Beyond broadband: towards a spectral decomposition of EEG microstates

*Victor Férat*¹, *Martin Seeber*¹, *Christoph M. Michel*^{1,2}, *Tomas Ros*^{1,2}

¹ Functional Brain Mapping Laboratory, Department of Basic Neurosciences, Campus Biotech, University of Geneva, Geneva, Switzerland

² Centre for Biomedical Imaging (CIBM) Lausanne-Geneva, Geneva, Switzerland

Credit authorship contribution statement

Victor Férat: Conceptualization, Formal analysis, Methodology, Visualization, Writing - original draft, Writing - review & editing.

Martin Seeber: Writing - review & editing

Christoph Michel: Writing - review & editing

Tomas Ros: Writing - Conceptualization, Formal analysis, Methodology review & editing.

Data availability statement

The data and code supporting our results are openly available in the OSF repository and can be found at: <https://osf.io/bfsge/>

Other 3rd party software and datasets used in this study can be found by following citations in the paper.

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29 **Conflict of Interest Statement**

30 The authors declare that the research was conducted in the absence
 31 of any commercial or financial relationships that could be construed
 32 as a potential conflict of interest.

33

Abstract: Originally applied to alpha oscillations in the 1970s, MS analysis has since been used to decompose mainly broadband EEG signals (e.g. 1-40 Hz). We hypothesized that MS decomposition within separate, narrow frequency bands could provide more fine-grained information for capturing the spatio-temporal complexity of multichannel EEG. In this study using a large open-access dataset (n=203), we decomposed EEG recordings into 4 classical frequency bands (delta, theta, alpha, beta) in order to compare their individual MS segmentations using mutual information as well as traditional MS measures (e.g. mean duration, time coverage). Firstly, we confirmed that MS topographies were spatially equivalent across all frequencies, matching the canonical broadband maps (A, B, C, D). Interestingly however, we observed strong informational independence of MS temporal sequences between spectral bands, together with significant divergence in traditional MS measures. For example, relative to broadband, alpha/beta band dynamics displayed greater time coverage of maps A & B, while map D was more prevalent in delta/theta bands. Moreover, by using a frequency-specific MS taxonomy (e.g. θA , αC), we were able to predict the eyes-open vs closed- behavioural state significantly better using alpha-band MS features compared with broadband ones (80% vs 73% accuracy). Overall, our findings demonstrate the value and validity of spectrally-specific MS analyses, which may prove useful for identifying new neural mechanisms in fundamental research and/or for biomarker discovery in clinical populations.

Keywords: EEG ; microstates; topography; Resting state ; eyes closed ; eyes open ; alpha; mutual information

1 Introduction

Multi-channel Electroencephalography (EEG) is a long-established tool for exploring the human brain's spatio-temporal activities. Microstate (MS) analysis (Michel and Koenig 2018), first introduced by Lehmann (Lehmann 1971) in 1971, takes advantage of EEG's high temporal resolution to segment EEG signals into short successive periods of time characterized by metastable scalp topographies. Initially applied to narrow-band alpha oscillations (8 -12 Hz)(Lehmann 1971), microstate analysis is nowadays usually performed on broadband EEG signals (1 - 40Hz) (Michel and Koenig 2018; Zanesco et al. 2020). Historically, only a limited number of studies (Javed et al. 2019; Merrin et al. 1990; Musaeus et al. 2020) have focused on applying MS analysis to the traditional frequencies associated with cortical oscillations (e.g. delta, theta, alpha, beta etc.). For example, in the 1990's, Merrin et al (Merrin et al. 1990) were the first to report on a significant difference in MS segments between schizophrenic patients and controls specifically in the theta EEG band. On the other hand, more recent work in healthy subjects found that MS dynamics were independent of EEG power fluctuations across the frequency spectrum (Britz, Van De Ville, and Michel 2010), which technically supported the rationale for performing broadband MS analysis. Neuroimaging studies have nevertheless emerged showing that anatomically-distinct cortical regions display different dominant EEG frequencies, with occipito-parietal regions more active in the alpha band, and prefrontal regions being biased more toward delta or theta power (Groppe et al. 2013; Keitel and Gross 2016; Mellem et al. 2017). Moreover, ongoing cortical dynamics have been reported to fluctuate from a local resting/idling alpha oscillatory state to task-specific active mode(s)

88 dominated by other rhythms (e.g. theta (Ribary, Doesburg, and Ward
89 2017), gamma (Hipp, Engel, and Siegel 2011)). As a consequence, cortical
90 regions could combine different frequencies for integrating/segregating
91 information across large-scale networks, a phenomenon termed
92 “oscillatory multiplexing” (Akam and Kullmann 2014). Finally, of more
93 clinical significance, a growing body of work has indicated abnormal EEG
94 spectral power in distinct frequencies across cortical regions in a variety
95 of brain disorders (Ros et al. 2014; Schulman et al. 2011). Therefore, given
96 that different spatial topographies uncovered by MS analysis imply
97 anatomically-distinct cortical generators (according to the forward-model
98 of EEG generation (Michel and Koenig 2018)), it is reasonable to
99 hypothesize that distinct MS topographies may display different spatial
100 and/or temporal profiles across the frequency spectrum.

101 To investigate this question as well as gain a deeper understanding of
102 frequency-specific MS signature(s), we sought to explicitly decompose MS
103 spatio-temporal dynamics within *discrete, narrow-band frequency bands*
104 (i.e. delta, theta, alpha, and beta), with the aim of comparing them to the
105 classical analysis of the broadband signal.

106 Here, we employed a validated, open-source dataset (Babayan et al.
107 2019) of resting-state EEG recordings from 203 healthy subjects during
108 both eyes opened and eyes closed conditions. These were then filtered in
109 the classical EEG bands (delta: 0-4 Hz, theta: 4-8 Hz, alpha: 8-12 Hz, beta:
110 15-30 Hz) to obtain band specific signals. These narrow-band signals, in
111 addition to the broadband (1-30 Hz) signal, were then independently
112 subjected to standard microstate analysis (Pascual-Marqui, Michel, and
113 Lehmann 1995). Map topography, mean duration, occurrence, time

114 coverage, and global explained variance (GEV) were used as quantitative
115 measures of spatiotemporal microstate dynamics. In summary, and using
116 spatial correlation analysis, we firstly demonstrate remarkably similar
117 microstate topographies across frequencies, closely matching the classical
118 broadband maps. Interestingly, however, we observed strong
119 informational independence of microstate sequences between
120 frequencies, in addition to significant differences in established measures
121 of temporal dynamics (mean duration, occurrence, and time coverage).

122 In conclusion, our results support a more diverse, frequency-specific
123 application of microstate analysis compatible with the narrow-band MS
124 analyses of early pioneers (Lehmann 1971; Merrin et al. 1990). We
125 anticipate this approach to provide a more fine-grained spectral
126 information not visible to the standard broadband analysis, for example in
127 the identification of biomarkers in clinical populations or for
128 understanding the mechanisms underlying EEG microstates.

129 **2 Methods**

130 **2.1 Dataset**

131 EEG recordings were obtained from 203 anonymized participants
132 enrolled in the Mind-Brain-Body study (Babayan et al. 2019). Detailed
133 protocol and inclusion criteria are reported in (Babayan et al. 2019). The
134 overall sample consisted of 227 participants divided into 2 groups: the
135 younger adults group with participant age ranging between 20 and 35
136 years (N = 153, 45 females, mean age = 25.1 years, SD = 3.1) and an older
137 adults group with age ranging between 59 and 77 years (N = 74, 37

138 females, mean age = 67.6 years, SD = 4.7). Medical and psychological
139 screening was conducted on all participants at the Day Clinic for Cognitive
140 Neurology of the University Clinic Leipzig and the Max Planck Institute for
141 Human and Cognitive and Brain Sciences in order to include only healthy
142 patients. The study protocol was approved by the ethics committee of the
143 University of Leipzig (reference 154/13-ff). Data were obtained in
144 accordance with the Declaration of Helsinki.

145 **2.2 Recordings**

146 Resting state EEGs were recorded using 61 scalp electrodes
147 (ActiCAP, Brain Products GmbH, Gilching, Germany), and one additional
148 VEOG electrode for recording right eye activity. All electrodes were placed
149 according to the international standard 10–20 extended localization
150 system with FCz reference, digitized with a sampling frequency of $f_s=2500$
151 Hz, an amplitude resolution of 0.1 microV, and bandpass filtered between
152 0.015 Hz and 1 kHz. The ground was located at the sternum and scalp
153 electrode impedance was kept below 5 K Ω . Recordings took place in an
154 electrically shielded and sound-attenuated EEG booth. Here, 60s blocks
155 alternated between eyes open (EO) and eyes closed (EC) conditions for a
156 total recording of 16 min (8 blocks EC, 8 blocks EO, starting with EC).
157 During the EO condition, participants were asked to stay awake while
158 fixating their eyes on a black cross presented on a white background.

159 **2.3 Preprocessing**

160 The preprocessing steps are extensively described in (Babayan et al.
161 2019), which we summarize below. All EEG recordings were down-

162 sampled from 2500 to 250 Hz and filtered between 1 and 45Hz (8th order,
163 Butterworth filter). Blocks sharing the same condition were concatenated
164 leading to the creation of 2 datasets per subject. After visual inspection,
165 outlying channels were rejected and EEG segments presenting noise
166 and/or artefacts were removed (except eye movements and eye blinks
167 that were kept for further preprocessing). PCA was used to reduce data
168 dimensionality, by keeping PCs ($N \geq 30$) that explain 95% of the total data
169 variance. Then, independent component analysis (ICA) was performed
170 using the Infomax (runica) algorithm. Components reflecting eye
171 movement, eye blink or heartbeat related artefacts were removed.

172 Before performing microstate analysis, the following additional
173 preprocessing steps were conducted using MNE-python (Gramfort et al.
174 2013): missing/bad channels were interpolated using spherical spline
175 interpolation, the reference was re-projected to average and recordings
176 were down-sampled to 100Hz. Finally, each recording was filtered into
177 broadband plus the 5 traditional EEG frequency bands: broadband (1-30
178 Hz), delta (1-4 Hz), theta (4-8 Hz), alpha (8-12 Hz), beta (15-30 Hz). Filter
179 design consisted of a two-pass forward and reverse, zero-phase, non-
180 causal band-pass FIR filter with the following parameters.

- 181 • **Broadband (1-30 Hz):** - Lower passband edge: 1.00 - Lower
182 transition bandwidth: 1.00 Hz (-12 dB cutoff frequency: 0.50
183 Hz) - Upper passband edge: 30.00 Hz- Upper transition
184 bandwidth: 7.50 Hz (-12 dB cutoff frequency: 33.75 Hz) Filter
185 length: 331 samples (3.310 sec)
- 186 • **Delta (1-4 Hz):** - Lower passband edge: 1.00 - Lower transition
187 bandwidth: 1.00 Hz (-12 dB cutoff frequency: 0.50 Hz) - Upper

188 passband edge: 4.00 Hz - Upper transition bandwidth: 2.00 Hz
 189 (-12 dB cutoff frequency: 5.00 Hz) - Filter length: 331 samples
 190 (3.310 sec)
 191 • **Theta (4-8 Hz):** - Lower passband edge: 4.00 - Lower
 192 transition bandwidth: 2.00 Hz (-12 dB cutoff frequency: 3.00
 193 Hz) - Upper passband edge: 8.00 Hz - Upper transition
 194 bandwidth: 2.00 Hz (-12 dB cutoff frequency: 9.00 Hz) - Filter
 195 length: 165 samples (1.650 sec)
 196 • **Alpha (8-12 Hz):** - Lower passband edge: 8.00 - Lower
 197 transition bandwidth: 2.00 Hz (-12 dB cutoff frequency: 7.00
 198 Hz) - Upper passband edge: 12.00 Hz - Upper transition
 199 bandwidth: 3.00 Hz (-12 dB cutoff frequency: 13.50 Hz) - Filter
 200 length: 165 samples (1.650 sec)
 201 • **Beta (15-30 Hz):** - Lower passband edge: 15.00 - Lower
 202 transition bandwidth: 3.75 Hz (-12 dB cutoff frequency: 13.12
 203 Hz) - Upper passband edge: 30.00 Hz - Upper transition
 204 bandwidth: 7.50 Hz (-12 dB cutoff frequency: 33.75 Hz) - Filter
 205 length: 89 samples (0.890 sec)

206 For all filters, a Hamming window with 0.0194 passband ripple and 53
 207 dB stopband attenuation was used to reduce border effects.

208 **2.4 MS segmentation**

209 **2.4.1 Segmentation**

210 Microstate segmentation was applied to each combination of
 211 frequency band (broadband, delta, theta, alpha, beta) x behavioural
 212 condition (EO, EC) leading to the computation of 10 optimal clusters using

the methodology described below. First, local maxima of the Global Field Power (GFP) known to represent portions of EEG data with highest signal to noise ratio (Koenig and Brandeis 2016), were extracted from each individual recording. Then, 20 epochs of 500 time points randomly drawn from the previous extraction were submitted to a modified k-means cluster analysis using the free academic software Cartool (Brunet, Murray, and Michel 2011). For each number of cluster centers K ranging from 1 to 12, 50 k-means initialisations were applied to each epoch. The initialisation with highest global explained variance (GEV) was selected and kept for further processing. A meta-criterion (Bréchet et al. 2019) was used to choose the optimal number of cluster centers k for each epoch. Individual optimal clusters were then merged within conditions and within frequencies to form 10 groups of 4060 clusters. Each group was then randomly re-sampled into 100 epochs of 5000 time points, and submitted to the same clustering algorithm (50 initialisations, with meta criterion selection), leading to the extraction of 100 optimal clusters per group. Finally, these 100 clusters were submitted to the modified K means clustering algorithm to extract, for each number of cluster centroids k, a set of maps which best represent the spatiotemporal variance of frequency specific EEG data within each condition.

2.4.2 Selection of “common” MS maps

Given that we found high spatial correlations between MS maps across all frequencies and EO/EC conditions, we fitted the broadband maps directly to all the frequency bands in order to have a common reference. This may be considered a heuristic approach for the sake of simplicity. An alternative approach we explored was to perform subject-level (i.e. 1st level) clustering on all data concatenated *within-subject* (across

240 frequencies, and/or conditions), followed by group-level (i.e. 2nd-level)
 241 clustering. We found this to once again produce identical maps to the
 242 broadband decomposition. This method could theoretically be used to find
 243 the most “common” clusters across different datasets, in case of variable
 244 k-means outputs (e.g. visually similar MS maps at different k-values). Since
 245 it is beyond the scope of this paper, we leave it to future studies to validate
 246 this method more rigorously.

247 **2.4.3 Back-fitting of MS Maps**

248 The common topographic maps selected above were then assigned
 249 to every time point from all individual recordings using the traditional MS
 250 back-fitting method (Van De Ville, Britz, and Michel 2010). First, the
 251 spatial correlation was computed between every timepoint and map.
 252 Using the so called ‘winner takes all’ algorithm, each timepoint was
 253 labelled according to the map with which it shared the highest absolute
 254 spatial correlation. Timepoints were labelled as “non-assigned” when the
 255 absolute spatial correlation was below $r < 0.5$ threshold. To ensure
 256 temporal continuity of MS segmentation, a smoothing step (Brunet et al.
 257 2011; Pascual-Marqui et al. 1995) was applied. Finally, segments with
 258 duration shorter than 3 samples (30ms) were assigned to neighbouring
 259 segments using the following rule: the segment was split into two parts,
 260 where each part was assigned to the neighbouring segment with the
 261 higher spatial correlation. With backfitting completed, we extracted 4
 262 spatiotemporal parameters for each microstate map, namely:

- 263 • **Global explained variance** (Gev) described as the sum of
 264 variances of the original recording explained by the considered

265 microstate map weighted by the Global Field Power at each
 266 moment in time. Units are percentages (%) between 0 and 1.
 267 • **Mean duration** (MeanDurs), defined as the mean temporal
 268 duration of segments assigned to each MS map. Units are in
 269 seconds (s).
 270 • **Time coverage** (TimeCov) is the ratio of time frames assigned
 271 to each MS map relative to the total number of time frames from
 272 the recording. Results are Units are percentages (%) between
 273 0 and 1.

274 2.5 Adjusted Mutual information score

275 Scikit-learn (Pedregosa et al. 2011) implementation of the adjusted
 276 mutual information score (AMI) (Vinh, Epps, and Bailey 2010) was used
 277 to quantify the mutual information (MI) shared between different MS
 278 temporal segmentations, whilst simultaneously accounting for random
 279 overlap due to chance. This metric, bounded between 0 and 1, is used to
 280 evaluate the statistical (in)dependence of two variables. In our case, AMI
 281 is estimated between the symbolic sequences of two different microstate
 282 segmentations (e.g. ABDCADB vs ABDBDAC). A high score (approaching
 283 1) indicates that the two segmentations agree on the temporal order of all
 284 labels while a low score (approaching 0) indicates that the segmentations'
 285 labels are not temporally aligned. We selected the corrected version of
 286 this metric in order to control for the impact of differences in label
 287 distribution due to chance (for example differences in overall time
 288 coverage between labels).

289 **2.6 Statistics**

290 Statistical analyses were performed on the 4 main spatiotemporal
 291 parameters (Global explained variance, Mean spatial correlation, Mean
 292 duration, Time coverage). Tests were conducted using a two sided
 293 permutation test for equality of means on paired samples (same subject,
 294 either between condition, either between frequencies) under the H0
 295 hypothesis that both frequency (i.e. condition) share the same mean
 296 against the alternative H1 that the distributions come from two different
 297 populations. P-values were estimated by simulated random sampling with
 298 10000 replications. As a large number of statistical tests were carried out
 299 without specific pre-planned hypotheses (Armstrong 2014), P values
 300 were corrected for multiple comparisons using the Bonferroni method.
 301 Corrected P-values are reported in the Results section, as well as the
 302 observed means (m) of both samples together with observed standard
 303 deviations. Effect sizes are reported as the standardised difference of
 304 means using Cohen's d (d).

305 **2.7 Neurobehavioral prediction models**

306 **2.7.1 Model**

307 Linear Support Vector Classification (SVC) with 'l2' norm
 308 penalization and squared hinge loss function were used to discriminate
 309 EO vs EC states using MS parameters pertaining to broad- as well as
 310 narrow- band EEG activity. Models were trained using 15 frequency
 311 specific features correspond to the 3 spatiotemporal MS metrics (Gev,
 312 MeanDurs, TimeCov) of each maps (A,B,C,D,C') of a given frequency. Band

specific prediction models were fitted with standardized features (after removing their respective mean and scaling them to unit variance).

2.7.2 Evaluation

As suggested by Bouckaer et al. (Bouckaert n.d.), 10 times repeated 10 fold cross validation tests were used to assess classification results. For each of the 100 runs, 9 folds of 20 subject's features each were used to train the model while 1 fold of 20 subject's features was used to evaluate the 3 diagnostic metrics:

- **Accuracy**: defined as number of the number of correctly predicted samples out of all the testing set. **The operating characteristic (ROC)** which the plot of true positive rate as a function of the false positive rate. It is used to illustrate the classification trade-off for different discrimination threshold.
- **Area under the curve (AUC)** defined as the area under the ROC curve: it is an aggregate measure of performance for all possible classification thresholds. AUC values are in the range of 0 to 1. A model with 100% error in its predictions has an AUC of 0.0. If all its predictions are correct, its AUC is 1.0.

95% confidence intervals were evaluated on each of the 3 metric distributions with 10 degrees of freedom.

Statistical comparison between models were conducted on both accuracy and AUC using a two- tailed permutation test for equality of means on paired samples under the H0 hypothesis that the alpha-band (8-

336 12 Hz) had a greater mean of the classification metric than the broadband
337 (1-30 Hz). P-values were estimated by simulated random sampling with
338 10000 replications.

3 Results

3.1 Spatial Similarity of Microstate Maps

Figure 1: Spatial correlation between MS topographies across behavioural conditions. Global cluster centroids of each frequency band within eyes-open (EO) or eyes-closed (EC) condition. Note that map polarity inversion is ignored in the classical analysis of spontaneous EEG.

Figure 1 illustrates the topographic results of MS segmentations in the different conditions and frequency bands. After visual inspection of optimal clusters at different cluster numbers (k), we identified that a value of $k=5$ revealed five MS topographies that were similar across all EEG bands and behavioural conditions, consistent with recent findings from our laboratory (Bréchet et al. 2019, 2020; D'Croz-Baron et al. 2019). MS maps were designated in line with the canonical prototypes from the literature and their respective symbols, featuring a left-right orientation (A), a right-left orientation (B), an anterior-posterior orientation (C), fronto-central maximum (D) and occipito-central (C') maximum.

Given the additional frequency dimension, we labelled the MS maps firstly according to the Greek letters traditionally used for narrow-band EEG (i.e. δ , θ , α , β) and then the Latin alphabet for the canonical map symbols (i.e. A, B, C, D). For example, αA denoted the left-right diagonal map from the alpha band (α) segmentation, and δC the anterior-posterior map from the delta band (δ) segmentation. The broadband segmentation was designated with the prefix 'bb'.

Figure 2: Spatial correlation between MS topographies across frequencies. Spatial correlation of cluster centers of each sub-frequency bands compared to broadband for eyes opened (EO) and eyes closed (EC) condition.

As shown in **Figure 2**, when comparing topographies between broadband and each narrow-band (i.e. the diagonal entries in the correlation matrix), all spatial correlations were $r > 0.98$. Consequently,

370 we fitted the broadband maps directly to all the frequency bands in order
371 to have a common reference.

372 We similarly observed common MS maps when comparing broadband
373 topographies between EO and EC conditions (**Suppl Figure 1**), with all
374 intraclass spatial correlations exceeding $r > 0.98$, thus providing
375 justification for comparing microstate parameters between behavioural
376 conditions while fitting condition specific broadband maps.

377 **3.2 Mutual Information of Microstate Sequences**

378

379 **Figure 3: Adjusted mutual information of MS symbolic sequences**

380 **a)** Mean adjusted mutual information (AMI) is depicted, for each
381 behavioural condition (EC: eyes-closed, EO: eyes-open) across $n = 203$
382 subjects.

383 **b)** Mean adjusted mutual information of MS symbolic sequences between all

384 *broadband and narrow-band combinations. Mean ($n = 203$ subjects)*
 385 *adjusted mutual information (AMI) for all frequency pairs.*

386 Briefly, Adjusted Mutual Information (AMI, bounded between 0 and 1)
 387 is an index of how similar two separate MS segmentations are, by
 388 estimating the degree of shared information (i.e. the number of time
 389 points assigned with the same MS) between their symbolic sequences (e.g.
 390 ABCD vs ABDA). The 'adjusted' aspect ensures the measure is unbiased for
 391 symbolic overlap(s) due to chance (Vinh et al. 2010). Higher AMI
 392 (approaching 1) indicates nearly identical MS temporal sequences, while
 393 lower AMI (approaching 0) indicates temporally independent sequences.
 394 (I.e. low overlap)

395 As shown in **Figures 3**, the AMI between broadband and narrow-band
 396 segmentations in the EO condition showed a value of $s = 0.06$ for delta, $s =$
 397 0.03 for theta, $s = 0.05$ for alpha, and $s = 0.01$ for beta. These values are
 398 surprisingly low and we can conclude that the broadband segmentation is
 399 comparatively independent of the narrow-band one. Similar conclusions
 400 of temporal independence can be made by examining the AMI between the
 401 narrow-bands *themselves*, with a maximum AMI value between theta and
 402 alpha bands (EO: $s = 0.006$, EC: $s = 0.009$), and a minimum AMI value of s
 403 $= 0.001$ for non-adjacent EEG bands (delta-alpha, delta-beta, theta-beta)

404 As a sanity check, when inspecting the EO vs EC transition, the shared
 405 information with broadband decreased for the delta band ($s = 0.03$) but
 406 increased for the alpha band ($s = 0.12$). The latter is in line with
 407 expectations, as alpha oscillations are known to increase considerably
 408 during eye closure, which would amplify their contribution to the
 409 broadband signal and consequently their shared dynamics.

410 **3.3 Between-frequency comparison of classical MS** 411 **measures**

412 Here we tested for significant differences between broadband and
413 narrow-band filtered EEG in the classical MS measures: Global explained
414 variance (Gev), Time Coverage (TimeCov), and Mean Duration
415 (MeanDurs). This was done by conducting paired t-tests between
416 broadband (bb) and respective narrow-band (delta to beta) MS measures
417 across all n=203 subjects. For each MS measure and MS map, results were
418 visualised using heat-plots as the narrow-band *absolute difference* from
419 the broadband mean value. Here, a red/blue background indicated
420 significant positive/negative differences at $p < 0.05$, while a white colour
421 indicated non-significant differences at $p > 0.05$. Exact p-values and effect
422 sizes are reported in Table 2 of the Supplementary Results.

423 **Global Explained Variance (Gev)**

Figure 4: Microstate map differences in Global Explained Variance (Gev) between broadband and narrow-band filtered EEG, for eyes open (EO) and eyes closed (EC) conditions. The first row (in grey) represents the mean Gev of the broadband segmentation. Coloured rows represent the mean Gev difference between the narrowband (δ , θ , α , β) and broadband segmentations, for each microstate (A – C'). Significant differences have red/blue backgrounds, while non-significant ones have a white/grey background.

Figure 4 illustrates the percent differences in global explained variance (Gev) between each narrow-band vs broadband, demonstrating the presence of specific “fingerprints” between frequencies (rows) or MS

435 maps (columns). , MS segmentation of **delta** band activity showed
 436 significantly higher GEV across most MS maps in both EO (+16 %) and EC
 437 (+ 16 %) conditions, compared to the broadband segmentation. A similar
 438 but less pronounced effect was found for the theta segmentation,
 439 suggesting that low-frequency EEG fluctuations in the 1-8 Hz (delta-theta)
 440 range may be accounted for more parsimoniously using the 5 canonical
 441 MS maps than 1-30 Hz (broadband) activity.

442 The profile of the **alpha** band segmentation depended on
 443 behavioural condition. During EC, microstate C had significantly increased
 444 Gev (+ 12%) relative to broadband, indicating that distinct MS
 445 topographies have stronger behavioural specificity at narrow-band
 446 frequencies (see section *Application to Behavioural Classification*).
 447 Conversely, during EO, microstates A (+ 2%) and B (+ 4%), expressed
 448 significantly more Gev compared to broadband.

449 Conversely, **or the beta** band, Gev was significantly greater compared to
 450 broadband for maps A (EO: + 2%, EC+ 3%) and B (EO: + 2%, EC: + 2%)
 451 while it was significantly reduced for maps D (EO: - 2%, EC: - 1%) and C'
 452 (EO: - 3%, EC: - 3%) . Microstate C explained less variance compared to
 453 broadband but the comparison was significant only for EC (- 2%).

3.3.1 Time Coverage (TimeCov)

Figure 5: Microstate map differences in Time Coverage (TimeCov) between broadband and narrow-band filtered EEG, for eyes open (EO) and eyes closed (EC) conditions. The first row (in grey) represents the mean TimeCov of the broadband segmentation. Coloured rows represent the mean TimeCov difference between the narrowband (δ , θ , α , β) and broadband segmentations, for each microstate (A – C'). Significant differences have red/blue backgrounds, while non-significant ones have a white/grey background.

463 During MS segmentation, each time-point is assigned to only *one*
 464 of the five canonical MS topographies through a winner-takes-all process
 465 (i.e. the map with the highest spatial correlation with that time-point
 466 *wins*). Time Coverage (TimeCov) refers to the *average* prevalence of each
 467 MS map over the whole EEG recording (**Figure 5**), expressed as a
 468 percentage (i.e. number of time-points assigned to a particular MS map
 469 divided by the total number of time-points).

470 Comparing the **delta** band segmentation to broadband, TimeCov was
 471 reduced for maps A (EO: - 3%, EC -0%), B (EO: - 2%, EC ns) , and C (EO:
 472 5% , EC: - 6 %) , while it was increased for maps D (EO: + 5%, EC: + 4%)
 473 and C '(EO: +4, EC: +2%).

474 Small differences were generally observed between **theta** and broadband
 475 MS distributions, with the notable exception of a significant increase in
 476 map D (EO: + 5%, EC: + 7%) and decrease in map C (EO: - 2%, EC: - 4%),
 477 consistently found across behavioural states. For the **alpha** band,
 478 TimeCov was particularly greater compared to broadband for maps A (EO:
 479 + 2%, EC ns) and B (EO: + 4%, EC: + 1%)

480 Finally, comparing the **beta** band to broadband, TimeCov was
 481 increased for maps A (EO: +4%, EC: +5% , $p < 0.05$) , B (EO: +4% , EC:
 482 +4%, $p < 0.05$) ,while it was reduced for maps D (EO: -4%, EC: -2%, $p <$
 483 0.05) and C '(EO: -6%, EC: -6%, $p < 0.05$)

3.3.2 Mean Duration (Mean Durs)

Figure 6: Microstate map differences in Mean Duration (MeanDurs) between broadband and narrow-band filtered EEG, for eyes open (EO) and eyes closed (EC) conditions. The first row (in grey) represents the mean MeanDurs of the broadband segmentation. Coloured rows represent the mean MeanDurs difference between the narrowband (δ , θ , α , β) and broadband segmentations, for each microstate (A – C'). Significant differences have red/blue backgrounds, while non-significant ones have a white/grey background.

493 While analysing MS mean duration (MeanDurs) we first observed that MS
 494 were significantly shorter in **delta** compared to broadband across all
 495 maps: map A (EO: -14ms, EC: -13ms), map B (EO: -14ms, EC: -14ms) , map
 496 C(EO:-15ms, EC: -17ms, map D (EO: -7ms, EC: -8ms) and map C' (EO: -
 497 8ms, EC: -11ms).On the contrary **theta** segments were significantly longer
 498 than broadband ones for map A (EO: +6ms, EC: +11), map B (EO: +6ms,
 499 EC: +11ms) and map D(EO: -7ms, EC: -8ms). Similar but non-significant
 500 increases were also observed for maps C and C'.

501 **Notably**, all MS maps had significantly increased duration in **alpha** band
 502 compared to broadband: map A (EO: +57ms, EC: +70ms), map A (EO:
 503 +62ms, EC: +70ms) map C (EO: +71ms, EC: +150ms) map D (EO: +42ms,
 504 EC: +72ms) and map C'(EO: +57ms, EC: +63ms).

505 Less pronounced and less consistent differences were found for the **beta**
 506 band, which revealed a single significant increase of map A duration in the
 507 EC condition (EO: ns, EC: +9ms).

508

509 **3.4 Within-frequency comparison of classical MS**
510 **measures during eyes-open (EO) versus eyes-closed (EC)**

511

512

513 **Figure 7: EO versus EC comparison using frequency specific microstate**
514 **parameters. a) Mean global explained variance (Gev (%)), and b) mean**
515 **time coverage (time coverage (%)) for each microstate (A – C') within each**
516 **frequency band (broadband, delta, theta, alpha, beta) for both eyes closed**
517 **condition (EC, blue) and eyes opened condition (EO, red). Significance values**
518 **are indicated from paired permutation test on mean between conditions: no**
519 **star: $0.05 > p$, *: $p < 0.05$, * color indicates the condition with highest value.**

520 Here, we directly compared EO vs EC conditions within each frequency
521 band, and only relevant cases where narrow-band measures were salient
522 compared to the broadband analysis are reported. Full results are
523 documented in Table 3 and Suppl Figure 2 of the Supplementary Results.

524 **3.4.1 Global Explained Variance (Gev)**

525 Across frequencies, map C' explained more variance during EC than
526 during EO for all bands (bb: $d = 0.59$, $p < .05$ | δ : $d = 0.43$, $p < .05$ | θ : $d =$
527 0.35 , $p < .05$ | α : $d = 0.35$, $p < .05$ | β : $d = 0.67$, ns) while map D expressed
528 less variance(bb: $d = -0.14$, ns | δ : $d = -0.07$, ns | θ : $d = -0.29$, $p < .05$ | α : $d = -$
529 0.42 , $p < .05$ | β : $d = -0.73$, $p < .05$). In contrast, the other MS maps had band-
530 specific modulations: during EC map C explained relatively less variance
531 in alpha ($d = -1.0$, $p < .05$) and broadband ($d = -0.7$, $p < .05$),but expressed
532 more variance in delta ($d = 0.20$, $p < .05$) and beta ($d = 0.21$, $p < .05$). In
533 addition, statistically significant effects were detected in the narrow-
534 bands which were not evident in the broadband. For example, : the Gev
535 of map B decreased from EC to EO ($d = -0.31$, $p < 0.05$) in in the beta band
536 while no significant effect was found in broadband for this map.

537 **3.4.2 Time coverage (TimeCov),**

538 Map C was relatively more prevalent in EC vs EO in alpha ($d = -0.71$, $p <$
539 $.05$) and broadband ($d = -0.48$, $p < .05$), but the effect size was significantly
540 stronger in the alpha band. In contrast, the opposite effect was observed
541 in delta ($d = 0.22$, $p < .05$) and beta ($d = 0.42$, $p < .05$) bands, which showed
542 increased coverage of map C during EO compared to EC. Diverging effects
543 of time coverage in narrow-bands compared to broadband appeared
544 across a number of MS maps and frequency bands, during the EO vs EC

545 transition: βA –where TimeCov decreased prevalence ($d = -0.20, p < .05$),
 546 bbA and βC –TimeCov increased, respectively ($d = 0.23, p < .05$) and ($d =$
 547 $0.21, p < 0.05$)., while bbC TimeCov decreased ($d = -0.71, p < .05$). Where
 548 non-significant differences between EO and EC conditions were found for
 549 bbB coverage, βB ($d = -0.17, p < .05$) and ΘB ($d = -0.35, p < .05$) were
 550 significantly increased in the EC condition while αB ($d = 0.57, p < .05$) was
 551 decreased.

552 All in all, the EO vs EC- comparison revealed significant differences
 553 between the broadband and narrow-band segmentations, which were
 554 frequently map- and/or band- specific.

3.5 Statistical classification of EO vs EC behavioural states

Figure 8: Classifying EO vs EC states using classical microstate measures. Binary classification performance, computed as the area under the curve (AUC) of the receiver-operating characteristic (ROC), for 2 support-vector machine models. Input features of the first model (red) were broadband MS parameters (see text) while the second model (blue) was evaluated on alpha-band MS parameters. Shaded areas represent 95% CI. Mean AUC $\pm$ standard deviation is reported in the legend.

As a proof-of-concept, we tested the applicability of band-specific microstates in the context of behavioural prediction, i.e. the binary discrimination of EO versus EC states using machine learning. Leveraging

the well-known effect of alpha-band modulation during eye opening/closure (Barry et al. 2007) we hypothesised that alpha-band specific MS parameters would be stronger and more specific predictors of the EO/EC transition than those derived from the broadband segmentation. As we did not have any MS map specific hypotheses, we selected as features the basic set of classical MS measures from our study: 5 maps (A, B, C, D, C') x 3 variables (Gev, TimeCov, MeanDurs). Then, using these 15 features, we applied a linear support vector machine (SVM) to classify EO vs EC recordings across all 203 subjects, separately for alpha-band and broadband models.

Following 10 fold cross-validation, we observed higher accuracy (i.e. sensitivity) for the SVM model tested with alpha-band MS parameters ($80 \pm 5\%$) than the one tested with broadband MS parameters ($73 \pm 6\%$). The superiority of the alpha-band model was reinforced by a separate analysis of the area under the curve (AUC) of the receiver-operating characteristic (ROC), which also incorporates the false-positive rate (i.e. specificity). Here alpha-band (AUC $87 \pm 5\%$) outperformed broadband ($77 \pm 7\%$) by a full 10%. Finally, these differences were statistically significant for both accuracy (Cohen's $d=1.75$, $p < 0.001$) and AUC (Cohen's $d=1.28$, $p < 0.001$) demonstrating that a narrow-band MS segmentation may provide higher sensitivity/specificity in differentiating behavioural state relative to a broadband one.

589 **4 Discussion**

590 Historically, the first microstate (MS) analysis was applied by
 591 Lehmann and colleagues to narrowband (alpha) oscillations (Lehmann
 592 1971), yet this “frequency-specific” approach appears to have been
 593 overlooked during the last decades of MS research in favour of
 594 decomposing broadband EEG signals (e.g. 2-40 Hz)(Michel and Koenig
 595 2018; Pascual-Marqui et al. 1995). Hence, the present study specifically
 596 explored the MS characteristics of narrow-band EEG signals, their
 597 quantitative interrelationship, and whether they provide any novel
 598 information compared to course-grained broadband dynamics. This was
 599 done by first filtering the broadband EEG signal into several narrow-band
 600 frequencies (delta, theta, alpha, and beta), with the goal of comparing MS
 601 symbolic sequences and classical measures (explained variance, mean
 602 duration, time coverage) between them, as well as across different
 603 behavioural conditions (eyes open (EO) vs eyes closed (EC)).

604 **4.1 The spatial dimension: microstate** 605 **topographies**

606 We first investigated whether analogous MS scalp topographies
 607 would be produced by segmenting broadband versus narrow-band EEG
 608 signals (including the alpha band (Milz et al. 2017)). Interestingly, we
 609 observed highly similar MS topographies (with minimum spatial
 610 correlations of $r > 0.98$) across all investigated broad- and narrow- band
 611 frequencies (broadband, delta to beta), as well as between EO/EC
 612 conditions. This is compatible with recent work by Brechet and colleagues
 613 (Bréchet et al. 2020), who observed that states of sleep and wake

614 exhibited significantly different spectral content (e.g. delta vs beta power)
615 but very similar MS maps. Moreover, these maps corresponded to the
616 canonical (broadband) topographies previously described in the
617 literature (Custo et al. 2017; Michel and Koenig 2018). It is therefore
618 tempting to assume that identical neuronal sources are involved in
619 generating the same topographies across frequencies. However, although
620 different maps imply different generators (forward problem), same
621 topographies do not necessarily imply identical generators (inverse
622 problem). Due to the ill-posed nature of EEG signals (constructive and
623 destructive electromagnetic fields), similar scalp potentials can still be
624 generated by different underlying brain mechanisms (Helmholtz 1853).
625 Hence, although we cannot unequivocally conclude that MS maps across
626 the EEG spectrum are generated by the same brain sources operate, this
627 would be the most probable and parsimonious interpretation. Moreover,
628 we must juxtapose our findings with work from other groups (Musaeus et
629 al. 2020) which applied a similar approach but didn't necessarily find the
630 same topographies across the EEG spectrum. From a methodological point
631 of view, it should be kept in mind that narrow-band MS analysis does not
632 *per se* require similar topographies between frequencies. In this case,
633 although cross frequency comparisons would not be possible due to
634 dissimilar maps, it would remain valid to study and quantify
635 spatiotemporal MS parameters within each frequency band separately, for
636 example, in the service of clinical biomarker discovery (Merrin et al.
637 1990). Reassuringly, the MS maps of our study replicate the ones derived
638 from independent work utilising the same EEG dataset (ZanESCO et al.
639 2020), further supporting the reproducibility of MS analysis despite
640 methodological variations between studies (e.g. absence of resampling).

641 **4.2 The temporal dimension: mutual information** 642 **of microstate sequences**

643 Milz and colleagues (Milz et al. 2017) recently proposed that alpha
644 oscillations were the major component driving microstate dynamics. In
645 general, adjusted mutual information (AMI) analyses reported in our work
646 reveal low values (near or below 0.1) of information shared between the
647 narrow-band segmentations, including alpha, and that of the broadband
648 decomposition. However, consistent with the work of Milz and colleagues
649 (Milz et al. 2017), the alpha-band during eyes-closed (EC) did indeed have
650 the highest shared information with broadband (around 0.125).
651 Importantly however, this relationship did not necessarily hold during
652 eyes-open (delta being highest). This indicates specific narrow-band
653 contribution(s) to broadband dynamics heavily depend on behavioural
654 state. Moreover, if narrow-band(s) topographies were directly
655 responsible for the origin of the spatial distribution of the broadband
656 signal, one would expect much higher AMI values (at least 0.5) than those,
657 we observed. In view of the results presented, it would be inaccurate to
658 claim that alpha band, or any other narrow-band as the dominant source
659 of broadband topographies.

660 In contrast, our results appear to support the ideas of Croce and colleagues
661 (Croce et al. 2020), who suggested that broadband MS dynamics could not
662 be extrapolated from one or a subset of EEG frequency bands. It remains
663 unclear how the interaction of several narrow-band-components leads to
664 a substantially different broadband MS decomposition. We speculate that
665 this might stem from the fact that i) different narrow band signals could

cancel each other at specific time points and ii) microstate assignment is non-linear given the winner-takes all approach.

Lastly and most intriguingly, no significant informational interrelations were found between the narrow-band topographical dynamics themselves (e.g. delta vs beta, theta vs alpha), indicating that each EEG band appears to have its own independent dynamics. This may not be surprising, considering that spontaneous EEG oscillations have been reported to dynamically switch from a resting signatures (e.g. alpha) to task-specific active mode(s) dominated by theta (Ribary et al. 2017), beta (Fernández et al. 1995) or gamma activities (Hipp et al. 2011)). In this context, our observations of spatiotemporal independence between narrow-band EEG components support the operation of “oscillatory multiplexing” (Akam and Kullmann 2014) mechanisms in the cortex, whereby brain regions could combine different frequencies for integrating/segregating information across large-scale networks (Le Van Quyen 2011)

4.3 Classical microstate measures: explained variance, time coverage, and mean duration

Global Explained Variance (Gev)

Overall, MS segmentations of low-frequency bands (delta, theta) explained more of the global topographical variance compared to the classical broadband segmentaion. Since Gev is normalised by and therefore independent of global field power, this suggests that the goodness-of-fit (i.e Gev) of the five-map MS model is clearly greater in the

690 delta/theta bands compared to broadband EEG. In higher frequencies,
691 effects are more map-specific, as for example we observed an increase in
692 Gev for the diagonal maps (A,B) and a decrease for midline (D,C') ones..

693 **Time Coverage (TimeCov)**

694 Different patterns of MS temporal coverage were observed according to
695 frequency. The delta and theta bands seem to exhibit greater prevalence
696 of map D and decreased incidence of maps A, B, and C. This is remarkable
697 insofar map D shares an intriguing overlap with the topography of the
698 well-known frontal-midline theta-rhythm (fm-theta) (Scheeringa et al.
699 2008; Töllner et al. 2017). Conversely, beta band dynamics seem to favour
700 the more frequent appearance of maps A and B in lieu of maps D and C'.
701 The appearance of alpha-band MS maps, on the other hand, appear to be
702 more state-dependent, as might be expected given the well-known
703 expression of the posterior alpha rhythm during eyes-closed. Accordingly,
704 there was a strong behavioural dissociation particularly for map C, which
705 displayed a relatively greater temporal prevalence during EC compared to
706 EO.

707 The presence of such “spectral fingerprints” suggests the existence of an
708 affinity between distinct MS topographies and EEG bands suggests that
709 different cortical generators (i.e. topographies) may be activated
710 preferentially in certain frequencies (Groppe et al. 2013; Keitel and Gross
711 2016; Mellem et al. 2017),..

712 **Mean Duration (MeanDurs)**

713 Microstates are defined as short periods of time during which the scalp
714 electric field remains quasi-stable. Traditional microstate analysis does
715 not suggest specific frequency filtering, thus resulting in various
716 broadband filter settings across studies (Michel and Koenig 2018). Our
717 findings demonstrate that temporally stable states (around 80ms or
718 longer) are present within all classical EEG narrow-bands (i.e. delta to
719 beta). It is established that such spatiotemporal structures do not appear
720 for randomly shuffled EEG (Wackermann et al. 1993). For most EEG
721 narrow-bands, mean MS durations were usually in the same range as the
722 typically reported 70–120 ms, but often longer. For example, the average
723 MS duration in the eyes open state was around 150 ms for the alpha-band,
724 compared to 90 ms for broadband. It will be therefore interesting for
725 future studies to examine the mechanistic links between the aggregated
726 dynamics of the broadband microstates and those of frequency-specific
727 modes.

728 **4.4 Discriminating between behavioural states:** 729 **eyes open versus eyes closed**

730 Within each EEG narrow-band, between 8 (for theta) and 14 (for alpha)
731 of the classical MS measures were found to be statistically significant. In
732 comparison, classical MS measures derived from broadband EEG had a
733 higher effect size for only one parameter (broadband microstate B mean
734 duration). For all other 14 parameters, at least one narrow-band
735 component showed a relatively stronger effect size.

736 Hence, the addition of the frequency dimension has the primary benefit
737 of increasing both the number and the specificity of potential neural

738 markers that could aid clinical prognosis or provide insight into brain
739 mechanisms. We therefore conclude that the extra frequency dimension
740 in itself leads to a more fine-grained decomposition of multichannel and
741 multiplex EEG signals than the standard broadband analysis.

742 This is directly supported by our behavioural classification results,
743 where we utilised alpha-band vs broadband MS parameters to predict EO
744 vs EC states using the recordings of all 203 subjects. The significant boost
745 in overall accuracy (alpha-band: 80% vs broadband: 73%) and area under
746 the ROC curve nicely demonstrate that frequency-specific MS measures
747 may provide higher behavioural predictive power than those derived
748 from the broadband analysis. Although beyond the scope of this paper, we
749 expect that this approach to provide advantages in other contexts, such as
750 event-related potential (ERP) analyses or for discriminating between
751 different clinical populations.

752 Interestingly, we found that in a few cases the narrow-band effects
753 were opposite in directionality to the broadband results. Thus, limiting
754 the analysis to only the latter could lead to incomplete (or even incorrect)
755 interpretations of underlying brain dynamics.

756 **5 Potential Limitations and Future Work**

757 The current study may technically be considered exploratory, given the
758 large number of tests that were carried out and in the absence of well-
759 defined hypotheses. However, we carried out Bonferroni correction for all
760 tests which may be considered the most conservative method for
761 controlling for multiple comparisons. Several studies have thus far

762 proposed explanations for the origins of broadband MS topographies
763 (Britz et al. 2010). We feel it is still too early to make analogies or
764 speculations between these results and those of the narrow-band
765 dynamics. However, we believe that the application of the methodology
766 proposed here may lead to valuable insights in order to more fully
767 understand the underlying spectral tapestry of EEG microstates.

768 **6 Conclusion**

769 Ultimately, we report a number of important and novel findings
770 between the classical broadband MS analysis, generally performed in the
771 EEG field, and its application to more narrow frequency bands relevant to
772 cortical oscillatory activities. In a nutshell, it appears that each canonical
773 EEG frequency band possesses its own independent spatiotemporal
774 dynamics, whilst the relative prevalence of MS topographies themselves
775 differ across frequencies. Moreover, it appears that broadband dynamics
776 cannot be appropriately explained by the simple summation of individual
777 narrow-band frequency components.

778 Analysis of narrow-band MS parameters revealed spatial and temporal
779 characteristics that both converged and diverged from broadband MS
780 findings. At the very least, our results indicate that narrow-band analysis
781 is justified as complementary to the usual broadband MS analysis. A
782 narrow-band decomposition into frequencies more specific for cortical
783 oscillatory activity could not only advance and consolidate findings in
784 clinical disorders e.g. (Merrin et al. 1990) (Musaeus et al. 2020), but also
785 enable a better understanding of the organization and functioning of
786 large-scale brain systems..

787 **Data and Code Availability Statement**

788 The data and code supporting our results are openly available in the OSF
789 repository and can be found at: <https://osf.io/bfsge/> (DOI
790 10.17605/OSF.IO/BFSGE).

791 Other 3rd party software and datasets used in this study can be found by
792 following citations in the paper.

793 **References**

794 Akam, Thomas, and Dimitri M. Kullmann. 2014. 'Oscillatory Multiplexing
795 of Population Codes for Selective Communication in the
796 Mammalian Brain'. *Nature Reviews Neuroscience* 15(2):111–22.
797 doi: 10.1038/nrn3668.

798 Armstrong, Richard A. 2014. 'When to Use the Bonferroni Correction'.
799 *Ophthalmic and Physiological Optics* 34(5):502–8.

800 Babayan, Anahit, Miray Erbey, Deniz Kumral, Janis D. Reinelt, Andrea MF
801 Reiter, Josefin Röbbig, H. Lina Schaare, Marie Uhlig, Alfred
802 Anwander, Pierre-Louis Bazin, and others. 2019. 'A Mind-Brain-
803 Body Dataset of MRI, EEG, Cognition, Emotion, and Peripheral
804 Physiology in Young and Old Adults'. *Scientific Data* 6:180308.

805 Barry, Robert J., Adam R. Clarke, Stuart J. Johnstone, Christopher A. Magee,
806 and Jacqueline A. Rushby. 2007. 'EEG Differences between Eyes-
807 Closed and Eyes-Open Resting Conditions'. *Clinical*
808 *Neurophysiology* 118(12):2765–73. doi:
809 10.1016/j.clinph.2007.07.028.

810 Bouckaert, Remco R. n.d. 'Choosing between Two Learning Algorithms
811 Based on Calibrated Tests'. 8.

812 Bréchet, Lucie, Denis Brunet, Gwénaél Birot, Rolf Gruetter, Christoph M.
813 Michel, and João Jorge. 2019. 'Capturing the Spatiotemporal

- 814 Dynamics of Self-Generated, Task-Initiated Thoughts with EEG
815 and fMRI'. *Neuroimage* 194:82–92.
- 816 Bréchet, Lucie, Denis Brunet, Lampros Perogamvros, Giulio Tononi, and
817 Christoph M. Michel. 2020. 'EEG Microstates of Dreams'. *Scientific*
818 *Reports* 10(1):17069. doi: 10.1038/s41598-020-74075-z.
- 819 Britz, Juliane, Dimitri Van De Ville, and Christoph M. Michel. 2010. 'BOLD
820 Correlates of EEG Topography Reveal Rapid Resting-State
821 Network Dynamics'. *NeuroImage* 52(4):1162–70. doi:
822 10.1016/j.neuroimage.2010.02.052.
- 823 Brunet, Denis, Micah M. Murray, and Christoph M. Michel. 2011.
824 'Spatiotemporal Analysis of Multichannel EEG: CARTOOL'.
825 *Computational Intelligence and Neuroscience* 2011.
- 826 Croce, Pierpaolo, Angelica Quercia, Sergio Costa, and Filippo Zappasodi.
827 2020. 'EEG Microstates Associated with Intra-and Inter-Subject
828 Alpha Variability'. *Scientific Reports* 10(1):1–11.
- 829 Custo, Anna, Dimitri Van De Ville, William M. Wells, Miralena I. Tomescu,
830 Denis Brunet, and Christoph M. Michel. 2017.
831 'Electroencephalographic Resting-State Networks: Source
832 Localization of Microstates'. *Brain Connectivity* 7(10):671–82.
- 833 D'Croz-Baron, David F., Mary Baker, Christoph M. Michel, and Tanja Karp.
834 2019. 'EEG Microstates Analysis in Young Adults With Autism
835 Spectrum Disorder During Resting-State'. *Frontiers in Human*
836 *Neuroscience* 13:173. doi: 10.3389/fnhum.2019.00173.
- 837 Fernández, Thalía, Thalía Harmony, Mario Rodríguez, Jorge Bernal, Juan
838 Silva, Alfonso Reyes, and Erzsébet Marosi. 1995. 'EEG Activation
839 Patterns during the Performance of Tasks Involving Different
840 Components of Mental Calculation'. *Electroencephalography and*
841 *Clinical Neurophysiology* 94(3):175–82. doi: 10.1016/0013-
842 4694(94)00262-J.
- 843 Gramfort, Alexandre, Martin Luessi, Eric Larson, Denis A. Engemann,
844 Daniel Strohmeier, Christian Brodbeck, Roman Goj, Mainak Jas,

- 845 Teon Brooks, Lauri Parkkonen, and others. 2013. 'MEG and EEG
846 Data Analysis with MNE-Python'. *Frontiers in Neuroscience* 7:267.

- 847 Groppe, David M., Stephan Bickel, Corey J. Keller, Sanjay K. Jain, Sean T.
848 Hwang, Cynthia Harden, and Ashesh D. Mehta. 2013. 'Dominant
849 Frequencies of Resting Human Brain Activity as Measured by the
850 Electroencephalogram'. *NeuroImage* 79:223–33. doi:
851 10.1016/j.neuroimage.2013.04.044.

- 852 Helmholtz, H. von. 1853. 'Ueber Einige Gesetze Der Vertheilung
853 Elektrischer Strome in Korperlichen Leitern, Mit Anwendung Auf
854 Die Thierisch-Elektrischen Versuche (Schluss.)'. *Annalen Der
855 Physik* 165(7):353–77.

- 856 Hipp, Joerg F., Andreas K. Engel, and Markus Siegel. 2011. 'Oscillatory
857 Synchronization in Large-Scale Cortical Networks Predicts
858 Perception'. *Neuron* 69(2):387–96. doi:
859 10.1016/j.neuron.2010.12.027.

- 860 Javed, Ehtasham, Pierpaolo Croce, Filippo Zappasodi, and Cosimo Del
861 Gratta. 2019. 'Hilbert Spectral Analysis of EEG Data Reveals
862 Spectral Dynamics Associated with Microstates'. *Journal of
863 Neuroscience Methods* 325:108317.

- 864 Keitel, Anne, and Joachim Gross. 2016. 'Individual Human Brain Areas Can
865 Be Identified from Their Characteristic Spectral Activation
866 Fingerprints'. *PLoS Biology* 14(6):e1002498.

- 867 Koenig, Thomas, and Daniel Brandeis. 2016. 'Inappropriate Assumptions
868 about EEG State Changes and Their Impact on the Quantification
869 of EEG State Dynamics'. *Neuroimage* 125:1104–6.

- 870 Le Van Quyen, Michel. 2011. 'The Brainweb of Cross-Scale Interactions'.
871 *New Ideas in Psychology* 29(2):57–63. doi:
872 10.1016/j.newideapsych.2010.11.001.

- 873 Lehmann, D. 1971. 'Multichannel Topography of Human Alpha EEG Fields'.
874 *Electroencephalography and Clinical Neurophysiology* 31(5):439–
875 49.

- 876 Mellem, Monika S., Sophie Wohltjen, Stephen J. Gotts, Avniel Singh
877 Ghuman, and Alex Martin. 2017. 'Intrinsic Frequency Biases and
878 Profiles across Human Cortex'. *Journal of Neurophysiology*
879 118(5):2853–64.
- 880 Merrin, Edward L., Patricia Meek, Thomas C. Floyd, and Enoch Callaway
881 III. 1990. 'Topographic Segmentation of Waking EEG in
882 Medication-Free Schizophrenic Patients'. *International Journal of*
883 *Psychophysiology* 9(3):231–36.
- 884 Michel, Christoph M., and Thomas Koenig. 2018. 'EEG Microstates as a Tool
885 for Studying the Temporal Dynamics of Whole-Brain Neuronal
886 Networks: A Review'. *NeuroImage* 180:577–93. doi:
887 10.1016/j.neuroimage.2017.11.062.
- 888 Milz, Patricia, Roberto D. Pascual-Marqui, Peter Achermann, Kieko Kochi,
889 and Pascal L. Faber. 2017. 'The EEG Microstate Topography Is
890 Predominantly Determined by Intracortical Sources in the Alpha
891 Band'. *Neuroimage* 162:353–61.
- 892 Musaeus, Christian S., Knut Engedal, Peter Høgh, Vesna Jelic, Arjun R.
893 Khanna, Troels Wesenberg Kjær, Morten Mørup, Mala Naik, Anne-
894 Rita Oeksengaard, Emiliano Santarnecchi, and others. 2020.
895 'Changes in the Left Temporal Microstate Are a Sign of Cognitive
896 Decline in Patients with Alzheimer's Disease'. *Brain and Behavior*
897 e01630.
- 898 Pascual-Marqui, Roberto D., Christoph M. Michel, and Dietrich Lehmann.
899 1995. 'Segmentation of Brain Electrical Activity into Microstates:
900 Model Estimation and Validation'. *IEEE Transactions on*
901 *Biomedical Engineering* 42(7):658–65.
- 902 Pedregosa, F., G. Varoquaux, A. Gramfort, V. Michel, B. Thirion, O. Grisel, M.
903 Blondel, P. Prettenhofer, R. Weiss, V. Dubourg, J. Vanderplas, A.
904 Passos, D. Cournapeau, M. Brucher, M. Perrot, and E. Duchesnay.
905 2011. 'Scikit-Learn: Machine Learning in Python'. *Journal of*
906 *Machine Learning Research* 12:2825–30.

- 907 Ribary, Urs, S. M. Doesburg, and L. M. Ward. 2017. 'Unified Principles of
908 Thalamo-Cortical Processing: The Neural Switch'. *Biomedical*
909 *Engineering Letters* 7(3):229–35. doi: 10.1007/s13534-017-
910 0033-4.
- 911 Ros, Tomas, Bernard J. Baars, Ruth A. Lanius, and Patrik Vuilleumier. 2014.
912 'Tuning Pathological Brain Oscillations with Neurofeedback: A
913 Systems Neuroscience Framework'. *Frontiers in Human*
914 *Neuroscience* 8. doi: 10.3389/fnhum.2014.01008.
- 915 Scheeringa, René, Marcel C. M. Bastiaansen, Karl Magnus Petersson,
916 Robert Oostenveld, David G. Norris, and Peter Hagoort. 2008.
917 'Frontal Theta EEG Activity Correlates Negatively with the Default
918 Mode Network in Resting State'. *International Journal of*
919 *Psychophysiology* 67(3):242–51. doi:
920 10.1016/j.ijpsycho.2007.05.017.
- 921 Schulman, Joshua J., Robert Cancro, Sandlin Lowe, Feng Lu, Kerry D.
922 Walton, and Rodolfo R. Llinás. 2011. 'Imaging of Thalamocortical
923 Dysrhythmia in Neuropsychiatry'. *Frontiers in Human*
924 *Neuroscience* 5. doi: 10.3389/fnhum.2011.00069.
- 925 Töllner, Thomas, Yijun Wang, Scott Makeig, Hermann J. Müller, Tzyy-Ping
926 Jung, and Klaus Gramann. 2017. 'Two Independent Frontal Midline
927 Theta Oscillations during Conflict Detection and Adaptation in a
928 Simon-Type Manual Reaching Task'. *The Journal of Neuroscience*
929 37(9):2504–15. doi: 10.1523/JNEUROSCI.1752-16.2017.
- 930 Van De Ville, D., J. Britz, and C. M. Michel. 2010. 'EEG Microstate Sequences
931 in Healthy Humans at Rest Reveal Scale-Free Dynamics'.
932 *Proceedings of the National Academy of Sciences* 107(42):18179–
933 84. doi: 10.1073/pnas.1007841107.
- 934 Vinh, Nguyen Xuan, Julien Epps, and James Bailey. 2010. 'Information
935 Theoretic Measures for Clusterings Comparison: Variants,
936 Properties, Normalization and Correction for Chance'. *The Journal*
937 *of Machine Learning Research* 11:2837–54.

- 938 Wackermann, J., D. Lehmann, CM Michel, and WK Strik. 1993. 'Adaptive
939 Segmentation of Spontaneous EEG Map Series into Spatially
940 Defined Microstates'. *International Journal of Psychophysiology*
941 14(3):269–83.
- 942 Zanesco, Anthony P., Brandon G. King, Alea C. Skwara, and Clifford D.
943 Saron. 2020. 'Within and Between-Person Correlates of the
944 Temporal Dynamics of Resting EEG Microstates'. *NeuroImage*
945 211:116631. doi: 10.1016/j.neuroimage.2020.116631.
- 946