Developmental Aspects of Renal β-Amino Acid Transport. V: Brush Border Membrane Transport in Nursing Animals—Effect of Age and Diet

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ABSTRACT. This study examines the Na^+-dependent accumulation of the β-amino acid, taurine, by brush border membrane vesicles isolated from nursing animals compared to uptake in adult animals. The diets fed to the mothers nursing these pups were altered so as to provide a low sulfur amino acid intake or a high taurine diet as well as conventional sulfur amino acid intake. Taurinuria is greater in nursing animals than in adult controls, but animals of all ages respond to exposure to the low sulfur amino acid intake by conservation of taurine and to the high taurine diet by hyperexcretion of taurine. Taurine uptake at 10 μM by brush border membrane vesicles is influenced by age in all groups and by diet in 14- and 21-day-old animals. A precession of uptake is seen both in terms of initial and peak rate of uptake with the lowest values in 7-day-old animals to the highest in adult. Greater brush border membrane vesicle uptake is found in 14- and 21-day-old rats after exposure to the low sulfur amino acid intake and reduced uptake after the HTD, whereas no dietary influence on uptake was found in 7-day-old rats. Neither the pattern of the time course of uptake nor the uptake values at equilibrium (45 min) are affected by age or diet. Kinetic analyses of concentration dependent uptake show that the maturational process involves a change in the Vmax of initial uptake. Kinetic analysis of the adaptive response reveals an increase in Vmax after low sulfur amino acid intake and a decline after high taurine diet in 14- and 21-day-old pups, but not in 7-day-old pups. Uptakes at high taurine concentrations (5 mM) which are 10-fold higher than the Km are uninfluenced by age or diet. This study indicates that the physiologic taurinuria of immature rats may relate, in part, to a lower rate of uptake at the brush border surface, but that after 1 wk and before 2 wk of age the kidney can adapt to changes in sulfur amino acid intake. (*Pediatr Res* 20:890–894, 1986)

Abbreviations

LTD, low sulfur amino acid diet
NTD, normal sulfur amino acid diet
HTD, high sulfur amino acid diet
BBMV, brush border membrane vesicle
ANOVA, analysis of variance

The renal tubular epithelium is involved in the reabsorption of various ions and nutrients, including amino acids that arise by virtue of filtration across the glomerular basement membrane. A "physiologic" aminoaciduria is evident in the young of all mammalian species. On the surface, aminoaciduria seems inappropriate in view of the need for a young, rapidly growing animal to conserve compounds that are important in growth (1, 2). Our lab has been concerned with those factors that contribute to the development of amino acid transport processes in the maturing animal and we hope to understand more fully whether maturation of the transport process can be accelerated by various physiologic manipulations (3–7). We have used as a transport probe, the β-amino acid, taurine, since one can manipulate the dietary intake of sulfur amino acids which results in a renal adaptive response for taurine (5, 8–13).

Full grown rats fed a limited sulfur amino acid intake reduce their urinary taurine excretion, a finding which is paralleled *in vitro* by augmented uptake of taurine by collagenase-isolated tubules (7) and by isolated brush border membrane vesicles (8, 9). A diet consisting of normal amounts of methionine and 3% taurine causes hyperexcretions of taurine accompanied by diminished uptake of taurine by both tubules and vesicles. This adaptive response at the level of the basolateral (7) and the brush border surface appears to relate to a change in the rate of transport (Vmax) rather than in the affinity of the transport site for taurine (Km) (8, 9, 12). These previous studies indicate that this renal adaptive response functions to conserve taurine during periods of diminished intake and dispose of this compound during periods of dietary surfeit.

Of considerable interest, young rats studied 1 wk postweaning (28 day old) show the same pattern of uptake and transport kinetics in their brush border membranes following ingestion of the same diet, but demonstrate an additional 5-fold greater degree of taurinuria in keeping with their age (5, 6). Although young rats fed a LTD lower the amount of taurine excreted into urine, taurinuria is excessive (5-fold higher) as compared to values in adult animals. On a NTD or HTD, urinary taurine losses are also higher in young animals. Thus, the renal adaptive response to changes in sulfur amino acid intake is found in the brush border membrane, but the urinary excretion pattern is only partially adapted. It is possible that delayed efflux of taurine across the basolateral surface accounts for this excessive taurinuria, since our previous studies have indicated reduced basallateral efflux in immature rats (4, 6, 7).

Although the adaptive response has been shown to partially exist in terms of urinary excretion and to fully exist at the apical surface in 28-day-old rats, little is known about the response in nursing animals at this membrane surface. Herein we describe the influence of the altered amino acid diets fed to the mothers of nursing rats on the renal handling and brush border accumu-

lation of taurine in these nursing rats and their mothers. In addition, we explored the ontogeny of taurine transport by examining the capacity of brush border vesicles from rats to aged 7, 14, and 21 days to accumulate this β-amino acid.

MATERIALS AND METHODS

Animals. Sprague-Dawley rats (King Laboratories, Fitchburg, WI) were used in all studies. Rats were fed one of three diets: LTD, NTD, or HTD prepared as described previously (5, 11, 12). Adult female rats were fed each diet from the point of impregnation (sperm positive vaginal smear). Nursing rats of ages 7, 14, and 21 days were also used. On the day of sacrifice animals were placed in metabolic cages. Animals remained in cages for 3 h at which time the timed urine sample was weighed and frozen. When using younger animals several animals were caged together and their urine pooled.

Urine taurine was measured by a high performance liquid chromatography method after post column derivatization with phenyl-iso-thiocyanate as described elsewhere (14), urine creatinine concentrations were measured by a previously described method (3).

Membrane vesicle preparation. Renal cortex BBMV were isolated by a series of differential centrifugations using a modification of the method of Booth and Kenny (15). Rats were placed under anhydrous ether anesthesia; their kidneys were removed, decapsulated, and placed in cold (4°) saline. Kidneys were pooled from 11–15 animals of age 7 days, seven to nine animals of age 14 days, four to six animals of age 21 days, and one adult animal. Renal cortex was cut free and samples between 1.5 to 6 g wet weight were homogenized in 20 volumes of 0.5 M D-mannitol, 2 mM Tris-HCl (pH 7.4), and 10 mM HEPES (THM buffer) for three times 30 s using a Brinkmann Polytron in an ice bath. Calcium chloride (final concentration 10 mM) was added to aggregate all membranes except the brush border membranes. The mixture was stirred on ice for 15 min. The details of membrane preparation are given elsewhere (8, 9). Freshly prepared membrane vesicles were employed for all uptake studies.

Membrane purity was routinely assessed from the relative enrichment of γ-glutamyltransferase and 5'-nucleotidase, brush border membrane markers using a previously described method (9). Other enzymes routinely examined are ouabain-inhibitable $Na^+ + K^+$-ATPase, malate dehydrogenase, succinyl-cytochrome C reductase, acid phosphatase, and DNA to examine for contamination from basolateral, microsomal, mitochondrial, lysosomal, and nuclear contaminants using assays described previously (9). Protein was determined by the method of Lowry *et al.* (16).

Vesicle uptake studies. The uptake of radiolabeled taurine (^{3}H) was assayed using the millipore filtration techniques of Chesney *et al.* (19). Usually, 200 μg of membrane suspension was preincubated at 25° C for 45 min in a medium containing 389 mM mannitol, 1 mM Mg SO_4, and 10 mM Tris-HEPES (pH 7.4). The incubation solution contained 100 mM NaCl, 1 mM SO_4, 45 mM mannitol, and 10 mM Tris-HEPES (pH 7.4) along with known amounts of cold and radiolabeled taurine. After a known time interval, a 50 μl aliquot was placed on a prewet 0.45 μ Millipore filter (HAWP). The filtered sample was washed thrice with 3.0 ml of iced wash solutions containing 300 mM mannitol,

1 mM Mg SO_4, and 10 mM Tris-HEPES (pH 2.4). Filters were dried overnight in scintillation vials and then dissolved in Aquasol and counted in a liquid scintillation counter. The values for the nonspecific retention of radioactivity were subtracted from values obtained after incubation of membranes with radiolabeled taurine. This nonspecific retention of label was usually less than 1% of counts.

All incubations were performed in triplicate and each experiment was performed four to six times. Uptake values are expressed as pmol/mg protein/unit of time. The data are expressed as the mean ± SE unless noted.

Data comparisons were made using Student's *t* test, ANOVA, and linear regression analysis using the least squares method, using a desk-top computer with established programs (Texas Instruments Users Guide).

Materials. [^{3}H]Taurine (specific activity 23.5 Ci/mM) was purchased from New England Nuclear, Boston, MA. Radiochemical purity was confirmed by comparing the chromatographic pattern on a Perkin Elmer HPLC with authentic reagent grade taurine (Sigma Chemicals, St. Louis, MO) and was found to contain > 98% of the label as taurine. All chemicals used to prepare media were reagent grade.

Acetonitrile was purchased from Pierce Chemicals, Rockford, IL and was further purified by Dowex column chromatography.

RESULTS

Urine excretion. The pattern of urinary taurine excretion is given in Table 1. Urine taurine excretion, expressed as μmol taurine/mg creatinine, in adult female rats fed the NTD was 9.04 ± 1.22 (SE). Pups nursing from mothers fed the LTD show conservation of taurine regardless of the age of the pup and have excretion values similar to their mothers. Pups nursing from mothers fed the NTD show a modest reduction in urine taurine excretion ($p < 0.05$) at age 7 days and hyperexcretion of taurine at ages 14 and 21 days ($p < 0.005$, respectively). Rats nursing from mothers fed the HTD have hypertaurinuria relative to the NTD fed adults; adult rats fed the HTD have significantly more taurine excretion than 7-day-old pups ($p < 0.02$), but not than 14- and 21-day-old animals. These results indicate that the renal adaptive response to altered sulfur amino acid intake by lactating dams is expressed in the offspring suckled by these mothers. In addition, hypertaurinuria is evident in 7-, 14-, and 21-day-old animals nursed from mothers fed the NTD or HTD, and in mothers fed the HTD.

Brush border transport studies. Analysis of brush border membrane preparations from 7-, 14-, and 21-day-old rats showed enrichment of γ-glutamyl transferase and 5'-nucleotidase of 8.1- to 11.6- and 4.8- to 5.9-fold relative to the starting homogenate. The activity of $Na^+ + K^+$-ATPase was 1.8- to 2.3-fold increased, but no enrichment of the other marker enzymes was evident.

At equilibrium (45 min) the accumulation of taurine by membranes from pups of the three ages was inversely related to the osmolarity of the incubation medium when sucrose was used to increase osmolarity. Uptake data were linear between 300 and 1200 mOsmol/liter at each age probably indicating that accumulation of taurine represents intravesicular transport. Extrapolation to infinite osmolarity suggests that binding is on the order

Table 1. *Urine taurine excretion in nursing and adult rats (% of value in adult rats fed NTD)**

Age	LTD	NTD	HTD	LTD vs NTD	NTD vs HTD
7 days ($n = 12$)	6.12 ± 0.47	207.89 ± 8.11	407.63 ± 39.01	<0.001	<0.01
14 day ($n = 12$)	3.45 ± 0.29	195.79 ± 45.32	462.83 ± 51.11	<0.001	<0.02
21 day ($n = 9$)	12.60 ± 3.37	309.00 ± 39.19	473.52 ± 65.30	<0.001	<0.05
Adult	13.05 ± 1.91	100.00 ± 11.2	821.68 ± 144.25	<0.001	<0.001

* Each value represents the mean ± SE of the number of pooled urine samples indicated. For 7 day = 11–15 pups, 14 day = 7–9 pups; 21 day = 4–6 pups; adult = 1 rat.

of 5–7% of uptake at 300 mOsmol and is not influenced by diet (data not shown).

The uptake of 10 μM taurine over time in vesicles from rats exposed to the NTD is shown in Figure 1. Uptake pattern by BBMV is similar at all ages, reaching a peak of the over-shoot between 180 and 360 s, but uptake is the highest in vesicles prepared from adult animals. Uptake by vesicles prepared from 21-day-old rats was significantly lower than in BBMV from adult rats ($p < 0.02$–0.05 by ANOVA) and significantly higher ($p < 0.05$–< 0.02) than in BBMV from 7- and 14-day-old rats at all time intervals examined except at equilibrium (45 min) where no differences were found.

The uptake of taurine relative to the uptake in NTD-fed adult BBMV is shown in Figure 2. No dietary influence on uptake by BBMV prepared from 7-day-old animals was evident; uptake values are highly significantly lower than those found in adult membranes, $p < 0.001$ at all times except equilibrium (Fig. 2A). By contrast, uptake by BBMV from 14-day-old animals shows higher accumulation in LTD-exposed animals ($p < 0.001$ by ANOVA except at 45 min) and lower uptake in HTD-exposed ($p < 0.01$ by ANOVA). The BBMV from 14-day-old uptake LTD-fed pups is actually similar to NTD fed adult values (Fig. 2B). The pattern of accumulation in BBMV from 21-day-old pups was similar to the results in 14-day-old pups (Fig. 2C).

The uptake of taurine at 15 s (initial rate values) for 10 μM taurine is shown in Figure 3. At all ages following 7 days of age accumulation is significantly greater in BBMV from LTD-fed or exposed rats and significantly lower in HTD animals. By contrast, when 15-s uptake values are examined at an external concentration of 5 mM taurine (Fig. 4) no influence of diet or of age is evident. Thus it appears that the influence of diet on initial rate uptake is expressed for uptake at low external taurine concentrations and after 7 days of age, but not in 7-day-old animal vesicles or at high taurine concentrations.

The influence of diet on concentration-dependent taurine uptake, over the range 10 to 250 μM, is shown in Figure 5. At 7 days of age no influence of diet is evident; neither the Km of uptake or the initial Vmax (15 s) is altered by diet (Table 2). By contrast, at 14 and 21 days and in adult animals, the Vmax of uptake is significantly higher in vesicles from LTD-exposed and significantly lower in HTD-exposed rats. No significant effect of diet on the affinity of the transport system for taurine (Km value) is detected by ANOVA at any age. These findings are consistent with the time course data discussed previously.
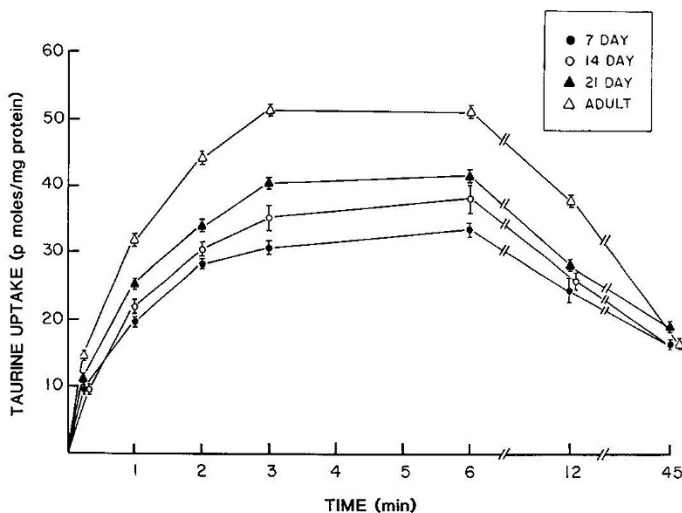

Fig. 1. Time course of taurine uptake by brush border membrane vesicles in 7-, 14-, 21-day-old, and adult rats fed the NTD. Each *point* represents the mean ± SE of four to five experiments performed in triplicate. Uptake is significantly lower in young animals as compared to adult at all time periods between 15 s and 12 min.
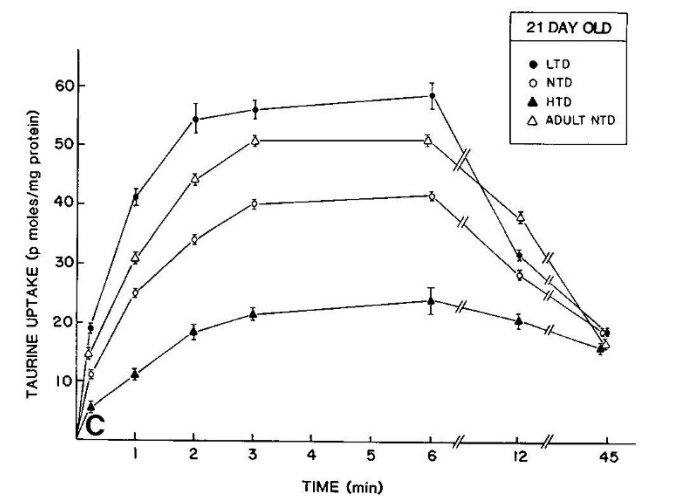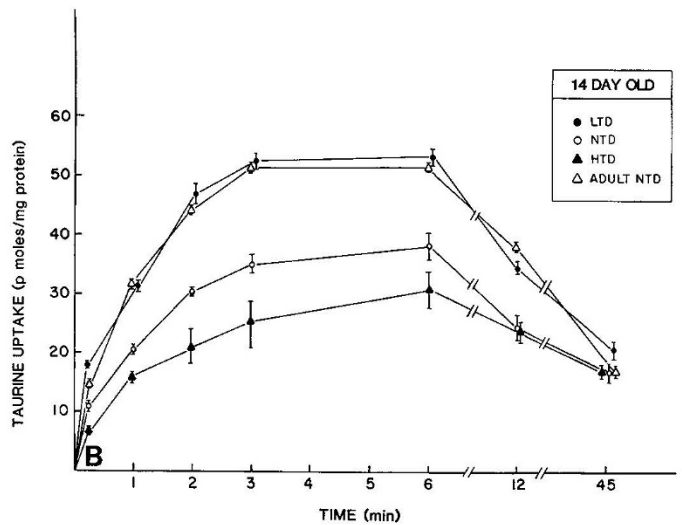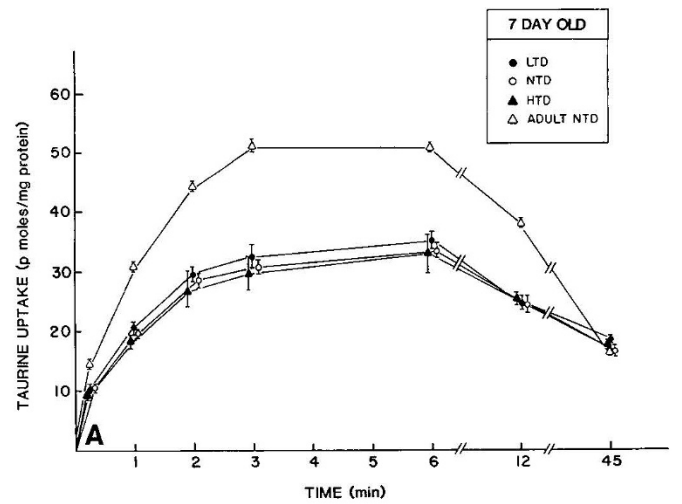

Fig. 2. *A*, uptake of taurine over time by BBMV in 7-day-old animals as influenced by diet. *B*, uptake of taurine over time in 14-day-old animals. *C*, uptake of taurine over time in 21-day-old animals. Each *point* is the mean ± SE of four to five determinations performed in triplicate.

DISCUSSION

The renal adaptive response to altered sulfur amino acid intake involves a change in the initial rate (15–60 s) of taurine uptake by BBMV (5, 6, 9, 10). This adaptive response is expressed for the low Km-high affinity portion of uptake (10–250 μM taurine

concentration range), but not for the high Km-low affinity uptake site (0.5–5.0 mM taurine concentration range) (9, 10). Further, at equilibrium (45 min), taurine accumulation within BBMV is not altered by dietary manipulation (10), indicating that the adaptive response occurs only with the early, Na⁺-gradient-energized portion of taurine accumulation (9, 10) or as an alteration in Na⁺-taurine symport. Accordingly, we have focused our studies in nursing animals on uptake at the low Km site where Na⁺-taurine symport occurs.
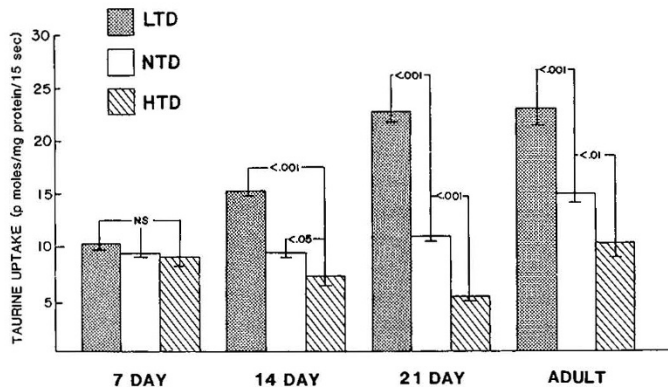

Fig. 3. Initial (15 s) taurine uptake at 10 μM as influenced by age and diet. Each *point* represents the mean ± SE of four to five determinations performed in triplicate.

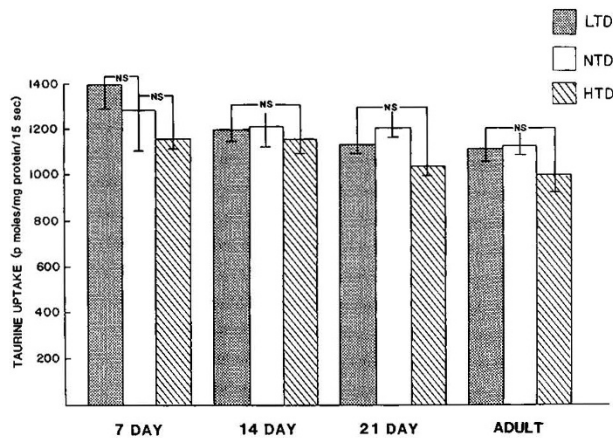Fig. 4. Initial (15 s) taurine uptake at 5.0 μM as influenced by age and diet. Each *point* represents the mean ± SE of five determinations.

This study examines the age-related characteristics of taurine transport into vesicles isolated from nursing rats of three different ages—7, 14, and 21 days—and examines the influence of dietary sulfur amino acid alteration on intravesicular uptake. We have recently shown that breast milk taurine content varies in accordance with the amount of taurine or one of its precursors present in the diet fed the lactating dam (17). Breast milk taurine content in rats ingesting the NTD was 0.21 ± 0.01 μmol/ml defatted milk in contrast to a level of 0.12 ± 0.01 μmol/ml in LTD fed and 1.26 ± 0.06 μmol/ml in HTD fed animals. The level of taurine in milk is not influenced by the length of lactation, being similar in dams nursing 7-, 14-, or 21-day-old pups (17). These results indicate that the dietary exposure of nursing pups to taurine in the milk they are ingesting varies widely and is not dissimilar to the levels found in plasma and urine of older animals (5). Thus, even though these pups are not directly ingesting these special diets, their exposure to varied quantities of taurine in their diet is apparent.

Taurine uptake by vesicles from 7-day-old rats is markedly lower than the values in older animals and no apparent effect of the type of diet on BBMV uptake is evident. These findings suggest that the aminoaciduria of immaturity may, in part, relate to this reduction in uptake. These findings are similar to those found in Segal's group (18) in their examination of proline uptake

Table 2. *Kinetics of taurine accumulation by BBMV from rats of various ages**

Age	Diet	Km†	Vmax‡
7 day	LTD	68 ± 8	87.71 ± 9.88
	NTD	64 ± 7	79.36 ± 8.61
	HTD	62 ± 9	67.56 ± 14.81
14 day	LTD	39 ± 7	86.20 ± 7.13§
	NTD	51 ± 7	67.10 ± 4.93
	HTD	60 ± 8	58.13 ± 5.72
21 day	LTD	35 ± 8	101.11 ± 9.65‖
	NTD	35 ± 6	54.04 ± 3.09
	HTD	55 ± 10	37.31 ± 2.12§
Adult	LTD	38 ± 11	95.83 ± 3.37§
	NTD	42 ± 8	78.12 ± 4.51
	HTD	52 ± 7	66.80 ± 2.11§

* Uptake of taurine over the range 10–250 μM. Each point is the mean ± SE of values of uptake at 15 s determined from four separate experiments performed in triplicate.
† Km in μM.
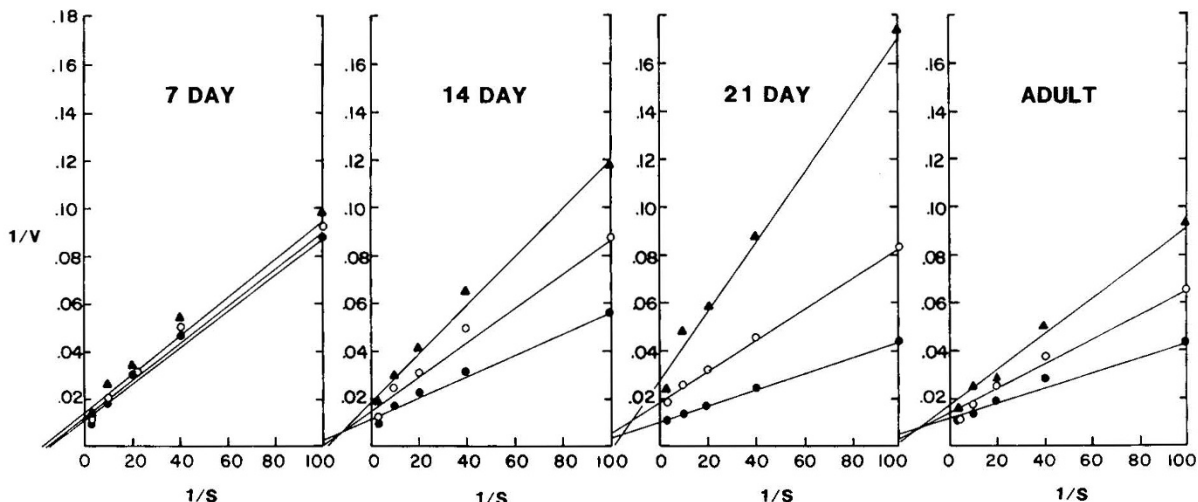‡ Vmax in pmol/mg protein/15 s.
§ $p < 0.05$ from NTD.
‖ $p < 0.02$ from NTD.

Fig. 5. Lineweaver Burk analysis of uptake data (15 s) over the range 10–250 μM by BBMV from animals fed the LTD O, NTD O, or HTD Δ. Each *point* is the mean of four to five determinations performed in triplicate.

in nursing rats (Meadow ME, personal communication). These results further suggest animals of this age may be appropriate for studies to determine the influence of various physiologic manipulations designed to enhance amino acid uptake. From our previous studies it is also clear that taurine efflux out of thin renal cortex slices is impaired at this age (4) and thus the aminoaciduria of immaturity may reflect a combination of reduced uptake at the luminal surface and an efflux block at the antiluminal surface.

Despite diminished BBMV uptake of taurine at 7 days, urinary excretion of taurine is lower in LTD nursed and higher in HTD nursed pups. No reason for this discrepancy between *in vivo* urinary taurine excretion and BBMV uptake is apparent, since the adaptive response to diet is only fully expressed at the luminal membrane surface in slightly older (14- and 21-day-old) nursing rats, in weanling (28 day old) and in adult animals. It is possible that taurine conservation or hyperexcretion is occurring at a nephron site distal to the brush border surface. Alternately the filtered load of taurine, not measured in the present study, may vary sufficiently to change tubular reabsorptions of taurine. Our previous study (17) indicates that plasma taurine values are significantly lower in LTD-nursed animals and thus the filtered load may be reduced. Renal cortex values of taurine are also lower in LTD-nursed pups (17), a finding in keeping with the hypothesis that cortex taurine pool size governs reabsorption and the renal adaptive response (10).

More likely the reduced taurine accumulation by BBMV prepared from 7-day-old animals, the failure to show diet-induced changes, and the discrepancy between *in vivo* and *in vitro* events may relate to changes in Na^+ entry into these membranes. Reduced Na^+-glucose entry into immature rabbit renal vesicles has been shown which relates to greater Na^+ permeability with reduction in the Na^+ gradient reducing initial uptake (20). Developmental studies in Sprague-Dawley rat jejunal BBMV also indicate that the decrease in the initial rate of Na^+-glucose uptake relates to the greater ^{22}Na permeability in membranes from suckling versus adolescent rats (21). This mechanism may also account for diminished L-proline uptake in one week old rats (Meadow ME, personal communication). We have not measured ^{22}Na entry at different ages, but it is possible that more rapid dissipation of a Na^+ gradient could account for the findings in young rats.

The pattern of accumulation found in 14- and 21-day-old rats is similar in shape to that evident in slightly older (28 day) and adult animals with a clear-cut difference in rate of uptake as related to dietary exposure. However, as in 7-day-old rat membranes, the rate of uptake is lower than in adult animals. The finding of intermediate uptake values—between 7 day or 28 day old and adult—indicates that the uptake process is not fully developed by age 14 or 21 days. Thus, a maturational precession for vesicle accumulation of taurine is apparent over the first 4 wk of life. Although uptake at early time points (15 s) and later at the peak of the overshoot (180 to 360 s) is significantly lower in 14- and 21-day-old animals than in the adult, the values at equilibrium (45 min) are similar indicating that vesicle size cannot account for these differences. Equilibrium values are also similar for 7 day animals and at all ages for each diet and hence the dietary adaptation also cannot be accounted for by age-related differences in vesicle size.

In contrast to uptake studies performed at taurine concentrations (10 μM) below the Km of the transport system [which is approximately 45 μM (5, 9)], studies performed at 5 mM taurine showed no influence of age or diet. This concentration of taurine is approximately 10-fold higher than the Km value and is a level of substrate which is predominately transported by a Na^+-independent diffusion process (9).

Kinetic analysis of concentration dependent uptake suggests that the progressive increase in transport into vesicles represents a change in the initial rate of uptake or Vmax. This process of maturation has been observed by us previously in slices (4) and in collagenase isolated tubules (22) as well as by Segal's group (1, 18) (Meadow ME, personal communication) as a major mechanism for the development of transport processes in renal epithelium. Whether this increase in Vmax represents an increase in the number of transport sites or a change in the configuration of the membrane that would permit greater taurine entry is unclear. This taurine transport site can be stimulated in the 14- and 21-day-old animals by exposure (through breast milk) to different diets which "up regulate" or "down regulate" transport sites as in the adult animals (6), but this change is not found in 7-day-old animal membranes. The nature of this adaptive change as well as the maturational increase in Vmax awaits studies directed at isolation, characterization, and quantitation of the transport site.

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