The ontogeny of the renal countercurrent system presents a unique problem because changes of thermodynamic parameters (9, 18, 22) occur during the postnatal period while the final arrangement of tubules within the medullary microarchitecture is attained (9, 41, 42). Some of these processes have been measured at the level of the single nephron segment and by tissue slice analysis (9, 11, 16, 21, 46, 53).

However, no attempts have been made to relate, in a quantitative way, geometry and transport processes in the medulla to the changing longitudinal osmotic gradients (9, 21, 58) within the countercurrent system. Specifically, loops of Henle from the outer cortical and midcortical layers appear by elongation in the outer medulla (9, 42, 43, 51) within a short period (rat) while the salt transport capacity of the individual loop segment increases (17, 59). These parameters have been studied, for technical reasons, in different species. The present model analysis, which is based on a differential equation model of the renal countercurrent system (35), incorporates structural changes of the rat kidney and thermodynamic parameters, as measured directly, of rabbit nephron segments. Medullary geometry and transport show the same developmental pattern in both species.

METHODS

Model Parameters

Developmental stages. According to anatomical studies renal development may be subdivided into several phases (9, 41, 43, 51). Phases in the rat kidney (51) are early (days 1–5), intermediate (days 5–10), and late development (days 10–20). The present model study has defined the initial points of each phase as stages I, II, III, and the final point (day 20) as stage IV, corresponding to the base case of a previous model simulation analysis (35).

Morphological Parameters

Medullary zones. The total length of the medulla increases by a factor of 2, from 5 to 10 mm, during development from stage I to IV. The length of the outer medulla (OM) is constant; the inner medulla (IM) increases as shown in Table 1. Within the outer medulla, the outer stripe (OS) and inner stripe (IS) are expressed only in stages III and IV (42, 43, 51).

Medullary Architecture

Distribution and number of medullary tubules. In the final stage, stage IV, short loops all turn in the lower third of the inner stripe (31). Only 30% of all loops of Henle (LH) reach the inner medulla (32), and it was assumed that about one-sixtieth of all loops turn at the tip of the papilla (38).

Figure 1 shows the change with development of the number of loops present at different medullary levels (9, 14, 15, 41, 43, 51, 52). It is apparent that the largest increase (fourfold) in the number of loops within the outer medulla occurs in stages II and III, whereas significant changes within the inner medulla take place up to stage II. From then on, the number of loops at the papillary tip is constant (9, 41, 51). The number of loops of Henle and vasa recta in stages I and II is equal (51); the increase of vasa recta is small up to stage III, whereas the major change occurs during the late phase of medullary development (43). The number of vasa recta at each medullary level in stage IV is higher by about 30% than the number of loops (31).

The collecting ducts do not merge in the outer medulla. Within the inner medulla, however, the number of collecting ducts (NCD) is reduced to 10 terminal ducts after...
TABLE 1. Developmental changes of medullary length

<table>
<thead>
<tr>
<th>Stage</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medulla</td>
<td>5.0</td>
<td>6.5</td>
<td>8.0</td>
<td>10.0</td>
</tr>
<tr>
<td>OM</td>
<td>4.0</td>
<td>4.0</td>
<td>4.0</td>
<td>4.0</td>
</tr>
<tr>
<td>OS</td>
<td>1.5</td>
<td>1.5</td>
<td>1.5</td>
<td>1.5</td>
</tr>
<tr>
<td>IS</td>
<td>2.5</td>
<td>2.5</td>
<td>2.5</td>
<td>2.5</td>
</tr>
<tr>
<td>IM</td>
<td>1.0</td>
<td>2.5</td>
<td>4.0</td>
<td>6.0</td>
</tr>
</tbody>
</table>

Length of medulla and the medullary zones at developmental stages I-IV is in millimeters. Data adapted from Ref. 42.

TABLE 2. Developmental changes of medullary tubule radii

<table>
<thead>
<tr>
<th>Stage</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>DLH</td>
<td>3.60</td>
<td>5.44</td>
<td>6.56</td>
<td>8.0</td>
</tr>
<tr>
<td>ALH</td>
<td>4.50</td>
<td>6.80</td>
<td>8.20</td>
<td>10.0</td>
</tr>
<tr>
<td>DCT</td>
<td>4.50</td>
<td>6.80</td>
<td>8.20</td>
<td>10.0</td>
</tr>
<tr>
<td>CNT*</td>
<td>3.60</td>
<td>5.44</td>
<td>6.56</td>
<td>8.0</td>
</tr>
<tr>
<td>CD</td>
<td>11.0</td>
<td>11.0</td>
<td>11.0</td>
<td>11.0</td>
</tr>
<tr>
<td>DVR</td>
<td>20.0</td>
<td>20.0</td>
<td>20.0</td>
<td>20.0</td>
</tr>
<tr>
<td>AVR</td>
<td>20.0</td>
<td>20.0</td>
<td>20.0</td>
<td>20.0</td>
</tr>
</tbody>
</table>

Tubular and vascular radii (μm) of medullary structures during development (stages I-IV). See METHODS for sources of data. *Values at the end of CNT.

Interstitial Geometry

The interstitial cross-sectional area in stage IV (final), including the cell volume, has been estimated to be 40% of the total tubular luminal cross-sectional area (27a, 38). Figure 2 depicts the quantitative changes of this parameter with medullary development (stages I-IV). The interstitial cross-sectional area within the inner medulla is constant in stages II-IV. In the outer medulla, a part of the interstitium (BZ, Bindegewebsszwikel) (43) decreases in size from stage II to IV while being replaced by tubules entering the interstitium.

Pelvic Geometry

In the final phase, the last 2 mm of the papilla reach into the pelvic fluid. The same geometry pertains to stage III, whereas papillary length in the renal pelvis is somewhat smaller in stage I (1.83 mm) and II (1.90 mm).

Thermodynamic Parameters

In contrast to changes within the medullary microarchitecture, only a few of the pertinent thermodynamic parameters have thus far been studied during medullary development. Therefore, values representing the final stage (Table 3), which were measured directly and discussed in a previous study (35), were incorporated into the present study with two exceptions. First, water conductivity (Lw, ADH) increases with development (Table 4) in the collecting duct (20). Second, active transport of salt in the thick part of the ascending limb of Henle’s loop (TALH), which occurs in the outer but not in the inner medullary segment, is lower at stage I by a factor of 5.8 when compared with the final stage (19). This factorial change was also assumed for the DCT and CNT. Active transport parameters, Vm and Km, are 22 × 10^-6 mmol·cm^-2·s^-1 and 50 mM, respectively, in the final stage. Values of Vm for stages II and III are 16 × 10^-6 and 19 × 10^-6 mmol·cm^-2·s^-1, respectively. The plasma concentrations of salt and urea were assumed to be 140 and 9 mM, respectively. Tubular fluid concentrations in the DLH were 140 mM for salt and 18 mM for urea at the corticomedullary junction. The volume flow rate at the entry into the countercurrent system is 10 nl/min and it is lower during the previous phases of develop-
TABLE 3. Thermodynamic parameters of medullary tubule segments and renal pelvis

<table>
<thead>
<tr>
<th></th>
<th>DLH*</th>
<th>tALH</th>
<th>TALH/DCT</th>
<th>CNT</th>
<th>OMCD</th>
<th>IMCD</th>
<th>Pelvis</th>
</tr>
</thead>
<tbody>
<tr>
<td>$L_p$, nl·cm$^{-2}$·min$^{-1}$·mosM$^{-1}$</td>
<td>247</td>
<td>0</td>
<td>0</td>
<td>lin. trans.*</td>
<td>48.4</td>
<td>7.37</td>
<td>0 (see Ref. 35)</td>
</tr>
<tr>
<td>$P_{\text{min}}$, 10$^{-6}$ cm/s</td>
<td>1.61</td>
<td>25</td>
<td>6.27</td>
<td>6.27</td>
<td>0</td>
<td>0</td>
<td>0 (see Ref. 35)</td>
</tr>
<tr>
<td>$P_{\text{area}}$, 10$^{-5}$ cm/s</td>
<td>1.5</td>
<td>6.7</td>
<td>0</td>
<td>lin. trans.†</td>
<td>0.097</td>
<td>2.4</td>
<td>30 (see Ref. 35)</td>
</tr>
<tr>
<td>$G_{\text{salt}}$, 0.96</td>
<td>0.5</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>$G_{\text{urea}}$, 0.95</td>
<td>0.7</td>
<td>1</td>
<td>0.74</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

Abbreviations are listed in Table 5. Numbers in parentheses indicate references. * Linear transition from DCT to OMCD (consistent with Ref. 30). † Linear transition from 0.0 to 1.0 (consistent with Refs. 7 and 57).

TABLE 4. Developmental changes of $L_p$ in the CT

<table>
<thead>
<tr>
<th></th>
<th>Stage</th>
<th>Stage</th>
<th>Stage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
<td>II</td>
<td>III</td>
</tr>
<tr>
<td>Outer medulla</td>
<td>12.97</td>
<td>32.04</td>
<td>48.4</td>
</tr>
<tr>
<td>Inner medulla</td>
<td>1.92</td>
<td>4.74</td>
<td>7.37</td>
</tr>
</tbody>
</table>

Water conductivity of the collecting tubule, nl·cm$^{-2}$·mosM$^{-1}$·min$^{-1}$.

The model and its description were validated by comparing model predictions with experimental data (35), as well as with other models of the renal countercurrent system (12, 37a, 38, 55, 55a). The model predictions were found to be in good agreement with experimental data, and the model was able to predict the changes in solute and water flows that result from transepithelial mass transport and are based on conservation of salt, urea, and water.

Central Core

As previously suggested (54), the highly permeable vasa recta (VR) can be functionally merged with the interstitium into a single fluid-filled space called the central core. It must be mentioned, therefore, that the model represents the cross-sectional area of the VR, whereas possible determinants such as incomplete osmotic equilibration between ascending and descending VR, or VR flow rates have not been incorporated. The consequences of the central core assumption for the mathematical modeling of the countercurrent system have been described in detail previously (24).

Loop Architecture

The loops of Henle turn at different levels of the renal medulla. This loop anatomy was described in the model by the function $N(x)$ shown in Fig. 1. Because of the large number of nephrons (some 30,000 in the rat kidney), it is not feasible to model each of the loops individ-
Results

Medullary Longitudinal Solute Gradients

Figure 4 shows the computed concentrations of salt and urea in stages I–IV of development along the medullary countercurrent system. Each point on these curves represents the computed “slice” concentration. This value is the mean concentration at a given transversal section, that is, including tubule lumens, vasa recta, and interstitium. The term “slice” concentration and its calculation has been extensively described in a previous report (35). Each curve describes the concentration gradient from the corticomedullary (c-m) boundary to the papillary tip for a given stage.

In stage I, salt concentration at the c-m border was 139.6 mM and it remained almost constant (141.7) at the outer-inner medullary (OM/IM) transition to the papilla (140.7). In stage II, salt at the c-m border was 136.8 mM, 140.7 at OM/IM, and 141.7 at the papilla. In stage III, salt at the c-m border was 129.7 mM and increased greatly to 418.4 at the OM/IM to reach 613.9 at the papilla. In stage IV, the salt concentration changed fur-
tion, similarly, did not change significantly in DLH and ALH during stages I and II. The principal change of the solute gradient occurred between stage II and III and continued up to stage IV. Salt and urea appeared to increase pari passu.

The same general mode of increase was seen for the concentrations in central core (Fig. 6). By contrast, the outer medullary rise of the CD salt concentration in stages III and IV was similar, and a further increase was seen in the inner medulla only during stage IV. The values for salt and urea concentration in pelvic urine are listed in Table 6.

To evaluate the role of active salt transport and of medullary geometry separately, two simulation analyses were performed.

Further from 128.5 mM at the entry level to 608.1 at the OM/IM transition to 900.4 at the papilla.

Urea concentration in stage I was 9.2 mM at the c-m border and remained in this low concentration range at the OM/IM (13.7) and papillary level (15.2). In stage II, urea concentration at the medullary entry level was 9.4 mM, 13.2 at the OM/IM, and a slight change to only 25.0 mM at the tip of the system was calculated. By contrast, urea concentration in stage III started at 14.0 mM at the c-m border and it rose to 104.0 and 240.2 at OM/IM and papilla, respectively. A further increase in the medullary urea gradient occurred in stage IV where the entry concentration was 18.9 mM, the OM/IM urea was 191.9, and urea at the papillary tip was 478.6.

A similar pattern of solute concentration changes was calculated for loop of Henle concentration (Fig. 5). In stages I and II, salt concentration at OM/IM and papillary tip ranged from 140.2 to 154.9 mM, urea concentration, similarly, did not change significantly in DLH and ALH during stages I and II. The principal change of the solute gradient occurred between stage II and III and continued up to stage IV. Salt and urea appeared to increase pari passu.

The same general mode of increase was seen for the concentrations in central core (Fig. 6). By contrast, the outer medullary rise of the CD salt concentration in stages III and IV was similar, and a further increase was seen in the inner medulla only during stage IV. The values for salt and urea concentration in pelvic urine are listed in Table 6.

To evaluate the role of active salt transport and of medullary geometry separately, two simulation analyses were performed.

Further from 128.5 mM at the entry level to 608.1 at the OM/IM transition to 900.4 at the papilla.
Changes of Active Salt Transport Rate

Figure 7 shows the changes of medullary salt and urea gradients in response to a reduction by 13.6% of the active salt transport rate in the TALH and DCT/CNT, reflecting the values of stage III. The major concentration difference for both salt and urea in this circumstance took place in the outer medullary gradient consequent to the localization of the transport change. The reduction in papillary concentrations was similar for salt and urea. Values were 900.4 mM for salt and 478.6 mM for urea with normal salt transport, and 798.3 mM for salt and 387.4 mM for urea in reduced salt transport.

Role of Medullary Geometry

The importance of the changing medullary geometry, that is, the changing localization of loops of Henle within the medulla and the increase in length of the medulla, is apparent from Fig. 8. The paired curves represent stage III with its measured normal salt transport and stage IV with an active salt transport reduced to that of stage III. The differences at the OM/IM transition are 95.1 mM for salt and 46.0 mM for urea; at the papillary tip, these values are 184.4 mM for salt and 147.2 mM for urea. It is of interest that the slope of the concentration profile increases toward the papilla, where the final 2 mm of medullary tissue in stages III and IV are immersed in the pelvic urine and hence reflect the influence of pelvic reflux (35).

TABLE 6. Developmental changes of pelvic solutes

<table>
<thead>
<tr>
<th>Stage</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>134.8</td>
<td>129.2</td>
<td>262.5</td>
<td>380.8</td>
</tr>
<tr>
<td>U</td>
<td>14.7</td>
<td>33.5</td>
<td>372.6</td>
<td>619.7</td>
</tr>
</tbody>
</table>

Salt (C) and urea (U) concentrations (mM) in the renal pelvis.

DISCUSSION

Medullary Solute Gradients in Vivo

Surprisingly few measured data are available on the pattern of longitudinal salt and urea gradients during medullary development (19). In the rabbit, salt concentration in the total outer medulla increases by a factor of about 3 from newborn to adult, while papillary salt and urea concentrations rise by factors of 4–4.5 (11). Comparable data in the rat have not been reported (9, 58). In the dog kidney, papillary salt and urea concentrations increase by a factor of about 3.5 (16). Therefore, the principal in vivo patterns of medullary and papillary solute gradients with ontogeny have been replicated in the present model simulation. In addition, the attainment of urinary osmotic concentration capacity with stage III of this model concurs with in vivo (rat, rabbit) observations (9, 19, 58, 59).

The major change in the computed medullary solute gradients is apparent between stages II and III (Fig. 4). Neither salt nor urea concentrations along the medullary longitudinal axis change significantly up to stage II. It is of interest that salt and urea do not increase equally between stages II and III; while the papillary salt concentration rises by a factor of 4, urea increases about 10-fold. This differential change of the principal solutes can be derived from measurements of urea and total solutes in the rat papilla (9). The rate difference calculated in the present model for salt and urea persists during stages...
III–IV in which salt changes by 47% and urea by 99%. Therefore, the changing contribution of papillary urea to urinary osmotic concentration is more important than that of salt.

This relationship is similar, albeit to a smaller extent, in the outer medulla (OM). The computed salt concentration at the OM/IM border increases by a factor of 2.7 during stages II and III whereas urea changes 7.9-fold. Subsequent concentration changes at the OM/IM transition during stages III and IV are smaller: 1.45-fold for salt and 1.85-fold for urea. In particular, these OM/IM changes are very similar to those of the papillary salt and urea. Therefore, the slopes of salt and urea concentrations along the medulla are similar in stages III and IV. Hence, in this region:

\[ J_n = L_{an} \times \sum_{r=1}^{2} n_r \Phi_{an} \times (C_n - C_0) \]  \hspace{1cm} (A3)

\[ S_n = P_{an} \times (C_n - C_p) + (1 - s_0) \times J_n \times \bar{C}_n + T_q \hspace{1cm} j = 1, 2 \]  \hspace{1cm} (A4)

For the reasons outlined previously (38) it was assumed that in the tubules axial movement of solute is by convection only:

\[ F_i = F_{pi} \times C_0 \hspace{1cm} i = 1, \ldots, 4, j = 1, 2 \]  \hspace{1cm} (A5)

Accordingly, the changing contribution of papillary urea to urinary osmotic concentration provides evidence for the assumption (18, 37, 50) that the increasing salt transport capacity of the thick ascending loop in conjunction with the organization of the microarchitecture, and its consequences for solute delivery, quantitatively account for the changing tissue solute accumulation in the renal medulla.

Evidence for Differential Role of Active Salt Transport and Medullary Geometry

The effect of a reduction in active salt transport in stage IV on medullary salt and urea gradients is illustrated in Fig. 5. There is a decrease in both salt and urea at the OM/IM border that is, already apparent in the inner stripe and persists throughout the inner medulla. Thus, changes in active salt transport of the thick ascending loop do not influence the characteristic but the level of the inner medullary solute gradients.

The role of changing medullary geometry for medullary solute gradients is apparent from Fig. 8. The difference in salt and urea gradients in these circumstances reflects the influence of medullary structural organization on medullary countercurrent function in two developmental stages. The major change appears to be in the inner stripe of the outer medulla for both salt and urea.

In conclusion, this model study on the ontogenetic evolution of urinary osmotic concentration provides evidence for the assumption (18, 37, 50) that the increasing salt transport capacity of the thick ascending loop in conjunction with the organization of the microarchitecture, and its consequences for solute delivery, quantitatively account for the changing tissue solute accumulation in the renal medulla.

APPENDIX

For i = 1, 2, 4 (medullary tubules) and i = 5 (pelvis) the transmural fluxes are given by:

\[ J_n = I_{an} \times \sum_{r=1}^{2} n_r \Phi_{an} \times (C_n - C_0) \]  \hspace{1cm} (A1)

\[ S_n = P_{an} \times (C_n - C_p) + (1 - s_0) \times J_n \times \bar{C}_n + T_q \hspace{1cm} j = 1, 2 \]  \hspace{1cm} (A2)

where \( \bar{C}_n = (C_n + C_0)/2 \).

The active transport, \( T_n \), is assumed to obey Michaelis-Menten kinetics, namely:

\[ T_n = \frac{V_{max} \times C_n}{K_{max} + C_n} \]

During passage through the DCT/CNT, the fluid interacts with the cortical interstitium, where the solute concentrations are assumed to be the same as in arterial plasma. Hence, in this region:

\[ j_n = L_{an} \times \sum_{r=1}^{2} n_r \Phi_{an} \times (C_n - C_0) \]  \hspace{1cm} (A3)

\[ S_n = P_{an} \times (C_n - C_p) + (1 - s_0) \times J_n \times \bar{C}_n + T_q \hspace{1cm} j = 1, 2 \]  \hspace{1cm} (A4)

The differential equations for the composite loop of Henle are (35)

\[ dF_{iw}/dx = -2\pi r_i x J_{iw} \]  \hspace{1cm} (A7)

\[ dF_{ow}/dx = -2\pi r_1 x S_{ow} \]  \hspace{1cm} \( j = 1, 2 \) \hspace{1cm} (A8)

The differential equations for the composite loop of Henle are (35)

\[ dF_{ow}/dx = -2\pi r_1 x S_{ow} \]  \hspace{1cm} \( j = 1, 2 \) \hspace{1cm} (A9)

The differential equations for the composite loop of Henle are (35)

\[ dF_{ow}/dx = -2\pi r_1 x S_{ow} \]  \hspace{1cm} \( j = 1, 2 \) \hspace{1cm} (A10)

The differential equations for the composite loop of Henle are (35)

\[ dF_{ow}/dx = -2\pi r_1 x S_{ow} \]  \hspace{1cm} \( j = 1, 2 \) \hspace{1cm} (A11)

The differential equations for the composite loop of Henle are (35)

\[ dF_{ow}/dx = -2\pi r_1 x S_{ow} \]  \hspace{1cm} \( j = 1, 2 \) \hspace{1cm} (A12)

The composite CD structure is described by

\[ dF_{ow}/dx = -2\pi r_1 x S_{ow} \]  \hspace{1cm} \( j = 1, 2 \) \hspace{1cm} (A13)

The total amount of pelvic urea reflux across the side wall of the papillary CC is determined by:

\[ PRUS = \int_{\theta_1}^{\theta_2} 2\pi r_1(x) x S_{ow}(x) \]  \hspace{1cm} (A15)

and across the cover wall

\[ PRUC = AC(x_{TP}) x P_{32} x [C_{32} - C_{eG}(x_{TP})] \]  \hspace{1cm} (A16)

The differential equations for the composite loop of Henle are (35)

\[ dF_{ow}/dx = \frac{4}{\sum_{i=1}^{4}} dF_{ow}/dx \]  \hspace{1cm} (A17)

\[ dF_{ow}/dx = \frac{4}{\sum_{i=1}^{4}} dF_{ow}/dx \]  \hspace{1cm} (A18)

\[ dF_{ow}/dx = \frac{4}{\sum_{i=1}^{4}} dF_{ow}/dx \]  \hspace{1cm} (A19)

\[ dF_{ow}/dx = \frac{4}{\sum_{i=1}^{4}} dF_{ow}/dx \]  \hspace{1cm} (A20)

\[ dF_{ow}/dx = \frac{4}{\sum_{i=1}^{4}} dF_{ow}/dx \]  \hspace{1cm} (A21)
The boundary conditions for the central core are
\[ C_0(0) = C_{\text{rh}} \quad j = 1, 2 \] (A22)
\[ F_0(x = 0) = 0, \quad F_k(x = 0) = 0, \quad F_k(x = a) = -\text{PRUS} \] (A23)

The boundary conditions for the pelvis result from the requirement of mass balance
\[ (x = x_p) \times C_0 - C_{\text{pr}}(x_p) - \text{PRUS} - \text{PRUS} \] (A24)

The boundary value problem, equations A1–A24, was solved numerically by multiple shooting (5, 56). The code includes a relaxation technique for the damped Newton method (8). The linear equations for the Newton corrections were solved in a direct manner (35a, 39). The initial value problems (56) were solved by a Runge-Kutta-Fehlberg method of seventh order (10) with an automatic control of the integration step sizes according to a prescribed tolerance. These techniques guarantee precise and reliable results, as pointed out for kidney models

(34). An important check is the overall conservation of mass in the entire medulla. In the results of the present study, mass inflow agreed with mass outflow to a relative accuracy of at least 4 \times 10^{-7} for both water and the solutes. The computations were performed on the CDC Cyber 175 (48-bit mantissa) of the Leibniz-Rechenzentrum der Bayerischen Akademie der Wissenschaften.

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