OESOPHAGEAL PRESSURE AND MOTILITY IN ANIMALS : A CINE-RADIOGRAPHIC AND MANOMETRIC STUDY

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Oesophageal motility in man has been studied by cineradiography[1-5] and by electro-mechanical manometry.[6-9] Botha, Astley, and Carré,[10] in 1957, were the first to combine these methods in an investigation of the gastro-oesophageal junction and Botha[11] subsequently applied the same technique to the pharyngo-oesophageal region. As yet manometry and cineradiography have not been widely employed in animals, and when this investigation was carried out there were no reports in the literature that they had been used in combination.

Direct experimental observation of oesophageal activity in man remains impracticable. However, by comparing cine-radiographic and manometric recordings in animals with those in man, and with the knowledge obtained from direct observation[12,13] of the characteristics of oesophageal peristalsis in animals, it is possible to obtain a better understanding of human oesophageal activity. In the present investigation synchronous cine-radiographic and manometric recordings were made in monkeys and rabbits. Manometric studies alone were also carried out in the rabbit, monkey, mouse, ferret, guinea-pig, cat and dog.

METHOD

Apparatus

Pressures were measured with an electro-manometer of the capacitance type (N.E.P. Ltd.) and a two-channel direct-writing pen recorder (Sanborn 'twin-viso cardiette'). Open-ended water-filled polythene tubes of 1·0 and 0·5 mm. bore were used in the great majority of experiments. Expanded tips[13] were used in an open-air system in a few experiments. Radio-opaque markers indicated the situation of the recording holes.

Cine-radiography was carried out by Astley's method for cine-angiocardiography,[14,15] using image intensification and intermittent radiation. Each cine frame was exposed as an individual high-speed radiograph with an exposure of 0·005 - 0·002 seconds. to reduce movement blurring. The precise instant of each picture was indicated below the pressure-tracing on the second channel of the pen recorder. Examinations were carried out at 16 frames per second.

Procedure

Animals were anaesthetized according to the method of Botha and Nunn[16] by intraperitoneal or intravenous veterinary pentobarbitone. All investigations were carried out in the supine or left lateral positions. A recording tube was attached to the manometer, filled with water and passed through the mouth into the stomach. The marker was located by fluoroscopy and the resting pressures recorded in the stomach, oesophagus and pharynx. The tube was also smoothly withdrawn from stomach to oesophagus at a uniform rate while simultaneous pressure and cine-radiographic recordings were taken, the instant of each frame being indicated on the pressure tracing. The procedure was repeated several times in each experiment. Oesophago-pharyngeal withdrawal curves were obtained in the same way. At the end of the examination barium was given to localize the gastric fundus, and further combined radiographic and manometric recordings were made. Combined recordings at all levels were also made during deglutition, swallowing being easily induced by thin barium suspension introduced into the pharynx.

The tube was flushed through after every few recordings, a minimum of water being used since the capacity of the stomach and oesophagus is limited in the smaller species. Careful and constant adjustments were made to the pressure head in order to eliminate as far as possible any errors due to the hydrostatic effect of the water column.

Analysis

Respiratory movements and vascular pulsations caused rhythmic pressure changes in the records obtained from the stomach, oesophagus and pharynx. Pressure changes due to the heart beat were relatively too small to interfere with the measurement of alimentary pressures or to influence the interpretation of the records. The amplitude of the respiratory deflections, however, was so large that it was difficult to find a suitable base-line for comparison of pressures at different anatomical levels. This was overcome by choosing certain fixed points in the respiratory cycle for making measurements. The end-inspiratory (EI) and the end-expiratory (EE) phases of respiration were selected because they (1) indicate the extremes of pressure, (2) are easily recognized, (3) are conveniently measured, and (4) reflect the longest stable period in the respiratory cycle.

Pressures at the junctional zones (gastro-oesophageal and pharyngo-oesophageal) were best demonstrated on slow withdrawal of the tube. The sphincteric high-pressure zone at the cricopharyngeus was easily identified. Localization of the diaphragmatic hiatus, on the other hand, was difficult, but the cardia was outlined by barium in the fundus.

Where simultaneous cine and pressure recordings were made, the cine films were projected frame by frame and composite tracings were made of each recording to show the site of salient points of the withdrawal curve relative to the diaphragm and barium in the gastric fundus. In the recordings of deglutition individual cine frames were correlated with the pressure changes. By counting the frames the duration of various phases of activity as well as the position of the bolus relative to that of the peristaltic contraction were studied. Final interpretation of results are based on cinematic projection of the films, by viewing consecutive frames in an enlarger after examination with a hand lens, and by photographic enlargement of film strips.

RESULTS: RESTING PRESSURE

Deglutition pressures are only significant if compared with resting oesophageal pressures, which are again intimately related to the pressure gradient across the oesophageal wall and the pressure in adjacent serosal cavities.

Stomach

The resting pressure varied considerably in different species and even in different animals of the same species. Even in a single animal the pressure varied from moment to moment, and was much more fluctuant than in man. This variation depended mainly on the depth of anaesthesia, and to a lesser extent on stomach fullness and peristaltic activity. In all animals the gastric pressure was positive (Fig. 1). During inspiration it became more positive as indicated by an upwards deflection. The end-inspiratory peak pressure was mainly dependent on the size of the animal, being proportionately higher in the larger species. A sighing type of respiration in a smaller species might, however, produce a much higher pressure than shallow respiration in a larger species. During expiration the pressure fell sharply and quickly reached the end-expiratory base-line. Another inspiration might follow directly so that the EE pressure trough was sharp; more commonly there was a conspicuous EE pause.

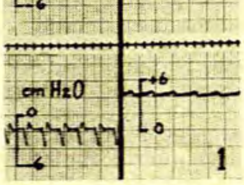

Fig. 1. Simultaneous pressure recordings in the rabbit with the open water system: (*a*) Pleural cavity (upper trace) and oesophagus (lower trace). (*b*) Pleural cavity (upper trace) and peritoneal cavity (lower trace).

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The introduction of relatively small amounts of fluid into the stomach did not affect the intragastric pressure. However, when the physiological threshold of distension was reached the pressure rose sharply with any further addition of fluid. Compression of the upper abdomen raised the intragastric pressure more than compression of the lower abdomen. The introduction of 5, 10, or 50 ml. of air into the peritoneal cavity had no effect on intragastric pressure in the larger species. Intraperitoneal and intragastric pressures were measured simultaneously before and after the introduction of air into the peritoneal cavity, and were found to simulate each other very closely. Elevation of the head of the animal caused the intragastric pressure to fall; if the tail was raised, the pressure increased immediately. Sudden linear pressure spikes were obtained during vomiting and sneezing, with peak pressures of 30 cm. of water in animals such as the ferret and rabbit.

Gastro-oesophageal Junction

In all the species examined by withdrawal of the tube across the gastro-oesophageal junction, a zone of pressure higher than that of the stomach was recorded immediately before the low pressure of the oesophagus was reached (Figs. 2 and 3). The incidence and form of this zone of higher pressure was variable not only in the different animals but also in the same animal from moment to moment (Fig. 2). The resting pressure here was more variable than anywhere else in the upper digestive tube. In the guinea-pig, ferret and rabbit the pressure rise was conspicuous and peak pressures of 6-10 cm. of water were not uncommon. In the cat and dog it was less marked and in the monkey it was commonly absent. At the high pressure zone, the curve often took the form of a 'saw-tooth or 'plateau' (Fig. 2). From the intragastric pressure level there was usually a gradual rising gradient with an increased respiratory excursion, the peak EI pressures rising more steeply than the EE pressures. Then the high pressure usually fell sharply to the negative intrathoracic level as soon as the recording hole had passed the hiatus into the thoracic oesophagus. The slower the withdrawal, the more convincing was the record of the high-pressure zone. Rapid withdrawals usually failed to demonstrate it; instead, the pressure fell with a 'step'. This was presumably due to the narrowness of the anatomical zone responsible.

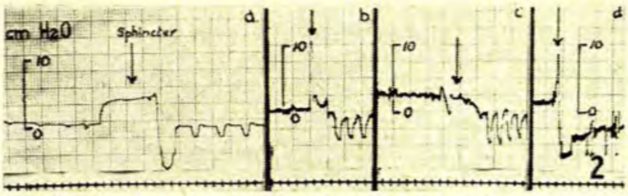


Fig. 2. Gastro-oesophageal withdrawal curves in the rabbit recorded with the open water system: (*a*) 'Plateau' curve. (*b*) 'Tooth' curve. (*c*) 'Step' curve showing no significant higher pressure zone. (*a*), (*b*) and (*c*) were all recorded in the same animal. (*d*) A well-marked tooth curve in another animal.

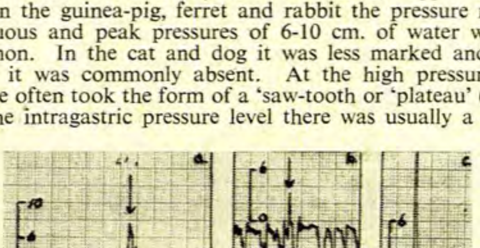
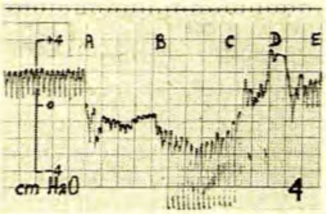


Fig. 3. (*a*) The gastro-oesophageal withdrawal curve in the guinea-pig shows a sharp, conspicuous rise at the junction. (*b*) The arrow indicates a primary peristaltic wave in the oesophagus. (*c*) A sneeze recorded from the stomach.

The reverse manœuvre, the advancement of a recording tube from the oesophagus into the stomach, also showed the high-pressure zone, but less convincingly (Fig. 4). The zone was most marked in the rabbit and ferret and in these two animals the greatest difficulty was also sometimes encountered in passing the tube down into the stomach; on several occasions all attempts failed to manipulate the polythene tube past the cardia. There is thus no question of a pure one-way valve in at least these two animal species, which are known to have excellent physiological sphincters at the cardia.[12,13] In the monkey the pressure rise on withdrawal was usually poor or absent; the tube was passed down into the stomach without any resistance in this animal.



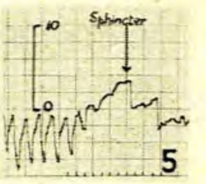


Fig. 4. Gastro-oesophageal withdrawal and advance curves in the rat. The tube is withdrawn from the stomach and passes the cardia at A without a rise in pressure. From A to B only small respiratory excursions are recorded in the abdominal oesophagus. At B the recording hole passes the hiatus, and the high negative pressures are recorded in the thorax. At C the tube is again advanced and it enters the abdominal oesophagus. At D it passes the high-pressure zone and enters the stomach E.

Fig. 5. The oesophago-pharyngeal withdrawal curve in the monkey. The arrow indicates the high pressure zone when the recording hole passes over the cricopharyngeal sphincter into the pharynx.

Slow gastro-oesophageal withdrawal curves in the rat showed an interesting two-stage pressure change (Fig. 4). When the tube was withdrawn from the stomach the pressure might or might not have a preliminary rise as the recording hole crossed the cardia; then it dropped to below the resting intragastric pressure when the tube passed into the long abdominal oesophagus. Here the deflections were still positive on inspiration but of much lower amplitude. On further withdrawal the pressure showed a second fall; it suddenly dropped to the negative intrathoracic level where the inspiratory deflections were negative. There was no zone of increased pressure when the recording hole passed the hiatus.

This two-stage pressure change might be absent for various reasons. For instance, if the stomach was empty, the difference between pressures in the stomach and the abdominal oesophagus might be less obvious. Another possible cause was increased pressure in the abdominal oesophagus and its shortening in length as a result of sustained contraction due to the irritation by the tube.

The two-stage pressure change, often with a high-pressure zone at the cardia, was also recorded when the tube was advanced into the stomach. However, it was less well defined and more irregular than in the withdrawal tracing.

The combined cine-radiographic and manometric recordings were carried out in the left oblique position with the stomach fundus outlined by barium. In the rabbit all the results were identical, with a high-pressure zone recorder over a distance of 5-7 mm. The rise always started as or just before the tip of the marker appeared outside the barium outline of the stomach, reached its peak a few mm. more cranially, and fell to the previous level about 5-10 mm. cranial to the barium outline. From this point to just caudal of the dome of the diaphragm the pressure remained more or less constant—higher than in the chest, yet lower than in the abdomen. Respiratory fluctuations were insignificant. In principle the results were similar to those obtained in man.[10]

In the monkey the pressure *started* to fall well outside the barium outline of the stomach, and reached the intrathoracic level only after the hole had passed through the 'empty segment' of the lower end of the gullet. The majority of withdrawal curves were 'steps'.

Oesophagus

Oesophageal pressure was always negative in the EI phase but often rose to positive values during expiration. The excursion depended mainly on the type of respiration, which again depended on the depth of anaesthesia. Thus in the rat a deep sighing respiration produced a negative pressure of -6 cm. of water, whereas the lowest pressure in the rabbit or cat during quiet shallow breathing was only -4 to -5 cm. of water. The intrapleural pressure closely resembled the intra-oesophageal pressure (Fig. 1).

Pharyngo-oesophageal Segment

The pharyngeal pressure in the larger species was always about atmospheric. Very minor respiratory fluctuations occurred. The pressure in the lower cervical oesophagus was equal to that in the thoracic oesophagus. On withdrawal of the tube from the oesophagus a constant high-pressure zone was recorded at the level of the cricopharyngeus (Fig. 5). It was much less variable than the high-pressure zone at the gastro-oesophageal junction, reached a much higher peak pressure, and remained the same for every animal during different withdrawals. Respiratory fluctuations were small or completely absent.

RESULTS: DEGLUTITION PRESSURES AND PERISTALSIS

The depth of anaesthesia markedly affected swallowing and oesophageal peristalsis. When too large a dose of pentobarbitone had been inadvertently used, no swallowing could be initiated. As the anaesthetic wore off, however, the power of swallowing returned, but the oesophageal peristalsis was still weak and ineffective, or even absent. Barium lingered indefinitely in the cervical and lower thoracic portions of the organ. Spontaneous localized contractions then occurred which narrowed the lumen but disappeared again without advancing the contents. Still later, primary peristalsis occurred, slow at first, but gradually increasing in force until motility was apparently normal.

Fluoroscopy and cine-radiography confirmed direct observations in the rabbit that the epiglottis folded dorso-caudally from its base and covered the superior laryngeal opening as a perfect lid.[13] The angle which was made by the base of the tongue, epiglottis and oesophagus was more obtuse during swallowing than at rest and provided a straighter and more vertical slope for the descending bolus. This change was brought about by the cranio-dorsal movement of the tongue, dorso-caudal folding of the epiglottis, and ventro-cranial movement of the larynx and proximal epiglottis and oesophagus. The cricopharyngeus was always firmly closed except when it opened to receive the bolus. Once the bolus has passed into the oesophagus, the cricopharyngeal sphincter closed and the larynx descended.

The oesophageal deglutition complex in the larger species was often almost identical with that in man: viz., a sudden initial positive deflection, then a gradually rising intermediate pressure zone, followed by a final conspicuous positive deflection which indicated the actual peristaltic contraction wave (Fig. 6). Primary peristaltic contractions were fairly uniform throughout the oesophagus when it contained only striated muscle (Figs. 7 and 8).

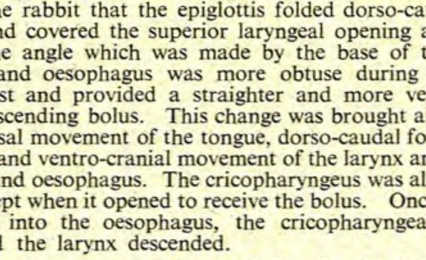


Fig. 6. A deglutition complex recorded about 2·5 cm. cranial to the cardia in a rabbit. Synchronous cine-radiographs at 16 frames per second are indicated in (Fig. 9).

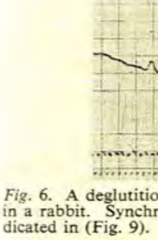


Fig. 7. 3 primary peristaltic contractions in the lower oesophagus of the rat. Swallowing in each case was initiated by the introduction of one minim of water into the pharynx.

Fig. 8. 3 primary peristaltic contractions in the ferret.

The force was greatest in the lower thoracic portion, where the positive peristaltic deflections were rapid and conspicuous. The rising gradient was usually as steep as the decline. No fall in pressure, either sudden or gradual, was seen immediately ahead of the peristaltic contraction in any species; on the contrary, the pressure usually increased just ahead of the contraction (Fig. 6). Thus no evidence was found of a localized wave of relaxation preceding the wave of contraction.

In the monkey the activity of the proximal oesophagus to the level of the hilum of the lung was typically that of striated muscle; caudal to this level the movements were slow and prolonged, and typical of smooth muscle.

In man a characteristic feature is an 'empty segment' seen just above the cardia in barium examinations. Fluoroscopy and cine-radiography showed that this was also constantly present in the animals. It did not disappear completely during the advance of a peristaltic wave; some constriction was always present (Fig. 10). In the rabbit (as in man) this segment contracted on its own as an independent part of the oesophagus, but the contraction was prolonged and sluggish and barium often lingered there for several minutes or until a further swallow carried it into the stomach.

The radiological appearance of the rabbit's gastro-oesophageal junction at rest and during peristalsis closely resembled those in the monkey, except that the movements in the striated organ were much more rapid than those in the organ which contains only smooth muscle at this level. If barium was slowly introduced into the oesophagus by means of a tube, the organ filled uniformly except at the vestibule. If more barium was introduced the distal portion gradually widened but the barium was always obstructed about 5-7 mm. cranial to the cardia, at exactly the site where the high-pressure zone was demonstrated on withdrawal. This empty segment was absolutely constant, of the same uniform length, and always located in the terminal 5-7 mm. of the oesophagus.

Primary peristaltic waves in the oesophagus of the rabbit were extremely rapid and forceful (Fig. 6).

The primary waves cleared the entire oesophagus of all barium, but secondary waves only cleared the organ distal to the point of origin, which was usually at or distal to the hilum of the lung. Once initiated, these secondary contractions proceeded to a normal completion, which was indistinguishable from that of the primary contractions (Fig. 10).

The rapidity, force and characteristics of the peristaltic contractions varied at different levels of the oesophagus, even in organs which contained only striated muscle. Thus in the rabbit the rising gradient in the upper thoracic oesophagus was very steep; the decline was more gradual. Peak pressures of 5-10 cm. of water were obtained, but the duration was short and a negative component was characteristic at the end of each wave. It was probably due to the rapid advance of the contraction, creating a transient vacuum in the proximal oesophagus after closure of the circopharyngeus. In the lower thoracic oesophagus higher peak pressures were usually recorded, often 15-20 cm. of water. The rising gradient of the peristaltic wave was more gradual, the wave was of longer duration, and the negative component less marked or absent. The gradual elevation of pressure immediately ahead of a peristaltic wave was present even in 'dry' swallows (saliva only).

In Figs. 6 and 9 are analysed the combined manometric and cine-radiographic recordings of a primary peristaltic contraction in the rabbit. When barium was swallowed, it rapidly accumulated in the supradiaphragmatic portion without entering the proximal vestibule. As the pressure in the oesophagus rose, this column of barium increased in diameter and shortened ahead of the advancing contraction. As the contraction approached the hilum of the lung, the distal oesophagus was gradually forced open and barium passed to the level of the sphincter, but still nothing entered the stomach.

Barium was then forced through the cardia in a thin steady stream (Fig. 10). The sphincter never dilated widely but stayed partially contracted, the X-ray appearances having a resemblance to those of achalasia in man. The contraction was uniform to the level of the vestibule, emptying the organ as it advanced. At the vestibule, however, the contraction changed; instead of the peristaltic wave advancing caudally, the vestibule itself contracted and slowly squeezed the last remaining drops of barium into the stomach. Traces of barium often remained behind, a phenomenon not seen elsewhere in the oesophagus. The completion of primary and secondary waves was usually similar, although primary waves might be of shorter duration and greater force.

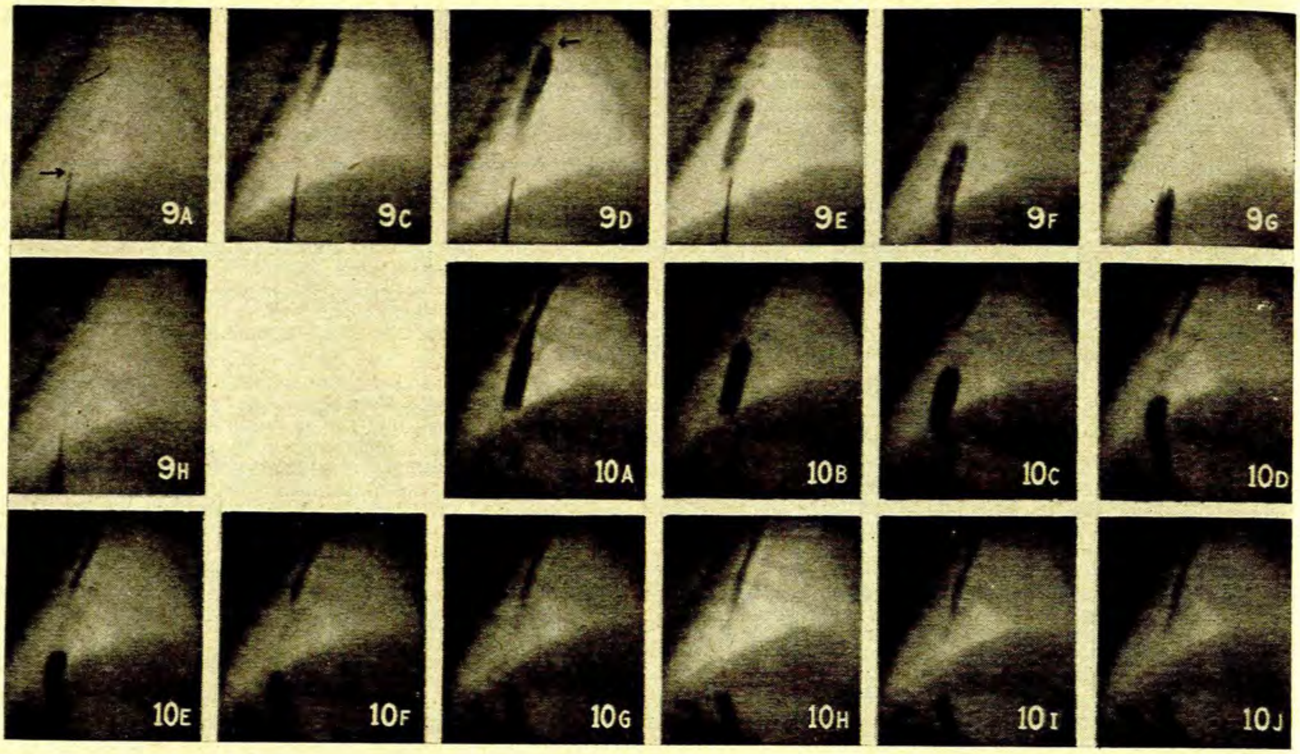


Fig. 9.

A. Frame 58: No barium has entered the thoracic oesophagus although the initial pressure rise is recorded 2·5 cm. above the cardia. The arrow indicates the recording hole just cranial to the marker. The gas bubble in the stomach and the diaphragm are clearly seen.

B. Frame 60: The pressure is rising but still no barium has arrived in the thoracic oesophagus. Same as (A), and not reproduced.

C. Frame 64: The barium has reached the hilum of the lung.

D. Frame 67: The distal head of barium has not moved much, but the contraction (arrow) has advanced to the level of the aortic arch. Frames 64 and 67 show unequivocally the initial rapid movement of the fluid bolus and the subsequent delay.

E. Frame 70: The bolus is now short and reaches the recording hole.

F. Frame 72: The head of barium enters the stomach.

G. Frame 75: The peristaltic wave reaches the recording hole and the pressure rises almost vertically.

H. Frame 77: The pressure starts to fall; the contraction is almost past the recording hole but the vestibule is not yet empty.

Fig. 10. The initiation, advance, and completion of a spontaneous secondary contraction in the lower oesophagus of the rabbit:

A. Frame 1: The thoracic oesophagus is distended with barium. A gas bubble is present in the vestibule. A narrowing is appearing at the level of the hilum.

B. Frame 2: A localized contraction ring has formed.

C. Frame 4: The secondary contraction moves distally and barium enters the vestibule.

D. Frame 6: The vestibule is distended with barium, which flows into the stomach through the narrow constricted sphincteric zone.

E. and F. Frames 7 and 8: The contraction of the sphincteric zone is maintained. The appearances resemble those of achalasia in man.

G. Frame 9: The peristaltic wave has reached the vestibule.

H., I. and J. Frames 10, 11 and 12: There is little change. The propagated peristalic wave has stopped; instead, the vestibule empties by generalized contraction and telescoping into the stomach.

DISCUSSION

The present investigation confirms the close relationship between the pressure in the abdominal and thoracic cavities and those within the hollow muscular organs which are normally present in these cavities. Thus the stomach and oesophagus may be conveniently used to measure intra-abdominal and intrapleural pressure. Cherniack *et al.*[17] and Fritts *et al.*,[18] however, have pointed out that in man, although the pressures are closely related during quiet respiration, the intra-oesophageal pressure may vary widely from the intrapleural pressure during forced respiration or hyperventilation. Although even the smallest variations in the gradient as well as the absolute peak values were faithfully reflected in the present investigation under different experimental conditions, it is possible that small qualitative discrepancies also exist in animals. In the small species examined it would be almost impossible to measure accurately such minor differences in pressure even with the most modern equipment. For practical purposes these pressures may therefore be regarded as the same.

The abdominal cavity fulfils the hydrostatic laws of a fluid container. The intragastric pressure therefore depends on the position of the subject. It is high when the head is downmost (Trendelenburg position) and drops in relation to the resting horizontal level when the head is raised. Whereas it is always positive in the supine position, it may change to an absolute negative value when the head is elevated. We could find no evidence that the introduction of small quantities of air or water into the peritoneal cavity affected the absolute pressure.

The negative oesophageal pressure was separated from the atmospheric pressure in the pharynx and the positive pressure in the stomach by two bands of higher pressure. These zones of high pressure were localized and fairly constant, and closely simulated those found in man.[10,11] They had all the physiological characteristics of functional intrinsic sphincters.

The high pressure band at the cranial end of the oesophagus was very constant, and corresponded exactly to the anatomical position of the cricopharyngeus muscle. The present findings support the view that the cranial part of the oesophagus is tonically closed off from the pharynx under resting conditions and further suggest that the musculus cricopharyngeus acts as the proximal oesophageal sphincter. The sphincteric pressure rise was always relatively higher than that at the gastro-oesophageal junction, a fact which was also observed in animals during oesophagoscopy and during direct studies of oesophageal motility; in cine films of the exposed oesophagus, the cricopharyngeus can be seen as a narrow constricted segment, corresponding with the zone of high pressure.

Our findings also suggest that this sphincter, as in man, is integrated into the pharyngo-oesophageal muscle complex during deglutition. Thus the sphincter actively relaxes ahead of the peristaltic contraction as part of the propagated peristaltic contraction which starts in the upper pharynx and proceeds to the distal oesophagus.

It is said that the main reason for this tonic closure is to avoid air being sucked into the oesophagus on inspiration, which would decrease the tidal volume and lead to marked ballooning of the organ. I should like to point out another very important reason, viz. that the tonic contraction of the cricopharyngeus prevents aspiration of ingesta from the oesophagus into the lungs, and may thus be looked on as a second closing mechanism of the stomach. In man the sudden escape of fluid from the stomach during eructation or reflux, especially in the supine or head-down positions, might be insufficiently returned by secondary peristalsis. Under these circumstances the cricopharyngeal sphincter is the only factor which will prevent a spill-over.

The high-pressure zone between stomach and oesophagus was never *at* the cardia only: it was always in the most terminal portion of the oesophagus. Furthermore it was never confined to a narrow band but always extended over a segment, varying in length according to the species. These findings completely exclude a localized flap-valve mechanism between the stomach and the oesophagus.

The diaphragm certainly influences this high-pressure zone and undoubtedly causes a pinching effect during inspiration, as indicated by the higher positive deflections at the hiatus than in the stomach. However, it is unlikely that the constricting effect of the crura would be fully appreciated in an empty oesophagus; the crura might have a greater pinching effect when the organ is distended.

Not much difference was noticed between gastro-oesophageal withdrawal recordings taken during inspiration and during expiration. A substantial deflection was sometimes obtained in the rat when the recording hole passed through the terminal oesophagus; since this part of the organ normally lies 1 - 1·5 cm. caudal to the crura, the diaphragm can have no possible compressing effect upon it. The high-pressure zone must therefore, in at least this species, be due to another factor. In many recordings the pressure spike was identical in form, although not in amplitude, with those obtained in other species, including man; this suggests identical causation by some factor other than the diaphragm.

The most conspicuous high-pressure zone was unquestionably in the rabbit. Whereas crural function in this animal is poor,[13] it possesses a most remarkable anatomical sphincter.[20] This anatomical sphincter, the most convincing that was found in 21 different animal species,[21] is therefore relatively speaking also physiologically the most powerful. Even where no anatomical sphincter is recognizable and the lower oesophagus contains only smooth muscle, for example in the cat, the high-pressure zone was unmistakable. All this evidence suggests that a functional, if not a structural sphincter exists in the terminal oesophagus.

The characteristic empty segment in the lower oesophagus which forms such a striking feature of the normal oesophagogram in man, was seen in all the species. The barium in the fundus was always smooth in outline; a horn of barium was never seen protruding into the terminal oesophagus. The only factor that could possibly close the distal oesophageal orifice so flush is folds of mucosa. These were adequately demonstrated by direct studies of the interior of the stomach in animals and by anatomical studies in man.[12] It therefore appears as if the mucosal folds at the cardia form a watertight seal at the cardiac orifice, being held in position and supported by the inferior oesophageal sphincter.[21] Together these two factors constitute the closing mechanism between stomach and oesophagus.

In none of the animals investigated was there any sign of a wave of relaxation preceding the wave of contraction. In fact, there was usually a gradual rise in pressure immediately ahead of the peristaltic wave at all levels of the oesophagus. This was even present when only saliva was swallowed. The manometric findings support the cine-radiographic recordings taken during direct studies of oesophageal peristalsis in many different animal species, and suggest that Bayliss and Starling's law of the intestine does not apply to the oesophagus. Instead, we suggest that there is a variable degree of active relaxation *via* the motor nerves in the entire oesophagus distal to the peristaltic contraction. In addition there is a further passive dilation of the oesophagus as the advancing peristaltic wave forces the contents through the obstruction of the inferior oesophageal sphincter. Similar observations were made in man and the conclusions are the same.

Although the form and characteristics of deglutition complexes were not studied in detail in this investigation, some complexes were recorded which closely simulate those in man. The initial positive deflection was quite marked and occurred long before the barium reached the recording hole. This pressure spike is not caused by the arrival of the bolus, although it might coincide with the arrival when the recording hole is in the cervical oesophagus. The deflection is due to the transmitted positive pharyngeal pressure which rapidly passes through the oesophagus when the pharyngo-oesophageal pressure gradient equalizes at the time that the cricopharyngeal sphincter opens. The marked positive-pressure wave indicates the actual primary peristaltic contraction—a localized, coordinated, propagated ring which starts in the pharynx and moves to the terminal oesophagus.

It is difficult to generalize about the anatomical and physiological landmarks of the 'gastro-oesophageal segment' in the different species. In general the features are the same as in man. The terminal oesophagus, or sphincteric region, which is characterized by a constant empty segment of varying length, seldom relaxes fully during the advance of a peristaltic wave. Some constriction is always maintained, and the swallowed contents are forced through as if under considerable pressure. At the upper level of the sphincteric zone the propagated wave apparently disappears and is replaced by a delayed concentric contraction which empties this part into the stomach much more slowly. As in man, the findings suggest that the high-pressure zone exhibits a characteristic motor function which is integrated in oesophageal peristalsis as the final act in deglutition. Thus the functional sphincter not only serves as a part of the means of transport of the oesophageal contents but, once the bolus has passed into the stomach, its tonically contracted fibres keep the door closed so that no abnormal reflux can take place.

This study has not yet been completed. The results are reported to stimulate further interest in the wide possibilities of this field of investigation.

SUMMARY

Cine-radiographic and manometric recordings of oesophageal pressure and motility were carried out in the rabbit, monkey, mouse, cat, ferret, guinea-pig and dog.

The characteristics of the gastro-oesophageal and oesophago-pharyngeal withdrawal curves, deglutition complexes and intraluminal pressure changes were of the same general pattern in all species. The results were very similar to those obtained in man, suggesting that the underlying physiological mechanisms correspond.

Functional, if not structural, sphincters exist at the cranial and caudal ends of the oesophagus. These sphincters are integrated into the mechanism of deglutition, relaxing and contracting as part of the propagated primary peristaltic wave which starts in the pharynx and moves to the terminal oesophagus.

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