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To cite this version:
J. Fioramonti, Y. Ruckebusch. DIET AND CAECAL MOTILITY IN SHEEP. Annales de Recherches Vétérinaires, INRA Editions, 1979, 10 (4), pp.593-599. <hal-00901237>

HAL Id: hal-00901237
https://hal.archives-ouvertes.fr/hal-00901237
Submitted on 1 Jan 1979

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DIET AND CAECAL MOTILITY IN SHEEP

J. FIORAMONTI and Y. RUCKEBUSCH

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Résumé

REGIME ALIMENTAIRE ET MOTRICITE CAECALE CHEZ LE MOUTON. — L'activité électrique de la paroi caecale a été enregistrée pendant des périodes de deux mois chez 5 brebis recevant différents régimes alimentaires. Par rapport à un régime témoin (foin distribué à volonté), la fréquence des contractions caecales (1 500/24 h) est diminuée pour l'ingestion d'une même quantité de matière sèche sous la forme de concentrés contenant de l'urée, mais elle n'est pas modifiée en l'absence d'urée. Elle est également diminuée lorsque le niveau d'ingestion de foin ou de concentrés sans urée est réduit. La distribution des aliments sous la forme d'un repas quotidien de durée limitée induit une hyperactivité dans le cas du foin et une inhibition pour les concentrés avec urée. Les effets excito-moteurs ont pour origine le rumen avec intervention des nerfs vagues. Les effets inhibiteurs de l'urée sont liés à la production dans le rumen d'ammoniac et à sa diffusion dans la cavité abdominale.

The caecum regulates the flow of digesta between the small intestine and colon. The frequency of peristaltic or antiperistaltic contractions (about 1/min) which results in mixing of caecal contents depends on intra-caecal pressure (Fioramonti and Ruckebusch, 1978). About 10 times per 24 h and during the propagation of a phase of regular spiking activity of a myoelectric complex on the terminal ileum, strong contractions in series evacuate the digesta towards the proximal colon in sheep (Mcrae et al., 1973). However the flow of digesta through terminal ileum varies with the diet. It averaged 1.5 kg/24 h with digestible dried grass, but nearly twice this amount with less digestible hay (Goodall and Kay, 1965). Accordingly, the pattern of motility of the ovine small intestine is controlled by the amount of food eaten (Bueno, 1977), its nature and/or end products (Bueno et al., 1977b).

Diets containing large amounts of grain cause the production of large amounts of volatile fatty acids which may lead to atony of the caecum (Svendsen, 1972).

These experiments investigate the effects on caecal motility of the amount and the nature of food eaten, especially in the case of an increased ammonia production by non-protein nitrogen overload. An attempt to elucidate the mechanisms involved will be described.
Material and Methods

Five lacaune ewes weighing 35-49 kg were used. Five pairs of electrodes 2 mm apart made of insulated nichrome wire were implanted under thiopentone anaesthesia on the ileum at 40 cm from the ileo-caecal valve (ICV), on the caecum near the blind pole, on the mid-caecum, in front of the ICV, and on the proximal colon at 40 cm from the ICV. In sheep n° 4 and 5, a cannula (int. diam. 2 cm) was inserted in the caecum and in the dorsal blind sac of the rumen.

After surgery, animals were placed in metabolism cages, ileo-caeco-colic electromyogram was recorded for 3 days each week during 2 months on an EEG machine (Reega VIII, Alvar, Paris). In addition, electrical activity of four chosen sites was automatically plotted each 20 sec by means of a four line integrator on a potentiometric recorder (Latour, 1973).

Three different feeding regimes were used in sheep n° 1, 2 and 3 (long hay of poor quality, concentrates with or without urea) ; their chemical composition is given in table 1. Each diet was given ad libitum or from 10:00 to 14:00 hr in equivalent quantity, or was limited (low intake) to 800 g/day for hay and 700 g/day for concentrates given in 3 meals at 08:00, 13:00 and 19:00 hr. In the latter case, owing to uneaten food, dried matter consumed was nearly similar (table 3). The influence of diet, of the level of food intake and of feeding pattern were studied according to the design shown in table 2. After this experiment, sheep n° 1 and 3 were fitted with a silastic muff around each vagus nerve in the neck ; the rumen was distended in these sheep by insufflation of air through a needle inserted through the left flank before and after injection of a local anesthetis into the muff.

In sheep n° 4 and 5 receiving hay ad libitum, a 20 % (w/v) solution of urea (0.3 g/kg body weight) and a 1 N solution of ammonia (200 ml, pH 11) were rapidly infused into the rumen. Ammonia was also infused into the caecum (0.1 N, pH 11, 200 ml in 10 min) and into the jugular vein (0.03 N, 250 ml over 120 min). The concentration of blood ammonia was determined from samples taken 10, 20, 30 min after the beginning of infusions then each 30 min during 4 hours. The same solutions of ammonia adjusted to pH 7 by HCl were infused into the rumen or the caecum and ammonia was also injected intraperitoneally (0.06 N, 20 ml). Each solution was tested 3 times in each sheep. After this experiment, samples of caecal contents were collected (4/day during 7 days) on hay diet then during 7 days on concentrates with urea diet ad libitum.

The pH of caecal contents were measured immediately after sampling ; the NH₃ concentration was determined by the Berthelot reaction using an autoanalyzer Technicon (Puyt, 1973).

Results

Diet, level of food intake and meal pattern

The amounts of dry matter ingested ad libitum were identical for the three diets (table 3). On hay diet ad libitum, the motor profile of the caecum was similar for the three ewes : 936 ± 92 contractions/24h at the blind pole and 1 497 ± 129 near the ICV, 10.2 ± 2.7 phases of hyperactivity per 24 h which appeared when a phase of regular spiking activity was propagated on the terminal ileum. An inhibition lasting 12.3 ± 4.1 min then occurred. The number of phases of hyperactivity and subsequent inhibition remained unchanged whatever the diet.

<table>
<thead>
<tr>
<th>Constituents</th>
<th>Hay</th>
<th>Concentrates</th>
<th>Concentrates + urea</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry matter (g/kg)</td>
<td>860</td>
<td>870</td>
<td>870</td>
</tr>
<tr>
<td>Composition of dry matter (g/kg)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crude protein</td>
<td>93</td>
<td>212</td>
<td>191</td>
</tr>
<tr>
<td>Cellulose (Weende)</td>
<td>380</td>
<td>88</td>
<td>95</td>
</tr>
<tr>
<td>Lipid</td>
<td>17</td>
<td>29</td>
<td>26</td>
</tr>
<tr>
<td>Nitrogen-free extract</td>
<td>452</td>
<td>571</td>
<td>567</td>
</tr>
<tr>
<td>Minerals</td>
<td>58</td>
<td>100</td>
<td>102</td>
</tr>
<tr>
<td>Urea</td>
<td></td>
<td></td>
<td>19</td>
</tr>
</tbody>
</table>
The frequency of caecal contractions was not significantly modified by ingestion of concentrates without urea (1 396 ± 116/24 h) compared with hay fed ad libitum. But on a concentrates ration with urea ad libitum, the number of contractions was 30% less. Reducing the food intake by 40% decreased the number of caecal contractions/24 h on hay and concentrates without urea rations by 38% and 43% respectively near the ICV and by 43% and 48% on the blind pole. There was no change in the frequency of contraction on the concentrates with urea ration on the reduced intake (table 3).

Whatever the diet given ad libitum, eating did not modify the caecal motility. When the time of feeding was limited to 4 h/day, ingestion of hay produced, after a delay of 15 min, an increase by 25% of the frequency of caecal contractions during 5 hours (fig. 1). After ingestion of concentrates with urea, the frequency of contractions was decreased by half during 5-8 h after a delay of about 2 hours. Ingestion of concentrates without urea did not modify caecal motility. For the three diets, the number of contractions per day remained unchanged when compared with the same diet ad libitum.

**Ruminal factors**

The ruminal distension obtained by increasing internal pressure to 20 cm H2O by the insufflation of air produced an hyperactivity of the whole caecum : the frequency of contractions reached 4.5/min and this effect persisted during all the time of distension (fig. 2). The bilateral vagal anaesthesia by injection of a local anaesthetic (procaine sol. 2% w/v, 2 ml) into the muff around each nerve, indu-

### Table 2. Diet and feeding pattern

<table>
<thead>
<tr>
<th>Period (Days)</th>
<th>Sheep no.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-15</td>
<td>Hay ad libitum</td>
</tr>
<tr>
<td>16-30</td>
<td>Hay ad libitum</td>
</tr>
<tr>
<td>31-45</td>
<td>Concentrates low intake</td>
</tr>
<tr>
<td>46-60</td>
<td>Concentrates + urea 10:00-14:00 hr</td>
</tr>
</tbody>
</table>

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### Table 3. Diet, dry matter intake and frequency of caecal contractions in sheep fed ad libitum or on reduced ration.

<table>
<thead>
<tr>
<th>Diet</th>
<th>Dry matter intake (kg/day) (n = 6)</th>
<th>Caecal contractions per 24 h near the ICV</th>
<th>blind pole</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hay ad libitum</td>
<td>1.04 ± 0.11</td>
<td>1497 ± 129</td>
<td>936 ± 92</td>
</tr>
<tr>
<td>low intake</td>
<td>0.64 ± 0.06</td>
<td>925 ± 82**</td>
<td>528 ± 66**</td>
</tr>
<tr>
<td>Concentrates ad libitum</td>
<td>0.94 ± 0.08</td>
<td>1396 ± 116</td>
<td>917 ± 81</td>
</tr>
<tr>
<td>low intake</td>
<td>0.61 ± 0.02</td>
<td>794 ± 72**</td>
<td>417 ± 46**</td>
</tr>
<tr>
<td>Concentrates + urea ad libitum</td>
<td>1.06 ± 0.08</td>
<td>1023 ± 101**</td>
<td>554 ± 56*</td>
</tr>
<tr>
<td>low intake</td>
<td>0.61 ± 0.02</td>
<td>919 ± 94</td>
<td>465 ± 83</td>
</tr>
</tbody>
</table>

Mean values significantly different (P < 0.05) from hay diet in ad libitum intake (*) and from ad libitum intake in the same diet (**).
ced an inhibition of the caecal motility during 10-15 min. The frequency of contractions was reduced to 0.2/min. Ruminal distension performed 2 min after vagal anaesthesia had no effect on caecal motility.

Effects of ammonia production

The ammonia concentration of caecal contents increased from 8.6 ± 2.3 mg/100 ml (n = 20) on hay diet ad libitum to 22.0 ± 6.1 mg/100 ml on concentrates with urea diet; the pH remained unchanged (7.55 ± 0.33 vs. 7.46 ± 0.41). Intracaecal infusion of ammonia (0.1 N, pH 11, 20 ml/min, 300 ml) did not modify the concentration of blood ammonia (0.091 ± 0.012 vs. 0.085 ± 0.018 mg/100 ml). After a slight excitatory effect increasing the frequency of caecal contractions during the first 5 min of infusion, the infusion induced a strong inhibition of caecal motility during 92 ± 13 min. The frequency of contractions was reduced to 0.1/min. If a phase of regular spiking activity of a myoelectric complex reached the terminal ileum during this inhibition, the caecal hyperactivity associated with the regular spiking activity still occurred. Infusion of disodium hydrogen phosphate buffer solution (pH 11) or ammonia solution at pH 7 into the caecum only produced a slight and short inhibition of caecal motility not longer that 10 min.

After addition of urea into the rumen (0.3 g/kg body weight), the caecum showed, after a delay of 15 min, a pronounced inhibition lasting about 2 hours. The intraruminal injection of a 1 N solution of ammonia (200 ml, pH 11) induced after 3-4 min a short phase of caecal hyperactivity (2-3 min) followed by an inhibi-
tion during 72 ± 14 min. (fig. 3); at pH 7, such an addition had no effect. Intraperitoneal injection of an isotonic solution of ammonia (0.06 N, 20 ml, pH 11) reproduced the effects of intraruminal administration, the delay of apparition of hyperactivity not exceeding 20-30 seconds. Perfusion of ammonia into a jugular vein (0.03 N, 250 ml, 2 ml/min.) did not modify the frequency of caecal contractions. In all the experiments performed, motor changes were similar for caecum and proximal colon.

The concentration of blood ammonia reached 0.35 ± 0.09 mg/100 ml 2 hours after addition of urea into the rumen, 0.31 ± 0.11 mg/100 ml 1 hour after the intraruminal injection of the alkaline solution of ammonia and 0.44 ± 0.15 mg/100 ml 2 hours after the beginning of the infusion of ammonia into the jugular vein.

Discussion

The present work shows that the caecal motor profile is altered during different regimes. The 3 factors concerned are the amount and nature of the food and the time of feeding.

The decrease in the frequency of contractions by 40 % when the level of food intake is reduced confirms the major role played by the pressure into the caecum (Fioramonti and Ruckebusch, 1978), its volume being reduced by 20 % (Hecker, 1971b). Concurrently, the transit time of digesta is increased by about 40 % (Grovum and Hecker, 1973). As transit time increases as caecal motility decreases, we suggest a simple inverse relationship between these both parameters on the caecum and proximal colon unlike the more complex relations observed on the colon of other species such as the rabbit (Fioramonti and Ruckebusch, 1976).

On hay fed once a day, the postprandial hypermotility is not caused by an increase in intraruminal pressure as the ileal flow of digesta is unchanged after feeding (Goodall and Kay, 1965). The artificial distension of the rumen confirms the ruminal origin of such response by a rumino-caecal reflex (Zalucki, 1963) mediated by the vagus nerves. The stimulus must be relatively strong e.g. distension or brushing of ruminal wall, as this response appeared only for rough hay diet. This explains the conflicting informations about the effects of a meal on the caecal motility in sheep (Ulyatt et al., 1974).

The amount of dry matter in the caecum is halved in concentrates diet vs hay diet, concentrate digestion being more important in proximal areas of the digestive tract (Topps et al., 1968). The absence of a reduction in caecal motility on concentrate diets, expected because of the decrease of caecal volume, may be attributed to a permanent ruminal excitatory effect, the quantity of ingested dry matter being similar for both regimes. This constant control may be mediated by the vagus nerves: their anaesthesia in cervical area decreasing the frequency of caecal contractions.

Amplitude of contractions is decreased by volatile fatty acids, the production of which is increased on a cereal diet (Svendsen, 1972). In this case, the concentrates do not induce any change in caecal motility; but an increase in ammonia production linked to urea addition is associated with a decrease in motility. Ammonia has a complex effect on caecal motility. The inhibitory effect of intracaecal ammonia depends upon pH of caecal contents as observed for the rumen (Bueno et al., 1977a); on a concentrates with urea diet ad libitum, the role of ammonia concentration in the caecum (2.5 times higher than for hay) is diminished when compared to the effects of an alkaline ammonia infusion by the persistence of a nearly neutral pH.

The inhibition of caecal motility by addition of urea or of ammonia into the rumen shows the importance of the role of intraruminal ammonia. Intraruminal ammonia acts through its diffusible fraction (NH₃); only injection of an alkaline solution is effective. Caecal inhibition occurring 15 min after urea addition correspond to an increase in ruminal pH (Repp et al., 1955), inducing an increase in NH₃/NH₄⁺ ratio. It is suggested that ammonia from the rumen acts after direct diffusion in the abdominal cavity (Chalmers and White, 1969); indeed, intraperitoneal injection reproduces the inhibition whilst ammonia by intravenous route has no effect despite an increase of the concentration of blood ammonia identical to that observed for the intraruminal injection of ammonia. Such a mechanism may be also considered for ammonia produced in the caecum, its absorption by the caecal wall occurring by simple diffusion (Hecker, 1971a). In addition, the persistence of a caecal response by means of an ileo-caecal reflex (Fioramonti
and Ruckebusch, 1978) at the occurrence of an ileal regular spiking activity and despite the inhibition due to intraluminal infusion of ammonia, shows that such a phenomenon has no relation with the metabolic control by ammonia.

In conclusion, feeding does alter caecal motility by altering caecal filling, by a rumino-caecal reflex mediated by the vagus nerves and possibly by the diffusion of ammonia produced from concentrate diets with urea into the abdominal cavity.

Accepted for publication September 10th 1978.

Summary

The electrical activity of the caecum was recorded during periods of two months in 5 ewes receiving different diets. For a similar amount of dry matter ingested, the frequency of caecal contractions was diminished on concentrates with urea versus hay ad libitum but not on concentrates without urea. The frequency also decreased when the level of food intake on hay diet or on concentrates without urea diet was reduced. On a daily meal food intake, induced caecal hyperactivity occurred or hay and inhibition for concentrates with urea. The postprandial hyperactivity had a ruminal origin and was mediated by the vagus nerves. The inhibitory effects of urea were correlated with the ruminal production and ammonia and its diffusion into the abdominal cavity.

References


