RESEARCHES ON THE CIRCULATION TIME IN ORGANS AND ON THE INFLUENCES WHICH AFFECT IT. BY G. N. STEWART, M.A., D.Sc., M.D.

I. Preliminary Paper.

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SOME time ago[1] I described a method of measuring the circulation time which I believe to have great advantages over the method of Hering in the cases to which it is suitable, and which I have found especially useful in studying the circulation in organs like the kidney, lungs, liver, intestines, etc. I wish here to give a preliminary account of some of the work I have done in this way during the past two years, without either quoting or discussing the results in detail, or making more than incidental references to the literature of the subject. The experimental arrangements will, however, be described with some minuteness. In future papers I hope to treat the matter more fully, with the aid of the considerable amount of material already in my possession and of that which I may be able further to accumulate. A discussion of the theory of the method, a critical estimate of its value, and an examination of possible objections to it will be attempted in one of these papers.

The principle on which the method is based is as follows.

Since the electrical conductivity of blood is practically that of a solution of the salts in it, it can readily be altered by the injection of a solution of common salt of sufficient strength. The alteration will travel on with the velocity of the blood stream, and the arrival of the altered blood at any point of the vascular system may be detected by an easy galvanometrical observation, without the necessity of opening the blood-vessel. If a pair of unpolarizable electrodes be put in contact with the vessel between which and the point of injection the circulation time is to be measured, and connected with the ordinary Wheatstone's bridge arrangement, the balance will be disturbed as soon as the altered blood has reached the piece of vessel between the electrodes;

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[1] *Proc. Physiol. Soc.* Nov. 8th, 1890.

and a deflection will take place, the beginning of which will indicate the moment of arrival. The interval between this time and the beginning of the injection, the time of which has been also noted, gives the circulation time.

So much for the general principle. We shall now describe the details of its application which a pretty extended experience of the electrical method has shewn to be of importance, reserving only the modifications which have been found necessary or convenient in special experiments to be mentioned when these experiments come to be spoken of.

The measurement of the time.

It was very desirable that the method of doing this should be at once simple and quick, and yet sufficiently accurate. The usual electromagnetic arrangement, with tuning-fork, revolving drum, and all the ordinary impedimenta, was rejected as too cumbrous, although undoubtedly very fairly accurate. A little trial and a little reflection sufficed to shew that it was foolish to attempt to measure to a hundredth of a second a quantity like the circulation time, which was probably subject to spontaneous and uncontrollable variations of a twentieth of a second or more. I therefore looked about for something more convenient; and found all that was required in a stop-watch graduated in fifths of a second, and made specially for scientific work by a Swiss firm. With this chronometer it was possible to read between the divisions to twentieths of a second, a degree of accuracy which I found sufficient. It was only necessary to press the release at the moment when injection was begun, and to stop the watch as soon as the galvanometer image began to move. The interval could then be read off at leisure. It will be seen, when we begin to quote the results, what long lists of concordant numbers we are able to get by successive observations made in this way.

The injection of the salt solution.

This is an equally important point. After a little trial, it was found perfectly easy to arrange the syringe or other injecting apparatus, so that the injection could be managed by one hand of the observer, always the right in these experiments, while the chronometer was held in the other, and the eye was applied to the telescope of the galvanometer. With practice no difficulty was found in setting the watch off at the very moment of injection, and the touch of the finger on the piston of the syringe was quite a sufficient guide, so that the eye was left free. In this way the observer not only rendered himself independent of the aid of an assistant, but also ensured greater accuracy in the time measurement than would have been possible had one person made the injection and another looked at the galvanometer, as was done in the preliminary work. As a matter of fact, it was only in a very few of the first experiments, and only during the operation in the others, that any assistance was employed; while many experiments were done from beginning to end without help. This is mentioned to shew that the proceeding is by no means a complicated one in practice, although it may look so in print—a point of importance in judging of the value of a method.

The details of the injecting arrangement used in the greater number of the experiments are so simple that a figure is unnecessary. A small syringe, with graduated piston, is connected with a **T** piece, one limb of which communicates by an indiarubber tube with the cannula inserted in the blood-vessel. By means of a cock this can be cut off from the syringe, or put into communication with it. The other limb of the **T** is connected with a tube dipping into a vessel containing the salt solution to be injected. This vessel is immersed in the water of the warm box in which the animal is fixed, and it is thus secured that the solution is always injected warm and at approximately constant temperature.

Before each observation the syringe is filled by closing the tube connected with the blood-vessel, and drawing up the solution through the other. The latter is then closed by a cock or clip, the former opened; and, in injecting, the piston is pushed down till it is stopped by a check, which can be previously adjusted, so as to make the quantity injected larger or smaller, from $\frac{1}{8}$ c.c. to 5 c.c.

The *solution* used was generally a 2·5 per cent. solution of common salt. For special purposes a weaker or a stronger solution was occasionally employed. In a few of the preliminary experiments, before the sensitiveness of the method was known, solutions as strong as 10 per cent. were used. This strength is, however, much too great, and quite unnecessary, at least for animals of the size of rabbits, cats, and small dogs. In fixing the strength and quantity of the solution to be injected, the rule is to use the minimum quantity of salt required to cause a sufficiently large and definite deflection. Since the amount of the deflection depends upon the ratio of the new resistance of the arm of the bridge containing the blood-vessel to the old, and since the only variable factor in this resistance is that of the blood contained in the vessel, so much salt must be added to the blood at the point of injection, that when the column of altered blood has reached the electrodes, it is still able to diminish the resistance in this arm by a sufficient fraction of its amount. It is evident that the necessary quantity will depend upon the total amount of blood in the animal, or, what is usually much the same, the size of the animal, upon the distance the blood has to travel before reaching the electrodes, and the amount of branching of the path. The larger the animal, the greater the distance between the cannula and the electrodes, and the freer the circulation of the injected salt by other routes, the greater must the quantity injected be. From experience I have found 1 to 2 c.c. of a 2·5 per cent. solution about the best quantity to use for a rabbit or a very small dog, when only one set of capillaries lies between the point of injection and the electrodes. When two sets of capillaries intervene, it has sometimes been found advantageous to use a 3, 4 or even 5 per cent. solution.

The quantity injected can be varied a good deal without affecting the reading of the circulation time, when injection is made into a vein like the jugular; for the considerable capacity of the right side of the heart, and the sealing up of the auricle and the mouths of the great veins during contraction, tend to prevent the pressure from being artificially raised, and the blood and salt solution forced through the lungs at more than the normal rate.

Experiment 1 is an example of this.

EXPERIMENT 1. Rabbit, 2000 grams. 1·5 gram. chloral hydrate in rectum. Cannula in right jugular vein. Right carotid prepared.

Time	Solution injected	Circulation time from right jug. to right carotid	Deflection
.59	1 c.c.	2·6	∞
1.1	1 ,,	2·7	
.9	1 ,,	2·7	
1.11	1·5 ,,	2·6	
1.15	1·5 ,,	2·5	∞
.18	2 ,,	2·4	∞
.20	2 ,,	2·5	∞
.22	3 ,,	2·7	∞
.24	3 ,,	2·7	∞
.26	0·5 ,,	3·4	
.28	0·5 ,,	3·	236
.30	0·5 ,,	2·8	283
.37	1 ,,	3·2	
.39	1 ,,	2·8	

The Electrodes.

Since it is the proportion of the diminution of resistance in the circuit including the piece of blood-vessel to the total resistance of that circuit which determines the amount of the deflection, it is important that the variable resistance should bear as great a ratio as possible to the fixed resistance. The latter is made up of the resistance of the electrodes and that of the vessel walls. The resistance of the vessel walls can be diminished, or at least prevented from increasing, as it is apt to do when the vessel is long exposed, by moistening with normal saline solution. This is not always desirable, however, except near the electrodes, as a drop of the solution would cause short circuiting of the current. The resistance of the electrodes, although it must of course be always rather high, since they must be unpolarisable, can be greatly diminished by properly choosing their form and dimensions.

I have found the ordinary clay and zinc sulphate electrodes the best. Where the diameter of the blood-vessel was small the electrodes were both hook-shaped; and the vessel was laid on them so that the current would pass, on the whole, longitudinally. With large blood-vessels, and especially where two pairs of electrodes had to be brought into contact with neighbouring cross sections of the same vessel, it was sometimes found advantageous to use a pair consisting of one hooked and one straight-pointed electrode, the vessel being laid in the hook, and the point of the other electrode being arranged vertically over it. Here the contacts of the two electrodes would be approximately at the ends of a diameter of the vessel, and the current would pass transversely.

Each pair of electrodes was fixed in proper position in a cork holder attached to a universal joint.

To make the hook-shaped electrodes, a glass tube of fairly wide bore is drawn out abruptly, and bent into a hook as near the full bore as possible. The hook is flattened, and its point fused. A hole is next made in the usual way with a wire, the bore being opened exactly at the bottom of the bend. When the electrode is filled with clay, the vessel makes contact with the latter through this hole.

All the details given are of importance, if the most suitable electrodes are to be obtained, although nearly any kind will give fair results. The hook is almost indispensable, in order to keep the vessel in position. If it is not made thin and fine there will be undue pressure, and the flow of blood will be hindered, especially if the vessel is a vein.

The bore should be fairly wide, and narrowed as near to the hook as possible, in order to keep the resistance of the electrodes low.

I also tried a form of d'Arsonval's electrodes made specially for these experiments, with vulcanite hooks for the vessels, but I did not find them satisfactory.

The Galvanometer.

It is perhaps well to use a galvanometer with a light magnet and mirror, where this can be obtained; but an ordinary Wiedemann does well enough; and the greater number of my experiments have been made with a Wiedemann. The galvanometer should be rendered fairly sensitive. For some purposes it is well to make it aperiodic; for other purposes this is unnecessary, and for some it is disadvantageous.

Whatever kind of galvanometer is used, the readings should be taken with a telescope and scale, as this simplifies the observations greatly. Theoretically the resistance of the galvanometer should be adjusted to the resistances in the bridge, if the greatest delicacy is to be attained; but in practice it is quite sufficient to take any ordinary high resistance galvanometer, of the kind used in muscle and nerve experiments and with a resistance of 4000 to 7000 ohms. Mine had a resistance of 4373 ohms.

The Wheatstone's bridge.

This was formed in the usual way with a resistance box of post-office pattern. Sometimes the resistance of the arms of the bridge was 1000 ohms each; but when the resistance of the circuit containing the blood-vessel was more than 10,000 ohms—and of course it varied greatly with the size of the vessel and the length of it between the electrodes—the bridge ratio had to be made 100 : 1000. Where nothing is said about the ratio, it is to be assumed that it was 100 : 1000.

The Battery.

This always consisted of a single pint Daniell, the current of which was subdivided by a rheochord before reaching the bridge, so that only a weak twig passed through it; and the current strength in the branch containing the vessel was always low.

The Warm Box.

This was a metal box standing on feet, and heated by two small flames below. A considerable quantity of water was put in it, so that no sudden changes of temperature could take place. The holder containing the animal was put in the box at a suitable height, and the holders of the electrodes having been passed in over the edge, the whole was covered with glass plates. Unfortunately, during a portion of the work I had not this arrangement for keeping up the temperature of the animal.

Insulation of the blood-vessels.

This was obtained by slipping strips of thin sheet indiarubber beneath them. Of course when the electrodes were longitudinally arranged on a vessel, a twig of the current would pass round by the general mass of the tissues where the isolated vessel joined them. The longer the piece of insulated vessel in proportion to the distance between the electrodes, the weaker would this twig be.

It is, therefore, of some consequence to isolate as long a piece of the vessel as is convenient, without damaging the circulation. But, since the change which the arrival of the salt can produce in the resistance of the part of the circuit formed by a great mass of tissue must be trifling in comparison with that produced in the resistance of the isolated blood-vessel, the beginning of a well-marked deflection must always indicate the time when the change of resistance has actually reached the isolated portion of the vessel; so that whenever this is long enough to leave room for the electrodes a sufficiently accurate observation may be made.

To get a preliminary notion of the meaning and possible magnitude of changes in the circulation time, I made a few experiments on an artificial scheme. It consisted of a system of tubes, chiefly elastic, through which a flow of water was kept up from a large reservoir. At one point in the system a piece of fresh artery was introduced, which was arranged on unpolarisable electrodes of the kind used in the experiments, and so connected with the Wheatstone's bridge. A cannula in connection with the injecting apparatus was inserted at another point of the apparatus. The artery could be introduced directly into the unbranched circuit, or put into a collateral circuit. The peripheral resistance was varied in different ways, by introducing or removing glass capillary tubes, or by compressing with clamps and strips of wood a part of the indiarubber tube.

Experiment 2 is an example of the results got in this way; and though only of course a very rough imitation of anything which could happen in an animal, it indicates clearly enough, I think, how we are to interpret changes of the circulation time occurring under certain conditions.

EXPERIMENT 2. (Artificial Scheme.)

Resistance	Circulation time	Deflection	Notes
Large	53·1″	850—∞	2 c.c. 3 $^0/_0$ NaCl injected; galv. coils at 2; Rh. 250.
Less	22·25	272—∞	
No	7·1	475—∞	
Some	14·7	605—∞	
More	25·85	492—∞	
No	7·1	400—∞	1 c.c. 3 $^0/_0$ NaCl injected.
No	7·05	109—976	·5 c.c. ,, ,,
Some	16·75	0—98	
Some	10·9	410—429	Galv. coils at 4; 1 c.c. 3 $^0/_0$ NaCl injected in all that follows.
No	7·9	398—567	
Some	10·15	446—932	
More	20·9	490—∞	
Same as last	19·35	612—∞	
No	8·3	545—∞	
No	6·8	475—∞	Rh. 50; deflection was about 100 divisions off scale.
Some	17·75	600—937	

Note. "Galv. coils at 2, at 4" &c. means that each coil of the galvanometer (Wiedemann) was 20 mm., 40 mm., &c. distant from the galvanometer magnet.

"Rh. 250, Rh. 50" &c. means that 250 mm., 50 mm., &c. of the rheocord wire was interposed in the battery circuit.

In order to test further the value of the method before proceeding by its aid to attack more difficult problems, it seemed well first of all to measure the circulation time in a number of vascular tracts under conditions which made comparative observations on one and the same animal easy, and which did not preclude, in properly selected cases, the comparison of results obtained on different animals.

All the experiments contained in this paper are concerned with the determination and comparison of the circulation time of various tracts, but not with the influence of section and stimulation of nerves upon that time, nor with any other influences beyond that of temperature.

The animal (Rabbit) was put under chloral, the vessel or vessels to be placed on the electrodes exposed, and the cannula inserted into a vein (the external jugular, or one of its branches, or other veins, according to the object of the experiment). Since chloral lowers the blood pressure, it might seem to be a bad narcotic for experiments on the circulation. But for comparative experiments, where a notion of the relation between the circulation time in different organs is wanted rather than absolute measurements, it is a good drug, as it may be supposed to cut out accidental variations of the calibre of the small vessels. In all experiments with section and stimulation of nerves curara or urethan was used.

The time of the lesser circulation was generally taken as a standard of reference with which to compare other circulation times. The carotid was therefore exposed on one side in addition to the vessels required for the special purpose of the experiment. When the cannula was in the main stem of the jugular, as was generally the case, it was always pretty low down, so that its point was only at a comparatively short distance from the heart. The carotid was also usually prepared for the electrodes not very far above its origin. So that the circulation time from jugular to carotid would exceed that of the lesser circulation only by the time which the blood takes to pass from the mouth of the jugular[1] to the right side of the heart, and from the left side of the heart to a point a little beyond the origin of the carotid.

If then we take the average length of the arterial path from the left ventricle to the electrodes on the carotid as 4 cm., and from the mouth of the external jugular to the right heart as 1·5 cm., and assume the velocity of the blood in the arterial part of the path to be 20 cm. per second, and that in the venous part, 10 cm. per second, we get $0{\cdot}2'' + 0{\cdot}15'' = 0{\cdot}35''$ as the excess of the circulation time from jugular to carotid over the true time of the lesser circulation. If this excess remains sensibly constant, that is, if, with the degree of sensitiveness used in the measurement of time in our experiments, it does not vary more than $\frac{1}{7}$ of its whole amount, no sensible error will be caused by taking the unreduced time as the measure of the true time of the lesser circulation. This is what has generally been done, although in all experiments in which it was thought necessary to have data for making a correction, the distances were actually measured on the blood-vessels.

When a comparison of two circulation times was to be made, the electrodes needed were either first of all put in position in the two vascular tracts, and one or the other set thrown on to the bridge by means of a commutator, or a single pair of electrodes was shifted about from one to the other.

When a vein had to be placed on the electrodes the former plan

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[1] The portion of the vein between the cannula and its junction with the subclavian must always remain pretty full of salt solution from one observation to the next; and in the very moment of injection as much solution must pass into the superior cava as passes from the syringe to the jugular. The *mouth* of this vein, or of any other in which the cannula is inserted, and the circulation stopped, is therefore to be taken as the starting-point of the injected salt.

was found to be safest; but with arteries perfectly good results were, with a little care, obtained by the latter method.

In Experiment 3 the circulation time from the mouth of the posterior facial branch of the left external jugular to the right carotid artery is compared with the time from the same point of origin to the right crural artery. The crural vessels were always prepared about the upper third of the thigh.

EXPERIMENT 3. Rabbit, 2 kilos. Morphia. Right carotid and right crural artery exposed. Cannula in left posterior facial vein.

Right crural artery on electrodes. Circulation time 4·5″

Now injected ·2 gram chloral hydrate subcutaneously and ·2 gram into blood through the cannula. Circulation time $\left\{\begin{array}{l}3\cdot3''\\3\cdot5''\\4\cdot3''\end{array}\right.$

Right carotid artery on electrodes. Circulation time $\left\{\begin{array}{l}2\cdot4''\\2\cdot5''\\2\cdot5''\end{array}\right.$

Right crural artery again on electrodes. Circulation time 3·7″

Right jugular vein on electrodes. Circulation time $\left\{\begin{array}{l}3\cdot3''\\3\cdot0''\\3\cdot2''\end{array}\right.$

P.M. Bladder contained 126 c.c. urine; much distended. Blood clots well and as rapidly as normal. All the organs normal in appearance.

The average pulmonary circulation time (uncorrected) is here 2·45″ (we only take account of twentieths of a second). The average time to the crural artery of the three observations taken first is 3·7″, which exactly agrees with the last observation. The difference, 1·25″, represents the time taken by the blood in passing to the crural artery from the section of the aorta at which the solution has arrived at the moment of its reaching the electrodes on the carotid. If we suppose the velocity up to this section in the descending aorta to be the same as in the carotid up to the electrodes, we get 1·25″ as the time required by the blood to pass to the right crural artery from a point of the descending aorta at the same distance from the heart as the position of the electrodes on the carotid. In the experiment this point would be about 4 cm. from the origin of the aorta, and the electrodes on the crural would be about 22 cm. from the origin of the aorta. The blood therefore takes 1·25″ to travel 18 cm., an average velocity of 14·4 cm. per second over this part of the path.

Experiment 4. Rabbit, 2003 grms. 1·2 grm chloral hydrate in rectum. Cannula in left jugular vein.

Time	Vascular tract	Circulation Time	Maximum Deflection	Notes
11.45	Left jugular vein to right crural artery	*3·9″	—	Bridge ratio 100 : 1000; Box 2400.†
11.50	,,	3·85	370	
.54	,,	4·	385	
12.1	Left jugular to right carotid	3·1	230	Bridge ratio 100 : 1000; Box 1200.
.6	,,	2·8	241	
.10	,,	2·5	218	Box 1300.
.18	,,	3·	216	1 gr. chloral hydrate subcutaneously, as animal restless.
.39	,,	2·4		
.42	,,	2·95	210	
.45	,,	2·9	143	Up to this point 1 c.c. of 2·5 $^0/_0$ NaCl solution was used for each injection.
1.21	Left jugular to right jugular	4·1		1 c.c. of 5 $^0/_0$ solution of NaCl. Box 2300. As blood not flowing freely through vein on electrodes, a small side branch was ligatured and put on one electrode, while jugular vein itself remained on the other.
.24	,,	4·9	170	Far slower movement than with carotid artery on electrodes. The return is especially slow.
.29	,,	6·1		Ligatured another small branch and put it on second electrode. Blood seems now to flow better through vein. Box 4300.
.43	,,	5·6		
.45	,,	4·8		Box 5000
2.2	Left jugular to right crural vein	7·8		The crural artery and vein were exposed a little below Poupart's ligament. Box 1800.
.16	,,	8·4		Box 1300.
.20	,,	8·8		Image somewhat unsteady, and this time reading is almost certainly a little too long.
.24	,,	8·4	202	Deflection pretty sharp.
.27	,,	8·5	200	Temperature in rectum 30·75°.
.34	Left jug. to right crural artery	5·4	∞	Here used again 1 c.c. of 2·5 $^0/_0$ NaCl. Box 1300.
.36	,,	5·4	∞	
3.10	,,			Rectum 29·9°.
4.27	Left jug. to right carotid	3·		Warmed animal now by hot water box. Temp. of rectum rose very slowly. Rectum 33°. Box 1100.
.30	,,	2·8		
.32	,,	2·6		
5.3	Left jug. to right crural vein	8·85		
5.10	,,			Rectum 35°.

In Experiment 4, the average circulation time of the first set of

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* In the whole of this experiment 0·4″ had to be deducted from the circulation time for error of null point of chronometer. The corrected readings are given.

† "Box 2400" means that 2400 ohms had to be put in from the resistance box to give the balance of the bridge.

observations from jugular to crural artery is 3·80″; the average of the first set of seven pulmonary readings is 2·80″. The difference, 1·00″, represents again the circulation time of the path to the right crural artery from the point on the descending aorta corresponding to the position of the electrodes on the carotid. As these were about 6 cm. from the beginning of the aorta, as compared with 4 cm. in the last experiment, the time, 1″, would correspond to a path about 2 cm. shorter than the time, 1·25″.

About three hours later, the average circulation time to the crural artery was considerably increased. It was now 5·4″, while that of the pulmonary circulation was precisely the same as before, viz. 2·8″. The lengthening of the circulation time to the crural artery must be attributed, partly at least, to the cooling of the animal (the hot box had not yet been used), which, as we shall see, has a great effect. The temperature had risen again very considerably before the corresponding pulmonary observations were taken, although not nearly to its old value during the first series, and this might be supposed to account for the fact that the pulmonary circulation time was undiminished. There is little doubt, however, and many of the observations to be quoted confirm this, that the pulmonary circulation time is far less affected by changes of body temperature, or at any rate by a fall of temperature, than that of most vascular tracts.

Circulation time between crural artery and crural vein.

The average circulation time from the jugular to the right crural vein in the set of five observations, beginning at 2·2 (Experiment 4), is 8·4″.

Deducting from this the average time to the crural artery in the second set, viz. 5·4″, we get 3″ as the circulation time from crural artery to crural vein. If we take the mean between the first average circulation time to the crural artery, 3·8″, and the second 5·4″, we get 4·6″. Deducting this from 8·4″, we get 3·8″ as the circulation time from crural artery to crural vein. What precise meaning we must attach to the expression "circulation time from crural artery to crural vein" will be better discussed in another paper, where the changes produced in this time by section and stimulation of nerves are described. It is enough to say here that the circulation time of a region containing systemic capillaries is generally more variable than that of a region containing pulmonary capillaries, although great variations can be caused in the latter by experimental means. Since 8·4″ must be less than the total circulation time by way of the leg, it is plain that the blood completes the lesser circulation in less than a third of the time required to complete the whole circulation by this long path.

Taking account of the time required by the blood to pass from the position of the electrodes on the crural vein to the right side of the heart, or about 2″, we get 10·4″ as the total circulation time by this long route. The ratio of the (uncorrected) pulmonary circulation time to this is 1 : 3·7, and its ratio to the systemic part alone (7·6″) is 1 : 2·7. If the small correction for the distance of the electrodes on the carotid from the left ventricle (about ·2″ in this case) is applied, these ratios become 1 : 4 and 1 : 3 respectively. To get the time spent in the lungs alone we must further take account of the stay of the salt in the heart. The longest time it could remain in one side of the heart would be a complete cycle; and this would happen when the salt arrived just at the end of the auricular systole. If it got in at the very beginning of the auricular systole, it would remain in the heart at most ½ and might remain only ¼ of a cycle. On the average of a number of observations we may assume that the mean time spent in each side of the heart would be not far from ½ of a cycle, or in a rabbit with a pulse rate of 200 per min. ·15″. Deducting the double of this from 2·6″, we get, say, 2·3″ as the nett circulation time for the lungs alone.

Without entering into a formal analysis of results sufficient to prove the statement, and indeed with the express reservation that it is only to be taken as approximate, we may say that in general the time of the pulmonary circulation is not far from a fourth of the mean systemic circulation time, nor far from a fifth of the mean time required by the whole of the blood to complete both circulations. Here the mean systemic circulation time is defined to be the sum of the products of the mean circulation times of all the vascular tracts into which the systemic circulation may be divided and the average quantity of blood in them, divided by the average quantity of blood in the systemic vessels. In symbols, if m_1, m_2, m_3, &c. represent the average quantity of blood in the various organs &c., exclusive of the lesser circulation, and t_1, t_2, t_3, &c. the mean circulation times through these organs, then the mean systemic circulation time

$$= \frac{m_1 t_1 + m_2 t_2 + m_3 t_3 + \&c.}{m_1 + m_2 + m_3 + \&c.}.$$

And it is clear that, if instead of taking absolutely the whole systemic circulation into account, we consider a sufficient number of representative organs, we can equally arrive at a knowledge of the mean systemic circulation time.

It may be added, although it is anticipating a little the results of the following sections, that the kidneys, portal system, and distal portions of the limbs are among the systemic paths which have the longest circulation time. The shortest systemic circulation time observed (through the muscles of the neck) is generally about equal to that of the lesser circulation; perhaps the coronary circulation time may be still less.

The evidence for these statements is contained partly in the experiments on rabbits quoted in this paper, partly in observations on dogs and rabbits given in the accompanying paper on "The Time of the Lesser Circulation," and partly on experiments not yet published. It is unnecessary to point out that the quantities dealt with are not constants.

In one or two experiments some abnormally short systemic circulation times were observed. The circulation time from one jugular to the other, for instance, in Experiment 3, for a set of three readings, is only 3·15″. Deducting the pulmonary circulation time, this would leave only 0·7″ as the time required for some of the solution to find its way from carotid to jugular. This, however, is so exceptionally short that one hesitates to accept it, although I do not know of any weak point in the experiment, except that it was one of the first, and therefore presumably more liable to error than the later work. What may be considered a normal value is that of Experiment 4. Here, for a first set of five readings, the average time from jugular to jugular is 5·1″. Taking away the pulmonary circulation time, 2·8″, we get 2·3″ as the time from carotid to jugular.

In Experiment 3 the cooling was less than in Experiment 4 and this might partly account for the smaller circulation time.

The fact noted in Experiment 3, that the bladder contained a large quantity of urine, was pretty often seen in the course of this research and was on the whole more striking than any abnormal collection of liquid in the serous cavities. No doubt the injection of the salt had a diuretic effect. In many cases, however, the bladder was not found more than normally distended, and in some experiments in which it was emptied at the beginning no considerable quantity of urine was found in it at the end. But in a good many instances the bladder was more than once evacuated involuntarily in the course of the experiment, and the aggregate quantity of urine passed in some of these cases was very large. The note as to the normal appearance of the internal organs is characteristic. Often after an experiment lasting 5 or 6 hours, in which 50 injections or more had been made, the animal was in good condition at the end, and the post-mortem examination revealed scarcely any mark of damage. The blood always clotted normally.

The circulation time of the kidney.

The renal vessels are very suitable for the determination, as they are comparatively long, are unbranched, and can be isolated with great ease, while the renal vein is of large calibre. The left kidney is better than the right owing to the greater length of its vessels. The operation I found best was an incision in the linea alba for about $\frac{3}{4}$ of its length, beginning at the xiphoid. The intestines are drawn over to the side, and kept in position by blunt hooks guarded by sponges. The renal artery and vein are readily isolated with a curved needle, and a piece of sheet indiarubber is slipped under them, or under one of them, in the usual way. The kidney may be left *in situ*. In some cases, however, better insulation is got by gently separating the kidney from the surrounding connective tissue, and laying it also on a piece of sheet indiarubber or on a plate of glass or in a watchglass, or by ligaturing a piece of the connective tissue at each end of the organ, and gently swinging the kidney clear of the other tissues by the threads.

A point of great importance in preserving the normal relations of the circulation in the kidney is to keep the temperature normal, or at least to prevent it from falling much. In no organ which I have worked with does cold seem to produce a greater effect on the circulation time.

In Experiment 5 the average circulation time from jugular to right renal artery is 5″ in the first set of three observations, 4″ in the second set of four observations, and 3·85″ in the third set of three observations. The first set being the very beginning of the work on the kidney, was more or less a "trial" set, and is probably not worthy of equal confidence with the second and third sets. If we take, therefore, the average of the mean values of the two last sets, we get 3·9″ as the average circulation time from jugular to right renal artery. Omitting for the same reason the first isolated observation on the vein, we have for the five following readings a mean of 11·9″. The circulation time from the position of the electrodes on the renal artery to their position on the renal vein, i.e. practically the circulation time in the kidney, is in this case 8″.

EXPERIMENT 5. Rabbit, 2500 grams.

Time	Vascular tract	Circulation time	Maximum deflection	Notes
12.20				1·2 gram chloral hydrate in rectum, and ·5 gram more before operating. Abdominal cavity opened by an incision parallel to vertebral column on right side, reaching from the tip of the last rib to the neighbourhood of the iliac crest. Right renal artery and vein isolated. Cannula in left jugular.
	Left jug. vein to right renal artery	5·35″		2·5 $^0/_0$ NaCl used for injection.
1.45	,,	5·2		Box 900. Bridge ratio 100 : 1000.
	,,	4·5		
	Left jugular to right renal vein	10·8		
	Left jugular to right renal artery	3·9		Kidney insulated entirely from surrounding tissues by indiarubber.
	,,	4·		
	,,	4·		Kidney insulated by means of glass plate.
	,,	4·		Kidney feels rather cold.
	Left jugular to right renal vein	12·7		Box 1000.
	,,	11·5 } 11·9		
	,,	11·65		
	,,	11·6		1 c.c. 5 $^0/_0$ NaCl here used.
	,,	12·05	90	Vein rearranged on electrodes. Box 1200. 5 $^0/_0$ NaCl again.
	Left jugular to right renal artery	3·8		2·5 $^0/_0$ NaCl again.
	,,	3·8	71	
3.28	,,	4·		
.34				Rectum 33·2°.
3.39	Left jugular to right carotid	4·		
.56	,,	3·6		
4.1	,,	3·9		
.4	,,	4·		
.10	,,	3·9		
5.5				Rectum 31·5°.

P.M. Bladder 30 c.c. urine. Length of inferior vena cava from heart to diaphragm 2·5 c.m.; from diaphragm to upper border of liver 1 c.m.

Experiment 6. Rabbit, 2500 grams. At 12.20 1·2 gram chloral hydrate in rectum. Abdominal cavity opened in linea alba from xiphoid nearly to pubis. This is a better operation for exposing kidney than the operation of Experiment 5.

Cannula in left jugular. Right carotid artery and left renal artery and vein exposed.

Time	Vascular tract	Circulation time	Maximum deflection	Notes
2.15	Left jugular to right carotid	2·7″		
.25	,,	3·1 } 2·85		
.27	,,	3·05		
.29	,,	2·5		
.31	,,	2·8		
2.47	Left jugular to left renal artery	3·4	210	Kidney insulated by indiarubber.
.48	,,	3·5 } 3·45		
.50	,,	3·45		
2.53	Left jugular to left renal vein	13·5	100	
.55	,,	13·3 } 13·45		
.57	,,	13·1		
3.	,,	13·9	35	Kidney very cold.

We see therefore that the kidney has a long circulation time. In fact it is longer than that of any other organ which I have investigated; and the blood may take nearly as long to pass through the kidney as to pass round the whole circulation by the leg. No doubt the explanation of this, for the part of the blood going through the glomeruli, is the great vascular resistance presented by the double set of capillaries. The blood which passes through the medulla, although it has only one capillary plexus in front of it, must also have an unusually difficult path through the long and narrow vasa recta.

If we compare the circulation time from jugular to carotid (Experiment 5) with that from jugular to right renal artery, we find that the former averages 3·9″, which is precisely the average we have brought out for the latter. We should expect, therefore, on the assumption that the velocity is uniform right up to the electrodes in each case, to find that the position of the electrodes on the renal artery is about the same distance from the origin of the aorta as that of the electrodes on the carotid. And as a matter of fact this is not far from being the case, the electrodes on the right renal artery being only 2 cm. farther from the heart than those on the carotid. In reality, however, this agreement is not so close as it seems, and is partly accidental, for in Experiment 6 there is a difference of 0·6″ between the average circulation time to carotid and to left renal, although the difference in length of the path is only 4 cm.

In Experiment 6, with a rabbit of the same size as that of Experiment 5, the average circulation time from jugular to left renal artery is 3·45″, which is less than that to right renal artery in Experiment 5, although the distance is 1·5 cm. or 2 cm. more. The mean of a series of five readings of pulmonary circulation time is 2·85″.

The average of four readings of the circulation time from jugular to left renal vein is 13·45″, which gives a renal circulation time of 10″, as compared with 8″ in Experiment 5; and this although the blood reaches the renal artery 0·45″ sooner in Experiment 6. The delay takes place, therefore, in the kidney itself; and the circulation time is doubtless lengthened by the low temperature of the organ.

In a series of observations at the end of Experiment 8 (p. 21), the influence of temperature is very well brought out, and it is there shewn how greatly the circulation time in the kidney may be increased by cold and diminished by heat. And although it is possible, for the reason mentioned in the note to the readings with heated kidney in that experiment, that these readings are not absolutely trustworthy, and that they may give too short a circulation time with the high temperature and so exaggerate the difference between this and the circulation time with low temperature, the difference is far too great to be entirely explained away.

The Circulation Time in the Liver.

It is difficult, and I think impossible, to place the ingoing and outgoing vessels of this organ on insulated electrodes. The method adopted for measuring the circulation time was therefore indirect.

It is plain that if we know the circulation time from the entrance of the portal vein, say, to the carotid, and can calculate or measure that from the exit of the hepatic veins to the same point on the carotid, we have only to do a sum in subtraction in order to arrive at the time of the portal circulation in the liver. Direct measurement, however, of the circulation time from hepatic veins to carotid would be only less difficult than direct measurement of the portal hepatic circulation time itself; and it could not even be attempted without opening the chest.

But a calculation of the time from hepatic veins to carotid, can be made with fair accuracy if we observe the (uncorrected) pulmonary circulation time, say from the jugular to carotid. And this was done in Experiment 8. A still better plan is to choose a second route involving the lesser circulation and the inferior vena cava from the liver onwards to the heart, but not including the liver, and to compare the circulation time along this route with the circulation time along the route which includes the liver. This plan was adopted in Experiments 7 and 9.

EXPERIMENT 7. Rabbit, 2010 grams. Stomach filled with food. 1·4 gram chloral hydrate in rectum. Abdomen opened in linea alba from xiphoid cartilage nearly to pubis. Cannulae put into superior mesenteric vein and left renal vein. The two cannulae connected by a T tube with the injecting apparatus, so that salt solution could be injected into either at will. Right carotid artery exposed.

Time	Vascular tract	Circulation time	Maximum deflection	Notes
	Left renal vein to right carotid artery	3″	372	
	Superior mesenteric vein to right carotid	22·1		Liver and intestines very cold; began now to warm them.
	,,	16·2		Temperature rising.
	,,	9·3	82	
3.31	,,	8·2	100	
.33	,,	6·7		Rectum 38·75°
3.35	Left renal vein to right carotid	2·8 } 2·65		
	,,	2·6		
	,,	2·5		
3.43	Superior mesenteric vein to right carotid	8·2 } 9·6		Temperature falling
	,,	9·3		
.53	,,	10·8	85	Rectum 37·23°
4.2	,,	11·		Rectum 36·7°
.12	,,	9·9?		Some polarisation, and not easy to get good reading.
.16				Rectum 36°.

P.M. Distance from point of cannula in superior mesenteric vein to entrance of vena portae into liver, 2 cm.

From cannula in left renal vein to inferior cava, 5 mm.

From junction of left renal vein with inferior cava to point where latter is connected with liver, 2·3 cm. and from this point along inferior cava to diaphragm, about position where hepatic veins open into it, 3 cm.

Inferior cava from diaphragm to heart 2·5 cm.

EXPERIMENT 8. Rabbit, 2010 grams. At 11.30 a.m. 1 gram chloral hydrate in rectum; at 11.45, ·5 gram; at 12.30, ·5 gram. Abdomen opened by incision in linea alba for one third of its length, beginning at the xiphoid cartilage. A loop of small intestine drawn out, and cannula put into a small vein in mesentery. Another cannula in posterior facial branch of left jugular.

Time	Vascular tract	Circulation time	Galvanometer reading	Maximum deflection	Notes
1.35	Left post. facial vein to right carotid	2·3			Except when otherwise mentioned, 2 c.c. of 2·5 $^0/_0$ NaCl was used for injection in this exp. although 1 c.c. was enough to give a good deflection.
	,,	2·7 } 2·6″			
	,,	2·8	420—788	368	
1.40	Intestinal vein to right carotid	5·7	630—874	244	
	,,	7 } 6·4	638—882	244	This reading of circulation time is a little too long.
1.48	,,	6·55			
1.49	Left post. facial vein to right carotid	3·2	160—502	342	Circulation time a little too long. Rect. 37·5°. Changed zinc of cell, and image is now steadier.
	,,	2·55*	278—703	425	
	Intestinal vein to right carotid	3·4 (1st)			There is a preliminary slow movement of small extent followed by a much larger and sharper deflection. The time here given is to the beginning of the first movement.
	,,	6·5*	421–643–547–565–original	0 (1st) 222 (2nd) 18 (3rd)	No preliminary movement. Unsteadiness of image had been removed by moistening artery on electrodes just before this observation.
1.8	,,	6·55*	466—711	245	No preliminary movement. Rectum 38°.
	,,	4 (1st)	218—240	32 (1st)	1 c.c. 2·5 $^0/_0$ NaCl.
	,,	7·5 (2nd)	240—365	125 (2nd)	,, ,,
	,,	4·4 (1st)	$60\overset{\text{1st}}{\frown}70\overset{\text{2nd}}{\frown}241$– $140\overset{\text{3rd}}{\frown}147$–original	10 (1st) 171 (2nd) 7 (3rd)	1 c.c. 2·5 $^0/_0$ NaCl. The first slow movement is evidently not the beginning of the second movement, as it is sharply separated off from it.
2.15	,,	6·95 (2nd)	$90\overset{\text{1st}}{\frown}100\overset{\text{2nd}}{\frown}374$– $280\overset{\text{3rd}}{\frown}297$–200	10 (1st) 274 (2nd) 17 (3rd)	
2.48	,,	2·85 (1st)	$420\overset{\text{2nd}}{\frown}578$– $463\overset{\text{3rd}}{\frown}474$	158 (2nd) 11 (3rd)	

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* Observations which for any reason, such as superior steadiness of the image, appear specially good are marked with an asterisk.

Time	Vascular tract	Circulation time	Galvanometer reading	Maximum deflection	Notes
2.53	Intestinal vein to right carotid	24·1 (3rd)	$\overset{\text{3rd}}{\overgroup{453-464}}$	11 (3rd)	
.55	,,	7·05 (2nd)			
.57	,,	23·1 (3rd)		10 (3rd)	
2.59	Left post. facial vein to right carotid	2·7 (I)	328—388	60	The connecting tubes were still filled with ·6 °/₀ NaCl sol. which had been used in washing back some blood accidentally withdrawn by filling the injecting syringe with the cock open.
	,,	3·05 (I)	$\overset{\text{I}}{\overgroup{220-420}}$- $\underset{\text{II}}{\undergroup{238-244}}$-	200 (I) 6 (II)	II is a second small movement.
	,,	18·95 (II)	$\overset{\text{II}}{\overgroup{146-158}}$	12 (II)	
3.5	,,	2·85 (I)	$\overset{\text{I}}{\overgroup{372-594}}$	222 (I)	
3.7	,,	19·2 (II)			Rectum 37·05°.
3.12	Intestinal vein to right carotid	6·4 (2nd)	451—592	141 (2nd)	
3.14	,,	22·45 (3rd)			
3.18	,,	6·2 (2nd)			
3.19	,,	22·3 (3rd)		9 (3rd)	
3.21					Rectum 36·6°. Now enlarged wound in linea alba slightly and isolated left renal vessels.
4	Left post. facial vein to left renal vein	11·5			
	,,	14·1			
	,,	15·5 } Kidney cooling			Rectum 37·2°.
	,,	16·9			Kidney swung by threads to insulate it from surrounding tissues.
	,,	18·1			Kidney very cold.
					Now warmed kidney.
	,,	5·7 } Kidney warmed			A good deal of polarisation and not easy to be quite sure of these two readings.
	,,	5·3			
5.2	,,	13·95 } Kidney cooled			Kidney again cooled.

In Experiment 8 the intestines and liver were not at all cooled, as only a small loop of intestine was taken out of the wound in the linea alba, and after the cannula was inserted into the intestinal vein the whole was pushed back and the wound closed. The circulation in the left external jugular vein was very little disturbed.

P.M. The point of cannula in intestinal vein is 5 c.m. from the junction of that vein with the superior mesenteric vein; from this junction to the liver along the latter vein is a distance of 3 c.m.

The superior mesenteric vein is full of blood and salt solution, portal vein not much distended. Liver red and full of blood. Intestines warm and filled with blood. Left kidney normal; no congestion.

EXPERIMENT 9. Rabbit, 2020 grams. 1 gram chloral hydrate in rectum; then ·5 gram more; then, as still not completely narcotised, ·5 gram more. Incision in linea alba for rather more than half its length, beginning at xiphoid cartilage. Cannula put into left renal vein, and another in a moderately sized vein coming from the transverse colon. Call this the intestinal vein. Right carotid artery exposed. Animal kept very warm during whole operation; intestines all put back into abdominal cavity, and wound in linea alba closed by sutures and a clamp, only the two cannulae being

Time	Vascular tract	Circulation time	Maximum deflection	Notes
2·8	Left renal vein to right carotid	2″		0·2″ had to be added to all readings in this experiment for error of null point of chronometer. The corrected readings are given.
.10	,,	1·95		
2.20	Intestinal vein to right carotid	3·35		Some polarisation. Rectum 39·0°.
.23	,,	2·65	371	A better observation than the last. Breathing very rapid.
2.25	Left renal vein to right carotid	1·5	∞	Rectum 39·15°.
.27	,,	1·7		
2.33	Intestinal vein to right carotid	2·65	202	Rectum 39·5°. Fresh electrodes now put on.
2.54	,,	2·6		Rectum 38·8°.
3.8	Left renal vein to right carotid	2·1		Rectum 37·9°.
	,,	1·65	332	
	,,	1·65	334	
	Intestinal vein to right carotid	2·7	240	In all observations from intestinal vein to carotid there were two deflections, the first small, the second much larger. The time recorded is that to beginning of first deflection; but the galvanometer reading includes the second.
	,,	3·2	142	
	,,	2·3		
				One of the middle-sized arteries in the mesentery was now carefully isolated from its accompanying vein and put on the electrodes. Call it "the intestinal artery".
	Left renal vein to intestinal artery	2·3	201	The intestinal artery was one of the middle sized arteries of the mesentery.
	,,	3·6		1 c.c. 5 $^0/_0$ NaCl injected.
	,,	2·4		
	,,	2·4		

Time	Vascular tract	Circulation time	Maximum deflection	Notes
4.2	Left renal vein to rt. carotid artery	2·05		Rectum 34·5°.
.3	,,	2·3		
4.6	Intestinal vein to rt. carotid artery	4·3		Intestines now pretty cold.
	,,	3·3	228	Better observation than the last.
4.15	Left renal vein to omental vessels	11·2		A very vascular strip of omentum was now laid on the electrodes after separating as much of the connective tissue as possible from the vessels. Call these "omental vessels."
	,,	12·3		
4.25	,,	12·7	32	Greatly exposed, and cooled rapidly.
4.43	Left renal vein to rt. carotid artery	5·2	112	Rectum 32·35°.
.45	,,	5·2		
	Intestinal vein to rt. carotid artery	6·65		
	,,	6·8		
4.50	,,	7·5	19	Rectum 31·5°.
				Now began to heat again.
5.10	Intestinal vein to rt. carotid artery	4·9 (1st)		Rectum 32·3°.
	,,	4·9 (1st)		
	,,	9·15 (2nd)		
5.18	,,	4·6 (1st)		Rectum 33°.
	,,	3·2		,, 33·7°.
5.31	,,	4		,, 34·2°.
5.37	,,	4·5		,, 34·4°.
5.38	,,	4·5		

allowed to project. These were connected as in Experiment 8 with the injecting apparatus.

Two movements of the image were seen in all the observations in which salt solution was injected into the intestinal vein, and the numbers given under the heading "Circulation Time" in this experiment refer to the commencement of the first movement. The first movement was small compared with the second; it was also slower and had sometimes begun to slacken, and even nearly to stop, before the second took place.

Rabbit quite warm and in good condition at 6 o'clock, when it was killed.

P.M. The intestinal vein in which the cannula was inserted was traced to the superior mesenteric vein, the distance from the point of the cannula to that vein being 2·5—3 cm.

In order to carry out this second idea a cannula was put into a tributary of the portal vein (superior mesenteric vein, or one of the veins of the stomach, or one of the middle-sized intestinal veins of the mesentery). Another cannula was put into the left renal vein, and the two were connected by a second T tube with the injecting apparatus, so that salt solution could be injected at will into either cannula. The path from the mouth of the left renal vein round to the carotid differs but little from the path between the superior mesenteric vein and the carotid, except that the liver is placed upon the latter route. The two paths, so far as they consist of large vessels, may be measured and a correction applied, but it will be small; and the difference of the uncorrected circulation time by the two routes will be practically the time of the portal circulation in the liver.

In Experiment 7 the mean value of a set of three observations from renal vein to carotid is 2·65″; that of a set of four trustworthy readings from superior mesenteric to carotid, 9·6″. The (uncorrected) portal circulation time in the liver is therefore 6·95″. The greatest correction which, on any assumption as to the treatment of the difference in the length of that part of the two paths which is made up of large vessels, would have to be applied to this could not exceed 0·3″ or 0·35″; and this would have to be added to the 6·95″.

In the first series of readings from superior mesenteric to carotid the effect of temperature is exceedingly well marked, and in the same direction as in the kidney.

The superior mesenteric is such a large vein that closing it must necessarily disturb more or less the circulation in the intestines and in the liver itself. I therefore attempted to put the cannula into the splenic vein, and again into one of the large veins of the stomach; but after several trials it was found best to use one of the middle-sized intestinal veins, which are very easily got at through a small wound in the abdomen. This had besides the great advantage of avoiding the cooling and exposure of the internal organs. In Experiment 8, instead of the renal vein the posterior facial branch of the external jugular was used for the second cannula. The average pulmonary circulation time for the first set of three observations is 2·6″; for the first five observations, 2·7″.

The average of three readings of the time from the intestinal vein to the carotid is 6·4″. The (uncorrected) portal hepatic circulation time is therefore only 3·8″ as compared with 6·95″ in Experiment 7 for a rabbit of the same size. The difference may be partly due to the smaller disturbance of the abdominal contents, and the avoidance of cooling, which the operation used in this experiment made possible. Perhaps too in Experiment 7 the closure of the superior mesenteric vein shewed the portal blood stream.

The further seven observations in Experiment 8 marked (2nd) give an average of 6·75″ for the circulation time from the intestinal vein to carotid, and the three pulmonary readings marked (I) an average of

2·85″, which again gives for the (uncorrected) circulation time of the liver the value 3·9″.

In the observations marked (1st) or (2nd) two deflections were caused by injection of the salt solution into the intestinal vein, a small one (1st) followed by a deflection of much greater size (2nd). The second was so sharply marked off from the first that there was no difficulty in fixing the moment when it started. There can be no doubt, from the remarkable agreement of the figures, that this second movement in the observations where two movements could be distinguished, represented the single movement where one only was present, as at the beginning of the experiment; and the circulation time reckoned up to its commencement is evidently that of the path by which the great bulk of the blood must pass from the portal vein to the carotid, i.e. through the capillaries of the liver. The first small deflection suggests that a short cut for a portion of the blood may normally exist, or under certain conditions become abnormally developed, between the portal area and the inferior cava, by which the comparatively tedious circulation of the liver is avoided. In man we know that, in addition to the anastomoses between the rootlets of the portal system and the systemic veins in the hæmorrhoidal plexus and at other points, a direct communication exists between certain superficial branches of the portal in the liver and the phrenic veins.

If there was such an anastomosis here, it must have been far from free, since the first movement was so small. It is possible that repeated injection of the salt solution into the small intestinal vein might open up communications only potentially present at the beginning of the Experiment; for at first the only deflection seen was that corresponding to the (2nd) of the later observations.

The average circulation time of four readings up to the 1st movement is 3·95″. Deducting from this the average pulmonary circulation time taken about the same stage of the experiment, viz. 2·85″, we get 1·1″ as the (uncorrected) circulation time for this supposed short cut.

In the pulmonary observations no such breaking up of the deflection was ever seen, from which the deduction seems obvious that it could not have been accidental in the case of the portal circulation, but must have had its ground in some circumstance peculiar to the latter. This is confirmed by the fact that in Experiment 9 in the portal observations the deflection was also broken up into two.

In some of the pulmonary observations of Experiment 8 a phenomenon which seems superficially allied to the above is noted, that is to say, a small second deflection (II) following, after a long and fairly constant interval, the first large deflection (I). But the second deflection here represents, in all probability, the arrival of salt which has completed the systemic circulation, and passes a second time through the lungs. Its small amount shews how rapidly the alteration produced by injection of the salt fades out in the systemic capillaries.

Of course a second deflection several times larger than the first could not possibly be an echo of the first, and therefore the second deflection of the portal observations cannot be explained in this way. But such an echo, in the shape of a third feeble deflection [marked (3rd) in the record] was also detected here. The average of four readings gives 23″ as the time from the beginning of injection to the beginning of this third movement. If we deduct from this 6·75″, the average circulation time for the second movement, we get 16·25″.

Now the average time for the second movement (II) of the pulmonary readings is 19·05″. Deducting from this the average for the first movement of the pulmonary observations 2·85″, we get 16·20″. The agreement is exceedingly striking; and the meaning of it can only be this. The blood which reaches the electrodes on the carotid from the posterior facial vein in 2·85″ from the beginning of injection of the salt solution, gets back by some route or other to the same point of the carotid in 16·2″. The blood which reaches the carotid in 6·75″ from the intestinal vein passes now by the same route and in practically the same time as the blood which reached the artery from the posterior facial. If then, 2·85″ is a true measure of the time required in the first circuit, as there is no doubt it is, 6·75″ must truly represent the time taken by the bulk of the blood to pass from the intestinal vein to the carotid.

Resuming the consideration of our record of results, let us now turn to Experiment 9.

Here the circulation time from the left renal vein to the carotid was compared with that from an intestinal vein to the carotid. Two deflections were again seen in the portal observations; and this time note was generally taken only of the beginning of the first, which was much the smaller of the two.

The first two readings from renal to carotid are practically the same, (say) 2″. The first set of two from intestinal vein to carotid give an average of 3″, which leaves 1″ for the (uncorrected) circulation time of the supposed short circuit. This agrees very well with Experiment 8.

The next two sets give respectively 1·6″ for renal to carotid, and 2·65″ from intestinal vein to carotid, a difference of 1·05″. The next two sets give respectively 1·8″ from renal to carotid, and 2·75″ from intestinal vein to carotid, a difference of 0·95″; again a very close agreement.

Circulation Time from left renal vein to one of the middle-sized arteries of the mesentery.

The average of four readings is 2·65″, while the circulation time from renal vein to carotid, at the same stage of the Experiment, is 2·15″.

The remainder of the Experiment shews again the influence of fall of temperature and exposure to the air on the circulation time in most of the internal organs.

E.g. the circulation time from renal vein to some of the omental vessels, after great exposure, averaged 12·05″; while that of the supposed short circuit from intestinal vein to carotid rose to 4·9″. On heating, it again fell somewhat. But now the circulation time from renal vein to carotid was also markedly lengthened.

Injection of the salt solution into an artery.

When a vein is used for injection, the salt must of course pass through the lungs before reaching the capillaries of any other organ. Now it is not always easy, in making observations where the salt has to pass through two sets of capillaries before reaching the electrodes, to obtain a deflection sufficiently prompt and large, to make the readings trustworthy. And, although in general this difficulty can be overcome by suitably choosing the quantity or strength of the salt solution, I thought it well to try injection into an artery—one of the main arteries of an organ supplied by several; or a branch, where the arterial supply is single; or, what is equally good in a small animal, a distant part of the arterial system.

I quote Experiment 10 (p. 28) as an illustration of this method. In measurements of the circulation time through the organs of large animals it is almost indispensable to inject into an artery; and no error will be caused by increase of pressure due to the injection itself. But in small animals only a very small quantity of solution must be thrown into an artery opening directly into the main vessel of the organ; otherwise the pressure is at once raised and the solution forced through the capillaries at a much quicker rate than that of the blood.

I have in view, and have partly carried out, a systematic series of measurements, under various conditions, of the circulation time in all the more important organs to which the electrical method can be applied, with the object of deducing probable values for the organs of the human body. This task can only be accomplished when a sufficient number of observations have been made to disclose the relations between the circulation time of the organs and the body-weight or pulse rate of animals like the dog, or possibly the monkey. The results quoted in this preliminary paper are given rather as illustrations of the method than with the intention of discussing them fully, or drawing from them in detail the conclusions they are capable of yielding. But it may be well to illustrate by one or two examples the kind of information which such experiments, supplemented by other data, might give.

Experiment 10. Rabbit, 2500 grams. 1·2 grams chloral hydrate in rectum. Cannula in peripheral end of right common carotid.

Time	Vascular tract	Circulation time	Maximum deflection	Notes
2.50	Right carotid to left carotid	6·9″		1 c.c. 2·5 $^0/_0$ NaCl injected. Rh. 250, except where otherwise noted.
3.22	,,	8·2	54	
.23	,,	7·2*	38	
.25	,,	7	45	Rh. (all plugs out).
.33	,,	7	129	1·5 c.c. 5 $^0/_0$ NaCl injected.
3.40	Right carotid to left jugular	2	500	1 c.c. 5 $^0/_0$ NaCl.
.42		2·25		1 c.c. 5 $^0/_0$ NaCl. Box 1500.
3.52	Right carotid to left carotid	7·9	49	Box 1200. Rectum 34·8°.
3.57	Right carotid to left jugular	1·9		Box 1500.
.59	,,	1·7	63	Cannula now put into left jugular vein.
4.22	Left jugular to left carotid	4·4		
.24	,,	4·6		Rectum 33·1°.
.31	,,	4·9		

When the average quantity of blood contained in an organ is known, the quantity passing through it in a given period can be calculated from the average circulation time.

For example, if we take the average quantity of blood in the kidneys of a rabbit at 1·6 p.c. of the whole blood (Ranke), and the mean renal circulation time at 6·5″, the whole blood would pass through the kidneys in about 7 minutes. In a two kilo rabbit this would correspond to about 22 kilos per 24 hours. We have the means of checking this result by another consideration.

The excretion of urea by a rabbit of this weight may be taken as 3·5 grm. per day. (Voit gives 1·8 grm. for a 1 kilo rabbit.) 22 kilos blood containing ·025 p.c. urea would carry to the kidney urea to the amount of 5·5 grm. If 3·5 grm. were separated there, the blood of the renal vein would still contain nearly ·01 p.c. of urea. So that the estimated blood flow would be sufficient without being excessive.

Knowing the mean circulation time through the lungs and the average quantity of blood in them, we can calculate the amount of blood passing through them per hour. In the rabbit Ranke found 22 p.c. of the blood in the heart, lungs and great vessels, which could not leave much less than $\frac{1}{6}$ of the blood for the lungs alone.

Suppose then that $\frac{1}{5}$ to $\frac{1}{6}$ of the total blood of a 2 kilo rabbit is contained in its lungs. This passes through in say 2·1″, which corresponds to 34 kilos per hour.

Heger[1] states that the lungs of a rabbit, when the vessels are ligatured during life, and without opening the pleural cavity, contain only $\frac{1}{12}$ to $\frac{1}{13}$ of the total blood during inspiration and $\frac{1}{15}$ to $\frac{1}{18}$ during expiration. Without questioning the validity of his conclusion as to the relative capacity of the pulmonary vessels in the two respiratory phases, which indeed my own observations on the circulation time corroborate, I think it necessary to say that his absolute quantities seem much too small. If on the average during the whole of respiration the lungs contain only say $\frac{1}{14}$ of the total blood, then with a pulmonary circulation time of 2·1″ the whole blood will only pass twice in a minute through the lungs, and the average total circulation time will be about 30″, which is far too long.

In fact the average quantity of blood in the lesser and systemic circulations must be directly proportional to their mean circulation times. If the ratio between the amount of blood in the lungs and the mean systemic vessels be 1 : 13, and the mean systemic circulation time be taken at 8″ (for the 2 kilo rabbit of course), the pulmonary circulation time can only be $\frac{8}{13}$″. Now I do not think I have ever found the latter so small as twice this figure; and it is easier to measure the (uncorrected) pulmonary circulation time with accuracy than that of almost any other vascular tract.

The capacity of the pulmonary circulation in an average man, so far as is known, agrees with the larger estimate for the rabbit better than with Heger's results. It has been estimated from the extent of the capillary surface at 1 litre; and the lungs may therefore contain something like a fifth of the total blood. Or if we take the weight of the two lungs with all their blood at 1400 grm., and assume that the blood forms 63 p.c. of the whole weight, as Ranke found for the heart, lungs

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[1] *Rech. sur la circulation du sang dans les poumons*, 1880; Heger and Spehl, *Arch. d. Biologie*, II. p. 153, &c.

and great vessels of the rabbit, we get approximately 900 grm. blood in the pulmonary circulation, or something between $\frac{1}{5}$ and $\frac{1}{6}$ of the total blood.

Taking the mean total circulation time of a 2 kilo rabbit at 10·5″, we get 342 as the number of times the whole blood passes through the lungs in an hour. A 2 kilo rabbit contains $\frac{1}{9}$ kilo blood (Ranke). Therefore 38 kilos of blood pass through the lungs per hour. Now a 2 kilo rabbit consumes 1350 c.c. oxygen per hour (Finkler and Ortmann); and this would be supplied if the blood in passing through the lungs took up 3·6 volumes of oxygen p.c. If we adopt the common statement that the blood takes up 8—9 volumes p.c. of oxygen in the lungs we must make the mean total circulation time in a rabbit of 2 kilos weight 23″ to 26″, which is out of the question.

If the same ratio between the circulation time by the shortest path (jugular to jugular) and the mean total circulation time which holds for rabbits and small dogs be assumed to hold for large animals, the mean total circulation time in an average man (on Vierordt and Hering's assumption that the circulation from jugular to jugular is accomplished in 27 heart beats) will be, in round numbers, 50″. Taking the quantity of blood at 5 litres and the pulse rate at 72 per min., we get 83 c.c. as the output of the ventricle, and 360 litres as the amount of blood passing through the lungs per hour. Without attaching any great weight to this calculation, the data of which are obviously open to error, it is perhaps worth while to point out that the result agrees rather with the moderate estimates arrived at by several recent investigators than with the undoubtedly excessive numbers of Vierordt.

The circulation time through a loop of intestine, when cooling is prevented, is probably not more than that of the lungs, and not more than $\frac{1}{3}$ of the circulation time through the liver. Since the blood from the intestines and stomach forms by far the greater part of that passing through the liver, it follows that at any given time the liver must contain, speaking roughly, three times as much blood as the gastro-intestinal tract. Now Ranke found in the dead rabbit about four times as much blood in the liver as in the intestines; and the agreement is sufficiently close to illustrate the inverse relation which must exist between the circulation time and the capacity of any part of a vascular tract in which there is a steady flow.

The above paper is based on experiments carried out by the author as George Henry Lewes Student. The expenses were partly met by a grant from the Royal Society. The paper was sent in as part of a Thesis for the Goodsir Memorial Prize in the University of Edinburgh, *April* 30, 1892.

RESEARCHES ON THE CIRCULATION TIME IN ORGANS AND ON THE INFLUENCES WHICH AFFECT IT.

By G. N. STEWART, M.A., D.Sc., M.D.

Plate I.

(*From the Physiological Laboratories at Cambridge and Strasburg.*)

II. The Time of the Lesser Circulation.

PERHAPS there is no vascular tract which can be better investigated by the electrical method of measuring the circulation time than the lesser circulation, in the case of such problems as the method is capable of solving. For it is not necessary to open the chest, and of course this is a great advantage in dealing with the lungs. Further, the electrodes are placed on an artery, so that it is easy to avoid compression of the vessel and interference with the flow. Again, the circulation time through all parts of the lungs seems to be practically the same, so that the deflection is exceedingly prompt.

A cannula is put into the external jugular low down in the neck, the electrodes are placed on the carotid of the same, or better of the opposite side; and the lesser circulation, with very little else, is included between the cannula and the electrodes.

In most of the experiments of this paper the animal was under curara, and the respiration was artificial. The circulation time had been previously determined in many rabbits under chloral and other anaesthetics. The preliminary operation was done under an anaesthetic, before the curara was given; in a few experiments urethan, which is said to possess all the good qualities of chloral without its effect on the blood pressure, was used throughout.

SECTION I.

The first problem taken up was an old one, but still a problem which has not received a definite and unquestioned solution, viz.

The influence of the Expansion and Collapse of the Lungs on the pulmonary circulation.

This question has generally been treated in connection with the respiratory waves in the systemic blood-pressure curve, the cause of which has long been a classical subject of discussion.

I intend to consider here only the manner in which the pulmonary circulation time varies with the position of the lungs, and the deductions which may be made from this as to corresponding variations in their vascular resistance, but not the general question of the respiratory waves.

Haller[1] injected coloured liquid into the vena cava of an animal just killed, and asserted that it passed more rapidly through the inflated than through the collapsed lungs.

Poiseuille[2] found, on the contrary, that more blood flows through the collapsed than through the inflated lungs in a given time. He concluded that the capacity of the pulmonary capillaries was less in inflation than in collapse. Inflation was always produced by blowing air into the lungs.

Poiseuille's results were confirmed by Gréhant[3] and others.

Quincke and Pfeiffer[4] shewed that when the excised lungs are expanded by causing a negative pressure, the opposite of Poiseuille's effect is got, that is less blood flows through the collapsed lung in a given time than through the expanded lung.

They point out, however, that in their experiments the pressure under which the defibrinated blood flows through the lungs is constant, while in the living animal this would not be the case, since the heart and great vessels are also subject to the changes of pressure in the thorax.

Funke and Latschenberger[5] repeated and extended the experiments of Quincke and Pfeiffer, and found an increase in the outflow from the lungs during distension, but decrease if the lungs were kept distended; decrease of the outflow while the lungs were collapsing, but increase if the lungs were allowed to remain collapsed. Their explanation is that the capacity of the pulmonary vessels is decreased during expansion of the lungs, and therefore more blood is squeezed out; but, the resistance being at the same time increased, as soon as this temporary increase is over, the outflow is permanently diminished, if the lungs are allowed to remain expanded.

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[1] *Halleri Elementa physiologiae.* Lausanne, 1761, T. III. p. 246.

[2] *Compt. Rend.* XLI. p. 1072, 1852.

[3] *Compt. Rend.* 1871, p. 274.

[4] *Arch. f. (Anat. u.) Physiol.* 1871, S. 90.

[5] *Pflüger's Archiv*, Bd. XV. p. 405 and XVII. p. 547.

Zuntz[1] criticised Funke and Latschenberger's experiments and conclusions adversely, while Bowditch and Garland[2] supported them.

Kuhn[3] from an examination of the alterations of systemic blood pressure which take place in the different phases of artificial respiration concluded that they are due only to mechanical changes in the lungs, viz. increase of resistance in the pulmonary capillaries in inflation and decrease of resistance in collapse, for they persist after section of the vago-sympathetics.

When, with thorax and abdomen both opened, the lungs are kept inflated, the blood pressure falls more and more, the greater the distension is; if the lungs are now kept collapsed, the blood pressure rises in proportion to the amount of the previous distension.

De Jager[4] distinguishes the effects of changes of capacity of the pulmonary vessels from the effects of changes of resistance in them. Partly from experiment and partly by argument he comes to the conclusion, that during natural inspiration the capacity becomes larger, the resistance less; while during natural expiration the capacity becomes smaller, the resistance greater. During artificial respiration (by means of a pair of bellows) the capacity in inspiration becomes smaller, and the resistance greater, while in expiration the capacity becomes larger, and the resistance less. He supposes that a complete explanation of the respiratory waves of the blood pressure can be founded on these propositions.

Heger and Spehl[5] have shewn that when the great vessels of the lungs of rabbits are ligatured close to the heart at the height of inspiration, the lungs contain more blood than when the ligatures are put on in collapse.

Talma[6] concludes that in expiration the resistance in the pulmonary vessels increases, and in inspiration diminishes; but he ascribes also a large share in the production of the respiratory waves to the influence upon the systole and diastole of the heart of the changes of intrathoracic pressure produced by the respiratory movements.

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[1] *Pflüger's Archiv*, Bd. XVII.

[2] This *Journal*, Vol. II. p. 91.

[3] *Over de respiratieschommelingen der slagaderlijke bloedsdrukking.* Amsterdam, 1875.

[4] *Pflüger's Archiv*, Bd. XX., XXVII., XXXIII. and XXXVI.

[5] *Arch. de Biologie*, II., 1881, p. 153.

[6] *Pflüger's Archiv*, Bd. XXIX.

Knoll[1] found the lateral pressure in the pulmonary artery of the rabbit increased by an increase of the intrapulmonary pressure, and diminished by a decrease of that pressure, whether the changes of intrapulmonary pressure took place in natural or in artificial respiration, during collapse or during inflation of the lungs.

Fuld[2] (under Ewald's guidance), who gives an excellent synopsis of previous work, of which I have to some extent availed myself, has recently come to the conclusion that the respiratory waves depend upon the variations in the inflow of blood to the thorax during respiration, and also to some extent on the variations of the capacity of the pulmonary vessels. The capacity of the pulmonary vessels depends chiefly on the intrapulmonary pressure and not on the volume of the lungs. The respiratory waves with opened thorax depend entirely on changes of capacity of the vessels of the lungs.

I come now to my own experiments made by measuring the pulmonary circulation time.

The circulation time from jugular to carotid (low in the neck) was determined first with undisturbed respiration—sometimes natural, but in most cases artificial. Then respiration was arrested, as nearly as possible at the height of inspiration or expiration, by clipping the side tube of the cannula and the tube leading to the respiration apparatus. An observation of the circulation time was now taken, either at once or after a measured interval.

In the quoted Experiments in the column headed "Respiration", "Insp.", "Exp." mean respectively that the observation was taken with the lungs distended or collapsed. Where "Insp.", "Exp." are not followed by a number denoting time, the interval between the stoppage of respiration and the injection of the salt solution was as short as possible, generally not more than 4 seconds. "Insp. for 20″," means that the injection was not begun till the respiration had been stopped for 20 seconds in the inspiratory phase. "Exp. for 20″" has a corresponding meaning. In no case was the respiration begun again till the observation of the circulation time had been completed. When the column headed "Respiration" is blank opposite an observation, it means that respiration was going on undisturbed. This is very often indicated in words. Sometimes the rate of respiration is also given. In the artificial respiration, unless a note is made to the contrary, only

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[1] *Sitzungsber. d. Wien. Akad.* XCVII. Abth. 3, 1888.

[2] *Inaug. Diss.* Strasburg, 1889.

inflation was used, the lungs being allowed to collapse through their own elasticity and that of the chest.

Most of the experiments were made on rabbits; one or two on dogs.

Experiments 1, 2, and 3 give fairly typical specimens of the majority of the observations made with artificial respiration; and by far the most striking result brought out in these Experiments is the great lengthening of the (uncorrected) pulmonary circulation time in expiration as compared with that in inspiration, when the observation is taken immediately after the stoppage.

Omitting the first three readings of Experiment 1 with uninterrupted respiration, as certainly too long owing to the blood not being sufficiently oxygenated (and we shall have repeated opportunities of seeing that the pulmonary circulation time is greatly lengthened by such a condition—see, e.g., the series of readings from 3.55 to 4.10 o'clock in Exp. 2 and Exp. 5), we get as the average of the next set of four observations, taken from 4.17 to 4.23 o'clock, 4·45″. The average circulation time in inspiratory standstill for the next two observations is 4·25″, and for the next four readings, 3·9″, which latter value is something, but not a great deal, less than the last average with uninterrupted respiration, and is exactly the same as the average of the second set of three readings with respiration going on, taken from 4.5 to 5.2 o'clock.

But the circulation time both in inspiratory standstill and with uninterrupted respiration has evidently decreased since the beginning of the experiment; and therefore it is better to compare the average of this set of three readings with the average of the three immediately preceding inspiratory observations, viz. 3″.

Experiment 1. Rabbit, 2040 grams. 40 mg. curara subcutaneously. Artificial respiration. Cannula in right jugular. Left carotid exposed.

Time	Respiration	Circulation time from right jugular to left carotid	Maximum deflection	Notes
3.50	slow (say, 12 per min.)	5·8″		1·5 c.c. of 2·5 $^{0}/_{0}$ NaCl sol. injected.
		6·1		Blood very venous in carotid; respiration slow
		6		
4.17	Undisturbed at 16·6 per min.	4·15		Blood in carotid now better oxygenated.
4.20		4·6	120	
.21		4·4	103	
.23		4·6	77	

Time	Respiration	Circulation time from right jugular to left carotid	Maximum deflection	Notes
4.25	Insp.	4·15	126	
.28	,,	4·4	117	Blood now well arterialised.
.30	Exp.	5·65	108	
.32	,,	6·6	118	
.35	Insp.	3·65	96	Deflection is quicker than in Exp. and seems to turn more sharply at the maximum and come back more quickly.
.37	Insp.	3·4	115	
.39	Exp.	6·8		
.42	,,	6·35	135	Check slipped, and 2·5 c.c. of the NaCl solution went in.
.44	Insp.	2·85	80	
.46	,,	3·2	68	This reading of circulation time is a little too long.
.49	,,	3*	118	
4.52	Undisturbed at 16·6 per min.	3·7		Reading of circulation time a little too short.
5		4·15	69	
5.2		3·85	70	
.4	Insp.	2·3	70	Rectum 37·1°. Box 900.
.12	,,	2·85	97	Box 1000.
.14	,,	2·5	83	
.17	Exp.	7·3	139	Reading of circulation time too long. Movement of image is distinctly slower than in Insp.
.20	,,	6·3*	112	
.23	Insp.	2·6*	79	The interval in all the above observations between the stoppage of respiration and the beginning of the injection would not be more than 4″.
5.24	Undisturbed at 15·8 per min.	3·65*	78	
.26		4	76	Circulation time too long.
.25	Insp. for 20″	7·85		This circulation time is probably somewhat too long. The deflection is slower and much smaller than when observation taken immediately after stopping of respiration.
.36	Insp.	2·6*	72	Deflection as quick as usual.
.40	Insp. for 15″	4·25	89	Fairly quick deflection.
.50				Rectum 37·2°. Injected 10 mg. curara into blood, as convulsions come on when respiration interrupted for more than 20″.
6.2	Insp.	2·8		
	Insp. for 20″	7·6		Small and slow deflection.
6.6	Exp.	4·85	61	Blood in carotid seems more venous than before; respiration apparatus working badly now, although up to this it had worked well and regularly.
.8	Exp.	4·05	64	
.11	,,	3·8		
.29	,,	3·3		
.31	Exp. for 20″	3·9		
.33	Insp.	2·85		
	Insp. for 20″	5		

* Specially good readings are marked with an asterisk.

The difference is now 0·9″; and if we go on a little farther in the experiment and compare the average of the four inspiratory readings taken from 5.4 to 5.23 o'clock, which is only 2·55″, with the average of the succeeding set of two readings with uninterrupted respiration, which is 3·8″, or with the average of the preceding set of three observations, which is 3·9″, we get an excess of circulation time during uninterrupted respiration over that during inspiratory standstill of 1·35″.

But the difference between the circulation time in inspiratory and in expiratory standstill is much more striking.

The average of the first four readings in Exp. is 6·35″, an excess of 1·9″ over the average of the first set with uninterrupted respiration and of 2·45″ over the first set of four inspiratory readings. The circulation time in expiratory standstill does not practically change at all as the experiment goes on, at least until very late in the experiment (set of four readings from 6.6 to 6.29 o'clock), while we have seen that the circulation time in inspiratory standstill and with respiration going on becomes less; and the difference between the circulation time in Exp. and Insp. when the latter has been reduced to 2·55″ is 3·8″, the circulation time in Exp. being exactly two and a half times the circulation time in Insp.

In Experiments 2 and 3 the difference between the circulation time in Exp. and Insp. is also very striking and in the same direction; and, so far as this point is concerned, we can omit a detailed examination of these experiments.

There is one other point brought out by Experiment 1 which is worthy of being noticed. In all the observations hitherto discussed the reading was made on the heel of the stoppage of respiration. When the respiration is interrupted for a comparatively long interval (15″ to 20″ for example), the inspiratory circulation time increases greatly, whereas the circulation time in expiratory standstill may not be notably affected.

The maximum deflection, as will be seen in the column under that heading, may be quite as large in expiratory as in inspiratory standstill. A point of more value is that the maximum is more slowly attained in Exp. This slow movement is very constantly associated with a long pulmonary circulation time. Its significance will be discussed in a later paper.

Experiment 2. Rabbit. 30 mg. curara subcutaneously. Cannula in left jugular near junction with subclavian. Right carotid exposed. Artificial respiration.

Time	Respiration	Circulation time from left jugular to right carotid	Maximum deflection	Notes
3.46		3·25″	162	2 c.c. of 2·5 $^0/_0$ NaCl injected in whole of this experiment.
.48		2·7	108	
.49		2·8	140	
.51		3	129	
.55	23·3 per min.	2·6	109	Blood better oxygenated than in preceding observations.
.56		2·15	104	
4		5·2	142	Blood allowed to get gradually less oxygenated.
4.2		6·9	160	
.4		7·5	97	
.7		3·95	93	Blood again normally oxygenated.
.10		3	99	
.12	Insp.	3·15	137	
.19	Exp.	6·05	147	
.21	Insp.	2·7		
.23	Exp.	7·35	140	The movement is very slow compared with that in Insp.
.25	Insp.	3	128	
.27	Exp.	7	146	
.29	Insp.	2·4	115	
.31	Exp.	8·55	147	This circulation time is a little too long.
.35	Insp.	3·15	150	
.38	Exp.	8·2*	129	
.47	Insp.	2·05	107	
.56	,,	2·85	114	
	Exp.	8·1	167	
				Injected 20 mg. curara into blood, as still respiratory movements when artificial respiration stopped in Exp. although not when stopped in Insp.
5.12	Insp.	2·65	136	No respiratory movements now in expiratory standstill.
.15	Exp.	5·5	112	
.19	,,	4·85	147	Respiration 18·7 per min.
.24	Insp.	2·4	85	
.27	Exp.	4·05	125	
.32	Insp.	2·6	92	
.36	Exp.	4·85	156	Injected 20 mg. curara into blood.
.53	,,	4·55	43	Deflection small because tubes full of ·6 $^0/_0$ NaCl used in washing out curara.
.57	Insp.	6·2	114	Seen that now circulation had almost stopped in carotid.

at 5.54 froth was noticed coming up in trachea and animal dying.

Experiment 3. Bitch, 3700 grams. 3 grams. urethan in rectum. Cannula in left external jugular. Right carotid exposed.

Time	Respiration	Circulation time from left ext. jug. to right carotid	Notes
4.45			Inj. 50 mg. morphia subcutaneously.
.52			Inj. 35 mg. ,, ,,
.56	Natural	5·65″	Vagina 37·95°.
.59		5.85	
			Put cephalic end of cut right sympathetic on stimulating electrodes.
5.5†		6·15	
.7		6·7	
.9		6·7*	
.10†		6·1	
			30 mg. curara injected into blood. Artificial respiration begun.
6.20	Undisturbed	4·65	
.22	Artificial	4·65	
	Insp.	2·95	
	Undisturbed resp.	5·35	
.33	Exp.	5·2	
.35	Insp.	2·55*	The deflection is more prompt in beginning, and larger than in Exp.
.39	Exp.	4·85*	
			Respiration 32·6 per min. Vagina 36·4°.
.42		5·45*	
.50	Insp.	3·45	
.53	Exp.	5·35	
7.1	,,	4·95	
.8	Insp.	4·55	
.10	Undisturbed resp.	5·45	Vagina 36·5°.
			Opened chest on both sides.
7.17	Insp.	2·65	
.20	,,	1·9*	
.23	Exp.	5·45	
.24	Undisturbed resp.	5·3	
.28	Insp.	2·45	
.31	Exp.	5·2	
.34	Undisturbed resp.	4·7	
.36	Insp.	2·95	Heart 195·6 per min.
.41	Undisturbed resp.	4·5	
			Cut both vagi (vago-sympathetic on left side; right symp. previously cut).
.50	Undisturbed resp.	4·45	
.51	Insp.	3·45	
.53	,,	2·55*	
.55	Exp.	4·25	This circulation time is a little too long.
8.1	Undisturbed resp.	4·45	
.3	Insp.	2·1	
.5	Exp.	4·1	
.6	Insp.	1·8	
.13	Exp.	3·95	
			In whole of above experiment, stoppage of respiration either in Insp. or in Exp. is followed by a movement in direction of increased electrical resistance of carotid.

† Stimulation (7), i.e. stimulation of the cephalic end of right sympathetic with 7 c.m. distance between coils of inductorium, (1 Daniell in primary).

P.M. Distance of electrodes on right carotid from left ventricle, 7·2 c.m. Distance of point of cannula in left external jugular vein from its junction with subclavian, 1·5 c.m.

From this junction to right auricle, 5·5 c.m.

In Experiment 3, one of those made with dogs, although the circulation time is markedly less in Insp. than in Exp., the average circulation time in Insp. in four readings being 3·35″, and in Exp. in four readings, 5·1″, there is no difference between the time in undisturbed respiration (mean of four readings 5·05″) and in Exp.

That the difference between the circulation time in Insp. and Exp. does not depend on the pleural cavity being unopened, is well shewn in the latter half of Experiment 3.

The average inspiratory circulation time with opened chest is 2·5″ for eight readings; the average expiratory circulation time for five readings is 4·6″. These numbers are both less than with unopened chest; and the circulation time with undisturbed respiration is also less, viz. 4·7″ for five readings.

Section of both vagi in this Experiment produces no change whatever in the circulation time, with artificial respiration going on and thorax opened. The difference between the circulation time in Insp. and Exp. persists after section of the nerves, which shews that this difference does not depend on impulses passing along the vagi.

Experiment 4 is quoted as an instance where only a slight difference between the circulation time in Insp. and Exp. can be detected, and this only by taking the mean of all the observations. Thus from six readings of circulation time in Insp. we get the mean value, 3·05″; from four Expiratory readings, 3·35″; and from nine readings with undisturbed respiration, 3″.

Exp. 4. Rabbit. 30 m.g. curara subcutaneously. Not completely paralysed. Artificial respiration. Cannula in left jugular. Right carotid exposed.

The circulation time recorded is that from left jugular to right carotid.

Time	Respiration	Circulation time	Maximum deflection	Notes
4.14	Undisturbed at 20 per min.	3·55″		·75 c.c. 2·5 $^0/_0$ NaCl.
		2·4		2 c.c. 2·5 $^0/_0$ NaCl in this observation and all the rest of the experiment.
		3·3		
		2·4	115	
		2·3	124	
		3·5	131	
4.50		3·2		Rectum 38·4°.

Time	Respiration	Circulation time	Maximum deflection	Notes
5.12	Insp.	3·6		
5.14	Exp.	4·1		Rectum 37·4°.
	Insp.	3		
				Respiration now made 24 per min.
	Insp.	3·1		
5.52	Exp.	3·35		
	Insp.	2·7		
5.54	Exp.	3·4		Rectum 36·5°.
	Insp.	3·3		
	Exp.	2·65		
	Insp.	2·6		
	Insp. for 15″	3·35		
	Exp. for 15″	4·9		
	Insp. for 35″	5·5		
				Injected 10 mg. curara into blood. After this animal was perfectly motionless.
6.18	Undisturbed at 24 per min.	3·2		Rectum 36·6°.
6.20		3·2		
	Insp. for 20″	1·9		
6.27	Exp. ,,	3·5		Rectum 36·7°.
	Insp. ,,	2·15		
	Exp. ,,	3·7		
	Insp. ,,	3·6		
6.36	Exp. ,,	4·3		
	Insp. ,,	4·5		
	Exp. for 1′	5·6		
	Insp. ,,	4·95	140	
6.45	Undisturbed at 24 per min.	3·2	41	
		3·4	32	
		2·4	39	
		2·4	51	
6.55				Rectum 36·2°.

Animal still in good condition when experiment had to be stopped.

P.M. Some small haemorrhages in lungs.

EXPERIMENT 5. Rabbit, 2000 grams. 50 mg. curara subcutaneously. Artificial respiration. Cannula in left jugular. Right carotid exposed.

Time	Respiration	Circulation time from left jug. to right carotid	Maximum deflection	Notes
1.49	Only inflation used; resp. undisturbed at 27·9 per min.	2·1″	94	Box 900.
1.53		2·2	94	
1.56		2·2	92	
2·10		4·15		
2.12		3·8	103	Rectum 37·7°.
2.15		6	97	When the circulation time began to lengthen the deflection began to be less prompt and slower and to resemble more the deflection seen when the vascular tract includes two capillary regions.

The blood is now seen to be very venous in the carotid; and circulation in it stopped very soon after last observation.

Put nearly empty carotid again on electrodes; balanced now with Box 1240.

P.M. Distance of point of cannula in jugular from junction of jugular and subclavian 4 c.m.

From this junction to heart, less than 2 c.m.

Here then apparently standstill in distension produces no change in the pulmonary circulation time, while standstill in collapse increases that time to a small extent.

When we look at the observations with longer stoppage of respiration the difference is found to increase. Thus the mean of six inspiratory readings, where the interval between stoppage and beginning of injection varied from 15 seconds to 1 minute, is 3·4″; the mean of five expiratory readings is 4·5″; the difference is 1·1″.

In Experiment 6 the first six readings in Insp. average 2·75″, and the first five in Exp. precisely the same. Before the next set of three inspiratory and two expiratory readings the respiration was made exceedingly slow (5·4 per minute), in order to test the effect on the circulation time. The depth of the respirations was at the same time

EXPERIMENT 6. Rabbit, 1560 grams. 20 mg. curara subcutaneously. Artificial respiration. Cannula in left jugular. Right carotid exposed.

Time	Respiration	Circulation time from left jug. to right carotid	Maximum deflection	Notes
2.30	27·7 per min.	3·4″	111	
.41		3·1*	85	
.42		3*	86	
.45	Insp.	3·05		This circulation time is a little too long.
.47	Insp.	2·75	96	
	Exp.	2·8	91	
	Insp.	2·95	88	
				Respiration now made 18·6 per min. Box 1000.
	Insp.	2·55		This circulation time is a little too long.
3.2	,,	3·3*	80	Box 1100.
.4	Exp.	2·65*	67	
.7	,,	2·6	78	
.10	Insp.	2	100	This circulation time is perhaps a little too short.
.12	Exp.	2·85	58	
.13	Insp.	2·95	87	
				Respiration now made 5·4 per min.

Time	Respiration	Circulation time from left jug. to right carotid	Maximum deflection	Notes
3.18	Insp.	3·95	101	
.20	,,	4·1	91	
.22	Exp.	4·35	137	
.23	Insp.	3·95*	97	
.27	Exp.	3·95	83	
.33	12·5 per min.	3·2	74	
.36	Insp.	2·15	102	
.40	,,	2·4	93	
.42	Exp.	3·3	65	
				Here began to use suction as well as inflation for the artificial respiration. Resp. 12·5 per min.
3.45	Exp.	3·05	63	
.47	Insp.	3·15	90	
.49	12·5 per min.	2·85	48	
.51		2·6	66	
.52	Exp.	3·5	41	This circulation time is too long.
.54	,,	2·85	74	
.56	Insp.	2·15	107	
.58	Exp.	3·25	54	
4	Insp.	3·85	81	
4.2	Exp.	3·2	64	
				Injected 10 mg. curara into blood.
.18	12·5 per min.	3·4*	56	
.21	Exp.	3·5	63	
.25	,,	4·15*	44	
.27	Insp.	4·05	101	
				Injected 10 mg. curara into blood.
4.40	Exp.	3·4	46	
.42	Insp.	4·1	78	
.44	Exp.	3·05	57	
.46	Insp.	4·1*	89	
.52	Exp.	3·2	62	
.53	Insp.	4·4	78	
.55	12·5 per min.	3·15	53	
				Here stopped suction. Now only inflation used in artificial resp.
5	18·7 per min.	3·75	66	
5.1		3·15*	78	
.10	Exp.	3·4	75	
.12	Insp.	2·65	102	
				Now increased the depth of the resp. the rate remaining the same, viz. 18·7
.20	Insp.	3·2	102	
.22	Exp.	3	90	
.24	Insp. for 15″	3·4	108	
.25	Exp. ,,	4·3	122	
.26	Insp. ,,	3·05	100	
.28	Exp. ,,	6	88	This circulation time is too long.
.29	Exp. ,,	3·5	72	

In this Experiment the animal was not completely paralysed till near the end of the experiment, and sometimes there were natural movements of respiration.

increased. The mean for the inspiratory readings is 4″, and for the expiratory, 4·15″, that is there is no clear difference, although both circulation times are greatly more than with respiration at a quicker rate. The meaning of such exceptions to the general rule as Experiment 6 (first half) will be sought for later on.

It is important that in no case have I found with artificial respiration (inflation only) the circulation time in expiratory standstill shorter than in inspiratory standstill, while in the majority of the experiments the circulation time in expiratory standstill was distinctly longer than that in inspiratory standstill.

In the latter half of Experiment 6 aspiration as well as inflation was used in the artificial respiration, i.e. inflation during inspiration, aspiration during expiration, in order to see how this would affect the circulation time.

The average of seven inspiratory readings is 3·7″, of ten expiratory readings 3·3″. So that with aspiration the circulation time is less than with inflation. The difference is indeed not great, but the number of readings from which the means are obtained is large; and averages of this sort are worthy of more confidence than a close agreement of two or even three consecutive readings.

There appears then to be a reversal of the usual relation between the inspiratory and expiratory circulation times, when collapse of the lung is brought about by aspiration, instead of being left to take place of itself. In connection with this the note that the image moves in the direction of diminished electrical resistance of the carotid when the respiration is stopped in expiration, and in the direction of increased resistance when it is stopped in inspiration, is interesting; for when only inflation is being used, stoppage of respiration either in inspiration or in expiration causes the image to move in the direction of increased electrical resistance of the carotid. Diminution of the resistance of the artery would mean that the pressure in it was increased, and that more blood was getting through the lungs.

But I do not feel that I can at present ground on a sufficient basis of fact the statement, that in collapse of the lungs produced by aspiration the circulation time is always less than in expansion of the lungs produced by inflation, however probable this may be; and in the summary I shall use the phrase "seems to be" instead of is, in order to indicate that the number of experiments on which the statement rests is small.

When respiration (inflation only) is stopped for some time before the readings are taken, the inspiratory circulation time, so far as the few observations at the end of this experiment go, is again sensibly less than the expiratory circulation time. This is interesting when we consider that the circulation times were exactly equal with the short stoppage.

We may here restate the main results of this section.

With artificial respiration (inflation only), either with unopened or open chest, the pulmonary circulation time is in general less in inspiratory than in expiratory standstill, when the observation is taken immediately after the stoppage of respiration; and this may be due either to the circulation time in inspiratory standstill being less than that in undisturbed respiration while the circulation time in expiratory standstill is not less, or to the circulation time in expiratory standstill being greater than that in undisturbed respiration while the circulation time in inspiratory standstill is not greater.

When collapse of the lungs in the artificial respiration (with unopened chest) is caused by aspiration, the pulmonary circulation time seems to be less in expiratory than in inspiratory standstill (inflation).

A "venous" condition of the blood causes an increase in the pulmonary circulation time, with respiration (artificial or natural) going on.

When artificial respiration (by inflation only) is arrested for more than a few seconds before the measurement of the pulmonary circulation time is made, the circulation time in inspiratory standstill increases with the interval of arrest, and may become as great as that in expiratory standstill.

The interpretation of the results.

Some of these results were to me unexpected. Most of the writers on the respiratory waves in the arterial blood pressure curve who have sought their explanation in mechanical conditions influencing the pulmonary circulation, and not in nervous impulses affecting the heart or the systemic arterioles, are agreed that these mechanical conditions can only be :—(1) Changes in the capacity and resistance of the pulmonary capillaries, depending on changes in the volume of the lungs or in the relation between the pressure on their alveolar and pleural surfaces. (2) Changes in the quantity of blood entering the thoracic cavity caused by alterations in the intra-thoracic pressure.

As to the first factor, the weight of evidence is undoubtedly in favour of an augmentation of the capacity and a diminution of the resistance of the pulmonary circulation in natural inspiration, that is when the lungs are distended by a diminution of pressure on their pleural surface, but an opposite effect when the lungs are distended by inflation as in ordinary artificial respiration. The resistance of the collapsed lung in natural respiration is generally admitted to be greater, and the capacity less, than in the distended lung; in artificial respiration, on the other hand, the capacity in collapse is said to be greater, and the resistance less, than in inflation.

As regards the second factor, we cannot doubt that anything which lowers the intra-thoracic pressure relatively to the blood-pressure in the extra-thoracic veins must lead to an increased flow of blood to the right heart.

Let us now consider how these things tally with our results on the circulation time; and I will omit here all detailed reference to normal respiration, because I have only as yet made a sufficient number of experiments on curarised animals, in which the absolute steadiness of the electrodes, during stoppage of respiration, so necessary for accurate work, could be counted upon. It will be well first of all to take the case of the unopened chest, and to enquire what the meaning is of the smaller pulmonary circulation time in inspiration than in expiration.

The blood-pressure in the carotid sinks sharply during inflation under the conditions of my experiments; generally remains constant at its minimum till respiration is again begun, then leaps up to a maximum beyond the original mean pressure; and soon falls again to the normal level (Fig. 1, Pl. I.). During collapse the mean pressure is but little changed; if anything, it rises slightly; and when the respiratory undulations disappear, the mean corresponds at least to the tops of the wavelets. On the other hand, when the trachea is closed, either in inspiration or expiration, in a chloralised rabbit which has been breathing naturally, little change occurs in the blood pressure; the respiratory waves only become more pronounced owing to the deep respiratory efforts.

There is no doubt then that a relatively short pulmonary circulation time may be associated with a relatively small blood-flow through the lungs. There is as little doubt, I think, that, other things being equal, more blood must pass per unit of time through the lungs, as through other organs, when the vascular resistance is small than when it is large; and also that the linear velocity of a cross section of the column of blood must be greater, and the circulation time less, when the small vessels are widened than when they are constricted. The explanation of the seeming paradox, that salt solution injected into the jugular finds its way to the carotid through the inflated lungs as quickly as with respiration going on, and perhaps more quickly, while the total quantity of blood passing round the lesser circulation is so much diminished that the arterial pressure falls, lies, I think, in the fact that the other things are not equal. A great and necessary peculiarity of the pulmonary circulation, as compared with any part of the systemic circulation, the renal vascular tract for instance, is the dependence of the blood-flow through the lungs upon the quantity of blood which reaches the right side of the heart. Within limits, the quantity of blood which the right ventricle can send through the lungs in a given time depends only, or at least chiefly, on the quantity which is available; and this is determined by the facility with which blood passes from the systemic arteries into the veins, and from the extra-thoracic veins into the chest. Since the ventricle in general is not working up to its maximum output, a certain portion of its energy of contraction is usually wasted[1]; and this would be available for driving on the blood, if either there was more blood to drive on, or a greater resistance to its passage. If then the vascular resistance of the lungs be increased by diminution of their capacity while the quantity of blood reaching the right ventricle is not diminished, the increase in the part of the energy of the ventricular contraction spent upon the blood may compensate for the greater resistance, and the same quantity of blood may pass per unit of time through the lesser circulation. In this case it is clear that any given cross section of the column of blood would move with greater velocity than before, and the circulation time would be diminished, while the total blood-flow through the lungs was unchanged. Again, suppose that the quantity of blood coming to the right ventricle is lessened, while the capacity of the pulmonary circulation is unchanged, it is clear that the pulmonary circulation time must be increased, and the total blood-flow to the left side of the heart diminished.

But thirdly, we can suppose that while the supply of blood to the right ventricle is lessened, the capacity of the pulmonary vessels is diminished still more. In this case, on the assumption that the

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[1] Roy and Adami. *Phil. Trans.* 1892, pp. 199 etc.

ventricle is still able to force through the lungs all the blood which it receives, the pulmonary circulation time must be lessened simultaneously with the total blood-flow to the left heart.

To treat the problem a little more strictly, the mean pulmonary circulation time is the time in which the whole of the blood in the lungs passes from pulmonary artery to pulmonary veins, in other words it is the time in which the right ventricle throws into the former a quantity of blood equal to that in the pulmonary circulation. Supposing then that the ventricle up to a certain limit is able to force through the lungs all the blood it receives, independently of the vascular resistance, the pulmonary circulation time must vary inversely as the quantity of blood flowing into the right side of the heart per unit of time and directly as the quantity of blood in the pulmonary circulation at the beginning of the observation. In any case, if Q represent the capacity of the pulmonary circulation, Q' the average output of the right ventricle during the measurement, r the number of beats of the heart per second, and T the pulmonary circulation time, we get

$$T = \frac{Q}{rQ'}.$$

Now let Q be diminished while r and Q' remain constant, that is let the vascular capacity of the lungs be lessened, while the ventricle, supposed to be previously working below its maximum, continues to receive, and therefore to expel, the same quantity of blood as before. T must in this case be diminished too. Lichtheim's experiment on closure of a portion of the vascular tract served by the pulmonary artery would probably afford an illustration of this case. He found that even when a very considerable proportion ($\frac{2}{3}$) of the whole tract was cut out, the blood-pressure in the carotid artery did not fall. Now here Q must have been notably diminished, for the unblocked third of the vessels of the lungs can hardly be supposed to have been so much distended as to keep the total capacity normal. Q' would be unchanged, since the carotid pressure remained the same; so that the ratio $\frac{Q}{Q'}$, would be diminished, and there is little doubt that if the pulmonary circulation time were measured under the conditions of Lichtheim's experiment, a decrease would be found. The same is true however Q and Q' may be changed, if only the ratio $\frac{Q}{Q'}$ is diminished while r remains constant.

Now when artificial respiration is arrested with the lungs inflated and the thorax unopened, Q and Q' are both lessened, Q' because the high intra-thoracic pressure hinders the return of blood from the systemic veins, Q because inflation of the lungs, by increase of the intra-alveolar pressure, diminishes the capacity of the pulmonary circulation. In this case the pulmonary circulation time, T, is diminished; which would indicate that Q has been lessened proportionally more than Q'. Heger's result, that the artificially inflated lungs may contain only $\frac{1}{4}$ the normal quantity of blood, shews how easily this may happen.

In arrest of respiration with opened chest and inflated lungs Q and Q' are both lessened, Q because of the decrease of vascular capacity of the lungs, Q' not perhaps because less blood is reaching the right heart than during regular respiration, but because the ventricle, although sending more blood through the lungs than in inflation with unopened chest, is unable to force through the whole of its now relatively abundant supply. The systemic blood-pressure therefore falls, while the diminution of the pulmonary circulation time (Exp. 3) is even greater than with unopened chest, since Q is presumably diminished to at least the same extent and Q' not proportionally so much.

In collapse, with unopened chest, the capacity of the pulmonary circulation is greater than in inflation. More blood also reaches the right ventricle; and it sends more through the lungs, though presumably not so much more as to counterbalance the increase in capacity. So that although the outflow in a given time by the pulmonary veins is greater than in inflation, and perhaps greater even than during regular respiration, and the carotid pressure accordingly does not fall, and may rise a little, the ratio $\frac{Q}{Q'}$ would seem to be upon the whole increased, or at least to remain the same as before; and the pulmonary circulation time is either greater than, or at anyrate not less than, the circulation time during undisturbed respiration, and therefore greater than that in inspiratory standstill.

In collapse with opened chest, the same quantity of blood may be supposed to reach the right ventricle as in inflation. Since the vascular capacity of the lungs, however, is greater in collapse than in inflation, $\frac{Q}{Q'}$, and therefore the pulmonary circulation time will be greater, unless Q' is increased in the same proportion as Q; which in general will not be the case.

When aspiration is used to produce collapse, with unopened thorax, the pulmonary circulation time seems to be rather less than in inflation. Since the carotid pressure is as great as during regular respiration or even greater, Q' cannot have diminished. On the contrary it will have increased, for aspiration reduces the intrathoracic pressure, and thus increases the flow of blood to the right heart. The same will be the case with Q; and it will depend upon the relative alteration in Q' and Q whether T is increased or diminished. Apparently Q' is in general increased more than Q; and the pulmonary circulation time is therefore less in collapse (by aspiration) than in inflation. The difference is not large, perhaps because Q is proportionally nearly as much increased in collapse as Q'. For there are two factors both tending to make the capacity greater, first that the collapsed lungs, even when collapse is produced under comparatively unfavourable conditions, by the recoil of the chest walls alone, have a greater vascular capacity than the inflated lungs, and, secondly, that lungs caused to collapse by aspiration, have a greater vascular capacity than when the collapse is brought about by a method which does not diminish the intra-alveolar pressure.

Next let us consider the increase in the pulmonary circulation time which takes place when the blood is not sufficiently oxygenated, although the movements of respiration (artificial or natural) are being kept up. I at first thought that this increase of circulation time was a clear proof of increase of vascular resistance in the lungs, and therefore a corroboration of the observations of Lichtheim and other writers, who have observed a rise of pressure in the pulmonary artery during suspension of respiration, not necessarily accompanied with an increase of pressure in the carotid. On further considering the subject, I believe that my observations, although certainly not inconsistent with the idea that poorly oxygenated blood causes narrowing of the pulmonary vessels, either by direct action or through vaso-motor nerves, will bear another explanation. We know that the systemic blood pressure rises when the blood becomes venous, because of the constriction of the small vessels and consequent increase of peripheral resistance. Now the effect of this constriction on the lesser circulation must be, except so far as it is balanced by the higher pressure, that less blood will pass into the systemic veins, and therefore less into the right ventricle and through the lungs. In other words, Q' is diminished. If now r and Q remain unaltered, T, the pulmonary circulation time, must be increased; as we find is the case. But it is not necessary that r and Q should remain absolutely unchanged; it is sufficient that the ratio $\frac{Q}{rQ'}$ should increase. Q may, therefore, also be diminished, but not so much as rQ'. When the deficiency of oxygen in the blood, or the increase of arterial pressure, has reached a certain point, slowing of the heart may take place, that is a diminution in r, accompanied, however, by an increase in Q'. But upon the whole rQ' tends rather to diminish than to increase with the time during which respiration is suspended; so does T; and the clear inference is that if Q is also diminishing, it must be at a less rapid rate than rQ'.

The lessening of the circulation time when the blood is "venous" may be seen also, though to a less extent, in systemic vascular tracts. When a tract including both the lungs and systemic capillaries is investigated, the total circulation time is not only found to be increased, as would of course necessarily be the case if the time of the lesser circulation alone were affected, but it is, sometimes at least, increased to a greater extent than can be accounted for by the slowing of the blood stream in the lungs alone.

As I have said, this does not shut out the possibility that the pulmonary vessels may be narrowed in asphyxia. It only does not support it. A rise of pressure in the pulmonary artery, during suspension of respiration, unaccompanied by a corresponding rise of general arterial pressure, could I think, only mean that in proportion to the vascular resistance of the lungs the output of the right ventricle had increased. This might happen either if the pulmonary vascular resistance increased while the ventricular output remained the same as before, or if the ventricular output increased while the resistance in the lungs was unchanged. A more than momentary increase in the output of the ventricle would not be conceivable without a change in the pressure in the carotid, unless it was balanced by a simultaneous increase in the outflow through the systemic capillaries, and this would not be easy to explain in accordance with the ordinary phenomena of asphyxia. A constriction of the pulmonary vessels must lead to a fall of systemic pressure, unless it is accompanied by either a simultaneous and proportional increase of constriction of the systemic arterioles or by an increased effort of the right ventricle which enabled it, in spite of the increase of pulmonary resistance, still to pass the same quantity of blood through the lungs. In the latter case the pulmonary circulation time would be diminished not increased, as it certainly is when respiration is suspended for any considerable time with the lungs in any position whatever.

The increase of the pulmonary circulation time, both in inspiratory and expiratory standstill, but especially in the former, when respiration is suspended for more than a few seconds, is connected, I think, with the effect of deficiency of oxygen on the circulation time while the respiratory movements are still going on, although, of course, this effect is superadded to the changes produced by the position of the lungs. The circulation time through the collapsed lungs, which is already relatively long, reaches its maximum sooner than that of the inflated lungs (with unopened thorax); the latter is as a rule lengthened even in 20″, and may ultimately equal the expiratory circulation time, which, if originally long, may not be much increased by continuing the suspension beyond the time necessary to make the measurement (say 4″ for a rabbit). Further, when the blood of an animal is neither well oxygenated nor very venous, the excess of expiratory over inspiratory circulation time may be greater after suspension of respiration for a very short period (4″ to 5″) than later on; while with well oxygenated blood the greatest difference may be found with a somewhat longer suspension (say 10″ to 15″).

These things suggest that when the deficiency of oxygen in the blood reaches a certain point, an increase of the pulmonary circulation time is caused both through the inflated and through the collapsed lungs; but the point at which this effect begins is reached sooner in collapse than in inflation.

This can be again explained as the consequence of vasomotor constriction of the systemic arterioles and consequent diminution of the output of the right ventricle, without the necessity of assuming a diminution of the calibre of the pulmonary vessels. And the curves in Figs. 2 and 3, Pl. I., shew that the blood pressure in the carotid may, when respiration is arrested in collapse, begin to rise in the typical curve of asphyxia, while after the same, or a considerably longer interval of suspension in inflation, no such rise may occur.

But why is the effect on the circulation time and on the systemic blood pressure delayed in expiratory as compared with inspiratory standstill? I think the answer to this question is that in full inflation the lungs contain much more oxygen than in collapse; not only is the volume of the included air greater, but the partial pressure of the oxygen is also a little greater. Now from this stock of oxygen the blood has to supply itself during the time that respiration is suspended. In inspiratory standstill the proportion of oxygen in the blood does not so soon fall to the point at which vasomotor stimulation begins as in expiratory standstill. When the blood is already poorly oxygenated, this point is very quickly reached with the lungs in collapse, but not so quickly when the lungs are inflated.

It is easy to see, by a rough calculation, that the difference in the quantity of oxygen is of an order of magnitude suitable to the production of the effect. Suppose that the quantity of air in the lungs of a 2 kilo rabbit in the deepest inspiration is $\frac{1}{35}$ of the quantity in the lungs of a 70 kilo man, or say $\frac{5000}{35} = 145$ c.c. This corresponds, the deficiency of oxygen in the residual air being left out of account, to nearly 30 c.c. of oxygen. In the position of deepest expiration only $\frac{1500}{35}$ c.c., say 45 c.c. of air or 9 c.c. of oxygen, would be present. Now the consumption of oxygen by a 2 kilo rabbit was found by Finkler and Ortmann[1] to be about 1350 c.c. per hour or 22 c.c. per minute. In the inspiratory position therefore there is enough oxygen in the lungs of a rabbit to supply the consumption for more than a minute, in the expiratory position not enough for half a minute.

A man, I suppose for the same reason, can hold his breath longer after a deep inspiration than after a deep expiration. A 70 kilo man uses say 350 c.c. of oxygen per minute. In deepest inspiration the lungs contain about 1000 c.c. oxygen; in deepest expiration 300 c.c., or not enough for 1 minute.

A man of 70 kilos weight, height 5 ft. 10 in., aet. 32, in rather weak health and suffering from a cold, was able to hold his breath,

$$\begin{array}{cc} \text{In Exp.} & \text{In Insp.} \\ \left.\begin{array}{rl} \text{Sitting} & \left\{\begin{array}{l} 9{\cdot}85'' \\ 10{\cdot}20'' \end{array}\right. \\ \text{Standing} & 13{\cdot}45'' \end{array}\right\}\begin{array}{l}\text{average}\\ 11{\cdot}16''.\end{array} & \left.\begin{array}{rl} \text{Sitting} & \left\{\begin{array}{l} 17{\cdot}45'' \\ 22{\cdot}10'' \end{array}\right. \\ \text{Standing} & 25{\cdot}50'' \end{array}\right\}\begin{array}{l}\text{average}\\ 21{\cdot}68''.\end{array} \end{array}$$

A healthy boy, of 52 kilos weight, height 5 ft. 2 in., aet. 16, held his breath,

$$\begin{array}{cc} \text{In Exp.} & \text{In Insp.} \\ \text{Standing}\left\{\begin{array}{l} 30{\cdot}35'' \\ 20{\cdot}10'' \\ 26{\cdot}90'' \end{array}\right\}\begin{array}{l}\text{average}\\ 25{\cdot}78''\end{array} & \text{Standing}\left\{\begin{array}{l} 35{\cdot}20'' \\ 38{\cdot}25'' \\ 45{\cdot}75'' \end{array}\right\}\begin{array}{l}\text{average}\\ 39{\cdot}7''.\end{array} \end{array}$$

The boy entered with greater enthusiasm into the experiment than the man and this, as well as the weak health of the latter, may partly account for the much longer time during which he held his breath.

In a few experiments no difference between the pulmonary circulation time in inspiration and expiration could be made out by taking the mean of a number of observations. In addition to the first half of Experiment 6 already alluded to, Experiment 6*a*, made on a dog, may be quoted as an illustration of this; and it is worthy of note that

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[1] *Pflüger's Archiv*, Bd. XIV. p. 62.

although the expiratory and inspiratory circulation times are practically equal on the average, they are both considerably greater than the circulation time with respiration going on.

EXPERIMENT 6*a*. Dog, 2030 grams. Morphia and curara. 1·5 c.c. 5 % NaCl solution used for injection.

Time	Circulation time from right ext. jug. to left carotid	Maximum deflection	Notes
5.40	2·8″	100	
.41	2·9	82	
.42	2·65		
.44	Exp. 3·35	101	
	Insp. 3·75		
.47	Exp. 3·1		
.48	Insp. 3·7	130	
.51	Exp. 3·3	110	
.53	Insp. 3·45	129	
			Ligatured both vago-sympathetics.
6.5	2·75	109	Rectum 40·5°.
.6	Insp. 3·35	109	
.8	Exp. 3·2	88	
.15	Exp. 4·05	126	
.16	Insp. 4·95	153	
.18	Exp. 3·7	132	
.20	Insp. 3·55	152	
			Central end right vago-sympathetic put on stimulating electrodes.
.24	Insp. Stim. 2	135	In the whole experiment when respiration is stopped either in Insp. or Exp. there is a movement in direction of increased electrical resistance of carotid; this movement is larger in Insp. than in Exp.
.22	Exp. ,, 3·3	124	
.32	Insp. ,, 2·7	87	
.33	Exp. ,, 3·25	103	
.37	3·25	100	
.38	Stim. 2·95	85	
.41	Insp. for 15″ stim. 3·9	91	
.43	Exp. for 15″ stim. 3·4	104	

"Stim." means stimulation of central end of right vago-sympathetic.

Here the mean of nine expiratory readings is 3·40″, of nine inspiratory readings 3·45″, of six readings with regular respiration 2·85″. Section of the vago-sympathetics and stimulation of their central ends in a curarised animal may be assumed, from other experiments, to have no effect on the circulation time or to have the same proportional effect upon the time in Exp., Insp. and uninterrupted respiration, so that all the observations may be drawn into the average. What is the meaning then of the negative result so far as a difference between the circulation time in Exp. and Insp. is concerned? In one or two cases in the earlier part of the work this may have been due to imperfect clipping of the tubes, so that the arrest of respiration was incomplete, or did not take place sufficiently near the maximum of inflation or collapse; or to natural respiratory movements being attempted during stoppage of the artificial respiration when the dose of curara was too small, or during closure of the tracheal cannula when the animal was breathing normally under chloral alone. Apart from experimental imperfections of this kind, the state of oxygenation of the blood previous to stoppage of the respiration might be such that before the observation could be taken the relative lengthening of the circulation time in inspiratory standstill had already equalised it with that of collapse. The fact that both circulation times are greater than in undisturbed respiration in the experiment just quoted, would seem to indicate that here this factor was at work. But it is not difficult to see from the principles by which we have already endeavoured to explain the other results that an apparently negative experiment may be occasionally looked for, from the interference of conditions not under control. For if Q_I, Q_E be the pulmonary capacity, Q'_I, Q'_E the output of the ventricle, respectively in inflation and collapse, we have $Q_I = mQ_E$ and $Q'_I = nQ'_E$ where m and n are proper fractions, since in inflation (with unopened chest) both the pulmonary capacity and the ventricular output are less than in collapse. Then $\frac{Q_I}{Q'_I} = \frac{m}{n} \cdot \frac{Q_E}{Q'_E}$, and r being supposed constant, the pulmonary circulation time is proportional to the ratios $\frac{Q_I}{Q'_I}$, in Insp., and $\frac{Q_E}{Q'_E}$ in Exp. In general m and n are unequal, and $m < n$, since the inspiratory circulation time is less than the expiratory. But it is conceivable that the relative changes of pulmonary capacity and ventricular output might, in a particular animal at a given time, that is with certain relations between the vascular resistance, blood-pressure and blood-flow in the greater and lesser circulations with inflated and with collapsed lungs, be such that upon the whole one change compensated another. Then m would be $= n$, within our somewhat wide limits of error. Reading to twentieths of a second, we cannot at most, for an average pulmonary circulation time, and then only with a large number of observations, come nearer than within 2 per cent. of the whole. If m ever becomes $> n$, the difference would not be detected unless it at least exceeded this amount.

This is perhaps the place to point out how much more strictly the circulation time of a portion of the systemic circulation increases and diminishes with the vascular resistance than does that of the lungs. The difference depends to a great extent upon the fact that there are many parallel paths for the blood to pass by in the systemic circulation. When the small vessels of the kidney are constricted, the renal circulation time is increased. The available supply of blood is the same as before; practically the propelling force is unchanged, for the general arterial pressure is little affected; and the effect of the greater vascular resistance comes out unmixed. A quantity of blood equal to that which lies between the electrodes on the renal artery and those on the renal vein must pass through the kidney in the renal circulation time; and although this quantity is less than when the renal arterioles are dilated, the outflow in a given time is still more diminished, and therefore the average linear velocity is lessened. If the outflow only diminished at the same rate as the average cross section of the vascular path, the linear velocity would not be altered by constriction; but in capillary tubes Poiseuille found that the outflow varies as the fourth power of the diameter, not as the square; and the linear velocity therefore varies as the cross section.

If there were a heart upon the renal artery, which, working at higher pressure when the renal vessels were constricted, continued to force through the kidney as much blood as before, the linear velocity would evidently be augmented and the circulation time diminished by constriction of the arterioles.

SECTION II.

Effects of the division and stimulation of Nerves on the Pulmonary Circulation Time.

Schiff and v. Wittich stated that the vasomotor nerves of the lungs run in the vagus; but this has been denied by various observers[1].

Couvreur asserted that stimulation of the vagus in the frog caused constriction of the vessels of the lung.

Most observers are agreed that the pressure in the pulmonary circulation is practically independent of the systemic blood-pressure. On the assumption that this is true, a rise of pressure in the pulmonary artery caused by suspension of respiration would mean increased vascular resistance in the lungs.

Lichtheim could get no rise of pressure in the pulmonary artery reflexly, by stimulation of the central stump of the vagus or sciatic, but got a rise by suspension of respiration[2].

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[1] Frey, Bókay, Lichtheim, Bradford and Dean, and others.

[2] Lichtheim. *Die Störungen des Lungenkreislaufs und ihr Einfluss auf d. Blutdruck*, 1876. Quoted in *Hermann's Handbuch*, Bd. IV. Th. 1.

Zuntz[1] could find no distinct alteration, even during suspension of respiration, in the filling of the pulmonary vessels or the outflow of blood from a small wound.

Bradford and Dean[2] confirm the statement that the pulmonary pressure is only little dependent on the aortic, and also that the pulmonary vasomotor nerves come from the upper dorsal cord (dog). Stimulation of the upper part of the cord causes great rise of pressure both in the pulmonary system and the aorta. If the cord is now cut at the level of the 7th dorsal nerve, and the lower end stimulated, there is only a rise of pressure in the aorta. If the upper part of the cord is now again stimulated, there is only a small aortic rise, while the pulmonary rise of pressure is as great as at first. They consider that this proves the direct influence of the cord on the pulmonary vascular system. Peripheral stimulation of the 2nd—7th dorsal roots causes a relatively great rise in the pulmonary blood-pressure. The vagus contains no vasomotor fibres for the lungs.

In my experiments the circulation time was determined by a sufficient number of readings before and after section of a nerve, and again during stimulation of the nerve.

Section and Stimulation of the Vagi.

Considering the profound effect which section of these nerves has on the respiration, I thought it possible that, vasomotor influences apart, a change in the circulation time might be found associated with the mechanical changes. And I think there is little doubt that the pulmonary circulation time (with natural respiration) is to some extent lengthened after section of both vagi.

In Experiment 8 (p. 66), for example, the circulation time with intact vagi was 2·25″ in three good readings. The mean of three readings following section of the first vagus is 2·45″; the mean of four readings following section of the second vagus is 2·7″; and the mean of the next four readings, 3·9″.

No doubt in the last two or three observations the imperfect oxygenation of the blood had begun to affect the circulation time.

In Experiment 7 (p. 64), the means of a first set of four and a second set of three readings are 4·05″ and 4·1″ respectively. (This is long for a normal pulmonary circulation time, but the rabbit was unusually large, over 3 kilos.)

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[1] *Pflüger's Archiv*, Bd. XVII. p. 399.

[2] This *Journal*, Vol. X. p. i. *Proc. Physiol. Soc.* 1889.

The mean of a set of three readings taken immediately after section of both vagi is 4·4″, and of a set of two marked readings taken a few minutes later, 5·7″.

In this experiment section of the vagi produced no effect whatever on the rate of respiration, although a note says that the depth seemed somewhat increased. This would perhaps suggest that lengthening of the circulation time after section of the vagi need not be due to mechanical changes in the respiration, but may be a result of the cutting out of impulses normally passing along these nerves and independent of the impulses concerned in maintaining the normal respiratory rhythm.

But if this is true, it is evident that we might expect to find changes in the pulmonary circulation time, after section of the vagi, with artificial as well as with natural respiration. But in Experiment 12 (p. 69), in which artificial respiration was used, the pulmonary circulation time was 3·15″ (eight readings) before section of the second vagus, and 2·95″ (mean of 35 readings) after section, while in other experiments no difference was found.

Taking everything into consideration, I do not think we can say more than that section of both vagi does, as a rule, cause a lengthening of the pulmonary circulation time with natural respiration; this may depend partly on mechanical or chemical changes produced in the respiration, but may possibly in part be due to the cutting off of impulses which more directly affect the vascular resistance in the lungs, or the activity of the heart.

It is not difficult to see that, given a vaso-motor mechanism for the lungs, it might be of importance that the variations of capacity and vascular resistance which the rhythmical mechanical changes in respiration entail should be to a greater or less extent compensated by reflex dilation and contraction of the pulmonary vessels; and of all afferent nerves which might be thought of as adequate to such a duty, none can compare with the pulmonary fibres of the vagi. I therefore endeavoured to find out whether stimulation of the central end of one vagus, the other being cut, had any effect upon the pulmonary circulation time, either with undisturbed respiration (natural or artificial), or in inspiratory or expiratory standstill. With natural respiration, however, the question is complicated by the reflex action of the vagus on the respiratory centre; and although this difficulty can be got over by curara and artificial respiration, the effect on the systemic blood-pressure remains.

So that although in some of my experiments with artificial respiration, there was an apparent shortening of the pulmonary circulation time during stimulation of the central end of the vagus, the interpretation of this result, even if it were shewn to be constant, would have to be carefully controlled.

In a dog of 6 kilos weight with natural respiration, stimulation of the central end of one vago-sympathetic, the other being intact, caused expiratory standstill with marked lengthening of the pulmonary circulation time—from 3·75″ (average of 3 marked readings) to 6·65″; but the heart was at the same time slowed from 163 to 62·5 beats per min.; and the circulation time from external jugular to internal jugular below the thyroid gland, on the side of the cut vago-sympathetic, rose from 7·35″ (mean of seven readings) to 18·2″. Here evidently the slowing of the heart is the cause of the increase in the circulation time.

Similarly, if we found that after section of both vagi the circulation time was diminished, this might merely be due to the increased rate of the heart. And although the rapidly beating heart of the rabbit may be little affected by section of the vagi, we could not accept a diminution in pulmonary circulation time as due to any other cause than increased cardiac activity, unless at least the rate of the heart was observed, and found not to be sufficiently altered to account for the diminution.

When, however, it is a case of increase in the circulation time this necessity does not arise so far as section of the vagus is concerned. But when we stimulate the peripheral end of the vagus, we cannot draw conclusions as to any effect on the pulmonary circulation time of other than cardiac origin, without eliminating the influence of the nerve on the heart, say by atropia.

For example, in Experiment 10, stimulation of the peripheral end of the cut left vagus raises the pulmonary circulation time from 4·35″ to 9·7″ (average of 2 readings). But we cannot at all conclude from this that there has been any direct effect on the vascular resistance in the pulmonary circuit. For the heart was greatly slowed, and this of itself would account for the increase.

In Experiment 12, after section of both vagi and the right sympathetic, and before the injection of atropia, the circulation time was 2·65″ (average of 3 readings from 2.10 to 2.17 o'clock, 2·65″; of 6 readings from 2.30 to 2.55 o'clock, 2·7″; and of 3 readings from 3.16 to 3.23 o'clock, 2·65″).

During stimulation of the peripheral end of the left vagus, the circulation time was 3·35″ (mean of 4 readings from 3.7 to 3.24 o'clock).

The excess during stimulation is therefore 0·7″. If we take only the readings marked with the asterisk, we get again an excess during stimulation of 0·7″.

After subcutaneous injection of $\frac{1}{25}$ mg. of atropia and immediately afterwards of $\frac{1}{17}$ mg. more, the pulmonary circulation time without stimulation of the vagus was 3·05″ (average of 12 readings from 3.33 to 4.48 o'clock). During stimulation of the peripheral end of the left vagus the circulation time was 3·55″ (mean of 9 readings from 3.47 to 4.49 o'clock).

The excess during stimulation is therefore still 0·5″.

If we take only the marked observations after the subcutaneous injection of atropia, we get as the mean of 4 readings without stimulation, 3″, practically the same as before; and for the mean of 7 readings during stimulation, 3·5″.

Here the excess during stimulation is again 0·5″.

But now it is possible that the two doses of atropia injected subcutaneously, although large doses, were not enough to paralyse the vagus action on the heart. Let us, therefore, separate the readings taken before from those taken after the intravenous injection of $\frac{2}{25}$ mg. of atropia at 4.15 o'clock, which certainly removed all traces of the inhibitory action.

We thus get 2·85″ as the average of 6 observations without stimulation before the atropine was put into the blood, and 3·5″ as the mean of 5 readings with stimulation; the excess being 0·65″.

After the injection of atropine into the blood, the mean of 6 readings without stimulation is 3·2″; and the average of 4 during stimulation, 3·6″, a difference of 0·4″.

If, however, we take only the marked readings after intravenous injection of atropia, we get for the average of 3 readings during stimulation of the peripheral end of the vagus, 3·35″; while the single marked reading without stimulation is 3·1″. We can probably accept with safety this single reading, as it agrees sufficiently with the average of all the marked observations without stimulation (3″) and with the average of marked and unmarked readings without stimulation (3·05″).

This would give an excess during stimulation of, say, only 0·3″ or 0·25″; while before the intravenous injection of atropia the excess of the mean of the 4 marked readings during stimulation (3·65″) over the mean of the 3 marked readings without stimulation (2·95″) is 0·7″, which is practically the same as that brought out by taking all the marked and unmarked readings together.

In brief then what we find is this. Before the first (subcutaneous) injection of atropia, the average excess of pulmonary circulation time during stimulation of the peripheral stump of the vagus over that without stimulation comes out by two different methods of treating the results as 0·7″.

The excess on the average of the readings from the subcutaneous injection to the intravenous injection, comes out 0·7″ by one method and 0·65″ by another; while after the intravenous injection it is 0·3″ and 0·4″ respectively.

It is evident, therefore, that the subcutaneous injection of atropia has here left the excess practically unaltered; and the apparent diminution in that excess when we take the mean of all the readings after the intravenous as well as after the subcutaneous injection must be due solely to the diminution after the intravenous injection. So that we must conclude that up to this latter injection the action of the atropia on the vagus was incomplete. After that injection we see the excess drop from 0·7″ to 0·4″, 0·3″ or 0·25″, that is to a half or a third of its original amount.

I have discussed this experiment at great length because it is the type of more in which the same difficulties of interpretation have to be met.

The general conclusion is that the greater part at any rate of the apparent increase in the pulmonary circulation time which may be caused by stimulation of the peripheral end of the cut vagus is due to the action of the vagus on the heart, and not to direct action on the vascular resistance in the pulmonary circuit. (Here we assume that the measures taken to cut out the vagus ends in the heart are such as are not likely to cut out at the same time the endings of pulmonary vasomotor nerve fibres possibly contained in the vagus.)

Whether there may not be in addition some slight direct effect I cannot certainly say. It is not likely, however.

It is of course conceivable that the action of the vagus fibres on the bronchial muscles which has been demonstrated by Roy and Brown, and by Sandmann[1], might to some extent affect the pulmonary circulation time as a whole. Sandmann states that in the cat and rabbit atropia does not paralyse the fibres of the vagus which cause constriction of the bronchi.

To be perfectly conclusive, perhaps these experiments ought to be repeated with simultaneous stimulation of the two vagi. For if stimu-

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[1] *Arch. f.* (*Anat. u.*) *Physiol.* 1890.

lation of one nerve caused an increase of circulation time only in the lung of the same side, this would be marked if the circulation time of the other lung remained unchanged.

Section and Stimulation of the Cervical Sympathetic.

Section of the cervical sympathetic on one or both sides has no effect on the pulmonary circulation time, nor has stimulation either of the caudal or cephalic stump of the nerve any effect.

This statement is based on observations such as those of Experiment 9 (p. 66) and of part of Experiment 12.

The mean of the first 8 readings in Experiment 9 is 3·3″. The mean of the next 3 readings following section of the right sympathetic is 3·4″; and of the next 6 observations following section of the left sympathetic, 3·5″. There is therefore practically no change produced, for a slight progressive lengthening of the circulation time as the experiment goes on is quite sufficient to account for the very small apparent increase. After 4.35 o'clock the rate of this progressive increase becomes rather abruptly greater, and the average circulation time springs from 3·5″ to 3·95″ for the next 3 readings, and to 4·1″ for the 6 readings from 4.35 to 5.2 o'clock.

The average of 11 observations, beginning at this time, during stimulation of the caudal end of the left sympathetic is 4·3″, while the mean of 12 observations without stimulation is 4·25″; and this close agreement derives great weight from the comparatively large number of readings from which the means are deduced.

In Experiment 12, 3 readings, taken from 2.10 to 2.17 o'clock without stimulation average 2·65″; 5 readings taken between 2.24 and 2.56 o'clock during stimulation of the cephalic end of the right sympathetic average 2·7″; and 6 readings taken in the same interval without stimulation average 2·7″. Here stimulation of the cephalic end of the cervical sympathetic has not the slightest effect on the pulmonary circulation time.

Effect of stimulation of the dorsal spinal cord on the pulmonary circulation time.

Here an undoubted effect upon the circulation time was obtained.

Experiment 13 is an example. The readings agree remarkably well with each other. This is doubtless due to the great steadiness mentioned in the "Notes."

The first 2 readings, without stimulation, are identical, viz. 3·7″.

The next 4, with stimulation, give a mean of 6·2″; while 4 taken within the same interval but without stimulation have a mean of 3·5″. The excess of the mean pulmonary circulation time during stimulation is therefore (say) 2·7″. In other words, stimulation of this part of the cord has in this instance increased the circulation time by about 75 p.c.

The last 2 observations shew a somewhat smaller, but still an unmistakeable increase, the average circulation time during stimulation being 4·8″. This falling off is probably due to exhaustion; and it is interesting to notice, that the movement of the image in the direction of increased electrical resistance of the carotid, which follows stimulation, begins also to diminish when the circulation time during stimulation begins to grow less. Another point of interest is the extreme slowness with which the deflection caused by the salt solution begins, when it is injected during stimulation. As has been more than once remarked, this is very typically associated with a long pulmonary circulation time. Any possible stimulation of cardiac inhibitory fibres by escape of current, and consequent lengthening of the pulmonary circulation in this way, was eliminated by the injection of atropia.

To sum up the results of Section II.:

Stimulation of the dorsal spinal cord greatly increases the (uncorrected) pulmonary circulation time.

Section of the cervical sympathetic or stimulation of either stump has no effect.

Section of both vagi generally lengthens the circulation time to some extent. This is due, in part at least, to the mechanical changes produced in the respiration. Stimulation of either stump has no undoubted effect when the influence of the vagus on the heart is eliminated.

It may be added that stimulation of the central end of a nerve like the sciatic usually affects the pulmonary circulation time but little. (In one rabbit 3·45″—6 readings—during stimulation; 3·7″—11 readings—without stimulation.). Here reflex constriction of systemic vessels and reflex augmentation of the heart would oppose each other.

The lengthening of the pulmonary circulation time which stimulation of the upper part of the dorsal cord causes, reminds one of the rise of pressure in the pulmonary artery observed by Bradford and Dean.[1]

When I made the experiments I had not fully appreciated the importance of the part which variations in the quantity of blood passing into the thorax must play in determining the pulmonary circulation time; and, impressed with the idea that a marked increase in this time could only mean, changes in the rate of the heart being eliminated, an increase of vascular resistance in the lungs, I did not attempt to separate the effect of stimulation of the cord on the systemic arterioles from any direct effect on the pulmonary vessels. I now see that an increase of pulmonary circulation time may be caused by constriction of systemic arterioles alone, and consequent diminution in the flow of blood to the right heart. For if Q and r remain constant while Q' is diminished, the ratio $\frac{Q}{rQ'}$, must be increased.

I hope therefore to make further experiments on the point.

EXPERIMENT 7. Rabbit, 3060 grams. 2·4 grams. chloral hydrate in rectum. Cannula in right jugular. Left carotid exposed. Tracheotomy; but natural breathing at first.

Time	Respiration	Circulation time from right jug. to left carotid	Maximum deflection	Notes
2.15	Natural	3·65″	52	2 c.c. of 2·5 $^0/_0$ NaCl injected.
.17		4·1	45	,, ,,
.19		4·05	62	,, ,,
.21		4·4		
.30		4·45	40	3 c.c. of 2·5 $^0/_0$ NaCl injected here and in all following observations in this experiment, except where otherwise mentioned.
2.34	Insp.	4·35*	69	
.36	,,	3·75	77	
.42	Natural	3·8	62	
.48	Insp.	2·85	122	
.51	,,	3·4	124	
.52	Natural 30 per min.	4	122	
.54	Insp.	3·8	119	
3				Cut both vagi.
3.10				Respiration 30 per min., i.e. the same as before section. The depth was perhaps somewhat increased.
.22	Natural	4·85	61	
.24		4·4	60	
.25		3·95	59	
.29	Insp.	6·3*	59	
.31	,,	6*	63	
.32	Natural	5·75*	60	
.34		5·65*	64	
.38	Exp.	5·25*	56	
.40	,,	6	58	This circulation time is too long.
.42	,,	5·35	60	,, ,, slightly too long.
.44	Insp.	6·35	53	
.46	,,	5·6	56	
.48	Exp.	5·55	54	
				3 c.c. of 5 $^0/_0$ NaCl used for injection in the rest of this experiment.

Time	Respiration	Circulation time from right jug. to left carotid	Maximum deflection	Notes
3.51	Exp.	6·1	60	In this observation the tubes would still be filled with 2·5 $^0/_0$ NaCl, which explains the comparative smallness of the deflection.
.53	Insp.	5·2	85	
.55	Exp.	5·5	89	
.57	Insp.	5·55*	97	
4	Exp.	5	80	Moistened artery on electrodes.
.3	,,	4·5	84	
.6	Insp.	5·4	102	
.10	Exp.	5	112	Rectum 35·3°.
.14	,,	4·6	90	
.17	Insp.	4·85	96	
.22	Exp.	4·5	95	
.25	Insp.	5·25	90	
.27	Exp.	4·6	87	Rectum 35·5°.
.34	Insp.	4·25?	89	Resp. 33·3 per min. In this observation it was doubtful whether the clips were put on at the height of inspiration.
.36	Exp.	3·95	84	Rectum 35·6°. Temp. of animal is rising; the anterior part containing the lungs is being warmed possibly more quickly than the rest.
.42	Insp.	4·3	87	
.47	Exp.	4·2	87	
5.5				Injected 30 mg. curara into blood. Respiratory movements stop almost at once. Artificial resp. now begun.
5.15	Insp.	4·3	100	
.20	Exp.	4·8	76	Rectum 35·8°. Artificial resp. 11·5 per min.
.34	Insp.	4·2	77	
.36	Exp.	4·1	64	
.38	Insp.	3·95	82	This circulation time is rather too long.
.42	Exp.	3·7	73	
.46	Insp.	3·15	89	
.48	Exp.	4·1	77	Rectum 35·4°.
.52	Insp.	3·35	105	
.54	Exp.	3·7	78	
.57	Insp.	5·	93	
6	Exp.	4·7		
6.7	Insp.	4·55	56	
.9	Exp.	4·15	49	
.11	Insp.	3·2	53	
				Suction as well as inflation now used in artificial resp.
.14	Insp.	3·4	59	
.16	Exp.	4·7	70	This circulation time is undoubtedly too long.
.17	Exp.	4·15	65	
.19	Insp.	3·5	65	
.20	Exp.	6·4	58	
.21	,,	6·4	62	
.23	Insp.	4·15	82	
.27	,,	2·7	64	
	Exp.	3·65	62	Rectum 35·9°.

The cannula was in right jug. vein close to its junction with the subclavian.

EXPERIMENT 8. Rabbit, 2010 grams. Natural breathing. Cannula in left jugular very near junction with subclavian. Right carotid exposed; electrodes placed on it low down in neck not far from its origin.

Time		Circulation time from left jug. to right carotid	Maximum deflection	Notes
2.58		2·25*	54	2 c.c. 2·5 $^0/_0$ NaCl solution injected in all this experiment.
.59		2·25*	66	Box 900.
3.1		2·25*	68	
.3	Cut left vagus			Respiration deeper; 73·1 per min., as before section.
.5		2·45	66	
.8		2·35	54	
.9		2·55	54	
.10	Cut right vagus			
.11				Respiration now 22·9 per min.
.16		2·45	72	
.18		2·95	82	
				Box now made 1000.
.19		2·7*	62	
.21		2·75*	58	
.37		3·3	115	The deflection is slower than before section of the second vagus.
.39		3·45	118	Respiration 34·4 per min.
.40		4·65	97	Blood very venous in carotid.
.44		4·3	74	Rectum 37·9°.
.50				Animal died, apparently from œdema of the lungs.

EXPERIMENT 9. Rabbit. 20 mg. curara subcutaneously and 5 mg. into blood. Artificial respiration. Cannula in left jugular. Right carotid exposed. Cervical sympathetic isolated on both sides.

Time		Circulation time from left jug. to right carotid	Maximum deflection	Notes
4.8		3·65″	165	Respiration 19·6 per min.
.10		2·95*	185	
.11		3·65	176	
.12		3·3	—	
.17		3·15	168	
.19		2·9*	154	
.20		3·6	145	
.22		3·25*	153	
	Cut right symp.			
.23		3·65	152	
.24		3·3	150	
.25		3·25	159	
	Cut left symp.			
.27		3·7	141	
.28		3·7	142	
.29		3·3	139	

Time		Circulation time from left jug. to right carotid	Maximum deflection	Notes
.30		3·45	152	
.31		3·7	140	
.33		3·15	146	
.35		3·9	148	
.36		3·95	137	
.40		4·05	97	Respiration now 19·4 per min.
.42		3·9	153	
.59		4·05	168	
5		4·5	155	
5.1		3·95	153	
.2		4·45	149	
.3	Stimulated, caudal end of left symp.	3·75	151	
.5	Ditto (stronger stim.)	4·55	138	
.7		4·25	149	
.8	Stimulated ,,	4·4	149	
.9		4·3	154	
·12	Stimulated ,,	4·1	162	
·14		4·2	158	
·15	Stimulated ,, (with strongest stim.)	4·05	168	
				Moistened artery freely with normal saline between electrodes as well as on them †. Also moistened nerve on stimulating electrodes.
5.19		4·1	68	
.21	Stimulated	4·75	71	
.23		4·4	65	
.25		4·75	59	
.27	Stimulated	5·1	46	
.29		4·3	49	
.31	Stimulated	4·25	66	
.32	,,	3·7	57	
.34		3·75	55	Rectum 32·7°.
.39		4·4	54	
.41		4·45	55	
.45	Stimulated	4·55	54	
.48		4·25	58	
.51	Stimulated	4·25	72	
.53		3·85	91	
				Now cut nerve below stim. electrodes and put the ends together.
.55	Stimulated	4·75	102	This circulation time is too long.
.57		4·5	102	
				Now pushed stimulating electrodes down near clavicle so as to favour escape of current.
.58	Stimulated	5·05	116	
6		4·05	111	
6.1	Stimulated	4·1	132	Rectum 32·2°. Blood in carotid still well oxygenated.

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† After artery was moistened the deflections became much smaller and markedly slower than before. Towards end of experiment as artery dried again the deflection increased.

EXPERIMENT 10. Rabbit, 1980 grams. Cannula in left jugular. Right carotid and both vagi prepared. Curara. Artificial respiration.

Time		Circulation time from left jug. to right carotid	Maximum deflection	Notes
1.2		4·25″	248	
.3		4·3	279	
	Cut left vagus			
1.7		4·35	442	
.8		4·35	456	
.12	Stimulated periph. end of left vagus	9·6		
.14	,,	9·85	568	
.18		15·85	571	Animal dying.
.28				Rectum 36·6°.

The artificial respiration was not satisfactory, and the blood in the carotid appeared from the beginning to be insufficiently oxygenated. Still there is no doubt that the two readings with stimulation of the vagus shew a real lengthening of the circulation time, for the heart recovered its old rate after the last of the two observations. Then the vagus was stimulated a third time. No reading was got, as the chronometer missed; and apparently the heart did not recover after this third stimulation, for immediately after the very long circulation time of 15·85″ was obtained, and it was seen that the carotid was almost empty.

When the peripheral end of the vagus was stimulated, the image always moved in the direction of increased resistance in the carotid.

EXPERIMENT 11. Rabbit. 30 mg. curara subcutaneously. Artificial respiration. Cannula in left jugular. Right carotid artery, and vagus and sympathetic on both sides prepared.

Time		Circulation time from left jug. to right carotid	Maximum deflection	Notes
1.4		3·35″	59	This reading of circulation time too long.
.5		3·05*	63	
.7		3·05*	63	
.9		3·35	42	Circulation time a little too long.
	Cut left vagus			
.15		3·05	74	
.20	Stimulated central end of left vagus	4·65		
.26		3·35	151	Here the piston of the syringe having become slack, the help of an assistant was needed to finish the experiment. This may account for the great increase in the deflection, as it is possible that more than the usual quantity of salt solution was injected.
.28	Stimulated	3·55	154	
.32		3·75	162	

Experiment 12. Rabbit, 1850 grams. 15 mg. curara subcutaneously. Artificial respiration. Cannula in left jugular. Right carotid artery, and vagus and sympathetic on both sides prepared.

Time		Circulation time from left jug. to right carotid	Maximum deflection	Notes
12.25		2·7″	293	Respiration 31·6 per min.
.27		2·75	228	
	Cut left vagus			
.42		3·25	291	
.44		2·5	292	
.45		3·35*	282	
.46		3·1*	270	Central end of left vagus put on stimulating electrodes.
.47	Stim. central end left vagus	2·75	212	Now rearranged nerve on stimulating electrodes.
.48	,,	2·3	225	
.52		3·85	253	
.53	Stimulation	2·3	204	
.56		3·7	252	All the above observations are good.
	Cut right vagus			Blood still rather poorly oxygenated.
.59		3·5	233	
1.1		3·35	211	
.2	Stimulation	2·35	189	
	Cut right symp.			Blood better oxygenated than before, as vol. of respired air made greater.
.18		2·7	395	
.21		3·1	239	
.23		2.35*	245	
.24		2.35*	—	
.26	Stimulation	2·8*	254	
				Moistened nerve on electrodes.
.29	Stimulation	2·25	273	
.31		2·3	302	
.33	Resp. stopped in exp. Stim.	3·05	286	
	Exp. No stim.	2·35	295	
				Stopped artificial resp. as natural respiratory movements are going on.
	No stimulation	2·65	287	
	Stimulation	2·7	260	
				All resp. stopped. Blood in carotid venous.
.41	No resp. Stim.	3·35	258	
.44	No resp. No stim.	4·9	300	
.52	,, ,,	4·45	316	
.56	,, ,,	3·35		This observation was taken sooner after stopping resp. than the preceding one.
				Cephalic end of right sympathetic put on stimulating electrodes.
2.10		2·25	386	
.15		2·95	69	Before this obs. taken the artery between and on the electrodes was freely moistened with normal saline.
.17		2·75	401	Before this obs. the excess of saline was removed.
.24	Stim. cephalic end of right symp.	2·8	365	

Time		Circulation time from left jug. to right carotid	Maximum deflection	Notes
.30		2·55	366	
.37		2·75	340	
.39	Stimulation	3·05	256	
.43		2·8	279	
.46	Stimulation	2·3*	299	
.47		3·05	290	
.49	Stimulation	2·6	290	
.50		2·45	285	
.55		2·7*	270	
56	Stimulation	2·7*		
				Peripheral end of left vagus now put on stimulating electrodes.
3.7	Stim. periph. end of left vagus	2·7	292	Rearranged nerve on electrodes.
.12	Stimulation	3·15*	361	
.15	,,	3·5	342	
.16		2·3*	288	Rectum 35·6^0.
.19		3·05	276	
.23		2·55*	295	
.24	Stimulation	4·1	362	
.27				Injected $\frac{1}{25}$ mg. atropia subcutaneously.
.33		2·9	316	
.35				Injected 20 mg. curara and $\frac{1}{17}$ mg. atropia subcutaneously.
.45		3·05*	347	
.47	Stimulation	3·05		
.49	,,	2·9*	331	
.51		2·35	366	
.53		2·55*	357	In all obs. where peripheral end of vagus is stimulated the first effect of stim. is to cause a movement of the image in the direction of increased elect. resist. in the carotid.
.57	Stimulation	4·3*	348	
4.3		3·1	303	
.4	Stimulation	3·3*	373	
.7		3·25*	356	
.8	Stimulation	4·05*	346	
.15				Injected into blood $\frac{2}{25}$ mg. of atropia.
.19		3·3	296	
				Stimulation does not affect the rate of the heart.
.32		3·3	301	
.33	Stimulation	3·7*	296	
.35		3·45	341	Moistened artery.
.38		2·7	151	
.44	Stimulation	3·05*	146	
.45		3·35	121	
.47	Stimulation	4·25	123	
.48		3·1*	132	
.49	Stimulation	3·3	145	
				Caudal end of left sympathetic put on stimulating electrodes.
5	Stimulation	3·7*	139	
5.1		3·6*	131	
.3	Stimulation	3·6*	129	
.4		3·3	133	
.6	Stimulation	2·95	128	
.7		3·4*	143	
.9	Stimulation	3·35*	127	Rectum 33·8^0.
				Began now to heat a little more.
.35				Rectum 34·7^0.

EXPERIMENT 13. Rabbit, curara, atropia.

Time		Circulation time from left jug. to right carotid	Maximum deflection	Notes
				Stimulating electrodes in the form of needles thrust into dorsal spinal cord
5.59		3·7″	169	Bridge ratio 1000 : 1000. Box 7000.
6.1		3·7*	166	Box now made 7200.
.2	Stimulation	5·6*	149	The movement is very slow in comparison to that seen when there is no stimulation.
.5	Stimulation	6·35*	150	Movement very reluctant at beginning just as in last observation.
.11		3·5*	156	
.13	Stimulation	6·45*	157	Movement begins with exceeding slowness.
.16		3·35*	158	
.19	Stimulation	6·45*	155	
.22		3·7	146	
.24	Stimulation	4·6	165	
.31		3·35	191	
.33	Stimulation	5·05	184	The deflection now is quicker than in the first obs. with stimulation.

In all the observations with stimulation of the dorsal cord soon after the commencement of stimulation the image begins to move in the direction of increased resistance in the carotid. The average amount of this movement was 40 divisions in the first four observations quoted. In the last two it was only 20 divisions. Everything was exceedingly steady throughout the whole experiment; and the observations are, therefore, very trustworthy.

P.M. Uppermost of stimulating electrodes was found in the spinal canal a little above the lower border of the 4th dorsal vertebra, and lowermost a little below the lower border of the 11th dorsal vertebra.

The point of the cannula in the jugular was quite close to its junction with the subclavian.

The experiments in the above paper were made by the author while holding the George Henry Lewes Studentship. The expenses were met by grants from the Royal Society and the British Medical Association. The paper was sent in as part of a Thesis for the Goodsir Memorial Prize in the University of Edinburgh, April 30th, 1892. In all the experiments performed in the Physiological Laboratory at Cambridge, and in most of those done in the Physiological Institute at Strasburg, the animals were anæsthetised with chloral, morphia, urethan, chloroform or ether. When curara was given, it was generally in addition to one of these anæsthetics.

EXPLANATION OF PLATE I.

Blood pressure tracings from carotid of rabbit. Time trace, seconds. The tracings are to be read in the direction of the arrows.

Fig. 1. Curara and chloral. Artificial respiration. Thorax unopened. At 1 respiration stopped with lungs inflated for 25″. Interval of 10″ between 2 and 3 not reproduced. At 4 artificial respiration begun again.

Fig. 2. Curara and chloral. Artificial respiration (inflation and suction). Chest unopened. Respiration stopped at 1 with lungs in maximum inflation. Kept thus for 60″. Interval between 2 and 3, during which the curve was almost a straight line, 51″. At 4 respiration again begun.

Fig. 3. Taken shortly before Fig. 2 from same rabbit. Respiration stopped in maximum collapse for 60″, beginning at 1. Interval between 2 and 3 (not reproduced) 34″. The line of mean pressure fell to the level of 3 in this interval. At 3 it began to rise. In the interval of 10″ between 4 and 5 it reached the level of 5. At 6 respiration resumed.

Fig. 4. Chloral. Natural respiration. Arrested at I_1 in inspiration (moderate expansion); at E_1 in expiration (moderate collapse). Deep efforts at respiration occurred during the 25″ for which the tracheal tube was closed. Respiration again begun at 2. There is only a slight rise of the mean pressure during expiratory arrest, little or no change during inspiratory arrest. The pulmonary circulation time measured under these conditions is about the same in both positions of the lungs.

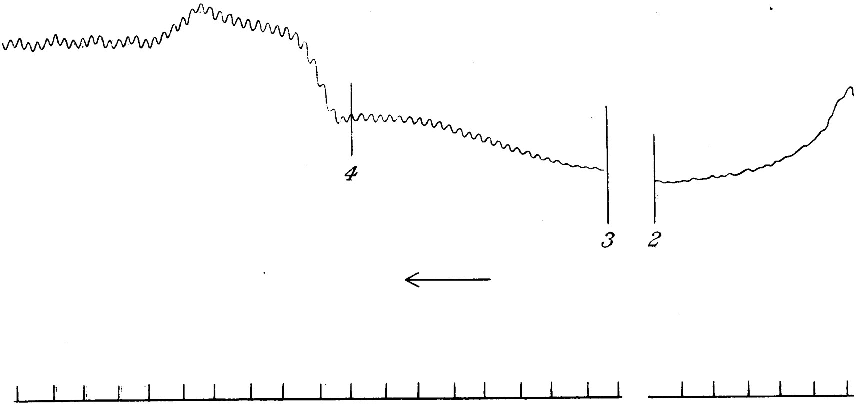


Fig. 1.

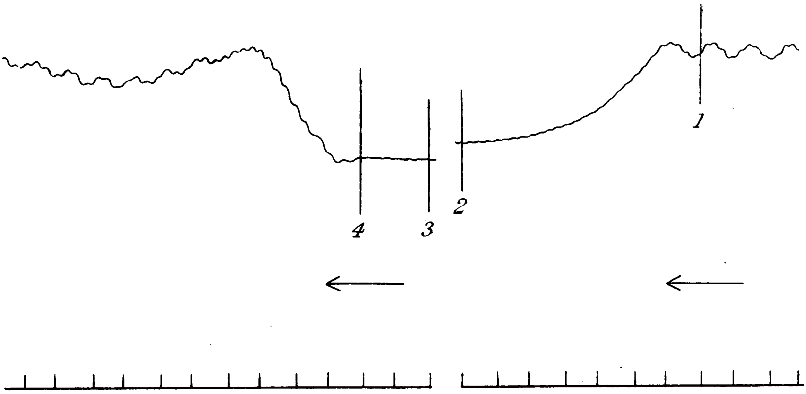


Fig. 2.

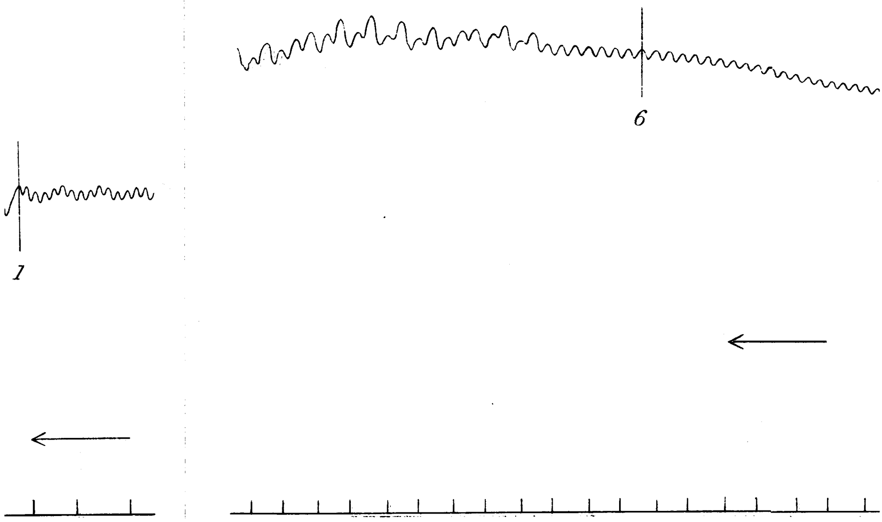


Fig. 3.

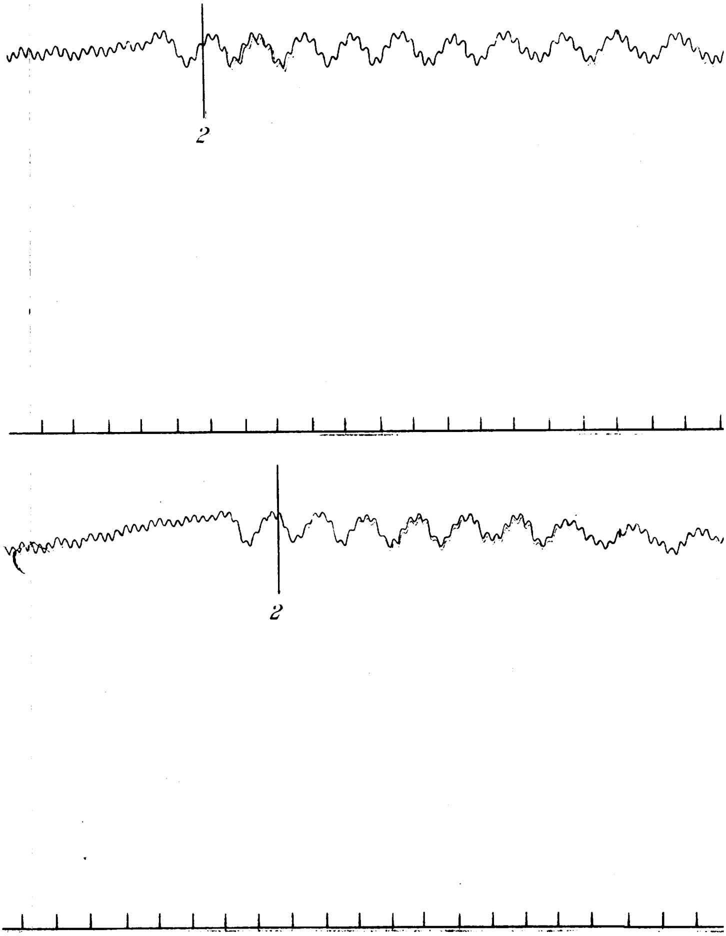
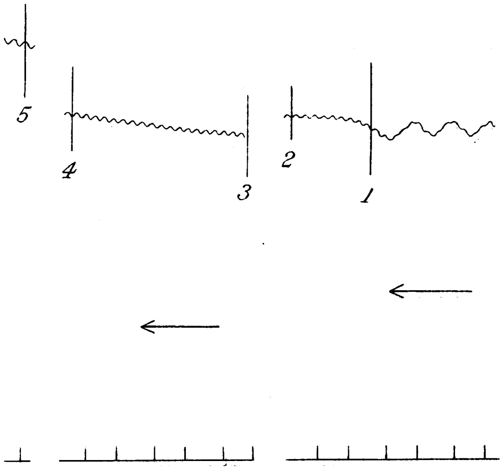
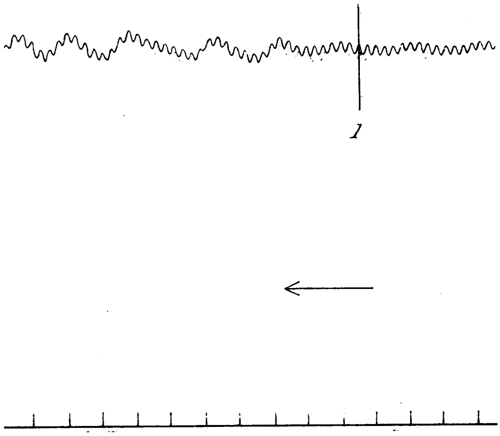
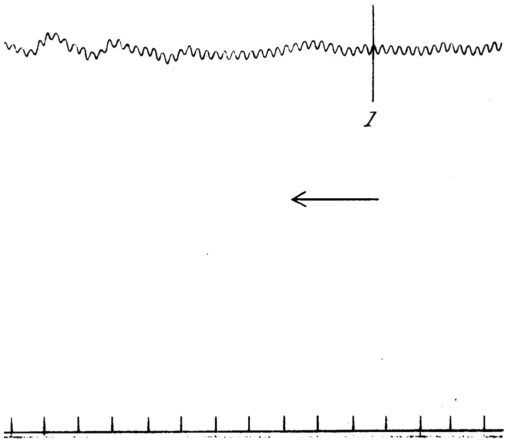


Fig. 4.







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THE CIRCULATION TIME IN ORGANS AND THE INFLUENCES WHICH AFFECT IT. By G. N. STEWART, M.A., D.Sc., M.D.

III. The circulation time in the thyroid gland, and the effects of section and stimulation of nerves upon it.

THE observations of this paper were made entirely upon dogs. None of the animals exceeded six kilos in weight, and most of them weighed much less. Hence it was possible to inject the salt solution into a vein. For large animals an artery would have to be used. The isthmus of the thyroid was absent in some cases, feebly developed in the animals in which it was present. The two lobes were therefore practically independent in their circulation; except that occasionally a common vein, running down over the trachea, and either joining the internal jugular or opening separately, received branches from both lobes.

Operation. An incision was made in the neck in the middle line, tracheotomy performed as far from the position of the thyroid as possible, and a cannula fixed in the trachea. The carotid was next exposed low down in the neck, and a sufficient length of it (say 2 to 3 cm.) isolated for the electrodes. Then the vago-sympathetic was isolated on one or both sides about the same level as the carotid; and in most cases the strong common sheath was removed, and the nerve split carefully into its two strands. Next, the internal jugular vein, or the strongest branch of it where there was no single trunk, was prepared for the electrodes, either below the level of the thyroid or opposite the gland. Care was necessary so as not to injure the vein, as any serious damage to it interfered with the blood-flow.

The irregularity of the veins draining the thyroid made it difficult to adhere to one vein all through. The rule was to take the largest, and, if necessary, to cut off by ligature any blood entering it from other organs than the corresponding thyroid lobe. By far the greater part of the blood in the internal jugular or its representatives, at least in these small and young dogs, comes from the thyroid, and generally only a very trifling proportion from the feeble continuation of the vein upwards from the thyroid to the brain, which for some purposes it is not necessary to tie; for the beginning of the deflection corresponds to the time of the shorter (thyroid) path, and in a control experiment it was found that the circulation time observed was not altered by ligature of the vein above the gland.

The cannula was generally put in the external jugular. In every case a dissection was made post mortem to shew the arrangement of the blood vessels, and to make sure that the vessels and nerves worked with had been properly identified.

The object of the experiments was to determine whether section or stimulation of nerves can be shewn to affect the circulation time in the gland. Changes in the circulation time produced in this way would indicate that vasomotor fibres for the thyroid were contained in the nerves. And, in general, it is easy to see that if the arterial blood pressure is unaffected, or increased, while the circulation time through a systemic vascular tract is lengthened, the vascular resistance in that tract must have increased; and if the arterial pressure is either unaffected or diminished while the circulation time is lessened, the vascular resistance must have diminished.

If, on the other hand, we find that a circumstance which causes a shortening of the circulation time in an organ also causes a rise of general pressure, we cannot conclude that the peripheral resistance in the organ has been diminished, unless we can calculate how much effect the general rise of pressure has, and whether there is a margin over which we must set to the account of vascular change in the organ itself.

Now although this considerably limits the information to be derived from a measurement of the circulation time, without a simultaneous registration of general blood-pressure, it yet leaves many cases which can be attacked by this method alone, and among them our present problem.

I shall now quote some of my experiments.

EXPERIMENT 1. Small adult dog, 2600 grams. 30 mg. morphia hydrochlorate subcutaneously at 12.30. Vago-sympathetic prepared on both sides in the neck below the level of the thyroid gland, and sympathetic carefully separated from vagus for some distance. Cannula in right external jugular vein. Left internal jugular vein and left carotid artery prepared below the level of the thyroid gland. 30 mg. curara injected into blood. Artificial respiration, 34 per minute.

Time		Vascular tract	Circ. time	Max. deflect.	Notes
1.55		Right ext. jug. to left int. jug. vein	9·25″	54	2 c.c. of 2·5 $^0/_0$ NaCl injected in this experiment except where otherwise mentioned.
,,		Right ext. jug. to left carotid	3·3		
2.5		Ext. to int. jug.	9·3	28	
	Cut right symp.				Put cephalic end of right symp. on stimulating electrodes.
.15		,,	8·1		
.19		,,	7·85	22	
.23		,,	7·95	31	
.47		,,	8·45	30	
.48		,,	8·5	34	
.50	Stim.	,,	7·95	39	
.53		,,	8·3	52	
.55	Stim.	,,	8·45	—	Stim. of cephalic end of right symp. causes image to move in direction of increased resistance in int. jug. vein. Blood was now allowed to become more venous in carotid, by diminishing ventilation.
.58		,,	11·45		
3.0	Stim.	,,	11·55	—	Here there is no movement of image in direction of increased resistance in vein. Blood again after this obs. allowed to be freely oxygenated.
.4		Ext. j. to carotid	2·7	91	
.7		,,	3·3		
.14		,,	3·1	79	
.16		,,	2·75	76	
.18		,,	3·05*	77	
.23	Stim.	,,	3·3	82	
.26	,,	,,	3·1	91	
.29		,,	3·25	78	
4.15					Rectum 40·3°.
.18		,,	2·85	94	
.20		,,	2·75		Box 800.
.24		,,	3·05*	89	Box 700.
.26		,,	2·7*	75	
.36		Ext. jug. to int. jug.	8·35*	66	
.49	Cut left symp.				Put cephalic end of left symp. on stimulating electrodes.
.53		Ext. jug. to left carotid	3·2		
.54		Ext. jug. to left int. jug.	6·7*	74	
5.0		,,	6·15*		
.3	Stim. (very weak)	,,	6·8	63	
.5	Stim. (stronger =5)†	,,	9·05	28	A movement of the image in the direction of increased resistance of the int. jug. vein follows stimulation.
.9	Stim. (5)	,,	11·1		2 c.c. of 5 $^0/_0$ NaCl injected in the remaining obs. of this exp.
.16		Ext. jug. to left int. jug.	6·1*	84	
.18		,,	6·15*	103	
.20	Stim. (5)	,,	9·1	69	

† Stim. (5) means that distance between coils of inductorium was 5 c.m.

Time		Vascular tract	Circ. time	Max. deflect.	Notes
.22	Stim. (5)	Ext. jug. to left int. jug.	10·05*	147	
.24			5·85*	58	
.29	Stim. (reversed cur. in primary) (5)	,,	7·7*	58	Nerve not so well on electrodes as before. Rearranged it now, and moistened vein on electrodes.
.37		,,	6·9	58	
.40		,,	6·5	73	This circ. time is a little too long.
.43		,,	6·1*	58	Now removed some saline sol. from vein.
.54		,,	6·85*	107	
					Injected 20 mg. curara.
6.11		,,	6·55*	100	
.13	Stim. (8)	,,	8·3	63	
.18	,,	,,	10·3*	40	Stimulation was kept up, before taking the obs., for a much longer time than in last case.
.21	Stim. (8)	,,	9·6*	32	Stim. not so long as last time.
.22		,,	7·2*	100	Box 970.
.30		Right ext. jug. to left carotid	2·85	93	
.32	Stim.	,,	3·3	82	Immed. after stim. there is first a movement of 6 divisions in direction of increased resistance and then a moderately slow movement of 34 div. in direction of diminished resistance of artery. This is typical.
.37		,,	2·7*	85	
.38	Stim.	,,	3·7*	82	Rectum 40·4°.
.43	Stim.	,,	3·15	94	
.46		,,	2·75	96	
.48	Stim.	,,	3·75*	100	
.51		,,	2·75*	103	
.53	Stim.	,,	3·5*	98	Box 730.
.55	Stim. (reversed cur. in primary)	,,	2·95*	100	The movement of image caused by stim. is not affected by reversal of primary current.
7.9		Right ext. jug. to left int. jug.	6·25	96	
.22	Stim.	,,	10·1	29	
.24	Stim.	,,	10·25	35	
					Seared left symp. nerve on cephalic side of electrodes.
.32		,,	6·85	47	
.35	Stim.	,,	8·55	53	
					Seared nerve again.
.37	,,	,,	6·7	62	
	Cut right vagus				Put central end of right vagus on stimulating electrodes.
8.5		Right ext. jug. to left carotid	3·05		
.7		,,	2·95	142	
.8	Stim.	,,	2·8	139	
.9	Stim.	,,	3·1*	143	
.10		,,	2·7	125	
.11		,,	2·55*	128	
.12	Stim.	,,	2·5*	131	
					Put peripheral end of right vagus on stimulating electrodes.
.15	Stim.	,,	6·75		
		,,	3·3	136	This obs. was taken immed. after stopping stimulation.

When peripheral end of vagus is stimulated, the image begins to move in the direction of increased resistance in the carotid, and the movement becomes very large, as much as 400 or 500 divisions or more. The image, however, now becomes unsteady, although before stimulation it was extremely steady. This was repeated again and again.

Apparently, when the blood-pressure falls through stimulation of the peripheral end of the vagus, the pulsatory oscillations in the half-empty carotid increase in size, and the changes of electrical resistance due to the pulse become greater. Besides, when the heart is slowed there is more time for the galvanometer to respond to each of such changes.

Although there was a well-marked pulse in the cardiac end of the internal jugular, a deflection never occurred immediately after the injection of the saline solution, even when the electrodes were placed on a distinctly pulsating piece of the vein. Although the pulse wave starting from the right auricle is able to reach the electrodes, or pass beyond them, there is not a regurgitation in mass of the auricular blood.

P.M. Point of cannula in right external jugular vein only 8 mm. from junction with subclavian. Distance of electrodes on left internal jugular from its junction with left external jugular, 2·5 cm.; from this junction to right auricle, 4·5 cm.

Distance of electrodes on left carotid from origin of that artery, 5·5 cm.

From electrodes on carotid to origin of superior thyroid artery, 4·2 cm.

Length of superior thyroid artery, 1·7 cm.

" " " vein, 2 cm.

The tissues in the neighbourhood of the thyroid had been very little disturbed in the operation for this experiment. The superior thyroid artery and vein were not isolated.

No isthmus of the thyroid was present.

In most of the experiments one or both vago-sympathetics were isolated in the neck below the level of the thyroid gland, and the vagus portion carefully separated from the sympathetic portion for a sufficient distance to allow of the laying of either on stimulating electrodes.

The circulation time from the right external jugular to the left internal jugular we shall for shortness call the "venous circulation time," and that from external jugular to right carotid the "arterial circulation time," the difference between the two being the (uncorrected) thyroid circulation time—in this case for the left lobe. The only corrections necessary to find the net thyroid circulation time would be the subtraction of the time taken by the blood to pass from the position of the electrodes on the carotid along the superior thyroid artery to its entrance into the gland, and of the time taken in the veins from the gland to the electrodes on the internal jugular. This correction would be small, and for our purpose it is not required.

In Experiment 1, the mean of 5 readings of venous circulation time after section of the right sympathetic is 8·2″, and that of 5 readings of arterial circulation time is 3″. The thyroid circulation time is therefore 5·2″.

During stimulation of the cephalic end (*i.e.* the end next the thyroid) of the cut right sympathetic the mean of 2 readings of venous circulation time is 8·2″. Stimulation has accordingly caused no change in it. The mean of 2 readings of arterial circulation time during stimulation is 3·2″, so that practically no change has been caused here either. In other words,

Stimulation of the cephalic end of the cut right sympathetic in the neck below the level of the thyroid, causes no change in the circulation time of the left thyroid lobe.

Of course this statement is not based merely upon the single experiment in the discussion of which it appears.

At 4.49 o'clock, the left sympathetic was cut below the level of the thyroid. Immediately before, a marked reading (a reading of circulation time marked in the record with an asterisk to denote that it is specially good) gives a venous circulation time of 8·35″. The mean of 2 marked venous readings taken after section is 6·4″, a difference of 1·95″; while a single arterial reading gives 3·2″, leaving the thyroid circulation time after section 3·2″. From this and similar experiments we deduce the following statement.

The venous circulation time of the left thyroid lobe is diminished by section of the left sympathetic in the neck below the level of the gland. The arterial circulation time is little, if at all, affected. The circulation time of the left thyroid lobe is therefore diminished.

The next point brought out by Experiment 1 is the effect of stimulation of the cephalic end of the cut left sympathetic.

The mean of 8 observations of venous circulation time during stimulation, taken between 5.5 and 6.21 o'clock, is 9·4″; that of 9 readings without stimulation, 6·45″; a difference of 2·95″.

The average of 6 readings of arterial circulation time, taken between 6.30 and 6.55 o'clock, during stimulation is 3·4″; of 4 readings without stimulation 2·75″; a difference of 0·65″. Deducting these values from the venous circulation time, we get 3·7″ as the thyroid circulation time without stimulation, and 6″ during stimulation.

Again, the mean of 2 observations of venous circulation time during stimulation, taken at 6.22 and 6.24 o'clock is 10·15″, that of 2 readings without stimulation taken about the same time 6·55″. The excess during stimulation is 3·6″.

These observations on the circulation time are confirmed by the fact that the image moves in the direction of increased electrical resistance of the left internal jugular vein, when the cephalic end of the left sympathetic is stimulated. For this shews that the blood-pressure in the vein has been lowered by the stimulation. The slight diminution of electrical resistance of the carotid is probably an index of increased blood-pressure due to increased peripheral resistance in the area supplied by it. Of course when the pressure in a vessel increases, its cross-section, unless the increase of pressure is counterbalanced by contraction of the circular muscular fibres, becomes slightly greater, and the electrical resistance of a given length of it becomes slightly less.

We conclude from experiments of this kind, that stimulation of the cephalic end of the cut left sympathetic below the level of the thyroid causes an increase in the circulation time through the left thyroid lobe. In other words, the cervical sympathetic contains vaso-constrictor fibres for the corresponding thyroid lobe.

Experiment 2 confirms the result of Experiment 1, that there are fibres in the cervical sympathetic which can affect the vascular resistance in the thyroid.

The venous circulation time of the right thyroid lobe, which is 7·1″ (mean of three readings) before ligature of the right sympathetic below the level of the thyroid, becomes 5·35″ after ligature (mean of four successive readings).

Weak stimulation of the cephalic end of the cut right sympathetic has no effect on this time, two observations giving 5·3″. Stronger stimulation (with a distance of 6 cm. between primary and secondary) has a marked effect, the mean of three observations during stimulation being 12·3″, while the mean of six readings without stimulation taken during the corresponding interval is 7·4″. (The diminution following ligature of the sympathetic has not apparently lasted very long in this experiment.) The difference is therefore 4·9″; and, as there is practically no change produced in the arterial circulation time, the whole of this difference represents the increase in the (uncorrected) thyroid circulation time.

EXPERIMENT 2. Bitch, 3708 grams. 50 mg. curara subcutaneously. Artificial respiration. Exposed right internal jugular vein, right carotid artery and right vago-sympathetic nerve, below thyroid gland. Carefully separated right vagus from sympathetic for some distance. Cannula in left external jugular vein.

Time		Vascular tract	Circ. time	Max. deflect.	Notes
2.2		Left ext. jug. to right int. jug.	8·45″	38	Rh. 1250. 2 c.c. of 4 $^0/_0$ NaCl injected in whole of this exp. except where otherwise noted.
.4		”	6·5	38	Rectum 39·23°.
.7		”	6·3	40	
	Ligatured right symp. below thyroid				
.16		”	4·8*	36	
.17		”	4·85*	33	
.19		”	5·9	36	
.20		”	5·95*	31	
					Put cephalic end of cut right symp. on stimulating electrodes.
	Stim. (weak)	”	5·3	—	
	”	”	5·3	—	
.32		”	8·1	27	
.36		”	8·15	42	
.37	Stim. (strong, 6)	”	13·6		Deflection consists only of slight, hesitating movements.
.38		”	5·95	50	
.42	Stim. (6)	”	12·5		Only slight, hesitating movements.
.45		”	5·95	29	
.54	Stim. (6)	”	10·95	11	The image ran gradually down from 300 to 60 during stimulation.
3.5					Injected 20 mg. curara into blood. Respiration 29·2 per min.
.42		”	8·1*	20	
.44		”	8·25*	36	
4.7		Left ext. jug. to right carotid	4·75	12	Rectum 38·3°.
.16		”	4·7*	11	
					Electrodes again set up. Cut right superior laryngeal nerve.
.40		Left ext. jug. to right int. jug.	8·7		Rh. 50.
.42		”	8·9	11	”
.47		”	8·65	10	”
.58					Injected 20 mg. curara into blood. Rh. made 1250.
5.0		”	8·35	13	Now put peripheral end of right sup. laryngeal nerve on stim. electrodes.
.15	Stim.	”	8·65*	13	
.17		”	9·05*	13	
.25		”	9·15		
.26	Stim. (6)	”	8·7		
.28		”	9·45		
.29	Stim. (6)	”	9·5		
					Cephalic end of right symp. put on stim. electrodes.

Time		Vascular tract	Circ. time	Max. deflect.	Notes
5.35	Stim. (6)	Left ext. jug. to right int. jug.	11·6*		
.38		,,	8·5*		Rectum 38·23°.
.40		,,	7·3		
.44	Stim.	,,	12·75*		
.49		,,	8·5*	21	
	Stim. (6)	,,	10·1		
.54	,,	,,	12·45		
.56		,,	6·35	32	
.58		,,	7·55		
6.9		Left ext. jug. to right carotid	3·7	15	This circulation time is a little too long.
.10		,,	3·5	13	
					Cephalic end of right symp. on stimulating electrodes.
.14	Stim. (6)	,,	3·6		
.15	,,	,,	3·55		These four obs. on carotid are better than those taken before, as image is now very steady.
					Put periph. end of right sup. laryngeal nerve on stimulating electrodes.
.20	Stim. (6)	Left ext. jug. to right carotid	4·1		Rectum 38·1°.
.22		,,	3·75		
.23	Stim. (6)	,,	4·05		
.27	,,	,,	3·15*		
.29		,,	3·1*		
.31		,,	2·9*		Curara action passing off; twitching of muscles.
.33	Stim. (6)	,,	2·55		Here it was found that from 6.20 to 6.33 (incl.) there was really no stim. of nerve, as the circuit was accidentally left open. Now put this right.
.40		,,	3·15		
.41	Stim. (6)	,,	3·5		
.42	,,	,,	3·65		This circ. time is a little too long.
.43		,,	3·5		
.46		,,	3·3		
.53					Injected 25 mg. curara into blood.
					Now isolated right symp. below sup. cervical ganglion before it joins the vagus; and put cephalic end on stimulating electrodes.
7.54	Stim. (6)	Left ext. jug. to right int. jug.	9·2*		4 c.c. of 4 $^0/_0$ NaCl injected in these observations.
.56		,,	6·35*		Stimulation is always followed by a well-marked movement in the direction of increased elect. resist. of the vein. This begins a second or two after beginning of stim.
.58	Stim. (6)	,,	8·85*		
.59		,,	6·85*		
8.3	Stim. (6)	,,	9·05*		
.6	Stim. (6)	,,	7·3*		Here stim. was kept up for 2 mins. before the observation was taken.
					Cephalic end of right symp. below thyroid now put on stimulating electrodes.
.13		,,	7·3		2 c.c. 4 $^0/_0$ NaCl.
.14		,,	6·25		4 c.c. ,,
	Stim.				No definite effect of stim. could be got. Rectum at 8·27, 37·2°.

P.M. On the right side a large lymphatic vessel, which passes close by the outer border of the thyroid, and is connected with the submaxillary lymphatic glands, is greatly distended with lymph. This is not the case on the left side. Query : Has section or stimulation of the cervical sympathetic increased the transudation (secretion) of lymph in the region supplied by it?

Traced fine branches of right superior laryngeal nerve down to the entrance of the thyroid artery into the right lobe. No doubt that these fibres enter the thyroid gland with the artery. But there seemed to be more fibres around the artery within the gland than could possibly have come from the slender branches of the superior laryngeal.

Fig. 1 shews the arrangement of the veins in this case.

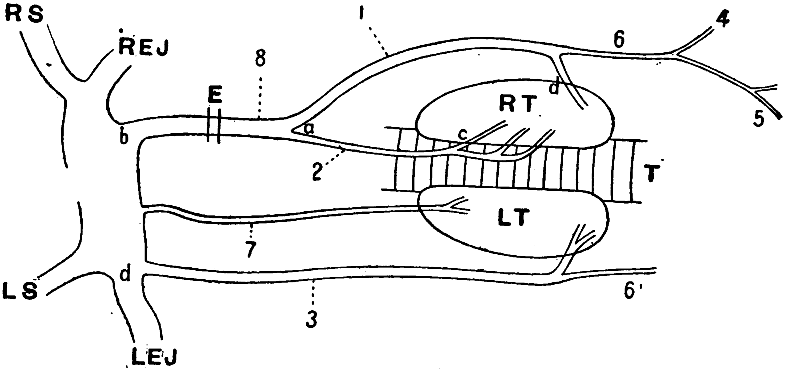

FIG. 1.

T, trachea. *RT*, *LT*, right and left thyroid lobes. *RS*, *LS*, right and left subclavian veins. *REJ*, *LEJ*, right and left external jugular veins. *E*, position of electrodes on 8, the right internal jugular vein below thyroid. 1 and 2, the veins which unite to form 8. 6, 6′, the continuation of internal jugular vein above thyroid—very small compared with 1, 2, or 3. 4, small vein from submaxillary lymphatic glands. 5, internal jugular coming from skull—very small. Internal jugular on left side is represented by two separate veins, 3 and 7.

Distance from *b* to *a*, 4 cm.

Distance from *a* to *c* along vein 2, 1·5 cm. (The figure is not intended to represent the relative length of the vessels, and is not drawn to scale.)

Distance from *a* to *d* along vein 1, 3·6 cm.
,, heart along superior cava to *b*, 3·5 cm.
,, heart to origin of right carotid, 2·8 cm.
,, electrodes on carotid to origin of superior thyroid artery, 6·5 cm.
,, origin of thyroid artery to thyroid gland, 0·7 cm.
,, electrodes on carotid to origin of carotid, 2·8 cm.
,, point of cannula in *LEJ* to *d*, 3 cm.

In this experiment, stimulation of the peripheral end of the right superior laryngeal nerve had no effect on the circulation time of the corresponding thyroid lobe. (Since branches of this nerve may be traced into the gland, entering it with the superior thyroid artery, and seeming more conspicuous than any of the pharyngeal twigs, it seemed worth while to see whether fibres capable of influencing the vessels were contained in them.)

The mean of three readings of venous circulation time during stimulation of the peripheral end of the superior laryngeal is 8·95″, that of seven readings without stimulation, 8·9″; while the average of six readings of arterial circulation time without stimulation is 3·3″, and of two during stimulation, 3·55″. That the apparent small excess of arterial circulation time during stimulation is not real, but almost certainly due to the small number of observations from which the average is drawn, is shewn by the "dummy" experiment unconsciously performed between 6.20 and 6.33 o'clock. Here the average of four observations marked "Stim.," but in which there was really no stimulation, is 3·45″, while the average without stimulation is, as before, 3·3″.

As we might expect, since stimulation of the peripheral end of the superior laryngeal does not affect the circulation time, stimulation of the sympathetic is still effective after section of that nerve.

Thus, the average of four observations of venous circulation time on the right side with stimulation of the cephalic end of the right sympathetic below the level of the thyroid, after section of the right superior laryngeal nerve, is 11·75″; that of five readings without stimulation, 7·65″, a difference of 4·1″. The mean of two readings of arterial circulation time during stimulation is 3·6″, and of the same number without stimulation, also 3·6″. In this case the (uncorrected) thyroid circulation time is 4·05″ without stimulation, and 8·15″ during stimulation. In other words, it is doubled during stimulation.

Passing up to the other end of the cervical sympathetic, we find that stimulation of its cephalic end just below the superior cervical ganglion also causes an increase in the circulation time of the thyroid lobe of the corresponding side.

In Experiment 2 the right sympathetic was isolated below the superior cervical ganglion, cut, and the cephalic end stimulated.

The average of three readings of venous circulation time during stimulation was 9·05″, and of two readings without stimulation, 6·6″. All these readings are marked, and, therefore, specially trustworthy. The clear difference is 2·45″; and the (uncorrected) thyroid circulation time is increased by 80 °/₀ during stimulation.

In one of the readings with stimulation, taken at 8.6 o'clock, the circulation time is only 7·3″; but it is of interest that here the stimulation had been kept up for two minutes; and there is little doubt that the fibres the excitation of which can increase the circulation time were in this case getting exhausted.

Exhaustion is sometimes indicated very strikingly by the movements of the image during stimulation. A second or two after stimulation has commenced (*i.e.* after a distinct latent period), the image (we are now supposing the electrodes to be on the internal jugular of the corresponding side) begins to move in the direction of increased electrical resistance of the vein. But if the stimulation is long kept up, the deflection may reach a maximum, and the image slowly fall back again towards its original position.

The slowness with which the deflection following injection of the salt solution during stimulation begins is important auxiliary evidence of increased vascular resistance.

Experiment 3 is an example of the want of effect of stimulation of the central end of the vago-sympathetic below the level of the thyroid, after section of the other vago-sympathetic, on the circulation time of the thyroid lobe of the opposite side, in a case in which a distinct isthmus was present. I do not think it is a waste of space to quote such experiments, for although the result is what might be expected, they afford a valuable control of the positive experiments.

EXPERIMENT 3. Young dog, about 6 months old, 2030 grams. 30 mg. morphia hydrochlorate subcutaneously. Cannula in right external jugular vein. Left internal jugular exposed above and below thyroid gland. Left carotid exposed in same situations. Vago-sympathetic isolated on both sides below thyroid.

20 mg. curara subcutaneously. Artificial respiration. In the course of the experiment 30 mg. curara injected into blood.

Ligatured both vago-sympathetics.

Distance of electrodes on internal jugular below thyroid, 3 cm. from junction with external jugular, and 2 cm. from level of lower end of thyroid gland.

Distance of electrodes on carotid below superior thyroid artery, 1·5 cm. from origin of latter, and 6·5 cm. from origin of carotid.

Distance of ligature on cephalic end of left sympathetic from upper end of inferior cervical ganglion, 2 cm. Distance of ligature on central end of right vago-sympathetic from inferior cervical ganglion, 2 cm.

Distance from point of cannula in right external jugular from its junction with subclavian, 3·5 cm.

Time		Vascular tract	Circ. time	Galvanom. reading	Max. deflec.	Notes
6.51		Right ext. jug. to left int. jug. below thyroid	8·9″*	223—352	129	The left internal jug. was previously ligatured opposite the thyroid gland and just below the entrance of the sup. thyroid vein, (which in this case was very small) so that all the blood from the left thyroid, and no other blood, passed the electrodes on the int. jugular.
.53		”	9·1*	823—967	144	Altered box. The deflections are now very distinct, and unusually large for "double capillary" obs.
.58	Stim.	”	9·1*	235—318	83	Central end of right vago-symp. on stimulating electrodes.
7.1		”	9·05*	112—213	101	
						Moistened nerve and put a fresh piece of it on electrodes.
.7	Stim.	”	9·3	—	—	
.9	Stim.	”	8·1*	181—277	96	
.11		”	8·65*	68—177	109	Rectum 34·6°.
						Moistened vein; altered box.
.18		”	8·5*	403—538	135	
						Cephalic end of left symp. put on stimulating electrodes.
.28		”	8·4	232—378	146	
.35	Stim.	”	9·6	402—463	61	
.37	Stim.	”	11·8	590—652	62	
.39		”	11·3	701—792	91	
.41		”	11·1	790—900	110	Box 1030.
.46		Right ext. jug. to left carotid just above origin of thyroid artery	4·15*	337—392	55	
	Stim.	”	4·15*	341—391	50	
.49		”	4·1*	342—393	51	
						Put central end of right vago-symp. on stimulating electrodes.
.53	Stim.	”	3·35	371—427	56	
.54		”	3·9	362—422	60	
.56	Stim.	”	3·9	373—427	54	
.57	Stim.	”	4·35	368—431	63	Rectum 34·3°.

The arrangement of the veins is shewn in Fig. 2.

In Experiment 4 we have an instance of the venous circulation time of the right thyroid falling from 10″ (average of four readings), before section of the right sympathetic, to 7·7″ after section; stimulation of the cephalic end of the same nerve below the gland at a later period in the experiment did not cause any distinct increase of the circulation time. The experiment is not a very good one, because in the heat of observation I did not give sufficient attention to the fact that the temperature of the animal was rising and the circulation time consequently falling; and I mention this to shew the importance of controlling the temperature.

Still there is something in the anatomical relations of the veins in this experiment which seems to be, partly at least, responsible for the result, and even goes far, I think, to raise the latter to the high if somewhat perilous dignity of "the exception which proves the rule." For this was one of the cases in which a big vein ran down on the trachea in the middle line, collecting blood from both lobes of the thyroid, and falling into the internal jugular above the position of the electrodes.

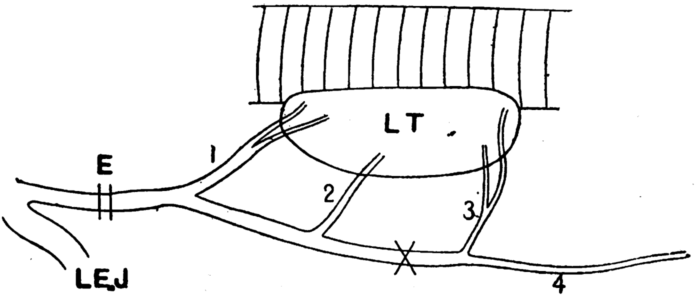

FIG. 2.

E, position of electrodes on left internal jugular vein. 1, 2, 3, veins from left thyroid lobe—3 is very small. *X*, position of ligature.

4, internal jugular vein above thyroid, very small.

Section of the right sympathetic, diminishing the vascular resistance in the right lobe, would allow of salt coming sooner through by that route than before; and this would not be affected by the vascular resistance remaining unchanged in the other lobe, for the beginning

EXPERIMENT 4. Dog, 3500 grams. Put under morphia for operation. Cannula in left external jugular. Exposed right internal jugular and right carotid below thyroid. 20 mg. curara into blood, as animal could not be got properly under morphia. Artificial respiration. Isolated right vago-sympathetic below thyroid and separated vagus from sympathetic.

Time		Vascular tract	Circ. time	Max. deflect.	Notes
2.42		Left ext. jug. to right int. jug.	9·75	—	2 c.c. 4 $^0/_0$ NaCl injected in all this exp. except where otherwise mentioned.
.46		,,	10·7	—	Rectum 37^0.
.48		,,	9·25*	41	
.50		,,	10·25*	61	
	Cut right symp. below thyroid				
3.20		,,	8·2	53	
.22		,,	8·15	—	

Time		Vascular tract	Circ. time	Max. deflect.	Notes
3.24		Left ext. jug. to right int. jug.	7·7	—	
.27		”	7·7*	—	
.31		”	6·85	48	
.38					Rectum 37·95°. Set up electrodes again, as some polarisation.
4.20		”	7·3*	88	
.25		”	8·05*	54	Box 900.
.34		Left ext. jug. to right carotid	5·35*	36	
.35		”	5·3*	29	Rectum 39·1°.
	Cut right vagus below thyroid				
5.49		”	4·35	—	
.51		”	3·9*	25	Rectum 39·7°.
.53		”	3·75*	41	
					Put central end of right vagus on stimulating electrodes.
.57	Stim. (15)	”	3·25	47	
.59		”	3·35	39	
6.0	Stim. (11·5)	”	3·35	39	
.3		”	3·4*	42	
.8		Left ext. jug. to right int. jug.	6·25	37	
.9		”	7·75	29	
.15		”	6·5	43	
.20		”	6·1	26	Central end of right vagus still on stimulating electrodes.
.21	Stim. (11·5)	”	6·1*	34	
.23	Stim. (7)	”	7·7	19	Unsteady.
.26	Stim. (7)	”	6·5*	42	
.28		”	5·85	—	
.30		”	5·8*	30	
.35	Stim. (5)	”	5·9	—	
					Cephalic end of right sympathetic put on stimulating electrodes.
.46		”	6·1	35	
					20 mg. curara injected into blood.
7.0		”	6·15		In this observation 4 c.c. of the NaCl sol. were accidentally injected instead of 2 c.c.
	Stim. (8)	”	5·7	31	
.4		”	4·2*		These obs. were taken after stim. was stopped, the first one being taken immediately after.
.5		”	5·15	29	
.8		”	5·95	21	
.12	Stim. (8)	”	5·5	28	
.14		”	4·7	26	
.19		”	5·7		
.21	Stim. (8)	”	5·7*	15	
		”	5·3	18	This obs. taken immediately after preceding one.
					Rectum 40°.
.31		Left ext. jug. to right carotid	2·75	28	
					Now moistened artery on electrodes and readjusted box.
.35		”	2·7	6	Rectum 40·1°. Pulse 211 per min. The high temp. has very greatly increased it.

Animal died suddenly at 7.55. Blood stream failed all at once in the carotid. The temperature in the rectum 10 minutes later was 40·2°.

of the deflection would correspond to the circulation time of the shorter path. But stimulation of the cephalic end of the right sympathetic, although it increased the vascular resistance in the right lobe, would, leaving it unaffected in the left lobe, not increase the apparent circulation time. For salt would still be able to come through the freer path of the left lobe, and would cause a deflection the time of commencement of which would correspond to this path.

The arrangement of the veins is shewn in Fig. 3.

Distance from cannula to *a*, 2·6 cm.
,, *a* to *b*, 1·8 cm.
,, *b* to heart, 1·7 cm.
Distance of electrodes from *c*, 2·5 cm.
,, electrodes from lower border of right thyroid lobe, 2·5 cm.
,, *c* from heart, 2·8 cm.
,, electrodes on right carotid from heart, 5 cm.
,, electrodes on right carotid from origin of thyroid artery, 4 cm.
Length of right thyroid artery, 1 cm.
No distinct thyroid isthmus was present.

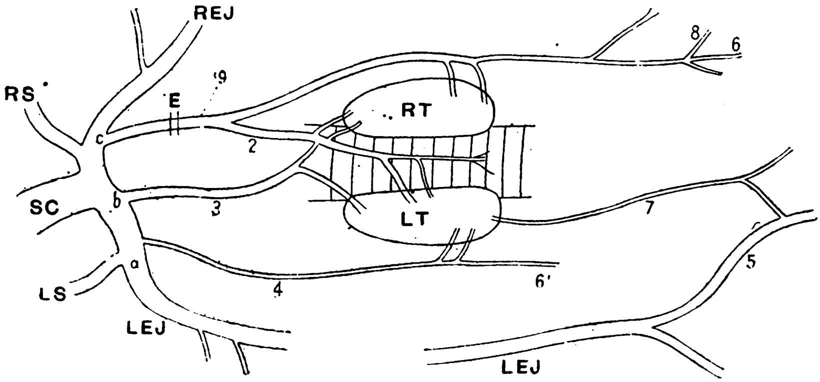

FIG. 3.

REJ, *LEJ*, *RS*, *LS*, *E*, same as in Fig. 1. *SC*, superior vena cava. 1 and 2, the branches which form the internal jugular, 9, below the thyroid. 9 is larger than usual. 2 receives branches from both thyroid lobes; it is a large vein. 3 is a vein which communicates both with 2 and with the left lobe and opens separately. It conveys most of the blood from the left lobe.

4 is a vein in the usual position of the left internal jugular, but it is very small; 6′ is its upper continuation.

5 is the left vena maxillaris externa. It receives a long thin vein, 7, from the upper part of the left thyroid lobe. 6 is the small continuation of 1 above the thyroid to skull. 8 is a small vein which communicates with the right external maxillary vein.

The above paper is based on experiments made by the author, while holding the George Henry Lewes Studentship, in the Physiological Institute at Strasburg. The results were embodied in a report to the Government Grant Committee of the Royal Society, dated March 22nd, 1892. The paper formed part of a Thesis sent in for the Goodsir Memorial Prize in the University of Edinburgh, April 30th, 1892, of which an abstract was read before the Physiological Society, June 25th, 1892.