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## RESPONSES OF THE GASTRIC MUSCULATURE OF THE SHEEP TO SOME HUMORAL AGENTS AND RELATED SUBSTANCES

By DOROTHY L. DUNCAN

*From the Rowett Research Institute, Bucksburn, Aberdeenshire*

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The number of published papers dealing with the pharmacology of the ruminant stomach is still small. An approach was made to the subject by Wester (1926), and later work includes that of Amadon (1930), Dougherty (1942) and the South African group, Quin & van der Wath (1938), Quin & Clark (1946) and Clark (1950*a*). The effects of choline esters and adrenaline were studied by Brunaud, Dussardier & Labouche (1950) and Brunaud & Dussardier (1951, 1953). The subject was reviewed by Clark (1950*b*). Except by Brunaud *et al.* (1950) most attention so far has been given to the responses of the rumen, and for this reason an extension of study to other parts of the stomach was needed. Because the work described here was done primarily as part of a wider study of gastric motility in the sheep, only those substances were studied which are believed to take part in the transmission of nerve impulses and to act as local hormones. Observations were also made on surviving gastric musculature *in vitro*.

### MATERIAL AND METHODS

*Experiments with sheep.* Scottish Blackface wethers were provided with ruminal and abomasal cannulae, usually of the ebonite type as described by Phillipson & Innes (1939), and were trained to stand quietly in a metabolism crate. Gastric motility was transmitted to air-filled rubber balloons and water manometers, pressure changes being recorded on a smoked paper. The ruminal cannulae had an internal diameter of about 2 cm and allowed simultaneous recording from balloons in the reticulum and rumen. The polythene tube connecting the reticulum balloon to the manometer system was supported by a stiff wire bent to allow the balloon to be passed through the rumino-reticular orifice. The rumen balloon was placed in the dorsal sac within a short distance of the cannula. A more sensitive, thin rubber balloon was preferred for the abomasum and this was placed in the mid-region of the organ. Two manometers were used and simultaneous records were made from any two of the three sites described.

The average weight of the sheep was 30 kg. Each substance was given to at least six sheep, and usually at least 48 hr elapsed between successive experiments on one sheep. Four sheep were used for pharmacological experiments after bilateral thoracic vagotomy, combined in three with bilateral splanchnic section; the history of these sheep has been given in an earlier paper (Duncan, 1953). One adrenalectomized ewe was made available by Mr J. V. R. Evans. Two sheep and a goat were used for acute experiments during which they were anaesthetized with sodium pentobarbitone.

*Experiments with isolated surviving gastric musculature.* Material was obtained either from the local slaughterhouse or from sheep killed at the Institute for experimental purposes. The tissue was removed almost immediately after slaughter and was placed in ice-cold Ringer-Locke solution for transport to the laboratory. Muscle strips were prepared as soon as possible, since good results could not be obtained with material stored overnight at about 1° C. To avoid stretching the muscle a strip of stomach was cut in the appropriate direction and the mucosa and unwanted muscle layer were gently clipped off with fine scissors. The strip of tissue was then mounted in a bath of 50 ml. capacity containing oxygenated Tyrode solution at 38° C. An isotonic lever was employed for recording.

## RESULTS

### *Experiments with sheep*

*Acetylcholine chloride* administered intravenously in doses of 0.5 mg or less had no effect. With doses of 1.0–10 mg activity in all parts of the stomach immediately decreased or stopped. With 3–5 mg complete inactivity of rumen and reticulum lasted only about 2–5 min, but the amplitude of subsequent

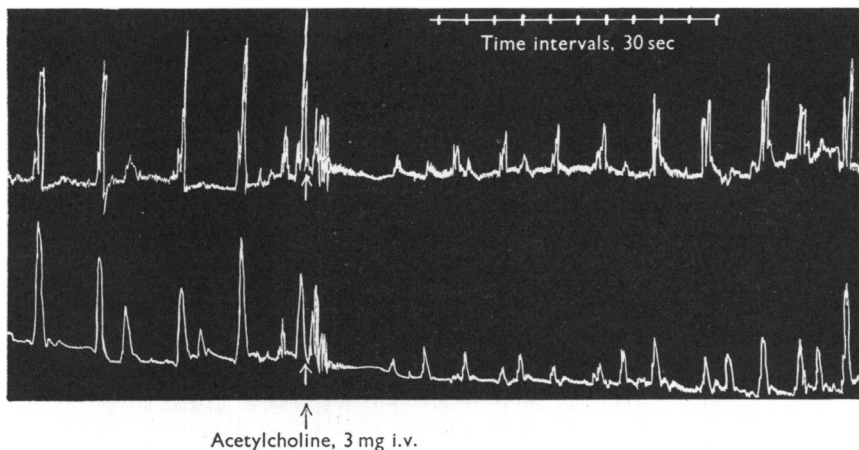


Fig. 1. Effect of acetylcholine, 3 mg intravenously, on reticulum (above) and rumen. The rapid movements immediately after the injection are the result of coughing.

contractions was depressed for about 30 min. Depression of abomasal activity was less. Immediately after the injection the sheep usually coughed violently, which masked the stomach movements for a few seconds, but on the rare occasions when coughing did not occur no sign of a rapid contraction could be detected in any part of the stomach.

In several experiments sheep received physostigmine sulphate (eserine) before acetylcholine. Since the effective dose of eserine alone was found to be at least 10 mg (see below) only 2–5 mg were given before acetylcholine. Some potentiation of the acetylcholine effect was seen, as slight depression of reticulo-ruminal motility was obtained in the eserinated sheep with only 0.1–0.2 mg acetylcholine.

One adrenalectomized sheep was studied 7 and 22 hr after removal of the second adrenal. Cortisone had been administered and blood chloride was in the normal range. During the first experiment the sheep was probably still affected by the anaesthetic (Nembutal) and motility of the rumen and reticulum was reduced, one contraction cycle occurring about every 5 min. Three successive injections, of 0.5, 1.0 and 1.5 mg acetylcholine, produced no effect on gastric motility. The general reaction to the third injection was fairly marked, with laboured breathing and signs of distress, and it was not considered safe to increase the dose. There was, however, no indication of sensitization to acetylcholine. The experiment was repeated on the following day; ruminal activity was normal and the sheep had been ruminating. The injection of 1 mg acetylcholine produced no rumen contraction, and only a very slight inhibition.

In vagotomized sheep with inactive rumen and reticulum, injection of acetylcholine had no effect on the stomach, but in one sheep in which intrinsic activity of the reticulum was present (Duncan, 1953) this was abolished for more than 30 min by injection of 2 mg acetylcholine.

Acetylcholine injected directly into the muscle of the reticulum in anaesthetized sheep, and in one goat, with open abdomen, invariably produced strong, localized contracture.

*Carbaminoylcholine chloride* (carbachol) was administered intramuscularly in doses of 0.25–0.5 mg. Owing to the prolonged action of carbachol, atropine was always given at the end of the experiment. Carbachol always increased both tonus and frequency of rumen contractions, sometimes to a state of incomplete tetanus. The increase in frequency of contractions outlasted the tone increase, so that a period of marked activity followed the tetanic condition when this occurred. The effect of carbachol upon the abomasum was less but was also one of increased tonus and activity. The effects upon the reticulum were more variable. The smallest dose employed, 0.25 mg, on several occasions increased activity in the reticulum, but in contrast to the effect in the rumen this was an increase in the amplitude, and not in the frequency, of contractions. Dosage at the upper end of the range, and indeed sometimes the small dose, after a brief initial stimulation inhibited movement in the reticulum. There was a sudden and complete cessation of contractions, and this was not a tetanic effect, since it was not accompanied by increased tonus. The dose of 0.5 mg was sufficient to induce profuse salivation and some respiratory embarrassment, so a larger dose was not employed. In two vagotomized sheep in which the rumen and reticulum were showing intrinsic activity, carbachol increased this activity.

*Physostigmine sulphate* (eserine) was also given intramuscularly, in doses varying from 2.0 to 20 mg. The experiments were terminated by administration of atropine. It was found that the action of eserine was not developed until approximately 40 min after injection, probably because of slow absorption.

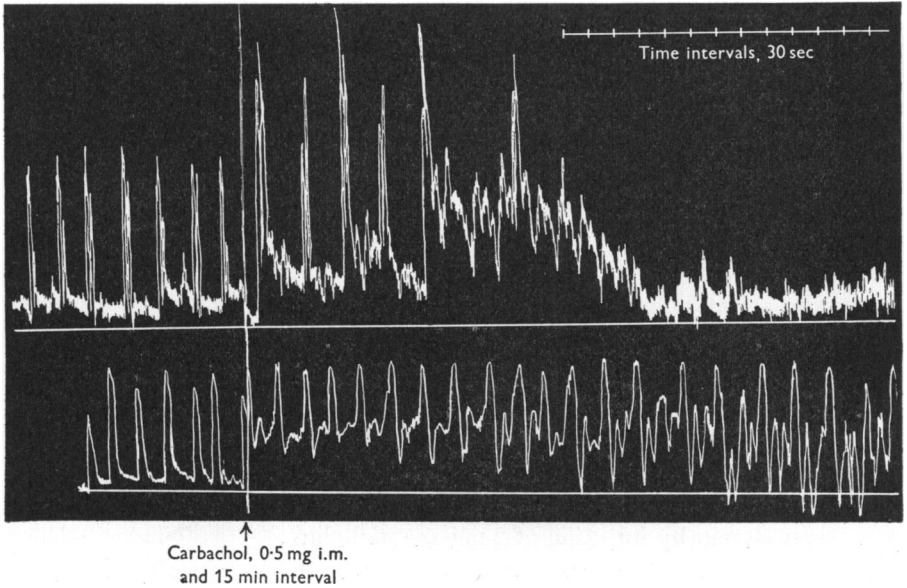


Fig. 2. Effect of carbachol, 0.5 mg intramuscularly, on reticulum (above) and rumen. The injection was given at the vertical stroke and 15 min elapsed before the second part of the tracing. The increase in tonus of the reticulum was not commonly seen but that of the rumen always occurred. The excursions of the reticulum lever after the drop in tonus are entirely due to respiratory movement.

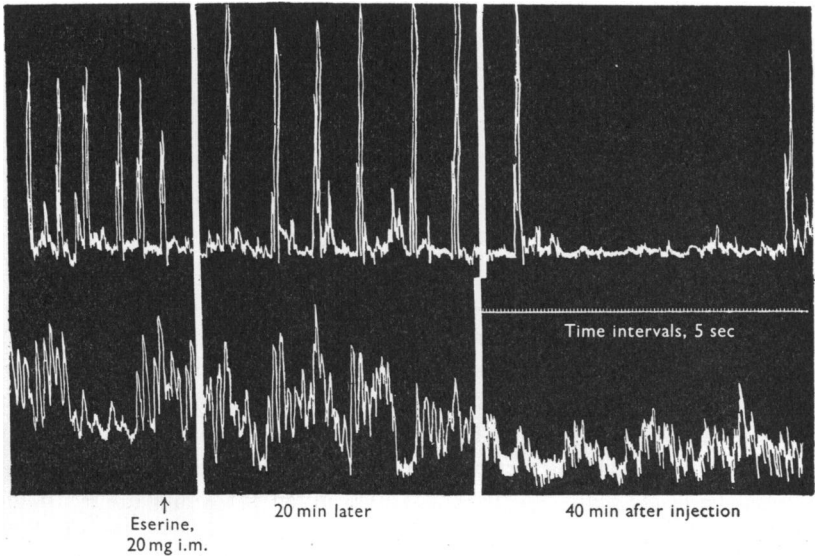


Fig. 3. The effect of eserine, 20 mg intramuscularly, on the reticulum (above) and abomasum. The injection was given at the end of the 'control' record. The second part was taken 25 min later and the third, 40 min after the injection. Time intervals, 5 sec.

The smallest effective dose was 10 mg and the effect upon the rumen was very similar to that of carbachol. The reticulum also responded as it did to carbachol, but the stimulatory phase, with increased amplitude of contractions, was most commonly seen, and periods of inhibition were relatively fewer and shorter. Only on a few occasions was abomasal activity noticeably increased.

*Atropine sulphate*, in doses of 10–20 mg subcutaneously, produced partial or complete inhibition of motility in all parts of the stomach. The effect was often more pronounced in the abomasum than in the rumen and reticulum. On two occasions sheep were observed to ruminate when contractions of the reticulum were reduced or absent as a result of atropine injection. In the animal which ruminated in total absence of reticular activity the reticulum balloon recorded

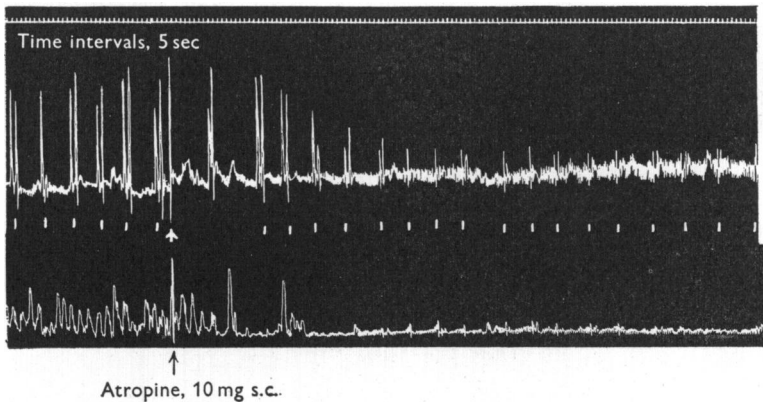


Fig. 4. The effect of atropine, 10 mg subcutaneously, on the reticulum (above) and abomasum. Rumination occurred before and after the injection; each signal (below reticulum record) indicates a regurgitation.

a slight and jerky pressure increase with each regurgitation: the movement was too sharp to be due to contraction of the reticulum itself and it appeared to indicate a transmitted diaphragmatic movement. In vagotomized sheep, atropine abolished the intrinsic activity of the reticulum and rumen.

*Adrenaline*. The effect of the commercial solution of 'Adrenaline B.P.', 1:1000 was studied first. Intravenous injection of 1–2 ml. inhibited contractions and tonus waves in all parts of the stomach. Subcutaneous injection of as much as 6 ml. was without effect. Later, fresh solutions of L-adrenaline and of L-arterenol bitartrate monohydrate (L-noradrenaline) were employed. Each caused inhibition on intravenous injection, but the dose of L-adrenaline required was lower than the estimated dose in the commercial solution, 0.5–1 mg sufficing to stop contractions of the rumen and reticulum for several minutes and to decrease the amplitude of contractions for about 1 hr. Injection of L-adrenaline often produced coughing, rarely seen with arterenol. Previous administra-

tion of atropine, 10–15 mg, abolished normal activity and no effect was then seen on injection of adrenaline.

In vagotomized sheep a striking reversal of the adrenaline effect was observed. In two such sheep, in which the normal rhythm of the reticulum was absent,

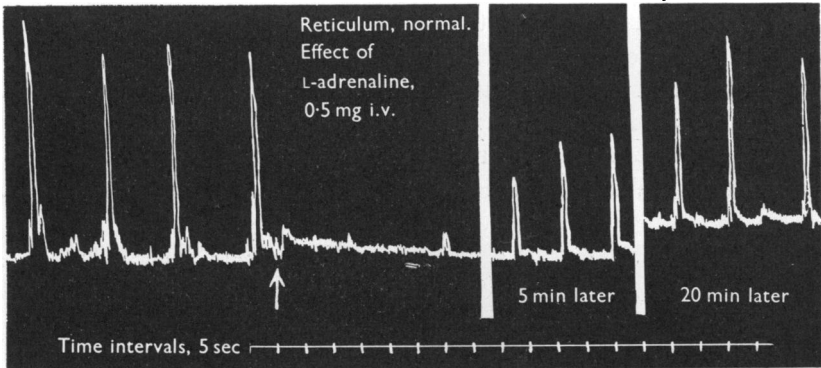


Fig. 5. The effect of L-adrenaline, 0.5 mg intravenously, on the reticulum.

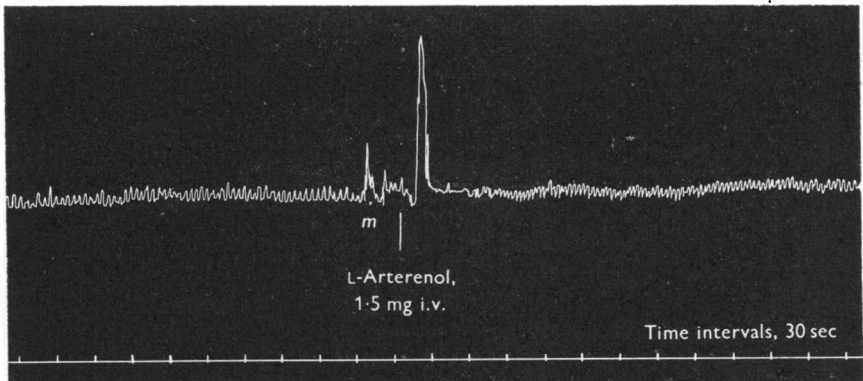


Fig. 6. The effect of L-arterenol, 1.5 mg intravenously, on the reticulum of a sheep in which normal reticulum motility was abolished by vagotomy. The movement (*m*) was caused by the animal struggling before the injection; the basal excursions are respiratory.

intravenous injection of 0.3–1.5 mg L-adrenaline or of 1 mg L-arterenol always resulted in a single slow contraction of all parts of the stomach and especially of the reticulum. When intrinsic activity of the reticulum and rumen was present this was inhibited for a time after the single contraction had occurred. One of these animals had also had the splanchnics cut. When intrinsic activity was abolished by atropine the adrenaline contraction persisted. A similar contraction was obtained in response to adrenaline injection from the reticulum of three sheep anaesthetized with sodium pentothal, in which normal gastric

motility was abolished by the anaesthetic; the effect was unchanged in one animal by subsequent cervical vagotomy. In two of these sheep adrenaline was injected locally into the reticulum muscle, where it failed to cause contraction such as that produced by acetylcholine.

*Histamine* acid phosphate was injected intravenously in doses of 0.1–0.5 mg. The effect was invariably one of inhibition of all gastric movements, without

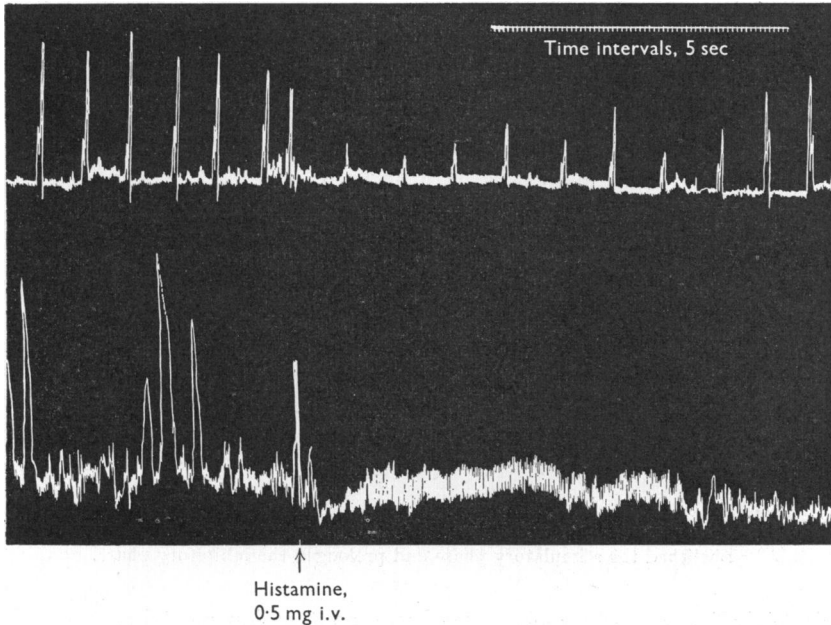


Fig. 7. The effect of histamine acid phosphate, 0.5 mg intravenously, on the reticulum (above) and abomasum. Note the increased frequency and amplitude of respiratory movements after the injection.

tonus increase. Inhibition was slight and transient with the smallest dose, but marked, although still brief, with larger doses. Unlike adrenaline, histamine caused no contraction of the reticulum or rumen in the vagotomized sheep.

*Experiments with isolated surviving gastric musculature*

The results of these experiments have not been satisfactory, but some support is given to the results of the work *in vivo*. The chief difficulty was in obtaining satisfactory preparations. Not all strips of muscle were spontaneously active, and it was observed that active strips usually gave good responses to added substances. The response with inactive or sluggishly active strips was reduced or absent; for this reason only results obtained from active strips, eighty in all, have been considered. The behaviour of strips depended to some extent on the site from which they were taken; the longitudinal or outer

muscle layer tended to be the more active. Strips from the abomasum readily commenced spontaneous activity and the longitudinal strips contracted 15–17 times a minute for several hours. Strips from the omasum and rumen were more erratic, but more than half of them showed spontaneous activity. This activity was often intermittent, bursts of activity alternating with quiescent periods. Little success was obtained with strips from the reticulum; in over twenty attempts only one active strip was obtained. Usually the strips contracted as soon as they were set up in the bath and never relaxed again. They were completely unresponsive to all the substances used in these experiments. The single exception was a strip showing spontaneous rhythm which commenced after the addition of histamine, 10  $\mu\text{g}/\text{ml}$ ., and continued for about 3 hr.

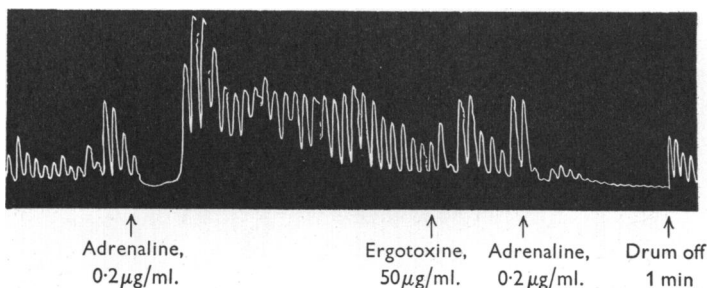


Fig. 8. Effect of adrenaline, 0.2  $\mu\text{g}/\text{ml}$ ., on abomasal strip *in vitro*. Ergotoxine, 50  $\mu\text{g}/\text{ml}$ ., abolished the stimulatory phase and prolonged the inhibitory phase.

*Acetylcholine*, 0.02–6.0  $\mu\text{g}/\text{ml}$ ., produced contraction of strips from all the chambers of the stomach, including the single active strip from the reticulum. Inhibition was never observed.

*Carbachol*, 0.01  $\mu\text{g}/\text{ml}$ ., produced strong contraction in strips of rumen, omasum and abomasum.

*Eserine*, 1  $\mu\text{g}/\text{ml}$ ., was used unsuccessfully in attempts to obtain active reticulum strips.

*L-Adrenaline*, 0.01–0.4  $\mu\text{g}/\text{ml}$ ., was somewhat variable in effect and the dose needed to produce a given reaction varied from one strip to another. However, the most characteristic effect, obtained from abomasum, rumen and omasum, was brief inhibition of spontaneous activity accompanied by a slight drop in tone and immediately succeeded by a partial or completely tetanic contraction lasting for some minutes. When such a response was obtained it was possible by decreasing the dose to reach a level at which brief inhibition was the only effect; on the other hand, increasing the dose gradually eliminated the initial inhibition so that large doses produced only strong tetanic contraction. Ergotoxin, 1  $\mu\text{g}/\text{ml}$ ., abolished the stimulatory effect of adrenaline, but not the



inhibitory effect. The single active reticulum strip in response to L-adrenaline, 0.1  $\mu\text{g/ml.}$ , gave a strong contraction followed by relaxation, quite unlike the tetanic contractions of the other strips.

*Histamine*, up to 60  $\mu\text{g/ml.}$ , gave inconclusive results, but never the strong contraction which it commonly produces in other types of gastro-intestinal musculature.

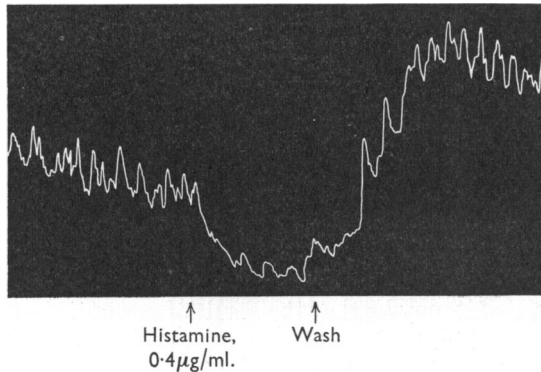


Fig. 9. Effect of histamine acid phosphate, 0.4  $\mu\text{g/ml.}$ , on abomasal strip *in vitro*.

#### DISCUSSION

While the experiments described above are to a certain extent repetitive of earlier work, the results appear to clarify the somewhat confused picture obtained from conflicting reports of the effects of 'parasympathetic stimulants' on the ruminant stomach. The inhibitory effect of injected acetylcholine upon all parts of the stomach, previously described for the sheep rumen by Quin & van der Wath (1938) and for the bovine rumen by Dougherty (1942), led Brunaud & Dussardier (1951) to conclude that acetylcholine is not the chemical mediator of the bovine vagus at the level of the stomach. This theory, however, would appear to be founded almost entirely upon negative evidence, since the action of acetylcholine *in vitro* or when injected directly into the muscle *in vivo*, and the effects of carbachol, eserine and atropine *in vivo* are all such as would be expected if acetylcholine or a very closely related substance were the vagal mediator. The close resemblance between the gastric effects of intravenous injections of acetylcholine and adrenaline and the observation that the effect of the former may persist for an hour, although acetylcholine is known to be destroyed in the body with great rapidity, suggested that the inhibitory effect was produced or enhanced by liberated adrenaline rather than by a direct effect of acetylcholine on the stomach.

The effect of acetylcholine in the adrenalectomized sheep supports the idea that acetylcholine is not in itself inhibitory to the stomach.

The stimulatory effects noted (Quin & Clark, 1946) when 100 mg acetylcholine was injected into a sheep intramuscularly were never observed by the writer.

Eserine, carbachol and related compounds have been administered to cattle or sheep by Wester (1926), Amadon (1930), Quin & van der Wath (1938), Dougherty (1942), Quin & Clark (1946), Brunaud *et al.* (1950), Brunaud & Dussardier (1951) and Brunaud & Navarro (1953*a*). A study of the apparently conflicting results shows that they arise from differences in the dosage levels and in the methods of recording gastric motility. The smaller doses of these substances increase ruminal tonus and activity, but larger doses produce tetanic contraction which amounts to depression of propulsive activity. Since the most detailed studies, those of the South African group and of Dougherty, were made by recording pressure changes in the rumen, the difference in sensitivity between rumen and reticulum has not until now been fully reported (Duncan, 1951). The mechanism by which carbachol and eserine depress activity in the reticulum differs from that involved in the depression following acetylcholine injection, and it may be that the result of eserine injection gives a truer picture of the effect of increasing acetylcholine concentration in the reticulum musculature. The initial increase in amplitude of contractions suggests an increased sensitivity to vagal impulses which would be expected if acetylcholine were the vagal mediator. The sharp transition from strong contractions to paralysis, not accompanied by increase in tone, suggests a sharply defined threshold between stimulatory and inhibitory concentrations, but no such threshold was detected in studies *in vitro* and the inhibition may be a central effect rather than a property of the muscle. The difference in response between rumen and reticulum has been observed also by Brunaud & Dussardier (1953) and Brunaud & Navarro (1953*a*). The latter authors administered eserine, 0.01–0.1 mg/kg body weight intravenously to anaesthetized sheep, and the effects on the rumen and reticulum appear to have been similar to those obtained in the present experiments with 0.3–0.5 mg/kg intramuscularly, though of shorter duration. They did not, however, obtain inhibition of the reticulum. They consider the *anarchie motrice* of the rumen to be a central effect. The present author considers, on the other hand, that the difference between rumen and reticulum is more readily understood in relation to the different degrees of specialization found in the musculature and discussed in an earlier paper (Duncan, 1953). The reticulum contracts almost exclusively in response to volleys of vagal impulses and this explains the difficulty, also mentioned by Brunaud & Dussardier, in obtaining active preparations *in vitro*, and the limited effect of choline esters in increasing its activity. The rumen, on the other hand, has a considerable capacity for independent contractions as well as carrying out co-ordinated contractions in response to vagal impulses; this is manifested in the normal rhythm, which shows extra contractions in

intervals of the cyclical rhythm, and also in the capacity of ruminal strips for independent activity. Since the reticulum rhythm shows that central discharges are not made more frequent by carbachol and eserine, it appears that the increased and often irregular activity of the rumen is due in the main to stimulation of the intrinsic activity, bringing about the increased tonus and partial tetanus.

These observations appear to have some clinical application. Clark (1950*b*) stated that 'as the whole gastrointestinal tract is activated by the parasympathetic system, these drugs [i.e. parasympathetic stimulants] are powerful ruminatorics...'. In the light of the effects observed upon the reticulum their clinical value appears somewhat doubtful. The reticulum probably plays a greater role than the rumen in the propulsion of digesta through the reticulo-omasal orifice (Balch, Kelly & Heim, 1951), and unless doses of drugs can be estimated with sufficient accuracy to ensure stimulation of both reticulum and rumen little advantage is likely to accrue from their use. Increased activity of the reticulum does not lead to rumination, and in fact the ability of atropinized animals to ruminate bears out Stigler's (1931, 1949) views on the mechanism of rumination. It suggests that the extra reticulum contraction, which normally precedes regurgitation but is eliminated by the action of atropine, is of less importance in rumination than the oesophageal and thoracic striped muscles, which are not affected by atropine. Wester (1926) also observed in cattle that 'wenn sich nach der Atropininjektion die Haube nicht mehr zusammenziehen kann, ist dennoch Wiederkauen möglich'.

Quin & van der Wath (1938) and Phillipson (1942) reported that adrenaline had little or no effect upon the stomach of the sheep. In both instances the drug was given intramuscularly; the present work shows that it is necessary to inject adrenaline intravenously to obtain its full effect. After the publication of work by Comline & Titchen (1951) describing contractions induced by adrenaline in the reticulum of the decerebrate or anaesthetized goat, it was confirmed that such contractions were obtained in the unanaesthetized, vagotomized sheep and were thus not due to a central effect of adrenaline. The two opposite effects of adrenaline appear to be due to two separate mechanisms, and both can occur as a response to a single injection, as in the sheep showing intrinsic gastric motility after vagotomy. The two effects also occur *in vitro*, but the order is reversed. The single instance of rapid contraction observed on the application of adrenaline to a reticulum strip *in vitro* is of course inconclusive, but it suggests yet again that the reticulum musculature differs fundamentally from the rest of the stomach.

The inhibitory effect of histamine upon ruminal activity was reported by Dougherty (1942) and investigated more fully by Clark (1950*a*). Histamine appears to have little effect upon the ruminal musculature *in vitro*, and the inhibition following intravenous injection might be a systemic effect. Neither

histamine nor acetylcholine reproduced the effect of adrenaline in the denervated reticulum.

#### SUMMARY

1. The motility of the rumen, reticulum and abomasum has been studied in normal and vagotomized sheep after the administration of a variety of drugs. Strips of muscle from various parts of the stomach have been used to study the effects of the same drugs *in vitro*.

2. The anomalous effects of parasympathetic stimulants have been further studied. The inhibitory effect produced by injection of acetylcholine is found to be due to liberation of adrenaline. Although acetylcholine when injected does not stimulate gastric motility, there seems no strong evidence that it is not the chemical mediator of the vagus in ruminants.

3. Additional evidence is presented to emphasize the highly specialized nature of the musculature, particularly that of the reticulum.

*Author's note.* Since this paper was prepared two papers have appeared, by Dussardier & Navarro (1953) and Brunaud & Navarro (1953*b*), which include a more complete study of the effects of adrenaline, acetylcholine and neostigmine on the ruminant stomach *in vitro*. Their results agree on the whole with those in the present paper.

I wish to thank Dr F. Alexander and Dr A. T. Phillipson for much helpful discussion during the course of this work. Mr J. V. R. Evans kindly performed the bilateral adrenalectomy on one ewe. I am indebted to Dr Kosterlitz for the provision of L-arterenol bitartrate. The sheep were ably cared for and technical assistance was given by Messrs W. Brown and W. Wilson.

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