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REFLEX CONTRACTION OF THE OESOPHAGEAL GROOVE IN YOUNG RUMINANTS

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In the suckling ruminant liquids such as milk, after being swallowed, pass directly to the abomasum or secretory portion of the stomach. This is in contrast to the delay which occurs in the adult ruminant in which the food undergoes preliminary bacterial digestion in the anterior compartments, the reticulum and rumen, before it passes to the abomasum and small intestine.

The rapidity with which milk appeared in the abomasum of the calf after suckling was noted by Home (1806) who appears to have been the first to postulate that the oesophageal groove was responsible for the diversion from the fermentation chambers. This groove extends with two well-defined lips or pillars from the cardiac end of the oesophagus over the dorsal wall of the reticulum to the entrance of the omasum, a compartment which lies between the fermentation and secretory portions of the stomach in most species of ruminant. The floor of the groove is continuous with a well-defined omasal canal so that, when the lips contract to form a tube, liquids pass directly from the oesophagus through the oesophageal groove and omasal canal to the relatively large abomasum and do not enter either the recticulum or the rumen which, in the young animal, are small and undeveloped.

The activity of the groove has been studied by using food stained with dyes and within recent years by radiological techniques (Phillipson, 1939; Watson, 1944). Direct evidence for its contraction in the conscious animal was obtained by Schalk & Amadon (1928) by palpation through a rumen fistula. The literature on the subject has been reviewed by Watson (1944).

It has generally been assumed that the contraction of the oesophageal groove is a reflex response to stimulation of the pharyngeal region, but direct evidence for this has been difficult to obtain in the conscious animal. In the experiments described below the reflex nature of the contraction of the oesophageal groove has been defined in decerebrate calves and lambs. Preparations of this type allowed a more detailed examination of the reflex response.

METHODS

Subjects. The majority of the experiments were performed on male Jersey calves 2–14 days old, weighing 20–25 kg.; three lambs 3–8 weeks old were also used. The animals were kept at the laboratory for 2–3 days but never more than 9 days before the experiment. During this period the animals were fed a mixture of equal parts of cow's milk and water which they suckled through a rubber teat. Care was taken that they did not have access to solid food or bedding.

Anaesthesia was induced and maintained during decerebration in the early experiments by the administration of chloroform or a chloroform and ether mixture. Later, induction with ethyl chloride and maintenance with ether through a tracheal cannula was found to be more satisfactory.

Decerebration was performed by sectioning the brain stem in a plane from the anterior colliculi dorsally to the mammillary bodies ventrally. This level of section was sufficiently high to avoid decerebrate rigidity, with the consequent difficulty in handling the preparation, but did not result in limb movements after the anaesthetic was withdrawn. Unless special precautions were taken the section of the brain stem resulted in profuse arterial and venous haemorrhage. The vertebral arteries could not be occluded in the majority of calves so that, despite clamping of the carotid arteries with bulldog clips, profuse haemorrhage occurred from the arterial rete mirabile lying under and anterior to the level of transection. In the technique finally adopted exposure of the dura mater over the dorsal aspect of both cerebral hemispheres allowed ligation of the dorsal sagittal sinus and, after removal of the brain anterior to the section, easy access to the rete mirabile and venous sinuses at the base of the cranial cavity. Haemorrhage from these points was controlled by the application, initially with pressure, of fibrin foam soaked in a thrombin solution. With this procedure the bulldog clamps on the carotid arteries could be removed within 5–10 min.

The oesophageal groove was exposed, after the animal was placed on its back, by reflection of the anterior part of the abdominal wall from an incision along both costal arches. After this an incision along the free relatively avascular ventral curvature of the reticulum provided a clear exposure of the groove. The abdominal viscera were kept moist and warm throughout the experiment by the continuous application of 0·9% (w/v) NaCl at 38° C.

Recording. A small hook attached to a fine linen thread was placed in the left lip of the groove. The thread was led through pulleys to a frontal writing lever. Swallowing movements and the respiratory excursion of the diaphragm were recorded by hooks in the thyroid notch of the larynx and the sternal part of the diaphragm respectively, attached to frontal writing or gimbal levers. The kymograph records were always checked by direct observation of the groove. Blood pressure was recorded from a femoral artery with a mercury manometer.

Stimulation of the pharyngeal region was obtained by a flow of water at a rate of 50 ml./min. through a rubber tube placed so that its end lay beyond the dorsum of the tongue in the isthmus faucium. This form of stimulation was continued for 15 sec. in most experiments. Nerves were stimulated through Lucas fluid electrodes, as modified by Porter & Allamon (1936), which delivered condenser discharges from a neon-tube stimulator or faradic stimulation from a Palmer coil.

Access to the phrenic and vagus nerves in the thorax was obtained by removal of the middle third of the ninth rib. When necessary the dorsal and ventral trunks of the abdominal vagus nerves were cut in the abdomen immediately behind the diaphragm. The splanchnic nerves and the adrenal glands were exposed by a modification of the method described by Liddell & Sherrington (1929). In calves, it is more convenient to remove the last rib before searching for the nerve, a modification which does not result in pneumothorax in this species.

L-Adrenaline base (B.D.H.) and L-noradrenaline bitartrate were dissolved with HCl in saline immediately before use and diluted to give the appropriate concentration before injection through a cannula into the femoral vein. Atropine sulphate (B.D.H.) was dissolved in saline.

RESULTS

Lambs were used in the initial experiments; thereafter the observations were restricted to calves which were available over a longer period of the year. Greater care was required in preparing the calves because, owing to the relatively deep situation of the reticulum within the abdomen, the other compartments of the stomach tended to obscure the groove after the reticulum was opened. If care was taken to empty completely the rumen and reticulum before setting up the preparation, the activity of the oesophageal groove could be continuously observed and recorded without further interference with the abdominal viscera. Provided these precautions were taken similar results were obtained with both species.

Reflex contraction

Oesophageal groove contraction was obtained either with a flow of water into the posterior part of the mouth cavity, or by stimulation of the central end of the superior laryngeal nerve. These stimuli also produced swallowing. The contraction of the groove usually started within 2–5 sec., rarely up to 10 sec. after application of the stimulus. The first swallow occurred within 1–2 sec. of stimulation of the superior laryngeal nerve and within 3 sec. of the entry of water into the pharynx.

In both calves and lambs the oesophageal groove contracted with two distinct movements. First, the lips of the groove, which before contraction were flaccid and easily separable, became firmly apposed; at the same time they shortened in their antero-posterior length. After a short pause this was followed by a second and more complicated movement in which the lips inverted and at the same time appeared to twist about an axis running the length of the right lip. This second movement drew the mucosa of the reticulum adjacent to the right lip over the groove, which disappeared from view. The two parts of the contraction were quite distinct and usually complete within 3–5 sec. although occasionally as much as 10 sec. was required for its completion. Each phase occupied about half the total contraction time. With rapid contractions, or a slowly moving kymograph, the biphasic form was not always clearly shown in the records.

A record of the biphasic contraction of the oesophageal groove is shown in Fig. 1. In this experiment, although a threshold stimulus to the superior laryngeal nerve evoked only one swallowing movement, the groove contracted in two distinct stages. In a resting state diaphragmatic respiratory movements were passively superimposed on the records from the groove. Since respiration was inhibited by the afferent stimulation this passive movement did not distort the record of the active contraction of the groove and may be separated from it by a comparison of the records from the oesophageal groove and diaphragm.

The groove did not contract maximally in the initial biphasic movement. If the stimulus was continued additional contractions of much smaller intensity, each succeeded by an equivalent degree of relaxation, were superimposed upon it. In many cases the small additional contractions were synchronous with swallowing. In other instances they were observed when swallowing movements did not occur throughout the whole period of afferent stimulation although respiration continued to be inhibited (Fig. 2).

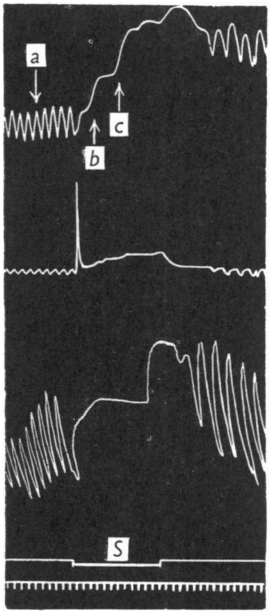

Fig. 1.

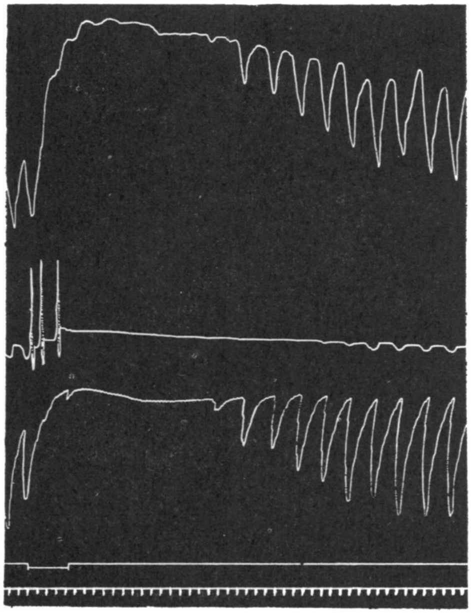

Fig. 2.

Fig. 1. Decerebrate calf. Reflex contraction of the oesophageal groove. Records from above downwards: oesophageal groove, swallowing, respiration, signal, time (1 sec.). Stimulation of superior laryngeal nerve with induction coil discharge, *S*. (Coil distance 12 cm.). *a* indicates passive movement of oesophageal groove with respiratory excursions of diaphragm. *b* and *c* indicate the first and second parts of the biphasic contraction of the oesophageal groove.

Fig. 2. Decerebrate calf. Reflex contraction of the oesophageal groove stimulated by introducing water into the mouth (signal). Records in same sequence as in Fig. 1. Time 1 sec.

The nature of the reflex

The reflex arc

The reflex nature of the oesophageal groove contraction was demonstrated by section and stimulation of possible afferent and efferent nerves.

The superior laryngeal nerve was the only afferent nerve stimulation of which consistently caused swallowing and groove contraction in the decerebrate calf. Stimulation of the central end of the chorda-lingual trunks and branches of the pharyngeal plexus other than that of the superior laryngeal nerve was usually ineffective. In the lamb, in one experiment, swallowing and groove contraction occurred on stimulation of the central end of a divided middle laryngeal nerve.

The efferent nerve fibres to the musculature of the oesophageal groove were confined to the dorsal vagus nerve. The contraction in response to all forms of afferent stimulation was abolished after section of this nerve in either the thorax or abdomen. On stimulation of the peripheral end of the cut nerve both the oesophageal groove and the rumen contracted, the contraction of the

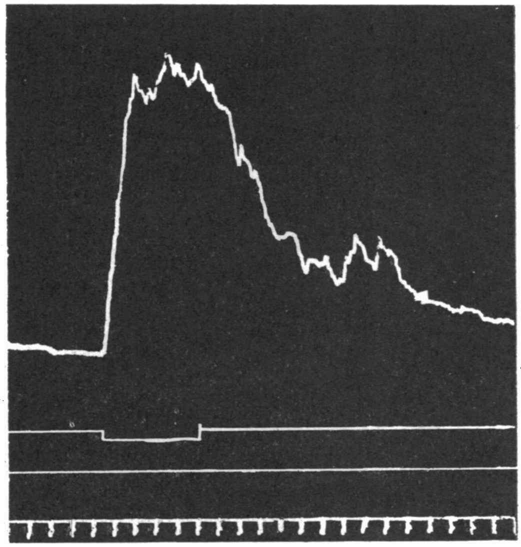

Fig. 3. Decerebrate calf. Contraction of the oesophageal groove evoked by stimulation of the dorsal vagus nerve in the thorax (signal). Coil distance 10 cm. Phrenic nerves sectioned in thorax. Positive pressure ventilation. Time 1 sec.

groove retaining the characteristic biphasic form noted on reflex stimulation (Fig. 3). The reflex contraction of the groove was not appreciably reduced after section of the ventral vagus nerve. On stimulation of the peripheral end only slight movements occurred of the lips of the groove close to the reticulo-omasal junction. Unilateral section of the cervical vagus had no observed effect on the reflex groove contraction.

The intravenous injection of from 2–5 mg. of atropine sulphate (80–200 μg./kg.) totally abolished contractions from the reflex and the dorsal vagus nerve stimulation. Swallowing movements induced by stimulation of the superior laryngeal nerve or by the introduction of water into the posterior mouth cavity were unaffected. The inhibitory effect of the atropine was at a maximum within five minutes of administration and remained for at least two hours, which was the longest period over which the experiments were continued after the injection. These effects are shown in Fig. 4.

Although contraction of the oesophageal groove was associated with swallowing, the reflex contraction occurred after the abolition of the bucco-pharyngeal movements by section of the appropriate nerves (pharyngeal and laryngeal rami of the vagus nerves, the glossal and pharyngeal rami of the glossopharyngeal and the hypoglossal nerves and mandibular branches of the trigeminal nerves). Section of these nerves abolished all responses to the introduction of water into the pharynx. The groove still contracted in response to stimulation of the central end of the superior laryngeal nerve (Fig. 5).

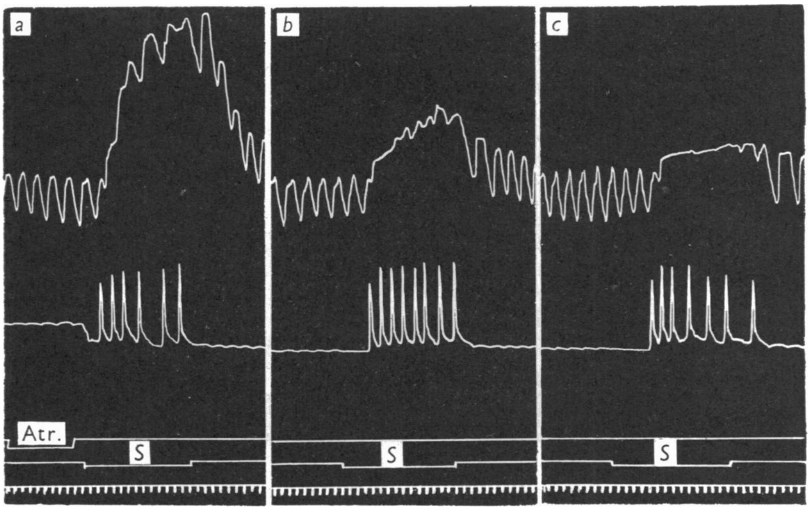

Fig. 4. Decerebrate calf. Effect of atropine. Records from above downwards, oesophageal groove, swallowing, injection signal (*Atr.*), stimulation signal, time (1 sec.). Superior laryngeal nerve stimulation, *S*, with a coil distance of 10 cm. *a*, during the injection of 2 mg. atropine; *b*, 2 min. after and *c*, 4 min. after the injection of atropine.

Inhibition

The reflex contraction of the oesophageal groove could be inhibited by afferent stimuli from either the pharyngeal region or from the abdomen. The effect on swallowing as well as groove contraction and the rate of recovery, after withdrawal, varied according to the inhibitory stimulus.

Stimulation of the glossal branch of the glossopharyngeal nerve inhibited the reflex contraction of the oesophageal groove. Swallowing and the incomplete respiratory movements, which in a few experiments occurred between a number of swallows, also ceased during such stimulation. The inhibition corresponded to the period of stimulation. The recovery was rapid and frequently marked by one or two large respiratory movements.

Stimulation of the glossopharyngeal trunk formed by the glossal and pharyngeal rami gave variable results. On most occasions an inhibition was found, but in a few experiments reflex swallowing and groove contraction occurred either during stimulation or immediately after it had ceased.

Manipulation of the abomasum and the reticulum inhibited the reflex contraction of the groove. The effect was prolonged and persisted on occasions for 10–15 min. after handling of the viscera had ceased. Stretching the

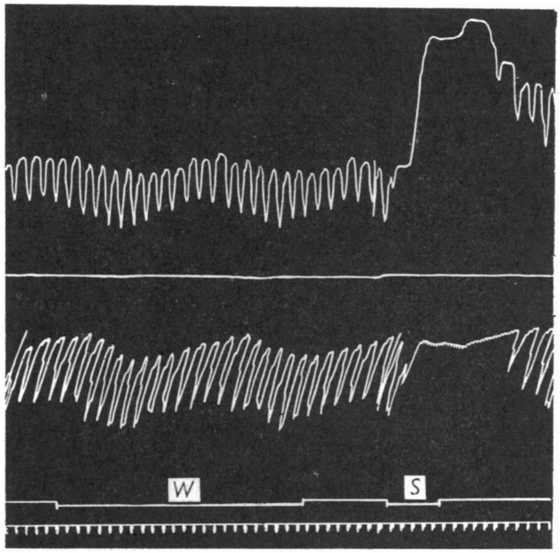

Fig. 5. Decerebrate calf. Denervation of pharynx and larynx. Records in same sequence as in Fig. 1. First signal, water into the mouth, *W*, 50 ml./15 sec.; second signal, superior laryngeal nerve stimulation, *S* (coil at 11 cm.). Time 1 sec.

reticulum between forceps so that no direct tension was exerted on the groove had a similar effect. Following these observations stimulation of the central end of a cut cervical vagus nerve was found to abolish reflex groove contraction but the effect could not be recorded in a satisfactory manner owing to the concurrent respiratory movements.

Since handling of the abomasum caused a profound inhibition of reflex groove contraction, the central end of the divided branch of the ventral vagus running over the lesser curvature of the abomasum was stimulated for varying periods. In calves more than 5–7 days old this always inhibited groove contraction, but in younger animals the inhibition was more irregular and did not occur on every occasion. The inhibition differed from that due to stimulation of the glossal branch of the glosso-pharyngeal nerve in that it was slower in onset, more prolonged once established and only affected reflex contraction of the groove, not respiration or swallowing (Fig. 6).

The inhibitory effect from stimulation of the abomasal nerve was demonstrated most effectively when a series of reflex-groove contractions was established by delivering periods of stimulation from the pharynx for 15 sec. at intervals of from 60 to 150 sec. This normally produced a sequence of separate and comparable groove contractions. If the abomasal nerve was stimulated for 15–20 sec. preceding the pharyngeal stimulus the contraction of the groove was either reduced or abolished and the next contraction in the

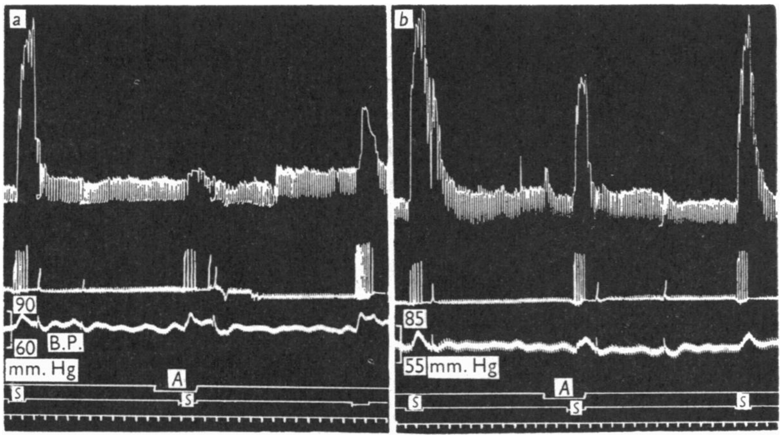

Fig. 6. Decerebrate calf. (*a*) Continuous record of, from above downwards, oesophageal groove, swallowing, blood pressure, abomasal nerve stimulation, *A* (coil at 10 cm.), superior laryngeal nerve stimulation, *S* (coil at 11 cm.). Time 5 sec. (*b*) As in (*a*) with coil at 12 cm. for abomasal nerve stimulation, *A*.

series was frequently smaller than normal. The effects of two strengths of stimulation of the abomasal nerve are shown in Fig. 6*a*, *b*. If both abomasal and pharyngeal nerve stimulation were simultaneous the immediate reflex closure of the groove occurred but the next contraction was either partially or completely inhibited. Stimulation of the abomasal nerve alone had no effect on blood pressure, respiration or swallowing. The inhibition remained after bilateral section of the splanchnic nerves but was eliminated by section of the ventral trunk of the vagus cranial to its division into the various abdominal branches. Stimulation of the central end of the ventral vagus nerve then produced inhibition.

Effect of section and stimulation of the splanchnic nerves

The action of sympathetic nerves on the oesophageal groove musculature was examined by noting the effect of bilateral section of the splanchnic nerves on the reflex contraction and by stimulating the peripheral end of these nerves, before and after removal of the adrenal glands. The nerves were cut immediately after decerebration, before the abdominal viscera were exposed.

When both splanchnic nerves had been divided, marked activity of the small intestine was observed immediately after the laparotomy. The reticulum was also active, but the contractions were localized to small groups of muscle fibres and never developed into a synchronous contraction of the whole organ. In contrast when the splanchnic nerves were left intact, activity of this type did not appear in either the small intestine or the reticulum until at least 30–45 min. after opening the abdominal wall, and was never as intense.

Immediately after the laparotomy had been completed, in the preparations in which both splachnic nerves had been cut, the lips of the oesophageal groove were in a state of slight sustained contraction which gradually increased with time and which was abolished by section of the dorsal abdominal vagus nerve. The reflex contraction was superimposed upon this slight sustained contraction, but the succeeding relaxation in many cases, although prolonged, was complete; the tonic contraction gradually returned within the course of a few minutes (Fig. 7).

Stimulation of the peripheral end of both splanchnic nerves did not affect the reflex contraction of the oesophageal groove induced by stimulation, at the same time, of a superior laryngeal nerve. The rapid blanching of the mucosa of the reticulum adjacent to the groove, the rise in blood pressure and the abolition of the slight continuous contraction or tone of the groove showed that stimulation of the splanchnic nerves had been effective. An inhibition, following splanchnic nerve stimulation, could be demonstrated, by noting the effects on a series of reflex groove contractions in a similar manner to that used with the abomasal nerve. When the splanchnic nerves were stimulated for 10–40 sec., a reflex contraction of the groove which occurred during this period remained unchanged but that which followed about 90–150 sec. later was either partially or completely inhibited (Fig. 8). A partial inhibition remained for 7–9 min. after cessation of the stimulation of one or both splanchnic nerves.

During prolonged stimulation of the splanchnic nerves the inhibition of the oesophageal groove gradually diminished and then, in several experiments, completely disappeared. The first sign of the reduced inhibition was the gradual return of a maximal contraction of the groove with a more rapid relaxation, so that the contraction of the groove followed more closely the period of afferent nerve stimulation. Thereafter the slight tonic contraction of the groove returned and cessation of stimulation had no effect on the time course of the reflex contraction (Fig. 7). The duration and intensity of the inhibition during prolonged splanchnic nerve stimulation varied with preparations of different ages. This was shown most clearly by comparing the effects of successive periods of splanchnic stimulation. In animals from 3–5 days old the period of

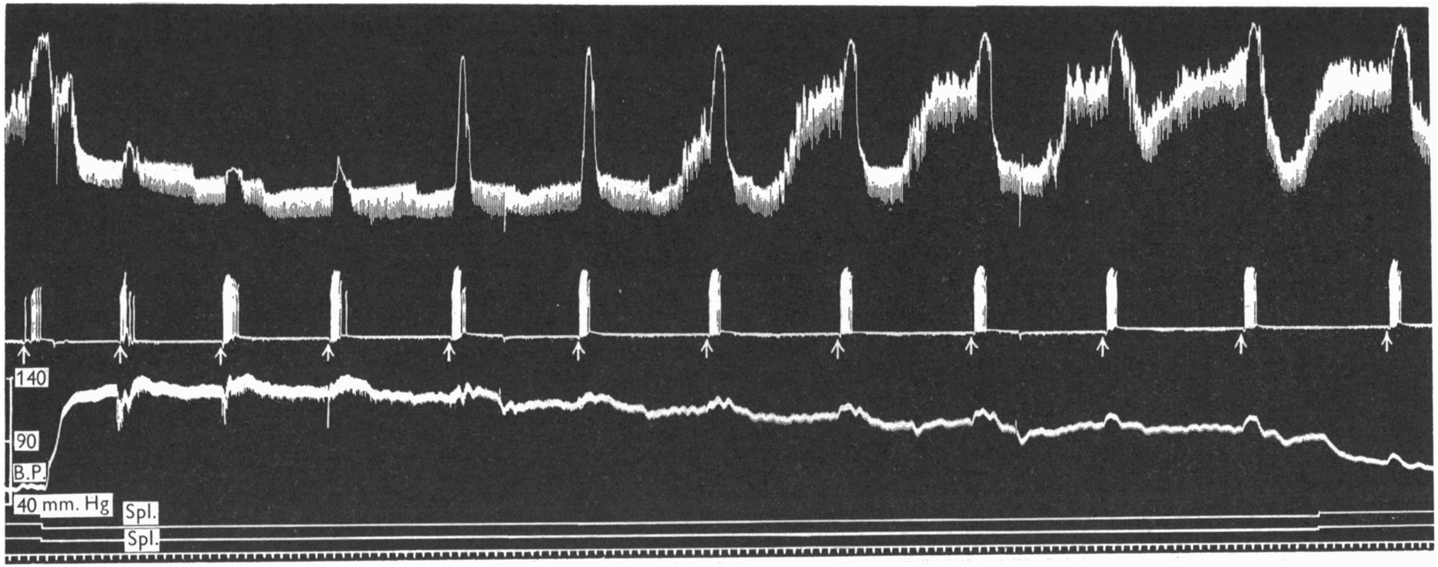

Fig. 7. Decerebrate calf. Prolonged stimulation of both splanchnic nerves. Records from above downwards, oesophageal groove, swallowing, blood pressure, stimulation of both splanchnic nerves (*Spl.*), with coils at 10 cm. Stimuli to swallowing (50 ml. water/15 sec.) indicated by arrows. Time 5 sec.

stimulation required before the inhibition disappeared in most experiments was about 10 min. and never exceeded 15 min. A second period of stimulation after an interval of 50 min. produced only a very slight and much more transient inhibition. In the older animals, from 10–14 days of age, the inhibition from the first period of prolonged stimulation persisted for 15–21 min., and a definite although reduced inhibition resulted from a second period of prolonged splanchnic stimulation. Thus in an experiment on a calf aged 14 days, the inhibition persisted with the first period of splanchnic stimulation

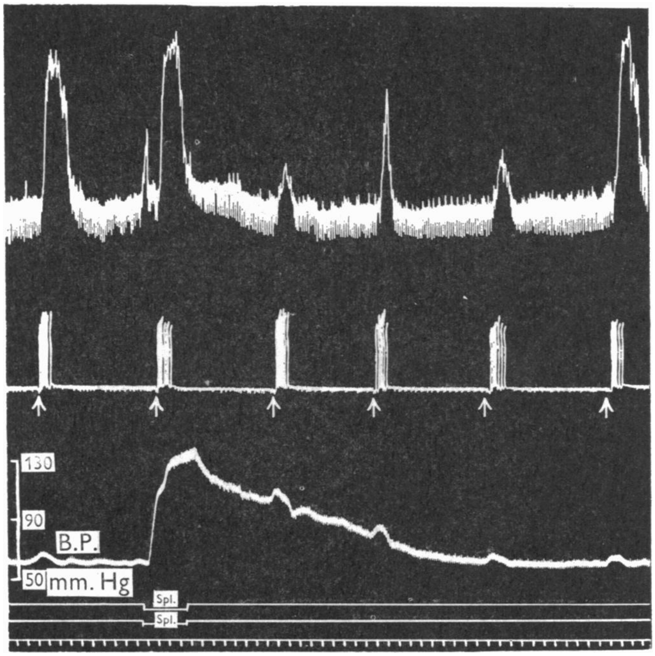

Fig. 8. Decerebrate calf. Short period of stimulation of both splanchnic nerves. Records in same sequence as in Fig. 7. Coil distances for stimulation of splanchnic nerves (*Spl.*) 10 cm. Stimuli to swallowing (water 50 ml./15 sec.) indicated by arrows. Time 10 sec.

for 21 min. When the prolonged stimulus was repeated after 55 min. the inhibition which developed persisted for only 10 min., and did not amount to a total inhibition at any stage. The pressor effect was similar in both cases.

The relation of the rise of blood pressure, which followed splanchnic stimulation, to the inhibition of the oesophageal groove musculature varied according to the duration of the stimulus to the splanchnic nerves. With short periods the inhibitory effect outlasted the pressor effect (Fig. 8). With prolonged periods of stimulation, however, the rise in blood pressure continued after the inhibition of the groove musculature had ceased. The secondary component of the pressor response, due to stimulation of the adrenal medulla, gradually failed although the effect was masked to some degree by the reflex response to increased blood pressure (Fig. 7).

The inhibitory effect of splanchnic stimulation on the reflex contraction of the oesophageal groove was abolished by removal of the adrenal glands; the pressor effect and blanching of the reticular mucosa remained. This was demonstrated more clearly by dividing the splanchnic nerves on both sides and removing the adrenal on one side before stimulating one or other of the splanchnic nerves.

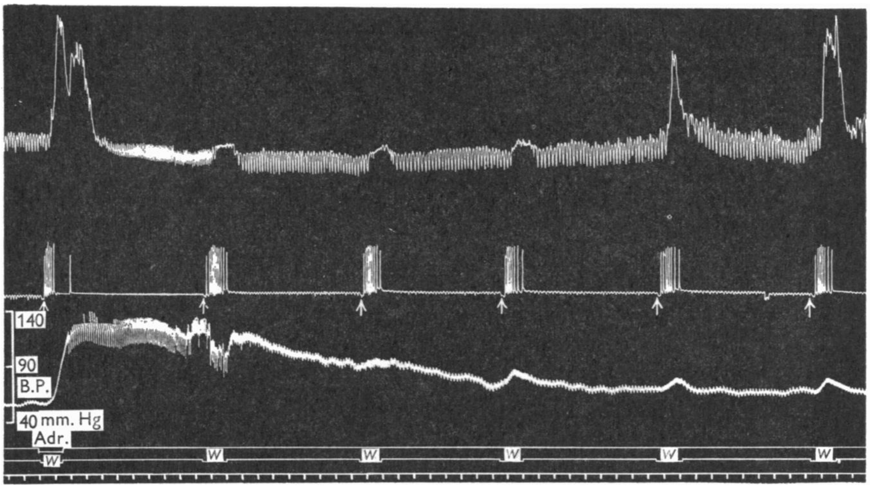

Fig. 9. Decerebrate calf. Effect of adrenaline. Records from above downwards, oesophageal groove, swallowing, blood pressure, injection (*Adr.*), water into mouth (*W*) also indicated by arrows, time 10 sec. At *Adr.* 250 μg. L-adrenaline was injected intravenously.

Both adrenaline and noradrenaline on intravenous injection inhibited the musculature of the oesophageal groove in a similar manner to that found with stimulation of the splanchnic nerves (Fig. 9). The intravenous injection of equal doses of these substances showed that the inhibitory action of adrenaline was slightly more prolonged than that of noradrenaline, although a similar pressor response was obtained with the same dose of each substance.

DISCUSSION

The use of decerebrate preparations has provided direct evidence for the reflex nature of oesophageal groove contraction in young ruminants. The reflex and the factors which affect it have only been studied in detail in calves, and in this species at least fibres in the dorsal abdominal vagal trunk are the principal efferent nerves to the musculature of the groove. Of all possible afferent fibres from the pharynx only those in the superior laryngeal nerve consistently caused groove contraction on stimulation. The afferent fibres may well be restricted to this nerve although the introduction of water into the mouth after unilateral section of one superior laryngeal nerve was more effective than maximal stimulation of the divided nerve in producing a reflex contraction. This greater efficiency of the normal sensory stimulus when compared to stimulation of the afferent nerve trunk is a common property of reflexes (Sherrington, 1906).

The experiments may, in part, be regarded as an extension of those of Miller & Sherrington (1916) to include a study of the visceral reactions which occur with reflex swallowing. In the young ruminant, reflex swallowing and closure of the oesophageal groove are closely integrated with one another although the mechanical movements of one reflex response can be abolished e.g. by section of efferent nerves, without affecting the other. This synchronism was shown by the parallel inhibition and rapid recovery from inhibition of both groove contraction and swallowing due to stimulation of the glossal branch of the glossopharyngeal nerve.

Contraction of the oesophageal groove is one part of a co-ordinated series of reflex responses, and Watson (1944) has pointed out that at least a relaxation of the reticulo-omasal orifice and other parts of the omasum is necessary for a free passage of liquid directly to the abomasum. In the experiments reported in this paper no records were taken of the movements of other parts of the stomach but the ridge between the rumen and reticulum contracted at about the same time as the groove. We have also observed, in decerebrate calves, especially after bilateral section of the splanchnic nerves, an increase in the activity of the small intestine on stimulation of the superior laryngeal nerve similar to that reported by Andersson, Langren, Neil & Zotterman (1950) in cats under chloralose anaesthesia.

While glossopharyngeal nerve stimulation inhibited respiration, reflex swallowing and closure of the oesophageal groove, the inhibition due to stimulation of the central end of the abomasal branch of the ventral vagus only abolished the visceral reflex response. The inhibition from the two sources differed in other respects; that from the abomasal nerve was characteristically slow in its onset and prolonged in its effect. The inhibition remained after bilateral section of the splanchnic nerves and thus it probably results from depression of a centre in the brain stem. The sensory receptors which normally stimulate the abomasal nerve have not been studied, but Phillipson (1939) reported that in the adult animal distension of the abomasum abolished contractions of the reticulum. The phenomenon may not be restricted to species with a compound stomach, since Veach (1925) found that stimulation of the central end of the divided vagus in decerebrate cats inhibited movements of the fundic part of the stomach, and Harper & Vass (1941) noted the inhibitory effect of stimulation of the central end of the ventral vagus on pancreatic secretion. More experimental evidence is required before a full interpretation can be given, but the inhibition of groove contraction may be part of a general mechanism in which stimulation of one region of the stomach modifies the reflex response of another, the integration of all the reflexes resulting in the activity which normally occurs. If this is the case, such an action may provide an explanation for the observation that the oesophageal groove does not as a rule contract in the adult unless a conditioned reflex has been established and maintained by training the adult animal to continue suckling.

The failure of the oesophageal groove to contract in the adult may also be due, in part, to an increase in the action of the sympathetic nervous system. In our experiments stimulation of the splanchnic nerves of calves up to 7 days old had only a slight and rapidly diminishing inhibitory action on the reflex contraction of the oesophageal groove. In this respect the reflex contraction differed from the increased tone which in many experiments followed section of the splanchnic nerves and which rapidly diminished either on stimulation of the splanchnic nerves or on the injection of adrenaline. Apart from this, no evidence was obtained which suggested a sympathetic innervation to the groove musculature with a direct inhibitory action. Characteristically the inhibition was delayed in onset and of comparatively short duration although the immediate effects, including blanching of the adjacent mucosa of the reticulum, demonstrated that the stimulation of the splanchnic nerves was effective. The reduction in the inhibition after removal of the adrenal and the delay in onset suggest that the secretion of the adrenal medulla was responsible for much of the inhibitory action.

In older calves the inhibition was more prolonged but even in these its diminution was more rapid than that reported by Dye (1935) for the pressor response and contraction of the nictitating membrane in the adult cat with continuous stimulation of the splanchnic nerve. He found that both the pressor response and contraction of the nictitating membrane remained after continuous stimulation for 160 min. Even after ligation of the adrenals the responses remained for at least 30 min. of continuous stimulation of a splanchnic nerve. This can be compared with the disappearance of the inhibitory effect in the young calf with adrenals intact and with similar forms of stimulation after 15 min. The phenomenon would appear to be associated with the youth of the animals and may be analogous with the results of Bauer (1938, 1939) who did not find a sympathetic action on the heart of young rabbits during asphyxia until 11 days after birth.

The point at which the failure occurred on continued stimulation of the splanchnic nerve cannot be deduced from the data of the preliminary investigations reported here. The adrenal glands of young calves contain a higher proportion of noradrenaline to adrenaline than those of adult animals (Holton

1951). Noradrenaline also inhibited groove contraction when injected intravenously so that release of this compound cannot provide the whole explanation. The diminution in response may have been exaggerated by stimulation of the adrenal medulla reflexly and by decerebration under ether anaesthesia (Elliott, 1912*a*, *b*). On the other hand, the splanchnic nerves were cut before the laparotomy, that is at least 2 hr. before they were stimulated; in any case the effects of ether anaesthesia on the adrenal medulla do not explain the results obtained with calves of different ages.

Much of the experimental work on the oesophageal groove in the last few years has been concerned with the curious action of copper salts which, when given in small amounts to young adult ruminants in which a conditioned reflex has not been established, facilitate the closure of the groove after swallowing in a large proportion of animals (Clunies Ross, 1931; Watson & Jarrett, 1944). This action of copper salts was not studied in any great detail in the experiments reported here as it was apparent that, in the decerebrate preparations of young animals at least, copper salts had no greater effect than water in stimulating reflex contraction of the groove. The action of the copper salts may be due to some change in the sensation from the mouth, which is not effective in the decerebrated animal. In our experiments solutions of the copper salts rapidly cleared the mucous membrane of the mouth and fauces by precipitating the mucus. It has also been reported that in man tobacco has a sweet taste after rinsing the mouth with weak solutions of copper salts (Winton & Bayliss, 1948). Before an explanation can be given for the action of copper salts more information is required on the factors which may affect reflex contraction of the oesophageal groove in the adult animal.

The activity of the oesophageal groove has been compared, especially in the older literature, with that of the homologous structure, the magenstrasse or gastric canal, of the simple stomach (Babkin, 1950). The function of the magenstrasse is now thought to be insignificant, at least in adults (Alvarez, 1939). The experiments reported here may offer a clue to its function in species with simple stomachs but this cannot be considered in detail until further experimental evidence is available.

SUMMARY

1. The reflex nature of the oesophageal groove contraction has been examined in decerebrate preparations of young ruminants. The reflex arc and the factors which affect it have been studied in detail in young calves up to fourteen days old.

2. The superior laryngeal was the only afferent nerve which, on stimulation, consistently produced a reflex contraction. The entry of water into the posterior part of the mouth was a more effective stimulus to reflex contraction

than stimulation of this nerve. The efferent fibres were confined largely to the dorsal abdominal vagus nerve.

3. The reflex contraction of the oesophageal groove was associated with swallowing but occurred after the bucco-pharyngeal movements had been abolished by section of the appropriate nerves.

4. Stimulation of the central end of the glossal branch of the glosso-pharyngeal nerve inhibited swallowing, respiration and the reflex contraction of the oesophageal groove. Both swallowing and groove contraction rapidly recovered on cessation of the stimulus.

5. Stimulation of the central end of the abomasal nerve inhibited reflex groove contraction but not swallowing or respiration. The inhibition was slow in onset and remained after bilateral section of the splanchnic nerves.

6. The inhibition which followed splanchnic stimulation was also slow in onset and progressively diminished with continued stimulation. The duration of the inhibition was increased in older animals. No evidence was found for the presence of a sympathetic innervation directly inhibitory to the groove musculature.

7. Contraction of the groove as a result of reflex excitation or direct stimulation of the dorsal vagus nerve was abolished by small doses of atropine. Reflex contraction was inhibited by the intravenous injection of adrenaline and noradrenaline.

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REFERENCES

Alvarez, W. C. (1939). *An introduction to Gastro-enterology*, 3rd ed. pp. 310, 327. London: Heinemann.

Andersson, B., Langren, S., Neil, E. & Zotterman, Y. (1950). *Acta physiol. Scand.* **20**, 253.

Babkin, B. P. (1950). *Secretory Mechanism of the Digestive Glands*, 2nd ed. pp. 115–16. New York: Hoeber.

Bauer, D. J. (1938). *J. Physiol.* **93**, 90.

Bauer, D. J. (1939). *J. Physiol.* **95**, 187.

Clunies Ross, I. (1931). *Aust. vet. J.* **7**, 122.

Dye, J. A. (1935). *Amer. J. Physiol.* **113**, 265.

Elliott, T. R. (1912*a*). *J. Physiol.* **43**, 32*P*.

Elliott, T. R. (1912*b*). *J. Physiol.* **44**, 374.

Harper, A. A. & Vass, C. N. (1941). *J. Physiol.* **99**, 415.

Holton, P. M. (1951). *Nature, Lond.*, **167**, 858.

Home, E. (1806). *Philos. Trans.* **96**, 357.

Liddell, E. G. T. & Sherrington, C. S. (1929). *Mammalian Physiology*, 2nd ed. Oxford: Clarendon Press.

Miller F. R. & Sherrington, C. S. (1916). *Quart. J. exp. Physiol.* **9**, 147.

Phillipson, A. T. (1939). *Quart. J. exp. Physiol.* **29**, 395.

Porter, E. L. & Allamon, E. L. (1936). *J. Pharmacol.* **58**, 178.

Schalk, A. F. & Amadon, R. S. (1928). *Bull. N. Dak. agric. Exp. Sta.* **216.**

Sherrington, C. S. (1906). *The Integrative Action of the Nervous System*, p. 9. Cambridge University Press, 1947.

Veach, H. O. (1925). *Amer. J. Physiol.* **71**, 229.

Watson, R. H. (1944). *Bull. coun. sci. industr. Res. Aust.* **180**, I.

Watson, R. H. & Jarrett, I. G. (1944). *Bull. coun. sci. industr. Res. Aust.* **180**, II.

Winton, F. R. & Bayliss, L. E. (1948). *Human Physiology*, 3rd ed. p. 539. London: Churchill.