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Postprandial Changes in the Duodenal Ionic Composition in Sheep

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Summary

Using six castrated male sheep with a T-shaped duodenal cannula, we assessed the postprandial changes in ionic composition in the duodenal digesta. Samples were taken every 15 min from animals fed either once a day or fasted over 24 hrs. The flow rate, pH and osmolality of the duodenal fluid were significantly increased after a meal, whereas these factors significantly decreased or changed little in fasted animals. The Na^+ concentration was significantly decreased, whereas the K^+ and Cl^- concentrations were significantly increased in fed animals. In fasted animals, however, the ionic composition of Na^+, K^+ and Cl^- changed in reverse to those seen in fed animals. There was a significant correlation between flow rate and Na^+, K^+, or Cl^- concentration, and a significant negative correlation also existed beween Na^+ and K^+ concentrations. From these results, we conclude that feeding significantly increases the duodenal digesta pH and osmolality as well as flow rate and that the postprandial changes in duodenal ionic composition would reflect the functional activity in the gastrointestinal tract, including the abomasum and the pyloric region in sheep.

The concentrations of H^+ and nutrients such as amino acids or fatty acids in the duodenal digesta are important pieces of information for the gastrointestinal tract in controlling the digestive activities (1, 2). For instance, the intestinal endocrine cells, which sense changes in the luminal H^+ concentrations, secrete the gastrointestinal hormone, secretin into the blood stream. This results in the secretion of HCO_3^--rich alkaline fluid from exocrine glands into the lumen to neutralize excess H^+ and consequently maintains the luminal H^+ concentration at a stable level.

It is currently accepted that duodenal pH decreases after feeding in dogs (3). In sheep, however, it has been reported that feeding causes an increase in duodenal pH, which is mimicked by an intravenous injection of secretin (4). This animal

species also exhibits a postprandial metabolic acidosis, i.e., the blood pH was decreased from 7.50 before feeding to 7.40 1 hr after feeding (5). The authors suggest that this might be caused by an excess loss of plasma HCO_3^-, such as occurs during an increased exocrine secretion of HCO_3^--rich fluids. These results also led us to the assumption that feeding could cause unexpected responses in the digestive tract in this animal species. The purpose of the present study was to assess the dynamic changes in ovine ionic composition of duodenal digesta after ingestion of feed, and discuss them with regards to the changes in the gastrointestinal function induced by a meal.

Materials and Methods

Six castrated male sheep weighing 45 to 84 kg were used. They were fed lucerne hay cubes (2% of the total body weight) and had free access to water. Animals were fed once a day at 12 am or were not fed at all on the experimental day to assess the respective effects of feeding or fasting on duodenal fluid ionic composition.

The surgical procedure for fitting a single T-shaped duodenal cannula at 5 cm distal to the pyloric sphincter was the same as described previously (6). The duodenal digesta sampling was carried out as described previously (6) with some modifications. Namely, every 15 min, the cannula cap was opened for 10 min to allow the digesta to flow out of the cannula. After measuring the volume of the digesta, a part of the digesta was centrifuged at 12,000 rpm for 20 min, and the supernatant was used for the determination of pH, osmolality and ionic concentrations. The concentrations of Na^+ and K^+ in duodenal fluid were determined by a flame photometer (AA-825, Nippon-Jarrell-Ash, Japan), while the concentration of Cl^- was photometrically determined with commercial kits (Wako Pure Chem., Japan). The osmolality of the duodenal fluid was measured by an osmometer (3L, Advanced Inc., USA).

The results are represented as the mean$\pm$S.E. (n=6). For statistical analysis, *t*-test (7) was employed to compare the difference between the values just before (at time 0 min) and after feeding, or between the values for fed and fasted animals. The difference was considered to be significant when the P value was less than 0.05.

Results

Effects of feeding and fasting on duodenal flow rete, pH and osmolality

Fig. 1 shows the changes in duodenal flow rate, digesta pH and digesta osmolality. Duodenal flow rate of fed animals was 111.5$\pm$19.1 ml/10 min prefeeding (time 0 min), which was significantly increased and peaked at a

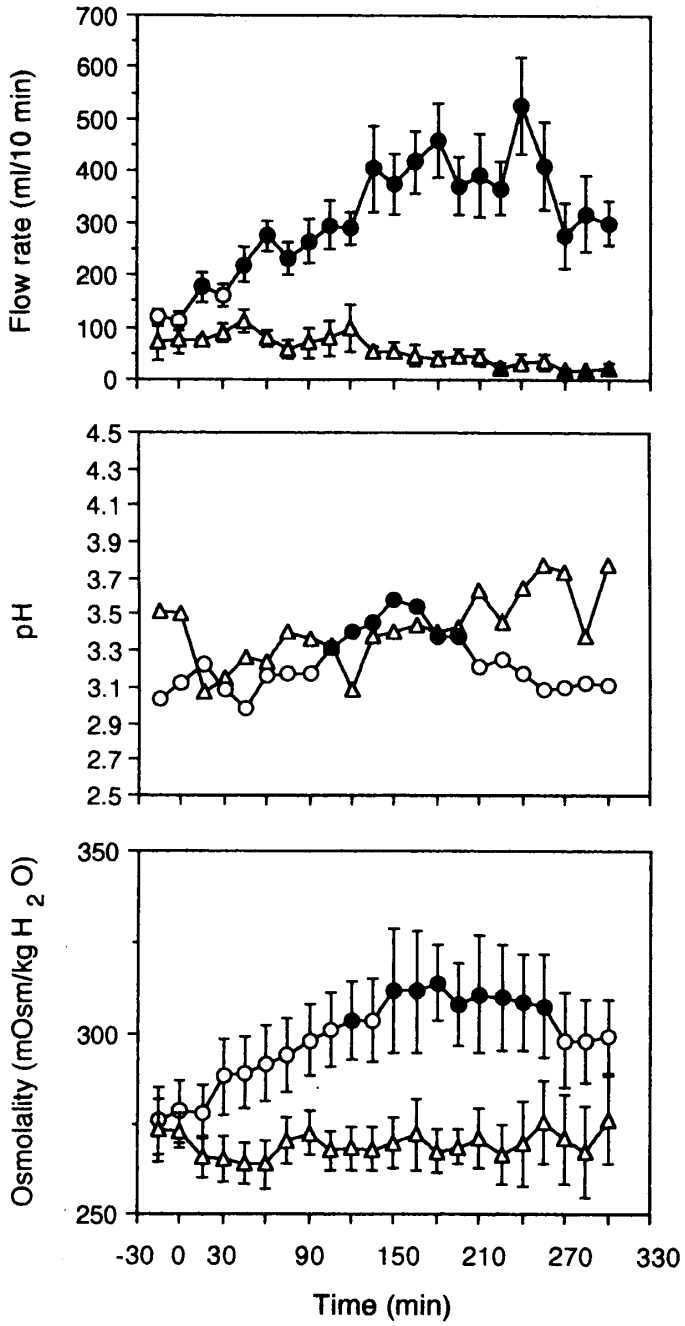

FIG. 1. Effects of feeding or fasting on the flow rate (upper), pH (middle) and osmolality (bottom) of the duodenal digesta in sheep. Animals were fed (circle) at time 0 with lucerne hay cubes (2% of body weight) or were fasted over 24 hrs (triangle). The parameters were measured in the digesta samples collected for 10 min through a T-shaped duodenal cannula as described in **Materials and Methods**. Results are represented as the mean with S.E. (vertical bar) at 15 min intervals (n = 6) except for pH where S.E. is omitted to avoid confusion. The closed symbols show the significantly different (t-test, $P < 0.05$) values from the control value just before feeding (0 min).

maximal value of 526.4±94.9 ml/10 min at 4 hrs postfeeding. On the other hand, in fasted animals, digesta flow rate (74.7±25.7 ml/10 min at time 0 min) was gradually decreased to 24.5±5.0 ml/10 min at 5 hrs postfeeding. There were

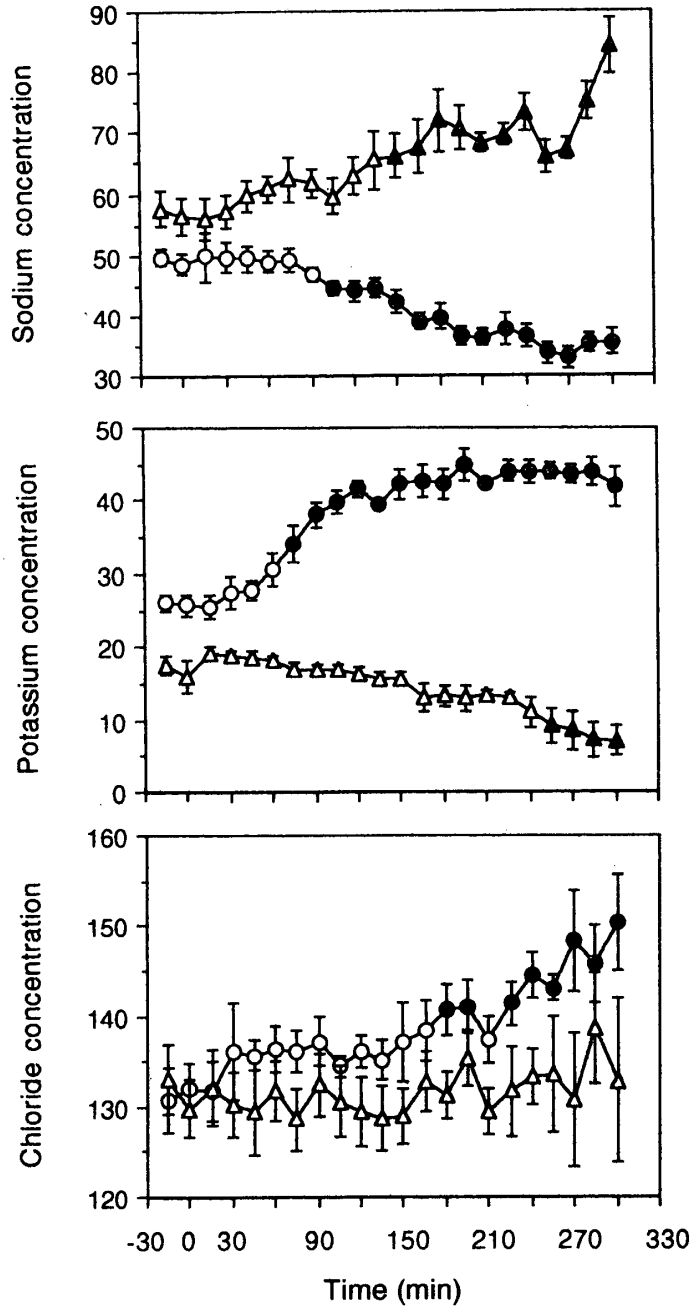

FIG. 2. Effects of feeding or fasting on the concentrations of Na^+ (upper), K^+ (middle) and Cl^- (bottom) of the duodenal digesta. Animals were fed or fasted, and the digesta samples were collected as in Fig. 1. Results are represented as the means±S.E. (n=6). The meanings of the symbols are also the same as in Fig. 1.

significant differences between the values for fed and fasted animals from 15 to 300 min postfeeding.

The duodenal pH was 3.12 ± 0.05 before feeding, which was transiently but significantly increased and peaked at 3.58 ± 0.05 at 2.5 hrs postfeeding. However, in fasted animals, it did not change significantly (3.51 ± 0.28 at time 0 min *v.s.* 3.77 ± 0.41 at 5 hrs).

The duodenal digesta osmolality prefeeding was 278.4 ± 8.5 mOsm/kg H_2O, which was substantially and significantly increased to 313.8 ± 10.6 mOsm/kg H_2O at 3 hrs postfeeding. On the other hand, it did not change significantly in fasted animals. There were significant differences between the values for fed and fasted animals from 30 to 240 min postfeeding.

Effects of feeding and fasting on the duodenal Na^+, K^+ and Cl^- concentrations

The Na^+ concentration of duodenal fluid (48.5 ± 1.6 mEq/l prefeeding) was gradually and significantly decreased to 32.9 ± 1.8 mEq/l at 4.5 hrs postfeeding. The Na^+ concentration in fasted animals (56.5 ± 3.0 mEq/l at time 0 min) was gradually and significantly increased to 84.3 ± 4.5 mEq/l at 5 hrs. There were significant differences between the values for fed and fasted animals from 30 to 300 min postfeeding.

The K^+ concentration (25.7 ± 1.4 mEq/l prefeeding) was significantly increased to 41.6 ± 1.2 mEq/l at 2 hrs postfeeding, which was maintained for a further 3 hrs. In fasted animals, the K^+ concentration (15.9 ± 2.1 mEq/l at time 0 min) was significantly decreased to 7.1 ± 2.0 mEq/l at 5 hrs.

The Cl^- concentration was significantly increased from 132.1 ± 2.6 prefeeding to 150.3 ± 5.3 mEq/l at 5 hrs postfeeding. In fasted animals, the Cl^- concentration (129.8 ± 3.3 mEq/l at time 0 hr) occasionally fluctuated, but did not change significantly. Occasionally, significant differences between the values for fed and fasted animals were observed.

Correlations between flow rate and ionic compositions

There was a significant correlation between the flow rate and Na^+ ($r = -0.81$), K^+ ($r = 0.78$) or Cl^- ($r = 0.70$) concentration. Furthermore, a significantly negative correlation ($r = -0.76$) was observed between the concentrations of Na^+ and K^+.

Discussion

It has been shown that duodenal fluid pH was significantly increased after feeding in sheep. This result is consistent with the previous findings confirmed by continuous measuring of the pH using an electrode inserted into the duodenum through a T-shaped cannula, and also through discontinuous measuring of the

digesta samples collected from the cannula at appropriate intervals (4). However, pH observed with an electrode was significantly increased 2 hrs postfeeding and was sustained over a further 3 hrs, whereas only a transient pH change was seen when the duodenal fluid pH change was seen when the duodenal fluid pH was measured in the digesta samples collected through a duodenal cannula (4). The reason for this difference remains unclear. The duodenal digesta pH observed in the present study (3.12 and 3.51) agrees with that reported by van Bruchem (8) (2.93–3.03), suggesting that duodenal pH is independent of the type of feed ingested.

As shown in the present data our previous paper on sheep (4), the pH change after feeding is quite different from that seen in dogs. In dogs, it has been reported that postprandial duodenal pH decreased in a pulsatile manner (3). This postprandial pH reduction is expected in this animals species because of an increased inflow into the duodenum of gastric juice with a lower pH resulting in the duodenal pH decrease. The difference in ruminant animal species would be due to the presence of forestomachs. In ruminants, volatile fatty acids produced by microbial fermentation of carbohydrate in the forestomachs, which results in an increase in fluid osmolality (9), are neutralized by a large amount of parotid saliva with a high HCO_3^- concentration of more than 100 mM (10). Therefore, the digesta pH of the forestomachs is maintained in the range between 6 and 7. The continuous flow of forestomach digesta with higher pH into the abomasum would overcome the reduction of pH induced by gastric acid, resulting in a postprandial increase in the duodenal pH. It is also possible that HCO_3^- secretion in the pyloric region is greater in sheep than in dogs.

Sasaki *et al.* (5) found that feeding caused a significant plasma pH reduction in sheep, which was accompanied by a reduction in plasma HCO_3^- concentration. Recently, it has also been reported in steers that blood pH reduction occured when animals were fed with either a concentrate or roughage diet (11). The authors (5) suggested that this metabolic acidosis accompanied by feeding was caused by a rapid loss of plasma HCO_3^- through saliva secretion. However, the previous data on the effect of secretin injection on plasma acid-base status reveals the possibility that metabolic acidosis is caused by an increase in HCO_3^- secretion not only through saliva but also through other gastrointestinal HCO_3^--rich fludis from the exocrine pancreas, gallbladder, Brunner's glands and other minor mucous glands. These glands are known to secrete HCO_3^--rich fluid in response to stimulation by secretin-family peptides (1, 12). It is also known that both feeding and secretin injection increase the secretion of HCO_3^--rich alkaline fluid from the ovine exocrine pancreas (13, 14). It has been shown more recently that the plasma secretin concentrations fluctuate and correspond well to an increase in exocrine pancreatic secretion and migrating myoelectric complex activity of the small intestine in calves (15). Furthermore, blood pH was significantly higher in sheep

than in cattle (16). This seemed, in part, to be attributed to lower P_{CO2} levels in the plasma. However, the physiological implications of these characteristics are not known.

The postprandial changes in Na, K and Cl concentrations are probably due to stimulated H^+ secretion, as discussed previously by Hill (17) and van Bruchem (8). That is, they found that the concentrations of Cl^- and K^+ increased with an increase in H^+ secretion, and Na^+ concentration showed a strong negative correlation with K^+ concentration. The present data on the effects of feeding on these ion concentrations could well be explained by these previous findings.

The capacity of HCO_3^- maintenance in ruminants might be more fragile than that of the monogastric animals, when fed once a day as mentioned above. However, it is not known whether this is related to a postprandial increase in the duodenal pH. With regards to the physiological significance of the pH increase in the duodenum, it is known that a luminal pH increase induced by $NaHCO_3$ in sheep and calves (18, 19) or NaOH injection in rats (20), stimulated abomasal motility and emptying, or pancreatic exocrine secretion, respectively. Cottrell and Iggo (21) suggested that the mechanism responsible for these responses involves the excitation of duodenal alkali receptors.

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