DIAPHRAGMATIC AND OESOPHAGEAL ACTIVITY IN REGURGI-TATION IN SHEEP: AN ELECTROMYOGRAPHIC STUDY

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SUMMARY

1. Electromyographic (e.m.g.) recordings of reactions of the oesophagus, vertebral and costal fibres of the diaphragm and from the reticulum – one of the cranial divisions of the stomach were made during the regurgitation of rumination in sheep.

2. E.m.g.s indicated that a contraction of the caudal thoracic oesophagus developed over a period of about 2 sec before, and ceased at the time of, the more forceful inspiratory effort associated with regurgitation.

3. This contraction was confined to the caudal region of the thoracic oesophagus in which it was characteristically more prolonged and intense in its most caudal part within 15-25 mm of the hiatus oesophageus. It is interpreted to contribute to development or intensification of a caudal thoracic oesophageal sphincter.

4. The more forceful inspiratory effort at the time of regurgitation was due to costal fibres of the diaphragm. Although active normally during inspiration the vertebral fibres of the hiatus oesophageus do not contribute to this more forceful inspiration. This may facilitate regurgitation of digesta. Similarly, inactivity of vertebral but not costal fibres detected during primary oesophageal contractions (of swallowing) may make for easier passage of digesta into the stomach.

INTRODUCTION

Regurgitation of digesta in the course of rumination is preceded by a gastric (reticular) contraction at the height of which a more forceful than usual inspiratory effort is made with a closed upper airway (Sellers & Stevens, 1968). Although differing views have been advanced on the importance of gastric and respiratory movements in generation of the pressure difference between the stomach and thoracic oesophagus at the time of regurgitation, it has been accepted that the movement of gastric digesta into the oesophagus occurs on relaxation of a caudal oesophageal sphincter (Bell, 1958, 1961; Stevens & Sellers, 1960; Sellers & Stevens, 1968).

Factors which influenced undertaking the present work included doubts about the forms of oesophageal and diaphragmatic activity during regurgitation. There has been a cineradiographic demonstration of constrictions of the thoracic oesophagus in sheep during insufflation of gas into the stomach (Dougherty & Meredith, 1955), but

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no evidence of a high pressure zone, characteristic of a sphincter, was obtained in 'pull through' manometric studies in the sheep or cow (Winship, Zboralske, Weber & Soergel, 1964); nor was evidence of a sphincter obtained from studies on activity in vagal efferent fibres innervating the oesophagus (Roman, 1966, 1967; Rousseau, 1970) and from oesophageal electromyograms (Rousseau, 1970).

It was also postulated that participation of vertebral fibres of the diaphragm forming the hiatus oesophageus, in the forceful contraction of the diaphragm at the time of regurgitation, would hinder rather than aid movement of digesta into the thoracic oesophagus. Thus it was of interest to compare the activity of vertebral and costal fibres of the diaphragm during the more forceful inspiratory effort associated with regurgitation.

Electromyography was applied to study directly, activity of the caudal regions of the oesophagus, the reticulum and of the diaphragm and to define inter-relations between the activity of these structures during regurgitation. A preliminary report of this work was communicated to the Physiological Society (Titchen, 1976).

METHODS

The observations reported were made in nine sheep, 9-15 months old (in Melbourne Australian Merinos, crosses of the Merino and British breeds and at the Royal Veterinary College, Cheviots). In each fifteen-strand fluorocarbon covered stainless-steel wire (o.d. 0.28 mm), Cooner Sales Company, Chatsworth, California, was used to record from two or more of the following: reticulum, cervical oesophagus within 45 mm of the thyroid cartilage, the caudal thoracic oesophagus at sites up to 60 mm rostral to the hiatus oesophageus, vertebral fibres of the diaphragm, both within 10 mm of the hiatus oesophageus and more peripherally, and costal fibres of the diaphragm. The wires were introduced during halothane (B.P.) anaesthesia with full precautions to maintain asepsis. Three wires were inserted at each site, in either an equilateral triangular arrangement with about 5 mm separating each, or in line similarly separated.

Introduction of the electrodes was facilitated by their preparation. After a knot was made about 30 mm from one end of a length of about 800 mm of the fluorocarbon covered wire, the insulation was stripped between this knot and the immediately adjacent end. The bared wires were soldered into the lumen of a 12 mm long, 23 or 25 gauge hypodermic needle detached from its hub. The needle was used to take the wire bared of its insulation through the muscle of the different structures. EutecRod 157-B was used with Eutectic flux 157 (Eutectic (Australia) Pty Limited, Melbourne) to solder the wires into the needle. The ease of soldering cables into the hypodermic needle tubing was greater with these materials than when ordinary core solders were used with metaphosphoric acid as a flux. Each of the three wires used to record from one site was tied with a reef knot into the muscle of the structures being studied. Once the wires had been placed, the hypodermic needle tubing used to insert them was cut from the cable. These electrode assemblies were sterilized by being autoclaved in paper envelopes.

The wires were taken from the structures into which they were inserted to a superficial position by being led through tissues in the eye of a needle about 300 mm long to pass through the skin in a mid-dorsal situation usually at the level of the dorsal process of the last thoracic vertebra. Each group of three cables was identified with a code of knots tied 75-100 mm from their free ends at the time of insertion; they were later soldered to edge connectors. Confinement of connectors, and the exteriorized wires, within a tubular expanding elastic net body bandage (Presnet, Eizai Lab., Tokyo) preserved them from interference by the animals, which apparently arose from curiosity rather than irritation. Electromyograms (e.m.g.s) were obtained within 120 min of insertion of the wires and were still being obtained in one sheep when it was killed 240 days after introduction of the wires. Recordings have been obtained for over 500 days using this technique (N. Anderson, personal communication), features of which, as applied to sucking lambs have been demonstrated to the Physiological Society (Harding, Johnson, McLelland & Titchen, 1976; Newhook & Titchen, 1976).

Grass and Cannon oscilloscope recording cameras were used to obtain photographic records of the electromyograms using film or sensitized paper. The amplifiers used were either Grass P15, Tektronix 122 or Devices AC8 differential amplifiers modified to permit oscillographic recording between 3 Hz and 3 kHz. The Tektronix 122 amplifiers were used with a Tektronix double beam oscilloscope at the Royal Veterinary College. A double beam Tektronix 565 oscilloscope was used in association with a 3A3 2-channel beam splitting amplifier and a 3A74 4-channel beam splitting amplifier in the University of Melbourne: in this way up to six e.m.g.s were recorded at the same time. All recordings were made whilst the animals were in the metabolism cages in which they were usually kept. Use of an audio monitor aided associations to be formed between e.m.g. changes and activity detected by observation of the animals.

Observations were made in three sheep of oesophageal and diaphragmatic e.m.g. activity during pentobarbitone sodium anaesthesia, of the effect of inflation of balloons in the oesophagus. Pressure recordings from these balloons were obtained using Bell and Howell transducers and Devices DC2D amplifiers or Siemens Schonander EMT 35 transducers in conjunction with their EMT 31 amplifiers.

RESULTS

Activity of the reticulum and of costal fibres of the diaphragm during the regurgitation of rumination is shown in Fig. 1. The reference point in these and descriptions



Fig. 1. Reticular and costal diaphragmatic e.m.g.s recorded from a sheep (Merino cross) during regurgitation. The uppermost record is from the right lateral aspect of the reticulum and the lower from the costal diaphragm. The sheep was indoors at an ambient temperature of 80 °F. Frequency of recording in this and later Figures, 3–3 kHz. Time bar 1 sec. The reticular e.m.g. shows three phases of activity. The first and longest ($2\cdot 2$ sec) precedes the more forceful inspiratory effort of the diaphragm, which is followed by briefer second and third phases. The inspiratory effort of regurgitation shows clearly on the costal diaphragmatic e.m.g. as a longer higher voltage burst.

which follow is the more intense inspiratory effort of the costal fibres of the diaphragm which occurred at the time of regurgitation, referred to here as 'the inspiratory effort of regurgitation'. This was readily observed and was used to identify the characteristic patterns of e.m.g. activity of the structures studied during regurgitation. Descriptions which follow, and the records shown, refer only to regurgitation seen to be succeeded by periods of mastication.

Activity of the reticulum during rumination

Three phases of reticular activity occur at the time of the regurgitation of rumination (Figs. 1 and 7). The first and longest precedes the inspiratory effort of regurgitation. It has been identified with every method applied in studies on reticular motility during rumination as an additional phase of reticular contraction which precedes

regurgitation. This contraction has been associated with the movement of digesta towards or into the oesophagus (Bell, 1958, 1961; Stevens & Sellers, 1960; Sellers & Stevens, 1968). It functions either to contribute to the gastro-oesophageal pressure gradient at the time of regurgitation or to move digesta towards the cardia. Data from three sheep on the duration of the phases of the reticular e.m.g. at the time of rumination are given in Table 1.

TABLE 1. Duration of the phases of reticular e.m.g. recorded during regurgitation of ruminationEach figure refers to the mean of fifteen observations $\pm s.e.$

| Sheep no. | First phase of reticular e.m.g. (sec) | Pause | Second phase of reticular e.m.g. (sec) | Pause | Third phase of reticular e.m.g. (sec) |
|--------------|---|------------|--|------------|---|
| 1. | 2.38 | 2.33 | 1.03 | 0.83 | 0.28 |
| | ± 0.04 | ± 0.02 | ± 0.05 | ± 0.01 | ± 0.01 |
| 2. | 2.44 | 2.22 | 1.10 | 0.92 | 0.25 |
| | ± 0.01 | ± 0.08 | ± 0.05 | ± 0.05 | ± 0.01 |
| 3. | 2.26 | 2.17 | 1.03 | 0.75 | 0.29 |
| | ± 0.01 | ± 0.02 | ± 0.08 | ± 0.06 | ± 0.01 |

Diaphragmatic activity during the regurgitation of rumination

The more forceful inspiration against a closed upper airway preceding regurgitation during rumination is due to contraction of costal and not of hiatal fibres of the diaphragm. The costal fibres exhibit an e.m.g. burst of increasingly higher voltage, which abruptly ceases before a regurgitation movement occurs in the oesophagus. The more forceful inspiratory effort of the diaphragm during regurgitation has the following features:

It occurs in the costal fibres of the diaphragm over about $0.5 \sec (0.55 \pm \text{s.e.})$ $0.01, 0.53 \pm \text{s.e.}, 0.02 \text{ and } 0.51 \pm \text{s.e.}, 0.04 \sec, n = 15$ in each of three different sheep, with e.m.g. recordings made at respiratory rates between 24 and 42 sec⁻¹).

It always follows the first or additional phase of the reticular contraction.

It may occur when an inspiration would have been expected, or be added to an already developing inspiration or occur independently, thus interrupting the rhythm of respiration. Relations between the e.m.g.s of costal and vertebral fibres of the diaphragm during the regurgitation of rumination can be seen in Fig. 2, in which it



Fig. 2. E.m.g.s of costal and vertebral fibres of the diaphragm of a Cheviot sheep at the time of the more forceful inspiration of regurgitation during which costal fibres of the diaphragm show an increased period of e.m.g. activity of higher voltage. Vertebral fibres forming and within 5 mm of the hiatus oesophageus are inactive both during the more forceful inspiration of regurgitation and for one respiration after. Time bar 1 sec. The upper record is the vertebral fibre e.m.g. and the lower that of costal fibres of the diaphragm.

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is clear that hiatal fibres did not contribute to the more forceful inspiration, being quiescent at the time of the more forceful inspiratory effort or regurgitation. Hiatal fibres showed a period of reduced activity or inactivity for up to 4.75 sec after the more forceful inspiration (Fig. 2). This reaction was characteristic of hiatal fibres within about 8 mm of the hiatus oesophageus. More peripherally located vertebral fibres continued to contract during the inspiratory effort of regurgitation; they did not however show the increase in activity seen in costal fibres.

Differing activity in hiatal and costal fibres of the diaphragm was also recorded during swallowing and oesophageal distension. Activity ceased in hiatal fibres during swallowing, especially at higher respiratory rates (Fig. 3).



Fig. 3. Reduction in activity of hiatal fibres of the diaphragm of a Merino sheep during a primary oesophageal contraction. E.m.g.s of from above downwards:costal region of the diaphragm, vertebral fibres forming the hiatus oesophageus, the thoracic oesophagus 15 mm rostral to the hiatus oesophageus and cervical oesophagus 20 mm caudal to the thyroid notch. Time bar 1 sec.

Distension of a balloon in the cervical and cranial (but not caudal) regions of the thoracic oesophagus was followed in sheep anaesthetized with pentobarbitone sodium by reductions in the activity of hiatal but not of the costal fibres of the diaphragm (Fig. 4). A similar reaction has been reported in the dog, in which costal but not hiatal fibres are active during the expulsive phase of vomiting (Monges, Salducci & Naudy, 1976*a*, *b*).



Fig. 4. Reduction in activity in the hiatal fibres of the diaphragm in a Merino sheep anaesthetized with pentobarbitone sodium during distension of the cervical oesophagus (50 mm caudal to the thyroid notch). The upper bar indicates 5 sec. The lower bar indicates the period during which 10 ml. water was introduced into the balloon and then removed. The upper recording is from costal fibres of the diaphragm, the lower from the hiatal fibres.

Caudal thoracic oesophageal activity during the regurgitation of rumination

Two bursts of e.m.g. activity consistently occurred in the caudal regions of the thoracic oesophagus at the time of the regurgitation of rumination (Figs. 5, 6 and 7). The first was typically most intense in the 15-25 mm of the oesophageus rostral to the hiatus oesophageus. It is interpreted to be virtually contraction of a caudal thoracic oesophageal sphincter which develops in advance of the more forceful inspiratory effort of regurgitation. This contraction develops over about 2 sec $(1.91 \sec \pm s.E. 0.22, 2.19 \sec \pm s.E. 0.08, 2.20 \sec \pm s.E. 0.13$ in three sheep with n = 15 in each).



Fig. 5. E.m.g.s recorded from the caudal thoracic oesophagus and costal fibres of the diaphragm of a sheep at the time of regurgitation. The upper record is of the e.m.g. of the thoracic oesophagus about 2 mm rostral to the hiatus oesophageus. The lower record is of costal fibres of the diaphragm. The oesophageal e.m.g. shows a progressive increase in activity preceding the inspiratory effort of regurgitation. The e.m.g. burst following the inspiratory effort is associated with regurgitation, the later burst is the primary contraction following swallowing of the liquid part of the regurgitated bolus. The costal fibres of the diaphragm have a longer higher voltage e.m.g. burst at the time of the inspiratory effort of regurgitation.



Fig. 6. E.m.g.s recorded in a Merino sheep from in the upper trace, the caudal thoracic oesophagus 20 mm and in the lower trace 5 mm rostral to the hiatus oesophageus preceding and during regurgitation and up to the time of the primary oesophageal contraction of the oesophagus following swallowing of the liquid part of the regurgitated bolus. Time bar 1 sec. Note the relatively greater e.m.g. activity in the oesophagus 5 mm rostral to the hiatus oesophageus preceding regurgitation.

It is typically confined to the most caudal region of the thoracic oesophagus. The most cranial point at which it was detected was 40 mm rostral to the hiatus oesophageus. At more cranial levels in the oesophagus the e.m.g. appeared later, sometimes disappeared earlier and generally was weaker (relative to the e.m.g.s of swallowing and regurgitation) than in the caudal part of the thoracic oesophagus. It was noted on three separate occasions in two sheep that whilst regions of the oesophagus 40 mm rostral to the hiatus oesophageus exhibited this activity before the first of a series of regurgitations they did not in subsequent regurgitations.

An oesophageal contraction which contributes to the propulsion of digesta towards the mouth followed the inspiratory effort of regurgitation. It occurred as a rapidly developing burst of higher voltage which, in regions of the oesophagus 2-5 mm from the hiatus oesophageus, persisted for about $0.2-0.3 \sec (0.31 \sec \pm \text{s.e.} 0.08, 0.24 \sec \pm \text{s.e.} 0.01$, and $0.23 \sec \pm \text{s.e.} 0.01$ in three sheep, n = 15 each). The rostral progression of this wave of activity was readily apparent in recording sites separated by 30-50 mm in which it was evident that the rostrally progressing oesophageal contraction of regurgitation was more rapid than the caudally sweeping contractions of swallowing (Figs. 6 and 7), a point shown in previous manometric studies (Winship *et al.* 1964; Stevens & Sellers, 1960).



Fig. 7. The association of reticular, diaphragmatic and oesophageal activity during regurgitation. Records from above downwards : reticular e.m.g., vertebral fibres of the diaphragm forming the hiatus oesophageus, costal fibres of the diaphragm and the caudal thoracic oesophagus at three sites :5 mm rostral to the hiatus oesophageus 15 mm and 25 rostral to the hiatus oesophageus. Time bar 1 sec. The first swallow (\uparrow Sw) follows completion of mastication of a previously regurgitated bolus. Regurgitation (\uparrow Reg) of another bolus of gastric contents to be further masticated and ensalivated is followed by swallowing (\uparrow Sw) of the liquid portion of the regurgitated bolus.

Swallowing regularly occurs during episodes of rumination in association with the other events recorded. Characteristically there is a swallow immediately following entry into the mouth of the regurgitated bolus. In addition there may be a number of swallows during the 40–50 sec of mastication. Both the primary contraction (of swallowing) of the oesophagus which occurs at the end of a period of mastication and that immediately after regurgitation are shown in Fig. 7 which demonstrates the association between the reticular, oesophageal and diaphragmatic activities at the time of rumination.

The duration of the e.m.g. activity of the primary contractions following swallowing was consistently greater than that of regurgitations. Thus in regions of the oesophagus 2-5 mm from the hiatus oesophageus the e.m.g. of the primary contraction associated with swallowing of the liquid portion of the regurgitated bolus occurred, in three sheep, over $0.47 \sec \pm s.E$. 0.05, $0.44 \sec \pm s.E$. 0.01, and $0.40 \sec \pm s.E$. 0.19 in three sheep (n = 15, in each). Similarly primary contractions associated with swallows at the end of the period of mastication of the chewed bolus were marked by e.m.g. activity over $0.53 \sec \pm s.E$. 0.12, $0.45 \sec \pm s.E$. 0.01, and $0.41 \sec \pm s.E$. $0.02 \sec \text{ in each}$ of these sheep (n = 15, in each).

DISCUSSION

E.m.g.s have provided direct evidence of a contraction of the most caudal regions of the thoracic oesophagus preceding the regurgitation of rumination. This contraction is interpreted as effectively leading, temporarily, to the development of a sphincter, which is important in the genesis of a gastro-oesophageal pressure gradient during the inspiratory effort of regurgitation and the additional phase of reticular contraction of rumination. There is no evidence from e.m.g.s that this region of the oesophagus displays tonic activity. It is possible that the exclusion of gastric digesta from the oesophagus for most of the time is due to mechanisms such as Botha discussed (1962). The effectiveness of these will be increased with caudal thoracic oesophageal contractions in response to distending or other stimuli (Code & Schlegel, 1968). Edwards (1970) commented in this connexion that 'the effective sphincter responds to a challenge by contracting'. The sensitivity of the sheep's oesophagus to mechanical stimuli has been established both in studies on salivary, gastric and oesophageal responses to its stimulation and from electrophysiological studies on vagal afferents (Iggo, 1957; Falempin, Mei & Rousseau, 1978). These afferents probably mediate reflex responses to oesophageal and specially caudal thoracic oesophageal stimulation, just as they do in the cat in which oesophageal contractions can be obtained as reflex (vago vagal) responses to gastric and oesophageal stimulation (Titchen & Wheeler, 1971).

Contraction of the diaphragm against a closed upper airway makes the main contribution to the gastro-oesophageal pressure gradient which aids aspiration of digesta into the thoracic oesophagus during regurgitation. This contraction is characteristically of costal and not vertebral fibres of the diaphragm, similarly Monges *et al.* (1976*a*) found that central fibres of the hiatus oesophageus participate in the more forceful contraction of the diaphragm in retching but not in the expulsive phase of vomiting in the dog. Both in rumination and vomiting relaxation of the vertebral fibres will allow easier passage of digesta past the hiatus oesophageus.

The absence of hiatal fibre activity during the inspiratory effort of regurgitation probably reflects the central co-ordination of events of rumination; hiatal fibre inactivity continuing after regurgitation has occurred could arise from oesophageal stimulation. In the dog (Monges et al. 1976b) and the sheep (Fig. 4) oesophageal distension has been shown to reduce activity of hiatal fibres; thus afferent stimulation of the oesophagus itself during swallowing and regurgitation could modify diaphragmatic activity. Oesophageal stimulation may arise both from distension by the bolus and oesophageal contraction since oesophageal receptors exhibit both 'in parallel' and 'in series' behaviour in the sheep (Falempin et al. 1978). This is possibly characteristic of oesophageal muscle receptors generally – similar sensitivities were found in the cat's oesophagus (Harding & Titchen, 1975).

Relaxation of hiatal fibres also occurs during swallowing, usually this is only clearly seen with faster respiratory rates or when there is co-incidence of primary oesophageal contraction and of inspiration. Whether this mechanism, which operates in regurgitation and swallowing in the sheep and in the expulsive phase of vomiting in the dog is also brought into play under still other circumstances, e.g. in secondary oesophageal contractions, to ensure free passage of material into the stomach has not been investigated. This and the possibility of other oesophago-phrenic associations require further study.

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