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Топологический анализ позволяет предположить реконфигурацию сетей мозга человека при переходе от состояния покоя к когнитивной нагрузке

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АННОТАЦИЯ

Обоснование. Адаптация нейронных сетей мозга к переменным условиям окружающей среды — ключевой аспект эффективного исполнения когнитивных функций. Сетевой подход в нейронауке, фокусирующийся на анализе структурных и функциональных характеристик сетей, которые связаны с когнитивными функциями, является весьма многообещающим направлением для понимания психофизиологических механизмов, лежащих в основе адаптивной динамики когнитивных процессов.

Цель исследования — изучить, как топологические особенности функциональных коннектомов мозга человека связаны с осуществлением различных когнитивных процессов. Основное внимание было уделено определению динамических изменений в мозговых сетях во время выполнения задач на рабочую память с целью выявления сетевых характеристик, присущих сетям при исполнении этой когнитивной функции.

Методы. На основе электроэнцефалографических данных подробно рассмотрены топологические характеристики функциональных мозговых сетей в состоянии покоя и при когнитивной нагрузке, обеспечиваемой выполнением теста Стернберга на рабочую память (Sternberg Item Recognition Paradigm). Записи ЭЭГ 67 здоровых взрослых были обработаны для оценки функциональной связности с помощью метода когерентности. Мы предполагаем, что топологические свойства функциональных сетей в человеческом мозге различаются между когнитивной нагрузкой и состоянием покоя с более высокой интеграцией в сетях во время когнитивной нагрузки.

Результаты. Исследование подтверждает, что топологические особенности функциональных коннектомов зависят от текущего состояния когнитивной обработки и изменяются в ответ на изменения когнитивной нагрузки, вызванной заданием. Анализ также продемонстрировал, что функциональные коннектомы, зафиксированные при выполнении задач на рабочую память, характеризуются более быстрым появлением генераторов групп гомологии. Это подтверждает идею взаимосвязи между начальными этапами выполнения задач на рабочую память и увеличением скорости сетевой интеграции, при этом решающую роль играют соединительные хабы (connector hubs).

Заключение. Различные уровни когнитивной нагрузки, в частности при задачах на рабочую память, связаны с разными топологическими свойствами функциональных сетей мозга, что подчёркивает важность сетевой динамики в когнитивной обработке.

Ключевые слова: когнитивная нейронаука; функциональная нейровизуализация; картирование биоэлектрической активности мозга; картирование коннектома; рабочая память.

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Topological data analysis suggests human brain network reconfiguration during the transition from resting state to cognitive load

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ABSTRACT

BACKGROUND: Neural networks of the brain continually adapt to changing environmental demands. The network approach in neuroscience, which focuses on the analysis of structural and functional network characteristics related to cognitive functions, is a highly promising avenue for understanding the psychophysiological mechanisms underlying the adaptive dynamics of cognitive processes.

AIM: We aimed to explore how the topological features of functional connectomes in the human brain are linked to different cognitive demands. The focus was on understanding the dynamic changes in brain networks during working memory tasks to identify network characteristics inherent to working memory.

METHODS: We examined the topological characteristics of functional brain networks in the resting state and cognitive load provided by the execution of the Sternberg Item Recognition Paradigm based on electroencephalographic data. Electroencephalogram traces from 67 healthy adults were processed to estimate functional connectivity using the coherence method. We propose that the topological properties of functional networks in the human brain are distinct between cognitive load and resting state, with higher integration in the networks during cognitive load.

RESULTS: The topological features of functional connectomes depend on the current state of cognitive processing and change with task-induced cognitive load variation. Moreover, functional connectivity during working memory tasks showed a faster emergence of homology group generators, supporting the idea of a relationship between the initial stages of working memory execution and an increase in faster network integration, with connector hubs playing a crucial role.

CONCLUSION: Collected evidence suggest that cognitive states, particularly those related to working memory, are associated with distinct topological properties of functional brain networks, highlighting the importance of network dynamics in cognitive processing.

Keywords: cognitive neuroscience; functional neuroimaging; brain electrical activity mapping; connectome mapping; working memory.

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INTRODUCTION

Network neuroscience, an approach aimed at analyzing the characteristics of structural and functional networks associated with cognitive functions, is one of the most promising ways of understanding the psychophysiological mechanisms of cognition. The tremendous complexity of brain neuronal structures, abundant with interconnections, renders the relation of cognitive functions to the activity of separate brain regions inefficient. It appears that interactions between the brain loci are a better way of understanding the brain mechanisms of cognition. Recently, a network approach that depicts the brain as a network of interconnected regions has become a popular method of brain activity analysis.

The widely used measure in functional network studies is the level of global segregation and integration in the network. Segregated networks are characterized by a more distinguished structure of processing modules, whereas the nodes of integrated networks are much more interconnected. Functional segregation in the network is characterized by higher modularity and clearly distinguishable clusters of nodes in which the number of intracluster connections significantly exceeds the number of intercluster connections. The integrated network is characterized by low modularity and a higher level of interconnection between all network nodes (Fig. 1). The new computational methodology has shown that the global topological properties of functional brain networks have some unique features, such as small-worldness, which implies a low path length and high clustering, and provides an optimal ratio of the efficiency of information processing and the costs of its transmission for brain networks [1]. In addition, convincing evidence shows that brain neural networks are complementary to global small-world architecture characteristics of topological organization such as high clustering and high global efficiency [2] and highly modular community structure [3], which indicates a high number of nodes with multiple connections — network hubs [4].

Increasing the level of integration within brain functional networks is often associated with cognitive activity [5]. The level of integration in the network can directly predict performance in cognitive tasks, including those for working memory (WM), such as the N-back task.

By applying the methods of network neuroscience, large amounts of data on the basic network architecture of the human brain, particularly the cerebral cortex, were collected. Neuroimaging studies have suggested that brain activity is topologically organized by functional networks, which are persistent in the cognitive load and resting states. These networks are commonly referred to as intrinsic connectivity networks (ICNs) [6], which denote functional brain networks detected regardless of the current cognitive load and separate them from resting state networks. Evidence shows that the topology of these functional networks is close to the anatomical neural topology of the corresponding brain regions [7–9], and these networks are associated with certain cognitive functions (e.g., networks of visual perception, long-term memory, cognitive control, and attention [10]), supporting global information processing and other aspects of cognition. Key features of ICN organization in the human brain include the seven most distinguished networks according to the study by Yeo

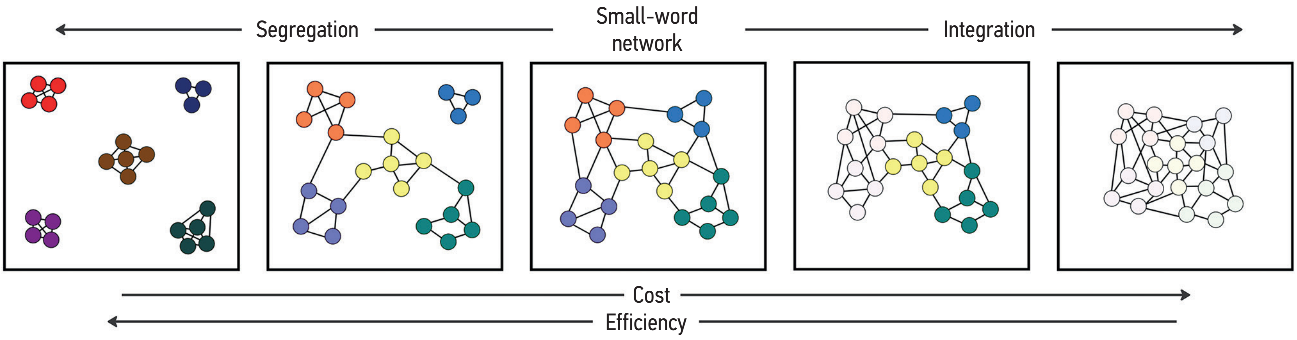

Fig. 1. Brain networks demonstrate a “small-world topology”, providing a balance between a regular network (*leftmost*), which promotes local efficiency in exchange for low costs, and a random network (*rightmost*), which delivers global efficiency at high cost. As segregation increases (*right-to-left*), the network is divided into modules, and its nodes are closely interconnected and poorly connected to the nodes in other modules. As integration increases (*left-to-right*), the number of connections between nodes increases, and individual modules merge into a single undifferentiated network. Rich clubs (*yellow*), formed by hubs of high centrality, provide global information pathways in the network. Figure adapted from [6].

Рис. 1. Сети мозга демонстрируют топологию «тесного мира» (“small-world topology”), обеспечивающую баланс между регулярной сетью (*слева*), которая способствует локальной эффективности в обмен на низкие затраты, и случайной сетью (*справа*), которая обеспечивает глобальную эффективность при высоких затратах. По мере увеличения сегрегации (*справа налево*) сеть делится на модули, узлы внутри которых тесно взаимосвязаны, но слабо связаны с узлами в других модулях. По мере увеличения интеграции (*слева направо*) количество соединений между узлами увеличивается, и отдельные модули объединяются в единую недифференцированную сеть. «Богатый клуб» (“Rich club”; показан жёлтым цветом), созданный узлами высокой центральности, обеспечивает поддержание эффективных глобальных информационных потоков в сети. Рисунок адаптирован из [6].

et al., where the more stable networks were distinguished in functional magnetic resonance imaging data [11]. These networks are roughly specified as visual, somatomotor, dorsal attention, ventral attention, limbic, frontoparietal, and default-mode networks. Although some of these networks are suggested to aggregate multiple topologically and task-specific subnetworks, research reveals that these networks can be attributed to specific functions. Nevertheless, these findings support the idea of topologically localized network organization of brain neural activity.

According to modern conceptions of brain network organization, the key elements of global brain networks are the highly connected zones in the brain, which are responsible for the transfer of information between specialized ICNs. Such zones, or hubs, can be either local (provincial hubs), connecting nearby nodes to a functional local subnetwork, or global (connector hubs), through which local subnets communicate with each other. Studies have shown that global hubs form the “rich club” [12], which includes approximately 70% of the shortest paths in the neural networks of the brain, and is the most important element ensuring the effective operation of the global network [13]. The connection of the features of rich club networks with cognitive functions lies in the fact that local hubs, having many strong connections within their subnets, ensure the transition of the network to easily accessible states [14], in which internalized knowledge and experience are available for processing by various means.

Working memory is a crucial cognitive function that makes a significant contribution to an individual’s cognition. Encoding, storage, and retrieval of information from memory are essential for various cognitive functions, including speech, reasoning, perception, and motor activity [15].

The prefrontal cortex, particularly its dorsolateral part, is considered to play a major role in the execution of WM. The dorsolateral prefrontal cortex appears to be involved in information storage, particularly regarding spatial positioning, whereas various parts of the ventral and lateral prefrontal cortices participate in storing nonspatial information (e.g., objects, faces, and words). On the contrary, each of these areas may have different functions, whereas the dorsolateral prefrontal cortex is involved in manipulating information, and the ventrolateral cortex is suggested to be involved in its retention [16].

According to recent studies, during the WM task, brain networks have some specific properties, particularly an increase in the integration between the frontoparietal and frontotemporal lobes, and an increase in reconfiguration in the frontal regions is positively associated with the performance of memorization [17]. The latest data suggest that the execution of WM tasks leads to an increase in segregation in functional brain networks compared with the networks in the resting state. The significance of the role of frontoparietal functional networks in WM performance is validated by the considerable accuracy of prediction models based on the topological characteristics of functional connectivity in these regions [18, 19]. In addition, Finc et al. showed that training affects network segregation, induced by WM tasks: after training, participants tend to have more modularity in functional networks, whereas the performance of the participants in WM tests also increases [20]. After the training, the integration between task-positive systems (frontoparietal, salience, dorsal attention, and cingulo-opercular) increased, whereas the integration of the listed ICNs with the default-mode network decreased.

Considering the abovementioned facts, we hypothesized that the topological characteristics of the functional networks of the human brain differ in WM tasks and resting state. Furthermore, we assumed functional connectivity in the WM load to demonstrate a more integrated organization with a distinct rich club of highly connected hubs.

Aim — to investigate the relationship between the topological features of functional connectomes in the human brain and cognitive processing. We sought to understand how the organization of functional networks within the brain changes depending on the type of cognitive task performed by the participants. One focus was on studying the patterns of functional connectivity during WM tasks, which are crucial for the temporary storage and processing of information in the brain. By analyzing dynamic changes in functional connectomes during different cognitive tasks, potential associations were identified between specific network characteristics and cognitive performance. This investigation provides valuable insights into the underlying mechanisms of cognitive processes, particularly in relation to WM, and contributes to a deeper understanding of brain functioning and its relevance to cognitive abilities.

MATERIALS AND METHODS

Participants

The study involved 67 people aged 18–34 years (m=21.7, SD=3.36), 20 females and 47 males, all right-handed, with no known injuries or neurological disorders.

Written consent was obtained from all the study participants before the study screening in according to the study protocol approved by the Bioethics Committee of the Lomonosov Moscow State University (protocol N 8–ch of 13.05.2021).

Working memory task procedure

The experiment involved 10-min recording of resting-state brain activity at 2-min intervals with closed and open eyes consecutively at 6 and 4 min of recording, respectively. Then, the participants were offered a task on WM — Sternberg item recognition paradigm (SIRP) [21]. In this paradigm, participants were shown sets of characters in the present study — a sequence of six digits (sample stimulus), and after a certain delay, one character (control

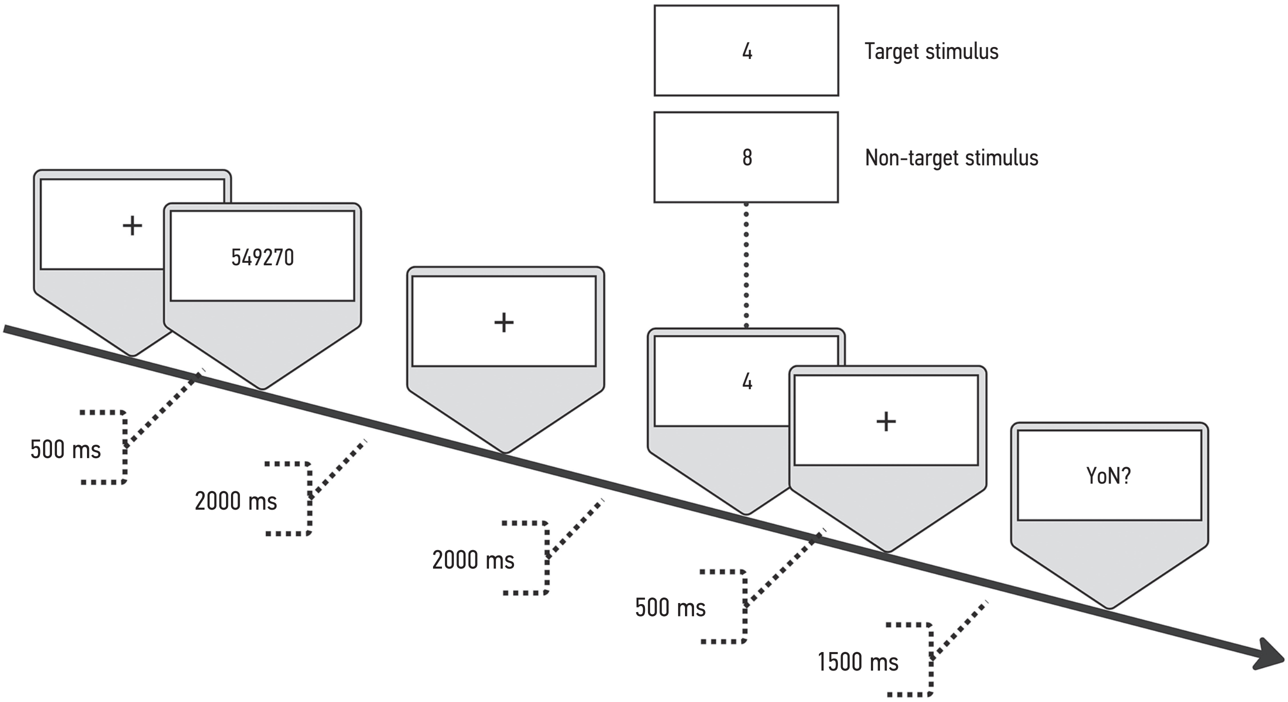

Fig. 2. Scheme of the presentation of stimuli of the Sternberg Item Recognition Paradigm working memory task.
Рис. 2. Схема предъявления стимулов теста Стернберга на рабочую память (Sternberg Item Recognition Paradigm).

stimulus) was presented, and the participants had to determine whether this character was a part of the original set (Fig. 2). Each task comprised the following stages:

1. Presentation of a fixation cross in the center of the screen (presented for 0.5 s).
2. Presentation of the sample stimulus (2 s).
3. Postponement with repeated presentations of the fixation cross (2 s).
4. Presentation of the control stimulus — target or non-target (0.5 s).
5. Time for the participant's response with repeated presentations of the fixation cross (1.5 s).

In total, 129 stimuli were presented to each participant.

PsychoPy version 2023.1.1 was used to program the experiment, present stimuli to the participants, and record behavioral data.

Neurophysiological data acquisition and processing

Brain activity was recorded using the 64-channel electroencephalographic (EEG) system actiCHamp (Brain Products GmbH, Germany). The recording was performed in the monopolar mode. The proprietary mounting of electrodes by Brain Vision (USA) based on the 10–10 system was used, with FCz as a reference electrode and AFz as a grounding electrode. An electromyogram was recorded using an electrooculography electrode placed under the right eye to correct artifacts from the oculomotor musculature. The frequency range of electrical signal registration was 0.1–1000.0 Hz.

During preprocessing, EEG data were manually processed to remove major artifacts. The recording sampling frequency was then changed from 1000 to 250 Hz, the frequency range was limited to 0 and 50 Hz, and the reference electrode was changed from FCz to a virtual averaged reference. This stage of the preprocessing procedure was performed using BrainVision Analyzer 1.0 by Brain Products GmbH.

At the final stage of preprocessing, oculomotor and other artifacts were removed by ICA, and damaged epochs and channels were restored using the Autoreject Library for Python [22].

Bioelectric signal sources were localized to more accurately determine the features of the distribution of neural electrical activity in the brain. The location of the sources was determined using the "average" head and brain magnetic resonance imaging model based on the "Buckner40" model. The "oct6" scheme was used (4098 points per hemisphere; the distance between sources was 4.9 mm, and the area for each source was 24 mm^2).

To calculate the forward operator using the boundary-element model, areas with different conductivities were divided into triangular geometric units. For EEG data, three layers were used: the intracranial space, skull, and scalp. After that, the boundary-element model layers were assigned a conductivity value: for the scalp and parts of the brain, the default value was 0.3 S/m; for the skull, the default value was 0.006 S/m.

The activity of the sources was calculated using the dSPM method [23]. The result of the algorithm is the assessment of the activity of individual sources in the hemispheres

(4098 per hemisphere), which were reduced to 75 zones in each hemisphere using the PCA method. The value of the first component was implemented. Zones in the brain cortex were extracted according to the Destrieux anatomical atlas [24]. Source localization procedures were performed using the MNE-Python 1.3.1 package.

Preprocessed EEG traces were subjected to connectivity estimation for each participant and condition (SIRP, closed eyes and open eyes), and adjacency matrices were constructed using the coherence method [25]. The connectivity for the entire interval for each condition, including SIRP execution, was estimated. This study focused on the evaluation of functional connectome differences linked to different cognitive states, not different levels of WM performance. Thus, no SIRP epochs were dropped, including those that were recorded during an unsuccessful trial of WM task execution. In this study, we focused on the alpha (8–13 Hz) and beta (13–30 Hz) frequency bands. EEG data were divided into 6-s epochs with a 0.5-window overlap to capture temporal dynamics. Coherence was calculated within each epoch and frequency band and averaged first with every single SIRP stimulus. Thereafter, coherence values were averaged across stimuli within the same frequency band, and adjacency matrices were constructed to represent functional connectivity.

At present, no consensus has been established on the optimal value of the bond strength threshold for constructing adjacency matrices, although this procedure is an established part of the connectivity analysis process. In recent studies of functional connectivity, authors more often use fairly high values of the threshold of the strength of connections, up to 0.80–0.95 [26, 27]. However, a high threshold value can lead to the loss of a significant share of information because weak functional connections in brain networks can play an important role in the neural mechanisms of cognitive functions [28]. In this study, a less conservative threshold value of 0.7 was used. Functional connectivity was estimated using the MNE-Python 1.3.1 package.

Topological data analysis

Topology is often colloquially described as representing the overall structure of the data. In addition to more localized and rigid geometric features, topological features are useful for capturing global, multiscale, and intrinsic properties of datasets. The usefulness of topological features has been acknowledged with the emergence of topological data analysis (TDA). Many researchers have attempted to use this information to gain a new perspective on their datasets. In recent years, an extension of TDA has emerged, which involves integrating topological methods to enhance traditional data analysis.

A fundamental assumption in data analysis is that data possess a shape, meaning that they are sampled from an underlying low-dimensional manifold, which is referred to as the “manifold hypothesis” [29]. Instead of solely relying on statistical descriptions, TDA seeks to explore the underlying manifold structure of datasets algebraically. This involves computing descriptors of datasets that remain stable even when subjected to perturbations, and these descriptors encode intrinsic multiscale information about the data shape.

Data shape is a significant property, particularly in the field of network science. Numerous studies have investigated the topological structure of different biologically inspired data, from structural [30] and functional connectomes to eye movements [31] and single-cell activities. TDA techniques have gained popularity in processing EEG signals because they can aid researchers in discovering new properties of complex and extensive data by simplifying the analysis by implementing a geometrical approach.

Fundamental topological data analysis definitions

Point clouds are a type of data representation in which data elements are represented as an unordered set of points in a Euclidean space with *n* dimensions, denoted as E^n. A point cloud refers to a finite subset of E^n. This type of data can be obtained from many natural experiments and can even be extracted from two-dimensional time series by disregarding the order of elements. The overall topology of point clouds can offer valuable insights into data structure.

The typical approach to transforming the data points in a cloud $\{x_i\} \subseteq E^n$ into a single, unified topological object is to use them as vertices in a combinatorial graph. To determine the edges in the graph, an ε-sized window of proximity is defined such that points x_i and x_j are connected by an edge if their distance $\rho(x_i, x_j)$ is less than or equal to ε. However, this graph has a two-dimensional structure and cannot adequately capture the high-dimensional properties of the original space from which the data points were sampled. To overcome this limitation, a mathematical object, known as a clique complex, can be constructed on any graph object using a specific method of creating a simplicial complex. Each clique on *n* vertices in the graph is interpreted as an (*n*–1)-dimensional combinatorial simplex. TDA methods work directly with these discrete constructions; however, their topological properties can be generalized to topological simplices, which are the topological realizations of such combinatorial simplices. Different methods of clique complex construction are available, and the most commonly used and useful ones are the Delaunay, Vietoris–Rips, Cech, and Alpha complexes. These indices are defined as follows:

Cech $$Cech_\varepsilon\,(X) = \{\sigma \subseteq X \mid \bigcap_{x\in\sigma} B\varepsilon(x) \neq \varnothing\}$$

Vietoris–Rips $$VR_\varepsilon(X) = \{\sigma \subseteq X \mid diam(\sigma) \leq 2\varepsilon\}$$

Delaunay $$Del(X) = \{\sigma \subseteq X \mid \bigcap_{x\in\sigma} V_x \neq \varnothing\},$$

$$V_x = \{y \in R^d \mid \,||y-x|| \leq ||y-z||, \forall z \in X\}$$

Alpha $$Alpha_\varepsilon(X) = \{\sigma \subseteq X \mid \bigcap_{x\in\sigma} (B_\varepsilon(\mathrm{x}) \cap V_x) \neq \varnothing\}$$

One of the main methods of TDA is persistent homology, which considers the existence of an ordered pair (X, f) where X is a set of data points and f is a filter function defined in the domain of interest X. The filter function induces filtration of the set X, i.e., a sequence of subspaces

$$\varnothing = X_0 \subseteq X_1 \subseteq X_2 \subseteq \ldots \subseteq X_n = X,$$

which are often the sublevel sets $X = f^{-1}(-\infty, \varepsilon]$ of this function for an arbitrary real valued threshold parameter $\varepsilon \in R$. For example, assume that $\{VR_i\}^N{}_1$ is a sequence of VR complexes associated with a point cloud X (data) for an increasing sequence of parameter values $\{\varepsilon_i\}^N{}_1$.

$$VR_1 \to VR_2 \to \ldots \to VR_N,$$

where i is the inclusion maps between these complexes. Persistent homology provides a tool for examining homology not for a single complex VR_i but for a whole sequence of homology groups in each dimension * and for all $i<j$

$$\iota\colon H^*(VR_i) \to H^*(VR_j).$$

The dimensions of homology vector spaces named Betti numbers $\beta = dim(H^*\ (X))$ play the role of the most common topological invariants in data analysis practice.

Persistent homology allows us to track and uncover the emergence and disappearance of topological features in various dimensions during filtration, where the threshold parameter ϵ changes from $-\infty$ to $+\infty$. Persistent topological features are those that persist over a long interval of the threshold parameter, hence, the name “persistent”. The persistence of a homology group element is measured as the difference between the values of the filter function f at its death and birth moments, denoted by d_i and b_i, respectively. In other words, it quantifies how long the homology group element has existed and how important it is for the overall topology of the space.

A concise method for summarizing information about the lifespan of elements in homology groups of a particular filtration is typically achieved using a “persistence diagram” (PD). These diagrams are used for any given dimension k the filtration and provide a compact representation of data descriptors.

$$\{D^k{}_{f(X)}\}_{k \in \{0 \ldots K\}},$$

which is called a k^{th} dimensional PD

$$D_{fk}(X) := \{(b_i, d_i)\}^k{}_{i \in I},$$

where $\{(b_i, d_i\}^k{}_{i \in I}$ is the multiset of birth-and-death intervals of topological features in the dimension k. An analogous way of thinking about PD is a multiset of points on the extended Euclidean plane $R^2 \cup \{+\infty\}$ in the birth-and-death coordinates.

To compare different PDs, different metrics, i.e., bottleneck and Wasserstein distances, are available. Given the two PDs D and D', their bottleneck distance is defined as

$$W_\infty(D, D') := inf_{\eta: D \to D'} sup_{x \in D}\ ||x - \eta(x)||_\infty,$$

where $\eta\colon D \to D'$ denotes a bijection between the point sets of D and D' and $||\cdot||_\infty$ refers to L_∞ distance between two points in R^2.

The Wasserstein distance is a generalization of the bottleneck metric and is defined as

$$W_p(D_1, D_2) := inf_{\eta: D_1 \to D_2}\Big(\sum_{x \in D_1} ||x - \eta(x)||_\infty{}^p\Big)^{1/p}.$$

In this study, TDA was used to analyze the topological structure of individual functional connectomes. Each functional connectome was interpreted as a simplicial complex; Vietoris–Rips complexes are mostly used in this study, and PDs in zero, one, and two dimensions were computed for each of them. Pairwise bottleneck distances between Vietoris–Rips complexes were computed and used to construct point clouds of the diagrams (Fig. 3). Finally, point clouds were compared using representation topology divergence (RTD), the topological measure of complex data representations, such as point clouds, which have topological and geometrical structures [32].

To vectorize PDs, different functions that represent diagrams in vector form, for example, Betti curves, can be used. Let D be a PD, then Betti curve in i^{th} dimension is a function $\beta_i\colon R \to N$, from real numbers to natural numbers, where $\beta_i\,(s)$ is the number, counted with multiplicity, of points $(b_i,\ d_i)$ in D such that $b_i \le s < d_i$. Betti curve values $\beta_i\ (s)$ describe the i^{th} Betti number or the count of the independent i-cycles in each graph after all cliques have been filled in or i-dimensional “holes” (A 1-cycle bounds a 2D area, a 2-cycle bounds a 3D volume, etc.).

All topological computations were performed using the Python gudhi 3.8.0 package [33].

RESULTS

The times of birth and death of one- and two-dimensional holes and connected components during the filtration process provide significant information about the graph structure and its possible functional roles. PDs correspond to two states of similar cognitive activity levels: the resting states with closed and open eyes form topologically and geometrically equal point clouds in a two-dimensional space, with the RTD distance between them equal to 9. By contrast, the distance between point clouds formed by PDs corresponding to different cognitive states drastically increases (for 25%) and equals 11 (Fig. 4).

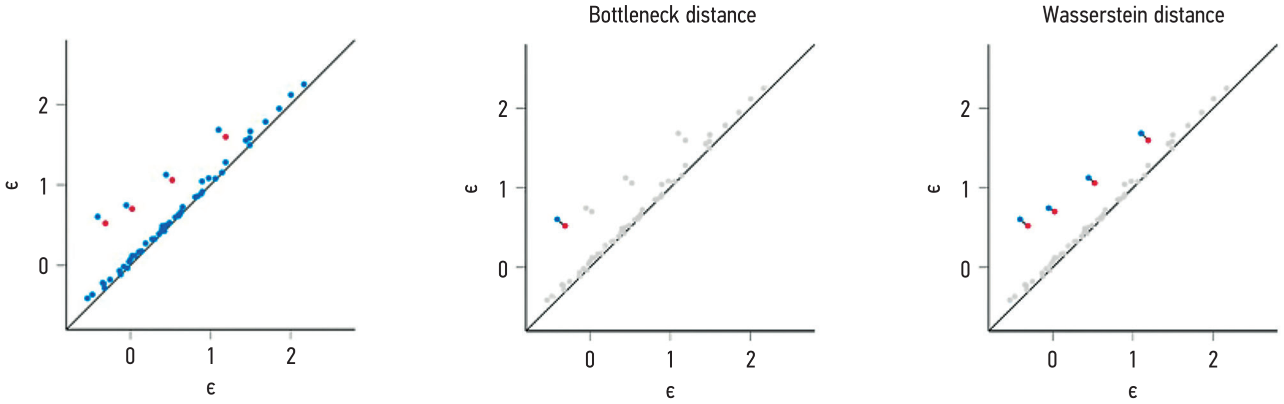

Fig. 3. The left picture represents the combination of two persistence diagrams: *D1* (*blue*) and *D2* (*red*), and the dots correspond to moments of the homology vector space basis elements death at specific filtration step ε. The two right pictures represent the difference between the information taken into account in Bottleneck and Wasserstein distances between diagrams.
Рис. 3. На рисунке слева представлена комбинация двух персистентных диаграмм (persistence diagrams): *D1* (*синим*) и D2 (*красным*), с точками, соответствующими моментам гибели базисных векторов пространства гомологий. На двух правых рисунках отображена разница между информацией, учтённой при расчёте расстояний бутылочного горлышка (Bottleneck) и Вассерштейна между диаграммами.

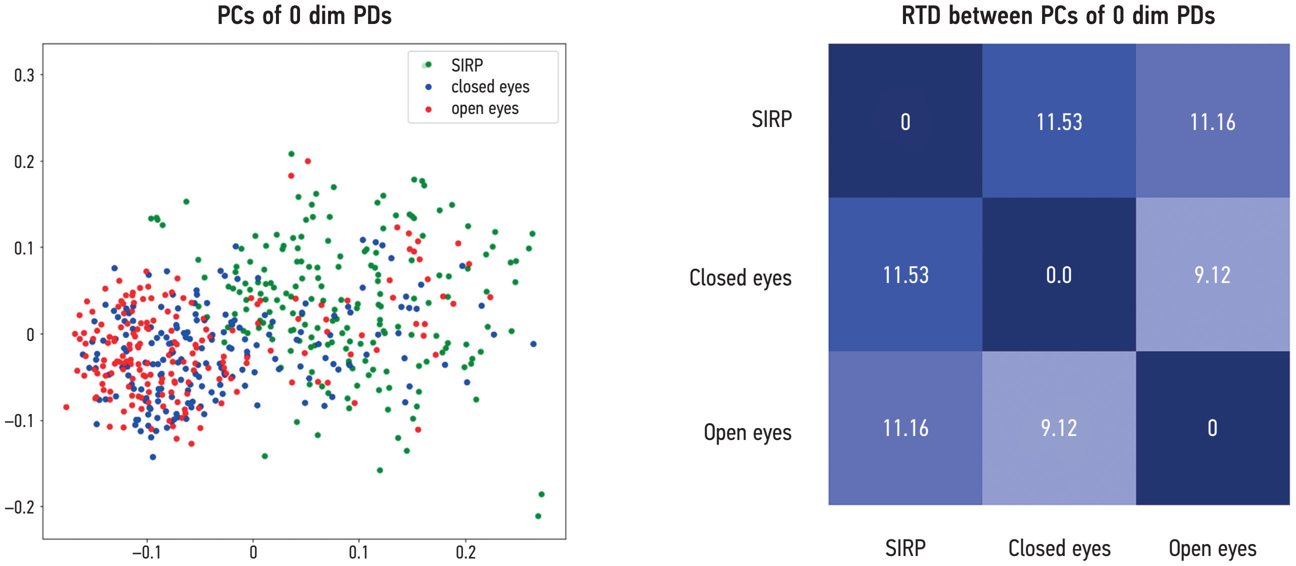

Fig. 4. The left picture shows the resulting point clouds for each of the three functional states (SIRP, closed eyes and open eyes) and clearly demonstrates the spatial discrepancy between persistence diagrams (points in the clouds), i.e., the cloud corresponding to the SIRP functional state is located far from the resting state clouds (closed and open eyes functional states). The right picture shows the matrix of pairwise distances (representation topology divergence metric [32]) between point clouds. Here: PCs, point clouds; PDs, persistence diagrams; RTD, representation topology divergence; SIRP, Sternberg item recognition paradigm.
Рис. 4. На рисунке слева показаны результирующие облака точек для каждого из трех функциональных состояний (SIRP, закрытые глаза и открытые глаза) и наглядно демонстрируется пространственное несоответствие между персистентными диаграммами (точки в облаках), т.е. облако, соответствующее функциональному состоянию SIRP, расположено далеко от облаков состояния покоя (с закрытыми и открытыми глазами). На правом рисунке показана матрица попарных расстояний (метрика Representation Topology Divergence [32]) между облаками точек. Здесь: PCs — облака точек; PDs — персистентные диаграммы; SIRP — тест Стернберга; RTD — representation topology divergence metric.

In addition, the speed of two- and three-dimensional hole deaths and appearance is significantly higher for functional networks during SIRP. The topological structure of connectomes during SIRP becomes equal to the resting-state networks only at the 20000th filtration step (Fig. 5). This supports the reconfiguration hypothesis, which states that functional networks of cognitively loaded tasks of solving reconfigure faster.

Conversely, little difference was observed between networks in the resting state with open or closed eyes.

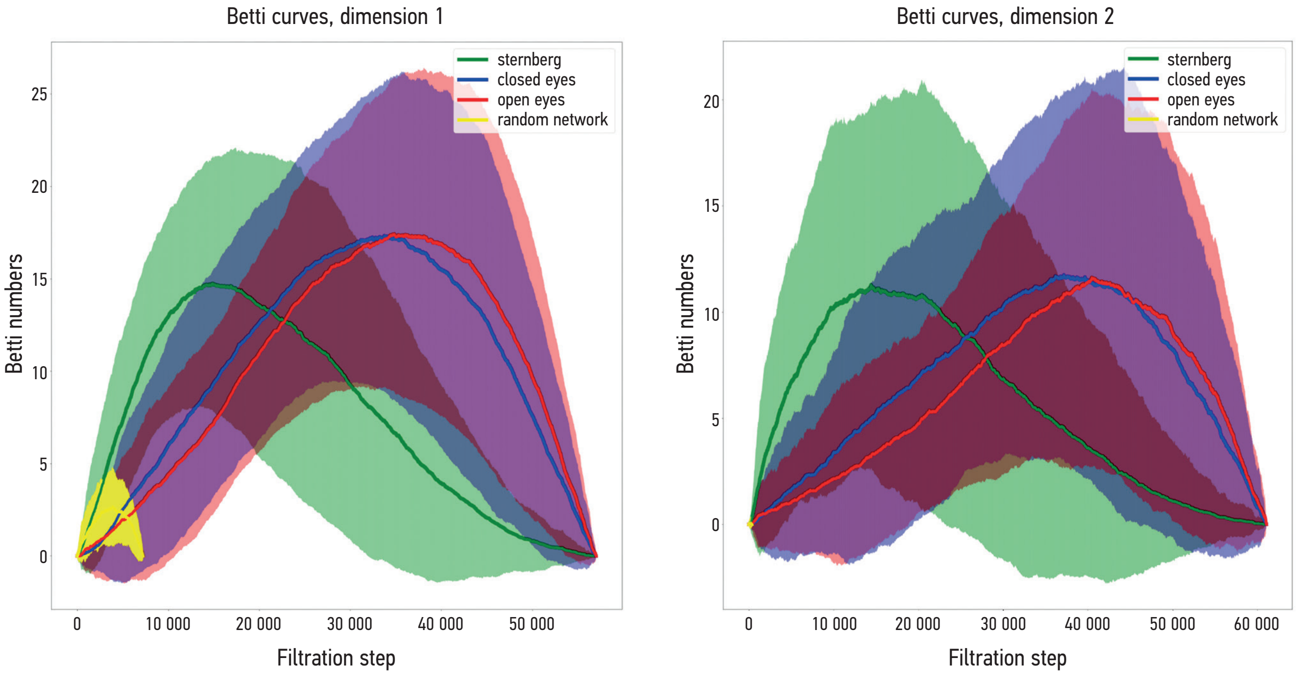

Fig. 5. Mean Betti curves for dimensions 1 and 2 averaged across all participants. The Y-axis corresponds to the Betti numbers of the specific dimension: 1 or 2. The X-axis corresponds to the filtration steps for an increasing sequence of parameter values $\{\varepsilon_i\}^N_1$, where N=60000. Here: sternberg, values for networks in Sternberg item recognition paradigm execution; closed eyes, values for networks in the resting state with closed eyes; open eyes, values for networks in the resting state with open eyes; random network, values for randomly generated networks of corresponding dimensions.

Рис. 5. Средние кривые Бетти для измерений 1 и 2, которые усреднены по всем участникам. Ось Y соответствует числам Бетти конкретного измерения: 1 или 2; ось X — шагам фильтрации для возрастающей последовательности значений параметров $\{\varepsilon_i\}^N_1$, где N=60000. Здесь: sternberg — значения для сетей при выполнении теста Стерберга; closed eyes — для сетей в состоянии покоя с закрытыми глазами; open eyes — для сетей в состоянии покоя с открытыми глазами; random network — для случайно сгенерированных сетей соответствующих размеров.

The general topological structure is quite similar, i.e., the times of the birth and death of the topological features do not differ during these states.

Real-world biological networks have significantly distinguished clique topologies compared with random networks [34]. If a correlation matrix is not random, it can uncover the “geometric” structure of data and indicate that neurons encode geometrically organized stimuli. To test the statistical significance of the observed topological properties, random distance matrices on the same number of vertices were generated as the number of vertices in the functional connectomes, and their Betti curves with similar dimensions were computed (See Fig. 5).

DISCUSSION

This study used a graph theory-driven approach to examine the complex causality patterns derived from EEG recordings. The aim of this study was to identify distinct topological properties of neural networks associated with the processing of information in WM and topological features of resting-state networks, captured in close vicinity of the moment of execution of the cognitive task. This was elicited during visual SIRP performed in healthy middle-aged adults.

Topological features, such as the time of birth of the zeroth, first, and second homology group generators, i.e., network-connected components, one- and two-dimensional holes, differ significantly depending on the current cognitive state. Furthermore, analysis has shown that functional connectivity in WM tasks demonstrates a higher speed of homology group generator appearance, providing evidence in favor of links between early phases of WM execution and increased global integration in functional networks. Moreover, because connector hubs are the nodes that highly participated in global network interconnections, we hypothesize that they contribute the most to the higher speed of birth and death of homology groups. Thus, the described topological properties can be linked with hub-based network configuration in the cognitive load.

These findings suggest that TDA, performed on EEG-derived functional connectivity, can represent the complexity of functional networks underlying cognitive functions, including WM, highlighting the peculiar properties of the topological features of brain networks in the resting state and selectivity to dynamics occurring during processing of memory items.

Networks in the resting state and cognitive load

Our data suggest that the functional networks of the human brain demonstrate a significantly distinct topology depending on the current level of cognitive load. Resting-state networks were constructed from data acquired when participants had their eyes closed or open. When a participant can visually inspect the surrounding space while not experiencing any cognitive load, brain activity changes and adapts in response to the need to support neural processes of visual perception. These changes express some whole-brain features, such as the suppression of alpha-band EEG activity, which is linked to preparatory visual attention [35]. From the perspective of complex network analysis, resting-state brain activity with open or closed eyes suggests differences in properties connected to specific cognitive ability networks. According to a previous study, the coordinated activity between the cingulo-opercular and right-frontoparietal networks is associated with visual processing, resulting in increased integration in visual perception [36].

On the contrary, topological analysis, performed in this study, showed a little difference between networks in the resting state with open or closed eyes. We speculate that the observed insensitivity of homology group generator death reflects a stronger linkage of given network characteristics to high-level information processing, which occurs during dedicated problem solving, but not background perception and processing.

Such results correlate with the predictions of the global workspace theory [37], according to which, when accessing the global workspace, the flow of information becomes an object of conscious processing and is available for conscious reporting and flexible behavior control. Moreover, entering the workspace enhances this flow relative to others, which are also inhibited. In many cognitive models, the concept of a workspace is associated with arbitrary attention and WM; therefore, the limits on the capacity of the workspace correspond to the limits usually set for focal attention or WM [38]. A dynamic model of workspace formation was proposed; accordingly, the community structure of locally synchronized modular subsystems for unconscious processing can be functionally rearranged by the launch of a globally synchronized system representing a consciously processed stimulus [39]. Such dynamic transitions from modular to global synchronization have been demonstrated in computational models, including those using data on the structure of anatomical networks of humans or model animals [40]. Thus, as observed in our study, the higher rapidity of birth of the zeroth and first homology group generators in WM task execution may reflect the abovementioned process of conscious processing of information in the workspace, which occurs alongside the suppression of other data flows.

Features of the network topology in working memory tasks

The human brain is a complex organ and can reorganize and adapt in response to environmental changes. Collected evidence suggests that ICNs are the functional basis of cognitive functions, with specific global states related to cognitive performance [41]. Our results support this hypothesis, showing faster local network integration during the processing of working tasks in contrast with lesser early functional network integration in resting states. The greater number of new connected components in the functional connectome in the early stages of WM task execution can be interpreted as a process of a faster establishment of high-degree hubs in functional networks. Thus, networks reconfigure faster to a topology with a more expressed, highly connected core of the “rich club”. Based on the asymmetrical distribution of the number of connected components over time with a shift to the left, we suggest that a greater number of new nodes are included in the “rich club”, moving from the status of being provincial hubs to being global hubs in the early stages of information processing in WM. Such features of network reconfiguration can indicate processes in the brain during which certain ICNs are included in the global functional network. The connection of topological changes with the phase of information processing in WM 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.

These findings correspond with those of recent network neuroscience studies, suggesting that a more globally integrated network with less specialized segregation may be effective in sustaining WM [42]. The content of WM is defined by the interaction between selective perceptual information processing (such as visual or auditory information) operated via selective attention and long-term memory representations that are in a state of “accessibility” and require persistent activity of specialized networks controlled by attentional processes [43]. Therefore, a whole-brain network with high global information transfer (integration) may better sustain an optimal interplay between locally specialized networks, as seen in the local organization of WM subnetworks.

CONCLUSION

This study used topological data analysis to analyze electroencephalographic recordings and identify the topological properties of neural networks involved in working memory processing. Sternberg item recognition paradigm was performed in healthy middle-aged adults. The study examined resting-state networks and connectivity in cognitive load to understand topological features specific to each state and the nature of network reconfiguration in the transition between states.

This study revealed a significant association between the topological characteristics of functional connectomes and the level of cognitive load undertaken by the participants. During working memory tasks, the analysis indicated a quicker emergence of homology group generators, suggesting a connection between the execution of working memory tasks and enhanced rapid integration of networks.

Overall, this study suggests that topological data analysis can represent the complexity of functional networks underlying cognitive functions, including working memory. This study highlights the unique properties of topological features of brain networks in the resting state and selectivity to dynamics during the processing of memory items.

ADDITIONAL INFORMATION

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Authors' contribution. I.M. Ernston — neurophysiological data acquisition and processing, visualization, collection and analysis of literary sources, writing and editing; A.A. Onuchin — neurophysiological data processing, visualization, preparation and writing of the text of the article; T.V. Adamovich — curation, neurophysiological data processing, editing. All authors confirm that their authorship meets the international ICMJE criteria (all authors have made a significant contribution to the development of the concept, research and preparation of the article, read and approved the final version before publication).

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Источник финансирования. Авторы заявляют об отсутствии внешнего финансирования при проведении исследования.

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Вклад авторов. И.М. Эрнстон — сбор и обработка электрофизиологических данных, визуализация данных, сбор и анализ литературных источников, написание текста и редактирование статьи; А.А. Онучин — обработка электрофизиологических данных, визуализация данных, написание текста и редактирование статьи; Т.В. Адамович — курация, обработка электрофизиологических данных, редактирование статьи. Все авторы подтверждают соответствие своего авторства международным критериям ICMJE (все авторы внесли существенный вклад в разработку концепции, проведение исследования и подготовку статьи, прочли и одобрили финальную версию перед публикацией).

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