Frequency space organization of the brain

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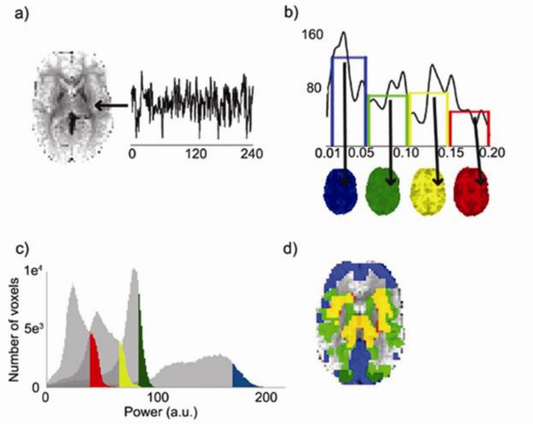
INTRODUCTION

- The brain is organized based on multiple anatomical and functional features.
- Frequency-specific oscillatory activity in the brain has been associated with different functions, however structural localization of such activity has remained elusive.
- Here, we present evidence of frequency-specific organization of the brain based on activity captured through functional magnetic resonance imaging (fMRI), and we show that certain frequency bands of activity may be related to specific functions.

METHODS

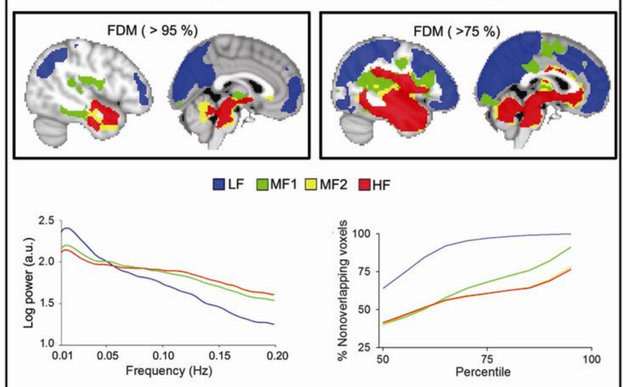
- Whole-brain functional MR data was acquired with a 3T Siemens Trio whole-body scanner on 17 healthy subjects (9 females, 8 males; average age = 36.6 years, SD = 8.5 years). Each scan was 10 minutes long and subjects performed no task other than to stay awake with their eyes open.
- Time-series of the BOLD signal was extracted at every voxel (Panel 1a). Frequency power of the BOLD signal at each voxel was determined using Welch's method and the average power at four frequency bands (LF: 0.01-0.05 Hz, MF1: 0.05-0.10 Hz, MF2: 0.10-0.15 Hz, and HF: 0.15-0.20 Hz) made up 4 different maps for each subject (Panel 1b). The power distribution at each frequency band was thresholded to show only the voxels with the highest power (Panel 1c). A frequency distribution map (FDM) was made for each subject (Panel 1d).
- Subject maps were transformed into standard space using FSL's FLIRT and multiplied by a standard gray matter mask to create an average map across subjects (Panel 2) and determine the frequency content of each brain area (Panel 3).
- We performed this analysis on both the entire brain and on isolated resting state networks (RSNs) to examine the frequency-space distribution of BOLD activity within networks (Panel 4). Functional connectivity was assessed within frequency bands of the DMN (Panel 5).

1 Method for generating frequency distribution maps



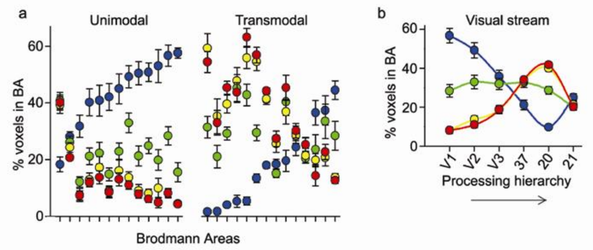
Method for generating frequency distribution maps. a) BOLD fMRI time-series are extracted at each voxel. b) Time-series data are Fourier-transformed into frequency space. Power at 4 different frequency bands (0.01-0.05, 0.05-0.10, 0.10-0.15, 0.15-0.20 Hz) is averaged and assigned to each voxel, generating 4 frequency distribution maps for each subject. c) Histograms for each frequency band are generated and power distributions are thresholded . d) An example of a thresholded frequency distribution map for a single subject. Maps are transformed into standard space and averaged across subjects (panel 2).

2 Spatial structure of BOLD signal frequency bands for the resting brain



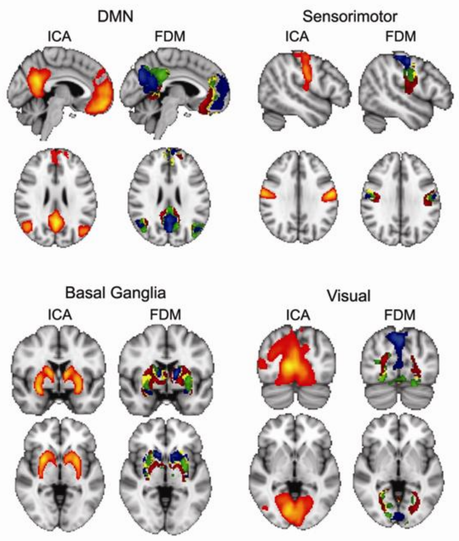
Frequency distribution of BOLD signal reflects anatomical and structural organization. *Upper panels*) FDMs at 2 different thresholds. Notice LF is restricted primarily to the association neocortex of the frontal and parietal regions, while higher frequencies are present in subcortical, temporal , and limbic regions. *Lower panel, left)* Average power spectrum of the entire brain for the 4 frequency bands. MF2 and HF are overlapped in this plot. *Lower panel, right)* Unique voxels within each frequency band as a function of percentile threshold. In general, as threshold increases, the number of non-overlapping voxels across frequency bands increases. The upper plots illustrate this, as the 95th percentile threshold clearly shows less overlapping of frequency bands than the 75th percentile.

3 Frequency characteristics of Brodmann areas are related to function



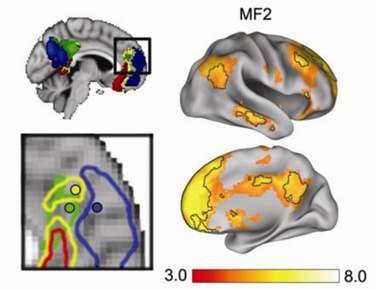
Distribution of BOLD signal power for the four frequency bands across Brodmann Areas (BA). *Left)* Mean power for each frequency band is shown for 27 BA-s, rank ordered by power in lowest frequency band, LF. BAs classified as unimodal and transmodal are shown (Mesulam, 1998). Unimodal BAs encode basic sensory features, while transmodal BAs have more complex anatomical and functional properties. Transmodal BAs are primarily high frequency, whereas unimodal BAs are dominated by low frequency. *Right)* Visual-cortical BAs are arranged in order of processing hierarchy. There is an overall decrease in LF and increase in MF2 and HF proceeding down the visual processing stream.

4 Resting state networks exhibit unique BOLD frequency distribution



FDMs for different resting state networks show unique distribution. Four resting state networks were determined using independent component analysis (*left panels*). Spatial structure of frequency distribution appears to be unique for each network (*right panels*). The analysis performed within network is identical to that performed for the entire brain.

5 Functional connectivity within the DMN is distinct for each frequency band



Neighboring areas of different frequency content exhibit frequency-specific connectivity. *Upper left)* 95th percentile FDM within the default mode network. The inset shows the location of functional connectivity seeds, all within non-overlapping regions of 3 different frequency bands and located within 5mm of each other in the MPFC. *Right)* Yellow regions indicate average functional connectivity across all subjects for the high-frequency MF2 seed. The black outline contours represent regions where connectivity was common across all frequency bands. While connectivity with the low frequency region returns the DMN, connectivity with the high-frequency MF2 seed shows more expansive connectivity, including connections to regions of higher-frequency dominance.

CONCLUSION

- The brain is organized based on frequency characteristics of the fMRI BOLD signal. At the whole-brain level low frequencies reside in neocortical association regions, and high frequencies are more dominant in temporal, subcortical, paralimbic, and limbic cortices.
- Brodmann areas associated with primary sensory functions tend to be dominated by low frequency, while more diverse and anatomically complex regions are higher frequency.
- At the RSN level, frequency band distribution reflects anatomical and functional organization, with each network exhibiting distinct frequency structure.
- We suggest frequency space as a new domain for organization of the brain.

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