Diet induced ruminal papillae development in neonatal calves not correlating with rumen butyrate

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ABSTRACT: The objective of this study was to investigate the development of rumen mucosa and the level of plasma IGF-1 in calves induced by different amounts and types of milk replacers and solid diet. Forty-five male Holstein calves 7 days of age were assigned to three groups: group I milk free replacer, late weaned; group II milk free replacer, early weaned, and group III milk replacer, early weaned. All animals received additional concentrate, water and maize silage were offered *ad libitum*. In each group, three calves were slaughtered at 41 days of age. The concentration of ruminal total SCFA and the molar proportion of butyrate did not differ between the groups, but the molar proportion of acetate was lower ($P = 0.01$) and the proportion of propionate was higher ($P = 0.02$) in early weaned calves. Compared to the late weaned calves (group I) the length, width and surface of the papillae of *atrium ruminis*, the length and width of the papillae of ventral ruminal sac and the length of the papillae of ventral blind sac were greater ($P < 0.05$) in the early weaned calves fed low amounts of milk and high amounts of concentrate (group III). Furthermore, there was a tendency of plasma IGF-1 concentration to be increased ($P = 0.1$) in early weaned calves. The plasma levels of glucose and insulin were decreased ($P < 0.01$, and $P = 0.03$, respectively). Positive correlations existed between papillae length and plasma IGF-1 concentrations ($P < 0.10$). Insulin and glucose concentrations were negatively correlated with parameters of papillae development ($P < 0.1$). In conclusion, the development of rumen papillae was stimulated in calves consuming increased amounts of concentrate. The effect was not correlated with the molar proportion of butyrate, but with the molar propionate proportion in the rumen and with the plasma IGF-1 concentration.

Keywords: calves; rumen fermentation; ruminal morphology; IGF-1

Newborn calves are subjected to various nutritional conditions. The early intake of solid feed, which is related to the development of microbial fermentation in the rumen, might positively influence the functional development of the rumen in calves (Roy, 1980; Zitnan et al., 1993a,b; Kohler et al., 1997). However, there is debate on the ratio of forage to concentrate and on the physical form of concentrates (Di Giancamillo et al., 2003). Forage consumption stimulates rumination, saliva production and muscular development of the rumen (Hodson, 1971; Hamada et al., 1976). On the other hand, forage fermentation does not provide sufficient concentrations of short chain fatty acids (SCFA). SCFA are chemical stimuli for the development of rumen epithelium, promoting its structural development and absorption activity (Kauffold et al., 1977; Jesse et al., 1995; Zitnan et al., 1998; Lesmeister and Heinrichs, 2004).

In a previous study we demonstrated a positive correlation between early weaning and progress of the morphological development of the rumen epithelium, as characterized by the number of papillae as well as their length and width (Zitnan et al., 1999). A recent report indicates similar ontogenic and physiological effects on sodium and chloride transport in the developing calf rumen epithelium (Breves et al., 2002). Increased sodium and chloride transport by the developing rumen epithelium could reflect an increase in the SCFA absorptive capacity by the rumen epithelium (Sehested et al., 1999).

Shen et al. (2004) observed higher IGF-1 concentration in plasma, increased papillae size and surface of rumen epithelium, and an enhanced net flux of Na^+ across the isolated rumen epithelium in kids fed high energy levels. Thus dietary energy-dependent alterations of rumen morphology and function are accompanied by corresponding changes in systemic IGF-1.

The aim of this investigation was to examine the effects of different amounts and types of milk replacers (milk free vs. milk containing ones) and solid diet on the development of rumen mucosa and level of plasma IGF-1 in calves during the first 7 weeks of age.

MATERIAL AND METHODS

Animals and nutrition

Forty-five male German Holstein calves (mean body weight 49.9 ± 0.3 kg) were used. The calves were 7 days old and were randomly assigned to one of the three treatment groups. Calves were housed outdoors in group hutches with straw bedding. Water and maize silage were offered *ad libitum*. The animals of group I (late weaned) were offered a maximum of 8 l of commercial milk free replacer (100 g/l) per day until seven weeks of age and a concentrate mixture (50% pellets + 50% flakes) *ad libitum*. Both in group II (early weaned) and group III (early weaned) calves were given a milk replacer until six weeks of age, which was milk free in group II. Groups II and III received flakes

Table 1. Feed intake by the calves (in g air dry matter per animal and day; maize silage in g fresh matter per animal and day)

	Age (weeks)					
	2	3	4	5	6	7
Late weaned, group I						
Milk free replacer[1]	554	730	776	770	758	779
Pellets[2] + flakes[3] (50:50), *ad libitum*	52	60	102	146	266	454
Maize silage, *ad libitum*		66	56	106	55	51
Early weaned, group II						
Milk free replacer[1]	528	600	366	289	91	
Flakes[3], *ad libitum*	57	60	159	463	1 030	1 449
Maize silage, *ad libitum*		30	54	144	79	52
Early weaned, group III						
Milk replacer[4]	514	565	364	270	112	
Flakes[3], *ad libitum*	107	147	386	703	1 224	1 735
Maize silage, *ad libitum*		62	63	128	129	104

[1]components: dried sweet whey, dried sweet whey (partial removal of lactose), oil (vegetable origin), wheat protein; in group I 100 g/l, in group II 120 g/l

[2]components: wheat, soybean meal (extracted), dried molassed sugar beet pulp, barley, soybean oil, minerals

[3]components: soybean meal (extracted), linseed expeller, cornflakes, wheat flakes, maize gluten, dried whey (protein-rich), wheat bran, soy lecithin, sugar beet molasses, vitamin and mineral mixture

[4]components: dried skim milk, dried sweet whey; oil (vegetable origin), wheat protein; 120 g/l milk

Table 2. Chemical composition and metabolizable energy of diet components (per kg air dry matter)

	Milk replacers		Concentrates	
	group I + II	group III	pellets	flakes
Organic matter (g)	895	925	940	933
Crude protein (g)	190	220	200	190
Crude fat (g)	150	160	50	26
Crude fibre (g)	3	2	35	46
Sugar (g)	n.d.	n.d.	70	60
Starch (g)	n.d.	n.d.	400	350
ME (MJ)	15.3	15.7	11.7	11.4

n.d. = not determined

ad libitum (Table 1). The chemical composition and metabolizable energy of feed are shown in Table 2.

Sampling and chemical analysis

In each group, 3 calves were slaughtered at 41 days of age. Rumen fluid was taken from the perforated rumen immediately after slaughtering. The rumen fluid was strained through 4 layers of gauze and prepared for SCFA analysis.

Samples of the rumen wall (1 cm^2 surface) were obtained from identical sites of the *atrium ruminis*, ventral rumen sac and ventral blind sac and fixed in a 4% neutral formaldehyde solution.

Blood samples were obtained from the non-sacrificed calves on day 42 of life. Blood was collected into 9-ml heparinized tubes (S-Monovette®, SARSTEDT, Numbrecht, Germany) (Li-heparin 10–30 I.U./ml blood). The samples were immediately put on melting ice and centrifuged at 3 000 × g at 4°C for 10 min to separate the plasma. Plasma samples were stored at –80°C until analysed for IGF-1, insulin, and glucose.

For SCFA analysis, a mixture of 5 ml rumen fluid and 2 ml iso-capronic acid (internal standard) was centrifuged at 3 000 × g at 4°C for 20 minutes. The supernatant was then filtered (0.22 µm pore size) to measure the SCFA concentration by gas chromatography (Shimadzu GC-14A, Shimadzu Corporation, Kyoto, Japan) on a capillary column (Free Fatty Acid Phase, 25 m × 0.25 mm, Machery-Nagel GmbH & Co. KG, Duren, Germany) (Geissler et al., 1976). The pH of rumen fluid was measured directly after sampling and prior to preparation for SCFA analysis with a glass electrode (N 1042A, pH meter CG 841, Schott, Mainz, Germany), and ammonia concentration was determined by the microdiffusion method (Voigt and Steger, 1967).

Plasma glucose concentrations were measured by the glucose oxidase method using a commercial kit (No. 115, Sigma Diagnostics, St. Louis, MO).

The determination of insulin was performed by the porcine insulin ^{125}RIA kit (PI-12K, Linco Research, Inc., St. Charles, MO, USA) which used purified human insulin as standard, first antibody raised in guinea pigs, and goat-anti-guinea pig IgG for the bound/free separation. A standard curve was prepared at concentrations from 2 to 200 µU. Cross-reactivity with bovine insulin was 90%. All samples were analysed in duplicates. The sensitivity of the insulin RIA was calculated at 2 µU/ml after measurements with a multi-crystal gamma-counter by a RIA program (LB 2104, Berthold, Bad Wildbad, Germany). Intra- and inter-assay coefficients of variation (precision and reproducibility) were 4.3 and 8.2%, respectively.

Plasma IGF-I was measured by a commercial ^{125}I-RIA kit (Nichols Institute Diagnostics, San Juan Capistrano, USA). IGF-I was separated from binding proteins through acid-ethanol (12.5% 2N HCl – 87.5% ethanol) precipitation. Each sample was analysed in duplicates (2 × 100 µl). All steps of RIA were performed according to the directional insert. Test on samples with two different IGF-I contents (undiluted and diluted, respectively) indicated parallelism. The coefficients of intra-assay and inter-assay variation were 4.4% and 9.9%.

Dietary dry matter (DM), crude protein (CP), crude fibre (CF) and ash were determined according

to the Weender standard procedure (Naumann and Bassler, 1993). The energy content was calculated by the prediction equation of metabolizable energy in mixed feeds (Kuhla and Weißbach, 1996).

Light microscopy and morphometry

After rinsing with water, the rumen wall tissues were dehydrated in a graded series of ethanol (30%, 50%, 70%, 90% and absolute ethanol), cleared with benzene, saturated with and embedded in paraffin. At each sampling sections of 5 µm thickness were made of 20 papillae and stained with haematoxylin/eosin. The length and width of papillae were determined by the computer-operated *Image C* analysis system (Intronic GmbH, Berlin, Germany) and the IMES analysis program, using a colour video camera (SONY 3 CCD) and a light microscope (Axiolab, Carl Zeiss Jena, Germany). The number of papillae per cm^2 of mucosa was estimated with video camera by an image analysis system. The total surface of papillae per cm^2 of mucosa was determined as length × width × 2, multiplied by the number of papillae/cm^2 (Hofmann and Schnorr, 1982).

Statistical analysis

The results were statistically analysed by STATISTICA-Software of StatSoft Inc. (version 6.0). A one-way analysis of variance ANOVA was used to determine the significance between the feeding groups. A significance level of $P < 0.05$ was set. The results are presented as means ± SD.

RESULTS

Intake and body weight gain

During the experimental period of 7 weeks the calves of late weaned group I and early weaned group II and group III daily consumed 675, 362, and 364 g of milk replacer per animal, respectively. The consumption of concentrate in late weaned group I was 294 g per animal and day. In early weaned group II and group III, the intake amounted to 715 g and 887 g per animal and day, respectively. The intake of maize silage in group I, II and III was 68, 78, and 109 g per animal and day, respectively. In group I, II, and III, the intake of total energy amounted to 13.4, 11.7 and 13.6 MJ ME per animal and day. The intake of crude protein amounted to 182, 181, and 219 g per animal and day for group I, II, and III, respectively. The body weight of the calves before slaughtering averaged 63.3 kg (group I), 60.7 kg (group II) and 61 kg (group III). Calves fed in group II had a lower average daily gain (310 g) than calves in group I (502 g) and in group III (521 g) ($P < 0.1$).

Rumen fermentation

No significant differences in the pH, total SCFA concentration and molar proportion of butyrate

Table 3. Effects of diet on ruminal parameters in calves at the time of slaughter at the age of 41 days (mean ± SD, $n = 3$)

	Group[1]			*P*-values
	I	II	III	
pH	5.30 ± 0.31	5.13 ± 0.08	5.34 ± 0.18	0.469
SCFA (mmol/l)	133.7 ± 43.2	175.2 ± 40.1	156.1 ± 13.5	0.403
C_2 (mol%)	59.2 ± 9.1[a]	42.0 ± 0.3[b]	43.1 ± 2.1[b]	0.013
C_3 (mol%)	27.9 ± 6.1[a]	41.6 ± 5.0[b]	43.9 ± 4.5[b]	0.020
C_4 (mol%)	8.8 ± 2.4	9.6 ± 3.4	8.2 ± 3.9	0.864
$C_2 : C_3$	2.24 ± 0.85[a]	1.02 ± 0.11[b]	0.99 ± 0.10[b]	0.035
NH_3(mmol/l)	13.9 ± 1.17[a]	3.9 ± 1.35[b]	10.4 ± 2.90[a]	0.002

[1]group I milk free replacer, late weaned; group II milk free replacer, early weaned; group III milk replacer, early weaned
[a,b]means with different superscripts within a row differ significantly ($P < 0.05$)

in the rumen contents were observed (Table 3). The molar proportion of acetate was increased (P = 0.013) and the proportion of propionate decreased (P = 0.020) in the late weaned calves (group I) when compared to the early weaned calves (group II and III). In the early weaned calves the acetate to propionate ratio also decreased (P = 0.035). Ammonia levels in the rumen contents were lower (P = 0.002) in the early weaned calves of group II.

Rumen mucosa

In the early weaned calves of group III the length, width, density and surface of rumen papillae of the *atrium ruminis* were increased (P < 0.05) when compared to the late weaned calves (group I). Both the papillae length and width of the ventral rumen sac were significantly greater in the early weaned calves (group III) than in the late weaned calves (group I). Likewise, the length of papillae in the ventral blind sac was larger in the early weaned calves of group III than in the late weaned calves (P < 0.05; Table 4).

Plasma IGF-1, insulin, and glucose concentrations

The plasma concentrations of insulin and glucose were lower (P = 0.03 and P < 0.01, respectively), but the plasma concentrations of IGF-1 tended to be higher (P = 0.10) in calves fed less milk and increased amounts of concentrate (Table 5).

Pearson correlation coefficients for selected parameters are presented in Table 6. Butyrate exhibited very low coefficients (–0.25 and 0.18) with IGF-1 and insulin. Correlation coefficients were negative for IGF-1 with acetate (–0.75) and for insulin with propionate (–0.77), but were positive for IGF-1 with propionate (0.85) and insulin with glucose (0.89) and acetate (0.69), respectively.

DISCUSSION

The results demonstrate the influence of the time of weaning on rumen fermentation, rumen mucosa development, and levels of glucose, insulin and IGF-1 in the plasma of neonatal dairy calves.

Table 4. Effects of diet on the number and surface of rumen papillae in calves at the time of slaughter at the age of 41 days (mean ± SD, n = 3)

	Group[1]			P-values
	I	II	III	
Atrium ruminis				
Length (mm)	1.14 ± 0.09^{a}	1.65 ± 0.21^{b}	1.89 ± 0.14^{b}	0.003
Width (mm)	0.53 ± 0.05^{a}	0.59 ± 0.11^{a}	0.81 ± 0.06^{b}	0.009
Density (n/cm^2)	156 ± 16^{a}	130 ± 16^{a,b}	105 ± 8^{b}	0.011
Surface (mm^2/cm^2)	189 ± 12^{a}	249 ± 48^{a}	321 ± 23^{b}	0.006
Ventral rumen sac				
Length (mm)	0.94 ± 0.12^{a}	1.10 ± 0.04^{a,b}	1.25 ± 0.08^{b}	0.014
Width (mm)	0.41 ± 0.05^{a}	0.50 ± 0.08^{a,b}	0.54 ± 0.06^{b}	0.105
Density (n/cm^2)	206 ± 12^{a}	174 ± 9^{b}	153 ± 6^{c}	0.001
Surface (mm^2/cm^2)	160 ± 29	191 ± 26	207 ± 28	0.197
Ventral blind sac				
Length (mm)	0.49 ± 0.08^{a}	0.56 ± 0.10^{a,b}	0.67 ± 0.08^{b}	0.108
Width (mm)	0.34 ± 0.03	0.38 ± 0.04	0.40 ± 0.07	0.291
Density (n/cm^2)	137 ± 7^{a}	111 ± 6^{b}	110 ± 13^{b}	0.020
Surface (mm^2/cm^2)	45 ±9	48 ± 12	59 ± 10	0.272

[1]group I milk free replacer, late weaned; group II milk free replacer, early weaned; group III milk replacer, early weaned
[a,b,c]means with different superscripts within a row differ significantly (P < 0.05)

Table 5. Effects of diet on plasma glucose, insulin-like growth factor 1 (IGF-1) and insulin concentrations in calves at the age of 42 days[1]

	Group[2]			*P*-values
	I	II	III	
Glucose (mmol/l)	5.20 ± 0.85[a]	3.41 ± 0.46[b]	3.83 ± 0.68[b]	< 0.001
IGF-1 (μg/l)	116 ± 44[a]	147 ± 32[b]	139 ± 25[a,b]	0.103
Insulin (μU/ml)	20 ± 16[a]	8 ± 3[b]	11 ± 9[b]	0.034

[1]values are means ± SD, group I and group II $n = 11$, group III $n = 12$
[2]group I milk free replacer, late weaned; group II milk free replacer, early weaned; group III milk replacer, early weaned
[a,b]means with different superscripts within a row differ significantly ($P < 0.05$)

Table 6. Pearson coefficients of correlation between selected parameters and probability of difference from zero[1] ($n = 9$)

	C_2 (mol%)	C_3 (mol%)	C_4 (mol%)	$C_2 : C_3$	Glucose (mmol/l)	IGF-1 (μg/l)	Insulin (μU/ml)
IGF-1 (μg/L)	–0.75 (0.02)	0.85 (<0.01)	–0.25 (0.52)	–0.80 (0.01)	–0.84 (< 0.01)		
Insulin (μU/mL)	0.69 (0.04)	–0.77 (0.02)	0.18 (0.64)	0.68 (0.04)	0.89 (< 0.01)	–0.84 (< 0.01)	
Atrium ruminis							
Length (mm)	–0.73 (0.02)	0.75 (0.02)	–0.09 (0.82)	–0.71 (0.03)	–0.69 (0.04)	0.58 (0.10)	–0.73 (0.03)
Surface (mm^2/cm^2)	–0.61 (0.06)	0.70 (0.04)	–0.19 (0.63)	–0.62 (0.08)	–0.51 (0.16)	0.45 (0.23)	–0.59 (0.10)
Ventral rumen sac							
Length (mm)	–0.58 (0.10)	0.73 (0.03)	–0.24 (0.53)	–0.61 (0.08)	–0.68 (0.05)	0.62 (0.08)	–0.79 (0.01)
Surface (mm^2/cm^2)	–0.48 (0.19)	0.60 (0.09)	–0.12 (0.77)	–0.50 (0.18)	–0.60 (0.08)	0.46 (0.22)	–0.78 (0.01)
Ventral blind sac							
Length (mm)	–0.29 (0.46)	0.41 (0.28)	–0.24 (0.54)	–0.26 (0.50)	–0.46 (0.21)	0.43 (0.25)	–0.44 (0.24)
Surface (mm^2/cm^2)	–0.10 (0.79)	0.24 (0.54)	–0.26 (0.50)	–0.09 (0.82)	–0.31 (0.42)	0.31 (0.42)	–0.30 (0.43)

[1]in parentheses

In our studies the pattern of rumen fermentation was significantly different between animals weaned early or late. Molar proportion of acetate was significantly lower and molar concentration of propionate was significantly higher in calves fed the low milk and high solid diets. Consequently, the acetate to propionate ratio was lowered in the early weaned calves. Different types of diets did not influence the molar proportion of butyrate nor the pH and total SCFA concentration.

The development of parakeratosis and strong mucosal proliferation were apparent after feeding high amounts of concentrate (groups II and III). This can be interpreted as a result of adaptive processes to the increased SCFA level (not significantly) and altered molar proportion of propionate and acetate in the rumen. In these calves the length, width, density, and surface of rumen papillae of the *atrium ruminis* were significantly increased when compared to the late weaned calves. Both the papillae length and width of the ventral rumen sac were significantly greater in the early weaned calves compared to the late weaned calves. Baldwin and Jesse (1992) considered the *stratum spinosum* to be responsible for metabolizing SCFA. Therefore, the efficiency of nutrient transport across the epithelium depends to a large extent on the integrity and degree of keratinization of the *stratum corneum*. While mucosal proliferation and parakeratosis are indications for physiological adaptations to the increased SCFA

production, they can lead to health impairment in response to pathophysiological changes of the rumen wall (Dirksen and Garry, 1987).

A higher proportion of butyrate usually causes the proliferation and keratinisation of papillae in the rumen of adult animals (Kauffold et al., 1977). This effect was not present in our examinations (Table 6). Papillae development and keratinisation of papillae were found without a change in the butyrate proportion. However, the higher proportion of propionate was related to an increased papillae size. It was earlier demonstrated that the intraruminal infusion of propionate, but not glucose resulted in a distinct development of the papillae in calves (Sander et al., 1959; Tamate et al., 1962).

The responsible mechanisms for the induction of papillary development are not fully understood. The plasma concentrations of insulin and glucose were lower ($P < 0.05$) and plasma concentrations of IGF-1 tended to be increased ($P = 0.10$) in calves with stimulated papillae development (Table 5). Shen et al. (2004) demonstrated in kids that circulating IGF-1 affected the rumen papillae development. The effect is probably mediated by IGF-binding proteins in tissue. As demonstrated in Table 6, a positive correlation existed between papillae length (*atrium ruminis*, ventral rumen sac) and plasma IGF-1 concentrations ($P < 0.10$). Insulin and glucose concentrations were negatively correlated with parameters of papillae (length, surface) development ($P < 0.10$). In contrast, ruminal epithelial proliferation in adult sheep was stimulated by *i.v.* infusion of insulin (Sakata et al., 1980) or by *in vitro* incubations with insulin (Baldwin, 1999). Obviously, differences exist in the metabolism of mature rumen papillae and neonatal rumen papillae. It seems that insulin is not a necessary factor controlling ruminal epithelial proliferation in neonatal calves.

CONCLUSION

In conclusion, the development of rumen papillae is stimulated in calves consuming less milk and increased amounts of concentrate. The effect is not correlated with the molar butyrate proportion but with the molar propionate proportion in the rumen and circulating IGF-1. Increased plasma glucose and insulin were not related to ruminal papillae development in neonatal calves consuming predominantly milk replacer.

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