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STUDIES IN THE MATHEMATICAL THEORY OF EXCITATION

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The general linear two-factor nerve-excitation theory of the type of Rashevsky and Hill is discussed and normal forms are derived. It is shown that in some cases these equations are not reducible to the Rashevsky form. Most notable is the case in which the solutions are damped periodic functions. It is shown that in this case one or more—in some cases infinitely many—discharges are predictable, following the application of a constant stimulus S. The number of discharges increases with S, but the frequency is a constant, characteristic of the fiber and independent of S.

1. *The general linear two-factor theory.* The two-factor nerve-excitation theories of Rashevsky (1933) and of Hill (1936) are natural generalizations of the single-factor theory of Blair (1932), which supply several of the deficiencies of Blair's theory. At the same time these have not appeared to yield repetitive discharges of the nerve fiber under constant stimulation, a phenomenon which is often met with empirically. It is the purpose of the present discussion to consider the most general possible linear two-factor theory, and to show in particular that for suitable choices of the parameters of the equations such repetitive discharges are predictable.

In its most general terms the two-factor theory postulates the capacity of the nerve fiber to develop two "substances" or "factors", the rate of development of each being a linear homogeneous function of the three quantities: the stimulus intensity, and the excess of each substance or factor over the resting value. Excitation is supposed to occur and to continue as long as a certain linear homogeneous function of the measures of these factors is positive.

We shall speak of the factors as substances, for convenience and definiteness of the picture, though they do not need to be such, and we shall speak of their concentrations as measures of the factors. Then if x_1 and x_2 are the concentrations at any time t, and if $S(t)$ is the stimulus intensity, then the development of the substances is governed by the linear differential equations

$$\frac{dx_1}{dt} = a_{11}(x_1 - x_1^0) + a_{12}(x_2 - x_2^0) + \alpha_1 S(t),$$
$$\frac{dx_2}{dt} = a_{21}(x_1 - x_1^0) + a_{22}(x_2 - x_2^0) + \alpha_2 S(t), \tag{1}$$

where x_1^0 and x_2^0 are the concentrations in the resting fiber. Since we are by no means insisting that they really are substances being developed, we shall not require that x_1 and x_2 be positive to be meaningful.

By suitable choice of units and of subscripts, it is no restriction to assume that the condition for excitation be of the form

$$x_1 - x_2 > 0\,, \tag{2}$$

the left member of the inequality being the linear homogeneous function referred to above.

Empirically only $S(t)$ and the resulting interval of excitation are measurable, that is to say, only $S(t)$ and the times at which the inequality (2) is satisfied. Hence we shall *define two forms* of the two-factor theory *as being equivalent in case the corresponding inequalities* (2) *are simultaneously satisfied.* With this definition of equivalence we shall investigate the conditions for equivalence of any two two-factor theories and deduce normal forms for these.

Blair's theory is obtainable by setting $a_{12} = a_{21} = a_{22} = \alpha_2 = 0$ in (1). Rashevsky's theory assumed $a_{12} = a_{21} = 0$, while Hill's theory had $a_{12} = \alpha_2 = 0$. Offner (1937), seeking to test Rashevsky's and Hill's theory experimentally, found that they were, in fact, equivalent in the sense defined above. Young (1937) then showed that the most general two-factor theory (1) could in general be formally reduced to the Rashevsky form. However, when the characteristic roots are complex so are the resulting coefficients in the Rashevsky form. Physically this is the case of (damped) periodicity with possible repetitive discharge, and is most conveniently studied by reducing to a non-Rashevsky form with real coefficients. Rashevsky (1938) has reviewed completely the case of the equations in his form with real characteristic roots, summarizing the equivalence proofs of Offner and of Young, and discussing empirical checks.

2. *Roots real and distinct.* Equations (1) can be written in matrix notation in the form

$$\frac{dx}{dt} = a(x - x^0) + \alpha S(t), \tag{3}$$

where S is a scalar, α, x and x^0 are column vectors, and a is a two-by-two matrix. Any linear substitution

$$y = c\,x\,, \qquad \frac{dy}{dt} = c\,\frac{dx}{dt}\,, \tag{4}$$

where the matrix c is a non-singular matrix of constants, transforms the linear differential equations (3) into the linear differential equations

$$\frac{dy}{dt} = b\,(y - y^0) + \beta\,S(t) \tag{5}$$

where

$$b = c\,a\,c^{-1}\,, \qquad \beta = c\,\alpha\,. \tag{6}$$

However, we can admit only those matrices c for which inequality (2) and the inequality

$$y_1 - y_2 > 0 \tag{7}$$

are simultaneously satisfied. Such matrices c will be said to define an *admissible substitution.* Any equations (3) and (5) obtainable one from the other by an admissible substitution are equivalent in our sense.

It is at once evident that a scalar matrix

$$c = \begin{pmatrix} \rho & 0 \\ 0 & \rho \end{pmatrix}, \qquad \rho > 0 \tag{8}$$

defines an admissible substitution. This has the effect only of multiplying the two coefficients α_1 and α_2 by the same positive scalar factor ρ. Hence, *only the ratio* $\alpha_1 : \alpha_2$ *is important,* and we may, for example, at any time assume α_1 and α_2 to be the sine and the cosine of some angle.

We next recall the well known theorem in algebra which states that for *any* non-singular matrix c, the characteristic roots of the matrices a and $c\,a\,c^{-1}$ are the same. These are the roots λ_1 and λ_2 of the quadratic equation

$$|a - \lambda\,I| = 0\,, \tag{9}$$

where I is the identity matrix. Hence if an admissible substitution exists such that the matrix b is diagonal, b has necessarily the form

$$\begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}. \tag{10}$$

We can easily write down the matrix c defining such an admissible substitution, when the roots λ_1 and λ_2 are real and distinct, by referring to some principles of projective geometry. Consider the transformation

$$\xi' = a\,\xi \tag{11}$$

of the elements (ξ_1, ξ_2) of a one-dimensional projective form into the elements (ξ_1', ξ_2') of this same form. When the roots λ_1 and λ_2 are real and distinct there are two real and distinct fixed elements, i.e. two elements of the one-dimensional form, (ξ_1^1, ξ_2^1) and (ξ_1^2, ξ_2^2) which are transformed into themselves by the transformation (11). These are given by the two pairs of dependent homogeneous equations

$$\lambda_i\,\xi^i = a\,\xi^i\,, \qquad (i = 1, 2), \tag{12}$$

If we introduce new coordinates into this projective form by the coordinate substitution

$$\eta = c\,\xi\,, \qquad \eta' = c\,\xi'\,, \tag{13}$$

then the transformation (11) is equivalent to

$$\eta' = c\,a\,c^{-1}\,\eta\,. \tag{14}$$

Now a projective coordinate system in a one-dimensional form is fixed when the projective coordinates of three elements of the form are assigned. Let us, therefore, assign to the point ξ^1 the η-coordinates *(1,0)*, to ξ^2 the η-coordinates *(0,1)* and to *(1,1)* the η-coordinates *(1,1)*. Evidently, then, the points *(1,0)* and *(0,1)* are the fixed points of the transformation (14), and therefore this takes the form

$$\eta_i' = \lambda_i\,\eta_i\,. \tag{15}$$

Since the required coordinate substitution changes the coordinates of ξ^1 and ξ^2 into *(1,0)* and *(0,1)* respectively, and leaves the coordinates of *(1,1)* unchanged, it is easy to write down this substitution explicitly in terms of the ξ_i^j by expressing the fact that the anharmonic ratio of an arbitrary ξ with ξ^1, ξ^2 and *(1,1)* is equal to the anharmonic ratio of the corresponding η with *(1,0)*, *(0,1)* and *(1,1)*. If we write, then, x and y in place of ξ and η for the variable point we obtain the desired form of the substitution (4):

$$y_1 = \rho\,\frac{\xi_2^2\,x_1 - \xi_1^2\,x_2}{\xi_2^2 - \xi_1^2}\,, \quad y_2 = \rho\,\frac{\xi_2^1\,x_1 - \xi_1^1\,x_2}{\xi_2^1 - \xi_1^1}\,, \tag{16}$$

where ρ is an arbitrary constant.

One thing remains to be determined. We observe that interchanging the notations ξ^1 and ξ^2 of the two fixed points, or, what comes to the same thing, interchanging the subscripts on the two characteristic roots λ_1 and λ_2, has the effect of interchanging y_1 and y_2. Whichever root is called λ_1 and whatever the sign of ρ, the *equations* $x_1 = x_2$ and $y_1 = y_2$ will be simultaneously satisfied, but unless these are properly associated the orders of the *inequalities* will be reversed. For definiteness we require that

$$\rho > 0 . \tag{17}$$

It is no restriction if we so choose the homogeneous coordinates of ξ^1 and ξ^2 that

$$\xi_2^i - \xi_1^i = 1 . \tag{18}$$

Then we have

$$y_2 - y_1 = \rho\{ (\xi_2^1 - \xi_2^2) x_1 - (\xi_1^1 - \xi_1^2) x_2 \} .$$

But by subtracting equations (18) one from the other we find that

$$\xi_2^1 - \xi_2^2 = \xi_1^1 - \xi_1^2 ,$$

whence

$$y_1 - y_2 = \rho (\xi_2^2 - \xi_2^1) (x_1 - x_2) . \tag{19}$$

Thus *in order that the inequalities* (2) *and* (7) *shall be simultaneously satisfied the designations* λ_1 and λ_2 *must be assigned to the characteristic roots in such a way that*

$$\xi_2^2 - \xi_2^1 > 0 \tag{20}$$

when the scalar factor ρ *is chosen positive and the homogeneous coordinates of the fixed points are chosen to satify* (18).

From equation (6) we have

$$\beta_1 = \rho (\xi_2^2 \alpha_1 - \xi_1^2 \alpha_2) ,$$
$$\beta_2 = \rho (\xi_2^1 \alpha_1 - \xi_1^1 \alpha_2) . \tag{21}$$

Varying the scalar factor ρ does not affect the matrix b, but only the magnitudes of the coefficients β. Hence, we may choose this scalar factor so that

$$\beta_1^2 + \beta_2^2 = 1 \tag{22}$$

and hence so that β_1 and β_2 are the cosine and the sine of some angle. This is in accordance with the statement made above that only the ratio of the coefficients of $S(t)$ is important. Note that

$$\beta_1 - \beta_2 = \rho (\xi_2^2 - \xi_2^1) (\alpha_1 - \alpha_2) , \tag{23}$$

so that *the quantities* $\beta_1 - \beta_2$ *and* $\alpha_1 - \alpha_2$ *have the same sign.* Nothing can be said, however, about the signs of β_1 and β_2 separately.

We have tacitly assumed, in the foregoing discussion, that the point (*1,1*) is not itself a double-point of the transformation (11). Postponing, for the moment, our consideration of this possibility, we may summarize:

Let the excitation equations in the explicit form (1) *or the matrix form* (3) *be such that the roots* λ_1 *and* λ_2 *of the quadratic equation* (9) *are real and distinct. Let the vectors* ξ^1 *and* ξ^2, *which satisfy the matrix equations* (12), *both have unequal components. Then their components can be chosen to satisfy* (18) *and the indices can be so adjusted that* (20) *is satisfied. Then the substitution* (16) *with an arbitrary positive scalar* ρ *is admissible and transforms the equations* (1) *into the equations*

$$\frac{dy_1}{dt} = \lambda_1(y_1 - y_1^0) + \beta_1 S(t) ,$$

$$\frac{dy_2}{dt} = \lambda_2(y_2 - y_2^0) + \beta_2 S(t) , \tag{24'}$$

where β_1 *and* β_2 *are given by* (21). *The scalar* ρ *can further be specified so that* (22) *is satisfied, and in this case the equations* (24′) *can be written*

$$\frac{dy_1}{dt} = \lambda_1(y_1 - y_1^0) + S(t) \cos \beta ,$$

$$\frac{dy_2}{dt} = \lambda_2(y_2 - y_2^0) + S(t) \sin \beta , \tag{24}$$

for some angle β. *This is the Rashevsky form of the excitation equations, and it contains five essential parameters. For stability to exist, and non-excitation in the resting state, it is necessary that*

$$\lambda_1 < 0 , \qquad \lambda_2 < 0 , \qquad y_1^0 < y_2^0 , \tag{25}$$

while from the nature of the substitution it follows that $\beta_1 - \beta_2$ *and* $\alpha_1 - \alpha_2$ *satisfy* (23) *and hence have the same sign.*

In the exceptional case when (*1,1*) is a fixed point of the transformation (11) there is no substitution (4) admissible in our sense which throws the excitation equations into the Rashevsky form. If λ_1 is the root corresponding to the fixed point (*1,1*) and if λ_2 is the other root, the equations (1) are in the form

$$\frac{dx_1}{dt} = a(x_1 - x_1^0) + (\lambda_1 - a)(x_2 - x_2^0) + \alpha_1 S(t) ,$$

$$\frac{dx_2}{dt} = (a - \lambda_2)(x_1 - x_1^0) + (\lambda_1 + \lambda_2 - a)(x_2 - x_2^0) + \alpha_2 S(t) , \tag{26}$$

where a is some constant. The other fixed point is then $(a - \lambda_1 , a - \lambda_2)$. We may make a substitution which gives to this point the coordinates $(0,1)$, in which case the excitation equations take the form

$$\frac{dy_1}{dt} = \lambda_1(y_1 - y_1^0) + \beta_1 S(t) ,$$
$$\frac{dy_2}{dt} = (\lambda_1 - \lambda_2)(y_1 - y_1^0) + \lambda_2(y_2 - y_2^0) + \beta_2 S(t) , \tag{27}$$

where the coefficients β are yet to be determined and we may still assign the projective coordinates of another point. But β_1 and β_2 are the projective η-coordinates of the point whose coordinates are (α_1, α_2) in the ξ-system. Hence the following statement is immediately evident:

In the exceptional case when $(1,1)$ is a fixed point of the transformation (11), the excitation equations cannot be given the Rashevsky form by any admissible substitution, but they can be given the form (27). In these equations λ_1 is the root of (9) corresponding to the fixed point $(1,1)$, and λ_2 is the other root. To obtain this form one has only to choose a substitution keeping fixed the coordinates of $(1,1)$ and giving to the other fixed point the coordinates $(0,1)$. As for the coefficients β, there are three possibilities:

a. if $\alpha_1 = \alpha_2$, then $\beta_1 = \beta_2$ whatever substitution of this type one employs;

b. if (α_1, α_2) is the second fixed point of the transformation (11) then $\beta_1 = 0$ and β_2 is -1 or $+1$ according as $\alpha_1 - \alpha_2$ is positive or negative;

c. if the coefficients α do not satisfy either relation, then β_1 and β_2 can be given arbitrary distinct values, $\beta_1 \neq \beta_2$, and in particular β_2 can be made equal to zero and β_1 equal to $+1$ or -1 according as $\alpha_1 - \alpha_2$ is positive or negative.

In case c the substitution is uniquely determined since the coordinates of the three points whose initial coordinates are $(1,1)$ $(a - \lambda_1, a - \lambda_2)$ and (α_1, α_2) are assigned. In cases *a* and *b* the point (α_1, α_2) coincides projectively with one of the other two, and the third point may be chosen at will.

3. *Roots real and equal.* If the characteristic roots are equal, $\lambda_1 = \lambda_2 = \lambda$, and the matrix b can be diagonalized, then it is a scalar matrix

$$c\,a\,c^{-1} = b = \begin{pmatrix} \lambda & 0 \\ 0 & \lambda \end{pmatrix},$$

whence

$$a = c^{-1}\,b\,c = b$$

since a scalar matrix is commutative with any matrix. Hence in the case of equal roots the excitation equations cannot be given the Rashevsky form unless they are initially in this form, and any (admissible) substitution leaves them in this form. If, in addition, $\alpha_1 = \alpha_2$, then the two quantities $x_1 - x_1^0$ and $x_2 - x_2^0$ satisfy the same differential equation, a case which is obviously of no importance. In the light of the discussion of the preceding section it is therefore evident that:

If the characterictic roots are equal, then the excitation equations cannot take the Rashevsky form unless they are initially of this form. In this case, however, it is physically necessary that $\alpha_1 \neq \alpha_2$, *and the equations can be given the form*

$$\frac{dy_1}{dt} = \lambda(y_1 - y_1^0) \pm S(t) ,$$
$$\frac{dy_2}{dt} = \lambda(y_2 - y_2^0) , \tag{28}$$

where the sign before $S(t)$ *in the first equation is that of the quantity* $\alpha_1 - \alpha_2$.

In the contrary case, when the excitation equations have equal characteristic roots but are not in the Rashevsky form, there is only one fixed element of the transformation (11). This can be given, say, the projective coordinates *(0,1)* by an admissible substitution, provided it is not the element *(1,1)*. The original equations in this case can be written

$$\frac{dx_1}{dt} = (\lambda + a)(x_1 - x_1^0) - \mu a(x_2 - x_2^0) + \alpha_1 S(t) ,$$
$$\frac{dx_2}{dt} = \frac{a}{\mu}(x_1 - x_1^0) + (\lambda - a)(x_2 - x_2^0) + \alpha_2 S(t) , \tag{29}$$

where λ is the characteristic root and $(\mu , 1)$ is the fixed element. If $\alpha_1 \neq \alpha_2$ the substitution

$$y_1 = \rho \frac{x_1 - \mu x_2}{1 - \mu} , \qquad y_2 = \rho \frac{\alpha_2 x_1 - \alpha_1 x_2}{\alpha_2 - \alpha_1} , \tag{30}$$

where

$$\rho(\alpha_2 \mu - \alpha_1)(1 - \mu)(\alpha_2 - \alpha_1) > 0 , \tag{31}$$

yields the form

$$\frac{dy_1}{dt} = \lambda(y_1 - y_1^0) \pm S(t)\,,$$
$$\frac{dy_2}{dt} = b(y_1 - y_1^0) + \lambda(y_2 - y_2^0)\,, \tag{32}$$

where

$$b = \frac{(\mu - 1)\,(\alpha_1 - \alpha_2\,\mu)a}{\alpha_2 - \alpha_1}. \tag{33}$$

In case $\alpha_1 = \alpha_2$ we obtain the form

$$\frac{dy_1}{dt} = \lambda(y_1 - y_1^0) \pm S(t)\,,$$
$$\frac{dy_2}{dt} = b(y_1 - y_1^0) + \lambda(y_2 - y_2^0) \pm S(t)\,, \tag{34}$$

with a different expression for b. If $\mu = 1$ in (29), the fixed element is $(1,1)$ and the substitution yielding the form (32) or (34) is no longer admissible.

If the characteristic roots $\lambda_1 = \lambda_2 = \lambda$ are equal, and the excitation equations are not in the Rashevsky form, they can be written in the form (29), *where* $(\mu,1)$ *is the single fixed element. If* $\mu \neq 1$ *and* $\alpha_1 \neq \alpha_2$, *a substitution of the form* (30) *yields the equations* (32). *If* $\alpha_1 = \alpha_2$, *it is possible to obtain the form* (34). *But if* $\mu = 1$, *neither of these forms is obtainable by an admissible substitution and one can only alter the form* (29) *by making the coefficients* α_1 *and* α_2 *equal to zero or unity.*

4. *The characteristic roots complex.* In this case the roots are necessarily distinct, being conjugate complex. Let these be $\lambda \pm i\,\mu$. Then we choose the substitution which gives the coordinates $(1\,, -i)$ to the fixed point corresponding to the root $\lambda + i\,\mu$, and the coordinates $(1\,, i)$ to the fixed point corresponding to the root $\lambda - i\,\mu$. The excitation equations then take the form

$$\frac{dy_1}{dt} = \lambda(y_1 - y_1^0) - \mu(y_2 - y_2^0) + \beta_1\,S(t)\,,$$
$$\frac{dy_2}{dt} = \mu(y_1 - y_1^0) + \lambda(y_2 - y_2^0) + \beta_2\,S(t)\,. \tag{35}$$

The explicit form of the equations of substitution can be derived as explained previously, but they are slightly more complicated and we do not write them here. The substitution is uniquely determined up to a scale factor ρ. It is convenient for the further discussion to adjust the time units so that

$$\lambda^2 + \mu^2 = 1 . \tag{36}$$

This can always be done by substituting

$$\tau = t \sqrt{\lambda^2 + \mu^2} \tag{37}$$

and writing the corresponding equations in τ instead of t. Suppose this has been done, and let us then rename the variables, calling the time variable in the new units t instead of τ and the new coefficients and functions again λ, μ, β, and $S(t)$. Equation (36) is then satisfied and by a further choice of the scale factor ρ we can suppose that

$$\beta_1{}^2 + \beta_2{}^2 = 1 . \tag{38}$$

Hence we may set

$$\begin{aligned} \lambda &= \cos\gamma , \qquad & \mu &= \sin\gamma , \\ \beta_1 &= \cos\beta , \qquad & \beta_2 &= \sin\beta , \end{aligned} \tag{39}$$

and write our equations (35) in the form

$$\begin{aligned} \frac{dy_1}{dt} &= (y_1 - y_1{}^0) \cos\gamma - (y_2 - y_2{}^0) \sin\gamma + S(t) \cos\beta , \\ \frac{dy_2}{dt} &= (y_1 - y_1{}^0) \sin\gamma + (y_2 - y_2{}^0) \cos\gamma + S(t) \sin\beta . \end{aligned} \tag{40}$$

The remainder of our discussion will deal with the properties of the solutions of the equations (40), or of equations (35) with (36) and (38) holding.

If $S(t) \equiv 0$, the homogeneous equations have the solutions

$$\begin{aligned} y_1 - y_1{}^0 &= e^{\lambda t}(A \cos\mu t - B \sin\mu t), \\ y_2 - y_2{}^0 &= e^{\lambda t}(B \cos\mu t + A \sin\mu t), \end{aligned} \tag{41}$$

as one can readily verify, with A and B constant. In fact, A and B are the values of $y_1 - y_1{}^0$, and $y_2 - y_2{}^0$, respectively, at the time $t = 0$. In the general case the solution still has this form, except that the A and B are no longer constant, but are functions of t defined by

$$\begin{aligned} A &= A_0 + \int_0^t e^{-\lambda x} S(x) \cos(\mu x - \beta)\, dx , \\ B &= B_0 - \int_0^t e^{-\lambda x} S(x) \sin(\mu x - \beta)\, dx . \end{aligned} \tag{42}$$

In these equations A_0 and B_0 are constant, and are the initial values of $y_1 - y_1^0$ and $y_2 - y_2^0$ respectively.

We are especially interested in the case when S is a constant and $A_0 = B_0 = 0$, i.e. when a constant stimulus is applied to a resting fiber. In this case the quadratures (42) can be effected, and one obtains

$$\begin{aligned} A &= S[\cos(\beta - \gamma) - e^{-\lambda t}\cos(\mu t - \beta + \gamma)]\,, \\ B &= S[\sin(\beta - \gamma) + e^{-\lambda t}\sin(\mu t - \beta + \gamma)]\,. \end{aligned} \tag{43}$$

Hence, on substituting these values of A and B into (41) we obtain

$$\begin{aligned} y_1 - y_1^0 &= S[e^{\lambda t}\cos(\mu t + \beta - \gamma) - \cos(\beta - \gamma)]\,, \\ y_2 - y_2^0 &= S[e^{\lambda t}\sin(\mu t + \beta - \gamma) - \sin(\beta - \gamma)]\,, \end{aligned} \tag{44}$$

or, somewhat more explicitly,

$$\begin{aligned} y_1 - y_1^0 &= S[e^{t\cos\gamma}\cos(t\sin\gamma + \beta - \gamma) - \cos(\beta - \gamma)]\,, \\ y_2 - y_2^0 &= S[e^{t\cos\gamma}\sin(t\sin\gamma + \beta - \gamma) - \sin(\beta - \gamma)]\,. \end{aligned} \tag{45}$$

Excitation will occur at the first, third, $\cdots$, roots of

$$y_1 = y_2$$

i.e. of

$$\begin{aligned} &e^{\lambda t}[\cos(\mu t + \beta - \gamma) - \sin(\mu t + \beta - \gamma)] \\ &\qquad = \cos(\beta - \gamma) - \sin(\beta - \gamma) + \frac{y_2^0 - y_1^0}{S}\,, \end{aligned} \tag{46}$$

and will continue until the second, fourth, $\cdots$, roots respectively. This equation can be simplified slightly, by means of a trigonometric identity, to the form

$$e^{\lambda t}\cos\left(\mu t + \beta - \gamma + \frac{\pi}{4}\right) = \cos\left(\beta - \gamma + \frac{\pi}{4}\right) + \frac{y_2^0 - y_1^0}{S\sqrt{2}}\,, \tag{47}$$

and if we set

$$\beta' = \beta + \frac{\pi}{4} \tag{48}$$

we have

$$e^{\lambda t}\cos(\mu t + \beta' - \gamma) = \cos(\beta' - \gamma) + \frac{y_2^0 - y_1^0}{S\sqrt{2}}\,. \tag{49}$$

For abbreviation set

$$f(t) \equiv e^{\lambda t} \cos(\mu t + \beta' - \gamma) \; , \qquad (50)$$

$$\phi(S) \equiv \frac{y_2{}^0 - y_1{}^0}{S\sqrt{2}} > 0 \; ,$$

and write (49) in the form

$$f(t) = f(0) + \phi(S) \; . \qquad (51)$$

The following statement is now immediate:

When the excitation equations (1) *have complex roots* $\lambda \pm i\mu$ *there is a unique admissible substitution* (4) *reducing these equations to the form* (35), *with* β_1 *and* β_2 *satisfying* (38). *By a further choice of time unit it is possible to obtain the somewhat simpler form* (40). *In these equations* $\lambda = \cos\gamma < 0$, $\mu = \sin\gamma \neq 0$, *and* $y_2{}^0 > y_1{}^0$, *but the parameters are otherwise independent and unrestricted as to sign. Excitation is assumed to occur and persist while* $y_1 \geq y_2$.

The general solution of these equations is given by (41) *and* (42), *but in the special case that a constant stimulus* S *is applied to a resting fiber the quadratures can be effected and the solutions are given by* (44). *The intensity-time relations are then given by an equation of the form* (51) *where* f *and* ϕ *are defined by* (50), *excitation lasting while* $f(t) - f(0) \geq \phi(S)$. *Since* $\phi(S) > 0$ *for all* S, *while vanishing asymptotically in* S, *and since* f(t) *fluctuates periodically in sign and vanishes asymptotically in* t, *we have the following possibilities*:

If $f(0) > 0$, f(t) *can exceed* f(0) *at most a finite number of times, and if* f(0) *is an absolute maximum of* f(t) *for all* $t \geqslant 0$, *no excitation is possible for any* S. *If, however,* f(t) *exceeds* f(0) *for some* $t > 0$, *then for sufficiently large* S *at least one discharge will be possible, and the rheobase is given by the value of* S *for which* $\phi(S) = f(t_1) - f(0)$, t_1 *being the value of* t *at the first maximum of* f(t).

If $f(0) = 0$ *the rheobase* S_1 *is given by* $\phi(S_1) = f(t_1)$, *and if* t_n *is the time of the* n-th *maximum,* n *discharges are obtainable by making* $S \geq S_n$ *where* $\phi(S_n) = f(t_n)$. *The solution* S_n *exists and is unique for any* n.

If $f(0) < 0$, *let* S_∞ *be the unique solution of* $\phi(S) + f(0) = 0$, *and* S_1 *the rheobase obtained as in the first case. If* $S < S_1$ *no excitation occurs; if* $S_1 \leq S < S_\infty$ *there will be a finite number of discharges; if* $S = S_\infty$, *there will be infinitely many discharges; and if* $S > S_\infty$, *then after at most a finite number of discharges a state of permanent excitation will result persisting as long as the constant stimulus* S *is applied.*

This last case of $f(0) < 0$ might seem to be physically impossible, but if it be supposed that an intensity S_∞ of the stimulus is injurious, then the mechanism breaks down for such stimuli and one still has only a finite number of discharges from any "physiologically admissible" stimulus.

It is to be noted that on this theory the frequency of the discharge under constant stimulation is a fixed characteristic of the nerve fiber, and is independent of the intensity S of stimulation. Only the number of discharges varies with S, and this is potentially infinite for fibers for which $f(0) \leq 0$, but limited in those for which $f(0) > 0$. In order to obtain variation of the frequency with S by a two-factor theory (or, in fact, by an n-factor theory) it is necessary to generalize equations (1) to a form

$$\frac{dx_1}{dt} = f_1(x_1 - x_1{}^0, x_2 - x_2{}^0, S),$$
$$\frac{dx_2}{dt} = f_2(x_1 - x_1{}^0, x_2 - x_2{}^0, S), \tag{52}$$

where it is supposed that the functions f vanish with their three arguments $x_1 - x_1{}^0$, $x_2 - x_2{}^0$ and S. If the functions f are expanded in power series of the three arguments, the linear equations discussed above may be regarded as first-order approximations.

Nevertheless, the linear theory in the periodic case yields, at least qualitatively, not only the possibility of repetitive discharges, but also the depressed state (relative refractoriness) and the ensuing supernormal phase. However for any quantitative checks it will be necessary to study the solutions (41) with A and B constant giving the recovery course after withdrawal of the stimulus, and also the course of development of the two substances with intermittent stimulation.

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