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ORIGINAL PAPER

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Relationship between glucose transporter and changes in the absorptive system in small intestinal absorptive cells during the weaning process

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Abstract In the present study, we investigated the changes in the localization of the glucose transporter GLUT2 and the fructose transporter GLUT5 in small intestinal absorptive cells during postnatal development, especially during the weaning period, using immunohistochemistry and confocal laser scanning microscopy. In the jejunum, GLUT2 was observed within the apical and basolateral membrane domain of absorptive cells, especially in the middle part of the villi. In the suckling rat ileum, GLUT2 was found within the apical and basolateral membrane domain of absorptive cells, but after 18 or 19 days after birth, GLUT2 was found mainly within the apical membrane domain. GLUT5 was observed within the apical membrane domain of absorptive cells in the suckling rat jejunum. In the 18- or 19-day-old rat jejunum, GLUT5 was localized within the apical and basolateral membrane domain of absorptive cells in the lower part of the villi, but after weaning, GLUT5 was found within the apical and basolateral membrane domain of absorptive cells throughout the entire villi. In the suckling rat ileum, there was little GLUT5 in the absorptive cells. In the 18- or 19-day-old rat ileum, GLUT5 was localized within the apical membrane domain of absorptive cells in the lower part of the villi, but after weaning, GLUT5 was observed mainly within the apical membrane domain of absorptive cells throughout the entire villi. These results suggest that the localization of glucose transporters corresponds with a shift from neonatal-suckling to weaned absorptive cells during postnatal development.

Key words GLUT2 · GLUT5 · Absorptive cell · Small intestine · Weaning

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Introduction

During postnatal development, the mammal gradually shifts its diet from maternal milk to other nutrition. To digest and absorb nutrients, the membrane properties, enzyme activities, and transporter activities of the absorptive cells of the small intestine change at each developmental stage.

We have previously shown that the structure and macromolecular uptake of absorptive cells varies according to the region of the small intestine during postnatal development.[1] In the suckling period, the absorptive cells of the small intestine absorb milk macromolecules and digest them in the lysosomes. The adult absorptive cells, on the other hand, absorb small molecules that are broken down in the digestive tract and on the surface of microvilli.

Dietary monosaccharides, e.g., glucose, galactose, and fructose, are transported across the absorptive cells through the activity of various carrier systems expressed in both the luminal and basolateral domains of the plasma membrane. In the apical membrane domain of absorptive cells, the presence of both the Na^+/glucose cotransporter, SGLT1, and GLUT5 has been demonstrated.[2–5] GLUT5 is a facilitative transport system for fructose in the apical membrane. Human GLUT5 transports fructose exclusively, whereas rat GLUT5 is able to facilitate the transport of both glucose and fructose.[6] In contrast, the basolateral domain of the plasma membrane of absorptive cells expresses GLUT2, but not GLUT5 or SGLT1.[5,7] GLUT2 facilitates mainly glucose transport from absorptive cells.[8]

During development, intestinal nutrient transporters can be classified into two categories: those that exhibit high transport rates before birth, such as SGLT1 and some amino acid transporters, and those which show high transport rates only after birth or weaning, such as the fructose transporter GLUT5 and bile acid transporters.[9] During postnatal development, SGLT1 and GLUT2 expression increases throughout the suckling period and peaks after weaning.[5,10] Insulin-like growth factor (IGF) alters the expression of SGLT1 and GLUT2[11] while luminal fructose

regulates the expression of GLUT5 during weaning.[12,13] Most previous studies, however, have focused mainly on the jejunum. Moreover, there are few reports about the relationship between glucose transporter and the absorptive system in small intestinal absorptive cells during weaning.

The aim of this study was to investigate changes in the absorptive system and localization of the glucose transporter, GLUT2, and the fructose transporter, GLUT5, in jejunal and ileal absorptive cells during postnatal development, especially during the weaning process, by electron microscopy, immunohistochemistry, and confocal laser scanning microscopy.

Materials and methods

Animals

The study used Wistar rats, some of which were 7- to 21-day-old (suckling to weaning), and some of which were 28-day-old (after weaning) rats, and these were reared under ordinary laboratory conditions. The rats were anesthetized with ether. The small intestine was exposed through a vertical slit in the abdominal wall and the entire small intestine was dissected intact. The proximal jejunum and distal ileum were cut into 3- to 4-cm pieces.

Transmission electron microscopy

For the transmission electron microscopic study, tissues were cut into 1.0 mm × 2.0 mm blocks. The specimens were fixed in a mixture of 2.0% formaldehyde and 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH 7.4) for 2 h at 4°C, washed in the same buffer, postfixed for 2 h at 4°C in an aqueous solution of 1.0% osmium tetroxide, dehydrated in a graded series of ethanol, and embedded in EPON 812. Thin sections were cut into 1-μm slices on a microtome, stained with toluidine blue, and observed under a microscope. For ultrastructural study, ultrathin sections were stained with uranyl acetate and lead acetate, and they were examined with a transmission electron microscope (JEOL-1200EX) at an accelerating voltage of 80 kV.

Immunohistochemistry

For detection of the glucose transporter, GLUT2, and the fructose transporter, GLUT5, tissues were cut into 1.0-cm-wide rings. The specimens were embedded in OCT compound medium (Sakura Fine Technical, Tokyo, Japan) and flush-frozen in dry ice-acetone. Sections were cut into 6-μm slices on a cryostat, transferred to a glass slide, air-dried, and fixed in acetone for 30 min at −20°C. The fixed sections were washed in phosphate-buffered saline (PBS, pH 7.4), and were then blocked with 5.0% dry-milk PBS for 30 min at room temperature. The primary antibody used was rabbit anti-GLUT2 or rabbit anti-GLUT5 (Chemicon International, Temecula, CA, USA). The sections were incubated with the primary antibody diluted 1:2000 in 1.0% bovine serum albumin (BSA)-PBS for 2 h at room temperature. Control sections were treated with only 1.0% BSA-PBS. After being washed three times with PBS, all the sections were incubated with secondary antibody diluted 1:2000 in 1.0% BSA-PBS for 30 min at room temperature. As secondary antibody, Alexa Flour 488-labeled goat antirabbit IgG (Molecular Probes, Eugene, OR, USA) was used. The sections were washed three times with PBS, mounted using a Vectashield Hard Set Mounting Medium (Vector Laboratories, Burlingame, CA, USA) and observed with a laser scanning confocal microscope (Fluoview FV300; Olympus, Tokyo, Japan).

Results

Light microscopy

In the suckling rat jejunum, numerous thin villi of various heights were observed in the lumen. Just before weaning and just after weaning, the villi became thicker and of equal height. In the suckling rat ileum, numerous thin villi of various heights were observed in the lumen, as in the jejunum. Throughout the 7- to 28-day period, the jejunal villi were longer than those of the ileum.

In the jejunal absorptive cells, there were no visible changes between the suckling and the weaned rats (Fig. 1a–c). There was, however, an obvious difference in the ileum. In the suckling rats, the ileal absorptive cells had a giant lysosome in the supranuclear region (Fig. 1d). As the weaning process progressed, the giant lysosome became larger and larger, as in the upper part of the villus. In the 18- or 19-day-old rat ileum, absorptive cells without a giant lysosome could be seen at the base of the villi (Fig. 1e). After 18 or 19 days, the ileal villi became covered with absorptive cells that had no giant lysosome (Fig. 1f).

Transmission electron microscopy

Transmission electron microscopic observations of the epithelium in the rat jejunum and ileum showed changes in the absorptive cells during weaning.

In the suckling jejunum, absorptive cells contained many lipid particles in the smooth endoplasmic reticulum, Golgi apparatus, and intercellular space, and an apical endocytic membrane system that decreased during weaning. After weaning, the apical membrane system was rarely observed in the jejunal absorptive cells. In the suckling ileum, absorptive cells contained an apical endocytic membrane system including a giant lysosome in the supranuclear region. During weaning, the apical membrane system became decreased in the ileal absorptive cells as it did in the jejunum. In addition, the giant lysosome decreased in electron density, even while it was enlarging in the ileal absorptive cells as the rats developed. In the 18- or 19-day-old rats, two types of absorptive cell were observed in the ileum. One

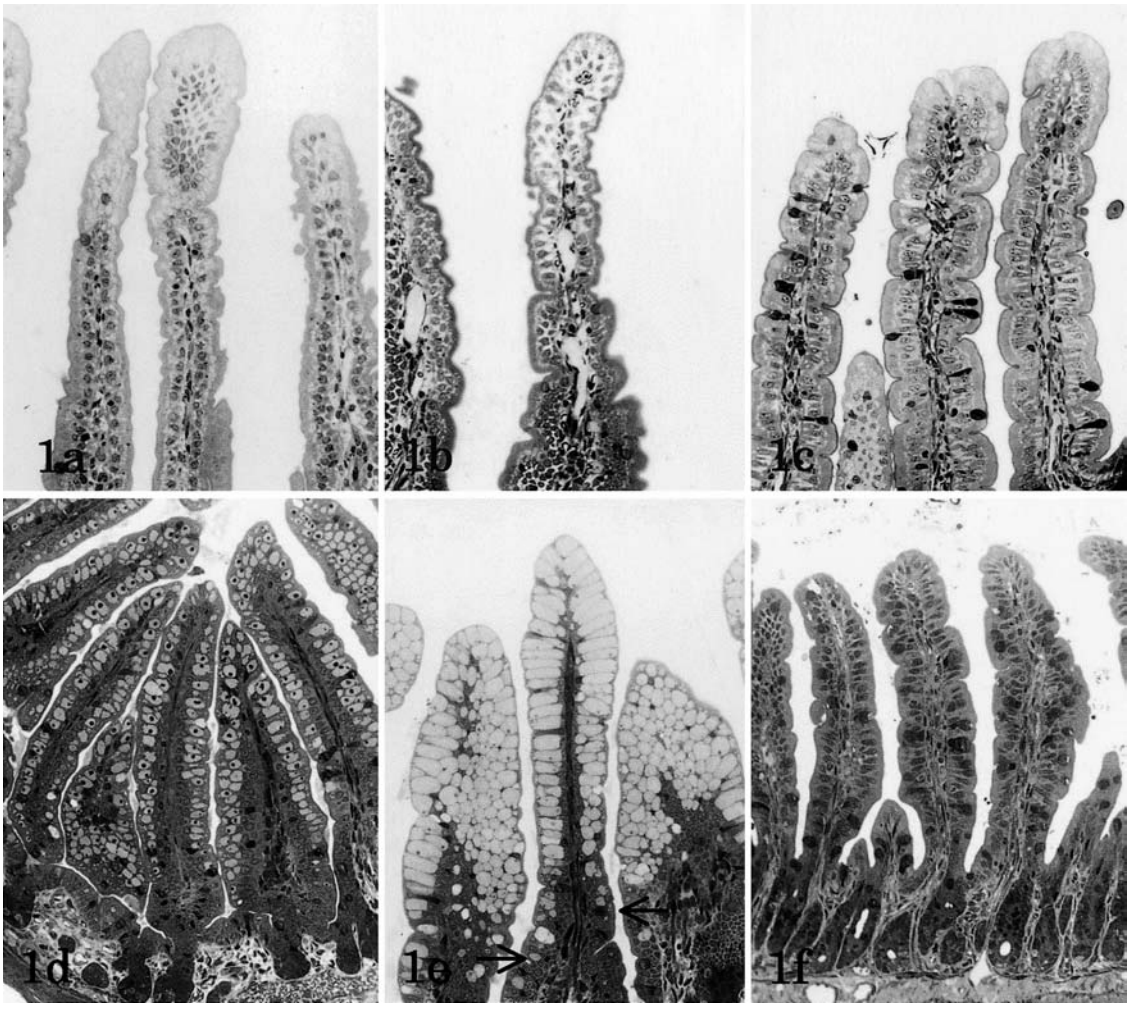

Fig. 1. Light micrographs of the small intestinal villi: **a** 7-day-old rat jejunum; **b** 19-day-old rat jejunum; **c** 21-day-old rat jejunum; **d** 7-day-old rat ileum; **e** 19-day-old rat ileum (*arrows* show the boundary of the two types of absorptive cells); **f** 21-day-old rat ileum

was observed in the upper part of the villi and had an apical endocytic membrane system, including an enlarged giant lysosome, while the other was observed in the lower part of the villi and had no apical endocytic membrane system. After 18 or 19 days, only the latter type of absorptive cell was observed throughout the villi.

Immunohistochemistry

Laser scanning confocal microscopic observations of the epithelium in the rat jejunum and ileum showed the localization of GLUT2 and GLUT5 during weaning.

In the neonatal to weaned rat jejunum, GLUT2 was observed within the apical and basolateral membrane domain of absorptive cells throughout the entire villi (Fig. 2a–c). In the suckling rat ileum, GLUT2 was observed at the apical and basolateral membrane domain of absorptive cells throughout the entire villi (Fig. 2d). After 18 or 19 days, GLUT2 was mainly found within the apical membrane domain of the absorptive cells from the lower part of the villi (Fig. 2e). In the weaned rat, GLUT2 was observed within the apical membrane domain of the absorptive cells (Fig. 2f).

GLUT5 was observed within the apical membrane domain of the absorptive cells in the suckling rat jejunum (Fig. 3a). In the 18- or 19-day-old rat jejunum, GLUT5 was observed within the apical membrane domain of the absorptive cells from the upper part of the villi, as in the suckling rat jejunum (Fig. 3b). On the other hand, GLUT5 was localized not only within the apical but also within the basolateral membrane domain in the absorptive cells from the lower part of the villi (Fig. 3b). After 18 or 19 days, GLUT5 was found within the apical and basolateral membrane domain of absorptive cells throughout the entire villi (Fig. 3c). In the suckling rat ileum, few GLUT5 reaction products were observed in the absorptive cells (Fig. 3d). In the 18- or 19-day-old rat ileum, few reaction products of GLUT5 were observed in the upper part of the villi; however, in the lower part of the villi, GLUT5 was localized within the apical membrane domain of the absorptive cells (Fig. 3e). After weaning, GLUT5 was observed mainly

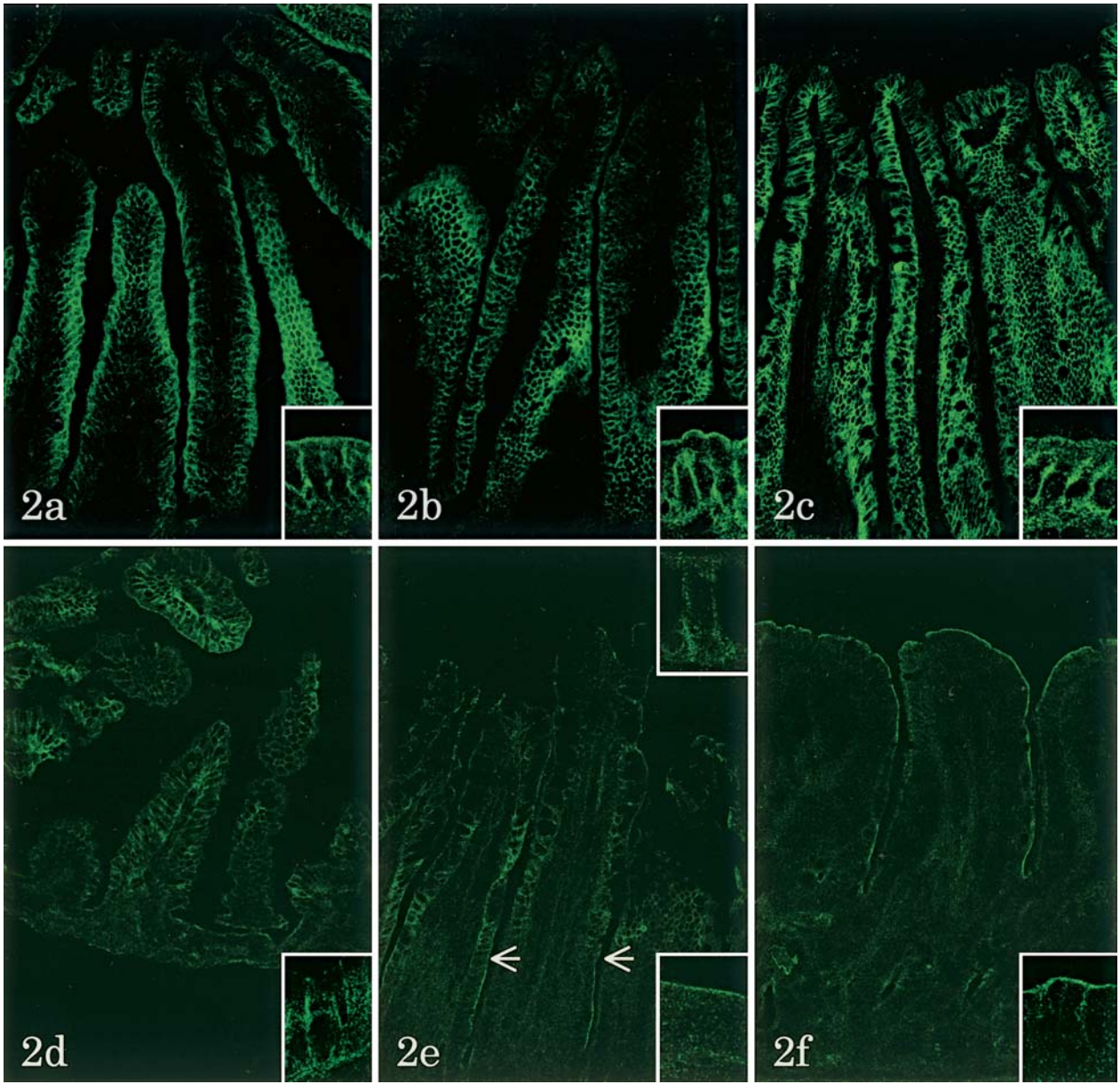

Fig. 2. GLUT2 localization of the rat small intestine: **a** 7-day-old rat jejunum (*inset*, jejunal absorptive cells); **b** 19-day-old rat jejunum (*inset*, jejunal absorptive cells); **c** 28-day-old rat jejunum (*inset*, jejunal absorptive cells); **d** 7-day-old rat ileum (*inset*, ileal absorptive cells); **e** 19-day-old rat ileum (*arrows* show the boundary of the localization of GLUT2; *upper inset*, ileal absorptive cells from the upper part of the villi; *lower inset*, ileal absorptive cells from the lower part of the villi); **f** 28-day-old rat ileum (*inset*, ileal absorptive cells)

within the apical membrane domain of ileal absorptive cells throughout the entire villi (Fig. 3f).

Discussion

During the suckling period, the immature gastrointestinal tract is offered maternal milk. The dietary shift from maternal milk to an adult diet occurs at weaning when neonatal properties are lost and mature ones are acquired. To digest and absorb nutrients, the dietary shift is accompanied by profound modifications of digestive and transport functions.

The neonatal intestine is capable of endocytosing macromolecules from milk, including immunoglobulins.[14–19] The expression of Fc receptors is regulated transcriptionally and is maximal within the proximal duodenum, but declines progressively in the distal bowel.[20] On the other hand, the absorptive cells specialize for macromolecular uptakes, as in the distal small intestine. Those cells are characterized by having the apical endocytic membrane system including the vesicles, early endosomes, late endosomes, multivesicular bodies, lysosomes, and a giant lysomsome.[1,16–19] Similar

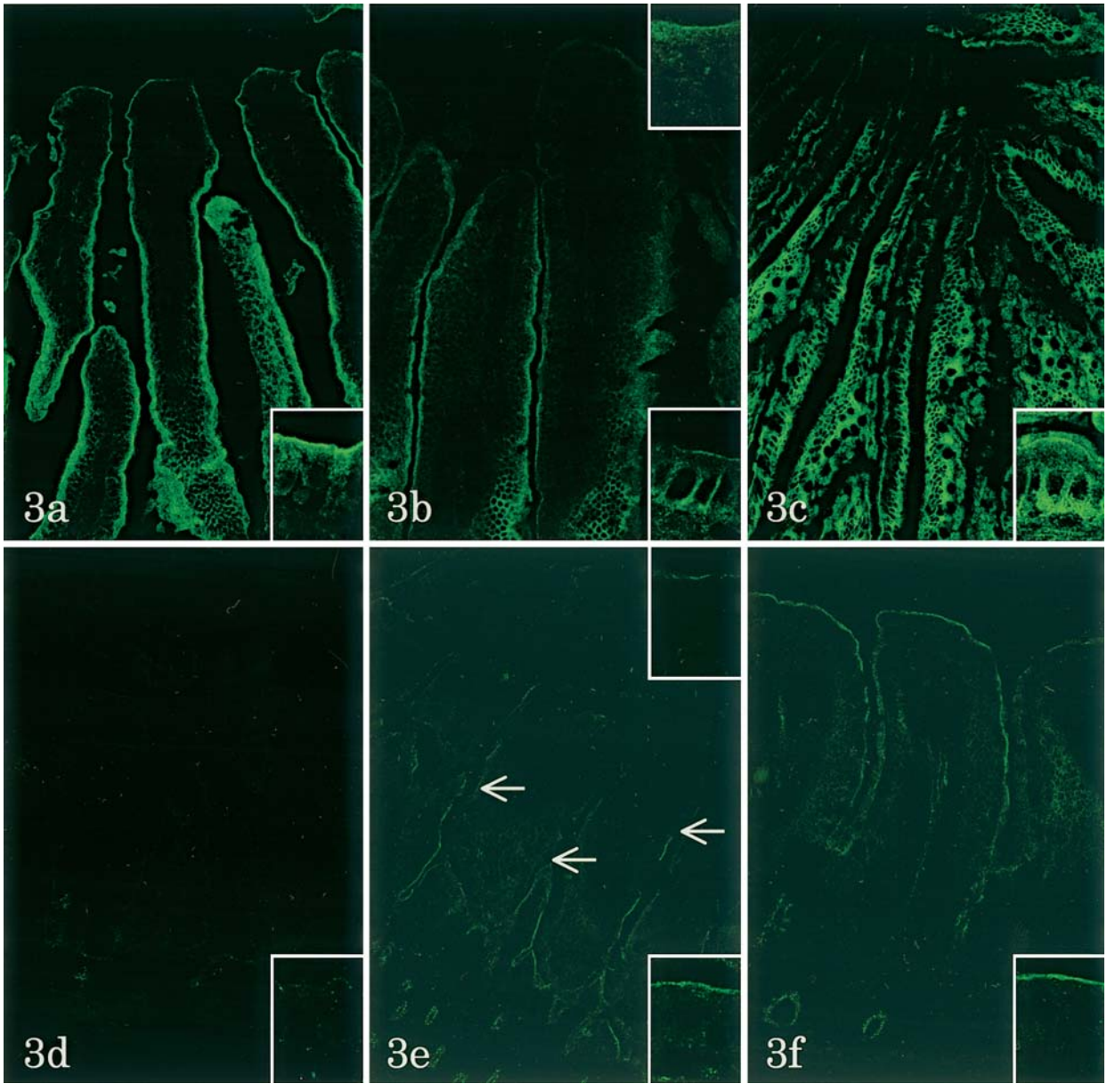

Fig. 3. GLUT5 localization of the rat small intestine: **a** 7-day-old rat jejunum (*inset*, jejunal absorptive cells); **b** 19-day-old rat jejunum (*upper inset*, jejunal absorptive cells from the upper part of the villi; *lower inset*, jejunal absorptive cells from the lower part of the villi); **c** 28-day-old rat jejunum (*inset*, jejunal absorptive cells); **d** 7-day-old rat ileum (*inset*, ileal absorptive cells); **e** 19-day-old rat ileum (*arrows* show the boundary of the localization of GLUT5; *upper inset*, ileal absorptive cells from the upper part of the villi; *lower inset*, ileal absorptive cells from the lower part of the villi); **f** 28-day-old rat ileum (*inset*, ileal absorptive cells)

cells were observed in the neonatal cecum and proximal colon.[21]

The permeability of the intestinal epithelium for macromolecules declines after birth. The transfer is terminated 21 days after birth in both rats and rabbits.[22–24] The developing intestine is able to establish and maintain differences in the differentiation programs of each lineage as a function of their location along the proximo-to-distal and crypt-to-villus gradient.[25,26] We have previously shown that the structure and macromolecular uptake of the small intestinal absorptive cells varies according to their location during postnatal development.[1] In the suckling rats, the absorptive cells of the small intestine had not only functional but also morphological differences along the proximal-to-distal gradient. The difference became more distinct in the upper part of the villi. The morphological difference, however, became unclear after weaning.

There are differences in the distribution of transporters along the crypt-to-villus axis between the immature and adult intestine. In the neonatal intestine, nutrient transport occurs along the whole crypt-to-villus axis, whereas in the adult intestine the absorption of nutrients is shifted to the upper part of the villi.[27] In the present study, the shift was only observed in the ileum with regard to GLUT2. A shift

of GLUT5 was not clearly found, although it is possible that it might take place after 28 days.

Although the absorption of glucose, galactose, and fructose across the apical membrane is mediated by two different proteins, their transport across the basolateral membrane may be mediated by a single protein, the facilitated glucose transporter GLUT2 that decreases during the late suckling period.[28] In the present study, the decrease in GLUT2 was not observed during the late suckling period. The localization of GLUT2, however, was changed in the ileal absorptive cells during the weaning process.

On the other hand, fructose utilizes GLUT5[4,29] for entering within the absorptive cells. Fructose absorption increases in the small intestine during weaning in both the rat and the rabbit.[30,31] Its expression is enhanced during weaning, and it is prematurely induced by dietary fructose.[29,32] With the exception of the perinatal development period, GLUT5 gene expression is regulated by the small intestinal region, circadian rhythm, and the effect of diabetes.[33] In the present study, GLUT5, localized within the apical membrane domain in the jejunal absorptive cells, was observed even in the early suckling period. Rat GLUT5 is able to facilitate the transport of both glucose and fructose.[6] It is suggested that GLUT5 mainly facilitates the transport of glucose in the early suckling period. On the other hand, GLUT5 was not observed in the absorptive cells from the suckling rat ileum. During weaning, absorptive cells with a different localization of GLUT5 appeared at the basal villus in both the jejunum and the ileum. After weaning, these absorptive cells were observed throughout the entire villi.

Recently, it was found that the brush border membrane contained not only GLUT5 but also GLUT2.[34–36] Our present observation that GLUT2 was localized in the absorptive cells from weaning to weaned rat jejunum is consistent with those earlier reports.

In the jejunum, the membrane domain of the absorptive cells that contained the glucose transporter spread during the weaning process. On the other hand, the membrane domain with the glucose transporter of the ileal absorptive cells was reduced during weaning. These results show that the jejunal absorptive cells absorb monosaccharide actively and transport it during the suckling period, and this monosaccharide transport is actually increased after weaning. On the other hand, the ileal absorptive cells absorb monosaccharide and transport it during the suckling period, but this monosaccharide transport is reduced after weaning. This finding suggests that the jejunal absorptive cells absorb monosaccharide to utilize it as energy not only for the cell but also for the whole body, whereas the ileal absorptive cells absorb monosaccharide simply for the cell.

The change in the localization of glucose transporters corresponded with the change in morphology and macromolecular uptake in the jejunal and ileal absorptive cells during postnatal development, especially during the weaning period. It can be assumed that these changes result from the shift from neonatal-suckling to adult absorptive cells during postnatal development. This result would seem to suggest that the developing intestine is able to establish and maintain differences in the differentiation programs not only along the proximal-to-distal and crypt-to-villus gradients but also along the suckling-to-adult gradient.

Conclusion

In this study, we investigated changes in the absorptive system and localization of the glucose transporter, GLUT2, and the fructose transporter, GLUT5, in jejunal and ileal absorptive cells during postnatal development, especially during the weaning process, by electron microscopy, immunohistochemistry, and confocal laser scanning microscopy. The changes in the localization of glucose transporters correspond with a shift from neonatal-suckling to weaning absorptive cells during postnatal development, especially during the weaning period.

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References

1. Baba R, Fujita M, Tein CE, Miyoshi M (2002) Endocytosis by absorptive cells in the middle segment of the suckling rat small intestine. Anat Sci Int 77:117–123
2. Semenza G, Kessier M, Hosang M, Schmidt U (1984) Biochemistry of the Na+, D-glucose cotransporter of the small-intestinal brush-border membrane. The state of the art in 1984. Biochim Biophys Acta 779:343–379
3. Hediger MA, Coady M, Ikeda TS, Wright EM (1987) Expression cloning and cDNA sequencing of the Na^+/glucose co-transporter. Nature (Lond) 330:379–381
4. Davidson NO, Hausman AML, Ifkovits CA, Buse JB, Gould GW, Burant CF, Bell GI (1992) Human intestinal glucose transporter expression and localization of GLUT5. Am J Physiol Cell Physiol 262:C795–C800
5. Matsumoto K, Takao Y, Akazawa S, Yano M, Uotani S, Kawasaki E, Takino H, Yamasaki H, Okuno S, Yamaguchi Y, Nagataki S (1993) Developmental change of facilitative glucose transporter expression in rat embryonal and fetal intestine. Biochem Biophys Res Commun 193:1275–1282
6. Rand EB, Depaoli AM, Davidson NO, Bell GI, Burant CF (1993) Sequence, tissue distribution, and functional characterization of the rat fructose transporter GLUT5. Am J Physiol 264:G1169–G1176
7. Thorens B, Cheng ZQ, Brown D, Lodish HF (1990) Liver glucose transporter: a basolateral protein in hepatocytes and intestine and kidney cells. Am J Physiol 259:C279–C285
8. Massimino SP, McBurney MI, Field CJ, Thompson AB, Keelan M, Hayek MG, Sunvold GD (1998) Fermentable dietary fiber increases GLP-1 secretion and improves glucose homeostasis despite increased intestinal glucose transport capacity in healthy dogs. J Nutr 128:1786–1793
9. Buddington RK, Diamond JM (1989) Ontogenic development of intestinal nutrient transporters. Annu Rev Physiol 51:601–619
10. Thorens B (1996) Glucose transporters in the regulation of intestinal, renal, and liver glucose fluxes. Am J Physiol Gastrointest Liver Physiol 270:G541–G553
11. Lane RH, Dvorak B, McLennan NK, Dvorakova K, Halpern MD, Pham TD, Philips AF (2002) IGF alters jejunal glucose transporter expression and serum glucose levels in immature rats. Am Physiol Regul Integr Comp Physiol 283:R1450–R1460
12. Shu R, David ES, Ferraris RP (1998) Luminal fructose modulates fructose transport and GLUT-5 expression in small intestine of

weaning rats. Am J Physiol 274: (Gastrointest Liver Physiol: 37) G232–G239
13. Jiang L, David ES, Espina N, Ferraris RP (2001) GLUT-5 expression in neonatal rats: crypt-villus location and age-dependent regulation. Am J Physiol Gastrointest Liver Physiol 281:G666–G674
14. Abrahamson DR, Rodewald R (1981) Evidence for the sorting of endocytic vesicle contents during the receptor-mediated transport of IgG across the newborn rat intestine. J Cell Biol 91:270–280
15. Oshikawa T, Baba R, Fujita M (1996) Apical endocytosis of lectins by the absorptive cells of the suckling rat jejunum *in vivo*. Okajimas Folia Anat Jpn 73:229–246
16. Fujita M, Reinhart F, Neutra MR (1990) Convergence of apical and basolateral endocytic pathways at apical late endosomes in absorptive cells of suckling rat ileum *in vivo*. J Cell Sci 97:385–394
17. Gonnella PA, Neutra MR (1984) Membrane-bound and fluid-phase macromolecules enter separate prelysosomal compartments in absorptive cells of suckling rat ileum. J Cell Biol 99:909–917
18. Wilson JM, Whitney JA, Neutra MR (1987) Identification of endosomal antigen specific to absorptive cells of suckling rat ileum. J Cell Biol 105:691–703
19. Hatae T, Fujita M, Okuyama K (1998) Study on the origin of apical tubules in ileal absorptive cells of sucking rats using concanavalin-A as a membrane-bound tracer. Cell Tissue Res 251:511–521
20. Martin MG, Wu SV, Walsh JH (1997) Ontogenetic development and distribution of antibody transport and Fc receptor mRNA expression in rat intestine. Dig Dis Sci 42:1062–1069
21. Baba R, Tanaka R, Fujita M, Miyoshi M (1999) Cellular differentiation of absorptive cells in the neonatal rat colon: and electron microscopic study. Med Electron Microsc 32:105–113
22. Teichberg S, Wapnir RA, Moyse J, Lifshitz F (1992) Development of the neonatal rat small intestinal barrier to nonspecific macromolecular absorption. II. Role of dietary corticosterone. Pediatr Res 32:50–57
23. Weström BR, Svendsen J, Ohlsson BG, Tagesson C, Karlsson BW (1984) Intestinal transmission of macromolecules (BSA and FITC-labeled dextrans) in the neonatal pig. Influence of age of piglet and molecular weight of markers. Biol Neonate 46:20–26
24. Weström BR, Tagesson C, Leandersson P, Folkesson HG, Svendsen J (1989) Decrease in intestinal permeability to polyethylene glycol 1000 during development in the pig. J Dev Physiol 11:83–87
25. Roth KA, Rubin DC, Birkenmeier EH, Gordon JI (1991) Expression of liver fatty acid-binding protein/human growth hormone fusion genes within the enterocytes and enteroendocrine cell populations of fetal transgenic mice. J Biol Chem 266:5949–5954
26. Simon TC, Gordon JI (1995) Intestinal epithelial cell differentiation: new insights from mice, flies and nematodes. Curr Opin Genet Dev 5:577–586
27. Smith MW (1981) Autoradiographic analysis of alanine uptake by newborn pig intestine. Experientia (Basel) 37:868–870
28. Miyamoto K, Hase K, Taketani Y, Minami H, Oka T, Nakabou Y, Hagihara H (1992) Developmental changes in intestinal glucose transporter mRNA levels. Biochem Biophys Res Commun 183:626–631
29. Shu R, David ES, Ferraris (1997) Dietary fructose enhances intestinal fructose transport and GLUT5 expression in weaning rats. Am J Physiol Gastrointest Liver Physiol 272:G446–G453
30. Buddington RK, Diamond JM (1990) Ontogenic development of monosaccharide and amino acid transporters in rabbit intestine. Am J Physiol Gastrointest Liver Physiol 259:G544–G555
31. Toloza EM, Diamond J (1992) Ontogenic development of nutrient transporters in rat intestine. Am J Physiol Gastrointest Liver Physiol 263:G593–G604
32. David ES, Cingari DS, Ferraris RP (1995) Dietary induction of intestinal fructose absorption in weaning rats. Pediatr Res 37:777–782
33. Castelló A, Gumá A, Sevilla L, Furriols M, Testar X, Palacnín M, Zorzano A (1995) Regulation of GLUT5 gene expression in rat intestinal mucosa: regional distribution, circadian rhythm, perinatal development and effect of diabetes. Biochem J 309:271–277
34. Helliwell PA, Richardson M, Affleck J, Kellett GL (2000) Stimulation of fructose transport across the intestinal brush-border membrane by PMA is mediated by GLUT2 and dynamically regulated by protein kinase C. Biochem J 350:149–154
35. Anita AU, Gupta A, Schembri P, Cheeseman CI (2002) Rapid insertion of GLUT2 into the rat jejunal brush-border membrane promoted by glucagons-like peptide 2. Biochem J 367:247–254
36. Affleck JA, Helliwell PA, Kellett GL (2003) Immunocytochemical detection of GLUT2 at the rat intestinal brush-border membrane. J Histochem Cytochem 51:1567–1574