

Neural oscillatory dynamics serving abstract reasoning reveal robust sex differences in typically-developing children and adolescents

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ABSTRACT

Fluid intelligence, the ability to problem-solve in novel situations, is linked to higher-order cognitive abilities, and to academic achievement in youth. Previous research has demonstrated that fluid intelligence and the underlying neural circuitry continues to develop throughout adolescence. Neuroimaging studies have predominantly focused on identifying the spatial distribution of brain regions associated with fluid intelligence, with only a few studies examining the temporally-sensitive cortical oscillatory dynamics underlying reasoning abilities. The present study collected magnetoencephalography (MEG) during an abstract reasoning task to examine these spatiotemporal dynamics in a sample of 10-to-16 year-old youth. We found increased cortical activity across a distributed frontoparietal network. Specifically, our key results showed: (1) age was associated with increased theta activity in occipital and cerebellar regions, (2) robust sex differences were distributed across frontoparietal regions, and (3) that specific frontoparietal regions differentially predicted abstract reasoning performance among males versus females despite similar mean performance. Among males, increased theta activity mediated the relationship between age and faster reaction times; conversely, among females, decreased theta mediated the relationship between age and improved accuracy. These findings may suggest that males and females engage in distinct neurocognitive strategies across development to achieve similar behavioral outcomes during fluid reasoning tasks.

1. Introduction

Fluid intelligence (*Gf*) is broadly defined as the ability to problem-solve in novel situations and is commonly described as “non-verbal” intelligence (Ferrer et al., 2009; Horn and Cattell, 1967). Researchers and clinicians commonly assess *Gf* abilities through abstract, relational reasoning tasks including figural matrices, numerical matrices, and figural analogies (for examples, see Gagol et al., 2018). There is a general consensus that *Gf* abilities interact with a wide array of higher-order cognitive abilities including attention, executive functions, and working memory (Conway et al., 2002; Crone and Richard Ridderinkhof,

2011; Duncan, 2013; Ferrer et al., 2009). Importantly, evidence shows that *Gf* has a major impact on academic achievement among children and adolescents (Gómez-Veiga et al., 2018; Green et al., 2017; Soares et al., 2015). *Gf* is also known to be particularly sensitive to changes in neurological functioning, including changes associated with normative development (Crone and Richard Ridderinkhof, 2011; Horn, 1968; Krawczyk, 2012). More specifically, neuropsychological assessments repeatedly show that *Gf* rapidly increases with age from early childhood through adolescence before reaching a plateau in young adulthood (Cattell, 1974; Mcardle et al., 2002).

Concerning the underlying neurophysiology of intelligence and

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reasoning abilities, Jung and Haier (2007) have proposed one of the most popular theories on the neural basis of intelligence: the parieto-frontal integration theory (P-FIT). This model outlines a dispersed frontoparietal network of brain regions including lateral portions of prefrontal cortex, posterior portions of parietal cortex, as well as areas of the occipital and temporal cortices, which largely support performance on measures of general intelligence (Jung and Haier, 2007). Subsequent research specifically examining *Gf* in the brain have largely corroborated the P-FIT model as a neural network serving abstract reasoning abilities across development (Basten et al., 2015; Dumontheil, 2014; Ferrer et al., 2009; Krawczyk, 2012; Tadayon et al., 2019). Further, regions within the P-FIT model and the connections between them are known to undergo dramatic structural maturation from childhood through adolescence, including changes in gray matter volume, cortical thickness, and white matter integrity (Casey et al., 2000, 2005; Dumontheil, 2016; Shaw, 2007), and those structural changes have been linked to differences in *Gf* abilities (Estrada et al., 2019; Wendelken et al., 2016). Furthermore, functional MRI (fMRI) studies have also shown fluctuations in blood-oxygenation level-dependent (BOLD) activity within P-FIT regions during abstract reasoning tasks. However, investigations using fMRI to examine *Gf* abilities across development have been mixed, with some showing increases in BOLD in key regions and others showing decreases (Bazargani et al., 2014; Ramchandran et al., 2019; Shaw, 2007). Although it should be noted that *Gf* abilities have only rarely been studied in developing youth, and thus some of these discrepancies may be due to differences in the age range being studied, developmental sex differences, or task design factors.

While fMRI studies of *Gf* are relatively common, there is a paucity of work examining the oscillatory dynamics of neuronal activity serving abstract reasoning and other *Gf* abilities. Of the existing studies, several have associated alpha (8–12 Hz) event-related desynchronizations, or decreases in band-limited power, during complex cognitive tasks with *Gf*, with some evidence for sex differences in adults (e.g., Dix et al., 2016; Neubauer and Fink, 2003; Ramos et al., 1993). Other adult studies using transcranial alternating-current stimulation (tACS) have suggested that both gamma (>30 Hz) and theta (4–8 Hz) frequency stimulation affect abstract reasoning and logical performance (Neubauer et al., 2017; Pahor and Jaušovec, 2014a,b; Santarnecchi et al., 2016, 2013), but these studies have not examined the inherent oscillatory dynamics of the underlying circuits during ongoing processing. Despite the known developmental changes in *Gf*, the neural oscillatory dynamics serving abstract reasoning and related abilities have seldom been studied in children and adolescents. Developmental changes in neural oscillatory dynamics are well appreciated (Embury et al., 2019; Heinrichs-Graham et al., 2018; Trevarrow et al., 2019; Uhlhaas and Singer, 2013; Uhlhaas et al., 2009; Wilson et al., 2010), with some evidence for changes in *Gf*-implicated processes such as working memory (Embury et al., 2019) and sex-specific patterns of correlation with cognitive abilities (Bódizs et al., 2014; Ujma et al., 2017). Additional studies have shown sexually-dimorphic age-related changes in spontaneous neural activity during rest (e.g., Eeg-Olofsson, 1971; Gasser et al., 1988; Gibbs and Knott, 1949; Matoušek and Petersén, 1973; Matsuura et al., 1985; Penuel et al., 1955). Such findings of sex differences in this domain are consistent with the literature on sex-specific developmental trajectories of cortical reorganization that directly relate to cognitive capacity in several high-order domains including attention and working memory (Blakemore and Choudhury, 2006; Blakemore et al., 2010).

In the current study, our goals were to elucidate the neural oscillatory dynamics serving *Gf* in a large sample of typically developing youth during middle childhood and adolescence. We begin by identifying the main neural oscillatory responses observed during a novel abstract reasoning task, and demonstrating that behavioral performance on widely accepted measures of *Gf* are correlated with performance on our abstract reasoning task. Then, we image these responses and examine whole-brain correlations between the strength of these neural

oscillations and chronological age. Next, we evaluate sex differences in the relationships between neural oscillatory activity, age, and behavioral performance. Based on the literature (e.g., Dix et al., 2016; Neubauer et al., 2017; Pahor and Jaušovec, 2014b), we hypothesized that our abstract reasoning task would elicit alpha desynchronizations (i.e., band-limited power decreases) and gamma and theta synchronizations (i.e., band-limited power increases) across frontoparietal regions. We also expected to see differential patterns of age-related change in neural oscillatory activity in males and females, demonstrating the sexually-divergent nature of neurodevelopment during the transition from middle childhood to adolescence.

2. Materials and methods

2.1. Participants

Seventy-two typically developing youth ages 10–16 years ($M_{age} = 12.74$ years, $SD = 1.59$; IQ: $M_{FSIQ-4} = 113.62$, $SD = 14.08$; 35 male) completed an abstract reasoning task as part of the National Science Foundation (NSF)-funded Developmental Chronnecto-Genomics (DevCoG) study. All participants were recruited from the University of Nebraska Medical Center (UNMC) site. Exclusionary criteria included inability to perform the task, any medical illness affecting CNS function, neurological or psychiatric disorder, history of head trauma, current substance abuse, any medication known to affect CNS function, and the MEG Laboratory's standard exclusion criteria (e.g., dental braces, metal implants, battery operated implants, and/or any type of ferromagnetic implanted material). Parents of child participants signed informed consent forms, and child participants signed assent forms before proceeding with the study. All procedures were approved by the UNMC Institutional Review Board.

2.2. Cognitive assessments

The complete four-scale Wechsler Abbreviated Scale of Intelligence (WASI-II; Wechsler, 2011) was administered by a trained research assistant in a quiet room. Normed composite scores were derived for Full-Scale IQ-4 (FSIQ-4) and the Perceptual Reasoning Index (PRI; a measure of fluid intelligence) in accordance with the publisher recommendations. The WASI-II is known to have high reliability and validity in children and adolescents (Irby and Floyd, 2013; McCrimmon and Smith, 2013). One child in our sample did not complete the WASI-II due to test anxiety.

2.3. MEG experimental paradigm

Participants completed a custom, MEG-compatible non-progressive abstract reasoning task that was adapted from the classic Raven's Progressive Matrices (Raven, 1936; Raven et al., 2003). Participants were shown a centrally-presented fixation cross in a 4×4 grid for a jittered period of $2750 \text{ ms} \pm 250 \text{ ms}$ (see Fig. 1). Either the bottom left or bottom right box was highlighted. An array of four complex figures was then presented for 4000 ms. Participants were instructed to determine whether the complex figure in the highlighted box accurately completed the 4×4 grid given the pattern of shapes/colors in the other three boxes. Participants responded by pressing a button with their right index finger if the highlighted figure correctly completed the matrix, or by pressing a button with their right middle finger if the highlighted figure did *not* correctly complete the matrix. There were a total of 120 trials, equally split and pseudorandomized between correct and incorrect matrix completions. The task lasted approximately 14 min total with a 30 s break at the mid-point.

2.4. MEG data acquisition

Neuromagnetic responses were acquired within a magnetically-

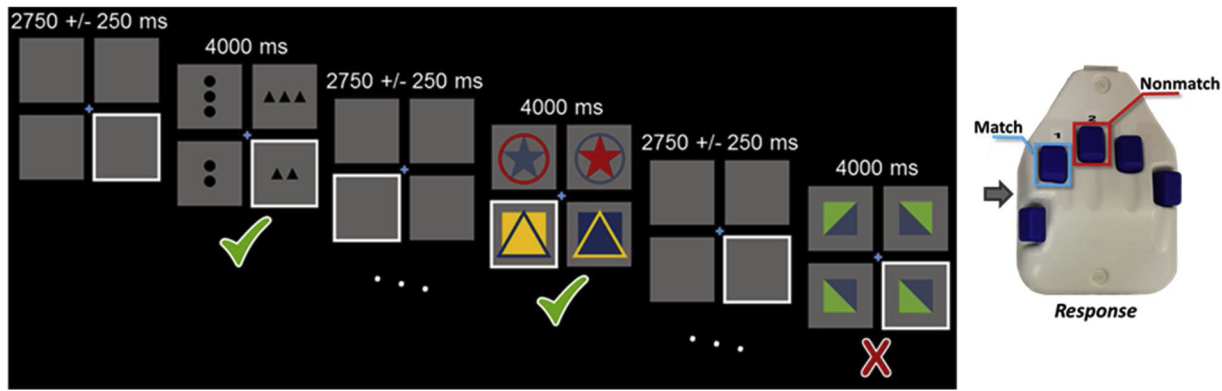


Fig. 1. The abstract reasoning task. Each trial began with a centrally-located fixation cross amid an empty 4×4 grid for 2750 ± 250 ms. One box, either the bottom left or bottom right, was highlighted with a white outline. The grid was then filled with complex figures for 4000 ms. Participants were instructed to respond as quickly as possible with a button press indicating whether the figure in the highlighted square correctly completed the matrix.

shielded room using an Elekta MEG system with 306 sensors (102 magnetometers and 204 planar gradiometers; Elekta, Helsinki, Finland). Signals were sampled at 1 kHz with an acquisition bandwidth of 0.1–330 Hz. Each MEG data set was corrected for head motion, and the signal space separation method with a temporal extension (tSSS; Taulu and Simola, 2006; Taulu et al., 2005) was applied for noise reduction. Further details are provided in several recent papers (Embury et al., 2019; Lew et al., 2019; Spooner et al., 2018; Wiesman and Wilson, 2020).

2.5. MEG coregistration and structural MRI processing

The MEG coregistration procedure, MRI acquisition and processing, and spatial normalization of images to Talairach space followed a standard pipeline that has been reported in previous manuscripts associated with the Dev-CoG project (Embury et al., 2019; Trevarrow et al., 2019).

2.6. MEG time-frequency transformation and statistics

The continuous magnetic time series was divided into epochs (duration: 6500 ms), beginning -2500 ms prior to the onset of the matrix stimuli and extending 4000 ms afterward. The baseline period was defined as -1800 to -800 ms prior to the onset of the matrix stimuli to minimize any anticipation effects. Signal-space projection (SSP) was used to remove cardiac and eye blink artifacts from the MEG data, and this was accounted for during source reconstruction (Uusitalo and Ilmoniemi, 1997). Artifactual epochs (e.g., those containing muscle artifacts, eye blinks/saccades, coughing, swallowing, etc.) were rejected based on a fixed-threshold method that was supplemented with visual inspection. Amplitude and gradient distributions per person were computed using all trials, and the trials with the highest amplitude and/or gradient values relative to the total distribution were excluded. Of note, individual signal amplitude ($M = 1432.61$ fT, $SD = 398.51$) and gradient ($M = 92.20$ fT/s, $SD = 24.63$) thresholds were set for each participant due to differences among individuals in sensor proximity and head size, which strongly affect MEG signal amplitude. An average of 96.25 trials ($SD = 7.97$) per participant remained for further analysis after artifact rejection.

Following artifact rejection, complex demodulation was used to transform all remaining epochs into the time-frequency domain (resolution: 2.0 Hz, 25 ms). The resulting spectral power estimations (per sensor) were averaged over trials and then normalized using the respective bin's baseline power, which was defined as the mean power during the -1800 to -800 ms window. Statistical analysis of the sensor-level spectrograms across all trials and gradiometers were used to determine the precise time-frequency windows used for source imaging.

This analysis was limited to the first 1000 ms following stimulus onset, which was selected to maximize focus on the abstract reasoning components, while minimizing the impact of other neural responses (e.g., motor) occurring during each trial. The sensor-level statistical analysis followed an established two-stage procedure that was designed to minimize the risk of false-positive results while also maintaining reasonable sensitivity (see McDermott et al., 2017; Proskovec et al., 2018; Wiesman et al., 2017). Briefly, two-tailed paired-sample *t*-tests versus baseline were performed on each data point per spectrogram, and the resulting *t*-values were thresholded at $p < .05$. The time-frequency bins that survived the threshold were clustered with temporally and/or spectrally neighboring bins that also exceeded the threshold. A distribution of cluster values was then derived using nonparametric permutation testing and the significance level of the observed clusters was tested directly using this distribution (Ernst, 2004; Maris and Oostenveld, 2007). At least 10,000 permutations were computed to build a distribution of cluster values for each comparison. The significant time-frequency windows that were identified through this analysis were subjected to the beamforming analysis (see “Sensor-Level Results” in the Results section).

2.7. MEG source imaging and statistics

An extension of the linearly constrained minimum variance vector beamformer (Gross et al., 2001; Hillebrand et al., 2005; Veen et al., 1997), called Dynamic Imaging of Coherent Sources (DICS; Gross et al., 2001) was used to image cortical activity. This approach uses spatial filters in the frequency domain to estimate source power across the whole brain volume. The technical details of this approach is described at length in the papers cited, and the specific application used here has been described in our recent papers (e.g., Embury et al., 2019; Heinrichs-Graham et al., 2018; Proskovec et al., 2018; Spooner et al., 2019; Wiesman and Wilson, 2020). MEG preprocessing and imaging were completed using BESA (V 6.1) software.

Using the statistically selected time-frequency bands (see below) normalized differential source power was computed over the entire brain volume per participant ($4.0 \times 4.0 \times 4.0$ mm). The resulting 3D volumes of neural activity were averaged across all participants to assess the neuroanatomical distribution of each significant oscillatory response that was identified through the sensor-level analysis. Whole-brain correlations were then computed between the participant-level maps and chronological age in hundredths of years to examine developmental changes in the neural responses, and then separately for males and females. Sex effects in correlational maps were tested using Fisher's *r* to *Z* transformations. All maps were threshold at a significance level of $p < .001$ and corrected for multiple comparisons using a cluster criterion (> 300 contiguous voxels), which was a conservative estimate based on the

spatial smoothness of the image.

Finally, we conducted follow-up analyses to examine whether the neural oscillatory activity identified in our developmental analyses related to behavioral performance on the task. Specifically, we examined whether oscillatory activity measured at the peak of each identified cluster mediated the relationship between age and task performance (i.e., reaction time and accuracy). Because traditional tests of indirect effects (e.g., the Sobel test) often violate the assumption of normality, we utilized asymmetrical confidence intervals which best represent the true distribution of the indirect effect (i.e., the product of coefficients from the “a” and “b” paths). Thus, we examined the 95 % confidence intervals of bias-corrected bootstrapped confidence intervals based on 1000 bootstrapped samples (Efron and Tibshirani, 1986), which provide a robust estimate of mediation effects and are asymmetrical (Fritz and MacKinnon, 2007). Mediation analyses were conducted in Mplus version 8.1.

3. Results

3.1. Demographic data and behavioral results

Of the 72 participants who completed the task, five participants were excluded due to poor performance on the task (< 60 % correct overall) and an additional 21 participants were excluded due to technical issues during MEG/MRI data collection, excessively noisy or artifact-riddled data, and/or other artifacts or errors during data processing. Thus, the final sample consisted of 46 youth ($M_{\text{age}} = 12.96 \pm 1.65$ years; fluid intelligence: $M_{\text{PRI}} = 109.31 \pm 15.20$; 22 male). Average accuracy on the

task was 82.55 ± 7.36 %, and average reaction times were 1966.09 ± 317.01 ms. All artifact-free trials were utilized in the final MEG analyses to maximize the signal-to-noise ratio, although we also ran the MEG analyses using the correct-only trials and this yielded very similar conclusions. The number of trials included in the final analyses did not significantly correlate with age, $r = 0.22$, $p = .14$.

There was a significant correlation between age and accuracy such that older youth tended to perform better on the task, $r = -0.34$, $p = .02$. Additionally, reaction time was correlated with age such that older youth tended to respond faster than their younger peers, $r = -0.41$, $p = .005$ (see Fig. 2a-b). Accuracy and reaction time were significantly related, suggesting that youth who were more accurate on the task also tended to respond more quickly, $r = -0.50$, $p < .001$ (i.e., reverse speed-accuracy tradeoff). Finally, both accuracy and reaction time correlated with participants’ *Gf* scores, as indexed by the PRI composite of the WASI-II. Youth with greater *Gf* abilities tended to have higher accuracy, $r = 0.50$, $p < .001$, and faster reaction times, $r = -0.31$, $p = .04$, than participants with lower *Gf* (see Fig. 2c-d). This finding is important as it supports the validity of our novel abstract reasoning task as a measure of *Gf* in this population. Finally, two-sample *t* tests revealed no significant differences between males and females in either reaction time or accuracy, nor were their sex differences in PRI scores or overall WASI-II 4-scale composite scores.

3.2. Sensor-level results

Statistical evaluation of the time-frequency spectrograms showed a significant theta increase from 4 to 8 Hz in central and frontal sensors

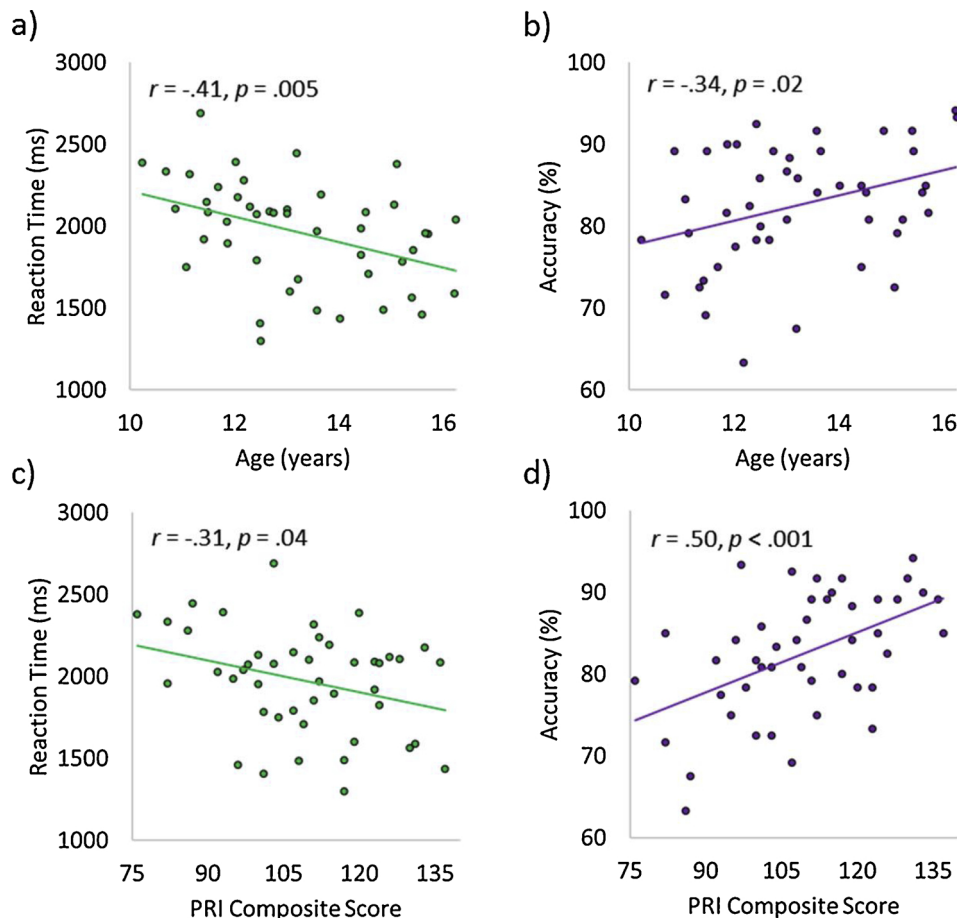


Fig. 2. Correlations between task performance, fluid intelligence, and chronological age. a) significant correlation between age and reaction time; b) significant correlation between age and accuracy; c) significant correlation between fluid intelligence (*Gf*) and reaction time; d) significant correlation between fluid intelligence (*Gf*) and accuracy.

from 100–500 ms. Additionally, there was an alpha/beta decrease between 475–1000 ms that spanned from 8 to 22 Hz, and a gamma increase between 175–975 ms from 64–92 Hz, both observed across bilateral posterior sensors (p 's < 0.001, corrected; Fig. 3). The neural populations generating each of these three time-frequency responses were then imaged separately in each participant, and examined statistically for developmental and sex effects.

3.3. Functional mapping results

Beamformer images per time-frequency bin were initially averaged across all participants. These grand-average maps revealed an early increase in theta that extended broadly across frontal and parietal cortices, with additional smaller peaks in temporal and occipital areas (see Fig. 3). There were also strong decreases in alpha/beta across bilateral occipital regions, with an additional peak in the left inferior parietal lobule. Finally, increased gamma activity was more isolated, with the grand-averaged beamformer reconstruction images implicating primarily occipital cortex (Fig. 3).

We evaluated developmental effects by correlating each of these functional maps (i.e., theta, alpha/beta, and gamma) with chronological age. Interestingly, theta activity along the calcarine fissure was positively correlated with age, as was a region of the right cerebellar cortices (p 's < 0.001, corrected; see Table 1 and Fig. 4). Thus, older youth tended to exhibit stronger theta responses compared to their younger peers within these regions during the abstract reasoning task. No brain regions in the alpha/beta nor gamma functional maps were statistically correlated with age at our conservative threshold. Next, we tested whether there were sex differences in the developmental trajectories by computing these correlations separately for males and females and then using Fisher's r to Z transformations. These analyses revealed robust sex differences in the correlations between theta activity and age. Specifically, males had significantly stronger positive correlations between theta activity and age in distributed areas of frontal, temporal, and parietal cortices (p 's < 0.001, corrected; see Table 1 and Fig. 5), including

Table 1

Significant clusters for each analysis.

| Region/Correlation of Interest | X | Y | Z | Statistic |
|---|-----|-----|-----|------------|
| Theta Activity with Chronological Age | | | | |
| L calcarine | -5 | -94 | 9 | r |
| R cerebellum | 18 | -84 | -35 | .52 |
| Sex Differences in Theta with Chronological Age (Male > Female) | | | | |
| R superior frontal gyrus | 20 | -11 | 65 | Fisher's Z |
| R superior frontal gyrus | 15 | 25 | 48 | 3.98 |
| L dorsolateral prefrontal cortex | -42 | 15 | 35 | 3.30 |
| L inferior frontal gyrus | -34 | 40 | 7 | 4.41 |
| L pre-supplementary motor area | -12 | 14 | 58 | 4.33 |
| L inferior temporal sulcus | -58 | -6 | -20 | 3.76 |
| R inferior parietal lobule | 49 | -31 | 52 | 4.09 |
| R inferior parietal lobule | 55 | -43 | 44 | 4.00 |
| R precuneus | 2 | -71 | 55 | 3.46 |
| L cuneus | -14 | -89 | 24 | 3.33 |
| | | | | 3.65 |

the left dorsolateral prefrontal cortices, left inferior and middle frontal gyri, left middle and inferior temporal gyri, superior and inferior parietal cortices, as well as visual cortices in the occipital region (Fig. 5). In other words, with increasing age, males exhibited greater theta synchronization across a distributed network of brain regions compared to their female peers.

3.4. Direct & indirect links between neurophysiology and abstract reasoning performance

Given the robust age-by-sex interactions in the distributed fronto-parietal network, we examined whether theta activity in the 10 significant clusters (Table 1) was associated with task performance, thereby deciphering the functional relevance of these neural signatures to abstract reasoning abilities. Thus, we performed a series of mediation analyses examining whether theta synchronization in the identified regions mediated the relationship between age and task performance (i.e., reaction time and accuracy) separately for males versus females. We first determined the direct effect of age on both accuracy and reaction time

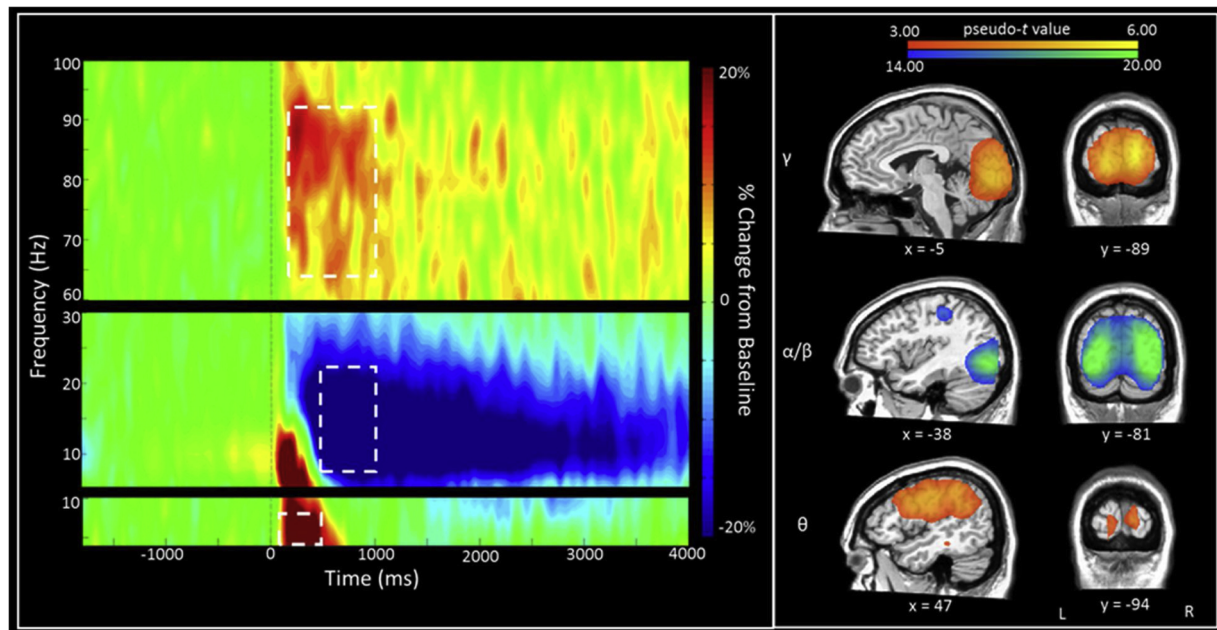


Fig. 3. Spectrograms and source reconstructions. Time-frequency decomposition and permutation-corrected statistical analyses indicated three time-frequency bins with significant responses (p < .05, corrected) relative to baseline during the first 1000 ms period of interest. These included theta activity (4–8 Hz; bottom left) from 100–500 ms, alpha/beta activity (8–22 Hz) from 475–1000 ms, and gamma activity (64–92 Hz) from 175–975 ms. The statistical analyses included all gradiometers, but shown here are the sensors most clearly showing the response (i.e., M1123 for theta, M2243 for alpha/beta, and M2042 for gamma). To the right are the grand-averaged source reconstructions per time-frequency bin across participants. As shown, theta responses were detected across a widespread network, whereas alpha/beta and gamma responses were largely constricted to parietal and/or occipital cortices.

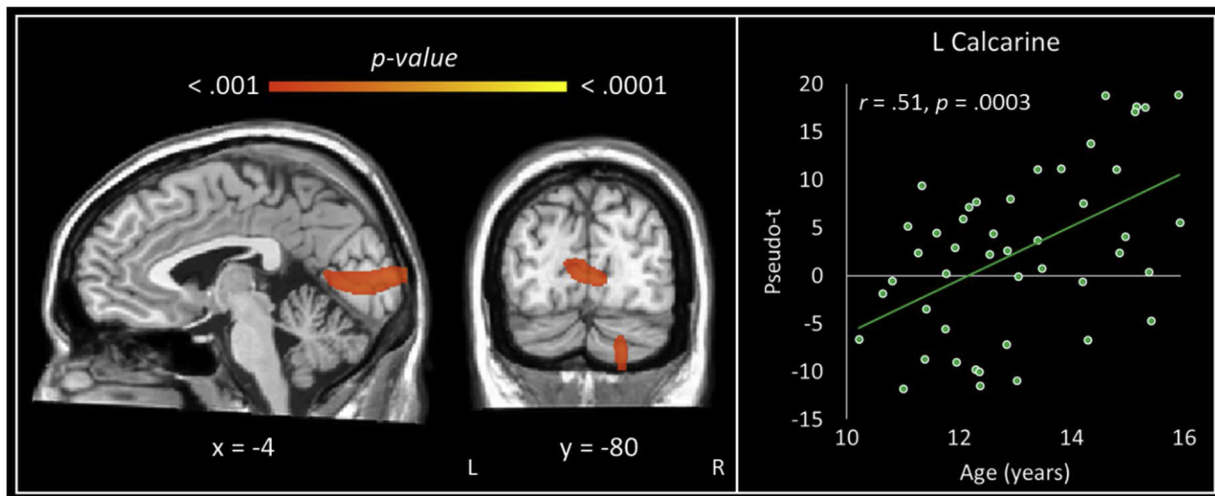


Fig. 4. Correlations between theta activity during task performance and chronological age for the full sample. (Left) Maps have been thresholded at $p < .001$, corrected, and show regions of occipital and cerebellar cortices. (Right) Scatterplot showing the correlation between the peak in occipital cortices and chronological age, with the r and p -values embedded.

using a simple group-based path analysis, which simultaneously calculated the effects for males versus females; these results are shown in Fig. 6. In short, there is a significant direct effect of age on reaction time, but not accuracy among males, whereas females showed the opposite effect. The data suggest an immediate differentiable pattern of developmental influences on task behavior between males and females. To reiterate the earlier findings noted above, males and females did not differ in *mean* reaction time or accuracy.

We then tested the conceptual model shown in Fig. 7, which assessed the extent to which theta synchronization measured at the peak of each of the identified clusters significantly mediated the effect of age on task performance. We found several statistically significant indirect effects of theta synchronization on the relationship between age and task performance (see Table 2). Among males in the study, theta activity within right superior frontal gyrus, left dorsolateral prefrontal cortex, and the right inferior parietal lobule fully mediated the relationship between age and reaction time during the abstract reasoning task. In each case, increasing age predicted increased theta synchronization, and increased theta synchronization predicted faster reaction times. There were no significant indirect effects of theta synchronization on the relationships between age and accuracy among males, which was not altogether surprising given that the direct effect of age on accuracy was not statistically significant in the original model (Fig. 6).

For females, we detected two statistically significant partial mediations on the relationship between age and accuracy (see Table 2). Specifically, increasing age predicted decreased theta synchronization in the left dorsolateral prefrontal cortex and inferior frontal gyrus, which then predicted increased accuracy on the task. There was also a significant indirect effect on the relationship between age and reaction times among females such that increasing age predicted decreased theta synchronization in the left pre-supplementary motor area, which then predicted faster reaction times on the task. Interestingly, the data suggest a significant suppressor effect; the original, direct effect of age on reaction time was not statistically significant for females. However, when accounting for the mediating effect of theta activity in left pre-supplementary motor area, the path from age to reaction time (c') increased in magnitude and achieved statistical significance *in addition* to the significant indirect effect of theta activity.

4. Discussion

The present study examined the neural oscillatory dynamics underlying abstract reasoning abilities using MEG in a cohort of typically

developing youth. Behaviorally, we found that greater *Gf* abilities and older chronological age were associated with both increased accuracy and faster reaction times on the abstract reasoning task, which supports the veracity of our novel task as a measure of *Gf*, and additionally suggests strong cognitive-developmental influences on task performance. Importantly, there were no significant differences in behaviorally assessed *Gf* abilities, or in accuracy or reaction time during the abstract reasoning task between males and females.

Examination of oscillatory activity during task performance revealed three distinct time-frequency windows of interest: 1) an early theta (4–8 Hz) synchronization from 100–500 ms, 2) an alpha/beta (8–22 Hz) desynchronization from 475–1000 ms, and 3) a high-frequency gamma (64–92 Hz) synchronization from 175–975 ms. Theta activity was relatively distributed across much of the cortex including frontal, parietal, and occipital areas, whereas alpha/beta and gamma responses were more confined to the bilateral occipital cortex. Alpha/beta activity was also found in the left inferior parietal lobule. These findings corroborate prior work examining the P-FIT model of the neurobiological basis of intelligence (Basten et al., 2015; Jung and Haier, 2007). Specifically, the abstract reasoning task in the present study elicited cortical responses within the frontal, parietal, and occipital regions of the cortex believed to serve *Gf* abilities.

Our key findings were the significant changes in oscillatory responses as a function of chronological age, both at the full-group level and differentially between males and females. For the full sample, theta activity surrounding the calcarine fissure and in cerebellar cortices increased as a function of increasing chronological age, suggesting that older youth generally had stronger theta oscillatory activity within these regions compared to their younger peers during task performance. Perhaps more interestingly, the data revealed a robust, differential pattern of cortical theta activity between males and females. Overall, males exhibited stronger theta oscillations with increasing age across a distributed network of regions, including many of the P-FIT model regions, whereas females showed *reduced* cortical theta with development across these same brain regions. Importantly, these findings emerged without any notable differences in mean task performance between sexes (either reaction time or accuracy), garnering support that the differences in cortical oscillatory activity likely reflect differences in either local neural efficiency or larger-scale network maturation, and were not confounded by performance differences.

Interestingly, our follow-up analyses indicated that only specific regions of neural oscillatory activity significantly mediated the relationship between age and abstract reasoning task performance. Among

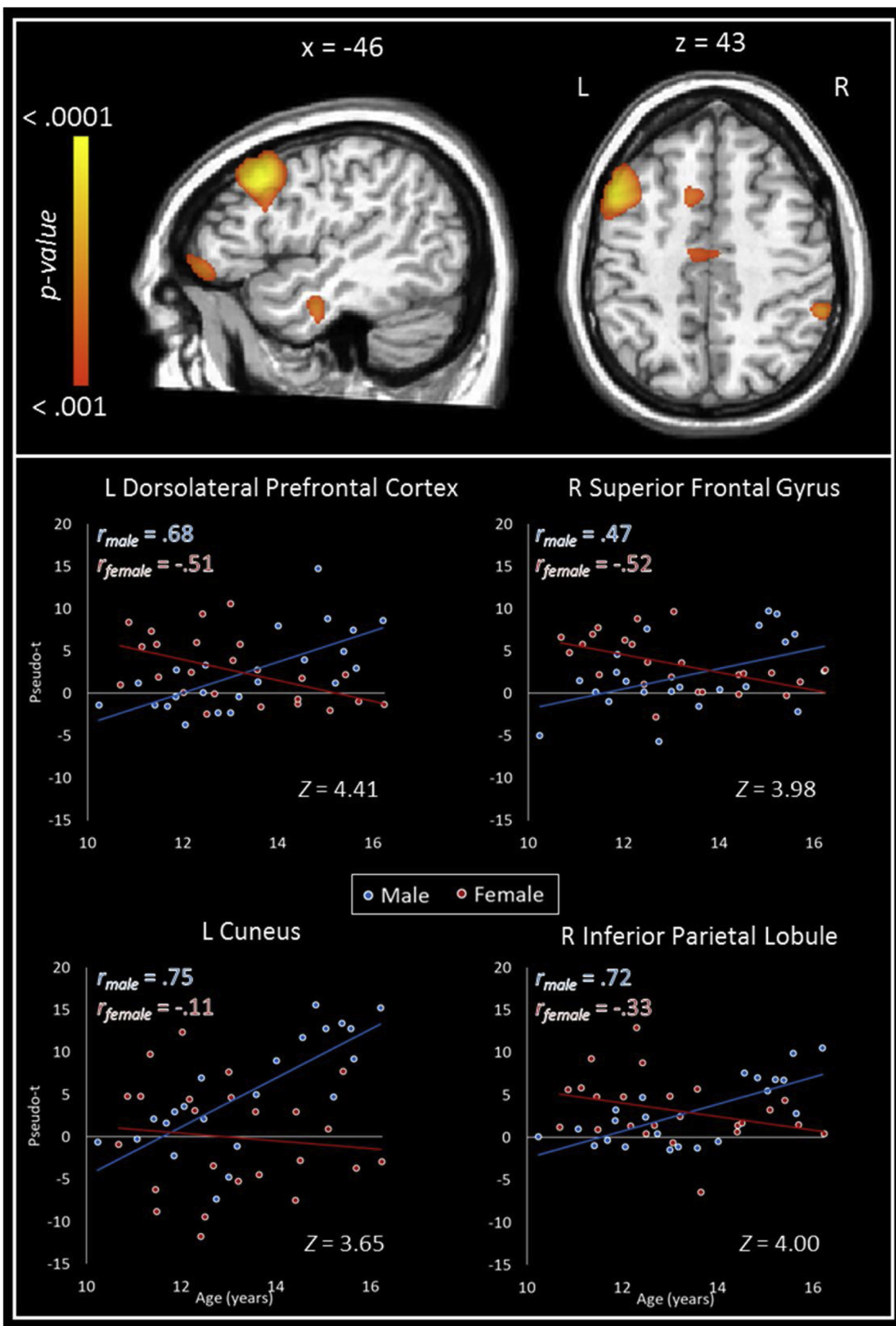


Fig. 5. Sex differences in the correlation between theta activity and chronological age. (Top) Fisher's r to Z map showing significant sex differences in the developmental trajectory of theta activity during abstract reasoning. In all cases, males exhibited a significantly greater positive correlation between theta amplitude and chronological age relative to females. Maps have been thresholded at $p < .001$, corrected. (Bottom) Scatterplots demonstrating specific correlations obtained from peak voxels within several representative regions.

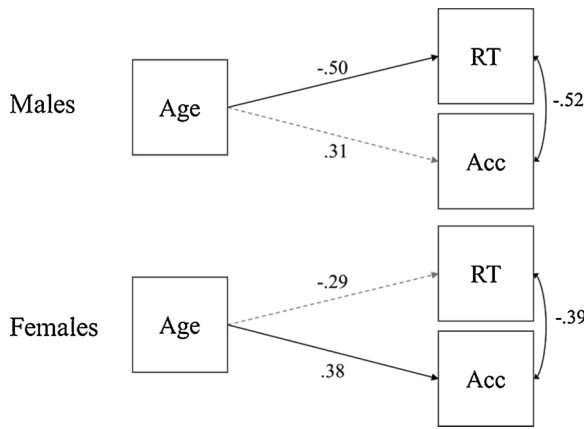


Fig. 6. Results of the group-based path analysis exploring the direct effect of age on both reaction time (RT) and accuracy (Acc). Dashed gray lines indicate a relationship that is not statistically significant at the $p < .05$ level; solid lines indicate statistically significant relationships. Single-headed arrows show predictive relationships, and double-headed arrows show correlations. All reported parameters are standardized coefficients.

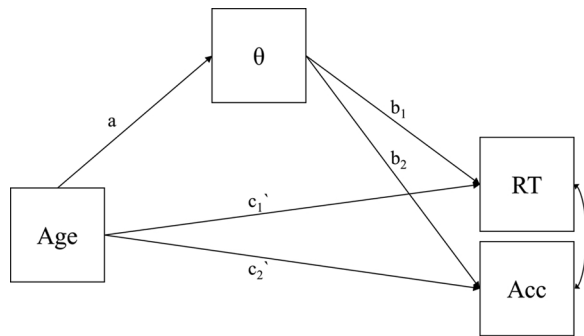


Fig. 7. The conceptual mediation model tested. Theta synchronization is assessed as a mediator of the relationship between age and reaction times (RT) and accuracy (Acc), separately for males versus females using a multi-group analysis approach.

males, increased theta synchronization in superior frontal gyrus, dorsolateral prefrontal cortex, and inferior parietal lobule fully explained the association between increasing age and faster reaction times. Conversely, among females, decreased theta synchronization in dorsolateral prefrontal cortex and inferior frontal gyrus partially explained the relationship between increasing age and better accuracy on the task. The specific relationship between activity in these regions and abstract reasoning task performance further corroborates the P-FIT model of fluid intelligence (Jung and Haier, 2007), and strengthens support for the conclusion that the neural networks underlying abstract reasoning abilities follow sexually-divergent developmental trajectories between during adolescence.

Similar developmental sex differences in cortical oscillatory activity during high-order cognitive processing were recently reported (Embury et al., 2019), although the prior study used a verbal working memory task and the key findings were restricted to the alpha band. Furthermore, the study found no developmental sex differences in performance on the task (Embury et al., 2019), which is in agreement with our findings and may also support the interpretation that the oscillatory differences are related to developmental changes in local neural efficiency (i.e., that the circuits are more efficient in young females) or network level maturational differences. Of note, another recent study examining the developmental trajectory of motor-related oscillations did not find sex differences (Trevarrow et al., 2019), which may indicate that such effects are limited to higher-order cognitive tasks.

Unfortunately, beyond this work, sex differences in the developmental trajectory of neural oscillatory dynamics related to intellectual capacity have scarcely been studied, with the literature primarily examining oscillations recorded during sleep (e.g., Bódi et al., 2014; Ujma et al., 2017). However, these studies do suggest that adolescence is a critical period for the development of cortical infrastructure serving higher-order cognitive abilities.

It is important to note that all of our neurodevelopmental findings were detected within theta-band activity. Theta has been associated with a variety of cognitive functions, including memory processing, coordinating streams of information processing, discretely sampling sensory information, and regulating activity within other brain structures (for reviews, see Colgin, 2013; Herrmann et al., 2016). Importantly, theta activity is thought to be critical in long-range communication between regions in distributed networks. For example, Mizuhara and Yamaguchi (2007) demonstrated that theta oscillatory activity specifically within frontoparietal areas coordinates higher-order cognitive abilities such as working memory and executive function. Given the literature, coupled with findings from the present investigation, it is possible that females develop theta oscillatory mechanisms serving high-order cognition earlier than their male peers, leading to more efficient neural processing at a younger age. Future work should examine a larger age-range of individuals, from younger in childhood through adulthood, to more definitively determine the nature of theta oscillatory dynamics across development between males and females.

Before closing, it is important to acknowledge some limitations of this study. First, the task utilized in the study was difficult and somewhat long in duration, which led to exclusion of a number of participants at early stages of processing. Future work may choose to optimize the task parameters to be more suitable for children and to avoid performance- and movement artifact-based exclusions. Second, the present study did not include a normative adult sample. The literature examining neural oscillatory dynamics underlying *Gf* across the lifespan is sparse at best. Thus, it is difficult to interpret the lifespan implications of the developmental effects discovered in the present study. Future work should examine the neural oscillatory patterns elicited during the abstract reasoning task in adult samples, as well as younger child samples, to obtain a clearer image of the developmental trajectory of cortical activity serving *Gf*. Third, neural oscillatory activity generally localized to frontoparietal regions of the brain. These regions are known to be involved in a number of higher-order cognitive processes (e.g., Breukelaar et al., 2018; Friedman et al., 2016; Petersen and Posner, 2012), thus it is difficult to ascertain whether activity in these regions is specifically tied to fluid intelligence, or may be better linked to other cognitive abilities (e.g., attention, cognitive control) required to successfully complete the task. Finally, the time-frequency bins which we statistically identified for beamforming (i.e., imaging) were defined using the full sample, rather than separately by sex. It is possible that males and females may exhibit differences in the spectro-temporal dynamics, and that our time-frequency windows were not optimal for detecting such differences in neural processing between males and females. Additional study could benefit from separately examining sex-specific time-frequency components.

To conclude, the current study examined the neural oscillatory dynamics serving abstract reasoning abilities in typically developing youth in the middle childhood and adolescent period. The findings corroborated prior structural and functional literature implicating a distributed frontoparietal network of cortical areas supporting intelligence and reasoning abilities, and provided new evidence on the underlying spectro-temporal dynamics, including widespread theta activity, alpha/beta dynamics, and high-frequency gamma responses. Further, theta oscillatory activity, which is known to underlie higher-order cognitive abilities in distributed neural networks, was identified as a critical oscillatory marker of *Gf*-related processing that varied by chronological age. Moreover, males and females in the study exhibited differential developmental trajectories of cortical theta oscillatory activity, despite

Table 2
Results of the mediation analyses, demonstrating the a, b, and c' paths as well as total indirect effects for each analysis.

| Reaction Time | | | | | | | | | |
|---------------|--------|----------------|------------------|----------|----------|--------|----------------|------------------|----------|
| Cluster | Male | | | | Indirect | Female | | | |
| | a | b ₁ | c ₁ ' | Indirect | | a | b ₁ | c ₁ ' | Indirect |
| R SFG | .47* | -.27 | -.37 | -.13 | -.52 | .090 | -.24 | -.047 | |
| R SFG | .59*** | -.39 | -.27 | -.23* | -.35*** | -.17 | -.35 | .059 | |
| L DLPFC | .68*** | -.56* | -.12 | -.38* | -.51*** | -.030 | -.30 | .015 | |
| L IFG | .61*** | -.35 | -.29 | -.21 | -.58** | -.068 | -.33 | .039 | |
| L Pre-SMA | .43* | -.21 | -.41* | -.092 | -.58** | -.41* | -.52** | .24* | |
| L ITS | .64*** | -.34 | -.28 | -.22 | -.49** | .13 | -.23 | -.063 | |
| R IPL | .72*** | -.24 | -.33 | -.17 | -.33* | -.23 | .18 | -.060 | |
| R IPL | .58** | -.49 | -.21 | -.29* | -.35* | .13 | -.24 | -.047 | |
| R Precuneus | .51** | -.35 | -.33 | -.18 | -.46* | .17 | -.21 | -.077 | |
| L Cuneus | .76*** | -.42 | -.19 | -.32 | -.11 | .48* | -.23 | -.053 | |

| Accuracy | | | | | | | | | |
|-------------|--------|----------------|------------------|----------|----------|--------|----------------|------------------|----------|
| Cluster | Male | | | | Indirect | Female | | | |
| | a | b ₂ | c ₂ ' | Indirect | | A | b ₂ | c ₂ ' | Indirect |
| R SFG | .47* | .24 | .11 | -.011 | -.52 | -.30 | .22 | .16 | |
| R SFG | .59*** | .26 | .13 | .063 | -.35*** | .20 | .45 | -.071 | |
| L DLPFC | .68*** | -.022 | .32 | .18 | -.51*** | .40* | .58** | -.20* | |
| L IFG | .61*** | .55* | -.025 | .33 | -.58** | .54** | .69** | -.32* | |
| L Pre-SMA | .43* | .35 | .16 | .15 | -.58** | .23 | .51 | -.13 | |
| L ITS | .64*** | .33 | .097 | .21 | -.49** | .30 | .52* | -.15 | |
| R IPL | .72*** | .29 | .096 | .21 | -.33* | .066 | .40* | -.022 | |
| R IPL | .58** | .089 | .26 | .052 | -.35* | -.035 | .37 | .012 | |
| R Precuneus | .51** | .028 | .29 | .014 | -.46* | -.001 | .38 | .001 | |
| L Cuneus | .76*** | .18 | .17 | .14 | -.11 | -.18 | .36 | .020 | |

Note: Indirect effects were calculated and assessed for statistical significant using the bias-corrected bootstrapped confidence intervals. Significant indirect effects have been bolded for visibility. All reported parameters are standardized coefficients.
*p < 0.05; ** p < .01; *** p < .001.

similar performance on the task. There was also specificity in the relationship between theta activity and task performance, with increased frontal and parietal theta activity supporting faster reaction times in males, and decreased frontal theta activity supporting better accuracy among females. This latter finding suggests that the neural circuitry serving abstract reasoning and Gf may develop at different rates in males and females, and be more locally efficient (i.e., more developed) in females during the critical developmental period connecting childhood to adolescence (i.e., puberty transition). Future studies should focus on younger and older participants to map the entire developmental trajectory, and/or employ longitudinal models to identify the precise changes in neural dynamics that occur and their relationship to underlying hormonal changes.

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References

Basten, U., Hilger, K., Fiebach, C.J., 2015. Where smart brains are different: a quantitative meta-analysis of functional and structural brain imaging studies on intelligence. *Intelligence* 51, 10–27.
Bazargani, N., Hillebrandt, H., Christoff, K., Dumontheil, I., 2014. Developmental changes in effective connectivity associated with relational reasoning. *Hum. Brain Mapp.* 35, 3262–3276.

Blakemore, S.-J., Choudhury, S., 2006. Development of the adolescent brain: implications for executive function and social cognition. *J. Child Psychol. Psychiatry* 47, 296–312.
Blakemore, S.-J., Burnett, S., Dahl, R.E., 2010. The role of puberty in the developing adolescent brain. *Hum. Brain Mapp.* 31, 926–933.
Bódizs, R., Gombos, F., Ujma, P.P., Kovács, I., 2014. Sleep spindling and fluid intelligence across adolescent development: sex matters. *Front. Hum. Neurosci.* 8.
Breukelaar, I.A., Williams, L.M., Antees, C., Grieve, S.M., Foster, S.L., Gomes, L., Korgaonkar, M.S., 2018. Cognitive ability is associated with changes in the functional organization of the cognitive control brain network. *Hum. Brain Mapp.* 39, 5028–5038.
Casey, B.J., Giedd, J.N., Thomas, K.M., 2000. Structural and functional brain development and its relation to cognitive development. *Biol. Psychol.* 54, 241–257.
Casey, B., Tottenham, N., Liston, C., Durston, S., 2005. Imaging the developing brain: what have we learned about cognitive development? *Trends Cogn. Sci. (Regul. Ed.)* 9, 104–110.
Cattell, R.B., 1974. Raymond B. Cattell. In: Lindzey, G. (Ed.), *A History of Psychology in Autobiography*, Vol VI. Prentice-Hall, Inc., Englewood Cliffs, pp. 61–100.
Colgin, L.L., 2013. Mechanisms and functions of Theta rhythms. *Annu. Rev. Neurosci.* 36, 295–312.
Conway, A.R.A., Cowan, N., Bunting, M.F., Theriault, D.J., Minkoff, S.R.B., 2002. A latent variable analysis of working memory capacity, short-term memory capacity, processing speed, and general fluid intelligence. *Intelligence* 30, 163–183.
Crone, E.A., Richard Ridderinkhof, K., 2011. The developing brain: from theory to neuroimaging and back. *Dev. Cogn. Neurosci.* 1, 101–109.
Dix, A., Wartenburger, I., van der Meer, E., 2016. The role of fluid intelligence and learning in analogical reasoning: how to become neurally efficient? *Neurobiol. Learn. Mem.* 134, 236–247.
Dumontheil, I., 2014. Development of abstract thinking during childhood and adolescence: the role of rostralateral prefrontal cortex. *Dev. Cogn. Neurosci.* 10, 57–76.
Dumontheil, I., 2016. Adolescent brain development. *Curr. Opin. Behav. Sci.* 10, 39–44.
Duncan, J., 2013. The structure of cognition: attentional episodes in mind and brain. *Neuron* 80, 35–50.
Eeg-Olofsson, O., 1971. The development of the electroencephalogram in normal adolescents from the age of 16 through 21 years. *Neuropediatric* 3, 11–45.
Efron, B., Tibshirani, R., 1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Stat. Sci.* 1, 54–75.
Embury, C.M., Wiesman, A.L., Proskovec, A.L., Mills, M.S., Heinrichs-Graham, E., Wang, Y.-P., Calhoun, V.D., Stephen, J.M., Wilson, T.W., 2019. Neural dynamics of verbal working memory processing in children and adolescents. *NeuroImage* 185, 191–197.

- Ernst, M.D., 2004. Permutation methods: a basis for exact inference. *Stat. Sci.* 19, 676–685.
- Estrada, E., Ferrer, E., Román, F.J., Karama, S., Colom, R., 2019. Time-lagged associations between cognitive and cortical development from childhood to early adulthood. *Dev. Psychol.*
- Ferrer, E., O'Hare, E.D., Bunge, S.A., 2009. Fluid reasoning and the developing brain. *Front. Neurosci.* 3.
- Friedman, N.P., Miyake, A., Altamirano, L.J., Corley, R.P., Young, S.E., Rhea, S.A., Hewitt, J.K., 2016. Stability and change in executive function abilities from late adolescence to early adulthood: a longitudinal twin study. *Dev. Psychol.* 52, 326–340.
- Fritz, M.S., MacKinnon, D.P., 2007. Required sample size to detect the mediated effect. *Psychol. Sci.* 18, 233–239.
- Gagol, A., Magnuski, M., Kroczyk, B., Kałamała, P., Ociepa, M., Santarnecchi, E., Chuderski, A., 2018. Delta-gamma coupling as a potential neurophysiological mechanism of fluid intelligence. *Intelligence* 66, 54–63.
- Gasser, T., Verleger, R., Bächer, P., Sroka, L., 1988. Development of the EEG of school-age children and adolescents. I. Analysis of band power. *Electroencephalogr. Clin. Neurophysiol.* 69, 91–99.
- Gibbs, F.A., Knott, J.R., 1949. Growth of the electrical activity of the cortex. *Electroencephalogr. Clin. Neurophysiol.* 1, 223–229.
- Gómez-veiga, I., Vila Chaves, J.O., Duque, G., García Madruga, J.A., 2018. A new look to a classic issue: reasoning and academic achievement at secondary school. *Front. Psychol.* 9.
- Green, C.T., Bunge, S.A., Briones Chiongbian, V., Barrow, M., Ferrer, E., 2017. Fluid reasoning predicts future mathematical performance among children and adolescents. *J. Exp. Child Psychol.* 157, 125–143.
- Gross, J., Kujala, J., Hämäläinen, M., Timmermann, L., Schnitzler, A., Salmelin, R., 2001. Dynamic imaging of coherent sources: studying neural interactions in the human brain. *Proc. Natl. Acad. Sci.* 98, 694–699.
- Heinrichs-Graham, E., McDermott, T.J., Mills, M.S., Wiesman, A.I., Wang, Y.-P., Stephen, J.M., Calhoun, V.D., Wilson, T.W., 2018. The lifespan trajectory of neural oscillatory activity in the motor system. *Dev. Cogn. Neurosci.* 30, 159–168.
- Herrmann, C.S., Strüber, D., Helfrich, R.F., Engel, A.K., 2016. EEG oscillations: from correlation to causality. *Int. J. Psychophysiol.* 103, 12–21.
- Hillebrand, A., Singh, K.D., Holliday, I.E., Furlong, P.L., Barnes, G.R., 2005. A new approach to neuroimaging with magnetoencephalography. *Hum. Brain Mapp.* 25, 199–211.
- Horn, J.L., 1968. Organization of abilities and the development of intelligence. *Psychol. Rev.* 75, 242–259.
- Horn, J.L., Cattell, R.B., 1967. Age differences in fluid and crystallized intelligence. *Acta Psychol. (Amst.)* 26, 107–129.
- Irby, S.M., Floyd, R.G., 2013. Test Review: Wechsler Abbreviated Scale of Intelligence, Second Edition. *Can. J. Sch. Psychol.* 28, 295–299.
- Jung, R.E., Haier, R.J., 2007. The Parieto-frontal Integration Theory (P-FIT) of Intelligence: Converging Neuroimaging Evidence. *Behavioral*. In Retrieved from http://www.gse.uci.edu/docs/Leak_Duncan_Li_Timing_Paper_APPAM_102810.Pdf Lessov-Schlaggar, (Psychological), pp. 1174–1177.
- Krawczyk, D.C., 2012. The cognition and neuroscience of relational reasoning. *Brain Res.* 1428, 13–23.
- Lew, B.J., Wiesman, A.I., Rezich, M.T., Wilson, T.W., 2019. Altered neural dynamics in occipital cortices serving visual-spatial processing in heavy alcohol users. *J. Psychopharmacol.* 34 (2), 245–253. <https://doi.org/10.1177/0269881119863120>.
- Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. *J. Neurosci. Methods* 164, 177–190.
- Matoušek, M., Petersén, I., 1973. Automatic evaluation of EEG background activity by means of age-dependent EEG quotients. *Electroencephalogr. Clin. Neurophysiol.* 35, 603–612.
- Matsuura, M., Yamamoto, K., Fukuzawa, H., Okubo, Y., Uesugi, H., Moriiwa, M., Kojima, T., Shimazono, Y., 1985. Age development and sex differences of various EEG elements in healthy children and adults — Quantification by a computerized wave form recognition method. *Electroencephalogr. Clin. Neurophysiol.* 60, 394–406.
- Mcardle, J.J., Ferrer-caja, E., Hamagami, F., Woodcock, R.W., Cattell, R.B., Data, T., 2002. Comparative longitudinal structural analyses of the growth and decline of multiple intellectual abilities over the life span. *Dev. Psychol.*
- McCrimmon, A.W., Smith, A.D., 2013. Review of the wechsler abbreviated scale of intelligence, second edition (WASI-II). *J. Psychoeduc. Assess.* 31, 337–341.
- McDermott, T.J., Wiesman, A.I., Proskovec, A.L., Heinrichs-Graham, E., Wilson, T.W., 2017. Spatiotemporal oscillatory dynamics of visual selective attention during a flanker task. *NeuroImage* 156, 277–285. <https://doi.org/10.1016/j.neuroimage.2017.05.014>.
- Mizuhara, H., Yamaguchi, Y., 2007. Human cortical circuits for central executive function emerge by theta phase synchronization. *NeuroImage* 36, 232–244.
- Neubauer, A.C., Fink, A., 2003. Fluid intelligence and neural efficiency: effects of task complexity and sex. *Personal. Individ. Differ.* 35, 811–827.
- Neubauer, A.C., Wammerl, M., Benedek, M., Jauk, E., Jaušovec, N., 2017. The influence of transcranial alternating current stimulation (tACS) on fluid intelligence: an fMRI study. *Personal. Individ. Differ.* 118, 50–55.
- Pahor, A., Jaušovec, N., 2014a. The effects of theta transcranial alternating current stimulation (tACS) on fluid intelligence. *Int. J. Psychophysiol.* 93, 322–331.
- Pahor, A., Jaušovec, N., 2014b. Theta-gamma cross-frequency coupling relates to the level of human intelligence. *Intelligence* 46, 283–290.
- Penuel, H., Corbin, F., Bickford, R.G., 1955. Studies of the electroencephalogram of normal children: comparison of visual and automatic frequency analyses. *Electroencephalogr. Clin. Neurophysiol.* 7, 15–28.
- Petersen, S.E., Posner, M.I., 2012. The attention system of the human brain: 20 years after. *Annu. Rev. Neurosci.* 35, 73–89.
- Proskovec, A.L., Heinrichs-Graham, E., Wiesman, A.I., McDermott, T.J., Wilson, T.W., 2018. Oscillatory Dynamics in the Dorsal and Ventral Attention Networks During the Reorienting of Attention. *Hum. Brain Mapp.* 39 (5), 2177–2190. <https://doi.org/10.1002/hbm.23997>.
- Ramchandran, K., Zeien, E., Andreasen, N.C., 2019. Distributed neural efficiency: intelligence and age modulate adaptive allocation of resources in the brain. *Trends Neurosci. Educ.*
- Ramos, J., Corsi-Cabrera, M., Guevara, M.A., Arce, C., 1993. Eeg activity during cognitive performance in women. *Int. J. Neurosci.* 69, 185–195.
- Santarnecchi, E., Polizzotto, N.R., Godone, M., Giovannelli, F., Feurra, M., Matzen, L., Rossi, A., Rossi, S., 2013. Frequency-dependent enhancement of fluid intelligence induced by transcranial oscillatory potentials. *Curr. Biol.* 23, 1449–1453.
- Santarnecchi, E., Müller, T., Rossi, S., Sarkar, A., Polizzotto, N.R., Rossi, A., Cohen Kadosh, R., 2016. Individual differences and specificity of prefrontal gamma frequency-tACS on fluid intelligence capabilities. *Cortex* 75, 33–43.
- Shaw, P., 2007. Intelligence and the developing human brain. *BioEssays* 29, 962–973.
- Soares, D.L., Lemos, G.C., Primi, R., Almeida, L.S., 2015. The relationship between intelligence and academic achievement throughout middle school: the role of students' prior academic performance. *Learn. Individ. Differ.* 41, 73–78.
- Spooner, R.K., Wiesman, A.I., Mills, M.S., O'Niell, J., Robertson, K.R., Fox, H.S., Swindells, S., Wilson, T.W., 2018. Errant Oscillatory Dynamics During Somatosensory Processing in HIV-infected Adults. *NeuroImage Clin.* 20, 85–91. <https://doi.org/10.1016/j.nicl.2018.07.009>.
- Spooner, R.K., Wiesman, A.I., Proskovec, A.L., Heinrichs-Graham, E., Wilson, T.W., 2019. Rhythmic Spontaneous Activity Mediates the Age-Related Decline in Somatosensory Function. *Cerebral Cortex* 29 (2), 680–688. <https://doi.org/10.1093/cercor/bhx349>.
- Tadayon, E., Pascual-Leone, A., Santarnecchi, E., 2019. Differential contribution of cortical thickness, surface area, and gyrification to fluid and crystallized intelligence. *Cereb. Cortex.*
- Taulu, S., Simola, J., 2006. Spatiotemporal signal space separation method for rejecting nearby interference in MEG measurements. *Phys. Med. Biol.* 51, 1759–1768.
- Taulu, S., Simola, J., Kajola, M., 2005. Applications of the signal space separation method. *IEEE Trans. Signal Process.* 53, 3359–3372.
- Trevarrow, M.P., Kurz, M.J., McDermott, T.J., Wiesman, A.I., Mills, M.S., Wang, Y.-P., Calhoun, V.D., Stephen, J.M., Wilson, T.W., 2019. The developmental trajectory of sensorimotor cortical oscillations. *NeuroImage* 184, 455–461.
- Uhlhaas, P.J., Singer, W.J., 2013. Developmental Changes in Neuronal Oscillations and Synchrony: Evidence for a Late Critical Period. p.
- Uhlhaas, P.J., Roux, F., Singer, W., Haenschel, C., Sireteanu, R., Rodriguez, E., 2009. The development of neural synchrony reflects late maturation and restructuring of functional networks in humans. *Proc. Natl. Acad. Sci.* 106, 9866–9871.
- Ujma, P.P., Konrad, B.N., Gombos, F., Simor, P., Pótári, A., Genzel, L., Pawlowski, M., Steiger, A., Bódizs, R., Dresler, M., 2017. The sleep EEG spectrum is a sexually dimorphic marker of general intelligence. *Sci. Rep.* 7, 18070.
- Uusitalo, M.A., Ilmoniemi, R.J., 1997. Signal-space projection method for separating MEG or EEG into components. *Med. Biol. Eng. Comput.* 35, 135–140.
- Veen, B.D.V., Drongelen, W.V., Yuchtman, M., Suzuki, A., 1997. Localization of brain electrical activity via linearly constrained minimum variance spatial filtering. *IEEE Trans. Biomed. Eng.* 44, 867–880.
- Wechsler, D., 2011. WASI-II: Wechsler Abbreviated Scale of Intelligence (PsychCorp).
- Wendelken, C., Ferrer, E., Whitaker, K.J., Bunge, S.A., 2016. Fronto-parietal network reconfiguration supports the development of reasoning ability. *Cereb. Cortex* 26, 2178–2190.
- Wiesman, A.I., Heinrichs-Graham, E., Proskovec, A.L., McDermott, T.J., Wilson, T.W., 2017. Oscillations During Observations: Dynamic Oscillatory Networks Serving Visuospatial Attention. *Hum. Brain Mapp.* 38 (10), 5128–5140. <https://doi.org/10.1002/hbm.23720>.
- Wiesman, A.I., Wilson, T.W., 2020. Attention Modulates the Gating of Primary Somatosensory Oscillations. *NeuroImage* 211, 116610. <https://doi.org/10.1016/j.neuroimage.2020.116610>. In press.
- Wilson, T.W., Slason, E., Asherin, R., Kronberg, E., Reite, M.L., Teale, P.D., Rojas, D.C., 2010. An extended motor network generates beta and gamma oscillatory perturbations during development. *Brain Cogn.* 73, 75–84.