EXPERIMENTAL PAPERS

The Motor Synergies' Organization Features at Different Levels of Motor Control during High Coordinated Human's Movement

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Abstract—The study considers the synergetic effects manifested at the level of interaction between the various parts of the musculoskeletal system with the patterns of bioelectrical activity of skeletal muscles within the framework of the concept of hierarchical, modular principle of control. Motor synergies were studied at the muscular, kinematic, and neuronal levels. The spatial and temporal structure of motor synergies during the performance of a short straight punch by highly skilled boxers was considered. Synergies were extracted using factor analysis by principal component extraction. It was found that the muscles that form the spatial structure of the first synergy have patterns of impulse activity of the control signals characteristic of the synergy. The spatial-temporal characteristics of the movements of the body segments, as well as the parameters of the electrical activity of the skeletal muscles in the structure of synergies, demonstrate high stability in repeated realizations of the motor action and low variability in the intra- and interindividual comparison. The intermuscular interaction characteristic of synergy can be achieved by different strategies for organizing the impulse activity of motor units. A movement that is complex in coordination can have different temporal patterns of synergy activation, but the patterns of one form can be shifted in time relative to each other when they are compared during multiple realizations of a model movement.

INTRODUCTION

The problem of coordination of human movements as overcoming the redundancy of degrees of freedom, formulated by N.A. Bernstein, is still relevant today [1]. One of the theories considering the solution of this fundamental problem is based on the notion of modular organization of neuronal networks coordinating a wide range of arbitrary movements, designed to reduce the computational load on the structures of the central nervous system. This can be realized by organizing a multilevel system, where the highest level in the hierarchy regulates only some parameters of the lower level functioning independently [2]. The undoubted advantage of the hierarchical organization of control can be traced when considering the interaction between the activity of

neuronal networks controlling the joint movements of one limb, two limbs of one pair innervated by one spinal cord segment, and, finally, the coordination that unites different spinal cord segments when performing complex multi-joint bilateral movements. The first two aspects are rather widely presented in the national and foreign literature. Convincing evidence in favor of the existence of a modular control structure was obtained by studying the synergetic effects (the effects of interaction between various motor output parameters) in the structure of movements carried out in isolation by one of the upper limbs when conditions of artificial limitation of degrees of freedom were created [3]. A striking example of consideration of the synergistic interaction of the links of one pair of limbs is locomotion, the study of which is devoted by many works [4–6]. However, the issue of integrating different levels of multi-joint motion control is represented by very few studies.

As a rule, synergetic effects are considered at one of three levels, and different characteristics and parameters of motor output are used as initial data. At the muscular level, these are the parameters of skeletal muscle bioelectric activity, and at the kinematic level, the spatial and temporal characteristics of movements. The neuronal level of synergy research includes consideration of central control signals using methods of electroencephalography and electroneuromyography. Recorded signals are considered in isolation or in combination, depending on the objectives and level of research, most often using methods of data factorization, which allow to present the structure of the studied movements in the form of temporal patterns of activation of extracted modules (synergies) and their spatial architecture [7, 8]. Although there are some disadvantages and limitations of this approach, it is widely used in the study of coordination of voluntary movements and can provide insight into how motor task parameters are encoded in the structure of motor synergies [9, 10]. Thus, motor synergies have characteristic features that can be identified using matrix factorization methods, which involve simultaneous, but not necessarily unidirectional, changes in the recorded motor output parameters at a particular level of synergy study. At the mus-

cular level, these are the characteristics of skeletal muscle bioelectroactivity, at the kinematic level, the interaction of joint angles and spatiotemporal motion characteristics, and at the neuronal level, the coordinated change of central control signals.

Based on the above, the objectives of this study were to identify the synergistic effects manifested at the level of interaction between different links of the musculoskeletal system (interlink synergistic effects) and to establish the relationship between specific functions (movement of body links with certain spatial and temporal characteristics) and patterns of skeletal muscle bioelectric activity within the concept of the hierarchical modular control principle.

MATERIALS AND METHODS

Experiments were carried out on 8 male boxers with the title of candidate master of sports and master of sports, aged from 19 to 24 years. The researches were carried out on the basis of Scientific-Research Institute of Sports and Recreational Physical Culture Problems of Velikolukskaya State Academy of Physical Culture and Sports in the laboratory of physiology of nervous and muscular systems. All studies were conducted in compliance with the requirements and principles of biomedical ethics formulated in the Declaration of Helsinki, 1964, and approved by the local bioethics committee. Each participant provided voluntary written informed consent to participate in the studies.

Subjects performed three series of direct short blows on paws held by an opponent, 11 in each, with rest intervals between them until the subjective sensation of complete recovery. The first and last punch in each series were excluded from analysis, and a total of 216 punches were analyzed. Electromyograms (EMG) of 16 superficial skeletal muscles of the trunk, upper and lower extremities were recorded during athlete's movements using a telemetric multichannel biomonitor ME6000 and MegaWin software (MegaElectronics LTD, Finland). EMG of the following bilateral muscles was recorded: biceps and triceps brachii, trapezoid (upper bundles), deltoid (anterior part), greater pectoralis, abdominal rectus (middle part), and biceps and rectus femoris. For

Table 1. Processing procedures applied to data rows and analyzed signals' number

Processing procedures	Variationrows				
	EMG	joint angle value	distance	speed	acceleration
Number	16	10	16	16	16
Bandpass filtering 30–450 Hz	+	–	–	–	–
Rectification (interval = 0.002 s)	+	–	–	–	–
LPF (15 Hz)	+	–	–	–	–
Exponential smoothing ($\alpha = 0.050$)	–	–	+	+	+

EMG retraction, we used cutaneous disposable self-adhesive electrodes with conductive gel and an active contact area of 2.5 cm^2, 36 × 45 mm (Swaromed, Austria). The electrodes were applied bipolar, with the active one placed in the projection area of the motor point of the studied muscle, and the reference one attached along the course of its fibers with 2 cm distance between the electrodes; an additional grounding electrode on each muscle was provided [11]. EMG signals were amplified by a biomonitor with a bandwidth from 10 to 10000 Hz and digitized at a frequency of 2000 Hz.

The recorded EMG were processed in two ways. In the first case, they were filtered with a bandpass filter with a bandwidth of 20–450 Hz and a suppression strength of 60 dB, then rectified with an averaging interval of 0.002 s, and a low-pass filter (LPF) of 15 Hz was repeatedly applied using the MegaWin software. In the second case, no filters were applied to the signals when considering the interaction effects of interference EMG potentials. Since the source of each potential deviation in interference EMG is a motor unit action potential, the dynamics of such deviations can provide information about the impulse activity of motor units (MU) in the EMG lead area [12]. The EMG variation series was divided into twenty equal segments, in each of which the number of tournaments (turns) was calculated. The change of EMG curve direction regardless of zero line crossing with peak-to-peak amplitude not less than 10 μV was taken as a turn unit [12, 13]. The

EMG processed by two methods were exported to the Statistica system (StatSoft, Inc., version 10).

Video capture of the athlete's movements was performed using the Qualisys 3D video capture system (Qualisys, Sweden), including 8 high-speed Oqus cameras. Reflective markers were attached to bilateral anthropometric points of body segments: frontal, cervical, brachial, radial, styloid, trochanteric, superior tibial, inferior tibial, and terminal [14]. The video capture frame rate was 500 Hz. The beginning of the athlete's movement (short direct kick) was determined by the beginning of the angle change in the knee joint of the right leg, and the end was determined by the moment when the styloid point on the target finished moving. The primary processing of the video sequences was performed in the Qualisys Track Manager software environment, and the movements of anthropometric points, their velocity and acceleration, and the values of articular angles were calculated. Digitized data containing variation series of movements, velocities, accelerations, values of articular angles, as well as markers determining the boundary moments of the start and end of movement were exported to the Statistica system.

A matrix of initial data (X) was formed in the Statistica system, with dimensions ($I \times J$), where I is the number of points (measurements at the moment of time) of motor action (for each movement—300 points), and J is the number of independent variables (variation series of EMG, joint angles, kinematic parameters—74 in total), the
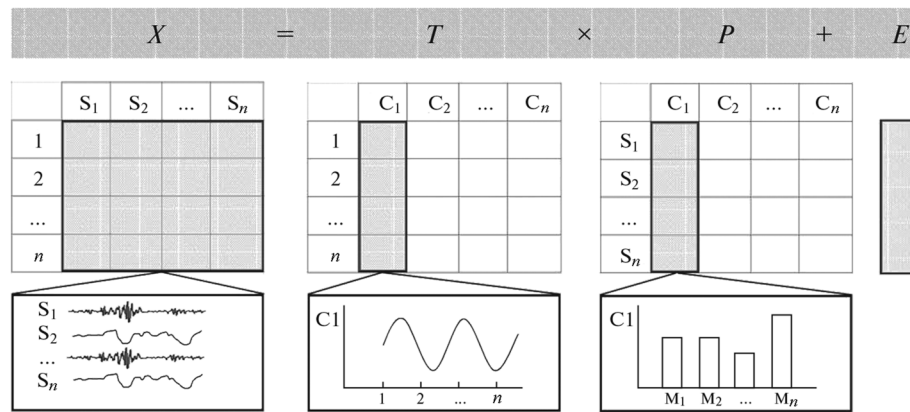
Fig. 1. The original matrix decomposition scheme. *X*—Initial matrix, *T*—the matrix of accounts, *P*—the matrix of loads, *E*—the matrix of residuals. S1,2,*n*—the initial signals data (EMG, angle values, etc.), C—the principle component, 1, 2, ... *n*—the value at the time.

total dimension of the matrix being 2700×74. All variation series were interpolated relative to a single point of reference. A simple exponential smoothing ($\alpha = 0.050$) was applied to the series containing data on displacement, velocity, and acceleration of points in the body segments. All data in the matrix were standardized to a unit standard deviation (Table 1).

Similarly, we formed a separate data matrix of the same dimensionality, where *I* is the number of points (measurements at a point in time) of motor action (for each movement—20 points), and *J* is the number of independent variables (variation series of the number of EMG turns—16 in total), the total dimensionality of the matrix is 180×16. The data in the matrix were standardized to one standard deviation.

Synergies were extracted from the matrices using factor analysis (FA) by principal component extraction without factor rotation. Factor analysis was used as a method to reduce the dimensionality of the data and as a method to classify the data. The percentage of total variance accounted for by each factor in the total data set (VAF) was used as a criterion of the efficiency of synergy extraction. A VAF of at least 80% was considered an acceptable level of efficiency for reconstruction of the original data. Factors with eigenvalues greater than one and accounting for at least 5% of the total variance were considered.

Matrix *X* was decomposed into the product of two matrices: $X = T \times P + E$, where *T* is the matrix of scores, *P* is the matrix of loadings, *E* is the matrix of residuals (Fig. 1). The loadings matrix carries information about the relationship or independence of variables in relation to new, formal variables obtained in the process of decomposition of matrices—"vectors of synergy". The matrix of accounts defines the temporal organization of the identified synergies and represents the projections of the original data on the subspace of the main components—"activation coefficients". The matrices were decomposed in the Statistica 10.0 environment, using the standard module "Advanced/Multivariate−Mult/Exploratory—Factor".

Mathematical and statistical data processing was performed in Statistica 10.0 and included calculation of arithmetic mean (*M*), arithmetic mean error (*SE*), standard deviation (*SD*), and coefficient of variation (*CV*). To compare the parameters of extracted synergies, we used Pearson correlation coefficient analysis and maximum values of cross-correlation functions, taking into account the bias against zero, where 1 is complete agreement, 0 is no correlation.

RESULTS

The decomposition of the data matrix resulted in three factors (synergies) with a total share of explained variance of 85.42 ± 1.28. The activation coefficients of the first synergy were characterized by one peak of activity falling in the first half of the movement, followed by a gradual decrease in its activity (Fig. 2c). We should note the high
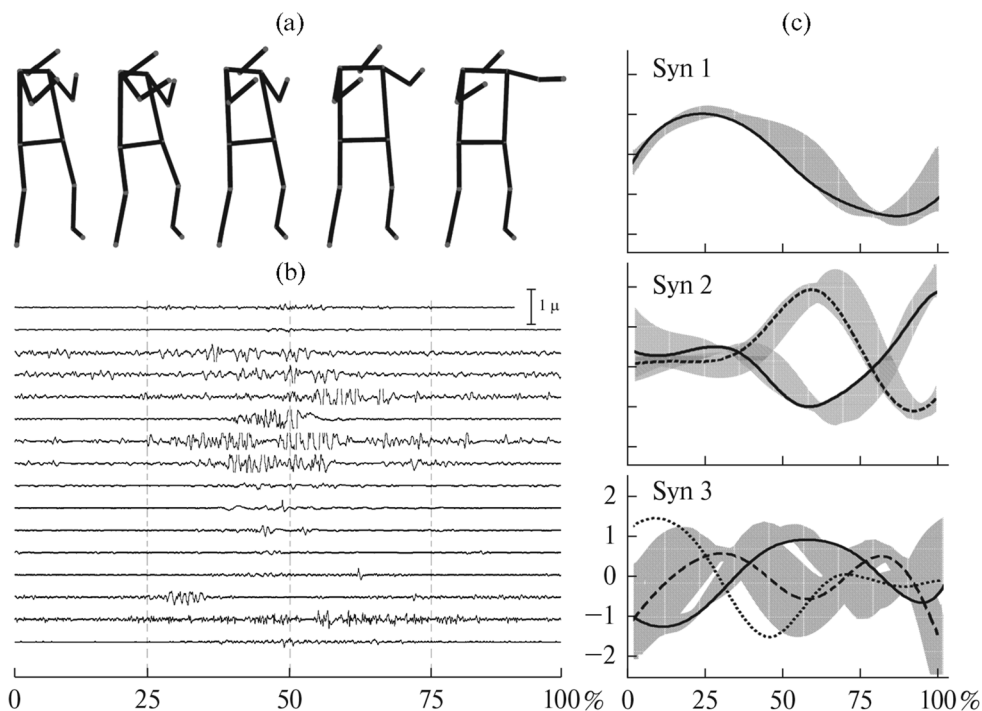
Fig. 2. Kinematogram (a), electromyogram sample (b) and activation coefficients of motor synergies (c) during "jab" performing in boxing. Syn 1,2,3—synergy number. *Abscissa*: the progress of the exercise (%), *ordinate*: c.u. In (b)—muscles from top to bottom: right biceps brachii, right triceps brachii, right trapezius (superior portion), right deltoideus (anterior portion), left biceps brachii, left triceps brachii, left trapezius (superior portion), left deltoideus (anterior portion), right pectoralis major, left pectoralis major, right rectus abdominis, left rectus abdominis, right biceps femoris, right rectus femoris, left biceps femoris, left rectus femoris. Solid and dotted lines on the chart are averaged patterns.

degree of reproducibility of the temporal structure of the first synergy during repeated beat realizations, where the maximum values of the cross-correlation functions averaged 0.83 ± 0.05 for the group, and *CV* did not exceed 15.73%.

The temporal structure of the second identified synergy showed two activation patterns with multidirectional peaks of activity in the second half of the movement (Fig. 2c). Both synergy activation patterns had high concordance coefficients when compared across attempts, 0.73 ± 0.05 and 0.71 ± 0.06, noting their low coefficients of variability of 12.20% and 15.31%, respectively. The activation coefficients of the third synergy were represented by three characteristic patterns. The first pattern was characterized by a smooth increase in the coefficients by the middle of the movement and their gradual decrease by the end of the movement, the second pattern had two pronounced peaks of activity in the first and second half of the exercise, the coefficients of the third pattern decreased by the middle of the exercise and

increased by the end of the third quarter of the motor action in question (Fig. 2c).

Based on the objectives of the work, the vectors of the extracted synergies were considered. The interaction of the six skeletal muscles included in the structure of the first synergy was established: the right and left triceps shoulder, the deltoid, the right biceps thigh muscle, and the left lower extremity straight thigh muscle (Fig. 3a). These muscles were included in the structure of the first synergy in 100% of the attempts realized by all subjects, with *CV* not exceeding 11.86%, while, for example, for the left-sided straight thigh muscle there was a very low variability and high degree of repeatability of its inclusion in the structure of the first synergy—4.79%.

It should be noted that in addition to the mentioned muscles, the structure of the first synergy in the range of 61% to 86% of the total number of attempts also included the left deltoid, large pectoral muscles, and rectus abdominis muscle of the right side of the body. Overall, the vectors of the
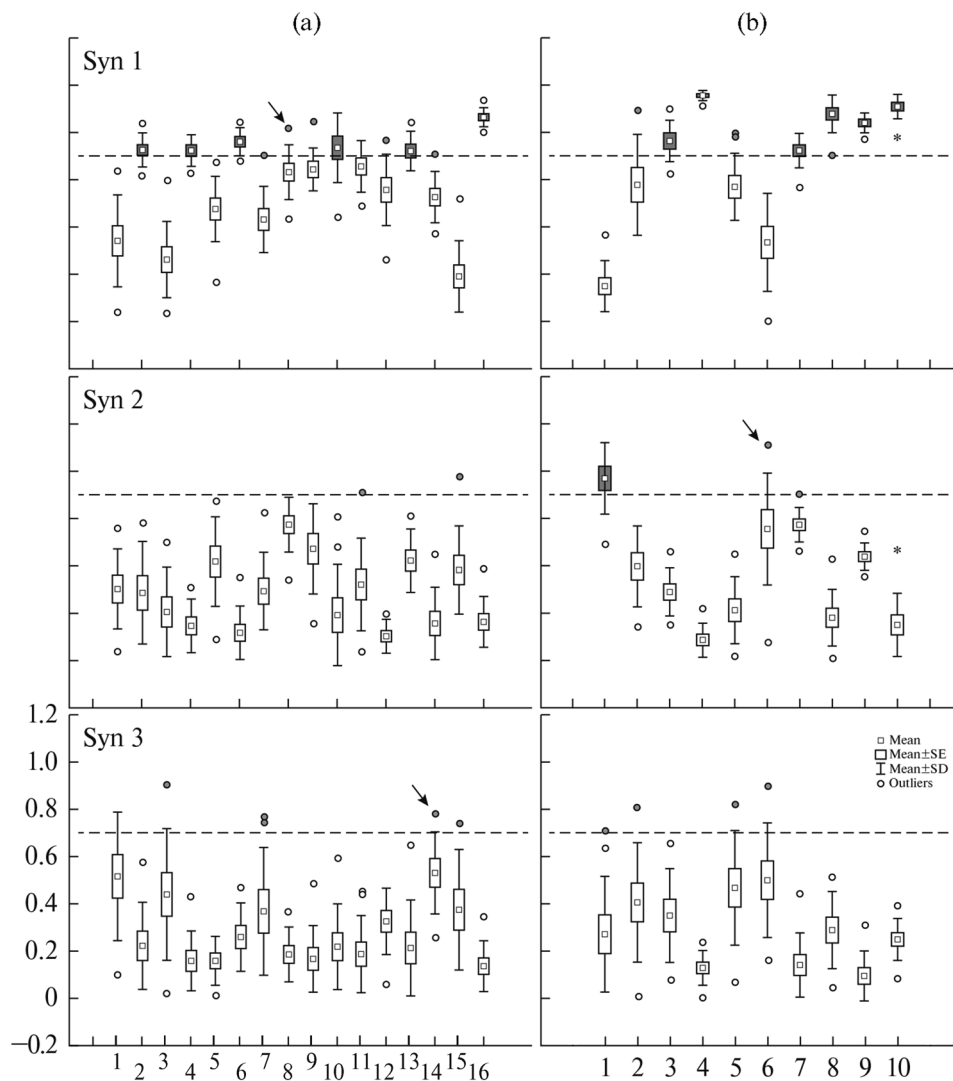
Fig. 3. Vectors of motor synergies when "jab" performing in boxing. Syn1,2,3—synergy number. (a) Muscle synergies, (b) kinematic synergies (coactivation of articular angles). In (a): 1—right biceps brachii, 2—right triceps brachii, 3—right trapezius (superior portion), 4—right deltoideus (anterior portion), 5—left biceps brachii, 6—left triceps brachii, 7—left trapezius (superior portion), 8—left deltoideus (anterior portion), 9—right pectoralis major, 10—left pectoralis major, 11—right rectus abdominis, 12—left rectus abdominis, 13—right biceps femoris, 14—right rectus femoris, 15—left biceps femoris, 16—left rectus femoris. In (b): 1—left hip joint, 2—right hip joint, 3—left knee, 4—right knee, 5—left ankle, 6—right ankle, 7—left elbow, 8—right elbow, 9—left shoulder, 10—right shoulder. *Ordinate*: factor loads. The data is presented as $M \pm SE \pm SD$.

first synergy showed low variability and high reproducibility, with correlation coefficients of 0.71 ± 0.02 and *CV* not exceeding 15.46%. The structure of the other identified synergies was predominantly represented by a single skeletal muscle with high correlation coefficients with the new (formal) component, the left deltoid (55.6% of cases, 0.57 ± 0.03, *CV*—20.62%) in the second synergy and the right double-headed arm in 54.6% of cases (0.51 ± 0.09, *CV*—52.46%) in the

third. The trapezius muscle, right abdominal rectus, right thigh rectus, and left lower extremity biceps muscle were found to be connected to the synergies in individual cases (Fig. 3a). These connections are shown as extremes (outliers) in the figure. The vectors of these synergies showed a medium degree of similarity, not more than 0.65 ± 0.02, and the variability was assessed as low, *CV* not more than 14.1%. Thus, the spatial structure of the second and third muscle synergies
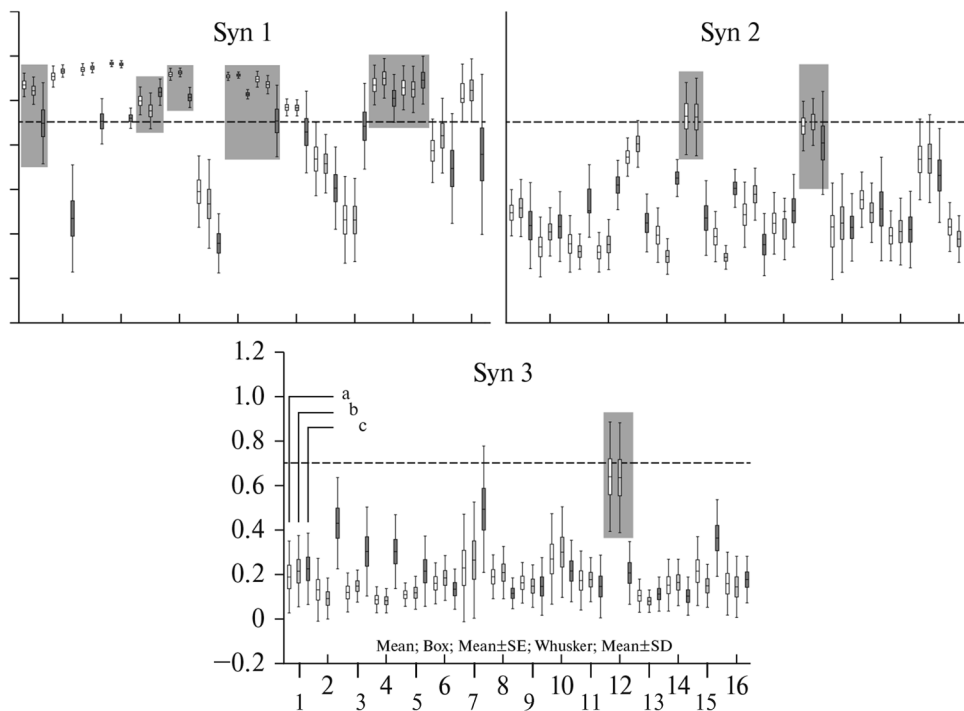
Fig. 4. Vectors of kinematic synergies when "jab" performing in boxing. a—Distance, b—speed, c—acceleration. Along the *abscissa* axis are anthropometric points: 1—metopion, 2—cervical, 3—right acromion, 4—left acromion, 5—right radiale, 6—left radiale, 7—right stylion, 8—left stylion, 9—right trochanterion, 10—left trochanterion, 11—right tibiale, 12—left tibiale, 13—right sphyrion, 14—left sphyrion, 15—right acropodion, 16—left acropodion. On the *ordinate* axis—factor loads. Syn1,2,3—synergy number. The data in Fig. is presented like $M \pm SE \pm SD$.

proved to be variable when considering their component composition and reproducibility in different attempts on average for the group of boxers.

The spatial organization of the first synergy was determined by the coactivation of the hip, shoulder, and elbow joints on both sides of the body in 100% of the cases (Fig. 3b). The named joint angles showed high factor loadings, and their variability was evaluated as low, e.g., the CV of the right ankle and left shoulder joints did not exceed 4.96% when comparing them in different realizations. Synergy vectors also showed high concordance in different attempts, 0.84 ± 0.03, and CV were 11.87%. It should be noted that the left elbow joint was involved in the first synergy in 87% of impact realizations and the hip joint on the right side of the body was involved less frequently—56% of cases. The second synergy was characterized by an interaction between the left hip joint (90% of cases, $CV = 19.8\%$) and the knee joints of both lower extremities (Fig. 3b). The vectors of this synergy showed a high degree of similarity, with correlation coefficients averaging at

least 0.92 ± 0.01 for the group, and their variability was rated as extremely low ($CV = 3.1\%$). The third synergy predominantly included the dynamics of hip and knee joint angles, but only in some realizations did the coefficients of these angles reach our established threshold of referring to synergy of 0.7. Nevertheless, the vectors of the third synergy demonstrated high reproducibility in different attempts (0.78 ± 0.02) and very low variability, CV not exceeding 9.92%.

The spatial organization of the identified kinematic synergies is shown in Fig. 4. It was found that the first synergy included synergetic patterns of movement of most of the anthropometric points. Thus, in all realizations, combined movements of the upper extremities, head, and lower extremities were observed by all subjects with the exception of the upper tibial anthropometric points. The factor loadings of the upper limb points, when examined inter- and intraindividually, showed very low coefficients of variability-no more than 7.63%, while the lower extremity and limb points showed somewhat larger values, rang-

ing from 10.14% to 24.84%. In general, the vectors of the first kinematic synergy determined by the combined movement of the anthropometric points of the body segments averaged 0.89 ± 0.01, and their variability was very low, 4.28% (Fig. 4a).

It was found that the body segments with characteristic synergistic movement patterns had similar dynamics of changes in the velocities and accelerations of the corresponding anthropometric points (Fig. 4b). Their variability was also low, and there was a high degree of similarity between the synergistic vectors (0.88 ± 0.01, CV—6.49% and 0.66 ± 0.05, CV—2.12%, respectively).

The second identified synergy was characterized by the corresponding movement patterns of the radial, styloid, and upper tibial anthropometric points on the right side of the body; synergistic interaction of these segments was noted in most of the recorded movements. Vectors of this synergy showed a high degree of correspondence—0.78 ± 0.03. It was also found that the structure of the second synergy was determined not only by movement patterns, but also by characteristic combined velocity changes of the same body segments, demonstrating high correspondence of the synergy vectors in repeated realizations of the impact—0.79 ± 0.03 (Fig. 4b). The coefficients of variation of the body segments in the structure of the second synergy in the different beat realizations were estimated to be low, with CVs ranging from 15.03% to 24.22%. Vectors of the second synergy also demonstrated low variability, 14.42%. It should be noted that in a number of realizations of the movement (not more than 34% of cases), the structure of the second synergy additionally included the right lower extremity endpoint, which has similar dynamics of movements and velocities.

The combined movement and velocity of the right styloid and upper tibial anthropometric points of the left lower extremity determined the structure of the third synergy considered (Fig. 4). The coefficients of variation of the factor loadings of these points were evaluated as average, both when considering movement patterns and velocities during repeated realizations of direct impact, while the other segments under consideration showed high variability. Vectors of the third synergy showed a high degree of similarity, $0.70 \pm$

0.03 and 0.73 ± 0.04 for displacements and velocities, respectively, and low variability, not more than 19.12%. The acceleration patterns of the recorded body segments were in most cases more variable and had no changes in the displacement and velocity indices characteristic of synergy.

The analysis of the temporal structure of the patterns of the synergistic interaction between the central control signals showed the presence of two different motion control strategies. The first one was characterized by an increase in the impulse activity of the MU in the second half of the movement and reached its maximum by its end; the second one demonstrated a gradual decrease in the activity (Fig. 5a).

Both activation patterns had a high degree of reproducibility, as evidenced by the high values of the maximum cross-correlation functions, 0.92 ± 0.23 and 0.84 ± 0.03. The coefficients of variation obtained by comparing the activation coefficients of these synergies of multiple beat realizations did not exceed 11.21%, which indicates low variability. It should be noted that, for the most part, maximum values of cross-correlation functions with their shift to the negative side were registered. The second and third established synergies had pronounced peaks of activity in the third and last quarters of the motion in question, their activation coefficients demonstrated average reproducibility from beat to beat, and CV were low, but reached slightly higher values than in the first synergy—25.32%.

In the absolute majority of cases, the spatial organization of the first synergy included characteristic patterns of impulse activity of the MU of the triceps brachii muscle of the left arm, great pectoral muscle of the right side, biceps femoris right, and rectus femoris muscle of the left lower extremity (Fig. 5b). In intra- and interindividual comparisons, the electrical activity of these muscles exhibited high factor loadings ranging from 0.84 ± 0.02 and above, in some realizations they reached 0.91 ± 0.01, with extremely low variability ranging from 4.68% to 7.95%. In general, the vectors of the first synergy showed high similarity in multiple repetitions of movement (0.74 ± 0.02), and their variability was rated as low. Between 50% and 80% of the total strokes recorded, the first synergy also included activity of
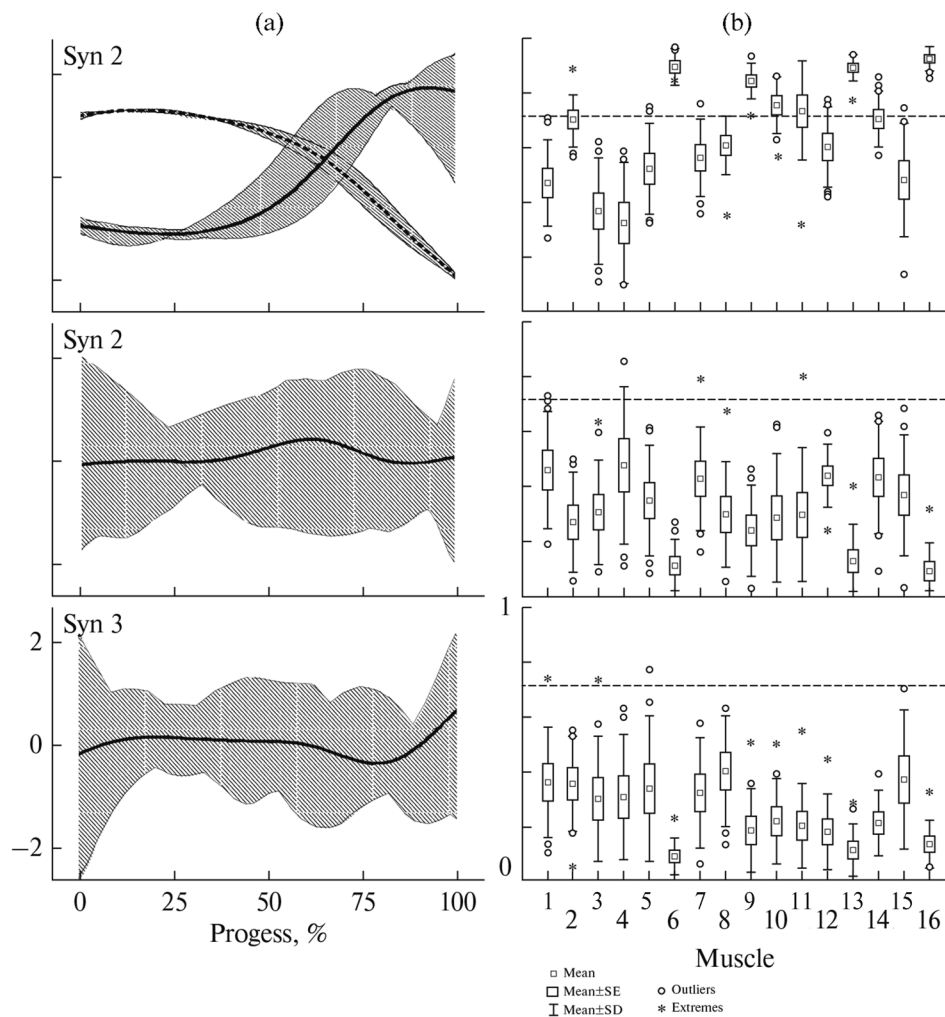
Fig. 5. Synergetic interaction patterns of motor units' impulse activity during "jab" performing in boxing. (a) Activation coefficients, *abscissa*: movement progress, *ordinate*: c.u. (b) Spatial structure of synergies, *ordinate*: factor loads, *abscissa*: skeletal muscles: 1—right biceps brachii, 2—right triceps brachii, 3—right trapezius (superior portion), 4—right deltoideus (anterior portion), 5—left biceps brachii, 6—left triceps brachii, 7—left trapezius (superior portion), 8—left deltoideus (anterior portion), 9—right pectoralis major, 10—left pectoralis major, 11—right rectus abdominis, 12—left rectus abdominis, 13—right biceps femoris, 14—right rectus femoris, 15—left biceps femoris, 16—left rectus femoris. Syn1,2,3—synergy number.

the right triceps shoulder muscle, left thoracic great muscle, right abdominal straight muscle, and right lower extremity thigh straight muscle. The second and third established synergies showed an average reproducibility of the synergy vectors (0.57 ± 0.06 and 0.31 ± 0.03, respectively) with a low variability reaching 27.95%. Note that the vectors of these synergies did not reach the established threshold of 0.7 on the average for the group, but in some realizations (up to 30% of the total number of movements), the second synergy can be attributed to the impulse activity of the right arm biceps and deltoid muscle, and the third

synergy includes the right arm biceps, trapezius, left arm biceps, deltoid, and left lower extremity biceps. In Fig. 5b, these values are represented as extreme, sharply different values from the mean (outliers extremes).

Thus, during repeated realizations of a direct blow in boxing, the structure of the first synergy was represented by two different temporal patterns of activation, and the spatial structure included more than half of the studied skeletal muscles with characteristic synergistic patterns of impulse activity of motor units. The other identified synergies demonstrated the temporal dynam-

ics characteristic of synergy, but were characterized by unstable spatial organization.

DISCUSSION

In our study, 4 to 5 extractable factors (synergies) were obtained in different implementations of direct impact, but three synergies were left for consideration, because the others in most cases did not meet the established requirements for extraction efficiency by factor analysis, and in addition, the data of these factors are difficult to give an acceptable physiological interpretation. A similar number of extracted modules was obtained when considering acyclic movements that involve different body segments, and it is noted that the synergies detected by factorization methods are not computational artifacts, but reflect the main aspects of the organization of muscle activation patterns that underlie motor behavior [15, 16].

A number of studies point to the need for caution when choosing the initial signals to be included in the analysis, since the number of EMG in the analysis of muscle synergies and the number of repetitions of the studied movement affect the results of their extraction and the adequacy of the interpretation of the data obtained. There is evidence of possible discrepancies in the results of synergy consideration even when considering biomechanically similar movements [10, 17]. Perhaps the results of synergy extraction are sensitive to the original data set due to the peculiarities of the factor analysis algorithm. Thus, in principal component analysis, factor extraction is performed sequentially with maximization of the residual variance, so that the newly extracted factors are orthogonal (uncorrelated). This suggests that, for example, muscle synergies extracted from an initial data set containing only EMG data will be different from those extracted from a broader set of signals. At first sight, this fact may seem as a disadvantage of the method, however, the approach with inclusion of various signals in the analysis and corresponding preliminary mathematical processing is, in our opinion, the most expedient, because only in this case the combined changes of movement parameters, reflecting all levels of its study, are taken into account.

The coordinated activation of skeletal muscles,

leading to the corresponding interaction of joint angles, characteristic patterns of movements and velocities of different body parts, is probably not a simple consequence of biomechanical interaction of body segments and even more a computational artifact, but is caused by the control of CNS structures. This question is quite often raised by researchers of movement coordination, and evidence in favor of neuronal control of control through formation and modulation of motor synergies is increasingly cited [18, 19]. Confirmation of the neuronal origin of synergies is found in our data when considering intermuscular coordination and characteristic patterns of impulse activity of the MU of a number of skeletal muscles. It turns out that the muscles that form the spatial structure of the first synergy also have characteristic for synergy combined patterns of impulse activity of control signals. In addition, the spatio-temporal characteristics of the body segments, as well as the skeletal muscles in the synergy structure, show high stability during repeated realizations of the standard movement and very low variability during intra- and interindividual comparisons. This pattern is traceable in different subjects, despite rather significant differences in their anthropometric data. Thus, the identified synergies are probably separate morphofunctional units whose functioning is based on the activity of neuronal networks that provide reliable control of a complex motor skill, integrating reflexes organized at different levels of the spinal cord and implementing a combined unidirectional change in motor output parameters.

In addition to the formation of functional synergies, the problem of redundancy of degrees of freedom can be solved by dividing the control parameters into essential and non-essential ones [20]. In fact, such control parameters can also be found in the structure of retrievable motor synergies, as indicated by the pattern of variability in their spatial and temporal architecture. In our studies, in most cases, the parameters exhibiting synergistic interaction in the structure of extracted synergies had a low or extremely low level of variability. In addition, there was a tendency for an increase in the variability of the parameters of those body segments that perform less movement—these are the lower extremities and the ter-

minal anthropometric points, while the upper shoulder girdle showed low variability in the structure of the synergies. Obviously, the latter are of decisive importance in the efficiency of the target movement realizations and the control system in this case has a tighter control of the parameters, but still allows a slight variability. The above is consistent, to a certain extent, with the concept of "motor equivalence", according to which the control system can generate different movement strategies even under unchanged external conditions [18]. In the structure of the motor synergies of the movement we considered, the dynamics of the EMG activity and the spatiotemporal characteristics of individual body segments demonstrated high stability during repeated realizations of the impact. Another control principle closely related to the manifestation of movement variability is the ability of the control system to achieve the goal through different strategies—"motor constancy". Our studies also confirm this principle with regard to the structure of motor synergies. It was found that in a number of movement realizations, additional muscles were involved in the synergy, which led to the appearance of additional coactivation effects of some joint angles. This pattern was also observed at the level of control signals. The temporal structure of some of the identified synergies also demonstrated this ability of the control system, which manifested itself in the formation of completely different temporal patterns of activation during the realization of the impact under standard experimental conditions. Thus, the structure of the first synergy at the muscular level was determined by a single activation pattern, whereas at the level of control signal interaction, the same synergy demonstrated two characteristic patterns. Thus, intermuscular synergy can be achieved by different strategies for organizing the impulse activity of motor units.

Different temporal patterns and spatial structure of synergies can be associated with the transition from discrete movements to rhythmic movements, which have different ways of control in the CNS. It has been reported that the generation of synergies in rhythmic movements may provide greater computational efficiency, i.e., reduce the load on the higher controlling departments to a greater extent [22, 23]. We do not exclude such a possibility, because the research protocol did not involve establishing the pace of the movements, and analysis of the time intervals between beats of one series showed their decrease compared to the beginning of the series. In addition, the so-called one-step synergies considered in this work, and synergies that change over time, are also known [24]. The detection of the latter is possible using the analysis of cross-correlation functions, where the shift of maximums relative to zero indicates the advance or delay of one process relative to another [12]. The obtained cross-correlation function coefficients in our studies were predominantly shifted to the negative side in a number of beat realizations. This indicates that a standard motion can have different temporal patterns of synergistic activation, but that patterns of the same form can be shifted in time relative to each other when they are compared during multiple realizations of the model motion.

CONCLUSION

The spatial structure of motor synergies organized at the muscular level and at the level of control signals demonstrates high similarity and stability during repeated realizations of a standard movement, which testifies in favor of the statement about the neuronal nature of movement control by combining different spinal cord segments into a single control system.

The high stability of the spatiotemporal structure of the extracted synergistic modules organized at different levels of the control system, as well as the formation of different temporal patterns of synergy activation during repeated realizations of a complex movement demonstrate the ability of the control system to generate different strategies for solving a motor task in standard, relatively unchanged conditions of its execution.

AUTHORS' CONTRIBUTIONS

S.A.M.—planning, organizing and participating in conducting experiments, recording and analyzing the data obtained, processing the data, preparing the text of the manuscript; R.M.G.—general control of experiments, participation in the preparation of the manuscript.

FUNDING

CONFLICT OF INTEREST

The author declares that there is no conflict of interest.

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Translated by A.V. Dyomina