posterior gastric plexuses in the stomach*

(*a*) *Human*

The presence or absence of anterior or posterior gastric plexuses is debated in the literature. This may be due to differences in the definition of what actually constitutes a plexus. In the present study, a plexus was considered to be present if a definite nervous network was identifiable.

An anterior gastric plexus was clearly evident in 18 of the 31 cadavers studied, on the anterior aspect of the cardia and the proximal quarter of the body of the stomach. It consisted of a complicated arrangement of interconnecting nerves linking the individual branches of the anterior gastric division. A similar posterior gastric plexus was found in a corresponding but posterior position in 20 cadavers. Rami passed from these plexuses to the fundus, cardia and the proximal half of the body of the stomach while the remainder was innervated by the anterior and posterior nerves of Latarjet.

(*b*) *Ferret*

No gastric plexus, either ventral or dorsal, occurred in any of the 23 dissections. Both the ventral and dorsal gastric divisions consisted of a number of discrete branches to the stomach.

(iii) *The nerve supply to the pyloric part of the stomach*

(*a*) *Human*

Kollmann (1860), Perman (1916) and Griffith (1964) have stated that the pyloric innervation is derived by a direct caudal continuation of the anterior and posterior gastric divisions along the lesser curvature, while Bourgery (1944), McCrea (1924, 1926) and Jackson (1948, 1949) described a descending hepatopyloric ramus from the hepatic division of the anterior vagal trunk and stated that the gastric divisions terminate in the region of the incisura angularis and do not extend any further distally.

More recently, Brizzi *et al.* (1973) and Skandalakis *et al.* (1974, 1980) have reconciled both viewpoints by concluding that the nerve supply to the pyloric region of the stomach is derived from both the hepatic division and the terminal branches of the gastric divisions.

The results of the present study tend to support those of Brizzi *et al.* (1973). Descending hepatopyloric rami from the hepatic plexus in the fissure for ligamentum venosum passed along the right gastric artery to reach the superior, anterior and posterior surfaces of the pyloric canal and sphincter, and the first part of the duodenum. These rami commonly communicated with the terminal branches of the anterior and posterior gastric divisions in the region of the pyloric antrum. The posterior gastric division extended only as far distally as the posterior aspect of the pyloric canal and sphincter in one dissection, although the corresponding anterior gastric division provided direct pyloric branches in this way in five cadavers.

No direct pyloric branches were seen to pass through the gastrohepatic ligament from either vagal trunk in any of the 31 dissections.

Direct branches from the posterior nerve of Latarjet passed to the anterior surface of the pyloric canal and sphincter in one cadaver and, in addition, small communicating nerves were usually evident between the main anterior and posterior gastric divisions as they passed along the lesser curvature in each cadaver.

Nerves could also be traced from the coeliac plexus along the common hepatic artery to reach the pyloric area on the right gastric and gastro-epiploic arteries, although the autonomic nature of these nerves could not be determined. It is therefore evident that the innervation of the pyloric canal and sphincter differs significantly from that of the pyloric antrum and the remainder of the stomach. Latarjet (1921) noted this point by stating that "the stomach reservoir and the pylorus differ in the manner of their nerve supply".

(*b*) *Ferret*

On gross anatomical inspection in the majority of animals, the sole nerve supply to the pylorus was via descending hepatopyloric rami derived from the hepatic plexus. The input to this plexus originates from two sources:

(1) The hepatic division of the anterior vagal trunk.

(2) Peri-arterial nerves from the coeliac plexus.

As in man, the hepatopyloric rami pass along the right gastric artery to the pyloric canal and sphincter.

In two ferrets, this supply was augmented by communicating branches to the peri-arterial nerves around the right gastric vessels from the ventral gastric division in the region of the incisura angularis.

The ventral and dorsal gastric divisions never continued any further caudally than the pyloric antrum, and, in addition, no direct pyloric nerves passed from either vagal trunk to the pyloric canal or sphincter.

(iv) *Distribution of the posterior vagal trunk to the stomach*

(*a*) *Human*

There is general agreement that the posterior vagal trunk supplies posterior gastric branches to the stomach, but the extent of the distribution of this division is the subject of some controversy.

Kollmann (1860) described branches from the posterior vagal trunk innervating the proximal half of the posterior surface of the stomach, with the remainder receiving only a sympathetic supply; but the majority of anatomists have endorsed the view of Latarjet (1921) that the posterior surface of the stomach as far distally as the pyloric antrum is supplied by the posterior nerve of Latarjet. Thus, Mitchell (1940) stressed that the gastric branches of the posterior vagal trunk are distributed in a similar way to their anterior counterpart, althoughly slightly less extensively.

Further reports (Jackson, 1948, 1949; Ruckley, 1964, 1970) confirmed the earlier work of Latarjet (1921) and Mitchell (1940). Their investigations, however, differed on one crucial point: Jackson (1948, 1949) maintained that the posterior nerve of Latarjet was present in only 19 of his 50 specimens whereas Ruckley (1964, 1970) found this nerve in all cases – a feature of all 31 cadavers in the present series.

More recently, Loeweneck, Ludinghausen & Mempel (1967) stated that the posterior vagal trunk occasionally supplies branches as far distally as the pylorus – a situation present in only one cadaver in our study.

From the above it is apparent that some controversy exists regarding the finer details of the posterior gastric division. The results of the present investigation agree with Latarjet (1921) and Mitchell (1940) in that the posterior gastric division is limited, in its distal distribution, to the pyloric antrum in all but one dissection, whilst the anterior gastric division is observed to extend as far distally as the pyloric canal and sphincter in five cadavers.

(*b*) *Ferret*

The distal limit of the distribution of this division is invariably the posterior aspect of the pyloric antrum, thus corresponding to the distribution in man.

A significant difference, however, is the presence in 15 of the ferrets examined, of a nerve that originates from the dorsal gastric division and crosses onto the ventral surface of the pyloric antrum. In addition, in two of these animals, this nerve constitutes a second ventral nerve of Latarjet and, as such, innervates the ventral surface of the body of the stomach and the pyloric antrum.

(v) *Summary of gross anatomical similarities of parasympathetic innervation in man and the ferret*

Although the previous sections of this discussion highlight differences between the parasympathetic innervation of man and the ferret, the following features are shown to be similar in both:

(1) The anterior and posterior vagal trunks can contain fibres from both the right and left cervical vagus nerves.

(2) Gastric branches of both vagal trunks are distributed predominantly along the lesser curvature of the stomach, although the relationship of these nerves to the branches of the left gastric vessels differs in man and the ferret.

The anterior and posterior nerves of Latarjet in man are separated by the vascular plane present in the gastrohepatic ligament, whereas, in the ferret, the ventral gastric division passes ventral to the main stem of the left gastric vessels while the dorsal gastric division passes amongst, and not dorsal to, these vessels.

In both man and the ferret, the terminal branches of the anterior gastric division ran oblique and anterior to the major blood vessels leaving the right and left gastric arteries. Similarly, the terminal branches of the posterior gastric division ran posterior and oblique to these major vessels.

(3) Branches from the subdiaphragmatic anterior vagal trunk run in the upper portion of the gastrohepatic ligament, cross the caudate lobe of the liver from left to right, and continue to the hepatic plexus. Nerves can then be traced from this plexus to the pyloric sphincter of the stomach along the right gastric vessels.

(2) *Histological and physiological studies*

The histological studies reveal that the predominant fibre type in the abdominal vagus nerves is unmyelinated in both man and the ferret. This is also found in other monogastric mammals, e.g. cat (Agostoni, Chinnock, De Burgh Daly & Murray, 1957), dog (Kemp, 1973*a*, *b*) and rat (Gabella, 1976). Interestingly, the predominant efferent fibre type in ruminants is myelinated (Dussardier, 1960); this may be related to the greater degree of central control of the stomach required for rumination. The function of the small myelinated fibres in the abdominal vagus nerves of monogastric animals is a matter for speculation, but it is tempting to suggest that they may form a sub-group of vagal afferents.

The presence of unmyelinated fibres in the abdominal vagus nerves is supported by recordings of vagal compound action potentials that show prominent potentials with latencies appropriate to conduction in unmyelinated nerve fibres. These results are consistent with the conduction velocities of fibres present in the abdominal vagus nerves of the rat and dog (see Andrews & Taylor, 1982, for summary).

Gastric motility studies in the ferret (Andrews & Scratcherd, 1980) have shown that the vagus nerve contains preganglionic nerve fibres (with conduction velocities in the range for C-fibres) capable of activating two types of postganglionic neurons via nicotine cholinergic synapses. Activation of the intrinsic cholinergic neurons (sensitive to atropine) evokes an overall increase in intragastric pressure with superimposed gastric contractions. Stimulation of the intrinsic non-cholinergic non-adrenergic inhibitory nerves evokes a decrease in intra-corpus pressure and inhibition of antral contractions. Human gastric motility was not investigated in the present study, but previous studies by Bennett & Stockley (1975) on strips of isolated human stomach and intestinal wall demonstrated the presence of the above two types of intramural neuron.

(3) *Is the ferret stomach a suitable model for the human stomach?*

For the ferret stomach to be a suitable model system for the study of the human stomach there should be a reasonable combination of points of similarity between the stomachs of the two animals with respect to their anatomical characteristics, innervation and physiological characteristics. These aspects are discussed below.

(*a*) *Anatomical characteristics of the stomach*

The anatomical characteristics of the stomach in man and the ferret have been shown to be similar in two main respects: (i) the ultrastructure of the gastric mucosal surface is shown to be identical, and in neither animal was evidence found for the discharge of mucus from the surface epithelial cells (Pfeiffer, 1970). (ii) The gross similarity between empty human and ferret stomachs was commented upon by Stephens & Pfeiffer (1968). Further studies by Andrews, Grundy & Scratcherd (1980) showed that the distribution of food in the ferret stomach immediately after a meal was similar to that demonstrated in man, i.e. approximately 80% of the food is accommodated in the body and fundus. In the ferret, this distribution was shown to be mainly due to the different length-tension properties of the muscle in the body and antrum, the body being more distensible. Because food distribution is similar in the ferret and human stomachs it is probable that the arrangement of the gastric musculature is similar in both animals. It is worth noting that the ferret, like other laboratory carnivores, is an intermittent feeder, as is man.

(*b*) *Innervation of the stomach*

The comparative innervation of the stomach in the two species has been discussed in detail above and will be described here only briefly. The gross vagal distribution to the stomach is similar in both animals although it is much simpler in the ferret, particularly in the region of the thoracic oesophagus. One of the interesting differences in the innervation is that, in the ferret, the ventral vagal trunk (at the macroscopic level) appears to supply only the body of the stomach in the majority of animals. This arrangement may provide a useful system for testing the interaction between the vagal innervation of the oxyntic cells and gastrin released from the antrum by local stimuli. In the ferret, electrical stimulation of the ventral vagal trunk should evoke acid secretion only by a direct route, whereas, in other animals, ventral vagal trunk stimulation evokes acid secretion from the corpus via both a direct innervation and a simultaneous release of antral gastrin.

This study has also demonstrated that the abdominal vagus nerves in both species contain predominantly unmyelinated nerve fibres with conduction velocities $< 2{\cdot}5$ m/sec. The innervation of the viscera by these slowly conducting fibres appears to be a feature common to monogastric mammals (Andrews, 1979).

(*c*) *Physiological characteristics of the stomach*

The two aspects of gastric physiology that will be considered here are motility and acid secretion. To summarise the motility results discussed above, the stomachs of both man and ferret contain cholinergic excitatory neurons and non-cholinergic, non-adrenergic inhibitory fibres, both of which can be activated by the unmyelinated preganglionic vagal fibres described above (Andrews & Scratcherd, 1980). The second point of similarity is that a number of vago-vagal reflexes observed in man have also been seen in the anaesthetised ferret (Andrews, Grundy & Scratcherd, 1980; Andrews, Grundy & Lawes, 1980). This work needs to be extended to studies on the conscious ferret, and further quantitative studies of motility need to be performed in man before these comparisons can be fully assessed. The ferret is also particularly useful as a model for man because it readily vomits under urethane anaesthesia in response to vagal afferent stimulation (Andrews, 1979) and, unlike the rat and cat, its vomiting can be evoked by administration of cis-platinum (Florczyk, Schurig, Lenaz & Bradner, 1981).

The secretory behaviour of the ferret stomach shows a combination of similarities to man that is not found in other common laboratory animals. The ferret, like man, is a basal secretor of acid and proteolytic enzymes in the fasting state (Pfeiffer & Peters, 1969). The basal acid and pepsin secretion is reduced by unilateral abdominal vagotomy as it is in the human (Pfeiffer & Peters, 1969). It has been suggested that the level of basal acid secretion may play a role in the aetiology of gastric ulcers and, in connection with this, spontaneous gastric ulceration has been observed in laboratory ferrets (Andrews, Illman & Wynne, 1976).

Gastric acid secretion in man is stimulated by low doses of histamine (40 μg/kg; Desai, Borkar & Jeejeebhoy, 1967) as it is in the ferret (67 μg/kg; Pfeiffer & Peters, 1969). The ferret has a similar sensitivity to histamine as dogs and cats but is many times more sensitive to histamine than the rat which is commonly used for gastric secretory studies. There is also a considerable increase in pepsin secretion in response to histamine in the ferret; 124 % above basal as compared to 65 % increase in the cat (Emas & Grossman, 1967).

Acid secretion is stimulated by pentagastrin in man and the ferret and in both animals the vagus nerves must be intact to achieve a maximal response to pentagastrin (Basso *et al.* 1971). The response to histamine was also reduced by unilateral vagotomy, but to a lesser extent than the response to pentagastrin (*ibid*); this discrepancy has also been observed in man (Konturek, 1967). Other similarities between gastric acid secretion in the ferret and man are: parenteral caffeine stimulates secretion, as it does in the cat but not in the dog or rat (Pfeiffer & Roth, 1970); the secretion of gastric acid evoked by vagal stimulation or pentagastrin is markedly reduced by prior administration of atropine or cimetidine (Andrews & Bower, 1979); intravenous calcium infusion raises serum gastrin levels and hence gastric acid secretion (this phenomenon is reported not to occur in dogs or rats and thus the ferret provides a useful model for the relationships that exist between calcium and gastrin in man, e.g. in Zollinger-Ellison syndrome, or hyperparathyroidism (Watson, Reeder & Thompson, 1973)).

In the ferret, the secretory response to calcium is completely inhibited by atropine, suggesting that calcium acts through a cholinergic system, as is thought to be the case in man (Basso & Passaro, 1972).

In conclusion, the stomach of the ferret displays many anatomical and physiological features that are similar to those found in man. Some of these features are also present in other common laboratory animals, but the value of the ferret stomach as a human model is the overall *combination* of similarities.

SUMMARY

The ferret stomach has been used recently as a model for the investigation of vagal control of gastric function in man. However, little is known of its parasympathetic innervation. This paper describes the vagal innervation of the ferret stomach. A quantitative study of the vagal innervation of the human stomach was also performed to provide a basis for comparison between the two animals. The studies were performed using gross dissection, light and electron microscopy, and, where possible, physiological techniques.

In man, the macroscopic dissections emphasised the complexity of the vagal supply to the stomach. Fibres from a peri-oesophageal plexus, which consisted of anterior and posterior components, united to form anterior and posterior vagal trunks at a variable level rostral to the diaphragm. These trunks passed, together with the oesophagus, through the diaphragm into the abdomen. Each of the two main vagal trunks gave rise to two primary divisions: the anterior trunk divided into hepatic and anterior gastric divisions; the posterior trunk divided into coeliac and posterior gastric divisions. These truncal divisions represented the primary pathways for the distribution of the vagus nerves to the abdominal viscera.

The nerves and vessels within the gastrohepatic ligament (which ran parallel to the lesser curvature of the stomach) had a trilaminar arrangement: the anterior and posterior gastric divisions of the vagal trunks lay, respectively, superficial and deep to the peri-arterial nerves which surrounded the left gastric artery in the supine position. The nerves passing along the lesser and greater curves may contain both sympathetic and parasympathetic fibres because both sets of nerves provide an input to the coeliac plexus.

The distribution of the vagus nerves to the ferret stomach closely resembled that observed in man. However, two major differences were observed. Firstly, the arrangement of nerves at the oesophageal plexus was grossly simplified. Secondly, in the ferret, the ventral vagus nerve appeared to extend only as far distally as the body of the stomach in the majority of specimens, while, in man, the corresponding anterior gastric division appeared to supply the body of the stomach and the pyloric antrum.

Light and electron microscopic studies revealed that the abdominal vagus nerves were similar in structure in both animals, with unmyelinated nerve fibres predominating.

The suitability of the ferret stomach as a model for the human stomach is reviewed in the light of this anatomical study and previous physiological investigations.

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