Motor profile of the ruminant colon: hard vs soft faeces production

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Summary. The spiral colon, despite its similarity in ovine and bovine species is only the site of pellet formation in sheep. This peculiarity is associated with a permanent and localized contractile activity of the ovine spiral colon instead of 5-min periods of continuous activity migrating slowly aborally in cattle.

Sheep excrete dry pellets containing about 40% of dry matter whereas in cattle the dry matter reaches only 20% despite the very similar anatomy of the large intestine. In both sheep and cattle the total length of the proximal colon, spiral and distal colon averages about 5 m. The use of markers showed that the amount of colonic content propelled corresponds to 1 kg of wet matter with a mean retention time of 9 h in cattle[3].

Post-mortem examination showed that pellets began to be moulded in the first coil of the spiral colon in sheep but not in cattle. No explanation has been proposed for these differences. The aim of this study was firstly to ensure the role of the spiral colon in the formation of pellets and secondly to elucidate the patterns of colonic motility involved in the production of hard versus soft faeces.

Materials and methods. 6 ewes weighing 50–60 kg of the Lacaune breed and 3 weaned calves weighing 110–140 kg were used. They received hay and water ad libitum and were housed in individual cages which permitted measurement of the daily fecal output. In 3 ewes, the whole spiral colon was isolated as a Thiry-Vella loop by section before the 1st and beyond the last coil, the continuity of the bowel being re-established by an end-to-end anastomosis. In the remaining ewes and in the calves, pairs of electrodes made of insulated nichrome wire were implanted[3] on each coil of the spiral colon under halothane anaesthesia. In cattle, 4 additional groups were implanted at 15-cm intervals on the 3rd coil of the spiral colon.

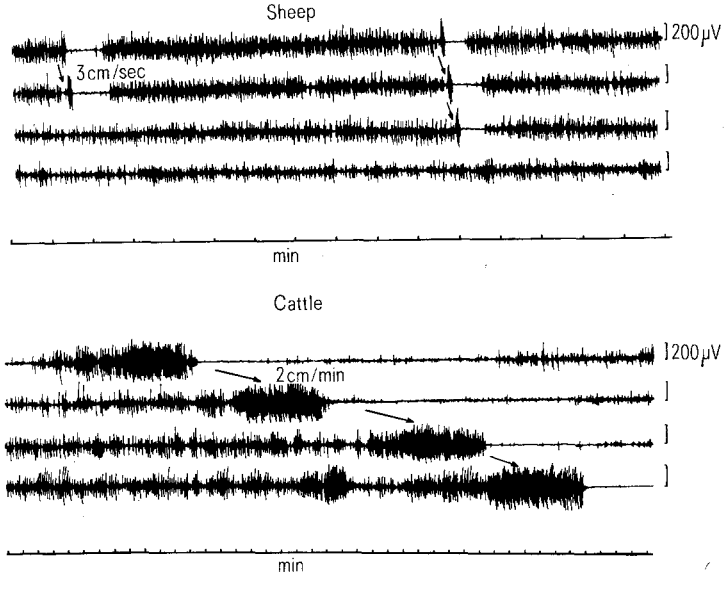
Commencing 1 week after surgery, the electrical activity was recorded continuously during 4 weeks on an electroencephalograph (Reega VIII, Alvar, Paris) at a paper speed of 2.4 or 0.9 cm/min. The dry matter of the faeces was determined by drying samples at 100 °C periodically twice a week during 5 months.

Results. Removal of the spiral colon in sheep was followed by the absence of pellet formation. The faecal dry matter decreased from 38±3% to 12±4% so that the daily weight of excreta averaged 1042±51 g (n=90) instead of 278±29 g. During the subsequent 4 months, the weight of excreta decreased to 496±37 g containing 26±3% of dry matter.

The electrical activity of the ovine spiral colon consisted mainly of bursts of spike potentials lasting 3.9±0.3 sec and recurring at a mean rate of 14.6±0.8/min. In the 3 ewes this pattern occupied 95% of the recording time so that the activity seemed to be nearly continuous. Only periods of quiescence lasting about 1 min were recorded; they followed spike bursts of potentials, lasting 15–30 sec and rapidly propagated along the colon at a velocity of 3 cm/sec (figure). The propagated spike bursts of potentials occurred at a mean hourly rate of 8–10, half of them being propagated along the entire spiral colon.

The pattern of electrical activity of the bovine spiral colon differed from that of the sheep by the presence of spike bursts of potentials which recurred only at a mean frequency of 7.0±0.6/min and occupied 22–27% of the recording time. At each electrode site, 8–10 daily periods of quiescence lasting 30 min were recorded. They were preceded by 5-min phases of continuous electrical spiking activity of high amplitude indicating an intense activity of the colon. These phases migrated slowly along the colon at a velocity of 2 cm/min, with less than 5% of intra- or inter-individual differences.

Discussion. The results show clearly that the spiral colon of the sheep is necessary in the formation of pellets. Its removal was followed within 5 months by an adaptation of the remaining colonic segments for the function of absorption, but not for the formation of pellets. Thus the spiral colon is probably responsible for pelleting in sheep by a permanent tonic activity of the colonic wall. Pellets could be moulded by the daily 200–300 peristaltic contractions moving rapidly along the colon. Such a duality between



Electrical activity recorded from 4 consecutive coils of the spiral colon in sheep and from 4 electrode sites at 15-cm intervals on the 3rd coil in cattle. The spiking activity was continuous in sheep except for spike bursts lasting 15 sec and propagated at a high velocity along 2 or 3 coils. The spiking activity was irregular in cattle, occupying 25% of the recording time with 8–10 daily phases of sustained activity lasting about 5 min and migrating very slowly along the colon.

permanent tonic activity and rapidly propagated bursts has already been observed in the proximal colon of the rabbit[4]. On the other hand, the slow migration of strong phases of continuous activity superimposed on a low level activity as seen in cattle, seems to be an alternative pattern for the aboral transfer of the large amounts of residual food found in herbivores, since such a pattern has never been recorded in dogs[5], pigs[6] or humans[7].

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May K^+ ions stimulate the formation of cyclic AMP in the brain independently on their depolarizing action?

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Summary. The effect of potassium ions on the formation of adenosine 3',5'-monophosphate (cAMP) in the rat cerebral cortex in vivo was studied under conditions where development of spreading depression had been blocked by pretreatment of the cerebral cortex by topically applied magnesium ions. A linear relationship between potassium concentrations applied to the cortical surface and levels of cAMP has been found. Moreover, potentiation of the K^+-effect by magnesium ions has been observed.

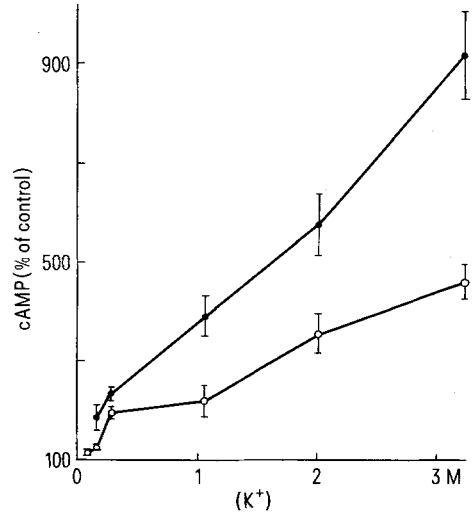
In a previous study, we have shown that a massive depolarization of cerebral cortex cells in vivo, manifested as spreading depression (SD)[1], is accompanied by an elevation of cAMP. Potassium ions, in contrast to the other depolarizing agents used, were able to stimulate the formation of cAMP, both at subthreshold concentrations for evoking SD, and at high concentrations where all the cells are completely depolarized[2-4]. This feature suggested that K^+ affects the cAMP generation system in a direct way as well as indirectly through its effect on depolarization. To test this hypothesis, the effect of K^+ on cAMP levels in the brain cortex was studied under conditions where K^+-evoked SD had been prevented by pretreatment of the cerebral cortex by topically applied magnesium ions.

Materials and methods. Male hooded rats (Druckrey strain) of 180-200 g b.wt were used throughout the experiments. Under pentobarbital anaesthesia (40 mg per kg, i.p.), trephine openings 3 mm in diameter were made in the frontal and the parieto-occipital areas. The dura was kept intact. SD was elicited by application of a filter paper (2×2 mm) soaked in KCl solutions of various concentrations into the trephine opening above the frontal cortex of one hemisphere. The contralateral frontal cortex was treated with saline in a similar way. Development of SD under the influence of K^+ was checked by the appearance of a slow potential change in the parieto-occipital cortex of the same hemisphere.

To prevent elicitation of SD by K^+, the frontal cortex was pretreated with $MgCl_2$ solutions. A concentration of 1.5 M Mg^{2+} sufficed to prevent K^+-induced SD even after concentrations of 3.2 M KCl. 2 types of experiments have been undertaken. In the first one, both frontal hemicortices were treated by topical application of a filter paper soaked with 1.5 M $MgCl_2$. After 30 min, the paper was removed, the cortical surface washed with saline and KCl applied to one of the trephine openings above the frontal hemicortex as mentioned above. The results were compared with the effects of KCl alone. In the 2nd type of experiment, the frontal cortex of only one hemisphere was pretreated with 1.5 M $MgCl_2$. After 30 min, 2.1 M KCl was applied on both frontal hemicortices. Thus the effect of Mg^{2+} on K^+-induced elevation of cAMP was studied in the same animal.

When SD did not appear in the parieto-occipital hemicortex 10 min after K^+ application, the rat was killed by immersion in liquid nitrogen. Samples of about 1 mg wet weight of frozen cortex were dissected at −20 °C and homogenized in 6% trichloracetic acid at 4 °C. cAMP was determined by a protein binding assay procedure as described earlier[3]. Protein was measured by the method of Lowry et al.[5].

Results and discussion. The figure demonstrates the effect of K^+ on cAMP levels in the brain cortex with and without Mg^{2+}-pretreatment. It appears that, in spite of the blocking of K^+-induced SD by Mg^{2+}, the stimulation of cAMP formation by K^+ in a dose-dependent manner proceeds as in the absence of Mg^{2+}, or similarly. Moreover, a remarkable potentiation of the K^+-effect by Mg^{2+} apparently occurs. This facilitation effect is rather striking and as yet unexplained. It could be due to permeability changes induced by the high $MgCl_2$-concentrations. Mg^{2+} alone did not influence cAMP levels significantly. cAMP content in



Cyclic AMP level in the brain cortex as a function of concentration of KCl solutions topically applied on to the surface of one hemicortex. Surface of both control and K^+-affected hemicortices pretreated with 1.5 M $MgCl_2$ (●—●). Surface of both hemicortices pretreated with saline (○—○).