DOI 10.1007/s11062-015-9538-6
Neurophysiology, Vol. 47, No. 4, August, 2015

Coordination of Activity of the Shoulder Belt and Shoulder Muscles in Humans during Bimanual Synchronous Two-Joint Movements

T. I. Abramovich,[1] I. V. Vereshchaka,[1] A. M. Tal'nov,[1] A. V. Gorkovenko,[1] M. Dornovski,[2] and A. I. Kostyukov[1]

Received April 20, 2014

We examined coordination of EMG activity of flexors and extensors of the shoulder and elbow joints during realization of synchronous bimanual ramp-and-hold movements within a horizontal plane similar to those in the course of rowing. A tested subject moved handles of two levers rotating on the vertical axes and traced a trajectory of the command signal presented on a monitor. Test movements included displacements of the lever handles "to the chest" (TCh) and "from the chest" (FCh) (durations 0.4, 1.0, or 2.0 sec), separated by a phase of fixation of the extremum position after the first phase (duration 6.0 sec); the amplitude of turns of the levers was equal to 30 deg. The movements were realized under conditions of application of external loadings (33–28 and 19–15 N) having FCh or TCh directions. During realization of the movements, EMG activity of the shoulder belt and shoulder muscles was recorded bilaterally; patterns of rectified and integrated EMGs were considered correlates of the central motor commands (CMCs) coming to the corresponding muscles. Analysis of EMGs recorded from 12 muscles (six for each limb) demonstrated that the activity of the latter is coordinated in a rather complex mode. The peculiarities of functional interactions (synergies) of muscles during coordinated displacements of the shoulder links and forearms under conditions of realization of the above-mentioned test movements are described. Significant effects of the velocity factor on the dynamic components of CMCs addressed to the examined muscles were observed. In each muscle, statistically significant differences between the EMG amplitudes during realization of the TCh and FCh movements were found. Differences between the dynamic and static EMG components under the action of external loadings of opposite directions were also significant. It was found that, in the course of realization of the movements, CMCs coming to the elbow flexors were more variable (flexible) compared with CMCs directed toward shoulder extensors. With increase in the duration of active phases of the test movement, the amplitude of these phases (D1 and D2) in EMGs of all examined muscles decreased at both directions of the external loading. The dependence of stationary EMG levels on the direction of action of this loading has been also demonstrated. Static components of EMG activity of all muscles were considerably greater at extending loadings compared to those at flexing ones.

Keywords: bimanual two-joint movements, shoulder belt and shoulder muscles, electromyography, central motor commands (CMCs), dynamic and static components of the movements, muscle synergies.

INTRODUCTION

Patterns of central motor commands (CMCs) coming to muscles of the limb during spatial voluntary (or close to those) motor effects (movements or efforts) in humans have been studied predominantly using experimental models of simple stereotyped movements [1–4]. The EMGs rectified and subjected to low-frequency filtration, which are recorded from the muscles involved in realization of these movements, can serve as correlates of CMCs responsible for the control of such movements.

Single-joint ramp-and-hold movements are usually interpreted as a transition from one equilibrium position of the limb link to the subsequent position. Our recent studies allowed us to hypothesize that the control of voluntary single-joint movements (in particular those in the elbow joint) is realized predominantly at the expense of coordinated interaction of dynamic CMC components. As some researchers believe, a transition of the limb link from one equilibrium

---

[1] Bogomolets Institute of Physiology, National Academy of Sciences of Ukraine, Kyiv, Ukraine.
[2] Academy of Physical Education and Sport, Gdansk, Poland.
Correspondence should be addressed to T.I. Abramovich
(e-mail: tatyana_abramovich90@mail.ru).

position to another (during both flexion and extension) is controlled by dynamic changes in the activity of motoneurons of the corresponding muscles, which are organized according to the principle of the three-burst pattern, independently of the motion velocity [5]. Concurrently, there is a hypothesis according to which a transition of the limb link from one equilibrium position to another is realized at the expense of static CMC components resulting from a change in certain parameters in the stretch reflex system [6–8]. In the context of some theories of motor control (e.g., hypothesis of the equilibrium point), it is believed that there is a single-valued interrelation between efferent motoneuronal activity received by the muscles responsible for the control of the corresponding joint and the mechanical parameters of the movement [9–11]. The analysis of EMG activity generated in the course of performance of stereotyped single-joint movements realized in a mode close to isotony was indicative, however, of an obvious ambiguity of the ratio between the level of EMG activity vs. parameters of positioning of the above-mentioned link. As was demonstrated in studies on the hip muscles of humans during movements realized with a permanent influence of external loading, one and the same equilibrium position of the foot can be achieved at significantly different levels of efferent activity coming to the muscles; the corresponding patterns depended, to a considerable extent, on the prehistory of the preliminary movement [12].

Changes in a joint angle during realization of elementary movements are due to coordinated contraction and relaxation of agonist and antagonist muscles. The patterns of activity of agonists are altered not only in the performance of different motor tasks; the intensity of activation of these muscles can vary significantly even in identical movements. Within certain phases of the movements, co-activation of antagonists, which increases the joint mechanical stiffness, is quite possible; this phenomenon is most important in the course of complex multijoint movements [13]. Such an increase in the stiffness of joints also neutralizes the instability in the position of a limb link under the action of one external force or another. This is why co-activation of the antagonistic muscles is an important factor increasing the accuracy of the movement [2, 14].

Despite the fact that the problem of control of simple single-joint movements has been subjected to intense investigations, a great number of questions in this sphere remain unresolved. Additional questions arise with respect to the mechanisms underlying the control of more complicated multijoint coordinated movements. As was found, the muscles controlling certain movements in various joints can form transient functional groupings well coordinated with each other (muscular synergies). Combination of the muscles in synergies is a relative phenomenon; muscles that form a certain synergy may demonstrate, during realization of one movement of another, not only identical but also appreciably different levels of activation [15–18]. A lesser effort developed by a certain muscle can be compensated by the intensified efforts of other muscles; in this case, final integral motor phenomena (movements of the limb or forces developed by the limb) will remain identical close to each other.

The patterns of CMCs in the course of real complex multijoint movements consist of strictly determined and random components. The latter are related to randomized re-distribution of the activity inside synergic muscle groups and between agonist and antagonist groups.

It is logical that the first stage in the analysis of such motor phenomena should be carried out on stereotyped two-joint movements. In particular, such approach can allow one to adequately compare dynamic and static components of activity of the involved muscles and to examine the variability of the characteristics of activity of these muscles during realization of identical movements. The intriguing aspect in examination of the corresponding motor phenomena is investigation of the similarity and dissimilarity of reactions of one muscle or another during identical synchronous movements performed by the two upper limbs. In this situation, the characteristics of movements can depend on the prevalence of similarity of or difference between the activities of one and the same muscle in two different limbs.

The main part of the studies dealing with examination of bimanual movements [19–22] was focused exclusively on biomechanical parameters of the above-mentioned motor phenomena. In our research, we tried to quantitatively analyze the characteristics of EMG activity of a number of shoulder belt and shoulder muscles generated during identical synchronous movements of the upper limbs of humans under conditions of alteration of the direction of an external loading. The test movements were initiated, and their trajectories were tracked according to a visual signal; the movements included phases of active displacements in two opposite directions separated by a phase of holding of the achieved position.

METHODS

Organization of the Tests. Seven volunteers (right-handed men, 19-27 years old) were involved in our tests. A mechanical part of the experimental device is shown schematically in Fig. 1. The tested subject sat in an armchair at a special table. The position of the chair seat could be regulated; the level of the armpits of the subject was 10–15 cm above the surface of the table. The subject held, by both of his hands, the handles of two movable levers fixed on the table on vertical axes and capable of rotating. The construction of the axis having ball-bearings provided minimization of the resistance during rotation. Distances from centers of rotation of the levers to middles of the handles were 60 cm. Rubber belts (length 4.0 m each) were fixed to the levers; the tested subject should develop certain efforts directed to the chest (TCh) or from the chest (FCh).

Angular displacements of the levers during realization of the test movements of both above kinds were about 30 deg and varied within a ± 5 deg range depending on the anthropometric characteristics of the tested subject (first of all, lengths of the limb links). The values of rotation angles of the levers were measured using precision potentiometer sensors fixed on the axes of rotation; zero levels of the signals corresponded to medium positions of the levers (Fig. 1A).

Synchronous test movements of both limbs were initiated from the position shown in Fig. 1B, when external angles between the axes of the shoulder and forearm (in elbow joints) and between the frontal plane of the chest and axes of the shoulder links of the limbs (in shoulder joints) were 60 deg each. According to a visual signal (appearance of a cursor on the screen of the control monitor), the tested subject began to move the handles to the chest (TCh) toward the extreme position shown in Fig. 1C. In the course of the performed movement, the tested subject should strictly track with maximum accuracy (by a motion of the signal from an angle sensor of the left lever on one of the beams of the monitor) the trajectory of the command trapezium-shape signal presented on the screen by the second beam. The duration of a TCh shift of the handles (*D1*) was 0.4, 1.0, or 2.0 sec; after this, the position of levers should be maintained stably for 6.0 sec. Then, the movement was realized in an opposite direction

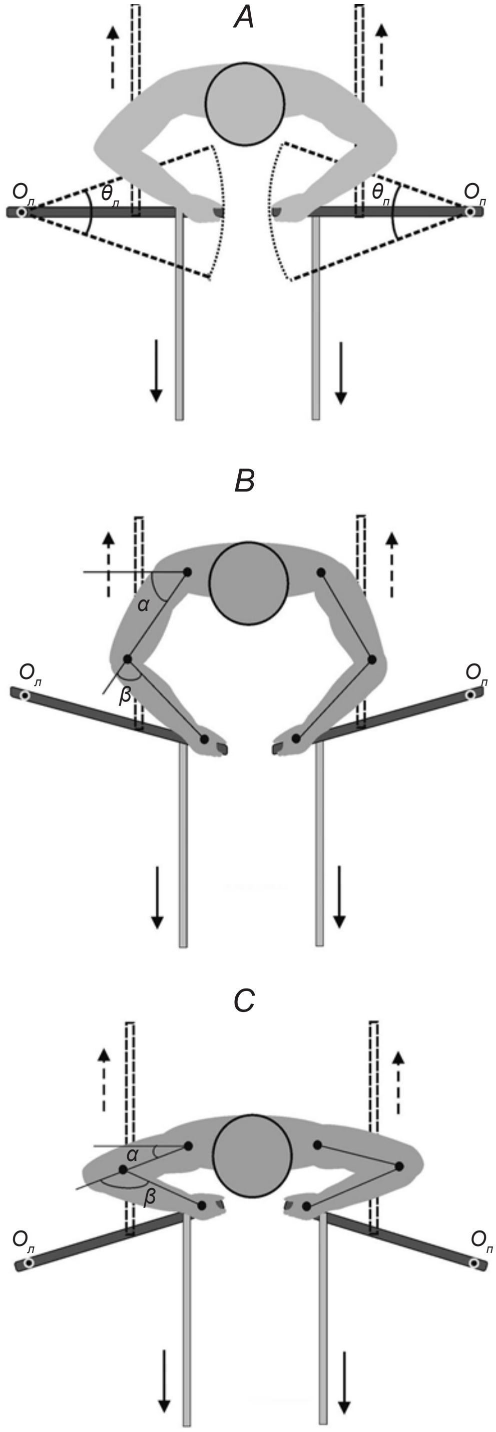

Fig. 1. Scheme of the experimental setup and organization of the tests. O_R and O_L) Rotation axes of the levers. In A, θ_R and θ_L are working ranges of the angular displacements of the levers. In B and C, positions of the hands of the tested subject and of the levers at initiation of the test movement (B) and at fixation of the position after the first phase of the latter (to the chest, TCh, C) are shown. Values of the angles in the shoulder and elbow joints (α and β, respectively) are also indicated. For details, see the text.

(FCh) toward the initial position. The duration of the backward movement (*D2*) was also 0.4, 1.0, or 2.0 sec.

Test movements were performed under conditions of application of an external loading in two opposite directions. In the case of test movement 1, the external loading developed by long extended rubber belts (4 m) was FCh-directed, i.e., impeded the first phase of the movement. At the beginning of test movement 1, the external loadings re-calculated with the respective points of application of efforts developed by the subjects (i.e., with respect to the handles) were 28 N, while with the achievement of the final handle positions and their fixation, they were 33 N. During realization of test movements 2, external loadings on the handles had the TCh direction; at the initial handle positions they were 19 N, while at the final position (after the lever movements in the TCh direction) they were 15 N.

As can be seen from Fig. 1, the bimanual test movements in our experiments were analogous, to a certain extent, to the movements of the limbs of a rower at sculling in a dinghy or in an outrigger racing boat. The movements of the levers in the TCh direction corresponded approximately to the phase of an active stroke, while the FCh movements corresponded to sweeping of the oars before the next stroke.

Recording of EMG Activity and Its Analysis. EMG activities of the shoulder belt and shoulder muscles were recorded bilaterally using a standard technique of electromyography, with the help of superficial electrodes (Biopac System EL 503, USA). We recorded EMGs from the following muscles: *mm. pectoralis major (Pect), deltoideus scapularis (Delt), biceps brachii, caput longum (Bic.l), biceps brachii, caput breve (Bic.b), brachioradialis (Br)*, and *triceps brachii, caput longum (Tric)*. The recorded EMG signals were amplified using a 16-channel amplifier (CWE Inc., USA) and filtered with a bandpass of 10 to 5,000 Hz. The EMGs and signals from sensors of the rotation angles of the levers were digitized using an ADC (Power 1401 data acquisition system) and Spike 2 software (Cambridge Electronic Design, Great Britain); digitization frequencies were 10^4 and $2 \cdot 10^3$ sec^{-1}, respectively. Signals from the above-mentioned sensors of the lever angles, taking into account the anthropometric characteristics of the tested subjects, were converted (recalculated) into values of the external joint angles for the shoulder and elbow joints. For off-line analysis of the obtained data, we used Origin 8.0 (OriginLab Corp., USA) and SPSS 17.0 softwares (IBM Business Analytics, USA). Digitized EMG samples were subjected to full-wave rectification and low-frequency filtration (fourth-order Butterworth filter, bandpass 0–10 Hz); this procedure led to a phase shift with respect to the initial EMG signal by about 130–150 msec [4]. After preliminary processing, signals were averaged by ten realizations of one and the same test. Prior to each group of tests, we recorded EMGs from all examined muscles at the maximum voluntary contraction (MVC) of the latter in order to normalize the averaged EMG records during test movements with respect to the MVC.

RESULTS

Figure 2 shows examples of realizations of the test movements under conditions where TCh displacements of the levers toward oneself, maintenance of a stationary position, and backward (FCh) movements were realized under conditions of application of external loadings of different directions (FCh and TCh). In such movements, changes in the angles of the left (traced) and right (untraced) levers were nearly of a similar trapezoid form. Within the framework of this experimental approach, two-joint movements of each upper limb were formed from single-joint components (i.e., from time-coordinated movements in the shoulder and elbow joints). The respective limb links moved synchronously and in an antiphase manner; values of the angles in the elbow joints changed in the flexion direction, while those in the shoulder joints changed in the extension direction. The achieved positions in both joints were maintained for 6 sec; then, links of limbs moved synchronously in the opposite directions; the elbow joints were extended, while the shoulder joints were flexed. In the case of a forward external loading, i.e., of the FCh direction with respect to the frontal plane of the body of the tested subject, this force extended the elbow joints and flexed the shoulder joints. Such action was, in fact, directed against the efforts developed by the elbow flexors and shoulder extensors.

Under these testing conditions, the analysis of EMG activity of the studied shoulder belt and shoulder muscles was indicative of their rather complex coordination. According to this direction of the external loading, movements of the levers were realized due to prevailing activation of the elbow

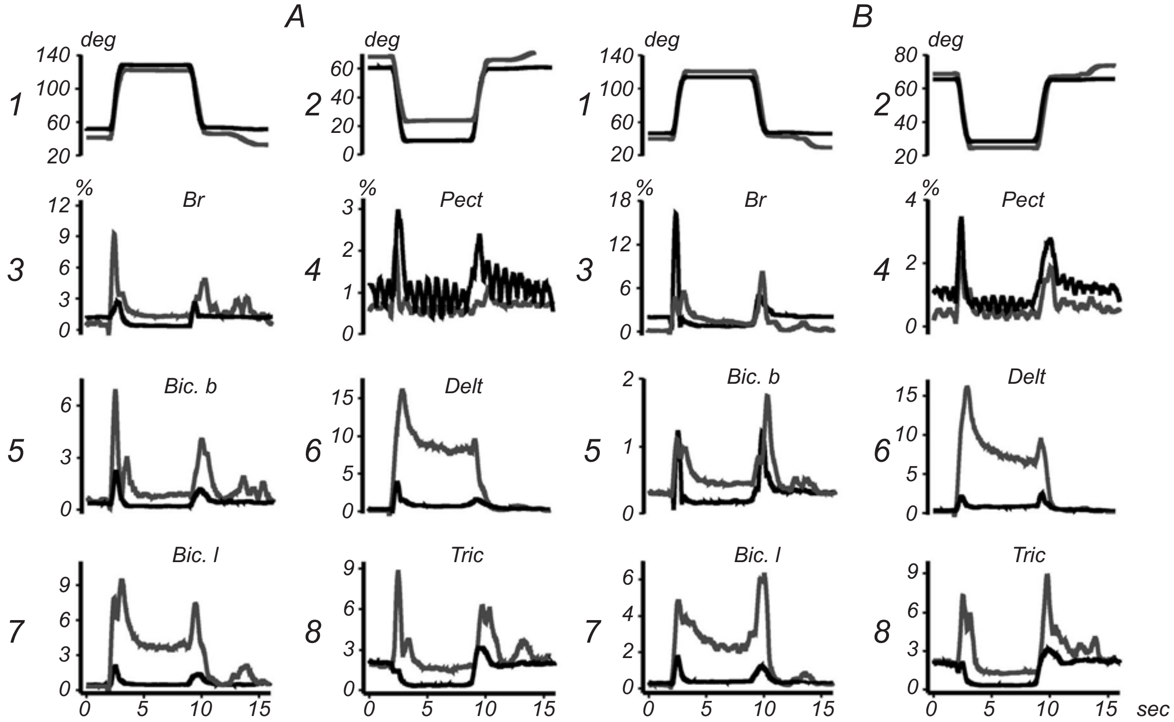

Fig. 2. Averaged records of values of the angles in elbow (1) and shoulder (2) joints and EMG activities of the shoulder belt and shoulder muscles (3–8) during realization of the test movements with 1.0-sec-long displacements of the levers. A and B) For the left and right hand, respectively). Black and gray lines show records under the action of external loadings “to the chest” and “from the chest,” respectively. Vertical scales in fragments 1 and 2) External angles in the above-mentioned joints, deg; vertical scales on fragments 3–8) Intensity of EMGs normalized with respect to those during maximum voluntary contraction of the above muscles, %. For designations of the muscles, see Methods.

flexors *(Br, Bic.b,* and *Bic.l*) and shoulder extensors *(Delt)*. It should be noted that the shoulder extensors (*Delt*) generated forces counteracting the external loading within the extension phase, stabilizing the position at the stationary level, and developing additional forces; this, in turn, allowed the external loading to flex the shoulder joints toward the initial position. Patterns of activities of the shoulder extensors (*Delt*) of both limbs were rather similar to each other.

The peculiarities of formation of EMG activity of the elbow flexors (*Br, Bic.b,* and *Bic.l*) were very similar to those in the case of activation of the muscles controlling the shoulder joints. We also observed their counteraction with the external loading force at the phase of flexion of the elbow joints, stabilization of their activity on the stationary level, and the development of an additional force at the phase of extension of the above joints. Under such conditions, all studied elbow flexors demonstrated rapid increases in their activity. It should be noted that, after the achievement of the stationary phase, holding of the attained position in the elbow joint of the right hand was mainly provided by a relatively stable level of activity of the *Bic.b* and *Bic.l* and due to simultaneous co-activation of the two-joint extensor (*Tric*), while the *Br* synchronously decreased its activity. However, the stationary position in the elbow joint of the left hand was maintained only due to a significant tonic activation of the *Bic.l.*

During realization of the trapezium-shape movements in the case where the external loading acted in the direction of flexion of the elbow joints and extension of the shoulder joints, i.e., it was directed backward with respect to the frontal plane of the body of the tested subject, the *Bic.b and Bic.l* of both limbs at the phase of flexion produced a small activity compared with that under the action of the extending external force (Fig. 2). At the same time, the *Br* of the right hand demonstrated a more pronounced high-amplitude dynamic component of activity than that in the left hand. Extension of the elbow joints was provided at the expense of increase in the activity of their extensor (*Tric*). These muscles helped to withdraw the joint out of the equilibrium position and generated the force that counteracted with the external loading. It should be noted that, after flexion of the elbow joints, the *Tric* demonstrated relaxation. At the phase of holding of the stationary position of the joints, these muscles continued to hold a relatively low activity, and EMGs returned to the initial level during extension of the elbow joints.

Extension of the shoulder joints was realized mostly at the expense of action of the external loading, while the *Delt* developed only some additional force to maintain the joints in the stationary position. We also observed simultaneous co-activation of the flexors of these joints (*Pect*). The withdrawal of the shoulder joints out of the equilibrium state and their flexion were controlled by activation of the *Pect* against the action of the external loading.

For quantitative estimation of changes in the amplitudes of the dynamic components of EMG activity of the examined muscles, we calculated values of these components separately. For this purpose, in each experiment and for each normalized EMG, we estimated the intervals of realization of the dynamic components, *D1* (2–4 sec, the phase of the TCh movement) and *D2* (9–12 sec, the phase of the FCh movement), within which we calculated the respective mean values. The obtained values of this index were averaged for each muscle and in each series separately. The same procedure was performed for calculation of mean values of the static component (time interval 5–8 sec).

To estimate possible dependences of the dynamic and static components on the experimental conditions, we used multifactor analysis of variance, ANOVA. As the first factor, lateralization, left (L) or right (R) hand, was considered. The second factor was the external loading direction, i.e., forward or backward with respect to the frontal plane of the tested subject's body, FCh or TCh. The third factor was the duration of the active phases of the movement (0.4, 1.0, or 2.0 sec), and the fourth factor was the first (*D1*) or the second (*D2*) dynamic component. Statistical calculations were performed using SPSS Statistics 17.0 software (IBM, USA). Intergroup differences were considered to be significant with $P < 0.05$ and $P < 0.01$.

Figures 3 and 4 illustrate results of comparison of the changes in the *D1* and *D2* amplitudes depending on the direction of action of the external loading and the duration of active phases of the movement. *In toto*, taking into account the effect of a velocity factor on the dynamic EMG components, statistically significant differences between the *D1* and *D2* amplitudes were observed in all examined muscles. With flexion of the elbow joints under the action of the extending external loading and at a minimum duration of the active phases of the realized movement (0.4 sec), a rather powerful

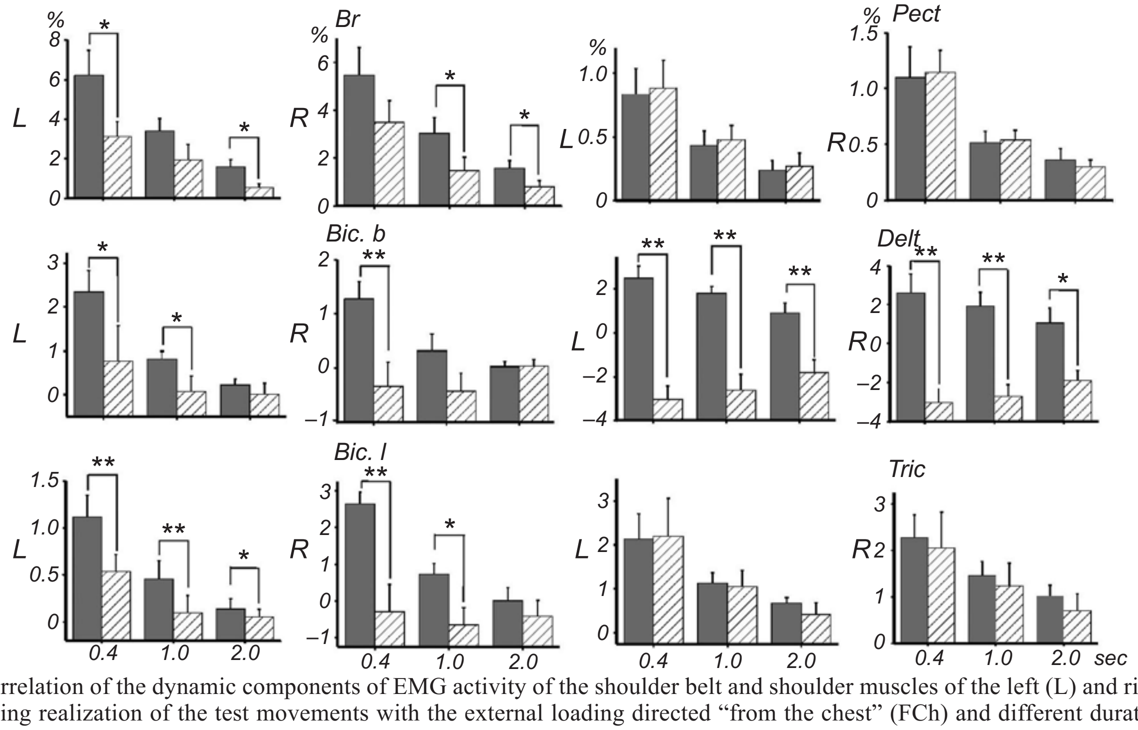

Fig. 3. Correlation of the dynamic components of EMG activity of the shoulder belt and shoulder muscles of the left (L) and right (R) hands during realization of the test movements with the external loading directed "from the chest" (FCh) and different durations of the active phases of the movements (*D1* and *D2*). Gray and dashed columns show averaged values of the amplitudes of the dynamic components within the TCh (phase *D1*) and FCh (phase *D2*) movements; horizontal scale) duration of the above-mentioned active phases of the movement (0.4, 1.0, and 2.0 sec). One and two asterisks show cases of significant differences between the *D1* and *D2* values with $P < 0.05$ and $P< 0.01$, respectively. Other designations are the same as in Fig. 2.

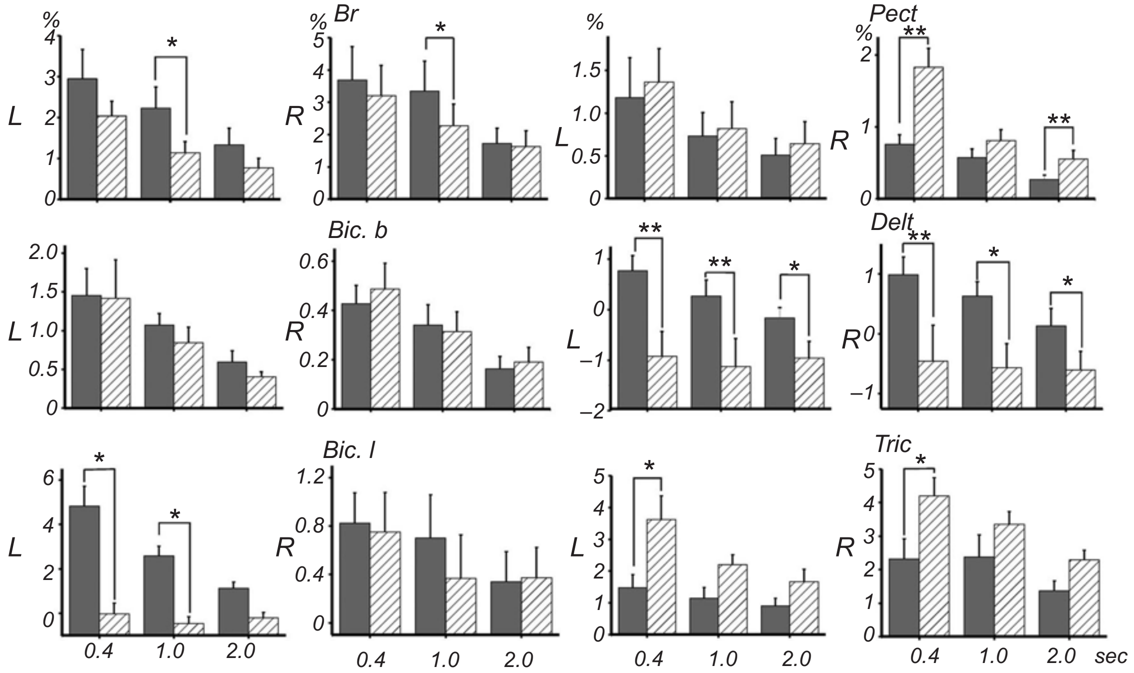

Fig. 4. Correlation of the dynamic components (*D1* and *D2*) of EMG activity of the shoulder belt and shoulder muscles of the left (L) and right (R) hands during realization of the test movements with the external loading directed “to the chest” (TCh) and different durations of the above-mentioned active phases of the movement. Other designations are the same as in Figs. 2 and 3.

dynamic component of EMG activity was observed within the *D1* phase in the flexors, i.e., in *Br, Bic.b,* and *Bic.l* (Fig. 3). The withdrawal from the equilibrium state of the examined joints and their return to the initial state were controlled by the same muscles, but the *D2* component was expressed to a lesser extent. The same pattern of correlation of the *D1* and *D2* amplitudes was observed in the shoulder extensors (*Delt*). The analogous dynamics were preserved in the case of both extending and flexing external loadings acting on these joints, which is confirmed by the significant differences between the values of *D1* and *D2* amplitudes for both limbs (Figs. 3 and 4). The amplitudes of the *D1* and *D2* phases in EMG activity of the *Tric* and *Pect* under conditions of action of the extending external loading were practically identical (Fig. 3). If the direction of the external loading during realization of the movements was changed by the opposite one, the *D2* amplitude in the activity of these muscles increased significantly. With rise in the duration of active phases of the movements, the amplitude of the *D1* and *D2* phases in all examined muscles decreased for both directions of the external loading. In addition, with a maximum duration of these phases of the test movement (2.0 sec), the amplitudes of *D1* and *D2* components in EMGs of the *Bic.b* were nearly the same.

ANOVA analysis was used for estimation of the dependence of static components of EMG activity on the direction of the external loading and the duration of active phases of the movement (Fig. 5,

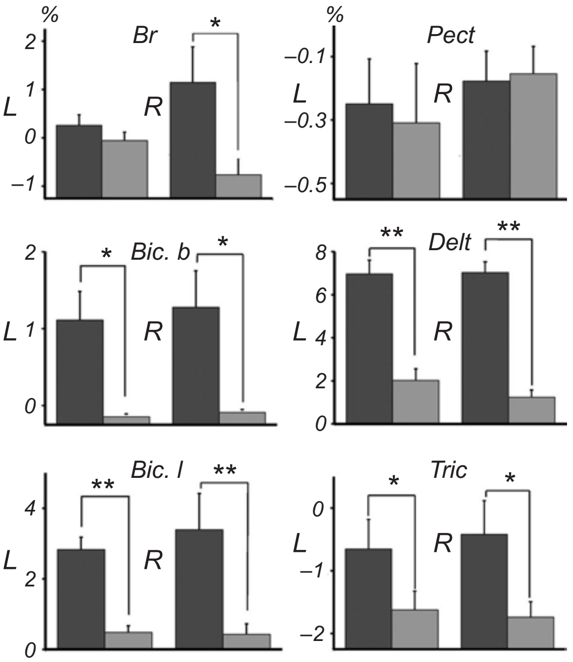

Fig.5. Correlation between the static components of EMG activity of the shoulder belt and shoulder muscles of the left (L) and right (R) hands during realization of the test movements with different directions of external loading and 1.0-sec-long active phases. Filled and gray columns correspond to the action of the external loading in the TCh and FCh directions, respectively. Other designations are the same as in Fig. 4.

Table 1. Correlation between Levels of the Static EMG Components of the Studied Muscles Depending on the Direction of the External Loading and Duration of Active Phases of the Test Movements (0.4 and 2.0 sec)

Muscles	Side	Loading	Duration of active phases of the movement	$M \pm m$	P
Bic. b	*L*	1	0.4	1.48±0.5	**0.008****
			2.0	0.91±0.4	**0.044***
		2	0.4	-0,07±0.1	**0.008****
			2.0	-0.14±0.1	**0.044***
	R	1	0.4	1.28±0.5	**0.028***
			2.0	0.98±0.3	**0.008****
		2	0.4	-0.04±0.0	**0.028***
			2.0	-0.06±0.0	**0.008****
Bic. l	*L*	1	0.4	2.46±0.3	**0.001****
			2.0	2.78±0.6	**0.004****
		2	0.4	0.48±0.1	**0.001****
			2.0	0.38±0.1	**0.004****
	R	1	0.4	3.83±1.3	**0.016***
			2.0	2.77±0.8	**0.007****
		2	0.4	0.65±0.4	**0.016***
			2.0	0.27±0.2	**0.007****
Br	*L*	1	0.4	-0.02±0.4	0.17
			2.0	0.30±0.4	0.367
		2	0.4	-0.10±0.2	0.17
			2.0	-0.12±0.2	0.367
	R	1	0.4	1.28±0.8	0.189
			2.0	0.94±0.6	0.102
		2	0.4	-0.73±0.3	0.189
			2.0	-0.70±0.3	0.102
Tric	*L*	1	0.4	-0.84±0.5	**0.006****
			2.0	-0.56±0.5	**0.023***
		2	0.4	-2.16±0.6	**0.006****
			2.0	-1.67±0.3	**0.023***
	R	1	0.4	-0.45±0.6	**0.035***
			2.0	0.05±0.4	**0.002****
		2	0.4	-1.84±0.3	**0.035***
			2.0	-1.59±0.2	**0.002****
Pect	*L*	1	0.4	-0.22±0.1	0.41
			2.0	-0.32±0.2	0.984
		2	0.4	-0.30±0.1	0.41
			2.0	-0.31±0.2	0.984
	R	1	0.4	-0.24±0.1	0.705
			2.0	-0.18±0.1	0.773
		2	0.4	-0.29±0.1	0.705
			2.0	-0.13±0.1	0.773
Delt	*L*	1	0.4	7.07±0.7	**0.005****
			2.0	6.63±0.8	**0.006****
		2	0.4	2.41±0.5	**0.005****
			2.0	2.04±0.5	**0.006****
	R	1	0.4	7.00±0.7	**0.004****
			2.0	7.02±0.8	**0.002****
		2	0.4	1.88±0.8	**0.004****
			2.0	1.54±0.7	**0.002****

Footnotes. L and R) Left and right hands, respectively; $M \pm m$) Means and s.e.m. of the level of normalized EMGs within the stationary phase. Cases of significant differences (*$P < 0.05$ and **$P < 0.01$) between the levels of EMG activity of the studied muscles at the phase of holding of the limb in the stationary position are shown boldfaced and by asterisks.

Table 1). In reactions of the examined muscles, a clearly pronounced dependence of the stationary EMG levels on the movement velocity was a general regularity. Increase in the velocity usually led to intensification of the stationary EMG phase. It was also found that the static components of EMG activity of all the examined muscles were significantly higher during the action of extending loading, compared with that under the action of the flexing force. This observation is confirmed by the statistical significance of the differences ($P < 0.05$). The levels of shoulder flexor (*Pect*) and of *Br* activity were exceptions. It should be noted that the static component of *Br* activity in the right hand was appreciably greater as compared with that in the left hand. This was observed at durations of the active phases of the movement equal to 0.4 and 1.0 sec. In other examined muscles, the levels of EMG at holding of the stationary phase of the test movements were nearly equal for both left and right hands.

DISCUSSION

We analyzed coordination of the CMCs addressed to the shoulder belt and shoulder muscles during realization of relatively simple bimanual two-joint movements. These movements were performed synchronously under conditions of the action of external loadings and included symmetric phases of TCh and FCh movements of the levers separated by a phase of static fixation of the position of the limbs. The main aim of our study was to estimate patterns of averaged EMGs in different shoulder belt and shoulder muscles and to compare the activity of the corresponding muscles of the right and left hands. In the case where the external loading acted in the direction corresponding to flexion of the shoulder joints and extension of the elbow joints (i.e., it had the FCh direction), angles in the latter joints in the flexed equilibrium position were maintained by a force developed by the flexors. In this case, among the examined muscles flexing the elbow joints, only the *Bic.b* and *Bic.l* demonstrated a high activity at the phase of holding of the limbs in a stationary position. During the maintenance of the elbow joints in the flexed position, the *Br* developed only a small activity or was inactive. In this situation, precisely the *Bic.b* and *Bic.l* synchronously decreased their activity prior to the beginning of extension. This, we believe, led to a withdrawal of the joints from the equilibrium position and allowed the external loading to begin to extend these joints. Practically synchronously with the beginning of extension, these muscles increased their activity; concurrently, the activity of the *Br* also increased. According to this scheme, flexion of the shoulder joints was also realized, but the process of flexion was controlled by the shoulder extensors (*Delt*) counteracting the external loading. In the case of change in the direction of this loading (from extension to flexion), extension of the forearms was realized at the expense of a rise in the activity of their extensors (*Tric*), which helped the joints to go out from the equilibrium state and generated the force counteracting the external loading. The flexors were eventually activated; this probably increased the controllability of the joints. It should be noted that the activity of the *Tric* in both left and right hands was significantly higher during the action of the extending loading on the elbow joints. In this situation, these muscles worked as antagonists and were co-activated during flexion due to the development of additional efforts in the course of extension of the joints. By analogy, after a change in the direction of the external loading (from flexing, with respect to these joints, to extending), the control of the process of flexion of the shoulder joints was passed from the extensors to the flexors.

In our experimental approach, when the two-joint movements of each upper limb were formed by the single-joint components, the forearm and shoulder links moved synchronously and in an antiphase mode. This allowed us to observe certain functional interaction of the muscles responsible for the control of different joints that are, from the anatomic aspect, antagonists. In this case, it is a matter of synergic interaction of the examined muscles responsible for flexion of the elbow joints (*Br, Bic.b,* and *Bic.l*) and extension of the shoulder joints (*Delt*) in the course of the movement of the levers in the TCh direction and of the muscles responsible for extension of the elbow joints (*Tric*) and flexion of the shoulder joints (*Pect*) within the phase having the FCh direction. Muscle synergies are qualified as transitional activation of certain muscle groups coordinated in time and space [23]. Under conditions of the performance of two-joint test movements in our experiments, the muscles responsible for flexion of the elbow joints and for extension of the shoulder joints provide the movements of levers in the TCh direction at the beginning of the test, maintain stable joint angles within the stationary phase, and work in an almost background mode during the phase of FCh movement of the levers. The other muscle group (*Tric* and *Pect*) is in an antagonistic interaction with flexors and extensors of the elbow and shoulder joints, respectively. Within the two phases of movements mentioned above, the muscles increase their activity at the expense of counteraction with forces generated by flexors of the elbow joints and extensors of the shoulder joints. The relatively significant variability of EMG activities of these muscles at the stationary phase of the test movement is obviously related to their auxiliary role in realization of this movement. Such functional interaction of the muscles, first of all, provides coordinated changes in the angles in the shoulder and elbow joints during realization of two-joint movements of the limb and, in turn, stabilizes certain characteristics of central motor control.

During realization of the movements, CMCs coming to the elbow flexors were more flexible and more variable compared with those addressed to the shoulder extensors. This is confirmed by the presence of constant statistically significant differences between the *D1* and *D2* levels in the *Delt* activity, independently of the movement velocity and direction of action of the external loading. However, with increase in the duration of active phases of the movements in the muscles responsible for flexion of the elbow joints, we observed some drop in their activity, while the amplitudes of the *D1* and *D2* remained nearly the same.

Recently, it has been found that the dynamic and static components of CMCs coming to the muscles during flexion ramp-and-hold movements depend significantly on the phenomenon of muscle hysteresis [7]. It has been hypothesized that the effects of hysteresis provide a decrease in the intensity of central efferent activity for fixation of the muscle length after muscle contraction [8]. It should be emphasized that, within our experimental paradigm, we recorded appreciably differing patterns of EMG activity within the phase of the FCh movement, when the muscles were stretched in a mode of additional work (Fig. 2).

In efferent activity controlling two-joint movements, certain time intervals may exist within which programs of co-activation of the agonists and antagonists prevail. Phases of active movements are, to a considerable extent, accompanied by co-activation of antagonists, while holding of the stationary phase is related to the predominant use of “normal” (reciprocal) activation. In our recent studies, we found that reciprocal activation can provide a considerably more linear pattern of the movement after a change in its direction and initiation of its rapid start. It was also found that the co-activation patterns can significantly decrease undesirable effects of ambiguity in the system of motor control; in particular, these modes can neutralize, to a certain extent, the effects of muscle hysteresis [6, 24]. Examination of the control of forward motions shows that tested subjects use co-activation of the muscles as a strategy in order to stabilize the position of the limb joints under conditions of action of external forces [25, 26]. During realization of the movements, tested subjects can create a certain balance of muscle co-activation to provide greater stiffness of the limb in different spatial directions [1] and in various joints [2]. There is a viewpoint that the CNS can rather widely use co-activation as a strategy to increase the accuracy of targeted limb movements [3].

In some studies, it has been demonstrated that, during the development of bimanual isometric efforts, tested subjects can use only the sensory feedback strategy for redistribution of generated forces between the muscles of both limbs [21, 27]. However, in the case where the action of an external factor is significant, the process of coordination of motor commands becomes dissimilar from that normally expected. In our tests, despite a rather high quality of performance of the test movements by the subjects, the patterns of EMG activity of analogous muscles controlling the right and left hands may differ somewhat from each other. It is most likely that such differences between CMCs addressed to the muscles during active phases of the test movements is related to attempts of the tested subject to use the strategy of redistribution of the activity between analogous muscles, in order to balance the action of external loadings and to neutralize differences between the efforts developed by the left and right hands; in such a way, simultaneous movements of both limbs are better coordinated.

It is obvious that movements performed under conditions of our tests should be considered only a relative analog of the movements of a rower. Under real conditions of sculling, handles of the oars move along cyclic trajectories in 3D space but not exclusively within a horizontal plane. Within the framework of our own experimental protocol, movements of the body and legs of the “rower” were absent. Nevertheless, examination of the temporal and spatial organization of activity of a number of the involved muscles during realization of synchronous bimanual movements can provide researchers with significant information on central control of such (rather complex) movements. A certain simplification of the conditions necessary for realization of such activity at the beginning of the respective studies is probably a necessary limitation.

Therefore, the analysis of records of EMG activity of the examined shoulder belt and shoulder muscles during bimanual cyclic movements showed that this activity manifests a rather complex pattern of coordination. This is confirmed by the patterns of CMCs controlling such rather complex motor phenomena. It should be noted that the data obtained in our study correspond to the modern concept that the CNS can control movements performed in modes close to isotony using a certain number of functional muscle synergies related appropriately to the motor task.

The stydy was carried out in accordance with the statements of the Helsinki declaration (1975, version of 2000) and national norms on bioethics. All participants were preliminarily informed in detail on the procedure of the study; their written consent was received.

The authors, T. I. Abramovich, I. V. Vereshchaka, A. M. Tal'nov, A. V. Gorkovenko, M. Dornovski, and A. I. Kostyukov, confirm the absense of any conflict related to comercial or financial interests, to interrelations with organizations or persons in any way involved in the research, and to interrelations of the co-authors.

REFERENCES

1. H. Gomi and R. Osu, "Task dependent viscoelasticity of human multijoint arm and spatial characteristic for interaction with environment," *J. Neurosci.*, **18**, 8965-8978 (1998).
2. P. L. Gribble and D. J. Ostry, "Independent coactivation of shoulder and elbow muscles," *Exp. Brain Res.*, **123**, 335-360 (1998).
3. P. L. Gribble, L. I. Mullin, and A. Mattar, "Role of contraction in arm movement accuracy," *J. Neurophysiol.*, **89,** 2396-2405 (2003).
4. A. N. Tal'nov, T. Tomiak, A. V. Maznychenko, et al., "Firing patterns of human biceps brachii motor units during isotorque ramp-and-hold movements in the elbow joint," *J. Neurophysiol.*, **46**, 212-220 (2014).
5. A. N. Tal'nov, D. A. Vasilenko, S. G. Sirenko, et al. "Roles of dynamic and stationary components of a motor command in establishing the equilibrium state at simplest targeted movements," *Neirofiziologiya/ Neurophysiology*, **30**, No. 6, 420-423 (1998).
6. A. I. Kostyukov, "Muscle hysteresis and movement control: a theoretical study," *Neuroscience*, **83**, 303-320 (1998).
7. A. I. Kostyukov and O. E. Korchak, "Length changes of the cat soleus muscle under frequency-modulated distributed stimulation of efferents in isotony," *Neuroscience*, **82**, 943-955 (1998).
8. W. Herzog, E. J. Lee, and D. E. Rassier, "Residual force enhancement in skeletal muscle," *J. Physiol.*, **574**, 635-642 (2006).
9. A. G. Feldman, "Functional tuning of nervous system with control of movement or maintenance of a steady posture: 2. Controllable parameters of the muscle," *Biophysics*, **11**, 565-578 (1966).
10. N. Hogan, "The mechanics of multi-joint posture and movement control," *Biol. Cybern.*, **52**, 315-331 (1985).
11. A. G. Feldman and M. F. Levin, "The equilibrium-point hypothesis−past, present and future," *Adv. Exp. Med. Biol.*, **629**, 699-726 (2009).
12. A. N. Tal'nov and A. I. Kostyukov, "Hysteresis aftereffects in human single-joint voluntary movements," *Neurophysiology*, **26**, 65-71 (1994).
13. N. V. Dounskaia, C. Ketcham, and G. E. Stelmach, "Influence of biomechanical constraints on horizontal arm movements," *Motor Control*, **6,** 366-387 (2002).
14. P. L. Gribble, L. I. Mullin, and A. Mattar, "Role of contraction in arm movement accuracy," *J. Neurophysiol.*, **89,** 2396-2405 (2003).
15. M. L. Latash, A. S. Aruin, and M. B. Shapiro, "The relations between posture and movements: study of a simple synergy in a two-joint task," *Hum. Mov. Sci.*, **14**, 79-107 (1995).
16. M. L. Latash, *Synergy,* Oxford Univ. Press, New York (2008).
17. G. Torres-Oviedo and L. M. Ting, "Muscle synergies characterizing human postular responses," *J. Neurophysiol.*, **98**, 2144-2156 (2007).
18. E. J. Weiss and M. Flanders, "Muscular and postural synergies of the human hand," *J. Neurophysiol.*, **92**, 523-535 (2004).
19. S. P. Swinnen, K. Jardin, and R. Meulenbroek, "Between-limb asynchronies during bimanual coordination: effects of manual dominance and attentional cueing," *J. Neuropsychol.*, **34,** 1203-1213 (1996).
20. N. V. Dounskaia, S. P. Swinnen, C. B. Walter, et al., "Hierarchical control of different elbow-wrist coordination patterns," *Exp. Brain Res.*, **121**, C239-C254 (1998).
21. D. S. Soteropoulos and M. A. Perez, "Physiological changes underlying bilateral isometric arm voluntary contractions in healthy humans," *J. Neurophysiol.*, **105**, 1594-1602 (2011).
22. M. Gueugnon, K. Torre, D. Mottet, and F. Bonnetblanc, "Asymmetries of bilateral isometric force matching with movement intention and unilateral fatigue," *Exp. Brain Res.*, **232**, 1699-1706 (2014).
23. A. d'Avella and E. Bizzi, "Shared and specific muscle synergies in natural motor behaviors," *Proc. Natl. Acad. Sci. USA*, **102**, 3076-3081 (2005).
24. A. V. Gorkovenko, S. Sawczyn, N. V. Bulgakova,

et al., “Muscle agonist-antagonist interactions in an experimental joint model,” *Exp. Brain Res.*, **222**, 399-414 (2012).

25. S. J. De Serres and T. E. Milner, “Wrist muscle activation patterns and stiffness associated with stable and unstable mechanical loads,” *Exp. Brain Res.*, **86,** 451-458 (1991).
26. T. E. Milner and C. Cloutier, “Damping of the wrist joint during voluntary movement,” *Exp. Brain Res.*, **122,** 309-317 (1998).
27. S. P. Swinnen, “Intermanual coordination: from behavioral principles to neural-network interactions,” *Nat. Rev. Neurosci.*, **3**, 348-359 (2002).