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Ontogenetic Development of Neurophysiological Mechanisms Underlying Language Processing

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Abstract

During the last 20 years, new data on the neurophysiological mechanisms underlying different types of cognitive activity, especially speech and its ontogenetic formation, were obtained in the Laboratory of Children's Neurophysiology headed by Prof. M.N. Tsitseroshin. Using the analysis of the spatial-temporal structure of regional interactions of cortical bioelectric potentials (so-called functional connectivity), we investigated how specific language levels, such as phonology, grammar, and semantics, are represented in the brain. The data obtained in children vs. adults indicate that the speech perception and production require joint and extremely coordinated activities of both hemispheres, along with the obligatory and differentiated involvement of "classic" speech centers in the left hemisphere, especially Wernicke's area. Another line of our research is to explore the differences, which arise during verbal processing in adults and children with impaired vs. non-impaired speech, particularly with alalia, dysarthria and stuttering, using behavioral and EEG data. Our data obtained in children vs. adults allow assessing the degree of maturity in the organization of the central processes of maintaining the studied types of verbal activity in children of different ages. These data allow expanding modern concepts about the brain mechanisms of verbal activity in children in the norm and pathology.

Keywords: speech processing, phonology, grammar, semantics, EEG, brain, development, interhemispheric interactions, speech pathology

1. Introduction

A study of the functional interaction between various parts of the cerebral cortex (so-called functional connectivity) is of fundamental importance for understanding the neural basis of cognition [1–14]. A growing number of studies that have appeared in the last decade testify the renewed interest in functional interactions among different brain parts, in both the background state and under cognitive activity [13, 15]. Unraveling functional connections in the human brain, with a main focus on the formation of the integrative brain mechanisms, has been a long-term research goal of the Laboratory of Child's Neurophysiology at the Sechenov Institute of Evolutionary Physiology and Biochemistry of the Russian Academy of Sciences headed by Prof. M.N. Tsitseroshin. The original methods designed in the laboratory to analyze the primary and secondary EEG parameters provided new insight into the genesis of these mechanisms. It was shown that the spatial-temporal structure of interregional interactions of cortical bioelectrical activity (i.e., functional connectome) in healthy subjects is highly spatially ordered (**Figure 1**).

It was shown for the first time that the structure of the distant EEG statistical relationships in adults does not arise randomly or chaotically, but occurs in a strictly ordered manner (**Figure 1A**). The implementation of various types of cognitive activity is associated only with transitional changes in the spatial structure of the interregional interactions while maintaining the integration processes of the brain activity characteristic of the resting state. Our studies have shown that this ordered structure of cortical interactions retains its topological invariance also in other background states of the brain, in particular, at different stages of natural and hypnotic sleep. Stable distortion of the ordered structure of intracortical interactions was detected only in case of cerebral pathology [5, 16–19] (**Figure 1B**).

During brain maturation, this order gradually increases, reflecting the formation of integrative relationships in the cortex and subcortical structures. This process creates a stable morphofunctional basis for the effective performance of learning processes and optimization of adaptive reactions. The authors consider this phenomenon as one of the fundamental features of the whole brain's functional organization required for the brain's normal activity. The orderliness of the spatial organization of brain biopotential field reflects the functioning of main integrative mechanisms of the brain. Based on the data obtained using factor analysis of EEG, it is possible to specify some morphofunctional brain systems (factors), which are directly involved in the processes of brain activity integration. According to these ideas, the factor I reflects general properties of the wave bioelectric processes occurring on the convexital surface of the cortex. It also reflects a degree of generalized nonspecific modulating influences of the brainstem and medulla on the cortical fields' activity. Factor II reflects the frontal-occipital relationships, that is, processes of activity integration for the anterior and posterior portions of each hemisphere by means of long association pathways and thalamo-cortical associative systems. Factor III reflects interhemispheric interactions, that is, processes providing coupled activity of the cerebral hemispheres by means of the commissural fibers with the involvement of the striopallidar and limbic systems.

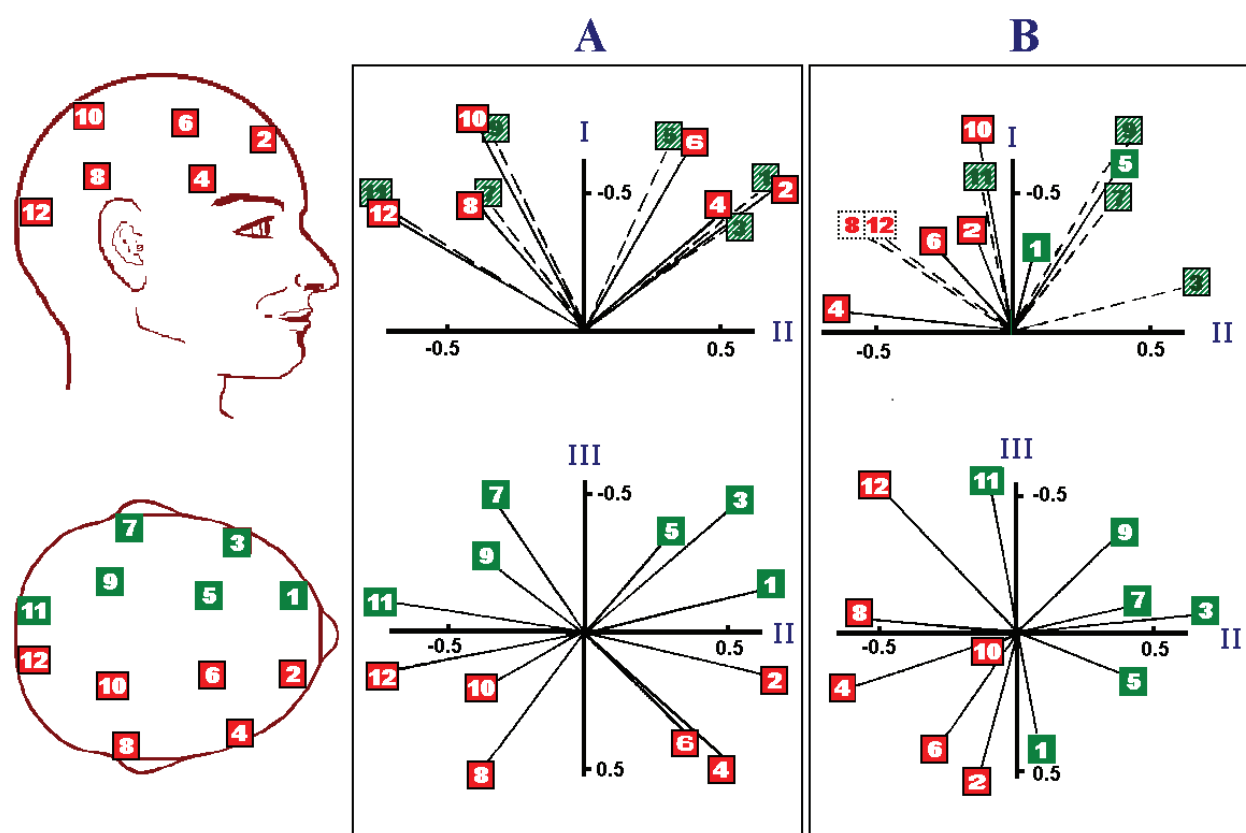


Figure 1. New method of EEG data representation in 3D factor space. (A) In the norm, the location of the radius vectors (the angles between vectors reflect the cross-correlation between EEG processes in different cortical areas) and electrodes is very similar, indicating strictly ordered spatial interactions of cortical areas' activity. (B) In case of cerebral pathology, the revealed topological violations of the radius vectors' location. At the top—projections of EEG radius vectors on the plane of factors I–II. At the bottom—same on the plane of factors II–III. Numbers of EEG radius vectors (1–12) that correspond to EEG leads in the left charts.

Methodological approaches used in our laboratory, including the priority methods (patent RU № 2177716 of 10.01.2002), allow quantitative assessment of the contribution of the left and right hemispheric cortical fields to the organization of neurophysiological mechanisms underlying various types of cognitive activity, including speech [7].

2. Neurophysiological mechanisms underlying language development

Current data on the principles of organization of the central nervous system and mental activities allow linking the processes of cognitive activity with the simultaneous involvement of numerous spatially distributed cortical and subcortical structures. An appropriate way to study patterns of cortical interactions is analysis of the spatiotemporal organization of brain activity oscillations. Currently, it is of no doubt that language processing relies on a widespread network of brain regions [1–5, 20–26]. Great importance is also attached to the role

of cortical networks and functional connections between different parts of the brain, in both adults and children [21, 22, 27–33].

Despite a long period of study, the question about a special role of the left and right hemispheres in providing the speech function as well as on the degree of involvement of interhemispheric relationships in these processes is still at the peak of interest [34]. Considering the well-known concepts of a greater significance of the right hemisphere for the speech processes in children vs. adults [35, 36], a study of the central mechanisms of the speech function formation in the children's ontogeny is of particular relevance.

The issues of the levels of involvement of the left and right hemispheres in supporting verbal activity are of continuing interest of investigators; however, their analysis sometimes yields mutually contradictory results. The use of the state-of-the-art neuroimaging methods, such as functional magnetic resonance imaging (fMRI), has unexpectedly increased the number of reports with the evidence of predominantly left-sided location of the neural centers responsible for speech perception and production [32, 37–39]. Thus, Binder et al. [37], while reviewing 120 articles on cortical locations of the areas associated with semantic speech processes, reported that 68% of 1145 fMRI or PET activations were detected in the left hemisphere cortex areas, 32% in the right hemisphere, and 10% in the cerebellum. The locations of right-sided foci were generally homologous to those of several left-sided foci—in the angular gyrus, posterior middle temporal gyrus, and cingulate gyrus. But, these data summation by a special algorithm led the authors to conclude mainly left-sided lateralization for verbal semantic processes. Price [38] has come to similar conclusions considering 100 fMRI speech studies reported in 2009. However, other authors, despite some left hemisphere advantages, defend the bilateral cerebral organization of language processing. This viewpoint was emphasized in the Hickock and Poeppel model [20]. The studies by Hagman et al. [40], using fMRI combined with diffusion tractography, pointed out that the subject gender has a significant influence on the speech processing lateralization. The results of spectral coherence and cross-correlation analysis of EEG-data provided a highly reproducible result associated with significant changes in both hemispheres during verbal processing, with increased levels of hemispheric interactions [21, 22, 30, 31]. Two earlier studies in this area [41, 42] emphasized that changes in EEG spectral power and coherence during speech processing are seen in both hemispheres showing no signs of any predominant lateralization (“These results do not indicate any lateralized EEG changes during verbal tasks”) ([42], p. 357). Our studies of cortex regional interaction organization in children and adults, during different verbal tasks, have been shown the long-distance connection activation between cortical biopotentials of the left and right hemispheres [1–5, 7, 43, 44]. According to Ross [24], “functional localization in the brain is a robust dynamic and four-dimensional process. It is a learned phenomenon driven over time by large-scale, spatially distributed neural networks seeking to efficiently maximize processing, storage, and manipulation of information for cognitive and behavioral operations.” Yourganov et al. [45] also pointed out that connectome-based approaches should be used in combination with lesion-based ones to fully elucidate whether structurally damaged or disconnected regions relate to the aphasic impairment and its recovery.

During the past 20 years, new data have been obtained in our laboratory on neurophysiological mechanisms underlying different types of cognitive activity, especially speech and

its formation in ontogenesis. Special attention was paid to analysis of interhemispheric interactions and the involvement of the left and right hemispheres in speech. Our investigations were focused on the central mechanisms underlying speech processing at different language levels: phonological, semantic, syntactical, and lexical. On the other hand, we investigated both analytical speech processing (auditory perception and analysis of verbal signals) and synthetic speech processing (mental formation of words from sets of phonemes, mental formation of sentences from sets of words). We also investigated EEG correlates of verbal task performance in healthy adults and children as well as children with dysarthria, alalia, and typical speech development. Our results obtained in children vs. adults allow us to assess the degree of maturity of the central processes providing the maintenance of the studied types of verbal activity in children at different ages. The results of our research allow expanding modern concepts about the brain mechanisms of verbal activity in children in the norm and pathology; they can also assist in developing effective approaches to early correction of speech disorders.

At the semantic and syntactical language levels, we investigated the spatial organization of brain biopotentials in healthy adults during the perception of sentences with syntactical or semantic mistakes. At the syntactical language level, we used sentences containing the following syntactical mistakes: (1) gender agreement errors: in personal endings of verbs, for example—“Pod stolom sidel sobaka” (“A dog [feminine] sat [masculine] under the table”) and in gender endings of adjectives—“Devochka nadela goluboe yubku” (“The girl put on a blue [neuter] skirt [feminine]”); (2) mistakes in Russian nouns: in inflections of nouns—“Ya prochital interesnuyu knizhku” (“I have read an interesting [accusative case] book [instrumental case]”). As for semantic, the stimulus material contained the following types of semantic mistakes: (1) mistakes in constructions reflecting the time sequence of events (“Winter comes after spring”) and (2) constructions containing a semantic paradox (“A tortoise overtook a deer”). Our results revealed changes in distant biopotential relationships, which were both similar and specific to the type of mistakes. In both cases, the interhemispheric biopotential relationships increased significantly as compared to eyes-closed resting conditions. At the same time, almost the total absence of changes in intrahemispheric EEG correlations was observed. An increase in contralateral interactions was particularly characteristic of the activity of Broca and Wernicke’s areas and the middle temporal zone of the right hemisphere. Distant EEG relationships in Broca’s area increased more significantly during the detection of semantic rather than grammar mistakes in adults. Obtained data also showed that detection of grammatical and syntactic mistakes was supported by the intercentral connections related to the functional system responsible for the detection not only of verbal but also any other stimuli [3] (**Figure 2**).

The recent data [46] provide evidence that sensitivity to syntactic complexity is widespread across the language system, contrary to many previous neuroimaging studies that reported only a few, localized foci of syntactic complexity effects.

The other line of our research addresses the neurophysiological mechanisms underlying the maintenance of mental speech activity associated with the synthesis of speech units from elementary components (mental composing words from a set of phonemes and composing sentences

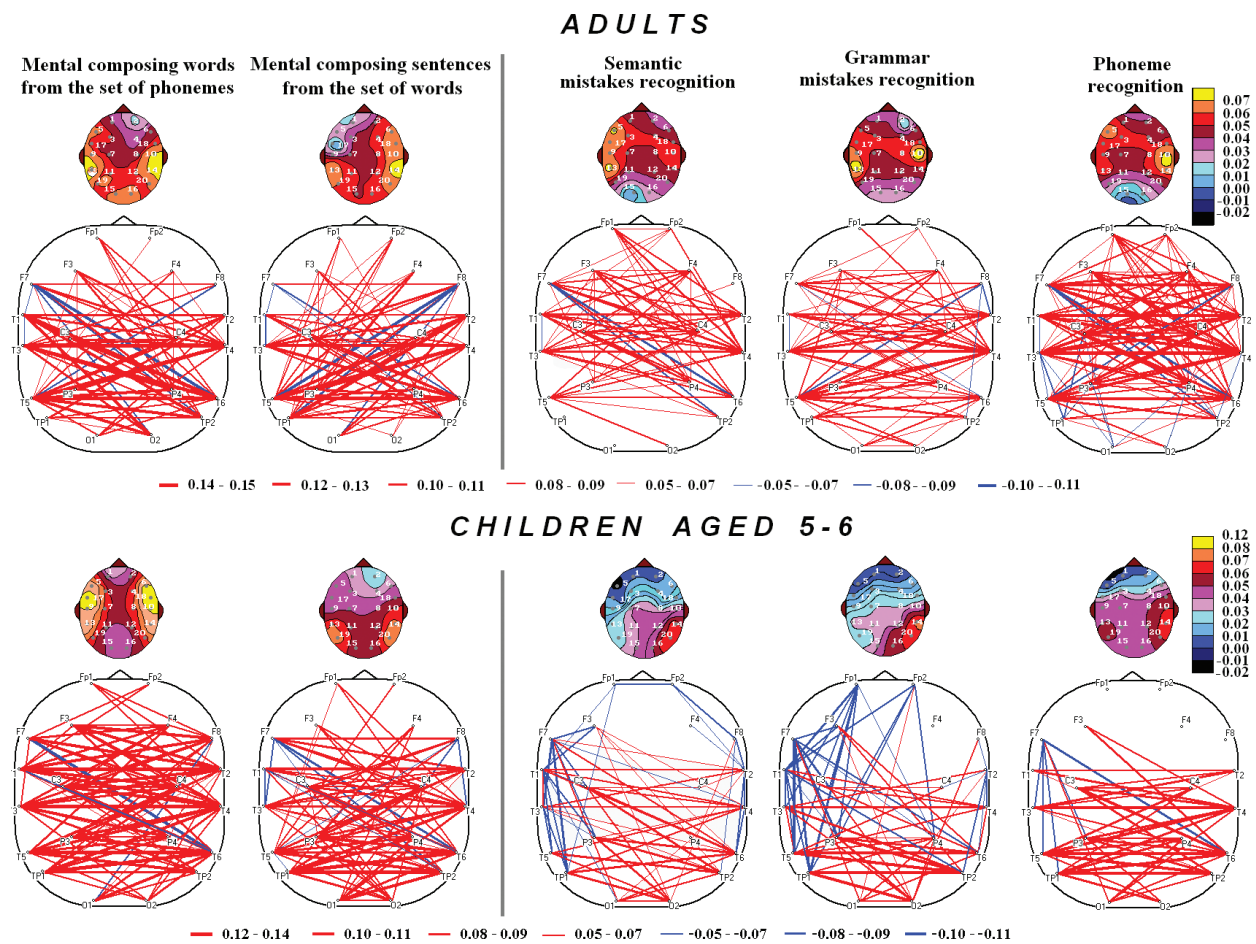


Figure 2. Increase in interhemispheric interactions during speech perception and production in adults and children aged 5–6 years. Left side—mental synthesis of speech units: composition of words from the set of auditory presented phonemes and composition of sentences from a set of auditory presented words. Right side—detection of semantic and syntactic mistakes in auditory presented sentences; analysis of verbal material during phoneme recognition in auditory presented words [4].

from a set of words) in healthy adults [2] and children aged 5–6 years [4]. During the mental composition of words from an auditory presented set of phonemes (phonemic synthesis) or sentences from a set of words, the adults exhibited specific changes in the spatial structure of the statistical EEG relationships with a significant increase in the interhemispheric interactions. During the performance of both tasks, changes in the interhemispheric interactions were typical for the temporal, temporo-parieto-occipital (TPO), inferofrontal, and occipital areas of both hemispheres (**Figure 2**). Phonemic synthesis was associated with a more pronounced increase in the contralateral interactions in the left hemisphere, as well as with generating sentences from words in the right hemisphere. The coherence analysis of EEG showed maximal changes in the delta, theta, and beta frequency bands with rather slight changes in the alpha frequency band (**Figure 3**, adults). For all frequency bands, changes in EEG coherence 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 EEG, especially in the temporal, inferofrontal, and TPO areas.

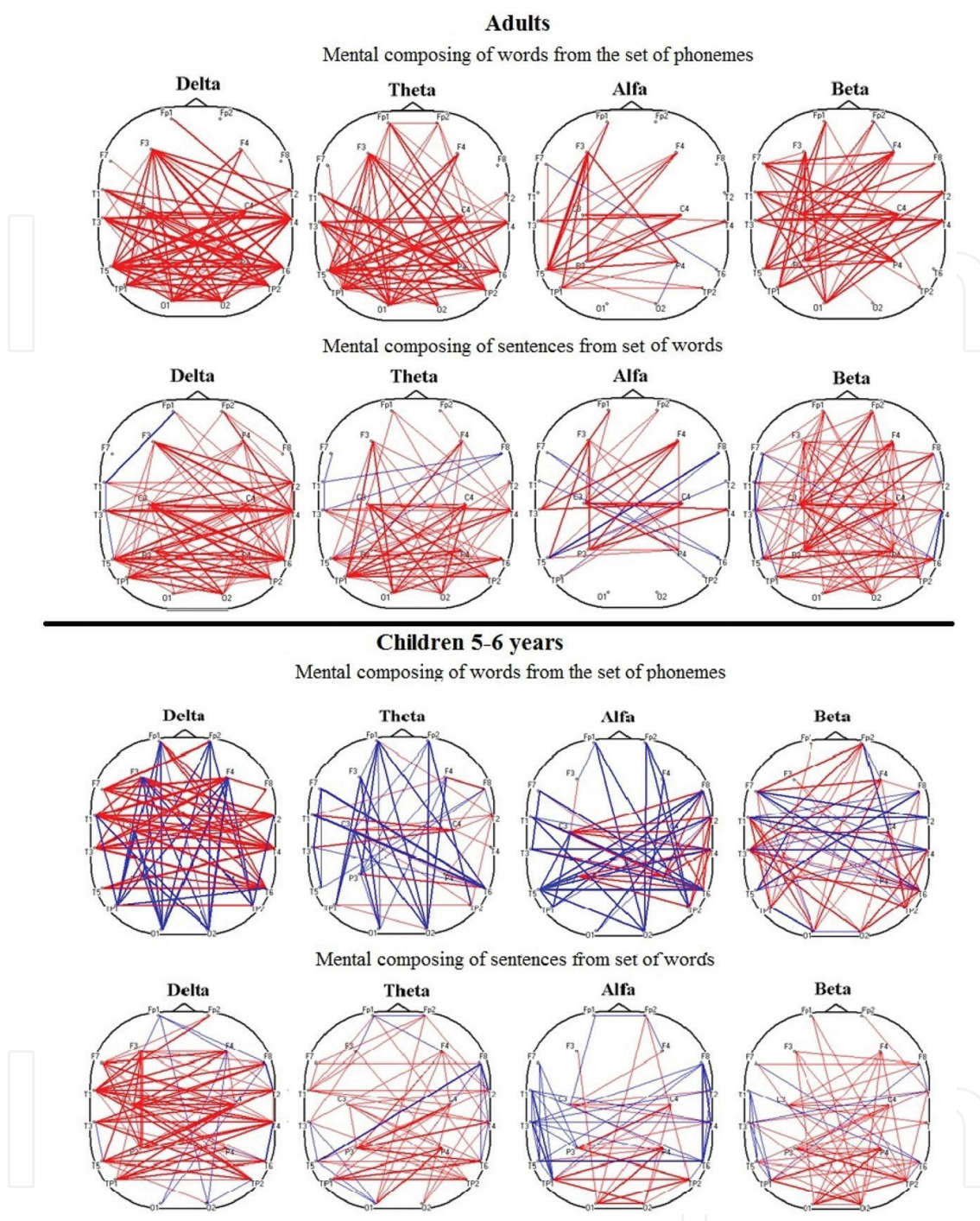


Figure 3. Changes in the spatial structure of EEG coherence connections in different frequency bands (delta, theta, alpha, beta) in adults while composing words from a set of phonemes and sentences from a set of words (baseline compared). Below — the same in children aged 5–6 years. Red lines show increases and blue lines show decreases of EEG coherence connections. Significant changes at $p \leq 0.05$ are shown.

In children aged 5–6 years, the composition of words from a set of auditory presented phonemes and of sentences from sets of words showed significant changes in the spatial structure of interregional EEG relationships [4] (**Figure 2**). Both tasks evoked significant increases in interhemispheric interactions between different cortical areas. Cross-correlation relationships

showed a particular increase in biopotential oscillations in the inferior frontal areas of both hemispheres, as well as in the anterior, intermediate, and posterior temporal areas, central and parietal areas of the cortex, and TPO areas of the left and right hemispheres. However, some differences in the topical features of changes in EEG cross-correlation relationships were also observed (**Figure 2**). In children, maximal changes toward increased interhemispheric connections were observed for EEG connections between the frontal areas (particularly inferior and posterior) and all temporal cortical of the right and left hemispheres (i.e., anterior, intermediate, and posterior) and TPO areas during word composition task. In turn, maximal increases while composing sentences from a set of words were characteristic of interhemispheric EEG connections in the posterior cortical areas (including the posterior temporal ones), TPO areas, and occipital areas of both hemispheres. It should be noted that in children, the activity associated with the formation of words represents a more difficult task than that associated with the formation of sentences. The rate of composing words from sounds was much slower in children than the rate of composing sentences from words. This may be due to the children preschool age, and they are still unable to read and write, so they do not operate with visual images while inventing words, comparing to adults [2].

This verbal task seems to be more abstract and difficult for children than for adults. Some EEG coherence interactions decrease (especially long distance) in children while composing words may be due to a greater subjective difficulty of the task being performed. Weiss and Mueller [22] pointed that successful creative speech activity is accompanied by increases in coherence between EEG signals from distant cortical zones while increased subjective difficulty in performing linguistic tasks correlates with a decrease of EEG coherence connections.

In children, some differences in theta and delta frequency bands were observed: mainly a decrease in coherent interactions during composing words and, conversely, an increase in the coherent interactions of EEG oscillations during composing sentences (**Figure 3**, children).

Bastiaansen et al. also demonstrated an increase in spectral power of the theta band during performing sentence-processing tasks [47]. Since the increase in theta activity during verbal tasks is associated with memory processes, it is likely that increase in the coherence of EEG oscillations in the theta range can be due to features of sentence composing associated with an increase in the efficiency of information processes [21, 22].

Thus, in children of preschool age, composing of speech units from more elementary components revealed complex patterns of changes in the distant interactions of bioelectrical activity in different areas of both hemispheres. The complexity of these patterns with the decrease and increase in the correlation and coherent EEG interactions seems to reflect the formation of the spatial structure of systemic interactions between these cortical areas, whose joint action is necessary to support verbal utterance generation during the postnatal ontogeny period.

To explore the regional brain interactions biopotentials at the phonological language level, we compared subject's performance results of three phonological tasks: phoneme recognition in words, composing a word from a set of phonemes, and controlled oral word association test. Cross-correlation and coherent analyses of EEG revealed differences in the spatial-temporal structure of brain biopotential interaction in adults. A significant increase of the interhemispheric

relations was observed during phoneme recognition, especially in theta and delta frequency bands between temporal areas of both hemispheres [44] (**Figure 2**). During word composition task, changes in the hemispheric interactions were most pronounced in the temporal, especially Wernike’s and temporo-parieto-occipital areas of both hemispheres [2] (**Figure 2**). A remarkable increase in regional interactions in the occipital areas accompanied by a decrease in interactions in frontal areas was observed during controlled word association. Our data showed that differences in the structure of regional interactions of brain biopotentials during verbal tasks at the phonemic language level depend on different task performance in spite of phonological specificity tasks.

The essential role of joint activity of both cerebral hemispheres in providing speech was also revealed during the analysis of the violations of systemic brain activity organization in children with developmental speech disorders such as alalia, dysarthria, and stuttering [1, 5, 6, 16]. A study of irregularities in the brain activity systemic organization, in children with various types of speech pathology, also allows deeper understanding of processes of formation of the neurophysiological mechanisms underlying language functions. In 12 children aged 3–4 years with motor alalia and 15 children aged 5–6 years with dysarthria were detected both significant differences in the nature and localization of violations of the systemic interaction of brain potentials and were revealed indicators of similarity (**Figure 4**) [16].

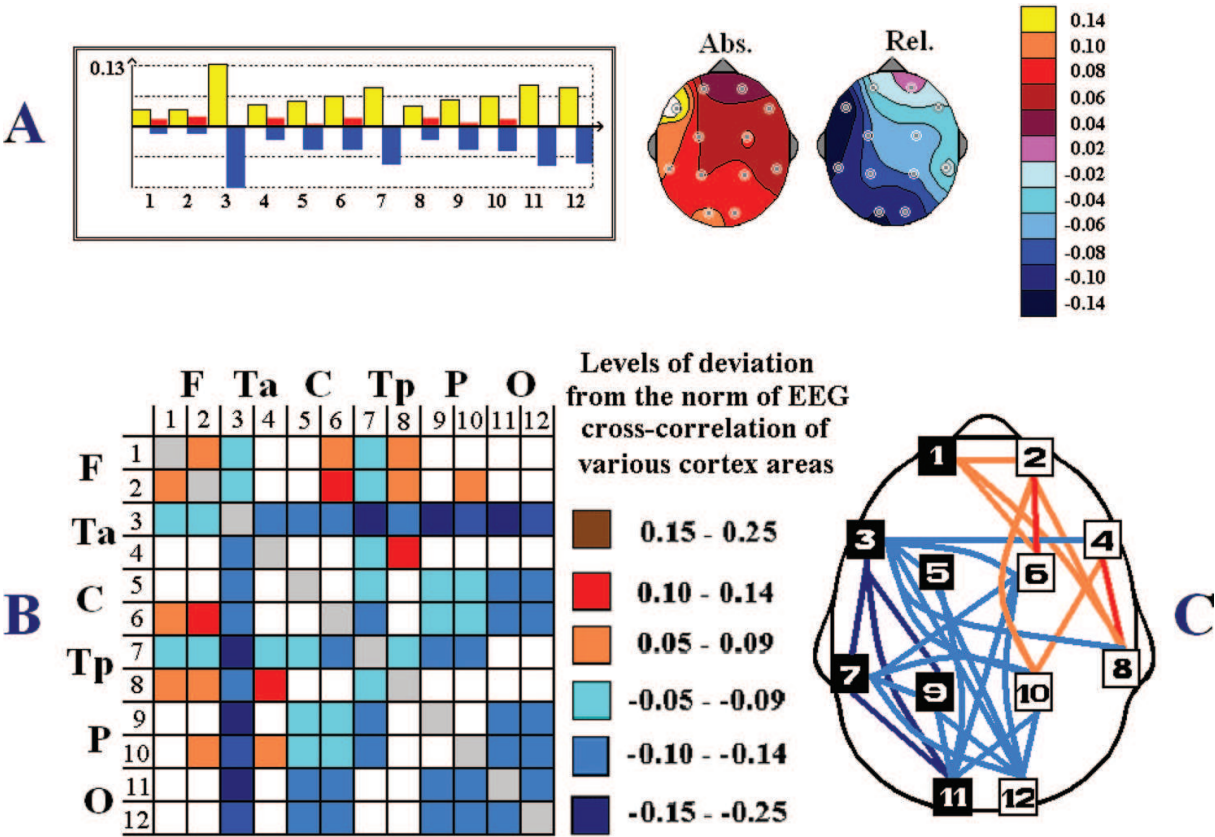


Figure 4. Disturbances in interregional interaction of cortical fields’ activity in 3-year-old children with motor alalia.

To specify the role of hemispheric interactions in pathogenesis of these verbal impairments, it is important to consider the data showing that in case of both alalia and dysarthria there were revealed two types of changes in systemic interaction of brain cortical biopotentials with the direction of these changes differing in the right and left hemispheres [1]. In all children with these types of verbal pathology, against the background of a decrease in EEG connections of one of the hemispheres, the interregional interaction of bioelectrical activity in the brain cortex also significantly exceeded the interaction in the contralateral hemisphere, as compared to the normative level; this was especially characteristic of children with dysarthria (Figure 5).

It cannot be ruled out that the revealed exceeding over the normal level of regional interaction of the cortical bioelectrical activity in children with alalia and dysarthria can be pathological, making the adequate development of verbal functions difficult.

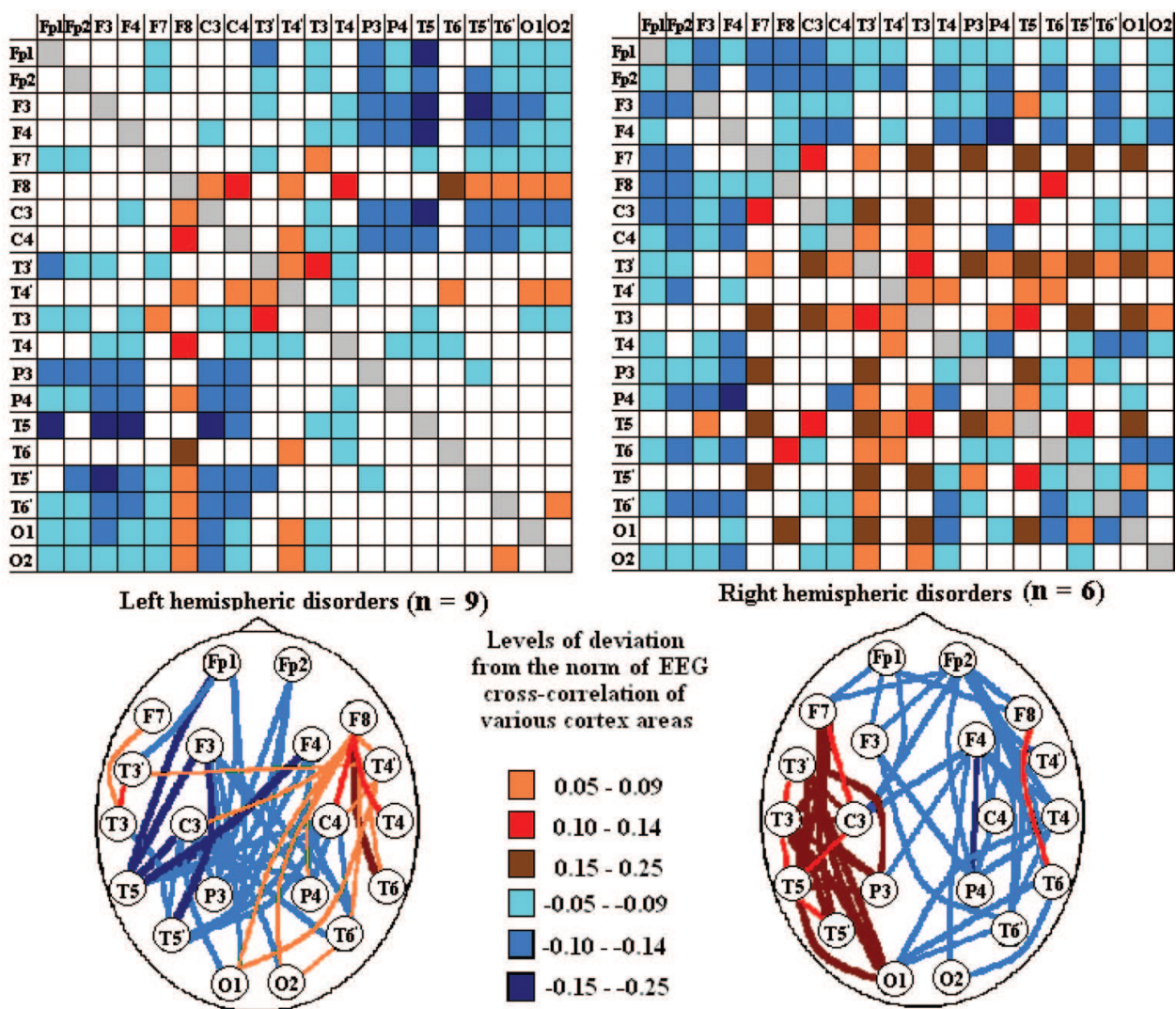


Figure 5. Infringements of systemic interaction of brain biopotentials in children aged 5–6 years with dysarthria.

Thus, the evidence of the essential role of joint activity of both brain hemispheres in providing speech was obtained by the analysis of the violations of the systemic organization of brain activity in children with deviations of speech development, such as alalia, dysarthria, and stuttering.

The other series of our studies [48, 49] addresses the role of multiple factors that determine the individual variety of neurophysiological mechanisms providing learning and using two languages. Speech formation is influenced by both common factors of bilingual and monolingual and bilingual special factors. Common factors include genetic and environmental effects explaining the individual differences in the morphofunctional organization of the speech function. Apparently, bilinguals have a large variability of the central mechanisms providing speech function due to various factors affecting language environment. These conditions include the age of the second-language acquisition, language proficiency, linguistic similarity of languages, the method of language acquisition, and the intensity and situation of use, and individual sensitivity to the above factors can be different. Unique features of the brain, existing only at the initial stages of postnatal ontogenesis, need for language acquisition, are effectively used in the situation of bilingualism. With age, the individual variability of EEG activation patterns during verbal activity in bilinguals increases. Perhaps with age during second-language acquisition, the brain is forced to manipulate a large number of additional cerebral mechanisms responsible for speech functions. There is a serious reason to believe that second-language acquisition contributes to the expansion of the functional capabilities of the brain and creates the basis for successful cognitive activity.

3. Conclusions

The results of long-term investigations conducted in our laboratory were presented in the collective monograph "The Formation of the Integrative Functions of the Brain" [7], edited by N.P. Bechtereva. According to the pivotal idea running through this monograph, the important feature of the integrative mechanisms of the brain consists in providing at the consecutive stages of postnatal ontogenesis a correlative formation of new functions and functional systems, including those that are not fully determined by the "phylogenetic laws." This idea, originating from the works by Severtsov and Schmalhausen, could account for evolutionary leap in the development of the brain in great apes, which led to rapid qualitative and quantitative changes resulted in the emergence of the perfect brain of modern men able to master and perform a variety of functions, including those that were not caused by long processes of phylogenetic development. These functions, in particular, include such aspects of abstract logical thinking as the ability to perform complex mathematical operations, create technical devices, and operate them at a distance. These functions also include those, which allow modern people to learn the principles of their own brain's organization. Based on our experimental data [50], we have suggested that speech could have evolved through the correlative phylogenetic development of stereognosis and language systems.

Thus, our recent data indicate that the implementation of complex verbal and mental activities associated with speech perception and production in children at different ages and in adults requires joint and extremely coordinated activities of both hemispheres along with an obligatory

and differentiated involvement of the classical speech centers in the left hemisphere. These findings support the view on the role of interactions between both hemispheres as decisive for speech processing, as well as on the involvement of both hemispheres in the organization of different language levels. A quantitative analysis of the results obtained on children vs. adults allows assessing the degree of maturity of the organization of central processes underlying verbal-mnemonic activity in preschool children. The new information about the formation of the lateralization of verbal processing in children's ontogenesis was obtained. The evidence for the essential role of joint activity of both brain hemispheres in providing speech was supported by the analysis of violations of the systemic organization of brain activity in children with impaired speech. The results of our research allow expanding modern concepts about the brain mechanisms of verbal activity in children in the norm and pathology. They can also assist in developing new and effective approaches to early correction of speech disorders.

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