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THE PHYSIOLOGICAL PRINCIPLE[1] OF MINIMUM WORK APPLIED TO THE ANGLE OF BRANCHING OF ARTERIES.

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In a recent paper[1] it has been proposed that the total work involved in the circulation of blood in a section of artery (sufficiently small so that the pulsating changes in the kinetic energy of the blood stream in it can be neglected as compared to the work required to overcome friction) can be expressed by the equation:

$$E = pf + bvol = \frac{f^2 \cdot l \cdot 8\eta}{\pi r^4} + bl\pi r^2 \qquad (1)$$

which embodies Poiseuille's law of flow and a term which covers the cost of maintenance of blood volume. p is the fall in pressure in dynes/cm.^{2}, b is the cost of blood volume in ergs/cc. sec. (considered constant), *vol* is the volume, r is the radius of the section of artery, and η is the viscosity of whole blood (also taken as "constant"). At constant flow, f (that is, for any given steady state), and at constant length of arterial section, l, the total energy, E, is a minimum when:

$$f^2 = \frac{r^6\pi^2 b}{16\eta} \qquad (2)$$

Substituting for f^2 in the original equation, we obtain:

$$E/l = r^2(3\pi b) \qquad (3)$$

Or, to avoid constants, we may use a different unit for E, and write:

$$(kE)/l = r^2 \qquad (4)$$

[1] Murray, C. D., *Proc. Nat. Acad. Sc.*, 1926, xii, 207.

This equation is a simple deduction from premises discussed at length in the paper referred to.[1] This equation can be used to develop a theoretical law for the angle of branching of arteries, on the assumption that the total work of the circulation is to be a minimum, that is, assuming the validity of equation (4). Let us consider the plan of arterial branching which is most efficient in allowing for the distribution of blood from a point S to two points, A and B (see Fig. 1). r_0, r_1, r_2 are the radii of the arteries; l_0, l_1, l_2, the lengths, and x and y

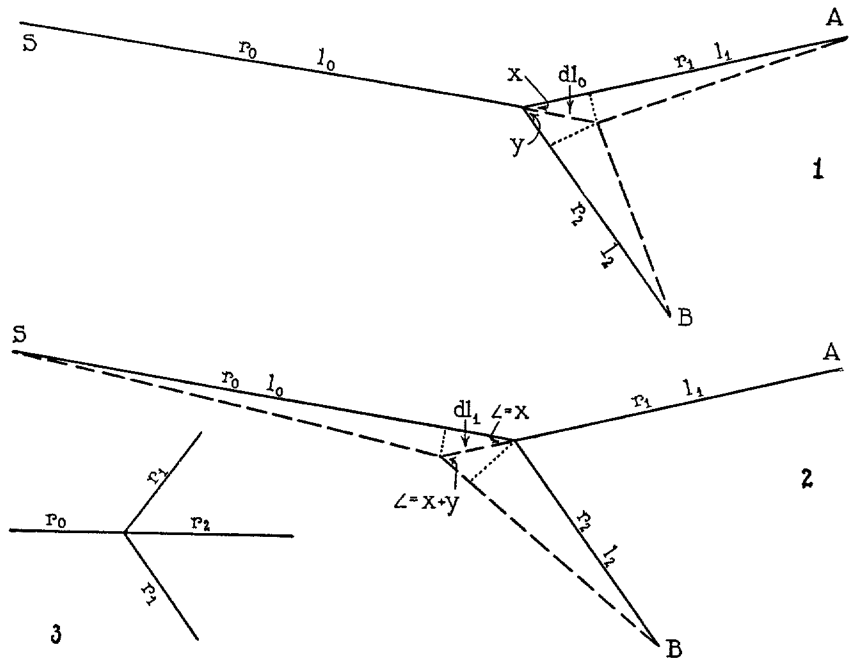

FIG. 1.

are the angles, to be determined, which the branches make with the line of direction of the main artery proceeding from S. Suppose Diagram 1 to represent the condition for minimum work, and then imagine an infinitesimal increment, dl_0, to be added to l_0 (l_1 and l_2 now assuming the positions indicated by the dashed lines). The "cost" (in the tentative unit of kE) of the section l_0 is now increased by the increment $dl_0 r_0^2$, and the costs of the branches are decreased (in this case) by $\cos x\ dl_0 r_1^2$ and $\cos y\ dl_0 r_2^2$ respectively. The dotted lines show the triangles constructed in order to arrive at this result. Two similar constructions (one of them illustrated by Diagram 2, Fig. 1) can be made, representing virtual increments added in turn to l_1 and l_2. By the principle of virtual work in mechanics (which states that, when conditions are such that the total work is a minimum, then a virtual change in the configuration of the system results in no change in the total work) we obtain one equation for each of the three constructions, as follows: (Only two of these equations are independent, since cos $(x+y)$ is a function of cos x and cos y, but the procedure is simplified by taking the three cases.)

$$dl_0r_0^2 = \cos x\, dl_0r_1^2 + \cos y\, dl_0r_2^2$$
$$dl_1r_1^2 = -\cos(x+y)\, dl_1r_2^2 + \cos x\, dl_1r_0^2$$
$$dl_2r_2^2 = -\cos(x+y)\, dl_2r_1^2 + \cos y\, dl_2r_0^2$$

These equations can be divided through by dl_0, dl_1, and dl_2 respectively, and by combining we arrive at the equations:

$$\cos x = \frac{r_0^4 + r_1^4 - r_2^4}{2\, r_0^2\, r_1^2};\ \cos y = \frac{r_0^4 + r_2^4 - r_1^4}{2\, r_0^2\, r_2^2};\ \cos\,(x + y) = \frac{r_0^4 - r_1^4 - r_2^4}{2\, r_1^2\, r_2^2}$$

Since the flow in the branches must equal the flow in the main stem, and since, from equation (2), at maximum efficiency $f = k'r^3$, then it follows that $f_0 = f_1 + f_2 = k'r_0^3 = k'(r_1^3 + r_2^3)$. Thus $r_0^3 = r_1^3 + r_2^3$. Substituting this last relation in the equations for the angles we obtain the final result:

$$\cos x = \frac{r_0^4 + r_1^4 - (r_0^3 - r_1^3)^{\frac{4}{3}}}{2\, r_0^2\, r_1^2};\ \cos y = \frac{r_0^4 + r_2^4 - (r_0^3 - r_2^3)^{\frac{4}{3}}}{2\, r_0^2\, r_2^2};\ \text{or,}$$

$$\cos\,(x + y) = \frac{(r_1^3 + r_2^3)^{\frac{4}{3}} - r_1^4 - r_2^4}{2\, r_1^2\, r_2^2} \qquad (5, 6, 7)$$

two of the three equations being sufficient to determine the plan.

If, instead of dividing into two branches, an artery, after giving off two *equal* branches on opposite sides, continues in its course, the ideal angle made by either branch with the main artery can be determined according to the following equations (see Diagram 3, Fig. 1):

$$dl_0r_0^2 = dl_0r_2^2 + 2\cos x\, dl_0r_1^2$$

$$\cos x = \frac{r_0^2 - r_2^2}{2\, r_1^2} = \frac{r_0^2 - (r_0^3 - 2\, r_1^3)^{\frac{2}{3}}}{2\, r_1^2} \qquad (8)$$

A few scale drawings are presented illustrating the application of the above equations. The equations yield results conforming to certain qualitative laws observed by Roux and quoted in a paper by Hess:[2] for example the rule that the larger the branch the more the

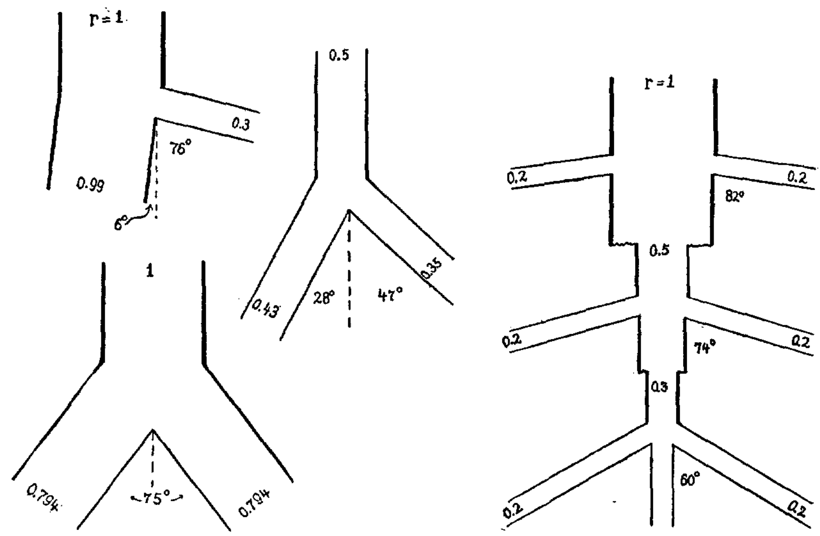

FIG. 2. Scale drawings of arterial branching. The drawings are based on the equations developed in the text, and illustrate the conditions, for free unobstructed branching of vessels, which make the work of distribution of blood a minimum. Values for the radii of the vessels and for certain angles are shown in the drawing. The sum of the cubes of the radii of the branches equals the cube of the radius of the main stem from which they arise. The confluence of veins appears to follow the same rules in a general way.

It is interesting to compare these branchings with branching in trees. (The drawing should be turned upside down for this comparison.) For blood vessels the minimum theoretical angle for a simple bifurcation is 75°, but in trees the actual angle is usually less than this, especially when the bifurcation occurs in a vertical plane and may therefore be supposed to be affected by both helio- and geotropic factors. Another interesting comparison is afforded by results obtained by Miss E. Hendee and Miss M. E. Gardiner in this laboratory. If a tree is cut through at any point of the trunk, of a branch, or of a small twig, the ratio of the weight of the whole part (peripheral to the cut section) to the cube of the radius of the cut section (taking the average ratio observed for each set of branches of similar weight) is a constant. Thus the rule for arteries, $r_0^3 = r_1^3 + r_2^3 + \ldots$, tends to hold also in *small* trees.

[2] Hess, W. R., *Arch. Entwcklngsmechn. Organ.*, 1903, xvi, 632.

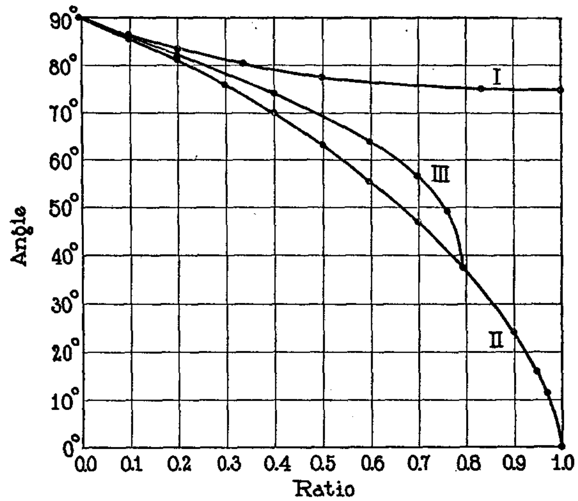

FIG. 3. Curve I shows the relation between the angle $(x+y)$ and the ratio r_1/r_2—the case illustrated by Diagram 1. The curve passes through a minimum when $r_1 = r_2$. See Table I. Note the small variation in the angle of bifurcation, whatever the value of the ratio.

Curve II shows the relation between angle x and the ratio r_1/r_0 (Table II, Diagram 1). Note that the larger the branch the less is the angle made with the line of direction of the main stem.

Curve III shows the relation between angle x and the ratio r_1/r_0 (Table III, Diagram 3). This is the only case considered where the direction of the main artery is unchanged. At the point when the ratio equals 0.7937, this case merges into the one illustrated by Curve II, the continuation of the main stem having been reduced to zero.

TABLE I.

See Diagram 1.

r_1/r_2	$\angle (x+y)$
1	74°.95
2 or 1/2	77°.6
3 " 1/3	80°.3
5 " 1/5	83°.5
10 " 1/10	86°.5
(∞ " 0.0)	90°.0

TABLE II.

See Diagram 1.

r_1/r_0 or r_2/r_0	$\angle x$ or $\angle y$
(0.00)	90°.0
0.20	81°.2
0.40	69°.9
0.60	55°.6
0.80	36°.7
0.90	23°.9
0.95	15°.5
(1.00)	0°.0

TABLE III.

See Diagram 3.

r_1/r_0	$\angle x$
(0.00)	90°.0
0.20	82°.3
0.40	74°.2
0.60	64°.1
0.70	56°.7
0.76	49°.2
(0.7937)	37°.5

main artery is deflected, and the smaller is the angle between the branch and the direction of the main stem before division; and the rule that branches of equal size make equal angles with the same main stem. Anatomically the angles are the variables which can be checked most readily, and it is not necessary here to consider the lengths, which are, in each case, easily determined, if the points have been given and the angles calculated.

An equation for the "ideal" angle for a single branching has been published by Hess, who took as his criterion of efficiency the condition which would make the fall in pressure, between a point in the main artery and a point in the branch, a minimum. He neglected to take into account the conditions in the continuing portion of the main artery, assuming implicitly also that the continuation was in a straight line. Owing to this error Feldman[3] has been somehow misled. He arrives at the result[4] that, as the ratio of the radius of a branch to the radius of the artery approaches unity, the angle of bifurcation should approach zero. He then cites as an instance the small angle between the external and internal carotid arteries. In contrast to this curious result, the rule arrived at in the present paper is that the angle in the bifurcation of an artery should not be less than 75° (74°.9 to be more exact). Miss M. Hardy and Miss M. S. Gardiner, in this laboratory, have prepared a corrosion model of the arterial and venous systems of a cat's lung,—an excellent organ in which to observe free branching of vessels. Examination of this preparation makes it apparent that for every bifurcation angle less than let us say 70° there are hundreds, if not thousands, of cases where the angle is between 75° and 90°, a fact consistent with the limits for the angle $(x+y)$ as given by equation (7). These limits are perhaps the most characteristic results of our analysis. There occur, of course, numerous and important branchings which do not agree exactly with the simple theory, *e.g.* the bifurcation of the pulmonary artery makes too wide an angle, and the common iliac arteries make an angle varying from 60°–75° (Piersol) and therefore preponderantly on the narrow side of the theoretical angle. It would be interesting, in the case of the carotids, to analyze factors of

[3] Feldman, W. M., Biomathematics, London, 1923.
[4] Feldman,[3] p. 172.

differential growth which make this case, and presumably others, singularly exceptional. One more point: in analyzing the minimum properties of physiological systems it seems preferable, when possible, to construct the problem in such terms that the *work* involved in the system becomes a central feature.