

Activity of Motor Units in Human Elbow Flexor and Extensor Muscles during Task-Dependent Unloading

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Surface EMGs and activity of 73 single motor units (MUs) of the *m. triceps brachii caput laterale (TBcl)* and 25 units of the *m. biceps brachii caput longum (BBcl)* were recorded in five adults during unloading within the ramp phase of the isotorque ramp-and-hold movements in the elbow joint (“movement” task) and during maintaining of a certain position (“position control” task). Analysis of the surface EMGs showed that patterns of the MU responses to unloading in different motor tasks are dissimilar. Depending on the responses to unloading, the examined MUs were classified into two groups. Motor units of the first group, including 14 *TBcl* MUs and 22 *BBcl* ones, were characterized as task-independent units. Their spiking was completely inhibited in response to unloading in both motor tasks. The second group (44 *TBcl* and 3 *BBcl* MUs) should be considered as a group of the task-dependent units. These MUs were active during unloading in the “movement” task but were fully inhibited in the “position control” task. This specificity in the reactions of MUs during movements may be related to their different functions. Presumably, the former group of MUs is mainly involved in the force control, while the latter one is associated with the control of the movement *per se*.

Keywords: elbow joint, isotorque movements, unloading, movement control, motor units, surface EMG

INTRODUCTION

The question of how activities of single motor units (MUs) are associated in integral (“gross”) muscle contractions (providing, e.g., movements of the limb link and/or maintenance of a certain joint angle) is one of the central problems in the physiology of motor control. At present, the development of techniques providing the possibility to record single MU activity during a sufficiently long time interval even under conditions of performance of relatively intense muscle contractions [1–5] opens certain possibilities for interpretation of at least some aspects of the above question. Various test paradigms allowed researchers to record activities of individual MUs in humans related to the performance of movements or to the maintenance of a stable position of a limb link and to compare

such activities. Some earlier studies [2, 3, 5] gave certain reasons to believe that the neural control of the above two situations (“movement” and “position control”) is characterized by some specificities. Significant additional information in the considered field of study can probably be obtained by application of an addition load in the course of the “movement” and/or “position control” tests and by removal of such loading. This may be indicative of the involvement of the stretch-reflex mechanisms in the observed changes in muscle activity.

Studies of oppositely directed changes (excitation or inhibition) in the activity of motoneurons while performing monotonous single-joint movements [6, 7] seem to be important for understanding certain peripheral processes of motor control. The possibility of task-dependent activation of the same MUs has been examined by many authors [2–4, 7–16]. It was shown that the recruitment thresholds of *m. biceps* MUs and the firing frequency of the latter after the recruitment are task-dependent. During the performance of slow movements, the recruitment thresholds were lower (3 deg/sec), and the MU firing frequencies during muscle shortening were higher than those during isometric

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contraction at the hold position [2]. For a given torque output, the discharge rate of the soleus MUs was significantly lower in isometric contractions than that in voluntary concentric contractions [4]. Tax et al. [2] noted that the recruitment thresholds and firing frequency of MUs in the hold position demonstrated an intermediate state between the respective values in the tasks of isometric force control and movement control. These authors proposed such an explanation for this finding: The hold position can be considered not purely isometric; there is a possibility for small displacements in the muscle. The authors also mentioned that the hold position should be considered a movement task with a zero velocity. The task-dependent activity of MUs during sustained isometric contractions was compared for two cases in detail, i.e., when muscles either supported an inertial load (position task) or exerted an equivalent constant torque against a rigid restraint (force task) [13–16]. However, comparative characteristics of MU activities under conditions of changes in the external load during the dynamic movement and position control have not been studied sufficiently.

An active ramp-and-hold movement with a constant velocity performed against a previously applied constant external load can be divided into three phases: i) compensation for the previously applied external load (static phase); ii) exit of the joint from the equilibrium position and transition with a constant velocity to a new position (movement *per se*, a dynamic phase), and iii) compensation of the external load to fix a new position with the agonist muscles being shorter than those in phase 1 (static phase). The first and the third phases of the “movement” task should be considered examples of approximately isometric states and are, in fact, hold-position tasks. The second phase is performed under conditions of anisometry with preferential movement control.

In the literature, it has been proposed [17, 18] that the alpha and gamma motoneuronal pools are controlled by separate descending systems. Elbow flexor motoneuronal pools might be activated differently in force and movement tasks either by one or by both of these separate control systems [8]. If the control of the slow movement tasks and force tasks is provided by separate synaptic drives, isolated modes of control of the movement (muscle length) and of an external load during a task with the active movement against the above load seem

to be quite possible. An idea that the external force is compensated separately by the action of specific central commands, which would control the length of the muscles, was suggested for the first time in a hypothesis of the fusimotor servo control proposed by Merton [19]. When investigating activities of the *m. biceps* MUs during flexion of the elbow joint [5], we observed a noticeable proportion of units whose activity was not related to the movement control. These MUs were activated in response to application of an external load; flexion was performed to oppose the latter. Such units, however, did not increase their discharge frequency within segments of the movement with a constant velocity. A part of these units demonstrated an activity decline during concentric contractions (voluntary elbow flexion). These units were characterized by relatively low thresholds of activation; the minimal recruitment threshold corresponded to only 4% of the maximum voluntary contraction. It seemed that such units mainly controlled opposition to the external load and were not involved in the actual movement control.

To verify the hypothesis on the possibility of separate modes in controlling the external load and of the actual working point displacement (velocity, amplitude), we decided to test the activity of single MUs under conditions of two experimental paradigms. First, an unloading was applied while performing a task of sufficiently slow (8 deg/sec) voluntary ramp-and-hold isotonic movement. Second, an unloading was applied when the force was created against the external load in order to maintain a given position. One of the purposes of such a study was to differentiate the MUs that would respond similarly to force manipulations in the “movement” task and in the “position control” task and the units that would react differently under such conditions. We assumed that the MUs whose activity compensates the external load should also respond clearly to unloading in these different movement tasks, i.e., they could be qualified as task independent. We tried to elucidate the possibility of separate modes of control of the force and the movement by units of the same muscle. Conversely, the units whose activity is clearly associated with the movement control were likely to be task dependent. During recordings of MU activity, surface EMGs were also recorded from the *m.m. biceps brachii caput longum (BBcl)* and *triceps brachii caput laterale (TBclat)* in a parallel manner.

METHODS

Subjects. In this study, five healthy 34- to 54-year-old men without neuromuscular disorders participated in twenty-five test sessions. The subjects performed two different motor tasks during each test session; each task included three tests, and each of the latter consisted of at least 10 trials.

Experimental Setup. Each subject sat in a comfortable-height adjustable chair. The right forearm was fixed on a lightweight platform; the latter could be rotated within the horizontal plane at a level where the subject's shoulder link could move strictly horizontally. The forearm was placed on the platform in a palm-down position; an adjustable armlet restrained the wrist at the platform, thus reducing the possible activity of the palm and finger muscles during test movements.

Surface and Intramuscular EMG Recordings (sEMG and iEMG). To record the integral muscle activity, pairs of EMG electrodes (Biopac System EL 503, USA) were placed on the skin covering the *BBcl* and *TBclat*; the interelectrode distance was 25 mm. Intramuscular EMG signals were recorded from the *BBcl* and *TBclat* using paired fine-wire electrodes inserted into distal thirds of the above muscles. We assumed, according to our empirical experience, that shifting of the electrode during a muscle contraction in this part of the muscle would be smaller than that in its central part. As a result, we were able to record long-lasting iEMG signals during relatively high-amplitude movements. Two 25- μm varnish-insulated Ni-Cr wires (A-M Systems Inc., USA) were glued together and cut, to expose only bare cross-sections of the wires. The electrodes were inserted into the muscle through a 22-gauge disposable injection needle that was withdrawn after the insertion procedure and left the recording wires in place. This arrangement allowed us to stably record the impulsion generated by MUs with minimum discomfort for the subject; the duration of the most successful recordings reached 3 hours.

Both sEMG and iEMG signals were recorded using a BrownLee 440 amplifier (BrownLee Precision, USA) with bandpass filtering within the following ranges: 10 Hz to 5 kHz (sEMG) and 100 Hz to 5 kHz (iEMG). The obtained signals together with the signals from transducers allowing us to measure the joint angle and torque value (filtering range, 0 to 500 Hz) were collected by a CED Power 1401 data acquisition system using Spike 2 software (Cambridge Electronic Design, Great Britain).

EMGs and signals from transducers were digitized at 10^4 sec^{-1} and 10^3 sec^{-1} frequencies, respectively.

Origin 8.0 (OriginLab Corporation, USA) and SPSS 17.0 (IBM Business Analytics software, USA) were used for off-line data analysis. To evaluate accurately central commands coming to the muscles, identical test movements were repeated ten times, and sEMG records were averaged after their preliminary full-wave rectification; as was believed, the amplitude of such rectified and filtered sEMGs rather strictly correlated with the intensity of the above commands (Fig. 1).

During iEMG (single MU) registration, the electrode used usually recorded spiking of three to ten MUs simultaneously. These units could be differentiated according to the form and amplitude of their action potentials. Spikes with amplitudes from 0.1 to 2.0 mV were chosen for off-line analysis. Spikes with similar amplitudes were discriminated from the total trains using the Spike 2 program (WaveMark option). Spike superposition was used to control the individuality of the MUs, which confirmed constant values of the spike amplitude and shape. Such a control mode was applied in earlier works using iEMG records [20]. As a result, up to three motor units belonging to one muscle were usually analyzed within each test.

Experimental Procedure. At the beginning of each test series, we measured the EMG levels in the *BBcl* and *TBclat* during an isometric maximum voluntary contraction (MVC). The maximum voluntary torque (MVT) was measured by an electronic dynamometer (LOTS01, Wuyi Lot Electronics, China) at the joint angle of 45 deg with respect to the completely extended position defined as 0 deg. In the main part of the testing procedure, the subject performed isotorque ramp-and-hold movements ("movement" task) or graded the force against an external load to maintain the limb link position ("position control" task) under visual guidance. The subject could observe two real-time traces on a monitor; one trace represented the target signal, while another displayed the signal from angle sensors. The subject was asked to move both traces together and to try to provide their coincidence; thus, the subject either performed an isotorque movement ("movement" task) or maintained the position ("position control" task). The programs for the "movement" task began from the elbow joint position of 10 deg for the flexion movements and from 82 deg for the extension ones. Seventeen seconds after the trial start, a ramp-and-hold movement was made with

the velocity of 8 deg/sec and a maximum value of the hold position of 82 deg or 10 deg, respectively. The subjects maintained the hold position for at least 8 sec (the time increased proportionally to the decrease in the amplitude of the motion) and then returned the limb link to the original position in the elbow joint. Each trial was 50 sec long. The “position control” task programs began by moving the elbow joint to the hold position corresponding to that of the “movement” task and continued by holding this position until the end of the trial (the trial was also 50 sec long). Simultaneously or after the joint displacement toward the hold position, a linear motor created a constant torque that acted on

the subject’s forearm in the direction of extension or flexion and was maintained until the end of the trial. Unloading was performed by a linear motor, from the operating constant torque to the zero value at a maximum rate of 30% MVT in the case of extension and 10% MVT in the case of flexion. The zero torque value was held for approximately 18 sec; then it was increased up to the initial state. In the “movement” task, the unloading was performed during the ramp phase, at least 3 sec after the start of movement; the interval was extended with a decreasing amplitude of the constant torque. In the “position control” task, unloading was performed during a stationary part of the hold position, 20 sec after the trial start.

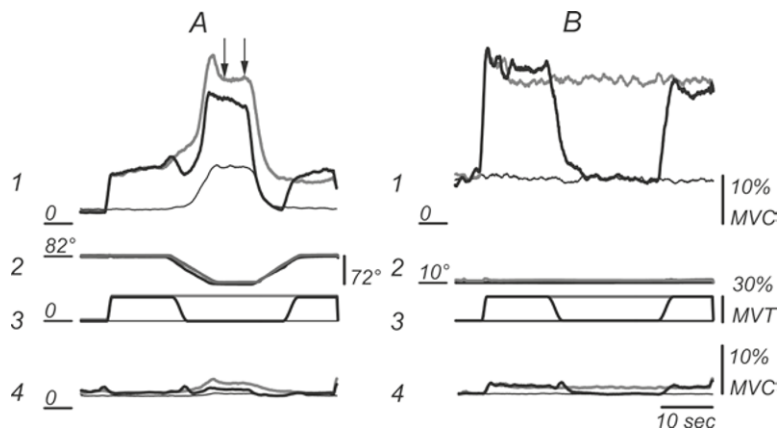


Fig. 1. Surface rectified EMGs recorded from the *m.m. triceps brachii caput laterale* (TBclat) and *biceps brachii caput longum* (BBcl) during ramp-and-hold movements (extension) of the elbow joint (movement task) (A) and while maintaining the joint equilibrium in a “hold position” (position control task) (B). An external load was absent in test 1 (thin black lines), a constant external load was applied in test 2 (grey lines), and unloading was performed in test 3 (thick black lines). 1) triceps EMGs, where 0 shows the zero level, while arrows indicate a quasi-stationary “hold position” section, from which values for the statistical analysis were taken, 2) changes in the joint angle, where 82° was the initial position of the joint and 10° was the “hold position”, 3) changes in the external load, where 0 corresponds to the zero-load level, and 4) BBcl EMGs.

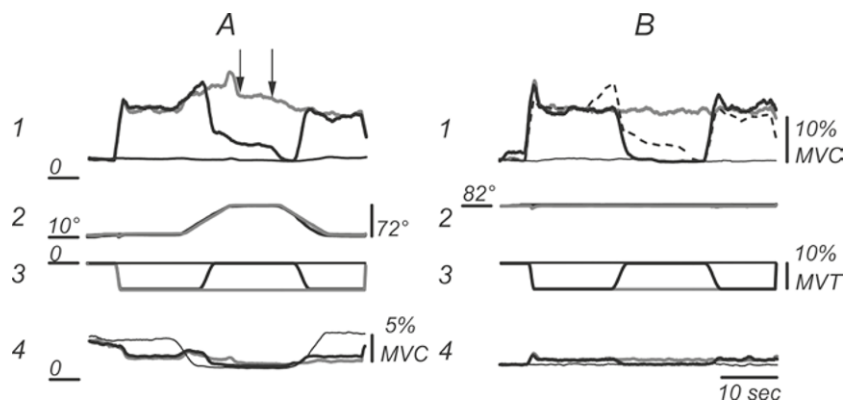


Fig. 2. Surface EMGs recorded from the *m.m. biceps brachii caput longum* (BBcl) and *triceps brachii caput laterale* (TBclat) during ramp-and-hold movements (flexion) of the elbow joint (“movement” task) (A) and while maintaining the joint equilibrium in a “position hold” (“position control” task) (B). 1) BBcl EMGs; a dotted line in B is BBcl EMGs during unloading in the “movement” task (shown in A); 2) changes in the joint angle, where 10° was the initial position of the joint, and 82° was the “hold position”. 4) TBclat EMGs. Other designations are the same as in Fig. 1.

The subjects performed the “movement” and “position control” tasks in the absence of an external load (test 1), under the influence of a constant external load (test 2), and during unloading (test 3). Tests 1–3 in both experimental tasks were performed in a pseudo-random order. The arm muscles were in a relaxed state for 30–50 sec between the repeated tests. In the “movement” task, while moving at a velocity of 8 deg/sec in the absence of an external load, a force pulse of 0.06 Nm appeared in the ramp phase. The recruitment threshold of individual MUs was estimated before the main part of the test series during the “movement” task. For this purpose, the movement task was executed with discrete rising of the external load from 0 (test 1) to 30% MVT at extension and from 0 to 10% MVT at flexion. The incremental load step was equal to 1% MVT. The units that were recruited without the external load were classified as “zero” units, while those that were recruited with the external load above zero were called “non-zero” ones.

Statistical Analysis. The sEMG levels and the firing rate of MUs were compared during the hold position in tests 1–3. We chose the area on the averaged graphs that was quasi-stationary (a rather uniform section of activity, generated after a dynamic segment before a decrease of activity related to returning to the start position) in all three tests. The minimal “stationary” area in one of three tests was chosen as the time interval for all three tests. In individual trials, we averaged all values in the selected area using the descriptive statistics programs (Origin 8.5). The obtained values were used in one-way ANOVA (Origin 8.5) to calculate the mean values, differences between the mean sEMGs for each subject (Bonferroni test), firing frequencies of individual MUs, and those for groups of units. Mean total firing rates of all units of the group were calculated by summing the average rates computed for individual MUs in the group (Table 2 and Fig. 3).

Table 1. Mean Differences between the Steady-State EMG Levels for the Same Length and Load Parameters in Two Different Movement Paradigms, 1) “Movement” Task after Previous Unloading at the Ramp Phase, and 2) “Position Control” Task after Previous Unloading.

Subject	<i>m. triceps brachii</i>		<i>m. biceps brachii</i>	
	test3mov-test3poz	Prob.	test3mov-test3poz	Prob.
	m ± SEM, % MVC		m ± SEM, % MVC	
1	1.347 ± 0.259	< 0.001	0.936 ± 0.068	< 0.001
2	5.666 ± 0.400	< 0.001	0.044 ± 0.036	= 0.231
3	9.369 ± 0.507	< 0.001	1.251 ± 0.286	< 0.001
4	7.989 ± 0.327	< 0.001	1.420 ± 0.176	< 0.001
5§	10.682 ± 0.407	< 0.001	3.565 ± 0.264	< 0.001

Footnotes. The results for the *m. triceps brachii caput laterale* (extension) and *m. biceps brachii caput longum* (flexion) are presented for five subjects (Bonferroni's test); §: data are presented in Figs. 1 and 2.

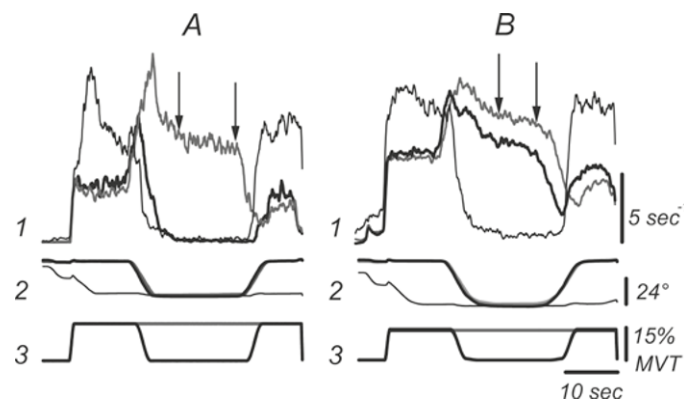


Fig. 3. 1) Summated data on the mean firing rates of 14 task-independent motor units (group 1) in tests 2 and 3 of the “movement” task and “position control” task (A) and the same graphs for 44 task-dependent motor units of group 2 (B). Grey lines, “movement” task, test 2; thick black lines, “movement” task, test 3, thin black lines – “position control” task, test 3; other designations are the same as in Fig. 1.

Table 2. Statistical Parameters for Averaged Mean Firing Rates of Motor Units in the Selected Groups in Tests 1–3 during the Movement Task and Position Control Task

Groups	Movement task					Position task		
	Load=0, test1, mean firing rate of the MUs \pm s.d., sec ⁻¹	Load>0, test2, mean firing rate of the MUs \pm s.d., sec ⁻¹	Unload, test3, mean firing rate of the MUs \pm s.d., sec ⁻¹	t2-t1 mean diff. \pm s.e.m., sec ⁻¹	t2-t3 mean diff. \pm s.e.m., sec ⁻¹	t3-t1 mean diff. \pm s.e.m., sec ⁻¹	Unload, test3 mean firing of the MUs \pm s.d., sec ⁻¹	move-poz test3-test3 mean diff. \pm s.e.m., sec ⁻¹
1	0	7.12 \pm 5.987	0.09 \pm 0.242	–	7.0 \pm 1.73***	–	0.11 \pm 0.191	0.0 \pm 0.10
2	–	9.61 \pm 4.452	7.52 \pm 4.835	–	2.1 \pm 0.89	–	0.75 \pm 1.285	6.8 \pm 0.88***
2a	0	8.54 \pm 4.015	5.66 \pm 3.021	–	2.9 \pm 1.39*	–	0.23 \pm 0.458	5.4 \pm 0.97***
2b	4.42 \pm 4.23	9.71 \pm 4.462	9.75 \pm 4.576	5.3 \pm 1.94*	0.0 \pm 0.11	5.3 \pm 2.25*	1.15 \pm 1.662	8.6 \pm 1.69***
2c	8.2 \pm 4.42	10.51 \pm 4.795	7.50 \pm 4.809	2.0 \pm 1.66	3.0 \pm 1.15*	1.0 \pm 1.64	0.76 \pm 1.233	6.7 \pm 1.50***

Footnotes. One-way ANOVA was used to calculate average values of the firing rate of motor units 1 and combined 2 (2a, 2b, 2c) groups in “position hold”; the table shows average values of the firing rate \pm Standard Deviation. The Bonferroni's test was used to calculate the mean differences between the average firing rates. The table shows the mean difference \pm s.e.m., the probability of the differences is shown by asterisks under the corresponding values. One asterisk corresponds to $0.05 > P > 0.01$, two asterisks – $0.01 > P > 0.001$, and three asterisks – $P < 0.001$, the absence of asterisks – the difference is insignificant.

RESULTS

In our study, we examined the effects of manipulations with the external load applied in different motor tasks, which affected sEMG activity and activity of individual MUs of the muscles operating the elbow joint. Each subject performed the “movement” task and the “position control” task in the absence of the external load (test 1), under the influence of a constant external load (test 2), and during unloading (test 3). The results of tests 2 and 3 allowed us to compare the extent of inhibition of MUs during unloading. Comparison of the results of tests 3 and 1 demonstrated differences in the levels of equilibrium activity under conditions of a zero external load. Comparison of the results of test 3 during the “movement” task and “position control” task allowed us to distinguish the task-dependent and task-independent reactions of MUs to unloading.

SEMG Activities of the *TBclat* and *BBcl* during Unloading in the “Movement” and “Position Control” Tasks. Examples of changes of *TBclat* and *BBcl* sEMGs (subject 5 in Table 1) during tests 1–3 in the “movement” task and “position control” task are illustrated in Fig. 1. Panel A in this figure shows that sEMG activities of the *TBclat* in the hold position with a zero external load at identical elbow joint positions (10 deg) were significantly dissimilar in tests 1 and 3. The mean difference was $15.30 \pm 0.58\%$ MVC ($P < 0.001$). Perhaps this situation was partly related to coactivation of the *biceps* and *triceps* (Fig. 1A, 4) because the activity of the former muscle in test 3 was greater than in test 1. This circumstance could increase the joint stiffness in test 3.

In the “position control” task (Fig. 1B), the subject maintained an equilibrium state in the hold position (10 deg) corresponding to that in the “movement” task. After unloading, the level of *TBclat* EMG activity in test 3 was reduced to the equilibrium level shown in the absence of an external load (thick and thin black lines, respectively). The sEMG activity in the *BBcl* was the same during coactivation with the *TBclat* in tests 1 and 3 (Fig. 1B, 4). The level of sEMG activity in the *TBclat* after unloading in the “movement” task (Fig. 1A, thick black lines) was significantly higher than that after unloading in the “position control” task (Fig. 1B, thick black lines). The mean difference was $15.72 \pm 0.57\%$ MVC ($P < 0.001$).

A similar situation was observed in the “movement” and “position control” tasks in tests 1–3 with *BBcl* EMG during elbow flexion. The mean difference between the respective EMG activities in tests 3 and 1 in the “movement” task (Fig. 2A) with the zero external load in the same elbow joint position (82 deg) was $3.31 \pm 0.26\%$ MVC ($P < 0.001$). The levels of *TBclat* sEMG activity during co-activation in the hold position in tests 1 and 3 were approximately the same (Fig. 2A, 4). In the “position control” task (Fig. 2B), unloading (test 3) led to a decrease in the level of muscle activity to the level shown in test 1, when the position was held in the absence of the external load. The antagonist muscle during coactivation in tests 1 and 3 showed the same activity level (Fig. 2B, 4). The level of *BBcl* sEMG activity after unloading in the “movement” task (Fig. 2A, thick black lines, B, dashed lines) was significantly higher than that after unloading in the “position control” task (Fig. 2B, thick black lines). The mean difference was $3.56 \pm 0.26\%$ MVC ($P < 0.001$).

The mean differences between steady-state EMG levels for the same length and load parameters have been compared for two different movement paradigms: i) “movement” task after previous unloading at the ramp phase, and ii) “position control” task after previous unloading. The results for five subjects are shown in Table 1; the activities of the *TBclat* (extension) and *BBcl* (flexion) were compared. The sEMG activity levels after unloading were significantly higher in almost all cases in the “movement” tasks, as compared with those in the “position control” ones. This fact is indicative of the existence of MUs whose responses to unloading were task-dependent.

Influence of Unloading on *TBclat* and *BBcl* MU Activity during Elbow Extension and Flexion in the “Movement” and “Position Control” Tasks. In the case presented in Fig. 1, *TBclat* activity during the position holding in test 1 was much higher than the background activity, while the level of *BBcl* EMG activity was comparable with the background level (Fig. 2A). This means that the number of “zero” motor units was greater in the *TBclat* than that in the *BBcl*.

Motor Units of the *TBclat*. In our study, 31 “non-zero” units and 42 “zero” units belonging to the *TBclat* were recorded. Two alternative types of MUs were arranged depending on the specificity of their reactions in test 3 in the “movement” and “position control” tasks.

The average rate of activity generated by 14 “non-zero” units is shown in Fig. 3A. Their firing rates during unloading (test 3) did not significantly differ from each other in both “movement” and “position control” tasks. In both tasks, these units were inhibited at unloading. Considering this fact, such units were classified as task-independent and formed MU group 1. These MUs certainly do not play a significant role in the ongoing movement control after unloading in the “movement” task. We hypothesized that such units were responsible mainly for the force control. The mean firing rate statistics of group-1 units for different motor tasks and tests are presented in Table 2. In Fig. 4, the upper row shows an example of the instantaneous and average rates of spike activity typical of group-1 units. The mean difference of its firing rate after unloading in two tasks was $0.05 \pm 0.09 \text{ sec}^{-1}$ ($P = 0.063$).

In contrast to the units of group 1, all (“non-zero” and “zero”) units of group 2 were task-dependent. Their activity after unloading changed slightly in the “movement” task and almost disappeared in the “position control” task (Fig. 3B). The statistics of the mean firing rate of group-2 units for different motor tasks and tests are given in Table 2.

The 2nd group was clearly heterogeneous. Units of this group could be divided according to the type of recruitment (“zero” or “non-zero”). Subgroup 2a included 13 “non-zero” units. The most important feature of these units was a decrease in the recruitment threshold in test 3 compared to that in test 1 in the “movement” task. The lower part of Fig. 4 represents an example of unit activity typical of subgroup 2a (Un13). Unloading during the ramp phase of the movement (test 3) curtailed the unit firing rate (Fig. 4B). In the “position control” task (Fig. 4C), the firing rate of this MU was reduced to

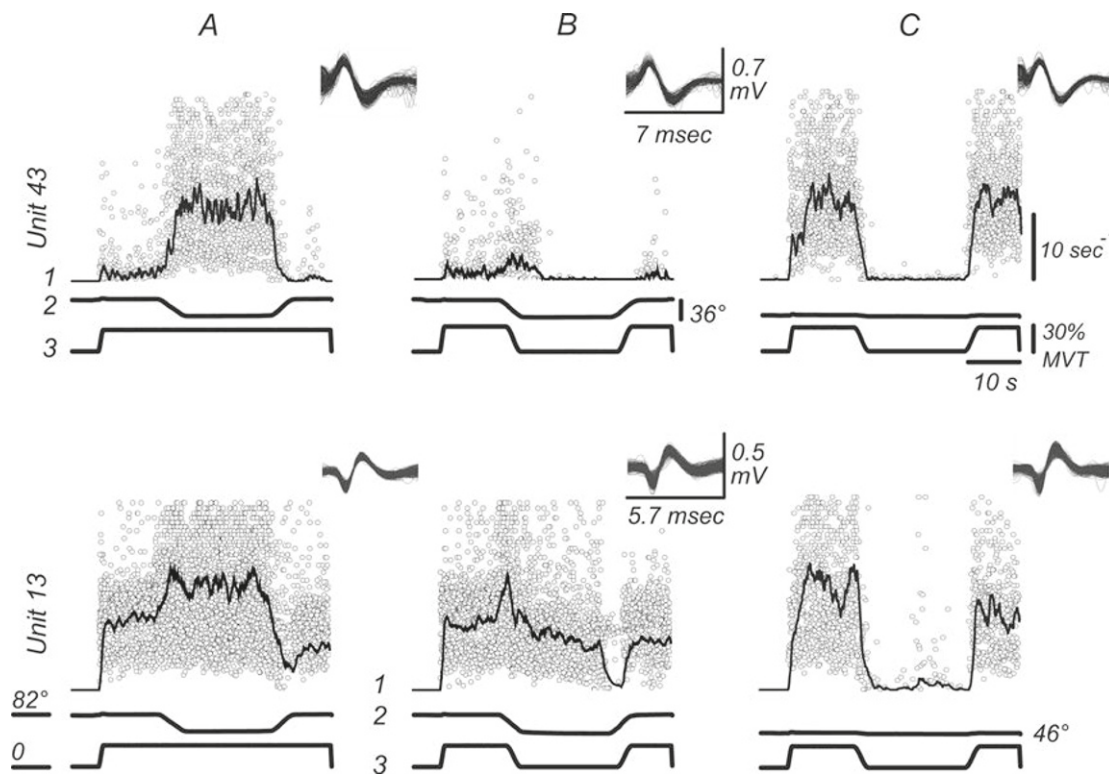


Fig. 4. Examples of activity of the task-independent (Un43) and task-dependent (Un13) “non-zero” motor units of the *m. triceps brachii caput laterale*. A) Instantaneous and averaged (10 trials minimum) mean firing rates during ramp-and-hold extension movements of the elbow joint (“movement” task) under the action of a constant external load (test 2). B) The same records during unloading in the “movement” task (test 3). C) Instantaneous and averaged (10 trials minimum) mean firing rates during unloading (test 3) and maintaining of the joint equilibrium in the hold position (“position control” task). 1) superposition of the instantaneous rates and recordings of the averaged mean firing rates, 2) changes in the joint angle, 3) changes in the external load. Superposition of the action potentials that were used to calculate the presented instantaneous and mean firing rates are shown in the upper right corner of each panel with superposition of the instantaneous firing rate.

$0.49 \pm 0.13 \text{ sec}^{-1}$ in response to unloading (test 3). The mean difference between the aforementioned value and the respective value for the “movement” task was $7.62 \pm 0.01 \text{ sec}^{-1}$ ($P < 0.001$).

Subgroups of 2b and 2c involved 16 and 15 “zero” units, respectively. In the “movement” task, spiking of units of subgroup 2b after unloading (test 3) remained significantly higher than the equilibrium level of activity shown in test 1 (Table 2). Units of the above subgroup demonstrated clearly visible hysteresis properties. Spiking of units of subgroup 2c in a similar situation decreased practically to the equilibrium activity level shown in test 1 (Table 2). In fact, units of subgroup 2c exhibited no hysteresis properties. The upper row in Fig. 5 shows an example of activity generated by Un55 belonging to subgroup 2b. This was a “zero” unit whose firing frequency slightly diminished during unloading in the “movement” task (Fig. 5B). Panel C shows a comparison of changes in the mean firing rate of Un55 during the performance of the “movement” task in tests 1, 2, and 3. Average values of the unit firing rate in the selected section (downward arrows) of the hold position were $13.05 \pm 0.82 \text{ sec}^{-1}$ in test 2 and $11.97 \pm 1.13 \text{ sec}^{-1}$ in test 3. The mean difference between values in tests 2 and 3 was $1.08 \pm 0.42 \text{ sec}^{-1}$ ($P = 0.018$). The mean difference between the firing rate during the hold position in test 3 (unloading towards the zero level) and test 1 (movement with

the zero external load) reached $5.27 \pm 0.23 \text{ sec}^{-1}$ ($P < 0.001$). In the “position control” task (Fig. 5D), the analyzed unit decreased its spiking to almost zero in response to unloading during the hold position (test 3). The mean difference between the aforementioned value and the respective value for the “movement” task was $11.92 \pm 0.17 \text{ sec}^{-1}$ ($P < 0.001$). The unit demonstrated significant hysteresis after unloading in the “movement” task (comparison of tests 1 and 3) and should be classified as task-dependent during unloading. The lower part of Fig. 5 illustrates the properties of a “zero” unit (Un9) belonging to subgroup 2c. During test 2, this MU was activated in response to application of the external load close to the threshold (6% MVC), but this was not observed in all trials (Fig. 5A). The firing rate of this unit, however, always increased in the ramp phase of the movement. Unloading performed in the ramp phase of the movement in test 3 resulted in a decrease in the firing rate in the hold position (Fig. 5B). A comparison of changes in the mean firing rate of Un9 during the “movement” task in tests 1, 2, and 3 is shown in Fig. 5C. The average value of the unit firing rate in the selected section of the hold position (downward arrows) was $13.14 \pm 0.50 \text{ sec}^{-1}$ in test 2 and $10.70 \pm 0.69 \text{ sec}^{-1}$ in test 3. The mean difference between values of the firing rate in tests 2 and 3 was $2.44 \pm 0.07 \text{ sec}^{-1}$ ($P < 0.001$). At the same time, the mean difference

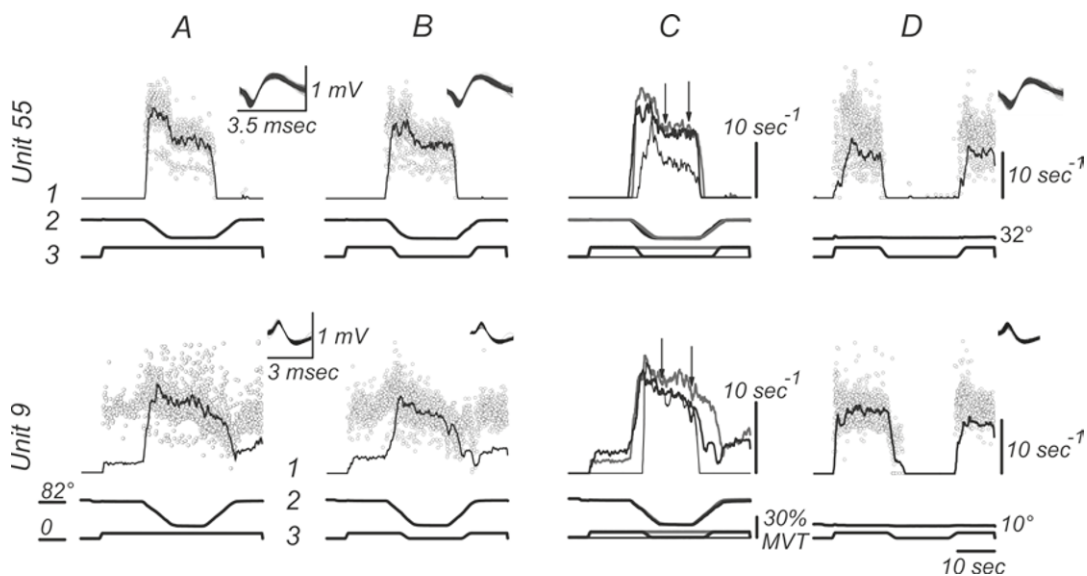


Fig. 5. Task-dependent activity of two “zero” motor units of the *m. triceps brachii caput laterale*, one of which (Un55) did not change its firing rate during unloading in the “movement” task (test 3), while another (Un9) reduced its firing rate to the values shown during the movement without the external load (test 1). A) “Movement” task, test 2. B) “Movement” task, test 3. C) “Movement” task, test 1 (thin black lines), test 2 (grey lines), and test 3 (thick black lines). D) “position control” task, test 3 other designations are the same as in Fig. 4.

between the firing rate levels in the hold position in tests 3 and 1 was $0.21 \pm 0.30 \text{ sec}^{-1}$ ($P = 0.497$). In the “position control” task (Fig. 5D), the unit increased its firing rate in response to application of the external load and decreased this value almost to zero in response to unloading during the hold position in test 3. The mean difference between the aforementioned value and the corresponding value for the “movement task” was $10.69 \pm 0.12 \text{ sec}^{-1}$ ($P < 0.001$). This unit showed no hysteresis properties. Its activity was inhibited to the level shown in test 1 during unloading in the “movement” task. However, this value remained significantly higher than the data shown during unloading in the “position control” task. The unit should be characterized as task-dependent during unloading.

The task-independent units of group 1 demonstrated significantly higher mean recruitment thresholds ($16.02 \pm 5.00\%$ MVT) in response to application of the external load than task-dependent units of group 2 ($7.27 \pm 4.12\%$ MVT). The mean difference between the above values was $8.75 \pm 1.39\%$ MVT ($P < 0.001$). The task-independent units of group 1 were activated, on average, $697 \pm 823 \text{ msec}$ after the movement beginning, while the

respective value for task-dependent ones of group 2 was $306 \pm 969 \text{ msec}$ before the movement. Thus, the mean difference was $1004 \pm 320 \text{ msec}$ ($P = 0.003$). We were able to measure the recruitment thresholds of units in group 2 during the “movement” and “position control” tasks. The respective average values were $5.10 \pm 1.63\%$ and $9.24 \pm 3.49\%$ MVT, with a mean difference of $4.14 \pm 1.30\%$ MVT ($P = 0.034$). The recruitment thresholds in response to the external load for all “zero” units were above zero, and the average thresholds of units in groups 2b and 2c were $7.56 \pm 4.72\%$ and $5.70 \pm 3.61\%$ MVT, respectively.

Motor units of the *BBcl*. We identified 25 “non-zero” MUs of the *BBcl*. All responses to unloading of these *BBcl* MUs could be divided into two groups. The first group included task-independent units. These were 22 MUs; seven of them were inhibited upon application of a constant external load during the ramp phase of the movement. Other MUs belonged to the task-dependent group (3 units). The upper row of Fig. 6 shows an example of the activity of a task-independent unit. This unit (Un7) was activated in test 2 in response to application of the external load (the recruitment threshold was

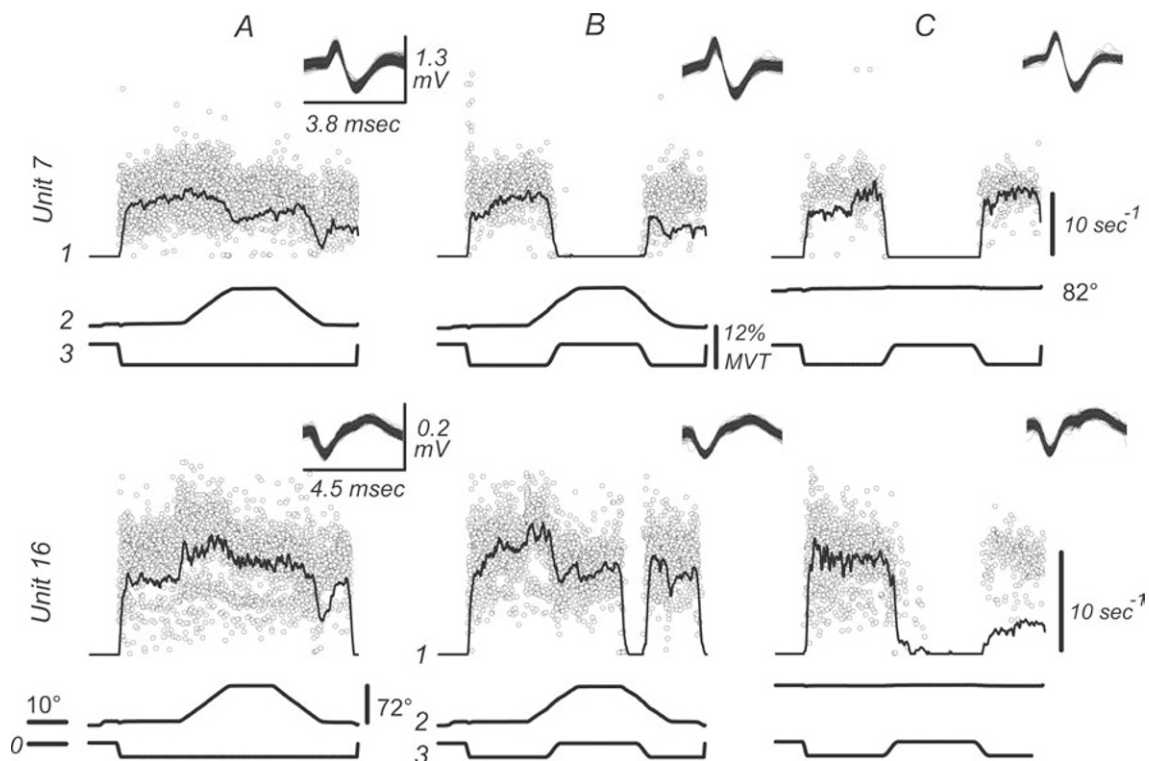


Fig. 6. Activity of task-independent (Un7) and task-dependent (Un16) “non-zero” motor units of the *m. biceps brachii caput longum*. Designations are the same as in Fig. 4.

$5.18 \pm 1.57\%$ MVT) and decreased its firing rate within the ramp phase in relation to implementation of the movement (Fig. 6A). This unit reduced its firing rate to zero in response to unloading during the ramp phase (Fig. 6B), and its activity was completely inhibited upon unloading in both “position control” and “movement” tasks (Fig. 6C).

The lower row of Fig. 6 shows an example of activity of the task-dependent unit. Such MU (Un16) was activated in response to application of the external load (recruitment threshold was $2.58 \pm 0.78\%$ MVC) and intensified its firing with implementation of the movement (Fig. 6A). This MU slightly diminished its firing rate in response to unloading during the ramp phase of the movement (Fig. 6B). The mean firing rate of this unit in the selected segments of the hold position in test 2 was $9.80 \pm 0.97 \text{ sec}^{-1}$, while it was $8.92 \pm 0.82 \text{ sec}^{-1}$ in test 3. The mean difference between these values was $0.88 \pm 0.31 \text{ sec}^{-1}$ ($P = 0.025$; Bonferroni test). Unit 16 was inhibited practically to zero in response to unloading in the “position control” task (Fig. 6C). The average value of the Un16 firing rate within the selected section of the hold position in test 3 (“position control” task) was only $0.01 \pm 0.021 \text{ sec}^{-1}$. The mean difference between the aforementioned value and the corresponding value in the “movement” task (test 3) was $8.91 \pm 0.30 \text{ sec}^{-1}$ ($P < 0.001$).

DISCUSSION

Analysis of sEMGs. Analysis of the parameters of surface EMGs recorded from the *TBclat* and *BBcl* during the ramp-and-hold movements (“movement” task) and the maintenance of hold positions (“position control” task) showed that the respective motoneurons in different motor tasks respond to unloading in a dissimilar manner. In the “position control” task, such MUs were mainly inhibited, while in the “movement” task they kept a fairly high level of activity. This is related not only to the dynamic pattern of the respective phase of activity but also to the spiking pattern in the hold position (Table 1). A comparison of results in tests 1 and 3 during the “movement” task revealed clear differences between the levels of equilibrium activity in the hold position, with maintaining the same joint angle and external load. The nonlinearity of muscular dynamics and statics (hysteresis of muscle contractions) has been demonstrated by

many researchers [21–24]. This property has been associated with different mechanical states of the muscles determined by the previous history of the movement. In our case, the ambiguity arose after unloading performed during the movement. According to the equilibrium point hypothesis [25, 26], it is suggested that a transition of the motoneuronal activity in test 3 should lead to the equilibrium level shown in test 1 and an automatic change in the joint angle corresponding to this equilibrium level of activity and the magnitude of the external load. In reality, the situation, however, was quite different. Figure 1A shows that motoneurons began to decrease the level of their activity in response to unloading, but this drop did not reach the corresponding equilibrium level shown in test 1. Such a drop is interrupted, and the spiking intensity began to increase and did not react to unloading. We can assume that the above-mentioned increase was necessary for providing the continuation of the movement and for the achievement of the preset value of the joint angle. The level of EMG activity in the hold position after reaching the set value of the joint angle in test 3 did not return to the equilibrium level shown in test 1. The above ambiguity could be related to a few reasons. Recording of MU activity showed that the performance of the “movement” task in tests 1 and 3 was provided by different groups of units. Exclusively “zero” units in test 1 were accompanied by “non-zero” units in test 3 in the proportion of approximately 1 to 3 of activated units (according to a rough estimate). Different compositions of the activated units could determine different mechanical parameters of the muscles involved in the test movements, and such an assumption may successfully explain the different equilibrium levels of the respective integral sEMGs in tests 1 and 3. Additionally, the difference in equilibrium levels could arise due to hysteresis properties of the activated units. Motor unit activities that manifested hysteresis properties are shown in Fig. 4 (Un13 and Un55). Their firing rates were significantly higher in the hold position after unloading during the movement (test 3) than the respective values observed in a similar ramp-and-hold movement performed under conditions of a constant zero external load (test 1). The same situation was reflected in the indices of the 2a and 2b groups of units (Table 2). As was shown earlier [27], the stiffness of a joint increased when the joint angle began to change in the opposite direction with respect to the direction of the preceding movement.

In our case, the hysteresis effect could arise due to a change in the mechanical state of units caused by a short initial relaxation of the muscle in response to unloading and subsequent contraction. The third source of differences between the equilibrium levels of sEMG activity in tests 1 and 3 could be related to the force developed by antagonists in test 3.

Analysis of changes in the firing rate of MUs of the *TBclat*. Classification of motor units on the basis of separate modes of the force and movement control: a hypothesis. Our tests showed that reactions of the studied MUs of the *TBclat* to unloading performed, on the one hand, during the ramp phase in the “movement” task and, on the other hand, during the hold position phase in the “position control” task (test 3) were significantly dissimilar. Some of the units (group 1) were inhibited almost completely to zero in response to unloading in both tasks; in other words, such MUs were task-independent. Since the units of this group reacted to unloading by termination of their activity in both force task and “movement” task, we suggest that these units are responsible for the force control in these tasks. This conclusion is supported by the fact that units of this group did not participate in the control of the ongoing movement after unloading in the “movement” task. Other units (group 2) were inhibited slightly or were not inhibited at all in response to unloading in the “movement” task. Unloading performed in the “position control” task led to almost complete inhibition of these units (i.e., the latter were task-dependent). We assumed that such MUs were responsible predominantly for the control of the movement *per se* in the movement task, since they generated the activity strictly associated with the ongoing movement after unloading. An additional proof for specific relations of the studied units to the movement control was the fact that their activity, on average, was much more intense than that at the beginning of the movement. In contrast, spiking of MUs of group 1 increased mainly during the movement itself. Based on the hypothesis of the existence of separate synaptic inputs to the neuronal circuits involved to the movement control and force control [2, 8, 9, 17–19], the observed task dependence of the unit responses in group 2 to unloading could be explained by activation of different synaptic inputs to the respective circuits in the movement task and in the position control task. This assumption is supported by the difference in the recruitment thresholds of the units of the respective groups in the two above tasks, which correlates well with the data of Tax et al. [2].

Comparison of the MU Activity of the *BBcl* and *TBclat*. The classified *BBcl* units could also be divided into task-independent and task-dependent ones with regard to unloading performed during the ramp phase in the “movement” task and to the hold position phase in the “position control” task (test 3). Despite the fact that sEMGs and responses of separate MUs were examined at different levels of the external load, the quantitative ratio of unit types in the *BBcl* and *TBclat* was found to be in good agreement with sEMGs of these muscles. We found a significantly greater number of “zero” units and task-dependent units in the *TBclat* than the respective number in the *BBcl*. These data are in accordance with the report of Wilson et al. [28], who showed that the neuromodulators that produce persistent inward currents (PICs) in motoneurons of the muscles of the human upper limb influenced the excitability of extensor units of the *triceps* rather than flexor units of the *biceps*. Earlier, studies in the ventral laminae of the spinal cord of decerebrated cats showed that the PIC amounts are greater in the extensor pools of limb motoneurons than those in the flexor pools [29]. The greater excitatory effect of the neuromodulation systems on synaptic inputs to neurons of the limb extensors during quadrupedal locomotion in most mammals should be explained by the necessity to support the body weight against the action of gravity. However, because humans are characterized by bipedal locomotion, there are no prerequisites for the participation of the upper limbs in the maintenance of antigravity trunk support. We suppose that PICs are greater in this case; the excitability of extensor MUs is higher, their recruitment threshold to external loads decreases and is close to zero, and this allows the extensor units to easily participate in manipulation movements under conditions where the force vector of the *triceps* coincided with the direction of the gravity vector.

We conclude that the MUs we have examined respond in a different mode to force perturbations during the movement. This statement is confirmed by the existence of oppositely directed motoneuronal reactions during monotonous movements in the joint [5]. We also observed oppositely directed activity changes manifested by different units under conditions of application of a constant external load in the “movement” task. In this case, one part of the units decreased the firing rate during the ramp phase, while another part increased this parameter. The heterogeneity of the state of MUs controlling

the contracting muscle has been previously shown [30, 31] and discussed [12]. Oppositely directed reactions of the motoneurons during monotonous displacements of a limb link (in our case, the elbow) allow us to hypothesize that functions of these neurons are different to a significant extent. All motoneurons that were inhibited during the ramp phase in the “movement” task, including those inhibited in response to unloading, were also inhibited in response to unloading in the force task (position control). Considering this, we speculate that such motoneurons are mainly related to the force control in the movement task, while motoneurons that were not inhibited in response to unloading in this task are mainly associated with the control of the movement itself.

All subjects read and signed an informed consent form prior to participation in the study. The study was approved by the Ethics Committee of the Bogomolets Institute of Physiology and performed in accordance with the Helsinki Declaration of 1975.

The authors, A. V. Maznychenko, G. V. Dovgalets, I. V. Vereshchaka, T. Tomiak, V. S. Mishchenko, M. Dornowski, and A. N. Talnov, confirm the absence of any conflict in commercial or financial relations, relationships with organizations or persons that in any way could be related to the study, and also in interrelations of the co-authors.

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