Developmental differences in patterns of electrophysiological connectivity profiles in children and adolescents

Dryden Arseneau
Faculty of Social Sciences and Humanities, Ontario Tech University

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Instructor: Dr. Shannon Vettor
Supervisors: Dr. Bobby Stojanoski and Dr. Taylor Heffer

Abstract

The transition from childhood to adolescence involves profound cognitive, social, and neural changes. While prior research has primarily used fMRI to examine the development of functional connectivity (FC), the temporal dynamics of these processes remain less understood. This study leverages the high temporal resolution of electroencephalography (EEG) and a naturalistic movie-watching paradigm to examine age- and sex-related differences in FC across six frequency bands in children and adolescents (n = 116, aged 5.0 to 16.99 years) from the Healthy Brain Network. Using generalized additive models (GAMs), we identified both linear and non-linear developmental changes within- and between-region connectivity, varying by frequency and region. Broadband analyses revealed general maturational trends, particularly in parietal and temporal regions, while frequency-specific analyses uncovered distinct profiles, such as increasing theta and alpha connectivity across long-range networks, decreasing gamma synchrony in local circuits, and nonlinear delta-band changes involving frontal-temporal integration. Beta-band FC showed no significant effects. Additionally, we observed sex-based differences in theta-band connectivity, with males exhibiting stronger frontoparietal coupling involving the right parietal region. These findings suggest sex-specific developmental trajectories in attentional and control networks. Right-lateralized effects were observed across multiple bands, supporting theories of hemispheric specialization. By combining ecologically valid stimuli with flexible, non-parametric modelling, this study provides a dynamic and temporally precise account of functional brain development, introducing a scalable framework for investigating both typical and atypical trajectories of connectivity in children and adolescents.

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The transition period from childhood to adolescence is marked by significant improvements in several cognitive and social processes, including executive functioning and theory of mind. Coinciding with improvements in cognition are massive changes to the brain structurally (Babiloni et al., 2003; Gilmore et al., 2018; Supekar et al., 2009) and functionally (Bathelt et al., 2013; Gilmore et al., 2018; Ismail & Karwowski, 2020). While many studies have examined age-related changes in functional brain development (e.g., Bathelt et al., 2013; Boersma et al., 2013; Chung et al., 2022), several important questions about the developmental trajectory and pace of brain maturation remain unanswered. In the present study, we aim to characterize non-linear age-related changes in brain-wise connectivity patterns during childhood and adolescence.

One common measure used to assess brain-wise connectivity patterns is functional connectivity (FC), which refers to the temporal correlation of neuronal activity between spatially distinct regions reflecting their functional communication (Chung et al., 2022; Grayson & Fair, 2017; Ponten et al., 2010; Sanders et al., 2022). Resting-state FC (rsFC) electroencephalography (EEG) studies have become a widely used tool for assessing FC across development due to their ability to capture nuanced dynamics of neural communication with high temporal resolution (Boersma et al., 2011; Chung et al., 2022; Davoudi et al., 2023). There is a growing consensus emerging from recent research that as children mature into adolescents, there is a shift from a globalized to a more localized functional organization of the brain (Boersma et al., 2011; Boersma et al., 2013; Liuzzi et al., 2023; Solé-Padullés et al., 2016; Stevens, 2016). These changes reflect maturational processes such as synaptic pruning and myelination (Cherchik et al., 1999; Boersma et al., 2011). For example, long-range connections, such as those involving the default mode network (DMN), tend to strengthen with age, supporting the development of higher-order cognitive functions (Boersma et al., 2011; Grayson & Fair, 2017). In contrast, short-range connections may weaken as the brain undergoes synaptic pruning (Chechik et al., 1999) and refines local processing hubs (Boersma et al., 2013). However, little is currently known about the precise nature and timing of these developmental changes.

Critically, most developmental studies of FC rely on linear statistical models to assess age-related changes (Adolph & Robinson, 2008). Linear models, by design, are limited to capturing constant and uniform rates of change (Adolph & Robinson, 2008; Marek et al., 2015; Supekar et al., 2009; Stevens, 2016). This limitation may oversimplify the complex and dynamic trajectories of brain development (Sanders et al., 2023). Generalized Additive Models address these limitations by using flexible, penalized spline bases that adapt to the data, enabling the characterization of continuous and non-linear developmental changes (Wood, 2017).

Notably, Sanders et al. (2023) contributed to our understanding of developmental FC using resting-state fMRI (rsfMRI) and GAMs. This study found evidence of non-linear age-related changes in various neural networks across development. Their findings demonstrated that long-range connections, such as those in the DMN and frontoparietal networks (FPN), strengthen while local connections, such as those in sensorimotor regions, diminish across childhood and adolescence. This indicates an ongoing integration of neural networks. They also identified key sex differences, with males displaying increased putamen (PUT) connectivity with age, while females displayed no significant change. This underscores the importance of considering age in developmental studies, as sex differences in FC have been observed in brain regions associated with emotional regulation and cognition, such as the prefrontal cortex (PFC) (Lopez et al., 2020) and PUT (Wierenga et al., 2018). While Sanders et al. (2023) use of GAMs provides a valuable tool for understanding non-linear developmental changes, their reliance on the low temporal resolution of fMRI limits the ability to capture rapid, dynamic shifts in connectivity. Conversely, the current study utilizes EEG, offering millisecond-level temporal precision to track these fast neural changes. Additionally, while Sanders et al. (2023) focused on rsFC, the present study introduces a naturalistic movie-watching paradigm, which enhances ecological validity and allows for a more engaged and realistic assessment of FC during development (Sonkusare et al., 2019). By combining these methodologies, this study aims to deepen our understanding of age and sex differences in FC, building upon and extending the findings of Sanders et al. (2023).

A movie-watching paradigm offers several advantages for studying FC, particularly in developmental neuroscience. Traditional paradigms (e.g. resting-state or task-based approaches) may not capture the complexity of real-world experiences. Movie-watching, on the other hand, provides a naturalistic and dynamic environment that can reflect everyday neural dynamics (Gao et al., 2022; Sonkusare et al., 2019; Tanner et al., 2023). Movies promote consistent and synchronized patterns of brain activity across participants due to shared audiovisual and narrative experiences, providing rich data for FC analysis (Tanner et al., 2023). This approach also enables researchers to examine how brain networks integrate and respond to dynamic stimuli, engaging regions related to attention, emotion, and memory in ways that mimic real-life contexts (Gao et al., 2022). The engaging nature of movie-watching makes it particularly useful for studies involving children and adolescents who may struggle with traditional tasks (Chung et al., 2022; Sonkusare et al., 2019).

An advantage of using EEG to track age-related changes in FC is its capacity to analyze oscillatory brain activity across multiple frequency bands with high temporal precision (Boersma et al., 2011; Chung et al., 2022; Hassan et al., 2014). These bands—Broadband (0.5–80 Hz), delta (0.5–4 Hz), theta (4–8 Hz), alpha (8–13 Hz), beta (13–30 Hz), and gamma (30–80 Hz)—are each associated with distinct neural functions and developmental patterns (Buzsáki & Wang, 2012; Klimesch, 1999; Michels et al., 2013). For instance, delta and theta activity have been linked to early cognitive and motivational processes (Güntekin & Başar, 2016; Harmony, 2013; Knyazev, 2012), alpha rhythms are associated with attentional control (Klimesch, 1999), beta activity reflects sensorimotor integration (Gaál et al., 2010), and gamma oscillations are related to local cortical computations and early cognitive and language skills (Benasich et al., 2008; Buzsáki & Wang, 2012). These oscillatory markers evolve throughout development, reflecting underlying maturational changes in neural structure and function (Boersma et al., 2013; Michels et al., 2013; Uhlhaas et al., 2009). By examining FC within and between brain regions across these frequency bands, this study can capture nuanced developmental dynamics that unfold at both local and global network levels.

The present study aims to advance our understanding of developmental changes in FC by leveraging a movie-watching paradigm and applying GAMs to EEG data. This approach offers a novel examination of how FC evolves with age and varies by sex in naturalistic contexts. To capture the full scope of developmental dynamics, we apply separate GAMs to each within- and between-region FC connection across all frequency bands. A central goal is to examine age- and sex-related differences in FC, hypothesizing that age will correlate with increased integration within large-scale brain networks, reflecting the ongoing maturation of neural systems (Bathelt et al., 2013; Lopez et al., 2020; Sherman et al., 2014). Furthermore, it is hypothesized that FC undergoes both linear and non-linear development, with distinct developmental trajectories for within- and between-brain regions. By combining the ecological validity of movie-watching with the temporal precision of EEG, this study provides a unique opportunity to characterize the non-linear patterns of neural development.

Method

Participants

Participants in the current study (N = 116, M_{age} = 10.39 ± 3.53, age range = 5.0-16.99, 35.3% female) were drawn from the Child Mind Institute (CMI) Release 10 from the Healthy Brain Biobank (described in detail in Alexander et al., 2017). Figure 1 displays the distribution of participants across age and gender. The Healthy Brain Network (HBN) is an ongoing initiative to collect an extensive database of children and adolescents aged 5 to 17. The Chesapeake Institutional Review Board approved the study. Details on the HBN biobank can be found at http://fcon_1000.projects.nitrc.org/indi/cmi_healthy_brain_network/. Secondary analysis of the HBN data was approved by the Institutional Research Ethics Board at Ontario Tech University. For the current study, participants were included if their EEG data for a movie-watching paradigm (*The Present*) were successfully acquired and they had a complete phenotypic profile (age, sex, handedness). Everyone in the current study has written consent from their legal guardians, and written assent was obtained from the participant. Participants were not excluded based on their handedness or any diagnoses they may have, including neurodevelopmental disorders, to ensure the sample remains representative of the population. Participants were excluded if they failed registration, had excessive motion, or if 25% or more of the data contained large “spikes” (significant fluctuations in signal intensity).

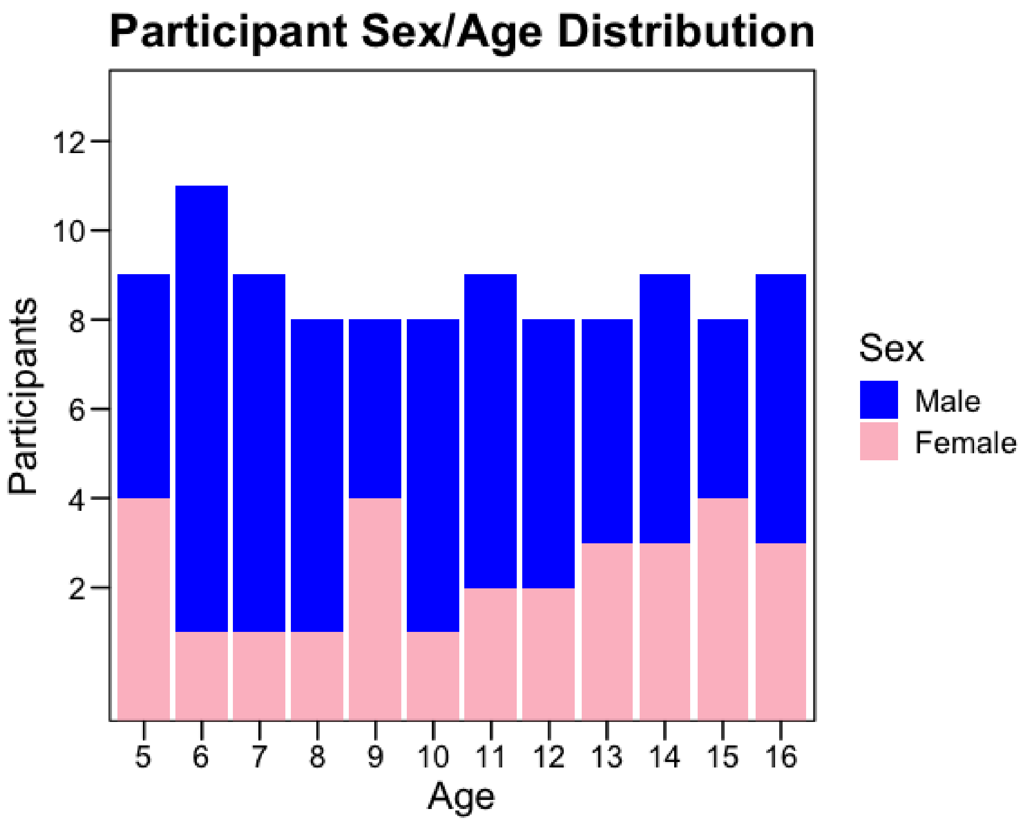


Figure 1. *Histogram of the age and sex distribution of the participants (N = 116). Participant ages were rounded down to the nearest whole age for clarity.*

Procedure

Participants were recruited from New York, NY, USA, using various methods, such as affiliate referrals, online advertising, and non-affiliate referrals. The participants completed various measures prior to data collection, including a clinical intake, mental health visit, learning and language assessment, cognitive evaluation, and neuroimaging examination (described in detail in Alexander et al., 2017). For neuroimaging data collection, participants completed multiple tasks over the course of their visit; however, for the current study, we are only concerned with the final task, which was a passive (task-independent) naturalistic movie-watching paradigm (see Alexander et al., 2017, Tables 2-6 for an entire breakdown of each participant's visit). The participants watched *"The Present" by Jacob Frey,* published by the Filmakademie Baden-Württemberg in Germany. Participants were instructed to remain as still as possible and to watch the movie. EEG recording began when the movie started and ended when the credits began. The movie is three minutes and twenty-three seconds long from start to finish of the EEG recording.

The EEG data were collected in a sound-shielded room with a sampling rate of 500 Hz and a bandpass of 0.1 to 100 Hz. The high-density EEG was recorded with a 128-channel EEG Geodesic Hydrocel system by Electrical Geodesics Incorporated (EGI). The recording reference is at Cz (central vertex of the head). The head circumference of each participant was measured, and an appropriately sized head cap was selected. The impedance of each electrode was checked before recording to ensure good contact and was kept below 40 kΩ. The time to prepare the EEG net is 30 minutes or less, and impedance was checked every 30 minutes of testing, with saline added as needed.

Pre-Processing

EEG data were acquired from the CMI's tenth release, which included 576 participants with complete phenotypical data. Of the 576 participants, 273 were downloaded and checked, with 116 (42.4%) being usable. Participants were deemed unusable if their files did not contain data for *The Present* (102 participants, 37.3%), were excessively noisy (47 participants, 17.2%), or were outside of our age range (8 participants, 2.9%). Data was downloaded from the release, and then MATLAB 2024b (The Mathworks Inc., 2024) and EEGLAB 2024.2 (Delorme & Makeig, 2004) were used to preprocess it. First, the data was rereferenced around the average of all channels. Then, the *pop_eegfilt* EEGLAB command was used to apply a highpass filter at 0.5 Hz and a lowpass filter at 80 Hz, as well as the pop_eegfiltnew command with the revfilt parameter to run a notch filter at 60 Hz, thereby eliminating environmental noise. Next, bad channels were removed through interpolation using the *eeg_interp* function in EEGLAB. Each channel was mapped on a histogram, and channels were manually selected for interpolation. A least mean squares (LMS) regression algorithm, *pop_lms_regression* in EEGLAB, was used to remove eye movement artifacts. Then, independent component analysis (ICA) was performed using the Extended Infomax algorithm, pop_runica, with the extended parameter in EEGLAB. Finally, ICA manual inspection was performed through *pop_topoplot* in EEGLAB to remove any remaining ocular artifacts.

Plan of Analysis

Functional Connectivity and Regional Grouping

We computed FC using the weighted Phase Lag Index (wPLI), which measures phase synchronization between signals while minimizing artifacts from volume conduction (Vinck et al., 2011). This metric was chosen because it provides a robust estimate of true neural interactions by downweighting zero-lag correlations that often reflect electrical spread rather than true connectivity. EEG channels were grouped into eight standard regions (left/right occipital, parietal, temporal, and frontal) based on their scalp positions (Figure 2, adapted from Popiel et al., 2021). We excluded central midline channels and non-brain electrodes (e.g., EOG channels) because these represent overlapping activity from multiple brain regions or non-neural signals, respectively, that could confound our connectivity measures (Popiel et al., 2021; Figure 2). Popiel et al.'s (2021) figure consists of 92 channels; conversely, our model considers 90, excluding additional midline channels. This conservative approach ensured that our connectivity estimates specifically reflected cortical activity patterns.

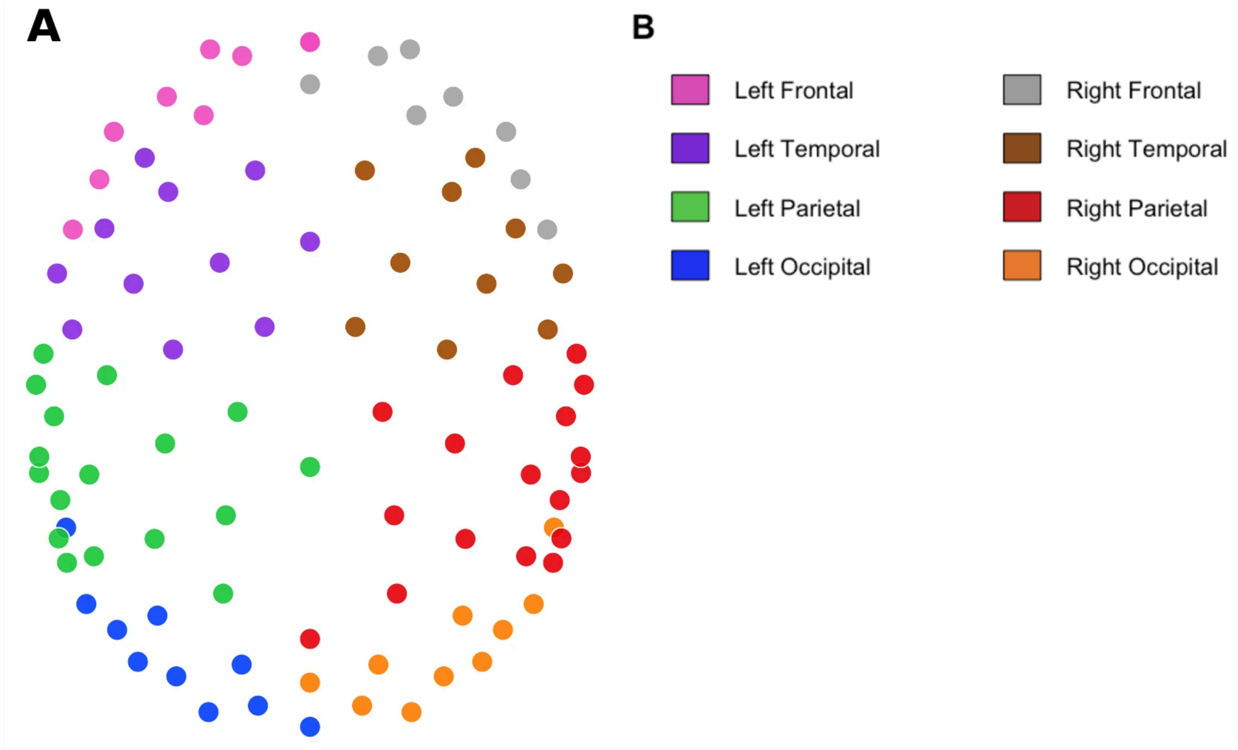


Figure 2. *(A) The clustering of the 90 channels used from the 128-channel geodesic hydrocel EEG cap (adapted from Popiel, N. J., Metrow, C., Laforge, G., Owen, A. M., Stojanoski, B., &*

Soddu, A. (2021). Exploring electroencephalography with a model inspired by quantum mechanics. Scientific Reports, 11(1), 19771). (B) Legend outlining the colour representation for the clustering.

Frequency Band Analysis

The EEG data were filtered into six standard frequency bands (delta: 0.5-4 Hz, theta: 4-8 Hz, alpha: 8-13 Hz, beta: 13-30 Hz, gamma: 30-80 Hz, and broadband: 0.5-80 Hz) using basic FIR filters in EEGLAB. We examined these bands separately because they are known to have distinct functional roles in cognition and show different developmental trajectories (Klimesch, 1999). For example, alpha rhythms are particularly relevant for attention processes, while gamma activity relates to local cortical computation. By analyzing each band independently, we could detect frequency-specific developmental effects that might be obscured in broadband analyses.

Developmental Modelling Approach

We used GAMs implemented in R's *mgcv* package (Wood, 2017) to capture connectivity changes across ages. GAMs were selected because they can capture non-linear developmental patterns that linear models might miss (Sanders et al., 2023). We ran separate models for within-region and between-region connectivity for each frequency band. Age was modelled using smooth terms (penalized regression splines) to allow flexible curve fitting, while sex was included as a categorical predictor. The models used restricted maximum likelihood (REML) for parameter estimation, which yields stable results even with smaller sample sizes. The significance of each smooth term was evaluated using an F-statistic. Below, the first value reported after the F-statistic is the effective degrees of freedom (EDF). This value corresponds to the complexity or "wiggliness" of the fitted curve. Notably, when edf = 1.00, the smooth term is roughly equivalent to a linear term. The second value reported is the reference degrees of freedom (Ref.df).

Results

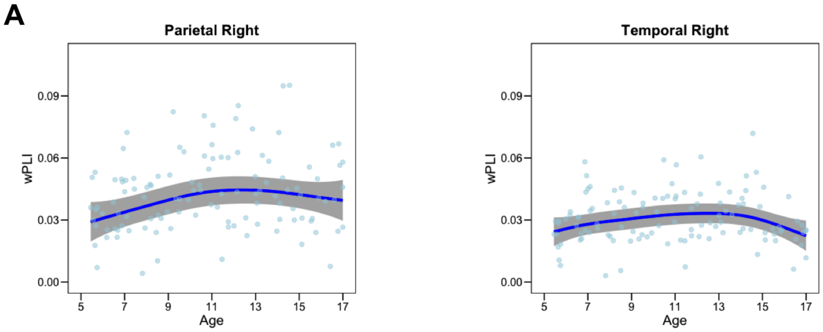
Broadband FC Development

Within-Region Connectivity

To examine age-related differences in within-region FC across the broadband spectrum (0.5-80 Hz), we computed GAMs for each of the eight clustered regions. We identified nonlinear age-related changes in both the right parietal region (*F*(2.27, 2.82) = 3.46, *p* = .020) and the right temporal region (*F*(2.91, 3.61) = 2.85, *p* = .040; see Figure 3A). The spline of age was not significant in any of the other remaining six regions (all *p* > .05).

Between-Region Connectivity

To examine age-related differences in between-region FC across the broadband spectrum (0.5-80 Hz), we computed twenty-eight GAMs, one for each between-region pairing. We identified five nonlinear age-related changes between the following regions: left occipital and right frontal (*F*(2.15, 2.67) = 2.98, *p* = .040), right parietal and right temporal (*F*(2.79, 3.47) = 4.00, *p* = .007), right parietal and right frontal (*F*(2.58, 3.21) = 3.62, *p* = .014), right temporal and right frontal (*F*(2.47, 3.07) = 2.70, *p* = .048), and right temporal and left frontal (*F*(2.62, 3.26) = 3.48, *p* = .017; see Figure 3B). Additionally, we found one linear change in the following pair: right parietal and left parietal (*F*(1.00, 1.00) = 4.62, *p* = .034). All other comparisons were non-significant (*p* > .05).



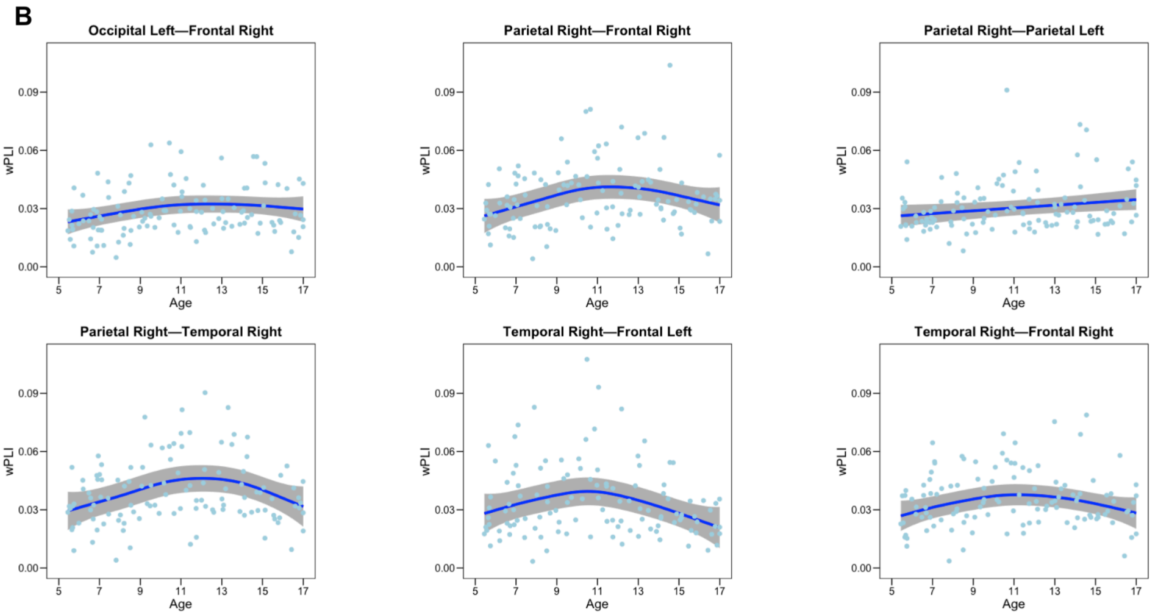


Figure 3: *(A) Significant age-related changes in broadband within-region FC. (B) Significant age-related differences in the between-region broadband FC. The shaded regions around the lines represent 95% confidence intervals. Continuous age is presented along the x-axis, and mean wPLI is presented along the y-axis. Raw scores for each participant are depicted in the background.*

Frequency-Specific Developmental Trajectories

Delta FC Development

Within-Region

No significant linear or non-linear developmental changes in within-region FC were observed across any of the eight clustered regions in the delta band (all $p > .05$).

Between-Region

Non-linear age-related changed were identified in four delta-band between region pairings: left parietal and left temporal ($F(4.08, 5.02) = 2.34$, $p = .047$), left temporal and left frontal ($F(4.11, 5.06) = 2.41$, $p = .043$), left temporal and right frontal ($F(2.49, 3.10) = 3.29$, $p = .023$), and right temporal and right frontal ($F(2.55, 3.18) = 2.87$, $p = .038$; see Figure 4). All other comparisons were non-significant (all $p > .05$).

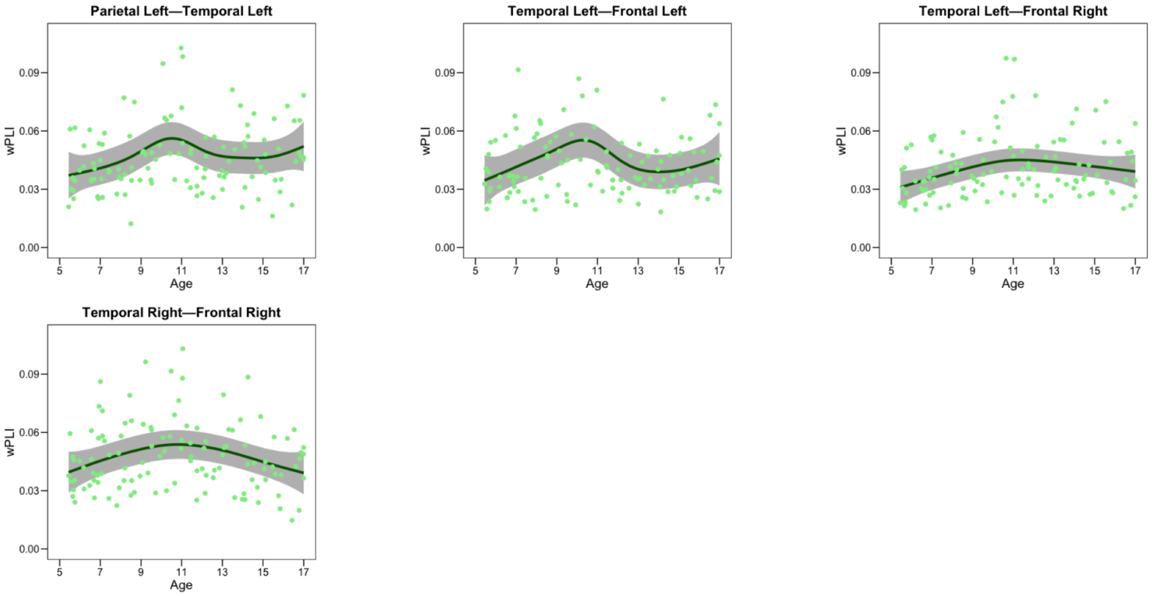


Figure 4. *Significant non-linear between-region age-related differences in delta-frequency FC. The shaded regions around the lines represent 95% confidence intervals. Continuous age is presented along the x-axis, and mean wPLI is presented along the y-axis. Raw scores for each participant are depicted in the background.*

Theta FC Development

Within-Region

Theta-band FC showed a significant linear age-related increase in the right parietal region ($F(1.00, 1.00) = 4.24$, $p = .042$; see Figure 5A). No other within-region effects were significant (all $p > .05$).

Between-Region

Theta-band between-region FC exhibited linear increases in seven region pairs: left occipital and right parietal ($F(1.00, 1.00) = 9.12$, $p = .003$), right occipital and right parietal ($F(1.00, 1.00) = 10.44$, $p = .002$), right occipital and right temporal ($F(1.00, 1.00) = 9.46$, $p = .003$), right parietal and left frontal ($F(1.00, 1.00) = 5.66$, $p = .019$), right parietal and right frontal ($F(1.00, 1.00) = 5.56$, $p = .020$), right parietal and left temporal ($F(1.00, 1.00) = 5.93$, $p = .016$), and, right parietal and right temporal ($F(1.00, 1.00) = 7.77$, $p = .006$; see Figure 5B). All other between-region comparisons were non-significant (all $p > .05$).

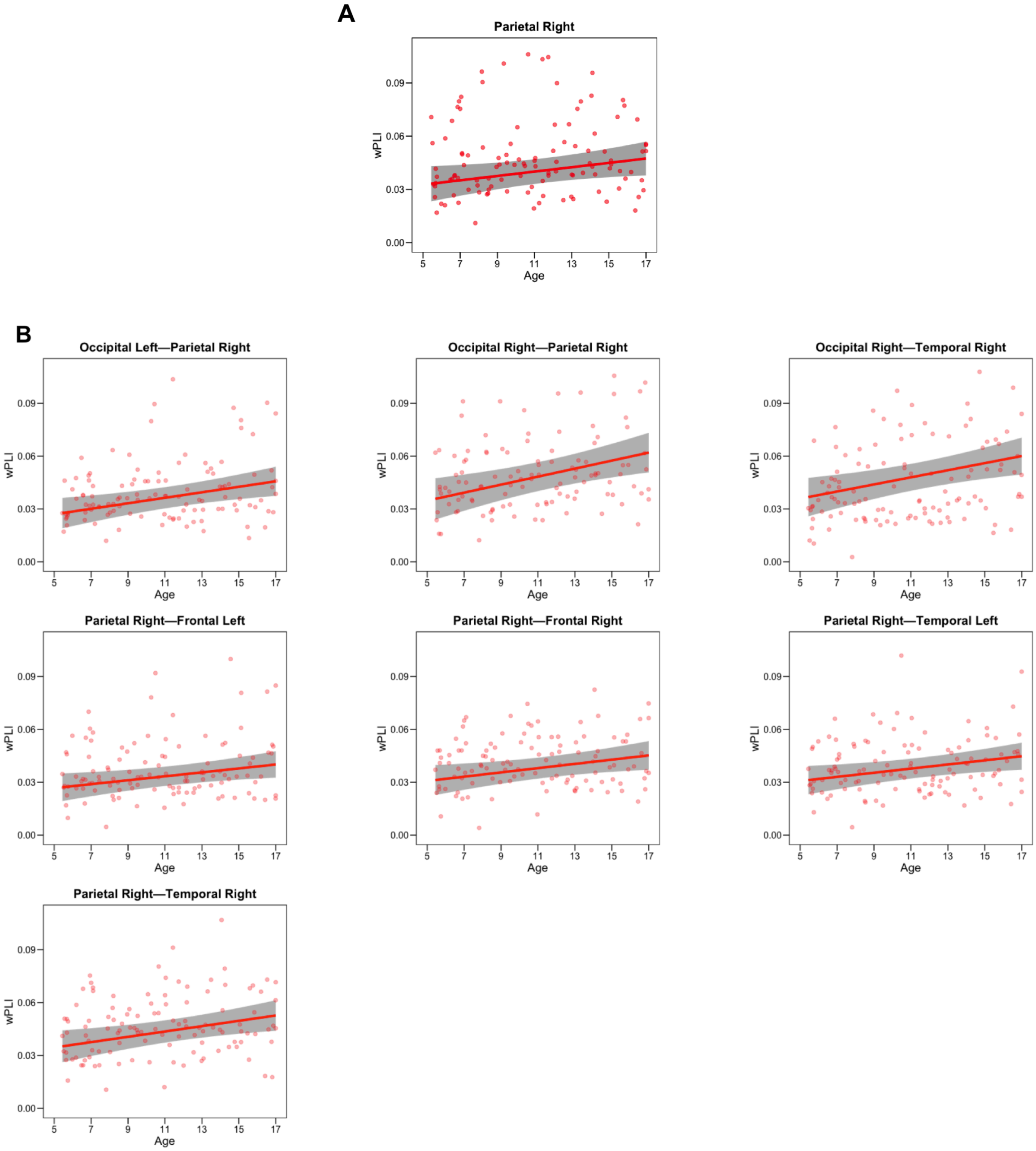


Figure 5. *(A) Significant age-related linear changes in theta within-region FC. (B) Significant non-linear between-region age-related differences in theta FC. The shaded regions around the lines represent 95% confidence intervals. Continuous age is presented along the x-axis, and mean wPLI is presented along the y-axis. Raw scores for each participant are depicted in the background.*

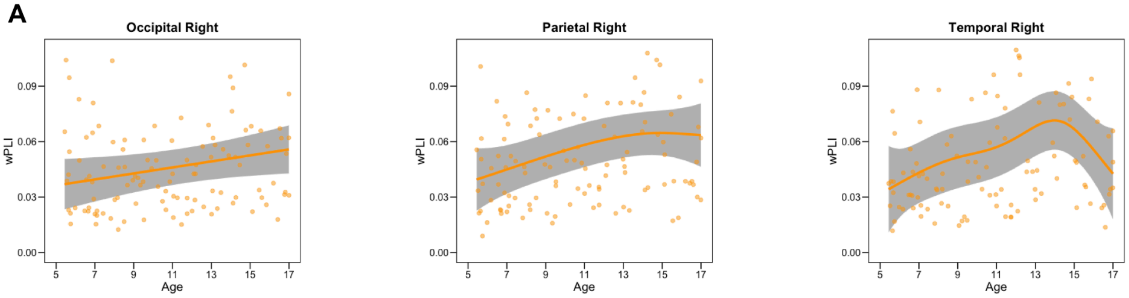
Alpha FC Development

Within-Region

Significant age-related changes in alpha-band within-region FC were observed in three regions: right occipital (*F*(1.00, 1.00) = 3.96, *p* = .049), right parietal (*F*(1.80, 2.23) = 3.54, *p* = .024), and right temporal (*F*(3.34, 4.14) = 2.79, *p* = .026; see Figure 6A). The remaining regions did not show significant effects (all *p* > .05).

Between-Region

Age-related linear and non-linear changes in alpha-band FC were found in seven pairings: left occipital and right parietal (*F*(1.00, 1.00) = 5.22, *p* = .024), right occipital and right parietal (*F*(2.32, 2.89) = 3.50, *p* = .016), right occipital and right temporal (*F*(2.29, 2.85) = 2.98, *p* = .031), right parietal and left frontal (*F*(1.00, 1.00) = 3.98, *p* = .048), right parietal and right frontal (*F*(1.20, 1.38) = 4.91, *p* = .014), right parietal and left parietal (*F*(1.00, 1.00) = 5.13, *p* = .025), and right parietal and right temporal (*F*(2.73, 3.40) = 3.08, *p* = .034; see Figure 6B). All other comparisons were non-significant (*p* > .05).



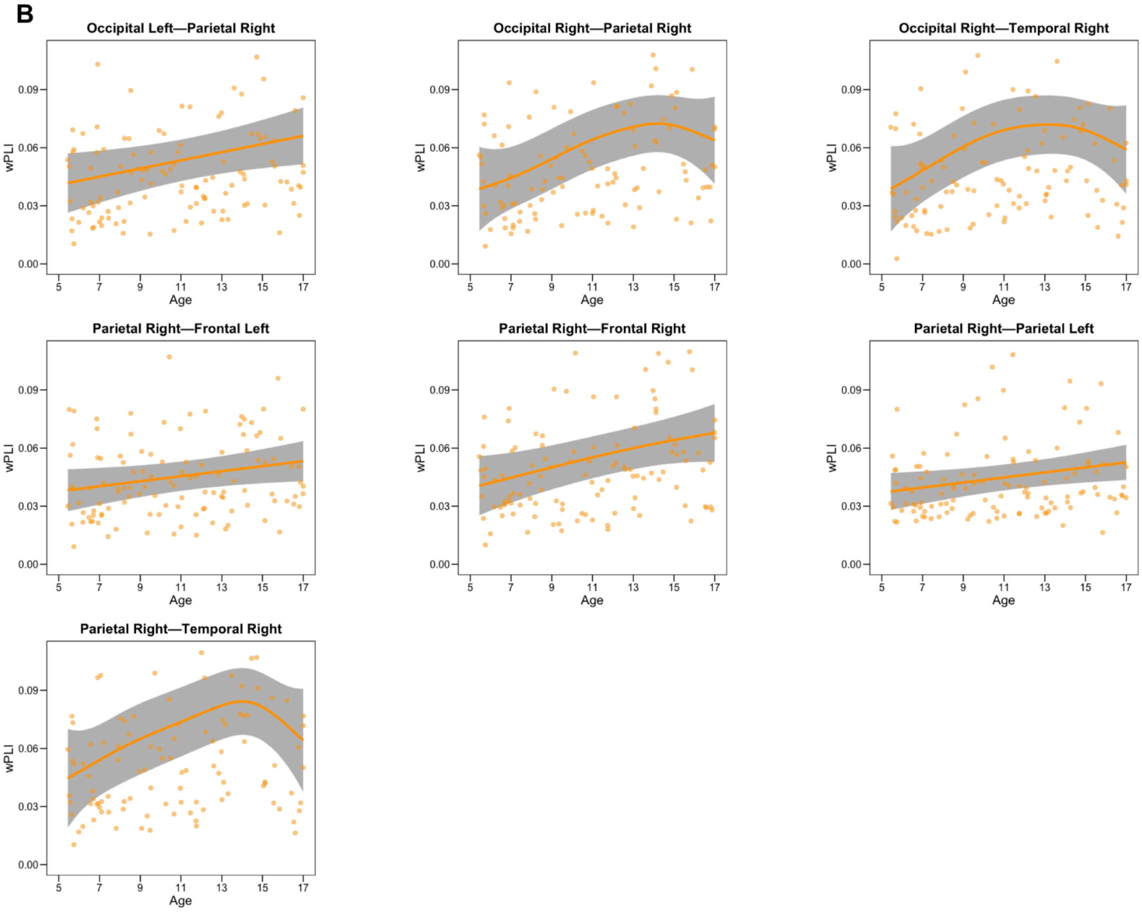


Figure 6. *(A) Significant age-related non-linear and linear changes in alpha within-region FC. (B) Significant non-linear and linear between-region age-related differences in alpha FC. The shaded regions around the lines represent 95% confidence intervals. Continuous age is presented along the x-axis, and mean wPLI is presented along the y-axis. Raw scores for each participant are depicted in the background.*

Beta FC Development

Within-Region

No significant developmental changes in the beta-band within region FC were identified (all $p > .05$).

Between-Region

All beta-band between-region GAMs returned non-significant results (all $p > .05$).

Gamma FC Development

Within-Region

Significant linear decreases in gamma-band FC were observed in the left occipital ($F(1.00, 1.00) = 4.07$, $p = .046$) and right parietal ($F(1.00, 1.00) = 6.15$, $p = .015$; see Figure 7). No other regions showed significant within-region changes (all $p > .05$).

Between-Region

No significant age-related effects were detected in the gamma-band between-region FC (all $p > .05$).

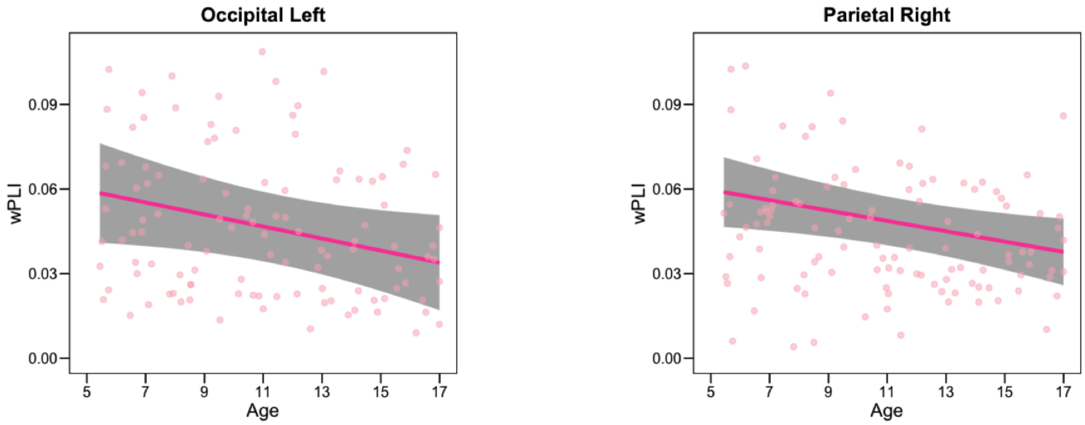


Figure 7. *Significant linear within-region age-related differences in gamma FC. The shaded regions around the lines represent 95% confidence intervals. Continuous age is presented along the x-axis, and mean wPLI is presented along the y-axis. Raw scores for each participant are depicted in the background.*

Sex Differences in Functional Connectivity

To evaluate potential sex-related differences in FC, sex was included as a predictor in all GAMs across frequency bands and region pairs. While most comparisons yielded non-significant results, three theta-band effects were found to be significant. Specifically, males exhibited greater theta connectivity within the right parietal region ($\beta = 0.013$, SE = 0.004, $t = 3.08$, $p = .003$), as well as between the right parietal and right frontal ($\beta = 0.009$, SE = 0.004, $t = 2.4$, $p = .02$), and right parietal and left frontal ($\beta = 0.007$, SE = 0.003, $t = 2.07$, $p = .04$) regions. For transparency, all sex effects—including non-significant ones—are reported in Tables S1-6 (Supplementary Materials), organized by frequency band.

Discussion

While many studies have examined age-related differences in functional brain development (Bathelt et al., 2013; Boersma et al., 2013; Chung et al., 2022), several questions still remain about the precise trajectories and temporal dynamics of functional connectivity (FC) maturation, particularly in relation to oscillatory frequency bands and individual differences. Prior work has primarily focused on resting-state data or fMRI-based approaches, which, while informative, may lack the temporal resolution to capture the rapid neural synchrony that underlies moment-to-moment cognitive processes (Sonkusare et al., 2019; Fries, 2015). In this study, we addressed this gap by using EEG data from a naturalistic movie-watching paradigm to characterize both linear and non-linear age-related changes in FC across six canonical frequency bands in children and adolescents. Our findings demonstrate that developmental change in FC is highly frequency- and region-dependent, emphasizing the value of temporally sensitive methods for mapping brain maturation.

We identified dynamic age-related changes in FC within and between temporal, parietal, and occipital regions—areas implicated in sensory integration and narrative comprehension (Tanner et al., 2023; Gao et al., 2022). Notably, frontal regions exhibited relatively stable within-region FC but increasing long-range connectivity with posterior regions, particularly in the theta and alpha bands. This supports prior findings suggesting that higher-order cognitive functions emerge through the gradual integration of distributed neural systems (Grayson & Fair, 2017; Marek et al., 2015; Michels et al., 2013). The prominence of non-linear effects across regions and frequencies further supports developmental theories emphasizing asynchronous and experience-dependent brain maturation (Adolph & Robinson, 2008; Chechik et al., 1999). Broadband analyses, although useful for summarizing general patterns, obscured many of these fine-grained developmental effects—highlighting the importance of examining frequency-specific contributions to FC development (Sanders et al., 2023; Klimesch, 1999).

Building on these findings, we next examined how developmental changes in FC varied across different frequency bands. Oscillatory systems are differently involved in cognitive and affective processes (Klimesch, 1999; Harmony, 2013), and emerging evidence suggests that age-related connectivity shifts may be frequency-specific rather than uniformly distributed across the spectrum (Michels et al., 2013; Sanders et al., 2023). By disentangling these patterns, we aimed to uncover how distinct rhythms contribute to cortical reorganization, long-range integration, and local specialization across development. The following sections interpret each frequency band in relation to known functional roles and developmental processes.

Frequency Band Interpretations

Theta and Alpha: Long-Range Integration of Cortical Networks

Theta and alpha bands exhibited significant linear increases in between-region FC with age, particularly involving frontal-parietal pathways. These findings align with research linking these oscillations to the development of large-scale attentional and executive control networks (Klimesch, 1999; Supekar et al., 2009). Right-lateralized changes in these bands further support theories of asymmetric neurodevelopment in attentional and emotional domains (Orekhova et al., 2014).

Frontal regions showed stable within-region FC but increased global connectivity with parietal and occipital regions, especially in theta and alpha bands. This suggests a growing need for inter-network coordination to support the maturation of cognitive control systems. Such long-range FC increases may reflect the gradual integration of neural systems responsible for emotional comprehension, abstract reasoning, and cognitive schema development (Adolph & Robinson, 2008; Grayson & Fair, 2017). In naturalistic tasks, such as movie-watching, these frequencies likely facilitate synchrony across networks involved in social cognition, visual interpretation, and narrative comprehension. These changes may also precede the maturation of higher-order executive functions, such as inhibitory control and working memory, which continue to develop throughout adolescence (Sherman et al., 2014).

Gamma: Local Pruning and Functional Refinement

Gamma-band FC demonstrated age-related decreases in within-region connectivity, particularly in parietal and occipital cortices. As gamma oscillations are tied to localized cortical computations (Buzsáky & Wang, 2012), this reduction may reflect local circuit refinement via synaptic-pruning—a key mechanism in adolescent brain maturation (Chechik et al., 1999; Uhlhaas et al., 2009).

Rather than indicating diminished function, this decline in gamma FC could suggest a shift toward more efficient, specialized processing. Strengthening of critical pathways and concurrent myelination may enhance information transfer, especially in domains such as visual perception, spatial reasoning, and attention. These findings support the interpretation of the gamma-band as a hallmark of localized functional optimization. It is also possible that gamma-related processes vary by cortical region or individual experience, reflecting environmental or cognitive differences across development.

Delta: Distributed Emotional and Homeostatic Integration

In the delta band, we observed non-linear developmental changes in between-region FC, especially involving frontal-temporal and frontal-occipital pathways. Delta rhythms are associated with motivational, emotional, and homeostatic processes (Harmony, 2013; Knyazev, 2012), and their non-linear trajectory may reflect tuning of long-range affective circuits. This pattern suggests that while frontal connectivity remains locally stable, it undergoes developmental reorganization with temporal and parietal regions at lower frequencies. The movie-watching paradigm, which included a socially and emotionally rich narrative, likely engaged these systems directly. For example, the story of a boy and his dog sharing a disability provided a context that resonated differently across age groups, prompting a variable engagement of emotional and social networks. Given the increasing complexity of affective demands during adolescence, delta-band connectivity may serve as a crucial biomarker for emotion-cognition integration and vulnerability to affective disorders. These findings may indicate inflection points in the development of limbic-prefrontal pathways and emotional-cognitive integration.

Beta: Null Effects and Potential Delay

Beta-band FC did not show significant age-related changes, which may reflect a combination of task-specific and maturational factors. The passive nature of the movie-watching paradigm, combined with the participant's instructions to remain still, likely minimized the engagement of motor-related beta processes. Additionally, beta-band systems supporting sensorimotor integration may mature beyond the sampled age range (Michels et al., 2013), with developmental effects emerging later in adolescence or early adulthood. Together, these factors may have contributed to the absence of detectable age-related changes in beta-band connectivity.

Hemispheric Lateralization and Frontal Integration

Right-lateralized developmental effects were prominent across multiple frequency bands, especially within parietal and temporal regions. This finding is consistent with prior work, which indicates that the right hemisphere matures earlier and plays a key role in attentional, spatial, and emotional processing (Orekhove et al., 2014; Grayson & Fair, 2017). Interestingly, while frontal regions exhibited little within-region FC change, they showed increasing global integration with posterior areas—particularly in delta, theta, and alpha bands. This suggests a developmental trajectory in which the frontal regions become a coordinating hub, facilitating long-range interactions necessary for higher-order functions such as narrative comprehension, social reasoning, and self-reflection. The shift toward global rather than local frontal reorganization may be a key marker of functional maturation. Taken together, the frequency-specific findings illustrate how brain development unfolds through parallel mechanisms of long-range integration, local specialization, and emotion-regulation tuning—each of which is captured by distinct oscillatory systems.

Taken together, these frequency-resolved findings underscore the multidimensional nature of brain development during childhood and adolescence. Rather than processing uniformly, neural maturation reflects the interplay of distinct processes—such as long-range integration, local refinement, and emotional-cognitive coupling—each of which is captured by specific oscillatory bands. This supports the idea that developmental change operates across parallel systems with unique temporal and functional signatures (Buzsáki & Wang, 2012; Harmony, 2013; Klimesch, 1999). Importantly, these patterns converged around the frontal regions as a hub for global coordination, reinforcing its role in supporting emergent executive functions and adaptive cognition (Grayson & Fair, 2017; Marek et al., 2015). By examining these trends across multiple frequency bands, we provide a more granular and biologically grounded account of how FC reorganizes with age, setting the stage for investigating potential modulators, such as sex, experience, and individual variability.

Sex Differences in Theta-Band Connectivity

Complimenting these hemispheric and network-level trends, we also identified significant sex differences in theta-band frontoparietal connectivity. Males exhibited stronger connectivity involving the right parietal region, suggesting possible sex-based divergence in the development of large-scale attentional and control systems. These findings align with previous literature linking theta oscillations to the maturation of cognitive control (Klimesch, 1999; Supekar et al., 2009) and with evidence of sex-based differences in prefrontal and parietal functional networks (Lopez et al., 2020; Wierenga et al., 2018). The fact that these effects emerged consistently within right-lateralized frontoparietal connections highlights both the specialty and potential functional relevance of sex-based developmental variation. Taken together, these results underscore the importance of modelling sex as a core biological factor in frequency-resolved analyses of brain development.

Methodological Contributions

By integrating EEG with GAMs and a naturalistic movie-watching paradigm, this study offers novel insights into the temporal dynamics of brain development. GAMs enabled the identification of subtle non-linear effects and inflection points that might be obscured in traditional linear models (Wood, 2017; Sanders et al., 2023). The naturalistic context further improved ecological validity, engaging participants in emotionally and socially relevant stimuli. While the film was broadly accessible across ages, developmental differences in emotional interpretation, social cognition, and narrative processing likely shaped the observed FC patterns. Together, the combination of GAMs and naturalistic stimuli enabled a more accurate, real-time depiction of how brain connectivity reorganizes with age.

Altogether, these findings contribute to a more nuanced understanding of developmental FC, capturing how age- and sex-related differences unfold across spatially distributed networks and oscillatory systems. By integrating frequency-resolved EEG with ecologically valid, naturalistic stimuli and non-linear modelling, this study demonstrates that brain development is not defined by a single trajectory, but by a confluence of processes that vary across frequency, region, and individual. These insights build upon and extend prior work by offering temporally precise evidence of how cortical networks reorganize during critical periods of childhood and adolescence, laying the groundwork for future longitudinal and translational research in developmental neuroscience.

Limitations and Future Directions

Several limitations warrant consideration. The cross-sectional design precludes within-individual modelling of development; longitudinal designs are needed to map FC trajectories over time. Additionally, the use of a single movie limits generalizability; future studies should examine how different types of content influence neural synchrony. Clinical and demographic heterogeneity, while increasing ecological validity, may introduce variability. Stratification by diagnosis or socioeconomic background could offer further insight into population-level differences. Finally, EEG's limited spatial resolution constrains anatomical interpretation. Combining EEG with modalities such as fMRI or MEG would enhance spatial precision and provide a fuller picture of developmental network reorganization. Future research should address these limitations through the use of longitudinal and multimodal designs, expanded stimulus sets, and targeted comparisons across clinical or developmental subgroups. Incorporating stimulus variability and developmental stratification could help clarify which observed effects are generalizable and which are context- or population-specific.

Conclusion

This study provides a comprehensive account of functional brain maturation during childhood and adolescence, highlighting distinct developmental trajectories across frequency bands. Theta and alpha bands showed linear increases in long-range FC, reflecting integration of attentional and control systems. Gamma-band FC declined locally, consistent with synaptic pruning and functional specialization. Delta-band FC demonstrated non-linear between-region reorganization, potentially supporting emotion-cognition integration. Beta-band FC remained unchanged, possibly reflecting task constraints or delayed maturation. Together, these findings support a model of neurodevelopment characterized by the co-occurrence of global integration and local refinement processes. By capturing both linear and non-linear changes and leveraging ecologically valid methods, this study contributes to a growing framework for understanding how large-scale brain networks mature. These findings may also contribute to identifying early neurophysiological markers of atypical development, enabling clinicians and educators to tailor interventions during key developmental windows. As research progresses, frequency-resolved EEG may become a powerful tool for scalable screening and monitoring of brain development. The integration of GAMs and naturalistic paradigms represents a promising methodological frontier in developmental neuroscience, enabling the discovery of individualized, context-sensitive patterns of brain maturation. Additionally, by modelling sex as a predictor across all frequency bands, this study identified distinct sex-based differences in theta-band frontoparietal connectivity. These findings underscore the importance of incorporating sex as a central variable in developmental neuroscience and highlight its potential role in shaping individual trajectories of neural maturation.

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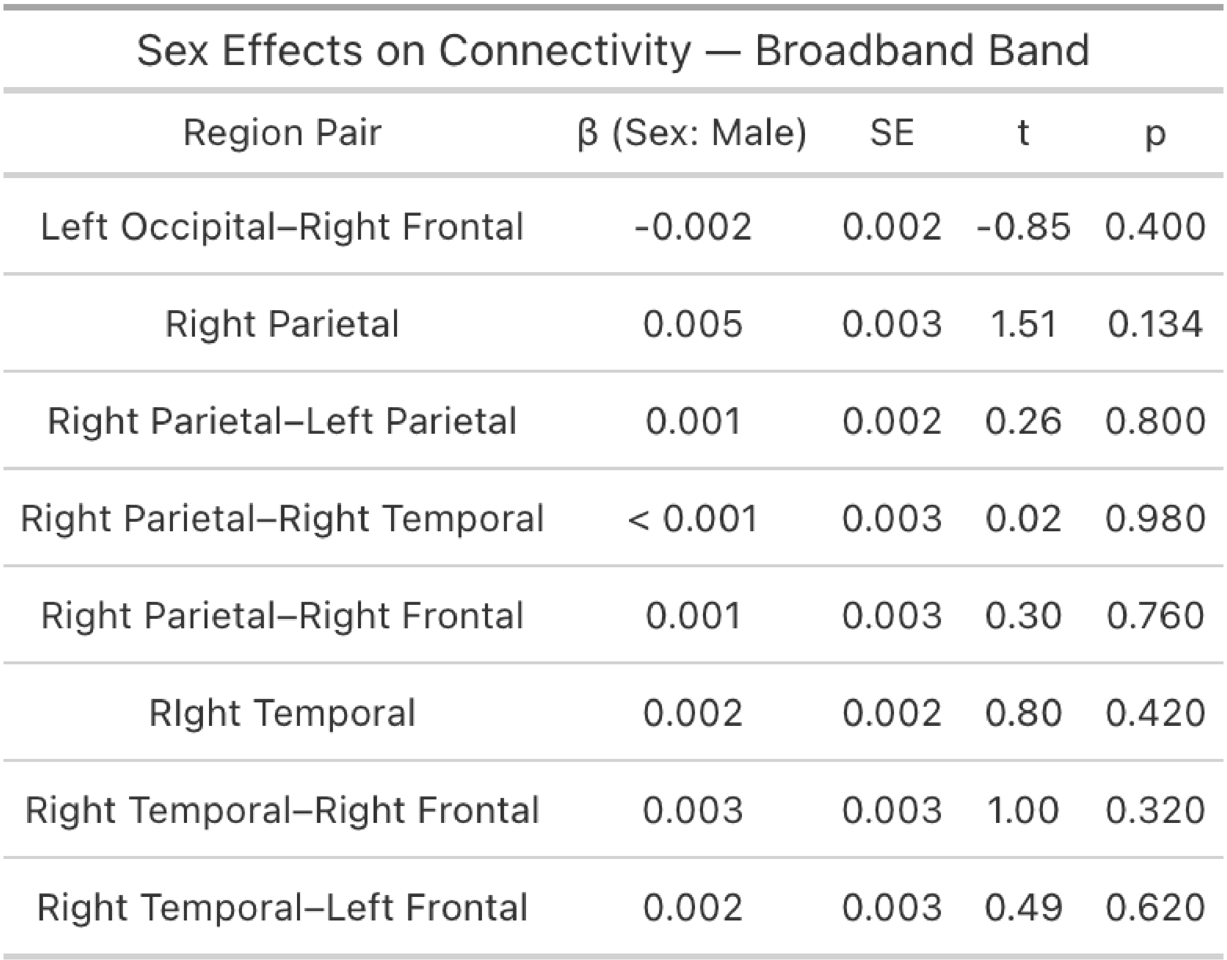
Supplementary Materials

Sex Effects on Functional Connectivity Across Frequency Bands

Note: All models included a smooth term for Age.

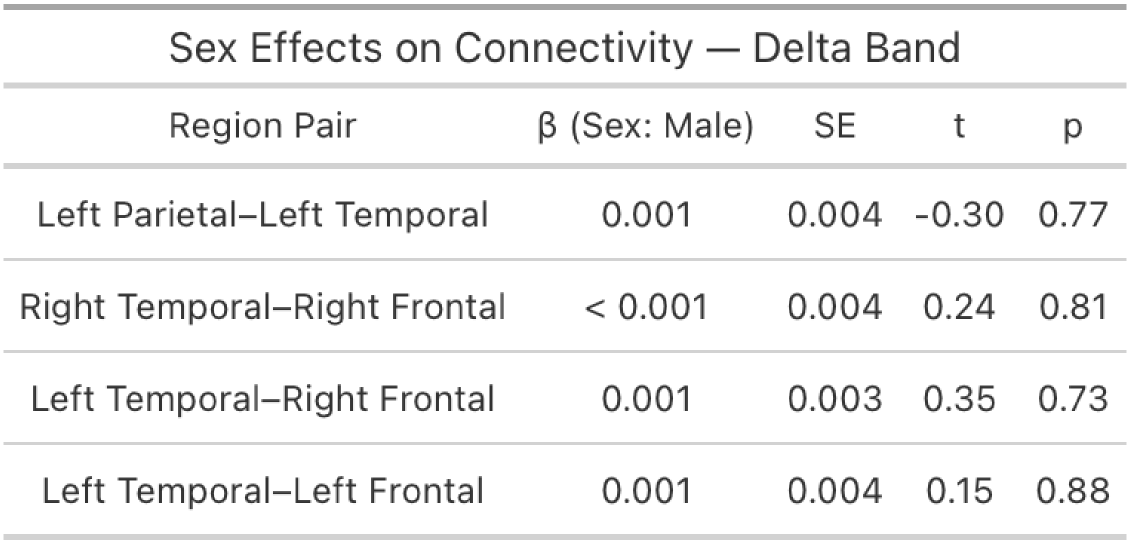
Table S1. Broadband (0.5-80 Hz)



Sex Effects on Connectivity — Broadband Band

Region Pair	β (Sex: Male)	SE	t	p
Left Occipital–Right Frontal	-0.002	0.002	-0.85	0.400
Right Parietal	0.005	0.003	1.51	0.134
Right Parietal–Left Parietal	0.001	0.002	0.26	0.800
Right Parietal–Right Temporal	< 0.001	0.003	0.02	0.980
Right Parietal–Right Frontal	0.001	0.003	0.30	0.760
RIght Temporal	0.002	0.002	0.80	0.420
Right Temporal–Right Frontal	0.003	0.003	1.00	0.320
Right Temporal–Left Frontal	0.002	0.003	0.49	0.620

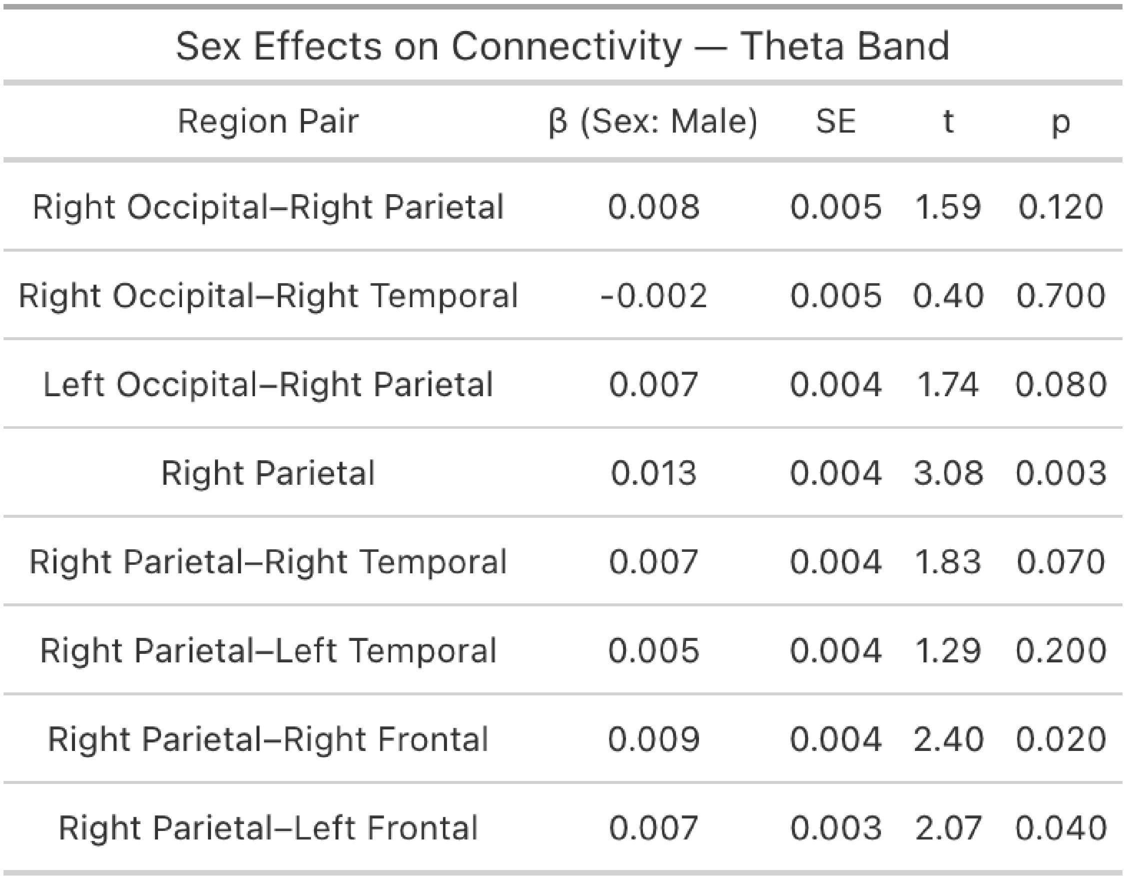
Table S2. Delta (0.5-4 Hz) Band



Sex Effects on Connectivity — Delta Band

Region Pair	β (Sex: Male)	SE	t	p
Left Parietal–Left Temporal	0.001	0.004	-0.30	0.77
Right Temporal–Right Frontal	< 0.001	0.004	0.24	0.81
Left Temporal–Right Frontal	0.001	0.003	0.35	0.73
Left Temporal–Left Frontal	0.001	0.004	0.15	0.88

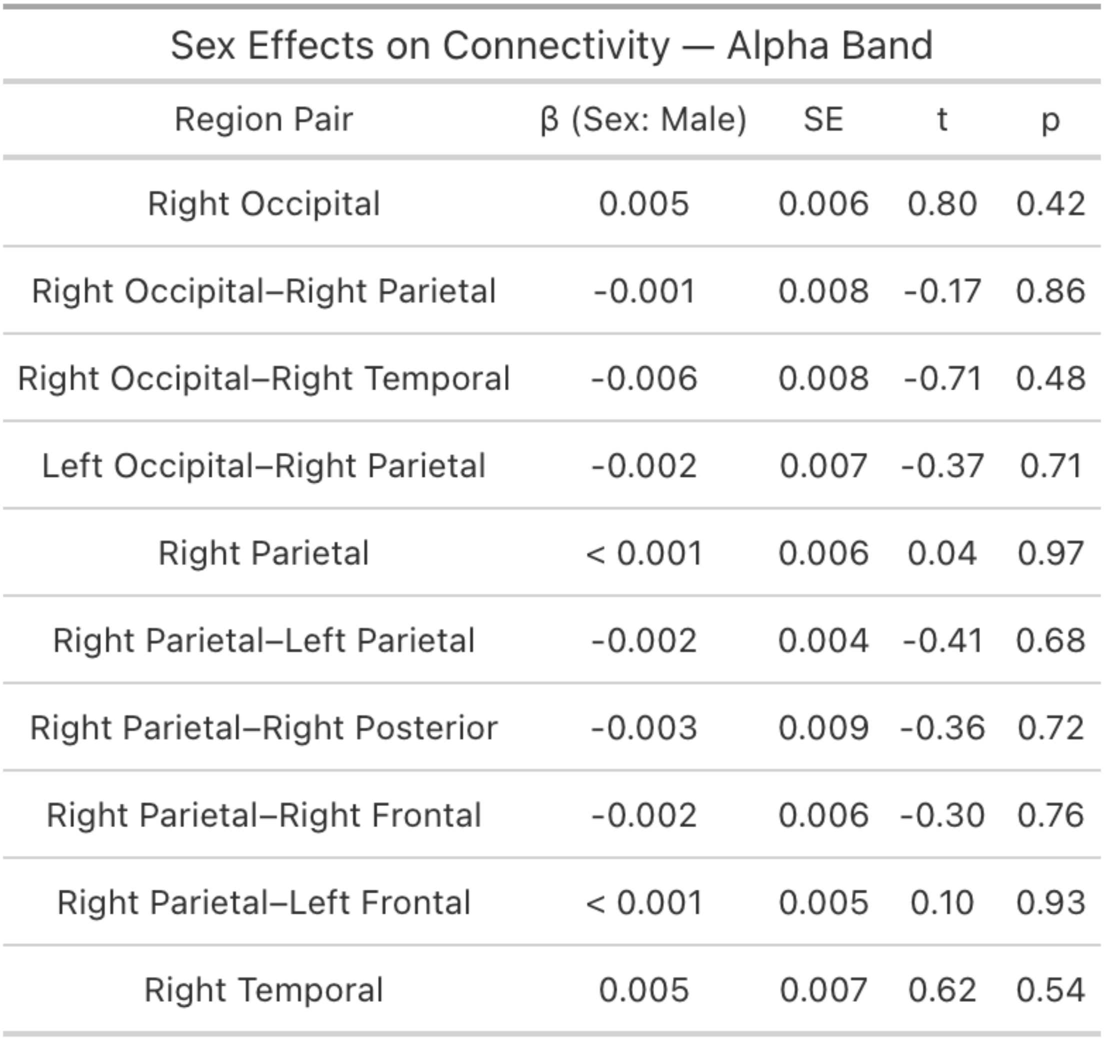
Table S3. Theta (4-8 Hz) Band



Sex Effects on Connectivity — Theta Band

Region Pair	β (Sex: Male)	SE	t	p
Right Occipital–Right Parietal	0.008	0.005	1.59	0.120
Right Occipital–Right Temporal	-0.002	0.005	0.40	0.700
Left Occipital–Right Parietal	0.007	0.004	1.74	0.080
Right Parietal	0.013	0.004	3.08	0.003
Right Parietal–Right Temporal	0.007	0.004	1.83	0.070
Right Parietal–Left Temporal	0.005	0.004	1.29	0.200
Right Parietal–Right Frontal	0.009	0.004	2.40	0.020
Right Parietal–Left Frontal	0.007	0.003	2.07	0.040

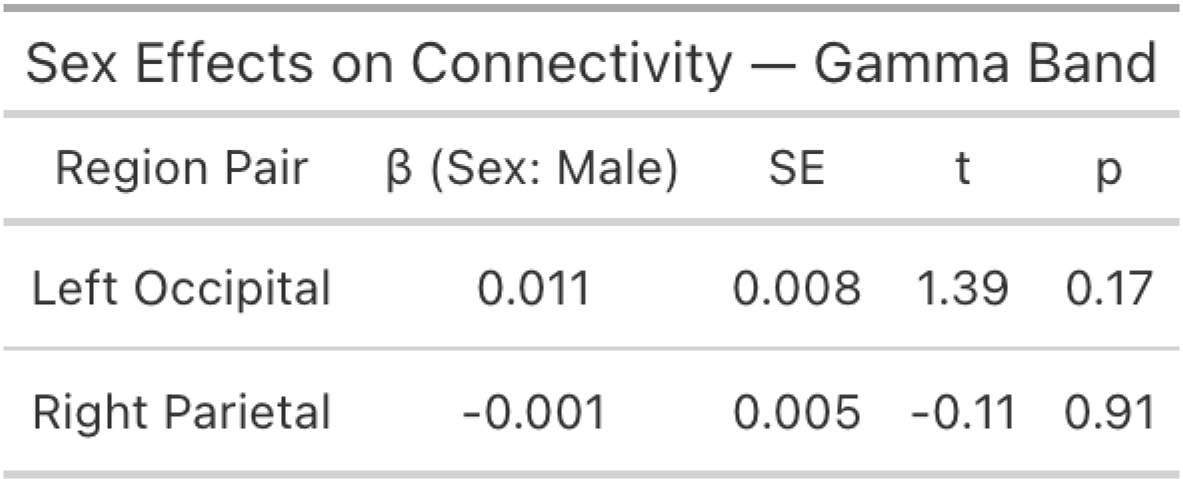
Table S4. Alpha (8-13 Hz) Band



Sex Effects on Connectivity — Alpha Band

Region Pair	β (Sex: Male)	SE	t	p
Right Occipital	0.005	0.006	0.80	0.42
Right Occipital–Right Parietal	-0.001	0.008	-0.17	0.86
Right Occipital–Right Temporal	-0.006	0.008	-0.71	0.48
Left Occipital–Right Parietal	-0.002	0.007	-0.37	0.71
Right Parietal	< 0.001	0.006	0.04	0.97
Right Parietal–Left Parietal	-0.002	0.004	-0.41	0.68
Right Parietal–Right Posterior	-0.003	0.009	-0.36	0.72
Right Parietal–Right Frontal	-0.002	0.006	-0.30	0.76
Right Parietal–Left Frontal	< 0.001	0.005	0.10	0.93
Right Temporal	0.005	0.007	0.62	0.54

Table S5. Gamma (30-80 Hz) Band



Sex Effects on Connectivity — Gamma Band

Region Pair	β (Sex: Male)	SE	t	p
Left Occipital	0.011	0.008	1.39	0.17
Right Parietal	-0.001	0.005	-0.11	0.91