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Kosar Sanjar

Vilnius University

Povilas Tarailis

Vilnius University

Inga Griskova-Bulanova

`inga.griskova-bulanova@gf.vu.lt`

Vilnius University

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Frequency-Specific Age Associations in EEG Microstate Dynamics Across the Adult Lifespan

Kosar Sanjar 1, Povilas Tarailis 2, Inga Griskova-Bulanova 1, 2*

1 Vilnius University, Institute of Bioscience, Life Sciences Center, Saulėtekio ave. 7, LT-10257, Vilnius, Lithuania.

2 Vilnius University, Translational Health Research Institute, Faculty of Medicine, Žaliųjų ež. str. 2, LT- 08406, Vilnius, Lithuania.

* Corresponding author: inga.griskova-bulanova@gf.vu.lt

Abstract

EEG microstates are conventionally derived from broadband signals, although their temporal dynamics may differ across frequency ranges. Whether age associations in conventional voltage microstates are similarly frequency specific remains unclear. We examined resting-state EEG from 60 healthy adults aged 20–78 years and derived microstates separately from broadband (1–30 Hz), delta (1–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), and beta (15–30 Hz) activity. The number of microstates was selected independently for each band using the Krzanowski–Lai criterion, yielding four classes for broadband, delta, alpha, and beta, and five for theta. Age associations were tested for duration, occurrence, coverage, global explained variance, observed transition probabilities, and transitions adjusted for those expected from class prevalence, with false-discovery-rate correction.

Age associations showed a marked spectral dependence. Of 84 state-level tests, 13 survived correction: one in broadband, six in delta, one in theta, none in alpha, and five in beta. In delta, increasing age was associated with greater expression of MS B and reduced expression of MS C across duration, occurrence, and coverage. In beta, age was associated with greater MS A expression and reduced MS C expression. All significant state-level associations remained after adjustment for sex, education, and band-specific spectral power. Eight observed transition associations survived correction, all in broadband and delta, but only three remained after accounting for transitions expected from state prevalence.

These findings indicate that age-related variation in EEG microstate dynamics is strongly frequency-specific and is expressed primarily through redistribution of state expression rather than through widespread alteration of transition preference. Frequency-resolved microstate analysis, hence, reveals age associations that are not evident in conventional broadband analysis.

Introduction

Aging is accompanied by systematic changes in spontaneous electrophysiological activity, many of which depend strongly on frequency. Alterations in oscillatory power, dominant frequencies, and spectral organization are among the most consistently reported features of healthy brain aging (Fernández-Rubio et al., 2025). This frequency dependence is important for interpreting electrophysiological changes associated with cognitive decline and neurodegenerative disease, because many EEG measures proposed as clinical markers are themselves sensitive to aging (Chetty et al., 2024; Fernández-Rubio et al., 2025; Yuan et al., 2025). Characterizing how aging is expressed across spectral components of ongoing EEG is therefore important both for understanding physiological aging and for interpreting disease-related abnormalities.

EEG microstate analysis provides a complementary description of spontaneous brain activity by representing the continuous EEG as a sequence of recurrent, quasi-stable scalp potential

configurations whose temporal properties have been linked to a range of cognitive, clinical, and experimental conditions (Koenig et al., 2002; Michel & Koenig, 2018; Tarailis et al., 2024). Their temporal expression is commonly characterized by duration, occurrence, coverage, and global explained variance, while sequential organization can be described using transition probabilities and other sequence-based measures (Michel & Koenig, 2018; Tarailis et al., 2026). Previous lifespan studies using conventional broadband EEG have demonstrated age-related variation in these measures (Koenig et al., 2002; Tomescu et al., 2018; Zanesco et al., 2020; Jabès et al., 2021). However, the specific classes and parameters associated with age have varied across studies, and broadband analyses provided limited information about the spectral components underlying these associations. This matters because broadband EEG combines activity from frequency ranges that show distinct age trajectories.

A less explored aspect of microstate analysis is the spectral composition of the EEG from which microstates are derived. Conventional microstate analysis predominantly uses broadband EEG, although broadband activity integrates contributions from multiple frequency ranges. Férat et al. (2022) derived conventional EEG microstates separately from delta-, theta-, alpha-, and beta-band activity and found highly similar topographies across bands and broadband EEG. Despite this spatial similarity, their temporal sequences showed substantial informational independence, and microstate parameters differed systematically across frequency bands. This suggests that broadband analysis may obscure frequency-specific differences in microstate dynamics.

Evidence that this spectral distinction matters for aging is beginning to emerge. Using resting-state MEG data from 624 participants aged 18–88 years, Huang et al. (2024) reported age-related differences in frequency-resolved microstate dynamics, with prominent alpha-band effects and additional changes in theta and beta. Together, these findings suggest that age effects on microstate dynamics may depend on frequency. However, whether comparable effects characterize conventional EEG voltage microstates remains less clear. It is also unknown whether spectral specificity extends beyond individual microstate parameters to the organization of transitions between states.

Transition probabilities provide information complementary to duration, occurrence, coverage, and GEV by quantifying how frequently one microstate follows another. Age-related transition differences have been reported in broadband EEG (Tomescu et al., 2018). However, observed transitions depend partly on the relative occurrence of the participating states. Comparing observed with expected transitions can therefore help distinguish changes in state prevalence from changes in transition preference (Antonova et al., 2022; Khazaei et al., 2021).

Recent work using instantaneous-frequency microstates has also identified age-related differences in frequency-specific transition dynamics (Nobukawa et al., 2026). Although this approach characterizes phase-derived frequency patterns rather than conventional voltage-topography microstates, it suggests that age-related changes in sequential EEG organization may themselves be frequency dependent. To our knowledge, however, frequency-specific age associations in the transition structure of conventional EEG voltage microstates have not been systematically examined across the major resting-state frequency bands. Thus, it is yet not clear whether spectral specificity in healthy aging is limited to the expression of individual microstates or also extends to their sequential organization.

The present study investigated the spectral organization of age-related variation in resting-state EEG microstate dynamics. Using a previously characterized adult EEG dataset (James & Burgess, 2025), we derived microstates from broadband EEG and separately from delta-, theta-, alpha-, and beta-band activity, with the number of microstate classes selected independently for each band. First, we examined associations between age and microstate duration, occurrence,

coverage, and GEV across spectral ranges. Second, we tested whether age-related differences extended to sequential organization by analyzing observed transition probabilities and deviations from expected transitions. We expected age associations to vary across frequency ranges; however, because existing evidence does not support reliable directional predictions for specific bands, classes, or transition pairs, these analyses were exploratory at the level of individual states and transitions.

Methods

Participants

Analyses used the previously characterized dataset of James and Burgess (2025), comprising eyes-closed resting-state EEG data from 60 healthy adults (36 female, 24 male) aged 20–78 years, uniformly sampled across age, with 10 participants per decade. The full published sample was analysed; no additional participant selection was applied, and no participant met the data-quality exclusion criterion described below. Age distributions did not differ between sexes (Mann–Whitney U, $p = .98$). For categorical analyses, participants were grouped as young (20–39 years), middle-aged (40–59 years), and older (60–78 years; $n = 20$ per group). Recordings comprised 66 channels sampled at 500 Hz; full acquisition details are provided in James and Burgess (2025).

EEG preprocessing

Preprocessing was performed in EEGLAB 2026.0.0 (Delorme & Makeig, 2004). Three non-scalp channels were removed, leaving 63 scalp electrodes at standard 10–10 positions. Data were high-pass filtered at 1 Hz and then low-pass filtered at 40 Hz (separate zero-phase Hamming-windowed FIR filters). Bad channels were detected with `clean_rawdata` (flatline criterion 5 s, channel-correlation criterion 0.8, line-noise criterion 4; burst correction and window rejection disabled) and removed before ICA to preserve data rank (median 2 channels per participant, range 0–12). Extended Infomax ICA was computed on the full-rank continuous data, and components classified by ICLabel (Pion-Tonachini et al., 2019) as ocular or cardiac with probability $> .70$ were removed (mean ≈ 2.9 components per participant); no artifact-subspace reconstruction was applied. Removed channels were then interpolated (spherical splines), data were re-referenced to the common average and resampled to 250 Hz. Recordings remained continuous throughout: no epoching or amplitude-based data rejection was applied. This choice was made a priori to avoid introducing age-dependent differences in retained data quantity through fixed amplitude-rejection thresholds. The mean analyzed recording length was 321.5 s ($SD = 43.5$, range 281.0–559.7) and was identical across frequency bands within each participant.

Frequency-band decomposition

The cleaned continuous data were filtered into five ranges following the band scheme of Férat et al. (2022): broadband (1–30 Hz), delta (1–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), and beta (15–30 Hz), using zero-phase Hamming-windowed FIR filters with fixed temporal lengths (3.31 s for broadband and delta, 1.66 s for theta and alpha, 0.90 s for beta; filter orders 828, 828, 414, 414, and 224 at 250 Hz). The 1–30 Hz broadband range was defined a priori as the span of the analyzed sub-bands, thereby limiting potential contamination from high-frequency muscle artifacts.

Microstate analysis

Microstate analysis was performed in MICROSTATELAB v2.1 (Nagabhushan Kalburgi et al., 2024). For each participant and band, individual microstate (MS) maps were identified by

modified k-means clustering restricted to topographies at global field power (GFP) peaks, using all available peaks, ignoring polarity, on amplitude-normalized data, with 20 random restarts, for cluster numbers $k = 4-7$ (fixed random seeds). The number of clusters was selected per band using the Krzanowski-Lai criterion (Krzanowski & Lai, 1988), computed for $k = 3-12$ on 10 random subsamples of 500 GFP-peak topographies per participant, with polarity-invariant k-means, and averaged across participants (Supplementary Table S2, Supplementary Fig. S1). The group-level optimum was $k = 4$ for broadband, delta, alpha, and beta, and $k = 5$ for theta, and these values were adopted for subsequent analyses. Band-wise group mean maps were computed using a permute-and-average procedure (polarity ignored) and labeled according to the canonical microstate classes of Custo et al. (2017) following visual inspection of the group topographies; the classes represented differed between bands (Figure 1). The group labeling was then propagated to all individual datasets. Because group-deviant topographies may themselves reflect age effects, participant exclusion was based only on an absolute quality criterion (polarity-invariant mean spatial correlation of the individual maps with the corresponding group mean maps below .50 in any band); no participant met this criterion (lowest value .531, beta band), and all 60 participants were retained.

The group mean maps were then fit back to each participant's continuous band-filtered data, with class assignment determined at GFP peaks and extended to the intervening samples by linear interpolation of class membership, consistent with the clustering procedure. For every class, we extracted mean duration (ms), occurrence (Hz), coverage (%), and individually explained variance (GEV), separately for each band. Transition probabilities were extracted both as observed matrices and as matrices expected under independence given class occurrence (e.g., Khazaei et al., 2021; Antonova et al., 2022). Chance-adjusted transition preference was quantified as the relative deviation from the expected value, $100 \times (\text{observed} - \text{expected}) / \text{expected}$, as implemented in MICROSTATELAB. Self-transitions were excluded, yielding 12 ordered class pairs at $k = 4$ and 20 at $k = 5$.

Spectral power estimation

For the power-control analysis, individual band power was computed for each participant from the cleaned continuous broadband (1-30 Hz) recording using Welch's method (4-s Hamming windows, 50% overlap). Power was averaged across all 63 scalp channels, then across the frequency bins within each band, and then log₁₀-transformed. This measure is distinct from global field power (GFP), which was used only to select the topographies included in clustering. Group-mean spectra are shown in Supplementary Fig. S5.

Statistical analysis

Age was uniformly sampled across adulthood by design. Spearman rank correlations were used for all age associations to assess monotonic relationships without assuming linearity and to reduce sensitivity to outliers. False-discovery-rate (FDR) control (Benjamini & Hochberg, 1995) was applied at $q = .05$ within a priori-defined inferential families based on the analytical structure. For state parameters, each band $\times$ parameter combination constituted a separate family comprising that band's microstate classes (20 families of 4 or 5 tests; 84 tests). For transitions, the directed class-pair transitions within each band constituted a separate family (12 pairs at $k = 4$, 20 at $k = 5$), with corrections applied separately to observed and chance-adjusted transition probabilities (5 families per metric; 68 tests per metric), for 220 primary-age tests in total. The robustness of FDR-significant state-level and transition-level age associations was evaluated in secondary sensitivity analyses using (a) partial Spearman correlations controlling for sex and

education, (b) three-group comparisons (young, middle-aged, and older) using one-way ANOVA with Tukey post-hoc tests, (c) Cohen's d for older versus young participants with bootstrap 95% confidence intervals (10,000 iterations), and (d) partial Spearman correlations additionally controlling the log10-transformed spectral power of the corresponding frequency band. For reference, the minimum detectable correlation for an individual two-tailed test at $n = 60$, $\alpha = .05$, and 80% power is $|r| = .355$. Secondary sex analyses used Mann–Whitney U tests with the rank-biserial correlation as effect size (positive values indicate higher values in males), FDR-corrected within band $\times$ parameter families.

Results

Microstate topographies

The Krzanowski–Lai criterion favored four clusters in broadband, delta, alpha and beta and five in theta (Supplementary Table S2, Supplementary Fig. S1). The group-mean maps of each band corresponded to canonical microstate classes (Figure 1): A, B, C and D in broadband, delta and beta; A, B, D and F in alpha; and A, B, D, E and F in theta. No participant met the exclusion criterion, and all 60 participants (300 participant $\times$ band datasets) entered the analyses.

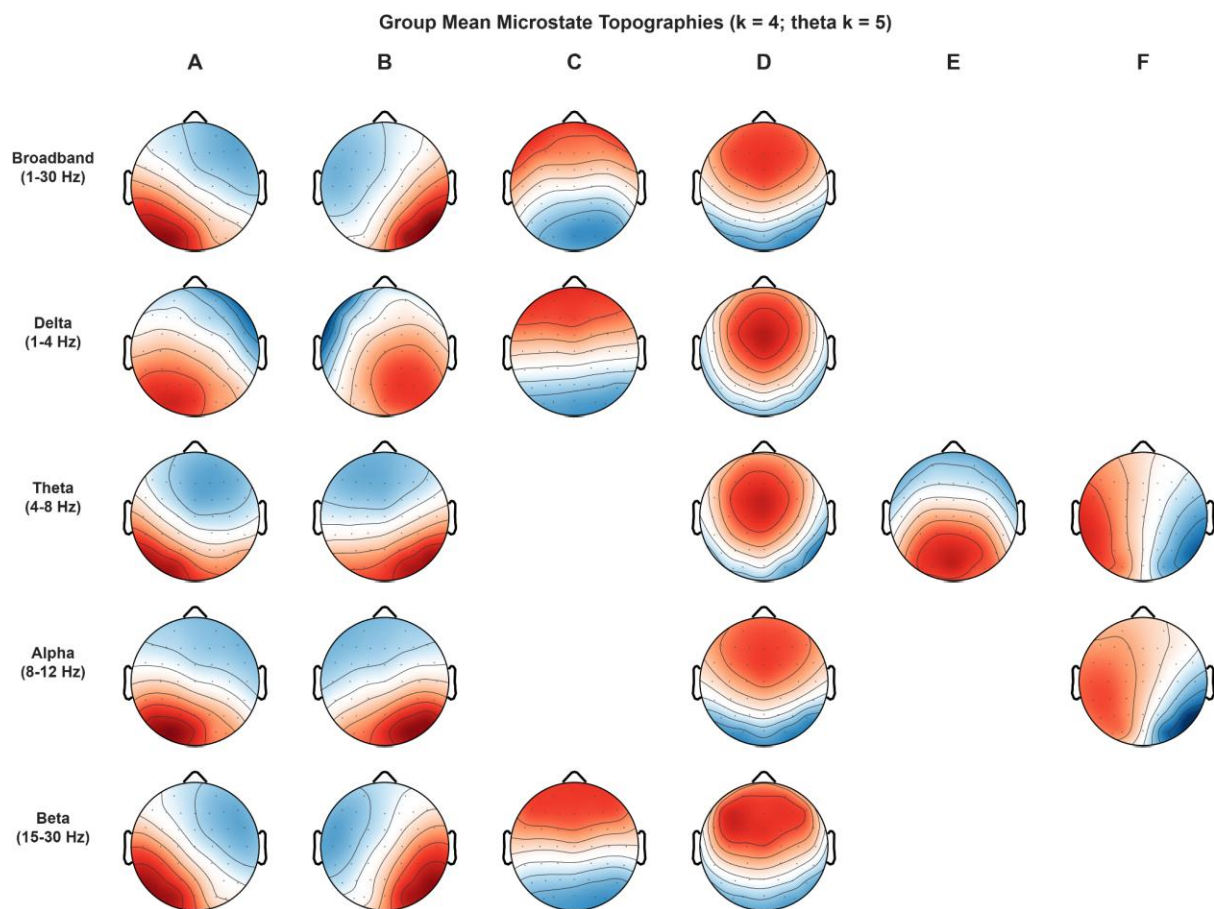


Figure 1. Group-mean microstate maps for each frequency band under the final cluster-number scheme ($k = 4$ for broadband, delta, alpha, and beta; $k = 5$ for theta; based on 60 participants), labeled according to the canonical classes of Custo et al. (2017); empty cells indicate classes not represented in that band. Maps are amplitude-normalized. Map polarity is arbitrary in microstate analysis; for display, each map is shown with the sign that aligns it with the corresponding template map. All analyses are polarity-invariant.

Age associations with microstate temporal parameters show a frequency-dependent distribution

Of 84 state-level age tests, 13 survived FDR correction (Figure 2, Table 1): one in broadband, six in delta, one in theta, none in alpha, and five in beta.

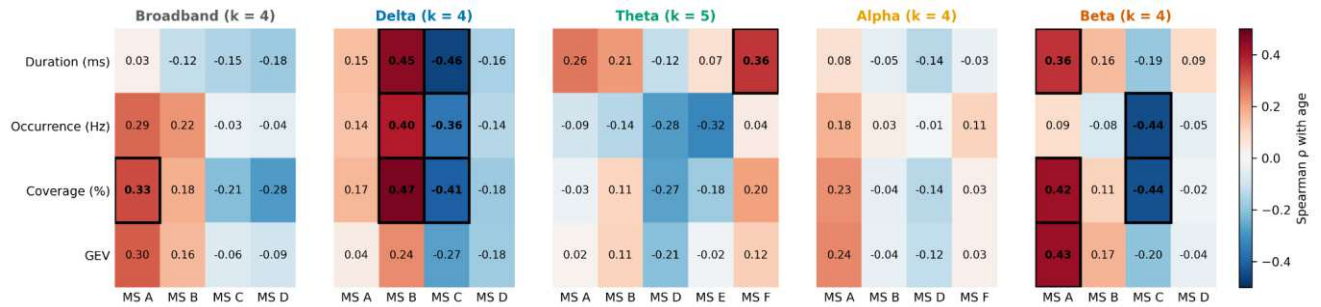


Figure 2. Heatmaps of Spearman ρ between age and each temporal parameter (duration, occurrence, coverage, GEV) for every microstate class and frequency band. Black outlines and bold values indicate FDR-significant associations ($q = .05$, within band $\times$ parameter families). Thirteen of 84 tests were significant (broadband 1, delta 6, theta 1, alpha 0, beta 5).

Broadband analysis yielded a single state-level association, an increase in the coverage of MS A with age ($\rho = .33$, $q = .042$). The delta- and beta-band state-level effects, which involve MS B and MS C in opposite directions, had no broadband counterpart. In the delta band, age was associated with greater expression of MS B (coverage $\rho = .47$, duration $\rho = .45$, occurrence $\rho = .40$; all $q \leq .007$) and reduced expression of MS C (duration $\rho = -.46$, coverage $\rho = -.41$, occurrence $\rho = -.36$; all $q \leq .010$). In the beta band, age was associated with greater expression of MS A (GEV $\rho = .43$, coverage $\rho = .42$, duration $\rho = .36$; all $q \leq .019$) and reduced expression of MS C (occurrence $\rho = -.44$, coverage $\rho = -.44$; both $q \leq .002$). In the theta band, only the duration of MS F increased with age ($\rho = .36$, $q = .025$), and no alpha-band parameter was associated with age. Figure 3 illustrates six of the strongest associations.

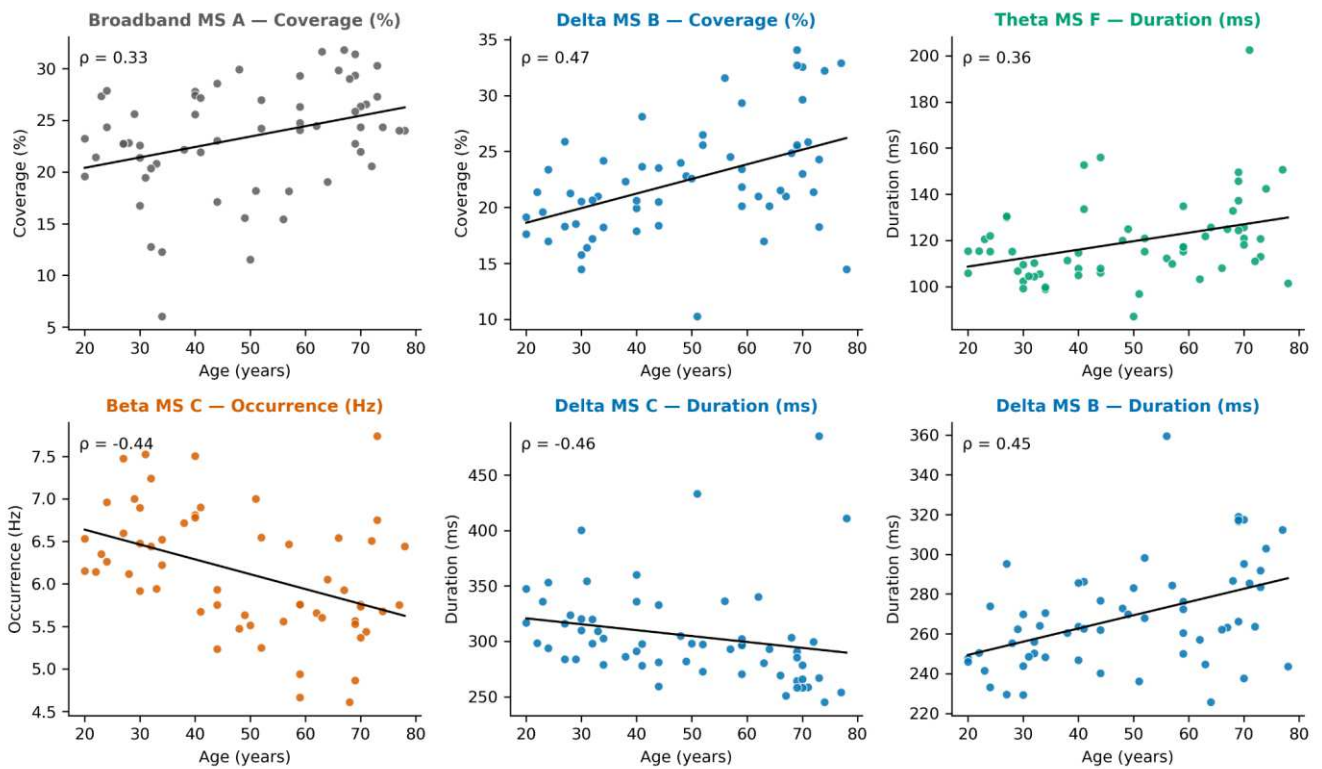


Figure 3. Scatterplots of age against six FDR-significant associations: the strongest association of each band (by absolute Spearman correlation), followed by the next strongest overall — broadband MS A coverage ($\rho = .33$), delta MS B coverage ($\rho = .47$), theta MS F duration ($\rho = .36$), beta MS C occurrence ($\rho = -.44$), delta MS C duration ($\rho = -.46$) and delta MS B duration ($\rho = .45$). Each point represents one participant ($n = 60$); least-squares fit lines are shown for visualisation.

Age-related reorganization of microstate transitions

For observed transition probabilities, 8 of 68 tests survived FDR correction (Figure 4, Table 1).

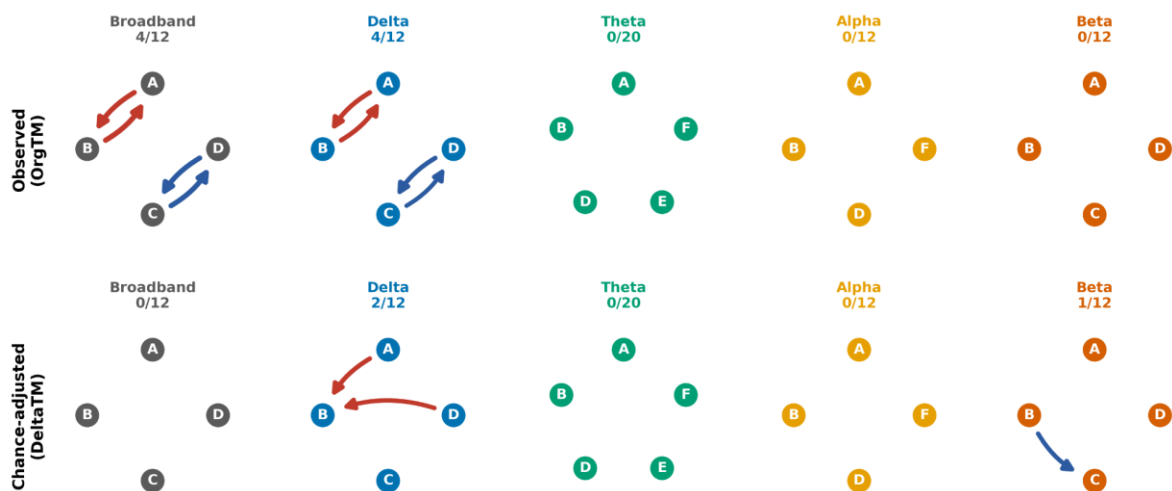


Figure 4. Network diagrams of FDR-significant age associations of transition probabilities by band. Top: observed transition probabilities (8 of 68 significant); bottom: chance-adjusted probabilities (3 of 68). Red edges indicate transitions that increase with age, blue edges decrease;

edge width is proportional to $|\rho|$. Directions are also given numerically in Supplementary Tables S3–S4.

In broadband, transitions between MS A and MS B increased with age ($A \rightarrow B \rho = .45$, $B \rightarrow A \rho = .47$; both $q = .001$) while transitions between MS C and MS D decreased ($C \rightarrow D \rho = -.45$, $D \rightarrow C \rho = -.45$; both $q = .001$). The delta band showed the same pattern ($A \rightarrow B \rho = .40$ and $B \rightarrow A \rho = .40$, both $q = .008$; $C \rightarrow D \rho = -.35$, $q = .019$; $D \rightarrow C \rho = -.39$, $q = .008$); no theta, alpha or beta transition was associated with age. When transitions were expressed as deviations from those expected from class prevalence alone, 3 of 68 associations were FDR-significant: delta MS A $\rightarrow$ B ($\rho = .39$, $q = .024$), delta MS D $\rightarrow$ B ($\rho = .36$, $q = .027$), and beta MS B $\rightarrow$ C ($\rho = -.37$, $q = .047$). Only delta MS A $\rightarrow$ B was significant in both analyses. Of the other seven observed-transition associations, three were substantially attenuated in the deviation analysis (broadband MS A $\rightarrow$ B, $\rho = .45 \rightarrow .18$; delta MS B $\rightarrow$ A, $\rho = .40 \rightarrow .21$; delta MS C $\rightarrow$ D, $\rho = -.35 \rightarrow -.06$), while four fell just short of the corrected threshold ($q = .063-.065$). Conversely, delta MS D $\rightarrow$ B and beta MS B $\rightarrow$ C were significant only as deviations (observed $q = .117$ and $.095$). All eight observed associations were weaker as deviations (mean $|\rho| .42 \rightarrow .27$), indicating that a substantial part of the apparent age-related change in the observed transition matrix reflects the age-related changes in class prevalence reported above, alongside a small number of transition associations that are not explained by prevalence alone (full transition tables in Supplementary Tables S3–S4).

Table 1. Overview of FDR-significant associations by frequency band ($q = .05$, within-band families). State: temporal parameters (duration, occurrence, coverage, GEV) of each class; classes with at least one parameter increasing ($\uparrow$) or decreasing ($\downarrow$) with age are listed. Observed / Chance-adj.: transition probabilities. Sex: Mann–Whitney differences.

Band	k	Classes	State tests	$\uparrow$ with age	$\downarrow$ with age	Observed transition s	Chance-adj. transition s	Sex difference s
Broadband	4	ABCD	1/16	MS A	—	4/12	0/12	1/16
Delta	4	ABCD	6/16	MS B	MS C	4/12	2/12	1/16
Theta	5	ABDEF	1/20	MS F	—	0/20	0/20	0/20
Alpha	4	ABDF	0/16	—	—	0/12	0/12	0/16
Beta	4	ABCD	5/16	MS A	MS C	0/12	1/12	8/16
Total			13/84			8/68	3/68	10/84

Secondary sex differences

Secondary sex analyses identified 10 of 84 FDR-significant differences; eight of them were in the beta band (Supplementary Table S5). Two sex-related differences coincided with age-associated parameters (beta MS A duration and beta MS C coverage), indicating limited overlap between the identified age- and sex-associated patterns.

Sensitivity analyses

In sensitivity analyses, all 13 FDR-significant state-level age associations remained significant in partial Spearman correlations controlling for sex and education (13/13), and in partial correlations additionally controlling the log10-transformed spectral power of the corresponding frequency band (13/13; Supplementary Table S6). The delta associations were unchanged or strengthened by the power adjustment (e.g., MS C duration, $\rho = -.46 \rightarrow -.52$), whereas the beta associations were attenuated but remained significant (e.g., MS C coverage, $\rho = -.44 \rightarrow -.35$).

Consistent with this dissociation, band power itself was associated with age only in the beta band ($\rho = .35$, $p = .007$; Supplementary Fig. S5).

Three-group comparisons were consistent with the continuous age associations for 12 of 13 parameters. Descriptively, older-versus-young effect sizes were large ($|d| \geq 0.8$) for the same 12 associations, with bootstrap 95% confidence intervals excluding zero; the single exception was delta MS C duration ($d = -0.51$ [$-1.90, 0.11$]; ANOVA $p = .25$). These effect sizes are reported to describe the magnitude of the age differences; the inferential tests are the FDR-corrected correlations above (Supplementary Table S1, Supplementary Figs. S2–S3). Tukey HSD comparisons localized these differences to the extremes of the age range: young versus older participants differed significantly for 12 of the 13 parameters, whereas young versus middle-aged differed for three and middle-aged versus older for one (Supplementary Table S8).

The transition-level findings were similarly robust: all 11 FDR-significant associations remained significant with sex, education, and band power controlled; all showed large older-versus-young effects with confidence intervals excluding zero, and 10 of 11 differed significantly across the three age groups (exception: chance-adjusted delta MS D→B, $p = .059$). In Tukey HSD comparisons, all 11 transition associations differed between young and older participants, including chance-adjusted delta MS D→B ($p = .049$), whereas only one differed between young and middle-aged participants and two between middle-aged and older participants (Supplementary Table S7, Supplementary Fig. S4, Supplementary Table S9).

Discussion

The present study shows that age associations with resting-state EEG microstate dynamics are strongly frequency dependent. Broadband microstate parameters showed comparatively limited associations with age, whereas effects were concentrated mainly in the delta and beta bands, with only limited evidence in theta and none in alpha. In delta, increasing age was associated with greater expression of MS B and reduced expression of MS C across several temporal parameters, whereas beta showed a distinct redistribution characterised by greater MS A and reduced MS C expression. Age was also associated with observed transition structure, although these effects were markedly reduced after accounting for transitions expected from state prevalence. Overall, age-related microstate variation was expressed primarily as frequency-specific redistribution of state expression.

Age-related variation in microstate dynamics has previously been demonstrated using conventional broadband EEG (Koenig et al., 2002; Tomescu et al., 2018; Zanesco et al., 2020; Jabès et al., 2021), although the specific microstate classes associated with age have differed across studies. Direct comparison is complicated by differences in model order and class definition, particularly in frequency-resolved analyses. In the present analysis, the Krzanowski–Lai criterion favored four classes for broadband, delta, alpha, and beta activity, but five for theta, and the resulting class compositions also differed across bands. Thus, identically labeled classes should not be assumed to represent strictly equivalent topographies across spectral ranges.

For this reason, the more informative finding is the distribution of age associations across frequency bands rather than the behaviour of any single canonical class. Férat et al. (2022) showed that recognizable microstate topographies can be recovered from delta-, theta-, alpha-, and beta-filtered EEG, despite clear differences in their temporal dynamics. Our findings extend this observation by showing that age associations are likewise unevenly distributed across the spectrum, with the clearest effects in delta and beta.

Notably, this spectral pattern differs from that reported by Huang et al. (2024), who found prominent alpha-band microstate effects in resting-state MEG, along with changes in theta and

beta bands. In contrast, the present EEG analysis showed clearer delta- and beta-band associations and no corrected state-level effects in alpha. Differences across studies may reflect recording modality, microstate definition, model order, age modeling, or frequency specification. More broadly, age effects are not expressed uniformly across electrophysiological measures or frequency ranges, as also shown for frequency-resolved resting-state connectivity (Ruuskanen et al., 2026). The lack of an alpha effect is particularly interesting because the same cohort showed clear age sensitivity of conventional spectral features and peak alpha frequency (James & Burgess, 2025). Moreover, all significant age–microstate associations remained after adjustment for band-specific power, suggesting that the observed effects were not simply a consequence of age-related differences in spectral amplitude.

Within delta and beta, age associations formed coherent within-class patterns rather than isolated parameter changes, consistent with a redistribution of recurrent scalp-field configurations within these frequency ranges. Functional attribution should nevertheless remain conservative because correspondence between individual scalp maps and specific cognitive systems remains limited (Custo et al., 2017; Michel & Koenig, 2018; Tarailis et al., 2024; Bréchet & Michel, 2026). Recent work has also shown that some noncanonical microstate topographies may be particularly susceptible to movement-related artifact contributions (Jordánek et al., 2025), reinforcing the need for caution when interpreting atypical narrow-band configurations. The transition analyses further showed that spectral specificity extended to the apparent sequential organization of microstates. Age associations with observed transition probabilities were confined to broadband and delta activity, with increased $A \leftrightarrow B$ and decreased $C \leftrightarrow D$ transitions in both bands. These effects were markedly attenuated after adjustment for transitions expected from state prevalence, leaving only three significant associations across all frequency ranges and indicating that much of the apparent age dependence of observed transitions was attributable to differences in state prevalence. The sparse significant associations in the chance-adjusted matrices indicate that more selective differences in transition preference may nevertheless be present. This interpretation is consistent with previous evidence that transition structure varies with age (Tomescu et al., 2018) and with recent frequency-specific state analyses showing age-related differences in occupancy and transitions (Nobukawa et al., 2026).

The spectral specificity observed here may also be relevant to the interpretation of microstate alterations in pathological aging. Microstate abnormalities have been reported across subjective cognitive decline, mild cognitive impairment, and Alzheimer’s disease, including frequency-dependent effects (Smailovic et al., 2019; Musaeus et al., 2020; Das et al., 2026). Microstate alterations have also been observed in presymptomatic carriers of autosomal-dominant Alzheimer’s disease mutations, suggesting that such changes may emerge before overt clinical impairment (Johansson et al., 2025). Because healthy age associations differ across frequency ranges, the spectral representation of EEG may influence how disease-related microstate abnormalities are interpreted. Direct comparison with clinical populations nevertheless requires caution because of differences in population characteristics and analytical procedures.

Several limitations should be noted. The cross-sectional design identifies age associations rather than intraindividual aging trajectories, and the modest sample size warrants replication in larger cohorts. Frequency-resolved microstate estimates may also be influenced by age-related differences in spectral amplitude and signal-to-noise ratio, particularly because spectral characteristics were age-sensitive in this cohort. However, the persistence of the significant state-level associations after controlling for band-specific spectral power argues against a simple power explanation. In addition, fixed canonical bands may not represent equivalent physiological

activity across adulthood; this is particularly relevant for the alpha range, because age-related slowing of peak alpha frequency (Sally et al., 2018; Knyazeva et al., 2018; Park et al., 2024) could reduce the comparability of the fixed 8–12 Hz band across participants and may have contributed to the absence of corrected alpha-band associations. Less stereotypical narrow-band topographies also limit direct class-wise comparisons across frequencies. Furthermore, narrow-band filtering alters temporal structure, so absolute durations should not be interpreted as directly comparable intrinsic timescales across bands. Sex effects were present, particularly in beta, but showed limited overlap with age-associated parameters.

In conclusion, age associations in EEG microstate dynamics were strongly frequency dependent, with the clearest state-level effects in delta and beta. The findings suggest that frequency-resolved microstate analysis captures aspects of age-related EEG organization not fully represented by broadband analysis alone, while differences in state prevalence appear to account for a substantial portion of the observed age-related variation in transition probabilities.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

Not applicable.

Competing interests

None

Funding

None

References

Antonova, E., Holding, M., Suen, H. C., Sumich, A., Maex, R., & Nehaniv, C. (2022). EEG microstates: Functional significance and short-term test-retest reliability. *NeuroImage: Reports*, 2(2), 100089. doi:10.1016/j.nirp.2022.100089.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, 57(1), 289–300. doi:10.1111/j.2517-6161.1995.tb02031.x.

Chetty, C. A., Bhardwaj, H., Kumar, G. P., Devanand, T., Sekhar, C. S. A., Aktürk, T., Kiyi, I., Yener, G., Güntekin, B., Joseph, J., & Adaikkan, C. (2024). EEG biomarkers in Alzheimer's and prodromal Alzheimer's: A comprehensive analysis of spectral and connectivity features. *Alzheimer's Research & Therapy*, 16, 236. doi:10.1186/s13195-024-01582-w.

Custo, A., Van De Ville, D., Wells, W. M., Tomescu, M. I., Brunet, D., & Michel, C. M. (2017). Electroencephalographic resting-state networks: Source localization of microstates. *Brain Connectivity*, 7(10), 671–682. doi:10.1089/brain.2016.0476.

Das, S., Mdawar, B., Diaconescu, A., Hill, A. T., Desarkar, P., Ma, C., Zrenner, C., De Luca, V., Zomorodi, R., & Rajji, T. K. (2026). Electroencephalogram microstates in Alzheimer's dementia

and mild cognitive impairment: A systematic review and meta-analysis. *Clinical Neurophysiology*, 117, 2111-2156. <https://doi.org/10.1016/j.clinph.2026.2111856>

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21. doi:10.1016/j.jneumeth.2003.10.009.

Fernández-Rubio, G., Vuust, P., Kringelbach, M. L., & Bonetti, L. (2025). The neurophysiology of healthy and pathological aging: A comprehensive systematic review. *Brain Structure and Function*, 230, 146. doi:10.1007/s00429-025-03012-5.

Férat, V., Seeber, M., Michel, C. M., & Ros, T. (2022). Beyond broadband: Towards a spectral decomposition of electroencephalography microstates. *Human Brain Mapping*, 43(10), 3047–3061. doi:10.1002/hbm.25834.

Huang, Y., Cao, C., Dai, S., Deng, H., Cambridge Centre for Neuroscience and Ageing, Su, L., & Zheng, J.-S. (2024). Magnetoencephalography-derived oscillatory microstate patterns across lifespan: The Cambridge Centre for Ageing and Neuroscience cohort. *Brain Communications*, 6(3), fcae150. doi:10.1093/braincomms/fcae150.

Jabès, A., Klencklen, G., Ruggeri, P., Michel, C. M., Banta Lavenex, P., & Lavenex, P. (2021). Resting-state EEG microstates parallel age-related differences in allocentric spatial working memory performance. *Brain Topography*, 34, 442–460. doi:10.1007/s10548-021-00835-3.

James, T. M., & Burgess, A. P. (2025). Estimating chronological age from the electrical activity of the brain: How EEG-age can be used as a marker of general brain functioning. *Psychophysiology*, 62(3), e70033. doi:10.1111/psyp.70033.

Johansson, C., Koenig, T., Smailovic, U., Hallström, V., Jelic, V., & Graff, C. (2025). Selective association of EEG microstates with clinical symptoms and mutation status in monogenic Alzheimer disease. *NeuroImage: Clinical*, 48, 103879. <https://doi.org/10.1016/j.nicl.2025.103879>

Jordánek, T., Lamoš, M., & Mareček, R. (2025). Vertical topography in EEG microstates: Physiology or artifact manifestation? *Human Brain Mapping*, 46(11), e70294. doi:10.1002/hbm.70294.

Khazaei, M., Raeisi, K., Croce, P., Tamburro, G., Tokariev, A., Vanhatalo, S., Zappasodi, F., & Comani, S. (2021). Characterization of the functional dynamics in the neonatal brain during REM and NREM sleep states by means of microstate analysis. *Brain Topography*, 34(5), 555–567. doi:10.1007/s10548-021-00861-1.

Knyazeva, M. G., Barzegaran, E., Vildavski, V. Y., & Demonet, J.-F. (2018). Aging of human alpha rhythm. *Neurobiology of Aging*, 69, 261–273. doi:10.1016/j.neurobiolaging.2018.05.018.

Koenig, T., Prichep, L., Lehmann, D., Valdes Sosa, P., Braeker, E., Kleinlogel, H., Isenhardt, R., & John, E. R. (2002). Millisecond by millisecond, year by year: Normative EEG microstates and developmental stages. *NeuroImage*, 16(1), 41–48. doi:10.1006/nimg.2002.1070.

Krzanowski, W. J., & Lai, Y. T. (1988). A criterion for determining the number of groups in a data set using sum-of-squares clustering. *Biometrics*, 44(1), 23–34. doi:10.2307/2531893.

Michel, C. M., & Bréchet, L. (2026). EEG microstates: From methodological foundations to clinical translation. *Trends in Neurosciences*, 49(6), 433–449. <https://doi.org/10.1016/j.tins.2026.04.003>

Michel, C. M., & Koenig, T. (2018). EEG microstates as a tool for studying the temporal dynamics of whole-brain neuronal networks: A review. *NeuroImage*, 180, 577–593. doi:10.1016/j.neuroimage.2017.11.062.

Musaeus, C. S., Engedal, K., Høgh, P., Jelic, V., Khanna, A. R., Kjaer, T. W., Mørup, M., Naik, M., Oeksengaard, A.-R., Santarnecchi, E., Snaedal, J., Wahlund, L.-O., Waldemar, G., & Andersen, B. B. (2020). Changes in the left temporal microstate are a sign of cognitive decline in patients with Alzheimer's disease. *Brain and Behavior*, 10(6), e01630. doi:10.1002/brb3.1630.

Nagabhushan Kalburgi, S., Kleinert, T., Aryan, D., Nash, K., Schiller, B., & Koenig, T. (2024). MICROSTATELAB: The EEGLAB toolbox for resting-state microstate analysis. *Brain Topography*, 37(4), 621–645. doi:10.1007/s10548-023-01003-5.

Nobukawa, S., Ikeda, T., Kikuchi, M., & Takahashi, T. (2026). Age-group differences between young and middle-aged adults in spatiotemporal EEG dynamics revealed by instantaneous frequency microstate analysis. *Frontiers in Aging Neuroscience*, 18, 1707228. doi:10.3389/fnagi.2026.1707228.

Park, J., Ho, R. L. M., Wang, W.-E., Nguyen, V. Q., & Coombes, S. A. (2024). The effect of age on alpha rhythms in the human brain derived from source localized resting-state electroencephalography. *NeuroImage*, 292, 120614. doi:10.1016/j.neuroimage.2024.120614.

Pion-Tonachini, L., Kreutz-Delgado, K., & Makeig, S. (2019). ICLabel: An automated electroencephalographic independent component classifier, dataset, and website. *NeuroImage*, 198, 181–197. doi:10.1016/j.neuroimage.2019.05.026.

Ruuskanen, S., Avendano-Diaz, J. C., Liljeström, M., & Parkkonen, L. (2026). Frequency-resolved cortical functional connectivity across the adult lifespan. *Human Brain Mapping*, 47(4), e70484. doi:10.1002/hbm.70484.

Scally, B., Burke, M. R., Bunce, D., & Delvenne, J.-F. (2018). Resting-state EEG power and connectivity are associated with alpha peak frequency slowing in healthy aging. *Neurobiology of Aging*, 71, 149–155. doi:10.1016/j.neurobiolaging.2018.07.004.

Smailovic, U., Koenig, T., Laukka, E. J., Kalpouzos, G., Andersson, T., Winblad, B., & Jelic, V. (2019). EEG time signature in Alzheimer's disease: Functional brain networks falling apart. *NeuroImage: Clinical*, 24, 102046. doi:10.1016/j.nicl.2019.102046.

Tarailis, P., Koenig, T., Michel, C. M., & Griškova-Bulanova, I. (2024). The functional aspects of resting EEG microstates: A systematic review. *Brain Topography*, 37(2), 181–217. <https://doi.org/10.1007/s10548-023-00958-9>

Tarailis, P., Artoni, F., Koenig, T., Michel, C. M., & Griškova-Bulanova, I. (2026). Short-term and long-term test-retest reliability of memory, complexity, and randomness of EEG microstates sequence. *Cognitive Neurodynamics*, 20(1), 19. <https://doi.org/10.1007/s11571-025-10391-2>

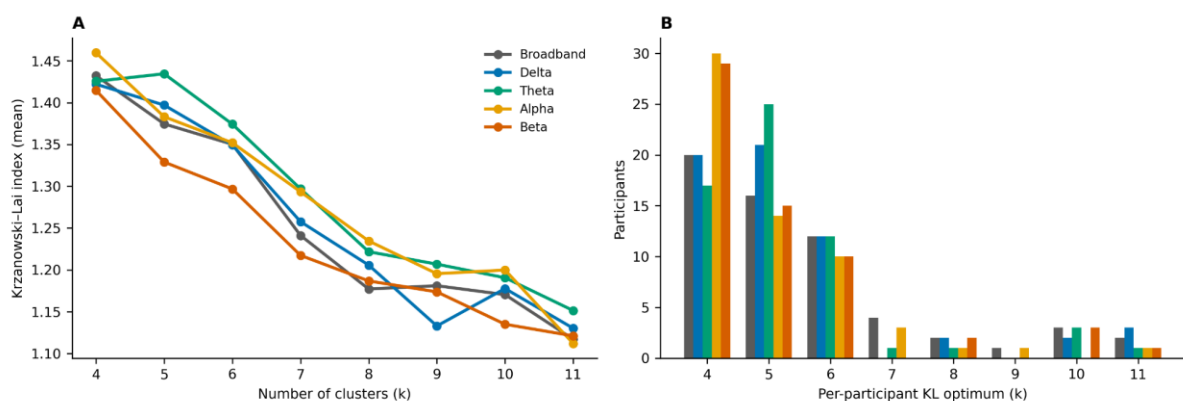
Tomescu, M. I., Rihs, T. A., Rochas, V., Hardmeier, M., Britz, J., Allali, G., Fuhr, P., Eliez, S., & Michel, C. M. (2018). From swing to cane: Sex differences of EEG resting-state temporal patterns during maturation and aging. *Developmental Cognitive Neuroscience*, 31, 58–66. doi:10.1016/j.dcn.2018.04.011.

Yuan, Y., & Zhao, Y. (2025). The role of quantitative EEG biomarkers in Alzheimer's disease and mild cognitive impairment: Applications and insights. *Frontiers in Aging Neuroscience*, 17, 1522552. doi:10.3389/fnagi.2025.1522552.

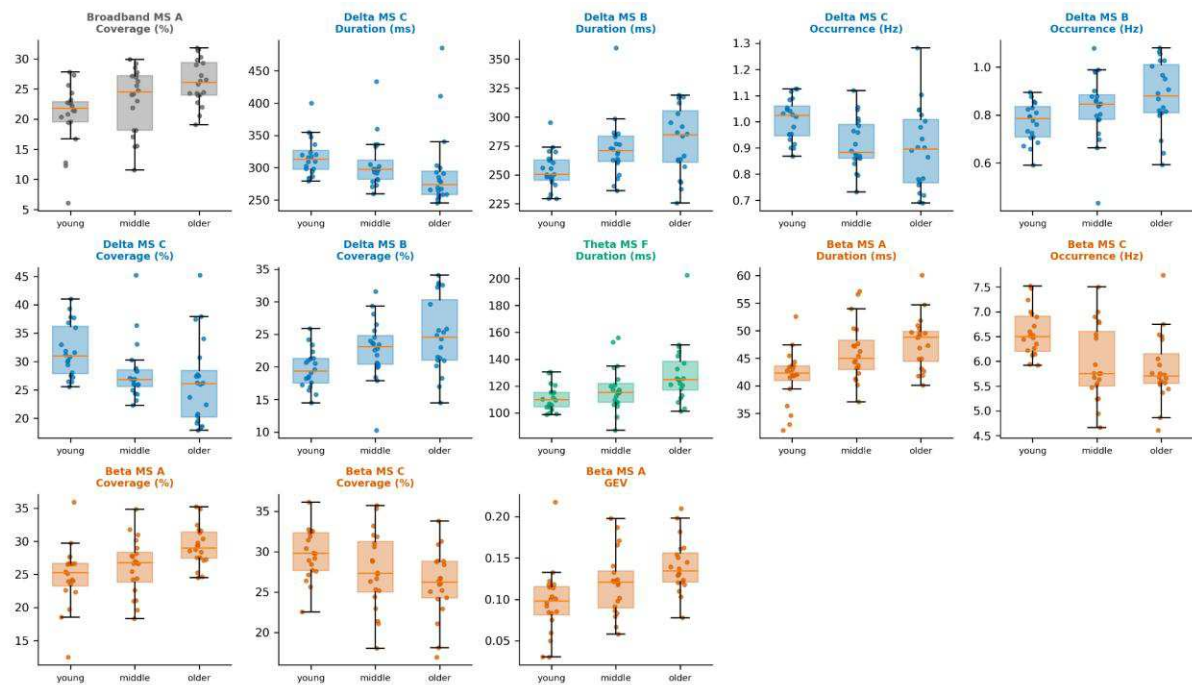
ZanESCO, A. P., King, B. G., Skwara, A. C., & Saron, C. D. (2020). Within and between-person correlates of the temporal dynamics of resting EEG microstates. *NeuroImage*, 211, 116631. doi:10.1016/j.neuroimage.2020.116631.

Supplementary Material

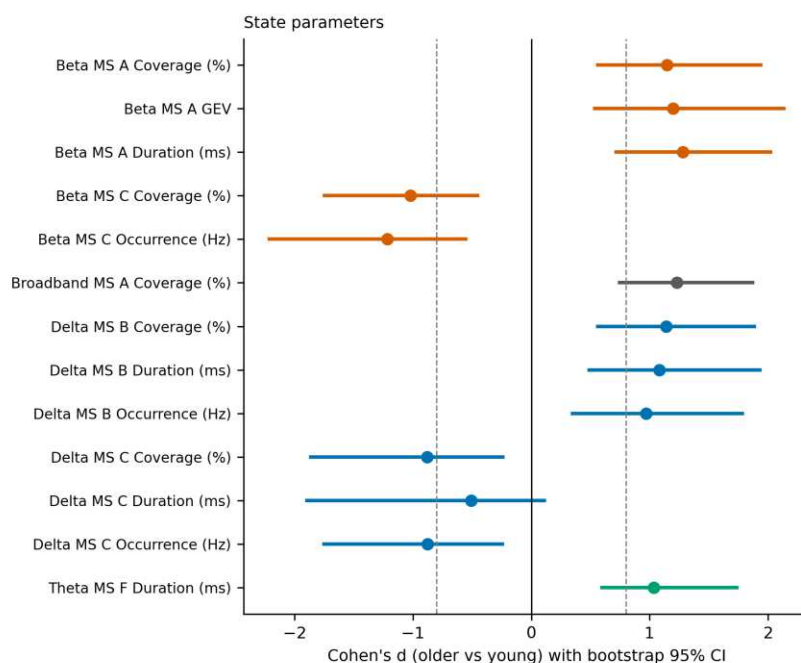
Supplementary figures



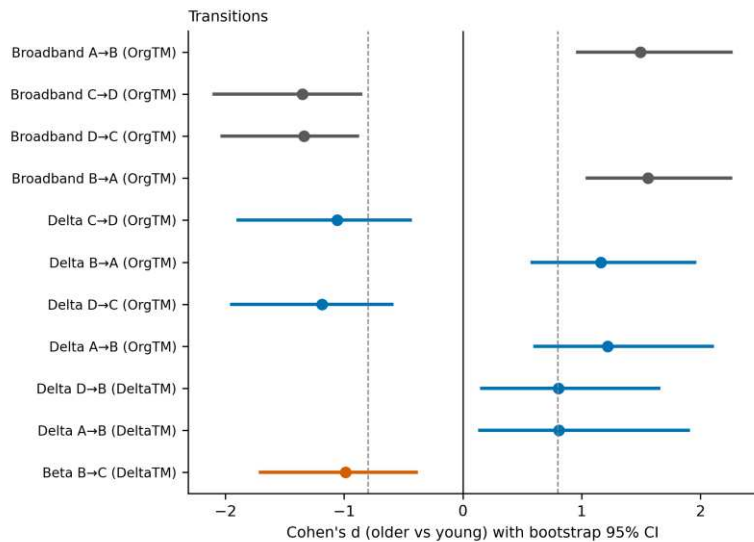
Supplementary Fig. S1. (A) Mean Krzanowski–Lai index by number of clusters ($k = 4–11$) for each frequency band. (B) Distribution of the per-participant Krzanowski–Lai optimum.



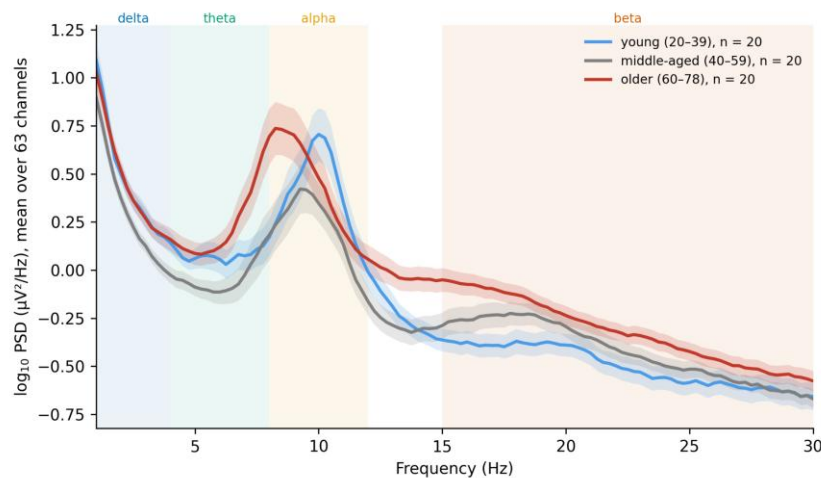
Supplementary Fig. S2. Distributions of all 13 FDR-significant state-level parameters in young (20–39), middle-aged (40–59) and older (60–78 years) participants ($n = 20$ per group); boxes = median and interquartile range, points = participants, colours follow frequency band.



Supplementary Fig. S3. Cohen's d (older vs. young) with bootstrap 95% confidence intervals for the 13 FDR-significant state associations; dashed lines mark $|d| = 0.8$.



Supplementary Fig. S4. Cohen's d (older vs. young) with bootstrap 95% confidence intervals for the 11 FDR-significant transition associations (8 observed, 3 chance-adjusted).



Supplementary Fig. S5. Mean power spectral density (log₁₀ PSD, Welch's method with 4-s Hamming windows and 50% overlap, averaged over the 63 scalp channels) of the cleaned continuous broadband recordings, by age group (n = 20 per group); shading shows ± 1 SEM. Coloured bands mark the frequency ranges used in the analyses.

Supplementary tables

Supplementary Table S1. FDR-significant age associations of microstate temporal parameters and their robustness. ρ : Spearman correlation with age; q : FDR-adjusted p within band $\times$ parameter families; ρ partial: controlling for sex and education; d : Cohen's d for older (60–78) versus young (20–39) participants with bootstrap 95% confidence interval (10,000 resamples); ANOVA: one-way ANOVA across the three age groups.

Band	Class	Parameter	ρ	q	ρ partial	p partial	d [95% CI]	p ANOVA
Broadband	MS A	Coverage (%)	+0.328	0.0421	+0.315	0.0160	+1.23 [0.75, 1.87]	0.0023

Delta	MS B	Duration (ms)	+0.446	0.0007	+0.462	0.0003	+1.08 [0.49, 1.93]	0.0046
Delta	MS B	Occurrence (Hz)	+0.398	0.0065	+0.443	0.0005	+0.97 [0.35, 1.78]	0.0213
Delta	MS B	Coverage (%)	+0.473	0.0006	+0.504	< .0001	+1.14 [0.56, 1.88]	0.0027
Delta	MS C	Duration (ms)	-0.461	0.0007	-0.521	< .0001	-0.51 [-1.90, 0.11]	0.2455
Delta	MS C	Occurrence (Hz)	-0.359	0.0097	-0.384	0.0029	-0.88 [-1.75, -0.25]	0.0102
Delta	MS C	Coverage (%)	-0.408	0.0024	-0.468	0.0002	-0.88 [-1.86, -0.24]	0.0144
Theta	MS F	Duration (ms)	+0.359	0.0245	+0.360	0.0056	+1.03 [0.60, 1.74]	0.0061
Beta	MS A	Duration (ms)	+0.361	0.0183	+0.388	0.0026	+1.28 [0.72, 2.02]	0.0008
Beta	MS A	Coverage (%)	+0.424	0.0015	+0.407	0.0015	+1.15 [0.56, 1.94]	0.0029
Beta	MS A	GEV	+0.429	0.0025	+0.460	0.0003	+1.20 [0.54, 2.14]	0.0021
Beta	MS C	Occurrence (Hz)	-0.442	0.0016	-0.459	0.0003	-1.22 [-2.21, -0.56]	0.0018
Beta	MS C	Coverage (%)	-0.435	0.0015	-0.456	0.0003	-1.02 [-1.75, -0.46]	0.0191

Supplementary Table S2. Cluster-number selection by the Krzanowski–Lai criterion (k = 3–12 searched; the index is defined for k = 4–11). Group optimum: k maximizing the mean index across participants; participant mode: most frequent per-participant optimum (n = 60). The k used in all analyses is given in the last column.

Band	Group optimum k	Mean KL at optimum	Participant mode k	n at mode	k used
Broadband	4	1.43	4	20	4
Delta	4	1.42	5	21	4
Theta	5	1.43	5	25	5
Alpha	4	1.46	4	30	4
Beta	4	1.41	4	29	4

Supplementary Table S3a. Spearman correlations between age and observed transition probabilities, Broadband band (k = 4). Rows: origin class; columns: destination class. * FDR-significant within the band's 12 directed pairs (q = .05).

	to A	to B	to C	to D
from A	—	+0.45*	+0.10	+0.06
from B	+0.47*	—	-0.05	-0.00
from C	+0.08	-0.01	—	-0.45*
from D	+0.09	-0.02	-0.45*	—

Supplementary Table S3b. Spearman correlations between age and observed transition probabilities, Delta band ($k = 4$). Rows: origin class; columns: destination class. * FDR-significant within the band's 12 directed pairs ($q = .05$).

	to A	to B	to C	to D
from A	—	+0.40*	-0.18	-0.04
from B	+0.40*	—	+0.03	+0.25
from C	-0.22	+0.01	—	-0.35*
from D	+0.04	+0.26	-0.39*	—

Supplementary Table S3c. Spearman correlations between age and observed transition probabilities, Theta band ($k = 5$). Rows: origin class; columns: destination class. * FDR-significant within the band's 20 directed pairs ($q = .05$).

	to A	to B	to D	to E	to F
from A	—	+0.13	-0.14	-0.11	+0.13
from B	+0.09	—	-0.22	-0.05	+0.19
from D	-0.17	-0.27	—	-0.26	+0.07
from E	-0.06	-0.13	-0.30	—	+0.14
from F	+0.21	+0.19	+0.04	+0.06	—

Supplementary Table S3d. Spearman correlations between age and observed transition probabilities, Alpha band ($k = 4$). Rows: origin class; columns: destination class. * FDR-significant within the band's 12 directed pairs ($q = .05$).

	to A	to B	to D	to F
from A	—	+0.15	+0.11	+0.15
from B	+0.14	—	-0.22	-0.06
from D	+0.10	-0.15	—	-0.03
from F	+0.17	-0.15	+0.09	—

Supplementary Table S3e. Spearman correlations between age and observed transition probabilities, Beta band ($k = 4$). Rows: origin class; columns: destination class. * FDR-significant within the band's 12 directed pairs ($q = .05$).

	to A	to B	to C	to D
from A	—	+0.30	-0.09	+0.30
from B	+0.33	—	-0.25	+0.12
from C	-0.03	-0.25	—	-0.29
from D	+0.25	+0.10	-0.24	—

Supplementary Table S4a. Spearman correlations between age and chance-adjusted transition probabilities, Broadband band ($k = 4$). Rows: origin class; columns: destination class. * FDR-significant within the band's 12 directed pairs ($q = .05$).

	to A	to B	to C	to D
from A	—	+0.18	-0.04	-0.14
from B	+0.33	—	-0.25	-0.15

from C	+0.28	+0.20	—	-0.34
from D	+0.28	+0.14	-0.31	—

Supplementary Table S4b. Spearman correlations between age and chance-adjusted transition probabilities, Delta band ($k = 4$). Rows: origin class; columns: destination class. * FDR-significant within the band's 12 directed pairs ($q = .05$).

	to A	to B	to C	to D
from A	—	+0.39*	-0.20	-0.16
from B	+0.21	—	-0.19	-0.03
from C	-0.10	+0.18	—	-0.06
from D	+0.13	+0.36*	-0.31	—

Supplementary Table S4c. Spearman correlations between age and chance-adjusted transition probabilities, Theta band ($k = 5$). Rows: origin class; columns: destination class. * FDR-significant within the band's 20 directed pairs ($q = .05$).

	to A	to B	to D	to E	to F
from A	—	+0.12	-0.02	-0.21	-0.00
from B	+0.03	—	-0.18	+0.15	+0.06
from D	+0.07	-0.10	—	-0.09	+0.19
from E	-0.05	+0.11	-0.28	—	+0.17
from F	+0.13	-0.15	+0.09	-0.06	—

Supplementary Table S4d. Spearman correlations between age and chance-adjusted transition probabilities, Alpha band ($k = 4$). Rows: origin class; columns: destination class. * FDR-significant within the band's 12 directed pairs ($q = .05$).

	to A	to B	to D	to F
from A	—	+0.06	-0.10	-0.07
from B	+0.19	—	-0.23	+0.06
from D	-0.04	-0.02	—	-0.01
from F	+0.06	-0.22	+0.25	—

Supplementary Table S4e. Spearman correlations between age and chance-adjusted transition probabilities, Beta band ($k = 4$). Rows: origin class; columns: destination class. * FDR-significant within the band's 12 directed pairs ($q = .05$).

	to A	to B	to C	to D
from A	—	+0.10	-0.24	+0.16
from B	+0.26	—	-0.37*	+0.16
from C	+0.20	+0.05	—	-0.20
from D	+0.21	+0.09	-0.24	—

Supplementary Table S5. FDR-significant sex differences in microstate temporal parameters (Mann–Whitney U; rank-biserial correlation, positive values = higher in males; FDR within band $\times$ parameter families).

Band	Class	Parameter	r_{rb}	p	q
Broadband	MS C	GEV	-0.403	0.0088	0.0354
Delta	MS A	GEV	-0.398	0.0097	0.0386
Beta	MS A	Duration (ms)	-0.336	0.0292	0.0390

Beta	MS A	Occurrence (Hz)	+0.350	0.0232	0.0463
Beta	MS B	Duration (ms)	-0.433	0.0049	0.0098
Beta	MS C	Duration (ms)	-0.697	< .0001	< .0001
Beta	MS C	Coverage (%)	-0.472	0.0021	0.0081
Beta	MS C	GEV	-0.625	< .0001	0.0002
Beta	MS D	Occurrence (Hz)	+0.604	< .0001	0.0003
Beta	MS D	Coverage (%)	+0.442	0.0040	0.0081

Supplementary Table S6. Band-power-controlled partial correlations. Partial Spearman correlation of each FDR-significant association with age, controlling for sex, education, and the log10-transformed spectral power of the corresponding frequency band. All 13 associations remained significant.

Band	Class	Parameter	ρ (primary)	ρ (partial)	p (partial)	Remains significant
Broadband	MS A	Coverage (%)	+0.328	+0.335	0.0109	Yes
Delta	MS B	Duration (ms)	+0.446	+0.460	0.0003	Yes
Delta	MS B	Occurrence (Hz)	+0.398	+0.439	0.0006	Yes
Delta	MS B	Coverage (%)	+0.473	+0.502	< .0001	Yes
Delta	MS C	Duration (ms)	-0.461	-0.518	< .0001	Yes
Delta	MS C	Occurrence (Hz)	-0.359	-0.392	0.0026	Yes
Delta	MS C	Coverage (%)	-0.408	-0.465	0.0003	Yes
Theta	MS F	Duration (ms)	+0.359	+0.284	0.0322	Yes
Beta	MS A	Duration (ms)	+0.361	+0.306	0.0207	Yes
Beta	MS A	Coverage (%)	+0.424	+0.364	0.0054	Yes
Beta	MS A	GEV	+0.429	+0.454	0.0004	Yes
Beta	MS C	Occurrence (Hz)	-0.442	-0.355	0.0067	Yes
Beta	MS C	Coverage (%)	-0.435	-0.348	0.0079	Yes

Supplementary Table S7. Robustness of FDR-significant transition associations: ρ partial (sex + education), ρ partial (+ log10 band power), Cohen's d older vs. young with bootstrap 95% CI, and one-way ANOVA across the three age groups.

Band	Metric	Transition	ρ	q	ρ partial	ρ partial (+power)	d [95% CI]	p ANOVA
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Broadband	observed	A→B	+0.446	0.0011	+0.459	+0.451	+1.50 [0.97, 2.26]	< .0001
Broadband	observed	C→D	-0.452	0.0011	-0.463	-0.467	-1.35 [-2.10, -0.86]	0.0005
Broadband	observed	D→C	-0.451	0.0011	-0.464	-0.468	-1.34 [-2.03, -0.89]	0.0007
Broadband	observed	B→A	+0.471	0.0011	+0.476	+0.471	+1.56 [1.05, 2.26]	< .0001
Delta	observed	C→D	-0.348	0.0191	-0.367	-0.362	-1.06 [-1.89, -0.44]	0.0111
Delta	observed	B→A	+0.398	0.0079	+0.425	+0.421	+1.16 [0.58, 1.95]	0.0020
Delta	observed	D→C	-0.392	0.0079	-0.411	-0.407	-1.19 [-1.95, -0.60]	0.0023
Delta	observed	A→B	+0.402	0.0079	+0.408	+0.404	+1.22 [0.61, 2.10]	0.0018
Delta	chance-adj.	D→B	+0.362	0.0266	+0.364	+0.372	+0.81 [0.16, 1.65]	0.0588
Delta	chance-adj.	A→B	+0.391	0.0240	+0.374	+0.374	+0.81 [0.14, 1.90]	0.0486
Beta	chance-adj.	B→C	-0.367	0.0470	-0.372	-0.314	-0.99 [-1.71, -0.39]	0.0166

Supplementary Table S8. Tukey HSD post-hoc comparisons for the 13 FDR-significant state-level associations. Adjusted p values for each pair of age groups (young 20–39, middle-aged 40–59, older 60–78; n = 20 per group); * p < .05. The one-way ANOVA result for each parameter is given in Supplementary Table S1.

Band	Class	Parameter	young vs middle-aged	middle-aged vs older	young vs older
Broadband	MS A	Coverage (%)	.234	.117	.002*
Delta	MS B	Duration (ms)	.046*	.654	.004*
Delta	MS B	Occurrence (Hz)	.277	.389	.016*
Delta	MS B	Coverage (%)	.091	.316	.002*
Delta	MS C	Duration (ms)	.729	.621	.216
Delta	MS C	Occurrence (Hz)	.050	.840	.012*

Delta	MS C	Coverage (%)	.110	.643	.013*
Theta	MS F	Duration (ms)	.439	.104	.005*
Beta	MS A	Duration (ms)	.018*	.531	.001*
Beta	MS A	Coverage (%)	.511	.049*	.002*
Beta	MS A	GEV	.134	.190	.001*
Beta	MS C	Occurrence (Hz)	.011*	.872	.003*
Beta	MS C	Coverage (%)	.243	.411	.014*

Supplementary Table S9. Tukey HSD post-hoc comparisons for the 11 FDR-significant transition associations. Adjusted p values for each pair of age groups (young 20–39, middle-aged 40–59, older 60–78; n = 20 per group); * p < .05. The one-way ANOVA result for each transition is given in Supplementary Table S7.

Band	Metric	Transition	young vs middle-aged	middle-aged vs older	young vs older
Broadband	observed	A→B	.454	.004*	< .001*
Broadband	observed	C→D	.145	.073	< .001*
Broadband	observed	D→C	.187	.068	.001*
Broadband	observed	B→A	.447	.004*	< .001*
Delta	observed	C→D	.113	.557	.009*
Delta	observed	B→A	.051	.417	.002*
Delta	observed	D→C	.032*	.603	.002*
Delta	observed	A→B	.073	.298	.001*
Delta	chance-adj.	D→B	.284	.655	.049*
Delta	chance-adj.	A→B	.565	.304	.039*
Beta	chance-adj.	B→C	.051	.944	.023*