Distinct roles of brain network flexibility in motor learning across age

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Abstract

Motor learning is a lifelong process, from infancy through old age. Acquiring new motor actions through repetitive practice requires adjusting motor output in response to sensory input and integrating them to facilitate learning. For this to occur, the central nervous system must flexibly predict and adapt to the dynamic interplay between sensory inputs and motor outputs. Although overall brain function changes with age, it remains unclear how the flexible brain network evolves and influences motor learning ability with aging. To address these open questions, we designed a visuomotor learning task involving both younger and older adults and quantitatively assessed brain network flexibility, leveraging multichannel electroencephalography (EEG) in humans. Here, we found age-group differences in motor learning properties, brain network flexibility, and their neural relationships. In younger adults, learning aftereffects were associated with brain network flexibility during the preparatory period of the task. However, this association was not observed in older adults. Together, our findings suggest that brain network flexibility during the preparatory period, rather than motor execution, was critical for acquiring and maintaining new motor actions in younger adults, but that this coupling was attenuated with aging.

Introduction

More recently, many people live well beyond the age of 60 and maintain good health. In our current reality, various types of motor and cognitive learning occur throughout a lifetime, spanning from early infancy to old age. Notably, learning new motor skills, such as playing musical instruments, remains feasible even in older adulthood. The definition of skill emphasizes reducing variability in action outcomes, and this variability progressively decreases throughout the learning process. However, the relationship between motor learning and movement variability remains a subject of debate at both the behavioral and neural levels. At the behavioral level, movement variability (i.e., exploratory behavior) is thought to play a pivotal role in facilitating motor learning (Ranganathan and Newell, 2010; Uehara et al., 2019; Ranganathan et al., 2020), as effectively promoting motor exploration leads to better outcomes (Wu et al., 2014). Nevertheless, conclusive evidence regarding the neurological rationale behind remains elusive. Our scalp electroencephalogram (EEG) study demonstrated that overall brain network flexibility reflects key neural processes involved in skill formation and predicts musical performance skill in proficient brass players. Notably, brain network flexibility primarily contributed to feedback control, rather than feedforward control, during skilled musical performance (Uehara et al., 2023). Together, this evidence suggests that brain network flexibility may underlie the sensorimotor integration and the control of the consolidated motor function. In this context, brain network flexibility, reflecting moment-to-moment reconfiguration of large-scale brain networks, emerges as a candidate neural mechanism supporting learning acquisition. This study utilized the brain network flexibility, which is defined as a quantitative index of node flexibility, capturing the frequency with which nodes change their community assignments over a given period. Here, nodes represent brain regions, and a module represents a group of brain regions that are more strongly interconnected with each other. While this mathematical framework initially seemed disconnected from biological mechanisms, growing empirical evidence suggests that it reliably

accounts for fundamental properties of brain function (Braun et al., 2015; Betzel et al., 2017; Reddy et al., 2018; Monteiro et al., 2019; Uehara et al., 2023). Notably, N-methyl-D-aspartate receptors, which play a main role in neural inhibition, have the potential to modulate the degree of brain network flexibility (Braun et al., 2016). Similarly, dopamine D1- and D2-receptor function also influences state transitions in brain networks (Braun et al., 2021). This implies that synaptic transmitter activity significantly impacts brain network flexibility. Because these neuromodulators and synaptic processes are themselves altered across the lifespan, brain network flexibility would also be expected to change with aging. With advancing age, elderly people undergo widespread changes in neuromuscular function even during healthy aging, which can disrupt the interplay between sensory input, motor output, cognition, and their neural integrations (Goble et al., 2009; Coxon et al., 2014; Serbruyns et al., 2015; Frolov et al., 2020; Zapparoli et al., 2022; Goelman et al., 2023). These age-related changes in sensorimotor function result in a gradual decline in sensorimotor function and learning ability (Vercillo et al., 2017; Hehl et al., 2020; Pauelsen et al., 2020). This decline is associated with reductions in white and gray matter volumes (Courchesne et al., 2000; Good et al., 2001; Jernigan et al., 2001) and alterations in white matter microstructural organization (Cox et al., 2016; Beck et al., 2021), changes in brain activity, and network dynamics (Garrett et al., 2013; Monteiro et al., 2019; Frolov et al., 2020; Goelman et al., 2023), and declines in dopaminergic and gamma-aminobutyric acid neurotransmission (Kaasinen and Rinne, 2002; Guitart-Masip et al., 2016; Hermans et al., 2018) even in healthy aging. These neural factors may individually or collectively disrupt the coordinated operation of brain networks across multiple levels, ultimately leading to behavioral changes (Marstaller et al., 2015; Shafiei et al., 2019; Yoshimura et al., 2020). Additionally, a human functional magnetic resonance imaging (fMRI) study has already demonstrated that the strength of brain network flexibility was reduced in older adults, and the flexibility of the brain area in the prefrontal cortex was associated with lower error during bimanual motor coordination (Monteiro et al., 2019). These findings allow

us to raise an open question whether age-group changes in brain network flexibility could hinder motor learning in the elderly. The majority of existing studies have focused on age-group–specific alterations in brain activity or connectivity and their relationship to behavioral performance. However, age-group differences in brain network flexibility and motor learning ability remain underexplored, and the neural mechanisms by which brain network flexibility supports adaptation through motor learning are still unclear.

Here, we aimed to investigate whether age-group changes in brain network flexibility affect motor learning ability in both young adults (YA) and older adults (OA). We utilized multichannel scalp EEG recordings while participants from both YA and OA groups engaged in learning an error-based visuomotor adaptation task. In the present study, we hypothesized that entire brain network flexibility would increase with aging due to excessive neural noise (Garrett et al., 2010) and compensatory reorganization (Cabeza, 2002), and that this increased flexibility becomes functionally ineffective in supporting motor learning in older adults. Additionally, based on previous works (Deco and Kringelbach, 2016; Sase and Kitajo, 2021), we posit that brain network flexibility reflects not just localized cortical activity, such as specific motor-related regions, but the broader, system-level organization of functional brain networks. Likewise, motor learning engages a distributed network of brain regions rather than being confined to a single cortical area. Specifically, the frontal area is implicated in planning and attentional processes, the cerebellum and basal ganglia are involved in prediction and motor adjustment, and the sensory cortices play a critical role in integrating sensory feedback (Cavanagh et al., 2010; Krakauer and Mazzoni, 2011; van de Vijver et al., 2011; Roth and Ding, 2024; Fukuda and Uehara, 2025). Focusing on whole-brain dynamics in terms of network flexibility is therefore essential for elucidating neural mechanisms of motor learning ability in the context of aging. Moreover, previous EEG studies suggest that the suppression of trial-by-trial neural variability, as indexed by event-related potentials (ERPs) in the present study, is closely associated with enhanced perceptual abilities (Arazi et al., 2017; Daniel and

Dinstein, 2021). Given this, the reduction in brain network flexibility during the motor learning process, relative to the early phase of learning, may help stabilize brain activity. We therefore hypothesized that these distinctive changes are modulated by aging and, in turn, impact motor learning abilities.

Materials and Methods

In this study, we selected an error-based visuomotor adaptation task to assess individual motor learning abilities. To estimate the number of participants required to reliably assess behavioral motor learning effects, we conducted an a priori power analysis using the G*Power program (Erdfelder et al., 2009) with the effect size set at 0.49 based on our prior data collection from seven healthy right-handed young individuals (26.4 ± 5.5 yrs, range: 22 -35 yrs, two females). Using the same experimental protocol described later (see *Experimental task and protocols*), the effect size was determined assuming changes in motor performance (i.e., the degree of the deviation of cursor position) between the early, middle, and late phases of motor learning. The statistical significance level was set at $p < 0.05$ (two-tailed) for a one-way repeated measures analysis of variance (ANOVA) with a within-subject factor (motor learning phase). Despite the sample size calculation being conducted only for a younger group, this a priori power analysis estimation showed that at least 25 participants were required for one group, and effect sizes were reported for each statistic to confirm the robustness of the results. Based on this procedure, fifty-four healthy participants were recruited and divided into two groups, each consisting of 27 participants, The groups were categorized as younger-aged (YA) (27.6 ± 5.8 yrs, range: 20 - 38 yrs, 13 females) and older-aged (OA) (66.8 ± 7.4 yrs, range: 58 - 80 years old, 12 females). All participants were naïve concerning our visuomotor learning task, had a normal or corrected-to-normal vision, no history of musculoskeletal or neurological disorders, and were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Before data collection, all participants in

the OA group underwent a Mini-Mental State Examination (MMSE) with a cutoff score of 25 points, as scores above 25 points indicate intact cognition (Folstein et al., 1975). All participants in the OA group scored above 25 points (29.1 ± 1.2 points), leading to older adults having normal cognitive functions, including orientation, memory, attention, language, and visuospatial skills. However, four out of 27 participants from each group were excluded from the final data analyses due to the failure of the motor performance or electrical noise in the EEG data that was difficult to remove. This paper therefore reports data from 23 participants in each of the groups. This experimental protocol was approved by the local ethics committee of the National Institute for Physiological Sciences in accordance with the guidelines established in the Declaration of Helsinki. Before data collection, written informed consent was obtained from all participants.

Experimental task and protocols

Experimental protocol, trial structure, and apparatus are illustrated in Figure 1. The electromagnetically shielded experimental room used in this study was completely darkened to minimize the availability of any visual information that was not projected on a PC monitor. Participants were seated 120 cm in front of a 24.5-inch (1920 x 1080 pixels resolution) computer display comfortably positioned on a chair with the right forearm supported by an armrest and a chin resting comfortably on a chin rest to ensure a consistent position throughout the experimental session.

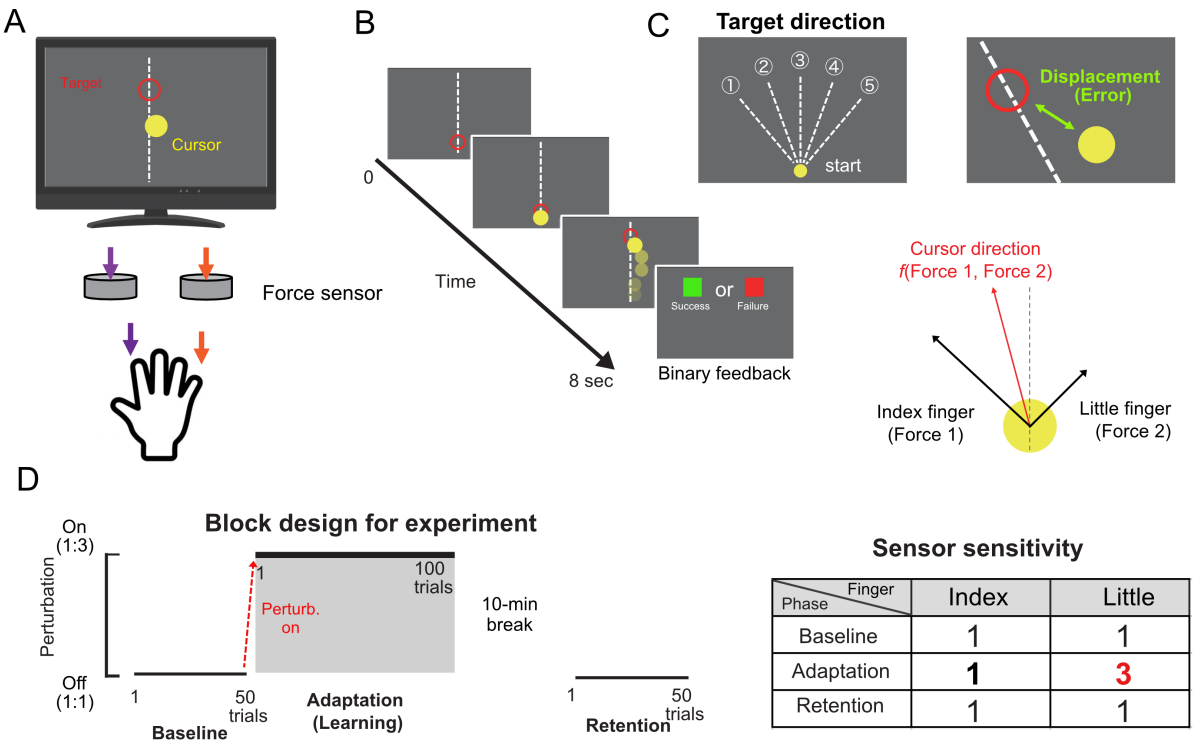
Prior to all data collection, participants underwent two sets of resting-state EEG recordings, involving 3-minute maintenance of the resting state while keeping their eyes open and closed, respectively, without focusing on any thoughts. During the eyes-open condition, participants were instructed to see the fixation cross placed at the center of the monitor. Following this, participants performed three times of maximal voluntary contraction (MVC) in the right index and little fingers, respectively. The maximum force was defined as an MVC

value and used to determine cursor control during the task.

On each trial, the target moved straight ahead at a constant speed of 10.8 cm/s in one of five directions (10, 11, 12, 1, or 2 o'clock) in a randomized order within each session. Participants were instructed to track a moving target on the screen by controlling the cursor as accurately as possible. Our experimental system allowed participants to freely control cursor speed and direction by pressing two force-torque transducers (USL06-H5, Tec Gihan, Co. Ltd., Japan) using their right index and little fingertips (Figure 1A). Our task design was inspired by O'Sullivan et al. (O'Sullivan et al., 2009), who demonstrated that the distribution of coordinated force made by the index and little fingers is greater when heterogeneous effectors (e.g., index and little fingers) are used together than when homonymous combinations are used. This finding implies that the nervous system must adaptively coordinate the muscles by integrating both effort and variability. By employing a non-habitual effector like the little finger, we investigated how the brain flexibly learns force mapping in unfamiliar coordination contexts. Force signals were amplified via an amplifier device (GDA-06B, Tec Gihan, Co., Ltd., Japan) and then stored on a computer via a NI-DAQ device (USB-6002, National Instruments, United States) at a sampling frequency of 1 kHz with analog-to-digital conversion. The index finger controls leftward cursor movement, while the little finger is responsible for rightward cursor movement. Therefore, the cursor direction was determined by the vector component calculated from the force applied by the index and little fingers. Cursor velocity was also controlled by varying the pressure applied to the force-torque transducers.

Visual cues, cursor control, cursor and target positions on the screen, and trigger signals sent to the EEG amplifier were managed by a dedicated software package (Graphical Design Lab, Japan), implemented in National Instruments LabVIEW software (version 2019, National Instruments, United States).

For the experimental protocol, participants were asked to learn the force mapping in their right index and little fingers through an error-based visuomotor adaptation task. The task



Phase \ Finger	Index	Little
Baseline	1	1
Adaptation	**1**	**3**
Retention	1	1

Figure 1: Experimental setup and trial structure. **A.** Participants were instructed to control a yellow cursor by pressing force transducers with their right index and little fingertips. **B.** Upon the ready cue (when the red open circle appeared), the yellow cursor was displayed on a monitor as the Go cue. After receiving the Go cue, participants began tracking the yellow target to keep the red cursor on the target throughout the trial. **C.** The cursor direction controlled by a participant was determined using a composite vector related to the force exerted in the z-direction output from the index and little fingertips. At the end of each trial, they received binary feedback on their performance, with green or red squares indicating success or failure, respectively. The two-dimensional space distance (i.e., horizontal and vertical) between the moving target and the cursor was used as an error index. We employed an error-based visuomotor adaptation task with five different target directions (10, 11, 12, 1, or 2 o'clock direction). **D.** In the first 50 trials, participants controlled the cursor with a force sensor sensitivity ratio of 1:1 for the index and little fingers during the baseline session. In the next 100 trials, which corresponded to the adaptation session, the force sensor sensitivity ratio was changed from 1:1 to 1:3 for the index and little fingers. After the 100 trials were completed, participants took a 10-minute break. Lastly, participants completed aftereffect testing consisting of 50 trials during which the force sensor sensitivity ratio was returned to the baseline session value (i.e., clear the perturbation).

began with a familiarization period consisting of null movement trials (no added sensor perturbation, approximately 25 trials). After the familiarization, we asked participants to complete a total of 200 trials. The experiment consisted of three conditions: baseline (unperturbed), adaptation (perturbed), and aftereffect. As shown in Figure 1B, at the beginning of each trial, the target circle appeared after a 5-second preparation period, signaling the "Go Cue". Participants were asked to accurately track the target by controlling the cursor. At the end of each trial, they received binary feedback on their performance, with green or red

squares indicating success or failure, respectively. Figure 1D illustrates the summary of the experimental schedule. In the baseline condition consisting of 50 trials, participants tracked the moving cursor with a force sensor sensitivity ratio of 1:1 between the index and little fingers. During the adaptation phase, participants completed 100 trials with the force sensor sensitivity ratio of 1:3 between the index and little fingers, requiring them to adapt to the de novo force mapping. After a 10-minute break, aftereffects were assessed in a 50-trial session with sensor sensitivity returned to baseline. This session was included to evaluate whether an internal model had been sufficiently formed through motor learning, as the presence of aftereffects is widely regarded as strong evidence of internal model formation. It is thought that the sensorimotor system adapts to the perturbation and updates its predictive control mechanisms, including an internal model (Salomonczyk et al., 2013; Leow et al., 2018; Krakauer et al., 2019; Tsay et al., 2024). Note that the luminance of the colors used for the cursor, target, and binary feedback was uniformly set to avoid any biases related to visual perception.

Data recording

Behavioral data. Time series of the two-dimensional target and cursor positions (x- and y-axes) on the screen were contentiously acquired at a sampling rate of 100 Hz using the dedicated software package as described above.

Electroencephalography. To recode neural activity during data collection, we utilized a multi-channel EEG amplifier system (actiCHamp, Brain Products GmbH, Germany). EEG signals were continuously recorded from 63 electrodes positioned on the scalp following the international 10/10 system, using active electrodes embedded in a wearable elastic cap (actiCAP, Brain Products GmbH, Germany). A ground reference electrode for data acquisition was placed at AFz. During the data recording, all electrodes were referenced to the right

earlobe while the left earlobe was also recorded as an electrode for re-referencing. Electrooculography (EOG) signals are widely used to detect activities of eye movements and are available to remove eye movement-related noises from the EEG signals. EOG signals were recorded using electrodes placed above and below the left eye for monitoring vertical eye movements and below the left and right eyes for monitoring horizontal eye movements. EEG and EOG signals were amplified and digitized with 24-bit resolution at a sampling rate of 1 kHz. These signals were continuously stored on a personal computer via BrainVision recorder software (Brain Products GmbH, Germany). Skin/electrode impedance was consistently maintained below 10 kΩ throughout the data collection.

Data analysis

Behavioral data were analyzed using custom-written code on MATLAB 2019b (MathWorks, Natick, United States). EEG data were also analyzed using functions from EEGLAB toolbox (Delorme and Makeig, 2004) implemented on MATLAB in combination with custom-written code. Statistical analyses for behavioral and EEG results were implemented using R environment (R Development Core Team, version 4.2.2, www.r-project.org/) unless otherwise noted.

Behavioral data. A 2-dimensional space distance (i.e., screen height and width) between the moving target (red circle) and the cursor (yellow circle) was utilized as an error index. Throughout the error-based visuomotor adaptation task, participants had to reduce this error. To quantify the magnitude of the error, the Euclidean distance (d) from the moving cursor to the moving target was calculated at each timepoint (t) between the "Go" cue (t_0) and end of the target tracking (t_{end}) at each trial. We then calculated the cumulative error for each trial as follows:

$$d(t) = \sqrt{(x_{2t} - x_{1t})^2 + (y_{2t} - y_{1t})^2},$$

where x_{1t} and y_{1t} are the cursor center coordinates and x_{2t} and y_{2t} are the target center coordinates. Subsequently, the cumulative error (CE) for motor performance within each trial was calculated in the following formula:

$$\text{Cumulative error (CE)} = \int_{t_0}^{t_{\text{end}}} d(t)dx \ .$$

To examine the effects of motor learning effects, we computed the average error over five consecutive trials, defining this as one epoch.

With regard to quantifying motor learning, the CE data obtained during the adaptation period were first normalized to the average CE from the baseline period, i.e., null movement trials. This correction was performed because significant individual differences in basic motor skills among participants were observed, as shown in Supplementary Figure 1. By normalizing the data using the average of the baseline session, we minimized the influence of these differences in essential motor skills between participants, thereby facilitating a more accurate assessment of the learning process itself. Following this mathematical adjustment, the learning curve of errors across the trials in the perturbation phase was then fitted for each participant using an exponential function (Bönstrup et al., 2020) as follows:

$$L(t) = k_1 - k_2 \cdot \left(1 - e^{-k_3 n}\right) ,$$

where L is the CE and k_{1-3} denotes initial performance (function intercept), maximum performance (function plateau), and learning rate (function slope), respectively. n represents trial number.

To further determine how brain network flexibility relates to the ability to maintain and recall a learned motor performance, we calculated the degree of aftereffect by averaging the first five

trials immediately after the 10-minute break (see Figure 1). This is because aftereffect is a hallmark of the effectiveness of motor learning. A high aftereffect value indicates that the motor performance and a related internal model have been solidly learned and can be recalled effectively.

EEG data. For preprocessing and artifact removal, consecutive EEG signals were re-referenced offline to the averaged signals of bilateral earlobes and segmented into 14-second epochs from 5 s before to 9 s after the “Go” cue. These segmented EEG data underwent band-pass filtering between 1-50 Hz while eliminating 60 Hz power line noise. Independent component analysis (ICA) was then applied to the filtered EEG signals associated with eye movements, blinks, and muscle contractions. The ICA-derived noise components were automatically identified using the ADJUST algorithm (Mognon et al., 2011). Across the individuals, at least two and up to six ICA components were removed from the filtered EEG signals. As a final preprocessing step, we applied the current source density transformation via the current source density (CSD) toolbox (version 1.1), utilizing the spherical spline algorithm (Perrin et al., 1989; Kayser and Tenke, 2006). This step minimizes the impact of volume conduction on EEG data. Subsequently, artifact-corrected EEG data were used for brain oscillation analysis. Given the necessity of maintaining the sequence of motor learning processes, no trials were removed.

To quantify functional brain networks and their flexibility, we utilized a neural oscillation with a phase-based approach for the analysis of neural oscillations (Lachaux et al., 1999; Varela et al., 2001; van Diessen et al., 2015). This approach aligns with the dynamical systems observed in the brain (Lachaux et al., 1999), where phase synchrony of neural activity significantly contributes to information processing within the brain (Rodriguez et al., 1999; Varela et al., 2001; van de Vijver and Cohen, 2019). First, to decompose the single-trial EEG signals into time-frequency representations of the instantaneous phase, we applied complex Morlet wavelet that can be defined as the product of a complex sine wave and

Gaussian window (Tallon-Baudry et al., 1996; Cohen, 2019). The CSD-transformed EEG signals were convoluted by a Morlet wavelet function $w(\tau, f)$:

$$w(\tau, f) = e^{2i\pi f\tau} e^{\frac{-\tau^2}{2\sigma^2}},$$

where i is the imaginary unit. τ and f denote time points and the center frequency, respectively. σ is the width of the Gaussian, which is defined as

$$\sigma = \frac{n_{co}}{2\pi f}.$$

The parameter n_{co} is defined as the number of cycles and represents a nontrivial choice in time–frequency analysis. In the present study, we set n_{co} = 3 and f increased from 1 to 50Hz in 1-Hz steps (Lachaux et al., 2000). It is well established that this parameter governs the trade-off between temporal and frequency precisions, such as that a larger number of cycles results in lower temporal resolution, and vice versa. A smaller number of n_{co} enables more precise localization of temporal dynamics compared to a larger number. Our primary aim is to capture transient changes in neural activity within a time-limited window during motor execution associated with learning. Drawing on established knowledge (Cohen, 2014), we therefore selected a smaller number of cycles. We then calculated the instantaneous phase synchrony index (PSI) at each frequency for all electrode pairs using the following formulas;

$$\mathrm{PSI}(\tau, f) = \frac{1}{T}\left|\sum_{\tau=1}^{T} e^{i\theta(\tau)}\right|,$$

$$\theta_{mn}(\tau) = \varphi_m(\tau) - \varphi_n(\tau),$$

where T denotes the total number of time points corresponding to three cycles of the center frequency, employing 90% overlapping windows, as per previous literature (Uehara et al., 2023). The utilization of 90% overlapping windows enables the generation of time-dense phase synchrony information, facilitating the observation of highly time-resolved brain network dynamics during the task. $\varphi_m(\tau)$ and $\varphi_n(\tau)$ represent the instantaneous phase of the m_{th} and n_{th} electrodes at time point τ. The PSI represents phase synchronization between EEG signals from two different electrodes at each time point within each time window. This

index ranges between 0 and 1, where a value of 0 indicates complete randomness, while a value of 1 denotes perfect synchrony (i.e., complete phase alignment) in EEG signals from the two electrodes and provides valuable information about functional connectivity within the whole brain (Lachaux et al., 2000; Varela et al., 2001).

As the final step, the whole-brain network flexibility was determined using the Louvain-like algorithm (Blondel et al., 2008; Mucha et al., 2010), which is a mathematical method for revealing the inherent community structure within complex networks. This approach is rooted in network analysis, employing graph theory and has recently been applied to analyze neuroimaging data, including fMRI and EEG, which is unveiling functional relationships between brain network flexibility and cognition as well as action (Bassett et al., 2011, 2013; Betzel et al., 2017; Paban et al., 2019; Uehara et al., 2023). Initially, the generalized Louvain algorithm was employed for multilayer community detection. In the present study, a multilayer community was defined wherein each network node (i.e., EEG electrode) in one time window is connected to itself in neighboring (preceding or following) time windows (i.e., layers). This step can be calculated using the following formula (Mucha et al., 2010; Bassett et al., 2013):

$$Q_{\text{multilayer}} = \frac{1}{2\mu} \sum_{nmlr} \left[(A_{nml} - \gamma_l P_{nml})\, \delta_{lr} + \delta_{nm} \cdot \omega_{mlr} \right] \delta(g_{nl}, g_{mr}),$$

where Q represents the multilayer modularity index, l denotes the number of layers in the multilayer network, and μ signifies the total edge weights encompassing both intra- and inter-layer connections. A_{nml} represents the time-by-time $N \times N$ PSI-derived functional connectivity matrices (where N denotes the number of EEG electrodes) between nodes n and m (i.e., PSI value). P_{nml} signifies the weight of the edge between nodes n and m under the null model, while γ_l denotes the structural resolution parameter that defines the weight of the intralayer connections. g_{nl} represents the community assignment of node n in

layer l while g_{mr} is the community assignment of node m in layer r. ω_{mlr} denotes the connection strength between nodes across two layers. In this study, the parameters ω and γ were set to 1, constituting their default values as per previous literature (Bassett et al., 2013). $\delta(g_{nl}, g_{mr})$ corresponds to the Kronecker delta, taking a value of 1 if $g_{nl} = g_{mr}$ and a value of 0 if $g_{nl} \neq g_{mr}$. Subsequently, we determined brain network flexibility by counting how often a node altered its module assignment throughout time, adjusting for the total potential changes. Given the heuristic nature of this algorithm, we ran the analysis 100 times and selected the best clustering based on the maximum Q value. Brain network flexibility was averaged in the theta (4-8 Hz), alpha (9-13 Hz), and beta (14-30 Hz) frequency bands across all EEG electrodes to capture the global flexibility of the whole cortical regions on every single trial. This flexibility index ranges from 0 to 1, where 0 indicates no change in communities, while 1 indicates a change in community across every layer. It is well accepted that the Louvain algorithm has a heuristic in nature. We therefore performed 50 repetitions of the algorithm for each participant. Before averaging across trials, the flexibility of the whole brain network was averaged within each trial across predefined frequency bands during the 5-second preparation period immediately preceding the onset of action and during the 3-second motor execution period. We presumed that the neural systems dynamically and flexibly reconfigure brain networks not only during motor execution but also during the preparation period throughout learning. Previous human behavioral studies demonstrated that the preparation of motor execution during a learning process plays a critical role in the ability to learn in an adaptation task (Haith et al., 2015). Preparatory neural activity patterns have the potential to retain motor memory (Sun et al., 2022). Focusing more directly on brain network flexibility, preparatory brain network flexibility for musical playing is necessary for feedback control, rather than feedforward control, in skilled motor performance by expert musicians (Uehara et al., 2023). These previous studies motivated us to investigate how the flexibility of neural preparatory activity affects motor learning ability across different ages. Moreover, we

quantified temporal changes in brain network flexibility throughout the trials during adaptation to identify how inter-trial brain network flexibility changes within the adaptation period and how these changes relate to motor learning ability with age. We performed this analysis to test the assumption that reduced flexibility may stabilize brain networks optimized by learning and enhance focus on relevant neural signals. This hypothesis is supported by a previous human EEG study, which suggests that the suppression of trial-by-trial neural variability is closely associated with perceptual abilities (Arazi et al., 2017). To test this, we calculated the differences in brain network flexibility values between the averages of the first and last 5 trials according to the predefined frequency bands at the individual level.

To enhance the interpretability of the physiological aspects of brain network flexibility, we first computed the multi-channel Lempel-Ziv complexity (LZC) index (Lempel and Ziv, 1976; Fernández et al., 2011). This index quantifies the dynamical complexity generated by brain networks in terms of randomness and compressibility. There is a possibility that our mathematical approach merely captures the apparent flexibility of brain networks. In other words, even if network nodes transition frequently within a small number of modules, our approach might incorrectly determine that the brain network is highly flexible. We assessed LZC in each frequency band across the group to rule out this false detection. Multi-channel LZC was calculated for the preparatory period of each trial using custom-written code available in the MATLAB environment. We then calculated the trial-averaged LZC at the individual level. In general, higher LZC values (normalized between 0 and 1) reflect greater randomness. Additionally, although the present study has a potential limitation in topographical interpretation since we did not perform source localization analysis, looking at the topographical characteristics of each network module will help in biologically interpreting the obtained results. To do so, leveraging insights into the community affiliations of each node (i.e., EEG channel) over the analytic time window, we visualized each network module associated with brain network flexibility in each group using a hierarchical clustering algorithm

(function *cluster* in MATLAB).

Statistics

Motor learning profiles. To test age-group differences in the motor learning profiles between the YA and OA groups, we used an independent-sample t-test for the learning slope and aftereffect, respectively.

Brain network flexibility. To test age-group differences in brain network flexibility during the resting state, we conducted a two-way repeated measures ANOVA with a mixed design on each resting EEG data with the AGE (2 levels: YA and OA) as the between subject-factor and FREQUENCY (3 levels: theta, alpha, and beta) as the within subject-factor. Next, a three-way repeated-measures ANOVA with a mixed design was conducted on the EEG data obtained during the visuomotor task, with AGE (2 levels: YA and OA) as the between-subject factor and STATE (2 levels: preparation and motor execution) and FREQUENCY (3 levels: theta, alpha, and beta) as the within-subject factors. Moreover, we are interested in the extent to which changes in brain network flexibility are associated with the progression of motor learning. To test this, a four-way repeated measures ANOVA for mixed design with the AGE (2 levels: YA and OA) as the between subject-factor and STATE (2 levels: preparation and motor execution), FREQUENCY (3 levels: theta, alpha, and beta) and PHASE (2 levels: mean of the initial and final 5 trials during the perturbation session) as the within subject-factors was conducted. A Greenhouse-Geisser correction for a series of ANOVA was used when the assumption of sphericity was violated. Post hoc explorations using Holland-Copenhaver correction for multiple comparisons were performed if a significant effect was detected from the ANOVA (Holland and Di Ponzio Copenhaver, 1988).

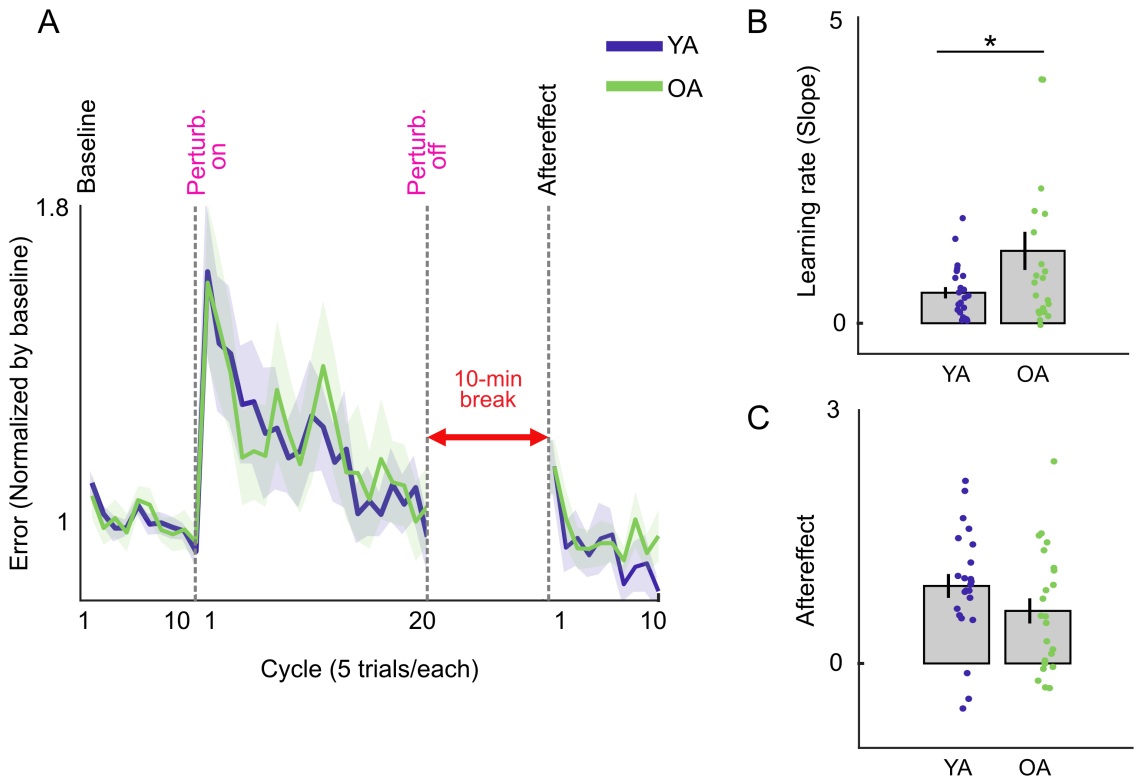


Figure 2: Behavioral results. **A.** Group-averaged performance error normalized by the baseline value throughout the data collection. Solid lines and shaded areas showed mean and SEM for five trials of epoch across participants (n=23 of each). **B.** Learning rate was determined by the slope value (k^3) of the exponential function. Group-averaged learning rates significantly differed between the groups. A lower value indicates continued performance improvement throughout the adaptation period. **C.** Group-averaged aftereffect was used as a hallmark of the effectiveness of motor learning. We calculated the degree of aftereffect by averaging the first five trials after the 10-minute break. A higher value indicates that the motor performance has been solidly learned and can be recalled effectively. Each dot represents an individual, and each error bar indicates the standard error of the mean across participants. Statistical significance is denoted by $*$ $p < 0.05$.

Neuro-behavioral relationship. The primary goal of this study was to determine the neural associations of preparatory brain network flexibility or inter-trial changes in brain network flexibility across the frequency bands and the ability of motor learning, including learning rate and aftereffect. To achieve this, we employed a least absolute shrinkage and selection operator (LASSO) regression model, which incorporates penalized regression (Tibshirani, 1996). LASSO regression enables the selection of explainable variables using a weighted combination of L1 norm regularization. The LASSO regression used in the present study was performed using the *glmnet* package implemented in R software package (Friedman et al., 2010). The trial-averaged brain network flexibility values at theta, alpha, and

beta frequencies at the individual level were treated as independent variables. The individuals' learning rate and aftereffect were treated as dependent variables, respectively. To ensure the goodness-of-fit of the model, a coefficient of determination value (R^2) was used. We repeated the regression 100 times and identified the median of R^2 across these repetitions because the results of LASSO regression are indeed sensitive to the choice of the hyperparameter. These repetitions can help to provide a more robust estimate of model performance. The optimal λ was chosen by performing k-fold cross-validation and selecting the one with the minimum generalization error. Based on this median R^2, we then reported the relevant brain network flexibility most associated with the motor learning profiles.

<Figure 2 around here>

Results

Behavioral results. Overall motor learning profiles are shown in Figure 2. A representative cursor trajectory during motor learning is depicted in Supplementary Figure 1B. Figure 2A shows the degree of behavioral performance across motor learning observed from the YA and OA groups. Motor learning was evaluated by the degree of baseline-normalized performance error. This is then transformed into parameters representing each profile. As predicted, the degree of error was attenuated along with the number of trials, and this was visible from the first few trials after the start of the adaptation period even though baseline accuracy (i.e., first 50 trials without the perturbation) differed between the groups (Supplementary Figure 1A). This indicates that motor learning occurred throughout the adaptation period in both groups. Subsequently, we found that the learning rate, parameterized by the slope (i.e., β value) of an exponential fit per individual, significantly differed between the groups (Figure 2B) according to an independent t-test (t = 2.574, p = 0.013, Cohen's d = 0.759). The YA group exhibited a lower slope value compared to the OA group, indicating that the YA group was able to sustainably attenuate performance error

throughout the adaptation period. No significant difference in aftereffect was detected between the groups (t = -0.504, p = 0.616, Cohen's d = 0.424) (Figure 2C). These results suggest that age had minimal impact on the effectiveness of motor learning and the ability to recall motor memory.

Brain network flexibility. We first sought to verify how brain network flexibility at the resting state differs between both groups (Supplementary Figure 2A). A two-way ANOVA found a significant main effect of FREQUENCY ($F_{1.9,87.2}$ = 10.53, p < 0.001, η_p^2 = 0.19), but no significant AGE effect ($F_{1,44}$ = 0.82, p = 0.36, η_p^2 = 0.018). The significant interaction between them was detected ($F_{1.9,87.2}$ = 3.52, p = 0.035, η_p^2 = 0.07). A posthoc test revealed that the theta band had significantly higher brain network flexibility compared to other frequency bands (p < 0.05, Holland-Copenhaver corrected). The alpha band tended to differ between the age (p = 0.052), whereas no differences were observed in the other frequency bands.

Next, we tested whether age-group differences in brain network flexibility emerged during the preparation (Figure 3A) and motor execution (Figure 3E) phases throughout the adaptation session. A three-way ANOVA found significant main effects of the STATE ($F_{1,44}$ = 11.11, p = 0.001, η_p^2 = 0.20) and FREQUENCY ($F_{1.48,64.9}$ = 25.66, p < 0.001, η_p^2 = 0.36), but no main effect of AGE ($F_{1,44}$ = 0.425, p = 0.42, η_p^2 = 0.014). A significant interaction between STATE and FREQUENCY was detected ($F_{1.27,55.9}$ = 50.97, p < 0.001, η_p^2 = 0.53). No significant interaction effects involving the age factor were observed (all p > 0.05). Despite no age-group differences being observed, significant differences in brain network flexibility were observed between the preparation and motor execution periods (Theta: $F_{1,44}$ = 33.06, p < 0.001, η_p^2 = 0.42; Alpha: $F_{1,44}$ = 64.08, p < 0.001, η_p^2 = 0.59; Beta: $F_{1,44}$ = 15.74, p < 0.001, η_p^2 = 0.26). In the present study, another important aim was to examine how the degree of brain network flexibility changed over time throughout the adaptation period.

Figure 3B-D and Figure 3F-H illustrate how brain network flexibility changes from the

initial to the later phase over the time course of the adaptation period. The four-way ANOVA detected significant main effects of PHASE ($F_{1,44}$ = 7.371, p = 0.009, η_p^2= 0.143) and FREQUENCY ($F_{1.45, 63.88}$ = 20.93, p < 0.001, η_p^2= 0.322) but no significant main effects of STATE ($F_{1,44}$ = 1.43, p = 0.237, η_p^2 = 0.031) or AGE ($F_{1,44}$ = 0.804, p = 0.374, η_p^2 = 0.018). Moreover, a significant interaction between STATE and FREQUENCY was detected ($F_{1.62,71.48}$ = 27.58, p < 0.001, η_p^2= 0.385), whereas no other statistically significant interactions were detected (all p > 0.05). To further examine the significant interaction observed in the four-way ANOVA, follow-up post hoc tests were conducted. Brain network flexibility was significantly modulated depending on the initial or late phases of adaptation ($F_{1, 44}$ = 13.22, p < 0.001, η_p^2 = 0.23). Brain network flexibility in the alpha frequency band significantly decreased toward the end of the adaptation period ($F_{1, 44}$ = 23.46, p < 0.001, η_p^2 = 0.34). On the other hand, during motor execution, there was no significant difference in brain network flexibility between the initial and late phases of the adaptation period ($F_{1, 44}$ = 0.63, p = 0.428, η_p^2 = 0.014). Together, these findings suggest that the brain network became more rigid as learning progressed, potentially reflecting that learning was accompanied by a transition from an exploration to an exploitation strategy.

Gaining additional insights into the characteristics of the functional brain network is crucial for interpreting the present findings. We therefore assessed how many network modules were mediated by the flexible nodes because there was a concern that the network could be considered highly flexible even if each node was only moving back and forth between a limited number of modules. To address this concern, the number of modules (Figure 4A) and network complexity (Figure 4B), as indicated by LZC, were reported, respectively. Figure 4B shows the LZC values during the preparation and motor execution periods throughout adaptation. The three-way ANOVA for the LZC values detected significant main effects of STATE ($F_{1, 44}$ = 174.3, p < 0.001, η_p^2= 0.798) and FREQUENCY ($F_{1.37,60.12}$ = 221.6, p < 0.001, η_p^2= 0.834) as well as significant interaction between them ($F_{1.53,67.11}$ = 55.71,

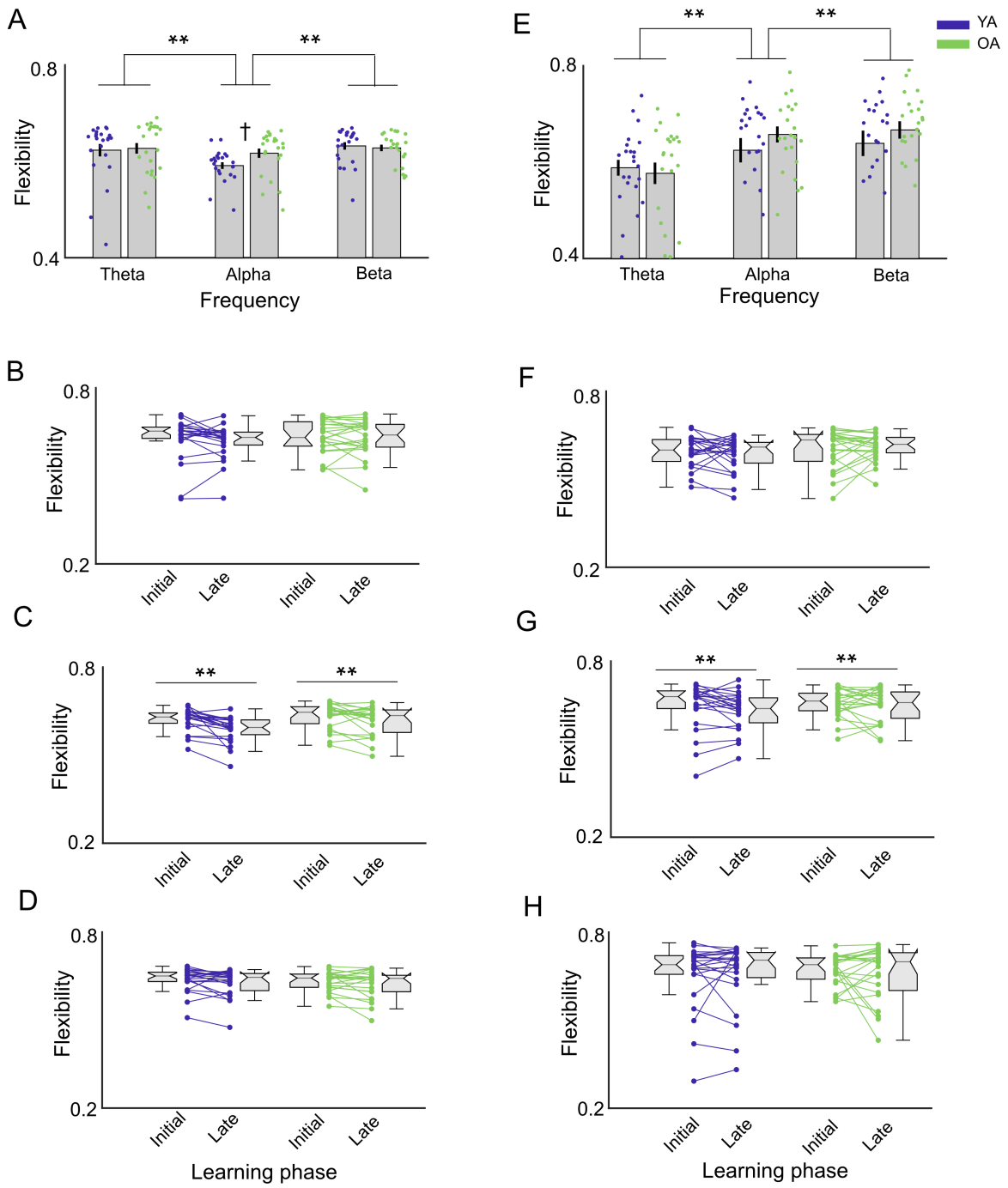


Figure 3: Group-averaged brain network flexibility during the preparatory period **(A)** and motor execution **(E)** in the visuomotor learning task in response to the predefined frequency bands. A higher value indicates greater flexibility among the networks. **B-D.** Changes in group-averaged brain network flexibility during the preparatory period from the initial to the late trials were compared for each frequency band (C: Theta, D: Alpha, and E: Beta). **E-H.** show similar patterns, but the results correspond to the motor execution. Each dot represents an individual, and each error bar indicates the standard error of the mean across participants. Statistical significance is denoted by ** $p < 0.001$.

$p < 0.001$, $\eta_p^2 = 0.55$). More concretely, the LZC values in motor execution were significantly lower than those in preparation across all frequencies. In contrast, no significant effects or interactions involving the factor AGE were observed (all $p > 0.05$). Together, although the properties of the

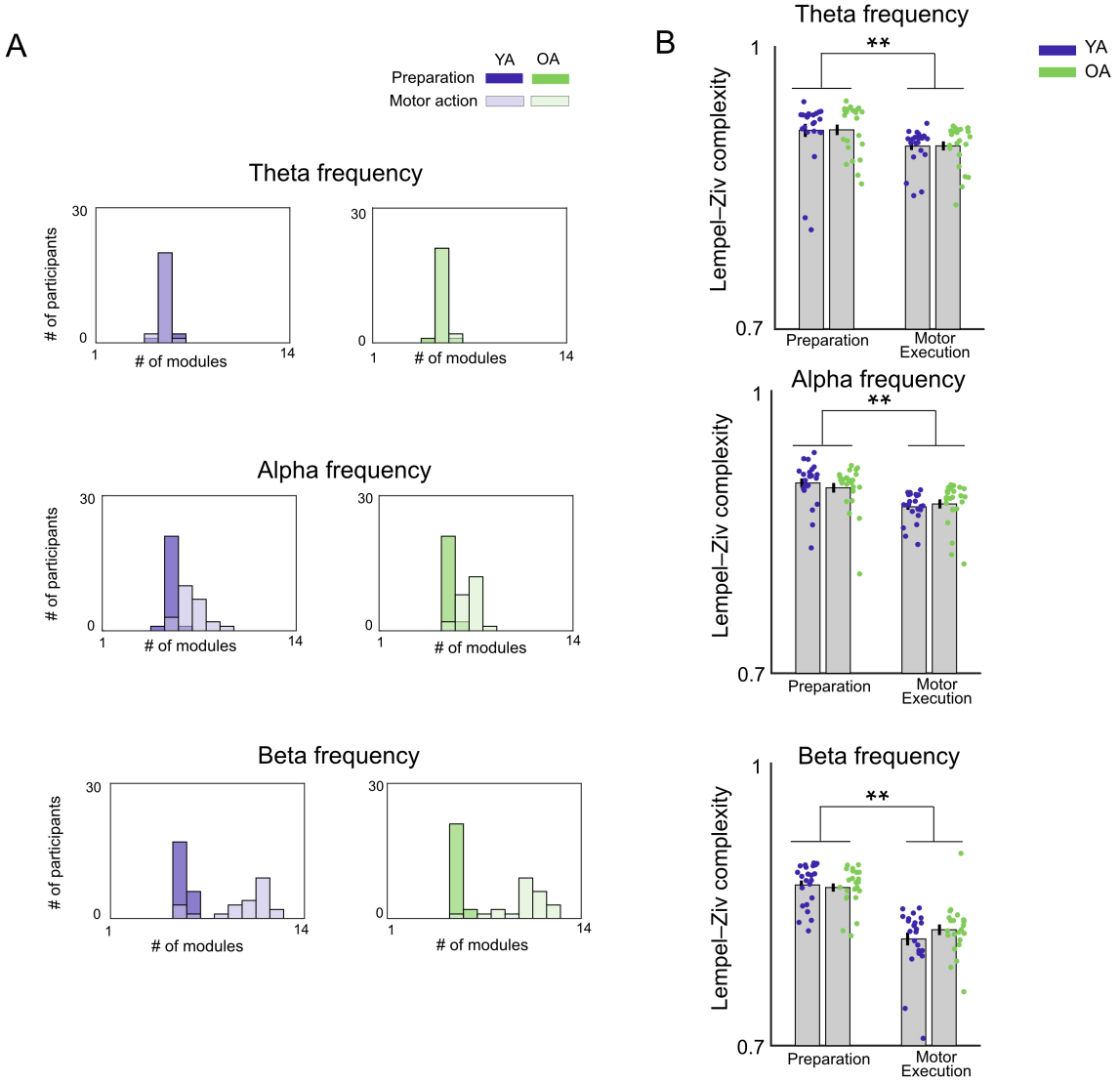


Figure 4: Characteristics of brain network structures. **A.** Number of modules in the extracted brain networks for predefined frequency bands under the preparatory and motor execution period during the motor learning. **B.** Comparisons of brain network complexity. A higher value indicates that the extracted brain networks are complex and contain many unique patterns. Each dot represents an individual, and each error bar indicates the standard error of the mean across participants. Statistical significance is denoted by ** p < 0.001.

brain network differed across task states and frequencies, the age-related differences in brain network flexibility during adaptation did not originate from differences in network complexity.

For the resting state, as shown in Supplementary Figure 2B, the two-way ANOVA for the LZC values detected significant main effects of AGE ($F_{1, 44}$ = 9.77, p = 0.003, η_p^2= 0.181) and FREQUENCY ($F_{1.45,63.71}$ = 619.2, p < 0.001, η_p^2= 0.933) and their significant interaction ($F_{1.45,63.71}$ = 20.49, p < 0.001, η_p^2= 0.31). The OA groups exhibited higher dynamical complexity, generated by brain network flexibility, than the YA group, suggesting that aging

may be accompanied by greater randomness in resting-state brain network dynamics. The post hoc test revealed significant age-group differences between the alpha and beta bands, but not the theta band (Theta: $F_{1, 44} = 2.48$, $p = 0.122$, $\eta_p^2 = 0.05$; Alpha: $F_{1, 44} = 12.33$, $p = 0.001$, $\eta_p^2 = 0.218$; Theta: $F_{1, 44} = 18.67$, $p < 0.0001$, $\eta_p^2 = 0.298$).

Neuro-behavioral relationship. Figures 5 and 6 summarize the relationships between brain network flexibility and the learning properties based on the results of the LASSO regression analyses. For clarity, the R^2 values obtained from the regression analyses are presented as percentages using a pie chart in the Figure 5 and 6. Figure 5A shows the extent to which brain network flexibility during preparation throughout the adaptation period predicted the behavioral outcomes. Figure 5 A shows that brain network flexibility across the entire frequencies accounted for 19% of the aftereffect in YA, whereas this relationship was scarcely explainable in OA (2%). Interestingly, the learning rate in OA was partially explained by brain network flexibility in the theta and beta bands (11%). Figure 5B shows the relationships between changes in brain network flexibility toward the end of the adaptation period and the behavioral outcomes. We found that the degree of change in brain network flexibility during the adaptation period predicted learning even more strongly. In the YA group, this relationship was highly explainable for a substantial portion of the aftereffect (51%), whereas in the OA group, it was primarily associated with the learning rate (25%). On the other hand, brain network flexibility during motor execution predicted only the learning rate, but not the aftereffect (Figure 6). Furthermore, its explanatory contribution of brain network flexibility during motor execution was clearly lower than during preparation across the age groups.

To summarize, we suggest that brain network flexibility during the preparatory period contributed more to motor learning as compared to that during the motor execution period. Brain network flexibility was effectively available to motor learning in younger adults as compared to older adults. Our observations determine that brain network flexibility plays an

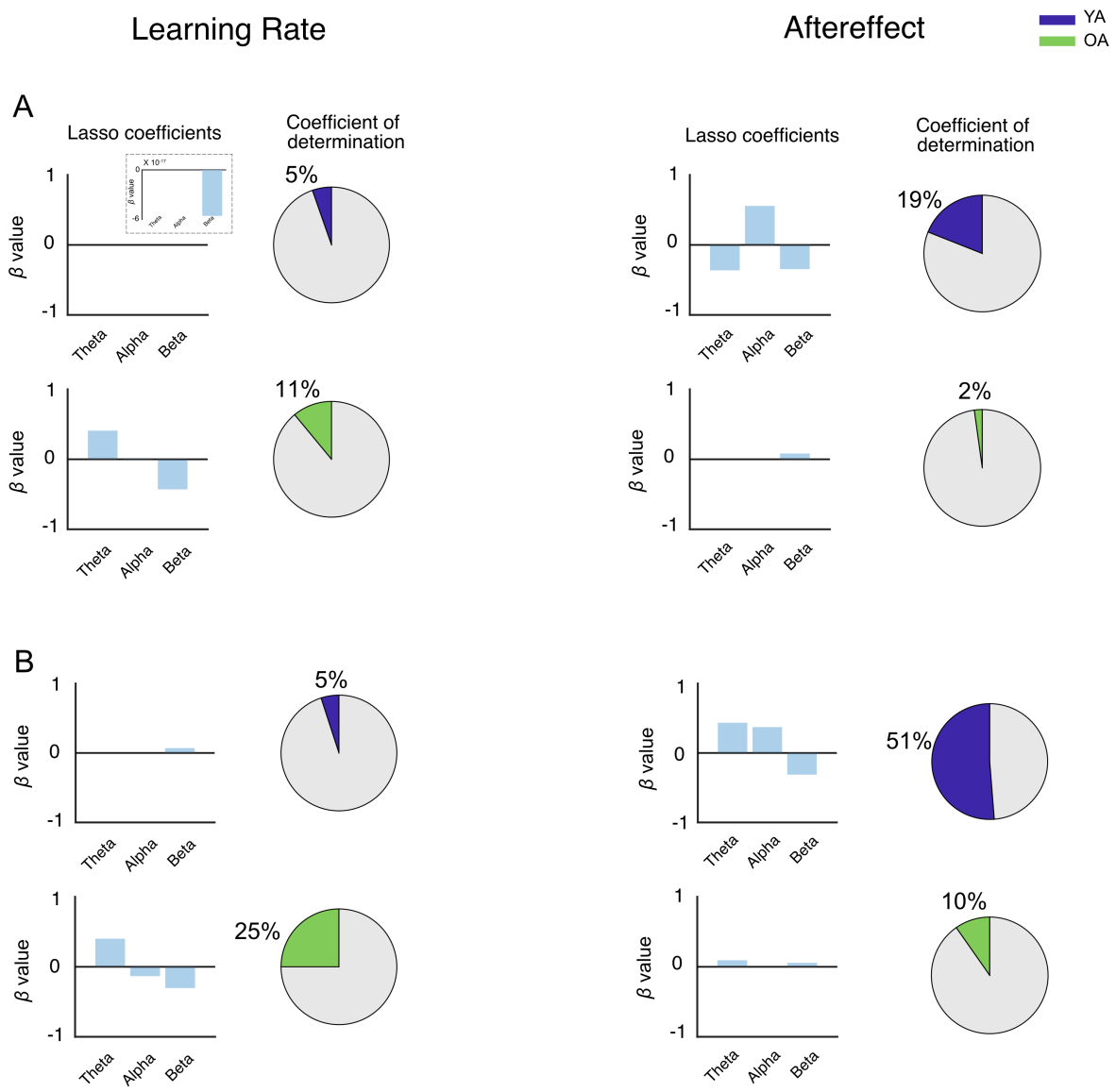


Figure 5: Results of the LASSO regression during the preparatory period. **A.** Relationships between brain network flexibility and motor learning outcomes. **B.** Relationships between changes in brain network flexibility throughout the learning period and motor learning outcomes. Bar plots display β coefficients estimated by LASSO, while pie charts summarize the explanatory power as the coefficient of determination (R^2). The small inset within the bar plot for the β coefficients provides an enlarged view of the region near zero.

active role in learning retention, i.e., aftereffect, in younger adults. However, this effect appears to be limited in older adults.

Based on the LASSO regression results, we are further interested in understanding what kinds of network modules contribute to forms of brain network flexibility, as this understanding would help clarify the functional and biological significance of our findings. Figure 7 displays the network modules observed during the preparation period throughout adaptation for each

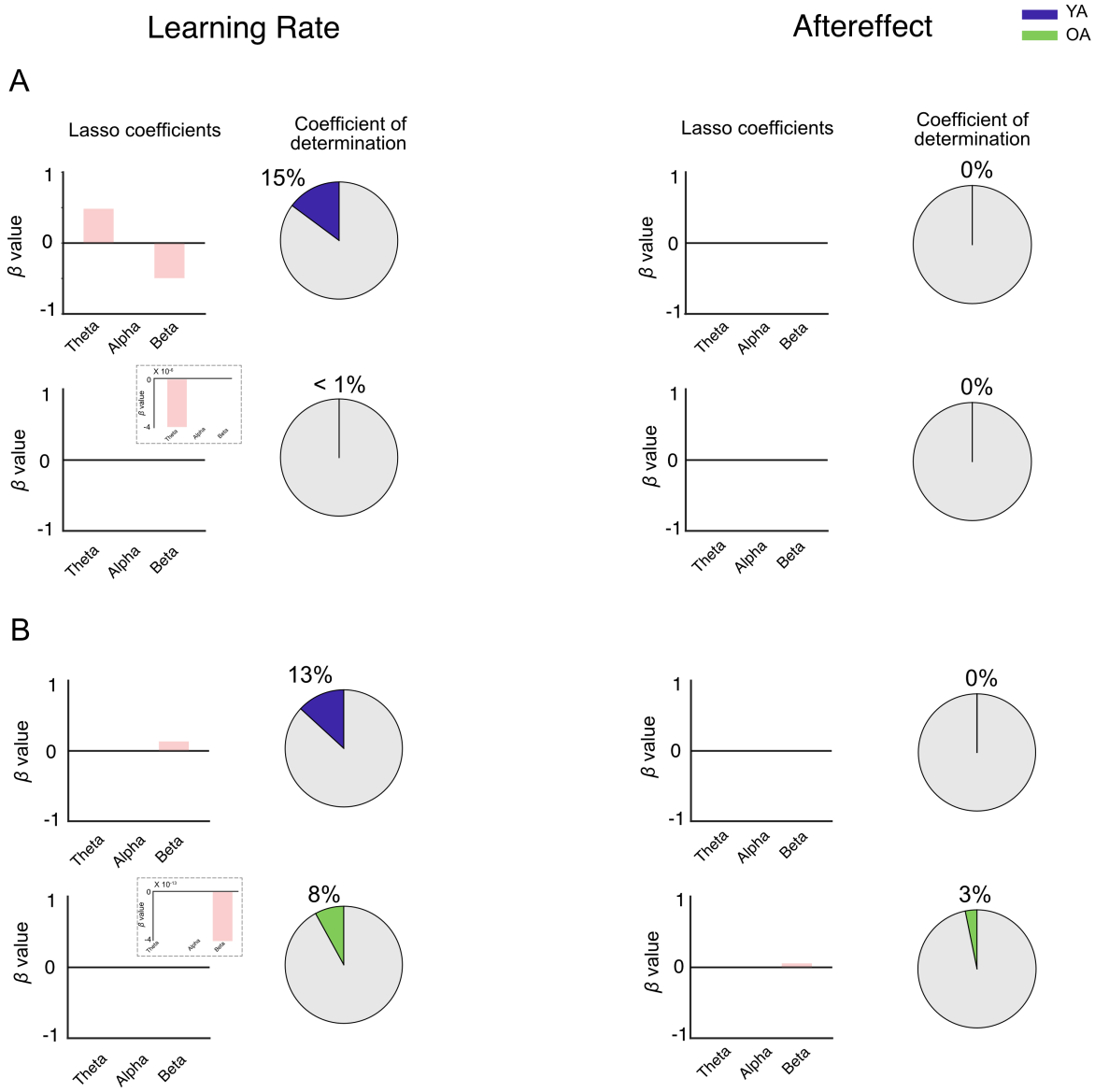


Figure 6: Results of the LASSO regression during the motor execution. **A.** Relationships between brain network flexibility and motor learning outcomes. **B.** Relationships between changes in brain network flexibility throughout the learning period and motor learning outcomes. Bar plots display β coefficients estimated by LASSO, while pie charts summarize the explanatory power as the coefficient of determination (R^2). The small inset within the bar plot for the β coefficients provides an enlarged view of the region near zero.

age group.

<Figure 7 around here>

Discussion

The goal of the present study was to examine whether age-group differences in brain network flexibility exist and how these differences were related to motor learning abilities by leveraging the visuomotor learning task and multichannel EEG recordings. Our key finding

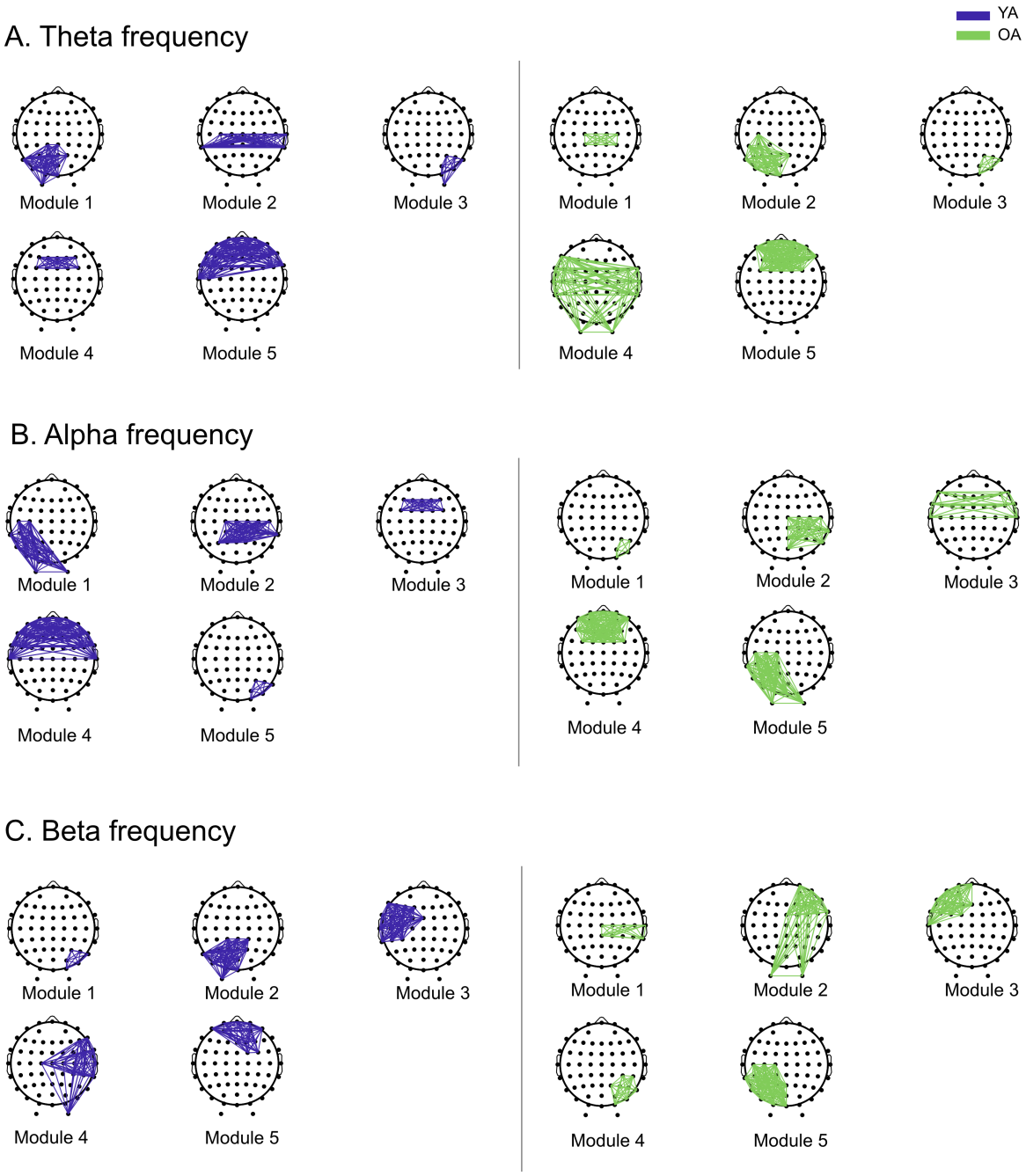


Figure 7: Extracted network modules across participants in each group. According to the brain network analysis results, five network modules, which are obtained during the preparatory period, are visualized in the alpha **(A)** and beta **(B)** frequency bands, respectively.

was that motor learning properties were tightly coupled with brain network flexibility during motor learning, although these associations differed across the age groups (Figures 5 and 6). More specifically, we identified the following distinctive neural–behavioral couplings. First, brain network flexibility emerging immediately before motor execution contributed more strongly to the acquisition of motor learning than the flexibility observed during motor

execution. Second, this effect was observed more prominently in younger adults than in older adults. Third, the modulation of brain network flexibility immediately before motor execution over repeated trials was essential for the consolidation of motor learning (Figure 5B). Taken together, we propose novel evidence that brain network flexibility plays a crucial role in acquiring and maintaining new motor execution in younger adults, but this relationship becomes less effective with aging. We further show that preparatory brain network flexibility could strongly predict the aftereffect rather than the learning rate, suggesting that brain network flexibility may contribute to the formation and stabilization of implicit internal models.

For the behavioral results, both groups were able to sufficiently adapt to the perturbation in response to changes in the sensitivity of force mapping. Interestingly, although older adults had less precise cursor control compared to younger adults at the baseline (Supplementary Figure 1), they exhibited motor learning effects similarly to those of younger adults as they could adapt to the novel force mapping (from the baseline of 1:1 to the adaptation of 1:3) (Figure 2). In principle, the learning slope quantifies the magnitude of trial-by-trial changes in performance across repeated action, reflecting how strongly motor behavior is updated in response to experienced errors, whereas the aftereffect reflects the maintenance and recall of the internal model for future use (Krakauer and Mazzoni, 2011; Krakauer et al., 2019; Leech et al., 2022). In the present study, older adults exhibited a significantly steeper learning slope than younger adults, indicating larger behavioral adjustments across trials during the acquisition phase. Based on our initial inspection, such a steeper slope observed in the older adults could be interpreted as indicating faster or more efficient learning. However, we assumed that the learning slope does not necessarily index the final level of learning or the extent of internal model formation. This is because, by integrating the observed learning slope with the aftereffect, we can propose different possibilities. Importantly, no age-related differences were observed in the aftereffect in the present study (Figure 2C). The aftereffect is commonly considered to reflect implicit sensorimotor adaptation and has been accepted as the retention

of the acquired internal model (Heuer and Hegele, 2008; Hegele and Heuer, 2010; Shadmehr et al., 2010). The dissociation between the steeper learning slope and comparable aftereffects suggests that the increased learning slope in older adults reflects larger trial-by-trial behavioral updates rather than a greater magnitude of implicit learning. This pattern is in line with the previous evidence showing that older adults rely more heavily on exploratory or strategic adjustments during learning (Voelcker-Rehage, 2008; Cirillo et al., 2011; Berghuis et al., 2019; Lee and Ranganathan, 2019; Bootsma et al., 2021), leading to larger immediate corrections, while the capacity for implicit adaptation and consolidation remains preserved. Thus, alternative learning strategies occur with aging. This observation will be discussed in the following section by incorporating evidence from age-related differences in neural activity.

Most previous studies investigating the biological function of brain network flexibility have relied on fMRI. However, BOLD-based measurements have limited temporal resolution due to the inherent characteristics of the measurement principle. Although age-related differences in brain network flexibility and their impact on motor skill have also been investigated using fMRI (Monteiro et al., 2019), a definitive conclusion has not yet been drawn. In the present study, our EEG-based investigation of brain network flexibility substantially advanced the understanding of its role in motor learning by revealing distinct patterns of brain network flexibility during preparation and motor action on a trial-by-trial basis.

We found that older adults exhibited significantly greater brain network flexibility than younger adults in the alpha frequency band during the preparatory period of the visuomotor learning task (Figure 3A). In principle, it has been accepted that alpha neural oscillations are ubiquitous throughout the entire brain and are involved in multiple functional processes (Klimesch, 1999; Başar, 2012; Bazanova and Vernon, 2014; Pascucci et al., 2025). Among them, one of the key roles is that alpha-band activity contributes to inhibitory processes, especially in sensory perception (Jensen et al., 2015; Clayton et al., 2018). We putatively presumed that the elevated alpha-band brain network flexibility observed in older adults may

indicate constrained information gating, rather than enhanced adaptive reconfiguration, potentially driven by age-related degradation of cerebellar–thalamocortical control (Mooney et al., 2022). An alternative perspective proposes that functional networks exhibit reduced neural network specificity (i.e., an increase in randomization) in older adults (Geerligs et al., 2014).

A key finding of the present study is the neurophysiological relationship between brain network flexibility and learning characteristics, and the extent to which this relationship is modulated by age. Preparatory brain network flexibility and its reduction toward the later learning period showed the identical patterns associated with aging (Figure 5). In young adults, a progressive reduction in brain network flexibility toward later learning was selectively associated with stronger aftereffects, but not with learning rate. This indicates that network stabilization primarily supports post-learning retention of the adapted internal model. Indeed, this finding is consistent with previous evidence showing that better visual perception abilities are associated with larger quenching of neural variability (Daniel and Dinstein, 2021). In contrast, older adults showed the opposite pattern. The learning-related reductions in network flexibility were strongly associated with learning rate but were unrelated to aftereffects. This dissociation suggests an age-related shift in the functional role of brain network flexibility from a post-learning stabilization mechanism in young adults to an online constraint on learning efficiency in older adults. This finding aligns with a previous EEG study showing that older adults with larger trial-by-trial auditory response variability are less accurate at sound localization (Anderson et al., 2012), indicating that aging alters the stability of brain activity, and these changes influence behavior. By contrast, such a strong association was not observed during the motor execution of the visuomotor learning task (Figure 6), suggesting that large-scale network reconfiguration across the brain primarily supports planning and post-learning stabilization, whereas execution-related neural dynamics reflect the implementation of already specified or planned motor commands. In other words, preparatory activity relies on the first stage in a chain of events that generates voluntary movement (Churchland and

Shenoy, 2024; Schimel et al., 2024).

Here, we will further discuss the frequency-specific contribution of brain network flexibility to learning properties. Despite the complexity of interpreting frequency-specific effects, identifiable roles emerge from our findings. Our LASSO regression analyses revealed that, in young adults, aftereffects were positively associated with alpha-band flexibility and negatively associated with theta- and beta-band flexibility, indicating that successful retention relies on alpha-mediated top–down gating. This pattern suggests an active exploitation of the internal model formed during adaptation. Indeed, alpha neural oscillations can influence the acquisition, retention, and efficiency of motor preparation (Deiber et al., 2014; Ghasemian et al., 2017). In contrast, older adults showed a weak but positive association between aftereffects and beta-band dynamics, with no significant contributions from the alpha or theta bands. Given the small effect, this finding suggests that aftereffects in older adults are not supported by an actively maintained internal model but rather by a passive persistence of the adapted motor state. The absence of alpha- and theta-band involvement further indicates a reduced ability to engage top–down gating or to suppress alternative control strategies after learning. These results point to an age-related shift from a frequency-specific, multi-band exploitation strategy in young adults to a limited, beta-dominated retention mechanism in older adults.

In the present study, interpreting LCZ as a proxy for neural complexity helps elucidate our findings. Intriguingly, the age-related elevations in LZC and preserved flexibility were confined to the resting state and the motor preparation phase, disappearing during actual execution. This selective manifestation suggests that the aging brain employs a proactive neural strategy characterized by hyper-complex idling. By maintaining a broader repertoire of dynamic states and high network reconfigurability before movement, older adults may create a functional buffer that compensates for age-related neurobiological declines (Goble et al., 2009; Coxon et al., 2014; Serbruyns et al., 2015; Frolov et al., 2020; Zapparoli et al., 2022;

Goelman et al., 2023). This heightened readiness may facilitate the successful transition into a stabilized, task-optimal state during execution, where performance becomes indistinguishable from that of younger individuals. Regardless of age, the coexistence of reduced LCZ and increased network flexibility during motor action (see Figures 3 and 4) suggests a brain state in which local neural dynamics are highly stereotyped and efficient, while large-scale functional interactions remain rapidly reconfigurable. This pattern indicates that motor execution relies on a repertoire of simple, reusable neural primitives that can be flexibly recombined in response to task demands. Moreover, we observed an increase in the number of modules alongside a decrease in intra-modular LZC, which we interpret as the emergence of specialized neural primitives for motor control. While each module becomes more dedicated to a specific sub-task (resulting in more stereotyped, lower-complexity dynamics), the overall network retains high flexibility. We therefore assumed that motor learning is characterized not by a global change in complexity, but by the efficient decomposition of tasks into simple, recruitable modules that can be dynamically rearranged.

The present study has potential limitations and caveats regarding the interpretation of the results. First, we could not mention the cerebellar function throughout the present study. It is accepted that the cerebellum plays a key role in the regulation of motor learning, including adaptation (Krakauer and Mazzoni, 2011; Tsay et al., 2024). However, non-invasive measurement of cerebellar electrophysiology is hindered by the limited spatial resolution of human scalp EEG recordings (Andersen et al., 2020). In principle, studies employing EEG delineate functional networks do not account for the cerebellum, as it is not reliably measurable using this technique. That said, the cerebellum is connected to broader cortical regions, including the motor cortex, frontal cortex, parietal cortex, and temporal lobe (Bernard et al., 2012; Schulz et al., 2014). Although we could not directly capture cerebellar function, assessing the dynamics of cortical networks, which receive extensive inputs from and send outputs to the cerebellum, is essential for understanding motor learning. Second, the present

study compared only momentary differences between the two age groups. To account for the entire lifespan, we employed a cross-sectional study design that assesses age-related changes across a continuum from infancy to old age.

In conclusion, the present study revealed dissociated roles of brain network flexibility in motor learning across different age groups. Brain network flexibility during the preparatory period, rather than motor execution, was critical for acquiring and maintaining new motor actions in younger adults, but this coupling was attenuated with aging. Understanding flexible brain dynamics could aid in the development of novel tools to enhance motor learning and mitigate age-related learning limitations.

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Conflict interests

The authors declare no conflicts of interest associated with this paper.

Data and code availability

The data and code that support the findings in this study are available from the corresponding author upon reasonable request.

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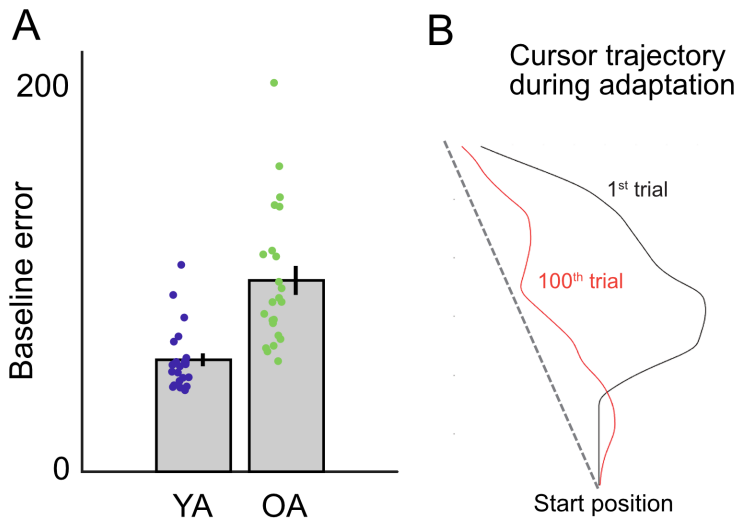
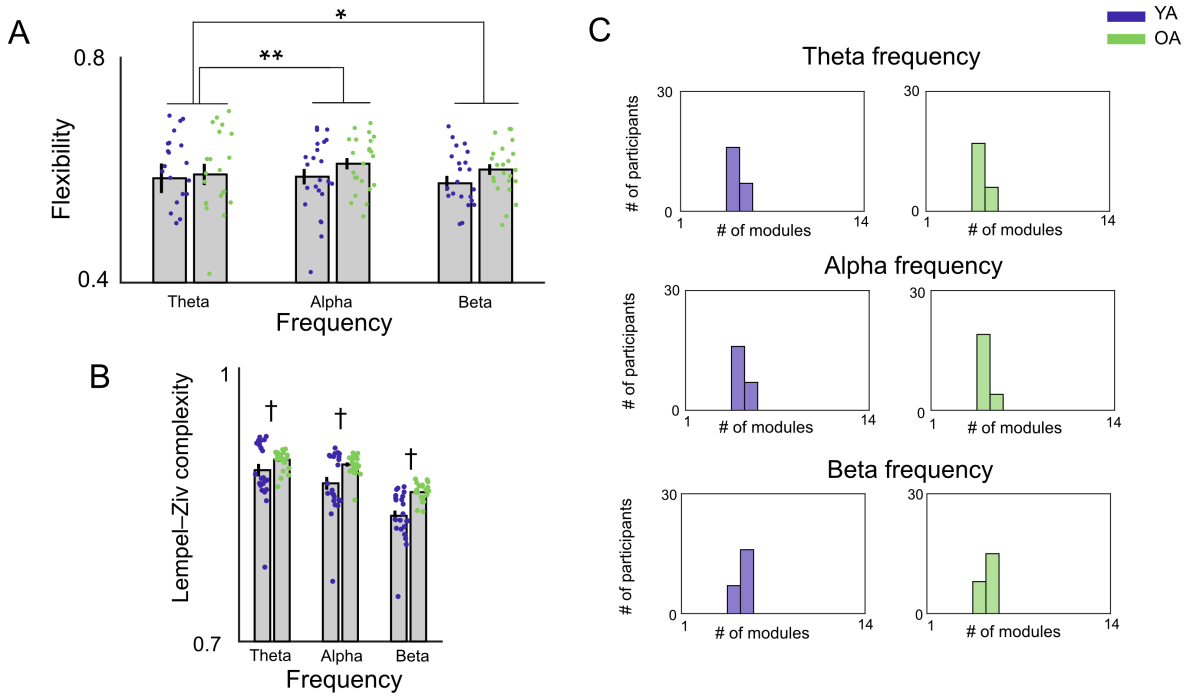
Supplementary Materials



Supplementary Figure 1: Baseline motor performance **(A)** and a typical cursor trajectory during adaptation **(B)**. **A**. Group-averaged error at the baseline across the fifty trials. Each dot represents data from an individual, and each error bar indicates the standard error of the mean across participants. **B**. A typical cursor trajectory during adaptation from a representative participant in the YA group. The deviation of the cursor was decreased consistently across the 100 trials.



Supplementary Figure 2: Group-averaged brain network flexibility during an eyes-open resting state in response to the predefined frequency bands **(A)** and their network properties (**B**: LZC, **C**: Number of network modules). Each dot represents an individual, and each error bar indicates the standard error of the mean across participants. Statistically significant differences between the frequency bands are denoted by ∗∗ $p < 0.001$. Statistically significant difference between the age groups is indicated by † $p < 0.05$.