Co-modulation of spectral power between maximally independent brain sources

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INTRODUCTION

It has been known since the first days of EEG research that the brain tends to oscillate at certain frequencies more than others. One such frequency band is the well-known alpha (~8-12 Hz) band which manifests with a slightly different peak frequency across subjects, and typically across scalp locations. The significance of the inter-subject difference is a disputed topic, some reporting improvements in performance to be associated with higher alpha frequencies (Klimesch et al., 1993) and others contending that there is no quantifiable advantage to having a faster mean alpha frequency (Posthuma et al., 2001).

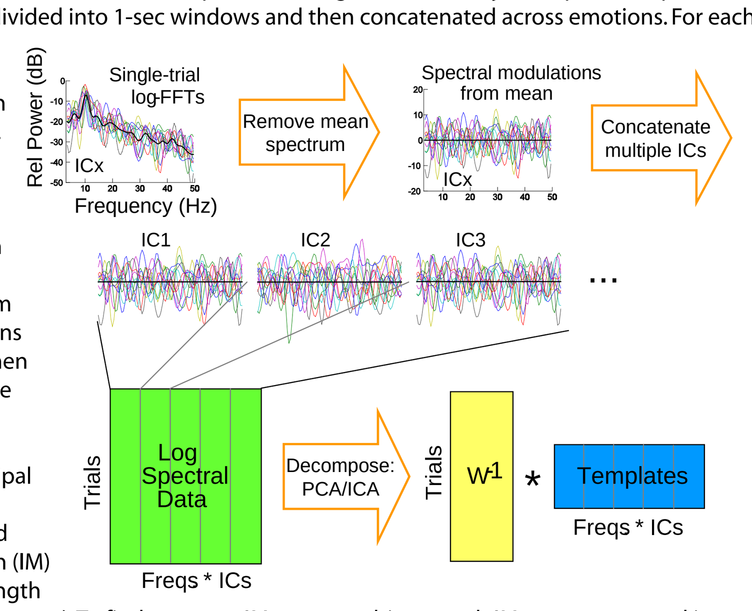
Regardless of the cognitive or behavioral consequences of alpha frequency, the fact that inter-individual differences are so prevalent presents a significant obstacle to frequency-domain EEG data analysis. This issue is frequently addressed in EEG literature by creating frequency bins relative to each subject's individual mean alpha frequency (IAF) (Doppelmayr et al., 1998), defined as the mean power spectrum from all scalp electrodes. Using this method, three alpha sub-bands have been defined and correlated to cognitive processes (Klimesch, 1997; Klimesch et al., 1997). Generally, the upper alpha band (IAF +) is associated with specific cognitive demands such as semantic memory while the lower alpha bands (IAF -) are associated with non-specific attentional load (Klimesch et al., 1998; Klimesch et al., 1999). This model assumes that the 'peak' alpha frequency is not a constant value but may be slightly higher or lower depending on the time period studied (Klimesch et al., 1993). This variability at the scalp electrodes could be explained by at least two different processes. First, multiple EEG sources projecting to the same channel with comparable strengths may express unique frequency characteristics that differ from one another by 1 Hz or more. If this were the case, a decrease in power of one but not the another alpha source would result in a shiftin the power spectrum recorded on the scalp. For example, a single EEG source with a relatively fast alpha frequency might be blocked during a semantic memory task while other sources would be unaffected. Else, each EEG source may produce alpha activity at vaying frequencies, possibly for specific cognitive or behavioral purposes. Both of these options are theoretically possible and also not mutually exclusive.

METHODS

Young adults from the San Diego area (male: 14, female: 20; age range: 18-38 (25.5 ± 5)) were guided through a series of emotional scenarios by a pre-recorded auditory narrative. Emotions were introduced with a short suggestion (~15-30 sec) of possible scenarios in which the emotion might arise and associated bodily sensations that might occur for the given emotion. Then during a self-paced silent period subjects attempted to imagine a suitable scenario, real or imaginary, and to experience the suggested emotion. Subjects were asked to maintain each emotional state for ~3-5 min. Data presented here were extracted from these emotional imagination periods

EEG data were submitted to extended infomax ICA (Lee et al., 1999) using the binica (Makeig et al., 1997) in the EEGLAB toolbox (Delorme, 2004).

For each subject, data were extracted from event-free periods during which the subjects reported experiencing the requested emotion. This data was divided into 1-sec windows and then concatenated across emotions. For each selected independent component (IC) process, a fast fourier transform (FFT, Welch method) was performed on each 1-sec window between 1 Hz and 50 Hz. The result of this decomposition was transformed into log power (dB = 10*log10(power)). For each component, the mean power spectrum was removed from each epoch so that only variations from the mean spectrum remained (see diagram). Power variations for 10-20 selected components were then concatenated to yield a matrix with size (windows by frequencies * ICs). The resulting matrix was submitted to ICA after removing all but the first 15 principal dimensions of the data by principal component analysis (PCA). ICA returned 15 maximally independent modulation (IM) modes or templates, as well as the strength of each IM in each time window (see diagram). To find common IMs across subjects, each IM was represented its IC template with the highest root mean squared value. In most cases, if an IM included spectral modulations from more than one IC, the modulation shapes were identical but of varying relative magnitude. Thus, each IM was reasonably well-represented by a single spectral modulation pattern. ICs of an IM that expressed the same activity with lesser relative magnitude were labeled as 'comodulated' when the dot product between their IM spectral pattern and the IM template was more than 50% the value of the template with itself. IM clusters were then found by calculating the Euclidean distance between these IM templates and using the Matlab linkage and dendrogram functions to find clusters.



1. IC contributions to the mean power spectrum at the scalp

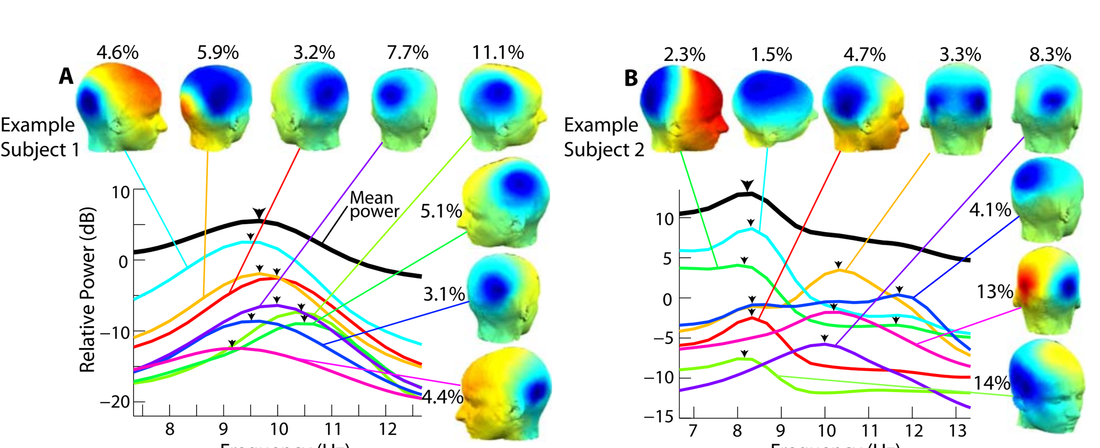


Figure 1. EEG activity recorded at scalp electrodes mixes activity from many EEG sources, each of which may have a distinct mean alpha band peak frequency. The thick black traces show the mean power spectrum for one subject, averaged over all time windows and scalp channels. Colored traces present the mean power spectra of the indicated independent component (IC) sources, connected to their respective near-dipolar scalp projection maps. For each IC, the percent residual variances unaccounted for by the projection of a single equivalent dipole is given. (A) IC sources contributing to alpha band power of one subject have peak frequencies (arrow heads) between 9.3 Hz and 10.4 Hz. (B) For a second subject, the IC alpha band peak frequencies range between 8.2 Hz and 11.7 Hz).

CITATIONS

Delorme A, Makeig, S. (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics. Journal of Neuroscience Methods 134:9-21.

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2. Log-spectral decomposition finds independent modulation (IM) templates

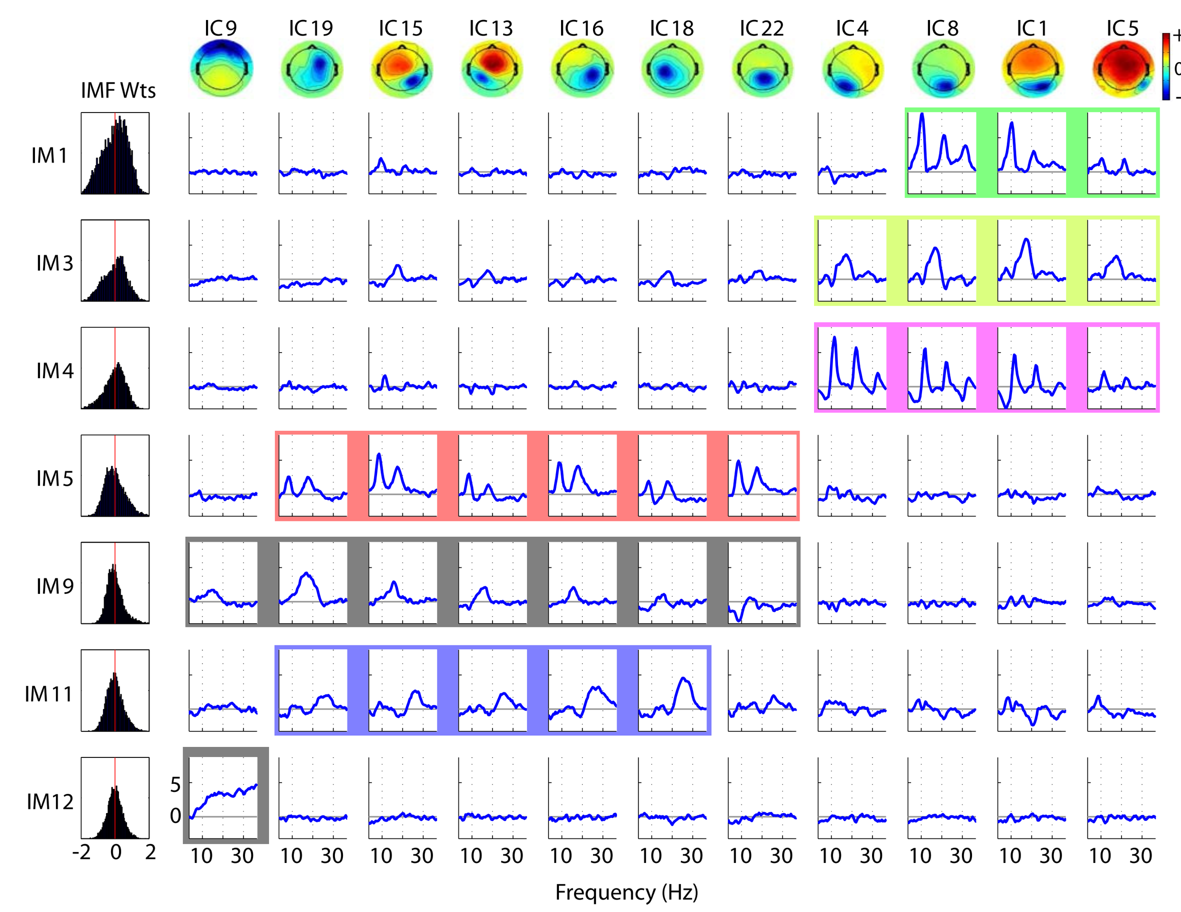


Figure 2. Spectral decomposition for one subject showing 7 of the 15 IMs produced by log-spectral decomposition. Each row represents an independent IM and each column a different IC. Thus, each IM contains a modulationtemplate for every IC, though often times a particular contribution may be near zero. The colored boxes indicate the significantly comodulated ICs for the different IMs. Many IMs show comodulation between ICs, while IM 12, comprises significant non-zero modulations for only one IC.

3. Moment-to-moment power fluctuations for a single subject and IC

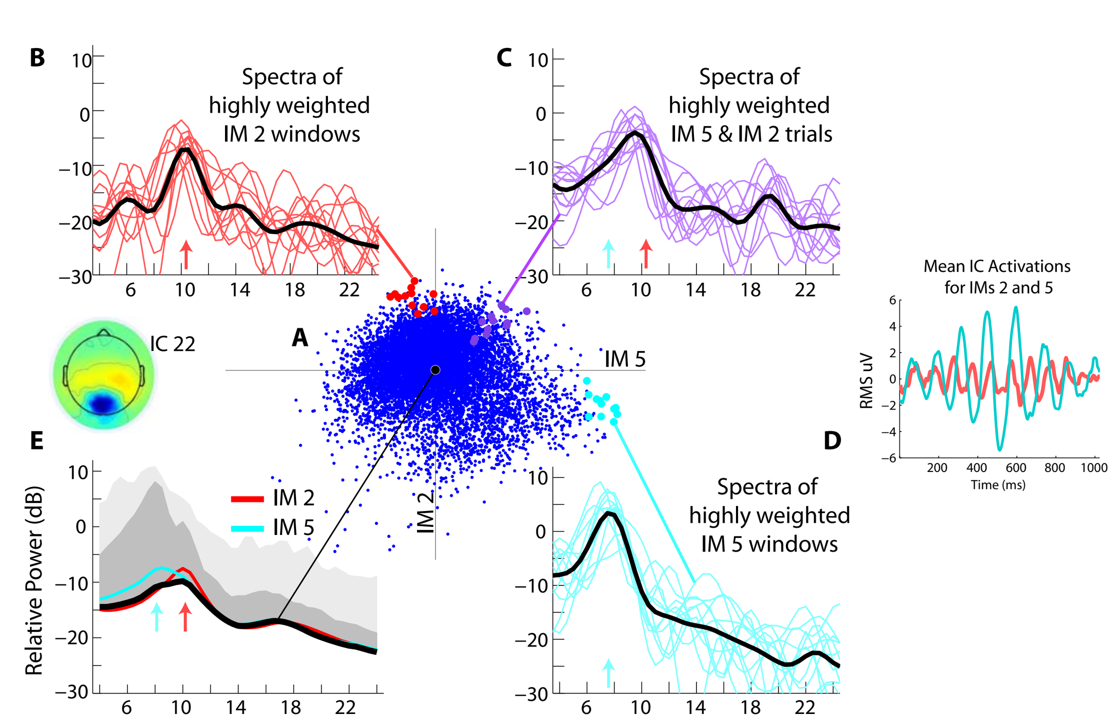


Figure 3. Variability of IC alpha band peak frequency in single time windows. (A) Scatter plot of IM window weights of two IMs for a central parietal IC (scalp map, left). Larger, colored dots represent the time windows whose spectra are plotted in panels B-D. (B-D) Power spectra for time windows with largepositive weights (colored traces) for IM2 (B), IM5 (D), or both IM2 and IM5 (C). Black traces show the mean spectra for the illustrated windows. Note thedifferences in alpha band peak frequency. (E) Mean IC22 power spectrum (black trace), mean IM2 and IM5 contributions (red and blue traces). Note the relation of mean power in the alpha band to the two IM spectra. *Grey outlines*: spectra of the whole (light grey) and PCA-reduced (dark grey) IC22 data. Note again the appearance of the two alpha band peak frequencies (near 8 Hz and 10 Hz).

4. independent modulation (IMs) separate variations from the mean log power spectrum

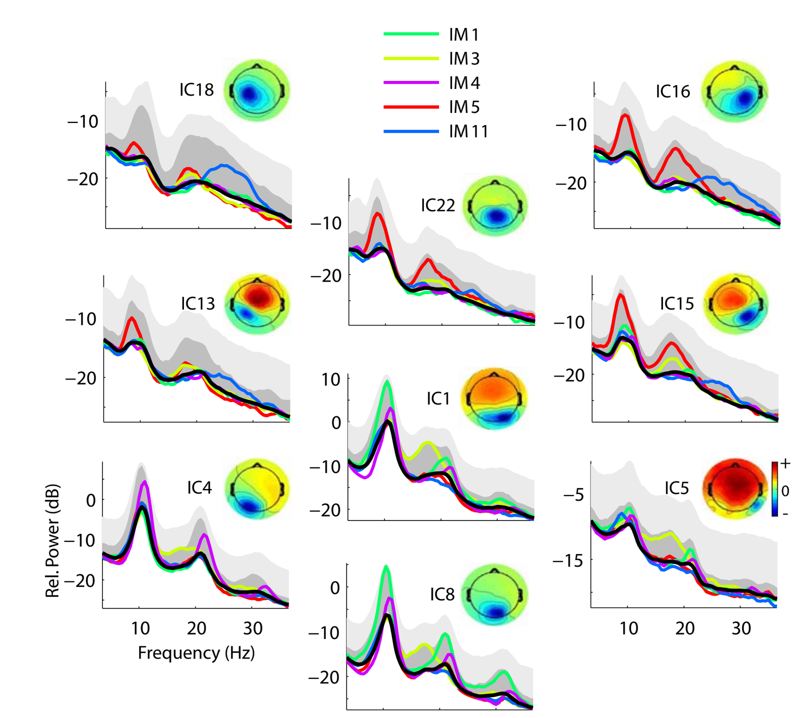


Figure 4. Contributions of five selected IMs to selected ICs (same subject as in Fig. 1). *Black traces*: IC mean power spectra. Grey outlines: 98th percentile window spectra for the whole (light grey) and PCA-reduced (dark grey) IC data. *Colored traces*: Contributions of the IMs to the 98th percentile data (dark grey). The IMs indicate which portions of the frequency spectra vary independently, for example (IC16, upper right) beta/gamma power (20-40 Hz) versus harmonically linked alpha and beta power (near 9 Hz and 18 Hz). Alpha and beta power variations across the ICs are modeled by four IMs (IM5, IM1, IM3, IM4) with slightly different alpha band peak frequencies (e.g., IC1) that may alternately or jointly affect the power spectrum of a particular time window.

5. Relative pattern and strength of IM templates across ICs

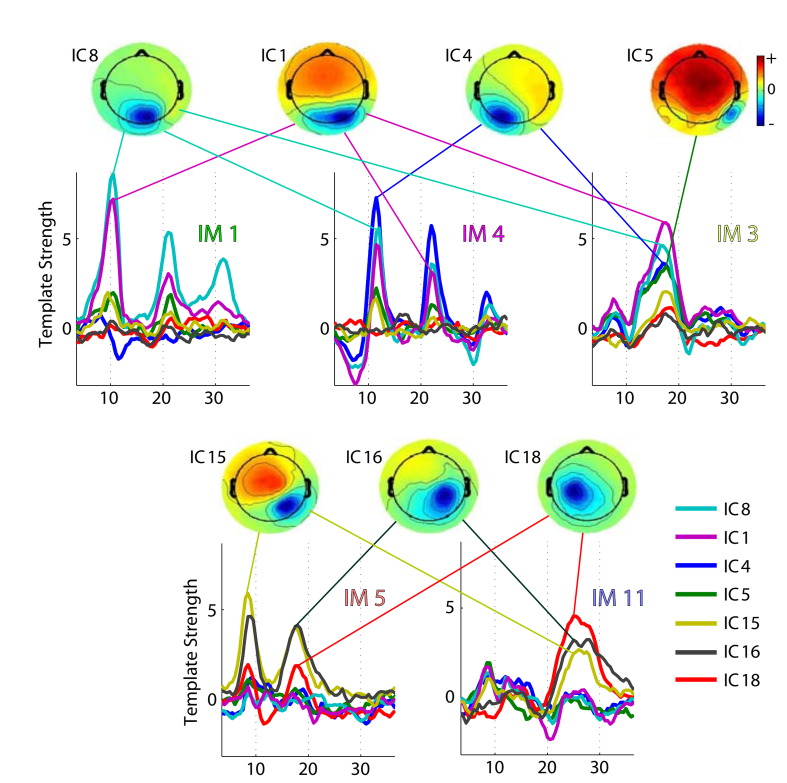


Figure 5. Differences in the relative strengths of IM contributions to individual IC processes. *Top row*: Actions of three IMs on power spectra for four posterior ICs (cf. Fig. 2). Note the difference in alpha band peak frequencies (10-11 Hz), the prominent harmonic modulations (20-22 Hz), the dominant beta (ca. 14 Hz) activity in IM3, and the compensatory decrease in low-alpha (< 10 Hz) activityin IM4, an 'alpha shift' IM. Each IM contributes most strongly to a different IC and comodulation occurs between different combinations of ICs. *Bottom row*: Effects of low-alpha (9-Hz) IM5 and high-beta (20-30 Hz) IM11 on three lateral central ICs.

6. Clusters of similar IMs appear across subjects

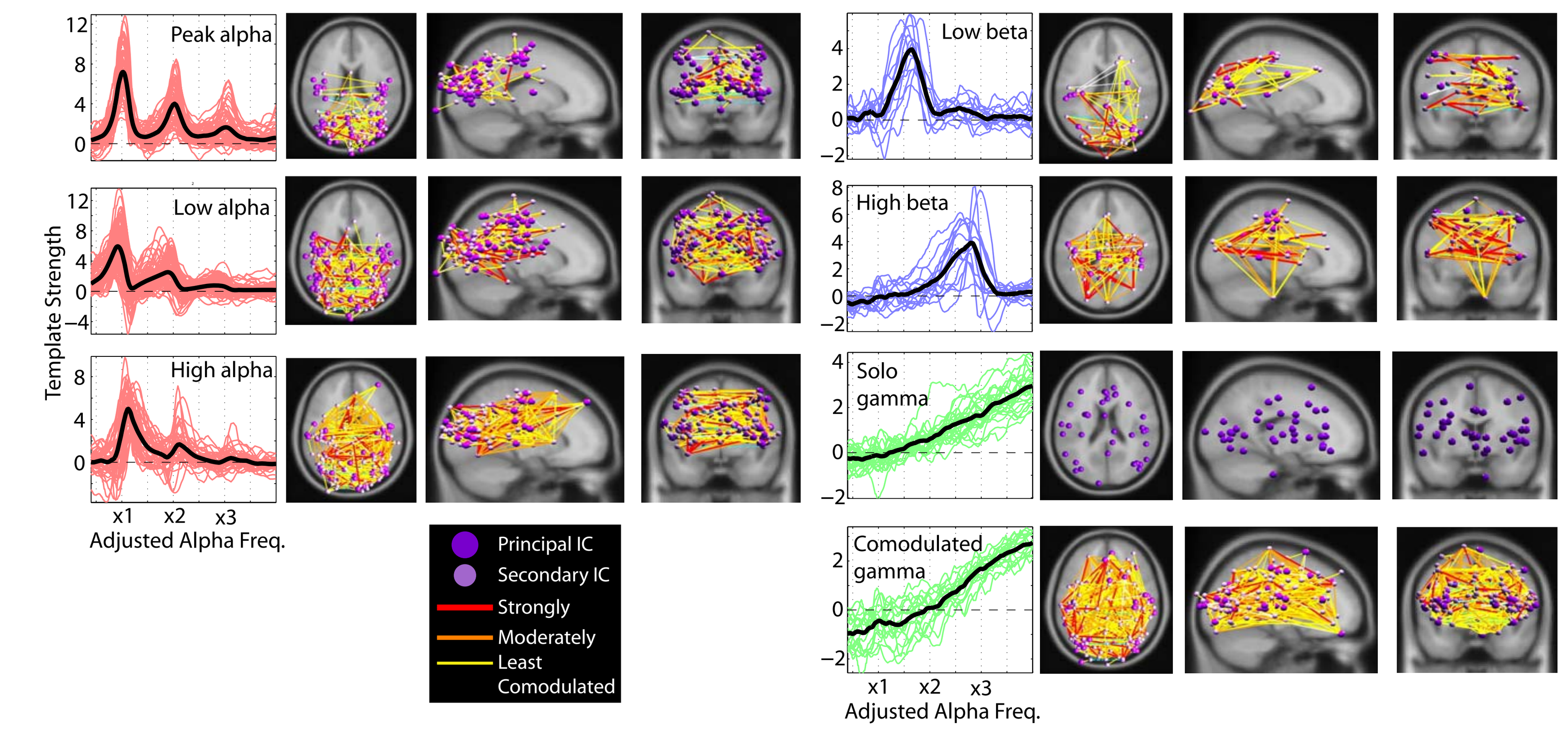


Figure 6. IM clusters. IMs for the 33 subjects were clustered based on similarities in their normalized frequency templates. IM template frequency axes were stretched to align the individual subject scalp mean alpha band peak frequency to 10 Hz ('x1'). Next, the strongest normalized IC templates for each IM were clustered by Euclidean distance (see methods), producing the 7 IM clusters shown here. Colored traces are frequency-normalized IM templates and their mean (black traces). MRI images display 3-D distribution of equivalent dipoles locations for principal (purple balls) and secondary (smaller balls, see legend) ICs for individual IMs. Colored lines connect comodulated ICs for the same IM (see legend). *Alpha clusters* (left, red): Three alpha modulation clusters affecting alpha band activity at, below, or above the alpha band peak frequency (x1) respectively. *Beta clusters* (upper right, blue): Two beta band IM clusters. *Gamma clusters* (bottomr right, green): Two broad-band or gamma band IM clusters that affect either just one (Solo) or multiple (Comodulated) ICs. Note the difference in IM templates (left) for these two clusters.

7. Dipole density differences between clusters

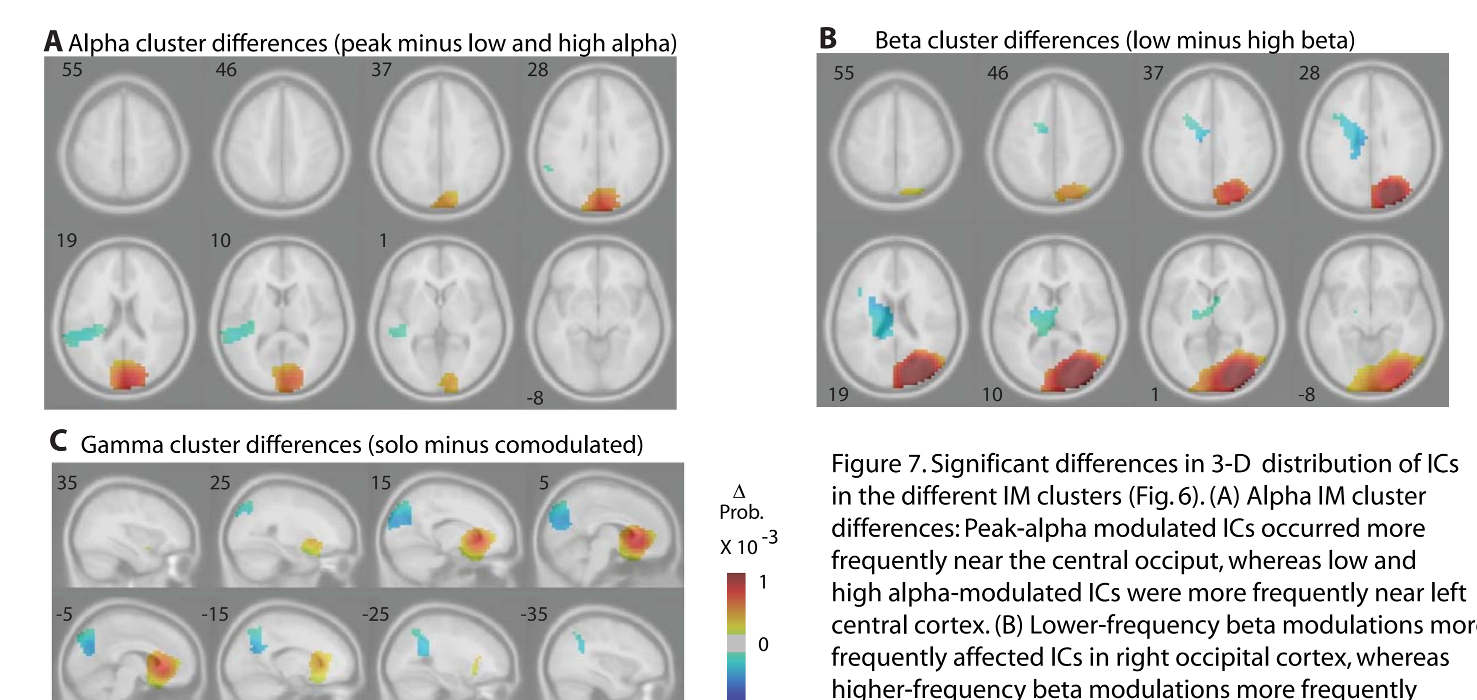
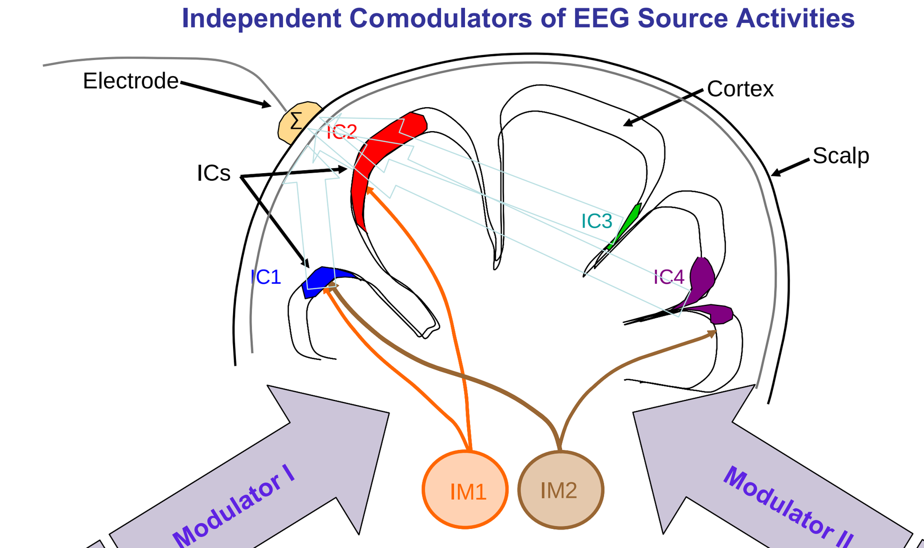


Figure 7. Significant differences in 3-D distribution of ICs in the different IM clusters (Fig. 6). (A) Alpha IM cluster differences: Peak-alpha modulated ICs occurred more frequently near the central occiput, whereas low and high alpha-modulated ICs were more frequently near left central cortex. (B) Lower-frequency beta modulations more frequently affected ICs in right occipital cortex, whereas higher-frequency beta modulations more frequently affected ICs with equivalent dipoles in left central cortex. (C) Solo gamma or broad-band IM clusters more often accounted for activity in ICs with equivalent dipoles in or near sub-genual medial cortex during the emotional imagination task, whereas co-modulated gamma or broad-band IMs more often affected ICs with equivalent dipoles located in left and right parietal cortex.

8. Conclusions



We suggest that the observed comodulations between ICs may be the product of separate neuromodulators (IM1 and IM2 in diagram). Each modulator projects to a unique set of cortical areas that may each be innervated by more than one modulator system. In this way, several source areas may be simultaneously induced to oscillate at the same frequency. Oscillatory activity may be mixed in cortical source areas that receive input from more than one neuromodulator (see 'IC1' above).

- Mean individual alpha frequencies (IAF) at scalp electrodes may represent the sum of ICs with variable peak frequencies
- Decomposition of IC log-spectral activities reveals independent modulations of IC power
- Mean IC spectra are composed of various modes of oscillatory activity
  - independent modes of a single IC may express power at neighboring frequencies independently (ie, 10 Hz and 11 Hz)
  - IMs also reveal independent modulation of non-alpha frequencies, (ie, 14 Hz)
- IM analysis indicates stable patterns of spectral comodulation between various combinations of ICs
- Independent modulation analysis can also be applied in event-related paradigms to describe single-trial dynamics following experimental stimuli or behavioral responses

Human Brain Mapping, Florence, Italy, 2006