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BIOELECTRICAL ACTIVITY OF LIMB MUSCLES DURING COLD SHIVERING ON STIMULATION OF THE VESTIBULAR APPARATUS

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16. Abstract

The effects of caloric and electric stimulation of the vestibular receptors on the EMG activity of limb muscles in anesthetized cats during cold-induced shivering involved flexor muscles alone. Both types of stimulation suppressed bioelectrical activity, more effectively in the ipsilateral muscles. The suppression of shivering activity seems to be due to the increased inhibitory effect of descending labyrinth pathways on the function of flexor motoneurons.

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BIOELECTRICAL ACTIVITY OF LIMB MUSCLES DURING COLD SHIVERING ON STIMULATION OF THE VESTIBULAR APPARATUS

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In experiments on anesthetized cats we studied the bioelectrical activity of the flexor and extensor muscles of the limbs during cold shivering on unilateral caloric and electrical stimulation of the vestibular apparatus. It was shown that stimulation of the labyrinthine structures suppresses the bioelectrical activity of the flexor muscles, which is more marked on the ipsilateral side. During cold shivering there was no bioelectrical activity of the extensor muscles both before and during stimulation of the vestibular apparatus. It was concluded that suppression of the activity of the flexor muscles of the limbs was brought about by an increase in the inhibiting labyrinthine effects on the function of the motoneurons of the studied muscles. /70

Key words: cold shivering, vestibular apparatus.

Cold shivering, brought about by the skeletal muscles, is a source of heat production of an organism when it is cold. In the limbs the shivering appears selectively in the flexor muscles, which promotes the formation of a posture that decreases heat loss [2, 3]. Central control of muscular shivering is effected by the hypothalamus, the effect of which on the spinal centers is mediated by supraspinal mechanisms that regulate muscular tone [6, 7, 9]. A special role in the regulation of tonic reflexes, which control body position in space, is played by the vestibular apparatus, the descending effects of which are directed at the activation of extensor reflexes and the suppression of the flexor reflexes [5, 11, 13, 16]. In an earlier work [1] we

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* Numbers in the margin indicate pagination in the foreign text.

showed that removal of the effects of the vestibular apparatus on spinal activity reduces cold shivering in the flexors of the limbs. It is therefore possible to propose that an increase in the descending effects of the labyrinthine structures will have an inhibiting effect on the function of the motoneurons of the limb flexors that are active during cold shivering.

Included in this investigation was the study of the bioelectrical activity of the flexor and extensor muscles of the front and back limbs during cold shivering on unilateral stimulation of the vestibular apparatus.

Procedure

The experiments were conducted on 48 cats that were anesthetized with a chloralose-urethane mixture (50 + 500 mg/kg) with premedication with metacin (2.5 mg/kg). We studied the bioelectrical activity of flexor muscles (the sartorius and the biceps of the shoulder) and extensor muscles (gastrocnemius, soleus and triceps muscle [long head]). EMG's were recorded by a "Medikor" M-21 electromyograph with the help of bipolar electrodes. During the preparation the animal was artificially warmed up, preserving its deep temperature at a level of 38-39°, and then, at the beginning of the experiment, it was cooled in /703 a thermal chamber. The temperature of the chamber was maintained at a level of 18-20°, and such moderate cooling was sufficient for the appearance of cold shivering in the anesthetized animals. The animal in the chamber was in an independent posture, on its side. With this position the tone of the limbs is average [4].

For stimulation of the vestibular apparatus we used caloric tests (20 animals) and electrical stimulation (28 animals). The selection of the two procedures was not accidental, since it is known that in caloric tests only the receptors of the semicircular canals are stimulated [8], and in electrical stimulation--

Table. Bioelectrical activity of the flexor muscles of the limbs during cold shivering in conditions of unilateral stimulation of the vestibular apparatus

Observed effect	Caloric tests				Stimulation by impulse current			
	sartorius muscle (no. of tests)		biceps muscle of shoulder (no of tests)		sartorius muscle (no. of tests)		biceps muscle of shoulder (no. of tests)	
	IS	CS	IS	CS	IS	CS	IS	CS
Activity decreased	[illegible]	29	23	[illegible]	37	38	30	34
Activity stopped	6	4	19	10	8	6	20	12
Activity did not change	10	13	0	1	6	1	0	4
Total tests	[illegible]	[illegible]	[illegible]	42	[illegible]	[illegible]	50	50

all the labyrinthine structures. For the caloric tests we first drilled 2 openings in the bulla into which we inserted plastic catheters (external diameter 1.8 mm). One of the catheters served for the inflow of water, the other for outflow. We irrigated the bulla with 10 ml of water at a temperature of 14-16° for 8-12 sec. As a control we implemented irrigation of a bulla with water with a temperature equal to the deep temperature of the animal.

During electrical stimulation of the labyrinthine structures we used an ESY-1 electrical stimulator. A bipolar platinum electrode (area of the end 0.03 mm^2, interelectrode distance 0.14 mm) was inserted into the round window of the bulla. The vestibular apparatus was stimulated by square-wave impulses with a frequency of 5-10 Hz, duration 20-100 msec. The voltage supplied to the stimulating electrodes (on the average it was 9-11 v) was increased until the appearance of distinct changes in the bioelectrical activity of the studied muscles, and then a recording was made for 10 sec. As a control electrical stimulation of 9-11 v was applied to the bony wall of the bulla.

The EMGs during cold shivering were evaluated visually by the change in the amplitude and frequency of the bioelectrical activity.

To avoid adaptation of the labyrinth to the effect of the caloric and electrical stimuli there was an interval of 10-15 min between tests.

During the entire experiment rectal and subcutaneous temperatures were recorded by an N-3020-3 recorder.

Results of the Investigation

In the warmed animal there was no bioelectrical activity of any of the studied muscles. Stimulation of the labyrinthine structures in these conditions did not evoke any responses in the studied flexor and extensor muscles. Bioelectrical activity appeared in the flexor muscles of the limbs in proportion to the cooling down of the anesthetized animal and reduction of the subcutaneous temperature below 30°. In this case the rectal temperature either was reduced to lower than 38° or in part of the animals remained at the initial level (38-39°). Bioelectrical activity in the extensor muscles was not observed in any of the experiments. Stimulation of the labyrinthine structures was begun on the appearance of regular activity of the flexor muscles. Rectal temperature at the beginning of stimulation was $37.7 \pm 0.18^{\circ}$, subcutaneous--$26.5 \pm 1.00^{\circ}$; at the end of the experiment, 36.6 ± 0.20 and $22.0 \pm 0.36^{\circ}$, respectively. The results of the experiments are presented in the table.

Caloric stimulation of the labyrinth during cold shivering. In the conditions of our experiment, in most tests caloric stimulation of the labyrinthine structures led to bilateral suppression of the bioelectrical activity of the flexor muscles of the limbs during cold shivering (Fig. 1). At the same time the caloric stimulus did not cause the appearance of bioelectrical activity of the extensor muscles of the limbs in any of the experiments (Fig. 2). Suppression of flexor activ- /704

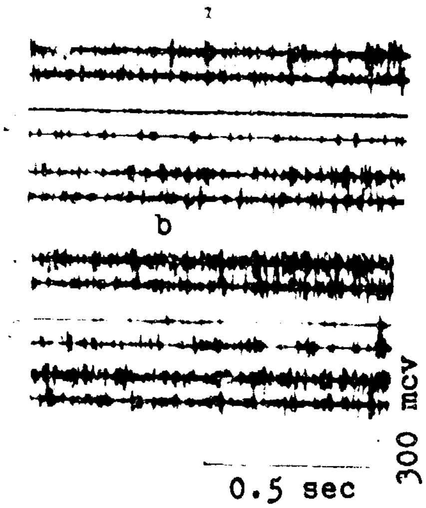

Fig. 1. Change in the activity of flexor muscles of the limbs of the ipsi- and contralateral side on caloric stimulation of the labyrinthine structures.

a - EMG of the biceps muscle of the shoulder, b - of the sartorius muscle. 1 - initial activity, 2 - activity during the stimulation, 3 - after cessation of the stimulation. Upper path - EMG of muscle of ipsilateral side, lower path - EMG of muscle of contralateral side.

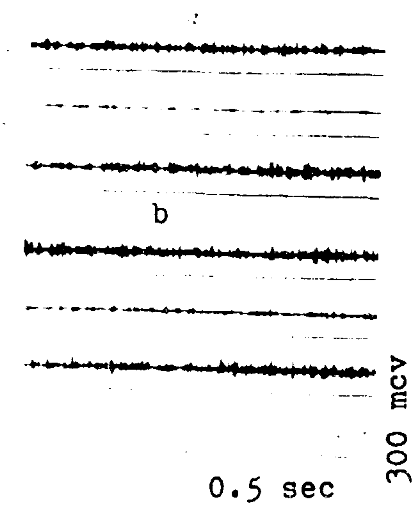

Fig. 2. Activity of flexor and extensor muscles of back limbs on caloric stimulation of the labyrinth.

a - on ipsilateral side, b - on contralateral side. 1 - initial activity, 2 - activity during the stimulation, 3 - after **removal of the stimulus**. Upper path - EMG of sartorius muscle (flexor), lower path - of soleus muscle (extensor).

ity was manifested in the form of its decrease or complete cessation (see table). In most tests the effect of the stimulation predominated in the muscles situated on the side of the stimulated vestibular apparatus (Fig. 1). Cessation of the bioelectrical activity of the muscles during caloric tests was not observed simultaneously in muscles of the ipsi- and contralateral side; as a rule, the activity was suppressed earlier in the muscles of the ipsilateral side and then the contralateral. Thus, inhibition of the activity of the sartorius muscle of the ipsilateral side was observed 2.1 $\pm$ 0.54 sec earlier than on the contralateral side. For the biceps muscle of the shoulder this difference was 0.9 $\pm$ 0.20 sec. On the average the bioelectrical activity of the flexors of the ipsilateral side during caloric stimulation of the labyrinths in the conditions of our experiment were decreased or completely stopped within 2-5 sec from the beginning of the stimulation.

During the action of the caloric stimulus we observed for the studied time segment the effect of the "escape" of the shivering from the effect of the stimulus. In the sartorius muscles the restoration of activity, despite the continuing stimulation, took place in 14 tests of 36; in 12 of them the activity of the sartorius muscle of the ipsilateral side appeared 1.7 ± 0.03 sec later than in the muscles of the contralateral side, and in two tests the activity appeared simultaneously. In the remaining 22 tests "escape" of the shivering was not observed. In the biceps muscle "escape" of the activity occurred only in 2 tests.

Also indicative of the more significant effect of the labyrinths on the motoneurons of "their" side is the fact that suppression of bioelectrical activity in the form of its complete cessation was more frequently observed in the muscles of the ipsilateral side (see table). /70 Thus, during unilateral caloric action on the vestibular apparatus, asymmetry of the inhibition of the bioelectrical activity of the muscles of the ipsi- and contralateral side is observed.

Thermal stimulation of the labyrinthine structures causes more marked suppression of the cold shivering of the biceps muscle of the shoulder than of the sartorius muscle (Fig. 3, a). This is evidenced by the fact, indicated above, of the absence of "escape" of shivering in the biceps muscle of the shoulder in most of the tests. In addition, complete cessation of the activity of the biceps muscle of the shoulder of the ipsilateral side was observed in 19 tests of 42, whereas the activity of the sartorius muscle was stopped completely only in 6 tests of 46. It should be noted that caloric stimulation of the labyrinths did not always suppress the bioelectrical activity of the sartorius muscles. In 10 tests the activity of the sartorius muscles of the ipsilateral side, and in 13--of the contralateral side, remained at the initial level during the stimulation. The activity of the biceps muscle of the shoulder, however, was suppressed in all the tests.

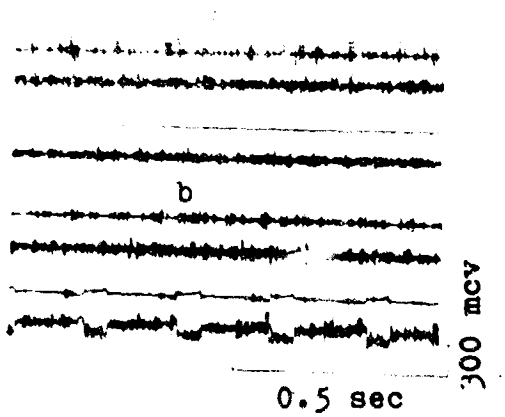

Fig. 3. Comparative characteristics of the bioelectrical activity of flexor muscles of the front and back limbs of the ipsilateral side on stimulation of the vestibular apparatus.

a - caloric stimulation, b - electrical stimulation. 1 - initial activity, 2 - activity during stimulation of labyrinth. Upper path - EMG of biceps muscle of shoulder, lower path - of sartorius muscle. On oscillogram 2, b - artifact of electrical stimulation.

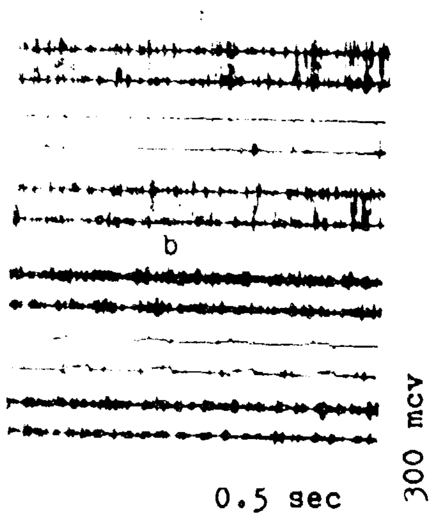

Fig. 4. Change in the activity of flexor muscles of the limbs of the ipsi- and contralateral side on electrical stimulation of the labyrinthine structures.

a - EMG of the biceps muscle of the shoulder, b - of the sartorius muscle. 1 - initial activity, 2 - activity during the action of the stimulus, 3 - after cessation of stimulation. Upper path - EMG of muscle of ipsilateral side, lower path - of muscle of contralateral side. On oscillograms 2, a and 2, b - artifact of electrical stimulation.

In control tests the thermal stimulus did not change the bioelectrical activity of the muscles. Increase of flexor activity was not observed in any of the conducted tests.

Electrical stimulation of the labyrinth during cold shivering. Electrical stimulation of the vestibular apparatus, similar to caloric tests, caused bilateral suppression of the bioelectrical activity of the flexor muscles of the limbs during cold shivering with predominance of the effect on the ipsilateral side (see table; Fig. 4). In this case stimulation of the labyrinth did not cause activation of the extensor muscles (Fig. 5).

The threshold intensity of stimulation that caused suppression of the bioelectrical activity of the biceps muscle of the shoulder was 8.8 ± 0.4 v, and for the sartorius muscle--11.6 ± 0.4 v. From Fig. 3, b, it is evident that an electrical stimulus of 9.0 v suppresses the activity of the biceps muscle of the shoulder, while the activity of the sartorius muscle remains at the initial level. During the electrical stimulation of the vestibular apparatus for the studied time interval (10 sec) we did not observe restoration of the shivering, as occurred in the caloric tests. /706

Electrical stimulation (9-11 v) of the bony wall of the bulla caused no changes in the bioelectrical activity of the studied muscles.

Disscussion of Results

It is known that the descending effects of the vestibular apparatus on spinal activity are manifested as tonic stimulation of the motoneurons that are connected to the antigravitation musculature during simultaneous reciprocal inhibition of the flexor motoneurons [5, 11, 13, 16]. As a result of our earlier experiments [1] it was shown that in conditions of unilateral destruction of the vestibular apparatus there is an increase in the bioelectrical activity of flexor muscles of the limbs during cold shivering. It was hypothesized that intensification of cold shivering after destruction of the labyrinthine structures is related to removal of the inhibiting effects of the vestibular apparatus on the flexor motoneurons. The results of the given experiments, in which suppression of the bioelectrical activity of flexor muscles was observed during cold shivering on stimulation of the labyrinths, are in agreement with previously conducted experiments and do not contradict the literary data on the inhibiting effect of the vestibular apparatus on the motoneurons of the flexors.

Activation of the vestibular structures did not bring about the appearance of bioelectrical activity of the extensor muscles. This is related, apparently, to the fact that vestibulo-motoneuron connections represent axodendritic synapses [15], and the effectiveness of the stim-

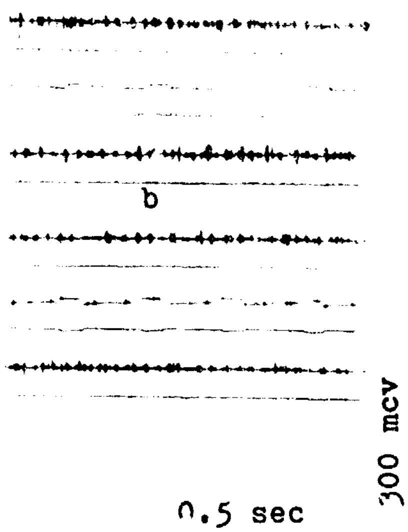

Fig. 5. Activity of flexor and extensor muscles of the front limbs during electrical stimulation of the labyrinth.

a - on the ipsilateral side, b - on the contralateral side. 1 - initial activity, 2 - activity during the action of the stimulus, 3 - after cessation of the stimulation. Upper path - EMG of the biceps muscle of the shoulder (flexor), lower path - of the triceps muscle (extensor). On oscillograms 2, a and 2, b - artifact of electrical stimulation.

ulation of the vestibular apparatus in our experiments was not high enough to evoke independently activity of the extensor muscles. In addition, increase in the activity of the cutaneous cold receptors could have an inhibiting effect on the pool of motoneurons of the extensors [17].

The bilateral effect of the suppression of the activity of the flexor muscles during cold shivering that was observed in most of the tests is related, in all probability, to the bilateral effects of the vestibular apparatus on spinal activity with predominance of the effect in muscles of "its" side [10, 12].

Stimulation of the vestibular apparatus had a greater inhibiting effect on flexor muscles of the front limbs than the back limbs. Such a phenomenon may be related to properties of the vestibular control of the activity of various regions of the spinal column. The motoneurons of the lumbar regions are connected primarily with neurons of Deiters' nucleus, whereas the motoneurons of the cervical and upper thoracic segments are subjected to the influence of both Deiters' nucleus and the medial vestibular nucleus [14, 15].

Such properties of the vestibular control of the activity of the /707
motoneurons of the spinal chord may also explain the absence of suppression of the activity of the sartorius muscle in some of the tests

and the "escape" of shivering in these muscles under the influence of a caloric stimulus. A caloric stimulus, as is known, causes stimulation of the receptors of the semicircular canals [8], which are connected to the spinal cord through the medial vestibular nucleus. Descending effects of the medial vestibular nucleus in the structure of the medial longitudinal fascicle were traced in the cervical and thoracic segments of the spinal cord, but not in the lumbar segments. It would seem that in this case thermal stimulation of the vestibular apparatus should not have inhibiting effects on the motoneurons of the lumbar regions of the spinal cord, and consequently the bioelectrical activity of the flexors of the back limbs during cold shivering should remain unchanged. The suppression of the activity of the sartorius muscles during caloric stimulation of the labyrinth that was observed in most of the tests could be caused by alteration in the activity of the reticulospinal system [11].

Thus, despite some peculiarities of the effect of caloric and electrical stimulation of the vestibular apparatus on muscle activity, both types of stimulation caused suppression of the pool of flexor motoneurons that are active during cold shivering, with maximum effect of the suppression of motoneurons that innervate the flexor muscles of the front limbs of the ipsilateral side.

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