SEVERAL MODES OF EXCITATION MOVEMENT IN IDEAL EXCITABLE TISSUE*

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IT IS very hard to make a detailed study of the pattern of movements of excitation in real excitable (nerve or muscular) tissue and therefore, to solve the specific problems it is appropriate to use theoretical models which have a strictly limited number of properties chosen in relation to the character of the problem. Such models may be discrete and continuous. By analogy with the ideal gas it is desirable to call them ideal excitable tissue.

The purpose of the present work is to show how in ideal excitable tissue modes of excitation movement may appear similar to certain pathological disturbances in cardiac rhythm.

Apparently, Lewis [1] was the first to call attention to the fact that in certain conditions the excitation wave appearing in the atrium moves in a circle around the site of entry of the vena cava. He is also responsible for the hypothesis that this phenomenon is linked to auricular flutter. Subsequently, the problem was investigated by Wiener and Rosenblut [2] who used for study of the excitation movement a model very similar to the ideal excitable medium considered below. An interesting continuous model with spontaneous activity was described by Gel'fand and Tsetlin [3].

Гельфанд и Цетлин

We shall consider a two-dimensional ideal excitable tissue which may be both finite and infinite. Each point of this tissue may be resting, excited or refractory. Only the resting points are excited, excitation is imagined as an instantaneous process abruptly passing from the resting to the refractory state. We shall call the totality of simultaneously excited points the leading edge of excitation which is the line separating the points which have still to be excited from the refractory ones. Excitation spreads in the resting tissue to all sides of the leading edge of excitation at a constant speed. After the point has been excited, it is in a refractory state for an interval of time τ after which it passes to the resting state.

The character of the movement of excitation in this tissue depends on the initial conditions. We shall first consider a mode which we will call normal. It appears if any point or group of points of such a medium is excited by an external agent. Excitation from the initially excited point O spreads in the form of a circle the radius of which increases at the rate v (see Fig. 1*a*). This circle is the external boundary of the ring-shaped refractory zone the thickness of which is $v \cdot \tau$. Because of the properties of the medium during time τ after the first excitation, point O cannot be excited. If it is

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excited two or more times with intervals greater than τ a few concentric rings appear. If it is excited at intervals τ, the leading edges of excitation move one directly behind the boundary of refractoriness of the other. After excitation of point O has ceased, around it forms an unexcited zone which increases until all the finite region of the medium considered is involved.

A characteristic feature of a normal mode of movement of excitation is that each leading edge is either closed or both ends abut against the boundaries of the medium

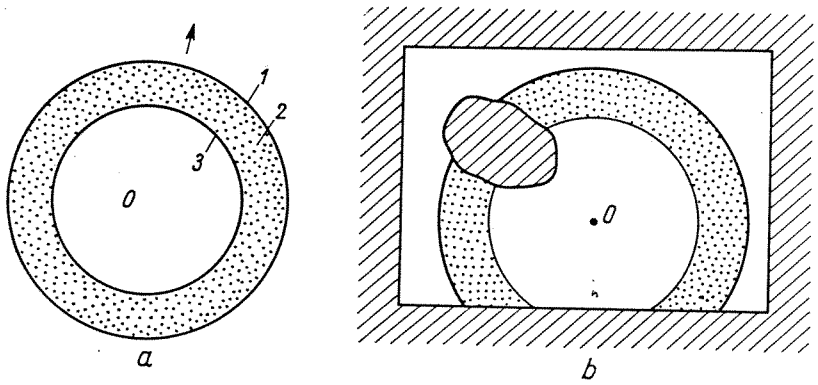

FIG. 1. *a*—Spread of excitation from point O; *1*—leading edge of excitation; *2*—refractory zone; *3*—rear boundary of excitation. Arrow denotes direction of spread of excitation. *b*—spread of excitation in bounded ideal excitable tissue with "hole".

(in the particular case in its non-excitable zones or "holes" (Fig. 1*b*). This property may be taken as a criterion of the normal mode.

The normal mode is stable. This means that small quantitative differences in the properties of the tissue do not change the character of movement of excitation. In fact, reduction in the rate of propagation of excitation in any restricted zones only leads to certain changes in the form of the leading edge of excitation. As can be seen from Fig. 1*b*, it goes round even the non-excitable zones of the "hole". By drawing the corresponding Figures it is easy to see that several independent leading edges of excitation sooner or later will merge into one. The abnormal mode of movement of excitation appears for other initial conditions. Let in an infinite medium there be a plane semi-finite leading edge of excitation. The initial picture is depicted in Fig. 2a. The leading edge of excitation has the form of a semi-infinite straight line one end of which at the initial moment of time is at point O_1 and the other passes to infinity. Behind the leading edge of excitation is the zone refractoriness the rear boundary of which begins at point O_2. The structure of the refractory zone is such that the further the point is away from the leading edge of excitation, the sooner it emerges from the state of refractoriness, i.e. the same as would occur on movement of excitation from point O_2 to point O_1.

We shall consider how this picture evolves. From all the points of the leading edge of excitation apart from O_1 it may move only to one side since the zone of refractoriness is on the other. This movement proceeds at the speed v. From point O_1 excitation may spread in a 180° sector moving at the "lateral" boundary of the refractory zone. Since

the rear boundary of refractoriness also moves at the speed v in the direction from point O_2 to O_1, at the moment of time $\frac{1}{2}\tau$ excitation emerging from point O_1 is encountered at point O_3 with the rear boundary of refractoriness. At this moment of time the leading edge will have the form depicted in Fig. 2*b*. After this, excitation at point O_3 will move behind the rear boundary of refractoriness from point O_3 to point O_1. To the right, excitation will spread freely forming a semi-circle; spread to the left will be impeded by refractoriness. At moment of time τ excitation again returns to point O_1 which precisely at this time emerges from the refractory state (Fig. 2*c*). Then

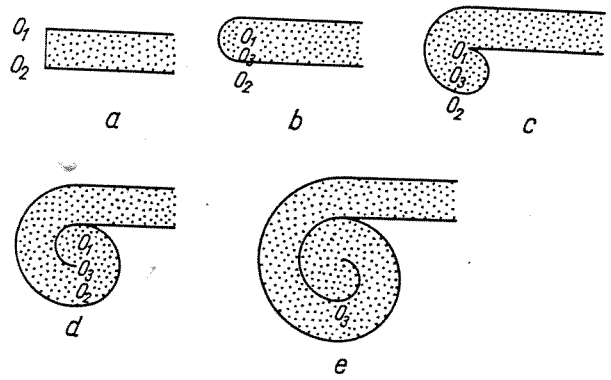

FIG. 2. Course of development of abnormal mode of excitation Unbroken bold line, leading edge of excitation; refractory zone shaded.

the extreme point of the leading edge of excitation again turns moving from point O_1 to point O_3. This will continue for as long as one likes and in the interval $0-\frac{1}{2}\tau$, $\tau-\frac{3}{2}\tau$, $2\tau-\frac{5}{2}\tau$, etc., the extreme point of the leading edge of excitation will move from point O_1 to point O_3 and in the interval of time $\frac{1}{2}\tau-\tau$, $\frac{3}{2}\tau-2\tau$, $\frac{5}{2}\tau-3\tau$, and so on it will move from point O_3 to point O_1. After a sufficient interval of time the leading edge of excitation will consist of two non-symmetrical systems of concentric semi-circles: on the left there will be semi-circles the centres of which are at point O_1 and on the right at point O_3.

A somewhat more complicated picture appears if the abnormal mode develops from rupture of the leading edge of excitation. The configuration of leading edges of excitation in this case is given in Fig. 3, here waves of excitation are formed coming from two symmetrical "eddies" each of which is similar to that depicted in Fig. 2.

The abnormal mode of movement of excitation which has once appeared cannot spontaneously cease and the waves from its centre will spread to all sides until the whole medium is embraced. Since they operate with a frequency $1/\tau$ one directly behind the other, all the points will operate in the maximum possible rhythm. Figures 2 and 3 show that these modes may appear only for portions of tissue not less than $\frac{1}{2}\tau v$. There is no fundamental difference between the abnormal mode of movement of excitation and the ring rhythm considered by Lewis and also by Wiener and Rosenblut in the studies quoted above; this can be readily seen by considering the case when point O_1 or O_3 is at the boundary of a small non-excitable zone.

In ideal excitable tissue all points of which are the same, the normal mode of movement of excitation cannot pass to the abnormal, but if it has sufficiently large zones with raised refractoriness such a transformation occurs. This happens when two normal leading edges of excitation follow one another directly. In the zone with raised refractoriness the second leading edge "strikes" it and is disrupted and the margins of disrup-

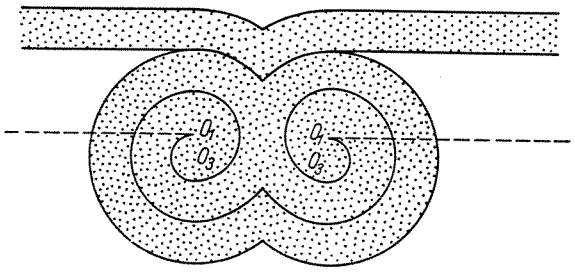

FIG. 3. Configuration of leading edges of excitation for abnormal mode developing from disruption of the leading edge of excitation. Broken line—line of leading edge of excitation at initial moment; unbroken line—after 3τ.

tion abut against the zone with high refractoriness. If at the termination of the period of refractoriness the leading edge of excitation does not have time to close, this may become the centre of the abnormal mode. For this it is necessary that the second leading edge of excitation be disrupted for a sufficient interval of time. Otherwise it simply closes (Fig. 4).

It is quite probable that such phenomena lie at the basis of flutter in certain forms of extrasystole. If the abnormal mode similar to that depicted in Figs. 2 and 3 appears

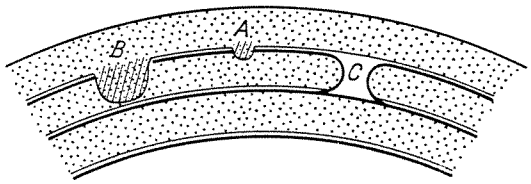

FIG. 4. Diagram illustrating stability of normal leading edge of excitation and appearance of abnormal modes. Double shaded region—zones with increased refractoriness, other notations as in Fig. 3. *A*—small zone of raised refractoriness, normal mode stable. *B*—large zone of increased refractoriness; if it passes into resting state before the second leading edge of excitation closes, an abnormal mode is set up. *C*—new centre of abnormal mode.

in a zone with normal values of the speed of conduction of excitation and of refractoriness then flutters appear. If the centre of the waves in Fig. 3 is in a pathologically changed zone where the refractoriness is high (high value of τ), the waves will travel with considerable intervals of time and resemble an atypical focus of excitation.

It has already been noted that the abnormal mode may appear only in sufficiently large volume of tissue in which the ring of the leading edge of excitation depicted in Fig. 2 can be accommodated, i.e. not less than $\frac{1}{2}\tau \cdot v$. If the tissue is damaged and

movement of excitation slowed down, this dimension shortens and the appearance of abnormal modes is facilitated.

The abnormal modes considered above occur only if the tissue is homogeneous; if the duration of the refractory period varies even within insignificant limits, the coherent picture illustrated in Figs. 2 and 3 is disturbed; the continuous leading edges are destroyed and centres of abnormal modes continuoulsy appear and shift. In fact, since each leading edge of excitation for an abnormal mode moves directly behind the boundary of refractoriness of the preceding one, any increase in duration of the refractory period leads to formation of rupture in the subsequent leading edge. The zones of the maintained leading edge are the centres of new abnormal modes which in a complex way interact with waves coming from the main centre. It is also not difficult to see that increase in the duration of refractoriness at point O_1 or O_3 in Fig. 2 leads to displacement of the centre of the "eddies". Apparently, such processes lie at the basis of the clinical phenomena united altogether under the wide designation of flutter and fibrillation.

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EFFECT OF MINERAL NUTRITION ON THE WATER REGIMEN OF THE PLANT*

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ONE of the most important problems in modern plant physiology is the search for optimal conditions of cultivation of plants which would ensure maximum productivity.

This problem may be solved with use of systems of automatic control one of the links of which must be the plant itself.

Some of the main conditions determining the productivity of plants are the water regimen and mineral nutrition and these conditions are intimately related.

Elements of mineral nutrition have a profound influence on the water regimen of plants. Salts present in the soil solution have varied effects on the plant. Usually, they osmotically hold back absorption of water and also raise the concentration at which in the cell the state of equilibrium with the salt solution occurs.

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