Many extensive investigations have been made for the purpose of
determining the electrical conductivity of cell suspensions such as
blood, body tissues, bacterial suspensions, and the like; the biological
importance of this constant being that it would give some idea
of the permeability of the cells (or the cell walls) in question. The
investigations of the conductivity of blood by Bugarszky and Tangl,¹
Fraenkel,² Oker-Blom,³ Roth,⁴ Stewart,⁵ and others are well known.
These investigators found that the red corpuscles act as perfect
insulators,⁶ so that the electric current exclusively passes in the
space between them. Oker-Blom, for instance, showed that the resis-
tance of a blood cell suspension of a certain volume concentra-

¹ Bugarszky, S., and Tangl, F., Eine Methode zur Bestimmung des relativen
² Fraenkel, P., Ueber die Bestimmung des Blutkörperchenvolumens aus der
³ Oker-Blom, M., Thierische Stoffe und Gewebe in physikalisch-chemischer
Beziehung, Arch. ges. Physiol., 1900, lxxix, 510.
⁴ Roth, W., Elektrische Leitfähigkeit tierischer Flüssigkeiten, Zentr. Physiol.,
1897–98, xi, 271.
⁵ Stewart, G. N., The behaviour of the hemoglobin and electrolytes of the
coloured corpuscles when blood is laked. J. Physiol., 1899, xxiv, 211. The relative
volume of weight of corpuscles and plasma in blood, 356. The mechanism of
hemolysis with special reference to the relations of electrolytes to cells, J.
Pharmacol. and Exp. Therap., 1909–10, i, 49.
⁶ It is to be understood that this apparently high resistance to an electric
current of low frequency may be wholly due to polarization at the surfaces of
the red corpuscles.

375
tion was equal to the resistance of a suspension of quartz sand of equal volume concentration in the same suspending medium. The ratio of the resistance of the blood suspension to the resistance of the suspending medium in this case is, therefore, a function of the volume concentration of the corpuscles alone. Experience shows that this function is independent of the size and only slightly dependent on the shape of the suspended particles. In the case of suspensions of cells such as bacteria, part of the current generally goes through the intercellular liquid and part goes through the cells. The resulting conductivity of the suspension is, therefore, a function both of the specific conductivity of the suspending medium and of the specific conductivity of the cellular substance as well as of the volume concentration.

The purpose of the present paper is to derive a formula whereby the specific conductivity of the cellular substance may be calculated from observed values of the specific conductivity of suspensions of the cells in question and of the suspending medium. This formula will be here derived for the simple case of a dilute suspension of spherical homogeneous cells. Nevertheless, the formula can be applied also with fair accuracy to the more general case of a suspension of homogeneous ellipsoids, for it is found that up to a quite large value for the eccentricity of the ellipsoids the same formula as that for homogeneous spheres is applicable. This is in accord with the findings of Oker-Blom and Fraenkel mentioned above, that the conductivity of suspensions of red corpuscles and of quartz sand depends only on the volume concentration of the suspensions.

It may be well at this point to consider briefly the assumption that the cells are homogeneous. In general, a single cell comprises many regions of varying conductivities, as indicated, for instance, by the very large polarization capacity of all living cells. Thus, it is probable that all cells are surrounded by a thin membrane which is semipermeable and in consequence has a comparatively high resistance. However, the formula applicable to a cell consisting of several concentric layers of different conductivities will be identical with that which we shall develop for a homogeneous sphere, the specific conductivity of the homogeneous sphere being replaced by a
certain average value of the conductivities of the different layers of the non-homogeneous cell.\(^7\)

We shall, therefore, consider the case of a suspension of homogeneous spheres (radius \(a\), specific conductivity of cell material \(k_1\)) in a medium of specific conductivity \(k_2\). We shall assume that the suspension is so diluted that each sphere acts as if it were alone in the suspending medium—that is, that the spheres are so far apart that the current lines become parallel in the space between them. As will be shown below, a comparison with experimental data shows that within an accuracy of a few per cent this assumption is fulfilled with concentrations from zero up to 30 per cent.

The treatment of the general case of an ellipsoid having a surface layer of a conductivity different from that of its interior will be taken up in a paper which will appear in the Physical Review. This case includes that of a homogeneous polarizable ellipsoid.

\(^7\) The treatment of the general case of an ellipsoid having a surface layer of a conductivity different from that of its interior will be taken up in a paper which will appear in the Physical Review. This case includes that of a homogeneous polarizable ellipsoid.
Let us consider first the case of a single sphere suspended in the medium (Fig. 1). We assume that the medium is placed in an electrolytic cell with a volume of 1 cc. and that a constant electrical current, \( i \), passes through the suspension. The difference in potential of the electrodes we shall designate as \( V \). Since the electrodes are 1 cm. apart, \( V \) is equal to the electric force. The surface of the sphere is the seat of a certain distribution of surface charges. The surface charge, \( S \), at an arbitrary point can be developed into a series of surface harmonics.\(^8\)

\[
S = \alpha_0 S_0 + \alpha_1 S_1 + \alpha_2 S_2 + \ldots + \alpha_n S_n + \ldots = \sum \alpha_n S_n.
\]

The potential at any point outside the sphere is\(^9\)

\[
V_{\text{ext}} = 4\pi \sum \frac{\alpha_n + 1}{(2n + 1)} \frac{S_n}{r^{n+1}}
\]  
\( r \) being the distance of the point from the center of the sphere. The potential at an internal point is

\[
V_{\text{int}} = 4\pi \sum \frac{\alpha_n}{(2n + 1)} \frac{S_n}{r^{n-1}}
\]

The component of the electric force perpendicular to the surface at a point situated on the external surface of the sphere is

\[
F_{\text{ext}} = -\frac{dV_{\text{ext}}}{dr} = 4\pi \frac{n + 1}{2n + 1} \alpha_n S_n
\]

At a point situated on the internal surface of the sphere we have for the same component:

\[
F_{\text{int}} = -\frac{dV_{\text{int}}}{dr} = -4\pi \frac{n}{2n + 1} \alpha_n S_n.
\]

These forces are the forces due to the electric charges on the spheres. The total forces are obtained by adding the component of the original electric force due to the surface charges on the electrodes of the electrolytic cell. This component is equal to \(-V\sin \varphi\) (Fig. 1).

The electric force has a discontinuity at the surface of the sphere. At the moment when the current through the suspension is started, the electric force is the same on the two opposite sides of the surface of the sphere. As soon as the current is started, since the conductivity of the substance of the sphere is different from the conductivity of the suspending medium, a different amount of electricity will be carried to the outside of an element of surface from that which is being carried away from the inside at the same instant. Thus, an accumulation of charge on the surface begins and is continued until the difference between the electric forces on the two sides of the surfaces of the sphere becomes so large that the same amount of electricity is carried to the outside of the surface as is carried away from the inside in the same time interval. That is, the equation of equilibrium is

\[
(F_{\text{ext.}} - V\sin \varphi) k_1 = (F_{\text{int.}} - V\sin \varphi) k_2
\]

or

\[
\left(4 \pi \sum_{n=1}^{\infty} \frac{n+1}{2n+1} \alpha_n S_n - V\sin \varphi \right) k_1 = \left(-4 \pi \sum_{n=1}^{\infty} \frac{n}{2n+1} \alpha_n S_n - V\sin \varphi \right) k_2 \tag{3}
\]

We have

\[S_2 = 1\]

\[S_1 = \sin \varphi\]

\[S_2 = \frac{1}{2}(3 \sin \varphi^2 - 1)\]

In order that the right and the left side of equation (3) be identities it is necessary that \(\alpha_n\) be made zero for all values of \(n\) except 1. Consequently equation (3) reduces to

\[
\left(4\pi \cdot \frac{3}{2} \alpha_1 \sin \varphi - V\sin \varphi \right) k_1 = \left(-4\pi \cdot \frac{3}{2} \alpha_1 \sin \varphi - V\sin \varphi \right) k_2
\]

from which we derive the value of \(\alpha_1\).

\[
\alpha_1 = \frac{V}{4\pi} \frac{(k_1 - k_2)}{3(2k_1 + k_2)}
\]

\(^9\) Jeans,\(^8\) p. 224.
Substituting this value for \( \alpha_1 \) in equation (1) and (2) for the potentials \( V_{\text{ext.}} \) and \( V_{\text{int.}} \) we now obtain

\[
V_{\text{ext.}}(\varphi) = a \cdot \frac{V (k_1 - k_2)}{(2k_1 + k_2)} \sin \varphi \quad \text{(1)}
\]

\[
V_{\text{int.}}(\varphi) = a \cdot \frac{V (k_1 - k_2)}{(2k_1 + k_2)} \sin \varphi \quad \text{(2)}
\]

The conductivity of the suspension can now be calculated by means of the following method. The space between the electrodes of the electrolytic cell is divided into an infinite number of volume elements, \( dS, dx \); \( dS \) being a surface element parallel to the electrodes and \( dx \) a line element perpendicular to the electrodes. If \( F_x \) is the component of the electric force along \( x \) then by using Ohm's law

\[
\int \int F_x \cdot dS \cdot dx \cdot k_1 + \int \int F_x \cdot dS \cdot dx \cdot k_2 = \int \int dx = V \cdot k
\]

\( k \) being the conductivity of the suspension. The first integration is taken over all volume elements outside the sphere, the second integration over all elements inside the sphere.

In carrying through this integration on the left side we integrate all elements situated in the cylinder defined by a fixed \( dS \). If this cylinder does not cross the sphere, its elements contribute solely to the first integral. This contribution is

\[
\text{Contr. 1} = \int \int F_x \cdot dS \cdot dx \cdot k_1 = \int k_1 \cdot dS \cdot \int F_x \cdot dx = k_1 V \cdot \int dS = k_1 V \cdot (1 - \pi a^2).
\]

The contribution of the cylinders crossing the sphere (as indicated in Fig. 1) to the left side of our equation is

\[
\text{Contr. 2} = \int \int F_x \cdot dS \cdot dx \cdot k_1 + \int \int F_x \cdot dS \cdot dx \cdot k_2 = \int (V - \Delta V) \cdot dS \cdot k_1 + \int \Delta V \cdot dS \cdot k_2
\]

\( \Delta V \) being the difference in potential between the two points, \( P_1 \) and \( P_2 \), where the cylinder crosses the surface of the sphere. Then, according to what was found above
\[
\Delta V = \int_{\phi=0}^{\phi=\pi} (\phi_2 - \phi_1) a \sin \phi + 2 V a \sin \phi
\]

Consequently taking
\[
dS = 2 \pi a \cos \phi \, d(\cos \phi)
\]

Contr. \(1 = \int V dS \cdot k_1 + \int_{\phi=0}^{\phi=\pi} \Delta V \left(\phi_2 - \phi_1\right) 2 \pi a \cos \phi \, d(\cos \phi)
\]

Contr. \(2 = \int V dS \cdot k_1 + \int_{\phi=0}^{\phi=\pi} \Delta V \left(\phi_2 - \phi_1\right) V a^3 \int_{\phi=0}^{\phi=\pi} \sin^3 \phi \, d(\sin \phi)
\]

Using the expressions obtained for Contr. \(1 \) and Contr. \(2 \), equation (4) becomes
\[
V \left(1 - a^3\right) k_1 + \pi a^3 V k_1 \left(1 + \frac{4 \left(k_3 - k_1\right)}{2 k_1 + k_3} a\right) = V k
\]

\[
V k_1 + \frac{4 \left(k_3 - k_1\right)}{2 k_1 + k_3} \pi a^3 V k_1 = V k
\]

\[
k = k_1 + \frac{4 \left(k_3 - k_1\right)}{2 k_1 + k_3} a^3 k_1
\]

Calling the volume of the sphere \( \rho \) we obtain
\[
k = \left(1 + \frac{3 \left(k_3 - k_1\right)}{2 k_1 - k_3} \rho\right) k_1
\]

or
\[
\frac{k}{k_1} = 1 + \frac{3 \left(1 - \frac{k_1}{k_3}\right)}{1 + 2 \frac{k_1}{k_3} \rho}\]
This formula with \( \rho \) being the total volume of spheres per cc. will hold for a suspension of spheres so diluted that each sphere deforms the current lines of the original current independently of every other.

We see that \( \frac{k}{k_1} \) is a linear function of \( \rho \).

From equation (5) we derive the value for \( \frac{k_2}{k_1} \)

\[
\frac{k_2}{k_1} = \frac{1 + 2 \frac{k}{k_1} - 1}{3 \rho} + \frac{k}{k_1} - 1 \quad (6)
\]

The above formula shows that for diluted cell suspensions \( \frac{k}{k_1} \) is independent of the concentration. In Fig. 2 \( \frac{k_2}{k_1} \) is plotted against \( \frac{k}{k_1} - 1 \) for values of \( \frac{k}{k_1} > 1 \), while \( \frac{k}{k_1} \) is plotted for \( \frac{k}{k_1} < 1 \).

A test of the theory here developed has been made by applying formula (6) to red corpuscles. As was stated above, red corpuscles are very nearly non-conductors; that is, \( k_2 = 0 \). According to our theory \( \frac{1}{3 \rho} \) should therefore have the constant value of \(- \frac{1}{3}\). In Table I are given the values of \( \frac{k}{k_1} - 1 \) calculated from data given by Fraenckel for red corpuscles of man, dog, horse, and cow. It is seen that the experimental value of \( \frac{k}{k_1} - 1 \) has the theoretical value
TABLE I.

<table>
<thead>
<tr>
<th>$\frac{b}{b_i-1}$</th>
<th>$\rho$ per cent</th>
</tr>
</thead>
<tbody>
<tr>
<td>$-0.53$</td>
<td>10</td>
</tr>
<tr>
<td>$-0.52$</td>
<td>20</td>
</tr>
<tr>
<td>$-0.50$</td>
<td>30</td>
</tr>
<tr>
<td>$-0.47$</td>
<td>40</td>
</tr>
<tr>
<td>$-0.44$</td>
<td>50</td>
</tr>
</tbody>
</table>
of $-0.50$ up to concentrations of between 30 and 40 per cent. The formula here developed can therefore be expected to hold up to this limit of concentration.

Experiments dealing with the applications of the theory here developed to colloids (especially graphite suspensions) and to suspensions of different living cells are at present being made in this laboratory and will be reported in a later paper.