CONDUCTIVITY AS A MEASURE OF VITALITY AND DEATH.*

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The use of electrolytic conductance measurements in physiological research may be said to date back nearly a century. Eduard Weber at Halle in 1836[1] conceived that galvanic energy like other forms of energy might be useful in the human body, and that if this were the case there should be paths of differing conductivity through the tissues. His thorough and ingenious experiments command admiration, and his conclusions as to the epidermal locus of most of the electrolytic resistance of the body, and as to the effects upon it of warmth and moisture, are still valid. After Weber came du Bois-Reymond[2] who studied the resistance of muscle during contraction; Hermann[3] who showed that the resistance of muscle was greater across the fibers than along them; Ranke[4] who made careful studies of the decrease in resistance of plant and animal tissues upon death; and many others.

In 1897 there appeared almost simultaneously a number of studies of the resistance of red blood cells [5,6,7] which may be taken as the

* Approved for publication by the Surgeon General.

[1] Weber, E., Quaestiones physiologicae de phaenomenis galvano-magneticis in corpore humano observatis, Leipsic, 1836.

[2] du Bois-Reymond, E., Untersuchungen über thierische Elektricität, Berlin, 1849.

[3] Hermann, L., *Arch. ges. Physiol.*, 1872, v, 223.

[4] Ranke, J., Tetanus—eine physiologische Studie, Leipsic, 1865.

[5] Stewart, G. N., *J. Boston Soc. Med. Sc.*, 1896–97, i, No. 16, 18. This and subsequent papers are summarized by Stewart, G. N., *J. Pharmacol. and Exp. Therap.*, 1909–10, i, 49.

[6] Róth, W., *Zentr. Physiol.*, 1897–98, xi, 271.

[7] Bugarszky, St., and Tangl, F., *Zentr. Physiol.*, 1897–98, xi, 297.

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prototypes of studies on unicellular organisms, with which erythrocytes are in many ways comparable.

Recently a great impetus has been given to the use of the conductivity methods by the important generalizations which Osterhout[8],[9],[10] has been able to deduce from his studies on the marine alga *Laminaria*.

Conductance measurements have been made upon a large number of types of living material; but the results, especially when unicellular forms were used, have not been wholly satisfactory. The conductance of bacteria, for example, is oftentimes not an easy thing to determine, or to interpret. The present paper attempts to obviate a certain confusion which threatens to permeate the field by defining a set of concepts which seem best adapted to express the physiological state of the tissue, and by pointing out certain facts whose recognition is fundamental to further study of the subject. Some of these have been very briefly referred to in a previous paper.[11]

I.

Definitions.

To avoid needless repetition of qualifying phrases let us define two concepts. By "net conductance" we shall mean the difference in conductance of the current path between the electrodes when suspending fluid alone is present and when the same fluid is partially replaced by cells (or tissue), *expressed in per cent of the conductance in the former case.* This will ordinarily be negative in sign, and unless otherwise stated the negative sign will be understood. It is to be noted that as the conductivity of a tissue decreases, its "net conductance" as here defined increases. In the absence of tissue the conductance is that of a solution the same as that which bathes the tissue; in the presence of tissue both solution and tissue probably take part in the conduction of electricity.

Theoretical equations derived in much the same way as those previously published by the writer,[11] but assuming uniformly spaced as well as regularly arranged cells, show, however, that the conductance of some types of cells may be very small. The least

[8] Osterhout, W. J. V., *Science*, 1912, xxxv, 112.

[9] Osterhout, W. J. V., *Science*, 1914, xl, 488.

[10] Osterhout, W. J. V., *J. Gen. Physiol.*, 1920–21, iii, 145, 415, 611.

[11] Brooks, S. C., *Proc. Soc. Exp. Biol. and Med.*, 1922, xix, 284.

conductive cells which the writer has measured were erythrocytes which in 24.2 per cent suspension gave a net conductance of 33.9 per cent. Applying the equations mentioned we may show that the resistivity of the cells was more than 11.3 times that of the solution; they would therefore conduct a very small part of the current, and changes in their resistivity would hardly affect the net conductance. The term "net resistance" has been used to express the difference in ohms found by subtracting "the resistance of the apparatus" from the resistance of the same apparatus containing *Laminaria*,[9] and represents in this case the actual resistance of the tissue in ohms. The net conductance as defined above will be shown to have the more general significance, and will be meant unless it is otherwise expressly stated.

The second concept which we wish to define is "dead conductance," by which we mean the net conductance of dead tissue in per cent of that of the same tissue in its normal living state; dead conductance is therefore 100 × (net conductance of dead tissue) ÷ (net conductance of living tissue).

II.

Methods.

In order to determine the net conductance of unicellular organisms it is necessary to know the conductance of the suspending fluid as well as that of the suspension. This may be done by filling the conductivity cell alternately with the suspension and with portions of suspending fluid obtained by centrifugation.[12,13,14] The same end is served by alternate centrifugation and resuspension of the organisms in an appropriate tube in which immersion electrodes may be placed in such a position as to lie wholly in the supernatant liquid after centrifugation; the resistance measurements are made immediately

[12] Green, R. G., Papers from the Mayo Foundation for Medical Education and Research and the Medical School, 1915-20, Philadelphia and London, 1921, 577. See also the paper by Green, R. G., and Larson, W. P., in *J. Infect. Dis.*, 1922, xxx, 550.

[13] Holland, D. M., personal communication.

[14] Shearer, C., *Proc. Cambridge Phil. Soc.*, 1916-19, xix, 263; *J. Hyg.*, 1919-20, xviii, 337.

before and immediately after resuspension. More concentrated suspensions may be used by the former method, but the latter involves less transfer of organisms from one vessel to another. It is also to be noted that during progressive changes in conductivity on the part of both cells and fluid, the observed conductance of the supernatant liquid, as found by the latter in contrast to the former method, is likely to be more nearly the same as the actual conductance of the fluid around the organisms at the moment when their conductance is being determined. The latter method is also more convenient, and has for all these reasons been selected in preference to the former method. In the writer's method two coaxial cylinders of bright platinum form the electrodes and are immersed in the suspension of cells. The tube containing the suspended cells may be removed, centrifugalized, and returned to its original position; the cells are thus brought to the bottom of the tube, and the electrodes lie wholly in the fluid which a moment before bathed the suspended cells. Successive readings may be made by alternate centrifugation and resuspension, and the supernatant fluid may be changed by decantation of the old and resuspension in the new fluid.

The electrical portion of the writer's apparatus is essentially a Wheatstone or, more properly, a Christie bridge circuit[15] in which one arm consists of the conductivity cell and another of variable resistance and capacitance in parallel. In some of the earlier experiments, one of which is described here, a variometer in series with the conductivity cell was used in place of the parallel capacitance in the adjacent arm. This parallel capacitance was substituted to simplify calculations not involved in this paper. This involves an error in apparent conductance which has been emphasized by McClendon,[16] and it therefore seems necessary to mention that this error is serious only in exceptional cases like that cited by McClendon; in the present experiments it is greatest in the experiments upon *Laminaria*, where it causes errors as great as several per cent. The results of these experiments are given in corrected form. In all the other experiments

[15] Christie, S. H., *Phil. Tr. Roy. Soc. London*, 1833, Part I, 95. Wheatstone called the attention of the public to Christie's paper, and his name has become associated with the bridge circuit there described.

[16] McClendon, J. F., *J. Biol. Chem.*, 1920, xliii, 317.

the error is less than that from other sources, *e.g.* about 0.6 per cent of the net conductance in the case of red blood cells, and the data are given in the uncorrected form.

It is probably always advisable to compensate for the shift of phase suffered by the current in the electrolytic cell by appropriate condensers or variometers. This affords a more definite end-point, although with large platinized electrodes good readings may be obtained without their use. Several methods of making such compensation are described by Taylor and Curtis,[17] Washburn,[18] and others. It is also essential to guard against changes in the electrode surfaces during an experiment. Platinized electrodes are notoriously difficult to keep clean, and it may often prove the safer course to use "blank" electrodes, especially in the presence of organisms like bacteria which continually set free into the solution complex organic substances, or which maintain unusual oxidation or reduction potentials.

Even blank electrodes are not free from errors of this sort. As an example an experiment upon the effect of mercuric chloride on a heavy suspension of *Bacillus butyricus* may be cited. Measurements were made upon the resistance of suspensions of bacteria in a 0.14 M solution of sodium chloride plus 0.1 per cent mercuric chloride, and as control, in a physiologically balanced solution having the same conductivity. In the former a gray coloration of the suspension was evident in about 1 hour and became steadily more pronounced, while at the same time the apparent resistance of both the suspending fluid and the suspension began to rise, and after about 7 hours became several times greater than at the beginning of the experiment. The exact extent of this rise could not be determined because the capacitance also increased, and ultimately exceeded the range of the available variometers used for compensation. Neither the gray color nor the rise in resistance was observed in the controls.

Electrodes previously used in the controls were then used in one of the suspensions containing mercuric chloride. The resistance measured with these fresh electrodes was nearly identical with the initial resistance. The affected electrodes were cleaned in boiling

[17] Taylor, W. A., and Curtis, H. L., *Phys. Rev.*, 1915, Ser. II, vi, 61.

[18] Washburn, E. W., *J. Am. Chem. Soc.*, 1916, xxxviii, 2431.

nitric acid for about 5 minutes, washed, and were then used for a resistance measurement. The readings were again identical with those of fresh electrodes.

Evidently reduction of mercuric chloride had occurred, presumably with deposition of a thin film of insoluble mercurous chloride upon the electrodes. A thin film of a relatively poor conductor would act like a leaky condensor and produce the observed phenomena, and it would be removed by the process of cleaning. The gray appearance of the suspension suggests that reduction was carried to the extent of depositing metallic mercury. Such difficulties as this are, of course, only occasional.

III.

EXPERIMENTAL.

Apparently the conductivity of cells in equilibrium with any non-injurious solution varies with that of the solution. If the conductivity of sea water were to be halved by dilution, the conductivity of a tissue immersed in it would also be approximately halved. In the case of organisms like bacteria this is peculiarly important since the conductivity of a new solution placed in contact with the organisms may be profoundly changed, and it would not be safe to assume that the conductivity of the bacteria was unaffected thereby. In fact the safest assumption seems to be that even in the case of tissue immersed in an injurious solution the conductivity of the tissue would vary as that of the surrounding solution if only the same degree of injury could be maintained long enough for equilibrium to be established.

That this equilibrium involves the conductance of the protoplasm itself appears probable, since it has been shown by Osterhout, using conductivity data,[19] and by the writer in his experiments on the free diffusion of salts through diaphragms of Laminaria tissue,[20] that the protoplasm, or at least some living substance forms a part of the pathway for the movement of ions in the tissue.

The following experiments upon several different organisms will serve to show how the principle operates.

[19] Osterhout, W. J. V., J. Gen. Physiol., 1921–22, iv, 1.

[20] Brooks, S. C., Bot. Gaz., 1917, lxiv, 306.

A unicellular green alga *Chlorella* was grown in pure culture in Chodat-Grintzesco solution[21] plus 2 per cent saccharose for a period of 2 weeks, and the conductance of a dense suspension determined first in the nutrient solution, then in a similar solution concentrated to half its original volume by evaporation, and then again in the original nutrient solution (Table I). The small amount of available material renders the result less striking than it might be, since the net conductance here depends directly upon a small difference between

TABLE I.

Effect of Conductance of the Surrounding Solution upon That of Chlorella.

Time.		Solution.	Net conductance.	
hrs.	*min.*		*per cent*	
0	30	Chodat-Grintzesco solu-	4.8	
0	50	tion.	4.7	
1	30		4.3	Average, 4.55
2	19		4.3	
2	33		4.7	
3	06		4.5	
3	27	Same; double strength.	6.2	
3	46		4.3	
4	04		4.1	Average, 4.27
4	20		4.4	
4	44	Same; original strength.	0.3	
5	01		3.6	

two relatively large quantities, and is therefore subject to unusually great error. In spite of this the net conductance approaches the same constant value in the different solutions. The first readings after each change of solution are seen to be affected by the previous condition; *e.g.*, when the change is to a more concentrated solution the apparent net conductance is high, since the protoplasm is still relatively too poor in electrolytes. The opposite variation occurs when the change is to a less conductive solution. (It is to be noted

[21] Chodat, R., and Grintzesco, I., Congrès International de Botanique à l'Exposition Universelle de 1900, Paris, 157–162.

that a high net conductance means not a highly conductive protoplasm but precisely the opposite.) The results are therefore just what would be predicted in the case of cells into and out of which salts diffuse rather slowly.

A somewhat more convincing proof was obtained when larger amounts of *Chlorella* were used. The material was raised in the same way, but Perrier's artificial sea water[22] diluted to one-eighth its original concentration was used as the more dilute, and double this strength (*i.e.* one-fourth strength) Perrier's solution as the more concentrated medium. The normal net conductance of *Chlorella*

TABLE II.

Effect of Conductance of the Surrounding Solution upon That of Chlorella.

Time.		Solution.	Net conductance.	
			Observed.	Mean.
hrs.	*min.*		*per cent*	*per cent*
2	40	Perrier's sea water; ⅛ strength.	28.8	
3	23		28.7	28.9
4	00		29.1	
5	10	Same; ¼ strength.	28.0	
5	50		27.8	27.2
6	27		27.0	
7	07		25.8	

is maintained for at least 24 hours in either of these solutions. Table II summarizes the experiment. Upon transfer to the stronger solution the cells shrank slightly, and since the net conductance is proportional to the volume of cells over short ranges in suspensions of the density used,[11] it is possible to correct for the change in volume. The corrected figure should tell us more nearly the conductance of the cell material itself. It is found to be 28.3 per cent, a figure which agrees well with the original figure of 28.9 per cent.

Table III shows that the behavior of *Bacillus butyricus* is similar. A 24 hour culture on glycerol agar was used. Again the net conductance in the two solutions coincides within the limits of error of the method.

[22] Perrier, E., *Compt. rend. Acad.*, 1890, cx, 1076.

The experiments were also extended to include *Laminaria aghardii*, which was studied in a manner essentially like that described by Osterhout,[8] the thalli being cut into discs and these piled like a roll of coins into a closely fitting glass tube. At each end of this tube was a paraffin block in which was a well open at the top and connecting with the lumen of the tube. Platinized platinum electrodes 1 cm. in diameter were inserted into the wells and held by means of rubber stoppers. Variation in the distance between the electrodes was not great enough to disturb the experiments. The current passed from one electrode through the glass tube to the other. The tube

TABLE III.

Effect of Conductance of the Surrounding Solution upon That of B. butyricus.

Time.		Solution.	Net conductance.		Net conductance corrected for change of cell volume.
			Observed.	Mean.	
hrs.	min.		per cent	per cent	per cent
0	00	Perrier's sea water; ½ strength.	16.0		
1	01		17.5	16.8	16.8
2	21		16.6		
3	24		17.2		
5	12	Same; ¼ strength.	14.6		
6	05		15.4	15.0	17.2
7	09		14.9		

was first filled with sea water and the conductance determined; then the discs of *Laminaria* tissue were inserted and another determination was made. After this the tissue was placed in half strength sea water (equal parts of distilled and sea water) for about one-half hour, and then the conductance in the half strength sea water determined as before. The experimental protocol (Table IV) not only serves to confirm the results of the previous experiments, but also furnishes a striking example of the fact, which also exists in the other cases cited, that the net resistance in ohms may be a very misleading quantity. The same remark applies to the net conductance in reciprocal ohms as opposed to the net conductance in per cent used by the writer. It is obvious that the vitality or injury of any tissue is

best expressed in terms of net conductance (or net resistance) in per cent. In comparing two lots of tissue allowance must, of course, be made for the relative volumes of tissue and solution present, but for comparative purposes, the sequence of changes in any one lot of tissue may be followed by taking the normal net conductance as a basis to which all other figures are referred.

Another point which seems to need emphasis, is that dead plant or animal cells of all the kinds which I have studied, and under all conditions which I have been able to create with one exception which will be discussed in a subsequent paper, offer more or less resistance

TABLE IV.

Effect of Conductance of the Surrounding Solution upon That of Laminaria aghardii.

Time.		Solution.	Gross resistance.		Change of resistance due to presence of tissue.	Net conductance.
			Solution only.	Solution plus tissue.		
hrs.	*min.*		*ohms*	*ohms*	*ohms*	*per cent*
0	20	Sea water.	148.5	933.7	785.2	84.1
1	03	Same; ½ strength.	289.6	1,788.0	1,498.4	83.3
2	02	Same; full strength.	151.2	949.7	798.5	84.1

to the passage of an electrical current. This is of particular interest in view of an impression which appears to have arisen, that dead tissue ordinarily has the same electrical resistance as the surrounding fluid. Such an impression may possibly have had its origin in too literal an interpretation of Osterhout's statement[8] regarding *Laminaria* that "In all cases the resistance after killing fell to *about*"[23] that of a similar cylinder of sea water. As a matter of fact, the resistance of suspensions of some unicellular forms hardly changes when they are killed. Under some conditions the resistance may be increased by the killing process.[2,3] It is necessary to select carefully the means used to kill the organism. Dense bacterial suspensions, for example, may survive doses enormously exceeding the traditional fatal concentrations; nor can one confidently say that any certain

[23] The italics are mine.

degree of heating is satisfactory since too much heat may raise the resistance of some forms rather than lower it.

For example, of two similar portions of a suspension in one-fifth strength unbuffered Ringer-Tyrode solution of *Bacillus coli* (20 hour culture on trypagar), one was kept at 62°C. for 5 minutes, while the other was left at 38.2°C., the temperature at which the readings were made. Subsequent measurements showed that the net conductance of the heated specimen even when decreased by correcting for a slight increase in volume was still 10.7 per cent as compared with 8.8 per cent for the control. Plate cultures showed that the bacteria in the heated portion were essentially all dead, only 57 colonies developing, whereas innumerable colonies appeared in the control. The exact reason for such a change is not apparent; but since the conductivity of the suspending fluid increased, just as found by Green,[12] electrolytes must be diffusing from the cell, and imperfect establishment of equilibrium would have decreased rather than increased the net conductance. This then is not the explanation.

It may be suggested that such a rise in net conductance is due merely to minute air bubbles developing in the solution. But the following experiment shows that similar effects may be produced by other agents, which would not cause the formation of air bubbles. A suspension of *Bacillus coli* of pH 7.7 was divided into four portions, of which two were reserved as controls. Before treatment the net conductance of the control tubes was 3.25 per cent, of the others 4.10 per cent. After 2 hours and 40 minutes in 0.015 M HCl the pH of the treated tubes was 3.4; that of the controls still 7.7. Plate cultures showed the controls to be increasing in numbers, while no colonies developed from the acidulated suspensions; yet the latter had a net conductance (8.15 per cent) more than double that of the controls (3.95 per cent). Still other examples will be found in Table V. An increase in the resistivity of the cells appears to be the only plausible explanation of such an increase of the net conductance.

Still other methods of killing were tried. Organic solvents and heavy metal salts were avoided because of the probability that they would extract fat-soluble substances from, or otherwise profoundly affect non-living material. Liquid air, affording a temperature of

about −190°C. seemed to offer an ideal means of killing.[24] Two portions of a suspension of *Bacillus coli* were both exposed to liquid air for a period of 15 minutes; the tubes were smartly struck several times in the meanwhile to promote formation of ice crystals, then

TABLE V.

"Dead Conductance" of Various Types of Cells.

Organism.	Killing agent.	Duration of action.	Dead conductance.		Notes.
			Observed.	Mean.	
		min.	*per cent*	*per cent*	
B. *butyricus*.	65–72°C.	65	54.7		
Same suspension.	65–80° "	105 additional.	70.7		
Saccharomyces cerevisiæ.	100° "	5	65.0		
Chlorella sp.	64–68° "	48	71.0		
"	75–80° "	60	109.7		
"	55–63° "	75	92.3	89.2	
"	55–61° "	46	90.8		
"	72–81° "	42	82.0		
"	Tricresol, 6.7 per cent.	35	136.9		
		1,320 additional.	203.8		
"	−190°C.±	20	95.0		(Liquid air.)
"	−190° " ±	45	91.0		Not all dead.
Rabbit erythrocytes.	73–75° "	15	45.8		
" "	70–72° "	30	46.6	45.8	
" "	68–76° "	30	45.0		
" "	63–67° "	30	46.0		

thawed, and were again given a 15 minute exposure to liquid air, after which they were brought to a temperature of 38°C. The immediate results were most gratifying. The net conductance fell

from 16.3 per cent immediately before exposure to 9.5 per cent immediately afterwards. This, by far the largest drop in net conductance observed up to that time, seemed to be the clew to the real "dead conductance." Unfortunately, plates made before and after exposure to liquid air showed more numerous colonies after the treatment than before.[25] Repetition of the experiment served but to confirm the disconcerting fact that the net conductance fell, but the bacteria lived and throve.

Recourse was again had to heating as a means of killing and evidence obtained that the net conductance of *Bacillus coli* could be lowered by heat. In one experiment, for example, the temperature rose slowly from 80–94°C. during 30 minutes. The bacteria were then washed several times in fresh suspending solution and plate cultures made. No colonies developed. The net conductance fell from an average of 4.15 per cent for the 4 preceding determinations to 2.10 per cent for the following two, after which the experiment was terminated. The dead conductance was accordingly 50.6 per cent.

Other organisms gave somewhat similar results which are condensed for the sake of brevity in Table V.

It will be seen that all these tissues retain some net conductance in spite of all attempts to find a means of killing which would leave the cells with none. It seemed desirable to make comparisons between the writer's method, and that of Osterhout to eliminate the possibility that there might be a difference in the results due to some systematic error. If both methods were sound, experiments upon *Laminaria* by the writer's method should agree with those of Osterhout[8] and in particular the dead conductance of killed *Laminaria* should be very small or entirely absent.

Accordingly, fresh healthy *Laminaria* thallus was cut into pieces about 1 mm. square, and the resistance of a suspension of such squares compared with that of the surrounding sea water. Since the small pieces settled completely to the bottom of the tube in 2 or 3 minutes, it was only necessary to stir up the suspension and make two determinations of the resistance, one immediately and one in about 5 minutes.

[25] Only one dilution was made and the colonies were so abundant as to defy more exact enumeration.

In the first experiment the normal net conductance was found to be 38.8 per cent, and after heating to 46–51°C. for 20 minutes it was 9.5 per cent. The "dead conductance" was therefore 24.5 per cent, whereas the tissue appeared to be dead. Repetition of the experiment lead to no fundamental change in this result. Since it seemed possible that fine cutting might have injured the tissue and thus lowered the assumed normal net conductance, experiments were tried in which a piece of thallus about 5 × 25 cm. was rolled up into a cylinder fitting tightly into the tube containing sea water, and leaving a space in the center just large enough to admit the electrodes and their supporting rod. The current was thus forced to pass chiefly through the tissues.

TABLE VI.

"Dead Conductance" of Laminaria Tissue According to the Writer's Method.

Killing agent.	Duration of action.		Dead conductance.
	hrs.	*min.*	*per cent*
Formaldehyde, 1 per cent.................	23	20	51.0
" 2 " "	24	10	44.6
Ethyl alcohol, 25 per cent..................	1	40	23.4
Heat 46–51°C.............................	0	20	24.5
" 45–50°C.............................	2	35	26.9

Tested in this manner a strip of thallus had a net conductance of 52.3 per cent before exposure for 135 minutes to a temperature of 45–50°C., and of 14.1 per cent after exposure; the dead conductance was therefore 26.9 per cent. The other killing agents tried and the results obtained are given in Table VI. These experiments were carried on in half strength, or in the last case in ¾ strength sea water. The net conductance in sea water at such dilutions remained normal for more than the duration of the experiments. In all cases the "killed" tissues were green and flaccid long before the close of the experiment, thus giving every visible evidence of being dead. The experiments with formaldehyde disagree with the others which in general suggest a characteristic dead conductance of about 25 per cent.

Since this figure was considerably in excess of the dead conductance expected, an apparatus essentially like that used by Osterhout was set up. This has been described above. Various killing agents were again tried, and the results agreed substantially with those found by the writer's method. They are summarized in Table VII. These experiments were all done in full strength sea water. Fig. 1 shows that during the progress of heating the net conductance approached a constant value which may be considered as indicative of death.

In the experiments on *Laminaria*, it will be noticed that the "dead conductance" is in all cases practically identical for all the experiments in which portions of the same lot of discs were used, irrespective

TABLE VII.

"Dead Conductance" of Laminaria Tissue According to Osterhout's Method.

Killing agent.	Duration of action.		Dead conductance.	
	hrs.	*min.*	*per cent*	
Formaldehyde, 4 per cent.........	4	0	64.5	} Same tissue.
" 4 " "	13	10	64.5	
Heat 45°C......................	1	0	35.0	}
" 37–39°C....................	2	0	36.5	} All from same original thalli.
Ethyl alcohol, 25 per cent.........	0	25	37.0	}
Heat 36–39°C....................	4	29	21.7	} From same thalli.
" 36–39°C....................	7	50	21.9	

of the manner of killing. In these experiments the dead conductance is probably determined by the state of the original tissue, which may have been in some cases in rather poor condition, rather than by the manner of killing. This would lead us to expect that under the most favorable conditions, *i.e.* with the original material having the maximum normal net conductance, the dead conductance might be as low as 10 or 20 per cent.

It will also be noted that in the case of *Bacillus coli* the existence of a considerable dead conductance is in agreement with the independent findings of other investigators in this country,[12],[13] but apparently in direct conflict with those of Shearer.[14] Certain of the writer's experiments on erythrocytes suggest that the conflict is only apparent,

and may easily be explained as a result of differing experimental conditions. Discussion of this point will be taken up in another paper.

It will be apparent from these data that the writer's method and that used by Osterhout agree in assigning to all the organisms and cells studied a certain net conductance, or resistance to the passage of current even when they are presumably dead. This dead conductance is least in *Laminaria* and is greater in other forms in the approximate order: blood cells, yeast, *Bacillus butyricus*, *Chlorella*,
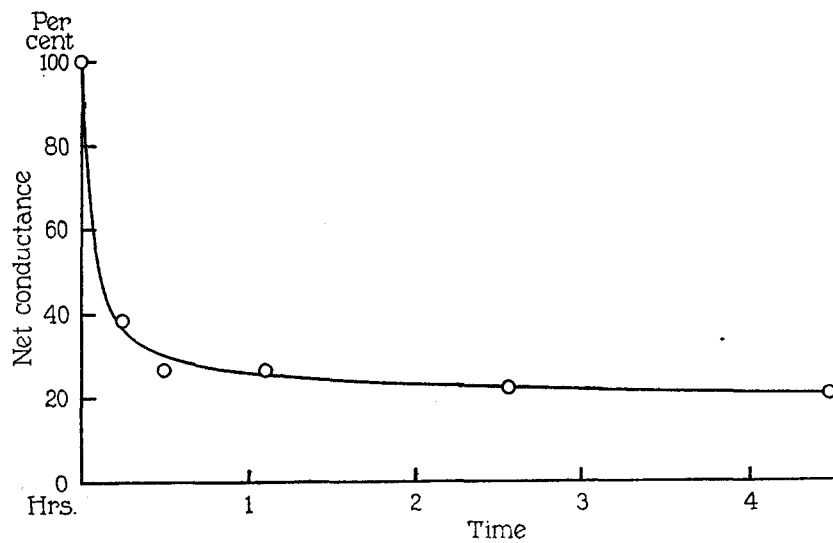

Fig. 1. The progressive decrease in the net conductance of *Laminaria* in sea water at 36–39°C. The measurements were made at room temperature.

Bacillus coli. As has already been pointed out in the case of all except *Laminaria* the dead conductance is relatively greater in those cells normally exposed to a fluctuating environment.[11] This correlation suggests the possibility that cell walls (or at least some non-living structure) might help to protect the protoplasm of such cells from injury due to abrupt changes in the electrolyte concentration, by impeding diffusion of the ions of electrolytes into and out of the protoplasm. This correlation may be only apparent, since similar effects might be produced by other than external structures, by the

presence of a certain proportion of dead cells in the population assumed to give the normal net conductance, or other causes which will suggest themselves to the reader. It is hoped that further studies will elucidate this point.

In order to forestall possible misconceptions it may be well to point out that the fact that *Laminaria* has, when dead, a resistance higher than that of sea water, in no wise affects the theory of injury and recovery based by Osterhout[10] upon calculations from data upon *Laminaria*. These calculations do not depend on the resistance of sea water, but allowance is made for the observed resistance of killed tissue.

IV.

SUMMARY.

The conductance of *Laminaria*, *Saccharomyces*, *Bacillus coli* and *Bacillus butyricus*, *Chlorella*, and of red blood cells has been studied by the writer's method, and *Laminaria* by that of Osterhout. For the material studied it has been found that:

1. The conductance of living tissue is closely proportionate to, and determined by that of the surrounding fluid with which it is apparently in equilibrium. Changes in the conductance of the fluid are quickly followed by compensatory changes in that of the tissue.

2. A quantity is defined which is independent of the conductivity of the fluid bathing the tissues. This is called the "net conductance."

3. All the tissues studied, even when dead, offer a resistance to the passage of current greater than that of the surrounding solution. Exceptions which occur under certain conditions will be discussed in a later paper.

4. In view of the wide variety of material studied it seems admissible, in the absence of any evidence to the contrary, to suppose that these conclusions are generally applicable.