Function of the Collecting Ducts

By Karl J. Ullrich, M.D.

Urine was sampled from microcatheters situated at different levels of the collecting ducts of golden hamsters. Appropriate analyses provided data concerning the function of the collecting ducts with respect to concentrating and acidifying the urine. The conclusion is reached that the collecting ducts serve 2 functions: a passive one, i.e., the back-diffusion of water and urea and an active one, i.e., the exchange of sodium for hydrogen ions and the formation of ammonia.

Heidenhain in 1874 injected indigo carmine into intact animals and found a strong concentration of color in the collecting ducts. His explanation was that there is relatively more urine in the collecting ducts and that some precipitated dye is collected by coagulation in a manner analogous to sand being swept along by a stream. He attributed no special function to the cells of the collecting ducts because of their clear appearance. This interpretation was accepted for 70 years.

In 1949 Vimtrup, in the laboratory of Bodil and Knut Schmidt-Nielsen, repeated experiments with dyes on Heteromyidae whose collecting ducts are very long and a good subject for experimental study. He concluded that the urine becomes concentrated as it flows through the collecting ducts. In 1951 Hargitay and Kuhn published their countercurrent hypothesis, showing by experiments performed in conjunction with Wirz that the urine was concentrated in the collecting ducts.

To obtain more information about the function of collecting ducts, Hilger, Klümper, Eigler, Pehling and Ullrich catheterized the collecting ducts of golden hamsters, whose papillae are easily accessible from the renal pelvis. The experimental procedure was as follows: 2 polyethylene microcatheters were passed from the renal pelvis into 2 collecting ducts, the tips reaching different levels. Both samples of urine which were obtained in this way were analyzed with respect to the depressions of the freezing point and the concentrations of inulin, sodium, and potassium.

The results are plotted in figure 1. In 33 cases, the concentration of inulin in urine from the superficially placed catheter averaged 1.5 times that from the deeper one. In a second series of animals with higher urinary osmotic pressure, the mean increase was threefold. If it is assumed that the increase in inulin concentration is due to the reabsorption of water, the results of both series indicate that between one-third and two-thirds of the water flowing into the portions of the collecting ducts under consideration is reabsorbed.

If water alone is reabsorbed from the fluid of the collecting ducts, the increase in osmotic pressure ought to parallel the increase in the concentration of inulin. But (fig. 2), such parallelism was not observed: the real osmotic pressures increase with much less of a slope. From this discrepancy one can conclude that some solutes must be reabsorbed too, thereby making the osmotic pressure of the reabsorbed solution equal to about two-thirds of that of the solution flowing into the corresponding segment of the collecting ducts.

In other experiments, Klümper, Ullrich, and Hilger measured the concentrations of inulin and urea in samples obtained from microcatheterization of collecting ducts. In all cases the increase in the concentration of inulin exceeded that of urea. The ratios of the rate of increase in the concentration of urea to the rate of increase in the concentration of inulin varied from 0.37 to 0.97, with an average of 0.65. These data indicate that the con-

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Relative changes in the concentrations of inulin in the urine within the collecting duct, and the corresponding reabsorption of water. The data illustrated on the right side of the figure are from animals excreting a more concentrated urine than those on the left. On the abscissa are plotted the distances of sampling points from the tip of the papilla. The straight lines represent the values of the simultaneously gained samples. Data taken from Hilger, Klümper and Ullrich.

What changes occur in the electrolytes during the passage of urine through the collecting ducts? On the average, the increases in the concentrations of potassium parallel the increases in the concentrations of inulin. This supports the view that potassium is concentrated only by reabsorption of water in the collecting ducts of the inner medullary region.

The concentrations of sodium in the urine, however, fall as the urine passes through the collecting ducts. As may be seen in figure 3, there is a steep slope, with high values for concentration in the outer medullary region. This fact indicates that a great deal of water is reabsorbed from the collecting ducts of the cortex and the outer medulla. The sodium concentrations are very low at the papillary tip. Thus, sodium must be reabsorbed from the collecting ducts. We may then conclude that the collecting ducts can regulate the excretion of sodium by the kidney.

But how can this drop in the concentration of sodium be reconciled with the coincidental rise in the osmotic pressure of urine in the same region? Simultaneous measurements of the concentrations of inulin and ammonium by Ullrich, Hilger, and Klümper indicate (fig. 4) that ammonium increases much more than inulin. Therefore, we may conclude that ammonium ions are secreted into the collecting ducts. In connection with this observation, it is interesting to note that Richterich-van Baerle, Goldstein, and Dearborn have de-
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Figure 2
Changes in the osmotic pressure of urine along the course of the collecting duct. The data used for the left side of the figure were calculated from the freezing-point depression of urine obtained from the deeper level and the respective concentrations of inulin in urine from both levels. This hypothesis figure would be expected if only water were reabsorbed. The observed increases in osmotic pressure (right) are less. Data taken from Hilger, Klümp and Ullrich.5

Figure 3
a. Changes in the concentrations of sodium during the passage of urine through the collecting duct (26 experiments on golden hamsters). On the abscissa is plotted the distance of the sampling point from the tip of the papilla. b. Changes in the concentrations of potassium during the passage of urine through the collecting duct (23 experiments). (Republished by permission of Pflüger's Archiv für die gesamte Physiologie des Menschen und der Tiere.5)

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scribed a high degree of activity of glutaminase I in the inner zone of the renal medulla of dogs and rabbits. Moreover, as may be seen in figure 5, acidification of urine within the collecting ducts was demonstrated by a decrease of pH. These observations were recently confirmed by Gottschalk10 and Giebisch,11 who have also shown that acidification can take place in the proximal and distal convolutions. The present data indicate that there is an exchange of sodium ions for hydrogen ions and a secretion of ammonia in the collecting ducts.

The findings by the stop-flow method12-15 are in accord with our results as far as the reabsorption of sodium and the secretion of hydrogen ions and ammonia are concerned. However, a discrepancy exists with respect to the site of secretion of potassium. According to the stop-flow method, potassium is secreted at the same site as hydrogen ions and ammonia. However, our results indicate that potassium is not secreted in the collecting ducts of the inner medullary region, but that secretion of potassium may occur at a site higher up in the collecting ducts.

Figure 4
Changes in the concentration of ammonia in urine during the passage through the collecting duct compared with the changes in the concentration of inulin and in the osmotic pressure in the same samples (4 representative experiments). Data taken from Hilger, Klümpcr and Ullrich.5
To summarize, the collecting ducts seem to have 2 functions: (1) a passive one, i.e., the back-diffusion of water and urea, and (2) an active one, i.e., the exchange of sodium ions for hydrogen ions and the formation of ammonia. Both functions, passive and active, seem to operate independently. It is particularly surprising that the cells of the collecting ducts, which are exposed to enormous changes in the concentrations of electrolytes and urea, and are threatened by an inadequate supply of oxygen and essential nutrients as a consequence of countercurrent diffusion, are entrusted with such essential functions as the exchange of sodium and hydrogen and the secretion of ammonia.

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The Animal that Fits

In 1926, Marshall, browsing through comparative anatomy, discovered that a number of fishes had been described which possessed purely tubular kidneys. This fact, of course, immediately evoked Marshall's interest in fish urine. Unfortunately, agglomerular fishes were rather rare, but we happened to have one species, the goosefish, at Salisbury Cove . . .

Work on the agglomerular fishes had been undertaken independently by J. G. Edwards in the Naples' laboratory, and within a short time it was clear that this purely tubular kidney, which does not even possess a significant arterial blood supply, but is perfused entirely by venous blood from the renal portal vein and at a pressure which is probably below the osmotic pressure of the plasma proteins, can excrete all the ordinary urinary constituents . . .

So, by 1930, the question of tubular excretion was answered in the affirmative. But, as Richards said in the discussion when Marshall read a paper at Woods Hole on the agglomerular fish, "At last he has found an animal that fits in with his theory."—H. W. Smith, Lectures on the Kidney. Lawrence, Kansas, University of Kansas Press, 1943, p. 73.
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