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DISTRIBUTION OF OSMOTIC FLOW IN STOMACH AND GALLBLADDER

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Summary

Stomach and gallbladder actively transport fluids which are nearly isotonic to plasma. Consideration of the measured areas of the appropriate transporting surfaces gives a more realistic view of the osmotic gradient required to account for the observed net flow of water. Simple osmosis may be adequate if the transporting membrane has an osmotic permeability in the range observed for synthetic lecithin-cholesterol bilayer membranes.

Recent work with frog gallbladder shows that Na^+ pumping sites are distributed in relatively uniform fashion over the basal-lateral surfaces of this epithelium [1]. Such experiments have not been carried out in stomach, but the correlation of apical membrane surface of oxyntic cells with rate of acid secretion suggests that HCl pumping sites are also uniformly distributed, in this case over the apical surface [2—6]. Stereological estimates of these surface areas are now available.

In the stomach, the apical surface area of oxyntic cells has been determined at the electron microscopic level for dog [2] and frog [6]. In dog the apical surface includes the area of the secretory canaliculi. These areas are expressed per unit macroscopic or chamber area in Table I.

For gallbladder, the results cited above suggest that the transporting surface is the basal-lateral membrane of the epithelial cells. Blom and Helander [7] have measured the lateral surface for rabbit gallbladder in vitro: the basal surface makes only a small additional contribution in this tissue. They give the lateral surface in units of $\mu m^2/\mu m^3$ cell volume. The cell volume per unit area measured along the epithelium may be obtained by combining their values for epithelial height and fractional cell volume (equal to 1-fractional paracellular channel volume). Averaging over crest

TABLE I

DISTRIBUTION OF ACTIVE TRANSPORT AND OSMOTIC FLOW OVER THE TRANSPORTING SURFACE OF STOMACH AND GALLBLADDER

	Frog stomach (in vitro)	Rabbit gallbladder (in vitro)	Dog stomach (in vivo)
Transporting surface* per macroscopic area (cm^2/cm^2)	129	173	350
Net active transport of HCl or NaCl (μequiv/cm^2 per h)	6.4	8.5	300
Net water flow with HCl or NaCl (μl/cm^2 per h)	53	53	1875
Net water flow per unit transporting surface (μl/cm^2 per h)	0.41	0.31	5.4
Osmotic excess** in transported fluid (mM)	1.8	1.3	23

*Apical surface of stomach oxyntic cells or lateral surface of rabbit gallbladder epithelial cells.
**Calculated from the osmotic permeability for a lipid bilayer of 230 μl/cm^2 per h per 1 M difference in concentration of HCl or NaCl [10].

and crypt epithelium, we find the lateral area to be 64 cm^2/cm^2 of epithelial area. Folds and crypts account for an enlargement factor of 2.7 in these unstretched bladders [7] so that the lateral area is 2.7 × 64, or 173 cm^2/cm^2 macroscopic area (Table I).

Optimal rates of active transport are listed in Table I for the three tissues. In vitro values were chosen for frog stomach [4] and rabbit gallbladder in an unstretched state [8], corresponding to the conditions in which stereological data were obtained. The value for dog stomach represents maximally stimulated acid secretion collected in vivo [2]. The net water flow associated with acid secretion into the empty gastric lumen, or NaCl absorption by the unilateral gallbladder preparation, is also shown. The transported fluid is assumed to be approximately isotonic, 120 mM in frog and 160 mM in mammal.

Table I also lists the net water flow averaged over the transporting surface. By the osmotic hypothesis, such net water flows are due to an osmotic excess in some region of the tissue. The simplest possible assumption is that osmosis occurs uniformly over a single membrane, the transporting surface. A conservative estimate for the osmotic permeability, P_f, of this membrane can be derived from measurement of this parameter in synthetic lipid bilayers. P_f varies greatly, however, depending on the composition of the bilayer: in particular, it is reduced if cholesterol is included [9]. We adopt for the present calculation the result obtained for a membrane-forming solution containing phosphatidylcholine and cholesterol in the molar ratio of 1:2, in which case P_f was about $1.8 \cdot 10^{-3}$ cm/s [9,10]. As pointed out before [10], this value falls midway in the range of values of P_f($3 \cdot 10^{-4} - 7 \cdot 10^{-3}$ cm/s) calculated by Dick [11] for a wide variety of animal membranes.

The value adopted here of $P_f = 1.8 \cdot 10^{-3}$ cm/s corresponds to an osmotic permeability of 230 μl/cm^2 per h per 1 M difference in concentration of HCl or NaCl across the transporting surface. This membrane is assumed to be impermeable to the electrolyte. Accordingly, the final row of Table I shows the osmotic excess in mM required to yield the observed net water flow. The osmotic excess ranges from about 1% for gallbladder to 14% for dog stomach when expressed in terms of the respective plasma molarity. An osmotic excess of a few percent might easily escape detection, and the transported fluid be considered isotonic. Thus it appears that net water flow in the two in vitro preparations could be driven by osmosis of the magnitude observed in a lipid bilayer.

Special morphological features such as a double membrane or standing gradient could improve osmotic equilibration of transported fluids, however. A mechanism of this kind may be required to account for secretion in dog stomach, where the calculated osmotic excess (Table I) is about twice that measured in gastric juice [12]. For example, suppose a standing gradient is present between the oxyntic cell and the entrance to the gastric gland, a distance of several hundred μm. The osmotic excess at the oxyntic cell surface (23 mM) would be partly dissipated as the secretion passes into the lumen, provided the cells lining the gastric tubules and pits are not completely impermeable to water. Only 7% of the total net water flow need be supplied in this manner to reduce the osmotic excess calculated above to that measured in gastric juice.

The presence of small aqueous pores in the transporting membrane will lead to a larger estimate of P_f, as inferred for the erythrocyte membrane [13] and toad urinary bladder [14]. The osmotic excess calculated here will be diminished in inverse proportion to the increase in osmotic permeability.

Definitive experimental evidence for the presence of pores or standing gradients in the tissues considered here is still lacking. Proliferation of the transporting membrane does occur, and it seems reasonable to suppose that this is at least one device by which the epithelium minimizes osmotic gradients.

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