DYNAMIC SPEECH NETWORKS IN THE BRAIN: DUAL CONTRIBUTION OF INCREMENTALITY AND CONSTRAINTS IN ACCESS TO SEMANTICS

ECE KOCAGÖNCÜ

QUEENS' COLLEGE
UNIVERSITY OF CAMBRIDGE

THIS DISSERTATION IS SUBMITTED FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY.

SEPTEMBER 2016

Aileme ve öğretmenlerime

DECLARATION

I hereby declare that this dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration, except where specifically indicated in the text. It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution. I further state that no substantial part of my dissertation has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University of similar institution, except where specifically indicated in the text. This dissertation contains less than 60,000 words as prescribed by the Biology Degree Committee excluding appendices, bibliography, footnotes, tables and equations.

Ece Kocagöncü
September 2016

ACKNOWLEDGEMENTS

I would like to give my thanks to all the people who contributed in some way to the creation of this thesis. First and foremost, I would like to express my deepest gratitude to my supervisor, Professor Lorraine K. Tyler, who offered advice throughout my PhD, provided insightful discussions, and systematic guidance. I am very thankful to Dr. Alex Clarke for all the friendly guidance he has given, the effort he put in training me, patiently putting up with my endless questions, and helping me develop as a researcher. I thank my thesis committee, Professor Piers Cornelissen and Dr. Olaf Hauk who kindly agreed to review and help improve my thesis. I am grateful for the generous support I received from the Istanbul Chamber of Commerce which funded my education.

I thank my office mates, Dr. Alex Clarke, Dr. Elisa Carrus and Dr. Andreas Maruchos for providing a friendly and cooperative atmosphere. I want to thank past and present members of CSLB especially Dr. Billi Randall, Dr. Barry Devereux, Dr. Darren Price, Dr. Karen Campbell, Dr. Elisabeth Fonteneau and many others for sharing their knowledge and their insightful discussions. They all helped in numerous ways during various stages of my PhD. Special thanks to Elisabeth, who has been my graduate advisor for the majority of my PhD, for the advices she has given in times of need, and for cordial listening. I would like to express my special appreciation and thanks to my tutor, Professor Lisa Hall, the Queens' College MCR, and my graduate advisor Dr. Dénes Szücs for providing a family-like atmosphere in Cambridge, and their support in difficult times.

I will forever be indebted to my former supervisors Professor Sacit Karamürsel and Dr. Gülüstü Kaptanoğlu; and teachers, Professor Reşit Canbeyli, Dr. Esra Mungan, and Dr. Adnan Kurt at Boğazici University and Istanbul University, who are responsible for my love of neuroscience and for being such great role models for becoming a scientist, mentor and teacher. I thank my friends, especially Deniz, Freya, Ruta, Salema and Vittoria for all the great times we shared, for making Cambridge feel like a second home, for your kindness, for being there for each other.

I especially thank my mum and dad, for the unconditional love, support and encouragement, for their sacrifices, for listening to my frustrations, and for believing in me. I would not have made it this far without them.

ABSTRACT

This thesis explores the spatiotemporal network dynamics underlying natural speech comprehension, as measured by electro-magnetoencephalography (E/MEG). I focus on the transient effects of incrementality and constraints in speech on access to lexical semantics. Through three E/MEG experiments I address two core issues in systems neuroscience of language: 1) What are the network dynamics underpinning cognitive computations that take place when we map sounds to rich semantic representations? 2) How do the prior semantic and syntactic contextual constraints facilitate this mapping?

Experiment 1 investigated the cognitive processes and relevant networks that come online prior to a word's recognition point (e.g. *"f"* for *butterfly*) as we access meaning through speech in isolation. The results revealed that 300 ms before the word is recognised, the speech incrementally activated matching phonological and semantic representations resulting in transient competition. This competition recruited LIFG, and modality specific regions (LSMG, LSTG for the phonological; LAG and MTG for the semantic domain). Immediately after the word's recognition point the semantic representation of the target concept was boosted, and rapidly accessed recruiting bilateral MTG and AG.

Experiment 2 explored the cortical networks underpinning contextual semantic processing in speech. Participant listened to two-word spoken phrases where the semantic constraint provided by the modifier was manipulated. To separate out cognitive networks that are modulated by semantic constraint from task positive networks I performed a temporal independent component analysis. Among 14 networks extracted, only the activity of bilateral AG was modulated by semantic constraint between -400 to -300 ms before the noun's recognition point.

Experiment 3 addressed the influence of sentential syntactic constraint on anticipation and activation of upcoming syntactic frames in speech. Participants listened to sentences with local syntactic ambiguities. The analysis of the connectivity dynamics in the left frontotemporal syntax network showed that the processing of sentences that contained the less anticipated syntactic structure showed early increased feedforward information flow in 0-100 ms, followed by increased recurrent connectivity between LIFG and LpMTG from the 200-500 ms from the verb onset.

Altogether the three experiments reveal novel insights into transient cognitive networks recruited incrementally over time both in the absence of and with context, as the speech unfolds, and how the activation of these networks are modulated by contextual syntactic and semantic constraints. Further I provide neural evidence that contextual constraints serve to facilitate speech comprehension, and how the speech networks recover from failed anticipations.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

NOMENCLATURE

AAL	Automated anatomical labelling atlas
ATL	Anterior temporal lobe
AG	Angular gyrus
BA	Broadmann area
BEM	Boundary element method
B model	Backward model
BMS	Bayesian model selection
BMA	Bayesian model averaging
CSA	Conceptual structure account
DCM	Distributed cohort model
DCM-ERP	Dynamic causal modelling for event related potentials
DCT	Discrete cosine transform
DM	Distributional memory
DOM	Dominant phrase
ECD	Equivalent current dipole
ECoG	Electrocorticography
ECG	Electro-cardiogram
EEG	Electroencephalography
EM	Expectation maximisation
EOG	Electro-oculogram
ELAN	Early left anterior negativity
ERF	Event-related field
ERP	Event-related potential
F model	Forward model
FB model	Forward-backward model
FC model	Fully connected model
fMRI	Functional magnetic resonance imaging
GLM	General linear model
HPI	Head position indicators
IC	Independent component
ICA	Independent component analysis

tICA	Temporal independent component analysis
IFG	Inferior frontal gyrus
IPL	Inferior parietal lobule
Iq	Quality index
ITS	Inferior temporal sulcus
LAN	Left anterior negativity
MDN	Multiple demand network
MEG	Magnetoencephalography
MTG	Middle temporal gyrus
MUC	Memory unification control model
MVPA	Multivariate pattern analysis
No C	No constraint
PMN	Phonological mismatch negativity
PPI	Psychophysical interaction
PWD	Pure word deafness
PWI	Picture-word interference
RDM	Representational dissimilarity matrix
RSA	Representational similarity analysis
S model	Serial model
SMG	Supramarginal gyrus
STG	Superior temporal gyrus
STS	Superior temporal sulcus
ssRSA	Spatiotemporal searchlight representational similarity analysis
Strong C	Strong constraint
SUB	Subordinate phrase
TMS	Transcranial magnetic stimulation
TSA	Transcortical sensory aphasia
UNAMB	Unambiguous phrase
UP	Uniqueness point
VLPFC	Ventrolateral prefrontal cortex
VOT	Voice onset time
WA	Wernicke's aphasia
Weak C	Weak constrain

CHAPTER 1

INTRODUCTION

1.1. SPEECH IS INCREMENTAL

Speech carries rich linguistic information such as the sentence structure, previous discourse content, rhythmic, prosodic and gestural cues as well as the meaning. This rich information is delivered rapidly between 125-400 words per minute (Foulke, 1968). Despite its richness and the high speed of the speech delivery, speech comprehension comes to us so natural and effortless. Our comprehension is not disrupted even when the speech is degraded to a degree (Strauß, Kotz, & Obleser, 2013; A. E. Wagner, Toffanin, & Başkent, 2016), presented in a noisy environment (Nahum, Nelken, & Ahissar, 2008; Obleser & Kotz, 2010), and when it is ambiguous (Rodd, Vitello, Woollams, & Adank, 2015; van Berkum, Brown, Hagoort, & Zwitserlood, 2003). Two main contributing factors make speech comprehension robust: speech's incremental nature and the contextual constraints. The incrementality of speech involves rapid unfolding of the speech input which requires us to process acoustic-linguistic information in parallel and in small segmented units at a time (M. H. Davis, Marslen-Wilson, & Gaskell, 2002). Rapid speech comprehension requires efficient online speech processing which is often aided by contextual cues that allow us to anticipate the upcoming speech and speed up comprehension.

Speech is delivered at a rapid rate, at about 10-15 phonemes per second. However, human memory for auditory events is limited. The human auditory working memory spans up to seven (plus or minus two) randomly ordered meaningful items (e.g. words, letters, digits) (Miller, 1956). In running span paradigms, participants are able to recall the last 3-5 digits they heard, which is equivalent to less than 2 seconds of listening (Baddeley & Hitch, 1974; Cowan, 2001). This suggests that as we listen to speech, the acoustic input needs to be processed rapidly, before it is overwritten by the incoming speech. This physiological limitation is referred to as the now-or-never bottleneck of speech (Christiansen & Chater, 2015). Thus, the physiological capacity of the verbal working memory and the transient nature of speech, forces multiple linguistic information to be rapidly processed online as the speech unfolds.

This thesis investigates the cortical network dynamics that underpin the incremental cognitive processes performed during speech-to-meaning mapping and the modulations of these processes by contextual constraints over time. In this chapter I will give an overview on and compare cognitive models of spoken word recognition. Then I will discuss the current neuroimaging and neuropsychology literature on the cortical regions underpinning speech-meaning mapping, temporal dynamics associated with underlying cognitive processes, and spatiotemporal modulations due to contextual constraints.

1.2. COGNITIVE MODELS OF SPEECH COMPREHENSION

Early models of speech comprehension included a precognition memory buffer which stored the linguistic information for later processing and integration (Cutting & Pisoni, 1978; Pisoni & Sawusch, 1975). This buffer was thought as a temporary storage where the acoustic information is preserved for a short period of time to be operated on at a later stage. However, this view of delayed processing with accruing behavioural evidence got superseded by incremental models of speech comprehension. Contemporary views of spoken word recognition agree that it involves incremental interpretation and that we do not wait until we reach the end of the sentence to process the acoustic signal (Altmann & Kamide, 1999; Marslen-Wilson & Tyler, 1980).

Here incremental interpretation refers to processing of linguistic representations on the fly as the speech accrues. For example, garden path sentences (e.g. *The man who whistles* *<u>tunes</u>* *pianos*) that contain local ambiguities that are quickly resolved by the upcoming speech, indicate that speech is processed online and meaning is constructed and updated as we listen. These sentences also show that whilst listening to continuous speech we consider multiple meanings/representations that match the speech input (e.g. *tuning pianos* and *whistling tunes*). Supporting the view of activation of multiple representations, priming studies report that both the lexical representations (e.g. *capital*, *captain*) that match the speech input (e.g. /*kæp*/) and their semantic associates (e.g. *money*, *ship*) are activated in parallel before the word is recognised (Zwitserlood, 1989). Further, the post-offset phonemes have been shown to activate the lexical representations of the embedded words (e.g. *bone* in *trombone*) and their semantic associates (e.g. *rib*) (Luce & Cluff, 1998; Shillcock, 1990). These results indicate that lexical and semantic representations that match the speech input are activated incrementally as the speech is heard irrespective of phonemes' positions in the word. Even though contemporary models of speech comprehension agree on the incremental processing of speech, they diverge by the proposed nature of lexical activations, lexical competition and the information flow between levels of processing. In the next section, for simplicity, I will discuss four key models that were behaviourally validated: the cohort model, TRACE, Shortlist and the Distributed Cohort Model (DCM).

1.2.1. THE COHORT MODEL

The cohort model was the first psycholinguistic model developed specifically for speech comprehension (Marslen-Wilson & Tyler, 1980; Marslen-Wilson & Welsh, 1978). According to the cohort model speech comprehension involves three processes: access, selection and integration. During access, lexical representations of words that match the speech input (e.g. /*hæ/)* are activated in the parallel (e.g. *hammer, ham, hamster, hangar*) (Figure 1.1). This set of words that have common word-onset phonemes is called *the cohort.* As the speech unfolds, the representations that no longer match the speech input or the sentential context are removed from cohort (i.e. selection). The selection ends when only one word remains in the cohort, the target word. The point on the spoken word, where the cohort size is one, is called the uniqueness point (UP). Finally, during integration, the syntactic and semantic representations of the target are integrated. This suggests that words can be recognised before their offset.

The challenges made to the cohort model were twofold. Firstly, it was suggested that word-onset or context match should not be crucial, as listeners can recognise words that are mispronounced (Levelt, 1983) or that mismatch with the context (Cole, 1973). Secondly, the model does not account for the finding that listeners recognise frequent words earlier than non-frequent words (Taft & Hambly, 1986). Subsequently, the cohort model was modified to account for these two challenges (Marslen-Wilson, 1987, 1990). In this modified version, words that phonologically diverged (e.g. *hammer* - *grammar*) from the speech input were added to the cohort. Moreover, to account for the word frequency facilitation in word recognition, the activation levels of the cohort candidates were weighted by their frequencies. Thus, frequent words were activated at a higher level compared to infrequent words, and were recognised earlier (Marslen-Wilson, 1987). The cohort model led to the development of subsequent computational models of speech comprehension.

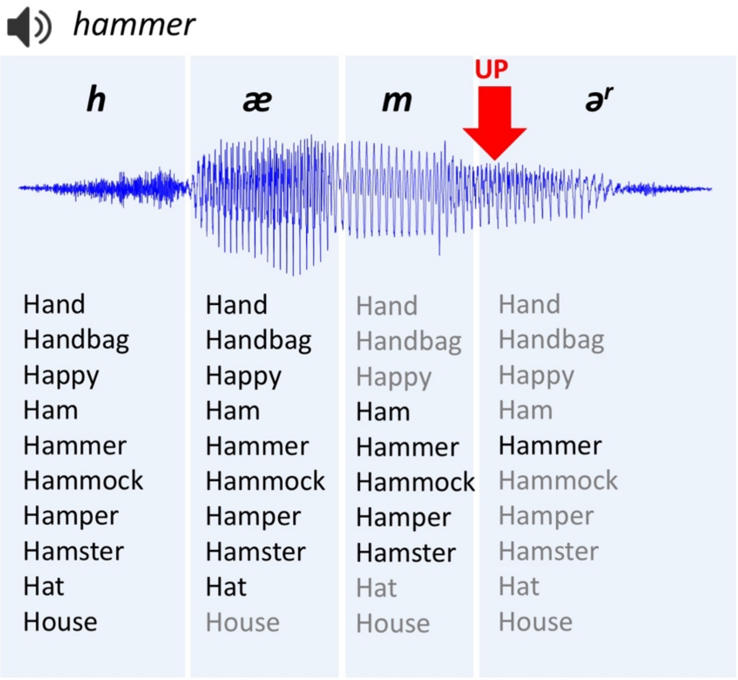


FIGURE 1.1. EXAMPLE DEPICTING THE COHORT ACTIVATION AND CHANGE OVER TIME FOR HAMMER. BLACK AND GREY WORDS INDICATE ACTIVATED AND DECAYING COHORT CANDIDATES RESPECTIVELY. HERE, HAMMER'S COHORT SIZE IS REDUCED TO A SINGLE ITEM AFTER HEARING THE LAST PHONEME, THEREFORE WORD'S UNIQUENESS POINT IS THE LAST PHONEME.

1.2.2. COMPUTATIONALLY IMPLEMENTED MODELS

The computational models aimed to implement the cognitive processes underlying speech comprehension and assess the model's behaviour against humans'. These models received the raw speech as input. However, the subsequent processing steps and the assumptions varied across models. TRACE is a computationally implemented model of speech comprehension which implements lexical activation in a three layered connectionist architecture, where the layers code features, phonemes and words (McClelland & Elman, 1986). Compared to the cohort model, TRACE accounts for the activation of post-word onset embedded words (e.g. *bone* in *trombone*), thus, any part of the speech input is allowed to activate lexical representations. In this architecture, phonemic features extracted from the speech input initially activate the nodes in the feature layer. This activation then spreads to the corresponding nodes in the phonemic and word layers. The level of node activation varies with the strength of match with speech input, which in turn results in different activation levels at the word layer. The word that is activated the strongest will inhibit the remaining words, and will be recognised. To account for the temporal extent of speech, TRACE uses reduplication where the linguistic representations at each layer are reduplicated at successive time slices.

Further, TRACE architecture allows information flow from higher to lower linguistic levels, which meant that prior lexical knowledge can influence speech perception via top-down modulations. In a later version, TRACE also accounts for the word frequency effects by weighting the resting activation levels of words (Dahan, Magnuson, & Tanenhaus, 2001), and for the time course effects of phonological competition (Allopenna, Magnuson, & Tanenhaus, 1998). However, the reduplication of phoneme templates to account for the temporal unfolding of speech, was thought to be an inelegant and inefficient solution (Norris, 1994; Strauss, Harris, & Magnuson, 2007).

The feedback connectivity of its architecture was criticised with the argument that this additional top-down information flow cannot speed up recognition or improve accuracy, as there is no way of increasing the information already available in the signal (Frauenfelder & Peeters, 1998; Norris, McQueen, & Cutler, 2000). Further it was suggested that feedback information flow can disrupt word recognition, and that sensory predictions can lead to perceptual hallucinations (Norris & McQueen, 2008; Norris et al., 2000). A study compared the accuracy and recognition time of a large set of words in TRACE, with feedback on and off (Magnuson, Strauss, & Harris, 2005). They added different levels of noise to the speech input, and found that recognition time and accuracy is better when the speech is noisy and feedback is on. Moreover, the fact that we can detect mispronunciations (Cole, 1973; Marslen-Wilson & Welsh, 1978), restore noise-replaced phonemes

(Samuel, 1981, 1996; R. M. Warren & Warren, 1970) indicate that the lexical knowledge informs pre-lexical processing.

Marslen-Wilson and Warren (1994) have investigated lateral inhibition in TRACE by cross-splicing spoken words to give participants coarticulatory misleading cues on the final consonant (Marslen-Wilson & Warren, 1994). There were three kinds of words created: cross-splicing of the same word from different recordings (e.g. *net+net*), of two meaningful words (e.g. *neck+net*) and of a nonword and a meaningful word (e.g. *nep+net*). The authors simulated TRACE's activations and compared them against lexical decision data. Lexical data showed equally high activations for neck+net and nep+net, followed by net+net. However, TRACE's simulations indicated that neck+net to have the highest activation followed by nep+net and net+net. The authors concluded that the lateral inhibition implemented in TRACE was too strong compared to data from humans.

Another computational model of speech comprehension, Shortlist, was developed to account for the challenges made to feedback connectivity (Norris, 1994). Shortlist's architecture consists of two layers: the input and word layer. As the speech unfolds, for each phoneme heard, a serial search is performed to find a small set of words (i.e. shortlist) that best match the phoneme onset. The activations of lexical representations are weighted by the degree to which the words match the speech input. Similar to TRACE, any part of the speech input is allowed to activate representations. Representation that were highly activated will reduce the activation levels of other candidates and will be recognised. Compared to TRACE the key difference is that Shortlist does not incorporate any feedback connections between layers. The second version of the model called the Shortlist B modified the model to operate under Bayesian principles (Norris & McQueen, 2008). In Shortlist B, speech comprehension is underpinned by phoneme and word probabilities, of which prior probabilities are modulated by their frequencies. Shortlist despite its modifications, due to its core premise that speech comprehension is a purely feed-forward system, appears to be in contrast to vast literature on the top-down modulations in speech comprehension (M. H. Davis, Johnsrude, Hervais-Adelman, Taylor, & McGettigan, 2005; de Zubicaray, McMahon, Eastburn, & Pringle, 2006; Noesselt, Shah, & Jäncke, 2003; Wild, Davis, & Johnsrude, 2012) and the existence of feedback white matter connectivity of the neural language system (Koziol & Budding, 2009; Salmelin & Kujala, 2006). Further, Shortlist B has been criticised to implement a Bayesian architecture by discarding key components to Bayesian approaches: the top-down and bottom-up information flows (Movellan & McClelland, 2001).

The final model I am going to discuss is the distributed cohort model (DCM) (Gaskell & Marslen-Wilson, 1997a). DCM, like TRACE and Shortlist, is a computational connectionist model. The architecture consists of three layers in a simple recurrent network design. The layers are the input layer that processes binary phonetic features, the hidden layer and the context layer. Its key difference from previous models and the cohort model is that the information is assumed to be represented in a distributed fashion than single nodes in the model. Therefore, in DCM, nodes of the layer represent phonological and semantic features of the words rather than phonemes and words themselves. The model's input layer activates the binary phonetic features extracted from the speech input, which in turn spreads to activate phonological features and semantic features (i.e. the blend) of the likely word candidates. This suggests that acoustic-phonetic features are directly mapped onto distributed lexical representations. Here as the cohort size increases, so does the competition, and in turn feature activation of the candidates decreases. Therefore, when the features of the cohort candidates are activated simultaneously, this results in an activated blend of features. As more of the speech input is heard, similar to the cohort model, the activation of the candidates' features that no longer match the speech input will decay over time, eventually

Model	**Reference**	**Model input**	**Pre-lexical representations**	**Word-form representations**	**Feedback**	**Competition**
Cohort	Marslen-Wilson & Welsh, 1978	Not specified	Features	Phonological representation	No	Competition does not impact activation
TRACE	McClelland & Elman, 1986	Phonetic features	Phonemes	Logogen	Yes	Lateral inhibition of competitors
Shortlist	Norris, 1994	Phonemes	Phonemes	Phoneme strings	No	Lateral inhibition of competition
DCM	Gaskell & Marslen-Wilson, 2002	Phonetic features	Phonetic features	Distributed feature vectors	No	Feature blending

TABLE 1.1. COMPARISON OF MAIN SPEECH COMPREHENSION MODELS.

narrowing down the cohort to a single word. When all the other cohort candidates gradually decay via mismatch elimination, only the semantic features of the target word will remain active, which will allow word recognition. DCM accounts both for the phoneme mismatch and the word frequency effects via the use of binary phonemic features and repeated presentation of the words in the model training. The authors' prediction that the activation of candidates that belong to a smaller cohort would be higher than those that belong to a large cohort (i.e. high competition) was validated through a priming study (Gaskell & Marslen-Wilson, 2002).

DCM further proposes that the lexical representations consist of dimensions that encode semantic and phonological features of the words. Compared to earlier models of speech comprehension that focus on the activation of lexical representations, the nature of lexical representations was a crucial and missing part of the puzzle. This has further implications on the competition processes. DCM suggests that as we hear speech, due to the match (i.e. goodness of fit) between the acoustic-phonemic features the partial activation of the phonological nodes of the architecture will be stronger than the activation of semantic nodes. This is due to the arbitrary mapping between the sound and the meaning of the words (i.e. words that sound similar do not have similar meanings). Due to this, DCM predicts strong effects of competition in semantics compared to phonology as the speech is heard over time (Gaskell & Marslen-Wilson, 1997b, 2002). Therefore, words that have a high number of cohort competitors will exhibit less semantic priming compared to words that have low number of competitors (Apfelbaum, Blumstein, & McMurray, 2011; Gaskell & Marslen-Wilson, 1999; Marslen-Wilson, 1990). A behavioural priming study provides evidence for distributed feature mapping of sound to meaning, by showing that different kinds of semantic properties (e.g. functional, perceptual) of words are activated over time before the word's UP (Moss, McCormick, & Tyler, 1997). The key features of the speech comprehension models described here are displayed in Table 1.1.

In summary, compared to earlier models of speech comprehension, DCM makes three key contributions: 1) the model takes a distributional approach -as opposed to a localist one- in the model architecture, and proposes a feature-based mapping between sounds and semantics (Masson, 1995; Plaut, McClelland, Seidenberg, & Patterson, 1996); 2) it models the transient temporal progression of competition processes rather than competition within the lexicon; and 3) it describes the organisational nature of the lexical representations as well as their retrieval processes. Because DCM is validated both behaviourally and computationally, and because it implements feature-based representations of both phonology and semantics, in this thesis, I have adopted DCM as the model of speech comprehension.

1.3. NEUROBIOLOGY OF SPEECH COMPREHENSION

A typical adult native English speaker knows about 30000 to 75000 words (Levelt, 1989; Oldfield, 1963). Due to speech's transient nature, we must rapidly process the sounds to recognise the word among thousands of words that we know. Sometimes the speech includes short term ambiguities (e.g. distinguishing words that sounds the same *knight/night*, or words that have multiple meanings *bark*) that can only be resolved post-hoc by the following speech input. Therefore, for the speech comprehension to occur smoothly the neural language system needs to perform rapidly and process and integrate acoustic information that is spread across time.

A considerable amount of evidence for the cortical regions involved in speech processing comes from studies on brain lesions. Broca describes his famous patients Tan and later Leborgne, who had a damage to the left inferior frontal gyrus (i.e. Broca's area; LIFG) which resulted in reduced speech fluency with spared speech comprehension (Broca, 1865). Wernicke's (Wernicke, 1874) seminal case study, on the other hand showed the opposite pattern, and have underlined the involvement of the left posterior temporo-parietal area (i.e. Wernicke's area) in speech comprehension, where damage results in spared fluent but unintelligible speech production and impaired speech comprehension.

Contemporary neurobiological models of speech were built on Wernicke and Broca's findings via numerous neuroimaging studies, and moved from a locationist view of language processing to a systemic one. Similar to the dual pathway structure of the visual system (Mishkin, Ungerleider, & Macko, 1983), speech is processed in two parallel streams: a ventral *what* stream that maps speech to meaning, and a dorsal *how* stream that maps speech to articulation (Ahveninen et al., 2006; Arnott, Binns, Grady, & Alain, 2004; Rauschecker & Scott, 2009; Saur et al., 2008). Therefore, they represent the receptive and expressive branches of speech processing. The dorsal how stream extends from the posterior superior temporal gyrus (STG), through the inferior parietal lobe (IPL), to premotor cortex and ends in the IFG (Hickok & Poeppel, 2007; Rauschecker & Scott, 2009) via the arcuate and superior longitudinal fasciculi (Saur et al., 2008). The what stream extends from middle temporal gyri (MTG), STG to the IFG via the extreme capsule (Saur et al., 2008). Within the interests of this thesis I will focus this review on the auditory what stream and its cortical dynamics involved in speech-meaning mapping (Figure 1.2).

1.3.1. ACOUSTIC-PHONEMIC ANALYSIS

In the earliest stage of speech processing acoustic-phonological characteristics of the speech input (i.e. pitch height, pitch chroma, intensity, timbre) are processed. Bilateral STG have been consistently reported to fulfil this function. Compared to silence, speech sounds including syllables, words and pseudowords activate STG bilaterally (Binder, 2000; Wise, Hadar, Howard, & Patterson, 1991). Neuroimaging studies relate STG activity to the rate of speech presentation (Dhankar et al., 1997; C. J. Price et al., 1992), changes in frequency (Zaehle, Wüstenberg, Meyer, & Jäncke, 2004), and spectral and temporal modulations (Britton, Blumstein, Myers, & Grindrod, 2009; Leaver & Rauschecker, 2010; Peelle & Davis, 2012; Su, Zulfiqar, Jamshed, Fonteneau, & Marslen-Wilson, 2014; Thwaites, Schlittenlacher, Nimmo-Smith, Marslen-Wilson, & Moore, 2016). Further, an electrocorticography (ECoG) study revealed that left mid STG's activity is sufficient to reconstruct intelligible speech forms indicating that the neural representation in STG is acoustic in nature (Pasley & Knight, 2013).

The cytoarchitectonic differences in the left and right STG indicate that STG's function in two hemispheres might not be identical; and as a result of these differences, these regions operate in different temporal windows. A hypothesis referred to as the *asymmetric sampling in time theory* (Poeppel, 2003) suggests that LSTG and RSTG respond to speech with gamma and theta dominant activity respectively, which makes these regions better equipped to process short (e.g. phonemes, syllables) and longer (e.g. harmonicity, periodicity) linguistic information respectively. These asymmetric temporal processing windows make LSTG more suitable to process rapidly unfolding speech segments, which was later validated by several fMRI studies (Boemio, Fromm, Braun, & Poeppel, 2005; DeWitt & Rauschecker, 2012; Giraud et al., 2007; Giraud & Poeppel, 2012).

Studies report that different kinds of acoustic information are processed in different subregions of STG. Comparison of non-speech sounds (e.g. tones, noise) with the speech specific sounds gives a clear indication on areas that process speech specific sounds. fMRI studies report higher activation for speech sounds compared to silence in bilateral STG (Binder, 2000; Wise et al., 1991). The activations are stronger in primary and belt auditory cortex, suggesting that the activation is due to acoustic processing. Primary and belt regions of the dorsal STG do not differentiate speech and non-speech sounds (Binder, Frost, Hammeke, Rao, & Cox, 1996); whereas ventral STG and neighbouring sulcus show more activity for speech sounds (DeWitt & Rauschecker, 2012). Further, an ECoG study reported that patches in STG respond selectively to different phonemic features and therefore phonemes (Chang et al., 2010; Mesgarani, Cheung, Johnson, & Chang, 2014). STG's role in acoustic-phonemic analysis is further corroborated by patient studies. A neurological disorder that results from bilateral STG damage is pure word deafness (PWD) (Auerbach, Allard, Naeser, Alexander, & Albert, 1982; Jones & Dinolt, 1952; Poeppel, 2001). Patients diagnosed with PWD cannot recognise or repeat spoken words, but have normal comprehension of written language. Since these patients have spared comprehension of text, the impairment can only be a result of impaired sublexical phonemic processing. Moreover, as we move from posterior-to-anterior of the STG, the cortical areas respond increasingly as a function of increasing complexity of the acoustic signal and intelligibility (i.e. tones and noise bursts to words and sentences) (Scott, Blank, Rosen, & Wise, 2000; Scott & Johnsrude, 2003; Scott, Rosen, Lang, & Wise, 2006). These findings demonstrate that subdivision in STG are differentially involved in perceptual acoustic processing of the sounds and phonological processing of the speech input.

Phonological contrasts (i.e. speech vs non-speech) in neuroimaging studies often reveal supramarginal gyrus (SMG) as well as STG (Dehaene-Lambertz et al., 2005; Démonet, Price, Wise, & Frackowiak, 1994). SMG is shown to be sensitive to changes in phonemes (Dehaene-Lambertz et al., 2005; Phillips, 2001), in syllables (Celsis et al., 1999), categorical perception of phonemes (Raizada & Poldrack, 2007), words that have greater phonological neighbourhood densities (Prabhakaran, Blumstein, Myers, Hutchison, & Britton, 2006), and phonological short-term memory (Buchsbaum et al., 2005; Hickok, Buchsbaum, Humphries, & Muftuler, 2003; Wise et al., 2001). Damage to the SMG, results in a syndrome called the conduction aphasia, which is characterised by impaired speech repetition, fluent spontaneous speech and preserved comprehension (Benson et al., 1973; Goodglass, 1992). The lesion often extends to the arcuate fasciculus underneath SMG (Benson et al., 1973; Damasio & Damasio, 1980). In conduction aphasia, Wernicke's area is typically spared, which accounts for the spared comprehension. Intact comprehension indicates that acoustic-phonological processing is carried out normally. However severe impairments in repetition, bolster the view that SMG underpins a post-phonological analysis deficit in phonological short-term memory.

Electrophysiological research relates perceptual acoustic processing of the sounds to the auditory evoked potential, N100 that peaks around 100 ms from the sound onset (Vaughan & Ritter, 1970). N100 is reported to reflect various dimensions of acoustic feature extraction and processing including frequency processing (Schönwiesner, von Cramon, & Rübsamen, 2002; Tramo, Shah, & Braida, 2002), perception of pitch chroma and height (Patel & Balaban, 2001; Tramo et al., 2002; J. D. Warren, Uppenkamp, Patterson, & Griffiths, 2003). N100 is also more sensitive to acoustic onsets of the signal, as it responds more strongly to the first syllable than middle syllables of the spoken word (Sanders & Neville, 2003). Further, its generators were located to bilateral supratemporal plane and the STG (Naanaten & Picton, 1987).

Another related electrophysiological response, the phonological mismatch negativity (PMN) is a negative deflection that peaks around 200-350 ms after the sound onset induced by the unexpected phonological representation of the spoken word (J. F. Connolly & Phillips, 1994). PMN in speech precedes the event related potential (ERP) induced by semantic incongruities, N400 which is observed around 400 ms (Kutas & Hillyard, 1980). For example, the last word in "*When the power went out the house became quiet*" is unexpected (i.e. as opposed to *dark*), and would evoke PMN followed by N400 (J. F. Connolly, Service, D'Arcy, Kujala, & Alho, 2001). Therefore, PMN is due to the mismatch between the expected and perceived phoneme, but not due to the semantic content of the word. Altogether, N100 and PMN findings indicate that as the speech is heard the acoustic processing is carried out around 100 ms, which is then followed by the phonological analysis between 200-350 ms.

1.3.2. COMPETITION IN SPEECH AND THE LIFG

As discussed in the earlier section, contemporary models of speech comprehension propose that as the speech is heard phonological and semantic representations that match the speech input are partially activated over time which creates competition (Gaskell & Marslen-Wilson, 1997a; McClelland & Elman, 1986). In this section I discuss the current evidence for the neural systems that underpin the lexical and semantic competition.

To tap into the network of regions involved in phonological competition, few studies used a picture-word interference (PWI) paradigm. In PWI the participants listen to words (e.g. *beaker*) whilst being displayed pictures of objects (e.g. *beaker, beetle, shoe, hammer*). On some trials the objects on the display include a lexical competitor that shared the first two phonemes with the spoken word (e.g. *beetle*). Studies show activity in LIFG, LSMG and LSTG when the spoken words are presented with a picture of a lexical competitor (Abel et al., 2009; Righi, Blumstein, Mertus, & Worden, 2010). Using the same paradigm de Zubicaray et al. (2002) have additionally shown activity in bilateral MTG, L anterior cingulate, and bilateral orbitomedial prefrontal cortex.

Studies that investigate semantic competition reveal a separate but overlapping network of regions. An fMRI study that presented participants spoken sentences that included local semantic ambiguities, found increased activity in bilateral IFG and MTG (Rodd, Davis, & Johnsrude, 2005). In a PWI study increased semantic competition (i.e. harder word retrieval), induced activity in LIFG (de Zubicaray & McMahon, 2009). Corroborating this finding, Moss et al. (2005) have manipulated competitor priming via order of picture presentation and showed increased LIFG activity to increased selection demands when naming objects. Further using verbal and category fluency tasks which increase the demand for word retrieval, Paulesu et al. (1997) found increased activity in the LIFG (Broadmann area 45; BA 45) for both tasks.

Patient studies provide further evidence for the cortical areas that are crucial for lexical access and resolving competition. Eye movements can be used to provide dynamic information on the lexical activation over time. When eye tracking is implemented in a PWI paradigm, one can calculate the time participants fixate on displayed items which in turn indicates the lexical representations activated due to the spoken word presentation. For example, when participants listen to "*Pick up the beaker*", they will fixate on the picture of *beetle* before settling on *beaker*; which suggests that the lexical representation of beetle is also activated. In these paradigms, aphasia patients show that compared to controls, the overall activation of lexical representations is lower in Broca's aphasics and higher in Wernicke's aphasics (Janse, 2006; McNellis & Blumstein, 2001; Misiurski, Blumstein, Rissman, & Berman, 2005). Similarly compared to controls, Broca's and Wernicke's aphasics show weaker and stronger word-onset competitor effects respectively (Yee, Blumstein, & Sedivy, 2008). This pattern might potentially be due to impaired lexical activation in Broca's aphasics and impaired lexical elimination (i.e. deactivation) in Wernicke's aphasics (Prather, Zurif, Love, & Brownell, 1997).

A couple of studies took a closer look at the issue of lexical activation in aphasia. Milberg et al. (1988b) used a semantic priming paradigm where they presented participants word pairs that were semantically related (e.g. *cat-dog*), where the first word was modified by one phonetic feature (e.g.

gat-dog), and where it was modified by multiple phonetic features (e.g. *wat-dog*). Healthy participants showed a graded decline in semantic priming as a function of increased phonetic modification; whereas Broca's aphasics showed priming only for the non-modified word pairs. The authors argue that Broca's aphasics suffer from inadequate lexical activation when the speech input does not perfectly overlap with the stored lexical representation, which is consistent with both DCM's and TRACE's assumptions (Gaskell & Marslen-Wilson, 1997a; McClelland & Elman, 1986). Another study used a similar paradigm and instead of modifying the phonetic features, it shortened the duration of the word onset phoneme (i.e. voice onset time, VOT) (Utman, Blumstein, & Sullivan, 2001). Here controls displayed a short-lived reduction in semantic priming as the VOT increased, whereas Broca's aphasics showed a long lasting reduction in priming. These studies demonstrate the central role of LIFG in lexical activation in speech comprehension.

In addition to its role in lexical activation, LIFG has been proposed to be involved in various executive functions including controlled retrieval of representations from memory (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005), unification of linguistic representations (Hagoort, 2005; Hagoort, Baggio, & Willems, 2009), and the resolution of competition among multiple likely representations by selection (Schnur et al., 2009; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). There is neuroimaging evidence corroborating all three major views. Thompson-Schill et al. (1997) have proposed that LIFG's role in comprehension is to select the relevant information among all competing representations to resolve the competition. A study using a picture naming paradigm, presented participants pictures either in the same semantic category (e.g. *truck, bike, boat*), or in a mixed order of categories (Schnur et al., 2009). Presenting subsequent objects from the different categories was assumed to increase competition whilst producing the object's name due to reduced category priming and increased demand for selection. They found increased activity in LIFG and LMTG with increased lexical competition and demand for selection. Further they reported that the degree of damage to the posterior LIFG significantly correlated with naming performance. The authors conclude that posterior LIFG's role is to resolve competition by selection. This view was later supported by numerous neuroimaging studies (Bedny, McGill, & Thompson-Schill, 2008; Grindrod, Bilenko, Myers, & Blumstein, 2008; Moss et al., 2005; Novick, Trueswell, & Thompson-Schill, 2005).

Badre and Wagner (2002), on the other hand propose that LIFG's role in comprehension is the controlled retrieval and activation of semantic and lexical representations from memory. The authors differentiate this form of retrieval from automatic retrieval. Automatic retrieval can be triggered by an external sensory cue, and therefore activate the representation in a purely bottom-up fashion and would not require LIFG. This theory therefore focuses on the controlled retrieval of representations. Bolstering this theory, LIFG activity was reported for conditions that require goal-directed access to semantics (Gabrieli, Poldrack, & Desmond, 1998; Poldrack et al., 1999), making semantic decisions (M. H. Davis & Johnsrude, 2003; M. H. Davis, Meunier, & Marslen-Wilson, 2004; Tyler, Bright, Fletcher, & Stamatakis, 2004), and classifications (Devlin, Matthews, & Rushworth, 2003; Gold & Buckner, 2002; Noppeney, Phillips, & Price, 2004).

Authors however add that the controlled retrieval can sometimes result in activation of multiple representations which causes competition. Similar to Thompson-Schill et al. (1997), Badre and Wagner (2002) suggest that in these instances, *post-retrieval selection* is required to resolve the competition. In an fMRI study Badre et al. (2005) have modulated the degree of selection and retrieval demands in their design, and revealed that left anterior (BA 47) and mid LIFG (BA 44/45) was sensitive to semantic retrieval and selection respectively. However a recent study have failed to replicate these findings. Whitney et al. (2011) have tested the involvement of LIFG subdivisions on tasks that vary in semantic and non-semantic control demands, and found that both LIFG (BA 45/47) and LpMTG are involved in the controlled retrieval and selection of semantic knowledge, and failed to find a distinction across LIFG subdivisions.

A third view is that LIFG is involved in unification (i.e. integration) processes in language (Hagoort, 2005). The theory proposes that linguistic manipulations like cloze probability and violations modulate the unification demands and induce activity in LIFG. Hagoort further proposes that there is a rostro-caudal gradient of sequence processing in the LIFG, where the BA 47, BA 45 and BA 44 unify semantic, syntactic and phonological sequences in language respectively (Hagoort, 2005; Hagoort et al., 2009; Uddén & Bahlmann, 2012).

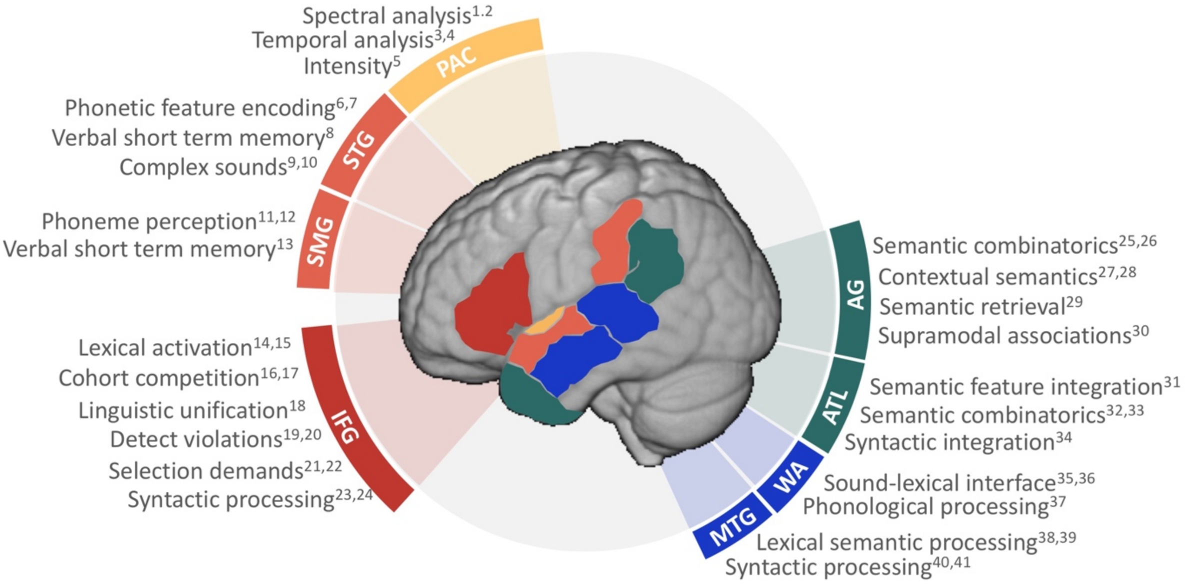


FIGURE 1.2. CORTICAL AREAS INVOLVED IN SPEECH COMPREHENSION AND THEIR REPORTED FUNCTIONS. AREAS SHOWN ARE THE PRIMARY AUDITORY CORTEX (PAC), SUPERIOR, MIDDLE TEMPORAL GYRI (STG AND MTG), SUPRAMARGINAL GYRI (SMG), ANGULAR GYRI (AG), INFERIOR FRONTAL GYRI (IFG), ANTERIOR TEMPORAL LOBES (ATL), AND WERNICKE'S AREA (WA). COLOURS INDICATE GROUPS OF COGNITIVE FUNCTIONS. YELLOW: ACOUSTIC ANALYSIS; ORANGE: PHONOLOGICAL PROCESSING AND VERBAL SHORT TERM MEMORY; RED: EXECUTIVE FUNCTIONS RELATED TO LANGUAGE; GREEN: COMBINATORIAL PROCESSES; BLUE: ACCESS TO SYNTAX AND LEXICAL SEMANTICS. 1 ZAEHLE ET AL. (2004); 2 FORMISANO ET AL. (2003); 3 BRITTON ET AL. (2009); 4 DHANKAR ET AL. (1997); 5 GUTSCHALK ET AL. (2002); 6 CHANG ET AL. (2010); 7 MESGARANI ET AL. (2014); 8 LEFF ET AL. (2009); 9 MIRZ ET AL. (1999); 10 SCOTT ET AL. (2000); 11 RAIZADA & POLDRACK (2007); 12 SLIWINSKA ET AL. (2012); 13 BUCHSBAUM ET AL. (2005); 14 PAULESU ET AL. (1997); 15 BADRE ET AL. (2005); 16 ZHUANG ET AL. (2011); 17 ZHUANG ET AL. (2014); 18 HAGOORT (2005); 19 PETERSSON ET AL. (2004); 20 FRIEDERICI ET AL. (2003); 21 MOSS ET AL. (2005); 22 THOMPSON-SCHILL ET AL. (1997); 23 GRODZINSKY ET AL. (1999); 24 PEELLE ET AL. (2004); 25 PRICE ET AL. (2015); 26 GRAVES ET AL. (2010); 27 OBLESER ET AL. (2007); 28 LAU ET AL. (2008); 29 BINDER ET AL. (2009); 30 ELSTON ET AL. (2001); 31 PATTERSON ET AL. (2007); 32 BARON & OSHERSON (2011); 33 BEMIS & PYLKKANEN (2011); 34 FRIEDERICI ET AL. (2000); 35 DAVIS & GASKELL (2009); 36 RISSMAN, ELIASSEN & BLUMSTEIN (2003); 37 BUCHSBAUM ET AL. (2001); 38 GOW (2012); 39 HICKOK & POEPPEL (2004); 40 TYLER ET AL. (2011); 41 TYLER ET AL. (2013).

In line with this proposed functional division, unexpected pitch accent in sentences (van Leeuwen et al., 2014), generating regularised pronunciations of words with irregular spellings (Gold, Balota, Kirchhoff, & Buckner, 2005) induced activity in BA 44/45. Morphological processing (Bozic, Tyler, Ives, Randall, & Marslen-Wilson, 2010), generation of inflected forms (Sahin, Pinker, Cash, Schomer, & Halgren, 2009), artificial grammar violations (Petersson et al., 2004), noun-verb ambiguities (Snijders et al., 2009) also activated BA 45. Lastly, processing high versus low cloze probability words in a sentence (Zhu et al., 2012), sentences with incongruent meaning (Tesink et al., 2009), and sentences with world knowledge anomalies (Menenti, Petersson, Scheeringa, & Hagoort, 2009) increased activity in BA 47. Even though the literature lacks a clear consensus of LIFG's functional role, the studies discussed above show that it is at the centre of language comprehension and competition.

1.3.3. MAPPING SPEECH TO MEANING

Speech comprehension occurs when sound patterns that we are familiar with are mapped onto stored meaning representations in the brain. This process however, is not straightforward. The sound patterns are acoustically and phonologically processed as the speech signal accrues over time, which is integrated as the input unfolds. Further, in the face of semantic ambiguity lexical access requires the listener to select the target meaning among multiple potential meanings. In the previous section I briefly discussed the regions proposed to subserve verbal short-term memory. In this section I will primarily discuss the neural underpinnings of speech-meaning mapping.

Neuroimaging experiments contrast the processing of words with pseudowords (i.e. lexical decision task) to show the cortical areas that underpin sound-to-meaning mapping. A meta-analysis overlapped the results of 11 fMRI studies that employed lexical decision (M. H. Davis & Gaskell, 2009) and found increased activation for words compared to pseudowords in LIFG, bilateral MTG, bilateral IPL and LSTG. Similarly, the comparison of making semantic decisions on words versus making phonological decision on nonwords recruits left middle, inferior temporal, LIFG and bilateral angular gyri (AG) (Démonet et al., 1992; Démonet et al., 1994). These studies demonstrate that speech-to-meaning mapping involves an extensive network of perisylvian regions. To dissociate the functional role of each individual region we need to take a closer look at various functional manipulations and selective neurological impairments.

Aphasia syndromes that are characterised by impaired speech comprehension include Wernicke's and transcortical sensory aphasia. Wernicke's aphasics have fluent but unintelligible speech production, and impaired comprehension (Wernicke, 1874). They produce phonemic (e.g. *top-dop*) and semantic paraphasias (e.g. *wife-sister*), and natural sounding neologisms (e.g. *tufbay*). Wernicke's aphasia has been associated with lesions in posterior superior temporal, middle temporal, angular and supramarginal gyri (Bogen & Bogen, 1976; Damasio, 1998; Dronkers, Redfern, & Ludy, 1995), with the core damage being in the Wernicke's area. Further evidence comes from the transcortical sensory aphasia (TSA) which is characterised by impaired speech comprehension and spared repetition due to lesions in posterior superior and middle temporal areas (Boatman et al., 2000; Coslett, Roeltgen, Gonzalez Rothi, & Heilman, 1987). The co-existence of semantic impairments in both comprehension and production, suggests that the posterior STG and MTG are involved in mapping sounds to meaning.

MTG, which is just ventral to the Wernicke's area, shows increased activity for word generation, picture naming (Indefrey & Levelt, 2004), for accessing high compared to low frequency words (Prabhakaran et al., 2006), semantic processing (Gow, 2012; Lau et al., 2008), and semantic priming of spoken words (Rissman et al., 2003; Wible et al., 2006). These studies underline MTG's role in semantic processing of speech. Further, lesion mapping studies show that following stroke and damage to MTG, patients show impaired speech comprehension (Bates et al., 2003; Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004). Similarly, propofol sedation that attenuates activity in the posterior temporal areas, disrupts comprehension of semantically ambiguous sentences (M. H. Davis et al., 2007). Building on the numerous corroborative findings, neurobiological models of language processing have proposed that posterior superior temporal sulcus-MTG acts as the interface between lexical and semantic representations (Gow, 2012; Hickok & Poeppel, 2004, 2007; Lau et al., 2008).

1.3.4. SEMANTIC PROCESSING AND INTEGRATION

In the previous sections I discussed how the word recognition occurs when the speech is mapped onto representations stored in memory. However, in everyday life we rarely encounter words in isolation. Words are almost always presented within a semantic and syntactic context. Due to the incremental nature of speech, we process and compute the semantic and syntactic relationships of the preceding sentential context with the following words as we hear speech. Then the upcoming words are integrated with both the syntactic and semantic context (Friederici, Steinhauer, & Frisch, 1999; Lau et al., 2008). Neuroimaging and patient studies shed light on potential neural substrates of linguistic combinatorial processes. Below I discuss semantic combinatorial processes in speech comprehension, which I differentiate from the conceptual combination where the combination of two concepts creates a new meaning (e.g. *mountain magazine*) that is more than the added meaning of the two concepts (Gagné, 2001; Murphy, 1990; Wisniewski & Love, 1998).

Neuroimaging studies on semantic combinatorics point to two key cortical areas: anterior temporal lobes (ATL) and AG (Lau et al., 2008). Studies show that both the superior and middle parts of ATL respond to intelligible speech, irrespective of changes in low level acoustics (M. H. Davis & Johnsrude, 2003; Evans et al., 2014). Listening to meaningful stories compared to non-meaningful speech induced activity in bilateral ATL (Mazoyer et al., 1993). Further, several neuroimaging studies have shown that the composition of basic adjective-noun phrases activate LATL (Baron & Osherson, 2011; Baron, Thompson-Schill, Weber, & Osherson, 2010; Bemis & Pylkkänen, 2011, 2013; Westerlund & Pylkkänen, 2014). These studies indicate that ATL is sensitive to the semantic content of speech.

ATL lesions lie at the centre of semantic dementia aetiology, a variant of frontotemporal dementia. Semantic dementia is associated with progressive loss of conceptual knowledge (Mummery et al., 2000), where the lesions originate from the ATL and gradually spread to posterior and ventral temporal areas (Snowden, Goulding, & Neary, 1989). Semantic dementia patients have word finding difficulties when naming objects and have difficulty understanding the meaning of spoken words (Lambon Ralph et al., 2001). Further, the loss of conceptual information is disproportional, as the recognition of specific concepts (e.g. ostrich) is more impaired than the recognition of basic level concepts (e.g. bird) (Hodges, Graham, & Patterson, 1995; Warrington, 1975). The neuroimaging findings together with the characteristics of semantic dementia patients, led to the proposal that ATL is a semantic hub that binds features of concepts, and semantic representations that are distributed across the cortex (Patterson et al., 2007). In addition to its role in semantics, ATL is widely reported in syntactic processing as well, which I will discuss in the next section.

AG, through a meta-analysis was found to be the area most commonly activated across studies on semantic processing (Binder et al., 2009); and was proposed to integrate semantic representations and contribute to retrieval of meaning (Davey et al., 2015; Noonan, Jefferies, Visser, & Lambon Ralph, 2013). AG is cytoarchitectonically well suited for combinatorial processes as it holds characteristics of heteromodal association cortices (e.g. larger dendritic fields) (Elston et al., 2001; Jacobs et al., 2001). AG activity is induced for semantically congruent stimuli (Humphries, Binder, Medler, & Liebenthal, 2006), meaningful compared to non-meaningful phrases (Graves et al., 2010) irrespective of the modifier's sensory modality (e.g. visual, tactile) (A. R. Price et al., 2015) or the modality of the presented stimuli (i.e. written or spoken words) (Devereux, Clarke, Marouchos, & Tyler, 2013; Fairhall & Caramazza, 2013). AG activity increases bilaterally as a function of the combinatorial strength of words (A. R. Price et al., 2015). Further, AG atrophy is associated with impairments in understanding combined rather than individual concepts (A. R. Price et al., 2015). Similarly, anodal stimulation of LAG with transcranial direct current stimulation speeds up comprehension of meaningful phrases (A. R. Price, Peelle, Bonner, Grossman, & Hamilton, 2016). In a transcranial magnetic stimulation study (TMS), Davey et al. (2015) found that stimulation of AG disrupted identification of objects at a specific level whilst not affecting the performance at the superordinate level. Authors conclude that AG is involved in automatic retrieval of semantic information. These studies show that AG has a prominent role in retrieving and constructing transmodal semantic representations.

Even though ATL and AG are reported individually in numerous studies, recent findings show that they operate jointly in semantic combinatorics. Bemis and Pylkkanen (2013) tested the magnetoencephalography (MEG) responses to written and spoken semantic combinations, and found increases in activity in both LATL and LAG in both modalities. Here LATL's activity peaked at 300 ms followed by a peak in LAG activity at 560 ms in the auditory domain. An fMRI functional connectivity study has recently shown that low-typical (e.g. *bright cave*) compared to highly typical combinations (e.g. *dark cave*) increases the LATL-LAG coupling (Molinaro, Carreiras, & Duñabeitia, 2012). The authors suggest that LATL is involved in constructing amodal abstract semantic representations, whereas AG contributes when the combined representation is complex but still meaningful.

In addition to simple phrasal semantic combinations, semantic representations also need to be incrementally integrated with the representation of the preceding sentential context. One way the brain achieves rapid incremental processing is by gathering semantic cues and use them to compute the likelihood of upcoming words and anticipate speech. Even though the facilitative effect of contextual information in speech comprehension is well established, earlier modular models of speech comprehension have initially proposed that words are recognised purely on the basis of the acoustic input; and that the contextual constraints can only have a post-lexical influence on the ease of integration of the word with the sentential context (Fodor, 1983; Forster, 1979). With accruing behavioural evidence supporting contextual facilitation in speech, later models of speech comprehension have adopted an interactionist architecture, that allow the auditory perception to be modulated by prior speech and knowledge (Gaskell & Marslen-Wilson, 1997a; McClelland & Elman, 1986).

Behavioural studies point toward a clear advantage in speech comprehension for supportive contexts (Marslen-Wilson, 1975; Marslen-Wilson & Tyler, 1980). Words that are highly predictable by the context are read more quickly (Ehrlich & Rayner, 1981; Lieberman, 1963; McDonald & Shillcock, 2003; Traxler & Foss, 2000; Tyler, 1984). Naming and lexical decision latencies are faster for words in supportive contexts (Fischler & Bloom, 1979; Jordan & Thomas, 2002; McClelland & O'Regan, 1981; Tyler & Wessels, 1983). Eye tracking studies on speech, indicate that the sentential context is used to narrow down the set of word candidates that are likely to follow (Altmann & Kamide, 1999; Kamide, Altmann, & Haywood, 2003).

Another example for contextual facilitation is the restoration in language. In a behavioural experiment, Warren and Warren presented participants spoken sentences that included a word where its first phoneme was replaced by the a cough sound (e.g. *It was found that the *eel was on the orange/shoe*) (R. M. Warren & Warren, 1970). Depending on the speech that followed the participants restored the missing phoneme with a contextually appropriate one (e.g. *peel/heel*). Similarly ambiguous speech sounds (e.g. a sound that is acoustically intermediate between /*k*/ and /*g*/) are perceived differently depending on the speech that follows (e.g. /*k*/ in /*_iss*/, and /*g*/ in /*_ift*/) (Ganong, 1980). Similarly Marslen-Wilson (1975) used a shadowing paradigm to investigate the effect of context on speech perception. The paradigm involved repeating sentences as the participants heard them. The study showed that participants restored sentences that contained word (e.g. *tomorrane* to *tomorrow*) and context disruptions (e.g. *put a stamp on the already* to *put a stamp on letter*) to words that better fit the context. Altogether these studies demonstrate that contextual information influences and facilitates online perception and semantic processing.

In electrophysiology contextual facilitation is consistently reflected on the N400 ERP, which is a negative deflection that is observed 200-500 ms post-stimulus onset (Kutas & Hillyard, 1980). N400 amplitude increases when the upcoming words do not match with the anticipated words constrained by the context, irrespective of the stimulus modality or the performed task (Hagoort & Brown, 1994; Kutas & Hillyard, 1980, 1984; van Petten, Coulson, Rubin, Plante, & Parks, 1999). During self-paced reading adjectives that are inconsistent with the anticipated noun slows down reading and induces larger N400 amplitudes (van Berkum, Brown, Zwitserlood, Kooijman, & Hagoort, 2005). An ERP study presented participants with sentences that were highly constraining (e.g. *They wanted to make the hotel look more like a tropical resort. So along the driveway, they planted rows of* …), which were completed by words that were highly anticipated (e.g. *palms*), not anticipated but belonging to the same semantic category (e.g. *pines*), and not anticipated and belonging to a different semantic category (e.g. *tulips*) (Federmeier, McLennan, De Ochoa, & Kutas, 2002). They found that the N400 amplitude was smallest for the highly expected continuation, *palms*. It was larger for *pines*, and largest for *tulips*.

N400 effect was suggested to be the result of two possible circumstances. First, N400 amplitude might reflect the ease of lexical access to the anticipated word from memory (Federmeier, 2007; Federmeier & Kutas, 1999; Kutas & Federmeier, 2000). Second view proposes that N400 amplitude reflects the difficulty in integrating the perceived lexical representation to the preceding sentential context (Brown & Hagoort, 1993; Hagoort, 2008; Kutas & Hillyard, 1980; Osterhout & Holcomb, 1992). However further ERP studies corroborate the former view by showing that variables that make lexical access more difficult increase N400 amplitude: high frequency words (Allen, Badecker, & Osterhout, 2003; van Petten & Kutas, 1990), and nonwords that sound like real words (Bentin, Mouchetant-Rostaing, Girard, Echallier, & Pernier, 1999; Holcomb & Neville, 1990). Another ERP study manipulated the predictability of indefinite articles (e.g. a, an) by the contextual constraint (e.g. *The day was breezy, so the boy went outside to fly an/a airplane/kite*) (DeLong, Urbach, & Kutas, 2005). In the example, context leads participants to anticipate that the boy would fly a kite, and the results show that the unexpected article produces a larger N400 prior to the noun's presentation. Given all sentences were grammatically correct, the effect cannot be due to grammatical or semantic violations. The authors conclude that as we hear speech, we use prior context to pre-activate the representations of words that are likely to follow. Therefore N400 studies indicate that 200-500 ms after we encounter a word, the semantic representation indicated by the preceding context is accessed.

Patients who have temporal lobe epilepsy in the left hemisphere do not show N400 changes, compared to patients who have seizure foci on the right (Olichney et al., 2002), which indicates that N400 is induced due to activity of the left temporal areas. In an fMRI study the participants were presented with spectrally degraded spoken sentences with either high or low contextual constraint (Obleser et al., 2007). They showed that as the speech degraded, contextual constraint of the sentence increased comprehension accuracy. Further, they showed increased activity in LAG, medial and lateral prefrontal areas and the posterior cingulate gyrus. These findings are in line with Lau et al's (2008) neural model of semantic processing in language. The proposed model is composed of five areas on the left hemisphere: LpMTG, LATL, LAG, anterior LIFG and posterior LIFG. LATL and LAG are proposed to be responsible for basic semantic combinatorial processes and integrating the lexical representations active in LpMTG. Anterior and posterior sections of LIFG are proposed to underpin the controlled retrieval of lexical information and selection of lexical candidates respectively.

Even though the cortical networks involved in speech-meaning mapping are well established and the ERP studies give clues as to the time windows when the speech input is semantically processed with respect to the preceded context, further research is needed to relate these findings to current cognitive models of spoken word recognition. Following the acoustic analysis, the incremental network dynamics that underpin the multiple parallel activation of lexical representations and the resolution of resulting competition remain unclear. Further, it is unclear how this dynamic network structure would be modulated by semantic context over time.

1.3.5. SYNTACTIC PROCESSING AND INTEGRATION

Syntactic processing in language recruits an extensive network of perisylvian regions. Neuroimaging studies show that LpSTG activity was induced by failure to integrate syntax due to ungrammaticality (Schlesewsky & Bornkessel, 2004), processing syntactically complex object-first sentences (Constable et al., 2004; Cooke et al., 2002), processing sentences with scrambled word order (Bornkessel, Zysset, Friederici, von Cramon, & Schlesewsky, 2005), and local syntactic violations (Friederici et al., 2003; M. Meyer, Friederici, & von Cramon, 2000).

In addition to its role in semantic processing, ATL is often reported for syntactic processing as well. Processing of progressively larger units of speech (i.e. syllables, words, sentences, paragraphs) is processed at a greater extent in the anterior regions of the lateral temporal cortex (DeWitt & Rauschecker, 2012; Friederici, Meyer, & von Cramon, 2000; Giraud & Price, 2001; Humphries, Love, Swinney, & Hickok, 2005; Lerner, Honey, Silbert, & Hasson, 2011; Vandenberghe, Nobre, & Price, 2002). Similarly, LATL is activated more for structured compared to scrambled sentences (Friederici, Meyer, et al., 2000; Humphries et al., 2005; Mazoyer et al., 1993). This finding might however also be linked ATL's role in semantic combinatorics (Pallier, Devauchelle, & Dehaene, 2011). This view is supported by language impairments of semantic dementia patients, which are more extensive for semantic processing (Hodges et al., 1995; Warrington, 1975) and that patients show spared nonsemantic linguistic processes such as syntax and phonology (Gorno-Tempini et al., 2004; Mummery et al., 2000).

LIFG activity is commonly reported in studies on syntactic processing. LIFG activity is reported for syntactically complex object-relative sentences (Peelle et al., 2004), unexpected syntactic structures (Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006; Friederici et al., 2003; Grewe et al., 2005), making decisions on grammatical class of the target word (Friederici, Meyer, et al., 2000), and for morphosyntactic computations (Moro et al., 2001). Patient studies corroborate these findings. The syntactic impairments in Broca's aphasics emphasise LIFG's role in syntactic processing. Broca's aphasics show good comprehension of single words and simple sentence structures, but impaired understanding of complex sentences (Grodzinsky et al., 1999).

In addition to LpSTG, ATL and LIFG, other studies have reported syntactic involvement of RIFG (Friederici, Meyer, et al., 2000; Kang, Constable, Gore, & Avrutin, 1999; Moro et al., 2001); bilateral planum polare (Friederici, Meyer, et al., 2000; M. Meyer, Zysset, von Cramon, & Alter, 2005), left caudate nucleus (Moro et al., 2001), basal ganglia (Friederici et al., 2003) and the superior frontal gyrus (Newman, Pancheva, Ozawa, Neville, & Ullman, 2001), however the distinct role of each region remains unclear. Further it was suggested that the pattern of activity reported in different neuroimaging studies might differ due to differences in task, experimental paradigm and control for confounding variables. Keller et al. (2001) showed that syntactic complexity of the sentences recruited a large network of regions consisting of LIFG, LSTG, LMTG, LIPL and L posterior middle frontal gyrus. The authors have also tested for the effect of lexical frequency, and reported activity in the LIPL and L posterior middle frontal gyrus have significantly correlated with frequency. Therefore, the cortical regions suggested to underlie syntactic processing might be confounded by linguistic third variables or task-related activity.

Syntax studies on chronic stroke patients with left hemisphere damage allow us to draw stronger inferences between brain regions and syntactic function. Wright et al. (2012) and Tyler et al. (2011) using a voxel-based correlation analysis, have related the structural integrity of both LIFG (primarily BA 45) and LpMTG to preserved syntactic performance. Further, the performance was also correlated with effective connectivity between LIFG and LpMTG (Papoutsi, Stamatakis, Griffiths, Marslen-Wilson, & Tyler, 2011), and the structural integrity of the white matter tracts, the extreme capsule and the arcuate fasciculus, that connect the two regions (Griffiths, Marslen-Wilson, Stamatakis, & Tyler, 2013). Altogether, these patient studies indicate that the core syntax network consists of LIFG, LpMTG and the connecting white matter tracts (Tyler & Marslen-Wilson, 2008).

ERP literature provides information of the temporal dynamics of the syntax network. Friederici (2002) put forward a neurocognitive model built on ERP evidence which suggests that the syntactic structure of the sentence is processed in three phases. In the first phase that takes place 100-200 ms, the initial automatic syntactic parsing is performed using the syntactic word category information. Violations detected in this phase elicit early left anterior negativities (ELAN) (Fonteneau, 2013; Friederici, Pfeifer, & Hahne, 1993; Hagoort, Wassenaar, & Brown, 2003; Hahne & Friederici, 1999). In the second phase that takes place between 300-500 ms, morpho-syntactic processing is performed. Processing difficulties of morpho-syntax such as inflection violations elicit left anterior negativities (LAN) (Gunter, Stowe, & Mulder, 1997). The second phase also involves the lexical conceptual semantic integration reflected in N400 which I discussed in the previous section. In the final phase, between 500-1000 ms, linguistic information from different streams is integrated. If the integrated information involves anomalies, and the sentential representation requires reanalysis and repair, then a late ERP, P600 (also referred to as the syntactic positive shift) is elicited. P600 is observed 500 ms after the presentation of the syntactically anomalous word (e.g. *The cats won't eating*) with a centroparietal scalp distribution. Similarly, increased P600 amplitudes are reported for violations of verb subcategorisation frame (e.g. *The banker persuaded/decided to sell the stock*) (Osterhout & Holcomb, 1992) and for incorrect subject-verb agreement (Hagoort, Brown, & Groothusen, 1993). Altogether ERP studies, if the syntactic structure is congruent with the sentential syntax, within 500 ms after the presentation of the word, the syntactic processing would be complete.

The studies discussed above establish the core cortical network underlying syntactic processing in speech as well as the temporal windows in which the processing takes place. Several studies have further investigated the connectivity dynamics within the syntax network. Two psychophysical interaction (PPI) studies in fMRI have manipulated sentential syntactic ambiguity, and revealed increased connectivity between LIFG and LMTG (Papoutsi et al., 2011; Snijders, Petersson, & Hagoort, 2010). Further studies have employed Dynamic Causal Modelling which uses a biologically informed causal model compared to PPI. These studies suggest that LIFG drives the increased connectivity in posterior temporo-parietal areas (David, Maess, Eckstein, & Friederici, 2011; den Ouden et al., 2012; Ohta, Fukui, & Sakai, 2013). These fMRI studies point toward increased effective connectivity from LIFG to LMTG during syntactic processing. However, further studies are needed to relate different phases of syntactic processing, their associated ERPs to changes in syntax network effective connectivity over time. This would clarify the temporal connectivity dynamics of the syntax network.

1.4. ISSUES ADDRESSED AND THE STRUCTURE OF THE THESIS

As discussed above, the rapid incremental nature of speech necessitates the cognitive processes underlying speech-meaning mapping to be performed online and in parallel fashion. These cognitive processes involve the initial acoustic-phonemic analysis of the speech signal, the use of phonological analysis to activate candidate lexical and corresponding semantic representation of words that match the speech input, and finally resolve the lexical-semantic competition to access the target meaning given in speech. Even though the cortical regions associated with these cognitive processes are well established, in order to fully elucidate the neural substrates of speech comprehension, further research is needed to understand how these regions operate dynamically as a network over time. The central premise in neuroimaging analyses is that a cognitive function can be localised to a cortical area (i.e. functional segregation), which suggests that the area is specialised for perform one function. However, increasing number of studies indicate that cognitive functions are underpinned by networks of regions that communicate with each other over time (i.e. functional integration). A complete understanding of speech-meaning mapping, similarly requires the 1) definition of cortical regions and networks in play, 2) how these networks interact with each other dynamically over time, 3) how these networks are modulated by preceding contextual information. In this thesis through three E/MEG experiments I investigate the cortical network dynamics that underpin these incremental cognitive processes performed during speech-meaning mapping and the modulations of these processes by contextual constraints over time.

In Chapter 3, I describe an E/MEG experiment where I investigated the spatiotemporal dynamics of sound-to-meaning mapping whilst we listen to single spoken words of concrete concepts (e.g. *hammer, lion*). In line with the lexicalist models of speech processing I predicted that the speech input would activate phonological and semantic representations of the cohort candidates in parallel, and that these candidates will be continuously assessed against the speech input. Over time as the candidates that no longer match the speech input decay, competition resolution will allow access to the semantics of the target word. In order to determine dynamic networks that are activated, and to relate these networks to cognitive processes, through a behavioural gating study I determined the uniqueness point (UP) of every word used in the study. The UPs were used to align the cognitive computations taking place in each trial. Here I used a novel multivariate pattern analysis method, the spatiotemporal searchlight representational similarity analysis (ssRSA), which allows us to relate theoretical models of cognition directly to the brain activity patterns. I constructed theoretical models that captured three key cognitive processes that underpin this mapping: lexical competition, semantic competition and access to target word's semantic representation. The ssRSA revealed early parallel networks for lexical and semantic competition prior to the UP that consist LIFG, LSMG and LMTG. Right after the UP, and therefore the resolution of competition, the target word's semantic representation was rapidly accessed via activity in MTG, AG and RIFG. I further discuss the neural substrates of lexical-semantic representations, and relate the findings to cognitive models of spoken word recognition.

Building on the findings of Experiment 1, in Chapter 4, I explore how the network dynamics underpinning access to meaning through speech, are modulated by degrees of contextual facilitation. Participants listened to two-word phrases in the form of [modifier +noun] and answered to occasional semantic relatedness questions. Three types of phrases were presented: phrases where the modifier provides a strong semantic constraint (e.g. *cycling helmet*), a weak semantic constraint (e.g. *plastic helmet*), and a word list condition where the words cannot be semantically combined to form a phrase (e.g. *shuffle helmet*). Here I aimed to define the cortical networks solely involved in contextual semantic processing, by first removing any domain general network activity induced by the experimental task. In line with the literature in the absence of task positive networks, I predicted to find effects of contextual facilitation in AG and LATL. Using an independent component analysis (ICA), I decomposed the data into independent temporal networks which I then tested for conditional modulations. The results revealed that bilateral AG were the only networks modulated by the degree of contextual semantic constraint. I further discuss the necessity and consequences of using tasks in E/MEG experiments.

In Chapter 5, I move on to the syntax domain, and investigate how the dynamic connectivity within the left frontotemporal syntax network is modulated by the anticipations on upcoming syntactic frames which are informed by the contextual syntactic structure. More specifically I explore how the connectivity dynamics change when the syntactic anticipations are confirmed or disproven by the upcoming speech. Participants listened to spoken sentences that were either unambiguous or contained local syntactic ambiguities (e.g. *Captains know that* *sinking submarines*…), which were resolved immediately by the words that followed. The disambiguating word either revealed the preferred (i.e. more anticipated) (e.g. …*are heading down to the seabed*) or less preferred reading of the structure (e.g. …*is nearly impossible*). To test how the information flow in the syntax network was modulated over time by the syntactic context, I performed a Dynamic Causal Modelling analysis with short time windows from the point of disambiguation. In line with the ERP literature on syntactic violations I predicted to find early connectivity changes driven by the top-down involvement of LIFG when the anticipations fail. Further I predicted that the connectivity patterns underlying confirmed anticipations will not differ from patterns underlying syntactically unambiguous sentences. The analysis revealed that when we fail to correctly anticipate the upcoming syntactic structure in a sentence, there was an early information flow to LIFG, followed by recurrent communication between LIFG and LpMTG. I discuss the results within the framework of prediction coding and relate the results to the ERP literature.

CHAPTER 2

GENERAL METHODS

This chapter covers all the commonalities between experimental methods. Additional differences unique to each experiment are given in their respective Methods section.

2.1. PARTICIPANTS

The participants were right-handed, healthy native British English speakers with normal hearing. The experiment was approved by the Cambridge Psychology Research Ethics Committee.

2.2. STIMULI

The stimuli were recorded by a female native speaker of British English onto a digital audio tape recorded at a sampling rate of 44100 Hz. The recordings were then transferred to a computer and downsampled to 22050 Hz, 16 bits, mono-channel format using the Cool Edit Software (Syntrillium Software Corporation, Phoenix, USA).

2.3. MEG PROCEDURE

The participants were seated in a magnetically shielded room (IMEDCO GMBH, Switzerland) and positioned under the MEG scanner. The auditory stimuli were delivered binaurally through MEG-compatible ER3A insert earphones (Etymotic Research Inc, IL, USA). To ensure good data quality, the participants were instructed to attentively listen to the spoken stimuli and follow instructions which were visually presented on the screen which was positioned 1 m in front of their visual field. E-Prime version 1 (Psychology Software Tools) was used to present the stimuli and record participants' responses when given task. The stimuli were presented in a pseudo-randomised order, in blocks where participants had the opportunity to rest in between. Further, the block order was also randomised for each participant.

2.4. MEG AND FMRI ACQUISITION

Continuous MEG data were recorded using the whole-head 306-channel Vector-view system (Electa Neuromag, Helsinki, Finland). The channel system consisted of 102 pairs of planar gradiometers, and 102 magnetometers. To monitor and record blinks and cardiac activity, electro-oculogram (EOG) and electrocardiogram (ECG) electrodes were used. To record subjects' head shape and movements five head position indicator coils (HPI) were attached onto the subjects' head. HPI coils recorded the head position every 200 ms. For coregistration of the subject head, to the MEG sensors, the three fiducial points (nasion, left and right pre-auricular) and additional points across the scalp were digitised. MEG signals were recorded continuously at 1000 Hz sampling rate with a high-pass filter of 0.03 Hz. To facilitate source localisation, T1-weighted MP-RAGE scans with 1 mm isotropic resolution were acquired for each subject using Siemens 3-T Tim Trio. Both the MEG and MRI systems were located at MRC Cognition and Brain Sciences Unit in Cambridge, UK.

2.5. MEG SSRSA PREPROCESSING AND SOURCE LOCALISATION

The raw data were processed using MaxFilter 2.2 (Elekta Oy, Helsinki, Finland) in three steps. In the first stage bad channels were detected. The signals of the bad channels were reconstructed using interpolation. In the second stage, signal space separation was applied to the data every four seconds to separate the signals generated from subjects' head from the external noise. Lastly head movements were corrected and each subject's data were transformed to a default head position.

In order to remove blink and pulse-correlated signals from the continuous MEG signals, an ICA was performed using the EEGLAB toolbox (Delorme & Makeig, 2004) where signal coming from each sensor type was decomposed to 60 ICs. The IC time series were correlated with the EOG and ECG time series. The components which had a Pearson's r-value higher than 0.5 (Jung et al., 1998) were removed from the data, and the remaining ICs were reconstructed.

Data were further preprocessed using SPM 8 (Wellcome Trust Centre for Neuroimaging, University College London, UK). They were band-pass filtered and notch filtered at 50 Hz using a 5th order Butterworth filter. The continuous data were separated into epochs for each trial of interest. The average of the baseline period was used for baseline correction of each trial. Trials contaminated by motion related artefacts were removed.

Each participant's data were prepared for source localisation. The source space was modelled by a cortical mesh consisting of 8196 vertices. The sensor positions were co-registered to individual subject's T1 weighted MP-RAGE scan using three fiducial points. Single shell model, as implemented in SPM8, was used for forward modelling. Inversion was completed over the entire epoch using the inversion methods implemented in SPM.

CHAPTER 3

MAPPING SOUNDS TO MEANING

Understanding speech involves the rapid transformation from low level acoustic-phonetic analysis to a meaning representation. When we hear a spoken word, our immediate percept is of the meaning of the word rather than its lexical form. This rapid speech-meaning mapping – within 200 ms of word onset (MacGregor, Pulvermüller, van Casteren, & Shtyrov, 2012) – is the end-product of a seemingly effortless set of computations, and yet little is known about the neural dynamics that underpin this essential human faculty.

3.1. BACKGROUND

3.1.1. SPOKEN WORD COMPREHENSION

One prominent cognitive model of the processes and representations involved in spoken language comprehension, the DCM, proposes that as the speech unfolds (e.g., *ro...*), lexical representations of word candidates (i.e. the cohort) that match the speech input will be partially activated (e.g., *robin, rock, rod*) (Gaskell & Marslen-Wilson, 1997b; Marslen-Wilson, 1987; Marslen-Wilson & Tyler, 1980), where the strength of partial activation is weighted by word's frequency and the cohort size. Lexical representations (i.e. phonological word forms) in turn activate semantic representations of the cohort candidates. The parallel activation of lexical and semantic representations creates a transient competition. As speech accumulates over time, the activation of candidates that no longer match the speech input will weaken and decay, eventually narrowing down the cohort (i.e. resolving competition) to a single item, the target word. The point in the spoken word where the cohort size is narrowed down to one item and therefore the word is uniquely identified is called the uniqueness point (UP) (Marslen-Wilson, 1987). The model proposes that the partial activation of the target word's representation prior to the UP, is boosted when the cohort competition is resolved and UP is reached.

These predictions of the DCM were previously validated through several behavioural studies (Connine, Blasko, & Titone, 1993; Marslen-Wilson, Moss, & van Halen, 1996; Marslen-Wilson & Zwitserlood, 1989; Tyler, 1983; Tyler & Wessels, 1983). These behavioural studies have demonstrated that as we hear speech we activate semantically associated words. One study showed that the recognition of spoken words (e.g. *bee*) are facilitated when the word is preceded by a semantically related word (e.g. *honey*) (D. E. Meyer & Schvaneveldt, 1971). Another study using a gating paradigm showed that after hearing /*kæp*/ semantic associates of both *captain* and *capital* (e.g. *ship, money*) were activated simultaneously as indicated by facilitation of word recognition (Zwitserlood, 1989). Therefore, these studies show that the listeners do not need to hear the entire word to access the meaning of the target word and its semantic associates. Further, the competition load was shown to modulate the strength of semantic activation. Words that have high lexical competition exhibited less semantic priming (Marslen-Wilson, 1990), suggesting that the strength of semantic access is determined by the target word's cohort size. Altogether these behavioural studies emphasise the incremental nature of semantic and lexical activation in comprehension of continuous speech.

Further evidence for incremental lexical activation and competition in speech and the associated cortical regions are provided by neuroimaging experiments and lesion studies. Numerous studies draw attention to the role of IFG in lexical competition. For instance, Broca's aphasics show impaired lexical access when lexical competition is high (McNellis & Blumstein, 2001) and general reduction in lexical activation strength (Misiurski et al., 2005). Further, a study investigating the relationship between speech comprehension impairments and left hemisphere stroke lesions have shown that the impairment in inhibiting words' semantic neighbours correlated with IFG lesions, whereas impairment in inhibiting lexical neighbours correlated with STG and IPL lesions (Mirman

& Graziano, 2013). Several fMRI studies provide additional evidence for LIFG's involvement in cohort competition, as its activity relates to target word's phonological density and word frequency (Prabhakaran et al., 2006), and cohort size (Zhuang et al., 2011). Finally, Reville et al (2008) tested the brain activation in response to lexical competition of learned novel motion related words. They showed that the target word's cohort competitors are activated in the MT/V5 motion area before the target word is recognised indicating that semantics of the cohort competitors are activated incrementally before the word is uniquely recognised. In summary, the lexical and semantic competition resulting from speech's incremental nature, has been shown to recruit left dominant set of regions including LIFG, STG and IPL.

3.1.2. SPEECH-MEANING MAPPING

Similar to the what and where pathways discovered in the visual system (Mishkin et al., 1983), the auditory system has a similar underlying spatial and semantic segregation (Alain, Arnott, Hevenor, Graham, & Grady, 2001; Rauschecker & Tian, 2000; Zatorre & Belin, 2005). One account proposes an auditory ventral stream (i.e. what pathway) that maps speech sounds to lexical semantic representations (Hickok & Poeppel, 2007). They propose that this sound-to-meaning mapping is undertaken by a bilaterally organised pMTG and posterior inferior temporal sulcus (ITS). They further explain that these two regions serve as an interface between lexical semantic representations and semantic representations that are encoded in a distributed fashion throughout the cerebral cortex. Rodd et al (2004) using semantically ambiguous sentences in fMRI revealed activity in the middle portion of LMTG. LMTG's role in accessing lexical semantics was further confirmed in various neuroimaging and neuromodulation studies (Kotz, Cappa, von Cramon, & Friederici, 2002; Whitney et al., 2011) and therefore MTG was included as the semantic interface in speech comprehension in semantic networks (Friederici, 2002; Lau et al., 2008; Tyler & Marslen-Wilson, 2008). In addition to MTG and ITS, AG and ATL were proposed to aid semantic processing by undertaking semantic combinatorial processes in language comprehension (Bemis & Pylkkänen, 2013; Seghier, 2013).

Further evidence for the cortical regions underlying sound-to-meaning mapping comes from neuropsychological disorders defined by impaired speech comprehension. One such disorder is Wernicke's aphasia (WA) that often occurs after a cerebrovascular insult to the left posterior temporo-parietal cortex (Ellis, Miller, & Sin, 1983). WA is characterised by impaired auditory comprehension, repetition, fluent speech incorporating phonological paraphasias and neologisms

(Goodglass, Kaplan, & Barresi, 1998). A similar disorder, PWD (also known as auditory verbal agnosia), is characterised by severely impaired speech comprehension and repetition with intact hearing, reading, writing and speaking (Buchman, Garron, Trostcardamone, Wichter, & Schwartz, 1986). In PWD the lesion involves bilateral posterior superior temporal lobe including the white matter tracts connecting STG to other auditory areas (Poeppel, 2001). Finally, TSA is characterised by impaired speech comprehension with intact repetition and speech production (Boatman et al., 2000). Therefore TSA distinguishes from both WA and PWD by intact repetition and caused by lesions to surrounding areas of Wernicke (Alexander, Hiltbrunner, & Fischer, 1989). Since in all three disorders the sound perception was intact, but the speech comprehension was selectively impaired, we conclude that Wernicke's area, bilateral STG and IPL have a crucial role in mapping sounds to meaning.

Electro- and magnetoencephalography research provides insights into the time scale of lexical access through speech. The negatively deflected ERP that occurs on average at 400 ms after the stimulus onset, N400 (Kutas & Federmeier, 2011), has been used as an anchor point to pin down semantic access (Lau, Almeida, Hines, & Poeppel, 2009; Lau et al., 2008). In addition to N400, the lexical decision tasks are useful to find out when the processing of words and nonwords start to diverge. Numerous studies that employed a lexical decision task showed a divergence that start from 385 ms (Tavabi, Embick, & Roberts, 2011) and 270 ms (Brennan, Lignos, Embick, & Roberts, 2014) post stimulus-onset. However since the spoken words will have varying UPs, these time points indicate the average time that the listeners take to resolve lexical competition and access the target semantics. One study, compared words with pseudowords after aligning them by their UPs, and revealed an early lexicality effect that started 50 ms after the UP (MacGregor et al., 2012). Therefore this rapid access to semantic representations of the target word requires the resolution of lexical and semantic competition.

Despite comprehensive findings regarding the cortical regions and temporal dynamics underpinning speech-meaning mapping, the spatiotemporal network dynamics that subserve transition from sound perception to lexical access, through semantic as well as cohort competition remains unclear.

3.1.3. CURRENT STUDY

With the current MEG study I aim to chart the spatio-temporal dynamics of the cognitive processes that underpin the access to meaning from speech: cohort competition, semantic competition and access to lexical semantics. Here I, 1) investigate the spatiotemporal dynamics of lexical and semantic competition as the speech unfolds; 2) ask whether the UP marks a transition between competition and the access to target word's unique semantic representation.

In order to model and test lexical semantic access, in the current study I adopt an anglicised neuro-cognitive feature-based model of semantics called the Conceptual Structure Account (CSA) (McRae, Cree, Seidenberg, & McNorgan, 2005; Taylor, Moss, & Tyler, 2007) which defines a concept as a set of semantic features in a large-scale distributed conceptual space. It is proposed that a conceptual representation is accessed when its constituent features coded in a distributed manner in the cortex are co-activated. These semantic features are used to compute feature statistics (Devereux, Tyler, Geertzen, & Randall, 2014), measures that capture relationships within features and concepts (e.g. sharedness, distinctiveness, number of features). Various studies have been carried out to test the predictions of CSA: the degree to which the feature of a concepts co-occur and are shared across other concepts facilitate conceptual processing; loss of distinctive feature information underlies the category-specific impairments for recognising living things; and that unique concepts identification is facilitated by concepts' distinctive features (Taylor et al., 2007). The predictions have been validated through numerous behavioural (Randall, Moss, Rodd, Greer, & Tyler, 2004; Taylor, Devereux, Acres, Randall, & Tyler, 2012), neuroimaging (Clarke, Taylor, Devereux, Randall, & Tyler, 2013; Clarke, Taylor, & Tyler, 2011; Clarke & Tyler, 2014; Kivisaari, Tyler, Monsch, & Taylor, 2012; Tyler, Chiu, et al., 2013) and patient studies (Bright, Moss, Longe, Stamatakis, & Tyler, 2007; Bright, Moss, Stamatakis, & Tyler, 2008; Noppeney et al., 2007; Wright, Randall, Clarke, & Tyler, 2015).

To relate our variables of competition and semantic access to brain data, I chose an analysis method that can capture the spatiotemporal activity patterns distributed across the brain. An innovative multivariate pattern analysis (MVPA) method called the spatiotemporal searchlight representational similarity analysis (ssRSA) (Su, Fonteneau, Marslen-Wilson, & Kriegeskorte, 2012) has the ability to detect specific oscillatory MEG signatures spread over the entire brain across time, and relate them to theoretical models of cognition. ssRSA compares the similarity structure observed in brain activity time courses, with the similarity structure of theoretically relevant cognitive models.

Representational similarity analysis (RSA) can reveal distinct representational geometries in different brain areas even when other MVPA methods seem to fail (A. C. Connolly et al., 2012). Using ssRSA I modelled key cognitive computations claimed to be involved in the transformation from speech to meaning by constructing model representational (dis)similarity matrices (RDMs) of our cognitive variables: lexical and semantic competition between activated cohort members, and target-specific semantic information. I tested these models over time against MEG activity patterns in the cortical surface (captured as brain data RDMs).

In line with the DCM of speech comprehension, I predicted that as the participants hear the speech, they would incrementally activate lexical representations that match the speech input. I predicted to find early effects of lexical competition prior to the UP in areas previously associated with lexical processing and competition, including LSTG, LIPL and LIFG. Consecutively I predicted that this lexical activation would lead to activation of cohort candidates' semantic representations prior to the UP which I expected to activate LMTG, LAG and LIFG. Since activation of phonology is a prerequisite for semantic activation, I predicted that although being parallel, the lexical competition effects to precede semantic competition effects. As I approach the UP I predicted that the competition effects would get reduced and the semantic activation of the target word would increase. Therefore, I predicted to find effects of semantic access after the UP.

3.2. METHOD

3.2.1. PARTICIPANTS

15 healthy participants volunteered in the study with a mean age of 23.7 (7 females, 8 males). Participants' ages ranged from 18 to 35. One participant fell asleep during the experiment. Three participants source estimates of the N100 time window (i.e. contrast window in 80-120 ms), did not localise correctly to the superior temporal gyrus indicating suboptimal estimation. A total of four participants were excluded from the following analysis.

3.2.2. BEHAVIOURAL PRE-TESTS

In order to align the cognitive processes across trials of the MEG data, prior to the MEG experiment, a behavioural gating task (Grosjean, 1980; Tyler & Wessels, 1985) was used to determine the UPs of each of the spoken words. In a self-paced procedure, 45 participants who did not take part in the MEG study, listened to incremental segments (i.e. gates) of an initial set of

372 spoken words and were asked to type in their best guess of the word and rate their confidence in their answer on a scale of 1 to 7 (7-very confident, 1-not confident at all). To optimally reduce the number of speech segments presented, the putative UP for each word was defined using CELEX (Baayen, 1995). The Celex UP was defined as the point where the cohort size was 1. In order to determine the gating UP, five gates were defined before and after the Celex UP. These gates were presented in 25 ms increments from the word onset.

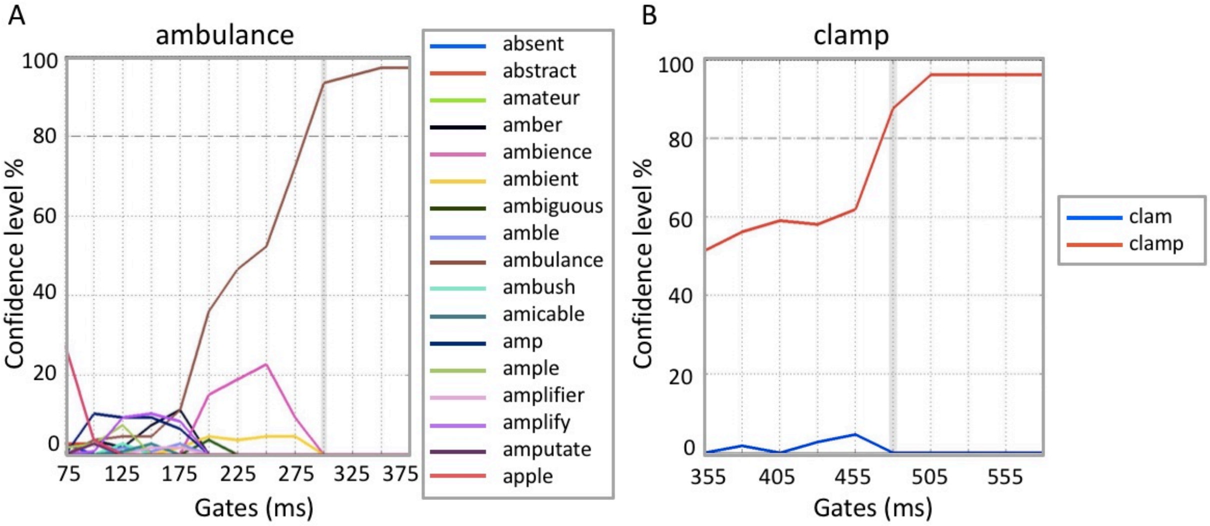


FIGURE 3.1. EXAMPLE GATING PLOTS OF AMBULANCE AND CLAMP. ON THE X AND Y AXES WE HAVE 25 MS INCREMENTAL GATES FROM WORD ONSET, AND THE PERCENT CONFIDENCE LEVEL GIVEN TO EACH COHORT COMPETITOR AT EACH GATE. NOTE THAT AMBULANCE SHOWS HIGHER COHORT COMPETITION COMPARED TO CLAMP, BECAUSE ITS COHORT SIZE (N = 17) IS LARGER THAN CLAMP'S (N = 2), AND IT BECOMES UNIQUE AT A LATER TIME POINT.

The words were taken from the Centre for Speech, Language and the Brain database of conceptual norms (Devereux et al., 2014). The gating UPs were defined as the gate where 80% of the participants correctly identified the word with an average confidence rating exceeding 80% (P. Warren & Marslen-Wilson, 1987, 1988). Using these criteria, the gating UPs (*M* = 408 ms; *SD* = 81 ms) of 296 spoken words were determined which were presented in the MEG experiment (Figure 3.1). The UPs of the remaining 76 words could not be determined, due to subthreshold confidence ratings and identification accuracy. With respect to the Celex UPs, the gating UPs were on average 69 ms delayed.

3.2.3. STIMULI

The stimuli consisted of 296 spoken single words which corresponded to names of concrete objects (e.g. *lion, hammer, cabbage*) and 30 English-sounding, phonotactically legal English nonwords (e.g. *rayber, chickle, tomula*). The nonwords were constructed de novo, and was previously used in an fMRI experiment. The words belonged to common object categories of clothes, animals, plants, vehicles, musical instruments, tools and weapons and were all names of concrete objects. The words were highly familiar (*M* = 477, *SD* = 73; MRC Psycholinguistic Database, (Coltheart, 1981)), frequent (*M* = 19.21, *SD* = 39.01; Celex, (Baayen, 1995)), semantically rich (number of features, *M* = 13, *SD* = 3.34 (McRae et al., 2005) concepts, with a mean duration of 601 ms ± 122 ms. Nonwords were matched to words by their duration, number of syllables and phonemes.

3.2.4. COGNITIVE VARIABLES

To investigate the speech-meaning mapping, the key cognitive processes of lexical competition, semantic competition, and access to semantic information were modelled. Lexical competition *(the LexComp model)* (Figure 3.2A) was defined as the change in entropy from the first presented gate (i.e. 5 gates before the Celex UP) until the UP. Here entropy represents the lexical uncertainty that results from changing lexical representations as speech unfolds (see Table 3.1 for example stimuli that show high and low LexComp).

It was calculated by adopting Shannon's entropy (Shannon, 1948; Willems, Frank, Nijhof, Hagoort, & van den Bosch, 2016) formula:

$$H = -\sum_{i=1}^{n} P(x_i) \log P(x_i)$$

where *H* refers to entropy, $P(X_i)$ refers to the summed confidence score for a cohort competitor *i* across participants divided by the total sum of confidence scores for all the competitors reported at one gate, and *n* refers to the total number of competitors at one gate. Here differences in entropy were inversely related to the level of lexical competition (Figure 3.2D). Entropy takes into account both the number of competitors and the change of confidence level relative to each other. For example, a word with a cohort size of 3 would have higher entropy if the candidate probabilities are similar (e.g. 33%, 33%, 33%) rather than probabilities that have larger gaps between them (e.g. 80%, 15%, 5%). The LexComp model was constructed using the change in entropy values between the first gate and the gating UP, and therefore the model was static over time.

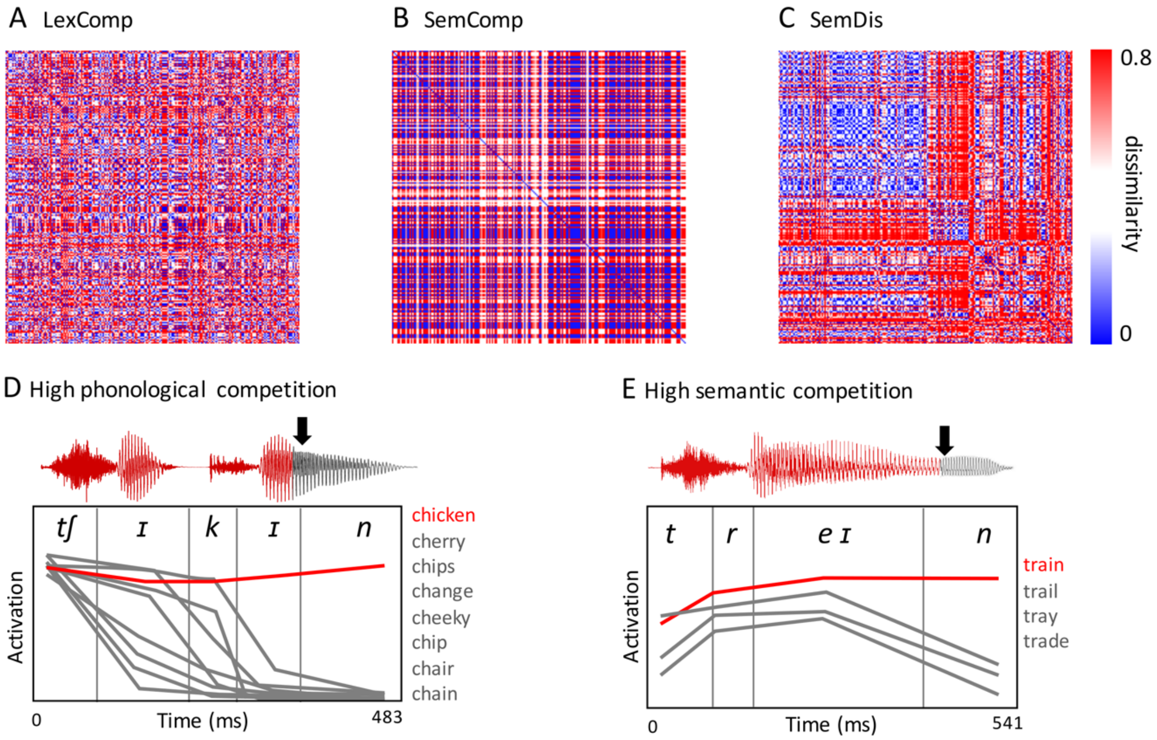


FIGURE 3.2. THE MODEL RDMS AND EXAMPLE COHORT PROFILES. A-C. THE MODEL RDMS TESTED IN THE CURRENT ANALYSIS WHERE ROWS AND COLUMNS OF THE MATRICES REPRESENT TRIALS (I.E. SINGLE SPOKEN WORDS), AND VALUES INDICATE PAIRWISE DISSIMILARITY VALUES ACROSS TRIALS. A. LEXCOMP MODEL, B. SEMCOMP MODEL, C. SEMDIS MODEL. D-E. REPRESENT COHORT ACTIVATION DIAGRAMS OF TWO EXAMPLE STIMULI: CHICKEN AND TRAIN. COHORT PROFILES INDICATE THE CHANGE IN ACTIVATION OF EVERY CANDIDATE WORD OVER TIME. D. AT THE WORD ONSET ALL MEMBERS IN CHICKEN'S COHORT ARE PARTIALLY ACTIVATED AT AN EQUAL LEVEL RESULTING IN HIGH LEXICAL COMPETITION. AS MORE OF THE SPEECH INPUT IS HEARD THE ACTIVATION OF THE COMPETITOR WORDS DROP, AND TARGET WORD'S ACTIVATION INCREASES. E. TRAIN'S COHORT PROFILE SHOWS HIGH SEMANTIC COMPETITION DUE TO LOW SEMANTIC OVERLAP BETWEEN OF THE TARGET WORD TRAIN AND ITS COMPETITORS. ARROWS MARK THE UPS.

Semantic competition *(the SemComp model)* incorporated feature-based semantic information of all competitor words included in target word's cohort (Figure 3.2B). Feature-based semantic similarity of the set of each word's competitors was computed using a corpus-based Distributional Memory (DM) database (Baroni & Lenci, 2010). The DM database represents 30686 concepts by a vector of 5000 semantic features. Here the entries in the semantic dimensions correspond to dimensionally reduced word co-occurrence data by the Random Indexing word space approach (Kanerva, Kristoferson, & Holst, 2000). Semantic competition was defined as the average cosine distance between pairs of feature vectors of competitors at the first presented gate. A smaller overlap between the vectors of features was proposed to create an average pattern of semantic activation from words that have a small resemblance to any single conceptual representation (Table 3.1), and therefore generating higher semantic competition (Figure 3.2E).

High LexComp	Low LexComp	High SemComp	Low SemComp
goat	fox	cigarette	eagle
shovel	olive	sledge	knife
cod	brick	bracelet	beetle
sofa	crocodile	skateboard	pistol
armour	alligator	pineapple	dandelion

TABLE 3.1: EXAMPLE STIMULI THAT SHOW HIGH AND LOW LEVELS OF SEMCOMP AND LEXCOMP.

Finally, *the SemDis model* (Figure 3.2C) was designed to tap into lexical access to target-specific unique semantic representations by incorporating target word's feature-based semantic representation. This measure was designed to capture the access to unique target specific semantic representations which involves the activation of the concept's shared features that highly co-occur with the features that distinguish the concept from close category members –therefore allowing unique identification-. This measure was computed using two feature-specific indices (McRae et al., 2005): feature distinctiveness and correlational strength (i.e. feature co-occurrence). Feature distinctiveness was defined as 1/[number of concepts in which a feature occurred] (e.g. *has stripes, has a hump*). Correlational strength of a feature, measured the degree to which two shared features co-occur (e.g. *has eyes, has ears*). SemDis measure was defined as the unstandardised slope of the regression line describing the scatterplot of showing all features of a concept where correlational strength and feature distinctiveness were plotted on the x and y axes respectively (Taylor et al., 2012). Therefore, the SemDis measure captured the relative contribution of a concept's feature co-occurrence to feature distinctiveness; and it was sensitive to the ease of feature integration of concepts (Taylor et al., 2012; Tyler & Moss, 2001). One needs to reiterate that the feature-based representations underlying the SemComp and SemDis models were inherently different. The DM database infers semantic features via corpus generated co-occurrences, whereas anglicised McRae norms directly instantiate semantic features with the use of a large scale behavioural norming study. Similar to the LexComp model, both the SemComp and SemDis models were static over time. Further three variables were correlated low to moderate levels. The SemDis had a correlation of $r = 0.12$ and $r = -0.09$ with LexComp and SemComp respectively. LexComp and SemComp on the other hand showed a moderate correlation of $r = -0.35$.

3.2.5. MEG PROCEDURE

Delay in sound delivery due to the length of earphone tubes and stimulus delivery computer's sound card was 32 ± 2 ms on average. To ensure that participants were attentively listening to the stimuli, a simple nonword detection task was performed. However, to reduce potential task effects on the neural response (Davis et al, 2014; Campbell et al, 2016) the nonwords were presented only on 10% of the trials. Participants were instructed to attentively listen to the speech and press a response key whenever they heard a nonword.

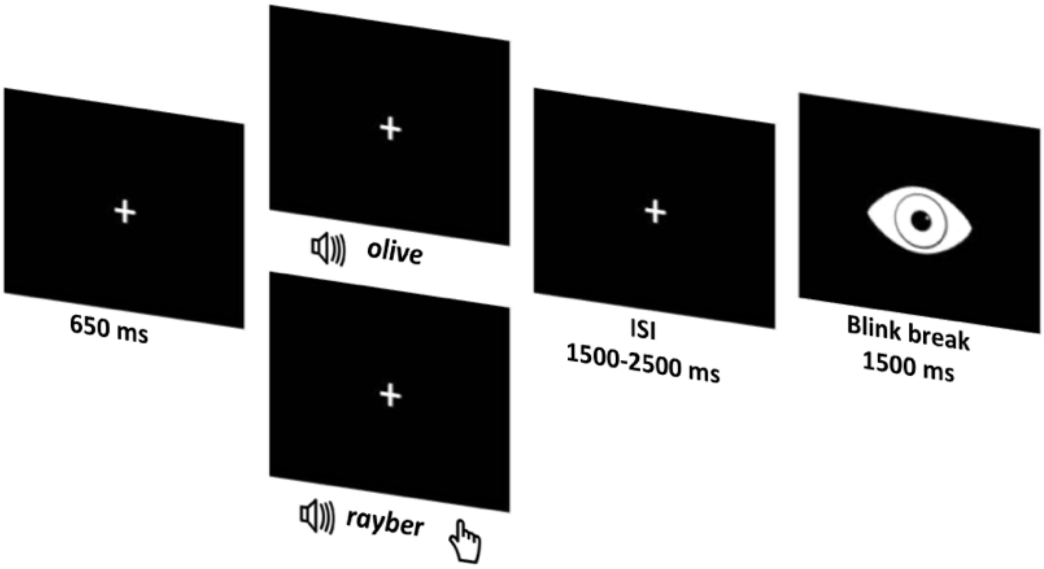


FIGURE 3.3. SCHEMATICS SHOWING STAGES OF THE EXPERIMENTAL PARADIGM. IN THE SECOND STAGE OF THE PARADIGM THE SPOKEN WORDS ARE PRESENTED, WHICH CONSISTED EITHER OF WORDS OR NONWORDS. PARTICIPANTS WERE ASKED TO PRESS THE RESPONSE KEY WHEN THEY HEARD A NONWORD.

To ensure a clean baseline prior to the speech presentation, before the presentation of the spoken stimulus, a cross appeared in the middle of the screen for 650 ms prompting the participant to focus his/her eyes on the cross (Figure 3.3). The inter-stimulus interval was randomised between 1500 and 2500 ms. Every interval was followed by a blink break that lasted for 1500 ms. The start of the blink break was indicated by an image of an eye that appeared in the middle of the screen. With the use of blink breaks the contamination of the signal by eye movement related artefacts was aimed to be minimised. Participants were also asked to refrain from movement during the entire block of recording. The stimuli were presented such that consecutive items were from different domains of semantics (living or nonliving concepts), and started with different phonemes. They were presented in two blocks, each containing 148 words and 15 nonwords.

3.2.6. MEG SSRSA PREPROCESSING AND SOURCE LOCALISATION

The data were band-pass filtered between 0.5-40 Hz using a 5th order Butterworth filter. The nonword trials were excluded from the imaging analysis. All the remaining real word trials were aligned by their UP (determined by the gating pre-test results) and segmented into epochs of 1200 ms duration. Since the aim of the analysis was to understand the spatiotemporal dynamics of lexical and semantic activation and competition processes over time – both before and after the UP – epochs were centred on the UP of each word, so that the epoch extended from 700 ms before the UP to 500 ms after it. The initial 200 ms baseline period of every trial corresponded to silence. The average of the baseline period was used for baseline correction of each trial. Trials contaminated by motion related artefacts were removed. On average 3.43 trials were removed due to artefacts (*SD* = 4.22). Finally, to speed up computations time courses were downsampled to 250 Hz. Each participant's data were prepared for source localisation by including both magnetometers and gradiometers.

3.2.7. SSRSA

RSA was originally developed to investigate the representational geometry of the hemodynamic data. The current analysis was carried out using an extension of RSA, the ssRSA, which allows us to apply the RSA method across the temporal dimension as well as space (Su et al., 2012). The analysis pipeline starting from the preprocessing steps is displayed in Figure 3.4.

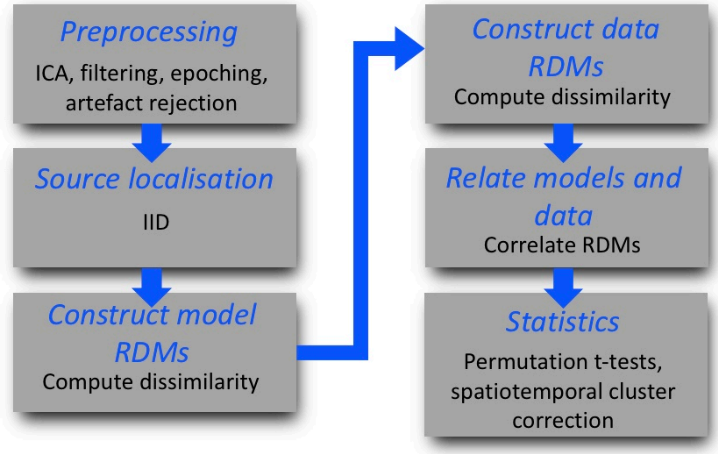


FIGURE 3.4. SSRSA PIPELINE SHOWING THE MAIN STEPS OF THE ANALYSIS.

The searchlight consists of 3 spatial and 1 temporal dimensions allowing the searchlight to move across both space and time. To construct the data representational dissimilarity matrices (data RDMs) the dissimilarity values were computed across every pair of the extracted data. These values were then compared against the dissimilarity values computed for the theoretically relevant models called the model representational dissimilarity matrices (model RDMs).

In the first step of ssRSA, model RDMs were constructed using pairwise dissimilarity values (1-euclidean distance[1]) (Kriegeskorte et al., 2008) for the theoretical measures of interest that correspond to the trials. Therefore, the entries of the model RDMs corresponded to dissimilarity values between trial which created a matrix which was symmetric across the diagonal. In the current analysis three models were tested (Figure 3.2A-C). LexComp and SemComp were constructed using the behavioural gating data and were predicted to be sensitive to lexical and semantic competition that took place prior to the UP. The SemDis model was predicted to tap into target word's unique semantic representations.

In the second step, to construct the data RDMs, the trials were extracted from source space using spatiotemporal searchlights that have 10 mm radius sphere and a sliding time window of 20 ms. The data extracted from each searchlight and each trial were vectorised. The data RDMs were constructed by computing the pairwise correlation distances (1-Pearson's r) (i.e. dissimilarities) between the vectorised brain activity patterns between trials for each searchlight. To speed up computations the analysis was restricted to a cortical space (Figure 3.4A) containing bilateral IFG, STG, MTG, ATL, SMG and LAG. These cortical regions have been consistently reported in studies investigating lexical and semantic processing during language comprehension, as revealed by meta-analyses of a large set of language neuroimaging studies (Binder et al., 2009; C. J. Price, 2010, 2012; Vigneau et al., 2006). The spatial definitions of these regions were taken from the Automated Anatomical Labelling (AAL) Atlas (Tzourio-Mazoyer et al., 2002), and were fused together as a contiguous mask with 1 mm isotropic spacing. For each participant, data RDMs were constructed for searchlights contained in the mask.

---

[1] In this analysis Euclidean distance was used to determine the similarity between trials. Alternative distance measures used previously in RSA include the correlation distance, Mahalanobis distance and cosine distance (Kriegeskorte et al., 2008).

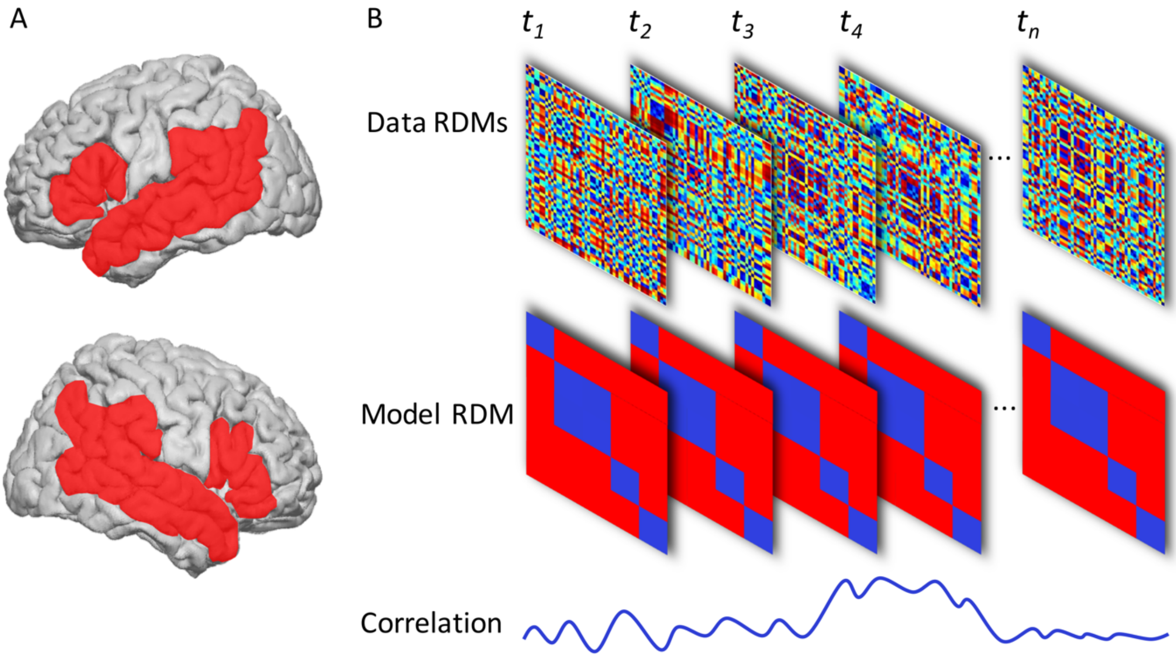


FIGURE 3.5. LANGUAGE MASK AND THE CARTOON DEPICTING MODEL-DATA CORRELATION A. LANGUAGE MASK USED IN THE CURRENT ANALYSIS. THE MASK CONSISTS OF BILATERAL INFERIOR FRONTAL, MIDDLE AND SUPERIOR TEMPORAL, SUPRAMARGINAL, ANGULAR GYRI AND ANTERIOR TEMPORAL POLES. B. CARTOON DEPICTING HOW DATA RDMS ARE CORRELATED WITH THE MODEL RDMS FOR EACH SEARCHLIGHT. NOTE THAT THE DATA RDMS CHANGE AT EVERY TIME POINT, BUT THE MODEL RDMS ARE STATIC. THIS PROCEDURE IS REPEATED FOR EVERY SEARCHLIGHT AND MODEL RDM.

To reduce within and cross category variance in the data, items belonging to semantic categories that have fewer items than 10 were removed from the set. The removed categories were plants, food, containers, furniture, outdoor artefacts, paper items, toys, rooms, buildings, and natural objects. The remaining was a set of 218 concepts, consisted of animals, birds, invertebrates, fruits, vegetables, clothing items, tools, vehicles, musical instruments and weapons. Similarly, the trials belonging to these categories were removed from data RDMs.

3.2.8. STATISTICS AND CORRECTION FOR MULTIPLE COMPARISONS

The data RDMs were then correlated with model RDMs using Spearman's rank correlation coefficient (Figure 3.4B). The correlations were computed independently for each model RDM. To allow computation of spatiotemporal clusters in 4–dimensional space, correlation time courses were placed in participant's cortical mesh. The 4-dimensional matrix consisted of 3 spatial dimensions of participant's cortical mesh (91x109x91[2] spatial points) and 1 temporal dimension

---

[2] The dimensions of this 91x109x91 matrix are the default dimensions used for cortical meshes in SPM8. In order to utilise SPM8's functions, the same dimensions were used in the current analysis.

(251 time points), adding up to over 226 million data points per participant. The extents of the data introduced a large multiple comparison problem, and therefore increased the amount of false positives. In order to overcome the multiple comparison problem and correct for the large number of data points tested, a cluster permutation based one-sample t-tests with 1000 permutations with $P = 0.01$ height and $P = 0.05$ significance threshold (Nichols & Holmes, 2004) was performed. At each permutation participant data were multiplied by either 1 or -1, and the resulting data set was tested using t-tests. The permutation vectors containing multipliers were kept constant across all tests of models, to preserve spatiotemporal autocorrelation of the data. The maximum sum of t-values, the cluster mass, from each permutation was pooled to create the permutation distribution. The significance levels of the observed spatiotemporal clusters that exceeded our height threshold were corrected using the permutation distributions of maximum cluster mass.

3.3. RESULTS

3.3.1. REPRESENTATIONAL SIMILARITY OF COMPETITION DURING SPEECH

Table 3.1 shows the details of all significant clusters revealed across tests of models. Figure 3.5 shows the corrected t-map snapshots aligned to the UP (0 ms) for each model RDM. Before the UP I found lexical and semantic competition effects, reflecting the early short-lived parallel activation of candidate lexical and semantic representations as speech is processed over time. The *LexComp* model showed early transient effects in LSTG and LSMG from -400 to -376 ms before the UP ($P = 0.023$) (Figure 3.5A), and later more sustained effects in LMTG between -224 to -180 ms $P = 0.031$) and LIFG (BA 45/47) from -244 to -172 ms ($P = 0.04$) prior to the UP. The early effects in LSTG reflect the acoustic phonetic computation of spectrotemporal features within speech (Hickok & Poeppel, 2007; Mesgarani et al., 2014). These computations are rapidly mapped onto lexical representations, involving the LMTG which engages later competitive processes between word candidates involving LIFG (Hickok & Poeppel, 2007; Howard et al., 1992). Sensitivity in LSMG is likely to reflect the sustained activation of the lexical token in verbal working memory (Deschamps, Baum, & Gracco, 2014).

Semantic competition effects captured by the *SemComp* model showed similar early effects prior to the UP starting at approximately the same time as the *LexComp* model in the LIFG (BA 47) from -420 to -392 ms ($P = 0.0009$) and -340 to -288 ms before the UP ($P = 0.005$) (Figure 3.5B). The

SemComp model revealed short-lived sensitivity in the RSTG/MTG from -332 to -292 ms (*P* = 0.029); and a sustained effect in the LAG and LMTG from -196 to -100 ms (*P* = 0.0009).

Models	**Cluster size**	p_{cor}	**Time window (ms)**	**Cluster majority**	**Cluster extent**
LexComp	19345	0.022	-400--376 ms	L superior temporal	L superior temporal L supramarginal L middle temporal
	15788	0.039	-244--172 ms	L inferior frontal pars tri	L inferior frontal pars tri L inferior frontal pars orb
	16527	0.031	-224--180 ms	L middle temporal	L middle temporal L superior temporal
SemComp	21267	<0.001	-420--392 ms	L inferior frontal pars orb	L inferior frontal pars orb L temporal pole
	18074	0.005	-340--288 ms	L inferior frontal pars orb	L inferior frontal pars orb L temporal pole
	10944	0.029	-332--292 ms	R middle temporal	R middle temporal R superior temporal
	24663	<0.001	-196--100 ms	L angular	L angular L middle temporal
	9690	0.036	-100--80 ms	L temporal pole	L temporal pole
	9371	0.041	-88--52 ms	R inferior frontal pars tri	R inferior frontal pars tri R inferior frontal pars oper
	10650	0.029	44-64 ms	L inferior frontal pars tri	L inferior frontal pars tri L inferior frontal pars oper
SemDis	21649	0.016	8-112 ms	L supramarginal	L supramarginal L angular L middle temporal
	38144	0.003	52-108 ms	R inferior frontal pars op	R inferior frontal pars op R inferior frontal pars tri
	15656	0.039	72-112 ms	R middle temporal	R middle temporal R angular
	17145	0.036	192-216 ms	R superior temporal	R superior temporal R middle temporal
	19380	0.025	200-248 ms	R supramarginal	R supramarginal R angular

TABLE 3.2: SSRSA RESULTS SHOWING SIGNIFICANT CLUSTERS FOR THREE MODEL RDMS.

There were transient effects in the LATL (*P* = 0.036) between -100 to -80 ms, in RIFG (*P* = 0.04) between -88 to -52 ms, and in LIFG (BA 44/45; *P* = 0.029) between 44 to 64 ms. These results show that the initial activation of low level lexical representations gives rise to later semantic representations as activity shifts from STG to LAG, LATL and bilateral MTG.

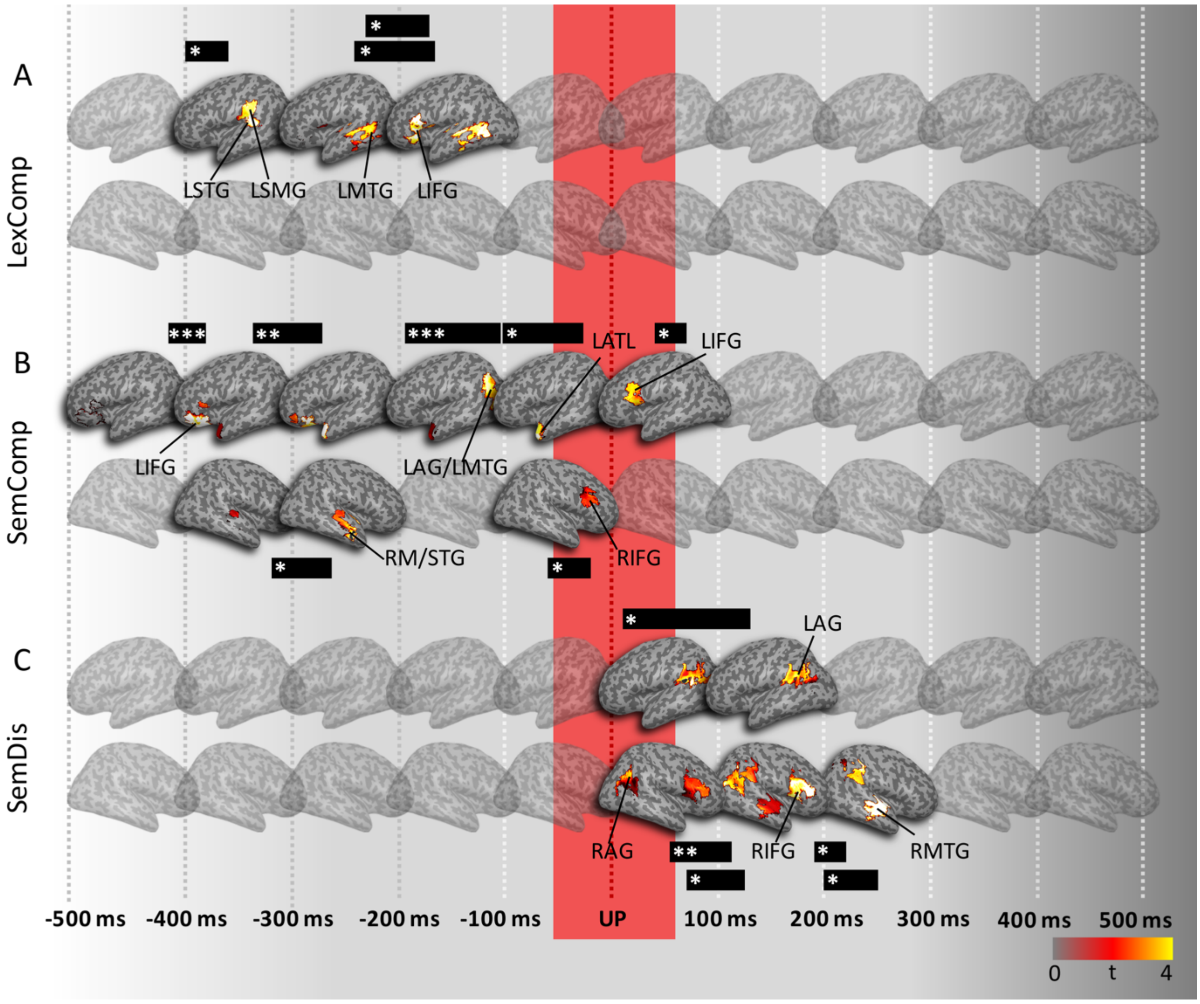


FIGURE 3.6. THE SSRSA RESULTS DISPLAYING THE CORRECTED T-MAPS EVERY 100 MS. * P<0.05, ** P<0.01, *** P<0.001. UP IS MARKED BY THE RED BORDER.

Together, the results of the SemComp and LexComp models indicate that prior to the identification of the spoken word multiple lexical and semantic representations of the cohort candidates are partially activated. This parallel activation recruits regions that have been previously associated with lexical semantic representation (Bonner, Peelle, Cook, & Grossman, 2013), phonological processing (Buchsbaum et al., 2001), and competition demands (Moss et al., 2005). Further two competition models show considerable overlaps in the LIFG which have been previously reported in neuroimaging studies investigating competition resolution and/or controlled retrieval of representations (Grindrod et al., 2008; Moss et al., 2005; Thompson-Schill, Aguirre, D'Esposito, & Farah, 1999).

3.3.2. TRANSITION FROM COMPETITION TO UNIQUE SEMANTIC ACCESS

After the UP, when the accumulating speech input enables the target word to be identified, there were significant effects of the model that captured the ease of target word's feature integration and therefore access to its unique semantic representation (SemDis). The results of the SemDis model revealed significant effects over time in bilateral AG and in RMTG and RIFG. There were early effects centered in the LIPL (Figure 3.5C), with the cluster extending from LAG, LSMG and LMTG ($P = 0.016$) and showing a sustained effect 8-112 ms after the UP. On the right hemisphere there were parallel effects in the IFG from 48 to 116 ms ($P = 0.003$). RIFG effects were followed by significant clusters in RAG from 72-112 ms ($P = 0.039$) and from 200-248 ms ($P = 0.025$), and in RS/MTG from 192-216 ms ($P = 0.036$). The SemDis results indicate that following the UP, reflects a process of individuation between the target concept and its cohort neighbours. Further, the overlapping effects of the SemComp and SemDis models in LAG confirm the prominent role of LAG in the conceptual retrieval (Bonner et al., 2013; A. R. Price et al., 2015) and show that UP marks a transition point between the lexical-semantic activation of the cohort candidates to boosting semantic activation and rapid access to target semantic representation (Marslen-Wilson, 1990).

3.4. DISCUSSION

This study investigated the spatiotemporal dynamics of the neural computations involved in the transition from speech to the target word's semantic representation by testing cognitive models of competition and semantics against the MEG data. Using spatiotemporal searchlight RSA I tested three theoretical models that captured key cognitive processes assumed to take place: lexical and semantic competition and access to lexical semantics of the target word. In line with lexicalist models of speech processing (Gaskell & Marslen-Wilson, 1995; Marslen-Wilson, 1987; McClelland & Elman, 1986), I predicted that as the participants heard the speech, they would partially activate lexical and semantic representations of the words that match the speech input. I predicted that only after the target word is uniquely identified (i.e. after the UP), the activation level of its unique semantic representation would be strongly boosted.

Consistent with these models of speech comprehension and our predictions I found that the sound-to-meaning mapping during natural speech processing involves rapid computations aligned around the UP. Prior to the UP speech processing was dominated by processes of lexical and semantic competition, reflecting the activation of multiple word candidates. In contrast, there were no competition effects of either phonology or semantics after the UP, supporting the claim that the UP marks the earliest point at which a word can be reliably differentiated from its cohort competitors (Tyler, 1984). I also found significant effects of the access to unique semantics of the target word only after the UP, suggesting that pre-UP the semantics of the target word was not differentiated from the semantics of the other words in the cohort.

3.4.1. COMPETITION IN THE ABSENCE OF CONSTRAINT

The lexical competition was modelled through the lexical entropy which captures uncertainty at the lexical level. As the number of competitors increased, and the lexical identity of the spoken word became more difficult to determine, which in turn increased the entropy. Therefore the LexComp model captured lexical competition as well as representational similarity of phonology within the cohort candidates. The LexComp results revealed a network of regions (LSTG, LSMG, and LIFG) commonly reported in studies investigating speech and phonology (Friederici, 2002; Hickok & Poeppel, 2000; C. J. Price, 2000; Scott & Johnsrude, 2003). I interpret the early LSTG and LSMG effects, as reflecting the initial acoustic-spectral processing of the continuous speech input (Leonard, Bouchard, & Chang, 2013; Leonard & Chang, 2014) and increasing load of the verbal working memory respectively (Henson, Burgess, & Frith, 2000).

The SemComp model on the other hand captured the average semantic similarity of the cohort candidates' feature co-occurrence vectors (Baroni & Lenci, 2010). I assumed that a lower semantic similarity of feature co-occurrence between members of the cohort would result in higher semantic competition prior to the UP. In line with our predictions, the SemComp results showed significant clusters only before the UP. The model recruited a large network of regions consisting of bilateral MTG, bilateral IFG, LAG and LATL. Functional neuroimaging and neuropsychological studies have previously associated MTG with the representation of lexical semantic information (Binder et al., 2009; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996; Visser, Jefferies, Embleton, & Ralph, 2012; Wei et al., 2012; Whitney et al., 2011). LAG on the other hand, has been often reported in studies that incorporate combining multiple semantic representations (Bemis & Pylkkänen, 2013; Graves et al., 2010) default mode network (Seghier, Fagan, & Price, 2010), spatial cognition (Ardila, Concha, & Rosselli, 2000) and many other cognitive functions (Seghier, 2013). Altogether these studies indicate that LAG acts as a heteromodal association cortex where information from multiple sensory and cognitive modalities converge (Bonner et al., 2013; Seghier, 2013). Similar to LAG, LATL has been also reported in studies looking at neural bases of conceptual combination (Baron & Osherson, 2011; Hickok & Poeppel, 2007; Lambon Ralph, Sage, Jones, & Mayberry, 2010; Patterson et al., 2007). Along the lines of findings in the literature, I can interpret the activity in bilateral MTG as activation of lexical semantic representations, which then becomes an amodal conceptual representation in LAG and LATL, although within the design of the current study their distinct functional roles in lexical semantics cannot be clarified.

Both SemComp and LexComp models showed effects in the LIFG. Although the literature lacks a clear consensus on LIFG's function in language comprehension, considering the nature of the models tested in this analysis LIFG's role in the networks unravelled in LexComp and SemComp can be explained with two theories. First theory suggests that LIFG is a part of a semantic executive network that subserves the online retrieval of semantic information from memory (Demb et al., 1995; A. D. Wagner, Paré-Blagoev, Clark, & Poldrack, 2001). This controlled semantic retrieval is suggested to be guided by top-down signals from LIFG to areas where semantic information is stored. Even though the focus of this theory is on the semantic aspect of memory, a similar retrieval effect has been previously shown for autobiographical memory as well (Greenberg et al., 2005). This theory would predict that the LIFG activity should precede the activity in the temporal areas during retrieval. The second theory suggests that the LIFG serves to select among competing alternatives, and eventually resolve any competition (Grindrod et al., 2008; Thompson-Schill, 2003; Thompson-Schill et al., 1997). Thompson-Schill et al (1997) argue that LIFG activity commonly attributed to memory retrieval operations might be confounded by parallel high demand for selection that is not controlled for in these experiments. According to the theory of selection and competition, the LIFG activity should be observed only when the experimental manipulation results in competition that is required to be resolved. Further, this theory would predict that the LIFG activity should become apparent in the final stages of competition -that is after multiple candidate representations are activated.

LIFG consists of three subdivisions proposed to serve different functions (Costafreda et al., 2006; Hagoort, 2005; Noonan et al., 2013; Uddén & Bahlmann, 2012). In a key fMRI study Badre et al (2005) test the distinction between selection and retrieval processes among LIFG subdivisions.

The study showed that left anterior ventrolateral prefrontal cortex (VLPFC; i.e. BA 47) activity was sensitive to top-down retrieval of semantically associated information, whereas the left mid VLPFC (i.e. BA 44/45) got activated in response to higher demand to select among multiple competitors. Both LexComp and SemComp results show a late cluster in the BA 45, which likely reflects the resolution of lexical and semantic competition by the selection of the target representation from the cohort. Further, the first cluster we see in the SemComp model (starting from -244 ms) is located in the BA 47. It is likely that this cluster shows the retrieval (i.e. activation) of multiple semantic representations of words that match the speech input. However, we do not see an early BA 47 cluster for LexComp, even at the uncorrected level. This might mean that the activation of lexical representations is an automatic feed-forward process that depends solely on the acoustic input. The early BA 47 cluster in SemComp demonstrates that the controlled retrieval of semantic representations that match the speech input requires top-down guidance from BA47.

An important issue here to remember is that in this experiment the spoken words were presented in isolation. Therefore, the lexical and semantic competition effects found were not modulated or facilitated by semantic contextual constraints. If the spoken words were presented within context (e.g. *helmet* versus *cycling helmet*) then we would expect to find reduced competition effects. If the prior context helps constrain the set of lexical candidates that could follow, then the cohort size should diminish and the word should become unique earlier. Even though in the current experimental design there was no intended contextual facilitation, it is possible that following the presentation of an initial small set of nouns that refer to concrete objects (e.g. animals, tools), the participants were primed to anticipate to hear more names of concrete objects. However, in the absence of semantic constraint and due to pseudo-randomised presentation of the stimuli participants would not be able to systematically constrain the set of likely upcoming words.

3.4.2. TRANSITION FROM COMPETITION TO SEMANTIC ACCESS

I predicted that following the resolution of cohort competition the partial activation of target word's semantic representation, would be boosted because the spoken token would allow a unique phonology-to-semantics mapping. The issue of interest here was the cortical dynamics of this mapping. The SemDis model captured the relative contribution of a concept's features in the distinctiveness to co-occurrence dimensions (Taylor et al., 2012). As the high co-occurrence and distinctiveness of the features facilitate semantic access, this measure was assumed to capture the ease of feature integration which is necessary for access to semantics.

SemDis model revealed a network of bilateral AG, MTG and RIFG. These effects indicate that these cortical regions underpin the access to target word's semantic representation. Further, the overlapping effects of the SemComp and SemDis models in LAG confirm the prominent role of LAG in the conceptual retrieval and show that UP marks a transition point between the lexical-semantic activation of the cohort candidates to boosting semantic activation and rapid access to target semantic representation.

An important outcome of the SemComp and SemDis tests is that the feature-level semantic activation is rapid. SemComp model that incorporated the target word's semantic representation shows effects of retrieval -244 ms before the UP. This indicates that the target word's semantic representation is partially activated to a degree before the UP along with the competitor representations. SemDis model starts showing effects only at 8 ms after the UP. The speed of semantic access through speech has been previously studied using MEG. These studies have shown that as soon as the word is uniquely identified, words and pseudowords are differentiated as early as 50 ms after the UP (MacGregor et al., 2012), and within 200 ms its semantic representation (verbs that are related to either actions of the mouth or the leg; e.g. eat and kick) activated (Pulvermüller, Shtyrov, & Ilmoniemi, 2005). The effects of the current analysis for lexical semantic access is even earlier than what's reported previously. It is possible that this is due to higher spatiotemporal sensitivity achieved by ssRSA compared to a more traditional ERP or event related field (ERF) approach. ERP/ERF approach involves averaging the signal across all sensors and channels, which results in losing the spatial information embedded in the signal.

The SemDis model fails to show any significant effects prior to the UP, which indicates that the level of activation before the UP, was too weak to be picked up by the ssRSA. However, this should not be interpreted that the semantic representations are accessed sequentially and that we wait until the spoken word is identified to access its meaning. That would be an inefficient and slow speech recognition system. The SemComp model, which includes the target concept's representation as well as the competitors', shows effects only before the UP. These results are consistent with DCM's predictions; they indicate that the boost of target word's semantic activation depends on the unique identification of the spoken word. This means that the semantic representations are only partially active prior to the UP. As the speech input accrues and we become more certain on the identity of the spoken word, this activation is boosted, reaching its peak after the UP. The preactivation of linguistic representations has been previously shown for written words following picture presentation (Dikker & Pylkkanen, 2013), the facilitation of prior sentential context in anticipating the upcoming word in written (DeLong et al, 2005), and in spoken sentences. Therefore, the results of the SemDis model show the crucial importance of the UP in the transition from partial semantic preactivation to complete activation of target semantics.

We need to further note that the SemDis model captured the ease of feature integration rather than the activation of semantic features, which is a necessary final step in accessing conceptual representations. If the model captured semantic activation instead, we would predict to find effects in a distributed network of regions in the inferior temporal cortex (Clarke et al., 2013; Tyler, Chiu, et al., 2013). The effects revealed a network involved in feature integration, mainly bilateral AG, that construct a supramodal conceptual representation and enabling semantic access. ATL has previously been proposed to perform the same function (Patterson et al., 2007), however there were no effects of ATL in the current analysis for the SemDis model. It is possible that ATL effects were transient to be picked by the ssRSA, as the pipeline involves both spatial and temporal smoothing which might not be sensitive to short lasting focal activity.

3.4.3. METHODOLOGICAL CONSIDERATIONS

Interpreting the competition results, we need to note the cross-model correlations. The SemDis model showed low correlations with the competition models ($r = 0.12$ with LexComp; $r = -0.09$ with SemComp). The LexComp and SemComp models on the other hand, were moderately correlated ($r = -0.35$). The overlapping effects for the competition models only restricted to LIFG and LMTG, and the activations in these regions did not temporally coincide across models. Since the competition models were not orthogonal, this spatial overlap of effects might be a result of model similarity. This interpretation requires further validation that involves a model fitting using a multiple regression rather than a serial correlational approach.

A second issue we need to consider is the alignment of trials by their respective UPs. The mean duration of the words was 601 ± 122 ms; whereas the mean UP was 408 ± 81 ms. This means that when the trials were aligned by their UPs the relative distance from the sound onset varied across trials. As we moved progressively away from the UP there was an increasing misalignment across trials. As ssRSA captures the pairwise dissimilarity across trials, it is possible that the word onset misalignment increased the dissimilarity across brain activity patterns. The misaligned word onsets possibly result in misaligned underlying cognitive processes. Therefore, it is possible that due to the jitter in the beginning and at the end of the epoch, ssRSA was not able to capture some of the effects. One way to deal with this issue in future studies would be to perform the analysis on the trials that have similar UPs, hence significantly reducing the word onset misalignment.

3.4.4. CONCLUSION

In conclusion, our findings argue that the sound-meaning mapping during natural speech recognition involves rapid dynamic computations aligned around the UP. I defined these computations through three fundamental processes: lexical and semantic competition prior to the UP, and access to feature-based semantic information following the resolution of competition. The findings show that prior to the UP both lexical and semantic representations of the cohort candidates are partially activated recruiting an extensive cortical network that include LSTG, LSMG, LIFG, bilateral MTG, and AG. However, as we accumulate speech input, the pool of candidate words is narrowed down to a single concept; the unique conceptual features of that concept alone are rapidly accessed which is underpinned by bilateral AG, MTG and RIFG.

CHAPTER 4

FACILITATION DUE TO SEMANTIC CONSTRAINTS

4.1. BACKGROUND

Whilst we perceive our environment, we constantly anticipate what we are likely to hear, see and the events likely to happen in the immediate future. In a car park we anticipate to see parked cars, in a forest we anticipate we will hear twittering birds and rustling leaves. Similarly, as we listen to speech we actively construct the sentential meaning by implicitly anticipating what the speaker will say next. The anticipation would involve the predictive preactivation of the anticipated lexical representations prior to hearing the words (Kamide, 2008; Kuperberg & Jaeger, 2016). These anticipations are affected by a series of contextual variables such as the content of the previous conversations had with the speaker, recent events that occurred related to the topic and the setting where the conversation is taking place. Therefore the brain operates like a proactive organ (Bar, 2007), allowing us to anticipate environmental stimuli and rapidly process and respond to them.

4.1.1. CONTEXTUAL FACILITATION IN LANGUAGE

In the previous experiment we investigated the neural dynamics that underpin the evolution of sound to meaning as we listen to spoken words in isolation. I showed that in the absence of any contextual cues (i.e. preceding semantic and syntactic context of the sentence) the lexical and semantic competition resulting from the parallel activation of cohort competitors, needs to be resolved before the meaning of the target word can be fully accessed (Marslen-Wilson, 1987; McClelland & Elman, 1986).

In everyday speech, we rarely encounter words in isolation. When we listen to continuous speech, understanding meaning of the words is aided by the preceding context. The set of lexical candidates (i.e. cohort) activated is restricted by both the speech input and the preceding sentential context. There are different forms of contextual facilitation such as knowing the voice you are listening to (Johnsrude et al., 2013), the temporal rhythm of the speech (Bendixen, Schröger, & Winkler, 2009), the facial expressions of the speaker (McGettigan et al., 2012) and her body gestures (Jessen & Kotz, 2013). In this chapter I focus on the semantic constraint provided by the prior speech only. In the current experiment I investigate how the semantic constraint modulates the network dynamics that underpin sound-to-meaning mapping.

Behavioural studies have previously shown that the lexical retrieval of words is facilitated when there is a discourse context (Bransford & Johnson, 1972). Words in supportive sentential context are processed faster than words in unsupportive contexts (Marslen-Wilson & Tyler, 1975, 1980; Tyler & Marslen-Wilson, 1986). A study shows that participants need to hear at least 50% of the word to identify the word in the absence of any context (Marslen-Wilson & Tyler, 1980; Wingfield, Aberdeen, & Stine, 1991). When context is provided the acoustic information needed to identify the word dropped to 20%. Similarly, speech presented in noise is understood better when it is provided within a helpful sentential context (Cohen & Faulkner, 1983; Miller, Heise, & Lichten, 1951). Moreover, disconfirmed anticipations about the identity of the upcoming word results in longer reaction times (Schwanenflugel & Shoben, 1985). Together these studies demonstrate that the preceding context of speech influences the processing and recognition of the upcoming words.

Further, electrophysiological studies investigating contextual facilitation in semantic processing during language comprehension focus on the N400 –a negative ERP deflection in the signal that on average peaks at 400 ms after the stimulus onset- (Kutas & Federmeier, 2000), which was previously linked to lexical semantic access (Brothers, Swaab, & Traxler, 2015) and facilitation of lexical integration (van Berkum, Hagoort, & Brown, 1999). N400 amplitude was consistently shown to decrease in response to words which were highly semantically predictable words in context (e.g. *She weighs/sifts the flour*) (Lau, Holcomb, & Kuperberg, 2013; Lau, Weber, Gramfort, Hamalainen, & Kuperberg, 2014). DeLong et al (2005) demonstrated that the N400 amplitude was directly linked to the expectancy of articles and nouns constrained by the prior sentential context. The authors suggest that since all sentences used in their study were grammatically and semantically plausible, the results cannot be attributed to semantic integration difficulties. Instead the results are suggested to reflect contextual facilitation of lexical access that allows pre-activation of likely upcoming lexical representations.

MEG studies aiming to define the neural generator of the N400 effects used semantic anomaly and priming paradigms and have localised N400 effects to LMTG, left superior temporal sulcus (STS) and LSTG in auditory presentation (Helenius et al., 2002; Uusvuori, Parviainen, Inkinen, & Salmelin, 2008), LATL and LSTG (Halgren et al., 2002; Lau et al., 2014), LIFG (Halgren et al., 2002). Similarly, fMRI studies varied cloze probability of the sentential context and found a reduction in activity in STG/STS (Obleser & Kotz, 2010); increased activity in LMTG (Gold et al., 2006) increased in activity in LAG, superior/medial frontal gyrus, LIFG and posterior cingulate (Obleser et al., 2007). Further, with increasing semantic constraint they showed that the connectivity of LAG with the other reported regions significantly increased. Altogether the neuroimaging findings show that the sentential semantic constraint modulates activity in an extensive network of perisylvian language related regions. Consistent with the neuroimaging findings, Lau et al (2008) suggest a neuroanatomical model of semantic processing guided by MEG, fMRI and intracranial research on contextual semantic manipulations. According to this model lexical representations stored in the LMTG are integrated with the sentential context by LATL and LAG.

4.1.2. CONCEPTUAL COMBINATION

Language comprehension in context, requires the combination of a word's meaning with the meaning acquired from the prior context. In the simplest case, two-word phrases are formed by combining the meaning of two words (e.g. *oven gloves*). The neural network underpinning this kind of semantic combination was previously tested by comparing sentences against word lists and meaningless sentences (i.e. Jabberwocky sentences) and these comparisons consistently show increased activations for meaningful combinations in LATL (Baron & Osherson, 2011; Bemis & Pylkkänen, 2011, 2013; Bottini et al., 1994; Friederici, Meyer, et al., 2000; Humphries, Willard, Buchsbaum, & Hickok, 2001) and LAG (Bemis & Pylkkänen, 2013; A. R. Price et al., 2015). LATL activity was shown to increase for infrequent and more abstract combinations of words (e.g. *dry rain*) (Molinaro et al., 2012). In MEG Bemis and Pylkkanen (2013) explored the brain response to spoken word lists and two-word phrases and demonstrated an early increased activity in LATL followed by LAG. In line with Lau et al's model of semantic processing (2008), LATL and LAG have crucial roles in semantic combinatorial processes in language, although their distinct roles are yet to be explained.

The studies reported above use various semantic tasks (e.g. sentence plausibility judgment, lexical decision task, metaphor plausibility, word-picture matching) and manipulations (semantic anomaly, semantic priming, semantic expectancy). Previous neuroimaging studies looking at the effect of task on cognitive brain networks have shown that tasks employed in the experiments are likely to recruit additional network of regions subserving domain general executive functions such as working memory, attention, decision making, and task difficulty (S. W. Davis, Zhuang, Wright, & Tyler, 2014; Miniussi, Marzi, & Nobre, 2005; Wright, Randall, Marslen-Wilson, & Tyler, 2011). Therefore, if the experimental design utilises tasks the cognitive network of interest might be contaminated by additional regions that perform executive functions. Despite recruiting additional network of regions, tasks are useful and required to keep participants attended to the experiment. Particularly in E/MEG designs tasks are needed to increase the signal-to-noise ratio by directing participants' concentration to the stimuli. In the current experiment I aim to distinguish cognitive networks that underpin semantic processing of speech in context, from cognitive networks that might be additionally recruited due to task. Making this segregation is key to define network of regions that underpin solely semantic processing.

4.1.3. CURRENT STUDY

In the current study I aim to define cortical networks that underpin semantic processing of speech in context. More specifically, I investigate the effect of the prior speech's semantic constraint on the network dynamics that underpin sound-to-meaning mapping. In order define the networks that come online over time I carried out an E/MEG experiment where I presented participants two-word spoken phrases in the form of [modifier + noun]. I varied the semantic constraint provided by the modifier. The modifier either provided strong (Strong C; e.g. *cycling helmet*) or weak (Weak

C; e.g. *plastic helmet)* semantic constraint and formed a meaningful phrase. In the third condition two words were unrelated, and did not form a meaningful phrase (No C; e.g. *shuffle helmet*). Thus, this condition was analogous to word lists. With these three conditions I aimed to manipulate both the degree of semantic constraint and semantic integration. Additionally, to keep participants attended to the stimuli, I asked them to answer semantic relatedness questions (e.g. school bus - children) that were presented only 10% of the trials. Results of Experiment 1 showed that in the in the absence of contextual facilitation, the access to target word's semantics occurs as soon as the word has is uniquely recognised. I expected that as the semantic constraint increased the words would be recognised faster, indicated by earlier UP and that the contextual semantics would induce activity in AG and ATL.

In line with the literature and Lau et al.'s model of semantic processing (2008) I predicted that the semantic constraint would facilitate the processing of meaningful phrases, and this facilitation would be underpinned by LAG and LATL. I predicted to find effects of integration, that is Strong and Weak C compared to No C, in LIFG (Hagoort, 2005). Lastly I expected that as the semantic constraint increased, the words would be recognised earlier and they would have less lexical competition. Even though the task used in this experiment was simple and presented infrequently, I predicted that it would still recruit additional executive network of regions that control attention and working memory.

Here I employed a temporal independent component analysis (tICA; (Hyvarinen, Karhunen, & Oja, 2001; Hyvärinen & Oja, 2000; Makeig, Jung, Bell, Ghahremani, & Sejnowski, 1997)) to investigate the effects of semantic constraint on the E/MEG brain activity patterns in the absence of domain-general activity. ICA is a blind source separation method originally developed for signal processing, but was later adopted by the neuroimaging community as a data-driven multivariate method of analysis that can decompose the data into statistically independent networks of brain signal. In E/MEG literature, it was previously utilised to uncover spatiotemporal networks that related to the resting state (Brookes et al., 2011; Ramkumar, Parkkonen, & Hyvärinen, 2014), artefacts resulting from cardiac activity, eye or body movement (Daly, Nicolaou, Nasuto, & Warwick, 2013; Ghaderi, Kim, & Kirchner, 2014; Lindsen & Bhattacharya, 2010) and to modulations due to experimental manipulations (Brookes et al., 2012; Luckhoo et al., 2012). Therefore, tICA applied at the group level, allows us to define and separate cortical networks common to all participants, and further determine the independent role of each network in a cognitive process. In the current experiment I use tICA at the group level to separate out temporal networks that are shared across participants that subserve contextual semantic processing from the task-positive networks.

4.2. METHODS

4.2.1. PARTICIPANTS

20 participants volunteered in the study with a mean age of 23.85 (9 males, 11 females). Participants' ages ranged from 20 to 34 years. Among these participants two were excluded due to technical problems during acquisition. A third participant was excluded because she misunderstood the task.

4.2.2. BEHAVIOURAL PRE-TESTS

To test the facilitating effects of semantic constraint on access to lexical semantic representations, the stimuli were presented in [modifier + head noun] (e.g. *toffee apple*) format. The modifiers belonged to three different conditions: strong constraint (Strong-C), weak constraint (Weak-C), and no constraint (No-C). One third of the modifiers formed meaningful phrases by applying strong semantic constraint on the head-nouns (e.g. *cycling helmet, cherry tomato, cruising yacht*). Weak constraint modifiers on the other hand, formed meaningful phrases (e.g. *ugly toad, broken spear, clean socks*) by only applying a weak semantic constraint. Lastly the no constraint modifiers failed to form meaningful word combinations (e.g. *lullaby wasp, pump sparrow, dining rake*). These phrases were included to allow modelling of the E/MEG activity in the absence of any helpful semantic constraint or integration. Therefore, the no-constraint phrases were essentially word lists rather than two-word phrases. The semantic constraint provided by the modifier was measured using the SemCons variable which was adopted from Price et al (2015). SemCons measures the probability of encountering the noun, given the modifier (i.e. transitional probability; see next section for more detail on the measure). SemCons measure was used to select modifiers that applied high and low semantic constraint.

Prior to the E/MEG study, to confirm that the level of semantic constraint applied by the modifier differed across conditions, to define the UPs of target words, and to measure the naturalness of the phrases, a behavioural gating study (Grosjean, 1980) was performed. The gating tests are especially useful in understanding online speech comprehension, as they allow us to investigate the transient online perception of continuous stream of sounds. During the gating study participants were instructed 1) to listen to chunks of the spoken words presented incrementally phoneme by phoneme; 2) to type in their best guess of what the word might be after each chunk (i.e. gate); 3) to rate their confidence in their answer; 4) and finally rate the naturalness of each phrase on a scale of 1-5 (5-high naturalness).

In the gating test, 111 spoken names of concrete concepts (e.g. *helmet*) were tested. The nouns used in Experiment 2 were a subset of the nouns used in Experiment 1. The nouns were presented with three different modifiers. Two meaningful and one irrelevant modifier (e.g. *shuffle helmet*) were selected for each concept. Among the two meaningful modifiers, one was aimed to apply stronger semantic constraint (i.e. high SemCons) on the head noun (e.g. *cycling helmet*) than the other (e.g. *plastic helmet*). 20 young participants (mean age 24.85 years, 13 females) who did not participate in the MEG experiment performed the task. Example plots from the gating results are given in Figure 4.1.

To confirm differences in semantic constraint across conditions, both the cohort size and the transitional probabilities were used as proxies. Transitional probability was defined as the percentage of participants who correctly guessed the target noun, at the modifier's offset, before hearing the noun the noun given the modifier. Naturalness ratings were used to exclude non-meaningful combinations of words. Further, the UPs were computed for each head-noun of each phrase, and were used for trial alignment of the following E/MEG analysis. Similar to the procedure used in Experiment 1, the UPs were defined as the first gate where a minimum of 80% of the participants have a summed confidence level that exceeds 80%. As expected, Strong and Weak C phrases on average were rated more natural compared to the No C phrases. Meaningful phrases with naturalness rating below 3.5 and non-meaningful phrases with naturalness ratings above 2.5 were removed from the set. 88 triplet phrases that showed clear differences between the cohort sizes and transitional probability across conditions remained from the larger set, to be used in the E/MEG experiment. These triplet phrases were assigned to three conditions that differed in the level of semantic constraint. The means and standard deviations of these measures across conditions are given in Table 4.1.

Condition	Naturalness	Cohort size	UP (ms)	Trans. P (%)
Strong-C	4.48 ± 0.42	5.59 ± 3.83	290.29 ± 130.55	33.19 ± 33.28
Weak-C	4.14 ± 0.38	11.14 ± 4.82	414.53 ± 139.01	4.98 ± 10.85
No-C	1.47 ± 0.30	14.76 ± 4.85	488.40 ± 103.87	0.44 ± 1.92

TABLE 4.1. GATING STUDY RESULTS. COLUMNS SHOW MEANS AND STANDARD DEVIATIONS OF NATURALNESS OF THE PHRASE, COHORT SIZE, UNIQUENESS POINT AND THE TRANSITIONAL PROBABILITY. UP = UNIQUENESS POINT.

The cohort size of a target word largely depends on its number of phonemes and therefore its length. As a word gets longer, the cohort size increases. When we take an average of the cohort sizes and UPs we do not take the length of the word into account. We can account for the word duration by normalising the cohort size and UPs within the triplets. Normalisation involved rescaling the values within every triplet to match the z-score distribution with a mean of 0 and standard deviation of 1. Table 4.2 shows the cohort size and UPs averaged across phrases after the values are normalised for the length of the target word. Even after normalisation change in cohort sizes and the UPs show the same linear pattern. As the semantic constraint increases cohort sizes shrink and UPs shift to an earlier time point. The cohort size, UP, their normalised versions and the Trans. P were tested across conditions using two-tailed paired samples t-tests.

Condition	N. cohort size	N. UP
Strong-C	-0.67 ± 0.87	-0.86 ± 0.87
Weak-C	0.22 ± 0.86	0.10 ± 0.86
No-C	0.92 ± 0.87	0.75 ± 0.86

TABLE 4.2. NORMALISED MEANS. COLUMNS SHOW MEANS AND STANDARD DEVIATIONS OF THE NORMALISED COHORT SIZE AND UNIQUENESS POINTS. UP = UNIQUENESS POINT, N = NORMALISED.

Results showed that as the semantic constraint increased, cohort size and UP decreased and the transitional probability increased. All condition differences were statistically significant (all $P < 0.00014$; see Table 4.3), confirming that the phrases have clear differences in the semantic constraint applied by the modifier at the stimulus level.

4.2.3. STIMULI

The final set of stimuli consisted of 264 spoken two-word phrases (see Appendix B) in the format of [modifier + head-noun]. 88 names of concrete concepts were randomly presented with three different modifiers. The conditions were matched ($P > 0.05$) by the number of syllables and the lexical neighbourhood density of the modifier (Table 4.3). There was a marginal difference in

Test	**UP**		**N. UP**		**Cohort size**		**N. Cohort size**		**Trans. P**	
	t	**P**	**t**	**P**	**t**	**P**	**t**	**P**	**t**	**P**
Strong-Weak C	-6.37	1.09e-08	-8.35	1.65e-12	-7.99	8.32e-12	-10.06	7.50e-16	8.67	3.84e-13
Strong-No C	-12.88	3.35e-21	-16.86	4.68e-28	-12.64	9.04e-21	-20.06	5.87e-33	9.87	1.70e-15
Weak-No C	-5.17	1.65e-06	-6.55	5.17e-09	-4.92	4.50e-06	-8.53	7.27e-13	4.01	1.37e-04

TABLE 4.3. STATISTICAL TESTS ON THE UP AND COHORT SIZE. TESTS INDICATE THAT THE UP, COHORT SIZE, THEIR NORMALISED VERSIONS AND TRANS P SIGNIFICANTLY DIFFER ACROSS ALL THREE COMPARISONS.

concreteness (Brysbaert, Warriner, & Kuperman, 2014) between the Strong C and Weak C modifiers ($P = 0.058$). Concreteness has been previously shown to facilitate word recognition (Feldman, Basnight-Brown, & Pastizzo, 2006; Palazova, Sommer, & Schacht, 2013). Moreover previous neuroimaging studies show that the word frequency facilitates semantic processing and retrieval (Carreiras, Mechelli, & Price, 2006; Halgren et al., 2002). However due to the nature of the experimental manipulation, the conditions were not matched by their word frequency. This is due to the fact that modifiers in the Weak-C condition are more commonly used in everyday language as they reflect general properties of many concepts (e.g. ugly, clean). Whereas modifiers in the Strong-C condition reflect properties of a small group of concepts, therefore are less frequent in everyday language. Since differences in modifier frequency and concreteness can cloud the effects of semantic constraint, in the following analyses the effects of these variables were accounted for (Table 4.3).

The presentation order of the phrases was pseudo-randomised and split into three blocks. Further, to minimise the effect of exhaustion and priming on the E/MEG signal, the blocks were presented in 6 different orders across participants. The mean duration of phrases was 1213 ms. Duration of each block was approximately 10 minutes.

The main experimental manipulations here were the degree of semantic constraint applied by the modifier word in the phrase and the ease with which modifier and the head noun are combined

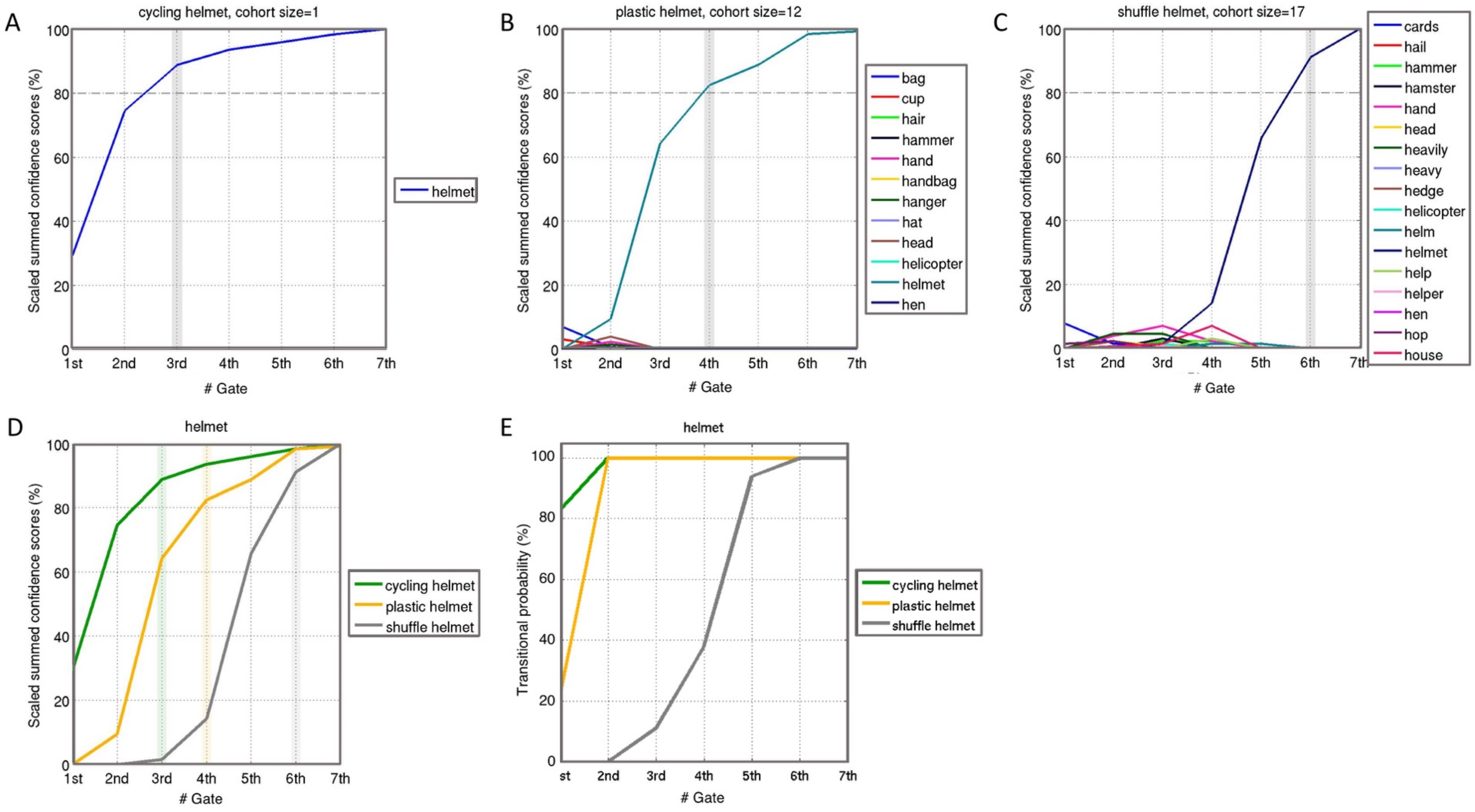


FIGURE 4.1. EXAMPLE GATING PLOTS. A. GATING PLOT OF THE STRONG C PHRASE FOR HELMET. B. GATING PLOT OF THE WEAK C PHRASE FOR HELMET. C. GATING PLOT OF THE NO C PHRASE FOR HELMET. D. SUPERIMPOSED CONFIDENCE TIME SERIES FOR TARGET WORDS ACROSS THREE CONDITIONS. E. TRANSITIONAL PROBABILITY CHANGES OVER TIME. DOTTED LINE AT 80% SHOWS THE CONFIDENCE SCORE CUTOFF THRESHOLD. UP WAS DEFINED AS THE FIRST GATE WHERE THE CONFIDENCE LEVEL EXCEEDS 80% FOR A MINIMUM OF 80% OF THE PARTICIPANTS. GREY BORDER MARKS THE UP FOR THAT PHRASE. GATES START FROM MODIFIER OFFSET AND END AT NOUN'S OFFSET. NOTE THAT AS SEMANTIC CONSTRAINT OF THE MODIFIER INCREASES, THE COHORT SIZE AND UP DECREASES. SUPERIMPOSED CONFIDENCE TIME SERIES SHOW THAT STRONG C PHRASE (CYCLING HELMET) HAS AN EARLIER UP THAN THE WEAK C PHRASE (PLASTIC HELMET), WHICH IS FOLLOWED BY THE NO C PHRASE (SHUFFLE HELMET). TRANSITIONAL PROBABILITY PLOT SHOWS THAT AT THE MODIFIER OFFSET STRONG C MODIFIER PROVIDES THE STRONGEST CUE FOR THE UPCOMING NOUN, FOLLOWED BY WEAK AND NO-C

into two-word phrases. The semantic constraint differences between the three conditions were confirmed through behavioural gating results, which showed that as the semantic constraint of the modifier increases the cohort size and UPs decrease and the transitional probability increases.

Using measures previously employed in the literature the semantic constraint of each phrase used in the experiment was quantified. For this the approach taken by Price et al (2015) was adopted. Accurately measuring linguistic properties of the modifier and the phrase require the use of a large corpus. The study mentioned, uses Google search results to quantify how often two words are used together, instead of a more conventional n-gram approach. The Google search offers two advantages over the conventional method. First, the frequency information is taken from websites that use more everyday language as opposed to formal language used in textbooks. Second, the frequency information that can be acquired from n-grams is sparse as we are limited by the number, topic, and the type of texts used to create the corpus. Therefore, Google search results provide a richer source of frequency information in everyday language. In their study Price et al (2015) were interested in measuring how often two words co-occur together. Here their method was used to calculate probabilistic information related to two-word phrase construction. The semantic constraint variable, the SemCons, was defined as below:

$$SemCons = -\log \left(P\left(C_{ij} \mid C_i\right)\right)$$

Where C_i and C_{ij} refer to the total number of search results for the modifier word on its own (e.g. cycling), and with the head noun (e.g. cycling helmet) respectively. Therefore, the variable measures the log posterior probability of encountering the two-word phrase, given the modifier. As the semantic constraint increases the SemCons values decrease (Table 4.3). Figure 4.2 shows the relationships of SemCons with cohort size and transitional probability. The SemCons measure is inversely related to transitional probability ($R^2 = 0.41$), and positively related to cohort size ($R^2 = 0.41$) (see Figure 4.2). Whereas cohort size is inversely related to transitional probability ($R^2 = 0.60$). All these measures showed significant differences across pairwise comparisons of conditions.

Condition	# Syllables	PND	Log frequency	Concreteness	SemCons	UP (ms)
Strong-C	1.80 ± 0.77	9.17 ± 11.62	0.70 ± 0.96	3.98 ± 0.76	2.29 ± 0.89	290.29 ± 130.55
Weak-C	1.83 ± 0.61	8.19 ± 11.70	1.76 ± 0.56	3.78 ± 0.77	3.78 ± 0.83	414.53 ± 139.01
No-C	1.85 ± 0.68	10.03 ± 12.60	0.71 ± 0.92	3.92 ± 0.53	5.52 ± 1.10	488.40 ± 103.87

TABLE 4.4. PSYCHOLINGUISTIC VARIABLES MEASURED FOR THE MODIFIERS.

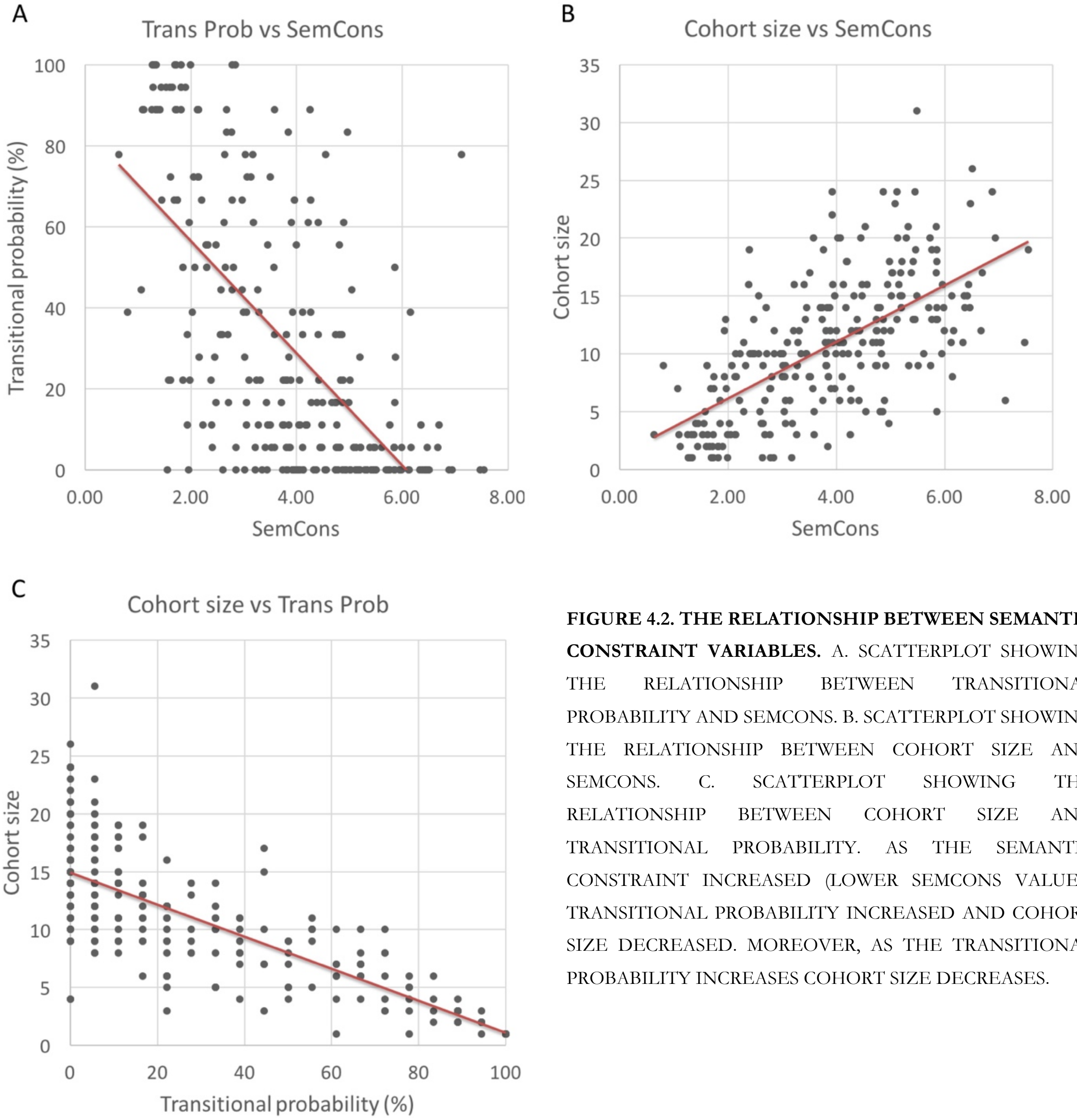


FIGURE 4.2. THE RELATIONSHIP BETWEEN SEMANTIC CONSTRAINT VARIABLES. A. SCATTERPLOT SHOWING THE RELATIONSHIP BETWEEN TRANSITIONAL PROBABILITY AND SEMCONS. B. SCATTERPLOT SHOWING THE RELATIONSHIP BETWEEN COHORT SIZE AND SEMCONS. C. SCATTERPLOT SHOWING THE RELATIONSHIP BETWEEN COHORT SIZE AND TRANSITIONAL PROBABILITY. AS THE SEMANTIC CONSTRAINT INCREASED (LOWER SEMCONS VALUES) TRANSITIONAL PROBABILITY INCREASED AND COHORT SIZE DECREASED. MOREOVER, AS THE TRANSITIONAL PROBABILITY INCREASES COHORT SIZE DECREASES.

4.2.4. PROCEDURE

Delay in sound delivery due to the length of earphone tubes and stimulus delivery computer's sound card was 26 ± 2 ms on average. To ensure that participants were attentively listening to the stimuli, on 10% of the trials they were presented with a semantic association question. In these catch trials after the spoken phrase (e.g. school bus) a single written word (e.g. children?) appeared in the middle of the screen. Participants were instructed to judge whether the the phrase they heard was semantically associated with the word displayed on the screen via button presses. The number of yes and no answers were equal. These semantic association questions were followed by a meaningful dummy spoken phrase, which was later removed from the analysis. The purpose of the inclusion of dummy phrases was to give participants time to focus back on natural listening. In the rest of the trials participants did not make any response. By instructing participants to make a response only on 10% of the trials, the involvement of domain general networks was minimised (S. W. Davis et al., 2014).

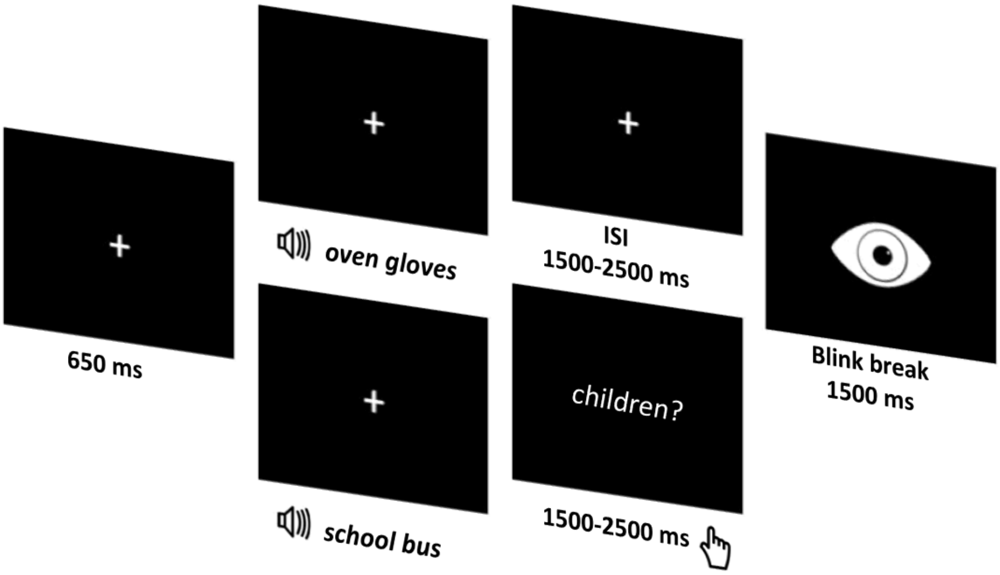


FIGURE 4.3. SCHEMATICS OF THE EXPERIMENTAL DESIGN. ON 10% OF THE TRIALS PARTICIPANTS WERE INSTRUCTED TO RESPOND TO A SEMANTIC RELATEDNESS QUESTION.

Before the presentation of the spoken stimulus, a cross appeared in the middle of the screen for 650 ms prompting the participant to focus his/her eyes on the cross (Figure 4.3). The inter-stimulus interval was randomised between 1500 and 2500 ms. Every interval was followed by a blink break that lasted for 1500 ms. The start of the blink break was indicated by an image of an eye that appeared in the middle of the screen. With the use of blink breaks, the contamination of the signal by eye movement related artefacts was minimised. Participants were also asked to refrain from movement during the entire block of recording. Participants started the experiment with a short practice run, which was followed by three experimental blocks. Duration of the entire experiment was approximately 40 minutes including breaks in between blocks.

4.2.5. E/MEG AND MRI ACQUISITION

Continuous electroencephalography (EEG) and MEG data were recorded simultaneously. EEG data was recorded using 64-electrode EasyCap (EASYCAP gmbH, Herrsching-Breitbrunn, Germany) setup. The Ag-AgCl electrodes were placed on the cap according to the 10/20 system.

The reference and ground electrodes were placed on the tip of the nose and on the lower right cheek respectively.

4.2.6. MEG PREPROCESSING AND SOURCE LOCALISATION

Data were further preprocessed using SPM 8 (Wellcome Trust Centre for Neuroimaging, University College London, UK). Data were band-pass filtered at 0-40Hz. The trials were aligned by the UP of the head noun. The epoch duration was -600 to 500 ms around the UP. Baseline period was set to -600 - -500 ms. On average 4.11 trials (*SD* = 3.33) were removed due to artefacts. Trials were averaged within conditions for every participant.

Each participant's data were prepared for source localisation by including magnetometers, gradiometers and EEG electrodes. Single shell model and EEG boundary element method (BEM) models were used for forward modelling of MEG sensors and EEG electrodes respectively. Inversion was completed over the period -500 to 500 ms around the UP.

4.2.7. WINDOWED SOURCE LOCALISATION

Using the inverse solutions, the source activity of each condition was averaged over 100 ms long non-overlapping time windows from -500 ms to 500 ms around the UP. The average activity was converted to 3D images using SPM8 (Wellcome Trust Centre for Neuroimaging, University College London, UK). The strength of source activity was compared across conditions via univariate contrasts, using permutation paired samples t-tests with 1000 permutations where initial height threshold was $P = 0.05$.

4.2.8. GROUP-LEVEL TICA

ICA is a blind source separation method that determines linear combinations of source components that are maximally independent to each other (Hyvärinen & Oja, 2000). When performed at the group level it can identify sources of activity that appear consistently across the group of participants. This method has been previously applied both to hemodynamic and MEG data to separate out networks that were shown to subserve different functional roles (Brookes et al., 2012; Calhoun, Eichele, Adalı, & Allen, 2012; Luckhoo et al., 2012).

The implementation of ICA on E/MEG data is not straightforward due to ICA's bias for finding non-Gaussian sources (Hyvärinen, Ramkumar, Parkkonen, & Hari, 2010). This bias makes ICA suitable for identifying components related to eye and body movement, cardiac activity and speech. Since brain activity has a highly Gaussian nature, the conventional ICA method is not sensitive enough to pick up independent focal brain activity patterns. One solution to overcome this problem is to incorporate the phase information of the signal to the data by taking the absolute value of the Hilbert transformed data (i.e. Hilbert envelope) (Hyvärinen et al., 2010). Since the phase values change considerably by the number of cycles of the oscillation, this computation has to be performed separately for narrow frequency bands. However, by decomposing the signal into frequency bands and then into ICs we would considerably increase the number of tests. For example, if we decompose the signal into 5 frequency bands and then separate every bands' signals to 20 ICs, we would have to perform 100 statistical tests. To reduce the number of multiple comparisons prior to the group-level ICA a time-frequency analysis was performed, which allowed us to focus on the frequency bands where experimental manipulation shows effects. The tICA analysis pipeline is displayed in Figure 4.4.

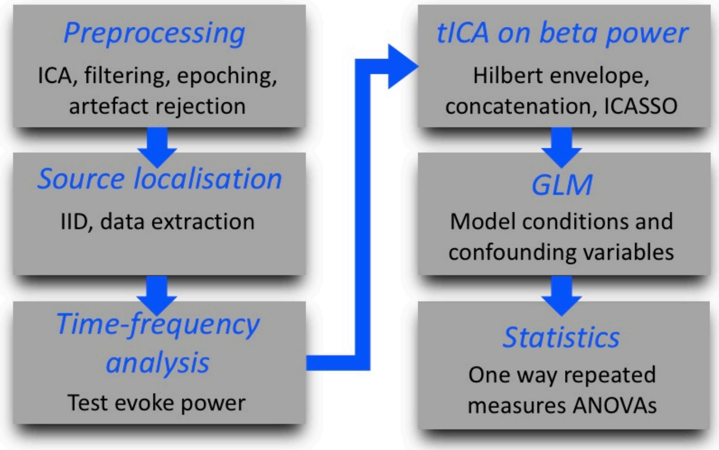


FIGURE 4.4. TICA PIPELINE SHOWING THE MAIN STEPS OF THE ANALYSIS.

4.2.8.1. TIME-FREQUENCY ANALYSIS

The power of all the frequencies from 5-40 Hz (i.e. theta up to gamma) was computed separately for each sensor type (EEG electrodes, magnetometers and gradiometers) across the epoch by applying Morlet wavelets with 5 cycles, implemented in SPM8. As the frequencies are reduced their power increases (i.e. power law). In order to test both high and low frequencies in the same representation the power needs to be rescaled (i.e. normalised) across frequencies. In this analysis the power of high and low frequencies were normalised using log rescaling (i.e. LogR method in SPM8) which computes the log of power and applies baseline correction to each frequency separately. Finally the power was averaged across all sensors of each sensor type. Therefore, the resulting time-frequency representations captured the power changes consistent across all sensors, but lost the spatial information. The time-frequency data were tested through univariate contrasts by using permutation based paired samples t-tests with two tails and 10000 permutations.

4.2.8.2. TEMPORAL ICA

The time-frequency results were used to constrain the analysis to bands where there were significant conditional differences. To prepare data for the group-level ICA the preprocessed epoched data were band-pass filtered into these bands and were inverted separately. Following the inversion, data time courses from every vertex (8196 vertices) were extracted by applying the inverse solution. Time courses at each vertex were Hilbert transformed to derive the analytic signal. The absolute value of the Hilbert transform was taken to compute the Hilbert envelope of the time course. This computation was performed for all of the source space vertices, and for every participant. To speed up computations the Hilbert envelopes were downsampled to 10 Hz, and concatenated across trials and participants in the time dimension. The downsampling rate was set to 10 Hz to allow ICA decomposition of this large dataset. In the literature this rate was previously set to 1 Hz (Brookes et al., 2011; Luckhoo et al., 2012), however any signal downsampled at 1 Hz cannot accurately represent the evoked signal. For example, if the epoch length is 1000 ms, 1 Hz rate would reduce the data to only the brain activity patterns at the 1st ms of every epoch. Therefore, as a compromise between increasing computational speed and representing evoked data accurately, I used a 10 Hz rate which means that the resulting time series will have values for every 100 ms.

Temporal ICA was performed on the concatenated dataset using the fastICA (Hyvarinen & Oja, 1997) algorithm, where the rows and columns of the dataset corresponded to concatenated temporal dimension and source space vertices respectively. Similar to pipeline used by Brookes et al (2011) the concatenated data were normalised across participants and were pre-whitened prior to ICA, by reducing the dimensions of the dataset to 30 principle components. 20 ICs were estimated. The spatial topography of each component was rendered by correlating the IC time series with every vertex of the data that was inputted to ICA. The resulting correlation values showed the relative contributions of time series of each vertex in the source space to create the independent time series. These correlation values were then rendered on a 3D brain template to visualise neural generators of the IC time series. Alternatively, one can use the unmixing matrix resulting from the ICA to retrieve the weights applied by each vertex into creating the IC time series. However, using correlation values in lieu of the weights in the unmixing matrix offers a more straightforward and familiar way to threshold the spatial maps. In this analysis the spatial maps were thresholded at an absolute r = 0.1.

4.2.8.3. RELIABILITY TEST OF THE ICA ESTIMATES

An issue to note with ICA is the unknown estimation reliability which arises from the lack of unique ICA estimation and statistical errors generated by the finite sample size. A toolbox implemented in MATLAB called ICASSO (Himberg, Hyvärinen, & Esposito, 2004) computes a metric of reliability by performing multiple runs of ICA with random initialisations. The similarities across estimates of multiple runs are calculated by ICASSO using agglomerative average linkage. The similarity value, σ_{ij} defined as the absolute value of two components' mutual correlation coefficient r_{ij}.

$$\sigma_{ij} = |r_{ij}|$$

The similarity values were used to compute the cluster quality index (I_q) using the formula below where C_m is the number of components in the m_{th} cluster, C_{-m} is the set of indices that do not belong to the m_{th} cluster. σ_{ij} is the similarity measured between the i_{th} and j_{th} components.

$$I_q(C_m) = \frac{1}{|C_m|^2} \sum_{i,j \in C_m} \sigma_{ij} - \frac{1}{|C_m||C_{-m}|} \sum_{i \epsilon C_m} \sum_{j \epsilon C_{-m}} \sigma_{ij}$$

The resulting Iq value will fall between 0-1, where values close to 1 indicate reliable ICs. Therefore, Iqs can be used as a criterion to define reliable ICs.

A second criterion is the cluster size, which here refers to the number of times a spatially similar component was detected throughout runs. Therefore, the cluster size in this context does not refer to the size of a brain region. Following multiple runs of ICA, ICASSO groups all IC estimates (20 ICs x 10 runs = 200 estimates) by computing spatial correlation as a measure of proximity. For example, if the same exact temporal pattern keeps coming up across multiple runs then the spatial proximity will be 0 and the estimates will cluster together. However, if slightly different temporal patterns come up across multiple runs then the spatial distance would be higher between estimates. Then, the estimates will either not cluster together, or form a large cluster with a low within cluster similarity. Ideally if the component is reliable, its cluster size should be equal to the number of runs. An appropriate cluster size was defined as ± 20 % of the number of multiple runs (Ma et al., 2011).

For example, if one performs 10 ICA runs, the range for appropriate clusters is 8-12. This criterion was incorporated as an additional measure to ensure that the ICs investigated will be the ones that were consistently identified by the ICA procedure across multiple runs. In the current analysis 10 runs of ICA were performed with random initialisations. Previously 0.7 was used as an Iq cut-off to define reliable components (Ma et al., 2011), which was adopted in the current analysis. Similarly, the range for appropriate cluster size was defined as 8-12. The components that fit both of these criteria were defined to be reliable, and were used in the following general linear model (GLM).

4.2.8.4. GENERAL LINEAR MODEL AND STATISTICS

The goal of the GLM following group level ICA was to investigate the response of cortical networks to experimental manipulations, in the absence of domain general activity such as maintaining attention, task related rules or decision making. To investigate the effect of varying degrees of contextual facilitation in sound-meaning mapping, the IC time series that were concatenated across trials and participants, were chopped up back into single trials. In a GLM, the trials were modelled by three dummy variables that represent three conditions, and two confounding variables (i.e. concreteness and log frequency) for every time point and IC separately. The resulting beta values were tested for differences across conditions by performing one-way repeated measures ANOVAs at each time point. The significant differences were further investigated using post-hoc Tukey's HSD comparisons. There were no multiple comparisons correction for the number of IC components. Note that previously by downsampling the data, the total data size was reduced. Therefore, the beta time series of each condition had only 11 data points, corresponding to every 100 ms.

4.3. RESULTS

4.3.1. WINDOWED SOURCE LOCALISATION

With this preliminary analysis I aimed to investigate the change in source activity (i.e. source strength) across the epoch, by testing for conditional differences every 100 ms time window. The t-maps of the univariate contrasts given in Figure 4.4 show uncorrected results at $P = 0.05$. Among these clusters the ones that reached significance at the corrected level following permutations are given in Table 4.4.

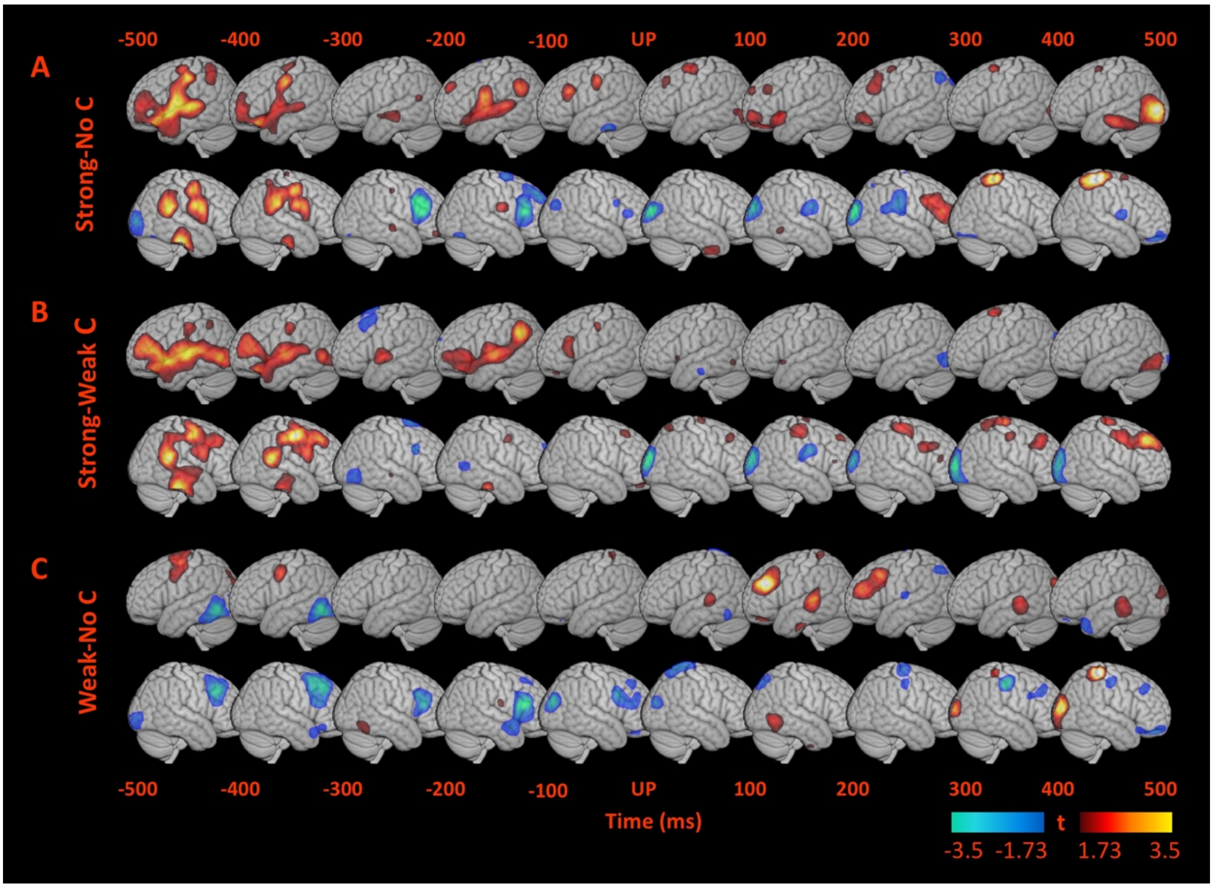


FIGURE 4.5. WINDOWED SOURCE LOCALISATION RESULTS (UNCORRECTED T-MAPS AT P=0.05). BLUE SCALE SHOWS INCREASES IN SOURCE ACTIVITY FOR THE SECOND CONDITION.

Compared to Weak C and No C, the Strong C condition displayed higher source activity in the bilateral STG, LIFG and LMTG between -500 to -300 ms before the UP. Strong C shows higher LAG activity compared to both condition after -200 ms, however this cluster was not significant at the corrected level.

Contrast	**Time window**	**k**	**p_{cor}**	**Cluster extent**
Strong-Weak C	-500--400 ms	15323	0.022	RSTG, R precentral, R postcentral
Strong-Weak C	-500--400 ms	19616	0.008	LMTG, LSTG, LIFG
Strong-No C	-500--400 ms	17667	0.005	LIFG, LIPL,LSTG,LMTG
Strong-Weak C	-400--300 ms	16071	0.011	LSTG, LMTG, LIFG
Strong-Weak C	-400--300 ms	12971	0.023	RMFG, RSTG, R precentral
Strong-No C	200-300 ms	9017	0.045	LIFG

TABLE 4.5. RESULTS OF THE WINDOWED SOURCE CONTRASTS. THE COLUMNS FROM LEFT TO RIGHT SHOW THE CONTRAST, TIME WINDOW OF THE CONTRAST, CLUSTER SIZE (K), CORRECTED CLUSTER P VALUE, AND THE CLUSTER EXTENT.

These results indicate that the increasing contextual semantic constraint recruits an extensive network of left dominant perisylvian regions 500 ms before the word is recognised. Whilst interpreting the results we have to keep in mind that the mean UP of the Strong C nouns was 290 ms, whereas the mean for No C and Weak C were 488 and 414 ms respectively. Therefore, -500 in Strong C corresponds to the period before the noun onset.

4.3.2. GROUP-LEVEL ICA

4.3.2.1. TIME-FREQUENCY ANALYSIS

Univariate time-frequency contrasts were performed to restrict the number of frequency bands tested in the following group-ICA and the GLM. 6 contrasts were performed for each sensor type separately. The results (Figure 4.5) showed increases in the beta band power for Strong-Weak C in both gradiometers and magnetometers starting from 254 ms to 16 ms before the UP (Table 4.5). The cluster found in magnetometers was largely overlapping with the beta/gamma band cluster in gradiometers; however the cluster's corrected p value was marginally significant. EEG electrodes showed a significant late effect for the Strong-No C contrast after the UP. This cluster was significant in the beta band from 224 to 456 ms after the UP. Overall the results of the time-frequency analysis helped to restrict the frequency bands tested in the following group-level ICA and the regression analysis. The following analyses were therefore restricted to the signal band-pass filtered to beta/gamma band at 15-34 Hz.

Contrast	Sensor	p_{cor}	k	Frequency window	Time window
Strong-Weak C	MAG	0.08	1788	15-27 Hz	-248 - -16 ms
	GRAD	0.04	2097	15-28 Hz	-254 - - 24 ms
Strong-No C	EEG	0.011	2815	16-34 Hz	224 – 456 ms

TABLE 4.6. RESULTS OF THE TIME-FREQUENCY ANALYSIS. THE COLUMNS FROM LEFT TO RIGHT SHOW THE CONTRAST, SENSOR TYPE, P VALUE CORRECTED WITH PERMUTATION T-TESTS, CLUSTER SIZE, FREQUENCY AND TIME WINDOWS OF THE CLUSTER.

4.3.2.2. GROUP ICA NETWORKS

As the time-frequency differences only occurred in the 15-34 Hz window, the temporal group-level ICA was performed only on the beta/gamma band (15-34 Hz) with 10 random initialisations (i.e. bootstrapped data sets). Following the multiple runs, using the reliability criteria I determined the ICs which were both coming up consistently across the multiple runs and were compact. Note that the ‘compactness’ of a cluster does not refer to the size of the brain region, but how temporally similar the estimates were across the runs. Results of the reliability tests are given in Figure 4.6.

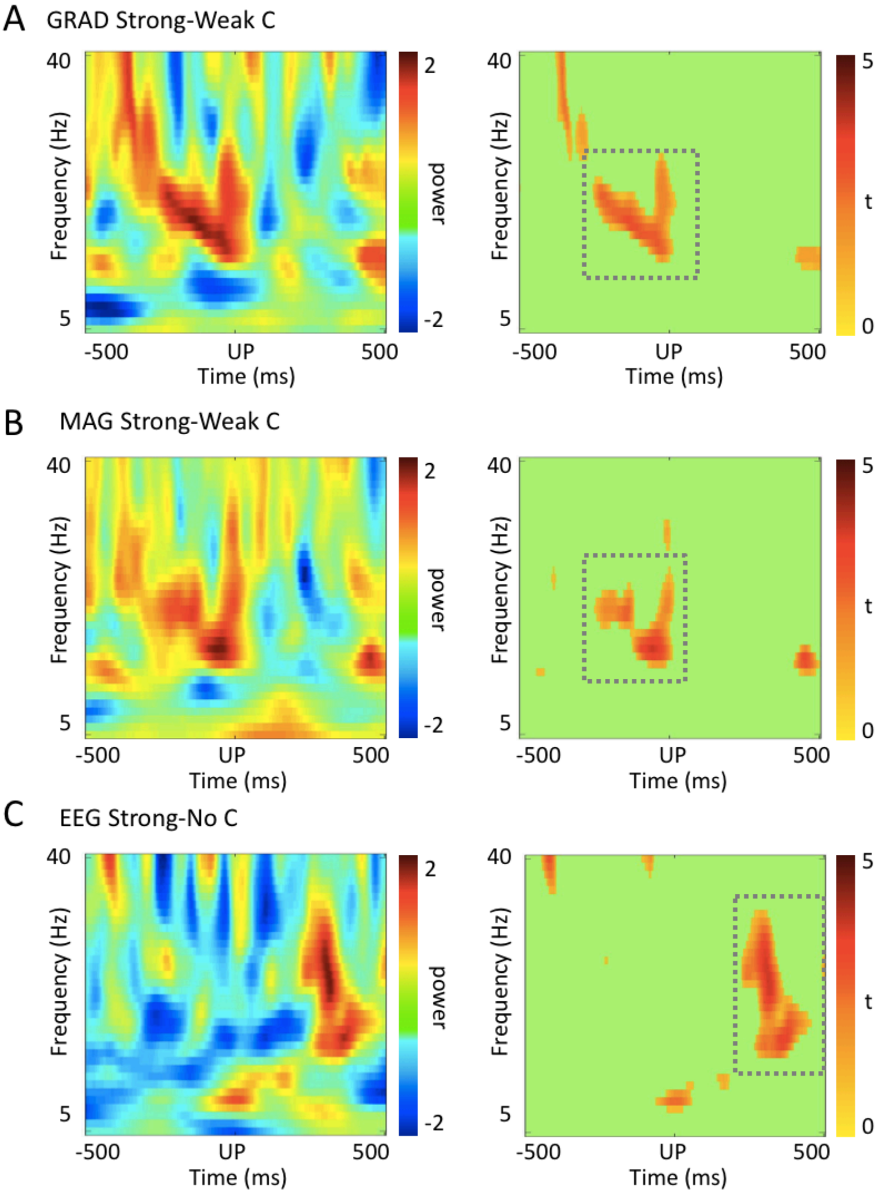


FIGURE 4.6. TIME-FREQUENCY REPRESENTATIONS OF THE SIGNIFICANT CLUSTERS. FIRST COLUMN SHOWS THE TIME-FREQUENCY REPRESENTATION OF THE CONTRASTS, AND THE SECOND COLUMN SHOW THE T-MAPS OF THE CONTRAST THRESHOLDED AT P=0.05. SIGNIFICANT AND MARGINALLY SIGNIFICANT CLUSTERS ARE INDICATED WITH THE DOTTED SQUARES.

Note that even though I specified 20 ICs, the Fast ICA algorithm decomposed the data to 14 components due to singularity of the covariance matrix. In this context singularity means that the columns of the matrix can be defined as linear combinations of each other. Therefore, if the number of components was higher than 14 then the components would not be statistically independent.

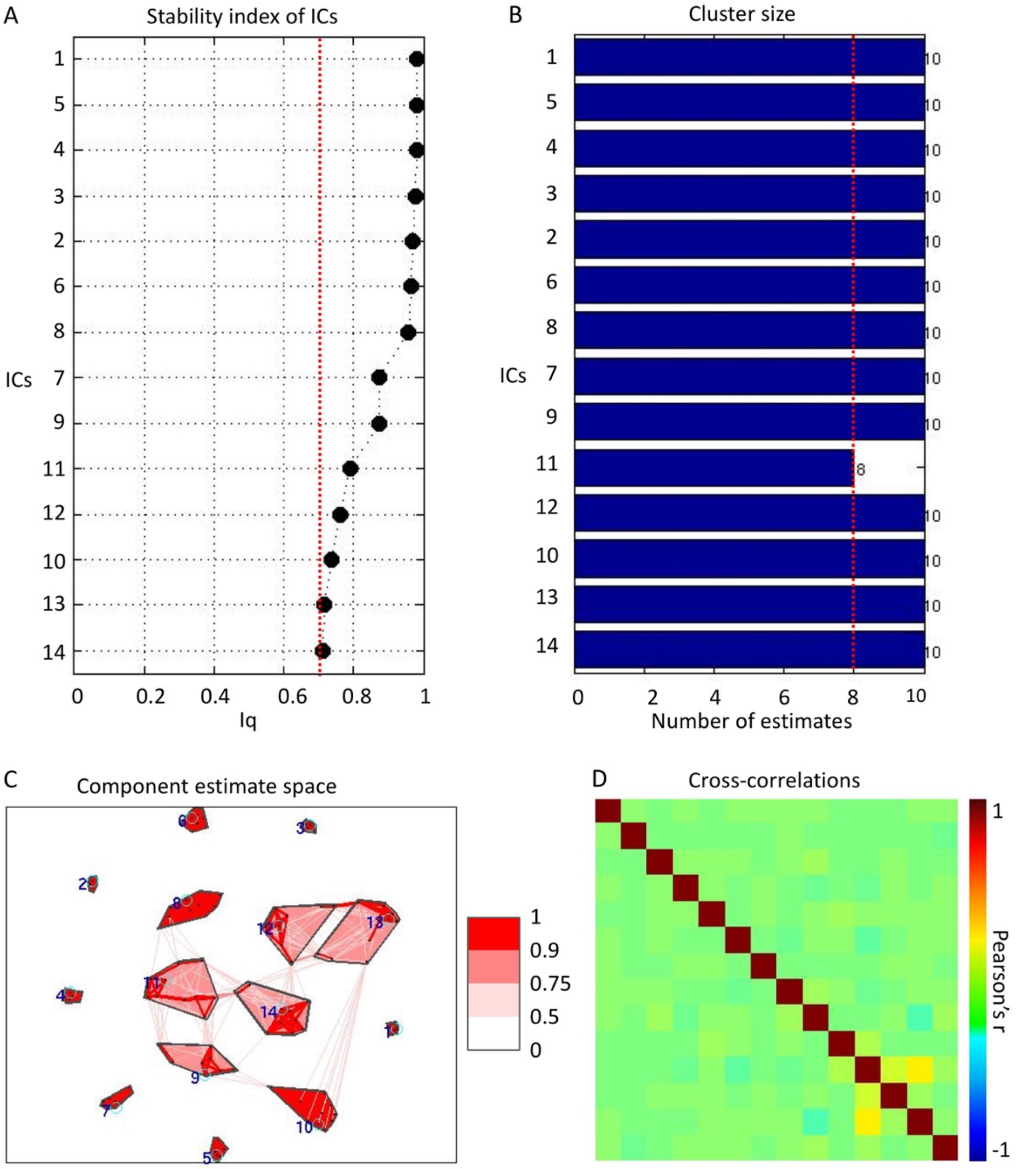


FIGURE 4.7. RESULTS OF THE ICA RELIABILITY TESTS PRODUCED BY THE ICASSO ALGORITHM. A. STABILITY INDICES OF THE INDEPENDENT COMPONENTS (ICS). RED LINE INDICATES THE IQ = 0.7 THRESHOLD. ACCORDING TO OUR CRITERIA ANY IC WITH AN IQ LOWER THAN THIS THRESHOLD IS UNRELIABLE. B. CLUSTER SIZES OF THE ICS. RED LINE INDICATES THE LOWER THRESHOLD OF THE CLUSTER SIZE RELIABILITY CRITERION. ANY COMPONENT WITH A CLUSTER SIZE OUTSIDE 8-12 RANGE IS UNRELIABLE. C. COMPONENT ESTIMATE SPACE PLOTTED AS A 2D PROJECTION, SHOWING PAIRWISE SIMILARITIES WITHIN AND ACROSS COMPONENTS. HERE CONVEX HULLS REPRESENT ESTIMATE CLUSTERS, COMPACT AND ISOLATED CLUSTERS SUGGEST RELIABLE ESTIMATES. NOTE THAT AS THE CLUSTER BECOMES MORE COMPACT AND ISOLATED THE COLOR GOES DARKER RED. D. PAIRWISE TEMPORAL CORRELATIONS BETWEEN IC TIME SERIES MEASURED BY PEARSON'S TESTS. CORRELATIONS ARE MINIMAL.

Figure 4.6A-B shows the Iq and the cluster size of every component was within the defined range, and therefore all components passed the reliability test. Figure 4.6C shows the temporal similarities of the components by projecting component estimates onto 2D space where the estimate positions depict within and across estimate similarities. Isolated clusters that are compact and that have high within cluster similarity are indicated by dark red. This means that across multiple runs of ICA decomposition the components that were acquired were highly similar within the cluster and highly dissimilar across components. Figure 4.6D shows the temporal correlations between ICs. As to be expected these correlations are minimal (<0.2), and therefore the temporal time courses are statistically independent.

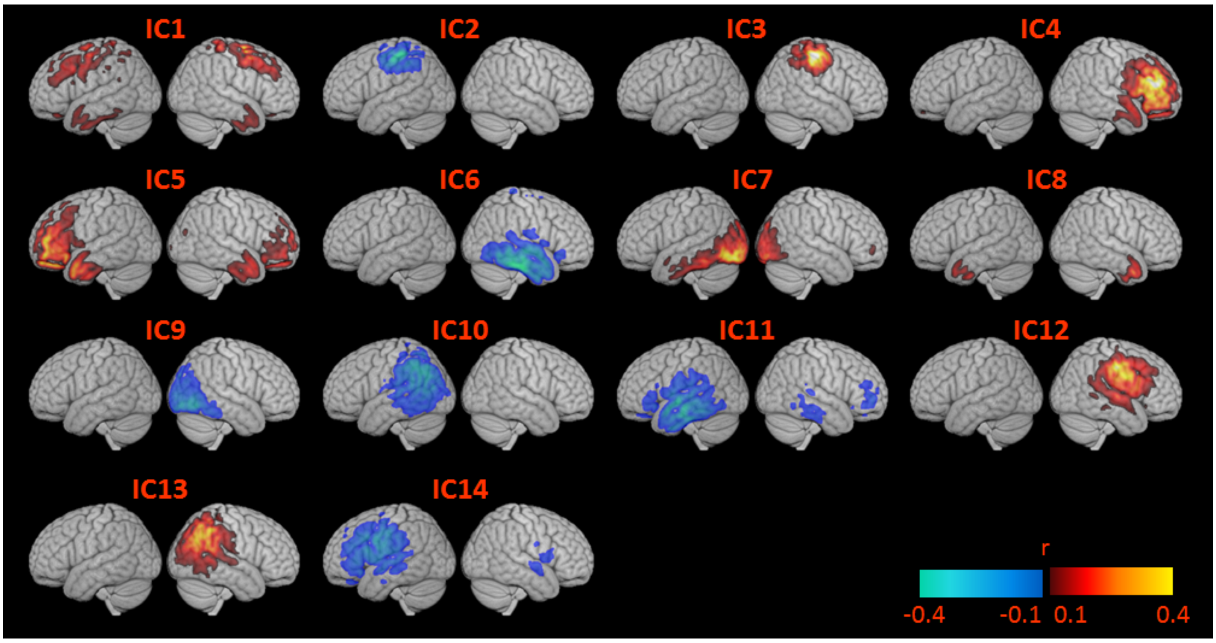


FIGURE 4.8. RESULTS OF THE GROUP-LEVEL ICA. THE PLOTS SHOW SPATIAL TOPOGRAPHIES OF INDEPENDENT COMPONENTS, GIVEN BY THE TEMPORAL CORRELATION OF IC TIME SERIES WITH THE ORIGINAL SIGNAL EXTRACTED FROM EACH VERTEX. THE VALUES SHOWN HERE ARE THRESHOLDED BETWEEN 0.1-0.4 AND -0.1- -0.4 FOR SIMPLICITY.

Figure 4.7 shows the spatial topographies of the ICs. These topographies are produced by correlating the IC time series with the source data at every vertex. These r values show the vertices that have greater contribution to construct the IC time series. Note that the spatial topographies overlap across components. This is due to the fact that tICA produces temporally independent but not spatially ICs. As the r values in a particular part of the cortex increase, its contribution to the IC time course increases. For this reason, the values shown in the topographies are thresholded between 0.1 to 0.4 magnitudes of r. The polarity of the weights indicates the relationship of the IC time course with the original signal. Therefore, negative and positive r values indicate negative and positive relationships between the IC time series and the input signal. Irrespective of the polarity, these spatial maps indicate the vertices that made the largest contributions to the IC time series.

Together the IC topographies covered a large area of the cortex that largely overlap with the networks uncovered in the windowed source localisation contrasts. The majority of the ICs represent processing in primary sensory areas: IC12-14 auditory network, IC7-9 visual network, and IC2-3 sensorimotor network. Given that the experimental design involves listening and answering occasional questions via pressing a button, it is expected to find activity in both the auditory and the sensorimotor network. Even though this was an auditory experiment, participants' eyes were open and focused on the cross presented in the middle of the screen. Since ICA picks up common networks across participants, finding visual networks among the ICs is to be expected as well.

Five of the ICs included regions associated with semantic processing in the literature: IC6-11 temporal cortices, IC10-13 AG, and IC8 bilateral ATL. Temporal cortices are proposed to store lexical representations, whereas ATL and AG proposed to combine semantic representations. Within the framework of this experiment, I would expect the activity of these five networks to be modulated by contextual semantic constraint.

Finally, tICA revealed three networks in the frontal cortex: IC1, IC4 and IC5. The regions in IC5 overlap partially with IC8 and IC4. These inferior frontal regions could be underpinning controlled retrieval of lexical representations and selection of the target representation among the activated cohort candidates (Badre & Wagner, 2002; Thompson-Schill et al., 1997). IC1 on the other hand shows more dorsal frontal regions with clusters in the IPL which altogether resembles the profile of the multiple demand network (MDN). MDN is a pattern of task-positive frontoparietal activity associated with planning and performing a series of small operations to achieve a goal (Duncan, 2010). Since experimental tasks involve performing additional mental operations (e.g. working memory, decision making, directing attention) MDN can be activated on top of the primary sensory and association areas. Despite the low frequency of the semantic relatedness questions included in the experiment (10%), it is possible that the use of the task recruited additional regions. However, eyeballing the networks is not enough to understand the role of these networks. If a network's activity is modulated by contextual semantic constraint, then that network's activity should differ across conditions. To find out if there are differences in constraint modulation, through the following GLM analysis, I removed the effects of the confounding variables and modelled the three conditions in each network.

4.3.2.3. GENERAL LINEAR MODEL AND THE UNIVARIATE CONTRASTS

The beta values were tested for differences using one-way repeated measures ANOVAs for each IC. Post-hoc Tukey's HSD tests were performed to determine the group means that differed. Results showed that among all 14 networks, only two showed significant differences across the conditions (Figure 4.8): IC10 and IC13 (i.e. bilateral AG).

Effects of semantic constraint occurred at 300 ms before the UP in both IC10 and 13. At -300 ms, in IC10 Strong C's amplitude (*M* = 0.60; *SD* = 0.49) was significantly higher (*F*(2,48) = 4.89, *P* = 0.011) than both Weak C (*M* = 0.31; *SD* = 0.34) and No C (*M* = 0.34; *SD* = 0.39). Simultaneously I found a similar pattern of activity in IC13 where Strong C's amplitude (*M* = 0.36; *SD* = 0.29) was significantly higher (*F*(2,48) = 3.79, *P* = 0.029) than Weak C's (*M* = 0.17; *SD* = 0.22). These indicate that the activity of both LAG and RAG are modulated by contextual semantics, and that as the semantic constraint increases so does the activity in these two networks. Therefore, when the words are presented within supportive semantic context, the contextual information is used 300 ms prior to word's recognition, to constrain the set of likely upcoming words.

In IC10 No C's amplitude (*M* = 0.40; *SD* = 0.27) was significantly higher (*F*(2,48) = 5.95, *P* = 0.004) than both Weak C (*M* = 0.19; *SD* = 0.26) and Strong C (*M* = 0.19; *SD* = 0.24) at 400 ms before the UP. Even though this pattern of effects might point to integration, evaluating these effects with the gating results I infer that this is unlikely. Since No C nouns have late UPs (see Behavioural pre-tests), -400 ms corresponds roughly to the noun onset. At this point participants start hearing the second word, and realise the mismatch between their anticipated and perceived word. Therefore, this increase of amplitude for the No C phrases might reflect semantic violation, and the initiation of recovery from this semantic mismatch rather than successful integration of word's meaning with the context.

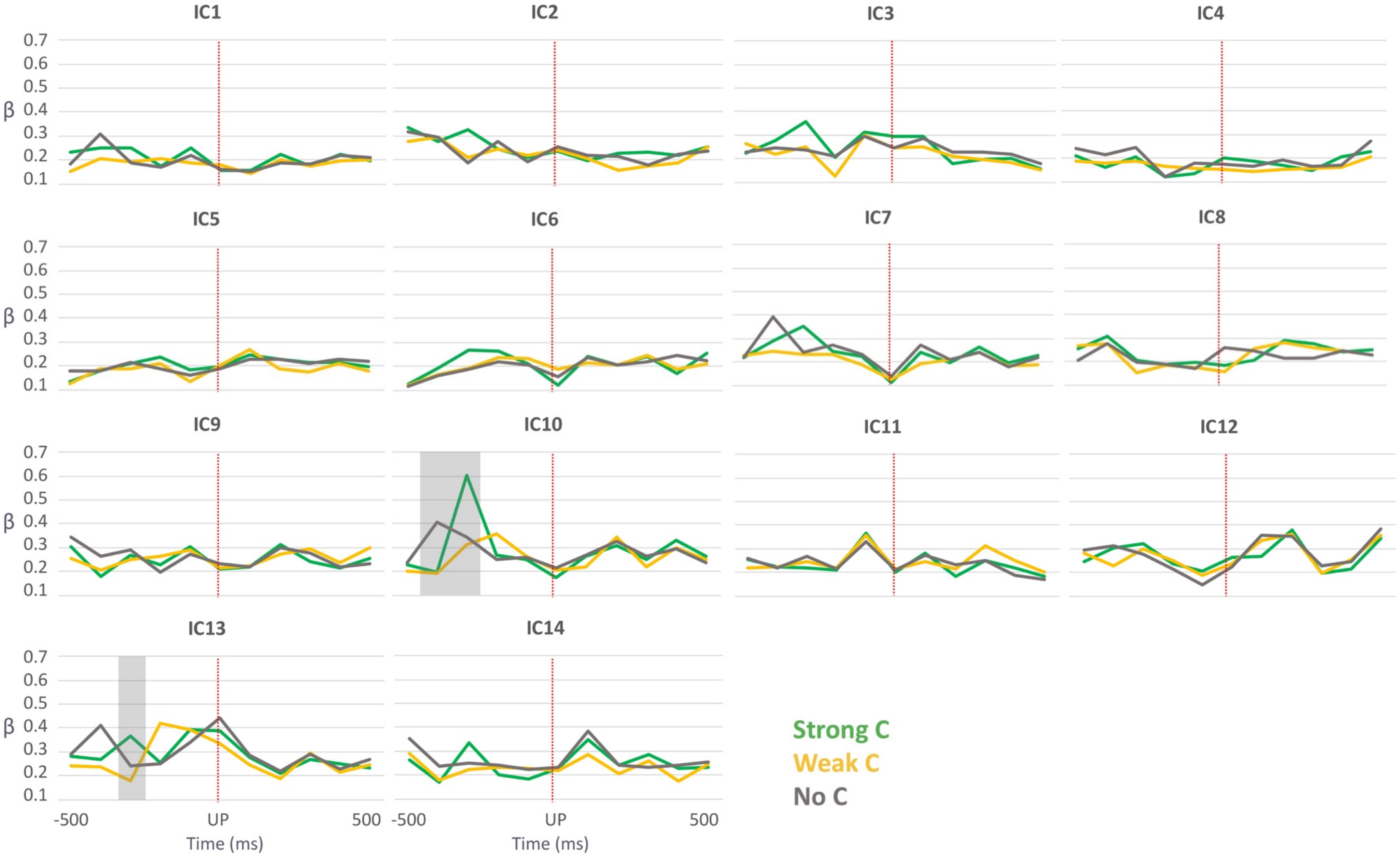


FIGURE 4.9. MEAN IC BETA TIME SERIES ACROSS THREE CONDITIONS. GREY BORDERS INDICATE THE TIME WINDOWS WHERE CONDITION BETAS DIFFERED SIGNIFICANTLY. RED DASHED LINE INDICATES THE UP. ONLY IC10 (LIPL/LAG) AND IC13 (RIPL/RAG) SHOWED SIGNIFICANT DIFFERENCES BETWEEN CONDITIONS. EFFECTS WERE FOUND BETWEEN -400 AND -300 MS.

4.4. DISCUSSION

In the current experiment I aimed to investigate the network dynamics of semantic processing of speech in context. I presented participants with two word spoken phrases where the first word, the modifier, provided varying degrees of semantic constraint. I predicted that increasing semantic constraint would result in earlier word recognition and integration of the noun's semantics with the modifier's. As a baseline for integration processes, a third condition, meaningless word pairs, was presented.

4.4.1. SPEED OF WORD RECOGNITION AND CONTEXT

As predicted and complementary to the behavioural literature (Marslen-Wilson & Tyler, 1980; Tyler, 1984; Tyler & Wessels, 1983) the behavioural gating results showed that as the semantic constraint increased, the target word's cohort size decreased and the UP shifted to an earlier time point. Replicating earlier effects (Tyler & Wessels, 1983), compared to Weak C, Strong C's average cohort size was almost halved, and its average UP (in ms) was approximately 125 ms earlier. These cohort size and UP effects were further validated by controlling for the duration of the noun. This additional check was done, because it is to be expected for long words to have bigger cohort sizes and therefore late UPs. Even when the UPs were normalised by the word durations, the effects and trends persisted. The behavioural results therefore demonstrate the facilitating influence of helpful semantic constraint on making speech comprehension faster and efficient by narrowing down the cohort candidates of the target word.

It is worth emphasising the "helpfulness" of the semantic constraint when we consider the case of No C phrases. Even though No C phrases were constructed as meaningless word pairs (e.g. *tune socks*), they were presented with the other meaningful phrases. This may have meant that when participants listened to these phrases they expected to encounter a meaningful phrase but realised at a later time point that the phrase was meaningless. Therefore, this condition may have reflected how the semantic network would respond to an unhelpful and misleading semantic context (e.g. semantic violation), and how it recovers from disconfirmed anticipations. The context may be unhelpful because participants may, by habit, listen to the phrases and expect a meaningful combination. As they heard the second word, the cohort members that did not fit both the speech input and the constraint decay. However, at a later time point when they realise the second word can not be semantically related to the preceding context, the participants tried to identify the second word by completely disregarding the contextual meaning. Due to this, the UPs of No C nouns were more delayed than UPs of the Weak C nouns. Even though the Weak C modifiers were semantically too broad, they were nonetheless more helpful than No C modifiers. The larger cohort sizes and late UPs of No C phrases, are complementary to previous behavioural findings that show longer reaction times to disconfirmed anticipations about the upcoming words in speech (Schwanenflugel & Shoben, 1985).

4.4.2. MULTIPLE NETWORKS OF LANGUAGE PROCESSING UNDER TASK CONDITIONS

After confirming behavioural differences between conditions, I performed a group-level tICA to test for semantic constraint and integration effects in the absence of induced task positive networks. Previous fMRI studies compared the networks activated in an auditory experiment, when participants naturally listened to sentences and when they performed a judgment about each sentence (Campbell et al., 2016; S. W. Davis et al., 2014). The studies showed that task-free speech comprehension activates the left frontotemporal and auditory networks. Only when participants made a judgment at the end of the sentence, the task recruited additional cognitive networks (i.e. task positive networks). When trying to define network of regions that perform a cognitive function, we need to make sure that all the regions that are part of the network serve a specific role in that cognitive process rather than domain general executive functions (e.g. working memory, decision making, maintaining attention). One solution to the problem of task-positive networks is to avoid using tasks in the experiments altogether. However, tasks are sometimes needed to ensure participants are indeed attending to the stimuli. In the absence of tasks participants are likely to get sleepy, lose concentration and think about things that are irrelevant to the experiment. In terms of electrophysiology, the diminishing alertness can be observed as increases in alpha and decreases in beta power (Huang, Jung, & Makeig, 2007). Thus, the use of an appropriate experimental task can improve participants' alertness and in turn improve performance and signal quality, which are of utmost importance in E/MEG experiments. For these reasons we may need to both use tasks and simultaneously apply caution in interpreting the results.

In the current experiment to keep the participants alert, and attending to the phrasal meanings, I used a simple semantic relatedness judgment task on 10% of the trials. To reduce the task impact on the participants' behaviour, these trials were followed by dummy trials. Both the catch and dummy trials were later removed from the data that was inputted to the tICA. In terms of data cleaning and preprocessing these pre-emptive measures might seem adequate to remove the task-positive effects. Yet, the results of the GLM analysis indicated that there were still traces of task-positive networks.

tICA revealed 14 temporally independent networks covering an extensive area throughout the cortex, including primary sensory and association areas, areas proposed to be part of the semantic processing network, and frontal networks. GLM was used to determine the networks that were modulated by differences in semantic constraint of the stimuli. Only two networks significantly related to conditional differences: left and right IPL with highest weights in the AG. This might be explained in two ways: either the remaining 12 networks were related to language processing but were not modulated by experimental manipulations, or they were subserving a domain general role. Networks where the former explanation might be true, would be the bilateral auditory cortices. Therefore, the lack of effects does not necessarily mean that these networks are task-positive but rather that they are not modulated by contextual semantics.

In order to determine which networks are task-positive we consult the previous research in systems neuroscience. The widely reported task-positive networks include multiple demand network (Blank, Kanwisher, & Fedorenko, 2014; Crittenden & Duncan, 2014; Duncan, 2010), dorsal and ventral attention networks (Ozaki, 2011; Ptak & Schnider, 2010; Szczepanski, Pinsk, Douglas, Kastner, & Saalmann, 2013; Weissman & Prado, 2012) and the salience network (Chand & Dhamala, 2016; Ham, Leff, de Boissezon, Joffe, & Sharp, 2013; Jilka et al., 2014). Among these networks IC1's spatial distribution overlaps with the frontoparietal MDN, which consists of bilateral inferior frontal sulcus, anterior insula, frontal operculum and intraparietal sulcus (Duncan, 2010; Hampshire & Sharp, 2015). MDN previously was shown to get activated in response to directing attention to stimuli in the absence of any behavioural response (Downar, Crawley, Mikulis, & Davis, 2000; Hon, Epstein, Owen, & Duncan, 2006; Thompson & Duncan, 2009) and is proposed to reflect planning and the control of program assemblies to achieve cognitive tasks. Further an fMRI study (Campbell et al., 2016) comparing the networks in natural listening to making judgments about sentences, have found increased MDN activity for trials that involve task. Even though the semantic relatedness judgment used in the current experiment is simple and infrequent, the presence of MDN suggests that any task that draws attention to stimuli can recruit additional network of executive control regions.

tICA revealed additional auditory (IC12, IC14), frontal (IC4, IC5) and temporal networks (IC6, IC11) which underpin acoustic-phonological and speech processing. These networks have previously reported in fMRI group-ICA studies that investigate changes in networks under natural listening and task conditions (Campbell et al., 2016; S. W. Davis et al., 2014). Both frontotemporal and auditory networks were found irrespective of the experimental design. However, the task design recruited additional networks including default mode, MDN, basal ganglia, frontal operculum, and motor networks. Therefore, the current study replicates previous fMRI findings using E/MEG and further reveals networks that underpin contextual semantic processing in the absence of task-positive networks.

It is worth noting the overlap of regions that came up in univariate source contrasts and the networks uncovered in tICA. Source contrasts showed increased activity for the Strong C phrases compared to the remaining conditions in LIFG, bilateral STG, bilateral IPL and LMTG. tICA revealed overlapping network of regions as well as additional networks including primary visual areas, fusiform gyri, RIFG and MDN. This demonstrates the power of tICA method in capturing network activity embedded in the signal, and how tICA can successfully separate regions that work together.

4.4.3. NEURAL DYNAMICS OF CONTEXTUAL SEMANTIC FACILITATION IN SPEECH

tICA revealed that left and right IPL networks were significantly modulated by semantic constraint. Spatial topographies of these networks (i.e. IC10 and 13) show that the highest weights are located in bilateral AG. AG has been reported to be one of the areas involved in heteromodal combinatorial processes including semantic combinations (Binder & Desai, 2011; Binder et al., 2009; Koenig & Grossman, 2007), and the most common cortical area to be functionally activated in studies investigating semantic processing (Binder et al., 2009). However lesion studies indicate that AG's role in cognition extends beyond semantics, as the lesions result in impairments in speech comprehension, finger agnosia, agraphia, acalculia and spatial disorientation (Ardila et al., 2000; Hart & Gordon, 1990; Luria, 1970). The extensive nature of AG related deficits supports the view that AG underpins the convergence of modality-specific information to construct a supramodal representation (Binder et al., 2009). This view has been validated by an fMRI study that showed that both concrete words that are related to sight, sound, manipulation modalities and abstract words have increased activity in the AG (Bonner et al., 2013). Both the findings of the current study and Experiment 1 emphasise AG's role in converging modality-specific semantic representations into a supramodal representation.

A previous fMRI study employed a similar experimental design, and presented participants written two-word pairs that were either meaningful or not (A. R. Price et al., 2015). This study provided evidence both from patients and controls that bilateral AG activity and structural integrity relate to the combinatorial strength of the words to form a phrase regardless of the modifier's sensorimotor modality. The authors define combinatorial strength as the two words' co-occurrence frequency, which relates to levels of semantic constraint of the current experiment. This is because words that have a higher likelihood of co-occurrence will result in higher transitional probabilities from the modifier to the noun. Complementary to Price et al.'s (2015) findings the current study shows higher activity in bilateral AG for Strong C. By combining powers of incrementality of speech and E/MEG, I further report that this contextual facilitation takes place 300 ms before the noun's UP with a stronger effect on the left than right AG. This may suggest that the semantic context facilitates speech comprehension and increases efficiency by restricting the cohort to likely candidates that match both the context and input, which leads to earlier lexical access. Therefore, AG activity prior to the UP may be a result of computations of cohort candidates' fit with the prior semantic context which would facilitate integration.

Lau et al.'s (2008) neuroanatomic model of semantic processing of words in sentential context puts forward both ATL as well as AG as centres for semantic combinatorial processes and integration of meaning with the context. Previous neuroimaging studies have reported increased activity for meaningful semantic combinations and sentential combinatorial processes in ATL (Baron & Osherson, 2011; Bemis & Pylkkänen, 2011, 2013; Bottini et al., 1994; Friederici, Meyer, et al., 2000; Humphries et al., 2001). In line with these studies I predicted to find increased activity in ATL for both Strong C and Weak C phrases compared to No C. However, the IC networks that included bilateral ATL (i.e. IC1, IC5, and IC8) have failed to show any conditional differences across the epoch. This might potentially be due to temporal downsampling of the signal. That is, if ATL involvement in semantic combinatorics is transient, and does not coincide with 100 ms time windows, then tICA would not be able to capture differences in ATL activity.

Further, the time-frequency contrasts showed that conditional differences occurred within the beta frequency band. Power decreases in alpha and beta bands has been previously shown as an indicator of increased neural activity (Hanslmayr, Staudigl, & Fellner, 2012; Hillebrand, Singh, Holliday, Furlong, & Barnes, 2005). Desynchronisation in the beta band have been observed for semantic anomalies (Luo, Zhang, Feng, & Zhou, 2010; L. Wang et al., 2012), strongly constraining sentences (Piai, Roelofs, Rommers, & Maris, 2015), processing unexpected words (Rommers, Dickson, Norton, Wlotko, & Federmeier, 2016). In the current experiment higher beta desynchronization was observed for weaker contextual semantic constraint, which is more in line with the Rommers et al. (2016) because the weaker context made the anticipation of the upcoming words harder. Moreover, it has been recently proposed that beta band subserves a predictive mechanism in language processing (Molinaro, Monsalve, & Lizarazu, 2015) where it is involved in top-down modulation of perception of language. From the perspective of predictive beta, the results of the current experiment might indicate that bilateral AG process the contextual semantic information to anticipate the upcoming speech that best fits the context.

It is possible that the contextual facilitation is not a result of early lexical access but instead is due to the ease of integration of the noun's semantic representation with the contextual semantics (Hagoort et al., 2009). These authors suggest that the semantic integration (which in this account termed *unification*) is underpinned by a left dominant network of regions that consists of LIFG, LSTG, LMTG and LIPL. No C phrases were formed of words that cannot be put together to form a meaningful combination. Only the Strong C and Weak C phrases required integration. Therefore, integration effect should be present for both Strong C and Weak C phrases and absent in the No C. We see this pattern of conditional differences at -400 prior to the UP in LAG, where No C displays higher activity than the remaining conditions. Given the average UP of the No C phrases (488.40 ms), this point roughly corresponds to the offset of the noun's first phoneme. Therefore, these early differences could not be attributed to failure to integrate as the nouns of No C phrases are yet to be recognised.

Consider the example *shuffle helmet*. Gating results show that at the noun onset participants' best guess of the second word was *cards*. After they started hearing the second word, they realise that the second word starts with *h*, which in return eliminates words that start with other phonemes. Due to the earliness of this effect it is unlikely that it reflects early integration of No C nouns with their context as the participants have yet to recognise the noun. Previous research similarly has shown an early increase in amplitude for unexpected adjective inflections (van Berkum et al., 2005). Similar increase in amplitude, albeit for N400, has been consistently reported for words in discourse that semantically violate their preceding context (Balconi & Caldiroli, 2011; Rösler, Pütz, Friederici, & Hahne, 1993) or world knowledge (Dudschig, Maienborn, & Kaup, 2016; Paczynski & Kuperberg, 2012). Thus, the early No C effect reported here may rather reflect the mismatch between the onset phoneme of the expected versus the perceived noun, and thus the initiation of a process to recover from disconfirmed semantic anticipations (i.e. semantic violation) due to misleading contextual semantic information.

Finally, it is important to note the differences between the regions revealed in source contrasts and the GLM. The source contrasts revealed an extensive network of regions in bilateral STG, LIFG, LSTG, LMTG, and LIPL for Strong C. However, GLM results only revealed significant differences in bilateral IPL only. The different effects are likely to be a result of differences in the analysis pipelines. tICA separates out statistically independent brain activity patterns and the GLM removes the effects of the confounding variables. In the case of source contrast we are testing solely the differences the source intensity. Therefore, the tICA will show a more restricted set of regions compared to the source contrasts.

4.4.5. METHODOLOGICAL CONSIDERATIONS

tICA successfully segregated the network of regions observed in the univariate source contrasts and uncovered additional network of regions. It allowed us to test the conditional modulation in each network and determine the regions that were solely modulated by semantic constraint and integration. To implement group tICA with MEG, and to make the data computationally manageable, the data was downsampled to 10 Hz. Due to high downsampling we are unable to find out where the effects occur within the 100 ms time windows, and potentially blind to transient weak differences between conditions. Therefore, with the current downsampling parameter we were not able to take full advantage of E/MEG's rich temporal information.

A second drawback of the current design is the use of stimuli that varied both in duration and the UPs. The variation in UP was a result of changes in contextual semantic constraint. This meant that as the semantic constraint increased the UP shifted to an earlier time point. When all the trials were aligned by their UPs, the beginning of the epoch of the words with early UPs corresponded to either the end of the previous word or the silence between. It is possible that the large amplitude differences we see prior to the UP are a result of increasing misalignment with respect to the word onset. To make sure that the beginning of the epoch corresponds to the same acoustic event across trials, in the future one can restrict the stimuli to words that have similar UPs.

4.4.6. CONCLUSION

With this experiment I explored the spatiotemporal network dynamics that are modulated by sentential semantic constraint. I showed that using tasks, regardless of their simplicity, can recruit additional domain general, task-positive networks of regions that are not necessarily involved in the cognitive process in question. In line with the literature I showed that bilateral AG are modulated by semantic constraint, and I further add that this modulation occurs 300 ms before the word is uniquely recognised. These findings indicate that sentential semantic constraint facilitates speech comprehension possibly by partially preactivating the anticipated semantic representation and further restricting the cohort; and that AG computes the semantic fit between the cohort candidates and the contextual semantics.

CHAPTER 5

ANTICIPATION DUE TO SYNTACTIC CONSTRAINTS

5.1. BACKGROUND

Comprehending speech requires the listener to rapidly carry out a series of different cognitive computations (e.g. acoustic-phonemic analysis, parallel computations of syntactic and semantic representations) as the speech input is transformed over time into a structured and meaningful representation (Marslen-Wilson, 1987; Marslen-Wilson & Tyler, 1980). Among these cognitive computations, syntax lies at the heart of the language system, providing constraints which enable the rapid incremental interpretation of words into structured, meaningful sentences.

A large body of neuroimaging and neuropsychological data have shown that syntactic processing involves a left hemisphere frontotemporal system, including LIFG (BA 44/45) and LpMTG (Caplan, Hildebrandt, & Makris, 1996; Tyler & Marslen-Wilson, 2008; Wright et al., 2012). The neuropsychological data shows that damage to any of these LH regions impairs syntactic processing and that neural sources underpinning syntax cannot reorganise to RH homologues or to other LH regions (Tyler et al., 2011; Tyler, Shafto, et al., 2010; Wright et al., 2012). Moreover, studies with patients who have left hemisphere damage have also shown that the integrity of the white matter pathways that connect BA 44, BA 45 and LpMTG – the arcuate fasciculus and the extreme capsule - play a critical role in syntactic comprehension (Griffiths et al., 2013). These data confirm that the LIFG, LpMTG and the structural connectivity between them constitute the core syntax network. While the cortical network that underpins syntactic processing is well established, little is known about the temporal dynamics of communication within this network.

A small number of fMRI studies have explored the effective connectivity changes between fronto-temporal cortical regions during syntactic processing using PPI and seed-based correlations (Antonenko et al., 2013; Papoutsi et al., 2011; Snijders et al., 2010; Xiang, Fonteijn, Norris, & Hagoort, 2010). A recent study (Snijders et al., 2010) using PPI on fMRI data found increased connectivity between the LIFG and the LpMTG when participants read syntactically (word-class) ambiguous compared to unambiguous sentences but not for word lists, suggesting that frontotemporal communication is required for constructing sentential syntactic representations. A related study with left hemisphere damaged patients (Papoutsi et al., 2011), in which a PPI analysis was performed on fMRI data with spoken syntactically ambiguous sentences, found that those patients who showed better syntactic performance (i.e. sensitivity to syntactic ambiguity) also showed increased effective connectivity between the LIFG and the LpMTG.

Note that PPI models static instantaneous relationships in the data; it does not incorporate biologically plausible dynamics and ignores the influence of previous states on the current state (Friston et al., 1997). Another effective connectivity method, dynamic causal modelling uses a biologically informed causal model to make inferences about neuronal generators of activity, and allows one to model the influence of experimental manipulations on the causal relationships (Friston, Harrison, & Penny, 2003). Only a few studies have looked at directionality of information flow during syntactic processing using dynamic causal modelling (David et al., 2011; den Ouden et al., 2012; Ohta et al., 2013), which have found that the LIFG is the driver for enhanced frontotemporal activity with increasing syntactic processing complexity. These effective connectivity studies confirm LIFG's pivotal role in syntactic processing as the driving force in frontotemporal information flow.

As discussed in Chapter 1, whilst listening to everyday speech, we use contextual constraints imposed by the prior speech to anticipate the likely upcoming words (Kutas & Federmeier, 2011; Osterhout & Holcomb, 1995). ERP studies show that words that violate contextual syntactic constraints induce an increased P600 potential (McKinnon & Osterhout, 1996; Osterhout, 1997). P600 is a positive ERP elicited around 600 ms after the onset of critical words that are incongruous to the anticipated sentential syntax (e.g. *The broker persuaded to sell the stock was sent to jail*) (Osterhout & Holcomb, 1992), that violate the prior syntax (e.g. *The spoiled child throw the toys on the floor*), expected word order (e.g. *the expensive very tulip)* (Hagoort et al., 1993), and the gender agreement (e.g. *The man reached her destination*) (Gunter, Friederici, & Schriefers, 2000). These studies indicate that anticipatory processing due to contextual syntactic constraints influence processing of the upcoming speech and that the fit of the critical word with the sentential context is evaluated around 600 ms after the word onset.

At the neural level, anticipatory processing was previously shown to influence long range oscillatory synchronisation between cortical regions (Gross et al., 2006), connectivity in cognitive networks (O'Reilly, Mesulam, & Nobre, 2008), and the activation threshold of relevant sensory cortices (Brunia, 1999). In this chapter, I will exchange the term anticipatory processing with predictive processing to refer to the use of available contextual information and prior linguistic probabilities to facilitate recognition and processing of the upcoming speech. Neuroimaging research suggests that this facilitation is a result of preactivation of likely linguistic representations before the words are recognised (DeLong et al., 2005; Dikker & Pylkkänen, 2013).

Predictive processing is assumed to involve three elements: 1) brain region(s) that make predictions, 2) brain region(s) modulated by the predictions, 3) communication between brain regions that predict and those that perform cognitive processing (Bubic, von Cramon, & Schubotz, 2010). The predictive coding account (Friston, 2005) proposes that predictive processing involves top-down information flow of the predictions made, and bottom-up information flow of perceived stimulus in a multi-layer hierarchical brain network. In this network higher regions in the hierarchy communicate predicted stimuli to lower regions in the hierarchy. In turn lower regions process the perceived stimulus, and communicate the goodness-of-fit of prediction to the perceived stimulus (i.e. prediction error) to the higher regions. In the case of syntactic predictive processing we would expect this communication to take place in left frontotemporal network. Further, syntactic ambiguities provide a useful proxy to investigate prediction in syntax, because they are ubiquitous to everyday grammatical speech, and their processing requires incorporating prior syntactic probabilities to facilitate the recognition and processing of upcoming speech.

Lexicalist accounts of spoken language comprehension propose that while listening to speech, listeners pre-activate the likely and contextually relevant syntactic representations –among other linguistic representations- of the sentence by using the speech input heard so far (Marslen-Wilson, 1987; Marslen-Wilson & Tyler, 1980). When the sentential syntax is ambiguous, multiple syntactic representations that fit the speech input are activated in parallel. These accounts suggest that the activation levels of these syntactic representations will be weighted by how likely and contextually relevant they are (MacDonald, Pearlmutter, & Seidenberg, 1994). Therefore, among these multiple syntactic representations, the most probable one will be highly preferred (i.e. predicted), and will have a higher activation level. If the prediction proves to be correct, the pre-activation of the predicted syntactic structure would speed up speech comprehension. If the prediction is incorrect, (i.e. prediction is inconsistent with the perceived speech), then the sentential syntax would need to be reanalysed by reactivating the less preferred syntactic representation and updating the sentential syntax. If we were to explain this process within the predictive coding framework, the inconsistent speech input would result in increased prediction error to be sent to higher regions in the syntax hierarchy. Through recurrent communication within the syntax network, this prediction error would be eventually minimised (i.e. reanalysis). Making use of common syntactic ambiguities in speech, we can investigate the changes in frontotemporal connectivity that underpin probabilistic syntactic constraints and predictive processing. Understanding the temporal as well as the causal relationships within the left frontotemporal syntax system is necessary if we are to fully elucidate the dynamics of syntactic processing in the left frontotemporal network.

In the current study I used MEG to determine the temporal flow of connectivity subserving syntactic predictive processing within the left frontotemporal system. MEG was preferred over fMRI as the neuroimaging method, because it can capture transient millisecond changes in brain activity over time and is a direct measure of neural activity. Because the LIFG is involved in many different cognitive functions as well as domain-general functions (S. W. Davis et al., 2014; Wright et al., 2012), participants were asked to attentively listen to spoken sentences without making any overt response. The sentences contained either a locally ambiguous syntactic phrase (e.g. In the afternoon *chasing dogs* are barking at the frightened cats) or an unambiguous phrase (e.g. Outdoors *marching soldiers* are frightening when they are noisy) (Figure 5.1B). Local syntactic ambiguities were resolved as soon as the following verb is heard. To manipulate the outcome of syntactic predictions, ambiguous sentences were further divided into two conditions in terms of the strength of how preferred (i.e. predicted) the disambiguating verb was: the dominant (i.e. preferred, DOM) and the subordinate (i.e. less preferred, SUB) reading or interpretation. Remaining stimuli were syntactically unambiguous sentences (UNAMB).

Previous studies that similarly manipulated syntactic ambiguity in speech have shown increased activity in LIFG and LpMTG for processing sentences with the more weakly preferred over the more strongly preferred syntax, indicating that this manipulation successfully reflects core syntax network processing (Rodd, Longe, Randall, & Tyler, 2010; Tyler et al., 2011). To test how syntactic processing modulates the frontotemporal syntax network over time I used dynamic causal modelling for ERPs (DCM-ERP) (David et al., 2006). DCM-ERP allows to test the effect of experimental manipulations on neural architecture and interactions among the regions by modelling the evoked

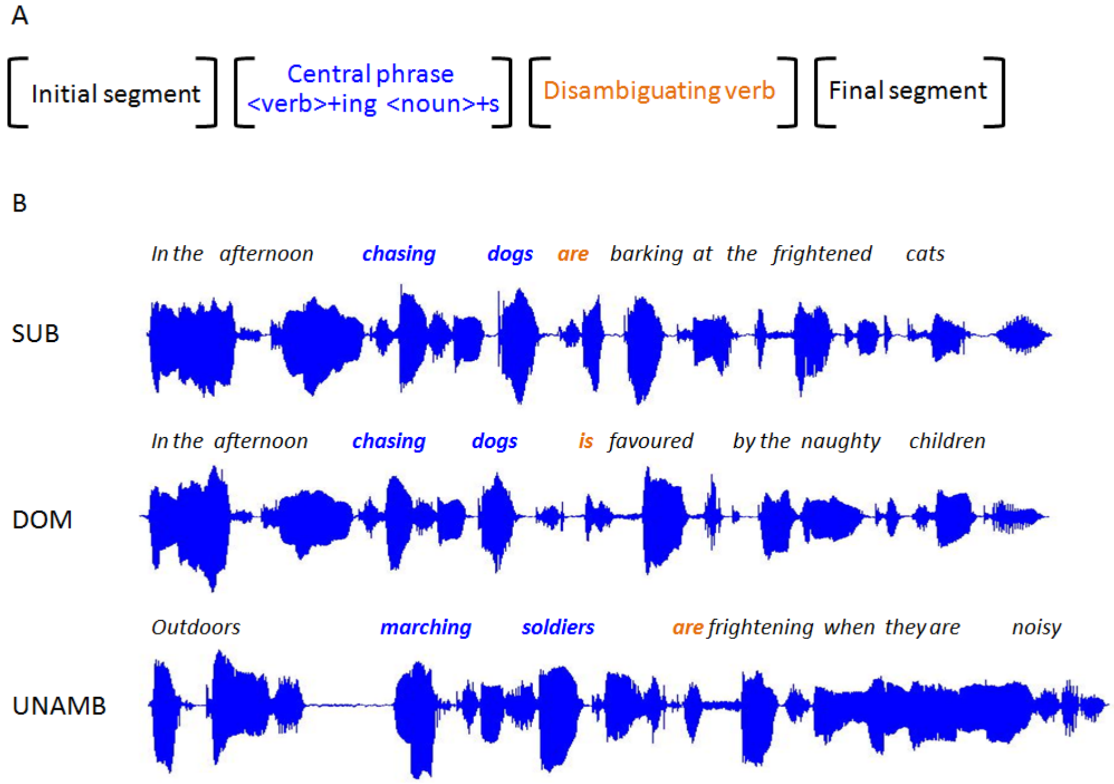


FIGURE 5.1. SENTENCE STRUCTURE AND EXAMPLE STIMULI. A. DIAGRAM SHOWING SENTENCE STRUCTURE. B. EXAMPLE STIMULI FROM EACH CONDITION. SUB, SUBORDINATE SENTENCES, DOM, DOMINANT SENTENCES, UNAMB, UNAMBIGUOUS SENTENCES.

potentials. I further adopted a windowing approach (Woodhead et al., 2014) where I fit the evoked responses to a series of time windows of increasing duration. Performing DCM-ERP in short time windows allowed to investigate how syntactic ambiguities and predictive processing modulate dynamic frontotemporal connectivity over time.

I tested modulations of the frontotemporal network connectivity by contrasting three conditions: SUB, DOM and UNAMB. It was hypothesised that processing SUB compared to DOM sentences would reflect the syntactic prediction error, and would require the reanalysis of the sentential syntactic structure. The reanalysis was expected to involve reactivation of the less preferred reading and the update of the sentential structure (MacDonald et al., 1994). Further, the comparisons of ambiguous and unambiguous phrases (i.e. SUB-UNAMB and DOM-UNAMB) were predicted to reflect the activation of multiple syntactic representations due to ambiguity. Since the processing of syntactically unambiguous phrases would not require activation of multiple representations and reanalysis, the SUB-UNAMB contrast was predicted to reflect both reanalysis and ambiguity effects. Syntactic reanalysis was predicted to be initiated early on following the disambiguating verb, through re-entrant activity in the LpMTG by top-down signals from LIFG which will reactivate the subordinate reading (Papoutsi et al., 2011). In line with the P600 studies, the reanalysis, and therefore prediction update was predicted to take place within 600 ms from the disambiguating verb onset.

5.2. METHODS

5.2.1. PARTICIPANTS

Twelve participants volunteered in the study with a mean age of 21.58 years (2 males, 10 females). Ages of the participants ranged from 18 to 28.

5.2.2. STIMULI

The stimuli consisted of 198 spoken sentences (Figure 5.1B). The sentences were formed of four continuous segments (Figure 5.1A): the initial segment, the central phrase, the disambiguating verb, and the final segment. In ambiguous sentences (e.g. "[In the afternoon] $_{\text{initial segment}}$ [chasing dogs] $_{\text{central phrase}}$...") the central phrase created a local syntactic ambiguity which could be interpreted either as a gerund ("is") or an adjective ("are"). This local ambiguity was resolved when listeners heard the disambiguating word [is/are] that immediately followed the central phrase. The main manipulation in the experiment was the degree at which the ambiguous phase (e.g. 'chasing dogs') predicted the following verb preference for one continuation rather than another (e.g. 'is' or 'are').

To determine the predictive strength of the local syntactic structure of each phrase, behavioural data was collected from 23 native British English subjects who did not participate in the MEG experiment. Participants were presented with the spoken sentences up to and including the central phrase, and were asked to complete the sentence. These sentence completions were subsequently coded as being consistent with either the gerund or adjective interpretation. Predictive strength was then computed for each phrase. The predictive strength of each sentence continuation was the percentage of number of subjects who produced "is" or "are" completions. These scores were then used to assign verb continuations to conditions. Sentence fragments with mean predictive strength score of 0.8 were assigned to the dominant condition (*M* = 0.79, *SD* = 0.12), and those with a mean score of 0.2 to the subordinate condition (*M* = 0.20, *SD* = 0.12). 66 sentences were assigned to each condition. The verb participles were matched on lemma frequency and duration across conditions. Unambiguous sentences had a dominance score of 1 (*M* = 1, *SD* = 0). Pre-test data were collected and coded by other members of the Centre for Speech, Language and the Brain in 2011.

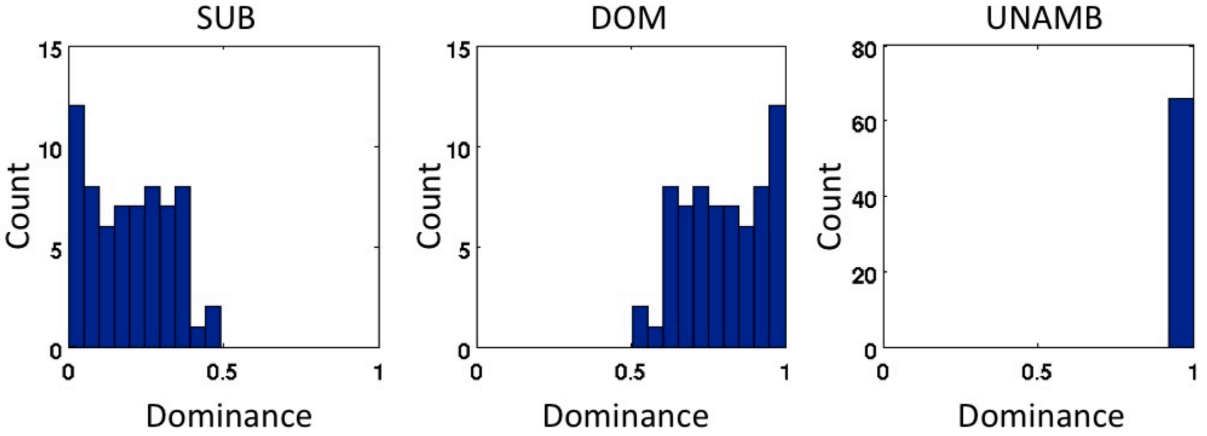


FIGURE 5.2. HISTOGRAMS SHOWING THE DISTRIBUTIONS OF DOMINANCE SCORES FOR EACH CONDITION. DOMINANCE SCORES RANGE BETWEEN 0 AND 1. UNAMB SENTENCES DISPLAY THE HIGHEST DOMINANCE SCORES FOLLOWED BY DOM AND SUB SENTENCES.

5.2.3. PROCEDURE

Delay in sound delivery due to the length of earphone tubes and sound card was 34 ± 2 ms. The inter-stimulus interval was randomised between 1500 and 2500 ms.

5.2.4. MEG AND MRI ACQUISITION

Data were collected by other members of the Centre for Speech, Language and the Brain in 2011, and were reanalysed by me.

5.2.5. MEG PREPROCESSING AND SOURCE LOCALISATION

Preprocessing was performed using SPM8 (Litvak et al., 2011). Data were first band-pass filtered between 0.5-100 Hz, then notch-filtered between 45-55 Hz using a 5th order Butterworth filter. The continuous data were then segmented into epochs of -200 ms to 1000 ms peristimulus period aligned to the onset of the disambiguating verb where the delay for stimulus delivery was corrected. Finally, trials were baseline corrected and the trials were averaged within each condition. There were no trials contaminated by the movement related artefacts across the sample. Each subject's gradiometer data were prepared for source localisation. Inversion was completed over the 0-500 ms time window and 0-100 Hz frequency window using multiple sparse priors as the inversion method (Friston et al., 2008).

5.2.6. NETWORK DEFINITION

DCM-ERP was used to identify modulated connections and time windows in which the effective connectivity within the left frontotemporal syntax network during processing of local syntactic ambiguities. Here the windowing approach of Woodhead et al (2014) and the model comparison method of Richardson et al (2011) were combined.

To identify the region that drives syntactic processing network architectures were defined by incorporating all possible regions and connections. The network architecture also referred to as *A matrix* models the average coupling among the nodes of the network across all conditions. Therefore, the A matrix allows us to discover the underlying network of a particular cognitive process. Here, the definition of A matrix, the neural architecture, was based on the neuroimaging findings on young controls (Dapretto & Bookheimer, 1999; S. W. Davis et al., 2014; Friederici, Fiebach, Schlesewsky, Bornkessel, & von Cramon, 2006; Humphries et al., 2005; Peelle et al., 2004; Segaert, Menenti, Weber, Petersson, & Hagoort, 2012; Snijders et al., 2009; S. Wang et al., 2008), mature controls (Meunier, Stamatakis, & Tyler, 2014; Shafto & Tyler, 2014; Tyler et al., 2011; Tyler, Wright, Randall, Marslen-Wilson, & Stamatakis, 2010) and patients (Griffiths et al., 2013; Rolheiser, Stamatakis, & Tyler, 2011; Tyler et al., 2011; Wright et al., 2012) during syntactic processing.

Therefore, our network consisted of LpMTG and LIFG and the left Heschl's gyrus (LHG, the primary auditory cortex) as the input node to our dynamic model.

The LIFG and LpMTG nodes (Figure 5.2B) in the network architecture were defined functionally using the results of a previous fMRI study in which 15 young participants (aged 19-24) heard the stimuli included in the current study (Tyler, Cheung, et al., 2013). The fMRI contrast revealed increased activity in LIFG (BA 44/45) and LpMTG for the SUB-DOM contrast (voxelwise $P < 0.01$, $P < 0.05$ FWE cluster corrected) (Figure 5.2A). MNI coordinates of peak activity were used to define the node locations: LpMTG [-54; -36; 0 mm] and LIFG [-51; 36; 9 mm] (BA 45). LHG, the input node of the model was anatomically defined [-48; -9; 7 mm] using the same coordinates as David et al (2011).

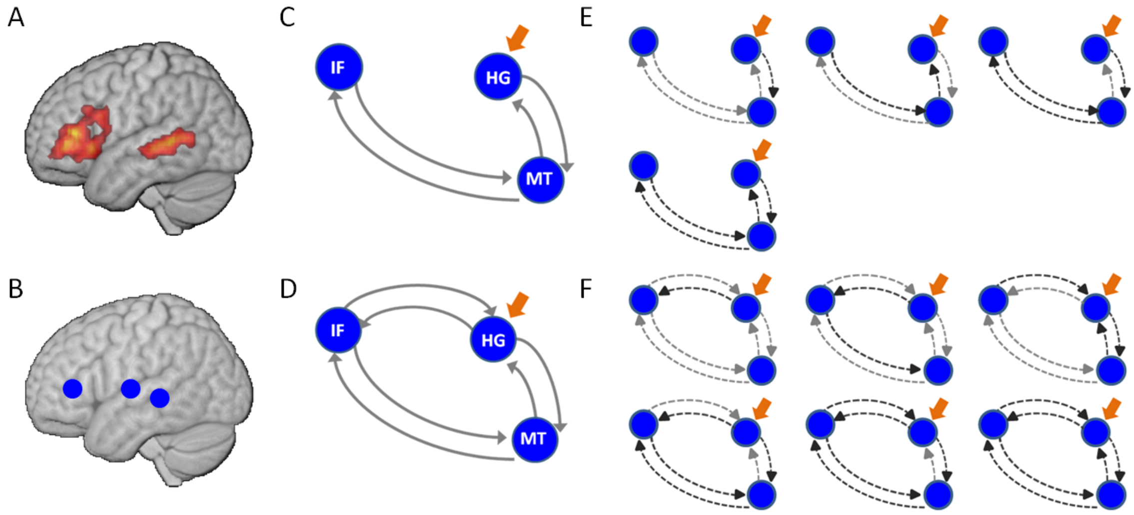


FIGURE 5.3. THE SYNTAX NETWORK AND MODEL ARCHITECTURES. A. SUB-DOM CONTRAST RESULTS OF OUR PREVIOUS FMRI STUDY USING THE SAME CONDITIONS (P<0.01 CLUSTER CORRECTED AT P < 0.05). B. DIPOLE LOCATIONS USED FOR DATA EXTRACTION. DIPOLES LOCATED IN LIFG, LPMTG AND LHG. C. SCHEMATIC REPRESENTATION OF THE SERIAL MODEL'S ARCHITECTURE. D. SCHEMATIC REPRESENTATION OF THE FULLY CONNECTED MODEL'S ARCHITECTURE. E. EXAMPLES OF SERIAL MODELS SELECTED FROM THE MODEL SPACE THAT CONSISTS OF 15 MODELS, WHICH HAVE 1-4 MODULATED CONNECTIONS. F. EXAMPLES OF FULLY CONNECTED MODELS SELECTED FROM THE MODEL SPACE THAT CONSISTS OF 63 MODELS, WHICH HAVE 1-6 MODULATED CONNECTIONS. ORANGE, GREY AND BLACK ARROWS INDICATE AUDITORY INPUT, NON-MODULATED AND MODULATED CONNECTIONS RESPECTIVELY.

Intra-regional connectivity of the network architecture was defined by consulting findings from previous connectivity studies: 1) human structural connectivity evidence for the connections between LpMTG and LIFG (i.e. extreme capsule and the arcuate fasciculus) (Griffiths et al., 2013); 2) human functional connectivity (Anwander, Tittgemeyer, von Cramon, Friederici, & Knösche, 2007; Frey, Campbell, Pike, & Petrides, 2008; Saur et al., 2008) and nonhuman primate structural connectivity evidence for connections between primary auditory cortex and prefrontal cortex (Petrides & Pandya, 2009; Romanski, Bates, & Goldman-Rakic, 1999); 3) resting state functional connectivity evidence from humans showing that LHG and LMTG are connected via the indirect segment of the arcuate fasciculus (Turken & Dronkers, 2011).

According to the predictive coding account, the information flow regarding the top-down prediction and bottom-up prediction error involves the whole network of regions for a specific cognitive function. To our knowledge the functional relevance of LHG-LIFG connection in syntactic processing is unknown. However this connection might have a role in syntactic prediction to facilitate and speed up auditory processing (Friston, 2005). To account for the possibility that the LHG-LIFG connection contributes to syntactic processing, two model architectures were constructed that differed with respect to their LHG-LIFG connections. The network architecture with bidirectional connections between LHG-LpMTG and LpMTG-LIFG was named the *Serial Model* (S) (Figure 5.2C). The architecture that has bidirectional connections between all three nodes was named the *Fully Connected Model* (FC) (Figure 5.2D).

5.2.7. NETWORK MODULATION

DCM-ERP models the MEG data as the response of a dynamic input-output system perturbed by experimental manipulations. This is done by defining modulations in a network (e.g. through the SUB-DOM contrast), also referred to as *B matrix*. Here, network architectures were used to define modulations in network connectivity in response to our syntactic manipulations. Two network architectures (the S and FC models) were then used to test all possible combination of modulations. For n number of connections, the total number of possible modulations is 2^n-1. Therefore, for S and FC the number of modulated models were 15 and 63 models per contrast respectively. 78 models were generated per contrast, adding up to 234 models in total (Figure 5.2E-F).

Model and family comparisons evaluate the goodness of fit of one model or family against others. Testing all possible modulations of connections within the model architecture was preferred for the following reasons: 1) to increase reliability of our family comparison results, 2) to account for all modulation effects, including the ones that I might have not predicted.

5.2.8. DCM-ERP SPECIFICATION

Once the models were defined, the data were extracted from each participant's source space from the node coordinates given above. The activity in nodes was modelled using the equivalent current dipole (ECD), and neural model for ERPs. ECD, as recommended by SPM, assumes that underlying neural sources are focal and are few, and that the activity of each source can be modelled by a single dipole[3]. The data were selected using eight modes, and one discrete cosine transform (DCT). Lastly the data were down-sampled to 500 Hz to speed up computations. DCM-ERP uses these parameters to estimate the model through the expectation maximisation (EM) procedure, where the negative free energy of the estimated model is aimed to be iteratively maximised (David et al., 2006). This means that DCM-ERP estimates the parameters iteratively until the disparity between the predicted and observed neural activity is minimised. The EM process outputs a free energy and posterior density estimate for each model, which then can be compared across the model space or families of models using a Bayesian framework. The DCM analysis pipeline is displayed in Figure 5.3.

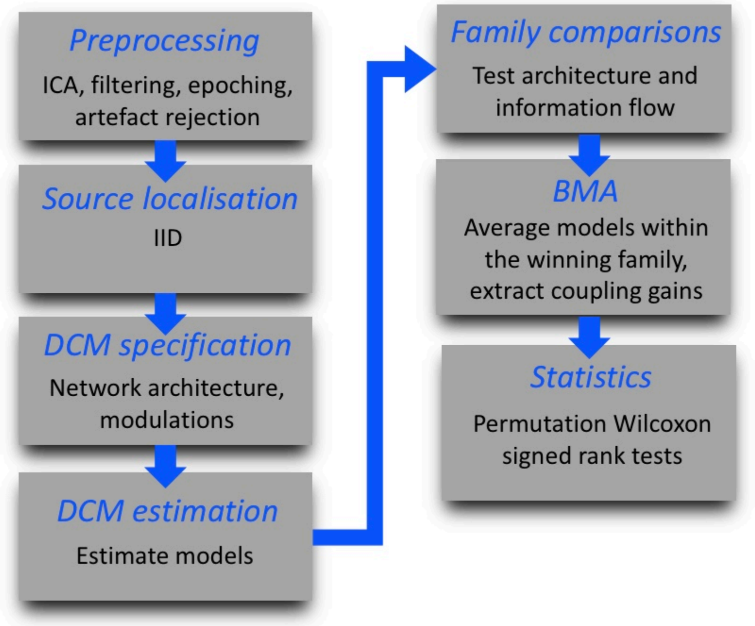


FIGURE 5.4. THE DCM PIPELINE SHOWING THE MAIN STEPS OF THE ANALYSIS.

---

[3] ECD approach in DCM can potentially be an oversimplification of the source neural activity. Other electromagnetic options in DCM include using cortical patches (IMG) and local field potentials.

Using the windowing approach, the conditions were fitted to five separate, but overlapping 100 ms long time windows, from the onset of the disambiguating verb. Time windows where the models were estimated are: 0-100 ms, 0-200 ms, 0-300 ms, 0-400 ms, and 0-500 ms. Instead of using a sliding time window, overlapping time windows were used because DCM-ERP's model estimation requires the activation of the input node to be included in the dynamic model. Therefore, all the time windows began from the onset of the disambiguating verb. The model estimation was performed separately for each time window. For each model SUB and DOM, SUB and UNAMB, and DOM and UNAMB conditions were fitted separately. One between condition effect was specified for each of these contrasts with the vector [1 0]. In these effects the second condition was regarded as the baseline condition.

5.2.9. MODEL COMPARISON AND STATISTICS

To determine the models that best explain the differences between high and low predicted syntactic phrases, the models were partitioned into families and then were tested for differences through family comparisons. The models were first partitioned by their network architecture (i.e. The S and FC models) and then by the direction of modulated connections within the network (forward, backward or both forward and backward).

A hierarchical selection procedure was followed where the model space was restricted in a stepwise fashion through family comparisons. That is, instead of starting the analyses with a conventional Bayesian Model Selection (BMS) (Stephan, Penny, Daunizeau, Moran, & Friston, 2009) across the entire model space and finding the winning model, the first step was comparing families of models, and then using the results at the family-level to restrict the model space. There were two reasons for preferring the hierarchical selection procedure over BMS. First, the winning model may differ across subjects, in which case the BMS is unlikely to find a winning model across the group of subjects. Second, the differences between the two model architectures (i.e. S and FC) and between the modulated models are subtle and therefore the log evidence would not change drastically across models, and BMS would be more likely to find a group of winning models rather than one clear winner. By employing family comparisons, both of these issues were accounted for, and common parameters were determined that explain the data.

Two family comparisons were performed consecutively using the random effects BMS with Gibbs sampling (Penny et al., 2010). The family comparison outputs an exceedance probability value for each family, which reflects the family's likelihood of generating the data. In family comparisons, the exceedance probabilities of all families add up to 100%. If one family's exceedance probability exceeds 95%, that family is deemed to be the winner (Penny et al., 2010). Family comparisons were performed sequentially to systematically restrict the model space. The results of each family comparison were used to restrict the model space of the consecutive family comparison. When a family's exceedance probability exceeded the significance threshold (%95), the families that have a subthreshold probability were removed from the following test. If none of the family exceedance probabilities exceeded the threshold, (which meant that all families were equally likely to explain our data) then all families were included in the following comparison.

In the final stage, a group level Bayesian Model Averaging (BMA) with random effects was used to gather average parameter estimates across subjects for the winning family of models. BMA computes the weighted average of the coupling gains of each connection by using the posterior distributions of model parameters (Penny et al., 2010). In cases where the second family comparison gave a clear winning family, the parameters were averaged within the winning family of models. In other cases, the parameters were averaged across all families from the second family comparison.

In order to make the interpretation of BMA output easier, the parameter averages were exponentiated (i.e. e^x), distributing the coupling values around a mean of 1. Exponentiation allows us to interpret the parameter averages in terms of either percent increases or decreases. For instance, a value of 1.36 means 36% increase in coupling strength for that connection. Whereas a value of 0.90 means 10% decrease.

Due to the small number of subjects in the study (n = 12), the nonparametric Wilcoxon signed rank test was used to test for significant increases or decreases in coupling strength. Wilcoxon signed rank tests were performed for each time window, contrast and connection separately, resulting in 108 tests. With an alpha level of 0.05, this would mean that 5.4 of these tests would give false positive results by chance due to multiple comparisons. In order to correct for the type I error, I used permutation tests with 5000 permutations, where raw coupling gains of each connection were randomly multiplied by either -1 or 1 and tested against a mean of 0 using the Wilcoxon signed rank test. A permutation distribution was constructed by taking the rank from each permutation and each connection. The permutation tests were preferred over family-wise error rate or false discovery rate corrections because the p distribution is unknown and not necessarily Gaussian.

5.3. RESULTS

5.3.1. FIRST FAMILY COMPARISON: MODEL ARCHITECTURE

The 78 models were separated to two families that differentiate two model architectures (i.e. Serial and Fully Connected). Family comparisons of all three contrasts showed that FC had higher exceedance probability than S with the exception of 0-500 ms window in SUB-DOM and SUB-UNAMB contrasts which suggests that after 400 ms the LIFG-to-LHG feedback coupling gains decrease, making the network function similar to a serial feed-forward model. In DOM-UNAMB contrast FC family had higher exceedance probability across all time windows. Figure 5.3 shows each family's exceedance probability for each contrast and time window. Each family's exceedance probabilities are given in Table 5.1. Higher exceedance probabilities broadly found for the FC family suggest that the connections between LIFG and LHG are modulated during the predictive syntactic processing of both preferred and less preferred readings.

		Time windows				
Contrast	**Families**	**0-100 ms**	**0-200 ms**	**0-300 ms**	**0-400 ms**	**0-500 ms**
SUB-DOM	**S**	0.024	0.283	0.013	0.135	0.848
	FC	**0.976***	0.717	**0.987***	0.865	0.152
SUB-UNAMB	**S**	0.170	0.001	0.302	0.291	0.723
	FC	0.830	**0.999***	0.698	0.710	0.277
DOM-UNAMB	**S**	0.014	0.042	0.043	0.290	0.024
	FC	**0.986***	**0.958***	**0.957***	0.710	**0.976***

TABLE 5.1. THE EXCEEDANCE PROBABILITIES OF THE FIRST FAMILY COMPARISON ACROSS THREE CONTRASTS. THE WINNING FAMILIES (P>0.95) ARE INDICATED WITH *.

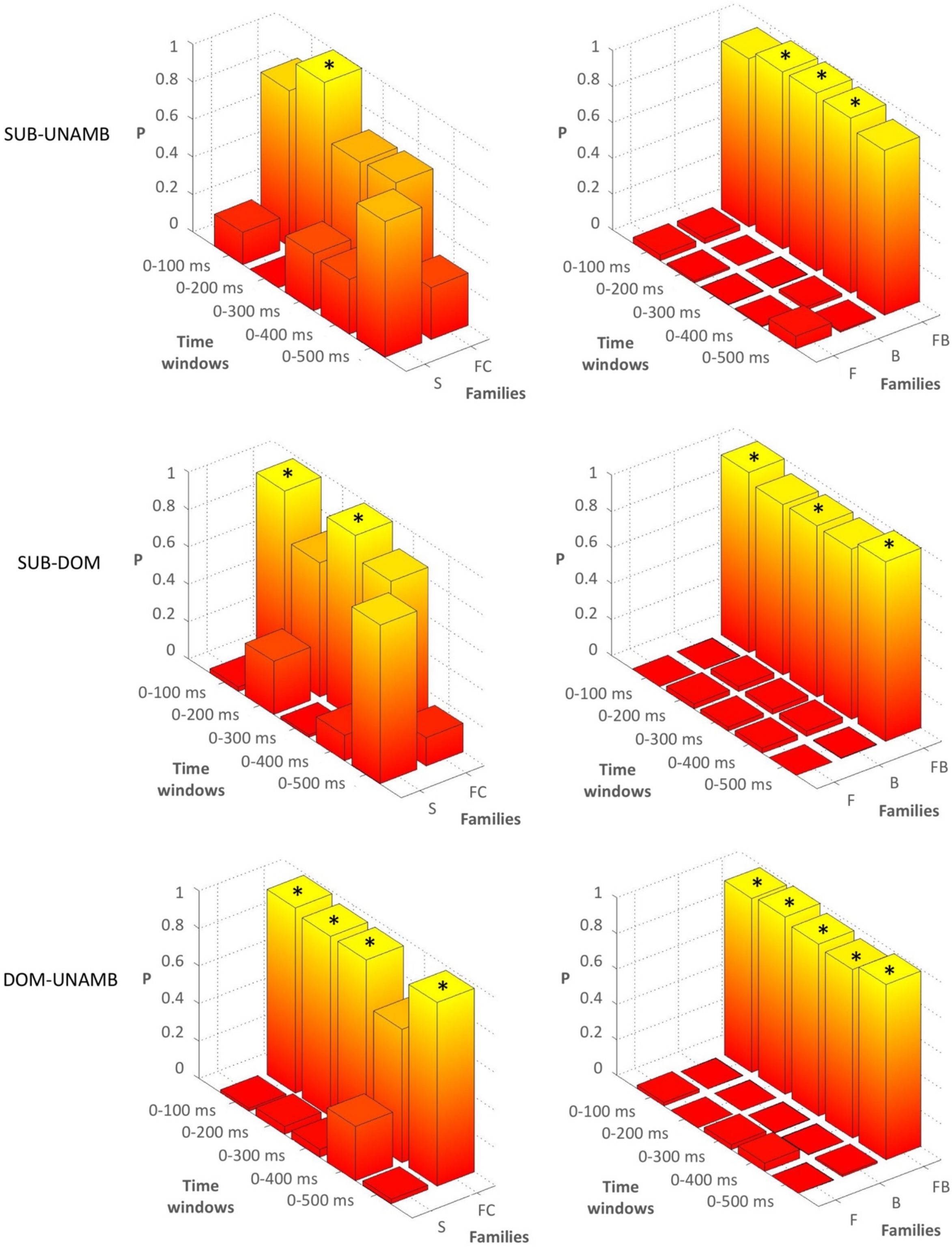


FIGURE 5.5. RESULTS OF THE FAMILY COMPARISONS. THE FIRST FAMILY COMPARISON RESULTS ON THE FIRST ROW SHOW THAT THE FULLY CONNECTED MODEL (FC) FAMILY HAS BROADLY HIGHER EXCEEDANCE PROBABILITY THAN THE SERIAL MODEL (S) FAMILY. THE SECOND FAMILY RESULTS ON THE SECOND ROW SHOW THAT THE FAMILY OF MODELS MODULATED BOTH IN FORWARD AND BACKWARD CONNECTIONS HAD THE HIGHEST EXCEEDANCE PROBABILITY IN ALL THREE CONTRASTS. ASTERISKS INDICATE THE THE WINNING FAMILY OF MODELS.

5.3.2. SECOND FAMILY COMPARISON: DIRECTION OF INFORMATION FLOW

The second family comparison asked whether differences between the three experimental conditions were due to modulation of either forward connections, backward connections or of both forward and backward connections in the winning model architecture. Only the models from winning families were included in the second family comparison. The exceedance probabilities are given in Table 5.2.

		Time windows				
Contrast	**Families**	**0-100 ms**	**0-200 ms**	**0-300 ms**	**0-400 ms**	**0-500 ms**
SUB-DOM	**F**	0.000	0.028	0.023	0.027	0.000
	B	0.000	0.032	0.027	0.029	0.003
	FB	**0.999***	0.941	**0.951***	0.944	**0.997***
SUB-UNAMB	**F**	0.033	0.011	0.003	0.005	0.071
	B	0.028	0.000	0.003	0.018	0.008
	FB	0.929	**0.989***	**0.994***	**0.978***	0.921
DOM-UNAMB	**F**	0.019	0.000	0.029	0.048	0.001
	B	0.000	0.000	0.002	0.001	0.011
	FB	**0.980***	**0.999***	**0.970***	**0.951***	**0.988***

TABLE 5.2. THE EXCEEDANCE PROBABILITIES OF THE SECOND FAMILY COMPARISON ACROSS THREE CONTRASTS. THE EXCEEDANCE PROBABILITIES OF FAMILY OF MODELS WITH MODULATED FORWARD CONNECTIONS (F), WITH MODULATED BACKWARD CONNECTIONS (B), AND BOTH FORWARD AND BACKWARD MODULATED CONNECTIONS (FB) ACROSS THREE CONTRASTS. THE WINNING FAMILIES (P>0.95) ARE INDICATED WITH *.

Figure 5.3 shows that in all three contrasts, the FB family (the family that has both forward and backward modulation of connections) displayed higher exceedance probability than both F and B families. Moreover, this pattern was not restricted to a specific time window, but rather was extended to all time windows up to 0-500 ms. The results of the second family comparison showed that predictive syntactic processing modulates both forward and backward connections of the left frontotemporal network and that the system involves recurrent communication rather than purely feed-forward information flow.

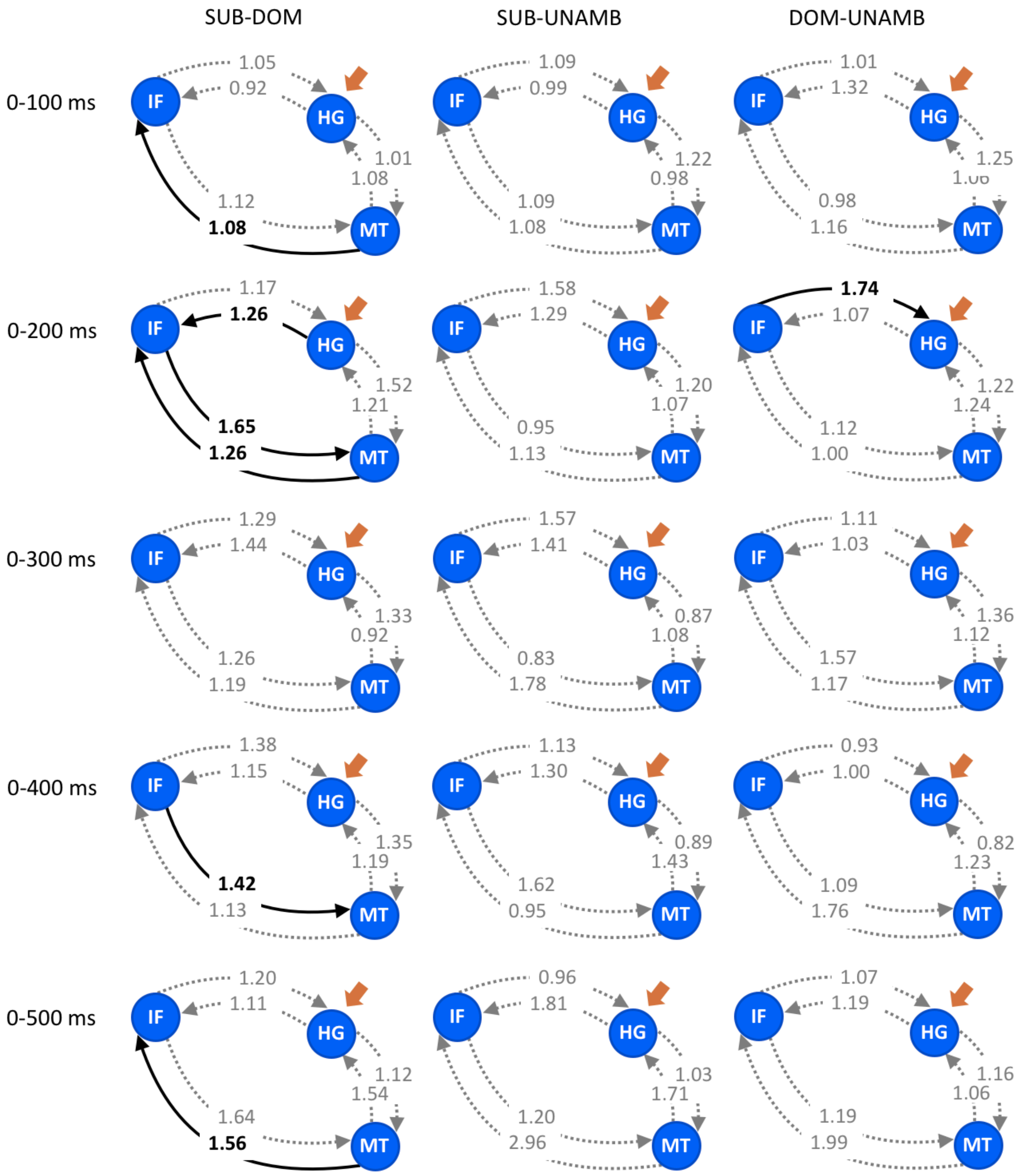


FIGURE 5.6. THE RESULTS OF THE PERMUTATION WILCOXON SIGNED RANK TESTS. SOLID LINES INDICATE THE SIGNIFICANTLY MODULATED CONNECTIONS. THE NUMBERS INDICATE THE MEDIAN COUPLING GAIN ACROSS SUBJECTS. NUMBERS GREATER AND SMALLER THAN 1 INDICATE INCREASES AND DECREASES IN COUPLING FOR THE FIRST CONDITION OF THE CONTRAST COMPARED TO THE SECOND. THE CONNECTIONS THAT WERE SIGNIFICANTLY MODULATED ARE DISPLAYED AS SOLID LINES. ORANGE ARROWS INDICATE AUDITORY INPUT. THERE WERE NO SIGNIFICANT COUPLING CHANGES FOR THE SUB-UNAMB CONTRAST.

5.3.3. BAYESIAN MODEL AVERAGING AND PERMUTATION WILCOXON SIGNED RANK TESTS

Figure 5.4 shows the mean coupling gains for each connection over the time windows and Table 5.4 shows the statistical results. The variability in coupling gains are given in Table 5.3. Figure 5.5 shows the time series of mean coupling changes. When interpreting the connectivity modulations, one needs to keep in mind that the time windows display the accumulated average of the estimated connectivity changes in a time window rather than independent averages of short time windows.

In Figure 5.4, the significant changes in coupling gain ($M = 1.08$; $P = 0.039$) for SUB-DOM contrast starts in the 0-100 ms window, where we see increased connectivity in the LpMTG-to-LIFG connection. In the 0-200 ms window I found increased information flow to LIFG both from LHG ($M = 1.26$; $P = 0.032$) and LpMTG ($M = 1.26$; $P = 0.029$). Meanwhile we see increased feedback connectivity from LIFG to LpMTG ($M = 1.65$; $P = 0.011$). Subsequently I found significant increases in coupling of the LIFG-to-LpMTG connection ($M = 1.42$; $P = 0.007$) in the 0-400 ms time window and in the LpMTG-to-LIFG connection ($M = 1.56$; $P = 0.014$). Even

SUB-DOM	0-100ms	0-200 ms	0-300 ms	0-400 ms	0-500 ms
LHG-LpMTG	0.67	1.11	0.96	1.20	0.43
LHG-LIFG	0.59	0.57	0.82	0.40	0.28
LpMTG-LHG	0.14	0.78	0.16	0.80	1.55
LpMTG-LIFG	0.15	0.48	0.58	0.57	0.82
LIFG-LHG	0.10	0.58	1.02	0.82	0.43
LIFG-LpMTG	0.26	1.04	0.88	0.81	2.39

SUB-UNAMB	0-100ms	0-200 ms	0-300 ms	0-400 ms	0-500 ms
LHG-LpMTG	1.00	1.38	0.51	0.27	0.67
LHG-LIFG	0.05	0.88	1.08	1.14	2.97
LpMTG-LHG	0.11	0.53	0.27	1.03	1.49
LpMTG-LIFG	0.19	0.33	1.43	0.33	5.05
LIFG-LHG	0.18	1.89	2.11	0.46	0.16
LIFG-LpMTG	0.26	0.39	0.28	1.37	0.54

DOM-UNAMB	0-100ms	0-200 ms	0-300 ms	0-400 ms	0-500 ms
LHG-LpMTG	0.95	0.82	1.07	0.54	0.94
LHG-LIFG	1.00	0.93	0.34	0.20	0.74
LpMTG-LHG	0.22	0.74	0.55	0.46	0.37
LpMTG-LIFG	0.40	0.22	0.36	1.61	2.50
LIFG-LHG	0.10	1.49	0.46	0.31	0.30
LIFG-LpMTG	0.21	0.96	1.91	0.51	0.66

TABLE 5.3. THE STANDARD DEVIATIONS OF COUPLING GAINS ACROSS CONTRASTS, CONNECTIONS AND TIME WINDOWS. THE MEAN STANDARD DEVIATION FOR SUB-DOM, SUB-UNAMB AND DOM-UNAMB WERE 0.71, 0.91 AND 0.73 RESPECTIVELY, INDICATING THAT VARIABILITY IN COUPLING GAINS IS HIGHER IN SUB-UNAMB COMPARED TO THE REMAINING CONTRASTS.

though we see increases in coupling of the LIFG-to-LpMTG connection up until the 0-400 ms time window (i.e. median coupling gain is above 1), the increases are more pronounced in the 0-200 ms and 0-400 ms time windows. This suggests that this drastic increase in coupling gain took place in 100-200 ms and 300-400 ms time windows.

In the 0-500 ms time window BMA showed significantly increased coupling from the LpMTG to the LIFG. Altogether the SUB-DOM coupling changes reflect that the syntactic reanalysis that follows failed syntactic predictions result in significant connectivity increases in the left frontotemporal syntax network, most information flow occurring as recurrent interactions between LIFG and LpMTG.

Coupling changes found in SUB-UNAMB, despite being large, were not significant. The mean coupling gains however, still show a similar pattern to the SUB-DOM contrast (Figure 5.5): 62% increase in connectivity in LIFG-to-LpMTG in 0-400 ms, and nearly 200% increase in connectivity in LpMTG-to-LIFG. The lack of significance for these large connectivity changes mean increased variance among the participants' connectivity patterns (Table 5.3).

In the DOM-UNAMB contrast I found a significant increase in early 0-200 ms LIFG-to-LHG connectivity ($M = 1.74$; $P = 0.031$). This change might reflect confirmed syntactic prediction, in the absence of increased subsequent feedback connectivity from LIFG to LpMTG (i.e. absence of syntactic reanalysis).

Altogether the results show that in the case of failed syntactic predictions, the frontotemporal communication is initiated by feedforward information flow from LHG and LpMTG to LIFG, which is later followed by recurrent communication between LIFG and LpMTG. This pattern of connectivity is complementary to the predictive coding account; and indicate that when the probabilistic syntactic predictions contradict with the perceived syntactic structure, the feedforward information flow underpins the transmission of prediction error, and the following recurrent information flow underpins the update of syntactic prediction, and therefore reanalysis within 500 ms after the verb.

SUB-DOM	Time windows				
Connections	0-100 ms	0-200 ms	0-300 ms	0-400 ms	0-500 ms
LHG to LpMTG	0.811	0.178	0.416	0.347	0.407
LHG to LIFG	0.923	**0.032***	0.061†	0.258	0.256
LpMTG to LHG	0.062†	0.429	1.000	0.562	0.219
LpMTG to LIFG	**0.039***	**0.029***	0.410	0.473	**0.014***
LIFG to LHG	0.144	0.367	0.548	0.149	0.116
LIFG to LpMTG	0.071	**0.011***	0.569	**0.007***	0.816

SUB-UNAMB	Time windows				
Connections	0-100 ms	0-200 ms	0-300 ms	0-400 ms	0-500 ms
LHG to LpMTG	0.654	0.942	0.936	0.967	0.803
LHG to LIFG	0.877	0.315	0.287	0.532	0.615
LpMTG to LHG	0.888	0.717	0.406	0.073	0.084
LpMTG to LIFG	0.579	0.153	0.084	0.838	0.073
LIFG to LHG	0.086	0.411	0.597	0.365	1.000
LIFG to LpMTG	0.279	0.916	0.935	0.181	0.184

DOM-UNAMB	Time windows				
Connections	0-100 ms	0-200 ms	0-300 ms	0-400 ms	0-500 ms
LHG to LpMTG	0.609	0.657	0.507	0.977	0.849
LHG to LIFG	0.451	0.842	0.525	0.693	0.541
LpMTG to LHG	0.145	0.235	0.431	0.122	0.526
LpMTG to LIFG	0.128	0.411	0.115	0.152	0.132
LIFG to LHG	0.546	**0.031***	0.424	0.878	0.414
LIFG to LpMTG	0.451	0.818	0.489	0.542	0.328

TABLE 5.4. THE CORRECTED P-VALUES FROM THE PERMUTATION WILCOXON SIGNED RANK TESTS. * SIGNIFICANT EFFECTS AT P = 0.05, † MARGINAL EFFECTS P < 0.07.

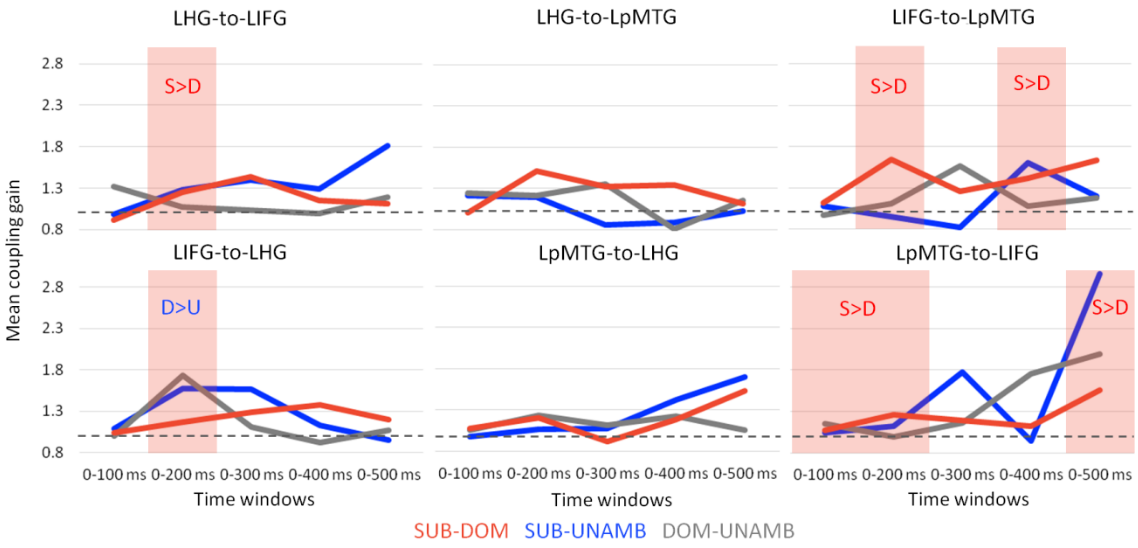


FIGURE 5.7. CHANGE IN MEDIAN COUPLING GAINS OVER TIME IN EACH CONNECTION. TIME WINDOWS WHERE SIGNIFICANT EFFECTS ARE FOUND ARE INDICATED BY ORANGE BORDERS. DOTTED LINE INDICATES MEAN COUPLING GAIN = 1. ANY VALUE ABOVE AND BELOW THIS LINE SIGNIFY INCREASE AND DECREASES IN CONNECTIVITY RESPECTIVELY.

5.4. DISCUSSION

In the current study I aimed to investigate how the effective connectivity in the left frontotemporal syntax network was modulated by syntactic predictive processing during natural speech comprehension. I predicted that: (1) Syntactic reanalysis resulting from failed predictions will be initiated through re-entrant activity in the LpMTG by top-down signals from LIFG and will reactivate the subordinate syntactic reading of ambiguity; (2) the activation of the subordinate syntactic reading will be subserved by increased feed-forward signals from LpMTG to LIFG resolving the ambiguity.

I employed DCM-ERP method with windowing approach on MEG data which allowed to draw inferences on direction and timing of transient coupling changes over time in response to probabilistic differences in syntactic predictions. The results of the two family comparisons showed that the fully connected models with modulations in both forward and backward connections explained the data better overall compared to remaining families of models. Further, I found that syntactic reanalysis (i.e. the SUB-DOM contrast) was underpinned by increased feedforward connectivity from LpMTG to LIFG in the 0-100 ms window; followed by increased recurrent connectivity between LIFG and LpMTG the disambiguating verb onset. I interpret these changes in connectivity within the predictive coding framework where in the first stage, the prediction error resulting from failed syntactic prediction is sent from LpMTG and LHG to LIFG in the first 200 ms. In the second stage, within 500 ms after the mismatch, the syntactic prediction is updated through recurrent frontotemporal information flow until the prediction error is minimised.

5.4.1. TOP-DOWN MODULATION OF THE FRONTOTEMPORAL NETWORK IN SYNTACTIC AMBIGUITY

Our interpretation of the early connectivity changes in the 0-400 ms window is complementary to the literature where the LpMTG is shown to play a crucial role in the storage and activation of lexico-syntactic representations (Hagoort, 2005; Indefrey & Levelt, 2004; Snijders et al., 2009; Tyler, Cheung, et al., 2013). I suggest that during reanalysis, LIFG prompts LpMTG to boost activation of the less preferred syntactic reading and later updates the sentential syntax. In the literature there are three prominent views regarding LIFG's role in cognition: conflict resolution with respect to the anticipated and observed stimulus (the cognitive control theory) (Novick, Trueswell, & Thompson-Schill, 2010), sentence-level unification of linguistic units (the Memory Unification Control Model, MUC) (Hagoort, 2005; Snijders et al., 2009) and providing a top-down bias mechanism to enable goal-directed control retrieval of task-relevant information from memory (Badre & Wagner, 2002). Further, predictive coding account puts forward a general biological framework that explains how a cortical hierarchy imposes top-down biases whilst perceiving and anticipating the external stimuli (Friston, 2005). The findings are consistent with both the cognitive control theory and the predictive coding account for the following reasons.

The cognitive control theory (Novick et al., 2005) proposes that LIFG is a part of frontal network subserving a domain general role in the detection and resolution of ambiguities (or misinterpretations) that arise when there is competition or incompatibility between the sensory input and anticipated input. In the case of ambiguous syntax, the syntactic continuation of the sentence conflicts with parsing preferences of a canonical sentence structure. Then LIFG is triggered to resolve the misinterpreted syntax. The theory suggests that LIFG should only be activated when there is a need to override the anticipated input and to revise the sentence. Complementary with this prediction, LIFG activity was reported for reading ambiguous sentences that had less preferred continuation (Mason, Just, Keller, & Carpenter, 2003; Thothathiri, Kim, Trueswell, & Thompson-Schill, 2012), for spoken sentences that had distant backward anaphoras (Matchin, Sprouse, & Hickok, 2014), and for written garden-path sentences (Christensen, 2010).

Within this framework, top-down signals from LIFG to LpMTG may reflect the early stage of reanalysis where the incompatibility between the anticipated syntactic structure and the structure of the incoming speech leads to the reactivation of the less preferred syntactic reading in memory. Whereas the bottom-up signals from the LpMTG to LIFG might reflect the communication of the less preferred reading to LIFG, for the update of sentential syntax.

Similarly within the predictive coding account, we can interpret the recurrent interaction between LIFG and LpMTG as information flow between top-down and bottom-up regions in the syntax hierarchy to minimise prediction error, following the realisation that the syntactic prediction was incorrect. Despite the similarity in their interpretations, the cognitive control theory and the predictive coding account differ in the roles they assign to regions carrying out executive domain general functions. Cognitive control theory suggests that LIFG is activated only when there is a cognitive conflict that needs resolving. Predictive coding account, on the other hand, proposes that the cortical regions in the hierarchy are constantly active and perform computations to anticipate the upcoming external stimuli irrespective of the level of competition. Despite being not significant, Figure 5.5 shows increases in coupling gain for DOM-UNAMB contrast in the frontotemporal network. Since DOM sentences do not involve any conflict resolution, these changes support the claims of the predictive coding account.

One might argue that increased frontotemporal coupling reflects the activation of task-relevant information. However, to avoid effects of domain-general processes clouding the linguistic effects, in the current study I employed a natural listening paradigm and grammatically correct sentences that had local syntactic ambiguities which are ubiquitous to spoken language comprehension (S. W. Davis et al., 2014). Further a recent fMRI study comparing the regions activated for syntactic processing during a natural listening and an acceptability judgment task, showed that the natural listening leads activation of LIFG and LpMTG, whereas the task resulted in activity in additional regions including bilateral prefrontal cortices, L parietal and motor cortices (S. W. Davis et al., 2014). Therefore, given the experimental design LIFG's top down modulation of LpMTG can only be attributable to LIFG's involvement in syntactic reanalysis following failed syntactic predictions rather than task induced domain-general cognitive processes.

5.4.2. FAILED PREDICTIONS IN SYNTACTIC PROCESSING AND RELATED CONNECTIVITY CHANGES

According to predictive coding account, failed predictions should result in greater prediction error to be communicated in a bottom-up fashion. This communication is assumed to be followed later by recurrent communication between higher and lower regions in the hierarchy, until the prediction error is minimised. Within the syntax network investigated in the current analysis, this would mean that 1) LIFG will communicate predictions to both LHG and LpMTG, 2) LpMTG will communicate predictions to LHG, and finally 3) LpMTG and LHG will communicate prediction errors to LIFG.

In this analysis SUB-DOM contrast allowed us to investigate the connectivity dynamics in response to failed predictions (i.e. increased prediction error) in syntactic processing. As the participants heard the first phoneme of the disambiguating verb (which differentiates two possible verb forms, *is* and *are*) they were able to implicitly tell whether their prediction was accurate. Since the average duration of disambiguating verbs across sentences was approximately 200 ms, I predicted that the bottom-up information flow of the prediction error for SUB phrases to occur within this time window. The results confirmed our predictions showing differences in coupling gains for the LpMTG-to-LIFG and LHG-to-LIFG connections in the 0-100 and 0-200 ms time windows between SUB and DOM.

The largest change in connectivity in LIFG-to-LpMTG connection (Figure 5.5) occurs between 0-100 ms to 0-200 ms windows, suggesting that this connectivity is increased between 100-200 ms after the disambiguating verb onset. In the following 0-300 ms and 0-400 ms windows we see sharp decreases of this coupling gain. The significant increase in connectivity of LIFG-to-LpMTG in the 0-400 ms suggests that up until 400 ms after the verb onset, despite getting weaker, there is still ongoing top-down information flow, indicative of prediction update. LpMTG-to-LIFG connection on the other hand displays a sharp increase in connectivity between 0-400 ms to 0-500 ms, suggesting that the bottom-up information flow occurs between 400-500 ms. Overall the results indicate that when predictions regarding the upcoming syntactic structure fail, within 500 ms from the word onset through recurrent frontotemporal interactions the syntactic reanalysis is completed.

Lastly, it is important to note that the natural stimuli used in the current experiment introduce a confounding variable. Even though the ambiguities were syntactic in nature, the participants still had to process the speech additionally in the semantic, phonological and acoustic domains. Therefore, even though the main experimental manipulation was syntactic, participants likely used all available linguistic information to anticipate the upcoming word (i.e. was/were/is/are). Whilst interpreting the results we need to consider that syntactic prediction making might not be entirely monolithic and instead benefit from acoustic, phonological and semantic information as well.

5.4.3. THE TIMING OF CONNECTIVITY CHANGES AND ITS SIGNIFICANCE

The temporal order of our connectivity changes indicate that the process of reanalysis is initiated by the prediction error communicated by the LpMTG and LHG to LIFG in the 0-100 ms and 0-200 ms windows, which is followed by LIFG's top down signalling of LpMTG in the 0-400 ms window, and is finalised by bottom-up signals from LpMTG to LIFG in the 400-500 ms window. The timings of the coupling changes between LIFG and LpMTG overlap with the results of our previous MEG study that employed the same syntactic ambiguity paradigm (Tyler, Cheung, et al., 2013). The study showed that the LpMTG activity correlated with the activation of multiple syntactic representations during the ambiguous central phrase. Following the disambiguating verb, the activity in LIFG correlated with the models of reanalysis and resolution of syntactic ambiguity from 300 ms peaking at 450 ms after the onset of the verb. This is consistent with the timings of the SUB-DOM contrast of the current study which showed increased recurrent communication between LpMTG and LIFG occurs between 400 to 500 ms window.

Further, our results are consistent with the ERP literature. The ELAN is a left lateralised anterior negativity that arises around 100-300 ms in response to syntactic structure violations (Friederici et al., 1993; Hahne & Friederici, 1999). Its role in syntax has been proposed to be initial parsing of sentential syntax (Hahne & Friederici, 1999). The window of top-down signalling of LIFG overlaps with ELAN's window, indicating that the initial parsing of the sentence has been interrupted by the failed syntactic prediction. Moreover using MEG the neural generators of ELAN have been localised to Broca's area (Friederici, Wang, et al., 2000) which bolsters our interpretation that the top-down signalling of LIFG reflects the same syntactic processes ELAN reflects in the ERP literature.

The results of the current study are consistent with the findings of the following PPI studies. Snijders et al (2010) compared syntactic processing of sentences and word lists, and have found that seed activity in LIFG revealed activity in LpMTG during unification of sentence structure. Further Papoutsi et al (2011) used the same syntactic ambiguity paradigm employed in the current study. For the comparison of sentences of subordinate versus dominant syntactic structure, using PPI they found increased activity in LpMTG when the seed region was set to LIFG. These two studies provide strong evidence for increased top-down frontotemporal connectivity during syntactic processing. A dynamic causal modelling study on fMRI data compared the connectivity changes related to the syntactic processing of object-cleft and subject-cleft sentences (Den Ouden et al., 2012). The results showed increased connectivity in the feedback connection going from LIFG to LpSTS for sentences with object-cleft structure. The LpSTS coordinates they used are slightly dorsal to the coordinates used for LpMTG in the current study. Considering that all three of these studies have used different tasks, and syntactic manipulations, the consistently emerging pattern of the top-down signalling of LIFG to drive activity in the L temporal cortex confirms that this connectivity change has a crucial role in syntactic processing.

5.4.6. THE PROCESSING OF SYNTACTICALLY UNAMBIGUOUS SENTENCES

In addition to the SUB-DOM effects, I predicted to find coupling changes for SUB-UNAMB and DOM-UNAMB contrasts. Since the DOM and UNAMB sentences did not require reanalysis, I expected the connectivity changes underlying the SUB-DOM and SUB-UNAMB differences would be similar. Even though the coupling gain differences we see in SUB-UNAMB are not significant, the connectivity changes 0-400 and 0-500 ms windows show similar patterns to SUB-DOM changes. In the 0-400 ms window for SUB compared to UNAMB sentences there is a 62% increase in LIFG-to-LpMTG connectivity, followed by almost 200% increase in LpMTG-to-LIFG connectivity in the 0-500 ms time window. These changes indicate that connectivity patterns underlying the SUB-DOM and SUB-UNAMB contrasts bear great similarities, however due to inter-subject variability (Table 5.3) in connectivity patterns of the SUB-UNAMB contrast, these changes fail to reach significance.

Since both DOM and UNAMB sentences were grammatically correct sentences that did not require syntactic reanalysis, I did not expect to see any differences in connectivity in the DOM-UNAMB contrast. However, one key difference between these conditions was that DOM sentences required multiple activation of the syntactic representations, with the highly predicted syntactic structure being activated more strongly. In the UNAMB sentences only one syntactic structure fit the preceding speech, therefore one syntactic representation was assumed to be predicted and activated. Therefore, any difference between the DOM and UNAMB sentences should be due to differences in syntactic prediction and the number of activated syntactic representations. Even though the predicted syntactic structure is correct in both types of sentences, the early LIFG-to-LHG connectivity increase might be a result of multiple activated representations.

5.4.7. CONCLUSION

With the current DCM-ERP study I investigated how the effective connectivity in the left frontotemporal syntax network is modulated by syntactic prediction when we encounter local syntactic ambiguities in continuous speech. I found that failed syntactic predictions led to increased information flow within the left frontotemporal syntax network which was initiated in the first 100 ms after the disambiguating verb onset by LpMTG-to-LIFG feed-forward communication. The failed predictions resulted in syntactic reanalysis that involved recurrent communication between LIFG and LpMTG until 500 ms after the verb onset. This recurrent communication, within the predictive coding account framework, reflects the prediction update to gradually minimise the prediction error on syntactic structure.

CHAPTER 6

CONCLUDING REMARKS

In this thesis using EEG and MEG, I have investigated 1) the cortical network dynamics associated with the cognitive processes that underlie speech comprehension; 2) and how the activity and connectivity of these networks are modulated by contextual semantics and syntax. In this final chapter I will aim to tie in all findings and highlight the novel contributions of this thesis to literature. Finally, I will discuss the study limitations and propose further research directions in understanding network dynamics of speech comprehension.

6.1. SUMMARY OF FINDINGS AND NOVEL CONTRIBUTIONS

6.1.1. NATURE OF LEXICAL REPRESENTATIONS AND COMPETITION

To investigate the cortical network dynamics that underpin sound-to-meaning mapping during speech comprehension (Experiment 1), I adopted the distributed cohort model as the model of spoken word recognition (Gaskell & Marslen-Wilson, 1997a, 2002). As discussed in detail in Chapter 1, DCM provides advantages over and above the other computationally implemented speech comprehension models (e.g. TRACE, Shortlist). DCM is both behaviourally and computationally validated (Apfelbaum et al., 2011; Gaskell & Marslen-Wilson, 1999; Moss et al., 1997); and more importantly it describes the nature of lexical and semantic representations. According to DCM the lexical and semantic representations of a concept are represented in distributed representational units. Therefore, DCM replaces nodes commonly used in computational models of speech with distributed feature-based representations. As the speech is heard, phonetic features decoded activate cohort candidates where those features consist the word form. In turn these partially activated lexical representations activate corresponding semantic representations. Multiple and parallel activation of representations create *blending* of representations, and therefore competition. When adequate amount of speech input accrues, the representations that do not match the available information, decay, and the input activates a single item in the cohort, the target representation.

Experiment 1 is the first study to validate DCM's propositions regarding both the nature of lexical and semantic representations and access to meaning. The LexComp and SemComp models captured the competition that results from parallel activation of feature-based representations of the cohort candidates (i.e. resulting from blending). These models successfully revealed the cortical networks that consist of regions previously reported for competition resolution (i.e. LIFG) (Zhuang et al., 2014), phonological (i.e. STG, SMG) (Rauschecker & Scott, 2009), and lexical semantic activation (i.e. MTG, AG) (Binder et al., 2009; Seghier, 2013). More importantly ssRSA allowed us to investigate the relative temporal dynamics of these cortical networks with respect to each other. Complimentary to DCM's propositions I found that the lexical and semantic competition start in parallel as soon as speech starts (about 400 ms before the UP). The results demonstrate the crucial importance of UP in speech comprehension, that it marks a transition point between processes of competition and access to target word's semantics. ssRSA further showed that the lexical semantic information that is partially activated prior to the UP, is boosted after the UP as soon as the competition is resolved. According to DCM, prior to the UP the degree to which lexical representations are activated depends on the size of activated cohort that inhibit each other through lateral inhibition. Therefore prior to UP target word's semantic representation remains weak due to lateral inhibition, but as the competitor representations decay, inhibition decreases and consequentially target word's semantic representation will be boosted after the UP.

In summary, Experiment 1 successfully 1) validates DCM's proposed cognitive processes and relates them to cortical network dynamics; 2) demonstrates that about 400 ms prior to UP lexical and semantic representations are partially activated in parallel; 3) show that UP is an important transition point in speech comprehension between competition processes and access to target semantics. These findings demonstrate that speech is processes by an optimally efficient language system (Gaskell & Marslen-Wilson, 1997a; Marslen-Wilson, 1984) that recognises words as soon as sufficient information is accumulated to differentiate them from the competitors. This optimally efficient system by enabling early activation of linguistic representations allows rapid integration of speech content and therefore online comprehension.

6.1.2. CONTEXTUAL FACILITATION IN SEMANTIC PROCESSING

Building on Experiment 1's findings in Experiment 2 and 3, I investigated the effect of contextual information on access to meaning in short phrases and sentences. Previous research shows that when words are presented within supportive contexts, lexical retrieval and processing is facilitated (Bransford & Johnson, 1972; Fischler & Bloom, 1980; Marslen-Wilson, 1975; Otten & Van Berkum, 2007; Tyler & Wessels, 1983; West & Stanovich, 1978). Neuroimaging studies that investigated the cortical areas underpinning contextual semantic processing and conceptual combination have indicated two areas: ATL (Baron & Osherson, 2011; Bemis & Pylkkänen, 2011, 2013; Humphries et al., 2005) and AG (Bemis & Pylkkänen, 2013; A. R. Price et al., 2015; Seghier et al., 2010). Most of these studies use tasks to help participants engage with the experiment and attend to the stimuli. Despite their advantages however, recent studies indicate that tasks might recruit additional networks of regions that subserve domain general executive functions (S. W. Davis et al., 2014; Miniussi et al., 2005; Wright et al., 2011). Using a network analysis, in Experiment 2, I aimed to discover cortical networks that underpin contextual semantic processing of simple two-word combinations in the absence of task induced domain general networks.

Firstly, the behavioural gating results showed that as the contextual semantics became more constraining, the cohort size decreased and the UP shifted to an earlier point, indicating that contextual support facilitates word recognition. Among 14 ICs revealed by ICA, only the bilateral AG networks showed significant modulations in activity in response to changes in semantic constraint. One network, IC8, picked up activity from bilateral ATL, however was not significantly modulated by semantic constraint. With respect to the extensive network of regions revealed in the univariate source activity contrasts, ICA only showed significant modulations in AG.

Altogether, the results of this study supports the literature that show AG as the locus of contextual semantic processing in language (Bemis & Pylkkänen, 2013; A. R. Price et al., 2015; Seghier, 2013), and further adds that when task induced network activity is accounted for, AG is modulated 300 ms before the word is recognised. Moreover, this effect was stronger in the left hemisphere. Altogether these findings demonstrate that as we hear speech, the cohort candidates that match the speech input are continuously assessed by the bilateral AG, against the meaning acquired from the prior context. This assessment might serve to restrict the cohort size to allow candidates that match both the speech input and the context; and to allow rapid integration of the target word's semantics with the sentential meaning.

6.1.3. SYNTACTIC PROCESSING AND RELATED NETWORK DYNAMICS

In speech processing, sentential syntactic structure is constructed on the fly. Listeners activate syntactic representations that match the contextual structure. However sentential syntax can sometimes be ambiguous, and multiple representations can fit the context. Similar to the propositions of the cohort model, when contextual syntax is ambiguous, multiple syntactic representations will be activated in parallel, and their activation levels will be weighted by how likely and how contextually relevant they are (MacDonald et al., 1994). The upcoming speech will be consistent with one syntactic representation. If the less preferred syntactic structure remains true, then the sentential syntax would need to be reanalysed. The reanalysis would involve reactivation of the less preferred syntactic representation and integration of the representation with sentential syntax.

The core neural system underlying syntax processing has been shown to involve a left hemisphere frontotemporal system, including LIFG and LpMTG (Caplan et al., 1996; Tyler & Marslen-Wilson, 2008; Tyler et al., 2011; Wright et al., 2012) and the white matter tracts connecting them (Griffiths et al., 2013). Even though the syntax network is well established the dynamics of the information flow is not well understood. Using DCM-ERP, Experiment 3 aimed to explore how anticipations regarding the upcoming syntactic frames and the match between the anticipations and the perceived speech modulates the connectivity in the syntax network. DCM-ERP revealed that when the anticipations about the upcoming speech were incorrect, the reanalysis of the sentential syntax led to an increased feedforward information flow in the first 100 ms, followed by increased recurrent communication between LIFG and LpMTG until 500 ms post verb onset. Previous research from Tyler et al. (2013) using the same stimuli and RSA, have reported early ambiguity and later reanalysis effects in LIFG. Current results further extend these findings, and demonstrate that early modulations result from the feedforward prediction error signal, and later recurrent modulations constitute the reanalysis processes that involve the reactivation of the unanticipated syntactic representation and its integration with the prior syntactic structure.

Altogether the results demonstrate that the listeners continuously process and assess the syntactic structure of the speech, and use the accumulated syntactic information to anticipate the upcoming words. Further the results indicate that when the upcoming speech is not consistent with our anticipations, then the error between the anticipated and perceived syntactic frame is minimised through recurrent frontotemporal interactions driven by the LIFG. Further, this is the first study that tests temporal dynamics of effective connectivity in the syntax network using a biologically informed causal model.

6.2. STRENGTHS AND LIMITATIONS

MEG data collected in all three experiments is a robust and dynamic measure of brain activity. MEG provides fast time resolution (in milliseconds) and compared to fMRI and PET, is a direct measure of brain activity. Compared to EEG, MEG recording does not have the issue of volume conduction across different tissues. All three analyses have been performed in MEG source space, which was constructed using individual participants' structural MRI scans that was later warped into a normalised plane. These steps allowed us to investigate brain activity both with high temporal and good spatial resolution.

Further to avoid confounding effects induced by tasks, in Experiment 1 and 2 employed simple natural tasks that were performed infrequently. Using nonword detection in Experiment 1, and semantic relatedness judgment in Experiment 2 participants were made sure to attend to the word meanings. These tasks were especially constructed to be simple and undemanding for memory.

Experiment 2 and 3 due to high computational resources required by the analyses, have not fully taken advantage of MEG's high temporal resolution. Group ICA required concatenation of all experimental trials across participants. To reduce the memory load and speed up computations, the data was downsampled to 10 Hz. Similarly, in the DCM-ERP analysis the coupling gains were computed for every 100 ms time window. If the time windows where the differences were expected to occur were known, then the epochs could be shortened accordingly and the data could be sampled at higher frequencies in the target time window.

6.3. FUTURE DIRECTIONS

Altogether the findings demonstrate the cortical networks as well as temporal dynamics that underpin speech comprehension in isolation and when aided by contextual information. Speech comprehension is shown to constitute incremental parallel processing of linguistic representations over time as speech accrues: before the word is uniquely identified the likely lexical, semantic and syntactic representations are activated in parallel, assessed against both the speech input and the sentential context, and rapidly integrated. This parallel incremental processing aided by the contextual support, makes speech comprehension rapid, efficient and robust. Experiments in this thesis aimed to answer questions on cortical network dynamics of speech comprehension, however there are several minor and major areas that remain open and require further research.

ssRSA used in Experiment 1 allows to construct theoretical models of variables of interest and test them against brain activity data. To define the time windows when the models relate to brain activity, the model RDMs need to be kept static. Therefore, the models captured the similarities across the stimuli at pre-specified time points. However, it is also possible to create dynamic model RDMs, which would reflect millisecond-by-millisecond changes in the modelled variable. For example, cohort competition can be modelled using the behavioural gating output at every gate, creating a time course of competition for each word. Although these dynamic model RDMs would introduce the issue of defining the right lag between the brain activity and the model, they have the potential of constructing a more accurate description of the modelled variable.

Analyses in this thesis have adopted DCM as the model of spoken word recognition. Even though the results of Experiment 1 successfully define the spatiotemporal brain dynamics of cognitive processes that underlie the model's propositions; they fail to reject the propositions of other models of speech comprehension. To address this issue, future studies should similarly model key cognitive processes (i.e. competition, lexical activation, and the nature of representations) as proposed by other prominent models of speech comprehension (e.g. TRACE, Shortlist). These models can be similarly tested these against the same brain data and through a goodness-of-fit measure future studies can determine which model of speech comprehension better account for the brain activity.

Results of Experiment 2 emphasise the central role of bilateral AG in processing contextual semantic constraints in speech. The analysis failed to find similar modulations in activity in ATL as widely reported in the literature, which might indicate that ATL is responsible for another semantic role in comprehension. Future research could aim to distinguish the functional roles of ATL and AG in speech comprehension (e.g. lexical retrieval, conceptual combination, syntactic integration, supramodal feature convergence), and determine the information flow between the two regions during speech comprehension.

To conclude, although many issues still remain to be addressed, the results presented in this thesis make novel contributions to our understanding of cortical network dynamics that underlie incremental processes of lexical activation and competition during the evolution of sound to meaning, contextual semantic processing of simple phrases, and the use of contextual syntactic structure to aid comprehension. This research will hopefully open up new directions of investigations to progress and enrich our neurobiological understanding of speech comprehension.

Ece Kocagöncü
September 2016

REFERENCES

Abel, S., Dressel, K., Bitzer, R., Kümmerer, D., Mader, I., Weiller, C., & Huber, W. (2009). The separation of processing stages in a lexical interference fMRI-paradigm. *Neuroimage, 44*(3), 1113-1124. doi:10.1016/j.neuroimage.2008.10.018

Ahveninen, J., Jääskeläinen, I. P., Raij, T., Bonmassar, G., Devore, S., Hämäläinen, M., . . . Belliveau, J. W. (2006). Task-modulated "what" and "where" pathways in human auditory cortex. *Proceedings of the National Academy of Sciences, 103*(39), 14608-14613. doi:10.1073/pnas.0510480103

Alain, C., Arnott, S. R., Hevenor, S., Graham, S., & Grady, C. L. (2001). "What" and "where" in the human auditory system. *Proceedings of the National Academy of Sciences, 98*(21), 12301-12306. doi:10.1073/pnas.211209098

Alexander, M. P., Hiltbrunner, B., & Fischer, R. S. (1989). Distributed anatomy of transcortical sensory aphasia. *Archives of Neurology, 46*(8), 885-892.

Allen, M., Badecker, W., & Osterhout, L. (2003). Morphological analysis in sentence processing: an ERP study. *Language and Cognitive Processes, 5*, 405-430.

Allopenna, P. D., Magnuson, J. S., & Tanenhaus, M. K. (1998). Tracking the time course of spoken word recognition using eye movements: evidence for continuous mapping models. *Journal of Memory and Language, 38*, 419-439.

Altmann, G. T., & Kamide, Y. (1999). Incremental interpretation at verbs: restricting the domain of subsequent reference. *Cognition, 73*(3), 247-264.

Antonenko, D., Brauer, J., Meinzer, M., Fengler, A., Kerti, L., Friederici, A. D., & Flöel, A. (2013). Functional and structural syntax networks in aging. *Neuroimage, 83*, 513-523. doi:10.1016/j.neuroimage.2013.07.018

Anwander, A., Tittgemeyer, M., von Cramon, D. Y., Friederici, A. D., & Knösche, T. R. (2007). Connectivity-Based Parcellation of Broca's Area. *Cerebral Cortex, 17*(4), 816-825. doi:10.1093/cercor/bhk034

Apfelbaum, K. S., Blumstein, S. E., & McMurray, B. (2011). Semantic priming is affected by real-time phonological competition: evidence for continuous cascading systems. *Psychonomic Bulletin & Review, 18*(1), 141-149.

Ardila, A., Concha, M., & Rosselli, M. (2000). Angular gyrus syndrome revisited: Acalculia, finger agnosia, right-left disorientation and semantic aphasia. *Aphasiology, 14*(7), 743-754.

Arnott, S. R., Binns, M. A., Grady, C. L., & Alain, C. (2004). Assessing the auditory dual-pathway model in humans. *Neuroimage, 22*(1), 401-408. doi:10.1016/j.neuroimage.2004.01.014

Auerbach, S. H., Allard, T., Naeser, M., Alexander, M. P., & Albert, M. L. (1982). Pure word deafness. Analysis of a case with bilateral lesions and a defect at the prephonemic level. *Brain, 105*(Pt 2), 271-300.

Baayen, R. H. (1995). The CELEX Lexical database. In P. L. D. C. University of Pennsylvania (Ed.).

Baddeley, A. D., & Hitch, G. (1974). Working memory. In G. H. Bower (Ed.), *The psychology of learning and motivation* (Vol. 8, pp. 47-89). New York: Academic Press.

Badre, D., Poldrack, R. A., Paré-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron, 47*(6), 907-918.

Badre, D., & Wagner, A. D. (2002). Semantic retrieval, mnemonic control, and prefrontal cortex. *Behavioral and Cognitive Neuroscience Reviews, 1*(3), 206-218.

Balconi, M., & Caldiroli, C. (2011). Semantic violation effect on object-related action comprehension. N400-like event-related potentials for unusual and incorrect use. *Neuroscience, 197*, 191-199. doi:10.1016/j.neuroscience.2011.09.026

Bar, M. (2007). The proactive brain: using analogies and associations to generate predictions. *Trends in Cognitive Sciences, 11*(7), 280-289.

Baron, S. G., & Osherson, D. (2011). Evidence for conceptual combination in the left anterior temporal lobe. *Neuroimage, 55*(4), 1847-1852.

Baron, S. G., Thompson-Schill, S. L., Weber, M., & Osherson, D. (2010). An early stage of conceptual combination: Superimposition of constituent concepts in left anterolateral temporal lobe. *Cognitive Neuroscience, 1*(1), 44-51. doi:10.1080/17588920903548751

Baroni, M., & Lenci, A. (2010). Distributional memory: A general framework for corpus-based semantics. *Computational Linguistics, 36*(4), 673-721.

Bates, E., Wilson, S. M., Saygin, A. P., Dick, F., Sereno, M. I., Knight, R. T., & Dronkers, N. F. (2003). Voxel-based lesion-symptom mapping. *Nature Neuroscience, 6*(5), 448-450. doi:10.1038/nn1050

Bedny, M., McGill, M., & Thompson-Schill, S. L. (2008). Semantic adaptation and competition during word comprehension. *Cerebral Cortex, 18*(11), 2574-2585. doi:10.1093/cercor/bhn018

Bemis, D. K., & Pylkkänen, L. (2011). Simple composition: a magnetoencephalography investigation into the comprehension of minimal linguistic phrases. *Journal of Neuroscience, 31*(8), 2801-2814.

Bemis, D. K., & Pylkkänen, L. (2013). Basic linguistic composition recruits the left anterior temporal lobe and left angular gyrus during both listening and reading. *Cerebral Cortex, 23*(8), 1859-1873. doi:10.1093/cercor/bhs170

Bendixen, A., Schröger, E., & Winkler, I. (2009). I heard that coming: event-related potential evidence for stimulus-driven prediction in the auditory system. *Journal of Neuroscience, 29*(26), 8447-8451. doi:10.1523/JNEUROSCI.1493-09.2009

Benson, D. F., Sheremata, W. A., Bouchard, R., Segarra, J. M., Price, D., & Geschwind, N. (1973). Conduction aphasia: a clinicopathological study. *Archives of Neurology, 28*, 339-346.

Bentin, S., Mouchetant-Rostaing, Y., Girard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP manifestations of processing printed words at different psycholinguistic levels: time course and scalp distribution. *Journal of Cognitive Neuroscience, 11*, 235-260.

Binder, J. R. (2000). The new neuroanatomy of speech perception. *Brain, 123 Pt 12*, 2371-2372.

Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences, 15*(11), 527-536. doi:10.1016/j.tics.2011.10.001

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex, 19*(12), 2767-2796.

Binder, J. R., Frost, J. A., Hammeke, T. A., Rao, S. M., & Cox, R. W. (1996). Function of the left planum temporale in auditory and linguistic processing. *Brain, 119 (Pt 4)*, 1239-1247.

Blank, I., Kanwisher, N., & Fedorenko, E. (2014). A functional dissociation between language and multiple-demand systems revealed in patterns of BOLD signal fluctuations. *Journal of Neurophysiology, 112*(5), 1105-1118. doi:10.1152/jn.00884.2013

Boatman, D., Gordon, B., Hart, J., Selnes, O., Miglioretti, D., & Lenz, F. (2000). Transcortical sensory aphasia: revisited and revised. *Brain, 123 (Pt 8)*, 1634-1642.

Boemio, A., Fromm, S., Braun, A., & Poeppel, D. (2005). Hierarchical and asymmetric temporal sensitivity in human auditory cortices. *Nature Neuroscience, 8*(3), 389-395. doi:10.1038/nn1409

Bogen, J. E., & Bogen, G. M. (1976). Wernicke's region-where is it? *Annals of the New York Academy of Sciences, 280*, 834-843.

Bonner, M. F., Peelle, J. E., Cook, P. A., & Grossman, M. (2013). Heteromodal conceptual processing in the angular gyrus. *Neuroimage, 71*, 175-186.

Bornkessel, I., Zysset, S., Friederici, A. D., von Cramon, D. Y., & Schlesewsky, M. (2005). Who did what to whom? The neural basis of argument hierarchies during language comprehension. *Neuroimage, 26*(1), 221-233. doi:10.1016/j.neuroimage.2005.01.032

Bottini, G., Corcoran, R., Sterzi, R., Paulesu, E., Schenone, P., Scarpa, P., . . . Frith, C. D. (1994). The role of the right hemisphere in the interpretation of figurative aspects of language. A positron emission tomography activation study. *Brain, 117 (Pt 6)*, 1241-1253.

Bozic, M., Tyler, L. K., Ives, D. T., Randall, B., & Marslen-Wilson, W. D. (2010). Bihemispheric foundations for human speech comprehension. *Proceedings of the National Academy of Sciences, 107*(40), 17439-17444. doi:10.1073/pnas.1000531107

Bransford, J., & Johnson, M. K. (1972). Contextual prerequisites for understanding - some investigations of comprehension and recall. *Journal of Verbal Learning and Verbal Behavior, 11*, 717-726.

Brennan, J., Lignos, C., Embick, D., & Roberts, T. P. (2014). Spectro-temporal correlates of lexical access during auditory lexical decision. *Brain and Language, 133*, 39-46. doi:10.1016/j.bandl.2014.03.006

Bright, P., Moss, H. E., Longe, O., Stamatakis, E. A., & Tyler, L. K. (2007). Conceptual structure modulates anteromedial temporal involvement in processing verbally presented object properties. *Cerebral Cortex, 17*(5), 1066-1073. doi:10.1093/cercor/bhl016

Bright, P., Moss, H. E., Stamatakis, E. A., & Tyler, L. K. (2008). Longitudinal studies of semantic dementia: the relationship between structural and functional changes over time. *Neuropsychologia, 46*(8), 2177-2188. doi:10.1016/j.neuropsychologia.2008.02.019

Britton, B., Blumstein, S. E., Myers, E. B., & Grindrod, C. (2009). The role of spectral and durational properties on hemispheric asymmetries in vowel perception. *Neuropsychologia, 47*(4), 1096-1106. doi:10.1016/j.neuropsychologia.2008.12.033

Broca, P. (1865). Sur le siège de la faculté du langage articulé. *Bulletin de la Societe d'anthropologie de Paris, 6*, 377-393.

Brookes, M. J., Liddle, E. B., Hale, J. R., Woolrich, M. W., Luckhoo, H., Liddle, P. F., & Morris, P. G. (2012). Task induced modulation of neural oscillations in electrophysiological brain networks. *Neuroimage, 63*(4), 1918-1930. doi:10.1016/j.neuroimage.2012.08.012

Brookes, M. J., Woolrich, M., Luckhoo, H., Price, D., Hale, J. R., Stephenson, M. C., . . . Morris, P. G. (2011). Investigating the electrophysiological basis of resting state networks using magnetoencephalography. *Proceedings of the National Academy of Sciences, 108*(40), 16783-16788. doi:10.1073/pnas.1112685108

Brothers, T., Swaab, T. Y., & Traxler, M. J. (2015). Effects of prediction and contextual support on lexical processing: prediction takes precedence. *Cognition, 136*, 135-149. doi:10.1016/j.cognition.2014.10.017

Brown, C., & Hagoort, P. (1993). The processing nature of the N400: evidence from masked priming. *Journal of Cognitive Neuroscience, 5*, 34-44.

Brunia, C. H. (1999). Neural aspects of anticipatory behavior. *Acta Psychologica, 101*(2-3), 213-242.

Brysbaert, M., Warriner, A. B., & Kuperman, V. (2014). Concreteness ratings for 40 thousand generally known English word lemmas. *Behavior Research Methods, 46*(3), 904-911. doi:10.3758/s13428-013-0403-5

Bubic, A., von Cramon, D. Y., & Schubotz, R. I. (2010). Prediction, cognition and the brain. *Frontiers in Human Neuroscience, 4*, 25. doi:10.3389/fnhum.2010.00025

Buchman, A. S., Garron, D. C., Trostcardamone, J. E., Wichter, M. D., & Schwartz, M. (1986). Word deafness - 100 years later. *Journal of Neurology Neurosurgery and Psychiatry, 49*(5), 489-499.

Buchsbaum, B. R., Hickok, G., & Humphries, C. (2001). Role of left posterior superior temporal gyrus in phonological processing for speech perception and production. *Cognitive Science, 25*(5), 663-678.

Buchsbaum, B. R., Pickell, B., Love, T., Hatrak, M., Bellugi, U., & Hickok, G. (2005). Neural substrates for verbal working memory in deaf signers: fMRI study and lesion case report. *Brain and Language, 95*(2), 265-272. doi:10.1016/j.bandl.2005.01.009

Calhoun, V. D., Eichele, T., Adalı, T., & Allen, E. A. (2012). Decomposing the brain: components and modes, networks and nodes. *Trends in Cognitive Sciences, 16*(5), 255-256. doi:10.1016/j.tics.2012.03.008

Campbell, K. L., Samu, D., Davis, S. W., Geerligs, L., Mustafa, A., Tyler, L. K., & Neuroscience, f. C. C. f. A. a. (2016). Robust Resilience of the Frontotemporal Syntax System to Aging. *Journal of Neuroscience, 36*(19), 5214-5227. doi:10.1523/JNEUROSCI.4561-15.2016

Caplan, D., Hildebrandt, N., & Makris, N. (1996). Location of lesions in stroke patients with deficits in syntactic processing in sentence comprehension. *Brain, 119 (Pt 3)*, 933-949.

Carreiras, M., Mechelli, A., & Price, C. J. (2006). Effect of word and syllable frequency on activation during lexical decision and reading aloud. *Human Brain Mapping, 27*(12), 963-972. doi:10.1002/hbm.20236

Celsis, P., Boulanouar, K., Doyon, B., Ranjeva, J. P., Berry, I., Nespoulous, J. L., & Chollet, F. (1999). Differential fMRI responses in the left posterior superior temporal gyrus and left supramarginal gyrus to habituation and change detection in syllables and tones. *Neuroimage, 9*(1), 135-144. doi:10.1006/nimg.1998.0389

Chand, G. B., & Dhamala, M. (2016). The salience network dynamics in perceptual decision-making. *Neuroimage, 134*, 85-93. doi:10.1016/j.neuroimage.2016.04.018

Chang, E. F., Rieger, J. W., Johnson, K., Berger, M. S., Barbaro, N. M., & Knight, R. T. (2010). Categorical speech representation in human superior temporal gyrus. *Nature Neuroscience, 13*(11), 1428-1432. doi:10.1038/nn.2641

Christensen, K. R. (2010). Syntactic reconstruction and reanalysis, semantic dead ends, and prefrontal cortex. *Brain and Cognition, 73*(1), 41-50. doi:10.1016/j.bandc.2010.02.001

Christiansen, M. H., & Chater, N. (2015). The now-or-never bottleneck: a fundamental constraint on language. *Behavioral and Brain Sciences*, 1-52.

Clarke, A., Taylor, K. I., Devereux, B., Randall, B., & Tyler, L. K. (2013). From perception to conception: how meaningful objects are processed over time. *Cerebral Cortex, 23*(1), 187-197.

Clarke, A., Taylor, K. I., & Tyler, L. K. (2011). The evolution of meaning: spatio-temporal dynamics of visual object recognition. *Journal of Cognitive Neuroscience, 23*(8), 1887-1899.

Clarke, A., & Tyler, L. K. (2014). Object-specific semantic coding in human perirhinal cortex. *Journal of Neuroscience, 34*(14), 4766-4775.

Cohen, G., & Faulkner, D. (1983). Word recognition: age differences in contextual facilitation effects. *British Journal of Psychology, 74*(Pt 2), 239-251.

Cole, R. A. (1973). Listening for mispronunciations: a measure of what we hear during speech. *Perception & Psychophysics, 1*, 153-156.

Coltheart, M. (1981). The MRC psycholinguistic database. *Quarterly Journal of Experimental Psychology, 33*(A), 497-505.

Connine, C. M., Blasko, D. G., & Titone, D. (1993). Do the beginnings of spoken words have a special status in auditory word recognition. *Journal of Memory and Language, 32*(2), 193-210.

Connolly, A. C., Guntupalli, J. S., Gors, J., Hanke, M., Halchenko, Y. O., Wu, Y. C., . . . Haxby, J. V. (2012). The representation of biological classes in the human brain. *Journal of Neuroscience, 32*(8), 2608-2618.

Connolly, J. F., & Phillips, N. A. (1994). Event-related potential components reflect phonological and semantic processing of the terminal word of spoken sentences. *Journal of Cognitive Neuroscience, 6*(3), 256-266. doi:10.1162/jocn.1994.6.3.256

Connolly, J. F., Service, E., D'Arcy, R. C., Kujala, A., & Alho, K. (2001). Phonological aspects of word recognition as revealed by high-resolution spatio-temporal brain mapping. *Neuroreport, 12*(2), 237-243.

Constable, R. T., Pugh, K. R., Berroya, E., Mencl, W. E., Westerveld, M., Ni, W., & Shankweiler, D. (2004). Sentence complexity and input modality effects in sentence comprehension: an fMRI study. *Neuroimage, 22*(1), 11-21. doi:10.1016/j.neuroimage.2004.01.001

Cooke, A., Zurif, E. B., DeVita, C., Alsop, D., Koenig, P., Detre, J., . . . Grossman, M. (2002). Neural basis for sentence comprehension: grammatical and short-term memory components. *Human Brain Mapping, 15*(2), 80-94.

Coslett, H. B., Roeltgen, D. P., Gonzalez Rothi, L., & Heilman, K. M. (1987). Transcortical sensory aphasia: evidence for subtypes. *Brain and Language, 32*(2), 362-378.

Costafreda, S. G., Fu, C. H., Lee, L., Everitt, B., Brammer, M. J., & David, A. S. (2006). A systematic review and quantitative appraisal of fMRI studies of verbal fluency: role of the left inferior frontal gyrus. *Human Brain Mapping, 27*(10), 799-810.

Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences, 24*, 87-114.

Crittenden, B. M., & Duncan, J. (2014). Task difficulty manipulation reveals multiple demand activity but no frontal lobe hierarchy. *Cerebral Cortex, 24*(2), 532-540. doi:10.1093/cercor/bhs333

Cutting, J. E., & Pisoni, D. B. (1978). An information-processing approach to speech processing. *Speech and language in the laboratory, school and clinic*, 38-72.

Dahan, D., Magnuson, J. S., & Tanenhaus, M. K. (2001). Time course of frequency effects in spoken-word recognition: evidence from eye movements. *Cognitive Psychology, 42*(4), 317-367. doi:10.1006/cogp.2001.0750

Daly, I., Nicolaou, N., Nasuto, S. J., & Warwick, K. (2013). Automated artifact removal from the electroencephalogram: a comparative study. *Clinical EEG and Neuroscience, 44*(4), 291-306. doi:10.1177/1550059413476485

Damasio, A. R. (1998). Signs of aphasia. *Acquired Aphasia, 2*, 27-43.

Dapretto, M., & Bookheimer, S. Y. (1999). Form and content: dissociating syntax and semantics in sentence comprehension. *Neuron, 24*(2), 427-432.

Davey, J., Cornelissen, P. L., Thompson, H. E., Sonkusare, S., Hallam, G., Smallwood, J., & Jefferies, E. (2015). Automatic and Controlled Semantic Retrieval: TMS Reveals Distinct Contributions of Posterior Middle Temporal Gyrus and Angular Gyrus. *Journal of Neuroscience, 35*(46), 15230-15239. doi:10.1523/JNEUROSCI.4705-14.2015

David, O., Kiebel, S. J., Harrison, L. M., Mattout, J., Kilner, J. M., & Friston, K. J. (2006). Dynamic causal modeling of evoked responses in EEG and MEG. *Neuroimage, 30*(4), 1255-1272. doi:10.1016/j.neuroimage.2005.10.045

David, O., Maess, B., Eckstein, K., & Friederici, A. D. (2011). Dynamic causal modeling of subcortical connectivity of language. *Journal of Neuroscience, 31*(7), 2712-2717. doi:10.1523/JNEUROSCI.3433-10.2011

Davis, M. H., Coleman, M. R., Absalom, A. R., Rodd, J. M., Johnsrude, I. S., Matta, B. F., . . . Menon, D. K. (2007). Dissociating speech perception and comprehension at reduced levels of awareness. *Proceedings of the National Academy of Sciences, 104*(41), 16032-16037. doi:10.1073/pnas.0701309104

Davis, M. H., & Gaskell, M. G. (2009). A complementary systems account of word learning: neural and behavioural evidence. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences, 364*(1536), 3773-3800. doi:10.1098/rstb.2009.0111

Davis, M. H., & Johnsrude, I. S. (2003). Hierarchical processing in spoken language comprehension. *Journal of Neuroscience, 23*(8), 3423-3431.

Davis, M. H., Johnsrude, I. S., Hervais-Adelman, A., Taylor, K., & McGettigan, C. (2005). Lexical information drives perceptual learning of distorted speech: evidence from the comprehension of noise-vocoded sentences. *Journal of Experimental Psychology: General, 134*(2), 222-241. doi:10.1037/0096-3445.134.2.222

Davis, M. H., Marslen-Wilson, W. D., & Gaskell, M. G. (2002). Leading up the lexical garden-path: segmentation and ambiguity in spoken word recognition. *Journal of Experimental Psychology: Human Perception and Performance, 28*, 218-244.

Davis, M. H., Meunier, F., & Marslen-Wilson, W. D. (2004). Neural responses to morphological, syntactic, and semantic properties of single words: an fMRI study. *Brain and Language, 89*(3), 439-449. doi:10.1016/S0093-934X(03)00471-1

Davis, S. W., Zhuang, J., Wright, P., & Tyler, L. K. (2014). Age-related sensitivity to task-related modulation of language-processing networks. *Neuropsychologia, 63*, 107-115. doi:10.1016/j.neuropsychologia.2014.08.017

de Zubicaray, G. I., McMahon, K., Eastburn, M., & Pringle, A. (2006). Top-down influences on lexical selection during spoken word production: A 4T fMRI investigation of refractory effects in picture naming. *Human Brain Mapping, 27*(11), 864-873. doi:10.1002/hbm.20227

de Zubicaray, G. I., & McMahon, K. L. (2009). Auditory context effects in picture naming investigated with event-related fMRI. *Cognitive, Affective, & Behavioral Neuroscience, 9*(3), 260-269. doi:10.3758/CABN.9.3.260

de Zubicaray, G. I., McMahon, K. L., Eastburn, M. M., & Wilson, S. J. (2002). Orthographic/phonological facilitation of naming responses in the picture-word task: an event-related fMRI study using overt vocal responding. *Neuroimage, 16*(4), 1084-1093.

Dehaene-Lambertz, G., Pallier, C., Serniclaes, W., Sprenger-Charolles, L., Jobert, A., & Dehaene, S. (2005). Neural correlates of switching from auditory to speech perception. *Neuroimage, 24*(1), 21-33. doi:10.1016/j.neuroimage.2004.09.039

DeLong, K. A., Urbach, T. P., & Kutas, M. (2005). Probabilistic word pre-activation during language comprehension inferred from electrical brain activity. *Nature Neuroscience, 8*(8), 1117-1121. doi:10.1038/nn1504

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods, 134*(1), 9-21.

Demb, J. B., Desmond, J. E., Wagner, A. D., Vaidya, C. J., Glover, G. H., & Gabrieli, J. D. (1995). Semantic encoding and retrieval in the left inferior prefrontal cortex: a functional MRI study of task difficulty and process specificity. *Journal of Neuroscience, 15*(9), 5870-5878.

den Ouden, D. B., Saur, D., Mader, W., Schelter, B., Lukic, S., Wali, E., . . . Thompson, C. K. (2012). Network modulation during complex syntactic processing. *Neuroimage, 59*(1), 815-823. doi:10.1016/j.neuroimage.2011.07.057

Deschamps, I., Baum, S. R., & Gracco, V. L. (2014). On the role of the supramarginal gyrus in phonological processing and verbal working memory: evidence from rTMS studies. *Neuropsychologia, 53*, 39-46. doi:10.1016/j.neuropsychologia.2013.10.015

Devereux, B. J., Clarke, A., Marouchos, A., & Tyler, L. K. (2013). Representational similarity analysis reveals commonalities and differences in the semantic processing of words and objects. *Journal of Neuroscience, 33*(48), 18906-18916. doi:10.1523/JNEUROSCI.3809-13.2013

Devereux, B. J., Tyler, L. K., Geertzen, J., & Randall, B. (2014). The Centre for Speech, Language and the Brain (CSLB) concept property norms. *Behavior Research Methods, 46*(4), 1119-1127. doi:10.3758/s13428-013-0420-4

Devlin, J. T., Matthews, P. M., & Rushworth, M. F. (2003). Semantic processing in the left inferior prefrontal cortex: a combined functional magnetic resonance imaging and transcranial magnetic stimulation study. *Journal of Cognitive Neuroscience, 15*(1), 71-84. doi:10.1162/089892903321107837

DeWitt, I., & Rauschecker, J. P. (2012). Phoneme and word recognition in the auditory ventral stream. *Proceedings of the National Academy of Sciences, 109*(8), E505-514. doi:10.1073/pnas.1113427109

Dhankar, A., Wexler, B. E., Fulbright, R. K., Halwes, T., Blamire, A. M., & Shulman, R. G. (1997). Functional magnetic resonance imaging assessment of the human brain auditory cortex response to increasing word presentation rates. *Journal of Neurophysiology, 77*, 476-483.

Dikker, S., & Pylkkänen, L. (2013). Predicting language: MEG evidence for lexical preactivation. *Brain and Language, 127*(1), 55-64. doi:10.1016/j.bandl.2012.08.004

Downar, J., Crawley, A. P., Mikulis, D. J., & Davis, K. D. (2000). A multimodal cortical network for the detection of changes in the sensory environment. *Nature Neuroscience, 3*(3), 277-283. doi:10.1038/72991

Dronkers, N. F., Redfern, B. B., & Ludy, C. A. (1995). Lesion localization in chronic Wernicke's aphasia. *Brain and Language, 51*, 62-65.

Dronkers, N. F., Wilkins, D. P., Van Valin, R. D., Redfern, B. B., & Jaeger, J. J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition, 92*(1-2), 145-177. doi:10.1016/j.cognition.2003.11.002

Dudschig, C., Maienborn, C., & Kaup, B. (2016). Is there a difference between stripy journeys and stripy ladybirds? The N400 response to semantic and world-knowledge violations during sentence processing. *Brain and Cognition, 103*, 38-49. doi:10.1016/j.bandc.2016.01.001

Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends in Cognitive Sciences, 14*(4), 172-179. doi:10.1016/j.tics.2010.01.004

Démonet, J. F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J. L., Wise, R., . . . Frackowiak, R. (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain, 115 (Pt 6)*, 1753-1768.

Démonet, J. F., Price, C., Wise, R., & Frackowiak, R. S. (1994). Differential activation of right and left posterior sylvian regions by semantic and phonological tasks: a positron-emission tomography study in normal human subjects. *Neuroscience Letters, 182*(1), 25-28.

Ehrlich, S. F., & Rayner, K. (1981). Contextual effects on word perception and eye movements during reading. *Journal of Verbal Learning and Verbal Behavior, 20*, 641-655.

Ellis, A. W., Miller, D., & Sin, G. (1983). Wernicke aphasia and normal language processing - a case study in cognitive neuropsychology. *Cognition, 15*(1-3), 111-144.

Elston, G. N., Benavides-Piccione, R., & DeFelipe, J. (2001). The pyramidal cell in cognition: a comparative study in human and monkey. *Journal of Neuroscience, 21*(17), RC163.

Evans, S., Kyong, J. S., Rosen, S., Golestani, N., Warren, J. E., McGettigan, C., . . . Scott, S. K. (2014). The pathways for intelligible speech: multivariate and univariate perspectives. *Cerebral Cortex, 24*(9), 2350-2361. doi:10.1093/cercor/bht083

Fairhall, S. L., & Caramazza, A. (2013). Brain regions that represent amodal conceptual knowledge. *Journal of Neuroscience, 33*(25), 10552-10558. doi:10.1523/JNEUROSCI.0051-13.2013

Federmeier, K. D. (2007). Thinking ahead: the role and roots of prediction in language comprehension. *Psychophysiology, 44*(4), 491-505. doi:10.1111/j.1469-8986.2007.00531.x

Federmeier, K. D., & Kutas, M. (1999). A rose by any other name: long-term memory structure and sentence processing. *Journal of Memory and Language, 41*, 469-495.

Federmeier, K. D., McLennan, D. B., De Ochoa, E., & Kutas, M. (2002). The impact of semantic memory organization and sentence context information on spoken language processing by younger and older adults: an ERP study. *Psychophysiology, 39*(2), 133-146. doi:10.1017/S0048577202001373

Feldman, L. B., Basnight-Brown, D., & Pastizzo, M. J. (2006). Semantic influences on morphological facilitation: Concreteness and family size. *The Mental Lexicon, 1*(1), 59-84.

Fischler, I., & Bloom, P. A. (1979). Automatic and attentional processes in the effects of sentence contexts on word recognition. *Journal of Verbal Learning & Verbal Behavior, 18*, 1-20.

Fischler, I., & Bloom, P. A. (1980). Rapid processing of the meaning of sentences. *Memory & Cognition, 8*(3), 216-225.

Fodor, J. A. (1983). *The modularity of mind.* Cambridge: MIT Press.

Fonteneau, E. (2013). Structural syntactic prediction measured with ELAN: evidence from ERPs. *Neuroscience Letters, 534*, 211-216. doi:10.1016/j.neulet.2012.11.055

Formisano, E., Kim, D. S., Di Salle, F., van de Moortele, P. F., Ugurbil, K., & Goebel, R. (2003). Mirror-symmetric tonotopic maps in human primary auditory cortex. *Neuron, 40*(4), 859-869.

Forster, K. I. (1979). Levels of processing and the structure of the language processor. In W. E. Cooper & E. Walker (Eds.), *Sentence processing: Psycholinguistic studies presented to Merrill Garrett* (pp. 27-85). Hillsdale, NJ: Erlbaum.

Foulke, E. (1968). Listening comprehension as a function of word rate. *Journal of Communications, 18*(3), 198-206.

Frauenfelder, U. H., & Peeters, G. (1998). Simulating the time course of spoken word recognition: An analysis of lexical competition in TRACE. In J. Grainger & A. M. Jacobs (Eds.), *Localist Connectionist Approaches to Human Cognition* (pp. 101-146). Mahwah: Erlbaum.

Frey, S., Campbell, J. S., Pike, G. B., & Petrides, M. (2008). Dissociating the human language pathways with high angular resolution diffusion fiber tractography. *Journal of Neuroscience, 28*(45), 11435-11444. doi:10.1523/JNEUROSCI.2388-08.2008

Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences, 6*(2), 78-84.

Friederici, A. D., Bahlmann, J., Heim, S., Schubotz, R. I., & Anwander, A. (2006). The brain differentiates human and non-human grammars: functional localization and structural connectivity. *Proceedings of the National Academy of Sciences, 103*(7), 2458-2463. doi:10.1073/pnas.0509389103

Friederici, A. D., Fiebach, C. J., Schlesewsky, M., Bornkessel, I. D., & von Cramon, D. Y. (2006). Processing linguistic complexity and grammaticality in the left frontal cortex. *Cerebral Cortex, 16*(12), 1709-1717. doi:10.1093/cercor/bhj106

Friederici, A. D., Meyer, M., & von Cramon, D. Y. (2000). Auditory language comprehension: an event-related fMRI study on the processing of syntactic and lexical information. *Brain and Language, 74*(2), 289-300. doi:10.1006/brln.2000.2313

Friederici, A. D., Pfeifer, E., & Hahne, A. (1993). Event-related brain potentials during natural speech processing: effects of semantic, morphological and syntactic violations. *Cognitive Brain Research, 1*(3), 183-192.

Friederici, A. D., Rüschemeyer, S. A., Hahne, A., & Fiebach, C. J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: localizing syntactic and semantic processes. *Cerebral Cortex, 13*(2), 170-177.

Friederici, A. D., Steinhauer, K., & Frisch, S. (1999). Lexical integration: sequential effects of syntactic and semantic information. *Memory & Cognition, 27*(3), 438-453.

Friederici, A. D., Wang, Y., Herrmann, C. S., Maess, B., & Oertel, U. (2000). Localization of early syntactic processes in frontal and temporal cortical areas: a magnetoencephalographic study. *Human Brain Mapping, 11*(1), 1-11.

Friston, K. J. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences, 360*(1456), 815-836. doi:10.1098/rstb.2005.1622

Friston, K. J., Buechel, C., Fink, G. R., Morris, J., Rolls, E., & Dolan, R. J. (1997). Psychophysiological and modulatory interactions in neuroimaging. *Neuroimage, 6*(3), 218-229. doi:10.1006/nimg.1997.0291

Friston, K. J., Harrison, L., Daunizeau, J., Kiebel, S., Phillips, C., Trujillo-Barreto, N., . . . Mattout, J. (2008). Multiple sparse priors for the M/EEG inverse problem. *Neuroimage, 39*(3), 1104-1120. doi:10.1016/j.neuroimage.2007.09.048

Friston, K. J., Harrison, L., & Penny, W. (2003). Dynamic causal modelling. *Neuroimage, 19*(4), 1273-1302.

Gabrieli, J. D., Poldrack, R. A., & Desmond, J. E. (1998). The role of left prefrontal cortex in language and memory. *Proceedings of the National Academy of Sciences, 95*(3), 906-913.

Gagné, C. L. (2001). Relation and lexical priming during the interpretation of noun-noun combinations. *Journal of Experimental Psychology: Learning, Memory and Cognition, 27*(1), 236-254.

Ganong, W. F. (1980). Phonetic categorization in auditory word perception. *Journal of Experimental Psychology: Human Perception and Performance, 6*(1), 110-125.

Gaskell, M. G., & Marslen-Wilson, W. D. (1995). *Modelling the perception of spoken words.* Paper presented at the 17th Annual Conference of the Cognitive Science Society.

Gaskell, M. G., & Marslen-Wilson, W. D. (1997a). Integrating form and meaning: a distributed model of speech perception. *Language and Cognitive Processes, 12*, 613-656.

Gaskell, M. G., & Marslen-Wilson, W. D. (1997b). Discriminating local and distributed models of competition in spoken word recognition. In M. G. Shafto & P. Langley (Eds.), *Proceedings of the 19th Annual Conference of the Cognitive Science Society* (pp. 247-252). Mahwah: Erlbaum.

Gaskell, M. G., & Marslen-Wilson, W. D. (1999). Ambiguity, competition, and blending in spoken word recognition. *Cognitive Science, 23*, 439-462.

Gaskell, M. G., & Marslen-Wilson, W. D. (2002). Representation and competition in the perception of spoken words. *Cognitive Psychology, 45*(2), 220-266.

Ghaderi, F., Kim, S. K., & Kirchner, E. A. (2014). Effects of eye artifact removal methods on single trial P300 detection, a comparative study. *Journal of Neuroscience Methods, 221*, 41-47. doi:10.1016/j.jneumeth.2013.08.025

Giraud, A. L., Kleinschmidt, A., Poeppel, D., Lund, T. E., Frackowiak, R. S., & Laufs, H. (2007). Endogenous cortical rhythms determine cerebral specialization for speech perception and production. *Neuron, 56*(6), 1127-1134. doi:10.1016/j.neuron.2007.09.038

Giraud, A. L., & Poeppel, D. (2012). Cortical oscillations and speech processing: emerging computational principles and operations. *Nature Neuroscience, 15*(4), 511-517. doi:10.1038/nn.3063

Giraud, A. L., & Price, C. J. (2001). The constraints functional neuroimaging places on classical models of auditory word processing. *Journal of Cognitive Neuroscience, 13*(6), 754-765. doi:10.1162/08989290152541421

Gold, B. T., Balota, D. A., Jones, S. J., Powell, D. K., Smith, C. D., & Andersen, A. H. (2006). Dissociation of automatic and strategic lexical-semantics: functional magnetic resonance imaging evidence for differing roles of multiple frontotemporal regions. *Journal of Neuroscience, 26*(24), 6523-6532. doi:10.1523/JNEUROSCI.0808-06.2006

Gold, B. T., Balota, D. A., Kirchhoff, B. A., & Buckner, R. L. (2005). Common and dissociable activation patterns associated with controlled semantic and phonological processing: evidence from FMRI adaptation. *Cerebral Cortex, 15*(9), 1438-1450. doi:10.1093/cercor/bhi024

Gold, B. T., & Buckner, R. L. (2002). Common prefrontal regions coactivate with dissociable posterior regions during controlled semantic and phonological tasks. *Neuron, 35*(4), 803-812.

Goodglass, H. (1992). Diagnosis of conduction aphasia. In S. E. Kohn (Ed.), *Conduction aphasia* (pp. 39-50). Hillsdale, NJ: Lawrence Erlbaum Ass.

Goodglass, H., Kaplan, E., & Barresi, B. (1998). Innovations in aphasia testing: Preview of the new BDAE. *Brain and Language, 65*(1), 27-30.

Gorno-Tempini, M. L., Dronkers, N. F., Rankin, K. P., Ogar, J. M., Phengrasamy, L., Rosen, H. J., . . . Miller, B. L. (2004). Cognition and anatomy in three variants of primary progressive aphasia. *Ann Neurol, 55*(3), 335-346. doi:10.1002/ana.10825

Gow, D. W. (2012). The cortical organization of lexical knowledge: a dual lexicon model of spoken language processing. *Brain and Language, 121*(3), 273-288. doi:10.1016/j.bandl.2012.03.005

Graves, W. W., Binder, J. R., Desai, R. H., Conant, L. L., & Seidenberg, M. S. (2010). Neural correlates of implicit and explicit combinatorial semantic processing. *Neuroimage, 53*(2), 638-646. doi:10.1016/j.neuroimage.2010.06.055

Greenberg, D. L., Rice, H. J., Cooper, J. J., Cabeza, R., Rubin, D. C., & Labar, K. S. (2005). Co-activation of the amygdala, hippocampus and inferior frontal gyrus during autobiographical memory retrieval. *Neuropsychologia, 43*(5), 659-674. doi:10.1016/j.neuropsychologia.2004.09.002

Grewe, T., Bornkessel, I., Zysset, S., Wiese, R., von Cramon, D. Y., & Schlesewsky, M. (2005). The emergence of the unmarked: a new perspective on the language-specific function of Broca's area. *Human Brain Mapping, 26*(3), 178-190. doi:10.1002/hbm.20154

Griffiths, J. D., Marslen-Wilson, W. D., Stamatakis, E. A., & Tyler, L. K. (2013). Functional organization of the neural language system: dorsal and ventral pathways are critical for syntax. *Cerebral Cortex, 23*(1), 139-147. doi:10.1093/cercor/bhr386

Grindrod, C. M., Bilenko, N. Y., Myers, E. B., & Blumstein, S. E. (2008). The role of the left inferior frontal gyrus in implicit semantic competition and selection: An event-related fMRI study. *Brain Research, 1229*, 167-178.

Grodzinsky, Y., Piñango, M. M., Zurif, E., & Drai, D. (1999). The critical role of group studies in neuropsychology: comprehension regularities in Broca's aphasia. *Brain and Language, 67*(2), 134-147. doi:10.1006/brln.1999.2050

Grosjean, F. (1980). Spoken word recognition processes and the gating paradigm. *Perception & Psychophysics, 28*(4), 267-283.

Gross, J., Schmitz, F., Schnitzler, I., Kessler, K., Shapiro, K., Hommel, B., & Schnitzler, A. (2006). Anticipatory control of long-range phase synchronization. *European Journal of Neuroscience, 24*(7), 2057-2060. doi:10.1111/j.1460-9568.2006.05082.x

Gunter, T. C., Friederici, A. D., & Schriefers, H. (2000). Syntactic gender and semantic expectancy: ERPs reveal early autonomy and late interaction. *Journal of Cognitive Neuroscience, 12*(4), 556-568.

Gunter, T. C., Stowe, L. A., & Mulder, G. (1997). When syntax meets semantics. *Psychophysiology, 34*(6), 660-676.

Gutschalk, A., Patterson, R. D., Rupp, A., Uppenkamp, S., & Scherg, M. (2002). Sustained magnetic fields reveal separate sites for sound level and temporal regularity in human auditory cortex. *Neuroimage, 15*(1), 207-216. doi:10.1006/nimg.2001.0949

Hagoort, P. (2005). On Broca, brain, and binding: a new framework. *Trends in Cognitive Sciences, 9*(9), 416-423.

Hagoort, P. (2008). The fractionation of spoken language understanding by measuring electrical and magnetic brain signals. *Philosophical Transaction of the Royal Society of London Series B Biological Sciences, 363*(1493), 1055-1069. doi:10.1098/rstb.2007.2159

Hagoort, P., Baggio, G., & Willems, R. M. (2009). Semantic unification. In M. S. Gazzaniga (Ed.), *The Cognitive Neurosciences* (4th ed., pp. 819-836). Chicago: MIT Press.

Hagoort, P., Brown, C., & Groothusen, J. (1993). The syntactic positive shift (SPS) as an ERP measure of syntactic processing. *Language and Cognitive Processes, 8*, 439-483.

Hagoort, P., & Brown, C. M. (1994). Brain responses to lexical ambiguity resolution and parsing. In C. Clifton, L. Frazier, & K. Rayner (Eds.), *Perspectives on sentence processing* (pp. 45-80). Hillsdale, NJ: Erlbaum.

Hagoort, P., Wassenaar, M., & Brown, C. M. (2003). Syntax-related ERP-effects in Dutch. *Cognitive Brain Research, 16*(1), 38-50.

Hahne, A., & Friederici, A. D. (1999). Electrophysiological evidence for two steps in syntactic analysis. Early automatic and late controlled processes. *Journal of Cognitive Neuroscience, 11*(2), 194-205.

Halgren, E., Dhond, R. P., Christensen, N., Van Petten, C., Marinkovic, K., Lewine, J. D., & Dale, A. M. (2002). N400-like magnetoencephalography responses modulated by semantic context, word frequency, and lexical class in sentences. *Neuroimage, 17*(3), 1101-1116.

Ham, T., Leff, A., de Boissezon, X., Joffe, A., & Sharp, D. J. (2013). Cognitive control and the salience network: an investigation of error processing and effective connectivity. *Journal of Neuroscience, 33*(16), 7091-7098. doi:10.1523/JNEUROSCI.4692-12.2013

Hampshire, A., & Sharp, D. J. (2015). Contrasting network and modular perspectives on inhibitory control. *Trends in Cognitive Sciences, 19*(8), 445-452. doi:10.1016/j.tics.2015.06.006

Hanslmayr, S., Staudigl, T., & Fellner, M. C. (2012). Oscillatory power decreases and long-term memory: the information via desynchronization hypothesis. *Frontiers in Human Neuroscience, 6*, 74. doi:10.3389/fnhum.2012.00074

Hart, J., & Gordon, B. (1990). Delineation of single-word semantic comprehension deficits in aphasia, with anatomical correlation. *Annals of Neurology, 27*(3), 226-231. doi:10.1002/ana.410270303

Helenius, P., Salmelin, R., Service, E., Connolly, J. F., Leinonen, S., & Lyytinen, H. (2002). Cortical activation during spoken-word segmentation in nonreading-impaired and dyslexic adults. *Journal of Neuroscience, 22*(7), 2936-2944. doi:20026244

Henson, R. N., Burgess, N., & Frith, C. D. (2000). Recoding, storage, rehearsal and grouping in verbal short-term memory: an fMRI study. *Neuropsychologia, 38*(4), 426-440.

Hickok, G., Buchsbaum, B., Humphries, C., & Muftuler, T. (2003). Auditory-motor interaction revealed by fMRI: speech, music, and working memory in area Spt. *Journal of Cognitive Neuroscience, 15*(5), 673-682. doi:10.1162/089892903322307393

Hickok, G., & Poeppel, D. (2000). Towards a functional neuroanatomy of speech perception. *Trends in Cognitive Sciences, 4*(4), 131-138.

Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. *Cognition, 92*(1-2), 67-99. doi:10.1016/j.cognition.2003.10.011

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience, 8*(5), 393-402.

Hillebrand, A., Singh, K. D., Holliday, I. E., Furlong, P. L., & Barnes, G. R. (2005). A new approach to neuroimaging with magnetoencephalography. *Human Brain Mapping, 25*(2), 199-211. doi:10.1002/hbm.20102

Himberg, J., Hyvärinen, A., & Esposito, F. (2004). Validating the independent components of neuroimaging time series via clustering and visualization. *Neuroimage, 22*(3), 1214-1222. doi:10.1016/j.neuroimage.2004.03.027

Hodges, J. R., Graham, N., & Patterson, K. (1995). Charting the progression in semantic dementia: implications for the organisation of semantic memory. *Memory, 3*(3-4), 463-495. doi:10.1080/09658219508253161

Holcomb, P. J., & Neville, H. J. (1990). Auditory and visual semantic priming in lexical decision: a comparison using event-related brain potentials. *Language and Cognitive Processes, 5*, 281-312.

Hon, N., Epstein, R. A., Owen, A. M., & Duncan, J. (2006). Frontoparietal activity with minimal decision and control. *Journal of Neuroscience, 26*(38), 9805-9809. doi:10.1523/JNEUROSCI.3165-06.2006

Howard, D., Patterson, K., Wise, R., Brown, W. D., Friston, K. J., Weiller, C., & Frackowiak, R. (1992). The cortical localization of the lexicons. Positron emission tomography evidence. *Brain, 115 (Pt 6)*, 1769-1782.

Huang, R. S., Jung, T. P., & Makeig, S. (2007). *Event-related brain dynamics in continuous sustained-attention tasks.* Paper presented at the 3rd International Conference on Foundations of Augmented Cognition.

Humphries, C., Binder, J. R., Medler, D. A., & Liebenthal, E. (2006). Syntactic and semantic modulation of neural activity during auditory sentence comprehension. *Journal of Cognitive Neuroscience, 18*(4), 665-679. doi:10.1162/jocn.2006.18.4.665

Humphries, C., Love, T., Swinney, D., & Hickok, G. (2005). Response of anterior temporal cortex to syntactic and prosodic manipulations during sentence processing. *Human Brain Mapping, 26*(2), 128-138. doi:10.1002/hbm.20148

Humphries, C., Willard, K., Buchsbaum, B., & Hickok, G. (2001). Role of anterior temporal cortex in auditory sentence comprehension: an fMRI study. *Neuroreport, 12*(8), 1749-1752.

Hyvarinen, A., Karhunen, J., & Oja, E. (2001). *Independent component analysis* (Vol. 46). New York: John Wiley & Sons.

Hyvarinen, A., & Oja, E. (1997). A fast fixed-point algorithm for independent component analysis. *Neural Computation, 9*, 1483-1492.

Hyvärinen, A., & Oja, E. (2000). Independent component analysis: algorithms and applications. *Neural Networks, 13*(4-5), 411-430.

Hyvärinen, A., Ramkumar, P., Parkkonen, L., & Hari, R. (2010). Independent component analysis of short-time Fourier transforms for spontaneous EEG/MEG analysis. *Neuroimage, 49*(1), 257-271. doi:10.1016/j.neuroimage.2009.08.028

Indefrey, P., & Levelt, W. J. (2004). The spatial and temporal signatures of word production components. *Cognition, 92*(1-2), 101-144.

Jacobs, B., Schall, M., Prather, M., Kapler, E., Driscoll, L., Baca, S., . . . Treml, M. (2001). Regional dendritic and spine variation in human cerebral cortex: a quantitative golgi study. *Cerebral Cortex, 11*(6), 558-571.

Janse, E. (2006). Lexical competition effects in aphasia: deactivation of lexical candidates in spoken word processing. *Brain and Language, 97*(1), 1-11. doi:10.1016/j.bandl.2005.06.011

Jessen, S., & Kotz, S. A. (2013). On the role of crossmodal prediction in audiovisual emotion perception. *Frontiers in Human Neuroscience, 7*, 369. doi:10.3389/fnhum.2013.00369

Jilka, S. R., Scott, G., Ham, T., Pickering, A., Bonnelle, V., Braga, R. M., . . . Sharp, D. J. (2014). Damage to the Salience Network and interactions with the Default Mode Network. *Journal of Neuroscience, 34*(33), 10798-10807. doi:10.1523/JNEUROSCI.0518-14.2014

Johnsrude, I. S., Mackey, A., Hakyemez, H., Alexander, E., Trang, H. P., & Carlyon, R. P. (2013). Swinging at a cocktail party: voice familiarity aids speech perception in the presence of a competing voice. *Psychological Science, 24*(10), 1995-2004. doi:10.1177/0956797613482467

Jones, J., & Dinolt, R. (1952). Pure word deafness. *The Laryngoscope, 62*, 194-203.

Jordan, T. R., & Thomas, S. M. (2002). In search of perceptual influences of sentence context on word recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 28*(1), 34-45.

Jung, T. P., Humphries, C., Lee, T. W., Makeig, S., McKeown, M. J., Iragui, V., & Sejnowski, T. J. (1998). Extended ICA removes artifacts from electroencephalographic recordings. *Advanced in Neural Information Processing Systems, 10*, 894-900.

Kamide, Y. (2008). Anticipatory processes in sentence processing. *Language and Linguistics Compass, 2*, 647-670.

Kamide, Y., Altmann, G. T. M., & Haywood, S. L. (2003). The time course of prediction in incremental sentence processing: Evidence from anticipatory eye movements. *Journal of Memory and Language, 49*, 133-156.

Kanerva, P., Kristoferson, J., & Holst, A. (2000). *Random Indexing of text samples for latent semantic analysis.* Paper presented at the 22nd Annual Conference of the Cognitive Science Society, Mahwah, New Jersey.

Kang, A. M., Constable, R. T., Gore, J. C., & Avrutin, S. (1999). An event-related fMRI study of implicit phrase-level syntactic and semantic processing. *Neuroimage, 10*(5), 555-561. doi:10.1006/nimg.1999.0493

Keller, T. A., Carpenter, P. A., & Just, M. A. (2001). The neural bases of sentence comprehension: A fMRI examination of syntactic and lexical processing. *Cerebral Cortex, 11*, 223-237.

Kivisaari, S. L., Tyler, L. K., Monsch, A. U., & Taylor, K. I. (2012). Medial perirhinal cortex disambiguates confusable objects. *Brain, 135*(Pt 12), 3757-3769. doi:10.1093/brain/aws277

Koenig, P., & Grossman, M. (2007). Process and content in semantic memory. In J. J. Hart & M. A. Kraut (Eds.), *Neural basis of semantic memory* (pp. 247-264). Cambridge: Cambridge University Press.

Kotz, S. A., Cappa, S. F., von Cramon, D. Y., & Friederici, A. D. (2002). Modulation of the lexical-semantic network by auditory semantic priming: an event-related functional MRI study. *Neuroimage, 17*(4), 1761-1772.

Koziol, L. F., & Budding, D. E. (2009). Automaticity and higher-order control on communication: A brief introduction to language and social cognition. In *Subcortical Structures and Cognition* (pp. 167-186). New York: Springer.

Kriegeskorte, N., Mur, M., Ruff, D. A., Kiani, R., Bodurka, J., Esteky, H., . . . Bandettini, P. A. (2008). Matching categorical object representations in inferior temporal cortex of man and monkey. *Neuron, 60*(6), 1126-1141. doi:10.1016/j.neuron.2008.10.043

Kuperberg, G. R., & Jaeger, T. F. (2016). What do we mean by prediction in language comprehension? *Language, Cognition and Neuroscience, 31*(1), 32-59. doi:10.1080/23273798.2015.1102299

Kutas, M., & Federmeier, K. D. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences, 4*(12), 463-470.

Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology, 62*, 621-647. doi:10.1146/annurev.psych.093008.131123

Kutas, M., & Hillyard, S. A. (1980). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science, 207*, 203-205.

Kutas, M., & Hillyard, S. A. (1984). Brain potentials during reading reflect word expectancy and semantic association. *Nature, 307*(5947), 161-163.

Lambon Ralph, M. A., Sage, K., Jones, R. W., & Mayberry, E. J. (2010). Coherent concepts are computed in the anterior temporal lobes. *Proceedings of the National Academy of Sciences of the United States of America, 107*(6), 2717-2722.

Lau, E. F., Almeida, D., Hines, P. C., & Poeppel, D. (2009). A lexical basis for N400 context effects: evidence from MEG. *Brain and Language, 111*(3), 161-172. doi:10.1016/j.bandl.2009.08.007

Lau, E. F., Holcomb, P. J., & Kuperberg, G. R. (2013). Dissociating N400 effects of prediction from association in single-word contexts. *Journal of Cognitive Neuroscience, 25*(3), 484-502. doi:10.1162/jocn_a_00328

Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (de)constructing the N400. *Nature Reviews Neuroscience, 9*(12), 920-933. doi:10.1038/nrn2532

Lau, E. F., Weber, K., Gramfort, A., Hamalainen, M. S., & Kuperberg, G. R. (2014). Spatiotemporal signatures of lexical-semantic prediction. *Cerebral Cortex*, bhu219. Retrieved from

Leaver, A. M., & Rauschecker, J. P. (2010). Cortical representation of natural complex sounds: effects of acoustic features and auditory object category. *Journal of Neuroscience, 30*(22), 7604-7612. doi:10.1523/JNEUROSCI.0296-10.2010

Leff, A. P., Schofield, T. M., Crinion, J. T., Seghier, M. L., Grogan, A., Green, D. W., & Price, C. J. (2009). The left superior temporal gyrus is a shared substrate for auditory short-term memory and speech comprehension: evidence from 210 patients with stroke. *Brain, 132*(Pt 12), 3401-3410. doi:10.1093/brain/awp273

Leonard, M. K., Bouchard, K., & Chang, E. F. (2013). Human superior temporal gyrus encoding of speech sequence probabilities. *The Journal of the Acoustical Society of America, 134*(5), 4234-4234.

Leonard, M. K., & Chang, E. F. (2014). Dynamic speech representations in the human temporal lobe. *Trends in Cognitive Sciences, 18*(9), 472-479. doi:10.1016/j.tics.2014.05.001

Lerner, Y., Honey, C. J., Silbert, L. J., & Hasson, U. (2011). Topographic mapping of a hierarchy of temporal receptive windows using a narrated story. *Journal of Neuroscience, 31*(8), 2906-2915. doi:10.1523/JNEUROSCI.3684-10.2011

Levelt, W. J. (1983). Monitoring and self-repair in speech. *Cognition, 14*(1), 41-104.

Levelt, W. J. (1989). *Speaking: From intention to articulation*. Cambridge: MIT Press.

Lieberman, P. (1963). Some effects of semantic and grammatical context on the production and perception of speech. *Language and Speech, 6*, 172-187.

Lindsen, J. P., & Bhattacharya, J. (2010). Correction of blink artifacts using independent component analysis and empirical mode decomposition. *Psychophysiology, 47*(5), 955-960. doi:10.1111/j.1469-8986.2010.00995.x

Litvak, V., Mattout, J., Kiebel, S., Phillips, C., Henson, R., Kilner, J., . . . Friston, K. J. (2011). EEG and MEG data analysis in SPM8. *Computational Intelligence and Neuroscience, 2011*, 852961. doi:10.1155/2011/852961

Luce, P. A., & Cluff, M. S. (1998). Delayed commitment in spoken word recognition: evidence from cross-modal priming. *Perception & Psychophysics, 60*(3), 484-490.

Luckhoo, H., Hale, J. R., Stokes, M. G., Nobre, A. C., Morris, P. G., Brookes, M. J., & Woolrich, M. W. (2012). Inferring task-related networks using independent component analysis in magnetoencephalography. *Neuroimage, 62*(1), 530-541. doi:10.1016/j.neuroimage.2012.04.046

Luo, Y., Zhang, Y., Feng, X., & Zhou, X. (2010). Electroencephalogram oscillations differentiate semantic and prosodic processes during sentence reading. *Neuroscience, 169*(2), 654-664. doi:10.1016/j.neuroscience.2010.05.032

Luria, A. R. (1970). *Traumatic aphasia: its syndromes, psychology and treatment*. Hague, Netherlands: Mouton and Co. N. V.

Ma, S., Correa, N. M., Li, X. L., Eichele, T., Calhoun, V. D., & Adalı, T. (2011). Automatic identification of functional clusters in FMRI data using spatial dependence. *IEEE Transactions in Biomedical Engineering, 58*(12), 3406-3417. doi:10.1109/TBME.2011.2167149

MacDonald, M. C., Pearlmutter, N. J., & Seidenberg, M. S. (1994). The lexical nature of syntactic ambiguity resolution. *Psychological Reviews, 101*(4), 676-703.

MacGregor, L. J., Pulvermüller, F., van Casteren, M., & Shtyrov, Y. (2012). Ultra-rapid access to words in the brain. *Nature Communications, 3*, 711.

Magnuson, J. S., Strauss, T., & Harris, H. D. (2005). *Interaction in spoken word recognition models: Feedback helps.* Paper presented at the the Annual Meeting of the Cognitive Science Society.

Makeig, S., Jung, T. P., Bell, A. J., Ghahremani, D., & Sejnowski, T. J. (1997). Blind separation of auditory event-related brain responses into independent components. *Proceedings of the National Academy of Sciences of the United States of America, 94*(20), 10979-10984.

Marslen-Wilson, W. D. (1975). Sentence perception as an interactive parallel process. *Science, 189*(4198), 226-228. doi:10.1126/science.189.4198.226

Marslen-Wilson, W. D. (1984). Function and process in spoken word recognition - A tutorial review. *Attention and Performance, 10*, 125-150.

Marslen-Wilson, W. D. (1987). Functional parallelism in spoken word-recognition. *Cognition, 25*(1-2), 71-102.

Marslen-Wilson, W. D. (1990). Activation, competition and frequency in lexical access. In G. A. Altmann (Ed.), *Cognitive models of speech processing: Psycholinguistics and computational perspectives* (pp. 148-172). Cambridge, MA: MIT Press.

Marslen-Wilson, W. D., Moss, H. E., & van Halen, S. (1996). Perceptual distance and competition in lexical access. *Journal of Experimental Psychology: Human Perception & Performance, 22*(6), 1376-1392.

Marslen-Wilson, W. D., & Tyler, L. K. (1975). Processing structure of sentence perception. *Nature*, 784-786.

Marslen-Wilson, W. D., & Tyler, L. K. (1980). The temporal structure of spoken language understanding. *Cognition, 8*(1), 1-71.

Marslen-Wilson, W. D., & Warren, P. (1994). Levels of perceptual representation and process in lexical access: words, phonemes, and features. *Psychological Review, 101*(4), 653-675.

Marslen-Wilson, W. D., & Welsh, A. (1978). Processing interactions and lexical access during word recognition in continuous speech. *Cognitive Psychology, 10*, 29-63.

Marslen-Wilson, W. D., & Zwitserlood, P. (1989). Accessing spoken words - the importance of word onsets. *Journal of Experimental Psychology: Human Perception and Performance, 15*(3), 576-585.

Mason, R. A., Just, M. A., Keller, T. A., & Carpenter, P. A. (2003). Ambiguity in the brain: what brain imaging reveals about the processing of syntactically ambiguous sentences. *Journal of Experimental Psychology - Learning Memory and Cognition, 29*(6), 1319-1338. doi:10.1037/0278-7393.29.6.1319

Masson, M. E. (1995). A distributed memory model of semantic priming. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 21*(1), 3-23.

Matchin, W., Sprouse, J., & Hickok, G. (2014). A structural distance effect for backward anaphora in Broca's area: an fMRI study. *Brain and Language, 138*, 1-11. doi:10.1016/j.bandl.2014.09.001

Mazoyer, B. M., Tzourio, N., Frak, V., Syrota, A., Murayama, N., Levrier, O., . . . Mehler, J. (1993). The cortical representation of speech. *Journal of Cognitive Neuroscience, 5*(4), 467-479. doi:10.1162/jocn.1993.5.4.467

McClelland, J. L., & Elman, J. L. (1986). The TRACE model of speech perception. *Cognitive Psychology, 18*(1), 1-86.

McClelland, J. L., & O'Regan, J. K. (1981). Expectations increase the benefit derived from parafoveal visual information in reading words aloud. *Journal of Experimental Psychology: Human Perception & Performance, 7*, 634-644.

McDonald, S. A., & Shillcock, R. C. (2003). Eye movements reveal the on-line computation of lexical probabilities during reading. *Psychological Science, 14*(6), 648-652.

McGettigan, C., Faulkner, A., Altarelli, I., Obleser, J., Baverstock, H., & Scott, S. K. (2012). Speech comprehension aided by multiple modalities: behavioural and neural interactions. *Neuropsychologia, 50*(5), 762-776. doi:10.1016/j.neuropsychologia.2012.01.010

McKinnon, R., & Osterhout, L. (1996). Constraints on movement phenomena in sentence processing: Evidence from event-related brain potentials. *Language and Cognitive Processes, 11*, 495-523.

McNellis, M. G., & Blumstein, S. E. (2001). Self-organizing dynamics of lexical access in normals and aphasics. *Journal of Cognitive Neuroscience, 13*(2), 151-170.

McRae, K., Cree, G. S., Seidenberg, M. S., & McNorgan, C. (2005). Semantic feature production norms for a large set of living and nonliving things. *Behavior Reseach Methods, 37*(4), 547-559.

Menenti, L., Petersson, K. M., Scheeringa, R., & Hagoort, P. (2009). When elephants fly: differential sensitivity of right and left inferior frontal gyri to discourse and world knowledge. *Journal of Cognitive Neuroscience, 21*(12), 2358-2368. doi:10.1162/jocn.2008.21163

Mesgarani, N., Cheung, C., Johnson, K., & Chang, E. F. (2014). Phonetic feature encoding in human superior temporal gyrus. *Science, 343*(6174), 1006-1010.

Meunier, D., Stamatakis, E. A., & Tyler, L. K. (2014). Age-related functional reorganization, structural changes, and preserved cognition. *Neurobiology of Aging, 35*(1), 42-54. doi:10.1016/j.neurobiolaging.2013.07.003

Meyer, D. E., & Schvaneveldt, R. W. (1971). Facilitation in recognising pairs of words: Evidence of a dependence between retrieval operations. *Journal of Experimental Psychology, 90*, 227-235.

Meyer, M., Friederici, A. D., & von Cramon, D. Y. (2000). Neurocognition of auditory sentence comprehension: event related fMRI reveals sensitivity to syntactic violations and task demands. *Brain Research. Cognitive Brain Research, 9*(1), 19-33.

Meyer, M., Zysset, S., von Cramon, D. Y., & Alter, K. (2005). Distinct fMRI responses to laughter, speech, and sounds along the human peri-sylvian cortex. *Brain Research. Cognitive Brain Research, 24*(2), 291-306. doi:10.1016/j.cogbrainres.2005.02.008

Milberg, W., Blumstein, S., & Dworetsky, B. (1988b). Phonological processing and lexical access in aphasia. *Brain and Language, 34*, 279-293.

Miller, G. A. (1956). The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review, 63*, 81-97.

Miller, G. A., Heise, G. A., & Lichten, W. (1951). The intelligibility of speech as a function of the context of the test materials. *Journal of Experimental Psychology, 41*(5), 329-335.

Miniussi, C., Marzi, C. A., & Nobre, A. C. (2005). Modulation of brain activity by selective task sets observed using event-related potentials. *Neuropsychologia, 43*(10), 1514-1528. doi:10.1016/j.neuropsychologia.2004.12.014

Mirman, D., & Graziano, K. M. (2013). The neural basis of inhibitory effects of semantic and phonological neighbors in spoken word production. *Journal of Cognitive Neuroscience, 25*(9), 1504-1516. doi:10.1162/jocn_a_00408

Mirz, F., Ovesen, T., Ishizu, K., Johannsen, P., Madsen, S., Gjedde, A., & Pedersen, C. B. (1999). Stimulus-dependent central processing of auditory stimuli: a PET study. *Scandinavian Audiology, 28*(3), 161-169.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision - 2 cortical pathways. *Trends in Neuroscience, 6*(10), 414-417.

Misiurski, C., Blumstein, S. E., Rissman, J., & Berman, D. (2005). The role of lexical competition and acoustic-phonetic structure in lexical processing: evidence from normal subjects and aphasic patients. *Brain and Language, 93*(1), 64-78. doi:10.1016/j.bandl.2004.08.001

Molinaro, N., Carreiras, M., & Duñabeitia, J. A. (2012). Semantic combinatorial processing of non-anomalous expressions. *Neuroimage, 59*(4), 3488-3501.

Molinaro, N., Monsalve, I., & Lizarazu, M. (2015). Is there a common oscillatory brain mechanism for producing and predicting language? *Language, Cognition and Neuroscience, 31*, 145-158.

Moro, A., Tettamanti, M., Perani, D., Donati, C., Cappa, S. F., & Fazio, F. (2001). Syntax and the brain: disentangling grammar by selective anomalies. *Neuroimage, 13*(1), 110-118. doi:10.1006/nimg.2000.0668

Moss, H. E., Abdallah, S., Fletcher, P., Bright, P., Pilgrim, L., Acres, K., & Tyler, L. K. (2005). Selecting among competing alternatives: selection and retrieval in the left inferior frontal gyrus. *Cerebral Cortex, 15*(11), 1723-1735. doi:10.1093/cercor/bhi049

Moss, H. E., McCormick, S. F., & Tyler, L. K. (1997). The time course of activation of semantic information during spoken word recognition. *Language and Cognitive Processes, 12*, 695-731.

Movellan, J. R., & McClelland, J. L. (2001). The Morton-Massaro law of information integration: implications for models of perception. *Psychological Review, 108*(1), 113-148.

Mummery, C. J., Patterson, K., Price, C. J., Ashburner, J., Frackowiak, R. S., & Hodges, J. R. (2000). A voxel-based morphometry study of semantic dementia: relationship between temporal lobe atrophy and semantic memory. *Ann Neurol, 47*(1), 36-45.

Murphy, G. L. (1990). Noun phrase interpretation and conceptual combination. *Journal of Memory and Language, 29*, 259-288.

Naanaten, R., & Picton, T. (1987). The N1 wave of the human electric and magnetic response to sound: a review and an analysis of the component structure. *Psychophysiology, 24*, 375-425.

Nahum, M., Nelken, I., & Ahissar, M. (2008). Low-level information and high-level perception: the case of speech in noise. *PLoS Biology, 6*(5), e126. doi:10.1371/journal.pbio.0060126

Newman, A. J., Pancheva, R., Ozawa, K., Neville, H. J., & Ullman, M. T. (2001). An event-related fMRI study of syntactic and semantic violations. *Journal of Psycholinguistic Research, 30*(3), 339-364.

Nichols, T., & Holmes, A. (2004). Nonparametric permutation tests for functional neuroimaging. In W. Penny (Ed.), *Human Brain Function* (2 ed., pp. 887-910). San Diego: Academic Press.

Noesselt, T., Shah, N. J., & Jäncke, L. (2003). Top-down and bottom-up modulation of language related areas--an fMRI study. *BMC Neuroscience, 4*, 13. doi:10.1186/1471-2202-4-13

Noonan, K. A., Jefferies, E., Visser, M., & Lambon Ralph, M. A. (2013). Going beyond inferior prefrontal involvement in semantic control: evidence for the additional contribution of dorsal angular gyrus and posterior middle temporal cortex. *Journal of Cognitive Neuroscience, 25*(11), 1824-1850. doi:10.1162/jocn_a_00442

Noppeney, U., Patterson, K., Tyler, L. K., Moss, H., Stamatakis, E. A., Bright, P., . . . Price, C. J. (2007). Temporal lobe lesions and semantic impairment: a comparison of herpes simplex virus encephalitis and semantic dementia. *Brain, 130*(Pt 4), 1138-1147. doi:10.1093/brain/awl344

Noppeney, U., Phillips, J., & Price, C. (2004). The neural areas that control the retrieval and selection of semantics. *Neuropsychologia, 42*(9), 1269-1280. doi:10.1016/j.neuropsychologia.2003.12.014

Norris, D. (1994). Shortlist: a connectionist model of continuous speech recognition. *Cognition, 52*, 189-234.

Norris, D., & McQueen, J. M. (2008). Shortlist B: a Bayesian model of continuous speech recognition. *Psychological Review, 115*(2), 357-395. doi:10.1037/0033-295X.115.2.357

Norris, D., McQueen, J. M., & Cutler, A. (2000). Merging information in speech recognition: feedback is never necessary. *Behavioral and Brain Sciences, 23*(3), 299-325; discussion 325-270.

Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2005). Cognitive control and parsing: reexamining the role of Broca's area in sentence comprehension. *Cognitive, Affective, & Behavioral Neuroscience, 5*(3), 263-281.

Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2010). Broca's area and language processing: Evidence for the cognitive control connection. *Language and Linguistics Compass, 4*, 906-924.

O'Reilly, J. X., Mesulam, M. M., & Nobre, A. C. (2008). The cerebellum predicts the timing of perceptual events. *Journal of Neuroscience, 28*(9), 2252-2260. doi:10.1523/JNEUROSCI.2742-07.2008

Obleser, J., & Kotz, S. A. (2010). Expectancy constraints in degraded speech modulate the language comprehension network. *Cerebral Cortex, 20*(3), 633-640. doi:10.1093/cercor/bhp128

Obleser, J., Wise, R. J., Dresner, M. A., & Scott, S. K. (2007). Functional integration across brain regions improves speech perception under adverse listening conditions. *Journal of Neuroscience, 27*(9), 2283-2289. doi:10.1523/JNEUROSCI.4663-06.2007

Ohta, S., Fukui, N., & Sakai, K. L. (2013). Syntactic computation in the human brain: the degree of merger as a key factor. *PLoS One, 8*(2), e56230. doi:10.1371/journal.pone.0056230

Oldfield, R. C. (1963). Individual vocabulary and semantic currency: A preliminary study. *British Journal of Social and Clinical Psychology, 2*, 122-130.

Olichney, J. M., Riggins, B. R., Hillert, D. G., Nowacki, R., Tecoma, E., Kutas, M., & Iragui, V. J. (2002). Reduced sensitivity of the N400 and late positive component to semantic congruity and word repetition in left temporal lobe epilepsy. *Clinical Electroencephalography, 33*(3), 111-118.

Osterhout, L. (1997). On the brain response to syntactic anomalies: manipulations of word position and word class reveal individual differences. *Brain and Language, 59*(3), 494-522. doi:10.1006/brln.1997.1793

Osterhout, L., & Holcomb, P. (1992). Event-related brain potentials elicited by syntactic anomaly. *Journal of Memory and Language, 31*, 785-806.

Osterhout, L., & Holcomb, P. J. (1995). Event-related brain potentials and language comprehension. In M. D. Rugg & M. G. H. Coles (Eds.), *Electrophysiology of mind: Event-related potentials and cognition* (pp. 171-215). Oxford: Oxford University Press.

Otten, M., & Van Berkum, J. J. (2007). What makes a discourse constraining? Comparing the effects of discourse message and scenario fit on the discourse-dependent N400 effect. *Brain Research, 1153*, 166-177. doi:10.1016/j.brainres.2007.03.058

Ozaki, T. J. (2011). Frontal-to-parietal top-down causal streams along the dorsal attention network exclusively mediate voluntary orienting of attention. *PLoS One, 6*(5), e20079. doi:10.1371/journal.pone.0020079

Paczynski, M., & Kuperberg, G. R. (2012). Multiple Influences of Semantic Memory on Sentence Processing: Distinct Effects of Semantic Relatedness on Violations of Real-World Event/State Knowledge and Animacy Selection Restrictions. *Journal of Memory and Language, 67*(4), 426-448. doi:10.1016/j.jml.2012.07.003

Palazova, M., Sommer, W., & Schacht, A. (2013). Interplay of emotional valence and concreteness in word processing: an event-related potential study with verbs. *Brain and Language, 125*(3), 264-271. doi:10.1016/j.bandl.2013.02.008

Pallier, C., Devauchelle, A. D., & Dehaene, S. (2011). Cortical representation of the constituent structure of sentences. *Proceedings of the National Academy of Science of the United States of America, 108*(6), 2522-2527. doi:10.1073/pnas.1018711108

Papoutsi, M., Stamatakis, E. A., Griffiths, J., Marslen-Wilson, W. D., & Tyler, L. K. (2011). Is left fronto-temporal connectivity essential for syntax? Effective connectivity, tractography and performance in left-hemisphere damaged patients. *Neuroimage, 58*(2), 656-664. doi:10.1016/j.neuroimage.2011.06.036

Pasley, B. N., & Knight, R. T. (2013). Decoding speech for understanding and treating aphasia. *Progress in Brain Research, 207*, 435-456. doi:10.1016/B978-0-444-63327-9.00018-7

Patel, A. D., & Balaban, E. (2001). Human pitch perception is reflected in the timing of stimulus-related cortical activity. *Nature Neuroscience, 4*(8), 839-844. doi:10.1038/90557

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience, 8*(12), 976-987.

Paulesu, E., Goldacre, B., Scifo, P., Cappa, S. F., Gilardi, M. C., Castiglioni, I., . . . Fazio, F. (1997). Functional heterogeneity of left inferior frontal cortex as revealed by fMRI. *Neuroreport, 8*(8), 2011-2017.

Peelle, J. E., & Davis, M. H. (2012). Neural Oscillations Carry Speech Rhythm through to Comprehension. *Frontiers in Psychology, 3*, 320. doi:10.3389/fpsyg.2012.00320

Peelle, J. E., McMillan, C., Moore, P., Grossman, M., & Wingfield, A. (2004). Dissociable patterns of brain activity during comprehension of rapid and syntactically complex speech: evidence from fMRI. *Brain and Language, 91*(3), 315-325. doi:10.1016/j.bandl.2004.05.007

Penny, W. D., Stephan, K. E., Daunizeau, J., Rosa, M. J., Friston, K. J., Schofield, T. M., & Leff, A. P. (2010). Comparing families of dynamic causal models. *PLoS Computational Biology, 6*(3), e1000709. doi:10.1371/journal.pcbi.1000709

Petersson, K. M., Forkstam, C., & Ingvar, M. (2004). Artificial syntactic violations activates Broca's region. *Cognitive Science, 28*, 383-407.

Petrides, M., & Pandya, D. N. (2009). Distinct parietal and temporal pathways to the homologues of Broca's area in the monkey. *PLoS Biology, 7*(8), e1000170. doi:10.1371/journal.pbio.1000170

Phillips, C. (2001). Levels of representation in the electrophysiology of speech perception. *Cognitive Science, 25*, 711-731.

Piai, V., Roelofs, A., Rommers, J., & Maris, E. (2015). Beta oscillations reflect memory and motor aspects of spoken word production. *Human Brain Mapping, 36*(7), 2767-2780. doi:10.1002/hbm.22806

Pisoni, D. B., & Sawusch, J. R. (1975). Some stages of processing in speech perception. In A. Cohen & S. G. Nooteboom (Eds.), *Structure and Process in Speech Perception* (pp. 16-35). Heidelberg: Springer.

Plaut, D. C., McClelland, J. L., Seidenberg, M. S., & Patterson, K. (1996). Understanding normal and impaired word learning: Computational principles in quasi-regular domains. *Psychological Review, 103*, 56-115.

Poeppel, D. (2001). Pure word deafness and the bilateral processing of the speech code. *Cognitive Science, 25*(5), 679-693.

Poeppel, D. (2003). The analysis of speech in different temporal integration windows: cerebral lateralization as 'asymmetric sampling in time'. *Speech Communication, 41*, 245-255.

Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage, 10*(1), 15-35. doi:10.1006/nimg.1999.0441

Prabhakaran, R., Blumstein, S. E., Myers, E. B., Hutchison, E., & Britton, B. (2006). An event-related fMRI investigation of phonological-lexical competition. *Neuropsychologia, 44*(12), 2209-2221. doi:10.1016/j.neuropsychologia.2006.05.025

Prather, P. A., Zurif, E., Love, T., & Brownell, H. (1997). Speed of lexical activation in nonfluent Broca's aphasia and fluent Wernicke's aphasia. *Brain and Language, 59*(3), 391-411. doi:10.1006/brln.1997.1751

Price, A. R., Bonner, M. F., Peelle, J. E., & Grossman, M. (2015). Converging evidence for the neuroanatomic basis of combinatorial semantics in the angular gyrus. *Journal of Neuroscience, 35*(7), 3276-3284. doi:10.1523/JNEUROSCI.3446-14.2015

Price, A. R., Peelle, J. E., Bonner, M. F., Grossman, M., & Hamilton, R. H. (2016). Causal Evidence for a Mechanism of Semantic Integration in the Angular Gyrus as Revealed by High-Definition Transcranial Direct Current Stimulation. *Journal of Neuroscience, 36*(13), 3829-3838. doi:10.1523/JNEUROSCI.3120-15.2016

Price, C. J. (2000). The anatomy of language: contributions from functional neuroimaging. *Journal of Anatomy, 197 Pt 3*, 335-359.

Price, C. J. (2010). The anatomy of language: a review of 100 fMRI studies published in 2009. *Annals of New York Academy of Sciences, 1191*, 62-88.

Price, C. J. (2012). A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *Neuroimage, 62*(2), 816-847.

Price, C. J., Wise, R., Ramsay, S., Friston, K. J., Howard, D., Patterson, K., & Frackowiak, R. (1992). Regional response differences within the human auditory cortex when listening to words. *Neuroscience Letters, 146*(2), 179-182.

Ptak, R., & Schnider, A. (2010). The dorsal attention network mediates orienting toward behaviorally relevant stimuli in spatial neglect. *Journal of Neuroscience, 30*(38), 12557-12565. doi:10.1523/JNEUROSCI.2722-10.2010

Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. (2005). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience, 17*(6), 884-892.

Raizada, R. D., & Poldrack, R. A. (2007). Selective amplification of stimulus differences during categorical processing of speech. *Neuron, 56*(4), 726-740. doi:10.1016/j.neuron.2007.11.001

Ramkumar, P., Parkkonen, L., & Hyvärinen, A. (2014). Group-level spatial independent component analysis of Fourier envelopes of resting-state MEG data. *Neuroimage, 86*, 480-491. doi:10.1016/j.neuroimage.2013.10.032

Randall, B., Moss, H. E., Rodd, J. M., Greer, M., & Tyler, L. K. (2004). Distinctiveness and correlation in conceptual structure: behavioral and computational studies. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 30*(2), 393-406. doi:10.1037/0278-7393.30.2.393

Rauschecker, J. P., & Scott, S. K. (2009). Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. *Nature Neuroscience, 12*(6), 718-724.

Rauschecker, J. P., & Tian, B. (2000). Mechanisms and streams for processing of "what" and "where" in auditory cortex. *Proceedings of the National Academy of Sciences of the United States of America, 97*(22), 11800-11806. doi:10.1073/pnas.97.22.11800

Revill, K. P., Aslin, R. N., Tanenhaus, M. K., & Bavelier, D. (2008). Neural correlates of partial lexical activation. *Proceedings of the National Academy of Sciences of the United States of America, 105*(35), 13111-13115.

Richardson, F. M., Seghier, M. L., Leff, A. P., Thomas, M. S., & Price, C. J. (2011). Multiple routes from occipital to temporal cortices during reading. *Journal of Neuroscience, 31*(22), 8239-8247. doi:10.1523/JNEUROSCI.6519-10.2011

Righi, G., Blumstein, S. E., Mertus, J., & Worden, M. S. (2010). Neural systems underlying lexical competition: an eye tracking and fMRI study. *Journal of Cognitive Neuroscience, 22*(2), 213-224. doi:10.1162/jocn.2009.21200

Rissman, J., Eliassen, J. C., & Blumstein, S. E. (2003). An event-related FMRI investigation of implicit semantic priming. *Journal of Cognitive Neuroscience, 15*(8), 1160-1175. doi:10.1162/089892903322598120

Rodd, J. M., Davis, M. H., & Johnsrude, I. S. (2005). The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. *Cerebral Cortex, 15*(8), 1261-1269. doi:10.1093/cercor/bhi009

Rodd, J. M., Longe, O. A., Randall, B., & Tyler, L. K. (2004). Syntactic and semantic processing of spoken sentences: an fMRI study of ambiguity. *Journal of Cognitive Neuroscience, 16*, C89.

Rodd, J. M., Longe, O. A., Randall, B., & Tyler, L. K. (2010). The functional organisation of the fronto-temporal language system: evidence from syntactic and semantic ambiguity. *Neuropsychologia, 48*(5), 1324-1335. doi:10.1016/j.neuropsychologia.2009.12.035

Rodd, J. M., Vitello, S., Woollams, A. M., & Adank, P. (2015). Localising semantic and syntactic processing in spoken and written language comprehension: an Activation Likelihood Estimation meta-analysis. *Brain and Language, 141*, 89-102. doi:10.1016/j.bandl.2014.11.012

Rolheiser, T., Stamatakis, E. A., & Tyler, L. K. (2011). Dynamic processing in the human language system: synergy between the arcuate fascicle and extreme capsule. *Journal of Neuroscience, 31*(47), 16949-16957. doi:10.1523/JNEUROSCI.2725-11.2011

Romanski, L. M., Bates, J. F., & Goldman-Rakic, P. S. (1999). Auditory belt and parabelt projections to the prefrontal cortex in the rhesus monkey. *Journal of Comparative Neurology, 403*(2), 141-157.

Rommers, J., Dickson, D. S., Norton, J. J., Wlotko, E. W., & Federmeier, K. D. (2016). Alpha and theta band dynamics related to sentential constraint and word expectancy. *Language, Cognition and Neuroscience*, 1-14.

Rösler, F., Pütz, P., Friederici, A., & Hahne, A. (1993). Event-related brain potentials while encountering semantic and syntactic constraint violations. *Journal of Cognitive Neuroscience, 5*(3), 345-362. doi:10.1162/jocn.1993.5.3.345

Sahin, N. T., Pinker, S., Cash, S. S., Schomer, D., & Halgren, E. (2009). Sequential processing of lexical, grammatical, and phonological information within Broca's area. *Science, 326*(5951), 445-449. doi:10.1126/science.1174481

Salmelin, R., & Kujala, J. (2006). Neural representation of language: activation versus long-range connectivity. *Trends in Cognitive Sciences, 10*(11), 519-525. doi:10.1016/j.tics.2006.09.007

Samuel, A. G. (1981). Phonemic restoration: Insights from a new methodology. *Journal of Experimental Psychology: General, 110*, 474-494.

Samuel, A. G. (1996). Does lexical information influence the perceptual restoration of phonemes? *Journal of Experimental Psychology: General, 125*(1), 28-51.

Sanders, L. D., & Neville, H. J. (2003). An ERP study of continuous speech processing. I. Segmentation, semantics, and syntax in native speakers. *Brain Research. Cognitive Brain Research, 15*(3), 228-240.

Saur, D., Kreher, B. W., Schnell, S., Kümmerer, D., Kellmeyer, P., Vry, M. S., . . . Weiller, C. (2008). Ventral and dorsal pathways for language. *Proceedings of the National Academy of Sciences of the United States of America, 105*(46), 18035-18040. doi:10.1073/pnas.0805234105

Schlesewsky, M., & Bornkessel, I. (2004). On incremental interpretation: degrees of meaning accessed during sentence comprehension. *Lingua, 114*, 1213-1234.

Schnur, T. T., Schwartz, M. F., Kimberg, D. Y., Hirshorn, E., Coslett, H. B., & Thompson-Schill, S. L. (2009). Localizing interference during naming: convergent neuroimaging and neuropsychological evidence for the function of Broca's area. *Proceedings of the National Academy of Sciences of the United States of America, 106*(1), 322-327. doi:10.1073/pnas.0805874106

Schwanenflugel, P. J., & Shoben, E. J. (1985). The influence of sentence constraint on the scope of facilitation for upcoming words. *Journal of Memory and Language, 24*, 232-252.

Schönwiesner, M., von Cramon, D. Y., & Rübsamen, R. (2002). Is it tonotopy after all? *Neuroimage, 17*(3), 1144-1161.

Scott, S. K., Blank, C. C., Rosen, S., & Wise, R. J. S. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain, 123*, 2400- 2406.

Scott, S. K., & Johnsrude, I. S. (2003). The neuroanatomical and functional organization of speech perception. *Trends in Neurosciences, 26*(2), 100-107. doi:10.1016/S0166-2236(02)00037-1

Scott, S. K., Rosen, S., Lang, H., & Wise, R. J. (2006). Neural correlates of intelligibility in speech investigated with noise vocoded speech--a positron emission tomography study. *Journal of the Acoustic Society of America, 120*(2), 1075-1083.

Segaert, K., Menenti, L., Weber, K., Petersson, K. M., & Hagoort, P. (2012). Shared syntax in language production and language comprehension--an FMRI study. *Cerebral Cortex, 22*(7), 1662-1670. doi:10.1093/cercor/bhr249

Seghier, M. L. (2013). The angular gyrus: multiple functions and multiple subdivisions. *Neuroscientist, 19*(1), 43-61.

Seghier, M. L., Fagan, E., & Price, C. J. (2010). Functional subdivisions in the left angular gyrus where the semantic system meets and diverges from the default network. *Journal of Neuroscience, 30*(50), 16809-16817. doi:10.1523/JNEUROSCI.3377-10.2010

Shafto, M. A., & Tyler, L. K. (2014). Language in the aging brain: the network dynamics of cognitive decline and preservation. *Science, 346*(6209), 583-587. doi:10.1126/science.1254404

Shannon, C. E. (1948). A mathematical theory of communication. *The Bell System Technical Journal, 27*, 379-423.

Shillcock, R. C. (1990). Lexical hypotheses in continuous speech. In G. Altmann (Ed.), *Cognitive Models of Speech Processing: Psycholinguistic and Computational Perspectives* (pp. 24-29). Cambridge: MIT Press.

Sliwinska, M. W., Khadilkar, M., Campbell-Ratcliffe, J., Quevenco, F., & Devlin, J. T. (2012). Early and sustained supramarginal gyrus contributions to phonological processing. *Frontiers in Psychology, 3*, 161. doi:10.3389/fpsyg.2012.00161

Snijders, T. M., Petersson, K. M., & Hagoort, P. (2010). Effective connectivity of cortical and subcortical regions during unification of sentence structure. *Neuroimage, 52*(4), 1633-1644. doi:10.1016/j.neuroimage.2010.05.035

Snijders, T. M., Vosse, T., Kempen, G., Van Berkum, J. J., Petersson, K. M., & Hagoort, P. (2009). Retrieval and unification of syntactic structure in sentence comprehension: an FMRI study using word-category ambiguity. *Cerebral Cortex, 19*(7), 1493-1503. doi:10.1093/cercor/bhn187

Stephan, K. E., Penny, W. D., Daunizeau, J., Moran, R. J., & Friston, K. J. (2009). Bayesian model selection for group studies. *Neuroimage, 46*(4), 1004-1017. doi:10.1016/j.neuroimage.2009.03.025

Strauss, T. J., Harris, H. D., & Magnuson, J. S. (2007). jTRACE: a reimplementation and extension of the TRACE model of speech perception and spoken word recognition. *Behavioral Research Methods, 39*(1), 19-30.

Strauß, A., Kotz, S. A., & Obleser, J. (2013). Narrowed expectancies under degraded speech: revisiting the N400. *Journal of Cognitive Neuroscience, 25*(8), 1383-1395. doi:10.1162/jocn_a_00389

Su, L., Fonteneau, E., Marslen-Wilson, W. D., & Kriegeskorte, N. (2012). *Spatiotemporal searchlight representational similarity analysis in EMEG source space.* Paper presented at the 2nd International Workshop on Pattern Recognition in Neuroimaging.

Su, L., Zulfiqar, I., Jamshed, F., Fonteneau, E., & Marslen-Wilson, W. (2014). Mapping tonotopic organization in human temporal cortex: representational similarity analysis in EMEG source space. *Frontiers in Neuroscience, 8*, 368. doi:10.3389/fnins.2014.00368

Szczepanski, S. M., Pinsk, M. A., Douglas, M. M., Kastner, S., & Saalmann, Y. B. (2013). Functional and structural architecture of the human dorsal frontoparietal attention network. *Proceedings of the National Academy of Sciences of the United States of America, 110*(39), 15806-15811. doi:10.1073/pnas.1313903110

Taft, M., & Hambly, G. (1986). Exploring the Cohort Model of spoken word recognition. *Cognition, 22*(3), 259-282.

Tavabi, K., Embick, D., & Roberts, T. P. (2011). Spectral-temporal analysis of cortical oscillations during lexical processing. *Neuroreport, 22*(10), 474-478. doi:10.1097/WNR.0b013e3283476b84

Taylor, K. I., Devereux, B. J., Acres, K., Randall, B., & Tyler, L. K. (2012). Contrasting effects of feature-based statistics on the categorisation and basic-level identification of visual objects. *Cognition, 122*(3), 363-374.

Taylor, K. I., Moss, H. E., & Tyler, L. K. (2007). The conceptual structure account: a cognitive model of semantic memory and its neural instantiation. In J. Hart & M. Kraut (Eds.), *The neural basis of semantic memory* (pp. 265-301). Cambridge: Cambridge University Press.

Tesink, C. M., Petersson, K. M., van Berkum, J. J., van den Brink, D., Buitelaar, J. K., & Hagoort, P. (2009). Unification of speaker and meaning in language comprehension: an FMRI study. *Journal of Cognitive Neuroscience, 21*(11), 2085-2099. doi:10.1162/jocn.2008.21161

Thompson, R., & Duncan, J. (2009). Attentional modulation of stimulus representation in human fronto-parietal cortex. *Neuroimage, 48*(2), 436-448. doi:10.1016/j.neuroimage.2009.06.066

Thompson-Schill, S. L. (2003). Neuroimaging studies of semantic memory: inferring "how" from "where". *Neuropsychologia, 41*(3), 280-292.

Thompson-Schill, S. L., Aguirre, G. K., D'Esposito, M., & Farah, M. J. (1999). A neural basis for category and modality specificity of semantic knowledge. *Neuropsychologia, 37*(6), 671-676.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proceedings of the National Academy of Sciences of the United States of America, 94*(26), 14792-14797.

Thothathiri, M., Kim, A., Trueswell, J. C., & Thompson-Schill, S. L. (2012). Parametric effects of syntactic-semantic conflict in Broca's area during sentence processing. *Brain and Language, 120*(3), 259-264. doi:10.1016/j.bandl.2011.12.004

Thwaites, A., Schlittenlacher, J., Nimmo-Smith, I., Marslen-Wilson, W. D., & Moore, B. C. (2016). Tonotopic representation of loudness in the human cortex. *Hearing Research*. doi:10.1016/j.heares.2016.11.015

Tramo, M. J., Shah, G. D., & Braida, L. D. (2002). Functional role of auditory cortex in frequency processing and pitch perception. *Journal of Neurophysiology, 87*(1), 122-139.

Traxler, M. J., & Foss, D. J. (2000). Effects of sentence constraint on priming in natural language comprehension. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26*(5), 1266-1282.

Turken, A. U., & Dronkers, N. F. (2011). The neural architecture of the language comprehension network: converging evidence from lesion and connectivity analyses. *Frontiers in Systems Neuroscience, 5*, 1. doi:10.3389/fnsys.2011.00001

Tyler, L. K. (1983). The development of discourse mapping processes: the on-line interpretation of anaphoric expressions. *Cognition, 13*(3), 309-341.

Tyler, L. K. (1984). The structure of the initial cohort: evidence from gating. *Perception & Psychophysics, 36*(5), 417-427.

Tyler, L. K., Bright, P., Fletcher, P., & Stamatakis, E. A. (2004). Neural processing of nouns and verbs: the role of inflectional morphology. *Neuropsychologia, 42*(4), 512-523.

Tyler, L. K., Cheung, T. P., Devereux, B. J., & Clarke, A. (2013). Syntactic computations in the language network: characterizing dynamic network properties using representational similarity analysis. *Frontiers in Psychology, 4*, 271. doi:10.3389/fpsyg.2013.00271

Tyler, L. K., Chiu, S., Zhuang, J., Randall, B., Devereux, B. J., Wright, P., . . . Taylor, K. I. (2013). Objects and categories: feature statistics and object processing in the ventral stream. *Journal of Cognitive Neuroscience, 25*(10), 1723-1735.

Tyler, L. K., & Marslen-Wilson, W. D. (1986). The effects of context on the recognition of polymorphemic words. *Journal of Memory and Language, 25*(6), 741-752.

Tyler, L. K., & Marslen-Wilson, W. D. (2008). Fronto-temporal brain systems supporting spoken language comprehension. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences, 363*(1493), 1037-1054. doi:10.1098/rstb.2007.2158

Tyler, L. K., Marslen-Wilson, W. D., Randall, B., Wright, P., Devereux, B. J., Zhuang, J., . . . Stamatakis, E. A. (2011). Left inferior frontal cortex and syntax: function, structure and behaviour in patients with left hemisphere damage. *Brain, 134*(Pt 2), 415-431. doi:10.1093/brain/awq369

Tyler, L. K., & Moss, H. E. (2001). Towards a distributed account of conceptual knowledge. *Trends in Cognitive Sciences, 5*(6), 244-252.

Tyler, L. K., Shafto, M. A., Randall, B., Wright, P., Marslen-Wilson, W. D., & Stamatakis, E. A. (2010). Preserving syntactic processing across the adult life span: the modulation of the frontotemporal language system in the context of age-related atrophy. *Cerebral Cortex, 20*(2), 352-364. doi:10.1093/cercor/bhp105

Tyler, L. K., & Wessels, J. (1983). Quantifying contextual contributions to word-recognition processes. *Perception & Psychophysics, 34*(5), 409-420.

Tyler, L. K., & Wessels, J. (1985). Is gating an on-line task? Evidence from naming latency data. *Perception & Psychophysics, 38*(3), 217-222.

Tyler, L. K., Wright, P., Randall, B., Marslen-Wilson, W. D., & Stamatakis, E. A. (2010). Reorganization of syntactic processing following left-hemisphere brain damage: does right-hemisphere activity preserve function? *Brain, 133*(11), 3396-3408. doi:10.1093/brain/awq262

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., . . . Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage, 15*(1), 273-289.

Uddén, J., & Bahlmann, J. (2012). A rostro-caudal gradient of structured sequence processing in the left inferior frontal gyrus. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences, 367*(1598), 2023-2032. doi:10.1098/rstb.2012.0009

Utman, J. A., Blumstein, S. E., & Sullivan, K. (2001). Mapping from sound to meaning: reduced lexical activation in Broca's aphasics. *Brain and Language, 79*(3), 444-472. doi:10.1006/brln.2001.2500

Uusvuori, J., Parviainen, T., Inkinen, M., & Salmelin, R. (2008). Spatiotemporal interaction between sound form and meaning during spoken word perception. *Cerebral Cortex, 18*(2), 456-466. doi:10.1093/cercor/bhm076

van Berkum, J. J., Brown, C. M., Hagoort, P., & Zwitserlood, P. (2003). Event-related brain potentials reflect discourse-referential ambiguity in spoken language comprehension. *Psychophysiology, 40*(2), 235-248.

van Berkum, J. J., Brown, C. M., Zwitserlood, P., Kooijman, V., & Hagoort, P. (2005). Anticipating upcoming words in discourse: evidence from ERPs and reading times. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 31*(3), 443-467. doi:10.1037/0278-7393.31.3.443

van Berkum, J. J., Hagoort, P., & Brown, C. M. (1999). Semantic integration in sentences and discourse: evidence from the N400. *Journal of Cognitive Neuroscience, 11*(6), 657-671.

van Leeuwen, T. M., Lamers, M. J., Petersson, K. M., Gussenhoven, C., Rietveld, T., Poser, B., & Hagoort, P. (2014). Phonological markers of information structure: an fMRI study. *Neuropsychologia, 58*, 64-74. doi:10.1016/j.neuropsychologia.2014.03.017

van Petten, C., Coulson, S., Rubin, S., Plante, E., & Parks, M. (1999). Time course of word identification and semantic integration in spoken language. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 25*, 394-417.

van Petten, C., & Kutas, M. (1990). Interactions between sentence context and word frequency in event-related brain potentials. *Memory and Cognition, 18*, 380-393.

Vandenberghe, R., Nobre, A. C., & Price, C. J. (2002). The response of left temporal cortex to sentences. *Journal of Cognitive Neuroscience, 14*(4), 550-560. doi:10.1162/08989290260045800

Vandenberghe, R., Price, C., Wise, R., Josephs, O., & Frackowiak, R. S. (1996). Functional anatomy of a common semantic system for words and pictures. *Nature, 383*(6597), 254-256.

Vaughan, H. G., & Ritter, W. (1970). The sources of auditory evoked responses recorded from the human scalp. *Electroencephalography and Clinical Neurophysiology, 28*, 360-367.

Vigneau, M., Beaucousin, V., Hervé, P. Y., Duffau, H., Crivello, F., Houdé, O., . . . Tzourio-Mazoyer, N. (2006). Meta-analyzing left hemisphere language areas: phonology, semantics, and sentence processing. *Neuroimage, 30*(4), 1414-1432.

Visser, M., Jefferies, E., Embleton, K. V., & Ralph, M. A. L. (2012). Both the middle temporal gyrus and the ventral anterior temporal area are crucial for multimodal semantic processing: distortion-corrected fMRI evidence for a double gradient of information convergence in the temporal lobes. *Journal of Cognitive Neuroscience, 24*(8), 1766-1778.

Wagner, A. D., Paré-Blagoev, E. J., Clark, J., & Poldrack, R. A. (2001). Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. *Neuron, 31*(2), 329-338.

Wagner, A. E., Toffanin, P., & Başkent, D. (2016). The timing and effort of lexical access in natural and degraded speech. *Frontiers in Psychology, 7*, 398. doi:10.3389/fpsyg.2016.00398

Wang, L., Jensen, O., van den Brink, D., Weder, N., Schoffelen, J. M., Magyari, L., . . . Bastiaansen, M. (2012). Beta oscillations relate to the N400m during language comprehension. *Human Brain Mapping, 33*(12), 2898-2912. doi:10.1002/hbm.21410

Wang, S., Zhu, Z., Zhang, J. X., Wang, Z., Xiao, Z., Xiang, H., & Chen, H. C. (2008). Broca's area plays a role in syntactic processing during Chinese reading comprehension. *Neuropsychologia, 46*(5), 1371-1378. doi:10.1016/j.neuropsychologia.2007.12.020

Warren, J. D., Uppenkamp, S., Patterson, R. D., & Griffiths, T. D. (2003). Separating pitch chroma and pitch height in the human brain. *Proceedings of the National Academy of Sciences of the United States of America, 100*(17), 10038-10042. doi:10.1073/pnas.1730682100

Warren, P., & Marslen-Wilson, W. D. (1987). Continuous uptake of acoustic cues in spoken word recognition. *Perception & Psychophysics, 41*(3), 262-275.

Warren, P., & Marslen-Wilson, W. D. (1988). Cues to lexical choice: discriminating place and voice. *Perception & Psychophysics, 43*(1), 21-30.

Warren, R. M., & Warren, R. P. (1970). Auditory illusions and confusions. *Scientific American, 223*, 30-36.

Warrington, E. K. (1975). The selective impairment of semantic memory. *Quarterly Journal of Experimental Psychology, 27*(4), 635-657. doi:10.1080/14640747508400525

Wei, T., Liang, X., He, Y., Zang, Y., Han, Z., Caramazza, A., & Bi, Y. (2012). Predicting conceptual processing capacity from spontaneous neuronal activity of the left middle temporal gyrus. *Journal of Neuroscience, 32*(2), 481-489. doi:10.1523/JNEUROSCI.1953-11.2012

Weissman, D. H., & Prado, J. (2012). Heightened activity in a key region of the ventral attention network is linked to reduced activity in a key region of the dorsal attention network during unexpected shifts of covert visual spatial attention. *Neuroimage, 61*(4), 798-804. doi:10.1016/j.neuroimage.2012.03.032

Wernicke, C. (1874). The aphasia syndrome complex: a psychological study on an anatomical basis. In G. H. Eggard (Ed.), *Wernicke's Works on Aphasia*. The Hague: Mouton.

West, R. F., & Stanovich, K. E. (1978). Automatic contextual facilitation in readers of three ages. *Child Development*, 717-727.

Westerlund, M., & Pylkkänen, L. (2014). The role of the left anterior temporal lobe in semantic composition vs. semantic memory. *Neuropsychologia, 57*, 59-70. doi:10.1016/j.neuropsychologia.2014.03.001

Whitney, C., Kirk, M., O'Sullivan, J., Lambon Ralph, M. A., & Jefferies, E. (2011). The neural organization of semantic control: TMS evidence for a distributed network in left inferior frontal and posterior middle temporal gyrus. *Cerebral Cortex, 21*(5), 1066-1075. doi:10.1093/cercor/bhq180

Wible, C. G., Han, S. D., Spencer, M. H., Kubicki, M., Niznikiewicz, M. H., Jolesz, F. A., . . . Nestor, P. (2006). Connectivity among semantic associates: an fMRI study of semantic priming. *Brain and Language, 97*(3), 294-305. doi:10.1016/j.bandl.2005.11.006

Wild, C. J., Davis, M. H., & Johnsrude, I. S. (2012). Human auditory cortex is sensitive to the perceived clarity of speech. *Neuroimage, 60*(2), 1490-1502. doi:10.1016/j.neuroimage.2012.01.035

Willems, R. M., Frank, S. L., Nijhof, A. D., Hagoort, P., & van den Bosch, A. (2016). Prediction During Natural Language Comprehension. *Cerebral Cortex, 26*(6), 2506-2516.

Wingfield, A., Aberdeen, J. S., & Stine, E. A. (1991). Word onset gating and linguistic context in spoken word recognition by young and elderly adults. *Journal of Gerontology, 46*(3), P127-129.

Wise, R. J., Hadar, U., Howard, D., & Patterson, K. (1991). Language activation studies with positron emission tomography. *Exploring Brain Functional Anatomy with Positron Tomography, 163*, 218.

Wise, R. J., Scott, S. K., Blank, S. C., Mummery, C. J., Murphy, K., & Warburton, E. A. (2001). Separate neural subsystems within 'Wernicke's area'. *Brain, 124*(Pt 1), 83-95.

Wisniewski, E. J., & Love, B. C. (1998). Relations versus properties in conceptual combination. *Journal of Memory and Language, 38*, 177-202.

Woodhead, Z. V., Barnes, G. R., Penny, W., Moran, R., Teki, S., Price, C. J., & Leff, A. P. (2014). Reading front to back: MEG evidence for early feedback effects during word recognition. *Cerebral Cortex, 24*(3), 817-825. doi:10.1093/cercor/bhs365

Wright, P., Randall, B., Clarke, A., & Tyler, L. K. (2015). The perirhinal cortex and conceptual processing: Effects of feature-based statistics following damage to the anterior temporal lobes. *Neuropsychologia, 76*, 192-207. doi:10.1016/j.neuropsychologia.2015.01.041

Wright, P., Randall, B., Marslen-Wilson, W. D., & Tyler, L. K. (2011). Dissociating linguistic and task-related activity in the left inferior frontal gyrus. *Journal of Cognitive Neuroscience, 23*(2), 404-413. doi:10.1162/jocn.2010.21450

Wright, P., Stamatakis, E. A., & Tyler, L. K. (2012). Differentiating hemispheric contributions to syntax and semantics in patients with left-hemisphere lesions. *Journal of Neuroscience, 32*(24), 8149-8157. doi:10.1523/JNEUROSCI.0485-12.2012

Xiang, H. D., Fonteijn, H. M., Norris, D. G., & Hagoort, P. (2010). Topographical functional connectivity pattern in the perisylvian language networks. *Cerebral Cortex, 20*(3), 549-560. doi:10.1093/cercor/bhp119

Yee, E., Blumstein, S. E., & Sedivy, J. C. (2008). Lexical-semantic activation in Broca's and Wernicke's aphasia: evidence from eye movements. *Journal of Cognitive Neuroscience, 20*(4), 592-612. doi:10.1162/jocn.2008.20056

Zaehle, T., Wüstenberg, T., Meyer, M., & Jäncke, L. (2004). Evidence for rapid auditory perception as the foundation of speech processing: a sparse temporal sampling fMRI study. *European Journal of Neuroscience, 20*(9), 2447-2456. doi:10.1111/j.1460-9568.2004.03687.x

Zatorre, R. J., & Belin, P. (2005). Auditory cortex processing streams: Where are they and what do they do? *Plasticity and Signal Representation in the Auditory System*, 277-290.

Zhu, Z., Hagoort, P., Zhang, J. X., Feng, G., Chen, H. C., Bastiaansen, M., & Wang, S. (2012). The anterior left inferior frontal gyrus contributes to semantic unification. *Neuroimage, 60*(4), 2230-2237. doi:10.1016/j.neuroimage.2012.02.036

Zhuang, J., Randall, B., Stamatakis, E. A., Marslen-Wilson, W. D., & Tyler, L. K. (2011). The interaction of lexical semantics and cohort competition in spoken word recognition: an fMRI study. *Journal of Cognitive Neuroscience, 23*(12), 3778-3790. doi:10.1162/jocn_a_00046

Zhuang, J., Tyler, L. K., Randall, B., Stamatakis, E. A., & Marslen-Wilson, W. D. (2014). Optimally efficient neural systems for processing spoken language. *Cerebral Cortex, 24*(4), 908-918.

Zwitserlood, P. (1989). The locus of the effects of sentential-semantic context in spoken-word processing. *Cognition, 32*(1), 25-64.

APPENDICES

APPENDIX A – THE LIST OF STIMULI USED IN EXPERIMENT 1

WORDS					NONWORDS
aeroplane	chisel	harpoon	pumpkin	telephone	alligus
alligator	cigarette	hawk	pyramid	tent	blacktrich
ambulance	clam	helicopter	rabbit	thermometer	carpikupe
anchor	clamp	helmet	radish	tiger	chay
apple	clarinet	hook	raft	tights	chickle
apron	cloak	horse	raisin	toad	chissor
armour	clock	housefly	rake	toaster	chow
avocado	coat	jacket	rat	toilet	dute
bag	cockerel	jeep	rattle	tomato	gazoolla
bagpipes	cockroach	kettle	rattlesnake	tongs	grasserine
balloon	coconut	knife	raven	tortoise	grattle
banana	cod	lamb	razor	tractor	honeyfut
barrel	coin	lamp	revolver	train	jarlif
basket	comb	lemon	rhubarb	tripod	jarpet
bath	cork	leopard	rice	trombone	jeye
beans	corkscrew	leotard	robin	trousers	kidge
beaver	courgette	lettuce	rock	trout	meecumber
bed	cow	lime	rope	trumpet	muckets
beetle	crab	lion	salmon	tuna	plaimp
belt	crocodile	lobster	sandals	turkey	plut
bench	crowbar	lorry	sandpaper	turnip	pumple
bike	cucumber	machete	sardine	turtle	pyther
bin	cup	mackerel	saxophone	typewriter	rashwerry
birch	cupboard	marble	scarf	umbrella	rayber
biscuit	curtains	menu	screwdriver	unicycle	remmob
blender	cushion	microwave	seagull	veil	rutterflake
blouse	dagger	mirror	seashell	violin	tomula
blueberry	dandelion	mittens	seaweed	walrus	ugualla
boat	dishwasher	moth	sellotape	wand	vess
bomb	dog	motorcycle	shawl	wasp	wols

book
boots
bottle
bowl
box
bracelet
bread
brick
broom
bucket
buckle
budgie
buffalo
bullet
butterfly
buzzard
cabbage
camel
candle
carpet
carrot
cart
cat
caterpillar
cauliflower
celery
certificate
chain
chair
chandelier
cheese
cherry
chicken
chipmunk
doll
dolphin
donkey
doorknob
dove
dress
drum
eagle
earmuffs
eel
elephant
envelope
falcon
fence
flute
fox
frog
garlic
gate
giraffe
gloves
goat
goldfish
goose
gown
grape
grapefruit
grasshopper
guitar
gun
hammer
hamster
harmonica
harp
mouse
mushroom
napkin
necklace
nectarine
nightingale
oak
octopus
olive
onions
otter
panther
partridge
peach
peacock
peg
pelican
pencil
penguin
piano
pie
pig
pigeon
pillow
pine
pineapple
pistol
platypus
pliers
porcupine
potato
pram
projector
prune
sheep
ship
shirt
shotgun
shovel
skateboard
skirt
skis
sledge
slippers
snail
socks
sofa
spanner
sparrow
spatula
spear
spider
spinach
spoon
squid
squirrel
starling
stick
stone
strawberry
submarine
surfboard
swan
sweater
sword
table
tangerine
taxi
wheel
wheelbarrow
whip
whistle
willow
woodpecker
worm
yacht
zebra

APPENDIX B – THE LIST OF STIMULI USED IN EXPERIMENT 2

Weak-C phrases	**Strong-C phrases**	**No-C phrases**
commercial aeroplane	crashed aeroplane	tsunami aeroplane
local ambulance	paramedic ambulance	sore ambulance
delicious apple	toffee apple	line apple
purple apron	chef's apron	rhythmic apron
silver armour	knight's armour	metric armour
yellow banana	peeled banana	heat banana
black beans	coffee beans	legible beans
adult beetle	dung beetle	rugby beetle
narrow belt	seat belt	wordy belt
summer blouse	chiffon blouse	tenor blouse
wooden boat	rowing boat	archer boat
shining boots	cowboy boots	thistle boots
yellow broom	witch's broom	numb broom
wounded butterfly	fluttering butterfly	layer butterfly
boiled cabbage	Savoy cabbage	sister cabbage
motor caravan	gypsy caravan	conifer caravan
orange carrot	sliced carrot	height carrot
open cart	go cart	bandana cart
sitting cat	tabby cat	nettle cat
cold chicken	fried chicken	aftershave chicken
metal clamp	wheel clamp	June clamp
hooded cloak	winter cloak	zigzag cloak
shining coat	fur coat	noise coat
noisy cockerel	crowing cockerel	parallel cockerel
brown cow	dairy cow	willow cow
little crab	hermit crab	apparel crab
fresh cucumber	pickled cucumber	scholar cucumber
massive dog	stray dog	clog dog
friendly donkey	stubborn donkey	modem donkey
pretty dove	cooing dove	number dove
expensive dress	silk dress	seal dress
desert eagle	bald eagle	cross eagle

mother elephant	bull elephant	clipper elephant
male falcon	swooping falcon	bottom falcon
passenger ferry	floating ferry	pastor ferry
country fox	arctic fox	ache fox
fresh garlic	peeled garlic	letter garlic
assorted gloves	oven gloves	gas gloves
grey goose	Canada goose	steam goose
cotton gown	ball gown	buffer gown
heavy hammer	sledge hammer	suburb hammer
giant helicopter	hovering helicopter	crop helicopter
plastic helmet	cycling helmet	shuffle helmet
pregnant horse	galloping horse	begonia horse
water jacket	tweed jacket	gluten jacket
small knife	bread knife	brush knife
beautiful leopard	man-eating leopard	midday leopard
strong lion	roaring lion	vessel lion
long lorry	delivery lorry	actor lorry
adult mouse	house mouse	chiller mouse
planted oak	evergreen oak	substance oak
rotten onions	chopped onions	weekend onions
lost pig	suckling pig	oboe pig
tiny pigeon	homing pigeon	cord pigeon
prickly pine	evergreen pine	walk pine
American potato	baked potato	calendar potato
carved pumpkin	Halloween pumpkin	repair pumpkin
little rabbit	frightened rabbit	base rabbit
floating raft	log raft	gender raft
garden rake	hay rake	dining rake
dirty rat	lab rat	dribble rat
women's razor	cutthroat razor	opera razor
pink rhubarb	stewed rhubarb	click rhubarb
powerful rocket	fuelled rocket	waste rocket
open sandals	leather sandals	drunkard sandals
neck scarf	cashmere scarf	notebook scarf
silver scissors	nail scissors	foggy scissors
electric screwdriver	Phillips screwdriver	colouring screwdriver

light shawl	prayer shawl	burrow shawl
large ship	sinking ship	splatter ship
pale shirt	polo shirt	trail shirt
rusty shovel	snow shovel	writer shovel
shortened skirt	pleated skirt	voice skirt
house slippers	satin slippers	clutch slippers
clean socks	smelly socks	tune socks
baby sparrow	chirping sparrow	pump sparrow
broken spear	thrusting spear	shampoo spear
jumping spider	tarantula spider	dentist spider
British submarine	nuclear submarine	bottle submarine
quiet swan	migrating swan	instrument swan
hungry tiger	Bengal tiger	melody tiger
ugly toad	horned toad	segment toad
red tomato	cherry tomato	gaming tomato
noisy train	freight train	son train
striped trousers	corduroy trousers	fang trousers
female wasp	stinging wasp	lullaby wasp
filthy worm	wriggly worm	blank worm
white yacht	cruising yacht	transplant yacht

APPENDIX C - THE LIST OF STIMULI USED IN EXPERIMENT 3

Condition	**Spoken sentences**
SUB	After an accident *flashing signs* is an excellent way to get noticed
DOM	After an accident *flashing signs* are usually distracting
SUB	As a rule *provoking suggestions* are necessary for lively debate
DOM	As a rule *provoking suggestions* is what TV presenters try to do
SUB	At cocktail parties *charming ladies* is what single men like to do
DOM	At cocktail parties *charming ladies* are attractive to older men
SUB	At demonstrations *irritating policemen* is a dangerous thing
DOM	At demonstrations *irritating policemen* are a common sight
SUB	At first *managing assistants* is a rewarding task
DOM	At first *managing assistants* are useless without extensive training
SUB	At night *attacking strangers* are not to be approached
DOM	At night *attacking strangers* is common in the city
SUB	Captains know that *sinking submarines* is nearly impossible
DOM	Captains know that *sinking submarines* are heading down to the seabed
SUB	Early in summer *growing flowers* is a great pleasure
DOM	Early in summer *growing flowers* are weeded regularly
SUB	Early in the morning *clinking bottles* is inconsiderate to neighbours
DOM	Early in the morning *clinking bottles* are annoying to neighbours
SUB	Even today *conquering countries* are threatening innocent civilians
DOM	Even today *conquering countries* is an impossible thing to justify
SUB	Everyone knows that *playing cards* are shiny when they knew
DOM	Everyone knows that *playing cards* is an excellent way to pass the time
SUB	Experts agree that *inspiring youngsters* are certain to encourage their friends
DOM	Experts agree that *inspiring youngsters* is certain to improve their chances
SUB	Fortunately *understanding parents* is easy today
DOM	Fortunately *understanding parents* are common nowadays
SUB	Friends heard that *slamming doors* are are annoying the neighbours next door
DOM	Friends heard that *slamming doors* is not allowed in John's house
SUB	He realised that *parking vans* were blocking the road nearby
DOM	He realised that *parking vans* is not encouraged in busy roads
SUB	Her brother told her that *drowning kittens* are seldom rescued
DOM	Her brother told her that *drowning kittens* is extremely immoral

SUB	His mum thought that *cleaning brushes* is important after painting
DOM	His mum thought that *cleaning brushes* were stored under the sink
SUB	In a quiet room *stimulating conversations* is often difficult
DOM	In a quiet room *stimulating conversations* are a big distraction
SUB	In some countries *kicking donkeys* are badly beaten
DOM	In some countries *kicking donkeys* is a serious offence
SUB	In stormy weather *sailing boats* is very difficult
DOM	In stormy weather *sailing boats* are tossed about on the waves
SUB	In the afternoon *chasing dogs* are barking at the frightened cats
DOM	In the afternoon *chasing dogs* is favoured by the naughty children
SUB	In the circus *juggling knives* are less sharp then people think
DOM	In the circus *juggling knives* is less dangerous than eating fire
SUB	In the long run *cheating partners* is likely to lead to divorce
DOM	In the long run *cheating partners* are likely to get caught
SUB	In warfare *advancing armies* is a difficult thing to achieve
DOM	In warfare *advancing armies* are destroying small villages
SUB	It accepted that *crashing vehicles* are likely to hit other vehicles
DOM	It accepted that *crashing vehicles* is likely to have serious consequences
SUB	It important that *training athletes* is a top priority for schools
DOM	It important that *training athletes* are given the correct diet
SUB	It pointed out that *appointing organisations* are required to ask for references
DOM	It pointed out that *appointing organisations* was accomplished through good advertising
SUB	It's a fact that *waking babies* are usually hungry
DOM	It's a fact that *waking babies* is usually tricky
SUB	John knew that *boring colleagues* was damaging his career
DOM	John knew that *boring colleagues* were approaching his office
SUB	Most experts agree that *failing students* is difficult for lecturers
DOM	Most experts agree that *failing students* are not to be rewarded
SUB	Normally *disturbing plans* are showed by senior managers?
DOM	Normally *disturbing plans* is a tactic to delay things
SUB	Not surprisingly *hunting eagles* are spotted over mountains
DOM	Not surprisingly *hunting eagles* is banned across Europe
SUB	On most roads *passing trucks* is impossible in small cars
DOM	On most roads *passing trucks* are a nuisance to other vehicles
SUB	On narrow roads *reversing lorries* is difficult for new drivers
DOM	On narrow roads *reversing lorries* are a problem for other road users

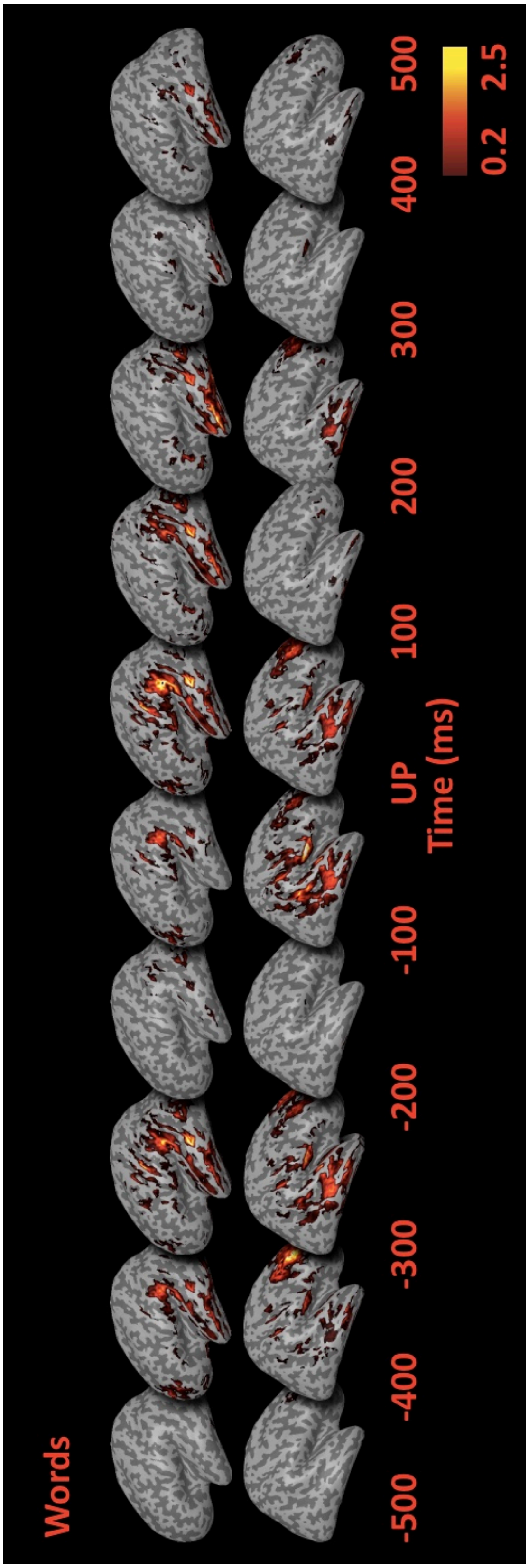
SUB	On some housing estates *abusing teenagers* are expected to go counselling.
DOM	On some housing estates *abusing teenagers* is perpetrated by rival gangs.
SUB	On the battlefield *exploding bombs* is a delicate life saving procedure
DOM	On the battlefield *exploding bombs* are directed behind enemy lines
SUB	On the parade ground *saluting officers* is important for discipline
DOM	On the parade ground *saluting officers* are acknowledged by their men
SUB	Outdoors *flying kites* are exciting when they soaring
DOM	Outdoors *flying kites* is superb way to entertain the children
SUB	Owners will tell you that *walking dogs* are usually well trained
DOM	Owners will tell you that *walking dogs* is a great way to get fit
SUB	She had heard that *breeding pigeons* are very noisy
DOM	She had heard that *breeding pigeons* is very popular
SUB	She remarked that *mocking boyfriends* are an embarrassment to their girlfriends
DOM	She remarked that *mocking boyfriends* is more trouble than she expected
SUB	She soon learned that *cutting boards* is a specialist job
DOM	She soon learned that *cutting boards* are easily broken
SUB	She soon learned that *packing cases* are heavier than shopping bags
DOM	She soon learned that *packing cases* is quicker than washing clothes
SUB	She told him that *shrugging shoulders* are a sign of boredom
DOM	She told him that *shrugging shoulders* is an easy way to be rude
SUB	Some people believe that *spinning coins* are more likely to land on heads than tails
DOM	Some people believe that *spinning coins* is more likely to get the attention of the bartender
SUB	Some teenagers think that *worrying parents* is an acceptable way to behave
DOM	Some teenagers think that *worrying parents* are a pain in the neck
SUB	The class observed *cooking apples* is an easy task
DOM	The class observed *cooking apples* are inedible without lots of sugar
SUB	The cook explained that *pickling onions* are sold in the supermarket
DOM	The cook explained that *pickling onions* is a way of preserving them
SUB	The developer knew *building services* is part of a successful project
DOM	The developer knew *building services* are supplied by the local council
SUB	The farmer explained that *hatching chicks* was a painstaking job
DOM	The farmer explained that *hatching chicks* were a wonderful sight
SUB	The gardener explained that *ripening tomatoes* is a tricky business
DOM	The gardener explained that *ripening tomatoes* are watered daily
SUB	The magazine said that *roasting potatoes* are tastiest with olive oil
DOM	The magazine said that *roasting potatoes* is traditional for Sunday lunch

SUB	The manager explained that *advertising awards* is the responsibility of the publicity department.
DOM	The manager explained that *advertising awards* are presented at fancy ceremonies
SUB	The manager told them that *developing ideas* were important to the company
DOM	The manager told them that *developing ideas* was much easier than they thought
SUB	The newspaper reported that *accelerating motorbikes* is dangerous in the rain.
DOM	The newspaper reported that *accelerating motorbikes* are becoming a nuisance
SUB	The newspaper reported that *bullying teenagers* is bad for their self esteem
DOM	The newspaper reported that *bullying teenagers* were a problem for the local school
SUB	The policeman knew that *racing cars* is illegal around the seafront
DOM	The policeman knew that *racing cars* are banned on public roads
SUB	The presenter argued that *trusting adolescents* are very likely to become volunteers
DOM	The presenter argued that *trusting adolescents* is not advisable for their teachers
SUB	The teacher explained that *rhyming words* is a standard poetic technique
DOM	The teacher explained that *rhyming words* are found at the end of each line
SUB	The teacher convinced that *interesting students* is an important part of teaching
DOM	The teacher convinced that *interesting students* are given the most attention
SUB	The tourist surprised that *overtaking buses* were travelling so fast
DOM	The tourist surprised that *overtaking buses* was allowed on the motor way
SUB	The woman discovered that *capsizing canoes* are very difficult to turn upright
DOM	The woman discovered that *capsizing canoes* is not difficult in the rapids
SUB	The woman found that *amusing youngsters* were the most popular pupils in the school
DOM	The woman found that *amusing youngsters* was the most time consuming aspect of her day
SUB	There many reasons why *boiling liquids* is an effective way to kill germs
DOM	There many reasons why *boiling liquids* are to be handled carefully
SUB	Tom noticed that *landing planes* is frightening to some pilots
DOM	Tom noticed that *landing planes* are deafening lots of people
SUB	Understandably *insulting neighbours* are not respected
DOM	Understandably *insulting neighbours* is not encouraged
UNAMB	After redundancy *acquiring debts* is a terrible way to get money.
UNAMB	As a rule *flowering trees* are perfect for bigger gardens
UNAMB	At Christmas parties *bringing presents* is what thoughtful people like to do
UNAMB	At first *establishing friendships* is an interesting undertaking
UNAMB	At school *sneering boys* are not to be tolerated
UNAMB	At the art auction *selecting paintings* is fun for everyone
UNAMB	Children know that *harming animals* is extremely bad

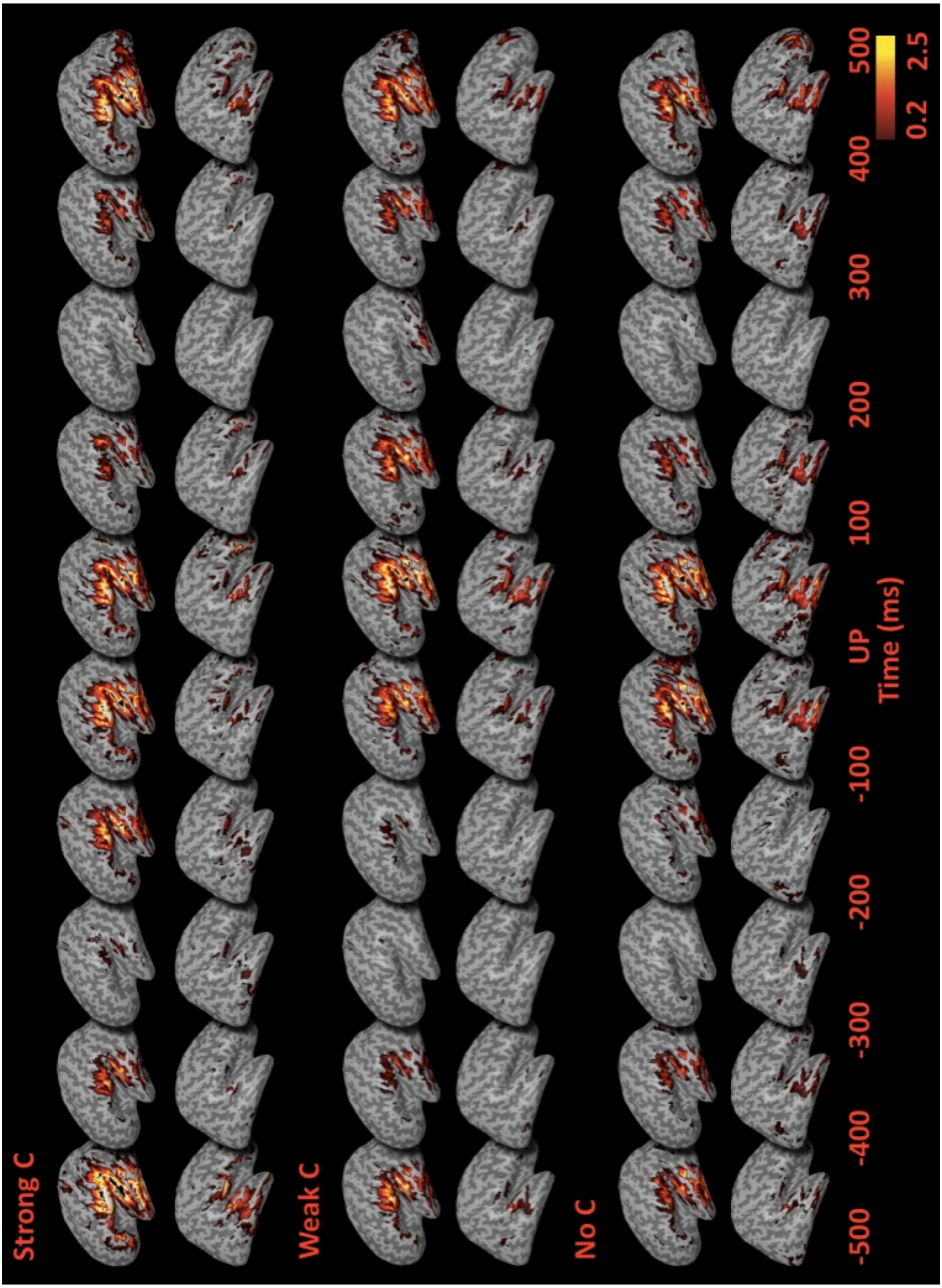
UNAMB	Criminals know that *regretting crimes* is sure to shorten their sentence
UNAMB	Even in the daylight *chuckling ghosts* are frightening to infants
UNAMB	Few teenagers think that *living poets* are more likely to get the attention of young people
UNAMB	For young people *inheriting fortunes* is a terrible burden
UNAMB	He found that *installing lights* is not easy in early February
UNAMB	He told her that *aching legs* are a problem for runners.
UNAMB	Her mother told her that *crying babies* are usually hungry
UNAMB	His father thought that *chairing meetings* was rotated among members
UNAMB	In cricket *bribing umpires* is a foolish thing
UNAMB	In difficult conditions *struggling swimmers* are rounded up by the lifeguard
UNAMB	In difficult times *rising costs* are a cause of many bankruptcies
UNAMB	In most companies *impressing employers* is essential to ambitious staff
UNAMB	In most families *resolving quarrels* is nearly impossible
UNAMB	In some big gardens *preventing weeds* is achieved through toxic chemicals
UNAMB	In some countries *denouncing traitors* is a patriotic duty
UNAMB	In the long run *employing craftsmen* is likely to get the job done
UNAMB	In the morning *speeding taxis* are rushing to the railway station
UNAMB	In the pub *joking comedians* are more entertaining than customers expect
UNAMB	It accepted that *releasing terrorists* is likely to enrage their victims
UNAMB	It pointed out that *competing teams* were instructed to desist from fighting
UNAMB	It's a fact that *emerging economies* are slowly developing
UNAMB	It's obvious that *clinging children* are lacking some reassurance
UNAMB	John knew that *gambling gangsters* were ruining his business
UNAMB	Just yesterday *gossiping housewives* were destroying people's reputations
UNAMB	Late in the evening *laughing friends* are shrieking loudly
UNAMB	Mary knew that *axing jobs* was saving lots of money
UNAMB	Most experts agree that *exploiting schoolchildren* is upsetting for parents
UNAMB	Normally *glistening bracelets* are displayed in the shop window
UNAMB	Not surprisingly *quarrelling sisters* are sent to bed
UNAMB	On the promenade *joking grannies* are heading towards the donkey ride
UNAMB	Outdoors *marching soldiers* are frightening when they noisy
UNAMB	Parents believe that *camping trips* are helping children develop
UNAMB	People know that *differing views* are acceptable these days
UNAMB	Secretaries would tell you that *functioning computers* are usually reliable
UNAMB	She knew that *despairing friends* are often neglected
UNAMB	She learned that *travelling businessmen* are very pushy

UNAMB	She noticed that *completing crosswords* was harder than she thought
UNAMB	She soon realised that *renting flats* is cheaper than buying houses
UNAMB	The article explained that *describing paintings* is encouraged in the gallery
UNAMB	The assistant knew that *discerning consumers* are tempted by the latest fashions
UNAMB	The chairperson announced that *adopting children* is the topic of this week's debate
UNAMB	The child said that *reminiscing grandfathers* were talking without wanting to stop
UNAMB	The employees believe that *interfering bosses* are a hindrance to their work
UNAMB	The gambler told him that *predicting results* is the only way to make money
UNAMB	The government knew that *working mothers* are happiest with short hours
UNAMB	The head teacher told that *reading problems* are hard to correct
UNAMB	The headmaster commented that *marking essays* is a daunting task
UNAMB	The judge argues that *imprisoning thieves* is a way of punishing them
UNAMB	The judge astonished that *hesitating criminals* were escaping so often
UNAMB	The nurse explained that *bandaging wounds* is an important first aid procedure
UNAMB	The reporter discovered that *blaming universities* is not fair on the lecturers
UNAMB	The secretary learned that *shredding files* is a standard requirement
UNAMB	The teacher knew that *rehearsing plays* is necessary for a good performance
UNAMB	The teacher sure that *allowing games* is a bad idea in the rain
UNAMB	The woman found that *glittering jewels* were the most expensive objects in the shop
UNAMB	The woman knew that *glowing references* are necessary for the best jobs
UNAMB	There many reasons why *torturing prisoners* is an unsatisfactory way to get information
UNAMB	Understandably *yawning audiences* are not welcomed
UNAMB	Workers understand that *neglecting risks* is a terrible way to carry on

APPENDIX D - ACTIVATION MAPS OF EXPERIMENT 1



APPENDIX E - ACTIVATION MAPS OF EXPERIMENT 2



APPENDIX F - ACTIVATION MAPS OF EXPERIMENT 3