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The relation between Scrabble expertise and brain aging as measured with EEG brain signal variability

Hongye Wang [a,*], Penny M. Pexman [a,b], Gary Turner [c], Filomeno Cortese [b,d], Andrea B. Protzner [a,b]

[a] Department of Psychology, University of Calgary, Calgary, Alberta, Canada
[b] Hotchkiss Brain Institute, University of Calgary, Calgary, Alberta, Canada
[c] Department of Psychology, York University, Toronto, Ontario, Canada
[d] Seaman Family MR Centre, Foothills Medical Centre, University of Calgary, Calgary, Alberta, Canada

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ABSTRACT

Recent empirical work suggests that the dynamics of brain function, as measured by brain signal variability, differs between younger and older adults. We extended this work by examining how the relationship between brain signal variability and age is altered in the context of expertise. We recorded electroencephalography from Scrabble experts and controls during a visual word recognition task. To measure variability, we used multiscale entropy, which emphasizes the way brain signals behave over a range of timescales and can differentiate the variability of a complex system (the brain) from a purely random system. We replicated previously identified shifts from long-range interactions among neural populations to more local processing in late adulthood. In addition, we demonstrated an age-related increase in midrange neural interactions for experts, suggesting greater maintenance of network integration into late adulthood. Our results indicate that expertise-related differences in the context of age and brain dynamics occur across different timescales and that these differences are linked to task performance.

1. Introduction

Considerable effort has been invested in identifying electroencephalography (EEG) measures that capture how brain function is altered during the course of healthy aging and how these alterations relate to cognitive decline. This work typically focuses on measures of central tendency in a given time series (e.g., event-related responses [ERPs]), spectral parameters (e.g., spectral power density [SPD]), or functional connectivity (e.g., correlation-based or graph theory metrics; independent component analysis [ICA]). Within-person variability of moment-to-moment brain responses often is ignored or is attributed to confounds that are deliberately removed to improve signal-to-noise ratio. However, an increasing body of work suggests that within-person brain signal variability is an important parameter, reflecting processing integrity and flexibility in the brain (Deco et al., 2013; Garrett et al., 2013). Variability facilitates the transition from one network configuration to another and enables the system to explore multiple states and thus generate multiple behaviors. In essence, variability provides the kinetic energy (McIntosh et al., 2010) for optimal brain responsiveness to our changing internal and external milieus.

In the context of neurocognitive aging, variability research suggests that young and old adults process information differently. Increasing age is associated with increased local information processing and decreased long-range interactions with other neural populations (McIntosh et al., 2014; Vakorin et al., 2011; Wang et al., 2016). Much of this research uses a measure of variability called multiscale entropy (MSE), which examines the predictability of brain signals (i.e., the variability, or the level of randomness in a time series) over different timescales. This last point is important as increased MSE (i.e., variability) at fine timescales, typically reflecting high frequencies, is associated with an increased reliance on local neuronal processing (McDonough and Nashiro, 2014; McIntosh et al., 2014; Vakorin et al., 2011). By contrast, increased MSE at coarse timescales, typically linked with lower frequencies, is associated with increased reliance on global or long-range processing. Thus, MSE is able to identify shifts in brain signal variability, reflecting changes in both local and distributed processing, a critical distinction in aging network neuroscience. Indeed, our

* Corresponding author at: Department of Psychology, University of Calgary, 2500 University Drive NW, Calgary, AB T2N 1N4, Canada. Tel.: +1 403 220 5566; fax: +1 403 282 8249.
E-mail address: hwang@ucalgary.ca (H. Wang).

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group and others have shown that with increasing age, MSE increases at fine timescales (e.g., across 2 ms intervals) but decreases at coarse timescales (e.g., across 50 ms intervals) throughout the brain, during cognitive tasks and resting state (Heisz et al., 2015; McIntosh et al., 2014; Sleimen-Malkoun et al., 2015; Wang et al., 2016). Thus, healthy aging is associated with both increases and decreases in variability, but at different timescales, reflecting a shifting balance between local and long-range processing.

The general trend is for increased age to be associated with neurocognitive decline; as such, identifying individual differences that may moderate this relationship is an important undertaking. To our knowledge, there is only 1 paper that has examined the influence of a potential moderator of age-related cognitive decline in the context of brain signal variability. Heisz et al. (2015) examined whether the age-related shift in brain signal variability from distributed to local processing was influenced by physical activity. They found that older adults who reported being more physically active showed greater task accuracy and greater local information processing (i.e., greater MSE at fine timescales). They suggested that the shift toward local processing was associated with better cognitive outcomes in aging and that this functional brain change was associated with greater physical activity.

Expertise also may have a moderating effect on neurocognitive decline. Although the behavioral research is mixed, several studies suggest that experts show an attenuated age-related performance decline within their area of expertise, even into very old age (Glisky, 2007; Salthouse, 1984; but see; Moxley and Charness, 2013). For example, Charness (1981) found that the quality of a move in chess was related to a player's expertise but not age. A study of age and aviation expertise demonstrated that age-related differences in performance declined in expertise-related tasks but not in other tasks (Morrow et al., 1994). A study with professional pianists (Krampe and Ericsson, 1996) failed to find a negative relationship between age and performance on expertise-related tasks, although both experts and novices showed an age-related decline in performance on non-expertise-related tasks. Work with structural MRI and ERP also suggests that expertise may be associated with moderating influences on the trajectory of age-related neurocognitive decline. For example, a structural MRI study on professional perfumers found that perfumers' olfactory expertise was related to increased gray matter volume from the gyrus rectus to the medial orbital gyrus (Delon-Martin et al., 2013). This increase offset the age effect as age was negatively correlated with gray matter volume in this region in controls but not in experts. An ERP study demonstrated that tactile expertise gained by dentists and watchmakers was associated with age-accompanied differences in the P300, a parietal ERP component that is related to attention and working memory (Reuter et al., 2014). Specifically, although P300 amplitude reduced with age and expertise, the reduction was positively correlated with performance only in older control participants, but not in experts. This indicates that the P300 amplitude reduction in experts may reflect reduced cognitive effort due to expertise. Finally, another ERP study targeting subcortical and cortical auditory brain regions demonstrated an association between long-term music experience and decreased reaction times for vowel categorization in older musicians, offsetting the age-related delay in neural responses to speech sounds (Biedelman and Alain, 2015). Considered together, these findings suggest that expertise may influence the trajectory of brain aging, especially in expertise-related tasks.

In the present study, we investigated the relationship between brain aging and expertise, in the context of visual word recognition with Scrabble experts. Scrabble is a popular board game that requires word recognition skills. What differentiates a competitive Scrabble player from a novice/casual player is that the former invests significant time memorizing words from the official Scrabble dictionary, practicing anagramming, and playing Scrabble (Halpern and Wai, 2007). Competitive Scrabble players show superior performance on a classic visual word recognition paradigm, the lexical decision task (LDT), as compared to age- and education-matched controls, especially for words presented vertically (Hargreaves et al., 2012). Findings from fMRI and ERP studies suggest further that the superior word recognition performance of Scrabble players is associated with different implicit task strategies: whereas both Scrabble experts and controls activate brain regions associated with meaning retrieval in visual word recognition, Scrabble experts additionally make use of brain regions associated with working memory and visual processing (e.g., superior parietal and extensive visual cortex; van Hees et al., 2017; Protzner et al., 2016).

Here, we acquired EEG from a lifespan sample of Scrabble experts and controls while they performed the LDT, using horizontally and vertically presented letter strings. We calculated MSE to characterize brain signal variability across the sample. We also calculated SPD as a complementary method, to examine the connection between MSE and a measure of central tendency (i.e., SPD) in the EEG signal (Courtiol et al., 2016). For our behavioral measures, we predicted age-related increases in reaction time (RT) during the LDT (Allen et al., 1991; Ratcliff et al., 2004) as well as increased accuracy due to the different speed-accuracy criteria settings between young and older controls (Ratcliff et al., 2004). We expected these differences to be attenuated in Scrabble experts (Bidelman and Alain, 2015; Halpern and Wai, 2007). For our brain measures, we predicted increased age to be associated with a shift toward local information processing (McIntosh et al., 2014; Vlahou et al., 2014; Wang et al., 2016). In older Scrabble experts, we expected the shift toward local processing to be amplified (Heisz et al., 2015).

2. Methods

2.1. Participants

Participants were 19 competitive Scrabble players and 19 age-matched, nonexpert controls. Scrabble experts ranged from 24 to 79 years of age (mean: 57.2, standard deviation [SD]: 18, 10 males) with a mean of 16.6 years of education (SD: 2.9). Controls ranged from 24 to 83 years of age (mean: 55.9, SD: 16.3, 9 males), with a mean of 17.4 years of education (SD: 3.3). Competitive Scrabble players were recruited from extensive advertising over a 1-year period at local and national Scrabble competitions held in the Calgary area. Controls were recruited through community advertising. All participants were right handed and underwent comprehensive screening to ensure that they had no neurological disorders, were not experiencing any psychiatric illnesses, were not taking any psychotropic medications, and did not have any vision or hearing deficits that might interfere with task performance. Ethical approval was obtained from the Conjoint Faculties Research Ethics Board of the University of Calgary. All participants gave written informed consent before participation and received monetary compensation for their time.

2.2. Scrabble expertise

On average, our Scrabble experts had played competitively for 12.32 years (SD: 6.63) and practiced 8.29 h/wk (SD: 5.79). We captured Scrabble expertise through an official ratings system called the North American Scrabble Players Association (NASPA) rankings. Our group had an average NASPA ranking of 1210 (SD: 299), placing most of them in the top quarter of all tournament-ranked Scrabble players (scrabbleplayers.org). NASPA rankings were not correlated with amount of practice or with age.

2.3. Stimuli and task

The EEG data collected were part of a larger project that included fMRI acquisition for a subset of the participants, and the tasks used here were described in detail in another study (van Hees et al., 2017). Briefly, participants completed 288 word and 192 nonword trails, with half presented horizontally, and half vertically. Word stimuli matched nonword stimuli for word length and visual characteristics such as orthographic Levenshtein distance (Yarkoni et al., 2008). Participants were seated approximately 80 cm from the computer screen, and the visual angle of the stimuli ranged between 3.2° × 0.6° for 4-letter strings and 6.4° × 0.6° for 8-letter strings. Each trial started with a fixation cross presented for variable durations between 250 and 750 ms (mean: 500 ms), followed by a letter string. Participants indicated whether the letter string was a word or nonword by pressing 1 of 2 response buttons as quickly and accurately as possible. The response triggered a 1000 ms blank screen, followed by the next trial (Fig. 1).

2.4. Cognitive tests

We tested participants on a battery of cognitive tests to confirm that group differences were restricted to Scrabble-specific expertise (van Hees et al., 2017). This battery included (1) Controlled Oral Word Association Test (COWAT; Spreen and Strauss, 1998)—participants generated as many words as possible that start with a given letter (“F”, “A”, “S”, and “UN”), or belong to a category (“animal”), within 1 minute; (2) Revised Author Recognition Test (Acheson et al., 2008)—participants identified real author names from a list of 130 names; (3) North American Adult Reading Test (Uttl, 2002)—participants pronounced 35 irregular English words; (4) WAIS III Digit Symbol test (Wechsler, 1997)—participants matched symbols to a list of numbers based on 9 digit-symbol pairs as fast as possible within 2 minutes; and (5) Anagramming skill (Tuffiash et al., 2007)—participants verbally solved 51 anagrams.

2.5. EEG acquisition and preprocessing

We collected EEG recordings from 64 active electrodes with an EasyCap 10/20 positioning system (actiCHamp; Brain Products GmbH, Gilching, Germany), in a dimly lit, quiet room. Cz was the reference, and the sampling rate was 500 Hz. For preprocessing, we bandpass-filtered continuous EEG recordings from 0.1 to 55 Hz and re-referenced to a common average reference, rejected data with excessive signal amplitude, and then performed artifact removal using ICA as implemented in EEGLAB (Delorme and Makeig, 2004). We removed components associated with eye blinks, saccades, horizontal eye movements, and muscle artifacts. We epoched the cleaned continuous EEG data into 1500 ms windows commencing at stimulus onset. After visual inspection of all epochs, we kept only artifact-free correct trials and separated epochs by condition. For our MSE analyses, we did not baseline the data because MSE measures are not influenced by the mean of the signal. For our SPD analyses, we normalized the data within epoch (mean: 0, SD: 1) to deal with age-related global signal power differences.

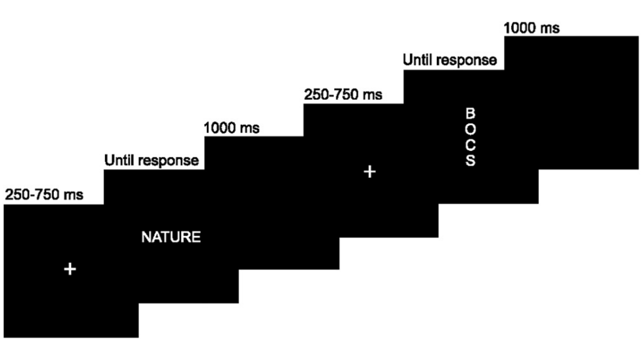

Fig. 1. The sequence of events for LDT trials. Abbreviation: LDT, lexical decision task.

2.6. Behavioral analysis

We first examined whether RT and accuracy differed across group, orientation, and word type by using a 2 (group: controls vs. experts) × 2 (orientation: horizontal vs. vertical) × 2 (word type: word vs. nonword) mixed-design ANOVA. Group was a between-subject factor, and orientation and word type were within-subject factors. Next, we examined whether age-related differences in performance varied between the 2 groups. As Scrabble experts are faster than controls at recognizing vertically displayed words and nonwords (Hargreaves et al., 2012; Protzner et al., 2016; van Hees et al., 2016), we hypothesized that group differences might be more evident in vertical conditions and ran general linear regressions on horizontal and vertical conditions separately. We examined whether the slopes of the regression lines between age and RT were different between the 2 groups, across word and nonword conditions.

2.7. MSE estimation of brain signal variability

Full details of MSE and its relevance for the analyses of signal complexity are provided in the study by Costa et al. (2005). The MSE method calculates entropy as a measure of regularity (predictability) of the EEG signal at different timescales, where greater MSE values represent greater entropy. The calculation of MSE involves 2 steps. First, data are resampled to create timescales. For each scale, data points within nonoverlapping windows are averaged. For example, scale 1 is the raw time series (i.e., 2 ms windows in the context of a 500 Hz sampling rate), scale 2 averages over 2 time points (i.e., 4 ms windows), scale 15 averages over 15 time points (i.e., 30 ms windows), and so on. Second, sample entropy is calculated for each epoch, measuring predictability by evaluating the appearance of repetitive patterns. Following parameter values used in several aging studies (Courtiol et al., 2016; McIntosh et al., 2014; Sleimen-Malkoun et al., 2015), we calculated MSE for each epoch using the algorithm available at www.physionet.org/physiotools/mse/, with parameter values m (pattern length) = 2 (Small and Tse, 2004) and r (tolerance) = 0.5 (Richman and Moorman, 2000). The length of the time series was 750 data points (corresponding to 1500 ms post-stimulus onset epochs). To ensure reliable MSE estimation, we included only those timescales for which we had at least 50 samples. Thus, for each participant, electrode- and condition-specific MSE estimates were obtained as a mean across within-epoch entropy measures for scales 1–15 (or 2–30 ms windows), where lower values represent fine timescales, and higher values represent medium timescales. Single trial estimates were averaged across trials to obtain mean MSE for each condition.

2.8. SPD estimation

We calculated SPD because a comparison of MSE and SPD results allowed us to examine how MSE measures relate to the frequency content of the EEG signal and to evaluate if age- and performance-related differences depend more on linear (assessed by both MSE and SPD) or nonlinear (assessed only by MSE) dependencies in the data (Courtiol et al., 2016). SPD of the signal was calculated using fast Fourier transform on single trial data. As described previously, the signal was first normalized (mean: 0, SD: 1) to deal with age-related global signal power differences. Relative contributions of different frequency bands to the total spectral power were calculated based on normalized data. Given a sampling rate of 500 Hz and 750 time points in 1500 ms per trial, the frequency resolution was 0.6667 Hz. Single-trial estimates were averaged to obtain mean SPD for each condition.

2.9. Partial least squares analysis

Analysis of MSE and SPD measures (i.e., MSE/SPD averaged across trials within condition) was carried out using a hypothesis-driven (i.e., nonrotated) version of behavioral partial least squares (bPLS; Krishanan et al., 2011; Lobaugh et al., 2001; McIntosh and Lobaugh, 2004; McIntosh et al., 2008). This is a multivariate technique that allowed us to examine group-dependent similarities and differences in correlations between MSE/SPD and age and between MSE/SPD, age, and RT measured during LDT performance. In a step that was separate from bPLS, we residualized task-specific RT from age. This process ensured that our measures of age and RT were orthogonal in our analyses and allowed us to examine the relation between age and brain function independent from age-related differences in performance, as well as the combined effects of age and age-related differences in performance on brain function (Ankudowich et al., 2016).

For bPLS, we first calculated the correlations between MSE/SPD and the age-residual, and MSE/SPD and RT across the entire sample, to quantify the strength of associations between our brain and behavioral measures. We then conducted inferential analyses on the product of correlation matrix and a predefined contrast matrix to identify latent variables (LVs) that show similarities or differences in MSE/SPD across electrode timescales/frequencies associated with individual differences in behavioral measures, across groups. Each LV contained 3 vectors: design saliences, electrode saliences, and a scalar singular value. Design saliences were the predefined contrasts between groups and/or conditions. Electrode saliences identified the particular pattern of electrodes and timescales/frequencies that were most related to the condition/group effect expressed in the LV. The scalar singular value indicated the strength of the effect expressed by the LV.

Statistical assessment in PLS was performed across 2 levels. First, the overall significance of each LV was assessed with permutation testing (Good, 2000). An LV was considered significant if the observed singular value exceeded the permuted singular value in more than 95% of the permutations ($p < 0.05$). Second, bootstrap resampling was used to estimate confidence intervals around electrode timescale/frequency weights in each LV, allowing for an assessment of the relative contribution of particular electrode timescales/frequencies, and the stability of the relation with the age-residual or performance (Efron and Tibshirani, 1986). No corrections for multiple comparisons were necessary because the electrode timescale/frequency weights were calculated in a single mathematical step on the whole brain. For the brain data, we plotted bootstrap ratios (ratio of the individual weights over the estimated standard error) as a proxy for z scores, with a threshold of 2.6 corresponding approximately to a 99% confidence interval, or $p < 0.01$.

3. Results

3.1. Behavioral results

We found no significant group differences for age, education, and cognitive tests that were not directly related to Scrabble practice (i.e., verbal fluency on the COWAT when probed with the category “animals,” perceptual speed, vocabulary, and print exposure). We found significant differences in cognitive tests that were directly related to Scrabble practice (i.e., verbal fluency on the COWAT with probes “F” ($t(36) = 2.9$, $p < 0.01$), “A” ($t(36) = 3.5$, $p < 0.01$), “S” ($t(36) = 2.5$, $p < 0.05$), “UN” ($t(36) = 3.0$, $p < 0.01$), and anagramming ($t(36) = 8.4$, $p < 0.001$)).

Performance measures (RT and percent correct) are presented in Table 1. Mixed-design ANOVA on RT yielded a significant three-way interaction between group, orientation, and word type ($F[1, 36] = 4.563$, $p = 0.04$, $\eta^2 = 0.112$). Further analyses revealed a significant simple interaction between orientation and group for words ($F[1, 36] = 8.843$, $p = 0.005$, $\eta^2 = 0.197$) and a significant simple interaction between orientation and group for nonwords ($F[1, 36] = 8.831$, $p = 0.005$, $\eta^2 = 0.197$). We then examined the second-order simple effects of group (Howell and Lacroix, 2012) and found significant differences for vertical words ($F[1, 36] = 5.299$, $p = 0.027$, $\eta^2 = 0.128$) and vertical nonwords ($F[1, 36] = 4.688$, $p = 0.037$, $\eta^2 = 0.115$). Mixed-design ANOVA on accuracy only yielded a significant main effect of orientation ($F[1, 36] = 22.094$, $p < 0.001$, $\eta^2 = 0.38$) and a significant main effect of word type ($F[1, 36] = 16.798$, $p < 0.001$, $\eta^2 = 0.318$). As accuracy was close to ceiling for both participant groups, we focused on RT for the remainder of the analyses.

General linear regression analysis demonstrated no group differences in the association between age and RT (i.e., the slopes of the regression lines were not significantly different between groups for horizontal conditions ($F[3, 68] = 0.822$, $p = 0.486$, $\eta^2 = 0.035$) or vertical conditions ($F[3, 68] = 1.011$, $p = 0.393$, $\eta^2 = 0.043$) (Fig. 2).

3.2. Expertise, age-residual, and MSE

We used 2 contrasts to examine group- and condition-dependent correlations between MSE and the age-residual: group similarities (contrast weights 1 1 1 1 1 1 1 1) and group differences (contrast weights 1 1 1 1 −1 −1 −1 −1). The group similarities LV (56.56% explained covariance, $p < 0.001$, Fig. 3A) revealed a positive correlation between MSE at fine timescales (2–18 ms) and the age-residual across all conditions for both groups. This pattern was stable at bilateral frontal, central, temporal, and parietal electrodes. The group differences LV (43.44% explained covariance, $p < 0.001$, Fig. 3B) revealed that for all conditions, MSE at fine (12–18 ms) and middle timescales (18–28 ms) decreased with the age-residual for controls but increased for experts in frontal, temporal, central, parietal, and occipital electrodes. Group differences identified at fine timescales did not overlap with those identified in the similarities LV.

3.3. Expertise, age-residual, LDT RT, and MSE

We used 2 contrasts to examine group- and condition-dependent correlations between MSE, the age-residual, and RT:

Table 1
Mean behavioral performance measures for LDT (standard deviation in parentheses)

Measure	Controls	Scrabble experts	F-value (1, 36)
a. Response time (ms)			
Horizontal word	713 (135)	674 (107)	0.979
Horizontal nonword	1004 (345)	895 (232)	1.296
Vertical word	1009 (311)	821 (174)	5.299[a]
Vertical nonword	1543 (644)	1175 (365)	4.688[a]
b. Percent correct			
Horizontal word	96.6 (6.2)	99.0 (1.1)	Not tested
Horizontal nonword	93.4 (5.8)	93.8 (4.1)	Not tested
Vertical word	93.6 (8.8)	98.4 (1.3)	Not tested
Vertical nonword	91.7 (7.3)	92.2 (3.9)	Not tested

Key: LDT, lexical decision task.
[a] $p < .05$. For the percent correct analysis, second-order simple effects for group were not tested because of a nonsignificant main effect of group. Abbreviation: LDT, lexical decision task.

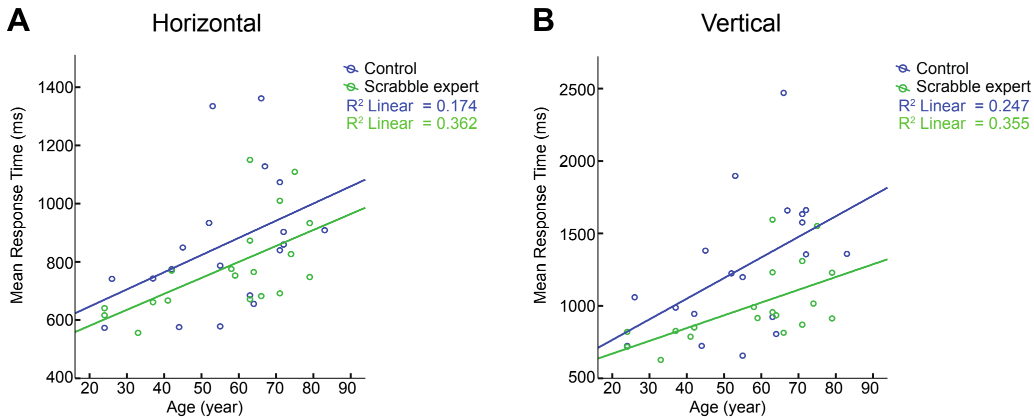

Fig. 2. Regression of mean LDT RT (averaged over word and nonword conditions) with age for each group in horizontal (A) and vertical conditions (B). Abbreviations: LDT, lexical decision task; RT, reaction time.

group similarities (contrast weights 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1) and group differences (contrast weights 1 1 1 1 1 1 1 1 −1 −1 −1 −1 −1 −1 −1 −1). The group similarities LV (51.61% explained covariance, $p < 0.001$, Fig. 4A) revealed a positive correlation between MSE at fine timescales (2–16 ms) and the age-residual across all conditions for both groups and a positive correlation between MSE and RT across all conditions for experts only. This pattern was slightly less extensive than the age-residual effect and appeared at bilateral frontal and some central and parietal electrodes. The group differences LV (48.39% explained covariance, $p < 0.001$, Fig. 4B) suggested that MSE was positively correlated with the age-residual and RT across all conditions for experts at fine timescales (2–18 ms) at 3 parietal electrodes (P2, CPz, and POz, which are different from the parietal electrodes identified in the previous LV) and at middle timescales (18–28 ms) in bilateral parietal and occipital electrodes. This LV did not show a reliable relationship for controls (see bar graph, Fig. 4B).

3.4. Expertise, age-residual, and SPD

We used 2 contrasts to examine group- and condition-dependent correlations between SPD and the age-residual: group similarities (contrast weights 1 1 1 1 1 1 1 1) and group differences (contrast weights 1 1 1 1 −1 −1 −1 −1). The similarities LV (65.56% explained covariance, $p < 0.001$; Fig. 5A) revealed a negative correlation between the age-residual and SPD in delta (1–4 Hz), theta (4–7 Hz), and upper alpha (12–14 Hz) bands and a positive correlation in beta (16–30 Hz) and gamma (30–50 Hz) bands across all conditions for both groups at frontal, temporal, central, and parietal electrodes. The differences LV (34.44% explained covariance, $p = 0.006$; Fig. 5B) demonstrated that the age-residual and SPD in upper alpha (11–15 Hz) and lower beta (15–22 Hz) bands were positively correlated in experts and negatively correlated in controls throughout the brain.

3.5. Expertise, age-residual, LDT RT, and SPD

We used 2 contrasts to examine group- and condition-dependent correlations between SPD, the age-residual, and RT: group similarities (contrast weights 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1) and group differences (contrast weights 1 1 1 1 1 1 1 1 −1 −1 −1 −1 −1 −1 −1 −1). The similarities LV (59.23% explained covariance, $p < 0.001$; Fig. 6A) revealed that SPD in delta (1–4 Hz), theta (4–7 Hz), and upper alpha (11–14 Hz) bands negatively correlated with the age-residual across all conditions for both groups and negatively correlated with RT across all conditions for experts in bilateral frontal, and some temporal, central, and parietal electrodes. In addition, SPD in beta (15–30 Hz) and gamma (30–50 Hz) bands positively correlated with the age-residual across all conditions for both groups and positively correlated with RT across all conditions for experts, mainly in frontal electrodes. The differences LV (40.77% explained covariance, $p < 0.001$; Fig. 6B) demonstrated that SPD in delta (1–4 Hz) and theta (5–7 Hz) bands negatively correlated with the age-residual and RT across all conditions except vertical nonwords for experts and positively correlated with the age-residual and RT across all conditions except vertical nonwords for controls. In addition, SPD in upper alpha (10–15 Hz) and lower beta (15–20 Hz) bands positively correlated with the age-residual and RT across all conditions except vertical nonwords for experts and negatively correlated with the age-residual and RT across all conditions except vertical nonwords for controls.

3.6. Degree of complementarity between MSE and SPD analyses

For the age-residual bPLSs, the correlation between brain scores from the MSE and SPD analyses is 0.9638 ($p < 0.001$) for the similarities LV and 0.7455 ($p < 0.001$) for the differences LV. For the age-residual and RT bPLSs, the correlation between brain scores from the MSE and SPD analyses is 0.9116 ($p < 0.001$) for the similarities LV and 0.8299 ($p < 0.001$) for the differences LV.

4. Discussion

We examined the relation between Scrabble expertise and brain aging in the context of brain signal variability and spectral power density measured during an expertise-related task. We replicated the previously identified shift toward more local neural processing with increasing age. We additionally demonstrated that experts showed greater midrange neural interactions with increasing age, suggesting that for this expert group, there was greater maintenance of network integration into late adulthood. While these brain differences emerged in the absence of age-related differences in task performance between experts and nonexperts, brain and performance associations were much stronger in experts than in controls.

4.1. Expertise, age, and task performance

LDT response accuracy was near ceiling, so we were unable to examine the relationship between accuracy, age, and expertise. We were able to replicate previously identified age-related increases in LDT RT (Allen et al., 1991; Ratcliff et al., 2004) and

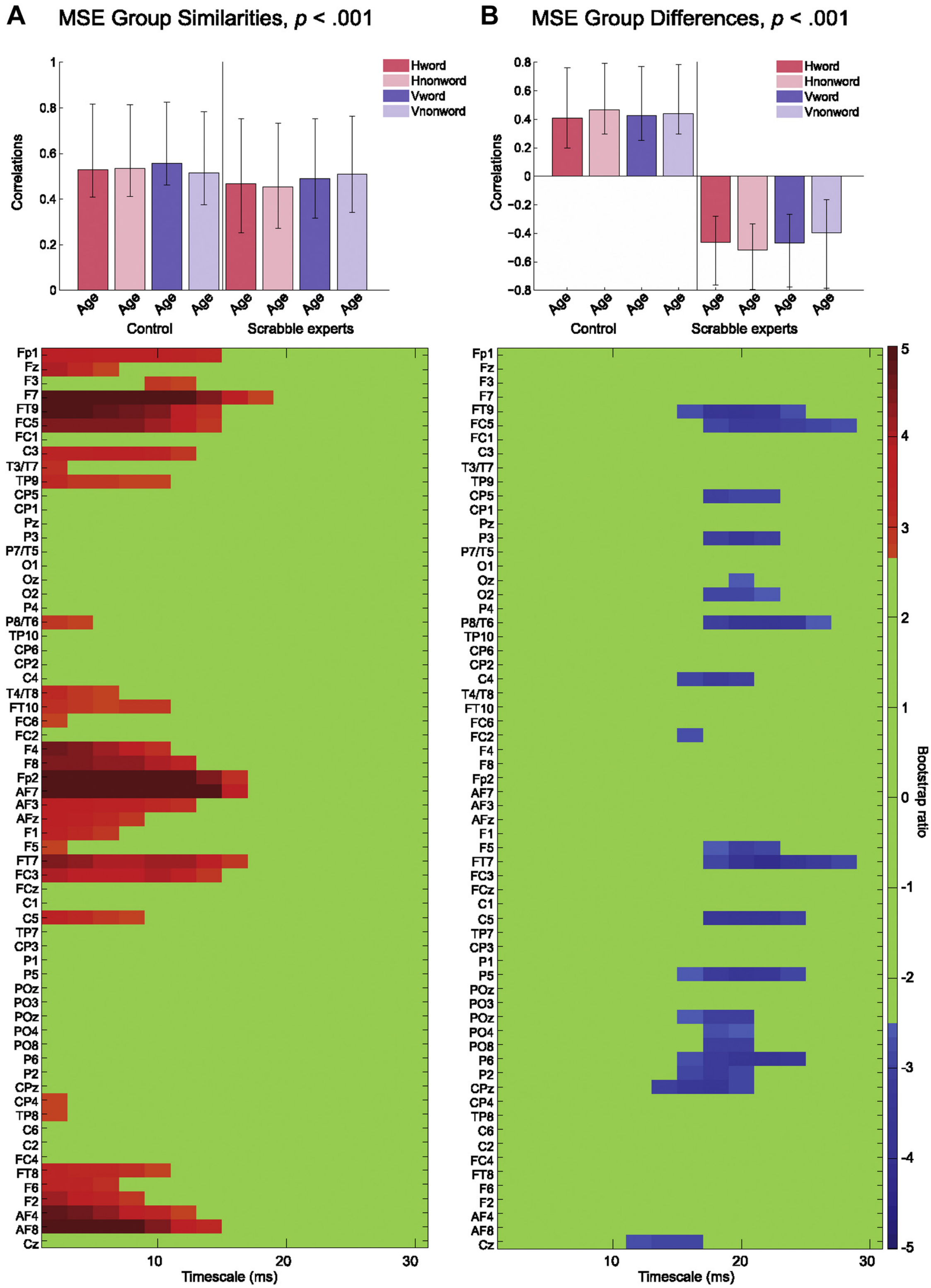

Fig. 3. bPLS results illustrating group similarities (A) and differences (B) in the association between MSE and the age-residual. The bar graphs depict the contrast between conditions and the age-residual that was significantly expressed across the entire data set as determined by permutation tests, with 95% confidence intervals. The statistical image plots (bootstrap ratio maps) represent electrodes and timescales at which the correlation between MSE and the age-residual was most stable as determined by bootstrapping. Values represent the ratio of the parameter estimate for the electrode divided by the bootstrap-derived standard error (roughly z scores). In panel A, positive values indicate electrodes and timescales showing increased MSE with the age-residual for both groups. In panel B, negative values indicate electrodes and timescales showing decreased MSE with the age-residual for controls but increased MSE with the age-residual for Scrabble experts. Abbreviations: bPLS, behavioral partial least squares; LDT, lexical decision task; MSE, multiscale entropy; RT, reaction time.

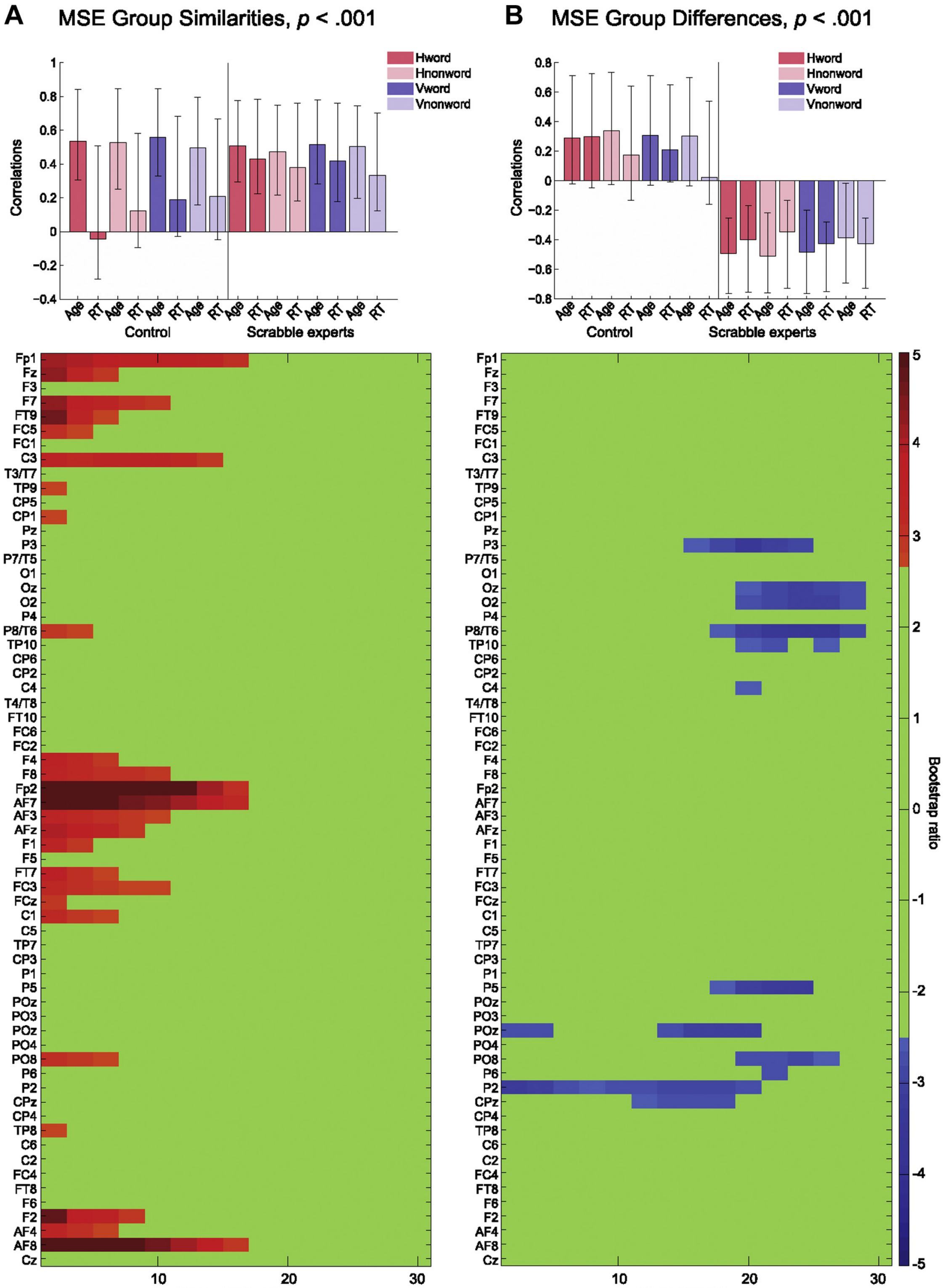

Fig. 4. bPLS results illustrating group similarities (A) and differences (B) in the association between MSE, the age-residual, and LDT RT. The bar graphs depict the contrast between conditions, the age-residual, and RT that was significantly expressed across the entire data set as determined by permutation tests, with 95% confidence intervals. The statistical image plots (bootstrap ratio maps) represent electrodes and timescales at which the correlation of MSE with the age-residual and RT was most stable as determined by bootstrapping. Values represent the ratio of the parameter estimate for the electrode divided by the bootstrap-derived standard error (roughly z scores). In panel A, positive values indicate electrodes and timescales showing increased MSE with the age-residual for both groups and increased MSE with increased RT for experts only. In panel B, negative values indicate electrodes and timescales showing increased MSE with the age-residual and increased RT for experts. Abbreviations: bPLS, behavioral partial least squares; LDT, lexical decision task; MSE, multiscale entropy; RT, reaction time.

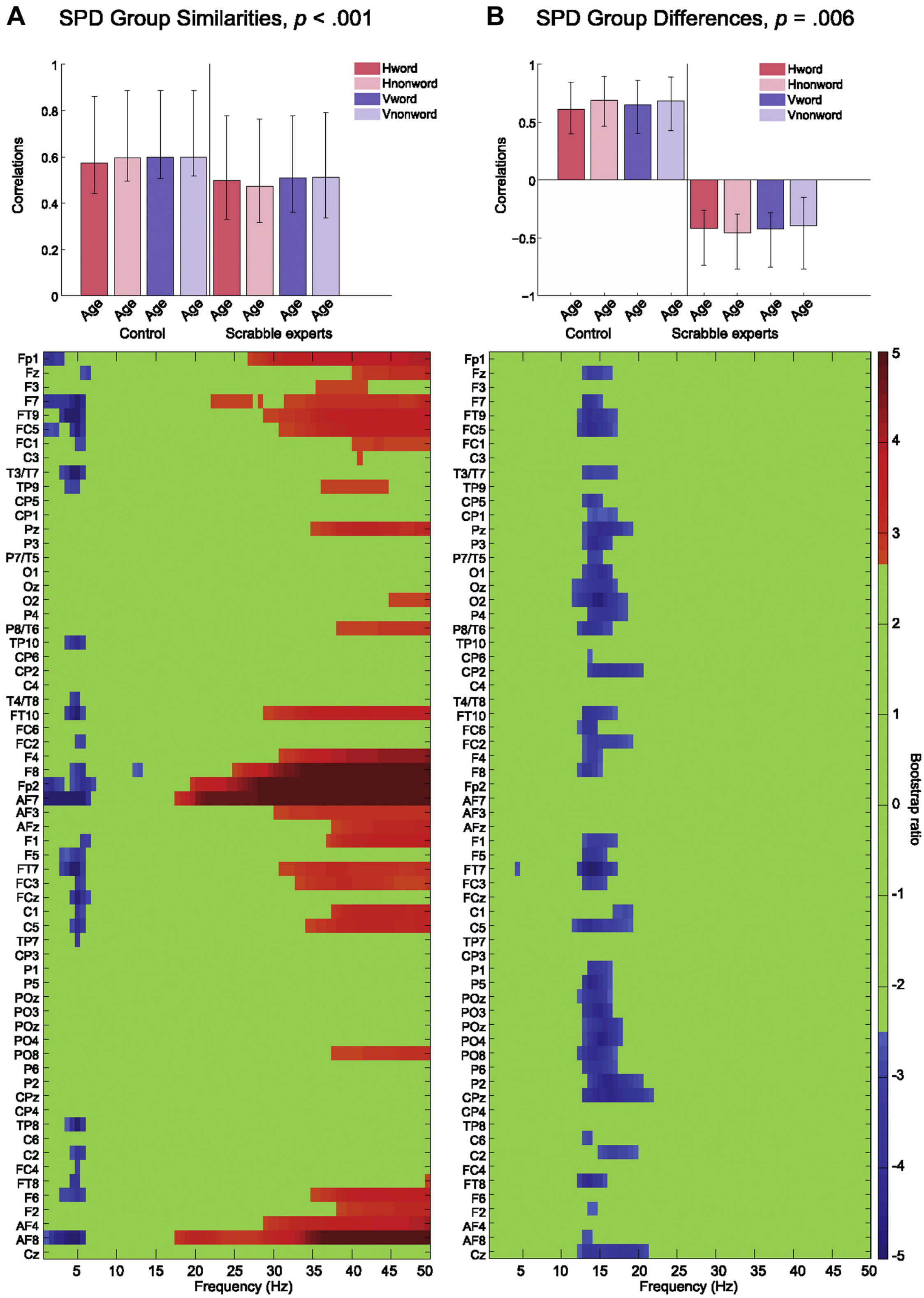

Fig. 5. bPLS results illustrating group similarities (A) and differences (B) in the association between SPD and the age-residual. The bar graphs depict the contrast between conditions and the age-residual that was significantly expressed across the entire data set as determined by permutation tests, with 95% confidence intervals. The statistical image plots (bootstrap ratio maps) represent electrodes and frequencies at which the correlation between SPD and the age-residual was most stable as determined by bootstrapping. Values represent the ratio of the parameter estimate for the electrode divided by the bootstrap-derived standard error (roughly z scores). In panel A, for both groups, positive values indicate electrodes and frequencies showing increased SPD with the age-residual and negative values indicate decreased SPD with the age-residual. In panel B, negative values indicate electrodes and frequencies showing decreased SPD with the age-residual for controls but increased SPD with the age-residual for experts. Abbreviations: bPLS, behavioral partial least squares; LDT, lexical decision task; RT, reaction time; SPD, spectral power density.

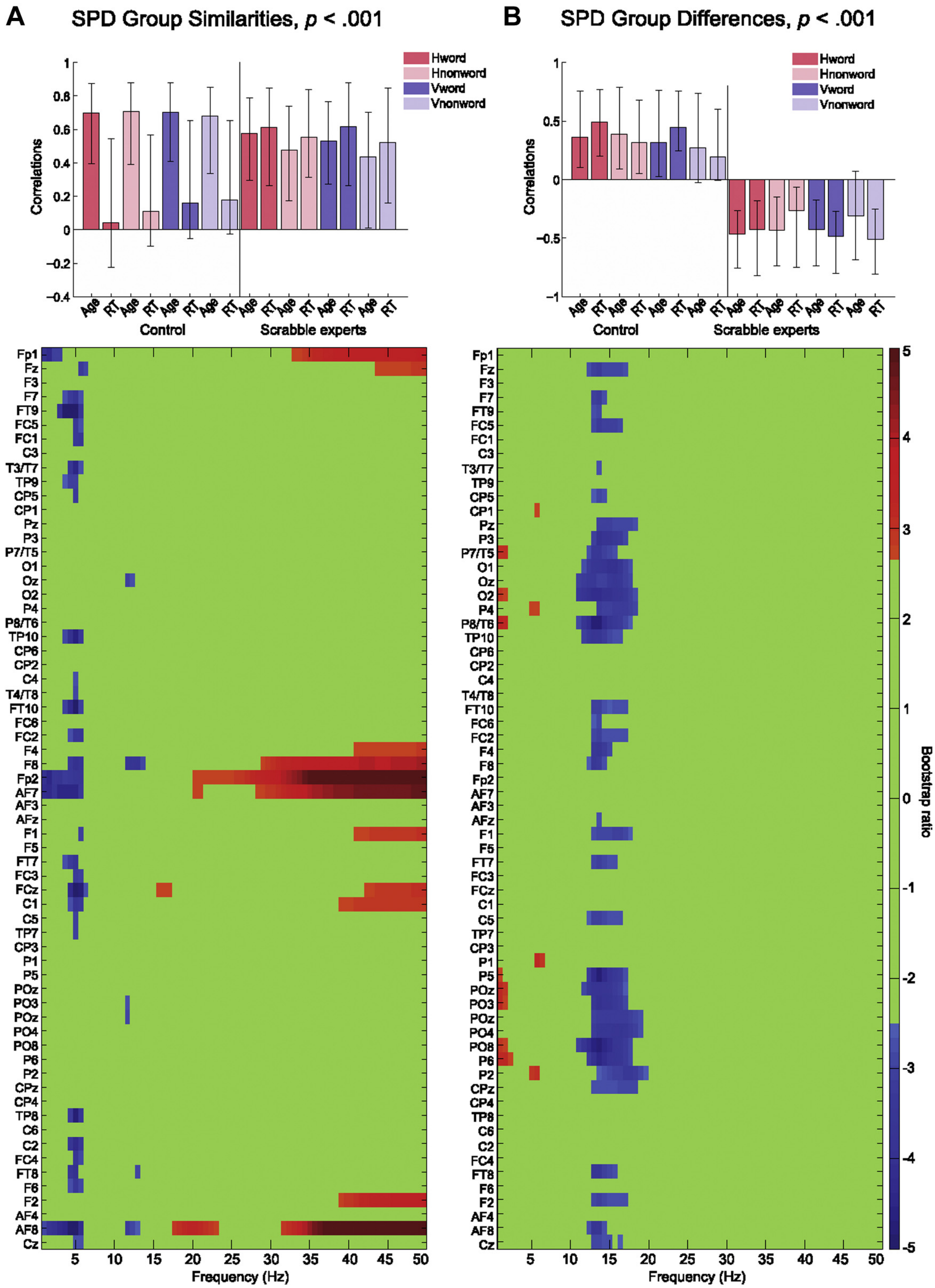

Fig. 6. bPLS results illustrating group similarities (A) and differences (B) in the association between SPD, the age-residual, and RT. The bar graphs depict the contrast between conditions, the age-residual and RT that was significantly expressed across the entire data set as determined by permutation tests, with 95% confidence intervals. The statistical image plots (bootstrap ratio maps) represent electrodes and frequencies at which the correlation of SPD with the age-residual and RT was most stable as determined by bootstrapping. Values represent the ratio of the parameter estimate for the electrode divided by the bootstrap-derived standard error (roughly z scores). In panel A, positive values indicate electrodes and frequencies showing increased SPD with the age-residual for both groups and increased SPD with increased RT for experts only. Negative values indicate electrodes and frequencies showing decreased SPD with the age-residual for both groups and decreased SPD with increased RT for experts only. In panel B, positive values indicate electrodes and frequencies showing increased SPD with increased age-residual and increased RT for controls but decreased SPD with increased age-residual and increased RT for experts; negative values indicate electrodes and frequencies showing decreased SPD with increased age-residual and increased RT for controls but increased SPD with increased age-residual and increased RT for experts. Abbreviations: bPLS, behavioral partial least squares; LDT, lexical decision task; RT, reaction time; SPD, spectral power density.

demonstrated that these increases were not modified in the context of expertise.

4.2. Expertise, age, and brain dynamics

In line with previous aging work (McIntosh et al., 2014; Sleimen-Malkoun et al., 2015; Wang et al., 2016), both Scrabble experts and controls showed increased MSE with age at fine timescales (2–18 ms) throughout the brain during LDT. Based on trial length, we measured MSE only up to medium timescales and did not assess the previously identified, age-related decrease in MSE at coarse timescales. Our MSE results suggest that for both experts and controls, there is a bias in older adults toward more local neural processing associated with specialization of functional networks (McIntosh et al., 2014; Vakorin et al., 2011).

Group similarities in SPD results were complementary to our MSE results. Specifically, both controls and competitive Scrabble players demonstrated a similar negative correlation between age and SPD in delta and theta bands (1–7 Hz) in frontal, temporal, central, and parietal electrodes and positive correlation between age and SPD in beta and gamma bands (16–50 Hz) in the same regions. These findings are consistent with the age-related EEG power shift, where increased age is associated with decreased power at lower frequencies (e.g., theta band) and increased power at higher frequencies (e.g., beta band) in frontal, central, and parietal electrodes (Polich, 1997; Vlahou et al., 2014; Zappasodi et al., 2015). Given suggestions that higher EEG frequencies modulate activity over small spatial regions in short time windows (McIntosh et al., 2014; Vakorin et al., 2011; von Stein and Sarnthein, 2000), increased SPD in beta/gamma may reflect relatively increased variability in more local networks.

Importantly, we also identified group differences in the relationship between age and MSE. Fine scale MSE (2–18 ms) in parietal electrodes increased with age for experts but decreased with age for controls, suggesting that the increase in local processing with age was greater for experts specifically in parietal regions. Midscale MSE (18–28 ms) also increased with age for experts but decreased with age for controls, with the strongest effects in bilateral parietal and occipital electrodes. Midscale MSE highlights frequencies in the lower beta band (e.g., MSE coarse grained at 28 ms is associated with frequencies around 18 Hz according to Courtiol et al., 2016, equation 11). Our SPD results suggest that power in upper alpha (10–15 Hz) and lower beta (15–22 Hz) bands also was negatively correlated with age in controls but positively correlated with age in experts, again with the strongest effect in bilateral parietal and occipital electrodes. These oscillations are involved in neighboring cortical synchronization and represent integration, but between more local brain networks (Buzsaki and Draguhn, 2004; Klimesch, 2012; von Stein and Sarnthein, 2000). Previous fMRI and EEG studies have established that Scrabble experts show a pattern of brain activity that is consistent with a de-emphasis of phonology and semantic information and greater reliance on working memory and visual perception (Protzner et al., 2016; van Hees et al., 2017), suggesting that experts have developed a different implicit approach to LDT. It is likely that Scrabble experts have greater integration between language, working memory, and perceptual networks during LDT performance. Thus, it is possible that the maintenance of expertise-related network integration into old age manifests as increased upper alpha and lower beta power, as well as increased midscale MSE. For Scrabble experts compared to controls, aging is therefore associated with greater local neural processing (specialization) and also greater midrange interactions with other neural populations (integration). Importantly, these age-related differences were not linked to performance but more directly reflective of a pure age effect.

4.3. Expertise, age, task performance, and brain dynamics

Interestingly, for both experts and controls, the relation between age and brain dynamics was associated with worse performance (i.e., increased RT). It is tempting to interpret this result as suggesting that the alterations in brain dynamics associated with increasing age observed here are disadvantageous, and more so for experts than nonexperts. However, this interpretation is inconsistent with the observation that Scrabble experts performed better than nonexperts, particularly during vertical word presentation. Furthermore, age-related increases in reaction times were similar for both groups across all conditions, making it unlikely that differences in brain dynamics were particularly harmful for the expert group. An alternate interpretation is that age-related reductions in speed of processing (Salthouse, 1996) and/or motor speed (Seidler et al., 2010) across both groups may have obscured more subtle differences in visual word recognition associated with Scrabble expertise. Yet, despite this common age-related slowing, we were able to demonstrate that the relationship between LDT performance and brain dynamics is stronger for Scrabble experts than for controls. Thus, our results, especially those from the expert group, are in line with previous work that suggests that individual differences in local and midscale processing can be linked with cognitive outcomes in aging (Heisz et al., 2015; Wang et al., 2016). Our work extends these findings by showing that these associations are stronger in experts than in controls.

4.4. Degree of complementarity between MSE and SPD analyses

Previous literature is mixed regarding the degree of complementarity between variability-based (e.g., MSE) and central tendency–based (e.g., SPD) analyses. While some studies show similar effects between the 2 approaches (e.g., McIntosh et al., 2008, 2014; Sleimen-Malkoun et al., 2015; Szostakiwskyj et al., 2017), others identified differences (e.g., Takahashi et al., 2009; Ueno et al., 2015; Wang et al., 2016). Potential inconsistencies between MSE and SPD results have been interpreted to reflect differences in the relative contribution of linear versus nonlinear dependencies in the data; changes in linear dependencies are evident in both MSE and SPD, whereas changes in nonlinear dependencies are evident only in MSE (Courtiol et al., 2016; Wang et al., 2016). In the context of the current work, the strong correlation between MSE and SPD results suggests that our age-related effects are more linear than nonlinear.

5. Limitations and conclusions

There are limitations in the present study. First, because accuracy was close to ceiling for both groups, we focused on RT alone as our measure of performance. RTs are likely influenced by expertise-related differences in LDT performance, as well as age-related motor slowing common to both groups. Thus, in the context of a more difficult task, it is possible that accuracy could have been a more sensitive indicator of the influence of expertise and may have allowed us to identify group differences in the rate of age-related performance decline. Second, our SPD analyses identify dominant age and RT effects in gamma (30–50 Hz) band. Previous research suggests that electromyogram (EMG) is a significant contributor to EEG power in this frequency range (Whitham et al., 2007), even when data separation methods (e.g., ICA denoising) are used for data cleaning. Importantly, EMG contamination is strongest at lateral and posterior electrodes and weakest at frontal and central electrodes (Whitham et al., 2007). Because our effects are mainly at frontal, and at some central electrodes (and not in lateral and posterior electrodes), it is unlikely that EMG effects are driving our results. Third, the pool of Scrabble experts is limited, and so despite extensive advertising over a 1-year period at local and national Scrabble competitions, our sample size was relatively small. That said, the distribution of age in each group was even (i.e., all decades were represented), and experts and controls were very well matched on age, education, and general cognitive function. Importantly, we were able to replicate previously demonstrated MSE and SPD age effects in both groups, suggesting that the obtained sample size was sufficient to explore the interplay between age and Scrabble expertise. Finally, although we focused our inferences on differential implicit strategy used in the expert and control groups, this is not the only potential explanation for our findings. That is, it is also possible that there are domain-specific age-related changes. This will be an important issue to resolve in future research.

We assessed Scrabble expertise as a potential moderator of neurocognitive decline because experts have demonstrated attenuated age-related performance declines and altered brain function, especially in expertise-related tasks (Bidelman and Alain, 2015; Charness and Bosnian, 1990; Delon-Martin et al., 2013; Reuter et al., 2014). Our behavioral data suggest that although Scrabble experts made lexicality decisions for vertically presented stimuli faster than controls, this effect did not differ across age. By contrast, our brain data showed differences in the interplay of age and expertise on brain dynamics. Aging in experts was associated with increased local neural processing (specialization), as well as increased midrange interactions with other neural populations (integration). This greater network integration may support an implicit task strategy that is unique to experts, involving greater reliance on a more distributed network architecture including brain regions associated with working memory and perception in addition to the more typical language network configuration (Protzner et al., 2016; van Hees et al., 2017). Interestingly, the coupling between brain dynamics and performance also was better preserved into advanced age in the expert group, possibly pointing to a potential for expertise in maintaining brain and cognitive health.

Disclosure statement

The authors declare no actual or potential conflicts of interest.

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References

Acheson, D.J., Wells, J.B., MacDonald, M.C., 2008. New and updated tests of print exposure and reading abilities in college students. Behav. Res. Methods 40, 278–289.
Allen, P.A., Madden, D.J., Crozier, L.C., 1991. Adult age differences in letter-level and word-level processing. Psychol. Aging 6, 261–271.
Ankudowich, E., Pasvanis, S., Rajah, M.N., 2016. Changes in the modulation of brain activity during context encoding vs. context retrieval across the adult lifespan. Neuroimage 139, 103–113.
Bidelman, G.M., Alain, C., 2015. Musical training orchestrates coordinated neuroplasticity in auditory brainstem and cortex to counteract age-related declines in categorical vowel perception. J. Neurosci. 35, 1240–1249.
Buzsaki, G., Draguhn, A., 2004. Neuronal oscillations in cortical networks. Science 304, 1926–1929.
Charness, N., 1981. Search in chess: age and skill differences. J. Exp. Psychol. Hum. Percept. Perform. 7, 467.
Charness, N., Bosnian, E.A., 1990. Chapter Eight expertise and aging: Life in the Lab. Adv. Psychol. 71, 343–385.
Costa, M., Goldberger, A.L., Peng, C.K., 2005. Multiscale entropy analysis of biological signals. Phys. Rev. E 71, 021906.
Courtiol, J., Perdikis, D., Petkoski, S., Müller, V., Huys, R., Sleimen-Malkoun, R., Jirsa, V.K., 2016. The multiscale entropy: guidelines for use and interpretation in brain signal analysis. J. Neurosci. Methods 273, 175–190.
Deco, G., Jirsa, V.K., McIntosh, A.R., 2013. Resting brains never rest: computational insights into potential cognitive architectures. Trends Neurosci. 36, 268–274.
Delon-Martin, C., Plailly, J., Fonlupt, P., Veyrac, A., Royet, J.P., 2013. Perfumers' expertise induces structural reorganization in olfactory brain regions. Neuroimage 68, 55–62.
Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Meth. 134, 9–21.
Efron, B., Tibshirani, R., 1986. Bootstrap methods for standard errors, confidence intervals and other measures of statistical accuracy. Stat. Sci. 1, 54–75.
Garrett, D.D., Samanez-Larkin, G.R., MacDonald, S.W., Lindenberger, U., McIntosh, A.R., Grady, C.L., 2013. Moment-to-moment brain signal variability: a next frontier in human brain mapping? Neurosci. Biobehav. Rev. 37, 610–624.
Glisky, E.L., 2007. Changes in cognitive function in human aging. In: Riddle, D.R. (Ed.), Frontiers in Neuroscience. Brain Aging: Models, Methods, and Mechanisms. CRC Press, Boca Raton, FL, US.
Good, P., 2000. Permutation Tests: A Practical Guide to Resampling Methods for Testing Hypotheses. Springer, New York.
Halpern, D.F., Wai, J., 2007. The world of competitive scrabble: novice and expert differences in visuospatial and verbal abilities. J. Exp. Psychol. Appl. 13, 79–94.
Hargreaves, I.S., Pexman, P.M., Zdrazilova, L., Sargious, P., 2012. How a hobby can shape cognition: visual word recognition in competitive scrabble player. Mem. Cogn. 40, 1–7.
Heisz, J.J., Gould, M., McIntosh, A.R., 2015. Age-related shift in neural complexity related to task performance and physical activity. J. Cogn. Neurosci. 27, 605–613.
Howell, G.T., Lacroix, G.L., 2012. Decomposing interactions using GLM in combination with the COMPARE, LMATRIX and MMATRIX subcommands in SPSS. Tutorials Quantitative Methods Psychol. 8, 1–22.
Klimesch, W., 2012. Alpha-band oscillations, attention, and controlled access to stored information. Trends Cogn. Sci. 16, 606–617.
Krampe, R.T., Ericsson, K.A., 1996. Maintaining excellence: deliberate practice and elite performance in young and older pianists. J. Exp. Psychol. Gen. 125, 331–359.
Krishanan, A., Williams, L.J., McIntosh, A.R., Abdi, H., 2011. Partial least squares (PLS) methods for neuroimaging: a tutorial and review. Neuroimage 56, 455–475.
Lobaugh, N.J., West, R., McIntosh, A.R., 2001. Spatiotemporal analysis of experimental differences in event-related potential data with partial least squares. Psychophysiology 38, 517–530.
McDonough, I.M., Nashiro, K., 2014. Network complexity as a measure of information processing across resting-state networks: evidence from the human connectome project. Front. Hum. Neurosci. 8. https://doi.org/10.3389/fnhum.2014.00409.
McIntosh, A.R., Kovacevic, N., Itier, R.J., 2008. Increased brain signal variability accompanies lower behavioral variability in development. PLoS Comput. Biol. 4, e1000106.
McIntosh, A.R., Kovacevic, N., Lippe, S., Garrett, D., Grady, C., Jirsa, V., 2010. The development of a noisy brain. Arch. Ital. Biol. 148, 323–337.
McIntosh, A.R., Lobaugh, N.J., 2004. Partial least squares analysis of neuroimaging data: applications and advances. Neuroimage 23 (Suppl 1), S250–S263.
McIntosh, A.R., Vakorin, V., Kovacevic, N., Wang, H., Diaconescu, A., Protzner, A.B., 2014. Spatiotemporal dependency of age-related changes in brain signal variability. Cereb. Cortex 24, 1806–1817.
Morrow, D., Leirer, V., Altiteri, P., Fitzsimmons, C., 1994. When expertise reduces age differences in performance. Psychol. Aging 9, 134.
Moxley, J.H., Charness, N., 2013. Meta-analysis of age and skill effects on recalling chess positions and selecting the best move. Psychon. Bull. Rev. 20, 1017–1022.
Polich, J., 1997. EEG and ERP assessment of normal aging. Electroencephalogr. Clin. Neurophysiol. 104, 244–256.
Protzner, A.B., Hargreaves, I.S., Campbell, J.A., Myers-Stewart, K., van Hees, S., Goodyear, B.G., Sargious, P., Pexman, P.M., 2016. This is your brain on scrabble: neural correlates of visual word recognition in competitive scrabble players as measured during task and resting-state. Cortex 75, 204–219.
Ratcliff, R., Thapar, A., Gomez, P., McKoon, G., 2004. A diffusion model analysis of the effects of aging in the lexical-decision task. Psychol. Aging 19, 278–289.
Reuter, E.M., Voelcker-Rehage, C., Vieluf, S., Winneke, A.H., Godde, B., 2014. Extensive occupational finger use delays age effects in tactile perception—an ERP study. Atten. Percept. Psychophys. 76, 1160–1175.
Richman, J.S., Moorman, J.R., 2000. Physiological time-series analysis using approximate and sample entropy. Am. J. Physiol. Heart Circ. Physiol. 278, H2039–H2049.
Salthouse, T.A., 1984. Effects of age and skill in typing. J. Exp. Psychol. Gen. 113, 345–371.

Salthouse, T.A., 1996. The processing-speed theory of adult age differences in cognition. Psychol. Rev. 103, 403–428.
Seidler, R.D., Bernard, J.A., Burutolu, T.B., Fling, B.W., Gordon, M.T., Gwin, J.T., Kwak, Y., Lipps, D.B., 2010. Motor control and aging: links t age-related brain structural, functional, and biochemical effects. Neurosci. Biobehav. Rev. 34, 721–733.
Sleimen-Malkoun, R., Perdikis, D., Müller, V., Blanc, J.L., Huys, R., Temprado, J.J., Jirsa, V.K., 2015. Brain dynamics of aging: multiscale variability of EEG signals at rest and during an auditory oddball task. eNeuro 2. ENEURO-0067.
Small, M., Tse, C.K., 2004. Optimal embedding parameters: a modeling paradigm. Physica D. 194, 283–296.
Spreen, O., Strauss, E., 1998. A Compendium of Neuropsychological Tests: Administration, Norms, and Commentary. Oxford University Press, New York.
Szostakiwskyj, J.M.H., Willatt, S.E., Cortese, F., Protzner, A.B., 2017. The modulation of EEG variability between internally- and externally-driven cognitive states varies with maturation and task performance. PLoS One. https://doi.org/10.1371/journal.pone.0181894.
Takahashi, T., Cho, R.Y., Murata, T., Mizuno, T., Kikuchi, M., Mizukami, K., Kosaka, H., Takahashi, K., Wada, Y., 2009. Age-related variation in EEG complexity to photic stimulation: a multiscale entropy analysis. Clin. Neurophysiol. 120, 476–483.
Tuffiash, M., Roring, R.W., Ericsson, K.A., 2007. Expert performance in Scrabble: implications for the study of the structure and acquisition of complex skills. J. Exp. Psychol. Appl. 13, 124–134.
Ueno, K., Takahashi, T., Takahashi, K., Mizukami, K., Tanaka, Y., Wada, Y., 2015. Neurophysiological basis of creativity in healthy elderly people: a multiscale entropy approach. Clin. Neurophysiol. 126, 524–531.
Uttl, B., 2002. North American adult reading test: age norms, reliability, and validity. J. Clin. Exp. Neuropsychol. 24, 1123–1137.
Vakorin, V.A., Lippe, S., McIntosh, A.R., 2011. Variability of brain signals processed locally transforms into higher connectivity with brain development. J. Neurosci. 31, 6405–6413.
van Hees, S., Pexman, P.M., Hargreaves, I.S., Zdrazilova, L., Hart, J.M., Myers-Stewart, K., Cortese, F., Protzner, A.B., 2016. Testing the limits of skill transfer for scrabble experts in behavior and brain. Front. Hum. Neurosci. 10, 564.
van Hees, S., Seyffarth, S., Pexman, P.M., Cortese, F., Protzner, A.B., 2017. An ERP investigation of vertical reading fluency in Scrabble® experts. Brain Res. 1667, 1–10.
Vlahou, E.L., Thurm, F., Kolassa, I.T., Schlee, W., 2014. Resting-state slow wave power, healthy aging and cognitive performance. Sci. Rep. 4, 5101.
von Stein, A., Sarnthein, J., 2000. Different frequencies for different scales of cortical integration: from local gamma to long range alpha/theta synchronization. Int. J. Psychophysiol. 38, 301–313.
Wang, H., McIntosh, A.R., Kovacevic, N., Karachalios, M., Protzner, A.B., 2016. Age-related multiscale changes in brain signal variability in pre-task versus post-task resting-state EEG. J. Cogn. Neurosci. 28, 971–984.
Wechsler, D., 1997. WAIS-III: Administration and Scoring Manual. Psychological Corp, San Antonio.
Whitham, E.M., Pope, K.J., Fitzgibbon, S.P., Lewis, T., Clark, C.R., Loveless, S., Broberg, M., Wallace, A., DeLosAngeles, D., Lillie, P., Hardy, A., Fronsko, R., Pulbrook, A., Willoughby, J.O., 2007. Scalp electrical recording during paralysis: quantitative evidence that EEG frequencies above 20 Hz are contaminated by EMG. Clin. Neurophysiol. 118, 1877–1888.
Yarkoni, T., Balota, D., Yap, M., 2008. Moving beyond Coltheart's N: a new measure of orthographic similarity. Psychon. Bull. Rev. 15, 971–979.
Zappasodi, F., Marzetti, L., Olejarczyk, E., Tecchio, F., Pizzella, V., 2015. Age-related changes in electroencephalographic signal complexity. PLoS One 10, e0141995.