ISSN 0022-0930, Journal of Evolutionary Biochemistry and Physiology, 2022, Vol. 58, No. 6, pp. 1775–1784. © Pleiades Publishing, Ltd., 2022.
Russian Text © The Author(s), 2022, published in Zhurnal Evolyutsionnoi Biokhimii i Fiziologii, 2022, Vol. 58, No. 6, pp. 549–557.

EXPERIMENTAL PAPERS

Spatio-Temporal Patterns of Intermuscular Interaction during Locomotion Induced by Spinal Cord Percutaneous Electrical Stimulation

S. A. Moiseev[a,*]

[a] *Velikiye Luki State Academy of Physical Education and Sports, Velikiye Luki, Russia*
**e-mail: sergey_moiseev@vlgafc.ru*

Received July 15, 2022

Revised September 16, 2022

Accepted September 27, 2022

Abstract—The paper considers the spatiotemporal muscle synergies' structure during voluntary locomotions in conditions of lower extremities horizontal support, and when step-like movements modulated by transcutaneous electrical spinal cord stimulation (TESCS). The synergies were extracted by matrix decomposition using the principal component method (PCA). Fewer synergies were found in locomotion initiated by percutaneous electrical stimulation of the spinal cord. It has been established that the temporal structure of extracted muscle synergies during locomotion under spinal cord electrical stimulation has evident peaks of activity and high reproducibility of activation patterns. In some cases, they are implemented in different time periods of the locomotive cycle while their repeated performing. The muscle loads in the identified synergetic modules' structure are significantly differing, however, the synergy vectors turn out to be highly similar in different experimental conditions. The muscle synergies' spatiotemporal structure differences during voluntary and induced locomotions are probably related to the reorganization of the rhythmogenerating part of the spinal neuronal network that controls the structure of the locomotor cycle.

DOI: 10.1134/S0022093022060096

Keywords: muscle synergies, spinal cord electrical stimulation, locomotion, intermuscular interaction, motion control

In the last decade, significant progress has been made in the research of synergetic effects in motion control, but a large number of unresolved issues remain, ranging from the methodological aspects of their extraction to conceptual questions about the nature of the synergetic phenomena under study. One of the most important for understanding the nature of the synergistic effects being detected is the area of interaction between different CNS levels in the generation and modulation of synergies. In the process of locomotor activity, such interaction can be achieved by introducing reciprocal and coactivation commands into the control system. The concept of these commands in the CNS as the main modes of interaction between the pools of motoneurons innervating muscle pairs in the agonist-antagonist system has been known for quite some time, and

recently the concept of such commands has been introduced to describe the control of arbitrary multi-joint movements [1, 2]. These data develop the notion of hierarchically organized control of automated movements through central pattern generators initiated by a simple command from higher-lying centers [3, 4].

We have previously shown that the application of transcutaneous electrical spinal cord stimulation (TESCS), probably affecting the motor manifestations of such commands, changes the reciprocal synergistic relationships of the lower limb muscles in the structure of synergistic modules [5]. However, the synergistic effects were considered under the conditions of arbitrarily performed movements during walking on the treadmill, which imposes certain restrictions on the operation of synergistic centers in the structure of spinal neural networks that regulate locomotor activity. In addition to biomechanical limitations, there are other factors affecting the operation of synergistic centers, such as afferentation from the support zones of the foot, central commands determining the voluntary component of locomotor movements, and several other factors, which results in rather variable motor output parameters even when they are considered intraindividually. A number of works suggest ways to minimize it, but they are mainly related to computational aspects of synergy extraction [6]. All this makes it difficult to obtain direct evidence of the synergistic control of muscle activity by the central nervous system.

By stimulating the structures of the spinal cord and brain of animals with different stimuli, it was possible to obtain spatiotemporal profiles of muscle activations characteristic of synergy and similar in structure to real movements [7, 8]. In spite of this, the nature of the observed synergistic effects remains largely unclear. The application of stimulation methods to CNS structures under conditions that minimize the influence of the above factors on the operation of synergistic centers may provide more accurate information on how the parameters of the motor task are encoded in the structure of muscle synergies. In this connection, the aim of the work was to study the synergistic effects of intermuscular interaction during involuntary locomotions induced by TESCS in the conditions of horizontal hanging of the lower limbs.

MATERIALS AND METHODS

The experiments were carried out on 8 male subjects aged 21–35 years old. The researches were carried out on the base of Research Institute of problems of sport and recreational physical education of Velikiye Luki State Academy of Physical Education 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 subject provided voluntary written informed consent to participate in the research. The subjects were placed in a horizontal lower extremity sign to minimize gravitational effects and to facilitate the step-like movements resulting from the electrical stimulation of the spinal cord structures [9, 10]. The research protocol involved performing arbitrary step movements in the horizontal sign of the lower extremities and under conditions minimizing the arbitrary component. In the latter case, subjects were instructed not to move arbitrarily and not to obstruct or concentrate on the movements of the lower extremities when they occurred. The absence of a voluntary component in the structure of evoked locomotion was monitored based on the assessment of the amplitude of movements in the joints, electromyographic activity of the skeletal muscles, and coordination between the lower extremities (Fig. 1). At least 8 full step cycles were analyzed in all experimental conditions. The boundary moments of the full step cycle were determined from the extreme positions of the metatarsal anthropometric point of the right leg in the sagittal plane.

Electromyograms (EMG) of the bilateral lower limb muscles were recorded: *tibialis anterior* (TA), *gastrocnemius mediale* (GM), *vastus lateralis* (VL), *biceps femoris* (BF), *rectus femoris* (RF). EMG was recorded using a wireless 16-channel ME6000 biomonitor (Finland) with a sampling rate of 2000 Hz. For EMG retrieval, we used cutaneous disposable self-adhesive electrodes

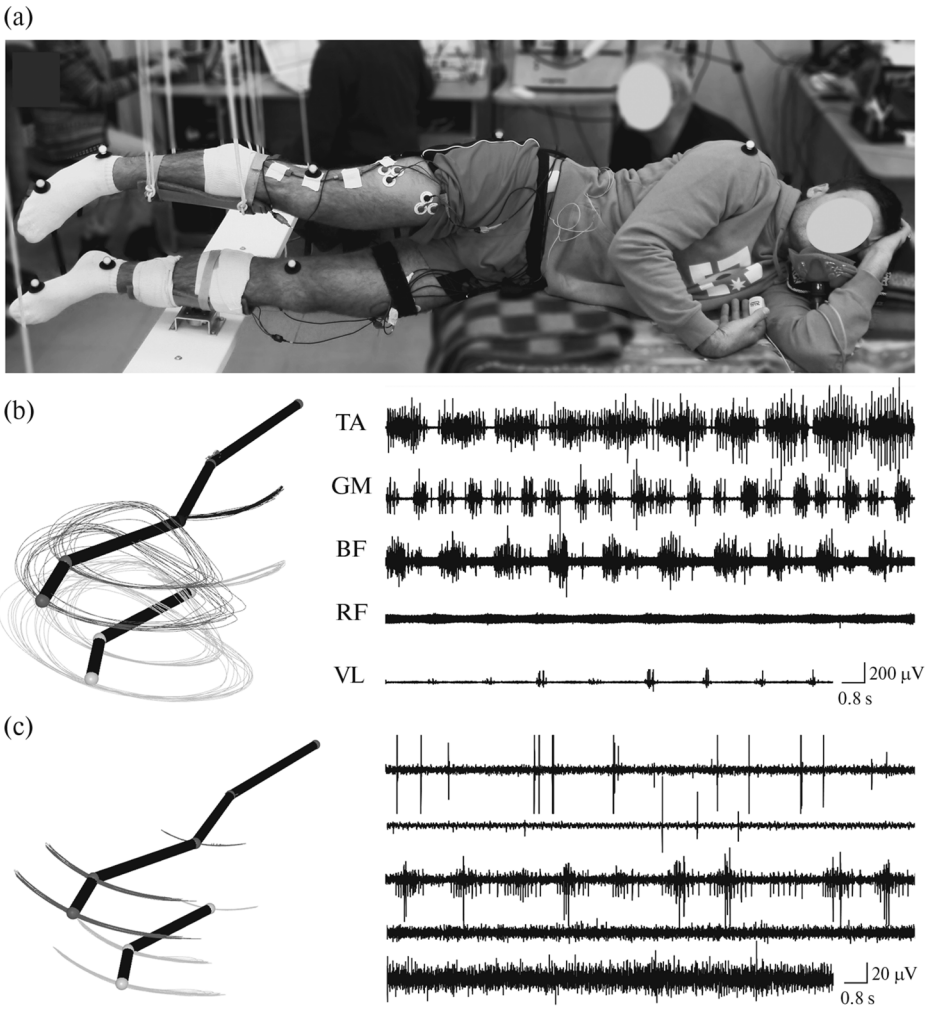

Fig. 1. The location of the subject in the lower extremities horizontal support (a), trajectories of moving anthropometric points and electromyogram samples of lower limb muscles during voluntary walking (b) and under conditions of TESCS (c).

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 muscle under study, and the reference one attached along the course of its fibers with an interelectrode distance of 2 cm; an additional grounding electrode on each channel was provided. All recorded EMG was filtered using the original software. The principle of filtering consists in searching for a pattern characteristic of a stimulation artifact and replacing the EMG fragment containing the tip with a dynamic average. The EMG were then filtered with a bandpass filter with a bandwidth of 30 to 450 Hz, 60 dB suppression strength with zero delay, then averaged in intervals of 0.002 s, and reapplied a 15 Hz low-pass filter using MegaWin software. All EMGs were normalized to the peak amplitude of each muscle in a particular experimental condition.

TESCS was performed using a Biokin ES-5 stimulator (Cosima LLC, Russia). The cathode was placed between vertebrae T11 and T12, two anodes were placed symmetrically over the crests of the iliac bones, the frequency of stimulation was 30 Hz. The intensity of stimulation was selected individually, increasing the current to a value that initiated a motor reaction but did not cause painful sensations, in the range of 30–90 mA. Based on previous results showing that involuntary stepping movements could be induced in healthy subjects using a 30 Hz TESCS

applied between vertebrae T11 and T12, we used the same stimulation parameters [4]. We synchronously performed video capture of movements of the main anthropometric points of the body segments of both lower limbs: metatarsal, lower extremity, upper extremity, and trochanter with a sampling rate of 500 Hz. We used a Qualisys 3D video analysis system (Sweden) including 8 high-speed Oqus cameras.

The recorded interference EMG, anthropometric point coordinates in the 3D system were exported to Statistica (StatSoft, Inc., version 10) and a matrix of initial data (X) was formed, the dimension ($I \times J$), where I is the number of points (measurements at a time point—500 for each experimental condition, step, subject), and J is the number of independent variables (variation series of EMG—8). In addition to the EMG variation series, additional variables were created in the matrix to identify the periods of the pacing cycle and the belonging of the data to a particular subject and step [11, 12]. All variation series were interpolated relative to a single reference point and standardized to a unit of standard deviation.

We extracted components (synergies) from the matrices using the principal components method (PCA). Components with eigenvalues greater than one and accounting for at least 10% of the total variance were considered. The following parameters were analyzed: the number of extractable components (synergies), the percentage of total variance accounted for by each factor in the total data set (VAF), loadings matrices, and scores matrices. The original matrix X was decomposed into the product of two matrices: $X = T \times P + E$, where T is the scores matrix, P is the loadings matrix, and E is the residuals matrix. The matrix of burdens carries information about the relationship or independence of the variables with respect to the new, formal variables obtained in the process of decomposition of matrices—"vectors of synergy".

When comparing the "vectors of synergy", the values of muscle loads in the established order in different experimental conditions served as the compared variation data series; in this case, cosine similarity analysis ($\cos\theta$) was used to compare variation series, where 1—complete similarity, 0—no similarity. The load matrix also includes weighting coefficients of each muscle, giving information about the degree of their involvement in the synergy, the higher the coefficient, the greater the relationship with the new component. We calculated the intraindividual mean values of the weight coefficients of each muscle for each extracted component during multiple realizations of a complete step cycle. One-factor ANOVA with Newman–Keuls post-hoc analysis was used to assess the significance of differences when comparing group mean weight coefficients. We considered p values < 0.05 to be statistically significant differences.

The scores matrix determines the temporal organization of the identified synergies and is a projection of the raw data on the subspace of the main components—the "activation coefficients" of synergies. The activation coefficients represent a dynamic process reflecting the change in the activity of synergies over time. Synergy activation coefficients were compared by analyzing the maximum values of cross-correlation functions (r), taking into account the bias against zero, where 1 is complete correspondence, 0 is no relationship. Simple exponential smoothing ($\alpha = 0.01$) was applied to variation series containing synergy activation coefficients before calculating the cross-correlation functions.

Mathematical and statistical data processing was performed using Statistica 10.0 and included calculation of arithmetic mean (M), standard error (SE), standard deviation (SD), and coefficients of variation (CV). Matrices were decomposed in Statistica using the standard module "Advanced/Multivariate—PCA".

RESULTS

On average, 4.4 ± 0.2 synergistic components were found in the random locomotion group, with an explained dispersion of $78.0 \pm 1.4\%$. Under the influence of TESCS, the number of synergies significantly decreased by 22.7% and reached 3.4 ± 0.2.

When considering the spatial structure of muscle synergies of arbitrary and TESCS-induced locomotion, the following regularities were established. The highest loads of the first synergy during arbitrary movements fell on the following

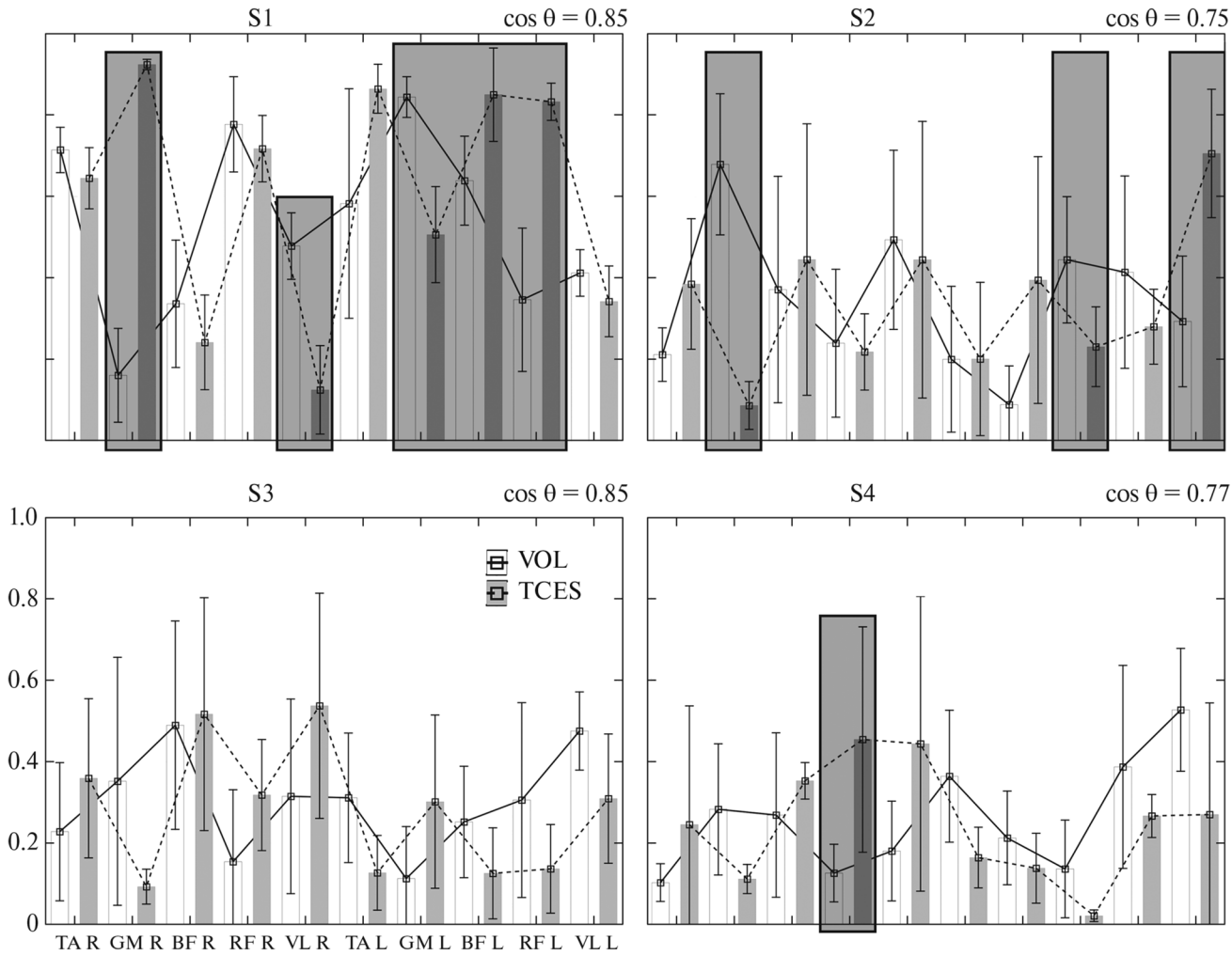

Fig. 2. Muscle loads and vectors of synergies (solid and dotted lines) during arbitrary walking in conditions of horizontal signification of the lower limbs and during locomotion induced by TESCS. *Abscissa*: skeletal muscles, *ordinate*: coefficients. VOL—Voluntary step-like movements, TCES—TESCS walking induced by stimulation. Fillings indicate significant differences in muscle loads at $p < 0.05$. S1, 2, 3, 4—synergy number.

muscles: TA and RF of the right leg, as well as GM and BF of the left leg (Fig. 2). Under TESCS conditions, along with these muscles, the GM R and RF L had high coefficients. A tendency was found to decrease the role of the VL R and the GM L in the first synergy during stimulation. At the same time, the role of the GM R, BF L and RF L increased significantly ($p < 0.05$). Analysis of the similarity of the vectors of the first synergy showed their high correspondence in both experimental conditions, where the coefficient was not less than 0.85.

In the second synergy, during voluntary walking, the greatest loads were detected in the GM R, and during stimulation—in the VL L. The vectors of the second synergy also demonstrated a high degree of similarity—0.75 (Fig. 2). In TESCS, there was a decrease in the involvement in the second synergy of the GM R and the RF L, and an increase in the role of the VL L ($p < 0.05$). In the third identified synergy, loads were low and did not exceed 0.5, but the vectors of synergy showed high similarity. In the fourth synergy, there was a significant increase in the role of the BF R during stimulation (Fig. 2).

It was found that the activation coefficients of the first synergy during arbitrary locomotions under the conditions of lower limb hanging had a pronounced peak of activity in the first quarter of the locomotor cycle (Fig. 3). Intraindividual pat-

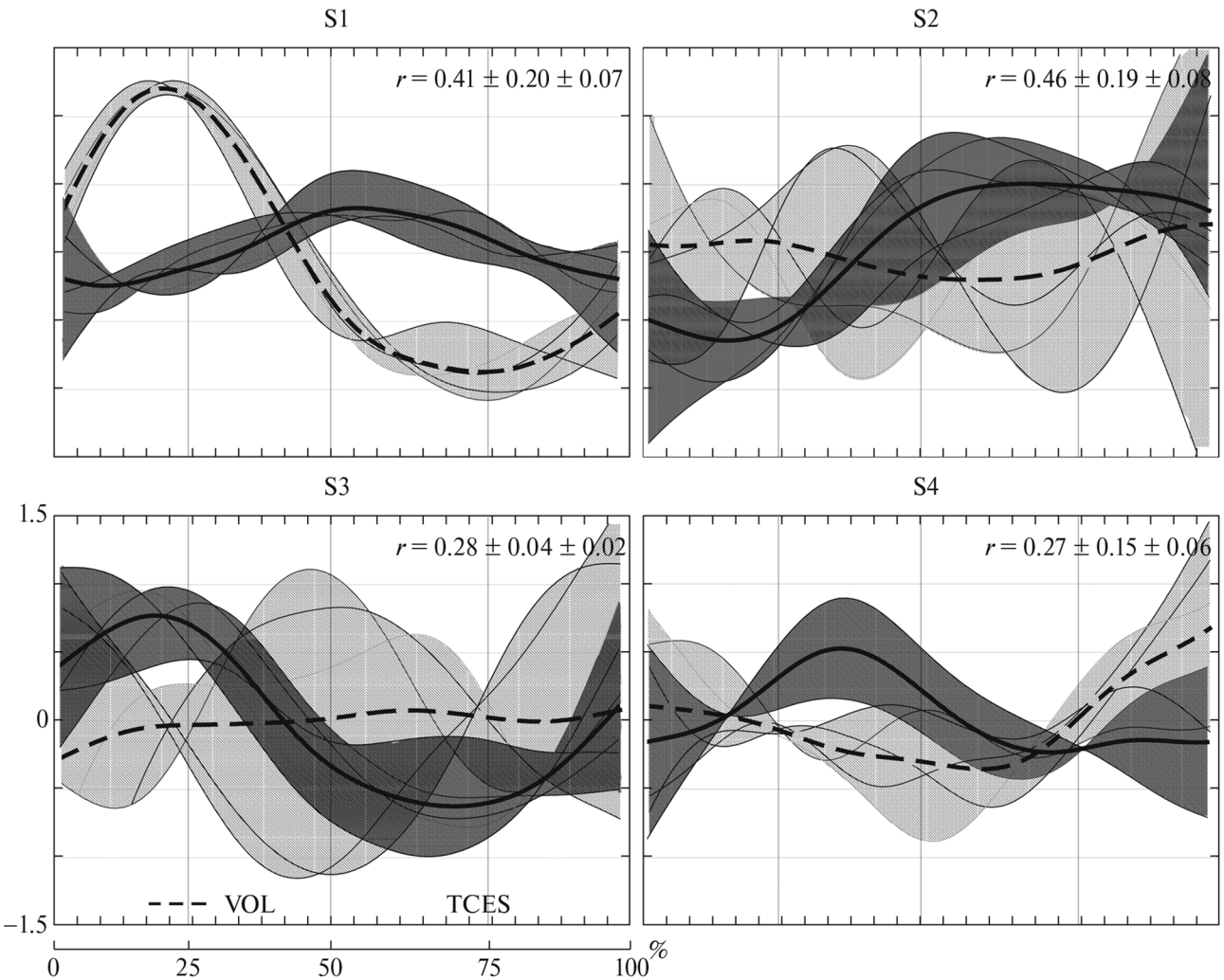

Fig. 3. Muscle synergies' activation coefficients during voluntary step-like movements in conditions of lower extremities horizontal support and during TESCS modulated locomotions. *Abscissa*: the progress of the step cycle, *ordinate*: VOL—voluntary step-like movements, TCES—TESCS modulated step-like movements. The fill shows the extreme intraindividual profiles of activation coefficients. The *r* values are represented as $M \pm SD \pm SE$. S1, 2, 3, 4 is the synergy number.

terns of temporal synergy activation showed high similarity, 0.79 ± 0.03, and *CV* did not exceed 9.17%. The activation profiles of the first synergy during TESCS-induced step-like movements were less similar, the cross-correlation function coefficients did not exceed 0.33 ± 0.01 on average, but were low-covariance (*CV*—9.93%). Analysis of the correspondence between the temporal profiles of voluntary locomotor movements and those evoked by TESCS showed an average correspondence of 0.41 ± 0.07, while the variability was assessed as average, with *CV* averaging 49.91%.

The temporal structure of the second muscle synergy during voluntary walking in the horizontal display of the lower limbs was characterized by the average reproducibility of step cycles and their low variability. A similar structure and intraindividual variability were also observed in involuntary locomotion. Thus, cross-correlation function coefficients were 0.48 ± 0.06, and variability coefficients did not exceed 23.81%. When comparing the structure of the second synergy obtained under different experimental conditions, their average correspondence and the average variability of the patterns of temporal activation were noted (Fig. 3). It should be noted that during voluntary walking, intraindividual examination

revealed peaks of synergy activity during different periods of the step cycle, while during evoked locomotion, there was predominantly one pronounced peak occurring in the third quarter of the movement.

During voluntary walking, the third muscle synergy was characterized by a single peak of activity, but the intraindividual profiles of the stride cycle structure were significantly shifted in time, as indicated by the mean values of cross-correlation functions with a shift relative to zero of 0.50 ± 0.03 and low coefficients of variation not exceeding 16.51% on the group average. During locomotions initiated by the TESCS, a similar pattern was observed, but with virtually no shift in the activation profiles (Fig. 3). There was a low similarity between the activation coefficients during arbitrary and evoked locomotions—0.28 ± 0.02, *CV*—17.45%.

The profiles of the temporal structure of the fourth set synergy demonstrated an increase in activity toward the end of the stride cycle, while the peak of synergy activity in movements induced by the TESCS occurred in the second quarter of the stride cycle. The low reproducibility of the cycle structure in the intraindividual consideration should be noted; the cross-correlation function coefficients in both locomotion conditions considered were estimated to be low, 0.29 ± 0.05 and 0.21 ± 0.01, respectively. A comparative analysis of the temporal structure of evoked and voluntary locomotions also showed its low similarity—0.27 ± 0.06, and *CV* reached 54.86%, which is estimated as an average variability.

DISCUSSION

When analyzing the number of extractable components (muscle synergies) and the proportion of variance described by each of them, we observed lower values of both parameters during locomotions initiated by the TESCS. In general, such results are expected because even the biomechanical structure of the stride cycle during artificially induced locomotions is somewhat different from arbitrary ones and the very conditions of their performance are not typical for walking in the upright position. Therefore, it would be logical to expect that the mechanism of locomotion control under such conditions would also have some peculiarities. The first thing that we would like to draw attention to is the decrease in the quality of reconstruction of initial data using PCA under ESCS. Under normal conditions, the synergistic relationships of lower limb muscle groups are regulated by spinal pattern generators, through reciprocal and coactivation commands, and the motor output is low-covariance stereotypic kinematic patterns and characteristics of muscle activity [1, 2, 9]. Data factorization methods under such conditions manage to account for most of the observed variance in muscle activity parameters; this has been shown in many studies, where VAF as a criterion of synergy extraction efficiency reaches 80% or more [6, 13, 14].

Electrical stimulation, affecting spinal neuronal networks, introduces changes in their organization (the frequency code of synergies), which is manifested by a decrease in the efficiency of synergies extraction. Moreover, these changes are not a confounding factor in the operation of spinal neural structures, but a means of targeting them. This assertion is supported by our results demonstrating clear outlines of the main peaks of synergies activity and high reproducibility of the temporal structure of the extracted muscle synergies during TESCS-induced locomotions. In arbitrary locomotions, this is observed only in the first synergy. Thus, artificially induced locomotions under conditions of horizontal hanging of the lower limbs have the so-called basic (fundamental) profiles of temporal activation, which can be observed during vertical walking under normal conditions, while arbitrary stepping movements under such conditions are more often characterized by high variability.

The concept of motor synergism implies reducing the computational load on the structures of the nervous system by combining elements of the system into modules with a smaller dimensionality. On this basis, it can be argued that the greater the number of modules, the higher the complexity of the control system. Four to five muscle synergies are recorded during walking under normal conditions. This is observed when analyzing the activity of the muscles of one limb or the muscles of one side of the body during running, walking, or pedaling on a bicycle ergometer [13, 15]. It is

likely that the structure of muscle synergies during locomotor movements may include most of the superficial muscles of the lower extremities in one way or another, but the participation of each of them in the structure of synergistic modules in different conditions of locomotion realization may differ. We have shown that when comparing the locomotions induced by TESCS and voluntary movements, the muscle loads in the structure of the first synergy differ significantly, namely, the role of right leg GM, BF and RB increases in evoked movements, and the role of right leg VL and left leg GM decreases. At the same time, the vectors of synergies turn out to be highly similar in different conditions. This indicates that the spatial structure of natural and evoked locomotion has a single control mechanism, probably implemented by neuronal networks localized at the level of T11–T12 vertebrae. In addition, the formation of a clear outline of the main activity peaks in the temporal structure of muscle synergies during movements evoked by TESCS testifies in favor of this statement.

Differences in the component composition of muscle synergies are observed even during repeated repetition of stereotypic movements, both discrete and cyclic. In this regard, it is quite expected that the muscle loads in the structure of the synergies we extracted during arbitrary and evoked movements turned out to be different. In addition, "step-like locomotor activity" can be represented by different patterns, similar in varying degrees to the biomechanical structure of real movements [16]. An important established fact in our study was the high concordance of the synergy vectors and the low variability with a clear outline of the main activity peaks of the synergy activation coefficients during evoked locomotor movements. Such results may be related to the following statements. One of the theories describing the complex interaction of control signals in the CNS during locomotion suggests the presence of two independent neuronal networks in the structure of spinal locomotor generators that control the rhythmic activity of flexor and extensor muscles, including the rhythm generating part and the network that generates locomotor patterns [17–19]. Drawing an analogy with the provisions of the concept of spatiotemporal synergy architecture, the activation coefficients of muscle synergies are the equivalent of the rhythm-generating part of the neural network that controls locomotion, and the synergy vectors and muscle loads that determine the ratio of activation of muscle groups will be the analogy of the pattern-forming network. Thus, electrical stimulation of the spinal cord at the level of T11–T12 vertebrae at least affects the rhythm-generating part of the neural network, which manifests itself in the formation of basic (fundamental) locomotor temporal patterns.

The variability of the temporal structure of synergies observed by us during random walking in the horizontal sign in a number of cases is associated with a shift in the activation coefficients detected by cross-correlation analysis. Such synergies are denoted as "time-varying synergies", i.e., synergistic patterns are realized in different temporal periods of the locomotor cycle during their repeated realization [14, 20, 21].

CONCLUSIONS

Thus, the temporal structure of the extracted muscle synergies during locomotion under conditions of electrical stimulation of the spinal cord has clearly expressed activity peaks and high reproducibility of the activation patterns. In a number of cases, they are realized in different temporal periods of the locomotor cycle during their repeated realization. The muscle loads in the structure of the identified synergistic modules differ significantly, but the vectors of synergies turn out to be highly similar in different experimental conditions. The differences in the parameters of the spatiotemporal structure of muscle synergies of arbitrary locomotion and modulated TESCS may be related to the reorganization of the rhythm generating part of the neuronal network that controls the rhythmic activity of flexor and extensor muscles in the structure of the complete step cycle.

ACKNOWLEDGMENTS

The author expresses his gratitude to the employees of the Research Institute of Sports and Recreational Physical Education Problems of Velikiye Luki State Academy of Physical Educa-

tion and Sports Pukhov A.M., Markevich V.V., Ivanov S.M. for their help in organizing the research.

AUTHORS' CONTRIBUTION

S.A.M.—idea of work, planning of the experiment, data collection and processing, writing and editing the article.

FUNDING

Funding was provided as part of the planned activities of the Velikiye Luki State Academy of Physical Education and Sports.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

REFERENCES

1. Feldman AG, Levin MF, Garofolini A, Piscitelli D, Zhang L (2021) Central pattern generator and human locomotion in the context of referent control of motor actions. Clin Neurophysiol 132(11): 2870–2889. https://doi.org/10.1016/j.clinph.2021.08.016
2. Madarshahian S, Latash ML (2022) Reciprocal and coactivation commands at the level of individual motor units in an extrinsic finger flexor-extensor muscle pair. Exp Brain Res 240(1): 321–340. https://doi.org/10.1007/s00221-021-06255-w
3. Arshavsky YI, Deliagina TG, Orlovsky GN (2015) Central Pattern Generators: Mechanisms of the Activity and Their Role in the Control of "Automatic" Movements. IP Pavlov J Higher Nerv Activit 65(2): 156–187. (In Russ). https://doi.org/10.7868/S0044467715020033
4. Gorodnichev RM, Pivovarova EA, Puhov A, Moiseev SA, Gerasimenko YP, Savochin AA, Moshonkina TR, Chsherbakova NA, Kilimnik VA, Selionov VA, Kozlovskaya IB, Edgerton VR (2012) Transcutaneous electrical stimulation of the spinal cord: a noninvasive tool for the activation of stepping pattern generators in humans. Human Physiol 38(2): 158–167. https://doi.org/10.1134/S0362119712020065
5. Moiseev SA, Gorodnichev RM (2017) Motor synergies structure variability in different intensity locomotions. Human Physiol 48(4): 22–33. https://doi.org/10.31857/S0131164622040087
6. Turpin N, Uriac S, Dalleau G (2021) How to improve the muscle synergy analysis methodology? Eur J Appl Physiol 121(4): 1009–1025. https://doi.org/10.1007/s00421-021-04604-9
7. Overduin S, d'Avella A, Carmena J, Bizzi E (2014) Muscle synergies evoked by microstimulation are preferentially encoded during behavior. Front Comput Neurosci 8:20. https://doi.org/10.3389/fncom.2014.00020
8. Cheung VC, d'Avella A, Bizzi E. (2009) Adjustments of motor pattern for load compensation via modulated activations of muscle synergies during natural behaviors. J Neurophysiol 101(3): 1235–1257. https://doi.org/10.1152/jn.01387.2007
9. Gurfinkel VS, Levik US, Kozennikov OV, Selionov VA (1998) Is there a locomotor circuitry in humans? Fiziol chelov 24(3): 42–50. (In Russ).
10. Minyaeva AV, Moiseev SA, Pukhov AM, Savokhin AA, Gerasimenko YP, Moshonkina TR (2017) Response of external inspiration to the movements induced by transcutaneous spinal cord stimulation. Human Physiol 43(5): 43–51. https://doi.org/10.7868/S0131164617050113
11. Moiseev SA, Ivanov SM, Gorodnichev RM (2022) The Motor Synergies' Organization Features at Different Levels of Motor Control during High Coordinated Human's Movement. J Evol Biochem Phys 58: 610–622. https://doi.org/10.1134/S0022093022020272
12. Moiseev S, Pukhov A, Mikhailova E (2022) Methodological and computational aspects of extracting extensive muscle synergies in moderate-intensity locomotions. J Evol Biochem Phys 58: 88–97. https://doi.org/10.1134/S0022093022010094
13. Ivanenko Y, Poppele R, Lacquaniti F (2006) Motor control programs and walking. Neuroscientist 12(4): 339–348. https://doi.org/10.1177/1073858406287987
14. Hogan N, Sternad D (2013) Dynamic primitives in the control of locomotion. Front Comput Neurosci 7: 71. https//doi.org/10.3389/fncom.2013.00071
15. De Marchis C, Schmid M, Bibbo D (2013) Interindividual variability of forces and modular muscle coordination in cycling: a study on untrained subjects. Hum Mov Sci 32(6): 1480–1494. https://doi.org/10.1016/j.humov.2013.07.018
16. Shapkova EY (2004) Localization and properties of spinal locomotion generators (SLG) revealed by electrical stimulation of the spinal cord in humans. Russ J Physiol 90(8): 420–432. (In

Russ).
17. Rybak I, Shevtsova N, Lafreniere-Roula M (2006) Modelling spinal circuitry involved in locomotor pattern generation: insights from deletions during fictive locomotion. J Physiol 577(2): 617–639. https://doi.org/10.1113/jphysiol.2006.118703
18. Churchland M, Cunningham J, Kaufman M (2012) Neural population dynamics during reaching. Nature 487(7405): 51–56. https://doi.org/10.1038/nature11129
19. Hogan N, Sternad D (2007) On rhythmic and discrete movements: reflections, definitions and implications for motor control. Exp Brain Res 181(1): 13–30. https://doi.org/10.1007/s00221-007-0899-y
20. Sternad D, Marino H, Charles S, Duarte M, Dipietro L, Hogan N (2013) Transitions between discrete and rhythmic primitives in a unimanual task. Front Comput Neurosci 7: 90. https//doi.org/10.3389/fncom.2013.00090
21. Overduin SA, d'Avella A, Roh J, Carmena JM, Bizzi E (2015) Representation of Muscle Synergies in the Primate Brain. J Neurosci 35(37): 12615–12624. https://doi.org/10.1523/JNEUROSCI.4302-14.2015

Translated by A. Dyomina