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Motor skill learning differentially modulates functional connectivity in cortical and corticospinal networks in children, adolescents, and adults

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ABSTRACT

Learning a new motor skill relies on functional reorganization of the human central nervous system (CNS). Plasticity may shape the transmission and communication between cortical regions and between cortical and spinal networks involved in sensorimotor control, but little is known about the influence of age on these adaptations. In a series of experiments, we investigated whether changes in cortical and corticospinal functional connectivity following motor practice differ among individuals at different stages of development (age range 8–30 years old). One hundred and one individuals practiced a visuomotor tracking task in a single experimental session. Functional cortico-cortical and cortico-muscular connectivity were quantified before and after motor training using non-zero lagged coherence estimated from source-reconstructed electroencephalographic (EEG) and electromyographic (EMG) time series. For cortico-cortical coherence, the focus was on sources in a pre-specified cortical network consistently implicated in motor learning. For cortico-muscular coherence, analyses were restricted to the contralateral primary motor cortex. The results showed that upregulation of connectivity in cortical and corticospinal networks, and improvements in motor performance following practice were more pronounced in adults compared to children. Control experiments demonstrated that these changes were dependent on motor practice rather than extended use and on changes in motor performance rather than absolute performance levels. We propose that the reported age-related differences reflect that the mature CNS is tuned to engage in adaptive processes, leading to increased sensorimotor connectivity and improvements in skilled performance during early motor learning. Our results contribute to a better understanding of age-related differences in the network adaptations underlying successful skill learning during human development.

1. Introduction

Motor learning plays a central role in everyday life, and humans acquire and refine motor skills throughout their lifespan. Changes in skilled motor capacity rely on the structural and functional properties of the central nervous system (CNS) and the ability to undergo neuroplastic changes (Dayan and Cohen, 2011). Practicing a new motor skill is accompanied by adaptations that shape the activity and connectivity between regions of the CNS involved in sensorimotor control; however, little is known about how development influences these processes. Here, we investigate the effects of a single session of motor skill practice on changes in the functional connectivity of sensorimotor cortical and corticospinal networks in humans at different stages of typical development.

The mechanisms of skill acquisition in humans have been investigated using neuroimaging and brain stimulation techniques. In adults, learning new motor skills is accompanied by changes in brain activity in an extended sensorimotor network (Hardwick et al., 2013; Lohse et al., 2014). Motor practice also leads to changes in the communication between these brain regions as can be seen as an increase in functional connectivity between them after practice (Albert et al., 2009; Sampaio-Baptista et al., 2015). Increased functional connectivity might

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represent functional reorganization, leading to more efficient communication in sensorimotor networks. The response to motor practice is not restricted to cortical sites. Plasticity in the primary motor cortex (M1) and corticospinal pathway, which plays a pivotal role in fine motor control (Lemon, 2008), has also been reported in adults following motor practice, leading to increases in corticospinal excitability (Jensen et al., 2005; Pascual-Leone et al., 1995) and cortico-muscular functional connectivity (Larsen et al., 2016; Perez et al., 2006). Collectively, these changes may reflect transient adaptations within the cortical and corticospinal networks accompanied by skill acquisition.

Investigations of the neurophysiological underpinnings of skill acquisition in humans have largely been restricted to adults, and current knowledge is sparse of the age-related differences in processes supporting improved motor performance following motor skill acquisition from childhood to adulthood. Consequently, although performance improvements following motor practice are typically reported to be greater (or occur at faster rates) in adults than in children (Beck et al., 2024; Du et al., 2017; Thomas et al., 2004; Vasudevan et al., 2011), the underlying neurophysiological correlates are not well understood. Non-invasive measures of the electrical activity of the brain and muscle acquired by means of electroencephalographic (EEG) and electromyographic (EMG) recordings provide a tool to assess the neural changes associated with motor skill acquisition in individuals of different ages. Owing to their high temporal resolution, EEG and EMG recordings are also particularly well suited to study communication between distant regions of the cortex and between the cortex and the spinal cord during motor tasks. Cortical and muscular oscillations and their synchronization in sensorimotor networks could reflect a functional state in the CNS that supports efficient neural interactions (Buzsáki and Draguhn, 2004; Fries, 2015, 2005; Siegel et al., 2012). This synchronization can be quantified using coherence, a frequency-domain metric quantifying the association between oscillatory activity in distant sources in the cortex, and between the cortex and the target muscle (representing the activity of the relevant alpha motoneuron pool). The results from such analyses provide a non-invasive measure of (changes in) cortical and corticospinal communication. For the sensorimotor system, oscillations and synchrony in the beta band (15–30 Hz) are particularly relevant (van Wijk et al., 2012). Movement is accompanied by a pronounced modulation of cortical beta power (Pfurtscheller and Lopes Da Silva, 1999), and beta-band coherence is present between the cortex and muscle during the maintenance of precise voluntary muscle contractions (Conway et al., 1995). In adults, improvements in skilled motor control through practice lead to a modulation of beta activity and synchrony in cortical networks (Bönstrup et al., 2019; Espenhahn et al., 2019; Gehringer et al., 2019; Rueda-Delgado et al., 2019; Veldman et al., 2018) and cortico-muscular circuits (Larsen et al., 2016; Mendez-Balbuena et al., 2012; Perez et al., 2006). These activity-dependent changes in rhythmic synchronization likely reflect functional reorganization of communication in cortical and corticospinal networks involved in controlling motor output, but it is unknown how these adaptations are affected by age. This is particularly relevant given that children, adolescents, and adults exhibit different neural control strategies (Beck et al., 2021b, 2021a) and acquire new motor skills at different rates (Beck et al., 2024). Understanding potential age-related differences in the mechanisms underlying motor skill acquisition may provide important insights into the neural adaptations and mechanisms underlying motor learning during typical and atypical human development.

Therefore, the aim of the present study was to investigate changes in motor-related functional connectivity in sensorimotor networks following practice of a novel motor task. Specifically, we investigated how non-zero lagged cortical and corticospinal coherence change following motor practice in children, adolescents, and adults (aged 8–30). Based on our previous report demonstrating greater performance improvements during skill acquisition with age (Beck et al., 2024), we hypothesized that greater increases in cortico-cortical and corticospinal coherence would be observed in older individuals than in younger individuals.

2. Methods

2.1. Participants

For the main experiment, we recruited 95 healthy individuals based on their age. Participants were included if they were–8–10yo; 12–14yo; 16–18yo or 20–30yo. In subsequent control experiments, we recruited 21 healthy adult participants between 20–30yo to assess changes in motor performance and in cortical and cortico-muscular connectivity in (1) individuals who did not practice the motor task and (2) individuals who practiced a more difficult version of the task to match the baseline performance of the 8–10yo. None of the participants had any known neurological, psychiatric, neurodevelopmental, or musculoskeletal conditions that could affect hand function and had normal or corrected-to-normal vision. Participants were excluded from the analyses if they failed to complete the motor practice paradigm as intended or if electrophysiological recordings were missing or corrupted by excessive noise. Before enrollment in the experiment, all participants were carefully informed about the purpose of the study. Participants or parents (for individuals aged <18 years) provided written informed consent. This study was approved by the regional ethical committee of the Greater Copenhagen Area (H-17,019,671) and was carried out in accordance with ethical standards of the Declaration of Helsinki. Behavioral data from some participants have been reported in a study investigating changes in performance following motor practice (Beck et al., 2024). Age-related differences at baseline in cortical and cortico-muscular connectivity from a subset of participants have also been presented elsewhere (Beck et al., 2021a, 2021b). In this study, we focus on changes in cortical and cortico-muscular coherence following a single session of motor practice. All data files were re-analyzed for the purposes of this study, as described below.

2.2. Experimental procedure

Participants reported to the lab and were informed of the purpose of the study. Participants completed the Edinburgh handedness inventory (Oldfield, 1971) to assess their laterality status and also filled out a sketched version of the Tanner stage (Marshall and Tanner, 1970, 1969) to assess their physical development. Participants were seated at a table in front of a computer monitor and were equipped with an EEG cap and EMG electrodes on the dominant and non-dominant hand (cf. 'EEG and EMG recordings' below). Participants were asked to complete two tasks: a visuomotor tracking task and a simple pinch task (Fig. 1A). Individuals practiced the visuomotor tracking task with their dominant hand, and their motor performance was evaluated by means of a baseline test and a test of immediate retention before and after approximately 26 min of motor practice (excl. breaks) (cf. 'Visuo-motor tracking task' below). These tests were performed on both the dominant and non-dominant hands (in that order), but in the present study, we focus on task performance on the trained, dominant hand. Just prior to the baseline performance test and immediate retention in the visuomotor tracking task, participants performed a simple pinch task (Fig. 1B). Analyses of functional connectivity using coherence were based on EEG and EMG data recorded while participants performed the simple pinch task with their dominant hand (cf. 'simple pinch task' below). Two additional control experiments were performed in adults. In control experiment 1, we aimed to control for potential differences in the response to practice due to different baseline performance levels and thereby differences in functional task difficulty (Guadagnoll and Lee, 2004). Participants in control experiment 1 followed the same procedure as those in the main experiment but practiced the motor task at a more difficult task level. In control experiment 2, we assessed whether changes in task performance and functional connectivity were related to practice, mere use, and/or the passage of time.

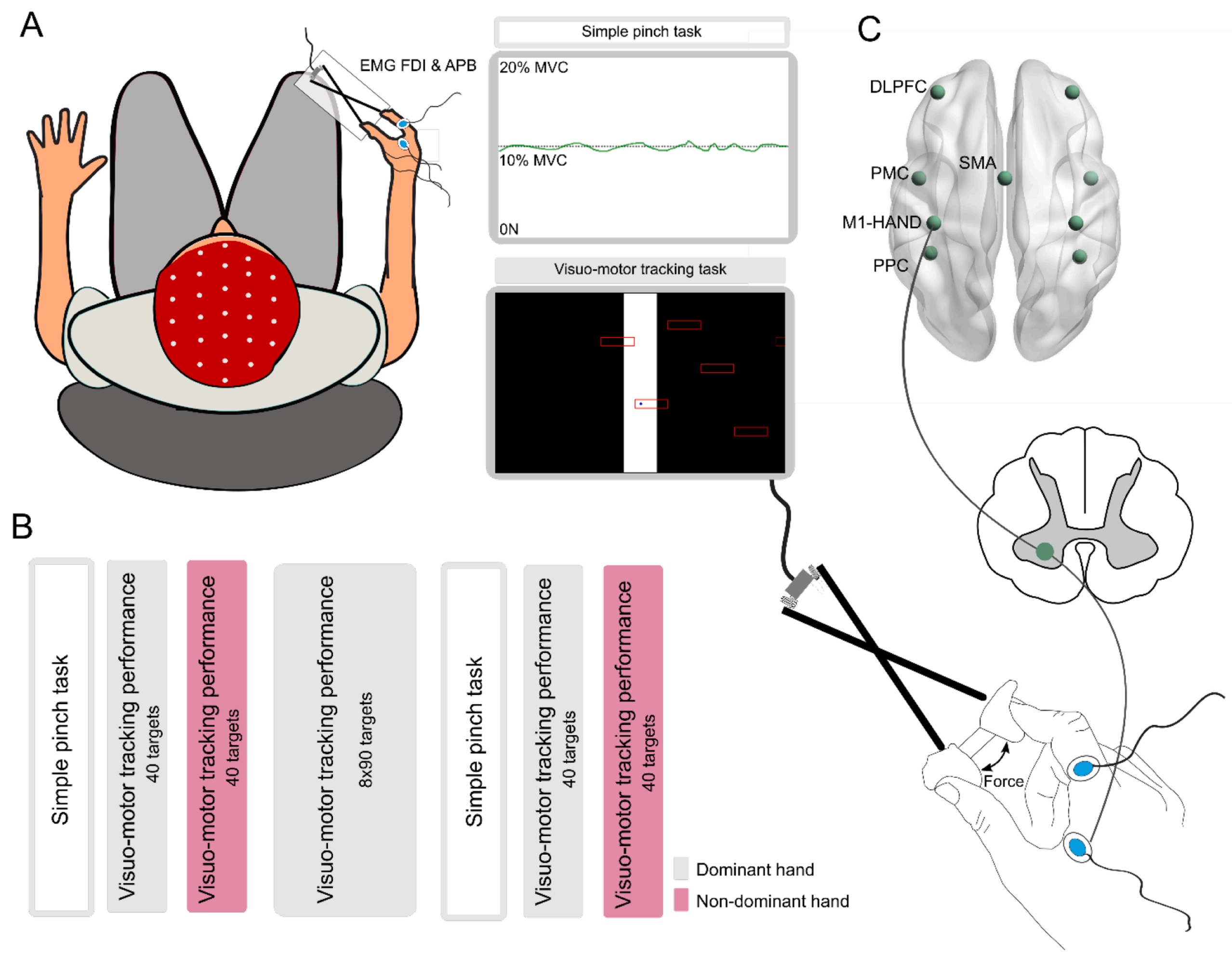

Fig. 1. Experimental setup and procedure. A) Experimental setup. The participants practiced a visuomotor tracking task, and EEG and EMG were recorded while they performed a simple pinch task. B) Experimental design. Displays the time course of the main experiment. In control experiment 1, adult participants followed a similar procedure but performed the task at a more difficult level. In control experiment 2, adult participants were tested at baseline and at immediate retention, but performed steady contractions instead of practicing the task. C) Cortical sources and cortico-muscular network from which coherence was estimated. EMG = electromyography; FDI = first dorsal interosseous; APB = abductor pollicis brevis; MVC = maximal voluntary contraction; PPC = posterior parietal cortex; M1 = primary motor cortex; PMC = premotor cortex; SMA = supplementary motor cortex; DLPFC = dorsolateral prefrontal cortex.

2.3. Visuomotor tracking task

A visuomotor tracking task was used to assess changes in motor performance. This task was chosen because pilot experiments demonstrated that both children, adolescents, and adults could understand and perform the task as intended, and because previous studies using comparable tasks have demonstrated changes in cortical and corticospinal connectivity following practice (Christiansen et al., 2018; Dal Maso et al., 2018). We used a dynamic task for motor practice, since we recently found that dynamic motor practice is accompanied by larger changes in cortico-muscular coherence compared to isometric motor practice (Nielsen et al., 2025). Participants controlled a circle on a 27'' computer monitor (S27D850T, Samsung, Suwon, South Korea)(resolution: 2560 × 1920) by applying force to a spring-loaded lever controlled by their index finger and thumb in a precision grip. The spring-loaded lever was connected to a load cell (UU2-K10, Dacell Co. Ltd., South Korea), and the signal from the load cell was amplified (x100), low-pass filtered (10 Hz) (AM-310, Dacell Co. Ltd., South Korea) and fed to a PC running the task via a custom-made Python application using a DAQ board (NI USB-6008, National Instruments, Austin, Texas) at a sampling rate of 90 Hz. Participants tracked a series of rectangular target boxes sliding horizontally from right to left at a fixed speed by adjusting the force applied to the lever (Fig. 1A). Squeezing the lever caused the circle to move up on the screen, and releasing the lever caused the circle to move down. The circle was red when it was not within the designated targets and turned blue when participants managed to steer the ball inside the rectangular targets, providing participants with augmented online feedback on their performance. The visible window was 1000 × 80 pixels tall and wide, and each target was 20 × 80 pixels tall and wide. First, participants performed a baseline motor performance test consisting of 40 targets for each hand (starting with the dominant hand). This was followed by 8 blocks of motor practice, with 90 targets in each block (8 × 90 targets). Participants rested for a minimum of 2 min between blocks of practice. Following the 8 blocks of motor practice, a ~10 min break was provided during which the simple pinch grip task was performed. Then, another test assessing participants' immediate retention was performed for each hand (starting with the dominant hand) (Fig. 1B).

To control for potential effects of different baseline performance levels between adults and children, adult participants in control experiment 1 followed the same procedure as those in the main experiment; however, the difficulty of the task was increased by lowering the height of the target boxes (12 × 80 pixels tall and wide). The specific target size was based on pilot experiments.

To control for the effects of prolonged use of the hand and/or passage of time, adult participants in control experiment 2 performed an isotonic contraction at a steady force level corresponding to the mean of the target positions from the main task. Participants did not receive any visual feedback on their performance during these contractions but were verbally instructed by the experimenter to ramp their force up or down if the applied force level was too high or too low, corresponding to approximately 75 pixels from the center of the target.

2.4. Simple pinch task

Estimation of functional connectivity using coherence was based on EEG and EMG data recorded while participants performed a simple pinch task with their dominant hand. The simple pinch grip task required the participants to maintain a constant force level using a precision grip at a low force output (10 % of the MVC) for 120 s (Fig. 1A) using real-time visual feedback of their force production. Participants were asked to apply force to a load cell (UU2-K10, Dacell Co. Ltd., South Korea) that they held in a precision grip between their index and thumb. The force produced (amplification: 1000; low-pass filter: 10 Hz; sampling rate: 1000 Hz) (Dacell, AM210, Dacell Co. Ltd., South Korea) was fed back to the participants on a computer screen in front of them to provide online visual feedback. A horizontal target line representing 10 % of the MVC was also displayed on the screen. Participants were instructed to match their force as precisely as possible to match the target line. The rationale for using this specific task was that cortical and corticomuscular coherence are most readily observed during isotonic muscle contractions (Baker et al., 1997; Brovelli et al., 2004; Kilner et al., 2000) and because coherence analysis generally assumes stationarity (Halliday et al., 1995). Furthermore, participants used the same muscles and were provided with similar forms of feedback (*i.e.*, online visual feedback on the produced force in response to a target) as they did in the visuomotor tracking task, providing functional similarity between the two tasks. As such, this task was suited to allow a steady and reliable quantification of functional sensorimotor connectivity while presumably engaging some of the same processes used in the task that participants practiced. Additionally, similar tasks have been found to be sensitive in detecting age-related differences in connectivity (Beck et al., 2021b, 2021a; Petersen et al., 2010; Spedden et al., 2019). Participants were instructed to relax their face and neck muscles during the task to avoid excessive muscle artefacts in the EEG (see below) and to place their inactive hand resting on the table in front of them.

2.5. EEG and EMG recordings

EEG and EMG measurements were obtained using a 64-channel BioSemi amplifier (ActiveTwo, BioSemi, The Netherlands). Sixty-four active EEG electrodes were mounted in an electrode cap that followed the 10–20 EEG cap system. Before placing the electrodes in their designated positions, a conductive electrode gel (SignaGel; Parker Laboratories, USA) was administered in the electrode cups. The electrode offset was below ~30 mV during recording. EMG was recorded from the first dorsal interosseous (FDI) and abductor pollicis brevis (APB) muscles of both the dominant and non-dominant hands using pairs of BioSemi FLAT Active electrodes (11 mm width, 17 mm length, 4.5 mm height). Before placing the electrodes, the skin was carefully prepared using Red Dot Trace Prep. EEG and EMG data were sampled as raw signals at 2048 Hz using ActiView software (v. 7.07). As per BioSemi amplifier design, the driven-right-leg (DRL) and common-mode-sensor (CMS) served as the system references. The sampled data were stored on a PC for offline analysis.

2.6. EEG and EMG preprocessing

Preprocessing of EEG and EMG data was performed in EEGLAB (v2020) (Delorme and Makeig, 2004) in MATLAB 2017b (MathWorks, Natrick, USA). The following preprocessing procedure was performed for each file. First, raw data were visually inspected, and periods with very high amplitude deviations across multiple electrodes (*e.g.*, transient movement or muscle artefacts) were removed from the time series. The EMG data were then separated from the EEG, filtered with a band-pass filter between 5–120 Hz and downsampled to 256 Hz. The EEG data were high-pass filtered at 2 Hz and low-pass filtered at 48 Hz before being downsampled to 256 Hz. EEG channels contaminated with apparent muscle activity based on visual inspection of signal amplitudes, topography and frequency content, over large parts of the time series were removed from the data and individual EEG channels were re-referenced to the average of the remaining electrodes. An independent component analysis (ICA) was performed (EEGLAB's *runica*-algorithm), and components reflecting eye blinks, lateral eye movements, residual muscle activity, and rare events were identified by visual inspection (using the guidelines presented in Chaumon et al. 2015) and removed from the data. Finally, EEG electrodes that had been removed were interpolated using the default spherical interpolation algorithm before merging the EEG and EMG data. These files were converted to Statistical Parametric Mapping (SPM) files using SPM software (SPM12, v. 7408) and divided into 1 s epochs.

2.7. EEG source reconstruction for the estimation of cortical and corticomuscular functional connectivity

Connectivity analyses were performed in the source space rather than the sensor space to mitigate the influence of volume conduction on connectivity estimates (Bastos and Schoffelen, 2016). We were interested in determining the global changes in connectivity in a bi-hemispheric network consisting of nine cortical regions of interest. This *a priori* selection of regions was based on previous meta-analyses that found consistent changes in BOLD activity in these regions with motor learning (Hardwick et al., 2013; Lohse et al., 2014) and on our previous work demonstrating that a similar network is developmentally sensitive (Beck et al., 2021a). These regions included the dorsolateral prefrontal cortex (DLPFC), premotor and supplementary motor areas (PMC and SMA), the hand area of the primary motor cortex (M1), and the inferior parietal lobule (IPL) of the posterior parietal cortex (PPC) in both hemispheres (Fig. 1C). SMA was modelled as a single midline source. Time series of cortical source activity from these regions were reconstructed using a linearly constrained minimum variance (LCMV) beamformer (Van Veen et al., 1997). Beamformers apply adaptive spatial filters to scalp-level data to estimate the maximal source activity for a specific location in the brain while minimizing the influence of other sources. The spatial filters used for beamforming were estimated from the data covariance matrix and the lead field or forward model. Lead fields were generated from a grid of points centered around the MNI coordinates from our regions of interest with a radius and resolution of 5 mm. MNI coordinates for the extracted time series are listed in Table 1. As we did not obtain individual structural brain scans, the SPM template MRI and a Boundary Element Model (BEM) was used to construct the forward model (Litvak et al., 2011). The sensor positions were automatically co-registered with the head model. The covariance matrix was regularized with 5 %. This analysis was performed using the Data Analysis in the Source Space (DAiSS) toolbox in SPM12.

Table 1
MNI-coordinates for reconstructed cortical time-series.

Region	x (mm)	y (mm)	z (mm)
Contralateral / Ipsilateral hemisphere			
DLPFC	−36/+36	46	18
PMC	−46/+46	0	30
SMA	0	0	56
M1-HAND	−38/+38	−24	60
PPC	−40/+40	−40	40

DLPFC = dorsolateral prefrontal cortex; PMC = premotor cortex; SMA = supplementary motor cortex; M1-HAND = primary motor cortex hand area; PPC = posterior parietal cortex.

2.8. Estimating cortical and cortico-muscular functional connectivity using coherence

Coherence was used as a measure of functional connectivity in the cortical and cortico-muscular networks. The coherence between the two signals of interest is defined as the magnitude squared cross-spectral density normalized by the product of the two power spectral densities. In the present study, non-zero lagged coherence was used to estimate changes in cortico-cortical and cortico-muscular connectivity. Non-zero lagged coherence was chosen over traditional measures of coherence to minimize the influence of volume conduction, leading to spurious coherence (with zero time and phase lag) (Bastos and Schoffelen, 2016; Schoffelen and Gross, 2009). Non-zero lagged coherence was estimated using non-parametric directionality analysis (Halliday, 2015; Halliday et al., 2016). This method separates coherence into three components: zero-lagged, forward lagging, and backward lagging, based on the time lag between the two signals of interest. The three coherence components were estimated by applying a pre-whitening filter to the cross-spectrum of the two signals. Following this step, an inverse Fourier transform was applied to convert the frequency estimates into the time domain. This allowed the separation of zero-lagged, forward-lagged, and backward-lagged contributions to coherence (please see Halliday, 2015; Halliday et al., 2016 for the mathematical foundation). Zero-lagged coherence can be contaminated by volume conduction (West et al., 2020) as there is zero time and phase lag between the two signals of interest. Therefore, it was discarded from the analysis (Bastos and Schoffelen, 2016; Schoffelen and Gross, 2009), leaving only the non-zero lagged coherence, that is, the sum of forward and backward coherence. Analyses of non-zero lagged coherence were performed using the open-source MATLAB-based software neurospec (v. 2.11) (http://www.neurospec.org/), with the signals being de-trended, normalized to unit variance, and multitapered.

We had no *a priori* hypothesis regarding regionally specific changes in cortico-cortical coherence. Therefore, we evaluated the changes in cortico-cortical non-zero lagged coherence across the entire (bi-hemispheric) cortical sensorimotor network. Specifically, we were interested in determining global changes in coherence between the nine cortical sources of interest (Fig. 1C). For this purpose, non-zero lagged beta-band coherence was assessed for each connection in the pre-specified bilateral network, and the area of beta band (15–30 Hz) coherence was computed (cumulative sum of coherence values between 15–30 Hz). We focused on changes in the beta band because earlier studies have implicated beta-band computations in motor control (Brovelli et al., 2004), because beta-band power and connectivity may change following motor practice (Espenhahn et al., 2019; Mendez-Balbuena et al., 2012; Perez et al., 2006; Rueda-Delgado et al., 2019), and because beta-band power and synchronization are sensitive in detecting developmental differences (Gehringer et al., 2019; Spedden et al., 2019; Trevarrow et al., 2019). The individual zero-lagged coherence beta-band areas for each of the connections in the network were then summed to obtain a single composite measure, that is, a cortical beta-connectivity index, reflecting global beta-band coherence between all the pre-defined cortical sources (a total of 36). Potential changes in the cortical beta-connectivity index therefore reflect the balance between up-and downregulation of cortico-cortical coherence across all combinations in the extended sensorimotor network of interest. As an exploratory follow-up analysis, we furthermore extracted individual coherence estimates from each of the 36 possible combinations in the network and performed mass-univariate statistical tests (controlling for the false discovery rate; see below) of all possible combinations.

Cortico-muscular coherence was also estimated using non-zero lagged coherence. As previous studies have robustly found cortico-muscular coherence to be focused around primary sensorimotor regions in the contralateral hemisphere (Conway et al., 1995; Mima and Hallett, 1999), we restricted the estimation of cortico-muscular coherence to a single source from the contralateral M1. To estimate non-zero lagged cortico-muscular coherence, the EMG signals were full-wave rectified (Boonstra and Breakspear, 2012; Halliday and Farmer, 2010). Again, we computed the beta-band area of non-zero lagged coherence (cumulative sum of coherence values between 15–30 Hz).

Please note that for left-handed individuals, the sources were flipped across the mid-sagittal line prior to all analyses to account for differences in hand used.

2.9. Statistical analyses

Statistical analyses were performed in Rstudio (R version 4.0.0). To investigate potential age-related differences in skill acquisition we fitted linear mixed models to the behavioral data reflecting the total time spent on target for the participants with Group (4 levels: '8–10yo', '12–14yo', '16–18yo', '20–30yo') and Time (2 levels: 'Baseline', 'Immediate retention') (Group x Time) as fixed effects. To account for the repeated-measurement (RM) design and the fact that individuals likely display different baseline performance values, we fitted random intercepts for each participant. A similar approach was used to evaluate changes in cortico-muscular and cortico-cortical connectivity. Following visual inspection of the *qq-plot* from the fitted mixed models, the residuals were deemed to be non-normal for models with both the global composite measure of cortico-cortical connectivity and areas of non-zero lagged beta-band cortico-muscular coherence. Therefore, a logarithmic transformation of the dependent variables was applied before the mixed models were re-fitted, and this successfully normalized the residuals. The final mixed-effects models were specified as follows:

$$\text{Time on target} \sim \text{Group } x \text{ Time} + (1|\text{participant}) + \varepsilon \tag{1}$$

$$\log(\text{area of beta corticomuscular coherence}) \sim \text{Group } x \text{ Time} + (1|\text{participant}) + \varepsilon \tag{2}$$

$$\log(\text{cortical beta connectivity index}) \sim \text{Group } x \text{ Time} + (1|\text{participant}) + \varepsilon \tag{3}$$

where x represents the interaction between the two fixed effects, (1|participant) reflects the individual random intercepts for each participant and ε the general error term.

As a follow-up analysis, to investigate which cortical connections displayed a change in coherence, a total of 36 individual mixed linear models were fitted with Time as the independent variable, and Participants added as random intercepts for all participants in the main experiment. For this mass-univariate approach, we controlled for the false-discovery rate (FDR) using the Benjamini-Hochberg procedure.

To assess performance and connectivity changes in the 8–10yo and the baseline-matched controls (control experiment 1), a linear mixed effect model with Group (two levels: '8–10yo', 'baseline matched controls'). Time (two levels: 'Baseline', 'Immediate retention') as independent variable was fitted to the data of these individuals.

To assess performance and connectivity changes in the group of adults not practicing the task up against adults practicing the task (control experiment 2), a linear mixed effect model with Group (two levels: '8–10yo', 'No practice controls'). Time (two levels: 'Baseline', 'Immediate retention') as independent variable was fitted to the data of these individuals.

Contrasts of interest were computed from the linear mixed-effects models. Specifically, contrasts reflecting between-group differences before or after motor practice, as well as within-group changes in performance and non-zero lagged cortico-cortical and cortico-muscular coherence, were estimated. Post hoc comparisons were performed using the *emmeans* and *multcomp* packages in RStudio. P-values were corrected for the FDR to control for multiple comparisons using the Benjamini-Hochberg procedure.

3. Results

Participants generally performed the motor learning task as intended. Fifteen individuals were excluded because they did not complete the full motor practice paradigm or because of excessive artefacts in the EEG data based on visual inspection, leaving 101 participants for whom the data were analyzed. Descriptive information on the participants' age, sex, developmental stage, and handedness is shown in Table 2.

3.1. Changes in skilled motor performance following motor training

Fig. 2AB depicts the changes in performance during motor practice as well as performance at baseline and immediate retention for all age groups. As already shown in (Beck et al., 2024), a main effect of age group was found ($F = 35.0$, $P < 0.001$) driven by greater performance levels across time points in the three oldest groups compared to the youngest ($\beta_{20\text{–}30yo\ vs\ 8\text{–}10yo} = 15.29 \pm 1.70; P < 0.001; \beta_{16\text{–}18yo\ vs\ 8\text{–}10yo} = 14.74 \pm 1.72; P < 0.001; \beta_{12\text{–}14yo\ vs\ 8\text{–}10yo} = 10.89 \pm 1.70; P < 0.001$), and in the two oldest age groups compared to the 12–14yo ($\beta_{20\text{–}30yo\ vs\ 12\text{–}14yo} = 4.41 \pm 1.72; P = 0.019; \beta_{16\text{–}18yo\ vs\ 12\text{–}14yo} = 3.86 \pm 1.74; P = 0.036$). A main effect of time was also seen ($F = 509.59$; $P < 0.001$), suggesting that all groups improved motor performance following motor training ($\beta_{8\text{–}10yo} = 12.8 \pm 1.41; P < 0.001; \beta_{12\text{–}14yo} = 16.4 \pm 1.44; P < 0.001; \beta_{16\text{–}18yo} = 17.7 \pm 1.48; P < 0.001; \beta_{20\text{–}30yo} = 18.3 \pm 1.44; P < 0.001$). Finally, an interaction between age group and time was found ($F = 2.97$, $P = 0.037$). Comparing between-group differences in the changes in motor performance revealed that the 20–30yo and the 16–18yo improved performance significantly more than the 8–10yo group ($\beta_{20\text{–}30yo\ vs\ 8\text{–}10yo} = 5.49 \pm 1.42; P < 0.001; \beta_{16\text{–}18yo\ vs\ 8\text{–}10yo} = 4.85 \pm 1.44; P = 0.004$)(Fig. 2C). Although the 12–14yo group displayed an absolute greater change in performance than the 8–10yo group ($\beta_{12\text{–}14yo\ vs\ 8\text{–}10yo} = 3.58 \pm 1.42; P = 0.06$), no significant differences were found for the changes in performance between the remaining groups (range of p-values: 0.06–0.97).

3.2. Changes in sensorimotor functional connectivity following motor training (main experiment)

Cortico-muscular as well as cortico-cortical connectivity were quantified for the simple pinch transfer task as non-zero lagged coherence in all participants before and after motor practice. For the purpose of readability, we simply refer to this as "coherence" in the results section. Fig. 3A displays individual cortico-muscular coherence spectra obtained before and after motor practice from four representative individuals (one from each age group). Fig. 3B displays the individual cortico-cortical coherence spectra (connection PMC-M1) before and after motor practice. As can be seen from these representative participants, increases in beta-band coherence following motor practice were seen in older individuals (>16 years old) but not in younger individuals (<14 years old). This was confirmed by the analysis of beta-band cortico-muscular coherence areas. A main effect of Time was observed ($F = 5.52$; $P = 0.021$), but within-group changes in cortico-muscular coherence following practice were only significant in the 16–18yo group ($\beta = 0.18 \pm 0.08$; $P = 0.028$). No significant changes were observed in the remaining age groups (range of p-values: 0.06–0.59) (Fig. 3B). A main effect of age group was also seen ($F = 3.05$; $P = 0.047$), but none of the group-wise post-hoc comparisons were significant after correcting for multiple comparisons (range of p-values 0.06–0.89). No significant interaction was observed between age group and time ($F = 1.60$; $P = 0.20$).

Similar results were obtained for the cortical beta connectivity index reflecting global cortico-cortical coherence: A significant effect of time was observed ($F = 20.44$; $P < 0.001$), but within-group changes in cortico-cortical coherence were only seen in the 16–18yo ($\beta = 0.19 \pm 0.07$; $P = 0.008$) and the 20–30yo group ($\beta = 0.22 \pm 0.07$; $P = 0.002$). This was not the case for the 8–10yo or the 12–14yo group (range of p-values: 0.12–0.14). No significant effects of age group ($F = 2.13$; $P = 0.10$) or interaction between age group and time were observed ($F = 0.76$; $P = 0.52$). Collectively, these results show a robust increase in beta-band sensorimotor connectivity in both cortico-muscular and cortical networks in older individuals (>16 years), but not in younger individuals (<14 years).

We further performed a mass-univariate post hoc analysis to explore between which cortical regions coherence was changed (up- or down-regulated). After correcting for the false discovery rate, this analysis revealed a significant upregulation of coherence between sources in a contralateral sensorimotor network, including PMC-DLPFC, PMC-M1, PMC-SMA, and M1-PPC, as well as in the ipsilateral connection between M1-PPC (Fig. 3D)(see Supplementary Table S1 for estimated differences and uncertainty of the estimates as well as uncorrected and corrected p-values).

Finally, we performed Pearson correlation analyses to investigate associations between changes in motor performance and changes in cortico-cortical connectivity and cortico-muscular connectivity. No statistically significant correlations were found from these analyses ($r = -0.03$, $P = 0.77$ and $r = 0.03$, $P = 0.79$ for cortical and cortico-muscular coherence, respectively).

3.3. Changes in task performance and sensorimotor functional connectivity following motor training at baseline-matched levels (control experiment 1)

The 8–10yo group displayed lower baseline performance in the visuo-motor tracking task and displayed smaller changes in task performance and cortical and corticospinal connectivity following practice. Therefore, we investigated whether the effects were contingent upon baseline performance levels in the motor learning task, and thereby on functional task difficulty by matching baseline task performance of adults in Control Experiment I to the 8–10yo (Guadagnoll and Lee, 2004). Visuomotor performance was not statistically different between the two groups at baseline ($\beta = -2.60 \pm 2.69$; $P = 0.34$). An interaction between group and time was found ($F = 11.13$; $P = 0.002$), which was driven by greater increases in task performance in the baseline-matched 20–30yo group compared to the 8–10yo group ($\beta = 8.22 \pm 2.47$; $P < 0.001$) (Fig. 4AB). Similarly, an interaction between group and time was found for cortico-muscular coherence ($F = 5.59$; $P = 0.025$). This was driven by the baseline-matched 20–30yo group displaying a significant increase ($\beta = 0.37 \pm 0.14$; $P = 0.015$), which was not seen in the 8–10yo group ($\beta = 0.04 \pm 0.10$; $P = 0.67$) (Fig. 4C). No significant interaction was found between group and time for the cortical connectivity index (F

Table 2
Characteristics of participants included in the main and control experiments.

Experiment	Main	Main	Main	Main	Control Exp 1: baseline-matched	Control Exp 2: no practice
Age group (yo)	8–10	12–14	16–18	20–30	20–30	20–30
Number of participants (n)	21	20	19	20	10	11
Age (years)	9.4 ± 0.6	13.0 ± 0.5	17.2 ± 0.5	24.4 ± 2.3	22.1 ± 4.7	25.1 ± 3.6
Sex (M/F)	10/11	8/12	10/9	9/11	5/5	5/6
Tanner stage	1.2 ± 0.4	2.7 ± 1	4.7 ± 0.6	5	5	5
Handedness (R/L)	17/4	18/2	18/1	20/0	10/0	10/1

Descriptive data of selected characteristics of participants in the main experiment and control experiments 1 and 2. Data are reported as mean ± SDs for continuous data and as counts for categorical data.

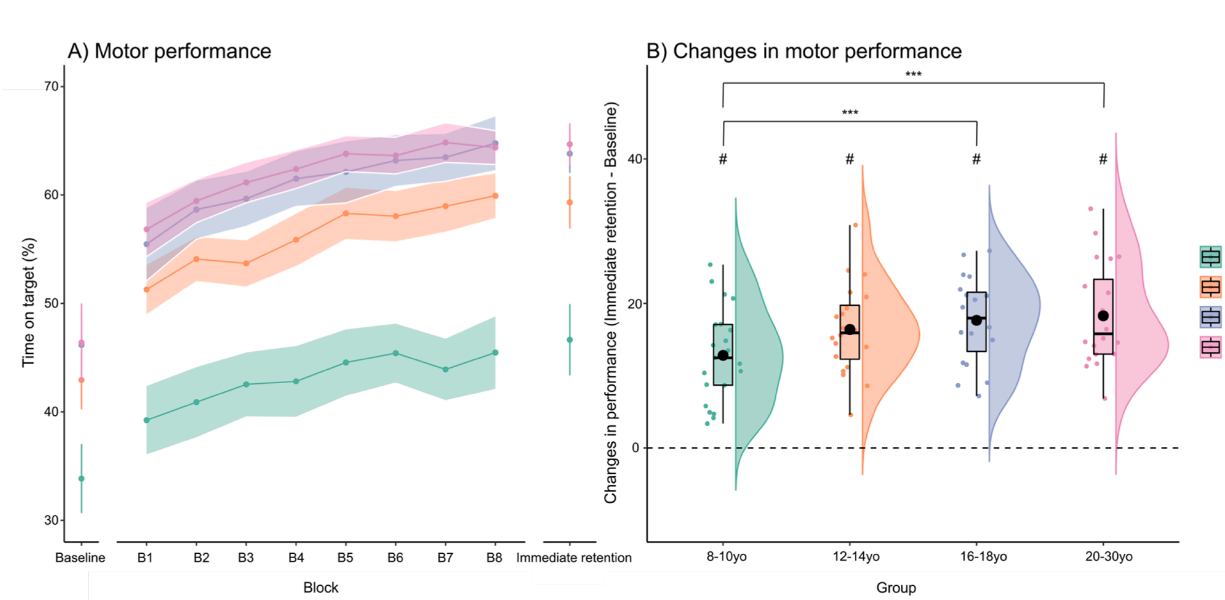

Fig. 2. Changes in motor performance with motor practice are greater in older individuals. A) Total time spent within the target boxes in percentage for each of the four age groups that practiced the visuomotor task. Dots represent group-mean values for each block, and error bars and shaded ribbons represent 95 % confidence intervals. B) Changes in motor performance from baseline to immediate retention. Boxplots with averages, density plots, and individual data points for each age group. # denotes significant changes from baseline to immediate retention within group ($P < 0.05$). *** represents significant differences in the performance changes between groups from baseline to immediate retention ($p < 0.05$).

= 0.01, $P = 0.91$) (Fig. 4D). The results demonstrated that when task level was adjusted to match baseline performance between adults and children, adults still displayed greater improvements in performance. At the same time, adults displayed an increase in cortico-muscular coherence.

3.4. Changes in task performance and sensorimotor functional connectivity without motor practice (control experiment 2)

A group of adults performed isotonic muscle contractions without practicing the task to investigate whether the effects observed in the main experiment could be explained by mere use or passage of time. The control group that did not practice the task still exhibited a significant increase in performance between baseline and immediate retention ($\beta = 6.90 \pm 1.99$; $P = 0.001$), but this was smaller than the improvement displayed by the 20–30yo practicing the task ($\beta = 11.40 \pm 2.48$; $P < 0.001$) (Fig. 5AB). Group-averaged data for cortico-muscular and cortico-cortical connectivity is displayed in Fig. 5CD. For cortico-muscular coherence (Fig. 5C), a significant main effect of Time was found ($F = 4.19$; $P = 0.05$), but although changes were largest in the 20–30yo practicing the task ($\beta = 0.15 \pm 0.08$; $P = 0.08$), none of the within-group comparisons revealed an increase in coherence (range of p-values: 0.08–0.24). No main effect of Group ($F = 0.37$; $P = 0.55$) or interaction between Group and Time was found ($F = 0.01$; $P = 0.92$). For cortico-cortical coherence, no main effect of Group was found ($F = 2.90$; $P = 0.09$), but a main effect of Time ($F = 8.85$; $P = 0.006$) and interactions between Group and Time were found ($F = 5.35$; $P = 0.028$). This was driven by a significant increase in the 20–30yo that practiced the task ($\beta = 0.22 \pm 0.05$; $P < 0.001$), but not in the individuals that did not practice the task ($\beta = 0.03 \pm 0.07$; $P = 0.68$) (Fig. 5D). Control Experiment 2 demonstrated that task introduction, performance tests, and extended use led to subtle improvements in motor performance in the adult control group. Importantly, these were significantly smaller than those of participants who practiced the motor task. Simple muscle activation without motor practice did not lead to changes in cortico-muscular or cortico-cortical coherence.

4. Discussion

We have previously shown that improvements in motor performance following a single session of motor training are greater in adulthood and late adolescence than in childhood (Beck et al. 2024). Here, we demonstrate that older adolescents and adults specifically also are characterized by an upregulation of non-zero lagged beta-band coherence in cortico-cortical and cortico-muscular networks following motor practice. In adults, upregulation of sensorimotor connectivity was not observed in individuals who did not practice the task, suggesting that the changes were dependent on motor skill acquisition rather than on mere use. Furthermore, adults who were matched in motor performance with children at baseline still displayed larger behavioral improvements with motor practice and changes in non-zero lagged cortico-muscular coherence, suggesting that the upregulation of connectivity was related to improvements in motor skill performance rather than absolute performance levels. That said, correlations between changes in connectivity and motor performance were not observed. This shows that changes in cortical and corticospinal connectivity accompanying motor practice are age dependent.

4.1. Increases in cortical and cortico-muscular connectivity following motor practice are age-dependent

Motor practice is accompanied by adaptations in the CNS that support performance improvements through changes in motor output (Krakauer et al., 2019; Schmidt, 1975). As we and others have previously reported, improvements in task performance following practice are greater in adults and older adolescents compared to children (Beck et al., 2024; Thomas et al., 2004; Vasudevan et al., 2011). Changes in motor performance can be ascribed to intrinsic processes in the CNS. Practicing a skill may lead to changes in the efficiency of interactions between central nervous regions through reorganization of functional connectivity in relevant networks that can be identified by neuroimaging and electrophysiological data (Guerra-Carrillo et al., 2014). We show increases in non-zero lagged beta-band coherence in both cortico-cortical and cortico-muscular networks following motor practice

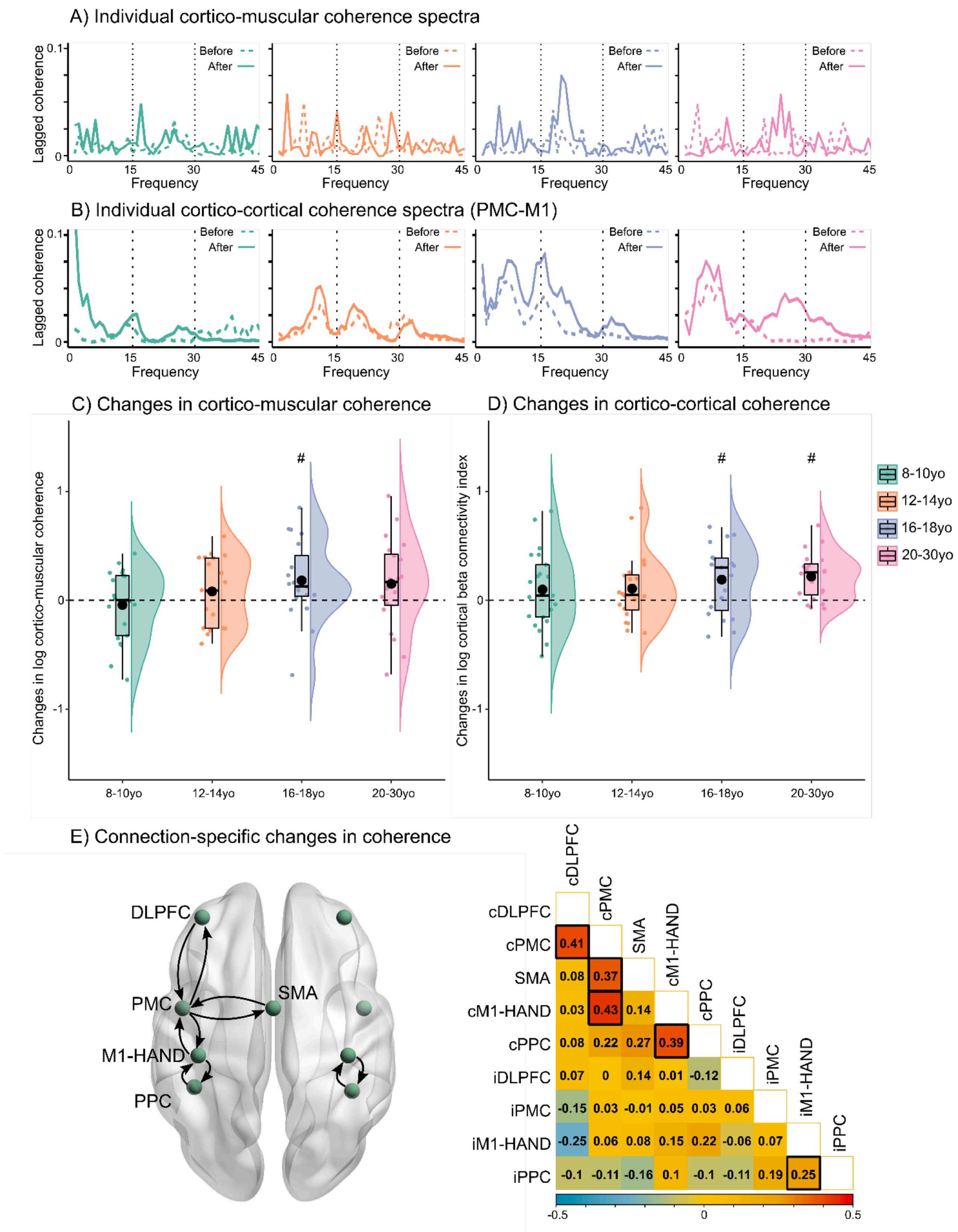

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Fig. 3. Changes in sensorimotor connectivity with motor practice are observed in older individuals. A) Examples of cortico-muscular coherence spectra from individuals in each of the four age groups before (dotted line) and after (full line) motor training. B) Examples of cortico-cortical coherence (PMC-M1) spectra from individuals in each of the four age groups before and after motor training. C) Changes in global cortico-cortical coherence (cortical beta connectivity index) from before to after motor training. D) Changes in cortico-cortical coherence index from before to after motor training. Boxplots with averages, density plots, and individual data points for each age group. # denotes significant changes from before to after motor practice within a group ($p < 0.05$). E) Schematic representation of the sources between which coherence was significantly changed following motor practice (left) and matrix with color-coded estimated changes in the log beta-band area of coherence for specific connections (right) across all age groups. Connections that survived FDR correction are highlighted with an arrow (left) and in a black box (right) (see Supplementary Table 1). The left hemisphere represents the hemisphere contralateral to the hand performing the task. The contralateral and ipsilateral sources of the matrix on the right are denoted as c and i, respectively. PPC = posterior parietal cortex; M1 = primary motor cortex; PMC = premotor cortex; SMA = supplementary motor cortex; DLPFC = dorsolateral prefrontal cortex.

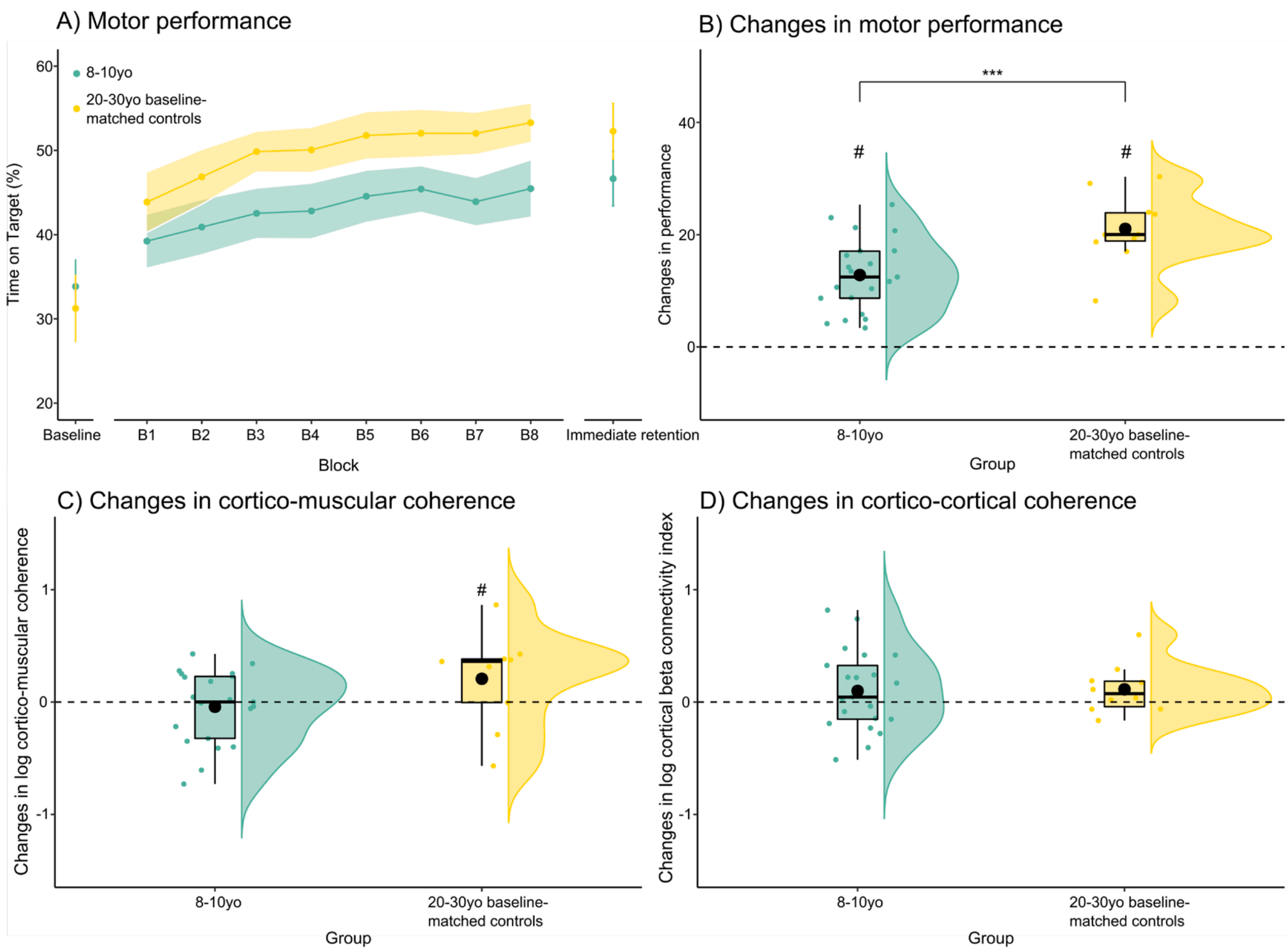

Fig. 4. Upregulation of cortico-muscular connectivity was also observed in adults with baseline matched performance. A) Group-averaged performance at baseline, motor practice, and immediate retention (mean and 95 % CIs). B) Changes in motor performance from baseline to immediate retention. C) Changes in global cortico-cortical coherence (cortical beta connectivity index) from before to after motor training. D) Changes in cortico-cortical coherence index from before to after motor training. Box plots with averages, density plots, and individual data points divided by group. # denotes a significant change from baseline to immediate retention within the group ($P < 0.05$). *** represents significant differences in the performance changes between groups from baseline to immediate retention ($p < 0.001$).

that depend on developmental stage. The theory of communication through coherence (Fries, 2005) suggests rhythmic synchronization as a mechanism to facilitate effective communication between neuronal populations (Fries, 2015, 2005; Schoffelen et al., 2005). From this, increases in network synchrony, as revealed by increased coherence, may reflect facilitation of communication between segregated areas of the CNS resulting from greater network coupling. Our results show that motor practice is accompanied by tuning of synchronization in networks relevant for sensorimotor control. Upregulation of functional connectivity following practice was observed in both cortical and corticospinal networks, and this is well in line with earlier findings using both fMRI (Albert et al., 2009; Sun et al., 2007) and EEG-EMG data (Larsen et al., 2016; Mendez-Balbuena et al., 2012; Nielsen et al., 2025; Perez et al., 2006; Veldman et al., 2018). These studies only tested how adult participants responded to practice. We add to the existing literature by demonstrating that the practice-induced changes in network connectivity indeed seem to be most pronounced in individuals at a later stage of development (*i.e.* older adolescents and adults). This is well in line with previous results from our group showing that cortico-muscular coherence does not increase following a single session of motor practice in preadolescents (Norup et al., 2023). Collectively, these results suggest that network adaptations to motor practice are age-dependent.

A recent study compared practice-induced changes in movement-related beta power in young adults and adolescents (aged 14 years), and found greater changes in adults (Gehringer et al., 2019). We extend the results from this study by showing that age-related differences in the

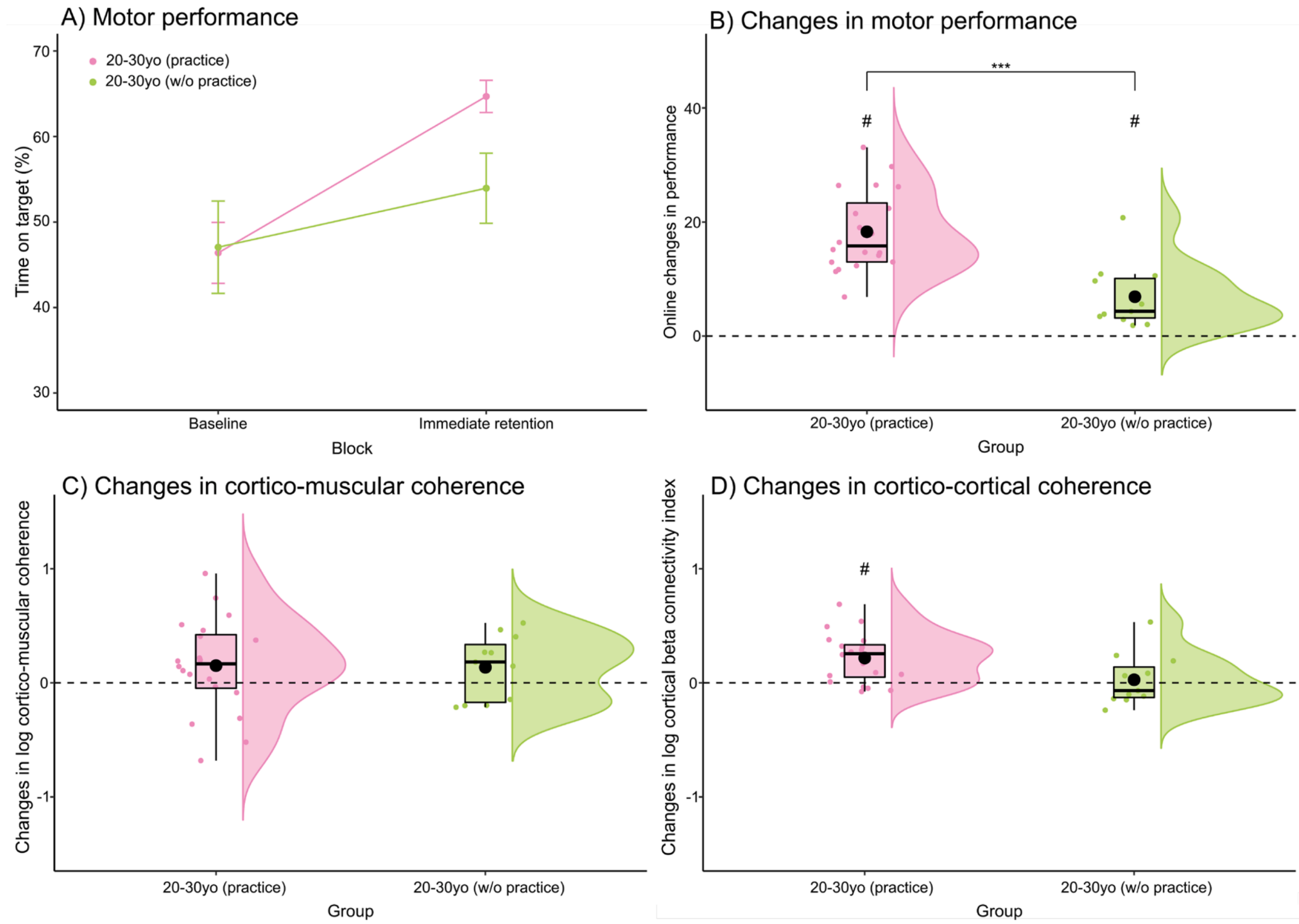

Fig. 5. No changes in sensorimotor connectivity without motor practice. A) Group average performance during baseline and immediate retention (mean and 95 % CI) for adults with and without (w/o) practice. B) Changes in online motor performance from baseline to immediate retention. C) Changes in cortico-muscular coherence from before to after motor training. D) Changes in global cortico-cortical coherence (cortical beta connectivity index) from before to after motor training. Boxplots with averages, density plots and individual data points divided by group. # denotes a significant change from baseline to immediate retention within group ($p < 0.05$). *** denotes significant differences between the changes between groups ($p < 0.001$).

response to motor practice are not restricted to changes in local motor-related beta activity but also involve a differential modulation of beta-connectivity in cortical and corticospinal sensorimotor networks. Upregulation of sensorimotor connectivity was only robustly demonstrated in individuals at a later stage of development, that is, from late adolescence (individuals aged 16–18yo and above). Processes occurring during puberty potently shape the structural and functional organization and properties of the CNS. For example, both resting-state (Miskovic et al., 2015) and task-related (Heinrichs-Graham et al., 2020, 2018; Trevarrow et al., 2019) oscillatory dynamics display protracted maturation and do not converge into adult-like patterns until late adolescence. These developmental adaptations may also influence how the CNS responds to motor practice, as suggested by the relationship between neural oscillations and synchrony and the induction of plasticity (Baur et al., 2020; Buzsáki and Draguhn, 2004; Zrenner et al., 2018). We interpret our findings to reflect that more mature central nervous sensorimotor networks are tuned to engage in the processes leading to early reorganization of sensorimotor connectivity with motor practice.

4.2. Motor practice upregulates functional connectivity in a contralateral fronto-parietal network

A post-hoc analysis was performed to explore where in the *a priori* defined sensorimotor network changes in connectivity was seen. These analyses revealed that changes in sensorimotor connectivity were primarily observed between intra-hemispheric sources in a fronto-parietal network contralateral to the trained hand that included prefrontal, premotor, primary motor, and parietal sources. The fact that the upregulation of connectivity was most prevalent in connections in the contralateral hemisphere supports earlier findings of neural reorganization in cortical sources contralateral to the trained effector (Pascual-Leone et al., 1995; Veldman et al., 2018).

In particular, the PMC displayed pronounced increases in connectivity with the other nodes in this contralateral sensorimotor network. Human neuroimaging studies have indeed emphasized the role of the PMC in motor skill acquisition (Hardwick et al., 2013). But what is the role of PMC in motor learning? In principle, PMC could directly alter motor output via direct mono-synaptic or indirectly via di-synaptic projections to spinal motor neurons, but these are sparse and contribute to a limited extent to direct modulation of movement (Boudrias et al., 2010; Shimazu et al., 2004; Strick et al., 2021). This suggests that PMC mediates (changes in) the motor output via alternative routes. PMC is known to be involved in processes related to sensorimotor integration and, in particular, in associating context-relevant sensory information with intended goals and expected motor outcomes (Davare et al., 2011; Olivier et al., 2007). In this way, processing in PMC might be involved in establishing and updating maps between higher-order goals, sensory information, and motor commands (Halsband and Lange, 2006). These processes also involve extensive interactions with prefrontal and parietal cortical regions (Davare et al., 2010; Rushworth et al., 2005; Tunik et al., 2005). The upregulation of coherence between sources in fronto-parietal circuits might reflect a reorganization of communication involved in sensory-motor mapping accompanied by motor training (Sun et al., 2007).

4.3. Individual changes in functional connectivity are not related to improvements in motor performance

It is interesting that changes in network connectivity were greatest – on the group-level - in those individuals that improved motor performance the most during motor training. This suggests that sensorimotor functional connectivity at the group level covaries with the development of performance over the course of practice. The fact that an upregulation of non-zerolagged cortico-muscular coherence was observed in adults, but not in children, performing at a lower baseline level also suggests that changes in connectivity are related to improvements in skilled performance rather than absolute task performance (Control Experiment 1; Fig. 4). The fact that increases in sensorimotor connectivity were confined to individuals practicing the visuo-motor task, further supports that they are related to motor learning rather than mere use (Control Experiment 2; Fig. 5). It is tempting to directly relate individual changes in sensorimotor connectivity to observed changes in motor performance as observed in previous studies (Houweling et al., 2010; Veldman et al., 2018). However, associations were not observed in the present study. This implies that the changes in sensorimotor connectivity observed in the present study may be a marker of processes occurring during practice that are not directly related to individual performance changes. Future research is needed to understand how changes in functional connectivity and skilled motor performance interact.

4.4. Peri-pubertal dissociation between increases in motor performance and connectivity

In the 12–14 years-old individuals, we observed greater improvements in motor performance compared to 8–10 year-olds but no significant changes in connectivity as observed in the older age groups. We speculate that this may be related to several non-mutually exclusive explanations. First, variability of physical development stage is greatest in this group, and inter-individual differences could mask group-level changes in coherence and motor performance. However, we observed no associations between Tanner scores and changes in connectivity or performance (see Supplementary Material, Fig. S1). Second, individuals in this age group could display differences in the temporal profile of plasticity. We only investigated connectivity before and after motor practice and therefore could not capture dynamic changes in connectivity occurring during training. Third, this group of individuals may rely on other networks than those examined in the present study. We included a broad network comprising several key cortical regions known to be relevant for skill learning, to increase the likelihood of detecting relevant changes across age groups.

4.5. Methodological considerations and limitations

Analyses of cortical connectivity from EEG data are challenged by the spatial spread of electromagnetic fields, leading to volume conduction that can cause spurious correlations in time series (Schoffelen and Gross, 2009; Siegel et al., 2012). This is especially the case for the estimation of cortico-cortical connectivity due to the relative adjacency of the regions of interest. To minimize this, we performed connectivity analyses in the source space rather than the sensor space and used a measure of connectivity (non-zero lagged coherence) that is insensitive to instant temporal (and phase) correlations (Halliday et al., 2016; West et al., 2020; Schoffelen and Gross, 2009; Bastos and Schoffelen, 2016; Van de Steen et al., 2019). From our analyses, it is difficult to dissociate changes in coherence from changes spectral power in one source or both. Furthermore, as connectivity was estimated from EEG activity, we restricted our analysis to spatially segregated sources at the cortical level coupled with EMG recordings. This approach allowed us to track changes in practice-related global connectivity in pre-defined cortical and cortico-motor networks. However, we cannot conclude on changes or age-related differences in connectivity between other cortical and/or subcortical regions, such as the cerebellum or basal ganglia. Finally, our results are also influenced by factors related to the applied analyses, including the chosen inverse method, head model, and estimator of connectivity (Brodbeck et al., 2011; Guggisberg et al., 2011). For example, a template MNI brain was used to construct our head models, as individual structural scans could not be obtained. This neglects age-related and individual differences in *e.g.* head anatomy that can affect the accuracy of the source reconstruction (Brodbeck et al., 2011; Guggisberg et al., 2011). However, we still believe that our approach provided physiologically reasonable results, as the group-level maximum of cortico-muscular coherence was localized close to the hand region of the contralateral M1 across age groups and did not differ qualitatively when compared to age-appropriate MRI templates (Richards et al., 2016) (see control analysis in the supplementary material, Fig. S2).

5. Conclusion

We have previously shown that improvements in skilled motor performance following a single session of motor training are greater in adulthood and late adolescence than in childhood (Beck et al., 2024). Here, we demonstrate that these age groups also display upregulation of functional cortical and cortico-muscular connectivity following motor practice. We propose that this reflects a greater capacity of the mature CNS to undergo short-term adaptations in sensorimotor networks and improve motor performance during motor training. These results contribute to an increased understanding of age-related differences in neurophysiological adaptations to motor practice, which may be used to guide the principles of motor training for individuals at different stages of typical or atypical motor development.

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CRediT authorship contribution statement

Mikkel Malling Beck: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Meaghan Elizabeth Spedden:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Mark Schram Christensen:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Jesper Lundbye-Jensen:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2025.121436.

Data availability

Data will be made available on request.

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