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ORIGINAL ARTICLE

Periodic and aperiodic contributions to theta-beta ratios across adulthood

Anna J. Finley[1] | **Douglas J. Angus**[2] | **Carien M. van Reekum**[3] | **Richard J. Davidson**[1] | **Stacey M. Schaefer**[1]

[1]Center for Healthy Minds, University of Wisconsin, Madison, Wisconsin, USA

[2]School of Psychology, Bond University, Gold Coast, Queensland, Australia

[3]School of Psychology and Clinical Language Sciences, University of Reading, Reading, UK

Correspondence
Anna J. Finleya and Stacey M. Schaefer
University of Wisconsin, Madison, WI, USA.
Email: ajfinley2@wisc.edu and stacey.schaefer@wisc.edu

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Abstract

The ratio of fronto-central theta (4–7 Hz) to beta oscillations (13–30 Hz), known as the theta-beta ratio, is negatively correlated with attentional control, reinforcement learning, executive function, and age. Although theta-beta ratios have been found to decrease with age in adolescents and young adults, theta has been found to increase with age in older adults. Moreover, age-related decrease in individual alpha peak frequency and flattening of the 1/*f* aperiodic component may artifactually inflate the association between theta-beta ratio and age. These factors lead to an incomplete understanding of how theta-beta ratio varies across the lifespan and the extent to which variation is due to a conflation of aperiodic and periodic activity. We conducted a partially preregistered analysis examining the cross-sectional associations between age and resting canonical fronto-central theta-beta ratio, individual alpha peak frequency, and aperiodic component ($n = 268$; age 36–84, $M = 55.8$, $SD = 11.0$). Age was negatively associated with theta-beta ratios, individual peak alpha frequencies, and the aperiodic exponent. The correlation between theta-beta ratios and age remained after controlling for individual peak alpha frequencies, but was nonsignificant when controlling for the aperiodic exponent. Aperiodic exponent fully mediated the relationship between theta-beta ratio and age, although beta remained significantly associated with age after controlling for theta, individual peak alpha, and aperiodic exponent. Results replicate previous observations and show age-related decreases in theta-beta ratios are not due to age-related decrease in individual peak alpha frequencies but primarily explained by flattening of the aperiodic component with age.

KEYWORDS

1/*f*, aging, beta, individual peak alpha frequency, theta, theta-beta ratio

1 | INTRODUCTION

The use of spontaneous resting electroencephalographic (EEG) activity as an objective measure of individual differences in psychological functioning has a long history (Davidson, 1984; Klimesch, 1999; Knyazev, 2007; Schutter & Knyazev, 2012). Resting EEG has typically been divided into standardized bands based on canonical (i.e., fixed)

spectral power bands, from the slowest frequencies in delta (0–4 Hz), through theta (4–7 Hz), alpha (7–13 Hz), beta (13–30 Hz), to the fastest frequencies in gamma (30+ Hz), but are also sometimes defined on an individual basis from the alpha peak frequency (Babiloni et al., 2020). A persistent but growing focus is on the use of these resting EEG measures (usually quantified from canonical bands) as biomarkers for optimal and suboptimal executive function, particularly in the context of identifying healthy versus unhealthy executive function development and decline with aging (Arns et al., 2013; Babiloni et al., 2006). Recent research suggests that individual and intraindividual differences in executive function broadly, and attentional control specifically, are associated with the ratio between fronto-central standard theta to beta oscillations, purported to represent differences in periodic activity within these frequency bands (Angelidis et al., 2016).

1.1 | Theta-beta ratios

The ratio between fronto-central theta and beta oscillations has been promoted as a marker of executive [dys] function associated with Attention-Deficit Hyperactive Disorder (ADHD; Arns et al., 2013) where higher ratios—indicating relatively greater fronto-central theta than fronto-central beta—are characteristic of ADHD. In nonclinical populations, theta-beta ratio has been found to be strongly negatively correlated with self-report and behavioral measures of executive function, while theta and beta alone are not (Perone et al., 2018), and smaller theta-beta ratios are indicative of better cognitive control, executive control, and increased vigilance (Angelidis et al., 2016, 2018; Putman et al., 2010, 2014; van Son, Schalbroeck, et al., 2018). Several studies have shown that beyond being a marker of attentional control, theta-beta ratios are negatively correlated with response-inhibition by threatening stimuli (Putman et al., 2010) and are positively correlated with attentional capture by mildly threatening stimuli relative to highly threatening stimuli (van Son, Angelidis, et al., 2018). Theta-beta ratios have also been found to negatively correlate with advantageous decision-making in reinforcement learning paradigms (Massar et al., 2014; Schutter & Van Honk, 2005). Other studies have reported that theta-beta ratios are positively associated with risk taking behavior, and that theta and beta alone do not (Massar et al., 2012). Recent studies have also shown that theta-beta ratios increase during mind-wandering (van Son, De Blasio, et al., 2019; van Son, de Rover, et al., 2019). Together, these studies suggest that theta-beta ratios are related to attentional control broadly, as well as to more specific emotional and rewarding contexts, such that lower theta-beta ratios are reflective of more control or focus.

Theta-beta ratios are argued to reflect the reciprocal regulation of bottom-up subcortical processes by top-down cortical processes (Knyazev, 2007; Schutter & Knyazev, 2012). Although much of the research supporting this subcortical–cortical model of theta-beta ratios and executive function has been indirect, a recent study has provided support for involvement of cortical networks (van Son, de Rover, et al., 2019). Specifically, van Son, de Rover, et al. (2019)) showed that not only are theta-beta ratios lower when participants exert attentional control compared to when they engage in mind-wandering, but that these changes are associated with decreased functional connectivity between dorsolateral prefrontal cortex (DLPFC) and the dorsal anterior cingulate cortex (ACC)—regions which have been associated with executive function in multiple domains (Seeley et al., 2007).

Given age-related decline in executive function (Buckner, 2004; Lustig & Jantz, 2015) and in cortical integrity (Fjell et al., 2017; Madden et al., 2009, 2012), one would assume a straight-forward relationship between theta-beta ratio and age. The mapping between age and the theta-beta ratio is more complicated, however. First, theta has been observed to increase with age, potentially through a migration of alpha activity to the upper frequencies of theta, discussed in more detail below (Klimesch, 1999). Second, resting theta recorded from the same fronto-central scalp locations used in theta-beta ratio research has been positively correlated with cognitive function in older adults (73 adults ages 56–70, Finnigan & Robertson, 2011; 53 adults ages 18–89, Vlahou et al., 2014). Third, in child and young adult samples, theta-beta ratios have been reported to be negatively correlated with age (41 young adults ages 18–31 years, Angelidis et al., 2016; 41 children ages 8–12 years, Clarke et al., 2001; 101 children ages 7–16 years, Ogrim et al., 2012; 162 children ages 3–9 years, Perone et al., 2018; 28 young adults ages 19–28 years, Putman et al., 2010, but see Putman et al., 2014 for a non-replication in 77 young adults with a mean age of 19.9 years), and with cognitive function (Angelidis et al., 2016, 2018; Putman et al., 2010, 2014; 128 young adults with a mean age of 22.3 years, Schutte et al., 2017). Thus, it remains unclear what drives any association between age and theta-beta ratio, complicated in part by the reliance on canonical frequency bands for calculating theta-beta ratio in populations with shifts in individual alpha peak frequencies in the existing literature.

1.2 | Individual alpha peak frequencies

The frequency at which power in the alpha band (7–13 Hz) peaks, known as individual alpha peak frequency, has

been found to be negatively correlated with age in adulthood (Clark et al., 2004; Klimesch, 1997), and is reduced in individuals with Alzheimer's disease (Klimesch, 1997). Higher individual alpha peak frequency across adulthood is associated with better working memory, better reading comprehension, and a larger general intelligence factor (Angelakis et al., 2004; Clark et al., 2004; Grandy et al., 2013; Klimesch, 1997), suggesting it is an indicator of cognitive capacity or preparedness.

Greater alpha power has been associated with reductions in blood flow across wide areas of the frontal and parietal cortex (Jensen & Mazaheri, 2010; Laufs et al., 2003). During working memory tasks, greater local alpha power during a trial was associated with better memory performance (Jensen & Mazaheri, 2010), and decreases in BOLD activation, particularly in areas of the default mode network (Anticevic et al., 2010; Daselaar et al., 2004). Together, these findings suggest that alpha power indexes the ability to inhibit task-irrelevant regions while performing cognitive tasks (Jensen & Mazaheri, 2010), processes which tend to decline with advancing age.

With regards to theta-beta ratios, because the peak alpha frequency is found in lower frequencies with age, some of the EEG power associated with the alpha band (commonly defined as 7–13 Hz) may be mistakenly attributed to power in the canonical theta band (commonly defined as 4–7 Hz) in older adults, driving increases in canonical theta band power with age and therefore changes in theta-beta ratios. While some work suggests that relative canonical theta in older adults may be positively correlated with measures of memory, attention, and executive functioning, the potential role of alpha leaking into the canonical theta band, as indexed by individual peak alpha frequency, remains unclear (Finnigan & Robertson, 2011). Therefore, understanding how resting canonical theta band power, canonical beta band power, theta-beta ratios calculated from canonical theta and beta band power, and individual peak alpha frequencies are cross-sectionally interrelated across the adult age-span is a key to beginning to understand how these EEG metrics may relate to healthy aging, particularly since the existing literature on theta-beta ratios in age relies on canonical power band definitions.

1.3 | Aperiodic and periodic neural activity

The association between traditional EEG metrics and healthy aging is further complicated by recent observations that frequency band measures of periodic activity are influenced by aperiodic activity present across all frequencies (Donoghue, Dominguez, & Voytek, 2020; Donoghue, Haller, et al., 2020; Keil et al., 2022; Voytek et al., 2015). In initial conceptualizations of aperiodic activity, steeper spectra were interpreted as indicating greater synchronization; flatter spectra were interpreted as indicating reduced synchronization (i.e., greater neural noise; Voytek & Knight, 2015). More recent data suggest that the slope of the EEG spectra is related to the ratio of excitatory to inhibitory neural activity, while the height of the spectra is related to neural spiking rates (Donoghue, Haller, et al., 2020; Waschke et al., 2021). Greater excitatory to inhibitory activity is reflected in flatter spectra (Gao et al., 2017), and greater spiking activity is reflected in greater overall spectral power (Manning et al., 2009; Miller et al., 2012). Aperiodic activity—in particular the slope of the spectra—has been associated with age, mediates cross-sectional associations between age and cognitive function (Voytek et al., 2015), and is associated with physiological markers of cognitive decline (Tran et al., 2020) and processing speed (Ouyang et al., 2020).

The impact of aperiodic activity on EEG metrics is particularly pronounced for theta-beta ratios. For example, the association between the exponent of aperiodic activity (i.e., the gradient of the spectra slope) and the theta-beta ratio has been found to be significantly stronger than the association between the periodic measures of both theta and beta (Donoghue, Dominguez, & Voytek, 2020). Beyond suggesting that measures of both theta and beta are severely confounded by aperiodic activity, the strong association between theta-beta ratios and aperiodic activity found in prior work implies that the individual differences in the theta-beta ratio may primarily reflect individual differences in excitatory to inhibitory neural activity (Donoghue, Dominguez, & Voytek, 2020). Furthermore, in the case of the lack of definable peaks within a given power band, it is ambiguous whether group or individual differences are due to changes in periodic power or instead the aperiodic component.

1.4 | The present study

Theta-beta ratios have been found to be negatively associated with age, such that larger ratios—indicating relatively greater theta power than beta power—are observed in samples of younger participants compared to older participants. However, child and young adult samples with restricted age ranges (e.g., children 3–9 years old in Perone et al., 2018; young adults 19–28 years old in Putman et al., 2010) that rely upon canonical band definitions, currently predominate the studies of age-related differences in theta-beta ratios. In the present study, we extend the research on fronto-central theta-beta ratios (calculated from canonical bands) by examining whether the negative association between age and

canonical fronto-central theta-beta ratios is observed in a large sample featuring a wide adult age range (from 36 to 84 years). Additionally, we examine to what extent any associations between canonical fronto-central theta-beta ratios and age are accounted for by age-related differences in fronto-central individual alpha peak frequency and in the fronto-central aperiodic (1/*f*-like) component of the neural power spectrum. Finally, we examine the unique associations between age and canonical fronto-central theta band power and canonical fronto-central beta band power individually and controlling for fronto-central individual alpha peak frequency and the fronto-central aperiodic component.

We conducted a partially preregistered[1] secondary analysis of data from the Midlife in the US Study's Neuroscience Project (see http://midus.wisc.edu/ and Ryff et al. 2021 for additional details), examining whether the correlation between canonical fronto-central theta-beta ratios and age is due to variation in associations between age and canonical fronto-central theta, age and canonical fronto-central beta, age-related decreases in individual peak alpha frequencies, or age-related flattening of the aperiodic component. Based on previous studies, we developed and tested two preregistered hypotheses. First, we tested whether the negative association between canonical fronto-central theta-beta ratios and age is replicated in a large sample of older adults ranging in age from 36 to 84 years old, hypothesizing that greater age will be associated with lower canonical fronto-central theta-beta ratios (Table 1, confirmatory hypothesis 1). Second, we used the RestingIAF package (https://github.com/corcorana/restingIAF; Corcoran et al., 2018) to test whether there would be a pattern of fronto-central alpha peak frequency "slowing" with age, predicting that older age would be associated with lower fronto-central individual alpha peak frequencies (Table 1, confirmatory hypothesis 2). We examined whether the association between canonical fronto-central theta-beta ratios and age was preserved when statistically adjusting for individual differences in fronto-central individual alpha peak frequencies, and examined if the relationships held controlling for gender and race.[2] We explored the relationship between the aperiodic 1/*f*-like component of the power spectrum and age, and if the association between canonical fronto-central theta-beta ratios and age was preserved when statistically adjusting for changes in the aperiodic component. Additionally, we examined if fronto-central individual alpha peak frequencies or fronto-central aperiodic component could mediate the relationship between canonical fronto-central theta-beta ratios and age. Finally, we examined the extent to which canonical fronto-central theta power and canonical fronto-central beta power are uniquely associated with age at time of recording (Table 1, additional hypothesis E1). Additional analyses are included in the supplemental materials to ensure the findings are not specific to analytical choices or specific EEG metric quantification methods described in the main manuscript.

Analyses and hypotheses regarding canonical fronto-central theta-beta ratio, fronto-central individual alpha peak frequency, and age (including the specific fronto-central ROI) were preregistered prior to the extraction of new EEG frequency metrics and their statistical analysis at https://osf.io/n57au. Additionally, the new EEG reprocessing pipeline for the extraction of canonical fronto-central theta power, canonical fronto-central beta power, and individual alpha peak frequencies was registered separately at https://osf.io/wfkmn. See Table 1 for a summary of the preregistration status of all analyses and exclusion criteria.

2 | METHOD

2.1 | Sensitivity power analysis

We used G*Power 3.1 (Faul et al., 2009) to conduct sensitivity power analysis prior to data processing for a sample of 300 participants as an estimate for the final usable sample size after applying our criteria for usable EEG data. This analysis indicated that we would have 95% power to detect a Pearson's correlation of 0.20, and 95% power to detect a small to medium sized effect in regression analyses ($f^2 = 0.06$).

2.2 | Participants

The present study used data collected during the second wave of Midlife in the US (MIDUS) in the Neuroscience Project (2004–2009), consisting of 331 participants from the main MIDUS cohort. These respondents included three distinct subsamples: the Main Longitudinal ($n = 135$), Twin ($n = 88$), and Milwaukee ($n = 108$) subsamples (see http://midus.wisc.edu/midus2/project5/ for additional details about sampling strategies within these subsamples). The Main Longitudinal and Twin subsamples

[1]All analyses regarding the aperiodic 1/*f*-like components were suggested by a reviewer and are therefore not included in the preregistration. Preregistered hypotheses and analyses regarding theta-beta ratios, individual alpha peak frequencies, and age are explicitly denoted, and outlined in Table 1.

[2]We did not explicitly register the exploratory analyses between canonical fronto-central theta-beta ratios and fronto-central individual alpha peak frequencies, nor did we explicitly register controlling for participant race.

TABLE 1 Summary of preregistration status of analyses (from https://osf.io/n57au) and exclusion criteria

Analysis	Preregistration status
Section 3.1: Pearson's pairwise correlations	*Preregistered*: Age with canonical fronto-central theta-beta ratio, with and without controlling for gender Age with RestingIAF defined fronto-central individual alpha peak frequencies, with and without controlling for gender *Post hoc, determined to be a useful additional analytic strategy*: Partial correlations controlling for gender and race Report all other additional pairwise correlation combinations and descriptive statistics *Post hoc, reviewer suggested*: Age with FOOOF defined fronto-central aperiodic exponent and offset Canonical fronto-central theta-beta ratio with FOOOF defined fronto-central aperiodic exponent and offset RestingIAF defined fronto-central individual alpha peak frequencies with FOOOF defined fronto-central aperiodic exponent and offset
Section 3.2: Partial correlations	*Implied in background of preregistration*: Due to author oversight, analyses regarding controlling for RestingIAF defined fronto-central individual alpha peak frequencies are implied in the preregistration introduction but not explicitly outlined *Post hoc, reviewer suggested*: Age with canonical fronto-central theta bet aeration, controlling separately for fronto-central aperiodic exponent and offset
Section 3.3: Mediational analyses	*Post hoc, determined to be a useful additional analytic strategy*: Relationship between age and canonical fronto-central theta-beta ratio mediated by RestingIAF defined fronto-central individual alpha peak, FOOOF defined aperiodic offset, and/or FOOOF defined aperiodic exponent
Section 3.4: Hierarchical regression analyses	*Preregistered*: Step 1 (canonical fronto-central theta and canonical fronto-central beta regressed on age) and Step 2 (RestingIAF defined fronto-central individual peak alpha added) *Post hoc, reviewer suggested*: Step 3 (FOOOF defined aperiodic exponent)
Supplemental material, S2: General estimating equation analysis	*Preregistered*: GEE analyses repeating main correlational analyses, controlling for genetic dependencies within family
Supplemental material, S3: Explore nonlinear age and theta-beta ratio relationships	*Preregistered*: Quadradic regression of canonical fronto-central theta-beta ratio with age
Supplemental material, sections S4-S10	*Post hoc, reviewer suggested*: Repeat analyses on eyes closed only, with different theta-beta ratio and individual alpha peak specification methods
Preregistered exclusion criteria (reproduced from https://osf.io/n57au and https://osf.io/wfkmn) 1. 50% epochs retained for spectral power density metrics 2. 50% of channels resulting in definable alpha peaks	
Post hoc exclusion criteria 1. Poor FOOOF model fit, defined as less than three standard deviations below the mean in R^2 model fit for the fronto-central composite	

contained individuals who participated in the initial wave of MIDUS data collection approximately 10 years prior. The Milwaukee subsample contained individuals who participated in the baseline MIDUS Milwaukee study initiated in 2005. Demographic information is presented in Table 2.

All data collection procedures were approved by the UW-Madison Institutional Review Board, and informed consent was obtained for all participants. Participants with unusable resting spectral power EEG data ($n = 12$, 3.6%), without identifiable alpha peak frequencies ($n = 48$, 14.5%), and/or without adequate FOOOF model fit ($n = 9$,

TABLE 2 Sample demographics

	Sufficient EEG data ($n = 268$)	Insufficient definable fronto-central individual alpha peaks ($n = 48$)	Insufficient epochs for spectral power ($n = 12$)	Poor fronto-central FOOOF algorithm fit ($n = 9$)
Age in years (*SD*)	55.8 (11.0) range = 36–84	52.5 (11.6) range = 38–82	58.8 (11.7) range = 44–81	59.8 (13.6) range = 40–82
Gender				
Male	122	18	7	4
Female	146	30	5	5
Race/Ethnicity				
White	172	33	6	5
Black	86	12	6	3
Hispanic/Black	4	–	–	–
Hispanic/White	1	–	–	–
Asian	2	–	–	–
Other	3	1	–	1
Handedness				
Right	252	43	10	9
Left	16	5	2	–
MIDUS Subsample				
Main	107	22	5	5
Twin	71	14	3	1
Milwaukee	90	12	4	3

Note: The sample sizes for each data quality exclusion criteria do not sum to the total $n = 331$ because six participants had both poor FOOOF algorithm fit at fronto-central sites and insufficient definable fronto-central individual alpha peaks.

2.7%) were excluded from analyses, yielding a final sample of $n = 268$ participants.[3]

2.3 | Materials

2.3.1 | Demographics

Demographic variables are publicly available via Colectica (http://midus.colectica.org/) and the Inter-university Consortium for Political and Social Research (ICPSR; https://www.icpsr.umich.edu/web/ICPSR/series/203). From the MIDUS 2 Neuroscience Project data set, we used age at time of EEG data collection, gender, race (dichotomized as White/Black, Indigenous, and People of Color [BIPOC] for analyses), and Family ID. Family ID was used to account for genetic dependencies in follow-up analyses in the supplemental materials. See Table 2 for a breakdown of demographics.[4]

2.4 | Procedure

2.4.1 | EEG recording

EEG data were collected using a 128 channel geodesic net of Ag/AgCl electrodes in the GSN200 montage (see preprocessing preregistration figure, https://osf.io/wfkmn; Electrical Geodesics, Inc, 2007) encased in saline dampened sponges (Electrical Geodesics, Inc [EGI], Eugene, OR) with impedances reduced to less than 100 KΩ while ensuring that electrolyte "bridges" (see Greischar et al., 2004) had not formed. After the net was placed, participants were escorted into a soundproof booth where

[3]The list-wise exclusion of participants failing to meet criteria for the number of epochs and identifiable fronto-central alpha peak frequency were specified in the preregistration. The list-wise exclusion of participants with poor fronto-central FOOOF model fit metrics were decided after preregistration in response to reviewer suggested additional analyses. See Table 1 for additional details on preregistered and post hoc exclusion criteria. Analysis without any FOOOF model fit exclusions are presented in the supplemental materials and do not change the pattern of results.

[4]Additionally, a histogram of age is available in the supplemental materials.

they were seated in front of a computer screen. A computer located outside the booth recorded the data. Signals were amplified and sampled at 500 Hz with an online bandpass filter from 0.1 to 100 Hz at 16-bit precision using an online vertex (Cz) reference. The participant was instructed to rest for six 1-min periods. During three of the 1-minute periods they were asked to keep their eyes open; for the remaining three 1-min periods they were asked to keep their eyes closed. The order of the eyes open/eyes closed was pseudorandomized, with two fixed orders counterbalanced across participants. Participants then completed an emotional picture viewing task (data not presented here), followed by another baseline resting recording for six 1-min periods. Prior data processing was restricted to alpha asymmetry variables from the first baseline recording, collapsed across the entire 6-minute period (e.g., Hostinar et al., 2017). The current analyses focus on metrics extracted from this first resting recording, collapsed across eyes open, and eyes closed periods. Additional analyses examining eyes closed only epochs are available in the supplemental material and do not change the interpretations of the analyses. Raw continuous data as well as the summary metrics described below in sections 2.5.2, 2.5.3, and 2.5.4 are available upon request. See https://osf.io/fxgnt/ for information about how to access the data used in the following analyses.

2.5 | Data reduction

2.5.1 | EEG preprocessing

Offline the EEG data were filtered (60 Hz notch, 0.5 Hz high-pass), bad channels identified and removed, and bad sections of data identified and removed. EEGLab6 was originally used to conduct a PCA/ICA to identify 20 components (such that PCA was first applied for the reduction constrained to 20 components, followed by an ICA for the differentiation of components), which were visually inspected to identify components to remove obvious blink, eye movement, and other artifacts. No further PCA or ICA dimension reduction was conducted after artifactual components were removed. Bad channels were replaced using a spherical spline interpolation. These are the original preprocessing steps from the initial alpha asymmetry pipeline that were preserved in the reprocessing pipeline, detailed in Ryff et al. (2021). Data from the eyes open and eyes closed conditions were collapsed.[5] The fronto-central ROI was preregistered to comprise of the average composite of the F3/Fz/F4 analog channels.[6]

2.5.2 | Spectral power for canonical fronto-central theta-beta ratio

Data processing for spectral power for canonical fronto-central theta-beta ratios was completed using EEGLab 2019.1 scripts implemented in MATLab 2019b. Data were re-referenced to the average reference and Cz was imputed. Continuous resting data were epoched into 2 s segments with 50% overlap, and bad segments were rejected if there was a voltage deviation on any channel of ±100 μV. As preregistered, participants with more than 50% of the total number of epochs rejected were excluded from analyses in a list-wise fashion ($n = 12$). EEG spectral power at each predefined canonical spectral band (theta: 4–7 Hz; beta: 13–30 Hz) was extracted using a 2 s Hamming window padded by a factor of 2 with 50% overlap. Spectral power was extracted individually for each channel, then averaged over the fronto-central composite ROI and were transformed to a theta-beta ratio by dividing the former by the latter and subsequently log-normalized.[7]

2.5.3 | EEG reprocessing: Individual alpha peak frequency

Fronto-central individual alpha peak frequency from the initial baseline recording was extracted using the RestingIAF package (https://github.com/corcorana/restingIAF; Corcoran et al., 2018), using adjustments to the parameters based on our sample of older adults as recommended by Corcoran et al. (2018). The RestingIAF package algorithmically identifies the peak activity within the alpha band using the Savitzky–Golay filter (SGF), a nonparametric curve fitting technique, whereby the PSD estimates are smoothed using the SGF before estimating the first and second order derivatives. These derivatives are then used to identify a spectral peak, and the first

[5]Alternative analyses on just the eyes closed conditions are available in the supplemental materials and do not change interpretations.

[6]As shown in the reprocessing pipeline registration (https://osf.io/wfkmn), the fronto-central composite of F3/Fz/F4 was comprised of the EGI GSN200 electrode montage (Electrical Geodesics, Inc, 2007) sensors 12, 20, 21, 25, 29 (comprising the analog for F3), sensors 4, 5, 118, 119, 124 (comprising the analog for F4), and sensor 11 (comprising the analog for Fz), and was selected based on existing theta-beta ratio literature. See Keil et al. (2022) for a discussion of the importance of preregistering ROIs in frequency-based EEG analyses.

[7]Alternative analyses using individually defined theta and beta bands based on individual alpha peak frequency to create the theta-beta ratio are available in the supplemental materials and do not change interpretations.

derivative is additionally used to identify the individual alpha band windows based upon where the "shoulders" of the alpha peak are located (see Corcoran et al., 2018 for additional information). We used a 2 s Hamming window with 50% overlap, as well as the following RestingIAF algorithm settings: $F_w = 11$ (SGF frame width, with larger numbers indicating more smoothing, results in a frequency span of ~2.69 Hz); $k = 4$ (SGF polynomial degree, higher values result in less smoothing and less peak height attenuation); $W_\alpha = [6, 14\,\text{Hz}]$ (the frequency domain within which evidence for peak activity was searched); fRange = [1, 40 Hz] (range of frequencies used to fit the algorithm), mpow = 0.6 (the minimum power value a local maximum needed to exceed to qualify as a peak candidate), $pDiff = 0.20$ (the minimum proportion of peak height by which the highest peak candidate had to exceed other peaks within the search window W_α to be assigned as the alpha peak frequency), $cMin = 3$ (minimum number of channel estimates necessary for returning results). Estimates were extracted individually for each channel, then averaged over the fronto-central composite ROI. As preregistered, individuals who did not exhibit a definable fronto-central individual alpha peak value in 50% of the sensors used for the composites or 50% of the overall scalp were excluded from analyses in a list-wise fashion ($n = 55$). Fronto-central individual alpha peak frequency for the current study was quantified as the average composite of the F3/Fz/F4 analog channels to assess the impact of age-related differences in individual peak alpha at fronto-central sites on canonical theta-beta ratio measured at the same fronto-central sites.

2.5.4 | Modeling periodic and aperiodic power spectrum components

Spectral power density was extracted individually for each channel using a 2 s Hamming window padded by a factor of 2 with 50% overlap using EEGLab 2019.1 scripts implemented in MATLab 2019b from 0 to 250 Hz in 0.25 Hz increments for all sensors then analyzed using FOOOF 1.0.0 (Donoghue, Haller, et al., 2020; https://fooof-tools.github.io/) in Python (version 3.9) to fit aperiodic and periodic components from 2 to 40 Hz.

FOOOF algorithmically fits a model to estimate both the aperiodic (1/*f*-like) component of EEG spectral power density as well as overlying periodic oscillatory "peaks", by first fitting an aperiodic component (modeled after a Lorentzian function) with a specific offset value (corresponding to the y-intercept of the aperiodic component) and exponent (corresponding to the "flatness" of the 1/*f* curve, equivalent to the sign-flipped slope of a linear fit in log–log space), which is then regressed out of the PSD, leaving behind periodic peaks. These peaks are then iteratively modeled by fitting a Gaussian around the central frequency of each peak, until the maximum number of peaks fit is reached or no more peaks meeting the algorithm's criteria are available (see Donoghue, Haller, et al., 2020 for additional details). Periodic and aperiodic components were estimated from the PSD ranging from 2 to 40 Hz, without a knee, with peaks limited in width from 1–6 Hz, a minimum peak height of 0.05, a relative peak threshold of 1.5 standard deviations, and a maximum number of six peaks fit. The resulting models were defined as having poor fit if they were less than three standard deviations below the mean in R^2 model fit for the fronto-central composite, resulting in $n = 9$ failing to meet the $R^2 = 0.862$ threshold and were excluded in a list-wise fashion. Finally, the aperiodic offset and exponent values for the frontal F3/Fz/F4 composite were extracted. Details regarding additional alternative EEG metrics are discussed in the supplemental materials.[8]

3 | RESULTS

As our preregistered analyses focused on metrics extracted from the resting data collapsed across eyes open and eyes closed periods, we report all analyses below on metrics extracted from the combined recordings. Parallel analyses were conducted on alternative EEG metrics are reported in the supplemental materials (see Supplemental Materials section S3). Overall, the pattern of results remained the same regardless of the choice of EEG metric quantification (e.g., canonical and individual band power, metrics extracted from eyes closed only data, etc.). All statistical analyses were performed in R (version 4.1.2). RMarkdown scripts and output for all analyses reported below and in the supplemental materials are available at https://osf.io/hdrax/. See Table 1 for a breakdown of which analyses were preregistered. We first report pairwise correlational analyses, including our two preregistered analyses regarding our hypotheses that: (1) resting canonical fronto-central theta-beta ratios will be inversely associated with age, and (2) fronto-central individual alpha peak frequencies will be inversely associated with age. Next, we report

[8]As detailed in the supplemental materials, use of the FOOOF defined individual alpha peak frequency instead of the RestingIAF defined individual alpha peak frequency did not change the analyses. Additionally, it was not possible to create a metric of aperiodic adjusted canonical theta-beta ratio using FOOOF defined aperiodic adjusted canonical fronto-central theta power and aperiodic adjusted canonical fronto-central beta power, as only $n = 42$ participants had a definable aperiodic adjusted canonical fronto-central theta peak. This results in a severe floor effect, with $n = 229$ participants with a FOOOF-derived aperiodic adjusted canonical fronto-central theta-beta ratio of zero.

our exploratory analyses examining partial correlations between canonical fronto-central theta-beta ratio and age controlling for fronto-central individual alpha peak frequency and the fronto-central aperiodic $1/f$ component. Then, we explore the extent to which fronto-central individual alpha peak frequencies and the fronto-central aperiodic component metrics mediate the relationship between canonical fronto-central theta-beta ratio and age. Finally, we explore the unique associations between canonical fronto-central theta and canonical fronto-central beta with age, with and without controlling for fronto-central individual alpha peak frequencies and the fronto-central aperiodic exponent. We report false discovery rate (FDR) corrected p values for pairwise and partial correlations, because FDR corrections have been shown to have increased power over other correction methods, particularly in cases with many comparisons and when the number of non-null hypotheses increase (Benjamini & Hochberg, 1995). Given the expectation that EEG metrics would be significantly intercorrelated, we opted for FDR to preserve as much statistical power as was feasible while controlling for false discoveries.

3.1 | Pairwise Pearson's correlation analyses

Our first confirmatory hypothesis was initially tested using Pearson's correlations between log-normalized theta-beta ratios and age. As shown in Table 3 and in Figure 1, resting canonical fronto-central theta-beta ratios were negatively correlated with age ($r = -0.24$, 95% CI [−0.35, −0.12], $p_{uncorrected} < 0.001$, $p_{fdr} < 0.001$), such that the ratio of slow-wave to fast-wave activity was lower for older participants. Consistent with our second confirmatory hypothesis, as well as consistent with a prior unpublished analysis of this data set and previous independent studies in adults (Clark et al., 2004; Klimesch, 1999), we also observed a significant negative correlation between individual alpha peak frequency and age ($r = -0.17$, 95% CI [−0.28, −0.05], $p_{uncorrected} = 0.006$, $p_{fdr} = 0.008$), such that fronto-central peak alpha frequencies were lower in older participants (Table 2, Figure 1). Additionally, consistent with prior work (Voytek et al., 2015), the fronto-central aperiodic exponent was negatively correlated with age ($r = -0.24$, 95% CI [−0.35, −0.13], $p_{uncorrected} < 0.001$, $p_{fdr} < 0.001$), consistent with a "flattening" of the aperiodic component with age. Finally, we replicated prior work (Donoghue, Dominguez, & Voytek, 2020) by finding that canonical fronto-central theta-beta ratio is more strongly correlated with the fronto-central aperiodic exponent ($r = 0.71$, 95% CI [0.64, 0.76], $p_{uncorrected} < 0.001$, $p_{fdr} < 0.001$) than with canonical fronto-central beta ($r = -0.28$, 95% CI [−0.38, −0.16], $p_{uncorrected} < 0.001$, $p_{fdr} < .001$), *Fisher's z* = 6.90, $p < .001$, or canonical fronto-central theta ($r = 0.50$, 95% CI [0.41, 0.59], $p_{uncorrected} < 0.001$, $p_{fdr} < 0.001$), *Fisher's z* = 3.89, $p < 0.001$, suggesting that canonical theta-beta ratios are highly confounded with the aperiodic exponent.

Generalized Estimating Equations (GEE) confirmed these relationships held when adjusting for genetic dependencies between twin and sibling participants in the sample ($n_{\text{twin/sibling}} = 71$; Supplemental Table S6 for details of the GEE analyses). We also examined the partial correlations controlling for gender and race, and still observed a significant negative correlation between age and canonical fronto-central theta-beta ratio ($r = -0.23$, 95% CI [−0.34, −0.11], $p_{uncorrected} < 0.001$, $p_{fdr} < 0.001$), a significant negative correlation between age and fronto-central individual alpha peak frequency ($r = -0.18$, 95% CI [−0.30, −0.06], $p_{uncorrected} = 0.003$, $p_{fdr} = 0.003$), and a significant negative correlation between age and fronto-central aperiodic exponent ($r = -0.23$, 95% CI [−0.34, −0.11], $p_{uncorrected} < 0.001$, $p_{fdr} < 0.001$), while the relationship between age and fronto-central aperiodic exponent remained nonsignificant ($r = -0.09$, 95% CI [−0.21, 0.03], $p_{uncorrected} = 0.155$, $p_{fdr} < 0.181$).

3.2 | Partial correlation analyses

Next, we examined the partial correlations between age and canonical fronto-central theta-beta ratio, controlling separately for fronto-central individual alpha peak, fronto-central aperiodic offset, and fronto-central aperiodic exponent. As shown in Table 4 and Figure 2, the partial correlation between canonical fronto-central theta-beta ratio and age becomes nonsignificant only when controlling for the fronto-central aperiodic exponent, $r_{partial} = -0.10$, 95% CI [−0.21, 0.02], $p_{uncorrected} = .110$, $p_{fdr} = 0.110$. This suggests that in adults, the flattening of the aperiodic curve with age, as denoted by the aperiodic exponent, may be largely driving the relationship between canonical theta-beta ratio and age.

3.3 | Mediational analyses

To further understand the relationship between age and canonical fronto-central theta-beta ratio, we conducted a series of exploratory mediational analyses to see if fronto-central individual alpha peak frequency, fronto-central aperiodic offset, or fronto-central aperiodic exponent would fully mediate the relationship between age

TABLE 3 Correlations and descriptive statistics between age and EEG metrics, collapsed across eyes open and eyes closed ($n = 268$)

	Mean (SD)	1. Age	2. Fronto-Central Theta	3. Canonical Fronto-Central Beta	4. Canonical Fronto-Central Theta-Beta Ratio	5. Fronto-Central Individual Alpha Peak Frequency	6. Fronto-Central Aperiodic Exponent
1. Age	55.8 (11.0)	—					
2. Canonical Fronto-Central Theta	0.77 (1.17)	0.01 [−0.11, 0.13] $p_{uncorr} = .849$ $p_{fdr} = .892$	—				
3. Canonical Fronto-Central Beta	0.22 (0.17)	0.23 [0.11, 0.34] $p_{uncorr} < .001$ $p_{fdr} < .001$	0.42 [0.32, 0.52] $p_{uncorr} < .001$ $p_{fdr} < .001$	—			
4. Canonical Fronto-Central Theta-Beta Ratio	1.09 (0.68)	−0.24 [−0.35, −0.12] $p_{uncorr} < .001$ $p_{fdr} < .001$	0.50 [0.41, 0.59] $p_{uncorr} < .001$ $p_{fdr} < .001$	−0.28 [−0.38, −0.16] $p_{uncorr} < .001$ $p_{fdr} < .001$	—		
5. Fronto-Central Individual Alpha Peak Frequency	9.31 (0.98)	−0.17 [−0.28, −0.05] $p_{uncorr} = .006$ $p_{fdr} = .008$	−0.38 [−0.48, −0.27] $p_{uncorr} < .001$ $p_{fdr} < .001$	−0.07 [−0.19, 0.05] $p_{uncorr} = .257$ $p_{fdr} = .284$	−0.42 [−0.51, −0.31] $p_{uncorr} < .001$ $p_{fdr} < .001$	—	
6. Fronto-Central Aperiodic Exponent	1.23 (0.26)	−0.24 [−0.35, −0.13] $p_{uncorr} < .001$ $p_{fdr} < .001$	0.44 [0.34, 0.53] $p_{uncorr} < .001$ $p_{fdr} < .001$	0.0008 [−0.12, 0.12] $p_{uncorr} = .893$ $p_{fdr} = .893$	0.71 [0.64, 0.76] $p_{uncorr} < .001$ $p_{fdr} < .001$	−0.25 [−0.36, −0.14] $p_{uncorr} < .001$ $p_{fdr} < .001$	—
7. Fronto-Central Aperiodic Offset	0.43 (0.44)	−0.11 [−0.23, 0.01] $p_{uncorr} = .071$ $p_{fdr} = .083$	0.65 [0.58, 0.72] $p_{uncorr} < .001$ $p_{fdr} < .001$	0.48 [0.38, 0.57] $p_{uncorr} < .001$ $p_{fdr} < .001$	0.54 [0.45, 0.62] $p_{uncorr} < .001$ $p_{fdr} < .001$	−0.30 [−0.40, −0.19] $p_{uncorr} < .001$ $p_{fdr} < .001$	0.75 [0.70, 0.80] $p_{uncorr} < .001$ $p_{fdr} < .001$

Note: 95% confidence intervals for pairwise correlations displayed in brackets followed by uncorrected and FDR corrected p values.

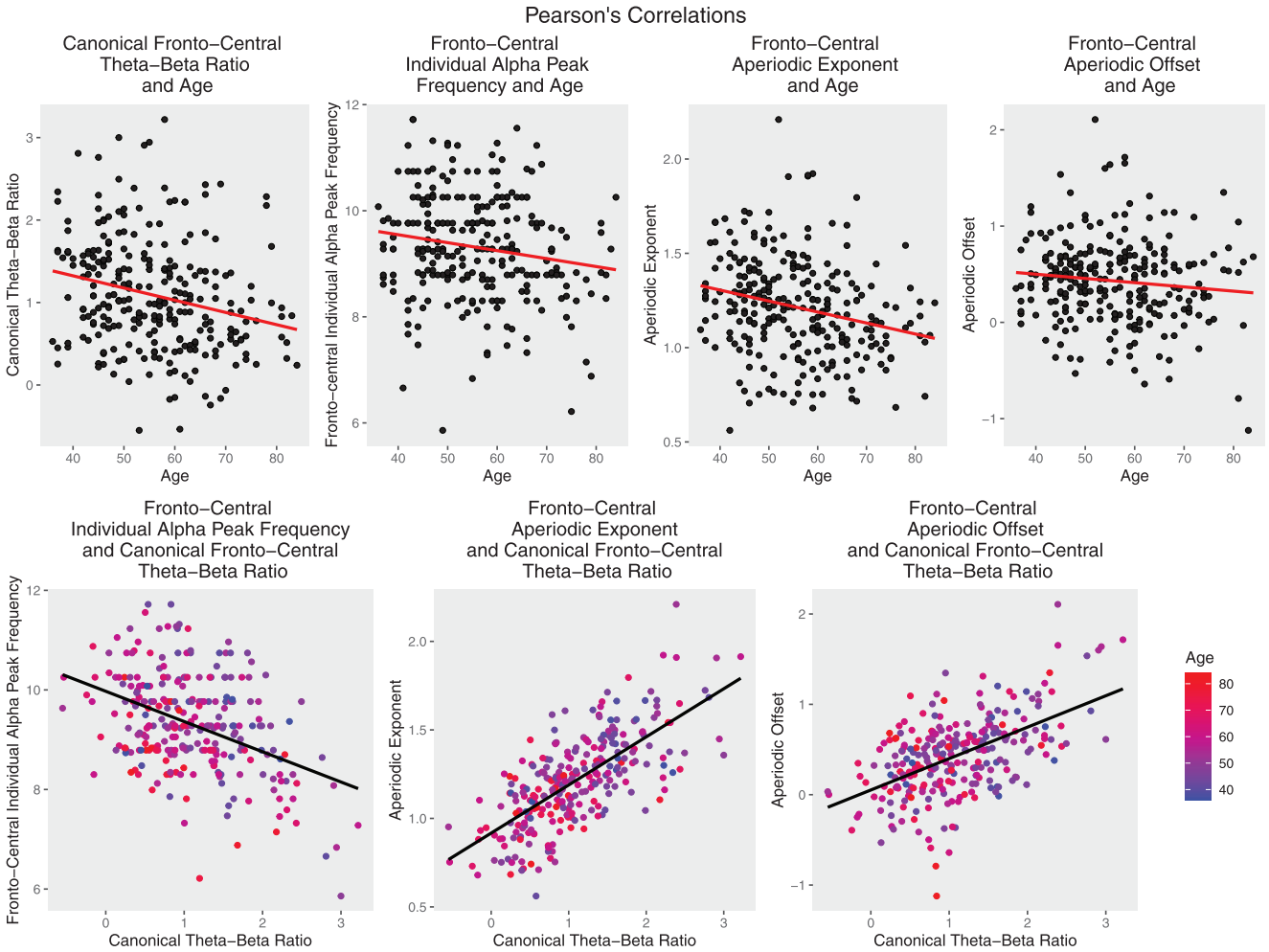

FIGURE 1 Pearson's correlation scatterplots between EEG metrics and age.

and canonical fronto-central theta-beta ratio. Mediation analyses were conducted using the processR package in R (Moon, 2021), with maximum likelihood estimation and 10,000 bootstrap estimates of standard error. See Figure 3.

As shown in Table 5, only the fronto-central aperiodic exponent fully mediated the relationship between age and canonical fronto-central theta-beta ratio, such that the direct effect (c') between age and canonical fronto-central theta-beta ratio was nonsignificant ($c' = -0.004$, 95% CI [−0.010, 0.001], $p = .121$). This suggests that the relationship between canonical fronto-central theta-beta ratio and age is driven primarily by the aperiodic exponent, not periodic activity in the canonical theta or beta band, and not from alpha power "leaking" into the canonical theta band as the individual alpha peak frequency shifts into lower frequencies with age.

3.4 | Hierarchical regression analyses

Taken together, the correlational and mediational analyses suggest that the relationship between canonical fronto-central theta-beta ratio and age in older adults is due to the underlying aperiodic exponent, not periodic activity in the canonical theta and beta bands or leakage of alpha into the canonical theta band with age. However, we wanted to determine the extent to which canonical theta and beta have unique associations with age, if any, apart from the theta-beta ratio. Therefore, we conducted a hierarchical regression, regressing age on canonical theta and beta, adding individual alpha peak frequency in the second block and adding the aperiodic exponent in the third block. The first two blocks of the analysis were preregistered as exploratory analysis E1 in the preregistration (https://osf.io/n57au), and the third block was added as an exploratory step to include the aperiodic component. Because controlling for aperiodic offset did not substantially change the relationship between canonical theta-beta ratio and age or mediate the relationship between age and canonical theta-beta ratio, and because the aperiodic exponent and offset are highly intercorrelated ($r = 0.75$, 95% CI [0.70, 0.80], $p_{uncorr} < 0.001$ $p_{fdr} < 0.001$), we conducted the stepwise

TABLE 4 Partial correlations between age and canonical EEG metrics, controlling for fronto-central individual alpha peak frequency, fronto-central aperiodic exponent, or fronto-central aperiodic offset, collapsed across eyes open and eyes closed ($n = 268$)

	Pairwise Pearson's correlation	Partial correlation controlling for fronto-central individual alpha frequency	Partial correlation controlling for fronto-central aperiodic exponent	Partial correlation controlling for fronto-central aperiodic offset
Canonical fronto-central theta-beta ratio and age	−0.24 [−0.35, −0.12] $p_{uncorr} < .001$ $p_{fdr} < .001$	−0.35 [−0.45, −0.24] $p_{uncorr} < .001$ $p_{fdr} < .001$	−0.10 [−0.22, 0.02] $p_{uncorr} = .110$ $p_{fdr} = .110$	−0.22 [−0.33, −0.10] $p_{uncorr} < .001$ $p_{fdr} < .001$
Canonical fronto-central theta and age	0.01 [−0.11, 0.13] $p_{uncorr} = .849$ $p_{fdr} = .892$	−0.06 [−0.18, 0.06] $p_{uncorr} = .356$ $p_{fdr} = .356$	0.14 [0.02, 0.25] $p_{uncorr} = .025$ $p_{fdr} = .030$	0.11 [−0.01, 0.23] $p_{uncorr} = .070$ $p_{fdr} = .070$
Canonical fronto-central beta and age	0.23 [0.11, 0.34] $p_{uncorr} < .001$ $p_{fdr} < .001$	0.22 [0.11, 0.33] $p_{uncorr} < .001$ $p_{fdr} < .001$	0.23 [0.12, 0.34] $p_{uncorr} < .001$ $p_{fdr} < .001$	0.32 [0.21, 0.43] $p_{uncorr} < .001$ $p_{fdr} < .001$

Note: 95% confidence intervals for pairwise correlations displayed in brackets followed by uncorrected *p*-values.

analyses with only the aperiodic exponent to avoid issues of multicollinearity.

As shown in Table 6, in Block 2 canonical fronto-central theta was significantly associated with age when controlling for fronto-central individual alpha peak frequency, $b = -1.86$, $t(264) = 2.84$, $p = .005$. However, canonical fronto-central theta was nonsignificantly associated with age when controlling for the fronto-central aperiodic exponent in block 3, $b = -0.53$, $t(264) = 0.75$, $p = .456$. In Block 3, there were significant relationships between canonical fronto-central beta and age, $b = 14.75$, $t(264) = 3.65$, $p < .001$, fronto-central individual alpha peak and age, $b = -2.71$, $t(264) = 3.96$, $p < .001$, and the fronto-central aperiodic exponent and age, $b = -11.80$, $t(264) = 4.32$, $p < .001$, suggesting that there is a significant increase in periodic activity in the canonical beta band with age, as well as the age-related flattening of the aperiodic component and "slowing" of the individual alpha peak frequency. The lack of unique variance associated with canonical theta power over and above the aperiodic component is consistent with the lack of definable peaks (with the FOOOF package) within the canonical theta band, as described in the supplemental materials.

4 | DISCUSSION

In the preregistered portion of the current study, we aimed to replicate and extend previous observations that canonical fronto-central theta-beta ratios and fronto-central individual alpha peak frequency are associated with age in a large sample of 268 adults featuring a wide age range (36–84 years). Consistent with preregistered predictions and previous studies, we found that both canonical fronto-central theta-beta ratios and fronto-central individual alpha peak frequencies were negatively correlated with age. Exploratory analyses indicated that the association between canonical fronto-central theta-beta ratios and age remained when controlling for fronto-central individual alpha peak frequencies, demonstrating that age-related decreases in canonical fronto-central theta-beta ratios are not due to age-related decreases in fronto-central individual alpha peak frequencies. Instead, the relationship between canonical fronto-central theta-beta ratios and age were reduced when controlling for the fronto-central aperiodic exponent. Additionally, mediation analyses found that only the fronto-central aperiodic exponent fully mediated the relationship between age and canonical fronto-central theta-beta ratios. Furthermore, this effect appears to be robust against multiple ways of defining theta-beta ratios and individual alpha peaks, and consistent across eyes closed only recordings, as described in the supplemental materials.

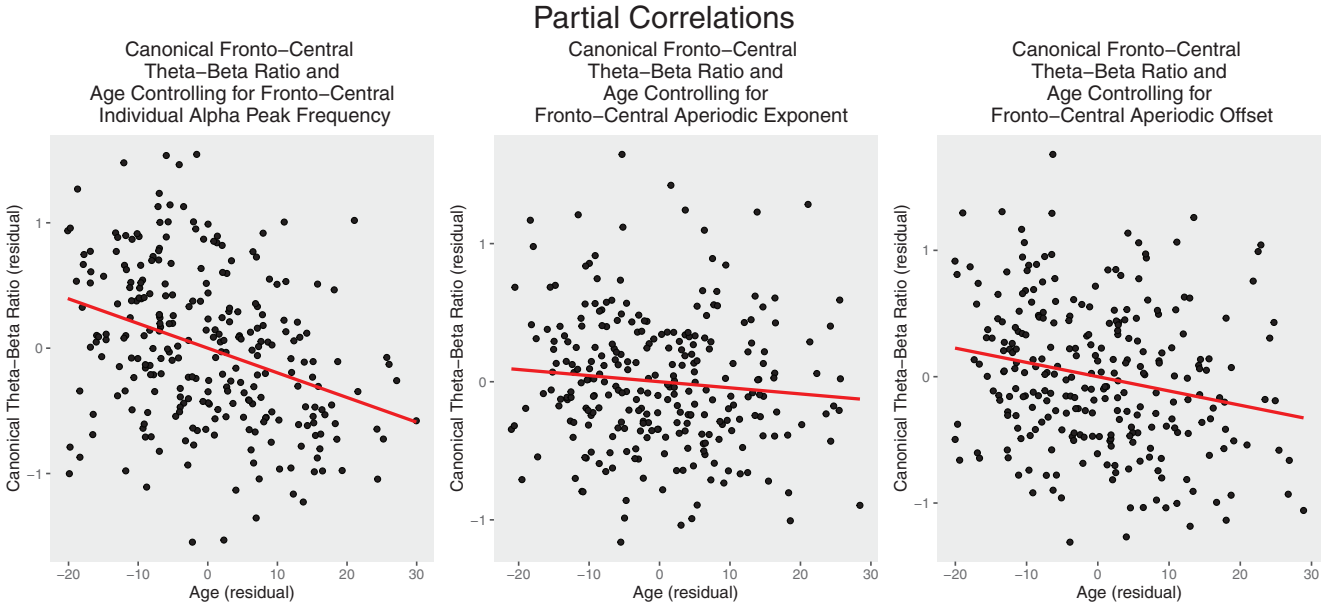

FIGURE 2 Partial correlation scatterplot between canonical fronto-central theta-beta ratio and age.

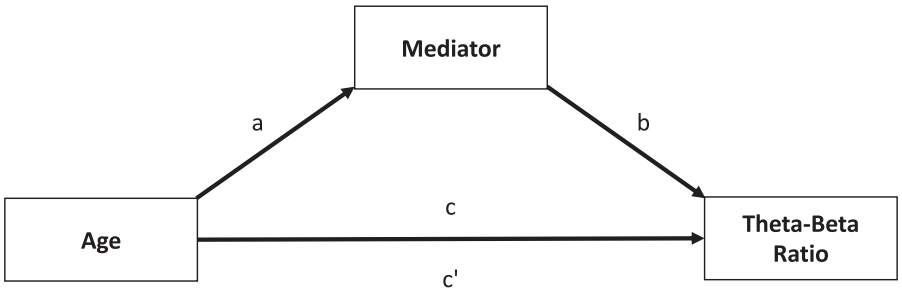

FIGURE 3 Diagram of mediation analyses. The total effect is *c*, and is the relationship between age and canonical fronto-central theta-beta ratio without any mediator. The indirect effect is the path *ab*, and the direct effect *c′* is the remaining relationship between age and canonical fronto-central theta-beta ratio after accounting for the indirect effect of the mediator.

4.1 | Understanding how aperiodic components, canonical theta-beta ratios and individual alpha peak frequencies change over the lifespan

Our results also reveal a complex pattern of associations between canonical fronto-central theta-beta ratios, fronto-central individual alpha peak frequency, fronto-central aperiodic activity, and age. Consistent with previous studies (Voytek et al., 2015), we observed that the aperiodic exponent was negatively associated with age, suggesting relatively synchronized aperiodic firing in younger versus older adults. However, the age-related differences in aperiodic offset reported by prior research (Voytek et al., 2015) were not significant in our sample ($p_{uncorr} = 0.071$, $p_{fdr} = 0.083$). We observed that the age-related differences in the aperiodic exponent are preserved into older adulthood, and are not limited only to the younger (e.g., <44 years of age) populations reported on in previous studies (Donoghue, Dominguez, & Voytek, 2020), or the relatively small samples used in others (Voytek et al., 2015). We also observed that the association between age and canonical fronto-central theta-beta ratios is reduced when statistically adjusting for the fronto-central aperiodic exponent, consistent with the observation that individual differences in ratio metrics are likely confounded with individual differences in aperiodic activity, especially when there is no clear peak within the particular power band. Critically, the association between age and canonical fronto-central theta-beta ratio is fully mediated by the fronto-central aperiodic exponent.

4.2 | Limitations of the current study

The current study has some methodological limitations, particularly regarding the preregistered decision

TABLE 5 Mediation analyses examining the relationship between canonical fronto-central theta-beta ratio and age, collapsed across eyes open and eyes closed ($n = 268$)

	Mediator											
	Fronto-central Individual Alpha Peak Frequency				Fronto-central Aperiodic Offset				Fronto-central Aperiodic Exponent			
	Est	SE	95% CI	*p*-value	Est	SE	95% CI	*p*-value	Est	SE	95% CI	*p*-value
a (age to mediator)	−0.015	0.005	[−0.026, −0.005]	0.006	−0.004	0.003	[−0.010, 0.001]	0.092	−0.006	0.001	[−0.008, −0.003]	< .001
b (mediator to canonical fronto-central theta-beta ratio)	−0.324	0.039	[−0.398, −0.244]	< .001	0.801	0.09	[0.152, 0.232	< .001	1.787	0.111	[1.576, 2.013]	< .001
ab (indirect effect)	0.005	0.002	[0.002, 0.009]	0.009	−0.004	0.002	[−0.008, < 0.001]	0.081	−0.01	0.002	[−0.015, −0.006]	< .001
c (total effect)	−0.015	0.003	[−0.021, −0.008]	< .001	−0.015	0.003	[−0.021, −0.008]	< .001	−0.015	0.003	[−0.021, −0.008]	< .001
c' (direct effect)	−0.019	0.003	[−0.021, −0.008]	< .001	−0.011	0.003	[−0.021, −0.008]	0.001	−0.004	0.003	[−0.010, 0.001]	0.121
Proportion Mediated (indirect/total)	−0.328	0.226	[−0.922, −0.084]	0.147	0.238	0.144	[−0.024, 0.548]	0.1	0.702	0.178	[0.458, 1.126]	< .001

to examine the data combined across eyes open and eyes closed periods and calculate individual alpha peak frequency from fronto-central ROI. Combining eyes open and eyes closed data results in unequal number of epochs between the two conditions. Additionally, alpha power is known to be strongest during eyes closed recordings from posterior sites, which may have impeded our ability to detect individual alpha peak frequency. However, additional analyses reported in the supplemental materials on only the eyes closed data, as well as from individual alpha peak frequency calculated from across all sensors, neither substantially increased the number of RestingIAF package definable peaks, nor changed the interpretation of the analyses. Using the FOOOF package to define individual alpha peak frequency did increase the number of definable individual alpha peaks to $n = 302$, but the results do not change with this alternative method of defining individual alpha peaks (see Supplemental Materials for full details). Additionally, the decision to use visual artifactual screening makes the preprocessing stream non-reproducible without getting a list of artifactual components. However, we decided to keep the original data preprocessing pipeline from the initial MIDUS 2 EEG data release the same to increase consistency with the publicly available MIDUS 2 alpha asymmetry metrics (http://midus.colectica.org/; https://www.icpsr.umich.edu/web/ICPSR/series/203). The current study is also limited by examining these relationships cross-sectionally across age. Additional longitudinal work is needed to tease apart the unique developmental trajectories of theta-beta ratio and individual peak alpha frequency.

4.3 | Implications for fronto-central aperiodic activity, canonical fronto-central theta-beta ratio, and fronto-central individual alpha peak frequency as markers of executive function and healthy aging

Taken together, our findings complicate the interpretation of fronto-central theta-beta ratio as a marker of executive function. In adolescents and young adults, higher theta-beta ratios are associated with more executive dysfunction and related to ADHD (Arns et al., 2013), and lower theta-beta ratios are associated with better attentional control (Perone et al., 2018). Considering older age-related decline in executive function (Buckner, 2004; Lustig & Jantz, 2015), fronto-central theta-beta ratios may exhibit a curvilinear relationship with executive functioning, such that better executive functioning is related to a moderate level of fronto-central theta-beta ratio. Additionally, it may be that adolescence and younger adults are more

TABLE 6 Hierarchical multiple regression, regressing age on canonical theta, canonical beta, individual alpha peak frequency, and aperiodic exponent

	b	SE	t	p	Adj. R^2
Block 1					0.055
Canonical Fronto-central Theta	−0.98	0.62	1.58	0.11	
Canonical Fronto-central Beta	17.23	4.13	4.17	< .001	
Block 2					0.093
Canonical Fronto-central Theta	−1.86	0.66	2.84	0.005	
Canonical Fronto-central Beta	18.76	4.07	4.61	< .001	
Fronto-central Individual Alpha Peak Frequency	−2.47	0.71	3.5	< .001	
Block 3					0.15
Canonical Fronto-central Theta	−0.53	0.71	0.75	0.456	
Canonical Fronto-central Beta	14.75	4.05	3.65	< .001	
Fronto-central Individual Alpha Peak Frequency	−2.71	0.69	3.96	< .001	
Fronto-central Aperiodic Exponent	−11.8	2.73	4.32	< .001	

prone to disruptions related to elevated theta-beta ratios and older adults are more prone to reductions in theta-beta ratios potentially driven by normative aging processes. The moderate level of theta-beta ratio may reflect an optimal balance in the bidirectional regulation of bottom-up subcortical processes by top-down cortical processes that theta-beta ratio is putatively suggested to index (Knyazev, 2007; Schutter & Knyazev, 2012).

However, considering recent data regarding the physiological mechanisms and functions of neural noise, the theta-beta ratio model advanced in previous studies is increasingly difficult to support. As Donoghue, Dominguez, and Voytek (2020) observed and we have replicated, the association between theta-beta ratios and age is confounded by age-related differences in aperiodic activity. Inter- and intraindividual differences in aperiodic activity have also been strongly and consistently associated with variation in cognitive function (Tran et al., 2020; Voytek et al., 2015), and provide a parsimonious and physiologically plausible mechanism for variation in cognitive function across the lifespan relating to the ratio of excitatory to inhibitory activity (Donoghue, Haller, et al., 2020; Gao et al., 2017; Waschke et al., 2021.

Given the relationships between aperiodic activity, individual alpha peak frequency, and theta-beta ratio with age, as well as existing research linking aperiodic activity to cognitive function (Tran et al., 2020; Voytek et al., 2015), individual alpha peak frequency with memory-related aspects of executive functioning (i.e., Clark et al., 2004) and theta-beta ratio with attention-related aspects of executive functioning (Angelidis et al., 2016), these markers appear to be promising, but potentially overlapping and redundant measures of healthy aging. Further research is needed to confirm the unique associations of aperiodic activity, individual alpha peak frequency and theta-beta ratio with memory, executive functioning, and measures of healthy and pathological aging.

5 | CONCLUSION

Overall, we found that both fronto-central theta-beta ratios and fronto-central individual alpha peak frequencies were cross-sectionally negatively associated with age, and that age-related decreases in fronto-central theta-beta ratios are not due to age-related decreases in fronto-central individual alpha peak frequencies. This suggests that changes in both theta-beta ratios and individual alpha peak frequencies may index differential components of healthy aging. Critically, our findings highlight confounds between theta-beta ratio and the aperiodic exponent, suggesting that both metrics should be considered in understanding power-based EEG metrics and aging. Future research should explicitly examine multiple facets of executive function (including working memory, attention control, and response inhibition) to determine how theta-beta ratios, aperiodic components, and individual alpha peak frequencies at rest relate to cognitive functioning in older adulthood, and if these measures are suitable as biomarkers for healthy and pathological aging. Additionally, we are limited by the cross-sectional nature of the study from determining if these cross-sectional relationships between age and resting EEG metrics reflect an underlying developmental trajectory in aging. Future longitudinal research is needed to trace the developmental trajectory of theta-beta ratios, aperiodic components, and individual alpha peak across the lifespan.

AUTHOR CONTRIBUTIONS

Anna J. Finley: Conceptualization; data curation; formal analysis; investigation; supervision; visualization; writing – original draft; writing – review & editing. **Douglas J. Angus:** Conceptualization; formal analysis; writing – original draft; writing – review and editing. **Carien Van Reekum:** Data curation; formal analysis; investigation; methodology; writing – review and editing. **Richard J. Davidson:** Funding acquisition; methodology; project administration; resources; writing – review and editing. **Stacey M. Schaefer:** Data curation; investigation; methodology; project administration; resources; supervision; writing – review and editing.

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ORCID

Anna J. Finley https://orcid.org/0000-0002-0881-9147
Douglas J. Angus https://orcid.org/0000-0001-9722-2475

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

TABLE S1 Supplemental materials table of contents

TABLE S2 Correlations between age and EEG metrics, collapsed across eyes open and eyes closed, only preregistered exclusions ($n = 271$)

TABLE S3 Partial correlations between age and EEG metrics, controlling for individual alpha peak frequency, aperiodic exponent, or aperiodic offset, collapsed across eyes open and eyes closed, preregistered exclusions only ($n = 271$)

TABLE S4 Mediation analyses examining the relationship between canonical fronto-central theta-beta ratio and age, collapsed across eyes open and eyes closed, preregistered exclusions only ($n = 271$)

TABLE S5 Hierarchical multiple regression, regressing age on canonical fronto-central theta, canonical fronto-cental beta, fronto-central RestingIAF individual alpha peak frequency, and fronto-central aperiodic exponent ($n = 271$)

TABLE S6 General estimating equations, age and EEG metrics, controlling for genetic dependencies across twins

TABLE S7 Sample demographics for additional analyses in supplemental materials, describing breakdown of the sample with sufficient data for analyses, combined data only, canonical fronto-central theta-beta ratio

TABLE S8 Sample demographics for additional analyses in supplemental materials, describing breakdown of the sample with sufficient data for analyses, combined data only, individual fronto-central theta-beta ratio

TABLE S9 Sample demographics for additional analyses in supplemental materials, describing breakdown of the sample with sufficient data for analyses, eyes-closed data only, canonical fronto-central theta-beta ratio

TABLE S10 Sample demographics for additional analyses in supplemental materials, describing breakdown of the sample with sufficient data for analyses, eyes closed data only, individual fronto-central theta-beta ratio

TABLE S11 Correlations between various fronto-central theta measures

TABLE S12 Correlations between various fronto-central beta measures

TABLE S13 Correlations between various fronto-central theta-beta ratio measures

TABLE S14 Correlations between various individual peak alpha frequency (IAF) measures

TABLE S15 Correlations between various aperiodic component measures

TABLE S16 Correlations between age and EEG metrics, collapsed across eyes open and eyes closed, good FOOOF fit, valid RestingIAF scalp individual alpha peak frequency,

canonical fronto-central theta and beta bands ($n = 276$)

TABLE S17 Correlations between age and EEG metrics, collapsed across eyes open and eyes closed, good FOOOF fit, valid RestingIAF fronto-central individual alpha peak frequency, individual fronto-central theta and beta bands ($n = 268$)

TABLE S18 Correlations between age and EEG metrics, collapsed across eyes open and eyes closed, good FOOOF fit, valid RestingIAF whole scalp individual alpha peak frequency, individual fronto-central theta and beta bands ($n = 276$)

TABLE S19 Correlations between age and EEG metrics, collapsed across eyes open and eyes closed, good FOOOF fit, FOOOF fronto-central individual alpha peak frequency, canonical fronto-central theta and beta bands ($n = 302$)

TABLE S20 Correlations between age and EEG metrics, collapsed across eyes open and eyes closed, good FOOOF fit, FOOOF whole scalp individual alpha peak frequency, canonical fronto-central theta and beta bands ($n = 305$)

TABLE S21 Correlations between age and EEG metrics, collapsed across eyes open and eyes closed, good FOOOF fit, FOOOF fronto-central individual alpha peak frequency, individual fronto-central theta and beta bands ($n = 276$)

TABLE S22 Correlations between age and EEG metrics, collapsed across eyes open and eyes closed, good FOOOF fit, FOOOF whole scalp individual alpha peak frequency, individual fronto-central theta and beta bands ($n = 276$)

TABLE S23 Correlations between age and EEG metrics, eyes closed only, good FOOOF fit, fronto-central RestingIAF individual alpha peak frequency, canonical fronto-central theta and beta bands ($n = 273$)

TABLE S24 Correlations between age and EEG metrics, eyes closed only, good FOOOF fit, whole scalp RestingIAF individual alpha peak frequency, canonical fronto-central theta and beta bands ($n = 282$)

TABLE S25 Correlations between age and EEG metrics, eyes closed only, good FOOOF fit, fronto-central RestingIAF individual alpha peak frequency, individual fronto-central theta and beta bands ($n = 271$)

TABLE S26 Correlations between age and EEG metrics, eyes closed only, good FOOOF fit, whole scalp RestingIAF individual alpha peak frequency, individual fronto-central theta and beta bands ($n = 276$)

TABLE S27 Correlations between age and EEG metrics, eyes closed only, good FOOOF fit, fronto-central FOOOF individual alpha peak frequency, canonical fronto-central theta and beta bands ($n = 303$)

TABLE S28 Correlations between age and EEG metrics, eyes closed only, good FOOOF fit, whole scalp FOOOF individual alpha peak frequency, canonical fronto-central theta and beta bands ($n = 306$)

TABLE S29 Correlations between age and EEG metrics, eyes closed only, good FOOOF fit, fronto-central FOOOF individual alpha peak frequency, individual fronto-central theta and beta bands ($n = 276$)

TABLE S30 Correlations between age and EEG metrics, eyes closed only, good FOOOF fit, whole scalp FOOOF individual alpha peak frequency, individual fronto-central theta and beta bands ($n = 276$)

TABLE S31 Partial correlations between age and EEG metrics, controlling for individual alpha peak frequency, aperiodic exponent, or aperiodic offset, collapsed across eyes open and eyes closed.

TABLE S32 Partial correlations between age and EEG metrics, controlling for individual alpha peak frequency, aperiodic exponent, or aperiodic offset, eyes closed only

TABLE S33 Mediation analyses examining the relationship between canonical theta-beta ratio and age, collapsed across eyes open and eyes closed.

TABLE S34 Mediation analyses examining the relationship between individual theta-beta ratio and age, collapsed across eyes open and eyes closed

TABLE S35 Mediation analyses examining the relationship between canonical theta-beta ratio and age, eyes closed only

TABLE S36 Mediation analyses examining the relationship between individual theta-beta ratio and age, eyes closed only

TABLE S37 Hierarchical multiple regression, regressing age on canonical fronto-central theta, canonical fronto-central beta, whole scalp RestingIAF individual alpha peak frequency, and aperiodic exponent, combined eyes open and eyes closed ($n = 276$)

TABLE S38 Hierarchical multiple regression, regressing age on individual fronto-central theta, individual fronto-central beta, fronto-central RestingIAF individual alpha peak frequency, and aperiodic exponent, combined eyes open and eyes closed ($n = 268$)

TABLE S39 Hierarchical multiple regression, regressing age on individual fronto-central theta, individual fronto-central beta, scalp RestingIAF individual alpha peak frequency, and aperiodic exponent, combined eyes open and eyes closed ($n = 276$)

TABLE S40 Hierarchical multiple regression, regressing age on canonical fronto-central theta, canonical fronto-central beta, fronto-central FOOOF individual alpha peak frequency, and aperiodic exponent, combined eyes open and eyes closed ($n = 302$)

TABLE S41 Hierarchical multiple regression, regressing age on canonical fronto-central theta, canonical fronto-central beta, whole scalp FOOOF individual alpha peak frequency, and aperiodic exponent, combined eyes open and eyes closed ($n = 305$)

TABLE S42 Hierarchical multiple regression, regressing age on individual fronto-central theta, individual fronto-central beta, fronto-central FOOOF individual alpha peak

frequency, and aperiodic exponent, combined eyes open and eyes closed ($n = 275$)

TABLE S43 Hierarchical multiple regression, regressing age on individual fronto-central theta, individual fronto-central beta, scalp FOOOF individual alpha peak frequency, and aperiodic exponent, combined eyes open and eyes closed ($n = 275$)

TABLE S44 Hierarchical multiple regression, regressing age on canonical fronto-central theta, canonical fronto-central beta, fronto-central RestingIAF individual alpha peak frequency, and aperiodic exponent, eyes closed only ($n = 273$)

TABLE S45 Hierarchical multiple regression, regressing age on canonical fronto-central theta, canonical fronto-central beta, scalp RestingIAF individual alpha peak frequency, and aperiodic exponent, eyes closed only ($n = 282$)

TABLE S46 Hierarchical multiple regression, regressing age on individual fronto-central theta, individual fronto-central beta, fronto-central RestingIAF individual alpha peak frequency, and aperiodic exponent, eyes closed only ($n = 271$)

TABLE S47 Hierarchical multiple regression, regressing age on individual fronto-central theta, individual fronto-central beta, whole scalp RestingIAF individual alpha peak frequency, and aperiodic exponent, eyes closed only ($n = 276$)

TABLE S48 Hierarchical multiple regression, regressing age on canonical fronto-central theta, canonical fronto-central beta, fronto-central FOOOF individual alpha peak frequency, and aperiodic exponent, eyes closed only ($n = 303$)

TABLE S49 Hierarchical multiple regression, regressing age on canonical fronto-central theta, canonical fronto-central beta, whole scalp FOOOF individual alpha peak frequency, and aperiodic exponent, eyes closed only ($n = 306$)

TABLE S50 Hierarchical multiple regression, regressing age on individual fronto-central theta, individual fronto-central beta, fronto-central FOOOF individual alpha peak frequency, and aperiodic exponent, eyes closed only ($n = 276$)

TABLE S51 Hierarchical multiple regression, regressing age on individual fronto-central theta, individual fronto-central beta, scalp FOOOF individual alpha peak frequency, and aperiodic exponent, eyes closed only ($n = 276$)

FIGURE S1 Histogram of age by whole sample ($n = 331$) and the sample reported in the analyses in the main manuscript ($n = 268$)

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