

Mechanisms of Reading in Persons with Different Levels of Written Text Comprehension

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Abstract—The aim of the present study was to investigate the reading mechanisms in adults (27 subjects; mean age, 19.5 ± 0.8 [SD] years) with different levels of written text comprehension using fMRI. The main objective was to analyze the basic brain mechanisms of verbal stimuli perception with and without semantic component during reading discrimination tasks. The BOLD signal changes during WORD and PSEUDOWORD reading comparing to GAZE FIXATION state were estimated using both analysis of whole brain activation and ROIs (structures connected with the brain system providing reading) in two groups of subjects, “good” and “poor” readers. It was revealed that activations were higher in “poor” readers in lingual gyrus, SMG, STG compared to “good” readers during PSEUDOWORD reading. It was supposed, that the strategies of words and pseudowords recognition differed in two groups of readers: “good” readers identified words or pseudowords already at the stage of visual analysis of “word” structure and demonstrated attempts to decode pseudowords (i.e., language lexical zones were not activated); “poor” readers, apparently, tried to read pseudowords using the same strategy as for the words reading referring to the lexicon, and after failure identified pseudowords as meaningless concepts. In that case, activations of both lexical “language” zones and visual word form area (VWFA) were observed.

Keywords: reading, words, pseudowords, gaze fixation, fMRI, reading competence, “good”/“poor” readers, regions of interests (ROI)

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The process of text comprehension during reading has been the object of study of psychologists, linguists, and, recently, neuroscientists for several decades. The contemporary scientific data suggest that text analysis during the reading represents a multi-level process [1–3]. Birvish [4] distinguished the following levels: phonetic (i.e., lexical), syntactic, semantic, and contextual. Multiple evidence suggest that the size of the structural units of text available for comprehension increases from the single words and short phrases to the text consisting of several sentences in children, which began to practice reading [5, 6]. What is behind these concepts of levels relative to a mature reader remains not quite clear: the stages of text processing or different submodules of the functional system of reading?

The level of individual’s word reading appears to be the most studied one from all the levels of text processing during reading from both psychological and physiological aspects [7]. The contemporary models of word reading with comprehension, i.e., lexical access, which is usually called decoding, include several operations including designation of several letters, actual-

ization of several sounds relevant to the letters in accordance with the rules of spelling, a subsequent synthesis of the phonetic word and its lexical access [8]. A direct association of the graphic word together with its lexical value as a shorter way was also considered [9]. It is assumed that both types of operations (the two route theory) are involved in the reading process at different degrees [10–12]. However, according to some data, another anticipation mechanism as a probabilistic prognosis of an entire word by its first one or two syllables is involved in decoding during the word reading even outside the context. This mechanism works only during the reading of words (rather than pseudowords), since it is based on the mental syllabary and motor images of the word forms in memory [13].

The study of the cerebral mechanisms of word reading using fMRI demonstrated that this process was provided by highly organized cortical system including the structures of the brain left hemisphere: the dorsal (temporal parietal), ventral (occipital temporal), and frontal subsystems focusing in inferior frontal gyrus (IFG) [14]. The dorsal subsystem

includes the angular and supramarginal gyrus, posterior part of the superior temporal gyrus (Wernicke's area). These structures are involved in the association of the visual image of letters with their phonemic referents and provide a connection between the phonological structures and semantic categories [15]. The ventral subsystem extends to the inferior and medial temporal gyri and also includes left inferior part of the occipital temporal region (fusiform gyrus) also known as the area of the visual images of words, which usually demonstrates higher activity to graphic images of words rather than to pseudowords or subjective images.

The frontal ventral (occipital temporal) subsystem is considered to be involved in semantics-associated reading [16, 17], while the posterior region selectively and quickly responds to the printed text, especially in "good" readers [14]. Frontal subsystem (IFG) integrates two functionally different areas: frontal IFG is mainly responsible for a decision in semantic task [18], while caudally located part of this multifunctional subsystem together with insula and opercular area [19, 20] and in accordance with literature data is more activated during pseudowords processing rather than high-frequency words [16, 21].

Several studies testified that the level of development of reading skills affected the structural organization of the cerebral word reading. An improvement of the behavioral parameters of reading might be accompanied by a decreased activity in left inferior frontal and supramarginal gyri, supplementary locomotor region and the cerebellum using fMRI [22]. Subjects with a low level of word reading demonstrated a reduced activity of the left parietal-temporal and parietal-occipital regions [23, 24]; however, an increased activity in the posterior regions of the right hemisphere and bilaterally in the frontal regions was observed [25, 26].

The present study aimed to analyze the mechanisms of comprehension during reading in subjects differing in the levels of scientific texts comprehension.

METHODS

The fMRI analysis involved 27 healthy subjects (7 men and 20 women) aged 19–23 years (mean age, $19.5 \pm 0.8[SD]$) with a normal or corrected to normal vision studying at one of St. Petersburg universities. In accordance with [27], 25 of them were right-handed and two were left-handed. All subjects reported Russian was the native language. The study was performed in accordance with the Helsinki Declaration and its subsequent additions. An informed consent for participation in the study was obtained from the enrolled subjects.

According to preliminary testing by the level of scientific texts comprehension, subjects were divided

into two groups: relatively "good" ($N = 14$, five men) and "poor" ($N = 13$, two men) readers. An estimate of comprehension and analysis of text information was conducted using the methodology of *Understanding Scientific Texts* (UST) [28], which included the reading of three scientific texts (250–300 words) followed by answering on questions. A group of relatively "good" readers consisted of subjects resulted at the level of 85–100 percentile, while a group of relatively "poor" readers included subjects resulted at the level of 1–15 percentile according to UST.

Tasks. The present study examines the level of reading of words out of context and pseudowords. WORDS task included individual's reading the word and determination whether it belonged to a living or non-living object. In PSEUDOWORDS task subjects had to read a set of letters and to decide whether it is a word from the Russian language. PSEUDOWORDS task also included a randomized presentation of the words in 2.5% of cases. It oriented subjects to perform a stimuli discrimination task, maintained their level of attention during the testing; however, it slightly affected homogeneity of the used linguistic material. When making decisions, subjects pressed the joystick button with their thumb on the right or left hand (depending on a decision). A change of stimulus occurred when the button was pressed (self-paced mode), in the case of exceeding the response time in 1500 ms stimulus change was conducted automatically.

The fMRI study was conducted using magnetic resonance imaging (Philips Ingenia, Netherlands) with a magnetic field intensity of 1.5 T. The study was carried out using 8-channel neurological coil, an individual was placed in MRI chamber in the reclining position, the subject's head in the magnetic headphones to protect hearing and communicate with staff was fixed by sealing modules.

For stimuli presentation a special InVivo SensaVue 30' monitor included in the InVivo ESys fMRI complex for conducting fMRI studies. The image from the monitor was projected to individual via a system of built-in mirrors. The presentation of stimuli was carried out based on e-Prime 1.1 software package. Before the study subjects performed training tasks (with distinct sets of stimuli) without turning the MR scanner on.

The examination of each task was designed according to the block paradigm and consisted of four alternating periods of rest (the task of gaze fixation on the image of a fixed black cross in the center of the screen) and periods of tasks performance (4 + 4) for 30 s each. In the GAZE FIXATION task individual was asked to press the joystick button in the free mode to compensate the activation of the motor cortex compared to the reading tasks.

Prior the functional study 6-s scanning without registration of *BOLD* (hemodynamic response) signal

(dummy scans) was conducted for the formation of MR signal. The total duration of one reading task was 4 minutes 6 s. The fMRI study protocol included the obtaining of T2, T1, Flair images to estimate the brain anatomy to exclude a severe organic pathology. The structural T1-WI (weighted image) were obtained in the 3D mode as thin slices, which made it possible to obtain high-resolution brain images in three orthogonal projections.

Directly functional scans were performed in EPI (echo-planar impulse sequence) mode under the following parameters: $TR/TE = 3000$ ms / 50 ms, reconstruction matrix 64×64 , FOV (field of view) $230 \times 230 \times 136$ mm. Slice thickness was 4 mm, voxel size after reconstruction was 3.59 mm. The performance of one task was accompanied by 80 dynamic scans (10 scans in each 30-s block). The primary estimate of individual's answers correctness based on the results of pressing the joystick buttons was conducted during the scan and the presence of coarse motion artifacts was evaluated visually.

The experiments output were recorded in the international standard format DICOM followed by transformation into Nifti format using specific MRiConvert software for post-processing of fMRI data using the SPM8 software package (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>). Statistical analysis was performed using the general linear model (GLM).

Preliminary processing of individual data. The first stage included the collection of anatomical and functional data for each individual. Functional data were adjusted for motion-associated artifacts, the comparison of functional data with the structural images, normalization to a standardized anatomical space, and spatial smoothing using a filter $8 \times 8 \times 8$ mm ($FWHM$) were carried out. Subsequently, *first-level analysis* included a composition of design matrix for the individual functional data. 80 scans per one task block were used, which comprised 40 scans (images) of WORD or PSEUDOWORD reading in each block and 40 scans (images) of GAZE FIXATION task in each block. A comparison of each task with GAZE FIXATION state was carried out.

Group statistical analysis (second-level analysis). Statistical analysis of changes in *BOLD* signal in the whole brain was conducted in the groups of "good" and "poor" readers via *T*-test. The results were obtained for direct (comparison of tasks with GAZE FIXATION state) and reverse *t*-contrasts. The results of statistical maps design were considered (at clusters level, clusters exceeding 100 voxels were considered) with a threshold of $p < 0.001$ and a threshold of $p < 0.05$ under FWE [29] correction at *peak level*. Coordinates topography of the maximums of the regions differences after *MNI* coordinates transformation into the coordinates of the Atlas of Talairach were determined using the Talairach Client freeware (<http://www.talairach.org/client.html>).

Intergroup comparisons. The analysis of changes in *BOLD* signal in the regions of interest (ROI) selected on the basis of published findings [7, 30, 31] based on the brain reading system and considering the selection of regions non-overlapping with detected activations during the analysis of the whole brain was performed. The structures appeared to be the regions of interest comprising the regions involved in the process of word reading were the following: lingual, fusiform, supramarginal, superior, middle and inferior temporal gyri, frontal cortical gyrus (triangular and operculum areas). The anatomical mask in the mentioned structures for selected ROI was designed in accordance with reported coordinates [7, 30, 31] using freely accessed Marsbar (<http://marsbar.sourceforge.net>). Subsequently, the differences in the level of *BOLD* signals between the groups of readers during the comparison of tasks (WORDS reading, PSEUDOWORDS reading and GAZE FIXATION) were estimated for each ROI via one-way analysis of variance (ANOVA). The effect of variables GROUP ("good"/"poor" readers) and TASK and their interaction were considered. A sphere with a center in the mentioned local maximum and 5 mm radius was used as ROI.

RESULTS

The results of the analysis of behavioral data. The fMRI was based on the paradigm of individual-controlled stimuli change (*self-paced*). The average values of reaction times in the WORDS reading were 624 ± 94 ms [*SD*] in the group of "good" readers and 693 ± 139 ms [*SD*] in a group of "poor" readers. The number of correct answers was $96.5 \pm 1.8\%$ [*SD*] and $95 \pm 2.5\%$ [*SD*], respectively. A task of PSEUDOWORDS reading was characterized by a time of reading and stimuli discrimination equal to 637 ± 109 ms [*SD*] in the group of "good" readers and 763 ± 171 ms [*SD*] in the group of "poor" readers. The analysis of behavioral data using non-parametric Mann-Whitney test revealed no statistically significant differences between the groups in the number of correct answers during reading and differentiation of living/non-living objects in WORDS ($z = 1.6$; $p < 0.1$) and PSEUDOWORDS task ($z = 1.02$; $p < 0.3$). The differences in the speed of response to WORDS ($z = 1.18$; $p < 0.23$) and PSEUDOWORDS task ($z = 1.7$; $p < 0.07$) between the groups also remained under the level of significance.

Comparison of BOLD signals during WORDS and PSEUDOWORDS reading compared to GAZE FIXATION in the group of "good" readers. The comparison of *BOLD* signals during the execution of tasks and GAZE FIXATION revealed the clusters of activation in the group of "good" readers during WORDS reading in the left occipital and insular regions, right parietal and limbic cortex and during PSEUDOWORDS reading—only in the occipital areas bilaterally (Table 1).

Table 1. Differences in the levels of *BOLD* signals during WORD and PSEUDOWORD reading compared to GAZE FIXATION in a group of “good” readers

Location	BA, hemisphere	Cluster size	$p(unc)$ cluster	Value at the maximal level (peak level)				Maximum coordinates		
				$p(FWE-corr)$	$p(FDR-corr)$	T	Z	x	y	z
WORD READING > GAZE FIXATION										
Middle occipital gyrus, Lingual gyrus, Fusiform gyrus	18L, 17L, 19L	11544	0.000	0.000	0.006	14.44	5.98	-30	-98	8
Insula	13L	1724	0.000	0.017	0.019	10.07	5.23	-36	22	6
Angular gyrus	39R	364	0.000	0.022	0.020	9.85	5.19	32	-62	36
Cingulate gyrus	32R	1132	0.000	0.047	0.032	9.15	5.03	10	20	44
PSEUDOWORD READING > GAZE FIXATION										
Inferior/middle occipital gyrus/Cuneus	19L	5404	0.000	0.000	0.001	16.84	6.29	-38	-82	-6
Cuneus/inferior/Middle occipital gyrus	18R	3568	0.000	0.004	0.006	11.38	5.49	24	-100	-4

Data including cluster size, location of their maximum and statistically significant changes in *BOLD* signal at the cluster level are presented ($p < 0.001(uncorr)$); L, left hemisphere; R, right hemisphere; BA, Brodmann area.

Table 2. Differences in the levels of *BOLD* signals during WORD and PSEUDOWORD reading compared to GAZE FIXATION in a group of “poor” readers

Location	BA, hemisphere	Cluster size	$p(unc)$ cluster	Value at the maximal level (peak level)				Maximum coordinates		
				$p(FWE-corr)$	$p(FDR-corr)$	T	Z	x	y	z
WORD READING > GAZE FIXATION										
Inferior occipital gyrus, Fusiform gyrus, Middle occipital gyrus	19L, 37L, 18L	3849	0.000	0.002	0.020	13.04	5.62	-44	-74	-6
Inferior/middle frontal gyrus	9/46L	1458	0.000	0.008	0.022	11.40	5.36	-54	22	26
PSEUDOWORD READING > GAZE FIXATION										
Fusiform gyrus Inferior occipital gyrus	37L 19L	10551	0.000	0.000	0.002	22.68	6.42	-42	-64	-14
Middle frontal gyrus	46R	817	0.000	0.014	0.040	11.75	5.26	48	38	22

Designations are the same as in Table 1.

Comparison of BOLD signals during WORDS and PSEUDOWORDS reading compared to GAZE FIXATION in the group of “poor” readers. Both “poor” and “good” readers groups demonstrated significantly higher level of *BOLD* signal during WORDS and PSEUDOWORDS reading compared to GAZE FIXATION: in the left occipital temporal and frontal regions during WORDS reading and in the left occipital temporal regions and right frontal regions during PSEUDOWORDS reading (Table 2).

The reverse contrasts of comparison in GAZE FIXATION task during WORDS and PSEUDOWORDS reading revealed no significant clusters of activation in both groups of subjects.

Comparison of BOLD signals during WORDS and PSEUDOWORDS reading in GAZE FIXATION state between “poor” and “good” readers. Analysis of the regions of interest. Significant effects ($p < 0.05$) of GROUP \times TASK interaction were revealed in the following ROI: left lingual gyrus [*MNI* coordinates of the center of ROI sphere: -22, -47, -1]: $F(2,44) = 5.62$,

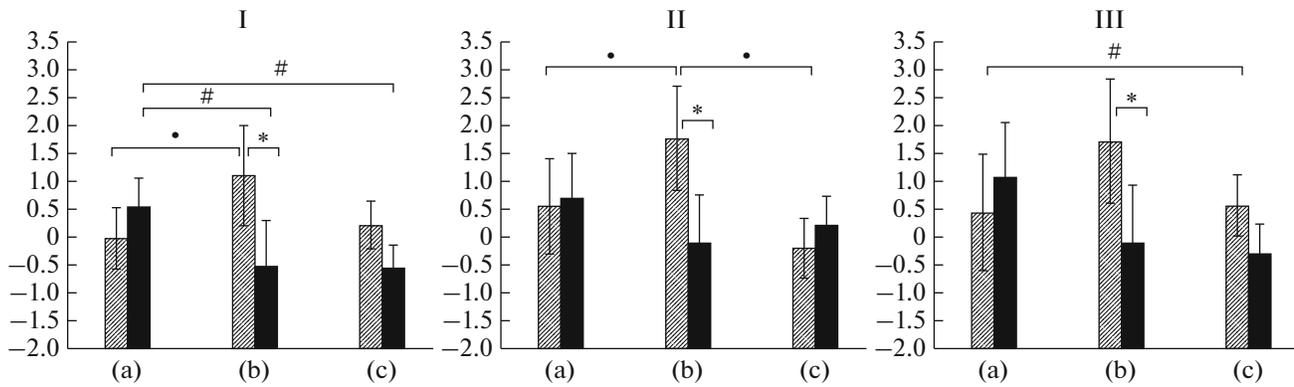


Fig. 1. Intergroup differences in *BOLD* signals and the difference among the tasks in explored ROI in “good” (shown in black) and “poor” readers (shown in gray). I, Lingual gyrus (L); II, supramarginal gyrus (L); III, superior temporal gyrus (L). Tasks: (a) word reading; (b) pseudoword reading; (c) gaze fixation on a cross. # Differences between the tasks in a group of “good” readers; • differences between the tasks in a group of “poor” readers; * differences in ROI between the groups of “good” and “poor” readers.

$e(G-G) = 0.78$, $p < 0.02$; left supramarginal gyrus [$MNI: -60, -41, 25$]: $F(2,44) = 5.1$, $e(G-G) = 0.81$, $p < 0.02$; left superior temporal gyrus [$MNI: -53, -13, 0$]: $F(2,44) = 2.69$, $e(G-G) = 0.79$, $p < 0.05$ (Fig. 1).

The following results of post-hoc analysis were revealed: *BOLD* signal was significantly higher in the left lingual gyrus during WORDS reading compared to GAZE FIXATION and PSEUDOWORDS reading in the group of “good” readers. Oppositely, in the group of “poor” readers the *BOLD* signal was significantly higher during PSEUDOWORDS reading compared to WORDS reading. *BOLD* signal appeared to be higher in the supramarginal gyrus in a group of “poor” readers during PSEUDOWORD reading compared to GAZE FIXATION and WORDS reading. No statistically significant differences in this ROI were observed in a group of “good” readers. A significant increase in the level of *BOLD* signal was observed in the left superior temporal gyrus during WORDS reading compared to GAZE FIXATION in a group of “good” readers. PSEUDOWORDS reading was accompanied by significant intergroup differences in all ROI: the level of activation in mentioned ROI was increased in a group of “poor” readers compared to “good” ones.

DISCUSSION

Differences in BOLD signal during WORDS and PSEUDOWORDS reading compared to GAZE FIXATION states in the groups of readers differing in written text comprehension. Activation of occipital and posterior temporal regions of the cerebral cortex (fusiform, lingual gyri; inferior and middle occipital gyri) was detected in the groups of “poor” and “good” readers (differing in the level of scientific texts comprehension) during WORDS/PSEUDOWORDS reading compared to GAZE FIXATION state. The obtained data correspond to other findings of the brain processes providing reading and activation of the

structures responsible for the perception of written text, which, in addition to the mentioned regions, also include superior and middle temporal gyrus, angular gyrus, inferior and middle frontal gyrus [7, 32]. According to some authors, words and pseudowords reading might be accompanied by the activations of the similar brain regions [33–36], which were also observed in the present study in the temporal – occipital regions of the cortex. The group of “poor” readers demonstrated activation in fusiform and inferior occipital gyri as a result of both WORDS and PSEUDOWORDS reading; while the left middle occipital gyrus was the common activation region during both WORDS and PSEUDOWORDS reading in the group of “good” readers. Activation of occipital-temporal regions is characteristic for the tasks requiring silence-associated reading of demonstrated stimuli [7, 30, 31]. The contemporary reading models [25, 30, 37] assume that the transfer of visual language information includes the left ventral occipital temporal region in a close proximity to the occipital temporal sulcus. This region is considered to be the one rather specific to reading [38, 39], since activation of these regions is higher during words perception compared to visually similar stimuli such as false fonts or letter sequences [39, 40]. The injury of the occipital temporal regions results in selective reading disorders without affecting of speech [41–44].

In the present study activation of the left occipital-temporal regions correlated with the processing of visual images of words was observed during WORDS and PSEUDOWORDS reading in the group of “poor” readers, and activation cluster by the number of included voxels was higher during PSEUDOWORDS reading. This is consistent with meta-analysis data [45]. Activation of occipital temporal regions during words reading in a group of “good” readers was detected only in the left hemisphere (in middle occipital, lingual and fusiform gyri),

while during pseudowords reading, in both hemispheres (in inferior/middle occipital gyri). Previously [46] an increased activation of the occipital regions in the left and right hemispheres was reported during reading in groups of children (aged 10–14 years) with the normal reading skills compared to children with specific comprehension impairment. Benjamin et al. [47] demonstrated that an enhanced reading speed was accompanied by an increased activity in the temporal occipital region of the left hemisphere (fusiform gyrus) among all brain regions involved in reading. In the study the activation of occipital temporal regions of the right hemisphere in the group of “good” readers during PSEUDOWORDS reading might be related to the comprehension of the graphic structure of pseudoword as alien in our language, i.e. as no word, based on the minimal orthographic signs.

The results obtained during the reading tasks in the group of “poor” readers together with activation of occipital temporal cortical regions point to the differences in the level of *BOLD* signal during WORDS reading in the middle and inferior cortical gyri of the left hemisphere BA46/BA9, while during PSEUDOWORDS reading, in symmetrical BA46 region of the right hemisphere. Activation of these regions was associated with semantic memory [48], working memory and attention control [49, 50], with speech understanding and formation [51, 52] in verbal fluency tasks [19]. Activation in the symmetrical regions in the right hemisphere (BA46) was identified during PSEUDOWORDS reading in a group of “poor” readers, which might correspond to increased load on the working memory during the recognition of meaningless set of letters comprising a pseudoword. In addition, activation of prefrontal cortex in “poor” readers during the reading of both WORDS and PSEUDOWORDS in stimuli discrimination tasks was congruent to published findings reported an enhanced activation in the frontal cortical regions in subjects with a lower level of reading skills [25, 26] during the performance of corresponding tasks.

WORDS reading compared to GAZE FIXATION task was characterized by activation of both visual regions in the left hemisphere and insular region (insula, BA13L), parietal (angular gyrus, BA39R), and limbic cortex (cingulate gyrus, BA32R).

The activation of insula was detected in several studies [16]. Presumably, this area is also involved in phonological processes [53] including low-frequent syllables [54] during reading. Insula activation in the group of “good” readers during word reading might be associated with phonological processes. The study [55] demonstrated the effect of task complexity (reading of frequent and rare words) on activation of this structure depending on the formation of reading skill. Activation of the insular cortex in the group of adolescents without reading impairments depended on the task complexity and remained unmodified depending

on the task complexity in the group of adolescents with impaired reading skills.

The involvement of the angular gyrus was shown in a wide range of cognitive operations [56], and is considered to be the center of crossmodal integration including the comparison of information obtained from different sensory systems: via formation of event occurrence, creation of mental images, redirection of attention to relevant information. However, right BA39 comprises associative cortex closely related to the processes of memory retrieval, conflict selection/differentiation of information [56], and verbal activity [57]. Considering activation in BA39 together with activation in the right BA32 [58] in the anterior cingulate gyrus, it could be assumed that stimuli discrimination task (living/non-living objects) was actively realized during word reading in a group of “good” readers.

Therefore, different pattern of activation was observed during WORDS and PSEUDOWORDS reading in comparison with GAZE FIXATION task in a groups of “good” and “poor” readers depending on the task and the level of reading comprehension. PSEUDOWORDS reading was accompanied by activation of visual cortical regions in both hemispheres in a group of “good” readers, while activation of the temporal occipital cortex was predominant in the left hemisphere in a group of “poor” readers. PSEUDOWORDS discrimination by “good” readers was provided by activation of occipital temporal cortical regions thus suggesting a high level of effective recognition of pseudowords by the minimal graphic parameters and their discrimination from the words. Together with activation of occipital temporal regions in the left hemisphere a group of “poor” readers in this task demonstrated activation in the right inferior frontal gyrus, which is probably caused by a stronger involvement in the processes of discrimination of words and pseudowords—working memory and cognitive control in this group of subjects.

Intergroup differences based on the data analysis in the regions of interest. Based on the results of *BOLD* signals assessment in the regions of interest relevant to the brain system of word and pseudoword reading, intergroup differences among “poor” and “good” readers were identified presented in lingual, supramarginal, and superior temporal gyri. The level of activation during PSEUDOWORDS reading was significantly higher in the group of “poor” readers compared to the group of “good” readers.

Interestingly, different ratio of *BOLD* signals in the groups of “poor” and “good” readers during WORDS and PSEUDOWORDS reading was detected in the left lingual gyrus. Activation of this ROI was higher in WORDS task compared to PSEUDOWORDS reading in a group of “good” readers, while an opposite observation was detected in a group of “poor” readers. The study [59] described activation of the lingual gyrus

as a result of perception of orthographically correct words and pseudowords and the absence of activation during the perception of sequence of consonants and pseudofonts. In the study [60] activation of this region was higher during word reading compared to pseudowords (among adults). The data suggest that recognition of words and pseudowords in the groups of “poor” and “good” readers differed by the organization of processes: probably, “good” readers could make a decision without reference to the lexicon or lexical analysis, based on several lingual statistical characteristics of pseudowords differentiating them from the spelling of the Russian language. At the same time, “poor” readers demonstrated a weak heuristic analysis by the minimal information supports. It might be indirectly confirmed by the results of eyes movement during reading of various types of texts in the analysis of oculomotor behavior in these subjects. According to the present study, “poor” readers were unable to adaptive changes in the reading strategy depending on a type of represented text compared to “good” readers [28].

The supramarginal gyrus (parietal region of the left hemisphere) was characterized by an increased activation level during PSEUDOWORDS reading in a group of “poor” readers compared to WORDS reading and compared to PSEUDOWORDS reading in a group of “good” readers. This brain region is involved in graphic-phonological decoding of visually presented stimuli [30], which, obviously, was significant during PSEUDOWORDS reading in a group of “poor” readers. PSEUDOWORDS reading in “poor” readers was accompanied by an increased activation also observed in superior temporal gyrus in the left hemisphere—a region known to be activated only during phonological analysis [61]. Accordingly, PSEUDOWORDS reading in a group of “poor” readers was characterized by a strong activation of the regions associated with graphic-phonological transformation of words during reading.

CONCLUSIONS

Obtained findings confirm an assumption that neurophysiological organization of the reading process in the readers differing in the skill of scientific texts analysis becomes different even at the level of reading of individual words and verbal stimuli without semantic component (pseudowords). Significant differences in the group of “strong” readers were identified during word reading and concepts discrimination (by living/non-living object) compared to the gaze fixation state in the insular cortex and left parietal and occipital cortical areas, right angular and cingulate gyrus. At the same time, pseudowords reading was characterized by the differences only in secondary and tertiary areas of left visual cortex, which may indicate the adoption of a categorical decision (word/pseudoword) even at the level of orthographic

analysis of the graphic word. Reading and discrimination of the words and pseudowords compared to the gaze fixation state involved both visual areas in the left and frontal cortex in the group of “poor” readers. In the first of these comparisons (word reading > gaze fixation) the differences were observed in the prefrontal cortex of the left hemisphere; while in the second — in the frontal cortex of the right hemisphere. It could be suggested that the involvement of symmetrical regions of the prefrontal cortex in the left and right hemispheres (BA46) during reading of words and pseudowords, respectively, in the group of “poor” readers evidence in the differences in stimuli processing in subjects with a low reader competence. An increased level of activation of the prefrontal cortex in subjects with a lower level of reading corresponds to several published data [25, 26].

Intergroup differences in activations of the lingual, supramarginal and superior temporal gyrus in the left hemisphere identified during the pseudowords recognition, obviously, evidence in the use of different strategies for pseudowords comprehension by “poor” and “good” readers.

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REFERENCES

1. Storch, S.A. and Whitehurst, G.J., Oral language and code-related precursors to reading: evidence from a longitudinal structural model, *Dev. Psychol.*, 2002, vol. 38, no. 6, p. 934.
2. Oakhill, J.V., Cain, K., and Bryant, P.E., The dissociation of word reading and text comprehension: evidence from component skills, *Lang. Cognit. Process.*, 2003, vol. 18, no. 4, p. 443.
3. Ouellette, G.P., What’s meaning got to do with it: The role of vocabulary in word reading and reading comprehension, *J. Educ. Psychol.*, 2006, vol. 98, no. 3, p. 554.
4. Bierwisch, M., How on-line is language processing? in *The Process of Language Understanding*, d’Arcais, G.B.F. and Jarvella, R.J., Eds., New York: Wiley, 1983, pp. 113–168.
5. Kornev, A.N., *Narusheniya chteniya i pis’ma u detei* (Disorder of Reading and Writing in Children), St. Petersburg: Karo, 2003.
6. Egorov, T.G., *Psikhologiya ovladeniya navykom chteniya* (Psychology of Reading Skillings), St. Petersburg: Karo, 2006.
7. Price, C.J., A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading, *Neuroimage*, 2012, vol. 62, no. 2, p. 816.
8. Luo, C.R., Johnson, C.R., and Callo, C.R., Automatic activation of phonological information in reading evi-

- dence from the semantic relatedness decision task, *Mem. Cognit.*, 1998, vol. 26, p. 833.
9. Daneman, M. and Reingold, E., What eye fixations tell us about phonological recoding during reading, *Can. J. Exp. Psychol.*, 1993, vol. 47, p. 153.
 10. Forster, K.I. and Chambers, S., Lexical access and naming time, *J. Verbal Learn. Verbal Behav.*, 1973, vol. 12, p. 627.
 11. Marshall, J.C. and Newcombe, F., Patterns of paralexia: a psycholinguistic approach, *J. Psycholing. Res.*, 1973, vol. 2, p. 175.
 12. Coltheart, M., Modeling reading: the dual-route approach, in *The Science of Reading: A Handbook*, Snowling, M.J. and Hulme, Ch., Eds., Oxford: Blackwell, 2005, p. 6.
 13. Levelt, W.J.M., Models of word production, *Trends Cognit. Sci.*, 1999, vol. 3, p. 223.
 14. Landi, N., Frost, S.J., Menc, W.E., et al., Neurobiological bases of reading comprehension: Insights from neuroimaging studies of word-level and text-level processing in skilled and impaired readers, *Reading Writing Quart.*, 2013, vol. 29, no. 2, p. 145.
 15. Black, S.E. and Behrmann, M., Localization in alexia, in *Localization and Neuroimaging in Neuropsychology*, Kertesz, A., Ed., New York: Academic, 1994, p. 331.
 16. Fiebach, C.J., Friederici, A.D., Mueller, K., et al., fMRI Evidence for dual routes to the mental lexicon in visual word recognition, *J. Cognit. Neurosci.*, 2002, vol. 14, p. 11.
 17. Simos, P.G., Fletcher, J.M., Bergman, E., et al., Dyslexia-specific brain activation profile becomes normal following successful remedial training, *Neurology*, 2002, vol. 58, p. 1203.
 18. Poldrack, R.A., Wagner, A.D., Prull, M.W., et al., Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex, *Neuroimage*, 1999, vol. 10, no. 1, p. 15.
 19. Paulesu, E., Goldacre, B., Scifo, P., et al., Functional heterogeneity of left inferior frontal cortex as revealed by fMRI, *Neuroreport*, 1997, vol. 8, p. 2011.
 20. Roskies, A.L., Fiez, J.A., Balota, D.A., et al., Task-dependent modulation of regions in the left inferior frontal cortex during semantic processing, *J. Cognit. Neurosci.*, 2001, vol. 13, p. 829.
 21. Fiez, J.A. and Petersen, S.E., Neuroimaging studies of word reading, *Proc. Natl. Acad. Sci. U.S.A.*, 1998, vol. 95, no. 3, p. 914.
 22. Katz, L., Lee, C.H., Tabor, W., et al., Effects of printed word repetition in lexical decision and naming on behavior and brain Activation, *Neuropsychologia*, 2005, vol. 43, no. 14, p. 2068.
 23. Shaywitz, B.A., Shaywitz, S.E., Pugh, K.R., et al., Disruption of posterior brain systems for reading in children with developmental dyslexia, *Biol. Psychol.*, 2002, vol. 52, p. 101.
 24. Turkeltaub, P.E., Gareau, L., Flowers, D.L., et al., Development of neural mechanisms for reading, *Nat. Neurosci.*, 2003, vol. 6, no. 7, p. 767.
 25. Pugh, K.R., Mencl, W.E., Jenner, A.R., et al., Functional neuroimaging studies of reading and reading disability (developmental dyslexia), *Ment. Retard. Dev. Disab. Res. Rev.*, 2000, vol. 6, p. 207.
 26. Sarkari, S., Simos, P.G., Fletcher, J.M., et al., The emergence and treatment of developmental reading disability: contributions of functional brain imaging, *Semin. Pediatr. Neurol.*, 2002, vol. 9, p. 227.
 27. Oldfield, R.C., The assessment and analysis of handedness: the Edinburgh inventory, *Neuropsychologia*, 1971, vol. 9, no. 1, p. 97.
 28. Kornev, A.N. and Oganov, S.R., Variability of strategies for processing written text: analysis of eye movements in 2–4 courses students reading descriptive texts, in *Aitrekning v psikhologicheskoi nauke i praktike* (Eye Tracking in Psychological Science and Practice), Barabanshchikov, V.A., Ed., Moscow: Kogito-Tsentr, 2015, p. 279.
 29. Friston, K., Ashburner, J., Kiebel, S., et al., *Statistical Parametric Mapping: The Analysis of Functional Brain Images*, London: Academic, 2007, p. 656.
 30. Jobard, G., Crivello, F., and Tzourio-Mazoyer, N., Evaluation of the dual route theory of reading: a meta-analysis of 35 neuroimaging studies, *Neuroimage*, 2003, vol. 20, no. 2, p. 693.
 31. Richardson, F.M., Seghier, M.L., Leff, A.P., et al., Multiple routes from occipital to temporal cortices during reading, *J. Neurosci.*, 2011, vol. 31, p. 8239.
 32. Choi, W., Desai, R.H., and Henderson, J.M., The neural substrates of natural reading: a comparison of normal and nonword text using eyetracking and fMRI, *Front. Hum. Neurosci.*, 2014, vol. 8, p. 1024.
 33. Mechelli, A., Gorno-Tempini, M.L., and Price, C.J., Neuroimaging studies of word and pseudoword reading: consistencies, inconsistencies, and limitations, *J. Cognit. Neurosci.*, 2003, vol. 15, no. 2, p. 260.
 34. Price, C.J., Noppeney, U., Phillips, J., and Devlin, J.T., How is the fusiform gyrus related to category-specificity? *Cognit. Neuropsychol.*, 2003, vol. 20, no. 3, p. 561.
 35. Levy, J., Pernet, C., Treserras, S., et al., Piecemeal recruitment of left-lateralized brain areas during reading: a spatio-functional account, *Neuroimage*, 2008, vol. 43, p. 581.
 36. Levy, J., Pernet, C., Treserras, S., et al., Testing for the dual-route cascade-reading model in the brain: an fMRI effective connectivity account of an efficient reading style, *PLoS One*, 2009, vol. 4, no. 8, p. e6675.
 37. Price, C.J., The anatomy of language: contributions from functional neuroimaging, *J. Anat.*, 2000, vol. 197, no. 3, p. 335.
 38. Cohen, L., Dehaene, S., Naccache, L., et al., The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients, *Brain*, 2000, vol. 123, no. 2, p. 291.
 39. Cohen, L., Lehericy, S., Chochon, F., et al., Language-specific tuning of visual cortex? Functional properties of the Visual Word Form Area, *Brain*, 2002, vol. 125, no. 5, p. 1054.
 40. Price, C.J., Wise, R.J., and Frackowiak, R.S., Demonstrating the implicit processing of visually presented words and pseudowords, *Cereb. Cortex*, 1996, vol. 6, no. 1, p. 62.

41. Damasio, A.R. and Geschwind, N., The neural basis of language, *Annu. Rev. Neurosci.*, 1984, vol. 7, p. 127.
42. Cohen, L., Martinaud, O., Lemer, C., et al., Visual word recognition in the left and right hemispheres: anatomical and functional correlates of peripheral alexias, *Cereb. Cortex*, 2003, vol. 12, p. 1313.
43. Cohen, L., Henry, C., Dehaene, S., et al., The pathophysiology of letter-by-letter reading, *Neuropsychologia*, 2004, vol. 42, no. 13, p. 1768.
44. Starrfelt, R., Habekost, T., and Leff, A.P., Too little, too late: reduced visual span and speed characterize pure alexia, *Cereb. Cortex*, 2009, vol. 19, no. 12, p. 2880.
45. Taylor, J.S., Rastle, K., and Davis, M.H., Can cognitive models explain brain activation during word and pseudoword reading? A meta-analysis of 36 neuroimaging studies, *Psychol. Bull.*, 2013, vol. 139, no. 4, p. 766.
46. Cutting, L.E., Clements-Stephens, A., Pugh, K.R., et al., Not all reading disabilities are dyslexia: distinct neurobiology of specific comprehension deficits, *Brain Connect.*, 2013, vol. 3, no. 2, p. 199.
47. Benjamin, C.F. and Gaab, N., What's the story? The tale of reading fluency told at speed, *Hum. Brain Mapp.*, 2012, vol. 33, no. 11, p. 2572.
48. Gabrieli, J.D., Poldrack, R.A., and Desmond, J.E., The role of left prefrontal cortex in language and memory, *Proc. Natl. Acad. Sci. U.S.A.*, 1998, vol. 95, p. 906.
49. Minamoto, T., Yanoi, K., Osaka, M., and Osaka, N., The rostral prefrontal cortex underlies individual differences in working memory capacity: An approach from the hierarchical model of the cognitive control, *Cortex*, 2015, vol. 71, p. 277.
50. Daniel, T.A., Katz, J.S., and Robinson, J.L., Delayed match-to-sample in working memory: A BrainMap meta-analysis, *Biol. Psychol.*, 2016, vol. 120, p. 10.
51. Abdullaev, Y.G. and Bechtereva, N.P., Neuronal correlate of the higher-order semantic code in human prefrontal cortex in language tasks, *Int. J. Psychophysiol.*, 1993, vol. 14, p. 167.
52. Buckner, R.L., Raichle, M.E., and Petersen, S.E., Dissociation of human prefrontal cortical areas across different speech production tasks and gender groups, *J. Neurophysiol.*, 1995, vol. 74, no. 5, p. 2163.
53. Borowsky, R., Cummine, J., Owen, W.J., et al., fMRI of ventral and dorsal processing streams in basic reading processes: insular sensitivity to phonology, *Brain Topogr.*, 2006, vol. 18, no. 4, p. 233.
54. Carreiras, M., Mechelli, A., and Price, C.J., Effect of word and syllable frequency on activation during lexical decision and reading aloud, *Hum. Brain Mapp.*, 2006, vol. 27, no. 12, p. 963.
55. Pugh, K.R., Frost, S.J., Sandak, R., et al., Effects of stimulus difficulty and repetition on printed word identification: an fMRI comparison of nonimpaired and reading-disabled adolescent cohorts, *J. Cognit. Neurosci.*, 2008, vol. 20, no. 7, p. 1146.
56. Seghier, M.L., The angular gyrus: multiple functions and multiple subdivisions, *Neuroscientist*, 2013, vol. 19, no. 1, p. 43.
57. Bechtereva, N.P., Shemyakina, N.V., Starchenko, M.G., et al., Error detection mechanisms of the brain: background and prospects, *Int. J. Psychophysiol.*, 2005, vol. 58, nos. 2–3, p. 227.
58. Khani, A. and Rainer, G., Neural and neurochemical basis of reinforcement-guided decision making, *J. Neurophysiol.*, 2016, vol. 116, no. 2, p. 724.
59. Petersen, S.E., Fox, P.T., Snyder, A.Z., et al., Activation of extrastriate and frontal cortical areas by visual words and word-like stimuli, *Science*, 1990, vol. 249, p. 1041.
60. Hagoort, P., Indefrey, P., Brown, C., et al., The neural circuitry involved in the reading of German words and pseudowords: a PET study, *J. Cognit. Neurosci.*, 1999, vol. 11, p. 383.
61. Wise, R., Chollet, F., Hadar, U., et al., Distribution of cortical neural networks involved in word comprehension and word retrieval, *Brain*, 1991, vol. 114, no. 4, p. 1803.

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