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## DEPENDENCE OF SINGLE MUSCLE RECEPTOR FUNCTION ON MUSCULAR ACTIVITY

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Spontaneous and evoked activity of single muscle spindles and Golgi receptors was recorded in cats anesthetized with chloralose and urethane and the effect of muscular activity evoked by direct or indirect stimulation on this activity was studied. The contractile activity of the plantaris (fast) and soleus (slow) muscles was shown to reduce the spike discharge both of muscle spindles and of Golgi receptors, and much more so in the case of muscle spindles of the fast muscles than of the slow.

KEY WORDS: single muscle receptors; muscular activity.

Investigators who have studied muscle reception in warm-blooded animals have given adequate descriptions of the basic principles governing function of single muscle receptors (muscle spindles, Golgi receptors), but no data can be found on the effect of contractile activity of a muscle on receptors located in it [4, 5]. Yet investigations in which afferent impulses are recorded from skeletal muscle receptors of cold-blooded animals have shown that during prolonged activity of a muscle the flow of afferent impulses diminishes, and the more strongly the muscle contracts, the more rapid and more marked the diminution and the faster the muscle becomes fatigued [6, 7, 10].

The object of this investigation was to study the effect of prolonged contractions of a muscle in warm-blooded animals, produced by direct or indirect electrical stimulation of the muscle, on discharges from single muscle spindles and Golgi receptors of the same muscle.

### EXPERIMENTAL METHOD

Cats were anesthetized with a mixture of chloralose (5  $\mu\text{g/kg}$ ) and urethane (500  $\mu\text{g/kg}$ ) intraperitoneally. The test objects were muscle receptors (muscle spindles and Golgi receptors) of fast (plantaris) and slow (soleus) muscles before and after contractile activity of the same muscles evoked by direct or indirect stimulation.

The ventral and dorsal spinal roots were dissected and divided at level  $L_5-S_1$ ; all muscles in both hind limbs were denervated except the soleus and plantaris. A weight of 200 g was attached to the tendon of these muscles, causing them to stretch and producing spontaneous activity of the receptors located in them; after attachment of the weight, the muscles contracted under isometric conditions.

To obtain impulses from single receptors the dorsal root was separated into filaments under oscilloscopic control, until impulses of equal amplitude were obtained. Activity was recorded on the UEF-5 electrophysiological system (transmission band 10-3500 Hz, sensitivity 2 mm/ $\mu\text{V}$ , amplifier noise 8  $\mu\text{V}$ ). Muscle

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TABLE 1. Discharges (spikes/sec) of Single Muscle Receptors Before and After Muscular Contraction Evoked by Electrical Stimulation

| Type of receptor | Muscle    | Activity of receptors | Before stimulation (background) | After direct stimulation | After indirect stimulation |
|------------------|-----------|-----------------------|---------------------------------|--------------------------|----------------------------|
| Muscle spindle   | Plantaris | S                     | 18.6 ± 1.86                     | 15.3 ± 1.25              | —                          |
|                  |           | E                     | 50.2 ± 2.82                     | 35.4 ± 3.2               | —                          |
|                  |           | E-S                   | 37.6 (100)                      | 20.1 (53.4)              | —                          |
|                  | Soleus    | S                     | 48.4 ± 2.47                     | 15.6 ± 1.47              | 11.9 ± 2.1                 |
|                  |           | E                     | 81.1 ± 3.52                     | 69.3 ± 3.7               | 64.4 ± 4.1                 |
|                  |           | E-S                   | 62.7 (100)                      | 53.7 (85.0)              | 49.5 (78.9)                |
| Golgi receptors  | Plantaris | S                     | 17.2 ± 1.2                      | 11.2 ± 3.3               | —                          |
|                  |           | E                     | 45.5 ± 3.2                      | 33.4 ± 2.8               | —                          |
|                  |           | E-S                   | 28.3 (100)                      | 22.2 (78.4)              | —                          |
|                  | Soleus    | S                     | 17.5 ± 0.8                      | 11.2 ± 3.3               | —                          |
|                  |           | E                     | 45.5 ± 3.2                      | 33.4 ± 2.8               | —                          |
|                  |           | E-S                   | 28.3 (100)                      | 22.2 (78.4)              | —                          |

Legend. S) Spontaneous activity; E) activity evoked by stretching muscle; E-S) increase in number of spikes in response to stretching (in spikes/sec, in parentheses in %).

spindles and Golgi receptors were identified from their response to muscular contraction, evoked by stimulation of the ventral root. If the contraction caused the spike discharge to cease, the response was ascribed to the muscle spindle, but if the discharge frequency increased it was ascribed to the Golgi tendon organ. Besides spontaneous activity, evoked afferent impulsion arising in response to additional muscle stretching of standard magnitude (by 5 mm at the rate of 40 mm/sec for 60 sec) also was recorded. This evoked activity was recorded 0.5-1 sec after the beginning of stretching (dynamic stage), then every subsequent 15 sec. The repetition frequency of the spikes per second and the increase in the number of spikes in response to stimulation were calculated from the recordings.

Contractile activity of the muscles was evoked by electrical stimulation of the muscle by a current of four times the threshold strength, with a frequency of 150 Hz in the case of direct and 75 Hz in the case of indirect stimulation. Contractions of the muscle were recorded by means of strain gauges and the UTS-VT-K tensometric units.

## EXPERIMENTAL RESULTS

Analysis of the receptor discharges, the results of which are given in Table 1, showed that before stimulation of the muscle, spontaneous activity of single muscle spindles and Golgi receptors of the plantaris and soleus muscles consisted of discharges of almost equal frequency. Additional testing stretching of the muscle caused an increase in the discharge frequency which was particularly marked in the dynamic phase. The frequency of evoked activity and the increase in the number of spikes differed for different receptors: they were greater for muscle spindles of the soleus muscle than for the plantaris muscle, and they were equal for Golgi receptors of both muscles, but less than for muscle spindles.

After direct stimulation of the muscle for 10 min all indices of receptor activity were reduced: spontaneous activity of plantaris muscle spindles by 17.8% and of soleus muscle spindles by 15.3%, activity of Golgi receptors of both plantaris and soleus muscles by 36.4%. The frequency of the evoked discharge in response to additional testing stretching of the muscle also was reduced: in the dynamic phase for plantaris muscle spindles by 37.1% and soleus muscle spindles by 14.6%, and for Golgi receptors of both muscles by 26.4%. The increase in the number of spikes in the response of the receptors to stretching, characterized by an increase in the percentages of evoked activity compared with the background, also was reduced (Fig. 1).

Indirect stimulation of the soleus muscle had the same effect as direct, but it was a little stronger (Table 1, Fig. 1).

Statistical analysis of the numerical data showed that the decrease in the indices of receptor spike activity is significant or there was a tendency for it to decrease.

The results of these experiments thus indicate that muscular activity depresses the function of receptors in the muscle: muscle spindles and Golgi receptors. A functional difference was found between the receptors: muscle spindles of the plantaris muscle reduced their activity to a much greater degree than those of the soleus

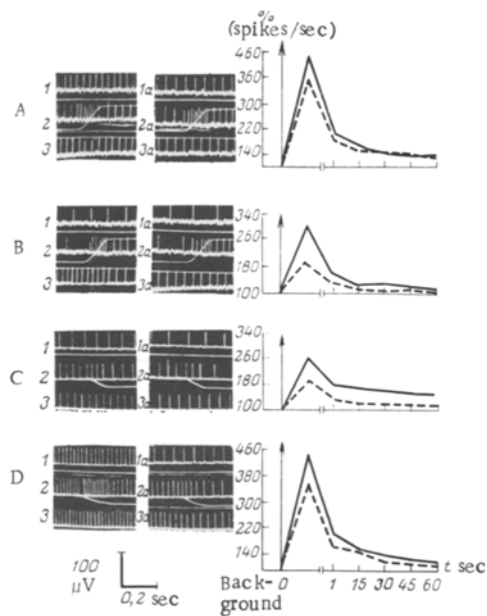


Fig. 1. Spike discharge (I) and graph of response of single muscle receptors to stretching of muscle (II) before and after stimulation. A, B, C) Direct stimulation of muscle; D) indirect stimulation; A and D) soleus muscle spindles; B) plantaris muscle spindles; C) soleus Golgi receptors. Tracings: 1, 2, 3) spike activity before stimulation, 1a, 2a, 3a) after stimulation (1 and 1a represent background receptor activity; 2 and 2a activity during dynamic phase; strain gauge readings shown also on these tracings; 3 and 3a) 15 sec after stimulation). Graphs show spike discharges during stretching of muscle (beginning of stretching shown by arrow) in percentages of background discharge frequency, taken as 100%; first measurement of spike discharge in dynamic phase, remainder at time intervals indicated on abscissa after first measurement; continuous line in all cases before, broken line after stimulation of muscle.

muscle; Golgi receptors of both muscles respond equally, but their function is depressed by a greater degree than that of the muscle spindles. The functional difference between the muscle spindles of the plantaris and soleus muscles was observed even before stimulation of these muscles: Soleus muscle spindles responded to testing stimulation of the muscle by a higher discharge frequency than plantaris muscle spindles. No such difference was found between the Golgi receptors. The functional difference between the plantaris and soleus muscle spindles, which other workers also have observed [1], is evidently attributable to morphological differences between these muscles, for the former is a fast (phasic) muscle, the second a slow (tonic) muscle [9, 11].

The results obtained in this investigation are similar to those obtained previously in experiments on cold-blooded animals, in which the total flow of afferent discharges was recorded [6, 7, 10]; they are complementary to them in the sense that they answer the question of which receptors are responsible for the reduction of the afferent flow. Experiments with single receptors showed that under the influence of muscular activity the spike discharges of both muscle spindles and Golgi receptors have a tendency to diminish.

In experiments on cold-blooded animals the depression of receptor function under the influence of muscular activity is caused by products of muscle metabolism formed during work of the muscle, the change in tone of the muscle, and the development of contracture [6, 7]. Since experiments on warm-blooded animals

were carried out under isometric conditions, the effect of contracture and of other factors changing the length of the muscle, and at the same time, changing the degree of activity of the muscle spindles, was ruled out. Metabolites are a possible cause of the change in the functional state of the receptors in the working muscle and in warm-blooded animals; it may be that it is the same substances which also influence neuromuscular synapses [2, 3, 8]. Dependence of the activity of muscle receptors on the state of metabolism in the muscle is also demonstrated indirectly by the functional difference observed between the muscle spindles of the fast (plantaris) and slow (soleus) muscles.

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#### EFFECT OF THE PRINCIPAL BLOOD COMPONENTS ON LUNG SURFACTANT

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The action of the principal blood components on surface activity of substrates containing lung surfactant was investigated. Mixing blood hemolysate, serum, albumin, and fibrinogen with extracts and washings from the lungs, application as a monolayer, or their injection into the hypophase of a monolayer of washings increased the surface tension (ST) of these substrates. Hemoglobin, serum lipids, and cholesterol had the opposite action. Contact of all these blood components, exhibiting opposite effects on ST of medium containing surfactant, with bubbles from the lungs during determination of their coefficient of stability (CS), by Pattle's method, led to an increase in CS.

KEY WORDS: lung surfactant; endogenous substances; blood components.

Of the endogenous substances with which alveolar surfactant can come into contact, with a change in its activity, the most important are the blood components. The incomplete and highly contradictory data given by different workers on interaction between lung surface-active substances (surfactants) with the principal blood components are difficult to compare, for many were based on methods of investigation which differed in principle or in their essential details [6-9, 11, 13]. The solution to this problem is highly relevant to the explanation of mechanisms of the changes in surfactant arising in pulmonary edema, inflammatory lesion of the lungs, alveolar proteinosis, the respiratory distress syndrome in newborn infants and adults, and so on. It was there-

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