

Resumen por el autor, John A. Kittelson.

Los efectos de la inanición y realimentación sobre el crecimiento del riñón de la rata albina.

El autor ha llevado a cabo un cuidadoso estudio volumétrico de la corteza y médula del riñón, así como una numeración completa de los corpúsculos renales (corpúsculos de Malpighi), basándose en cortes seriados del riñón de la rata albina hambrienta a consecuencia de una alimentación insuficiente administrada desde el nacimiento hasta las tres y seis semanas de edad, y en los del riñón de ratas en las cuales se ha mantenido constante el peso del animal desde el nacimiento hasta las tres semanas de edad. También ha estudiado el riñón de una rata realimentada hasta pesar 25.6 gramos, después de sometida a una alimentación insuficiente desde el nacimiento hasta las tres semanas, y el de otra rata realimentada hasta pesar 74 gramos y sometida previamente a alimentación insuficiente desde el nacimiento hasta las seis semanas, así como los riñones de ratas normales escogidas como término de comparación. Durante la alimentación insuficiente puede cesar la formación de nuevos corpúsculos en la corteza. Los esbozos de los corpúsculos que aparecen al comienzo de la alimentación defectuosa continúan su desarrollo, pero no aparecen nuevos esbozos. Los corpúsculos renales aumentan de tamaño durante el periodo de hambre y presentan una hipertrofia suficiente para compensar su escasez. Cuando el periodo de hambre es largo ocurre sin embargo que, con un aumento algo mayor de peso total y de peso del riñón, el impulso para formar nuevos corpúsculos vence a la inhibición producida por el hambre. De este modo el riñón hipertrofiado tiende a producir el número de corpúsculos normal para su peso. Los datos recogidos parecen demostrar que, manteniendo el mismo peso en el animal, la mayor parte del crecimiento del riñón tiene lugar en la médula. Esto está de acuerdo con los resultados obtenidos en las ratas normales. Parece pues que la inanición severa no es suficiente para inhibir el impulso de crecimiento de la médula.

EFFECTS OF INANITION AND REFEEDING UPON THE GROWTH OF THE KIDNEY OF THE ALBINO RAT

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INTRODUCTION

The normal postnatal development of the rat's kidney, including renal corpuscles and volumetric growth of cortex and medulla, was described in a previous paper (Kittelson, '17). No detailed data on the kidney after conditions of inanition and refeeding seem to be available. Jackson ('15) found a slight increase in the weight of the kidneys in young rats held at maintenance (constant body weight) by underfeeding from three to ten weeks of age. Stewart ('16) found that the kidneys are of practically normal percentage weight in rats after maintenance from three to twelve weeks of age and throughout the period of refeeding. In underfeeding begun at earlier periods, however, he (Stewart, '18, '19) found a definite increase in the kidney weight. The effects of inanition and refeeding on the volumes of cortex and medulla and on the total number and volume of the renal corpuscles in young rats are the special problems for which data have been collected in the present investigation.

The work was done in the Anatomical Laboratory of the University of Nebraska. The problem was suggested by Prof. C. M. Jackson, University of Minnesota, and carried out under his supervision. I thank Doctor Jackson for his valuable aid and criticism. The material was given to me by Dr. C. A. Stewart, University of Minnesota, who fed, cared for, and autopsied the rats in connection with his inanition studies. I wish to express my thanks to Doctor Stewart for his generosity. I am also very grateful to Dr. C. W. M. Poynter, University of Nebraska, for his interest in the problem and for valuable suggestions.

MATERIAL AND METHODS

The material used included the kidneys of eight albino rats (*Mus norvegicus albinus*) from the rat colony in the Institute of Anatomy at the University of Minnesota. In addition to these test rats, six normal rats used in my previous study (V 2.1; V 2.2; V 1.3; V 13.1; V 1.7; V 1.8) were employed as controls. The kidneys of another new-born control rat (K 2.1) were studied and the number of renal corpuscles at birth more definitely determined. Data from Donaldson ('15) on kidney weights were also used for comparison. The general data are given in table 1. Of the test rats, two belonging to the same litter were stunted by underfeeding from birth to three weeks, a male (St 101.3) and a female (St 101.5). Two rats belonging to another litter were stunted by underfeeding from birth to six weeks, a male (St 100.1) and a female (St 100.2). Two female rats (St 214.2 and St 239.10) were held at maintenance (constant body weight) from birth to approximately three weeks (eighteen and twenty days, respectively). One female rat (St 106.1) was stunted by underfeeding from birth to three weeks (body weight 10.9 grams) and then refed to 25.6 grams (at five weeks of age). A male rat (St 91.8) was then stunted by underfeeding from birth to six weeks (body weight 13.5 grams) and then refed to 74 grams. This rat was killed at the age of thirteen weeks. During the underfeeding, the young nursing rats were at first removed from the mother for various periods up to the age of three weeks. Those in which the stunting continued to six weeks were fed

(after the weaning period) limited amounts of whole-wheat bread soaked in whole milk.

The identification numbers of the rats were used in the following way: the letters 'K' (Kittelson), 'St' (Stewart), and 'V' (Vaughn) indicate the series, the number preceding the decimal point designates the litter, while the number following the decimal point designates the individual rat.

The rats were killed with chloroform, weighed, and their nose-anus lengths measured. The two kidneys were then weighed together, and the weight of each kidney may be assumed to be one-half of the combined kidney weight. Individual kidney weights were not recorded.

One kidney (no record made of whether right or left) in each case was fixed in Zenker's fluid for eighteen to twenty-four hours, depending on the size. It was then imbedded in paraffin and cut in serial cross-sections $10\ \mu$ in thickness. The sections were then mounted in complete series and stained with haematoxylin and eosin.

The total volume of cortex and medulla was obtained by using the paper method explained in detail in a former paper (Kittelson, '17). The sections were enlarged by means of a Bausch & Lomb projection apparatus and the outlines of cortex and medulla were drawn on 'Byron Weston Ledger, Substance no. 32' (sheets 18 x 23 inches). The paper outlines were then cut out, weighed, and the data computed as explained in my previous paper. The paper used was slightly different from that formerly used. In order to reduce weight in grams to square area in centimeters, the weight was multiplied by 80.32, this representing the average area in square centimeters of one gram of the paper.

In table 1, the volumes of the kidneys used appear much smaller than might be expected from the corresponding weights. This difference is due to three factors: 1) the volume of the capsule and of the renal sinus (pelvis), both of which were excluded; 2) shrinkage of material in the process of preparation; 3) the specific gravity of the kidney, making the volume of the kidney in cubic centimeters somewhat less than the corresponding weight in grams.

In counting the number of malpighian corpuscles, the method used by Miller and Carlton ('95) was modified as in my former paper (Kittelson '17). In finding the average diameter of the malpighian corpuscles in the two zones, the paper method as used by Jackson ('17) was again followed.

Ferry ('13) showed that in rats refed after stunting the rate of growth is a function of size rather than of age. So far as possible, therefore, the test rats were compared with rats of about equal body weight. The limited number of observations make it impossible to draw any final conclusions, but the results are interesting and suggestive.

DATA AND DISCUSSION

1. Weights of the kidneys used

The weights of the kidneys in the normal (control) rats (table 1) correspond fairly well to those in rats of similar body length or weight in the tables of Donaldson ('15). Of the test rats, those stunted to three weeks (especially St 101.3) have kidney weights somewhat below the normal for corresponding body weight or length. Those stunted to six weeks have kidney weights below those for corresponding body length, but more nearly in agreement with the corresponding body weight. The two rats held at maintenance (constant body weight) for three weeks have kidney weights much above those for corresponding body weights (as found by Stewart, '19), but more nearly in agreement with those for body length. The two rats refed after stunting have kidneys slightly above the normal for corresponding body weight. The rats stunted to three and six weeks therefore appear exceptional, in that they fail to show the increase in weight of the kidneys as found by Stewart ('18). This must be kept in mind in interpreting the results.

2. Effects on cortex and medulla

The data showing the absolute growth in volume of medulla and cortex of the kidney are given in table 1. Data in terms of relative growth, which may be more easily comprehended, are also given in table 2.

The ratio between the volumes of medulla and cortex of the two rats stunted by underfeeding from birth to three weeks (St 101.3 and St 101.5) is 1:1.79, while the rats stunted from birth to six weeks (St 100.1 and St 100.2) show a ratio of medulla to cortex of 1:1.63. The rats held at maintenance from birth to three weeks (St 214.2 and St 239.10) show ratios of medulla to cortex of 1:1.44 and 1:1.47, while in normal rats of about equal body weight the ratio of medulla to cortex is 1:2.75 or 1:3.05. In normal rats of body weight about equal to those stunted from birth to three weeks the ratio between medulla and cortex is 1:2.91 or 1:2.02. The stunted rats of both periods therefore show a relative volume of cortex apparently below normal and this is more marked at the end of the longer inanition period and still more marked after the period of maintenance. A comparison of the absolute data (table 1) shows this to be due to an increase in the medulla rather than a decrease in the cortex.

The rat refed to 25 grams (St 106.1), after stunting from birth to three weeks, shows a ratio between medulla and cortex of 1:1.81. A normal rat of about the same body weight (V 13.1) has a ratio between medulla and cortex of 1:1.50. On refeeding to 74 grams (St 91.8), after stunting from birth to six weeks, the ratio between medulla and cortex becomes 1:1.95. This is very near the ratio between medulla and cortex in the normal twelve weeks' rat (V 1.8), which is 1:2.00. The cortex of the kidney has therefore increased at a more rapid rate than the medulla, on refeeding after inanition, so as to restore the normal ratio.

The volumetric relations between medulla and cortex are similarly evident from the percentages which each forms of their combined volume (table 2). In rats stunted from birth to three weeks, the medulla forms 36 per cent and the cortex 64 per cent, and in those stunted to six weeks the medulla forms 38 per cent and the cortex 62 per cent. In normal rats of similar body weight (V 2.2; V 1.3), the medulla forms 26 to 33 per cent and the cortex forms 67 to 74 per cent of the volume of the kidney. In rats held at maintenance for three weeks the medulla forms 41 or 42 per cent, while the cortex forms only 58 or 59 per

TABLE 1

RAT NUMBER	SEX	AGE	NOSE-ANUS LENGTH	GROSS BODY WEIGHT	WEIGHT OF BOTH KIDNEYS	TOTAL VOL- UME OF ONE KIDNEY, COR- TEX, AND MEDULLA	VOLUME OF MEDULLA IN ONE KIDNEY	VOLUME OF CORTEX IN ONE KIDNEY	TOTAL NUM- BER OF RENAL COR- PUSCLES PER ONE KIDNEY	NUMBER OF RENAL COR- PUSCLES PER CU. MM. OF CORTEX
1. Normal rats (controls)										
K 2.1	M	Newborn	52	5.4	0.058	cu. mm. 13.7614	cu. mm. 3.6628	cu. mm. 10.0986	{ 15,940 ¹ 12,124 ²	1,578 ¹ 1,201 ²
V 2.1	F	Newborn	51	5.2	0.055	13.1709	3.2504	9.9205	{ 15,533 ¹ 10,465 ²	1,586 ¹ 1,057 ²
V 2.2	M	1 week	67	10.3	0.156	25.6952	6.5662	19.1290	19,682	1,028
V 1.3	M	2 weeks	69	11.8	0.169	44.5020	14.7160	29.7860	24,061	802
V 13.1	F	3 weeks	94	22.6	0.290	76.3424	30.5852	45.7572	25,930	566
V 1.7	M	7 weeks	122	44.6	0.498	131.7852	41.3524	90.4328	28,583	316
V 1.8	F	12 weeks	166	122.2	1.207	325.6988	106.6100	219.0888	28,863	131
2. Rats stunted from birth to three weeks										
St 101.3	M	3 weeks	66	11.5	0.1240	29.5572	10.6020	18.9552	14,661	773
St 101.5	F	3 weeks	67	11.0	0.1406	30.0716	10.7948	19.2768	14,428	748
3. Rats stunted from birth to six weeks										
St 100.1	M	6 weeks	80	13.4	0.1862	43.5330	16.5460	26.9870	26,071	966
St 100.2	F	6 weeks	78	13.6	0.2046	44.5610	16.9310	27.6300	26,165	946
4. Rats held at maintenance from birth to three weeks										
St 214.2	F	18 days	56	5.1	0.0900	20.7536	8.5056	12.2480	15,325	1,252
St 239.10	F	20 days	56	5.0	0.0750	17.6255	7.0502	10.5753	14,916	1,420
5. Rat stunted from birth to three weeks and refed										
St 106.1	F	5 weeks	95	25.6	0.3611	99.0500	35.1800	63.8700	31,447	492
6. Rat stunted from birth to six weeks and refed										
St 91.8	M	13 weeks	133	74.0	0.7794	170.780	57.7300	113.0500	32,826	290

¹ Including renal corpuscles still in stages of formation.² Including only fully formed corpuscles.

TABLE 2
Volumetric ratio of cortex and medulla in the kidney of normal and inanition rats.
Data derived from table 1

RAT NUMBER	AGE	RATIO OF MEDULLA TO CORTEX	PERCENTAGE OF KIDNEY VOLUME FORMED BY		INDEX OF GROSS BODY WEIGHT (GRAMS) DIVIDED INTO VOLUME (CU. MM.) OF	
			Cortex	Medulla	Cortex	Medulla
1. Normal rats (controls)						
K 2.1	Newborn	1:2.75	73	27	1.87	0.64
V 2.1	Newborn	1:3.05	75	25	1.91	0.63
V 2.2	1 week	1:2.91	74	26	1.86	0.64
V 1.3	2 weeks	1:2.02	67	33	2.52	1.25
V 13.1	3 weeks	1:1.50	60	40	2.01	1.35
V 1.7	7 weeks	1:2.10	69	31	2.03	0.93
V 1.8	12 weeks	1:2.00	67	33	1.79	0.83
2. Rats stunted from birth to three weeks						
St 101.3	3	1:1.79	64	36	1.65	0.92
St 101.5	3	1:1.79	64	36	1.75	0.98
3. Rats stunted from birth to six weeks						
St 100.1	6	1:1.63	62	38	2.01	1.23
St 100.2	6	1:1.63	62	38	2.03	1.24
4. Rats held at maintenance from birth to three weeks						
St 214.2	18 days	1:1.44	59	41	2.40	1.66
St 239.10	20 days	1:1.47	58	42	2.11	1.41
5. Rat stunted from birth to three weeks and refeed to 25.6 grams						
St 106.1	5 weeks	1:1.81	64	36	2.49	1.37
6. Rat stunted from birth to six weeks and refeed to 74 grams						
St 91.8	13 weeks	1:1.95	66	34	1.53	0.78

cent. In new-born control rats of about equal body weight the medulla forms 25 to 27 per cent and the cortex 73 to 75 per cent. Kidneys of stunted rats therefore show a somewhat greater percentage of medulla as compared with kidneys from normal rats of corresponding body weight. This condition is most marked after maintenance (body weight held constant). In the refeed rats the percentages are within the normal limits.

The relative growth of medulla and cortex may also be studied from a different point of view by comparing the volume of each with the corresponding total body weight. An arbitrary index of their relative growth is thus obtained, as shown in the last two columns of table 2. Some differences between the test animals and the normal controls are evident, but the data are too scanty to justify any definite conclusions, on account of the individual variability.

3. Effects on the renal (malpighian) corpuscles

a. Total number of renal corpuscles after inanition and refeeding.

As shown in table 1, the total number of renal corpuscles at the end of stunting from birth to three weeks is 14,661 for rat St 101.3 and 14,428 for rat St 101.5. These numbers are intermediate between the number of fully formed corpuscles in the normal new-born rat (V 2.1), which is 10,465 (Kittelson '17) and the number of fully formed corpuscles in the normal rat of corresponding body weight (with somewhat larger kidney) at one week (V 2.2), which was found to be 19,682. If, however, the number of renal corpuscles still in stages of formation in V 2.1 (new-born) is added to the number of fully formed corpuscles, the resulting total number of corpuscles (15,533) is seen to be but slightly in excess of that found after underfeeding from birth to three weeks. In these cases, although the kidney failed to increase in weight, the maturation of renal corpuscles continued, although no new anlagen were formed.

In rats stunted by underfeeding from birth to six weeks (St 100.1, St 100.2), the number of corpuscles is 26,071 and 26,165, respectively. In these cases, the body weight and especially the kidney weight have increased, and the number of corpuscles approaches the full quota usually found in the normal rat kidney (28,000). No corpuscles in stages of formation were seen in the kidneys after either period of underfeeding.

In the rats held at maintenance from birth to three weeks (St 214.2 and St 239.10) the number of corpuscles are 15,325 and 14,916, respectively. The body weight has been stationary in

this case while the kidney weight has increased greatly. The number of corpuscles is practically the same with that found after stunting from birth to three weeks. From the above data it would seem that during underfeeding of greater or less severity the formation of new renal corpuscles may cease for a time, while those already partly formed become fully developed. If the period of underfeeding is lengthened, however, and the body weight be allowed to increase somewhat more, the kidneys increase in size and the formation of renal corpuscles may continue until the final number reached is practically normal, in spite of the continued underfeeding.

In the rat refed to 25.6 grams (St 106.1) after stunting from birth to three weeks, the number of renal corpuscles is 31,447. In the rat refed to 74 grams (St 91.8), after stunting from birth to six weeks, the number is 32,862. Both these numbers are in excess of the number found in the normal adult (28,000, according to Kittelson, '17). The differences are probably too great to be considered as due to individual variations or to errors in counting, although the data are too scanty to be certain. It is possible that the stimulus of underfeeding and refeeding leads to an overproduction of the renal corpuscles.

Noé ('00) noted considerable 'compensatory reparation' in body weight upon refeeding after inanition in rabbits, but in rats he found it to be less evident. He concluded that the compensation depends on the rate of restoration—when the recovery is more rapid, the compensation is less marked. Morgan ('06) points out that the greater power of assimilation of a regenerated part makes it possible for this part to draw the necessary nourishment from the blood, although the amount of nutriment in the blood is below that which is necessary to maintain a status quo in the differentiated tissues. "These slowly decrease in size and in the number of their cells, while the new part is increasing in size and in the number of its cells."

b. Number of renal corpuscles per cubic millimeter of cortex. The data are shown in table 1. The number of renal corpuscles per cubic millimeter of cortex in St 101.3 is 773 and in St 101.5 is 748. These two rats, which were stunted from birth to three

weeks, have an average total number of corpuscles of 14,580, which would normally occur somewhere between birth and one week of age. The number of renal corpuscles per cubic millimeter of cortex, however, would normally occur between two and three weeks of age (V 1.3 and V 13.1). This rapid extension or spreading out of cortical elements is due in part to the growth of the renal corpuscles themselves, but mostly to the rapid growth of the cortical tubules. The rats stunted by underfeeding from birth to six weeks (St 100.1; St 100.2) have 966 and 946 renal corpuscles per cubic millimeter of cortex, respectively. These are larger numbers than are found in the rats underfed for the shorter period. However, the rats stunted from birth to six weeks have almost twice as many corpuscles (total number) as the rats stunted from birth to three weeks. This would largely account for the greater number of corpuscles per cubic millimeter, which are in these rats more closely crowded together than in the normal rats at one week of age (V 1.3).

The rats held at maintenance from birth to three weeks (St 214.2 and St 239.10) have a total of 15,325 and 14,916 corpuscles, respectively, and 1252 and 1420 corpuscles per cubic millimeter of cortex. This condition would normally occur during the first week of life. It seems to show that during early maintenance by underfeeding the cortex nearly ceases to grow except for maturation of the anlagen of corpuscles present at birth. This is clearly indicated by the data for total volume of the cortex (table 1).

Upon refeeding to 25 grams, the number of corpuscles per cubic millimeter of cortex falls to 492. This corresponds very nearly with the normal number found in rats of similar body weight (V 13.1). In the rat refed to 74 grams after underfeeding from birth to six weeks, there are 290 corpuscles per cubic millimeter of cortex, which is somewhat higher than the number (131) seen in rat V 1.8, with a greater body weight, and slightly below that (316) seen in rat V 1.7, with a smaller body weight. This rapid decrease in the number of renal corpuscles per cubic millimeter of cortex during refeeding therefore corresponds to that found during the normal process of growth.

c. Diameter of the renal corpuscles. The diameters of the renal corpuscles are shown in table 3. After the stunting period from birth to three weeks, the diameters are very similar to those in the controls (V 2.2, V 1.3). The differences are small and of doubtful significance.

After underfeeding from birth to six weeks, there is in general an increase in the diameters of the renal corpuscles, especially in rat St 100.2, in which the average diameter exceeds that of the normal at three weeks (V 13.1) with much greater body weight and kidney weight.

After maintenance at constant body weight from birth to three weeks (St 214.2 and St 239.10) there is in general a decrease in diameters when compared with the controls of same body weight (K 2.1 and V 2.1).

After refeeding to 25 grams following stunting from birth to three weeks (St 106.1), the average diameter greatly exceeds this diameter in the normal rat with slightly lower body weight (V 13.1) and is practically equal to that in rat V 1.7, with much higher body weight and kidney weight.

After refeeding to 74 grams following underfeeding from birth to six weeks (St 91.8), the diameters of the renal corpuscles have increased so as to approach those of V 1.8, and are probably approximately normal for corresponding body or kidney weight.

In column g of table 3, the ratio between the number of corpuscles in equal areas of the outer and inner zones of the cortex are shown. They do not differ materially in the test rats and corresponding controls.

From the above data it would seem that underfeeding of young rats does not prevent the growth of renal corpuscles in size, which tends rather to exceed that in the normal kidney of corresponding weight. The shortage in numbers of the renal corpuscles in certain stages of underfeeding may be compensated in this way by increase in volume of the corpuscles. Also on refeeding after underfeeding from birth to three weeks, there is apparently some overgrowth or hypertrophy on the part of the renal corpuscles. That there is a relation between the total number of renal corpuscles and the average diameter of the renal cor-

TABLE 3.
Comparative data on the size of the renal corpuscles in the kidney of normal and inanition rats

BAT NUMBER	AGE	DIAMETER OF RENAL COR- PUSCLES FROM THE OUTER ZONE			DIAMETER OF RENAL COR- PUSCLES FROM THE INNER ZONE			(g) RATIO OF NUMBER OF COR- PUSCLES IN EQUAL AREAS OF OUTER AND INNER ZONE	(h) AVERAGE DIAMETER OF CORPUSCLES (ZONES CON- SIDERED EQUAL IN VOL- UME)	(i) AVERAGE DIAMETER OF CORPUSCLES CORRECTED FOR DIFFERENCE IN VOL- UME OF OUTER AND IN- NER ZONES (ESTIMATED)	(j) TOTAL VOLUME OF COR- PUSCLES IN ONE KIDNEY	RATIO OF TOTAL VOLUME OF COR- PUSCLES TO	
		(a) Maxi- mum	(b) Mini- mum	(c) Average	(d) Maxi- mum	(e) Mini- mum	(f) Average					Kidney	Cortex
1. Normal rats (controls)													
K 2.1	Newborn	80	40	60	98	56	72	57:43	63	62	1.50241	1:9	1:6.7
V 2.1	Newborn	78	40	59	104	56	73	57.5:42.5	64	62	1.29475	1:10	1:7.6
V 2.2	1 week	70	40	49	105	58	65	56.5:43.5	54	52	1.46708	1:11	1:13
V 1.3	2 weeks	70	40	51	89	51	58	56:44	54	53	1.85960	1:23	1:16
V 13.1	3 weeks	89	51	56	93	68	76	55.5:44.5	65	61	3.36586	1:22	1:13
V 1.7	7 weeks	92	72	76	103	74	87	53:47	81	79	6.84566	1:19	1:13
V 1.8	12 weeks	123	91	94	125	93	98	51:49	96	95	12.84648	1:12	1:17
2. Rats stunted from birth to three weeks													
St 101.3	3 weeks	63	39	54	72	55	61	56.5:43.5	57	56	1.33894	1:22	1:14
St 101.5	3 weeks	70	37	55	75	57	65	56:44	59	57	1.38942	1:21	1:13

3. Rats stunted from birth to six weeks

St 100.1	6 weeks	75	42	58	81	54	62	54:46	60	59	2.78430	1:19	1:12
St 100.2	6 weeks	78	46	67	81	58	73	54:46	70	69	4.46964	1:10	1:6

4. Rats held at maintenance from birth to three weeks

St 214.2	18 days	74	40	54	75	54	62	56:44	58	56	1.48957	1:13	1:8
St 239.10	20 days	72	38	52	75	50	60	56:44	57	55	1.29049	1:13	1:8

5. Rats stunted from birth to three weeks and refeed to 25.6 grams

St 106.1	5 weeks	85	67	81	86	70	83	54:46	81	81	8.69003	1:11	1:7
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6. Rats stunted from birth to six weeks and refeed to 74 grams

St 91.8	13 weeks	104	76	85	118	79	97	50:50	91	89	12.03349	1:14	1:9
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puscles is indicated by the fact that while during normal development the number of corpuscles is increasing from birth to two weeks the average diameter of the corpuscles does not increase (Kittelson, '17).

d. Total volume of renal corpuscles and its ratio to that of the cortex and to the total kidney volume. Table 3 shows the total volume of the renal corpuscles and their ratio to the volume of the cortex and to that of the entire kidney. Those stunted by underfeeding from birth to three weeks and six weeks, and by maintenance to three weeks, correspond in general to the normal ratios, excepting rat St 100.2. In this rat, on account of the larger average diameter, the total corpuscular volume appears nearly twice the normal relative size. This hypertrophy of the corpuscles may be an effect of the experiment, although it does not appear in rat St 100.1, which was similarly treated.

The two rats refed after stunting both also show abnormally large relative volumes of the corpuscles, in proportion to kidney or cortical volume. This increase may be due in part to increase in the number of corpuscles, but is due chiefly to increase in average diameter (or volume) of the renal corpuscles.

DISCUSSION AND CONCLUSIONS

The variability of organs as to loss of weight during inanition has been explained in several ways. Manassein ('69) thought that the organs which are most active lose least during inanition. Paschutin ('81) thought that the organs lose in weight in proportion to their storage of available food. If the change in weight were due to the variation in food supply from the blood, then the renal corpuscles ought to maintain themselves much better and grow much faster than the tubules in young animals stunted by underfeeding. Huber ('06) proved conclusively by corrosion preparations (rat, dog, cat, guinea-pig, rabbit) that practically all the blood which nourishes the tubules of both cortex and medulla passes first through the renal corpuscles. The results in the longer underfeeding and refeeding experiments, in which the volume of the corpuscles is disproportionately large, may be due in part to this factor.

The present data indicate that during underfeeding the formation of new corpuscles in the cortex may cease (rats St 101.3, St 101.5, St 214.2, St 239.10). This is in general agreement with the well-known fact that inanition tends to prevent mitosis. For example, Jackson ('17) found that mitosis in the hypophysis ceases in rats held at maintenance by underfeeding from three to ten weeks of age, and reappears again on refeeding for one-half week or more. In these cases the anlagen of corpuscles present at the beginning of the underfeeding continue their process of development, but no new anlagen appear. The renal corpuscles grow in size during the underfeeding period and show a hypertrophy sufficient to overcome their lack in number (as shown by total volume of corpuscles). Sometime during the longer underfeeding period, however, with a somewhat greater increase in body weight and kidney weight, the impulse to form new anlagen (corpuscles) overcomes the inhibition caused by the underfeeding. Thus the hypertrophied kidney during underfeeding tends to develop the number of corpuscles normal for its weight.

Stewart ('19) has found that in new-born rats held at maintenance by underfeeding for two or three weeks the growth impulse in the kidney is very marked, so that it may even double its weight. The present data seem to show that only a small part of this growth takes place in the cortex and that it occurs mostly in the medulla. This is in accord with what was found from birth to three weeks in normal rats (Kittelson, '17). It would seem that the severe inanition of maintenance is not sufficient to inhibit the growth impulse of the medulla. Refeeding after stunting results not only in a hypertrophy of the renal corpuscles, but also in an increase in number, which may even exceed the normal. The data on this point are too few to be conclusive, but the indication is interesting.

SUMMARY

A careful volumetric study of the cortex and the medulla, together with complete enumeration of the renal (malpighian) corpuscles, was made upon serial sections of the kidney of the albino rat after stunting by underfeeding from birth to three weeks, from birth to six weeks, and after maintenance (constant body weight) from birth to three weeks. A rat which had been refed to 25.6 grams after stunting from birth to three weeks and a rat refed to 74 grams after stunting from birth to six weeks were also studied, together with normal controls. The principal results may be summarized as follows:

1. During underfeeding, especially when severe (maintenance), the loss in rate of growth in the medulla is less than in the cortex, which becomes relatively smaller in volume. The normal proportion is restored upon refeeding.

2. During the shorter underfeeding periods, formation of new renal corpuscles ceases, although the anlagen incompletely formed become fully developed. The deficiency in number of corpuscles is apparently overcompensated by a corresponding increase in the size of the corpuscles.

3. During the longer underfeeding period, with somewhat greater body and kidney weight, the formation of new corpuscles continues until practically the normal number is reached. Growth in size of the corpuscles also continues.

4. Refeeding after underfeeding apparently results in hypertrophy of the renal corpuscles, and an increase in their number even beyond normal.

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