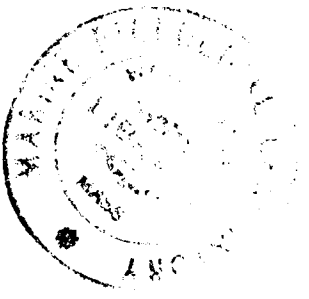
THE PHYSICS OF BLOOD FLOW IN CAPILLARIES

II. THE CAPILLARY RESISTANCE TO FLOW



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ABSTRACT A previous communication described the peculiar motion of the plasma trapped between erythrocytes in a capillary (bolus flow). In this paper the effect of this motion on capillary resistance to flow, as well as on dissipative effects associated directly with the cells, are described. The resistance that would be associated with plasma in bolus flow at high Reynolds numbers (relative to a capillary value of 0.01) was studied in a model, in which air bubbles, separated by short segments of water, passed along a glass tube. The resistance to flow, especially with short boluses, was at least ten times greater than that associated with Poiseuille flow. In a second series of experiments at lower Reynolds numbers, a single bolus of liquid was forced by air pressure along a glass tube. In these latter experiments, which more closely simulate biological conditions, the mean resistance to flow was only 30 per cent greater than that associated with Poiseuille flow. In the final series of experiments human blood and plasma, diluted in acid-citrate dextrose (A.C.D.) in varying degrees, were forced through glass micropipettes of capillary dimensions. The mean apparent viscosity of whole blood was found to exceed that of plasma by only about 5 per cent, thus verifying a conjecture to this effect made by Fahraeus and Lindqvist in 1931.

1. INTRODUCTION

In the first paper (1) of this series the peculiar eddy-like motion of plasma trapped between two red cells in a capillary and the effect of this motion on the equilibration of gases in the capillary were discussed. In bolus flow (*i.e.* red cells in single file) the velocity distribution in the plasma is not parabolic, so that it cannot be assumed a priori that Poiseuille's law is at all applicable. In addition to the resistance to flow associated with the trapped plasma there will be 'friction' between the walls of the red cells and the endothelial lining of the capillary. A third possible contribution to resistance to flow exists if the contents of the red cell are set in motion in bolus flow. Finally, energy is required to deform the discoid red cell in order that it may enter a capillary of smaller diameter. This last factor is the subject of the final paper (2) in the series.

It is well known from the work of Landis (3) that the pressure drop in the capillary circulation represents 20 to 30 per cent of the total pressure drop across a vascular bed. On the other hand it has been known since the work of Fahraeus and Lindqvist (4) that the apparent viscosity of blood decreases as the radius of the vessel decreases. Thus the pressure drop in the capillary circulation depends jointly upon two quantities, namely the cross-sectional area of the capillary bed and the apparent viscosity of blood. Landis (5) postulated that the apparent viscosity is greater in the capillaries than in the arteries, whereas Fahraeus and Lindqvist (4) postulated a smaller apparent viscosity for blood in capillaries than in arterioles. No theoretical basis for the postulate of Landis has been advanced. But for the opposite postulate of Fahraeus and Lindqvist, in so far as large tubes (*i.e.* wide enough for several cells abreast) are concerned, at least two theories have been advanced (6); one theory attributes the decreased viscosity to the fact that the "integration" in the derivation of Poiseuille's law should be replaced by a "summation," the other attributes it to the formation of a cell-free zone near the wall. Evidently neither of these theories is applicable to flow through those capillaries which permit red cells to pass only in single file. There is abundant experimental evidence for the decrease in apparent viscosity of blood as the radius decreases, but only down to radii of about 25 microns. However, Bayliss (7) has reported a few measurements made in tubes of about 10 microns diameter.

There has been little discussion (see reference 8) of the general relevance of the Reynolds number to a discussion of the circulatory system, although the importance of the Reynolds number as a criterion of the onset of turbulence has been realized (9). Of greater present interest is the fact that the Reynolds number is an index of whether inertial or viscous dissipation may be expected to predominate in a given situation. The Reynolds number associated with flow through the aorta is of the order of 1,000, whereas that associated with the capillary circulation is certainly less than 0.01. In the aorta it may be expected that inertial dissipation in blood is of considerable importance, whereas in the capillary circulation viscous dissipation may be expected to predominate.

Consider the case of bolus flow. The radial velocity components associated with the "mixing" motion indicate that the fluid is being accelerated and decelerated within the trapped plasma. This acceleration will be associated with an inertial loss. At large Reynolds numbers this inertial loss may be expected to be large, whereas at small Reynolds numbers it may be expected to be rather small in comparison to viscous dissipation. Evidently an experimental study of the resistance to flow offered by the plasma in bolus flow would be valuable, as well as measurements of the resistance to flow offered by whole blood in very small tubes.

2. MODEL EXPERIMENTS

The Reynolds number has a further significance. It may be shown (10) that dynam-

ical similarity (*i.e.* same relative importance of inertial and viscous forces) between the fluid behaviour of the model and that of a prototype is achieved when the Reynolds number is the same in both cases. Thus dynamical similarity between a model and the plasma of the capillary circulation is achieved if the Reynolds number is of the order of 0.01 or less.

In the model experiments to be described it is again desirable to compare the results obtained with bolus flow to those which would be obtained with Poiseuille flow (as was done in the first paper (1) for the thermal analogue). In order to make this comparison it is convenient to express Poiseuille's law in terms of the dimensionless parameters P, L, and R.

The "pressure coefficient" P is given by:

$$P = 2\,\Delta P/\rho u_0^2 \tag{1}$$

in which ΔP denotes the pressure drop along the length l of the tube; the fluid having density ρ and average velocity u_0. Similarly the axial ratio L is given by:

$$L = l/a \tag{2}$$

wherein a is the radius of the tube. The Reynolds number R is given by:

$$R = 2\rho a u_0/\eta \tag{3}$$

wherein η is the viscosity of the fluid. Poiseuille's law, expressed in terms of P, L, and R is given by:

$$P = 32L/R \tag{4}$$

These same dimensionless parameters may be employed to describe bolus flow. Thus it is possible to compare the results obtained in bolus flow experiments with those which would be obtained in Poiseuille flow experiments by expressing the data in terms of P, and L/R. It is of interest to compute the value of L/R for the capillary circulation. The axial ratio 'L' may be taken as unity, which would correspond roughly to the average axial ratio of the plasma boluses in a sample of blood having 50 per cent hematocrit in capillaries of 10 microns diameter. Thus, with an axial ratio of unity and a Reynolds number of 0.01, the parameter L/R has the value 100. A nominal range then for the capillary circulation may be taken as:

$$10 \leq L/R \leq 1000 \tag{5}$$

The results of model experiments now to be described will be expressed in terms of the above formalism.

Method

Two series of experiments were carried out with the apparatus already described and illustrated in Paper I of this series (1). Water, under constant pressure, was allowed to flow through a long horizontal glass tube (3 mm in diameter). Bolus flow

(in which a regular train of air and water bubbles flowed down the tube) was obtained by injecting compressed air into the water through thermometer tubing and a hypodermic needle. The Reynolds number associated with this flow was relatively high (order 100).

In the second series the apparatus again consisted chiefly of a horizontal glass tube. In this case, however, a *single* bolus of liquid was forced along the tube under constant air pressure. Alcohol was employed as the liquid phase in order to reduce surface tension effects. The Reynolds number associated with the flow in this second series of experiments was much smaller (order 5).

In each series of experiments it was a simple matter to determine the driving pressure (by the level of a liquid manometer), the average length of the boluses (by calipers), and the average velocity of the bolus (by timing individual boluses over a given length). The density and viscosity of the fluid at the given temperature were taken from standard tables, and the average radius was computed from the weight of water in a given length of tube. Thus all of the parameters required to describe bolus flow in terms of P, L, and R could be determined.

Observations

The results of the first series of experiments (Reynolds number about 100) are shown in Fig. 1 wherein the ratio of the resistance to flow with bolus flow (R) to the resistance to flow with Poiseuille flow (R') is plotted against the axial ratio ($1/a$).

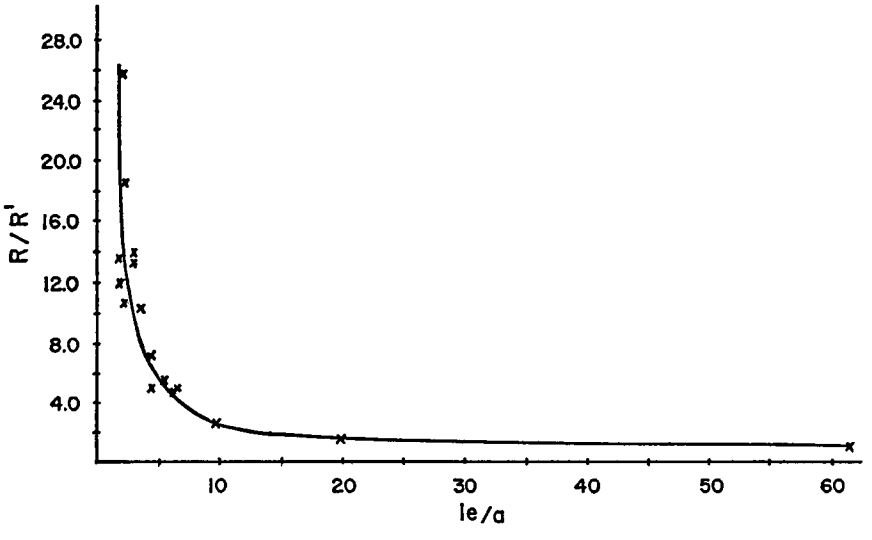

FIGURE 1 Viscous resistance associated with bolus flow. Data obtained in bolus flow experiments in which the Reynolds number was of the order of 100. The ratio of the bolus flow resistance to the Poiseuille resistance is plotted against the axial ratio.

The combined result of both series of experiments is plotted logarithmically in Fig. 2. The smooth curve represents Poiseuille's law adjusted to take into account the kinetic energy correction (*i.e.* the corrected equation is given by:

$$P = 32L/R + 1, \text{ (cf. reference 11)}$$

A regression line was fitted through the data (*i.e.*, P, a linear function of L/R) over the nominal range of capillary blood flow. The mean value of P obtained from this regression line was 30 per cent greater than for the Poiseuille-law flow over the same range (shown in Fig. 2).

Discussion

In the model experiments with bubbles of air in water, or the single bolus of water or alcohol in air, the shape of the meniscus at the end of the bolus is affected by surface tension and by its motion, and may not correspond with the case of red cells deformed in a capillary. If the pattern of flow between the boluses were sufficiently different, the resistance to flow in the two cases might not correspond. Also

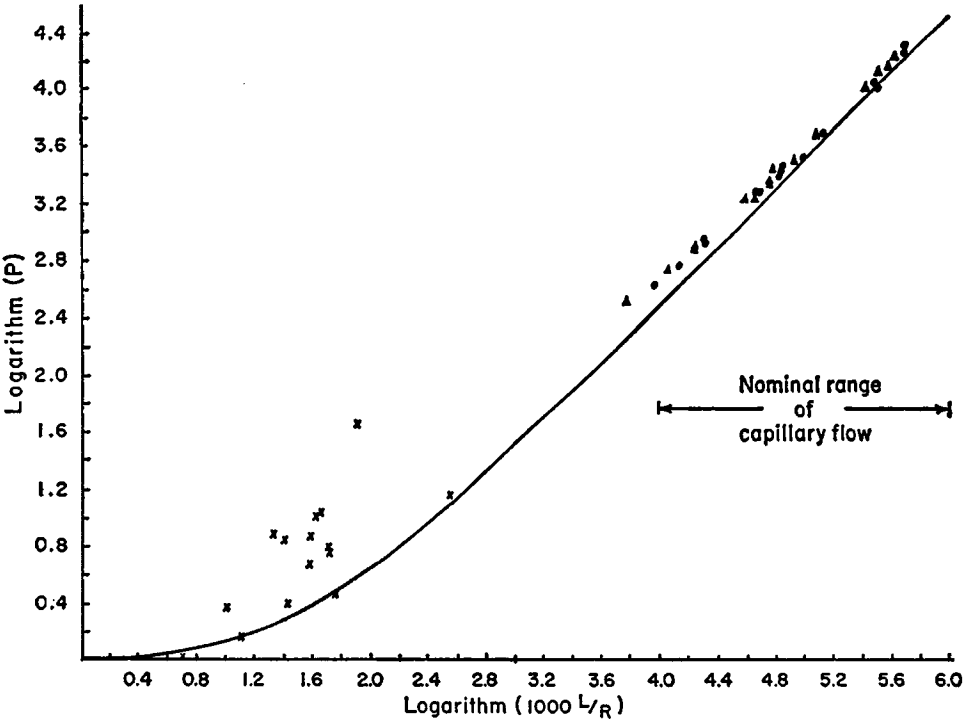

FIGURE 2 Summary of data obtained in bolus flow experiments. The smooth curve represents Poiseuille-law flow corrected by a kinetic energy term. The crosses correspond to the experiments at high Reynolds numbers, the circles and triangles to those at low Reynolds numbers.

part of the resistance to flow might be attributed to pressure drops across the series of meniscuses. Early in the work, attempts were made to assess this factor by using interfaces with different interfacial tensions. For example, the surface tension of air-alcohol is only 25 per cent of that of air-water. No consistent relation of the resistance to flow to surface tension was found. We can only hope that this means that this "end effect," dependent on surface tension and on the shape of the meniscus at the ends of a bolus, is not important, and that the results in the models, scaling down to the dimensions of the capillary by the 'modeling theory,' indicate reliably the effects in actual blood flow through capillaries.

At the larger Reynolds numbers (smaller values of L/R) the viscous resistance associated with bolus flow may be as much as ten times that associated with Poiseuille-law flow. At smaller Reynolds numbers on the other hand the resistance to flow associated with bolus flow is only 30 per cent greater than that associated with Poiseuille-law flow. The smallest Reynolds number obtained in the experiments was still considerably larger (500 times) than those which obtain in the capillary circulation. However, if data were available at lower Reynolds numbers it is to be expected that they would fall on the same curve (Fig. 2) as the present data inasmuch as the plot depends only on the ratio of L to R (cf. equation 5).

Thus, in so far as the *plasma* of the capillary circulation is concerned, the departure from Poiseuille's law is 30 per cent or less. This estimate is consistent with the results of a theoretical calculation of the resistance to flow associated with bolus flow being carried out with the collaboration of Dr. J. Blackwell of the Department of Physics and Applied Mathematics. This calculation is based upon a solution to the Navier-Stokes equations obtained with boundary conditions similar to those of bolus flow.

3. MICROPIPETTE EXPERIMENTS

When blood flows through the capillaries, dissipation is associated with the motion of the cells as well as with the motion of the plasma. Thus the resistance to flow may be appreciably greater than that associated with just the plasma. In order to investigate this possibility an apparatus was designed to permit blood flow measurements to be made in a tube of capillary dimensions. A few measurements of a somewhat similar nature have been described by Bayliss (7).

Theory

Fluids may be forced through glass micropipettes (of the type employed for intracellular electrodes) so that a droplet of gradually increasing radius forms on the tip (see Fig. 3). The flow may be calculated from the time required for a drop of given radius (as determined microscopically with an eyepiece reticule) to form on the tip. This technique permits flow of the order of 10^{-6} cc/sec. to be determined. However, this flow rate is still 10 times as great as the flow through capillaries *in vivo*.

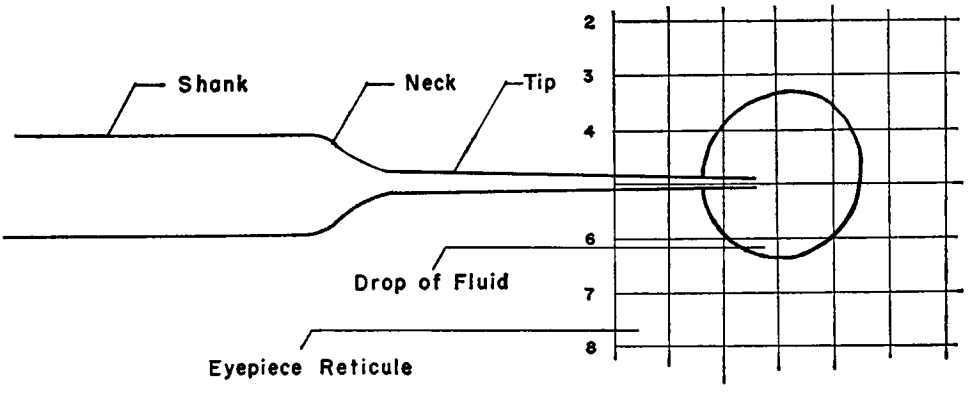

FIGURE 3 The "drop method" of measuring flow in the micropipette experiments. The radius of the drop is estimated through the eyepiece reticule. The spacing in the reticule represents about 100 microns.

There are two corrections to the method, both of which are made possible by adopting the method of timing from the start, when the meniscus is on the tip of the micropipette, to a standard radius of droplet (usually 600 microns). The first correction is for evaporation of the droplet. This was evaluated by measuring the shrinkage of a drop, without any flow entering, over the same size range. Evaporation diminished the apparent rate of flow by 3 per cent. The droplet method for flow was checked against collection of the efflux in a calibrated 0.1 ml pipette, with very good agreement. The second correction is for the pressure-drop, diminishing the total driving pressure, across the surface of the droplet. This is large (150 mm Hg for a tip of 7 microns radius) when the droplet radius approaches that of the tip, but decreases as the droplet grows ($2T/r$). The true mean for the correction is a very complicated function of time, but using the time to a standard size of droplet ensures that for a given size of micropipette tip, the mean correction is the same for all the flow determinations made at different driving pressures. Thus, while the capillarity correction leads to the positive intercept on the graphs (*e.g.* Figs. 4 and 5), capillarity cannot affect the slope of the flow pressure lines, upon which the subsequent calculations are based.

The relative viscosity of the fluid may be calculated directly. A pressure-flow relation is first obtained with a standard solution, (in this case acid-citrate-dextrose (A.C.D. *cf.* (12)). The slope (m_1) of this line is computed. Then a second pressure-flow relation is obtained with the fluid under study (in this case either diluted plasma or diluted blood). The slope (m_2) of this second line is computed. The relative viscosity (η_{rel}) is given by:

$$\eta_{rel} = m_1/m_2 \tag{6}$$

The apparent viscosity (η_{app}) is calculated from the relative viscosity by multiplying by the viscosity of the standard solution (A.C.D.) *i.e.*

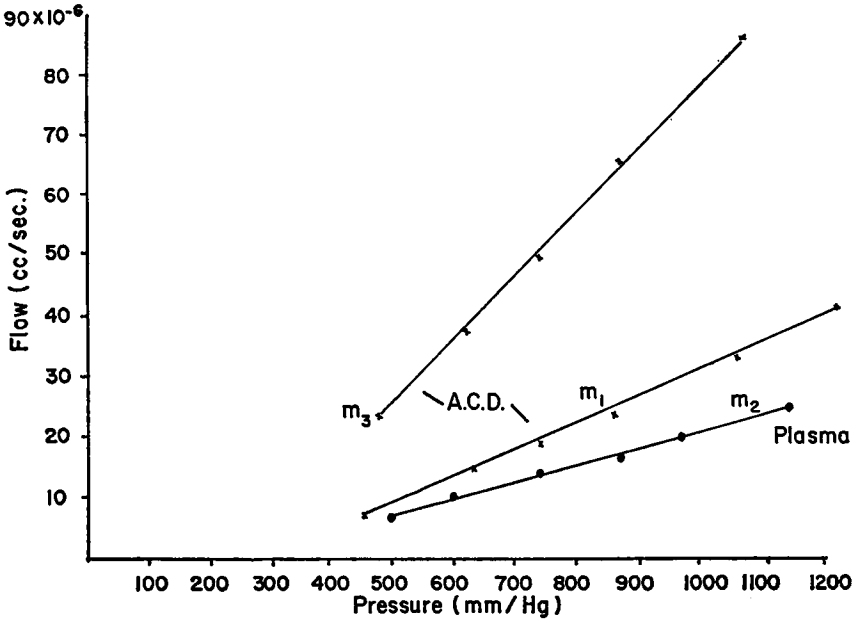

FIGURE 4 A typical result obtained with diluted human plasma in the micropipette experiments. The first pressure-flow relation (denoted by m_1) was obtained with A.C.D. Then a pressure-flow relation was obtained with plasma (denoted by m_2). Finally after cutting a portion off the tip (575 microns in this case) another pressure-flow relation was obtained with A.C.D. (denoted by m_3). The plasma had, in this experiment, a protein concentration of 6.0 gm per cent.

$$\eta_{app} = 100 \times \eta_{rel} \times \eta_{A.C.D.} \quad \text{centipoise} \tag{7}$$

Note that the term "apparent viscosity" includes, in the case of blood, the effects within the plasma and cells, as well as the effects of friction between the cells and glass walls. In principle the apparent viscosity is proportional to the mean rate of shear for a given applied stress.

It is also possible to determine the radius of a relevant portion of the micropipette tip. The first step is to carry out a pressure-flow determination with water, after which a known length (of the order of 200 microns) is cut from the micropipette tip (by microscissors under microscopic observation). Then another pressure-flow determination with water is carried out. If the slope of the first and third pressure-flow relations are denoted by m_1 and m_3 (cc/sec. $\times$ 10^6/mm Hg respectively, and the length cut off is denoted by l (microns), then the average radius of the segment (*cf.* Appendix I) is given by:

$$a = \sqrt[4]{\frac{20.89l}{\frac{1}{m_1} - \frac{1}{m_3}}} \quad \text{microns} \tag{8}$$

Procedure

(*a*) In the first series of experiments the apparent viscosity of human plasma was determined. Venous blood, collected into varying amounts of the acid-citrate-dextrose (A.C.D.) solution was centrifuged, after which the supernatant plasma was injected into a micropipette. A series of pressure-flow determinations was made with plasma, and then, after cutting a portion off the tip, another series was made with A.C.D. Protein determinations were carried out by the Department of Pathological Chemistry, Victoria Hospital, London, Ontario.

Thus a schedule for these experiments consisted in making three pressure-flow determinations, a first with A.C.D., a second with plasma, and finally, after cutting a known length from the tip, a third with A.C.D. The two determinations made with A.C.D. permit one to calculate the radius of a portion of the micropipette tip, as described above.

(*b*) The second series of experiments differed from the first in two ways; human blood (diluted in A.C.D.) was employed rather than plasma and furthermore (with four exceptions) only two pressure-flow determinations were made, one with A.C.D. and a second with blood. Thus it was not possible in most cases to calculate the radius of the tip in this second series. The diameter could however be estimated microscopically.

Both series of experiments were carried out in a temperature-controlled room. The temperature was 21.0 ± 0.5°C during the experiments with plasma and 23.5 ±5°C in the experiments with blood.

Observations

Typical results obtained in an experiment with diluted plasma and in another experiment with diluted blood are shown in Figs. 4 and 5, respectively. All of the results obtained in both series of measurements are summarized in Fig. 6.

The tips of the micropipettes employed in the first series of experiments (with plasma) were found to have a mean radius of 6.8 microns with a standard deviation of 2.3 microns. The four pipettes for which the radius was determined in the experiments with blood were found to have a mean radius of 4.7 ± 1.0 microns.

Discussion

The linear relation observed between pressure and flow both for blood and plasma is of interest. The large intercept on the pressure axis (Fig. 4 and 5) may be attributed to surface tension (13), since the pressure applied to the micropipette is plotted rather than the true driving pressure.

The straight lines plotted in Fig. 6 represent the regression equations calculated for the data obtained with plasma and blood. These equations are:

$$\eta_{bl.} = 0.020\ He + 1.00 \qquad (10)$$

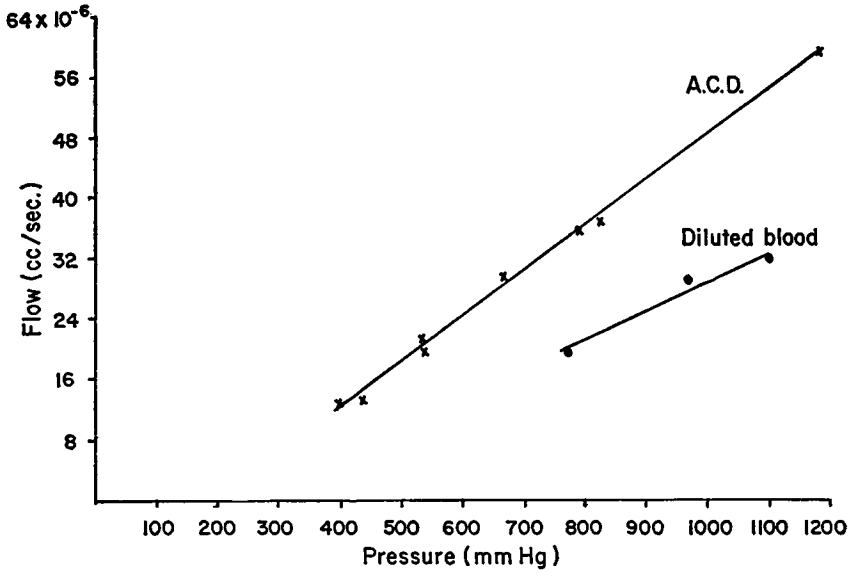

FIGURE 5 A typical result obtained in the experiments with diluted human blood. In this example the blood had a hematocrit value of 37 per cent.

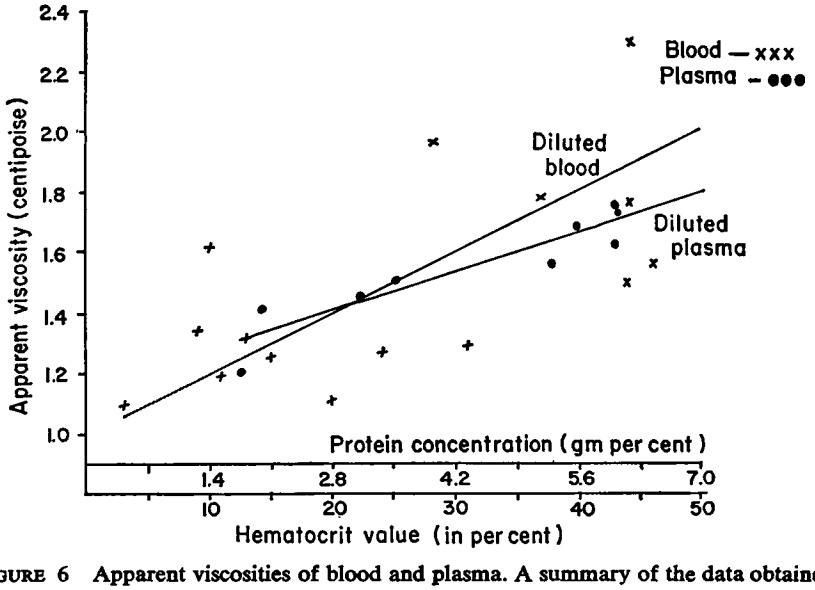

FIGURE 6 Apparent viscosities of blood and plasma. A summary of the data obtained in experiments with human blood and plasma. Note that two axes are plotted along the abscissa. The results obtained with plasma are to be referred to the upper axis, those with blood to the lower axis.

$$\eta_{pl.} = 0.091\ \mathrm{Pr} + 1.16 \qquad (11)$$

Since in the data of Equation (10) the whole blood was diluted, the protein concentration Pr is proportional to the hematocrit He. η_{pl} and η_{bl} represent the viscosities in centipoise of plasma (at 21°C) and blood (at 23.5°C) respectively, and Pr and He the corresponding protein concentration (gm per cent) and hematocrit value. The coefficients of correlation were 0.74 and 0.93, respectively. The reasons for the poorer correlation coefficient obtained in the experiments with blood are not understood.

The regression equation may be employed to estimate the excess apparent viscosity which whole blood exhibits over the apparent viscosity of plasma. Let us take a nominal value of 7.0 gm per cent for the normal protein concentration of plasma. Then from equation (9) it is found that the apparent viscosity of the plasma is 1.80 centipoise at 21.0°C (*i.e.* 1.9 centipoise at 23.5°C). Similarly it is found that the apparent viscosity of blood at a hematocrit of 50 per cent is 200 centipoise (at 23.5°C). Thus the apparent viscosity of whole blood as determined in these experiments exceeds that of the plasma by only about 5 per cent.

CONCLUSIONS

A considerable proportion of the data obtained in this laboratory on the *in vitro* behaviour of blood (suspended in A.C.D.) is summarized in Fig. 7. The upper four curves are taken from the work of Haynes (14). The lowest line of Fig. 7 is another plot of the regression line (for blood) given in Fig. 5. The data is seen to form a consistent family of curves, the apparent viscosity increasing both with increasing hematocrit values and increasing radius.

Both in the model experiments and in the micropipette experiments the Reynolds numbers were some 500 × greater than those which characterize capillary blood flow. It is possible that the apparent viscosity of whole blood is even somewhat less in the capillary circulation than observed in these experiments. This may be the case in those capillaries where in the red cells do not touch the capillary wall (we have termed this regimen "slug flow"). In slug flow the dissipation must occur chiefly in the plasma. However it is considered unlikely that the apparent viscosity figure for capillary blood will be less than the value for plasma (*i.e.* 1.9 centipoise at 23.5°C) in any case.

It is concluded that human capillary blood has an apparent viscosity of 2.0 centipoise (at 23.5°C) with a standard error of estimate of ±0.27 centipoise. Furthermore (see Figs. 4 and 5) the flow is a linear function of the pressure so that a relation of the same form as Poiseuille's law may be applied to the capillary circulation. Thus if the average velocity of the blood in a capillary of known dimensions is determined, the above figure for the apparent viscosity may be employed in Poiseuille's law in order to calculate the pressure drop. However, this is not meant

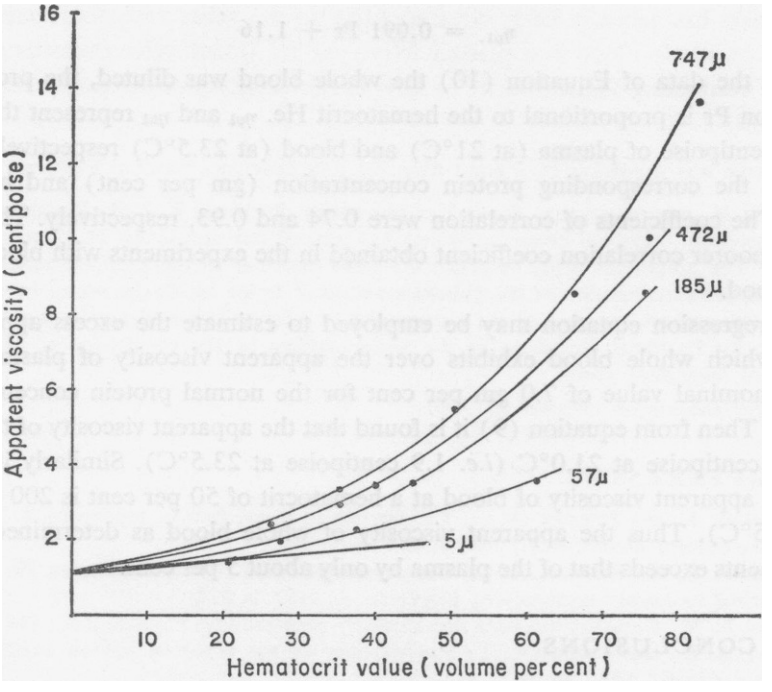

FIGURE 7 A summary of a number of measurements of the apparent viscosity of blood made in this laboratory. The top four curves represent data obtained in tubes of different radii (microns) by Haynes. The bottom line corresponds to the regression equation plotted (for blood) in Fig. 7, for which the average radius of the tip is estimated to be 5 μ.

to imply that the resistance to flow varies as the inverse fourth power of the radius. If a diameter much greater than, say, 15 microns is considered, then a different and no doubt higher figure for the apparent viscosity must be employed. For capillaries of diameter less than 15 microns the figure of 2.0 centipoise (at 23.5°C) should give the correct resistance to flow to within about 15 per cent.

The experiments described above do not permit one to evaluate the friction between the cells and the walls of the micropipette. However, the small difference (*i.e.* 5 per cent) observed in these experiments between the apparent viscosity of whole blood and that of plasma suggests that wall friction and internal motion in the red cell (16) (as well as inertia loss in the plasma) makes little contribution to the resistance to flow.[1] Furthermore it has been reported by Bloch (15) that adhesion between blood cells and the endothelial lining is also negligible in healthy capillaries *in vivo*.

[1] Though the mean diameter of the micropipette tips used (8.4 microns) was not less than the mean diameter of the erythrocytes (7.2 microns) the tubes tapered somewhat and some contact with the walls probably occurred.

Attention has recently been directed (16) to the shear rate dependence of the viscosity of whole blood and plasma. However the quantitative importance of this factor in computing the resistance to flow in the capillary circulation remains to be established.

This research was supported by a grant from the Life Insurance Medical Research Fund.

Note added in press relevant to Paper I of this series: Professor F. J. W. Roughton of Cambridge University (personal communication) has pointed out that in his Ph.D. thesis of 1925 he wrote "The corpuscles being of about the same diameter as the capillary make it almost certain that turbulent motion of the plasma must occur in the capillaries where indeed it is so needed." The authors are glad of the opportunity to refer to this evidence of the well known pioneering by Professor Roughton in the understanding of the physiology of the capillary exchange of respiratory gases.

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REFERENCES

1. PROTHERO, J., and BURTON, A. C., The physics of blood flow in capillaries. I. The nature of the motion, *Biophysic. J.*, 1961, **1**, 565.
2. PROTHERO, J., and BURTON, A. C., The physics of blood flow in capillaries. III. The force required to deform erythrocytes, *Biophysic. J.*, 1962, **2**, 213.
3. LANDIS, E. M., Capillary pressure and capillary permeability, Physiol. Rev., 1933, **14**, 404.
4. FAHRAEUS, R., and LINDQVIST, T. The viscosity of the blood in narrow capillary tubes. *Am. J. Physiol.* 1931, **96**, 562.
5. LANDIS, E. M., Poiseuille's law and the capillary circulation, *Am. J. Physiol.*, 1933, **103**, 432.
6. HAYNES, R. H., Physical basis of the dependence of blood viscosity on tube radius. *Am. J. Physiol.*, 1960, **198**, 1193.
7. BAYLISS, L. E., Deformation and flow in Biological Systems, New York, Interscience Publishers, Inc., 1952, chapter 6, 371.
8. STACY, R. W., WILLIAMS, D. T., WORDEN, R. E., and MCMORRIS, R. Q., Essentials of Biological and Medical Physics, New York, McGraw-Hill Book Company, 1955, chapter 30, 368.
9. STEHBENS, W. E., Turbulence of blood flow, *Quart. J. Exp. Physiol.*, 1959, **44**, 110.
10. MILNE-THOMSON, L. M., Theoretical Hydrodynamics. New York, The MacMillan Co., 1955.
11. GOLDSTEIN, S., Modern Developments in Fluid Dynamics. Oxford, Clarendon Press, 1957, **1**, chapter 7, 299.
12. BRAY, W. E., Clinical Laboratory Methods. St. Louis, C. V. Mosby Co., 1951, 183.
13. PROTHERO, J., The Physics of the Capillary Circulation. Ph.D. thesis, University of Western Ontario, London, Canada, 1960.
14. HAYNES, R. H., The Rheology of Blood. Ph.D. thesis, University of Western Ontario, London, Canada, 1957.
15. BLOCH, E. H., Visual changes in the living microvascular system in man and experimental animals as they are related to thrombosis and embolism, *Angiology*, 1954, **10**, 421.
16. WELLS, R. E., JR., and MERRILL, E. W., Shear rate dependence of the viscosity of whole blood and plasma. *Science*, 1961, **133**, 763.

APPENDIX I

One may, given certain information, calculate the *average* diameter of a portion of the micropipette tip. This calculation depends upon knowing the resistance to flow associated

with the micropipette before *and* after a known length is cut off the tip. In this case the *change* in resistance may be attributed to the segment cut off. The *Poiseuille* resistance is a function only of the fluid viscosity and of the tube's length and radius. Therefore, given the change in Poiseuille resistance, the fluid viscosity, and the segment's length, the average radius (*i.e.* fourth root average) of the segment cut off may be calculated. The appropriate formula is given by:

$$m_1 = \text{initial slope cc/sec.} \times 10^6/\text{mm Hg}$$

$$m_3 = \text{final slope cc/sec.} \times 10^6/\text{mm Hg}$$

$$a^4 = \left[\frac{10^{-6}}{\frac{1}{m_1} - \frac{1}{m_3}}\right]\left(\frac{8\eta l}{\pi}\right)\left(\frac{0.943}{1.333 \times 10^3}\right) \tag{1}$$

Where 0.943 is the reticule calibration factor and 1.333×10^3 converts the pressure in mm Hg to dynes/cm^2. The experiments were carried out in a temperature-controlled room. The average temperature, as determined from continuous temperature recording charts was 21.0 ± 0.5°C. (plasma experiments). The viscosity of A.C.D. at this temperature is 1.16 centipoise. Equation (1) therefore reduces to:

$$a = \sqrt[4]{\frac{20.89l}{\left(\frac{1}{m_1} - \frac{1}{m_3}\right)}} \quad \text{microns} \tag{2}$$

where a and l are in microns.