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EMG Patterns of the Elbow- and Shoulder-Operating Muscles in Slow Parafrontal Upper Limb Movements under Isotonic Loading

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Averaged EMGs were recorded from the elbow- and shoulder-operating muscles in 10 adult men during parafrontal slow test movements of the hand performed within the horizontal plane. The movements between the left and right end-point positions were carried out with a constant 4 cm/sec velocity in both directions consequently; two identical isotonic loads (10.2 N) were applied to the hand along the rightward and leftward movement traces (F_r and F_l) with respect to the subject's body. The elbow and shoulder flexors demonstrated a synergic unification, reacting predominantly to the F_r loads; a similar synergy was manifested by the extensors of both joints in their reactions to the F_l loads. Under the action of the corresponding loads, EMGs of both flexor and extensor muscle groups showed strong hysteresis (counterclockwise and clockwise loops, respectively). The muscles acting as agonists for a given direction of loading (flexors for the F_r loads, extensors for the F_l loads) participated also in a co-contraction mode as antagonists in the movements fulfilled under oppositely directed loads; the direction of hysteresis loops was reversed in this case, and their amplitude decreased. The obtained results allow us to conclude that hysteresis properties of muscle contraction and the related characteristics of signal transmission in the motor control system lead to strong hysteresis-associated modifications of central commands coming to the muscles in various movement tasks.

Keywords: motor control, upper limb, muscles, electromyography, two-joint movements, joint torques

INTRODUCTION

Registration of the parameters of slow movements of the upper or lower limbs and parallel EMG analysis are ordinarily used to find the relationships between the movement *per se* and central commands providing its performance in humans. Such an approach becomes especially effective when test movements can be repeated many times and then averaged. Recently, slow repetitive movements of the hand with a fixed wrist have been studied during the action of elastic loads acting tangentially with respect to the movement trajectory [1]. Such an experimental approach allowed us to define the torques acting around the shoulder and elbow joints, basing on the load value and lengths of the upper limb segments. The above-cited study demonstrated the existence of a strict correspondence between the shoulder and elbow joint torques (JTs) and EMGs recorded by surface electrodes from the shoulder- and elbow-controlling muscles. During a complete movement period, each of the torques includes two components, positive and negative, which correspond to the activities of flexor and extensor muscles, respectively. Timings and relative durations of both torque and EMG waves for different joints are dissimilar. Analytical methods for computation of the torque waves have been proposed in theoretical studies of our group [2, 3]. Additionally, a geometrical method was developed to define points of the movement trajectory where JTs change their signs [4]. To distinguish various combinations of activity of the flexors and extensors acting upon different joints, we proposed to separate movement traces into phases

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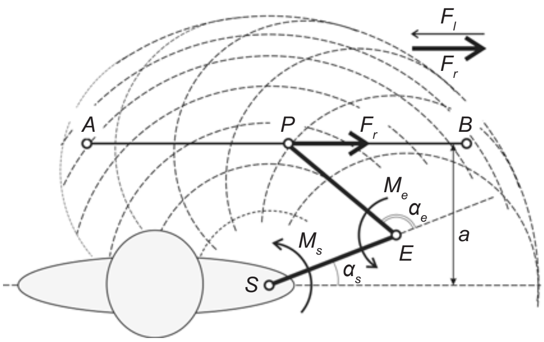
with two different types of synergy, the coinciding and opposing ones, which describe activation of the muscles of the same (flexor-flexor, extensor-extensor) or opposing (flexor-extensor, extensor-flexor) functionality in different joints, respectively [1, 2, 5]. A similar procedure allowing one to identify the interrelationships between the JTs and EMGs has been extrapolated on the conditions of nearly isometric muscle contractions [6, 7], when a subject should slowly change the direction of the end-point force. For circular turnings of the force vector, changes in the shoulder and elbow JTs demonstrated sinusoidal patterns and equal durations of the positive and negative components.

In this our study, we analyze averaged EMGs of the elbow- and shoulder-operating muscles in the course of performance of slow linear parafrontal movements under the action of loads, whose direction coincides with or is opposite with respect to the movement direction. A specially developed experimental setup allowed us to compare EMG activity of the muscles in four possible combinations of directions of the load and the movement. Such an approach was found to be especially effective for the analysis of hysteresis-associated variations of the central commands related to an important class of linear isotonic movements.



F i g. 1. General scheme of the experimental setup. *A* and *B*, points restricting the test movement; *S* and *E*, positions of the axes of the shoulder and elbow joints; *P*, point of application of the external force to the hand; *F*, externally applied force; thick and thin arrows indicate forces of rightward/leftward directions. Later on, EMGs and joint torques will be indicated in a similar way (by the line thickness in accordance with the external force direction; see Fig. 2); α_s, and α_e are the shoulder and elbow joint angles; *a* is the distance of the movement trace from the shoulder joint; M_s and M_e are the joint torques, which the subject must create to produce the test movement. More detailed description is given in the text.

METHODS

Ten adult young volunteer men (23 to 28 years old) without neurological or musculoskeletal diseases participated in the tests. The tested subject sat before a table, the upper plane of which was at a 5- to 8-cm level below his shoulder joint (Fig. 1), and gripped a handle placed at the moving carriage by his right hand. The vertical position of the shoulder joint was adjusted using a special chair with an adjustable seat height. The upper limb of the subject was suspended at the level of the elbow joint by a special cable loop hanged to the room ceiling. The carriage was based on a system of ball bearings; it could easily move over the table strictly along the line; the path trajectory was restricted using two aluminum rails installed at both sides of the carriage. The test movements were realized along a parafrontal line *AB* situated at a distance a = 0.37 m from the frontal plane passing via the shoulder joint (Fig. 1). Points *A* and *B* were placed at distances of 0.4 and 0.44 m, respectively, from the projection of the shoulder joint axis *S* on the movement trace.

A standard test corresponded to a slow steady movement from *A* to *B*, a 3-sec-long stay in *B*, and a similar returning movement from *B* to *A*; the movement velocity was 4 cm/sec. The test was repeated 10 times with the load F_r acting in the *A*–*B* direction. Then the direction of the load changed to the opposite one (F_l), and the test was again repeated 10 times. A precise potentiometric sensor served for exact estimation of the position of the subject's hand (*P* in Fig. 1) during the test movement; the subject also used this signal for visual tracking of the command signal on the monitor screen. External loads were created in either *A*–*B* or *B*–*A* directions using the weights (10.2 N, i.e., 1 kg force), which created the horizontally directed forces F_r or F_l, respectively. The forces were applied to the carriage along the movement trace via a system of cables and pulleys.

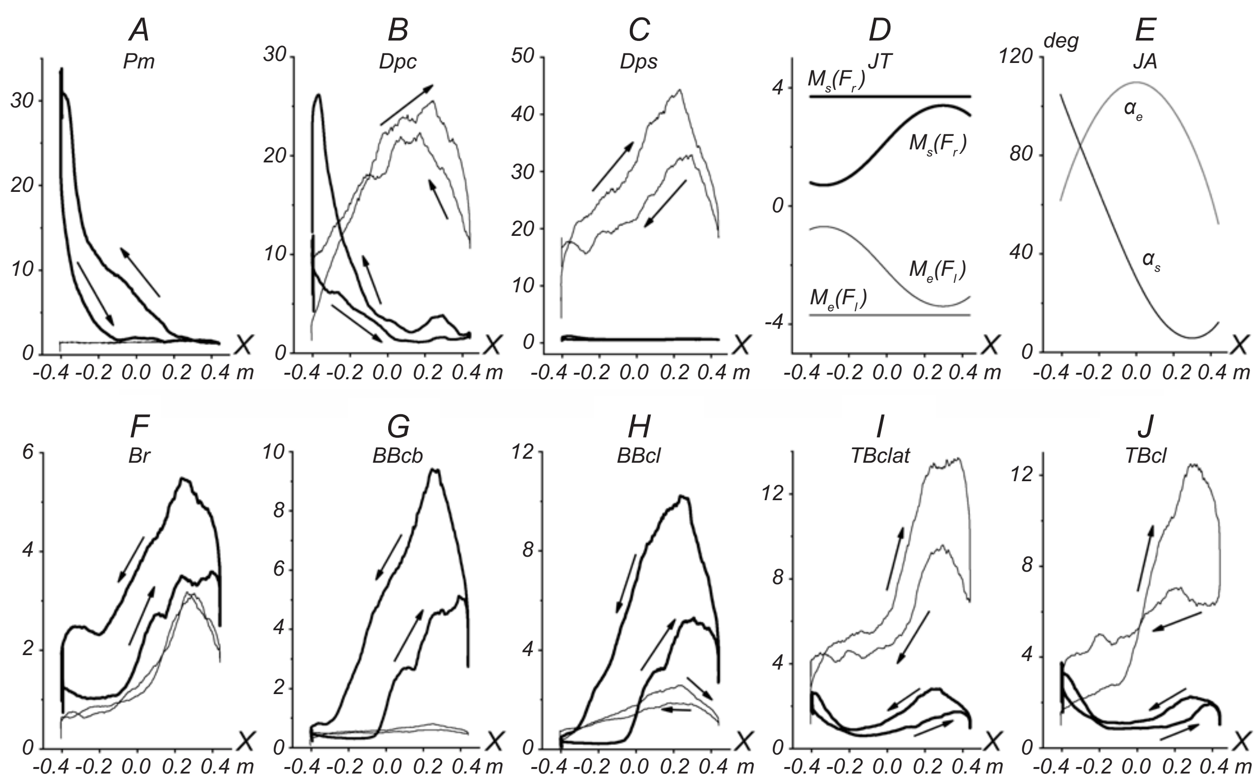
In the tests, two computers were used. One of them was used for recording the reference trajectory of the movement displaying it in real time by a light marker on the monitor screen; another marker corresponded to the target end-point position, thus showing the necessary trajectory of movement to the subject. The movement task was to provide the most strict correspondence of the positions of the above two markers. The second computer was used for displaying the position signal and EMGs recorded from eight muscles operating the subject's upper limb, namely *mm. brachioradialis (Br), biceps brachii cap. breve(BBcb), biceps brachii cap. longum (BBcl), triceps brachii cap. laterale (TBclat), triceps brachii cap. longum (TBcl), pectoralis major (Pm), deltoideus pars scapularis (Dps),* and *deltoideus pars clavicularis (Dpc)*.The EMGs were recorded by surface bipolar electrodes, Skintact F-301 (Austria); the interelectrode distance was 2.0 cm. The bandpass of the amplifiers corresponded to 0.1 to 1000 Hz range; the recorded signals were digitized and registered using PCI 6071E and 6023E ADCs (National Instruments, USA; sampling rate $2 \cdot 10^3$ sec^{-1}). The software for signal recording was based on LabView 6 and 7 software packages (National Instruments, USA). The EMG signals were subjected off-line to (i) high-pass filtering (a fourth-order Butterworth filter with a 20 Hz cutoff frequency), (ii) full-wave rectification, and (iii) low-pass filtering (a fourth-order Butterworth filter with a 5 Hz cutoff frequency). Then, EMG signals were normalized with respect to the EMG maximum voluntary contraction (MVC) levels of the corresponding muscles taken at 100%. Offline computations and graphical plotting were performed using Origin 8.5 software (OriginLab Corporation, USA). For better visualization of changes in the EMG intensities, averaged EMGs were additionally smoothed using a sliding averaging procedure with a 200-point window. Previously developed methods of analysis of the two-joint movements [3, 8] were applied; in all movement tests, we also defined current changes in the biomechanical parameters, namely the JTs acting around the shoulder and elbow joints (M_s, and M_e) and the corresponding joint angles (JAs, α_s, and α_e).

RESULTS

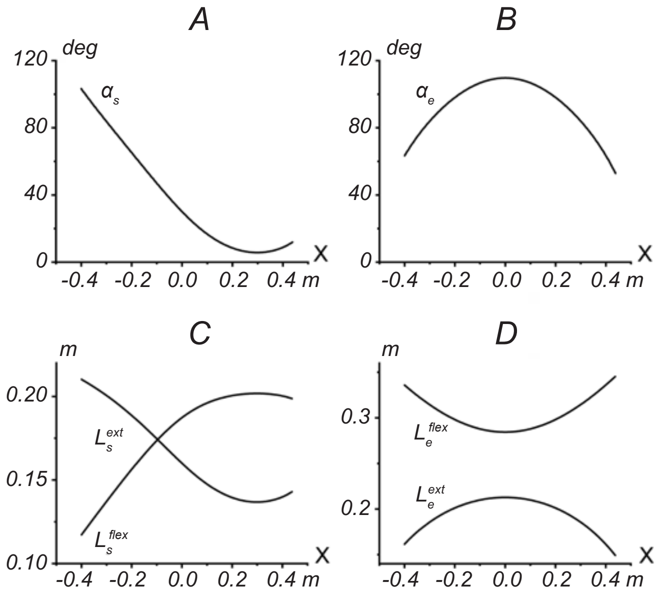
Considering the reciprocating pattern of the test movements (*A–B–A*) and their execution under consecutive applications of two oppositely directed external loads (F_r and F_l), we had the opportunity to analyze all possible combinations of the load and movement directions (Fig. 2). Both shoulder (Fig. 2A–C) and elbow (Fig. 2F–J) flexors demonstrated predominant activation under the F_r action. Under these conditions, extensors were either completely passive or showed slight coactivation. On the contrary, in the case of F_l forces, mostly extensors were activated, while flexors were predominantly inactive. Between the examined shoulder muscles, the *Pm* (flexor) and *Dps* (extensor) showed the clearest respective specificity, while the *Dpc* demonstrated a "mixed" activity pattern. The latter peculiarity might be related to the complex nature of this muscle that participates in providing both flexion and extension of the shoulder. In a group of the studied elbow flexors, the *Br* activities were less predictable; both amplitudes and current changes in its EMGs during the F_r action in different subjects were variable. On the other hand, coactivation of this muscle during the F_l action was more expressed compared with the respective activity of both *biceps* heads. Different parts of the *biceps* demonstrated quite similar EMG activities, despite the fact that one part of this muscle, the *BBcl*, operates exclusively at the elbow joint, while another one, the *BBcb*, is a two-joint muscle; it participates at least partly in the movements around the shoulder joint. Similarly to the shoulder extensors, the elbow ones (*TBclat* and *TBcl*) demonstrated predominant activation during the action of the F_l force (Fig. 2I-J). Their coactivation with the flexors was, however, also noticeable at an opposite force direction, F_r (thick lines in the same panels).

One can see that all EMGs recorded from the muscles activated by application of a force of the given direction demonstrated clearly expressed hysteresis. It was typical of both flexors in the case of the F_r or of extensors when the force acted in an opposite direction (F_l). It is interesting that hysteresis loops in the flexors of both joints had an anticlockwise direction with respect to the end-point position (X), while those of the extensors were directed in a clockwise manner.

It seems to be clear that the hysteresis patterns manifested in central commands coming to the joint muscles (under conditions of our tests, EMG magnitudes are correlates of these commands) are first of all dependent on the direction of end-point forces; at the same time, these commands were essentially modified by the direction of changes in the muscle lengths. Purely qualitatively, a combination of the force and length changes might be evaluated by positional dependences of the JTs (Fig. 2D) and JAs (Fig. 2E). Methods for computation of these parameters were described in our previous communications [3, 8]. Because of the insufficiency of the respective anatomical information, we did not search in detail for both specifications of the force generation processes and precise changes in the muscle lengths and velocities of these indices. However, a simplified geometrical model for the shoulder- and elbow-operating muscles (Fig. 3) can provide us with information on the movement direction within different segments of the test traces. The constant value of the shoulder JTs shows that these shoulder muscles work in fact under purely isotonic conditions. Significant values of changes in EMGs of both shoulder flexors and extensors (Fig. 2A–C) are probably related to substantial length changes in these muscles, as can be concluded when analyzing the respective JAs (Fig. 2E). A strong decrease in the angle at the beginning of the test movement was accompanied with the respectively increased length of the shoulder flexors (L_s^{flex} in Fig. 3C). According to classic statements of neuromuscular physiology, an isotonically lengthening muscle generates a greater force compared to that in isometric contractions; the latter force is in turn greater than that in a shortening movement. Therefore, within this phase of the movement, the shoulder muscles might be less active, which corresponds to a rapid decrease of their EMG intensities (Fig. 2A). Moreover, the drop in activation of these muscles is so rapid that their EMGs completely disappeared; this fact correlates with a more noticeable involvement of the elbow flexors in force generation (Fig. 2F–H, lower branches of the hysteresis loops). Within the phase of a reverse movement (*B–A*), the pattern of activation of the shoulder flexors was opposite. In proximity to point *B*, the muscles were maximally lengthened, and then they began to actively shorten, which inevitably required their additional activation. As a result, the EMG intensities during the reverse phase of the movement were rising much higher than the respective parts of the curves belonging to the direct phase. Therefore, if we consider a complete cycle of the test movements (*A–B–A*), we notice that changes in the intensity of EMG activity looked like counterclockwise hysteresis loops.



F i g. 2. Averaged EMGs recorded from the muscles operating the shoulder (A–C) and elbow (F–J) joints during six repetitions of the standard test movements with right- and leftward external loads (F_l and F_r, as shown in Fig. 1) and the respective biomechanical characteristics. Panels D and E illustrate results of theoretical computation of the joint torques acting around the shoulder and elbow joints (JTs, M_s and M_e) and corresponding joint angles (JAs, α_s and α_s). Abscissa in all plots defines the positioning along the movement trace, m; a zero point corresponds to the projection of the right shoulder joint axis on the movement trace. The EMGs (A–C and F–G) and computed torque traces (D) are shown by thick and thin lines for F_r and F_l loads, respectively. Arrows on the recorded EMG loops signify their circumvention directions within the framework of a standard pattern of the movement: *A–B–A*) Values of the ordinates; EMGs are measured in % of those observed at MVC; JTs are indicated in Nm, and JAs, in degs.



F i g. 3. Trajectories of the joint angle changes (A and B, deg) and the modeled lengths of the shoulder (C) and elbow (B) flexors and extensors (m; for the simplicity, only single-joint heads of the muscles are considered). Computation of the joint angles based on the well-calibrated position signal (X, m) in the experimental setup is sufficiently accurate, while estimations of shoulder and forearm muscle lengths L (C and D) are only approximative because of a lack of basic anatomical parameters necessary for modeling. Nonetheless, graphs C and D create a correct impression on the directions of the movement within different segments of the test traces.

The patterns of length changes in the shoulder extensors were opposite those in the flexors (L_s^{ext} in Fig. 3C). Within the direct movement phase (*A–B*), these muscles were shortened, while they were lengthened within the reverse phase (in *B–A*), which corresponds to clockwise hysteresis of the EMG intensity changes with respect to the position coordinate (Fig. 2C). It is interesting that activity of the *Dpc* demonstrated the presence of two hysteresis loops of almost equal amplitude for both forces (F_r, and F_l); moreover, the directions of the loops coincided with their usual directions in the flexors and extensors. This fact may be indicative of the mixed nature of the given muscle, with the presence of independent, both flexing and extending, compartments (Fig. 2B).

The dynamics of the movement in the elbow joint are somewhat more complicated than those described above; this is due to the fact that both lengths of the muscles and forces acting on them are changing during the test movement. This is not the case for the shoulder muscles, for which actions of the external forces are invariable within the entire movement (compare curves M_s and M_e in Fig. 2D). Instead of pure isotonic movements, which are described above for the case of the shoulder flexors, the length of the elbow flexors increases under the action of background wave-like changes in the external force. Such lengthening is to a lesser extent dependent on efferent activation; therefore, EMGs of all flexors within the initial phase of movement (*A–B*) show an evident slowdown (Fig. 2F–H). One can notice that transition to lengthening of the elbow flexors (after the achievement of an apex by the α_e curve) leads to dome decreases in the increments of their EMGs (Fig. 2E, 3D). The beginning of the return movement from point B was accompanied by a fast active shortening of the elbow flexors; these muscles began to produce work against the external load. This requires a quick rise in the muscle activity (and, naturally, in the EMG intensity). Then, the EMGs attained extremal values, which was followed by clear drops despite the continuation of muscle shortening that proceed up to an about zero position. This drop in the activation intensity might be related to a noticeable decrease in the elbow torque values (Fig. 2D). Then, the elbow flexors began to lengthen; however, averaged EMG records continued to be significantly greater than the corresponding values achieved within the first phase (*A–B*) of the movement. One can assume that such an increment is manifested due to the presence of the same kind of after-effects in the action of central commands.

Similarly to the muscles of the shoulder joint, the elbow extensors are more subjected, in general, to the action of the F_l forces. In this case, both examined heads of the *triceps* demonstrated opposite directions of the position–EMG hysteresis loops, as compared with those of the elbow flexors under the action of F_r forces. On the other hand, the hysteresis effects were well noticeable in co-contraction activation of these muscle heads in response to the F_r loads (EMGs marked by thick lines in Fig. 2I-J). It seems important that hysteresis loops changed their direction to the opposite one in the coactivation patterns (when the antagonists are predominantly activated); thus, in this case, the hysteresis direction coincided with that of the antagonists.

Statistical analysis of EMG parameters in the studied group of ten subjects (Fig. 4) showed that the type of EMG patterns described above for one of the subjects is rather typical. For comparison of the EMG intensities in various muscles, we calculated the average levels of EMGs (defined in % MVC) by the following expression using an algorithm of numerical integration:

$$\overline{E}_i = \frac{1}{T} \cdot \int_0^T E_i(t)dt, \tag{1}$$

where E is the current EMG intensity (in % MVC) in the ith muscle, and T is the total duration of the test including both phases of the movement (*A–B* and *B–A*).

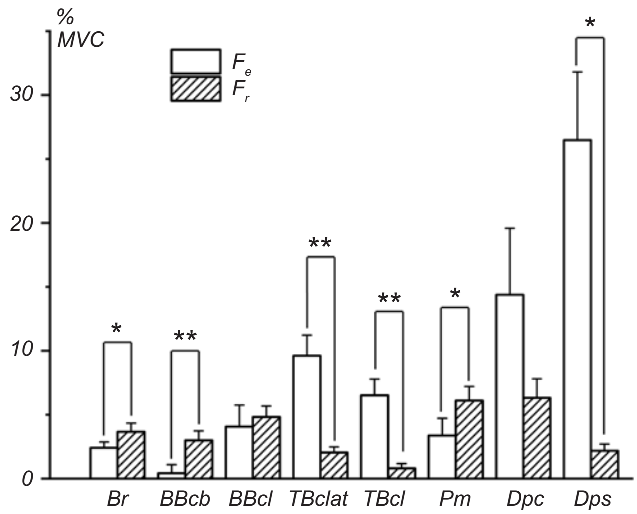
These differences were expressed better in the flexors of both joints when the external force was directed rightward, i.e., at F_r (dashed columns for the *Br, BBcb, BBcl,* and *Pm* in Fig. 4), while the extensors were more active during the action of leftward loads, F_l (open columns for the *TBclat, TBcl,* and *Dps*). Despite significant amplitudes of *Dpc* EMGs, their differences related to opposite directions of the load were statistically insignificant. This fact might be explained by the complex composition of this muscle, with the presence of both flexor and extensor compartments in its structure. The absence of a significant difference between EMGs of the *BBcl* muscle at opposite loads could be related to a high level of individual variability of the pattern of activation of this muscle.

The following expression can be used to define the normalized integral values (areas) of the hysteresis loops at EMG records:

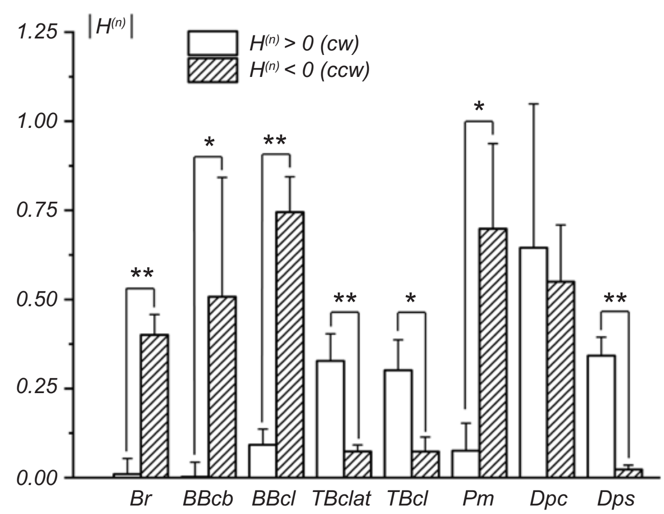
$$H_i^{(n)} = \frac{\int_{X_A}^{X_B} E_i(X)dX - \int_{X_B}^{X_A} E_i(X)dX}{(X_B - X_A)\overline{E}_i}; \tag{2}$$

where the integrals define the areas under EMG records within the first (A–B) and second (B–A) phases of the test movement, while E is defined by Eq. (1).

One can see that the parameter defined by Eq. (2) is equal to zero in the absence of hysteresis; it is negative for the counterclockwise hysteresis loops and positive for the clockwise ones. Statistical characteristics of the parameter were compared for situations with the action of F_r and F_l loads in the group of all ten tested subjects; the paired t-test was used to evaluate the statistical significance of differences between the corresponding values (Fig. 5). One can notice the clear prevalence of negative values of the analyzed parameter in EMGs of the flexor muscles operating both joints during the action of the F_r forces (counterclockwise loops). At the same time, the extensors demonstrated positivity of the parameter (the clockwise loops; predominance of the reactions under the action of F_l forces). It seems important that our study demonstrated a quite interesting reversal in the direction of hysteresis loops observed after transition from a predominant force (F_r in flexors and F_l in extensors) to an opposite one (F_l in flexors and F_r in extensors).



F i g. 4. Diagram of the mean EMG magnitudes (% of those at MVC) generated by muscles in the test movements during the action of loads F_r, and F_l. Data for the entire group (ten subjects) and 10 test movements for each of the loads. Asterisks designate cases where the difference between EMG levels for different loads (F_r and F_l) was statistically significant (paired t-test, $*P < 0.05$, $**P < 0.01$).



F i g. 5. Diagram of absolute values of the normalized areas of the EMG intensity-position hysteresis loops registered during the test movements in the examined group (ten subjects). The parameter was defined by Eq. (2) for responses recorded during the action of F_r (dashed columns) and F_l (open columns) loads (paired t-test; $*P < 0.05$, $**P < 0.01$). Note the prevalence of negative values of the parameter in the activity of the flexor muscles at both joints (counterclockwise loops, F_r loads); on the contrary, the extensors demonstrated the prevalence of positivity of the parameter (clockwise loops; F_l loads).

If we neglect the activities of the "mixed" *Dpc* muscle, we see that the opposite character of events was more pronounced in the flexors (*BBcl* and *Pm*) and extensors (*TBclat*, *TBcl*, and *Dps*) (Fig. 5). On the other hand, such a hysteresis reversal can be easily explained by an assistance function of the antagonists with respect to their agonists, which are the main "performers" in a given movement task. The antagonists generate co-contraction forces that "reflect" the patterns of agonist contractions.

DISCUSSION

Our communication describes results of further analysis of the control of two-joint upper limb movements, which was begun in our previous studies [1, 2, 5–7]. In this investigation, we considered the parafrontal end-point movements of the upper limb within the horizontal plane and compared the EMGs recorded from the shoulder- and elbow-operating muscles during consecutive application of the opposite external loads to the subject's hand directed along the movement trajectory. Such movement tests allowed us to consider simultaneous actions of changes in the JTs and JAs and to analyze the hysteresis effects in the formation of central commands accompanying execution of this kind of upper limb movements.

The averaged integrated EMG records in our study served to evaluate central commands coming to the muscles; the respective EMG traces changed depending on the load and movement directions. It was found to be useful to consider muscle actions within an entire cycle of the movement, including its direct (*A–B*) and reverse (*B–A*) phases (Fig. 1), and to compare these actions during application of the right- and leftward loads (F_r and F_l). In the position – EMG intensity coordinates, well-expressed hysteresis loops were observed; the amplitudes and directions of the loops appeared to be strongly dependent on the load direction. The elbow and shoulder flexors demonstrated a synergic unification, predominantly at the F_r loads; a similar synergy was manifested by the extensors of both joints in their reactions to the F_l loads. Under the action of the corresponding loads, the EMGs of the above muscles demonstrated strong hysteresis dependences on the end-point position; the direction of the respective hysteresis loops depended on the functional modality of the muscles, being counterclockwise in the flexors and clockwise in the extensors of both joints. The muscles acting as agonists for a given direction of loading (flexors for F_r loads and extensors for F_l loads) were also involved in a co-contraction mode at the action of oppositely directed loads; the directions of the hysteresis loops demonstrated reversion in this case.

Earlier, we have proposed a classification of the force synergies in accordance with the functional modality of the muscles acting on different joints, which were activated simultaneously [4]. The coinciding synergy corresponds to simultaneous activation of the muscles of the same functional modality at both joints (flexors-flexors; extensors-extensors); in the case of opposing synergy, simultaneous activation develops in muscles of the opposite modality (flexors-extensors; extensors-flexors). Muscle combinations in both types of synergy effects depended on the direction of the end-point force; a change in the direction resulted in a natural exchange between active and non-active muscles. Theoretical analysis of the muscle dynamics and related synergies for generation of the isometric forces [2–4] allowed us to assume that the coinciding patterns of synergy were often prevailing, and experimental results obtained in this our study might be considered as a support for this assumption.

In this study, we used a rather significant level of muscle loading in order to record distinct EMG signals. When the applied forces are small or absent, the system formally may stay in an uncertain state; therefore, in this case, the end-point positions within the working space are not predetermined. The elements of uncertainty can also be inherent to the conditions of low-intensity efferent inflows to the relaxed muscles. On the other hand, a powerful source of the uncertainty effects may be the interaction of agonist-antagonist pairs of muscles or muscle groups, when reciprocal changes in their lengths during the movement can in some cases modify the expression of the hysteresis aftereffects [9–12]. Behavioral studies with the use of the postural test tasks demonstrated that subjects may frequently use muscle co-contraction as a strategy for stabilization of the limb joints in the presence of external loadings [13]. Humans are also able to vary independently the relative balance of co-contraction and limb stiffness in different spatial directions [14] and at different joints [15]. In our study, we observed inversion of the direction of EMG hysteresis when synergic groups of the muscles participated in the co-contraction mode as antagonists. It seems that one can hardly find additional functional consequences of this phenomenon, except for a general property of the co-contraction in supporting the joint stability during the movement [4, 10, 14]. At the same time, one should bear in mind that co-contraction of the antagonistic muscles inevitably increases the energy costs in the performance of real movements.

Despite the existence of close relationships between the JTs and muscle length changes, on the one hand, and the EMG intensities, on the other hand (this was shown by our group earlier [1, 5, 6] and in the present study), a noticeable muscle activity might be encountered outside the boundaries predicted by the above biomechanical parameters. This phenomenon may be related to a more complicated arrangement of the joints and their muscles compared with that in a simple pivotal model used to define the JTs or the muscle lengths. It seems that the biomechanics of the elbow and shoulder joints can introduce additional elements of indeterminacy in the processes of force generation; similarly, this may introduce noticeable errors in the evaluation of the muscle lengths. The geometry of rotation in the shoulder joint is not simple [16]; the elbow joint is also considered an assemblage of three interactive joint components [17]. It should be noted that the model of two-joint movements with muscles operating exclusively of the constituent joints is certainly oversimplified. Fixed sites of the force applications can be considered only for the monoarticular muscles, while the procedure of their identification for the biarticular muscles is much more complex [18].

Under conditions of relatively slow parafrontal movements (as in our study), both position-dependent changes in the JTs and direction of changes in the muscle lengths define patterns of the respective EMGs (Fig. 2). In the case of the shoulder joint, the JTs remain unchanged; therefore, the EMGs generated by the shoulder muscles are mainly determined by the required trajectory of the muscle length changes. For the distal muscles, the program of activation is somewhat more complex; both the muscle lengths and related JTs change simultaneously and, at first sight, independently of each other. Real movements with nonzero velocities inevitably need significant modifications of the central commands; therefore, dynamic methods of analysis would be required in this case [19–22].

At least partly, our results described in this communication might be consistent with the so-called “leading” joint hypothesis [23] that has been introduced for description of the multijoint movements. This hypothesis proposes that planning of a complex movement can be considerably simplified by choosing one “leading” joint, the neuromuscular control of which provides a dynamic basement for the control of the entire movement. In movements of the upper limb, the shoulder joint is usually considered the “leading” one due to the more massive musculature and higher inertia of the proximal limb link (shoulder) [24–26].

In conclusion, we would like to emphasize that the obtained results allow us to assume that hysteresis properties of muscle contraction and the related characteristics of the signal formation and transmission in the motor control system can lead to a strong hysteresis-related modification of the central commands coming to the muscles in various movement tasks simulating natural movements.

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All tests were carried out in strict compliance with the existing international ethical norms for investigations with the involvement of humans. All participants were volunteers and gave their written consent for their partnership in the tests

The authors, I. V. Vereshchaka, A. V. Gorkovenko, O. V. Lehedza, T. I. Abramovych, W. Pilewska, M. Zasada, and A. I. Kostyukov, declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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