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NON-LINEAR EXCITATION THEORY: NON-ACCOMMODATIVE, SUB-THRESHOLD EFFECTS

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The standard two factor excitation theories should be called "pre-excitation" theories since they apply only to those events occurring just up to excitation. A true phenomenological excitation theory which describes the *whole* excitation cycle must involve non-linear equations. The nature of these non-linearities is suggested by B. Katz's subthreshold response data. From this data is constructed a "local phenomenological characteristic" which is analogous to the current-voltage characteristic of a non-linear electrical or mechanical system capable of displaying relaxation oscillations. Excitation by constant currents is shown to occur where the slope of the characteristic changes sign. The variation of the time constant of excitation with degree of response, explained by W. A. H. Rushton in terms of a liminal length, is described here in purely formal terms. The theory as presented explicitly treats only those events in the excitation cycle up to and a little beyond excitation; the complete excitation cycle (including recovery and repetition) is mentioned as being amenable to mathematical treatment by an extension of the present theory.

The formal two-factor theory of nerve excitation, (e.g., Rashevsky, 1933) while being adequate to predict time-intensity relations for a variety of stimulating currents, is generally assumed to be inadequate to deal with phenomena occurring after "physiological" response has begun. (See, however, Katz, 1936). That this inadequacy must be fundamental is apparent from a consideration of the physical basis underlying excitation: profound structural changes are known to accompany excitation and recovery (Cole and Curtis, 1938), yet the excitation equations involve parameters which are constant and, therefore, independent of these changes. A possible way out of this dilemma has been suggested by several authors (Monnier and Coppée, 1939; Arvanitaki, 1939; Householder, 1939): viz., that the excitation equations are really *non-linear*, and that the usual linear equations, which are valid only during the "physical" response, are first approximations to the exact equations. (This statement may be taken to imply a definition of physical response: i.e., physical response is that response representable by linear equations.) Such a non-linear theory could presumably describe the processes accompanying breakdown and recovery; however, so far as the writer is aware,[1] no attempt has been made to investigate the specific nature of the required non-linearities. In the present paper we shall investigate some possible non-linear modifications of the formal excitation theory; the discussion will be confined to non-accommodative (single-factor) cases, and for the most part, to sub-threshold effects.

Phenomenological character of excitation theory. The "state of excitation" of a nerve, ε, is defined operationally by

$$\varepsilon(t) = \frac{E_0 - E(t)}{E_0}, \tag{1}$$

where E_0 is the resting threshold cathodal impulse (measured either in volts or coulombs), and $E(t)$ is the impulse required to just bring the nerve to threshold at time t. Before excitation $E(t)$ is the shock required to just produce a propagated excitation, and so $E(t)$ is cathodal and $\varepsilon(t) < 1$; during the early stages of excitation $E(t)$ is the shock required to just quench the excitation, $E(t)$ is anodal, and $\varepsilon > 1$. Thus, although the intrinsic physical nature of ε is a matter of conjecture, ε can be defined operationally over a considerable portion of the excitation cycle; over this portion of the cycle it is a perfectly valid variable to use as the basis of a mathematical theory of excitation (Monnier, 1934; Schaefer, 1940, p. 166).

It has been shown (Young, 1941) that if ε is assumed to vary according to

$$\frac{d\varepsilon}{dt} = KI - k\varepsilon, \tag{2}$$

then ε defined by (1) is consistent with (2). Proof of this is required because any dynamic equation such as (2) implies a relation between ε and the current I [or $E(t)$] which, in general, will not reduce to (1) for impulsive stimuli. If (2) is modified by assuming that k is itself a function of ε, but K is not, then we have

$$\frac{d\varepsilon}{dt} = KI - k(\varepsilon)\varepsilon \cdot \tag{3}$$

it remains to show that ε defined by (3) is consistent with (1).

Let us define two quantities ε' and ε'' which vary according to

$$\frac{d\varepsilon'}{dt} = KI - k'\varepsilon'$$

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[1] During the preparation of this manuscript I have had the opportunity to read a very interesting manuscript by Dr. B. Katz in which a semi-physical approach to the problems discussed here is given.

and

$$\frac{d\varepsilon''}{dt} = KI - k''\varepsilon''$$

where k' and k'' are the maximum and minimum values, respectively, of $k(\varepsilon)$ on the range 0 to ε. Then it is clear that

$$\varepsilon' \leqq \varepsilon \leqq \varepsilon'',$$

the equality holding, for any arbitrary $I(t)$, only for constant $k(\varepsilon)$. Moreover, for impulsive shocks (Young, 1941),

$$\varepsilon' = \varepsilon'' = \frac{E_0 - E(t)}{E_0}$$

and so $\varepsilon(t)$ of equation (3) is also given by (1). We have therefore proved that *the dependent variable of the non-linear excitation equation* (3) *is operationally definable by* (1). We shall refer to a theory which concerns itself only with variables definable in terms of the state of excitation as a *phenomenological* theory; from this point of view, the single-factor theory or its non-linear generalization (3) is phenomenological.

The fact that k is a function of the electrode spacing (Katz, 1939, p. 75) would decrease the operational significance of ε, unless we agree upon some standard electrode spacing; in the remaining discussion we shall assume that this standard electrode spacing is maintained.

Subthreshold effects. Experiments by B. Katz (1937), A. L. Hodgkin (1938), R. J. Pumphrey et al (1940), and others on subliminal responses of nerve have strongly indicated that the linear equation (1) should be replaced by the more general equation (3). Their evidence may be briefly summarized as follows: after an impulsive conditioning shock, ε will attain some value, ε_1, and according to (2), will then subside exponentially, i.e.,

$$\frac{d\varepsilon}{dt} = -k\varepsilon; \quad \varepsilon = \varepsilon_1 e^{-kt}, \tag{4}$$

where k is the time constant of excitation. (Note that our k is the reciprocal of Hill's k). This statement is the starting point of A. V. Hill's (1936) discussion of excitation. The exponential subsidence of the excitatory state is certainly correct if ε_1 is small or negative (anodal); but, as Katz's (1937) Figure 4 shows, when $\varepsilon_1 > .5$ marked deviations from (4) occur, while for $\varepsilon_1 > 1$, ε actually increases with time. An interpretation of these deviations from linearity in terms of a "local" response in accordance with Rushton's notion of liminal length (1937) has been fairly general (Katz, 1939); but from the strictly *phenomenological* viewpoint such considerations are somewhat irrelevant. All that can be concluded from these curves is that the differential equation (4) should be replaced by a non-linear equation in which the time constant is itself a function of ε, (or, a possibility which will not be discussed here, K is a function of I). The physical interpretation of such a non-linearity is outside the scope of a *formal* theory. For example, from the point of view of a formal non-linear theory, it is immaterial whether a variable k is due to an all-or-none local response extended over a gradually increasingly area, or a graded local response, or (as would appear to be most likely a priori) a combination of both.

From the $\varepsilon(t)$ curves of Katz's experiment, the function $k(\varepsilon)$ (which we shall call the instantaneous time constant) can be found since, by (4),

$$k(\varepsilon) = -\frac{1}{\varepsilon}\frac{d\varepsilon}{dt}, \tag{5}$$

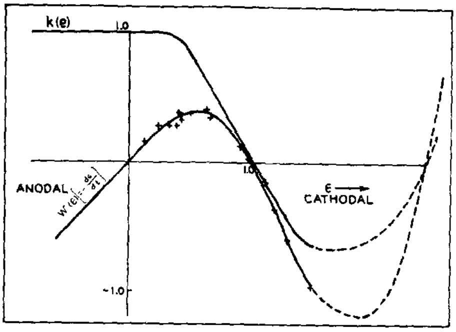

FIGURE 1

The "local phenomenological characteristic", $w(\varepsilon)$ vs. ε, and the instantaneous time constant $k(\varepsilon)$, from Katz's data. Indicated points are experimental. The dotted portions of these curves are hypothetical. The function $k(\varepsilon)$ for anodal shocks is a constant whose value is uncertain (cf. Katz, 1937); for this reason no experimental points are shown on the anodal side.

and the value of $d\varepsilon/dt$ for each value of ε can be ascertained by graphical differentiation. If k is a function of ε alone, these $\varepsilon(t)$ curves should consist of a family of "parallel" curves, in which the slope of each member of the family is the same for a given value of ε. To what extent this is true can be judged from Figure 1, where $-d\varepsilon/dt$ vs. ε and $k(\varepsilon)$ are plotted from Katz's data; very much the same results are found from the giant axon data of R. J. Pumphrey *et al.* The scattering of the points taken from different members of the decay curve suggests that k may depend on some variable besides ε (e.g., $d\varepsilon/dt$, ε_1, or I) or that even in this range K is not constant; however, the scattering is not bad between $\varepsilon \backsim .5$ and $\varepsilon \backsim 1.4$ and so we shall suppose k to be determined by ε alone in the present discussion.

A semi-analytic approximation to $k(\varepsilon)$ together with the response curves obtained by using this approximation in integrating (5) are shown in Figure 2. A general resemblance to the experimental curves is apparent here; improving the fit by bettering the approximation to $k(\varepsilon)$ is of no particular theoretical value, however.

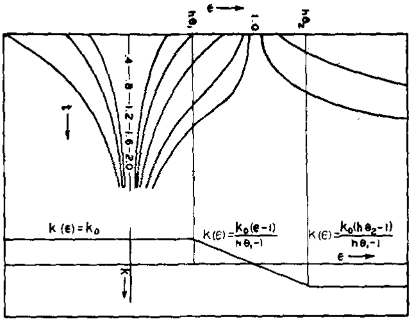

FIGURE 2

Local decay curves obtained by integrating (5) with $k(\varepsilon)$ given by the piecewise linear function on the right. (The positive direction on the k-axis is right to left.) The notation $h\ \theta_1$ and $h\ \theta_2$ for the points at which $k(\varepsilon)$ changes slope is suggested by Rushton (1937), Figure 6.

The nerve "phenomenological characteristic". In the non-linear theory of electrical oscillations and related phenomena it is customary to introduce a "characteristic curve", a knowledge of which is sufficient to predict the behavior of the system provided the dynamical equations of the system are known. In general, the characteristic gives the relation between a current and a potential variable; if the current variable is a multiple valued function of the potential variable, the characteristic is usually denoted by the letter N (north), while if the potential variable is a multiple valued function of the current, the characteristic is denoted by S (south) (cf. le Corbellier, 1931, p. 32). For systems possessing a linear characteristic, the variational resistance (defined as the slope of the characteristic) is constant and equal to the ordinary resistance. While the system is in a state characterized by positive resistance, energy must be supplied from the outside to maintain the activity of the system; while the system is in a state characterized by negative resistance, the system supplies its own energy. From the definition of the characteristic, it follows that the variational resistance (or conductance) changes sign at a turning point of the characteristic.

In attempting to arrive at a corresponding "characteristic" for nerve based on phenomenological principles (assuming that one exists), we are guided by certain requirements, suggested by the electrical analogies, which must be satisfied by any curve which plays the role of a characteristic in the theory. First, the characteristic must be a relation between some variable which behaves like a potential (cf. Herrenden-Harker, 1940), and a variable which has the dimensions of current (in a generalized sense). Second, the slope of the characteristic must reduce, in the linear case, to a variational conductance (or a time constant, in circuits with constant capacitance). This means that a theory based on a linear characteristic must be identical with the linear theory already known. Third, at the turning points of the characteristic, the direction of the energy flow must reverse, and the nerve phenomenon must become self-sustaining.

We can treat the quantity ε as a potential variable without compromising our ideas of potential too seriously. For the equilibrium state of the nerve is characterized by the condition $\varepsilon = 0$, and the value of ε is a measure of the deviation from equilibrium. Consequently, the potential energy of the system (in a strict physical sense) can be expanded in powers of ε, thus establishing a connection between ε and the potential energy which is valid even though ε is a purely phenomenological variable. The quantity ε is analogous to the displacement variable in a spring near equilibrium.

On the other hand, the choice of current variable is not so clear. The quantity $w(\varepsilon) = k(\varepsilon)\,\varepsilon \left[= \frac{-d\varepsilon}{dt} \text{ by (5)} \right]$ satisfies the dimensional requirement, and when k is constant, it does give rise to a linear "characteristic" which yields the original linear theory. However, if we plot $w(\varepsilon)$ vs. ε (Figure 1), we find that the turning point of this "local phenomenological characteristic" (l.p.c.) occurs almost where the physiological local response begins, but certainly *not* where the excitation has become self-sustaining. The origin of this difficulty seems to lie in the fact that the self-sustaining nerve response is a propagated disturbance; *the criteria for physiological response and for propagated response are not identical.* This fact was pointed out by W. A. H. Rushton in 1937.

Stability and instability of the characteristic. If we assume that K is independent of ε, (an assumption which is certainly incorrect for $\varepsilon >> 1$, and may be incorrect even for smaller ε), we can indicate the effect of a constant current I by means of a straight line drawn across the l.p.c. parallel to the ε axis, (Figure 3); the line KI intersects the characteristic at the points A and B. Point A is seen to be stable, for if the state of the nerve is represented by some point A, and if we displace this point toward the right (ε increasing), $KI - w(\varepsilon)$, or by equation (3), $d\varepsilon/dt$, becomes negative and the point returns to A; similarly if ε is decreased slightly, $KI - w(\varepsilon) > 0$ and again the point returns to A. On the other hand, a displacement in either direction from the point B will tend to increase the displacement ($d\varepsilon/dt$ and $\Delta\varepsilon$ have the same sign) and so B is unstable. The argument presented here can easily be generalized to show that for steady current stimulation any point on an ascending branch of the l.p.c. ($dw/d\varepsilon > 0$) is stable while any point on a descending branch ($dw/d\varepsilon < 0$) is unstable.

Suppose a graded series of constant stimuli are applied to a resting nerve; these may be represented by a family of horizontal lines as in Figure 3. From the preceding discussion, it is clear that a constant current, I, will not stimulate if KI intersects the ascending branch of the l.p.c. The rheobase will be represented by the line which is tangent to the l.p.c., or, from the figure,

$$I_0 = \frac{w_0}{K}$$

where w_0 is the maximum value of $w(\varepsilon)$ and I_0 is the rheobase. From a knowledge of the l.p.c. we can predict the response to a constant current stimulus: if $I > w_0/K$, excitation will occur, otherwise not.

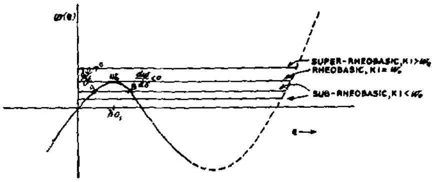

FIGURE 3

Stability and instability of the l.p.c. for steady current stimulation.

The response to impulsive stimuli presents certain difficulties if we wish to make our interpretation depend on the properties of the l.p.c. As we have said, the turning point of the local characteristic is known experimentally to occur at about $\varepsilon = .5$ instead of $\varepsilon = 1$; in other words, instability to steady current stimulation occurs before instability to impulsive stimulation. Just such a possibility was suggested by Rushton (cf. his θ_1 with $h\,\theta_1$) in discussing the "liminal length"; if stimulation is impulsive, the entire liminal length must be excited for instability to set in (i.e., the representative point must be brought to the zero of the l.p.c.) while if stimulation is steady, instability induced at any one point is sufficient to ensure propagation (i.e., the representative point need merely be brought to the *turning point* of the l.p.c.). This picture is very suggestive—but since it is based on the assumption that the local response is all-or-none, we are not justified in accepting it as the complete explanation of the difference in response to impulsive and steady stimuli.

Thus far we have intentionally neglected any discussion of what happens to the representative point an appreciable time after instability has set in. To answer this question we would have to know the shape of the l.p.c. during the later part of the action. It is difficult to assign operational significance to the quantity ε during the later stages of the action, since, as far as the writer is aware, it is impossible to block propagation by impulsive anodal shocks applied at the point of stimulation after a certain point in the action has been reached. If it eventually proves possible to give an operational definition of ε during the subsidence of the action (Monnier, 1934), we would certainly find it hard to refrain from extending the characteristic to include a second ascending branch (dotted line, Figure 1). Such a characteristic (S type), together with suitable assumptions concerning the variation of K with ε, would enable us to give a phenomenological theory of such processes as recovery and repetitive discharge. The analogy with systems capable of displaying relaxation oscillations would be complete. However, we do not feel justified in going further into these possibilities until some evidence is given for extending the characteristic in the manner just described.

Relations between linear and non-linear theory. It is an empirical fact that the linear equation (2) predicts excellent strength-duration and voltage-capacity curves. If (2) is only an approximation to the non-linear (3), why should this be the case?

Suppose voltage-capacity or strength-duration experiments are performed in which the index of response is not necessarily the propagated disturbance ($= 1$), but some arbitrary value of the excitatory state, ε_h, as measured by the test shock method. Voltage-capacity measurements of almost this type have been performed by H. Rosenberg (1937) but technical difficulties have made the corresponding strength-duration experiments unfeasible (although cf. Rushton, 1932). If ε_h is small ($< .5$) so that the linear theory applies, the time constant found from such experiments would simply be the initial slope of the l.p.c., and would be independent of degree of response. As ε_h increases, the linear theory no longer applies: the effective time constant will depend on ε_h and, in general, on the shape of the stimulating current.

To determine exactly what intermediate value of k must be used in a linear theory strength-duration curve so that it will deviate as little as possible from the non-linear strength-duration curve, we must require that the duration of a constant stimulus according to the non-linear theory,

$$\int_0^{\varepsilon_h} \frac{d\varepsilon}{KI - k(\varepsilon)\,\varepsilon}$$

and the duration according to the approximating linear theory

$$\int_0^{\varepsilon_h} \frac{d\varepsilon}{K_l I - k_l(\varepsilon_h)\,\varepsilon}$$

be as nearly alike as possible, for a given index of response ε_h. The quantities K_l and $k_l(\varepsilon_h)$ are the approximating linear theory constants for the index of response ε_h. An exact solution of this minimum problem for all currents $I(t)$ seems to be very difficult, and so we shall simply write down an approximate solution which is valid for large values of the stimulating current:

$$k_l(\varepsilon_h) = \frac{2}{\varepsilon_h^2} \int_0^{\varepsilon_h} k(\varepsilon)\,\varepsilon\, d\varepsilon\,, \qquad K_l = K\,. \tag{6}$$

This integral is the first moment of the function $k(\varepsilon)$. The fact that $k_l(\varepsilon_h)$ is not independent of I in the next approximation (small values of I) may be related to H. A. Blair's (1936) contention that the simple linear theory is inadequate, even for strength-duration data.

To determine voltage-capacity or strength-duration curves accurately we should integrate (3) with the function $I(t)$ replaced by the particular current used as stimulus. The result of this integration for constant currents of various intensities, is given in Figure 4*a*. (The $k(\varepsilon)$ function of Figure 2 was used here.) These curves are practically the same as those given by W. A. H. Rushton (1937, Figure 6).

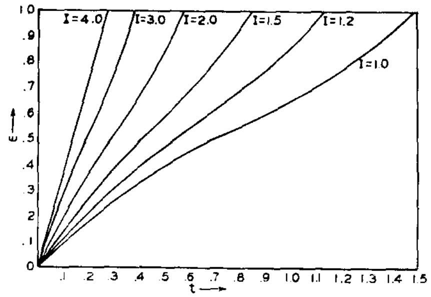

FIGURE 4*a*

The variation of ε under constant current stimulation obtained by integrating (3) with the $k(\varepsilon)$ of Figure 2. The parameters in Figure 2 are arbitrarily taken: $k_0 = 1$, $h\,\theta_1 = .5$, $K = 1$, and the units of t and I are arbitrary.

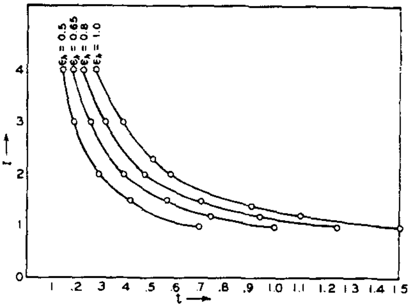

FIGURE 4*b*

Strength-duration curves for indices of response $\varepsilon_h = 1$, .80, .65, .50. Points obtained directly from the curves of Figure 4*a* are represented by circles. The curves were obtained by using the Table 1 values of $k_l(\varepsilon_h)$ in the ordinary condenser formula (2).

From the curves of Figure 4*a*, we can construct strength-duration curves for any arbitrary index of response; the curves for $\varepsilon_h = 1$, .8, .65, .5 are given in Figure 4*b*. The values of $k_l(\varepsilon_h)$ determined directly from these curves, together with theoretical values of $k_l(\varepsilon_h)$ calculated from (6), are given in the accompanying Table 1. The magnitude of the variation in $k_l(\varepsilon_h)$ which may be expected is seen to be of the order of 100%; this agrees with the results of H. Rosenberg (1937) and of B. Katz (1937).

Table 1: Values of $k_l(\varepsilon_h)$ from strength-duration curves (Figure 4*b*) compared with values of $k_l(\varepsilon_h)$ from (6).

ε_h	$k_l(\varepsilon_h)$ (Fig. 4*b*)	$k_l(\varepsilon_h)$ (Eq. 6)	% difference
.5	1.0	1.0	0
.65	.86	.92	6+
.80	.74	.79	6+
1.0	.54	.58	7+

It is seen from Figure 4*b* that the non-linear strength-duration curves are practically identical with the linear curves which are obtained by integrating the linear equation (2), after replacing k_0 by $k_l(\varepsilon_h)$. This must be considered rather fortuitous, since, by taking some different approximating function for $k(\varepsilon)$, we could get a different non-linear strength-duration curve. Thus it appears that Rushton's prediction of a strict linear theory strength-duration curve, even when the liminal length is taken into account, must depend on the assumption of an all-or-nothing response at a point.

Physical interpretations. Although the theory which we have outlined is phenomenological, certain connections with physical interpretations seem to be inevitable. As an example, we may ignore the difficulties for the moment, and identify ε with the condenser voltage, V, in a circuit consisting of a condenser, C, shunted by a non-linear resistance. For this circuit, assuming no current flow from the outside,

$$\frac{dV}{dt} = -\frac{V}{R(i)C}$$

where i is the current through the variable resistance $R(i)$ and, by definition, $iR(i) = V(i)$. Since $i = C\frac{dV}{dt}$, the $V(i)$ characteristic may be determined exactly as we determined $w(\varepsilon)$—by graphically differentiating a family of voltage decay curves. The $V(i)$ curve may be identified with our $w(\varepsilon)$ provided we plot ε vertically and w horizontally; on the other hand, this characteristic bears little resemblance to the steady state $V(i)$ curve found by K. S. Cole and H. J. Curtis (1940) for squid axon.

The direct measurement of the $V(i)$ characteristic in nerve is analogous to the usual direct measurement (with ammeter and voltmeter) of the characteristic of a neon tube shunted by a resistance and a condenser. However, there is another "phenomenological" method of measuring the characteristic of such a neon tube which, while highly impractical, is analogous to the scheme we have used here to get at the "characteristic" of nerve (cf. also Blinks and Skow, 1940). Suppose, instead of directly measuring the current as a function of the steady voltage across the tube, we determine the time course of the discharge of the condenser through the neon tube and its shunting resistance. This may be done either by actually measuring the time decay of the initial charge with a ballistic galvanometer, or, by determining the extra charge required at each time to just cause the neon tube to flash. In this way we can obtain "local excitatory decay" curves entirely analogous to those found by Katz, and from these we can determine the instantaneous voltage across the tube as a function of the current through it. For a simple neon tube circuit this phenomenological method and the previous direct method should give identical characteristics. If the experiments of K. S. Cole and H. J. Curtis may be considered the proper analogue, in the nerve, to the direct measure of the characteristic of the neon tube, then as we have mentioned, the direct and the phenomenological methods in nerve *do not* lead to the same characteristics. The explanation of this difference probably lies in the inadequacy of the structural assumptions required to make the transition from the phenomenological to the physical characteristics. A complete elucidation of this difference will be a major task of any adequate theory of nerve activity.

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