ISSN 0362-1197, Human Physiology, 2007, Vol. 33, No. 1, pp. 10–19. © Pleiades Publishing, Inc., 2007.
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Reorganization of Interhemispheric Interactions during Verbal–Mental Activity Aimed at Synthesis of Words and Sentences

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Received July 17, 2006

Abstract—Correlation and coherence analyses of multichannel electroencephalogram (EEG) recordings from 18 subjects (mean age 25 years) were used for investigating the reorganization of systemic interactions between bioelectric potentials of the cortical areas of both hemispheres (20 EEG derivations) during verbal–mental activity connected with generating verbal units from simpler components. When generating either words from aurally presented phonemes or sentences from a set of words, the subjects exhibited specific changes in the spatial structure of the statistical relationships in the EEG, with a significant increase in the interhemispheric interactions. During performance of both tasks, the changes in the interhemispheric interactions were most pronounced in the temporal, temporo-parieto-occipital (TPO), inferofrontal, and occipital areas of both hemispheres. Phonemic synthesis was associated with a more marked increase in the contralateral interactions in the left hemisphere, and generating sentences from words, in the right hemisphere. The coherence analysis of the EEG showed the greatest changes in the Δ, θ, and β frequency bands, with rather slight changes in the α frequency band. For all frequency bands, changes in the EEG coherences were the greatest in Wernicke's and the TPO areas of the right and left hemispheres during the performance of both tasks, especially during the phonemic synthesis. These findings suggest that neurophysiological processes underlying mental generation of words and sentences require coordinated activity of the left and right hemispheres, which is accompanied by an increase in the interhemispheric interactions in the EEG, especially in the temporal, inferofrontal, and TPO areas.

DOI: 10.1134/S0362119707010021

INTRODUCTION

Current methods for studying neurophysiological mechanisms responsible for verbal production and comprehension of oral and written language allow identification of specific features of the structure of intercentral interactions related to the analysis and synthesis of verbal signals with various phonetic, syntactic, and semantic elements [1–12].

A detailed study of these processes seems most promising for understanding the principles of organization of thinking. Study of the spatial structure of the bioelectric potential field of the brain may help to reveal the principles of systemic interactions of distant cortical areas during various types of verbal activity.

According to our previous findings, performance of verbal–mnemonic tasks such as mental counting; listening to, memorizing, and recalling verses; tasks relating to verbal fluency; and searching for homonyms leads to an increase in statistical relationships between the bioelectric potentials of the posterior cortical area of the left hemisphere and those of the frontal cortical area of the right hemisphere [13–16]. This type of interhemispheric interactions during verbal activity was described in [12, 17, 18].

Other types of verbal activity lead to the activation of interhemispheric interactions in the EEG of other cortical areas of both hemispheres. For example, performance of tasks related to the analysis of aurally perceived verbal material, i.e., recognition of either phonemes in a word context or grammatical or semantic errors in aurally presented sentences, was associated with an increase in the interhemispheric interactions between the EEG recorded from Broca's, Wernicke's, and the temporal areas of the left hemisphere and that of the antero- and midtemporal areas of the right hemisphere, with no changes in the intrahemispheric interactions in the EEG [19].

Neurophysiological mechanisms responsible for various aspects of verbal function, e.g., generation of complex verbal units from simpler components, have been poorly studied and need further research.

The objective of this work was to study the reorganization of the spatial structure of systemic interactions between various cortical areas of both hemispheres during performance of tasks related to mental synthesis of verbal material, i.e., generating either words from phonemes or sentences from a set of words.

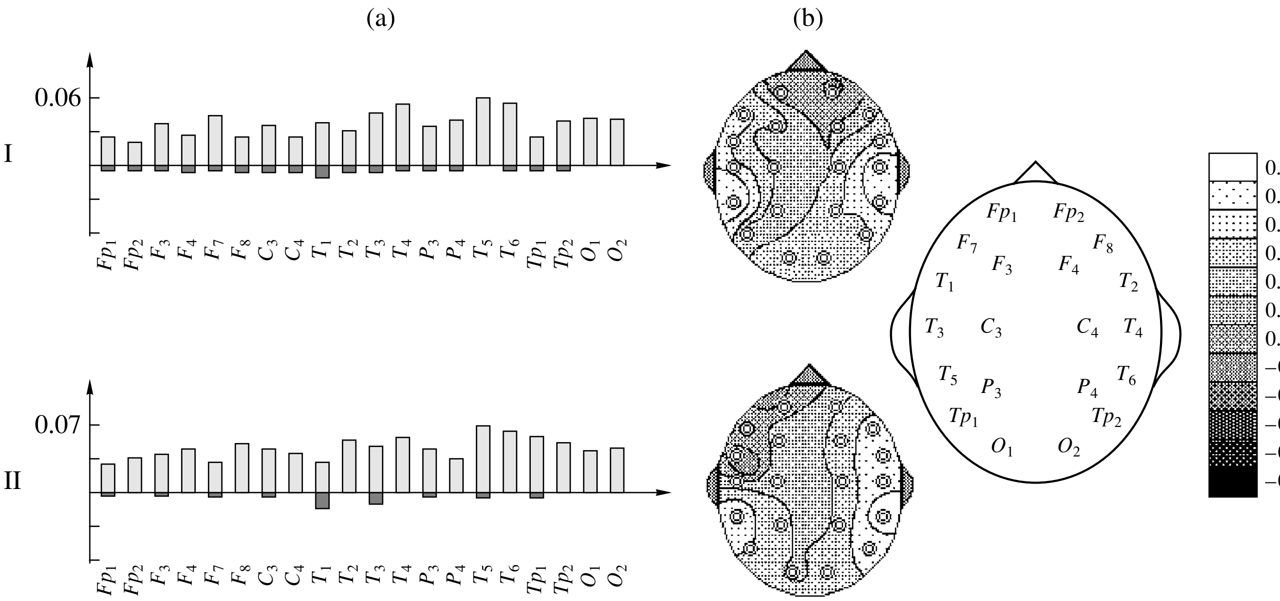


Fig. 1. Involvement of various cortical areas of both hemispheres in systemic brain activity during performance of verbal tasks, as revealed by the correlation analysis of the EEG. (I) Synthesis of words from phonemes; (II) generation of sentences from words; (a) changes in the intensity of interactions between the EEG of each cortical area and that of other areas. Upward columns, an increase in the coefficient of cross-correlation (CC); downward columns, a decrease in the CC. Ordinate, differences between the EEG CC in the state of relative rest and during performance of tasks; abscissa, EEG derivations placed in accordance with the scheme of placing electrodes from the right side. (b) Maps of the mean (relative to a given derivation) changes in the EEG CC in the tested state as compared with the baseline (according to the scale at the top right of the figure). Maps are plotted using the data from (a).

METHODS

EEG recordings from 18 healthy right-handed subjects aged 22–35 years were analyzed using multiparametric analysis in two series of observations.

The EEG was recorded monopolarly in the bandwidth 0.5–30 Hz with a 24-channel computer-aided electroencephalograph. The EEG signals were fed into the computer at a sampling rate of 185 samples per second. For EEG recording, 16 of 20 electrodes were placed symmetrically in accordance with the international 10–20 system in the anterofrontal (Fp_1 and Fp_2), posterofrontal (F_3 and F_4), inferofrontal (F_7 and F_8), central (C_3 and C_4), midtemporal (T_3 and T_4), posterotemporal (T_5 and T_6), parietal (P_3 and P_4), and occipital (O_1 and O_2) areas. For a detailed analysis of the importance of temporal areas for verbal function, four electrodes (Fig. 1) were additionally placed in the anterotemporal (T_1 and T_2) areas of both hemispheres and in the TPO (TP_1 and TP_2) areas, i.e., at the junction of the temporal, parietal, and occipital lobes. A coupled earlobe electrode was used as a reference. The EEG was continuously recorded in the following states: keeping awake with the eyes closed (the baseline EEG) and performing tasks in a lying position in a soundproof and darkened room.

All subjects were given two tasks. The first was phonemic synthesis (PS), i.e., generating words from aurally presented phonemes. A subject listened to four or five Russian phonemes that were binaurally presented through earphones in random order and then had to mentally compose two words (nouns) from these phonemes. For example, the phonemes **v**, **a**, **p**, **r**, and **o** were presented to a subject, from which he/she had to compose words (*povar* and *pravo*) and then relate the results. Five or six sets of phonemes were presented. The second task was sentence synthesis (SS), i.e., generating sentences from a set of words presented in the basic form and in random order. For example, several words such as *kompozitsiya, sostavlyat', original'nyi, salon, florist*, and *krasivyi*, were presented to a subject, from which he/she had to compose a finished, grammatically correct sentence containing function words if necessary. A total of 20 sets of words were presented with a changing semantic context.

The EEG was recorded when phonemes and words were presented to the subject and when he/she mentally composed words and sentences. No EEG was recorded when the subject related the results of the tasks performed.

For each 4-s analysis epoch, cross-correlation (CC) coefficients were calculated for all pairs of EEG derivations (190 EEG CC values) to give a 20×20 matrix.

For each epoch, we also calculated a matrix of the EEG coherence (Coh) in the Δ, θ, α, and β frequency bands. For this purpose, the following calculations were performed for all pairs of the 20 EEG derivations: (a) auto- and cross-covariance functions of the EEG

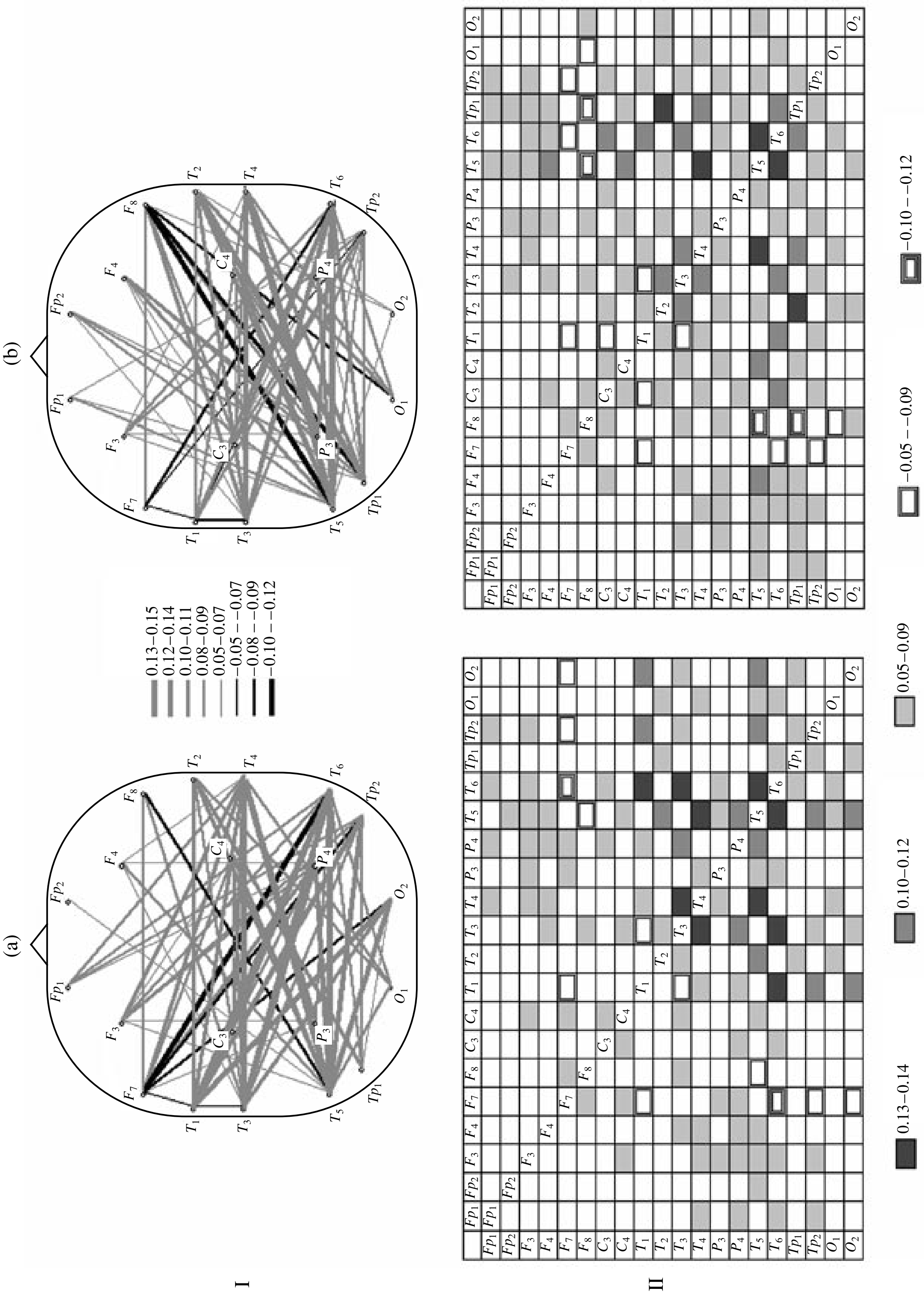

(a)
(b)
0.13–0.15
0.12–0.14
0.10–0.11
0.08–0.09
0.05–0.07
–0.05 – –0.07
–0.08 – –0.09
–0.10 – –0.12
I
II
0.13–0.14
0.10–0.12
0.05–0.09
–0.05 – –0.09
–0.10 – –0.12

Fig. 2. Changes in the structure of interhemispheric interactions of the cortical bioelectric potentials of both hemispheres during performance of verbal tasks. (a) Synthesis of words from phonemes; (b) generation of sentences from words. (I) Changes in the interregional interactions in the EEG; here and in Fig. 3, gray and black lines correspond to an increase and a decrease in the level of the EEG correlations, respectively, as compared to the baseline; the scale of changes is given in the center. (II) Difference matrices. Columns and rows are EEG derivations according to the scheme in Fig. 1. The scale of an increase or decrease in the EEG CC is given below. In the schemes and matrices, changes in the EEG CC are significant at $p = 0.01$.

were calculated; (b) after the functions were smoothed, the fast Fourier transform was used to determine the relevant auto- and cross-spectra and to calculate the Coh function in the frequency range from 0.5 to 30.0 Hz at an interval of 0.5 Hz; (c) mean Coh was calculated for the main frequency bands of the EEG, i.e., Δ (0.5–3.5 Hz), θ (4.0–7.5 Hz), α (8.0–12.5 Hz), and β (13.0–30.0 Hz); and (d) mean Coh for all pairs of the EEG derivations were then summed into a 20×20 Coh matrix.

Thus, for each EEG analysis epoch, one CC matrix and four Coh matrices were calculated. A total of 30–60 artifact-free epochs per subject were processed using the above algorithms for every tested state (baseline or performance of tasks). As a result, the duration of the analyzed EEG periods corresponding to a certain type of activity of the subject varied from 2 to 4 min.

Hierarchical agglomerative cluster analysis[1] was used to exclude from processing those CC matrices for which no significant statistical differences were observed at the baseline and during the performance of tasks. The above method made it possible to avoid any impact that short-term changes in the uniformity of the subject's state may have had on the results obtained.

The elements in the recorded correlation and coherence matrices of the multichannel EEG were averaged across the tested states and all subjects, the means and the EEG CC and Coh variances being calculated. To calculate correlation and coherence coefficients, Fisher's z-transform was used.

To estimate changes in the distant interactions in the EEG during the performance of the tasks, the elements in the EEG CC and Coh matrices averaged across the baseline state (relaxed wakefulness) were subtracted from the cell values in the mean EEG CC and Coh matrices corresponding to the performance of the tasks. In this way, EEG CC and Coh difference matrices were formed that reflected the changes in the spatial organization of the EEG detected during the performance of various tasks. For each cell of the difference matrices, Student's t-test ($p \leq 0.05$) was used to estimate the significance of changes in the EEG CC and Coh during the performance of the tasks as compared to the baseline EEG CC and Coh.

To plot an equipotential map of the changes in the distant interactions between bioelectric potentials, all the elements in a given column (corresponding to a certain EEG derivation) were averaged across the columns of the EEG CC and Coh difference matrices, the sign being taken into account. Thus, we determined the mean changes (across all 19 interactions between a given cortical area and the other areas) in the distant interactions in the EEG of a given area as compared to the results obtained at the baseline. These data were used to plot charts and maps. The maps were plotted with regard to the spatial gradient of the mapped parameters, with an optimal form of the interpolating surface.

On the basis of the statistically significant differences in the EEG CC and Coh between the baseline and tested states, a chart of changes in the interregional interactions was plotted using a special program.[2]

RESULTS

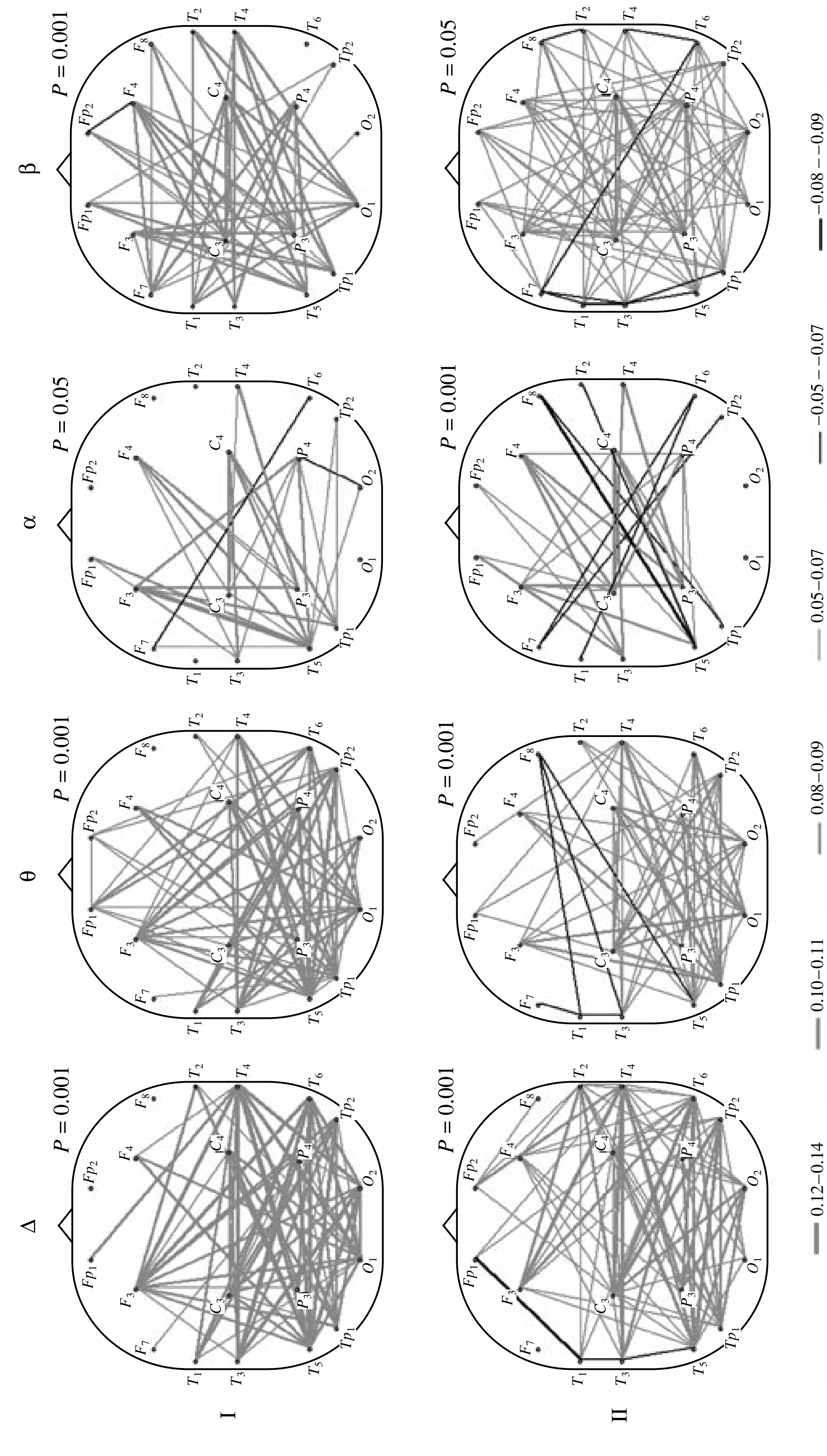
During the performance of the tasks related to PS and SS, the location of the cortical areas involved was substantially similar, with maximum changes in the spatiotemporal interactions of bioelectric potentials (Fig. 1). In both cases, there was a considerable increase in the spatial interactions between the bioelectric potentials of cortical areas of both hemispheres as compared to the baseline state. During the performance of both tasks, the maximum increase in distant interactions in the EEG was typical of the posterotemporal areas of the left and right hemispheres (Fig. 1, derivations T_5 and T_6). There was also a considerable increase in the interregional interactions of the bioelectric potentials of the middle temporal areas (T_3 and T_4). Notably, a greater involvement of the anterotemporal (T_2) and inferofrontal (F_8) areas of the right hemisphere was observed during the performance of the task involving SS rather than PS (Fig. 1, IIb).

Analysis of the changes in the interregional interactions in the EEG during the performance of both tasks (Figs. 2a, 2b, I) also showed a great similarity in their spatial structure, which can be explained by a considerable increase in the interhemispheric interactions, mainly in the diagonal relations.

During PS, both an increase and a decrease in the interhemispheric diagonal relations occurred mainly from left to right (mainly between the EEG of the frontal and antero- and midtemporal areas of the left hemisphere and that of the mid- and posterotemporal, TPO, parietal, and occipital areas of the right hemisphere);

[1] The methods and program were developed by A.A. Pogosyan at the Sechenov Institute of Evolutionary Physiology and Biochemistry.

[2] The program was developed by V.P. Rozhkov at the Sechenov Institute of Evolutionary Physiology and Biochemistry.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–0.08 – –0.09

during SS, the changes occurred mainly from right to left (Figs. 2a, 2b, I). Thus, during the performance of both tasks, there was a mirror symmetry in the structure of changes in the interhemispheric interactions in the EEG, which were more pronounced in the left hemisphere during PS and in the right hemisphere during SS.

The performance of both tasks was associated with an increase in the statistical relationships between the bioelectric potentials in bilaterally symmetrical cortical areas, primarily, between the EEG of the inferofrontal, temporal, central, and TPO areas of both hemispheres, with a maximum increase in the mutual correlation between the EEG of the mid- and posterotemporal areas.

During the performance of verbal tasks, a decrease in the statistical relationships of the bioelectric potentials was typical mainly of the long diagonal relations in the EEG of the inferofrontal areas of the left (F_7) and right (F_8) hemispheres (Figs. 2a, 2b, I). Again, as in the analysis of the spatial structure of increasing interregional interactions, a mirror symmetry in decreasing interhemispheric interactions in the EEG was observed during the performance of each task. There was a decrease in the interhemispheric interactions between the EEG of the inferofrontal areas and that of the posterotemporal (either T_5 or T_6), TPO (TP_1 and TP_2), and occipital (O_1 and O_2) areas of the contralateral hemisphere as compared to the baseline state. The changes were more pronounced in the left hemisphere (a greater decrease in the interactions in the EEG of the left versus the right inferofrontal area) during PS and in the right hemisphere during SS.

Note that, during the performance of both tasks, the same cortical areas exhibited a slight but statistically significant ($p = 0.01$) decrease in the intrahemispheric interactions, although only in the left hemisphere was there a decrease in the interactions between the bioelectric potentials from the F_7 and T_1 derivations and the T_1 and T_3 derivations as compared to the baseline state (Fig. 2).

During the performance of both tasks, there was also a certain mirror symmetry in changes in the interregional interactions in the bioelectric activity of the occipital cortical areas (Fig. 2). During PS, the statistical relationships in the EEG of the occipital area in the right hemisphere (O_2) increased to a greater extent than in the left hemisphere (O_1). The interactions in the EEG of this cortical area (O_2) were contralateral: there was an increase in the interactions with the temporal (T_1, T_3, and T_5) areas of the left hemisphere and a slight but significant decrease in systemic interactions with the inferofrontal area (Broca's area, F_7) of the same hemisphere. During SS, the changes in the contralateral interactions in the EEG of the occipital (O_1) area of the left hemisphere dominated.

Coefficients of similarity (CSs) between changes in the spatial structure of the EEG coherences in various frequency bands and the matrix of changes in the cross-correlations of the total EEG during performance of verbal tasks

Task	EEG frequency band			
	Δ	θ	α	β
Synthesis of words from phonemes	**0.71**	0.63	0.43	0.67
Generation of sentences	**0.66**	0.58	0.31	0.63

Note: Maximum values of the CS for each task are boldfaced.

Thus, during both PS and SS, the structural changes in the interregional interactions of the cortical bioelectric potentials of both hemispheres were expressed in an increase in the diagonal relations and interhemispheric interactions in the EEG of bilaterally symmetrical areas, mainly the temporal and TPO areas of the left and right hemispheres and, to a lesser extent, the inferofrontal, occipital, and frontal areas. For both tasks, there were only slight changes in the intrahemispheric interactions in the EEG.

Analysis of the EEG CC difference matrices shown in Fig. 2 may be helpful for observing the specific features of the reorganization of the spatial structure of systemic interactions between the cortical areas during the performance of verbal–mnemonic tasks related to the synthesis of verbal units from simpler components. These matrices were used as the bases for plotting charts and maps (Fig. 1) and schemes of interregional interactions (Fig. 2, I).

For example, analysis of the difference matrices related to both states demonstrated marked differences in the involvement of the parietal areas of the left and right hemispheres in each of the types of verbal activity under study. During PS, the P_4 column, corresponding to the right parietal area, displayed considerably more changes in the distant interactions in the EEG than the P_3 column, corresponding to the left parietal area; during SS, the opposite was true. The analysis of the difference matrices also showed that, during SS, the changes in the distant interactions in the EEG of the TPO areas (TP_1 and TP_2) of both hemispheres considerably exceeded those during SP.

Fig. 3. Specific changes in the spatial structure of the coherence relationships between the bioelectric potentials in various EEG frequency bands during performance of verbal tasks as compared to the baseline. (I) Synthesis of words from phonemes; (II) generation of sentences from words; abscissa, the main EEG frequency bands (Δ, θ, α, and β). The scale of the changes in the EEG coherences is given below. The significant changes in the EEG coherences are given in accordance with the symbols at the top right of the figure.

The coherence analysis of the EEG recorded during the performance of both tasks also showed considerable changes in the spatial organization of the bioelectric potential field of the brain in the main frequency bands (Fig. 3, I and II). The observed changes were rather similar, e.g., the performance of both tasks was associated with relatively few changes in the structure of the EEG coherences in the α frequency band (Fig. 3, I and II). The coefficient of similarity between the changes in the distant interactions in the EEG for this frequency band and the changes in the correlations of the total EEG was 0.43 during PS and 0.31 during SS (table).

However, each of the EEG frequency bands had its own specific features. For example, the greatest similarity between the changes in the spatial structure of the EEG coherences and the above changes in cross-correlations of the total EEG was observed in the Δ and β frequency bands (Figs. 2, 3). This was in line with the greatest values of the coefficients of statistical similarity (CSs) and the EEG Coh and CC matrices (the Δ frequency band: the CS was 0.71 and 0.66 for PS and SS, respectively (table)). During PS, the CS was also greater than 0.60 in the θ frequency band, indicating that the spatial changes in the coherences between the bioelectric potentials of various cortical areas of both hemispheres in the θ frequency band were rather similar to the changes in the cross-correlations of the total EEG.

Again, as in the analysis of EEG cross-correlations, there was a significant increase in the interhemispheric coherences. However, compared with the correlation analysis, the coherence analysis of distant interactions in the EEG was more helpful for detecting an increase in the intrahemispheric interactions, especially in the left hemisphere. For example, during PS, there was a significant increase in the ipsilateral coherences between the bioelectric potentials of the frontal (Fp_1 and F_3) areas of the left hemisphere and the activity in Wernicke's (T_5) and the TPO (TP_1), parietal (P_3), and occipital (O_1) areas of the left hemisphere (Fig. 3, I). During SS, the EEG coherences between these areas of the left hemisphere were expressed to a lesser extent and mainly in the α, β, and θ frequency bands (Fig. 3, II).

A decrease in the diagonal coherences between the bioelectric potentials of the inferofrontal (F_7 and F_8) areas of both hemispheres and the posterotemporal (T_5 and T_6) and TPO (TP_1 and TP_2) areas of the contralateral hemisphere was observed in the α frequency band, especially during SS. During PS, a decrease in the diagonal coherences was observed in the α frequency band only between the EEG of Broca's area (F_7) and that of the posterotemporal area (T_6) of the contralateral hemisphere. In the θ frequency band, a decrease in the coherences between the EEG of the inferofrontal (F_8) area of the right hemisphere and that of Wernicke's and the antero- and midtemporal areas of the left hemisphere was observed only during SS.

In the Δ, θ, and β frequency bands, the EEG coherences of the occipital areas of both hemispheres increased during PS to a greater extent than during SS. As was noted above, during the performance of these tasks, a mirror symmetry was typical of distant interactions between the left and right occipital areas, as evidenced by the correlation analysis of the total EEG (Fig. 2).

However, in the tested EEG frequency bands, the spatial structure of the constellations of coherence relationships of bioelectric potentials substantially differed both in the location of the areas involved and in the extent to which the contralateral and ipsilateral interactions increased. During the performance of both tasks, especially during PS, Wernicke's area (T_5) was activated more often than other cortical areas, as evidenced by its functional interactions with other brain regions.

DISCUSSION

The results obtained show that the neurophysiological processes underlying verbal–mental activity aimed at the synthesis of verbal units, i.e., words and sentences, proceed at a high level of systemic interaction between the bioelectric activities of the cortex in both hemispheres, especially in the temporal and inferofrontal areas. Broca's and Wernicke's areas and, to the same or even a greater extent (during SS), symmetrical areas of the right hemisphere are involved in these close interhemispheric interactions.

Mental generation of either words from phonemes or sentences from aurally presented sets of words includes several sequential and parallel operations. They begin with the perception, identification, and analysis of the acoustic characteristics of signals and their recognition as verbal units. For this purpose, it is necessary to compare the sound patterns of presented signals with the memory engrams of phonemes and words [20]. Then, the programming and generation of a word or phrase from sets of recognized elementary units are likely to occur. When these processes occur, the semantic context and grammatical norms learned earlier are taken into account. Finally, the synthesized word or composed phrase is mentally compared with linguistic norms.

Undoubtedly, these sophisticated psychophysiological processes require a continuous exchange of information between the left and right hemispheres and activate, to a greater or lesser extent, almost all cortical areas. According to our findings, verbal–mental processes, including analysis, synthesis, programming, and control, are specifically reflected by the spatiotemporal organization of oscillations of the cortical bioelectric potentials of both hemispheres.

During the performance of both tasks, there was a great similarity between the changes in the interregional interactions of the cortical areas, which were expressed in a considerable increase in the interhemispheric interactions in the EEG, with slight changes in the intrahemispheric interactions. In both cases, the contralateral interactions in the EEG of the temporal, TPO, inferofrontal, and occipital areas of both hemispheres changed maximally as compared to the baseline state. The changes in the interhemispheric interactions, mainly in the diagonal relations, were the greatest, although the statistical relationships in the EEG of bilaterally symmetrical cortical areas also increased.

We have already reported that the performance of verbal tasks related to the analysis of aurally perceived verbal material (recognition of either phonemes in a word context or grammatical or semantic errors in sentences) is associated with a significant increase in the interhemispheric interactions between the EEG of the temporal and Broca's areas of the left hemisphere and that of bilaterally symmetrical areas of the right hemisphere [19]. In these cases, the changes in the intrahemispheric interactions were insignificant.

Although the observed changes in the interhemispheric interactions in the EEG are rather similar to those described earlier (more pronounced during the performance of tasks related to phonemic analysis and synthesis, i.e., generating words from aurally presented phonemes and recognizing phonemes in aurally presented words [19]), we found specific differences in the spatial structure of interhemispheric interactions during the verbal activity of synthetic nature studied in the present work. For example, generation of words and sentences was associated with a considerably greater increase in the contralateral diagonal relations of the EEG of the TPO areas of both the left (mainly during generation of sentences from words) and the right (during generation of words from phonemes) hemispheres. These findings are in line with those reported in neuropsychological studies according to which a lesion of the left TPO area leads to impaired comprehension of complicated logical–grammatical constructions. Notably, the TPO areas are involved in simultaneous analysis and synthesis of supramodal information [21, 22]. Our findings suggest that synthesis of verbal units requires the involvement of the TPO area of not only the left but also the right hemisphere.

One more difference was found for the occipital areas: the performance of tasks related to analysis of aurally perceived material [19] was associated with few changes in the interregional interactions between the above areas, while the performance of tasks related to mental synthesis of phrases and especially words was associated with a marked increase in the distant interactions between the EEG of the occipital areas and that of the temporal areas, mainly of the contralateral hemisphere. This was proved by the correlation and coherence analyses of the EEG. The coherence analysis of the EEG showed activation of the ipsilateral interactions in the EEG of the occipital areas in all frequency bands except α (in the case of PS, within the left hemisphere).

The fact that the occipital areas of the left and, especially, the right (during synthesis of words) hemispheres were involved in the verbal activity indicates that the mechanisms responsible for imaginative thinking are substantially involved in synthetic verbal activity. Indeed, most of the subjects reported that, when generating words from aurally presented sets of sounds, they used mental visual images of letters and syllables. Interestingly, the task related to PS was difficult for all subjects.

During PS and SS, there was a considerable increase in the statistical relationships between the bioelectric potentials of Wernicke's area and the symmetrical posterotemporal area of the right hemisphere with many contralateral cortical areas. There was also an increase in the relationships of the other temporal areas of both hemispheres with many cortical areas, mainly of the contralateral hemisphere.

As was shown in [23], the available neurovisualization methods confirm clinical data that auditory perception and recognition of speech require involvement of not only Wernicke's and other temporal areas of the left hemisphere, but also cortical areas in the right hemisphere homologous to Wernicke's area and sometimes the anterotemporal area of the right hemisphere [24].

Our findings suggest that not only auditory perception of verbal signals but also mental generation of verbal phrases requires active involvement of the temporal areas of the right hemisphere. An important point is that there is a significant increase in systemic interactions between the bioelectric activities of these homologous areas of the left and right hemispheres, as evidenced by the correlation and coherence (mainly in the Δ, θ, and β frequency bands) analyses.

Morphologically, these systemic interactions are ensured by the caudal parts of the corpus callosum and the pathways in the posterior part of the anterior commissure [25].

As described in the review article by Mesulam [6], in studies by other authors involving tasks where subjects were asked to name various colors or specific features of the movement of objects or pictures of faces and animals, selective activation of the cortical areas responsible for perceptual decoding of the relevant features and properties of the objects occurred. Very few of these regions of the temporal lobe appear to overlap with Wernicke's area. According to Mesulam [6], this indicates that lexical information retrieval is a complicated function with a broad spatial representation.

Special attention should be focused on positron emission tomography–based clinical observations evidencing that lesions that spare Wernicke's area but interrupt its connections with other parts of the association cortex impair speech comprehension and the ability to translate thoughts into words [6]. Such observations have led to the conclusion that Wernicke's area is not a central repository for neurophysiological processes responsible for verbal function, but a neural gateway that performs a switching function, where impulses of various sensory and associative fields converge and neuronal patterns of images are transformed into word forms. It is clear that such a multiprogram task requires the extensive connections of Wernicke's area, which cover not only many regions in the temporal lobe of the left hemisphere [6] but also, as evidenced by our findings, most of the distant areas of both hemispheres, especially the contralateral hemisphere.

Of special interest are the inferofrontal areas (F_7 and F_8), where the distant interactions in the EEG considerably and selectively decreased, as evidenced by the correlation and coherence analyses. During PS, there was a decrease in the interactions between the EEG of the inferofrontal area of the left hemisphere and the bioelectric potentials of certain areas of the contralateral hemisphere (T_6, TP_2, and O_2), and during SS, there were mirror relationships, i.e., a more marked decrease in the interactions between the EEG of the inferofrontal area of the right hemisphere and that of the same areas of the left hemisphere (T_5, TP_1, and O_1). In the latter case, the interactions in the EEG of the right inferofrontal area (F_8) selectively decreased in the α and θ frequency bands, as shown by the coherence analysis.

The coherence analysis of the spatial structure of the bioelectric potential field of the brain showed certain differences for all EEG frequency bands during the performance of the two tasks. During PS, there was a more marked reorganization of the structure of interactions in the β, θ, and Δ frequency bands; during SS, an increase (or, less frequently, a decrease) in the interhemispheric interactions in the EEG (compared to the baseline) was less pronounced and could be explained by the lower complexity of the task, as reported by the subjects.

PS was associated with a relatively greater increase in interhemispheric correlations between the EEG of the antero- and midtemporal areas of both hemispheres, slightly more marked in the left hemisphere. Compared with SS, PS was associated with a greater increase in the interhemispheric interactions of the inferofrontal (Broca's) and posterofrontal areas of the left hemisphere, while the level of interhemispheric interactions of the inferofrontal and postero- and midtemporal areas of the right hemisphere was lower.

During SS, the contralateral interactions in the EEG of the inferofrontal areas of the right hemisphere, especially with the mid- and posterotemporal areas of the left hemisphere, changed to a greater extent. As shown in Results, the spatial structure of the bioelectric potential field of the brain during SS differed from that during PS.

These distinctive features can be explained using Chomsky's hypothesis [26] on the principles of phrase generation based on the rules for widening a kernel sentence, which, as Chomsky conceives of it, is noun and verb phrases. After the above rules are used for each part of the kernel sentence (by using other auxiliary parts of the sentence), it is transformed into a complete sentence. It may be suggested that a strategic choice for each branch node requires consistent and regulated activation of cortical areas responsible for both the storage of verbal information and the control of adherence to grammatical and semantic rules. These processes can be reflected by an increase in bilaterally symmetrical and diagonal relations of many cortical areas of both hemispheres during PS.

A systemic integration of the activity of various areas of the right and left hemispheres during generation of sentences can be explained using the ideas described in [27] on the necessity of interhemispheric information exchange involving an intricate multiphase transformation of phrase deep structure, ensured mainly by the right hemisphere, into surface structure, associated mainly with the left hemisphere.

CONCLUSIONS

Combined activity of various cortical areas of the left and right hemispheres was detected during the performance of complicated linguistic tasks involving synthesis of verbal units from simpler components. The performance of tasks related to either synthesis of words from aurally presented phonemes or generation of semantically coherent sentences from a set of aurally presented words was associated with specific changes in the spatial structure of systemic interactions of cortical bioelectric potentials, with an active involvement of both hemispheres.

These changes were expressed primarily in an increase in the interhemispheric interactions between cortical areas, with a relatively small increase in the ipsilateral interactions. In both cases, the most marked changes in the contralateral interactions in the EEG were typical of the temporal areas, including Wernicke's area, and the TPO, inferofrontal, and occipital areas of both hemispheres. There was an increase in the statistical relationships between the oscillations of the bioelectric potentials of bilaterally symmetrical cortical areas, mainly in the diagonal relations. We found a mirror symmetry in the structure of changes in the interhemispheric interactions in the EEG during the performance of each task, i.e., a more marked dominance of the left hemisphere during PS and of the right hemisphere during SS.

An active involvement of the temporal areas of the right hemisphere and a significant contribution of the occipital areas of the left and right hemispheres indicate that the mechanisms responsible for imaginative thinking are substantially involved in synthetic verbal activity.

The fact that the distant interactions in the EEG of the inferofrontal areas of the right hemisphere changed more markedly during SS suggest that the generation of meaning-bearing sentences from a set of words requires involvement of the cortical areas of the right hemisphere responsible for prosodic and tonal characteristics of speech.

Our findings indicate that verbal–mental activity related to the synthesis of complex verbal constructions from simpler components requires coordinated combined activity of the temporal and inferofrontal areas of both hemispheres, with an essential but differentiated involvement of the classical speech regions of the left hemisphere, specifically, Wernicke's area. Our findings confirm the current ideas on the great importance of interhemispheric interactions for verbal–mental activity and on involvement of both hemispheres in all levels of language organization.

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