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THE BLOOD-PRESSURE IN THE EYE AND ITS
RELATION TO THE CHAMBER-PRESSURE

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(Continued from p. 26)

IN the first part of this article certain physical principles essential to the study of blood-pressure were demonstrated by experiment. In accordance with these principles and with anatomical and physiological data, a schematic line was laid down to represent in a general way the fall of pressure suffered by the blood in travelling from the left ventricle to the right auricle. It was shown that such a line can be true only in a general sense because different blood-circuits would give different pressure-lines and the line for any one circuit would vary with contraction and dilatation of the vessels.

The next step is to test this schematic line by comparing it with actual measurements of blood-pressure in different regions. The test cannot be a very rigid one because, apart from physiological variations, different observers have arrived at different results. Moreover, the instruments employed for this purpose do not tell us exactly what we want to know; they raise the lateral pressure of the blood-stream in the act of measuring it. In clinical work, where the object is to compare the pressure in an individual with

the normal average rather than to learn its absolute value, this source of error is probably of small importance; in an enquiry like the present it cannot be disregarded. The methods must be considered.

In measuring the blood-pressure in an artery of an animal it is usual to divide the vessel transversely and to bind the central end on to the canula of a manometer. The column of mercury or other liquid rises or falls until it balances, and so measures, the pressure of the blood. The flow through the artery is thereby stopped. Between the manometer and the point where the artery leaves its parent trunk or gives off its last branch, the blood-column, though receiving a pulsatory impulse, has no onward flow. The indicated pressure is that of the arrested blood column, not that which was present in the vessel when the blood was moving. It is higher. This is easily demonstrated.

FIG. 25

Shows the effect of closing one branch of a bifurcating tube.

Tube T (Fig. 25) consists of an afferent trunk and two equal-sized branches. In each branch a short length of rubber tube is introduced on the distal side of the point *d*, so that either branch can be closed here by pressure from without. When both branches are open the lower pressure-line is obtained. When one branch is closed the trunk and the closed branch give the upper line. It is pushed up because the total resistance in the tube is now greater than before, the driving-force remaining the same. Over the trunk the upper line slopes less steeply than the lower because the velocity here is now reduced; over the branch it is horizontal because the water here is now stationary. For the open branch we get the broken line: it is steeper than the corresponding part of the original line because the velocity here is now increased. When both branches are closed the line (not shown in the chart) is pushed up to the level of the water in the cistern; it is horizontal throughout because the water is stationary throughout. Suppose this tube to represent an artery

having two equal branches, and the lower line in the chart to represent the lateral pressure of the undisturbed blood-stream. Now suppose one branch to be severed at *d* and tied on to a manometer. The pressure at *d* will rise; the reading obtained, if regarded as a measure of the pre-existing pressure at this point, will be erroneous. It will not even be true for the pre-existing pressure in the trunk above the bifurcation, for the pressure in the trunk is itself raised by the closure of the branch. The amount of the error will be represented by the vertical distance between the upper and lower pressure-lines over the point *d*, and will depend on several circumstances:—

It will depend on the steepness of the normal pressure-line in the region in question. Since the pressure falls more quickly in small vessels than in large, and in short circuits than in long, the errors will be greater in small vessels and in short circuits, provided that equal lengths of the blood-stream are immobilised in the several cases.

It will depend on the length of the immobilized blood-column, i.e., the distance between the cut end of the artery and the last point of branching, for the normal pressure-line for this region would slope downward whereas the manometric is horizontal. Thus in the case of Tube T, if the manometer were placed at *c* instead of *d*, the error would be smaller, while if it were placed at *e* the pressure-line would be lengthened and the error would be greater.

Again, it will depend on the relative capacities of the occluded channel and of the channel or channels remaining open to the

FIG. 26

Shows the effect of closing one or more of several branches.

blood. Tube U (Fig. 26) has four equal branches. When all are open we get the lower pressure-line; when one is closed we get the middle line; when three are closed, the upper line.

And again, it will depend to some extent on the angle at which

the occluded branch springs from the parent trunk. If at a right-angle, then the pressure of the stationary blood will equal the lateral pressure of the moving stream, as in our experimental apparatus. If at a slope in the forward direction, then the stationary blood will bear not only the lateral, but also a part of the forward pressure, and accordingly will be pushed up somewhat more.

Moreover, our experiment omits a factor which is often present in the case of the blood-stream. When we close a branch in our artificial system the driving force remains unaltered, and the increased resistance leads to a proportionate reduction of the output from the cistern. On the other hand, when a large artery is closed, the driving force of the heart usually increases—a purposive reaction tending to maintain the previous output—and a rise of pressure additional to that here demonstrated takes place.

FIG. 27

Pressure-chamber by means of which known degrees of external pressure can be applied to a compressible tube transmitting a stream of water.

The air-bag sphygmometer errs in like manner. In Lockhart Mummery's well-known experiment⁵ the canula of a mercurial manometer was tied into the right femoral artery of a dog, and at the same time a sphygmometer having a special narrow cuff was applied to the animal's left thigh. The sphygmometric reading was taken at the moment when the pulse became imperceptible in the

popliteal or posterior tibial artery. Three dogs were examined in this way. Ten pairs of simultaneous readings were recorded, and in only one instance did the two instruments differ by more than 2 mm. Hg. The agreement shows, of course, not that these instruments are capable of measuring the normal blood-pressure correctly, but that in so far as they err they are likely to err about equally.

The following experiments exhibit the kind of way in which the armlet of the sphygmometer disturbs the pressure in the vessels it compresses. Fig. 27 shows an arrangement in which a portion of our usual horizontal glass tube was replaced by a piece of pigeon's gut. Surrounding the gut was a glass chamber with two outlets, one connected with an adjustable reservoir, the other with a graduated vertical tube showing the pressure in the chamber. By this means we could subject the membranous tube to any desired external pressure, and observe the effects on a stream of water flowing through it. Obstruction of the flow was shown by changes of pressure at *a* and *b*, by diminished outflow, and by alteration in the contour of the gut. To understand the latter, one must realize that even in this short length of gut the lateral pressure is lower at the distal than at the proximal end.

FIG. 28

Represents pressure-changes induced by progressive compression of an artery without compression of the corresponding vein.

In Tube V (Fig. 28) a chamber of this kind was placed about midway along the proximal half. When the chamber-pressure stood at 0, the long heavy pressure line was obtained. The pressure in the gut would then be about 15 c.m.—i.e., a little above the mean of the pressures at *a* and *b*, for the lumen of the gut was greater than that of the glass tube. The chamber-pressure was raised step by step, 2 cm. at a time. When it reached 16 cm. it began to affect the flow through the tube; the gut showed slight compression at its distal end, the pressure-line was altered, the

outflow was reduced ; at 18 and 20 cm. these changes became more pronounced. The three thin lines were obtained with chamber-pressures of 16, 18 and 20 cm. respectively ; the dotted part of each is inferential. At 22 cm. the flow almost stopped ; at 24 cm. it stopped completely, the gut being completely closed. The pressure-line (upper heavy line) was then horizontal, standing like the water in the cistern at 23 cm.

If the air-bag of the sphygmometer could be so applied as to compress an artery without compressing the corresponding vein, the pressure-changes induced would be of the kind seen in Tube V ; during gradual compression of the artery the blood-pressure would rise more and more in the region above the bag, and fall in that below it ; at the moment of occlusion the pressure above the bag would equal the air-pressure in the bag. But this illustration is not quite satisfactory, for a distended artery has more elastic resilience than a distended gut, and for this reason external pressure would find a stronger auxiliary in the wall of the artery than in that of the gut, and the lumen of the artery would begin to diminish under a relatively lower external pressure.

But the air-bag as ordinarily used compresses veins as well as arteries, and except for some difference in their embedding, the two sets of vessels are subjected to the same degree of external pressure. Their relation to the armlet might therefore have been imitated by turning the tube round upon itself in the half-way region, leading it back through the same compression-chamber, and placing a second piece of gut alongside the first, but it was simpler to place a second chamber in the distal half of the tube and to make equal pressures in the two ; the principal is the same.

FIG. 29

Represents pressure-changes induced by the armlet of the sphygmometer.

Tube W (Fig. 29) shows what happened when increasing external pressure was applied equally at corresponding parts of the proximal and distal halves—representing the air-bag pressing equally

on arteries and veins. As before, the pressure was raised step by step. When it stood at 0 the pressure-line was almost identical with that of Tube V. The pressure in the distal gut would then be about 7 cm. As was to be expected, disturbance of the flow now began when the chamber-pressure reached 8 cm.; the distal gut showed compression at its distal end, the pressure-line was altered, the outflow was diminished. At 12, 16, and 20 cm. we got respectively the three thin pressure-lines, and the outflow progressively diminished. So far the proximal gut showed no sign of compression; not until the chamber-pressure rose nearly to 24 cm. was it noticeably altered; then it collapsed and the outflow stopped completely.

With these results in view one can easily realize what happens when the air-bag of the sphygmometer is placed round the arm or fore-arm and *slowly* inflated. As soon as the air-pressure in the bag exceeds the blood-pressure in the underlying veins it begins to reduce their lumen in that situation. It does not close them because the venous pressure below the air-bag, being driven up by the oncoming blood, rises with the external pressure. Below the armlet the pressure is driven up in all the vessels—most in the veins, less in the capillaries, least in the arteries—and so tends towards a common level. Above the armlet, while the arterial pressure rises, the venous falls. As soon as the air-bag pressure exceeds the diastolic pressure in the artery the vessel collapses during the diastole, and refills during the systole; when it exceeds the systolic pressure the vessel remains closed. The stationary arterial blood above the armlet has then the same pressure as it would have if the vessel were severed and connected with a mercurial manometer. By inflating the armlet *rapidly*, it is possible to close the artery before the capillaries and veins have had time to become greatly overfilled; and so to avoid painful congestion of the limb.

The object of this digression, the reader may need to be reminded, was to demonstrate that the manometer and sphygmometer raise the blood-pressure in the act of measuring it. Let us now turn to actual readings, and first, to certain remarkable observations published by Poiseuille in 1826⁶. They are sometimes cited, I think, with insufficient reserve.

Working with the U-shaped mercurial manometer invented by himself, Poiseuille investigated the pressure in the larger arteries in a number of dogs and a horse. Using two manometers simultaneously he connected them with different arteries by means of glass tubes filled with salt-solution, and so compared the pressures in different regions. The arteries compared were the common carotid and the brachial, common iliac and brachial, carotid and crural (=femoral of man), carotid and aorta, carotid and renal, axillary and crural, and in the horse the carotid (diam. 10 mm.) and a branch of the crural (diam. 2 mm.). In every instance a

series of readings was taken and the average was struck. In every instance, so far as the record goes, the average pressures at the two points compared were equal. He concluded that "the force with which the blood is driven from the heart retains the same intensity throughout the arteries as far as their smallest ramifications." This conclusion is irreconcilable with well-established laws. Where did the fallacy lie?

Wishing to test Poiseuille's results and knowing the difficulty of making accurate comparisons with separate instruments, Claude Bernard⁷ devised a differential manometer which brought the two ends of a single U-shaped mercurial column into connection with the two arteries to be compared; preponderance of pressure in either artery displaced the mercury and was thereby measured. He found that in fellow arteries, e.g., the carotids, the pressures were equal, while in different arteries, e.g., the carotid and the crural, the pressure was higher in the vessel nearer the heart. But on experimenting further with an instrument which showed the rise and fall occurring with each heart-beat, which apparently Poiseuille's did not, he found that the difference between the carotid and the crural pressures was much greater at the moment of maximum than at that of minimum pressure—it belonged to the systole rather than to the diastole.

Further it is important to notice that the smallest artery Poiseuille tested had a diameter of 2 mm., whereas the chief fall of pressure takes place in smaller vessels still. Also that the pressures he observed were not normal pressures; they were raised by the arrest of the blood-stream, and being raised would be more nearly level with each other and with the aortic pressure than are the normal pressures. And after all, even if the mean-pressures in such arteries as the carotid and the femoral *were* proved to be equal or nearly so, this would not justify Poiseuille's conclusion even for the larger arteries. The carotid and the femoral belong to different circuits one longer than the other, but these circuits have identical end-pressures, aortic and caval. Assuming that they are destined to supply their respective capillary areas with blood at about equal pressures, we should reasonably look for equal arterial pressures not at *equal*, but at *proportional*, distances from the heart. But such equality, if proved, would tell us nothing of the fall occurring between the heart and these arteries. To ascertain the form of the pressure-line we must know the pressures at different distances from the heart in one and the same circuit, and it is the mean pressure that we want to know.

What is the mean pressure in the *arch of the aorta*? Since the innominate and common carotid arteries spring from the aorta at right angles, a mercurial manometer applied to either of these branches would show the aortic pressure correctly, were it not that

obstruction of so considerable a branch must raise the pressure in the trunk (see Tube T). In an animal thus tested the normal pressure in the aorta must be rather lower than that indicated by a manometer applied to the innominate or common carotid artery. In healthy young men the average mean aortic pressure is estimated by Leonard Hill⁸ at 120 mm. Hg., or a little more, on the supposition, apparently, that it cannot be much higher than the brachial pressure. It increases with age, and some authorities put the normal average a good deal higher, but to run no risk of over-estimating it, let us take it as 120 mm. Hg. in healthy young men.

In the *brachial artery* of healthy young men Leonard Hill—using the armlet-sphygmometer, and taking the maximum oscillation of the pointer as his indication—found mean pressures varying from 110 to 130 mm. Hg.: say, average about 120, and from this something may be deducted on account of the arrest of flow. George Oliver's figures⁹ give a lower average: about 108 mm. Hg. according to his earlier measurements; about 95 when the auditory method of determining diastolic pressure had been adopted. These figures are not expressly given by him, but represent the half-way between the mean of his diastolic and the mean of his systolic pressures in the young adult.

Between the *upper arm* and the *forearm* Oliver could detect no fall of pressure. Between the *wrist* and the *first phalanx* of the finger, a much shorter distance, he found a fall of 5 to 15 mm. Hg., *i.e.*, to 90 or 85 mm. Hg. Why this sudden step downward, instead of an even descent? Possibly it was more apparent than real. In the fore-arm, where there are two bones, the arteries are said to be rather less accessible to the pressure of the air-bag than in the upper arm, where there is only one. If this be so, they may need the same degree of bag-pressure for their occlusion, although their blood-pressure is a little lower. As to the fall at the wrist, it is worth noting that an air-bag round the wrist obstructs the whole of the blood-supply to the fingers, whereas one round a single finger obstructs about one-fifth of it; the pressure may therefore be more pushed up at the wrist than at the finger (see Fig. 26).

In the *second and third phalanges* of the finger, Oliver found a rapidly-increasing fall; the pressure in the *ungual phalanx* was rather less than half that in the brachial artery, *i.e.*, somewhere about 50 mm. Hg.

In the *cabillaries of the finger* von Kries¹³ measured the pressure by laying a small glass plate of known area on the pink skin at the root of the nail and weighting it progressively until the skin grew pale. On a level with the heart, in the sitting position, it appeared to be about 38 mm. Hg., *i.e.*, nearly one-third of that in the aorta. But the method is not very trustworthy, for since the cuticle has

some rigidity, the pressure of the plate is not accurately confined to the area it covers, and since this area is small the error so arising may be considerable. Oliver measured capillary pressure by noting the height above the apex of the heart at which the matrix of the nail grows pale. The height in inches multiplied by 2 gives an approximate equivalent in mm. Hg. It was found to vary much with the temperature of the hand, and with degrees of muscular effort; in the sitting position, when the hand was warm, it was commonly from 25 to 30 mm. Hg.

In the *dorsal veins of the hand* Oliver measured the pressure by the same method. The hand is raised gradually and the observer notes the height at which the veins visibly collapse—a method obviously good in principle, but applicable only if the veins are fairly prominent. In the sitting position the pressure was commonly 15 to 20 mm. Hg.

For the pressures in the *larger veins* we have to look to experiments on animals. In a sheep, during normal quiet respiration, Jacobson¹¹ found 9 mm. Hg. in a branch of the brachial vein; 4 in the brachial itself; and amounts hardly distinguishable from 0 in the subclavian, jugular and innominate. In these latter, and in the main trunks near the heart, the pressure is negative during inspiration, positive during expiration, and on the average probably not far from 0.

These figures, though wanting in precision, suffice to show that a pressure-line for the circuit in question would bear a general resemblance to the one we arrived at by other means for the bloodstream as a whole. Thus they show a slight fall in the region of large and middle-sized arteries, a much greater fall in the region comprising arterioles, capillaries, and veins, and again only a very slight fall in the middle-sized and large veins. Speaking roughly, they show a fall of about 30 mm. Hg. between the aorta and the base of the finger, 70 or 75 in the finger itself, and 15 or 20 between the base of the finger and the vena cava. They agree with our schematic line in placing the average capillary pressure at something between one-fourth and one-fifth of the aortic, though on this last point no stress can be laid, for capillary pressures vary greatly. Perhaps our original line (Fig. 24) falls rather too quickly in the first third of its course. In Fig. 30 it is a little modified in that respect, and the pressures are shown in mm. Hg. instead of percentages of the total fall.

The general form of the line (Fig. 30) finds a rational explanation when the requirements of the body are considered. The blood performs its essential work in a very small part of each circuit; the minute channels near the half-way point are its place of business, the larger tubes merely carry it to and fro. But in this small part great variations of supply are needed, e.g., for temporary activity in

a secreting gland, for repair of a lesion, or for defence against an irritant, and it is just because the pressure of the blood is maintained at a high level so far along every arterial path that dilatation of small vessels can greatly increase the volume and the pressure of

FIG. 30

Schematic pressure-line of blood-stream in a long and a short circuit.

the blood in a limited area that needs it, without disturbing the flow in neighbouring regions that do not. High pressure is everywhere near at hand. Did the pressure of the blood-stream fall evenly from aorta to vena cava—as it might do if the dimensions of the channels were adapted to that end—this isolated flooding of small areas would be far less possible than it is.

The steepness of the line, as already said, varies with the path taken; the shorter the path the steeper the line. A particle of blood that is carried from the left ventricle to the right auricle through the coronary vessels, travels perhaps one-tenth as far as one that goes by way of the arm and finger tips, yet the fall of pressure is the same in the two cases for the end-pressures are the same. Hence if the continuous line in Figure 30 is fairly true for the longer circuit the dotted line will be so for the shorter.

One is apt to imagine that capillaries remote from the heart, e.g., those of the finger-tips or nose, have, *by reason of their remoteness*,

FIG. 31

A long and a short circuit with equal pressures at the half-way points.

a lower lateral blood-pressure than those lying nearer to it, but the idea is ill-founded. It is easy to show that in circuits having the same end-pressures the halfway pressures are independent of the distances travelled. In Tube X (Fig. 31) the water passes from

A to V by two paths, one longer than the other. The trunks A and V are equal: the branches a, a', v, and v', are all of equal diameter, and in each case the aggregate cross-section of the two branches equals that of their stem. The pressures are measured at A, V, c and c'. Under a certain driving force the pressures at A and V were respectively 18 and 6 cm., and in each circuit—as was to be expected—the half-way pressure was equal to the mean of the end-pressures, viz., 12cm. We then enlarged the whole of the distal (venous) half of the system so that its cross-section was everywhere double that of the proximal (arterial) half: the half-way pressures were then of course no longer equal to the mean of the end pressures, but they were still equal to each other.

This may seem paradoxical. Since the fall of pressure between A and V is the same whichever path the water takes, the resistances in the two circuits must be equal. How can they be equal, it may be asked, when one circuit is longer than the other? The answer is that the velocities are unequal. The stream in the longer circuit is the slower by an amount which equalizes the resistances. But such differences of velocity, it may still be urged, cannot be the rule in the blood-stream, for the needs of the body would not be met if the more distant capillaries had always to accept a slower current than the nearer. No, they are not under that disadvantage. In our tube X we could equalize the velocities at c and c' without disturbing the equality of pressure by increasing the lumen of the tubes a' and v'. And so it is with the blood-vessels; where an artery divides to feed regions at unequal distances it usually divides unequally, the blood for the remoter region being provided with a larger channel. By this means (with adjustments to compensate the effects of gravity) the capillaries in all parts of the body might be supplied with blood under equal pressure and equal velocity were this requisite; in reality differences are required. We know that *temporary* variations are constantly occurring, and there is reason to suppose that different parts need *persistent* differences.

In Fig. 30 the part of the pressure-line relating to the capillaries cannot be differentiated, for whereas the line there shown relates to a circuit of 1,000 mm. or more in length, the length of a capillary is usually less than 1 mm. If it is to be distinguished it must be shown on a larger scale as in Fig. 32. Should this part of the line be steeper or less steep than the adjacent parts? In other words, does the pressure of the blood fall more rapidly or less rapidly in the capillaries than in the arterioles and venules? It is a question of relative resistance. If a group or plexus of capillaries, 1 mm. in length, offers more resistance to the blood-stream than does 1 mm. of the arteriole that feeds them, the line will be steeper over the capillary region (aa), if less, it will be less steep (bb). We know that the lowering of velocity in the capillaries tends *per se* to lower

the resistance, and that the increase of friction-surface tends to increase it, but what is the net result?

Fig. 33 is schematic. It is so proportioned as regards the size and number of the tubes as to offer equal resistance per unit of distance in the several regions. Thus, in travelling 1 mm. through the 16 tubes in region *e* a liquid would encounter the same amount of resistance as in travelling 1 mm. through the single tube *a*, or the two tubes *b*, and so on. The proportions are determined by

FIG. 32

Possible changes in slope of pressure-line over capillaries. Schematic.

the rule: *square the total cross-section in each region and divide by the number of tubes in that region; the products are inversely proportional to the resistances.* Experimental proof that these proportions give the result stated is given by tube *Q* where the four branches bear the same diameter-ratio to the main trunk as do those in Fig. 33 and the pressure line is straight (Fig. 17, page 20).

At first sight this figure suggests a contradiction. The right half is an exact counterpart of the left, and the cross-section at the half-way point is four times greater than at each end; therefore, according to the principle already demonstrated (p. 11) the pressure at the half-way point must be greater than the mean of the end-pressures—the pressure-line must be pushed upwards towards the middle. Yet if the resistances are equal in the several regions the corresponding segments of the pressure-line will slope equally, and it would seem that the whole line should be straight. The paradox

disappears when we regard not only the resistances calculable from the size and number of the tubes, but the additional resistances arising at the points of bifurcation and reunion.

FIG. 33.

A schematic ramification which would offer equal resistance (per unit of length) in each region. The proportions are as follows :—

Region	a	b	c	d	e
Number of tubes	1	2	4	8	16
Diameter of each tube ...	1	0·84	0·71	0·6	0·5
Total cross-section of tubes	1	1·42	2	2·9	4
Velocity	1	0·78	0·5	0·34	0·25
Aggregate resistance ...	1	1	1	1	1

To ensure accuracy the figure was drawn on a much larger scale and reduced by photography.

The steepness of the pressure-line is here reduced for convenience ; it would vary with the velocity of the stream.

FIG. 34.

Proportions as in Fig. 33. Analysis of pressure-line.

By means of Tube Y (Fig. 34) we experimented with a single bifurcation and a single reunion having the same proportions as those in Fig. 33. We had thus a symmetrical system comparable with

Tubes D, E, and F (p. 8), but by measuring the pressures immediately above and below the points of branching we analysed the pressure-line more minutely than before. The two lines shown in the chart were obtained with two different degrees of driving-force; the upper represents a stream disturbed to some extent by eddies, the lower an approximately steady stream. It is evident that the

FIG. 35

Schematic ramification for comparison with branching blood-vessels. Proportions as in Fig. 33. Resistances equal in the several regions.

additional resistance was smaller at *b c*, where the trunk divides, than at *d e* where the branches reunite, although the stream is equally deflected in the two regions. Why this difference? The velocity alters differently in the two regions; the *diminution* of velocity between *b* and *c* tends to counteract the additional resistance due to the deflection, whereas the *increase* of velocity between *d* and *e* supplements it. Proof of this is afforded by Tube D where the branching involves no change of velocity and the additional resistance is the same in the two regions.

Applying this observation to the case of Fig. 33 we may infer that the pressure-line of that system would be of the character there shown, i.e., approximately straight in the proximal half, step-like (or rather sinuous) and somewhat steeper in the distal, and thus showing a half-way pressure greater than the mean.

Fig. 35 reproduces the proportions of Fig. 33 in a form more easily comparable with ramifying blood-vessels. Observe that each stem divides into two equal branches, and that the diameter-ratio of stem to branch is always 1 to 0.84 (approximate); also, that after four bifurcations, whereas the number of tubes is increased from 1 to 16, the diameter only falls from 1 to 0.5.

By comparing these proportions with those of branching blood-vessels it is possible, in favourable situations, to ascertain whether the resistance offered to the blood-stream increases or diminishes as the channels increase in number. In the case of good-sized arteries that bifurcate symmetrically there is no difficulty. We measured stem and branches near to the bifurcation of the following arteries, taking the average diameter of the branches when they were not quite equal; abdominal aorta (two), common iliac (two), popliteal, innominate, small arteries from the surface of the brain, and some from muscles. In every instance the diameter-ratio of stem to branch was greater than that in the schematic figure; it varied from 1 : 0.8 to 1 : 0.6; in other words, in every case the resistance was greater in the branches than in the stem.*

Comparison with arterioles and capillaries is more difficult, partly because of the difficulty of obtaining adequate material, and partly because the free anastomoses of these small vessels upset one's computations. Figure 36 is from an injected preparation. In this specimen the arterioles bifurcate symmetrically in many places, and, as a rule, the diameter-ratio of stem to branch is greater than in the schematic figure, e.g., 1 : 0.75, 1 : 0.66, etc., as in the larger arteries. With regard to the capillaries—better seen in the specimen than in the photograph—precise computation is impossible, but in proportion to their numbers they are certainly small in diameter as compared with Figure 35. Unfortunately artificial injection cannot be trusted to show these small vessels in their natural proportions; in this specimen some vessels are unequally distended in different places and many of the capillaries, though injected, remain too small to admit a blood-corpuscle. One wants to see them injected with their own blood.

Figure 37 shows a group of capillaries in the web of a frog's foot. The frog having been pithed, the web was examined while the blood was still circulating. When the movement ceased a

*In the case of the larger arteries we cut rings from stem and branches a few mm. above and below the fork. Each ring was opened and laid out flat between two plates of glass and measured as to the length of its inner surface; this gave the circumference. In the case of smaller vessels the entire fork stripped of its adventitia was flattened between plates of glass and measured with the micrometer; this gave the external semi-circumference. The diameters were calculated. They were, of course, not those proper to the vessels during life, but the ratio of stem to branch was probably unaltered. In the case of microscopic preparations the measurements were made by projecting the image on to millimetre paper by means of the Leitz drawing-prism, the magnification for each power having been previously ascertained.

FIG. 36

Blood-vessels in sub-mucous coat of small intestine of cat, injected. $\times 36$ diams.
(Specimen from Prof. Carlier's collection.)

FIG. 37

Prism-drawing of capillaries in web of frog's foot, not artificially injected, but containing blood. $\times 60$ diams. The figures show diameters as measured in the specimen.

ligature was applied to retain the blood in the foot, and the part was removed and placed in normal saline with 4 per cent. of formalin; it was mounted in glycerine jelly. The capillaries were of various sizes. Those of about 0.008 mm. diameter contained a single file of well-shaped corpuscles, some smaller ones contained compressed sausage-shaped corpuscles, and a few smaller still were blocked at the ends by corpuscles which had been unable to enter them. All the channels seen in the drawing contained blood. The stem on the left has a diameter of 0.03 mm. Its resistance (per unit of length) would be equalled by that of 8 capillaries of 0.018 mm. diameter, or 16 of 0.015, or 32 of 0.012. It is possible

FIG. 38

Retinal capillaries of a child, six months old—after W. His. Reproduced from Leber's article in the Graefe-Saemisch Handbook, 1903, Vol II, Section ii, p. 14. *Aa*—arteriæ afferentes. *Ve*—Venæ efferentes. The arrows show direction of flow. In the original the artery is coloured red, the vein blue. Here the artery is darker than the vein.

that the stem served a few more capillaries than are here shown, but according to the measurements it is probable that in this membrane, as in the previous example, the capillaries offered a somewhat higher resistance than the corresponding arterioles.

This probability is the greater because the calculation applies to the resistances in a homogeneous fluid, whereas the blood contains particles which make the resistance relatively higher in the smaller

capillaries ; where the corpuscles move in single file and nearly fit the channel, the resistance is relatively greater than where the blood can move like a homogeneous liquid—more rapidly in the axis than at the periphery of the channel.

FIG. 39

Drawing of the retinal vessels in the neighbourhood of the macula lutea, from an injected preparation by H. Mueller. Reproduced from Leber's article in the Graefe-Saemisch Handbook (see above) p. 11. In the original the arteries are coloured red, the veins blue ; here the letters A & V are added to distinguish them. $\times 50$ diams.

Figure 38 shows part of a small artery in the retina giving off at right-angles a series of branches Aa much smaller than itself—three are included in the picture. What are the relative resistances in one of these arterioles and the capillaries it feeds? Here the branches are so little smaller than their stem, and are yet so numerous, that if we may trust the drawing it seems probable that

the arteriole offers (per unit of length) as much resistance as the capillaries, if not more; and this seems probable for other reasons also, when the position of these capillaries is considered. They lie between an artery and a vein much larger than themselves, in other words, between relatively high arterial and low venous pressures—as compared, for example, with the capillaries in the following figure. The pressure-line of the blood that crosses from artery to vein in this place must therefore be comparatively steep, and the velocity in these capillaries, unless it is checked by resistance in the arteriole, must be comparatively high, higher than in the capillaries around the macula, which is not likely. (See description of tube X, Fig. 31.)

Figure 39 shows the retinal vessels in the neighbourhood of the macula. Here there is no sudden fall in size; the arteries diminish gradually as they branch, and there is no evident reason for supposing that the resistance in the capillaries differs greatly from that in the ultimate arterioles. The same impression is received, I think, when the vessels around one's own macula lutea are scrutinised by the pinhole method, or better, perhaps, in the clear field of a microscope while the head is slightly moved.

FIG. 40

Drawing of hyaloid artery, and its branches on posterior surface of lens—from an injected preparation by Lawson Tait. $\times 16$ diams.

Figure 40, drawn from a well-injected preparation of the hyaloid artery and its ramification on the posterior surface of the lens, shows quite exceptional proportions; the stem, which has a diameter of 0.035 mm., divides and subdivides until, near the lens-margin, there are about 70 branches; the majority of these measure about 0.015 mm., some rather less, and some as much as 0.02 mm.; if they all measured 0.015 mm., the resistance in the stem would be to that in the 70 branches about as 2.4 to 1.

This question as to the relative resistances in arterioles, capillaries and venules has been variously answered. Some writers assume that the maximum resistance occurs in the arterioles, some attribute it to the capillaries; one has even placed it in the venules. B. Lewy¹² attempted to solve the problem mathematically, but unfortunately the data he adopted are inadmissible. He assumed, for example, that every artery has two corresponding veins, and that the diameter of each vein is to that of the artery as 1.5 to 1, proportions widely differing from those which exist in the retina and other parts where accurate measurements have been made. The evidence given in the present paper, although scanty, shows, I think, that no sweeping statements on the subject are safe.

When all the factors are considered—the proportions of the channels as to size and number, the increasing frequency of bends and tortuosities towards the half-way point, and the disproportionately high resistance in channels that admit only a single file of corpuscles—the probability seems to be that the blood-stream, as a rule, encounters more and more resistance (per unit of distance travelled) as it sub-divides, and finds the maximum where the channels are most numerous, and where its essential work is done, namely, in the capillaries; but that variations in this respect are present in different parts, and occur in the same part at different times.

There is no reason, then, to deflect the schematic line (Fig. 30) over the capillary region. It reaches its greatest steepness here. At the point, not precisely determinable, but probably near to the middle of the capillary region, where the resistance begins to diminish, its curvature passes insensibly from convexity to concavity. There is no reason to introduce a sudden deflection at any point. Such modifications of the line as different organs or parts may give must be separately studied.

The reader who has persevered so far may suspect that the original purpose of this paper has been abandoned, but that is not so. It appeared indispensable to consider the blood-stream as a whole before attempting to learn its special characters in the eye.

(To be concluded.)

REFERENCES.

5. Mummery, P. Lockhart.—*Jl. of Physiol.*, Vol. 32, p. XXIII, 1905.
6. Poiseuille.—“Recherche sur la Force du Cœur aortique,” Paris, 1828.
7. Bernard, Claude.—“Leçons sur les Propriétés Physiologiques,” etc., Paris. 1859, p. 208.
8. Hill, Leonard.—In Schaefer's *Text-Book of Physiol.*, Vol. II, p. 40, 1900.
9. Oliver, George.—“Studies in Blood-pressure,” London, 1916, also earlier edition, 1906.
10. von Kries.—See L. Hill, as above, p. 116.
11. Jacobson.—See L. Hill, as above p. 120.
12. Lewy, Benno.—“The resistance and fall in the smallest vessels,” *Archiv f. die gesammte Physiol.*, Vol. LXV, 1896.