COMPENSATORY PHENOMENA IN THE DISTRIBUTION OF THE BLOOD DURING STIMULATION OF THE SPLANCHNIC NERVE

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A study of the transfer of the blood from the arterial to the venous side, during periods of vasoconstriction affecting the splanchnic area, requires the special consideration of two factors; namely, the quantity of blood that flows through the portal circuit, and the quantity of blood that traverses other divisions of the circulatory system.

The blood flow in the portal vein of the dog has been carefully studied by Burton-Opitz,[1] measurements having been made upon the flow in the main trunk as well as in the tributaries. It has been shown that vasoconstriction in the abdominal viscera causes a marked diminution in the portal flow. The amount of decrease during a period of about 20 seconds of moderate stimulation of one splanchnic nerve was as much as one-fourth of the quantity normally flowing through this vein. In work upon the magnitude of the portal flow it is stated "that a dog having an average body weight of 14.3 kgm. possesses a portal flow of 268.2 cc. per minute." If we assume that the total quantity of blood is one-thirteenth of the body weight, it is obvious that about one-fourth of the entire blood-supply normally passes through the portal circuit. This would mean that about one-sixteenth of the blood of the animal, or approximately

[1] Burton-Opitz: Archiv für die gesammte Physiologie, cxxiii, p. 553, 1908; cxxiv, p. 495, 1908; cxxix, p. 189, 1909; cxxxv, p. 205, 1910; and Quarterly Journ. Physiol., 1911, iv, p. 113.

68 cc. per minute, must find its way into the venous channels during splanchnic vasoconstriction through some other course, because the accumulation of this quantity of blood on the arterial side would soon produce a greatly diminished venous return to the heart and consequently a diminished ventricular output.

The large vascular area over which the splanchnic nerve exercises a powerful vasomotor influence, has been regarded as occupying a reciprocal relation to other parts of the body. Thus Dastre and Morat[2] state that a vasoconstriction in the abdominal portal vessels is accompanied by a dilatation of the cutaneous vessels, and they postulate that a vasoconstriction of the cutaneous vessels denotes a dilatation of the splanchnic area. A similar view has been expressed by Bayliss and Bradford[3] who state that there is an antagonism of a physiological character existing between the vessels of the limb and those of the splanchnic area—the latter exercising the predominant influence. v. Anrep[4] similarly describes the splanchnic nerve as the regulator of the blood-supply of the body.

By means of the plethysmographic method it has been demonstrated that the volume of the intestine,[5] kidney,[6] and spleen,[7] is greatly diminished during stimulation of the splanchnic nerve, and a similar phenomenon has been shown with the hind limbs.[8] These observations are of interest in this connection because of the bearing they have upon the use of the changes in the volume of an organ as an index of the quantity of blood flowing through it. If an increase or a decrease in volume were an infallible index of respective changes in the blood-flow, then obviously the simultaneous diminution in the volume of the internal organs and the extremities would produce a condition of arterial stagnation. The present paper presents some results of a study of the blood-flow through other parts of the body during periods

[2] Dastre and Morat: Arch. de Physiol., 1882, p. 337.
[3] Bayliss and Bradford: Journ. Physiol, 1894, xvi, p. 10.
[4] v. Anrep: Journ. Physiol., 1912, xlv, p. 307.
[5] Hallion and Francois-Franck: Arch. de Physiol., viii, p. 493.
[6] Cohnheim and Roy: Arch. f. Pathol. Anat., xcii, p. 424, 1882.
[7] Roy: Journ. Physiol., 1880–82, iii, p. 203.
[8] Bayliss: Journ. Physiol., 1902, xxviii, p. 220 and v. Anrep; loc. cit. p. 310.

in which there is a lessened flow through the portal circuit. I have experimented with the circuits of the head and posterior extremity. Measurements of the blood-flow were taken from the carotid artery, jugular vein, femoral artery, and femoral vein. The data obtained from these divisions of the circulatory system enable us to determine the extent of compensation for the diminished transfer of blood through the portal circuit.

Method of investigation. The experiments were performed upon dogs weighing 6 to 12 kgm. Narcosis by means of ether was maintained in all animals throughout the experiments. The general blood-pressure was determined in the left femoral artery by means of a mercury manometer. The left greater splanchnic nerve was exposed through the peritoneal cavity, isolated for about 1 cm. centrally to the left suprarenal capsule, and placed in shielded electrodes. In some experiments the nerve was divided and in others it was left intact, but in the two cases the general character of the results did not differ materially.

At the outset information was sought regarding circulatory conditions by registering venous pressures in different parts of the body. Such determinations, however, serve only as an index of qualitative changes in the volume of the blood-flow through a part; for example, an increased venous pressure is indicative of a greater flow, and decreased pressure an indication of a lessened flow. In addition I have made quantitative determinations of the blood-flow in the circuits of the head and posterior extremity by means of the recording stromuhr described by Burton-Opitz.[9]

The determinations of venous pressure were made in all cases by means of an ordinary manometer filled with saline solution and connected in most cases with the blood-vessel by means of a T-canula. The readings were made at short intervals and inserted directly beneath the tracing of the arterial blood pressure.

[9] Burton-Opitz: Arch. f. d. gesammte Physiol., 1908, cxxi, p. 150.

OBSERVATIONS OF VENOUS PRESSURE

1. Femoral vein. Vasoconstriction in the splanchnic area produces a gradual increase in the lateral blood pressure in this vein which attains its maximum value shortly after the maximum height of the systemic arterial pressure has been reached. It is followed by a fall, which is essentially identical in character with the phase of increasing pressure. While the changes in venous pressure pursue a course that is practically parallel to that of the arterial pressure, a slight difference in the time relationship is noticeable. For example, an average of a series of ten readings taken after stimuli of slightly different intensity and duration, shows the maximum arterial pressure in twenty-four seconds after the beginning of the stimulation, while the corresponding venous readings show the maximum pressure in thirty-three seconds after the beginning of the stimulation.

The readings of arterial pressure in this set of experiments show an average increase of 25.2 mm. Hg, while the average venous pressure is 13 mm. water or approximately 0.96 mm. Hg. This increase in venous pressure is proportionally large, because the average normal pressure in this series of experiments was 4.9 mm. Hg, a value that may be regarded as representing a normal pressure since it is only 0.5 mm. Hg less than the average pressure obtained by Burton-Opitz[10] in eighteen dogs ranging in weight from 6 to 24 kgm.

In table I are compiled the changes in pressure in the femoral vein upon stimulation of the splanchnic nerve.

In view of the work of v. Anrep[11] upon the relation between the changes in the volume of the posterior extremity and the activity of the adrenal glands, I have paid especial attention to any possible change in venous pressure coincident with the second phase in the rise of arterial blood-pressure. I have been unable to observe any indication of an alteration in the blood-flow at this period. v. Anrep attributes the secondary rise in general pressure which follows stimulation of the splanchnic, to

[10] Burton-Opitz: Amer. Journ. Physiol., 1903, ix, p. 198.
[11] v. Anrep: loc. cit. p. 310.

TABLE I

EXPERIMENT	NERVE STIMULATED	DURATION OF STIMULATION IN SECONDS	SECONDS AFTER BEGINNING OF STIMULATION	PRESSURE IN FEMORAL ARTERY IN MM. Hg.	PRESSURE IN FEMORAL VEIN IN MM. H_2O
				74	85
			6	84	90
			17	90	95
I	L. splanchnic nerve undivided	27	27	84	100
			32	76	95
			41	70	90
			47	70	85
				90	80
			9	74	85
			23	80	95
II	L. splanchnic nerve undivided	40	34	72	93
			39	70	90
			51	68	85
				95	65
			6	114	70
			11	120	80
III	L. splanchnic nerve divided	53	25	146	85
			37	144	80
			50	132	72
			102	102	70
			108	98	65
				130	50
			16	166	55
			24	168	55
IV	L. splanchnic nerve undivided	46	32	160	60
			40	154	55
			58	134	55
			66	134	50
				66	50
			11	76	55
			26	88	60
V	L. splanchnic nerve divided	37	36	80	64
			45	72	60
			64	66	55
			82	66	50

a powerful vasoconstriction in the peripheral blood vessels as a result of an increased quantity of adrenalin in the circulating blood at this time. In support of this view he has shown a decrease in the volume of the extremities. If the diminished volume of the posterior extremities were accompanied by a marked decrease in the transfer of blood within the limb, we would expect to obtain a drop in the blood-pressure in the femoral vein following closely upon the second phase in the arterial blood-pressure rise. But the absence of such a drop in pressure should not be interpreted, I believe, as opposed to the conclusions of v. Anrep; on the contrary, it indicates that changes in the volume of the posterior extremity cannot be relied upon to give an index of the quantity of blood flowing through it.

2. External jugular vein. It has been shown by Tschuewsky[12] that the blood supply of the head is about four times greater than that of the posterior extremity. If one reasons from analogy, it is evident that the head must play an important part in compensating for the diminished transfer of blood through the portal system. The external jugular vein was selected, because it is the principal vessel for the return of blood from the head.

The results obtained from five experiments on the external jugular vein are arranged in table II.

It will be seen that there is a marked increase in pressure during the stimulation of the splanchnic nerve, which is evident in this particular set of experiments as an average rise in pressure of 1.8 mm. Hg. If contrasted with the increase in femoral venous pressure, the external jugular vein shows an absolute rise that is much greater. The quantitative variation in pressure indicated in this table is characteristic of all of the experiments upon this vein. It can readily be observed that the difference in the degree of increase in the three different animals from which these observations were taken is comparatively small.

The rate of increase in pressure in the external jugular vein as compared with that in the femoral is significant in showing

[12] Tschuewsky: Arch. f. d. gesammte Physiol., 1903, xcvii, p. 386.

TABLE II

EXPERIMENT	NERVE STIMULATED	DURATION OF STIMULATION IN SECONDS	SECONDS AFTER BEGINNING OF STIMULATION	PRESSURE IN FEMORAL ARTERY IN MM. Hg	PRESSURE IN FEMORAL VEIN IN MM. H_2O
I	L. splanchnic nerve undivided	28		60	20−
			7	76	15−
			12	80	10−
			14	80	5−
			18	88	0
			23	90	5
			30	82	0
			33	76	5−
			38	64	10−
			44	60	15−
II	L. splanchnic nerve undivided	30		66	20−
			5	82	15−
			9	92	10−
			12	96	5−
			14	98	0
			20	102	5
			33	86	0
			36	78	5−
			39	72	10−
			44	68	20−
III	L. splanchnic nerve undivided	17		56	5−
			4	70	0
			7	72	5
			12	72	10
			26	70	13
			30	64	10
			42	58	5
			68	60	0
IV	L. splanchnic nerve divided	37		86	20−
			5	104	15−
			10	120	10−
			14	120	5−
			16	120	0
			19	118	5
			24	116	10
			30	110	12
			46	100	10
			53	96	5
			62	94	0
			77	98	5−
V	L. splanchnic nerve undivided	37		136	30
			2	140	35
			6	156	45
			9	162	50
			12	162	55
			26	152	50
			35	140	45
			41	136	40
			64	136	30

a very close relationship between the two. For example, the time required for a 5-mm. increase in pressure in each vein is directly proportional to the total increase in pressure in each vein. It is evident, therefore, that the accelerated flow through the limb and that through the head are dependent upon essentially identical haemodynamic factors. Moreover, the comparatively large jugular flow might well be expected to show any temporary fluctuations in pressure that would result from a vasomotor action either in other parts of the body exclusive of the splanchnic area, which would tend to shift the blood-stream, or any possible vasomotor changes that might occur in the head circuit. The uniform character of the records during the entire phase of changed pressure makes the existence of such secondary alterations extremely doubtful.

The absence of secondary variations in the blood-pressure, and particularly of a decrease, is taken to mean that the circuit of the head offers at no time an effectual hindrance to the blood-flow through this part. Furthermore the degree of increase in pressure in the external jugular vein, permits of rating the head circuit as a most important factor in counterbalancing the diminished transfer of blood through the portal system.

In some experiments venous pressures were determined in the vicinity of the right auricle by inserting a catheter through the right external jugular vein into the superior vena cava. The most striking feature of these measurements is an initial rise in pressure amounting to only from 5 to 10 mm. of water. Subsequently the pressure returns rapidly to normal, and may even at times reach a value very slightly below the normal for a short period. It is evident, therefore, that the change in blood-pressure close to the heart is very slight. The temporary increase is probably due to a squeezing out of the blood from the portal vessels from vasoconstriction in the splanchnic area. From these considerations it appears that other channels have equalized the transfer of blood so that the pressure close to the heart, and therefore, the volume of the blood returned, is affected very little.

3. Pancreatic and renal veins. A few experiments were made upon these veins to obtain information regarding the pressure conditions in them, because they represent venous channels in which a decrease in the blood-flow is known to occur during splanchnic vasoconstriction. The results were somewhat varied, showing in some cases fairly regular, in others fluctuating changes. One set of readings (table III) will illustrate the essential character in the pancreatic vein.

It will be noted that the changes in venous pressure occur simultaneously with those in the general pressure, but in an inverse relation. While the fall in pressure was not always so great as shown in this set of readings, an initial drop was observed in every case—a result the opposite of that obtained with the femoral and jugular veins.

Similarly in the renal vein there was obtained a drop in pressure. In this case, however, the fall was usually small and after

TABLE III

Left divided splanchnic nerve stimulated for twenty-three seconds

Seconds after beginning of stimulation		11	16	21	32	36	40
Pressure in femoral artery in mm. Hg	86	110	118	124	116	112	108
Pressure in pancreatic vein in mm. H_2O	100	95	90	80	90	100	110

this initial drop of a few millimeters there was in many cases a partial return to the normal before the rise in general pressure reached a maximum. It is evident from readings taken from the central end of the renal vein, and from a catheter inserted into the inferior vena cava, that the pressure does not change markedly in the latter vessel during vasoconstriction in the splanchnic area. The pressures in the renal vein were of necessity measured close to the vena cava, therefore the small drop in renal pressure was due, I believe, to the equalizing tendency of the nearly uniform pressure in the large vena cava.

The experiments upon the pancreatic and renal veins show an unmistakable drop in pressure. The fall is in many cases small but the principal significance lies in the fact that it shows a direct relationship between the changes in venous blood-pressure and the volume of the blood-flow.

MEASUREMENTS OF THE BLOOD-FLOW

1. Flow through the head. The experiments upon the blood-pressure in the external jugular vein gave results that indicate an increased flow through the head during stimulation of the splanchnic nerve. The method, however, was not applicable to quantitative determinations. The experiments now to be described were undertaken with this end in view. It was also hoped that the data obtained would give information regarding the proportional amount of compensation for the diminished portal flow which is afforded by the head circuit.

The blood-flow in the external jugular vein was taken as the index of flow through the head, because it is the principal vessel for the return of the blood from this part. In the results of these experiments three things are obvious—first, vasoconstriction in the splanchnic area produces a marked increase in the blood-flow through the head; second, the changes in the flow occur in the same general manner as the changes in blood-pressure within the vein; and third, there is no evident diminution in the flow coincident with the second phase in the increase in arterial blood pressure.

It will be seen from table IV that the average blood-flow prior to the stimulation of the splanchnic nerve was about 1.99 cc. in a second and the average systemic blood pressure corresponding to this blood-flow was 0.89 mm. Hg. In terms of a systemic pressure of 100 mm. Hg, this would give a flow of 2.23 cc. per second, a value that is close to the average normal of 2.4 cc. per second obtained by Burton-Opitz.[13] Stimulation of the splanchnic nerve with current of moderate strength for an average period of forty-four seconds gave an increase of about 12.5 per cent in the amount of blood-flow through this vein.

In table IV are arranged the results of five experiments upon the flow in the jugular vein.

Let us turn for a moment to the proportional compensatory action afforded by this circuit. If we take the average normal flow in the external jugular as 144 cc. per minute, 2.4 cc. per

[13] Burton-Opitz: Amer. Journ. Physiol.. 1902, vii, p. 435.

TABLE IV

Experiment 1

PHASE OF STROMUHR	DURATION OF PHASE	QUANTITY OF BLOOD PER PHASE	QUANTITY OF BLOOD PER SECOND	PRESSURE IN FEMORAL ARTERY IN MM. Hg.	CONDITIONS
	seconds	*cc.*	*cc.*		
1	10.2	21.75	2.13	82	Before stimulation of left splanchnic nerve
2	13.6	21.75	1.60	82	
3	12.0	21.5	1.79	82	
4	12.4	21.75	1.75	95	During stimulation
5	9.8	21.75	2.22	104	
6	10.4	21.50	2.06	106	
7	9.5	21.75	2.28	106	
8	11.0	21.75	1.97	106	
9	10.5	22.5	2.14	100	After stimulation
10	12.2	22.5	1.84	94	
11	12.8	21.75	1.62	90	
12	14.0	21.2	1.51	88	

Experiment 2

1	9.2	21.0	2.28	70	Before stimulation of left splanchnic nerve
2	10.4	19.7	1.89	70	
3	9.8	20.0	2.05	72	
4	10.0	20.5	2.05	80	During stimulation
5	8.2	21.5	2.62	84	
6	9.0	20.7	2.30	90	
7	7.6	21.5	2.83	94	
8	8.8	21.7	2.41	96	
9	6.2	20.2	3.25	98	
10	8.5	19.5	2.29	94	After stimulation
11	7.5	20.7	2.76	90	
12	10.8	22.0	2.10	86	

Experiment 3

1	12.4	20.75	1.67	84	Before stimulation of left splanchnic nerve
2	20.0	21.2	1.06	84	
3	13.6	21.2	1.56	98	During stimulation
4	17.0	21.75	1.28	106	
5	11.2	21.5	1.92	106	
6	16.5	21.0	1.27	104	After stimulation
7	15.0	20.75	1.38	98	

TABLE IV—Continued

Experiment 4

PHASE OF STROMUHR	DURATION OF PHASE	QUANTITY OF BLOOD PER PHASE	QUANTITY OF BLOOD PER SECOND	PRESSURE IN FEMORAL ARTERY IN MM. Hg.	CONDITIONS
	seconds	*cc.*	*cc.*		
1	11.8	22.2	1.96	76	Before stimulation of left splanchnic nerve
2	15.6	21.2	1.36	76	
3	11.5	21.0	1.73	76	During stimulation
4	14.0	21.75	1.55	94	
5	9.5	22.5	2.36	98	
6	13.8	22.0	1.59	100	
7	9.3	21.2	2.27	100	After stimulation
8	16.0	21.5	1.33	88	

Experiment 5

1	8.4	20.0	2.38	136	Before stimulation of left splanchnic nerve
2	5.2	19.7	3.78	136	
3	6.8	19.7	2.89	136	
4	5.5	19.2	3.48	136	
5	7.5	18.7	2.49	136	
6	5.0	18.7	3.74	144	During stimulation
7	6.8	19.2	2.82	154	
8	5.2	19.7	3.78	160	
9	8.4	19.5	2.32	144	
10	5.5	19.5	3.54	122	
11	8.5	19.2	2.25	120	After stimulation
12	7.5	18.7	2.65	130	

second, then during the period of stimulation of the splanchnic nerve there is an increase of approximately 17 cc. in a minute. The compensation offered by the head circuit as figured on this basis would amount to 34 cc. in a minute for the two external jugular veins. This value, however, would probably not represent the total compensation afforded by the head portion of the circulatory system, because the internal jugulars may be expected to take a part proportional to their normal volume of flow. Bearing in mind now the fact stated in the early part of this paper that splanchnic vasoconstriction may produce a diminished transfer of blood through the portal circuit, to the extent of about 68 cc. in a minute, it is obvious that the head circuit alone is capable of compensating for more than one-half of this quantity.

The average flow in these experiments during stimulation of the splanchnic nerve was 2.26 cc. per second, and the average systemic pressure for the same period, obtained by taking the mean pressure for each phase of the stromuhr, was 107 mm. Hg. These values give a volume of flow per 100 mm. Hg pressure, of 2.11 cc. per second. If we now compare this with the normal flow of 2.23 cc. per second, obtained in these experiments, it is evident that there is a greater volume of flow per second with

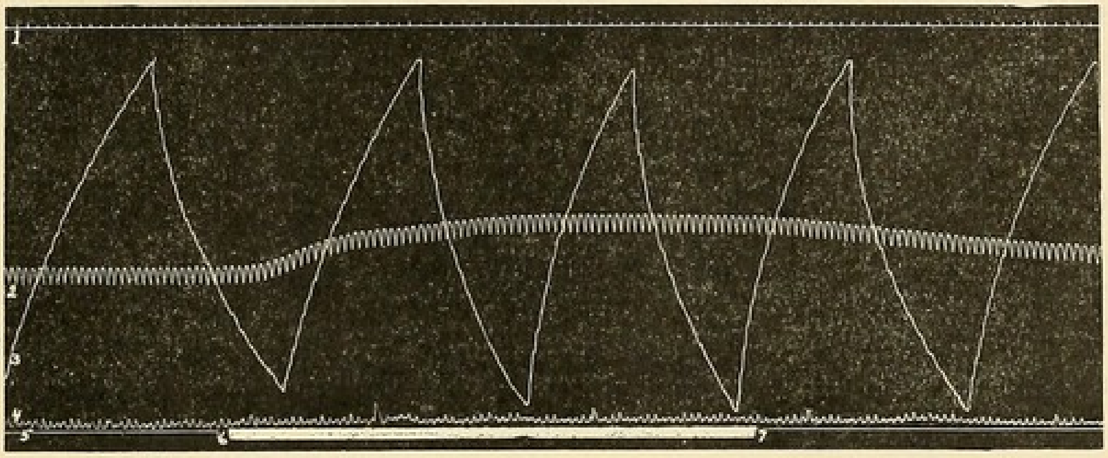

FIG. 1 RECORD OF THE ACCELERATED BLOOD-FLOW IN THE EXTERNAL JUGULAR VEIN DURING STIMULATION OF THE L. SPLANCHNIC NERVE

1, Time in seconds; *2*, blood-pressure in femoral artery (mercury manometer); *3*, stromuhr; *4*, blood-pressure in jugular vein (membrane manometer) *5*, zero blood pressure; *6* to *7*, period of stimulation.

the high systemic blood-pressure, yet in proportion to the head of pressure there is a diminished efficiency. The increase in the flow bears a close relation to the corresponding changes in blood-pressure, as is illustrated in figure 1. There is first a short latent period which is followed by a gradually increasing flow. The maximum flow is usually attained at about the time of highest systemic blood-pressure. If the period of stimulation is short, e.g., ten to fifteen seconds, the maximum flow does not appear until after the cessation of the stimulation.

The graphic tracing of the blood-flow, with respect to the two phases in the increase of systemic blood-pressure, shows no indication of a variation that could be associated with a vasomotor activity in the carotid circuit. The first phase in the rise of blood-pressure is so short that it is questionable whether its effect could be demonstrated with the stromuhr, but in case of the second phase, there is obviously no marked change in the volume of blood-flow. If the diminished volume of the extremities, said to occur at this time, were accompanied by a pronounced decrease in the blood-flow in these parts; then secondary alterations in the already accelerated blood flow through the head circuit might be expected to occur. The fact that no such secondary changes in the flow have been recorded in these experiments, if taken together with the results obtained upon the femoral vein which are to follow, support the view that the volume decrease of the limb is insufficient to cause a marked change in the blood-flow through these parts.

2. Flow through the posterior extremity. This series of experiments was made upon the femoral vein and femoral artery. In brief the results show an increased flow through this part during splanchnic stimulation, and no retardation coincident with the second rise in general blood-pressure. The total compensation through this circuit is much smaller than that afforded by the head circuit, because the total blood-flow is relatively small.

Femoral vein. The average obtained from five experiments upon the flow in this vein shows an increase of a fraction less than 15 per cent with an initial mean systemic pressure of 91 mm. Hg, a period of stimulation of thirty-three seconds, and a mean systemic pressure during this period of 130 mm. Hg. The graphic record of this increase in blood-flow is very similar in character to the record of the same phenomenon in the jugular vein. Likewise there is shown in the actual percentage increase in the blood-flow in the two cases a difference of about 2.5 per cent which is well within the limit of experimental error.

The average normal blood-flow in the femoral has been determined[14] as 0.85 cc. per second This value taken with the per-

[14] Burton-Opitz: Amer. Journ. Physiol., 1903, ix, p. 161.

centage of increase obtained in this set of experiments permit of quantitative data upon the compensatory flow through the posterior extremities. Each extremity upon this basis would afford a compensation of about 7.6 cc. per minute or 15.2 cc. per minute for the two posterior extremities. If we assume that the circulation of the anterior extremity gives an increase of blood flow, during stimulation of the splanchnic nerve, approximately the same as obtained from the posterior extremity, the total quantity of blood prevented from returning to the venous side by way of the portal vein (see p. 15) during vasoconstriction in the splanchnic area, is practically all compensated for by the circulations of the head and extremities.

In table V are compiled data from four experiments to show the increase in flow in the femoral vein during the period of stimulation of the splanchnic nerve.

A final feature evident from the records of the experiments now under discussion is a lack of correlation between the rate of the blood-flow through the limb and the changes, said to occur, in its volume. It has been demonstrated[15] that the second phase in the general rise of blood-pressure resulting from stimulation of the splanchnic nerve is accompanied by a diminished volume of the limb, and such changes have been associated with a diminished blood-flow. But in my experiments the blood-flow was not diminished at this phase in the blood-pressure rise; on the contrary the flow was always accelerated during the entire phase of raised systemic blood-pressure, and in many cases the maximum flow was recorded towards the end of or immediately following the second phase in the blood-pressure increase. This fact has a greater significance when the total blood exchange is considered. A diminished volume of some of the abdominal organs has already been referred to on page 16, and moreover it has been shown[16] that in these organs there is a decrease in blood-flow following stimulation of the splanchnic nerve. If the volume of the limb were likewise accompanied by a significant diminution in the blood-flow through it, then the circulation of

[15] v. Anrep: loc. cit. p. 307.
[16] Burton-Opitz: loc. cit.

TABLE V

Experiment 1

PHASE OF STROMUHR	DURATION OF PHASE	QUANTITY OF BLOOD PER PHASE	QUANTITY OF BLOOD PER SECOND	PRESSURE IN FEMORAL ARTERY	CONDITIONS
	seconds	*cc.*	*cc.*	*mm.*	
1	22.0	18.7	0.85	114	Before stimulation of left splanchnic nerve
2	23.0	18.5	0.80	114	
3	17.0	17.2	1.0	124	During stimulation
4	12.5	17.5	1.40	124	
5	11.0	19.5	1.70	110	
6	15.0	19.5	1.30	108	
7	17.0	8.7	1.10	106	After stimulation

Experiment 2

1	25.0	18.0	0.72	114	Before stimulation of left splanchnic nerve
2	21.5	18.0	0.86	122	During stimulation
3	16.6	19.0	1.14	126	
4	14.5	19.2	1.32	118	
5	19.3	19.72	1.00	112	After stimulation
6	24.2	17.2	0.71	112	

Experiment 3

1	38.0	15.5	0.40	90	Before stimulation of left splanchnic nerve
2	12.0	5.5	0.46	94	
3	19.0	11.0	0.60	108	During stimulation
4	22.0	18.0	0.82	104	
5	25.0	18.5	0.74	118	After stimulation

Experiment 4

1	22.8	21.0	0.91	84	Before stimulation of left splanchnic nerve
2	17.2	20.7	1.20	84	
3	18.2	22.2	1.22	86	During stimulation
4	9.3	23.0	2.5	106	
5	11.8	22.2	1.88	104	
6	10.0	21.5	2.15	94	
7	13.2	21.2	1.60	90	After stimulation
8	12.0	22.0	1.66	90	
9	14.2	21.5	1.51	90	
10	13.2	20.5	1.55	90	

the extremities would antagonize the circulation of the splanchnic area and there would result a greatly lessened transfer of blood to the venous side. The pressure conditions in different parts of the venous system, as set forth in the first part of this paper, indicate that the venous return is not materially lessened during splanchnic vasoconstriction.

The absolute decrease in the volume of the limb is not evident in the studies[17] upon this subject. But from the method employed in registering this change, and the solid character of the organ itself, it seems probable that the change is very small. From these considerations the conclusion seems warranted that the diminution in the volume of the limb is not sufficient to affect appreciably its blood-flow.

Femoral artery. A few experiments were made upon the blood-flow in this artery to determine whether the inflow to the posterior extremity corresponds, at all closely, to the outflow; since the possibility exists that a part of the accelerated outflow may be due to a squeezing out of the contained blood from vasoconstriction in this organ. The records show an increase in the arterial blood-flow, which is essentially identical in character with that obtained from the femoral vein. An average of three experiments shows an increase of 16.8 per cent, a value that is likewise very close to similar determinations upon the femoral vein. In fact this uniformity in the general character of the records, and the close agreement in the percentage increase in the blood-flow, are the most significant features of the results. These observations make it probable that the accelerated flow in the femoral vein is independent of mechanical factors within the limb.

3. Flow through a denervated kidney. In this series of experiments the left kidney was used in all cases. It was isolated from nervous influences by dividing all the nerve fibers leading to it. The blood-flow through such an organ might be expected, a priori, to follow the changes in general blood-pressure. I proceeded to investigate this by first making use of the oncometric

[17] Bayliss: loc. cit. p. 222; v. Anrep: loc. cit. p. 310.

method to record the changes in the volume during stimulation of the splanchnic nerve. In this feature my results agree essentially with those of v. Anrep. Figure 2 shows a graphic record of a typical experiment of this kind. Here the rapid increase in volume during the initial rise in systemic pressure is attributed to a passive dilatation of the blood-vessels produced by the increased systemic blood-pressure. The sudden decrease in the volume coincident with the second phase in the rise of general blood-pressure is attributed to the augmented secretion of ad-

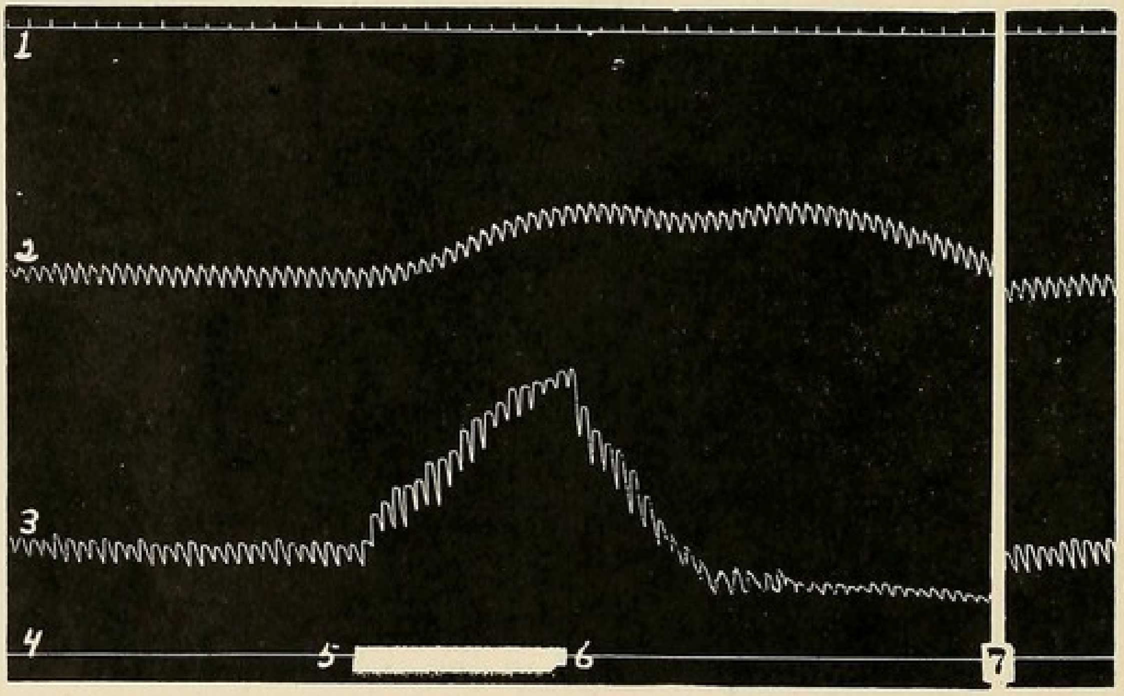

FIG. 2 RECORD OF THE CHANGES IN THE VOLUME OF A DENERVATED KIDNEY DURING STIMULATION OF THE L. SPLANCHNIC NERVE

1, Time in seconds; *2*, blood-pressure in femoral artery (mercury manometer); *3*, volume of the kidney (oncometer); *4*, zero of blood pressure; *5* to *6*, period of stimulation; *7*, interval of 40 seconds.

renalin from stimulation of the splanchnic nerve. This phase, namely, the decrease in the volume, I have been able practically to abolish by using a short series of stimulations. Each stimulation was maintained for a period of about twenty seconds, and repeated four to six times at intervals of about fifty seconds. In this case the supply of adrenalin had evidently become exhausted, because the splanchnic vasomotor mechanism was still capable of producing the initial rise in general pressure but the secondary rise was not shown.

In order to determine whether there is a correlation between these changes in volume of the kidney and the quantity of blood traversing it, I made records of the blood-flow by inserting the stromuhr into the renal vein. The results show a moderate increase in flow during practically one phase of the record of the stromuhr. This increase follows very closely upon the application of the stimulation to the splanchnic nerve, and its duration is apparently identical with the increase in the volume described above. Subsequently there is a marked diminution in the flow, which continues during the remainder of the stimulation period and for a time thereafter. In fact this retarded, yet gradual, return to the normal flow is one of the striking features of the experiment. The decrease in flow occurs simultaneously with the second phase in the rise in systemic blood-pressure. In this feature it coincides, therefore, with the decrease in the volume of this organ described by v. Anrep and corroborated by experiments given in this paper. It can hence be accepted without question that this diminished blood-flow is produced by the action upon the renal blood vessels of the adrenalin, which is present in the circulating blood in larger quantities at this time.

The observations described above make it, I think, clear that the rate of the blood-flow through a denervated kidney does not passively follow the rise in general blood pressure, as it might at first thought be expected to do. In this feature my records differ slightly from those obtained by Burton-Opitz[18] but this discrepancy is more apparent than real since it has been shown that the decrease in flow occurs during longer periods of time than were used in the experiments of Burton-Opitz. Further it is to be noticed that there is an unquestionable relationship between the relative volume of this organ, and the quantity of blood flowing through it at any given time during the period of splanchnic stimulation. This is no contradiction to the conclu-

[18] Burton-Opitz: Arch. f. d. gesammte Physiol., 1909, cxxvii, p. 143.

sion reached on page 32 regarding the change in the volume of the posterior extremity and its blood-flow. The two cases are essentially different, in that the kidney presents a small, flaccid, and highly vascular organ, in which the absolute changes in volume are proportionally large; while the limb is large its tissue is much firmer in character, and from the evidence obtainable it appears that the absolute changes in volume are proportionally small. For these reasons it seems probable, that the total vascular area of the limb would be insufficiently affected by the diminution in volume, from the increased adrenalin in the blood, to produce a retarding action upon the blood-flow through it.

The facts here reported seem to emphasize the necessity of using caution in drawing conclusions regarding the blood-flow through an organ from determinations of its changes in volume.

SUMMARY

Stimulation of the splanchnic nerve produces changes in the distribution of the blood that permit of the following conclusions:

1. The blood-pressure in the femoral vein shows an average increase of 0.96 mm. Hg from stimulation for forty seconds. The phases of increase and final return to normal closely agree with similar changes in the general pressure.

2. An average increase of 1.8 mm. Hg was obtained in the external jugular vein by stimulation for thirty seconds.

3. In the pancreatic and renal veins a fall in pressure results, which is usually small and variable in character. A few determinations in the inferior and superior vena cava indicate slight changes in the pressure.

4. The measurements of the blood-flow in the external jugular vein show an increase of 12.5 per cent. Estimated from the normal flow this gives for the two jugular veins a compensatory flow of 34.4 cc. per minute.

5. The blood-flow in the femoral vein showed an increase of 15 per cent. The estimated compensatory flow in this case gave a value for the two posterior extremities of 15.3 cc. per minute.

6. If we assume that the circulation of the anterior extremities affords an accelerated flow approximately equal to that of the posterior extremities, then the increased transfer of blood permitted by the vascular circuits of the head and extremities together is sufficient to compensate for the diminished flow through the portal circuit.

7. There is no indication in either the readings of venous pressure or the stromuhr records from the jugular and femoral veins of a change in flow coincident with the second phase in the rise of the general blood-pressure.

8. The denervated kidney showed a correlation between its relative volume and the quantity of blood flowing through it. There was a temporary increase in flow coincident with the initial increase in volume, and a marked decrease in the flow corresponding to the similar change in the volume.

9. A change in the volume of an organ is not an infallible criterion of the relative quantity of blood flowing through it.

I wish to express my sincerest thanks to Prof. Frederic S. Lee for his kind advice and criticism. I have much pleasure also in thanking Prof. R. Burton-Opitz for suggesting the problem and for invaluable help he has given me throughout the work.

VITA

I was born on September 7th, 1882, in Oxford, Maine, and was graduated from Hebron Academy with the class of 1902. I entered the University of Maine in the same year and received the degree of Bachelor of Science in 1906. In the summer season of 1905 I completed the course in Invertebrate Zoology, and in 1906 the course in Embryology, at the Marine Biological Laboratories, Woods Hole, Massachusetts.

I entered upon my duties as assistant in biology at the University of Maine in 1906, was advanced to instructor in 1907, and was appointed assistant entomologist in the Maine Agricultural Experiment Station in June, 1908. I resigned this position in the autumn to accept an assistantship in zoology in Columbia University for 1908-09, and in the summers of 1909 and 1910, I received appointment to the same position for the Summer School session. In the autumn of 1909 I was appointed tutor in the College of the City of New York, and have now been advanced to instructor for 1914-15.

I have spent several summers at the research laboratories of the Marine Biological Association, and the United States Bureau of Fisheries, at Woods Hole, Massachusetts. During a part of this time I studied the anatomy and the vasomotor phenomena of the sympathetic nervous system in the turtle, and the results of this were published in the American Journal of Physiology, volume thirty-three, 1914.

August 20th, 1914 (Sigeed) DAYTON JAMES EDWARDS