

Absorption of inorganic ions and volatile fatty acids in the rabbit caecum

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1. Rabbit caecal segments in situ were used to measure absorption rates of volatile fatty acids (VFA) and inorganic ions from a saline solution comparable in composition to normal caecal fluid.
2. Results confirm the importance of VFA absorption from caecal material found by other workers.
3. Like the mammalian colon, the rabbit caecum conserved large amounts of sodium, chloride and water. Bicarbonate was also absorbed.
4. VFA replacement studies showed that net water absorption was reduced, net electrolyte absorption was hardly influenced.
5. Na replacement completely inhibited net water absorption and decreased net VFA and Cl absorption, HCO_3 was heavily secreted.
6. These findings indicate that VFA absorption in the rabbit caecum is partly dependent on Na absorption and that in the absence of Na an anion-exchange mechanism occurs.

One of the most important functions of the mammalian large intestine is the conservation of electrolytes and water from intestinal contents (Edmonds, 1967; Turnberg, 1970; Giller & Phillips, 1972; Binder & Rawlins, 1973; Frizzell, Koch & Schultz, 1976). Moreover, the large intestine is the site of microbial breakdown of cellulose-containing foodstuffs (Jühr & Haas, 1976). This aspect is especially important for non-ruminant herbivores. The rabbit, for example, obtains up to 30% of its maintenance energy requirement from volatile fatty acids (VFA), which are produced by fermentation of carbohydrates in the caecum (McBee, 1970; Parker, 1976) and which are already absorbed to a great extent through the caecal wall (Henning & Hird, 1972*b*; Parker, 1976). Other mammalian species, however, also show high concentrations of organic anions in colon and faecal contents (Rubinstein, Howard & Wrong, 1969). In the goat colon, it seems well established that VFA influence net sodium and water absorption (Argenzio, Miller & von Engelhardt, 1975). Until now, there have been no investigations concerning ion fluxes in vivo in rabbit caecum nor studies of VFA absorption in absence of caecal micro-organisms. The aim of the present study was primarily to analyse net movements of electrolytes and VFA from a saline solution in isolated segments of rabbit caecum in situ and, in addition, to give indications for possible relationships between inorganic ion and VFA absorption by means of ion-replacement experiments.

EXPERIMENTAL

Operative preparation of animals

Male cross-bred rabbits weighing 3.0 ± 0.2 kg were used for the experiments. Food (Altromin® K; Altromin, Soest) was withheld for 24 h before commencement of the experiments, but water was available *ad lib*. The animals were anaesthetized with pentobarbital sodium (20 mg/kg in 2 ml saline (9 g NaCl/l) intravenously). Throughout the experiments they were placed on heated operating tables. The abdomen was opened along the linea alba and a caecal segment was prepared by closing the caecum with intestinal forceps applied

Table 1. *Composition (mmol/l) of saline solutions A, B and C in the control samples at the beginning of the 60 min incubation periods*

(Mean values and standard deviations, no. of experiments in parentheses)

	Solution A (20)		Solution B (24)		Solution C (24)	
	Mean	SD	Mean	SD	Mean	SD
Sodium	131.4	17.0	147.0	5.8	5.7	3.6
Potassium	19.3	2.4	16.7	2.8	63.4	10.2
Calcium	1.0	0.3	0.5	0.2	0.5	0.4
Magnesium	12.4	2.3	11.6	1.4	9.7	2.2
Chloride	74.2	10.4	119.8	8.6	80.8	7.8
Bicarbonate	8.7	2.1	21.4	3.1	18.9	2.9
Phosphate	22.6	1.9	17.5	1.8	18.0	1.9
Acetate	38.8	1.9	—	—	36.9	2.4
Propionate	8.8	0.5	—	—	8.8	0.6
Butyrate	13.2	0.9	—	—	13.4	0.9
Osmolality (mosmol/kg)	309	9	320*	8	316†	8
pH	6.61	0.09	7.07	0.08	6.99	0.13

* Adjusted with mannitol.

† Adjusted with choline chloride.

between the 10th and 11th and the 17th and 18th spiral folds. A silicone injection tube (internal diameter 2.5 mm) was inserted into the proximal end of the caecal segment and an irrigation tube (internal diameter 4.5 mm, Nelaton catheter; Braun, Melsungen) was inserted into the distal end. The bowel contents were washed out with saline (9 g NaCl/l) warmed to 38°. Experiments with Na-free solution were preceded by additional irrigation of the bowel with isotonic choline chloride solution. When the bowel had been cleaned, the irrigation tube was removed and the resulting opening was closed by moving the distal intestinal forceps. Care was taken to ensure that larger blood vessels were not damaged.

Experimental procedure

The test solution was heated to 38° and 20 ml were introduced into the caecum through the injection tube. This volume was seen to distend the caecal segment to an extent found under normal physiological conditions. After thorough mixing of the residue of the irrigation fluid with the test solution, a control sample of 5 ml was withdrawn. The bowel was then replaced in the abdomen and the abdominal wall was closed. When the incubation period had been completed, all the fluid was withdrawn anaerobically.

The first series of experiments was undertaken to determine the time course of concentration of the VFA and inorganic ions. Because of the small initial volume and the rapid absorption of water from the caecum it proved impossible to withdraw successive samples sufficient for all analyses during one prolonged period, without influencing the absorption conditions. Therefore, separate periods of 10, 20, 30, 40, 50 and 60 min were chosen. For each saline solution these periods were distributed at random among twelve rabbits, so that the total duration of the tests in each animal was no more than 150 min.

In a second series of experiments, the absorption rates during a 60 min period were studied in more detail. Again, ten to twelve rabbits were used for each saline solution, with two consecutive 60 min test periods for each animal.

Test solutions

Three different saline solutions were used (Table 1). The composition of solution A largely corresponded to that of normal caecal fluid (Leng & Hörnicke, 1975), except for a noticeable difference in calcium content (1 mmol/l instead of 20 mmol/l) and chloride content (70–120 mmol/l instead of 15 mmol/l). Cl was used to replace unknown anions (probably acid mucopolysaccharides) in the normal caecal fluid. The pH was adjusted to 6.6–7.0 with sodium hydroxide (solutions A and B) or potassium hydroxide (solution C). This resulted in the precipitation of most of the calcium chloride of the electrolyte solution as calcium phosphate. Osmolality in solution B (VFA-free) was adjusted with mannitol, in solution C (Na-free) with choline. All three solutions were slightly hypertonic to correspond to normal caecal fluid. A non-absorbable marker substance, polyethylene glycol (PEG) 2 g/l and [^{14}C]PEG 20 $\mu\text{Ci/l}$ (molecular weight 4000; New England Nuclear, Dreieichenhain, Frankfurt) were added to each saline solution.

Analyses

The samples were centrifuged under liquid paraffin for 2 min (Eppendorf-Zentrifuge 3200; Eppendorf, Hamburg) and their pH and pCO_2 values were measured in a blood-gas analyser (Corning-EEL Model 165; IMA, Neuss). Chloride content was determined coulometrically (Chlor-o-counter; Marius, Utrecht) and phosphate and magnesium contents photometrically (Merckotest 3331; Merck, Darmstadt and Roche-Diagnostica 1019; Hoffman-La Roche, Basle, Switzerland). The analysis of Na, K and Ca was carried out by flame photometry (Eppendorf-Photometer; Eppendorf, Hamburg). Osmolality was measured cryoscopically (Osmometer; Knauer, Berlin). VFA content was determined by gas-liquid chromatography (Model 5750 G; Hewlett-Packard, Frankfurt) after acidification of a 1 ml sample with 0.1 ml concentrated formic acid. Injection volume was 1 μl , injector temperature 220°, column temperature 118°, detector temperature 230°, carrier gas was nitrogen. The glass column (length 1.5 m, diameter 2.7 mm) was packed with 20% neopentylglycolsuccinate (NPGS) containing 2% phosphoric acid on 60/80 mesh firebrick. Peak areas were determined by an electronic integrator (Model 3370 G; Hewlett-Packard, Frankfurt). Standards with known VFA concentrations and blanks (aqua bidest) both acidified with formic acid were analysed in the same way and used to calculate the absolute VFA concentrations of the samples. The [^{14}C]PEG activity was measured in a sample of 100 μl + 10 ml Instagel (Packard Instruments) in a liquid-scintillation counter (Tri-Carb 3380; Packard, Frankfurt). All analyses were performed at least in duplicate. The area of the incubated caecal segment was measured by planimetry after the experiment. Finally, the dry weight of the segment was determined by drying to constant weight at 80°.

Calculations

The volume of liquid injected at the beginning of each experiment was corrected by means of [^{14}C]PEG dilution in the control sample to include the residue of the irrigation liquid in the bowel. The formulas used in calculating net water and electrolyte transport were:

$$\begin{aligned} \text{net water transport (ml)} &= V_o - V_o \text{PEG}_o / \text{PEG}_i, \\ \text{net solute transport } (\mu\text{mol}) &= c_o V_o - c_i V_o \text{PEG}_o / \text{PEG}_i, \end{aligned}$$

where V_o is the volume of fluid in bowel at start of the experiment (ml), PEG_o and PEG_i are the PEG concentrations in terms of specific radioactivity (counts/min) at the beginning and at the end of experiment and c_o and c_i are the solute concentrations ($\mu\text{mol/ml}$) at the start and at the end of experiment. To facilitate comparison of the transport rates of

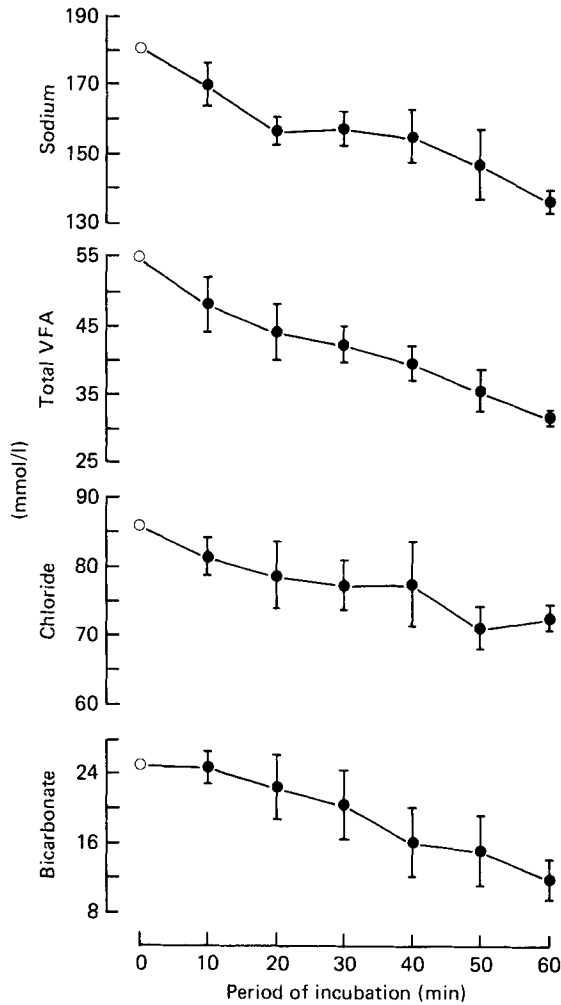


Fig. 1. Relation between incubation period (min) and concentration (mmol/l) of electrolytes and volatile fatty acids (VFA) in rabbit caecum incubated in vivo with saline solution A (for details, see Table 1).

different electrolytes irrespective of their concentrations, clearance values were calculated in addition:

$$\text{clearance (ml/h)} = \text{net transport rate}/c_m h,$$

where c_m is the algebraic mean of solute concentrations at the start and at the end of the 60 min incubation period.

All net transport values were calculated in terms of 1 g dried bowel substance. The mean dry weight of incubated caecal segments was 1.38 ± 0.38 g; the mean serosal area was 5000 ± 1300 mm² ($n35$). The net flux rates over 60 min for solutions B and C were compared with the corresponding flux rates for solution A using the Student's t test and the U test of Wilcoxon, Mann & Whitney. Mean values and standard deviations are given.

Table 2. Net flux/h per g dry weight of caecal segment of water, electrolytes and volatile fatty acids from saline solutions A, B and C† in rabbit caecum in vivo

(Mean values and standard deviations, no. of experiments in parentheses. Positive values represent absorption, negative values secretion)

	Solution A		Solution B		Solution C	
	Mean	SD	Mean	SD	Mean	SD
Water (ml)	5.0	1.6 (20)	3.9	1.8 (24)*	0.1	1.1 (23)***
Sodium (μmol)	902.0	313.0 (19)	1025.0	334.0 (24)	-42.4	51.8 (20)***
Potassium (μmol)	17.0	53.1 (19)	2.6	34.8 (24)	158.0	186.0 (22)**
Calcium (μmol)	6.0	4.7 (15)	2.6	3.0 (24)**	1.6	4.0 (22)**
Magnesium (μmol)	38.3	32.7 (20)	20.3	22.3 (24)*	19.9	23.4 (23)*
Chloride (μmol)	433.0	207.2 (19)	789.3	278.0 (24)***	322.0	202.0 (22)
Bicarbonate (μmol)	61.2	38.3 (20)	179.6	84.0 (24)***	-358.0	117.0 (23)***
Phosphate (μmol)	65.1	54.6 (20)	15.1	36.9 (24)***	5.0	41.6 (23)***
Acetate (μmol)	249.3	59.3 (17)	—	—	151.0	51.0 (22)***
Propionate (μmol)	75.0	14.9 (17)	—	—	51.9	12.5 (22)***
Butyrate (μmol)	124.0	25.6 (17)	—	—	107.0	19.0 (22)***

Values were statistically significantly different from those for solution A: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† For details, see Table 1.

RESULTS

Time-course of concentrations

In the first series of experiments, an approximately linear relationship between time period and end concentration for each period was found for Na, Cl, HCO_3 and VFA, in all three saline solutions within a period of 60 min. As for the other electrolytes, variations of concentration were small and did not behave uniformly. The same is valid for Na in solution C. The time-course of the main electrolytes and the VFA in solution A is shown in Fig. 1. Na and HCO_3 concentrations of solution A used in these experiments were higher than indicated for solution A used in the 60 min incubation periods (see Table 1). This was probably due to different batches of chemicals and to a more careful addition of NaHCO_3 to the experimental solution. If HCO_3 was added to the saline solution before adjustment of the pH, a considerable loss of CO_2 occurred.

However, as a similar slope between initial and end concentration of Na in solution A as recorded from the 60 min incubation periods could be established, it can be assumed that the time-dependent decrease of Na concentration shown in Fig. 1 is valid at least for a range of 180–90 mmol/l. For HCO_3 , a non-linear decrease in the concentration range of 10–3 mmol/l within 60 min cannot be excluded.

Net flux of electrolytes and VFA

In the second series of experiments, net fluxes of water, electrolytes and VFA were measured using an incubation period of 60 min. Results are shown in Table 2 and Fig. 2. In the Na- and VFA-containing solution A, the VFA were heavily absorbed (65–95%). Net absorption of water, Na, Cl and HCO_3 amounted to 50–60% and net absorption of Mg and PO_4 to 25–30%. Net Ca flux was also directed serosally, but in relation to its initially low concentration and the great variations, the absorption rate of $49 \pm 28\%$ was of no importance. Movements of K were not observed to have any definite direction.

VFA clearance increased threefold with increase in chain-length. Na clearance corresponded approximately to the acetate and Cl clearance, while the clearance of HCO_3 exceeded that of Cl and acetate. K, Mg and PO_4 clearances were low. Ca clearance amounted to 7.1 ± 8.0 ml/h.

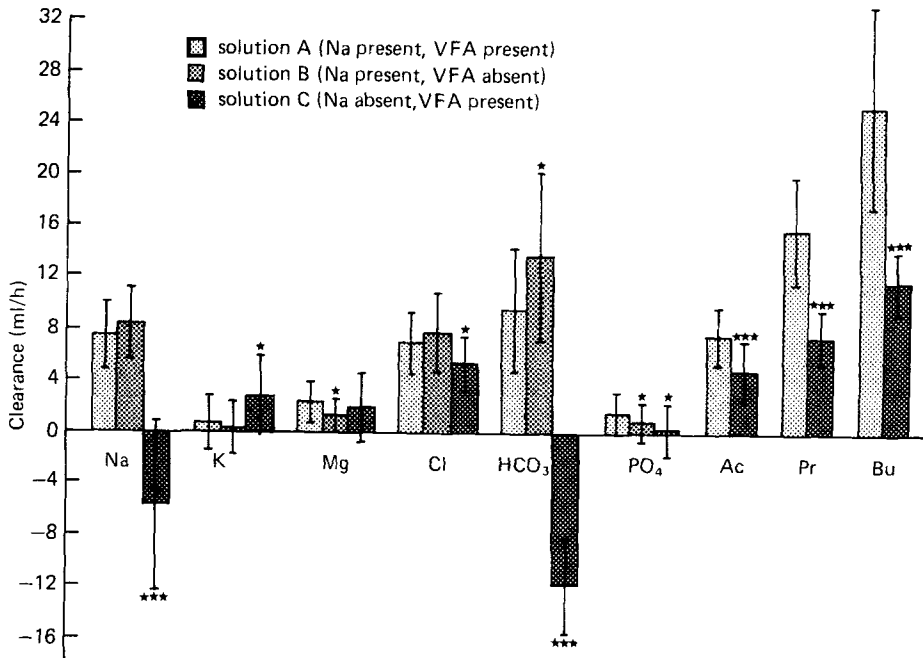


Fig. 2. Clearance (ml/h) of electrolytes and volatile fatty acids from saline solutions A, B and C (for details, see Table 1) in rabbit caecum in vivo. Ac, Acetate; Bu, butyrate; Pr, propionate. Mean values and standard deviations; values were significantly different from those for solution A: * $P < 0.05$, *** $P < 0.001$.

In the VFA-free solution B, net Na and net Cl clearance did not change, whereas HCO_3 clearance increased by half. Net water absorption decreased by approximately one-quarter of that for solution A.

Na was secreted into the Na-free solution C. Within 1 h, Na concentration increased from 5.6 ± 3.6 to 8.5 ± 5.6 mmol/l ($P < 0.001$). Net water movement was completely absent. VFA clearance decreased by half and Cl clearance by a quarter. In contrast to solutions A and B, K was evidently absorbed. The most remarkable fact was the heavy secretion of HCO_3 into the Na-free solution. HCO_3 concentration increased from 18.9 ± 2.9 to 43.1 ± 7.0 mmol/l and total CO_2 concentration from 21.5 ± 3.2 to 44.4 ± 7.0 mmol/l. Soluble CO_2 concentration consequently decreased during the 60 min incubation period, whereas in solutions A and B the HCO_3/CO_2 relation largely remained constant. There was also no appreciable change in pH in solutions A and B (pH at the end of the 60 min incubation period was 6.8 ± 0.2 for solution A and 7.0 ± 0.2 for solution B), but there was an increase to 7.7 ± 0.1 for solution C.

Relationships between solute movements

Net absorption of water was closely correlated with the net absorption of osmotically-active material (Fig. 3). All three saline solutions which had been slightly hypertonic at the beginning of the experiments, reached a level of 282 ± 13 mosmol/kg at the end of the incubation period, a value which corresponds to the osmolality of the blood. Correlation between net water absorption and net acetate absorption was better than between water and Na (Fig. 4). However, absorption of VFA was still evident, even when there was no net

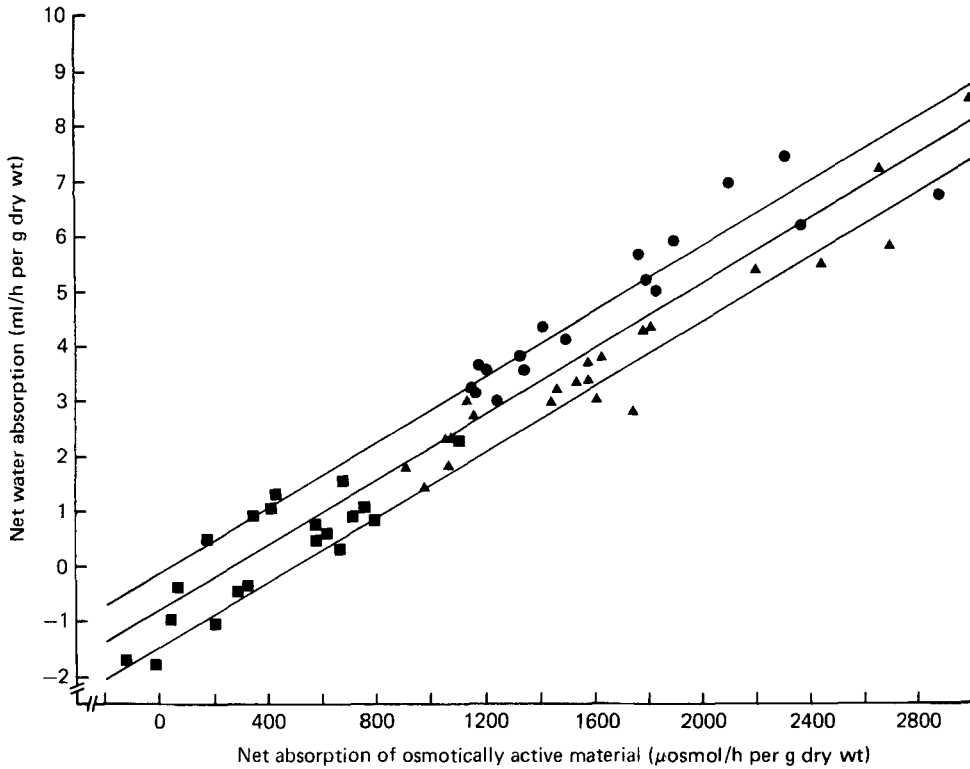


Fig. 3. Correlations between net water absorption (ml/h) and net absorption of osmotically active material ($\mu\text{osmol/h}$) from saline solutions A, B and C (for details, see Table 1) in rabbit caecum in vivo. ●, Solution A (Na present, VFA absent); ▲, solution B (Na present, VFA absent); ■, solution C (Na absent, VFA present). All values related to 1 g dried caecal segment. Regression equation: $y = 0.003x - 0.861$, where y is water absorption, x is absorption of osmotically active material. Deviation of $yv.x$ was 0.698, coefficient of correlation was 0.959.

water absorption or when water was secreted. There was also a large intercept in the instance of HCO_3 secretion. On the other hand, net water flux was not significantly different from zero when net Na absorption was zero. The same result has been found for the net flux of Cl and water. Net Na absorption and net Cl absorption were well correlated in solutions A and B (Fig. 5). Regression lines were calculated separately because of the 60% higher concentration of Cl in solution B. A similar relationship existed between net Na and net VFA absorption (Fig. 5).

DISCUSSION

The present results showed that the rabbit caecum, like the colon of this and other mammalian species, conserved water, Na and Cl to a great extent. Ca, Mg and PO_4 also disappeared from an electrolyte solution equivalent in composition to that found in the caecum under normal physiological conditions. However, it cannot be concluded from these experiments whether the decrease of Ca and Mg was due to real absorption or to adsorption onto the mucosa or secreted mucus (Rübsamen, 1976). Finally, the rapid absorption of VFA confirms the importance of VFA absorption from normal caecal contents in vivo and in vitro (Henning & Hird, 1972*b*; Parker, 1976). The rate of absorption increased with the size of the molecule.

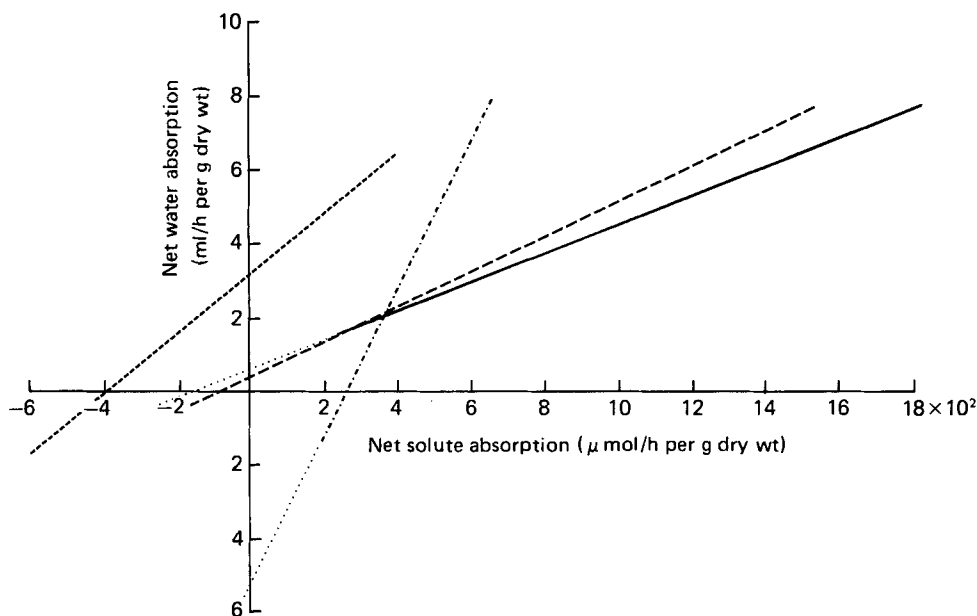


Fig. 4. Relationships between net movement of ions ($\mu\text{mol/h}$) and water (ml/h) in rabbit caecum in vivo incubated with three saline solutions (for details of solutions, see Table 1). All values related to 1 g dried caecal segment. Regression lines ($y = bx + a$), deviations of y v. x (s_{yx}) and coefficients of correlation (r) were calculated for Na (—) from experiments with saline solutions A and B, for VFA (---) with solutions A and C, and for Cl (····) and HCO_3 (-·-·) with all three solutions. Regression lines are shown over the range of values recorded, (····) extrapolated region.

x	b	a	s_{yx}	r
Na	0.004	0.68	1.35	0.69
Cl	0.005	0.39	2.06	0.60
HCO_3	0.008	3.28	1.62	0.62
VFA	0.020	5.14	1.46	0.82

Cation- and anion-exchange mechanisms have often been discussed in relation to gastrointestinal absorption phenomena. A relationship between Na absorption and K secretion was proposed for the rat colon (Edmonds, 1967), whereas in the human colon the direction of K movement seems to be more dependent on mucosal K concentration than on Na absorption (Devroede & Phillips, 1969; Edmonds & Pilcher, 1972; Salas-Coll, Kermode & Edmonds, 1976). In the rabbit, an inverse diurnal variation was found for the concentrations of Na and K in the normal caecal contents (Leng & Hörnicke, 1975). Na concentration was high, when K concentration was low and vice versa. This might indicate a relationship between Na and K absorption, but this could not be proved in the present investigation. The mean of K flux was approximately zero in solutions A and B with a mean K concentration of 18 mmol/l. In human colon, this was also shown to be the critical concentration for K secretion or absorption (Devroede & Phillips, 1969). K absorption was significantly increased only in the Na-free solution C, when there was Na secretion. At the same time, however, K concentration was considerably higher.

From Table 2 it is seen that in solution A half of the Na uptake is balanced by Cl as anion and the other half by the VFA absorbed. In the VFA-free solution B, Na absorption was unaffected and Cl absorption was doubled, so that net Cl absorption corresponds almost entirely to net Na absorption. It seems, therefore, that in the rabbit caecum uptake

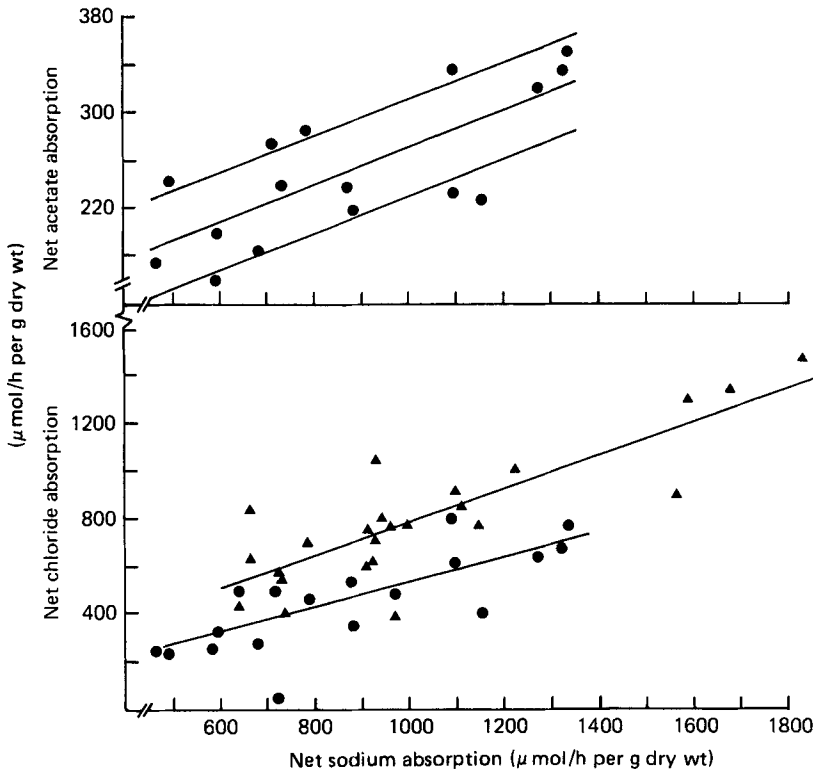


Fig. 5. Correlations between net Na absorption ($\mu\text{mol/h}$) and net Ac absorption ($\mu\text{mol/h}$) and net Cl absorption ($\mu\text{mol/h}$) in rabbit caecum in vivo. All values related to 1 g dried caecal segment. Regression line ($y = bx + a$), deviation of y from x (s_{yx}) and coefficient of correlation (r) was calculated for Na/Ac from solution A (●), for Na/Cl from solutions A (●) and B (▲). (For details of solutions, see Table 1). Ac, acetate.

solution	x	y	b	a	s_{yx}	r
A	Na	Ac	0.153	117	42	0.743
A	Na	Cl	0.514	18	190	0.818
B	Na	Cl	0.682	109	135	0.874

of VFA occurs at the expense of Cl. In contrast to the rabbit, the presence of VFA has a marked stimulatory effect on net Na absorption in the goat colon (Argenzio *et al.* 1975). A relationship between Na absorption and VFA absorption was also determined in other species and various bowel segments (Smyth & Taylor, 1958; Ventura, Schlegel, LaForce & Code, 1973; Schmitt, Soergel & Wood, 1976). It was suggested by Argenzio *et al.* (1975) that the absorbed VFA may supply an energy source for the active transport of Na, as it is known that VFA are partly metabolized in the colon and caecal mucosa (Henning & Hird, 1972a; Argenzio, Southworth & Stevens, 1974; Argenzio & Southworth, 1975). In the rat colon in vitro, Na and fluid absorption were increased in the presence of VFA as well as in the presence of glucose (Parsons, 1967; Binder & Rawlins, 1973) which appears to support the theory of an energy coupling between Na absorption and substrate absorption. On the other hand, net Na absorption in the perfused guinea-pig caecum and colon in vivo did not change in the presence or absence of glucose (Powell, Malawer & Plotkin, 1968). Moreover, Na transport in the present study was not influenced by VFA, and recently Argenzio, Southworth, Lowe & Stevens (1977) demonstrated even an inhibitory

effect of acetate on net Na transport in equine caecal musoca in vitro. Therefore, no general conclusions can be drawn concerning the influence of substrate availability on actively absorbed electrolytes in the large intestine.

Nevertheless, there was a relationship between Na and VFA absorption in the present results, which is apparent from Fig. 5 and from the fact that VFA absorption was markedly reduced in Na-free solution. VFA absorption is thought to occur by passive diffusion (Sallee & Dietschy, 1973; Naupert & Rommel, 1975; Mottaz & Worbe, 1977). This diffusion is dependent on the concentration gradient between lumen and mucosa and, in addition, on free water movement. Consequently, VFA absorption may become smaller with reduced Na-coupled water flux in the caecum. The existence of an Na-H exchange, whereby an absorption of VFA in non-ionic form would be facilitated, could offer another explanation. Without measurements of electrical phenomena, however, the mechanism of VFA absorption cannot be completely clarified.

As in the large intestine of several species and under various experimental conditions, Na transport appears to account for the short-circuited current and as Cl absorption often is associated with simultaneous secretion of HCO_3^- , a Cl- HCO_3^- -exchange mechanism has been proposed (Swallow & Code, 1967; Devroede & Phillips, 1969; Wingate, Krag, Mekhjian & Phillips, 1973; Frizzell *et al.* 1976). Moreover, carbonic anhydrase (EC 4.2.1.1) inhibitors reduce both Cl absorption and HCO_3^- secretion (Parsons, 1956; Phillips & Schmalz, 1970). In the present study, however, HCO_3^- was not seen to be secreted under physiological conditions (solution A). The increased HCO_3^- absorption in solution B is probably due to the higher HCO_3^- concentration and not to an effect of VFA absence. Yet, the lack of Na in solution C caused a striking reversal in the direction of HCO_3^- flux, though its concentration remained the same as in solution B. Balance calculations show that under these experimental conditions HCO_3^- secretion equals Cl absorption. On the other hand, a VFA- HCO_3^- -exchange mechanism such as that proposed by Ash & Dobson (1963) for VFA absorption in the rumen and confirmed by Rübtsamen (1976) for the llama gastric pouch, must also be taken into consideration. According to the equilibrium $\text{CO}_2 + \text{H}_2\text{O} \rightleftharpoons \text{H}_2\text{CO}_3 \rightleftharpoons \text{H}^+ + \text{HCO}_3^-$, the dissociation of CO_2 would produce H^+ ions which would favour the absorption of VFA in their undissociated form, as at a neutral pH the VFA would be present to more than 99% as ionized molecules. As a consequence, CO_2 concentration should decrease and HCO_3^- concentration should increase. Comparisons of HCO_3^- and CO_2 concentrations in the VFA-free solution B show, that the relation of HCO_3^- (90% of the total CO_2) and CO_2 (10% of the total CO_2) did not change during the experiment, whereas in solution C there was a shifting from 88% HCO_3^- and 12% CO_2 at the start of the experiment to 97% HCO_3^- and 3% CO_2 at the end of the 60 min incubation period. Because of the high net appearance of total CO_2 in the caecal lumen using solution C, it must be postulated that an increased CO_2 diffusion from the blood side took place. A similar absorption mechanism of VFA in equine large intestine was recently discussed by Argenzio *et al.* (1977). Yet, until now, it has not been possible to determine whether CO_2 hydration takes place within the intestinal lumen or within the mucosal cells. Carbonic anhydrase, which accelerates this process, is present in high concentrations in the colon mucosa (Maren, 1967; Lönnerholm, 1977).

From the present experiments it cannot be decided, which anion-exchange mechanism in the absence of Na may be more involved in HCO_3^- secretion. It seems that in normal caecal contents of rabbits, where high concentrations of Na are present and CO_2 is continuously produced by microbial digestion, anion-exchange processes are of secondary importance for VFA absorption.

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