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The increase in brain network modularity leads to improved memory performance in the volitional eyes-closed state

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Abstract

Previous research has shown that participants exhibit better memory performance when consciously closing eyes (EC) compared to keeping eyes open (EO). However, the underlying dynamical mechanism remains unclear. Here, we propose a reservoir computing (RC) algorithm based on EEG-derived functional connectivity of brain networks in resting state to simulate the brain's memory processes and reproduce the EC-related memory advantage. Our findings indicate that, compared to EO-based connectivity, the RC constructed from EC-based resting-state connectivity demonstrates superior memory performance. Further graph-theoretical analysis reveals that the EC networks exhibit stronger modularity and the modularity index are positively correlated with memory ability. Therefore, we conclude that the functional connectivity of whole brain underlies memory function and the broad reorganization of connectivity in the EC state leads to its memory advantage over the EO state.

Keywords: Volitional eyes closing, Memory capability, Reservoir computing, Modular brain network

Introduction

Conscious eye closure (EC) is a behavior unique to humans, which is rarely observed in other animals (Feng et al., 2021). When facing difficult tasks, participants often close their eyes to avoid unnecessary distractions, thereby achieving a better performance (Lavie, 2005; Clapp, Rubens, & Gazzaley, 2010; Perfect et al., 2008). Previous studies have confirmed that EC significantly enhances participants' memory abilities (Vredeveldt, Hitch, & Baddeley, 2011). For example, Mastroberardino and Vredeveldt (2014) found that child participants in the EC state showed more accurate recall of videos played earlier. In another well-designed eyewitness event test, the EC state raised the number of correctly reported details without compromising the accuracy of the testimony (Vredeveldt & Penrod, 2013). Furthermore, several studies have confirmed the advantages of EC in memory retrieval tasks (Glenberg, Schroeder, & Robertson, 1998; Vredeveldt, Baddeley, & Hitch, 2012; Perfect, Andrade, &

Eagan, 2011; Vredeveldt et al., 2011; Bastarrika-Iriarte & Caballero-Gaudes, 2019; Wagstaff et al., 2004).

There are two potential explanations for the memory advantage of eye closure: 1) The EC state avoids unnecessary cognitive load, thereby enhancing memory performance (Perfect et al., 2008, 2011). 2) Eye closure reduces visual interference, which aids in the visualization and memory performance of past events (Bastarrika-Iriarte & Caballero-Gaudes, 2019; Vredeveldt et al., 2011). With the widespread application of fMRI and graph theory methods, we can reconsider the origin of the EC advantage from the perspective of whole-brain functional connectivity reconstruction, testing and integrating the above two hypotheses at the network topology level. It is widely believed that eye closure alters the brain's information processing pattern, shifting from an "external sensory" state to an "internal sensory" state, because of the functional connectivity reorganization of whole brain (Marx et al., 2003, 2004). Activity changes associated with EC and EO states have been observed in several resting-state networks, including the default mode network (Yan et al., 2009), visual network (Patriat et al., 2013), and dorsal attention network (Nakano, Kato, Morito, Itoi, & Kitazawa, 2013). At the whole-brain level, the EC state exhibits higher global efficiency and lower local efficiency, and cross-modal functional connectivity (FC) changes as eye-opening (Xu et al., 2014). Zhang et al.'s study indicates that during EC, modular integration significantly increases, including a decrease in modularity index, an increase in participation coefficient, a reduction in provincial hubs and an increase in connector hubs (Zhang et al., 2024). Considering that FC is an intuitive reflection of the brain's functional dynamic transitions, we believe that the memory advantage in the EC state must be closely related to changes in FC. However, determining the potential relationship between memory ability and FC remains a significant challenge. The fundamental reason is that

it is difficult to change the participant's functional connectivity according to our predetermined intentions without causing other effects. Therefore, experimental studies involving human participants can generally perform correlation analysis only, rather than causal inference.

A potential solution is to simulate brain memory processes based on functional connectivity of brain networks with an appropriate mathematical model. Thus the relationship between network structures and memory capability (MC) is obtained. To achieve the target, we introduce reservoir computing (RC) to quantify memory ability. The computational framework of RC was independently proposed by Bertschinger and Natschl ger (2004), and Jaeger (2001), corresponding to Liquid State Machines and Echo State Networks, respectively. The network consists of an input layer, a reservoir, and an output layer. This model has been widely used in natural language processing (Tong, Bickett, Christiansen, & Cottrell, 2007), spatial navigation (Antonelo & Schrauwen, 2014), and working memory simulation (Zeng, Huang, Jiang, & Yu, 2019) and so on.

Model

Here, we present a memory task based on reservoir computing, which quantitatively compares the MC of participants' resting-state functional connectivity in the EC and EO states. The reservoir computing algorithm consists of three components which are the input layer, the intermediate layer (reservoir) and the output module. The input layer is responsible for feeding random signals into specific nodes of the reservoir. Through the nonlinear dynamics of interconnected nodes in the reservoir, the memory signals are mapped into a high-dimensional space. Finally, the output module generates the output by decoding from this high-dimensional space, restoring the input signal. The memory capacity is quantitatively represented by the Pearson correlation coefficient between the input and output signals. Unlike traditional reservoir computing, which uses sparse and normally distributed connection weights in the intermediate layer, we use the resting-state functional connectivity matrix ($\mathbf{R}$) constructed from resting-state EEG data with 61 channels of valid signals as the connection matrix for the intermediate layer. The EEG data preprocessing is detailed in the Materials and Methods section.

The model diagram of RC is constructed in Figure 1 to help readers understand the RC framework. We randomly generate 10,000 data points as input signals. To eliminate the effect of initial transients, we select 4,000 data points within the range from 4001 to 8000 as the memory target, which are inputted into the receiving nodes of the intermediate layer through the input matrix $\mathbf{W}_{in}$. Specifically, the input connection weights for the receiving node are set to 1, and the remaining weights are set to 0. The dynamics of the intermediate layer nodes are determined by the following equation.

$$x(t+1) = \tanh(\mathbf{W}_{in}u(t+1) + \mathbf{R}x(t)), \quad (1)$$

where $x(t)$ represents the dynamic state of a node at time t ,

and the connectivity between nodes are determined by the correlation coefficient matrix $\mathbf{R}$ constructed from resting-state EEG data. For an $n \times n$ matrix $\mathbf{R}$, $\lambda_1, \lambda_2, \dots, \lambda_n$ are its eigenvalues. The spectral radius (SR) of $\mathbf{R}$ is defined as follows.

$$SR = \max_{1 \leq i \leq n} (|\lambda_i|), \quad (2)$$

Previous studies have shown that the SR of the intermediate layer's connectivity matrix affects the system's memory performance. When the spectral radius of the matrix approaches 1, the system is in a critical state, and memory performance is optimal (Sompolinsky, Crisanti, & Sommers, 1988; Su  rez, Richards, Lajoie, & Misic, 2021). To regulate the system's performance, we modify Equation (1) to the following form.

$$x(t+1) = \tanh(\mathbf{W}_{in}u(t+1) + \frac{SR}{SR_0}\mathbf{R}x(t)), \quad (3)$$

where SR_0 is the spectral radius of the connectivity matrix $\mathbf{R}$. After a delay time τ , the states of all the nodes in the intermediate layer are output through the output matrix $\mathbf{W}_{out}$, and the output signal y is decoded as follows.

$$y = \mathbf{W}_{out}\mathbf{X}, \quad (4)$$

where $\mathbf{X}$ is the internal state of the intermediate layer with the delay time τ for an input signal. More specifically, $\mathbf{X}(t + \tau), \mathbf{X}(t + \tau + dt)$ corresponds to $[u(t), u(t + dt)]$. The output weight matrix $\mathbf{W}_{out}$ is obtained by linear regression.

$$\mathbf{W}_{out} = (\mathbf{X}^T\mathbf{X})^{-1}\mathbf{X}^T\mathbf{u}, \quad (5)$$

The magnitude of the delay time is related to the difficulty of the task. Here, we set $\tau = 20$, corresponding to the task at a level of medium difficulty. Since an input signal is added, the dynamic states of the intermediate layer nodes are read after 20 iteration steps. Finally, the memory capacity (MC) of the system is measured by the Pearson correlation coefficient $\rho(u, y)$ between the output signal y and the input signal u :

$$MC = \rho(u, y) = \frac{\sum_{t=1}^T (u(t) - \bar{u})(y(t + \tau) - \bar{y})}{\sqrt{\sum_{t=1}^T (u(t) - \bar{u})^2} \sqrt{\sum_{t=1}^T (y(t + \tau) - \bar{y})^2}}, \quad (6)$$

where $\bar{u}$ and $\bar{y}$ are the average values of u and y .

Experimental Hypotheses

Previous research related to RC based on structural brain networks has revealed a preliminary relationship between brain network structures and task performance. Su  rez et al. established an RC framework based on the structural network of the human brain. By comparing its performance in encoding and decoding tasks with that of a random network, they discovered that the brain's structural network is significantly superior to random networks, particularly when considering wiring costs (Su  rez et al., 2021). Similarly, Damicelli et al.

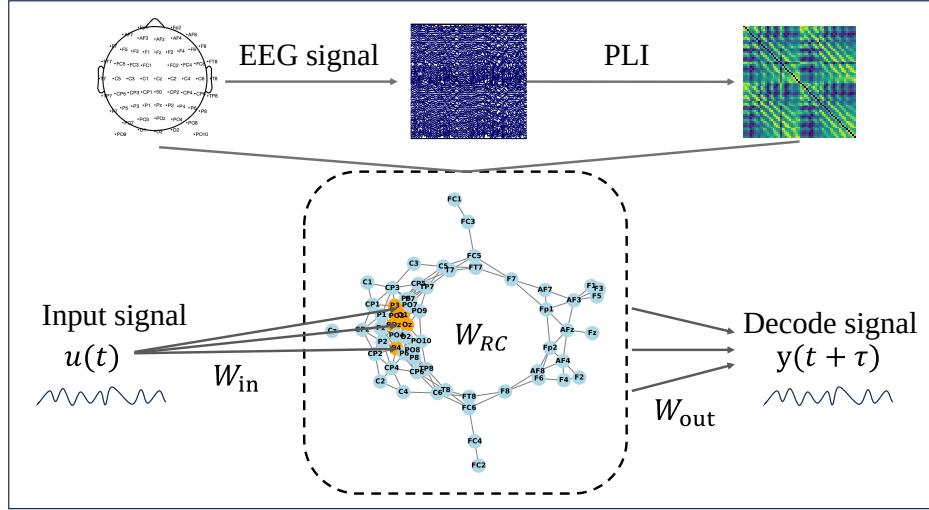


Figure 1: Schematic diagram of a memory task based on the functional connectivity from resting-state EEG. The yellow nodes represent receiving nodes, which are the six nodes with the highest degree in the resting-state functional connectivity. The dynamic states of all nodes in the intermediate layer are output through the output matrix after a delay time τ , resulting in the decoded signal. Finally, the Pearson correlation coefficient between the output signal y and the input signal u is calculated to characterize MC.

conducted similar studies on various biological neural networks, which also supported the superiority of brain networks (Damicelli, Hilgetag, & Goulas, 2022). The aforementioned two works only involved fixed brain structural networks. Although the results demonstrated the superiority of brain networks, it is unclear that how the dynamical changes in the structure of a brain network enhance its efficiency. To elucidate how changes in FC affect MC, we use the EEG-based resting state functional connectivity matrices of the subjects in the EO and EC states as the connection structures of the intermediate layer in RC to simulate memory tasks. By analysing the differences on MC of the two states, we try to establish a causal relationship between the altered FC and the MC enhancement in EC state.

We propose the following two hypotheses, 1) the brain's functional network serves as the dynamic foundation for memory functions, 2) the enhancement of memory performance in subjects in the EC state is caused by the wide reorganization of the functional networks. To test these hypotheses, we design a memory task based on the model presented in Section **Model**. By comparing memory performance based on resting-state functional connectivity in the EC state with that of the EO state, we aim to determine whether the model can replicate the memory advantages observed in the EC state. Subsequently, we calculate graph-theoretical properties of the functional networks in both states and obtain the correlation between graph-theoretical metrics and memory performance. The causal relationship between changes in the topology of functional networks and improvements in memory performance is therefore revealed.

Materials and Methods

Participants

All data used in this study are obtained from the publicly available dataset (<https://fcon.1000.projects.nitrc.org/indi/retro/MPILEMON.html>), which includes preprocessed resting-state EEG data from young participants. To ensure data stability and avoid potential impacts of interpolation on network structures, we excluded all recordings with bad channels. The final sample comprise 39 participants (27 males), aged 20 – 40 years. For additional participant information and preprocessing details, please refer to (Babayan et al., 2019).

EEG data acquisition and preprocessing

A 16-minute resting-state EEG recording was obtained using a BrainAmp MR plus amplifier inside an electromagnetically shielded, sound-attenuated booth. Sixty-two active ActiCAP electrodes (61 scalp electrodes plus one for vertical electrooculogram below the right eye; Brain Products GmbH, Gilching, Germany) were positioned in accordance with the extended 10 – 20 system (also known as the 10 – 10 montage), with FCz as the reference and a sternum-based ground. Electrode impedances remained below 5 k Ω , and the amplifier resolution was set to 0.1 μ V. The data were recorded with a 0.015 – 1000 Hz bandpass and digitized at 2500 Hz. The recording session comprised 16 one-minute segments, alternating between EC and EO conditions (eight each), beginning with an EC block. Instructions and block transitions were managed via Presentation software (version 16.5, Neurobehavioral Systems Inc., Berkeley, CA, USA). Participants were asked to remain awake and, during EO periods, to fix their gaze on a black cross against a white background.

For the remaining participants, raw data were downsampled from 2500 Hz to 250 Hz, bandpass filtered between 1 and 45 Hz using an 8th-order Butterworth filter, and separated by condition (EO vs. EC). Channels showing frequent abrupt shifts or poor signal quality were discarded based on visual review. Time segments with large peak-to-peak deflections or high-frequency bursts were also removed, while intervals containing blinks and eye movements were retained at this stage. Subsequent processing employed EEGLAB (v14.1.1b) for MATLAB. Principal component analysis (PCA) was carried out to retain enough components to account for 95% of the total variance (commonly > 30 principal components). Independent component analysis (ICA) was then applied using the Infomax (runica) algorithm to identify and remove components reflecting ocular and cardiac artifacts. The remaining components (mean: 19.7 for EO, 21.4 for EC) were back-projected to electrode space for downstream analyses.

Note that the data used in this study are resting-state EEG data already preprocessed by the authors of the publicly available dataset. The above text is a restatement of the data collection and preprocessing procedures, more detailed information can be found in (Babayan et al., 2019).

After obtaining the 61-channel resting-state EEG data, we calculate the Phase Locking Value (PLV) among the 61 channels, resulting in a 61×61 resting-state connectivity matrix. Finally, we rank the connection edges based on their weights, retaining the top 10% of the connection strength while discarding the rest. Thus a binarized connectivity matrix with 0 or 1 is obtained, in which the connection weight with 1 indicates a connection between two nodes, and 0 indicates an absence of the connection. We then use this matrix as the adjacency matrix for the intermediate layer and obtain the MC of 39 participants under both EC and EO states with the method described in Section **Model**.

Results

Memory capability

Previous studies have demonstrated that the spectral radius of the connectivity matrix in the intermediate layer significantly impacts the system's MC (Suárez et al., 2021; Damicelli et al., 2022). To identify optimal MC, we calculate the system's MC under different SR . The results, shown in Figure 2, reveal that as SR increases, MC in both EC and EO states initially rises, reaching a maximum near $SR = 1$, and subsequently declines. When SR approaches 1, the system transits to a critical state between order and chaos, as previously reported (Sompolinsky et al., 1988). Our RC-based method, constructed from resting-state connectivity, aligns well with these findings.

We then examine the MC differences between EC and EO states. As shown in Figure 2, the MC in both states exhibits a consistent trend, peaking near $SR = 1$ and declining thereafter. However, as SR increases, the advantage of the EC state becomes more pronounced, reaching its maximum near the critical state, as illustrated in Figure 3.

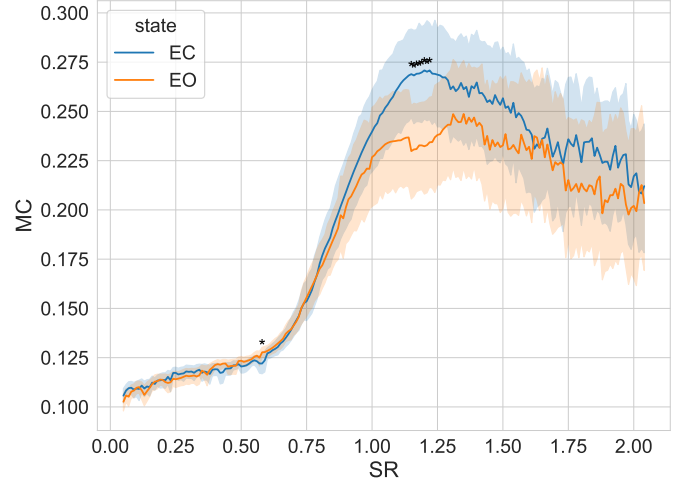


Figure 2: The curves of MC with different SR . An asterisk (*) indicates that the t-test p-value is less than 0.05.

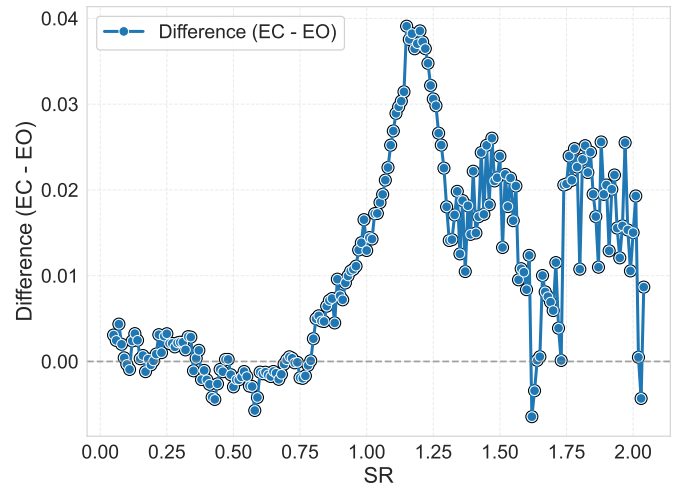


Figure 3: The MC difference between EC and EO states under different SR .

Notably, in our experimental results, the optimal MC does not strictly occur at $SR = 1$. The reason is that we employ a binary critical matrix composed of 0s and 1s, whereas the prior theoretical derivation is based on an intermediate-layer connectivity matrix with strictly normally distributed weights (Sompolinsky et al., 1988). The difference results in a slight deviation from the theoretical predictions. But in summary, these results collectively validate our two hypotheses. First, the functional connectivity of whole brain serves as the foundation for the brain's memory capacity, and second, the memory advantage of the EC state over the EO state can be effectively reproduced using an RC algorithm based on functional brain connectivity.

Graph theory analysis

Because our model remains identical in all aspects except for the connection structures of the intermediate layer in RC, we can conclude that compared to EO state, the structural reorganization of whole brain networks in EC condition underlies its advantage in MC. To pinpoint which kinds of structural changes lead to the increase in MC, we calculate graph-theoretic metrics, such as characteristic path length, clustering coefficient, betweenness centrality and the modularity index (Q value) for the EC and EO functional connectivity networks. The Q value of a network is defined as follows.

$$Q = \sum_{m \in M} \left[e_{mm} - \left(\sum_{m' \in M} e_{mm'} \right)^2 \right], \quad (7)$$

where e_{mm} represents the proportion of links between nodes within module m , and $e_{mm'}$ represents the proportion of links between nodes located in module m and module m' respectively. A higher Q value indicates a greater degree of network modularity.

We observe a significant difference on modularity between the EC and EO states. Specifically, we apply the Louvain algorithm to partition each connectivity matrix into communities, and then calculate the Q value based on these partitions. Results reveal that the Q value of EC is significantly higher than that of EO (see Figure 4), indicating that the brain in the EC state exhibits more distinct functional subdivisions and enhanced local integration, thereby strengthening local information processing. In addition, we calculated other metrics, including global efficiency, clustering coefficient, and characteristic path length. However, no significant differences were observed between the EC and EO states.

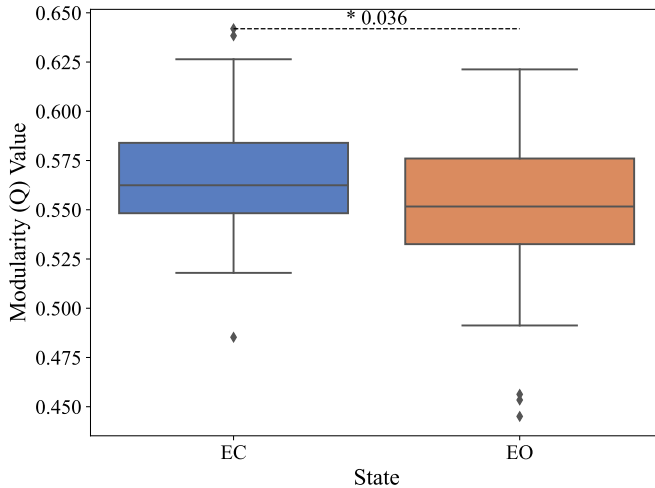


Figure 4: Differences in Q values of resting-state connectivity between EC and EO states.

To validate this conclusion, we further examine the correlation between MC and Q value. In brief, we first calculate the Q value for each resting state connectivity matrix, then

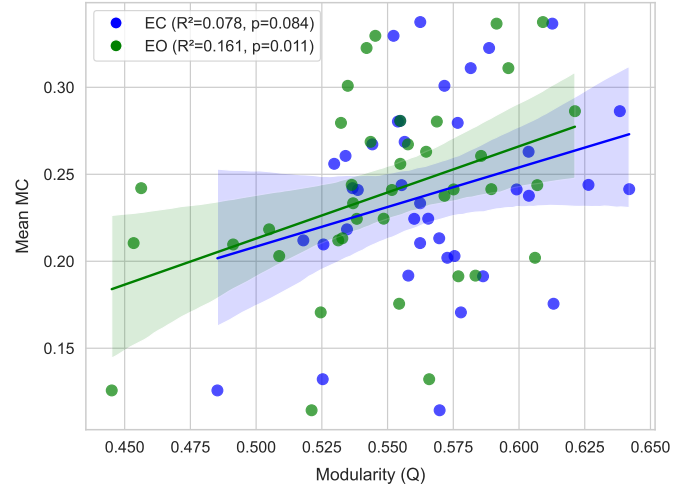


Figure 5: Correlation between Q values and the mean MC in the SR range of 0.9 – 1.2.

derive the mean MC (SR from 0.9 – 1.2) for each matrix, defined as the maximum MC within an SR range of 0 – 2. Next, we perform a linear regression analysis of MC and Q value, and the results are presented in Figure 5. We find a positive correlation between the mean MC and Q value in both EC and EO states. Compared to the EO state, the EC state have a higher Q value and a corresponding increase in the mean MC. Given that no other differences exist aside from the intermediate layer structures, we infer that the increase in modularity is the key factor driving the MC enhancement in the EC state.

Discussion

In this work, we propose two fundamental assumptions: 1) Functional connectivity across the whole brain provides the basis for MC. 2) wide reorganization of the functional brain networks underlies the MC advantage in the EC state. To test these assumptions, we employ EEG-based resting-state connectivity to perform RC simulations of a memory task and successfully prove the MC advantage observed in the EC state. We then calculate various graph-theoretic measures of resting-state connectivity in the EC and EO conditions and find that the modularity of the EC network is significantly enhanced. Further analyses reveal that MC is positively correlated with the modularity index, suggesting that the increase in modularity is a key factor driving the heightened MC in the EC state. Taken together, these findings validate our two basic assumptions.

The relationship between the level of modularity and participants' memory abilities has been widely explored. The study of Stevens, Tappon, Garg, and Fair (2012) showed that the modularity level of resting-state functional brain networks can predict participants' working memory capacity, higher modularity leads to a more optimized organizational structure, thereby enhancing working memory capacity. For older adults, one study reported that individuals with more segre-

gated sub-networks in the brain (i.e., more modular networks) at baseline exhibited greater training improvements in synthesizing complex information (Gallen et al., 2016). In addition, both brain modularity and memory performance decline in parallel with advancing age (Onoda & Yamaguchi, 2013). These findings collectively demonstrate a positive correlation between MC and modularity. Our results aligns with above experiment findings regarding the origin of the MC advantage in the EC state.

However, some other studies have reported contradictory results. For instance, Stanley et al. found that the difference on brain network modularity levels between the 2-back and 1-back tasks is negatively correlated with the decline in task performance of the participants (Stanley, Dagenbach, Lyday, Burdette, & Laurienti, 2014). Additionally, Gamboa et al. (2014) demonstrated a negative correlation between resting-state network modularity and memory task performance among patients with multiple sclerosis. Explaining these seemingly inconsistent findings remains a major challenge.

Here, we propose a potential explanation. The study of Rodriguez, Izquierdo, and Ahn (2019) has shown that there exists an optimal level of modularity for memory performance in RC, striking a balance between local cohesion and global connectivity such that optimally modular networks can retain information for longer durations. We therefore posit that in healthy individuals, the level of modularity is near this optimal point. Factors such as brain development or targeted cognitive training may shift the brain's modularity closer to the optimum, whereas pathological conditions or brain aging drive it away from this ideal point. The differential shifts in modularity may explain why the relationship between modularity and MC varies across different populations. Improving our model and validating above hypothesis with more extensive multimodal data are the goals of our future research.

Although our reservoir computing model is capable of replicating the memory advantages observed in the EC state, it inevitably exhibits certain limitations similar to those found in other computational models. While random signals are employed as the standard input for RC, they do not constitute a detailed simulation of the brain's memory processes. Consequently, further modifications to the model are required to simulate the brain's memory processes with as much detail as possible.

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