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Water Absorption in the Proximal Tubule: Effect of Bicarbonate, Chloride Gradient, and Organic Solutes (41536)

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Abstract. Simultaneous *in vivo* capillary and luminal microperfusion studies were performed in the superficial proximal convoluted tubule of the rat to determine the effect of intraluminal bicarbonate, the imposition of a transepithelial chloride gradient, and the addition of organic solutes to the luminal perfusion solution on the rates of water absorption (J_v). The capillary perfusion solution contained NaCl, $NaHCO_3$, and KCl. Perfusion of both capillary and lumen with the same solution resulted in a J_v of 3.01 ± 0.24 nl/min/mm. Imposition of a transepithelial chloride gradient (equimolar substitution of NaCl for $NaHCO_3$ in the luminal solution) resulted in a J_v of 3.18 ± 0.21 nl/min/mm (P = NS). Addition of cyanide to both solutions in the presence of a chloride gradient resulted in a significantly lower J_v of 2.21 ± 0.19 nl/min/mm. Luminal substitution of Na cyclamate for $NaHCO_3$ resulted in a solution containing no bicarbonate and no chloride gradient. J_v averaged 0.34 ± 0.08 nl/min/mm. Addition of cyanide to the solution totally inhibited J_v. The addition of D-glucose, L-alanine, or both, to luminal solutions containing bicarbonate or in the presence of a chloride gradient did not significantly affect J_v. Addition of both organic solutes to the NaCl–Na cyclamate luminal solution resulted in a significantly higher J_v of 0.77 ± 0.14 nl/min/mm. These studies indicate that J_v in the rat superficial proximal tubule is influenced by active sodium transport, by the presence of bicarbonate in the lumen, and/or by the imposition of a transepithelial chloride gradient. The organic solutes D-glucose and L-alanine also influence water absorption, but this effect could only be demonstrated under some experimental conditions.

Considerable investigative effort has recently been focused on the role of intraluminal factors in water absorption in the proximal convoluted tubule. Specific interest has centered around the possible effects of substances cotransported with sodium, such as D-glucose and L-alanine, and the role of intraluminal bicarbonate and the chloride gradient, on the rates of water absorption (J_v) in the proximal tubule. It has been concluded, at least by some investigative groups, that passive processes may account for a significant percentage of the total rate of water absorption in some subsegments of the proximal tubule (1–4). As will be reviewed in the Discussion, conflicting data exist as to the possible role of the above factors. The present microperfusion studies were performed in the superficial proximal convoluted tubule of the rat to attempt to define more clearly the effect of organic solutes, bicarbonate, and the chloride gradient on water absorption. Accordingly, peritubular capillary and tubular lumens were simultaneously microperfused with simplified electrolyte solutions of known composition.

Methods. All studies were performed on male Sprague–Dawley rats, anesthetized with sodium pentobarbital (50 mg/kg body wt) injected intraperitoneally, and prepared for micropuncture as previously described (5). During preparation for study, animals received an intravenous infusion of isotonic saline equal to 1% of body weight. An infusion of saline at a rate of 1.2 ml/hr was then continued for the duration of the study.

Peritubular capillaries and their adjacent proximal tubules were microperfused simul-

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TABLE I. COMPOSITION OF PERFUSION SOLUTIONS (m*M*)

	Na^+	HCO_3^-	Cl^-	K^+	D-Glucose	L-Alanine	Cyclamate	Cyanide
Luminal perfusion solutions								
$NaCl/NaHCO_3$	150	25	129	4	—	—	—	—
NaCl	150	—	154	4	—	—	—	—
NaCl/Na cyclamate	150	—	129	4	—	—	25	—
NaCl/Na cyclamate/Na cyanide	150	—	129	4	—	—	25	0.1
NaCl/Na cyanide	150	—	154	4	—	—	—	0.1
$NaCl/NaHCO_3$/D-glucose	150	25	129	4	5.6	—	—	—
NaCl/D-Glucose	150	—	154	4	5.6	—	—	—
$NaCl/NaHCO_3$/L-alanine	150	25	129	4	—	8.0	—	—
NaCl/L-alanine	150	—	154	4	—	8.0	—	—
NaCl/D-glucose/L-alanine	150	—	154	4	5.6	8.0	—	—
NaCl/Na cylamate/D-glucose/L-alanine	150	—	129	4	5.6	8.0	25	—
Capillary perfusion solution	150	25	129	4	(5.6)[a]	(8.0)[a]	—	(0.1)[b]

[a] Glucose and alanine added to the capillary solution in some studies when the luminal perfusion was NaCl/D-glucose/L-alanine or NaCl/Na cyclamate/D-glucose/L-alanine.

[b] Cyanide added to the capillary perfusion solution only when the luminal perfusion solutions contained cyanide.

taneously, as previously described from this laboratory (5). The peritubular capillary perfusion rate was approximately 3 μl/min. The tubular lumens were microperfused between oil blocks with a Hampel microperfusion pump set to deliver fluid at a rate of 18 nl/min. The peritubular capillary perfusion solution contained 125 m*M* NaCl, 25 m*M* $NaHCO_3$, 4 m*M* KCl.[5] The solution was gassed with 95% O_2/5% CO_2 and the pH was adjusted to 7.4. The measured osmolality was 288 mosm/kg H_2O. Where indicated, D-glucose (5.6 m*M*) and L-alanine (8 m*M*) were added. The tubular lumens were microperfused with solutions of varying composition formulated to alter the concentrations of bicarbonate, chloride, and organic solutes (Table I). Where examined, sodium cyclamate was substituted for sodium bicarbonate in equimolar amounts in the luminal perfusion only. Where examined, sodium cyanide (0.1 m*M*) was added to both the capillary and luminal perfusion solutions following the protocol of Green *et al.* (6). [^{3}H]Methoxyinulin (New England Nuclear Corp., Boston, Mass.), 6 μCi/ml, was added to the luminal perfusion solution to permit calculation of the rates of water absorption. At the conclusion of each perfusion, the lumen was filled with latex and the distance between the luminal perfusion and the collection sites determined subsequently by microdissection. Only one set of solutions was examined in any individual animal.

Radioactivity was determined in Biofluor (New England Nuclear Corp.) in a Tri-Carb liquid scintillation counter (Packard Instruments, Downers Grove, Ill.). For each microperfusion, the following calculations were made:

$$\text{Perfusion rate (nl/min)} = \text{collected rate} \times CF/PF,$$

where *CF* and *PF* are the disintegrations per minute per nanoliter in the collected and initial luminal perfusion solutions, respectively.

$$\text{Water absorption (nl/min/mm)} = (1 - PF/CF) \times \text{perfusion rate} \times \text{length}^{-1}.$$

The results are expressed as the mean ± SEM. Statistical analysis was performed using the *t* test for unpaired data.

Results. The results are summarized in Table II. Water absorption averaged 3.01 ± 0.24

[5] No calcium was added to the microperfusion solution. Analysis of the solution by X-ray fluorescence spectrometry, however, indicated that it contained 0.25 m*M* calcium. Although the minimal concentration of calcium necessary to maintain the integrity of the cell is not known with certainty, a value of 0.02 m*M* calcium appears to be sufficient for the colon (28).

TABLE II. WATER ABSORPTION IN THE RAT PROXIMAL TUBULE[a]

Luminal perfusion solution	n	l (mm)	PR (nl/min)	J_v (nl/min/mm)
$NaCl/NaHCO_3$	14	1.6 ± 0.1	17.6 ± 0.5	3.01 ± 0.24
NaCl	20	1.6 ± 0.1	17.4 ± 0.3	3.18 ± 0.21
NaCl/Na cyclamate	19	1.4 ± 0.1	17.7 ± 0.4	0.34 ± 0.08
NaCl/Na cyclamate/Na cyanide	18	1.6 ± 0.1	17.0 ± 0.3	−0.19 ± 0.11
NaCl/Na cyanide	22	1.4 ± 0.1	17.2 ± 0.4	2.21 ± 0.19
$NaCl/NaHCO_3$/D-glucose	15	1.6 ± 0.1	17.8 ± 0.4	3.14 ± 0.24
NaCl/D-glucose	15	1.5 ± 0.2	17.9 ± 0.3	2.97 ± 0.34
$NaCl/NaHCO_3$/L-alanine	8	1.7 ± 0.2	17.4 ± 0.5	2.87 ± 0.25
NaCl/L-alanine	14	1.5 ± 0.1	18.1 ± 0.3	3.18 ± 0.32
NaCl/D-glucose/L-alanine	19	1.7 ± 0.1	17.1 ± 0.3	3.23 ± 0.15
NaCl/D-glucose/L-alanine[b]	11	1.6 ± 0.1	18.2 ± 0.5	2.99 ± 0.16
NaCl/Na cyclamate/D-glucose/L-alanine	19	1.7 ± 0.2	17.3 ± 0.2	0.77 ± 0.14
NaCl/Na cyclamate/D-glucose/L-alanine[b]	10	1.6 ± 0.1	16.3 ± 0.1	0.77 ± 0.11

[a] Values represent mean ± SEM. n, Number of tubules studied. PR, luminal perfusion rate; J_v, water absorption; l, length of tubule.
[b] Results obtained when the capillary perfusion solution also contained D-glucose and L-alanine.

nl/min/mm from a solution containing bicarbonate but no chloride gradient. When chloride was substituted for bicarbonate in the luminal perfusion solution, water absorption was not significantly different and averaged 3.18 ± 0.21 nl/min/mm. To create conditions where no bicarbonate was present initially in the lumen and no transepithelial chloride gradient was imposed, cyclamate was substituted for bicarbonate in the luminal solution. Water absorption under these conditions averaged 0.34 ± 0.08 nl/min/mm, a value significantly lower than when bicarbonate was present or when a chloride gradient was imposed ($P < 0.001$). This value, however, is significantly greater than zero. The addition of cyanide to both the capillary perfusion solution and to the cyclamate-containing luminal perfusion solution resulted in a J_v of −0.19 ± 0.11 nl/min/mm ($P < 0.01$). The addition of cyanide to the capillary and luminal perfusion solutions under conditions whereby a chloride gradient was present resulted in rates of water absorption which averaged 2.21 ± 0.19 nl/min/mm. This value is significantly lower than that obtained from the same solution not containing cyanide ($P < 0.005$).

The possible effect of organic solutes on water absorption was determined by adding D-glucose and L-alanine to the luminal perfusion solution. In the presence or absence of luminal bicarbonate, the addition of D-glucose or L-alanine to the luminal perfusion solution did not significantly affect water absorption as compared to the comparable solutions not containing the organic solutes. The addition of both D-glucose and L-alanine either to the NaCl luminal perfusion solution alone or to both the capillary and NaCl luminal perfusion solutions did not result in any significant change in water absorption. The addition of both glucose and alanine to the luminal perfusion solution containing cyclamate but no bicarbonate resulted in a significantly higher rate of water absorption (0.77 ± 0.14 nl/min/mm) as compared to the cyclamate solution not containing these organic solutes ($P < 0.02$). The addition of the organic solutes to the capillary solution in addition to the luminal solution containing cyclamate had no additional effect.

Discussion. Several prior studies have examined the influence of alterations in the composition of the luminal fluid on the rates of water absorption in the proximal tubule. It has been suggested by at least some investigative groups that the rate of water absorption is influenced by the rate of sodium absorption, mediated by an active transport mechanism for sodium and/or sodium absorption co-transported with organic solutes,

the rate of hydrogen ion secretion and bicarbonate absorption, and the generation of lumen-to-interstitium chloride gradient (1–4, 6–19). Different estimates exist, however, as to the relative importance of these factors in the rates of water absorption (4, 6, 13, 18). It has been reasoned that the secretion of hydrogen ion and the absorption of bicarbonate significantly influence water absorption in the proximal tubule. Bicarbonate has a higher reflection coefficient than does chloride and the addition of bicarbonate to the interstitium would create an effective osmotic gradient for water absorption (20). In addition, the absorption of bicarbonate from the luminal fluid results in an increase in the chloride concentration in the lumen such that, under free-flow conditions, the TF/P chloride concentration ratio exceeds unity by the end of the proximal tubule. Chloride permeability exceeds that of sodium in the superficial nephrons, and it has been proposed that the generation of a chloride gradient creates conditions for passive chloride diffusion out of the lumen, presumably by a paracellular route (4, 6). More recently, however, it has been suggested that chloride might also exit from the lumen by a mechanism linked to an anion exchanger in the brush border of proximal tubule cells (18, 21). This anion exchanger, linked to an independent sodium-for-hydrogen exchanger, could result in neutral sodium chloride absorption. Whatever the mechanism, the generation of a chloride gradient has been estimated to account for between 30 and 70% of the net rate of water absorption in the proximal tubule (4, 7, 18). In the present studies, under circumstances where $NaHCO_3$ and NaCl were exchanged in equimolar amounts, water absorption was not significantly affected. Moreover, despite the higher reflection coefficients for bicarbonate as compared to chloride, the presence of bicarbonate in the capillary solution only did not appear to alter the rates of water absorption. We did not determine the chloride or bicarbonate concentrations in the collected perfusion solutions, but it seems reasonable to suggest that hydrogen ion secretion and the generation or imposition of a chloride concentration gradient are mechanisms of approximately equal magnitude. This conclusion is consistent with that of Bank *et al.* (1).

It is agreed by most investigators that the generation of a chloride concentration gradient (by active secretion of hydrogen ion) influences water absorption by passive chloride diffusion (4, 13, 18). The magnitude of this influence, however, is disputed. Jacobson has reported that water absorption in the superficial rabbit proximal convoluted tubule is essentially zero if the luminal perfusion solution contains no organic solutes and no chloride gradient is imposed across the tubule (2). In the present studies, we substituted sodium cyclamate for sodium bicarbonate, thus yielding a luminal perfusion solution with the same concentration of sodium and chloride as in the capillary perfusion fluid. Under such circumstances, water absorption was significantly lower and was approximately 10% of control values. In a somewhat analogous but not identical study, Green *et al.* found that water absorption from a similar cyclamate-containing solution was reduced to approximately 25% of control values (6). The mechanism subserving the residual water absorption from the cyclamate-containing solution is not known, but we reasoned that it could represent the component of water absorption due to sodium absorption. Cyanide has been demonstrated to inhibit the active transport of sodium (12). When cyanide was added to both the capillary and luminal perfusion solutions, the latter containing cyclamate, water absorption was reduced to zero.

These studies, then, provide confirmatory evidence that water absorption in the superficial proximal convoluted tubule of the rat is mediated by active sodium absorption and by bicarbonate absorption with the subsequent generation of a transepithelial chloride gradient. The importance of the chloride gradient is further supported by the finding that the addition of cyanide to both perfusion solutions under conditions where the chloride gradient was present reduced water absorption by approximately 30%. Thus, water absorption derived in large measure from the chloride gradient and the contribution of active sodium transport could account for only 10–30% of the net rate of water absorption. It is important to note, however, that these conclusions must be considered in light of the experimental conditions. The question as to the contribution of active sodium transport is

a relative one. Whereas Green and Giebisch, Green *et al.*, and Bank *et al.* concluded that active sodium transport significantly affected water transport, our results would suggest a lesser role (1, 6, 13). In the studies of Green and Giebisch and of Bank *et al.*, the peritubular capillaries contained protein. It is conceivable that protein is required in the capillaries for active transport or that protein indirectly affects local sodium gradients across the basolateral surface of the renal tubular cells. Moreover, in the studies described above, the composition of the luminal perfusion solution was different from that in our studies, possibly accounting for the differences in the estimates of active versus passive transport.

In addition to the role of bicarbonate and chloride, considerable recent interest has centered around the possible role of organic solutes on water absorption. D-Glucose and L-alanine are reabsorbed in the proximal tubule of the rat, a process which is mediated by a sodium-dependent carrier located in the brush border (22–25). It has also been confirmed that the presence of these organic solutes is responsible for a lumen-negative electrical potential difference (7, 17). The relationship between potential difference and water and sodium absorption, however, is not clear (26). Moreover, the relationship between the presence or absence of these substances on water absorption in the proximal tubule is uncertain at the present time (8, 9, 11, 13, 14, 16, 19, 22, 27). In a prior study in the rat we reported that elimination of glucose from the luminal perfusion solution resulted in a 25% decrease in water absorption (19). Imai *et al.* reported that, in the rabbit proximal tubule, the selective omission of glucose from the luminal perfusion solution resulted in a significant decrease in sodium flux and a decrease (albeit not significant) in water absorption (14). Burg *et al.* also suggested that the elimination of glucose from both the bath and luminal solutions of the isolated rabbit proximal tubule was associated with a decrease in water absorption (9). However, studies in the rat superficial proximal tubule by Bank *et al.*, Green and Giebisch, and Bishop *et al.*, and in the rabbit tubule by Dennis *et al.*, have not supported the results of previously cited studies (1, 8, 11, 13). As noted earlier, in the studies of Imai *et al.*, the change in water absorption when glucose was omitted from the luminal perfusion solution did not reach statistical significance (14). Moreover, alanine was still present in the lumen and glucose was present in the bath in these studies. In the experiments of Burg *et al.*, elimination of glucose from the lumen alone resulted in only a small decrease in water absorption (9). Significant changes in water absorption were observed only when glucose was omitted from both the bathing and luminal perfusion solutions. In the present studies, we were unable to demonstrate an effect when glucose was present in the lumen only, either in the presence or absence of an initial chloride gradient.

As is the case for glucose, the role of L-alanine is uncertain. In the studies of Imai *et al.*, elimination of both alanine and glucose resulted in a significant decrease in sodium flux and the rate of water absorption (14). The relative contribution of alanine to the decreased fluxes appeared to be greater than that of glucose. In the studies of Burg *et al.*, elimination of alanine was associated with a significant decrease in water absorption (9). Both of the above studies were performed in the rabbit proximal tubule. We are unaware of specific studies on the role of alanine in water absorption in the rat. The results of the present studies do not provide evidence that the presence of alanine alone in the luminal perfusion solution is an important determinant of water absorption.

When both glucose and alanine were added together to a high-chloride luminal perfusion solution, water absorption was not significantly different than that obtained when the solution contained no organic solutes. In all the studies where an organic solute was added to the luminal perfusion solution only, a lumen to capillary osmotic gradient was imposed. The presence of such an osmole gradient would tend to retard water absorption. It is possible, then, that the demonstration of any enhancing effect of glucose and/or alanine would be minimized by the osmole gradient imposed across the tubule. This does not appear to be the case, however, since similar results were obtained when glucose and alanine were added to both perfusion solutions. It is possible that an effect of the organic solutes would not be discernible under conditions where either bicarbonate absorption

or passive chloride absorption are the major factors affecting water absorption. We reasoned that an effect of the organic solutes might be more evident under conditions where water absorption was low, no chloride gradient was present, and the luminal solution did not contain bicarbonate. The addition of D-glucose and L-alanine to the NaCl–Na cyclamate solution resulted in a significantly higher rate of water absorption than that obtained from the same solutions not containing the organic solutes. Thus, the present results, in conjunction with the prior studies cited earlier, suggest that in the superficial proximal tubule of the rat, an effect of organic solutes on water absorption probably does exist.

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