Decrease of Lactase Activity in the Small Intestine of Jejunum-Bypassed Rats

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Summary The effect of jejunum-bypass operation on lactase in rat small intestine was examined. Three groups of four or five rats were designated as jejunum-bypassed, sham-operated and normal rats. All animals including normal rats received by pair-feeding 5% glucose/1% NaCl for 5 days following the operation; thereafter they were fed ad libitum the laboratory chow diet. Three weeks after the jejunal bypass operation, the proximal ileum exhibited a hyperplasia as evidenced by a concomitant increase in mucosal contents of both total proteins and DNA. The specific activity of lactase in this segment was significantly lower in the operated rats than sham-operated controls, whereas the specific activity of sucrase in this segment was significantly elevated. The reduction of lactase activity was also evident in the proximal jejunal segment as well as in the distal jejunum which was deprived of luminal nutrition, suggesting that some hormonal factor(s) might be involved in the decrease of lactase activity in jejunum-bypassed animals. Electroimmunoassay revealed that the amount of immunoreactive lactase also declined in the operated rats relative to the sham-operated controls. Our results thus suggest that lactase activity in residual ileum is not only unable to compensate for the loss of digestive-absorptive surface of jejunum, but lactase activity even decreases following jejunum-bypass operation.

Key Words lactase, sucrase, jejunum-bypass, rat intestine

Among small intestinal disaccharidase complexes located in the brush border membranes, lactase-phlorizin hydrolase is the only β-glycosidase that catalyzes the hydrolysis of lactose. It is well known that lactase activity in small intestine declines during the periods of weanling in most mammals, and in adulthood lactase activity is usually within a very low range where capability of digestion and absorption of lactose depends strictly on the level of lactase activity present in the small intestine (1). Previous studies have shown that lactase activity can be
modulated in adult rats by various factors; carbohydrate intake positively correlates
with lactase activity (2) and pancreatic insufficiency is accompanied by elevated
lactase activity (3), whereas thyroxine treatment leads to the decrease of lactase
activity (4). However, the mechanism whereby these changes in lactase activity
occur is not well characterized at present.

Jejunal resection and jejunal bypass are assumed to cause various changes in
the luminal environment around the surface of brush border membranes of absorp-
tive cells in residual small intestinal segments. These changes might include the
increase in the nutrient supply to the enterocytes of distal parts of small intestine,
and the variation of the amounts and/or distribution along the proximo-distal axis
of luminal proteases and biles. It was reported that in the rats with bypassed
jejunum the specific activities of sucrase and maltase are elevated in the ileum (5).
Our previous study (6) demonstrated that the increased sucrase activity observed in
jejunum-bypassed rats was mainly ascribed to the decrease in the degradation of
sucrase-isomaltase complex which was possibly caused by the decrease of luminal
proteases. These findings led us to a question as to whether lactase activity is also
modified by jejunal bypass operation in the residual small intestine to compensate
for the loss of absorptive surface.

In the present paper, we have explored the adaptability of lactase activity
following jejunal bypass operation in the residual jejunal and ileal segments remain-
ing in continuity as well as in the disconnected jejunal segments deprived of luminal
nutrition.

MATERIALS AND METHODS

Animals and operation procedure. Six-week-old male rats of Sprague-Dawley
strain (Japan SLC, Inc., Hamamatsu) were housed individually in metal hanging
cages and had free access to a standard laboratory diet (MF, Oriental Yeast Co.,
Tokyo). At 7 weeks of age, the animals were starved for 24 h and anesthetized with
an intraperitoneal injection of 5 mg/100 g body weight sodium pentobarbital. A
jejunal bypass operation was performed according to the procedure described by
Lambert (7). In short, at 5 cm distal to the ligament of Treitz, an incision was
carried out on the wall of the intestine, with care being taken not to cut small
vessels. A second incision was made in the middle of the jejunoileal segment,
separating jejunal and ileal segments. The proximal jejunal segment (5 cm) and the
proximal ileal segment were then sutured end-to-end with 6-0 thread by means of
two guiding threads (7). The excluded loop, sutured at one end, was anastomosed
by an end-to-side anastomosis at the level of the sigmoid colon. Control animals
were anesthetized after a 24-h fasting, and transections were carried out at the two
sites of the small intestine corresponding to the anastomosis of the jejunum-
bypassed rats. The third group of animals were starved for 24 h and they
underwent no operation; this group was designated as normal.

Following the operation, all rats including the normal rats received 5%
glucose/1% NaCl solution for 5 days. In a preliminary experiment, we observed that the operated rats consumed only a small quantity of diet during the 5-day period following the operation. Therefore, during this postoperative period, the same amounts of the glucose/NaCl solution that the operated rats consumed were given to the sham-operated rats and the normal rats. Five days after the operation, all animals received free access to the standard laboratory diet. Ad libitum food intake of operated rats, expressed as an average daily intake of day 5 through day 20, was $22.7 \pm 0.8$ g/day (mean $\pm$ SEM, $n=4$). This value did not differ significantly from those of sham-operated rats ($24.4 \pm 0.8$, $n=5$) and the normal rats ($25.2 \pm 0.3$, $n=4$). Deionized water was provided ad libitum through the entire experimental period. The animals were killed by decapitation between 10:00 am and 11:30 am 20 days after the operation.

**Preparation of intestinal samples.** The small intestine was quickly removed and duodenum was discarded. The ileal segment of operated rats extending from the anastomosis to the ileo-cecal valve was divided into two segments of equal length, being referred to as proximal ileum and distal ileum, respectively. The corresponding segments were obtained from the sham-operated rats and the normal rats. In addition, a proximal jejunal segment (5 cm) and the rest of jejunal segment (distal jejunum) were obtained from the sham-operated rats and the normal rats. Each segment was flushed with ice-cold 0.9% NaCl solution. Mucosa was scraped from each segment using a microscopic glass slide. Intestinal mucosa was weighed and provided for brush border preparation. The brush border membrane fractions were prepared according to the method of Kessler et al. (8). The mucosa was homogenized in 10 volumes (w/v) of ice-cold 5 mM mannitol/2 mM Tris HCl buffer (pH 7.1). An aliquot of the homogenate was stored at $-20^\circ$C for the assay of lactase and sucrase activities. The membrane pellet was suspended in 10 mM potassium phosphate buffer (pH 7.0) containing 1% Triton X-100. The Triton X-100-treated brush border membrane vesicles were then incubated at 4°C for 90 min with frequent stirring. The insoluble material was removed from the membranes by centrifugation at 105,000 $\times$ g for 60 min. The resulting supernatant was used for the determinations of lactase activity and the quantification of immunoreactive lactase.

**Enzyme assays.** Lactase and sucrase activities were assayed as described by Dahlqvist (9), with 28 mM lactose and sucrose, respectively. Immunoreactive lactase was quantified by electroimmunoassay using the rocket technique as described previously (10). The specific antiserum against lactase was raised in a rabbit immunized with lactase preparation purified from rat small intestine.

**Other assays.** Protein was determined by the method of Lowry et al. (11), with bovine serum albumin as standard. DNA was assayed according to the method of Burton (12), with calf thymus DNA as standard. Serum total protein and albumin were measured by a biochemical analyzer (CL 7000, Shimadzu Manufacturing Co.) using the reagent kits purchased from Wako Pure Chemical Co. Serum concentrations of thyroxine ($T_4$) and triiodothyronine ($T_3$) were
determined by enzyme immunoassays using reagents purchased from Boehringer Mannheim.

Statistical analysis. All results were subjected to one-way analysis of variance. Differences in mean values between groups were tested using Tukey's multiple range test (13).

RESULTS

Postoperative body weight changes

All rats including the animals which were subjected to jejunum-bypass operation showed a weight loss during the postoperative 5-day period. After this period, the operated rats consumed sufficient amount of standard laboratory diet; the food intake of the operated rats did not differ from those of other groups. Consequently, the operated rats gained their weights at a rate comparable to that of sham-operated rats (Fig. 1). Therefore, we considered that the surgical treatment was well tolerated by the animals.

Serum levels of total protein, albumin, A/G ratio and thyroid hormones (T₄, T₃)

To evaluate the effect of jejunal bypass operation on rat metabolic status, we measured serum levels of total protein, albumin, A/G ratio, thyroxine (T₄) and triiodothyronine (T₃) (Table 1).

Serum total protein concentration of the jejunum-bypassed rats was slightly lower than that of normal rats, but serum albumin level and A/G ratio were unaffected by the operation (Table 1). Serum levels of T₄ and T₃ were slightly

![Fig. 1. Changes in body weight of normal, sham-operated and jejunum-bypassed rats. △, normal rats (n=4); □, sham-operated rats (n=5); ○, jejunum-bypassed rats (n=4). J. Nutr. Sci. Vitaminol.]
higher in sham-operated rats than normal rats. In jejunum-bypassed rats, the serum level of T₄ tended to be low as compared to those in normal and sham-operated rats. The serum T₃ level of jejunum-bypassed rats was similar to that of normal rats (Table 1).

Adaptive changes in intestinal mucosa

Jejunoileum was divided into four segments, i.e., proximal jejunum (5 cm), distal jejunum, proximal ileum and distal ileum, and mucosa was obtained from each segment. As shown in Table 2, mucosal weight in the distal jejunum, which was removed from the intestinal continuity and bypassed to sigmoid in the bypassed rats, was decreased to half that of sham-operated rats and normal rats \( (p < 0.01) \). In contrast, the proximal ileum of operated rats exhibited a remarkable increase in the mucosal weight relative to other groups \( (p < 0.05; \) Table 2). In proximal ileum of bypassed rats, the increase of mucosal weight was accompanied by the increase in the amounts of mucosal total proteins and DNA (data not shown), suggesting that hyperplastic change had occurred in this segment. The proximal jejunum and distal ileum did not show notable modifications of mucosal weight following jejunum-bypass operation (Table 2).

Lactase and sucrase activity in the mucosal homogenate

Lactase activity in proximal jejunum of jejunum-bypassed rats was about 50% lower than those of sham-operated and normal rats, whereas sucrase activity in this segment was similar among the three groups (Table 2). In the distal jejunum of the operated rats, which was deprived of luminal nutrition, both lactase and sucrase activities declined as compared to sham-operated and normal rats (Table 2). The proximal ileum of jejunum-bypassed rats showed a low lactase activity which was again 60% lower than those of sham-operated and normal rats, whereas sucrase activity in this segment was significantly greater \( (p < 0.05) \) than those of sham-operated and normal rats (Table 2). In distal ileum, neither lactase activity

**Table 1.** Serum levels of total protein, albumin, albumin/globulin (A/G) ratio, T₄ and T₃ levels in normal, sham-operated and jejunum-bypassed rats.  

|                   | Normal     | Sham-operated | Bypassed  |
|-------------------|------------|---------------|-----------|
| Total protein (g/100 ml) | 5.93 ± 0.14ᵃ | 5.70 ± 0.11ᵇ | 5.43 ± 0.04ᵇ |
| Albumin (g/100 ml)        | 4.14 ± 0.12 | 3.90 ± 0.08   | 3.81 ± 0.10  |
| A/G ratio*               | 2.33 ± 0.08 | 2.20 ± 0.13   | 2.39 ± 0.18   |
| T₄ (μg/100 ml)           | 7.88 ± 2.12 | 8.99 ± 1.08   | 6.71 ± 1.06   |
| T₃ (μg/100 ml)           | 0.13 ± 0.003ᵃ| 0.16 ± 0.009ᵇ| 0.14 ± 0.005ᵇ|

* A/G ratio was calculated by (albumin)/(total protein−albumin). Results are shown as means ± SEM of 4 rats in normal and bypassed groups and 5 rats in sham-operated group. Values not sharing a common superscript are significantly different from each other at \( p < 0.05 \) by Tukey's multiple range test.
Table 2. The mucosal weight and the activities of lactase and sucrase in mucosal homogenate of rat small intestine in normal, sham-operated, and jejunum-bypassed rats.

|                | Mucosal weight (g) | Lactase activity | Sucrase activity |
|----------------|-------------------|-----------------|-----------------|
| Proximal jejunum |                   |                 |                 |
| Normal          | 0.42 ± 0.01       | 0.37 ± 0.02*    | 1.69 ± 0.09     |
| Sham-operated   | 0.40 ± 0.03       | 0.31 ± 0.05*    | 1.37 ± 0.14     |
| Bypassed        | 0.47 ± 0.02       | 0.15 ± 0.05b    | 1.93 ± 0.40     |
| Distal jejunum  |                   |                 |                 |
| Normal          | 1.57 ± 0.12*      | 0.79 ± 0.08*    | 4.27 ± 0.09*    |
| Sham-operated   | 1.69 ± 0.07*      | 0.82 ± 0.09*    | 4.20 ± 0.29*    |
| Bypassed        | 0.86 ± 0.11b      | 0.35 ± 0.02b    | 2.87 ± 0.14b    |
| Proximal ileum  |                   |                 |                 |
| Normal          | 0.77 ± 0.07*      | 0.61 ± 0.12*    | 3.06 ± 0.21*    |
| Sham-operated   | 0.86 ± 0.03*      | 0.67 ± 0.15*    | 2.91 ± 0.25*    |
| Bypassed        | 1.33 ± 0.19b      | 0.26 ± 0.05b    | 4.02 ± 0.26b    |
| Distal ileum    |                   |                 |                 |
| Normal          | 0.63 ± 0.06       | 0.02 ± 0.01     | 0.38 ± 0.04     |
| Sham-operated   | 0.69 ± 0.02       | 0.02 ± 0.01     | 0.41 ± 0.01     |
| Bypassed        | 0.72 ± 0.09       | 0.01 ± 0.01     | 0.49 ± 0.05     |

The rats were killed 3 weeks after surgery. Results are shown as means ± SEM of 4 rats in normal and bypassed groups and 5 rats in sham-operated group. Values not sharing a common superscript in the corresponding segment are significantly different from each other at p < 0.05 by Tukey's multiple range test. Activities of lactase and sucrase are given in μmol/h per mg of protein.

nor sucrase activity showed any significant alteration following the jejunum-bypass operation (Table 2).

**Lactase and sucrase activities in the brush border membranes**

To determine the characteristic of the changes in lactase activity, we prepared brush border membranes from distal jejunum and proximal ileum. The enzyme activity recovered in the brush border membranes, expressed as a percentage of that in the initial homogenate, varied in the range of 35–44% for lactase and 28–41% for sucrase activity. The average recovery of each enzyme activity was similar among the three groups, and the yields of these enzyme activities were unaffected by the operation. Lactase activity in the brush border membranes of distal jejunum was significantly lower (p < 0.01) in jejunum-bypassed rats than in sham-operated and normal rats (Table 3). By contrast, brush border membrane sucrase activity in this segment did not differ significantly among the three groups (Table 3).

In the brush border membranes of proximal ileum, lactase activity was again significantly lower in jejunum-bypassed rats than in sham-operated and normal rats, whereas brush border membrane sucrase activity in this segment was significantly
Table 3. Lactase and sucrase activities in the brush border membranes of distal jejunum and proximal ileum in the normal, sham-operated, and jejunum-bypassed rats.

|                | Normal         | Sham-operated | Bypassed      |
|----------------|----------------|---------------|---------------|
| Distal jejunum |                |               |               |
| Lactase activity | 20.4±2.50<sup>a</sup> | 19.8±0.46<sup>a</sup> | 14.0±0.28<sup>b</sup> |
| Sucrase activity | 100±7.1       | 103±4.2       | 122±9.4       |
| Proximal ileum |                |               |               |
| Lactase activity | 11.0±2.67<sup>a</sup> | 13.3±1.61<sup>a</sup> | 5.9±0.82<sup>b</sup> |
| Sucrase activity | 44.1±2.67<sup>a</sup> | 50.4±4.02<sup>a</sup> | 61.9±1.35<sup>b</sup> |

The rats were killed 3 weeks after surgery. Results are shown as means±SEM of 4 rats in normal and bypassed groups and 5 rats in sham-operated group. Values not sharing a common superscript in the corresponding segment are significantly different from each other at p<0.05 by Tukey's multiple range test. Activities of lactase and sucrase are given in μmol/h per mg of protein.

Fig. 2. Effects of jejunum-bypass on lactase activity and the amount of immunoreactive lactase in the brush border membranes of proximal ileum. Results are shown as means±SEM. □, normal rats (n=4); ■■■, sham-operated rats (n=5); ■■■■, jejunum-bypassed rats (n=4). * denotes a significant difference from sham-operated rats at p<0.05.

LACTASE FOLLOWING JEJUNUM-BYPASS

Effects of jejunal bypass on the amounts of immunoreactive lactase in proximal ileum

In order to explore the mechanism whereby lactase activity is decreased in elevating the jejunal bypassed rats as compared with those in the corresponding segment of other groups (p<0.05; Table 3). Thus, jejunal bypass operation evoked a decline in lactase activity in brush border membranes of both hyperplastic proximal ileum and distal jejunum with hypoplasia.

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jejunum-bypassed rats, lactase of proximal ileum was solubilized with Triton X-100 from the brush border membranes, and the amount of immunoreactive lactase was determined (Fig. 2). The recovery of enzyme activities in the Triton X-100-solubilized supernatant against the activities in the brush border membranes was 61–88% for lactase activity among all animals. The yields of solubilized microvillar lactase activity were unaffected by the operation. The specific activity of lactase solubilized from the brush border membranes of proximal ileum was remarkably decreased in the operated rats relative to the sham-operated rats (Fig. 2). The amounts of immunoreactive lactase solubilized from the microvillar membranes also showed a significant decline ($p<0.05$) in the operated rats, as compared to normal and sham-operated rats (Fig. 2). The lactase catalytic activity per $\mu g$ of immunoreactive lactase tended to decrease by the operation, and the value of bypassed rats was significantly lower ($p<0.05$) than that of sham-operated rats (Fig. 2).

**DISCUSSION**

It has been demonstrated that after resection or bypass operation of small intestine the experimental animals and humans exhibit remarkable structural and functional changes in the residual small intestine (14). These changes include hyperplasia of distal small intestine and the increases in sucrase and maltase activities in ileal segments (5,15). Associated with the hyperplastic changes, enhanced ileal absorption may permit the animal to compensate for the loss of proximal transport function to maintain normal growth of the whole body (16). The proposed mechanisms responsible for the adaptive functional changes in the residual small intestinal segments may include increased amounts of nutrients provided to absorptive cells in the distal small intestine, trophic effects of enteric hormones and increased blood flow (14).

In the previous study, we demonstrated that the adaptational increase of sucrase activity in the proximal ileum of jejunum-bypassed rats is not only due to the increase in the number of enterocytes, but also attributed to the decreased degradation of sucrase-isomaltase complex (6). Thus the intestinal adaptive response after jejunum-bypass operation appears to involve a complex interaction between luminal, hormonal and pancreaticobiliary factors. In the present study, we have demonstrated that, in sharp contrast to sucrase activity, the lactase activity in the hyperplastic proximal ileum is not capable of compensating for the loss of digestive-absorptive surface caused by jejunum-bypass operation. It should be noted that the lactase activity in the proximal ileum rather showed a significant decrease after jejunum-bypass operation (Tables 2, 3). Since the amount of immunoreactive lactase in this segment was also remarkably decreased, the decrease in lactase activity was mainly due to a reduction in the amount of lactase protein, which could have occurred either due to the decrease in the rate of synthesis or due to the increase in the rate of degradation of lactase enzyme protein.
It has been speculated that the level of jejunal lactase activity is possibly controlled by thyroid hormones (17). Indeed, the normal decrease in lactase activity at weaning period is inversely correlated with the rise in the serum concentration of thyroxine (18). Furthermore, modifications of serum levels of thyroid hormones, e.g., thyroxine administration (4) or starvation (19) have been shown to accompany the modulation of lactase activity in small intestine. Therefore, it was suspected in the present study that the decrease of lactase activity in the jejunum-bypassed rats might be associated with some modifications of serum level of thyroid hormones. However, the serum levels of T₄ and T₃ of the jejunum-bypassed rats were similar to those in sham-operated controls (Table 1). At present the mechanism whereby lactase activity decreased after jejunum-bypass is unclear, but we speculate that some systemic factor(s), presumably hormonal, should be involved in the reduction of the lactase activity after jejunum-bypass surgery, since the decrease in lactase activity occurred not only in the hyperplastic proximal ileum, but also did in the proximal jejunum where no hyperplastic change was detected and in the distal jejunum where even hypoplasia was present.

In conclusion, the present study strongly suggests that lactase and sucrase differ in their adaptability to jejunal bypass, and that lactase activity rather decreases following the jejunal bypass surgery.

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