SOME MEASUREMENTS OF CILIARY ACTIVITY

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In the preceding paper (White, 1929) were reported two measurements of the propulsive action, as evidenced by their effect on lowering intracapsular pressure, of the cilia in the ciliated neck of Necturus renal tubules during a period of normal rate of flow of liquid through the tubules. The present paper reports some measurements of maximum pressures which ciliary activity can maintain.

In the first set of experiments a dye-containing pipette connected with a leveling bulb was inserted into a glomerular capsule and enough dye run in to identify the corresponding proximal tubule. The capsule was then torn wide open, the pipette, with the tip toward the capsule, inserted into the proximal tubule a short distance below its junction with the ciliated neck, and the tubule occluded distal to the pipette by pressure with a fine glass rod. Ringer’s solution was kept dripping over the kidney surface. The height to which the pressure in the proximal tubule now rises is a measure of the pressure difference which the cilia can build up by forcing liquid down into the tubule. This intratubular pressure is measured by noting the height of the leveling bulb at which the dye in the pipette tip is in equilibrium with the intratubular liquid. In six such experiments, done on four animals, the tubule pressures were 5.2, 4.0, 4.6, 5.4, 4.8 and 5.7 cm. H₂O. The pressure rises gradually, reaching the maximum in from 1 to 2 minutes and then remaining constant; at the time of maximum pressure the tubule above the occlusion is widely distended. It is thus seen that the pressure difference which the cilia can build up is much greater than the extent (4 or 5 mm. H₂O) to which they lower the intracapsular pressure with a normal rate of flow through the tubule.

It may be pointed out here that this demonstration answers an objection which has been raised (Pütter, 1926) against regarding the fluid collected by a pipette in a capsule as being purely capsular fluid; it has been objected that the fluid may be in part that which has been drawn back from the tubule. This objection appears reasonable in the case of the experiments of Wearn and Richards (1924), against which it was directed. They employed suction pressures of 20 to 30 mm. Hg in drawing the capsular
fluid into the pipette, an unnecessarily high degree of suction. If, however, the fluid is drawn into the pipette with a negative pressure of not more than 1 mm. Hg it is evident that it will not be contaminated by tubular fluid, since the cilia of the ciliated neck can resist a pressure of several millimeters Hg. And since the findings of Wearn and Richards on the capsular fluid of frogs have been found to hold in Necturus, where the fluid was collected under a negative pressure of not more than 1 mm. Hg, it appears probable that even with the suction pressures which they employed there was no significant contamination of capsular by tubular fluid.

Another set of experiments was carried out to determine the maximum pressure against which the cilia of the nephrostome can prevent liquid from passing out, in the reverse of the normal direction, from the ciliated neck to the mouth of the nephrostome. In these experiments a dye-containing pipette connected with a leveling bulb was inserted into a capsule and dye run in to identify the proximal tubule, which was then occluded by a glass rod a short distance below its junction with the ciliated neck. The leveling bulb was then raised until dye was seen passing out from the ciliated neck through the nephrostome and the pressure at which this occurred was observed. After this observation, in some of the experiments the same determination which was carried out in the first set of experiments was also obtained, i.e., after tearing open the capsule, removing the pipette from the capsule and removing the tubular occlusion until the tubule had been washed clear, the pipette was inserted into the proximal tubule, which was again occluded and the intratubular pressure determined. Also, in some of these experiments the intracapsular pressure was determined before and after occluding the proximal tubule.

1. December 10. Female. Dye came out of nephrostome when intracapsular pressure was 8.5 to 9 cm. H$_2$O, was slowly swept back into ciliated neck when bulb was lowered to 8 cm.

2. December 14. Male. Intracapsular pressure before proximal tubule occlusion was 3.4 cm. H$_2$O, after occlusion rose to 8.6 cm. H$_2$O. Dye moved out of nephrostome with intracapsular pressure of 10.2 cm. H$_2$O, was slowly swept back into ciliated neck when bulb was lowered to 0.7 cm.

Another capsule in the same animal showed intracapsular pressure of 3.8 cm. H$_2$O before tubule occlusion, 9 cm. afterwards. Dye moved out of nephrostome when bulb was raised to give intracapsular pressure of 10.8 cm. H$_2$O, slowly swept back when bulb was lowered to 10.3 cm.

3. December 14. Female. Intracapsular pressure 2.2 cm. H$_2$O before tubular occlusion, 7.8 cm. afterwards. Dye came out of nephrostome with intracapsular pressure of 8.5 to 9 cm. H$_2$O, came back at 8 cm. Next tore capsule, removed tubular occlusion and let tubule wash out, then put pipette into proximal tubule and again occluded tubule distal to pipette. Tubular pressure rose to 4.4 cm. H$_2$O.

In another capsule intracapsular pressure was 3.0 cm. H$_2$O before tubular occlusion and 8.5 cm. afterwards. Dye left nephrostome at intracapsular pressure of 11.0 to 11.5 cm. H$_2$O, came back at 10.5 cm. Next tore capsule, removed tubular occlusion and let tubule wash out, then put pipette into proximal tubule and occluded tubule distal to pipette. Tubular pressure rose to 5.3 cm. H$_2$O.
It is seen that the nephrostome cilia can prevent an outward passage of liquid against a considerable pressure. It may be pointed out that the maximum pressure against which the nephrostome cilia can prevent the outward passage of liquid is even somewhat greater than the pressure indicated by the height of the leveling bulb, since, due to the activity of the cilia in that portion of the ciliated neck between the capsule and the origin of the nephrostome, the pressure in the ciliated neck at the origin of the nephrostome is somewhat greater than the intracapsular pressure determined by the height of the leveling bulb.

The intracapsular pressures with the tubule unoccluded are of course those pressures due to the passage of fluid into the capsule across the glomerular membrane. An interesting point arises in regard to the interpretation of the intracapsular pressure after the tubule is occluded. At first thought one might consider this procedure analogous to the determination of maximum ureteral pressure with the ureter occluded, the pressure being due to the entrance of fluid into the capsule across the glomerular membrane. It must be remembered, however, that with the tubule occluded, the nephrostome cilia will sweep liquid into the tubule until the intratubular pressure reaches the maximum height against which the nephrostome cilia are able to move liquid. The intracapsular pressure will always, of course, be somewhat less than this, due to the activity of the cilia in that portion of the ciliated neck between the capsule and the origin of the nephrostome.

It thus appears that the maximum intracapsular pressure with the tubule occluded cannot be taken as a measure of the maximum pressure against which liquid can enter the capsule through the glomerular membrane for the former can never exceed the maximum pressure against which the nephrostome cilia can prevent the escape of liquid into the body cavity; it will, in fact, be somewhat less than this, due to the activity of the cilia in that portion of the ciliated neck between the capsule and the origin of the nephrostome. If the glomerulus can still pass liquid into the capsule against the maximum intracapsular pressure which the nephrostome cilia can build up with the tubule occluded, the liquid thus entering the capsule will escape into the body cavity through the nephrostome, thus preventing any rise of intracapsular pressure above that which the nephrostome cilia can build up. The present experiments do not permit us to decide whether or not this may happen; a crucial experiment to determine the maximum pressure against which the glomerulus can eliminate liquid would necessitate occlusion of the nephrostome as well as of the tubule and up to the present time this has not been technically possible.

The above observations do not exclude the possibility that in the capsules from which pass tubules not bearing nephrostomes (and these are in the great majority, only the primary tubules having nephrostomes) the pressure due to the passage of liquid across the glomerular membrane
may rise, with the tubule occluded, higher than the pressure which the nephrostome cilia were observed to exert. These secondary capsules in Necturus are not accessible for manipulation.

Such a consideration does not, of course, enter into an interpretation of maximal ureter pressure with the mammalian kidney; there (if ureteral contractions, the valve-like action of the papillae of the kidney pelvis, possible osmotic effects between tubule contents and blood, and perhaps other factors are allowed for) it is truly a measure of the maximum pressure against which the glomeruli can eliminate fluid.

**SUMMARY**

The cilia in the first segment of the renal tubule of Necturus can, with the capsule torn and the proximal tubule occluded, raise the pressure in the proximal tubule proximal to the occlusion to 4.0 to 5.7 cm. H$_2$O. It is pointed out that this demonstration proves that capsular fluid withdrawn under suction of not more than 1 to 2 mm. Hg cannot be contaminated with tubular fluid.

The nephrostome cilia can exert pressures of 8 to 11 cm. H$_2$O. The complication which this introduces into an interpretation of the maximum intracapsular pressure with the tubule occluded as a measure of the maximum pressure against which the glomeruli can eliminate fluid is discussed.

**BIBLIOGRAPHY**


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