IONIC THEORY OF ACTIVITY OF NERVE CENTERS AND OF
PROPAGATION OF NERVE IMPULSE.

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In this article I intend to give an explanation of the ionic theory of
function of nerve centers in connection with propagation of nerve
stimulation. The experiments of many authors and our observations
show that during continuous action of nerve centers there takes place
a periodic process of stimulation which results in a periodic electro-
motive force. The periods of different centers are not identical and
vary from 0.01 to 1 second.

From the view-point of ionic theory of stimulation, the periodicity
of actions of centers must depend on the periodic changes of the
concentration of ions in the centers. These changes are brought
about by periodic chemical reactions. The kinetics of such a periodic
reaction is not well known. The attempt of many authors to develop
the doctrine of this reaction, based on the kinetics of ordinary chemi-
cal reactions, does not give definite results and if we want to apply
the kinetics of periodic reactions to the domain of physiology of the
nervous system, it suffices to assume that in the nerve cells during
activity there takes place a periodic chemical reaction resulting in a
periodic change of ionic concentration.

The equation of this periodic change of concentration \( C \) can be
written as follows:

\[ C = f(t) \]  \hspace{1cm} (1)

in which \( f(t) \) is a periodic function of time, \( t \).

The simplest case of this function is that in which

\[ C = f(t) = C_0 (1 + \sin nt) \]  \hspace{1cm} (2)

\(^1\)Lasareff, P., Ionentheorie der Reizung, in Lipschütz, A., Sammlung von
Abhandlungen aus dem Gebiete der Biologie und Medizin, Bern and Leipsic, 1923.

349

The Journal of General Physiology
In this case \( C \) varies between 0 and \( 2C_0 \).

The value of \( C \) given by the equation (2) satisfies the following equation of kinetics.

\[
\frac{dC}{dt} = n^2 (C_0 - C)
\] (2a)

We can conclude from the equation (2) that every period of this reaction consists of two phases: During the first phase of the period (part a) we have a destruction of substance in the nerve and the concentration of \( C \) rises (from 0 to \( 2C_0 \)); during the second phase (part b) complete restitution takes place, when \( C = 0 \). In other words, in every period we have the time of fatigue (part a) and the time of rest (part b). If we observe nerve cells in which a periodic reaction takes place, in periods of time \( nt = 2\pi A \) in which \( A \) is a whole number, we find that \( C \) has the constant value \( C_0 \) and we can conclude that this center is not fatigued.

The indefatigability and the periodic function are, from this theory, in a close connection. In our paper published recently, we have given a proof of the indefatigability of the visual centers of peripheral vision, predicted by the ionic theory of adaptation developed by us in 1914. It was found that during adaptation when the sensitiveness of the visual apparatus varies 100,000 times, the sensitiveness towards electric stimulation does not vary.

It may be assumed by the analogy in the kinetics of the reactions that also other centers of the brain are not fatigued during their activity. We therefore arrive at the conclusion of the indefatigability of brain centers either by starting from the theory of adaptation or from the general doctrine of periodic action of nerve cells.

In conclusion, it is necessary to point out that the influence of physical and chemical agents upon the course of ordinary periodic reactions is identical with their influence upon the activity of the

\[ ^2 \text{Lasareff, P., Arch. ges. Physiol., 1923, cc, 119.} \]
\[ ^3 \text{Lasareff, P., Recherches sur la théorie ionique de l'excitation, Edition de l'Institut Scientifique de Moscou, Moscow, 1918.} \]
nerve centers. As an example of this identity, we may take the case of the influence of electric stimulation. In both cases we have a minimal effect when the amplitude of the periodic electrical current, \( a \), and the frequency, \( n \), have the following relation.

\[
\frac{a}{\sqrt{n}} = \text{const. (law of Nernst)}
\]

Furthermore, the action of temperature on both phenomena is the same. Also, many chemical substances produce an analogous effect on the rate of pulsation of nerve centers and of periodic chemical reactions. Thus, we can conclude that the chemical and the dynamic conditions in active nerve cells are similar to those of periodic chemical reactions.

Stimulation of nerve centers results in a propagation of the stimulus into the nerve. The derivation of the equation for the propagation of nerve impulses can be based on the following experimental facts. First, the velocity of propagation of the stimulus is constant, and second, the form of the electric impulse accompanying the stimulation is not changed during its propagation. We can express these data mathematically if we write that the impulse propagates in the form of a wave. The differential equation of propagation then is

\[
\frac{\partial C}{\partial t} = v^2 \frac{\partial^2 C}{\partial x^2} \tag{2b}
\]

in which \( v \) is the velocity of propagation and \( x \) the distance from point \( x = 0 \). The integral of this equation is

\[
C = \phi \left( t - \frac{x}{v} \right)
\]

The function \( \phi \) must satisfy the conditions in the beginning of the coordinates, where we may imagine the nerve cell to be located and where, therefore, there must exist the condition

\[
C_1 = C_2 (1 + \sin nt) \tag{3}
\]

The concentration $C$ in the nerve is obtained if we make

$$C = C_0 \left[ 1 + \sin \left( \frac{t \pm \frac{x}{v}}{
u} \right) \right]$$

(4)

This concentration satisfies the two conditions: the constancy of velocity of propagation and the condition at the beginning of the coordinates given in equation (3).

If $C$ has the character not of a simple sinoidal function but that of a more complicated general periodic function, we can write

$$C_1 = f(t) = C_0 + C_1 \sin (nt + \alpha_1) + C_2 \sin 2(nt + \alpha_2) + \ldots$$

and in this case, we have

$$C = C_0 + C_1 \sin \left[ n \left( t \pm \frac{x}{v} \right) + \alpha_1 \right] + C_2 \sin 2 \left[ n \left( t \pm \frac{x}{v} \right) + \alpha_2 \right] + \ldots$$

This $C$ satisfies the equation (2b) and the condition at the beginning of the coordinates.

Our assumption is that the chemical reaction in the nerve cell brings about a chemical reaction in the nerve. In order to obtain the equation of the kinetics of this reaction in the nerve, we must assume that in the nerve, the concentration of the sensitive substance is uniform on all points. The relation between $\frac{dC}{dt}$ and $C$ determines the character of this reaction. The assumption of equality of $C$ in all points of the nerve is identical with the one that in the nerve $C$ is a function of $t$ only and does not depend on $x$. Therefore,

$$\frac{\delta^2 C}{\delta x^2} = 0$$

Then the time variation of $C$ is expressed by the equation

$$\frac{\delta C}{\delta t} = 0$$

or

$$\frac{\delta C}{\delta \tau} = A$$

(5)

and

$$C = A t + B$$

$A$ and $B$ are constants.
We see from equation (5) that the velocity of reaction is constant and therefore the reaction beginning at the time, \( t \), cannot stop and ends when the sensitive substance in the nerve is entirely decomposed. The stimulation in the nerve from this point of view cannot vary in intensity.

If the stimulus is too small to provoke the stimulation there is no reaction; if, on the other hand, it is sufficient to produce stimulation, then there always results a maximum ionic concentration. In this way we may explain the “all or nothing” law.