CHANGE OF THE FUNCTIONAL STATE OF THE PERIPHERAL NEUROMUSCULAR APPARATUS DURING THE FORMATION OF A DOMINANT IN THE SPINAL CORD

Communication I. Influence of Spinal Cord Dominant on the Parameters of Excitability of the Nerve and Muscle

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In their studies of the dominant, Ukhtomskii's school paid particular attention to the laws of the reorganization of intracentral relationship [5-8, 12, 13]. Only the work of Aristova [1, 2], from Vasilev's laboratory, was concerned with the question of the influence of the dominant center on the peripheral neuromuscular apparatus connected with such a center.

It was determined by one investigator [11] that a prolonged cooling of the frog, which led to the formation of a natural flexor dominant, was accompanied in the majority of cases by a change in the ratios of the chronaxies of the antagonistic muscles of the hind limb. If the frog were maintained at room temperature, the values for chronaxies of the extensor muscles were greater than those of the flexors, and the relationship of these values to each other was close to 2. According to the data of this worker, when the frog was kept at a low temperature, this relationship - the coefficient of Bourguignon - became equalized or less than unity, as a result of the rise of chronaxie of the flexors and the lowering of chronaxie of the extensor muscles. In the experiments of Aristova, rheobase and chronaxie changed in opposite directions. Unfortunately, this author recorded the rheobase and chronaxie of the muscles of only one extremity and did not examine the excitability of the motor nerve.

It thus remained unclear from the experiments of Aristova whether the dominant produced by cooling, which was reflected in the results obtained, was due to the presence of a dominant in both flexor centers for the hind limbs or in one of them only. Furthermore, the experimental arrangement was such as to preclude the possibility of following the dynamics of the changes in excitability of the muscles during formation and extinction of the dominant in one and the same animal, for the author compared the values of Bourguignon's coefficient in normal and preliminarily-cooled animals.

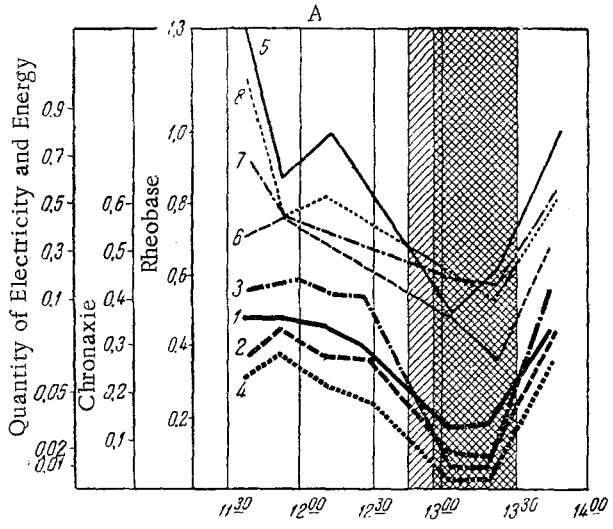
In our work, we set ourselves the task of studying changes of the functional state of the peripheral neuromuscular apparatus in the process of the appearance, development and extinction of an experimental, artificially produced dominant.

The dominant was produced by the action of rhythmic subliminal stimuli to the tibial nerve of the frog, according to the method of Vetyukov [4, 5], as modified by Verzilova [3]. The presence of a dominant was shown in the perversion of the reciprocal relations among the centers for the antagonists, which was expressed as a heightened contraction of the semitendinosus muscle to test stimulations of the nerves.

METHODS

The cerebral hemispheres of frogs Rana ridibunda were ablated and on both sides the semitendinosus muscles, peroneal nerves, ulnar nerves, and the motor branches of the sciatic nerve (deep posterior twigs) which innervate the semitendinosus muscles were prepared. The frogs were fastened to a cork board and placed in a moist chamber. Induction currents at a frequency of 50 cps and of an intensity 2-3 cm below threshold were used for subliminal excitation. These stimuli lasted for 10-20 min and generally were applied repeatedly. In the intervals between the action of subliminal stimulations reflex contractions of the semitendinosus muscles were recorded, against the background of which test stimuli were applied to the ulnar and contralateral peroneal nerves. The rheobase and chronaxie of the motor nerve (deep posterior branch of the sciatic nerve) and of the semitendinosus muscle innervated by it served as the characteristic of the functional state of the peripheral neuromuscular apparatus.

Silver chloride electrodes were used. Rheobase and chronaxie of the muscle were determined by means of



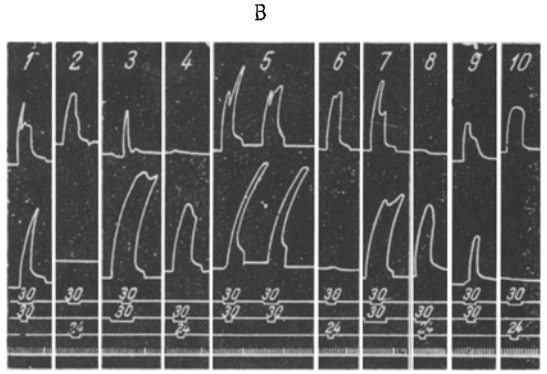


Fig. 1. Change of parameters of excitability of the motor nerve and muscle during formation of a dominant focus in the ipsilateral flexor center of the spinal cord. Experiment 34, April 9, 1957.

A. Reduction of rheobase, chronaxie, threshold quantity of electricity, and threshold energy of stimulating current of the semitendinosus muscle and its motor nerve during formation of a dominant in the flexor centers of the corresponding limb. The ipsilateral peroneal nerve was subjected to subliminal tetanization for 10 min (12:50 to 13:00, first hatched column). As a result of this a dominant arose (second hatched column).

1. Rheobase of the nerve; 2) chronaxie of the nerve; 3) threshold quantity of electricity of the stimulating current for the nerve; 4) threshold energy of the stimulating current for the nerve; 5) rheobase of the muscle; 6) chronaxie of the muscle; 7) threshold quantity of electricity of the stimulating current for the muscle; 8) threshold energy of the stimulating current for the muscle.

B. Kymograms from same experiment.

1st-4th sequences, reflex contractions of semitendinosus muscle at start of experiment, before formation of dominant; 5th-8th sequences, the same, after formation of dominant in the ipsilateral flexor center of the spinal cord due to influence of subliminal stimulation of peroneal nerve (frequency, 50 cycles; strength, 2 cm below threshold); 9th and 10th sequences, the same, after extinction of the dominant.

Significance of the curves (from above downward): myogram of the reflex contractions of ipsilateral semitendinosus muscle; myogram of reflex contractions of contralateral semitendinosus muscle; signal marker for stimulation of ipsilateral peroneal nerve; signal for stimulation of contralateral peroneal nerve; signal for stimulation of ulnar nerve; time marks (1 sec). Numbers above stimulation markers: distance between coils of inductorium (in centimeters).

needle electrodes, stuck into the belly and tendon of the muscle and separated by a distance of 10 mm. Measurements of excitability were carried out repeatedly — at the beginning of the experiment, at the time of formation of the dominant, and after its extinction. On the basis of the data obtained the threshold quantity of electricity (V_t) and the threshold energy (V^2_t) of the stimulating current required for excitation of the nerve and muscle were calculated. In all, 160 experiments were carried out. In the first series of experiments rheobase and chronaxie of the nerve and muscle of one limb were studied. These same parameters for nerve and muscle of one hind limb and of the motor nerve of the opposite extremity were determined simultaneously in the second series of experiments.

RESULTS

The experiments showed that the formation of a dominant in the flexor centers of the spinal cord was accompanied by a precise change in the parameters of excitability of the nerve and muscle. During this process there is a decrease of rheobase of the motor nerve and the muscle of the hind limb innervated by it, on the side ipsilateral to the dominant. Chronaxie was shortened, and the liminal quantity of electricity and energy of the stimulating current was reduced. The parameters of excitability of the motor nerve changed most sharply. Thus, in experiments carried out in the winter months (December-February), the values for rheobase and chronaxie of the motor nerve were reduced by 2-10 times. This observation is in good agreement with the fact that the spinal flexor dominant is established best in the winter.

When the dominant was formed, excitability of the muscle was heightened to a lesser extent than that of its motor nerve. With a deepening of the dominant state of the center there was an accompanying greater expression of the reduction of the parameters of excitation, but a weakening, on the other hand, of their expansion. The data from experiment 34 (Fig. 1) may be given as an illustration of this. At the beginning of the experiment, before application of subliminal stimulation, reciprocal relationships took place: reflex contractions of the ipsilateral muscle were weakened during stimulation of the contralateral peroneal nerve and ulnar nerve (Fig. 1B, 1st and 2nd strips of the myogram). Contraction of the contralateral muscle was reduced during test stimulation of the ipsilateral nerve (Fig. 1B, 3rd and 4th strips of the myogram). A ten min subthreshold tetanization of the ipsilateral nerve then led to the formation of a flexor dominant in the spinal centers for this extremity. Now, as is evident from the myogram, stimulation of the contralateral, peroneal, and ulnar nerves (Fig. 1B, 5th and 6th strips of the myogram) evoked an augmentation of the contraction of the ipsilateral muscle instead of inhibiting it, while at the same time the inhibitory effect was preserved in the opposite limb (Fig. 1B, 6th-8th strips of the myogram.). The rheobase of the ipsilateral motor nerve was reduced by 2.5

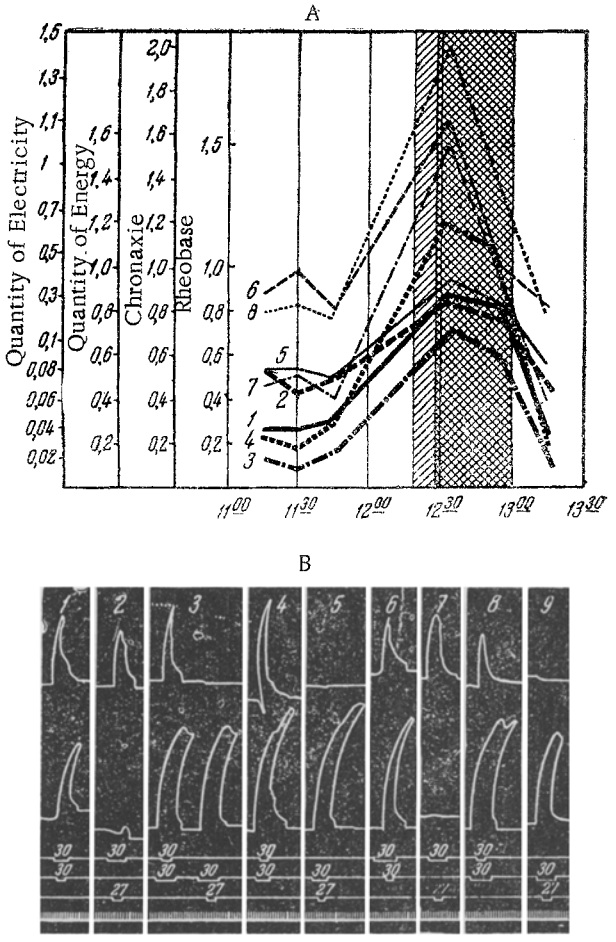


Fig. 2. Change of parameters of excitability of nerve and muscle during formation of a dominant focus in the contralateral flexor center of the spinal cord. Experiment 33, May 1, 1957.

A. Increase of rheobase, chronaxie, threshold quantity of electricity and threshold energy of stimulating current for semitendinosus muscle and its motor nerve during formation of dominant in flexor centers of the opposite limb.

The contralateral peroneal nerve was subjected to subliminal tetanization for 10 minutes (12:20 to 12:30, first hatched column). As a result of this a dominant was formed (second hatched column).

Designations on graph same as in Fig. 1A.

B. Kymograms of same experiment.

1st-3rd sequences, reflex contractions of semitendinosus muscle at beginning of experiment, before formation of dominant; 4th-7th sequences, the same, after establishment of the dominant under the influence of subthreshold stimulation of the contralateral peroneal nerve; 8th and 9th sequences, the same, after extinction of the dominant.

Significance of curves same as in Fig. 1B.

times (Fig. 1A, curve 1), and the chronaxie by 4 times (Fig. 1A, curve 2). In this experiment the threshold quantities of electricity (Fig. 1A, curve 3) and energy (Fig. 1A, curve 4) of the stimulating current were especially sharply reduced - by 10 and 25 times respectively.

Although less clearly expressed than the above, the parameters of excitability of the semitendinosus muscle also changed in the same direction during formation of the dominant. Rheobase of the muscle in this experiment was lowered by 2 times (Fig. 1A, curve 5), chronaxie by 1.6 times (Fig. 1A, curve 6), threshold quantity of electricity of the stimulating current by 2.5 times (Fig. 1A, curve 7), and threshold energy of the stimulating current by 5 times (Fig. 1A, curve 8). After extinction of the dominant the reciprocal relations between the centers of the muscle antagonists was again restored (Fig. 1B, 9th and 10th strips) and correspondingly reached the baseline levels of rheobase and chronaxie (see Fig. 1A).

Further experimentation showed that changes in the parameters of excitation of the motor nerve of the extremity contralateral to the flexor center in which the dominant was worked out were of an opposite character: rheobase increased, chronaxie lengthened, and threshold amount of electricity and threshold energy of the stimulating current increased.

Thus, for example, in experiment 33, of May 1, 1957, the rheobase of the nerve contralateral to the dominant of the extremity increased three-fold, chronaxie lengthened by 1.7 times, threshold quantity of electricity and energy of the stimulating current was augmented 5 and 15 5imes respectively (Fig 2A). Rheobase and chronaxie of the semitendinosus muscle change in the same direction.

These phenomena were demonstrated especially effectively in those experiments in which rheobase and chronaxie were measured in the nerve and muscle of an extremity in whose centers a dominant had been worked out, and in which the chronaxie of the motor nerve of the opposite limb was also studied at the same time (Fig. 3, experiment of May 11, 1957).

Changes in parameters of excitation are presented in Fig. 3. In each group pairs of columns show in sequence the changes of rheobase, chronaxie and threshold quantity of electricity and energy of the stimulating current. In each pair of columns the first shows the baseline value of the parameter before formation of the dominant, and the second, when the dominant is present. As is seen in Fig. 3, with the dominant formed in the ipsilateral flexor center, all parameters of excitation in this extremity were reduced. (Fig. 3A, hatched columns), whereas, on the contrary, they were increased on the opposite side (Fig. 3A, black columns).

When the dominant changed over from the ipsilateral to the contralateral flexor center, the opposite changes took place immediately (Fig. 3B). The parameters of excitability of the ipsilateral limb increased, whereas those of the contralateral side decreased. Such a transfer of the dominant from the flexor centers for one extremity to those of the other side often arose either spontaneously, or under the influence of repeated subliminal tetanization.

In some experiments subthreshold tetanization did not lead to the formation of a dominant in the spinal cord. When this occurred the values for rheobase, chronaxie, threshold quantity of electricity and of threshold energy of the stimulating current did not undergo significant changes. On the other hand, appearance of a "spontaneous" dominant (not dependent on subliminal tetanization) was accompanied by the characteristic reduction in the values for the indicated parameters.

The table above indicates changes of parameters of excitability of the nerve and muscle during formation of a dominant in the flexor center of one extremity. In 50 of the 64 cases reduction of the rheobase occurred and in 53 there was shortening of the chronaxie of the motor nerve of the ipsilateral limb. At the same time in 23 of a total of 34 experiments the rheobase increased and in 21 cases the chronaxie of the opposite side was lengthened. The parameters of excitation of the muscle also changed in the same direction during formation of the dominant. It should be exphasized that those experiments in which a dominant was formed simultaneously in the flexor centers for both limbs ("mixed dominant") are not entered in the data of this table. In such cases changes in excitability were of a more complicated character. They depended on the stage of expression of the dominant in one or another center. In some of these experiments we observed changes in rheobase and chronaxie which were in different directions.

The sum total of the data we have obtained leads to the conclusion that, during the formation of a dominant, important displacements can also be observed in the state of the peripheral neuromuscular apparatus along with those occurring in the reorganization of intracentral relationships (impairment of reciprocal inhibition). In such conditions excitability of the motor nerve, on the side of the dominant was increased, and was lowered on the opposite side. This also happened to a somewhat lesser degree with regard to excitability of the muscle.

Attention should be directed to displacements in the same direction of the parameters of rheobase and chronaxie at the time of appearance of the dominant - to their simultaneous shortening or lengthening, as the case may be. In contrast to Aristova's work changes of rheobase and chronaxie in opposite directions occurred in our experiments only in those cases where a mixed dominant was present. In various alterations of the nerve, rheobase and chronaxie often did change in opposite directions - chronaxie lengthened while rheobase decreased, and became shorter at a time when the rheobase was in-

Change of Rheobase and Chronaxie of a Motor Nerve and Muscle during Formation of a Dominant in the Spinal Cord

Parameters of excitability	On side of the dominant								On opposite side			
	Nerve				Muscle				Nerve			
	Number of cases			Character of change	Number of cases			Character of change	Number of cases			Character of change
	Total	of which			Total	of which			Total	of which		
Rheobase	64	50		Decrease	37	27		Decrease	34	23		Increase
			1	1:10			1	1:10			1	4:1
			3	1:5			1	1:4			3	3:1
			7	1:4—3			2	1:3			6	2:1
			14	1:2			3	1:2			7	1,5:1
			11	1:1,5			7	1:1,5			6	1—1,5:1
			14	1:1—1,5			13	1:1—1,5				No change
		7		No change		4		No change		6		Decrease
				Increase				Increase				
			2	2—3:1			1	2:1			1	1:1,5
		7	1	1.5:1		6	5	1:1—1,5		5	4	1:1—1,5
			4	1—1,5:1								
Chronaxie	64	53		Decrease	37	27		Decrease	34	21		Increase
			1	1:8			1	1:8			1	13:1
			3	1:4			1	1:4			3	3:1
			7	1:3			2	1:3			7	2:1
			14	1:2			4	1:2.5			6	1,5:1
			11	1:1,5			5	1:1,5			4	1—1,5:1
			17	1:1—1,5			14	1:1—1,5				
		3		No change		5		No change		5		No change
				Increase				Increase				Decrease
			2	3—2:1			2	2:1			1	1:3
		8	2	1,5:1		5	3	1,5:1		8	3	1:2
			4	1—1,5:1							4	1:1,5

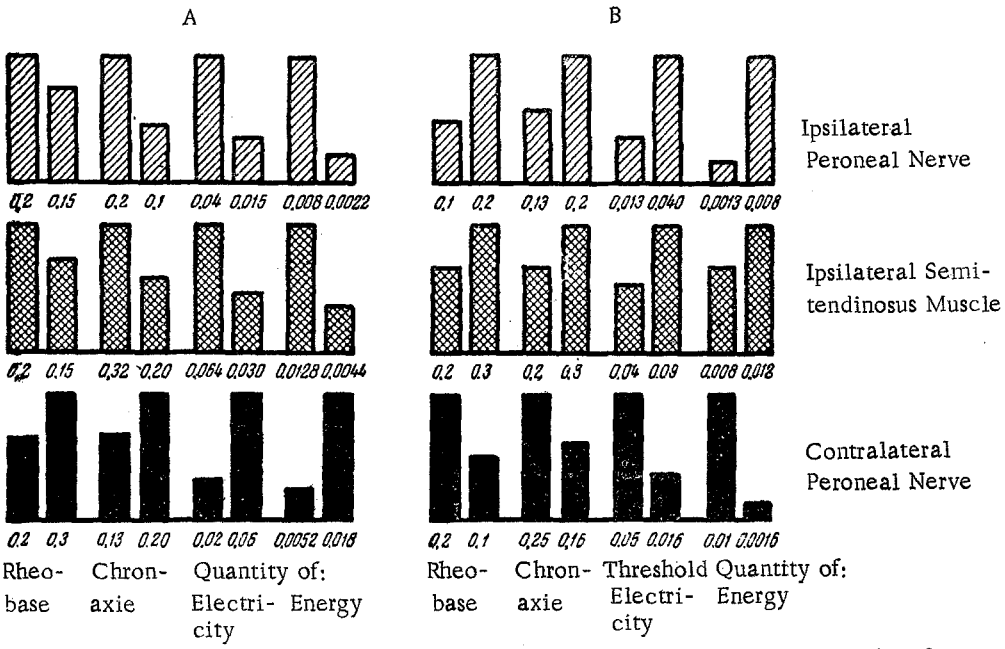


Fig. 3. Change of parameters of excitability of nerve and muscle during transfer of dominant from the flexor center for one limb to flexor center of the other side. Experiment 42, April 11, 1957.

A. Dominant in ipsilateral flexor center of spinal cord.

B. Dominant in contralateral flexor center of spinal cord.

In each group the pairs of columns designate, in order: rheobase, chronaxie, threshold quantity of electricity and threshold energy of the stimulating current. In each pair of columns, the first shows the baseline value of the parameter and the second, its value in the presence of the dominant. Figures under columns, the corresponding values of the parameters.

Legends: slanting hatched columns, parameters of excitability of the ipsilateral motor nerve; cross hatched columns, parameters of excitability of ipsilateral semitendinosus muscle; black columns, parameters of excitability of the contralateral motor nerve.

creased. On the basis of these facts Nasonov [9, 10] stated that the parameter of chronaxie was inversely dependent on the value of the rheobase and therefore could not be used as an indicator of the speed of rise of excitability in the nerve. In our experiments chronaxies shortened in spite of the fact that rheobase was reduced. It thus appears to us that this gives us a basis to consider that, during the rise of the dominant, a heightening of excitability (decrease of rheobase) takes place along with a decrease in the time of origin of excitation (chronaxie).

The changes which we have observed in the functional state of the neuromuscular apparatus during the working out of a dominant in the centers of the spinal cord may have an important adaptive significance, guaranteeing the preparation of an organ executing some task for the realization of an active effect. Further research is required for an understanding of the physiological mechanism of the action of the dominant center on the peripheral apparatus.

SUMMARY

The authors studied changes of the functional state of the peripheral neuromuscular apparatus during elaboration of the spinal cord dominant. The dominant was built up in one of the flexor centers of the frog's hindleg through application of rhythmic subliminal stimuli. The formation of the dominant manifested itself by inversion of the reciprocal relations between the centers of antagonists. It was found that, as the dominant appears in a flexor center of the spinal cord in a motor nerve and in the muscle innervated by it in the corresponding limb, rheobase, chronaxie, the threshold quantity of electricity, and the threshold energy of the stimulating current decrease, with simultaneous increase of all these parameters in the contralateral extremity. Disappearance of the dominant is accompanied by restoration of the initial level of excitability of the nerve and muscle, while the transfer of the dominant from a flexor center in one extremity to the centers of the other extremity

leads to corresponding modifications in their excitability.

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