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Existing theories of mammalian renal collecting duct function are based upon micropuncture or microcatheterization studies (see Jamison et al., *Am. J. Physiol.* 237: F247-F261, 1979) in which the renal pelvis surrounding the papilla has been removed or otherwise disrupted. We have used a simple technique to visualize urine flow in the papillary collecting ducts through the intact pelvic wall (Schmidt-Nielsen et al., *Bull. MDIBL*, 18: 89-91, 1978). Our findings show that there are serious misunderstandings about the processes involved in the formation of urine.

In our experiments anesthetized (Inactin, 150 mg/kg, I.P.), male hamsters were intravenously infused with isosmotic lissamine green-saline solutions in order to produce a brightly colored urine. The right kidney was exposed and isolated from respiratory movements by a plastic shield which pressed against the liver and diaphragm. The lower renal pelvis with about 1.3 mm of papilla was cleared of surrounding fat and illuminated with a fiber optic light. Urine flow rates were determined by measuring changes in bladder diameter ( $V = 2.99 \times 10^{-6} W^{5.27}$ ,  $n=45$ ,  $r^2 = .93$ , where  $V$  = bladder volume in ml and  $W$  = bladder width in mm) and, simultaneously, the movements of urine in the papillary collecting ducts were observed and filmed. The rate of urine formation was manipulated by altering the infusion rate (2-50  $\mu\text{l}/\text{min}$ ) with appropriately diluted lissamine green solutions (.5 - 2%). Prior to the experimentation, hamsters were maintained on water and either a low or normal protein diet (Jackson Lab #96; 21.3% protein or Zeigler Bros., NIH-104-76; 8% crude protein).

Our observations clearly show that urine moves as discreet boluses in a pulsatile fashion through the medullary collecting ducts. The urine boluses are propelled by peristaltic waves sweeping periodically down the renal pelvis (mean contractions/min  $\pm$  S.E.M. =  $12.5 \pm 0.5$ ). These observations, made on the kidney *in situ*, were in sharp contrast to the continuous flow of urine that was seen when the pelvis was excised. Our direct observations confirm the recent electrical capacitance measurements of pulsatile flow in the ducts of Bellini of the rat kidney (Jensen, *Acta Physiol. Scand.* 106: 5-9, 1979).

Previously, it has been assumed that urine flows in the collecting duct as a continuous stream. As a consequence of this assumption, it would be predicted that urine flows through the papillary collecting ducts at a low velocity during low urine and flow and at an increased velocity during diuresis. Analysis of our films show that the frequency and velocity of fluid movement in the collecting ducts are independent of urine flow rate (mean trailing edge velocity =  $1.6 \pm 0.1$  mm/sec). Furthermore, the percentage of time the papillary collecting ducts are in contact with urine is directly related to urine flow (Fig. 1). At the lowest flow rates the papillary collecting ducts were empty 94% of the time. The length of urine boluses also increased with urine flow.

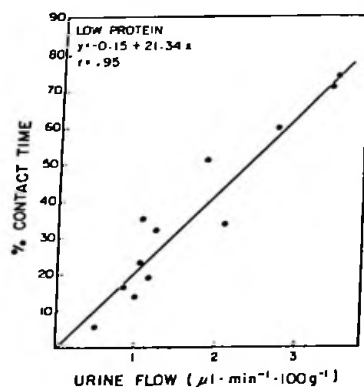


Figure 1. Relationship between contact time of papillary collecting ducts with urine and urine flow in hamsters fed a low protein diet ( $P < .01$ ). A similar relationship was seen in the normal protein group.

We feel that our findings have profound implications for understanding urinary concentrating mechanisms, for all previous models assume continuous urine flow in the collecting ducts. In addition to the pulsatile flow in the collecting ducts, we observe that the peristaltic wave moving down the pelvis also causes discontinuous and even retrograde movements of blood in the vasa recta and therefore effects intraluminal hydrostatic pressures. By analogy, we assume similar disruptions in fluid movements also are imposed upon the loops of Henle by these peristaltic waves. This work was supported by NIH grant 5 RO1 AM15972-09.

#### FLUID REABSORPTION IN THE PAPILLARY COLLECTING DUCTS IN THE HAMSTER KIDNEY WITH INTACT RENAL PELVIS

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In the preceding paper (Reinking and Schmidt-Nielsen, this volume) we have shown that urine moves discontinuously through the papillary collecting ducts, due to the milking action of the pelvis surrounding the papilla. Since the urine is propelled through the collecting ducts by the peristalsis of the pelvis, the linear velocity of the trailing edge of the urine bolus equals the velocity of the propagation of the peristaltic wave. Velocity was found to be independent of urine flow. Contact time between collecting ducts and urine, however, was found to be directly proportional to urine flow rate. This finding showed that the time for fluid reabsorption in the collecting ducts of the papilla could be as low as 1/20 (at the lowest urine flow rate) of that one would assume if the urine were to flow continuously through the collecting ducts, and it raised the question if there were time for any fluid reabsorption in the papillary collecting ducts. It then became clear to us that measurements of contact time and urine flow could be used to determine fluid reabsorption in the collecting ducts in the visible part of the papilla if the total area of the collecting duct lumen at different distances from the tip of the papilla were known.

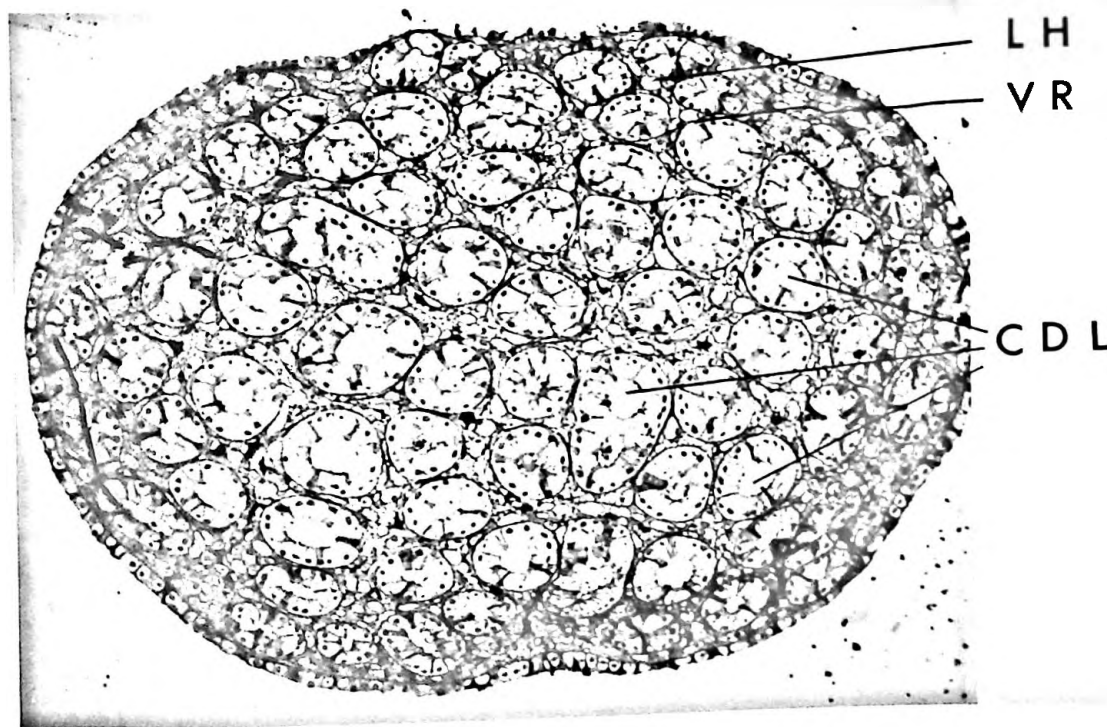


Figure 1. Cross-section of hamster renal papilla 900  $\mu$ m from tip. Collecting duct lumen (CDL), vasa recta (Vr), loop of Henle (LH). Magnification 130 X.