ON THE QUANTITY OF ELECTRICITY AND THE ENERGY
IN ELECTRICAL STIMULATION

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The quantity of electricity and the energy have been assigned considerable significance in the problem of electrical excitation on account of the circumstance that these quantities appeared in or were easily derivable from two noteworthy early attempts to correlate the strength-duration relations, namely, the laws of Weiss (1901) and Hoorweg (1892). It does not appear that the significance of these laws has been discussed adequately with respect to the dynamics of the excitatory process. There arises the question, therefore, as to whether the origin of these ideas about quantity and energy has a logical basis; and if it has not, there is another question as to whether any special significance can be assigned to the quantity and the energy from a point of view which is in conformance with more recent ideas about the nature of the excitatory process. It is the present purpose to consider these questions.

Weiss's law is easily derived as follows: let

$$\frac{dp}{dt} = KV - k$$

(1)

where $p$ is the state of excitation, $V$ is the applied voltage, and $K$ and $k$ are constants. If it is assumed further that a constant amount, $h$, of the local excitatory state is required for excitation, Equation (1) gives on integration,

$$Vt = \frac{h}{K} + \frac{k}{K} t$$

(2)

which is Weiss's law.

1 A quantity law by Dubois of Bern appeared earlier than these but it was soon found to be inadequate (see Lapicque, 1926; Hoorweg, 1892).
Weiss's law, therefore, is the logical consequence of the assumptions, that the rate of growth of the excitatory state varies as the strength of the stimulus, that there is a simultaneous spontaneous subsidence of the excitatory state at a constant rate, \( k \), and that equal amounts of the excitatory state are adequate for all threshold stimuli. The second, at least, of these assumptions is probably invalid for it implies that following an inadequate stimulus \((KV = 0 \text{ in (1)})\), the local excitatory state subsides at a constant rate, while the data of latent addition are interpreted as indicating the existence of an exponential rate, e.g. Chauchards (1925), Lapicque (1925). It must be admitted that the direct information on latent addition is far from satisfactory but there is very good indirect evidence of the exponential subsidence which will be discussed later. It is conceded in addition that equation (2) represents the data rather poorly (Lapicque, 1926). It is therefore very likely that the basis of Weiss's law is unsatisfactory and that any derivations from the law will be equally unsatisfactory.

In particular with regard to the minimal energy, which is easily shown from (2) to occur when \( t = \frac{h}{k} \) and \( V = \frac{2k}{K} = 2R \), the rheobase, being the minimal voltage for times indefinitely long, it cannot be expected either that the experimental minimal energy will occur at exactly \( V = 2R \), or that the duration for which it occurs can be related through Weiss's law to any parameter of the process of excitation.

It has been shown already by Strohl (1932) that Weiss's and Hoorweg's laws are inconsistent. His reasoning was on the basis of the quantities of electricity, but it can be shown equally well by the present method. For, if Weiss's and Hoorweg's laws have a common basis, the latter should be derivable, using the same assumptions as previously, from the equation,

\[
\frac{dp}{dt} = KV_0 e^{-\frac{\pi}{r} t} - k
\]

where \( V_0 \) is the initial voltage of the stimulating condenser and \( k \) and \( r \), are the capacity and resistance, respectively, of the circuit. The solution with \( p = 0 \) at \( t = 0 \) is

\[
p = ce KV_0 \left( 1 - e^{-\frac{\pi}{r} t} \right) - kt
\]
This function, \( p \), has a maximum value at a time \( t_0 = \alpha r \log \frac{KV_0}{k} \). If \( p = h \) at this time, \( t_0 \), the utilization time of the discharge, it will be just adequate. These conditions in (4) give

\[
h = \alpha r KV_0 \left(1 - \frac{k}{KV_0}\right) - \alpha r \log \frac{KV_0}{k}
\]

but this is not Hoorweg’s law. Therefore the bases of these laws are not the same.

It was pointed out by Strohl (1932) that putting the utilization time, \( t_0 = \alpha \sigma r, \alpha \), a constant, gives the form of Hoorweg’s law. In this case this is equivalent to putting \( \log \frac{KV}{k} = \alpha \), which gives from (5)

\[
V_0 = \frac{h}{K\alpha r} + \frac{k}{K} (1 + \alpha)
\]

which is Hoorweg’s law. The assumption above concerning the utilization is, however, entirely illogical with respect to the present argument as it implies that the excitatory state is more adequate at some value other than its maximal. Thus if it appeared desirable to extend Weiss’s law it should be done by applying (5) to condenser data. The application of Hoorweg’s law, equation (6), is quite irrelevant.

With regard to the question as to whether Hoorweg’s equation may be derived from some basis other than equation (3) by a more logical assumption than that the utilization time is proportional to the \( \alpha r \) of the circuit, independently of the voltage, it will be observed that any basis in which the growth of the excitatory process depends on the current or voltage of the discharging condenser involves a term \( e^{-\alpha r} \). Since the integral of this expression will also contain \( e^{-\alpha r} \), and since Hoorweg’s equation does not, it follows that some assumption has to be used which will get rid of it. The necessary assumption is \( t_0 = \alpha r \times \text{constant} \). It therefore seems unlikely that Hoorweg’s law can be given a better interpretation than has been given. This conclusion does not apply, of course, to empirical integral expressions equivalent to Hoorweg’s law in which various interpretations can be
given to the parameters without regard to the underlying dynamics. Such an expression is given, for example, by Ebbecke (1927).

It seems, therefore, that lacking a consistent common basis, the quantity laws and the energy relations derived from them are likely to be very misleading. Since they show, however, approximate relations involving the quantity and the energy, it will be of interest to examine a more exact representation of the data in order to determine whether or not these quantities will appear in a simple way. The writer's representation (1932) is chosen because it is the only one which has been shown to be consistent for more than one type of stimulus on the same preparation (1935a, b).

The basis of this representation is the equation,

\[ \frac{dp}{dt} = KV - kp \]

in which the symbols have the same meanings as before. The upper limit of integration (the threshold) is, however, \( h - \alpha V \), where \( \alpha \) is a constant and \( V \) is the voltage at the utilization time. This gives for direct current stimuli and condenser stimuli, respectively, the relations,

\[ \log \frac{V}{V - R} = kt + \log \left( \frac{K + ka}{K} \right) \]

and

\[ \frac{V}{R} = \left( \frac{ka}{\alpha} \right)^{\frac{1}{\alpha - 1}} \]

These equations in which an exponential decay of the inadequate excitatory state is implied represent the data very adequately. Therefore, as mentioned above, both the direct evidence for latent addition and the indirect evidence from the strength-duration curves indicate the existence of the exponential rather than the constant decay of Weiss's law.

Considering (9), the condenser equation, first it will be seen that

2 This has been written \( h + \alpha V \) previously because some data required the + sign. The cases requiring this sign are so uncommon, however, that they may be due to experimental errors.
when \( crk < 1 \), \( \frac{V}{R} = \frac{1}{crk} \), approximately, or \( cV = \) constant. The prediction is, then, that the quantity of electricity necessary for condenser stimulation approaches a constant value as the capacity becomes small. In the case of the frog's sciatic nerve, \( k = 1000 \), approximately, so that if \( cr = 10^{-5} \) seconds, approximately, \( crk = 0.01 \), in which case the exponent of equation (9) \( = \frac{1}{0.99} = 1 \), approximately. Therefore the quantity of electricity, \( cV \), should be constant, approximately, for time constants, \( cr \), of the order of \( 10^{-5} \) seconds and less with this tissue.

That this result is obtained experimentally is illustrated by the work of Scott (1934). He plotted condenser curves as log \( V \) against log \( c \) in which case \( cV = \) constant appears as a line of slope, \(-1\). His data on the frog's sciatic show \( cV \) to be constant in close approximation for voltages from about 10 to 100 rheobases, or as it is remarked,\(^3\) for time constants, \( cr \), shorter than \( 2 \times 10^{-5} \) seconds.

These results indicate that equation (9), which has been shown previously to represent the data adequately (Blair, 1932 b, d; 1934; 1935 c) up to about 20 rheobases, is valid to about 100 rheobases, at least. They explain also why a formula such as Hoorweg's, which predicts a constant quantity at the limit as the capacity diminishes will fit at least part of the voltage-capacity curve.

Hoorweg's law, in common with Weiss's, predicts an energy minimum at \( V = 2R \). It appears to be assumed generally that this is borne out experimentally. Equation (9) will be examined therefore in this regard.

Since the energy is proportional to \( cV^2 \), equation (9) is written, after squaring both sides and multiplying by \( c \),

\[
\frac{crkV^2}{R^2} = (crk)^{\frac{1}{crk-1}} = \text{constant} \times E
\]

(10)

\( E \) being the energy. On differentiating and putting in the condition for a minimum,

\[
\frac{(crk + 1)(crk - 1)}{2crk} = \log crk
\]

\(^3\) Scott, D., J. Physiol., 1934, 82, 325.
But this is true in the limit as $crk$ approaches 1. But as $crk$ approaches 1, the right hand of (9) approaches $e = 2.718$ etc., the base of the natural logarithms. Therefore according to (9) the energy is a minimum not when $V = 2R$, but when $V = 2.718R$.

Those data which have been shown to conform to equation (9) (Blair, 1932 b, d; 1934; 1935 c) in close approximation will have the minimal energy at this point to a similar approximation. Since this matter has not been discussed previously, however, there is plotted in Fig. 1 a group of examples from the data of several observers on several different tissues using condenser stimuli. Only a few of these data have been related previously to equation (9).

In each case of Fig. 1 there is plotted the energy\textsuperscript{4} of the discharge against the initial voltage of the condenser on a scale of rheobases. The use of this scale requires that the rheobase should have been given. Some of the older data such as Hoorweg's (1892) do not satisfy this condition, so they could not be used. The scale of energies in the figure is arbitrary, the value, 1, being given to a point at about 1.5 rheobases so that the curve will be well defined in the region around 2 to 3 rheobases. The legend gives the sources of the data and the types of tissues.

It will be observed that in accordance with equation (9) the minima of these curves are close to the points $e$ rheobases which are marked on the graph by short lines. The energy curves are so flat toward the higher voltages in many cases, however, that the minima are poorly defined and the best that can be said, sometimes, is that they occur from about 2.5 to 3 rheobases. Obviously they are not near to 2 rheobases as predicted by Hoorweg's law and as is usually assumed.

In regard to the quantity of electricity with direct currents it will be seen that according to (8),

\begin{equation}
V = \frac{-Re^{at+c}}{1 - e^{at+c}}
\end{equation}

so that as $t$ becomes very small $V$ becomes approximately constant, as long as $C$ is not equal to zero, and $Vt$, the quantity of electricity, becomes proportional to the time. This is contrary to Weiss's law.

\textsuperscript{4} In case 0 the square of the energy is used because the energy curve is very flat.
but is in accord with experiment, as the curve of quantities plotted against the time tends to go toward the origin instead of cutting the axis of ordinates at the required point (Lapicque, 1926).

How far this prediction can be taken depends, however, on the dynamics of the process giving rise to $C$; i.e., to the process lowering the threshold from $h$ to $h - \alpha V$. This process has been complete with the data so far considered in relation to equation (8) but it cannot be assumed that it is instantaneous.

With direct currents on writing equation (8) as,

$$\log \frac{V}{V - R} = kt + C$$

it can be shown similarly that the condition for minimum energy is given by,

$$1 + 2 kt = e^{kt+C}$$

In the special case, $C = 0$, this is true for $kt = 1.25$, approximately, which corresponds to $V = 3.5 \frac{R}{2.5}$, approximately, or about 1.5 rheobases. With the threshold, $h - \alpha V$, $C$ is positive so that $kt$ will be greater than 1.25, and consequently $V$ will be greater than 1.5 rheobases. Therefore, since $C$ is usually positive, the minimum energy will be with voltages somewhat greater than 1.5 rheobases, but its position will be variable, since $C$ is variable and is very seldom zero. This variability was observed by Lapicque (1926) experi-

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5 Chapter 5.

6 A. V. Hill (1932) in reviving Lapicque's (1907) leaky condenser hypothesis, assumes that $C = 0$ in equation (13) (in which case this equation would represent the condenser hypothesis) because of data by Rushton (1932). For these data, this assumption is almost true, but not quite (Blair, 1932c). These data, taken from the frog's sciatic nerve near 0°C. are unusual in this respect, however. Most direct current data are not representable by the leaky condenser hypothesis with constant charge for adequacy, even in rough approximation (Blair, 1932a, c; 1935a, b). It should be observed also that equation (9) is true both for this condenser hypothesis and for the hypothesis of equation (7) along with the threshold, $h - \alpha V$ (Blair, 1934). Equation (9) cannot decide, therefore, between the condenser hypothesis and the present one. This ambiguity does not arise with other stimuli, however, which leave the inadequacy of the condenser hypothesis in no doubt, as Lapicque (1907) concluded long ago. Hill's (1935) conclusion that an equation like (13) with $C = 0$ must fit direct current data because equation (9)
mentally, who remarks that his results with direct currents did not give minima at the same place consistently. It is evident now why this result was obtained. The situation is illustrated in Fig. 2, in which four direct current curves are plotted with the energy as ordinates against the voltage in rheobases as abscissae. Curve A is fits condenser data appears superficially to be quite valid, but it can be invalid, and there is little doubt that it is invalid except in a few special cases. As Hill was concerned chiefly with the effects due to currents of relatively long application (accommodation) this conclusion does not affect his general argument. This matter is discussed again more fully later in the text.

Fig. 2. The energy minima with strength-duration curves. A. Sciatic nerve of frog, C = 0 (Blair, 1935a, p. 761). B. Sciatic nerve of frog, C = 0.03 (Blair, 1935a, p. 761). C. Sartorius muscle of frog, C = 0.12 (Benoit, 1934, p. 339). D. Sartorius muscle of frog, C = 0.103 (Benoit, 1934, p. 339; Experiments 1 and 3; or Blair, 1935d, p. 304).
from the sciatic nerve of the frog, and \( C = 0 \). The minimal energy should be at 1.5 rheobases, according to equation (12). Curve B is also from the sciatic nerve of the frog, but \( C \) is greater than zero. The minimum should be displaced to a higher voltage. Curves C and D are \( \alpha \) excitabilities in which (as is usual) \( C \) is very large. It will be observed that the minimal energy here is at about 4 rheobases, at least. The curves are not extensive enough to get beyond the minima again in order to determine their positions exactly.

Since the minimal energy for rectangular currents is a variable point greater than or equal to 1.5 rheobases while the minimal energy for condenser stimuli is near \( e \) (2.718) rheobases, this particular energy can no longer be considered to have a special significance with respect to the strength-duration curves of various kinds of stimuli expressed on scales of rheobases.

The chronaxie is not at or simply related to the minimal energy point, but this is of no particular consequence, except insofar as they are usually supposed to be coincident. As was pointed out previously (Blair, 1932c) the direct current chronaxie does not determine uniquely the excitability factor, \( k \), because of the variable parameter, \( C \), of equation (13). With condenser discharges, however, \( crk = 2 \) when \( V = 2 R \), i.e. for chronaxie, and \( crk = 1 \) for minimal energy. Either of these points give directly, therefore, the parameter, \( k \), which is inversely proportional to condenser chronaxie. It will be observed, incidentally, that the minimal energy point gives \( k \) without the necessity of the rheobase being known.

The effective energy in the case of rectangular currents is the total energy, but with the condenser stimuli the energy actually utilized is less than the total by the amount still remaining in the condenser at the utilization time. The utilization time for the condenser discharges is,

\[
\tau = \frac{cr}{crk - 1} \log crk = cr \frac{V}{R}
\]

(Blair, 1932d)\(^t\)

\(^t\) P. 178.
But according to the equation of the discharge of the condenser \( V = V_0 e^{-\frac{t}{\tau}} \) the potential remaining at the utilization time is

\[
V = V_0 e^{-\frac{t}{\tau}} \frac{V_0}{R} = R
\]  

(14)

The condenser discharge is utilizable, therefore, until its potential descends to the rheobase. The utilizable energy consequently is

\[
0.5 c (V^2 - R^2)
\]  

(15)

This deduction from the theory can be easily verified directly as follows: The rheobase suffices on long application just to raise the local excitatory state, \( p \), to its threshold. Therefore, if with a greater stimulus, \( p \) has not reached the threshold before the potential has dropped to the rheobase it can never do so thereafter. On the other hand, if \( p \) has not reached the threshold it will continue to grow as long as the stimulus exceeds the rheobase. Therefore, a just adequate stimulus has raised \( p \) just to the threshold just as it itself has decayed to the rheobase. This conclusion was reached by Bouman (1928)\(^8\) in a similar way. When applied to the equation of the condenser discharge it gives directly the utilization time, the utilizable potential, and the utilizable energy as they are above without reference to any theory of excitation.

This utilizable energy of the condenser discharge (Equation 15) does not present features of particular interest in a simple way so that it need not be discussed further. Equation (14) is of interest, though, with respect to footnote 6, in which it was stated that equation (9) was equally representative of the condenser hypothesis\(^9\) and the

\(^8\) P. 421.

\(^9\) Equation (7) has the same form as the differential equation of the rise of potential in a leaky condenser. If the threshold is assumed constant, i.e. if the condenser, on reaching a certain potential, \( h \), is assumed to set off the process of conduction the corresponding integral (\( C = 0 \) in (13)) would represent Lapicque’s (1907) condenser hypothesis. This hypothesis is not adequate, but the leaky condenser with a variable threshold \( h - \alpha V \) (\( C \) existing in equation (13)) appears to be apart from accommodation. It cannot be inferred, however, on these grounds, that the excitatory mechanism is a leaky condenser with a variable threshold because equation (7) may represent other mechanisms.
It will be evident that with the condenser stimuli, since the excitatory state always becomes adequate when \( V = R \), the threshold will always at that moment be \( h - \alpha R \) which is a constant. Thus with the condenser discharges the threshold is constant, not because it is unaffected by the stimuli but because it is equally affected by all the stimuli. This is the reason why Equation (9) cannot distinguish between the condenser hypothesis, which assumes a constant threshold, and the present one which assumes a threshold \( h - \alpha V \). The threshold for each hypothesis is a constant, although a different constant.

This is the reason also that the condenser equation (9) has but one arbitrary constant, \( k \), while the direct current equation, (8) or (13), has the two, \( k \) and \( C \). The second factor, \( C \), is required to express the relations arising from the circumstance that the threshold, \( h - \alpha V \), is different for each direct current stimulus because each stimulus has a different value at the utilization time.

It will be evident also that this is the basic reason that condenser chronaxie and direct current chronaxie do not have the same meaning. The former is adequate because it can express a relation determining the single parameter, \( k \), while the latter is not, because it cannot express the two independent parameters, \( k \) and \( C \) (Blair, 1932). The variability of the minimal energy with direct currents is related to the existence of \( C \) as was shown above, therefore it also is fundamentally due to a variable direct current threshold.

Thus it will be seen that these differences between the integral relations for the direct current and the condenser stimuli are easily explainable quite directly on the basis of the hypothesis that the threshold is not a constant but of the form, \( h - \alpha V \). This hypothesis is well confirmed because it has been shown to be consistent for direct currents, and linearly rising currents (1935b), in both of which cases the threshold should be variable at the utilization time because each stimulus has a different value at that time; and it is confirmed also by the fact that a constant threshold appears with condenser stimuli, in which case \( h - \alpha V \) should be constant.

This alteration of the threshold by the stimulus is not the process of accommodation, the dynamics of which have been discussed recently again by Hill (1935). Accommodation involves a raising of the
threshold, among other things, and is a slow process compared to the 
excitatory process proper; so slow that its effect on the strength-
duration curve is apparently negligible (Blair, 1935 b). The present 
process on the other hand is very fast relative to the excitatory process 
and it involves a lowering of the threshold.

It appears to be well established, therefore, that there are two ex-
citatory processes apart from accommodation. The principal one is 
that represented by the equation,

\[
\frac{dp}{dt} = KV - kp
\]

The other one, whose dynamics are not known because it is always 
complete with existing data at the utilization time, involves a lowering 
of the threshold from \( h \) to \( h - \alpha V \). There is some indication from 
unpublished data on the alpha excitability that this threshold process 
is not complete with the very short stimuli, so its dynamics may be 
found in this way. The question of its existence does not depend, 
however, on a knowledge of its dynamics.

CONCLUSIONS

It will be evident, in conclusion, that the quantity of electricity and 
the energy do not appear from excitation data in a way nearly so 
simple as has been generally supposed on the basis of Weiss's and 
Hoorweg's laws and that in consequence the attachment of any 
special significance to these factors is likely to be very misleading. 
The situation given by the data is explainable quite directly on the 
basis of the hypothesis that the rate of growth of the excitatory state 
varies directly as the instantaneous strength of the stimulus, that 
there is a simultaneous subsidence of the excitatory state at a rate 
proportional to its magnitude, and that the threshold amount of the 
excitatory state is a constant decreased by an amount proportional 
to the strength of the stimulus at the utilization time. The present 
considerations, therefore, lend further support to this hypothesis.

SUMMARY

Weiss's and Hoorweg's laws are discussed with respect to the 
dynamics of the excitatory process. The former is shown to have a 
simple basis which is inadequate, however, because it implies a con-
stant rate of subsidence of the state of excitation. Hoorweg's law does not follow logically from the same basis so the two laws do not represent the same excitatory mechanism. Experimental data do not give minimal energies at 2 rheobases as predicted by each law. The experimental minima with direct currents are at 1.5 or more rheobases, while with condenser stimuli they are from 2.5 to 3.0 rheobases. These minima conform to the predictions of the writer's equations which give the direct current minima as variable with a lower limit at 1.5 rheobases and the condenser minima as constant at $e = 2.718$ rheobases. The reasons for these differences are discussed and it is concluded that considerations of the quantity of electricity and the energy, *per se*, do not lead to any simple concepts with regard to the excitatory mechanism. The existing quantity and energy relations are, however, easily correlated in terms of the dynamics of the excitatory mechanism.

**BIBLIOGRAPHY**