BLAIR'S "CONDENSER THEORY" OF NERVE EXCITATION

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In four recent papers, Blair (1931–32; 1932–33) has developed a mathematical concept which he believes to underlie the excitation process in nerve and muscle, and he urges that a deeper insight will be gained into this process if observations are expressed in terms of the equations which he has derived. Since on the one hand many experimenters do not easily digest the somewhat rich diet of mathematics provided in these papers, and since on the other the author appears to have overlooked certain defects in his theory, it is proposed in this note to point out in non-mathematical terms some qualitative advantages and quantitative objections to Blair's treatment.

Prolonged Currents

When a constant current is applied to a tissue, the excitatory state first quickly rises and then (if the threshold is not reached) slowly declines, though not to zero. It is thus possible by increasing a current in small steps to apply without response a current much in excess of the rheobase. If the steps are infinitesimal the case becomes that of slowly rising currents. This property appears to be one of the fundamental facts to be answered in any comprehensive theory. It enters into all discussions of Nernst's hypothesis under his term "accommodation" and has proved the stumbling block in many treatments. In particular one of the limitations of the "condenser theory" is that it will not contemplate this property of nerve and muscle.

If a tissue is represented as a shunted condenser (Fig. 1) it is apparent that when a certain voltage is applied and retained constant, the charge on the condenser will rise to a value characteristic of that voltage, and become quite independent of whether the voltage initially rose suddenly or exceedingly gradually. And this which is intuitively clear from electrical considerations equally follows from Blair's equa-

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tions which are the exact mathematical equivalent. It is consequently obvious that the condenser theory is quite inapplicable to cases of prolonged currents, because the tissue "accommodates" and the condenser does not.

Blair, however, attempts to apply his equations to the cases of slowly rising currents, but shelves the only significant aspect of the question—the minimum gradient—by suggesting that this is due to some phenomenon different from the local excitatory process.

With regard to the opening excitation, which originates at the anode, it has been usual to regard this as some sort of rebound after the process of "accommodation." If this is the case the consideration were well postponed until some clearer views are available concerning the minimum gradient—which is probably closely related. Blair, how-

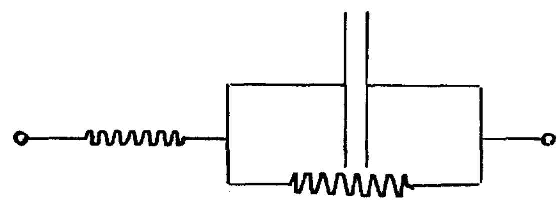

FIG. 1

ever, supposes that the opening excitation is due to a sudden shift in the sensitivity of the tissue so that a certain magnitude of the excitatory process, inadequate to excite while the current is flowing, suddenly becomes adequate owing to the threshold falling faster than the rate of decay of the excitatory process.

Since this requires that the opening excitation should occur at that electrode where excitability was enhanced during the current flow, namely the cathode, this concept is quite untenable.

These considerations emphasise that whatever may be the advantages of the condenser theory for brief currents, the theory unmodified has no place at all in relation to prolonged currents.

It is very easy to make a suitable modification, for instance by the assumption that there is polarisable connective tissue in series with the tissue. This accounts qualitatively for all the chief results with prolonged currents—the minimum gradient, the opening excitation, etc.,—and if this polarisation is represented as a leaky condenser it is easy to derive the appropriate equations. But what is required is the physical investigation of what polarisation does in fact occur, not what equations result from supposing that such a polarisation behaves like a parallel plate condenser.

Brief Currents

The fact that the condenser theory is inapplicable to conditions involving "accommodation" does not in any way invalidate it as a theory applicable only to brief currents, for in these cases "accommodation" whatever it is, may be regarded as insufficiently developed to be significant.

I wish to suggest that in this domain the condenser theory is a useful qualitative guide, and a valuable basis upon which to build a more accurate concept of the excitatory process. But both in its simplest form and in the modification by Blair it is quantitatively inadequate.

Blair does not explicitly assume that the tissue is to be regarded as a shunted condenser (Fig. 1), but he postulates that it obey the mathematical law which governs the flow of electricity in such a condenser system, and hence all the results which he derives are identical with those on the condenser theory.

Actually he claims that a nerve cannot be regarded as a condenser since otherwise an alteration in series resistance would change the time relations. This argument falls to the ground if the condenser is assumed shunted by a resistance small compared with the series resistance. The recent papers of Umrath (1930) and Eichler (1931) deal with this matter experimentally and in detail.

Turning now to Blair's form of the condenser theory, we note that he first makes the assumption that the condenser must attain a certain fixed charge h in order that excitation may occur. This is a very reasonable physical concept (and by no means a new one) but it has the disadvantage that it does not accurately fit the facts. To remedy this the assumption is now modified, and the charge must attain not h but $h + \alpha V$, where V is the applied voltage at the moment of excitation, and α is a constant. There is no physical justification for this assumption nor can I find a physical meaning to it. It appears, moreover, to be contrary to facts.

In many preparations Blair claims that α is positive; let us consider what happens in this case according to Blair's hypothesis. If the tissue is excited by a constant current of voltage V, the threshold during the whole period of current flow will be $h + \alpha V$, but the instant after the current ceases the threshold will have fallen to h. Now the excitatory process takes a finite time to decay, hence it will not have diminished appreciably between the instant before and the instant after breaking the stimulating circuit. Consequently, if the excitatory process had attained the value h before breaking, it would have attained this value the instant after breaking and consequently would cause excitation. We must therefore conclude that where α is positive the threshold required will not be $h + \alpha V$ but still h.

But not only does the hypothesis which we are considering bring the results no nearer the facts but it also involves two conclusions of a very startling kind. For if the rheobase current be stopped after flowing for a duration just greater than the utilisation period it need only be such a strength as will cause the excitatory process to attain h. If, however, the rheobase be continued indefinitely so that excitation is observed to occur while the current is still flowing, then the excitatory process must attain the value $h + \alpha V_R$ where V_R is the rheobase in this case. It is obvious that according to this a *higher* threshold is required for a current which continues than for one which is stopped, which is very contrary to experience.

Again it appears that at the instant of starting the stimulus the threshold will rise from h to $h + \alpha V$. If V is negative (*i.e.* the point we are considering is anode) the threshold will not rise but fall when the current starts, and if V is made large enough the threshold will fall below zero; *i.e.*, the tissue will be excited by the resting value of the excitation process. This result is surprising; it signifies that with strong currents, excitation should arise at the anode, the current need not flow for any finite duration, nor is the threshold reduced by increased duration of flow.

Nothing would be served by dwelling further upon Blair's modification of the condenser theory, for we have seen that it is unrelated to any likely physical mechanism, that it does not in fact fit observations any better than the unmodified theory and that it involves consequences of a totally inadmissible kind.

CONCLUSIONS

With regard to the advantages of the condenser theory, they have been urged by so many authors from time to time in connection with so many different experimental investigations, that it is impossible to treat the matter in this place. Suffice it to state that although it rarely happens that the theory fits accurately the observations, yet over a very large range there is a good qualitative correspondence, and this is illustrated in the papers of Blair. In particular in the calculations relating to strength-duration curves and voltage-capacity curves, the latter relation was determined from the former without any arbitrary constants at all, and the correspondence is sufficiently striking.

The following conclusions therefore seem permissible.

The condenser theory in its simple form though quite misleading when applied to cases of prolonged currents is a useful qualitative guide where brief currents are concerned.

The semiquantitative correspondence which subsists between theory and observation in a very wide field suggests that something equivalent to the condenser mechanism may underlie the phenomena of excitation as commonly measured. The particular modification of this theory put forward by Blair, however, is not physically plausible and leads to inadmissible conclusions.

SUMMARY

Blair's recent theory of excitation is analysed with the following conclusions:

1. The theory is inapplicable to currents of long duration; *i.e.*, slowly increasing currents and the opening excitation.

2. The theory is a modification of the condenser theory of excitation but the modification is to be rejected on three grounds:

(*a*) The modification has no obvious physical significance.

(*b*) It does not in fact remedy the divergence between calculation and observation.

(*c*) It leads to certain conclusions of a surprising kind which are contrary to observed fact.

3. The qualitative value of the condenser theory is demonstrated by the fairly close agreement between calculation and observation over a considerable field of enquiry.

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