The shape of the mammalian erythrocyte and its respiratory function.*

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In a note on the shape of the mammalian red cell, Hartridge (1) has suggested that the erythrocyte has a form which is a compromise between that of a sphere and that of an infinitely thin disc. Gas diffusing from the surface of either of these figures would reach the central regions at the same time. The sphere, however, offers a small surface compared to its volume, while in the thin disc, the surface layers forming the envelope would be greatly increased at the expense of the contents. In the disc, moreover, gas would gain access too readily at the ends, so that the peripheral regions would be reached soonest. A body of the shape of the normal red cell meets the difficulties of the problem, for not only is the surface comparatively large for the volume, but the ends are thickened, so that gas diffusing from the surface reaches the central regions in a uniform manner.

The red cell being greatly concerned with gas transportation, it is obviously important to consider whether its special shape offers any special advantages. This we propose to do in this short paper, thus following up the suggestion of Hartridge.

Consider two equal and isolated sinks, $S_1$ and $S_2$. They will set up lines of flow,

$$\cos \theta - \cos \theta' = \text{Constant},$$

and lines of equal velocity potential

$$\frac{1}{r} + \frac{1}{r'} = \text{Constant.}$$

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Supposing that a gas starting from a line of equal velocity potential passes along a line of flow, it will thus pass at right angles to all the lines of equal velocity potential which it traverses, and finally reach one of the sinks.

If the strength of the sink $S_1$ be $m_1$, and that of $S_2$ be $m_2$, then, if the sinks are apart by a distance $a$, the lines of equal velocity potential will be

$$\frac{m_1}{r_1} + \frac{m_2}{r_2} = \frac{k}{a}.$$

Such an equation gives, for various values of $k$, a series of curves known as the equipotential curves of Cayley, who first described them in 1857 (2). In our case, the strength of the sinks is equal, or $m_1 = m_2$.

![Fig. 1. Equipotential lines for various values of $\psi$, the velocity potential. Lines above the abscissa alone are shown; the lines below the abscissa are identical with those above.](image)

Taking as a convenient strength that of 24 units, and placing the sinks 12 units = $a$, apart, one can plot these equipotential lines for various values of $\psi$, the velocity potential. This is done in Fig. 1, lines for a series of values of $\psi$ being shown. The method of plotting these lines is similar to that used for obtaining lines of equal potential due to two similar and equal magnetic poles (3): in the figure, lines above the abscissa alone are shown, the lines below the abscissa being identical with those above. These lines are, of course, identical with the lines of equal velocity potential produced by two equal sources.

It will be seen that as $\psi$ decreases, the line representing equal values of $\psi$ passes from an oval (not shown in the figure) to a curve presenting a concavity; as $\psi$ continues to decrease, the concavity becomes
deeper, and ultimately the curve splits into two loops with a double point on the abscissa mid-way between the sinks. A further decrease in \( \psi \) causes the curve to assume the form of two ovals, one lying about each sink, and finally, when the velocity potential is zero, the curve becomes two points, \( S_1 \) and \( S_2 \). From the equation of the curve, it will be seen that, if the sinks are equal in strength,

1. when \( k > 4m \), the curve consists of a large oval, with or without biconcavities;

2. when \( k = 4m \), the curve has a double point;

3. when \( k < 4m \), the curve consists of two ovals.

It will further be observed that the series of lines for equal values of \( \psi \) may be regarded as a wave surface converging on \( S_1 \) and \( S_2 \), as \( \psi \) decreases, and hence particles of gas commencing to move towards the sinks from any one line of equal velocity potential will arrive at the sinks at the same moment.

Apart from the theoretical aspect of the case, curves very similar to these equipotential curves of Cayley can be produced by a very simple experimental device, in which the conditions are analogous to
those which we are considering. A uniform ground of gelatin containing potassium chromate is formed on a glass plate, and on this is placed either one or two drops of 4 N silver nitrate, the drops being made as small as possible. The whole preparation is then kept in a moist chamber. As the silver salt diffuses from the droplet into the gelatin, a series of rings appears arranged round the drop or drops. These are shown in the photographs, for which I have to thank Dr. W. W. Taylor, who first called my attention to the Liesegang phenomenon. In the first case, a single drop was used; in the second, two drops a small distance apart. The lines which appear etched on the ground are lines of equal salt concentration, analogous, in a general way, to lines of equal velocity potential. It will be seen that in the case of the single drop, these lines are circles, but that when there are two drops, which we can look upon as two equal and similar sources, the lines are similar to the equipotential curves mentioned above. Reversing the process, and making the sources become sinks, will plainly give the same form of lines around the sinks as round the two sources. This experiment must, of course, be taken merely as an illustration, for the primary condition that the sources shall be points is not fulfilled; nevertheless, it shows the general result very well.

Selecting the curve $\psi = 7.5$, and rotating it about its minor axis
we obtain a solid of a shape approximately that of the erythrocyte. In the process, the sinks $S_1$ and $S_2$ become a circular sink, and the equipotential line which forms the curve becomes the equi-velocity potential surface of the solid of revolution. Gas starting from any point of this surface and moving inwards at right angles to it along lines of flow will reach this circular sink in the same time, irrespective of the point on the surface from which it started. Further, taking account of Fick's law of diffusion across a membrane, it will be seen that any line of equal velocity potential must also be a line of equal gas concentration; since the surface of the solid of revolution is a surface of equal velocity potential, as much gas will pass across any one unit of the surface in a given time as will pass across any other unit. The gas thus passing across the membrane will proceed along lines of flow, and reach the circular sinks.

Now, turning to the erythrocyte, which may be imagined as containing no oxygen, and floating in a fluid containing a certain quantity of dissolved gas, it is obvious that the surface of the cell must be one of equal gas concentration, and that therefore gas will pass across the surface towards the inner parts of the cell to form a series of surfaces of equal gas concentration, and of equal velocity potential. The gas starting from the equipotential surface of the cell must converge on the circular sink, which will be reached simultaneously by all particles of gas which start from the surface at the same moment. If, then, the form of the erythrocyte were that of the solid produced by the rotation of the curve $\psi = 7.5$, or, indeed, any curve of equal velocity potential, about $yy'$, that form would be one peculiarly suited to the even and orderly distribution of gas throughout its contents.

The passage of gas from the surface of a solid of this form results, of course, in a progressive loss of strength of the circular sink. This, however, in no way alters the general nature of the diffusion process, for if, by gas entering the cell, the strength of the sink becomes halved, then the surface $\psi = 7.5$ will become the surface $\psi = \frac{7.5}{2}$ but will remain of the same form. Alterations in the numerical strength of the sink, such as would be produced by gas entering the cell, do not, therefore, affect the form of the surface, but only its numerical strength. Nor does the fact that the sink may become a source
influence the manner of diffusion of gas across the surfaces of equal
velocity potential, except as regards the direction of the flow.

It now remains to be seen to what extent the equipotential curves
of Cayley can provide a satisfactory fit to the shape of the red cell,
for the nearer the shape of the cell to that of the curves, the better
will it be adapted for the purposes of the flow of gases within it. The
goodness of fit of the curves may be tested in two ways: by comparing
the dimensions of the curves with those of the cell, as ascertained by
measurement, and by comparing the volume enclosed by the different
equipotential curves with that of the red cell. It is, to begin with,
clear that the only one of the equipotential curves with which we need
care is $\psi = 7.5$, curves for other values of $\psi$ being obviously inapplicable to the shape of the cell.

Photomicrographs show that the erythrocyte is not quite so
rounded at the ends as is this curve, and that its concavity is not
quite so deep. It is admittedly difficult to judge of these matters from
even the most carefully taken photomicrographs, for one is very apt
to be deceived, as regards the general contour of the cell, by the slight
flattening which occurs when the cells are in rouleaux—it being diffi-
cult to obtain them in profile unless thus arranged—and also to under-
estimate the depth of the concavity. Nevertheless, one cannot help
coming to the conclusion that the equipotential curves are too great
at their greatest ordinates, and too narrow at the point where $x = 0$,
to represent the red cell with great accuracy.

The crucial test, however, lies in the comparison of the volume en-
closed by the rotated curve $\psi = 7.5$, with the surface of the erythro-
ocyte. The equipotential curve lends itself to neither rectification nor
quadrature, which is not surprising, as it is of the eighth degree, and
very complicated in Cartesians. The volume of the solid of revolution
produced by its rotation about $yy'$ must therefore be found by graphi-
cal methods and the use of the theorems of Pappus. In a like manner
we can find the surface of the solid of revolution.

For the curve $\psi = 7.5$, rotated about $yy'$,

<table>
<thead>
<tr>
<th>Description</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Major axis</td>
<td>20 units.</td>
</tr>
<tr>
<td>Area of quadrant</td>
<td>34.45 units².</td>
</tr>
<tr>
<td>C. gr. of area</td>
<td>5.33</td>
</tr>
<tr>
<td>Arc of quadrant</td>
<td>13.0 units.</td>
</tr>
</tbody>
</table>
Reducing this to the scale of a human red cell of diameter 8.8μ, the volume of the solid of revolution works out at approximately 196μ³. The volume of the erythrocyte can be obtained with considerable accuracy by converting it into the spherical form by immersion in isotonic saline (4, 5) and calculating its volume from measurements while it is in this spherical state. Such a procedure gives, as an average volume for the human red cell, about 110μ³, and, even if experimental error be allowed for, to the fullest extent, no figure greater than 120μ³. Comparing this with the volume for the solid of revolution derived from the curve ψ = 7.5, it is plain that the discrepancy, which amounts to about 60 per cent, is too great to be allowed. It must therefore be concluded that the shape of the erythrocyte cannot be described by one of the equipotential curves of Cayley, convenient though such a description would be: on the other hand, the general resemblance between the erythrocyte and these solids with equipotential surfaces should not be overlooked, for the more complete the resemblance, the better is the cell adapted in its function of gas exchange. The resemblance which does in fact exist is such as to make the efficiency of the cell very great compared with that of most other figures of the same volume, and very much greater than that of a spherical form, for, in order to obtain the same rapidity of gas diffusion for the same volume distributed in spheres, we would require approximately nine spheres each of one-ninth the volume. Even allowing for the fact that there is not a perfect agreement of the form of the red cell with that of a body with an equipotential surface, the efficiency of the cell for gas interchange is very great, as Hartridge has noted.

Taking a body of exactly the form of the red cell, it ought to be possible to determine the manner in which gas will pass throughout its contents by proceeding on lines similar to these. The lines of flow and the surfaces of equal velocity-potential will be nearly, but not quite, the same as those for a body with a surface given by the revolution of one of Cayley’s curves, and the diffusion of gas will take place according to the same general scheme. But the sinks will have to be
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postulated as something other than points, and in their neighbourhood the phenomena will become very complex: we have therefore not thought it worth while to pursue the study further, as in purpose this paper is more suggestive than complete.

This consideration of the advantage produced by the form of the cell approximating to that of a solid with an equipotential surface does not, of course, offer any explanation as to why this form should be taken up. The rotation of the line \( \psi = 8 \) about \( yy' \) would produce an even more adapted solid, but yet the form of this solid is far from that of the red cell. The reason for the assumption of the special shape of the erythrocyte is to be sought along very different lines, and though the approximation to the form of a solid with an equipotential surface may be very interesting, that approximation may be nothing but a coincidence.

BIBLIOGRAPHY.