Onderstepoort Journal of Veterinary Science and Animal Industry, *Volume* 11, *Number* 2, *October*, 1938.

Printed in the Union of South Africa by the Government Printer, Pretoria.

Studies on the Alimentary Tract of Merino Sheep in South Africa. V.—The Motility of the Rumen under Various Conditions.

By J. I. QUIN and J. G. VAN DER WATH, Section of Physiology, Onderstepoort.

Introduction.

In a previous article (No. IV) appearing under this series, a description was given of the technique which was followed in studying various aspects of ruminant digestion. As far as the motility of the rumen was concerned, accurate records of this could be obtained from sheep with closed ruminal fistulae. By a direct connexion of the registering apparatus (tambour and water manometer) to the ruminal fistula and without the use of a balloon in the rumen, all pressure changes in this organ could be recorded in detail.

According to recent work conducted by Krzywanek and Quast on sheep with ruminal fistulae, contractions of the rumen are characterised by a series of rhythmically occurring phases in each of which one large contraction precedes two smaller ones. Moreover, it was shown that a close relationship exists between the rumen and the abomasum as far as their motility was concerned, contraction in the latter usually following on that in the former. Wester, in his earlier work on the forestomachs of ruminants, also established the presence of a relationship between the rhythmic movements of different parts of the forestomachs.

Mangold and Klein, and also Czepa and Stygler, on the other hand, were not able to demonstrate any definite and significant type of rhythm for the forestomachs of ruminants.

Due to the fact, therefore, that the characteristic features in ruminal motility are as yet not fully appreciated, it was decided to undertake a series of experiments on fistula sheep with the object of gaining more knowledge in respect of this very important aspect of ruminal physiology.

For the sake of convenience it is proposed to discuss the various experiments concerned with ruminal motility under the following sub-divisions: —

(*a*) The normal motility of the rumen.

(*b*) The influence of food and water (or their absence).

(*c*) The effect of mineral salts.

(*d*) The effect of drugs and poisons.

(*a*) The Normal Motility of the Rumen.

Of the various aspects of ruminal function, that concerned with the movements of the forestomachs is of primary significance seeing that the normal process of food fermentation, including the control of the pH and the eructation of gas, is intimately associated with it. Moreover, as will be shown presently, the rumen is extremely susceptible to a wide variety of factors, each of which may influence the motility in a specific manner and hence also the chemical changes occurring within this organ.

In studying the characteristic features of large numbers of kymographic records obtained from the rumen of clinically healthy and well nourished Merino sheep, it is found that the well-known rhythmic contractions may from time to time undergo significant changes in spite of the animal having been kept under constant conditions.

As a rule it may be accepted that for Merino sheep 5 to 7 ruminal contractions per 5-minute period constitutes the average rate when recorded during the morning and before feeding.

The force and magnitude of the contractions may, however, vary considerably from day to day, although on an average fluctuations between pressures of -10 mm. H_2O during quiescence and $+70$ mm. H_2O pressure at the height of ruminal contraction are commonly encountered. A negative pressure within the rumen, occurring between the periods of contraction, is an interesting feature and one constantly observed in the majority of sheep. Usually it ranges from -5 mm. to -20 mm. H_2O pressure. In a minority of animals, however, the pressure rarely falls below the zero level.

With regard to the rhythm of the movements, a considerable degree of variation may be revealed. Thus it may change from an evenly spaced rhythm in which all the contractions are of approximately the same magnitude to one in which both rate and size of movements become irregular. At times, however, the rhythm described by Krzywanek and Quast may be assumed, although as a rule only for brief periods during which a large movement is followed by two smaller contractions, the first of which takes place soon after the large movement.

With regard to the effect of rumination itself on the movements, the findings of Krzywanek and Quast could be confirmed, in which it was shown that regurgitation of the food mass into the mouth

invariably precedes a contraction of the rumen frequently only by a second. Similarly it could be established that contraction of the abomasum was closely related with that occurring in the rumen, the abomasum as a rule showing three waves of contraction immediately after that of the rumen.

Eructation of gas from the mouth usually coincides with a strong ruminal contraction, the frequency of eructation depending upon fermentation activity within the rumen.

Apart from the actual contractions revealed, no significant deviation in the general tonus of the ruminal musculature is noticeable in animals kept under constant conditions.

External stimuli such as repeated pin pricks into the skin over the gluteal region or even fairly intense faradic stimulation of the skin, provoked no significant effect on ruminal movement. The sight of a dog may accelerate ruminal movement considerably, an effect which, however, varies with individual animals.

(*b*) The Influence of Food and Water on Ruminal Motility.

Due to the general significance of ruminal function to nutrition, considerable attention has been devoted in this study to the possible relationship existing between the diet and the motility of the forestomachs. In order to investigate this matter, the procedure adopted throughout was to record ruminal movements firstly before feeding, then during actual feeding and finally at different periods after feeding had been stopped. In all the accompanying graphs, these periods are denoted by arrows, which actually indicate the point at which the conditions were changed. From an analysis of many graphs obtained in this way, it may be stated that in every animal used in the experiment ruminal motility was significantly accelerated from the moment that feeding was commenced until it was stopped again, the average increase ranging from a normal 8 movements per 5 minutes before feeding to 20-25 movements per 5 minutes during feeding, i.e., approximately a threefold increase in the rate of concentration (see graph No. 1). That this acceleration is intimately associated with mastication and deglutition and not with the increased state of filling of the rumen is clearly evident from the subsequent rapid retardation as soon as feeding is stopped again (see graph No. 1). Thus it is frequently found that within 10-15 minutes after feeding the rate of contraction has returned to the normal 8 per 5 minutes, although the individual contractions may still be larger than before feeding. In spite of the fact that the movements are much accelerated during feeding, there is, however, no significant increase in ruminal tonus and intraruminal pressure. On the contrary, there may be a temporary accommodating decrease in tone as shown in graph No. 1, in which the minimal pressure decreases from zero before food to -10 mm. H_2O pressure during actual feeding. This, however, is not consistent for all animals. From these observations, there appears strong evidence that this increased motility of the forestomachs during feeding is associated primarily with vagal reflex action, in which the reflex is initiated probably in the pharynx, during deglutition.

On the other hand, the type of food ingested seems to exert little if any specific influence on ruminal movements, since lucerne (both dry and green), poor veld hay and crushed maize all provoke an equally significant acceleration of ruminal movement during feeding. This, however, is noticed only in hungry animals. Apart from acceleration during actual feeding, some animals, which through repeated handling have become well acquainted with the experimental procedure, show in addition a well-defined psychic response to food, whenever this is shown to it. In such cases ruminal movements are also accelerated, although not to the same extent as during actual feeding. In fistula sheep recently brought under experimental conditions this response may be either absent or not so easily elicited, which indicates that it originates as a type of conditional reflex.

By maintaining animals on any one particular type of food even for prolonged periods at a stretch, the normal rhythm is not disturbed as long as the appetite remains satisfactory. Thus in graph No. 2 the ruminal movements are recorded, both before and after feeding, of a sheep that had been kept on a diet comprised of poor quality wheat chaff only for 8 weeks. As will be noticed, both the rhythm and the size of the excursions were well maintained in spite of the poor diet. When, however, animals are kept on an exclusive grain ration, e.g. crushed maize, for a considerable period, the size of the ruminal excursions become much reduced although the rhythm itself is not significantly altered. In graph No. 3 the ruminal records are shown of two sheep kept on a diet of crushed maize only for several weeks. Where animals are forced to exist for prolonged periods on an unbalanced ration comprised either of crushed maize only or of poor quality straw only, ruminal movements may disappear completely and without warning, this being determined very largely by the idiosyncrasy of individual animals, since cessation of ruminal movement and loss of appetite appear much sooner in some animals than in others.

The dosing of finely ground food, e.g. 200 grams powdered grass hay, directly into the rumen through the fistula opening, causes no change whatever in the ruminal rhythm as shown in graph No. 4, although due to the greater filling of the organ the excursions themselves may be augmented, the maximal pressure increasing from +90 mm. H_2O to +127 mm. H_2O. If, instead of the grass hay, 50 grams of sugar such as glucose is dosed into the rumen, an interesting response may be noted as far as the motility is concerned. In well-nourished animals on a normal diet of lucerne and maize, the usual effect of glucose is that of a rapid rise in intraruminal pressure which may be maintained from 15 to 30 minutes, during which time the contraction resemble an incomplete tetanus which gradually passes of again (see graph No. 5). This increased pressure is due, at least partly, to the rapid increase in the rate of fermentation and the accumulation of extra volumes of gas as clearly shown in volumetric determinations of ruminal gas both before and after the dosing of glucose. The possibility of a direct stimulating effect of the glucose on the ruminal musculature as partly responsible for this effect is, however, not excluded. When, on the other hand, the same amount of glucose is administered to low-conditioned sheep accustomed to a diet of poor quality veld hay only, and in which

the animals already show definite signs of body wastage, the opposite response to that described above is very frequently noticed, i.e. there is no sign of an increase in ruminal pressure while the normal contractions themselves may be completely inhibited for periods up to 24 hours or longer. Subsequent determinations of the fermentation rate in the rumen of such animals have moreover shown that the evolution of gas after glucose dosing is either much delayed or even completely kept in abeyance.

Complete starvation of well-nourished animals usually causes no significant effect on the ruminal rhythm for periods ranging from 72-96 hours (3-4 days), although the individual contractions tend to show a progressive decrease in amplitude. After this period a complete cessation of ruminal movement may, however, take place at any time, depending largely on individuality. Through subsequent feeding of such starved animals, ruminal motility usually reappears only after a considerable delay, as the appetite itself may be seriously disturbed after such prolonged fasting.

The Effect of Water.—Whereas food and the process of feeding, exert such well-defined effects on the movements of the rumen, no such response has been noticed for water. Thus neither the actual drinking of water nor the sight of it provokes any significant change in ruminal movement. Moreover, even wide extremes in temperature cause little effect. Thus the dosing of one litre iced water (0° C.) through the ruminal fistula may cause only a slight and transitory acceleration of movement as shown in graph 6. Similarly 1 litre of water at 50° C. provokes little response only, as revealed in graph No. 7. The effects of complete withholding of water for several days is not so easily ascertained, being complicated by the fact that the appetite also soon becomes disturbed, especially when a dry ration only is provided.

(*c*) The Effect of Different Mineral Salts on Ruminal Motility.

Seeing that it has been shown that sodium salts were effective in causing the closure of the oesophageal groove in cattle (Wester) and that copper sulphate produced a similar effect in sheep, it was decided to ascertain what action, if any, different mineral salts exerted on normal ruminal motility. For this purpose small amounts, usually not more than 2 to 3 c.c. of a 10 per cent. solution of the various salts, were dosed on to the back of the tongue as described by Mönnig and Quin and the response of the rumen to it recorded kymographically, both before and after dosing.

Copper Sulphate.—By dosing copper sulphate solutions to sheep as described above, a striking response is elicited as far as ruminal movement is concerned. This response, however, varies between different animals falling into one of two types: (*a*) In which dosing is immediately followed by a significant acceleration of ruminal movement frequently up to 20 contractions per 5 minutes, closely resembling that noticed during feeding. This effect usually passes off within 5 to 15 minutes, after which the contractions may be somewhat slower and smaller than normal (see graph 8).

(*b*) In this case dosing with $CuSO_4$ solution causes a primary complete inhibition of ruminal movement lasting up to 3 or 4 minutes, after which a secondary stimulation results in the typical acceleration effect as described under (*a*). This is clearly shown in graph No. 9. Moreover it has been found that the response of individual animals to repeated dosing with copper sulphate, when tested out over a period of many months, shows no change whatever, i.e. there is no interchange in response from group (*a*) to group (*b*) or vice versa. That this difference in reaction is closely associated with the closure of the oesophageal groove, is shown by the fact that small glass beads when dosed immediately after the copper sulphate, appear in the faeces of animals showing the (*a*) response, considerably earlier than in those in which the (*b*) response is normally elicited. Thus in the (*a*) group the majority of the beads may be eliminated within 48 hours after dosing, whereas in the other groups small numbers of beads are continually passed out over a period of 7 to 14 days or even longer.

Apart from its effect on ruminal movement, copper sulphate solutions, when dosed on to the tongue, provoke an equally sifinificant acceleration in the movements of the *abomasum* (sometimes after a period of primary inhibition) as shown in graph No. 10, while even the *caecum* is immediately stimulated to a more rapid rate of contraction following the dosing of copper sulphate, as revealed in graph No. 11.

On testing out various other mineral salts, it has been ascertained that silver nitrate solutions provoke a response identical to that of copper sulphate, as revealed in graph No. 12. Apart from the mineral salts, nicotine sulphate also causes a similar reaction in ruminal motility, as shown in graph No. 13. Of all the other mineral salts, such as magnesium sulphate, sodium sulphate, sodium chloride, ferrous sulphate and aluminium potassium sulphate (alum), when dosed in the above manner, none of these provoke any significant change in normal ruminal motility (see graphs Nos. 13, 14, 15, 16, 17). Thus it appears to be clearly established that only a limited few substances such as copper, silver and nicotine are capable of eliciting the vagal reflex in sheep when swallowed.

In addition to the above mineral salts, the effect of potassium cyanide on ruminal movement has also been ascertained. By dosing amounts ranging from 150 to 200 mgs. potassium cyanide dissolved in a few cubic centimeters of water directly into the rumen, an extremely rapid decrease in the rhythm and size of the contractions may be noticed which soon culminates in complete paralysis of the organ, while the respirations become much deeper and dyspnoeic in nature. See graph No. 18. Depending upon the dose and the general severity of the reaction, a return of the ruminal movements may be expected usually in 10 to 40 minutes after dosing, the size of the contractions gradually increasing with recovery. Equal doses of KCN may, however, provoke distinctly different effects on animals kept on different diets. Thus it has been found that a dose of 180 mgs. KCN, when dosed to a sheep on a diet of lucerne hay only, causes an effect much milder than that noticeable in animals on a

mixed diet of lucerne and crushed maize. Due to the slightly more acid reaction of the ruminal contents on the latter diet, it would appear that the more severe reaction is associated with a correspondingly more rapid formation, and hence a higher concentration of easily diffusible hydrocyanic acid gas from the KCN within the rumen.

(*d*) The Influence of Drugs on Ruminal Movement.

As certain drugs are reputed to exert a powerful effect on plain muscle, experiments were undertaken in which several well-known drugs in addition to various other substances were tested out for their action on ruminal motility. Of these, three vagal stimulants, viz. acetyl-choline, Lentin (Merck), and Esmodil (Bayer) may be regarded as comprising one group. Acetyl-choline, now generally accepted to be constantly liberated under parasympathetic stimulation was tested out on ruminal fistula sheep either alone or in combination with eserine sulphate. It was found that acetyl-choline in doses of 10 mgs. and more intravenously (dilution 1 : 1,000) caused an immediate and complete paralysis of ruminal movement, similar in all respects to the action of HCN on the rumen.

The effect of the acetyl-choline is, however, of very short duration, since rapid recovery of ruminal movement may be expected within 10 minutes after administration (graph No. 19).

Esmodil (Bayer) in a dose of 3 mgs. (dilution 3 : 1,000) intramuscularly was found to cause a progressive acceleration of ruminal movements accompanied by a rise in the general tone of the rumen. Although somewhat similar to Lentin (Merck) in its action, Esmodil appears to exert a milder effect on the plain muscle of the rumen (graph No. 20).

Lentin (Merck) in a dose of 1 mg. (1 : 1,000) injected subcutaneously, causes a practically instantaneous change both in ruminal tone and in rhythm. The tone which rises to well above the normal level may remain in a spastic state for a period of one hour or longer during which the normal movements are replaced by a series of rapidly recurring, shallow, wave-like contractions resembling those noticeable during a state of incomplete tetanus (graph No. 21). That these cramp-like peristaltic contractions are present at least also in the large bowel is proved by the fact that repeated purgation may set in within 45-60 minutes after injection. At the same time glandular activity is markedly stimulated as evidenced by the profuse and continued salivation and lachrymation. However, all the effects are usually passed off within 2½ to 3 hours, leaving the rumen with its normal rhythm of contraction.

Apart from the above-mentioned three substances, various other drugs were tested out on the rumen. Of these, pilocarpine hydrochloride (graph No. 22) and arecoline hydrobromide (graph No. 23) in doses of 25-40 mgs. per sheep intramuscularly provoked a response resembling that caused by Lentin, except that in no instance has purgation been noticed in sheep following the injection either of arecoline or pilocarpine.

The results with eserine sulphate have been disappointing in that even large doses of 10-15 mgs. intramuscularly failed to provoke any definite response from the rumen except augmentation of the ruminal movements (graph No. 24).

Veratrine hydrochloride, in doses of 5 mgs. subcutaneously, produced intense local irritation and a definite slowing down of the ruminal movements (graph No. 25).

Adrenalin (1:1,000) in doses of 2 c.c. subcutaneously, failed to provoke any change in the normal rhythm or tonus of the rumen (graph No. 26).

A poisonous principle isolated from the plant *Lippia rehmanni* (Verbenaceae), termed *icterogenin*, was found to produce a complete and prolonged inhibition of ruminal movement associated with loss of appetite when given *per os* in an amount of 4 grams (graph No. 27). This substance, which has been shown to be in the nature of a resinic acid, likewise causes inhibition in the bile excretory mechanism of the liver associated with a progressive severe type of regurgitative jaundice.

Discussions and Conclusions.

Experiments conducted on sheep with ruminal fistula have shown that normal ruminal movement may undergo very considerable variations from any rhythm that may be temporarily established. In this respect it is essentially the strength of the individual contractions as well as the spacing of the movements which may undergo a sudden change rather than the rate and the tonus of the rumen both of which remain far more constant. An interesting feature is the extensive degre of relaxation undergone by the ruminal musculature between the actual contractions. During these periods of rest the intra-ruminal pressure usually falls well below zero, values of -5 to -15 mm. H_2O pressure being frequently encountered. At the height of contraction the intra-ruminal pressure may rise from $+20$ to $+129$ mm. H_2O, with an average of ± 70 mm.

Feeding in every instance causes a very significant acceleration in the movement of the rumen, this being due in all probability to vagus reflexes initiated in the pharynx and oesophagus, and closely associated with mastication and deglutition. In some animals the mere sight of food may initiate reflex acceleration of ruminal movement. This effect is, however, neither as constant nor as strong as that noticeable during actual feeding. The type of food exerts little, if any, effect on the ruminal rhythm, although contractions tend to become small when animals are kept on a ration comprised exclusively of concentrates.

Complete starvation as a rule causes no definite change in the rate of ruminal movement up to the third or even the fourth day, although the excursions may become progressively smaller. After this period all movements may, however, disappear completely. Following renewed feeding after such prolonged starvation, a definite delay in the return of movements and also of the appetite is frequently noticeable.

The influence of water on the rumen is much less specific seeing that neither the sight of water nor actual drinking causes any appreciable change in the motility of the rumen. Moreover, wide extremes of temperature ranging from 0° C. to 50° C. following the dosing of 1 litre of either iced or warm water cause very little change in normal motility.

With regard to the influence of various mineral salts, it has been established that small doses of a copper sulphate solution, as well as similar solutions of silver nitrate and nicotine sulphate, when dosed on to the back of the tongue all cause very profound changes in ruminal rhythm, due again probably to a vagal reflex. All other mineral salts tested out so far have failed to provoke this charecteristic response from the rumen.

Potassium cyanide in small doses *per os* causes a rapid though transitory paralysis of all ruminal movements.

In addition to the mineral salts, various other substances have also been tested for their action on the rumen. Of these, Lentin (Merck) and Esmodil (Bayer) have been found to cause a well-marked stimulation of ruminal movement, while acetyl-choline causes an acute though transitory paralysis. Pilocarpine and arecoline also cause significant stimulation of ruminal movement. Adrenaline subcutaneously in doses of 2 c.c. (1:1,000) was found to exert little, if any, change in ruminal motility.

LITERATURE.

ALVAREZ, W. C. (1928). The mechanics of the digestive tract. 2nd Ed. Paul B. Hoeber, Inc., New York.

BERGMAN, H. D., AND DUKES, H. H. (1925). Observations on certain diurnal phases of rumination. *Jnl. Amer. Vet. Med. Assn.*, Vol. 67, pp. 364-366.

BERGMAN, H. D., AND DUKES, H. H. (1926). An experimental study of the mechanism of regurgitation in rumination. *Jnl. Amer. Vet. Med. Assn.*, Vol. 69, pp. 600-612.

BRÜGGEMANN, J. (1935). Über eine Methode zur Registrierung der Magen bewegungen beim kleinen Wiederkäuer. *Arch. Tierheik.*, Vol. 69, pp. 296-298.

COLUMBUS, A. (1934). Der quantitative Verlauf der Entleerung des Pansens bei Schafen und Ziegen mit Berucksichtigung der Gesamtentleerung des Magen-Darmkanals. Thesis: Handelsdruckerei G.M.B.H., Wiesbaden.

CZEPA, A., AND STIGLER, R. (1929). Der Verdauungstrakt des Wiederkäuers im Röntgenbild. Urban und Schwarzenberg Berlin u. Wien.

DUKES, H. H. (1935). Physiology of the ruminant stomach. *Lederle Vet. Bull.*, Vol. 4, No. 6, pp. 1-6.

DUKES, H. H. (1937). The physiology of domestic animals. 4th Ed. Comstock Publishing Co., Ithaca, New York.

DUKES, H. H., AND SAMPSON, J. (1937). Gastrointestinal motility in the ruminant. *Cornell Vet.*, Vol. 27, No. 2, pp. 139-149.

KRZYWANEK, F. W. (1932). Das Wiederkauen. *Handbuch der norm u. pathol, Physiologie*, Vol. 18, pp. 36-44.

KRZYWANEK, F. W., AND QUAST (1936). Die Bewegungen des Pansens und Labmagen beim Schaf und ihre Beziehungen zueinander und zum Wiederkauen. *Pflüg. Arch. Ges. Physiol.*, Vol. 238, No. 3, pp. 333-340.

LENKEIT, W., AND COLUMBUS, A. (1934). Zur Prüfung des Schlundrinnen reflexes. *Arch. Wiss. Prakt. Tierh.*, Vol. 68, No. 2, pp. 126-133.

MAGEE, H. E. (1932). Observations on digestion in the ruminant. *Jnl. Exp. Biol.*, Vol. 9, pp. 409-426.

MANGOLD, E. (1929). Handbuch der Ernährung und des Stoffwechsels der Landwirtschaftlichen Nutztiere. Vol. 2. Verlag Julius Springer, Berlin.

MANGOLD, E. (1935). Die Verdaulichkeit der Futtermittel in ihrer Abhängigkeit von verschiedenen Einflüssen. "*Der Forschungsdienst.*" Sonderheft 2, pp. 35-48.

MANGOLD, E., UND KLEIN, W. (1927). Bewegungen und Innervation des Wiederkäuermagens. Georg. Thieme, Leipzig.

MÖNNIG, H. O., AND QUIN, J. I. (1933). Studies on the alimentary tract of merino sheep in South Africa. I. Investigations into the physiology of deglutition. *Onderstepoort Jnl. Vet. Sc. and An. Ind.*, Vol. 1, No. 1, pp. 117-133.

MÖNNIG, H. O., AND QUIN, J. I. (1935). Studies on the alimentary tract of merino sheep in South Africa. II. Investigations into the physiology of deglutition. *Onderstepoort Jnl. Vet. Sc. and An. Ind.*, Vol. 5, No. 2, pp. 485-499.

SCHALK, A. F., AND AMADON, R. S. (1928). The physiology of the ruminant stomach (ovine). Study of the dynamic factors. *North Dakota Agr. Expt. Sta. Bull.* 216, pp. 1-64.

SCHEUNERT, A. (1927). "Das Wiederkauen." *Handb. Norm. u. Pathol. Physiol.*

TRAUTMANN, A., AND SCHMIDT, J. (1933). Beitrage zur Physiologie des Wiederkäuermagens. III. Über den Schlundrinnen reflex bei kleinen Wiederkäuer. *Arch. Tierernähr. u. Tierzucht.*, Vol. 9, No. 1, pp. 1-10.

TRAUTMANN, A. (1933). Beiträge zur Physiologie des Wiederkäuermagens. V. Die Bewegungsformen des Pansens und der Haube beinm Säugenden Wiederkaüer. *Arch. Tierernähr. u. Tierzucht.*, Vol. 9, No. 1, pp. 19-30.

WESTER, J. (1926). Die Physiologie und Pathologie der Vormägen beim Rinde. Berlin, Richard Schoetz.