Investigating changes in the functional organisation of brain networks during illusory perception

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CERTIFICATE

This is to certify that the dissertation entitled **"Investigating changes in functional organisation of brain networks during illusory perception"** is the result of work carried out by **Akanksha Gupta** in National Brain Research Centre, Manesar, Haryana, India.

The work presented herein is original and has not been submitted previously for the award of any degree or diploma to **National Brain Research Centre (Deemed to be University)** or to any other University. This work is completely based on the guidelines given by **National Brain Research Centre** and is a record of the candidate's own efforts.

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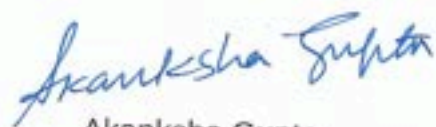Place : NBRC, Manesar

Date : 1/06/2020

DECLARATION

I, **Akanksha Gupta**, hereby declare that the work presented in the thesis entitled *"Investigating changes in the functional organisation of brain networks during illusory perception"* is carried out by me under the guidance of **Dr. Arpan Banerjee, National Brain Research Centre (Deemed to be University)**, Manesar, Haryana, India.

I also declare that no part of this dissertation has been previously submitted for the award of any degree or diploma to **National Brain Research Centre** or any other University.
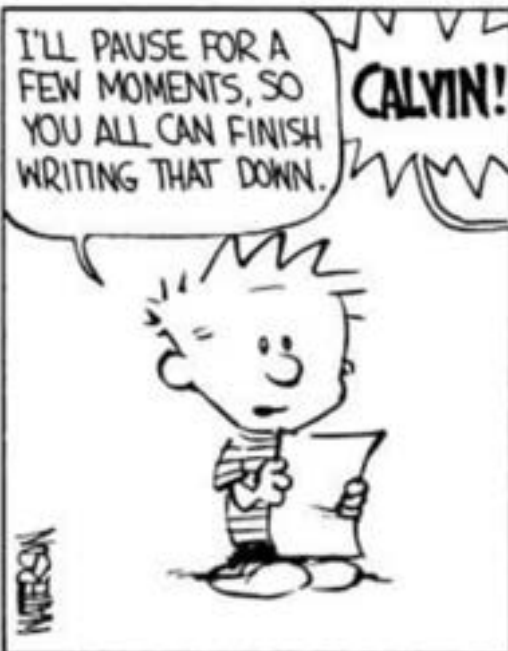
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ABSTRACT

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Human perception is veritably multi-sensory and multi-modal. Integration of sensory information from various modalities facilitates the production of a coherent picture of the outside world. McGurk effect, an illusion where visual speech information influences the auditory speech perception, is a conventional assay to measure audiovisual integration. In this dissertation, we study the McGurk effect from a network perspective. We apply the concepts derived from graph theory to investigate the changes in various global and local network metrics of network segregation and integration. We found that there is enhanced functional segregation with cross-modal perception. The global network parameters were also related to the illusory /ta/ perception using Pearson correlation analysis. We found significant correlations between network measures and rate of illusory perception.

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Chapter One

Introduction

Hauf his soul a Scot maun use

Indulgin' in illusion

And hauf in getting rid o them

And comin' to conclusions.

(Hugh McDiarmid, 1928)

Perception acts as an interaction channel through which we connect to the outside world. Human perception is veritably multi-sensory and multi-modal. At any given moment, we are inundated with multiple sensory signals through various sensory modalities. Concomitantly, a series of labyrinthine events leads to the production of a percept, coherent representation of external stimuli. In terms of evolution, the *raison d'être* is to provide us with unambiguous information about the characteristics of our surroundings to usher in propitious action. Nonetheless, there are frequent departures from the accuracies of perception leading one to experience false percepts or illusions [1].

1.1 Speech Perception

"Human speech is like a cracked kettle on which we tap crude rhythms for bears to dance to, while we long to make music that will melt the stars."

— Gustave Flaubert (Madame Bovary)

Understanding the enigma behind how speech is produced and perceived entails that we do not discount its visual concomitants. In the context of spoken discourse, acoustic signals follow hard on the heels of facial gesticulations [2]. Humans invariably rely on information from lips, teeth, tongue and non-mouth facial features to comprehend spoken language [3]. Offsetting of suboptimal acoustic signals by visual speech information is quite evident in a noisy milieu. In such circumstances, visual signals serve as a supplement for the loss of auditory information [4]. However, auditory perception is influenced by vision even when audio signals are intelligible, and some audio-visual pairing leads to illusory perceptions [5]. The merging of information from auditory modality and visual modality during speech perception is termed as audio-visual integration.

1.1.1 McGurk effect: The quintessence of cross-modal illusion

McGurk effect was discovered fortuitously in 1976 by two psychologists, Harry McGurk and John MacDonald while researching on speech perception in young infants [6]. When the participants were presented with a video of a woman repeating the sound of phoneme /ga/ with an auditory sound of phoneme /ba/ dubbed over, they reported a novel auditory syllable /da/. In another instantiation, the sound of phoneme /pa/ was combined with the lip movement of phoneme /ka/. Observers of this complex discordant bimodal stimuli perceived the sound of the phoneme /ta/. Thenceforwards, this illusion came to be known as the McGurk effect [5, 6].
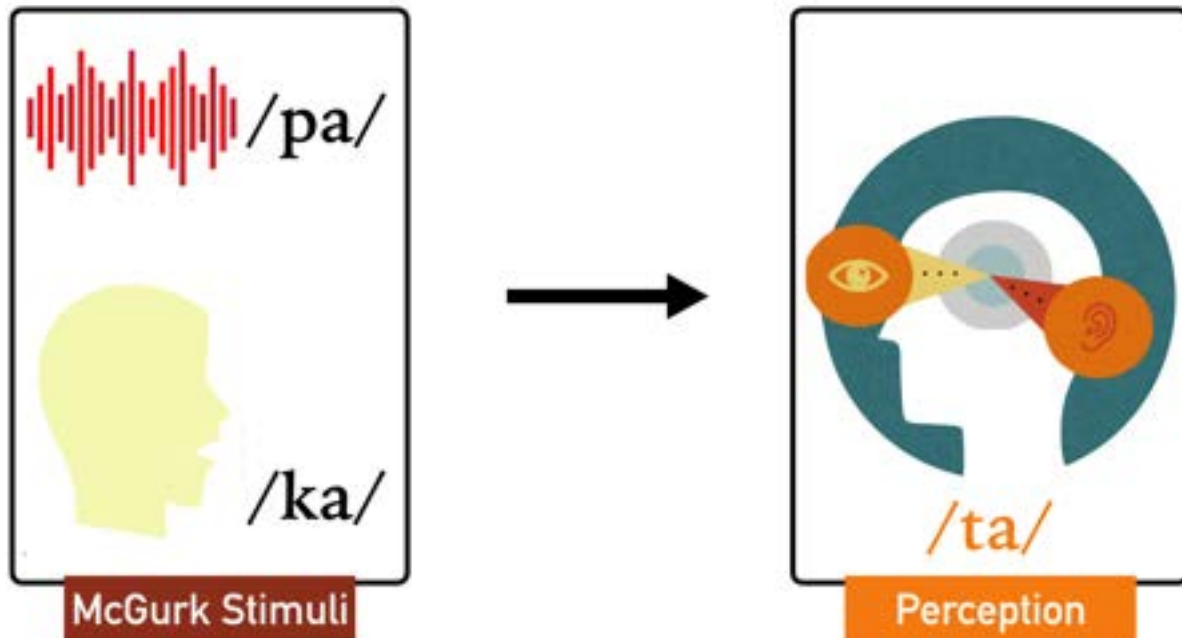
Figure 1.1 The McGurk Effect. The speaker mouths the syllable /ka/ with the sound of syllable /pa/ dubbed over, so the participant usually report the percept /ta/.

The McGurk effect reveals how visual experience shapes auditory perception. The McGurk percept corresponds to neither the auditory token nor the visual token evincing that speech perception is a multi-modal phenomenon. On numerous occasions, participants are aware of the attributes of the stimulus, but that does not disarticulate their unified percept. Thereby, it serves as a practical approach for measuring audio-visual integration in healthy and clinical populations [7]. Furthermore, the effect remains robust even when the auditory and visual signals are spatially [8] and temporally [9] not coextensive. However, presentation style of the stimulus, individual differences and the brain state of the participant can significantly affect the intensity of McGurk illusion [10].

1.1.2 Temporal asynchrony and audio-visual integration

In any classroom demonstration of the McGurk effect, the audio and visual signals of the McGurk stimuli are spatially and temporally synchronous seemingly originating from a single speaker. One might assume this synchrony of sensory information to be the cause of unified percept [11]. Time and again, researchers have modified the classic McGurk stimuli to scrutinise various constraints on the McGurk effect. When considering temporal discrepancies, the audio-visual integration of speech remains intact with desynchrony. For instance, Munhall et al. examined asynchronous stimuli extending between -360ms (auditory lead) to 360ms (visual lead) in intervals of 60ms. They reported that the effect persists from -60ms to +240ms with higher tolerance to visual-led asynchronies [9]. This continuum of asynchronies can be regarded as a window of perceptual integration. Thus, regarding audio-visual integration, this window albeit large is inordinately asymmetric [9, 2, 12]. The rate of illusory response change across this temporal window. In a recent study by Thakur et al. illusory percept was reported to be maximum at 0ms and 150ms time lags [13].
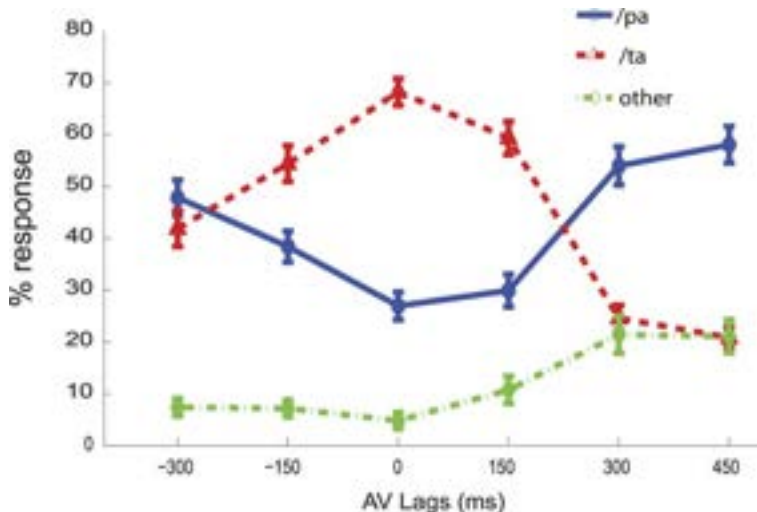
Figure 1.2 Normalized behavioral responses across AV lags. Figure adapted from Thakur, B., Mukherjee, A., Sen, A., and Banerjee, A. (2016) [13]

1.2   Network basis of Human Brain

Human brain is undoubtedly one of the most complex natural systems. As neuroscientist David Eagleman describes it in his book *Incognito*:

> *Your brain is built of cells called neurons and glia—hundreds of billions of them. (. . .) The cells are connected in a network of such staggering complexity that it bankrupts human language and necessitates new strains of mathematics. A typical neuron makes about ten thousand connections to neighboring neurons. Given billions of neurons, this means that there are as many connections in a single cubic centimeter of brain tissue as there are stars in the Milky Way galaxy.*

Our brain executes perception and higher-level cognition without a hitch owing to efficient network architecture. Understanding how the functional organisation of the brain effectuate this arsenal of functions has been a long-drawn-out pursuit in neuroscience.

The quest began in the 1700s when Franz Joseph Gall proselytised the idea that every mental function resides in a particular brain "organ". Although the academic community later jettisoned phrenology as pseudoscience, the underlying principle of functional localisation inside the brain remained unchanged [14, 15]. Paul Broca's identification of the inferior frontal gyrus for expressive aphasia engendered focal brain lesion studies, proffering empiric evidence for localised brain function [15]. Electrophysiological stimulation experiments further bolstered this notion.
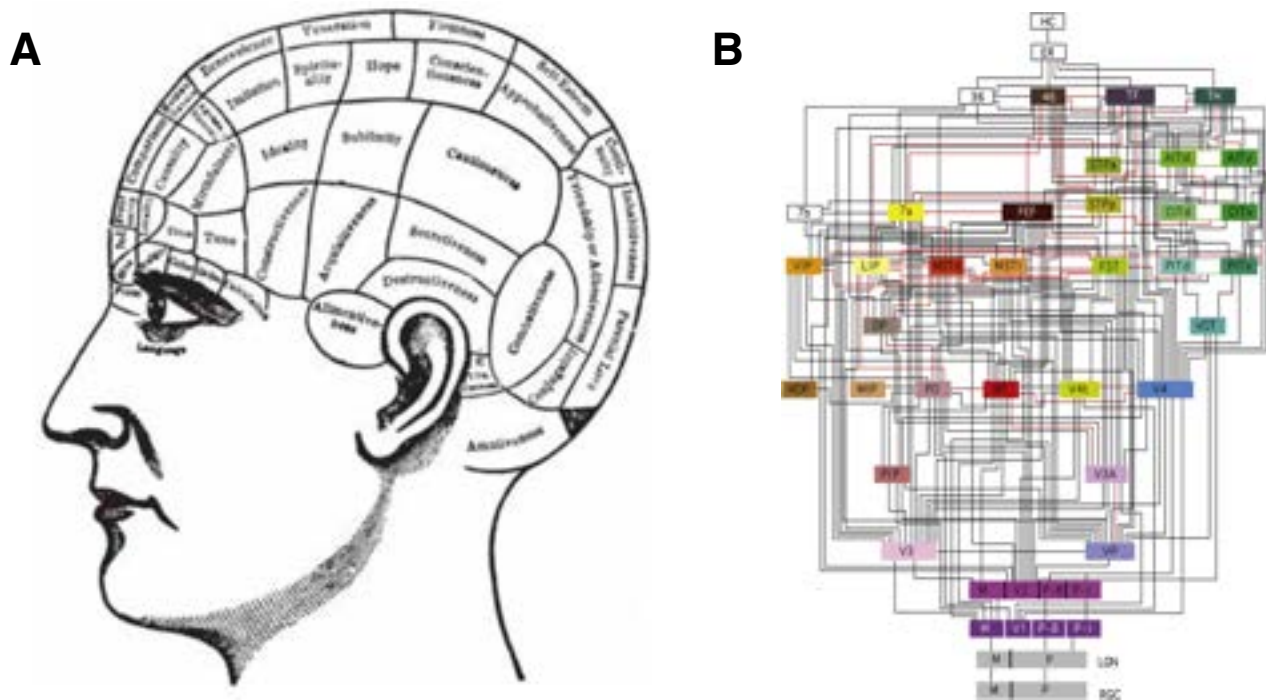
Figure 1.3

Localizationist and Holistic approach in describing mental functions (A) Phreno-logical Map Gall described that every mental function resides in a specific part of brain. Figure adapted fromClarke, E., O'Malley, C. D. (1996). [16] **(B)** 32 cortical area comprising the macaque visual system distributed over 10 hierarical levels. Figure adapted from Felleman, D. J., Van, D. E. (1991). [17]

The provenance of non-invasive brain imaging tools led to the development of sophisticated maps depicting that at least some brain functions can be dovetailed to a specific brain area.

In recent times, further improvements in electroencephalography (EEG), diffusion tensor imaging (DTI), positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) caused a seismic shift in our understanding of neuronal operations from discrete to a distributed phenomenon.

Following these modern advances, we are now aware that brain regions do not operate in isolation but rather are a part of dynamic brain networks.

1.3 Functional Segregation and Integration

The vicissitudes of the brain network organisation in response to the ever-shifting environment makes human life possible on this planet [18]. For efficient action, our brain incessantly integrates information coming from various sensory modalities to generate coherent percepts. Concurrently, it also segregates information to execute modality-specific computations. Thus, the two fundamental principles that are the building blocks of brain organisation are functional segregation and functional integration [19, 20, 21].

Functional segregation essentially explains the existence discrete and specialised sub-systems for similar function. Investigation at any network scale depicts substantial evidence for network segregation. This range from selective response of individual reurons to visual stimuli [22] to mini columns to macroscopic brain regions specific for processing faces [23]. One reason for the necessity of functional specialization for specific tasks can be the computationally distinct nature of these tasks requires specialised machinery.

The prevalence of modules or communities in the brain networks can be thought of as specialised machineries to carry out local computations. However, a completely segregated system would restrict brain function since information from specific modules would not be able to reach other modules to drive adaptive

behaviour. For instance, if someone walking across a forest hear a low rumble, this information from the auditory cortex could not be utilised by the visual and the motor cortex to locate and face the potential danger. [24]. Therefore, communication between the segregated units is of the utmost importance.

Functional integration describes the communication between these specialised neural elements to execute perception and facilitate adaptive behaviour [25]. Evidences of functional integration can be found by looking at the anatomy of thalamo-cortical systems, where reciprocal connections promote parallel information transfer [25].

Investigation of structural and functional networks derived from fMRI data has notably helped shape our understanding of the system-wide functional architectures which enable the brain to balance the segregation and integration of information. Human brains have been shown to demonstrate small-world character. The presence of modules along with long range integrative connections ensures both conservation of cellular material and space and time respectively. Furthermore, it augments resilience and robustness of a network [26].

Network neuroscience derives the concepts from graph theory to study brain network architecture to understand the principles of functional organisation i.e., segregation and integration responsible for perception and higher-level cognition.

1.4   Neuron to Node: Brain Networks and Graph Theory

> Some citizens of Königsberg
>
> Were walking on the strand
>
> Beside the river Pregel
>
> With its seven bridges spanned.
>
> "O Euler, come and walk with us,"
>
> Those burghers did beseech.
>
> "We'll roam the seven bridges o'er,
>
> And pass but once by each."
>
> "It can't be done," thus Euler cried.
>
> "Here comes the Q.E.D.
>
> Your islands are but vertices
>
> And four have odd degree."
>
> -William T. Tutte

Leonard Euler's solution to the seven bridges of Königsberg problem is assumed as the *fons et origo* of graph theory, the mathematical study of networks, or graphs [27, 28]. In graph theory, a graph 'G' is represented by a set of vertices/nodes (V) and their interactions by a set of edges (E). In modern times, graph theory has forged ahead as an effective method to decipher the underlying structure and function of complex systems [27, 28]. Many such complex networks like the internet, flight networks, social networks, and communication

and distribution networks are working behind the scenes in our daily lives. The introduction of the "The Human Connectome" [29] was a definitive moment in using graph theory to analyse complex brain networks. Graph measures notably provide significant intuitions about brain network architecture, evolution, development, and clinical disorders [27]

The brain network comprises of a set of nodes(vertices) and their pairwise links(edges) [27]. Brain nodes can be defined as voxels, large parcels from an anatomically based brain atlas or random interpolations between voxels and parcels. The links can be anatomical, functional, or effective connections [19, 30]. The associations between nodes can be converted into an adjacency or connection matrix. The edges between nodes can take weighted or unweighted values, and they can be directed or undirected [27]. The topological analysis of brain networks can be done through various graph measures.

In this dissertation, network analyses on fMRI derived data, which are considered to be undirected and unweighted are reported, focussing on the changing topology of brain networks during illusory perception.

Chapter Two

Methods

2.1 Participants

The data were collected by Abhishek Mukherjee and Arpan Banerjee for a brain imaging study at the National Brain Research Centre [13]. Fifty-two dextro-manual healthy adults(27 males; 25 females) aged from 22 to 29 years(mean age=24.5; SD=3.12), participated in the study. They all reported 20/20 vision, with no record of auditory or neurological disorders. The study was authorised by the Institutional Human Ethics Committee (IHEC), NBRC and was consistent with their guidelines and in strict adherence to the declaration of Helsinki. An informed consent was collected from all participants.

Participants were classified as McGurk perceivers if they reported the illusory /ta/ percept for at least 60% of the total responses at any audio-visual lag. Eighteen participants failed to perceive the McGurk percept. We used the data from the remaining 34 participants for network analyses[Due to some faults during stimulus presentation, only 31 participants were taken for -300 lag].

2.2 Stimuli

Six discordant stimuli(auditory /pa/ and visual /ka/) ranging from -300 ms(audio lead) to 450 ms(visual lead) in increments of 150 ms and a congruent stimulus called as PureTa(auditory /ta/ and visual /ta/) were created. The audio-visual lag conditions were labelled as: -L2(-300 ms), -L1(-150 ms), L0(0 ms), L1(150 ms), L2(300 ms) and L3(450 ms) **(Figure 2.1)**. Every participant had one AV lag where they had minimum and maximum /ta/ perception, these data were grouped to yield two perceptually sorted categories: MinTa(minimum illusory) and MaxTa(maximum illusory). The audio files of an Indian native male speaker repeating the sound of phoneme /pa/ and /ta/ were recorded, digitised at 44kHz and edited using Audacity. The videos of him articulating the phoneme /ka/ and /ta/ were recorded(25 frames/second) and edited using the software Videopad. For every condition, a stimulus video with 2 s duration with a display of 1280 x 720 pixels resolution was created by syncing appropriate audio and video files.

2.3 Experimental Design

The study was a block design experiment. Each activation block was of 20 s and comprised of ten concatenated videos of the same AV lag(each of 2s duration). For every stimulus condition, four activation blocks were prepared making a total twenty-eight activation blocks. A 20 s resting block followed every activation block **(Figure 2.2)**.
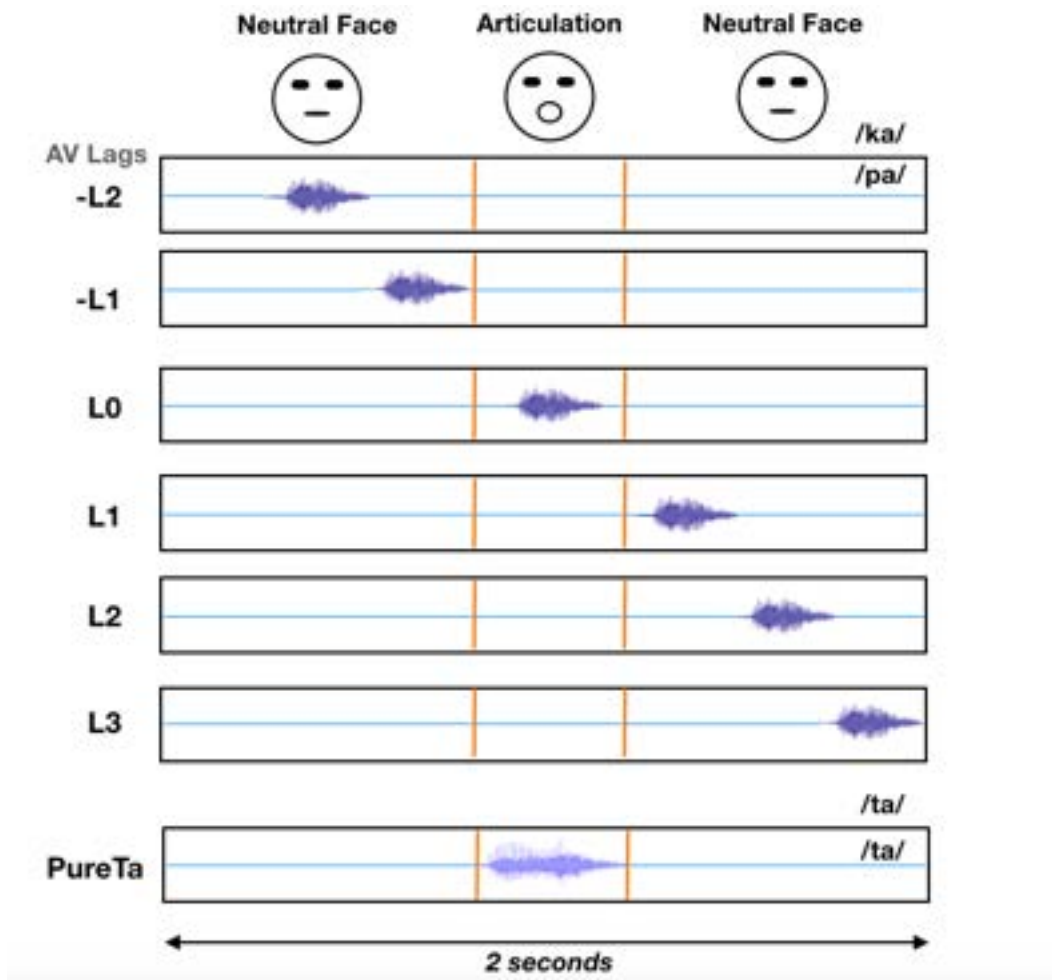
Figure 2.1 The McGurk Stimuli.
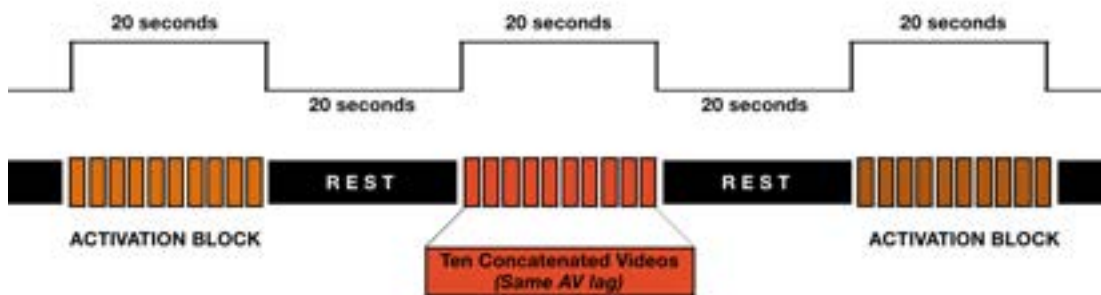
Figure 2.2 Schematic diagram of functional magnetic resonance imaging(fMRI) block design paradigm.

The presentation of stimulus blocks was random with no repetition in their order. All the stimuli were displayed using Presentation software. Participants viewed stimulus videos through an INVIVO MRI-compatible CRT screen with MRI-compatible headphones. The participants responsed either /ta/, /pa/ or "any other" using a fibre-optic button pad.

2.4   Data Acquisition and Pre-processing

The data were collected inside a 3T MRI scanner and preprocessed using SPM.

2.5   Network Construction

The Brainnetome atlas was utilised to demarcate the 210 nodes in our graph. The noisy signals led to the exclusion of the sub-cortical regions. For each stimulus condition, we measured the mean signal from the 210 regions in the Brainnetome atlas. A 210-by-210 correlation matrix was generated by measuring the Pearson r between all pairs of signals. Fisher's z-transformation on this correlation matrix yields a normal distribution of Pearson's r. For every stimulus condition, 34 matrices were created(N=34). The matrices were then group averaged and reverse Fisher transformed. A sample t-test was performed with multiple correction(FDR) to get the significant interactions. Lastly, a threshold of 0.45 was applied on the mean matrix to create a binary adjacency matrix representing whole brain functional connectivity **(Figure 2.3)**.
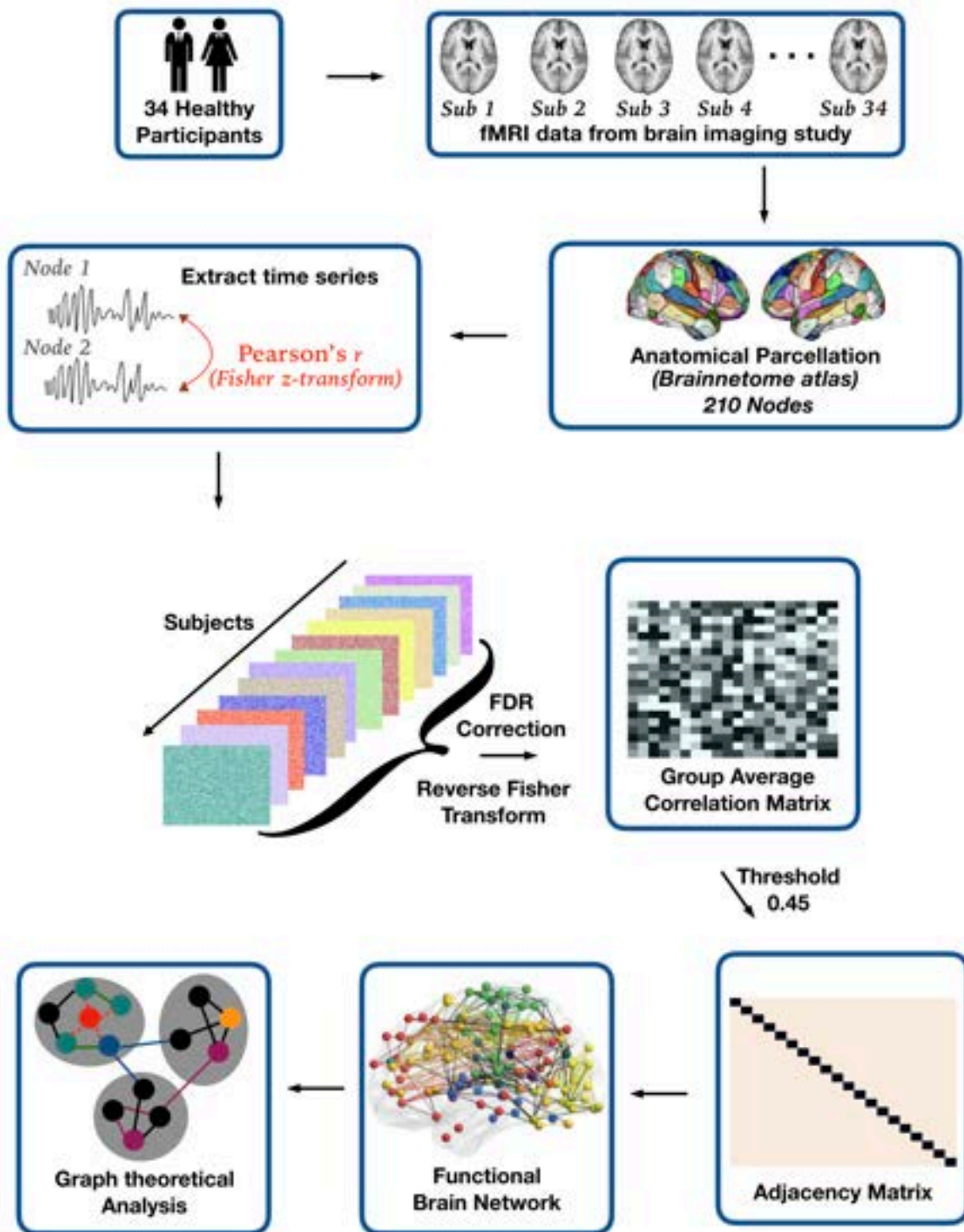
Figure 2.3 Schematic diagram of the dissertation workflow

The standard errors were computed for each condition using a bootstrap subsampling method. The sub-samples were generated by a random selection of 24 correlation matrices out of the 34 matrices created, and the correlated activity was then averaged to generate a sub-sample correlation matrix. Then, the same procedure, as stated above, was repeated to generate sub-sample adjacency matrices (50 replications for each AV lag).

2.6 Graph theory analyses

The network analyses were executed on the adjacency matrices using the iGraph library for Python.

2.6.1 Integrative Measures

Characteristic Path Length

Shortest path length is defined as the minimum number of edges to be traversed to reach from one node to another in a network. Characteristic path length(L) is nothing but the average of shortest path lengths for all possible node pairs [31].

$$L = \frac{1}{n} \sum_{i \in N} L_i = \frac{1}{n} \sum_{i \in N} \frac{\sum_{j \in N, j \neq i} d_{ij}}{n - 1} \qquad (2.1)$$

where d_{ij} is the shortest path between two nodes i and j [30].

A small characteristic path length invokes more integrated and expeditious communication within a network [32].

Global Efficiency

The global efficiency measure was introduced to give the concept of small-world a clear physical meaning [32]. It is quantified using the characteristic path length and can be simply given as:

$$E = \frac{1}{n}\sum_{i \in N} E_i = \frac{1}{n}\sum_{i \in N} \frac{\sum_{j \in N, j \neq i} d_{ij}^{-1}}{n-1} \tag{2.2}$$

where E_i is the efficiency of node i [30]. Global efficiency thus estimates inter-network connections and gives us an idea about the global information transfer.

2.6.2 Segregative Measures

Clustering Coefficient

Clustering can be quantified at both nodal levels and for the entire network. In an undirected and unweighted network, the clustering coefficient for each node is given by the number of links between its neighbours divided by total such links possible. The clustering coefficient of a graph is merely the average clustering coefficient of all the nodes.

$$C = \frac{1}{n}\sum_{i \in N} C_i = \frac{1}{n}\sum_{i \in N} \frac{2t_i}{k_i(k_i - 1)} \tag{2.3}$$

where C_i is the clustering coefficient of node i [30]. Clustering coefficient represents the fraction of possible interconnections among the neighbours of a node. Thus, a high number of interconnection between its neighbours indicates a higher tendency to form a local cluster [31].

Modularity

In brain networks, the nodes are banded together into a diverse network of communities or modules [27, 28]. These dense subsets of nodes are tightly connected with each other and simultaneously sparsely connected to the rest of the network, thus proffering compartmentalisation that decreases interdependence of modules and augments robustness [33]. However, detecting and characterising the clustering of nodes is a non-deterministic polynomial time-hard problem [34]. Out of a plethora of heuristic approaches, Newman-Girvan algorithm, which is based on optimising a quality function is the most popular [35]. It quantifies modularity as:

$$Q = \frac{1}{l} \sum_{i,j \in N} (a_{ij} - \frac{k_i k j}{l}) \delta_{m_i m_j} \tag{2.4}$$

where m_i is module containing node i, $\delta_{m_i m_j}$=1 if m_i=m_j and 0 otherwise [30]. In this dissertation, we used community multilevel algorithm of iGraph package(Python), which is based on another standard algorithm known as the Louvain method [36].

Modularity is perhaps the most elegant method to evaluate segregation of a network. Generally, the network architecture is said to be modular if the modularity index is above 0.3 - 0.4 [37]. It reflects the degree to which a network can be split into diverse modules. Furthermore, it reduces the wiring cost and enhances the adaptability of a system [24].

2.6.3 Node-wise Participation

Participation Co-efficient

The participation coefficient evaluates how distributed the links of a node are among different communities. Participation coefficient is given as:

$$y_i = 1 - \sum_{m \in M} \left(\frac{k_i(m)}{k_i}\right)^2 \tag{2.5}$$

where M is the set of modules, and $k_i(m)$ is the number of links between i and all nodes in module m [30]. Thus, a node's participation coefficient is maximum if its links are uniformly distributed and 0 if all its links are in a single community [24].

Within-module degree

Within-module degree is nothing but the z-scores that give an estimate of intra-network connections. It is defined as:

$$z_i = \frac{k_i(m_i) - \overline{k}(m_i)}{\sigma^{k(m_i)}} \tag{2.6}$$

where m_i is the module of node i, $k_i(m_i)$ represents the number of connections within the node's own module and $\overline{k}(m_i)$ and $\sigma^{k(m_i)}$ are the mean and standard deviation of the within-module degree distribution of module m_i [30]. We classified nodes with within-module degree, z $\geq$ 1 as hubs and nodes with z $<$ 1 as nonhubs.

2.6.4 Small Worldness

The brain is viewed as a small-world network as it maintains an optimal balance between segregation and integration. Here, we define small-worldness as networks with higher functional clustering but comparable characteristic path lengths. Small-worldness can be quantified using the scalar index:

$$S = \frac{C/C_{rand}}{L/L_{rand}} \tag{2.7}$$

where C and C_{rand} are the clustering coefficients, and L and L_{rand} are the characteristic path lengths of the respective tested network and a random network [38].

2.7 Normalization of Graph Measures

The number of connections in the brain networks of all the stimuli conditions largely vary, and therefore normalisation of these graph metrics was required for accurate comparisons of these measures across all the AV lags [39]. One hundred random networks with an identical number of nodes and degree distribution as bootstrapped subsamples were created to normalize the graph measures.

The modularity index was normalized using the following procedure [40]:

$$Q_m = \frac{Q_{real} - Q_{rand}}{Q_{max} - Q_{rand}} \tag{2.8}$$

where Q_{real} is the modularity index of the network, Q_{rand} is the average modularity of randomized networks and Q_{max} is the maximal possible modularity

of the real network. Q_{rand} was computed by averaging Q over hundred random networks that preserve the degree distribution of the real network. Q_{max} was estimated as 1 - 1/M, where M is the number of modules in the real network. The characteristic path length and clustering coefficient were normalized by dividing the observed characteristic path length and clustering coefficient values by their respective mean values of hundred random networks [38].

$$L_{norm} = L/L_{rand} \qquad (2.9)$$

where L and L_{rand} are the characteristic path lengths of the tested network and a random network.

$$C_{norm} = C/C_{rand} \qquad (2.10)$$

where C and C_{rand} are the clustering coefficients of the tested network and a random network [38].

Chapter Three

Results

3.1 Characteristic Path Length and Global Efficiency

The characteristic path length and global efficiency are measures of network integration. The path length reveals the ease of parallel information transfer whereas, global efficiency tells us how efficiently information is transferred across the network. The less the number of links one has to peregrinate around the entire network, the higher is the global efficiency and less is the characteristic path length.

Global efficiency in synchronous AV stimulus network significantly decreased while it significantly increased in the asynchronous AV stimuli networks. In contrast, the characteristic path length increased for the synchronous audio-visual presentation and decreased for the asynchronous stimuli. In the behavioural conditions, the global efficiency is maximum for PureTa and minimum for MaxTa. An opposite trend is observed for the characteristic path length for behavioural conditions. Collectively, these results depict that the

functional brain network becomes less integrated and more self-sufficient with cross-modal perception. **(Figure 3.1)**.

Figure 3.1 Changes in Integrative Measures. **(A)** Characteristic Path Length **(B)** Global Efficiency
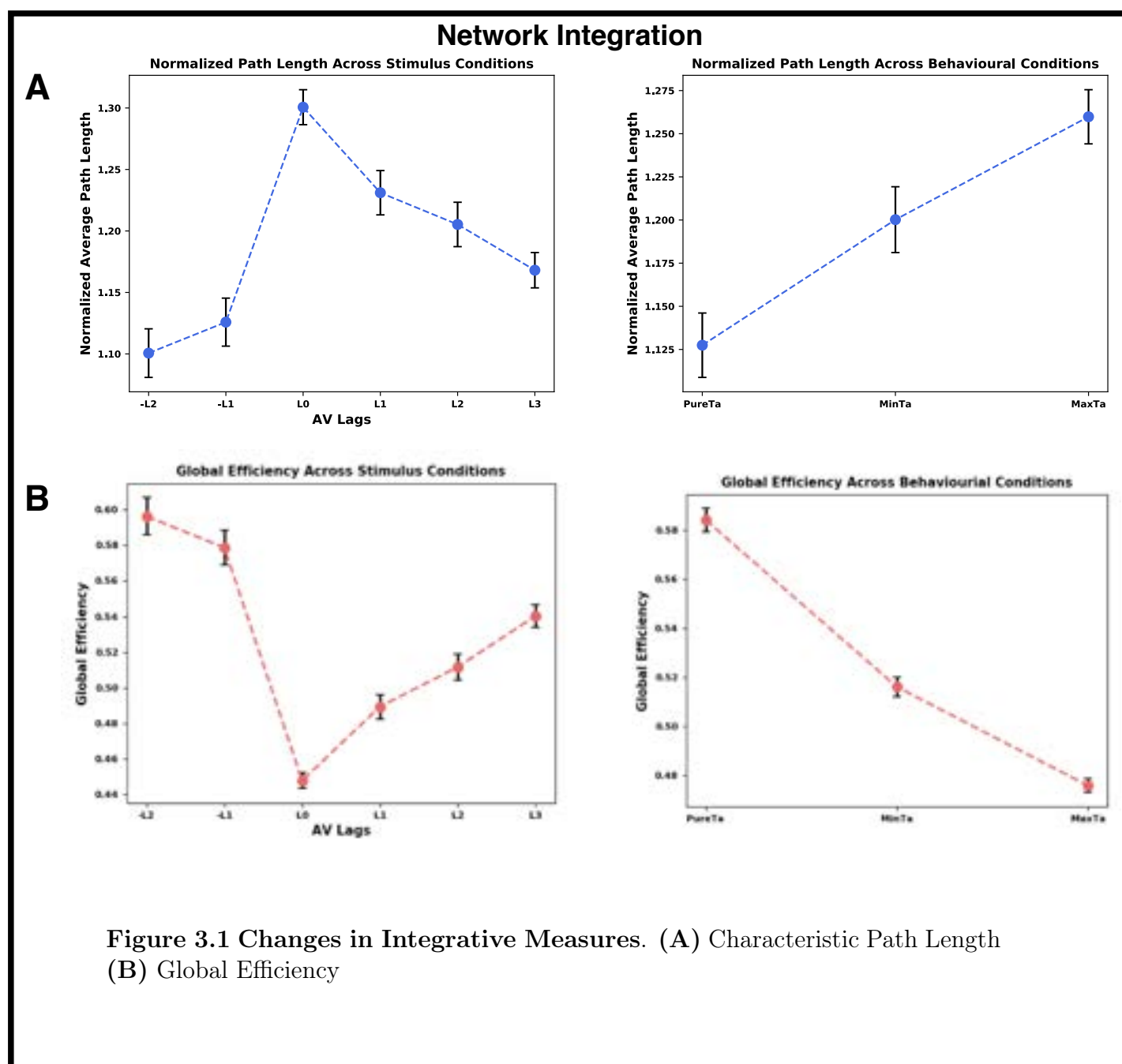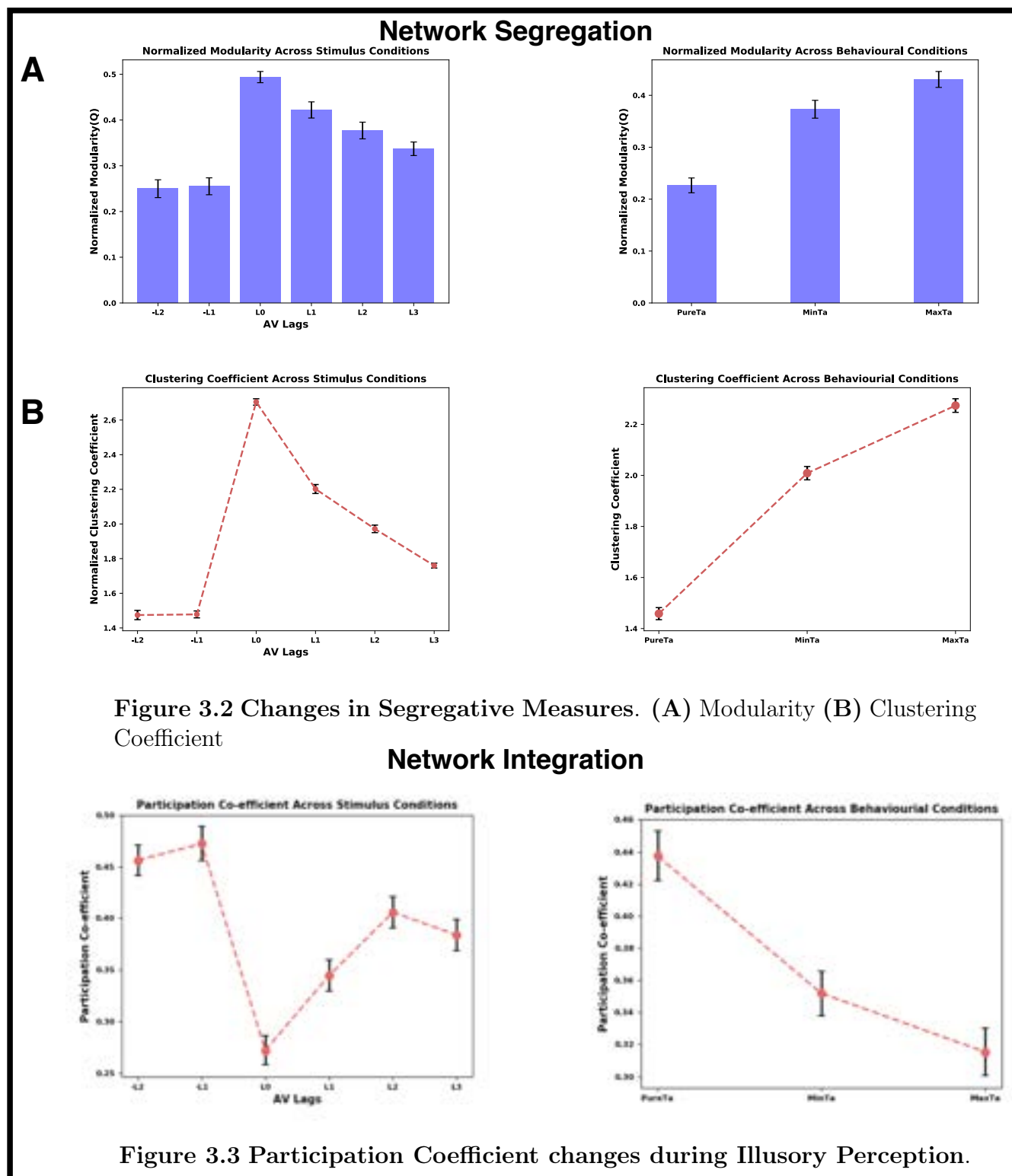
3.2   Changes in Segregative Measures

Modularity defines the ability of a system to be divided into dense internal clusters with limited connections to the other modules and clustering coefficient reveals the systems tendency to form local clusters. In quantitative terms, modularity index greater than 0.3 -0.4 points to a modular network architecture. The modularity index and the clustering coefficient were maximum for the synchronous condition and least for auditory-led asynchronies. They were notably higher at L0 . The modularity index of less than 0.3 for -L2 and -L1 suggest that the network architecture shifts from a modular to random for audio-led asynchronies. Moreover, there is an increase in network segregation of functional brain networks during cross-modal perception **(Figure 3.2)**.

3.3   Participation Coefficient

Once a network was divided into modules, the topological role of the 210 putative nodes was determined by the participation coefficient. The nodes with high participation coefficient act as information liaison between different modules in the network. The higher the participation coefficient, the more uniform is the distribution of the nodes' links across the entire network leading to expeditious information transfer. Thus, participation coefficient is one of the most efficient way to examine global integration **(Figure 3.3)**.

Network Segregation

A

B

Figure 3.2 Changes in Segregative Measures. **(A)** Modularity **(B)** Clustering Coefficient

Network Integration

Figure 3.3 Participation Coefficient changes during Illusory Perception.

We also plotted the distribution of various nodes across all the stimuli and behavioural conditions **(Figure 3.4)**.
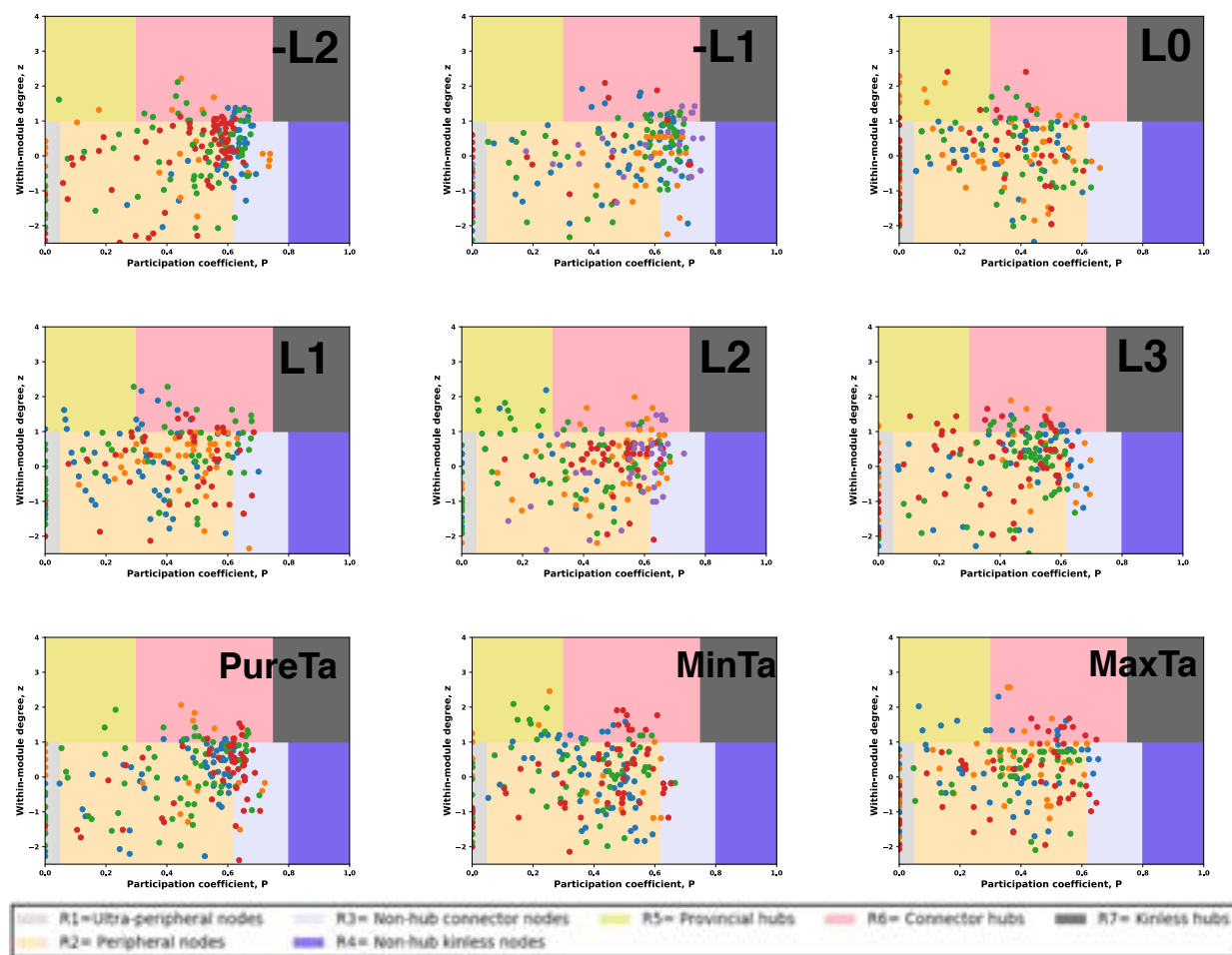
Figure 3.4 Functional Cartography maps.

3.4   Small World Index

We defined small-worldness as a property with enhanced local clustering and comparable path lengths. This is depicted by a slight difference in the characteristic path length with a significant change in clustering coefficient across different conditions. The small worldness is greater than 1 showing that the small-world architecture remains preserved across all the perceptual states. The small worldness was maximum for L0 depicting optimal segregation and in-

tegration when audio and visual signals are synchronous to each other. For behavioural conditions, the small world index was maximum for maximum illusory and minimum for PureTa. The brain seems to go towards a more random architecture as the time lag increase indicated by a decrease in small world index during asynchronous conditions.
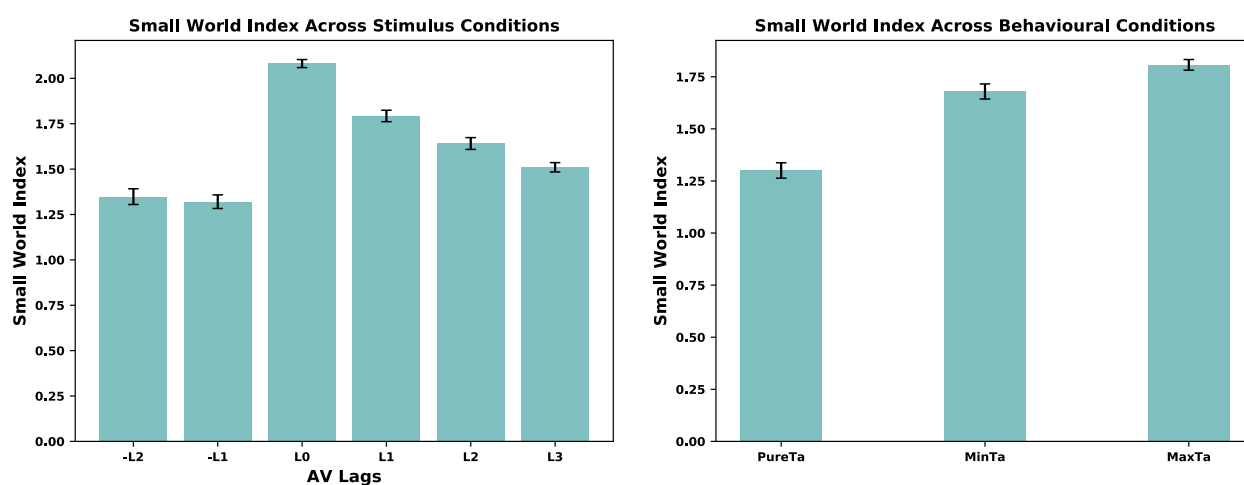
Figure 3.5 Small Worldness Increases during Cross-modal Perception.

3.5 Correlation between network characteristic and behavioural /ta/ perception

Pearson correlation analysis were performed to check the relationship between the global parameters and illusory /ta/ perception.

For modularity, characteristic path length, clustering coefficient and small-worldness, we observed significant positive correlation and for global efficiency we saw significant negative correlations.

Network Measure	Correlation*	SEM	p-value
Clustering Coefficient	0.41	0.02	<0.0001
Global Efficiency	-0.39	0.03	<0.0001
Path Length	0.41	0.05	<0.0001
Modularity	0.34	0.03	<0.0001
Small World Index	0.38	0.03	<0.0001

*These values are the average correlation of the 50 subsamples.

Table 3.1 Correlation between network characteristics and behavioural perception.

Chapter Four

Discussion and Conclusion

This study purported to investigate the changes in brain network organisation during illusory perception. We applied several graph theoretical measures to recognise the differences in segregation and integration of brain networks across a repertoire of perceptual states. The main findings of this study are:

1) The functional organisation of brain networks changes for different stimuli conditions.

2) Functional segregation was greater for synchronous AV lag and functional integration was higher for asynchronous AV lags.

3) For behaviourial conditions, segregation was higher for maximum illusory(MaxTa) and least for PureTa.

4) When comparing across asynchronous stimuli, segregation was higher for visual-led asynchronies and integration was higher for audio-led asynchronies.

5) Across all the conditions, the modular and small-world organisation remains preserved.

4.1 Integration versus Segregation

The network analysis revealed enhanced segregation and reduced integration with temporal congruity of the audio-visual stimulus. The increased segregation with synchronous audio-visual stimuli is a probable mechanism to circumvent cross-talk and ensure communication between specific local modules processing information to generate a unified percept.

A recent study by Morís Fernández et al. illustrated enhanced activation of brain areas involved in general conflict processing namely, anterior cingulate cortex coupled with AV speech specific conflict regions like inferior frontal gyrus with the presentation of asynchronous audio-visual stimuli [41, 42].

A plethora of behavioural studies have demonstrated diminishing illusory perception with temporal incongruity depicting a more resource-intensive processing during asynchronous AV lags than with congruent stimuli [13, 42]. All this points to the requirement of a more distributed processing of information with incongruent stimuli. Thus, there is an increase in functional integration with asynchronous audio-visual stimuli to ensure a stable and reliable percept.

Moreover, an increase in modularity, clustering coefficient and characteristic path length coupled with a decrease in global efficiency and participation coefficient during synchronous conditions and vice-versa during asynchronous conditions is brain's way to make best possible prediction about the stimulus in a cost-effective manner.

4.2 Modular Brain Organisation

Biological systems show a penchant for modular network organisation. The modules are structurally segregated and functionally specialised. Therefore, modular organisation proffers various advantages such as increased adaptablility with changing environment(rapid and restricted changes in confined modules) [40] and reduced wiring cost(a decrease in the length and number of connections) [24].

An increase in modularity with illusory perception is essentially to enhance accuracy and speed of perception with minimised wiring cost. Parallel information processing can take place in distinct modules and specific information can be rapidly integrated to generate coherent percept.

4.3 Small-World Architecture : the acme of segregation and integration

The small world architecture is nature's solution to balance segregation and integration. The nodes in a small-world network are banded together to form local clusters whereas, a few long range connections ensure a faster communication across network. The small world architecture remains preserved across all the perceptual states evincing that the brain organises itself in the most optimal manner possible to generate a unified coherent view of the world.

4.4   Limitations

Our graph theoretical analysis approach has obvious limitations. First, we only used a single brain atlas i.e., Brainnetome atlas to demarcate the nodes in our graph. Since there is no general consensus about the most optimal and accurate parcellation strategy, an analysis with multiple atlases would further substantiate our results may provide Second, the choice of threshold and z-score to classify hubs albeit based on generally accepted definitions were arbitrary. Therefore, a general conundrum is to develop efficient strategies of network characterisation to avoid a smidgen of arbitrary.

In conclusion, we performed graph-theoretical analyses to quantify changes in the principles of functional organisation i.e., functional segregation and functional integration with cross-modal perception

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