

rocks have been observed which had any such effects. Cyrus N. Ray records such patination in finds about Abilene, Texas, and Dr. A. H. Godbey read a paper before the Society for American Archeology, indicating similar observations. Both of these could have been accessible to flints derived from Coastal Plains deposits.

After a study of several thousand artifacts, we believe we are upon the track of a yard-stick for the dating of several Indian civilizations in the Southern United States, but I doubt the validity of the same set scale for other locations. The existence of Folsom man in Georgia seems very probable, though the data in

Minnesota and New Mexico apparently give a much longer time than seems indicated at Macon and at other places in this vicinity. We set a provisional date of 6,500 years, but await further study to claim this, and it may be exceeded.

I ask information bearing on the matter of weathered or patinated flints in America and their probable source. The weathering of quartz and obsidian arrows does not seem to be related to that of the flints from the Coastal Plain.

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## SPECIAL ARTICLES

### ELECTRIC IMPEDANCE AND PERMEABILITY OF LIVING CELLS

OWING to the lack of agreement between recent papers on the electrical impedance of living cells it seems pertinent to indicate the value of the Wheatstone bridge and centrifuge in analyzing impedance. I took a university course in radio engineering and spent seven years in improving a Wheatstone bridge for high frequency currents.<sup>1</sup> It was shown by Richardson<sup>2</sup> that there is no "skin effect" in electrolytic conductors up to 8 megacycles.

A living cell is not merely a spherical drop of electrolyte solution, but the surface layer has a greater impedance than the interior. It is therefore difficult to apply Clerk Maxwell's formula for the electrical resistance of a suspension of spheres to a suspension of living cells. It simplifies the problem to centrifuge down the cells until they touch one another. I showed that erythrocytes may be centrifuged down in 6 minutes at 20,000 revolutions per minute,<sup>3</sup> and recently that the cells of the thyroid gland may be centrifuged down at less than 100,000 revolutions per minute.<sup>4</sup>

In experiments on sea urchin eggs I found<sup>5</sup> that the electric impedance (resistance to an alternating current) of sea urchin eggs decreased on fertilization. In order to simplify the interpretation it was necessary before the first determination of impedance to wash off the glyco-protein jelly that surrounds the egg. The method used was that of quickly (to avoid lack of oxygen) packing the unfertilized eggs down by centrifugal force in the electrode vessel, marking a line at the upper border of the eggs, determining the impedance, dispersing the eggs in sea water of the

same electric conductivity as that in which they had been before packing, but to which spermatozoa had been added, and after the necessary lapse of time quickly packing them down again to the same level and determining the impedance. In this way the total impedance was more nearly that of the eggs themselves and was little affected by the film of sea water between them. It was thus not necessary to use any formula for the ratio of eggs to sea water, since sea water was in a vanishingly small quantity. This work was confirmed by Gray,<sup>6</sup> but later denied by Cole<sup>7</sup> with the words, "No specific change has been found in the interior resistance or the surface impedance which can be related either to membrane formation or cell division." In later papers, however, Cole has come to the opposite conclusion. He finds that the impedance of the surface is *reduced* on fertilization. In a study on Hipponeo eggs<sup>8</sup> he states, "The membrane of the fertilized egg is practically non-conducting at low frequencies and shows a static capacity 2.5 times that of unfertilized egg." Since the impedance,

$$Z = \sqrt{R^2 + (2\pi fL - \frac{1}{2\pi fC})^2}$$

(where  $R$  = resistance,  $C$  = capacity,  $L$  = inductance and  $f$  = frequency), where  $C$  is increased the impedance is diminished. In a study of Arbacia eggs<sup>9</sup> Cole states: "The unfertilized egg has a static plasma membrane capacity of  $0.73 \mu\text{f}/\text{cm}^2$ , which is practically independent of frequency. The fertilized egg has a static membrane capacity of  $3.1 \mu\text{f}/\text{cm}^2$  at low frequency which decreases . . . at high frequencies.

In electric impedance measurements of erythrocytes

<sup>1</sup> Hemingway and McClendon, *Physics*, 2: 396, 1932.

<sup>2</sup> Proc. Am. Physical Soc., *Physical Review*, 35: 297, 1930.

<sup>3</sup> *Am. Jour. Physiol.*, 91: 83, 1929.

<sup>4</sup> *SCIENCE*, 83: 283, 1936.

<sup>5</sup> *Am. Jour. Physiol.*, 27: 240, 1910.

<sup>6</sup> *Phi. Tr. Roy. Soc. London*, (B) 207: 481, 1916.

<sup>7</sup> *Jour. Gen. Physiol.*, 12: 37, 1928.

<sup>8</sup> *Jour. Gen. Physiol.*, 18: 877, 1935.

<sup>9</sup> *Jour. Gen. Physiol.*, 19: 625, 1936.

I showed that with a Wheatstone bridge with equal ratio arms the only impedance that would balance the erythrocytes with a change of frequency of the measuring electric current from 500 to a million cycles

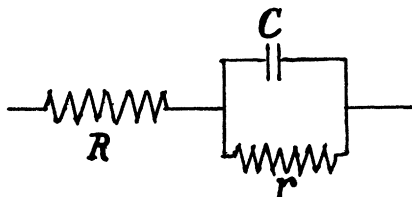


FIG. 1

per second (Fig. 1) was a resistance  $R$  in series with a "leaky condenser" consisting of a capacity  $C$  and a parallel resistance  $r$ , which must be discovered by trial and error. But time was saved by first setting  $R$  equal to the total impedance at the highest frequency. For instance, when the total impedance at a million cycles was 124 ohms,  $R$  was found to be 105 ohms. The closeness of these values is striking when it is noted that the total impedance at 500 cycles was 734 ohms.<sup>10</sup> At infinite frequency the total impedance would equal  $R$ , but technical difficulties with the Wheatstone bridge method and theoretical difficulties such as change of specific inductive capacity of water at very high frequencies led me to limit the high frequency at 1,500,000 cycles<sup>11</sup> and assume the total impedance at this frequency to equal  $R$ .

In a study of frog's skeletal muscle I showed<sup>12</sup> that the electric impedance decreased on stimulation, and in a later paper,<sup>13</sup> that the electric impedance of turtle's curarized skeletal muscle decreased when it was stimulated. This decrease in impedance was localized in the plasma membrane by showing that, on stimulation,  $R$  remained unaltered but  $r$  decreased whereas  $C$  appeared to increase.<sup>14</sup> This has been denied by Bozler<sup>15</sup> but confirmed by Dubuisson,<sup>16</sup> who made a great improvement in the technique by the use of the cathode ray oscillograph, with which he could determine the changes in impedance during a thousandth of a second ( $\sigma$ ).

Dubuisson used the high frequency impedance for  $R$ , and then at low frequency determined  $C$  and  $r$ . On stimulating the muscle there was no change in  $R$ , but there were two time-changes in the other values.

<sup>10</sup> McClendon, *Jour. Biol. Chem.*, 69: 745, 1926, written before the paper by Philipsson was read.

<sup>11</sup> McClendon, *Protoplasma*, 7: 561, 1926.

<sup>12</sup> *Am. Jour. Physiol.*, 29: 302, 1912.

<sup>13</sup> *Am. Jour. Physiol.*, 82: 525, 1927.

<sup>14</sup> McClendon, *Protoplasma*, 7: 561, 1926.

<sup>15</sup> The variation of electrical resistance of muscle during contraction. *Proc. Am. Physiol. Soc., Am. Jour. Physiol.*, 109: 14, 1934.

<sup>16</sup> Ionogrammes de la contraction musculaire: Actualités scientifiques et industrielles 246, Paris (1935) contains references to other workers.

Three  $\sigma$  after stimulation  $r$  dropped 0.2 per cent. of its former value and rose again at 13  $\sigma$  but fell again at 16  $\sigma$  8 per cent., and then rose again at 1000  $\sigma$ . The changes in  $C$  were equal and opposite to those in  $r$ . The first wave is apparently due to increased permeability of plasma membranes of muscle *fibers* (corresponding to R wave of electromyogram), and the second wave to increased permeability of the *fibrillae* (corresponding to T wave of electromyogram).

It thus appears that the decrease in reactance (increased capacity) of the plasma membrane, as shown by Cole and others, represents an increased conductivity of the plasma membrane. The same conclusion was drawn by Hemingway and Collins.<sup>17</sup> They state that the tissue may be considered as a series of leaky condensers (namely, the cell membranes) and the low resistance cell interiors. In such a case one condenser, if considered as a thin plate of specific conductivity  $s$  and dielectric constant  $k$ , would have a resistance  $r$  and a capacity  $C$ .

$$C = \frac{ks}{4\pi} \frac{1}{r}$$

In other words, the less the resistance  $r$  the greater the apparent capacity  $C$ .

By spectral analysis I showed that the permeability of the unfertilized frog's egg to ions is low<sup>18</sup> but when fertilized, Na, K, Mg, Ca, Cl came out of them at an increased rate. Fahr<sup>19</sup> showed that resting skeletal muscle is impermeable to Na and K, but Fenn and Cobb<sup>20</sup> showed that stimulated muscle lost about 15 per cent. of its K, which was replaced by Na from the medium. In other words, the electric impedance studies are harmonious with chemical studies of permeability in the same way as I have shown for the blood corpuscles. Although the plasma membrane of the blood corpuscle is probably as highly resistant as serpentine stone, which may be used in electrical insulation, still it is sufficiently conducting to account for the diffusion of chloride ions (chloride shift) which takes place in the blood during its passage through the lungs.

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### EXTRACTION OF VITAMIN B<sub>1</sub> FROM ADSORBATES

IN studies of concentration of vitamin B<sub>1</sub>, the adsorption method of Seidell has been extensively used. There have been several methods of extraction of the vitamin from the adsorbate, including the original Seidell method of extraction with alkaline solutions, the aqueous alcoholic hydrochloric acid method of

<sup>17</sup> *Am. Jour. Physiol.*, 99: 338, 1932.

<sup>18</sup> *Am. Jour. Physiol.*, 38: 163, 1935.

<sup>19</sup> *Z. Biol.*, 52: 72, 1909.

<sup>20</sup> *Am. Jour. Physiol.*, 115: 345, 1936.