A PHYSICAL MODEL OF NERVE AXON—I.
IONIC DISTRIBUTION, POTENTIAL PROFILE, AND RESTING POTENTIAL†

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A theory which is based on a set of assumptions different from those of the sodium theory is developed. Here the mobile ions are considered to be distributed at Donnan equilibrium and the axoplasm is regarded as an analog of a cation-exchanger. Following the spirit of the Debye–Hückel theory, some important features of the ionic distribution and electrical potential of the nerve fiber have been calculated. The results appear to be in better agreement with the experimental observations than the Goldman–Hodgkin–Katz equation.

1. Introduction. Since the discovery of the demarcation potential of muscle cell over a hundred years ago, many mechanisms have been proposed to explain the origin and the propagation of electrical potential in the excitable tissues. At the time being, the best-known and most widely accepted view is the ionic theory of Hodgkin and his co-workers (Hodgkin and Katz, 1949; Hodgkin and Huxley, 1952a, b, c, d; Hodgkin and Keynes, 1955). This theory, although it was able to yield good numerical agreement with some experimental observations, does not describe the microscopic mechanism of the excitation. In addition, many discrepancies with this theory have also been found (see Discussion

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Several investigators have developed alternative theories which treat the cellular potential and excitation on a more physicochemical basis (Ling, 1962; Karreman, 1964, 1973; Tasaki, 1968; Wei, 1971). Different degrees of success for these alternative theories have been reported.

This paper presents the first part of a theory which attempts to explain the origin of the cellular potential on a physical basis. The electrical potential profile at and near the cell surface will be calculated in the spirit of the Debye–Hückel theory. The resting potential is shown to follow a simple equation. The approach of this theory is basically different from that of the ionic theory. Here the axon is viewed as a semi-closed physical system which does not require artificial mechanisms such as membrane-situated “pumps” (Dean, 1941). The basic assumptions of this model are

(1) In the resting state, the electrolyte distribution across the axon membrane is at Donnan equilibrium.
(2) The axoplasm behaves as an ion-exchanger. (Therefore, the activity coefficient of an ion in the axoplasm is significantly different from that in a dilute electrolyte solution.)

The justification for these assumptions will be discussed in detail in the discussion section.

2. Theory

(A) Electrolyte distribution across the cell membrane. For a solution, the chemical potential of an ion $j$ is

$$\mu_j = \mu_j^0 + RT \ln f_j C_j,$$

where $\mu_j^0$ is the standard chemical potential of ion $j$, $f_j$ and $C_j$ are the activity coefficient and concentration of that ion, respectively. The corresponding equation for ions in the axoplasm may be expressed in a similar form:

$$\mu'_j = \mu'_j^0 + RT \ln f'_j C'_j.$$  (2)

Since the axoplasm here is considered to differ from a dilute electrolyte solution (assumption no. 2), then $f'_j \neq f_j$, and $\mu'_j^0$ may or may not equal to $\mu_j^0$. According to our assumption no. 1, the electrochemical potentials of an ion on both sides of the membrane are equal. Then,

$$\mu'_j + FZ_j V = \mu_j,$$  (3)

where $F$ is Faraday’s constant, $Z_j$ is the valence of ion $j$ and $V$ is the potential