HHS Public Access

Author manuscript

*Neuroimage*. Author manuscript; available in PMC 2025 September 12.

Published in final edited form as:

*Neuroimage*. 2025 September ; 318: 121389. doi:10.1016/j.neuroimage.2025.121389.

# Developmental trajectory of neural activity underlying motor control differs by sequence complexity and motor stage

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## Abstract

Primary motor areas in the brain mature relatively early in development, yet the control of complex movements improves through early adulthood. Neural oscillations in higher-order regions are refined in adolescence and contribute to executive processes important for complex motor control, but the neural dynamics among these regions and primary motor cortices remain poorly understood in youth. We recorded magnetoencephalography during a motor sequencing task in 68 healthy youth from ten to 17 years of age. Significant changes in oscillatory activity relative to baseline were identified at the sensor level and source reconstructed with a beamformer. Whole-brain maps of beta (18–24 Hz) and gamma (74–84 Hz) oscillatory activity were subjected to voxel-wise repeated-measures ANCOVAs to identify brain areas in which the developmental



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Declaration of competing interest

The authors of this manuscript acknowledge no conflicts of interest, financial or otherwise.

trajectory of oscillatory power differed by sequence complexity (simple/complex) or motor stage (planning/execution). Beta activity in bilateral prefrontal cortices was weaker with age during the planning of complex movements. Across simple and complex conditions, older youth tended to have stronger beta in posterior areas during planning. Finally, gamma activity across conditions was stronger with age in occipital and weaker in temporal cortices. These results suggest that the functional refinement of association cortices may drive improvements in motor control by enabling more efficient attentional and inhibitory control during formulation of the motor plan.

**Keywords**

Beta; Gamma; Oscillations; Development; Magnetoencephalography; MEG; ERD

## 1. Introduction

Control over complex movements of the hands and fingers is one of the main ways humans interact with objects in the environment. Such control aids in performing simple actions like grasping or reaching and is extremely important for tasks that require intricate coordination of multiple muscle groups (e.g., typing). Motor competency gradually improves from infancy to adulthood, beginning with improvements in more gross motor functions that enable ambulation and eventually the acquisition of increasingly more complex motor skills that are often used in sports and other adolescent and adult activities (Adolph and Robinson, 2015). Aside from enabling new motor skills, greater motor proficiency has been linked to cognitive development (Bornstein et al., 2013; Koziol and Lutz, 2013; Simpson et al., 2019), and vice versa (Gaul and Issartel, 2016; Rinne et al., 2018; Schulte et al., 2020). Thus, refining the capacity for coordinated multi-muscle movements is essential for normative development.

In typically developing youth, manual dexterity emerges fairly early in childhood (Fuelscher et al., 2021; Gerber et al., 2010), and indeed, the primary motor cortices display signs of gross structural maturity as early as nine years of age (Shaw et al., 2008). However, hand and finger control, especially for complex finger movements, continues to be refined well into adolescence (Fuelscher et al., 2021; Heinrichs-Graham, McDermott, et al., 2018). This is at least partially due to a collection of nonmotor association areas that mature later and are responsible for various cognitive processes that are active during motor control, such as visuomotor integration in the parietal cortex (Beurze et al., 2007; Cui and Andersen, 2011), behavioral inhibition and response selection in the dorsolateral prefrontal cortex (DLPFC; (Bartoli et al., 2018; Kaller et al., 2011), and attentional control in the superior and middle temporal gyri (Ramezanpour and Fallah, 2022; van Kemenade et al., 2019). Further, adolescence is widely accepted as a critical period for the refinement of higher-order cognition (Blakemore et al., 2010; Fuhrmann et al., 2015; Knudsen, 2004; Larsen et al., 2023; Larsen and Luna, 2018; Luna et al., 2004, 2010, 2015), and such functional maturation of the association cortices leads to improvements in executive processes that directly support better control over complex sequential movements.

The dynamics of motor control has been widely studied. Beginning several hundred milliseconds before the onset of a voluntary movement, populations of synchronously active pyramidal neurons in the motor cortex exhibit robust decreases in band-limited beta (~15–30 Hz) power relative to baseline, termed the peri-movement beta event-related desynchronization (ERD). This response persists until after movement termination and is strongest in the contralateral primary motor cortex, but is also present in the ipsilateral motor cortex, albeit to a lesser extent (Cheyne, 2013; Gaetz et al., 2010; Heinrichs-Graham, McDermott, et al., 2018; Heinrichs-Graham and Wilson, 2015; Heinrichs-Graham and Wilson, 2016; Kurz et al., 2016; Pfurtscheller et al., 2003; Trevarrow et al., 2019). The beta ERD has been linked to planning and response selection, and is modulated by multiple parameters, such as the certainty of the upcoming response (Doyle et al., 2005; Tzagarakis et al., 2010, 2015). The beta ERD is also important for motor execution, responses are often stronger during movement execution versus planning (Heinrichs-Graham et al., 2016; Heinrichs-Graham and Wilson, 2015; McCusker et al., 2021). Further, executing more complex movements tends to elicit stronger ERDs in higher order brain regions like the DLPFC than executing simple movements (Heinrichs-Graham and Wilson, 2015; Wilson et al., 2010). Following the termination of the movement, there is a subsequent increase in beta power that has been termed the post-movement beta rebound (PMBR). The response typically peaks in the postcentral gyrus, slightly posterior to the beta ERD (Gaetz et al., 2010; Wilson et al., 2010, 2011; Wilson, Fleischer, et al., 2011). The functional role of the PMBR is generally thought to reflect either inhibitory motor control processes (Gaetz et al., 2010; Heinrichs-Graham et al., 2017) or the processing and integration of somatosensory feedback (Cheyne, 2013).

Beyond oscillations in the beta range, there is a transient gamma (roughly 60–90 Hz) response that is tightly locked to movement onset and centered on the primary motor cortex contralateral to movement (Cheyne et al., 2008; Gaetz et al., 2013; Heinrichs-Graham, Hoburg, et al., 2018; Muthukumaraswamy, 2010; Spooner and Wilson, 2022, 2023; Wiesman et al., 2021; Wilson et al., 2010). This response is often termed the movement-related gamma synchronization (MRGS). The MRGS is observed during cued and self-paced movements and is typically strongest during the first movement in a repetitive sequence (Muthukumaraswamy, 2010). It is also present at the onset of, but is not sustained throughout, an isometric contraction (Muthukumaraswamy, 2010). Due to these properties, the MRGS is generally thought to reflect the motor output signal (Cheyne, 2013; Muthukumaraswamy, 2010). Interestingly, recent evidence suggests that the MRGS is modulated by cognitive interference and movement certainty, reflecting a potential role in cognitive-motor integration (Grent-’t-Jong et al., 2013; Heinrichs-Graham, Hoburg, et al., 2018; Wiesman et al., 2020, 2021). However, not all motor paradigms elicit this response (Heinrichs-Graham et al., 2016, 2020; Heinrichs-Graham, McDermott, et al., 2018; Heinrichs-Graham and Wilson, 2015; Killanin et al., 2023; McCusker et al., 2021; Ward et al., 2023; Zhang et al., 2025) and additional work is needed. The latter is especially true in the case of development, as far more is known about the development of motor-related beta oscillations during childhood and adolescence compared to the MRGS response. Of the few developmental studies that have examined the MRGS, the general finding is that it

becomes weaker with increasing age from childhood to late adolescence (Trevarrow et al., 2019; Wilson et al., 2010; Zhang et al., 2025).

Regarding the impact of development on these processes, many studies have shown that the strength of primary motor responses scale with age in youth (Bardouille and Bailey, 2019; Barlaam et al., 2018; Cheyne et al., 2014; Fung, Heinrichs-Graham, et al., 2022; Gaetz et al., 2010; Heinrichs-Graham, McDermott, et al., 2018; Heinrichs-Graham et al., 2020; Johnson et al., 2020; Killanin et al., 2023; Trevarrow et al., 2019), but only three have examined the oscillatory dynamics serving sequential finger movements as opposed to isolated single movements. The neural parameters for programming sequential movements are much more complicated than single, repetitive movements, as they require a higher level of inter-muscle coordination and thus planning activity for successful execution. Further, the corpus of possible movements becomes much larger in the case of three or more sequential movements per trial, which decreases the predictability and increases the motor planning burden. Heinrichs-Graham et al. (2018) found that the overall strength of the beta ERD in bilateral primary motor cortices increased linearly with age across the lifespan during a motor task consisting of three sequential finger movements that involved the second through fifth digit of the right hand (i.e., index finger to pinky) and did not systematically vary in complexity or other factors (Heinrichs-Graham, McDermott, et al., 2018). A later study from the same group (Heinrichs-Graham et al., 2020) used the same task and structural equation modeling to evaluate relationships between motor and parietal cortex activity, age, and behavioral performance. They found that age predicted beta planning activity in the superior parietal cortices, but not the primary motor cortices, although planning activity in the left primary motor cortex predicted execution activity in the right motor cortex. Further, older youth had stronger beta planning activity in the right parietal cortex, which predicted stronger execution activity, predicting shorter movement durations (Heinrichs-Graham et al., 2020). These results suggest that the primary motor cortex has an important role in guiding oscillatory activity throughout the motor network, and further solidified that the right superior parietal cortex as a hub for such sequential movements (Heinrichs-Graham and Wilson, 2015). Lastly, Killanin et al. (2023) measured testosterone via saliva and showed that higher levels mediated the direct relationship between age and beta ERD in the motor cortex during movement execution, and that older youth had greater testosterone levels, which predicted faster reaction times and shorter total movement durations during a motor sequencing task that involved three finger movements (Killanin et al., 2023). These results build upon the previous study's motor cortex and behavioral findings, suggesting that the increase in testosterone levels in adolescence is a driving factor behind age-related changes in motor-related beta activity and behavioral performance.

Though these three studies provided important information about how development modulates motor oscillations and behavioral performance during coordinated sequential movements of the fingers, none of them tested whether motor-related oscillations in youth are modulated by different levels of sequence complexity. In other words, all of these previous studies involved a series of three-movement sequences, but all three had only one task condition and thus did not manipulate complexity of the sequence, type of movement, starting position, or other factors. They also focused on beta oscillations and did not distinguish pre-movement beta responses from those occurring during and/or

after movement onset. In contrast, sequential movement studies in adults have examined how factors such as sequence complexity and/or movement phase (i.e., planning versus execution) modulate beta ERD power and the extent to which non-primary motor areas are recruited (Heinrichs-Graham and Wilson, 2015; McCusker et al., 2021; Ward et al., 2023). These adult studies have shown greater involvement of prefrontal and superior parietal cortices during more complex movements, as well as robust differences in response strength between planning and execution time windows in such higher order areas (Heinrichs-Graham and Wilson, 2015; Ward et al., 2023). Presumably, such sequence complexity and time window effects would be even more robust in the less refined motor systems of children, but to date no such studies have been conducted.

To address these gaps, we collected high-density magnetoencephalography (MEG) data during a motor sequencing paradigm with two levels of sequence complexity in nine to 17 year-old youth to investigate whether varying complexity affected the neural oscillatory dynamics underlying volitional motor control. To this end, we used a whole-brain, voxel-wise statistical approach to identify brain areas in which oscillatory activity underlying motor control covaried with age and evaluated whether these relationships differed as a function of sequence complexity (i.e., simple versus complex) or movement stage (i.e., planning versus execution). We hypothesized that the complex sequences would be comparatively more difficult for younger participants, and that this would be reflected by stronger beta ERDs in cognitive control regions during movement execution, but not during planning, and that stronger MRGS would be present in the contralateral motor cortex. However, our data-driven approach to identifying neural oscillations and whole-brain, voxel-wise statistical modeling was equally sensitive to non-hypothesized effects. Thus, our analytical approach was consistent with a more discovery-oriented framework, which we believe is appropriate given the field's limited knowledge on how experimental factors affect the development of motor-related oscillations in children and adolescents.

## 2. Methods

### 2.1. Participants

A total of 68 typically developing participants (36 female; four left-handed) between nine and 17 years of age (mean age: 13.08; SD: 1.66) completed all study procedures. All participants were enrolled in the Developmental Chronnecto-Genomics (DevCoG) study at the Omaha, Nebraska, USA site (Stephen et al., 2021). Potential participants were excluded from the study based on the following criteria: any diagnosed neurological or psychiatric disorder, any medical illness associated with CNS dysfunction, history of head trauma, current substance use, pregnancy, and standard MEG/MRI contraindications (e.g., metallic implants that could impede MEG or MRI data acquisition). All study procedures were approved by the local Institutional Review Board (IRB) and all ethical regulations relevant to human research participants were followed in accordance with the Declaration of Helsinki. Prior to participating, participants and their parent or legal guardian provided written informed assent and consent.

### 2.2. Experimental paradigm

We used a motor sequencing paradigm designed by Heinrichs-Graham and Wilson (2015) that has been used in several adult studies (Heinrichs-Graham and Wilson, 2015; McCusker et al., 2021; Son et al., 2025; Spooner and Wilson, 2023; Ward et al., 2023). Participants were instructed to place their right hand on a button pad that was positioned on a tray directly in front of them, and to respond to the stimuli as fast and as accurately as possible. Note that the participant's hand was visible to them throughout the recording. During each trial, participants viewed a fixation cross for 3750 ms during MEG recording. Three numbers, each corresponding to a finger on the right hand (i.e., "1″ for index, "2″ for middle, etc.), were shown on the screen for 500 ms. The numbers on the screen then changed color, indicating the cue to move, and participants had 2250 ms to tap out the sequence with the corresponding fingers. After the 2250 ms, the numbers disappeared, leaving only the fixation cross on the screen (Fig. 1A). The experiment consisted of two conditions, simple and complex sequences. The simple sequences included three numbers corresponding to adjacent fingers on the right hand (e.g., "2–3–4″; middle-ring-pinky finger), whereas the complex sequences consisted of three numbers corresponding to nonadjacent fingers on the right hand (e.g., "4–1–2"; pinky-index-middle finger). There was a total of 160 trials that were pseudo-randomized (i.e., no more than three of the same trial type could be presented sequentially) and equally split between condition, resulting in a task duration of approximately 16 min.

### 2.3. MEG and MRI data acquisition

Functional MEG data were collected using a 306-sensor MEGIN MEG system (Helsinki, Finland) equipped with 204 planar gradiometers and 102 magnetometers. Data were acquired at a 1 kHz sampling rate with an acquisition bandwidth of 0.1 – 330 Hz in a one-layer magnetically shielded room. Prior to recording, four coils were attached to the participants head and localized along with fiducial and scalp surface points using a 3D digitizer (FASTRAK, Pollhemus Navigator Sciences, Colchester, Vermont). Once participants were seated in the MEG chair for recording, an electric current with a unique frequency label (i.e., 322 Hz) was fed to each coil, inducing a measurable magnetic field. This allowed each coil, and therefore the head, to be localized in reference to the MEG sensor array throughout the entire recording session. Further, throughout the session, a real-time audio-video feed was used to monitor participant motion and to ensure the participant followed the task instructions.

A 3.0T Siemens Prisma scanner equipped with a 32-channel head coil was used to collect high-resolution structural T1-weighted MRI data from each participant (TR: 24.0 ms; TE: 1.96 ms: field of view: 256 mm; slice thickness: 1 mm with no gap; resolution: 1.0 × 1.0 × 1.0 mm). Structural volumes were aligned parallel to the anterior and posterior commissures and underwent inhomogeneity correction, segmentation, surface reconstruction, and transformation into standardized space. Each participant's MEG data were co-registered with their MRI data using BESA MRI (v3.0). After source imaging, each subject's functional images were also transformed into standardized space using the transform previously applied to the structural MRI volume, and spatially resampled.

### 2.4. Time-frequency transformation and statistics

MEG data were subjected to environmental noise reduction and corrected for head motion using the signal space separation method with a temporal extension (Taulu and Simola, 2006). Eye blinks and cardiac artifacts were removed from the data using signal space projection (SSP), which was accounted for during source reconstruction (Uusitalo and Ilmoniemi, 1997). The time series was then divided into 6400 ms epochs, including a baseline window from −2250 to −1750 ms, with the onset of movement defined as 0 ms. Epochs containing artifacts were rejected based on a fixed amplitude and gradient threshold method that was set per participant and supplemented with visual inspection. Briefly, the raw signal amplitude is strongly affected by the distance between the brain and the sensor array, as the magnetic field strength falls off sharply as the distance from the current source (i.e., brain) increases. Thus, to account for this and other sources of variance across participants, we used individualized thresholds based on the signal distribution for both amplitude ($M$ = 1487.13 fT/cm, SD = 338.85) and gradient ($M$ = 590.66 fT/(cm*ms), SD = 206.83) to reject artifacts. Trials where the participant completed the sequence incorrectly or too slowly (> 3000 ms) were also excluded from further analysis. The average number of accepted trials used for analysis was 121.75 (SD 23.21) and did not differ by sex ($t$ = −0.66, $p$ = .51) or condition ($t$ = −0.63, $p$ = .53), and was not correlated with chronological age ($r$ = 0.21, $p$ = .092).

Artifact-free epochs were transformed into the time-frequency domain using complex demodulation (Kovach and Gander, 2016; Papp and Ktonas, 1977). The resulting spectral power estimations per sensor were averaged across trials, generating time-frequency plots of mean spectral density. The sensor-level data were then normalized per time-frequency bin using the respective bin's baseline power, which was calculated by averaging the power during the 500 ms baseline period. The specific time-frequency bins used for source reconstruction were determined using a data-driven method based on the general linear model. Specifically, to reduce the risk of false-positive results while maintaining reasonable sensitivity, a two-stage procedure was followed to control for Type-1 error. In the first stage, two-tailed paired-sample $t$-tests against baseline were conducted across both conditions and all participants on each data point per spectrogram, and the output spectrogram of t-values was thresholded at $p < .05$ to define time-frequency bins containing potentially significant oscillatory deviations across all participants and both conditions. In stage two, the spectrogram data points that survived the threshold were clustered with temporally and/or spectrally neighboring data points that were also above the threshold ($p < .05$), and a cluster value was derived by summing the t-values of all data points in the cluster. Nonparametric permutation testing was then used to derive a null distribution of cluster values, and the significance level of the observed clusters (i.e., time-frequency windows) from stage one were tested directly using this distribution (Ernst, 2004; Maris and Oostenveld, 2007). For each comparison, 10, 000 permutations were computed. Based on these analyses, the time-frequency windows containing significant oscillatory events relative to baseline across all participants and both conditions were subjected to beamforming. For further details on our data processing pipeline, see (Wiesman and Wilson, 2020). Note that the goal of our sensor-level analyses were to identify the time-frequency windows where there were significant movement-related changes in MEG signal strength relative to the baseline

period for subsequent beamforming analyses. We did not compare the different movement conditions (i.e., simple/complex), examine developmental effects, or time window effects (i.e., planning/execution) at the MEG sensor-level because we were most interested in these effects at the cortical level and conducting the same statistical tests at both the sensor- and source-level can lead to inflated Type I error and is generally discouraged (Gross et al., 2013; Kriegeskorte et al., 2009).

### 2.5. MEG source imaging and statistical analyses

Oscillatory neural responses were imaged using the dynamic imaging of coherent sources (DICS) beamformer (Gross et al., 2001; Van Veen et al., 1997), which utilizes spatial filters in the time-frequency domain to calculate voxel-wise source power for the entire brain volume. The single images were derived from the cross-spectral densities of all combinations of MEG gradiometers averaged over the time-frequency range of interest and the solution of the forward problem for each location on a grid specified by input voxel space. Following convention, we computed noise-normalized source power for each voxel per participant using active (i.e., task) and passive (i.e., baseline) periods of equal duration and bandwidth (Hillebrand et al., 2005) at a resolution of 4.0 × 4.0 × 4.0 mm. Such images are referred to as pseudo-*t* maps, with units (pseudo-*t*) reflecting noise-normalized power differences (i.e., active versus baseline) per voxel. To assess the neuroanatomical basis of the significant oscillatory responses identified through the sensor-level analysis, grand-average whole-brain pseudo-*t* maps were computed. MEG preprocessing, coregistration, and imaging used the Brain Electrical Source Analysis (BESA Research v7.1, Statistics v2.1, MRI v3.0) software.

Behavioral data were analyzed using separate 2 × 1 analyses of covariance (ANCOVAs) for each metric (accuracy, reaction time, movement duration, and inverse efficiency), with condition as the within-subjects factor and age as the covariate of interest in IBM SPSS Statistics (v29.0.0.0).

A whole-brain, voxel-wise, 2 × 2 × 1 ANCOVA model was used to examine the within-subjects effects of sequence complexity (i.e., simple vs. complex) and window (i.e., movement planning vs. execution) on beta oscillatory activity supporting motor control, with age as a between-subjects covariate of interest. Note that the time-frequency windows used for imaging the beta response were determined via a data driven method (see previous section), with the exception that we divided pre-movement (−500 to 0 ms) and post-movement (0 to 500 ms) onset data to determine if there were developmental and/or conditional differences between the movement planning and execution phases, as this parameter was central to our primary hypotheses. Regarding the gamma response, a whole brain, voxel-wise, 2 × 1 ANCOVA was used to examine the within-subjects effects of sequence complexity on gamma oscillatory activity with age as a between-subjects covariate of interest. The time-frequency window used for imaging the gamma response was also determined via a data driven method (see previous section). Note that the gamma response was centered on movement onset and much more transient than the beta response, so we were unable to examine the window variable (i.e., planning/execution). For the resultant statistical maps, a stringent *p*-value threshold of $p < .005$ in conjunction with a cluster

threshold of 9 contiguous voxels (approximately 575 $mm^3$ of tissue) was used to account for multiple comparisons (Poline et al., 1995; Worsley et al., 1996, 1999). All whole-brain ANCOVAs were performed using R (R Core Team, 2022). Data plots were created in R using ggplot2 (Wickham, 2016). Finally, to reduce the impact of outliers on statistical analyses, participants with values 3 SDs above or below the respective sample mean were excluded.

## 3. Results

### 3.1. Participant characteristics and behavioral performance

All 68 participants (35 female; mean age 13.08 years, SD 1.66 years) successfully completed the motor sequencing task with a mean accuracy, reaction time, and movement duration of 92.95 % (SD 6.98 %), 658.93 ms (SD 238.00 ms), 867.22 ms (SD 178.18 ms), respectively. We also computed inverse efficiency scores using the reaction time (IES-RT mean: 672.83 ms, SD 273.0 ms) and the movement duration data (IES-MD mean: 889.97 ms, SD 176.47 ms). For each behavioral metric (i.e., accuracy, reaction time, movement duration, and inverse efficiency), an 2 × 1 ANCOVA with movement condition as a two-level within-subjects factor (simple/complex) and age as a covariate of interest was computed. These revealed a main effect of condition on movement duration ($F = 11.79$, $p = .001$), IES-RT ($F = 7.25$, $p = .009$), and IES-MD ($F = 9.25$, $p = .003$), but not accuracy ($F = 2.36$, $p = .13$) or reaction time ($F = 1.99$, $p = .16$), with complex movements having longer durations than simple (Fig. 1B) and worse efficiency in terms of both initiating (i.e., reaction time) and completing (i.e., movement duration) the sequence. There was also a main effect of age on movement duration ($F = 12.11$, $p < .001$), reaction time ($F = 7.39$, $p = .008$), IES-RT ($F = 8.06$, $p = .006$), and IES-MD ($F = 6.70$, $p = .012$), but not accuracy ($F = 1.39$, $p = .24$). These main effects of age indicated that independent of condition, older youth were faster to react, completed sequences in less time than younger participants, and were more efficient in both starting and completing the sequences. Finally, there was an age-by-condition interaction in movement duration ($F = 7.42$, $p = .008$) and IES-MD ($F = 6.65$, $p = .012$). These effects were such that younger participants were much slower and less efficient in completing the full sequence in the complex condition, but as age increased, movement duration and efficiency in completing the complex sequence approached that of the simple (Fig. 1B). Lastly, to assess whether reaction time and movement duration were related, we computed Pearson correlations per complexity condition. These indicated that reaction time and movement duration were positively correlated in both the simple ($r = 0.417$, $p < .001$) and complex ($r = 0.551$, $p < .001$) conditions.

### 3.2. Sensor- and source-space analyses

Statistical analyses of the sensor-level time-frequency spectrograms across all participants and both conditions were conducted to identify the time-frequency windows for beamformer source reconstruction. As described in the Methods section (*Time-frequency transformation and statistics*), these analyses used a two-stage procedure consisting of two-tailed paired-sample *t*-tests against baseline in stage one to define time-frequency bins containing potentially significant oscillatory deviations ($p < .05$), followed-up with nonparametric permutation testing on the resulting clusters to control for multiple comparisons. These

analyses revealed significant decreases in power relative to baseline (i.e., ERD) in sensors near the left motor cortex ($p < .001$, corrected; Fig. 2A). These power decreases, or ERDs, began about 500 ms before movement onset and terminated about 1000 ms after onset. The beta ERD bandwidth was 18–24 Hz, and we divided this into separate pre-movement planning (−500 to 0 ms) and execution (0 to 500 ms) phases as part of our hypotheses. We also observed a significant event-related synchronization (ERS), or increase in power relative to the baseline, in the gamma band (74–84 Hz) from −250 to 250 ms in sensors near the left motor cortex (all $p$s < 0.005, corrected). Note that we did not examine the post-movement beta rebound response (visible from 2000–3000 ms in Fig. 2A) because our two movement conditions (simple vs. complex) differed significantly in movement duration and this would bias the amplitude of the response and obscure interpretation. Likewise, there was also an alpha response from 9–12 Hz that can be seen in Fig. 2A, but this response was much weaker and previous work has generally linked it to somatosensory processing, thus we did not further examine (McCusker et al., 2021; Pineda, 2005; Salmelin et al., 1995). Finally, to ensure the older youth did not bias the frequency windows toward higher or lower values, we computed the peak frequency in each participant for beta and gamma activity and found that the peak frequency was not correlated with age across our sample for either beta or gamma responses (all $p$s > 0.62), which is consistent with the gamma findings of Gaetz et al. (2010).

To assess data quality and identify the anatomical regions generating the strongest beta and gamma responses, we imaged these significant time-frequency windows using a beamformer and averaged the resulting maps across the whole sample (Fig. 2B). Since we were interested in distinguishing motor planning from execution, we imaged the beta ERDs in two separate 500 ms windows. This revealed robust decreases in beta power in the primary motor cortices contralateral to movement across both time windows, with weaker responses in the ipsilateral motor cortex as well during the execution of complex sequences. Strong increases in gamma power were also observed in the contralateral primary motor cortex, slightly anterior to the peaks observed for the beta ERD.

### 3.3. Whole-brain analyses

For the beta maps, we conducted a whole-brain, voxel-wise 2 × 2 × 1 ANCOVA (condition, window, age) with movement condition (simple/complex) and time window (planning/execution) as within- subjects two level factors and age as a between-subjects continuous covariate of interest. Similarly, for the gamma maps, a 2 × 1 whole-brain, voxel-wise ANCOVA with movement condition (simple/complex) as a within-subjects factor, with age as a between-subjects covariate of interest. Note that there was no time window (planning/execution) factor for gamma because the neural response was more transient. In both models, we examined both main effects and all interactions.

There were no main effects of age on beta activity; however, there were several interaction effects. First, there were two beta clusters with a significant age-by-condition-by-window interaction, the left superior frontal ($F = 12.24$, $p < .001$) and right superior frontal gyri ($F = 11.05$, $p = .002$; Fig. 3). To further probe these three-way interactions, we extracted each participant's pseudo-$t$ values at the coordinates of the peak voxel and input these values

into two separate 1 × 2 ANCOVAs (condition, age) per region (i.e., one for planning and another for execution). This follow-up analysis revealed that in both clusters, a significant age-by-condition interaction was only present during planning (left: $F = 4.64$, $p = .035$; right: $F = 4.55$, $p = .037$; Supplementary Figure 1). Finally, we tested the correlation of age and beta activity separately by condition in the planning window of both peaks. None of these relationships were significant, but those in the complex condition were somewhat trending (left superior frontal: $r = 0.19$, $p = .15$; right superior frontal: $r = 0.144$, $p = .27$).

There were significant age-by-window interactions in the left lingual gyrus ($F = 12.46$, $p < .001$), right posterior cingulate cortex (PCC; $F = 12.12$, $p < .001$), left superior cerebellum (Crus I of lobule VII; $F = 11.46$, $p = .001$), and the left middle occipital gyrus ($F = 14.68$, $p < .001$). Follow-up correlations in each region showed that the relationship between age and beta activity during the planning phase was only significant in the PCC ($r = -0.28$, $p = .025$), although it approached significance in the cerebellum ($r = -0.19$, $p = .14$) and occipital gyrus ($r = -0.24$, $p = .064$). Fisher $r$ to $Z$ transformations indicated that none of the pairs of correlation coefficients differed significantly, though the difference between beta activity in planning versus execution approached significance in the left middle occipital cluster ($Z = -1.9$, $p = .057$). Overall, the significant interaction effects in these four regions were such that when controlling for sequence complexity, increasing age tended to be associated with stronger beta oscillations during motor planning, whereas during motor execution beta activity was not associated with age. Though again, it is important to note that the simple slopes during planning were rarely significant (Fig. 4).

In the 1 × 2 ANCOVA (condition, age) on the MRGS maps, there were no significant age-by-condition interactions on gamma activity. However, there were two clusters in which there was a significant main effect of age on gamma oscillatory activity (Fig. 5). Independent of sequence complexity, gamma activity decreased with age in the left superior temporal gyrus ($F = 12.31$, $p < .001$), but increased with age in the left superior occipital gyrus ($F = 10.67$, $p = .002$).

## 4. Discussion

In this study, we recorded MEG in 68 healthy adolescents during the performance of a motor sequencing paradigm with simple and complex conditions and used a whole-brain statistical approach to identify areas in the brain that exhibited developmental changes in the strength of motor-related oscillatory responses. We found condition- and time window-specific differences in age-related changes in beta activity in frontal, cingulate, occipital, and cerebellar areas. We also found developmental alterations in gamma oscillations in temporal and occipital regions that were not specific to sequence complexity. In what follows, we will discuss our findings and their implications.

Behaviorally, we found that older youth generally performed better on the task, measured by faster reaction times, shorter movement durations, and overall greater efficiency across both conditions. Average reaction times did not differ between condition, but the average movement duration was significantly slower in the complex condition, and movement duration and its associated inverse efficiency metric improved more rapidly with age in the

complex condition. There was no difference in accuracy by condition, and accuracy was not related to age in either condition. This pattern of findings suggests that all participants took longer to make the first movement in the complex relative to simple condition, potentially indicating a greater degree of motor planning to initiate the first movement. Further, once started, the younger participants could perform the simple condition at near ceiling levels, while the complex condition was more challenging for them. In contrast, once started, the older youth participants performed the sequences equally quick in both conditions. Finally, we found that reaction and movement duration were strongly correlated, which indicates that participants who were fastest to make the first movement also completed the full sequence in the least amount of time.

Key findings were the three-way age-by-condition-by-window interactions in the left and right superior frontal gyri, such that the developmental trajectory of beta activity significantly differed by condition only during the planning window. In both clusters, planning-related beta activity showed a trend towards becoming weaker with age in the complex condition, although the simple slopes were not significant in either condition. The lack of significance with the simple slopes likely reflected that the age-related conditional and window effects were present when considered from a within-subject perspective, but that the between-subject variance with age was high and thus the simple slopes were not significant. In other words, the age effect was more variable when considered in isolation, which is a common finding in developmental neuroimaging and has led our group and others to consider metrics beyond age in recent work (e.g., testosterone or DHEA levels; Fung, Heinrichs-Graham, et al., 2022; Fung, Rahman, et al., 2022; Killanin et al., 2024; Picci, Ott, Penhale, et al., 2023). Regardless of the simple slopes, the two superior frontal regions involved were near cortical areas implicated in cognitive control and the supplementary motor area (SMA), with the latter being particularly true for the more posterior right superior frontal cluster. Thus, these findings could reflect less involvement of this higher-order motor area in generating complex sequences as children progress through adolescence (Heinrichs-Graham et al., 2020). This interpretation is particularly attractive since the effects only emerged in the planning phase, which notably was contrary to our hypotheses where we predicted effects during movement execution. In retrospect, such differences in the planning phase are not surprising for these higher-order brain regions. The prefrontal cortices and SMA in particular are much more likely to be involved in planning movements, especially complex movements (Wilson et al., 2014), and less likely to be involved in movement execution, which would be more reliant on the primary motor cortices. Further, across the cortex, developmental beta effects during the motor planning stage are more commonly reported than the execution stage (Heinrichs-Graham, McDermott, et al., 2018; Wilson et al., 2010, 2011). However, a major complication to comparing the current finding and existing work is that most developmental studies did not vary the difficulty or complexity of the movement, and our current finding is that the effect varies based on sequence complexity. In perhaps one of the most comparable developmental studies, 8–15 year-old participants performed simple movements with their dominant and non-dominant hands (Wilson et al., 2010). They found significant beta planning responses in the SMA during unilateral movement of both the dominant and non-dominant hands, but that only SMA responses during movement of the non-dominant hand were correlated with age,

becoming weaker with increasing age in their cross-sectional study (Wilson et al., 2010). Similar findings emerged in a fMRI study of simple movements in children and adults (Turesky et al., 2018). Specifically, they found greater SMA activation in children relative to adults during finger tapping using the nondominant left hand, but not the dominant right hand (Turesky et al., 2018). Such non-dominant hand movements would be slightly more challenging and at a minimum require more planning in this age range; thus, they are at least comparable to our simple/complex distinction. Beyond these two studies, few developmental motor studies have found the SMA/SFG to be involved, but it is difficult to interpret this absence because the vast majority of such studies have focused on the primary motor cortex and not performed whole-brain statistics. Based on this limited work, the consensus seems to be that SMA responses do not differ in children relative to adolescents or adults during simple tasks with the dominant hand, but are stronger in children than adults (Turesky et al., 2018) and become weaker with increasing age from childhood to adolescence (Wilson et al., 2010) during simple movements of the nondominant hand or complex movements of the dominant hand (current findings). We propose that this pattern reflects compensatory recruitment to help control the nondominant hand during basic movements in young children, as well as the dominant hand during more complex movements in the same age range. Future developmental studies should vary the difficulty of the movement and use whole-brain approaches to probe higher-order regions, as the literature in this area is particularly sparse.

In addition to the three-way interactions, we also found age-by-window interactions in the left lingual gyrus, right PCC, left superior cerebellum, and left middle occipital gyrus. Independent of condition, beta activity in these regions tended to be stronger with age during planning, although the simple slopes with age only reached significance in the PCC, whereas in the execution phase age was not related to beta activity. As suggested above, these trends in the simple slopes that were conducted to follow-up the significant ANOVA findings may reflect higher between-subject variance in regard to age effects and future work should consider integrating pubertal or hormonal indices of development in an effort to offset this. The lingual gyrus is early in the ventral visual pathway and thus likely reflects processing of the visual stimuli, which would have been more critical during the planning phase when the visual input was being transformed into a motor plan (Grill-Spector et al., 2008; Simic and Rovet, 2017). Presumably, the age interaction indicates that the older adolescents more strongly directed attention to the visual input during the planning stage. Nonhuman primate studies suggest the PCC is involved in managing attention and response planning processes (Leech and Sharp, 2014), with stronger activity being linked to vigilance state and monitoring for changes in the environment (Hayden et al., 2009), such as behaviorally relevant cues and tracking behavioral responses over time (Pearson et al., 2009). Such roles in response planning are consistent with the current findings, as beta responses became stronger with increasing age during motor planning. Regarding the occipital cluster, this also likely reflects stronger visual processing of the numerical stimuli with age, similar to the lingual gyrus finding, particularly pertaining to the visual encoding aspect of motor planning (Tallon-Baudry et al., 2005). Lastly, lobule VII Crus I of the cerebellum has reciprocal connections and is frequently co-active with frontal, parietal, and temporal association cortices during higher-order processing, supporting action planning for

goal-directed behavior (Gao et al., 2020; Schmahmann, 2019; Stoodley and Schmahmann, 2009).

The MRGS response was not modulated by sequence complexity and was transient, restricted to a short time window surrounding movement onset. The superior temporal and superior occipital gyri exhibited opposite relationships with age, with gamma activity being weaker in older youth in the temporal cortex, and stronger in the occipital cortex. Gamma activity is known to be a signature of active processing across the brain (Buzsáki and Wang, 2012; Muthukumaraswamy and Singh, 2013). Decreased gamma activity in the temporal cortex likely indicates reduced reliance on extended attentional networks and related processes (Picci, Ott, Petro, et al., 2023; Ramezanpour and Fallah, 2022), at least for the initiation of the first movement in the sequence. It is possible that this decreased reliance is part of the typical developmental trajectory of motor-related oscillations throughout the brain. The few adult studies that utilized whole-brain statistical approaches in evaluating contributions to motor control did not report superior temporal cortex, but none of these studies examined correlations with age and likely these analyses would not have identified this region since our work suggests it is becoming less involved with increasing age. Developmental increases in the occipital gamma response concurrent with movement onset likely reflects improvements in top-down attentional control or visuomotor integration (Engel et al., 2001; Roelfsema et al., 1997). Better visuomotor integration is likely beneficial to behavioral performance, and may facilitate faster reaction times and shorter movement duration in sequential movements in adolescents (Heinrichs-Graham et al., 2020). However, more work is needed in order to substantiate this claim. One possible approach to identifying the impact of such increased gamma in this region would be to apply transcranial direct-current stimulation (tDCS) to the occipital while individuals perform a similar or identical motor task, as previous tDCS studies have shown that anodal stimulation increases occipital gamma locally (Arif et al., 2022; Wilson et al., 2018).

In summary, this study is the first to map the oscillatory dynamics serving sequential motor control of varying difficulty in youth. Regarding limitations of this study, we investigated developmental changes using a cross-sectional approach, which is advantageous in terms of cost and shorter study durations, but also has the downside that it may not accurately capture the developmental trajectory observed the average participant. Future studies should consider collecting neuroimaging data at multiple timepoints, which will offer a richer view of individual developmental trajectories. Along the same lines, we focused on linear effects with age and future work should consider quadratic and/or spline models. The detection of such higher-order effects often requires larger samples and thus future work in this area should consider higher enrollment targets. Another limitation is that a growing body of literature reports evidence for other developmental factors influencing the development of oscillatory activity beyond chronological age, such as pubertal hormones (Fung et al., 2020; Fung, Rahman, et al., 2022; Killanin et al., 2024; Penhale et al., 2022; Picci, Ott, Penhale, et al., 2023), yet very little is known how these endogenous hormones contribute to the refinement of motor-related activity throughout the cortex (Fung, Heinrichs-Graham, et al., 2022; Killanin et al., 2023). Future studies should investigate whether there is evidence to suggest pubertal hormones, or other developmental factors underlie the age-related changes identified in this study. Such studies should also include measures of pubertal stage, as these

can help guide interpretation of the hormonal data, and sex as there are known sexually dimorphic effects within this age range. Finally, some of our findings involve the cerebellar cortices and other deeper structures and the sensitivity of MEG to activity in these regions is reduced compared to the cortex. Thus, some caution is warranted, although there is evidence that MEG is adequately sensitive to such cerebellar responses (Samuelsson et al., 2020). Overall, using high-density MEG and dynamic functional mapping, we found that higher-order regions implicated in response selection and attentional control exhibit differential age-related changes in beta and gamma activity by sequence complexity and motor stage. These findings provide important new evidence for the involvement of higher-order areas in supporting developmental improvements in motor and cognitive control, and a foundation for the further differentiation of other modulatory factors in the developing motor network.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

## Funding statement

This work was supported by the National Institutes of Health [grant numbers R01-MH121101 to Wilson and P20-GM144641 to Wilson and Heinrichs-Graham; F30-MH134713 to Son], and the National Science Foundation [award number 1539067 to Wilson, Calhoun, Wang, and Stephen].

## Data availability

The data used in this article will be made publicly available through the COINS framework at the completion of the study (https://coins.trendscenter.org.

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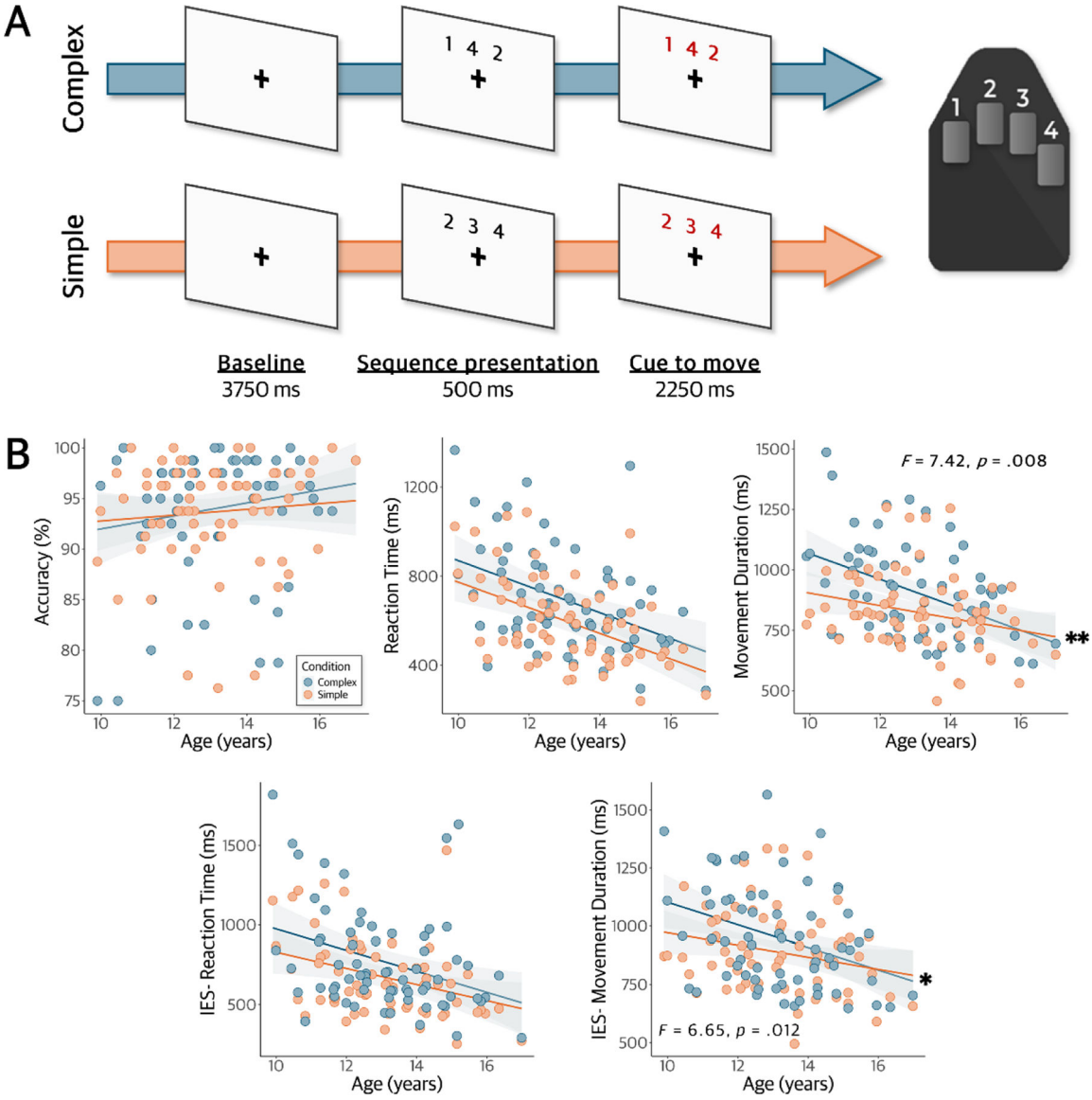


**Fig. 1.**

Motor sequencing task and behavioral results. (**A**) Participants fixated on a crosshair for 3750 ms. After this period, a three number sequence, with each number corresponding to a finger on the right hand, was displayed for 500 ms. The sequence then changed color, indicating the cue to move, and the participant had 2250 ms to tap the sequence. There were two conditions; simple, in which the numbers were adjacent button presses (e.g., 2–3–4), and complex where the numbers were nonadjacent (e.g., 4–1–2). (**B**) On the top row, percent correct (accuracy) is on the left, reaction time (time between cue to move and movement onset) in the middle, and movement duration (time to complete the sequence) on the right. On the bottom row, inverse efficiency scores (IES) based on the reaction time (bottom left; IES-RT) and movement duration (bottom right; IES-MD) data are shown. ANCOVAs revealed age-by-condition interactions on movement duration and IES-MD, as

well as multiple main effects. Grey shaded areas depict the standard error of the mean. Asterisks denote significance level of the age-by-condition interactions; * $p < .05$, ** $p < .01$.

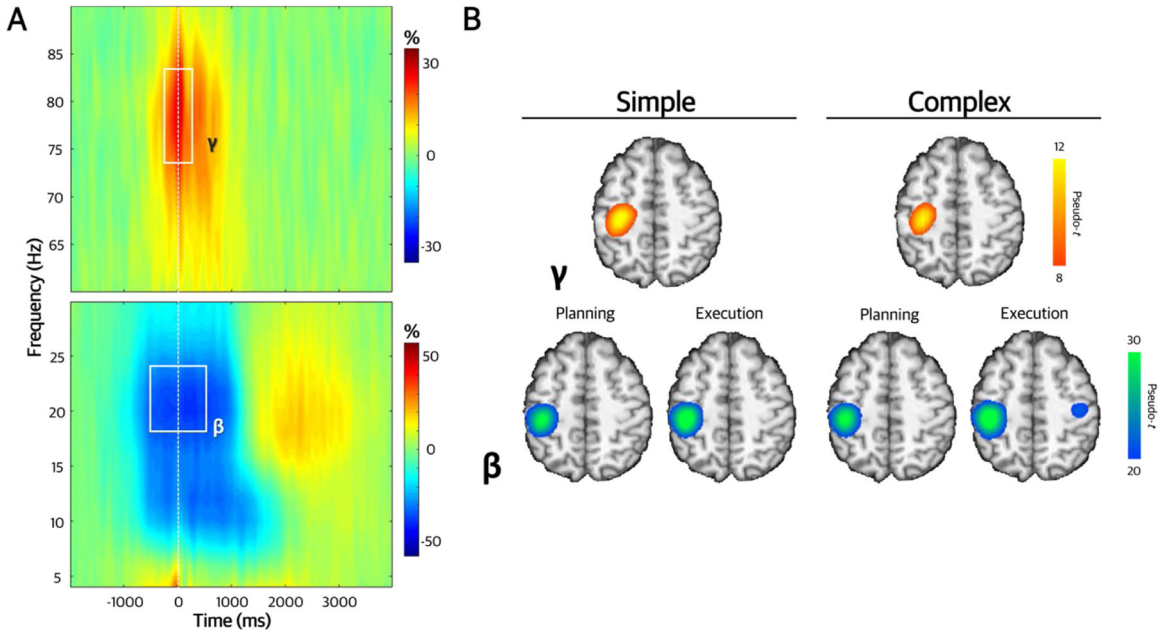


**Fig. 2.**

Sensor- and source-space analyses. (A) Grand-averaged time-frequency spectrograms across all participants and both conditions from sensors near the left sensorimotor cortex (i.e., MEG0423 for beta, MEG0432 for gamma). Time (ms) is displayed on the x-axis with frequency (Hz) on the y-axis. Signal power is expressed on the color scale as percent change from baseline. Before and during movement, there was a strong beta ERD. There was also a brief gamma ERS centered around movement onset at 0 ms. The white boxes display the significant time-frequency bins selected for beamforming analyses (beta planning: −500 to 0 ms, 18–24 Hz; beta execution: 0–500 ms, 18–24 Hz; gamma: −250–250 ms, 74–84 Hz). (B) Beamformer images averaged across all participants for both conditions in beta and gamma, as well as the two windows in beta, showed that the responses were strongest in the primary motor cortices contralateral to the movement.

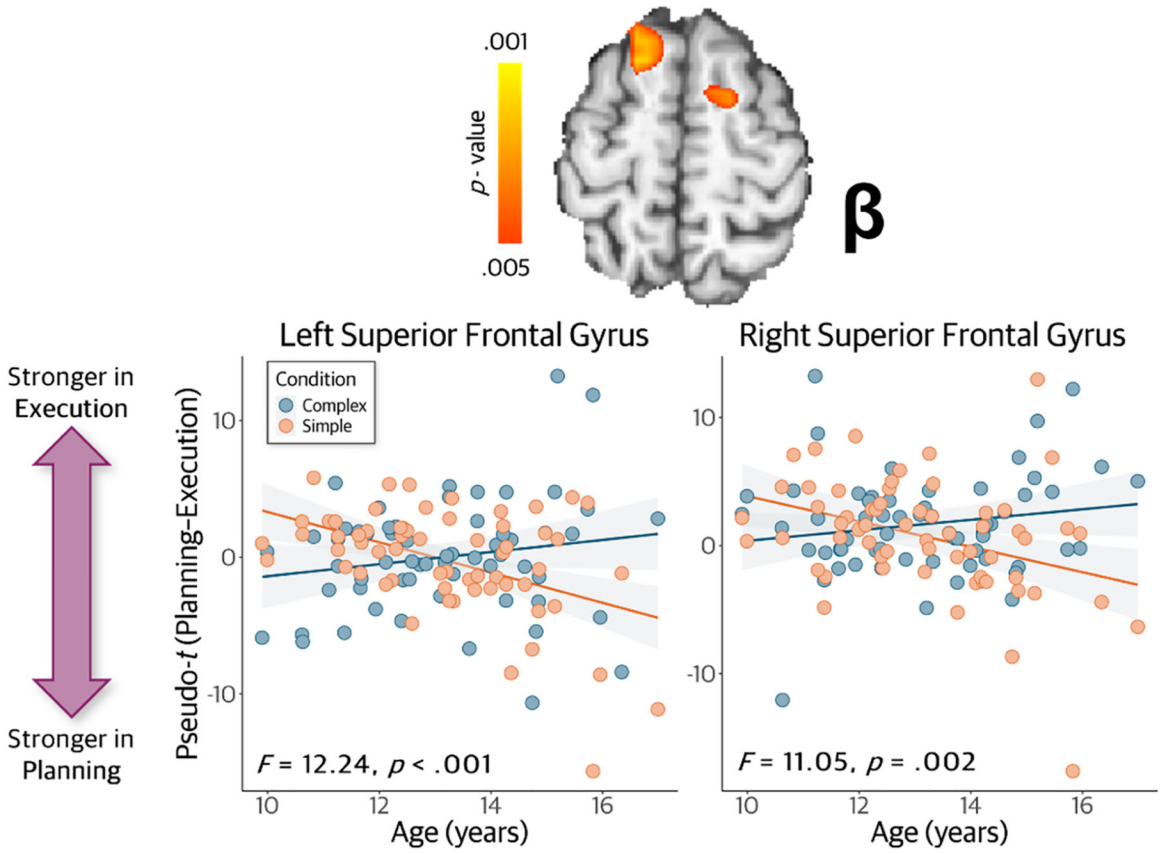


**Fig. 3.**

Significant three-way interaction in the bilateral superior frontal gyri. Whole-brain ANCOVAs revealed significant age-by-condition-by-window interactions on beta activity in the left and right superior frontal gyri. Scatterplots depict the difference in beta power during planning and execution on the y-axis by age on the x-axis. Difference scores for each peak were calculated by subtracting the pseudo-t values during execution from the values during planning. Thus, a larger positive value indicates that the beta response was stronger (more negative) during execution, while larger negative values indicate a stronger response in the planning phase. Please refer to Supplementary Figure 1 for a figure of the pseudo-t values plotted separately by window. Grey shaded areas depict the standard error of the mean.

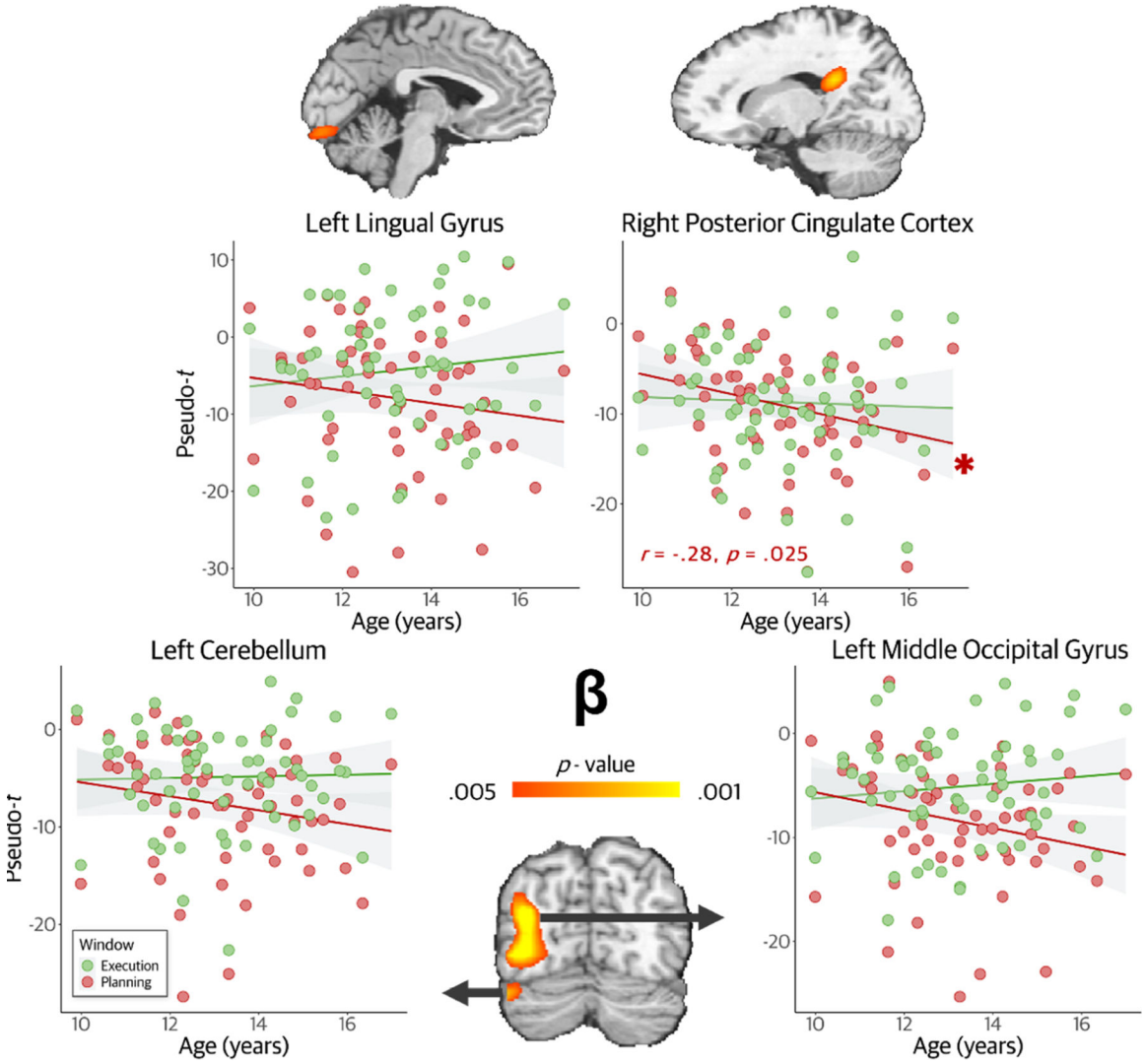


**Fig. 4.**

Significant age-by-window interactions on beta activity in the occipital, cingulate, and cerebellar cortices. Age-by-window interactions in beta activity in the left lingual gyrus (top left), right PCC (top right), left cerebellum Crus I (bottom left), and left middle occipital gyrus (bottom right). The interaction effects were such that independent of condition, beta activity tended to be stronger with age during planning, whereas in the execution phase age was not related to beta activity. Grey shaded areas depict the standard error of the mean. Asterisk denotes significance level of the simple slope. * $p < .05$.

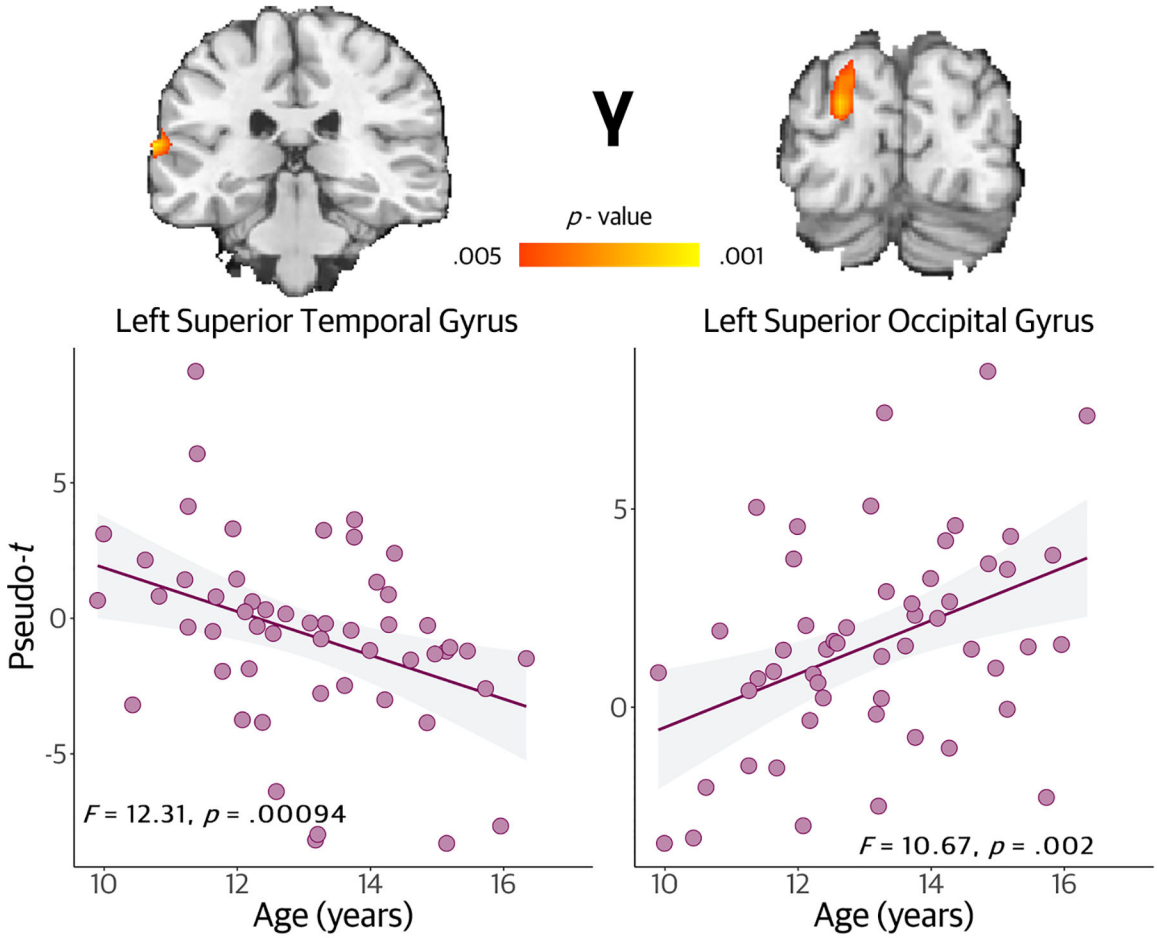


**Fig. 5.**

Main effects of age on gamma oscillations in temporal and occipital cortices. Significant main effects of age on gamma activity were present in the left superior temporal gyrus (left) and superior occipital gyrus (right). These effects were such that collapsing across conditions, gamma oscillations in the superior temporal gyrus became weaker with increasing age. Conversely, gamma oscillations in the superior occipital became stronger with age. Grey shaded areas depict the standard error of the mean.