CORTICAL NETWORKS UNDERLYING EEG ALPHA FREQUENCIES DURING REST

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DECLARATION BY CANDIDATE

I, **Tanmay Singhal** hereby declare that the work presented in the dissertation report entitled '*Cortical networks underlying EEG alpha frequencies during rest'* was carried out by me under the guidance of **Dr. Arpan Banerjee, National Brain Research Centre (Deemed to be University), Manesar, Haryana, India**. I declare that no part of the thesis contains any plagiarised material. Any previously published or other material sourced from anywhere else has been appropriately attributed to the source. I also declare that no part of this thesis has been previously submitted for the award of any degree of diploma to National Brain Research Centre (Deemed to be University) or to any other university.

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ABSTRACT

Studies on functional connectivity have largely been limited to fMRI based measures. However, this method has poor temporal resolution and an indirect relationship to electrical activity. Thus there is a need for EEG-based measures of directed functional connectivity, which would resolve both issues.

In the present study, we investigate open-eye resting state EEG data for the presence of networks in alpha frequency range. A power-spectral density analysis revealed alpha bands to be prominent primarily in the occipital regions. These were source-localised using sLORETA to specific anatomical brain regions. Implementation of Granger Causality revealed directed functional connectivity between brain regions—previously associated with the Default Mode Network. These findings suggest activation of DMN components under resting state. In conclusion, this study adds insights into the understanding of neural activity and functional connectivity patterns in the brain during rest, filling a gap in the existing literature on resting state EEG studies.

ABBREVIATIONS

BOLD	Blood Oxygenation Level Dependent
DMN:	Default Mode Network
EEG:	Electroencephalography
fMRI:	Functional Magnetic Resonance Imaging
GC:	Granger Causality
GCA:	Granger Causality Analysis
ICA:	Independent-Component Analysis
RSN	Resting State Network
sLORETA	Standardized LOw Resolution brain Electromagnetic TomogrAphy

AIMS AND OBJECTIVES

1) To investigate sources of alpha frequency during the resting state
2) To identify resting state networks associated with alpha frequency

CHAPTER 1

INTRODUCTION

1.1 Electroencephalography

EEG is a reflection of the accumulation of excitatory and inhibitory postsynaptic potentials at the dendrites of groups of parallel-oriented neurons (Cohen, 2014). Ionic flow across the membrane leads to generation of an electric field around the neuron. The electric field generated around a single neuron cannot be captured by electrodes because the magnitude is not high, therefore, the electrical activity recorded by the scalp electrodes in EEG is the synchronous activity of an ensemble of neurons. EEG was invented in 1929 by a German psychiatrist Hans Berger (Hans Berger (1873-1941)—the History of Electroencephalography], 2005). It is a non-invasive brain-activity recording technique, which has high temporal resolution—providing insight into brief oscillatory changes in the neuronal populations.

EEG signals can be classified into different waves based on the spectral characteristics and their association with different cognitive modalities. They can be characterized into the following; Alpha waves (7-12 Hz), Beta waves (13-30 Hz), Gamma waves (30-100Hz), Theta waves (4-7 Hz) and Delta waves (0.5-4 Hz). EEG has its applications in research, and in clinical setups as it can be used for the diagnosis of several neurological disorders. It can be used to monitor brain activity during seizures in case of disorders like epilepsy. It can be used to monitor normal brain functioning during different stages of arousal such as wakefulness, sleep, etc. It has diagnostic utility in detecting brain associated disorders.

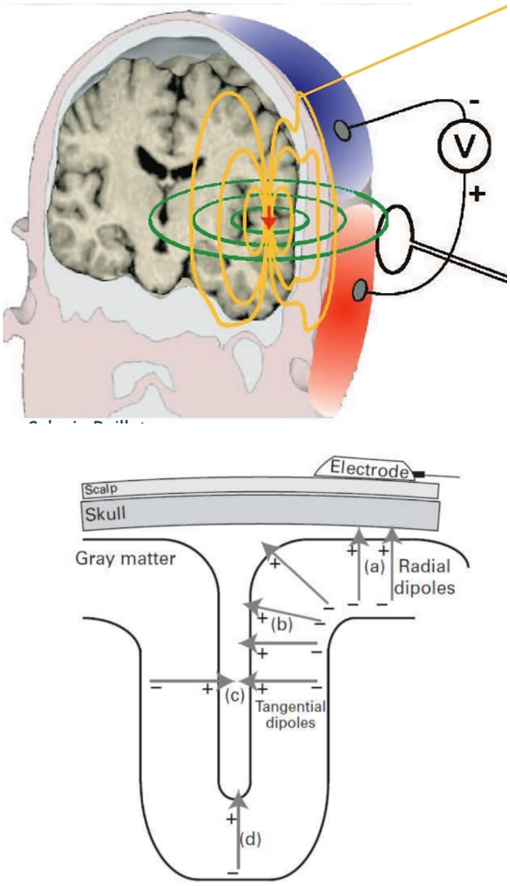

Fig 1: Electrophysiological aspects of EEG and Dipoles responsible for generating EEG and MEG signals. *Adapted from Mike X Cohen (2014), Analysing neural time series data*

1.2 The Resting State

"The fact that the body is lying down is no reason for supposing that the mind is at peace. Rest is… far from restful."
 - Seneca

A plethora of research previously conducted on brain function has exclusively focused on brain function during tasks. This can give us a robust understanding on the organisation and functioning of brain areas, but it ignores the fact that the brain has an intrinsic activity which in itself is a rich source of information (Raichle, 2015). At rest, the brain shows spontaneous fluctuations in the BOLD response even in the absence of a specific, task-based stimulus (Fox & Greicius, 2010); such patterns are referred to as *resting state networks* (RSN). Identification of resting state networks has been previously done using resting-state fMRI studies. These networks are associated with slow fluctuations in BOLD signals and not only appear both during rest and during tasks (Niazy et al., 2011).

The nomenclature of resting state networks depends on their topologically corresponding counterparts. Hence, the networks seen in the resting state are; Default Mode Network (DMN), the Dorsal Attention Network (DAN), the Somato-Motor Network (SMN) and the Visual Network (VN). While fMRI has excellent spatial resolution, the BOLD response is an indirect correlate of neural activity. Hence, looking at resting state networks using EEG provides us with the capability to directly measure neural oscillations with the added benefit of having a higher accuracy with respect to temporal resolution (Samogin et al., 2020). In addition to this, the EEG setup is cheaper and portable than MRI which allows experimentation on a larger number of healthy and diseased participants (Pirovano et al., 2022).

With regards to RSNs, extensive studies have been conducted on the *default mode network* (DMN). The DMN is associated with self thought and idling in the absence of an attentive state (Rosazza & Minati, 2011). The structural connectivity maps onto the functional connectivity when it comes to the DMN. fMRI and DTI studies have identified three regions primarily active in the DMN; the area comprising the posterior cingulate cortex (PCC) and precuneus, the medial temporal lobe (MTL), and the medial prefrontal cortex (Vincent et al., 2010). The DMN is active in the resting state as compared to task-related activity (Smith et al., 2018). The functional connectivity in the resting-state network changes with the level of arousal. For instance, the functional connectivity between hippocampus and DMN drops during slow wave sleep (Snyder, 2015). The activity of the DMN is also highly dependent on the nature of the task performed before data acquisition (Rosazza & Minati, 2011).

Another network of interest in the resting state is the *ventral attention network* (VAN) due to its ability to regulate attention towards behaviourally irrelevant stimuli. It has the ability to detect unattended and unanticipated stimuli and guide the dorsal attention network as to where it should utilize its attentional resources (Bavelier & Green, 2019). The VAN consists of the inferior frontal cortex, the temporal-parietal junction (TPJ) and the anterior insular region. The temporoparietal junction is responsible for sustained attention while the anterior insula works as a salience detector (Krall et al., 2014). In mild traumatic brain injury, changes have been observed in the VAN thus highlighting the role of VAN in serving as a marker for the pathology (Borich et al., 2015).

Although studying the resting state might seem counterproductive at first glance, it provides rich information of changes in functional connectivity particularly, during pathological conditions like schizophrenia, bipolar disorder and depression (Fox & Greicius, 2010). Functional connectivity refers to synchrony existing between brain regions that are far apart whose activity is statistically dependent on each other. It can give us crucial information on how distal brain regions communicate without being anatomically linked (Babaeeghazvini et al., 2021). However, in order to attempt understanding the changes in connectivity in diseased conditions, we first need to build a robust understanding of the functional connectivity observed in healthy individuals at the resting state.

1.3 Alpha Oscillations

During the resting state the regions of the human cortex show oscillations at 7-12 Hz; these oscillations are alpha oscillations which can be measured by EEG and MEG (Klimesch, 2012). Alpha oscillations were first discovered in 1929. It is the most dominant and resonant frequency in the awake, conscious brain (Klimesch, 2012). The primary source of alpha in the brain is thought to be the thalamus (Halgren et al., 2019).

The alpha rhythm has typically been characterized as a form of 'idle' activity as it was first observed in posterior electrodes when eyes are closed (Klimesch, 2012). Alpha rhythm is prominent over occipito-parietal cortices during a state of wakefulness (Klimesch, 2012).

A plethora of evidence has been accumulated which suggests that alpha oscillations play a pivotal role in working memory and attention (Wianda & Ross, 2019). One of the major ways by which alpha oscillations play a major role in attention is by inhibiting unattended stimuli (Händel et al., 2011). This indicates that alpha is primarily involved in attentional allocation in the brain and its power increases in regions which need to be suppressed during attention. Interneurons' GABAergic feedback has been strongly linked to the physiological process generating the alpha rhythm.

Alpha oscillations play a prominent role in resting state networks (Goldman et al., 2002). The brain regions involved in the default mode network (DMN) such as posterior cingulate cortex, precuneus, bilateral superior frontal gyrus and the medial frontal gyrus have shown positive correlation with alpha. The angular gyrus, which is an important region of the DMN, is involved in the modulation of alpha rhythm (Capotosto et al., 2014). Thus, alpha oscillations are one of the most prominent brain waves associated with the resting state and studying them using EEG can provide us with a vast amount of information on the functional organisation and synchronization of different brain areas in maintaining intrinsic homeostatic activity during rest.

An argument can be made that a common generator exists that produces oscillations throughout the brain to increase connectivity across all regions. For this to take place, the alpha generator must be highly connected to other brain regions. One such region is the thalamus, which has been suggested to produce alpha activity that propagates throughout the resting state network. (Halgren et. al., 2019).

1.3.1 Networks in the Alpha frequency range

Several studies have been performed to show that alpha band connectivity is the most prominent during the resting state and associated with default mode network and other *Resting State Networks* (RSN) (Samogin et al., 2020).

The alpha frequency band is prominent during relaxed wakefulness with closed eyes and is typically associated with a state of calmness and reduced sensory processing. Resting state alpha networks are thought to reflect the functional connectivity and communication between brain regions involved in attention, perception, and inhibitory processes. It has been seen that the global topography of RSN does not largely change in presence of extreme perturbations in behavioural states such as anaesthesia or sleep (Deco & Corbetta, 2011).

Alpha oscillations are also shown to have inhibitory functions (Klimesch, 2012). With respect to attention, alpha plays a role in the brain's ability to selectively attend to specific stimuli (Foxe & Snyder, 2011).

A few salient features about alpha oscillations in the resting state are;

1. Externally oriented ***attentional processes*** are associated with a decreased alpha power (Magosso et al., 2019). A task-associated reduction in alpha power is termed as alpha desynchronization (Holling et al., 2011). In contrast to this, there’s an increase in alpha power in absence of a task i.e. resting state (Holling et al., 2014).

2. Alpha band associated connectivity exhibits a high amount of ***inter-individual variability*** (Haegens et al., 2014). Some individuals may show more widespread alpha network connectivity, while others may have weaker or less coherent alpha networks. These individual differences may be related to factors such as age, cognitive abilities, and personality traits (Reineberg et al., 2018). For instance, change in functional connectivity in externally directed and internally directed attention networks has been associated with changes in working memory (Keller et al., 2015).

3. ***Clinically***, disorders of the brain are associated with an alteration in functional connectivity (Fox & Greicius, 2010). Changes in functional connectivity in brain areas in comparison to healthy subjects can be correlated to clinical symptoms and can thus be used as a biomarker for identifying different stages of diseases (Hinkley et al., 2011).

Studying resting state alpha networks provides insights into the brain's intrinsic functional organization and its relationship with attention, perception, and cognitive processes. It offers a valuable tool for understanding brain function and dysfunction, as well as potential applications in clinical research and diagnostics.

Given this diverse role of alpha oscillations, it is important to understand how it dictates the hierarchy of cortical organisation in information processing.

CHAPTER 2

METHODS

2.1 Data Acquisition

The electroencephalography (EEG) data of the participants was collected in Cognitive Brain Dynamics Lab, National Brain Research centre. 60 participants were subjected to a five-minute collection of resting-state EEG data with their eyes open. During this period, a blank screen was displayed on the monitor. The participants were asked to relax or think at free will while viewing the monitor screen placed before them. They were requested to make minimal head, body and eye movements. The experimental environment in the EEG recording room was carefully controlled to ensure consistent levels of ambient noise, light, and other potential disturbances.

Data was collected from two different study sessions.

Session 1

In session 1, behavioural and EEG data were acquired in the EEG recording room from 28 subjects where ambient noise, lights and other interferences were strictly controlled during the experiment to the same levels for all recording sessions. A Neuroscan EEG recording and acquisition system which included an elastic cap (EasyCap) with 64 Ag/AgCl sintered electrodes and amplifier (SynAmps2), was used. The 64-channel EEG signals were recorded according to the International 10–20 system of electrode placement. The reference electrode was present on the z line between Cz and CPz (closer to Cz), grounded to AFz and the impedances of all channels were monitored to be below 10 kΩ. The data were acquired at a sampling rate of 1000 Hz. A Polhemus Fastrak system was used to record the 3D location of electrodes using a set of fiducial points (Cz, nasion, inion, left and right pre-auricular points) while the EEG cap was placed on the participant's head.

In session 2, continuous EEG activity of 32 subjects was acquired in a noise-proof isolated room using a BrainVision Recorder acquisition system consisting of actiCHamp module with 63 active channels placed according to the International 10-20 electrode placement system.

SuperVisc electrolyte gel (EASYCAP) was used to make contact between EEG sensors and the scalp. EEG data were acquired at a sampling rate of 1 kHz, and each sensor's impedance was kept below 10 kΩ. The reference electrode was at the vertex (Cz), and the forehead (AFz) electrode was selected as the ground.

2.2 Data Preprocessing

All preprocessing steps were performed using Brainstorm (a MATLAB-based toolbox).

Raw EEG data was imported to brainstorm where it was first filtered by a band pass filter of 7-12 Hz since we were interested in looking at the networks in the alpha frequency range. After the filtering step, the data was observed and any jitters and abnormal segments from the time series data were removed. Afterwards, an averaged re-referencing was performed. Further, Independent component analysis (ICA) was performed to remove artifacts corresponding to eye blinks, ocular, and muscular movements. Finally, a detrending step removed slow, varying components from the EEG signal.

A bandpass filter is the combination of a high pass filter and a low pass filter. A high pass filter is used to remove low frequencies from the signal; it removes DC offset and the artifacts occurring at low frequencies such as breathing or eye movements. A low pass filter is used to remove high frequencies from the signal; it removes artifacts of higher frequency such as muscle contractions. It is also used to extract out the component of the interest by removing higher frequency components.

Averaged re-referencing was done to avoid any common reference problem by computing the average of signals at all electrodes, and subtracting it from the EEG signal at each electrode.

ICA is used to decompose mixed signals into the independent components. Here ICA was used to identify and remove artifacts from the data, making it more suitable for further analysis steps.

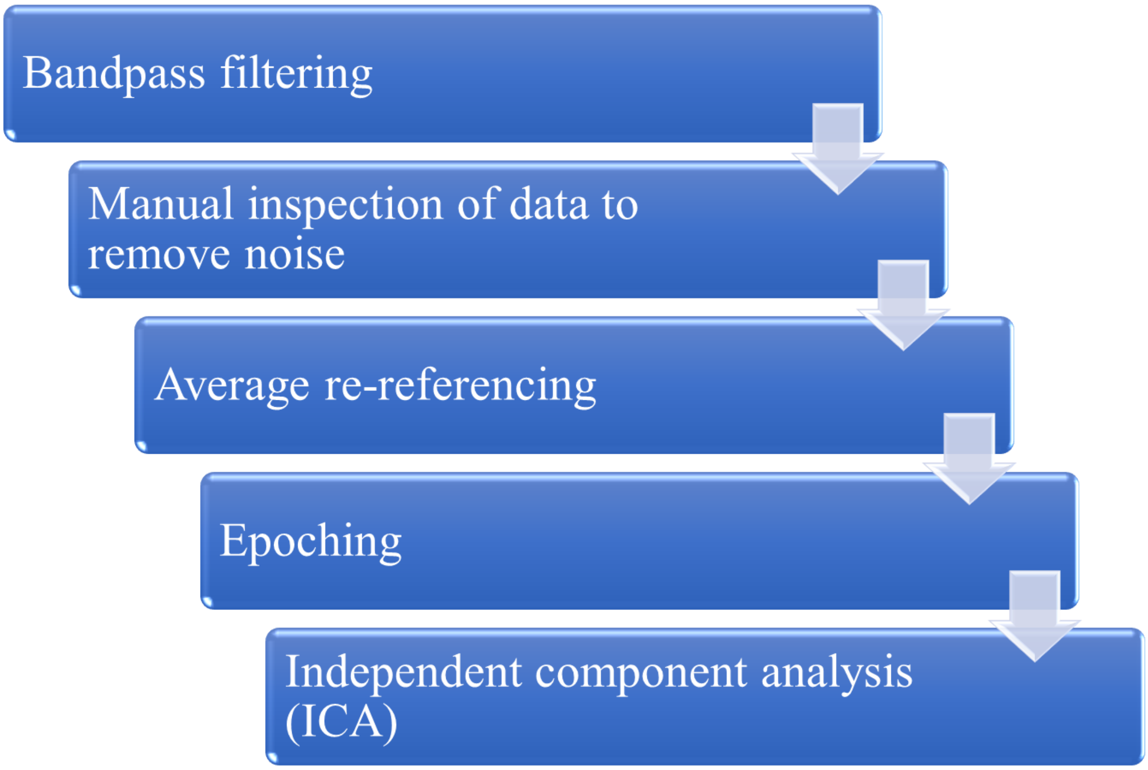

Figure 2.1: Preprocessing pipeline for EEG data

2.3 Spectral Analysis

The power spectrum, or the power spectral density (PSD) is a distribution of power across different frequency bands in a signal. It provides information about the strength of frequency components in the signal.

To detect the presence of the alpha band oscillations, power spectra were calculated using Welch's method. Peaks within the 7-12 Hz frequency range were then identified.

Welch’s method divides the input signal into several segments of equal length. A multiplication of each segment by a window function reduces spectral leakage, following which, each multiplied segment is Fourier-transformed. This calculates the frequency content of each segment. The results of individual segments are averaged together to obtain the final power spectrum density map.

2.4 Source Reconstruction and Extracting the Scout time Series

For localization of the sources of alpha frequencies, we used Minimum Norm (MN) imaging method. It estimates the amplitude hence of the signal sources, across the brain or within the cortex. It achieves source estimation by minimizing the overall activity amplitude over the brain, hence selecting for relevant sources of the signals.

EEG forward head models were generated with the overlapping spheres approach (Huang et al. 1999) and using default anatomy provided in Brainstorm (Tadel et.al. 2011).

Current density maps represent the distribution of current densities in the brain. Here, Standardized LOw Resolution brain Electromagnetic TomogrAphy approach (sLORETA) (Pascual-Marqui, 2002) was applied in Brainstorm. sLORETA limits the estimated activity to predefined brain regions, through incorporation of standardized head models. The generated current density maps are normalized to overall data covariance (a summation of both brain signal and noise covariance). Current density values over the brain can thus be compared, reflecting relative levels of neural activity.

Source time series were extracted based on pre-defined anatomical parcellation in accordance with the Desikan-Killiany parcellation scheme (Desikan et.al., 2006) consisting of 68 brain regions.

2.5 Directed Functional Connectivity Analysis

Granger Causality (GC) was employed to look at the connectivity patterns of the networks in the alpha frequency range. It is a statistical method to evaluate whether one signal causes another based on predictive utility. The basic principle can be understood from the following formulation,

$$\mathrm{X(t)} = \sum_{n=1}^{k} \alpha X(t-n) + \sum_{n=1}^{k} \beta Y(t-n) + exyt \qquad (2.6.1)$$

$$Y(t) = \sum_{n=1}^{k} \gamma Y(t-n) + \sum_{n=1}^{k} \delta X(t-n) + eyxt \qquad (2.6.2)$$

Consider two time series X(t) and Y(t) which can be fit into a bivariate auto-regressive model through the following expressions. Here, k is the model order while 'exy' and 'eyx' represent error terms. 'α', 'β', 'Ƴ' and 'δ' are the weighting coefficients. The timeseries 'X' is said to 'Granger cause' time series 'Y' if the error term 'eyx' is significantly lower than the error term of an autoregressive model of Y.

Significance here is determined by an F-test, a statistical method where the ratio between two variances is used to determine the 'F-statistic'. This follows the F-distribution under the null hypothesis and the likelihood of the observed F-statistic appearing in the F-distribution is used to establish significance. In Granger Causality, the ratio of error variances is used to calculate this statistic, and the log of the f-statistic is used to estimate the magnitude of the causal interaction. The variable Granger Causality can be performed on the time domain and frequency domain. In the time domain, the prediction is made for powers at a certain frequency. An extension of bivariate GC is multivariate GC, which is able to incorporate additional conditions into the test of causality. In this study the spectral GC algorithm seen in Ghosh et. al., 2021, was applied to determine functional connectivity in the resting state.

Intensity thresholding for Granger Causality determines the significance of resultant causal interactions. Connections with values below the set intensity threshold are considered insignificant. The intensity threshold was set at 90% in Brainstorm, and a connectivity map was generated.

2.6 Statistical Analysis

The mean spectral density at 10 Hz for 8 occipital electrodes and 8 frontal electrodes was computed for each participant and the difference between sets of means were tested for significance with a one-tailed independent samples t-test. A significance threshold of 0.05 was used. The results of the Granger Causality analysis were intensity thresholded to the top 10% of values to reveal the most prominent connections.

CHAPTER 3

RESULTS

3.1 Power Spectrum Density

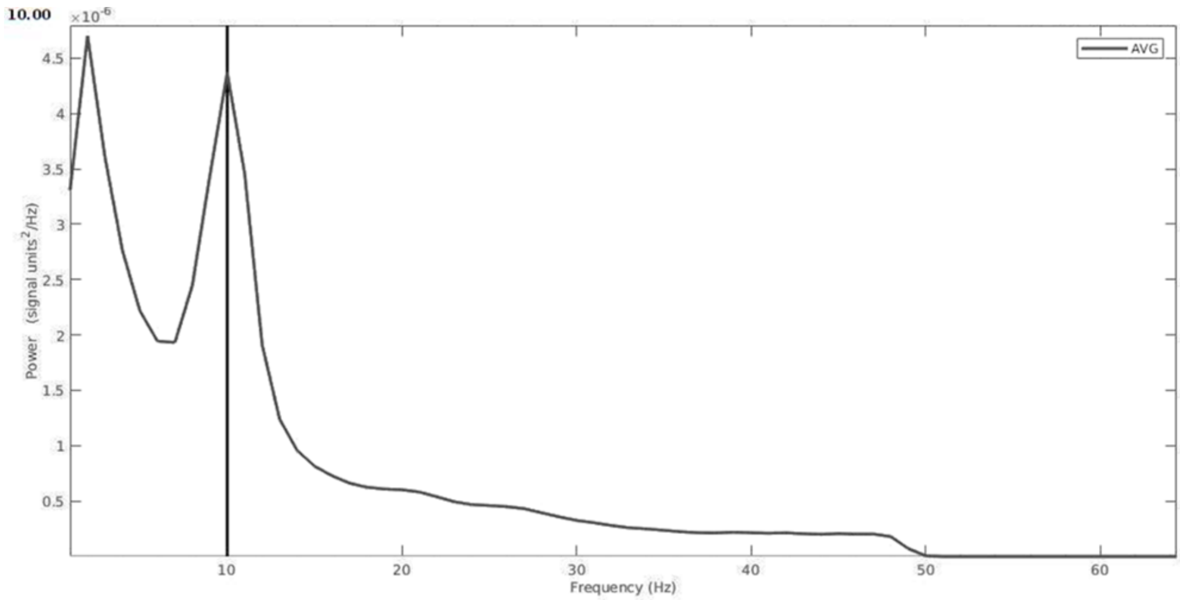

Figure 3.1: Power spectral density. The mean global power spectrum was plotted. A peak was observed at 10 Hz indicating the presence of alpha band.

The power spectra represent the most dominant frequency . The most dominant neural oscillations associated with resting state are alpha oscillations. Thus, to validate this, power spectra were calculated for each participant and averaged and collapsed across all sensors to obtain a global power spectrum. Figure 3.1 shows a prominent peak at 10 Hz indicating that alpha oscillations are prominent during the resting state. The orange areas on the topoplots indicate areas of high spectral power of alpha. Previously, the resting state has been associated with an enhancement in alpha power in the occipital regions (Goldman et. al., 2002). Consistent with this, we found a robust increase in alpha power in the occipital areas.

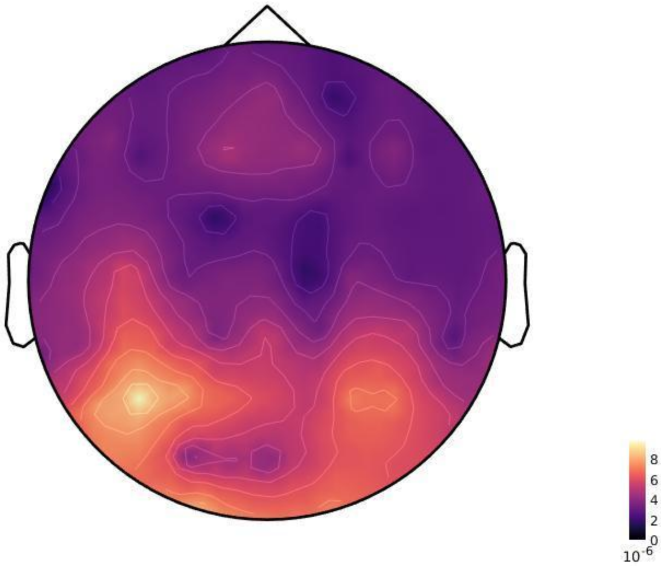

Figure 3.2: Sensor topography plotted using alpha power. Activation in the alpha band can be observed in the occipital region

Figure 3.2 shows the topoplot . The alpha band is enhanced in the occipito-temporal regions. In order to examine if the activation observed in the occipital area was significant, a sample independent t-test was applied by comparing the alpha power of individual participants at 8 frontal and 8 occipital sensors. A significant difference (p value = 0.0361) was detected between the frontal and occipital alpha power, indicating that alpha activity is indeed prominent in the occipital region during resting state EEG.

3.2 Source Localization

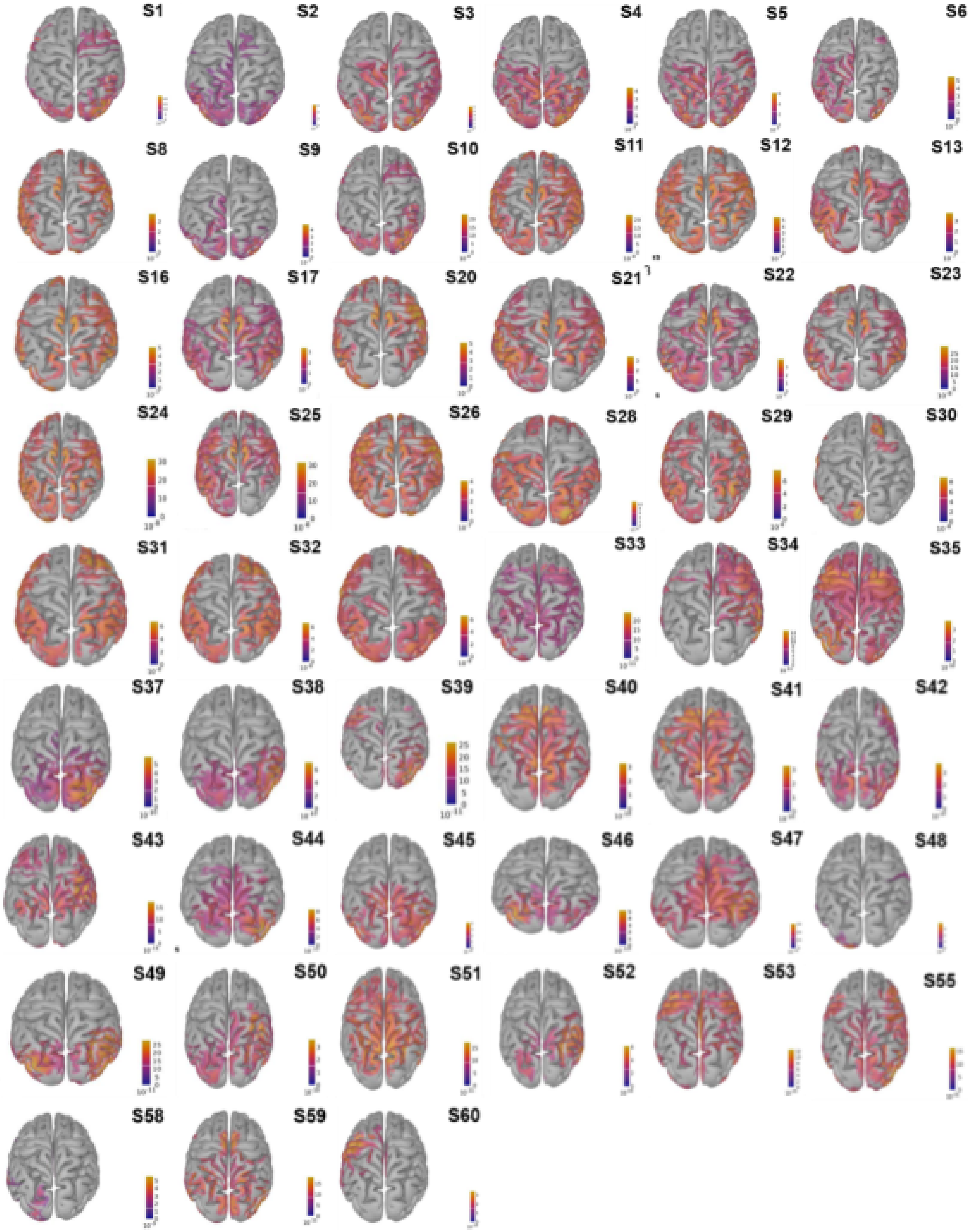

Figure 3.3: Cortical sources of alpha activity.

Source localization was performed to uncover the specific brain areas that show alpha power enhancement during resting state. sLORETA was used to locate the sources of alpha in anatomically demarcated brain regions. Source maps were generated for each participant. Data from five participants was discarded on account of excessive noise. It is a simple method of source localization along with being highly accurate (Sadat-Nejad & Beheshti, 2021). For further denoising , the maps were thresholded.

3.3 Connectivity Maps

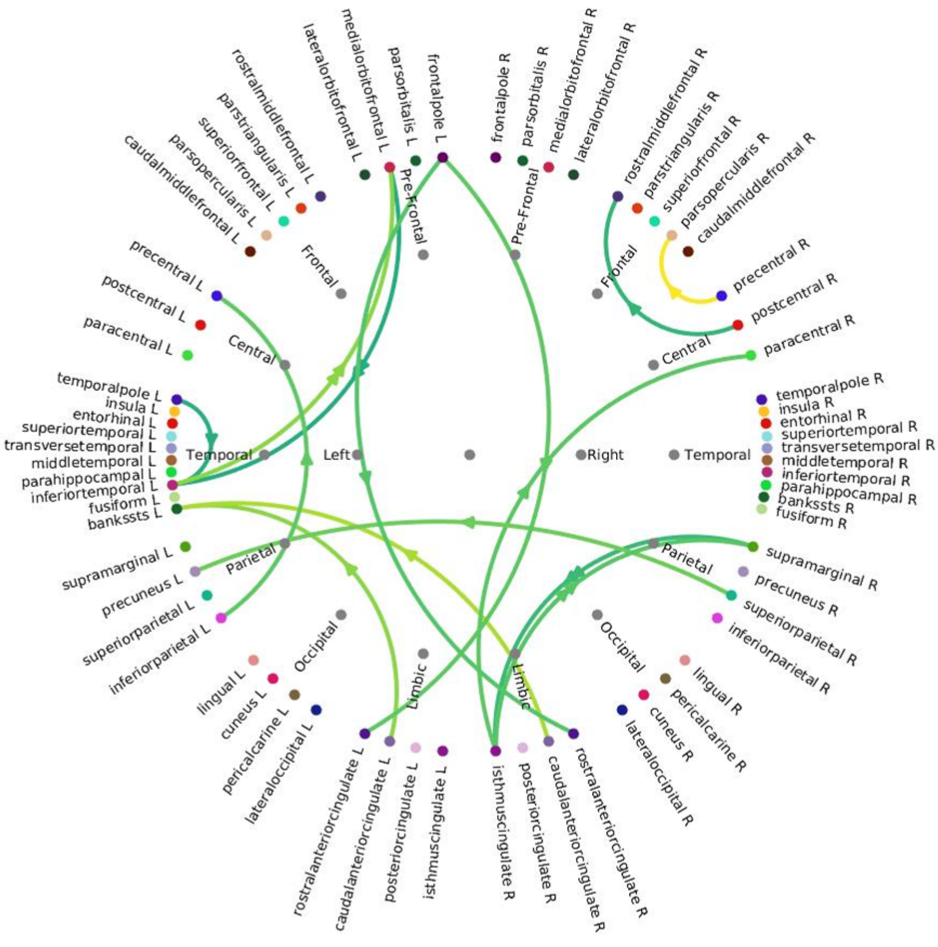

Figure 3.4: Whole brain connectivity map. Whole brain connectivity were generated by applying Granger causality.

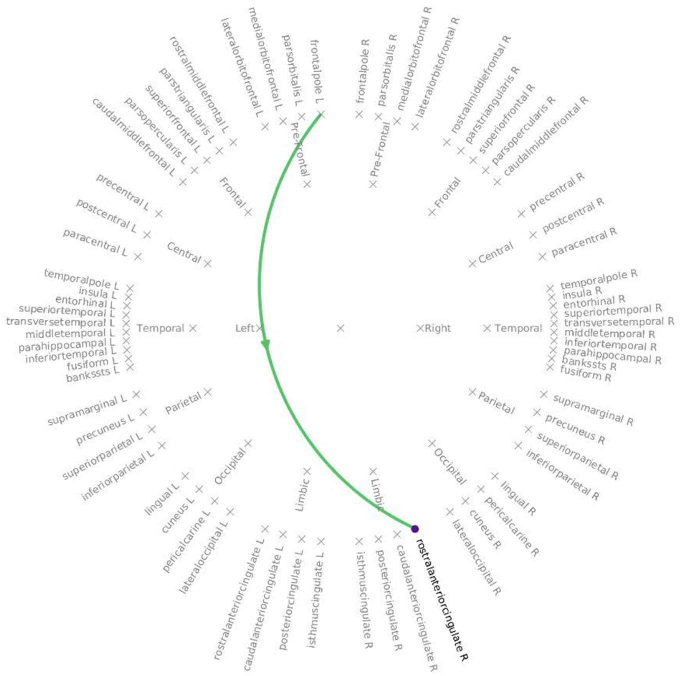

Fig 3.5: Connectivity between the rACC and the frontal pole

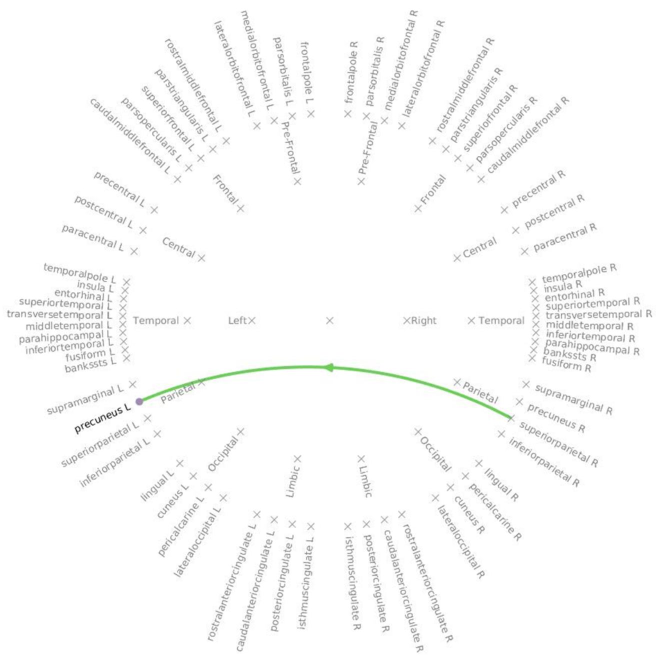

Fig 3.6: Connectivity from right superior parietal gyrus to left precuneus

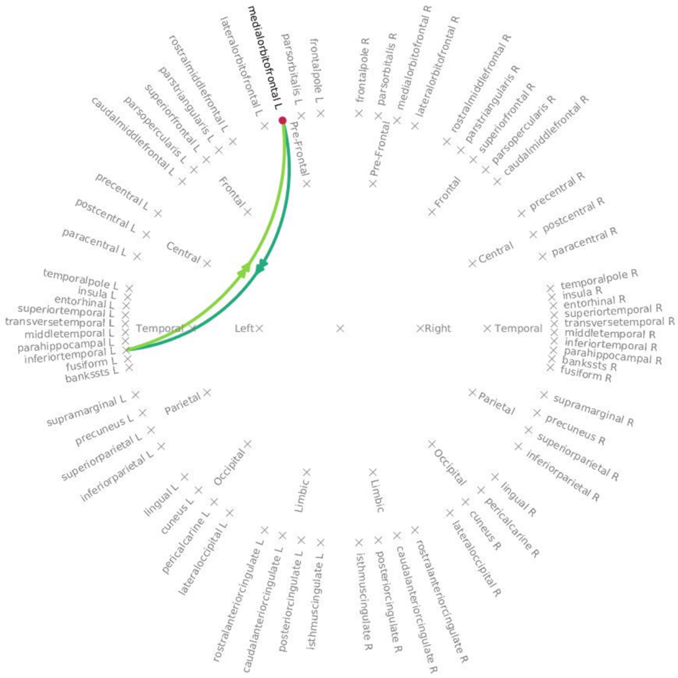

Fig 3.7: Connectivity from left medial orbitofrontal to left inferior temporal cortex

The resting state is characterized by a group of networks which show high activity in the absence of a specific task. Thus, it is important to identify if the sources of alpha oscillations identified are parts of any existing resting state network. Areas showing synchronous activity are considered to be functionally connected. It provides important information on the hierarchical organization of different networks in the brain. One of the methods to study functional connectivity in the brain is Granger causality. Granger causality analysis helps in identifying the functional interactions between anatomically distant brain areas by looking at the statistical dependence of the time series values of one area with respect to another area. In the present study, we wanted to characterize the brain regions in the alpha band into functionally connected networks. It was found that a high amount of connectivity was found between occipital, parietal and temporal areas.

One of the most prominent networks present during resting state is the *default mode network* (DMN). The primary areas that belong to the DMN are the posterior cingulate cortex, the precuneus, inferior temporal gyrus and the medial orbitofrontal cortex. **Fig. 3.7** shows connectivity between left inferior temporal to left medial orbitofrontal cortex which are both parts of the DMN (Xu et al., 2016) Another connectivity pattern observed which further strengthens the presence of DMN is the connectivity between the precuneus and the superior parietal region (Zhang & Li, 2012 (Fig 3.6). Anterior cingulate cortex and the frontal pole which is a part of the prefrontal cortex also shows strong connectivity which is another part of DMN (Liu et al., 2013) (Fig 3.5). Thus, existence of directed functional connectivity between the above mentioned regions suggest the activation of the DMN.

CHAPTER 4

DISCUSSION

In the present study, we wanted to identify the networks present during resting state which showed activation in the alpha frequency range. Previously, alpha power has been linked to resting state and has positive correlations with the default mode network (Bonnard et al., 2016). Furthermore, it has also been shown to be the most dominant frequency detected in the EEG during a state of rest (Grandy et al., 2013). The averaged power spectrum density graph that was generated for all 60 participants exhibited a peak at 10 Hz which corresponds to the alpha band.

There was significantly more alpha activity in the occipital region as compared to the frontal regions (p value < 0.05). This is in agreement with previous literature which locates alpha rhythm during rest in the occipito-parietal regions (Ben-Simon et al., 2008).

Source localized maps obtained using sLORETA for individual participants and connectivity maps were generated. The present study utilizes Granger causality measure which is a less ventured approach towards studying connectivity analysis. Granger causality (GC) analysis allows us to segregate regions in the brain into functional networks. Moreover, it is a method to find directed connectivity between brain regions. Directed functional connectivity gives us an idea of the organizational and functional hierarchy of hubs in a network.

The connectivity maps show directed functional connectivity between regions of the brain which have been previously implicated in the DMN:

1. between left inferior temporal cortex and left medial orbitofrontal cortex,
2. between the left precuneus and right superior parietal cortex, and
3. between the anterior cingulate cortices and the left frontal pole.

This result validates our use of GCA as DMN is the characteristic network which is almost always observed in resting state (Luo et al., 2015). The default mode network is less extensively engaged in tasks and is active in ‘mind-wandering.’

Future Prospects and Limitations

Connectivity maps show a strong link between the right pars opercularis and the right precentral sulcus. Additionally, a bidirectional connectivity is observed between the right supramarginal gyrus and the right isthmus cingulate cortex. Implications of these connections in various RSNs remain a trajectory of inquiry.

The validation of an EEG measure of functional connectivity also holds promise as a method for investigating network dynamics in an affordable and temporally resolute way. Future studies could investigate network dynamics during a variety of tasks and leverage the temporal resolution of EEG to reveal high frequency connections.

Source localisation for the obtained EEG data was performed using sLORETA. However, connectivity estimates vary depending on the method of source localisation method. Further, Sekihara et. al., suggest that sLORETA demonstrates certain source-localisation bias in the presence of measurement noise.

Granger causality, used here to explore causal relationships within the obtained data, also presents with certain drawbacks. Inferences are correlation-based, opposed to establishment of a purely causal relationship. Additionally, its interpretations may not capture non-linear relationships between variables.

In the future, a replication of the results of this study through implementation of different source localization algorithms and connectivity methods could be pursued.

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