Peculiarities of Activation of Muscles of the Shoulder Belt in Voluntary Two-Joint Movements of the Upper Limb

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We studied coordination of central motor commands (CMCs) coming to muscles of the shoulder and shoulder belt in the course of single-joint and two-joint movements including flexion and extension of the elbow and shoulder joints. Characteristics of rectified and averaged EMGs recorded from a few muscles of the upper limb were considered correlates of the CMC parameters. Special attention was paid to coordination of CMCs coming to two-joint muscles that are able to function as common flexors (*m. biceps brachii, caput breve, BBcb*) and common extensors (*m. triceps brachii, caput longum, TBcl*) of the elbow and shoulder joints. Upper limb movements used in the tests included planar shifts of the arm from one spatial point to another resulting from either simultaneous changes in the angles of the shoulder and elbow joints or isolated sequential (two-stage) changes in these joint angles. As was found, shoulder muscles providing movements of the elbow with changes in the angle of the elbow joint, i.e., *BBcb* and *TBcl*, were also intensely involved in the performance of single-joint movements in the shoulder joint. The CMCs coming to two-joint muscles in the course of two-joint movements appeared, in the first approximation, as sums of the commands received by these muscles in the course of corresponding single-joint movements in the elbow and shoulder joints. Therefore, if we interpret the isolated forearm movement performed due to a change in the angle of the elbow joint as the main motor event, while the shoulder movement is considered the accessory one, we can conclude that realization of a two-joint movement of the upper-limb distal part is based on superposition of CMCs related to basic movements (main and accessory).

Keywords: two-joint movement of the upper limb, elbow joint, shoulder joint, muscles of the shoulder and shoulder belt, superposition of central motor commands.

INTRODUCTION

As is known, shoulder muscles (*m. biceps brachii, caput breve, BBcb,* and *m. triceps brachii, caput longum, TBcl*) in humans not only provide, respectively, flexion and extension of the elbow joint but also are involved in movements in the shoulder joint [1-4]. In our earlier publications, we described some peculiarities of central activation of these muscles providing single-joint movements in the elbow joint under conditions of immobilization of the shoulder and absence of the angle changes in the shoulder joint [5-7]. In fact, the above muscles are, respectively, flexors and extensors of both joints; thus, it can be supposed that central motor commands (CMCs) coming to these muscles in the course of two-joint movements differ significantly from commands providing local movements in the elbow joint. Nonetheless, there are practically no data on the characteristics of CMCs sent to these muscles in the course of complex movements including changes in the position of the forearm and in the shoulder joint angle. Usually, the related studies dealed only with kinematic analysis of the movements; characteristics of CMCs (the latter can be described by analyzing the EMG activity of the corresponding muscles) were not analyzed [8]. In our study, we examined CMCs coming to the *BBcb* and *TBcl* in the course of sequential and simultaneous performances of voluntary movements in the elbow and shoulder joints. Tracking movements (those accompanied by the corresponding visualization) of the upper limb in the horizontal plane were used as the test events. The trajectory of the necessary displacement of the manipulandum handle held by the hand of the tested subject was programmed. At first, movements in one of the joints (either elbow or shoulder one) were performed under conditions of fixation of the angle in another joint. Realizations of

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two sequential movements in the above joints were compared with the movement with simultaneous changes in the angles of both joints. In these cases, the initial and final positions of the hand reference point in the sum of two single-joint movements and in the combined two-joint movement were considered. We analyzed three motor programs including flexions of both joints, extensions of both joints, and flexion of the elbow joint and extension of the shoulder joint. Taking into account the fact that interaction of the arm links in the course of a two-joint movement produced additional kinematic loadings upon the joints, which are absent in single-joint movements [9, 10], the velocities of the changes in joint angles used in our tests were sufficiently low (not more than 15 deg/sec). This circumstance allowed us to minimize the effects of dynamic inertial components in the structure of the test movement. Our study required the development of a corresponding equipment set including a relatively complicate mechanical device and also the corresponding mathematical calculations and development of the specialized software. This is why we describe below only general principles of the techniques used, while their more detailed description is given in the *Supplementum*.

METHODS

Experimental Set. Four volunteers took part in the tests. All these subjects were dextrals, with no neurological diseases and disorders in the functions of the support/motor apparatus. In the course of the experiment, the subject sat on a chair with an adjusted height of the seat. By the right hand, he/she held a manipulandum handle; the latter could freely move with minimum friction along a light metal cantilever. The cantilever could rotate around its axis within a horizontal plane (see the *Supplementum*, Fig. 1). We tried to maximally fit the positions of the cantilever axis and axis of rotation of the shoulder joint. The end of the cantilever was suspended to the ceiling at the point of projection of the rotation axis with a 3-m-long thin steel rope. The elbow of the subject was put in a strap also suspended with a thin rope to the ceiling (to the same point as the former cantilever rope). This allowed us to neutralize the action of the arm's weight and avoid deviations of the forearm position from the plane of the realized movements.

To record the position of the reference point (RP) of the hand of the subject within the movement plane, potentiometric transducers were used. This allowed us to measure the angle of rotation of the cantilever with respect to the initial position and the linear displacement of the handle along the cantilever. Signals from transducers were entered into one of the two PCs. The position of the hand was calculated on-line using the corresponding specially developed software. Anthropometric parameters of the arm of the given subject were taken into account, and this allowed us to measure the values of the angles in the elbow and shoulder joints with necessary accuracy (see the *Supplementum*). The position of the hand, after being calculated in such a way, was visualized for the subject as the position of the marker (light point) on the screen of a monitor (position marker). The necessary test trajectory of the movement was visualized by displacements of another light point (target marker) within the monitor screen. The subject should track the movements of the latter target marker along the test trajectory by providing maximally possible approximation (coincidence) of two of the above-mentioned markers.

In the course of test movements, muscles of the subject's arm can be subjected to additional force loading. External loadings were produced using two preliminarily extended long (4 m) rubber ropes. The stiffness of the rope producing the loading directed along the cantilever was 4.8 N/m, while the respective parameter for the rope producing the loading directed normally to the cantilever axis was 25.0 N/m. The forces produced by ropes were applied to the end of the cantilever (this force extended the shoulder joint) and to the manipulandum with the handle (this force extended the elbow joint) by a system of the ropelets and pulleys. Values of the loadings in different nodal points of the test trajectories, as well as values of the joint angles considered as zero ones, are mentioned in the *Supplementum*.

Recording of EEG and Parameters of the Movements. EEG signals were recorded from four muscles of the arm, *BBcb, TBcl, m. delteoideus, pars scapularis (Dps)*, and *m. pectoralis major* (*PM*); surface electrodes providing long-lasting stable recording (Biopac System EL503, USA) were used. The bandpath of the amplifiers was 0.1 to 1000 Hz; after amplification, signals were recorded using the second computer and an input/output unit, PCI 6071E (National Instruments, USA), with digitization frequency $2 \cdot 10^3$ sec^{-1}. The recorded signals were off-line subjected to full rectification and low-frequency digital filtration (integration). The same computer was used for recording of the signals from potentiometric transducers and subsequent calculation of current values of the joint angles and final digital filtration of the recorded samples. In both cases, low-frequency fourth-order Butterworth filters with a 15 Hz cut frequency were used. The respective signals were averaged for ten realizations of identical motor tests. Current amplitudes of the obtained rectified and integrated EMG signals were considered correlates of the current intensities of the CMCs coming to the given muscle at a definite moment. In the course of the analysis of superposition of the CMCs, two segments of averaged EMG traces obtained from the same muscle under different motor conditions could be artificially shifted in time and algebraically summed.

Trajectories of the Movements. In the course of the experiments, we tested two-joint movements of three types; these were flexions of both joints (elbow and shoulder), extensions of both joints, and flexion of the forearm and extension of the shoulder. Trajectories of the movement within the horizontal plane looked like a curve-sided quadrangle ABCD (Fig. 2 in the *Supplementum*). In the first part of the test procedure, the subject should track the trajectories with the movement in one of the two joints and immobilization of another joint. Then, the position in the former joint was fixed, and the movement toward the terminal target point was performed due to subsequent changes in the angle of the second joint. In the second test part, the transition of the limb RP toward the same target point was performed due to simultaneous changes in the angles of both joints. The subject should track every given trajectory ten times. Clearly unsuccessful trials were eliminated, and the respective test movement was repeated.

RESULTS

As was mentioned, coordination of the activity of muscles of the shoulder and shoulder belt was analyzed for three types of the test movements. In two modes, the directions of changes in the angles of the elbow and shoulder joints were analogous (either flexion or extension), while in the third mode these directions were opposite (flexion of the elbow joint and extension of the shoulder joint). An example of realization of the motor tasks with flexions of both joints is shown in Fig. 1. In this case, the subject should move the hand from an external region of the operational space (i.e., from the position were both joints were mostly extended) to the internal region, and this transition can be performed due to flexion of both joints (transition from point A to point C; see the scheme in Fig. 2 in the *Supplementum*). The initial position (point A in the scheme) was determined by angles of the elbow and shoulder joints 55 and 10 deg, while the final point corresponded to the angles of 100 and 40 deg, respectively. Figure 1A illustrates the activity of arm muscles related to isolated flexion of the elbow joint (trajectory A-D in the scheme in Fig. 2 of the *Supplementum*) and subsequent flexion of the shoulder joint (trajectory B-C). Test movements were performed against the background of application of mild external loadings directed toward extension of both joints (see the *Supplementum*). Flexion of the elbow joint to 45° was performed mostly at the expense of activation of the *BBcb* against some coactivation of the extensors of both joints (*TBcl* and *Dps*) and flexor of the shoulder (*PM*). The second phase of the test movement, where a 30-deg flexion the shoulder joint was performed, was mostly provided by activation of the *PM*. This movement was also accompanied by some coactivation of other muscles. In the course of the movement, the activity of the *BBcb* (common flexor of the elbow and shoulder joints) noticeably increased; this is readily observable on a fragment of the trace after blow-up (Fig. 1A, 2, a).

A change in the sequence of single-joint movements (first, isolated flexion of the shoulder moving the RP of the hand along the A-B segment, and, second, flexion of the forearm moving the hand along the B-C trajectory segment) did not crucially change the peculiarities of coordination of the muscle activity (Fig. 1B). In this case, flexion of the shoulder was also performed mostly due to activation of its flexor (*PM*) and coactivation of the *BBcb* (panel 2, a). The subsequent flexion of the forearm was provided by the activity of the *BBcb* with simultaneous activation of the shoulder extensor (*Dps*) and flexor (*PM*).

The next motor task allowed us to study coordination of the activity of the shoulder and shoulder muscles in the performance of a two-joint movement (Fig. 1C) at the expense of simultaneous flexions of the elbow and shoulder joints. In this case, values of the corresponding joint angles in the start and target points of the movement coincided with those used in the subsequent realizations of single-joint movements. In the corresponding positions, the elbow and shoulder joints were flexed to 55 and 10 deg (A) and 100 and 40 deg (C). The subject was asked to perform tracking of the A-C segment (Fig. 2 in the *Supplementum*, diagonal on the scheme of motor tasks). In the course of realization of the two-joint movement, a clearly pronounced relatively linear pattern of summation of the respective CMCs (visualized according to the

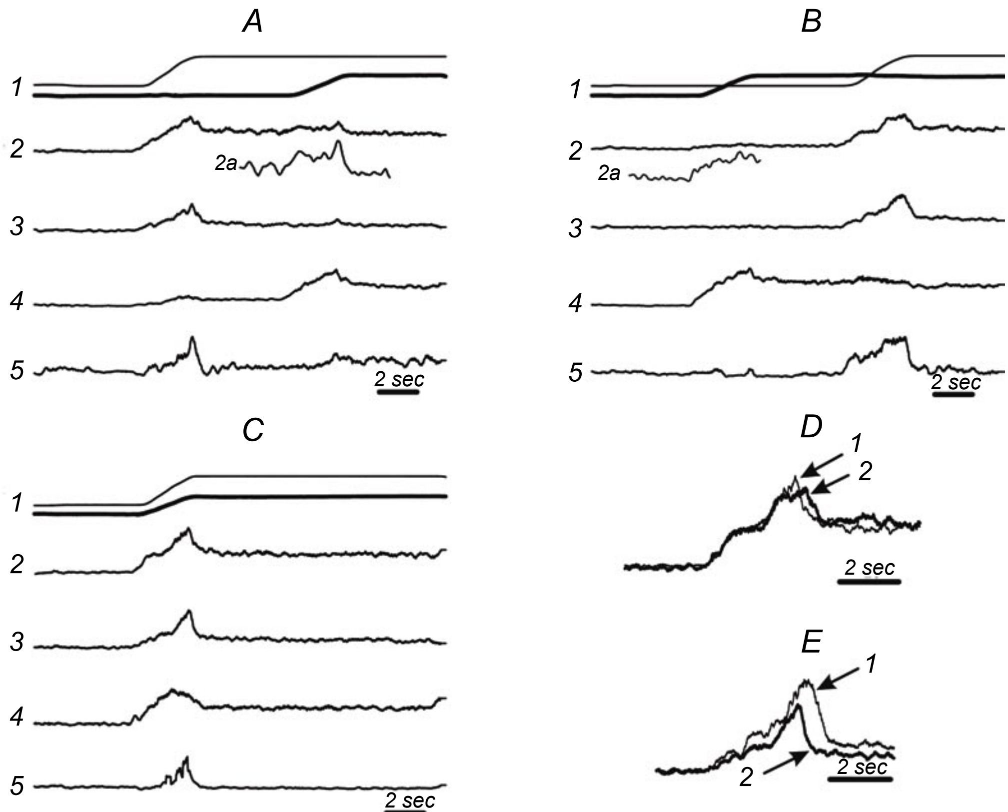

Fig. 1. EMG activities of muscles of the shoulder and shoulder belt related to the movements of the hand from an external region of the two-dimensional operational space of the arm to an internal one (from point A to point C on the scheme shown in Fig. 2 in the *Supplementum*). Three types of transition movements are illustrated: (i) sequential flexions of the elbow and shoulder joints (A, trajectory A-D-C in Fig. 2 in the *Supplementum*), (ii) sequential flexions of the shoulder and elbow joints (B, trajectory A-B-C in the above figure), and (iii) combined flexion of both joints (C, diagonal trajectory A-C in Fig. 2 in the *Supplementum*). In D, a real trace of the EMG activity of the *m. biceps brachii, caput breve (BBcb)* recorded in combined flexion of the elbow and shoulder joints is compared with an artificial curve obtained by summation of the fragments of recording from this muscle (B, 2) corresponding to separate flexions of the shoulder and elbow. In E, the EMG activity of the *m. triceps brachii, caput longum (TBcl)* recorded in combined flexion of the elbow and shoulder joints is compared with an artificial curve obtained by summation of the fragments of EMGs of the same muscle (B, 3) corresponding to isolated flexions of the shoulder and elbow. In A-C, 1 are changes in the joint angles (thick and thin lines for the elbow and shoulder joints, respectively); 2-5 are EMGs recorded from *BBcb* (2), *TBcl* (3), *m. deltoideus, pars scapularis* (4), and *m. pectoralis major* (5). In A and B, fragments of record 2 with a higher amplification and the same sweep (2a) are shown. In B and E, a thick line corresponds to EMG recorded in real combined flexion of both joints (arrow 1), while a thin one corresponds to the result of algebraic summation of EMGs recorded in sequential movements (arrow 2).

characteristics of muscle activity) was observed in the performance of subsequent single-joint movements transferring the RP of the limb to the same target (Fig. 1A, B). Records of EMG activity of the *BBcb* and *TBcl* in the course of combined flexions of the elbow and shoulder joints (D1, E1) were found to be rather close to the results of artificial summation of the fragments of EEG activity of the same muscles related to subsequent separate movements (D2, E2).

Within the same geometry of motor tasks, which was described above, we analyzed extensor movements in both joints. The subjects moved the hand RP from point C to point A (Fig. 2 in the *Supplementum*) using extensor movements performed either in an isolated sequential manner or simultaneously, by parallel changes in the angles of both joints (Fig. 2). In sequential test movements, the subjects extended the elbow joint from 100 to 55 deg; this movement was realized before (A, trajectory C-B-A) or after extension of the shoulder joint by 30 deg (B, trajectory C-D-A). Independently of the sequence of the forearm movement (isolated extension of the elbow joint; A, b), EMG reactions of the muscles providing these movements in the tests were rather similar to each other. Extension was provided by relaxation of the *BBcb* and noticeable activation of the *TBcl*. When

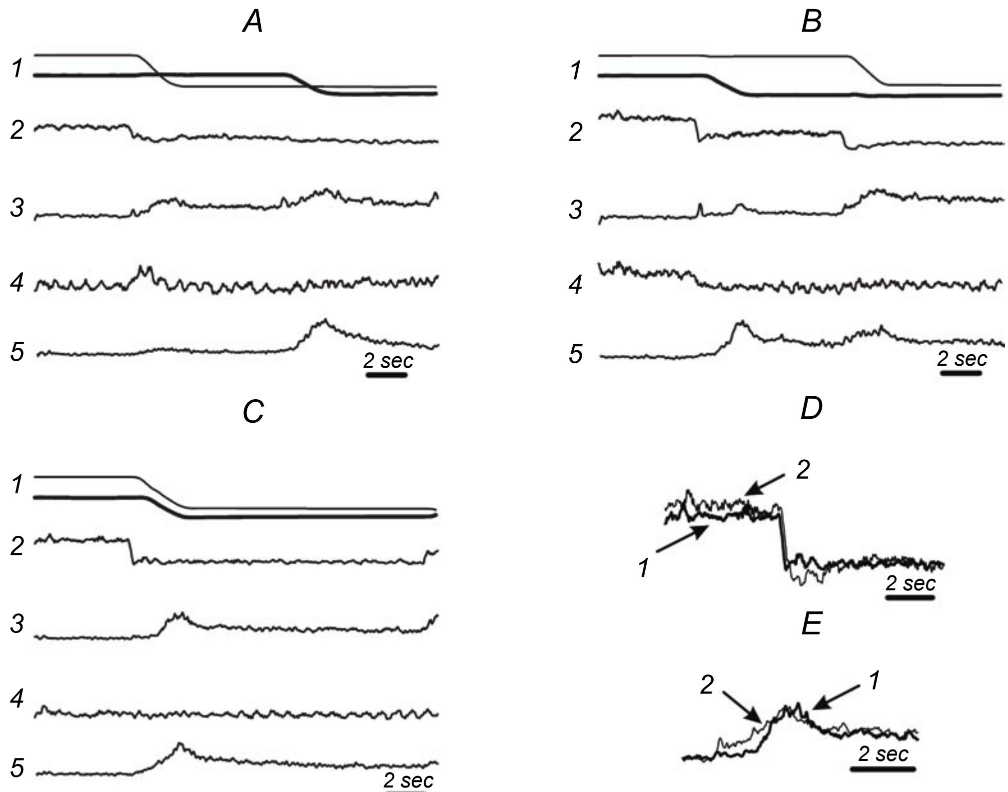

Fig. 2. EMG activities of the muscles of the shoulder and shoulder belt related to the movements of the arm from an internal region of the two-dimensional operational space of the hand to the external one (from point C to point A on the scheme shown in Fig. 2 in the *Supplementum*). Three types of transition movements are illustrated: (i) sequential extensions of the elbow and shoulder joints (A, trajectory C-D-A in Fig. 2 in the *Supplementum*), (ii) sequential extensions of the shoulder and elbow joint (B, trajectory C-B-A in the above figure), and (iii) combined extension of both joints (C, a diagonal trajectory C-A shown in Fig. 2 in the *Supplementum*). D and E are comparisons of EMG activities recorded from the *m. biceps brachii, caput breve* (*BBcb*) and *m. triceps brachii, caput longum* (*TBcl*) in combined extensions of the elbow and shoulder joints with an artificial curve obtained by summation of the fragments of EMGs recorded from the *BBcb* and *TBcl* (B, 2, 3) corresponding to isolated extensions of the shoulder and elbow. Other designations are the same as in Fig. 1.

realization of the motor program was begun by the movement in the elbow joint (A), an accompanying coactivation of the shoulder-belt muscles (*Dps* and *PM*) was noticeable. This, probably, provided the necessary, in this case, level of immobilization of the shoulder (A, 4, 5). The subsequent extension of the shoulder joint was probably performed mostly due to activation of the shoulder extensor (*PM*). In this situation, parallel activation of the *TBcl* was noticed; this muscle can function as an extensor of both joints (A, 3, 5). Realization of extension of the forearm (i.e., extension of the elbow joint) performed after preliminary extension of the shoulder joint was provided by a more complex pattern of activation of the shoulder muscles (B). In this case, coactivation of the shoulder extensors remained rather clearly expressed (B, 5) despite the fact that the activity of the corresponding flexors (*Dps*) was poorly visible (B, 4). It cannot be ruled out that this pattern was related to long-lasting inhibition of the activity of the above muscle after active extension of the shoulder joint.

A combination of the activity of different muscles similar to the above-described EMG patterns observed in the performance of the consecutive movements was found in the case of simultaneous extension of both joints in realization of the two-joint movement (Fig. 2 in the *Supplementum*, trajectory C-A). The *BBcb* was relaxed, while the *TBcl* and *Dps* increased their activity (Fig. 2C). In this case, the time course of a decrease in the level of activity of the *BBcb* in the course of simultaneous extension of both joints (D, 1) was rather close to the integral pattern obtained by superposition of the traces of activity of the above muscle in separated motor tests (curve 2 in B was

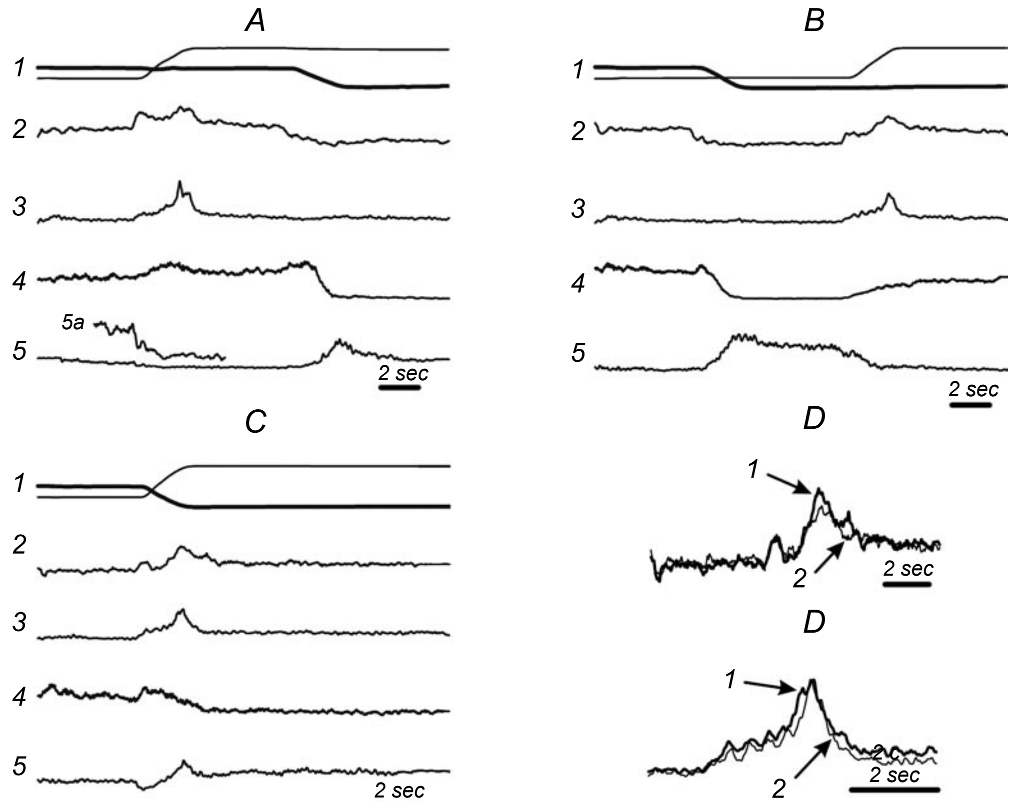

Fig. 3. EMG activities of the muscles of the shoulder and shoulder belt related to the movements of the hand from an external region of the two-dimensional operational space of the arm to an internal one (from point B to point D on the scheme shown in Fig. 2 in the *Supplementum*). Three types of transition movements are illustrated: (i) initial flexion of the elbow joint followed by extension of the shoulder joint (A, trajectory B-C-D in Fig. 2 of the *Supplementum*), (ii) initial extension of the shoulder joint followed by flexion of the elbow joint (B, trajectory B-A-D in the above figure), and (iii) combined flexion of the elbow point and extension of the shoulder joint (C, a diagonal trajectory B-D in Fig. 2 of the *Supplementum*). In A, an amplified fragment of record 5 with the same sweep is shown. D and E are comparisons of EMG activities recorded from the *m. biceps brachii, caput breve (BBcb)* and *m. triceps brachii, caput longum (TBcl)* in combined flexion of the elbow joint and extension of the shoulder joint with artificial curves obtained by summation of the fragments of EMGs of the *BBcb* and *TBcl* (B, 2, 3) corresponding to initial flexion of the shoulder and subsequent flexion of the forearm. Other designations are the same as in Fig. 1.

obtained by artificial summation of the corresponding fragments shown in B, 2). At combined extension of the joints, the time course of the rise in the EMG activity of the *TBcl* (E, 1) practically coincided with the respective curve obtained by summation of the EMG trace fragments related to realization of separate movements in each of the joints (E, 2).

Examining of more complex two-joint movements, with flexion of one joint combined with extension of another joint, was of special interest. In the experiment shown in Fig. 3, test movements included flexion of the forearm (i.e., flexion of the elbow) and extension of the shoulder (trajectories B-C-D, B-A-D, and B-D shown in the scheme of Fig. 2 in the *Supplementum* were tracked). In the B-C-D movement (Fig. 3A), EMG activity related to single-joint flexion of the elbow, in general, did not differ from that shown in the respective test traces in Fig. 1. Subsequent isolated extension of the shoulder (Fig. 3A, trajectory C-D) was provided by well-expressed activation of extensors of the shoulder belt (A, 5); this was accompanied by a mild increase in the activity of the extensor shoulder muscles (extensors of the elbow joint) and a noticeable “drop” in the activity of the flexor muscles of the shoulder and shoulder belt. The rather complex dynamics of the increases and decreases of EMG activity of different muscles under conditions of realization of the above-mentioned isolated movements in two joints was probably predictive of the multicomponent pattern of EMG activities of all examined muscles in C-D. In this case, the time course of sufficiently synchronous increases in the activity of flexors and extensors of the elbow joint in the beginning of realization of such a motor program showed, in fact, no difference from the course of EMG activity related to the corresponding single-joint movements. An initial "drop" in the activity of the shoulder extensors looked, however, somewhat unexpected (C, 5). We can only assume that a short-lasting decrease in the level of activation of the above muscle could be compensated by activation of other extensor muscles from which we did not record EMGs in these experiments. Besides this, we cannot rule out that the activity of the two-joint *TBcl* muscle could somewhat contribute to extension of the shoulder. This activity demonstrated a noticeable rise in its level within the initial phase of the test movement. Similarly to what was observed in the preceding tests with analogous directions of the movements in the elbow and shoulder joints (Figs. 1 and 2), the activity of shoulder muscles in the course of the two-joint "flexion-extension" movement could be rather adequately described by the algebraic sum of the respective fragments of EMG activity recorded in the performance of corresponding isolated single-joint movements (Fig. 3D, E).

DISCUSSION

Results of our tests showed that muscles of the shoulder providing movements of the forearm, the *BBcb* and *TBcl*, were significantly activated also in realization of isolated single-joint movements in the shoulder joint. Such a pattern of their activity is, at least partially, determined by anatomical peculiarities of these heads of the biceps and triceps muscles. Zones of fixation of their tendons to bones of the forearm and shoulder belt allow these muscles to provide movements related to changes in the angles of both the above-mentioned joints [1-4]. Therefore, the *Bbcb* and *TBcl* muscles cannot be considered as exclusively a flexor and an extensor of the forearm, respectively; they are *partially* two-joint muscles. Consequently, each active change in the angles of the elbow and shoulder joints is, in one manner or another, related to corresponding changes in the levels of EMG activity of these muscles. Using background force loading of the upper limb muscles in our tests showed the necessity of initial activation of the flexor muscles (those flexing both elbow and shoulder joints). Fixation of the shoulder made it necessary to activate the muscles flexing and extending the shoulder joint (*Dps* and *PM*) in a parallel manner with activation of the muscles immediately involved in the movements in the elbow joint.

Rather powerful accompanying activation of extensors of the elbow joint, i.e., coactivation of the antagonist muscles, is, as a rule, observed in the movements related to flexion of the elbow joint and realized with no fixation of the shoulder; such a pattern has rather frequently been used for the analysis of single-joint movements [6, 7]. At the same time, when the shoulder was fixed by an external force, and flexion of the elbow joint was performed against the action of an external extending loading, activation of the extensor muscles was insignificant [5-7]. A mostly coactivatory pattern of the muscle activity in flexor movements was recorded independently of the consequence of the movements, i.e., of the performance of the forearm movement before or after the movement in the shoulder joint (Fig. 1A, B). It seems probable that the observed difference is related to the necessity for immobilization of the shoulder, under the experimental conditions used, due to the force counteracting with the shoulder extensors (whose function can be partially performed also by the forearm extensors) (A, 4; B, 4). The observed activation of the extensors was frequently accompanied by simultaneous activation of the shoulder joint flexors.

In our tests, we observed rather general (common) patterns of activation of the muscles providing flexor and extensor movements in the elbow and shoulder joints. When both joints were flexed, coactivation of the antagonist muscles was usually observed. In this case, the force reaction of the flexors met the counteraction of the force created by contraction of the extensors. Combinations of the muscle activity in the extensor movements were quite dissimilar. Naturally, these movements were performed due to predominant activation of the extensors of the given joint, but a clearly manifested effect of relaxation of the muscles flexing the same joint assisted (practically in all cases) this action. Drops in the activity of the muscles flexing both elbow and shoulder joints were especially noticeable in the case where some level of background activation of the muscles was recorded before the beginning of the movement. One of the possible reasons for the above-mentioned specificities of EMG activity of the muscles controlling the above joints in the course of extensor and flexor movements can be related to using external loadings directed toward extension of the elbow and shoulder joints. In future, this supposition can be checked out in more detail in experiments with changed directions of the external loading used.

We should note that muscles controlling the shoulder joint, the *Dps* in particular, could noticeably change their activity related to fixation of the shoulder in different tests, and this feature differentiated these muscles from those immediately providing flexion of the elbow joint. For example, in the experiment illustrated in Fig. 1A, B, a rise in the activity of this muscle was observed in the case of flexion of the elbow, while this activity decreased in the similar test shown in Fig. 3A, B. It is important that specificities of activation of the *Dps* noticed in the course of single-joint movements were preserved after transition to two-joint test movements. A complex anatomical composition of the muscles responsible for movements in the shoulder joint can be one of the reasons for this peculiarity. In our experiments, we recorded EMGs only from a small part of the activity of this complex. Earlier, when we examined tracking movements in the elbow joint, we mentioned the probability of redistribution of the activity among different antagonist muscles in the course of realization of identical motor programs [6].

In this study, two-joint movements were formed from single-joint components under conditions of relatively low velocities of the changes in joint angles; this allowed us to neglect dynamic inertial interactions between the upper limb links. Within this experimental paradigm, we should mention that averaged EMG reactions recorded in the performance of two-joint movements from the muscles common for the above-mentioned joints (*BBcb* and *TBcl*) can be rather adequately described by an algebraic sum of the corresponding EMGs recorded in the course of single-joint movements in each studied joint, which are components of the two-joint motor act. If we consider an isolated movement of the forearm (i.e., a change in the elbow joint angle) as the main component and a movement in the shoulder joint as the accessory component, we can believe that a principle of superposition of the central commands for basic movements (main and accessory) works in the case of realization of two-joint motions of the distal part of the limb. It cannot be ruled out that this principle of the formation of CMCs should be taken into account in the analysis of multijoint movements with arbitrary changes in the angle joints. Naturally, the question remains open: Is this peculiarity of central programming of the movement related exclusively to the fact that the examined muscles moving the forearm are, in fact, two-joint ones, or can this principle be manifested in the case of purely single-joint muscles?

The above-described results allow one to believe that configurations of the CMCs depend, to a considerable extent, on biomechanical parameters, such as the joint angle and velocity of its change, and also on the field of external forces influencing the limb. If the mechanical parameters of the movement remain constant, central commands coming to the muscles controlling the limb link undergo no fundamental changes independently of the involvement of this limb in one complex multijoint movement or another. On the other hand, our findings show that similar movements can be mediated by different combinations of the activity of several antagonist muscles controlling the given joint.

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