Intestinal apical amino acid absorption during development of the pig

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1Department of Biological Sciences, Mississippi State University, Mississippi State, Mississippi 39762–5759; 2Division of Nutrition, Department of Animal Science and Animal Health, The Royal Veterinary and Agricultural University, DK-1870 Frederiksberg C, Denmark; and 316 Ferram Agullo, Barcelona, Catalonia, Spain

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Buddington, Randal K., Jan Elnif, Anna A. Puchal-Gardiner, and Per T. Sangild. Intestinal apical amino acid absorption during development of the pig. Am J Physiol Regulatory Integrative Comp Physiol 280: R241–R247, 2001.—Amino acids originating from the diet are the principal metabolic fuels for the small intestine, and although the developing intestine is exposed to dramatic changes in the types and amounts of protein, there is little known about rates of amino acid absorption across the apical membrane during development. Therefore, rates of absorption were measured for five amino acids that are substrates for the acidic (aspartate), basic (lysine), neutral (leucine and methionine), and imino (proline) amino acid carriers using intact tissues from the proximal, mid-, and distal small intestines of pigs ranging in age from 90% of gestation to 42 days after birth (12 days after weaning). Rates of absorption (sum of carrier-mediated and apparent diffusion) were highest at birth, and then declined. The contribution of apparent diffusion to amino acid absorption was lowest at birth, then increased after onset of suckling. There were continuing declines for leucine, methionine, and proline but not for aspartate and lysine. Due to rapid growth of the intestine, absorption capacities for all amino acids increased faster than predicted from gains in metabolic mass. Regional differences for rates of absorption were not detected until after birth, and only for aspartate and proline. Maximum rates of saturable absorption (nmol·min⁻¹·mg tissue⁻¹) by the midintestine increased during the last 10% of gestation, were highest at birth, and then declined. The contribution of apparent diffusion to amino acid absorption was lowest at birth, then increased after onset of suckling.

aspartate; leucine; lysine; methionine; proline; transport; uptake; ontogeny; small intestine

INTESTINAL GROWTH AND MATURATION before birth prepare neonates for the abrupt transition from acquiring the majority of nutrients via the placenta and umbilical vein and effectively bypassing the intestine to complete dependence on the intestine for processing and absorbing the components of milk. Corresponding with this, apical transporters for amino acids and sugars can be detected at ~40% of gestation in pigs (2), even earlier in humans (25% of gestation), and much later for altricial rats and mice (80%) (4). The prenatal appearance of transporters also provides a mechanism for absorption of the dilute nutrients present in swallowed amniotic fluid, which are critical for normal growth and maturation of the intestine and fetus (11). For pigs and most mammals, the period between birth and weaning is characterized by rapid growth of the intestine (12, 22), with rates of protein synthesis and deposition exceeding those measured at other stages of development (13). During this period, there are changes in the composition and dynamics of the enterocyte population (16), with concurrent shifts in the functional characteristics of the mucosa including generalized declines in rates of nutrient absorption per unit of intestine (5). Another set of changes in intestinal structure and functions occurs at weaning, as exemplified by the well-known increase in sucrase and decline in lactase (18).

Although amino acids are recognized as essential substrates for intestinal anabolic and catabolic processes (21, 21), particularly for early postnatal growth (17), considerably less is known about ontogenetic development of amino acid absorption compared with monosaccharides (5). Therefore, we sought to characterize age-related changes for absorption of four classes of amino acids using intact tissues from three regions of the small intestine of pigs, which are commonly used as models for humans. The age groups studied spanned three critical phases of intestinal development (late gestation, birth and suckling, and weaning) with different dietary inputs (amniotic fluid, colostrum, milk, and solid food) that vary in composition [respective protein levels of 1%, 15%, 6% (mainly casein and whey), and 21% (mainly from plants)] and thereby place different functional demands on the intestine. The carrier-dependent and apparent diffusion pathways of absorption were defined for the midintestine by examining the relationship between amino acid concentration and rates of absorption. Aspartate, leucine, methionine, lysine, and proline were selected as sub-

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strates for the acidic, neutral, basic, and imino amino acid transporters (6) and as essential and nonessential amino acids. Intestinal dimensions were recorded to gain insights about the relationship between postnatal growth and functional development and to estimate absorption capacities. The results are compared with our previous reports for age-related changes of sugar transport in pigs (2, 12).

**MATERIALS AND METHODS**

All aspects of the research involving animals at the Danish Royal Veterinary and Agricultural University (RVAU) followed the guidelines approved by the Member States of the Council of Europe. Preliminary studies conducted at Mississippi State University (MSU) were approved by the Institutional Animal Care and Use Committee.

**Animals and Their Care**

A total of 40 pigs (Sus scrofa; Large White × Danish Landrace) was obtained from the Research Farm (Sjælland III, Denmark). Fetal pigs (n = 11 from 4 sows) were collected by caesarean section at 102–106 days of gestation (90–92% of term) while the sows were under anesthesia (pentobarbital sodium, 10 mg/kg iv). The remaining 29 pigs were vaginally delivered at term and consisted of five postnatal age groups. These included newborn unsuckled pigs studied within 3 h after birth (n = 6 from 3 litters), 1-day-old pigs (20–26 h after birth and onset of suckling; n = 6 from 3 litters), 7-day-old pigs (n = 6 from 2 litters), 28-day-old pigs (n = 5 from 2 litters), and 42-day-old pigs (n = 6 from 2 litters). During suckling, the pigs had access to water and a solid feed provided ad libitum to the sow that was composed of 75% protein and 5.7% fat that was prepared with barley, wheat, ground barley and 25% fish meal (Roskilde Andel, Denmark). The pigs were isolated from the sow at 32–35 days of age and provided with excess solid feeding diet containing 20.5% protein and 5.7% fat that was prepared with barley, wheat, toasted soybeans, fish meal, and animal fat (Startlett, KFK, Nykøbing, Denmark).

Another 18 crossbred pigs were used for preliminary studies that were conducted at (MSU) to determine an appropriate length of time to incubate tissues for measuring rates of absorption and to establish the regional distribution of amino acid absorption. The preliminary pigs were of three ages (24 h after birth and onset of suckling (n = 6), 10-day-old sucklings (n = 6), and 30 days, which was 9 days after weaning (n = 6), with pigs in each age group originating from at least three litters. Although the MSU pigs were from a herd of mixed and less-defined genetics (various combinations of Duroc, Hampshire, Yorkshire, Landrace), the resulting data were considered to be applicable to the Danish pigs.

**Tissue Collection**

Pigs were euthanatized 0–4 h after removal from the sow (fetal and suckling pigs) or from the weaning crate (weaned pigs) by pentobarbital sodium (200 mg/kg iv at RVAU) or by Beuthanasia (Schering-Plough, 1 ml/4 kg at MSU). Immediately after death, the entire small intestine was removed, the associated mesenteries were severed, and cold (2–4°C) Ringer aerated with a mixture of 95% O2 and 5% CO2 was flushed through the small intestine to remove the contents. Total wet mass was recorded, length was measured in a relaxed state on a horizontal surface, and three segments of 30 cm were placed in cold, aerated Ringer solution. The first segment originated 20 cm distal to the pyloric sphincter, the second was from the midpoint of the intestine, and the third was from 20 cm proximal to the ileocolonic junction.

**Measurements of Intestinal Dimensions**

From each of the three segments a 10-cm section was opened along the mesenteric border, and adherent fluid was removed by carefully blotting the mucosa. The circumference and wet mass were recorded before the mucosa was removed by gentle scraping with a glass slide and dried (50°C, 72 h) to determine the percentage of mucosa. Regional values for wet mass per centimeter, circumference, and percent mucosa were used to calculate regional and total small intestinal wet mass and mucosal mass and nominal surface area (not accounting for surface area amplification due to villi and microvilli).

**Measurements of Amino Acid Absorption**

Rates of amino acid absorption were measured using intact tissues from each of the three regions. The smaller intestines of fetal, neonatal, and 24-h-suckled pigs were everted and mounted as 1-m sleeves on stainless steel rods with diameters that approximated those of the intestinal segments (4 and 5 mm). The larger diameter intestines of older pigs were opened, and patches of tissue were secured by silk ligatures over the ends of 5-mm-diameter rods such that the mucosa was exposed.

Beginning 45 min after death, the tissues were incubated for 3–4 min in 36°C aerated Ringer solution before they were suspended in tubes with 36°C aerated Ringer solution containing one of the amino acids at 50 mM (to insure saturation of carriers) and a stir bar rotating at 1,200 rpm. Absorption was quantified by adding trace levels of 14H-labeled amino acid. Polyethylene glycol (molecular weight 4,000) labeled with 14C was included to correct for amino acid associated with the adherent fluid. The tissues were exposed to the incubation solutions for 2 min based on the preliminary studies at MSU that showed that, for the ages studied, 1 min was long enough to equilibrate the extracellular fluid with the incubation solution and that absorption (nmol/mg) was linear out to at least 2 min. After the incubation, the tissues were gently blotted to absorb adherent fluid, cut from the rods, placed in vials, and wet mass was recorded. The tissues were solubilized (Optisol, Fisher Scientific, Loughborough, UK at RVAU; TS-2, Research Products International, Mount Prospect, IL at MSU), scintillant was added (Optisafe 2, Fisher Scientific at RVUA; 4A20, Research Products International at MSU), and radioactivity was determined by liquid scintillation counting. Calculated rates of amino acid (8) were normalized to wet tissue mass and represent the sum of carrier-mediated influx and an “apparent diffusion” component that does not show saturation kinetics (4).

**Absorption Capacities**

Rates of absorption in each region were multiplied by regional wet mass to estimate the capacities of each region to absorb the amino acids, and these values were summed to estimate the absorption capacities of the entire small intestine.

**Kinetics of Amino Acid Absorption**

The contributions of the carrier-mediated and apparent diffusion components of absorption were determined by exposing tissues to Ringer solution containing tracer amino acid only and in the presence of 0.25, 2.5, 25, and 50 mM unlabeled amino acid. The solutions were made isosmotic by
adjusting the NaCl fraction of the Ringer solution. These studies used midintestine because rates of amino acid absorption in this region of the pig are comparable with or exceed those of the other regions (preliminary study). The data were fit to a model for a single transporter plus a diffusion component (Enzfitter, Biosoft, Elsevier, 1987). It was not possible to improve the fit by using linear equations, by models lacking the diffusion component, or by including more than one transporter into the model. In addition, tracer accumulation ratios were calculated for the absorption of tracer when present alone relative to in the presence of 50 mM unlabeled amino acid. Accumulation ratios significantly >1.0 were considered to indicate that a saturable component of absorption was present. In contrast, values not different from 1.0 indicate that tracer influx is not inhibited by 50 mM amino acid, which could occur if the majority of absorption is independent of carriers or if the affinities of the carriers are sufficiently low that they are not saturated at 50 mM.

**Chemicals**

Unlabeled chemicals were purchased from Sigma Chemical Company (St. Louis, MO) and were of the highest purity available. Radiolabeled tracers (14C-labeled polyethylene glycol and 3H-labeled amino acids) were obtained from New England Nuclear (Boston, MA).

**Statistics and Data Analysis**

Values presented in tables and figures are means ± SE. The main effects of intestinal region and age on the measured dimensions and their interactions were evaluated using the general linear means model procedure of the SAS statistical software package (SAS, Version 7, Cary, NC, 1998). When a significant main effect was detected, differences between ages or regions were identified by Duncan’s multiple-range test. Comparisons were also restricted to specific ages to gain insights about critical phases of development. For example, fetal pigs were compared with newborn, unsuckled pigs to determine whether tracer-accumulation ratios differed patterns of change during suckling and weaning.

The PROC-univariate analysis procedure of SAS was used to determine whether tracer-accumulation ratios differed significantly from a value of 1.0. For all comparisons, P < 0.05 was accepted as the critical level of significance.

**RESULTS**

Pigs were from litters within the normal range (7–13 pigs). All animals were healthy, and postweaning diarrhea was not observed. An examination of stomach and intestinal contents showed that at day 28 the pigs had started to supplement the sow’s milk with solid food. Fluid was present in the stomachs and intestines of the fetal and newborn pigs.

**Body Weights and Intestinal Dimensions**

Newborn pigs averaged 22% heavier than the fetuses. This suggests a growth rate of ~2% per day during the last 10% of gestation. Although birth weights were not recorded, pigs studied at 24 h averaged 24% heavier than the neonates (Table 1).

Small intestinal length increased throughout development, but values normalized to body mass (cm/kg) were similar for fetuses, neonates, and after 24 h of suckling (average of 270 cm/kg) and were lower for older pigs. Surface area expanded during development due to increases in small intestinal length and circumference. Total surface area normalized to body mass (cm²/kg) was 23% higher for neonatal pigs compared with fetuses and increased 70% during the first 24 h of suckling but did not change between then and day 42.

Absolute and weight-specific intestinal mass (g, g/kg) increased throughout development. The percentage of total intestinal mass represented by the mucosa was highest at 24 h (60%), with similar values for the other postnatal ages (average of 50%; P < 0.05 for comparison with 24 h). Total intestinal mucosal mass increased

### Table 1. Body weights and intestinal dimensions of fetal (−11), newborn, and postnatal pigs

<table>
<thead>
<tr>
<th>Age, days</th>
<th>−11</th>
<th>0</th>
<th>1</th>
<th>7</th>
<th>28</th>
<th>42</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of animals</td>
<td>11</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Body mass, kg</td>
<td>1.10 ± 0.08a</td>
<td>1.35 ± 0.15ad</td>
<td>1.68 ± 0.04d</td>
<td>3.02 ± 0.19f</td>
<td>6.70 ± 0.48b</td>
<td>10.25 ± 0.15a</td>
</tr>
<tr>
<td>Length, cm</td>
<td>292 ± 18°</td>
<td>359 ± 32°</td>
<td>464 ± 21°</td>
<td>575 ± 39°</td>
<td>985 ± 47b</td>
<td>1189 ± 18a</td>
</tr>
<tr>
<td>Wet mass, g</td>
<td>21.7 ± 2.5a</td>
<td>45.1 ± 7.3ad</td>
<td>83.7 ± 5.3cd</td>
<td>146.3 ± 9.5c</td>
<td>449.3 ± 36.2b</td>
<td>861.7 ± 74.3a</td>
</tr>
<tr>
<td>Proximal &amp; Middle &amp; Distal &amp; Relative wet mass, g/kg</td>
<td>19.1 ± 1.6a</td>
<td>32.3 ± 2.8ad</td>
<td>49.9 ± 2.8c</td>
<td>48.2 ± 2.0a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Mucosa</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proximal</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Middle</td>
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<td>Distal</td>
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<td></td>
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<tr>
<td>Circumference, mm</td>
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<td></td>
<td></td>
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<tr>
<td>Surface area, cm²</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thickness, mm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Values are means ± SE. Means with different superscript letters indicate difference between ages. Mucosa is calculated as proportion of mucosal dry mass per total intestinal dry mass. Circumference is calculated as the mean intestinal circumference for the proximal, middle, and distal small intestine. The nominal intestinal surface area was calculated as intestinal length multiplied by mean intestinal circumference. Intestinal thickness was calculated as total tissue wet mass divided by nominal surface area, assuming a tissue density of 1 g/cm³. ND, not determined.
during postnatal development and, when normalized to body mass (g/kg), increased more than 80% between birth and 24 h with another significant increase between days 7 and 28.

Wet mass did not differ among the three regions between 90% of gestation and day 7, but the proximal region weighed more than the midregion at day 28 and more than the mid- and distal regions at day 42. The percentage of mucosa was higher in the middle region (58.7%; average for all postnatal ages) compared with the proximal and distal regions (47.7% and 50.7%, respectively). As a consequence, during the first 7 days after birth, mucosal mass in the midregion averaged 31% more than that in the distal intestine \( (P < 0.05) \) and 15% more than the proximal region (difference not significant). The percentage of mucosa at 28 and 42 days remained higher for the midregion (57%) compared with the proximal (45%; \( P < 0.05 \)) and distal (48%; \( P < 0.05 \)), but total mucosal mass did not differ among the three regions.

**Absorption of Amino Acids**

**Effect of age.** Between 90% of gestation and birth, rates of absorption (nmol·mg\(^{-1}\)·min\(^{-1}\)) averaged for the three regions increased for leucine but not for lysine and proline (Fig. 1, left). Rates of absorption declined during the first 24 h after birth by an average of 30% (±3%) for all five amino acids, but at day 7 they had recovered slightly and for proline were actually higher compared with newborns. Rates of absorption between days 7 and 42 remained stable for aspartate and lysine but declined for leucine, methionine, and proline. At all ages, rates of absorption were lower for aspartate compared with the other amino acids.

**Regional distribution of absorption.** Regional differences were not detected in fetuses or newborns for any of the amino acids. A significant effect of region was detected in 24-h and older pigs for aspartate and proline, with values for distal intestine lower than those for proximal and midintestine, which were similar (data not presented). Regional differences were not detected at any age for leucine, methionine, and lysine.

**Absorptive capacities for the entire length of small intestine.** Uptake capacities normalized to body mass (mmol·d\(^{-1}\)·kg\(^{-1}\); Fig. 1, right) increased significantly during the last 10% of gestation for leucine, lysine, and proline but not between birth and day 7, except for proline. Absorptive capacities normalized to body mass increased between days 7 and 42 for aspartate, lysine, and methionine but not for leucine and proline.

**Kinetics of absorption.** A saturable pathway of absorption was present in the midintestine at all six ages for the five amino acids studied. Specifically, accumulation of tracer was inhibited by 50 mM unlabeled amino acid, and accumulation ratios exceeded 1.0, ranging from an average of 2.0 for proline to 13.9 for methionine. Correspondingly, a model equation that included a single transporter and a nonsaturable, apparent diffusion pathway \( (P) \) provide a better fit for rates of amino acid absorption as functions of amino acid concentration than a linear regression or the Michaelis-Menten equation alone. Maximum rates of absorption \( (V_{max}) \) for all five amino acids were highest at birth before onset of suckling, with values higher for proline and lower for aspartate (Table 2).

Affinity constants \( (K_m) \) for weaned pigs were lower compared with those for sucklings. However, the values must be considered as apparent due to the presence of unstirred layers (8) that represent a rate-limiting step for absorption (1) and would be affected by postnatal changes in mucosal mass and architectural complexity (Ref. 22 and present study).

At 90% of gestation, 80–90% of leucine, lysine, and proline absorption by midintestine at 50 mM was by apparent diffusion. At term, carrier-mediated absorption contributed 70–80% of absorption; with the exception of aspartate absorption, which was estimated to be
and postnatal pigs

Table 2. Kinetic constants for absorption of the five amino acids by the midintestine of fetal (−11), newborn, and postnatal pigs

<table>
<thead>
<tr>
<th>Amino Acid</th>
<th>Age, days</th>
<th>0</th>
<th>1</th>
<th>7</th>
<th>28</th>
<th>42</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspartate</td>
<td>$V_{max}$</td>
<td>ND</td>
<td>0.52 ± 0.92</td>
<td>0.35 ± 0.02</td>
<td>0.24 ± 0.07</td>
<td>0.52 ± 0.21</td>
</tr>
<tr>
<td>$V_{max}$</td>
<td>ND</td>
<td>12.1 ± 1.7</td>
<td>19.7 ± 1.4</td>
<td>6.7 ± 3.3</td>
<td>12.8 ± 7.7</td>
<td>5.3 ± 5.1</td>
</tr>
<tr>
<td>$P$</td>
<td>ND</td>
<td>0.012 ± 0.001</td>
<td>0.013 ± 0.001</td>
<td>0.015 ± 0.001</td>
<td>0.013 ± 0.003</td>
<td>0.018 ± 0.001</td>
</tr>
<tr>
<td>Leucine</td>
<td>$V_{max}$</td>
<td>0.59 ± 0.23</td>
<td>2.22 ± 0.38</td>
<td>1.62 ± 0.80</td>
<td>1.95 ± 0.44</td>
<td>1.60 ± 0.62</td>
</tr>
<tr>
<td>$K_m$</td>
<td>0.8 ± 0.9</td>
<td>1.3 ± 0.6</td>
<td>6.9 ± 5.9</td>
<td>2.5 ± 1.3</td>
<td>12.6 ± 7.2</td>
<td>1.9 ± 1.9</td>
</tr>
<tr>
<td>$P$</td>
<td>0.038 ± 0.006</td>
<td>0.020 ± 0.009</td>
<td>0.007 ± 0.013</td>
<td>0.018 ± 0.009</td>
<td>0.004 ± 0.001</td>
<td>0.022 ± 0.007</td>
</tr>
<tr>
<td>Lysine</td>
<td>$V_{max}$</td>
<td>0.23 ± 0.49</td>
<td>2.20 ± 1.70</td>
<td>0.29 ± 0.30</td>
<td>0.98 ± 0.36</td>
<td>0.09 ± 0.001</td>
</tr>
<tr>
<td>$K_m$</td>
<td>4.5 ± 1.9</td>
<td>13.4 ± 6.6</td>
<td>3.3 ± 0.51</td>
<td>8.3 ± 5.0</td>
<td>0.4 ± 0.01</td>
<td>0.66 ± 0.76</td>
</tr>
<tr>
<td>$P$</td>
<td>0.043 ± 0.009</td>
<td>0.013 ± 0.009</td>
<td>0.023 ± 0.001</td>
<td>0.020 ± 0.005</td>
<td>0.022 ± 0.001</td>
<td>0.024 ± 0.006</td>
</tr>
<tr>
<td>Methionine</td>
<td>$V_{max}$</td>
<td>ND</td>
<td>2.68 ± 0.48</td>
<td>0.58 ± 0.34</td>
<td>1.55 ± 0.48</td>
<td>0.93 ± 0.55</td>
</tr>
<tr>
<td>$K_m$</td>
<td>ND</td>
<td>2.7 ± 1.1</td>
<td>1.7 ± 2.5</td>
<td>2.4 ± 1.7</td>
<td>1.4 ± 0.5</td>
<td>0.6 ± 0.1</td>
</tr>
<tr>
<td>$P$</td>
<td>ND</td>
<td>0.012 ± 0.010</td>
<td>0.026 ± 0.007</td>
<td>0.019 ± 0.010</td>
<td>0.017 ± 0.008</td>
<td>0.033 ± 0.005</td>
</tr>
<tr>
<td>Prolin</td>
<td>$V_{max}$</td>
<td>0.41 ± 2.6</td>
<td>4.8 ± 1.2</td>
<td>1.1 ± 2.6</td>
<td>0.83 ± 0.12</td>
<td>0.15 ± 0.03</td>
</tr>
<tr>
<td>$K_m$</td>
<td>15 ± 18</td>
<td>22 ± 8</td>
<td>30 ± 10</td>
<td>8.8 ± 2.2</td>
<td>0.53 ± 0.34</td>
<td>0.4 ± 0.4</td>
</tr>
<tr>
<td>$P$</td>
<td>0.060 ± 0.029</td>
<td>0.001 ± 0.003</td>
<td>0.020 ± 0.028</td>
<td>0.072 ± 0.002</td>
<td>0.048 ± 0.001</td>
<td>0.054 ± 0.001</td>
</tr>
</tbody>
</table>

Values are means ± SE. Maximum rate of absorption ($V_{max}$) values are expressed as mmol·min⁻¹·mg tissue⁻¹. $K_m$ values are given as mM. $P$, passive influx of nutrients calculated as mmol·min⁻¹·mg tissue⁻¹·mM⁻¹.

DISCUSSION

Extraterine survival and growth are, to a large extent, dependent on growth and maturation of the small intestine, with postnatal changes necessary for processing increasing amounts of food that shift in composition. Despite facing similar developmental challenges, comparative studies have shown that, among mammals, there are different patterns of intestinal development. The present study shows that, at 90% of gestation, the intestine of pigs is largely but not completely developed, and although survival ex utero is possible, intensive care is required (15). In comparison, at 90% of term, the human intestine is at an advanced stage of development and rates of extraterine survival are high, whereas altricial species (e.g., laboratory rats and mice) born at the same stage of gestation (day 19 of a 21-day gestation) (4) have an intestine that is underdeveloped and survival can be expected to be very low, regardless of care.

Structural Development

The amount of intestinal tissue is a critical determinant of functional capacities, and during the last 10% of gestation, the intestinal mass increased from 1.9% of total body mass to 3.2% at birth. Although the percentage of intestine represented by mucosa was not measured for the preterm intestine, it is known to increase during the final weeks of gestation (2). The most rapid increases in intestinal dimensions occur during the early postnatal period, particularly the first 6 h of suckling (23). Compared with unsuckled newborns, the intestines of 24-h-old pigs were 29% longer, 86% heavier with 130% more mucosa, and had a 60% greater circumference with 108% more nominal surface areas but were not thicker. Although histological observations were not made, the changes during the first 24 h after birth are consistent with a reduction in the thickness of the tissue layers under the mucosa. It is possible that the circular and longitudinal muscle layers are contracted in utero to minimize the space occupied by the intestine and reduce body volume. Relaxation of the muscle layers after birth would result in a longer intestine with a greater internal diameter and volume, and the rapid increase in the amount of mucosa would provide more tissue for absorption.

Intestinal mass continued to increase rapidly during the period of development studied and represented 6.8% and 8% of body mass at day 28 and 42, respectively. Correspondingly, slopes of double-log plots for intestinal and mucosal mass versus body mass (1.50 ± 0.12 and 1.31 ± 0.12) exceeded the predicted value of 1.0 for nonruminant eutherian mammals ($P < 0.05$) (10). Similarly, slopes of double-log plots for intestinal length (0.60 ± 0.04) and nominal surface area (1.20 ± 0.11) were greater than the predicted values of 0.33 and 0.6 ($P < 0.05$). Sometime after 42 days the rate of intestinal growth declines, and, in adult pigs, intestinal mass represents 2.6% of body mass (13).

Functional Development

Regional distribution of amino acid absorption. The distribution of nutrient absorption and other functions change during development of the pig. One of the more
AMINO ACID ABSORPTION DURING PIG DEVELOPMENT

The absorptive capacities of the mature pig intestine are not in great excess and can be saturated at high dietary intakes (19). Furthermore, the capacities of the pig intestine to absorb a protein hydrolysate are saturated at lower concentrations than those for simple carbohydrates and fats. It is possible that at 90–92% of gestation and before, intestinal absorptive capacities, particularly for amino acids, may represent a bottleneck that limits growth. If so, the rapid increases in intestinal dimensions from 90% of gestation to shortly after weaning may be critical for young pigs to increase their abilities to absorb nutrients. There is a need to determine whether this is true and how relevant these and other findings for the pig are for humans.

The present study examined amino acid absorption, but the majority of dietary amino acids is apparently absorbed as components of peptides (6). Because proteolytic capacities of newborn mammals are less developed than those of adults (7), there is a need to quantify peptide absorption, particularly during early development when it may be of greater importance.

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REFERENCES