Features of EEG Activity Related to Realization of Cyclic Unimanual and Bimanual Hand Movements in Humans

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Received July 15, 2015

In 10 tested dextral subjects, EEG activity was recorded during the performance of unimanual and bimanual cyclic movements of the hands and fingers. The movements corresponded to clenching the fingers into a fist and the subsequent unclenching of the fingers. The test consisted of four successive stages, the resting state, movement of the left hand, that of the right hand, and movement of both hands. The dependences between the spectral power and coherence of the respective EEG samples on the type of the test performed, on the type of the movement (uni- or bimanual), and on the laterality of the latter in the case of the unimanual movement were examined. The results obtained allow us to propose the following conclusions: (i) α and β EEG rhythms are characterized by different functional importance with respect to manual motor activity; (ii) neural control of bimanual movements cannot be considered "a sum of the controls" of unimanual movements, and (iii) control of bimanual movements may be largely based on the control of the movement by a subdominant upper limb.

Keywords: bimanual and unimanual movements, shoulder and elbow joints, EMG, EEG, spectral power, coherence, cyclic movements.

INTRODUCTION

Movements of the distal parts of the upper limbs constitute one of the most important components of the motor repertoire in humans. Functional organization of the mechanisms responsible for the control of uni- and bimanual movements still constitutes one of the crucial problems in modern neurophysiology. Studies of bimanual movements were based on examination of mechanical parameters of the limb motions [1], analysis of the muscle activity involved in their realization [2], and analysis of EEG activity related to these motor phenomena [3, 4]. There were also attempts to apply mathematical modeling for the analysis of CNS functions related to coordination of bimanual movements [5]. Elucidation of the questions of how the CNS coordinates movements of the two extremities in the case of bimanual performance and also of how the control of this movement is related to that of unimanual movements of the dominant and subdominant limb is believed to be specially important [6, 7].

Earlier, we examined the features of bimanual coordination in the course of performance of movements mimicking those in rowing [2]. In this work, we analyzed mechanograms of movements of oar "equivalents" and EMG activity of the respective muscles of both upper limbs. It should be noted that such a model of bimanual movements was probably rather simple from the aspect of central coordination (the subject in the course of testing should perform in-phase mirror-symmetrical movements) [8].

It is obvious that results of examination of mechanograms and activity of the limb muscles can help to understand the CNS mechanisms involved in the control of uni- and bimanual movements only to a limited extent. It can be expected that the research of activity of various cerebral structures with the use of the corresponding techniques may provide us with greater information in this respect. We used electroencephalography in such studies. Earlier, similar techniques were applied under conditions of temperature (cold) stimulation of the fingers [9] and in the performance of cyclic movements by the fingers of one hand [10]. Using EEG recording allows one to compare features of cortical activities related to bimanual movements and unimaual movements of the dominant and subdominant hand. Such an approach can open certain possibilities for better understanding of what are relations

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between central CNS mechanisms in the control of uni- and bimanual movements. It is clear that such comparison is rather difficult in the case where only movement mechanograms and EMG activity of the upper limb muscles are recorded.

A low amplitude of EEG signals is the main methodological difficulty in the course of EEG recording and analysis. These signals can be distorted by both external interferences and various electrical signals generated in the human body during its normal activity. In particular, these are electrical activity of the heart (ECG) and "parasitic" EMG signals coming from muscles during head movements, eye movements, blinking, and jaw movements. EEG records may also be distorted because of the displacements of recording electrodes. Because of this, the repertoire of the examined movements of the upper limbs is, unfortunately, rather limited. High-quality registration of EEG samples related to "massive" upper limb movements is very problematic. Considering this, we tested the EEG correlates of successive cyclic clenching of the subject's fingers in a fist and the reverse movements (straightening of the fingers). In our study, we chose, perhaps, the simplest, in terms of coordination, function of the CNS in the control of such movements, namely bimanual movements with an in-phase mirror symmetry of the latter. We compared the activities of the cerebral cortex in the course of such cyclic movements with the activity recorded under similar conditions, but in the course of unimanual movements performed by the dominant and subdominant limb. The main hypothesis was the following: the activity of the mechanisms used by the CNS in the organization of a bimanual movement may not be a simple superposition of the activity of the mechanisms involved in the control of unimanual movements.

METHODS

Tested Subjects. Ten volunteers, six men and four women (age 27.8 ± 6.7 years; mean \pm s. d.) took part in the tests. All participants had no neurological diseases and, according to the conventional tests, were dextrals.

EEG Recording. A computerized encephalograph, MITSAR-EEG-10/70-201 (MITSAR Co., Russia), was used. Positioning of the electrodes corresponded to the standard 10–20 scheme; 19 recording electrodes (OHRE-26) and two reference electrodes (also OHRE-26) fixed on the earlobes were used (Fig. 1, A). The electrodes were placed on the scalp using an EEG helmet, MultiCap-Cup; Ag/AgCl-electrodes were 10 mm in diameter, with 150 cm-long connecting wires. The entire set of electrodes was produced by GVB-geliMED KG (Germany). Before positioning of the electrodes, the scalp skin was degreased by ethyl alcohol; reduction of the skin-electrode resistance (≤ 5 kΩ) was provided by a special gel. The encephalograph was controlled by EEG StudioVersion 1.9 software (MITSAR Co., Russia). EEG signals were stored in a computer for further analysis. The sampling frequency for EEG signals was 500 sec^{-1} .

EMG Recording. In the course of the tests, we recorded EMG activity from *m. extensor carpi ulnaris* (ECU) and *m. flexor digitorum profundus* (FDP) of both forearms. Paired electrodes (Biopac System EL 503, USA) fixed on both forearms (distance between the centers 25 mm) were used. Before electrode positioning, hair was removed from the skin, and the latter was degreased with alcohol. Before the beginning of the testing series, EMGs related to the development of the maximal voluntary contraction (MVC) by the above muscles were recorded. To obtain the MVC samples for the ECUs, the subject was asked to perform maximum extension of the hand and fingers in both upper limbs. Correspondingly, to obtain such samples for the FDPs, the subject was asked to most strongly clench both fists. The EMG signals were amplified by amplifiers specially developed and manufactured in the laboratory; the bandpass was 5.0–2000 Hz. The above signals, after their digitization at a 2.10^3 sec⁻¹, were stored on a disk of a separate computer. Special synchronization pulses were introduced via separate channels in both EEG and EMG records to provide precise synchronization of the latter. In the course of EMG recording, an input-output device 6023E (National Instruments, USA) guided by LABVIEW 7 software (National Instruments, USA) was used.

Protocol of the Tests. Testing was carried out in a special room at low-light illumination. The subject was sitting in a comfortable chair with his/her forearms on the armrests in a position making no interference for EMG recording. During the tests, the eyes were closed. The tests were interrupted with 2- to 3-min-long resting intervals. The test series consisted of four tests lasting 2 min

Fig. 1. Details of the techniques. A) Scheme of localization of the recording EEG electrodes used in the test. B) Example of EMG activity recorded from the *m. extensor carpi ulnaris* (ECU) and *m. flexor digitorum profundus* (FDP) during the performance of two subsequent voluntary cycles of clenching a fist and unclenching and extension of the right hand fingers; performance of the bimanual test (CB) by one of the subjects. Vertical arrows show moments of the beginnings of a series of 1.0-sec-long time windows, within which the subsequent harmonic analysis was performed. Ordinate) Magnitude of EMG activity normalized with respect to that at the performance of maximum voluntary contractions of the respective muscles, %. C) Example of the power spectrum of EEG activity recorded by leads C3 and C4 at the performance of the mentioned test by the same subject. Frequency borders of the α and β rhythms (8–13 and 13–30 Hz, respectively) are shown above the abscissa; ordinate) logarithm of the spectral power of the respective signals. D) Spectrum of coherence of EEG oscillations recorded from the C3 and C4 cites; ordinate) hyperbolic values of the coherence (see Methods).

each. The first test corresponded to EEG recording in the resting state (RS). During the second test, the subject had to perform rhythmic clenching (flexion) of the left hand into a fist accompanied by unclenching of the fist and fingers (cycling left, CL), while the third test included similar rhythmic movements but performed by the right hand (cycling right, CR). During the fourth test, the subject performed synchronous bimanual rhythmic clenching/unclenching in a mirrorsymmetrical manner (cycling bimanual movements, CB). The rate of cyclic movements was chosen by the subject voluntarily, and there were no special signals determining the rate and synchronization of the movements (so, the mode corresponded to the so-called self-paced movements).

Processing of the Electrographic Signals. The program WinEEG (MITSAR, Russia) was used to estimate the quality of EEG recording and for removal of artifact-containing EEG segments. All records were subjected to thorough visual control, and segments containing clear artifacts were labeled for subsequent removal in the course of analysis. EMG signals were subjected to program filtering (high-pass filter with a 10 Hz cutoff frequency). Then these signals were subjected to full rectification and final program low-frequency filtering with a 20 Hz cutoff frequency. Additionally, EMG signals were normalized with respect to the levels of MVC signals taken as 100%. These processed signals were transformed into new samplings with the 500 sec^{-1} digitization frequency, synchronized with EEG records, and combined into a single file for subsequent analysis.

The moments of initiation of ECU activation, which approximately coincided with the beginning of the fist unclenching, where visually labeled in EMG records. Then, these labels were considered beginnings of the one-sec-long time windows for subsequent analysis of EEG samples; this provided a possibility for harmonic analysis of movementrelated (event-related) EEG samples [11] (Fig. 1 B).

For harmonic analysis, we used digital Fourier transform of the earlier labeled time windows using the Hamming window function. To obtain the respective averaged spectra, the spectra of 50 to 60 separate artifact-free windows were united. The event-related power spectrum was calculated using the formula:

$$
P_{x}(f) = \frac{1}{N} \cdot \sum_{n=1}^{N} C_{xn}(f) \cdot C_{xn}^{*}(f), \qquad (1)
$$

where is the frequency, Hz, and are the digital Fourier transform of the sample and its complex conjugate, respectively, and is the number of time windows.

For calculation of the spectrum of coherence of two EEG signals, we used a cross-spectrum function, for two signals, and ; this function was calculated according to the formula similar to formula (1):

$$
P_{xy}(f) = \frac{1}{N} \sum_{n=1}^{N} C_{xn}(f) \cdot C_{yn}^*(f).
$$
 (2)

Designations in formula (2) are similar to those in formula (1). Finally, the coherence spectra for two signals were calculated using the formula:

$$
\gamma_{xy}^2(f) = \frac{|P_{xy}(f)|^2}{P_x(f) \cdot P_y(f)},\tag{3}
$$

where $|\cdot|$ operation means calculation of absolute values for each definite frequency.

To obtain subsequent statistical estimates, values of the power spectra were subjected to decimal logarithmic transformations (formula (4)). This operation was performed for limitation of the range of variation of the values characterizing the spectral power:

$$
L_x(f) = \lg P_x(f),\tag{4}
$$

where L_x is logarithmic power spectrum (LPS).

For the same purpose, values of the coherence spectra were transformed according to the formula:

$$
z_{xy}(f) = arctgh\left(\gamma_{xy}^2(f)\right),\tag{5}
$$

where $arctgh(\cdot)$ is the hyperbolic arctangent function, and z_w is the hyperbolic coherence spectrum (HCS). It should be noted that such a mode for estimating the spectrum characteristics of EEG signals was used earlier [11]. We analyzed averaged values of the LPS and HCS for the α and β EEG rhythms $(8-13$ and $13-30$ Hz, respectively).

We should mention that the LPSs were calculated for each EEG signal, while the HCSs were estimates for each possible pair of all 19 leads (*in toto*, for 171 pairs). MathCad 2001 software (MathSoft, USA) was used for calculation of spectral characteristics of the signals. Examples of the respective results are shown in Fig. 1, C and D.

Statistical Estimates. These were obtained using a procedure of ANOVA with repeated measurement. *Post-hoc* analysis was done using the Bonferroni test. Intergroup differences were considered significant at $P \leq 0.05$. The specific types of the variance analysis, including the number of factors and their levels, depended on the task type; these aspects are mentioned and described in more detail in the Results section. Statistical calculations were performed using SPSS Statistics 17.0 (IBM Analytics, USA).

RESULTS

In the realization of rhythmic voluntary fist clenching/unclenching, the averaged period of the movements in the examined group was $1.17 \pm$ \pm 0.10 sec (mean \pm s.e.m.). The analysis of variance with repeated samples did not reveal any significant dependence of the movement rate on the test type $(F(2, 18) = 0.794, P = 0.467)$. As was mentioned, the fourth (bimanual) test was performed with the simplest mode of synchronization of the movements performed by two hands (the so-called in-phase mirror mode).

Analysis of EEG activity depending on the type of tests showed that the total power of α-range oscillations decreased noticeably during the above motor performance by the hands (Fig. 2 A); in other words, the α rhythm was desynchronized. **82 T. Tomiak et al.**

Fig. 2. Toposchemes of desynchronization of EEG activity related to the performance of the motor tests. A) Distribution of the decrements of α-range activity; B) that of β-range activity. *CL*, *CR*, and *CB* are motor tests performed by the left hand, by the right hand, and by both hands. Each scheme is the result of averaging of EEG activity for the entire group of subjects. The gradient of density marks the decrement of the logarithmic power spectrum (shown in the scale at the right).

To quantitatively characterize, in general, the level of such desynchronization, we took into account the differences between the LPSs for a definite range measured during realization of the respective test and in the resting sate (RS). The above figure demonstrates results of total averaging of the respective desynchronization values for the entire tested group. It can be noticed that the desynchronization levels in tests CL and CB were somewhat higher than that in the case of movements by the dominant hand (test CR). At the same time, it should be mentioned that this trend did not reach the confidence level. The following circumstance probably also deserves attention. Desynchronization of α-range oscillations showed the highest intensity in leads C3 and C4. In test CR, desynchronization observed in the contralateral cortical motor area (C3) was somewhat greater than that in the ipsilateral area (C4). In general, desynchronization of α oscillations attained statistically significant values in leads T3, C3, and C4. This was confirmed by results of the corresponding ANOVA with repeated measurement where the test type with four levels (RS, CL, CR, and CB) was considered the factor. Results of this test for leads T3, C3, and C4 were the following: *F*(3, 27) = 3.704, *P* = 0.024; *F*(3, 27) = 6.247, *P* = $= 0.002$, and $F(3, 27) = 4.583$, $P = 0.010$, respectively.

Desynchronization of the α rhythm in the parietal and occipital leads (electrodes P3, P4, O1, and O2) was more pronounced in the CB test, as compared with that in test CL; this difference, however, did not reach the level of statistical significance.

Oscillations of the β range demonstrated somewhat different dynamics of desynchronization. In contrast to that of α oscillations, the general level of movement-related desynchronization of the β rhythm did not depend noticeably on the type of the test performed (Fig. 2 B). In this case, the power of β activity in the parietal and occipital leads showed nearly no decrease, as compared with that measured in the resting state (RS). Against such a background, rather strong β desynchronization in the temporal T3 lead deserves attention. It should, however, be mentioned that the variability of the

		Factor ot the test (T)		Factor of the lead (E)		$T \times E$		Levene's test	
Leads	EEG range	F(3, 27)	p	F(2, 18)	D	F(6, 54)	P	F(11, 108)	P
C3, C4, and Cz	α	4.46	0.011	36.00	0.000	3.39	0.007	0.40	0.953
		2.76	0.061	1.83	0.189	1.55	0.180	0.29	0.987
F3, F4, and Fz	α	1.22	0.322	79.19	0.000	0.57	0.751	0.16	0.999
		1.88	0.157	1.13	0.344	1.51	0.194	0.64	0.795

Table 1. Results of Statistical Analysis of the Power Spectrum of EEG Activity.

Footnotes: Results of the analysis of variance of the power spectra and those of the Levene's test for the homogeneity of dispersion of the respective power indices for the signals of the shown range recorded by the mentioned electrodes are indicated. $T \times E$ denotes interaction between the factors of the test and lead.

desynchronization level in the examined group was rather high, as confirmed in the analysis of variance: $(F(3, 27) = 1.732, P = 0.184)$. Desynchronization of β oscillations acquired the level of statistical significance only in lead C3: $(F(3, 27) = 3.232)$, $P = 0.038$.

Separately, we compared the relations of the LPS values in the groups of central (C3, C4, and Cz) and

frontal (F3, F4, and Fz) leads. The respective results are presented in Fig. 3. Two-factor ANOVA with repeated measurement was carried out. In this case, the test type and site of recording were considered the factors. The test factor had four levels (tests RS, CL, CR, and CB), while the lead factor had three levels (electrodes C3, C4, and Cz or F3, F4, and Fz). Additionally, Levene's test was performed,

Fig. 3. Dynamics of changing in EEG activity recorded by two groups of electrodes; dependence on the test type. A and C) Activity recorded by electrodes C3, C4, and Cz; B and D) that recorded by electrodes F3, F4, and Fz. A and B) Activity of the α range; C and D) that of the β range. In each graph, s.e.m. values for the respective tests are shown for the respective points. Abscissa) Test types; RS is the resting state, CL, CR, and CB are movements by the left hand, right hand, and both hands. Ordinate) Values of the logarithmic power of the respective spectra.

which allowed us to estimate the homogeneity of dispersion of the LPS values. The results of such analysis are summarized in Table. 1. According to the respective results, the dispersions of all s.e.m. levels (see Fig. 3) were homogeneous; the respective values are shown in panels of the figure. The LPS value for the α range in lead Cz was greater than those in leads C3 and C4; this was confirmed by the *post-hoc* test ($P < 0.05$). The α SP values in the RS test were also higher than those in other tests. Note

Footnote: $T \times P$ denotes interaction between the factors of the test and lead pair.

that the level of desynchronization of oscillations of this range in lead C4, when measured in tests CR and CB, was somewhat lower than that in lead C3, but this difference did not reach the level of significance (A). Let us also note that the level of α-desynchronization in the CR test was somewhat smaller than those in all leads of the abovementioned group.

The α-range activity recorded by the group of frontal electrodes (F3, F4, and Fz) demonstrated

Table 2. Results of Analysis of the variance of Conerent Relations between EEG Activities Recorded by Different Lead Pairs.									
		Factor of the test (T)		Factor of the pair (P)		$T \times P$			
Lead pairs	EEG range	F(3, 27)	P	F(2, 18)	P	F(6, 54)	P		
$C3-C4$, $C3-Cz$, and $C4-Cz$	α	8.77	0.000	166.86	0.000	1.19	0.362		
	β	8.52	0.000	266.90	0.000	2.57	0.029		
	α	1.68	0.195	431.28	0.000	0.44	0.851		
$F3-F4$, $F3-Fz$, and $F4-Fz$	β	0.92	0.443	504.45	0.000	2.54	0.031		
	α	7.18	0.001	17.78	0.000	3.28	0.008		
$C3-F3$, $C4-F4$, and $Cz-Fz$		3.35	0.033	49.15	0.000	2.90	0.016		

Table 2. Results of Analysis of the Variance of Coherent Relations between EEG Activities Recorded by Different Lead Pairs.

Fig. 4. Dynamics of the indices of coherence of EEG oscillations recorded by different lead pairs; dependence of the test type. A–C) indices of coherence of α oscillations; D–F) those of β oscillation. A and C) Recordings by electrode pairs C3–C4 (1), C3–Cz (2), and $C4-Cz$ (3); B and E) those by pairs F3–F4 (1), F3–Fz (2), and F4–Fz (3), and C and F) those by pairs C3–F3 (1), C4–F4 (2), and Cz–Fz (3). Abscissa) Type of the test (RS, resting state; CL, CR, and CB, movements by the left hand, right hand, and both hands); ordinate) hyperbolic values of the coherence; means of the respective value and their s.e.m. are shown.

a similar trend (Fig. 3, B). In this case, the LPS level in the sagittal lead Fz was higher than the corresponding levels in leads F3 and F4 (this was also confirmed by *post-hoc* analysis, *P* <0.05). Such dependence, however, did not reach the confidence level, in contrast to the respective relations observed in the central group of electrodes (Table. 1).

Unlike α -range oscillations, β activity recorded by electrodes of the mentioned groups did not demonstrate statistically significant trends in the course of movements (Fig. 3, C, D, Table. 1). This was confirmed by the analysis of EEG activity of the latter range (Fig. 2, B). In general, it can be stated that β activity undergoes no significant changes related to realization of cyclic voluntary movements of the hand and fingers.

Separately, we studied functional relations between the cortical areas according to estimates of the coherence spectrum for the signals recorded by lead pairs. We took into account two electrode groups, central (C3, C4, and Cz) and frontal (F3, F4, and Fz). In total, the coherence of oscillations recorded by nine electrode pairs: (i) by the central group $(C3-C4, C3-Cz, and C4-Cz)$; (ii) by the frontal group $(F3-F4, F3-Fz, Fz, and F4)$, and (iii) by the central-frontal pairs (C3–F3, C4–F4, and Cz– Fz) was estimated. The average HCS values were analyzed for the α and β ranges. Results of such analysis are illustrated in Fig. 4, while results of their statistical processing are shown in Table 2; the two-factor ANOVA with repeated measurement was applied. The test type and the lead pair were taken as the factors. The former and latter were four- and three-degree factors, respectively.

It should be noted that interhemisphere coherent relations (C3–C4 and F3–F4) were noticeably weaker than sagittal-hemispheric relations (C3–Cz, C4– Cz, F3–Fz, and F4–Fz). The coherence of activity recorded by a sagittal electrode with that recorded from the respective site of the right hemisphere (C4–Cz and F4–Fz) was somewhat closer than that found for the left hemisphere (C3–Cz and F3–Fz). Such trends were typical of both α and β ranges (Fig. 4, A, B, C, and D). It should be noted that, for the α range, the difference between coherence indices for pairs C3–Cz and C4–Cz did not reach the confidence level; this was confirmed by results of the respective *post-hoc* analysis ($P > 0.05$). The dependence of coherence relations for the α range on the test type was the following: the coherence in the course of the RS test was smaller than that in other

tests. We should note that the factor "test type" did not exert a statistically significant influence on the dynamics of the coherence in the β range. For this rhythm, the coherence relations were approximately equal to each other in all tests.

The dynamics of coherence relations between activity recorded by the groups of central and frontal electrodes (Fig. 4, C and F) were rather interesting. Statistical analysis demonstrated that there was certain interaction between the factors of lead pairs and type of the test. In pairs C3–F3, C4–F4, and Cz–Fz, the dynamics of the values of the respective average coherence indices at testto-test transitions was noticeably specific. In the α range, the coherence in pairs C3–F3 and Cz–Fz was approximately constant in the tests with movements; in all these cases, it was greater than that in the "rest" test (RS). At the same time, the coherence in pair C4–F4 first became greater in test CL, then decreased in test CR, and again became greater in test CB (C). In the β range, separate pairs of leads also demonstrated certain individual dynamics dependent on the test type. In pairs C3–F3 and C4– F4, increases in the coherence were observed in the motion tests compared to that in the resting state. In this case, the levels of coherence in the motion tests were approximately equal to each other. At the same time, the lead pair Cz–Fz showed somewhat different dynamics of the coherence. In this case, the latter increased in test CL compared to that under RS conditions, remained at nearly the same level in test CR, and slightly decreased in test CB (F). It should be noted that the above results corresponded only to a trend mode; the respective *post-hoc* tests did not confirm the statistical significance of the respective differences. It should be specially emphasized that the intensity of coherence relations in both α and β ranges was positioned in an ascending order so that the lowest values were observed in pair C3– F3, medium values were typical of C4–F4, and the largest values were observed for Cz–Fz. In this case, the probability of the null hypothesis found in the respective *post-hoc* comparisons reached the *P* < 0.05 value.

DISCUSSION

In tests conducted on 10 dextral volunteers, we studied the specificity of EEG activity recorded during simple cyclic movements of the hands and fingers. These cycles included initial clenching of the fingers into a fist with their subsequent unclenching and extension. The test set included movements by the right hand, by the left hand, and by both hands; bimanual movements were in-phase and mirror-symmetric. Results of the previous research showed that coordination of such bimanual movements is rather simple [8]. In addition, the organization of cyclic movements is simpler than that of discrete movements where each movement has a clearly defined beginning and termination. The reaching motions are examples of the latter movement type; in these motions, the subject moves his/her hand toward some definite region of the operational space and then returns the hand back. It was suggested that organization of the cyclic and discrete movements and their control performed by the CNS differ significantly from each other [12, 13]. It can be assumed that the relative simplicity of the movements examined in our tests can provide some benefits for observation of the peculiarities of activation of the cerebral cortex associated with the control of these movements. Of course, further research should include comparison of the process of control of discrete and cyclic movements. There was an important feature of the examined test movements; in their realization, there was no feedback capable of determining the frequency of movements or influencing coordination of the right hand and left hand movements. Earlier, it was suggested that processing of proprioceptive information in the CNS, which was related to the performance of bimanual movements, cannot be interpreted as simple association of the respective signals coming from the sensory apparatus of each hand [7]. As was stated in the cited publication, central transformation of information in the CNS related to the above (bimanual) movements is mostly based on processing of the signals coming from the dominant hand. Such a conclusion contradicts, to a certain extent, our results, because cortical activity of the α range observed in our tests during the performance of cyclic bimanual movements was more similar to the activity observed at unimanual movements by the subdominant hand (Fig. 2, A, B).

Two main conclusions can be drawn considering the results of our tests. The first one was described above. The type of activation of the cerebral cortex in the α range during the performance of bimanual movements is more similar to that observed during test movements by the subdominant (left) hand. Under conditions of motions by the dominant (right) hand, the level of desynchronization of the α rhythm was noticeably lower (Fig. 2, A; 3, A, B). According to this, one can assume that certain neuronal mechanisms used in the organization of movements by the subdominant hand may be crucially involved in the control of bimanual movements. Another important feature was that the β-range cortical activity was subjected to rather mild modifications during the performance of motor test tasks (Fig. 2, B; 3, C, D). The above conclusions were partly confirmed in studies where magnetic resonance imaging (MRI) of the brain was used. It was noticed that activation of the cerebral zones related to realization of such movements begins from the dominant brain hemisphere; at the same time, such activity does not look like a direct superposition of the brain activities related to the unimanual hand movements [14]. The analysis of our observations also allows us to conclude that EEG cortical activity (at least that of the α range) in the case of performance of simple bimanual movements cannot be considered a simple "sum" of the activities observed during the respective unimanual movements. There are data that cerebral activity recorded using MRI does not, in general, depend significantly on whether the movements are unimanual or bimanual [15]. In the cited publication, it was mentioned that precisely the type of synchronization of bimanual movements may significantly influence the cortical activity. In particular, it was mentioned that in-phase movements of the fingers were accompanied by cerebral activation of a type noticeably differing from that observed in anti-phase movements. In our tests, we did not observe sufficiently clear dependences of the β range activity on the movement type (unior bimanual). Beside this, our data suggest that the α and β components of EEG possess dissimilar functional importance in the motor control. The formation of these rhythms is likely to result from the functioning of different cortical/subcortical mechanisms. Such assumptions related to generation of different EEG rhythms are rather common [16].

Many studies were focused on the analysis of possible neuronal pathways responsible for activation of the hand muscles. In these studies, coherence relations between EMG signals recorded from the respective muscles and EEG signals recorded by electrodes positioned above the primary motor and accessory motor cortical zones (close to

the cortical projections of the involved muscles) were specially examined [17, 18]. In the 10–20 system of positioning of EEG electrodes, central leads C3, C4, and Cz approximately correspond to the above zones. In the above-mentioned and many other publications, it was shown that the coherence relations between electrical activity of the muscles, on the one hand, and EEG activity of the β and γ ranges in the respective cortical zones, on the other hand, do exist. We have also carried out a similar analysis, the technique of which was described in detail in other papers [19, 20]. Our study, however, failed to find values of the cortico-muscular coherence reaching the levels of statistical significance. It should be noted that the respective values of coherence are much lower than those for signals of EEG *per se* presented in the above-mentioned publications [19, 20]. The coefficients of cortico-muscular coherence were smaller than 0.1; when the windows of harmonic analysis were expanded, these values could drop additionally, somewhere to 0.02 (i.e., the coherence was negligible). This, in turn, resulted from increase in the total time of the experiment. As can be supposed, the absence of significant coherence relations between EEG and EMG signals is determined by the fact that the movements in our experiments were simple and performed in a cyclic mode. Considering this, these movements were controlled, to a great extent, by spinal neuronal mechanisms, namely spinal central pattern generators, with a relatively limited involvement of the cortical mechanisms. Such movements are more "ancient" from the phylogenetic aspect. [21] It should also be mentioned that cortico-muscular coherent relations were studied earlier with the use of movements qualified as discrete ones [22].

When comparing our results with the data of previous studies, we should take into account that the coherence relations between neuronal mechanisms of the brain hemispheres in the course of the bimanual motor performance may noticeably depend on the type of the respective motor task. In our tests, the intensity of coherence in different lead pairs, when measured during active hand movements, increased, as a rule, as compared with that in the resting state (Fig. 4). This was especially visible within the α range. Earlier, interhemisphere relations of α-range activity were examined under conditions of development of bimanual static efforts of various levels [3]. In this case, it was mentioned that the respective relations in central leads were

weakened, as compared with those at rest.

In addition, it was found earlier that the level of interhemisphere coherence in the α and β ranges can vary significantly in the process of training for the realization of bimanual movements. This was believed to be associated with functional changes in the system of the callosal tract [7]. In our tests, the movements were rather simple, and their realization did not require some special training. Probably because of this we did not observe dramatic changes in the coherence levels throughout the testing period. Note that the above-mentioned report emphasized especially the existence of the functional difference between the α and β rhythms, and this aspect agrees with our data.

In our tests, the dominant role of the right hand was reflected in a certain way in the levels of coherence of EEG phenomena (Fig. 4). In particular, the coefficients of coherence for the lead pairs corresponding to intrahemisphere relations within the right hemisphere (pairs C4–Cz, F4– Fz, and C4–F4), were noticeably greater than the respective values in the left hemisphere (pairs C3–Cz, F3–Fz, and C3–F3, respectively), and this feature was manifested with respect to both α and β oscillations. Also, we should note that the levels of desynchronization of EEG oscillations in the corresponding leads/areas practically did not differ from each other in opposite hemispheres (Fig. 3). At the same time, we should emphasize that bimanual movement-related desynchronization of α activity (a measure of the involvement of α rhythm-related cortical mechanisms in the movement control) was more intense in the hemisphere controlling the subdominant hand. At present, these data do not allow us to formulate some single-value conclusions. Perhaps, this fact emphasizes the importance of precisely the left hemisphere for the performance of simple movements by both dominant and subdominant hands, as well as by both hands. It is known that a significant activation of the left hemisphere in dextrals occurs during the movements of the subdominant hand. From this aspect, our results agree with those of the recent work by Serriyena et al. [4]. In the latter paper, the analysis of the data of EEG recording during the performance of different-type bimanual movements by different groups of the subjects (dextrals and sinistrals) allowed the authors to conclude that the left hemisphere plays an especially important role in the planning and control of sequential motor events in humans, independently of the dominating role of one hand or another.

Results of our study allow us to formulate the following conclusions: (i) α and β EEG rhythms are probably generated by dissimilar functional subdivisions of the cerebral cortex; (ii) control of the bimanual movements is not based on simple "superposition" of the commands providing the control of unimanual movements; (iii) mechanisms responsible for the control of movements performed by the subdominant limb can play a key role in the control of bimanual movements, and (iv) when cyclic manual movements are performed, a greater level of intrahemisphere functional relations between neuronal mechanisms of the subdominant brain hemisphere is observed; this fact may emphasize the special role of the opposite dominant hemisphere in the performance of these movements.

Acknowledgement. The work was supported by grant 0024/RSA2/2013/52, program Rozwój Sportu Akademickiego (Poland).

All experimental procedures were conducted in full accordance with the Helsinki Declaration (1964 and its later amendments), and also in compliance with the national ethical standards. All participants were preliminarily informed about the content and process of experimentation, agreed to participate in them, and gave their written concent.

The authors, T. Tomiak, A. V. Gorkovenko, V. S. Mishchenko, and D. A. Vasilenko, confirm that they did not have any conflicts regarding commercial or financial relations, relationships with organizations or persons, which in any way could be related to the study, and the relationships between co-authors.

REFERENCES

- 1. N. V. Dounskaia, K. G. Nogueira, S. P. Swinnen, and E. Drummond, "Limitations on coupling of bimanual movements caused by arm dominance: When the muscle homology principle fails," *J. Neurophysiol.*, **103**, No. 4, 2027-2038 (2010).
- 2. T. I. Abramovich, A. V. Gorkovenko, I. V. Vereshchaka, et al., "Peculiarities of activation of human muscles in realization of cyclic bimanual movements with different organization of the cycles," *Neurophysiology*, **48**, No. 1, 31-42 (2016).
- 3. J. Long, T. Tazoe, D. S. Soteropoulos, and M. A. Perez, "Interhemispheric connectivity during bimanual isometric force generation," *J. Neurophysiol.*, **115**, 1196- 1207 (2015).
- 4. D. J. Serrien and M. M. Sovijärvi-Spapé, "Hemispheric asymmetries and the control of motor sequences,"

Behav. Brain Res., **283**, 30-36 (2015).

- 5. B. A. Kay, J. A. Kelso, E. L. Saltzman, and G. Schoener, "Space-time behavior of single and bimanual rhythmical movements: data and limit cycle model," *J. Exp. Psychol. Human Percept. Perform.*, **13**, No. 2, 178-192 (1987).
- 6. S. C. de Oliveira, "The neuronal basis of bimanual coordination: recent neurophysiological evidence and functional models," *Acta Psychol.*, **110**, Nos. 2/3, 139- 159 (2002).
- 7. J. D. Wong, E. T. Wilson, D. A. Kistemaker, and P. L. Gribble, "Bimanual proprioception: are two hands better than one?" *J. Neurophysiol.*, **111**, No. 6, 1362- 1368 (2014).
- 8. Y. Li, O. Levin, A. Forner-Cordero, R. Ronsse, and S. P. Swinnen, "Coordination of complex bimanual multijoint movements under increasing cycling frequencies: the prevalence of mirror-image and translational symmetry," *Acta Psychol.*, **130**, No. 3, 183-195 (2009).
- 9. V. Garkavenko, O. Man'kovskaya, T. Omel'chenko, et al., "Effect of cold stimulation of the arm fingers on the spectral/coherent EEG characteristics in humans," *Neurophysiology*, **40**, No. 3, 228-230 (2008).
- 10. V. Garkavenko, E. Man'kovskaya, T. Omel'chenko, et al., "Modifications of EEG in humans performing cyclic movements by the fingers of the right arm: Effect of local contralateral cooling," *Neurophysiology*, **40**, Nos. 5/6, 369-376 (2008).
- 11. C. Gerloff, J. Richard, J. Hadley, et al., "Functional coupling and regional activation of human cortical motor areas during simple, internally paced and externally paced finger movements," *Brain*, **121**, No. 8, 1513-1531 (1998).
- 12. S. Schaal, D. Sternad, R. Osu, and M. Kawato, "Rhythmic arm movement is not discrete," *Nat. Neurosci.*, **7**, No. 10, 1136-1143 (2004).
- 13. E. G. James, "Nonstationarity of stable states in rhythmic bimanual coordination," *Motor Control*, **18**, No. 2, 184- 198 (2014).
- 14. R. R. Walsh, S. L. Small, E. E. Chen, and A. Solodkin, "Network activation during bimanual movements in humans," *NeuroImage*, **43**, No. 3, 540-553 (2008).
- 15. M. Toyokura, I. Muro, T. Komiya, and M. Obara, "Relation of bimanual coordination to activation in the sensorimotor cortex and supplementary motor area: analysis using functional magnetic resonance imaging," *Brain Res. Bull.*, **48**, No. 2, 211-217 (1999).
- 16. F. G. Andres, T. Mima, A. E. Schulman, et al., "Functional coupling of human cortical sensorimotor areas during bimanual skill acquisition," *Brain*, **122**, No. 5, 855-870 (1999).
- 17. M. A. Perez, D. S. Soteropoulos, and S. N. Baker, "Corticomuscular coherence during bilateral isometric arm voluntary activity in healthy humans," *J. Neurophysiol.*, **107**, No. 8, 2154-2162 (2012).
- 18. T. W. Boonstra, "The potential of corticomuscular and intermuscular coherence for research on human motor control," *Front. Human Neurosci.*, **7**, 855 (2013).
- 19. B. A. Conway, D. M. Halliday, S. F. Farmer, et al., "Synchronization between motor cortex and spinal motoneuronal pool during the performance of a

maintained motor task in man," *J. Physiol.*, **489**, No. 3, 917-924 (1995).

- 20. A. M. Amjad, D. M. Halliday, J. R. Rosenberg, and B. A. Conway, "An extended difference of coherence test for comparing and combining several independent coherence estimates: theory and application to the study of motor units and physiological tremor," *J. Neurosci. Methods*, **73**, No. 1, 69-79 (1997).
- 21. A. de Rugy and D. Sternad, "Interaction between discrete and rhythmic movements: reaction time and phase of discrete movement initiation during oscillatory movements," *Brain Res.*, **994**, No. 2, 160-174 (2003).
- 22. K. von Carlowitz-Ghori, Z. Bayraktaroglu, F. U. Hohlefeld, et al., "Corticomuscular coherence in acute and chronic stroke," *Clin. Neurophysiol.*, **125**, No. 6, 1182- 1191 (2014).