Narrowband multivariate source separation for semi-blind discovery of experiment contrasts

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Abbreviated title: Narrowband contrasts using multivariate methods

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Acknowledgments: MBZ and MXC are funded by ERC-StG 638589. We thank Nadine Dijkstra for supplying the empirical data and providing insightful comments during analysis and writing.

The authors declare no competing financial interests.

Type of article: Research article
Keywords: Source separation; Multivariate analysis; Oscillations

Abstract

Background

Electrophysiological recordings contain mixtures of signals from distinct neural sources, impeding a straightforward interpretation of the sensor-level data. This mixing is particularly detrimental when distinct sources resonate in overlapping frequencies. Fortunately, the mixing is linear and instantaneous. Multivariate source separation methods may therefore successfully separate statistical sources, even with overlapping spatial distributions.

New Method

We demonstrate a feature-guided multivariate source separation method that is tuned to narrowband frequency content as well as binary condition differences. This method — comparison scanning generalized eigendecomposition, csGED — harnesses the covariance structure of multichannel data to find directions (i.e., eigenvectors) that maximally separate two subsets of data. To drive condition specificity and frequency specificity, our data subsets were taken from different task conditions and narrowband-filtered prior to applying GED.

Results

To validate the method, we simulated MEG data in two conditions with shared noise characteristics and unique signal. csGED outperformed the best sensor at reconstructing the ground truth signals, even in the presence of large amounts of noise. We next applied csGED to a published empirical MEG dataset on visual perception vs. imagery. csGED identified sources in alpha, beta, and gamma bands, and successfully separated distinct networks in the same frequency band.

Comparison with Existing Method(s)

GED is a flexible feature-guided decomposition method that has previously successfully been applied. Our combined frequency- and condition-tuning is a novel adaptation that extends the power of GED in cognitive electrophysiology.

Conclusions

We demonstrate successful condition-specific source separation by applying csGED to simulated and empirical data.

Introduction

EEG and MEG are prized for their high temporal precision, allowing us to link fast brain dynamics to cognition. However, their spatial precision is low compared to that of other measurement methods, with each sensor recording a linear and instantaneous mixture of populations of neurons from spatially distributed regions (Nunez & Srinivasan, 2006). Thus, many functionally diverse neural assemblies can contribute to the activity recorded from each MEG sensor. Fortunately, disparate neural sources generally produce unique electromagnetic fields, which have stable though spatially overlapping distributions at the scalp. Multichannel decomposition methods leverage these properties to attempt to isolate the component sources.

Many source separation approaches exist, and different approaches are designed to optimize different features (e.g., Beckmann & Smith, 2004; Brunton et al., 2016; Wang & Guo, 2019; Yang et al., 2004). We espouse the use of generalized eigendecomposition (GED), an advanced feature-guided multivariate source separation method. GED distinguishes itself from other methods by finding sources that maximally dissociate user-specified data of interest from reference data. This hypothesis-driven source separation provides improved flexibility and sensitivity over other multivariate source separation methods such as PCA and ICA.

Preparing multivariate data for GED requires the creation of two covariance matrices. One is constructed from data containing the features to be maximized (such as narrowband activity, a particular time window, or a subset of trials) and the other from data containing the features to be minimized (such as broadband activity, the entire trial, or another subset of trials). A GED applied to these covariance matrices returns a set of components, each consisting of an eigenvalue (indicating importance) and an eigenvector (a spatial filter, i.e., a set of sensor weights). These components capture sensor combinations that maximize the energy ratio between the covariance matrices. The eigenvectors can be used to construct component topographies and time series, the latter of which can be time-frequency decomposed for further inspection.

GED can identify frequencies of interest in the data by scanning the frequency spectrum for sources that maximally separate narrowband from broadband data (de Cheveigné & Arzounian, 2015; Nikulin et al., 2011). We adapted this technique to concurrently optimize for not only

frequency content, but also condition differences. This choice was driven by the observation that experimental designs in neuroscience commonly harness binary condition differences to quantify the impact of a task feature (e.g., stimulus period vs. baseline period, high vs. low levels of conflict, familiarity vs. novelty, or houses vs. faces). The resulting implementation of GED (which we designate *comparison scanning GED*, csGED) identifies the frequencies at which two conditions are maximally separable, lending insight into differences in frequency content between conditions. Furthermore, csGED allows for exploration of the nature of the sources contributing to these frequency differences, by computing and analyzing source-specific time courses and topographies.

We aim to demonstrate the value of csGED to identify sources (i.e., spatial filters) of oscillatory frequencies that maximally differentiate two conditions. We quantified the accuracy of csGED source reconstructions in simulated data with a known ground truth, and we demonstrated the practical applicability of the method on a published MEG dataset. We thus show that csGED can reveal the frequency spectrum of condition differences in a data-driven way.

Methods

Description of problem statement and mathematical solution

M/EEG and LFP are subject to signal mixing effects. Such mixing complicates the relation of measured signals to cognition, as many functionally independent neural sources may contribute to the signal at any sensor. Because mixing is instantaneous and linear (Nunez & Srinivasan, 2006; Parra et al., 2005), multivariate linear source separation methods are able to approximate the constituent statistical sources, decomposing the mixed signal into linearly separable components. Blind source separation methods (PCA, ICA) are optimized to capture salient features in the full dataset, but this is not ideal for all purposes: in neuroscience, we are often interested in only a subset of the data, namely that related to a cognitive or behavioral phenomenon. We here validated a feature-guided source separation method based on generalized eigendecomposition (GED, also known as joint decorrelation; de Cheveigné & Parra, 2014). GED allows for the specification of features of interest in the data, which we here harnessed to tune the source separation to both condition differences and frequency content of the signal. To distinguish the general method from the specific condition-contrasting and frequency-scanning application in this work, we refer to our approach as *comparison scanning GED* (csGED).

The goal of csGED is to map the frequency spectrum of source differences between two conditions, designated A and B. The data in each condition must be broadband; it can be taken from subsets of trials in an experiment, or from time windows within trials. First, the sensor-level signal $\mathbf{X}$ (channels-by-time-by-trials) is filtered, through Morlet wavelet convolution (or any other suitable narrowband filter), at a range of frequencies f that span the frequency spectrum to be investigated. This filtering yields narrowband datasets $\mathbf{X}_f$, from which condition-specific narrowband subsets $\mathbf{X}_{Af}$, $\mathbf{X}_{Bf}$ can be extracted. To improve sensitivity, data can be restricted to time windows during which the condition differences are expected to be present; this should be done after filtering in order to avoid edge artifacts.

Next, two sensor-by-sensor covariance matrices $\mathbf{K}_{Af}$ and $\mathbf{K}_{Bf}$ are constructed from the mean-centered narrowband data $\mathbf{X}_{Af}$, $\mathbf{X}_{Bf}$ for each frequency f. (eq. 1, see also Figure 1A):

(1)

$$\mathbf{K}_{Af} = n^{-1}\mathbf{X}_{Af}\mathbf{X}_{Af}^{T}$$
$$\mathbf{K}_{Bf} = n^{-1}\mathbf{X}_{Bf}\mathbf{X}_{Bf}^{T}$$

where *n* is the number of time points minus one in $\mathbf{X}_{Af}$ and $\mathbf{X}_{Bf}$, respectively, normalizing the covariance matrices with regard to duration (to facilitate comparison of eigenvalues for time windows of different length). Trials in $\mathbf{X}_{Af}$, $\mathbf{X}_{Bf}$ can be concatenated and used to compute the covariance matrix at once, or covariance matrices can be computed for each separate trial and averaged; we find that the latter option tends to produce cleaner covariance matrices with more stable solutions.

As GED finds sources that maximize the "multivariate power ratio" between two covariance matrices, one of the matrices must be chosen to be optimized (the *signal matrix*) and the other is chosen to be minimized (the *reference matrix*). To investigate two conditions of interest in csGED, the generalized eigenvalue equation is solved once using $\mathbf{K}_{Af}$ as signal matrix and $\mathbf{K}_{Bf}$ as reference matrix, and once with $\mathbf{K}_{Bf}$ as signal and $\mathbf{K}_{Af}$ as reference. The reference matrix can be shrinkage-regularized to improve separability and stability; details are provided in the next subsection.

By maximizing the Rayleigh quotient between $\mathbf{K}_{Af}$ and $\mathbf{K}_{Bf}$ ($\mathbf{K}_{Af}$ being signal and $\mathbf{K}_{Bf}$ being reference; eq. 2), a single set of weights $\mathbf{w}_{Af>Bf}$ is found. This $\mathbf{w}_{Af>Bf}$ captures the direction in which $\mathbf{K}_{Af}$ and $\mathbf{K}_{Bf}$ are maximally separable, i.e., where the power ratio between them is highest. The associated scalar value $\lambda_{Af>Bf}$ (eq. 3) quantifies this power ratio. For our purposes, $\mathbf{w}_{Af>Bf}$ describes a spatial filter that captures the maximal energy ratio between conditions A and B filtered at frequency *f*. As such, it provides a spatial weighting that attempts to isolate the source that generates the most *f*-Hz energy in condition A compared to condition B. Conversely, maximizing the Rayleigh quotient between $\mathbf{K}_{Bf}$ and $\mathbf{K}_{Af}$ yields weights $\mathbf{w}_{Bf>Af}$ and power ratio $\lambda_{Bf>Af}$, and isolates the source that generates most *f*-Hz energy in condition B compared to condition A.

$$\mathrm{w} = \arg\max_{\mathrm{w}} \frac{\mathrm{w}^{\mathrm{T}}\mathbf{K}_{\mathrm{Af}}\mathrm{w}}{\mathrm{w}^{\mathrm{T}}\mathbf{K}_{\mathrm{Bf}}\mathrm{w}} \tag{2}$$

$$\lambda = \frac{\mathrm{w}^{\mathrm{T}}\mathbf{K}_{\mathrm{Af}}\mathrm{w}}{\mathrm{w}^{\mathrm{T}}\mathbf{K}_{\mathrm{Bf}}\mathrm{w}} \text{ at } \mathrm{w} = \mathrm{w}_{\max} \tag{3}$$

Equations 2 and 3 can be extended from a single vector computation to a matrix computation (eqs. 4 and 5; see also Figure 1B). The resulting generalized eigenvalue equations, when solved, each yield a matrix of weights **W** and a diagonal matrix of associated eigenvalues **Λ**.

$$\mathbf{K}_{\mathrm{Af}}\mathbf{W} = \mathbf{K}_{\mathrm{Bf}}\mathbf{W}\boldsymbol{\Lambda} \tag{4}$$

$$\mathbf{K}_{\mathrm{Bf}}\mathbf{W} = \mathbf{K}_{\mathrm{Af}}\mathbf{W}\boldsymbol{\Lambda} \tag{5}$$

This generalized eigendecomposition equation is solved once for $\mathbf{K}_{Af} > \mathbf{K}_{Bf}$ (eq. 4) and once for $\mathbf{K}_{Bf} > \mathbf{K}_{Af}$ (eq. 5) at each frequency *f*. From each resulting $\boldsymbol{\Lambda}_{Af>Bf}$, $\boldsymbol{\Lambda}_{Bf>Af}$, the largest eigenvalue is extracted, as a measure of the maximum energy ratio between $\mathbf{K}_{Af}$, $\mathbf{K}_{Bf}$ (i.e., maximum separability between conditions) in that frequency. The associated set of weights (i.e., an eigenvector, or component) in $\mathbf{W}_{Af>Bf}$, $\mathbf{W}_{Bf>Af}$ is the spatial filter that attempts to isolate the source maximally separating the conditions at that frequency. To facilitate magnitude comparisons between components, extracted eigenvectors **w** are normed to unit length (eq. 6):

$$\hat{\mathbf{w}} = \frac{\mathbf{w}}{\|\mathbf{w}\|} \tag{6}$$

Plotting the largest eigenvalue found at each temporal filter frequency results in a frequency spectrum of separability, with peaks around frequencies where sources are found that strongly differentiate the conditions (Figure 1D). Components driving the spectral peaks can be further inspected by using the eigenvectors to compute component topographies and time courses.

Shrinkage regularization

The reference matrix can optionally be shrinkage-regularized (eq. 7) to improve separability and stability and, if necessary, correct potential rank-deficiency. Shrinkage regularization shifts the reference matrix towards a scaled version of the identity matrix (e.g., 1%), and thus shifts the GED procedure towards a PCA. The signal matrix is best left intact to retain an accurate representation of the signal to be maximized.

(7)

$$\tilde{\mathbf{K}} = (1-\gamma)\mathbf{K} + \gamma\alpha\mathbf{I}$$

Here **K** is the original reference matrix, **K̃** is the regularized reference matrix, γ is the degree of shrinkage (we used 0.01, which corresponds to 1%), **I** is the identity matrix of equal size to **K**, and α is the average of the eigenvalues of **K** (eq. 8):

$$\alpha = \frac{1}{\mathrm{n}}\sum_{\mathrm{i}=1}^{\mathrm{n}} \lambda_{\mathrm{i}} \tag{8}$$

Following regularization, the regularized matrix is used in place of the original reference matrix in Equations 2 through 5.

Computing component topographies

From each component eigenvector **w**, a component topography **q** can be constructed as a linear combination of the covariance matrix weighted by the eigenvector (cf. Haufe et al., 2014); see also Figure 1C):

$$\mathbf{q} = \mathbf{w}^{\mathrm{T}}\mathbf{K}_{\mathrm{Af}} \tag{9}$$

Computing component time courses

Component time series **c** can be constructed as linear combinations of the sensor-level time courses in **X**, weighted by the eigenvector **w** (see also Figure 1C):

$$\mathbf{c} = \mathbf{w}^{\mathrm{T}}\mathbf{X}_{\mathrm{Af}} \tag{10}$$

where **X** is the original (unfiltered, broadband) channels-by-time-by-trials data, and **c** is the component-by-time-by-trials result. Note that while **w** is computed from narrowband data, the fact that **X** is broadband results in the component time series **c** being broadband. The broadband nature of the component time series allows for time-frequency decomposition, which

can serve both to verify that activity in **c** occupies a narrow range of frequencies, and to explore activity in other frequencies captured by the same spatial filter.

Time-frequency decomposition

Component time series can be further characterized through time-frequency decomposition. We implemented this by narrowband-filtering the time series **c** at a range of frequencies, through trial-by-trial convolution with complex-valued Morlet wavelets spaced throughout the frequency range of interest. Morlet wavelets were constructed as follows (eqs. 11 and 12):

$$\Psi_f = e^{i2\pi ft} e^{-t2/2s^2} \tag{11}$$

$$s = \frac{n}{2\pi f} \tag{12}$$

where *t* is time, *f* is frequency, *s* is the standard deviation of the Gaussian that modulates the complex sine wave, and *n* is the number of wavelet cycles. The number of cycles per wavelet governs the tradeoff between temporal and spectral precision. Both datasets considered in this paper were decomposed at 40 different frequencies. These frequencies were linearly spaced from 2 to 20 Hz for the simulated data and logarithmically spaced from 4 to 80 Hz for the empirical data. Wavelet widths were logarithmically spaced from 4 to 10 cycles.

Convolving the component time series with the created Morlet wavelets produces a (temporally smoothed) power time series for each frequency. To correct for the higher power observed at lower frequencies (Cohen, 2014), the signal power at each frequency is dB-scaled relative to the average baseline power at that frequency. Baseline windows should be relatively free from perturbations, last at least as long as one full cycle at the lowest decomposition frequency, and be far enough removed from trial epoch edges to avoid filtering-related edge artifacts. We selected a baseline window of 0.8 to 0.2 seconds prior to stimulus onset for the simulated data, and 0.8 to 0.2 seconds prior to fixation cross onset for the empirical data.

<u>Simulations</u>

Before analyzing empirical data (where the ground truth is unknown), we validated and explored

our methods in simulated data, in which the ground truth is known and where it is possible to arbitrarily control the signal-to-noise ratio (SNR). To this end, we simulated MEG data for two conditions ("A" and "B") with unique signal and shared noise characteristics. The csGED procedure was applied once for A > B and once for B > A. Peaks in the eigenvalue spectra were identified, and the peak-associated component time series were compared to the ground truth signals (by computing shared spatial variance R^2), yielding a measure of reconstruction accuracy. This reconstruction accuracy was compared to the accuracy at best sensor for each dipole, i.e., the sensor to which the dipole projected most strongly (positively). We varied the signal amplitude relative to the noise amplitude to evaluate results for different SNR.

Dipole selection

A model containing 15000 cortical surface-level dipole locations, and each dipole's associated projection weight matrix (leadfield matrix) to sensor locations corresponding to the CTF 275 system, was generated using Brainstorm (Tadel et al., 2011). As a detailed anatomical representation of the cortex was not necessary, the model was downsampled to 3000 dipoles, improving simulation speeds. The leadfield projection weights for each dipole were normalized by that dipole's maximum projection weight across sensors, so that all dipoles projected to the scalp comparably strongly (eq. 13):

$$\hat{\mathbf{d}} = \frac{\mathbf{d}}{\max(\mathbf{d})} \tag{13}$$

where $\mathbf{d}$ are the original and $\hat{\mathbf{d}}$ are the normalized projection weights for a single dipole.

To demonstrate the efficacy of csGED in separating sources with partially overlapping topographies, we selected two signal-generating dipoles with a reasonable amount of overlap (squared spatial correlation $R^2 = 0.4$), of which one would be active on condition A trials and one would be active on condition B trials. Dipole projection topographies are shown in Figure 2A.

In addition to these signal dipoles, a random set of 1000 "distractor" dipoles was selected for each simulation, of which a randomized 30% on average would be active on any given trial. A signal dipole could not also be a distractor dipole.

Signal and noise generation

We simulated 200 3-second trials, of which the first 100 represented condition A and the last 100 represented condition B. Stimulus presentations were simulated during the 1– 2 s time window. This meant that on each trial in condition A, the first signal dipole was active during this time window while the second remained quiet. This was reversed for trials in condition B, where the second dipole was active while the first remained quiet. The activity each dipole generated was the time-domain representation of a uniformly randomly generated frequency spectrum, bandpass-filtered (through frequency-domain Gaussian convolution, Gaussian FWHM of 2) at a given frequency. Signal frequencies were chosen to be 6 Hz for dipole A and 10 Hz for dipole B.

On each trial, each of the distractor dipoles had a 30% chance of being active. An active dipole generated a waveform centering on a randomly chosen frequency with a maximum of 25 Hz, during a randomized time window of >0.3 s duration. These waveforms were scaled to a fixed root mean square (RMS) amplitude of 3. Additionally, white noise with a fixed SD of 0.5 was added to all (signal, distractor, and inactive) dipoles for the entire duration of the trial. The total activity for each dipole was projected to the scalp through multiplication with the leadfield matrix, resulting in a mixed sampling of dipole activity at each of the 275 simulated sensors.

To vary the SNR, the simulated signal was scaled to a specific RMS amplitude. The SNR for a given simulation was computed as the power ratio between total signal dipole amplitude and total distractor dipole amplitude (eq. 14), accounting for the fact that distractor dipoles were on average 300 times as plentiful as signal dipoles on a given trial and that scalp projection magnitudes for all dipoles were normalized. White noise amplitudes were not taken into consideration for the SNR value.

$$\mathrm{SNR} = \frac{{\mathrm{RMS_{sig}}}^2}{(300 \times \mathrm{RMS_{dist}})^2} \tag{14}$$

Here $\mathrm{RMS_{sig}}$, $\mathrm{RMS_{dist}}$ are the root mean square amplitudes for the signal and distractor dipoles, respectively. Note that signal and noise dipoles were distributed throughout the brain. Thus, the SNR at the topographical level reflects a mixture of all dipoles and thus in practice varies between sensors.

Contrasting conditions at each frequency

The previously described GED procedure was applied to the simulated data. The scalp-level signal **X** (channels-by-time-by-trials) was filtered at each frequency *f* using Morlet wavelet convolution, at 50 frequencies linearly spaced from 4 to 20 Hz. A time window of interest (1–2 s) was extracted from each trial, exactly matching the simulated stimulus duration. Covariance matrices $\mathbf{K}_{Af}$ and $\mathbf{K}_{Bf}$ were constructed from the A and B trials, and the eigendecomposition equation was solved. From the largest eigenvalues, a frequency spectrum was constructed, allowing us to derive at which frequencies the power ratios for A > B and B > A were maximal (Figure 1D).

Selecting frequencies of interest

To identify the components of interest, we first identified the frequencies of interest. We selected eigenvalue peaks in the frequency spectrum to determine at which frequencies A > B and B > A were maximal. An eigenvalue in the spectrum that was higher than the eigenvalues at both neighboring frequencies was considered a peak, with no additional constraints. The single highest peak in each spectrum was selected, and the corresponding eigenvector was dubbed “component A” for the A > B spectrum, and “component B” for the B > A spectrum. These components were used to construct component time series, which were then time-frequency decomposed for visual inspection, as described earlier.

Comparing reconstruction accuracy

We compared the GED-derived approximation of the ground truth dipole signals to the signals as measured at a single simulated MEG sensor. The simulated sensor to which each signal dipole projected most strongly (positively) was selected as the best sensor for that dipole.

Reconstruction accuracy was quantified as the shared temporal variance (R^2, squared correlation coefficient) between the ground truth dipole time series and the component time series in the relevant condition, and between the ground truth dipole time series and the signal measured at the best sensor in the relevant condition. R^2 values were plotted against the simulation SNR, to compare the accuracy of each measure in the presence of noise.

<u>Empirical data</u>

We selected a previously published dataset (Dijkstra et al., 2018) to analyze. Grounds for selection included the type of data collected (MEG, suited to source separation) and the binary task condition difference (perception vs. imagery of visual stimuli). Furthermore, imagery data can be challenging to analyze, as it is weakly time-locked to external stimuli or instructions (Dijkstra et al., 2019; Vidaurre et al., 2019). The absence of time-locking is not an issue for GED, as the method harnesses spatial covariance rather than temporal characteristics (beyond the selection of a general time window to analyze) to identify spatial filters. It is thus well-suited to the analysis of fluctuating neural dynamics, such as those exhibited during imagery.

Subjects

30 human subjects with normal or corrected-to-normal vision participated in this study. Subjects provided written informed consent. The Committee Human Research (CMO) Arnhem-Nijmegen approved the study, and all research was conducted according to the appropriate guidelines. Five subjects were rejected (for movement, failure to follow task instructions, or technical problems), leaving 25 subjects.

Task design

Full details are available in the original publication (Dijkstra et al., 2018); we here provide a brief summary that is relevant for our analyses. Subjects were sequentially shown two stimuli (face and house, or house and face; 0.8 s each, taken from a set of 8 possible stimuli), and were then cued to imagine either the first or second stimulus shown to them (0.3 s). Visual stimuli were separated by a random 0.4–0.6 s interval. The visual stimuli were separated from the imagery cue by a 0.5 s noise mask and another 0.4–0.6 s interval. Subjects completed 240 trials (120 per category; stimulus order counterbalanced) in blocks of 10.

Data acquisition

MEG data were acquired in a shielded room using a whole-head 275 axial gradiometer MEG system (MEG International Services Ltd., Coquitlam, BC, Canada) at a sampling rate of 1200 Hz. Data from five sensors were not recorded. Head location was monitored and corrected during between-block breaks. Electro-oculograms (EOG), an electrocardiogram (ECG), eye position, and pupil size were recorded to facilitate the removal of eye- and heart-related artifacts.

Data cleaning and preprocessing

Data were preprocessed using MATLAB (MATLAB 2014a, The MathWorks, Natick, 2014) and the FieldTrip toolbox (Oostenveld et al., 2011). Data were high-pass filtered at 0.5 Hz. 50 Hz line noise was filtered out with the ZapLine method (de Cheveigné, 2019), by removing a single noise component from each trial. Trial epochs were defined as lasting from 1 s prior to the appearance of the fixation cross (2 s prior to stimulus onset) to 1 s after the imagery time window, for a total of 15 s. Trial rejection was based on Dijkstra et al., 2018: if any of the relevant time windows (first visual stimulus, second visual stimulus, or imagery) had been rejected in the original study, we here rejected the full trial. After data cleaning and trial rejection, 192.4 ± 34.3 (mean ± SD) trials remained for each of the 25 subjects (minimum of 98 trials) each of which included a perception (P) and an imagery (IM) time window.

After trial rejection, data were downsampled to 300 Hz and independent component analysis (ICA) was performed. ICs capturing clear heart and eye artifacts were removed, based in part on correlations with the ECG/EOG/eye-tracking data and in part on visual inspection of the IC topographies. Data were scaled from Tesla to picoTesla prior to analysis, to prevent precision loss from rounding errors.

Contrasting conditions at each frequency

The csGED procedure was performed separately on each subject. First, the full-length trials were filtered at a range of frequencies through Morlet wavelet convolution. To optimize the trade-off between frequency resolution and computation speed, we first performed low-resolution scans with a frequency interval of 2 Hz (from 2 to 80 Hz), and then re-scanned in an 8 Hz range (4 Hz on either side) around identified peaks, with a frequency interval of 0.5 Hz.

Next, at each frequency, three relevant task windows were extracted from the full-length trial: one during the presentation of the first visual stimulus (“perception 1”, P1; 0.8 s duration), one during the second visual stimulus (“perception 2”, P2; 0.8 s duration), and one during the imagery window (IM; 3.5 s duration). To allow the GED to optimize for general perception-related processes, P1 and P2 were concatenated into a single “perception” (P) window. Sensor-by-sensor covariance matrices $\mathbf{K}_{Pf}$, $\mathbf{K}_{IMf}$ were computed per trial and then averaged. Then, for each subject, the eigendecomposition equation was solved once to find spatial filters that maximized $\mathbf{K}_{Pf} > \mathbf{K}_{IMf}$, and once for $\mathbf{K}_{IMf} > \mathbf{K}_{Pf}$. Each solution yielded a set of eigenvalues and

eigenvectors, of which the largest eigenvalue and corresponding eigenvector were retained and the others were discarded.

Selecting frequencies of interest

Subject-specific eigenvalue spectra typically contained multiple peaks. Local maxima in each spectrum were selected by identifying eigenvalues that 1) were flanked by lower eigenvalues at neighboring filter frequencies, 2) had a prominence (a measure of peak independence, defined as height relative to the lowest neighboring trough that is not separated by a higher peak) of at least 0.01, and 3) were separated by at least 2 Hz. If multiple eigenvalue peaks fell within 2 Hz of each other, the largest eigenvalue was selected. Selected eigenvalue peaks indicated a locally maximal power ratio for P > IM or IM > P at that frequency, meaning a spatial filter specific to that frequency was found that strongly maximized energy in one condition and minimized energy in the other. Components at the peaks were used to compute component topographies and component time series as described previously. Component time series were time-frequency decomposed for visual inspection, as described earlier.

Kernel density smoothing

To reconcile variability in the subject eigenvalue spectra and the extracted peak frequencies, we computed a kernel density estimate from the previously selected peaks per individual subject. Kernel density estimates are useful because they remove the biases resulting from different raw eigenvalue magnitudes across subjects and across frequencies. By applying this method of combining components, we made the assumption that components in different subjects are functionally similar when 1) they occupy the largest eigenvalue and 2) the frequencies to which they most contribute are close together.

Kernel density estimation was performed by taking the eigenvalue peak frequencies from all subjects, representing each as a Gaussian with a height of 1 and SD of 2 Hz (chosen to create a reasonably smooth plot), and summing over Gaussians. This procedure is illustrated in Supplementary Figure S1. The resulting kernel density functions (KDFs) reflected a combination of the proportion of individual-subject peak components around a given frequency, and how close to that frequency the peak components were located.

Averaging over components

Upon visual inspection, the KDFs exhibited multiple salient peaks (subjectively defined as exceeding 0.01, a.u.), reflecting frequencies near which many subjects presented with eigenvalue peaks. To facilitate comparing component characteristics, we averaged together component time courses, topographies, and time-frequency decompositions based on the components' distance to the KDF peak frequency. Specifically, frequency boundaries around each KDF peak were defined so that the ratio between the center frequency and the frequency band width was 2.33 (following the "golden rule"; (Klimesch, 2018). Each subject's peak component closest to the KDF center frequency was included in the average, as long as it remained within frequency boundaries. As such, each subject contributed a maximum of one component; a given peak average might therefore not include components from all 25 subjects. In practice, 16.8 subjects on average contributed components to a KDF peak, with a minimum of 7 and a maximum of 23.

Code accessibility

The custom-written MATLAB analysis code will be made available upon publication on GitHub at `http://www.github.com/marrit-git/csGED`.

Results

Simulation results

At SNR = 1×10^{-5}, the GED-derived eigenvalue spectra exhibited clear peaks centering on the frequency of the active dipole in that condition (Figure 1D). The csGED procedure thus successfully identified the frequencies at which covariance power in condition A was maximal compared to condition B and vice versa, without a priori expectations about these frequencies.

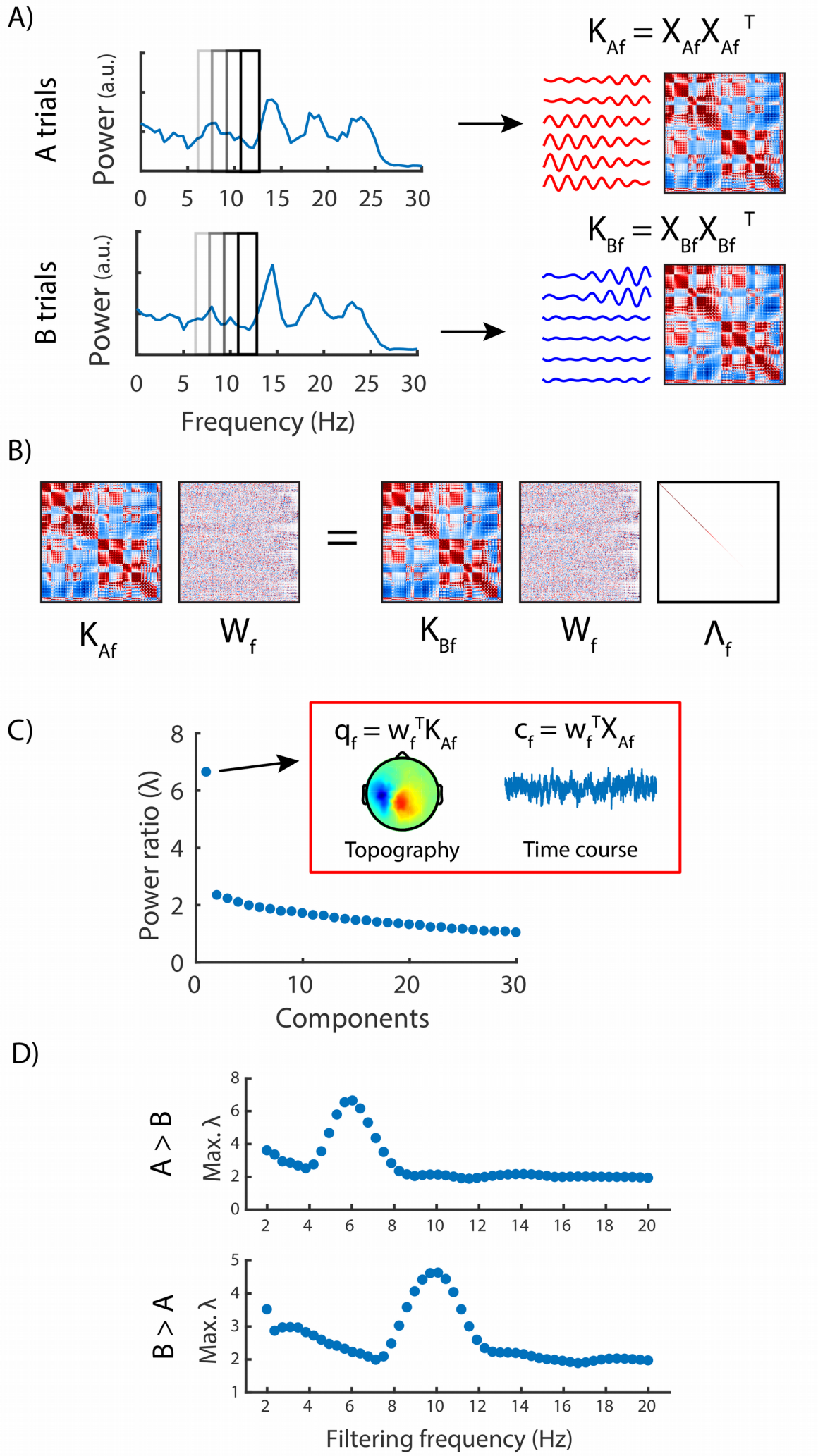
A)
A trials
Power (a.u.)
0 5 10 15 20 25 30
$K_{Af} = X_{Af} X_{Af}^T$
B trials
Power (a.u.)
0 5 10 15 20 25 30
$K_{Bf} = X_{Bf} X_{Bf}^T$
Frequency (Hz)
B)
K_{Af}
W_f
=
K_{Bf}
W_f
Λ_f
C)
Power ratio (λ)
0 2 4 6 8
0 10 20 30
Components
$q_f = w_f^T K_{Af}$
$c_f = w_f^T X_{Af}$
Topography
Time course
D)
A > B
Max. λ
0 2 4 6 8
2 4 6 8 10 12 14 16 18 20
B > A
Max. λ
1 2 3 4 5
2 4 6 8 10 12 14 16 18 20
Filtering frequency (Hz)

Figure 1. *Illustration of the method as applied to simulated MEG data with unique signal and shared noise characteristics.* ***A)*** *Trial data from conditions A and B (*$\boldsymbol{X}_A$ *and* $\boldsymbol{X}_B$*) are filtered at specific frequencies f. Covariance matrices* $\boldsymbol{K}_{Af}$, $\boldsymbol{K}_{Bf}$ *are constructed from the narrowband data* $\boldsymbol{X}_{Af}$, $\boldsymbol{X}_{Bf}$. ***B)*** *Matrices* $\boldsymbol{K}_{Af}$ *and* $\boldsymbol{K}_{Bf}$ *are entered into the generalized eigenvalue equation, yielding a set of eigenvectors* $\boldsymbol{W}_f$ *and corresponding eigenvalues* $\boldsymbol{\Lambda}_f$ *that maximize the energy ratio between* $\boldsymbol{K}_{Af}$ *and* $\boldsymbol{K}_{Bf}$ *(or* $\boldsymbol{K}_{Bf}$ *and* $\boldsymbol{K}_{Af}$*, respectively).* ***C)*** *Each eigenvector (component) can be used to construct a component topography* $\boldsymbol{q}_f$ *and time course* $\boldsymbol{c}_f$. *The component with the largest eigenvalue* λ *is retained to construct a spectrum of maximum eigenvalues.* ***D)*** *The maximum eigenvalues at each filtering frequency* f *peak around 6 Hz when maximizing A > B and at 10 Hz when maximizing B > A, reflecting the ground truth signals present in conditions A and B respectively.*

The components corresponding to the eigenvalues at these maxima represented the GED-identified approximation of the original dipole signal as a linear mixture of sensor data. The topographical reconstructions (spatial filters) were highly similar to the original dipole projections (Figure 2A; squared spatial correlation R^2 = 0.99 and 0.97, respectively). Time-frequency decompositions (Figure 2B) allowed for visual comparison of the original time courses to the reconstructions. At a SNR of 1×10^{-5}, the reconstructed time courses provided a closer fit to the ground truth signal (temporal R^2 = .028, .041 for dipole A and B, respectively) than the signal at the best sensor did (temporal R^2 = .006, .007 for A and B; p = 0.023, one-sided $t(2)$ = 4.47). The low R^2 values are attributable to the noise and distractors in other frequencies: narrowband-filtering all signals at 6 and 10 Hz (FWHM 2), respectively, provided closer fits (R^2 = .547 and . 730 for the reconstructed time courses; R^2 = .278 and .300 for the sensor-level signals). These results show that at this specific SNR, source separation components captured the ground truth brain signal better than single-sensor analyses did.

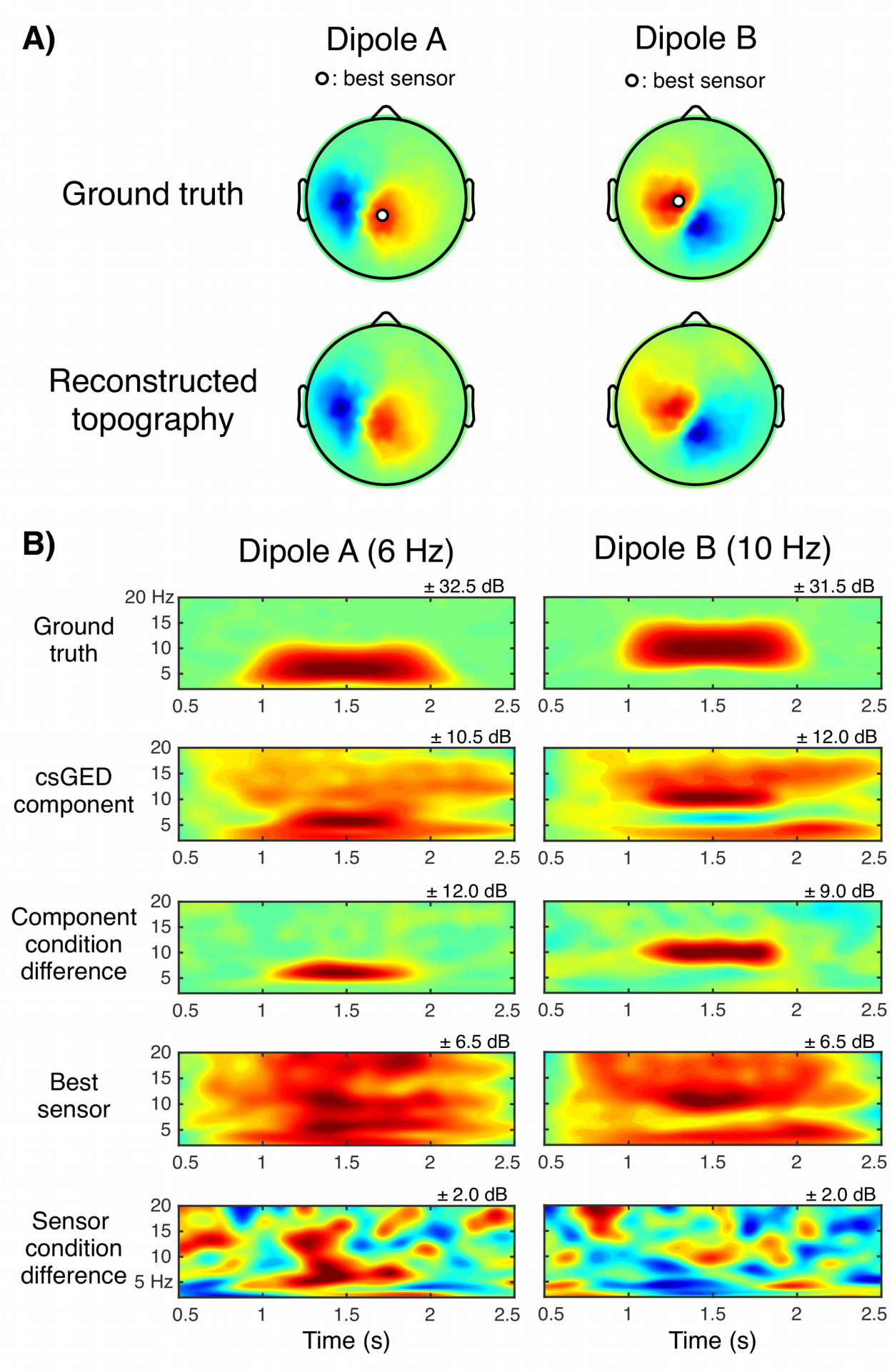
A)
Dipole A
o: best sensor
Dipole B
o: best sensor
Ground truth
Reconstructed topography
B)
Dipole A (6 Hz)
Dipole B (10 Hz)
Ground truth
± 32.5 dB
± 31.5 dB
csGED component
± 10.5 dB
± 12.0 dB
Component condition difference
± 12.0 dB
± 9.0 dB
Best sensor
± 6.5 dB
± 6.5 dB
Sensor condition difference
± 2.0 dB
± 2.0 dB
20 Hz
15
10
5 Hz
0.5
1
1.5
2
2.5
Time (s)

Figure 2. *Ground truth signals and signal reconstructions in simulated MEG data.* ***A)*** *Top: scalp projections of the signal-generating dipoles in both conditions. The circle marks the location of the best sensor for that dipole, at which the comparison signal is measured. Bottom: GED-reconstructed topographies of the signal dipoles for SNR* 1×10^{-5} *are highly similar to the ground truth topographies (shared spatial variances* R^2 *= 0.99 and 0.97 for dipole A and B respectively).* ***B)*** *Time-frequency (TF) decompositions illustrate that the GED component time series better approximate the ground truth signals (temporal* R^2 *= .028, .041 for dipole A, B) than the signals at the best sensors do (temporal* R^2 *= .006, .007 for dipole A, B). Condition difference plots (obtained by subtracting TF-decomposed A trials from B trials and vice versa; third and fifth rows) provide an even closer approximation of the ground truth.*

Next, we quantified the influence of the SNR on the reconstruction accuracy of both methods. Parametrically varying the SNR showed that the GED-derived reconstructions outperformed the best sensor at reconstructing a given signal, for all but the lowest and highest SNRs (Figure 3).

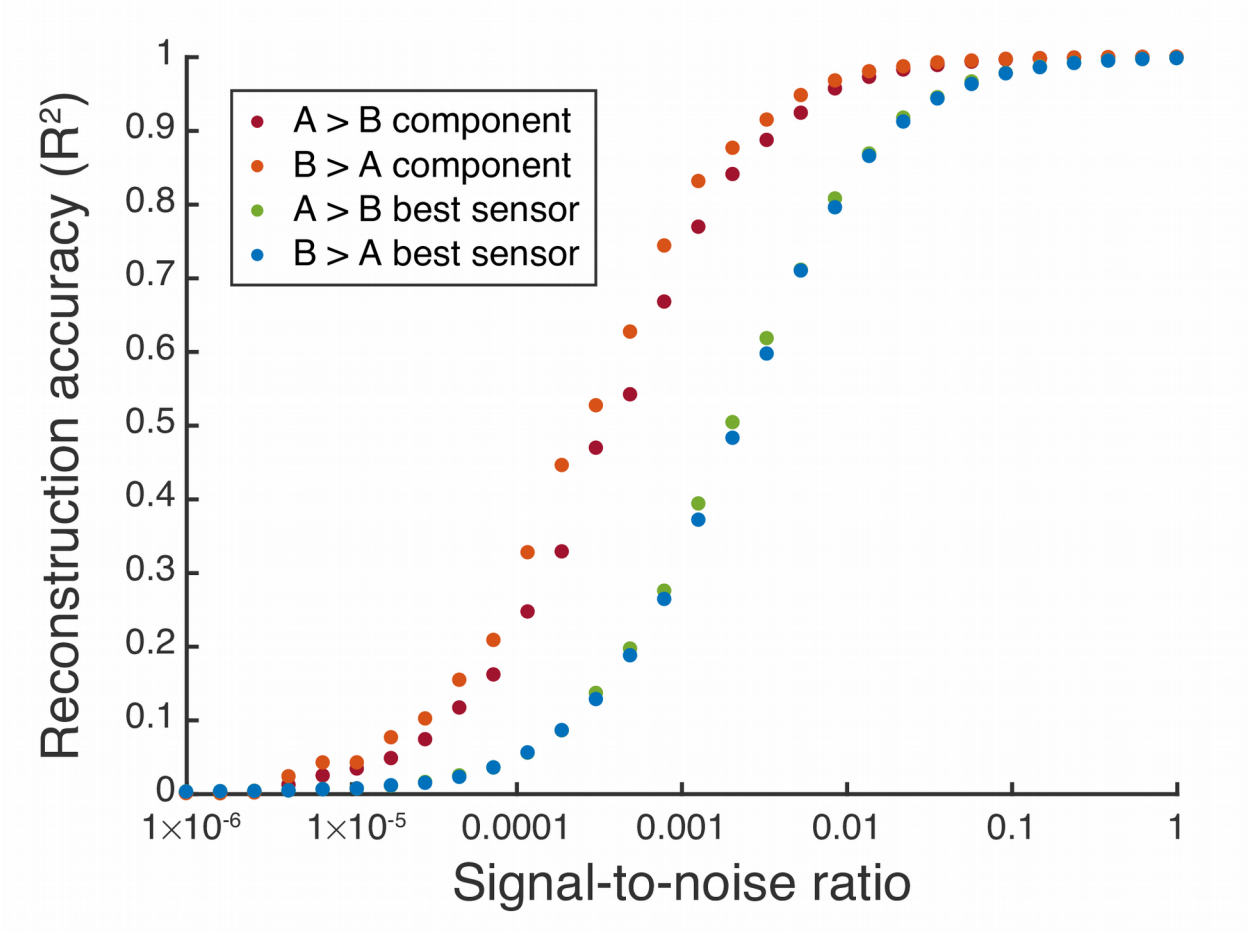

Figure 3. *In simulated MEG data, the csGED-derived component time series captured the ground truth more accurately than the signals at the best sensors did, even in the presence of large amounts of noise (300 noise dipoles for 1 signal dipole).*

Together, these simulation results demonstrate that csGED successfully identified the frequency content that maximally differentiated task conditions, without a priori expectations about the relevant frequencies. Furthermore, the ground truth signal at a given frequency was approximated more accurately with multivariate than with single-sensor analysis.

<u>Empirical results</u>

Each trial in our empirical dataset contained a time window during which subjects perceived visual stimuli (P) and a time window during which subjects imagined one of the stimuli (IM).

csGEDs contrasting the P and IM time windows on each trial were applied to data filtered at a range of frequencies, effectively scanning the frequency spectrum for high eigenvalues. This scan was performed once at low resolution (from 2 to 80 Hz with frequency intervals of 2 Hz) and then repeated at high resolution (frequency intervals of 0.5 Hz) around identified peaks, as described in the Methods section. P > IM and IM > P frequency spectra for individual subjects were variable (Figure 3A), likely reflecting intra-individual variability in peak oscillatory frequency.

A KDF was constructed from the eigenvalue peak frequencies, as illustrated in Supplementary Figure S1. Local maxima in the KDF (Figure 3B) indicate the frequencies at which subjects commonly exhibited an eigenvalue peak, while ignoring peak magnitude. KDF peak frequencies are listed in Table 1. The spectra exhibited peaks at similar frequencies for both condition contrasts. As the GED explicitly normalizes out commonalities between the conditions, this observation suggests that sources with different topographical distributions were active at the same frequencies in the two conditions.

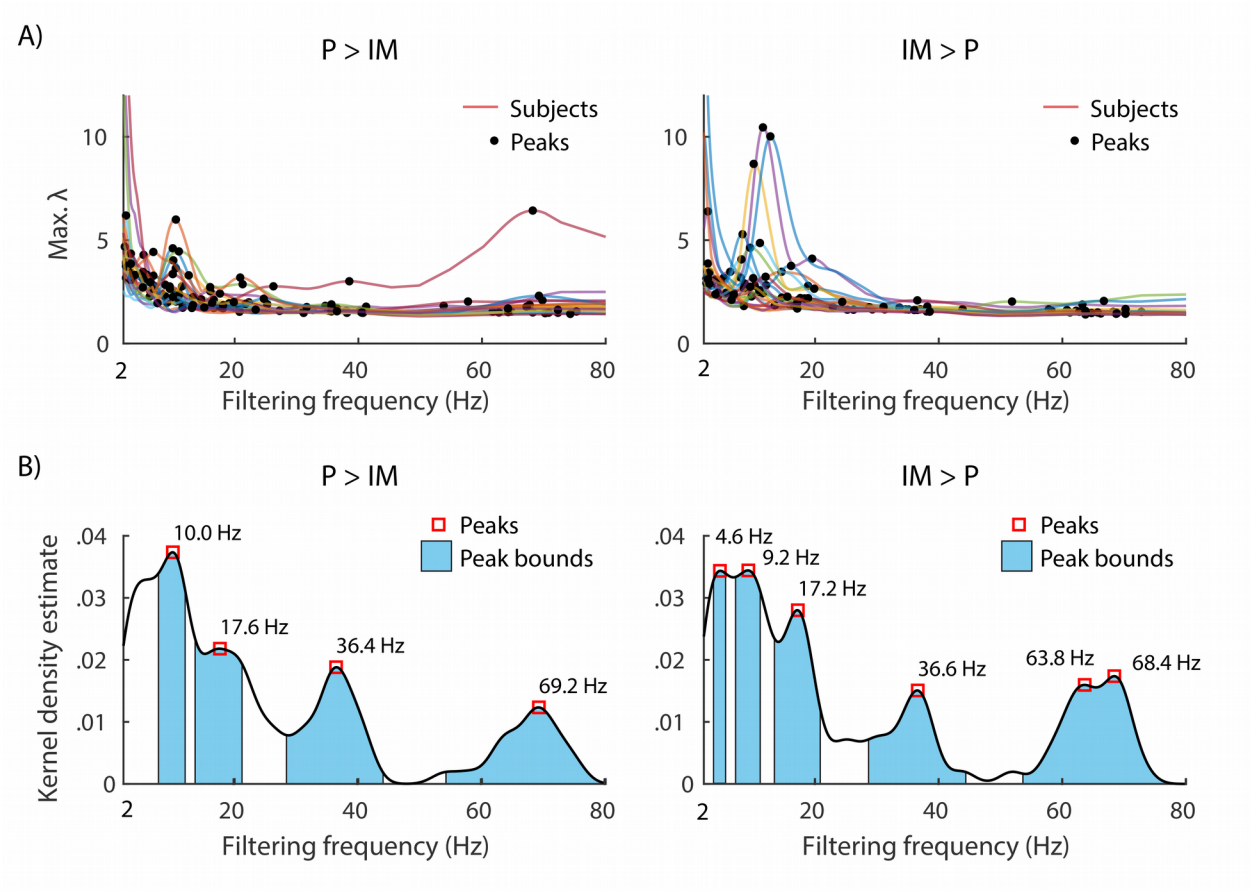

Figure 4. *Results of condition-specific spectral scanning on empirical MEG data, contrasting perception (P) against imagery (IM) time windows.* ***A)*** *Eigenvalue spectra per subject. Peaks were identified and transformed using a KDF.* ***B)*** *Kernel density estimates show multiple peaks, with each peak indicating that multiple subjects had high-eigenvalue components around that frequency. Notably, peaks for P > IM and IM > P were observed at similar frequencies, indicating condition-differentiating, spatially dissociable networks, resonating at nearly identical frequencies. Blue marks the frequency boundaries for each peak, which were later used to constrain averaging across components. IM > P gamma frequency ranges (with peaks at 63.8 and 68.4 Hz) overlapped substantially (sharing 22 out of 23 components) and were merged together.*

KDF-peak-related component topographies and time-frequency decompositions were averaged together for visual inspection. To do so, we selected components presumed to contribute to

each KDF peak, by identifying the component for each subject that was closest to the KDF peak as well as within frequency band boundaries (specified as 2.33 x peak frequency, following Klimesch, 2018). Table 1 lists the number of components included per peak and the average component frequencies. Individual components included in select peak averages (alpha, 10.0 and 9.2 Hz; and gamma, 69.2 and 66.6 Hz) are shown in Supplementary Figures 1 and 2. Note that we here operated on the assumption that components occupying the highest eigenvalue and centered around the same frequencies are functionally similar, and thus can be meaningfully averaged.

Comparison	KDF peak frequency	Component frequency (mean ± SD)	Component *n*
P > IM	10.0 Hz	10.2 ± 0.95 Hz	21
	17.6 Hz	17.8 ± 2.09 Hz	18
	36.4 Hz	36.0 ± 3.07 Hz	20
	69.2 Hz	68.4 ± 3.96 Hz	17
IM > P	4.6 Hz	4.4 ± 0.49 Hz	7
	9.2 Hz	9.5 ± 1.09 Hz	15
	17.2 Hz	17.4 ± 1.43 Hz	17
	36.6 Hz	34.9 ± 3.30 Hz	13
	66.6 Hz	64.5 ± 4.70 Hz	23

Table 1. *Overview of peak frequencies extracted from the KDF, and characteristics of the components selected as contributing to each peak frequency.*

Individual components, as well as component averages for each peak, varied both in topography and in time-frequency characteristics (Figure 5; Supplementary Figures S2 through S5), suggesting that csGED captured functionally diverse networks. Notably, csGED was able to harness condition differences to separate sources with overlapping spatial projections and frequencies (e.g., the P > IM and IM > P alpha components for subjects 1, 7, 15, and 19 in Figures S2 and S3). Conversely, it was able to harness frequency differences to separate

spatially overlapping sources active in the same condition (e.g., the P > IM components for subjects 4 and 9 in alpha and gamma; Figures S2 and S4).

Averaged component time-frequency dynamics (Figure 5) tended to show power increases during the condition of interest as well as power decreases during the other condition. This appeared to be a result of averaging, as individual component dynamics (Figures S2 through S5) tended to exhibit either power increases or power decreases, and rarely showed both. Many of the observed source dynamics were most pronounced during the perception time windows. Several features of these components are commonly linked to perception, such as short-lived alpha power decreases during perception (e.g., Fries et al., 2008; Klimesch et al., 2007) and gamma power increases during perception (Fries et al., 2008; Hoogenboom et al., 2006; Sedley & Cunningham, 2013). However, the persistent increases in alpha power and the decreases in gamma power are not typically observed in perception tasks. These may reflect perception-related source dynamics that are normally obscured, or they may reflect other processes; for example, the alpha increases may be related to attentional orienting (Thut et al., 2006). Gamma power decreases are rarely reported, regardless of task, and may be a novel observation.

Dynamics during the imagery time window generally remained closer to baseline than dynamics during the perception time window. The identified IM > P sources were thus characterized more by suppression during perception than by imagery-related power changes. It is possible that csGED recovered sources driven by imagery-related dynamics, but that these spatial filters were associated with smaller eigenvalues and were therefore not included in our analyses.

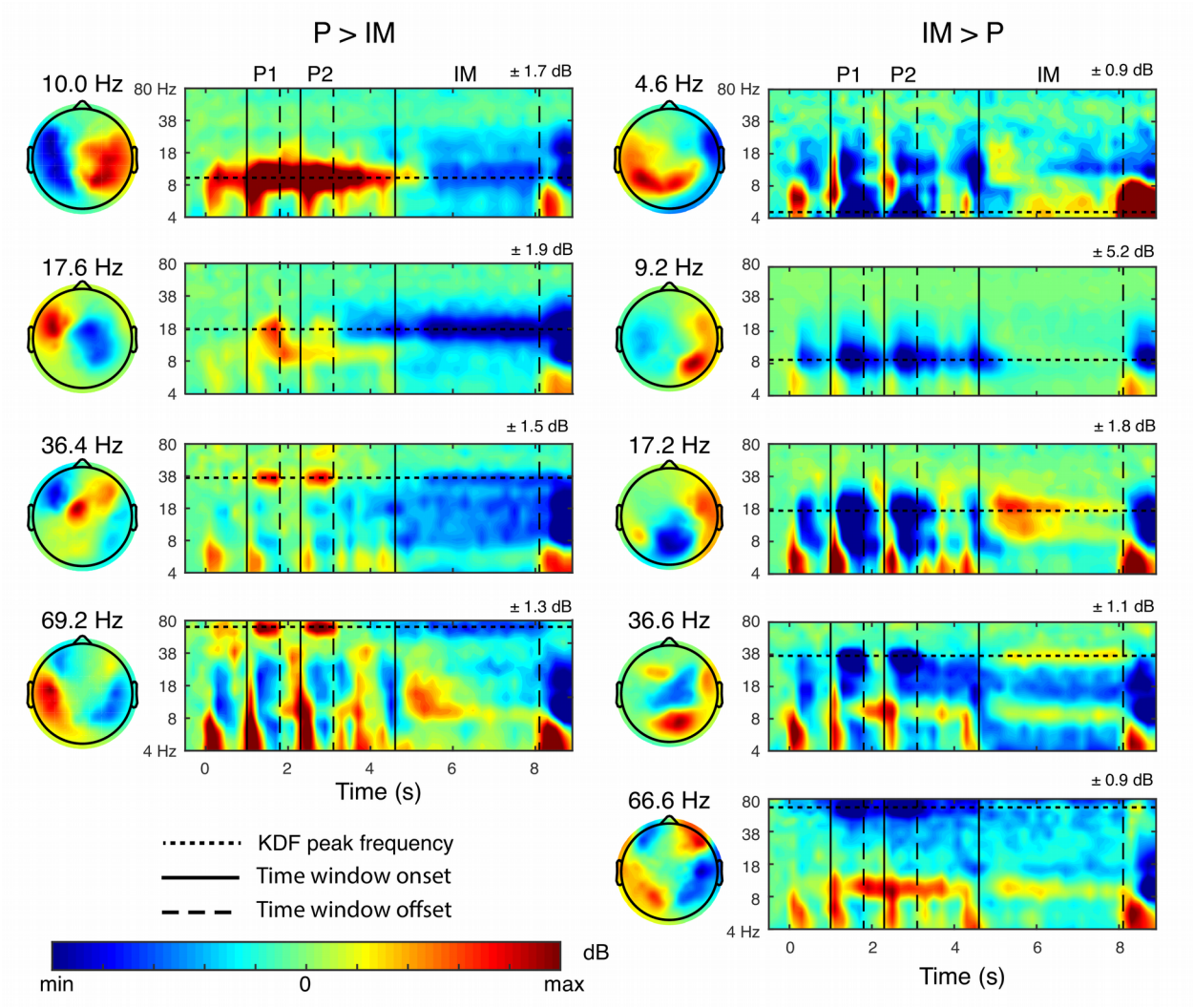

Figure 5. *Average component topographies and time-frequency decompositions, encompassing each subject's peak component closest to the overall KDF peak within frequency bounds. Average time-frequency decompositions tended to show power increases during the relevant condition and decreases during the other condition, indicating that csGED optimized for both.*

Discussion

<u>Summary</u>

We here presented csGED, an analysis method that scans the frequency spectrum for sources

that maximally differentiate two task conditions. While GED as a general method has been validated for different applications and on different types of neural data (Cohen, 2017a; de Cheveigné & Arzounian, 2015; de Cheveigné & Parra, 2014; Nikulin et al., 2011), this study is the first to concurrently combine frequency- and condition-sensitivity.

We first validated the source separation performance of csGED in simulated MEG data, for which the ground truth is known. We specified the operating frequency of signal-generating dipoles that were active in different conditions. csGED correctly identified the frequencies that differentiated the conditions, without a priori hypotheses about these frequencies. Next, we examined the top sources that csGED found at these frequencies and quantified how accurately the sources captured the ground-truth signals. This source reconstruction accuracy was compared to the accuracy at the best single sensor for each signal (which is commonly taken to be representative for phenomena detectable in M/EEG; e.g., Asanowicz et al., 2019; Tiedt et al., 2016)). For all but the highest and lowest signal-to-noise ratios, the csGED source reconstruction was markedly more accurate than the single-sensor representation of the source.

We next demonstrated the practical applicability of csGED in an empirical MEG dataset that compared visual perception and mental imagery (Dijkstra et al., 2018). As a result of its combined condition- and frequency-specificity, csGED was able to separate sources with overlapping topographies even when these sources generated activity at the same frequency or in the same condition. In sensor-level analyses, these separable sources would have remained linearly mixed (and thus confused) on account of their spatial co-occurrence. Furthermore, time-frequency decomposition of the source time series confirmed the presence of established neural signatures of perception in the source dynamics, suggesting that linear separation resulted in functionally meaningful segmentation.

In sum, csGED is able to successfully index the frequency spectrum of condition differences, and can accurately reconstruct signal sources whose dynamics may then be further inspected. We next highlight several features and idiosyncrasies that may be relevant to future applications of csGED.

<u>The interpretation of sources</u>

It should be kept in mind that csGED is performed without any anatomical constraints or biases;

thus, isolated statistical sources may, but do not necessarily, correspond to individual, spatially restricted, anatomical generators. As csGED is a covariance-based method, the spatial filters found may reflect distributed networks that generate covarying signal. Furthermore, the *inverse problem* applies: multiple combinations of dipoles exist that can drive a given spatial distribution. For these reasons, we prefer more conservative statistical and topographical interpretations over anatomical speculations.

One assumption underlying csGED is that the sources are covariance stationary, that is, that the covariance structure is constant over the selected time windows and over repeated trials. Violations of this assumption—for example through head movements or traveling waves—may decrease reconstruction accuracy or may be captured as two statistical sources. We have previously investigated this possibility in empirical data (Zuure et al., under review) and found it unlikely to be a significant issue.

Other spatial filter methods

There are several spatial filtering methods used in electrophysiology research, including principal components analysis (PCA) and independent components analysis (ICA). Owing to different assumptions, different methods highlight different features of a dataset. csGED differs from unsupervised methods like PCA and ICA primarily in that it is hypothesis-driven, i.e., optimizes for a given condition contrast at a set range of frequencies. This optimization essentially maximizes the signal-to-noise ratio for that contrast (de Cheveigné & Parra, 2014) and lends GED increased distinguishing power for hypothesis-relevant sources. In an entirely hypothesis-free exploration, PCA and ICA may be better suited to detect salient sources of activity. However, it is rarely the case that even exploratory analyses cannot be targeted towards a contrast, such as a task vs. baseline window. We have previously found that GED reconstructs simulated sources with higher accuracy than PCA or ICA (Cohen, 2017b), lending further validity to the csGED method.

Overfitting and underfitting

csGED is performed through the repeated solving of the generalized eigenvalue equation: once at every frequency. In this work, we have chosen to retain only the source with the largest eigenvalue (corresponding to the spatial filter explaining the most variance) from each of these solutions. The spectrum of separability was then constructed from these largest sources.

Selecting a single source at each frequency and contrast carries risks of overfitting and underfitting: it is possible that we retain a source where in reality there is only noise (overfitting), and it is possible that we retain just one source where in reality there are multiple relevant sources (underfitting).
Retaining a single source overfits the data if, in actuality, there is no source differentiating conditions at that frequency. This scenario can occur because the GED equations can be solved even for complete noise, essentially yielding sorted noise components. By assuming that the source with the largest eigenvalue meaningfully describes the data, we may mistake noise for a pattern. We mitigated potential overfitting by focusing on group-consistent peaks in the frequency spectra, relying on consistency across subjects to filter out noise-driven sources.

Conversely, retaining a single source underfits the data if multiple dissociable sources are active at that frequency. A single GED solution finds as many sources as there are sensors, more than one of which can be meaningful (de Cheveigné & Parra, 2014; Zuure et al., under review). By retaining the largest source per frequency and discarding the rest, potentially valid sources are excluded from the model describing the data. We retained a single source per frequency regardless, on the theoretical grounds that the source with the largest eigenvalue is likely to be the most relevant, and on the practical grounds of convenience. Notably, this means that further interesting and relevant dynamics may exist that csGED is able to recover, but that we did not focus on.

By retaining a single source at each frequency in the spectrum, csGED may be subject to overfitting at some frequencies and underfitting at others. Future applications of csGED may simultaneously mitigate over- and underfitting through permutation testing. In this procedure, a null distribution of eigenvalues is constructed for each frequency, and sources with eigenvalues exceeding this null distribution are retained (e.g., Hayton et al., 2004). Permutation testing may thus facilitate the detection of condition-relevant sources that do not occupy the largest eigenvalue.

<u>Pooling data across subjects</u>
Like most source separation methods, csGED is a method to be applied to single subjects for which the results later have to be combined across subjects (cf. Parra et al., 2018). There are many possible approaches to pooling sources (e.g., clustering by topography, time series

characteristics, or time-frequency characteristics; see also (Bigdely-Shamlo et al., 2013; Huster et al., 2015; Huster & Raud, 2018; Onton et al., 2005; Pion-Tonachini et al., 2019). We here relied on the assumption that empirical sources occupying the largest eigenvalue and sharing a frequency are functionally similar. As the standard approach in electrophysiology is to aggregate data based purely on frequency band, our approach is consistent with standard practice. Other approaches may highlight additional consistencies across subjects. For example, sources may exist that share similar topographies and temporal characteristics between subjects, but that manifest at different frequencies.

Extension beyond binary condition differences

csGED relies on the construction of a “signal” and a “reference” covariance matrix, meaning that the method lends itself to optimizing for a binary condition difference. One way to apply this method to multiple conditions is to compare all conditions pooled together against a baseline period; this would create a task-vs-baseline spatial filter that can be applied to the data from each individual condition. This approach also has the advantage of avoiding overfitting to a particular condition, albeit with a cost of reduced sensitivity to detecting subtle condition differences. csGED could also be extended to maximize a correlation with a variable over time or over trials, for example by integrating our frequency-specific spatial filters with the SPoC method (Dähne et al., 2014).

Conclusions

csGED is a multivariate source separation technique that is optimized to reveal the frequency spectrum of binary condition differences. While demonstrated here in MEG data, it is a general method that is equally applicable to the analysis of multivariate neuroscience data at any spatial scale and with any measurement technique that provides repeated measurements. It carries the dual advantage of being hypothesis-driven in terms of conditions, which enhances its sensitivity to sources of interest, and being hypothesis-free in terms of frequency, which adds exploratory value. csGED thus has the potential to push the boundaries of our understanding in the analysis of cognitive electrophysiology.

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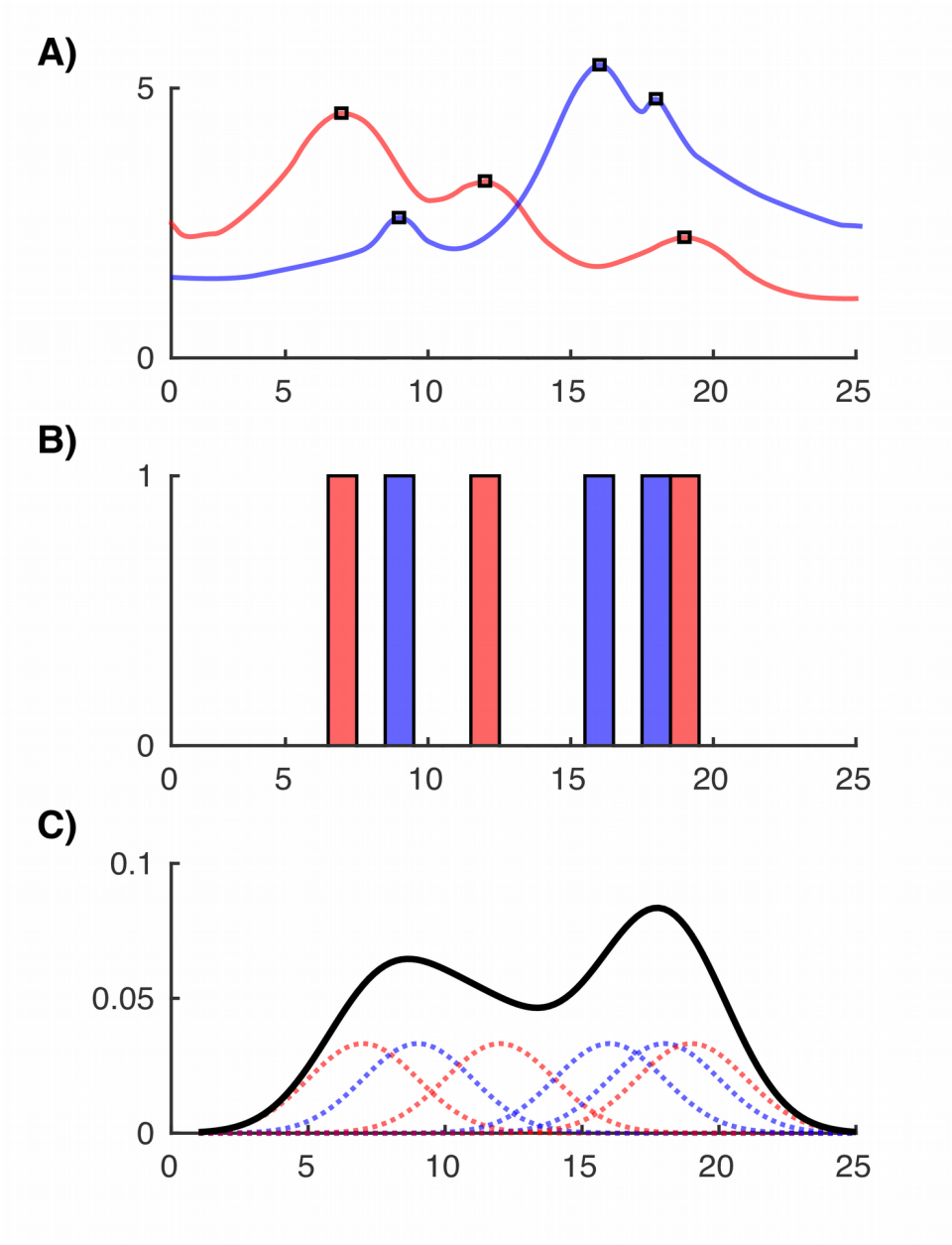
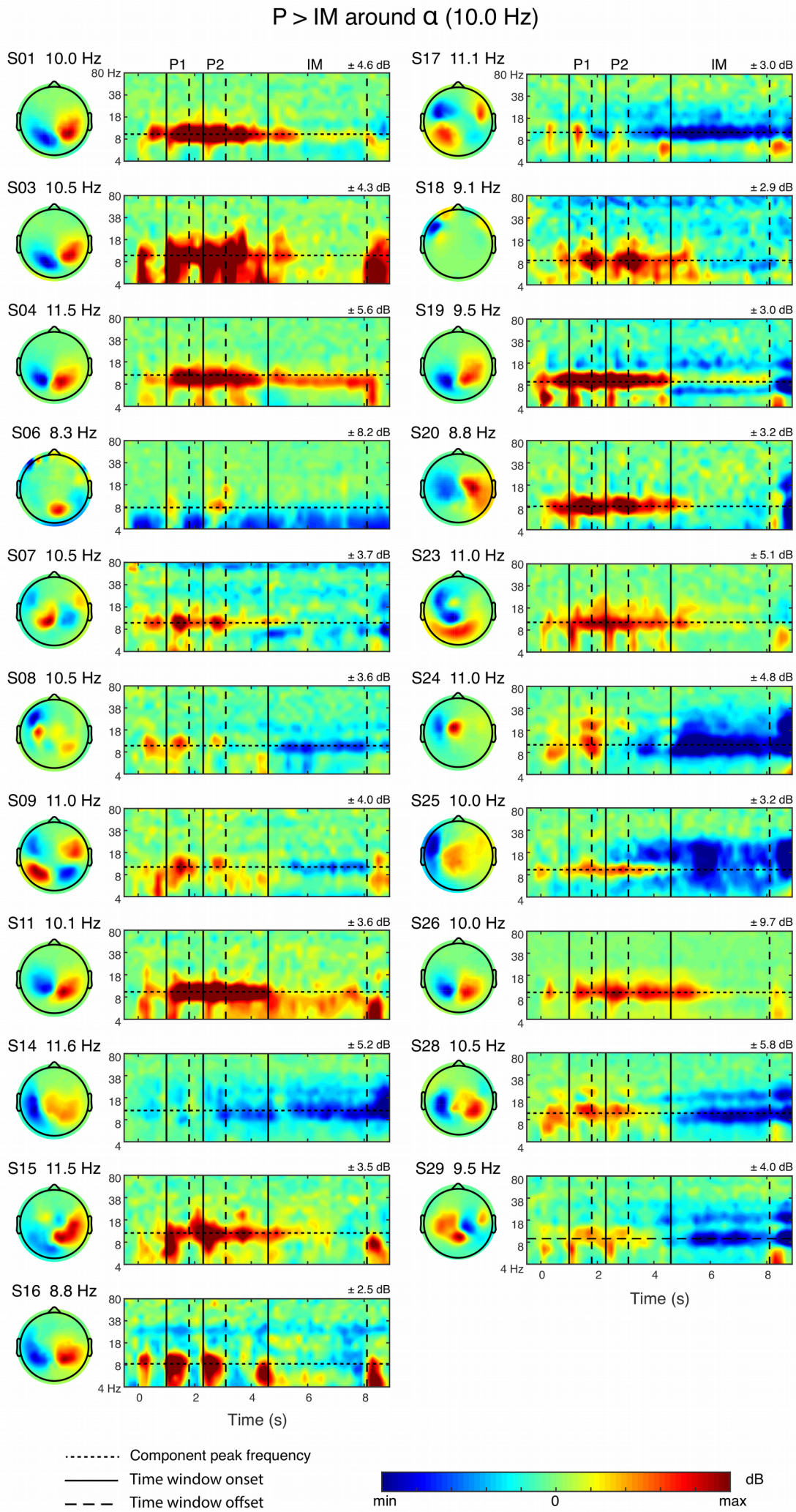
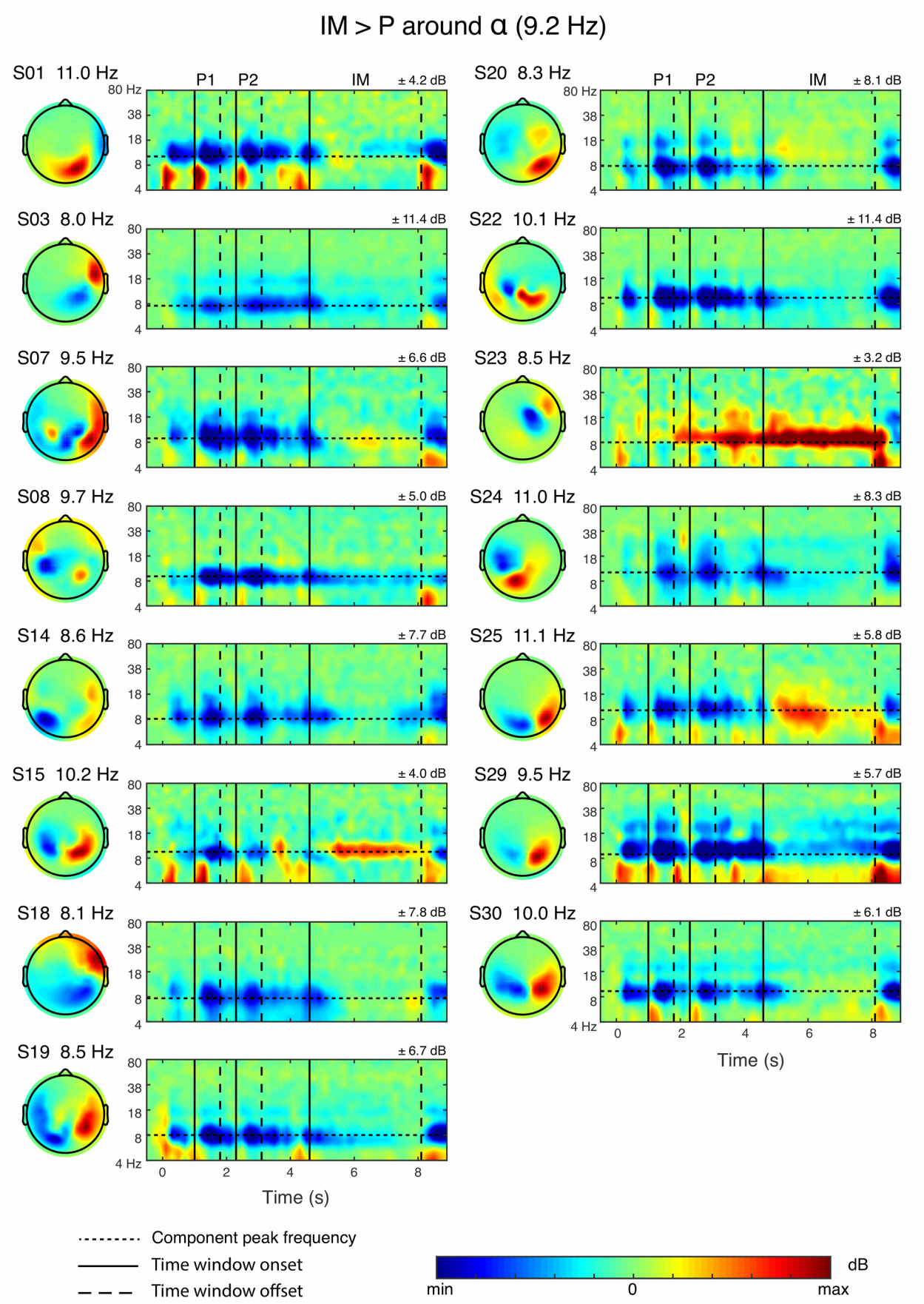
Supplementary material



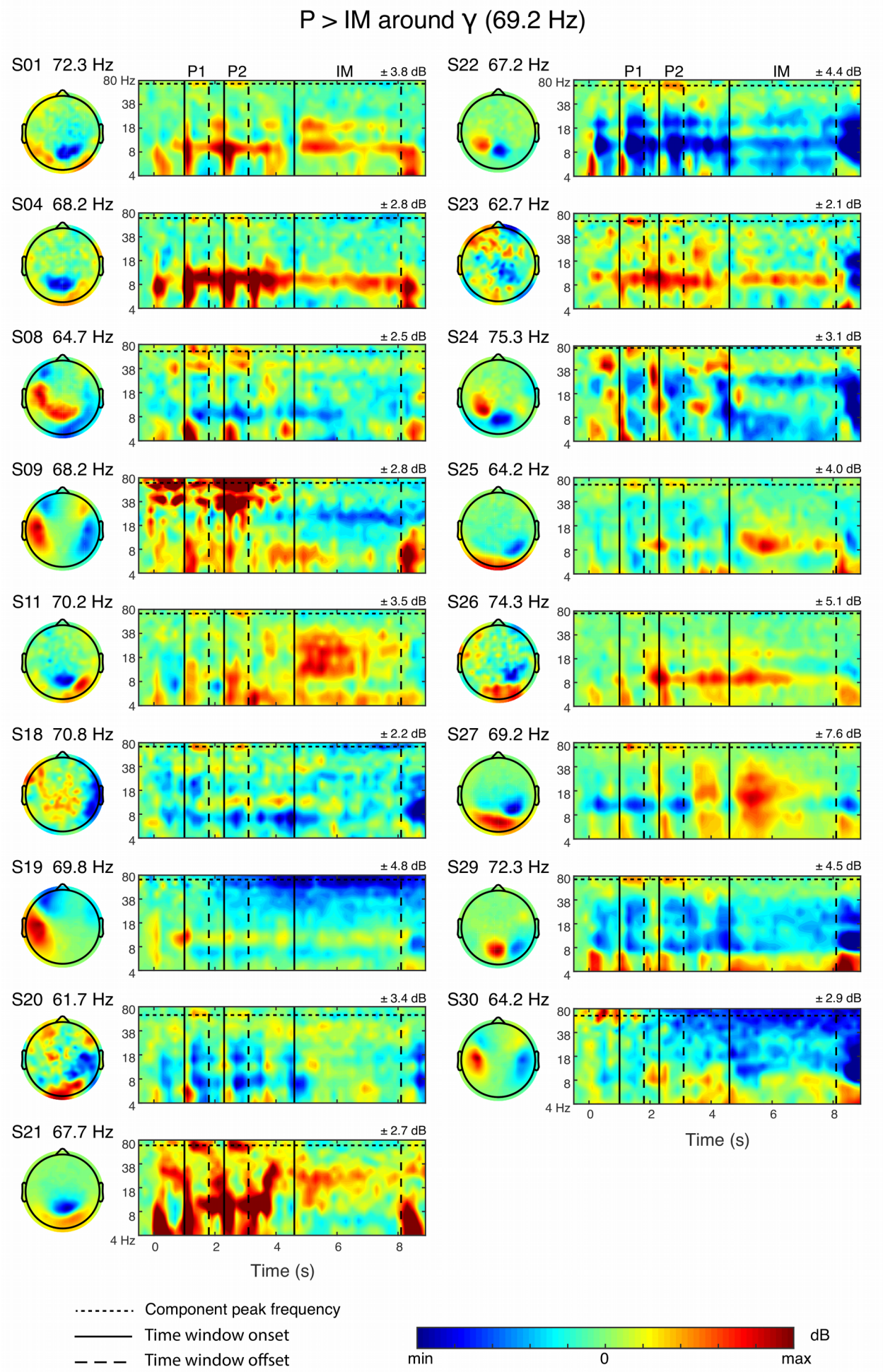
Supplementary Figure S1. Illustration (using fabricated data) of the kernel density estimation procedure. **A)** The individual data (i.e., the eigenvalue spectra for each subject) to be transformed. **B)** The spectra are converted to a binary representation of the presence of eigenvalue peaks at each frequency. **C)** Gaussian distributions (dotted lines) that center on the individual peak frequencies are constructed. The sum of the Gaussian distributions, normalized by the number of peaks, is the KDF (black line).


P > IM around α (10.0 Hz)
S01 10.0 Hz
S03 10.5 Hz
S04 11.5 Hz
S06 8.3 Hz
S07 10.5 Hz
S08 10.5 Hz
S09 11.0 Hz
S11 10.1 Hz
S14 11.6 Hz
S15 11.5 Hz
S16 8.8 Hz
S17 11.1 Hz
S18 9.1 Hz
S19 9.5 Hz
S20 8.8 Hz
S23 11.0 Hz
S24 11.0 Hz
S25 10.0 Hz
S26 10.0 Hz
S28 10.5 Hz
S29 9.5 Hz
P1
P2
IM
± 4.6 dB
± 4.3 dB
± 5.6 dB
± 8.2 dB
± 3.7 dB
± 3.6 dB
± 4.0 dB
± 3.6 dB
± 5.2 dB
± 3.5 dB
± 2.5 dB
± 3.0 dB
± 2.9 dB
± 3.0 dB
± 3.2 dB
± 5.1 dB
± 4.8 dB
± 3.2 dB
± 9.7 dB
± 5.8 dB
± 4.0 dB
80 Hz
4 Hz
Time (s)
Component peak frequency
Time window onset
Time window offset
dB
min
0
max

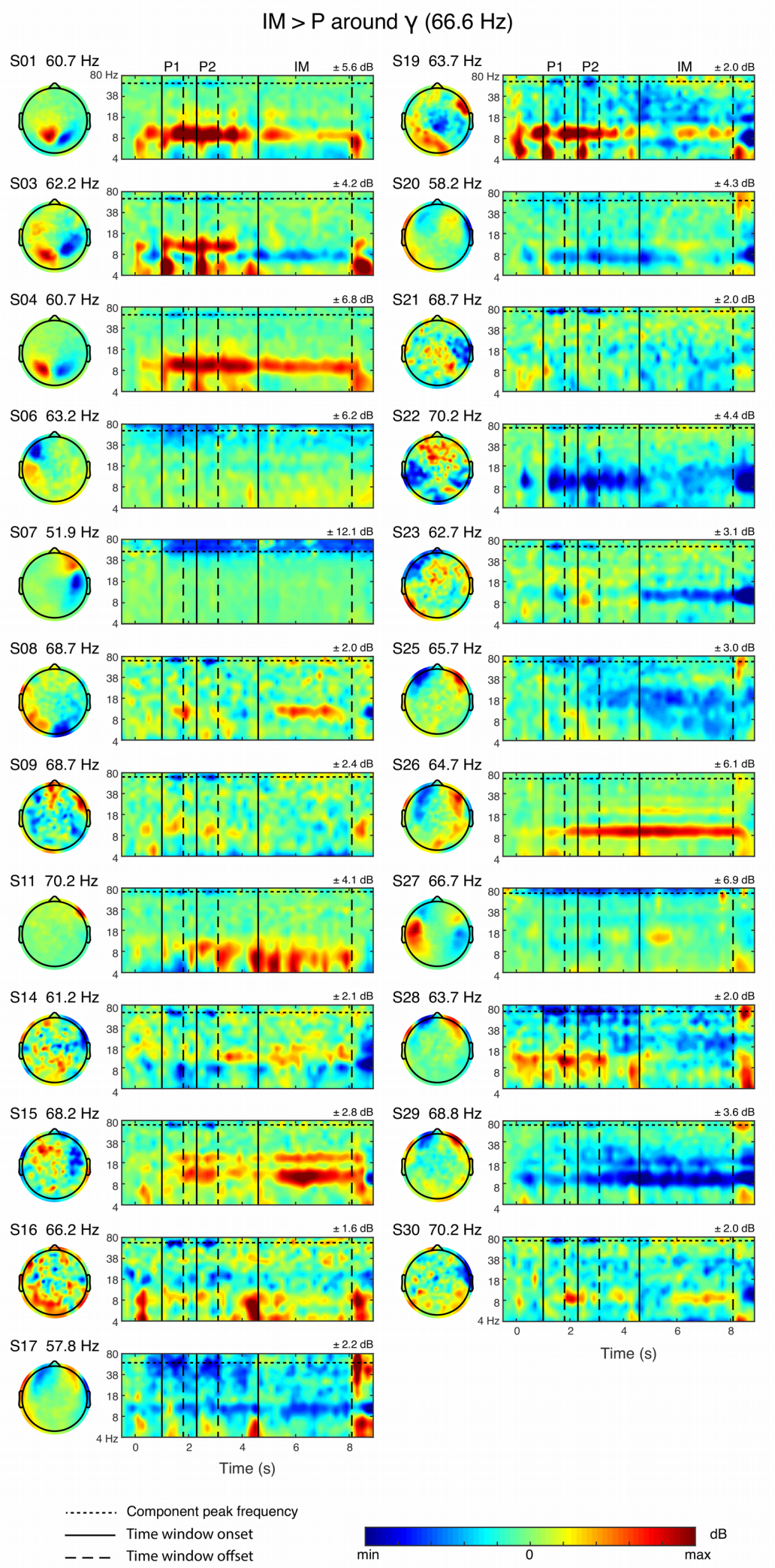
Supplementary Figure S2. Individual subjects' P > IM components around 10 Hz were diverse, but exhibited partial consistency in topography and time-frequency dynamics. Component spatial filters commonly captured an occipital topography. Components were characterized by alpha power increases during perception, alpha power decreases during imagery, or a combination of both. Horizontal dotted lines mark the filtering frequency at which each component was found. Vertical lines mark time window onset (solid) and offset (dashed), corresponding to the stimulus presentation for perception time windows (P1, P2) and the instructed imagery duration for the imagery time window (IM).


IM > P around α (9.2 Hz)
S01 11.0 Hz
S20 8.3 Hz
S03 8.0 Hz
S22 10.1 Hz
S07 9.5 Hz
S23 8.5 Hz
S08 9.7 Hz
S24 11.0 Hz
S14 8.6 Hz
S25 11.1 Hz
S15 10.2 Hz
S29 9.5 Hz
S18 8.1 Hz
S30 10.0 Hz
S19 8.5 Hz
P1
P2
IM
± 4.2 dB
± 8.1 dB
± 11.4 dB
± 6.6 dB
± 3.2 dB
± 5.0 dB
± 8.3 dB
± 7.7 dB
± 5.8 dB
± 4.0 dB
± 5.7 dB
± 7.8 dB
± 6.1 dB
± 6.7 dB
80 Hz
38
18
8
4 Hz
0
2
4
6
8
Time (s)
Component peak frequency
Time window onset
Time window offset
dB
min
0
max

Supplementary Figure S3. Same as Figure S2 but for the IM > P alpha peak. Component topographies were again commonly associated with an occipital topography. Components were characterized primarily by alpha power decreases during perception, and do not appear to be driven by imagery-related power changes.


P > IM around γ (69.2 Hz)
S01 72.3 Hz
P1
P2
IM
± 3.8 dB
S22 67.2 Hz
± 4.4 dB
S04 68.2 Hz
± 2.8 dB
S23 62.7 Hz
± 2.1 dB
S08 64.7 Hz
± 2.5 dB
S24 75.3 Hz
± 3.1 dB
S09 68.2 Hz
± 2.8 dB
S25 64.2 Hz
± 4.0 dB
S11 70.2 Hz
± 3.5 dB
S26 74.3 Hz
± 5.1 dB
S18 70.8 Hz
± 2.2 dB
S27 69.2 Hz
± 7.6 dB
S19 69.8 Hz
± 4.8 dB
S29 72.3 Hz
± 4.5 dB
S20 61.7 Hz
± 3.4 dB
S30 64.2 Hz
± 2.9 dB
S21 67.7 Hz
± 2.7 dB
80 Hz
38
18
8
4 Hz
0
2
4
6
8
Time (s)
Component peak frequency
Time window onset
Time window offset
dB
min
0
max

Supplementary Figure S4. Same as Figure S2 but for the P > IM gamma peak. Components were characterized primarily by short-lived gamma power increases during perception.


IM > P around γ (66.6 Hz)
S01 60.7 Hz
S03 62.2 Hz
S04 60.7 Hz
S06 63.2 Hz
S07 51.9 Hz
S08 68.7 Hz
S09 68.7 Hz
S11 70.2 Hz
S14 61.2 Hz
S15 68.2 Hz
S16 66.2 Hz
S17 57.8 Hz
S19 63.7 Hz
S20 58.2 Hz
S21 68.7 Hz
S22 70.2 Hz
S23 62.7 Hz
S25 65.7 Hz
S26 64.7 Hz
S27 66.7 Hz
S28 63.7 Hz
S29 68.8 Hz
S30 70.2 Hz
P1
P2
IM
± 5.6 dB
± 4.2 dB
± 6.8 dB
± 6.2 dB
± 12.1 dB
± 2.0 dB
± 2.4 dB
± 4.1 dB
± 2.1 dB
± 2.8 dB
± 1.6 dB
± 2.2 dB
± 2.0 dB
± 4.3 dB
± 2.0 dB
± 4.4 dB
± 3.1 dB
± 3.0 dB
± 6.1 dB
± 6.9 dB
± 2.0 dB
± 3.6 dB
80 Hz
38
18
8
4 Hz
0
2
4
6
8
Time (s)
Component peak frequency
Time window onset
Time window offset
dB
min
0
max

Supplementary Figure S5. Same as Figure S2 but for the IM > P gamma peak. Components were characterized primarily by short-lived gamma power decreases during perception, and do not appear to be driven by imagery-related power changes.