

A CONTRIBUTION TO THE PHYSIOLOGY OF THE
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A NUMBER of researches carried out in the Cambridge laboratory have pointed to the conclusion that the spleen has a very definite function which is, after all, but the expression of the two chief features in the structure, namely the muscular character of its framework and the extravascular condition of the red blood corpuscles which it contains. This function may be described briefly as that of acting as a reservoir for erythrocytes. J. and H. Barcroft⁽¹⁾ elaborated a technique for comparing the percentage of CO hæmoglobin in the spleen with that in the general circulation under known conditions of carbon monoxide inhalation and showed that there was a much greater lag in the rate at which CO entered the hæmoglobin of the spleen, than that of other organs. This presumably was due to the fact that the blood was outside the general circulation and indicated that the separation was functionally much more complete than was usually supposed. Hanak and Harkavy⁽²⁾ expanded these experiments and showed that in animals which were at rest, two hours' respiration of concentrations of CO sufficient to raise the COHb in the blood to 20 p.c. might elapse before any CO appeared in the spleen pulp. In such cases there could be no actual circulation through the parenchyma of the pulp, the blood was therefore held in a reservoir. This observation yielded no information as to whether the reservoir were large or small, important or unimportant. Hanak and Harkavy did show, however, that the reservoir was evacuated on struggling, a fact which suggested its functional nature.

These facts together with others to be referred to later on the effect of temperature pointed to the spleen expelling its corpuscles under such circumstances as increased the demand on the blood relatively to the quantity of functional hæmoglobin in circulation. There were however

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certain difficulties about this view. The first difficulty was the current idea that possession of a spleen "makes no difference." Barcroft, Murray, Orahovats, Sands and Weiss⁽³⁾, however, showed that guinea-pigs from which the spleen had been excised died sooner in an atmosphere charged with coal gas than did normal guinea-pigs or operated controls from which a portion of pancreas, or omentum, or one horn of the uterus had been excised; whilst in hydrocyanic gas, the lethal nature of which is quite unconnected with the carriage of oxygen by hæmoglobin, the normal animals enjoyed no greater tenure of life than the splenectomised ones. Faced therefore with such an emergency as we conceived it to be the purpose of the spleen to meet, the splenectomised animals were at an evident disadvantage. The second difficulty about our view lay in the size of the spleen, which appeared to be too small to admit of any very significant mass of corpuscles being evacuated from its substance. On looking into this matter it appeared that no knowledge was forthcoming as to what size the spleen actually was in the normal body, untouched by operation.

Since contraction of the spleen follows on anoxæmia of the central nervous system as shown by de Boer and Carroll⁽⁴⁾ almost any form of death might be expected to be accompanied by contraction of the spleen—certainly any death which was caused by a general anoxæmia, *e.g.* hæmorrhage, carbon monoxide poisoning, etc. Further, if our view is correct, it should be possible to demonstrate a considerable contraction of the spleen on exercise, for exercise would be the most obvious condition, in the ordinary circumstances of life in which an increased demand is made on the supply of oxygen-carrying hæmoglobin.

The present paper describes experiments, designed partly to ascertain whether there is a sufficiently definite relation between the size of what may be considered as the resting spleen in life to that after death, to allow of the size after death to be used as a measure to the resting size during life, and whether the spleen during rest might on occasions be much larger than would be inferred from its size in the dead animal. Secondly some experiments were made on the effect of exercise on the volume of the spleen during life and a comparison was drawn between the size of the organ under conditions of exercise or impaired oxygen supply with those of the resting and the dead spleens respectively. These points form the preliminary to a more general discussion of the spleen regarded as a regulator of the blood volume.

In order to discover the size of the spleen in the normal living body two techniques seem to be possible, (1) to replace a portion of the body

wall with a celluloid window¹, (2) to resort to radiography. The experiments described in the present paper were all carried out with X-rays. We would like here to thank Dr Dale for a suggestion as to the actual X-ray technique which we adopted and which has proved quite satisfactory, namely that of performing a preliminary operation in which a number of metal indices are placed round the edge of the spleen. The animal is then allowed to recover from the operation and photos have been taken usually about a week afterwards. The animal makes a complete recovery. The health of the spleen does not appear to suffer; we have one rabbit which was operated upon more than six months ago and which has shown no ill effect from the abnormal metallic contents of its abdomen. The actual indices which we used were surgeons' metallic sutures. These are easily placed on the spleen and can be filed beforehand into distinctive shapes, if necessary. The preliminary operation was carried out under chloroform and ether anæsthesia.

Preliminary experiments were carried out upon rabbits. These animals frequently have spleens which are rather long in relation to their breadth, and become almost cord-like when contracted. At first we put but two sutures into the spleen, one at each end. When the rabbit was placed on the X-ray table either on its side or on its stomach the two sutures could easily be seen on the fluorescent screen. Moreover they were seen invariably to approximate either after exercise, or when blood was withdrawn from the jugular vein. These experiments were of course of doubtful interpretation inasmuch as in order to obtain views in perpendicular planes of space the rabbits were rotated, nevertheless the alteration in the position of the sutures was very remarkable and convinced us of the desirability of carrying out more exact experiments.

Technique. Our final technique was as follows: Cats were used for the most part; rabbits, monkeys and one dog being used for confirmatory tests. Usually five, six, or seven sutures were put round the edge of the spleen. The operations were carried out in the Cambridge Physiological Laboratory; when the wound had been healed they were taken up to the X-ray department in the Anatomical Laboratory at University College, London, there to be photographed. The installation gives good records with an eighth of a second exposure. Records can be taken from the lateral and dorsal aspects within 10 seconds of one another. Care was taken in every case to discard all results in which the animal was

¹ Since the above was written by the kindness of Dr Florey who had such a cat, I have seen the spleen contract when the cat took exercise.

seen to have moved between the two exposures. In our earlier experiments the cats were placed in a cardboard box. Later we held them in position, the fore legs in one hand and the hind legs in the other.

The records were treated in the following way. Prints were made from the films. The print of the lateral aspect was laid on a block of paraffin with a level horizontal surface. The position where the teeth of the suture met was marked in the case of each suture, a sewing needle was driven vertically through the mark, so that a needle marking the position of each suture stood up from the block, perpendicularly to its surface. The corresponding sutures were identified and marked on the dorsal view, a line was drawn on the print either through or parallel to the middle line of the spinal cord, the distance of each suture was measured from this line. The needle corresponding to that suture was then driven into the block until the distance of its head from the paraffin surface was the same as that of the suture from the line on the antero-posterior print. The heads of the needles then gave a slightly magnified but relatively correct register of the positions of the sutures in space. The magnification was the same for all photos of the same animal. A thread was tied into the eye of each needle and a copper wire was fitted to the heads and tied in place, making a figure which represented the edge of the spleen.

In obtaining this wire figure due regard had to be paid to the orientation of the sutures for in some cases the spleen was more than usually curved, and in one or two there was obviously a considerable change in the dimensions of the spleen without very much alteration in the positions of the sutures. A simplified example may explain. Thus if *A* and *B* are two needles, they might correspond to sutures the same distance apart in two successive photos of the spleen, yet the aspects of which might be as in Figs. 1 and 2 respectively, in which case the sutures would indicate spleens of very different configuration.

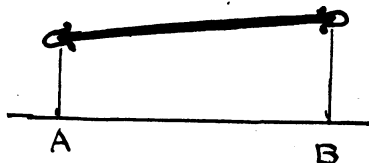


Fig. 1.

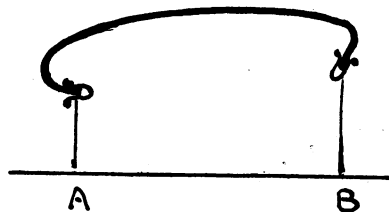


Fig. 2.

The wire figure is tied across in sufficient places in order to insure its retaining its shape, the threads are then cut and the figure removed.

Sheet lead of standard thickness is fitted to it, the figure marked on the lead, and a lead figure is cut which when flattened represents as a rough approximation the surface which the spleen would cover if taken out and laid flat on the table. As we became more expert it was possible in the simpler cases to leave out the step of making the wire figures and fit the lead directly to the heads of the needles. In a few cases thick paper was used instead of lead.

The method indicated above is of course a very crude one and it would be quite incapable of dealing with small changes in the size of the organ. The following are some examples of instances in which duplicate lead models were made independently by different persons from the same pair of films.

Orahovats	32.9	28.1	21.7	28.0
Barcroft	34.3	28.2	23.0	28.7

Barcroft's results, which were made from the wire tend to be larger than Orahovats's, in which the lead is fitted directly to the top of the needles. The wire models tend to give a more rounded figure. The ratio of the weights of any pair of models made by a single method is as a rule less affected than the individual models.

So far we have dealt only with two planes. There seems to be no reason, judging from the histology of the spleen, why a general contraction should affect the third plane differently from the other two and therefore one may get an idea of the actual percentage change in the volume of the organ by taking as a basis for comparison, the cube of the square root of the weight of the lead model. If one of the photos taken in any series be that of the spleen in the dead animal and if the weight of the spleen *post mortem* be known, a computation may be made on the lines indicated above, of the weights of the spleens previously photographed under the other conditions.

Some notion of the accuracy of the method may be obtained by taking two pairs of photos of the spleen in the body, *post mortem*, and comparing the models obtained from them. In such a case the separate estimates of

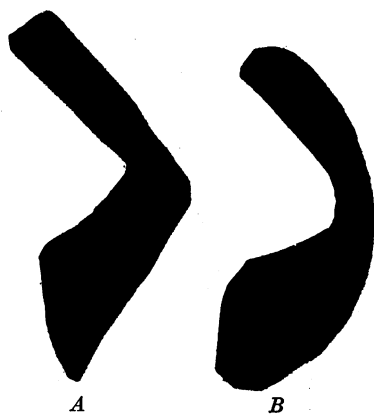


Fig. 3. Photos of lead models reconstructed from the same photos. *A*, without wire; *B*, with wire weighing respectively 28.0 and 28.7 gm.

the spleen made from photos taken an hour after death, and the day after, but in both cases before the body was opened gave 6.6 and 6.5 gm. respectively.

The resting spleen.

In the living animal a greater difference may be expected in successive computations of the volume of the spleen, for the spleen itself may vary somewhat from time to time even under nearly similar conditions, owing to a greater or less degree of tone in its muscle. Its shape and position also will be influenced by the degree of distension of adjacent organs such as the stomach. The following are some such computations:

Animal		Cat				Monkey	Dog
		(1)	(2)	(3)	(4)	(1)	(1)
Weight of spleen (gm.)	<i>a</i>	26.4	19.8	40.5	32.9	7.5	66
	<i>b</i>	24.1	22.7	44	28	6.9	75
	<i>c</i>	—	—	—	—	—	60

From the above instances it appears that the computations of the spleen in the resting animal differ by about 20 p.c. of the maximum measurement. Fig. 6, p. 454, shows four photographs of lead models of the spleen of the dog cited above when at rest. Of these *C*, *A* and *D* form the basis of the determinations given above (*a*, *b* and *c* respectively).

What size then is the spleen in the resting cat? The limits according to our observations are very wide. In full grown cats from about 2 kilos upwards (1990 gm.) nineteen estimations were made; the smallest spleen appeared as 11.9 gm. and the largest 45 gm., nine were between 14 and 20 gm., four were between 20 and 30 gm. and four were over 30 gm. The average is 21 gm., the median 18 gm. One may picture the spleen in the resting cat therefore as being of the order of 20 gm. in size with the possibility of large variations in different animals. The extent to which this size is correlated with definite factors such as age has not been worked out.

In fourteen of these cases we had the weights of the cats which average 2.9 kilos and the median 2.7. The weight of the spleen then appears to be about .7 p.c. of the weight of the cat in good sized adults. In two monkeys it appeared to be definitely smaller; they were 7.5 gm. and 5.7 in monkeys of 4.6 (old) and 2.0 (young) kilos respectively. In dogs only one experiment was performed; in this the spleen weighed 1.5 p.c. of the weight of the dog.

Relation of the living to the dead spleen.

In all cases of cats the spleen in the cadaver was lighter than the organ as computed in life. So far as our observation went the difference depended to some extent on the way in which the cats were killed.

Histamine. The least change, somewhat to our surprise, was in the case of cats killed by histamine.

Serial number	W Weight of cat (kilos)	A Weight of spleen in resting cat (grams)	B Weight of spleen in dead cat (grams)	D Difference (grams)
5	36.0	12.3	9.8	4
6	28.5	17.8	13.0	4.8

Coal gas poisoning. Two series of experiments were carried out in coal gas poisoning.

In the first series the concentration of gas was great and death was sudden, taking place in 1½ to 4 minutes, in most cases about two. In the second series, which consists of three experiments, the poisoning was more gradual, in all cases the spleen contracted on death, the degree of contraction however differed greatly in different animals. The data are as follows the headings being as in the table above:

Series	Cat	W (kilos)	A (grams)	B (grams)	D (grams)
I.	7	2.4	14.3	11.7	2.6
	8	2.7	14.0	12.1	1.9
	9	3.1	34.0	19.7	14.3
	10	2.0	22.1	12.2	11.9
	11	—	11.9	8.0	3.9
	12	—	17.4	8.0	9.4
III.	13	2.5	17.9	12.5	5.4
	14	2.4	14.8	10.0	4.8
	15	2.6	15.4	13.0	2.4

Among the spleens which contracted least was the last. The experiment deserves a word of comment as shedding some light on the variableness of the results. As will be shown later, exercise is one cause of contraction of the spleen. The cat in question greatly resented being photographed and it proved impossible to obtain records without holding her in position by main force. It is probable therefore that the spleen of the imprisoned cat was considerably contracted. The inconsiderable amount of contraction in some of the earlier experiments may have had to do with the suddenness of the poisoning; we have no real knowledge of the time relations of the contraction in the intact animal. The important thing to notice is that some of the spleens squeezed out 9–15 c.c. of their contents into the circulation.

Drowning. Four experiments were carried out in which the cat was drowned by tying a weight round its neck and placing it in the sink. They gave the following result:

Cat	W (kilos)	A (grams)	B (grams)	D (grams)
16	4.4	45.1	32.2	12.9
17	3.5	16.7	9.4	7.3
18	—	20.5	10.1	10.5
19	—	30.5	12.1	18.4

Drowning combines muscular exertion and anoxæmia. It is not surprising therefore that the shrinkage of the organ is very great, amounting in one case to 18·4 c.c.

Hæmorrhage. The form of death which in cats gave the most striking results was hæmorrhage. The subject may be dealt with in somewhat greater detail than the other forms of death which have been considered. As a sample experiment the following may be taken; a cat 2·9 kilos in weight, was photographed twice at rest, it was then given urethane and photographed again, in this case with little change in the size of the spleen. Under urethane the spleen was computed as weighing 28·3 gm., before the urethane 32·9 and 28·1 gm. respectively. On one occasion out of four we obtained a noticeable contraction in the "urethane" animal. The cat was then subjected to successive bleedings at intervals of about 10–15 minutes. The extent of the bleedings may be seen from the following table.

Cat 4	Time	Blood lost	A	B	Weight of spleen $B \times 10/36.2$ (grams)
			Relative weight of model	Relative weight spleens = $\frac{B}{\sqrt[3]{A}}$	
Rest 1	—	—	24.5	124	34.3
Rest 2	—	—	21.9	102	28.2
Urethane	2.50	—	22.0	103	28.5
1st bleeding	3.20	10	16.4	66.7	18.7
2nd "	3.30	22	14.1	53.0	14.6
3rd "	3.40	36	—	—	—
4th "	3.53	41	14.5	55.1	15.2
5th "	4.10	71	13.8	51.3	14.2
6th "	4.28	83	12.1	42.2	11.6
7th "	4.40	95	13.1	47.5	13.1
8th "	4.53	100	9.9	31.4	8.7
P.M.	—	—	11.0	36.2	10

Weight of spleen P.M. = 10 gm.

Weight of cat 2.87 kilos.

It may be interesting to give the relative weights of the living spleen, the spleen at death and the *post mortem* spleen in the four cases of hæmorrhage which we have studied.

Cat	A	B	C	Ratio C/A	Ratio C/B
	Weight of spleen P.M. (gm.)	Weight of spleen at death (gm.)	Weight of spleen at rest (gm.)		
1	6.6	6.7	25.3*	3.8 : 1	3.7 : 1
2	6.6	6.5	19.8	3 : 1	3.1 : 1
3	17.5	13.6	42	2.4 : 1	3.1 : 1
4	10	8.5	30.5	3.1 : 1	3.6 : 1
Dog	13.3	13.3	66	5.0 : 1	5.0 : 1

* Average of two determinations.

To us it came as a great surprise, that the *post mortem* spleen gave so paltry an idea of the spleen in the living animal: if there is so great a shrinkage one may ask, what actual decrease is there in the volume of the blood during hæmorrhage? Some idea of this may be obtained by comparing the volume of the blood lost in hæmorrhage with that added by the contraction of the spleen. Thus in Cat 4, 10 c.c. of blood were withdrawn, the spleen weight decreased by 9.8 gm. The volume of blood, therefore, was not appreciably altered by the hæmorrhage. Fig. 4 shows the extent to which hæmorrhage was balanced by contraction of the spleen in Cat 4. The broken line showing the volume of blood withdrawn, naturally goes diagonally across the figure; the contribution made by

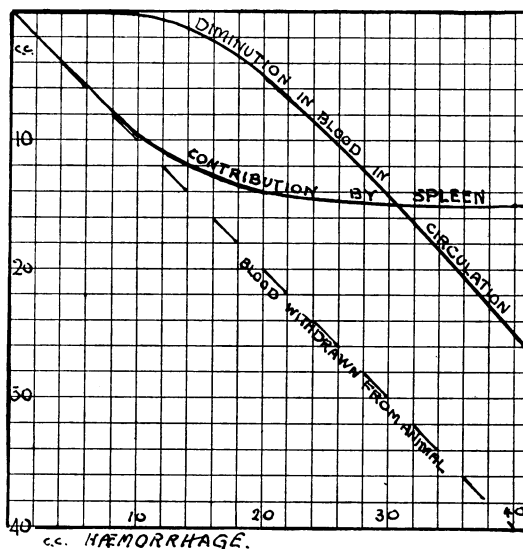


Fig. 4. Effect of hæmorrhage on spleen volume and blood volume. If the blood volume be taken as 150 c.c. the figures in the ordinate $\times \frac{2}{3}$ represent percentages of the blood volume.

the spleen at first so nearly coincides with this line, that when the blood contributed is added to the blood lost the quantity of circulating fluid scarcely changes.

Comment may be made on two points which are not unconnected.

(1) The spleen gives up the principal mass of blood at the commencement of the hæmorrhage. This is of course no measure of the actual force of contraction which at the end may be as great as, or greater than, at the commencement of the period of contraction.

(2) In the case of the cat one fact has come out pretty consistently, namely that over the first ten cubic centimetres of hæmorrhage, the blood volume appears to undergo little or no sensible diminution, *i.e.* the amount of fluid added by the spleen is almost the same as that lost in the hæmorrhage. A cat of course can lose very much more than ten cubic centimetres of blood, yet a hæmorrhage of that degree would be a very large one in the ordinary accidents of feline life; it would amount to about one-fifteenth of the whole blood volume of the animal and would therefore correspond to about 300 c.c. in man.

In the one dog which we investigated the variations in the size of the spleen were proportionately greater than in the cat, for the resting spleen at its largest was more than five times the weight of the *post mortem* spleen. The animal was bled to death under urethane, the main features being much as in the cat though on a larger scale. Here again the greatest loss from the spleen was at the earlier part of the hæmorrhage, though not quite so early as in the cat; the figures are as follows:

Hæmorrhage	(1)	(2)	(3)	(4)	(5)	(6)
Total quantity of blood lost by dog	20	40	68	133	200	230
Total quantity of blood lost by spleen	5	25	39	44	50	52

The dog being 4.45 kilos, the blood volume at rest was of the order of 300 c.c. The hæmorrhage extended over two hours. We need not here enter into the discussion as to the ratio of the blood volume to the body weight; the blood volume by some observers has been placed as low as 1/20 of the body volume, which for this dog would be 223 c.c. or rather less than the actual amount of blood which was obtained from the dog. We mention the matter here because it illustrates in a striking way the fact that much still remains to be discovered as to the rate at which blood is made during a hæmorrhage which lasts over two hours and we hope to undertake work on this subject.

The principal interest in the foregoing pages lies in the light which they throw on the general thesis, that the spleen has as one of its functions the adjustment of the volume of circulating blood to the needs of the animal. Our general conception is that while the majority of the red blood corpuscles are circulating, as "currency" a fraction of them are held in reserve, "banked", so to speak, and that one "bank" is the spleen.

So far as exercise is concerned we have performed experiments on the dog, the cat and the rabbit. The method has been that described above. In preliminary experiments on the rabbit the animal was laid on the X-ray table, the distance of sutures at the two ends of the spleen

was measured, the rabbit was then encouraged to "kick about," as rabbits do, and a second measurement taken, there was no difficulty

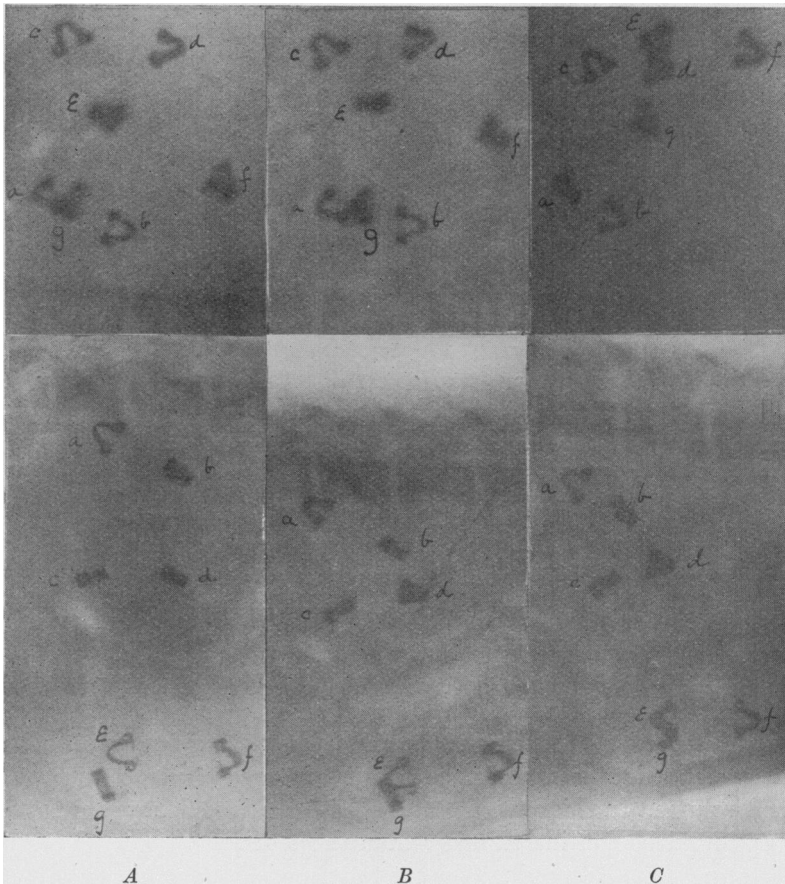


Fig. 5. $\times \frac{3}{2}$. Photos showing the clips in the margin of the spleen of a dog *A* at rest, *B* after severe exercise, *C* after severe hæmorrhage. Upper photos take in antero-posterior plane. Lower photos in the later plane. The photos of the lead models are shown in Fig. 7 *C* and *A* respectively.

in demonstrating that in whatever position the measurement was made, the sutures were nearer together after the exercise than before it. These preliminary experiments have been entirely confirmed on the dog, the cat and the rabbit by the reconstruction method.

In the dog two sets of photos were taken at rest which gave the spleen a weight of 68 and 75 gm. respectively (Fig. 6 *A* and *D*). The dog

then ran about, but the exercise was not so great as to make it perceptibly out of breath; photos at this stage showed the spleen to have a weight of

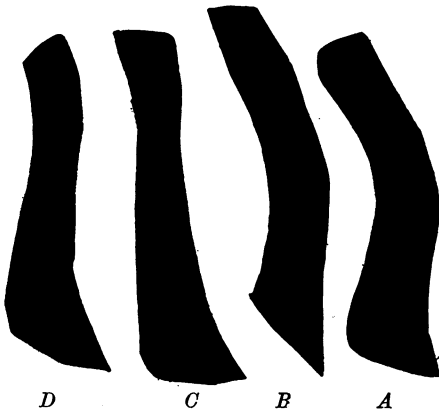


Fig. 6. Photos of four lead models of resting spleen of the same dog observed on different occasions (*B* under urethane). The actual length of *B* was 11.8 cm.

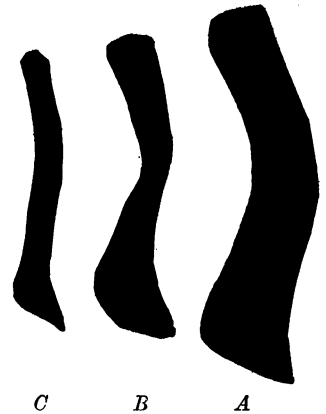


Fig. 7. *A* as in Fig. 6, *B* after severe exercise, *C* after severe hæmorrhage.

35 gm.; it was then exercised more vigorously so that at the end it was panting and its tongue was hanging out. The spleen had shrunk to 28 gm. In round numbers after mild exercise the spleen expelled half its substance, after severe exercise two-thirds. The actual quantity of material which left the organ as between the largest resting measurement and that after mild exercise was 40 c.c. whilst 8 more c.c. were expelled as the result of severe exertion. Taking the blood volume of this dog as 300 c.c. the amount contributed by contraction of the spleen was 15 p.c. of the blood volume. In this experiment there is no reason to suppose that any factors need be considered other than those of purely natural exercise. It is more difficult to induce the cat to take violent exercise without the possibility of inducing some degree of apprehension which would cause an adrenalin secretion and we know that adrenalin causes contraction of the spleen, but on the other hand it must be remembered that in the course of nature the same may be said; fear is the usual incentive to considerable exercise in a cat. In the first three of the four experiments which are cited below the cat was chased about the room in a very moderate way, in the fourth it was made to fight by placing it standing on a sheet which was then lifted by the corners. The cat finding itself on an unsteady surface became extremely active. In all cases the spleen contracted.

Cat	Weight of spleen (grams)		C, weight of material lost by spleen (grams)	Approximate proportion of C to blood volume taken as 150 c.c.
	A, before exercise	B, after exercise		
1	26.4	13.7	12.7	8.5 %
	24.1	7.1	17.9	12
2	19.8	9.9	9.9	6.6

In the rabbit the degree of shrinkage, expressed as a proportion of the size of the spleen, is of the same order as in the cat and dog, but the absolute amount of material expelled is less proportionately to the blood volume for the spleen is a smaller, and often a very much smaller, organ relatively.

Rabbit	Relative weight of the spleen before and after exercise	
	Before	After
1	100	56
2	100	60

In the two monkeys at our disposal we found it impossible to induce exercise uncomplicated by rage, possibly such could be accomplished on a tread mill, but it must at once be confessed that the spleens of these monkeys were so small that a 50 p.c. contraction would add but little to the blood volume; we never found it possible to photograph the spleens unless the monkeys were under the influence of a narcotic. Moreover the monkey's spleen offered special difficulties on account of its shape. As we saw it, it approximated to a tetrahedron, each facet of which was an equilateral triangle. This figure could easily have changed into a sphere without any alteration in the positions of the sutures at its corners. The alterations in volume of the monkey's spleen and therefore its volume when at rest may then have been much greater than we suppose.

Summing up what we have said above, it would seem that during strong exercise the spleen may expel more than half its volume of blood and shrinks to about the size of the spleen after death. We conclude that the *post mortem* volume of the spleen may be taken as a minimum estimate of the volume of blood it drives into the circulation during strong exercise. On this basis the spleen in man would expel from 110-258 c.c. of blood. If, as is possible, some concentration of blood takes place in the spleen pulp, the volume of red corpuscles passed out will be greater than corresponds to the decrease in spleen volume taken as blood. We arrive then at the general conclusion that the importance of the spleen as a reservoir of blood depends upon its size. The ratio of *post mortem* weight of spleen to body weight varies, as is known, in

different animals. The data seem to us to suggest that the ratio is greater, the greater the normal activity of the animal.

In the animals we observed the ratio was as follows: In the two monkeys it was $\frac{1}{333}$ and $\frac{1}{700}$. The extreme variation in cats was $\frac{1}{437}$ and $\frac{1}{70}$, but in eight cats it only varied between $\frac{1}{200}$ and $\frac{1}{300}$. In the one dog experimented on, the ratio was $\frac{1}{330}$.

SUMMARY.

1. A method is described for the computation of the size of the spleen in the dog, cat, rabbit and monkey, during life without the necessity of an anæsthetic or an operation synchronously.

2. The normal spleen is usually much larger than that of the dead animal. The forms of death studied were in most cases such as induced one or other type of general anoxæmia, *e.g.* CO poisoning, drowning, hæmorrhage.

3. In the case of hæmorrhage the living spleen in the dog, cat or rabbit is two, three or even five times the size of that of the dead animal.

4. In the earlier stages of hæmorrhage (in the cat up to 10 c.c. or 8 p.c. of the blood volume) the spleen contributes an amount of material to the circulating blood approximately equal to that of which the hæmorrhage deprives it. In the dog also the principal evacuation is at the commencement of the hæmorrhage.

5. During exercise also, the spleen expels its contents into the circulation in a great degree. Estimates in the cat and dog show that in exercise the shrinkage of the spleen corresponds to 6–15 p.c. of the blood volume.

6. The view is put forward that the spleen exercises a real function in adjusting the volume of circulating blood, or more correctly circulating functional hæmoglobin according to the needs of the animal.

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