THE PHYSIOLOGY AND PATHOLOGY OF THE SPLEEN.

(*First communication.*) By CHARLES S. ROY, M.D., *Professor-Superintendent of the Brown Institution.* Pl. XIV., XV., XVI.

(*From the Cambridge Physiological Laboratory.*[1])

It is fully recognized by physiologists that, under normal conditions, there is a certain relation between the degree of functional activity of an organ or tissue and the degree of expansion of its blood vessels. It was only, however, after making a long series of observations upon this subject in the case of the kidney, comparing the activity with which the renal circulation is being carried on with the rapidity of secretion of the urine, that I learned how surprisingly closely these two phenomena correspond. The method employed in these kidney experiments (which are not yet published) permitted of even excessively slight changes in the calibre of the renal vessels—as expressed by the changes in volume of the whole organ—being recorded graphically, while, at the same time and on the same paper, the number of drops of urine was also recorded, each drop of urine, which fell from a narrow cannula tied in the ureter, closing for an instant an electric current which flowed through the bobbins of an electro-magnetic signal. These observations showed that an excessively minute change in the rapidity of the urinary secretion—that an increase, for example, in the rapidity of the flow of urine, such as could barely be discovered by this exact method of counting the drops, was invariably accompanied by an increase in the calibre of the renal vessels, causing a very evident rise in the line which represented the volume of the kidney. In other words—paradoxical as it may appear—it was found that the rapidity of the flow of urine could be followed indirectly, by observing the changes in the calibre of the blood vessels of the kidney, with very much greater convenience than could be done directly by counting the number of drops of urine which escaped from a cannula tied in the ureter.

This fact naturally suggested to me that a study of the changes in the circulation through an organ or tissue (a matter which, in the case of many organs, presents but little difficulty) offers to us a method, from

[1] From observations made while the author held the post of *George Henry Lewes Student.*

which much may be expected, of obtaining information regarding the functions of certain organs.

Even in the case of the kidney, where the study of the changes in quantity and quality of the urine presents to us so convenient a means of investigating the functions of the organ, the indirect method of inquiry referred to above is fitted, according to my experience, to teach us much regarding the mechanism of the renal secretion and the relation which the kidney bears to the rest of the body. But very much more is *a priori* to be expected from the employment of this indirect method of investigation when it is applied in the case of organs whose functions cannot be studied by any direct method with which we are as yet acquainted—by any method directed towards the investigation of variations in the results of the functional activity of the organ. The spleen, it need scarcely be said, is a typical example of an organ of this latter kind, and it is, moreover, especially well situated, owing to its very complete mechanical isolation, for permitting the changes in its circulation being conveniently studied by the method which I made use of for this purpose.

This method is identical in principle with that which I had already used for the kidney[1] as well as with that which I have since employed, amongst other organs, for the intestine and foot of the dog, cat, or rabbit. It consists in inclosing the spleen (or other suitable organ of the living animal) in a rigid metal box, of appropriate shape, and of such a construction that, while no hindrance is offered to the entrance and exit of blood by the splenic arteries and veins, any change in the volume of the organ causes a rise or fall, corresponding in extent, of a recording lever writing upon the moving paper of the kymographion. The spleen, as already remarked, offers exceptional facilities for the employment of a method of this kind, seeing that, having once exposed the organ by cutting through the abdominal walls, no further dissection is required to isolate the organ, such as, for example, is required in the case of the kidney or intestine.

In the present communication I propose to confine myself chiefly to the characteristics of the normal splenic circulation and to the vasomotor mechanism of the organ. The effect upon the splenic circulation which is produced by the injection of various chemical substances into the blood, as well as the more important question of the bearing of these observations upon our knowledge of the function of the spleen, I prefer to leave for consideration in my next communication upon this subject.

[1] The first series of these experiments on the renal circulation was made in conjunction with Prof. Cohnheim.

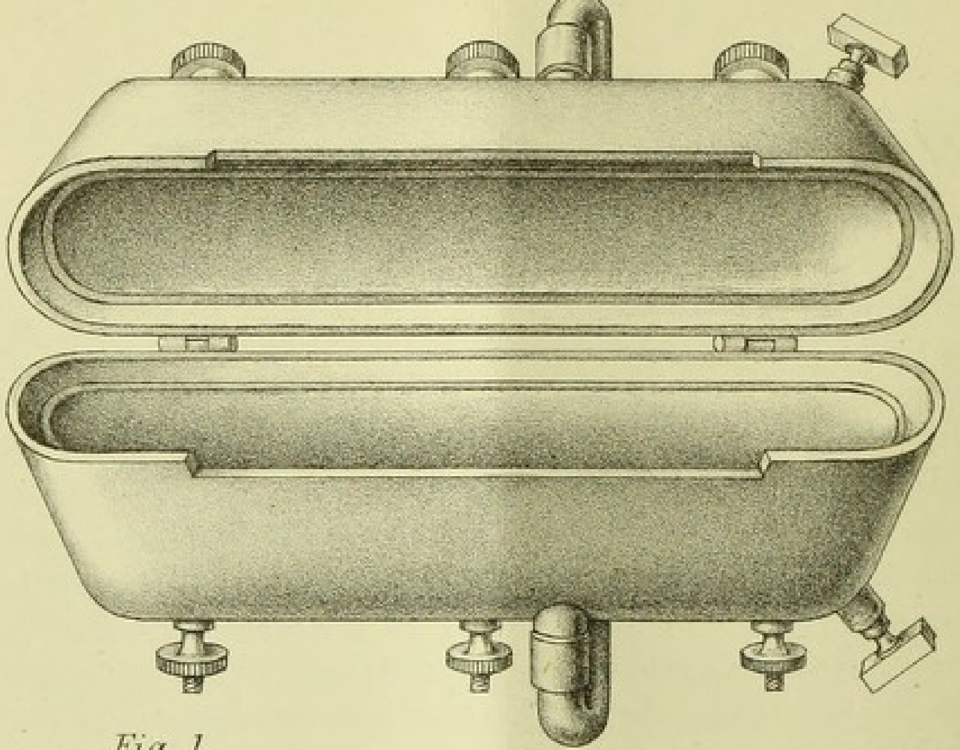


Fig. 1.
(½ natural size)

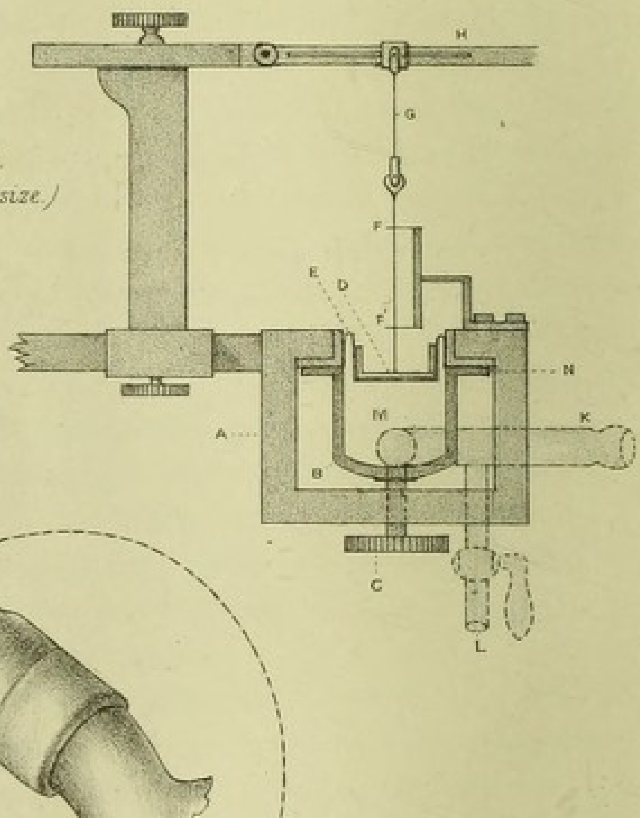


Fig. 3.
(½ natural size.)

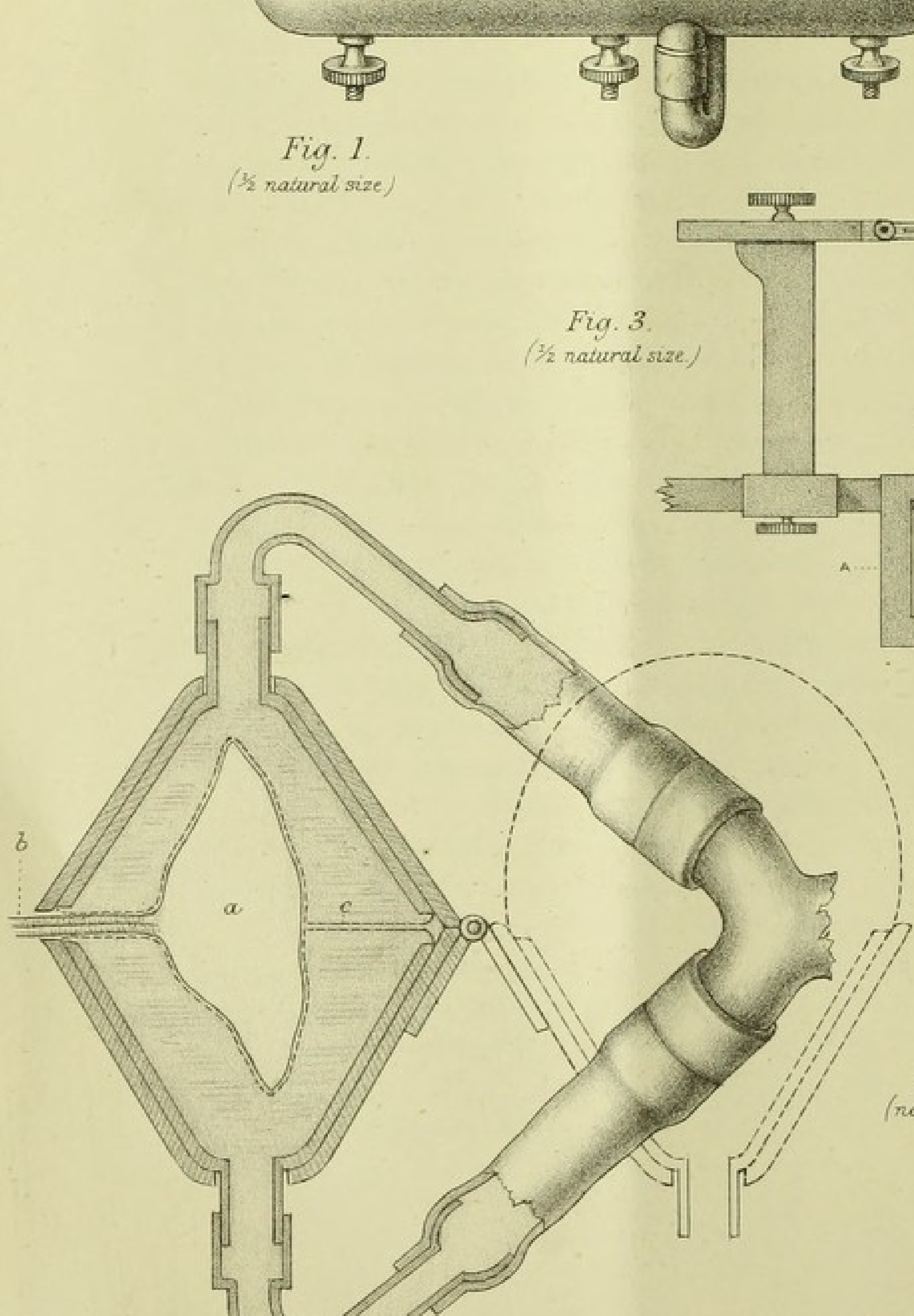


Fig. 2.
(natural size.)

METHOD EMPLOYED.

In all cases the arterial blood-pressure was recorded on the same paper as the changes in volume of the spleen. Unless this be done the most serious errors may be made in drawing conclusions regarding the nature of various changes in volume of the organ. For recording the changes in volume of the spleen two separate instruments were employed, one inclosing the organ, and the other (which I have been in the habit of employing for similar investigations on other organs) for recording graphically the changes in its volume. As the description of neither of these apparatus has yet been published, I must here refer briefly to their construction. The diagrams 1 and 2 of Pl. XIV. are intended to illustrate that form of the spleen box[1] which, after one or two other arrangements had been tried, was found most convenient. It consists of an elongated sheet-metal box composed of two symmetrical halves, which are joined together by a couple of hinges. Each of these halves is composed of an outer and an inner shell, the latter of which fits accurately into the former, and the two being capable of being firmly screwed to one another by means of the screws seen at the upper and lower rounded edges of the box. Between the two shells is clamped the edge of a thin flexible membrane of a kind which I have already had occasion to refer to repeatedly[2]. Suffice it to say here that it is prepared from the peritoneum of the calf, and that, when moistened with water, it is as flexible and delicate as the living peritoneal membrane. The following is the method which I have usually employed in fastening it in the instrument in question.

The inner shell of one half of the box having been removed, its outside is smeared with thick caoutchouc varnish, and a piece of membrane of appropriate size, having been moistened with water, is laid over its hollowed aspect so as to form with the metal shell a closed cavity. By gently sucking the air out of this cavity the membrane is made to apply itself smoothly to the inside of the shell, after which the edges of the membrane are turned over and applied to the outside of the

[1] For convenience of description I have been recommended to give a name to this form of instrument, and will, therefore, refer to it under the name of Oncometer, from the Greek word *Onkos*, bulk. The recording instrument, which is used along with it and with other instruments of a similar kind, I will refer to in the text as Oncograph. Both of these instruments may be obtained from the *Cambridge Scientific Instrument Company*, 18, Panton Street, Cambridge.

[2] This journal, Vol. I., p. 454, and Vol. II., p. 325, as well as elsewhere.

metal shell, which is then replaced in the outer shell, and tightly screwed to it. In this way an air-tight chamber is formed which is bounded on the one side by the flaccid membrane, and on the other by the metal wall of the box, as indicated by the dotted lines in the sectional diagram, Fig. 2. Pl. XIV. This process of applying the membrane is repeated with the other half of the box. Into each of the two chambers thus formed there are two openings, one pair of which are connected, as shown in Fig. 2, with a T tube, and thereby with the recording instrument. The other two openings, placed at the end of the box, are fitted with small taps, as shown in Fig. 1, and are simply intended to allow of the air escaping when the chambers are filled with oil after the spleen has been introduced into the box. At the point of junction of the two halves of the box on the side opposite to the hinges is a narrow slit formed by a long indent in the edges of the two halves, which slit is intended to permit of the passage of the splenic vessels.

It can easily be seen how the two membranes will dispose themselves when the elongated spleen of a dog or cat is placed in the box with its mesentery lying in the slit, when oil is introduced into the two chambers of the instrument. This is indicated by the sectional diagram, Fig. 2, Pl. XIV., in which the membranes are represented in the position they occupy when the instrument is in use, viz., closely applied to the surface of the organ. In this diagram the spleen is seen in section as *a*, the splenic vessels as *b*, while the membrane is represented as *c*. It need scarcely be added that any increase in the volume of the organ will force out a quantity of the oil from the two chambers through the openings which connect them with the recording instrument, and that, the other openings into the box being closed, any contraction of the organ will admit of more oil entering the interior of the instrument.

The recording instrument, the oncograph, which is in communication, by a flexible tube (made up of pieces of glass tube joined by short bits of india-rubber tubing), with the interior of the two chambers of the spleen box, is represented in the diagram, Fig. 3, Pl. XIV., which shows it in section and half the natural size. The light vulcanite piston, D, which is connected with the recording lever by means of the steel needle, G (which latter passes through the two guides, F, F^1, and is jointed as shown in the figure), floats on the surface of the oil contained in the cavity M, any escape of the oil by the side of the piston being prevented by a membrane, seen in section as E, of the same kind as that already referred to in describing the spleen box. The membrane is clamped tightly by the screw, C, between two flat ring-shaped surfaces at N, and is so arranged that, within the limits required, it does not interfere in the least with the movements of the piston. The advantage which is offered by an arrangement of this kind is, that while both exceedingly slight or very considerable changes in the volume of the spleen or other organ can be recorded with it, no change is produced in the pressure of the fluid which is contained in the oncometer, and which surrounds the organ whose volume is being recorded.

One practical difficulty in connection with experiments of this kind consists in the fact that the spleen of animals, even of the same species, varies in size to a very considerable degree in different individuals. It is well, therefore, to have spleen boxes of two or more sizes ready for use. It should be added that, having once arranged the membranes of the spleen box for an experiment, it may be used daily for weeks or months without its being necessary to apply fresh membranes, provided that the instrument be well washed with water and a few drops of glycerine be placed on the membranes before it is put aside at night.

Finally, a word may be added regarding the method of making the experiment. The animal having been anæsthetized by chloroform, ether, morphia, or a combination of two of these, a cannula is fixed in the jugular or facial vein in order to be able to inject any substance desired into the blood, and at the same time a glass cannula is fastened in the carotid artery. An oblique incision running downwards and outwards is then made in the skin of the left hypochondrium, the length of the incision depending upon the expected size of the spleen. The abdominal muscles are then separated layer by layer, any vessels which show themselves being double ligatured and cut between the ligatures. The spleen having been exposed is gently introduced into the box, which has previously been warmed to the temperature of the body by immersion in tepid water. The two chambers of the instrument are then filled with warm olive oil, which also fills the tube connecting the box with the recording instrument. Finally, the carotid cannula is fastened to the leaden tube of the kymograph and the observation can be commenced.

In many experiments the spleen box was simply allowed to lie upon the front of the abdomen; in those cases, however, where it could not be so placed without causing some twisting or stretching of the splenic vessels contained in the mesentery, the box was suspended by string from an appropriate holder. In a certain number of instances in which the involuntary muscular movements of the animal interfered with the observation of the volume of the spleen, curare was employed in addition to an anæsthetic agent. In these latter experiments I was fortunate enough to have placed at my disposal one of Mr. H. Darwin's artificial respiration instruments, the perfect action of which greatly lightens the difficulties of making such experiments, seeing that the artificial respiration is carried on with the regularity of clockwork, while the degree to which the natural respiration is copied is infinitely greater than is the case with any instrument of the kind with which I am acquainted.

I. The Normal Splenic Circulation.

All the observations which I have as yet been able to make by the above described method concur in showing that the splenic circulation differs in one fundamental particular from that of other organs.

In the case of the kidney, for example, the volume of the organ remains, *cæteris paribus*, practically constant, with exception of those comparatively slight expansions and contractions which are produced by the pulse and respiration waves in the arteries distending mechanically the walls of the renal vessels. And this appears to be the case, under normal conditions, with all other organs and tissues of the body. In the spleen, on the other hand, we have to do with an entirely different state of things. It is rare to find that the volume of this organ remains fairly constant for even a very short period of time; it is continuously expanding and contracting with a rhythm which, in so far as the element of time is concerned, is remarkably constant. This rhythmic contraction and expansion of the spleen is found in all the three different species of animals which I have employed for these experiments, viz., the dog, the cat, and rabbit.

The tracing which is reproduced (natural size) in Fig. 4, Pl. XV., obtained from a rather small-sized dog, will illustrate the characteristics of this rhythmic contraction and expansion of the organ in question better than can be done by a mere verbal description.

In this tracing the upper line, describing large waves, is the splenic curve, each ascent of the line corresponding to an increase, and each descent of the curve to a diminution, of the volume of the spleen. The curve beneath this is that of the arterial blood pressure from the carotid artery. The lowest line of the tracing gives the time, the interruptions of the marker recurring at intervals of one second. The vertical lines *a* and *b* give the relative positions of the lever-point of the *oncograph* and of the point of the recording style of the kymograph respectively.

From this tracing it can be seen that both the systole and the diastole of the spleen are gradual, and that, in this particular instance, the time which elapsed from the commencement of the splenic systole to the end of the succeeding diastole, or in other words, the time corresponding to the distance from apex to apex of the waves described by the lever-point of the *oncograph* is about 62 or 63 seconds. A closer examination of the tracing shows also that the duration of the systole of the organ is somewhat less than that of the diastole.

With the recording instrument " set " as it was while this experiment was being made, an increase in the volume of the organ by 2 c.c. caused the lever-point to rise 10 mm.[1]; so that, since the lever-point in this tracing falls and rises about 25 mm. with each contraction and expansion of the spleen, we know that the changes in volume of the organ which were thus produced were equivalent to about 5 c.c. The spleen of this animal was found after death to weigh 27 grammes, so that, at the time when the tracing was taken, each splenic systole caused a diminution in the volume of the organ equivalent to about 18½ per cent. (where no correction for specific gravity of the spleen is made) of its volume after death.

This tracing may be taken as fairly representative of the characteristics of the rhythmic changes in volume which the spleen is found to undergo. As might naturally be anticipated, however, the splenic contractions and expansions are subject to various more or less striking modifications. These differences appear, in most cases, to express simply the normal physiological reaction of the mechanism by which this splenic systole and diastole is regulated and maintained, seeing that they usually correspond to more or less evident changes in the conditions which either occur spontaneously or have been produced intentionally at different periods of the experiment.

We find, for example, that the rapidity of the splenic rhythm is subject to changes within certain very narrow limits. The extent of the contractions, or, in other words, the quantity of blood which is forced out at each systole of the organ, is, for any given individual, also subject to modification, and the differences in this respect which are produced by some change in the conditions of the experiment may be very considerable. It is found, moreover, that this rhythmic contraction and expansion of the spleen is subject to certain forms of irregularity, both as regards the time occupied by each successive systole and diastole, as well as in so far as the amount of blood forced out of the organ at each

[1] Measured by injecting fluid from a graduated syringe into the instrument before commencing the experiment.

contraction is concerned. I will first refer somewhat more in detail to rapidity of the rhythm of the splenic systole and diastole, and to the changes in it which are found to present themselves under the influence of varied conditions.

a. *The rapidity of the rhythm of the splenic systole and diastole.*

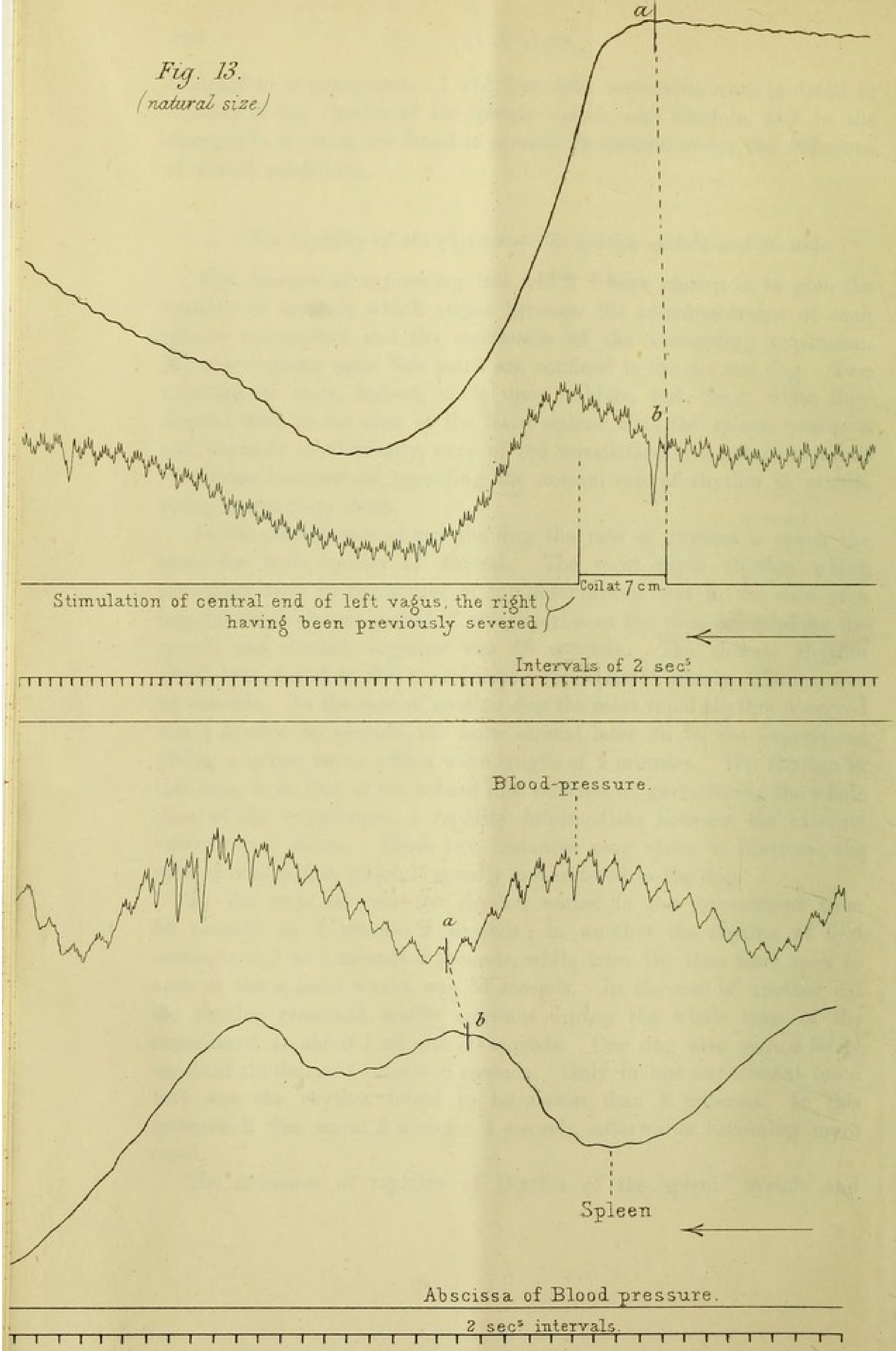
The manner of expressing this which I have chosen is, to give the number of seconds which elapse between the commencement of each splenic contraction and the conclusion of the succeeding expansion. My observations upon this point are confined to the cat and dog. Two experiments were, indeed, made upon rabbits, but these, while they showed that, in the case of the latter animal also, the spleen contracts and expands rhythmically, were of too unsatisfactory a nature to admit of definite conclusions regarding the normal rate of rhythm in rabbits being drawn from them.

In the case of the cat and the dog the rate of rhythm is much the same for both species of animal. The most rapid rhythm which presented itself in the course of my observations was in the case of a dog, in which at one period of the experiment the time occupied by the systole and diastole together was 46 seconds. The slowest rhythm which was found in this experiment, which lasted nearly 4 hours, was 55 seconds. In the case of another dog the most rapid rhythm observed was 1 minute 40 seconds, the same animal later on in the experiment giving a spleen curve with a wave length of 2 minutes. The rhythm in this case, as in that of the animal first referred to, gave, during the whole time of the experiment, a rapidity intermediate between the extreme values noted above. These two instances may serve to illustrate the rate of contraction which is usually encountered in the dog.

In the case of cats the rhythm varied in one experiment from 58 seconds to 1 minute 2 seconds; in another the rhythm at first corresponded to 1 minute 2 seconds, while later the time from apex to apex of the splenic waves was 54 seconds. In the case of another cat the rhythm remained nearly constant during the whole time of the experiment at about 1 minute 30 seconds. One dog also gave a fairly constant rhythm of 1 minute 8 seconds. Only in one experiment (on a cat) was the rhythm found to be slower than 2 minutes. In this instance it was about 2 minutes 3 seconds, afterwards becoming more rapid.

The extremes of rapidity of rhythm of the splenic systole and

Fig. 13.
(natural size)



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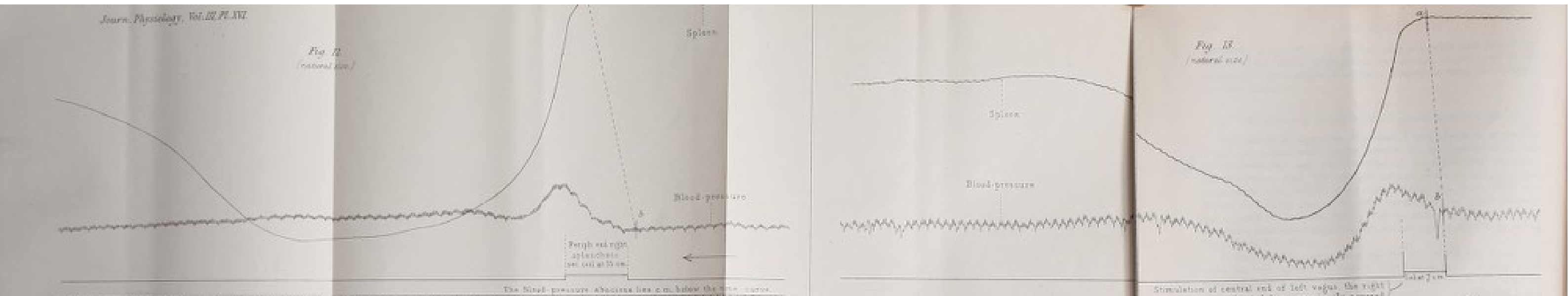
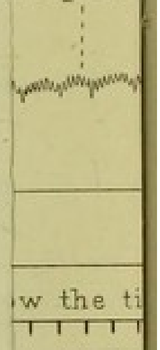


Fig. 11
(natural size.)
Spleen
Blood-pressure
Periph. end right splanchnic sec. coil at 15 cm.
The Blood-pressure abscissa lies c.m. below the time curve.
Fig. 9
(½ natural size.)
Spleen
Blood-pressure
Abscissa of Blood-pressure curve.
2 sec. intervals
Fig. 10
(½ natural size.)
Spleen
Blood-pressure
Spleen
Blood-pressure
Blood-pressure abscissa was 20 m.m. below the time
Fig. 13
(natural size.)
Stimulation of central end of left vagus, the right having been previously severed
Intervals of 2 sec.
Blood-pressure
Spleen
Abscissa of Blood-pressure.
2 sec. intervals.

pleen.

d-pres



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diastole were, therefore, 46 seconds for the most rapid, and 2 minutes 3 seconds for the slowest.

It is worthy of note that, except in cases where irregularity presents itself (a subject which will be referred to further on), the rhythm of the spleen is subject to gradual changes only. It is not too much to say that for any given short period of time, *e.g.*, $\frac{1}{4}$—$\frac{1}{2}$ an hour, the rhythm of the spleen *cæteris paribus* remains constant in so far as the element of time is concerned. It may be reasonably assumed that were it possible to keep the conditions fairly uniform throughout the experiment the changes in the rate of rhythm of the spleen would be very much less than they were found to be in my observations.

One may say that the average rate of the splenic rhythm is, therefore, speaking roughly, about 60 contractions an hour in the case both of dogs and cats. Certain forms of irregularity in the rate of rhythm of the spleen which occasionally present themselves may most conveniently be considered after the extent of the splenic systole has been referred to.

b. *The amount of the diminution of volume produced by each splenic systole.*

This element, viz., the extent of the splenic contractions, distinguishes itself from the time-element of the splenic rhythm by the fact that it is subject to very great variations. Not only may the contractions differ much in extent in different animals, but great differences in this respect may show themselves in the same individual at different periods of the experiment, and, what is still more striking, the amount of blood which is forced out at one systole may, under certain circumstances, differ to an appreciable degree from that forced out by the contraction which follows it. This may be seen in Fig. 10, Pl. XVI. (reduced to one-half natural size), which is intended to illustrate one effect of stimulation of a sensory nerve, viz., that which is usually produced when the spleen has by some cause or other been brought to a state approaching that of maximal contraction.

The appearance of this curve, together with a knowledge of the conditions under which it was obtained, make it probable that the gradual diminution in the extent of the successive waves was due to a gradual diminution in the force of the successive muscular contractions, the resistance offered by the splenic pulp, blood-pressure in the portal vein, &c., remaining practically constant. When the spleen is not greatly contracted, it is found that stimulation of a sensory nerve causes a more or less powerful contraction of the organ lasting for a longer or shorter time. With a powerfully contracted spleen, however, we find, as might be expected, that an influence which under other circumstances caused a strong contraction is no longer able to do so.

We find in its place, as is seen in Fig. 10, what appears from the curve to be simply a stronger natural systole of the organ, followed by others of gradually diminishing extent.

Various facts of a kind similar to that shown by the curve of Fig. 10 would seem to indicate strongly that a certain number at least of the changes which so readily present themselves in the extent of the splenic waves are due to variations in the force of the muscular contractions.

Another element regulating the extent of the splenic systoles, and one of the very greatest importance, is, naturally, the rapidity with which the blood is permitted to enter the *vasa serosa*. Even in absence of other evidence the character of the curves obtained from the spleen by the method employed by me would suffice to prove that the amount of blood entering the spleen in a given time by the arterioles is always exceedingly small in comparison with the rate at which it passes through other organs. If, for example, a kidney, a portion of intestine, or the foot of a dog or cat be inclosed in a box of a suitable construction, and the changes in its volume be recorded by an *oncograph*, it is found that there is a well-marked pulse-wave in the curve which represents the volume of the organ, and, *a fortiori*, a well-defined respiration-wave. In the case of the spleen[1], however, even when the organ is of large size, and the recording instrument is so arranged that it magnifies considerably the changes in volume of the organ, we find little or no indication of a pulse-wave, and only in cases where, using artificial respiration, the rise and fall of pressure in the lungs has been made tolerably great, do we even find, as in Curve 4, indications of a respiration-wave.

This imperfect reproduction in the changes in volume of the organ of changes in the arterial pressure indicates to us that the passages by which the arterial blood enters the substance of the spleen are comparatively very narrow.

A more striking evidence of the same fact is obtained by the simple experiment of closing for a moment the aorta at its point of passage

[1] It need scarcely be said that in comparing thus the curves obtained from the spleen with those of other organs, the degree to which the changes in volume have been magnified by the recording arrangement is supposed to bear the same relation to the size of the organ in all cases.

through the diaphragm, thereby producing, of course, a very considerable fall in the pressure of the blood in those arteries which are situated on the distal aspect of the compressed point—a fall which, in the case of the kidney, portion of intestine, or foot, leads to an exceedingly rapid contraction of the organ, causing an almost vertical descent of the oncograph curve, and indicating to us how free is the communication between the large arteries and the mass of small vessels with highly elastic walls which make up the bulk of the vascular territories of these organs. In the case of the spleen, on the other hand, the diminution in volume takes place very slowly—there is no sudden fall, such as would be produced were the large branches of the splenic arteries in free communication with a relatively large cavity whose elastic walls were distended with a pressure approaching that within arteries. Indeed, where the spleen is expanding at the moment of closure of the aorta, the lever may remain nearly stationary until the time comes for the commencement of the splenic systole.

This experiment of closing the aorta for a few seconds and observing the effect upon the volume of the spleen seemed fitted to give some information upon the question as to whether or not the splenic arterioles rhythmically contract and expand with each contraction and expansion of the organ, as well as upon some other points, and I was therefore led to repeat it as often as occasion offered. The following are some of the *data* which were thus obtained. When the aorta is closed during the systole of the organ, the descending line recorded by the *oncograph* lever tends to become more vertical, from which one would conclude that the entrance of blood from the splenic arteries does not cease completely during the time of contraction of the splenic muscular fibres. The rapidity with which the lever-point falls on closing the aorta is never so great as the rapidity with which it descends on stimulating the vasomotor nerves of the spleen. Naturally, also, the more extensive the vertical movements of the lever-point of the *oncograph,* the more marked is the effect produced upon the curve by closure of the aorta. But even when the splenic waves are very high, closure of the aorta, either during the time of ascent or of descent of the lever-point, never causes the rapid fall of the latter which can be produced by stimulation of the various nerves which cause contraction of the organ.

The very imperfect degree to which the volume of the spleen responds to variations in the height of the blood pressure shows us that the mass of the blood in the organ is practically cut off from the arterial system, and that, therefore, the circulation through the organ must be carried on almost exclusively, if not exclusively, by the rhythmic contractions of the smooth muscular fibres which are found in the splenic capsule and trabeculæ.

At an early period of my investigations I sought to find some means of influencing independently of one another these two factors, viz., the degree of dilation of the splenic arterioles and the extent of the splenic contractions, but soon found that the connection between them is exceedingly close. And this must necessarily be the case if, as seems more than probable, the arterial blood pressure takes no part in forcing the blood through the spleen.

All of the nerves which act upon the spleen influence apparently both the calibre of the arterioles and the rhythmic contractions of the muscular fibres. The spleen reacts, for example, with great readiness to reflex or direct vasomotor influences, but the effect produced in my experiments by stimulating vasomotor nerves directly or reflexly was always a contraction of the spleen, accompanied or followed by an increase in the extent of the rhythmic contractions, as will be described more fully when I come to refer to the vasomotor nerves of the spleen. To all appearance the arterioles are caused to contract if they be influenced at all, while at the same time the force of the rhythmic muscular contractions is increased. It is possible enough, it is true, that vasomotor influences affect the splenic muscles alone, and that the calibre of the arterioles is unaffected by them. At all events the comparatively rough method of section or stimulation of the various nerves which were found to influence the spleen failed to supply me with a satisfactory means such as I sought of separating, so to speak, the variations in calibre of the splenic arterioles from the variations in force of the splenic contractions in order to be able to investigate the part played by each.

That they do not under all circumstances bear one definite relation to one another is shown by the fact that various chemical substances and poisons, when injected into the blood, produce the most contrary effects upon the spleen—curare, for example, causing a temporary *expansion* of the organ, which is followed by an increase in the extent of the rhythmic contractions, while other substances, on the other hand, when injected into the blood, produce effects similar to those caused by stimulation of the splenic nerves, viz., a *contraction* of the organ, followed by an increase in the amount of blood pumped out at each systole.

Another proof that the amount of blood which enters the spleen by the arterioles may vary to some degree independently of the extent of the rhythmic contractions consists in the fact that the volume of the spleen is subject to slow variations, which would scarcely be the case if the relation between the amount of blood entering the organ and the amount pumped out at each systole were a rigidly fixed one.

And I may here refer briefly to these slow changes in volume of the spleen. That enlargement of the spleen occurs with very great readiness in a large variety of pathological conditions has long been known, but that changes in the volume of the organ may, and do, occur in health does not seem to be so fully recognized, and, indeed, the circumstances do not admit of our obtaining anything more than indirect evidence on the subject.

In the course of my observations I was constantly being reminded of the fact, that the volume of the spleen is subject to very considerable changes (I do not, of course, refer here to the rhythmic changes in volume which have been spoken of in the foregoing pages). In many experiments the organ continued to expand slowly for an hour or more, and this slow expansion would then, in some cases, be followed by a slow contraction. Or, the organ might at first slowly diminish in volume, this afterwards, perhaps, giving place to a gradual expansion. Little or no weight could, of course, be placed upon such gradual changes in the volume of the spleen as proving that similar changes take place under absolutely physiological conditions ; but, from the fact that the spleen may be made to expand or contract by relatively slight changes in the chemical constitution of the blood, such, for example, as those produced by injection into the veins of a small quantity of salt solution, &c., &c., certain deductions appear to me permissible.

It was found that, in cases for instance where the organ was steadily expanding, the injection into the veins of various substances which occur normally in the blood caused the spleen slowly to contract, and this gradual contraction might either continue until the end of the experiment, or might be replaced by gradual expansion. It is perfectly certain, then, that the spleen very readily changes in volume, and that such changes in volume may be brought about by very slight changes in the chemical constitution of the blood. The probability is, therefore, very great that gradual changes in the volume of the spleen are constantly taking place under normal, healthy conditions.

One other point in connection with these changes in volume of the spleen comes naturally to be referred to here, viz., the relation between the volume of the spleen and the extent of the rhythmic contractions. So far as I have been able to discover, there is absolutely no fixed relation between these two. The spleen may have increased enormously in size since the time of commencement of the experiment without any increase, and even with a considerable diminution, in the amount of blood which is being forced out at each systole of the organ. On this point also, therefore, as in so many others, the spleen differs from other organs, the amount of blood contained in it at any given time giving no indication whatever regarding the activity with which the circulation through it is being carried on. In one case, for example (of a dog), the height of the splenic waves was greater, after the organ had become contracted to the extent of more than 45 per cent. of its post-mortem volume, than the height of these waves before this contraction took place.

In one exceedingly limited sense some relation may be said to exist, however, between the volume of the spleen and the extent of its rhythmic contractions. When the organ has become nearly as strongly contracted as it is capable of becoming, the extent of the contractions is always very small (except in such a case as that illustrated in Fig. 10, where one or two unusually powerful contractions are produced by reflex stimulation of the splenic nerves). The cause of this diminution in the extent of the splenic systoles may lie either in the fact that the splenic pulp offers a resistance preventing the muscular fibres contracting beyond a certain point; or it may be that the muscular fibres of the capsule and trabeculæ, on undergoing considerable shortening, contract much less powerfully in response to a stimulus of given strength than would otherwise be the case. Both of these causes probably come into play in the case of the greatly contracted spleen, but one would naturally be inclined to lay most weight upon the first-mentioned.

With regard to the degree of contraction which results from stimulation of a sensory nerve, or of the splanchnics, for example, the contraction is much greater with a large spleen than with one which has already become considerably contracted. In one case, for instance, the contraction of the spleen produced by stimulating the peripheral end of one of the splanchnics was equal to more than 60 per cent. of the volume of the organ as measured after death, while in other cases where the spleen has already become "contracted up," only a slight effect, like that seen in Fig. 10, is produced.

Some of the influences, besides those already mentioned, which assist in regulating the amount of blood forced out of the organ at each systole will be referred to when describing the effect upon the volume of the spleen of stimulation of various nerves, and also in referring to the effect upon this organ of various chemical substances and poisons which have been injected into the blood.

Before coming to speak of certain kinds of irregularity of the splenic rhythm, I may remark briefly upon the absolute amount of blood, calculated in percentage of the volume of the spleen, which is forced out at each systole. This, as will have been gathered from the above pages, is subject to endless changes, and it is only of interest to state the extreme amount which I have encountered. This amount in one case was equal to a little over 36 per cent. of the volume of the organ as measured after death. I know of no reason for supposing, however, that this value represents the extreme amount of blood which the spleen is capable of expelling at each systole. In all probability with a larger number of observations a higher maximum will be found.

c. *Irregularity of the splenic rhythm.*

Before leaving the description of the more or less spontaneous changes which are found to take place in the volume of the spleen I have to refer to a form of irregularity of the splenic rhythm which is of considerable interest, and also, I believe, of some importance, from the light which it throws upon the mechanism of the rhythmic systole and diastole of the spleen. The form of irregularity referred to shows itself only when Traube-Hering curves of the blood pressure present themselves. These Traube-Hering curves, it need hardly be said, are caused by a rhythmic contraction and expansion of the blood vessels of various organs and tissues, but little being known of their nature further than that they are of central origin, being apparently due to rhythmic vaso-constrictor impulses emanating from the vasomotor centre or centres in the medulla and cord. Amongst those blood vessels which take part in producing the Traube-Hering blood-pressure waves by a rhythmic contraction and expansion of their component vessels are the vessels of the kidney. Whenever we find the blood-pressure curve rising and falling with the peculiar, and often very regular, rhythm which characterizes the Traube-Hering blood-pressure curve we find also that the kidneys undergo a rhythmic expansion and contraction.

In order to illustrate the close correspondence of the changes in volume of the kidney with the rise and fall of the blood pressure under the circumstances in question, I give a curve taken from the kidney by a method of the same kind as that which I have employed for the spleen. In Fig. 7, Pl. XV., the upper curve is that of the *oncograph* lever, the curve beneath it being that of the blood pressure. The letters *a* and *b* show the relative positions of the two recording pens. This tracing shows that with each rise of the blood pressure the volume of the kidney diminishes, and that with each fall of the blood pressure the volume of the organ increases. The very exact correspondence of the changes in volume of the organ with the changes in the arterial blood pressure is well shown in the tracing.

The spleen also takes part in the production of the Traube-Hering curves of the blood pressure, showing, like the kidney, a rhythmic contraction with each rise and an expansion with each fall of the blood-pressure curve. And this rhythmic contraction and expansion of the spleen is quite distinct from the rhythmic contractions of the organ which have already been described as occurring independently of any change in the height of the blood pressure.

In order to avoid confusion while referring to these two forms of rhythmic changes in the volume of the spleen, I will speak of that which is proper to the spleen, and which has no relation to changes in the height of the blood pressure as the specific splenic rhythm, while that which occurs in conjunction with the Traube-Hering blood pressure curves will be referred to as the Traube-Hering splenic rhythm.

In order to show that these two forms of rhythmic systole and diastole of the spleen are quite distinct from one another, the following facts may be mentioned.

In the first place: in those of my experiments in which the Traube-Hering splenic rhythm showed itself, the length of the waves of which it was made up was always different from the length of those of the specific splenic curves, the waves in the latter case being much longer than in the former. The difference in the wave-length was in every instance very considerable. For example, in the case of a dog, the specific splenic waves were, at the beginning of the experiment, of a length corresponding to 1 min. 40 secs., while three hours later they had become longer, the distance from apex to apex being equal to 2 min. Immediately after these waves had been described upon the paper, the Traube-Hering waves spontaneously appeared, these latter waves being, however, only 58 seconds long.

In the case of another dog, the specific spleen waves varied in length, in the course of the experiment, from 48 to 56 seconds, while the Traube-Hering waves, which appeared towards the end of the experiment, varied in length from 24 to 28 seconds only.

The simple fact of the difference in length of the two kinds of waves would not, perhaps, suffice to prove that they are different

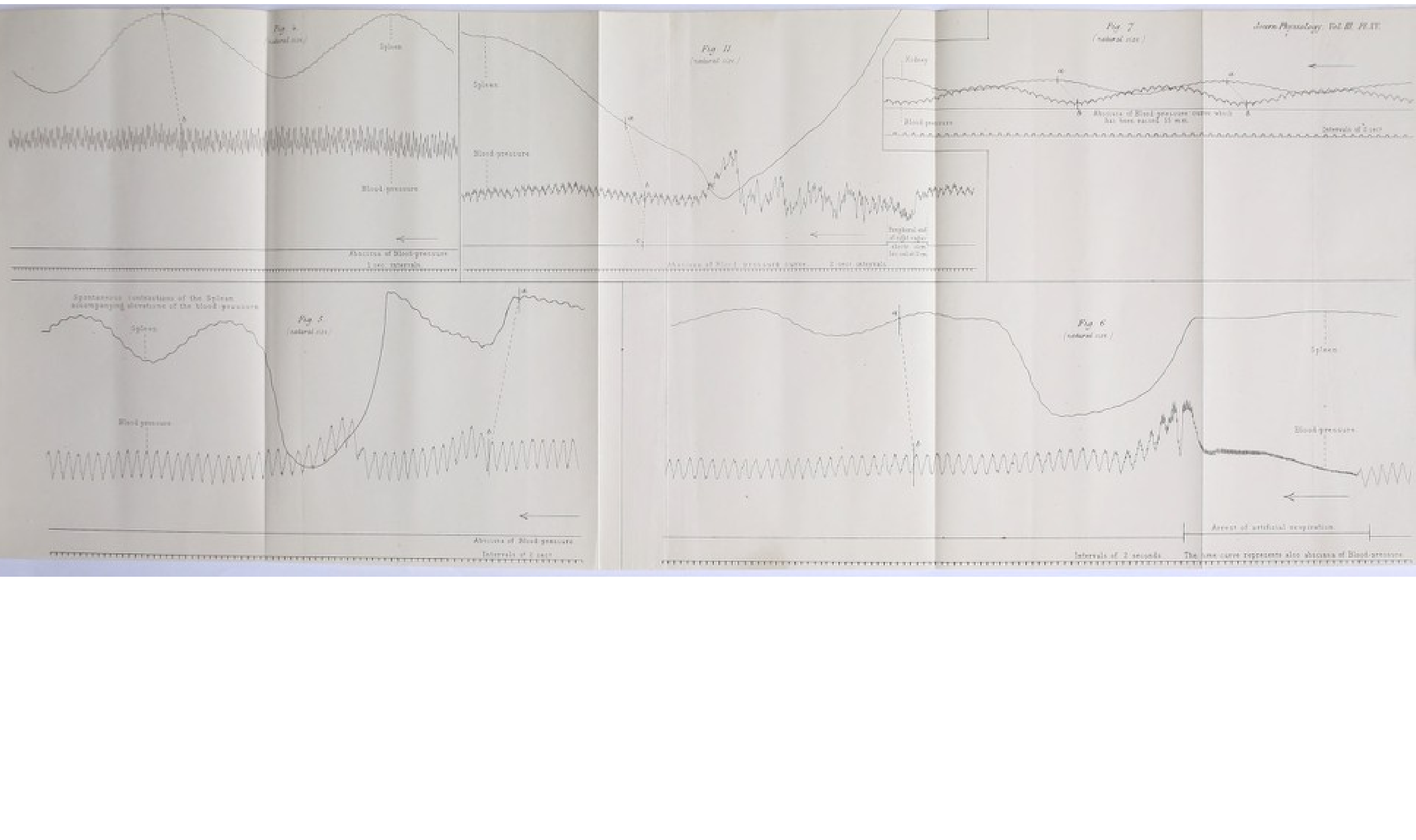
Fig 4
(natural size)
Spleen
Blood-pressure
Abscissa of Blood-pressure
1 sec. intervals
Fig 11
(natural size)
Spleen
Blood-pressure
Abscissa of Blood-pressure curve. 2 sec. intervals
Fig 7
(natural size)
Kidney
Blood-pressure
Abscissa of Blood-pressure curve which has been raised 15 mm.
Intervals of 2 sec.
Spontaneous contractions of the Spleen accompanying elevations of the blood-pressure
Fig 5
(natural size)
Spleen
Blood-pressure
Abscissa of Blood-pressure
Intervals of 2 sec.
Fig 6
(natural size)
Spleen
Blood-pressure
Arrest of artificial respiration.
Intervals of 2 seconds
The time curve represents also abscissa of Blood-pressure

in nature, since it might be supposed that the change in the condition of the animal, which leads to the appearance of the Traube-Hering curves, had caused a quickening in the rhythm of specific contractions and expansions of the spleen. This is, indeed, highly improbable, considering how constant is the rapidity of the splenic rhythm, even where great differences in the condition of the animal have taken place.

All possible doubt, however, as to the distinctness from one another of the specific and the Traube-Hering splenic rhythm ceases when we proceed to examine more closely the details of the Traube-Hering splenic waves. We find that on these curves presenting themselves, the waves of which they are made up are by no means regular in so far as strength, or rather extent, is concerned; there is also a certain degree of irregularity in the length of the waves.

In this respect the spleen presents a marked contrast to what is found to take place in the case of the kidney, in which, as the tracing in Fig. 7, Pl. XV., shows, the waves described by the *oncograph* lever are of the greatest regularity in time and height, and the correspondence with the changes in the blood pressure is exceedingly close. That a different state of things occurs in the case of the spleen can be seen at a glance in Fig. 8, Pl. XVI.

This tracing shows that, while the volume of the organ is evidently acted upon by the same kind of rhythmic vasomotor influence with each successive rise and fall of the blood pressure, as is seen in kidney curve, yet the degree to which the spleen curve corresponds with that of the blood pressure is very much less complete than is the case with the kidney. In most cases a simple inspection of the tracing suffices to convince one that the splenic curve, when the Traube-Hering waves of the blood pressure show themselves, is the result of the superposition of two series of waves, one being of a more rapid rhythm than the other. The curve which is produced is in fact an interference curve composed of the specific and of the Traube-Hering spleen waves. Even so short a portion of tracing as that reproduced in Fig. 8, suffices to illustrate this, although, of course, the fact is much more strikingly evident when a longer tracing is examined.

The fact that these two forms of rhythmic contraction and expansion of the spleen may be present at one and the same time, and that they produce an *interference curve*, is sufficient of itself, I believe, to prove that the specific splenic rhythmic systole and diastole is distinct in nature from those contractions and expansions which the spleen, in common with various other organs and tissues of the body, presents when the Traube-Hering blood-pressure waves appear.

At first, indeed, the meaning of the curious form of *regular irregularity* of the spleen curve, which is illustrated in Fig. 8, caused me no little perplexity, which was due to the fact that, although it seemed clearly an *interference curve*, yet there was often an apparent discrepancy between the extent of the specific spleen waves before the Traube-Hering rise and fall of the blood-pressure curve appeared, and the often very striking and even predominant effect of the former waves upon the latter in the interference curve. In one case, for example, the specific splenic waves were barely appreciable in the curve described by the *oncograph* lever before the appearance of the Traube-Hering waves; but on these latter commencing spontaneously, the interference curve showed a very marked participation of the specific spleen waves—much greater, in fact, than could possibly have resulted had the splenic waves remained so small in extent as they were before the *interference curve* commenced.

The meaning of this apparent discrepancy, however, disappeared when, with further investigations, I found that vasomotor influences of short duration, such as that produced by very brief stimulation of the peripheral end of one of the splanchnics, produces two effects upon the spleen, viz.: 1st, a contraction of the organ; and, 2nd, a temporary increase in the extent of the specific spleen waves. This latter effect is apparently always present, but is most readily seen in cases where the spleen has contracted to nearly a maximal extent, so that it can no longer diminish much in volume on stimulating its vaso-constrictor nerves. In such a case, as can be seen in Fig. 10, we have no great contraction of the organ, the most striking effect of the vasomotor stimulation being a temporary increase in the extent of the specific splenic waves.

As soon as this fact was made evident to me by repeated experiment, it was no longer difficult to see why the *interference curve* might show a much greater participation of the specific splenic waves than we would have anticipated from the extent of these latter before the rhythmic vasomotor influences which cause the Traube-Hering curves began to act upon the spleen. As in the case of electric stimulation of one of the vasomotor nerves of the spleen, so also each vaso-constrictor influence causing the rise of blood pressure in the Traube-Hering waves would have two effects, viz.: 1st, a contraction of the organ; and, 2nd, an increase in the force of the specific splenic waves. It seems clear that, with so complicated a relation between the two forms, above referred to, of rhythmic contraction and expansion of the organ, the production of a regular form of irregularity such as stamps those curves at first sight as interference curves, is chiefly due to the fact that the rhythm of the specific splenic systole and diastole is so remarkably constant in so far as the *duration* of the waves is concerned.

Before leaving this part of my subject it may be mentioned that certain differences may present themselves in the relative participation of the two component series of waves which make up the *interference* curve in question. In some of these curves the specific splenic waves are predominant, in others the Traube-Hering waves take the most prominent place; and between these extremes all varieties are apparently possible.

Leaving for the present those changes in the volume of the spleen which take place more or less spontaneously, I come to refer to those changes which can be produced experimentally through the medium of the nervous system.

II. Vasomotor Mechanism of the Spleen.

a. *Direct stimulation of the vasomotor centre.*

Perhaps the simplest way of stimulating the vasomotor centre is to cause dyspnœa of the animal, by interrupting for a short time the artificial respiration in cases where curare has been employed in addition to an anæsthetic agent. The tracing which is reproduced in Fig. 6 is an example of the effect which is produced upon the volume of the spleen by such temporary arrest of the respiration. As in the other tracings given, *a* and *b* give the relative positions of the *oncograph* lever-point and the point of the kymograph style respectively. It can be seen that, simultaneously with the sudden rise in the blood pressure, which occurred after the respiration had been stopped for about 50 seconds, the spleen contracted rapidly, and that, on recommencing the artificial respiration, the organ expanded to pretty nearly its former bulk. This tracing shows the usual effect produced by cessation of the respiration. And it may here be noted that, in the case of the spleen, the diminution in the volume of the organ is to all appearance not due exclusively to a contraction of the walls of the arterioles. In the case of the contraction produced by asphyxia, as in that which is produced by electric stimulation of the vasomotor nerves of the organ, the diminution in volume is far too rapid to permit of our supposing it to be due to a simple cessation of the entrance of blood into the pulp of the organ through the arterioles.

As has already been remarked, the rapidity with which the blood enters the spleen is, under normal conditions, relatively slight. When we find that even so great a fall in the blood pressure in the splenic arteries, as results from a closure of the aorta at its point of passage through the diaphragm, produces a relatively slow contraction of the organ, we can scarcely suppose that even a complete closure of all the splenic arterioles will produce so sudden a fall of the *oncograph* lever as usually results from stimulation of the vasomotor nerves of the spleen. The rapidity with which the spleen contracts on stimulation of its vasomotor nerves is well shown in Fig. 12, Pl. XVI.

The question naturally arises, whether this contraction of the spleen, which results from a cessation of the artificial respiration, be due to a vasomotor influence emanating from the cerebro-spinal centre, or whether it be not caused in part at least by the diminution of oxygen or increase of carbonic acid in the blood acting directly upon the muscular fibres of the organ. That a direct action of the latter kind takes place is possible enough, and it would be difficult to prove absolutely that it is absent without investigating the effect of asphyxia upon the volume of the spleen after section of all the splenic nerves—an operation which I have not as yet been able to accomplish satisfactorily. That the contraction in question is, at least in good part, due to a vaso-constricting influence emanating from the cerebro-spinal centre or centres may safely be concluded from the close correspondence in time of the sudden fall of the *oncograph* lever with the sudden rise in the arterial blood pressure.

Direct stimulation of the *medulla oblongata*, by passing an induced current through it (in curarized animals), also produces a rapid and powerful contraction of the spleen, which is synchronous with the rise of arterial blood pressure.

b. *Reflex stimulation of the vasomotor nerves of the spleen.*

Figs. 10 and 13 are intended to illustrate the effect produced upon the volume of the spleen by electric stimulation of the central end of a sensory nerve. Fig. 10, which has already been referred to, shows the effect of stimulating the central end of one of the sciatic nerves when the spleen is in a contracted condition. It shows that, under these circumstances, the principal if not the only evident effect of the stimulation is a temporary increase in the extent of the splenic waves. Fig. 13 shows the effect of stimulating, for about 16 secs., the central end of one of the vagus nerves (in this case the left), the nerve of the other side having been severed to prevent reflex inhibition of the heart. It can be seen that the effect in this case was that the spleen contracted rapidly and powerfully, afterwards expanding gradually, finally reaching more or less exactly the volume which it presented before the nerve was stimulated. Reference has already been made to the difference in the effect of stimulating the vasomotor nerves of the spleen according as the organ is or is not in a greatly contracted condition, and it is unnecessary to return at length to this subject here. With regard to these two curves, Figs. 10 and 13, it may be said that the difference between them is not due to the fact that the effect of stimulation of the sciatic differs in any appreciable manner from the effect of stimulation of the central end of one of the vagi (the nerve of the other side having been cut). The difference, in so far as the spleen is concerned, is apparently due exclusively to the different condition of the organ at the time of the stimulation. If instead of the sciatic, in the case of Fig. 10, I had stimulated the central end of the vagus, the change in volume of the spleen would have been the same as that given in Fig. 10. And the same holds good *mutatis mutandis* in the case of Fig. 13.

In cases where, as in Fig. 13, a tolerably powerful contraction of the organ results from stimulating a sensory nerve, we occasionally see but little increase in the extent of the specific splenic waves after the organ has expanded to its former volume, although some increase in the extent of these waves is, according to my experience, almost always present. This predominance of one of the effects of stimulating the vasomotor nerves of the spleen—viz., the contraction of the organ--over the other effect of stimulation of these nerves, viz., the temporary increase in the extent of the specific splenic waves,—it is difficult to explain satisfactorily. It is of importance to note, in connection with this point, that when a powerful contraction of the spleen is produced by stimulation of a vasomotor nerve, we very rarely find that the spleen goes on contracting and expanding in its contracted condition. No matter how long the contraction of the organ lasts, it is only after the spleen has again expanded to a volume approaching that which it presented before the nerve was stimulated that we find the splenic waves returning, and usually, as already said, with a temporarily increased extent. Stimulation of one of the vasomotor nerves of the spleen may cause therefore either an inhibition or an increase in force of the normal splenic contractions and expansions. The former effect, viz., inhibition, according to my experience, only results in cases where the spleen is not greatly contracted before the nerve is stimulated—to the case, in other words, where there is no hindrance to the contraction of the organ.

It may further be added with regard to the effect produced by stimulation of a sensory nerve that, with electric currents of equal strength, the effect of stimulating one sciatic, for example, is identical with that produced by stimulating the nerve of the other side. Careful comparison of the degree of contraction produced by stimulating the two sciatic nerves alternately with currents of the same strength and for the same period of time, showed that the resulting contraction of the spleen was the same in amount for both nerves.

With regard to the effect produced by stimulation of the central end of the vagus after the corresponding nerve of the other side has been cut, it may be mentioned that contraction of the spleen is always produced, whatever be the effect of the stimulation upon the blood pressure. As need scarcely be said, stimulation of the central end of the vagus of the dog sometimes causes a rise, sometimes a fall of the blood pressure, while, in some cases, as in Fig. 13, Pl. XVI., a combination of these two results is produced, a rise of the blood pressure being followed by a more or less marked fall. The effect on the volume of the spleen, however, appears to be always the same, viz., a contraction.

A word of explanation regarding Fig. 5, Pl. XV., may here be introduced. The changes in the height of the blood pressure and the corresponding changes in the volume of the spleen in this case are more or less spontaneous in nature.

Simultaneously with each rise of the medium blood pressure and the accompanying contraction of the spleen the animal struggled slightly. So that the rise of blood pressure which usually accompanies muscular movements is due in part to a contraction of the spleen. It is needless to refer further to this tracing, the meaning of which is sufficiently obvious.

c. *Direct stimulation of vasomotor nerves of the spleen.*

a. The splanchnic nerves.

There are at least four different nerve trunks the stimulation of which produces contraction of the spleen. By both right and left splanchnics and by the right and left vagus nerves vasomotor fibres pass from the cerebro-spinal centres to the organ in question.

Stimulation of the peripheral end of either the right or left splanchnic produces a very powerful and rapid diminution in the volume of the spleen. Fig. 12 is intended to illustrate the effect of stimulation by an induced current of the peripheral end of the right splanchnic. A precisely similar effect on the spleen was produced in the case of this animal by stimulating the peripheral end of left splanchnic. I have not made any extended series of observations upon the effect of stimulating the roots of the splanchnics in the thorax, but in one experiment I found that three of the roots of the left splanchnic (all that were tried) caused, on being stimulated, a marked contraction of the organ in question.

The effect of simple section of both splanchnic nerves did not, in two experiments, result in any expansion of the spleen; so that there did not appear to be any vasomotor "*tonus*" passing along these nerves from the cerebro-spinal centres to the spleen. Simple section of one or both splanchnic nerves does not cause any cessation or change in rapidity of the specific splenic systole and diastole. After both splanchnics have been cut the rhythmic contractions and expansions of the spleen are as regular and apparently as powerful as when both of these nerves are intact. It may be added that stimulation of the peripheral end of one of the splanchnics produces the same combination of effects upon the volume of the spleen, viz., contraction of the organ and temporary increase in the extent of the specific splenic contractions and expansions as was described as resulting from stimulation of a sensory nerve. Stimulation of the central end of one of the splanchnics has the same effect on the volume of the spleen as stimulation of the central ends of other sensory nerves.

b. The Vagi.

The relation of the vagi to the spleen is a very curious one; and I am by no means inclined to believe that the facts which have come to light in the course of my experiments on this subject permit of our drawing final conclusions as to the nature of this relation.

Stimulation of the peripheral end of either vagus causes a contraction of the spleen, as is illustrated by the tracing of Fig. 11. This tracing shows that the effect of stimulating the peripheral end of one of the vagus nerves (in this instance the right vagus) has a similar effect to that produced by stimulating the peripheral end of one of the splanchnics. That the contraction of the spleen, which is produced by stimulating the peripheral end of one of the vagi in the neck, is not due simply to the fall in the blood pressure, resulting from the action of the vagus on the heart, is evident from the fact that the contraction of the spleen does not by any means coincide, in regard to time, with the changes in height of the blood pressure. As has already been remarked, moreover, the volume of the spleen is but little influenced by changes in the height of the arterial pressure. The point, however, of principal interest in connection with the action of the vagus upon the spleen, lies in the fact that there is apparently some curious relationship between the rhythmic contractions of this organ and the nerves in question. Fig. 9, Pl. XVI., is intended to illustrate one of the peculiar phenomena which leads me to believe that some such relationship as that referred to exists. This figure reproduces the tracing reduced to one half the natural size. It shows that with each rhythmic contraction of the spleen there is an increase in the height of the pulse waves of the blood pressure curve, accompanied by a slight slowing of the cardiac rhythm. The appearance in this case of "vagus heart beats" synchronously with each successive contraction of the spleen, shows that some peculiar relation exists between the spleen and the vagus. In this case, section of both vagi, while causing, as was to be expected, a cessation of the rhythmic vagus beats of the heart, had no appreciable effect upon the rhythmic contractions of the spleen; from which one would be inclined to suppose that there exist centripetal nerve fibres, running from the spleen and having a close connection with the vagus-centre in the medulla, and that a centripetal nervous influence may, under certain conditions, be produced by each contraction of the splenic muscles. It should be added that in no case have I found that section of one or both vagus nerves causes an arrest of the specific splenic contractions, nor, on the other hand, does any expansion of the spleen result on these nerves being severed.

It is of importance to add that, after cutting both splanchnic nerves at their point of passage through the diaphragm, as well as both vagus nerves in the neck, stimulation of the central end of a sensory nerve, *e.g.*, the sciatic, still causes a reflex contraction of the spleen. There must therefore be at least a fifth route by which vasomotor influences may travel from the cerebro-spinal centres to the spleen.

I have intentionally avoided, in the course of this communication, making any statement regarding the time required for the transmission of vasomotor impulses, from the sciatic to the spleen, or from the vagus, or splanchnic, to that organ. The method employed admits of these measurements being made with convenience and considerable accuracy, but I prefer reserving the data which I have obtained upon this point, as I believe it may be better considered in a future paper, on the duration of the latent period for vasomotor impulses affecting the kidney, intestine, foot, &c., &c.

CONCLUSION.

In concluding, I may refer to some of the principal facts contained in the foregoing pages.

The circulation through the spleen differs from that of other organs in the important particular that the force which impels the blood through the organ is not that of the blood pressure in the arteries. The splenic circulation is carried on chiefly, if not exclusively, by a rhythmic contraction of the muscles contained in the capsule and trabeculæ of the organ.

This rhythmic contraction is exceedingly regular in so far as the rapidity of the rhythm is concerned, varying as it does in any given individual but very slightly even during an experiment lasting many hours, and in which the condition of the animal has necessarily changed considerably. Roughly speaking, each contraction with the succeeding expansion lasts about one minute in the case of dogs and cats.

As has also been pointed out, changes in the arterial blood pressure have comparatively little influence on the volume of the spleen, from which it may be concluded that the passages by which the arterial blood enters the substance of the organ are relatively very narrow, and that the pressure of the blood contained in the pulp of the spleen is not so closely connected with that of the arterial blood pressure as would be the case did the latter play a predominating part in carrying on the circulation through the organ.

The rhythmic contraction and expansion of the spleen is different in nature from the rhythmic contraction and expansion which may be observed in various organs on the "Traube-Hering" blood-pressure curves showing themselves. The spleen also takes part in the production of the "Traube-Hering" curves of the blood pressure, contracting with each rise, and expanding with each fall of the arterial pressure, but these contractions are readily distinguishable from those which are proper to the spleen and which are independent of changes in the blood pressure. Very frequently the combination of the Traube-Hering contractions of the spleen and the "specific splenic" contractions results in an "interference" curve being described by the instrument which records graphically the changes in volume of the organ.

Stimulation either of the central end of a cut sensory nerve or of the medulla oblongata causes a rapid contraction of the spleen. The paths by which such vaso-constrictor influences may travel from the cerebro-spinal centres are various. As has been shown, stimulation of the peripheral ends of both splanchnics and of both vagi causes a rapid contraction of the spleen. After section of these four nerves (the vagi in the neck and the splanchnics at their point of passage through the diaphragm) stimulation of a sensory nerve still causes a contraction of the spleen, showing that vaso-constrictor influences may pass from the cerebro-spinal centres to the spleen by some other route or routes than by the nerves named. It is not my intention, however, to give a résumé of the contents of the foregoing pages, and I will only remark in conclusion, that the fact that section of the principal nerves which convey vasomotor influences from the cerebro-spinal centres to the spleen has so little effect on the rhythmic contractions and expansions of the organ, would seem to indicate that these latter are regulated and maintained by some mechanism contained in the spleen itself.

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