

FIRING PATTERNS OF HUMAN *BICEPS BRACHII* MOTOR UNITS DURING ISOTORQUE RAMP-AND-HOLD MOVEMENTS IN THE ELBOW JOINT

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The activity of 18 motor units (MUs) of *m. biceps brachii* was studied in four adults during high-amplitude isotorque ramp-and-hold movements in the elbow joint. The recorded MUs had low isometric thresholds (below 6% of maximal voluntary contraction). During the examined movement, MUs of group I responded to application of subthreshold loads by increases in their firing rates, MUs of group II reacted to suprathreshold loads by decreases in the attained activity level, and background firing of MUs of group III at application of suprathreshold loads did not change. Dependences between the joint angle and firing rate, as well as between the velocities of these parameters, were positive in group I MUs and negative in those of group II. A decrease in the firing rate of MUs during flexion movements is likely to be related to nonlinear effects during the torque generation by the elbow flexors due to the specificity of geometrical arrangement of MU fibers with respect to the joint.

KEYWORDS: elbow flexors, isometric contractions, isotorque movements, motor control, motor units.

INTRODUCTION

The human CNS generates complex efferent commands to muscles even during execution of relatively simple single-joint movements. This complexity is better manifested at relatively fast movements usually produced by alternating excitations of antagonistic muscle groups [1-3]. Complex patterns of EMG activity are, however, also observed in agonist muscles producing slow ramp movements [4]. During slow ramp flexion in the elbow joint against a constant load, a surface EMG (sEMG) recorded from one or two elbow flexors usually demonstrates an angle-dependent exponential increase, while the activity of other agonist(s) can noticeably decrease within an intermediate range of the joint angles. Such a non-monotonic change in the EMG intensity could be mostly related to nonlinear angle-dependent changes in moment arms of the forces that are generated by elbow flexors [4, 5]. For the *biceps brachii*, the dependence of the moment arm on the joint angle has a bell-shaped form with an apex near 90 deg. In addition, the force developed by contracting flexors during flexion decreases in a nonlinear manner. These

two nonlinearities, of the angle-moment arm and angle-generated force, interact with each other. By applying a simple mechanical model, one may predict the non-monotonic changes in the torque generated by elbow flexors during flexion movements [5].

The MUs discharge rates in humans are commonly studied during voluntary isometric contractions rather than during real movements, mostly because of methodical difficulties in recording of MU firing during significant changes in the muscle length. The variability and fatigue-related modulation of the firing of MUs of the elbow flexors were described by Miller et al. [6] who also mentioned essential differences between the MU firings during movements and isometric contractions [7-9]. A detailed review of the studies comparing the MU firing in shortening and lengthening muscles has been recently presented by Duchateau and Enoka [10]. However, the activities related to movements in the elbow joint were predominantly studied at the amplitudes of these movements below 20-25 deg. Akazawa and Okuno [11] studied the activity of MUs in elbow flexors during large-scale isokinetic flexion movements; the authors demonstrated cessation of firing in the earlier activated MUs long before reaching the apexes of the movement trajectories. During isometric contractions, the activity of recruited MUs never stopped during the subsequent increase in the contraction force [1, 2, 10].

On our study, we analyze the origin of non-monotonic

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behavior of gross EMG activities of isotonically shortened muscles [4] in comparison with single MU activities. The experiments described were restricted to low-intensity contractions with torques that did not exceed 6% of the maximal voluntary contraction (MVC).

METHODS

Subjects. In this study, four healthy 23- to 34-year-old men without neuromuscular disorders participated in fourteen experiments.

Experimental Setup. Each subject sat in a comfortable chair, which was adjustable in height. His right forearm was fixed on a lightweight platform that rotated within a horizontal plane at a level such that the subject's shoulder could also move strictly horizontally. The forearm was placed on the platform in a palm-down position; an adjustable armband restrained the wrist at the platform thus reducing the activity of the palm and finger muscles during testing movements. The fixation of the subject's forearm excluded supination-pronation movements that could also influence the activity of the *m. biceps brachii* (BB). The rotation axis of the elbow was in coincidence with that of the platform; the subject's shoulder was placed horizontally within the frontal plane passing through the gle-

no-humeral joint and was supported from below by an additional immovable plate. The rotating platform was connected through a system of pulleys and steel cables to a servo-controlled linear motor. The system could function in two modes allowing command signals to control either the external torque or the rotation angle.

Surface and Intramuscular EMG Recordings (sEMG, iEMG). To record global muscle activity, pairs of EMG electrodes (Biopac System EL 503, USA) were placed on two heads of the BB, *caput breve* (BBcb) and *caput longum* (BBcl); the electrodes were separated by a 25-mm distance. Intramuscular EMG signals from the BB muscle were recorded using paired fine-wire electrodes inserted into the distal third of the BBcl; this part of the muscle occurred to be more suitable for long-lasting records of iEMG signals during high-amplitude movements. The electrodes consisted of two 25- μ m-diameter varnish-insulated Ni-Cr wires (A-M Systems Inc., USA) that were glued together and cut to expose only cross-sections of the wires. The electrodes were inserted into the muscle via a 25-gauge disposable hypodermic injection needle that was withdrawn after insertion, leaving the recording wires in place. This arrangement allowed us to reliably record impulsion of motor units with a minimal discomfort to the subject and provided stable recordings for up to three hours. Both sEMG and iEMG signals were recorded using a

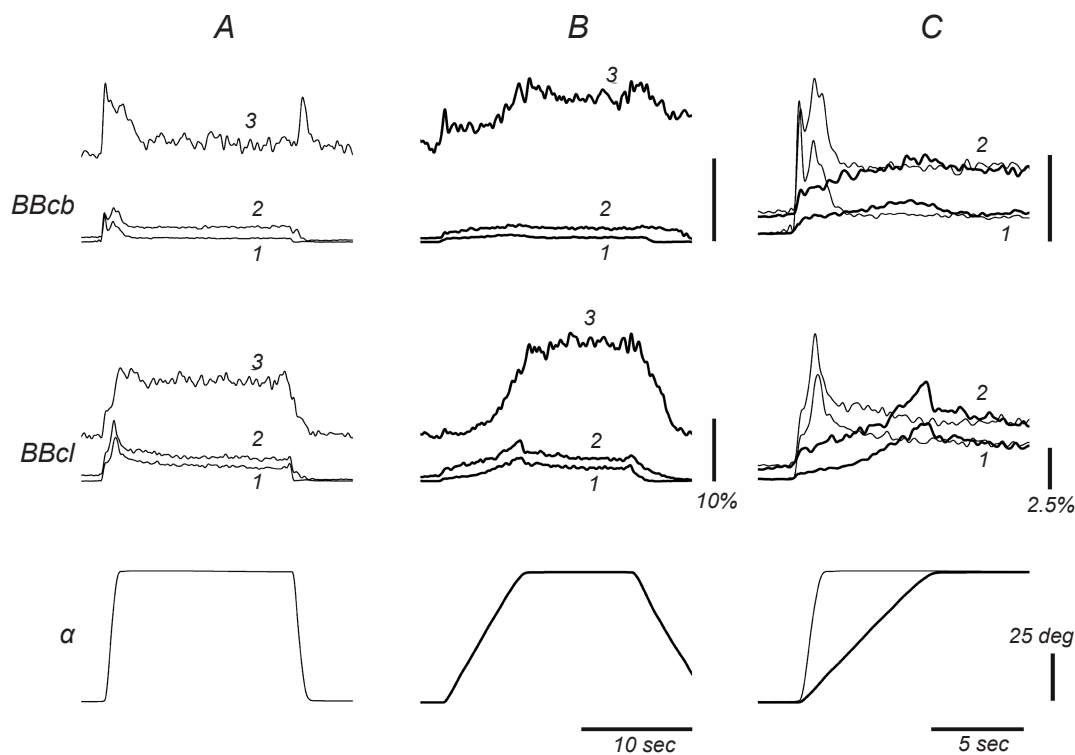


Fig. 1. Averaged sEMGs ($n = 10$) recorded from the BBcb and BBcl during ramp-and-hold flexion movements (changes in angle α) in the elbow joint. A, B) Superposition of the records for three different levels of the isotorque load (1, 2, 3) corresponding to 2, 4 and 12% MVC, respectively; parts of the records 1 and 2 are shown in an extended scale in C. Calibration of the sEMG is given in percentage of its intensity in MVC. Thin and thick lines are related to "fast" (velocity 70 deg/sec) and "slow" (10 deg/sec) test movements.

Рис. 1. Усреднені записи поверхневих ЕМГ, відведених від м'язів ВВсб та ВВкл під час трапецієдальних згинальних рухів (змін кута α) у ліктьовому суглобі.

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 sEMG and iEMG records together with the signals from the joint angle and torque sensors (filtering range, 0-500 Hz) were collected by a CED Power 1401 data acquisition system, using Spike 2 software (Cambridge Electronic Design, Great Britain); EMGs and sensor signals were digitized at 10^4 and 10^3 sec⁻¹, respectively. Origin 8.0 (OriginLab Corporation, USA) and SPSS 17.0 (IBM Business Analytics software, USA) were used for off-line data analysis. For evaluation of the central commands coming to the muscles, the identical test movements were repeated ten times, and sEMG records were averaged after their preliminary rectification (Fig. 1).

Experimental Procedure. At the beginning of each experiment, we defined the EMG levels in both heads of the *biceps* during an isometric MVC. The MVC was measured by an electronic dynamometer (LOT-S01, Wuyi Lot Electronics, China) at the joint angle 90 deg with respect to the completely extended position qualified as 0 deg. In the main part of the experimental procedure, the subject performed isotorque movements or produced isometric contractions under visual guidance. The subject observed two real-time traces on a monitor; one trace represented a target signal, while another displayed the signal from angle or torque sensors. The subject was

asked to move both traces together and thus either performed an isotorque movement (T1 mode) or produced a necessary isometric force (T2 mode).

The T1 movement programs began from the position of a fully extended elbow joint (0 deg), and the arm muscles were in a relaxed state between repeated tests for 30-40 sec. The linear motor created a constant torque, acting on the subject's forearm in the extending direction: due to a mechanical stopper that fixed the rotating platform, the torque was not applied to the joint between tests. Next, the stopper was removed, and a constant load acted on the subject's forearm during the subsequent test procedure. Flexion movements of a ramp-and-hold profile started 5 sec after the loading beginning. The experiments with force tracking in the T2 mode were performed using a fixed forearm position when the elbow joint angle was 90 deg; the subject generated a trapezoidal torque profile in accordance with the command signal on the monitor.

Motor unit discrimination was accomplished with a spike-sorting algorithm of Spike 2 (Cambridge Electronic Design, Great Britain). Single motor unit action potentials (APs) were identified based of their amplitude, duration, and waveform shape. During ramp contractions, each motor unit was analyzed on a spike-by-spike basis, and only units that could be clearly identified were included in the analysis; all records were supplied by superimposed traces of the identified spikes (Figs. 2; 3).

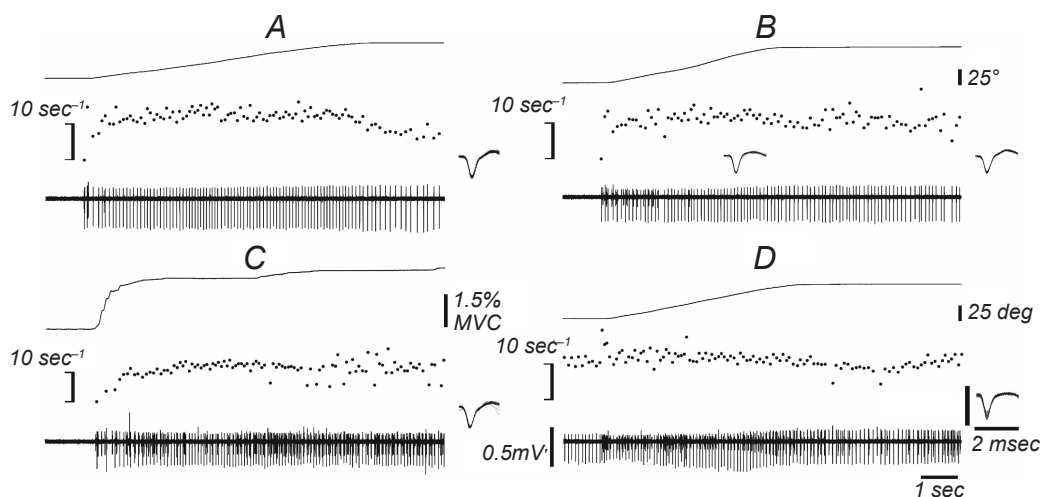


Fig. 2. Activity of a type-I MU recorded during flexion movements in the elbow joint (No. 1 in Table 1; mean isometric threshold for this unit was 1.9% MVC). A, B, and D) Isotorque movements with linear transitions between steady states at 10 and 70 deg of the joint angle and various durations of the movement phase; external torques were 0.8% (A and B) and 2.2% (D) MVC. C) Isometric flexion contraction at the 10 deg joint angle. In all panels, the lowest traces are iEMG records, middle traces are instantaneous firing rates, and upper traces are joint angle (A, B, and D) or torque (C) records. Superimpositions of all identified spikes for each record (waveform identification, Spike 2 software) are shown near the corresponding iEMG traces. Note changes in the MU activation patterns during similar movements produced under different external loads (B and D).

Р и с. 2. Активність м'язової одиниці типу 1, відведена протягом згинальних рухів у ліктьовому суглобі.

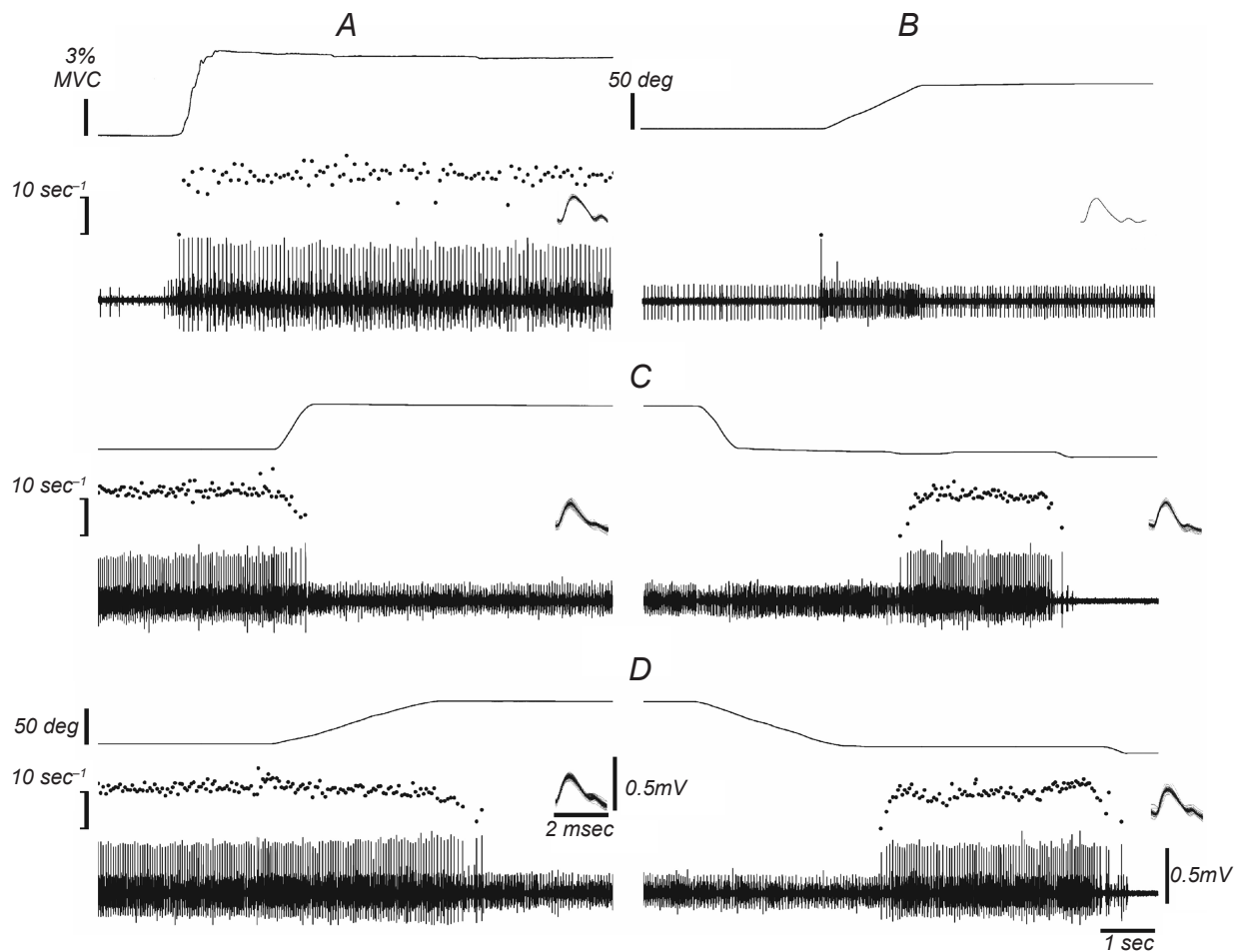


Fig. 3. Activity of a type-II MU recorded during flexion movements in the elbow joint (No. 9 in Table 1; mean isometric threshold for this unit was 3.7% MVC). A) Activity recorded during isometric muscle contraction at the 10 deg joint angle. B) Isotorque movement at a 1.7% MVC load. Note a single-spike response at the beginning of the movement. C and D) Two linear-transition isotorque movements between the 10 and 70 deg steady states; the movements were produced with different velocities for changing the joint angle; the loading level was 4% MVC. Designations are the same as in Fig. 1.

Р и с. 3. Активність м'язової одиниці типу 2, відведена протягом згинальних рухів у ліктьовому суглобі.

The motor unit recruitment thresholds (mean \pm s.d.) were measured in percentage of the MVC for ten-time repetitions of the isometric ramp contractions (T2 mode).

RESULTS

Relatively weak external loads that did not exceed 6.0% MVC were applied during recording of MU activity. In order to match our results with previous data related to surface EMGs in similar movements produced under more significant loads [4, 12], we compared the reactions in BBcb and BBcl muscles in identical movement tests for different levels of loading (Fig. 1). A subject produced standard ramp-and-hold flexion

movements in the elbow joint at two ramp velocities (70 and 10 deg/sec) and three loads (2, 4, and 12% MVC). During transition from "fast" to "slow" test movements, the dynamic EMG components clearly changed their shape, and their amplitude decreased. The steady-state EMG levels during the hold phase remained unvaried for loads 2 and 4% MVC (Fig. 1C) and raised for 12% MVC (traces 3 in B). During slow ramp movements under 12% MVC, the EMG intensity increased almost monotonically in the BBcl, whereas a fast initial rise of EMG intensity in the BBcb muscle was followed by a zone of relative steadiness, changing to a steep rise before the movement cessation. Earlier, when studying EMG activities in three elbow flexor muscles (with the addition of the *m. brachioradialis*)

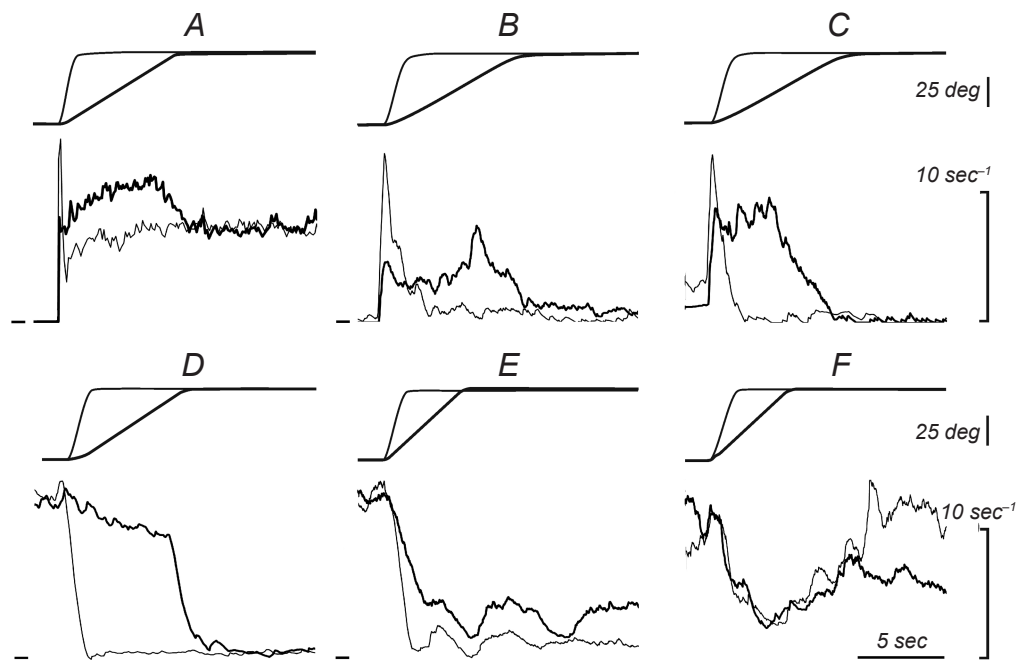


Fig. 4. Examples of averaged firing rates observed in six different MUs. A-F) Reactions recorded during fast and slow test movements (shown by thin and thick lines, respectively). All traces were obtained from ten time-averaged sliding mean frequency records (bin width 0.5 sec, Spike 2 software). A-C) Records from type-I MUs; reactions were recorded at external loads of 0.8 (A and B) and 1.2% (C) MVC; note the presence of obvious non-monotonic components in the MU reactions during slow movements. In all cases, the intensities of firing began to diminish before termination of the ramp phases. The MU in A is the same as in Fig. 1. D-F) Records from type-II MUs; initially, these units were activated by loading the elbow joint by 4 (D and E) and 5% (F) MVC. Note decreases in the firing rate of these MUs during flexion of the elbow joint. The MU in D is the same as in Fig. 2.

Рис. 4. Приклади усереднених частот розрядів, що спостерігалися в шести різних м'язових одиницях.

under similar conditions [4], similar clear-cut non-monotonic EMG components were observed usually in one of the agonists, while the activities in the two other ones raised mostly monotonically. The non-monotonic EMG components were also well observed in the BBcb reactions during movements produced under small loads (thin lines in upper panel C).

At a low extent of recruitment of different MUs under minimal loads, it was possible to identify reliably the activity of single units during high-amplitude movements (Figs. 2-4). All recorded MUs ($n = 18$) had low isometric thresholds for the appearance of steady firing (mean thresholds ranged from 0.44 to 6.29% MVC) and demonstrated quite similar reactions in the T2 mode when the subjects produced weak isometric contractions of the ramp-and-hold profile (compare Figs. 2C and 3A). The MUs were divided into three groups, groups I ($n = 7$) and II ($n = 4$), whose units discharged during test movements (these units are included in Table 1), and group III including non-responding units ($n = 6$). The main difference between MUs of groups I and II consisted in opposite directions of the firing rate changes during

the movement, a rise in the first case (Fig. 2), and a decrease in the second one (Fig. 3). At the same time, we would like to emphasize that the reactions of all MUs (groups I, II, and III) related to isometric contractions (T2 mode) were quite similar.

The MUs of group I responded well in the course of standard test movements (T1 mode) under weak loads (0.8-2.0% MVC) smaller than the corresponding discharge thresholds for isometric contractions (Fig. 2). Activation of these MUs usually preceded the movement beginning. The MU firings accompanying both ramp and hold phases of the tests are shown in Figs. 2 and 4A. Statistical analysis of firing of this unit is presented in Table 1, 1. For weak external torques (Figs. 2A, B), firing of this MU began with double or triple spikes generated at a high rate and was followed by a slow-rate increase during the movement. During slower test movements, the averaging procedure revealed a paradoxical increase in the discharge rate of this MU (Fig. 4A). Firing in this MU continued during angle fixation at the apex of the movement trace, although firing activity of other MUs could decrease, down to generation of sporadic spikes or even

Table 1. Statistical parameters of firing of the MUs of groups I and II during isometric tests and isotorque movements

Т а б л и ц я 1. Статистичні параметри розрядів м'язових одиниць груп 1 та 2, що спостерігалися протягом ізометричних тестів та рухів із постійним моментом навантаження

| ISOMETRY | | ISOTORQUE MOVEMENTS | | | | | |
|----------|-----------------------------|-------------------------|----------------------------|------------------------|----------------------|------------------------------|---------------------|
| No. MU | discharge threshold (% MVC) | external torque (% MVC) | $\frac{F_{PRE}}{F_{HOLD}}$ | F(a) linear regression | | $V_f(V_a)$ linear regression | |
| | | | | slope | ANOVA | slope | ANOVA |
| 1 | 1.90 ± 0.14 | 0.8 | – | 0.07 ± 0.01 | F = 87.19 | 0.15 ± 0.02 | F = 46.2 |
| | | | 10.3 ± 2.3 | r = 0.43 | P < 0.0001 | r = 0.81 | P < 0.001 |
| 2 | 1.61 ± 0.13 | 1.0 | – | 0.01 ± 0.02 | F = 0.61 | 0.12 ± 0.07 | F = 2.88 |
| | | | – | r = 0.02 | P = 0.80 | r = 0.49 | P = 0.11 |
| 3 | 1.92 ± 0.30 | 1.4 | – | 0.21 ± 0.08 | F = 6.50 | 0.09 ± 0.05 | F = 3.46 |
| | | | – | r = 0.15 | P < 0.01 | r = 0.34 | P = 0.07 |
| 4 | 0.44 ± 0.13 | 0.9 | sporadic 8.8 | 0.21 ± 0.07 | F = 7.71 | 0.13 ± 0.04 | F = 12.81 |
| | | | ± 1.1 | r = 0.15 | P < 0.01 | r = 0.53 | P < 0.005 |
| 5 | 0.56 ± 0.18 | 0.8 | sporadic | 0.02 ± 0.04 | F = 0.51 | 0.01 ± 0.03 | F = 0.17 |
| | | | sporadic | r = 0.14 | P = 0.70 | r = 0.07 | P = 0.68 |
| 6 | 0.64 ± 0.12 | 0.8 | sporadic | 0.04 ± 0.01 | F = 11.51 | 0.12 ± 0.05 | F = 7.19 |
| | | | sporadic | r = 0.14 | P < 0.001 | r = 0.39 | P < 0.01 |
| 7 | 1.42 ± 0.14 | 1.2 | – | 0.05 ± 0.07 | F = 0.75 | 0.07 ± 0.10 | F = 0.51 |
| | | | – | r = 0.05 | P = 0.42 | r = 0.14 | P = 0.48 |
| 8 | 2.29 ± 0.26 | 4.0 | 10.2 ± 1.4 | –0.2 ± 0.11 | F=3.11 | –2.49 ± 1.23 | F = 4.11 |
| | | | 8.8 ± 1.0 | r = –0.14 | P=0.08 | r = –0.52 | P = 0.07 |
| 9 | 3.70 ± 0.72 | 5.0 | 11.4 ± 1.0 | –0.47 ± 0.06 | F=59.19 | –1.99 ± 0.59 | F = 11.16 |
| | | | – | r = –0.36 | P < 0.0001 | r = –0.38 | P < 0.001 |
| 10 | 2.14 ± 0.26 | 4.0 | 12.2 ± 1.3 | –0.07 ± 0.00 | F=293.14 | –0.54 ± 0.01 | F = 27.71 |
| | | | sporadic | r = –0.56 | P < 0.0001 | r = –0.72 | P < 0.001 |
| 11 | 2.12 ± 0.31 | 4.0 | 10.1 ± 1.2 | –0.04 ± 0.01 | F=10.14 | –2.22 ± 0.54 | F = 10.12 |
| | | | sporadic | r = –0.21 | P < 0.01 | r = –0.46 | P < 0.01 |

Footnotes. The MUs of group I and II are separated by line; MUs Nos. 1-7 and Nos. 8-11 belong to group I and II, respectively. The discharge thresholds for all units were defined during the isometric tests; means ± s.d. are given as the statistical parameters. Linear regression analysis using one-way ANOVA was applied to define the F(a) and $V_f(V_a)$ dependences. For the first case, the instantaneous firing records were used (velocity range, 6–15 deg/sec); for the second one, the mean frequency records (velocity range, 6–55 deg/sec) were used. The separation between groups is described in the text; statistically significant correlations are highlighted by bold fonts. Irregular activities with mean rates below 6 sec⁻¹ are noted as sporadic.

complete silence (Fig. 4B, C). During slow movement tests, the firing rates could start to decrease before the movement finished, and this phenomenon was sometimes observed more clearly at higher loadings (Fig. 2D). Both the dynamic and steady-state firing components could vary between separate movement tests. The patterns of activity of various MUs were rather different. During suprathreshold loads evoking steady background activation of the type-I MUs, the dynamic firing components related to the ramp phase could include high-rate bursts followed by steady firing with an intensity close to the background activity level. Moreover, the firing rate might diminish

during the movement and after fixation of the joint angle (Fig. 2D).

During test movements, type-II MUs responded only to preliminary loading of the joint that evoked their steady background activation. The steady firing of the MU shown in Fig. 3 was evoked by a 4% MVC torque; the mean rate threshold for this unit was 2.14% MVC (MU 10 in Table 1). Under such loading, the firing rate of this MU decreased during flexion movements (Fig. 3C, D). Despite the presence of small dynamic increments in the firing rate at the very beginning of the movement, subsequent activity rapidly decreased. (Figs. 3C, D; 4D). For “fast” test movements, spiking

disappeared at the final joint position (Fig. 3C, right panel); for “slow” movements, decelerating firing was also observed after movement cessation (Fig. 3D, left panel). Inhibition of the discharge persisted in this MU even after returning of the limb link to the initial position (Fig. 3C and D, right panels). The duration of silent periods varied among different tests, and these periods were obviously longer after faster extension movements.

Comparison of the averaged firing rates for “fast” and “slow” test movements demonstrates additional differences in the behavior of MUs of groups I and II (Fig. 4). The dynamic components of reactions of the type-I MUs were more pronounced, and the rate increases at the start of the movement were clearly enhanced during faster-movement tests. During early stages of the movement, the group-II MUs showed weaker rate increments; the discharges consisted two or three spikes, and a change in the movement velocity almost did not influence these spike bursts. Linear regression analysis using one-way ANOVA was applied to define the $F(a)$ and $V_f(V_a)$ dependences for the MUs of groups I and II (Table 1). The signs of the slopes of the regression lines remained the same for all units in each given group; these were positive in group I and negative in group II. Statistical significance in one type of linear regression corresponded to a similar significance in the other type (see parameters highlighted by bold in Table 1).

We would like to emphasize that the above-proposed classification of the recorded MUs into three groups is inevitably artificial, it cannot represent a real spectrum of the MU activities during real movements. However, it can be concluded that differences between the reactions of various MUs during movements are much more pronounced, as compared with their responses during isometric contractions. Some MUs did not participate in the movement at all (group III); a part of them could paradoxically decrease their activity during active muscle shortening (group II). Even those MUs that are directly involved in the execution of the movements (group I) can often demonstrate unstable patterns of firing during repetitions of identical movement programs.

DISCUSSION

The above-described experiments were designed to analyze activation patterns of single BB MUs during high-amplitude movements in the elbow joint. Tax et

al. [7], Ivanova et al. [8], and van Bolhuis et al. [9] analyzed the differences in MU activities related to isometric contractions and isotonic movements; in their tests, a small range of movements with rather high angular velocities was tested. Actively contracting muscles are activated much more intensely during movements than in the course of isometric contractions [9, 13]. General information about elbow flexor activation in isotorque and isometric modes can be derived from sEMG recordings related to multiple repetitions of identical movement programs. The comparison of MU discharges related to ramp-and-hold isotorque movements with those at isometric muscle contractions of a similar time profile demonstrated the following. Powerful dynamic EMG components do exist in the first case and are insignificant in the second one [4, 14]. At least partly, such differences might be related to stronger manifestation of hysteresis-dependent suppression of the muscle contractile efficiency during real muscle shortenings than during isometric contractions; in the latter, the constituent myofilaments shorten to a smaller extent [5]. To overcome the hysteresis-related depression effects in muscles during isotonic movements, the CNS must generate noticeable dynamic components in efferent commands coming to the muscles. Real movements with changes in the joint angle could be provided by much more complex central commands including a variety of co-activation and/or reciprocal activation patterns in antagonistic muscle groups [10, 15].

At rather small external loads used in our study, a significant proportion of MUs either does not respond at all or generates only single spikes at the beginning of the movement. We did not observe close correlation between the sEMG patterns [4] and activities of single MUs. The firing intensities in various MUs could either increase or decrease during flexion movements. Moreover, many units ceased firing after the joint angle had been fixed. Some of the MUs (group III) responded only during test movements when the joint was loaded by an above-threshold external torque. In contrast, these units did not fire at all at lower loadings. The MUs activated during the movement at loads below their isometric thresholds (group I) demonstrated predominantly small rate increases; in addition, their firing rates often dropped before movement termination. Even after the averaging procedure, the activation patterns of MUs were essentially more variable than quite stable sEMG records [4, 12]. This difference could be considered an indicator of the activity rearrangement between

various MUs within the same movement programs.

Our data agree with the results of Akazawa and Okuno [11] who showed constant MU firing rates over a wide range of the elbow angles. Furthermore, our data demonstrate a wide variability of the MU reactions, some of which decreased their firing during elbow flexion. Moreover, even in the MUs with obvious initial rate increases, the subsequent movement could lead to rate decreases long before the movement ended, and many MUs were either silent or discharged irregularly at the apexes of the movement.

Significant decreases in the firing intensity in many MUs or even cessation of their activity within an intermediate range of the joint angle changes can be related to the nonlinear dependence of the flexor moment arm on the joint angle [4, 5, 11]. One can hypothesize that the behavior of MUs of the elbow extensors during extension movements will be quite different because of dissimilarity of the respective sEMG patterns and those of the elbow flexors [12]. The differences in the efferent commands sent to the muscles under isotonic and isometric conditions [16] could be mainly related to strong movement-dependent modification of the muscle dynamics. An active muscle generates stronger efforts during eccentric (lengthening) contractions and weaker ones during concentric (shortening) movements [5]. Minimal efferent firings are observed during stretches of the active muscle by an overwhelming external force; in contrast, maximal activity is required for the actively shortening muscles. Isometric states may occupy an intermediate position in this scheme. In this case, it is necessary to take into account the activation prehistory that directly determines internal movements of the constituent muscle fibers [5, 15].

In conclusion, we would like to emphasize that the activity patterns of the elbow flexor MUs during high-amplitude flexion movements are probably determined, to a considerable extent, by the bell-shaped dependence of the moment arm on the joint angle. This dependence corresponds to previously described angle-dependent local decreases in the sEMG intensities [4, 12]. The position-dependent increase in the flexor efficiency for torque generation leads to the cessation of firing in some MUs along with a decrease in the rate at which these units maintain their activity. For reciprocating movements, firing of MUs can terminate within the flexion phase, and the silence period is continued during the subsequent extension movement. In contrast, the beginning and cessation of firing in MUs correspond to approximately equal

torque levels during similar isometric contractions [1, 2].

All subjects involved in the tests provided informed consent, and the study was approved by the Institutional Review Board at the Bogomolets Institute of Physiology. The experimental procedures were also in accordance with the standards of the Committee on Human Experimentation of the Institution in which the experiments were performed and in accordance with the Helsinki Declaration of 1975.

The authors, A. N. Tal'nov, T. Tomiak, A. V. Maznychenko, G. V. Dovgalets, and A. I. Kostyukov, confirm that they have no conflict of interests.

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АКТИВНІСТЬ РУХОВИХ ОДИНИЦЬ ДВОГОЛОВОГО М'ЯЗА ПЛЕЧА ЛЮДИНИ В РУХАХ ТРАПЕЦІЄПОДІБНОЇ ФОРМИ В ЛІКТЬОВОМУ СУГЛОБІ ПРИ ПОСТІЙНОМУ МОМЕНТІ ЗОВНІШНЬОГО НАВАНТАЖЕННЯ

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Резюме

Досліджували активність 18 рухових одиниць (РО) *m. biceps brachii* у чотирьох дорослих чоловіків під час високоамплітудних згинальних і розгинальних рухів (по трапецієподібній траєкторії) у ліктьовому суглобі. Під час ізометричних зусиль зареєстровані РО мали низькі пороги активації (менше 6 % сили максимального довільного скорочення м'язів). Впродовж руху РО групи I реагували на підпорогові навантаження, збільшуючи частоту активності, а РО групи II реагували на надпорогові навантаження зменшенням досягнутого рівня активності. Фонова активність у РО групи III при прикладанні надпорогових навантажень не змінювалась. Залежності як між суглобним кутом і частотою активності РО, так і між відповідними швидкісними параметрами були позитивними в групі I та негативними в групі II. Зменшення частоти імпульсації РО в перебігу згинальних рухів, ймовірно, пов'язано з нелінійною зміною моменту сили згиначів ліктя, зумовленої геометричним розташуванням цих м'язів.

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