

THE ELECTRICAL CONDUCTANCE OF SUSPENSIONS OF
ELLIPSOIDS AND ITS RELATION TO THE STUDY
OF AVIAN ERYTHROCYTES*

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I

INTRODUCTION

The electrical conductance of a colloidal suspension is a function not only of the individual conductances of the particles and the suspending medium, and of the fraction of the volume occupied by the particles, but also of the shape of the particles, their orientation, and at high concentrations, because of electrical interaction between particles, their array. In the cases where the equations have been developed the electrical conductance measurements on suspensions can provide information either on volume, symmetry, or conductance of the colloidal particles if the values of the other variables are known.

Maxwell (1) derived the equation

$$\frac{(k/k_1) - 1}{(k/k_1) + 2} = \rho \frac{(k_2/k_1) - 1}{(k_2/k_1) + 2} \quad (1)$$

for homogeneous suspensions of non-polarizable spheres where k , k_1 , and k_2 , are specific conductances of suspension, medium, and particles respectively and ρ is the fraction of the total volume occupied by the suspended phase. The equation was experimentally verified for fat globules in cream by Fricke and Morse (2). Parallel equations for the dielectric constant of suspensions have been experimentally verified by Millikan (3) for emulsions of water in benzene and chloroform.

In order to apply the method to suspensions of non-spherical particles

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Fricke (4) considered the case of spheroids and expressed his results in the form

$$k = k_1 + \frac{1/3\rho}{1-\rho} \sum^{\alpha=a,b,c} \frac{2(k_2 - k)}{2 + abcL_\alpha(k_2/k_1 - 1)} \quad (2)$$

where ρ , k , k_1 , and k_2 are the same as above, a , b , and c are the axial lengths of the ellipsoid, and L_a , L_b , and L_c are integrals which are functions of a , b , and c and are dependent not upon the absolute magnitudes of these quantities but on the ratios, a/c and b/c . Equation (2) reduces to the form

$$\frac{(k/k_1) - 1}{(k/k_1) + x} = \rho \left[\frac{(k_2/k_1) - 1}{(k_2/k_1) + x} \right] \quad (2')$$

in which x , the form factor, is a function of the axial ratio of the particles and of the conductance ratio (k_2/k_1). Choosing as his model the oblate spheroid he showed that the conductance of suspensions of the biconcave discoidal red cells of mammals closely fitted his equations when a suitable value for the axial ratio of the cells was chosen. Due, however, to deviations of his model from the actual form of the cell the axial ratio which gave the best results in determining ρ differed slightly from the ratio obtained by direct measurement.

To make the method more widely applicable we have extended Fricke's development and have obtained solutions for a more general model, an ellipsoid with three axes different which rather closely approximates the normal shape of the avian erythrocyte. For the case most often met with in practice, k_2 is zero. The equation for ellipsoids assumes the form

$$\rho = \frac{(r/r_1) - 1}{(r/r_1) - 1 + f} \quad (3)$$

where r/r_1 is the ratio of the specific resistance of the suspension to that of the medium, ρ is as before the fraction of the volume occupied by the particles, and f is a factor which depends upon the axial ratios of the ellipsoids. Tables of f for various values of the axial ratios will be presented.

It was observed in confirmation of previous workers that marked changes in conductance occur when the suspension is stirred. The silky reflection pattern from the surface of a suspension swirled in a beaker suggested that the motion of the liquid orients the particles. Orientation was confirmed by light transmission measurements in a specially designed flow cell. We have therefore considered in the theory the effect of orientation upon the electrical conductance of the suspension. Conductivity cells were designed in which the suspension was allowed to flow during the measurements.

Changes in the direction predicted by the theory were observed and the effect shown to be a function of the degree of asymmetry of the particles. When the particles were converted to the spherical form the flow effect, as would be expected, disappeared.

Tables showing the dependence of the form factor, f , upon the axial ratios of the particles in random and four types of directed orientation are presented. With properly designed conductivity cells it should be possible to extend the method to shape studies of submicroscopic particles.

II

Theory

Fundamental Equation

Following Fricke's derivation which neglects the presence of ions inside and outside the particle and also neglects the electrical interaction between the particles themselves, Laplace's equation is used to obtain formally the potential inside and outside the particle due to charges on its surface. By superposition of these potentials upon that of the external field the electric force can be expressed as a function of the volume fraction, ρ , occupied by the particles, the axial ratios, the applied potential V , and the conductances of the particle and medium. For the case in which the a axis of the ellipse is oriented parallel to the external field the equation

$$(F/V)(1 - \rho) + \frac{2(F/V)\rho}{2 + abcL_a[(k_2/k_1) - 1]} = 1 \quad (4)$$

results, where L_a is the integral

$$\int_0^\infty \frac{d\lambda}{(a^2 + \lambda) \sqrt{(a^2 + \lambda)(b^2 + \lambda)(c^2 + \lambda)}}$$

and F is the electrical force. By applying Ohm's law the additional relation involving F/V and the other quantities is obtained:

$$k = k_1 + \rho \left(\frac{2k_1[(k_1/k_2) - 1]F/V}{2 + abcL_a[(k_2/k_1) - 1]} \right). \quad (5)$$

Eliminating F/V between the equations (4) and (5) we get the final result

$$k = k_1 + \left(\frac{\rho}{1 - \rho} \right) \left(\frac{2(k_2 - k)}{2 + abcL_a[(k_2/k_1) - 1]} \right) \quad (6)$$

In the corresponding equations for the cases in which the axes b and c are parallel to the electric field the integral L_a is replaced by L_b and L_c which are of the same form.

For random orientation averaging is accomplished by assuming that one-third of the particles is oriented in each direction. It follows that

$$k = k_1 + \frac{1/3\rho}{1 - \rho} \sum_{\alpha=a,b,c} \frac{2(k_2 - k)}{2 + abcL_\alpha[(k_2/k_1) - 1]} \tag{7}$$

Evaluation of the Integrals

In order to apply these equations the three integrals

$$L_a = \int_0^\infty \frac{d\lambda}{(a^2 + \lambda)^{3/2}(b^2 + \lambda)^{1/2}(c^2 + \lambda)^{1/2}}$$

$$L_b = \int_0^\infty \frac{d\lambda}{(b^2 + \lambda)^{3/2}(c^2 + \lambda)^{1/2}(a^2 + \lambda)^{1/2}}$$

$$L_c = \int_0^\infty \frac{d\lambda}{(c^2 + \lambda)^{3/2}(a^2 + \lambda)^{1/2}(b^2 + \lambda)^{1/2}}$$

must be evaluated. This is equivalent to evaluating any one of the L_α integrals, let us say L_a , for the three cases in which a takes successively the values of the three axes of the ellipse, and b and c take the values of the other two axes.

Letting $\lambda = (1/y) - a^2$ the integral becomes when simplified

$$L_a = \int_1^{1/a^2} \frac{y^{1/2} dy}{\sqrt{[(b^2 - a^2)y + 1][(c^2 - a^2)y + 1]}} \tag{8}$$

With the substitution $y = \frac{-\psi^2}{b^2 - a^2}$ we obtain eventually

$$L_a = \frac{2}{(a^2 - b^2)^{3/2}} \int_0^{\sqrt{a^2 - b^2}/a} \frac{\psi^2 d\psi}{\sqrt{(1 - \psi^2)(1 - q^2\psi^2)}} \tag{9}$$

where

$$q^2 = (c^2 - a^2)/(b^2 - a^2).$$

Rearranging we get

$$L_a = \frac{2}{q^2(a^2 - b^2)^{3/2}} \left[\int_0^{\sqrt{a^2 - b^2}/a} \frac{d\psi}{\sqrt{(1 - \psi^2)(1 - q^2\psi^2)}} \right. \tag{10}$$

$$\left. - \int_0^{\sqrt{a^2 - b^2}/a} \sqrt{\frac{1 - q^2\psi^2}{1 - \psi^2}} d\psi \right]$$

The integrals *i* and *ii* are standard elliptic integrals of the first and second kind respectively. To convert them to the forms in which they are most frequently tabulated¹ let $\sin \varphi = \psi$

$$L_a = \frac{2}{q^2(a^2 - b^2)^{3/2}} \left[\int_0^{\sin^{-1}[(a^2 - b^2)^{1/2}/a]} \frac{d\varphi}{\sqrt{1 - q^2 \sin^2 \varphi}} - \int_0^{\sin^{-1}[(a^2 - b^2)^{1/2}/a]} \frac{d\varphi}{\sqrt{1 - q^2 \sin^2 \varphi}} \right]$$

or

$$L_a = \frac{2}{(c^2 - a^2)(a^2 - b^2)^{1/2}} \left[F \left(\sqrt{\frac{c^2 - a^2}{b^2 - a^2}}, \sin^{-1} \frac{\sqrt{a^2 - b^2}}{a} \right) - E \left(\sqrt{\frac{c^2 - a^2}{b^2 - a^2}}, \sin^{-1} \frac{\sqrt{a^2 - b^2}}{a} \right) \right] \tag{11}$$

Case I, $a > c > b$

Equation (11) is real only for the case in which q is positive and can only be evaluated when $q < 1$; *i.e.*, $a < c < b$ or $a > c > b$. Of these two only the second case can be evaluated directly from the tables, for when $a < c < b$ the upper limit of the integrals becomes imaginary. Since b and c are interchangeable there remain only two other cases to be evaluated, namely $a < c < b$ and $b < a < c$.

Case II, $a < c < b$

For $a < c < b$ let $i\varphi = \psi$ in equation (10). The equation becomes

$$L_a = \frac{2}{q^2(b^2 - a^2)^{3/2}} \left[\int_0^{\sqrt{(b^2 - a^2)}/a} \frac{\sqrt{1 + q^2 \varphi^2}}{\sqrt{1 + \varphi^2}} d\varphi \tag{i} - \int_0^{\sqrt{(b^2 - a^2)}/a} \frac{d\varphi}{\sqrt{(1 + \varphi^2)(1 + q^2 \varphi^2)}} \tag{ii} \right] \tag{12}$$

The second integral (ii) in equation (12) is equivalent to

$$F [l, \tan^{-1} (\sqrt{b^2 - a^2}/a)]$$

where l is given by $l^2 = 1 - q^2 = (b^2 - c^2)/(b^2 - a^2)$ when $0 < l < 1$. The requirement $0 < l < 1$ is met when $a < c < b$.

¹ Pierce, B., A short table of integrals, Boston, Ginn and Co., 3rd revised edition, 1929.

To evaluate the first integral in equation (13) we make the substitution $\varphi = \tan \psi$ and obtain

$$(12)_i = \int_1^{\tan^{-1}(\sqrt{b^2 - a^2}/a)} \frac{\sqrt{1 - q^2} \sin \psi}{\cos^2 \psi} d\psi$$

which has been evaluated,²

$$(12)_i = (\sqrt{b^2 - a^2}/a) \sqrt{1 - p^2} \sin^2 (\tan^{-1} \sqrt{a^2 - b^2}/a) + F[p, \tan^{-1} (\sqrt{b^2 - a^2}/a)] - E[p, \tan^{-1} (\sqrt{b^2 - a^2}/a)] \tag{13}$$

where

$$p^2 = 1 - q^2 = (b^2 - c^2)/(b^2 - a^2)$$

Case III, $b < a < c$

The third case to be solved is $b < a < c$. We return to equation (10) and make the following substitutions and transformations

$$m^2 = -q^2, \quad \sqrt{a^2 - b^2}/a = u, \quad \text{and} \quad \psi = \sqrt{1 - p^2}$$

The first integral of (10) becomes

$$(10)_i = \int_1^{\sqrt{1-u^2}} \frac{-dt}{\sqrt{(1-p^2)(1+m^2-m^2p^2)}} \tag{14}$$

or after rearrangement

$$(10)_i = \frac{1}{\sqrt{1+m^2}} \int_0^1 \frac{dt}{\sqrt{(1-p^2)(1-p^2m^2)/(1+m^2)}} - \frac{1}{\sqrt{1+m^2}} \int_0^{\sqrt{1-u^2}} \frac{dt}{\sqrt{(1-p^2)(1-p^2m^2)/(1+m^2)}} \tag{15}$$

It follows immediately that in standard form

$$(10)_i = \sqrt{\frac{(b^2 - a^2)}{(b^2 - c^2)}} \left[F \left(\frac{\sqrt{a^2 - c^2}}{\sqrt{b^2 - c^2}}, \pi/2 \right) - F \left(\frac{\sqrt{a^2 - c^2}}{\sqrt{b^2 - c^2}}, \sin^{-1} b/a \right) \right]$$

Integration of (10)_{ii} is achieved by the substitution $m^2 = -q^2$, and the transformation $\cos \varphi = \psi$. The integral, (10)_{ii}, becomes

$$\sqrt{1+m^2} \int_{\cos^{-1}(\sqrt{a^2-b^2}/a)}^{\pi/2} \sqrt{[(1-m^2)/(1+m^2)] \sin^2 \varphi} d\varphi$$

or

$$(10)_{ii} = \sqrt{\frac{b^2 - c^2}{b^2 - a^2}} \left[E \left(\sqrt{\frac{a^2 - c^2}{b^2 - c^2}}, \pi/2 \right) - E \left(\sqrt{\frac{a^2 - c^2}{b^2 - c^2}}, \cos^{-1} \frac{\sqrt{a^2 - b^2}}{a} \right) \right] \tag{16}$$

² Potin, L., Formules et tables numerique, Paris, G. Doin, Gauthier, Villars and Co., 1925, 712.

Summing up, the three integrals necessary for calculations with equations (7), (6), or (8) are given below in terms of the standard elliptic integrals of the first and second kind $F(q, \varphi)$ and $E(q, \varphi)$, respectively

$$a > c > b \quad L_a = \frac{2}{(a^2 - c^2)(a^2 - b^2)^{1/2}} \left[F \left(\sqrt{\frac{c^2 - a^2}{b^2 - a^2}}, \sin^{-1} \frac{\sqrt{a^2 - b^2}}{a} \right) - E \left(\sqrt{\frac{c^2 - a^2}{b^2 - a^2}}, \sin^{-1} \frac{\sqrt{a^2 - b^2}}{a} \right) \right]$$

$$a < c < b \quad L_a = \frac{2}{(c^2 - a^2)(b^2 - a^2)^{1/2}} \left[\frac{\sqrt{b^2 - a^2}}{a} \sqrt{1 - \frac{b^2 - c^2}{b^2 - a^2} \sin^2 \left(\tan^{-1} \frac{\sqrt{b^2 - a^2}}{a} \right)} - E \left(\sqrt{\frac{b^2 - c^2}{b^2 - a^2}}, \tan^{-1} \frac{\sqrt{b^2 - a^2}}{a} \right) \right]$$

$$b < a < c \quad L_a = \frac{2\sqrt{c^2 - b^2}}{(c^2 - a^2)(a^2 - b^2)} \left[E \left(\sqrt{\frac{a^2 - c^2}{b^2 - c^2}}, \pi/2 \right) - E \left(\sqrt{\frac{a^2 - c^2}{b^2 - c^2}}, \sin^{-1} b/a \right) \right] - \frac{2}{(c^2 - a^2)(c^2 - b^2)^{1/2}} \left[F \left(\sqrt{\frac{a^2 - c^2}{b^2 - c^2}}, \pi/2 \right) - F \left(\sqrt{\frac{a^2 - c^2}{b^2 - c^2}}, \sin^{-1} b/a \right) \right]$$

The values of $abc L_a$ for different sets of axial ratios and for the three orientations in the external field are given in Table I. Instead of absolute values of the absolute length we use the axial ratios referred to the smallest axis as unity.

Ellipsoids of Revolution

For ellipsoids of revolution (rods and discs) we arrive at a similar set of equations. Considering the prolate spheroid with axes a, b, c and with $b = c$ and $a > b$ we have

$$k = k_1 - \frac{1/3\rho}{1 - \rho} \sum^{\alpha=a_1, b, b} \frac{2}{2 - ab^2 L_a} \tag{17}$$

The two integrals to be obtained are

$$L_a = \int_0^\infty \frac{d\lambda}{(a^2 + \lambda)^{3/2}(b^2 + \lambda)} \tag{18}$$

$$L_b = \int_0^\infty \frac{d\lambda}{(b^2 + \lambda)^{3/2}(a^2 + \lambda)^{1/2}} \tag{19}$$

Integrating by parts

$$L_a = \frac{2}{ab^2} - 2 \int_0^\infty \frac{d\lambda}{(a^2 + \lambda)^{1/2}(b^2 + \lambda)^2} = \frac{2}{ab^2} - 2L_b$$

Let $b^2 + \lambda = \delta$, then

$$L_b = \int_{b^2}^{\infty} \frac{d\delta}{(\sqrt{a^2 - b^2 + \delta})\delta^2} = \frac{a}{b^2(a^2 - b^2)} + \frac{1}{2(a^2 - b^2)^{3/2}} \log \frac{a - \sqrt{a^2 - b^2}}{a + \sqrt{a^2 - b^2}} \quad (20)$$

For the oblate spheroid, the approximate model of the mammalian red cell, the axes are a, b, c ; $b = c$ and $a < b$. The integral (20) assumes the form

$$\int_{b^2}^{\infty} \frac{d\delta}{\delta^2 \sqrt{a^2 - b^2 + \delta}} = \frac{a}{b^2(a^2 - b^2)} - \frac{1}{(b^2 - a^2)^{3/2}} \tan^{-1} \sqrt{\frac{a^2}{b^2 - a^2}} + \frac{\pi}{2(b^2 - a^2)^{3/2}} \quad (21)$$

Values of L_α for various sets of axial ratios are also given in Table I.

TABLE I
Dependence of $abcL_\alpha$ on the Axial Ratios a/c and b/c

a/c	b/c	c/c	$abcL_a$	$abcL_b$	$abcL_c$
2	2	1	0.472	0.472	1.069
3	2	1	0.318	0.535	1.158
4	2	1	0.222	0.574	1.208
5	2	1	0.175	0.593	1.253
6	2	1	0.136	0.607	1.291
7	2	1	0.110	0.617	1.328
3	3	1	0.360	0.360	1.263
4	3	1	0.277	0.396	1.326
5	3	1	0.217	0.417	1.371
6	3	1	0.167	0.433	1.406
7	3	1	0.138	0.442	1.438
4	4	1	0.297	0.297	1.404
5	4	1	0.233	0.318	1.453
6	4	1	0.191	0.331	1.482
7	4	1	0.157	0.343	1.500
5	5	1	0.250	0.250	1.500
6	5	1	0.211	0.273	1.532
7	5	1	0.176	0.282	1.552

Suspensions of Erythrocytes

The suspensions of ellipsoids used for experimental study were suspensions of the red blood cells of birds in serum and in isotonic solutions of sodium chloride. At the frequencies at which the resistance measurements were made the red cells behave as non-conductors and therefore $k_2 = 0$. The simplified equation for random orientation is

$$k_1 = k + \frac{\rho k f_1}{1 - \rho} = k \left(1 + \frac{\rho f_1}{1 - \rho} \right) \quad (22)$$

where $f_1 = \frac{2}{3} \sum_{\alpha=a,b,c} \frac{1}{2 - abcL_\alpha}$ is the form factor. Expressed as electrical resistance instead of conductance

$$\rho = \frac{(r/r_1) - 1}{(r/r_1) - 1 + f_1} \tag{23}$$

where ρ is the same as before and r and r_1 are the resistances of the suspension and medium respectively, measured in the same conductivity cell.

Orientation

The types of orientation of the ellipsoids with respect to the electrodes are shown in Fig. 1.

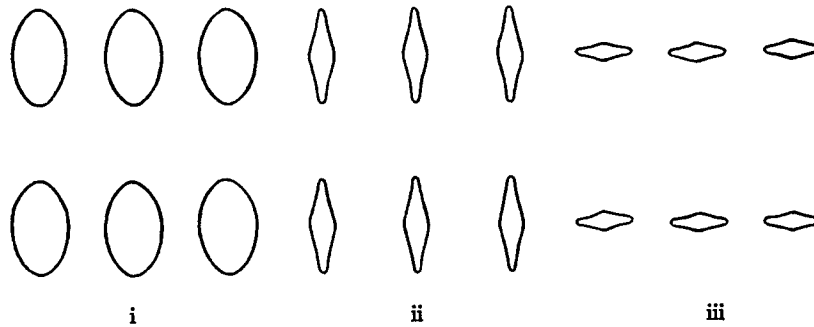


FIG. 1. The three projections of an ellipsoidal red cell with three axes different

When the ellipsoids are oriented at random in the field we take, in effect, the average of the three positions, i, ii, and iii (Fig. 1). If a special orientation is obtained by allowing the blood to flow past the electrodes the type of orientation obtained with respect to the electrodes depends upon the position of the electrodes in the stream. If the arrangement is such that the external field is parallel to the long axis of the particles the effective target area presented by the cells to the lines of electrical force is shown (Fig. 1) in iii the field being directed into the page, or in i or ii when the field is in the plane of the page from top to bottom.

The equation in this case (external field parallel to long axis) is

$$k = k_1 - \frac{2k\rho}{1 - \rho} \left(\frac{1}{2 - abcL_\alpha} \right) \tag{24}$$

Or in the form of equation (23)

$$\rho = \frac{(r/r_1) - 1}{(r/r_1) - 1 + f_2} \tag{25}$$

where

$$f_2 = \frac{2}{2 - abcL_a}$$

when a is taken as the long axis of the ellipsoid.

When the electrodes are arranged so that the long axis of the ellipsoid is perpendicular to the electrical field the target area offered by the cells to the lines of electrical force is the average of i and ii (Fig. 1) if the field is taken as normal to the page. The corresponding equation is

$$2k = 2k_1 - \frac{2k\rho}{1 - \rho} \sum^{\alpha=b,c} \frac{1}{2 - abcL_\alpha} \quad (26)$$

which reduces to

$$\rho = \frac{(r/r_1) - 1}{(r/r_1) - 1 + f_3} \quad \text{where} \quad f_3 = \sum^{\alpha=b,c} \frac{1}{2 - abcL_\alpha} \quad (27)$$

taking b and c as the intermediate and short axes of the ellipsoid respectively.

If the orientation is further restricted so that at the same time either the intermediate or short axis is parallel to the external field the conductance equation again assumes the form of equation (6) with a taken as the axis parallel to the external field.

Application of the conductance equation to suspensions of non-conducting ellipsoids requires the evaluation of the form factor f which is determined solely by the axial ratios of the particles. In Table II are presented the values of the form factors for various combinations of axes and for the various possible orientations of the cells.

III

EXPERIMENTAL

Determination of Volume Fraction and Form Factor

The working equation, $\rho = \frac{r/r_1 - 1}{r/r_1 - 1 + f}$, contains four experimentally (5) determinable quantities that can be approached by independent methods. When used to determine the volume concentration of the suspended phase, the appropriate form factor, f , must first be obtained. For spheres the value of f has been deduced and confirmed experimentally (see page 753). The functions for spheroids evaluated by Fricke have been tested only on the non-conducting discoidal red blood cells of mammals which are rough approximations of the spheroidal model. The chief difficulty in working with red cells is that accurate measurements of the short axis of the cell

have not been obtained. Deviations of the cell from the mathematical model occur along the short axis. It is therefore necessary to use an average value for this dimension. Confirmation of the theory for spheroids resides in the fact that when a suitable value for the short axis is chosen a single form factor can be selected which gives a close correspondence be-

TABLE II
Form Factors for Various Axial Ratios and Orientations

Axial ratios	Random orientation	Long axis parallel to external field, particle free to rotate	Long axis perpendicular to external field, particle free to rotate	Long axis perpendicular, intermediate axis parallel	Long axis perpendicular, short axis parallel	Model
1:1:1	1.500	1.500	1.500	1.500	1.500	Sphere
2:2:1	1.589	1.308	1.729	1.308	2.150	Oblate spheroid
3:2:1	1.643	1.188	1.870	1.364	2.376	Ellipsoid
4:2:1	1.684	1.124	1.964	1.402	2.526	"
5:2:1	1.731	1.096	2.049	1.422	2.676	"
6:2:1	1.776	1.072	2.128	1.436	2.820	"
7:2:1	1.827	1.058	2.211	1.446	2.976	"
3:3:1	1.718	1.220	1.967	1.220	2.714	Oblate spheroid
4:3:1	1.791	1.160	2.106	1.246	2.966	Ellipsoid
5:3:1	1.855	1.122	2.222	1.264	3.180	"
6:3:1	1.911	1.090	2.322	1.276	3.368	"
7:3:1	1.973	1.074	2.422	1.283	3.560	"
4:4:1	1.901	1.174	2.265	1.174	3.356	Oblate spheroid
5:4:1	1.992	1.132	2.422	1.189	3.656	Ellipsoid
6:4:1	2.054	1.104	2.529	1.198	3.860	"
7:4:1	2.097	1.086	2.603	1.207	4.000	"
5:5:1	2.195	1.142	2.572	1.143	4.000	Oblate spheroid
6:5:1	2.183	1.118	2.716	1.158	4.274	Ellipsoid
7:5:1	2.242	1.096	2.815	1.164	4.466	"
2:1:1	1.539	1.210	1.703	1.703	1.703	Rod
3:1:1	1.577	1.122	1.805	1.805	1.805	"
4:1:1	1.597	1.086	1.853	1.853	1.853	"
5:1:1	1.615	1.059	1.894	1.894	1.894	"
6:1:1	1.627	1.045	1.919	1.919	1.919	"
7:1:1	1.633	1.035	1.932	1.932	1.932	"

tween experiment and theory over a wide range of concentrations. The value for the short axis so chosen falls within the limits imposed by direct measurement.

It was hoped in extending the theory to cover the case of ellipsoids with three axes different that the avian red cell would fit the ellipsoidal model more closely than the mammalian cell fits the spheroidal model and such was found to be the case (see Fig. 2). However, the difficulty in determin-

ing the value of the short axis still exists. Table III shows the range of dimensions of cells in a single sample of blood and the individual variation from bird to bird. The average axial ratios of the cells in the above sample are $a/c: b/c: c/c = 4.8:2.9:1$ which correspond to a form factor (Table II) of 1.85. This form factor (1.85) is to be compared with the one obtained directly from conductance measurements on the same duck blood.

The form factor, f , and the volume fraction, ρ , can be determined independently by conductance measurements, alone. To accomplish this, a relatively concentrated suspension is taken and r/r_1 is obtained. Then the suspension is diluted by the addition of known amounts of medium. The ratio, r/r_1 , is determined for each mixture. Dilution is continued until a volume fraction of about 0.15 is reached. From the data, ρ and f are obtained in the following way. Let ρ' and (r'/r'_1) be the volume fraction

TABLE III
Dimensions of Red Blood Cells of Ducks

Bird	Length		Width		Thickness	
	Average	Extremes	Average	Extremes	Average	Extremes
1	13.7	12.3-15.4	8.0	6.9- 9.1	2.8	2.4-3.0
2	13.9	12.1-14.9	8.1	6.5-10.0	3.1	2.7-3.6
3	13.4	12.9-14.3	8.3	7.8- 9.2	2.8	2.0-3.0
4	13.6	12.5-14.6	8.4	7.6- 9.0	2.7	2.1-2.9

and conductance ratio, respectively, for the most dilute member of the series and ρ and (r/r_1) be the same for any other member of the series. From equation 23 it follows that

$$\rho'/\rho = \rho' \left(\frac{1 - r/r_1 + f}{1 - r/r_1} \right)$$

or

$$v/v' = \rho' \left(1 + \frac{f}{(r/r_1 - 1)} \right) \quad (28)$$

where v' is the total volume to which 1 cc. of the original suspension was diluted in the case of the most dilute member of the series and v is the total volume containing 1 cc. of the original suspension for any other member of the series. The quantities v/v' and r/r_1 are known and experimentally determined, respectively. Then v/v' is plotted against $\frac{1}{r/r_1 - 1}$. A straight line should result of intercept ρ' and slope $\rho'f$.

In Fig. 2 a dilution series on duck erythrocytes in 0.90 per cent NaCl is plotted as outlined above. It may be seen that the first six points fall on a straight line within the experimental error and that the last three points are

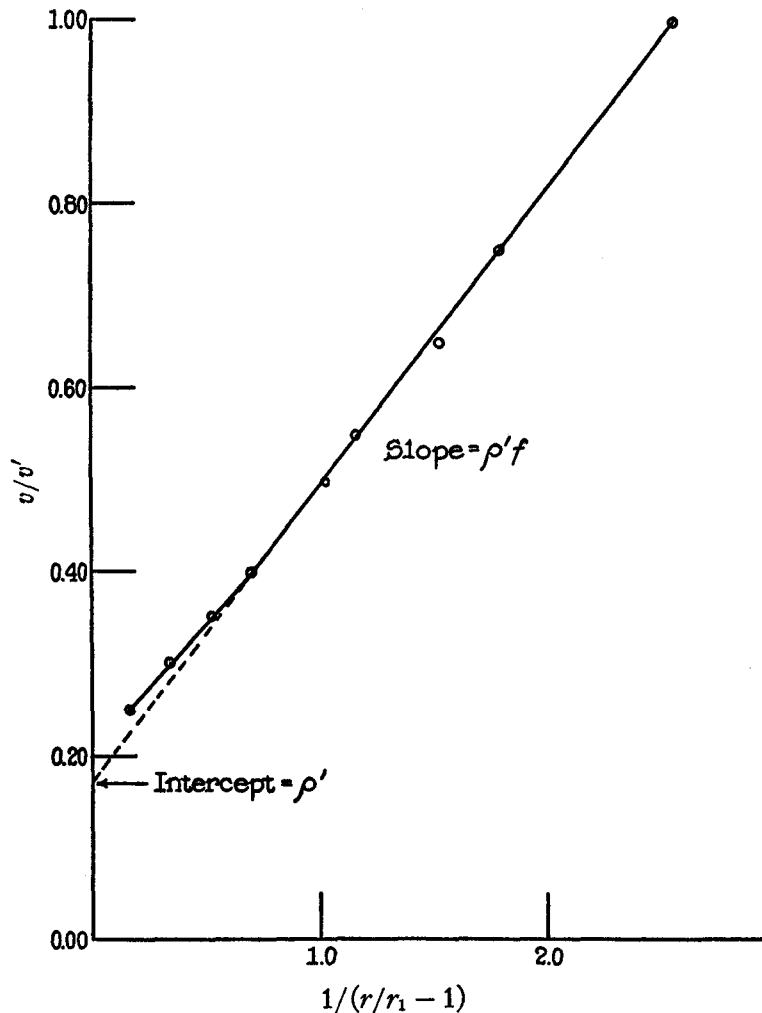


FIG. 2. Dilution series on duck erythrocytes

slightly but definitely above the line. The intercept is 0.172 ± 0.002 and the slope 0.323 ± 0.001 . Therefore $\rho' = 0.172 \pm 0.002$ and $f = 1.88 \pm 0.02$. The agreement between this value obtained by conductance measurements, 1.88, and the value predicted by the theory from direct measurements of the cells, 1.85, is satisfactory. The same data are presented in Table IV.

It may be seen that the agreement is good except for the last three points. The deviations at high concentrations are probably caused in part at least by a distortion of the cells as they crowd together. It should be noted that the deviations are opposite in direction to those which would occur if the cell membrane were not completely non-conducting under the conditions of measurement.

Orientation of Cells

When a blood suspension in a cylindrical conductance cell is stirred by a pulsating air jet and then resistance measurements made at 30 second intervals it is found that the resistance slowly rises until a constant value

TABLE IV
Dilution Series of Red Cells of Duck in 0.90 Per Cent NaCl

0.9 per cent NaCl added to 5.0 ml. of suspension	r_s resistance of suspension	r_s/r_m	Calculated from conductance	Calculated from dilution
<i>ml.</i>	<i>ohms</i>			
0	5460	6.68	0.732	0.688
1	3200	3.91	0.607	0.573
2	2350	2.88	0.500	0.491
3	1980	2.42	0.436	0.430
5	1620	1.98	0.343	0.344
6	1530	1.87	0.316	0.313
8	1360	1.66	0.259	0.265
10	1280	1.56	0.229	0.229
15	1140	1.39	0.172	0.172

is obtained. The phenomenon is what would be expected to occur if the cells were oriented by stirring and then slowly assumed random orientation after the cessation of stirring.

That orientation occurs is indicated by the silky moiré pattern on the surface of blood as it is swirled in a beaker. It is further demonstrated by consecutive light transmission measurements through a thin flat chamber containing blood at rest and then in laminar flow. The optical cell is mounted in place of the absorption cell in a photoelectric photometer (6). In the dilute suspensions of duck erythrocytes employed the transmission increases 15 to 20 per cent as soon as the suspension is allowed to flow and remains constant during flow. When the flow is stopped the transmission slowly decreases until the original resting value is attained, indicating that the orientation has again become random. The effect is not strikingly dependent upon the wave length.

In order to study the effect of orientation upon conductance similar flow cells were constructed. In the first cell (Fig. 3) coaxial conical electrodes of the Shedlovsky type (7) were fused into a cylindrical tube so that the electrical field would be parallel to the line of flow. In a second conductance (Fig. 4) cell the flow chamber was flattened and the electrodes placed at the sides to make the electrical field perpendicular to the line of flow of the suspension. The chamber actually was identical with that of an Abramson electrophoresis cell (8). When the flow is laminar the particles line up with their long axes parallel to the stream lines, and if the particles are flat the flat surface orients parallel to the wall of the flow chamber. In cell I the effective target area offered by the particles in distorting the electrical field is shown in Fig. 1 (iii) which represents the projection of the oriented cells on the electrode. The corresponding projection for cell II is shown in Fig. 1 (ii).

In Table V are presented the predicted resistances in cells I and II containing suspensions of particles of different shapes in equal volume concentration, oriented at random and in the positions obtained in the flow chambers. The calculations are made

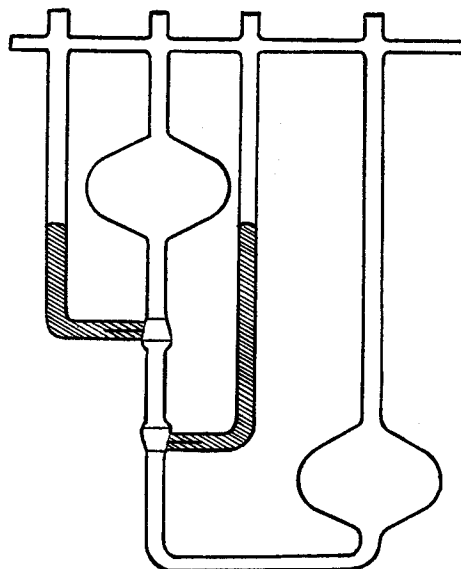


FIG. 3. Cell I—viscometer form of conductance cell for flow measurements with long axis of particles parallel to the electric field.

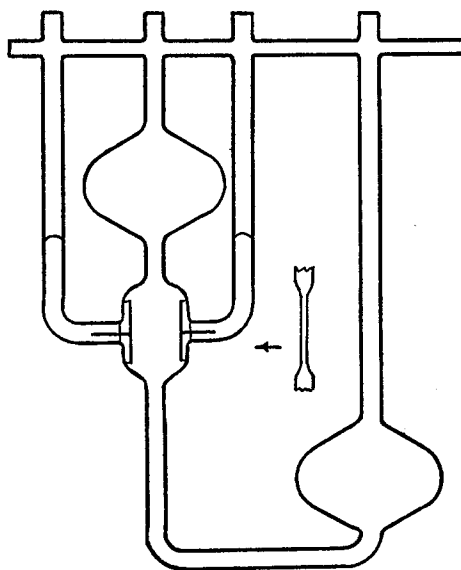


FIG. 4. Viscometer cell II. The orientation of particles is with the long axis perpendicular to the external field and the other two axes are either randomly or explicitly oriented.

for 30 per cent suspensions in which the resistance of the medium is 1000 ohms as directly measured in both conductance cells. It is assumed that the orientation is complete and the lines of electrical force are either parallel or perpendicular respectively to the stream lines at every point.

It is seen that under ideal conditions the resistance measurements of resting and flowing suspensions can provide information on particle shape independently of other methods. The hydrodynamic properties of the flat conductance cell II are such that both spheroidal and ellipsoidal erythro-

TABLE V
Theoretical Effect of Particle Shape and Orientation on the Electrical Resistance of a 30 Per Cent Suspension

Shape	Axial ratio	Resistance of suspension		
		Random	Long axis parallel to field (cell I)	Long axis perpendicular to field, intermediate axis parallel (cell II)
Sphere	1:1:1	2071	2071	2071
Rod	2:1:1	2088	1947	2158
	4:1:1	2113	1894	2223
	6:1:1	2126	1876	2251
Disc (oblate spheroid)	2:2:1	2110	1989	1989
	3:3:1	2165	1951	1951
	4:4:1	2243	1932	1932
Ellipsoid	5:5:1	2369	1918	1918
	4:2:1	2150	1910	2029
	6:2:1	2190	1888	2044
	4:3:1	2196	1926	1963
	6:3:1	2248	1896	1975
	5:4:1	2282	1914	1938
	7:4:1	2327	1894	1946
	6:5:1	2364	1908	1925
	7:5:1	2389	1898	1927

cytes project only their thin edges on the electrodes and suspensions of both therefore decrease in resistance during flow. Rods on the other hand offer a maximum target area to the electrical field under these conditions and correspondingly the resistance of a suspension of rods is increased during flow. It is thus possible to differentiate between platelets and rods.

Flow experiments in the present conductance cells have in the cases studied produced effects in the predicted directions but the magnitude of the effects is less than what would occur if the orientation were complete. Actually the flow cells are not hydrodynamically perfect and the electrical fields are not completely controlled so that the maximum effect is not to be

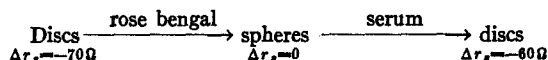
expected. Data for the various orientation effects are presented in Table VI.

The method may be used to follow experimentally produced shape (9) changes of particles in a suspension. The red blood cells of rabbits suspended in isotonic sodium chloride are approximately discs and the resistance of the suspension decreases during flow. If a small amount of the medium is pipetted off after centrifugation and replaced with an equal volume of dilute rose bengal in isotonic sodium chloride the cells become spherical and, having become completely symmetrical, can no longer be oriented. Correspondingly there is no decrease in resistance when the suspension is allowed to flow. If now the suspension is again centrifuged and some of the medium replaced with dilute serum the effect of the dye is counteracted and the cells again assume the discoidal shape. When the

TABLE VI
Experimental Flow Effects

Particles	Shape	Axial ratios	Ran- dom	Flow cell I	Flow cell II	Medium
Duck erythrocytes	Ellipsoid	4.8:2.9:1	1760	1660	1655	1025
Rabbit erythrocytes	Oblate spheroid	4.3:4.3:1	1820	1680	1671	983
<i>E. coli</i>	Rod	4:1:1	987	968	994	790
Cream	Sphere	1:1:1	4521	4528	4529	2360
Spherical red cells	Sphere	1:1:1	1260	1262	1261	830

suspension is allowed to flow its electrical resistance again decreases as it did in the original state



When horse erythrocytes are washed in isotonic saline they become almost spheres. If a suspension of such cells is placed in flow cell I and the decrease in resistance during flow is measured a slight effect is obtained corresponding to the slight asymmetry of the cells (random orientation conductance measurements indicate an axial ratio of about 1.7:1.7:1). The cells resume the discoidal shape when serum is added. Correspondingly after the addition of the limiting amount of serum one suddenly begins to get a marked decrease in resistance during flow. When more serum is added one begins to get erratic results due to the extensive rouleaux formation that horse erythrocytes undergo in the presence of sufficient amounts of serum. The flow effect thus provides an objective method for following

shape changes of erythrocytes and should provide an objective means of titrating the antisphering factor of rabbit cells (10).

When erythrocytes are aggregated in rouleaux the effective shape of the suspended particles is that of rods. The theory predicts that in cell II an increase in resistance is obtained during flow of a suspension of rods and such was found to be the case with heparinized horse blood in which all of the erythrocytes are in rouleaux. However the tendency to rouleaux formation is so great that the rouleaux themselves aggregate in irregular forms so that a simple mathematical treatment is impossible. The experiments with horse blood are further complicated by the exceedingly rapid rate of sedimentation.

The conductance measurements were made on a grounded bridge using a vacuum tube audio oscillator and two stages of amplification. Since ratios of resistances rather than absolute magnitudes were required it was sufficient to make the measurements in air in a closed room in which the temperature varied only a few tenths of a degree during a series of measurements. Blood was drawn by heart puncture, defibrinated, and the erythrocytes suspended either in serum or isotonic sodium chloride.

Addendum.—In connection with the conductance of suspensions of oriented rods it is of interest that Curtis and Cole (11) measured the transverse resistance of a single *Nitella* cell and found that the data fitted a modified form of Raleigh's equation (12) for infinite rods oriented with their long axis perpendicular to the electrical field. Raleigh's equation when thrown into the form of equation (3) gives a form factor, f , of 2, which may also be obtained by equation (17) as the limiting value for large axial ratios. Similar equations were applied to muscle and to nerve fibers (13).

SUMMARY

1. The theory of electrical conductance of colloidal suspensions has been extended to cover the case of ellipsoids with three axes different.
2. The results have been applied to suspensions of ellipsoidal erythrocytes of birds.
3. It has been shown that fluctuations in electrical resistance of suspensions of erythrocytes after stirring are due to streaming orientation of the cells.
4. The theory has been extended to cover four cases of orientation and tested experimentally in specially designed flow cells by electrical and optical methods.
5. Application of the flow method to the study of the shape of colloidal particles is discussed.

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