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EFFECTS OF STIMULATION OF EFFERENT FIBRES OF THE VAGUS ON THE RETICULO-OMASAL ORIFICE OF THE SHEEP

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SUMMARY

1. The reticulo-omasal orifice has been observed and its activity recorded in decerebrate and spinal preparations of lambs and in lambs and sheep anaesthetized with chloralose.

2. Spontaneous closure movements at about 6/min were seen, or recorded from balloons placed in the orifice in all types of preparation when both vagus nerves had been cut and after atropine, hexamethonium, phentolamine and propranolol had been given I.V.

3. The effects on the reticulo-omasal orifice of stimulation in the neck of efferent fibres of the vagus nerves on either side differed according to the form of the stimulus applied.

4. Threshold stimulation of the vagus nerve caused closing of the orifice which was blocked by atropine.

5. Opening of the orifice and disappearance of spontaneous closing movements followed more intense stimulation of the vagus nerves.

6. Vagal opening effects were obtained after atropine was given and after adrenergic opening and closure effects had been blocked with phentolamine and propranolol.

INTRODUCTION

A potentially narrow sphincter, the reticulo-omasal orifice, separates the more cranial divisions of the ruminant stomach, the reticulum and rumen from the omasum. The considerable passage of digesta through this orifice (Bost, 1970) is thought to depend on the development of pressure gradients between the reticulum and omasum, during reticular contractions

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or following omasal canal contractions at times when the orifice is open (Stevens, Sellers & Spurrell, 1960; Bost, 1970). Flow of digesta into the omasum is marked during the second phase of the regularly recurring contractions of the reticulum (Stevens *et al.* 1960; Phillipson, 1966). At this time there is an opening of the reticulo-omasal orifice both in the ox (Balch, Kelly & Heim, 1951; Stevens *et al.* 1960; Ruckebusch & Kay, 1971) and in the sheep (Ohga, Ota & Nakazato, 1965; Laplace, 1970; Ruckebusch, 1970).

The regular association of opening of the orifice and of reticular contractions could be expected to involve the vagal innervation of both of these structures. The vagus nerves are essential for the occurrence of the diphasic contractions of the reticulum and cyclical contractions of the rumen (Duncan, 1953) which are generated as vago-vagal reflex responses (see Titchen, 1968; Iggo & Leek, 1970). The experiments described in this paper were undertaken in an attempt to define, from stimulation of their efferent fibres, influences the vagus nerves have on the reticulo-omasal orifice in the sheep.

METHODS

Lambs from 7 to 30 days of age and adult sheep of the Romney breed or its crosses were used in both laboratories. Anaesthesia was induced by inhalation of ethyl chloride or halothane and was maintained with ether if decerebration or spinal cord transection was to be undertaken. Halothane was used for maintenance of anaesthesia when a volatile anaesthetic agent was used for a shorter period and only continued until chloralose (70 mg/kg) was given through a venous cannula. The experimental observations were made with the preparations in dorsal recumbency.

The reticulo-omasal orifice was exposed by a mid line laparotomy incision and an incision made in the free ventral pole of the reticulum. In both young and adult animals stomach contents had to be removed by aspiration and this was aided by the introduction of saline at 38° C into the rumen through the reticulum gastrostomy incision. Both observation of the reticulo-omasal orifice and the introduction of a recording balloon into it were conveniently accomplished with the approach described.

Records of the activity of the orifice were obtained with a Devices heat stylus chart recorder or a Mingograph (Elema Schönander) jet writing recorder using transducers in conjunction with water-filled balloons constructed from a length of a Latex finger stall (London Rubber Co.) which distended to a diameter of 20 mm and a length of 15 mm at a pressure of 10 cm water. The balloons were tied to vinyl tube (about 4 mm o.d., 3 mm i.d.) on which rubber disks (20 mm diameter, 4 mm thick) were mounted at each end of the balloon. These disks served to retain the balloon in the orifice.

A tracheal cannula was inserted in every experiment. In spinal preparations a Palmer (London) Ideal respiratory pump was used to ventilate the preparations with air or 95 % oxygen, 5 % carbon dioxide.

The carotid or femoral arterial blood pressure, and pressure changes within the balloon in the reticulo-omasal orifice, were recorded with the aid of Statham or Elema Schönander transducers. The method used for the reticulo-omasal orifice followed that described by Setekliev (1964) for isometric recording from a balloon in the rabbit uterus. In the experiments reported in this paper the distension of the balloon in the reticulo-omasal orifice was limited to 0·5–1·5 ml. In some experiments a water manometer in series with the pressure transducer permitted records to be obtained with a volume displacement system against increasing pressure.

Atropine sulphate (Parnell Laboratories, Sydney), adrenaline hydrochloride (Parke Davis & Co.), L-noradrenaline (Levophed, Winthrop Laboratories), isoprenaline (Isoprel, Winthrop Laboratories) phentolamine (Regitine, Ciba), propranolol (Inderal, I.C.I.) and hexamethonium bromide (Koch Light) were administered I.V. in the doses stated.

Nerve stimulation was undertaken with the aid of fluid electrodes as described by Porter & Allamon (1936) using silver wire electrodes in conjunction with either a Palmer student's stimulator or a Grass Model S4E stimulator.

RESULTS

Spontaneous rhythmically recurring closing and opening movements of the reticulo-omasal orifice of a frequency of about 6/min were observed in anaesthetized, spinal and decerebrate preparations with both vagus nerves cut and with one or both splanchnic nerves intact. This spontaneous activity was recorded in anaesthetized lambs and sheep in which it was also shown to be present after the administration of atropine (0·1–2·0 mg/kg), phentolamine (1·0 mg/kg), propranolol (0·3 mg/kg) and hexamethonium bromide (4–10 mg/kg).

Stimulation of the peripheral end of either vagus nerve cut in the neck modified the activity of the reticulo-omasal orifice. The simplest form of response of the orifice with threshold stimulation of efferent cervical vagal nerve fibres consisted of a single episode of narrowing of its lumen recorded as an increase in pressure. This will be referred to as contraction or closing of the orifice. Such evoked contractions occurred with latencies as short as 0·7 sec, reached their peak within 3 sec and were complete within 6 sec.

The identification of closing of the reticulo-omasal orifice as a response to stimulation of the vagus nerves involved distinguishing evoked contractions from spontaneously recurring closing movements. This was aided by delivering stimuli to a vagus nerve so that (*a*) the evoked contraction would be interpolated between members of a series of rhythmically recurring contractions (Fig. 1), or (*b*) the evoked contraction would be superimposed on a pre-existing contraction (Fig. 3), or (*c*) the contraction was evoked during a period of inhibition of spontaneous contractions by the means described later (Fig. 5). In many experiments evoked contractions were of a greater magnitude than any which occurred spontaneously. In some experiments the rate of development of stimulated contractions was also faster than that of spontaneous contractions, although this was not a constant feature in all experiments and was not used to distinguish between evoked and spontaneous contractions.

Closing responses of the reticulo-omasal orifice were distinguished from effects of the vagus on blood pressure or the reticulum since they were obtained on occasions when the stimulus applied either had no effect, or barely detectable effects on heart rate, blood pressure and also on the reticulum as well as on occasions when the effects on all three were marked.

The simple form of response described was characteristically obtained when one or a series of pulses of up to 1 msec duration was delivered to a vagus nerve. Frequencies of stimulation used were 2–20/sec applied for up to 30 sec. Once a set of conditions of stimulation had been established which produced a simple closure response, increases in the duration of the pulses, their frequency, voltage or the period for which they were applied were shown to increase the complexity of the responses. Most attention was paid to the effect of increasing the pulse duration or of prolonging the period of stimulation (Figs. 2 and 4).

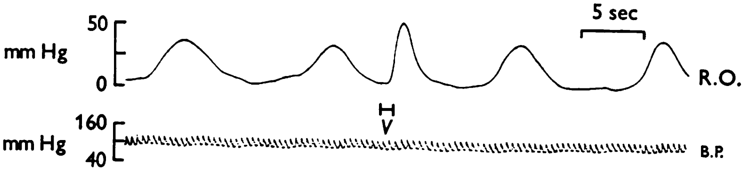

Fig. 1. Sheep 16 kg, chloralose anaesthesia. Responses of reticulo-omasal orifice (R.O.) and femoral arterial blood pressure (B.P.) to stimulation of peripheral end of left cervical vagus nerve (*V*) for 1 sec, with 20 pulses/sec, pulse duration 1 msec, 10 V. Time bar 5 sec. Note the faster rise time of the contraction evoked by stimulation of the vagus nerve than observed with spontaneous contractions between which it is interpolated. Volume of distension of reticulo-omasal balloon 0·5 ml.

Increases in the duration of pulses used to stimulate the vagus nerves resulted in the simple contraction of the reticulo-omasal orifice being followed by a period during which spontaneous contractions were absent. In the experiment in which Fig. 2 was obtained, comparisons were made of responses to stimulation of the vagus with pulses of 0·1 and 1·0 msec duration. With the shorter pulses after the initial contraction there was a sustained increase in pressure upon which a later contraction was superimposed (Fig. 2*a*). This later contraction was presumably a spontaneous one. In contrast, stimulation with the longer pulse durations resulted in the initial contraction being succeeded by periods during which spontaneous contractions were absent and the reticulo-omasal orifice remained open (Fig. 2*b*).

The inhibitory effects of vagus nerve stimulation on spontaneous contractions persisted in some preparations after the stimulus ceased. This inhibition was for a time which lengthened as the period of stimulation of the vagus nerves increased. Thus in the records shown in Fig. 4 stimulation of the vagus for 4 sec caused closing of the orifice and then loss of both tone and spontaneous contractions for 31 sec; stimulation for 1·5 sec caused a similar contraction, a lesser effect on tone and disappearance of spontaneons contractions for only 20 sec. In some experiments, such as that from which the record shown as Fig. 5 was obtained, spontaneous contractions were absent for 240 sec or more following stimulation of the vagus for 15 sec. In the later stages of such periods of prolonged

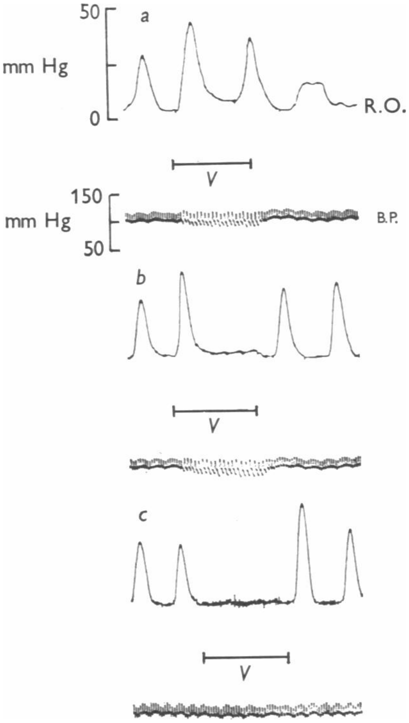

Fig. 2. Sheep 18·0 kg, chloralose anaesthesia. Responses of the reticulo-omasal orifice (R.O.) to stimulation of the peripheral end of the left cervical vagus trunk for 15 sec, 5 pulses/sec, 5 V. (*a*) Pulse duration 0·1 msec; (*b*) Pulse duration 1·0 msec; and (*c*) Pulse duration 1·0 msec, record obtained 3 min after the I.V. injection of 0·1 mg atropine/kg body wt. between (*b*) and (*c*). Stimulation with shorter pulses (*a*) caused an initial rapid contraction and an elevation (closure) of the base line from which the next contraction occurred.

Stimulation with the longer pulse duration (*b*) caused a contraction of the orifice succeeded by a loss of spontaneous contractions, in this case for about the duration of the stimulation. After atropine the contraction was blocked; the opening still persisted with stimulation of the vagus nerve. B.P., femoral arterial blood pressure.

absence of spontaneous contractions stimulation of a vagus nerve was shown to evoke a contraction of the reticulo-omasal orifice (Fig. 5) which was followed by the re-appearance of the rhythmically recurring contractions of the orifice.

Atropine injected I.V. in doses of 0·1–2·0 mg/kg body wt. blocked closure produced by stimulation of the vagus nerves but not their effects of abolishing spontaneous contractions (Fig. 2*c*). Effects of stimulation of the vagus nerve which persisted after the administration of atropine were observed within 3 min of its administration, within which time atropine-sensitive responses had been blocked. Judged by the form of the fall in the

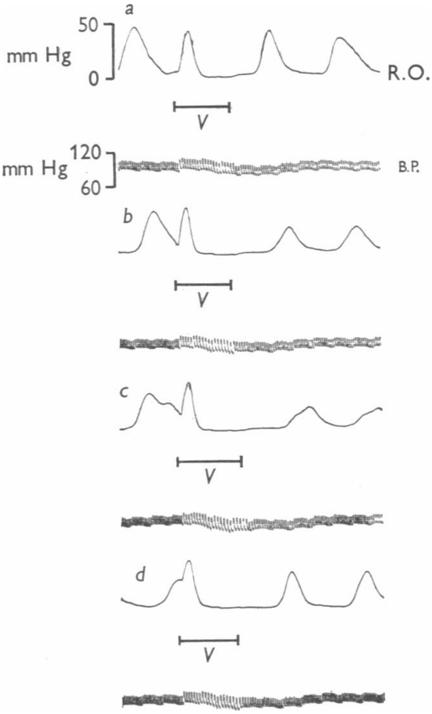

Fig. 3. Sheep 35 kg, chloralose anaesthesia. Changes in the reticulo-omasal orifice evoked by stimulation of the peripheral end of the left vagus nerve (*V*) cut in the neck. Each evoked contraction was succeeded by a period of diminished spontaneous activity of the orifice during which the orifice was widely open.

The stimuli were delivered so that the contractions occurred (*a*) independently and (*b*, *c* and *d*) were added to previous spontaneous contractions successively closer to the peak of each contraction.

R.O., reticulo-omasal orifice (balloon distension 1 ml.). B.P., femoral arterial blood pressure. Stimulus details: *a*, 5 pulses/sec, 5 V, 1 msec for 9·5 sec; *b*, *c* and *d*, 5 pulses/sec, 10 V, 1 msec, for *b*, 9·5 sec, *c* 11 sec, *d* 10 sec.

base line of the recording sometimes seen on stimulation of the vagus nerves after the administration of atropine these 'atropine resistant' effects appeared within 2 sec of the start of stimulation of the vagus nerves.

Both before and after the administration of atropine, marked changes were seen in some experiments following the withdrawal of stimulation of the vagus nerves, as post-stimulation increases in the amplitude of rhythmic contractions of the orifice. This after-effect of stimulation has a parallel in studies such as Campbell (1966) made with *in vitro* preparations of guinea-pig caecum in which cessation of inhibitory stimuli was followed by greater activity. Conditions which lead to inhibitory stimuli being followed by a period of continuing inhibition or enhanced activity have not been defined in the present study.

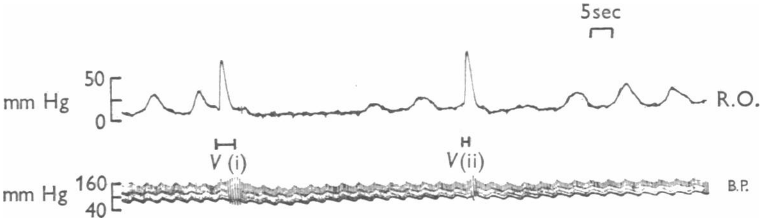

Fig. 4. Sheep 18·5 kg, chloralose anaesthesia. Contractions of the reticulo-omasal orifice (R.O.) evoked by stimulation of the peripheral end of the right cervical vagus nerve with 20 pulses/sec, 1 msec duration, 10 V for 4 sec (*V*i) and 1·5 sec (*V*ii). The reticulo-omasal recording balloon was distended with 0·7 ml.

Stimulation of the vagus nerve for 4 sec (*V*i) evoked contraction of the orifice succeeded by loss of tone and spontaneous activity for 31 sec. In contrast, stimulation for 1·5 sec led to a contraction, had a less marked effect on tone and caused the disappearance of major spontaneous contractions for 20 sec. B.P. femoral arterial blood pressure. Time bar 5 sec.

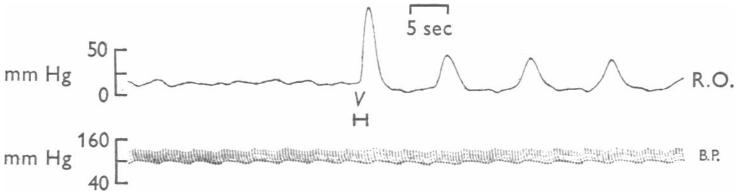

Fig. 5. Sheep 32 kg, chloralose anaesthesia. Contraction of the reticulo-omasal orifice (R.O.) evoked by stimulation of the peripheral end of the left vagus nerve trunk (*V*) during a period of maintained diminution of spontaneous contractions of the orifice resulting from stimulation of the vagus nerve for 15 sec, 120 sec before this stimulus was applied. The stimulus (*V*) which evoked a contraction and which was succeeded by a resumption of spontaneous contractions was for 2 sec. The stimuli were applied at 10 pulses/sec, 10 V, 1 msec pulse duration. 5 sec time bar.

Loss of spontaneous closure movements of the reticulo-omasal orifice with stimulation of the vagus nerves was observed after the intravenous injection of (in addition to atropine at up to 2 mg/kg) phentolamine (1·0 mg/kg) and propranolol (0·3 mg/kg) in doses reported by Titchen & Newhook (1968) to annul both the closure effects of adrenaline and noradrenaline and their effects (and those of isoprenaline) in reducing spontaneous contractions of the reticulo-omasal orifice.

Neither closing nor loss of spontaneous contractions was obtained with stimulation of the vagus nerves after the I.V. injection of hexamethonium bromide (4–10 mg/kg).

DISCUSSION

The recording system used in these experiments detected narrowing of the reticulo-omasal orifice as an increase in pressure; the extent of the opening which could be detected was limited by the diameter of the recording balloon introduced into and retained in the reticulo-omasal orifice. However, all of the major responses to vagus nerve stimulation interpreted to have occurred from pressure recordings – closure of the orifice, loss of spontaneous closure or contraction movements and its maintained opening – were in addition directly observed.

Evidence has been obtained of possible efferent vagal control of both closing and opening of the reticulo-omasal orifice. The effects of the vagus nerves appear to have been distinguished (by the use of pharmacological blocking agents) from the adrenergic closing and opening responses of the orifice described previously (Titchen & Newhook, 1968). The reactions of the reticulo-omasal orifice to stimulation of the vagus nerves are similar to effects of these nerves on the stomach of other species (Kosterlitz, 1968) consisting as they do of atropine sensitive (closing) and atropine resistant (opening) responses. The persistence of the atropine resistant opening of the orifice after blockade of the closing and opening effects of catecholamines is another respect in which there is a similarity in the reaction of the orifice and the stomach of other species. Relaxation of the cat's stomach in response to stimulation of the vagus nerves persisted both after atropine had been given and adrenergic blockade was produced (Martinson, 1965). Martinson & Muren (1963) concluded from the use of stimuli of different pulse durations that higher threshold fibres of the vagus were involved in the relaxation of the cat's stomach. The observation of a change from a simple closing to closing followed by opening of the orifice with increased duration of the pulses applied to the vagus nerves suggests that higher threshold fibres may also be concerned in opening of the orifice. In common with other atropine-resistant vagal effector mechanisms, that acting on the reticulo-omasal orifice of the sheep still remains to be identified as due to the post-ganglionic release of a particular transmitter substance, reactions occurring at ganglia or some other phenomena or combination of them.

Inhibition *and* differing mechanical responses of the ruminant stomach in response to stimulation of vagal efferent fibres have both been described. Brunaud & Dussardier (1951) and Comline & Titchen (1951*b*) showed an atropine-resistant inhibition of the reticulum produced by stimulation of efferent fibres of the vagus. This was also shown to suppress or reduce contraction of the reticulum evoked by adrenaline (Comline & Titchen, 1961). Different directions of contraction of the rumen were evoked by stimulation of the vagus nerves in an efferent sense at different frequencies (Reid & Titchen, 1965). Both forms of contraction, however, were abolished by atropine, as are the naturally occurring contractions of which they were interpreted to be the experimentally stimulated counterparts – the *A* and *B* sequences of contraction (Titchen & Reid, 1965).

It has not been shown how opening of the reticulo-omasal orifice is brought about. Our observations provide evidence of the existence of an inhibitory vagal innervation: stimulation of the vagus nerves led to diminution or disappearance of spontaneous activity of the orifice, this effect and the opening of the orifice persisting after atropine was given. No evidence has been obtained, however, that the two (opening of the orifice and inhibition of spontaneous contractions) are the same phenomenon. Electromyographic studies in conscious sheep revealed activity of muscle of, or near, the reticulo-omasal orifice at a similar frequency to that of spontaneous closing movements reported here. Laplace (1970) recorded bursts of electrical activity from the orifice lasting 3–6 sec, recurring every 8–10 sec, and noted additional prolonged discharges at the time the orifice would be expected, from endoscopic observation, to be open during the second phase of contraction of the reticulum. Ruckebusch (1970) also recorded electrical activity from near the orifice at 6–8 sec intervals and commented on its probable association with opening and closing of the orifice.

Recurring 'spontaneous' activity is not unique in the cranial parts of the ruminant stomach near to the reticulo-omasal orifice and its presence is not indicative that the e.m.g. recordings referred to were of muscle of the reticulo-omasal orifice. Structures contiguous to the reticulo-omasal orifice whose activity is of interest in this connexion are the reticular (oesophageal) groove and the reticulum. Small spontaneous contractions have been noted in the reticular groove in decerebrate preparations in which the splanchnic nerves had been cut (Comline & Titchen, 1951*a*); in partially separated slips of the reticulum in spinal preparations of kids and in kids anaesthetized with chloralose (Comline & Titchen, 1951*b*); and in the reticulum in decerebrate preparations in which they increased in activity immediately before the occurrence of diphasic contractions (Titchen, 1958) which they have also been observed to do in conscious animals in which exteriorizations of the reticulum were used to observe and record the activity of the reticulum (Reid, 1962). Leek (1969) observed contractions of local regions of the reticulum and cranial part of the rumen in sheep anaesthetized with halothane and he associated them with bursts of activity in afferent fibres of the vagus nerves lasting 2–5 sec and recurring at intervals of 4–10 sec. It seems clear from such observations that spontaneous activity is a characteristic feature of a number of regions of the cranial parts of the ruminant stomach and that its intensity may vary with the occurrence of the characteristic major contractions of the reticulum.

Both inhibition of spontaneous closing of the orifice and muscular contraction could contribute to opening of the reticulo-omasal orifice. Laplace (1970) associated two bursts of electrical activity, recorded electromyographically, with opening of the orifice. This supports the idea of opening being an active process due to muscular contraction. Ruckebusch (1970) was less categorical in his association of the electromyographic records and the condition of the orifice. There are considerable movements of structures near the orifice at the time of the reticulum contraction (Stevens *et al.* 1960) and, as argued above, their activity could contribute to interpretations being less clear cut than might have been hoped with the electromyographic techniques applied in conscious animals.

Although some aspects of the control of the reticulo-omasal orifice remain obscure it is clear from the present experiments that it exhibits considerable spontaneous activity which is subject to modification through its extrinsic vagal innervation. This modification could be expected to be achieved in part through vagal efferents that Iggo & Leek (1967) classed as Types II and III. The firm closing of the orifice which has been described during the first phase of the reticulum contraction could be ascribed to reinforcement of closing by Type III fibres, and the subsequent opening to fibres of Type II, from which Iggo & Leek (1967) recorded impulses preceding and in the early part of the second phase of contractions of the reticulum.

The present experiments on the efferent vagal innervation of the reticulo-omasal orifice add to an understanding of how its activity may be coordinated with reflex contractions of other structures of the ruminant stomach, such as the reticular groove (Comline & Titchen, 1951*a*) and the reticulum (Iggo, 1956; Titchen, 1958), and to the complex control of the motility of the ruminant stomach as a whole.

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REFERENCES

BALCH, C. C., KELLY, A. & HEIM, G. (1951). Factors affecting the utilization of food by dairy cows. 4. The action of the reticulo-omasal orifice. *Br. J. Nutr.* **5**, 207–216.

BOST, J. (1970). Omasal physiology. In *Physiology of Digestion and Metabolism in the Ruminant*, pp. 52–65, ed. PHILLIPSON. Newcastle upon Tyne: Oriel.

BRUNAUD, M. & DUSSARDIER, M. (1951). Recherches sur le médiateur chimique du nerf pneumogastrique des ruminants. *J. Physiol., Paris* **43**, 281–302.

CAMPBELL, G. (1966). Nerve mediated excitation of the taenia of the guinea-pig caecum. *J. Physiol.* **185**, 148–159.

COMLINE, R. S. & TITCHEN, D. A. (1951*a*). Reflex contraction of the oesophageal groove in young ruminants. *J. Physiol.* **115**, 210–226.

COMLINE, R. S. & TITCHEN, D. A. (1951*b*). Contractions of the reticulum of the young goat. *J. Physiol.* **115**, 24*P*.

COMLINE, R. S. & TITCHEN, D. A. (1961). Nervous control of the ruminant stomach. In *Digestive Physiology and Nutrition of the Ruminant*, pp. 10–22, ed. LEWIS, D. London: Butterworths.

DUNCAN, D. L. (1953). The effects of vagotomy and splanchnotomy on gastric motility in the sheep. *J. Physiol.* **119**, 157–169.

IGGO, A. (1956). Central nervous control of gastric movements in sheep and goats. *J. Physiol.* **131**, 248–256.

IGGO, A. & LEEK, B. F. (1967). An electrophysiological study of single vagal efferent units associated with gastric movements in sheep. *J. Physiol.* **191**, 177–204.

IGGO, A. & LEEK, B. F. (1970). Sensory receptors in the ruminant stomach and their reflex effects. In *Physiology of Digestion and Metabolism in the Ruminant*, ed. PHILLIPSON, A. T. Newcastle upon Tyne: Oriel.

KOSTERLITZ, H. W. (1968). Intrinsic and extrinsic nervous control of motility of the stomach and intestines. In *Handbook of Physiology*, section 6: Alimentary Canal, vol. IV, Motility, pp. 2147–2172. Washington: American Physiological Society.

LAPLACE, JEAN-PAUL (1970). Omaso-abomasal motility and feeding behaviour in sheep: a new concept. *Physiol & Behav.* **5**, 61–65.

LEEK, B. F. (1969). Reticulo-ruminal mechanoreceptors in sheep. *J. Physiol.* **202**, 585–609.

MARTINSON, J. (1965). Vagal relaxation of the stomach. Experimental re-investigation of the concept of the transmission mechanism. *Acta physiol. scand.* **64**, 453–462.

MARTINSON, J. & MUREN, A. (1963). Excitatory and inhibitory effects of vagus stimulation on gastric motility in the cat. *Acta physiol. scand.* **57**, 309–316.

OHGA, A., OTA, Y. & NAKAZATO, Y. (1965). The movement of the stomach of sheep with special reference to the omasal movement. *Jap. J. vet. Sci.* **27**, 151–160.

PHILLIPSON, A. T. (1966). The mechanical phenomena of the rumen. In *World Congress of Animal Feeding. I.* pp. 10–17.

PORTER, E. L. & ALLAMON, E. L. (1936). Barbiturate-strychnine antagonism in the spinal cat. A quantitative study. *J. Pharmac. exp. Ther.* **58**, 178–191.

Reid, C. S. W. (1962). The influence of the afferent innervation of the ruminant stomach on its motility. Ph.D. Thesis, University of Cambridge.

Reid, C. S. W. & Titchen, D. A. (1965). Reflex stimulation of movements of the rumen in decerebrate sheep. *J. Physiol.* **181**, 432–448.

Ruckebusch, Y. (1970). The electrical activity of the digestive tract of the sheep as an indication of the mechanical events in various regions. *J. Physiol.* **210**, 857–882.

Ruckebusch, Y. & Kay, R. N. B. (1971). Étude critique de la motricité gastrique chez les bovins. *Annls Rech. vétér.* **2**, 99–136.

Setekliev, J. (1964). Uterine motility of the estrogenized rabbit I Isotonic and isometric recording *in vivo* – influence of anesthesia and temperature. *Acta physiol. scand.* **62**, 68–78.

Stevens, C. E., Sellers, A. F. & Spurrell, F. A. (1960). Function of the bovine omasum in ingesta transfer. *Am. J. Physiol.* **198**, 449–455.

Titchen, D. A. (1958). Reflex stimulation and inhibition of reticulum contractions in the ruminant stomach. *J. Physiol.* **141**, 1–21.

Titchen, D. A. (1968). Nervous control of motility of the fore-stomach of ruminants. In *Handbook of Physiology*, section 6: Alimentary Tract, vol. v, Bile: Digestion: Ruminal Physiology, pp. 2705–2724. Washington: American Physiological Society.

Titchen, D. A. & Newhook, J. C. (1968). Adrenergic effector mechanisms in the stomach of the sheep. *J. Pharm. Pharmac.* **20**, 947–8.

Titchen, D. A. & Reid, C. S. W. (1965). The reflex control of the motility of the ruminant stomach. In *Physiology of Digestion in the Ruminant*, pp. 68–77, ed. Dougherty, R. W. Washington: Butterworths.