THE PHYSICS OF BLOOD FLOW IN CAPILLARIES

I. THE NATURE OF THE MOTION

J. PROTHERO *and* A. C. BURTON

From the Department of Biophysics, University of Western Ontario, London, Canada

ABSTRACT In many capillaries erythrocytes travel singly, separated by segments of plasma (bolus flow). The peculiar flow pattern, within the plasma, has been studied visually in a model in which air bubbles separated by short columns of liquid flow through a glass tube. Injection of dye reveals an "eddy-like" motion, in that each fluid element repeatedly describes a closed circuit. The possible significance of this "mixing motion" in relation to gaseous equilibration (*e.g.*, in pulmonary capillaries) has been studied in a thermal analogue. A copper tube passed first through a constant temperature bath which brought the fluid to a uniform temperature T_1, and then through a second smaller bath at a lower temperature T_2. From the final temperature T_3 of the fluid, which was collected in a thermally insulated flask, a calculation of the heat transfer was made (*i.e.*, from the flow and the temperature drop (T_1-T_3)). Bolus flow was up to twice as effective in transferring heat as Poiseuille flow (no bubbles in fluid). The theory of modelling was employed in order to apply this thermal data to gaseous equilibration, especially in pulmonary capillaries. It was concluded that gaseous equilibration may be considerably accelerated by bolus flow, though this may be more of a limiting factor in peripheral capillaries than in the pulmonary circulation. The result supports the assumption of complete mixing in plasma made by Roughton and Forster in 1957.

1. INTRODUCTION

It is now three hundred years since Malpighi first described the capillary circulation, and forty years since Krogh (1) initiated modern studies in this field. Remarkably little attention has been directed since to the biophysical factors which govern capillary flow. Landis (2) has been concerned with the general problem, and Bayliss (3) has made some measurements of blood flow through very small micropipettes.

Recent studies (4, 5) have clarified the role of the important variables influencing the resistance to flow in relatively large tubes (down to 50 microns diameter); *i.e.*, the rate of shear, the hematocrit, and the tube radius. In the systemic circulation both the rate of shear and tube radius are large compared to the values in the capillary circulation. Indeed it is probable (6, 7) that an appreciable fraction of the capillaries permit only one red cell to enter at a time. Furthermore, the average velocity of flow of blood in capillaries is only about a thousandth of that in the aorta. Thus the dynamic conditions which characterize capillary flow are very different from those which have been studied heretofore. It is important to note that the relative importance of the inertial forces and the viscous forces in the dissipation of energy in flow depends on the "Reynolds number" (see details later), so that the physics of such very slow rates of blood flow may be quite different from the physics of the flows usually encountered.

In those capillaries where only one red cell may enter at a time, the plasma is effectively "trapped" between successive red cells and thus moves along in segments. We have used the term bolus flow for this regimen, in which a fluid element of one phase separates two elements of another phase in their flow down a tube. When bolus flow of blood occurs in the capillaries, the red cells are deformed, and presumably there is a frictional force between the endothelial wall and the membrane of the cell. Also the plasma which is trapped between the red cells must undergo a peculiar motion. This motion of the plasma may be expected to contribute to an increased rate of gaseous equilibration within the plasma, as well as to an increased viscous resistance. These various effects associated with the bolus flow of blood are to be discussed separately. The flow pattern and rate of equilibration which must be associated with bolus flow of *plasma* are discussed in this paper. The viscous resistance associated with capillary blood flow (whether bolus flow or not) is discussed in the second paper (8), and finally, measurements of the pressure required to force red cells into narrow pores are discussed in the third paper (9).

The experimental study of bolus flow is possible, since this type of flow is easily produced in a model. This type of motion also lends itself to theoretical treatment. By employing a larger model it is possible to circumvent many technical difficulties associated with working with a structure of capillary dimensions. In such a model the flow pattern associated with bolus flow may be easily visualized. Another type of model permits the effect of hydrodynamic transport in facilitating equilibration to be distinguished from the effect of diffusion. Finally the observations made in the models may, by employing the theory of models (10), be applied to the capillary circulation.

2. THE PATTERN OF THE FLOW IN THE TRAPPED PLASMA

(*a*) *Method*

The first model (Fig. 1) studied employed a long horizontal glass tube, 4 mm in diameter, down which water flowed under a constant pressure head. A hypodermic needle (No. 22 gauge) was inserted through the wall of a plastic tube at the entrance. The needle was connected through narrow "thermometer tubing" to a reservoir of air under pressure, so that it emerged into the stream at a pressure close to that of the water. It was found that an oscillatory condition could be set up, in which bubbles of air entered the stream rhythmically, forming a train of "boluses." Adjustment of the relative pressures allowed bubbles of different lengths and spacing to be obtained. Dye (methyl blue) was injected from a syringe into the stream at a point beyond the entrance of the bubbles, and entered in a thin stream near the axis, trapped in each segment of water. The subsequent motion of the dye, in its segment, could be easily seen, but this proved difficult to photograph. For the photographs of the motion, a second model was used. The model consisted of a vertical glass tube 1 cm in diameter and 60 cm long, through which water was forced upwards by a constant-flow pump. A scale placed beside the tube allowed distances travelled to be measured. Illumination was provided by a fluorescent lamp mounted behind the tube.

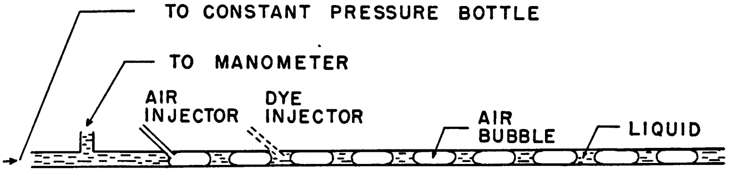

FIGURE 1 A diagram of the model first employed to study the flow pattern associated with bolus flow.

In this second model, designed for making photographic records, a bolus was produced by overlaying kerosene onto the upper surface of water. This bolus, it may be noted, is delimited by a water-kerosene interface on the bottom, a kerosene-glass interface on the sides, and an air-kerosene interface on the top. As water is pumped into the glass tube the kerosene bolus moves steadily up the tube. The flow pattern associated with this upward movement of the bolus was revealed by injecting a small quantity of Sudan black into the kerosene. The path of the dye, as it is transported within the bolus, was then recorded in a series of photographs.

(*b*) *Observations*

The type of flow observed in the first (visual) model resembled closely that seen in the second model (photographic) for which a typical series of pictures is shown in Fig. 2. Initially the dye is in the "core" of the bolus, wherein it is observed to be carried through the bolus at a velocity roughly twice the *average* (or "transport") velocity of the bolus. Soon the dye reaches the upper interface, where it is carried radially towards the walls of the glass tube (symmetrically, if the dye is exactly on the axis). Upon reaching the wall, the dye adheres to the glass and there remains until the bottom interface of the bolus arrives. Then the radial components carry the dye back into the core, after which the "circuit" is repeated. The complete flow pattern may be described briefly as eddy-like, or as a mixing motion. A circuit was completed every time the bolus had travelled about twice its own length.

(*c*) *Discussion*

The flow pattern which characterizes bolus flow is in contrast to that in Poiseuille flow, inasmuch as there are radial components of velocity associated with bolus flow. The radial velocity components which exist at the terminal surfaces of the bolus will increase the rate of transfer of a material (*e.g.* oxygen) from the periphery of the bolus into the interior. The effectiveness of the radial velocity components in facilitating transport is shown in the next section. Since the dye completes its circuit in the bolus in about the time required for the bolus to travel twice its own length, the circuit of the plasma trapped between two red cells would be completed at least 10 times in the average length of a capillary.

3. RATE OF EQUILIBRATION

Each of the different transport mechanisms to be considered, *i.e.* transport by hydrodynamic flow and transport by diffusion, must operate in the same way for transport of heat and for transport of mass, since the differential equations are identical in the two cases. Therefore the extent to which *mass* transport is enhanced in bolus flow, as compared to Poiseuille flow, may be deduced from a study of heat transport. Thermal measurements are technically much simpler since temperatures are more easily measured than, for example, O_2 concentrations. For this reason the present study was carried out on a "thermal analogue." In order to apply the results to the capillary circulation, it was then necessary to take into account not only the difference in scale, but also the difference in diffusion coefficients (thermal *vs.* gaseous).

(*a*) *Method and Theory*

In the thermal model employed (Fig. 3) a fluid is made to flow through a horizontal copper tube, the walls of which are kept, by water baths, at a temperature T_1 over one portion, and at a lower temperature T_2 over a second portion. Thus the fluid is first brought to a uniform temperature T_1, after which the fluid tends to cool, especially near the walls, to the temperature T_2. When the fluid is collected and mixed in an insulated flask it has in general an intermediate average temperature T_3. A general expression for the heat transfer coefficient C in cal/min/°C gradient, regardless of the type of flow, is given by:

$$C = 60\rho C_v m F \qquad \text{cal/min./°C} \tag{1}$$

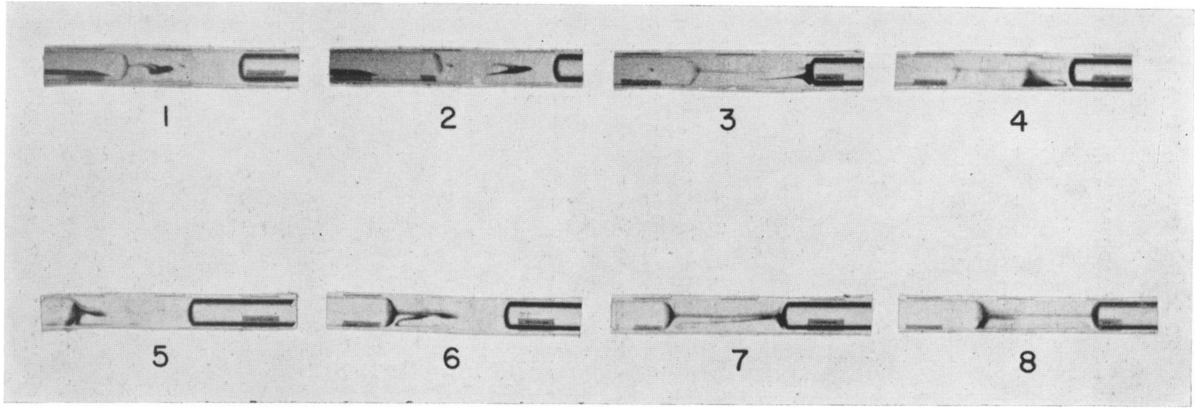

FIGURE 2
1. A slug of dye is shown immediately after injection into an upward moving bolus of kerosene.
2. The dye is being carried through the core of the bolus.
3. Then the dye reaches the upper interface and moves sideways.
4. The dye adheres to the wall of the glass tube.
5. When the bottom interface reaches the point at which the dye has adhered to the wall, the dye is immediately carried into the bolus. The whole bolus has now travelled a distance roughly equal to twice its own length.
6. The dye is again carried through the core of the bolus.
7. The upper interface is encountered once more.
8. The cycle is starting for the third time.

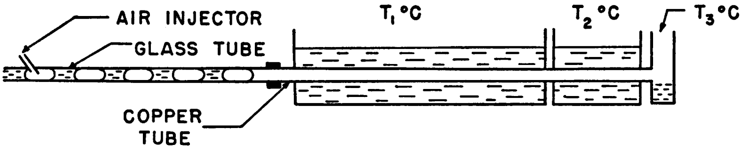

FIGURE 3 A diagram of the thermal analogue.

where ρ is the density in gm/cc, C_p is the specific heat in cal/gm/°C, F is the flow in cc/sec., and m is a dimensionless ratio given by:

$$m = (T_1 - T_3)/(T_1 - T_2) \tag{2}$$

In the case of Poiseuille flow (here represented by primed quantities) the heat transfer coefficient C' associated with a flow F' may be calculated from theory (11) (*i.e.,* given the dimensions of the tube and the thermal coefficients of the fluid). The calculation is summarized by the equation:

$$C' = f(F') \qquad \text{cal/min./°C} \tag{3}$$

where $f(F')$ is a known function (given in Appendix I). The transfer coefficient C' is a monotonically increasing function of the flow F'.

It was readily verified that the experimental data obtained in the present model, using Poiseuille flow, were described by equation (3), within the experimental error (*i.e.* 10 per cent). This fact is taken for granted throughout the subsequent discussion.

Special consideration must be given to one detail in order to compare the heat transport associated with bolus flow to that associated with Poiseuille flow. As will appear, when bolus flow is produced in the model the boluses of liquid are separated from one another by boluses of air. The heat transported by the air may safely be neglected, so that only a fraction, say α of the total fluid (air plus water) is transporting heat. This complicating factor may be taken into account by defining an "idealized bolus flow" in which the velocity profile across the bolus is parabolic; *i.e.,* of the Poiseuille type. In any given case the α and average velocity u_0 associated with the idealized bolus flow (F_i) will be identical with those of the actual bolus flow. The heat transfer coefficient (C_i) associated with this idealized bolus flow may be calculated from the parametric equations:

$$F_i = \alpha F' \tag{4}$$

$$C_i = \alpha C' \tag{5}$$

For example, if the bolus flow F had the value 1 cc/sec., with α equal to 0.5, then F' would be 2 cc/sec. Thus C' would be given by $f(2)$, and hence the idealized heat transfer would be given by:

$$C_i = 0.5f(2) \qquad \text{cal/min./°C} \tag{6}$$

The actual heat transfer associated with bolus flow in this case should then be compared with the value predicted by equation (6). In essence we compare the heat transfer in the two cases, Poiseuille or bolus flow, on the basis of the same average velocity (u_0) of the water, rather than on the basis of the same total volume flow of water.

(*b*) *Apparatus*

The apparatus is illustrated diagrammatically in Fig. 3. Water flows from a constant pressure bottle through a horizontal glass tube and then through a copper tube. Bolus flow is produced by injecting air through a hypodermic needle into the glass tube, thus producing a "train" of alternate air-water boluses. At a given pressure, the character of the bolus flow, as observed through the glass tube, remained unchanged for periods up to half an hour.

When a stable bolus flow was obtained at a given pressure, the procedure was to lower the temperature of the cooling bath and record the average temperature of the outflow. Then the temperature of the cooling bath was further reduced and the

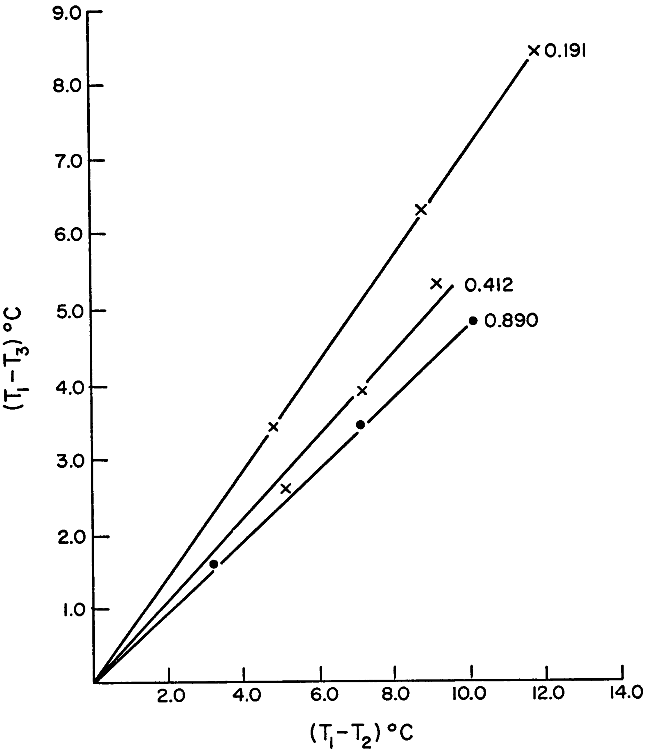

FIGURE 4 A graph of the temperature drop ($T_1 - T_3$) versus the driving function ($T_1 - T_2$). The numbers on the curves are flow rates given in cubic centimeters of fluid per second.

average temperature of the outflow again recorded. In this manner a series of values of T_1, T_2, and T_3 was obtained at the given flow. These measurements were repeated over a range of flows. The heat transfer which occurred was calculated from equations (1) and (2). At the end of each experiment the flow was stopped and the lengths of the air and water boluses determined. It was shown beforehand that the initial bath, at temperature T_1, produced complete equilibration of the water even at the highest flows. The temperature T_2 of the second bath was chosen so that the final temperature T_3 was close to room temperature. Typical temperatures would be $T_1 = 25°C$, $T_2 = 18°C$, $T_3 = 21°C$.

(*c*) *Observations*

The results of a series of measurements with water undergoing bolus flow are shown in Fig. 4. When the temperature difference $(T_1 - T_3)$ is plotted *vs.* $(T_1 - T_2)$, a linear relation is found except for points corresponding to large values of temperature difference, where the change in viscosity with temperature becomes of consequence. From the slope m of the lines, the heat transfer coefficients were calculated, and these coefficients are plotted *vs.* flow rate in Fig. 5. The smooth curves represent the heat transport coefficients which would occur if transport were solely due to diffusion in parabolic flow. Three smooth curves have been calculated (*i.e.*,

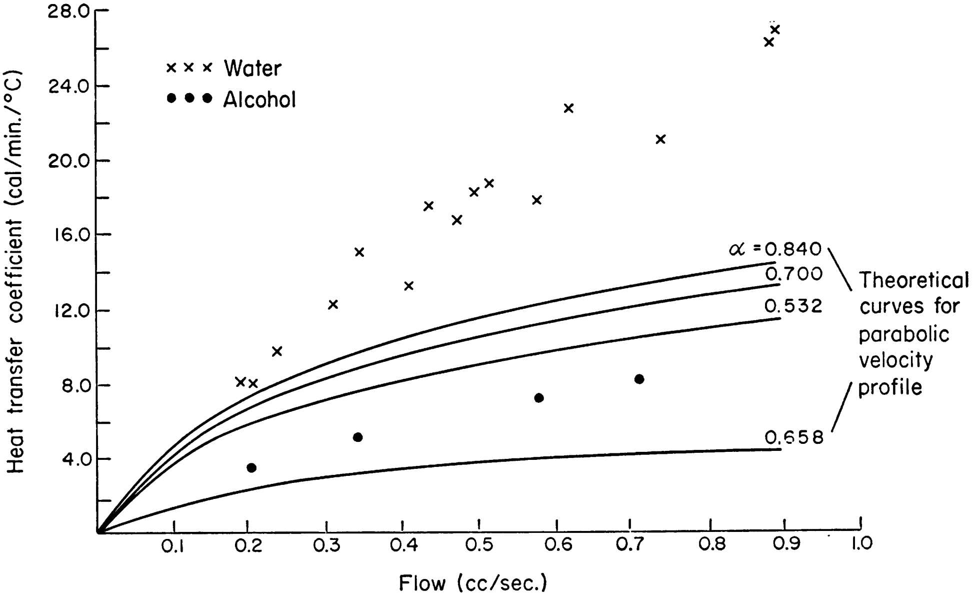

FIGURE 5 A graph of the heat transfer coefficient *versus* the flow. The values 0.840, 0.700, and 0.532 correspond to the maximum, average, and minimum values of α respectively in the experimental data for water. Only the average value of α has been employed in the calculation of the theoretical curve for alcohol.

from equations (3), (4), and (5) corresponding to different values of α in the experimental data. In practice it was not possible to produce bolus flow having a constant α over a range of flows. The values of $\alpha = 0.840$, 0.700, and 0.532 correspond to the maximum, average, and minimum values respectively present in the data.

(*d*) *Discussion*

It is clear from Fig. 5 that, at the higher flows, equilibration in the model is enhanced by about 100 per cent in bolus flow as compared to flow in which the velocity profile is parabolic. At lower flow rates the increase is less, falling to approximately zero at very low flows. It remains to apply these data to the capillary circulation.

4. DIMENSIONLESS FORMULATION

The theory of models (10) permits one to establish a correspondence between the behaviour of a model and that of a prototype. The essential step in establishing this correspondence is to express the data in terms of the appropriate dimenless parameter. The appropriate dimensionless parameter (11) in this case is termed the Nusselt number (*Nu*) or transfer coefficient. In terms of equation (2) this is defined by the relation (see Appendix I):

$$Nu = \left(\frac{2}{\pi Kl}\right)\left(\frac{m}{2 - m}\right)F \tag{7}$$

where l is the length over which the temperature T_2 is maintained and K is "thermometric conductivity" (or "thermal diffusivity"; *i.e.,* conductivity divided by density times specific heat).

Again in computing the transfer coefficient *Nu* it is necessary to allow for the fact that only a proportion α of the fluid is transferring heat. If the Poiseuille flow transfer coefficient is denoted by Nu', then, as before, the idealized transfer coefficient Nu_i is given by:

$$Nu_i = \alpha Nu' \tag{8}$$

It is thus a straightforward calculation to express the data of Fig. 5 in terms of the transfer coefficient and the dimensionless parameter β, equal to $Kl/4u_0a^2$, where K is the thermometric conductivity, u_0 the average fluid velocity, and a the tube radius. The data, thus expressed, are shown in Fig. 6. As would be expected the transfer coefficient is larger for bolus flow than for idealized bolus flow, especially for the larger values of $Kl/4u_0a^2$. The per cent difference between the curve and the experimental points is a measure of the greater transporting efficiency of bolus flow as compared to Poiseuille flow. This measure of the transport efficiency

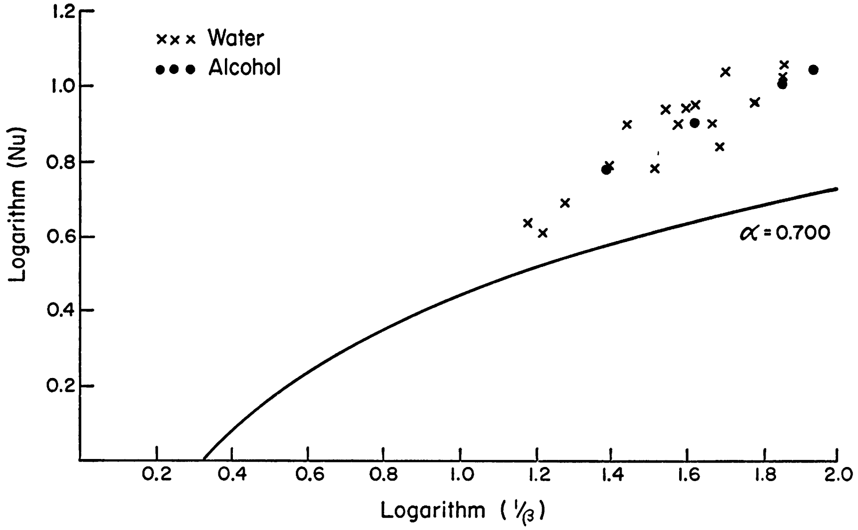

FIGURE 6 A graph of the heat (mass) transfer associated with bolus flow, plotted in terms of the dimensionless parameters *Nu* and β.

is dependent only on the value of the dimensionless parameter β. If we calculate β for the capillary, the transport efficiency will be given by this graph.

The form of behaviour in the model suggests application particularly to the pulmonary capillary. (Conditions of diffusion are more complicated in peripheral capillaries.) However, the model imitates the diffusion and mixing in the plasma only, and ignores the diffusion into the red cells adjacent to the trapped segment of plasma. These red cells will act as large "sinks" for O_2. The plasma enters a pulmonary capillary and is abruptly exposed to a higher concentration of oxygen on its periphery (this is analogous to the point at which the fluid in the model enters the cooling bath). The resistance to diffusion of O_2 through the wall is neglected. If the plasma undergoes Poiseuille flow, then it is possible to calculate, from equation 24 of the Appendix, the per cent saturation of the plasma at any point along the capillary. Let us take a capillary diameter of 10 microns, an average velocity of 0.1 cm/sec., and a diffusion constant for oxygen through plasma of 2×10^{-5} cm^2/sec. (*cf.* reference 12). The average per cent saturation of the plasma in Poiseuille flow at any distance up to 10 microns along the capillary is given by the lower curve of Fig. 7. For any point on this graph it is possible to calculate from Fig. 6 how much greater the per cent saturation would be in bolus flow. The upper curve of Fig. 7 has been calculated in this manner.

During the first micron or so bolus flow considerably facilitates equilibration. Thereafter the plasma rapidly becomes saturated. Of course in the capillary circulation the red cells act as sinks for oxygen, so that a greater total amount of O_2

is required for saturation, and in addition the gradient of O_2 tension is maintained longer. In this circumstance saturation occurs much less rapidly, and thus it is possible that bolus flow in the plasma may increase the rate of equilibration by as much as 100 per cent over the rate which would obtain if the motion in the plasma was that of Poiseuille flow.

However, it is known (*cf.* reference 13) that the pulmonary capillary blood has essentially reached gaseous equilibration with the O_2 tension in the alveolar space in the course of traversing only a fraction of the length of the capillary (perhaps one-third to one-half). Evidently the mixing motion of the plasma in bolus flow, though it may greatly facilitate the equilibration in this part of the total pathway of diffusion, may not be necessary to remove any limiting factor of the whole process.

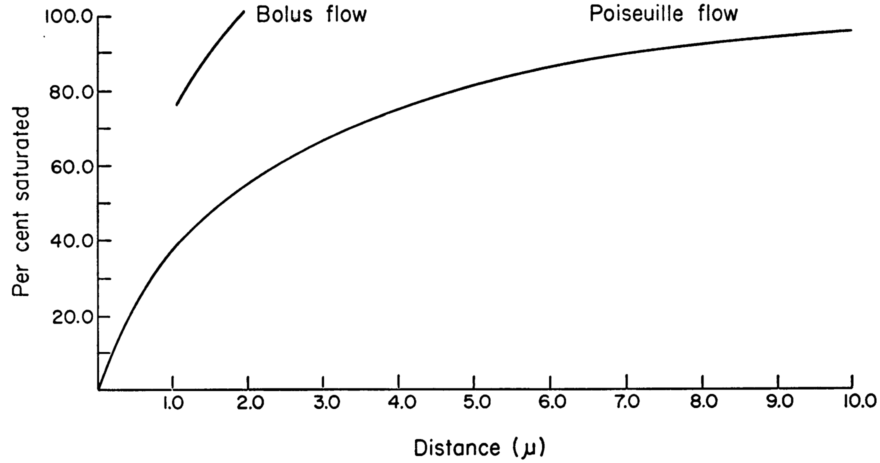

FIGURE 7 A graph, deduced from Fig. 6, depicting approximately the rate of oxygen equilibration in plasma undergoing bolus flow as compared to that undergoing Poiseuille flow (see text).

The consideration of this mixing, however, does have some theoretical importance. Roughton and his colleagues (14) have considered the series of resistances to diffusion in the whole process, namely the diffusion through the vessel wall from alveolus to lumen, the diffusion through the plasma, into the body of the red cell, and the kinetics of chemical association with haemoglobin in the red cell. They conclude that of all the factors, this last, the chemical combination of Hb, is likely to be an important factor. In their analysis of the problem they assume that the mixing in the plasma is complete. The demonstration of mixing in bolus flow gives additional support to the validity of this assumption.

The problem of diffusion of gases between blood and tissues is much more complicated in peripheral capillaries than in the lungs. Instead of an alveolar space where a uniform O_2 tension down the length of a capillary may be assumed, there will be gradients of PO_2 in the tissues surrounding the capillary, not only in a direction at right angles to the axis of flow, but also along the length of the capillary. These gradients will probably be considerable, since modern measurements of the PO_2 of cells indicate levels often far below the venous PO_2. It appears that equilibration is never achieved even in the full length of the capillary. In these circumstances the existence of "mixing" due to the peculiarities of bolus flow may be of great importance.

Forster (15) has proceeded to analyse the diffusion into the red cell, with the continuous sink of the hemoglobin throughout the cell, to derive the successive "shells" of O_2 tension within the discoid erythrocytes. This is of considerable academic interest. However, microscopic observation of red cells proceeding in bolus flow through narrow capillaries suggests that the red cell is continually changing shape, due to the non-uniformity of the capillary. It is obvious that mixing of the contents of the cell is likely to occur. Even when the capillary is larger than the red cell, a transfer of the energy of motion to the contents of the cell resulting in flow and mixing in the red cell, may well occur. Mason (16) has shown that such a circulation occurs within oil droplets suspended in water, when the suspension is flowing.

Though the model and analysis have been concerned only with the effect of true bolus flow (corresponding to the case where the capillary is smaller than the red cell) the same type of motion, though modified, will occur in the plasma between cells, when the capillary is large enough to permit these to travel through without contact with the wall, but still one at a time. In fact, a motion of this type in plasma between the cells probably occurs even in a large vessel. The importance of the radial components of the motion, however, will be less in these cases than in true bolus flow.

We gratefully acknowledge the technical assistance of Mrs. D. Elston, and of assistance in the research at one stage, of Mr. R. Kosan.
This research was supported by a grant from the Life Insurance Medical Research Fund.
Received for publication, March 20, 1961.

REFERENCES

1. Krogh, A., The Anatomy and Physiology of Capillaries, New Haven, Yale University Press, 1922.
2. Landis, E. M., Poiseuille's law and the capillary circulation, *Am. J. Physiol.*, 1933, **103**, 432.
3. Bayliss, L. E., Deformation and Flow in Biological Systems, New York, Interscience Publishers, Inc., chapter 6, 371.
4. Haynes, R. H., The Rheology of Blood, Ph.D. thesis, University of Western Ontario, London, Canada, 1957.
5. Haynes, R. H., and Burton, A. C., Role of the non-Newtonian behaviour of blood in hemodynamics, *Am. J. Physiol.*, 1959, **197**, 943.

6. Irwin, J. W., Barrage, W. S., Aimar, C. E., and Chestnut, R. W., Jr., Microscopical observations of the pulmonary arterioles, capillaries and venules of living guinea pigs and rabbits, *Anat. Rec.*, 1954, **119**, 391.
7. Muirhead, E. E., and Stirman, J. A., Pulmonary Circulation—An International Symposium, New York, Grune and Stratton, Inc., 1959, 109.
8. Prothero, J., and Burton, A. C., The physics of blood flow in capillaries. II. The capillary resistance to flow, data to be published.
9. Prothero, J., and Burton, A. C., The physics of blood flow in capillaries. III. The force required to deform erythrocytes, data to be published.
10. Langhaar, H. L., Dimensional Analysis and Theory of Models, New York, John Wiley and Sons, Inc., 1954.
11. Goldstein, S., Modern Developments in Fluid Dynamics, Oxford, Clarendon Press, 1957, **1**, chapter 7, 299; **2**, chapter 14, 616.
12. Höber, R., Physical Chemistry of Cells and Tissues, Toronto, The Blakiston Co., 1945, 13.
13. Comroe, J. H., Forster, R. E., Dubois, A. B., Briscoe, W. A., and Carlsen, E., The Lung, Chicago, The Year Book Publishers, 1955, chapter 5, 86.
14. Roughton, F. J. W., and Forster, R. E., Relative importance of diffusion and chemical reaction rates in determining rates of exchange of gases in the human lung, with special reference to the true diffusing capacity of the pulmonary membrane and the volume of blood in the lung capillaries, *J. Appl. Physiol.*, 1957, **11**, 290.
15. Forster, R. E., personal communication.
16. Rumscheidt, F. D., and Mason, S. G., Particle motions in sheared suspensions. XI. Internal circulation in fluid droplets, *Pulp and Paper Research Institute of Canada*, Montreal, Technical Report 177, 1960.

APPENDIX I

A. HEAT TRANSFER EQUATIONS

i. *General Expression*

Consider a temperature drop of $(T_1 - T_3)$ °C associated with a flow F ml/sec. of a fluid. The heat transfer is given by:

$$Q = 60\rho C_p F(T_1 - T_3) \qquad \text{cal/min.} \tag{1}$$

where ρ and C_p are the density and specific heat respectively of the fluid. In the model this heat transfer is a function of the temperature drop $(T_1 - T_2)$. We therefore define a heat transfer coefficient (C) by the relation:

$$\begin{aligned} Q &= C(T_1 - T_2) \\ \therefore\ C &= 60\rho C_p m F \qquad \text{cal/min./°C} \end{aligned} \tag{2}$$

where

$$m = (T_1 - T_3)/(T_1 - T_2)$$

ii. *Poiseuille Flow*

Theoretical relations (reference 11) are available which permit the Poiseuille heat transfer coefficient to be calculated. If the Poiseuille quantities are denoted by m', F', and C', then:

$$\begin{aligned} C' &= f(F') \\ &= 60\rho C_p m' F' \qquad \text{cal/min./°C} \end{aligned} \tag{3}$$

where

$$m' = 1 - g(\beta') \tag{4}$$

$$g(\beta') = 0.819e^{-14.627\beta'} + 0.097e^{-89.27\beta'} + \cdots . \tag{5}$$

$$\beta' = Kl/4u_0a^2 = (\pi/4)(Kl/F') \tag{6}$$

$$K = k/\rho C_p \qquad \text{cm}^2/\text{sec}. \tag{7}$$

These equations apply not only to heat diffusion but also to mass diffusion.

iii. *Idealized Bolus Flow*

In practice bolus flow in the model consisted of alternate segments of air and liquid. The air segments transfer only a negligible quantity of heat. Let the average length of the air and liquid segments be l_a and l_l respectively. Thus the proportion α of the fluid which is effective in transferring heat is given by:

$$\alpha = l_l/(l_a + l_l) \tag{8}$$

This fraction may be determined by measurements made at the end of each experiment.

When comparisons are to be made between the heat transfer coefficient associated with bolus flow and that associated with Poiseuille flow, it is important that the existence of α be taken into account. One method of doing this is to define an idealized bolus flow for which the velocity profile is parabolic, but which is otherwise identical with the given bolus flow. Such an idealized bolus flow is defined by the parametric equations:

$$F_i = \alpha F' \tag{9}$$

$$C_i = \alpha C' \tag{10}$$

where F_i and C_i are the "idealized" parameters. In a given case a comparison may be made between bolus flow (F) and idealized bolus flow by enforcing the condition:

$$F_i = F \tag{11}$$

Any difference between C and C_i may then be properly attributed to the hydrodynamic transport associated with bolus flow.

B. NUSSELT NUMBER

i. *General Expression*

When the data are expressed in terms of C, C_i, and F the results are dependent upon the physical constants of the fluid. For example a different set of curves is obtained when alcohol is employed rather than water as the liquid phase (*cf.* Fig. 5). Similarly another family of curves would be obtained if the scale of the model were altered. However, by expressing the data in the appropriate dimensionless form it is possible to obtain a single representation of all the data. When this step is taken estimates may be made of the extent to which hydrodynamic transport facilitates gas transfer within the plasma.

In the present instance the appropriate dimensionless parameters (11) are the Nusselt number (Nu) and β. These are defined by the equations:

$$Nu = Qd/kA\,\Delta T \tag{12}$$

$$\beta = (\pi/4)(Kl/F) \tag{13}$$

In so far as the present model is concerned the various terms may be defined as follows:—

$$Q = \rho C_p(T_1 - T_3)F \qquad \text{(heat transfer)} \tag{14}$$

$$A = 2\pi a l \qquad \text{(tube area)} \tag{15}$$

$$d = 2a \qquad \text{(tube diameter)} \tag{16}$$

$$\Delta T = (T_1 - 2T_2 + T_3)/2 \qquad \text{(temperature gradient)} \tag{17}$$

If the quantities defined by (3), (7), (13), (14), (15), (16), and (17) are substituted into (12) it is found that:

$$Nu = m/2\beta(2 - m) \tag{18}$$

ii. *Poiseuille Flow*

In the particular case of Poiseuille flow the Nusselt number is given by:

$$Nu' = m'/2\beta'(2 - m') \tag{19}$$

where m' and B' are given by equations (4) and (6).

iii. *Idealized Bolus Flow*

Although the Nusselt number takes account of the diffusion coefficient and the scale of the model, it does not take account of the fact that in bolus flow only a proportion α of the fluid is transporting heat (*cf.* equation 8). As in the previous case (A, iii) this factor may be taken into account by calculating the dimensionless parameters (Nu_i, β_i) associated with idealized bolus flow; that is,

$$Nu_i = \alpha Nu' \tag{20}$$

$$\beta_i = \beta'/\alpha \tag{21}$$

These equations may be deduced directly from equations (6), (9), (10), and (14).

The bolus flow data, expressed in terms of Nu and β, are depicted in Fig. 6. As expected, both the alcohol and water data fall on one curve. The theoretical curve has been calculated from equations (20) and (21). These dimensionless graphs form the basis upon which the hydrodynamic transport in the plasma is now to be estimated.

C. OXYGEN TRANSFER TO THE PLASMA IN A PULMONARY CAPILLARY

i. *Poiseuille Flow*

In the present study the effect of red cells will be neglected. The simplest case to consider is that of plasma undergoing Poiseuille flow. The plasma may be supposed to be at zero concentration initially, after which it is abruptly exposed to a constant concentration (C_2) of oxygen on its periphery. The average concentration of oxygen in the plasma (C_3) will approach that of the alveolus. In fact, with one slight modification the solution to this problem is given by equations (4) to (7). This modification consists in defining

m' in terms of concentrations. The temperatures T_1, T_2, T_3 may be replaced by the concentrations C_1, C_2, and C_3 respectively, *i.e.*,

$$m' = (C_1 - C_3)/(C_1 - C_2) \tag{22}$$

but by hypothesis $C_1 = 0$

$$\therefore\ m' = C_3/C_2 \tag{23}$$

Thus the per cent saturation of the plasma at any distance l after the plasma enters the capillary is given by:

$$\text{Per cent saturation} = 100\ m' = 100[1 - g(\beta')] \tag{24}$$

where $g(\beta')$ is specified by equations (5), (6), and (7).

Values of the various constants which are suitable for the present purposes are given by:

$$\begin{aligned} K &= 2 \times 10^{-5} \quad \text{cm}^2/\text{sec.} \quad (cf.(12)) \\ d &= 10 \times 10^{-4} \quad \text{cm} \\ u_0 &= 0\cdot 1 \quad \text{cm/sec.} \\ \beta &= 0.2l \quad (l \text{ in microns}) \end{aligned} \tag{25}$$

The lower curve of Fig. 7, which represents the rate at which equilibration with plasma takes place (in Poiseuille flow) has been calculated from equations (24) and (25).

ii. *Bolus Flow*

Consider the ordinates of an upper curve through the experimental points of Fig. 6 for a given value of β. In principle the ratio of the ordinate of the upper curve to that of the lower curve is a measure of the greater rate of equilibration associated with bolus flow compared to Poiseuille flow.

Thus in order to estimate the per cent saturation of the plasma when this undergoes bolus flow, the lower curve of Fig. 7 may be multiplied by the above ratio. When this is carried out the upper curve of Fig. 7 is obtained. It is evident that for short distances (order of 1μ) bolus flow may increase the rate of equilibration appreciably. When blood flow occurs the red cells act as sinks for oxygen. In this case the oxygen gradients are maintained for a much greater distance so that hydrodynamic transport would also be effective over much greater distances.