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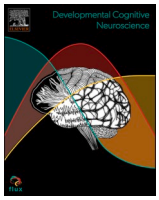

Cognitive interference elicits developmental sex differences in inhibitory control

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ABSTRACT

Inhibitory control is a key component of cognitive control that enables children and adolescents to develop increasingly complex skills throughout development. These processes are subject to insult via endogenous and environmental stressors (e.g., puberty, trauma) and alterations can lead to significant behavioral impairments that persist into adulthood. Despite this, the normative developmental course of neural oscillatory activity underlying interference control, a critical subcomponent of inhibitory control, and potential sex differences along this course, remain poorly understood. Herein, we utilized high-density magnetoencephalography (MEG) during the Eriksen flanker task to map the developmental sensitivity of neural processes supporting interference control in a large sample of children and adolescents (N = 121). MEG data were transformed into the time-frequency domain and significant oscillatory responses were imaged using a beamformer. Whole-brain analysis of flanker interference maps (i.e., incongruent - congruent trials) revealed age-related decreases in theta power in the supplementary motor area and cerebellum. Furthermore, regions known to be critical for supporting cognitive control, including the prefrontal and parietal cortices, exhibited age-by-sex interactive effects, suggesting modulation of interference control throughout development in a sex-dependent manner. Taken together, these data contribute to the characterization of the electrophysiological mechanisms supporting the development and refinement of interference control.

1. Introduction

The acquisition and refinement of increasingly complex motor, cognitive, and social skills is an essential component of healthy development in children and adolescents. Fundamental skills associated with cognitive domains such as attention and memory emerge relatively early in toddlers and children, and provide the necessary scaffolding for the development of more complex skills that promote mental and physical health (Diamond, 2013). Cognitive control is among the domains that takes the longest to reach maturity, with behavioral improvements (e.g., accuracy and latency) that continue into early adulthood (Diamond, 2013; Luna et al., 2004; Tervo-Clemmens et al., 2023; Zanolie and Crone, 2018). Cognitive control refers to flexible, goal-oriented behaviors that are necessary when prepotent or automatized responses are insufficient. A prominent theoretical framework identifies working memory, inhibitory control, and flexibility or performance monitoring as three key facets that comprise cognitive control (Miyake et al., 2000; Zanolie and Crone, 2018; Zelazo et al., 2003). There is also compelling

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work to support the presence of both domain-general (Tervo-Clemmens et al., 2023) and domain-specific (Huizinga et al., 2006; Miyake et al., 2000) developmental trajectories of cognitive control, with maturational differences between the latent factors (i.e., components).

As early as 1927, lesion studies gave early hints regarding the importance of the prefrontal cortex (PFC) in cognitive control, as structural damage of the PFC was linked with deficits in task switching (Milner, 1963). Indeed, structural and functional neuroimaging work supports the importance of the PFC in the development of cognitive control, including age-sensitive gray matter, blood oxygenation level-dependent (BOLD) signal, and electrophysiological changes during assessments taxing executive function (Best and Miller, 2010; Crone and Dahl, 2012; Friedman and Robbins, 2022; Miller, 2000; Paus, 2005; Sotiras et al., 2017; Taylor et al., 2020, 2021, 2022; Zanolie and Crone, 2018; Zelazo et al., 2003). Importantly, the PFC does not work in isolation and relies on distributed processing that enables successful cognitive control, integrating lower-order visual and somato-motor regions with higher-order association cortices (Ezekiel et al., 2013; Milham et al., 2003; Ridderinkhof et al., 2004; Son et al., 2023; Spooner et al., 2020; Wiesman and Wilson, 2020a). Specifically, the parietal cortex is consistently identified in cognitive control tasks and acts in conjunction with the PFC to modulate attention allocation and goal-directed behaviors as part of the central executive network (Arif et al., 2023; Embury et al., 2019; Wiesman and Wilson, 2020b; Zanolie and Crone, 2018).

Inhibitory control appears to play an especially important role in cognitive control. The results of a comprehensive analysis ($N > 10{,}000$) of four independent developmental datasets indicated that inhibitory control tasks are associated with some of the largest developmental effects and load strongly onto domain-general factors, highlighting their importance across various aspects of cognitive control (Tervo-Clemmens et al., 2023). Adequate inhibitory control is essential for normative function (Diamond, 2013) and is highly susceptible to developmental alterations during the critical periods of childhood and adolescence, when the brain undergoes rapid structural and functional reorganization and specialization due to hormonal changes and other factors (Fung et al., 2020; Fung, Heinrichs-Graham, et al., 2022; Fung, Rahman, et al., 2022; Killanin et al., 2023). Importantly, extensive literature indicates that inhibitory control is not a unitary construct and is not synonymous with global inhibitory function (Bari and Robbins, 2013; Friedman and Miyake, 2004; Howard et al., 2014; Nigg, 2000; Tiego et al., 2018). A seminal conceptual framework detailed in Nigg (2000) differentiates interference control, the focus of the current study, from behavioral and cognitive inhibition, reflecting different stages of information processing. Interference control, which is sometimes referred to as resistance to interference or attentional inhibition in the literature, refers to the aspect of cognitive control needed to suppress interference due to the competition of task-relevant and task-irrelevant stimuli during goal-oriented behavior (Nigg, 2000). Behavioral inhibitory control, which is sometimes referred to as response inhibition, has been further conceptualized as two distinct components (Sebastian et al., 2013), including the inhibition of prepotent responses (i.e., action restraint) and stopping actions that have already been initiated (i.e., action cancellation, e.g., stop-signal task). Indeed, neuroimaging work indicates the recruitment of distinct brain regions according to the subcomponent of inhibition being probed, as well as the involvement of other brain regions regardless of the subcomponent of inhibitory processing being engaged (Brydges et al., 2012, 2013; Nee et al., 2007; Sebastian et al., 2013; van Velzen et al., 2014; Wager et al., 2005). However, there are also conflicting results, as some work utilizing structural equation modeling has suggested that one latent variable parsimoniously captures variance in both response inhibition (i.e., behavioral inhibitory control) and resistance to interference (i.e., interference control; Friedman and Miyake, 2004).

Despite conceptual disagreements regarding the taxonomy of inhibitory control, aberrant inhibitory control is consistently observed in a wide range of mental health disorders, including attention-deficit hyperactivity disorder (ADHD), alcohol and substance use disorders, and mood disorders (Li et al., 2021; Lipszyc and Schachar, 2010; McTeague et al., 2016, 2017; Nigg, 2001, 2017; Verdejo-García et al., 2008). Most characterizations of inhibitory control in clinical settings approach it in a global sense, despite the fact that specific subcomponents are likely associated with particular disorders and may develop along distinct trajectories across the lifespan (Brydges et al., 2013; Dempster, 1993; Sebastian et al., 2013). The flanker task is one of the most widely used paradigms for measuring interference control, whereby participants exhibit decisional latency in the presence of stimulus-stimulus interference (Eriksen and Eriksen, 1974). Unfortunately, many studies using the flanker task do not specify the subcomponent of inhibitory processing that is being probed, which is a critical omission as it can undermine the identification of specific diagnostic and/or developmental relationships. For instance, an early methylphenidate study of attention-deficit hyperactivity disorder (ADHD) showed selective improvements in behavioral performance on action cancellation, but not interference control (Scheres et al., 2003). Thus, leveraging more precise differentiations of the subcomponents of inhibitory control may lead to critical insights on the emergence of specific patterns of inhibitory control with development, as well as alterations that are present transdiagnostically (Nigg et al., 2007). Furthermore, the use of time resolved methods such as magnetoencephalography (MEG) may lead to unique insights, as these tools can often distinguish elements of interference control from behavioral outputs, which may lead to a finer differentiation of the subcomponents of inhibitory control (Lindquist et al., 2009). A key barrier to progress in this area is that the normative developmental trajectory of interference control is only beginning to be characterized. Given the widespread developmental sex differences reported across subcomponents of inhibitory control (Embury et al., 2019; Taylor et al., 2020, 2021) and in the emergence of psychopathology in the presence of disinhibition (Bangasser and Wicks, 2017; McEwen and Milner, 2017; Rutter et al., 2003; Shulman et al., 2015; Zahn-Waxler et al., 2008, 2015), mapping the healthy developmental trajectory of interference control and identifying the neural dynamics and circuitry is critical.

In the current study, we used high-density MEG to map the neural oscillatory markers of interference control in a large sample of children and adolescents ($N = 121$). All participants completed a modified version of the Eriksen flanker task during MEG and the neural dynamics of interference control were analyzed using a whole-brain, voxel-wise full factorial model to probe for potential effects of age, sex, and their interaction. We hypothesized that there would be neural oscillations that varied with age across both male and female participants, as well as others that differed by sex. We expected these effects to emerge primarily in the PFC and parietal cortex, with potential for additional changes in lower-order visual and somato-motor regions. We hypothesized that all participants would exhibit significant flanker interference effects in their behavior, with slower and less accurate responses during incongruent relative to congruent trials. Further, we hypothesized that there would be neural oscillations that varied with age across both male and female participants, as well as others that differed by sex. We expected these effects to emerge primarily in the PFC and parietal cortex, with potential for additional changes in lower-order visual and somato-motor regions. More specifically, we hypothesized that the amplitude of neural activity supporting inhibitory control will decrease throughout development, reflecting more efficient allocation of neural resources. Further, we anticipate that these changes will be largely driven by alterations during the incongruent condition, while the congruent condition will not be as developmentally sensitive given its relative ease. We anticipate that the age-related changes in neural activity will diverge in male and female participants, such that sex differences become more readily appreciable in later adolescence, though we do not have specific hypotheses regarding the directionality of such sex differences per region given the substantial heterogeneity in the literature. Such findings

would directly contribute to the growing body of work aimed at understanding normative sex differences in the neural mechanisms serving interference control.

2. Materials and methods

Participants A total of 121 healthy children and adolescents (mean age: 9.83 years, 66 male) between the ages of 6 – 9 and 11 – 13 years-old were recruited as part of an accelerated longitudinal study. Exclusion criteria included individuals with any medical illness affecting central nervous system function, history of significant head trauma, current substance use, a formal diagnosis of neurological or psychiatric disorders, or metal implants (e.g., retainer, pacemaker) that would negatively affect MEG data acquisition or be an MRI safety concern. The study was reviewed and approved by the Institutional Review Board in accordance with the Declaration of Helsinki. Children and adolescents who participated in the study provided signed assent forms and parents signed informed consent forms prior to data collection.

2.1. Experimental paradigm and stimuli

Seated participants completed a 13-minute numeric version of the Flanker task in the MEG scanner (Eriksen and Eriksen, 1974; Wiesman et al., 2020; Wiesman and Wilson, 2020b). Each trial began with a central fixation presented for a randomly varied interstimulus interval of 2200 ms (randomized jitter of ± 200 ms). The fixation was then replaced by a vertically centered horizontal row of three equally spaced integers between 0 and 3. Two of these integers were always identical (task irrelevant) and the third was different (task relevant). Participants were instructed that the objective was to indicate the "odd-number-out" on each trial by pressing the button corresponding to its numerical identity on a five-finger button pad, where the index, middle, and ring finger locations represented the integers 1, 2, and 3, respectively (Fig. 1). In all trials, the spatial position and numerical identity of the task relevant stimulus was identical. Specifically, in the incongruent condition, the task relevant stimulus was always flanked by distractors (e.g., 1 2 2/1 1 3/3 2 3), while in the congruent condition, the task relevant stimulus was the only available button press (i.e., no interference; e.g., 1 0 0/0 2 0/0 0 3). The trials were pseudorandomized such that a given condition or response was not repeated more than twice in a row. Each participant completed 100 trials of each condition for a total of 200 trials. Matlab version 2018b was used to program custom visual stimuli (Mathworks, Inc.) using Psychophysics Toolbox V3 (Brainard, 1997) and back-projected onto a nonmagnetic screen.

2.2. Behavioral data analysis

For each participant, only correct trials were included for calculating the reaction time for each condition. Accuracy per condition was computed as the percentage of correct trials / total trials. On the single participant level, a standard reaction time threshold of three standard deviations was used to remove outlier trials. Mean reaction times were subsequently calculated for each participant and condition. Reaction time and accuracy data were then analyzed using paired samples *t*-test to identify conditional effects. Furthermore, behavioral measures were correlated with age and compared by sex to probe for developmental and/or sex effects on successful completion of the modified Flanker task. All behavioral analyses were implemented in Python using the SciPy package (Virtanen et al., 2020).

2.3. MEG data acquisition

All MEG data were collected in a one-layer magnetically shielded room with a 306-sensor MEGIN VectorView MEG system (Helsinki, Finland) sampled at 1 kHz with an acquisition bandwidth of .1–330 Hz. The system included 204 planar gradiometers and 102 magnetometers,

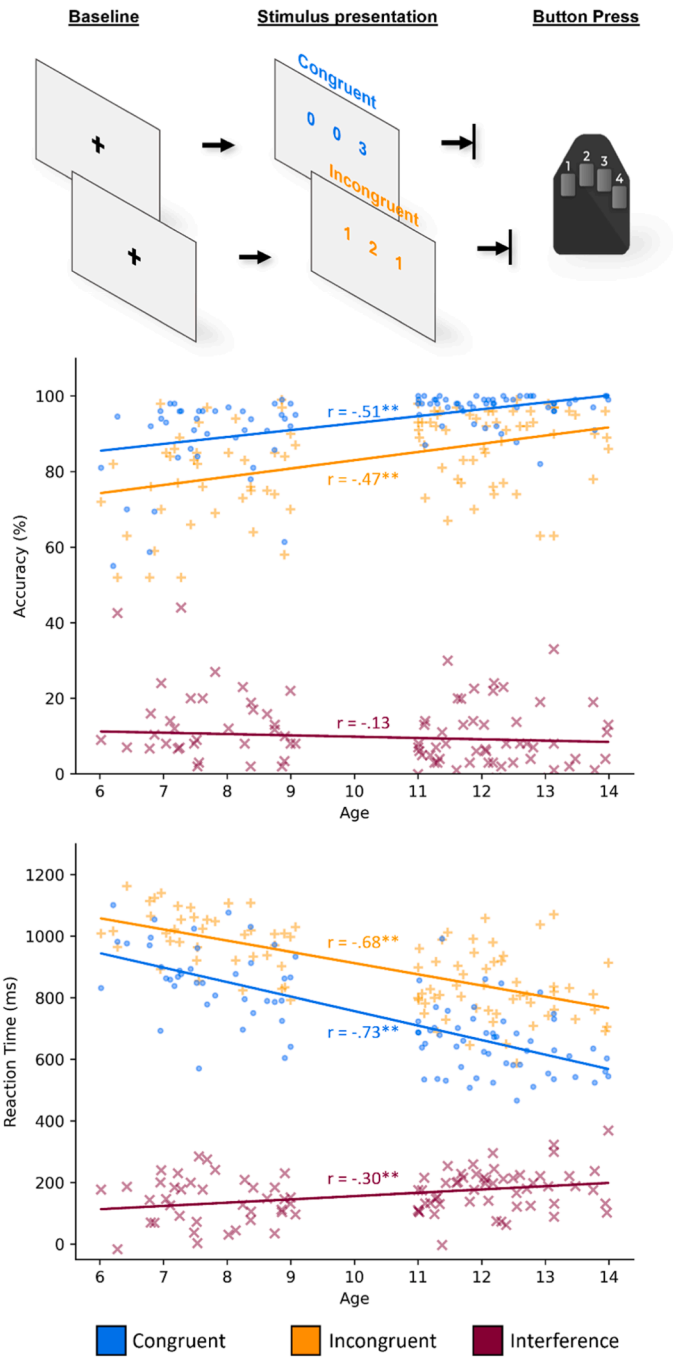

Fig. 1. Experimental paradigm and behavioral results. (**Top**) Participants completed a modified flanker task designed to probe interference control during MEG. (**Middle**) Correlations between age and accuracy (%) in the congruent and incongruent trials, as well as the flanker accuracy interference effect (i.e., incongruent – congruent accuracy). (**Bottom**) Correlations between age and reaction time (ms) in the congruent and incongruent trials, as well as the flanker reaction time interference effect. $^{**}p < .005$.

but we focused on the planar gradiometers in this investigation given their decreased sensitivity to distant (i.e., non-brain) sources compared to magnetometers. During data collection, study participants were monitored in real-time via audio-visual stream from within the magnetically shielded room. Raw MEG data were corrected for head motion and extraneous noise using the signal space separation method with a temporal extension (Taulu et al., 2005; Taulu and Simola, 2006).

2.4. Structural MRI processing and MEG coregistration

Prior to MEG measurement, four head-position indicator (HPI) coils were attached to the participant's head and localized in head space together with the three fiducial points and scalp surface using a 3D digitizer (Fastrak 3SF0002, Polhemus Navigator Sciences, Colchester, VT, USA). Once the participant was positioned for MEG recording, an electric current with a unique frequency label (e.g., 322 Hz) was fed to each of the coils, whose corresponding magnetic fields were then localized relative to the sensor array throughout the recording session. Each participant's MEG data were co-registered with their T1-weighted structural MRI prior to source space analysis using BESA MRI (Version 2.0). The MRI data were collected using a 3 T Siemens Prisma magnet with a 32-channel head coil (TR = 2400 ms; TE = 2.05 ms; FOV = 256 mm; slice thickness = 1 mm with no gap; in-plane resolution = 1.0 ×1.0 mm). Structural MRI data were aligned parallel to the anterior and posterior commissures and transformed into Talairach space. Following MEG source imaging (i.e., beamforming), the same spatial transformation that was applied to the structural MRI volume was applied to each participant's functional MEG images and then the standardized volumes were spatially resampled.

2.5. MEG preprocessing and time-frequency transformation

Cardiac and ocular artifacts were removed from the data using signal space projection and this was accounted for during source reconstruction (Uusitalo and Ilmoniemi, 1997). The continuous MEG time series was then epoched into 1500 ms segments, extending from 500 ms before stimulus onset to 1000 ms after. The baseline period was defined as the −500–0 ms window, while the active period ranged from 0 to 1000 ms. Epochs containing remaining artifacts were rejected based on amplitude and gradient thresholds that were set per participant, supplemented with visual inspection. Briefly, for each participant, the amplitude and gradient distributions were determined across all trials and approximated a normal distribution. Given that trials containing the highest amplitude and/or gradient values relative to the participant's own distribution are most likely to contain artifactual data (e.g., residual movement artifact, non-physiological artifact), these trials were rejected based on a participant-specific threshold. This approach was employed to help account for differences in head size and the proximity of the array to the scalp, which greatly impacts MEG signal amplitude at the sensor level. Across all conditions and participants, the average amplitude threshold was 1387.17 fT/cm (SD = 413.31), and the average gradient threshold was 238.52 fT/(cm*ms) (SD: 135.49). To avoid condition and age-related differences in signal to noise ratio (SNR), trials were randomly excluded from participants with the highest number of accepted trials so that the number of total trials did not differ by age or condition. Following artifact rejection and trial count adjustment, an average of 68.52 (SD: 6.92) trials remained in the congruent condition and 68.08 (SD: 10.69) trials remained in the incongruent condition. For completeness and to aid with interpretability, we also ran the same analyses using all correct accepted trials without balancing SNR (see Supplement). We drew similar conclusions from both models; thus, we used the model with trial balancing such that any effects could be attributed to variables of interest and not potential differences in SNR.

Artifact-free epochs were transformed into the time-frequency domain using complex demodulation, a mechanism that employs heterodyning with incrementally increasing carrier frequencies to build band-limited estimates of spectral power, with a time-frequency window of 25 ms by 2 Hz and a bandwidth of 3–100 Hz (Kovach and Gander, 2016). The resulting spectral power estimates per sensor were averaged across trials per person to generate mean spectral density plots. These normalized spectral power plots were then examined statistically to determine windows of interest for subsequent source analysis.

2.6. MEG sensor-level statistics

For a complete description of MEG sensor-level statistics and source imaging, we refer the reader to our previous MEG work (Spooner et al., 2020; Springer et al., 2022; Wiesman and Wilson, 2020b). Briefly, a two-stage procedure was followed to control for Type-1 error. Paired-sample t-tests relative to baseline power were conducted for each data point prior to nonparametric cluster-based permutation testing to build a null distribution based on 10,000 permutations for temporally and/or spectrally neighboring significant time-frequency bins (all $p < .05$) and neighboring sensors. The significance level of the observed clusters (from stage one) was then tested directly using this distribution within the BESA Statistics 2.1 toolbox. The resulting time-frequency windows that contained statistically significant oscillatory events across all participants and conditions were subjected to a beamforming analysis.

2.7. MEG source imaging and statistics

Neural responses were imaged using the dynamic imaging of coherent sources (DICS) beamformer, which uses the sensor-level cross-spectral density matrices to estimate source power per voxel for the entire volume (Gross et al., 2001; Van Veen et al., 1997). Each task condition was imaged separately per participant using the statistically defined time-frequency bins (see Results; Fig. 2). For each location in the input voxel space, we computed noise-normalized source power per participant using active (i.e., flanker task) and passive (i.e., baseline) periods of equal duration and bandwidth at a resolution of 4 mm isotropic (Hillebrand et al., 2005). Such images are typically referred to as pseudo-t maps, with units (pseudo-t) that reflect noise-normalized power differences (i.e., active versus baseline) per voxel. MEG pre-processing and imaging used the BESA (version 7.0) software. The resulting 3D maps of brain activity were averaged across all participants and both conditions to assess the neuroanatomical bases of the neural oscillatory responses identified using the time-frequency spectrograms. We then calculated interference maps (i.e., incongruent - congruent) for each participant to evaluate the flanker effect. These interference maps were subjected to whole-brain analysis of covariance (ANCOVA) statistical analyses using SPM12, with sex as a categorical variable of interest, age as a continuous variable of interest, and the age-by-sex interaction term as a variable of interest, resulting in whole-brain statistical maps. To account for multiple comparisons, we implemented a stringent *p*-value threshold of.005 to identify significant clusters in the whole-brain statistical maps, followed by a cluster threshold of at least 8 contiguous voxels (> 500 mm) based on the theory of Gaussian random fields (Poline et al., 1995; Worsley et al., 1996). In short, time-frequency windows determined via non-parametric cluster-based permutation testing at the sensor level were beamformed, resulting in whole-brain estimates of source power. These beamformed images were submitted for voxel-wise ANCOVAs for each voxel in the input space, with statistical thresholding applied to identify significant clusters.

3. Results

3.1. Behavioral results

Of the original sample of 121 participants, 25 participants were removed after artifact correction and movement compensation. The remaining 96 participants performed the flanker task well, with a mean accuracy of 92.85 % (SD: 9.54 %) in the congruent condition and 82.82 % (SD: 13.24 %) in the incongruent condition. This difference in accuracy was significant (paired *t*-test, $p < .001$). Accuracy was also significantly correlated with age such that the average accuracy across both conditions was higher in older participants ($p < .001$; Fig. 1, Middle). Mean reaction times for the congruent and incongruent conditions were 747.78 ms (SD: 158.32 ms) and 906.81 ms (SD:

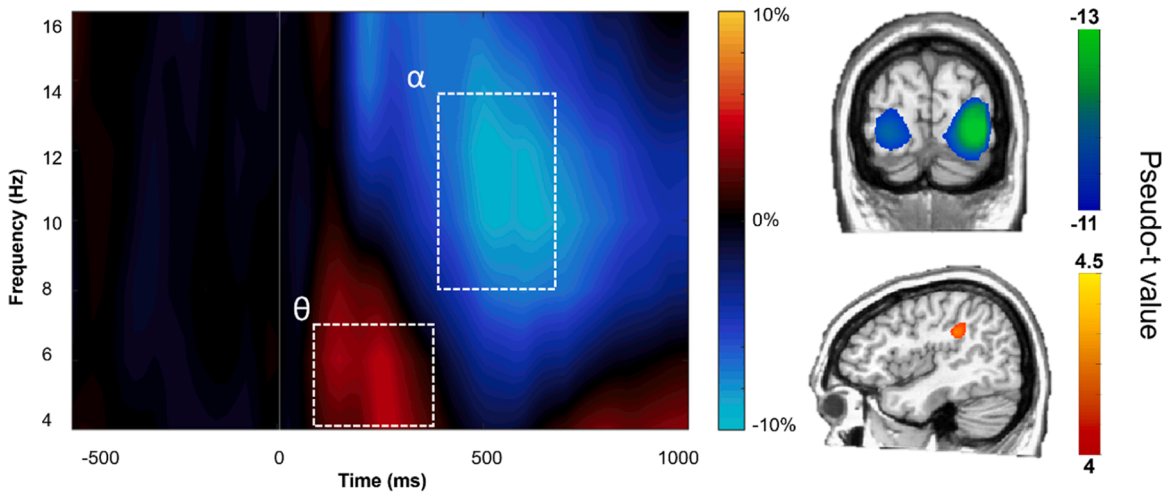

Fig. 2. Time-frequency spectrogram and grand-averaged source image maps. A two-step statistical analysis following complex demodulation of planar gradiometer data indicated two significant time-frequency clusters ($p < .05$, corrected) in the active period relative to the baseline period. There were significant increases in theta power (4–7 Hz) from 100 to 350 ms and significant decreases in alpha power (8–14 Hz) from 350 to 650 ms. To assess data quality, we grand-averaged the functional maps for each time-frequency component (to the right of the spectrogram), which indicated theta responses near the right supramarginal gyrus and the strongest alpha responses in the bilateral occipital cortices.

135.49 ms), respectively. This difference was significant (paired *t*-test, $p < .001$; Fig. 1, Bottom). Reaction time data were also significantly correlated with age such that reaction time decreased as a function of age in the congruent and incongruent conditions (*p*s < .001). Finally, we calculated the accuracy and reaction time interference effects (i.e., incongruent - congruent), which was found to be significantly correlated with age ($p = .003$), such that older participants exhibited a greater interference effect (Fig. 1, Bottom). The accuracy interference effect was not correlated with age, and no sex differences were found in any behavioral measures.

3.2. MEG sensor-level results

An average of 136.60 (SD: 15.00) trials were available per participant for subsequent sensor-level and source-level analyses. To derive the time-frequency bins for beamforming analyses, sensor-level spectrograms were probed using non-parametric permutation testing (see *Methods: MEG Sensor-Level Statistics*). These analyses revealed significant clusters ($p < 0.05$, corrected) of sustained increases in the theta (4–7 Hz; 100–350ms) and decreases in the alpha (8–14 Hz; 350–650ms; Fig. 2) range. Note that we did not consider time windows after 750 ms (i.e., latency of participants' button response) in order to focus on attention processes during flanker performance and limit sensitivity to movement planning and execution responses.

3.3. Task effects and flanker interference effects

To evaluate the dynamics and determine the precise brain regions generating the oscillatory responses observed at the sensor level, each time window was imaged using a baseline period of equal bandwidth and duration (theta: −250–0, alpha: −300–0). To assess data quality and regions generating the strongest responses, the beamformed images across all participants and both conditions were averaged to calculate the grand-averaged map separately for the theta and alpha bands. These showed increases in theta power relative to the baseline period in the supramarginal gyrus, as well as decreases in alpha power relative to the baseline period in the bilateral occipital cortices (Fig. 2). To examine the flanker interference effect, whole-brain subtraction maps (i.e., incongruent - congruent) were generated for each participant and time-frequency bin.

3.4. Theta flanker interference effects

The interference maps were subjected to a whole-brain ANCOVA to probe the main effects of age and sex, as well as the interactive age-by-sex effect. In regard to developmental effects, theta power was significantly associated with age in the right cerebellum ($F = 11.19$, $r = -.34$, $k = 32$, $p = .002$), such that theta power was weaker with older age (Fig. 3). Furthermore, theta power in the left medial superior frontal gyrus was significantly negatively associated with age ($F = 13.34$, $r = -.34$, $k = 8$, $p = .002$). No main effect of sex or age-by-sex interaction effects were identified. To examine possible neurobehavioral relationships, the neural interference effect from both the cerebellar cluster and

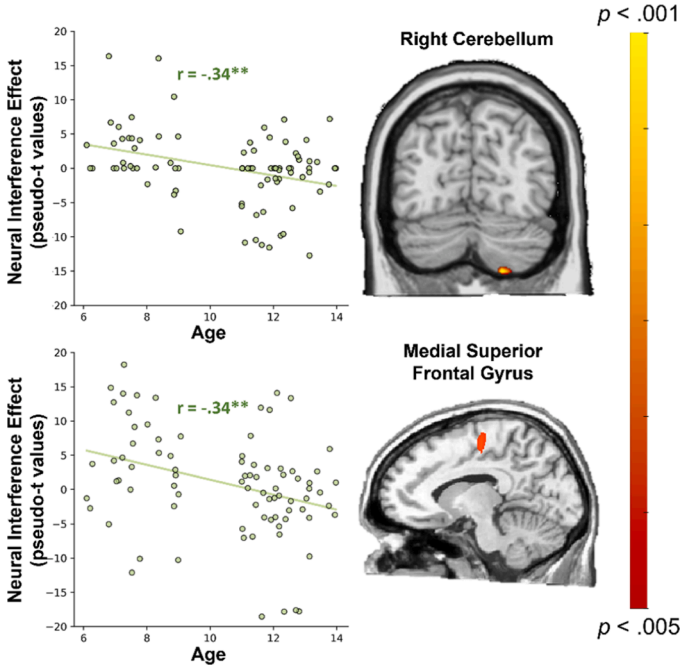

Fig. 3. Age-related flanker interference effects in the theta frequency. The flanker interference effect (i.e., incongruent - congruent) decreased as a function of age in the right cerebellum (top) and the left medial superior frontal gyrus (bottom). ** $p < .005$.

the left superior medial frontal gyrus were correlated with the reaction time interference effect (i.e., incongruent – congruent reaction times), but neither were significant (*ps* > .05). We did not identify any main effects of sex, or any interaction effects in the theta interference maps.

3.5. Alpha flanker interference effects

The alpha interference maps were subjected to a similar whole-brain ANCOVA, which revealed age-by-sex interaction effects (Fig. 4). There was a significant age-by-sex interaction in the right superior temporal cortex ($F = 16.40$, k = 77, $p < .001$), such that alpha interference effects were weaker (i.e., more positive) with older age in males ($r = .49$, $p < .001$), while the interference effect was stronger (i.e., more negative) with older age in females ($r = -.36$, $p = .027$). There was also a significant interaction effect in the left inferior frontal cortex ($F = 11.35$, k = 57, $p = .001$), such that alpha power was positively correlated with age in males ($r = .38$, $p = .009$), while the opposite relationship was significant in females ($r = -.34$, $p = .038$). In both of the aforementioned peaks, there was a significant main effect of sex, though post-hoc hierarchical regression revealed that the main effect of sex was not significant when controlling for the age-by-sex interaction term. Finally, there were significant age-by-sex interactions in the right inferior ($F = 10.03$, k = 8, $p = .002$) and superior parietal cortices ($F = 10.83$, k = 14, $p = .001$). In the right inferior parietal cortex, alpha power was positively correlated with age in males ($r = .32$, $p = .030$), while the opposite relationship was significant in females ($r = -.35$, $p = .031$). In the right superior parietal cortex, alpha power was positively correlated with age in males ($r = .50$, $p < .001$), but no significant relationship between age and alpha power was found in females ($r = -.22$, $p = .188$). Finally, we correlated the neural and behavioral interference effects for each of the four age-by-sex clusters separately by sex. In the superior temporal cortex, the neural interference effect was positively correlated with the behavioral interference effect in males ($r = .32$, $p = .032$), while the relationship was not significant in females ($r = .07$, $p = .658$). No other regions exhibited significant neurobehavioral relationships in either male or female participants (all *ps* > .05). We did not identify any main effects of age or sex in the alpha interference maps.

4. Discussion

In the present study, we probed the spatiotemporal oscillatory dynamics serving interference control using source-reconstructed MEG data collected during a flanker task in a sample of children and adolescents. We observed significant oscillatory responses in both the theta (4–7 Hz) and alpha (8–14 Hz) frequency bands, with beamformer imaging indicating age and age-by-sex effects in a distributed network of brain regions that have been implicated in interference control. In the theta range, we identified age-sensitive neural responses in the cerebellum and left medial superior frontal gyrus near the supplementary motor area (SMA). Furthermore, in the alpha range, we identified age-by-sex interaction effects in prefrontal, parietal, and temporal cortices. In both the theta and alpha bands, these developmental effects were driven by decreases in oscillatory response strength with increasing age in the incongruent condition, while no changes were identified in the congruent condition. Taken together, these results indicate the presence of developmentally-sensitive neural oscillatory responses that are shared by males and females, while other oscillatory responses exhibit distinct developmental changes in a sex-dependent fashion, and that these alterations are specifically elicited in the presence of stimulus-stimulus interference. Importantly, the excellent temporal resolution of MEG and our analytical focus on the neural dynamics preceding the behavioral responses provided a uniquely nuanced perspective on the neurodevelopmental changes primarily supporting interference control, while limiting overlap with behavioral inhibition. Below, we discuss the implications of these findings for understanding the neural dynamics underlying interference control during development.

Our behavioral results align with classic flanker findings, such that participants responded more slowly on incongruent relative to congruent trials. Furthermore, participants responded more quickly as they got older in both conditions, in line with existing developmental work showing improvements in cognition and processing speed. Interestingly, the flanker interference effect, or the difference in reaction time due to the presence of interference, increased as a function of age. Though the interference effect itself has been widely shown in children and adults, the literature regarding the impact of development on the magnitude of the interference effect is mixed. Interestingly, some studies that have specifically examined interference control in youth have found no developmental differences in the interference effect (Taylor et al.,

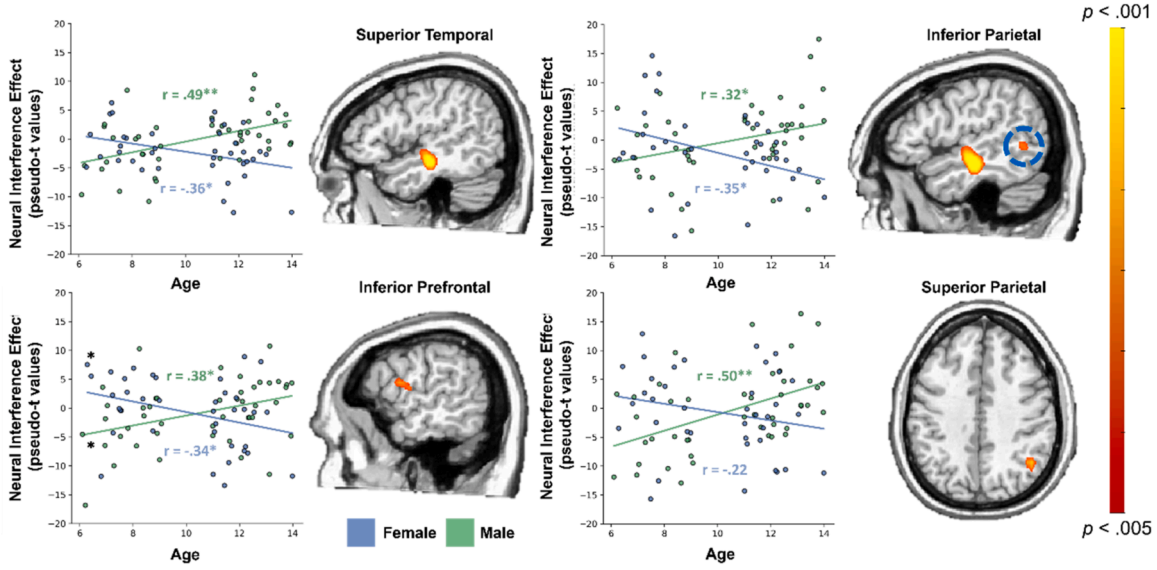

Fig. 4. Age-by-sex interaction effects in the right superior temporal cortex, left inferior prefrontal cortex, and right inferior and superior parietal cortices. In males, age was positively correlated with the alpha interference effect in all four regions. In females, age was negatively correlated with the alpha interference effect in the superior temporal, left inferior prefrontal, and right inferior parietal cortices. ** $p < .005$, * $p < .05$.

2021), while others have identified a decrease in interference with changes in inverse efficiency scores (Yeung et al., 2020) and a decrease in the interference effect itself throughout development (Ridderinkhof et al., 1997). It is well-established that the flanker interference effect is sensitive to various task parameters, including the cued attentional window (Dye et al., 2009), stimulus type (McDermott et al., 2007; Simmering et al., 2023; Spooner et al., 2020), and stimulus features (Simmering et al., 2023), which may explain in part the heterogeneity of findings. From a developmental perspective, our observation of an increased interference effect as a function of age can be interpreted as an increase in the susceptibility to interference with increasing age. Specifically, the older children and adolescents would be expected to have much stronger representations of the digit stimuli than the youngest participants due to increased educational exposure and this would likely be associated with higher implicit (i.e., automatic) activation of the representations of interfering digits. Such greater neural responses to the interfering digit stimuli would require stronger interference control, which would be associated with slower responses. This interpretation would suggest that the inconsistency across studies in whether interference effects get larger in this age range depends on whether the stimuli used in the task are equally familiar to children across the whole age range used in the study. However, some caveats with this interpretation are warranted, as the measured behavioral response cannot be fully parsed into developmental changes in interference control versus behavioral inhibition, and these subcomponents of inhibitory control are likely distinct (Brydges et al., 2012, 2013; Nee et al., 2007; Sebastian et al., 2013; van Velzen et al., 2014; Wager et al., 2005).

The developmental effects observed in the theta frequency range indicate that neural interference effects near the SMA and cerebellar cortices decrease with age, and this was primarily driven by age-related decreases in the strength of theta oscillations during the incongruent condition, while theta during congruent trials remained stable. These regions are critical for an array of higher-order cognitive functions, including the selection and execution of target behaviors, while inhibiting inappropriate responses (Heinrichs-Graham and Wilson, 2015; Huang et al., 2025; Mostofsky and Simmonds, 2008; Nachev et al., 2008; Son et al., 2024). Specifically, theta oscillations have been widely established as an index of cognitive control and are developmentally sensitive (Cavanagh and Frank, 2014; Liu et al., 2014), though many of these electroencephalography (EEG) studies have limited spatial precision. While there is a substantial literature supporting the sensitivity of medial prefrontal theta dynamics to task demands involving distinct elements of cognitive control (Cavanagh and Frank, 2014; Oehrn et al., 2014), our MEG results suggest that developmental changes in the theta dynamics supporting interference control may lie largely outside of canonical inhibitory control regions. Specifically, we found developmental alterations near the SMA and cerebellar cortices during interference control, and these regions are largely independent from those frequently reported in behavioral inhibition studies. While additional studies are needed, such differences may reflect our focus on the interference control component of the task, which was possible due to the unique spatiotemporal precision of MEG. While the earliest theta oscillations emerge in the visual cortex following stimulus onset and are known to become stronger with increasing age in youth (Killanin et al., 2020, 2024), these responses are likely too “early” in the cortical hierarchy to show sensitivity to interference. Taken together, these results indicate that the role of the SMA and cerebellum in early interference control decreases throughout development, likely indicating refinement and increased efficiency of these neural systems during the transition to adolescence and early adulthood (Wilson et al., 2010).

In the alpha band, we observed age-by-sex interaction effects in multiple brain regions associated with visuospatial processing and top-down regulation of attention. Interestingly, these alpha interference effects were primarily driven by age-related alterations in the incongruent condition. In the right superior parietal and right superior temporal cortices, both male and female participants exhibited significant correlations between age and neural power in the incongruent, but not the congruent condition. In the left prefrontal and right inferior parietal cortices, female participants exhibited significant correlations between age and neural power in only the incongruent condition. In contrast, male participants did not exhibit significant relationships between power in the congruent or incongruent conditions with age, though these effects were trending, such that alpha oscillations became stronger with age (i.e., more negative) in the congruent condition and weaker with age (i.e., less negative) in the incongruent condition. In sum, these findings may indicate that neural processes involved in inhibitory control exhibit greater developmental sensitivity. Sex differences in neural activity and connectivity during development have been observed during both basic sensory processing (Fung et al., 2021; Killanin et al., 2020) and higher-order cognition (Embury et al., 2019; Taylor et al., 2020, 2021), as well as during the resting state (Rempe et al., 2023; Satterthwaite et al., 2015). Furthermore, it appears that these age-by-sex interactions may continue throughout the aging process in multiple brain regions (Wiesman and Wilson, 2019). In line with previous findings (Fung et al., 2021), we identified an age-by-sex interaction in the inferior and superior parietal cortices. The parietal cortex is a key node of the dorsal visual stream and organizes spatial information dynamically through multiple reference frames (Goodale and Milner, 1992). Given that these spatial representations are subject to refinement through development and that there are sex differences in spatial learning and navigation tasks, our results could be early indicators of neural sex differences in regions critical for these functions and related behavioral differences as they emerge and persist into adulthood (Duff and Hampson, 2001; Linn and Petersen, 1985; Moffat et al., 1998; Shaqiri et al., 2018). Critically, alpha oscillations have been broadly linked to visual attention and are developmentally sensitive (Cellier et al., 2021). Furthermore, parietal alpha activity has been shown to index stimulus-stimulus interference, but not stimulus-response interference (Wiesman and Wilson, 2020b). The PFC also exhibited age-by-sex effects and is well-known to be sensitive to developmental and psychopathological processes (Badre and Wagner, 2004; Ezekiel et al., 2013; Kaczkurkin et al., 2019; Ridderinkhof et al., 2004; Satterthwaite et al., 2015; Schantell et al., 2023; Sheridan et al., 2014; Zanolie and Crone, 2018). Importantly, the parietal and PFC are known to be engaged in multiple forms of inhibitory control (Wager et al., 2005), indicating that the sensitivity of these regions to developmental changes in interference control may have downstream implications on other subcomponents of inhibitory control (e.g., response inhibition). Taken together, our findings suggest that there are marked age-by-sex interactions in interference control and contribute to a burgeoning literature examining the neural substrates that underlie sex differences in healthy brain function and psychopathology.

There are some limitations of our work. Primarily, the ongoing study from which these data were aggregated employs an accelerated longitudinal design, though the present research utilizes only a cross-sectional sample from one year of the data collection. Thus, while these results demonstrate general trends in neurodevelopmental processes by age, sex, and their interactive effects, future work will probe for longitudinal intra-individual differences in these processes upon completion of the study. Importantly, pediatric brain templates and atlases for structural and functional imaging (Chu et al., 2022; Doucet et al., 2025; Molfese et al., 2021) are becoming increasingly available and their use may highlight more subtle developmental changes that may be obscured by relying on an adult template for standardization. Additional specificity afforded by these developmentally specific templates will likely enhance our understanding of changes in the degree of functional dispersion (e.g., more distributed to localized) and should be incorporated in future analyses. Furthermore, this study does not incorporate endocrine data, which would provide complementary information regarding the complex developmental processes in children and adolescents. Future work should examine the impact of hormones during the pubertal transition to help disentangle the developmental

changes associated with age, hormones, and sex. Finally, these neurodevelopmental changes in interference control should be directly compared with those supporting response inhibition to more comprehensively assess potentially distinct trajectories underlying subcomponents of inhibitory control. Overall, this study contributes to the growing literature focused on the impact of age and sex on the neural substrates of interference control, a specific subcomponent of inhibitory control, and their potential contributions to sex and age-related differences in adolescent and adult psychopathology.

CRediT authorship contribution statement

Son Jake J: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Coutang Anna T:** Writing – review & editing, Data curation. **Stephen Julia M:** Writing – review & editing, Funding acquisition. **Yu-Ping Wang:** Writing – review & editing, Funding acquisition. **Calhoun Vince D:** Writing – review & editing, Funding acquisition. **Killanin Abraham D:** Writing – review & editing, Formal analysis, Conceptualization. **Wiesman Alex I:** Writing – review & editing, Conceptualization. **Mikki Schantell:** Writing – review & editing, Visualization. **Tony W. Wilson:** Writing – review & editing, Supervision, Investigation, Formal analysis, Conceptualization. **Yasra Arif:** Writing – review & editing, Conceptualization. **Ward Thomas W:** Writing – review & editing, Visualization. **Rempe Maggie P:** Writing – review & editing. **Ende Grace C:** Writing – review & editing, Data curation. **Okelberry Hannah J:** Writing – review & editing, Data curation. **Rice Danielle L:** Writing – review & editing, Data curation.

Declaration of Competing Interest

The authors have no competing interests to declare.

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Data availability

I have shared a link in the attach file step.

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