



## Age-related trends in aperiodic EEG activity and alpha oscillations during early- to middle-childhood

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### ABSTRACT

Age-related structural and functional changes that occur during brain development are critical for cortical development and functioning. Previous electroencephalography (EEG) and magnetoencephalography (MEG) studies have highlighted the utility of power spectra analyses and have uncovered age-related trends that reflect perceptual, cognitive, and behavioural states as well as their underlying neurophysiology. The aim of the current study was to investigate age-related change in aperiodic and periodic alpha activity across a large sample of pre- and school-aged children ( $N = 502$ , age range 4–11-years-of-age). Power spectra were extracted from baseline EEG recordings (eyes closed, eyes open) for each participant and parameterized into aperiodic activity to derive the offset and exponent parameters and periodic alpha oscillatory activity to derive the alpha peak frequency and the associated power estimates. Multilevel models were run to investigate age-related trends and condition-dependent changes for each of these measures. We found quadratic age-related effects for both the aperiodic offset and exponent. In addition, we observed increases in periodic alpha peak frequency as a function of age. Aperiodic measures and periodic alpha power were larger in magnitude during eyes closed compared to the eyes open baseline condition. Taken together, these results advance our understanding of the maturational patterns/trjectories of brain development during early- to middle-childhood.

### 1. Introduction

Spectral analyses of the electroencephalogram (EEG) characterize cortical brain activity in terms of frequency, and offer a valuable approach for investigating underlying neural organization and functional maturation across development. Previous EEG and magnetoencephalography (MEG) studies have highlighted the utility of power spectra analyses and have uncovered age-related trends that reflect perceptual, cognitive, and behavioral states as well as their underlying neurophysiology (Buzzell et al., 2019; Clarke et al., 2001; Cohen Kadosh et al., 2015; Donoghue et al., 2020a; Dustman et al., 1999; Gómez et al., 2017; He et al., 2010; Jensen, and Mazaheri, 2010; Klimesch, 2012; Leno et al., 2021; Marshall et al., 2002; Schäfer et al., 2014; Segalowitz et al., 2010;

Whitford et al., 2007). Traditional approaches to spectral power analyses typically describe absolute and/or relative power within pre-defined frequency bands of interest (e.g., delta, theta, alpha, beta, gamma) and ignore the background *aperiodic activity* also present in the power spectrum. This background aperiodic activity, commonly referred to as “1/f-like noise” due to its decreased power with increased frequency, contains important and meaningful physiological information that has been shown to dynamically change with age (Cellier et al., 2021; Dave et al., 2018; Donoghue et al., 2020a, 2020b; He et al., 2010; He, 2014, 2019; Hill et al., 2022; McSweeney et al., 2021; Ostlund et al., 2022).

Background aperiodic activity present in the raw power spectrum is often characterized by two parameters, an aperiodic offset and a slope exponent. The offset, measured as the y-intercept of lower frequency

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bound of the model fit, denotes “the uniform shift in power across frequencies” (Donoghue et al., 2020a) and is believed to reflect overall rates of neuronal population spiking (Manning et al., 2009; Miller et al., 2014). In contrast, the aperiodic exponent, defined as  $X$  in the  $1/f^X$  formulation, where  $X$  reflects proportional decreases in power with increases in frequency (i.e., the slope of the linear fit in log-log space), is thought to reflect the integration of synaptic currents in the brain, an index of excitatory (E) and inhibitory (I) balance (Gao et al., 2017). Parametrization of the power spectrum also allows for the measurement of aperiodic-adjusted periodic activity, hereon referred to as periodic activity. Periodic activity describes rhythmic components in the power spectrum (neural oscillations) measured as spectral peaks above the aperiodic exponent (Donoghue et al., 2020a). For a more detailed description of background aperiodic activity and reasons for parametrization see (Donoghue et al., 2020a; Ostlund et al., 2022).

Changes in E:I ratios, as indexed by the aperiodic exponent, have been shown to change substantially during the first year of life (Schaworonkoff and Voytek, 2021). These changes are thought to reflect changes in myelination, brain volume and cortical thickness. There is evidence that E:I imbalances are associated with neurodevelopmental and psychiatric disorders; attention-deficit/hyperactivity disorder (ADHD; Mamiya et al. 2021; Ostlund et al. 2021; Robertson et al. 2019), schizophrenia (Molina et al., 2020) and Fragile X Syndrome (FXS; Wilkinson and Nelson 2021). E:I imbalances are particularly evident in instances where pharmaceutical interventions have led to the “normalization” of E:I ratios in schizophrenia (Molina et al., 2020) and in ADHD (Mamiya et al., 2021; Robertson et al., 2019) when compared to typically developing controls. These findings suggest that aberrant changes in the E:I balance found in neurodevelopmental disorders like ADHD and schizophrenia suggest that an optimal E:I balance may be of particular importance in typical brain development. Accordingly changes in the balance between synaptic excitatory and inhibitory currents of the cerebral cortex are critical for normal cortical development and function. It should be noted that the “balance” in excitation to inhibition doesn’t mean that excitation is equal to inhibition (Gao et al., 2017). Further, from a developmental perspective, the regulation of E:I ratios during critical periods of brain development may be the result of greater change in inhibitory activity rather than changes in excitatory neurotransmission (Zhang et al., 2011).

Although age-related decreases in absolute power tend to occur across all frequencies (Rodríguez Martínez et al., 2012), prior developmental EEG and MEG studies have noted a more nuanced and complex relationship between brain maturation and relative slow and fast wave activity. Most notably, age-related decreases in relative slow-wave/low-frequency activity (delta and theta) emerges from approximately 4-years of age, followed by developmental increases in higher-frequency activity (alpha, beta, and gamma) (Dustman et al., 1999; Gómez et al., 2017; Hill et al., 2022; Marshall et al., 2002; Schäfer et al., 2014; Whitford et al., 2007). Moreover, a recent study that accounted for background aperiodic activity has shown that the peak frequency and power of the dominant neuronal oscillation (4–12 Hz range) increases with age, with an inflection/transition point from lower to higher frequency band activity occurring at approximately 7-years of age (Cellier et al., 2021). Both increases and decreases in EEG band power have been shown to be functionally significant. For example, in addition to being most prominent during eye-closure, the alpha rhythm is associated with the inhibition of task-irrelevant stimuli that impede attention allocation and working memory (Haegens et al., 2022; Jensen, and Mazaheri, 2010; Klimesch, 2012; Iemi et al., 2022; Voytek et al., 2017). Alpha oscillations have also been found to show age-related increases in peak frequency during childhood (Marshall et al., 2002) and age-related decreases in older adulthood linked to a diminution in executive function (Aurlen et al., 2004). These findings suggest that the alpha rhythm is an important index of cognitive development. Maturation of electrophysiological measures such as alpha oscillatory activity likely reflect age-related structural and functional change aligned to the burgeoning

of perceptual, cognitive, and behavioural abilities across development (Segalowitz et al., 2010).

The current study examined baseline (resting-state) aperiodic and periodic activity in a sample of 502 children from the Northern Plains of America (South Dakota, USA). The focus of the current study is on three estimates derived from our spectral power analyses; aperiodic offset and exponent and periodic alpha oscillatory activity. We focus on alpha oscillations as this is the band most commonly studied in baseline EEG analyses. With this focus, the purpose of the current work was two-fold. First, we examined age-related effects on aperiodic components from ages 4- to 11-years. In line with previous studies, we hypothesized decreases in aperiodic offsets and exponents with age (Cellier et al., 2021; Donoghue et al., 2020a, 2020b; He et al., 2010; He, 2014; Hill et al., 2022; McSweeney et al., 2021; Schaworonkoff and Voytek, 2021). Second, we investigated age-related effects on alpha oscillatory activity (alpha peak frequency and periodic power estimates). Based on previous findings (Cellier et al., 2021; Dustman et al., 1999; Gómez et al., 2017; Hill et al., 2022; Marshall et al., 2002; Schäfer et al., 2014; Whitford et al., 2007), we hypothesized a positive shift in periodic alpha peak frequency as a function of age, but did not hypothesize increases in periodic alpha power as the children grew older (Cellier et al., 2021; Hill et al., 2022). We conducted additional power spectra analyses for periodic theta, beta and gamma activity. These results are not reported in the main body of the text but are provided in supplementary materials.

## 2. Methods

### 2.1. Participants

Participants were originally enrolled in the Prenatal Alcohol in SIDS and Stillbirth (PASS) study described previously (Dukes et al., 2014). A subset of these subjects was then reenrolled as part of the Environmental Influences on Child Health Outcomes (ECHO) study in South Dakota (Blaisdell et al., 2021). As part of the larger study, children were invited to participate in an EEG assessment at one of five assessments based on their age. Assessments were at 4-, 5-, 7-, 9-, and 11-years-of-age. EEG data collection was conducted in Sioux Falls and Rapid City (South Dakota) by the Avera Center for Pediatric and Community Research (CPCR). The initial sample included 510 children ( $M_{\text{age}} = 6.88$  years;  $SD_{\text{age}} = 2.21$ ; 279 (54.7%) girls). Of the 510 participants, 3 were excluded due to insufficient length of EEG recordings ( $< 1$  min) and 5 were excluded due to poor model fits ( $R^2 < 0.90$ ) and mean squared error (MAE)  $> 0.10$ ). The final sample comprised 502 children (272 girls;  $M_{\text{age}} = 6.92$ ;  $SD_{\text{age}} = 2.21$ ;  $\text{Range}_{\text{age}} = 4.0\text{--}11.5$  years). The sample was predominately White (82.3%), followed by American Indian (13.3%), and other (4.4%). Mothers reported the following level of education: beyond high school = 84.5%, completed high school = 9.8%, some high school = 5%, any primary school = 0.8%. Monthly income reported at time of EEG data collection was as follows: less than \$500 = 2.4%, between \$501 and \$1000 = 5.6%, between \$1001 and \$2000 = 16.7%, between \$2001 and \$3000 = 19.1%, between \$3001 and \$4000 = 20.1%, between \$4001 and \$5000 = 15.5% and greater than \$5001 = 18.9%. A more detailed description of the demographic information for each age-group is presented in Supplementary Table 1.

### 2.2. Protocol/procedure

Prior to data collection, primary caregivers provided informed consent and children provided assent. After EEG cap placement, children were seated ~70 cm in front of a computer monitor and completed a total of 3 min of alternating blocks of eyes open (EO) and eyes closed (EC) baseline (resting) recording. Instructions were presented in E-Prime 2.0.10 (Psychology Software Tools, Pittsburgh, PA). Families were compensated for their participation and children were given a small gift

(e.g., toy). The Avera Institutional Review Board approved all study procedures.

### 2.3. EEG data acquisition

EEG data was acquired using a 64-channel HydroCel Geodesic Sensor Net (vertex-reference), sampled at 500 Hz via EGI software (Net Station Version 5.4; Electrical Geodesics, Inc., Eugene, OR). The nets had the four face channels (61–64) removed to measure other psychophysiological measures (e.g., heart rate) and were not used to collect EEG. Prior to data collection, impedance values were checked for all EEG channels and confirmed to be below 50 k $\Omega$ . The equipment used and protocols followed during EEG acquisition were identical across both data collection sites.

### 2.4. EEG preprocessing

EEG preprocessing was conducted using the EEGLAB toolbox (Delorme and Makeig, 2004) with custom MATLAB scripts (The MathWorks, Natick, MA). EEG data were preprocessed following the procedures described in the Maryland Analysis of Developmental EEG (MADE) pipeline (Debnath et al., 2020, <https://github.com/ChildDevLab/MADE-EEG-preprocessing-pipeline>). In short, continuous EEG data were high-pass filtered offline at 0.3 Hz and low-pass filtered at 49 Hz. Bad channels in the data were identified and removed using the EEGLAB plug-in FASTER (Nolan et al., 2010). To remove ocular artifacts, independent component analysis (ICA) was performed on a copied dataset with a 1 Hz high-pass filter to improve ICA decomposition. Prior to ICA, the copied dataset was segmented into 1 s epochs. Noisy segments of the data were rejected using a combined voltage threshold of  $\pm 1000 \mu\text{V}$  and spectral threshold (range -100 dB to +30 dB) within the 20–40 Hz frequency band to delete activity likely generated by muscle artifacts. If this artifact rejection procedure identified an artifact in more than 20% of the epochs for a given channel, that channel was removed from both the ICA copied dataset and the original dataset. ICA decomposition was then run on the copied dataset and the ICA weights copied back to the original, continuous dataset. Artifactual ICs were removed from the original dataset by using the Adjusted-ADJUST algorithm (Leach et al., 2020; Mognon et al., 2011).

EEG data were segmented into 2 s epochs and subjected to two additional steps of artifact rejection. First, to capture the presence of residual ocular activity not removed through ICA, we completely rejected any epochs in which ocular channel (EGI electrodes 1, 5, 10, and 17) voltages exceeded  $\pm 150 \mu\text{V}$ . Second, for any epoch in which only non-ocular channel voltages exceeded  $\pm 125 \mu\text{V}$ , we interpolated these channels at the epoch level. However, if more than 10% of the channels (not considering globally rejected channels) exceeded  $\pm 125 \mu\text{V}$ , we rejected the entire epoch instead. Any remaining missing channels were then interpolated using the spherical spline method (Perrin et al., 1989) and data were referenced to the average reference.

### 2.5. Parameterizing the power spectra

Power spectra were estimated from 1 to 49 Hz using Welch's method with a hamming window (50% overlap) as implemented using the *spec\_topo.m* function in EEGLAB. Frequency resolution was set to 0.5 Hz. This resulted in a power x channel matrix for each participant. EEG power was then averaged across all electrodes to compute a single power spectrum (global measure) for each condition (eyes closed, EC and eyes open, EO). The *specparam*<sup>1</sup> algorithm (Donoghue et al., 2020a) – an open

<sup>1</sup> The name of this toolbox has been recently updated to *specparam*, previously known as Fitting Oscillations and One-Over-F (FOOOF) (<https://github.com/foof-tools/foof/issues/193>).

source Python package (<https://github.com/foof-tools/foof/>) – was then applied to these data files in Python (v3.7.0) with the frequency range set to 3–40 Hz. The following FOOFGROUP settings were used: *peak\_width\_limits*=[1, 8], *min\_peak\_height*=0.05, *peak\_threshold*=0.5, *max\_n\_peaks*=6. In summary, *specparam* treats the power spectrum as a linear combination of aperiodic components (in log-log space) and periodic activity (oscillations above the aperiodic signal). An initial aperiodic fit was applied to the power spectrum and subsequently removed resulting in initial peak fits, to which Gaussian functions were iteratively fit and then removed. Once these fitted oscillatory peaks were removed from the power spectrum, a second aperiodic fit was applied to the data. Finally, the fitted components (aperiodic and periodic activity) were combined at which point goodness of fit measures were computed – variance explained (R squared) and mean absolute error (MAE). For each participant, estimates of aperiodic activity (aperiodic offset and exponent) were extracted in addition to measures of periodic activity for the theta, alpha, beta and gamma frequency bands. To investigate whether these global measures qualitatively differed at different scalp locations, we conducted additional parametrization at the following electrode locations, frontal (E3, E6, E8, E9), fronto-central (E4, E7, E54), centro-parietal (E33, E34, E36, E38), and occipital (E35, E37, E39) clusters. All four clusters showed similar age-related patterns and did not qualitatively differ substantially from the global estimates. In addition, the Cellier et al. (2021) results showed no significant age by electrode cluster interactions (frontal-midline versus parietal-midline) for aperiodic offset and exponent, and Hill et al. (2022) observed no significant interaction between age and three electrode clusters (anterior, central, posterior) for aperiodic offset and exponent, again suggesting that age-related change in aperiodic activity measured via scalp electrodes appear to be a global phenomenon (Cellier et al., 2021). Therefore, all of the results reported in the main body of text are derived from the global measures. Further, we chose to report global results as we did not have any *a priori* hypothesis regarding age-related scalp location differences (Cellier et al., 2021; Hill et al., 2022). Using global measures also helped with the issue of multiple comparisons that arises when comparing activity across sixty electrodes. Please see Supplement 2 (Supplement\_2\_global\_electrode\_cluster\_model\_fits) for age-group grand average model fits, MAE for each age-group (estimates of model fit error across frequencies), and periodic theta and alpha estimates, for each of the baseline conditions. For topographic maps depicting aperiodic activity and alpha estimates for each age-group and condition, please see Supplement 3 (Supplement\_3\_topomaps). Statistical analysis of global aperiodic and periodic activity estimates was performed via R Version 3.6.1 (R Core Team, 2019).

### 2.6. Statistical analyses

To examine the relationship between age and aperiodic and periodic activity, we employed a series of multilevel models (MLMs) using the *nlme* package in R (Pinheiro et al., 2007). Models were performed separately for each outcome of interest: aperiodic offset (eyes closed, EC, eyes open, EO), aperiodic exponent (EC, EO), and aperiodic-adjusted alpha peak frequency and power (EC, EO). All models included the following covariates; age in years, condition (EC/EO), sex, birthweight (in grams), maternal education level, number of epochs in each condition, and data collection site. All predictor variables were entered as fixed effects, and participant ID was included as a random effect (random intercepts). All models included interactions terms for age by condition (EC/EO). Prior to running each model, Mahalanobis distance was used to account for multivariate outliers. If outliers were found ( $\chi^2 < 0.001$ ), these were removed before each model was run. In total 11 outliers were excluded, 1 four-year-old, 3 five-year-olds, 3 seven-year-olds, and 4 eleven-year-olds. We employed both linear and quadratic models to investigate whether linear or non-linear trends better explained the data. Maximum likelihood estimation was used to allow for model comparison. Restricted maximum likelihood estimators were used for



the final model. The resulting  $p$  values were adjusted for multiple comparisons using  $p_{adjust}$  ( $p$ , "BH"; Benjamini and Hochberg 1995). If linear age-related effects (including interactions) proved to be significant these were then examined using *emmeans*, part of the *emmeans* package (Russell and Lenth., 2021) in R. Additional correlations were run to investigate the relationship between aperiodic and periodic measures (See Supplement 4). Results for aperiodic-adjusted periodic theta, beta and gamma are presented in Supplement 5.

### 3. Results

A series of one-Way ANOVAs were conducted to investigate age-group and collection site differences in terms of data quality. Data quality was assessed by the number of epochs retained after EEG preprocessing in each of the two baseline conditions, eyes open (EO) and eyes closed (EC). There was a statistically significant difference between age-groups for both the EO condition ( $F(4497) = 14.576, p < 0.001$ ) and the EC condition ( $F(4497) = 13.665, p < 0.001$ ) with the trend in the data showing greater data retention as the children grew older. In terms of data collection site differences, there was a statistically significant difference for the EO condition ( $F(1500) = 4.643, p = 0.032$ ) but not the EC condition ( $F(1500) = 2.111, p = 0.14$ ). In addition, a series of one-Way ANOVAs were conducted to investigate age-group and collection site differences for birthweight in grams and gestational age in weeks. There were no statistically significant age-group nor collection site differences in terms of birthweight or gestational age ( $P_s > 0.05$ ). To examine associations between the categorical variables at the time of data collection, the results of a series of Pearson Chi-Square analyses revealed no significant association between age-group and ethnicity ( $\chi^2(8) = 7.944, p = 0.43$ ), age-group and reported monthly income ( $\chi^2(24) = 20.914, p = 0.64$ ), nor age-group and maternal education level ( $\chi^2(12) = 11.969, p = 0.44$ ).

Among covariates included in each model (sex, birthweight (grams), maternal education level, number of epochs retained, data collection site), for the aperiodic offset, only sex was a significant predictor ( $p_{adjust} = 0.001$ ). For the aperiodic exponent only data retention, i.e., number of epochs retained after preprocessing, was a significant predictor ( $p_{adjust} = 0.01$ ). For alpha center frequency no covariates were significant predictors. For periodic alpha power data retention was a significant predictor ( $p_{adjust} = 0.01$ ). For periodic beta center frequency collection site was a significant predictor ( $p_{adjust} = 0.01$ ). See Table 1 for a breakdown of sample characteristics, measures of aperiodic and periodic activity and model fits.

#### 3.1. Aperiodic offset

The likelihood ratio test was used to compare the linear MLM model to the same model with a quadratic term for age. The model with the quadratic term fit the data significantly better than the linear model,  $\chi^2(15) = 13.579, p = 0.001$ . As predicted, we observed significant main effects for age ( $F(2, 491) = 16.761, p_{adjust} < 0.001$ ) and condition ( $F(1, 491) = 470.721, p_{adjust} < 0.001$ ) showing that offset values demonstrated a concave non-linear trend when collapsing across EC and EO conditions. For illustrative purposes, both conditions are plotted in Fig. 1, C. Offset values were significantly greater in magnitude during the EC compared to the EO condition ( $b = 0.288, SE = 0.017, CI[0.253 0.323]$ ). No significant two-way interaction was found between age and condition ( $F(2, 491) = 3.071, p_{adjust} = 0.092$ ).

#### 3.2. Aperiodic exponent

Similarly, the likelihood ratio test was used to compare the linear MLM model to the same model with a quadratic term for age. The model with the quadratic term fit the data significantly better than the linear model,  $\chi^2(15) = 22.673, p < 0.001$ . As predicted, we observed significant main effects for age ( $F(2, 491) = 12.075, p_{adjust} < 0.001$ )

and condition ( $F(2, 491) = 427.016, p_{adjust} < 0.001$ ) showing that exponent values demonstrated a concave non-linear trend when collapsing across EC and EO conditions. For illustrative purposes, both conditions are plotted in Fig. 1, C. Exponent values were significantly greater in magnitude during the EC compared to the EO condition ( $b = 0.248, SE = 0.015, CI[0.216 0.279]$ ). No significant two-way interaction was found between age and condition ( $F(2, 491) = 3.592, p_{adjust} = 0.056$ ).

#### 3.3. Aperiodic-adjusted periodic alpha peak frequency

Again, the likelihood ratio test was used to compare the linear MLM model to the same model with a quadratic term for age. The model with the quadratic term did not fit the data significantly better than the linear model,  $\chi^2(22) = 3.213, p = 0.200$ . For periodic alpha peak frequency, we observed a significant main effect for age ( $F(1, 454) = 107.117, p_{adjust} < 0.001$ ) but not for condition ( $F(1, 385) = 1.162, p_{adjust} = 0.511$ ) showing that periodic alpha peak frequency increased with age when collapsing across EC and EO conditions. For illustrative purposes, both conditions are plotted in Fig. 2B. Examining the estimates of slopes for this age-related linear trend confirmed this was the case ( $b = 0.135, SE = 0.013, CI[0.109 0.160]$ ). See Fig. 2, B. No significant two-way interaction was found between age and condition ( $F(1, 385) = 1.447, p_{adjust} = 0.229$ ).

#### 3.4. Aperiodic-adjusted periodic alpha power

For periodic alpha power estimates the linear MLM model proved to be sufficient. That is, including the quadratic term for age in the model did not significantly improve the model fit  $\chi^2(15) = 1.353, p = 0.508$ . For periodic alpha power, we observed a significant main effect for condition ( $F(1, 385) = 9.888, p_{adjust} = 0.007$ ) but not for age ( $F(1, 454) = 0.017, p_{adjust} = 0.893$ ) showing that alpha power was significantly increased during EC compared to the EO condition ( $b = 0.310, SE = 0.011, CI[0.288 0.332]$ ) (Fig. 2, D). We observed a significant two-way interaction between age and condition ( $F(1, 385) = 33.128, p_{adjust} < 0.001$ ). Examining the estimates of slopes for this age-related linear trend showed that periodic alpha power pattern of change over time differed between EC and EO conditions ( $b = 0.310, SE = 0.011, CI[0.288 0.332]$ ). See Fig. 2D.

## 4. Discussion

In the current cross-sectional study, we adopted a novel approach to examine age-related change in aperiodic and periodic activity across a relatively large sample of pre- and school-aged children. Previous studies that employed parametrization of the power spectrum to investigate aperiodic EEG activity identified negative relationships between aperiodic activity and age during different developmental stages (Cellier et al. 2021, age-range 3–24 years; Donoghue et al. 2020a, age range 20–30, 60–70 years; Donoghue et al. 2020b, age-range 6–44 years; Hill et al. 2022, age-range 4–12 years; McSweeney et al. 2021, age-range 13–15 years; Schaworonkow and Voytek 2021, age range 1–7 months). Here, in a large sample of children from 4- to 11-years, we observed non-linear age-related trends for both aperiodic offsets and exponents. Convergent with prior developmental work at other ages (Hill et al., 2022; McSweeney et al., 2021), we also observed condition-dependent differences in both offset and exponent, such that aperiodic offsets were greater in magnitude during EC compared to EO conditions. Aperiodic exponents were greater in magnitude (steeper 1/f-like spectral slopes) in EC compared to the EO condition.

We observed linear increases with age in alpha peak frequency which was not condition-dependent. That is, periodic alpha peak frequency did not differ between EC and EO conditions. For periodic alpha power, we observed the expected condition-dependent effects with periodic alpha power greater during EC compared to the EO condition. We also observed a significant two-way interaction between age and condition

**Table 1**  
Sample size, aperiodic and aperiodic-adjusted periodic activity, and model fits.

Age (years)	Aperiodic activity Mean(SD)				Aperiodic-adjusted periodic activity Mean(SD)			
	N	Offset	Exponent		Theta (3–8 Hz)	Alpha (8–13 Hz)	Beta (13–30 Hz)	Gamma (30–40 Hz)
4 years	87	1.82(0.40)	1.72(0.33)	EC	n = 80	n = 70	n = 55	n = 80
				CF	6.34(1.17)	8.88(0.50)	19.66(4.08)	34.15(3.85)
				PW	0.50(0.26)	0.77(0.30)	0.14(0.08)	0.22(0.13)
EO	87	1.52(0.35)	1.47(0.29)	EO	n = 71	n = 66	n = 52	n = 85
				CF	6.07(1.30)	8.94(0.55)	22.59(3.03)	33.16(3.67)
				PW	0.41(0.21)	0.54(0.17)	0.14(0.08)	0.18(0.10)
5 years	126	1.77(0.36)	1.76(0.26)	EC	n = 111	n = 112	n = 88	n = 107
				CF	6.59(1.19)	9.01(0.61)	18.74(3.51)	33.63(3.65)
				PW	0.41(0.25)	0.82(0.27)	0.17(0.10)	0.21(0.14)
EO	126	1.48(0.41)	1.50(0.33)	EO	n = 97	n = 98	n = 85	n = 116
				CF	6.05(1.18)	9.12(0.61)	21.12(3.22)	32.68(3.84)
				PW	0.33(0.20)	0.58(0.25)	0.15(0.10)	0.18(0.10)
7 years	164	1.86(0.33)	1.84(0.24)	EC	n = 127	n = 151	n = 137	n = 127
				CF	6.56(1.16)	9.23(0.68)	17.75(2.91)	33.67(3.79)
				PW	0.45(0.60)	0.84(0.27)	0.23(0.13)	0.19(0.15)
EO	164	1.57(0.36)	1.60(0.29)	EO	n = 121	n = 138	n = 132	n = 128
				CF	6.12(1.21)	9.21(0.66)	19.36(3.72)	33.44(3.53)
				PW	0.30(0.18)	0.54(0.25)	0.19(0.13)	0.19(0.13)
9 years	69	1.66(0.30)	1.73(0.25)	EC	n = 44	n = 68	n = 58	n = 49
				CF	6.36(1.31)	9.45(0.73)	17.34(2.74)	33.32(4.16)
				PW	0.35(0.24)	0.83(0.31)	0.28(0.16)	0.24(0.19)
EO	69	1.40(0.32)	1.52(0.27)	EO	n = 45	n = 60	n = 53	n = 49
				CF	5.84(1.34)	9.43(0.76)	18.13(3.49)	33.21(3.58)
				PW	0.23(0.12)	0.48(0.25)	0.25(0.16)	0.25(0.19)
11 years	56	1.54(0.33)	1.62(0.29)	EC	n = 33	n = 55	n = 53	n = 37
				CF	6.72(1.16)	9.98(0.89)	17.44(3.06)	33.69(4.08)
				PW	0.32(0.25)	0.94(0.32)	0.30(0.14)	0.20(0.14)
EO	56	1.35(0.34)	1.47(0.31)	EO	n = 33	n = 51	n = 45	n = 44
				CF	6.07(1.38)	10.01(1.09)	17.70(3.56)	33.23(3.68)
				PW	0.20(0.14)	0.55(0.25)	0.23(0.13)	0.21(0.15)
Model fit								
R <sup>2</sup>		4 years	5 years	7 years	9 years	11 years		
EC		0.98(0.01)	0.99(0.00)	0.99(0.00)	0.99(0.00)	0.99(0.01)		
EO		0.98(0.01)	0.98(0.01)	0.99(0.01)	0.99(0.0)	0.98(0.01)		
MAE								
EC		0.03(0.01)	0.03(0.01)	0.03(0.00)	0.03(0.00)	0.03(0.00)		
EO		0.03(0.01)	0.03(0.01)	0.03(0.01)	0.03(0.00)	0.03(0.01)		

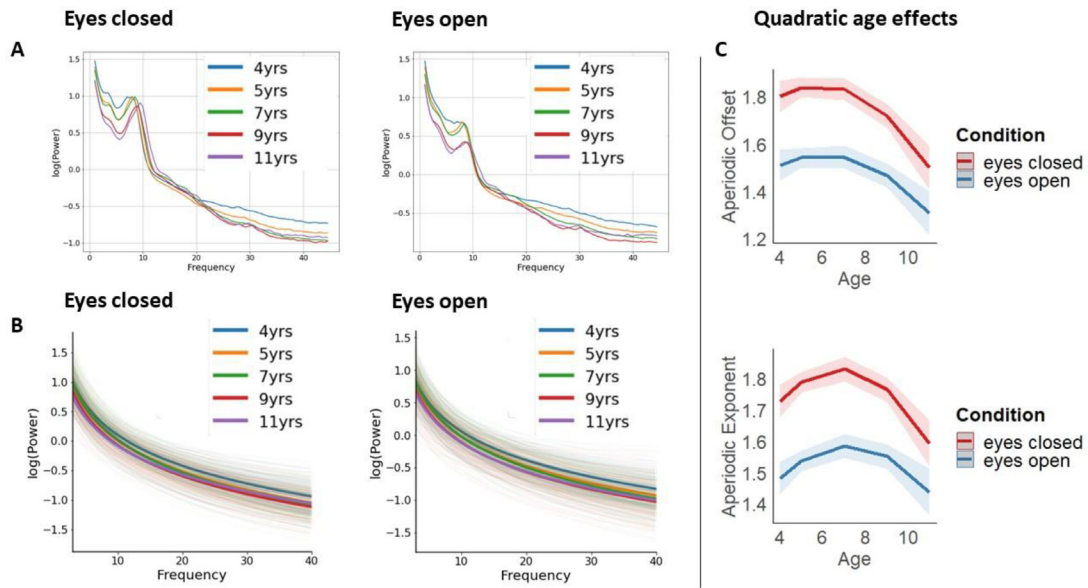
Note: EC = eyes closed condition; EO = eyes open condition; CF = center frequency; PW = log power; R<sup>2</sup> = variance explained by specparam model fit; MAE = mean absolute error of specparam model fit.

such that periodic alpha power increased as a function of age during the EC condition but not the EO condition.

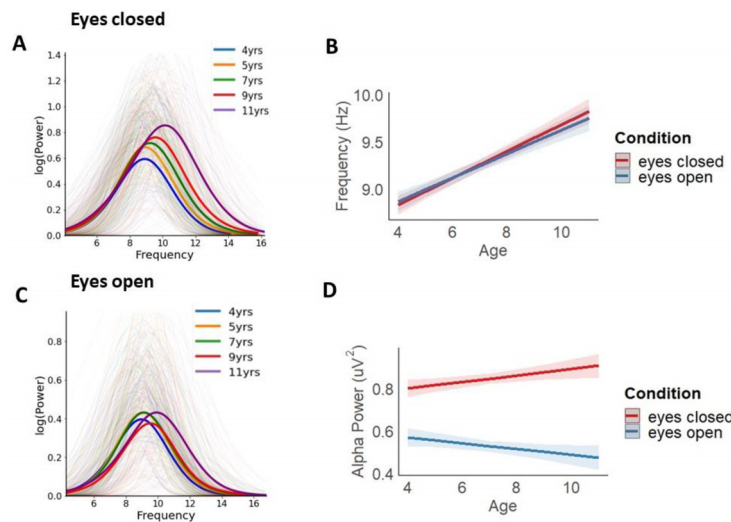
#### 4.1. Age-related change in aperiodic activity

In the current study, quadratic age-related trends were found for both offset and exponent values. The direction of these results is not in agreement with previous findings that have shown negative linear trends with increases in age. For example, previous studies have observed negative linear trends during early-to-middle childhood (Hill et al., 2022), when comparing early childhood to young adults (Cellier et al., 2021; He et al., 2019), young adults to older adults (Dave et al., 2018) and when examining longitudinal change during early-adolescence (McSweeney et al., 2021). Instead, we observed increases in aperiodic offsets and exponents from 4-years-of-age ~7-years-of-age followed by decreases in both aperiodic components up to 11-years-of-age. Age-related increases in aperiodic activity followed by age-related reductions in offset and exponent may be indicative of an inflection point or shift/transition from greater power at lower frequencies to increases in power at higher frequencies that occurs at approximately 7-years-of-age (Cellier et al., 2021).

Reductions in broadband power (aperiodic offset) are likely to be driven not only by changes to neural communication but also may reflect developmental changes to brain morphology. For example, a multimodal study using both EEG and magnetic resonance imaging (MRI) of 138 participants aged 10–30-years-of-age, noted that age-related changes in absolute EEG power in slow-range frequency bands during baseline were associated with declines in gray matter volume (Whitford et al., 2007). Moreover, while age-related changes in pre-pubescent cortical thickness (CT), surface area (SA) and overall cortical volume (CV) appear to show differing levels of complexity of cortical growth that is spatially defined, other studies have shown linear, quadratic and cubic developmental trajectories in cortical development (Shaw et al., 2008; Sussman et al., 2016). In a sample of 375 typically developing children and young adults (age range 3.5–33-years), Shaw et al. (2008) showed that increases in CT occur during early childhood with peak thickness across several regions occurring between the ages of 7- and approximately 10-years-of-age followed by CT decreases with advancing age. A second study by Sussman et al. (2016) utilizing a sample 192 gender-matched participants (age range 4–18-years, 96 females) showed quadratic changes in CV in different brain regions. Structural age-related non-linear trends (at the level of the cortical ar-



**Fig. 1.** (A) Power spectral density (PSD) for each age group during eyes closed and eyes open baseline conditions (B) Aperiodic fits by age-group eyes closed and eyes open conditions (C) Age-related change in the aperiodic offset and exponent (quadratic age effect) for eyes closed and eyes open conditions.



**Fig. 2.** (A) Plot showing periodic alpha power for eyes closed (EC) condition (B) Plot showing linear increases in periodic alpha peak frequency with increases in age (C) Plot showing periodic alpha power for eyes open (EO) condition (D) Plot showing age-related change in periodic alpha power for eyes closed and eyes open (EC and EO) conditions.

chitecture) may help to explain the age-related quadratic trajectory we observed for offset values. Therefore, it is possible that maturational changes in the aperiodic offset as measured via scalp EEG recordings index underlying morphological change and synaptic pruning, leading to increased efficiency in neuronal transmission associated with reductions in superfluous activity (Segalowitz et al., 2010). A note of caution relates to the fact that brain maturation occurs in concert with thickening of the skull. Increases in skull thickness leads to higher resistance which results in lower amplitude EEG signals. Additional research is needed to clarify whether decreases in broadband power as measured with scalp EEG reflect changes in underlying brain morphometry and are partially explained by changes in resistance/bone density.

We observed that offset magnitudes were significantly reduced during EO compared to the EC condition. Why this was the case is not immediately apparent. However, one important consideration is that changes in offset and exponent values are often highly correlated when there is a rotation of the power spectrum around a non-zero frequency (Donoghue et al., 2020a; Ostlund et al., 2022). In the current study, offset magnitudes positively correlated with exponent magnitudes during both baseline conditions (EC  $r^s = 0.838$ , EO  $r^s = 0.845$ ). Condition-

dependent reductions in offset magnitudes during the EO condition occurring in concert with reductions in exponent, may be indicative of a rotation in the power spectrum (flatter spectral slope) or the engagement of attentive processes and/or arousal levels (Hill et al., 2022) or both. For example, the active processing of visual stimuli has been shown to result in flatter spectral slopes (He et al., 2010; Podvalny et al., 2015). That is, increases in excitation relative to inhibition during EO compared to the EC condition may be indicative of greater engagement/arousal. This proposition is supported by our findings that exponent values were significantly greater in magnitude during the EC compared to the EO condition. With offset and exponent values showing such high correlations, one would expect that decreases in exponent occur in concert with decreases in offset. See Supplement 4.

As reported above, significant monotone decreases in exponent magnitudes with increases in age were not found. These findings may at first appear somewhat surprising given that previous developmental studies comprising participants (or sub-populations) of similar age have shown linear decreases in exponent magnitude with increases in age (Cellier et al., 2021; Dave et al., 2018; Donoghue et al., 2020a, 2020b; He et al., 2010; He, 2014, 2019; Hill et al., 2022; Ostlund et al., 2022).

However, differences in sample size (particularly during early childhood, for example 4-, 5- and/or 7-years-of-age) and/or sample characteristics may help to explain the inconsistency between the current study and the two earlier studies. Cellier et al. (2021) had a smaller sample ( $N = 25$  for 4–7 years and wider age range which included adolescents and adults). Hill et al. (2022) also had significantly smaller sample size ( $N = 139$ ). The quadratic age-related effects on exponent values suggest that developmental changes in background aperiodic activity may be more complex and developmentally dynamic than previously described. Future studies using a comparative and/or larger sample size should investigate further what appears to be an inflection point that occurs at approximately 7-years-of-age, possibly pointing to changes that might occur during specific developmental periods (see Cellier et al., 2021).

Changes in exponent have been associated with changes in the balance between excitatory and inhibitory neurotransmission (Donoghue et al., 2020a; Gao et al., 2017; He, 2014; Voytek et al., 2015b). Excitatory and inhibitory currents in neural populations are largely driven by excitatory (glutamate) and inhibitory (GABA) neurotransmitter levels and changes in this ratio are likely to occur during brain maturation and may play an important role for the acquisition of new skills. For example, using single-voxel proton magnetic resonance spectroscopy ( $^1\text{H-MRS}$ ), Cohen Kadosh et al. (2015) found that increase in glutamate/GABA ratios in the inferior frontal gyrus (IFG) positively correlated with face processing proficiency during childhood ( $N = 14$ , age range 7–10-years) but not during adulthood ( $N = 14$ , age range 20–23-years). In addition, the authors also note that this relationship was not found in other brain regions such as the inferior occipital gyrus (IOG), a phylogenetically older region of the brain (Gogtay et al., 2004). Further, this relationship was dissociable from cortical gray matter volume leading to the speculation that not only are glutamate/GABA ratios important during early developmental stages, but those changes in E:I ratios may precede structural change and the acquisition of new cognitive abilities. A study by Voytek et al. (2015b) reported associations between changes in the spectral slope (flattening of the slope) and cognitive decline as measured via a working memory task. This was evident in the older adult participants (60–70-years) but not in the younger adults (20–30-years).

In sum, these studies point to the importance of dynamic alterations in excitatory/inhibitory balance during different developmental periods and cognitive stages of human brain development, as well as the role E:I ratios may play in instigating morphological change. Moreover, significant differences between typical and atypical neurodevelopment have been previously noted when examining comparative change in the power spectra in ADHD (Mamiya et al., 2021; Ostlund et al., 2021; Robertson et al., 2019) and schizophrenia (Molina et al., 2020) when compared to typically developing controls. Based upon the current findings of age-related quadratic effects and previous work, we speculate that changes in exponent may be more evident during specific developmental periods or within particular clinical populations, for example during infancy (Schaworonkoff and Voytek, 2021), early-adolescence (McSweeney et al., 2021) or during older adulthood (Voytek et al., 2015b), or in clinical groups with ADHD (Mamiya et al., 2021; Ostlund et al., 2021; Robertson et al., 2019) and schizophrenia (Molina et al., 2020), in which E:I ratios may be particularly important. Furthermore, when compared to typically developing controls, group differences in spectral slope have been observed in certain genetic conditions. For example, Rett syndrome is associated with a steeper  $1/f$ -like slope. This condition is characterized by developmental regression that occurs approximately between 6 and 18 months of age (Roche et al., 2019). FXS is a genetic neurodevelopmental condition caused by an expansion of the CGG triplet related FMR1 gene on the X chromosome resulting in a FMRP protein deficiency. FXS is associated with an E/I imbalance and mouse models have reversed phenotypes in FMR1 knock-out mice through the administration of GABA agonists (Wilkinson and Nelson, 2021). Notably, in FXS the aperiodic spectral exponent appears to be reduced, a flatter  $1/f$ -like spectral slope (Wilkinson and

Nelson, 2021). Furthermore, there is some evidence suggesting that a steeper spectral slope in preterm infants is associated with autism risk (Shuffrey et al., 2022). Future studies using multimodal imaging approaches such as EEG and MRS may better elucidate the relationship between excitatory and inhibitory neural activity during specific developmental periods and/or between select clinical populations and healthy controls.

#### 4.2. Age-related change in periodic alpha oscillatory activity

We observed linear age-related change in alpha peak frequency. That is, alpha peak frequencies increased with age. These changes in alpha peak frequency are largely in agreement with previous findings (Cellier et al., 2021; Cragg et al., 2011; He et al., 2019; Hill et al., 2022; Marcuse et al., 2008; Marshall et al., 2002; Miskovic et al., 2015; Perone et al., 2018; Rodríguez-Martínez et al., 2017; Soroko et al., 2014). It has been proposed that shifts in alpha peak toward higher frequency coincide with increases in speed in neuronal communication (Segalowitz et al., 2010). Furthermore, previous work has shown the association between alpha peak frequency and cognitive ability in children with autism spectrum disorder (ASD) and age-matched non-autistic controls (Dickinson et al., 2018). The observed age-related effect in alpha peak frequency in the current study corroborate the proposition that alpha peak frequency may be an informative metric of neurodevelopmental change linked to increases in neuronal communication efficiency and presumably cognitive ability (Leno et al., 2021; Dickinson et al., 2018; Marshall et al., 2002; Segalowitz et al., 2010). Empirical results showing increases in alpha peak frequency with age appear to be replicable and robust findings, and indicate a shift from lower to higher frequency activity during neurotypical development. Consequently, developmental trajectories in alpha activity may point to the maturation and/or refinement in cognitive control, goal-directed behavior, impulsivity and working memory capacity.

For periodic alpha power, we observed a significant main effect of experimental condition showing the expected increased periodic alpha power during EC compared to the EO condition (Isler et al., 2022). We also observed a significant two-way interaction between age and condition showing that periodic alpha power increased with increases in age during the EC condition but not during the EO condition. This is not altogether consistent with a previous finding showing no age-related increases in periodic alpha power during the EC baseline condition (Hill et al., 2022) but is consistent for the EO baseline condition (Cellier et al., 2021; Hill et al., 2022), i.e., no significant age-related increases in periodic alpha power. It should be noted that in the Hill et al. (2022) study, although not meeting the threshold for significance, the association between increases in periodic alpha power with age during the EC condition approached significance ( $p = 0.08$ ), possibly indicating an age-related trend in their sample. However, and again, differences in sample size and/or sample characteristics may help to explain these inconsistencies.

Notably, not all participants in our sample exhibited aperiodic-adjusted alpha peak activity during resting state eyes closed and eyes open EEG recordings. For example, alpha activity (8–13 Hz) was present in 80% of 4-year-olds, 89% in 5-year-olds, 92% in 7-year-olds, and 98% in both the 9- and 11-year-old participants. For eyes open resting state recordings alpha activity was present in 76% of 4-year-olds, 78% of 5-year-olds, 84% of 7-year-olds, 87% of 9-year-olds and 91% of 11-year-olds. On average, aperiodic-adjusted alpha peaks were detected in 91% of participants during eyes closed recordings and in 82% of participants during eyes open recordings. It should also be noted that peak detection above the aperiodic signal in the theta band (3–8 Hz) decreased as the children grew older. For example, during eyes closed resting state recordings, theta peaks were detected in 92% of 4-year-olds, 88% of 5-year-olds, 77% of 7-year-olds, 64% of 9-year-olds and 59% of 11-year-olds. During eyes open resting state recordings, theta peaks were detected in 92% of 4-year-olds, 77% of 5-year-olds, 74% of 7-year-olds,



65% of 9-year-olds and 59% of 11-year-olds. On average, aperiodic-adjusted theta peaks were detected in 79% of participants during eyes closed recordings and in 73% of participants during eyes open recordings.

When we compare our findings to those of the Hill et al. (2022) study which comprised participants with a very similar age-range (4–12-years-of-age) and which also examined resting state eyes open and eyes closed EEG recordings, across all participants ( $N = 139$ ) alpha peaks were detected in 94% of participants during eyes open and 99% of participants during eyes closed resting state recordings. Moreover, in the Hill et al. (2022) study far fewer participants exhibited peaks within the delta (1–3 Hz), theta (3–7 Hz), and gamma (>30 Hz) frequency bands. This is consistent with the Ostlund et al., 2022 study which reported less than half of their sample showing clear aperiodic-adjusted theta peak activity. Again, in our sample ( $N = 502$ ), on average, aperiodic-adjusted alpha peaks were detected in 91% of participants during eyes closed recordings and in 82% of participants during eyes open recordings. Other than the differences in how bands were defined (Hill et al. 2022 alpha band was defined as 7–13 Hz), the lower percentages of peak detection in the alpha band in our sample may have resulted from the much larger sample size. This is consistent with the notion that there appears to be a shift from lower to higher frequency activity as a function of age.

#### 4.3. Limitations and future directions

The current study has a number of limitations. First, the findings are limited to spontaneous neural activity. Second, we did not account for other exposure which may have significantly contributed to earlier changes in EEG activity. e.g., maternal psychological states during infancy or during early-to-middle childhood or psychotropic medications taken during pregnancy. In addition, we did not adjust for other environmental factors such as parenting styles. Third, the current study was cross-sectional and was therefore unable to track individual longitudinal change. Also, the EC and EO baseline conditions were not counterbalanced. Lastly, there are some earlier data that suggest that the estimation of the aperiodic slope may differ for very low frequencies relative to higher frequencies (e.g., 0.1–1 Hz compared to 3–40 Hz, Gerster et al. 2022; He et al. 2010). There is the possibility that this might lead to a misestimation of the offset. Future studies should examine the relationships between spontaneous and task-related EEG activity longitudinally and, where possible, investigate how changes in brain morphology (cortical thickness and/or curvature) covary with aperiodic and periodic activity. Future investigations may also want to explore how aperiodic activity changes during wake versus sleep states across infancy or during early-to-middle childhood. If we assume aperiodic activity indexes both shifts in broadband power and the relative inhibitory to excitatory neurotransmission activity, one might expect to see condition-dependent change in aperiodic activity during different wake and sleep states with sleep states possibly resulting in increased inhibitory activity (steeper 1/f-like spectral slopes). Some evidence for this comes from a recent study by Colombo et al. (2019) that investigated changes in spectral exponent during baseline and after the administration of three anaesthetics (propofol, xenon, and ketamine). In a sample of fifteen healthy participants (age range 18–28) steeper spectral slopes were evident during anesthesia when compared to eyes closed and eyes open baseline conditions. Much less is known in relation to early neurodevelopmental stages and therefore investigating condition-dependent change in aperiodic activity during different wake and sleep states during early neurodevelopmental stages may prove to be informative.

## 5. Conclusion

Spectral analyses offer a valuable approach to investigating brain functioning across development. Parametrization of the power spectrum is a useful tool that can uncover significant maturational patterns in EEG

activity that have been largely overlooked by traditional approaches. The current study corroborates and extends previous findings showing shifts from lower to higher frequency activity in a unique sample of children from 4- to 11-years-of-age. We found predictably complex quadratic age effects for both aperiodic offsets and exponents. In addition, we observed significant age-related effects on alpha peak frequency. Taken together, these results advance our understanding of the maturational patterns/trajectories of brain development during early-to middle-childhood. Furthermore, the approach adopted highlights the utility of parametrization of the power spectrum to investigate 1/f-like background cortical activity to independently quantify important neurodevelopmental phenotypes.

#### Data statement

De-identified data is available from the authors upon reasonable request. A data sharing agreement would be required between institutions prior to releasing the dataset.

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#### Declaration of Competing Interest

The authors declare no conflicts of interest

#### Credit authorship contribution statement

**Marco McSweeney:** Conceptualization, Methodology, Writing – original draft, Formal analysis, Writing – review & editing. **Santiago Morales:** Conceptualization, Methodology, Formal analysis. **Emilio A. Valadez:** Conceptualization, Methodology, Formal analysis, Writing – review & editing. **George A. Buzzell:** Conceptualization, Methodology, Writing – review & editing. **Lydia Yoder:** Writing – review & editing. **William P. Fifer:** Writing – review & editing. **Nicolò Pini:** Writing – review & editing. **Lauren C. Shuffrey:** Writing – review & editing. **Amy J. Elliott:** Writing – review & editing, Funding acquisition. **Joseph R. Isler:** Writing – review & editing. **Nathan A. Fox:** Conceptualization, Methodology, Writing – review & editing, Supervision.

#### Data availability

Data will be made available on request.

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#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2023.119925.

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