EFFECT OF DURATION OF STIMULATING IMPULSES ON THE REACTION OF SKELETAL MUSCLE

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(Received October 21, 1954. Presented by V. N. Chernigovsky, Member Acad. Med. Sci. USSR)

The generally accepted way of evaluating the functional possibilities of an excitable system is from a study of the way in which the excitation develops in the system. When we apply any form of stimulator to the study of the functional properties of a physiological substrate, the course of the excitation process developing will depend to a considerable extent on the properties of the stimulating agent. It is for this reason necessary in each case to make a precise evaluation of the stimulator used.

Until recent times, such evaluations were confined to a consideration of the frequency and the intensity of the stimulation, the significance of which for the response reaction of the excitable substrate was not appreciated in the 19th century. References may, however, be found in the literature to the circumstance that the nature of the response given by an organ is also significantly affected by the duration of the stimulating impulses [5, 11, 12, and 13].

The present paper is devoted to a study of the effect of varying the duration of stimulating impulses on the response to rhythmic stimulation.

EXPERIMENTAL METHODS AND RESULTS

Our experiments were carried out on adults and on children of the age groups 7-8, 11-12, and 14-15. Stimulating impulses of given durations were tested on each subject not less than 5-6 times. The source of rhythmic indirect stimulations of the muscles was an electric generator of square wave impulses. As the frequency of the impulses rises, for a given duration of stimulation, the kymograph records of tetanic contraction of muscle gradually rose to a maximum, after which the height of the contractions began to fall with increasing frequency; at very high frequencies the reaction was either totally abolished, or it took the form of "initial contraction." The object of our research was to find the frequencies at which the height of contraction first began to fall, and at which the response either abolished, or was of the "initial contraction" form. The former frequency gave us the threshold for the partial pessimum of the muscle, and the latter frequency the threshold for the full pessimum.

We stimulated the lower point of the median nerve of human subjects, and registered the movements of the thumb. The intensity of stimulation amounted to $1^1/_2$ times the tetanization threshold. The duration of the stimulating impulses was from 1 to 8 milliseconds.

We found that the lower the age of the subject, the sooner did increase in frequency of impulses, at constant duration, bring about a pessimal reaction. As the duration of the impulses was increased, however, both the partial and the full pessima were achieved at lower frequencies of stimulation, for all age groups (Table 1).

Increase in the period of stimulation had a greater effect on the partial and full pessima than did increase in the duration of the impulses. It follows that increase in the period of stimulation took place during the impulse and during the pause (Figure 1).

In passing from a shorter to a longer duration of impulse, the increase in the pause for which pessimal reaction of the muscle was found was not the same for children of different age groups: it was greater for 7-8-year olds than for older children. This observation may serve as an indirect indication of the lower lability of muscles of 7-8-year old children.

The same effect was found in adults when the duration of the impulses was raised to 8 milliseconds – the greater the duration of the impulse, the longer was the pause during which the muscle responded with a pessimal reaction (Figure 2).

TABLE 1

Mean Values of the Thesholds of Partial and Full Pessimum at Different Durations of Stimulation

Age	Duration of impulses, in msec.	Pressimum			
		partial		full	
		frequency	duration of pause, in. msec.	frequency	duration of pause, in msec.
7—8 years	1	224	3.46	613	0.63
	$2^1/_2$	155	3.95	292	0.92
11—12 years	1	367	1.72	712	0.40
	$2^1/_2$	219	2.06	329	0.54
14—15 years	1	505	0.98	757	0.32
	$2^1/_2$	261	1.33	335	0.48
Adults	1	466	1.14	764	0.31
	$2^1/_2$	259	1.36	343	0.42
	4	125	4.00	—	—
	8	77	4.99	—	—

Thus the experiments in which duration was kept constant and frequency was varied showed clearly the dependence of the rate of onset of the pessimal reaction on the duration of the stimulating impulses.

Experiments in which we changed the duration of the impulses from one value to another, without interrupting stimulation or varying its frequency, showed that with relatively infrequent impulses the amplitude of the contractions increased when we switched over from shorter to longer durations. When the impulses were more frequent, increase in their duration had no effect on the amplitude of the contractions. At still higher frequencies, increase in duration led to a fall in the amplitude of the contractions.

Varying the frequency of the stimulation at constant duration showed that the greater duration of the impulses, the smaller was their frequency needed to give maximum amplitude of contraction. This evidently explains the strengthening of the motor reaction observed after increasing the duration of infrequent impulses. The data of the control experiments permitted two explanations of the absence of changes in the amplitudes of the contractions. In some cases both the durations applied, at the given frequency, gave an optimum effect, whereas in others the given frequency, in conjunction with the shorter duration, still gave a suboptimal effect, but at longer durations a pessimal one; both effects were of equal intensity.

The most pronounced changes in the amplitude of contraction were found in those cases in which the shorter duration gave an optimal effect, and the longer duration a marked pessimal one.

For example, application to one subject of stimulation of a frequency of 338 impulses per second, and a duration of 1 millisecond gave an optimal muscular reaction, whereas at the same frequency but with a duration of 2.5 msec. only a relatively small contraction resulted. For this reason at a frequency of 338 impulses per second the change in duration from 1 to 2.5 msec. resulted in a marked fall in the amplitude of the contraction. It follows that in order to demonstrate the effect of change in the duration of the stimulating impulse on the nature of the response reaction it is essential that the experiments should be performed using a wide range of frequencies, and not an arbitrarily selected one only.

We verified the results of our experiments by performing short experiments on 15 cats under anesthesia. We recorded the contractions of the anterior tibialis major muscle, in response to stimulation of the tibialis minor nerve, using a silver–silver chloride electrode. The indifferent electrode (a zinc sheet, area 6 sq. cm) was applied to the shaved skin in the lower abdominal region. The intensity of the stimulations was maximal, and the duration of the impulses was varied from 0.5 to 8 msec.

The animal experiments fully confirmed our findings, described above, with an even greater fall in the pessimum thresholds on increasing the duration of the stimulating impulses than for human subjects (Table 2).

The thresholds for full pessimum were determined only for durations of impulse of 1 to 8 msec. The values found were 175 and 74 impulses per second, respectively.

We also verified the dependence of the effect of stimulation on the duration of the impulses switching over from one duration to another without interrupting the experiment, without changing the frequency. As for humans, the change in amplitude of the tetanic contractions on switching over from a shorter to a longer duration of impulse depended on the frequency selected. Thus in one of the experiments (Figure 3), diminution in the amplitude of contraction first appeared with frequencies of 85 impulses per second, for duration of stimulating impulses of 1 msec. Increase in the duration of the impulses to 8 msec. led to a lowering of the partial pessimum threshold; a fall in amplitude was already evident at 50 impulses per second. Changing the duration of the impulses from 1 to 8 msec., at a frequency of stimulation of 30 impulses per second caused an increase in the motor reaction, while at a frequency of 50 impulses per second the amplitude of contractions fell, after an initial rise.

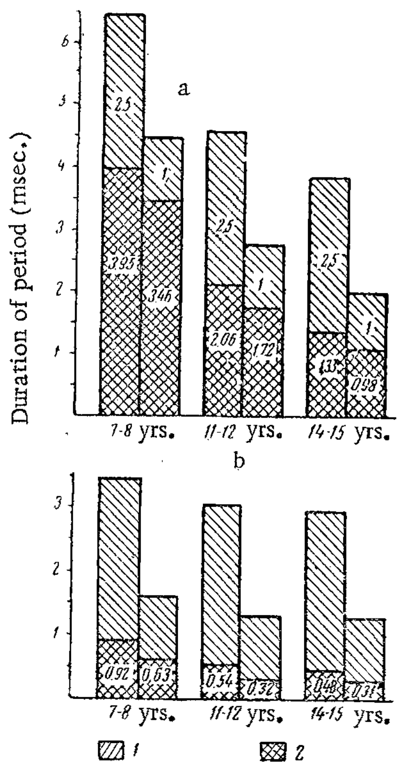

Fig. 1. Relation of the duration of the impulse to that of the pause at the frequency threshold of partial and full pessimum in children of different ages. a) Partial pessimum; b) full pessimum; 1) duration of impulses, in msec.; 2) duration of pauses, in msec

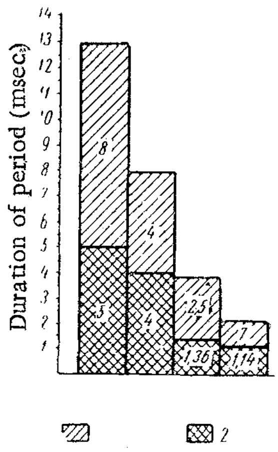

Fig. 2. Relation of the duration of the impulse to that of the pause at the frequency threshold of partial pessimum in adults. 1) Duration of impulse, in msec.; 2) duration of pause, in msec.

TABLE 2

Thresholds of Partial Frequency Pessimum in Cats

Duration in msec.		Pessimum threshold in imp./sec.	
impulses	pulse	mean value	range
0.5	6.91	135	104—150
1	8.71	103	75—132
4	12.67	60	50—75
8	13.74	46	10—55

Thus our observations on human subjects, and our experiments on cats, both with constant duration of impulses and variable frequency, and with constant frequency but variable duration, showed that the response reaction of the muscle is determined largely by the reciprocal relation of these two parameters. The greater the duration of the stimulating impulses, the smaller is the frequency necessary to produce a maximum response, and vice versa; the lower the frequency, the more does duration have to be increased to achieve a pessimal effect.

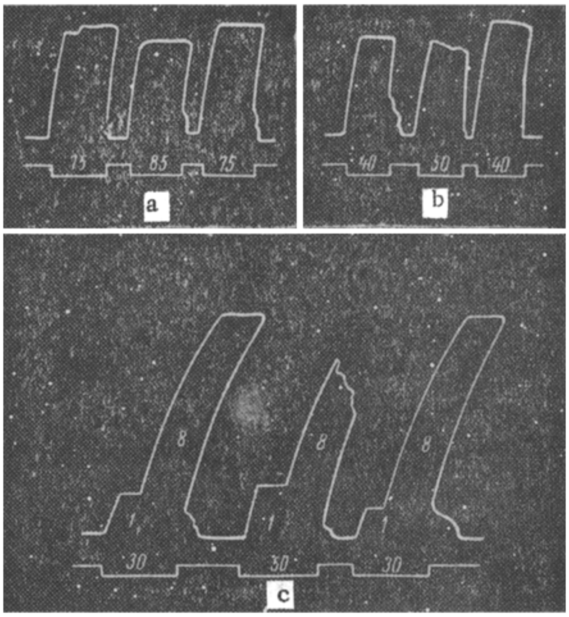

Fig. 3. Effect of varying the duration of impulses on the strength of contraction in response to stimulations of different frequency, in the cat. a) Partial pessimum threshold for duration of impulses of 1 msec.; b) the same, for durations of 8 msec.; c) switching over the durations from 1 to 8 msec., at frequencies of 30, 50, and again 30 imp./sec.
Explanation of tracings (from above down): muscle contractions, stimulation signals.

The more pronounced lowering of functional lability of the peripheral motor apparatus observed on raising the frequency or the duration of impulses in 7-8-year-old children is evidence of the lower resistance of neuromuscular elements to altering factors at this age.

It is of interest to consider this finding in conjunction with that of A. G. Ivanov-Smolensky [3], who showed that superlimiting inhibition occurs in the cerebral cortex more readily and frequently in school children of the younger age groups. This form of inhibition, according to I. P. Pavlov [10], has a protective effect, as it prevents the harmful action of excessively strong stimulation.

Other authors [8, 9] have shown that the same part is played by pessimal inhibition. It may be supposed that pessimal, or protective, inhibition arises in the neuromuscular apparatus more readily when the individual is younger [4].

These regular changes in the courses of the inhibitory process in children of different age groups are quite clearly shown in our experiments.

The lowering of the pessimum thresholds when the duration of stimulating impulses is increased may be explained, on the basis of N. E. Vvedensky's teachings on parabiosis, as a general reaction of living organisms to any factor, of either the internal or external environment [2].

The view that there is a close relationship between rhythmic stimulation and the parabiotic process is becoming increasingly widely held [1, 6, 7]. The excitation wave is regarded as a reversible parabiotic process. From this standpoint, the response reaction of the organ to the rhythmic stimulation depends on which particular phase of the reverse parabiotic reaction coincides with each successive impulse. If the second of a rhythmic series of stimulating impulses coincides with an inhibitory stage of the parabiotic process, a pessimal reaction results. Since each of the successive impulses intensifies the parabiotic process, maintaining it in the inhibtory stage, the pessimal reaction persists over the whole duration of stimulation. The longer the inhibitory phase of the parabiotic process is maintained, the smaller is the frequency which gives rise to a pessimal effect.

In our experiments, when we increased the duration of the stimulating impulses we thereby increased the duration of action of the dc cathode on the excitable substrate, and this, acting as a parabiotic agent, stopped the reverse parabiotic process.

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ELECTROPHYSIOLOGICAL PHENOMENA IN NERVES DURING THE ACTION OF ANTIGENS ON SKIN RECEPTORS

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(Received March 16, 1956. Presented by V. N. Chernigovsky, Member Acad. Med. Sci. USSR)

With each year, more and more experimental evidence of the reflex mechanism of the action of antigens is being published, as well as of the development of processes of infection along these lines (A. D. Speransky, and co-workers, V. S. Galkin, G. V. Peshkovsky and co-workers, and others). Our laboratory has devoted many

* In Russian.