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Spontaneous alpha oscillations and low-frequency activities are related to complementary aspects of cognitive control in younger and older adults

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Abstract

Resting-state EEG is dominated by sustained alpha oscillations, and low-frequency activities (short theta bursts and non-oscillatory 1/*f* slope). Resting alpha power decreases with age and correlates with intelligence. We propose that alpha facilitates proactive control (requiring task-set *maintenance* in preparation for *expected* conditions), whereas theta bursts relate to reactive control, requiring task-set *updating* in response to *unexpected* demands. Less is known about 1/*f* slope. To investigate these relationships, we recorded eyes-open and eyes-closed resting EEG from younger and older adults and subsequently tested their performance on a cued flanker task, expected to elicit proactive and reactive control processes. Alpha power and 1/*f* slope were smaller in older adults, whereas theta power did not show age-related reductions. Resting alpha power and 1/*f* slope predicted proactive control performance, whereas theta predicted reactive control. Resting theta may indicate greater sensitivity to distraction, reflected in frequent spontaneous updating operations. All predictive associations were present beyond the effect of age, suggesting that these EEG correlates may serve as biomarkers of individual differences in cognitive control.

Keywords: EEG alpha power, EEG theta bursts, cognitive control, proactive control, reactive control, aging

1. Introduction

Three main features dominate the resting-state EEG power spectrum: alpha oscillations (8-12Hz), theta bursts (Cavanagh and Frank, 2014) and 1/*f* activity (He, 2014). Alpha oscillations and theta bursts have been extensively investigated in relation to cognition, whereas the relationship between 1/*f* activity and cognition is emerging. Alpha and theta power are often measured during tasks to elucidate moment-to-moment neural variability yoked to certain stimuli or conditions. This is true of studies investigating cognitive control, a set of processes involved in focusing attention and updating representations to meet task demands, among others (Gratton et al., 2018). Critically, however, in the current study we investigate alpha and theta power *at rest* and show their ability to predict different aspects of cognitive control, highlighting the possibility of using resting state brain activity as a biomarker of *individual differences* in cognitive control in both younger and older adults.

Alpha oscillations reflect local field potentials (LFPs) of large neuronal populations receiving synchronous inputs over broad cortical areas (Klimesch et al., 2007). At rest, alpha power decreases with open eyes and is correlated with IQ (Doppelmayr et al., 2002). Task-based evidence demonstrates alpha blocking during working memory encoding, attentional engagement, and proactive inhibition (Sauseng et al., 2005; Foxe and Snyder, 2011; Vissers et al., 2016; Wöstmann et al., 2019). In contrast, sustained alpha activity has been observed during the foreperiod of cued spatial attention tasks (Worden et al., 2000) and the maintenance period of working memory tasks (Bonnefond and Jensen, 2012). It is well documented that alpha power decreases with age (e.g., Polich, 1997) and also in various stages of clinical impairments as dementia develops (Babiloni et al., 2006). Healthy older adults have been shown to have greater

resting state alpha power compared to those with Mild Cognitive Impairment (MCI), and they, in turn, have greater alpha power than those with Alzheimer's Disease (AD) (Moretti et al., 2004; Babiloni et al., 2006). Thus, resting state alpha power has been used as a biomarker for individual differences in older adults, having clinical relevance in distinguishing various degrees of age-related pathologies. Research during the last decade points to theta bursts as critical for propagating cognitive control operations across cortical regions, in response to stimuli with high levels of conflict or when task settings require updating (Cavanagh et al., 2009; Cooper et al., 2016). However, the relationship between resting-state theta activity and cognitive control is less clear. Theta at rest has been associated with lower IQ (Jaušovec et al., 2001). This leads to the hypothesis that theta may reflect the occurrence of shifting or updating operations (Miyake & Friedman, 2012), which may increase in highly distractible individuals. Differently from alpha, the evidence for resting-state theta changes with age is mixed (Babiloni et al., 2006; Finnigan and Robertson, 2011). Theta power has been reported not to differ in healthy older adults compared to that in individuals with MCI or AD (Babiloni et al., 2006), but also to undergo a relative *increase* with disease progression (Kwak, 2006).

A 1/*f*-type power spectrum indicates scale-free dynamics (He, 2014). In EEG it reflects non-oscillatory activity without a predominant center frequency and it may occur when oscillatory LFPs and spikes are decoupled (Voytek and Knight, 2015). The characteristic 1/*f* slope reflects the wavelength of the activity, with longer-wavelength activity (i.e., lower frequency) having greater power than shorter wavelength activity. 1/*f* slope has been related to task performance, cognitive state, and recently shown to decrease with age (Miller et al., 2015; Voytek et al., 2015; Dave et al., 2018).

Here we propose that these major components of the resting-state EEG spectrum reflect complementary aspects of *cognitive control*. Cognitive control refers to processes used to focus on task-relevant information while avoiding distraction (Gratton et al., 2018), and is related to both maintaining and updating task representations. Braver (2012) proposed a dual-mechanism framework that distinguishes proactive control (the anticipation and prevention of interference) from reactive control (the detection and resolution of interference). Proactive control is related to maintaining representations or goal-states, whereas reactive control is critical for updating representations following interference (Braver, 2012). With age, proactive control tends to decline (Manard et al., 2017) whereas reactive control is relatively spared (Bugg, 2014).

Gratton (2018) proposed that representations are maintained for intervals up to several seconds (working memory) by stabilizing mechanisms instantiated through continuous oscillatory activity involving cortico-thalamic loops (alpha). When unpredictable information occurs, these stability intervals are interrupted by sporadic bursts of low-frequency, inhibitory activity (in the theta and delta ranges), leading to suppression of the cortico-thalamic excitatory patterns. Here we propose that deviations from oscillatory stability are reflected by theta bursts, disrupting the temporal synchrony indexed by alpha. Functionally, in those instances, the cortex can update representations (either endogenous or exogenous) because the stability pattern is interrupted, allowing new incoming information to be processed. Within this framework, alpha oscillations reflect the maintenance of cortical representations, while theta reflect their updating.

A cued flanker task may be used to assess both proactive and reactive cognitive control. In a flanker paradigm, a central target stimulus is flanked by irrelevant distractors that are either congruent (e.g., >>>>> or <<<<<) or incongruent with the target (e.g., <><< or >><>>). The

subject's task is to ignore the flankers and respond based on the direction of the central arrow. The difference in performance between incongruent and congruent trials, known as the *congruency effect* (CE), reflects the extent to which distractor information is processed up to the point it influences responses (Eriksen and Eriksen, 1974). The less the distractor information is processed, the smaller the CE, and here this is taken as a measure of *reactive cognitive control*. Smaller CEs indicate more effective reactive control.

In a *cued* flanker paradigm, as used in the current study, the reaction stimulus arrays are preceded by a cue that indicates the probability that the array will contain congruent flanker information. Gratton, Coles, & Donchin (1992) showed that these probability cues influence the size of the CE. Cues indicating a high probability of congruency lead to larger CEs compared to cues indicating a high probability of incongruency. In other words, when participants are warned that the irrelevant distractors are likely to be incongruent, they adopt a strategy that limits the influence of the distractor information, reducing the CE. In contrast, when they are informed that the irrelevant distractors are likely to be congruent, they adopt a strategy that allows more distractor information to be processed, because on the majority of trials this information will facilitate performance. This is of course at the cost of hindering performance on the infrequent incongruent arrays, leading to a larger CE in such instances. These effects are similar to the conflict adaptation effect (also called the congruency sequence effect, or the Gratton effect) which is characterized by a reduced CE on trials immediately following an incongruent array as opposed to following a congruent array (e.g., Egner, 2007; Ullsperger, Bylsma, & Botvinick, 2005). We refer to the difference in probability cue-based congruency effects as the *conflict expectation effect* (CEE), which is taken here as a measure of *proactive control*.

Given the hypothesis that alpha indicates the maintenance of representations and theta bursts their updating, we predicted that individual differences in resting-state alpha power would be related to individual differences in proactive control, whereas individual differences in theta would be related to reactive control. Age should lead to a reduction of both phenomena, although potentially less so for reactive control (Bugg, 2014). Given the unexplored relationship between 1/*f* slope and cognitive control, we did not have *a priori* predictions for this analysis. As such, we investigated the association of resting-state alpha power, theta, and 1/*f* slope with cued-flanker task performance in healthy younger and older adults.**2. Materials and Methods**

2.1 Participants

Twenty-one younger and 20 older adults were recruited and underwent the procedures described below. Participants reported no history of psychiatric or neurological disorders and had no signs of dementia (scores ≥51 on the modified Mini-Mental Status Examination [mMMSE]; Mayeux, Stern, Rosen, & Leventhal, 1981), or depression (younger adults assessed with the Beck's Depression Inventory, Beck, Steer, & Brown, 1996; and older adults with the Geriatric Depression Scale, Yesavage et al., 1983; Yesavage & Sheikh, 1986). The study received ethical approval from the Institutional Review Board at the University of Illinois Urbana-Champaign. All participants provided written informed consent and were compensated for their time.

One younger adult and one older adult were excluded for excessive EEG artifacts: eye movements, muscle activity, and/or amplifier saturation. The remaining 20 younger adults (age range = 18-30, 14 females) and 19 older adults (age range = 65-80, 11 females) constituted the final sample. See Table 1 for age-group characteristics. Older and younger adults were well matched in cognitive status, although older adults, as is typical, had a slight advantage over

younger adults in tests relying on vocabulary knowledge[1], $t(35) = 4.29$, $p = .0001$. Older adults had slightly more years of education, $t(37) = -2.15$, $p = .04$, as expected, given that most younger adults were college students. Older adults also had higher composite age-adjusted IQ, $t(37) = -2.25$, $p = .03$, than younger adults.

INSERT TABLE 1 ABOUT HERE

2.2 Data Acquisition and Analysis

Participants underwent two separate sessions: a resting-state EEG recording session, followed by a behavioral testing session.

2.2.1 Resting-State EEG

Participants sat in a dimly lit, sound- and electrically attenuated recording chamber. Each session included 1-minute eyes-open recording of resting EEG followed by 1-minute with eyes-closed. These recording periods were conducted at the beginning of a recording session that involved other experiments that will not be reported here.

2.2.2 EEG Recording and Analysis

EEG and EOG were recorded continuously from 64 active electrodes in an elastic cap (Acti-Cap) using BrainAmp amplifiers (BrainVision Products GmbH). EEG was recorded from scalp electrodes referenced to the left mastoid, with off-line re-referencing to the average of the two mastoids. Two electrodes placed above and below the left eye measured vertical EOG to detect blinks and vertical eye movements. Two electrodes placed approximately 1cm to the left and right of the outer canthi of the eyes measured horizontal eye-movements (saccades).

[1] Two older adults did not take the Shipley Vocabulary Scale, resulting in fewer degrees of freedom for this *t*-test

Impedance was kept below 10kΩ. The EEG was filtered on-line using a 0.1-250 Hz bandpass and was sampled at 500Hz.

Off-line EEG processing was done using EEGLAB Toolbox (version: 13.6.5b; Delorme & Makeig, 2004), ERPLAB Toolbox (version: 6.1.3) and custom Matlab16a scripts (The MathWorks, Inc., Natick, Ma, USA). A 30 Hz low-pass filter was applied. The data were epoched into 4096 ms contiguous segments to facilitate usage of our artifact detection scripts. Epochs with amplifier saturation were discarded. Ocular artifacts were corrected using the procedure described in Gratton et al. (1983). After eye movement correction, epochs with voltage fluctuations exceeding 200µV were excluded from further analysis to minimize the influence of any remaining artifactual activity. This resulted in the exclusion of 1.23% of the epochs.

Power spectral densities were determined using a fast Fourier transform across the entire spectrum, using Welch's method at parietal (Pz, POz, P1, P2, PO3, PO4) and frontocentral (Fz, FCz, Cz, CPz, FC1, FC2, C1, and C2) electrode clusters. The segments were zero-padded and multiplied with a Hamming taper, with 0% overlap. These clusters were selected because alpha power is largest at parietal locations (e.g., Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014), and 1/*f* slope and theta are typically largest at frontocentral locations (Pertermann, Mückschel, Adelhöfer, Ziemssen, & Beste, 2019). This was confirmed by a review of topographical plots.

The power spectrum can be decomposed into non-oscillatory activity, alpha and theta oscillatory peaks, and noise and modeled using the following equation: $Power(f) = 1/f\ effect\ (f) + theta\ power(f) + alpha\ power(f) + \boldsymbol{\varepsilon}$, where f is frequency and $\boldsymbol{\varepsilon}$ is noise.

To accurately measure alpha and theta power, the 1/*f* component was removed from the spectrum. We first modeled the 1/*f* component on the raw power spectrum, excluding 4-13 Hz, which represents most oscillatory power in the spectrum, using a least-squares method (Figure 1). The slope of the1/*f* component from this procedure was retained for analysis. The 1/*f* trend was then subtracted from the spectrum, allowing for more reliable alpha and theta estimates (Nikulin and Brismar, 2006; Haegens et al., 2014). Mean alpha and theta power were quantified on the detrended spectra and then log-transformed. The log mean alpha and theta power were used for analyses because power has a positively skewed distribution. Using the logarithm attenuates the skew and allows for an ANOVA to be conducted without violating the assumption of normality. Similarly, 1/*f* slope was log-transformed.

INSERT FIGURE 1 ABOUT HERE

Assessing alpha power scalp topographies separately at 8, 9, 10, 11, and 12 Hz revealed very small power variations across the scalp at 8 Hz and 12 Hz in both younger and older adults. Thus, we estimated alpha power based on the average power between 9-11 Hz. For theta, which did not show a very prominent peak in the spectra, we used a broader frequency window encompassing the full, canonical theta band, 4-8 Hz.

2.2.3 Behavioral Task Session, Stimuli, and Related Analyses

At the beginning of testing, participants were seated 100 cm in front of a computer monitor centered at eye-level and were read instructions by the experimenter to supplement on-screen instructions. The imperative stimulus consisted of five horizontal arrows that were either congruent (<<<<< or >>>>>) or incongruent (<<><< or >><>>) on any given trial. Participants indicated, as quickly and accurately as possible, which direction (left or right) the central, target stimulus was pointing by pressing one of two keypads located on either side of the participant.

Stimulus-response mapping was constant across all participants (i.e., a left-pointing target stimulus always required a left-button press, and vice versa) to eliminate the possibility of a confounding Simon effect in some participants (Simon, 1969).

Three neutral, low-arousing images of inanimate objects (fire hydrant, dresser, and screw, from the International Affective Picture System database, IAPS; Lang, Bradley, & Cuthbert, 2008) served as cues and preceded the imperative stimulus array. These images represented a 75% (predict-congruent; PC), a 50% (predict-neutral; PN), and a 25% (predict-incongruent; PI) probability of a congruent stimulus array, respectively. The three cue types were equiprobable and participants were explicitly told the congruency probability represented by each cue prior to commencing the task. PC and PI cue images were counterbalanced across subjects.

Each trial began with a 499 ms cue, followed by a 999 ms fixation. Then, the imperative stimulus appeared for 149 ms and was followed by 1848 ms of fixation before the onset of the next trial. The response window began with the onset of the imperative stimulus and continued until the onset of the next cue (i.e., the next trial). The global probability of a congruent trial within each block was 50%. The imperative stimulus arrays were presented in white typeface on a black computer screen and subtended 2.23° x 0.46°. Each cue overlaid a gray background with uniform dimensions such that each composite image subtended 6.98° x 5.35°. All stimuli were presented on a monitor (19-in. CRT, refresh rate 60 Hz, screen resolution 1280 x 960; Dell Computer, Round Rock TX) using the E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA).

Accuracy feedback was displayed on-screen at the end of each block. If their accuracy was below 75% across all trial types, participants saw a message that read “respond more slowly and more accurately.” If they scored between 75 and 95%, they saw “continue to respond as

quickly and accurately as you can." If they scored above 95%, they saw "respond more quickly". The feedback was designed to encourage participants to prioritize speeded responses and elicit a reasonable number of errors, a requirement for accurately assessing speed of processing. Participants could take breaks between blocks, as needed.

Before the flanker task, younger adults completed 96 practice trials at the experimental speed. Older adults completed two sets of practice trials. Additional practice was added for older adults to offset difficulties (apparent in preliminary data) for them to complete the task at the experimental speed. As such, we added a slower-paced practice block to familiarize this group with the task. In the first set (48 trials), the inter-stimulus interval (ISI) was increased by 30%, but the cue and imperative stimulus presentation times remained at experimental speed. In the second set (96 trials), each trial ran at the experimental speed. Subsequently, all participants completed three blocks of 288 experimental trials.

Incorrect trials and all trials with reaction times $\leq$ 200 ms (i.e., fast guesses) were discarded before statistical analysis. Data were collapsed across target stimulus direction (i.e., response hand) to create six trial-types: 3 cue types (PC, PI, PN) x 2 flanker congruency conditions (congruent, incongruent). In addition to recording reaction time (RT) and calculating error rates for each trial-type, the inverse efficiency score (IES), an integrated measure of RT and accuracy, was also calculated (Townsend and Ashby, 1978, 1983; Bruyer and Brysbaert, 2011). IES is insensitive to speed-accuracy tradeoffs and results in a measure of RT that is not biased by fast decisions. IES is computed by dividing the mean RT of correct responses by the proportion of correct responses for each trial type (IES = RT/proportion correct), thereby providing an index of processing speed that estimates the "true" processing speed when the effects of speed-accuracy tradeoffs are minimized.

For our measure of reactive control, we calculated the congruency effect (CE) by subtracting congruent trials from incongruent trials (Incongruent - Congruent), so smaller differences in RT, error rate, and IES indicate greater reactive control. For the measure of proactive control, we calculated the conflict expectation effect (CEE) by subtracting the predict congruent CE from the predict incongruent CE (PC_{CE} - PI_{CE}). Here, a larger difference indicates greater proactive control.

2.4 Statistical Analyses

Two-way mixed ANOVAs were computed, with age (young, old) as a between-subjects factor, eye position (open, closed) as a repeated measure, and alpha power, theta power, or $1/f$ as dependent variables. Alpha analyses were restricted to the parietal cluster, whereas theta and $1/f$ analyses were restricted to the frontal cluster. Spearman's *rank-order* correlation coefficients were computed between alpha power, theta power, $1/f$ and behavioral performance measurements (CE and the conflict expectation effect for error rate, RT, and IES), in order to assess the effects of individual variability in resting-state EEG parameters and subsequent cognitive control processing. Spearman's rho was used instead of Pearson's r because assessment of normality with the Shapiro-Wilk test indicated that the behavioral measures were not normally distributed. These correlations were calculated both with and without partialing out the effects of age. Behavioral analyses of congruency effects and conflict expectation effects were assessed with age (young, old), cue-type (PC, PI, PN), and trial-type (congruent, incongruent) in three-way mixed ANOVAs.

3. Results

3.1 EEG Power Spectrum Decomposition

After decomposing the power spectrum into alpha power, theta power and 1/*f* slope we quantified the variance in the power spectrum captured by these components across all participants. With eyes open, three parameters (alpha power, theta power, and 1/*f* slope) accounted for 90% of the spectral variance at the parietal electrode cluster and 93% at the frontocentral cluster. Alpha, theta, and 1/*f* slope accounted for slightly less variance with eyes closed: 89% at both the parietal and frontocentral electrode clusters. Therefore, although the EEG signal is rich and complex, it can be largely described by these three parameters. Power spectra (after removing 1/*f* slope) for each electrode cluster are shown in Figure 2.

Scalp distribution maps of alpha, theta and 1/*f* are presented in Figure 3. As can be seen from these maps, for both younger and older adults the scalp distribution of alpha is posterior, and the one for theta more anterior, as typically observed. The scalp distribution of 1/*f* has both anterior and posterior aspects. All effects are larger around the midline.

INSERT FIGURES 2-3 ABOUT HERE

Alpha power and 1/*f* slope with eyes closed at the parietal cluster are marginally positively correlated with one another across participants, $r(37) = .302$, $p = .062$: Participants with greater resting-state alpha power with eyes closed tend to have steeper 1/*f* slopes, suggesting that both the main oscillatory (alpha) and non-oscillatory (1/*f*) activity in EEG vary together within individuals. However, this small correlation appears mostly due to the fact that both are larger in younger relative to older adults, and it disappears when age is partialed out $r(36) = .075$, $p = .655$. With eyes open, this relationship is not evident before [r (37) = .185, p =

.260] or after [$r(36) = .251$, $p = .129$] controlling for age. Unlike alpha power, frontocentral theta power is not correlated with frontocentral $1/f$ slope with either eyes open or eyes closed both before and after partialing out the effects of age.

Theta power was positively correlated with alpha power both with eyes open, $r(37) = .361$, $p = .024$, [$r(36) = .386$, $p = .017$ after partialing out age], and with eyes closed, $r(37) = .423$, $p = .007$, [$r(36) = .386$, $p = .017$ after partialing out age]. Thus, theta and alpha power, which are the main oscillatory activities represented in the power spectrum, are correlated with each other, both before and after accounting for age effects and in both eye conditions.

3.2 Oscillatory Activity - Alpha Power

A 2(age) x 2(eye status) mixed effects ANOVA was run for alpha power at the parietal electrode clusters. As expected, at the parietal cluster, alpha power was greater with closed compared to open eyes, $F(1, 37) = 24.865$, $p = .000$, partial $\eta^2 = .402$ (see Figures 2-3). Although there was no main effect of age $F(1, 37) = 1.056$, $p = .311$, partial $\eta^2 = .208$, there was an age by eye status interaction, $F(1, 37) = 10.260$, $p = .003$, partial $\eta^2 = .217$. With eyes open, there was little difference in alpha power between younger and older adults, $F(1, 37) = .255$, $p = .616$, partial $\eta^2 = .007$. When younger adults closed their eyes, they had a substantial increase in alpha power that was not evident in older adults, $F(1, 37) = 11.225$, $p = .002$, partial $\eta^2 = .233$. This may indicate that older adults modulate their resting-state alpha power less than younger adults, which, in turn, may reflect a weakening of the neural system giving rise to the alpha rhythm, or of the mechanisms for controlling it.

3.3 Oscillatory Activity - Theta power

A similar analysis was run for theta power measured at the frontocentral cluster. The results indicated a main effect of eye condition, $F(1,37) = 25.438$, $p < .001$, partial $\eta^2 = .407$ with greater power with eyes closed than eyes open. However, there was no significant difference between the two age groups, $F(1,37) = 0.064$, $p = .801$, partial $\eta^2 = .002$, and the interaction between age and eye condition did not reach significance, $F(1,37) = 2.850$, $p = .100$, partial $\eta^2 = .072$. Thus, the data suggest no effect of age on theta power at rest.

3.4 Non-oscillatory Activity - 1/f Slope

The 1/*f* slope was analyzed with a 2(age) x 2(eye status) mixed ANOVA at the frontocentral cluster to determine potential group differences and the effect of eye condition on 1/*f* slope. The ANOVA revealed that 1/*f* slope was greater with eyes closed than eyes open, $F(1, 37) = 8.223$, $p = .007$, partial $\eta^2 = .182$. There was also a main effect of age, $F(1, 37) = 12.363$, $p = .001$, partial $\eta^2 = .250$, such that younger adults had steeper 1/*f* slopes than older adults. This age effect has been previously shown during visual working memory tasks (Voytek et al., 2015) and language processing tasks (Dave et al., 2018), but to our knowledge this is the first time it has been demonstrated in the absence of an explicit cognitive task.

3.5 Behavioral Effects

Evidence from behavioral ANOVAs replicated the well-established congruency effect for accuracy [$F(1, 37) = 29.018$, $p = .000$], error rate [$F(1, 37) = 187.176$, $p = .000$], and IES [$F(1, 37) = 82.955$, $p = .000$, partial $\eta^2 = .835$]. The congruency effect interacted with age when measured with error rate, $F(1, 37) = 7.129$, $p = .011$, partial $\eta^2 = .162$, such that older adults had a larger congruency effect than younger adults.

Similar results from behavioral ANOVAs indicated that the conflict expectation effect was present for reaction time [$F(1, 37) = 6.603$, $p = .014$, partial $\eta^2 = .151$] and IES [$F(1, 37) = 12.478$, $p = .001$, partial $\eta^2 = .252$]. The conflict expectation effect was not apparent for error rate, $F(1, 37) = 2.382$, $p = .131$, partial $\eta^2 = .060$.

Age did not affect the conflict expectation effect for error rate [$F(1, 37) = .038$, $p = .847$, partial $\eta^2 = .001$] or IES [$F(1, 37) = 2.206$, $p = .146$, partial $\eta^2 = .056$]. However, the conflict expectation effect on RT was bigger in older adults, $F(1, 37) = 5.717$, $p = .022$, partial $\eta^2 = .134$.

3.6 Correlations between Resting-State Alpha Power, Theta Power, and 1/f Slope and Cognitive Control

Critically, the current study explored the relationship between alpha power, theta power and 1/*f* slope and proactive and reactive cognitive control processes. The results reported here are exclusively for the eyes open condition, as the eyes closed condition did not predict behavior (it should be noted here that this is not surprising, as the behavioral measures were obtained in an eyes-open condition). As shown in Figure 4A, alpha power at rest with eyes open predicted the size of the conflict expectation effect for both RTs, r_s (37) = .321, $p = .046$ and IES, r_s (37) = .491, $p = .002$. This is consistent with the prediction that alpha is related to proactive control. These relationships remained significant even after partialing out the effects of age (RT CEE: r_s (36) = .335, $p = .040$; IES CEE: r_s (36) = .487, $p = .002$) suggesting that the ability to engage proactive control is not driven by age per se, and may instead reflect individual differences in proactive cognitive control capacity. However, alpha power did not predict the size of the RT CE, r_s (37) = .174, $p = .289$, or IES CE, r_s (37) = .118, $p = .473$. This was also true after partialing out the effects of age. Thus, alpha power appears specifically related to proactive

control abilities rather than to cognitive control in general, with greater proactive control in individuals with larger alpha power at rest (with open eyes).

For resting theta power (with open eyes), there was a significant positive relationship with the error rate CE, r_s (37) = .406, p = .010, which varied little when age was partialed out, r(36) = .410, p = .010. A marginally significant positive relationship with IES and CE emerged after partialing out age, r_s (36) = .306, p = .062. This effect was not present for RT with CE, r_s (37) = .020, p = .902. In contrast, theta power was not significantly correlated with conflict expectation effect for either error rate CEE, r_s (37) = .226, p = .166, IES, r_s (37) = .182, p = .268, or RT, r_s (37) = -.040, p = .809. These effects remained non-significant after partialing out age. These results indicate a relationship between theta activity at rest and reactive, but not proactive, control. Interestingly, the data indicate that individuals with high theta power at rest are more affected by distractors than individuals with low theta power. These data are shown in Figure 4B.

It is important to illustrate the dissociation between both alpha and theta power and their relationships to proactive and reactive control, respectively. Therefore, partial correlation analyses were conducted to further illustrate the effect of alpha power on proactive control processes while holding theta power constant and the effect of theta power on reactive control processes while holding alpha power constant. As throughout this entire section, these analyses were conducted on the eyes-open measurements. Alpha power was positively related to the IES conflict expectation effect [r_s (36) = .464, p = .003] and the RT conflict expectation effect [r_s (36) = .368, p = .023] after partialing out the effects of theta power. As before, the error rate conflict expectation effect was not related to alpha power, even after partialing out theta power [r_s (36) = .198, p = .234].

The relationship between theta power and reactive control processes also varied little after partialing out the effects of alpha power. As before, there was a positive relationship between theta power and the error rate CE [r_s (36) = .402, p = .012], an effect nearly identical to the effect shown both before and after partialing out the effect of age. Theta power again showed a marginally positive relationship with the IES CE [r_s (36) = .208, p = .088] after partialing out the effects of alpha power. Taken together, these results indicate that alpha power is indeed related to proactive control processes, in a way that is independent from the contributions of theta power, and, conversely, that theta power is related to reactive control processes, in a way that is independent from the contributions of alpha. This provides strong evidence that alpha and theta power *at rest* are uniquely related to proactive and reactive control, respectively. As such, they could be used as separable biomarkers for these two aspects of cognitive control.

INSERT FIGURE 4 ABOUT HERE

Exploratory analyses indicated that 1/*f* slope marginally predicted the error rate CEE, r_s (37) = .271, p = .096, an effect which reached significance after controlling for age, r_s (36) = .368, p = .023. This may indicate that steeper 1/*f* slope is predictive of greater proactive control (Figure 4C). Additionally, 1/*f* slope was not related to the error rate CE before, r_s (37) = .233, p = .153, or after partialling out age, r_s (36) = .119, p = .477. This suggests that 1/*f* slope may be more related to proactive rather than reactive control processes. It should be noted, however, that there was no clear *a priori* prediction for the 1/*f* slope, and that the effects reported were not corrected for multiple comparisons. Therefore, these findings require additional replications.

4. Discussion

Most (>89%) of the resting-state EEG power spectrum can be described by only three parameters: the amplitude of the oscillatory spectral activity in the alpha and theta bands and the

slope of the non-oscillatory 1/*f* component. Interestingly, these features differ between younger and older adults, such that older adults have less alpha power (at least with closed eyes) and flatter 1/*f* slopes than younger adults (but no differences were found for theta activity). Consistent with our hypotheses, these electrophysiological characteristics were related to different aspects of cognitive control processing: increased alpha power (and, to a lesser extent, 1/*f* slope) predicted greater modulation of distractor processing given the cue information (conflict expectation effects), whereas theta power predicted greater distracter interference (congruency effects). Under the dual-mechanisms framework proposed by Braver (2012), our evidence suggests that alpha power (and perhaps 1/*f* slope) is related to proactive control processes and theta power is related to reactive control. A compelling picture emerges from these data: separate parameters from the decomposed EEG power spectrum *at rest* predict separable cognitive control processes during a behavioral task, independent of participant's age. The alpha results resonate with previous work done in our lab, which showed that alpha power predicted subsequent learning in a complex task (Mathewson et al., 2012).

This dissociation suggests a complementary role of alpha and theta oscillations in cognitive processing. Recently, Gratton (2018) proposed that alpha oscillations may help maintain currently active representations via thalamocortical circuits. Results from this, as well as previous studies (i.e. Deiber, Ibañez, Missonnier, Rodriguez, & Giannakopoulos, 2013; Polich, 1997; Volf & Gluhih, 2011) indicate that younger adults have greater alpha power than older adults (at least with closed eyes), suggesting that younger adults are better able to maintain and control their attention and avoid distractions, a result which is largely supported by extensive behavioral and cognitive neuroscience evidence (e.g., see Fabiani, 2012, for a review). This would result in higher-fidelity sensory representations and improved performance on cognitive

tasks, at least for those conditions in which stable stimulus representations need to be maintained over time. In the current study, this is instantiated in the conflict expectation effect, in which information from the cue is used to influence the settings of the information processing system *in advance* of the presentation of response stimuli, which will occur sometime later. In fact, as expected, alpha power predicted the conflict expectation effect and thereby proactive control. Even in our relatively small sample this effect is evident, supporting previous literature on the relationship between alpha power and proactive control (Cavanagh et al., 2009; Compton et al., 2011) .

It is important to note, however, that both the conflict expectation effect per se and its relationship with alpha power were independent of age (i.e., they were present in roughly equal amounts in both younger and older participants). It should also be noted that these alpha measures were taken under an eyes-open condition, and that the resting-state age-related alpha differences were only observed with closed eyes. This may indicate that individual difference in resting-state open-eyes alpha may predict cognitive control occurring when eyes are open. It remains to be shown that age-related differences in alpha obtained with eyes closed are instead more likely to be predictive of cognitive phenomena that can occur when the eyes are closed, and not in situations in which visual attention is involved.

Resting-state EEG has been used to investigate individual variability in cognitive status and cognitive performance in healthy older adults and those with MCI and AD. Most often, these recordings are conducted in the eyes closed condition and have illustrated a shift in the EEG power spectrum as participants progress from a healthy cognitive status to MCI to AD, such that alpha power is further reduced and lower frequency activity is increased (Babiloni et al., 2006; Kwak, 2006). This suggests that, as older adults change in cognitive status, their resting-state

EEG spectrum changes concurrently, and that these changes can be used as indices of cognitive performance. However, it is important to note that the predictability of the power spectrum characteristics on cognitive control processes occurred in *both* younger and older adults, which suggests that this informative neural variability exists already in younger adults and may continue to provide predictive power as individuals age. In this respect, resting-state alpha and theta power could be interpreted as biomarkers for a reserve capacity for cognitive control (Stern, 2009). In our study, these relationships were evident with eyes-open alpha and theta power, which is a condition often understudied in resting-state EEG and should be an avenue for continued research.

In previous studies, alpha power fluctuations have been investigated during ongoing cognitive control tasks using a time-frequency approach. These experiments often report phasic posterior alpha power reductions following error trials (i.e., Cooper et al., 2016; van Driel, Richard Ridderinkhof, & Cohen, 2012). These decreases in alpha power have been conceptualized as a mechanism associated with the refocusing of attention after an error occurred and when the updating of ongoing working memory task-related representations is needed. Gratton (2018) proposed that a temporary *blocking* of alpha is required for (or at least favors) the updating of representations. This is consistent with the idea that alpha per se is associated with the maintenance of existing representations over time (a phenomenon that would resist the updating process). Gratton's (2018) proposal links alpha mechanisms with the maintenance of representations, which would be required during proactive but not reactive control. This is consistent with the findings of the current study, in which alpha power at rest was predictive of the size of the conflict expectation effect (which requires maintenance of task-related

representations in the interval between cues and response stimuli) but not of the congruency effect per se (which requires direct handling of conflict, without a delay).

According to Gratton (2018), bursts of low frequency activity, in this case frontocentral theta, may provide a mechanism by which alpha is temporarily suspended to facilitate the updating of representations. As such, theta bursts would provide an opportunity for sustained alpha oscillations to be interrupted and for the maintenance of a representation to either be changed in favor of a new task-relevant representation, or in favor of a task-irrelevant distractor, which may happen more often in aging. Although a flexible engagement of theta interruption mechanisms is a useful process integral to cognitive control, its excessive engagement may lead to maladaptive responses (i.e., distractibility) in conditions in which such refocusing is not needed. This effect may be evident during resting-state situations: In such conditions engagement of theta activity and blocking of alpha activity are not required, and the trait-like propensity to do so may be correlated with lower control abilities during tasks. It may also explain previously reported results, which indicate that IQ is negatively correlated with resting-state theta, and positively correlated with resting-state alpha (Jaušovec et al., 2001; Doppelmayr et al., 2002). Our results also inform the trait-like spectral differences in adults with ADHD, which indicate both increased theta power and decreased alpha power (Woltering et al., 2012), and could explain the tendency for increased distractibility in these individuals. In the present study, such a propensity may be associated with increased susceptibility to the interference caused by incompatible flankers in the flanker task.

Although we did not find a difference in theta power with age, we did find an effect of reduced $1/f$ slope with age, replicating the age effect reported by Voytek et al. (2015) and Dave et al. (2018). Given that low-frequency activities may manifest as $1/f$ slope, this reduction fits

well with other literature reporting reduced delta power across the adult lifespan (Polich, 1997; Babiloni et al., 2006). Interestingly, in both datasets referred to here, alpha power was also shown to decrease with age, which we have reported as well.

Intriguingly, Prichep et al. (2006) reported reductions in theta power in cognitively typical older individuals with subjective memory complaints seven years later, but only for those individuals whose mental status declined during the seven year interval. This may address why our sample did not show theta power differences between younger and older adults – our older individuals were cognitively intact and not reporting memory complaints. Additionally, Finnigan and Robertson (2011) reported that relatively higher resting theta power in healthy older adults was related to better performance on verbal recall, attention, and executive function measures. It is possible that the older adults in this sample had sufficient resting theta power and were thus able to engage in the reactive control processes necessary to sufficiently complete the cued flanker task. Additionally, we show for the first time a relationship between $1/f$ slope and cognitive control processes, specifically proactive control. This is of interest because it suggests that another electrophysiological mechanism – besides alpha power – may be involved in proactive control processing. We have shown that alpha power and $1/f$ slope are not related to each other (in the eyes open condition), indicating that although they both predict proactive processing, they are likely distinct electrophysiological signals. There may be two neural mechanisms supporting proactive control processing: that generating alpha power and that generating $1/f$ slope.

Some limitations of the current study should be pointed out. First, our study is limited by its sample size. Nonetheless, predictive relationships were still present in this sample, suggesting that their effect size is sufficient. It is clear, however, that further testing with larger samples and

other cognitive control tasks may be very useful to validate the results reported here. Additionally, time-frequency analyses of EEG recorded during cognitive control tasks will allow us to investigate the dynamics of these electrophysiological parameters and assess whether alpha and 1/*f* slope and theta power selectively mediate proactive and reactive control. These analyses may also be useful to demonstrate that EEG parameters measured at rest are predictive of possible trait-like individual differences in event-related time-frequency phenomena during cognitive control tasks.

4.1 Conclusions

Resting-state EEG contains three dominant – and largely separable – electrophysiological signals: oscillatory alpha and theta power, and non-oscillatory 1/*f* slope. We found independent and separable predictive relationships between *resting-state* alpha power and proactive control, and theta power and reactive control, which existed regardless of participants' age. The fact that these dimensions of cognitive control can be predicted from EEG activity *at rest*, and therefore unrelated to specific task characteristics, suggests that they may represent important trait-like biomarkers. As such, they may prove useful in understanding life-span individual differences in cognition and may help researchers investigate variability in cognitive aging.

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Table 1

Descriptive characteristics of the sample. Mean (SD).

	Younger Adults	**Older Adults**	***p*-value**
N	20 (14 females)	19 (11 females)	
Age (years)	22.4 (*3.3*)	69.4 (*4.3*)	< .001
Education (years)	15.6 (*2.4*)	17.3 (*2.4*)	.038
IQ (age-adjusted)*	115.2 (*10.7*)	124.0 (*15.4*)	.030
Shipley's Vocabulary Scale	31.4 (*3.4*)	36.1 (*3.2*)	< .001

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Figure Legends

Figure 1: Detrending Procedure: A) Illustration of the raw power spectrum (solid black line) with the characteristic 1/*f* phenomenon in the lower tail of the spectrum. The 1/f phenomenon was modeled with the dashed line, excluding 4-13 Hz, and was subtracted from the raw power spectrum, resulting in the detrended power spectrum (solid blue line). Alpha and theta measurements were made on the detrended power spectrum. **B)** Illustration of the same raw power spectrum (solid black line) as in (A) but with 1/frequency as the scale on the abscissa. The 1/*f* phenomenon was modeled with the dashed line, as in (A). The gray box highlights the portion of the spectrum excluded in fitting the model (4-13 Hz) because most oscillatory activity occurs in this frequency band.

Figure 2: Detrended Power Spectra: Detrended power spectra at the parietal (A-B) and frontocentral (C-D) electrode clusters with eyes open (A, C) and eyes closed (B, D). Note that younger adults have greater alpha power than older adults with both eyes open and eyes closed. However, theta power was not significantly different between younger and older adults. Both alpha and theta powers were reduced by opening the eyes.

Figure 3: Topographic maps of alpha, theta, and 1/*f* slope: Alpha and theta amplitude, and 1/*f* slope with eyes open (top) and closed (bottom) are shown for both younger and older adults. Amplitude was used instead of power because power differences between younger and older adults were too large to be plotted using the same scale, impeding interpretation.

Figure 4: Relationship between EEG and cognitive control: (A) Parietal alpha power was correlated with the conflict expectation effect (shown here as the difference between IES on compatible and incompatible cues). Individuals with greater alpha power had a larger difference in IES between compatible and incompatible trials. The greater this difference, the better able were these individuals to use the information contained in the cue, which improved their behavioral performance. This effect is age invariant. **(B)** Frontocentral theta power was correlated with the congruency effect, after partialing out the effect of age. Greater theta power was predictive of a larger congruency effect, indicating that participants with large theta power at rest had a greater difference in error rate between incompatible and compatible trials, such that they were more likely to engage in reactive control processing. **(C)** Frontocentral 1/*f* slope was correlated with the conflict expectation effect, after partialing out the effect of age. The steeper the 1/*f* slope, the greater difference in error rate between incompatible and compatible trials, such that these participants were more likely to engage in reactive control processing.

Statement of conflicting interests: None of the authors of this article has any financial or other conflicts of interest regarding this work.

Figure 1
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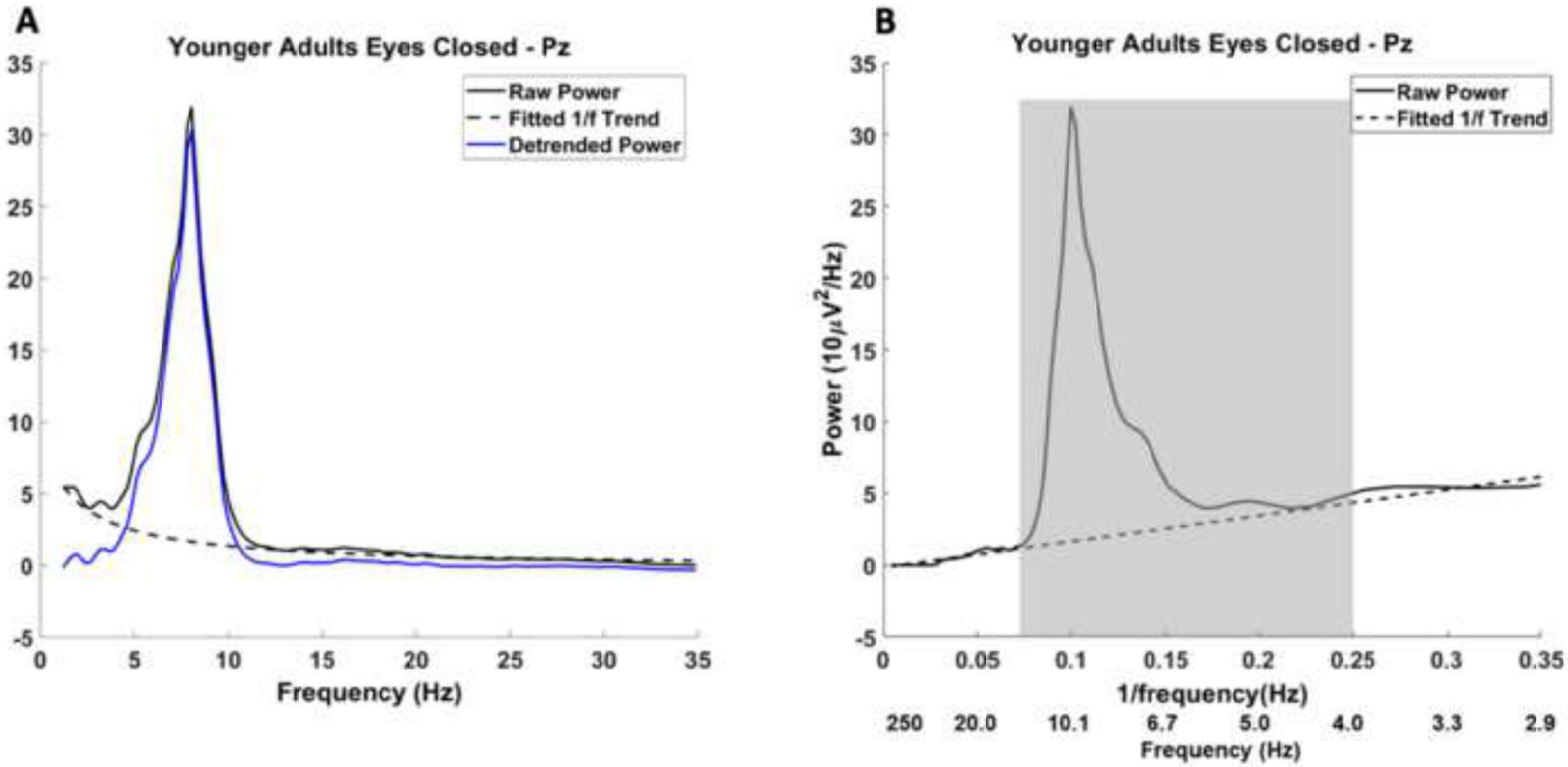

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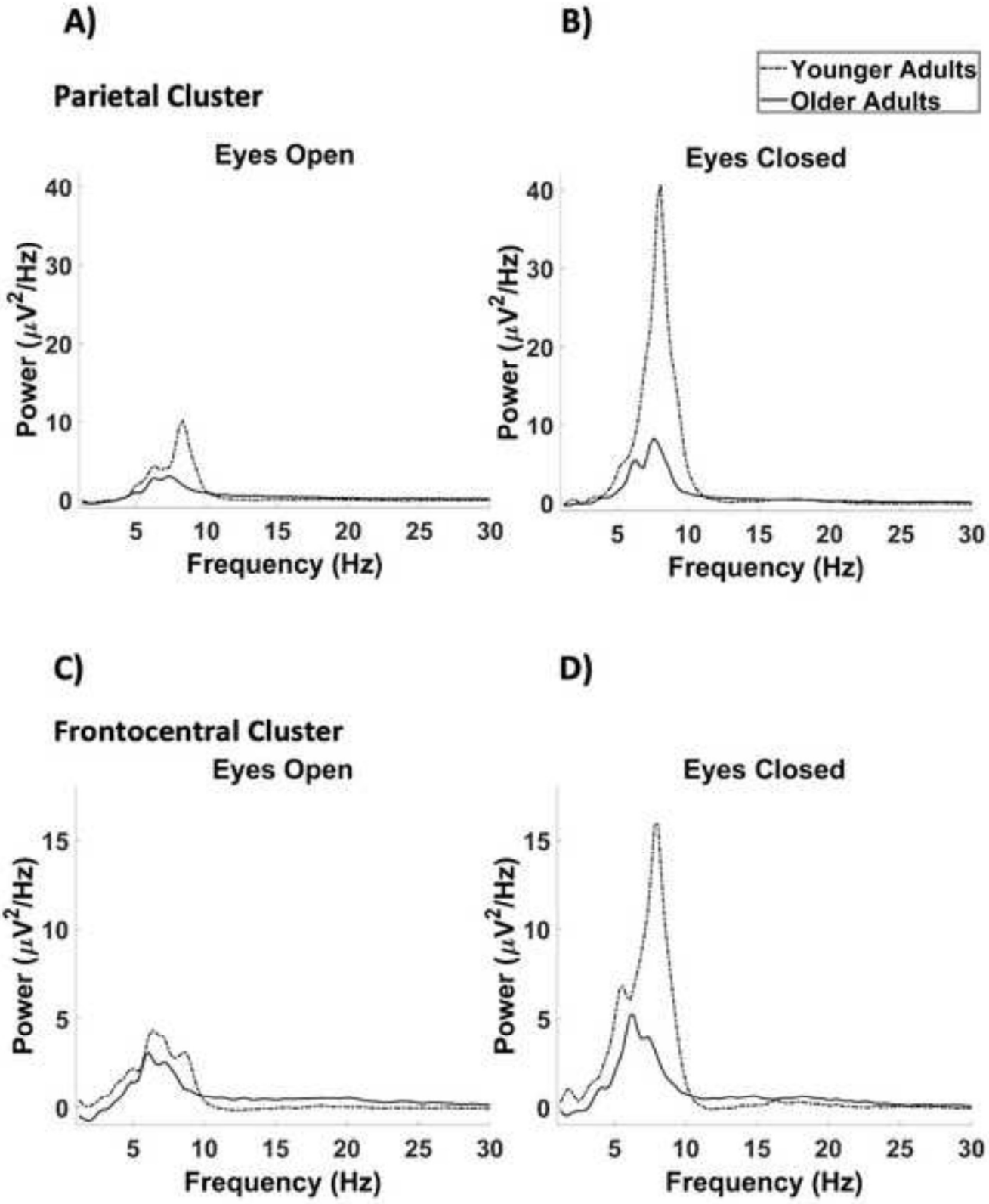

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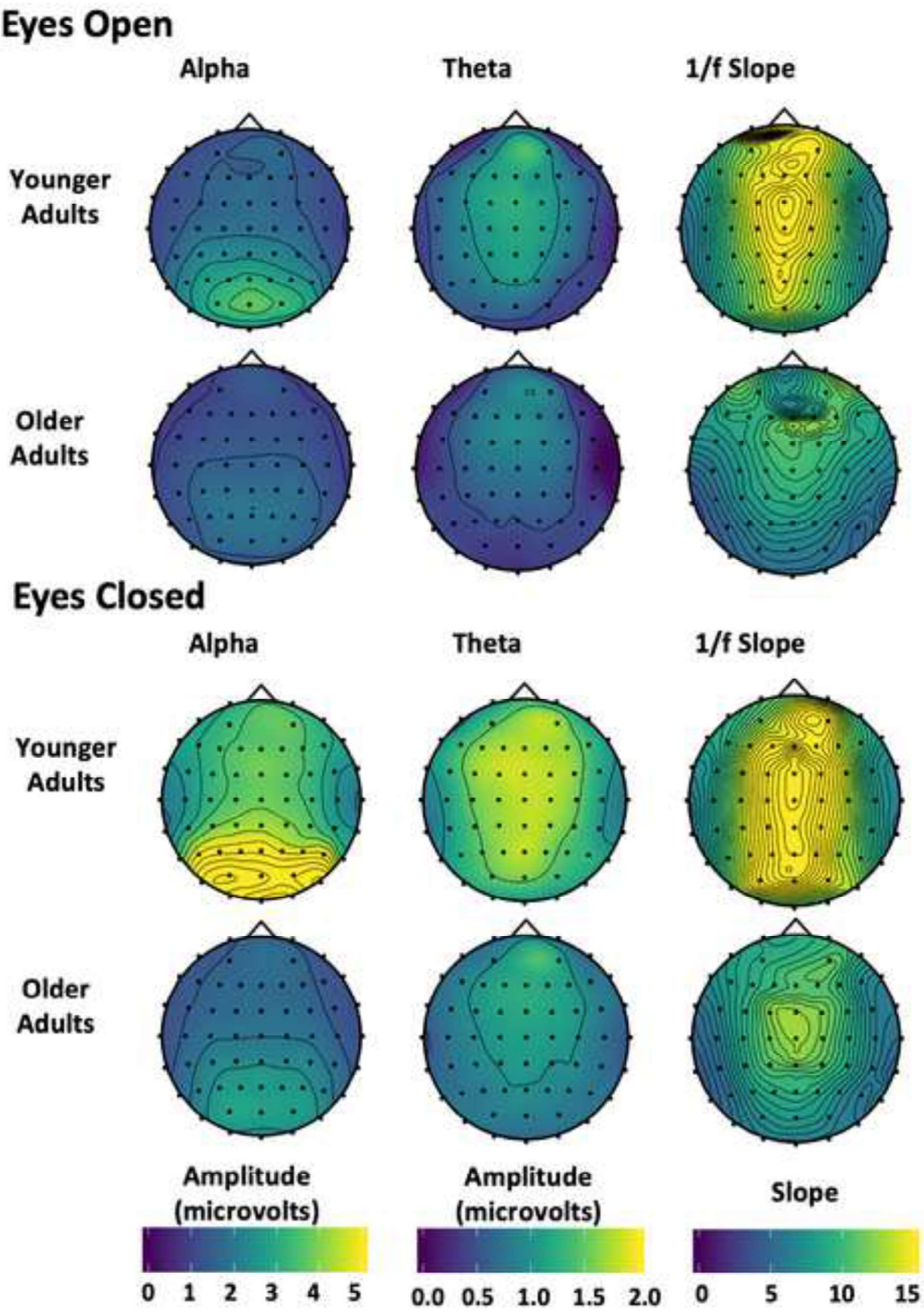
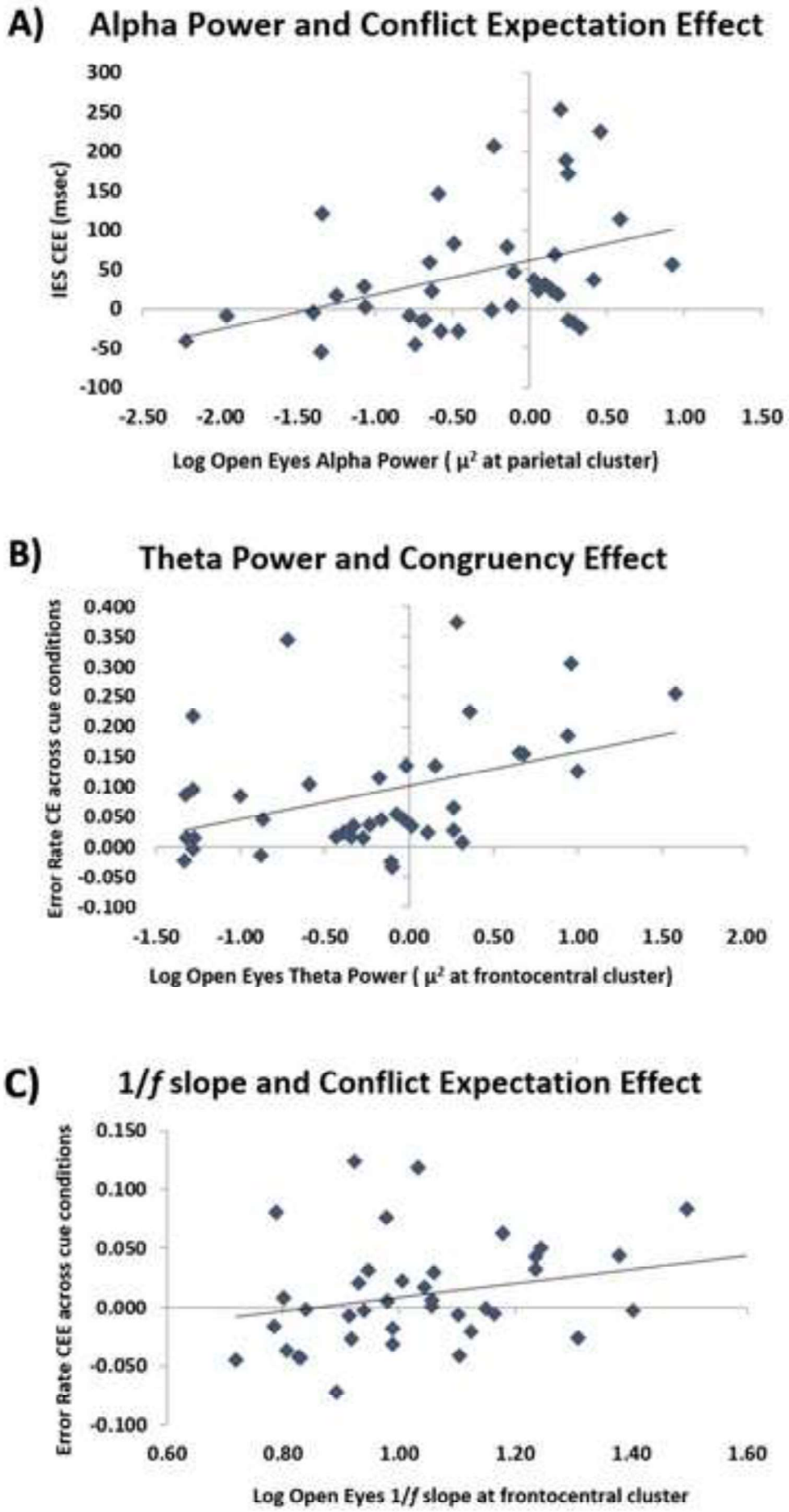
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