Lurian Journal. 2023. Vol. 4. No. 2. P. 46–58
DOI 10.15826/Lurian.2023.4.2.3
УДК 612.821 + 612.825.8 + 612.825.26:159.953 + 159.953.4 + 004.032.26:004.81

Differences in Brain Functional Network Topology in High and Low Working Memory Performance

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Различия топологических характеристик функциональных сетей мозга у людей с высоким и низким уровнем рабочей памяти

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To cite this article: Ernston, I. M., & Adamovich, T. V. (2023). Differences in Brain Functional Network Topology in High and Low Working Memory Performance. *Lurian Journal, 4*(2), pp. 46–58. doi: 10.15826/Lurian.2023.4.2.3

Abstract. Nowadays the network approach in neuroscience provides a promising way of analyzing neurophysiological mechanisms that underlie psychological functions and is widely used to study working memory. To date, data obtained in neuroimaging studies links working memory with topological features of brain networks, such as increased connectivity between frontal, parietal, and temporal regions, as well as increased integration in brain networks as a whole. The present study examines the relationship between the topological characteristics of functional brain networks with the performance in the Sternberg item recognition paradigm based on electroencephalographic data. It is shown that the higher performance in Sternberg paradigm, implying a higher efficiency of the processes of encoding, storage, and retrieval of information from working memory, is associated with an increase in the integration of functional networks, expressed in differences in the clustering coefficient, participation coefficient, Wiener index and eigenvector centrality between the groups of high and low working memory task performance ($p < .01$). In addition, our data suggest the variability in the topological pattern of connectivity, which can be traced through changes in the magnitude of the standard deviation of the values of topological metrics during the task.

Keywords: *cognitive neuroscience; network neuroscience; functional connectivity; working memory; topology of neural networks*

Аннотация. В настоящее время сетевой подход в нейронауках предоставляет многообещающий способ анализа нейрофизиологических механизмов, лежащих в основе психологических функций, и широко используется для изучения рабочей памяти. На сегодняшний день данные, полученные в ходе исследований с применением методов нейровизуализации, связывают рабочую память с топологическими особенностями мозговых сетей, такими как повышенная связность между лобной, теменной и височной областями, а также повышенная интеграция сетей мозга в целом. В данной статье рассматривается взаимосвязь между топологическими характеристиками функциональных сетей, полученными путем электроэнцефалографических исследований, и успешностью решения задач Стернберга на рабочую память. Было показано, что более высокая успешность в парадигме Стернберга, подразумевающая более высокую эффективность процессов кодирования, хранения и извлечения информации из рабочей памяти, связана с увеличением интеграции функциональных сетей, выражающейся в различиях в коэффициенте кластеризации, коэффициенте партиципации, индексе Винера и степени влиятельности между группами с высокой и низкой успешностью решения задач на рабочую память ($p < .01$). Кроме того, наши данные свидетельствуют об изменчивости топологической структуры связности, которую можно проследить по изменению величины стандартного отклонения значений топологических показателей во время выполнения задачи.

Ключевые слова: *когнитивная нейронаука; сетевая нейронаука; функциональная связность; рабочая память; топология нейронный сетей*

Introduction

The extreme complexity of the human brain neural structure, replete with interconnections, makes it impossible to study its functioning by tracking activity in individual brain loci. To date, cognitive neuroscience has found a comprehensive method of processing such neurophysiological data in network science methodology. Implementation of the network approach in the latest neuroscientific research provides promising results, bringing us closer to the understanding of the neurophysiological mechanisms of behavior. The application of graph theory formalism to multichannel activity records in many regions of the brain has revealed new patterns and mechanisms of cognitive functions and provides a better understanding of the neurophysiological foundation more fully explaining the functioning of the brain when providing a particular cognitive function (Bassett & Sporns, 2017).

Substantial evidence has been accumulated indicating the connection between the topology of functional brain networks and the current cognitive state. To date it is shown that brain networks demonstrate a small-world topology, providing a balance between a regular network, which promotes local efficiency in exchange for low costs, and a random network, which delivers global efficiency at high cost (Bullmore & Sporns, 2012). Important features of brain network topology are integration and segregation of the network. With the increase of segregation, the networks separate into several modules or node clusters. Nodes in these clusters are tightly interconnected as connections between modules are sparser. As integration increases, the number of connections between modules increases, merging them into a single undifferentiated network (*Fig. 1*). It was previously shown that integration and segregation are closely related to cognitive abilities and performance (Rizkallah et al., 2019; Vatansever, Manktelow, Sahakian, Menon, & Stamatakis, 2017; Wig, 2017).

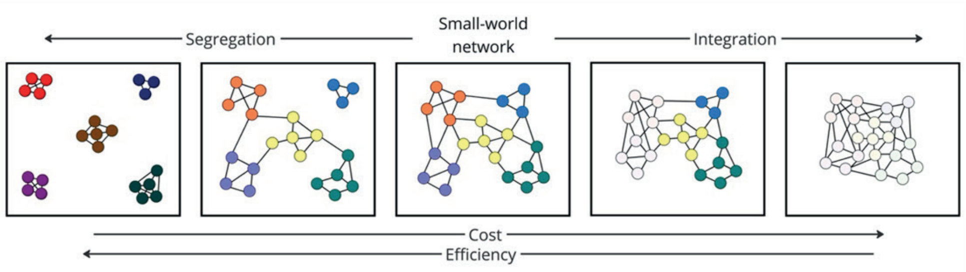

Fig. 1. Integrated and segregated topological organization of networks: on the left network is highly segregated, that is split into several separate modules; on the right network is highly integrated with lots of random interconnections between all the modules; typically, human brain networks demonstrate small-world topology (in the center), which is more cost-efficiency balanced

In the previous studies, network topology was estimated within some cognitive state or resting state, providing information regarding typical brain topology associated with this state, changes between brain topologies were usually overlooked. However, the reconfiguration of networks between states might be essential for cognitive functioning and individual differences in cognitive abilities.

For example, J. A. Thiele and co-authors (Thiele, Faskowitz, Sporns, & Hilger, 2022) found an inverse relationship between the level of reconfiguration of functional networks between states (measured through cosine distance) and the level of cognitive abilities (assessed by a battery of cognitive tests, including working memory tasks) on fMRI data, while K. Finc and co-authors (Finc et al., 2020), using the experimental design with the n-back task, showed that during the execution of the working memory task, the functional networks of the brain have a more segregated network.

This approach is applicable to the study of working memory, one of the important cognitive functions that contribute to the level of intelligence of an individual. Processes of encoding, storage, and retrieval of information from memory are necessary for many cognitive processes, including speech, thinking, planning, and implementation of motor activity. To date, there are data obtained in neural network studies that link working memory with the topological features of brain networks (Godwin, Kandala, & Mamah, 2017; Hampson, Driesen, Skudlarski, Gore, & Constable, 2006; Yamashita et al., 2018). The connection of handedness with the topology of functional networks was revealed in neuroimaging studies with working memory tasks. Thus, right-handers showed greater segregation and localization of activity in the leading hemisphere, while left-handers were inclined to greater integration and bilateral activation (Shirzadi, Einalou, & Dadgostar, 2020).

There is evidence indicating that the topological organization of functional networks in the states of execution of working memory is similar to that for episodic memory and primarily includes networks of insular and parietal regions (Stark et al., 2021). The relationship between performance in working memory tasks and integration in intrinsic connectivity networks (*ICNs*) was shown depending on the level of subjects' training (Finc et al., 2020). After the training, the integration between task-positive ICNs (frontoparietal, salience, dorsal attention, cingulo-opercular) increased against the background of a decrease in the integration of the listed ICNs with the default-mode network. At the same time, successful respondents showed a lower level of integration.

In our study, we have focused on the changes in network topology between the resting state and the state of cognitive task execution in relation to task performance. With that in mind, we have two main hypotheses:

(1) The higher performance of working memory tasks is associated with a higher level of integration in an individual's functional network.

(2) A greater variability in the characteristics (a higher level of reconfiguration) of the functional network over time is associated with a higher performance of working memory tasks.

Materials and Methods

Subjects

The sample included 67 people aged 17–34 years ($\overline{x}$ = 21.7, *SD* = 3.36), 20 of whom were female, all right-handed, with no known injuries and neurological disorders. Data collection and analysis were approved by the Ethics Committee of the Lomonosov Moscow State University.

Data Acquisition

Brain activity was recorded using a 64-channel EEG system BrainVision ActiCHamp by Brain Products Gmb H. Reference electrode — FCz, the ground electrode — AFz, eye movement interferences detected with EOG-electrode placed under the right eye.

Experimental Paradigm

The scheme of the experiment involved recording 10 minutes of resting-state brain electrical activity at 2-minute intervals with closed and open eyes, a total of 6 and 4 minutes of recording two types of resting-state activity, respectively. After that participants were presented with a working memory task (Sternberg item recognition paradigm, *SIRP* (Sternberg, 1966)), a total of 129 stimuli (*Fig. 2*).

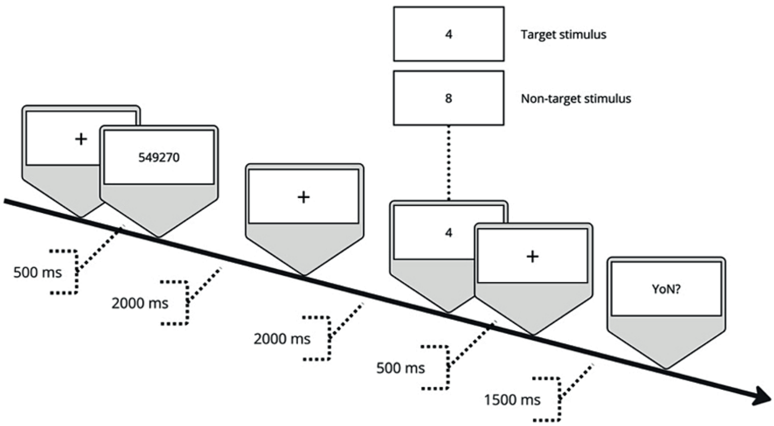

Fig. 2. Scheme of presentation of stimuli of the SIRP working memory task

Data Analysis

Source localization was performed using the average brain model Colin-27 (Holmes et al., 1998), and hemispheres were divided into 75 zones per hemisphere with the use of Destrieux Atlas (Destrieux, Fischl, Dale, & Halgren, 2010). A BEM model of the brain was built using the MNE package (standard settings were applied: three layers, standard permeability, 4096 points per hemisphere). The inverse operator was computed, after which the forward operator and noise covariance were found individually for every participant. The activity of points was calculated using the dSPM method. The activity of the hemispheric zones was approximated through the first PCA component, resulting in 75 time series per hemisphere.

The EEG recording for each stimulus (cognitive working memory task) was divided into epochs using the sliding window algorithm with a time interval of 250 ms and a single shift of 0.5 of the window.

Functional connectivity matrices were constructed for each epoch using methods for estimating signal synchronization (method based on mutual information (Wang, Alahmadi, Zhu, & Li, 2015)). A connectivity graph containing 30 % of the strongest connections in the matrix was constructed (*Fig. 3*) and then analyzed using topological

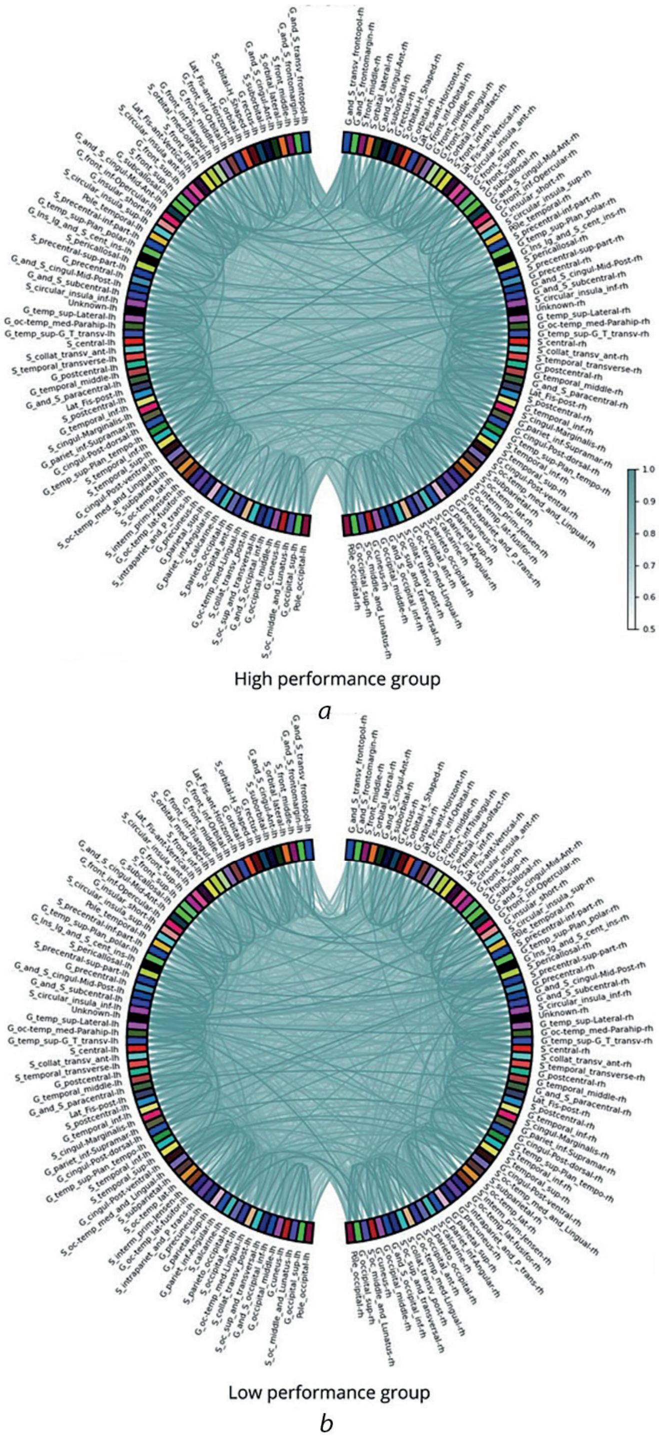

Fig. 3. Average network topology for individuals of high (*a*) and low (*b*) performance groups. The darker the tone of the line, the stronger the connection between modules

metrics, which indicate different aspects of the brain's functional network integration and segregation. The analysis is performed in the range from 8 Hz to 13 Hz (α-rhythm band).

The applied set of graph topology metrics included the following ones: average path length, clustering coefficient (Saramäki, Kivelä, Onnela, Kaski, & Kertész, 2007), participation coefficient (Thompson et al., 2019), Wiener index (Wiener, 1947), betweenness centrality (Brandes, 2001), eigenvector centrality (Bonacich, 1987), global efficiency (Latora & Marchiori, 2001).

The level of network integration increases with an increase in values of global efficiency and Wiener index and a decrease in average path length, clustering and participation coefficients; the reverse dynamics is an indicator of an increase in segregation. Betweenness and eigenvector centrality metrics are the measures to indicate how close on average are the nodes to the center of the graph (Rubinov & Sporns, 2010).

To assess network reconfiguration, *SD* for metrics was calculated individually for every participant. Greater *SD* values indicated a higher level of network reconfiguration.

Results

Behavioral Data

Key behavioral indicators for present investigation were the proportion of correct responses in the SIRP, as well as the average reaction time (*RT*) upon presentation of the test set (that is, the time from the appearance of a set of numbers on the screen to the response by the participant of the study by pressing a key on the keyboard). On average, the study participants gave correct answers in 91.71 % of cases, the median value was 92.2 %, $SD = 4.21$, min = 79 %, max = 99 %. The average RT was 0.8798 seconds, the median value was 0.8007 seconds, $SD = .25704$. The variability of behavioral parameters found in this work is consistent with the data acquired with SIRP in other studies (Tuladhar et al., 2007).

Based on behavioral data, participants were divided into groups of high and low performance in the SIRP (hereinafter referred to as high-performance and low-performance groups, respectively). The groups were identified using K-means clustering based on both the proportion of correct responses and the average RT of the study participants. The size of groups was 20 people in the low-performance group and 42 people in the high-performance group.

The examination of the influence of demographic characteristics of the study participants showed that differences in gender and age have no effect on behavioral data. As a result of the *regression analysis* of the influence of age on the proportion of correct answers, the following data were obtained: $t = .174$; $p = .862$; adjusted coefficient of determination = −.01615. These data indicate that there is no statistically significant influence of age on behavioral indicators.

The analysis of the influence of age on the average RT showed the following data: $t = -.854$; $p = .397$; adjusted coefficient of determination = −.004471. The data also do not allow us to claim the existence of a statistically significant influence of the age of the subject on the value of the average RT.

The application of one-factor analysis of variance to the data on the gender of the subjects shows that there is no significant relationship between the RT (for the main factor "gender" $p = .926$, $F(1, 60) = .009$, $MSE = .02523$) and the proportion of correct answers (for the main factor "gender" $p = .541$, $F(1, 60) = .378$, $MSE = .0000156$).

Functional Connectivity Features

Statistical differences in values of connectivity metrics were tested using ANOVA, regarding the behavioral group as fixed factor. The data on the p-levels of statistical significance, adjusted using the Tukey criterion, are presented.

Comparison of the values of connectivity metrics revealed the existence of significant differences depending on the behavioral group in a number of features (see *Fig. 4*). Thus, significant differences were found in the levels of the participation coefficient ($p < .001$), as well as the clustering coefficient and the Wiener index ($p < .05$) between behavioral groups: the high-performance group of is characterized by a higher level of integration relative to the low-performance group.

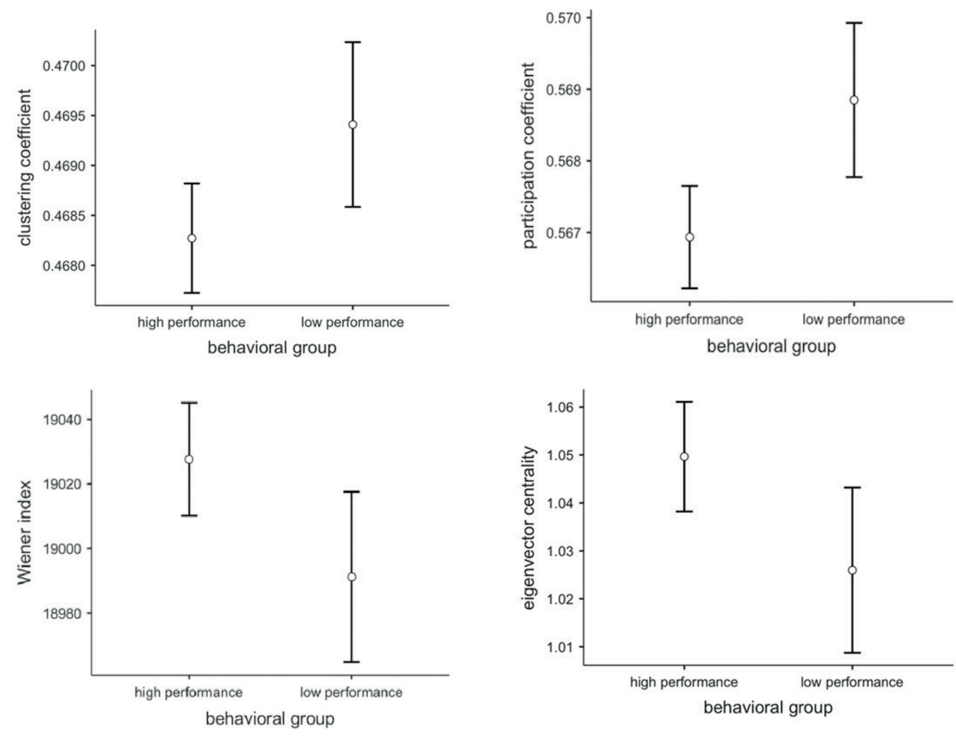

Fig. 4. A graph of estimated marginal means for the clustering coefficient, participation coefficient, Wiener index and eigenvector centrality (metric values on the *y* axis), fixed factor: the behavioral group (on the *x* axis). The points reflect marginal means, vertical segments — the 95 % of the confidence interval

Significant differences were also found in the values of centrality and rich-club metrics in different behavioral group. The analysis of variance indicates significant differences in the values of the eigenvector centrality index ($p < .05$).

However, no significant differences were found in the *SD* of topological metrics. Thus, a machine learning (*ML*) clustering algorithm was used to further test whether respondents could be divided into two groups based on metrics of reconfiguration level. The hypothesis was that if ML-based groups would match ones formed based on behavioral data about cognitive performance in WM tasks, reconfiguration level metrics shall reflect functional connectivity features connected to WM execution. Firstly, feature selection with the Boruta package was applied to form the mass of variables that are most important for the ML task (in our case, classification of participants on the basis of reconfiguration level). At this step following topological characteristics of reconfiguration level were selected: APL, PC, eigenvector centrality. It is worth noting that most of the characteristics were marked as important for clustering when considering averages of topological metrics. Finally, the Support Vector Machine (*SVM*) (Statnikov, 2011) ML algorithm was applied to selected metrics, forming two groups with an accuracy of 0.73 (share of participants in ML-based groups to match behavioral data-based groups).

Discussion

The results of the study support the existence of the dynamics of functional networks of the human brain when processing information in working memory. The topological characteristics of functional connectivity in working memory tasks differ depending on the performance in the cognitive task. Topological metrics which differ significantly in high and low cognitive performance groups form two sets, each of which describes whether a segregated or integrated network. Thus, patterns of functional connectivity demonstrated by the brains of individuals who perform better in WM tasks are comprehensively more integrated.

At the same time, no statistically significant differences in *SD* of topological metrics between the two groups of participants were found. This direct comparison of measures of dispersion of topological features doubts the hypothesis of reconfiguration level interconnection with the level of cognitive performance. However, it seems that more research on this topic is necessary because ML methods provide data in favor of the above-mentioned hypotheses. Thus, the application of the SVM classification algorithm resulted in the classification of participants based on reconfiguration-level metrics with a reasonably high accuracy of 73 %.

Such results support the concept of neuronal efficiency (Achard & Bullmore, 2007), and also complement recent studies that indicate the connection of a high level of intelligence with the lesser reconfiguration of networks against the background of their greater integration in solving various types of cognitive tasks, primarily requiring the performance of cognitive functions of fluid intelligence (Finc et al., 2020; Thiele et al., 2022). This is consistent with the results of other studies of the properties of networks at different load levels, which show that an increase in cognitive effort leads to a more globally efficient, less clustered, and less modular network configuration with greater synchronization over long distances between brain regions (Kitzbichler, Henson, Smith, Nathan, & Bullmore, 2011). Taken together, the described facts suggest that the modular structure of functional brain networks may be a factor in the success of tasks related to working memory, since brain network modules can be specialized for a certain type of information, therefore, when perceiving new stimuli, the nervous system faces the task of distributing incoming information to the appropriate modules for further processing, in particular in the case of working memory — storage. This specific task of modules associated with working memory causes an increase in segregation when they are active in the process of information processing. If the brain needs to access the stored information again, it is again brought together, which causes the reconfiguration of the functional networks of the brain into a more globally integrated state.

The current study shows significant differences in such features of the topological organization of networks as centrality. The values of eigenvector centrality index suggest that brain networks are not just becoming globally integrated or segregated, but also moving from a topology with a more pronounced highly connected core of the "rich club" to more randomly organized topologies and vice versa. In addition, the mentioned core changes not only by the strength of the connections of its constituent nodes (connecting hubs). Based on changes in global centrality metrics, new nodes are included in the "rich club," which cease to serve as provincial hubs and become global connecting hubs. Such features of network reconfiguration can be indicators of processes in the brain, during which certain ICNs are included in the global functional network. The connection of changes in topology with the level of performance in working memory task suggests that the described process is specific depending on the cognitive function performed, which is consistent with the concept of ICNs specific to various cognitive functions.

Conclusions

In conclusion, it can be noted that the results of the study confirm the importance of the topological characteristics of the functional networks of the brain for the successful performance of tasks related to working memory. The results of this study confirm the hypothesis of a close connection between the structure of functional brain networks and working memory.

The analysis revealed that more efficient memory work is associated with certain topological features of brain networks, including an increase in global integration and reconfiguration of functional connectivity according to the network pattern of the "rich club" with an increase in the centrality of connecting hubs. Data on the characteristics of brain networks indicate that individuals from the group with higher results in cognitive tests showed a higher level of integration in functional networks when solving this task.

Secondly, no clear exact conclusions can be made regarding the connection between cognitive performance in working memory tasks and the level of functional connectivity reconfiguration. The present study showed the absence of significant differences in the *SD* metrics of networks depending on the level of performance in WM tasks, while a fairly promising result was obtained in ML-based classification, suggesting that it is possible to distinguish individuals who demonstrate high cognitive performance from the ones who are less successful in cognitive tasks.

However, these findings require further investigation and verification. The results of the current study show that the use of connectivity indicators derived from EEG and related topological metrics can offer a reliable and at the same time affordable approach to monitoring working memory. It is also worth noting that the identified connections can be used to further study the mechanisms of brain work related to the execution of working memory within the framework of network neuroscience.

Limitations

The experimental design of the present study implies certain limitations, which shall be considered when interpreting the abovementioned findings. The nature of these limitations consists in: (a) the limited number of participants in the experimental sample; (b) methodological limitations in the calculation of connectivity matrices using sliding window algorithm; (c) EEG frequency range limited to only α-rhythm (8 to 13 Hz), while analysis in the wider range from θ-rhythm up to β-rhythm (3 to 30 Hz) is being planned; (d) *SD* was calculated for all stimuli, while it is likely that the calculation of metric deviations within a single stimulus may be more illustrative.

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Original manuscript received March 15, 2023
Revised manuscript accepted May 01, 2023

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