THE EXCITATION WAVE ANALYZED AS A PARABIOTIC PROCESS

A. N. Kabanov and N. N. Leontyeva

From the Laboratory of Growth Physiology (Head - Prof. A.N. Kabanov), the Institute of Physical Education and School Hygiene, the RSFSR Academy of Pedagogical Sciences, Moscow.

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N. E. Vvedensky [2] considered the theory of parabiosis which he worked out on a neuromuscular preparation to be a master mode of phenomena occurring in all sections of the nervous system. Further studies [1,5,6] experimentaly confirmed the validity of Vvedensky's basic conception concerning the importance of steady state excitation to the activity of the central nervous system. A series of researchers including L. L. Vasilyev [1], A. N. Magnitsky [6] and especially L. V. Latmanizova [5] found that many signs common to both steady and spontaneous stimulation appear during the spread of an excitatory wave.

This is a reason for regarding the stimulation wave as a peculiarly proceeding parabiotic process. We agree with L. V. Latmanizova that complete parabiosis develops immediately upon the appearance of a stimulatory wave and that it almost as immediately ceases, the stimulated portion of the organ then gradually passing through the stages of the parabiotic process in the reverse direction. It has been established that the relative duration of the parabiotic process depends on the agent used. With the action of some stimuli (anode of a continuous current, $CaCl_2$, heat, etc.), the first phase of parabiosis development is extraordinarily long, and the transition of the stimulated part into the second, or heightened excitability, stage is very slow (A in Fig.1). The action of other agents (cathode of a continuous current, KCl, cold, etc.) produces a short first phase and a very long second, or catelectrotonic, phase (B in Fig. 1). One can propose that the first two phases of the parabiotic process are extraordinarily brief with the development of a stimulatory wave, the inhibition condition occurring almost immediately (C in Fig. 1), after which, but more slowly, the substrate returns to its original condition by passing through the same stages in reverse order.

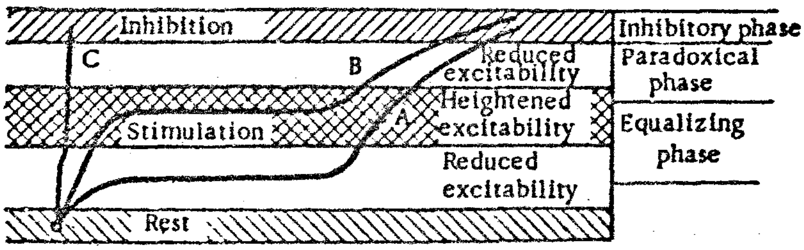

Fig. 1. Development of the parabiotic process under the influence of: A) anode of a continuous current; B) cathode of a continuous current; C) superthreshold stimulation.

When one compares the electric phenomena attending a single impulse with this process (Fig. 2), it appears that the maximal electronegativity, i.e., the peak of the action potential (point a) corresponds to the developed parabiosis, while the ensuing changes of the action potential will correspond to the stages of the reverse parabiotic process. The rapid fall of the high-voltage potential corresponds to the parabiotic process stage of profound inhibition, with its characteristic sharp decline of excitability. The negative after-potential period reflects the paradoxical and equalizing stages; excitability rapidly increases during this period – it is lower than the original (relative refractability) at first, but then exceeds it (heightened excitability or exaltation stage). The positive after-potential period corresponds to the first, or reduced excitability stage of the parabiotic process.

If the excitatory wave is considered to consist of parabiosis developing immediately and as immediately checking to pass through all the stages described above in reverse order with ever-decreasing speed, the features of the biological substrate's rhythmic reaction caused by both the substrate's inherent activity and by artificial stimulation can be explained.

EXPERIMENTAL METHODS AND RESULTS

We succeeded in proving the parabiotic nature of the phenomena developing during a stimulation wave in experiments conducted on animals and people in which we induced rhythmic excitation by continuous current impulses of a definite duration. With square wave impulse generator of variable duration and frequency, we used indirect, rhythmic stimulation of the muscle in such a way that the effect of each shock of current would consist of useful time, i.e., of the initial stimulation effect, causing the development of an impulse, and of the

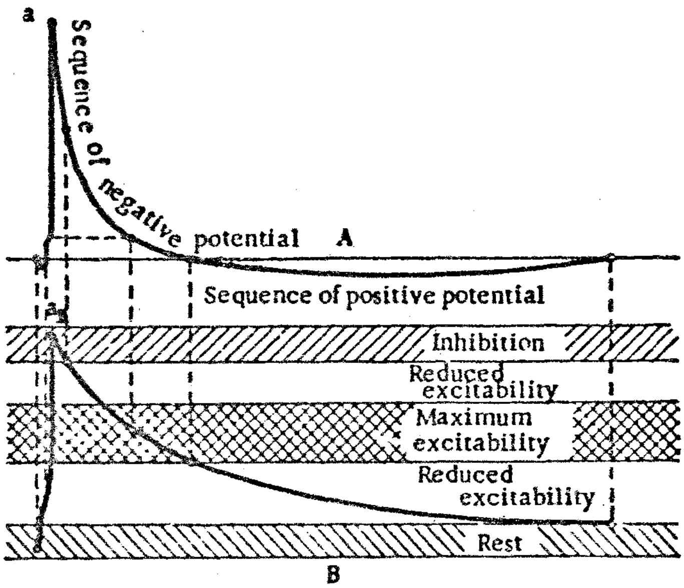

Fig. 2. Scheme illustrating comparison of electrical effect (A) in path of parabiotic process (B) in course of a single wave stimulation.

subsequent effect, not causing a new excitation wave to appear. As the continuous current action included this second phase, which lasted a very brief, exactly computed period of time, it can be considered to correspond to the introduction of a parabiotic agent [2,3,4,7,8,9]. In other words, with such an experimental setup, the rhythmic introduction of brief continuous current shocks not only causes the appearance of an impulse, but also affects the restorative processes. Our aim was to establish what effect different durations of these shocks had on the magnitude of the frequency threshold of muscle partial pessimum, which effect was estimated by the initial decrease in the contraction in response to an increased frequency of stimulating impulses.

In each of the 15 short experiments which we conducted on cats by means of indirect stimulation of the anterior tibialis muscle, the frequency threshold caused by stimulating impulses lasting 0.5, 1, 4 and 8 sec was determined several times. In all of the experiments, without exception, the frequency required to maintain maximal contraction with short impulses was comparatively high, but the longer the impulses were, the lower the frequency causing contraction height to diminish. It was clearly demonstrated that the longer the stimulating impulses, the greater the pause between them should be in order to maintain the maximal reaction. The total results of these experiments are summarized in Table 1 in which each figure shown for the thresholds and pauses represents the average from 50-60 observations.

Similar results were obtained from observations on people, recording the movements of the thumb in response to stimulation of the distal motor point of the median nerve, with stimulation impulses from 1 to 8 m sec in duration. However, with all of the experimental durations, a considerably greater frequency was required to obtain partial pessimum in the people than was required in the cats. It also appeared that the threshold of partial pessimum changed with age in humans. Table 2 gives the average amounts from 65 observations conducted on 12 subjects, varying from 25 to 30 years of age. We observed a similar picture, but with lower frequencies, in children of different ages and in adolescents.

TABLE 1

Experiments on Cats (Average Amounts)

Frequency threshold of partial pressimum	Duration in msec		
	Impulse	Pause	Total period (impulse + + pause)
135	0.5	6.91	7.41
103	1	8.71	9.71
60	4	12.67	16.67
46	8	13.74	21.74

TABLE 2

Observations on Adult Humans

Frequency threshold of partial pressimum	Duration in msec		
	Impulse	Pause	Total period (impulse + + pause)
466	1	1.14	2.14
259	2.5	1.36	3.86
125	4	4.00	18.00
77	8	4.99	12.99

The data presented indicate that increasing the duration of the stimulating impulses retards the restoration of the organ to the original state, i.e., decreases the rate of reverse parabiosis. The graphs in Figure 3 illustrate the reverse course of the parabiotic process during the time interval between two alternating stimulation impulses in which the pessimal reaction was first observed.

The upper graph represents the experiments with animals, the lower, those with people. The line AF, in the upper graph, represents the lower boundary of the inhibition stage, or the moment of absolute refractability termination. The point O represents the parabiosis immediately appearing under the influence of the alternating stimulation impulse. OC_1E_1, OC_2E_2 etc. are the restoration curves, i.e., show the reverse course of the parabiotic process with different durations of the stimulating impulses and intervening pauses. The impulse durations are shown by the sections AB_1 (0.5 m sec), AB_2 (1 m sec), AB_3 (4 m sec), AB_4 (8 m sec), and the pause durations by the sections B_1E_1 (6.91 m sec), B_2E_2 (8.71 m sec), B_3E_3 (12.67 m sec), and B_4E_4 (13.74 m sec).

Therefore, the left portion of each restoration curve (sections OC_1, OC_2, etc) represents the action period of the continuous current, and the second portion (sections C_1E_1, C_2E_2, etc) represent the pause period.

Since the 0.5 m sec duration of the impulse is actually only net stimulation time, one can consider the curve $O_1C_1E_1$ to show the speed of the reverse parabiotic process uncomplicated by the effect of the continuous current. The longer stimulating impulses, however, have a dual effect: they cause stimulation and have a parabioticizing effect, i.e., retard the reverse course of the parabiotic process. The protracted action of a continuous current gradually weakens its parabiotic effect due to the phenomenon of accomodation, as the graph shows (gradual descent of curve OC_1, C_2,C_3,C_4). Moreover, the longer the action of the continuous current, the greater the time needed for the restoration process: $C_4E_4 > B_3E_3 > B_2E_2 > B_1E_1$.

Similar results were obtained from the observations on people, as can be seen from the lower graph in Figure 3, constructed in the same way as the upper graph.

Comparing the two graphs, the first thing one notices is that the rate of the reverse course of the parabiotic process is considerably faster in people than in cats. This is in conformance with the greater lability of human muscles.

In this way, starting with the conception of the stimulation wave as an immediately developing, reversible, parabiotic process, we have attempted to explain how the duration of the stimulating impulses affects the character of the organ's responding reaction.

Instead of the metaphysical principle, "all or nothing", or, in other words, the principle concerning the alternation of assimilation and dissimilation (and therefore, the presence and lack of activity and the presence

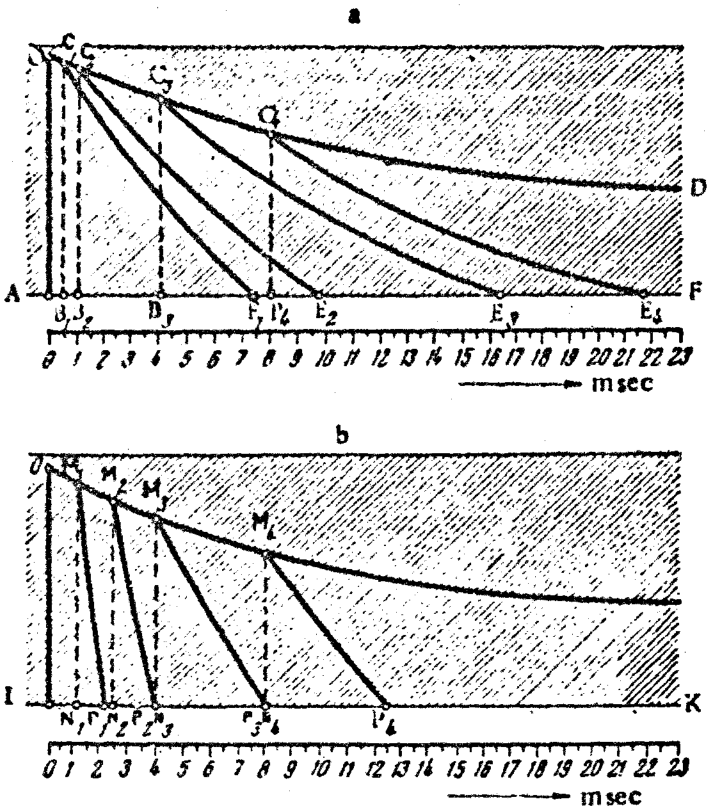

Fig. 3. Speed of reverse parabiotic process in relation to duration of stimulating impulses.
a) experiments on cats; b) observations on humans.

and lack of ability to react to stimulation) as a conclusion reached from the position that a live organ always reacts to stimulation, we propose the presence of the reversible parabiotic process. Excitability is only a particular phase of the reactivity of live matter, just as wave stimulation is a particular phase of an active, energetic condition.

A stimulated substrate reacts in response to any stimulating action by a single parabiotic process, but the form of this process can vary; in some cases, it develops in a wave-like manner, in others, in the form of a local, nonfluctuating process.

SUMMARY

The aim of this study was to verify the hypothesis that the excitatory wave is a reversible parabiotic process. Experiments were performed on people and cats. A nerve was subjected to serial frequent short stimuli by a constant current for 0.5, 1.4 and 8 msec. and the frequency of stimuli resulting in the appearance of a pessimal muscular reaction was determined. Pessimum appeared at much lower frequencies if stimuli were prolonged — the pause between stimuli being larger. This phenomenon is considered as a delayed reversible course of the parabiotic process, caused by the constant current.

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