Linking sentence production and comprehension: The neural mechanisms underlying production and comprehension control processes

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Abstract

This thesis investigated the relationship between sentence production and comprehension. A combination of behavioural and neuroimaging techniques were used to examine the extent to which sentence production and comprehension engage common or distinct mechanisms, with specific focus on the processes engaged by semantic/syntactic competition. Behavioural studies in Chapter 2 indicated that high-competition cases were more difficult to understand and produce than low-competition cases, and that difficulty varied as a function of the number of alternative associations entertained during performance in both tasks. In Chapter 3, an fMRI study indicated that production and comprehension shared a common competition mechanism within left inferior frontal gyrus (LIFG). However, they engage distinctive networks that interact with LIFG, with production eliciting a larger network including areas involved in sentence planning and memory retrieval. Further asymmetries across tasks were revealed in Chapter 4, in which behavioural results and neural networks were compared across adults and adolescents. This study also demonstrated the occurrence of shifts in the neural networks involved in competition resolution throughout development, thereby providing a strong link between poor behavioural performance and the underdevelopment of pre-frontal inhibitory mechanisms in adolescents. Chapter 5 used an improved experimental paradigm from that in Chapters 3 and 4. The results showed that production elicits more activity than comprehension in the dorsal language route thus confirming the engagement of task-specific control processes. Interestingly, this study also revealed a common area of LIFG involved in both tasks, but also differences within LIFG, suggesting the possibility of task-specific circuitry. Together, the findings suggest that production and comprehension share fronto-temporal areas that store and manage abstract linguistic associations between words and structures. However, they differ in the manner in which linguistic information is used, as is evident by the recruitment of distinct networks. Implications for models of language processing are discussed.

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Author's Declaration

This thesis comprises the candidate's own original work and has not, whether in the same or different form, been submitted to this or any other University for a degree. Selected aspects of the research described in this thesis have been presented at conferences.

Conference Talks

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Conference Posters

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Chapter 1

Literature Review

1.1 Introduction

Our understanding of the neurocognitive basis for language processing has progressed dramatically over the last decades. However, the relationship between generating language oneself and understanding language spoken by others, however, has been largely overlooked. Understanding the relationship between producing and comprehending language is clearly important to our understanding of language more generally, and should form a key component of any model of language processing. The purpose of this thesis was to examine more closely the potential commonalities and differences in the underlying mechanisms engaged by the two tasks with the aim of improving our understanding of the relationship between production and comprehension processes. The findings from this work not only have implications for psycholinguistic and neurocognitive models of language processing, but may also have a wider impact, for instance, in developing our understanding of cases of brain injury, or of child language developmental difficulty with respect to their production and comprehension skills.

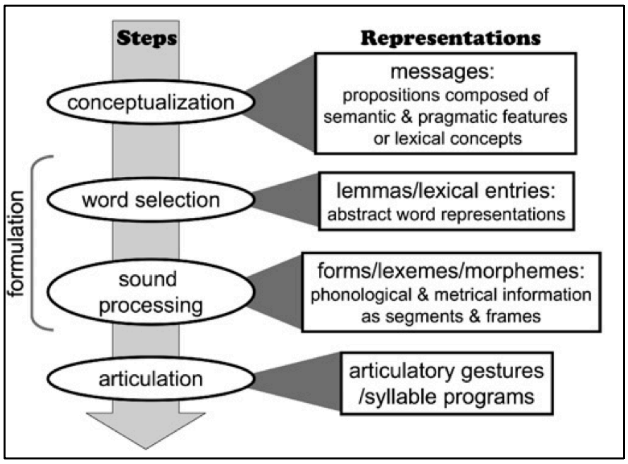
1.2 Psycholinguistic Approaches to Production and Comprehension

Traditionally in the psycholinguistic literature, production and comprehension have been studied as separate processes. As a result, independent psycholinguistic models have been proposed which emphasise differences rather than commonalties in the underlying mechanisms recruited by each task. This section summarises the dominant psycholinguistic models and highlights the key similarities and differences in the processes engaged across task domains.

1.2.1 Production models.

Psycholinguistic models of production suggest that word-production can be broken down into certain stages; conceptualisation, lexical and phonological processes, and articulation (see Figure 1.1; top-panel). Production begins with message conceptualisation, which is generally regarded to be pre-linguistic in nature (Garrett, 1975; Levelt, 1989). This is followed by a formulation stage, which is subdivided further into two components; lexical-retrieval (message-based processes) and phonological-retrieval (form-based processes) (Caramazza, 1997; Dell, 1986; Levelt, Roelofs, & Meyer, 1999). Lexical-retrieval involves the selection of the corresponding word that maps onto the activated concept. This word representation, known as a lemma, can be likened to a dictionary entry in that it specifies word-meaning and grammatical properties associated with the word. The phonological retrieval process involves retrieving sounds and relating them to the corresponding motor programme (phonetic encoding). Finally, there is an articulatory component during which the sounds are vocalised.

In sentence production, the basic stages are the same but the situation is more complex with the addition of syntactic processing. Following conceptualisation there is a grammatical component that is made up of two sub-processes; functional processing and positional processing (Bock, 1995). Functional processing is similar to the lemma level, but instead involves, as this is a model of sentence production, the activation of multiple lemmas. This is depicted schematically in the bottom panel of Figure 1.1, where multiple concepts have been activated. Here, the lexical representations needed for the sentence are flagged (lexical selection), and the grammatical roles such as subject or object are assigned (function assignment). Positional processing involves the allocation of each word to their specific slot in the sentence, based on the assigned grammatical properties.



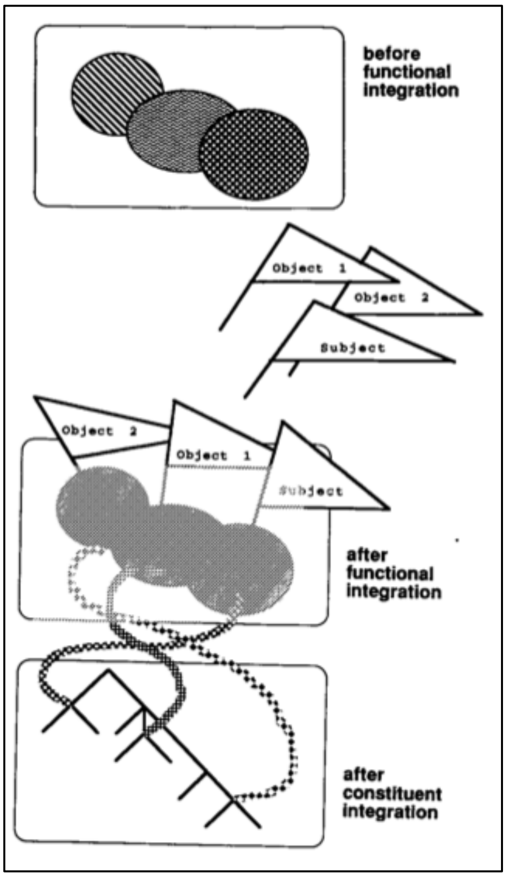


Figure 1.1 Top: A serial model of word production (Levelt et al., 1999) (figure taken from Griffin and Ferreira (2006)). Bottom: A schematic depiction of the processes involved in functional assignment during sentence production: Concepts are assigned grammatical flags that denote syntactic functions, the flags are used to assign word position during positional encoding (Bock, Loebell, & Morey, 1992). The example illustrates the stages in generating a subject-verb-object sentence such as “the boy is kissing the girl”.

Although production theories agree broadly on the core components of production (conceptualisation, lexicalisation, syntax, and phonology), they differ with regard to the manner in which information can flow through the production system. Models fall into two main categories; serial/encapsulated models (Bock & Levelt, 1994; Garrett, 1975; Levelt, 1999) and interactive/cascaded models (Dell, 1986; Dell, Burger, & Svec, 1997; Harley, 1993; Vigliocco & Hartsuiker, 2002). In serial models, information flow is unidirectional such that higher processing levels can influence lower levels, but the opposite cannot occur; lemma selection can influence syntactic processing, which in turn can influence phonological processing but not visa versa. These theories typically specify that the distinct components are encapsulated, which is defined as "not having access to facts that other systems know about" (Fodor, 1983, pg. 73). Encapsulation means that only information that has been uniquely selected is passed from one level onto the next. These models argue that encapsulation is critical for production efficiency as information at each level is protected from interference from different types of information from other levels.

Interactive models argue that information flow is bidirectional such that, for example, phonological processes can influence lemma selection (Dell, 1986). It is argued that an influence of phonological processes on lemma retrieval can aid production efficiency by, for example, leading to the selection of a lemma with high phonological frequency. These theories also specify a cascaded flow of information, that is, information can flow freely between meaning, lexical, and sound levels (Dell, 1986; Harley, 1993). The implication of cascaded activation is that multiple partially activated items, which are not ultimately selected, can propagate the system. In this model the target item and its' semantic competitors are activated during the lemma level. Then, activation from all competitors is passed on to the phonological level before a lemma has been uniquely selected. The item that is ultimately selected is the one that reaches a critical threshold of activation above the competing items.

1.2.2 Comprehension models.

The majority of researchers support an interactive model of comprehension where phonology, syntax, and semantic interact to influence each other in a mutual manner. The dominant theory of sentence comprehension, the constraint-satisfaction model, proposes that comprehension proceeds incrementally with multiple processes activated in parallel and interactively (syntax, semantics, phonology) (Boland, 1997; Boland, Tanenhaus, Garnsey, & Carlson, 1995; MacDonald, 1994; MacDonald, Pearlmutter, & Seidenberg, 1994; McRae, Spivey-Knowlton, & Tanenhaus, 1998; Spivey-Knowlton & Sedivy, 1995; Tanenhaus & Trueswell, 1995). With this approach, alternative interpretations are activated in parallel and competitively, with the level of activation of each interpretation determined by probabilistic information derived from real-world experience. By this view, multiple sources of information (e.g. context, plausibility, frequency) operate to constrain the domain of interpretation, and ambiguities arise when the correct interpretation is infrequent or implausible given a particular context.

One example of how multiple constraints operate to constrain interpretation in comprehension is provided in sentences 1a-1b (MacDonald et al., 1994). Here, the verb *examined* is ambiguous as it has equally frequent main verb or reduced relative clause meanings. However, in the case of 1a the ambiguity is reduced because *evidence* is inanimate and is therefore unlikely to be the agent of the verb *examined*, making this sentence more compatible with the reduced relative clause interpretation. This process is illustrated schematically in Figure 1.2 showing how the alternative interpretations of *examined* are constrained by the plausible thematic roles served by *evidence*. This example illustrates how semantic information, such as the plausible roles served by inanimate entities in an event, interact with structural information to constrain the domain of interpretation of a sentence. However, in the case of 1b, *The defendant* is animate, and animate entities tend to be agents of actions, thereby leading to ambiguity between the main verb and reduced relative clause interpretation (in Figure 1.2 *defendant* would activate the “agent” thematic role). Thus, in comprehension multiple interpretations are activated in parallel based on their frequency, and interact to constrain the interpretation of a sentence.

1a) The evidence examined by the lawyer turned out to be unimportant.

1b) The defendant examined by the lawyer turned out to be unimportant.

According to constraint-based models, comprehension proceeds incrementally, whereby each new word is semantically integrated into an interpretation, and it involves the generation of predictions regarding the plausible sequence of upcoming material based on real-world knowledge (Altmann & Kamide, 1999; DeLong, Urbach, & Kutas, 2005). For example it has been shown that in processing *It was windy. The boy went out to fly a…*, comprehenders process *plane* with more difficulty than *kite*, as the former conflicts with the expectation generated by real-world experience. Therefore, comprehension can be viewed as a rapid and interactive process whereby multiple information sources are activated in parallel and competitively, and predictions regarding upcoming information are generated.

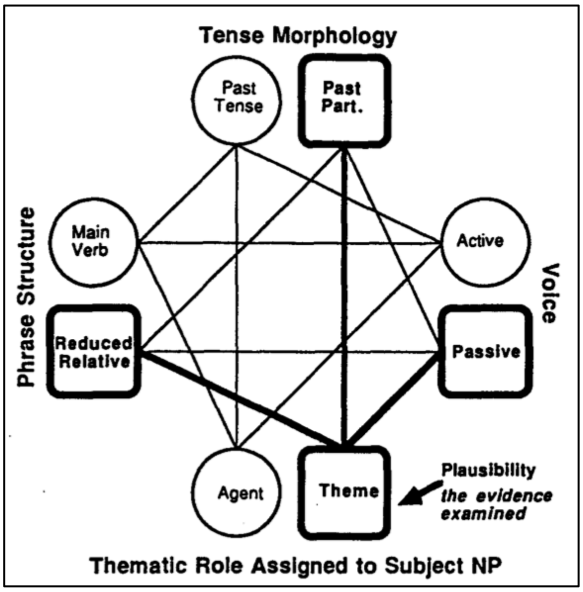


Figure 1.2 The influence of plausibility information on the alternative interpretations of the verb *examined*. Manipulating the plausibility of the head-noun biases the parser towards different structural interpretations, in this case *evidence* biases towards the "theme" interpretation thereby resulting in a reduced relative clause interpretation (MacDonald, et al., 1994).

1.2.3 The link between production and comprehension processes.

In terms of the link between production and comprehension processes, they have been modelled largely as separate processes (Bock, 1995; Dell, Burger, et al., 1997; Levelt, et al., 1999; McDonald, Bock, & Kelly, 1993; Thornton & MacDonald, 2003; Vigliocco & Hartsuiker, 2002). Indeed, Levelt et al. (1999) argued that whilst production and comprehension share conceptual and lexical representations (production lemmas are also comprehension lemmas), the systems are otherwise independent. Moreover, the assumptions made by constraint satisfaction model of comprehension differ greatly from the assumptions of serial/encapsulated production models. For instance, serial models are fundamentally incompatible with the notion of shared production and comprehension mechanisms as they argue that information flow is strictly unidirectional, from meaning to output, and the flow cannot be transferred in the reverse direction i.e. from input to meaning.

There are more similarities between comprehension models and the interactive/cascaded production models. Indeed, in the Dell model experience-based distributional knowledge of, for instance, likely syllable orders in words, or word orders in phrases, is a prominent influence on production, as is also the case in constraint-based models in comprehension (Dell, Reed, Adams, & Meyer, 2000). However, interactive production models do differ from constraint-based comprehension models in certain respects. Unlike constraint-based models, the Dell model is not fully interactive, in that each level can influence only the level that directly precedes or follows it. Furthermore, in the Dell model semantic processing always precedes syntactic and phonological processing. This contrasts with interactive comprehension models where all processes are activated in parallel.

Therefore, major psycholinguistic models are not entirely compatible with the notion of shared production and comprehension processes. Indeed, in certain respects there are good reasons to assume asymmetries in processes. Production is a more difficult task than comprehension. Production skills lag behind comprehension skills during development and second-language learning (Bates et al., 1988; Fenson, Dale, Reznick, Bates, & et al., 1994). Also, production is prone to errors. In fact there is an entire literature dedicated to the study of speech errors, involving problems with lexical retrieval (such as in the tip-of-the-tongue phenomenon) and phonological retrieval (e.g. phonological blends such as

Justice, instead of *Justin and Travis*), as well as errors in syntactic processes (such as name-agreement errors) and linearisation (e.g. *We forgot to add the list to the roof*) (Dell, et al., 2000; Dell, Schwartz, Martin, Saffran, & Gagnon, 1997; Garrett, 1975; Harley, 1984). Such errors are virtually unheard of in comprehension.

Beyond differences in processing difficulty there are also qualitative differences between production and comprehension tasks. Firstly, production is a task of word retrieval whereas comprehension is a task of word recognition. Word recognition is a faster process than retrieval; comprehenders are able to recognise a referent even before the speaker has completed articulation (Tanenhaus, Spivey-Knowlton, Eberhard, & Sedivy, 1995). However, naming an object in a picture takes around 900 ms for word initiation (Snodgrass & Yuditsky, 1996). These task-differences might lead to differences in the underlying processing systems (Bock, 1995; McDonald, et al., 1993; Thornton & MacDonald, 2003; Vigliocco & Hartsuiker, 2002). Secondly, production and comprehension have very different inputs. In comprehension, the processor must piece-together potentially ambiguous inputs, whereas the producer starts with a conceptual representation which is presumably free from ambiguity (Thornton & MacDonald, 2003). Furthermore, the systems differ in terms of the degree of precision that is required. As expressed by Garrett (1980), "The production system must get the details of form 'right' in every instance, whether those details are germane to sentence meaning or not" (p. 216). Comprehension, on the other hand, relies more on prediction rather than fine-grained analysis, and needs only to be “good-enough” (F. Ferreira, Bailey, & Ferraro, 2002). For instance comprehenders will often classify a sentence such as *The dog was bitten by the man* as plausible as their real-world knowledge is used to direct their interpretation.

Therefore production and comprehension appear distinct in some respects. However, despite these asymmetries it is implausible that the two systems will operate in isolation and independently of the other. The simple fact that the message that a person comprehends will be the result of another’s production suggests that at the very least production and comprehension must be sensitive to the same linguistic statistics. Indeed, certain models suggest strong links between the two processes. The Production-Distribution-Comprehension (PDC) model (Gennari & MacDonald, 2009; MacDonald & Thornton, 2009) suggests that constraints that operate on production choices lead to certain distributions in the language which influence comprehension difficulty. They argue that when planning a production, the producer is influenced by variables such as the accessibility of a word or concept. The accessibility of an item is known to be influenced by many factors including repetition, context (Haskell, Thornton, & MacDonald, 2010), imageability (Bock & Warren, 1985), and animacy (McDonald, et al., 1993). According to the PDC model, variables, such as accessibility, which reflect ease of retrieval due to previous experience, lead to distributional patterns in the language to which comprehenders are sensitive. As such, production preferences are strongly related to comprehension difficulty in that the structures that speakers do not produce are the ones that cause more difficulty to comprehenders. This point has been supported by behavioural data showing that production preferences predict comprehension difficulty (Gennari & MacDonald, 2009; Race & MacDonald, 2003). The PDC model thus suggests that the distributional regularities in the language impose shared constraints on both production and comprehension.

However, it is important to note that whilst the PDC model suggests a large degree of interactivity and interdependence between production and comprehension it does not necessarily suggest that they rely on the same processing system or mechanisms. Saying this, others have suggested that production and comprehension engage shared mechanisms (Bock, Dell, Chang, & Onishi, 2007; Chang, Dell, & Bock, 2006). Evidence for this comes from studies of syntactic priming, the tendency to re-use recently produced/heard syntactic structures. Bock et al. (2007) showed that syntactic priming effects occur across production and comprehension modalities such that comprehending a particular structure primes production of the same structure. Furthermore, the extent of priming effect across modalities was of the same magnitude as from production to production. This was taken as evidence for a shared production and comprehension sequencing system for syntactic processing.

1.2.4 Summary of psycholinguistic approaches.

To summarise, traditional psycholinguistic approaches have studied and modelled production and comprehension as largely independent systems. There are good theoretical reasons to assume some asymmetries in processes. For instance, production is a more difficult task. Also, production involves word retrieval and lexical, syntactic and phonological planning, whereas comprehension involves recognition and prediction. Despite these differences there is certainly a close relationship between the two tasks. However, the question remains as to the extent at which production and comprehension rely on shared or separate (but interactive) systems. Neuroanatomical investigations can help answer this question by demonstrating common or distinct neural engagement across tasks. In contrasts to the psycholinguistic approaches, neuroanatomical models tend to emphasise more the commonalities between production and comprehension processes.

1.3 Neuroanatomical Approaches to Production and Comprehension.

1.3.1 Comprehension-based models.

1.3.1.1 The fronto-temporal network.

The majority of neuroanatomical models of language processing are largely/exclusively comprehension-based, and are heavily biased towards comprehension data, although, many of these models assume common processes in production (Hagoort, 2005; Hickok & Poeppel, 2000, 2004, 2007; Jefferies & Lambon Ralph, 2006; Price, 2010; Snijders et al., 2009; Thompson-Schill, 2003; Thompson-Schill, Bedny, & Goldberg, 2005). Comprehension-based models refer to a core left-lateralised fronto-temporal network as being the neuroanatomical basis for language processing (Binder, Desai, Graves, & Conant, 2009; Friederici, 2002; Hagoort, 2005; Jefferies & Lambon Ralph, 2006; Price, 2010; Snijders, et al., 2009; Thompson-Schill, 2003; Thompson-Schill, et al., 2005; Tyler & Marslen-Wilson, 2008; Vigneau et al., 2006) (see Figure 1.3). Within the network different areas serve distinct functions, although there is considerable disagreement regarding the precise roles of different regions.

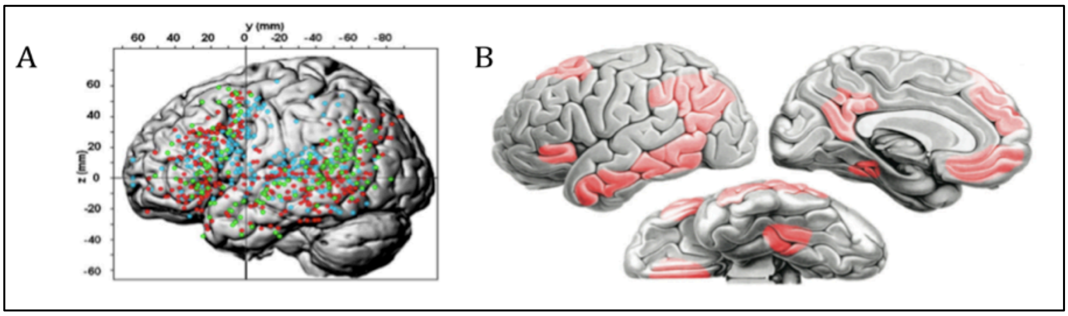


Figure 1.3 a) Model proposed by Vigneau, et al. (2006) showing the areas involved in phonology (blue), semantics (red), and syntax (green). b) Model proposed model by Binder et al (2009) showing the semantic network.

1.3.1.1.2 Temporal areas.

Neuroanatomical models of language processing agree that production and comprehension share a common semantic knowledge base. Left temporal areas are thought to play an important role in semantic processing, as highlighted by several reviews and meta-analyses (Binder, et al., 2009; Binney, Embleton, Jefferies, Parker, & Lambon Ralph, 2010; Friederici, 2002; Hickok & Poeppel, 2000, 2004, 2007; Indefrey & Levelt, 2004; Rogers et al., 2004; Vigneau, et al., 2006). In particular these theories highlight the importance of posterior temporal areas, such as posterior middle temporal gyrus (pMTG), and also anterior temporal lobe in semantic processing. However, there is some disagreement regarding the roles of the anterior and posterior temporal areas. Certain models suggest that conceptual knowledge is distributed throughout the cortex, but that posterior temporal areas, in particular pMTG and/or posterior inferior temporal sulcus (pITS) are important for lexical semantic access, that is, linking words to meaning or the lemma level of representation (Friederici, 2002; Hagoort, 2005; Hickok & Poeppel, 2000, 2004, 2007; Indefrey & Levelt, 2004). Whilst anterior temporal regions are involved in sentence level combinatorial processes i.e. the composition of sentence meaning (Hickok & Poeppel, 2000, 2004, 2007). In other models this "unifying" role has been assigned to the inferior frontal cortex (Hagoort, 2005; Snijders, et al., 2009).

However, other theories suggest different functions. For instance, some suggest that the posterior temporal areas are involved in pre-lexical semantic processes, for instance retrieving event-representations (Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003). Others still, have argued that the primary function of posterior temporal areas is in executive processes, that is semantic control (Jefferies & Lambon Ralph, 2006; Noppeney, Phillips, & Price, 2004), whilst anterior temporal areas form a semantic "hub" which stores amodal semantic representations (Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000; Rogers, et al., 2004). Therefore, whilst there is agreement that temporal areas are involved in semantic processes in language, the exact involvement of each area in conceptual, lexical, or executive processes is disputed.

1.3.1.1.3 Frontal areas.

Whilst temporal areas are thought to store and retrieve semantic and lexical representations, frontal portions of the "language network", in particular the left inferior frontal gyrus (LIFG), are thought to serve executive functions, although models disagree on the exact role. Certain theories suggest that the LIFG is important for sentence-level syntactic processes. For instance, claims have been made that the LIFG sequences information during the building of syntactic structure (Friederici, 2002, 2009). In support of the viewpoint that LIFG is involved in syntactic processing, there is evidence of increasing LIFG activation with increasing syntactic complexity in comprehension (Makuuchi, Bahlmann, Anwander, & Friederici, 2009). Furthermore, damage to LIFG has been shown to disrupt the sequencing of information in sentence production and comprehension suggesting potentially shared systems (Thothathiri, Schwartz, & Thompson-Schill, 2010). A related theory also suggests LIFG is critical for sentence level processes and in particular, the unification of information in multi-word structures (with distinct sub-components controlling phonological, syntactic and semantic unification) (Hagoort, 2005; Snijders, et al., 2009). Unification refers to the combinatorial processes required to bind multiple entities into a single form, for instance binding syntactic frames into a single syntactic structure, or integrating lexical information with context and real-world knowledge. This unification role is akin to the role assigned to anterior temporal areas in models discussed above (Hickok & Poeppel, 2000, 2004, 2007).

However, the evidence suggests that LIFG is not specialised for syntactic processing, for instance, studies have shown activation of this region for single words (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997) and for non-linguistic tasks when the executive demands are high (Duncan, 2010; Duncan & Owen, 2000; Owen, Schneider, & Duncan, 2000), and also the absence of activity here for sentences when task-demands are low (Binder et al., 2000; Scott, Blank, Rosen, & Wise, 2000; Scott & Johnsrude, 2003). Furthermore, studies have shown that syntactic complexity effects in LIFG can be overridden by semantic factors such as agent-patient plausibility (Caplan, Chen, & Waters, 2008; Caplan, Stanczak, & Waters, 2008). This suggests that LIFG is not responsible for syntactic processing *per se*, but rather that there is some aspect of a syntactically complex sentence to which LIFG responds, for instance increased control demands. Based on these observations, the majority of researchers do not assign sentence-specific processes to LIFG, rather they suggest that LIFG is involved in performing multiple general regulatory control functions, including memory maintenance, controlled retrieval and encoding, integration and selection/inhibition (Barde & Thompson-Schill, 2002; D'Esposito, Postle, Jonides, & Smith, 1999; Fiebach, Rissman, & D'Esposito, 2006; Fuster, 2001; Miller & Cohen, 2001; Thompson-Schill, et al., 2005; A. D. Wagner, Pare-Blagoev, Clark, & Poldrack, 2001).

Two of the functions often assigned to LIFG, which is relevant for the studies presented here, are verbal working memory and competition resolution. There is indeed extensive evidence that LIFG (pars opercularis and pars triangularis) is involved in maintaining and manipulating verbal information (Buchsbaum, Olsen, Koch, & Berman, 2005; Fiebach, Schlesewsky, Lohmann, von Cramon, & Friederici, 2005; Rogalsky, Matchin, & Hickok, 2008; E. E. Smith & Jonides, 1997), and is sensitive to working memory-based interference (Badre & Wagner, 2005; Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001; Jonides, Smith, Marshuetz, Koeppe, & Reuter-Lorenz, 1998; Thompson-Schill et al., 2002). For instance, LIFG activity is increased during proactive interference, where the presence of related information in a previous trial interferes with a response in the current trial (Badre & Wagner, 2005; Jonides, et al., 1998), and damage or stimulation of these areas disrupts performance on proactive interference tasks (Feredoes, Tononi, & Postle, 2006; Thompson-Schill, et al., 2002).

There is also good evidence to suggest that LIFG is involved in resolving competition between alternative interpretations/responses, and it acts as a mechanism that selects task-relevant information and inhibits information that is task-irrelevant. Neuroimaging and neuropsychological evidence has highlighted that LIFG is involved in tasks that require the selection of an appropriate response from alternative possible responses (Bedny, McGill, & Thompson-Schill, 2008; Demb et al., 1995; Gennari, MacDonald, Postle, & Seidenberg, 2007; Gold & Buckner, 2002; Hoenig & Scheef, 2009; Rodd, Davis, & Johnsrude, 2005; A. D. Wagner, et al., 2001). With regard to sentence level processes, LIFG is modulated by the presence of alternative possible meanings or syntactic structures (E. Chen, West, Waters, & Caplan, 2006; Fiebach, Vos, & Friederici, 2004; January, Trueswell, & Thompson-Schill, 2009; Mason, Just, Keller, & Carpenter, 2003; Obleser & Kotz, 2010; Rodd, et al., 2005; Rodd, Johnsrude, & Davis, 2010, 2011; Tyler et al., 2010; Ye & Zhou, 2009a). For instance, Rodd et al., (2011) found increased LIFG activity when comprehending sentences containing semantically ambiguous words (e.g. *She quickly learnt that injured calves moo loudly*) compared to sentences with low ambiguity (e.g. *He quickly learned that green fruits ripen slowly*), presumably because alternative interpretations of *injured calves* compete for selection. Whilst the majority of evidence in favour of LIFGs involvement in resolving competition comes from studies of comprehension, there is also evidence from brain injury and fMRI that the same region might serve similar function in production (Jefferies & Lambon Ralph, 2006; Novick, Kan, Trueswell, & Thompson-Schill, 2009; G. Robinson, Blair, & Cipolotti, 1998; G. Robinson, Shallice, Bozzali, & Cipolotti, 2010; G. Robinson, Shallice, & Cipolotti, 2005; Thompson-Schill, et al., 1997).

Evidence suggests that LIFG control processes such as memory maintenance and/or response selection are domain- and task-general, rather than language-specific; that is, the same LIFG conflict resolution processes are engaged across different tasks (Gold, Balota, Kirchhoff, & Buckner, 2005; Novick, et al., 2009; Rodd, Johnsrude, et al., 2010; Wright, Randall, Marslen-

Wilson, & Tyler, 2011; Ye & Zhou, 2009b). Evidence in favour of domain- and task-general functions comes from findings of common LIFG engagement for syntactic ambiguity and Stroop conflict (January, et al., 2009; Ye & Zhou, 2009a), as well as many non-linguistic cognitive control tasks (Duncan, 2010; Duncan & Owen, 2000; Owen, et al., 2000). Such general approach is consistent with developmental theories arguing that the role of LIFG and pre-frontal cortex more generally might shift with development. In particular, a growing body of research has shown that age-related changes in prefrontal neurodevelopment lead to variations in LIFG involvement in a variety of tasks that require cognitive control processes. For instance, the prefrontal cortex, including LIFG, does not fully develop until early-adulthood, and as a result children and adolescents show reduced recruitment of LIFG compared to adults (Durston et al., 2006; Rubia et al., 2006; Schroeter, Zysset, Wahl, & von Cramon, 2004; Stevens, Kiehl, Pearlson, & Calhoun, 2009; Tamm, Menon, & Reiss, 2002). This suggests that as inhibitory control improves during development, the recruitment of prefrontal structures especially LIFG also increases, indicating a strong link between domain general inhibitory mechanism and LIFG.

However, others suggest that LIFG is made up of distinct sub-regions serving distinct control functions. For instance, some claim that posterior LIFG is engaged in controlled selection, whereas more anterior regions are engaged more in controlled retrieval (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Badre & Wagner, 2007). Also, others have argued that different sub-regions are engaged by semantic, syntactic, and phonological control processes, that is BA45/47, BA44/45, and BA44/6 respectively (Gough, Nobre, & Devlin, 2005; Xiang, Fonteijn, Norris, & Hagoort, 2010). Furthermore, certain sub-regions have been further subdivided. For instance, Price (2010, 2012) suggested that dorsal, but not ventral, BA44 is involved in the formation of top-down predictions regarding the plausible sequences of linguistic and non-linguistic events. Therefore, LIFG appears involved in domain-general executive processes, but distinct sub-areas within LIFG may serve more specific control processes. However, given the scarcity of production studies, particularly at the sentence level of processing, whether or not production and comprehension engage the same sub-regions is unclear.

1.3.1.2 Summary.

To summarise, neuroanatomical models suggest that language engages a core fronto-temporal network. However, they disagree on the precise contribution of each area to language processing. The temporal lobes are thought to store semantic representations (although the locus is disputed), and play a role in lexical-semantic access. Executive functions, such as cognitive control, memory maintenance, syntactic sequencing, or unification, are served by frontal areas, and in particular LIFG. However, the extent to which sub-regions of LIFG serve task-specific functions remains unclear, and there is also evidence that LIFGs involvement in control may be age-dependent. Furthermore, since the majority of neuroanatomical models have been based largely on comprehension results, it is unclear whether assumptions of similarity across production and comprehension actually hold (Hagoort, 2005; Hickok & Poeppel, 2000, 2004, 2007; Jefferies & Lambon Ralph, 2006; Price, 2010; Snijders, et al., 2009; Thompson-Schill, 2003; Thompson-Schill, et al., 2005). The scarcity of production studies in the literature, particularly in terms of sentence-level processes does not allow strong claims to be made regarding the extent to which production and comprehension share fronto-temporal processes. The few production-based models that have been proposed are discussed in the next section. These models suggest that there may in fact be substantial differences in the neural processes engaged by production and comprehension.

1.3.2 Production-based models.

1.3.2.1 The fronto-temporal network.

Although the majority of models assume shared fronto-temporal processes for production and comprehension, there are a few notable exceptions. Based on the results of a meta-analysis of word-production studies, Indefrey and Levelt (2004) propose a neuroanatomical basis for Levelt’s psycholinguistic production model (see also Indefrey, 2011 for an updated model). They argue that whilst comprehension and production engage the same fronto-temporal areas, beyond the level of conceptual representation the activity reflects distinct underlying processes. Here they argue that left MTG is involved in lemma level processes (shared between production and comprehension), the posterior superior temporal sulcus (pSTS) is engaged by phonological retrieval, and that IFG is engaged by phonological encoding.

Other models have also argued for distinct production-comprehension processes within the fronto-temporal network. Hickok and Poeppel (2000, 2004, 2007) proposed a dual-stream model of language processing arguing for partially separable production and comprehension mechanisms. According to the dual-stream model, (auditory) comprehension is achieved via a ventral route involving structures in the posterior middle and superior temporal lobe bilaterally, whereas production is achieved via a dorsal route involving left-lateralised dorsal aspects of the posterior temporal lobe, parietal and posterior frontal areas (see Figure 1.4). Within the ventral route, sound-to-meaning is achieved in the posterior temporal lobe where phonological representations are mapped onto lexical concepts, and then more anterior regions perform combinatorial processes such as syntactic and compositional semantics. Production also engages the same phonological encoding areas within pSTS to guide articulatory sequencing during production by providing state feedback and also forward sensory predictions (Hickok, Houde, & Rong, 2011). However, beyond pSTS, production and comprehension engage distinct areas. In the dorsal stream, left frontal areas are involved in articulatory components of production. The BA44 region of LIFG engages motor syllable programs (Hickok, 2012; Hickok, et al., 2011). This model makes the strong claim that frontal areas serve a primarily motor role, and are therefore critical for language production but are not critical to language comprehension. They argue that frontal activity is epiphenomenal for comprehension tasks; it occurs because of the dense interconnections between production and comprehension systems, but is non-essential for successful speech comprehension, which is defined as those processes necessary and sufficient to lexico-semantic access (Okada & Hickok, 2006). This viewpoint contrasts strongly with that discussed in the previous section, whereby LIFG is important for both production and comprehension processes.

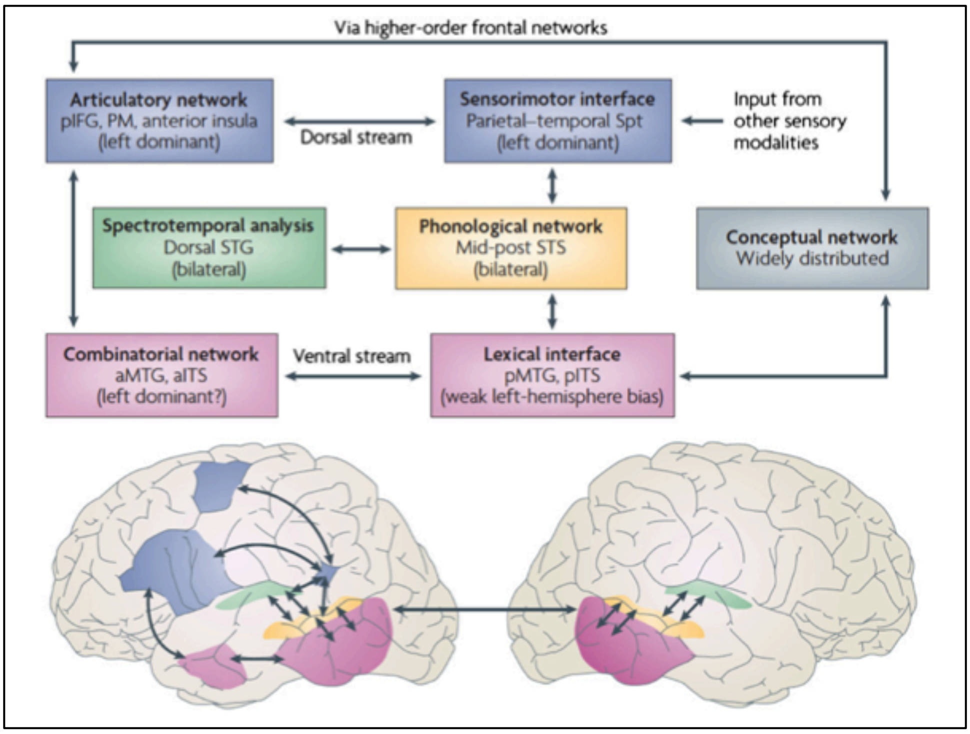


Figure 1.4 The dual-stream model of language processing (Hickok & Poeppel, 2000; 2004; 2007). Production engages in the dorsal stream in blue, whereas comprehension engages the ventral stream in pink (image from Hickok et al. (2011)).

1.3.2.2 Beyond the fronto-temporal network.

Studies of word-production highlight a further network of areas that go beyond the fronto-temporal network, and are not typically highlighted in comprehension studies (See reviews Indefrey, 2011; Indefrey & Levelt, 2004). This includes precentral gyrus, supplementary motor areas (SMA), middle frontal gyrus, anterior cingulate, and also subcortical structures such as basal ganglia, thalamus, insula, and cerebellum. These areas are thought to be involved in motor aspects of production, such as phonetic encoding and articulation. For instance, precentral gyrus, thalamus and cerebellum are proposed to be involved in syllabification, whereas, SMA and insula are involved in articulatory planning and coordination (Indefrey, 2011). Also, others have suggested that premotor and motor areas are involved in lower level phonemic processes (Hickok, 2012; Hickok, et al., 2011). However, several researchers have suggested that this motor-related network plays a more active role in production, beyond articulatory output. For instance, the SMA is engaged by tasks involving response conflict, suggesting a role for this area in selecting the appropriate responses (Simmonds, Pekar, & Mostofsky, 2008). Moreover, this sensitivity is not limited to the motor domain, as it has also shown responds to cognitive manipulations that do not require overt motor execution, for example, for decision-making tasks, and a variety of tasks involving verbal, numerical, visual or spatial mental operation (Derrfuss, Brass, & von Cramon, 2004; Donohue, Wendelken, & Bunge, 2007; Hanakawa et al., 2002; Tanaka, Honda, & Sadato, 2005). Also, relevant to the current study, SMA is sensitive to syntactic complexity in sentence production (Ye, Habets, Jansma, & Munte, 2011), and some have also suggested that it can be divided in to functionally segregated regions for different production processes, linearization, lexical selection, or motor control (Alario, Chainay, Lehericy, & Cohen, 2006). Therefore, it is possible that the role of the SMA in production is not simply in terms of articulatory control, as suggested by some (Hickok, 2012; Hickok, et al., 2011; Indefrey, 2011), but rather that this region may play a more active role in those more "linguistic" aspects of language production.

Other areas that have typically been associated with motor planning may also be actively involved in cognitive aspects of production. For instance, it has been suggested that the ACC and basal ganglia play a role in inhibiting inappropriate verbal response, as they show increased activity for bilingual speakers compared to monolinguals (Abutalebi et al., 2008; Ali, Green, Kherif, Devlin, & Price, 2009; Garbin et al., 2011; Price, 2010), and they may be involved in cognitive control processes in production (Robles, Gatignol, Capelle, Mitchell, & Duffau, 2005). Also, the thalamus might play a more central role in production; it is sensitive to linguistic violations in sentences, and stimulation of the thalamus causes the production of erroneous words, perseveration, or misnaming depending on the stimulation-site (Johnson & Ojemann, 2000; Munte & Kutas, 2008). Therefore, it might be that these production-specific regions are not peripheral, and play a more central role in language production that is credited by neuroanatomical production theories.

Regardless of the role of motor-related structures, the models described thus far agree that these areas serve productions-specific processes. However, there are certain models that argue that comprehension will also recruit these areas. As mentioned previously, sentence comprehension is anticipatory, in that the parser actively generates predictions regarding the plausible sequence of upcoming material (Altmann & Kamide, 1999; DeLong, et al., 2005). According to the simulation approach, these forward predictions involve simulations of production planning processes or covert imitation (D'Ausilio et al., 2009; Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967), thus recruiting motor control systems (Pickering & Garrod, 2007). Therefore, according to this approach production and comprehension will engage common motor planning systems. Support for this theory has come from studies showing activation of premotor areas when comprehending speech (Pulvermuller et al., 2006) and TMS to these areas has been shown to disrupt speech sound discrimination (D'Ausilio, et al., 2009). However, others have argued that motor cortex does not play a necessary role in comprehension, and that an activation of these structures is epiphenomenal (Okada & Hickok, 2006). Therefore, the role that motor related structures play in production and comprehension remains to be established.

1.3.3 Summary of neuroanatomical models.

The prevailing view within the neuroanatomical literature is that production and comprehension tasks share processes within a common fronto-temporal neural network; however this is based largely on data from comprehension studies. Certain models do highlight the differences between production and comprehension networks, but these tend to focus on motor aspects of production such as phonetic encoding and articulation. Whilst other models suggest that motor areas are also recruited for comprehension. Additionally, the psycholinguistic literature suggests that production and comprehension differ in more central respects, engaging task-specific component processes such as retrieval vs. recognition, planning vs. prediction, and it is unclear how these differences are instantiated in neural terms. Elucidating the extent of the similarities and differences between production and comprehension processes requires a direct comparison of production and comprehension tasks using well-controlled psycholinguistic variables.

1.3.4 Direct comparisons of sentence production and comprehension.

There is a scarcity of neuroimaging studies that have directly contrasted production and comprehension, particularly with regard sentence level processes. Sentence level studies are important as some of these similarities and differences between production and comprehension are likely to only be revealed when factors such as syntactic/semantic planning or prediction come into play. Only a handful of neuroimaging studies have contrasted production and comprehension beyond the word-level. The majority of these have looked at narrative production/comprehension (Awad, Warren, Scott, Turkheimer, & Wise, 2007; Braun, Guillemin, Hosey, & Varga, 2001; Braun et al., 1997; Kim, Relkin, Lee, & Hirsch, 1997; Kircher, Brammer, Levelt, Bartels, & McGuire, 2004; Papathanassiou et al., 2000; Tamas, Shibasaki, Horikoshi, & Ohye, 1993). Although this can provide some broad insights into the brain areas generally involved in the two tasks, little can be concluded regarding the underlying mechanisms. This requires stimuli that are well controlled in terms of psycholinguistic properties. To date, only three fMRI studies have directly contrasted sentence production and comprehension using well-controlled stimuli. These highlight some potential commonalities and differences between the neural processes engaged by production and comprehension tasks.

Firstly, Indefrey, et al. (2004) aimed to determine the extent to which the LIFG is recruited during the production or comprehension of identical sentences. Here, in the production tasks participants either described scenes consisting of interacting coloured shapes, using a complete sentence (e.g. *The red square launches the blue ellipse.*), or with a sequence of words without any syntactic relationship (e.g. *square, red, ellipse, blue, launch*). In the comprehension condition the participants heard auditory descriptions of the scenes. The results showed that whilst the LIFG is activated during the production of sentences (sentence > words), no difference was found in the comprehension task between the sentence and the word condition. These results might suggest some difference in the processes engaged by the two tasks, and that LIFG may be recruited more strongly in the encoding of syntactic structures in production compared to the decoding of syntactic structure in comprehension, at least in the current context. The explanation for the effect is unclear, but the results might reflect syntactic generation processes that are production-specific, for instance, in positional encoding or grammatical function assignment.

The remaining two studies, however, found data to suggest common LIFG processes in production and comprehension. The authors of these studies utilised a syntactic priming paradigm that has been used extensively in the psycholinguistic literature (Bock, et al., 2007; Chang, et al., 2006), whereby encountering a particular syntactic structure primes the processing of the same structure in successive presentations. Using the same paradigm in fMRI, the researchers demonstrated neural adaptation effects within fronto-temporal areas to repeated syntactic structure, both within and across production and comprehension modalities (Menenti, Gierhan, Segaert, & Hagoort, 2011; Segaert, Menenti, Weber, Petersson, & Hagoort, 2011). The authors argued that the engagement of a common fronto-temporal network across production-comprehension suggests shared syntactic processing. These studies also found production-specific adaptation beyond the fronto-temporal network, within SMA. This may suggest that motor-related regions such as SMA are involved in syntactic encoding processes that are specific to production, although the authors explained this effect in terms of phonetic processes in line with production models (Hickok, 2012; Hickok, et al., 2011; Indefrey, 2011).

Therefore, only a handful of studies have directly compared the neural processes engaged by sentence production and comprehension, and with differing results. The results from studies that have directly contrasted sentence production and comprehension are inconclusive as to whether and how subcomponent processes in production and comprehension relate. Therefore, the objective of this thesis is to further examine the extent to which sentence production and comprehension engaged common processes.

1.4 The current research objective

To summarise, historically in the psycholinguistic literature, production and comprehension were studied separately, and as a result many psycholinguistic models have emphasised task differences rather than commonalities, for instance production involves retrieval and syntactic planning, whereas comprehension involves recognition and prediction. There are, however, some clear similarities between production and comprehension, both tasks involve semantic, syntactic, and phonological processing and the two tasks act upon a common knowledge base. Recently, certain psycholinguistic theories have attempted to account for these commonalities (Bock, et al., 2007; Chang, et al., 2006; Gennari & MacDonald, 2009; MacDonald & Thornton, 2009). Their proposals, however, are consistent with either common processing or separate systems that are heavily interactive. Indeed, there are good motivations to assume strong interactions between tasks. For example, given that what we comprehend is a result of what others have produced means that both language systems will at the very least share access to the same linguistic statistics.

A greater degree of commonality between the two tasks is assumed within the neuroanatomical literature where the assumption is of common processes within core fronto-temporal network, and that any differences between the networks are peripheral to the core components of the task. However, these conclusions are often speculative as neuroimaging investigations of production are scarce, particularly at the sentence level, and very few studies have directly contrasted the two tasks. These models also fail to account for the task-specific component processes that are clearly highlighted in the psycholinguistic literature. The current work seeks to address this gap in the literature and further investigate the relationship between production and comprehension, with specific attention to the potential common and distinct subcomponent processes that might be engaged. For this purpose the current research focussed on "competition processes" in sentence production and comprehension.

Why Competition?

Language processing studies have often used paradigms that manipulate competition as a means to investigate the mechanisms involved in language processing (Barch et al. 2000; Gennari et al. 2007; Gennari et al., 2012; Rodd et al. 2005; Rodd et al. 2010; Spalek et al. 2008 Thompson-Schill et al. 1997). This is because competition is considered an important process that plays a central role in both models of production and comprehension. Essentially, these models argue that the level of competition experienced is a major determiner of language difficulty both in production and comprehension tasks. In comprehension, constraint-satisfaction models highlight that comprehension is a competitive process whereby meanings and/or sentence structures are activated in parallel based on probabilistic information that derives from language and real-world experience (Boland, 1997; Boland et al., 1995; MacDonald, 1994; MacDonald et al., 1994; McRae et al., 1998; Spivey-Knowlton & Sedivy, 1995; Tanenhaus & Trueswell, 1995). Comprehension difficulty occurs when multiple equally frequent alternatives are activated and therefore compete for selection (e.g. in cases of ambiguous words such as *bowl*), or when multiple linguistic and/or contextual cues are associated with alternative conflicting interpretations (as in the example *The defendant examined by the lawyer* described above). Thus competition is a major determiner of comprehension difficulty. Competition also plays a central role in production processes (Bock & Levelt, 1994; Dell, 1986; Dell et al., 1997; Garrett, 1975; Harley, 1993; Levelt, 1999; Vigliocco & Hartsuiker, 2002). Specifically, strongly associated items compete during lexical or phonological selection. For instance, picture-word interference paradigms show that picture naming is interfered with by the presence of semantically related distractors (Costa, Alario, & Caramazza, 2005; Glaser & Düngelhoff, 1984; Glaser & Glaser, 1989; Jescheniak & Schriefers, 1998; Schriefers, Meyer, & Levelt, 1990). Competition may also occur in production when alternative utterances, e.g., alternative sentence structures, are associated with the intended meaning (Gennari et al. 2012), or in the case of cued production, when alternative utterances are strongly associated with the cue (Barch et al. 2000; Spalek et al. 2008). For example, in elicitation studies where participants must produce a verb/action in response to a noun, strong associations like scissors-cut are easier to utter than weaker associations, e.g., wheel-turn, because these weaker associations compete with other available alternatives, and thus also engage inhibition/selection processes (Thompson-Schill et al. 1997; Barch et al. 2000). Therefore, the domain of competition is a useful method for investigating language processing and it is also useful to investigate the relationship between sentence production and comprehension, as competition is thought to occur in both tasks thus allowing the potential for parallel processes. The goal of this work was to examine the extent to which production and comprehension share processes to resolve competition. Finding evidence of brain regions and behaviours that are similarly sensitive to competition demands in both production and comprehension would suggest shared processes.

1.4.1 Thesis Outline.

The following chapters of this thesis describe a series of behavioural and neuroimaging studies that were designed to investigate the degree that sentence production and comprehension share common processes. In particular, they evaluate the extent to which sentence production and comprehension shared competition resolution mechanisms.

Chapter 2 presents a behavioural experiment where word-by-word reading and sentence-completion paradigms were used to investigate whether parallel effects of semantic competition can be identified across production and comprehension tasks. Having established the presence of parallel behavioural competition effects, Chapter 3 presents an fMRI study that investigates the extent at which the effects derive from common or distinct neural mechanisms by comparing activation and functional connectivity patterns. These results reveal some commonalities between production and comprehension but also highlight some important differences. Chapter 4 presents a behavioural and fMRI study that investigate the development of competition resolution mechanisms in production and comprehension by comparing data from adults and adolescents using the same paradigm as described Chapter 2 and 3. These experiments show a shift through development in the mechanisms used to resolve competition in both tasks, and also highlight some more general differences between production and comprehension processes, which were not evident in the adult data alone. Chapter 5 describes the results from two behavioural studies and an fMRI study using an improved paradigm. The results from these studies show that despite the presence of parallel behavioural effects, production and comprehension engage largely distinct neural mechanisms to resolve competition. Finally, Chapter 6 presents a general discussion of the thesis and future directions for research.

Chapter 2

Cue-based competition in sentence production and comprehension: a behavioural investigation.

2.1 Introduction

This chapter examines the extent to which sentence production and comprehension share common processes to resolve competition in a sentence. Previous psycholinguistic studies have indicated that producers and comprehenders recruit similar lexical and grammatical information (Bock, et al., 2007; Chang, et al., 2006; Gennari & MacDonald, 2009; MacDonald, 1999; Seidenberg & MacDonald, 2001). Gennari and MacDonald (2009) for example, showed that the sentential configurations that comprehenders find difficult are those that producers do not naturally produce suggesting that the way of mapping concepts into sentence structure is shared across tasks. The issue here, however, is not whether these processes share a common knowledge base such as the lexicon or grammatical rules but rather whether producers and comprehenders use this knowledge in different ways. Traditional models have approached production and comprehension separately, and argue for separate processes, for instance production is thought to be a task of word retrieval, whereas comprehension is a task of recognition. However, other models such as those discussed below assume a larger degree of commonality between production and comprehension tasks. To address this issue this chapter focuses on one area that is critical to successful sentence processing, the ability to resolve ambiguities in a message.

2.1.1 Competition in comprehension

Competition between lexical items or syntactic structure is known to play a large role in determining comprehension difficulty. Comprehenders are constantly predicting upcoming information in order to efficiently understand a message (Altmann & Kamide, 1999; Altmann & Mirkovic, 2009; Kutas & Van Petten, 1994). During this predictive process multiple constraints operate to restrict the domain of interpretation. According to the constraint satisfaction approach multiple alternatives are activated in parallel as a function of their frequency or plausibility, and compete with each other for selection in a probabilistic manner derived from distributional properties of the language (MacDonald, et al., 1994; McRae, et al., 1998; Tanenhaus & Trueswell, 1995; Trueswell, Tanenhaus, & Garnsey, 1994). Thus, competition between alternative lexical items or syntactic structures is thought to be one of the major influences on comprehension speed and accuracy. Indeed, the impact of competing alternatives on comprehension has been well documented in the comprehension literature (MacDonald, 1994). This issue here is the extent to which competition has parallel effects in production, as those found in comprehension.

2.1.2 Competition in production

Traditional psycholinguistic models assume distinct production and comprehension processes (Bock, 1995; Dell, Burger, et al., 1997; Levelt, et al., 1999; McDonald, et al., 1993). However, certain models predict similar effects in production and comprehension tasks (although the claims are not specific to ambiguity effects). According the to the Production-Distribution-Comprehension (PDC) model (Gennari & MacDonald, 2009; MacDonald & Thornton, 2009), difficulties that arise in comprehension can be explained by limitations on the production system leading to distributional patterns in the language to which comprehenders are sensitive. In this view, comprehension difficulty is linked to the frequency by which a particular utterance occurs in the language; this means that comprehension difficulty is related directly to production difficulty, and that the constraints that operate on the comprehension system derive from constraints on the production system. Therefore, according to this approach patterns of results found in comprehension tasks would be mirrored in production tasks. Indeed, cases of parallel effects have been found in the literature. For instance, Thornton and MacDonald (2003) found that plausibility had a similar effect on name-agreement in both sentence production and comprehension tasks.

However, with regard to the process of conflict/ambiguity resolution there is reason to assume there may be asymmetry in production and comprehension processes. The task faced by producers is very different in nature compared to comprehenders. Comprehending involves piecing together information as efficiently as possible to understand a message. Producers on the other hand already know the message they wish to convey, and rather their task is one of planning the words and structures to be used to convey a message (Allum & Wheeldon, 2007; Bock & Levelt, 1994; F. Ferreira & Swets, 2002; V. S. Ferreira, 1996). Production therefore, is a process of planning rather than predicting, and given that a major source of competition in comprehension derives from the conflict between input and ones' predictions might suggest that ambiguity resolution is less of a concern in the production system, or perhaps when it does act, the nature of the effect might differ to that observed in comprehension (Thornton & MacDonald, 2003). Therefore, whilst certain models, such as the PDC model, might be used to predict parallel effects in production and comprehension, there are nevertheless reasons to expect asymmetries in the processes engaged.

Evidence that competition processes affect production is mixed. Support has come from studies of single word production. For instance, numerous studies have demonstrated picture-word interference effects whereby the presence of semantically related distractors interferes with picture naming (Costa, Alario, & Caramazza, 2005; Glaser & Düngelhoff, 1984; Glaser & Glaser, 1989; Jescheniak & Schriefers, 1998; Schriefers, Meyer, & Levelt, 1990). However, the extent to which competitors affect production at the sentential level, such as during the assignment of syntax and grammatical role, has been less well documented. The studies that have been conducted have shown that conceptual factors, such as noun similarity, affect processing. For instance, production of a sentence is more difficult when the two nouns are conceptually related presumably due to similarity-based interference (e.g. *saw* and *axe* in the sentence *the saw and the axe move together*) (M. Smith & Wheeldon, 2004). This effect is also thought to partially explain the difficulty associated with particular forms of complex sentence structures such as relative clauses. Gennari, Mircovic, and MacDonald (2012) demonstrated that the degree of similarity between two nouns in a relative clause influenced production choices. Therefore, there is evidence of competition at the conceptual or lemma level of production. The presence of competitors has also been shown to influence syntactic choices in production. When alternative syntactic structures are available production becomes slower and more disfluent (Montag & MacDonald, in prep.; Stallings, MacDonald, & O'Seaghdha, 1998).

However, consistent effects of competition have not always been found. The influence of competitors is not always present, and can be heavily influenced by task demands such as memory load (V. Wagner, Jescheniak, & Schriefers, 2010). Also, speakers are often insensitive to ambiguities in the messages they produce (V. S. Ferreira & Dell, 2000; V. S. Ferreira, Slevc, & Rogers, 2005). Furthermore, in some cases the presence of alternative possible structural choices has been found to actually facilitate rather than to interfere with production (V. S. Ferreira, 1996). In this case, it has been argued that the presence of alternative syntactic options increases flexibility in the production system and increases the speed by which one of the alternatives can be selected. In this study, participants were faster to initiate productions and made fewer errors in the condition where a sentence could be constructed using two alterative syntactic structures (either a double object structure, such as *I gave the children the toys*, or a prepositional dative structure, such as *I gave the toys to the children*) compared to instances when only one structure was permissible (prepositional datives structure). According to Ferreira (1996), "having more ways to express a message permits the speaker to choose a sentence that accommodates variation in the way the message evolves" (pg. 751). These points suggest that the presence of multiple alternatives might differently influence production compared to comprehension, where the presence of alternative interpretations leads to interference (MacDonald, et al., 1994).

Similar inconsistencies have been shown for competition at the lemma level using the picture-word interference paradigm. Here, the extent of interference from semantically related words in picture naming depends on the time at which the word is presented. If the word and picture are presented simultaneously, or the word precedes the picture onset, then competition will occur and naming is slowed; however presenting the word shortly after the picture can facilitate naming (Glaser & Düngelhoff, 1984; Roelofs, 1992; Starreveld & La Heij, 1995, 1996). Therefore, the influence of competition on production appears to be more variable than that found during comprehension, and the extent to which production and comprehension engage similar processes when multiple alternatives interpretations/utterances are possible is a yet unresolved issue.

2.1.3 The present study

The goal of the current work is to address this issue by directly comparing the influence of ambiguity on production and comprehension of the same sentences. Specifically, this chapter focuses on the competition processes involved in determining the semantic roles of the nouns in a sentence (who is doing what to whom), which result from conflicting lexical semantic cues (such as animate vs. inanimate nouns) and structural cues (such as word order in the structure) (MacDonald, et al., 1994; Tanenhaus & Trueswell, 1995; Trueswell, Tanenhaus, & Kello, 1993). We chose to examine the processing of object relative clauses such as those in (1), because these structures are well known in psycholinguistics to differ in comprehension difficulty with (1b) being more difficult than (1a) (Gennari & MacDonald, 2008, 2009; Mak, Vonk, & Schriefers, 2002; Traxler, Morris, & Seely, 2002).

(1a) The movie that the director watched received a prize. (Inanimate-head, low-competition)

(1b) The director that the movie impressed received a prize. (Animate-head, high-competition)

The difficulty in sentences such as (1b) stems from the fact that animate and inanimate nouns are strongly associated with agent and patient roles respectively as animates tend to be the entity that perform actions and inanimate are the recipients of the action performed. Therefore, when the animate entity *The director* is first encountered in (1b) the comprehender incorrectly assumes it to be the agent of the action, as this is the most probable option. However, as the sentence proceeds with *that the* it becomes clear the animate entity is not in fact the agent of the action, but instead it is perhaps the object that is being acted upon, and consequently an upcoming agent is expected. Yet, when the inanimate noun is encountered, it’s meaning is initially inconsistent with an agent role because inanimate nouns are typically patients or affected participants in the event. This generates difficulty in determining the relationship between the movie and the director, and even more so when the verb *impressed* is reached: multiple competing alternative roles are evaluated, with strongly associated roles for the nouns (animate = agent, inanimate = affected participant) having to be inhibited in favour of the less frequent roles indicated by the verb (e.g. the inanimate noun *movie* receives an agent-like role of cause). In contrast, in structures such as (1a), the first encountered inanimate noun receives the expected patient role, and the structure is easily interpreted based on noun meaning and structure. Thus, the difference in processing difficulty between (1a) and (1b) is thought to derive from the difference in the number of alternative semantic role interpretations entertained as the sentence unfolds, with case (1b) having a greater number of alternative interpretations as the sentence unfolds.

The presence of the aforementioned competition mechanisms is confirmed by previous comprehension studies (Gennari & MacDonald, 2008). These authors found that the number of alternative thematic role relationships that speakers entertain predicted the reading times for these sentences. They conducted a completion study in which participants were presented with the initial fragment of a sentence taking the form *The N that the N…* (where N = noun), e.g. *The movie that the director…*, and were then asked to complete the sentence. The responses were coded in terms of the number of alternative thematic role relations that were produced for each item (e.g. Experiencer-Theme in *The director that the movie impressed…* or Agent-Theme in *The director that the movie was written by…*). This provided a measure of the number of alternative interpretations of who-is-doing-what-to-whom that could be entertained during comprehension of the sentence. It was shown that the number of alternative thematic role completions predicted the reading times of subsequent words after *The N that the N* during a word-by-word self-paced reading task. Therefore, these results suggest that the level of semantic indeterminacy regarding who-is-doing-what-to-whom predicts difficulty in comprehension, presumably because each of the alternatives is competing for selection. What is unclear, however, is the extent to which similar competition processes are engaged during production. Do speakers' entertain alternative utterances? And do these utterances compete with one another?

This study aims to investigate whether competition between alternative interpretations influences the comprehension of subordinate relative clauses such as those in (1), as previously shown (Gennari and MacDonald, 2008), and more critically, whether competition between alternative utterances also takes place in production. The comprehension task had the self-paced word-by-word reading design used by Gennari and MacDonald (2008) but with more items. The configuration of animate and inanimate nouns within the structures in (1) provides conflicting cues as to who-is-doing-what-to-whom in the sentence and hence causes competition: In (1b), the semantic roles strongly associated with the animacy of the nouns (the expected interpretation) must be inhibited when the verb *impressed* is reached, giving rise to competition between the various alternatives (Gennari & MacDonald, 2008, 2009; Mak, et al., 2002; Traxler, et al., 2002). Thus, it was predicted that from the relative clause verb onwards that longer reading times and more comprehension errors should be observed for the high-competition condition compared with the low-competition condition, thereby replicating previous results. Furthermore, inline with previous results it was expected that the number of alternative semantic role interpretations from the sentence should predict comprehension difficulty with a greater number of alternatives predicting longer reading times at critical portions of the sentence, in particular the relative clause verb.

A sentence completion paradigm was used as the production task. In this task, the initial portion of the comprehension stimuli were presented (e.g. *The movie that the director…* or *The director that the movie…*) and the task was for the participant to complete the sentence fully. These sentences varied in the ease of continuation, and required assigning sentential roles to the nouns of the fragments, as in the comprehension task. The completion task requires selecting an appropriate verb phrase to continue the fragment in such as way that the roles implied by the verb matches the meaning of the nouns. Finally, previous data (Gennari & MacDonald, 2008) indicate that there are various alternative ways to continue these fragments, particularly in the high-competition condition, suggesting that speakers have to select one alternative among many, potentially leading to competition. This might lead to similar competition effects being found in both production and comprehension tasks. It was predicted that if competition similarly effects production and comprehension processes, this should be indexed in longer production initiation times and greater number of production errors in the high-competition cases compared to low-competition cases. Furthermore, these measures should correlate with the number of alternative semantic role interpretations in a similar manner in production and comprehension.

Nevertheless, there are differences in the task demands between production and comprehension. The competition in comprehension involves competition between the predicted and the incoming interpretation, whereas in the completion task, the competition involves alternative possible utterances given the constraints provided by these nouns and the syntactic structure. Therefore, in both tasks there is competition between alternative roles assigned to the nouns, but speakers' must select and plan a structure to utter, whereas comprehenders' select an interpretation to continue semantic integration and prediction as the sentence unfolds.

2.2 Methods

2.2.1 Participants.

Thirty-nine native English speakers completed the study. All were students at the University of York (UK).

2.2.2 Materials.

Forty items with subordinate clauses such as that in (1) were used in the reading comprehension task. Each item had two versions varying in noun animacy and subordinate verb, yielding a high-competition version and a low-competition version, as in (1) (see Appendix A for full list of items). The same items have been used in several related experiments (Gennari & MacDonald, 2008, 2009; Mak, et al., 2002; Traxler, et al., 2002) and the manipulation is well known to show robust effects of processing difficulty that are driven by thematic role competition as processing times are predicted by the number of possible alternative thematic role relationships. Thus, this manipulation is regarded a good test of thematic role competition. The nouns of the stimulus sentences were matched for length and frequency across conditions as shown by *t*-tests, and the same was true of the verbs (see Table 2.1 for descriptive statistics: all *t*s < 1.5, all *p*s > .14). The 80 experimental sentences were randomly intermixed with 80 filler sentences. The majority of the filler sentences (57%) were subject-verb-object main clause structures. The production task included the same items as the comprehension task but only the initial fragment of the sentence was presented taking the form *The Noun that the Noun…* (e.g. *The director that the movie…*).

Table 2.1 The mean log word frequencies and length for the nouns and verbs from the high-competition and low-competition conditions.

	Condition	Example	Log word frequency	Length
Nouns	High-competition	*director*	4.18	6.88
	Low-competition	*movie*	4.27	6.02
Verbs	High-competition	*impressed*	4.05	7.64
	Low-competition	*watched*	4.08	7.57

2.2.3 Procedures.

The tasks were presented using E-prime software. Each participant performed two tasks, a production and a comprehension task, in varying order. In the comprehension task, stimulus sentences were presented word-by-word using a self-paced reading paradigm. We measured the reading times for each word position. Each sentence was followed by a comprehension question that required a YES/NO response. 53% of these questions referred to the content of the subordinate clause. For instance, for the sentence *The director that the movie pleased received a prize* the question was *Did the movie receive a prize?*. This was done to ensure that participants understood the meaning of the subordinate clause. In the production task, participants were presented with the initial fragment of a sentence in a word-by-word self-paced paradigm. The fragments had the form *The Noun that the Noun*, e.g., *The director that the movie….*

Participants were instructed to read the fragment very carefully and to complete the fragment aloud into a full sentence. We recorded the content and the planning time (speech onset time, from the offset of the final word) of their utterances using a microphone as the input in the E-prime experiment.

Note, it is possible that differences in initiation times between conditions are a spill over from differences in the speed at which participants comprehend the fragment. Whilst this is an inherent problem with the sentence completion task design, there is good reason to assume that this problem does not explain the results obtained. Firstly, the difficulty in comprehension did not arise until the subordinate verb (e.g., *impressed* in (1b)), thus suggesting that the high- vs. low-competition fragments used in the production task did not differ in reading difficulty. Secondly, as shown below, comparable results were found when analysing production error data to those found from the production initiation times, and it is unlikely that the production errors can be so easily explained in terms of problems comprehending the sentence fragment. Finally, and perhaps most convincingly, the reading times at each word position did not correlate with the planning time in the completion task, suggesting that the competition processes in these two tasks are sufficiently distinct, even though these timing measures are predicted by other measure reflecting competition (as shown below).

2.2.4 Design.

For each task, the items were split across two lists with each list containing 40 experimental items (20 high-competition and 20 low-competition sentences) and 40 fillers. Each participant saw only one list for each task. The lists were constructed in such a way that the high-competition and low-competition version of the same item would be on a separate list for a given task (Latin Square design), but both versions would be seen once in the production task and once in the comprehension task. Thus, within a task every subject saw one version of each item but equal number of cases in each condition, and across tasks, no participant saw the same version of any item. The item order was randomised, and the order of the production and the comprehension task was counterbalanced across participants. There was found to be no significant effect of task order; the results from mixed ANOVAs with processing times as the dependent variable, competition conditions as repeated factors, and task order as between subjects factor revealed no interaction of competition with task order, either in production or comprehension.

2.2.4.1 Data coding.

To analyse the production responses, we identified completion errors by simple inspection of the transcribed utterances. Continuations that were nonsensical were considered as errors. For example, for a fragment such as *The scientist that the book…*, the completion *had written* was considered an error, as books cannot plausibly write scientists. Two independent researchers coded the data and they agreed on more than 95% of the cases coded (cases in which the coders disagreed were discussed until a code was agreed upon). Additionally, we computed a measure indexing competition: the production data was manually coded to obtain information about the number of alternative semantic role interpretations that speakers associate with the prompt fragments. This information was then correlated with the dependent measures to establish whether the number of available alternative interpretations predicts processing difficulty, thus suggesting that these alternatives were indeed entertained during processing, with more alternatives engendering more competition (see below). We specifically coded for each item the semantic roles implied by the subordinate verbs of the produced completions. We used the coding criteria of Gennari and Macdonald (2008), where standard linguistic definitions of agent, patient, experiencer, cause and theme sentential roles are provided. For each item, we thus computed the number of semantic role pairs assigned to the relevant nouns across speakers. For example, a verb like *impress* in *the director that the movie impressed* assigns an experiencer role to *director* and cause role to *movie* and these two roles were computed as one possible interpretation of the subordinate clause, whereas a different pair of roles assigned to these nouns such as agent and patient (e.g., *the director that the movie was written by)* was computed as a different interpretation. For instance, *The director that movie…* example was found to be associated with three alternative thematic role interpretations, those being “experiencer-theme” as in *The director that the movie pleased…*, “theme-

theme” as in *The director that the movie was about…*, or “agent-theme” as in *The director that the movie was made by….*

2.2.4.2 Data analysis.

Data analyses of processing times (planning and reading times) were all carried on correct responses only (correct production trials, and sentences for which participants answered the comprehension question correctly). For the analysis of reading times, residual reading times were used as the dependent measure, as standard in psycholinguistics, although raw reading times display the same effects, as shown in Figure 2.1. Residuals are calculated from regressing out word length from raw reading times by calculating a regression equation for each subject across all items to predict their reading times for each word length, and then subtracting the word-length predicted reading times from the actual reading times. Although the conditions were matched for length across conditions, calculating the residual reading times is useful as it adjusts for baseline differences in reading rates across individuals and also controls for inter-subject variability in sensitivity to word-length (Pearlmutter & MacDonald, 1995). Furthermore, residual reading data is more normally distributed compared to raw reading data (Fedorenko, Piantadosi, & Gibson, 2012). For the analysis of production planning times, we used LOG transformed times to approximate normally distributed data points, although analyses of raw planning times yield similar statistical results. Responses that deviated by more than 3 SDs from the mean initiation times were removed from the analysis.

2.3 Results

2.3.1 Sentence comprehension task

2.3.1.1 Comprehension accuracy.

The overall mean accuracy across participants for the comprehension questions was 89% (SD 2.71). Response accuracy to the high-competition items was significantly lower compared to the low-competition items suggesting increased processing difficulty in the high competition case (item analysis: animate M = 84%, SD = 16.15; inanimate M = 94%, SD = 11.22; $t(39) = -3.23$, $p < .005$; subject analysis: animate M = 84.33%, SD = 10.41; inanimate M = 93.86%, SD = 6.60; $t(38) = -5.01$, $p < .001$).

2.3.1.2 Reading times.

The analyses were conducted across items and also across subjects and the results were found to be similar. Figure 2.1 plots the reading times for each word position as a function of condition. A repeated measures ANOVA was performed with residual reading time as the dependent variable and condition (high- vs. low-competition) and word-position (subordinate noun, e.g. *movie*, subordinate verb, e.g. *pleased*, and the main verb region, e.g. *had received a*) as factors. A main effect of condition was found ($F1(1, 38) = 10.34$, $p < .01$; $F2(1, 39) = 7.55$, $p < .01$). No main effect of position was found ($F1(2,76) = 1.47$, ns. ; $F2(2,78) = 1.42$, ns.), and there was no condition x position interaction ($F1(2,76) = 1.74$, ns.; $F2(2,78) = 1.82$, ns.). Planned comparisons showed significantly slower residual reading times for the high-competition vs. low-competition condition at the subordinate verb (item analysis: $t(39) = 2.31$, $p = .03$; subject analysis: $t(38) = 2.54$, $p = .02$), and also at the main verb region (item analysis: $t(39) = 2.80$, $p < .01$; subject analysis: $t(38) = 3.85$, $p < .001$). No difference was found at the subordinate noun across items or across subjects. Taken together, these results replicate similar effects reported in the literature (Gennari & MacDonald, 2008, 2009; Mak, et al., 2002; Traxler, et al., 2002) and clearly indicate that as the sentence proceeds, readers encountered more difficulty in the high-competition condition when the subordinate verb is encountered due to the difficulty in determining who is doing what to whom in the subordinate structure. This difficulty continues into the main verb phrase of the sentence.

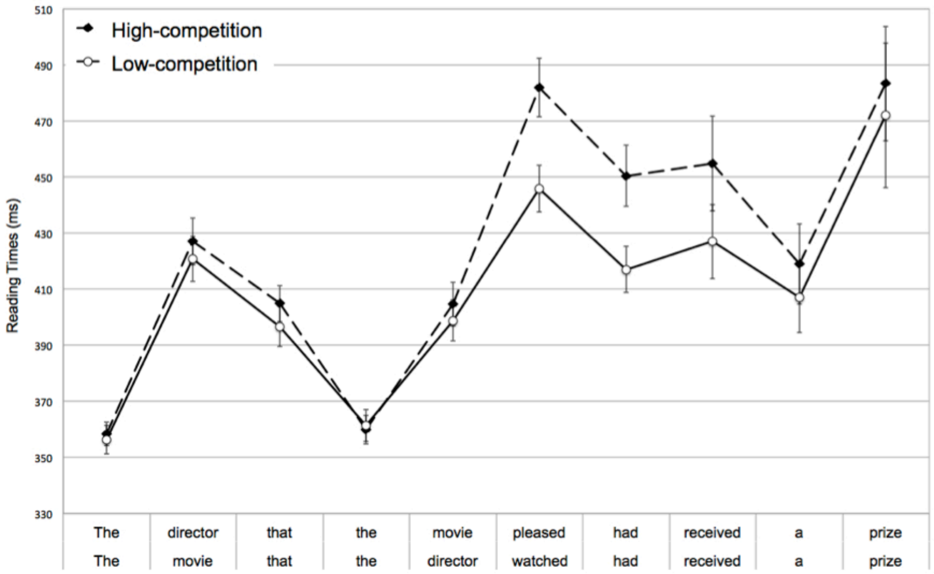


Figure 2.1 The average reading times for each word position from the comprehension task.

2.3.2 Sentence-completion task

2.3.2.1 Production responses.

The log-transformed production data was coded for accuracy and length (number of characters in the subordinate verb). Across participants the mean proportion of correct responses was 0.89 (SD .13). There were significantly fewer correct responses for the high-competition items relative to the low-competition items (item analysis: high-competition M = .81, SD = .16; low-competition M = .97, SD = .06; $t(39) = -6.47$, $p < .001$; subject analysis: high-competition M = .81, SD = .21; low-competition M = .97, SD = .09; $t(36) = -5.92$, $p < .001$), confirming the expectation that high-competition structures are more difficult to complete. Across items, the majority of errors (60.4%) were semantic role errors, for instance *The director that the movie… "watched was good"*. This clearly suggests that the participants attributed incorrect roles to the prompt nouns because they were unable to inhibit the more prepotent verb response.

2.3.2.2 Production planning times.

The log-transformed initiation times were longer for the high-competition compared to low-competition items (item analysis: high-competition M = 3.46, SD = .17; low-competition M = 3.31, SD = .12; subject analysis: high-competition

M = 3.34, SD = .26; low-competition M = 3.17, SD = .20). This difference was found to be significant with a paired-samples *t*-test (item analysis: *t*(39) = 5.13, *p* < .001; subject analysis: *t*(38) = 6.51, *p* < .001). The untransformed data from the item analysis are summarised in Figure 2.2.

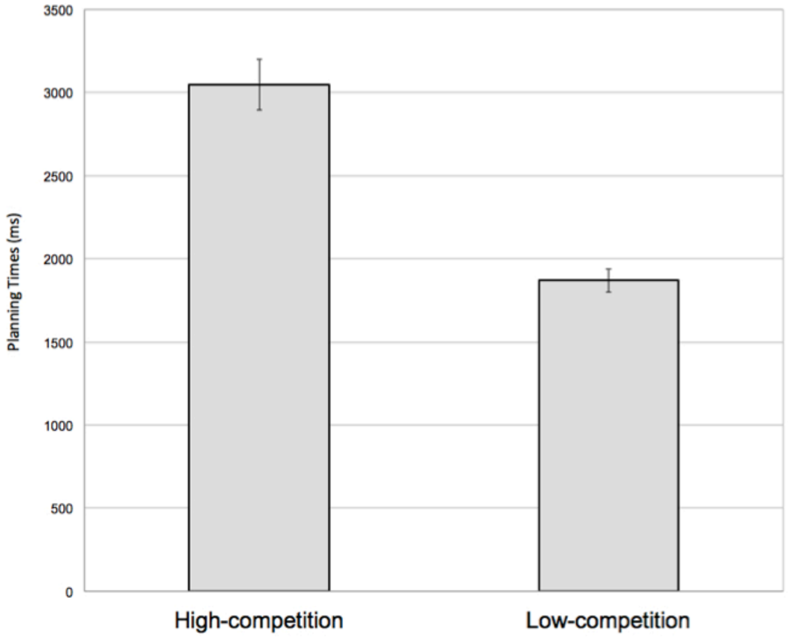


Figure 2.2 The average initiation times from the production task in milleseconds.

To establish that planning times were not unduly influenced by the length of the uttered completions (longer phrases take longer to plan), we used utterance length for each item and participant as nuisance regressor in a hierarchical multiple regression. In the item analysis, length alone explained 13% of the variance in planning times, a significant predictor (*F*(1, 78) = 11.73, *p* < .001). Yet, adding condition (high-competition vs. low-competition) into the model significantly increased the variance explained to 22% (*F*change(1, 77) = 8.85, *p* < .01). In the subject analysis, length alone did not significantly predict the planning times (R-square = .1%; *F*(1,76) = .05, ns.). Adding condition into the model significantly increased the variance explained to 14% (*F*change(1,75) = 12.22, *p* < .001). Therefore, the high-competition condition was more difficult to plan compared to the low-competition condition regardless of utterance length.

2.3.3 Predicting processing difficulty in comprehension and production.

To establish whether the differences in difficulty that we have revealed in both production planning and reading comprehension are indeed due to competition processes, we computed the number of alternative semantic role interpretations (roles such as agent, patient, experiencer, etc.) from our production data to correlate with either production and comprehension time measures (see *Data coding* section). These alternatives represent frequent preferences across speakers when speakers' choices converge, but indicate variable preferences when they do not, and hence, more potentially viable alternatives. We reasoned that if comprehenders entertained alternative semantic roles for the nouns at the point in which the subordinate verb is encountered (e.g., *impressed* in example 1b.), then, the reading time of this verb should correlate with the number of viable alternative semantic roles. This is because these alternatives enter in competition with the meaning of the verb being processed, particularly when this verb is not part of the active alternative set (indeed, verbs like *impress* for cases like (1) are infrequent in the completion data). Similarly, we reasoned that if speakers in the completion task entertained alternative verb continuations implying different semantic roles before speaking, their planning times should also correlate with the number of viable alternative interpretations provided across different speakers. In both cases, regularities obtained across speakers could be inferred to play a role in on-line reading and planning.

A significant correlation was found between the number of alternative thematic role relationships and the production planning times ($r = .467, p < .001$), and also residual reading times at the subordinate verb position thus replicating Gennari and MacDonald (2008) ($r = .236$, $p < .05$). Note that the relationship between planning times and number of alternative interpretations remains significant even if length of production is included into the regression model (the variance explained increased from 13% to 24% when number of interpretations is added into the model; change statistics: Fchange(1, 77) = 11.10, $p < .001$). These results suggest that the greater number of alternative interpretations regarding who-is-doing-what-to-whom in our stimulus sentences, the more difficult it is to produce and comprehend these sentences.

It is interesting to note, however, that despite finding a correlation with the number of thematic role alternatives in both production and comprehension tasks, production and comprehension measures do not correlate directly with each other, regardless of how the correlation is computed: whether the correlation is performed across items or subjects, when only the animates are selected, or by calculating the difference score, there is no correlation between the production initiation times and the residual reading times at any word-position (all *r*s < .20, all *p*s > .12). This might suggest some differences in production and comprehension processes.

2.4 Discussion

This study investigated the extent to which competition between alternatives plans/interpretations similarly affects comprehension and production processes. A similar pattern of results was found across production and comprehension tasks. The animate-head condition (high-competition condition), in which multiple alternative thematic role relationships can be entertained, was both harder to comprehend and harder to produce relative to the inanimate-head condition (low-competition condition), in which fewer alternatives are possible. In comprehension, there were longer reading times and an increased error rate for the animate compared to inanimate condition, replicating Gennari and MacDonald (2008). A similar pattern was found in the production task; longer speech initiation times and more errors were found for the animate condition relative to the inanimate condition. Furthermore, an analysis of error types revealed that the majority of production errors were thematic role errors, of the kind *The director that the movie… "watched was good"* (see section 2.3.2.1 Production responses). This clearly suggests a failure to resolve the semantic competition from the alternative interpretations regarding the relationship between *director* and *movie*, and a tendency for the participants to attribute incorrect roles as they were unable to inhibit the more prepotent verb response. Finally, a correlation was found between processing difficulty in each task (reading times and initiation times) and the number of alternative thematic role relationships that were entertained for each item. This suggests that the degree of semantic role competition in a sentence modulates processing difficulty in a similar manner across production and comprehension tasks. Together these results might be used to argue for shared processing mechanisms in production and comprehension.

The results from the current study clearly show that during production speakers' entertain alternative choices, which compete for selection, in a manner that parallels affects that have been found in comprehension (Gennari & MacDonald, 2008). Previous evidence has shown that semantic competition occurs between related concepts and words at the lemma level of representation during production, however, the extent to which competition occurs at the level of functional assignment where grammatical roles and structures are assigned is less clear. Some studies have shown that alternative syntactic choices compete and thus increase production difficulty (Montag & MacDonald, in prep.; Stallings, et al., 1998), however others have argued that the presence of alternative structures can facilitate production by increasing the flexibility in production choices (V. S. Ferreira, 1996). The initiation time date from the current study clearly suggests that alternative choices compete to negatively influence production processes; the greater the number of alternatives, the longer it takes to initiate production. It is worth noting that whilst our manipulation of alternative choices was semantic in nature, in that it represented the variation in the different semantic roles assigned to the two nouns in a sentence, this also impacts on the syntactic structure assigned. The nature of thematic roles assigned controls the type of syntactic structure permitted, for instance, the assignment of agent-patient roles as in 2) means that only a passive relative clause structure is permitted, whereas the assignment of experiencer-cause roles as in 3) permits an active relative clause structure. Therefore, the present results suggest that in sentence production, as in comprehension, alternative thematic role relationships and/or syntactic structures compete for selection, thereby influencing processing difficulty.

2) *The director that the movie was written by was well renowned*

3) *The director that the movie impressed was well renowned*

2.4.1 Production-comprehension overlap

Finding parallel effects of competition in production and comprehension tasks might be taken as evidence of shared processing mechanisms. This is incompatible with the opinion of many in the psycholinguistic literature who have suggested that production and comprehension are separate tasks (Bock, 1995; Dell, Burger, et al., 1997; Levelt, et al., 1999; McDonald, et al., 1993), but is more consistent with the PDC approach, mentioned in the introduction. Here it is argued that comprehension is sensitive to distributions in the language that fundamentally derive from limitations and pressures on the production system. Thus, parallel production and comprehension effects are predicted. Note, however, that whilst this theory predicts strong production-comprehension interactions, it does not necessarily predict shared processing systems; there may be separable but interacting systems, although claims of shared processing systems have been explicitly made (Bock, et al., 2007; Chang, et al., 2006).

The comprehension difficulty in the current task has been explained using a constraint-satisfaction framework, and has been attributed to conflicting semantic (animacy) and structural (word-order) cues (Gennari & MacDonald, 2008). According to constraint-satisfaction approaches, multiple constraints, such as semantics and syntax, are activated in parallel and interact to influence language processing. The power of each constraint is probabilistic, determined from distributional information from real-world experience. In the case of the animate condition, based on linguistic and real-world experience, the most strongly associated roles for the nouns (*director* = agent, *movie* = affected participant) are not compatible with the structure of the relative clause, and also with the roles indicated by the verb (*pleased*). This results in a situation whereby multiple alternative thematic role relationships and syntactic structures are activated, and the most frequent animacy interpretation must be inhibited in favour of a less frequent alternative. Thus, a constraint-based argument for cue-based competition easily accounts for the findings from the comprehension task that the number of alternative interpretations predicts reading difficulty. Finding a parallel effect in the production task suggests that cue-based competition might act on production as in comprehension. That conceptual and syntactic information interact to influence production is hard to account for in a strictly encapsulated production model where conceptual and grammatical information do not have bi-directional influence (Bock & Levelt, 1994; Levelt, et al., 1999), and appears more consistent with an interactive constraint-satisfaction approach. Indeed, the argument that both production and comprehension can be incorporated into a single constraint-based model has been presented by others, showing semantic-syntactic interactions in production (Haskell & MacDonald, 2003) and parallel effects of constraints in production and comprehension tasks (Thornton & MacDonald, 2003).

However, it is important to note that finding parallel behavioural effects in production and comprehension tasks does not necessarily imply a common processing system. Indeed, the fact that production and comprehension tasks did not directly correlate might hint at differences in the manner in which the competition arises in each task, and/or differences in the mechanisms used to resolve competition. For instance, the conflict in comprehension might reflect competition between predicted and actual input, whereas in production there is competition between alternative plans and in memory retrieval.

It is important to highlight some potential limitations of the task-design that may have implications for the interpretations of the results. Specifically, there are obvious limitations to the sentence-completion task in the context of the current objective of examining production-comprehension overlap given that the production task itself includes a comprehension component and because it somewhat artificially constrains the sentences that can be produced. Whilst this issue cannot be ignored there are certain arguments as to why the results do have relevant implications for the current research question. Firstly, whilst the sentence-completion task may itself be unnaturalistic, by forcing the producer to structure a sentence in a particular way it shows which structures would go against their natural structural preferences and their desired thematic role arrangement. Therefore, with this respect the results do inform on production processes more generally. Furthermore, the results have implications for thematic role assignment in production. In particular, the results show that during production, as in comprehension, animate entities automatically activate a greater number of plausible event roles and that these associations influence the ease by which sentences can be formed in production (or understood in comprehension). Indeed, it is exactly because of these automatic associations that the competition arises here when the producer is forced to inhibit alternative activated relationships i.e. competition could not arise unless the producer had automatically activated alternative thematic role relationships. Therefore, whilst it is important to bear in mind the obvious limitations of the paradigm it could be argued that the results do inform to some extent on structural preferences and thematic role assignment in production.

Therefore, to conclude, this data provides evidence that both production and comprehension are affected by competition, however, the results are inconclusive with regard the nature of the competition effect, and the notion of separate underlying processes cannot be rejected. The following chapter describes the results from an fMRI experiment that aimed to more conclusively determine whether production and comprehension rely on common or distinct systems for competition resolution processes.

Chapter 3

The neural processes engaged by cue-based competition in sentence production and comprehension: an fMRI investigation.

3.1 Introduction

The relationship between sentence production and sentence comprehension in terms of common/distinct neural processes has received limited attention in the literature. Those studies that have directly compared the two tasks have shown that both recruit a common fronto-temporal network including the posterior temporal lobe and LIFG (Menenti, et al., 2011; Segaert, et al., 2011). However, the recruitment of common brain regions does not necessarily imply that similar processes take place in both production and comprehension; they could reflect the recruitment of common semantic and grammatical knowledge, common processes such as meaning access and sentence assembly, or a mixture of both. It remains unclear therefore whether and how subcomponent processes in production and comprehension are related. This chapter describes the results from an fMRI experiment that investigates the extent to which production and comprehension share neural processes to resolve competition in sentences using an adapted version of the paradigm described in the previous chapter. Finding evidence of brain regions that are similarly sensitive to competition demands in both production and comprehension would suggest shared inhibition/selection processes across tasks.

Competition may occur in comprehension when multiple alternative interpretations are activated and selection between them takes place. In studies of lexical ambiguity, for example, equally frequent meanings of an ambiguous word like *bowl* are activated initially, and subsequent inhibition/selection processes are required to arrive at the intended meaning, often with the help of contextual cues. As discussed in Chapter 1, the LIFG is thought to play a critical role in resolving competition between alternative meanings by selecting the appropriate response and inhibiting inappropriate information. Several studies have shown that LIFG is recruited when processing sentences that contain semantically ambiguous words (Rodd, et al., 2005; Rodd, et al., 2011; Rodd, Longe, Randall, & Tyler, 2010). For instance, LIFG (BA44/pars opercularis) shows increased activity for sentences such as *She quickly learnt that injured calves moo loudly* presumably as it is involved in resolving the competition between alternative interpretations of *calves* (Rodd, Longeb, et al., 2010).

LIFG is also involved in resolving ambiguities between alternative possible syntactic structures (Fiebach, et al., 2004; January, et al., 2009; Mason, et al., 2003; Rodd, Longeb, et al., 2010). For instance, LIFG is responsive to syntactically ambiguous sentences, such as *The experienced soldiers warned about the dangers conducted the midnight raid*, where *warned* can be interpreted as either a main verb or as a reduced relative clause verb, compared to unambiguous sentences such as *The experienced soldiers who were told about the dangers conducted the midnight raid.* Particularly relevant for this study, LIFG is activated in cases where alternative possible thematic role relationships could be entertained, for instance using similar stimuli to those used in this study, LIFG has been shown to show increased activation for relative clauses with an animacy configuration that conflicts with the relative-clause structure, as in the case of *The director that the movie…* compared to *The movie that the director…* (Caplan, Chen, et al., 2008; Caplan, Stanczak, et al., 2008; E. Chen, et al., 2006).

LIFG is thought to be involved in resolving competition in production as well as comprehension. Damage to this area disrupts performance in both production and comprehension tasks involving high-competition (Jefferies & Lambon Ralph, 2006; Novick, et al., 2009; G. Robinson, et al., 1998; G. Robinson, et al., 2010; G. Robinson, et al., 2005; Schnur et al., 2009). For example, patients with LIFG damage perform less well when naming objects with low-name-agreement (e.g. *couch*, *sofa*, *settee*) compared to naming objects with high-name-agreement (e.g. *apple*), presumably due to their inability to resolve the competition from alternative responses (Novick, et al., 2009). Production deficits are also evident at the sentence level. For example, LIFG patients (but not patients with posterior damage, or damage to frontal areas other than LIFG) show deficits in sentence generation tasks when the sentence contains a word associated with multiple alternative senses, compared to a word with fewer senses (G. Robinson, et al., 2010). In terms of fMRI, there is evidence that common LIFG regions are modulated by competition in word-generation and word-classification tasks, suggesting possible shared involvement across production and comprehension tasks (Thompson-Schill, et al., 1997). Therefore, LIFG plays a critical role in tasks that require the ability to resolve competition between alternatives, and may be involved in both sentence production and comprehension.

Whilst production and comprehension might share processes to resolve competition in LIFG, there is reason to assume distinct patterns of activity elsewhere based on task differences. It seems likely that competition resolution is the result of a multi-faceted process involving the interaction of multiple areas depending on task demands. Psycholinguistic approaches have typically assumed that production and comprehension tasks involve distinct component processes (Bock & Levelt, 1994; MacDonald, et al., 1994). Indeed, production requires word retrieval and planning of a sentence structure, whereas comprehension involves word recognition and the understanding of syntactic-semantic relations between words. These processes have been long argued to give rise to marked asymmetries between these tasks. Sentence production, for example, often involves false starts, disfluencies, and errors, which are thought to arise from production planning processes that are not shared with comprehension (Bock & Levelt, 1994; Garrett, 1980; Levelt, et al., 1999). Competition processes also differ in that in production the conflict arises from the generation of competing sentence plans, whereas in comprehension competition occurs due to the conflict between linguistic predictions and the external input. These observations suggest differences in the mechanisms engaged by production and comprehension tasks. This is consistent with many production studies recruiting partially distinct neural networks from those found typically in comprehension studies, including supplementary motor regions, the cingulate cortex, parietal areas, and subcortical structures that are associated with motor planning and memory retrieval (Barch, Braver, Sabb, & Noll, 2000; Sörös et al., 2006; Tremblay & Gracco, 2009; Tremblay & Small, 2011a, 2011b; Whitney et al., 2009).

Together these findings suggest that the LIFG may play a role in both production and comprehension when resolving competition, but that there may also be differences in the networks implementing each task and cooperating with LIFG. To evaluate this possibility, fMRI was used to compare the production and comprehension of high- and low-competition sentences (as described in Chapter 1). Here we investigated whether LIFG was commonly modulated by competition across production and comprehension tasks. To do this, a region of interest of LIFG was defined in each individual based on data from an independent Stroop task (localiser scan). This guarantees a high degree of anatomical and functional specificity that is not influenced by normalisation procedures (Juch, Zimine, Seghier, Lazeyras, & Fasel, 2005; Swallow, Braver, Snyder, Speer, & Zacks, 2003). Additionally, functional connectivity analyses were conducted using the LIFG as seed region to determine the networks cooperating with LIFG as a function of competition condition. Based on the view outlined above, it was predicted that the levels of competition should modulate activity in LIFG for both tasks. Critically, if production and comprehension implement competition processes differently and contain task-specific component processes, as suggested by psycholinguistics research, distinct neural networks should interact with LIFG as a function of competition resolution demands.

3.2 Methods

3.2.1 Participants.

17 right-handed native English speaking students at the University of York, who did not take part in Experiment 1, participated in this study. No participants had any history of psychiatric illness nor any known neurological damage (10 males, 7 females, mean age = 23.2 years).

3.2.2 Materials.

The same 42 items and fragments used in Chapter 2 (see Table 2.1) were used in this experiment (84 experimental items in total).

3.2.3 Task design.

Three fMRI scans were conducted: comprehension task, production task, and a colour Stroop task. The Stroop task was used as a localiser to identify a region of interest within the LIFG that is involved in competition resolution independently of our manipulation. The order of the production and comprehension scans was counterbalanced across participants, and the Stroop task was always the last to be completed. The production and comprehension scans were presented in an event-related design. The most efficient ordering of events was determined using Optseq (http://www.freesurfer.net/optseq). Null time was intermixed between trials and randomly varied between 0 and 18 seconds, with an averaged inter-trial time of 4.67 seconds (Josephs & Henson, 1999). Every event type followed each other with equal probability (e.g., for three event types, every type followed every other across the experiment 33% of the time).

3.2.3.1 Comprehension task.

In each event a sentence was visually presented (white font on a black background) split into two consecutive halves of 3 seconds each. The first half contained the subordinate clause (e.g. *The movie that the director watched*) and the second half contained the remaining of the sentence. In order to ensure that the participants were processing the meaning of the sentences, 16 catch-trials were intermixed randomly with the experimental trials. Catch trials took the form of YES/NO comprehension questions as in Experiment 1. The participants were given 4 seconds in which to answer the question. Between trials a series of "+"s was presented which was the same length as the average sentence length. This acted as a visual baseline. In total the scan lasted 906 seconds. For each subject, the high-competition and low-competition version of an item was assigned to different halves of the experiment so that when one version appeared in the first half of the experiment, the remaining version appeared in the second half. The two halves of the experiments were counterbalanced across subjects so that each subject saw the two versions of an item in a different order. This eliminates potential influences of item order on group statistics, and similar techniques have been used successfully in related studies in the literature (E. Chen, et al., 2006).

3.2.3.2 Production task.

Each trial presented a sentence fragment (e.g. *The director that the movie…*) for 2 seconds after which the symbols "???" appeared for 4 seconds. Participants were instructed to covertly complete the sentence fully and meaningfully when they saw these symbols and to press a button when they were finished. To act as a reading baseline, 84 read-only items were intermixed with the production items. Here, the participant was instructed to simply read the fragment for meaning and press a button when they were finished. The read-only condition was made up of the same 84 experimental stimuli from the completion task except that they were presented in red font and followed by "XXX" rather than "???" as was the case in the production trials. After practice, the font colour thus indicated clearly from the beginning of the trial whether participants would complete or read the stimulus fragments. By contrasting the activity from the completion trials and the read-only trials, we aimed to remove the reading component of the trial, revealing only production-related activity. Note that the high- and low-competition condition were contrasted with the same read-only control condition, thus the baselines were identical across conditions. Note that regions found to be active only in the completion task, as compared to the comprehension task above, which constitute the majority of our results, cannot be attributed to any influence of the reading component of the completion task. If for example the reading component of the completion task was unsuccessfully removed (via the contrast between the completion trials and the read-only trials), we would expect the production results to be similar to the comprehension results from the main comprehension task above, which was clearly not the case. Furthermore, in areas that did show a parallel pattern of activity across tasks, when only the reading component of the trial was compared in the production task no effect of competition was found (see results section), thus clearly demonstrating that the production results cannot be explained in terms of reading difficulty.

The production scan was divided into two runs, one lasting 842 seconds and the other lasting 830 seconds. The order of the runs was counterbalanced across participants and the high- and low-competition experimental items were presented in separate runs. The order of event types was determined by Optseq and was such that each event type followed each other with equal frequency.

3.2.3.3 Stroop task (localiser).

This task was taken from previous studies (Milham et al., 2001), and has been used successfully as an LIFG localiser in similar language studies in the literature (Hindy, Altmann, Kalenika, & Thompson-Schill, 2012; January, et al., 2009). The responses were restricted to three font colours -yellow, green and blue. The task was to indicate the font colour pressing a button on a button box, whilst ignoring the word meaning. There were three conditions: incongruent-eligible, incongruent-ineligible, and neutral. In the incongruent-eligible trials, the word and ink colour were incongruent and the word denoted a colour that was a potential response (yellow, green, or blue). In the incongruent-ineligible trials, the word denoted a colour that was not a potential response (orange, brown, or red). The distinction between eligible and ineligible trials is that eligible trials will involve both conflict at the motor response level (since the word indicates a possible response), as well as conflict at the representational level (since both the word and the ink involve colour representations). However, ineligible trials will only involve conflict at the representational level (January, et al., 2009). Neutral trials consisted of non-colour words that were length and frequency matched to the colour items (e.g. plenty, horse, deal).

3.2.3.4 Acquisition parameters.

Imaging was carried out using a 3T Signa Excite MRI scanner at the York Neuroimaging Centre (YNiC). High-resolution whole brain T1-weighted structural images were obtained for all participants (1mm x 1mm x 1mm). Functional images were obtained using a gradient-echo EPI sequence with 38 contiguous axial slices per volume (TR = 2000 ms, TE = 20 ms, flip angle 90°, matrix 64x64, FOV 24cm, slice thickness = 3.5mm). A T1-weighted FLAIR image was also obtained to aid co-registration.

3.2.3.5 Data analysis.

Data analyses were carried out using FSL tools (the software library of the Oxford Centre for Functional MRI of the Brain (FMRIB); www. fmrib.ox.ac.uk/fsl). First- and higher-level analyses were carried out using FEAT

(FMRI Expert Analysis Tool). The two production runs were combined by concatenating their demeaned data. Pre-processing of the data included motion correction (Jenkinson, Bannister, Brady, & Smith, 2002), slice-timing correction, brain extraction to remove scalp tissue and improve the coregistration, spatial smoothing using a Gaussian kernel of full-width-half-maximum (FHWHM) 8 mm, and high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, sigma=25.0 seconds). Time series analyses were conducted using FILM (FMRIB's Improved Linear Model) with local autocorrelation correction (Woolrich, Ripley, Brady, & Smith, 2001). The data was spatially re-aligned and normalised to the MNI standard space for group comparisons.

The data from each task were modelled separately with event-based explanatory variables corresponding to the condition and trial structure, which were convolved with a hemodynamic response function (HRF) (gamma function) with temporal derivatives added which account for small variations in the timing of the HRF. For all tasks, HRFs were aligned to the beginning of the event and lasted for the duration of the event except for the production trials, which were modelled as 4.5 seconds. This aimed to capture the reading portion of the trial (2 seconds) plus the planning and initial encoding of the utterance (2.5 seconds), rather than the articulation. This timing was determined using data from Experiment 1 in Chapter 2 as it was an intermediate between high- and low-competition conditions (3 seconds and 2 seconds respectively). Note that variations in the timing of the response across trials and conditions should be accounted for by inclusion of temporal derivatives into the model which adjust for variations in the timing of the HRF. Furthermore, it is unlikely that fMRI has the temporal resolution to detect such small variations in response timings (i.e. deviances of 500ms from the model). Also, if it were true that the modelled response was too long in the low-competition items and too short in the high-competition condition then this would have resulted in a greater proportion of the articulatory component being included in the results fro the low- compared to the high-competition condition (i.e. motor activity would be stronger in the low-competition condition) which was not the case. Several contrasts were computed for each data set. For the comprehension task, all the sentences were contrasted relative to the visual baseline (language - baseline (1, 1)), each condition separately relative to baseline (high-competition - baseline (1, 0); low-competition - baseline (0, 1)), and the direct competition contrast (high-competition – low-competition (1, -1). Similar contrasts were performed with the production data but this time contrasting the experimental trials with the read-only control trials (2 sets of control trials, one each for high- and low-competition). There were four production contrasts: all production > control (1, 1, -2), high-competition production > control (1, 0, -1), low-competition production > control (0, 1, -1), and the direct competition contrast in which high competition was contrasted with all other conditions (2, -1, -1). The Stroop data was modelled with covariates for each condition. The main contrast of interest was the representational competition contrast in which incongruent ineligible items were contrasted with neutral items.

3.2.3.6 Region of interest analysis.

The Stroop data was used to identify a region of LIFG - the pars opercularis (BA44) – which was sensitive to semantic conflict in each participant. This region was consistently activated in all participants and is considered to play a central role in competition resolution in language processing and other cognitive tasks (Miller & Cohen, 2001; Thompson-Schill, et al., 2005). We identified this region in each individual brain by visual inspection of the contrast images for the ineligible vs. neutral Stroop trials overlapped on the structural image from each participant. We initially drew a mask on the active cluster falling within the pars opercularis, which was delimited by the inferior pre-central sulcus posteriorly, the inferior frontal sulcus dorsally, the lateral fissure ventrally and the vertical ramus of the lateral fissure anteriorly. From these clusters, we then extracted the 35 most active voxels, as described by (Hindy, et al., 2012). Within each ROI, we computed average measures of language activity for each participant. For the comprehension results, we extracted the mean contrast parameter estimates for the high-competition vs. baseline and low-competition vs. baseline contrasts. For the production results, we extracted the corresponding parameter estimates, i.e., high-competition vs. read-only control and low-competition vs. the read-only controls. These mean contrast parameters estimates were then converted into percent signal change and used as dependent variables in random-effect group analyses reported for each task to test whether there was an effect of condition across participants.

3.2.3.7 Psychophysiological interaction analyses.

In order to examine the networks that are engaged during competition resolution in the production and the comprehension tasks, we conducted functional connectivity analyses using the psychophysiological interaction method. Specifically, we aimed to determine whether the functional coupling between the pars opercularis and other brain regions interacts with task demands (levels of competition) in different ways for production and comprehension. This allows an examination of differences and similarities across production and comprehension in the underlying connectivity of the pars opercularis during competition resolution. The PPI analyses were carried out in FSL using the methods described in the FSL documentation. A mask of pars opercularis was used as the seed region (as defined by the Harvard-Oxford atlas). Note that the atlas mask was used for this analysis in order for the results to be directly comparable with those reported from a similar analysis in Chapter 4. First level analyses were carried out in FEAT for each of the tasks (http://www.fmrib.ox.ac.uk/Members/joreilly/how-to-run-a-ppi-analysis-in-feat). The average time course of the seed region was used as physiological variable in the analysis of both the production and comprehension data. In comprehension, the contrast high-competition > low-competition was used as the psychological variable (using the contrast 1, -1) to examine interactions of our physiological regressor with levels of competition. In the production task, the psychological variable was the contrast of the high-competition condition with the low-competition condition and the reading control condition (2, -1, -1). The psychological regressor was convolved with the gamma function and temporal derivatives with temporal filtering added in order to simulate the hemodynamic response function (HRF). Note that temporal derivatives account for small variations in the timing of the HRF. The PPI regressor was the interaction term between the zero-centred psychological regressor and the demeaned physiological regressor. (Note that FSL differs from SPM in convolving the psychological regressor rather than deconvolving the physiological regressor. Although this has been suggested to lead to loss of statistical power for event-related designs, the results that do survive are nevertheless valid (Gitelman, Penny, Ashburner, & Friston, 2003)). To evaluate group statistics, higher-level analyses were carried out using a threshold of $p < .001$ (uncorrected) and of $p = .05$ (cluster corrected, $Z = 2.3$).

3.3 Results

3.3.1 Behavioural performance during scanning sessions.

During the comprehension task, participants responded correctly to the catch trials 90% of the time on average, indicating that they maintained attention on the task. In the production task, participants took 5.35 seconds on average to complete the fragments and took about 2.60 seconds to read the fragments in the read-only control trials. Both these measures are consistent with our behavioural results in Exp. 1. Interestingly, there was a significant difference between the completion times of the high- and low-competition fragments, as measured from the beginning of the trial to the end of the production response (M=5.58 vs. 5.11 sec, $t(16) = 6.06$, $p < .0001$). In the Stroop localiser, we observed the typical competition effects in which incongruent trials, both eligible and ineligible, elicited longer response times than the neutral trials (M incongruent (eligible and ineligible) = 689ms, M neutral = 627ms, $t(16) = 2.17$, $p < .05$). Overall, the behavioural measures suggest that participants remained focused on the tasks at hand and followed the instructions.

3.3.2 Whole brain results.

To examine the extent to which the comprehension and production networks overlap, we conducted whole brain analyses contrasting each task vs. baseline or controls (cluster-corrected, $Z > 2.3$, $p < .05$). These broad contrasts guarantee that potential commonalities across tasks are not missed in more specific or direct contrasts, where common activity may be cancelled out. This analysis revealed that both sentence comprehension and production recruited a wide network of left-lateralised fronto-temporal areas (see Figure 3.1 and Table 3.1). Both tasks shared the involvement of several regions - the left inferior frontal gyrus (BA44, BA45, BA47), the precentral gyrus (BA6) and the posterior and anterior divisions of the middle temporal gyrus - although more extensive pMTG activity was found for comprehension. This is consistent with multiple studies reporting this core fronto-temporal network in language processing, which is thought to implement interactions between lexico-semantic retrieval and prefrontal control or competition processes (Gennari, et al., 2007; Tyler & Marslen-Wilson, 2008; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011). However, the production task also recruited an additional network of medial structures, including the supplementary motor area (SMA, BA6), the anterior cingulate cortex (ACC), the caudate and the thalamus, which were not active during comprehension. These regions have long been associated with production (Ketteler, Kastrau, Vohn, & Huberd, 2008; Murphy et al., 1997; Sörös, et al., 2006; Wise, Greene, Buchel, & Scott, 1999), and the recruitment of the SMA and ACC in particular, is well-known to play a critical role in response conflict or competition resolution in action and speech planning (Barch, et al., 2000; Botvinick, Cohen, & Carter, 2004; J. D. Cohen, Botvinick, & Carter, 2000; de Zubicaray, McMahon, Eastburn, & Pringle, 2006; Mostofsky & Simmonds, 2008; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010; Murphy, et al., 1997; Simmonds, et al., 2008; Tremblay & Small, 2011a; Wilson, Isenberg, & Hickok, 2009). Overall, the pattern of results indicates that although a fronto-temporal network is common to production and comprehension, a more extensive network including motor control regions is recruited in sentence production.

With regard competition effects, a whole-brain analysis was conducted separately for the production and comprehension task using the competition contrast (see Data Analsysis section for details) (Cluster corrected, $Z = 2.3$, $p < .05$). In comprehension, this analysis revealed a significant cluster of activation within LIFG, pars opercularis and no other region (see Appendix B). However, in production no areas of activation were revealed using the same level of correction (although activation was revealed in the left SMA using a reduced statistical threshold ($Z = 2.6$, uncorrected, $p < .01$)).

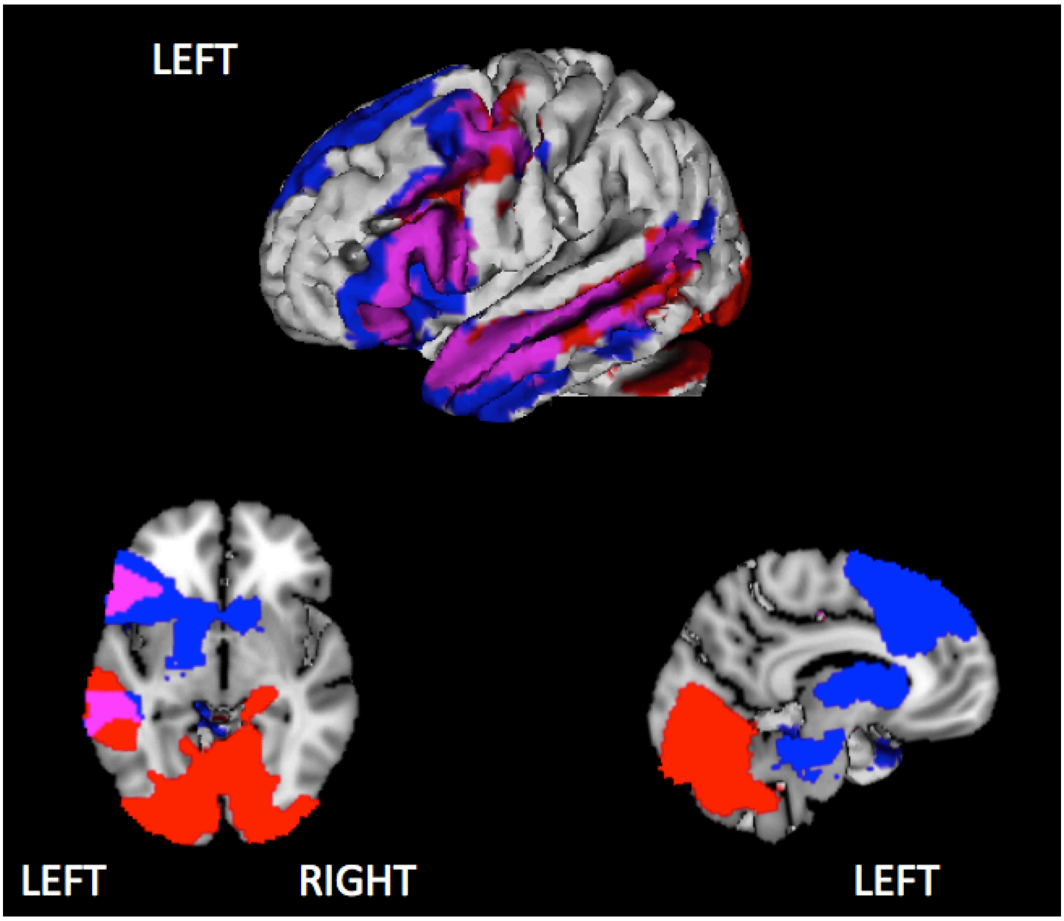


Figure 3.1 The comprehension network (red; all comprehension > baseline) and the production network (blue; all production > control) and the overlap between the two tasks (purple). Results from a whole-brain analysis (cluster corrected, $Z = 2.3$, $p < .05$).

Table 3.1 The production and comprehension whole-brain analysis (cluster corrected, *p* <.05).

Contrasts	Brain area	*Z*	Voxel (MNI) *x*	*y*	*z*
Comprehension > Baseline	Inferior frontal gyrus, left (BA44/BA45)	5.01	-50	14	24
	Inferior frontal gyrus, left (BA 47)	3.94	-54	26	-2
	Precentral gyrus (BA 6)	5.03	-46	-2	32
	Middle temporal gyrus, left posterior (BA 32)	5.81	-52	-44	2
	Middle temporal gyrus, left anterior (BA 21)	4.71	-56	-16	-10
	Anterior temporal lobe, left (BA 21)	4.18	-50	14	-22
	Hippocampus, left	3.80	-30	-24	-10
	Inferior parietal lobule, left (BA 39)	3.07	-36	-60	44
Production > Control	Inferior frontal gyrus, left (BA44/BA45)	5.37	-58	20	10
	Inferior frontal gyrus, left (BA 47)	4.21	-54	34	-12
	Precentral gyrus, left (BA 6)	2.65	-54	-4	48
	Middle frontal gyrus, left (BA 6)	3.51	-46	6	52
	Superior frontal gyrus, left (BA 9)	4.28	-10	56	38
	Superior frontal gyrus, left (BA 6)	4.72	-12	16	60
	Super temporal gyrus, left posterior (BA39)	3.47	-44	-62	16
	Middle temporal gyrus, left (BA 21)	4.46	-56	-30	-10
	Anterior temporal lobe, left (BA 21)	4.52	-50	12	-30
	Inferior temporal gyrus, left (BA 20)	3.96	-42	-8	-42
	Caudate, left	4.43	-16	12	12
	Caudate, right	3.46	6	14	4
	Anterior cingulate cortex, left (BA 32)	4.49	-10	26	32
	Anterior cingulate cortex, right (BA 39)	3.09	14	36	20
	Thalamus, left	3.31	-2	-12	10
	Right Cerebellum	4.23	36	-58	-40

3.3.3 ROI results.

To establish whether the high- and low-competition conditions modulated activity within the Stroop-defined pars opercularis region in both production and comprehension, the percent signal change for each condition across participants was compared. This was obtained for each individual participant from contrasting each condition relative to its baseline or control within the 35 most active voxels in the Stroop task (see Methods, Region of Interest analysis). We found a similar pattern of results across the production and comprehension tasks, as shown in Figure 3.2. In comprehension, the activity elicited by the high-competition items relative to baseline was higher than that of the low-competition items relative to baseline (M = .37, SE = .08; M = .28, SE = .05; *t*(16) = 2.31, *p* = .03). Similarly, production revealed higher activation for the high-competition condition than the low-competition condition relative to their read-only controls (M = .084, SE = .017; M = .069, SE = .014; *t*(16) = 2.90, *p* = .01). Note that the overall mean activity in the production task is much smaller than that of comprehension due to removal of common reading activity (production minus reading-control contrast). Furthermore, the effect of competition in the production task cannot be explained in terms of difficulty associated with reading the sentence prompt, as no difference in activity between high-competition and low-competition conditions is found when only the sentence prompt is modelled (M = .18, SE = .031; M = .17, SE = .026; *t*(16) = 0.77, *p* = .45). Taken together, these results provide evidence of common mechanisms across tasks operating at the level of each individual brain in a confined anatomical area.

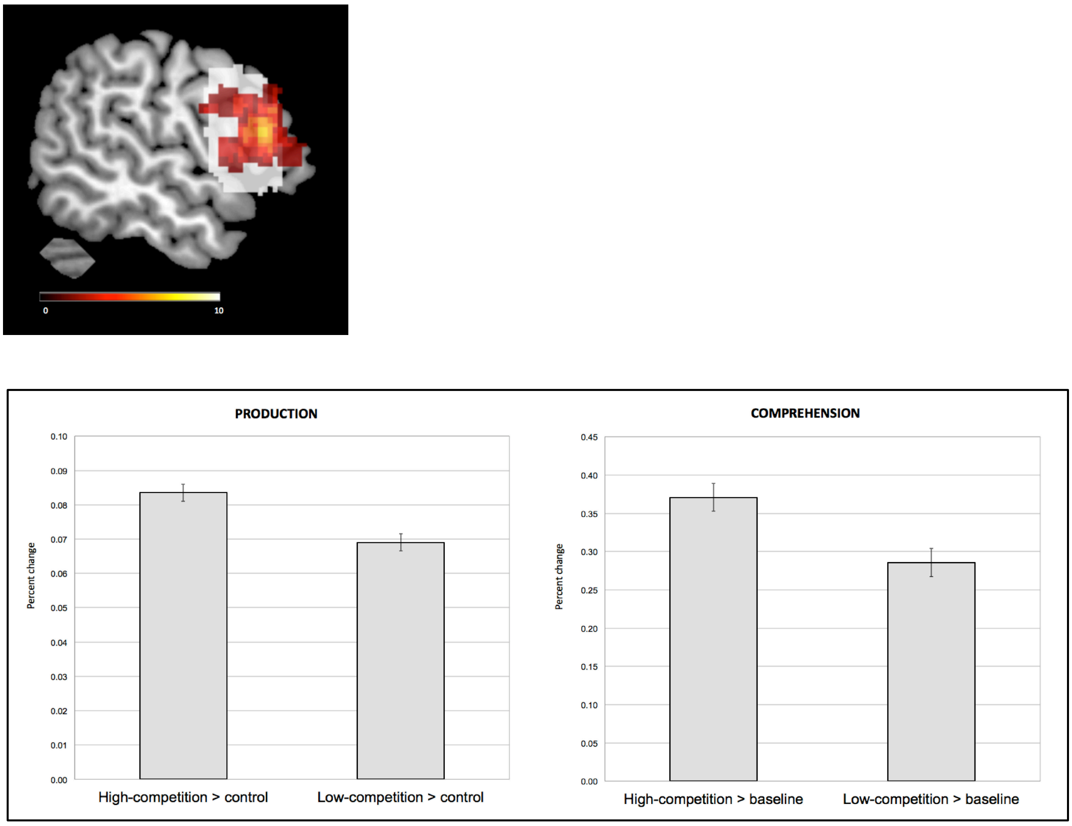


Figure 3.2 Top) The location of individual subject ROIs transformed to standard space overlapped on the Harvard-Oxford map of IFG, pars opercularis. The colour indicates the number of participants who recruited that area. Bottom) The percent signal change from each task from within the ROI.

3.3.4 PPI results.

PPI analyses were conducted using LIFG, pars opercularis as a seed region to establish how it interacts with high vs. low task demands in production and comprehension. The results of the comprehension task revealed a stronger coupling of activity between pars opercularis and the pMTG as a function of competition (uncorrected, p = .001), consistent with numerous studies indicating the involvement of this fronto-temporal network in comprehension (see references above). In contrast, the production results indicated that a much more distributed network of regions was coupled with the pars opercularis as a function of competition (uncorrected, p = .001). These results were stronger than those in comprehension, surviving more stringent correction thresholds (cluster corrected Z =2.3, p = .05) (see Figure 3.3 and Table 3.2). This production network included bilateral medial superior frontal gyrus, middle and superior temporal gyrus, left parietal cortex (postcentral gyrus, precuneus and insular cortex) and subcortical areas including the left basal ganglia, thalamus and bilateral hippocampus. All these regions have been typically shown to be involved in in speech planning, particularly when competitive processes are involved, e.g., lexical selection (de Zubicaray, et al., 2006; de Zubicaray, Wilson, McMahon, & Muthiah, 2001; Heim, Eickhoff, Friederici, & Amunts, 2009; Murphy, et al., 1997; Tremblay & Small, 2011a; Whitney, et al., 2009; Wilson, et al., 2009; Wise, et al., 1999). Note that although the posterior temporal clusters show slightly different centres for each task, there was considerable overlap, particularly if the thresholds are lowered. This was despite the fact that reading was removed from the completion task and thus potential regions of common involvement could have also been removed. Overall, these results indicate that whereas pars opercularis and portions of the posterior temporal cortex are recruited by both sentence production and comprehension, the network of regions effectively connected to pars opercularis is quite different in each task.

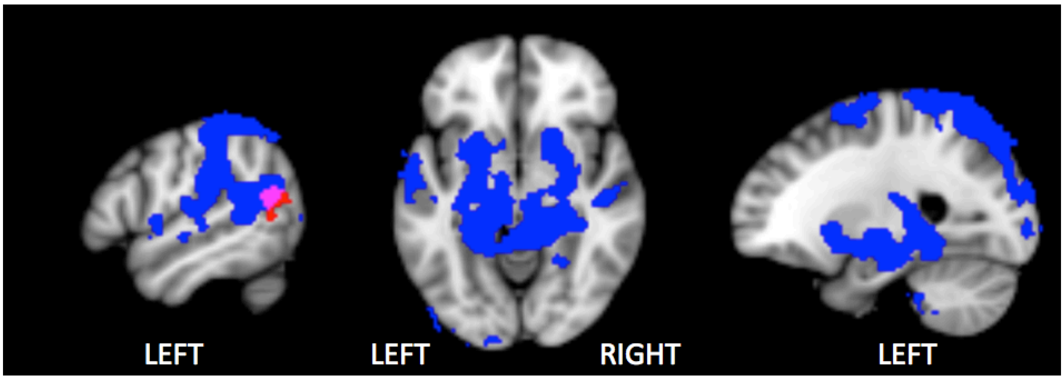


Figure 3.3 Results from whole-brain PPI analysis (uncorrected, *p* <.001): regions that show an interaction between level of competition (high vs. low) and the time-series of activity within BA44 in comprehension (red) and production (blue).

Table 3.2 Results from whole-brain PPI analysis (uncorrected, *p* <.001): regions that show an interaction between level of competition (high vs. low) and the time-series of activity within BA44.

Brain area	*Z*	Voxel (MNI)		
		X	*y*	*z*
Comprehension (animate > inanimate)				
Posterior Middle Temporal Gyrus, left	3.81	-60	-62	12
Production (animate > inanimate and control)				
Frontal				
Superior Frontal Gyrus, right	3.90	24	12	60
Superior Frontal Gyrus, left	3.50	-22	-2	66
Temporal				
Posterior Middle temporal Gyrus, left	3.87	-44	-60	10
Superior Temporal Gyrus, left	3.93	-52	-24	0
Subcortical				
Caudate, left	3.10	-8	14	-2
Putamen, left	3.43	-22	4	-10
Hippocampus, left	3.80	-20	-38	-6
Hippocampus, right	3.67	18	-34	-8
Thalamus	4.01	-4	-8	4
Parietal				
Postcentral Gyrus, left	3.78	-42	-36	68
Insular Cortex, left	3.56	-32	12	-10
Precuneus, left	4.01	-4	-66	50

3.4 Discussion

The present study aimed to investigate whether sentence production and comprehension share competition mechanisms in LIFG but differ in LIFG's supporting networks. Comparisons of the production and comprehension networks relative to rest or controls indicated that these tasks shared a fronto-temporal network, including LIFG, middle and superior temporal areas, and the pre-central gyrus (Figure 3.1). Within this network, the posterior temporal lobe is thought to store lexical knowledge, particularly that associated with verbs and their event structures (Bedny, Caramazza, et al., 2008; Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004; Tyler & Marslen-Wilson, 2008), whereas the LIFG is thought to perform general regulatory functions, including memory maintenance, controlled retrieval and encoding, integration and selection/inhibition (Barde & Thompson-Schill, 2002; D'Esposito, et al., 1999; Fiebach, et al., 2006; Fuster, 2001; Miller & Cohen, 2001; Thompson-Schill, et al., 2005; A. D. Wagner, et al., 2001). However, only production additionally engaged brain regions known to be critically involved in motor control and/or speech planning such as the medial superior frontal regions (SMA), the ACC and subcortical regions such as the basal ganglia and thalamus (Alario, et al., 2006; Barch, et al., 2000; Botvinick, et al., 2004; C. Y. Chen, Muggleton, Tzeng, Hung, & Juan, 2009; Ketteler, et al., 2008; Mukamel, et al., 2010; Murphy, et al., 1997; Nachev, Wydell, O'Neill, Husain, & Kennard, 2007; Simmonds, et al., 2008; Sörös, et al., 2006; Wahl et al., 2008; Wise, et al., 1999).

Critically, competition modulated activity in the Stroop-defined pars opercularis for both tasks, suggesting common competition mechanisms in LIFG. However, the strength and the extent of the LIFG's functional coupling differed across tasks. Indeed, PPI analyses revealed that the pars opercularis established distinct patterns of connectivity in production compared to comprehension (Figure 3.3). In comprehension, LIFG was found to functionally interact with posterior temporal areas as a function of competition. In production, LIFG also showed increased connectivity with posterior temporal areas for high competition relative to low competition cases. However, in addition to this, increased connectivity was also found with a further network of areas that was absent for the comprehension comparison. This included the medial superior frontal gyrus (SMA), parietal areas such as precuneus and angular gyrus, basal ganglia structures such as the caudate, and the hippocampus. Together these results suggest that production and comprehension share competition mechanisms in LIFG and posterior temporal areas, but that beyond these areas distinct functional networks are recruited for task-specific aspects of production and comprehension processes.

3.4.1 The fronto-temporal network.

Production and comprehension thus share competition mechanisms in LIFG and the posterior temporal lobe. The finding of common fronto-temporal activity is consistent with studies that have directly compared production and comprehension (Awad, et al., 2007; Braun, et al., 2001; Braun, et al., 1997; Kim, et al., 1997; Kircher, et al., 2004; Menenti, et al., 2011; Papathanassiou, et al., 2000; Segaert, et al., 2011; Tamas, et al., 1993). It is also consistent with studies that have explicitly manipulated control demands in either production or comprehension domains (Bedny, McGill, et al., 2008; de Zubicaray, et al., 2006; Gennari, et al., 2007; Thompson-Schill, et al., 1997; Zempleni, Renken, Hoeks, Hoogduin, & Stowe, 2007), as well as neuropsychological and TMS studies reporting that damage or stimulation of these areas creates production or comprehension impairments in tasks that require the ability to resolve competition (Jefferies & Lambon Ralph, 2006; Novick, et al., 2009; G. Robinson, et al., 1998; G. Robinson, et al., 2010; G. Robinson, et al., 2005; Schnur, et al., 2009).

These results illuminate the nature of the processes that might be common or distinct in production and comprehension. What LIFG processes are common to production and comprehension? Production and comprehension are sensitive to the same linguistic statistics regarding, for example, the association between nouns and event-roles. This is evident from observations that comprehension difficulty is predicted by distributional probabilities derived from the likelihood of a particular sequence being produced (Gennari & MacDonald, 2008, 2009; MacDonald, et al., 1994; Tanenhaus & Trueswell, 1995; Trueswell, et al., 1994). Therefore, the role of the LIFG may be for mediating the association between linguistic cues, such as word-meaning and syntactic structures, across production and comprehension tasks. This is consistent with the general executive functions often attributed to LIFG in mediating contingencies between cues and their associations (Fuster, 2001; Koechlin & Jubault, 2006; Passingham, Toni, & Rushworth, 2000). The LIFG is indeed involved in establishing linguistic contingencies during language learning (Opitz & Friederici, 2003, 2004), and it is necessary for producing word sequences and comprehending word order, grammatical cues and grammatical relations (Caplan, Hildebrandt, & Makris, 1996; Thothathiri, et al., 2010). Therefore, the LIFG, and its interactive networks, manage linguistic contingencies, and thus, the anticipation or activation of information associated with semantic and syntactic cues.

The mechanism used by LIFG to mediate these associations may be one that inhibits interference from inappropriate information and selects the appropriate alternatives. This is consistent with the more general view of LIFG as an inhibition/selection mechanism in language (Bedny, McGill, et al., 2008; Demb, et al., 1995; Gennari, et al., 2007; Gold & Buckner, 2002; Hoenig & Scheef, 2009; Rodd, et al., 2005; A. D. Wagner, et al., 2001). In the current study, the increased activation of LIFG for the high-competition cases presumably reflects the additional processing required to over-rule strong semantic associations, i.e. for animate entities to play the agent role and inanimate entities to be patients or affected participants, and select the alternative thematic roles that fit syntactic constraints of the context. Indeed, the importance of LIFG as a mechanism for checking and selecting the appropriate thematic role interpretations has been highlighted elsewhere (Caplan, Stanczak, et al., 2008). Finding common LIFG modulation by competition across production and comprehension tasks thus suggests that the inhibition/selection mechanisms used to resolve competition are common across production and comprehension.

The effect of competition was localised within the pars opercularis of LIFG (BA44), rather than other LIFG subsections (pars triangularis or orbitalis) (see Appendix B). Other studies that have manipulated competition in sentences have also found pars opercularis activity (Fiebach, et al., 2004; January, et al., 2009; Mason, et al., 2003; Obleser & Kotz, 2010; Rodd, et al., 2005; Rodd, et al., 2011; Rodd, Longeb, et al., 2010; Tyler, et al., 2010; Ye & Zhou, 2009a). Suggestions have been made that pars opercularis might be specialised for specifically syntactic processes, whereas more anterior areas are involved in processing semantic level representations (Friederici, 2009; Hagoort, 2005; Indefrey, Hagoort, Herzog, Seitz, & Brown, 2001). Here, the competition in the sentences was derived from conflicting lexical-semantic (animacy) and structural information, and is thus at the interface of semantic and syntactic level processes. The current findings are therefore not incompatible with a view that pars opercularis is involved in syntax, semantics, or both. However, the opinion that pars opercularis is specialised for syntactic level analyses is inconsistent with studies that showed overlapping activity in pars opercularis for semantically or syntactically ambiguous sentences (Rodd, Longeb, et al., 2010). Furthermore, whether it is possible to truly separate competition at the syntactic level from semantic level processes is unclear, given that different syntactic interpretations will necessarily result in different sentence meaning. Indeed, others have suggested that this area is not specialised for either syntactic or semantic level processes, instead it plays a top-down role in the plausible sequencing of information across both linguistic and non-linguistic domains (Price, 2010, 2012).

3.4.2 Task-specific activity.

Production alone engaged a further network of areas that interacted with LIFG as a function of competition. This suggests task-specific production processes that differ to comprehension processes inline with psycholinguistic perspectives. This network included bilateral medial prefrontal cortex (SMA), left anterior cingulate, left insula, subcortical structures within the basal ganglia (left caudate and putamen), thalamus, bilateral hippocampus, and parietal areas (precuneus, angular gyrus, and postcentral gyrus). This suggests that whilst production and comprehension share control processes within LIFG and posterior temporal lobe, beyond this distinct control processes are engaged.

This result provides some insights into the differences in processes engaged by production and comprehension. The hippocampus is well known to serve memory retrieval (Nadel & Moscovitch, 2001; Paller & Wagner, 2002; Whitney, et al., 2009), as is the precuneus in the parietal lobe (Cavanna & Trimble, 2006). Therefore, activation of these structures by production will likely reflect the increased retrieval demands in the production task. This is inline with psycholinguistic perspectives that production is a task of word retrieval, whereas comprehension engages recognition processes. The recruitment of parietal areas by the production task could also reflect increased processing demands in production relative to comprehension as precuneus and angular gyrus have been implicated in tasks with high attentional demands or when information is maintained in short term memory (Brownsett & Wise, 2010; Cavanna & Trimble, 2006; Cristescu, Devlin, & Nobre, 2006; Jacquemot & Scott, 2006; Nee, Wager, & Jonides, 2007). Production is indeed a more difficult task, as evidenced by the high proportion of false starts, disfluencies and errors in psycholinguistic studies of sentence production (Bock & Levelt, 1994; Garrett, 1980; Levelt, et al., 1999). Therefore, the fact that LIFG showed increased connectivity with parietal areas in production, particularly for the high-competition cases, might reflect the increased attentional resources required to resolve the competition.

The SMA, subcortical structures (basal ganglia, insula, thalamus) and parietal areas are involved in motor/speech planning (Alario, et al., 2006; Barch et al., 1999; Basho, Palmer, Rubio, Wulfeck, & Muller, 2007; Botvinick, et al., 2004; Brownsett & Wise, 2010; C. Y. Chen, et al., 2009; Dogil et al., 2002; Geranmayeh et al., 2012; Haller, Radue, Erb, Grodd, & Kircher, 2005; Hickok, 2012; Indefrey, 2011; Ketteler, et al., 2008; Kielar, Milman, Bonakdarpour, & Thompson, 2011; Mukamel, et al., 2010; Murphy, et al., 1997; Nachev, et al., 2007; Simmonds, et al., 2008; Sörös, et al., 2006; Wahl, et al., 2008; Wise, et al., 1999). Therefore, activity here in the production task likely reflects planning processes that are absent for comprehension. In particular these areas have been found to be responsive to tasks that involve response conflict in the motor domain, suggesting a possible role for these areas in managing competition between alternative motor plans. For instance, the SMA is engaged by tasks such as the Go/NoGo task, which involves the inhibition of inappropriate motor response and suggests a critical role for this area in response control and selection (C. Y. Chen, et al., 2009; Nachev, et al., 2007; Simmonds, et al., 2008). Production studies have highlighted the importance of SMA in production processes such as linearization, lexical selection or motor control depending on the SMA area (Alario, et al., 2006), and studies using bilingual participants have identified SMA, as well as anterior cingulate cortex (ACC) and the caudate as playing an important role for these areas in response selection and inhibiting inappropriate verbal response (Abutalebi, et al., 2008; Ali, et al., 2009; Garbin, et al., 2011; Price, 2010). Others have also highlighted the importance of subcortical structures in production (S. Robinson, Nichols, Macleod, & Duncan, 2008; Robles, et al., 2005) suggesting that whilst the putamen is important for motor aspects of production the caudate plays an important role in cognitive control, as stimulation of the caudate results in the failure to inhibit inappropriate verbal responses. Similar linguistic functions have also been assigned to the thalamus (Johnson & Ojemann, 2000; Ketteler, et al., 2008; Munte & Kutas, 2008; Wahl, et al., 2008). Together these observations suggest that the production-specific network highlighted in the current study plays an active role in resolving competition in production by selecting the appropriate production plan and inhibiting interference from competitors.

Therefore, the production-specific areas of activity reported here likely reflect production-specific processes such as word or structure retrieval and motor planning. The increases recruitment of these areas for the high-competition presumably reflects the additional processing required by the increased retrieval demands and the inhibition of competing responses.

3.4.3 Implications for current models

The current data has implications for neuroanatomical production models. The notion that the motor-planning network is actively engaged in cognitive control processes in production is in contrast to others that suggest that these structures play only a peripheral role in the production system such as motor output (Hickok, 2012; Indefrey, 2011; Segaert, et al., 2011). Rather, the current data suggests that they form a core component of a network that engages interactively with fronto-temporal areas to resolve competition during sentence production.

The data also has implications for psycholinguistic production models. That the influence of competition was found to pervade the entire production system challenges the assumption of major production models that assume information flow is encapsulated (Bock & Levelt, 1994). Encapsulation means that influence from competing information is restricted to only one level of representation (semantic, syntactic, phonological) and does not pervade the system. In the current study, the fact that semantic properties modulated activity in areas that are not associated with conceptual representations, such as various motor-related regions, suggests that semantic competition percolates the entire production system. Thus, competition resolution does not appear restricted to word selection, nor to the event role choices implied by the verb, but instead, reverberates across a large network involving linguistic representations at different levels. This result challenges serial models of sentence production arguing for distinctive stages of lexical retrieval, planning and word sequencing and instead suggests parallel processing and interactivity across the network.

More generally, the current results have implications for other approaches discussed widely in the literature, such as the simulation approach. This approach has argued that language comprehension involves simulation of production planning or covert imitation (D'Ausilio, et al., 2009; Liberman, et al., 1967), thus recruiting motor control systems (Pickering & Garrod, 2007). In the current study, motoric regions did not interact with pre-frontal cortex as a function of competition in comprehension, although the pre-motor cortex was engaged in both tasks in the whole brain analysis. This suggests that motor-related regions were specific to production and that the pre-motor cortex plays a supporting but not critical role in competition resolution during reading. This may be the case because task demands did not specifically require attending to motor-based sound properties, as in some previous studies (D'Ausilio, et al., 2009; Pulvermuller, et al., 2006), and thus motoric associations that may be ignited in both task are nevertheless not central to resolving semantic competition. Indeed, children learn to read by sounding out letters, so it is clear that associations between letters, sounds, articulatory plans and meanings are established early in life (Daneman & Newson, 1992). Nevertheless, the necessity of such associations for the comprehension of sentential meaning remains to be established.

Limitations.

As discussed in the previous chapter, there are obvious limitations to the sentence-completion task in examining sentence production. This means that it is important to be cautious when interpreting the results from this paradigm. However, it was argued that whilst it is very important to keep these issues in mind the paradigm still has some useful implications for the current research question. This argument is strengthened by the current data as production and comprehension were shown to engage clearly distinct networks beyond LIFG. This suggests that the production data cannot be explained by difficulty in comprehending the sentence-prompt. Furthermore, the production-specific areas identified here are regions that are known to play an important role in sentence planning and lexical selection in other studies thus further supporting the reliability of the data. Sentence production is a difficult process to investigate as it hard to control experimentally what participants might produce. The sentence-completion paradigm is a useful first step to investigating these issues. Nevertheless, it is important to demonstrate that these results replicate to alternative more naturalistic paradigms. This issue is addressed in Chapter 5 of the thesis in which a more naturalistic paradigm is used.

3.4.4 Conclusions.

In summary, production and comprehension share competition mechanisms in a fronto-temporal network typically engaged in language processing. This network appears to manage the myriad of activations elicited by various types of linguistic cues, including the association between noun meanings and their event roles in a sentence. However, production recruits several additional regions to retrieve information and generate linguistically-based plans. Therefore, competition in production and comprehension reverberates across distinct functional networks, as determined by task demands. It is important to note, however, that the functional networks engaged by production and comprehension competition processes change with development as maturational changes in neural processes can lead to functional changes in the neural networks engaged for control processes. The next chapter describes studies that investigate the influence of neurodevelopmental changes on production and comprehension control processes.

Chapter 4

The development of control mechanisms in sentence production and comprehension

4.1 Introduction

The previous chapters have shown that in healthy adults, sentence production and comprehension engage common and distinct control mechanisms to resolve cue-based competition. Yet, control processes are not a static mechanism, they continuously change through development. In particular adolescence is thought to be a time of particularly large neurostructural changes, especially in the prefrontal cortex. Neurodevelopmental theories have suggested that underlying structural changes from adolescence and into adulthood result in qualitative and quantitative shifts in the control processes that are engaged to resolve competition. The impact of these changes on language-related competition processes has not been explored. However, it is likely that neurodevelopmental changes influence the ability to resolve competition in language. Furthermore, the extent to which production and comprehension control processes show a common or distinct neurodevelopmental trajectory is unclear. For instance, the previous chapter showed that production and comprehension engage common LIFG control processes, but task-specific control mechanisms elsewhere. This raises the question, do the underlying LIFG control mechanisms show a similar pattern of development across production and comprehension tasks? Furthermore, what are the influences of neurodevelopmental changes on task-specific control processes? This chapter describes a behavioural and neuroimaging study that investigates the influence of neurodevelopmental changes on production and comprehension control processes by contrasting adult and adolescent performance. These studies combine behavioural, structural, and functional imaging techniques to help determine the influence of neurodevelopment on the ability to resolve competition in sentence production and comprehension, and the qualitative and/or quantitative shifts in the control mechanisms that are engaged.

4.1.1 Neurodevelopmental changes in brain structure from adolescence to adulthood.

Structural imaging studies have shown that major neural maturational changes take place between adolescence and early adulthood. Beginning at around age 12, adolescence and early adulthood are associated with age-related decreases in grey matter volume and density, accompanied with parallel increases in white matter (as shown in Figure 4.1) (Casey, Tottenham, Liston, & Durston, 2005; Giedd et al., 1999; Lebel & Beaulieu, 2011; Paus et al., 1999; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999; Thompson et al., 2000). Regressive maturational changes in grey matter volume are thought to reflect processes of synaptic pruning; the elimination of overabundant and unimportant synaptic connections thereby leading to greater processing efficiency (Tamnes et al., 2010), whilst white matter increases reflect axonal myelination, which leads to improvements in the speed and efficiency of information transfer (Casey, et al., 2005). These changes are particularly apparent in prefrontal cortex, the areas involved in higher-level cognitive functions. Indeed, using techniques such as Voxel Based Morphometry (VBM), which measures regional changes in grey and white matter volume and /or density, studies have shown that structural changes during adolescence are correlated with functional changes in brain activity and task performance in a range of tasks including relational reasoning (Dumontheil, Houlton, Christoff, & Blakemore, 2010), working memory (Edin, Macoveanu, Olesen, Tegner, & Klingberg, 2007; Nagy, Westerberg, & Klingberg, 2004; Olesen, Nagy, Westerberg, & Klingberg, 2003), intelligence (Shaw et al., 2008), inhibition (Tamnes, et al., 2010), and language (Lee et al., 2007).

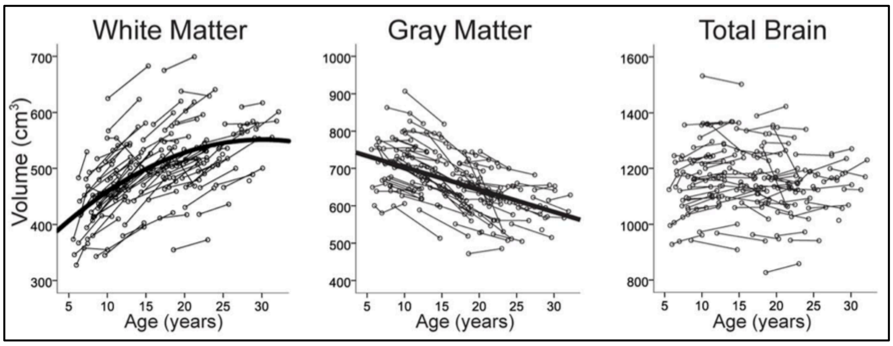


Figure 4.1 Correlations between age and grey and white matter volume (Taken from Lebel & Beaulieu, 2011).

4.1.2 Developmental changes in cognitive control processes.

As highlighted in earlier chapters, prefrontal cortex, and in particular the LIFG plays a critical role in inhibitory control processes and in the ability to select an appropriate response from alternatives. Prefrontal immaturity is thought to lead to deficits in the performance of cognitive control tasks. For instance, compared to adults, in behavioural studies adolescents show larger interference effects from competing responses in the Stroop and Go/NoGo task (Rubia, et al., 2006; Tamm, et al., 2002). In terms of neural processes, it has been suggested that adolescents compared to adults show both qualitative and quantitative differences in brain activity in cognitive control tasks. In particular, adolescents show reduced magnitude but a more diffuse pattern of activation (Bunge & Wright, 2007; Casey, et al., 2005; Durston, et al., 2006). Age is associated with increasing recruitment of pre-frontal control areas reflecting the fine-tuning of core systems and increased efficiency in inhibitory processing. For instance, studies have shown age-related increases in activation in LIFG, as well as in task-specific supporting networks in a range of cognitive control tasks such as the Go/NoGo task, target detection, and the Stroop task (Durston, et al., 2006; Rubia, et al., 2006; Schroeter, et al., 2004; Stevens, et al., 2009; Tamm, et al., 2002).

However, age-related increases in core pre-frontal processes are accompanied with age-related decreases in areas that are not considered part of the core control network in adults, thereby reflecting a shift from a more diffuse to more focal control network with age. In particular, comparisons of adults and adolescents have shown that adolescents recruit additional areas for control tasks that are absent in the adult groups, such as in medial prefrontal and posterior temporo-parietal cortex (Bunge & Wright, 2007; Durston, et al., 2006; Rubia, et al., 2006; Tamm, et al., 2002). The recruitment of this additional network in adolescents might serve a compensatory role, or it may reflect group-differences in processing strategies (Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002; Bunge & Wright, 2007; Durston, et al., 2006). Figure 4.2 shows the fMRI results from a Go/NoGo task showing increasing activity with age within LIFG (red) and age-related decreases in activity within a distributed network of areas including medial prefrontal structures (blue) (Durston, et al., 2006). Therefore, there is good evidence that control networks engaged during conflict resolution change with development; from adolescence to adulthood there is a shift from a more diffuse to a more focal control network with age (qualitative change), and this is accompanied with increased activity within core processing areas (quantitative change).

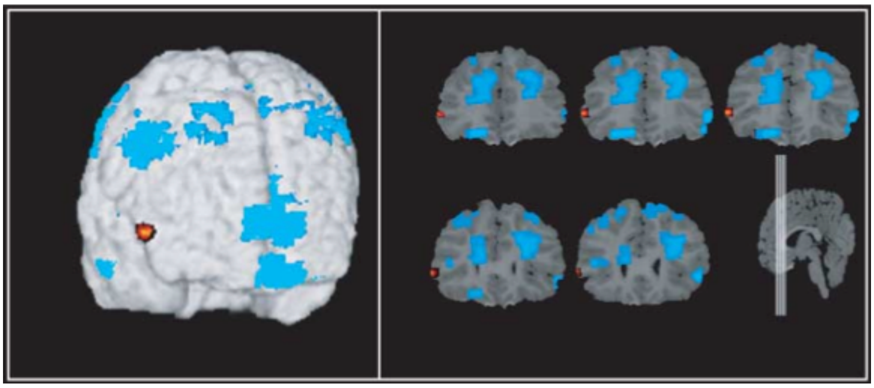


Figure 4.2 Figure taken from Durston et al. (2006) showing age-related changes in adolescent activity in LIFG (red) and age-related decreases in activity (blue) within a distributed network of areas. This suggests that activity becomes more focal with age.

4.1.3 Developmental changes in language processing.

The implication of adolescent neurodevelopmental changes on their ability to resolve competition in language has received little/no empirical investigation, neither in the domain of language production nor in comprehension. There has, however, been some work investigating age-related changes in the networks engaged by word production and comprehension more generally. For instance, in a word-generation study, Brown et al., (2005) compared age-related changes in activity from participants aged 7- 32 years. Similar to what has been reported in the cognitive control literature, activity was found to increase with age in “core” adult production regions, such as LIFG, and this was accompanied with age-related decreases in activity within a distributed network of areas that were absent for adult production, including occipito-temporal cortex, frontal pole, and posterior cingulate. Comparable results have been found for narrative and word comprehension tasks, showing age-related increases in activation in fronto-temporal language areas and increased fronto-temporal functional connectivity (Booth et al., 2001; Gaillard et al., 2003; Schmithorst, Holland, & Plante, 2006; Schmithorst, Holland, & Plante, 2007). These are sometimes accompanied with age-related decreased in activity in a mixture of areas that are not typically associated with adult comprehension, such as the precuneus in the parietal lobe (Schmithorst, et al., 2006).

Although no studies have directly investigated the influence of neurodevelopmental changes on language control processes, some researchers have proposed that certain observations of child difficulty in sentence comprehension might be linked to deficits in inhibitory control (Mazuka, Jincho, & Oishi, 2009; Novick, Trueswell, & Thompson-Schill, 2005). For instance, five-year-old children are unable to override initial misinterpretations of temporarily ambiguous sentences. For instance, in a sentence such as *Put the frog on the napkin in the box* children interpreted *on the napkin* as the goal of the action rather than as a modifier phrase, and unlike adults were unable to override this misinterpretation (Trueswell, Sekerina, Hill, & Logrip, 1999). Some have suggested that this deficit is related specifically to underdeveloped LIFG function, citing evidence of comparable effects in patients with LIFG damage (Novick, et al., 2005). However, no study has directly linked sentence processing difficulty with neurodevelopmental changes. Furthermore, the implication of these neurodevelopmental changes on the relationship between production and comprehension control processes have never been investigated. The goals of the current studies were to investigate the influence of neurodevelopment on production and comprehension control processes. These findings would hopefully have implications for the development of language control processes, and also for the more general relationship between production and comprehension control mechanisms.

4.1.4 The current experiments.

The studies described in this chapter had two primary aims. Firstly, to investigate the influence of neurodevelopmental changes on the ability to resolve competition in language. Secondly, to investigate whether parallel maturational trajectories are apparent in sentence production and comprehension tasks. Finding a parallel influence of neurodevelopment on both production and comprehension control processes would provide support for the notion of shared processes across tasks. However, if production and comprehension show divergent developmental trajectories, this would suggest asymmetries in the processing mechanisms engaged by production and comprehension tasks, at least during neural development. To investigate these issues a behavioural study (Experiment 3) and an fMRI study (Experiment 4) were conducted contrasting adult and adolescent performance on sentence production and comprehension tasks, using the same tasks and stimuli described in the preceding chapters. In particular, we examined the abilities of adolescents to resolve cue-based competition in relative clauses with conflicting animacy and structural information, such as *The director that the movie…*, where they must overcome the more prepotent thematic role associations for animate and inanimate entities. Experiment 3 showed that adolescents are indeed less able than adults to resolve cue-based competition in production and comprehension tasks. Experiment 4 demonstrated that adolescents show qualitative and quantitative differences compared to adults in the networks engaged by production and comprehension control processes. Importantly, functional differences were found to relate to differences in grey matter density thereby suggesting that neurodevelopmental changes in brain structure lead to functional changes in the control networks engaged to resolve competition in language. Finally, the results from both studies also highlight some important differences between production and comprehension mechanisms, which may have wider implications for production and comprehension processes more generally.

4.2 Experiment 3

A behavioural study was conducted to investigate whether adolescents show behavioural deficits in their ability to resolve cue-based competition in language, and to compare the developmental trajectories of production and comprehension processes. This was done by contrasting the behavioural performance of adult and adolescent participants in the sentence production and comprehension tasks described previously in chapter 2. It was predicted that if adolescents have deficits in resolving cue-based competition in sentences, then they should perform more poorly than adults in the language tasks (longer processing times, more errors), particularly for the high-competition items. Furthermore, if production and comprehension share competition resolution mechanisms, then they should show parallel behavioural effects and developmental trajectories.

4.2.1 Methods

4.2.1.1 Participants.

A total of 23 adolescents completed the behavioural comprehension and production study (mean age = 14.18 years, range = 12 - 16 years, SD = 1.19, 9 female). The adolescents were recruited from local schools and from University advertisements. The data from these subjects was compared to 23 randomly selected subjects from the adult study described in chapter 2 (mean age = 22.87 years, range =19-32 years, SD = 3.52, 14 female). The materials and tasks were exactly the same as in the adult experiment. Groups were matched in terms of verbal IQ scores from the Wechsler Abbreviated Scale of Intelligence (WASI; Wechsler, 1999) ($t(44) = -0.30$, ns). Table 4.1 shows a summary of participants' standardised verbal IQ scores. One adolescent participant was removed from the reaction time data due to excessively poor accuracy on the high-competition items for both the comprehension and production tasks (comprehension = 52.38% correct for high-competition items when chance = 50%, production = 4% correct for high-competition items). The same participant performed within the normal range for the low-competition condition suggesting that the poor performance was specific to the high-competition items rather than reflecting a general deficit in task performance (comprehension accuracy = 90.48%; production accuracy = 57% correct for low-competition items). Given the good levels of performance on the low-competition items, the accuracy data was considered to be meaningful and was therefore included in the accuracy analyses. Note, however, that the key results remained the same regardless of whether or not this subject was excluded.

Table 4.1 Verbal IQ scores for the adult and adolescent groups.

Verbal IQ		
Age group	Mean (SD)	Range
Adults (N = 23; age = 19-32)	121.04 (12.12)	94 – 145
Adolescents (N = 23; age = 12-16)	119.96 (12.64)	85 – 136

4.2.1.2 Procedures.

The tasks and procedures were identical to those described in Chapter 2. Briefly, all participants completed the comprehension (self-paced reading) and production (sentence-completion) tasks. For the comprehension task, the accuracy and residual reading time data was calculated as before, and 3 x 2 x2 mixed-design ANOVAs were conducted using group (adult and adolescent) as the between subject factor and condition (high- and low-competition) and word-position (RC noun, RC verb, and the Main verb region) as within subjects factors. As before, residual reading times were used as the reading time measure. This is obtained by computing the residuals after removing the effect of word length for each individual participant. Whilst word-length was matched across conditions and groups this analysis has the useful effect of removing inter-subject variability in sensitivities to word-length, therefore making it the method of choice in psycholinguistic experiments investigating individual differences in reading times (Pearlmutter & MacDonald, 1995; Wells, Christiansen, Race, Acheson, & MacDonald, 2009). For production, the responses were coded for accuracy, as described in Chapter 2, and the accuracy and the initiation times were contrasted across groups and conditions using 2 x 2 mixed-design ANOVAs, with group (adult and adolescent) as the between-subjects factor and condition (high- and low-competition) as the within-subjects factor. Data that deviated from the mean by the more than 3 SDs was excluded from the analyses, and only accurate responses were included in the RT analyses. Initiation time data were missing from three of the adolescent participants due to equipment failure, and the production recordings from one adolescent and two adults were lost due to faults with the recording equipment.

4.2.2 Results

4.2.2.1 Sentence comprehension

Comprehension accuracy. The overall mean accuracy across participants for the comprehension questions for the adolescent group was 83.23% (SD = 7.94) and for the adult group was 89.03% (SD = 6.95). The results from the 2 x2 mixed design ANOVA showed a significant main effect of group ($F1(1, 44) = 6.94$, $p < .05$; $F2(1, 78) = 5.26$, $p < .05$), a main effect of condition ($F1(1, 44) = 40.58$, $p < .001$; $F2(1, 78) = 26.64$, $p < .001$), and a marginal group x condition interaction ($F1(1, 44) = 3.61$, $p = .06$; $F2(1, 78) = 2.81$, $p = .09$) (see Figure 4.3). Planned t-tests found that both groups were significantly more accurate on the low-competition compared to high-competition trials (Adolescent group: High-competition accuracy = 75.57%, SD = 14.31; Low-competition accuracy = 90.89%, SD = 4.29; $t(22) = -5.28$, $p < .01$; Adult group: High-competition accuracy = 84.89%, SD = 10.32; Low-competition accuracy = 93.17%, SD = 7.15; $t(22) = -3.60$, $p < .01$). However, across groups adults showed increased accuracy on the high-competition items compared to adolescents ($t(44) = -2.53$, $p < .02$), but there was no significant difference in response accuracy for the low-competition items ($t(44) = -1.31$, ns). These results show that whilst both groups are affected by competition, adolescents are marginally poorer than adults at comprehending the high-competition items.

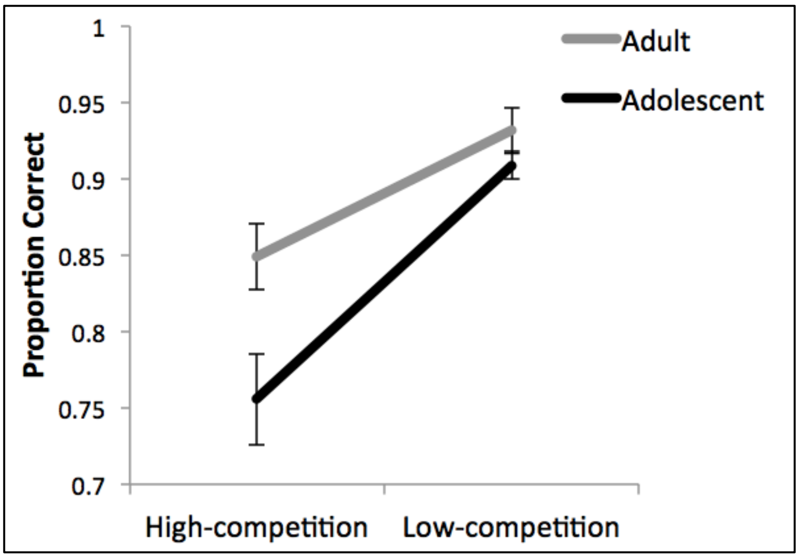


Figure 4.3 The proportion of correct responses to the comprehension questions for the adult and adolescent groups.

Reading times. The residual reading times were compared across groups and conditions for each word position (see Figure 4.4). The 2x2x3 mixed design ANOVA showed a significant main effect of condition ($F1(1, 43) = 16.41$, $p < .001$; $F2(1, 78) = 6.95$, $p < .01$), and a marginal effect of position in the subject analysis only ($F1(2, 43) = 2.75$, $p = .09$; $F2(2, 156) = .73$, $p = .49$). There was also a significant condition x word position interaction in the subject analysis only ($F1(2,43) = 4.46$, $p = .02$; $F2(2, 156) = 1.87$, $p = .16$). However, there was no significant main effect of group and no significant interactions with group in either the subject or item analysis (all *F*s < 1 and all *p*s > .05). Post-hoc comparisons were used to explore the condition x position interaction. These showed significantly slower residual reading times for the high-competition vs. low-competition condition at the RC verb ($t(44) = 3.78$, $p < .001$), and also at the main verb region ($t(44) = 4.55$, $p < .001$) but no difference at the RC noun ($t(44) = 1.28$, $p = .23$). Between-subject t-tests confirmed that there were no differences in reading times between groups for any condition or word-position (all *t*s < 1.5, *p*s > .15). Therefore, these results suggest that in terms of reading times, adult and adolescent participants are affected equally by competition.

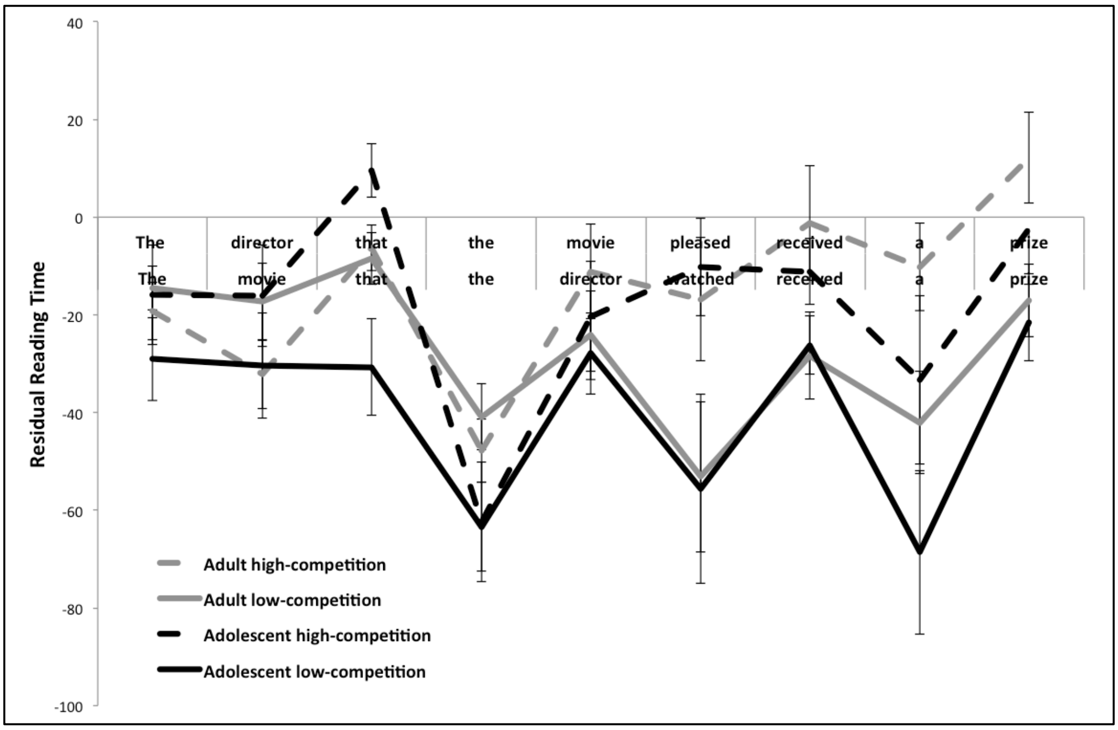


Figure 4.4 The residual reading times for each word position for the adult and adolescent groups.

4.2.2.2 Sentence Production

Production accuracy. Across conditions the average percent correct responses for the adolescent group was 79.52% (SD = 22.17) and 89.89% for adults (SD = 17.02). A 2 x 2 mixed design ANOVA was performed with response accuracy as the dependent variable, and group (adolescent or adult) and condition (high-competition or low-competition) as factors. This revealed a significant main effect of condition (*F1*(1, 41) = 27.33, $p < .001$; *F2*(1, 78) = 57.42, $p < .001$) and group (*F1*(1, 41) = 5.16, $p < .05$; *F2*(1, 78) = 27.59, $p < .001$) but no significant interaction (*F1*(1, 41) = .10, $p = .75$; *F2*(1, 78) = .03, $p = .88$). Planned comparisons were conducted to further explore the main effects in the subject analysis. These revealed that both groups showed a deficit in accuracy for the high-competition relative to low-competition items (adults: $t(20) = 4.0$, $p < .001$; adolescent: $t(21) = 3.42$, $p < .01$) (see Table 4.2). However, comparisons across groups showed that adults were more accurate than adolescents in their responses to the low-competition items ($t(41) = -4.90$, $p < .001$), but there was no significant difference in response accuracy for the high-competition items, although there was a numerical difference in the expected direction ($t(41) = -1.25$, ns).

Table 4.2 **Production accuracy scores (% correct) for the adult and adolescent groups.**

Production accuracy: percent correct

Group	High-competition (SD)	Low-competition (SD)
Adults	81% (20.52)	99% (3.37)
Adolescents	72% (27.90)	88% (20.52)

Production initiation times. The log transformed initiation time data were compared across groups and conditions (see Figure 4.5). Table 4.3 shows the raw initiation times across conditions for each group, for reference purposes. The 2x2 ANOVA showed a significant main effect of condition ($F(1, 40) = 28.69$, $p < .001$; $F2(1, 78) = 13.38$, $p < .001$), a marginally significant effect of group in the subject analysis only ($F(1, 40) = 2.87$, $p = .09$; $F2(1, 78) = 2.31$, $p = .13$), and a significant group x condition interaction ($F(1, 40) = 4.20$, $p < .05$; $F2(1, 78) = 2.90$, $p = .09$). Within subject t-tests of the subject analysis revealed that both groups showed a significant competition effect (adolescent ($t(18) = 2.29$, $p = .03$); adult ($t(22) = 5.39$, $p < 0.01$). Between-group comparisons showed that adults had faster initiation times on the low-competition items compared to adolescents ($t(40) = 2.28$, $p = .03$), however there was no significant difference for the high-competition items ($t(40) = 0.30$, ns). Therefore, the significant group x condition interaction can be explained by there being a larger effect of competition in the adult compared to the adolescent group who have more similar difficulty in both conditions.

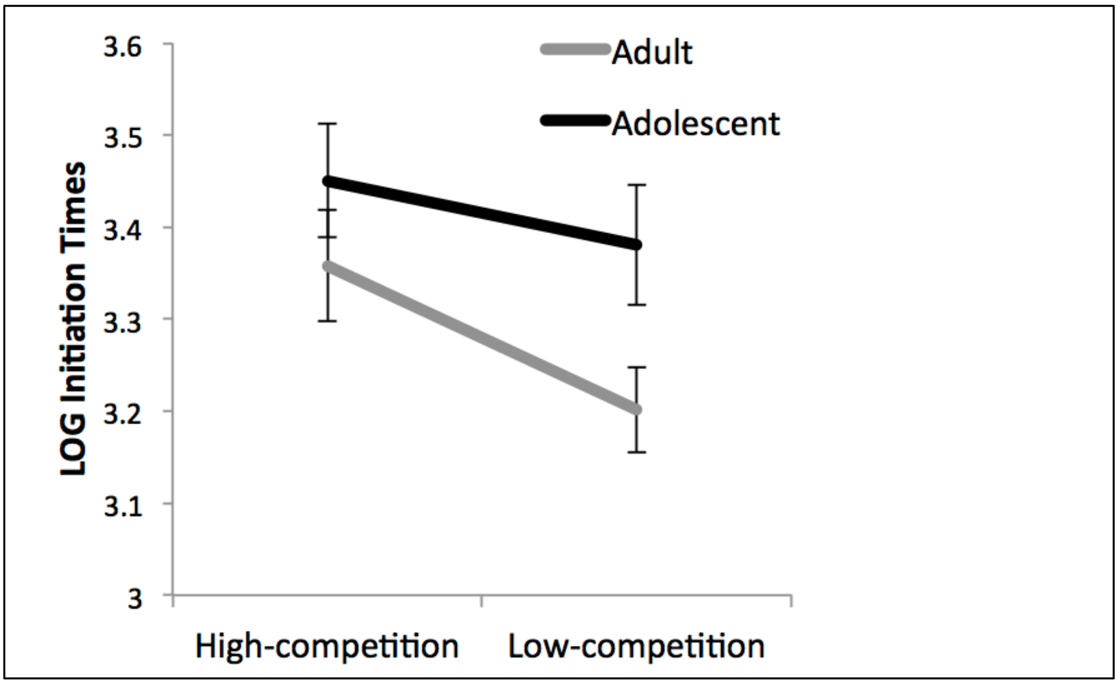


Figure 4.5 The Log-transformed production initiation times for the adult and adolescent groups.

Table 4.3 The raw production initiation times for the adult and adolescent groups.

Production initiation times (ms)		
Group	High-competition (SD)	Low-competition (SD)
Adults	3160 (1660)	2002 (763)
Adolescents	4732 (2950)	3293 (2444)

4.2.3 Discussion

The aim of this study was to investigate the influence of age on the ability to resolve competition in sentence production and comprehension by comparing adult and adolescent performance. In comprehension, compared to the adults, adolescents showed marginally decreased accuracy in comprehending the high-competition items, thereby suggesting a deficit in the ability to resolve competition in the high-competition cases. However, no between-group difference was found in the reading times, suggesting that despite the difference in accuracy data, the adolescent comprehension deficit might be comparatively mild and is not reflected in speed of processing. In the production task, adolescents demonstrated an overall slower and more error-full performance, accompanied with a smaller influence of the competition manipulation compared to adults (i.e., a smaller difference across competition conditions). This effect can be explained in terms of a general difficulty in production, as adolescents were slower overall and find the low-competition condition more difficult relative to adults. Possible explanations for these effects are explored in the general discussion at the end of the chapter.

Overall, the results provide tentative evidence to support the prediction that adolescents have deficits in the ability to resolve competition in comprehension (the production results might reflect a more general control deficit that effects both conditions: see the General Discussion at the end of this chapter). This is consistent with the wider literature suggesting that adolescents have increased difficulty in a range of cognitive control tasks, such as the Stroop task, the Go/NoGo task, and the Simon task (Rubia, et al., 2006; Tamm, et al., 2002). Furthermore, the findings extend previous results to apply to a very different form of competition processing, that is the ability to resolve cue-based competition in sentences. Specifically, adolescents have difficulty in resolving conflicting semantic and syntactic cues in the sentence, and in particular, in inhibiting the more prepotent thematic role interpretation of *director* and *movie*, which is that animate entities are agents and inanimate entities are patients of an event.

Adolescent behavioural deficits are thought to reflect the underdevelopment of neural inhibitory processing systems (Bunge & Wright, 2007; Casey, et al., 2005; Durston, et al., 2006). However, an alternative explanation for the current results is that it relates to group-differences in language experience, rather than to underlying neurodevelopmental differences. Indeed, language experience is known to be a major predictors of relative-clause processing difficulty, with increased experience decreasing difficulty (Wells, et al., 2009). In the next study, we investigate the extent to which adults and adolescents differ in terms of the neural processes engaged by competition in production and comprehension by contrasting adult and adolescent neural activity from the production and comprehension tasks. Importantly, age-related changes in functional activity are related directly to measures of structural development, specifically grey matter density, thereby linking functional changes in the control networks engaged by each group to structural changes in neurodevelopment.

4.3 Experiment 4

4.3.1 Introduction.

The functional activity was compared for adult and adolescent groups in an fMRI study using the same production and comprehension tasks described in Chapter 3. The aim of this study was to investigate the influence of neurodevelopmental changes on the functional networks engaged by language control processes, by comparing adult and adolescent neural responses to cue-based competition. This study also aimed to investigate the extent to which neurodevelopment has a parallel effect on production and comprehension control processes by comparing the pattern of data from each task. Importantly, variations in neural activity were directly related to structural development by correlating brain activity with measures of grey matter density using VBM, thereby linking the group-differences in functional activity to underlying differences in neural development. This is the first study to investigate functional and structural changes in language, although this method has been used successfully in other domains to determine the relationship between functional and structural changes (Dumontheil; Eckert et al., Lee et al., 2007).

Based on data from the developmental cognitive control literature, it was predicted that adolescents would show decreased activity within core parts of the adult language control network. Specifically, areas such as LIFG and pMTG that play a core role in both production and comprehension tasks should show reduced activity in adolescents compared to adults. A similar group-difference might also be found within areas engaged in production-specific processes, such as medial prefrontal cortex, but this effect might be specific to the production task. Beyond the “core-network”, however, it was predicted that adolescents would recruit a generally more distributed network of regions to resolve competition compared to adults. Critically, this being the first study of its kind, it is not known which regions might be additionally recruited in adolescents for language processing, if indeed they proved to show a more distributed network.

4.3.2 Methods

4.3.2.1 Participants.

Eighteen adolescents took part in the fMRI experiment that did not take part in the behavioural experiment (10 females, mean age 13.7, SD = 1.26, range = 12 - 16 years). This data was compared to that from the adult group described in Chapter 3 (7 females, mean age 23.7, SD = 3.72, range = 19 – 33 years). All participants were assessed on verbal ability using the verbal subtests (vocabulary and similarities) of the Wechsler Abbreviated Scale of Intelligence (WASI; Wechsler, (1999) (see Table 4.4)). Whilst both groups had above average verbal intelligence (the average being a score of 100 point), scores were found to be significantly higher in the adult group (*t*(33) = 2.92, *p* < .01). However, when analyses were run that controlled for these variations, using verbal IQ as a covariate in ANCOVA analyses, variations in verbal intelligence proved to not account for any of the results reported below, unless otherwise stated explicitly.

Table 4.4 The Verbal IQ scores for the adult and adolescent groups.

Verbal IQ

Age group	Mean (SD)	Range
Adults (N = 17)	127.29 (6.74)	117 – 146
Adolescents (N = 18)	118.77 (10.09)	97 – 136

4.3.2.2 Procedures.

All subjects took part in the production and comprehension fMRI tasks using the high- and low-competition stimuli. The stimuli, tasks, and scanning protocols were identical to those described in Chapter 3. Behavioural responses from within the scanner were recorded for the comprehension catch trials, and also for the production completion times (as indexed by button presses).

4.3.2.3 Data analysis.

The data was analysed using the same parameters as described in the previous chapter. Several contrasts were computed for each data set. For the comprehension task, all sentences were contrasted relative to the visual baseline (language - baseline), and each condition considered separately relative to baseline (high-competition - baseline; low-competition - baseline). Similar contrasts were performed on the production data but this time contrasting the experimental trials with the read-only control trials. There were three production contrasts: all production > control, high-competition production > control, low-competition production > control. Whole-brain analyses were conducted to compare the general pattern of results for the comprehension and production networks, i.e., the qualitative group-differences, and ROI analyses were conducted to investigate the more specific experimental predictions and test for quantitative differences between groups.

Region of interest analyses. Four ROIs were defined based on Harvard-Oxford probabilistic cortical structure atlas built into FSL. ROIs were defined for LIFG (inferior frontal gyrus, pars opercularis), left pMTG (posterior middle temporal gyrus, temporooccipital part), the left medial prefrontal cortex (superior frontal gyrus, (LSFG)), and the left anterior temporal lobe (LATL). LIFG and pMTG were selected due to their central role in adult production and comprehension control processes. Medial prefrontal cortex (LSFG) was selected due to its core role in adult production competition processes (as shown in Chapter 3), and also as this area has been found to be hyper-activated in adolescent groups in non-linguistic cognitive control tasks (Durston, et al., 2006). The predictions regarding SFG are therefore unclear; it may be hyper-activated in adolescents as in previous studies, or it may show a similar pattern as other core language areas i.e. reduced adolescent involvement. The left anterior temporal lobe (LATL) was included post-hoc, to further investigate potential group-differences in regions that were identified in the initial whole-brain analysis. Group differences in LATL activity are more generally also interesting, given the role of this area in semantics and sentence-level combinatorial processes (Hickok and Poeppel, 2000; 2004; 2007; Vandenberghe, Nobre, & Price, 2002).

Within each ROI, average measures of language activity were computed for each participant. For the comprehension results, we extracted the mean t-value for the contrast of high-competition vs. baseline and low-competition vs. baseline. For the production results, we extracted the corresponding t-value, i.e., high-competition vs. read-only control and low-competition vs. the read-only controls.

The advantage of using the *t*-value as a dependent measure is that it normalises for variations in within-subject noise, therefore making it a more powerful measure of the effect size for a contrast (Postle, Zarahn, & D'Esposito, 2000). The average *t*-values for each participant were used as the dependent variable in a 2 x 2 mixed design ANOVA where group (adult and adolescent) was the between subjects factor and condition (high- and low-competition) was the within subjects factor. For completeness, the same analyses were also performed using the contrast parameter estimates rather than the t-values. The results are reported using both methods for comparison. The two analyses techniques yielded consistent statistical results for the comprehension data (except in one case) however certain results were inconsistent in production suggesting that the production data may be less reliable. The possible explanation and impact of these differences is discussed in the results section. However, when inconsistent results were found, greater weight was placed on the results found using the t-values as the dependent variable given the evidence that this method as it can account for a greater proportion of the unexplained inter-subject variance thereby making it a more powerful estimate of effect size (see Postle et al., 2000).

Psychophysiological interaction analyses. PPI analyses were conducted to investigate group-differences in the networks that interact within LIFG as a function of competition. Note that these analyses were performed only for the comprehension task (using the method described in Chapter 3), as there was found to be no significant LIFG competition-effect for the adolescent group in the production task.

Voxel-based morphometry. Grey matter density was calculated in a VBM analysis using the VBM8 toolbox within SPM8. Measures of grey matter density were used to confirm the presence of age-related difference in grey matter, and were also used to correlate with the task-related activity to test directly for a relationship between language-activity and neurodevelopment. Images were processed using a generative model that combines bias correction, image regulation and tissue segmentation (Ashburner & Friston, 2005). Grey matter was segmented and smoothing was applied using a 10 mm full width at half maximum (FWHM) smoothing kernel. The analysis was performed using the unmodulated volumes, so that the data reflected a measure of tissue density/concentration (i.e. the proportion of grey/white matter) rather than a measure of tissue volume, as when modulated volumes are used (Mechelli, Price, Friston, & Ashburner, 2005). To control for possible edge effects, images were masked using an absolute masking threshold of <.01. In order to confirm expectations of age-related decreases in grey matter density as described in the introduction to this chapter, regressions were run on the smoothed grey matter volumes using age as a predictor of grey matter density. In order to test the relationship between grey-matter density and functional activation, the activity extracted from each ROI for each of the language tasks was regressed onto the grey-matter data for the same ROI in a VBM analysis. This revealed voxels within each ROI where functional activity correlated with grey matter density. This analysis reveals the extent to which functional activation varies as a function of grey matter density, and suggests that the functional differences between groups are due to structural differences in neurodevelopmental, as opposed to say, reduced linguistic experience in adolescents.

4.3.3 Results

4.3.3.1 Behavioural data from fMRI scans.

Table 4.5 shows the behavioural data across groups from the production and comprehension fMRI tasks. This revealed that the groups were matched in terms of their behavioural performance. In the comprehension task, accuracy in responses to the catch trials was on average high and did not differ across groups for either the high-competition (*t*(33) = .26, *p* = .79) or the low-competition items (*t(*33) = .64, *p* = .52). Similarly, for the production task, the time taken to complete the sentence fragments did not differ significantly between adults and adolescents for either condition, as indexed by the button-presses at the end of the completions (high-competition: *t*(33) = 1.05, *p* = .30; low-competition: *t*(33) = .80, *p* = .42).

Table 4.5 **In-scanner behavioural performance for the adult and adolescent groups.**

Task	**Adults** Mean (SD)	**Adolescents** Mean (SD)	***t***	***p***
Comprehension catch trials				
High-competition (accuracy)	84.82% (21.47)	86.60% (13.39)	.26	.79
Low-competition (accuracy)	93.75% (13.64)	96.72% (7.64)	.64	.52
Production button responses				
High-competition (RT)	3.55s (.75)	3.84s (.81)	1.05	.30
Low-competition (RT)	3.02s (.62)	3.22s (.76)	.80	.42

4.3.3.2 General language networks.

To examine the qualitative differences in the language networks engaged by adult and adolescent groups regardless of competition, analyses were carried out contrasting the comprehension and production tasks relative to baseline or control separately for each group. These analyses were restricted to voxels within the left hemisphere in order to increase statistical power (cluster-corrected, $Z > 2.3$, $p < .05$). Note that neither group activated the right hemisphere for either the production or comprehension tasks, except for early visual areas in comprehension for both groups (cluster corrected, $Z = 2.3$, $p < .05$) as revealed by a separate right hemisphere analyses. Therefore, only the left hemisphere results are reported here.

For the comprehension task, the results from the analysis of all items > baseline showed that adults and adolescents both recruited the same core front-temporal network, including lateral areas of the frontal cortex (LIFG, and precentral gyrus) and posterior and anterior areas of the temporal cortex, centered around middle temporal gyrus but extending to superior and inferior regions. Although, despite this similar pattern LIFG activity was found to be significantly stronger in the adults compared to the adolescents. Furthermore, as predicted, adolescents alone recruited an additional network of regions beyond the core network. In particular, the medial prefrontal cortex (supplementary motor cortex, and posterior and anterior superior frontal gyrus) and a more extensive pattern of activity within the temporal pole, especially in inferior regions (see Figure 4.6; the corresponding table is presented in Appendix C). Direct group contrasts showed that the activity was significantly stronger in the adolescents compared to the adults within both of these areas (see Appendix C). This suggests qualitative differences in the comprehension networks engaged by adults and adolescents; whilst adolescents do recruit the standard fronto-temporal “language network”, they show a more distributed pattern of activity with additional involvement of medial prefrontal cortex (SFG) and anterior temporal pole.

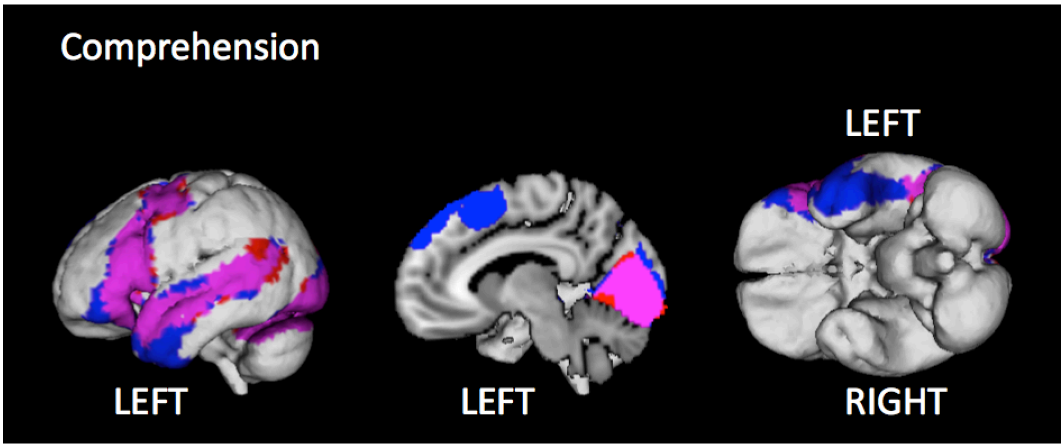


Figure 4.6 Group analyses showing the contrast of all comprehension items relative to baseline for the adult group (red) and the adolescent group (blue) and the overlap between the two (purple) (cluster corrected, *Z* = 2.3, *p* <. 05).

For the production task, for the contrast of all production trials vs. controls both groups recruited lateral frontal areas, including LIFG and precentral gyrus, as well as medial prefrontal structures within SMA, superior frontal gyrus and anterior cingulate gyrus, and also regions within the anterior temporal lobe. The adolescents showed marginally more distributed activity with medial prefrontal cortex. However, contrary to what was observed with comprehension, the pattern of activity was found to be moderately more extensive in the adult group, who recruited additional temporal areas and subcortical structures (caudate, putamen, thalamus) that were absent in the adolescent data (see Figure 4.7). Direct comparisons of groups yielded no significant differences. Therefore, the observation from the comprehension task that adolescents recruit a more distributed network of areas is not replicated for the production task (See tables in Appendix D for summaries of these results).

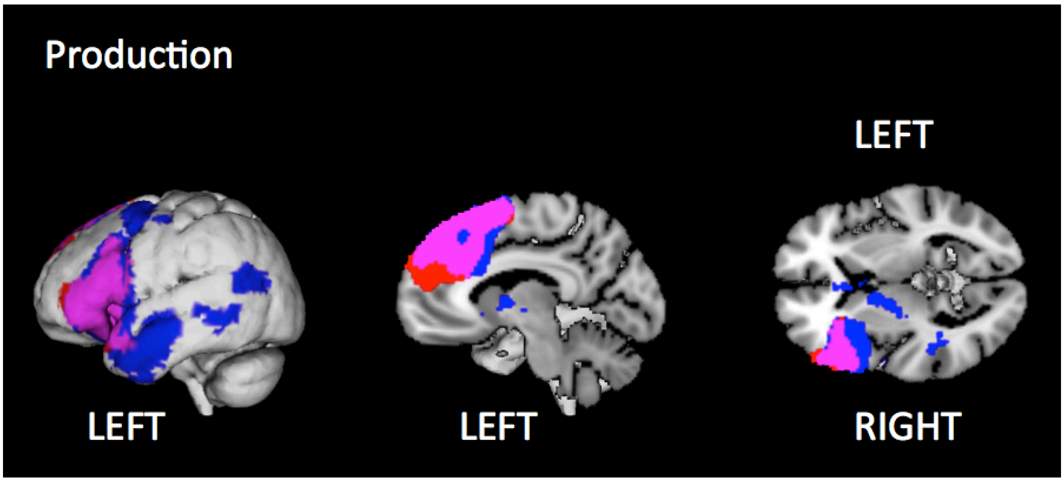
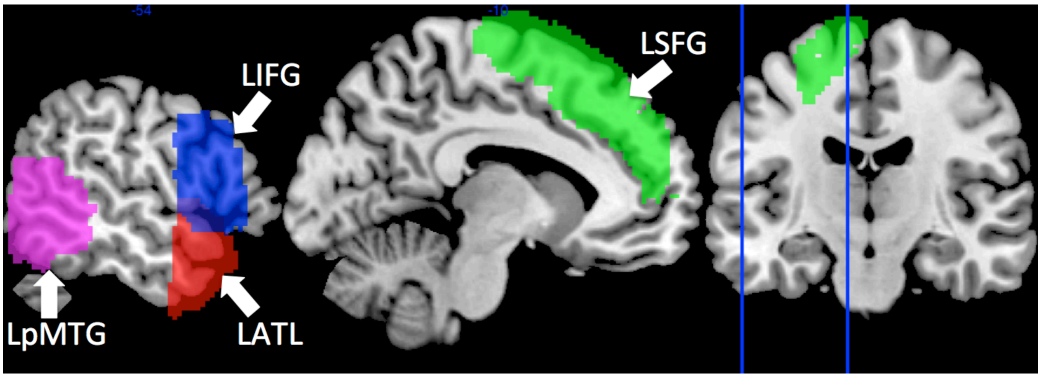
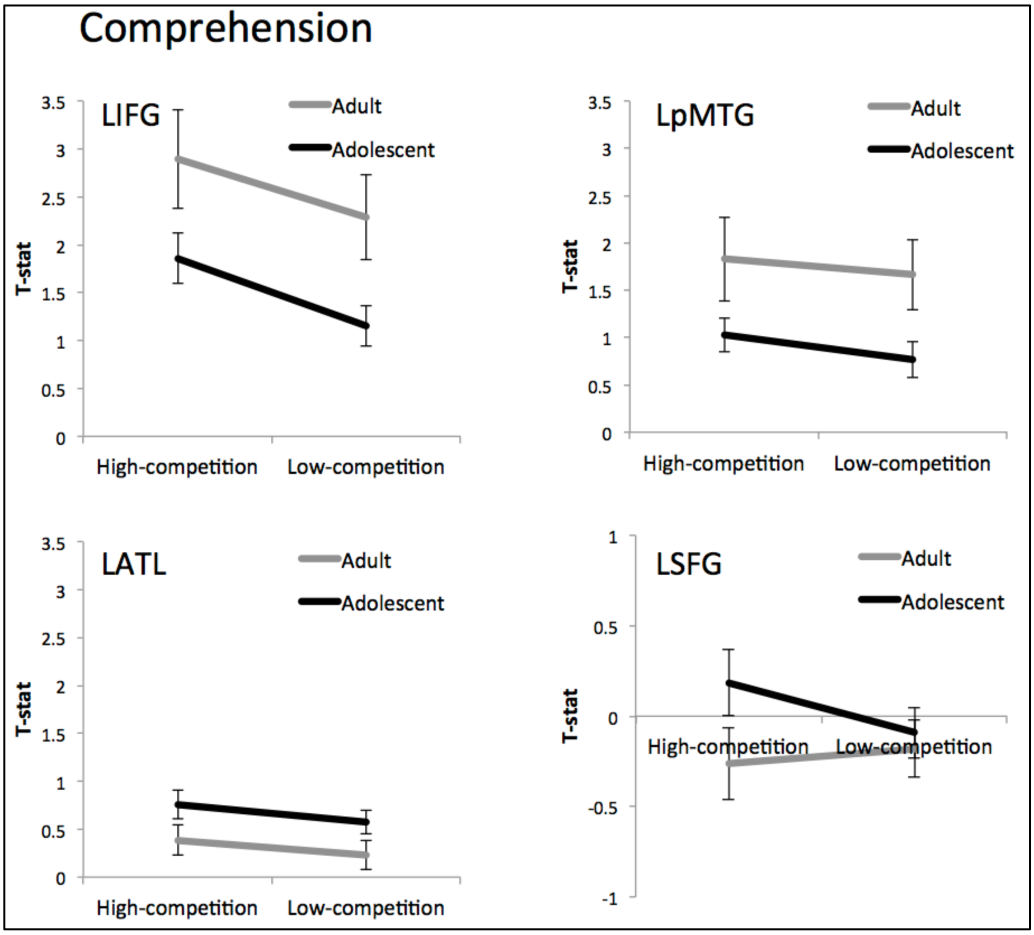


Figure 4.7 Group analyses showing the contrast of all production items relative to the control trials for the adult group (red) and the adolescent group (blue) and the overlap between the two (purple) (cluster corrected, $Z = 2.3$, $p <. 05$).

4.3.3.3 ROI analyses.

ROI analyses were conducted in order to directly compare groups and to test for effects of competition in the comprehension and production tasks. Four ROIs were defined based on Harvard-Oxford cortical maps: LIFG, LpMTG, LATL, and LSFG (see Figure 4.8; Top-panel). Across participants, the average *t*-value was extracted from within each ROI for each of the conditions relative to baseline or controls and 2 x 2 ANOVAs were performed using group (adult and adolescent) and condition (high-competition and low-competition) as factors, and the average *t*-value as the dependent variable. The average *t*-value for each group and condition from each ROI are shown in Figure 4.8. The results from the analyses performed using the contrast parameter estimates (COPEs) as the dependent variable are also reported.


LIFG
LpMTG
LATL
LSFG


Comprehension
LIFG
Adult
Adolescent
T-stat
3.5
3
2.5
2
1.5
1
0.5
0
High-competition
Low-competition
LpMTG
Adult
Adolescent
T-stat
3.5
3
2.5
2
1.5
1
0.5
0
High-competition
Low-competition
LATL
Adult
Adolescent
T-stat
3.5
3
2.5
2
1.5
1
0.5
0
High-competition
Low-competition
LSFG
Adult
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T-stat
1
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-0.5
-1
High-competition
Low-competition

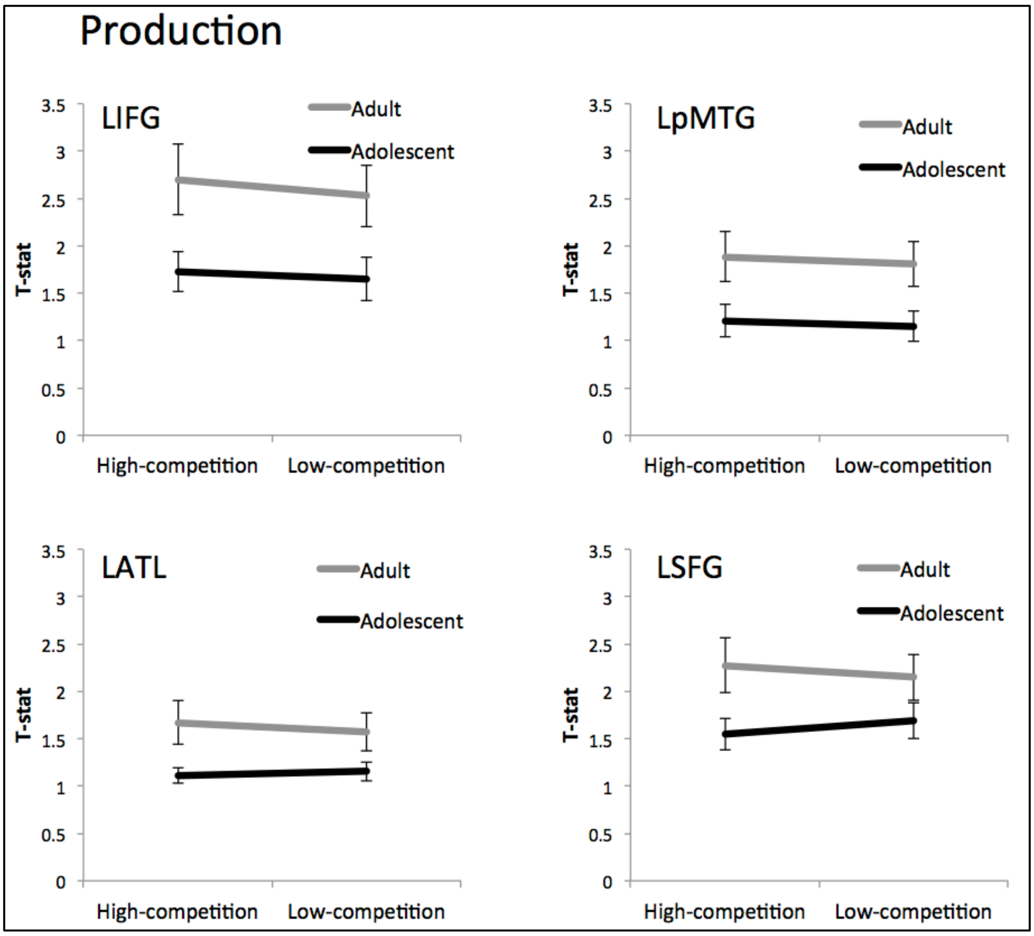


Figure 4.8 Top) The four anatomical ROIs. Middle) The results from the comprehension ROI analysis. Bottom) The results from the production ROI analysis.

4.3.3.3.2 Comprehension ROI analyses.

Results from the t-value analyses.

LIFG. Beginning with the comprehension data, within the LIFG ROI, as was predicted, the ANOVA revealed a significant effect of group, with adults showing increased activity relative to adolescents ($F(1,33) = 4.44$, $p < .05$), and also a significant effect of condition with increased activity for the high- compared to the low-competition condition ($F(1,33) = 38.96$, $p < .001$). There was no significant group x condition interaction ($F(1,33) = .22$, $p = .65$). Therefore, these results support the experimental predictions; whilst both groups recruit LIFG as a function of competition, adolescents show a weaker recruitment of this area. Planned t-tests were conducted to explore this effect further, and also to examine how it compares to the LIFG production results reported below. Within-subject t-tests showed a significant effect of competition in each group (Adults: $t(16) = 4.03$, $p < .001$) adolescents $t(17) = 4.83$, $p < .001$), and between group comparisons showed a marginally significant effect of group for both conditions (high-competition: $t(33) = 1.83$, $p = .08$; low-competition: $t(33) = 2.36$, $p = .03$ two-tailed).

LpMTG. As predicted a similar pattern was found within left pMTG to that in LIFG; the ANOVA showed a significant effect of group ($F(1,33) = 4.02$, $p < .05$) and a marginal effect of condition ($F(1,33) = 3.34$, $p = .08$), but no interaction ($F(1,33) = .19$, $p = .67$). However, these effects became non-significant when including verbal-IQ has a covariate in an ANCOVA (group: $F(1,32) = 1.52$, $p = .23$; condition: ($F(1,32) = 1.92$, $p = .18$).

LSFG. Within the left superior frontal gyrus, there were no significant main effects (group: $F(1,33) = 1.37$, $p = .25$; condition: $F(1,33) = 1.53$, $p = .23$). There was, however, a significant group by condition interaction ($F(1,33) = 5.06$, $p < .05$). Post-hoc t-tests showed that the interaction could be explained by a significant effect of competition in the adolescent group ($t(17) = 2.38$, $p = .03$) but not for the adult group ($t(16) = -0.75$, $p = .47$). This suggests that adolescents recruit this additional region within medial prefrontal cortex for competition processes, which is absent in the adult comparisons. It is interesting to note that non-linguistic control studies have also found that medial prefrontal cortex is hyper-activated in adolescents (Durston, et al., 2006).

LATL. Within the anterior temporal lobe the effect of group was reversed compared to the results from LIFG and pMTG. The ANOVA showed a marginally significant group effect, with increased activity for the adolescent group relative to the adults ($F(1,33) = 3.54$, $p = .07$). There was also a significant effect of condition ($F(1,33) = 5.36$, $p < 0.05$) but no significant interaction ($F(1,33) = .04$, $p = .85$). Therefore, within an area that is important for language processing, but is not considered as part of the core conflict network in adults, adolescents show increased recruitment than adults for competition. This pattern has not been identified by non-linguistic control studies suggesting a language-specific effect.

Results from the COPE analyses.

LIFG: As was the case in the analysis using the t-statistic, a mixed design ANOVA with condition as a within subject factor and group as a between subject factor showed that within the LIFG, there was trend effect of group ($F(1,33) = 2.96, p = .09$) and a significant effect of condition ($F(1,33) = 22.57, p < .001$) but no interaction ($F(1,33) = 1.08, p = .31$).

LpMTG: Unlike in the t-statistic analysis, within the LpMTG the results revealed no significant main effects (Group: $F(1,33) = 1.87, p = .18$; Condition: $F(1,33) = 1.48, p = .23$), and no interaction ($F(1,33) = .89, p = .36$).

LSFG: As was the case in the analysis using the t-statistic, a mixed design ANOVA with condition as a within subject factor and group as a between subject factor showed that within the LSFG there were no significant main effects (Group: $F(1,33) = .31, p = .58$; Condition: $F(1,33) = .01, p = .97$) but there was a significant group x condition interaction ($F(1,33) = 4.36, p < .05$).

LATL: As was the case in the analysis using the t-statistic, within the LATL there was a significant effect of group with increased activation for adolescents relative to adults ($F(1,33) = 4.81, p < .05$). There was, however, no effect of condition ($F(1,33) = 2.38, p = .13$) and no interaction ($F(1,33) = .01, p = .91$).

Summary. In support of the predictions adolescents were found to show reduced involvement of areas that play a central role in adult comprehension competition processes, specifically within LIFG and also pMTG (although the results are more tentative for pMTG as no group difference was found in the COPE analysis). However, this is accompanied with the increased recruitment of additional areas by adolescents that are not central to adult comprehension control, including LATL and LSFG. The LSFG has also been found to be hyper-activated in adolescents in non-linguistic control studies. However, this is not the case for the LATL thereby suggesting a language-specific change in control processes.

4.3.3.3.3 Production ROI analyses.

Results from the t-value analyses.

LIFG. In production, the results from the ANOVA showed the predicted effect of group, with significantly increased activity in adults relative to adolescents ($F(1,33) = 5.27$, $p < .05$), and a marginally significant effect of condition in the predicted direction ($F(1,33) = 3.70$, $p = .06$). There was, however, no significant group by condition interaction ($F(1,33) = 0.50$, $p = .48$) (Note that this interaction becomes significant in the COPE analysis). Planned comparisons were conducted to explore the data further. In the behavioural study, adolescents were found to show a smaller effect of competition relative to adults for the production task. To examine whether adolescents showed a neural competition effect within subject t-tests were conducted for each group to compare responses to the high- and low-competition conditions. These showed the predicted effect of competition in the adult group ($t(16) = 1.92$, $p = .06$ two-tailed), but no effect in the adolescent group ($t(16) = .84$, $p = .42$). Therefore, the LIFG production results appear to mirror what was found behaviorally, where adolescents show little influence of competition.

LpMTG. A significant effect of group was also found in left pMTG for the production task, with increased activation for the adult group ($F(1,33) = 5.31$, $p = .03$). There was, however, no significant effect of condition ($F(1,33) = 1.19$, $p = .28$) and also no interaction ($F(1,33) = .02$, $p = .88$). Therefore, as in in LIFG, LpMTG is more strongly activated by adults than adolescents, but at least from this analysis, pMTG does not appear sensitive to competition in either group.

LSFG. Within the LSFG the results revealed a marginal effect of group ($F(1,33) = 3.71$, $p = .06$), and also a marginal group x condition interaction ($F(1,33) = 3.39$, $p = .07$). There was no overall main effect of condition ($F(1,33) = .01$, $p = .93$). Post-hoc comparison showed that the adults had greater activity than the adolescents for the high-competition condition ($t(33) = 2.21$, $p = .04$), but there was no difference for the low-competition condition $t(33) = 1.51$, $p = .14$).

Note that this is a different pattern to what was shown in comprehension, where the adolescents showed increased activation.

LATL. A similar pattern was found in the LATL, as that found in the pMTG. The ANOVA showed an overall main effect of group, with increased activation for the adults (*F*(1,33) = 4.74, *p* = .04). However, no effect of condition (*F*(1,33) = .24, *p* = .63) and no interaction was found (*F*(1,33) = 1.78, *p* = .19). This pattern is different to what was found in comprehension, where adolescents showed increased activity.

Results from the COPE analyses.

LIFG. As in the analysis using the t-values, the results from the LIFG ANOVA showed a marginal effect of group (*F*(1,33) = 3.42, *p* = .07), a significant effect of condition in the predicted direction (*F*(1,33) = 10.93, *p* < .05). Unlike in the analysis using the t-values, there was also a significant group by condition interaction (*F*(1,33) = 4.48, *p* < .05). Within subject t-tests were conducted for each group to compare responses to the high- and low-competition conditions. These showed the predicted effect of competition in the adult group (*t*(16) = 3.77, *p* < .01), but no effect in the adolescent group (*t*(16) = .86, *p* = .41). Therefore, the LIFG production results appear to mirror what was found behaviorally, where adults showed a larger influence of competition compared to adolescents. This differs to what is found for the LIFG in comprehension where competition-effects were found for both adult and adolescent groups.

LpMTG. Unlike in the t-value analysis, the LpMTG showed no significant effect of group (*F*(1,33) = 1.64, *p* = .21). There was, however, no significant effect of condition (*F*(1,33) = 1.79, *p* = .19) and also no interaction (*F*(1,33) = 1.14, *p* = .29). Therefore, as in in LIFG, LpMTG is more strongly activated by adults than adolescents, but at least from this analysis, pMTG does not appear sensitive to competition in either group.

LSFG. Unlike in the t-value analysis, within the LSFG the results revealed no significant main effects (Group: *F*(1,33) = .02, *p* = .89; Condition: *F*(1,33) = .71, *p* = .41), and no interaction (*F*(1,33) = 1.88, *p* = .18).

LATL. In this analysis, the LATL showed no significant main effects (Group: $F(1,33) = 1.18$, $p = .29$; Condition: $F(1,33) = .59$, $p = .45$). There was, however, a significant group x condition interaction ($F(1,33) = 4.24$, $p < .05$). Post-hoc comparisons suggest that the interaction can be explained by marginally significantly increased activation for the adults compared to adolescents in the high-competition condition ($t(33) = 2.11$, $p = .04$) but not in the low-competition condition ($t(33) = .12$, $p = .90$).

Summary. In production, adolescents showed reduced activity within all four ROIs in the t-value analysis, and within the LIFG for the COPE analysis. Furthermore, adolescents appear to show no influence of competition within LIFG, with no difference in activity for the high- and low-competition conditions. This is a different pattern to that found in comprehension where LIFG was sensitive to the competition manipulation. The finding of an LIFG group-difference was consistent across the t-value and COPE analysis methods. This suggests that adolescents show reduced recruitment of the neural area regarded to play a central role in resolving competition in adult production. However, for the other ROIs the significant group-difference found using the t-value analysis became non-significant using the COPE method. Whilst the t-value analysis might be regarded the more powerful technique the effects from the pMTG, ATL, and SFG should be interpreted with caution given their unreliable nature. The inconsistencies likely arise due to high levels of noise in the production data, especially in the adolescent group. As was shown in the behavioural study, the adolescents show high error rates in the production task and this would add noise to the fMRI data thereby making the statistical results unstable.

4.3.3.4 Psychophysiological interaction analyses.

It is possible that adults and adolescents not only differ in terms of which regions are recruited during language processing, but also in the way in which these regions interact as part of a functionally connected network. PPI analyses were conducted examine variations across groups in those networks that interact within LIFG as a function of competition (high-competition vs. low-competition). These analyses were performed separately for the adult and adolescent groups, and for only the comprehension task. This analysis revealed that in comprehension LIFG interacted with different regions for the adult and adolescent groups. In adults the LIFG was found to functionally connect with the pMTG (as discussed in detail in Chapter 3). However, in adolescents a different pattern of fronto-temporal connectivity was found, with LIFG showing connectivity with the temporal pole, rather than pMTG (see Table 4.6). Therefore, this provides evidence of qualitative differences in the networks that cooperate with LIFG to resolve competition in comprehension in adult and adolescent groups.

Table 4.6 Results from whole-brain PPI analysis (uncorrected, *p* < .001): regions that show an interaction between level of competition (high vs. low) and the time-series of activity within BA44 in adult and adolescents in the comprehension task.

Brain area	*Z*	Voxel (MNI)		
		x	*y*	*z*
Adult Group				
Posterior Middle Temporal Gyrus	3.81	-60	-62	12
Adolescent Group				
Temporal Pole, left	3.00	-32	4	-22
Lateral Occipital Cortex	3.52	-20	-68	62

4.3.3.5 VBM analyses

4.3.3.5.1 Grey matter density.

Regressions were run in a VBM analysis using age as a predictor of grey matter density. This analysis revealed that as expected, an extensive network of neural regions showed a negative correlation between age and grey matter density with the strongest correlation in lateral and medial prefrontal cortex (LIFG, middle frontal, and superior frontal gyrus) and parietal cortex (angular and supramarginal gyri) (*p* < .05, cluster corrected) (see Figure 4.9). This therefore confirms that the adult and adolescent groups differed in terms of grey matter development, with a higher density of grey matter in the adolescent group, which steadily decreases with age.

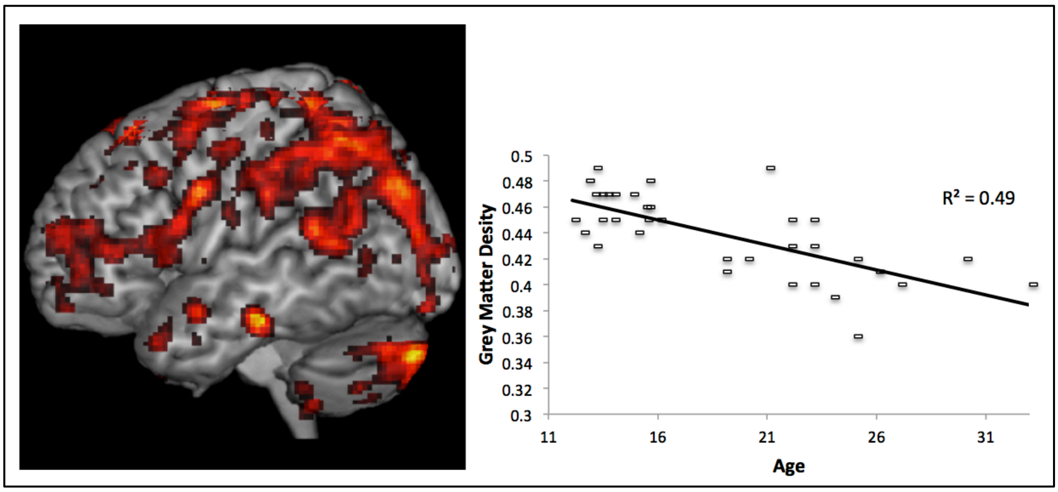


Figure 4.9 Left) VBM analyses showing a negative correlation between age and grey and matter density. Right) Negative correlation between age and grey matter density in the LIFG ROI.

4.3.3.5.2 Correlations between grey matter density and functional activity.

The aim of this study was to investigate the influence of neurodevelopmental changes on language processing. In the previous analyses, age group was used as an indirect measure of neurodevelopment. However, age groups will differ not only in neurodevelopment but also in other factors such as language experience. In order to examine whether variations in activity in the language tasks relate to a more direct measure of neurodevelopment, the activity from each ROI was correlated with grey matter density measures of the same region. This was achieved by regressing the language data from each participant onto the grey matter density measures for each ROI (by restricting the VBM analysis to a mask of the same region as the ROI language data) (uncorrected, t =3.31, $p < .001$). Analyses were performed separately for the comprehension and production data. The language contrast that was used to correlate onto the grey matter data varied depending on the ROI. In the case of ROIs that showed an overall group difference but no interaction with condition (LIFG, LpMTG, and LATL for production and comprehension tasks) the overall contrast of language vs baseline or control was used as the predictor. However, in the case of the LSFG, where significant interactions were found, the contrast of high-competition > low-competition were used, as this contrast more accurately captured the group differences in activation.

Given that increasing age is associated with decreases in grey matter density (see Figure 4.9 above), it was predicted that within ROIs showing age-related increases in functional activity, a negative correlation should be found between functional activation and grey-matter density. Indeed, in support of this prediction, the language activity was found to correlate in the predicted direction with grey matter density in each of the ROIs, and for both language tasks (see Figure 4.10). Specifically, for the comprehension data, a significant negative correlation was observed between grey matter density and language activity within the LIFG and pMTG ROIs, where adults showed increased activity compared to adolescents. However, positive correlations were found in LATL and LSFG ROIs where adolescents showed increased sensitivity compared to adults. For production, where adults showed greater activity than adolescents in all regions, the activity from all four ROIs correlated negatively with grey matter density. These results suggest that individual differences in activity are related to changes in neurodevelopment, and not simply to reduced linguistic experience in adolescents, or any other unforeseen group differences. That is, the effects observed in the language data across participants appear to vary as a function of grey matter development.

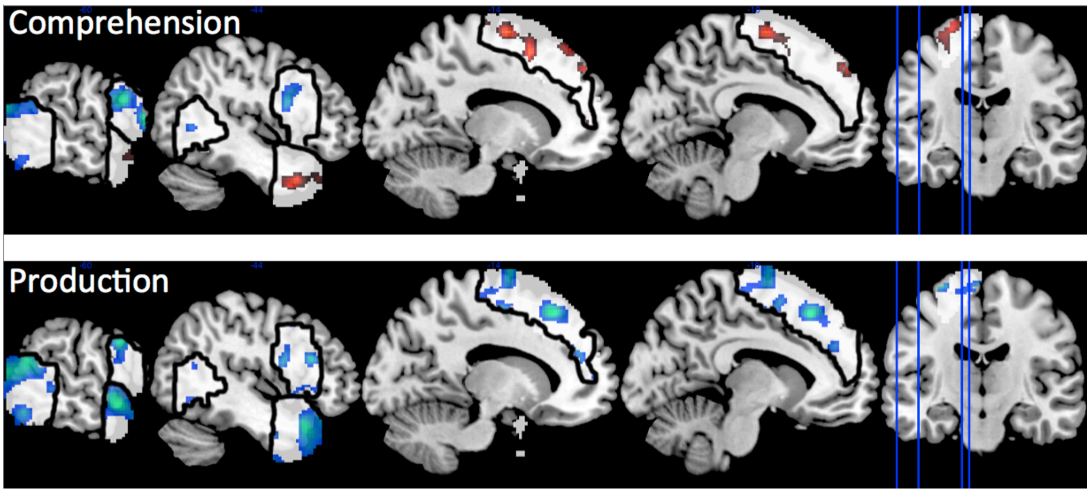


Figure 4.10 VBM analysis showing the voxels in which language activity correlated with grey matter density in each of the four ROIs (thresholded at an uncorrected level of *p* < .001). Red colours indicate positive correlations, and blue colours indicate negative correlations.

4.3.4 Summary

This study aimed to compare adult and adolescent brain responses to cue-based competition in sentence production and comprehension tasks. Based on the existing neurodevelopmental cognitive control literature, it was predicted that in each task, adults would show increased activity compared to adolescents within areas that play a core role in resolving competition. In other words, LIFG and pMTG in both tasks, with the medial prefrontal cortex (SFG) in production also possibly involved. It was also predicted that adolescents would show a more distributed pattern of activity, with the recruitment of additional processing areas for task performance.

The results from the comprehension task largely supported these predictions. Comparisons of the general adult and adolescent comprehension networks showed that whilst both groups recruited core fronto-temporal areas, the adolescent group showed increased involvement of regions within medial prefrontal cortex and inferior anterior temporal lobe. The ROI analyses directly compared the responses for the two groups as a function of competition. These revealed that as predicted, adults had increased activity compared to adolescents within core control regions (LIFG and pMTG), although these regions were equally sensitive to competition in both groups. However, beyond the core adult network, adolescents showed increased activity within the anterior temporal lobe and medial prefrontal cortex, and these areas were also involved in competition processes in adolescents, as confirmed by the ROI and functional connectivity analyses. The results from the comprehension task thus support the prediction that adolescents show decreased involvement of core control regions, but a generally more distributed pattern of activity recruiting an additional network for competition resolution.

The results from the production task support in part the predictions. It was confirmed that adults showed increased involvement of core production region. Although the adults and adolescents recruited similar core networks, the ROI analyses showed that as predicted, activity was found to be significantly greater in the adult compared to the adolescent group. However, in contrast to what was found in comprehension, there was little evidence of adolescents recruiting additional processing networks in production, as adolescents were not found to show increased activity compared to adults in any of regions tested. Interestingly, in production adolescents were found to be insensitive to the influence of competition within LIFG, where equal activity was found for both conditions. This differs to what was found for the comprehension task, where adolescents show a significant competition effect in LIFG.

Overall, the results support the general prediction that adolescents show decreased activity within those areas known to play a central role in cue-based competition in adults. Although, the prediction that adolescents will recruit additional networks was only supported for the comprehension task. Finally, age-related differences in activity were found to relate to variations in grey matter density as measured by VBM. Whilst causality cannot be inferred from correlational analyses, this result does suggest at least that the patterns of brain activity found here in some way relate to neurodevelopmental differences.

4.4 General Discussion

This chapter aimed to investigate the influence of neurodevelopmental changes on conflict resolution processes in sentence production and comprehension, by comparing adult and adolescent groups. The results from the behavioural study provide tentative evidence that, compared to adults, adolescents have mild deficits in the ability to resolve competition in comprehension tasks, and a general deficit in production. The behavioural data also highlighted some potential divergences between production and comprehension tasks. Whereas the comprehension deficit was found to relatively mild and specific to the high-competition items, the production deficit was more general as adolescents showed difficulty in both the high-competition and low-competition condition. The implications of this difference are discussed below. In terms of neural responses, adolescents showed decreased activity within core-processing areas in both production and comprehension tasks, and this was accompanied with the additional recruitment of a further network of areas in comprehension alone. For adolescents, LIFG was sensitive to competition in the comprehension task, but there was no evidence of a competition effect in the production task.

The present results demonstrate tentative evidence that adolescents have deficits in the ability to resolve competition between alternative sentence interpretations in comprehension. The findings support the more general theory that the underdevelopment of inhibitory control mechanisms in adolescents leads to poorer performance on tasks that involve selecting a response from competing alternative responses (Bunge & Wright, 2007; Casey, et al., 2005; Durston, et al., 2006). The current results extend current models to a linguistic domain and a more semantic level of processing, where the conflict derives from conflicting sematic and structural sentence cues. Importantly, the current fMRI effects were found to relate to underlying structural differences in grey matter density between groups, suggesting that the adolescent deficit may be caused by the underdevelopment of key neural structures. Indeed, the adolescent behavioural deficits found here are comparable, albeit less severe, to those found in patients with LIFG lesions (G. Robinson, et al., 1998; G. Robinson, et al., 2005).

This data therefore adds to the existing literature showing that the prefrontal cortex plays a critical role in resolving competition between alternative sentence interpretations/plans. However, it is important to note that despite finding a correlation between functional activity and grey matter density in the current study, the current data cannot fully disentangle the influence of age-related differences in maturation from age-related differences in language experience. Studies have shown that relative-clause processing difficulty relates closely to the level of experience that one has with these structures, with increased experience leading to decreases in processing difficulty (Wells, et al., 2009). Furthermore language experience is known to lead to structural changes in grey matter volume (Lee, et al., 2007; Mechelli et al., 2004; Richardson, Thomas, Filippi, Harth, & Price, 2010). It is therefore likely that the current results are the outcome of an interaction between age-related changes in neurodevelopment and variations in language experience.

4.4.1 Qualitative and quantitative shifts in language control processes.

Neurodevelopmental models of cognitive control have suggested that between adolescence and adulthood, there are qualitative and quantitative shifts in the control networks (Bunge & Wright, 2007; Casey, et al., 2005; Durston, et al., 2006). The current data lends support to the notion of quantitative differences between adult and adolescent control processes. In both production and comprehension tasks, adolescents showed a decreased involvement of areas that play key roles in adult comprehension and production control processes. These age-related changes presumably reflect the fine-tuning of core control systems and increased efficiency in inhibitory processing (Bunge, et al., 2002; Bunge & Wright, 2007; Durston, et al., 2006). Thus the mechanisms used to select an appropriate sentence interpretation/plan amongst competing alternatives become more efficient through development.

The current data also provide partial support for notion of qualitative differences between adult and adolescent control networks. Specifically, in comprehension, adolescents showed hyper-activation of the anterior temporal lobe and medial prefrontal cortex, and also the recruitment of these structures for competition resolution (as illustrated in the ROI and PPI results). There was, however, no evidence for the same pattern in production, where adolescents showed no evidence of increased activity relative to the adults. Whilst this pattern in production was not predicted, it is consistent with a number of studies that have found no evidence of adolescents recruiting additional processing areas. Rather these studies find evidence of only age-related increases in activity (Adleman et al., 2002; Gaillard, et al., 2003; Kwon, Reiss, & Menon, 2002; Schroeter, et al., 2004; Stevens, et al., 2009). The factors that determine whether or not adolescents recruit additional processing networks for cognitive control tasks are not clear. However, there has been some suggestion that the recruitment of additional neural networks serve a compensatory role for the inefficient processes elsewhere in the network (Bunge, et al., 2002; Bunge & Wright, 2007; Durston, et al., 2006). Indeed, this explanation may account for some of the current findings, as the recruitment of compensatory processes in comprehension but not production could account for why the comprehension behavioural deficit appears less severe compared to the production deficit. The reasons that compensatory processes are recruited in comprehension but not production may be because production is a far more difficult task compared to comprehension (see section below for further discussion; Wider implications for production and comprehension control processes) and perhaps the production task here is so difficult that it is beyond compensation.

Given that this is the first study of its kind, there were no specific predictions regarding which areas (if any) would be additionally recruited in adolescents. The results showed that in comprehension, adolescents have hyper-activation of medial prefrontal cortex and the temporal pole for control processing. Medial prefrontal cortex has been found to be hyper-activated in adolescents in a range of cognitive control tasks (see reviews by Bunge and Wright (2007) and Durston et al. (2006)), and it is therefore possible that this region plays a domain general role in adolescent control processing, with function shifting to LIFG during later development. However, it is also notable given the current research question that this area has a similar location to that found for production-specific processes in adults. The explanation for this observation is unclear, but it may suggest that the production and comprehension systems become more specialised, and thus more divergent, with development. Indeed, there is evidence of this pattern in other language systems. For instance, Booth et al. (2001) found that whilst adults recruit separate specialised system for visually presented words (occipital- and lingual gyri, and inferior- and middle temporal gyri) and auditorily presented words (superior temporal gyrus), 9-12 year old children activated all of these regions, irrespective of stimulus modality. It is, therefore, possible that systems that serve task-specific processes in adults do not show this level of specialisation in adolescents, and comprehension and production systems might rely on more largely overlapping systems in adolescents compared to adults.

The finding of adolescent hyper-activation within the anterior temporal pole for control processing is a novel result. Unlike the medial prefrontal region, hyper-activation of the temporal pole has not been found in previous adolescent cognitive control studies, suggesting that this region may play a language-specific function in adolescent competition resolution processes. The temporal pole is thought to be involved in sentence level combinatorial semantic processes (Hickok & Poeppel, 2000, 2004, 2007; Vandenberghe, Nobre, & Price, 2002). Therefore, the results suggest that adolescents have particular difficulty in assigning the semantic roles of the sentence, when multiple alternative semantic interpretations are possible. The heightened involvement of anterior temporal structures in adolescent comprehension, accompanied by the reduced involvement of posterior temporal cortex, might also relate to maturational differences in the development of different white matter pathways. In particular, the arcuate fasciculus, the major tract that links LIFG to posterior temporal cortex, shows a steep rate of development during this period, with rapid increases in myelination and axon density continuing throughout adolescence and well into a persons 20s (Ashtari et al., 2007; Lebel & Beaulieu, 2011). These maturational advancements in white matter could explain age-related increases in functional connectivity between frontal and posterior temporal regions (Schmithorst, et al., 2006; Schmithorst, et al., 2007). In contrast, the uncinate fasciculus, which links LIFG to anterior temporal regions, develops earlier and shows a slower rate of change during the same developmental period (Ashtari, et al., 2007; Lebel & Beaulieu, 2011). Therefore, a post-hoc explanation for the current pattern of data is that maturational changes in the development of white matter pathways might lead to functional shifts in the control networks engaged by adult and adolescents, with a shifting reliance from anterior to posterior temporal areas with age. This issue warrants further investigation by directly linking functional and anatomical connectivity measures, using techniques such as diffusion tenser imaging (DTI).

4.4.2 Wider implications for production and comprehension control processes.

The current results also have implications for the wider research question concerning the relationship between production and comprehension control processes. In adolescents, LIFG shows an effect of competition in comprehension but not in production.. This finding mirrors what was found in the behavioural study where adolescents showed a comparable (or larger) influence of competition in the comprehension task to adults, but a smaller influence in the production task where they had difficulty in both conditions.

The observed LIFG production-comprehension asymmetry might be explained in terms of a difference in task difficulty; production is generally a more difficult task compared to comprehension. Indeed, this is consistent with a large body of research showing that production skills lag-behind comprehension skills throughout child development (Fenson, et al., 1994). The difference in difficulty may arise due to the fact that production generally places stronger demands on control processes. For instance, control mechanisms might only be engaged by comprehension in cases where there is competition between alternative interpretations (as in the high-competition cases here, where the animacy associations conflict with the sentence structure) but not in cases with low-competition as the correct interpretation is automatically activated. Indeed, there is evidence that comprehension processes occur automatically and do not engage LIFG control processes in situations with low task-demands (Binder, et al., 2000; Scott, et al., 2000; Scott & Johnsrude, 2003). Production, however, is more effortful and may therefore place demands on control mechanisms more generally, even in cases with a lower-degree of competition. This is because the processes required to accurately retrieve and sequence information are more demanding than those involved in recognition, as is evident from the high occurrence of production-errors (Dell, et al., 2000; Dell, Schwartz, et al., 1997; Garrett, 1975; Harley, 1984). Therefore, according to this account, the adolescent control-processing deficit causes general difficulty in production, regardless of competition as both conditions place demands on the control system. However, in comprehension only the high-competition cases are affected. Indeed, the notion that production places more general demands on LIFG control processes is consistent with the literature showing that LIFG damage often results in severe production deficits without the presence of comparable deficits in comprehension (Blank, Bird, Turkheimer, & Wise, 2003; Crinion, Warburton, Lambon-Ralph, Howard, & Wise, 2006; Mohr et al., 1978). It is also consistent with fMRI studies showing that LIFG is activated when producing sentences with even a simple subject-verb-object structure, such as *The square pushes the circle*, however, not when comprehending the same sentences, presumably as they can be parsed with little difficulty (Indefrey, Hellwig, Herzog, Seitz, & Hagoort, 2004). Also, note that this theory is also supported by data from Chapter 5 in which production and comprehension tasks are directly compared. Together these results suggest that whilst it may be true that production and comprehension engage LIFG control mechanisms, the contexts and extent to which the mechanisms are engaged vary across tasks.

4.4.3 Limitations.

This chapter examines the influence of neurodevelopmental changes on conflict resolution processes in sentence production and comprehension, by comparing adult and adolescent groups. These studies are the first of their kind, and therefore provide a useful contribution to our understanding of the development of linguistic control processes. It is important to highlight, however, that there were significant limitations in the task design that restrict the conclusions that can be drawn. In particular, as the production responses were covert, there was no method of demonstrating the content or accuracy of the responses. Covert production is a commonly used method as it avoids the methodological problems from motion-artifacts associated with conducting studies of overt production in fMRI, and it has been shown to yield comparable networks beside the obvious motor output differences (Dogil, et al., 2002; Kielar, et al., 2011). However, the fact that response accuracy could not be determined meant that brain responses were averaged across correct and incorrect responses, thereby adding noise to the data. This is particularly problematic for the adolescent data, where production accuracy is known to be lower than adults. Therefore, whilst the current results are novel, caution must be drawn in over-interpreting the adolescent production data, and future research is required with improved designs to investigate the issues raised here more thoroughly.

Another limitation relates more generally to the sentence-completion paradigm, and can also be applied to the results from the previous chapters. The sentence-completion task is a useful method to control and manipulate production choices. However, in the context of production/comprehension comparisons, an obvious limitation of the sentence-completion task is that it includes a comprehension component that potentially could contaminate the production data. Another drawback of the design is that it is not a particularly natural production task. In natural sentence production, the speaker begins with a conceptual representation, and will then map this representation onto the appropriate lexical items and syntactic structure. This process is to some extent reversed in the sentence-completion task, where the lexical items and syntactic structure are given, and instead one is required to map these items onto a conceptual representation that fits the imposed semantic and syntactic constraints. Therefore, whilst the results from this experiment provide useful insights regarding the commonalities and differences in the processes engaged by sentence production and comprehension for cue-based competition, the extent to which the results will generalise to other designs is unclear. The experiments described in the next chapter attempt to address these limitations with improvements in task design, and by investigating the extent to which the results from the adult data generalise to a different form of semantic competition.

4.5 Conclusions.

The chapter examined the influence of neurodevelopmental changes on conflict resolution processes in sentence production and comprehension, by comparing adult and adolescent groups. The results suggest that adolescents have behavioural deficits in the ability to resolve competition in both production and comprehension tasks. In terms of neural processes, the networks used to resolve competition in language show qualitative and quantitative shifts with development, which is indicative of the fine-tuning and increased efficiency of language control processes. Furthermore, these results were found to relate to variations in structural neurodevelopment. Together these results suggest that the underdevelopment of neural inhibitory processing systems in adolescents affects their ability to resolve competition in language. The results also provide some wider insights into production and comprehension control processes; whilst it may be true that production and comprehension engage common control mechanisms, the extent to which control mechanisms are engaged may vary across tasks, with production showing a more general recruitment of control processes, but comprehension recruiting control processes only in cases of high-competition.

Chapter 5

Similarity-based competition in sentence production and comprehension

5.1 Introduction

The results described in Chapter 2 and 3 suggest some potential similarities but also some differences in the processes engaged by sentence production and comprehension to resolve competition. They show that in adults LIFG, in conjunction with temporal areas, mediates the contingencies associated with linguistic cues by selecting the appropriate cue-associations and inhibiting irrelevant information. This process appears common to both production and comprehension tasks, particularly where the constraints to production were contextually given by the prompt, as was the case in the sentence-completion paradigm. Therefore, in the case of cue-based competition, similar fronto-temporal control processes are recruited across production and comprehension tasks. However, the extent to which production and comprehension engage common competition mechanisms is likely task dependent. Our previous sentence-completion production task emphasised the conflict between semantic and syntactic cues. However, competition in production is not normally cued by external linguistic cues, rather it derives from internally generated processes such as the activation of multiple competing lexical items or syntactic structures during lexical retrieval or syntactic planning. Therefore, the question remains the extent to which production and comprehension share processes to resolve competition, originating not from external linguistic cues but rather from internally generated processes that may nevertheless involve competition.

This chapter describes a behavioural and fMRI study investigating the extent to which production and comprehension engage common mechanisms to resolve a different type of competition from that examined previously, namely, similarity-based competition. Similarity-based competition, or similarity-based interference, refers to the process by which the accessibility of an item is reduced following the co-activation of a semantically related item. The negative impact on performance from semantically related competitors has long been established in the verbal working memory literature. For instance, the short-term memory for a list of items is reduced when the list is made up of semantically related items, also accurate recall of an item is reduced by semantically-related distractors (Baddeley, 1966; Baddeley & Dale, 1966; Bartha, Martin, & Jensen, 1998; Crowder, 1979; Murdock, 1976).

5.1.1 Similarity-based competition in comprehension

Similarity-based competition is known to influence language processing. Inspired by working memory research, theories of sentence comprehension have argued that sentence processing difficulty is increased when maintaining in mind semantically or syntactically overlapping information, particularly in cases of high memory load (Gordon, Hendrick, & Johnson, 2001; Gordon, Hendrick, & Johnson, 2004; Gordon, Hendrick, & Levine, 2002; Lewis, 1996; Van Dyke & Lewis, 2003; Van Dyke & McElree, 2006, 2011). Similarity-based competition effects on sentence comprehension have been investigated mainly for object- and subject-relative clauses (such as those in 1a-b). Object relative clauses are associated with greater processing difficulty compared to subject relative clauses (Gordon, et al., 2001; King & Just, 1991; MacWhinney & Pleh, 1988; Traxler, et al., 2002), and this is thought to be due to two main factors that are not mutually exclusive: (a) the non-canonical word order and thematic role configuration in object relative clauses, whereby the head-noun is the object rather than the subject of the sentence, which creates difficulty in thematic role assignment (MacDonald & Christiansen, 2002; Wells, et al., 2009), and (b) because of demands on memory maintenance and interference in these structures, as neither noun can be integrated until after the RC verb (Caplan & Waters, 1999; Gibson, 1998; King & Just, 1991; Wanner & Maratsos, 1978; Waters & Caplan, 1996a, 1996b).

Several studies have shown that processing difficulty in object relative clauses is increased when the structure contains two semantically related nouns. For instance, Gordon et al., (2001, 2004) presented sentences where the two nouns in object and subject relative clauses were referred to using either proper names (e.g. John or Bill), or occupations (e.g. barber or lawyer), as in the example below. The critical manipulation was whether the two nouns were from matching or mismatching noun class.

1a) It was the barber/John that saw the lawyer/Bill in the parking lot. (subject RC)

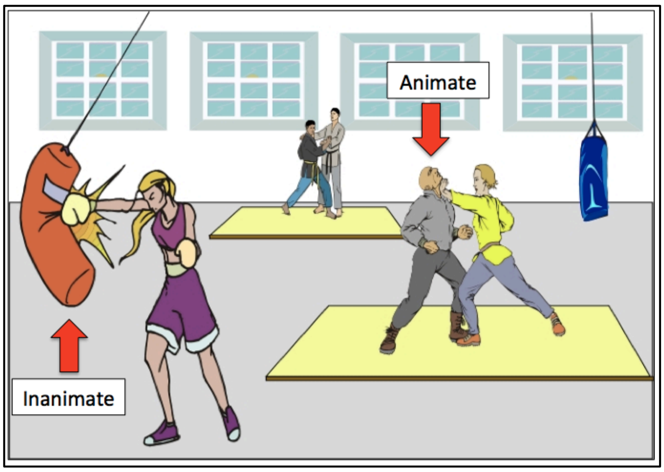
1b) It was the barber/John that the lawyer/Bill saw in the parking lot. (object RC)

The results showed that the object relative clauses that contained nouns from a matching category created greater processing difficulty compared to those where the nouns mismatched (the mismatching object relative clauses were actually equal in difficulty to the subject relative clauses) and this was explained in terms of the occurrence of similarity-based competition between nouns from a similar category. The fact that the difficulty was specifically associated with object relative clauses led researchers to suggest that the difficulty arises from a working memory interference effect associated with maintaining unintegrated nouns that are semantically related in working memory (Fedorenko, Gibson, & Rohde, 2006; Gordon, et al., 2001; Gordon, et al., 2004; Gordon, et al., 2002; Lewis, 1996; Van Dyke & Lewis, 2003; Van Dyke & McElree, 2006, 2011). Although, the results are also consistent with a thematic role competition explanation. That is, the non-canonical thematic role configuration in object relative clauses creates difficulty in determining who-is-doing-what-to-whom, especially when nouns are semantically related as they will share agent-patient associations that compete for selection. Therefore, similarity-based competition has been shown to be a major influence on comprehension difficulty, and this occurs due to competition between alternative thematic roles and/or from interference in working memory.

5.1.2 Similarity-based competition in production

Similarity-based competition is also thought to impact on language production. At the word-level, evidence for similarity-based competition comes from the picture-word interference paradigm where picture naming is slowed by the simultaneous presentation of semantically related distractors (Costa, et al., 2005; Glaser & Düngelhoff, 1984; Glaser & Glaser, 1989; Schriefers, et al., 1990). Similar effects of lexical competition have been shown at the sentence level. For example, Smith and Wheeldon (2004) showed that production initiation times are longer when producing a sentence containing highly related nouns, such as in *The saw and axe move down*, compared to unrelated nouns, such as *The saw* *and cat move down*. Furthermore, this effect is strongest when the nouns are mentioned in the same phrase thus suggesting that similarity-based competition has larger effects on information with a high degree of temporal overlap. Therefore, conceptually related entities compete for lexical selection during production, particularly if the entities occur in close temporal proximity in the sentence.

Similarity-based competition effects might also be particularly strong in relative clause production because the nouns in relative clauses occur in close proximity and are planned together (Meyer, 1996). Several studies have demonstrated similarity-based competition effects in relative clause production (Arnold & Griffin, 2007; Fukumura, van Gompel, Harley, & Pickering, 2011; Gennari, et al., 2012; Slevc, in press). For instance, Gennari et al. (2012) conducted a study using a picture-based relative clause elicitation paradigm, where the participants provided description of actions being performed upon either an animate or inanimate entity by an animate agent (as in 2). The conceptual relatedness between the participants of the action is higher in the animate-animate condition relative to the inanimate-animate condition. In the experiment participants produces relative clauses like in 2a-d using active or passive constructions (note that the use of a relative clause was encouraged by the presence of distractor items).



2a) The man that the woman is punching. (Animate-animate: Active)

2b) The man being punched by the woman. (Animate-animate: Passive)

2c) The bag that the woman is punching. (Inanimate-animate: Active)

2d) The bag being punched by the woman. (Inanimate-animate: Passive)

The conceptual relatedness between the participants of the action was found to influence production responses in a manner that suggests the occurrence of similarity-based competition. Specifically, participants produced a greater proportion of passive relative clause constructions for the animate-animate pairs compared to inanimate-animate cases, where there were an equal number of active and passive constructions. The increased use of passive constructions for the animate-animate condition is thought to occur due to similarity-based competition, as competition between conceptually related nouns leads to the inhibition of the second noun, and this results in the demotion of the second noun to final structure position or its omission altogether, thereby creating a passive construction (e.g. *The man being punched (by the woman)*). However, to more directly investigate whether this effect was due to variations in agent-patient semantic similarity, rather than other factors associated with varying animacy configurations (e.g. frequency), the researchers also manipulated the degree of agent-patient similarity within the animate pairs. The results showed that the degree of agent-patient similarity predicted the participants' choice of relative clause construction. Therefore, the presence of conceptually related items leads to similarity-based competition in sentence production.

What causes similarity-based competition in production? At the word-level, production models argue that similarity-based competition occurs because semantically related representations, such as *man* and *woman,* share overlapping conceptual features and therefore compete for lexical retrieval and selection (Dell, 1986; Levelt, et al., 1999). In sentence production, in addition to lexical-competition, competition could also occur at the functional level of processing during grammatical role encoding. This is because semantically related concepts share agent/patient associations, and as such compete for the allocation of grammatical functions and sentence positions (subject or object) (Acheson & MacDonald, 2009; Garrett, 1975; Gennari, et al., 2012). The influence of similarity-based competition on positional encoding during production is represented schematically in Figure 5.1, where *boy* and *girl* share agent features and therefore compete for the subject position in the sentence. Therefore, similarity-based competition in sentence production arises due to difficulty at the lexical level during word retrieval and selection, and/or at the functional level during grammatical assignment and positional encoding.

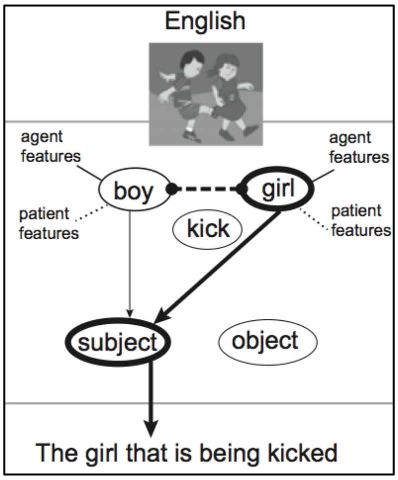


Figure 5.1 Schematic representation of how similarity-based competition influences positional encoding in production due to overlapping agent-patient features (image taken from Gennari et al., 2012).

5.1.3 The present study

Therefore, there is evidence that similarity-based competition influences both sentence production and comprehension. However, the source of the competition-effect in each case may be the result of distinct underlying processes. Semantic competition in relative clause comprehension arises due to working memory interference effects, and/or competition between alternative thematic role interpretations. However, similarity-based competition in production has been attributed to different processes that are production-specific, such as lexical retrieval and positional encoding. This chapter describes a series of experiments that seek to determine the extent to which parallel or distinct processes occur across production and comprehension paradigms to resolve similarity-based competition. First, a behavioural experiment was conducted using an adapted version of the production paradigm used by Gennari et al. (2012) which replicated the effects of Gennari et al. (experiment 5a) and tested whether a parallel behavioural effect would be demonstrated in comprehension using the same picture-based design (experiment 5b). Following this, an fMRI study (experiment 6) investigated the extent to which production and comprehension engage common/distinct neural processes for similarity-based competition.

The results from these studies advance those from the earlier chapters for several reasons. Firstly, compared to the sentence-completion design in the previous chapters the picture-based paradigm adopted here might better reveal the distinctions between production and comprehension processes. In the new paradigm the production task is more naturalistic as the competition derives from internally generated processes, rather than from conflicting external cues. Secondly, the picture-based task does not suffer from the same methodological limitations as the sentence-completion task as it does not include a "reading component". This makes it possible to conduct more accurate production/comprehension comparisons. Therefore, using this design it should be possible to determine with greater specificity the similarities and differences in the processes engaged by sentence production and comprehension.

5.2 Experiment 5a and 5b

5.2.1 Introduction

The aims of experiment 5 were to establish a paradigm to examine the extent to which parallel influences of similarity-based competition could be established in production and comprehension tasks. Gennari et al. (2012) used a picture-based task to demonstrate the occurrence of similarity-based competition in relative clause production. The aim of Experiment 5a was to investigate whether a comparable influence of similarity could be found in a comprehension task using a comparable paradigm. Finding a paradigm that elicited parallel effects across tasks was critical in order to directly compare production and comprehension in the fMRI experiment. Experiment 5b sought to replicate the key production findings from Gennari et al. using the new stimulus set, and also to pre-test the experimental design for the fMRI experiment (Experiment 5b).

To this end, here we manipulated the degree of similarity between agent-patient pairs in relative clauses, using an adapted version of the paradigm used by Gennari et al. (2012). The items varied in terms of animacy configuration and similarity; in the animate-animate condition (hereafter known as the animate condition) there is a greater degree of semantic similarity compared to the inanimate-animate condition (hereafter known as the inanimate condition). Furthermore, within the animate condition the degree of agent-patient similarity was systematically varied. This was done so that correlations could be performed with the degree of agent-patient similarity, without also varying animacy.

The tasks were based on the picture-based paradigm that was used by Gennari et al. (2012). The participants were presented with a picture, and either read active or passive relative clauses that did/did not accurately describe a highlighted entity within the picture (Experiment 5a), or provided descriptions of the highlighted entity themselves (Experiment 5b). In the comprehension task we measured the time-taken to respond to the sentence, and in the production task we measured the structural preferences associated with each item. It was predicted that similarity-based competition would lead to increases in reading times in the comprehension task, and an increase in the proportions of passive structures produced in production task for the animate relative to the inanimate conditions. Furthermore, if these results relate to variations in similarity, rather than another variable associated with varying animacy, then correlations should be found between the degree of agent-patient similarity in the animate items and the language measures.

5.2.2 Methods

5.2.2.1 Design and materials.

Pictures. Forty-two grey-scale scenes were constructed using images from clipart.com. Twenty-one of the scenes were taken from Gennari et al. (2012) and an additional 21 items were constructed in order to increase the statistical power for the fMRI study. Each scene contained two animate entities performing the same action (e.g. punching in the example). In one case the action was performed on an animate entity (e.g. a man) and in the other case the action was performed on an inanimate entity (e.g. a punch bag) (see Figure 5.2). The scenes also included distractor versions of the action objects in order to encourage the production of relative clause modifiers. In each picture, the animate or inanimate entity to be described was highlighted by a red box. Within the animate items, the degree of agent-patient similarity was varied so that it would be possible to correlate the degree of similarity with the language measures. For example, some animate cases were highly semantically and functionally similar (e.g. a boy and a girl), and in other cases they were less related (e.g. a man and a lobster) (see Figure 5.3).

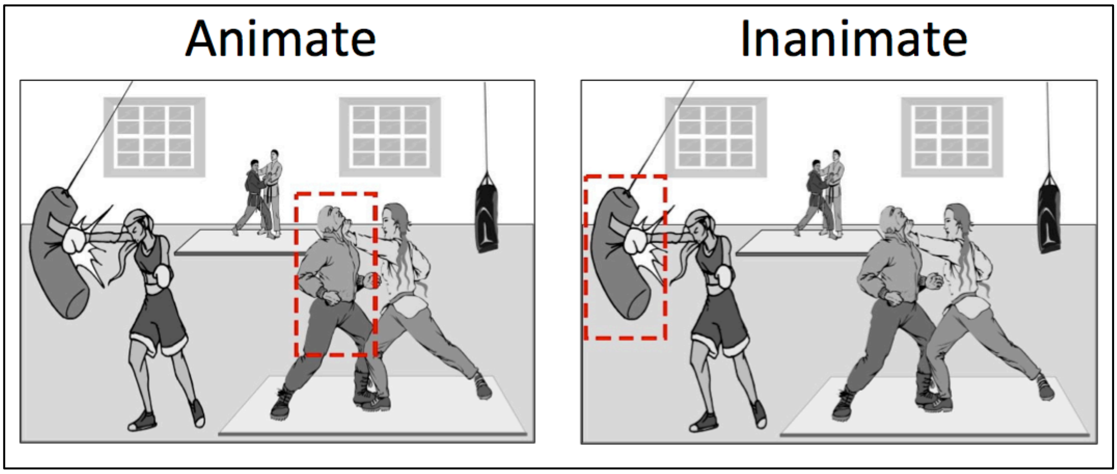
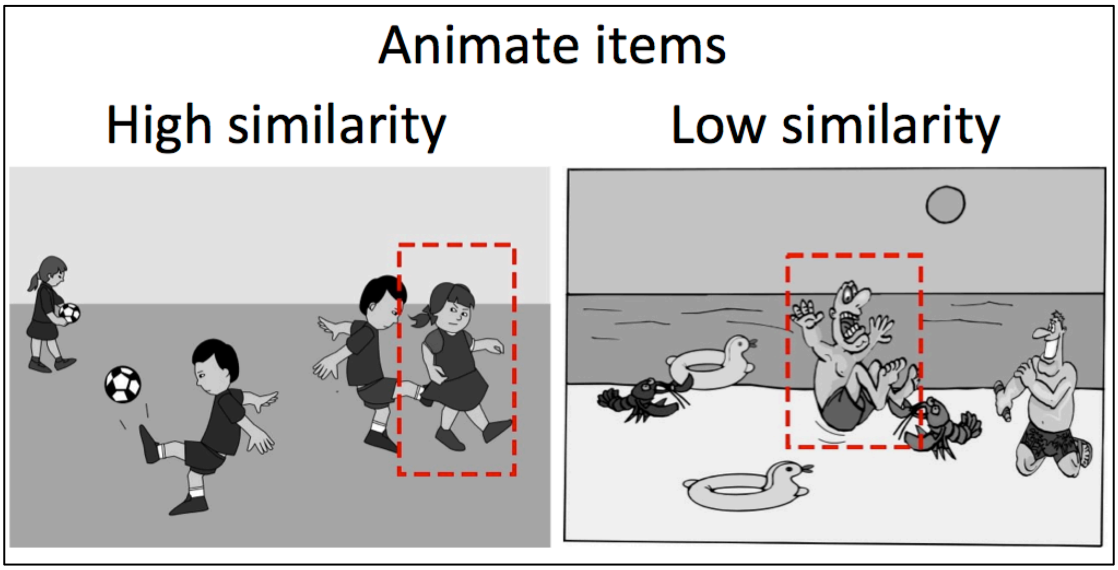


Figure 5.2 An example of the animacy manipulation. Participants provided descriptions (production trials), or read descriptions (comprehension trials) of the highlighted entity.


Animate items

High similarity

Low similarity

Figure 5.3 Agent-patient similarity was systematically varied across items within the animate condition. Figure depicts an example of a high-similarity and low similarity item.

*Similarity rating study***.** An online similarity rating study was conducted in order to gain accurate measures of the similarity of the two items. Here, the participants were presented with the pictures in which the to-be-rated entities were highlighted by a red box, and ratings were given on a 7 point scale with 1 being “not at all similar” and 7 being “highly similar”. When giving their ratings the participants were encouraged to focus on not only any physical similarity between entities but also their semantic similarity (e.g. similarity in function) (see instructions in Appendix E). Ratings were collected from 25 participants. There were two lists of items (11 participants completed list 1 and 14 completed list 2) with the animate and inanimate versions of each picture presented on separate lists. An item analysis showed that as expected the difference in similarity between the animate-animate pairs and the inanimate-animate pairs was highly statistically significant (M animate = 4.70, SD = 1.13; M inanimate = 1.79, SD = .42; $t(41,1) = 15.77$, $p < .001$). Also, as intended, within the animate condition there was found to be a good degree of variability in similarity ratings across items. This was important for the correlations with language measures (see Figure 5.4).

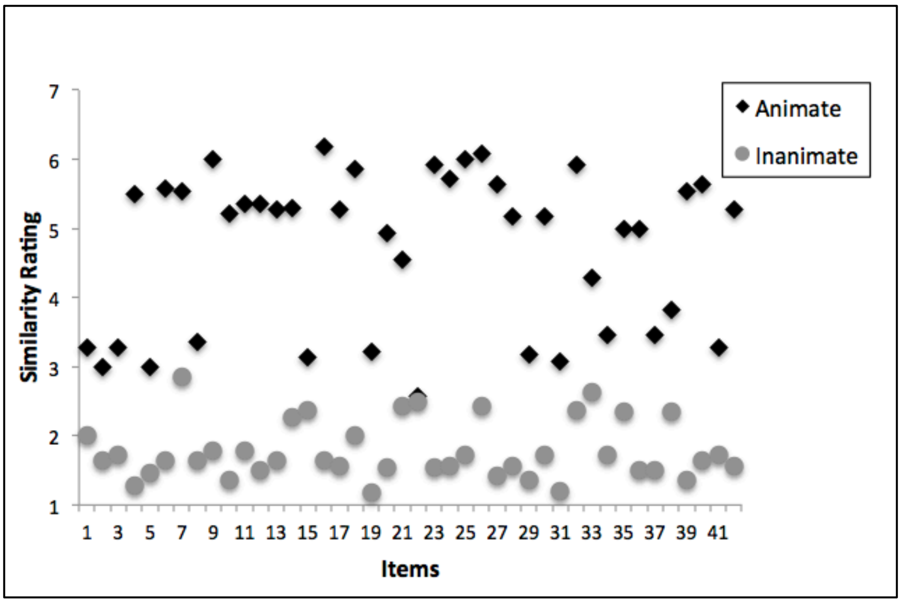


Figure 5.4 The similarity rating score for each item in the animate and inanimate conditions.

Comprehension sentences. For the comprehension trials, each of the pictures was paired with a relative clause that described either the animate or inanimate entity being acted upon. Passive and active descriptions were constructed for each of the 84 items. Thus, there was a 2x2 design with animacy (animate or inanimate) and syntactic structure (active or passive) as factors, as in 3a-d.

3a) The man that the woman is punching. (animate-active)

3b) The man being punched by the woman. (animate-passive)

3c) The bag that the woman is punching. (inanimate-active)

3d) The bag being punched by the woman. (inanimate-passive)

The sentences were developed by taking the most frequent noun and verb responses given by participants in a pilot production study (N = 13), thus providing the most natural words to describe the pictures. In this study the participants provided relative clauses to describe each of the animate and inanimate recipients of the action (using the same task and instructions as described in Experiment 5a below). The participants provided descriptions for all 84 experimental pictures. Across participants, the verbs used to describe the actions had a high name agreement, which was matched across conditions (Mean animate = 78.83%, SD = 22.24; Mean inanimate = 82.36%, SD = 35.40; *t*(82) = -.55, ns). There was also high name agreement both for noun1 and for noun2 in the relative clause, and these were also matched across conditions (N1: mean animate = 85.35%, SD = 22.72; mean inanimate = 80.95%, SD = 21.30; *t*(82) = .91, ns; N2: mean animate = 76.61%, SD = 22.28; mean inanimate = 83.74%, SD = 23.43; *t*(82) = -1.43, ns). This is important as it ensures a high likelihood that participants would use the same verbs and nouns to describe the pictures in the production task as was used in the comprehension tasks. However, the desire to create the comprehension sentences based on the most frequent production responses meant that it was impossible to match the conditions in other respects. In particular, the animate and inanimate conditions differed in sentence length (number of characters) for the active items, with the inanimate condition being longer than the animate condition (Active items: mean length animate (SD) = 34.0 (1.65), mean length inanimate (SD) = 35.5 (2.47), *t*(82) = 3.23, *p* < .01; Passive items: mean length animate (SD) = 33.7 (2.00), mean length inanimate (SD) = 35.0 (2.89), *t*(82) = -.72, *p* = .47). They also differed in terms of noun1 word frequency with noun1 having a lower word frequency in the inanimate compared to the animate conditions (Mean log-transformed word frequency (SD): animate = 4.87 (0.42), inanimate = 4.12 (0.65); *t*(82) = -6.24, *p* < .001) (Cobuild Corpus: 20 million words)). Note, however, that the word frequency and length differences act in the opposite direction to the similarity manipulation and therefore cannot account for any of the results.

5.2.3 Experiment 5a: Comprehension study

The comprehension study was conducted in order to examine whether a comparable similarity-based competition effect would be found in comprehension to those found when using a similar paradigm in production (Gennari et al., 2012). Whilst evidence suggests that similarity-based competition occurs during relative clause comprehension, the materials in previous experiments were rather indirect manipulations of semantic similarity, e.g., Gordon's noun class manipulation. Here, we directly tested the influence of similarity-based competition on the comprehension of relative clauses. Finding a paradigm that elicited parallel effects across tasks was critical in order to directly compare production and comprehension in the fMRI experiment.

Here, the participants were presented with the relative clauses in the context of the pictures. It was predicted that similarity-based competition should lead to increased difficulty in comprehending the animate condition relative to the inanimate condition as indexed by increased response times. Also, the effect should be larger in the object relative with active structure compared to passive structure, as the actives involve maintaining multiple unintegrated nouns in working memory before the verb is encountered. More importantly, if the results were explained in terms of similarity-based competition then the degree of agent-patient similarity should predict reading difficulty within the animate items, as determined by correlation analyses.

5.2.3.1 Experiment 5a Procedures.

The items were spread across four lists using a Latin Square design. Each participant therefore experienced 11 items from each of the 4 conditions. 42 catch trials were also included, and in these cases the sentences provided an inaccurate description of the highlighted entity. The task was to indicate whether or not the sentence provided an accurate description of the highlighted part of the pictures. The pictures for the catch trials were similar to the experimental trials, in that they included images in which at least two entities were interacting. The sentences were all relative clauses and constructed in such a way that either the thematic roles were reversed (e.g. *The shark that the fish is eating* when the correct description would be *The fish that the shark is eating*), or the verb or nouns were incorrect (e.g. *The man that is lifting the woman* when the correct description would be *The man that is lifting the weights*; or *The bride that is being tickled by the princess* when the correct response would be *The bride that is being kissed by the princess*).

Forty participants completed the experiment (10 per list) (mean age = 20.4, male = 15). During each trial, the pictures were presented in the centre of the computer screen for 3 seconds. Then one of the events was highlighted by a red square for 1 second. Finally, a whole sentence was presented for 3 seconds (or until button press). The task was to indicate “YES” or “NO” as to whether or not the sentence accurately described the highlighted event in the picture. Only the data from the "YES" experimental trials was analysed. It is important to note that the results cannot be explained in terms of difficulty in understanding the pictures, as the same pictures were used across the active and passive conditions.

The accuracy and reaction time data was analysed in both item and subject analyses to test for effects of animacy and structure. The results were analysed using the raw reaction time data, or by calculating the residual reading times after regressing out phrase length. The results are directly comparable in every respect so only the raw reaction time data is reported. To test if the time taken to process the sentences related to agent-patient similarity, correlation analyses were performed between the RT data and the similarity ratings from the animate items.

5.2.3.2 Experiment 5a Results

Accuracy. The results were analysed in terms of accuracy and reaction time data across items and across subjects. The average accuracy was found to be high across conditions (item analysis: M = 93.63%, SD = 10.35; subject analysis: M = 93.58%, SD = 8.79) (see Table 5.1). A 2x2 repeated measures ANOVA with condition (animate and inanimate) and syntactic structure (active and passive) showed a main effect of animacy, with the responses to the animate items being less accurate than the responses to the inanimate items (*F1*(1,39) = 8.38, *p* < .01; *F2*(1,41) = 5.58, *p* < .05). There was no significant main effect of structure or an interaction (all *F*s < .3, ns).

Table 5.1 Average percentage correct responses from the comprehension task.

	Animate-Active	Inanimate-Active	Animate-Passive	Inanimate-Passive
Accuracy (SD)	92.62% (7.98)	95.24% (7.73)	91.43% (1.57)	95.24% (7.40)

Comprehension decision time. For the reaction time data, only accurate responses were included, and responses were excluded that deviated from the mean by more than 3 SDs or were faster 900ms, which was considered a conservative cut-off for the time taken to read the entire sentence. This resulted in the removal of fewer than 3% of responses. The average RTS across items fro each condition are shown in Figure 5.5. The results are reported from both subject and item analyses. A repeated-measures ANOVA with condition and structure as factors showed a significant main effect of condition (item analysis: $F(1,41) = 9.57$, $p < .01$; subject analysis: ($F(1,39) = 18.74$, $p < .001$) and structure (item analysis: $F(1,41) = 19.53$, $p < .001$; subject analysis: ($F(1,39) = 29.66$, $p < .001$), and a significant condition x structure interaction (item analysis: $F(1,41) = 8.76$, $p < .01$; subject analysis: ($F(1,39) = 20.40$, $p < .001$). Post-hoc t-tests showed that as predicted responses were slower to the animate-active condition relative to the inanimate-active condition (item analysis: M animate = 1748ms, SD = 254.42; M inanimate = 1555ms, SD = 154.94; $t(41) = 4.03$, $p < .001$; subject analysis: M animate = 1737ms, SD = 276.14; M inanimate = 1541ms, SD = 268.49; $t(39) = 6.54$, $p < .001$). However, there was no significant difference between the passive conditions (item analysis: M animate = 1524ms, SD = 201.77; M inanimate = 1501ms, SD = 196.78; $t(41) = .53$, ns.; subject analysis: M animate = 1514ms, SD = 246.41; M inanimate = 1484ms, SD = 243.55; $t(39) = .89$, ns.).

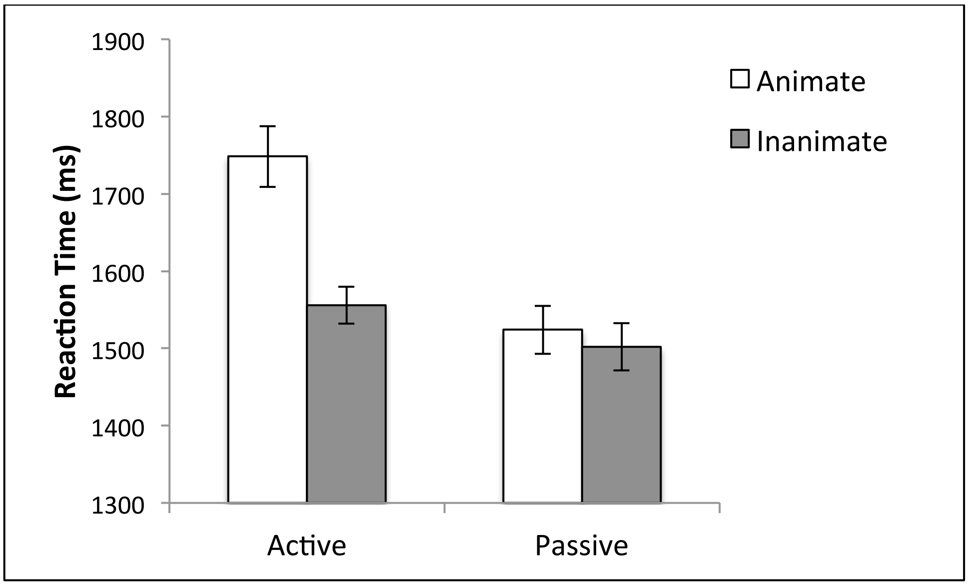


**Figure 5.5	Average reaction time data from the comprehension task.**

Correlation analysis. If processing difficulty is related to similarity-based competition, then a correlation should be found between the degree of agent-patient similarity in the animate items and the reaction time data. Indeed, in support of the prediction, a significant positive correlation was found between the degree of agent-patient similarity and the reaction time data for the animate-active condition ($r(42) = .345$, $p = .02$), and no correlation was found in the animate-passive condition ($r(42) = .121$, ns.).

5.2.3.3 Experiment 5a Discussion

This experiment aimed to investigate whether similarity based interference occurred in relative clause comprehension using a task comparable to that used in production studies (Gennari et al, 2012). The results confirmed the presence of a similarity-based competition effect. It was shown that comprehending object relative clauses with an animate-animate configuration is more difficult than those with a mismatch in animacy. Furthermore, the correlation analysis showed that the degree of agent-patient similarity predicted processing speed within the animate items. This is important as it demonstrates that the results are related to similarity-based competition rather than to other factors associated with the animacy configurations e.g. frequency differences as object relative clauses with an animate-animate configuration are less frequent structures compared to inanimate-animate constructions (Fox & Thompson, 1990; Gennari & MacDonald, 2008, 2009; Mak, et al., 2002; Roland, Dick, & Elman, 2007).

The similarity-based competition effect was found to be present only in the object relative structures with an active rather than a passive structure. This suggests that similarity has a particular impact on sentences with a non-canonical thematic role arrangement, as is the case in object relative clauses, and causes a difficulty in maintaining multiple unintegrated nouns in working memory before encountering the relative clause verb. This data thus adds to the existing literature and provides more conclusive evidence that noun similarity is a major influence on relative clause comprehension (Fedorenko, et al., 2006; Gordon, et al., 2001; Gordon, et al., 2004; Gordon, et al., 2002; Lewis, 1996; Van Dyke & Lewis, 2003; Van Dyke & McElree, 2006, 2011). The next experiment was conducted in order to demonstrate that parallel effects of similarity-based competition occur in the production task using a similar paradigm

5.2.4 Experiment 5b: Production study and fMRI pre-test.

This study sought to replicate the production results of Gennari et al. (2012) using the new stimuli set and a modified task. It was predicted that a greater proportion of passive structures would be produced for the animate condition relative to the inanimate condition. Furthermore, if these production preferences are related to semantic similarity rather than just varying animacy, then the level of agent-patient similarity within the animate items would predict the participants' production choices (proportions of passives).

A secondary aim of this study was to pre-test the design of the fMRI experiment. In the fMRI experiment alternating blocks of production and comprehension trials were presented. This was desirable as earlier piloting of the production task without comprehension trials revealed substantial influences of structural priming between production trials, meaning that participants tended to produce passive constructions for every trial. This is problematic as structural priming reduces the normal processing difficulty associated with processing relative clauses (Bock, et al., 2007). Intermixing comprehension trials with the production trials introduced some variability between active and passive structures which may reduce the structural priming effects. Therefore, a secondary aim of this study was to behaviourally pre-test the fMRI presentation order in order to confirm that the task could be performed accurately and to confirm the absence of structural priming effects in production.

5.2.4.1 Experiment 5b Procedures.

The 84 production items were presented in a web-based questionnaire. Thirty-two participants completed the questionnaire. The participants were recruited from an undergraduate population at the University of York and received course credit. The animate and inanimate versions of each item were spread across two different lists, but each participant experienced an equal number of trials from each condition (Latin Square design). In the questionnaire, each picture was presented in the centre of the screen, with an empty text box below the picture. The participants were instructed to look at the picture and answer the question *Who or what is the highlighted person/object?* and type their response in the text box provided. Before beginning the study participants were presented with instructions that gave several examples and encouraged the use of relative clause structures (the instructions were identical to those used by Gennari et al., 2012; see Appendix F for details).

Blocks of comprehension trials were intermixed with the production trials. In these trials the relative clauses were presented below the corresponding picture (active and passive versions). Comprehension trials were included in order to mimic the event order used in the fMRI experiment (see Experiment 6 for details), where alternating blocks of production and comprehension trials were presented. The task for comprehension trials was to indicate the trials in which the sentence did not accurately describe the highlighted part of the picture, which was the same task as in the fMRI study. Thirty catch-trials were intermixed with the comprehension trials in which the sentence and picture did not match.

5.2.4.2 Experiment 5b Results

The production data was coded for syntactic structure (active or passive), and accuracy. Production responses were considered as errors and removed from the analysis if they did not include a relative clause or provided an inaccurate description of the highlighted entity. Production accuracy overall was very high (M = 96.7%; SD = 5.46). Accuracy to the comprehension catch trials was also high (M accuracy = 95.8%; SD = 8.32).

The proportion of passive structures produced was compared for the animate and inanimate conditions (see Figure 5.6). This showed that as predicted, there were a significantly greater proportion of passive structures produced for the animate items compared to the inanimate items, thereby replicating Gennari et al. (2012) (M animate = 60.01%, SD = 22.17; M inanimate = 46.36%, SD = 16.05; $t(40) = 3.42$, $p < .001$). Gennari et al. claimed that the increased preference for passive structures in the animate cases could be explained by increased noun similarity. To test this, we correlated the proportions of passive structures produced for each item with the similarity rating within the animate items. The results supported the prediction; the higher the similarity rating the greater the proportion of passive structures produced for the animate cases ($r = .471$, $p < .01$). Importantly, the results mirror the effect of similarity-based competition from the comprehension study (Experiment 5) (see Figure 5.7).

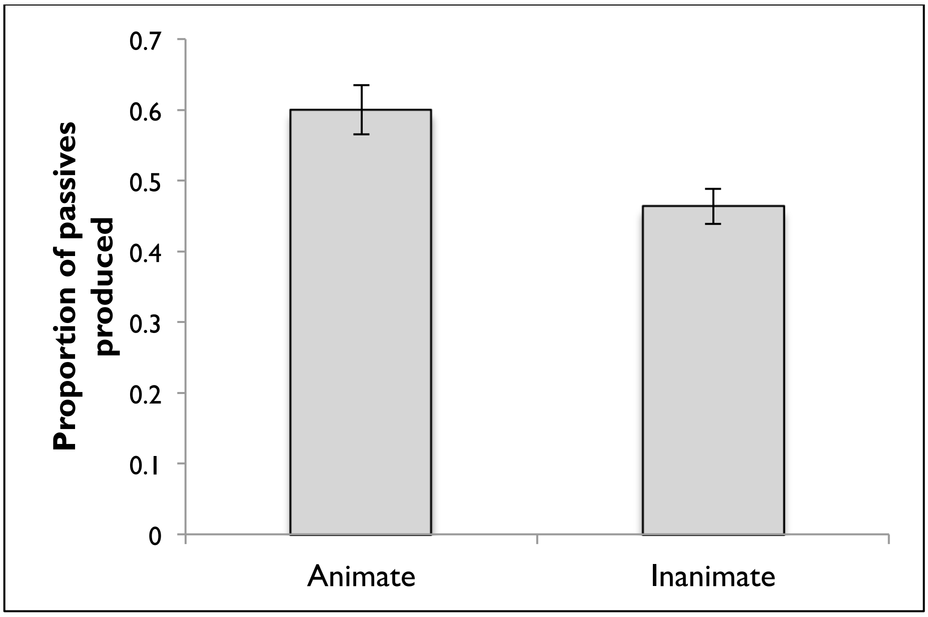


Figure 5.6 The proportion of passive structures produced in the production task

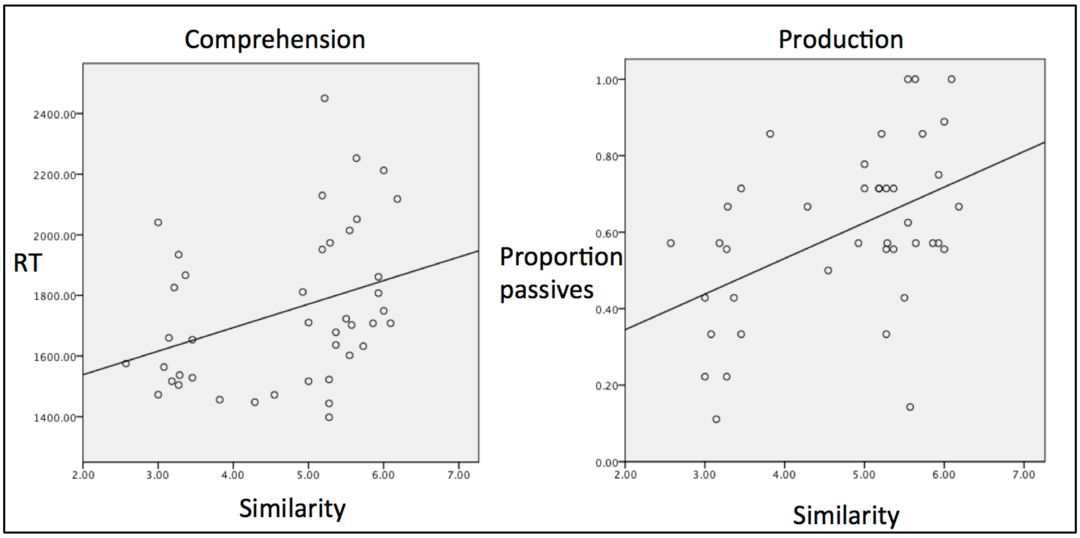


Figure 5.7 Correlation between agent-patient similarity in the animate items and RT data from the comprehension behavioural study (left) and proportions of passive structures produced from the production behavioural study (right).

5.2.3 Experiment 5 Discussion

This study aimed to replicate the production results from Gennari et al. (2012) using a modified task and a new stimulus set. This was successfully achieved; an increased proportion of passive constructions were produced for the animate items relative to the inanimate items. The use of passive constructions is thought to reflect an influence of similarity-based competition in the animate items; competition between conceptually related nouns leads to the inhibition of the second noun resulting in its demotion to final structure position (e.g. *The man being punched by the woman*). This conclusion is supported by the findings from the correlation analysis showing that the degree of semantic similarity within the animate items predicted the choice of syntactic structure. A secondary aim of this study was to behaviourally pre-test the design for the fMRI experiment and verify the absence of structural priming effects. This was also successful; response accuracy was found to be high for the production trials and also for the comprehension catch-trials, and structural priming effects were found to be minimal based on the fact that there was a good degree of variability in the use of syntactic structure.

Overall the results from experiment 5a and 5b establish a paradigm that is sensitive to similarity-based competition across production and comprehension tasks. It is important to note, however, that the presence of a parallel behavioural similarity effect across tasks does not necessarily suggest shared processing mechanisms. In particular, as different measures were used as evidence of similarity-based competition (structural choices in production vs. RTs) the data might reflect different underlying processes (or at different processing levels), even if both engage competition. The next section of this chapter describes an fMRI experiment designed to investigate the extent to which shared/distinct neural processes are engaged by similarity-based competition across production and comprehension tasks.

5.3 Experiment 6

5.3.1 Introduction

The behavioural evidence from Experiment 5 has established that similarity-based competition affects both the production and comprehension of relative clauses. It is unclear, however, the extent that this parallel behavioural effect is caused by processes that are common to production and comprehension tasks, or by distinct processes that happen to have a parallel behavioural manifestation. Here, an fMRI experiment was conducted with the aim at determining the extent to which production and comprehension engage common or distinct neural processes for similarity-based competition. This data will validate the findings from previous chapters using an improved methodological design, and extend them to a different form of competition that is more internally generated and not dependent on perceptual cues in production. Indeed, the present experiment substantially alters the nature of the production task thereby having the potential to reveal further distinct mechanisms present in production but not comprehension. A secondary aim was to further examine the general networks engaged by sentence production and comprehension by directly contrasting activity from the two tasks. Direct comparisons were not possible in the earlier fMRI study due to the different baselines used for each task.

In comprehension similarity-based competition is thought to arise due to interference from maintaining unintegrated semantically-related nouns in working memory and/or due to competition between alternative thematic role interpretations, (Fedorenko, et al., 2006; Gordon, et al., 2001; Gordon, et al., 2004; Gordon, et al., 2002; Lewis, 1996; Van Dyke & Lewis, 2003; Van Dyke & McElree, 2006, 2011). In terms of neural mechanisms, no neuroimaging study has directly investigated the influence of similarity-based competition in sentence processing. However, there is reason to assume that LIFG will be involved in both the working memory and thematic role selection components. In terms of thematic role competition, our results (Chapter 3) and others in the literature (Caplan, Chen, et al., 2008; Caplan, Stanczak, et al., 2008; E. Chen, et al., 2006) have shown that LIFG is sensitive to competition between alternative thematic role interpretations, and may be involved in selecting between alternative representations more generally (Badre & Wagner, 2005; Fletcher, Shallice, & Dolan, 2000; Moss et al., 2005; Schnur, et al., 2009; Thompson-Schill, D'Esposito, & Kan, 1999).

There is also extensive evidence that LIFG (pars opercularis and pars triangularis) is involved in verbal working memory (Fedorenko, Behr, & Kanwisher, 2011; Fiebach, et al., 2005; Rogalsky, et al., 2008; E. E. Smith & Jonides, 1997), and is sensitive to working memory-based interference (Badre &

Wagner, 2005; Bunge, et al., 2001; Jonides, et al., 1998; Thompson-Schill, et al., 2002). For instance, LIFG activity is increased during proactive interference, where the presence of related information in a previous trial interferes with a response in the current trial (Badre, et al., 2005; Jonides, et al., 1998), and damage or stimulation of this area disrupts performance on proactive interference tasks (Feredoes, et al., 2006; Thompson-Schill, et al., 2002). Furthermore, it has been shown that damage to LIFG leads to increased interference from semantically related probes, suggesting that LIFG is involved in resolving interference from semantic competitors (Hamilton & Martin, 2007). Therefore, given LIFGs involvement in both thematic role competition and working memory interference, it is likely that LIFG will be sensitive to similarity-based competition in the comprehension task.

In production, researchers have attributed similarity-based competition to distinct processes to those described above for comprehension (Gennari et al., 2012). However, it is likely that certain processes will be common to both tasks. For instance, as in comprehension, working memory is an important component of sentence production, as during production information must be maintained until the previously planned phrase has been outputted, and as a consequence this information may therefore be susceptible to interference (Acheson & MacDonald, 2009). Thus, it is likely that the processes involved in resolving interference from maintaining information in working memory are common to production and comprehension tasks. Furthermore, as discussed in earlier chapters, production and comprehension share a linguistic knowledge base (Bock, et al., 2007; Chang, et al., 2006), which includes the association between concepts and their agent-patient features. Therefore, it is likely that production and comprehension share some sensitivity to competition from semantically related items, as those items will ignite shared associations in semantic memory. Indeed, the mechanisms used to manage these linguistic contingencies may well be common to production and comprehension tasks, as shown by the finding of common LIFG involvement in Chapter 3. Therefore, it was predicted that production and comprehension would show common LIFG processes for managing linguistic contingencies and resolving working memory-based interference.

However, despite the common recruitment of certain general regulatory mechanisms, production and comprehension are likely to engage different processing mechanisms and thus distinct processes beyond LIFG. Firstly, unlike in comprehension, it is unlikely that production involves thematic role competition as a speaker already has a conceptual representation of who-is-doing-what-to-whom in the event and is therefore is unlikely to entertain alternative thematic role relationships (Thornton & MacDonald, 2003). Rather, as suggested by production models (Acheson & MacDonald, 2009; Dell, 1986; Garrett, 1975; Gennari, et al., 2012; Levelt, et al., 1999), competition in production derives from production-specific processes, such as those involved in lemma retrieval and selection, and in assigning grammatical features and word-order during grammatical sequencing, or the "functional level" of processing (refer to Chapter 1, section 1.2.1, for a full description of the levels of processing). According to this explanation, semantic similarity may lead to interference in lexical and/or positional selection. This is because related concepts such as *man* and *woman* share overlapping semantic and agent/patient associations and therefore compete for lemma selection during word retrieval and/or grammatical function assignment during positional encoding (animate nouns tend to be equally good subjects).

Thus, although production and comprehension both involve similarity-based competition, they might engage distinct underlying mechanisms. This might be reflected in distinct patterns of neural activity. Specifically, lexical retrieval and selection are thought to rely on posterior temporal areas. Word production studies that manipulate lexical competition have found recruitment of these areas (Hagoort, 2005; Indefrey, 2011; Indefrey & Levelt, 2004; Kircher, et al., 2004; Snijders, et al., 2009; Spalek & Thompson-Schill, 2008; Wilson, et al., 2009). For instance, using the picture-word interference paradigm, studies have shown that the presence of semantically related distractors increases activity in pMTG in a picture naming task presumably due to increased demands on lexical retrieval and selection mechanisms (de Zubicaray, et al., 2006; de Zubicaray, et al., 2001). Therefore, if similarity-based competition occurs in production due to difficulty in lexical retrieval/selection this might be reflected by activation of the pMTG activity.

In terms of functional assignment, processes such as linearisation and positional coding are thought to recruit areas involved in motor planning and articulation (Acheson & MacDonald, 2009), in particular the SMA (Alario, et al., 2006; Dogil, et al., 2002; Heim, et al., 2009; Kielar, et al., 2011; Menenti, et al., 2011; Segaert, et al., 2011). This suggestion is based on evidence showing the role of the SMA in sequencing information in the action domain. For instance, SMA activity increases when new motor sequences are learned (Hazeltine, Grafton, & Ivry, 1997), and TMS or lesions of this area disrupt the performance of motor sequences from memory (Exner, Koschack, & Irle, 2002; Gerloff, Corwell, Chen, Hallett, & Cohen, 1997). Furthermore, SMA is also activated when learning new sequences not in the motor domain, for instance sequences of abstract symbols (Bahlmann, Schubotz, Mueller, Koester, & Friederici, 2009; Forkstam, Hagoort, Fernandez, Ingvar, & Petersson, 2006). In terms of positional coding in production, studies have shown increasing SMA activity for increasing syntactic complexity in production (Ye, et al., 2011), and syntactic priming studies that have shown that the SMA and lateral premotor areas are involved in the generation of syntactic structures, but not in the comprehension of the same structures (Menenti, et al., 2011; Segaert, et al., 2011). Therefore, if similarity-based competition places demands on positional sequencing in production, then one would predict increased recruitment of these areas in the production task.

Therefore, to summarise, it is likely that certain processes are common to production and comprehension in similarity-based competition, such as those involved in maintaining information in working memory and also managing the linguistic contingencies associated with particular concepts. It was predicted that commonality would be reflected by shared LIFG modulation. However, beyond these general commonalities it is likely that production and comprehension engage distinct processes. In particular, in comprehension alternative thematic role interpretations might compete for selection. In production, however, similarity-based competition is thought to derive mainly from production-specific processes, such as those involved in lexical retrieval/selection and/or grammatical sequencing. Therefore, we predict that whilst production and comprehension will share some processing components within LIFG, they will recruit distinct networks for task-specific processes, such as lexical retrieval within pMTG, and positional planning within motor-planning structures, in particular the SMA. To evaluate this possibility, fMRI was used to compare the production and comprehension of sentences that varied in terms of animacy and similarity (as described in the previous section). Here, we examined activation that was predicted by the degree of agent-patient similarity in a whole-brain analysis, and in specific ROIs (LIFG, pMTG and SMA). In particular, we examined whether LIFG showed a common or distinct pattern across tasks, and also whether pMTG and motor-related areas such as SMA show production-specific processes, as predicted. It was hoped that the results from this study would contribute to our understanding of the similarities and differences in the competition processes engaged by sentence production and comprehension.

5.3.2 Methods

5.3.2.1 Participants.

Seventeen right-handed native English speakers students at the University of York, who did not take part in Experiment 5, participated in this study. No participants had any history of psychiatric illness or neurological damage (six male, mean age = 20.94 years).

5.3.2.2 Materials.

The items used in this experiment were described in detail in Experiment 5 (Figure 5.8). There were 84 production items (42 animate-animate, 42 inanimate-animate) and 164 comprehension items, as active and passive versions of each item were included. The passive structures were included to increase structural variability across items and thereby decrease any influence of structural priming on production and comprehension. As a similarity effect was found for only the active structures in Experiment 5a only the active items were included in the analysis of similarity-based competition effects. Behavioural pre-tests within Experiment 5b using the same item order as the fMRI task showed that the task could be performed accurately and verified the minimal effect of structural priming (see Experiment 5a).

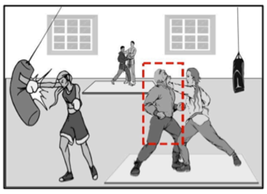
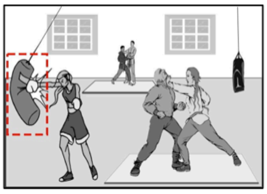
Example	Active RC	Passive RC
Animate		
	*The man that the woman is punching.*	*The man being punched by the woman.*
Inanimate		
	*The bag that the woman is punching.*	*The bag being punched by the woman.*

Figure 5.8 An example of the experimental items

5.3.2.3 Task design.

Alternating mini-blocks of comprehension and production trials were presented. The participant was cued before the beginning of each block as to the task they will be performing (either *Describe the highlighted entity in the picture* or *Does the sentence match the picture?*). Within a mini-block, conditions were presented using an event-related design. The most efficient block order and condition order within blocks was determined using Optseq. The production and comprehension tasks had the same trial structure: A picture was presented for 2 seconds, this was replaced by a fixation cross for a jittered interval of time (varying from 1.5 – 5 seconds in 500 ms intervals; mean jitter = 3.2 seconds, SD = 1.14). The picture would then return for 1 second but this time with a read square highlighting one of the participants in the picture. Finally, on comprehension trials, a sentence was visually presented for the 3 seconds, or on production trials, the symbol “???” was presented for 3 seconds indicating that the participants should covertly produce a sentence that describes the highlighted entity in the picture. Figure 5.9 shows the trial structure for the production and comprehension tasks. The use of the same trial structure across tasks thus makes it possible to perform direct task comparisons. During the null time between trials, a series of “+”s were presented that was the mean length of the sentences and acted as a visual baseline. The null time between trials was inserted using Optseq and varied from 0 – 22 seconds in 500 ms intervals (mean null time = 3.5 seconds, SD = 3.5).

The task for the comprehension trials was to indicate by button-press when the sentence did not refer to the highlighted object in the picture. There were 30 such trials and these acted as catch trials and ensured that every picture and sentence was attended to. In the production task, the participants were instructed to covertly describe the highlighted person/object using enough detail such that it could be uniquely identified. The instructions encouraged the use of relative clause structures and were the same as those used in Experiment 5. After the fMRI experiment, the participants also completed an abridged version of the production task outside the scanner. The responses to these items were analysed for accuracy, and it was assumed that if the participants could perform the task accurately outside of the scanner then they would also show accurate responses during the fMRI scan.

The language task had four separate runs each lasting 1136 seconds, 1092 seconds, 1010 seconds, and 1086 seconds respectively. The block and item order varied between runs, and the same item was never presented within the same run for production and comprehension tasks. The runs were presented in a counterbalanced order across participants to avoid order effects.

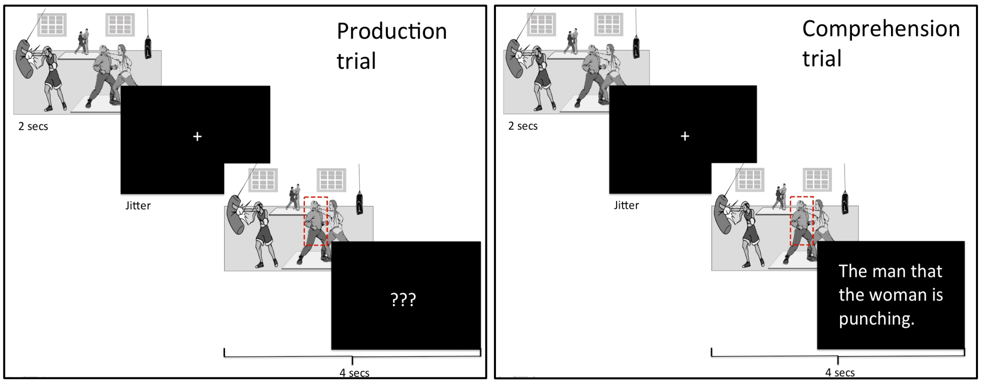


Figure 5.9 Trial structure for fMRI production and comprehension task.

5.3.2.4 Acquisition parameters.

Imaging was carried out using a 3T Signa Excite MRI scanner at the York Neuroimaging Centre (YNiC). High-resolution whole brain T1-weighted structural images were obtained for all participants (1mm x 1mm x 1mm). Functional images were obtained using a gradient-echo EPI sequence with 35 contiguous axial slices per volume (TR = 2000 ms, TE = 20 ms, flip angle 90°, matrix 64x64, FOV 24cm, slice thickness = 3.5mm). A T1-weighted FLAIR image was also obtained to aid in registration.

5.3.2.5 Data analysis.

Data analyses were carried out using FSL tools (the software library of the Oxford Centre for Functional MRI of the Brain (FMRIB); www. fmrib.ox.ac.uk/fsl). First- and higher-level analyses were carried out using FEAT (FMRI Expert Analysis Tool). The runs were combined by aligning and concatenating the demeaned (i.e. intensity normalised) raw sessions' data. Note that it is important to demean the cross-session data before concatenation because different sessions vary in their mean signal intensity. Pre-processing of the data included motion correction (Jenkinson, et al., 2002), slice-timing correction, brain extraction, spatial smoothing using a Gaussian kernel of full-width-half-maximum (FHWHM) 8 mm, and high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, sigma=25.0 seconds). Time series analyses were conducted using FILM (FMRIB's Improved Linear Model) with local autocorrelation correction (Woolrich, et al., 2001). The data from each task were modelled separately with event-based explanatory variables (EVs) corresponding to the condition and trial structure, which were convolved with a hemodynamic response function (gamma function). Each HRF was aligned to the beginning of the event and lasted the duration of the event. EVs were defined for each of the experimental conditions and the fillers. Separate EVs were defined for the initial 2 second picture presentation and the later 4 second "picture plus language" portion of the trials. Only this latter portion of the trial was entered into the analysis.

General language networks and animacy contrast. In order to examine the more general similarities and differences in the production and comprehension networks, we first conducted broad contrasts across all items in the production and comprehension tasks. Specifically, we performed the general contrast of all comprehension items > baseline, and all production items > baseline in order to replicate the findings from the previous experiment (Chapter 3). Also, in order to directly compare the activity patterns across tasks, we performed the direct contrast of all production > comprehension, and all comprehension > production (Cluster corrected, $Z = 2.3$, $p < .05$). To investigate the influence of animacy across tasks we directly contrasted the animate and inanimate conditions (animate > inanimate) separately for each task (Cluster corrected, $Z = 2.3$, $p < .05$).

Similarity correlation. To investigate the influence of similarity-based competition on production and comprehension a correlation analysis was performed using the similarity rating score for each of the 84 items as a covariate, separately for the production and comprehension tasks. This analysis thus reveals voxels that are sensitive to the degree of agent-patient similarity across items. Given the high degree of variability in similarity within the animate items, this model would achieve a better fit with the data compared with directly contrasting all animate and inanimate items. The analysis was restricted to the key anatomical regions mentioned in the introduction, specifically LIFG, pMTG, and SMA (voxel corrected, $p < .05$) that were defined based on the Harvard-Oxford structural atlas built within FSL (left inferior frontal gyrus, pars opercularis; left middle temporal gyrus, temporoccipital part; and left juxtapositional lobule, formerly supplementary motor cortex).

ROI analyses. In the similarity correlation analysis, variations in similarity are confounded by variations in animacy. This is potentially problematic as the animate items might be more difficult to process compared to the inanimate items for reasons other than similarity-based competition. For instance, because animate-animate object relative clauses are less frequent structures compared to inanimate-animate constructions (Fox & Thompson, 1990; Gennari & MacDonald, 2008, 2009; Mak et al., 2002; Roland et al., 2007; Gennari et al., 2012). Therefore, separate ROI analyses were conducted where the data was modelled differently to examine influences of similarity without the confounding effects of changing animacy, by restricting the analysis to only the animate items. This was done by splitting the animate items into a high-and low-similarity condition based on their similarity rating score and directly contrasting activity from these conditions (referred to as the animate-high-similarity > animate-low-similarity contrast). The data from this model was analysed in a ROI analysis to test the predictions about similarity-based competition within LIFG, pMTG, and SMA.

The ROIs consisted of a combination of functionally and anatomically defined regions. Functional ROIs for LIFG (pars opercularis) and the left SMA were defined based on data from a group analysis using animate-high-similarity > animate-low-similarity contrast from the production task to test for comparable results within comprehension. The contrast of animate-high-similarity > animate-low-similarity in production revealed two significant clusters of activity; one within LIFG (pars opercularis) and the other within the left SMA (cluster corrected, *p* < .05) These clusters of activation were separated into two separate functional ROIs to test for a parallel effect in the comprehension task (Note, that no regions were activated by this contrast in comprehension). The ROIs are shown in Figure 5.10). The pMTG was activated in neither production nor comprehension analyses and was therefore defined anatomically using the Harvard-Oxford atlas built into FSL, as described above.

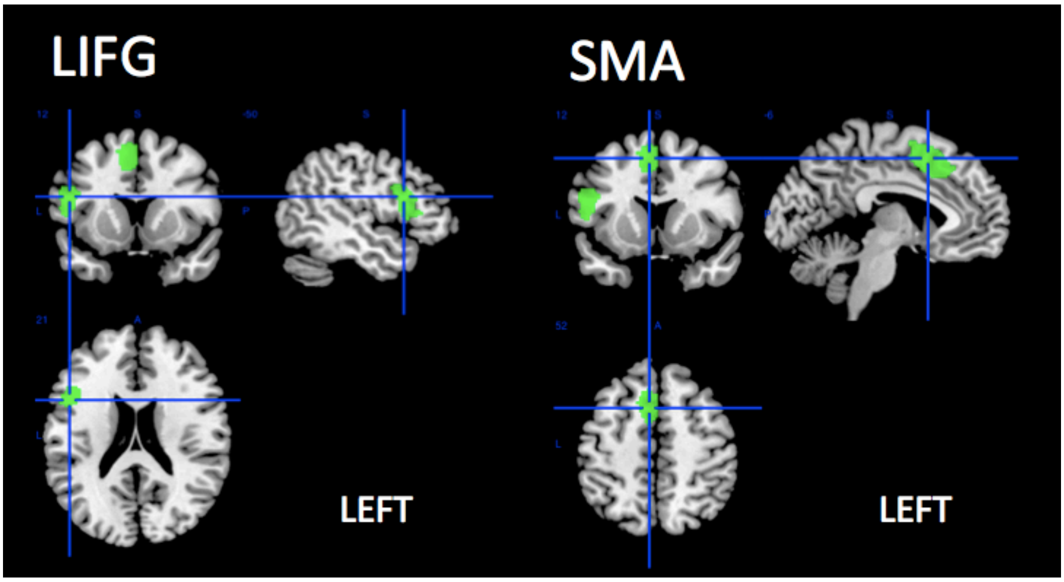


Figure 5.10 Functional ROIs for LIFG and SMA defined from the contrast of high-similarity > low-similarity animate items in the production task (Cluster corrected, *p* < .05).

5.3.3 Results

5.3.3.1 Behavioural data.

Behavioural responses to the comprehension catch trials were found to be accurate across participants (M % correct = 89.22%, SD = 8.21). Production responses to the same items outside the scanner were also highly accurate demonstrating that the participants were able to perform the production task accurately (M % = 91.93%, SD = 20.12).

5.3.3.2 fMRI Results.

Similarities and differences in overall production and comprehension networks. To examine the general similarities and differences in the overall networks engaged by production and comprehension whole brain analyses were performed contrasting each task separately against baseline, and also directly contrasting the two tasks with each other (cluster-corrected, $Z > 2.3$, $p < .05$). These broad contrasts guarantee that any potential difference between the production and comprehension tasks are not missed in more specific contrasts. Contrasts with baseline demonstrated that production and comprehension engage a common network of lateral fronto-temporal areas, including LIFG (pars opercularis, pars triangularis), left precentral gyrus and pMTG, as well as bilateral visual areas (occipital fusiform gyrus), whereas production alone engaged a further network of motor structures (see Table 5.2). This suggests a common left-lateralised fronto-temporal network, but production engages a further motor-related network, thus replicating the results from the previous chapter. These results thus replicate the effects observed in Chapter 3.

Table 5.2 The results from a whole-brain analysis (cluster corrected, *Z* > 2.3, *p* < .05): Regions activated for the contrast of production > baseline and comprehension > baseline.

Contrast	Brain Area	Z	Peak voxel (MNI) *x*	*y*	*z*
Comprehension > baseline	Occipital Fusiform Cortex, Bilateral	3.26	-38	-64	-24
	Precentral Gyrus, Left	2.75	-42	-2	58
	Inferior Frontal Gyrus, pars opercularis, Left	2.74	-54	12	26
	Inferior Frontal Gyrus, pars triangularis, Left	2.58	-54	22	-4
	Insular Cortex, Left	2.55	-32	20	-2
	Posterior Middle Temporal Gyrus, Left	2.84	-54	-58	8
Production >baseline	Occipital Fusiform Cortex, Bilateral	3.05	44	-46	-26
	Precentral Gyrus, Left	2.89	-60	10	18
	Inferior frontal Gyrus, pars opercularis, Left	2.87	-58	12	20
	Middle Frontal Gyrus, Left	2.5	-46	30	36
	Supplementary Motor Area, Left	3	-4	-2	62
	Posterior Middle Temporal Gyrus, Left	2.79	-58	-58	10
	Putamen, Left	2.5	-22	6	0
	Supramarginal Gyrus, Left	2.49	-42	-40	38
	Precuneus, Bilateral	2.79	6	-74	52

The direct contrast of production and comprehension tasks revealed some substantial differences in the networks engaged (see Figure 5.11; also see table in Appendix G). Production showed stronger activity than comprehension in a widely distributed network of areas, including lateral and medial frontal cortex (left SMA, bilateral precentral gyrus, left ACC, bilateral frontal pole, left SFG, left MFG, left IFG (pars opercularis, pars triangularis), and bilateral insular cortex), parietal areas (bilateral supramarginal gyrus, right precuneus, left superior parietal lobule), left inferior temporal cortex, subcortical structures (bilateral putamen and left thalamus), and right cerebellum. The reverse contrast revealed a far smaller network of areas that were more strongly engaged for the comprehension compared with the production task, and included mainly visual areas, including lower level visual areas and areas associated with reading (bilateral occipital pole, bilateral lingual gyrus, left occipital fusiform gyrus, left temporal occipital fusiform gyrus), as well as left cerebellum and bilateral hippocampi. Overall, the pattern of results indicates that whilst production and comprehension both engage a lateral fronto-temporal network, production shows a stronger and more extensive pattern of activity, apart from the obvious engagement of visual areas for the comprehension task.

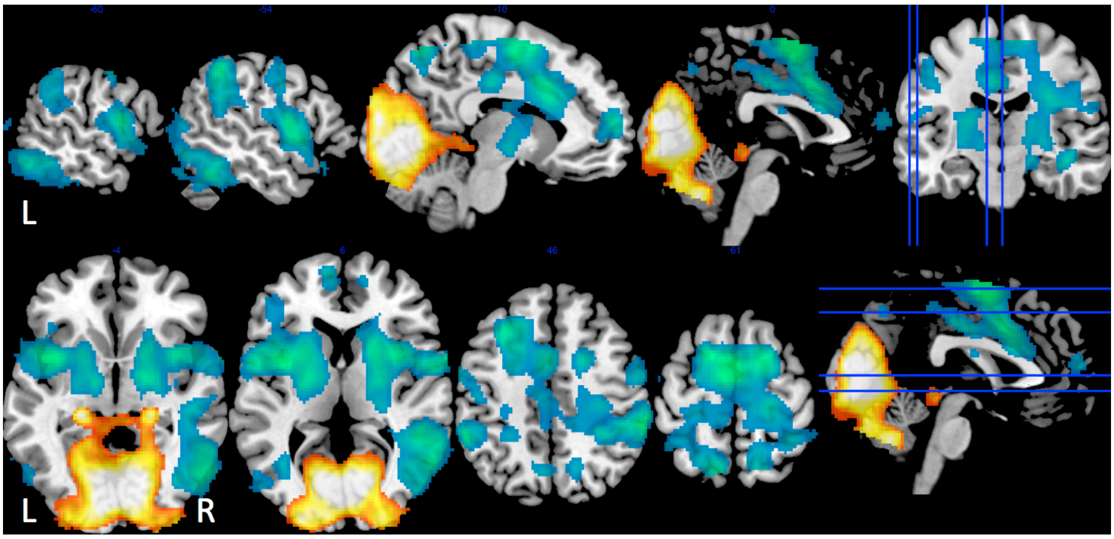


Figure 5.11 Whole-brain analysis: contrast of production and comprehension tasks (cluster corrected, *p* < .05). Production > comprehension in blue, and comprehension > production in red.

Animacy contrast. The contrast of animate vs. inanimate conditions failed to yield any significant results in either production or comprehension using the cluster corrected threshold. However, when the statistical threshold was reduced, a significant influence of animacy was found within the left SMA in production ($Z = 2.8$, $p = .005$; MNI coordinates: -14, 0, 62), and in comprehension within LIFG (pars triangularis; MNI coordinates: -54, 30, 20) and pMTG (MNI coordinates: -46, -64, 10) ($Z = 3.1$, $p = .001$). The failure to find results at an appropriate statistical threshold can be explained by the high degree of variability in similarity within the animate condition reducing the efficiency of the model. This variability is accounted for within the similarity-correlation analyses thus making it a better test of similarity-based competition effects.

Similarity-correlation analyses. In order to test the predictions regarding similarity-based competition in production and comprehension a correlation analysis was performed using similarity-rating score as a predictor within the key regions; LIFG (pars opercularis), pMTG, and SMA (voxel corrected, $p < .05$) (for the results of a whole-brain analysis using a more lenient threshold see Appendix H). As predicted, similarity was found to predict activity within the LIFG (pars opercularis) for both the production and comprehension tasks. Interestingly, however, the location of the clusters varied, with production recruiting a more dorsal and posterior area that bordered premotor cortex, and comprehension recruiting a more ventral and anterior area that bordered pars triangularis (see Figure 5.12), although some overlap was found in the clusters at a reduced statistical threshold (see Figure 5.13).

It was predicted that if similarity-based competition in production occurs at the level of lexical retrieval or positional encoding then the SMA and pMTG would show production-specific sensitivity to similarity. The results support this prediction for the SMA, as here a significant cluster of activation was revealed for the production task (see Figure 5.12) with no significant activity for comprehension. This suggests that production alone recruits motor-related structures for similarity-based competition, thus providing evidence of task-specific competition processes. The pMTG, however, was found to be insensitive to similarity in either task.

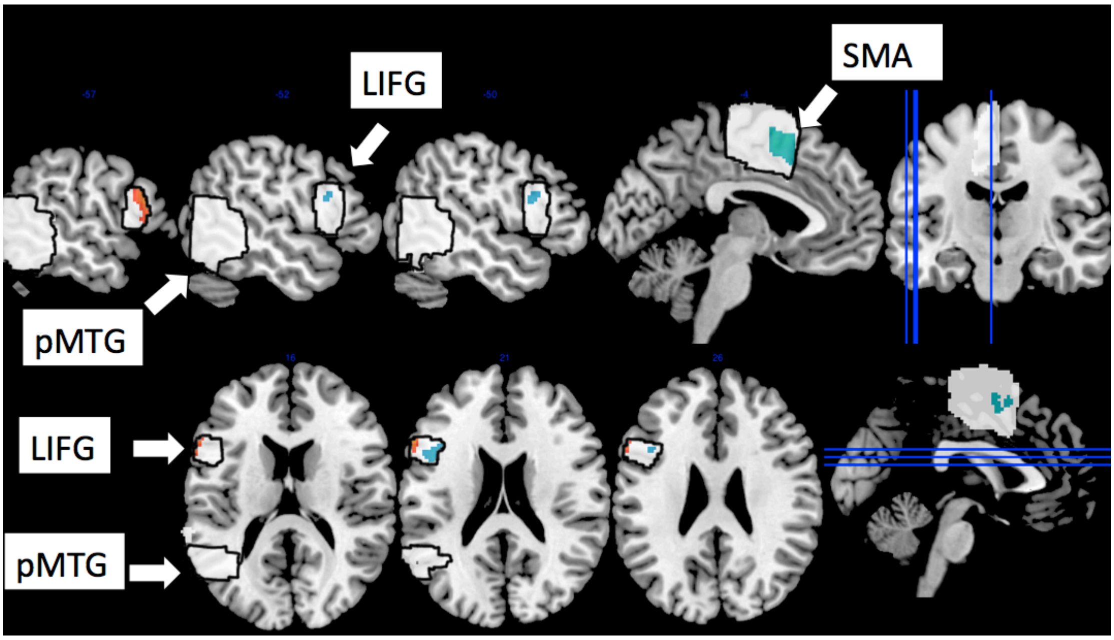


Figure 5.12 The similarity correlation analysis for production (blue) and comprehension (red) within LIFG, pMTG, and SMA (voxel corrected, *p* < .05).

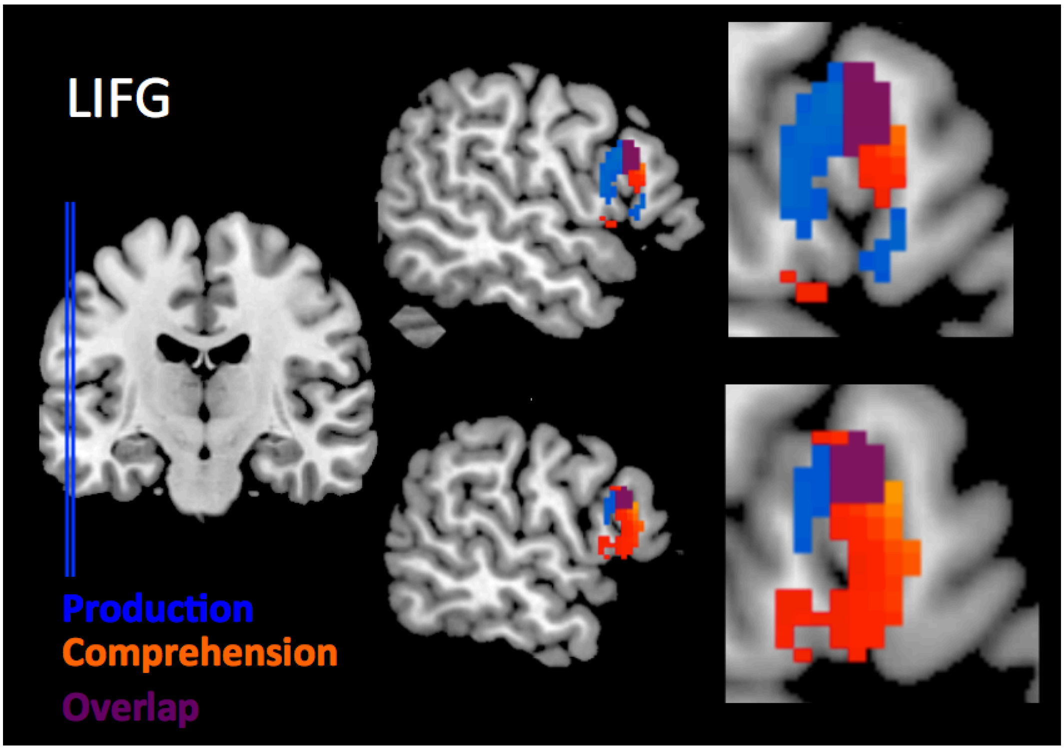


Figure 5.13 The similarity correlation analysis showing partial overlap between production (blue) and comprehension (red) and the overlap (purple) within LIFG (pars opercularis) (uncorrected, *p* < .05).

ROI analysis: High- vs. low-similarity in the animate items only. The contrast of high- and low-similarity animate items was performed to examine similarity effects without variations in animacy within ROIs for LIFG, SMA, and pMTG. Functional ROIs were defined for the LIFG and SMA based on the results from this contrast in the production group analysis to test for a comparable effect in the comprehension data. The pMTG region was defined anatomically based on the anatomical atlases (refer to Methods Section, ROI analysis). Percent signal change was extracted from each ROI for the high-similarity and low-similarity conditions. The results showed that within the LIFG ROI, as was the case in the production, an effect of similarity-based competition was found in the comprehension task. A paired-sample t-test showed a significant difference between the high-similarity and low-similarity condition in the comprehension task (*t*(16) = -1.90, *p* = .08, two-tailed) (see Figure 5.14).

Within the SMA, however, comprehension did not show the same effect as production. Here, a paired-sample t-test revealed that in the comprehension task there was no significant difference in activity for the high- and low-similarity conditions ($t(16) = -1.01$, $p = .33$). A repeated-measures ANOVA was used to confirm that the SMA responded differently to the production and comprehension tasks; this analysis revealed a significant main effect of task ($F(1,16) = 13.02$, $p < .01$) and condition ($F(1,16) = 6.41$, $p < .05$), and a significant task x condition interaction ($F(1,16) = 17.73$, $p < .01$) (see Figure 5.14). Therefore, the SMA is sensitive to similarity-based competition only in production.

Within the pMTG a repeated-measures ANOVA showed no effect of task ($F(1,16) = .98$, $p = .34$). However, there was a significant effect of condition ($F(1,16) = 6.38$, $p < .05$), and a significant task x condition interaction ($F(1,16) = 5.63$, $p < .05$). As predicted, planned t-tests showed a significant effect of similarity within the production task ($t(16) = 3.65$, $p < .01$), but no difference in comprehension ($t(16) = .36$, $p = .73$) (see Figure 5.14). Therefore, at least for this contrast, pMTG appears sensitive to competition in the production task but not in comprehension.

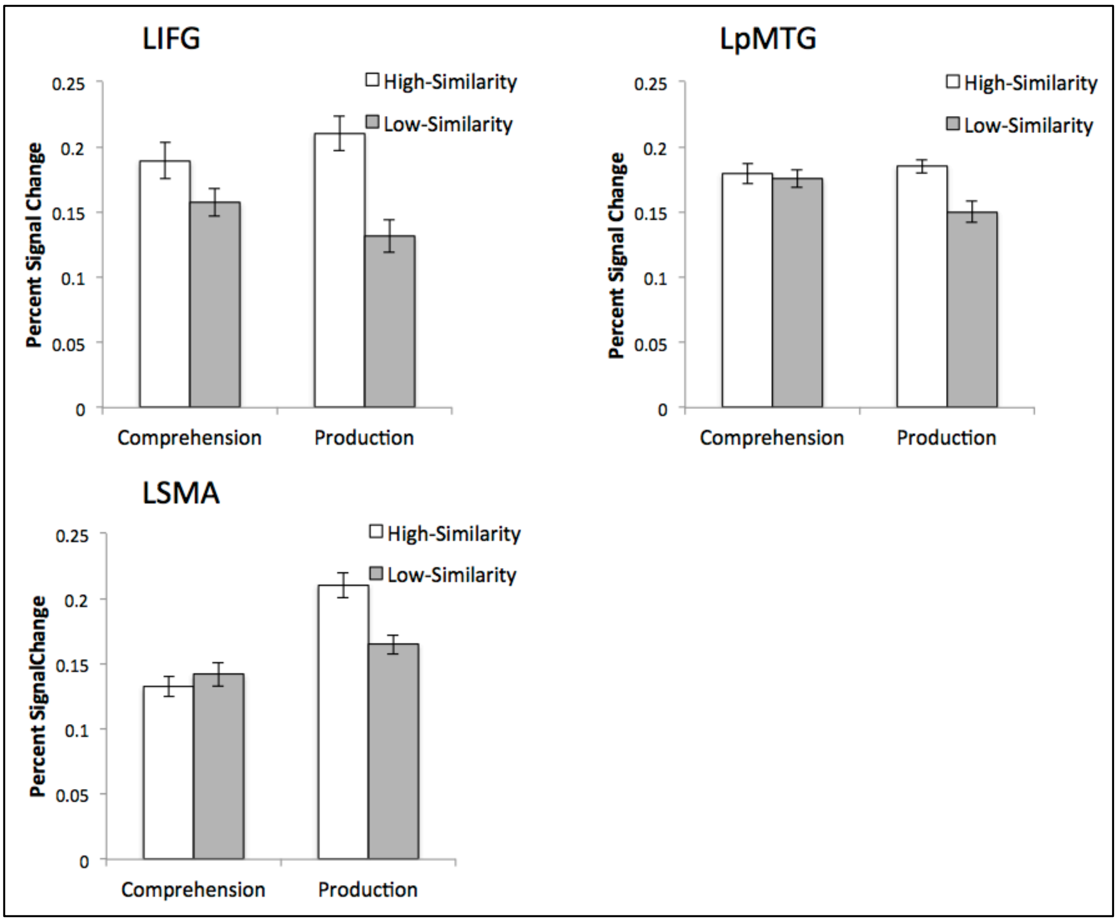


Figure 5.14 ROI analyses for the contrast of high-similarity and low-similarity animate items.

5.3.4 General Discussion

The aims of this study were two fold. The first general aim was to use an improved paradigm to directly compare the neural networks engaged by sentence production and comprehension. The results showed that whilst production and comprehension engage a common fronto-temporal network, production shows increased and more extensive activity across a wide network of frontal, temporal, parietal and subcortical structures. The second and more specific aim was to compare the neural processes engaged for similarity-based competition for production and comprehension tasks. The results from the similarity-correlation analysis and the contrast of high- and low-similarity animate items showed that both production and comprehension engage LIFG for similarity-based competition. Interestingly, however, although there was some overlapping activity the production and comprehension clusters had a slightly different location within pars opercularis. Specifically, production recruited a more dorsal and posterior section, bordering premotor cortex, whereas comprehension recruited a more anterior and ventral section bordering pars triangularis. Thus, despite some shared processing, the LIFG results also suggest a degree of divergence in the underlying processes engaged by each task.

The results also show, as predicted, that production and comprehension show diverging responses in other cortical areas. Specifically, it was predicted that pMTG and SMA would show sensitivity to similarity in production, but not comprehension due to their role in production-specific processes, in particular lemma retrieval and positional coding respectively. The results largely supported the predictions. The SMA selectively responded to similarity in the production task but not in comprehension in both the similarity-correlation analysis and also the contrast of high- and low-similarity animate items. With regard the pMTG analysis, no influence of similarity was found for either task in the similarity-correlation analysis. However, a similarity effect was found for production and not comprehension in the contrast of high- and low-similarity animate items. Thus, the results provide partial support for the pMTG predictions.

5.3.4.1 General production and comprehension networks.

As expected production and comprehension were both shown to engage the core fronto-temporal language network, thus replicating previous results from chapter 3. As mentioned previously, within this network the posterior temporal lobe is thought to store lexical knowledge, particularly that associated with verbs and their event structures (Bedny, Caramazza, et al., 2008; Dronkers, et al., 2004; Tyler & Marslen-Wilson, 2008), whereas the LIFG is thought to perform general regulatory functions, including memory maintenance, controlled retrieval and encoding, integration and selection/inhibition (Barde & Thompson-Schill, 2002; D'Esposito, et al., 1999; Fiebach & Schubotz, 2006; Fuster, 2001; Miller & Cohen, 2001; Thompson-Schill, et al., 2005; A. D. Wagner, et al., 2001). However, the direct comparisons of production and comprehension revealed that production displayed stronger and more extensive activity compared to comprehension in a wide network of areas including “core” language areas, such as LIFG, and additional regions such as lateral and medial prefrontal cortex, subcortical structures, parietal areas and inferior temporal lobe. Some of these production-specific areas were highlighted in Chapter 3, however, the improvements in experimental design in the current study now permit direct statistical comparisons.

The structures that were sensitive to production here likely serve multiple processes. For instance, certain areas are known to be involved in motor planning and coordination, as well as conflict control, and articulatory processes (SMA, cingulate gyrus, premotor cortex, basal ganglia, insula, thalamus, superior parietal lobule, cerebellum) and are likely involved in sentence planning during production (Alario, et al., 2006; Barch, et al., 1999; Basho, et al., 2007; Brownsett & Wise, 2010; C. Y. Chen, et al., 2009; Dogil, et al., 2002; Geranmayeh, et al., 2012; Haller, et al., 2005; Hickok, 2012; Indefrey, 2011; Indefrey & Levelt, 2004; Ketteler, et al., 2008; Kielar, et al., 2011; Mukamel, et al., 2010; Murphy, et al., 1997; Nachev, et al., 2007; Simmonds, et al., 2008; Sörös, et al., 2006; Wahl, et al., 2008; Wise, et al., 1999). In contrast, other areas are thought to be involved in word/syntactic retrieval and selection, processes that play a more prominent role in production compared to comprehension (middle frontal gyrus, LIFG, basal ganglia) (Abutalebi, et al., 2008; Ali, et al., 2009; Badre, et al., 2005; Garbin, et al., 2011; Price, 2010; Schnur, et al., 2009). Furthermore, the fact that LIFG was more active in production suggests that production places greater general demands on control processing compared to comprehension. This likely reflects differences in task-difficulty.

Production also showed increased recruitment of other areas that likely reflect differences in task difficulty. For instance, activity was found in areas that direct attention (supramarginal gyrus, precuneus), presumably reflecting the general increased processing demands associated with production compared to comprehension tasks (Brownsett & Wise, 2010; Cavanna & Trimble, 2006; Jacquemot & Scott, 2006; Nee, et al., 2007; Ye, et al., 2011). Therefore, the increased recruitment of this wide network of areas for production compared to comprehension likely reflects a combination of production-specific planning and retrieval processes, as well as differences in task difficulty, as reflected by increased attentional processes in production.

Certain areas were activated more strongly for the comprehension relative to the production task. Unsurprisingly these included lower level visual areas, as well inferior fusiform regions associated with reading (visual word form area) (L. Cohen et al., 2000). One surprising result was that bilateral hippocampi were recruited more strongly for comprehension compared to production. This result is in contrast to what was found in the previous experiment (Chapter 3), and with evidence of hippocampal involvement in retrieval aspects of production generally (Nadel & Moscovitch, 2001; Paller & Wagner, 2002; Whitney, et al., 2009). Saying this, increased hippocampal involvement for comprehension compared to production has been observed elsewhere in the literature, and has been explained in terms of demands on linking incoming information to information held in working memory (Awad, et al., 2007). Therefore, the current finding might be explained in terms of aspects of the comprehension task, which involved matching sentence-picture matching. Therefore the hippocampal activity found here likely reflected the maintenance of picture-related information in memory during sentence comprehension.

An interesting observation is that the production network was found to be more strongly bilateral compared to the comprehension network. This is in contrast to what has been suggested elsewhere in the literature where comprehension was found to be more bilaterally organised than production (Lambon-Ralph, McClelland, Patterson, Galton, & Hodges, 2001). This difference is likely explained in terms of comprehension modality; studies that have argued for bilateral comprehension have used auditory stimuli which are processed bilaterally (Hickok & Poeppel, 2004, 2007). Written stimuli, in contrast, show a greater left-hemisphere bias even in early processing areas such as the visual word form area (L. Cohen, Dehaene, et al., 2000; Michael, Keller, Carpenter, & Just, 2001).

To summarise, sentence production and comprehension engage a common fronto-temporal network of areas. However, task-specific differences mean that production shows stronger recruitment of a wide network of areas reflecting production-specific planning and retrieval processes, as well as the increased task difficulty and attentional demands. These results thus extend and confirm the results from Chapter 3 using an improved experimental design.

5.3.4.2 Similarity-based competition mechanisms

5.3.4.2.1 Shared production and comprehension processes.

The results from the similarity-correlation analysis, as well as the analysis using only the animate items, showed (at least partially) common LIFG activity for production and comprehension, thereby providing evidence of shared processing. The fact that certain processes are common to production and comprehension is unsurprising given some clear commonalities between the tasks. For instance, comprehension and production both engage certain general regulatory processes that are known to engage LIFG, such as those involved in maintaining information in working memory. For instance, both tasks involve maintaining information in memory during sentence processing, and this is therefore liable to interference from semantic competitors (see references in Experiment 6; Introduction).

Furthermore, certain linguistic processes are also likely common to production and comprehension (as described in previous chapters). In particular, the tasks are known to share knowledge regarding the associations between concepts and their agent-patient features (Bock, et al., 2007; Chang, et al., 2006; Gennari & MacDonald, 2009). The data here, combined with that from earlier chapters (see Chapter 3) suggest that the mechanisms used to mediate these linguistic associations may be common to production and comprehension tasks. This is consistent with the general executive functions often attributed to LIFG in mediating contingencies between cues and their associations, both in linguistic and non-linguistic domains (Fuster, 2001; Koechlin & Jubault, 2006; Opitz & Friederici, 2003, 2004; Passingham, et al., 2000).

Therefore, the current results suggest that the mechanisms involved in working memory maintenance as well as those involved in managing linguistic contingencies are common to production and comprehension. Note that these descriptions may in fact be referring to the same processing mechanism; one that both maintains activated linguistic information in working memory and manages the linguistic associations between that information.

5.3.4.2.2 Distinct production and comprehension processes.

Despite some commonalities between production and comprehension, the current results also emphasise the differences in the underlying processes engaged by production and comprehension. In particular, beyond some common LIFG recruitment, production and comprehension were shown to engage distinct areas for similarity-based competition suggesting task-specific processing. Specifically, production-alone engaged motor-related structures such as SMA, as well as areas thought to be involved in lexical retrieval such as pMTG (although the evidence regarding pMTG responses is less conclusive). Furthermore, some evidence was found for task-specific LIFG responses (despite partial overlap), with production engaging a more dorsal and posterior area of pars opercularis that bordered premotor cortex and comprehension engaging a more ventral and anterior area that bordered pars triangularis. Together these findings suggest that production and comprehension engage task-specific processes for resolving semantic competition.

As discussed in the introduction to the chapter, there are two alternative explanations for the similarity-based competition effect in production, which are not necessarily mutually exclusive. Firstly, competition might arise at the level of lexical retrieval as semantically related lexical items, such as *man* and *woman*, compete for lexical selection. Secondly, competition might arise at the functional level of processing during positional encoding, as semantically related items share subject/object associations and therefore compete for grammatical roles during function assignment. As discussed below, the current results provide good support for the latter positional explanation, but there is only partial evidence to support the lexical retrieval account.

5.3.4.2.3 Lexical retrieval account of similarity-based competition in production.

The current study provides only partial support for the lexical retrieval explanation of similarity-based competition in production. According to production models, lexical retrieval is carried out by the pMTG (Hagoort, 2005;

Indefrey, 2011; Indefrey & Levelt, 2004; Kircher, et al., 2004; Snijders, et al., 2009; Spalek & Thompson-Schill, 2008; Wilson, et al., 2009). Here, there was some evidence of pMTGs involvement in production; an effect of similarity was found in production for the pMTG ROI analysis when using only the animate items. However, the pMTG was insensitive to similarity in the similarity correlation analysis. These inconsistent results make it hard to draw firm conclusions regarding the extent of competition at the level of lexical retrieval in production. Of course, one possibility for the absence of a pMTG effect in production is that this area is not critically involved in lexical retrieval processes. Indeed, multiple functions have been assigned in pMTG in the literature, including pre-lexical accounts and accounts that assign semantic control processes to pMTG (Bedny, Caramazza, et al., 2008; Jefferies & Lambon Ralph, 2006). Therefore, the current results provide only partial support for the diverging involvement of left pMTG in semantic competition across production and comprehension tasks.

5.3.4.2.4 Positional encoding account of similarity-based competition in production.

That similarity-based competition arises in production due to difficulty in positional encoding and function assignment is supported by results showing the engagement of the motor-related areas, in particular the SMA, for similarity-based competition in production. The role of the SMA in sequencing information is well-established in the action domain; SMA activity increases when new motor sequences are learned (Hazeltine, et al., 1997) and TMS or lesions to this area disrupt the performance of motor sequences from memory (Exner, et al., 2002; Gerloff, et al., 1997). Based on this data it has been suggested that the motor system is an obvious candidate for serial order processing in production given the role of these areas in sequencing information in other domains (Acheson & MacDonald, 2009; Alario, et al., 2006). Indeed, the SMA has been shown to be involved in the generation of syntactic structures in production, and is not involved in comprehension (Menenti, et al., 2011; Segaert, et al., 2011), and is sensitive to increasing syntactic complexity in production (Ye, et al., 2011).

The importance of positional encoding processes in production is consistent with observations from the behavioural literature. In particular, studies of production errors have shown that word exchange errors, such as *Give the mother to your letter,* tend to occur only for highly related words that share a grammatical category, suggesting that items that share grammatical features compete for sentence positions in production (Garrett, 1975). Therefore, together these results suggest that similarity-based competition in production arises due to production-specific processes, and in particular from difficulty in the assignment of grammatical function and the positional coding of words in a sentence when the words share agent-patient features.

5.3.4.2.5 Task-specific LIFG activation for production and comprehension.

The current study found evidence that production and comprehension engage distinct (although overlapping) regions of LIFG, pars opercularis. In particular, production engaged a more dorsal and posterior region of pars opercularis that bordered on premotor cortex, whereas comprehension engaged a more ventral and anterior portion, bordering with pars triangularis. Whilst this result was not predicted it may be consistent with existing neurocognitive models.

The current pattern of data is compatible with the dual-stream model of language processing where production engages a dorsal route for planning and motor sequencing and comprehension engages a more ventral route for semantic processing (Hickok & Poeppel, 2000, 2004, 2007). The dorsal and ventral routes have been shown to converge upon distinct LIFG regions. The dorsal route connects motor and posterior temporal areas to dorsal regions of LIFG (BA44), whereas the ventral route connects semantic areas in the temporal lobe to more ventral LIFG regions (BA44 and 45) (Catani, Jones, & ffytche, 2005; Friederici, 2009; Petrides & Pandya, 2009; Saur et al., 2008; Wilson et al., 2011). Figure 5.15 shows the dorsal and ventral projections into the LIFG from a DTI study (Wilson, et al., 2011). Therefore, the distinct pattern of LIFG involvement found in the current study might reflect the differential involvement of the dorsal and ventral language pathways for each task. In production, similarity-based competition arises due to difficulty in "dorsal" processes such as sentence planning and positional sequencing, whereas comprehension difficulty arises due "ventral" processes such as the competition between alternative thematic role interpretations. The common activation pattern that was highlighted above (see above section: Shared Production and Comprehension Processes) might reflect the convergence zone between dorsal and ventral routes.

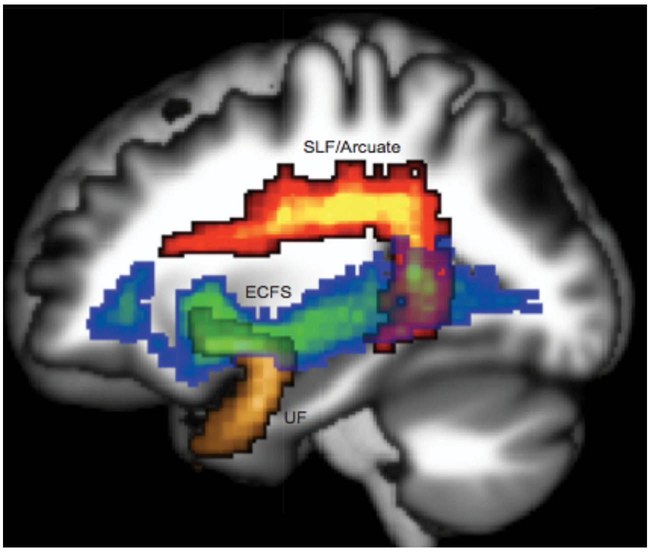


Figure 5.15 The dorsal and ventral white matter tracts, as revealed by DTI (Wilson, et al., 2011).

The possibility that dorsal and ventral regions of LIFG pars opercularis serve distinct roles in language is supported by a variety of evidence. Studies of the cytoarchitecture of pars opercularis have shown that dorsal and ventral areas have a different cellular structure suggesting functional differences (Amunts et al., 2010; Amunts & Zilles, 2012). In particular, ventral areas of pars opercularis have been claimed to serve semantic aspects of sentence processing, whereas dorsal aspects are involved hierarchical structure building in linguistic and non-linguistic domains (Price, 2010). For instance, dorsal opercularis is active to violations in syllable sequences and when learning new sequences in conjunction with SMA (Bahlmann, Schubotz, & Friederici, 2008; Bahlmann, et al., 2009; Tettamanti et al., 2009). In contrast, the more ventral region has been implicated in tasks involving semantic ambiguity resolution, and might therefore be more involved in selecting the appropriate interpretation amongst competing alternatives (Rodd, et al., 2005; Rodd, Longe, et al., 2010). Therefore, the differential pattern of LIFG recruitment found here is consistent with the notion of differences in the underlying processes engaged by production and comprehension. In particular, the current data suggests that dorsal pars opercularis, in conjunction with motor-planning structures such as SMA, may be involved in the positional sequencing of information in production, whereas the activation from the more ventral region might reflect semantic processes in comprehension such as the competition between alternative thematic role interpretations.

5.3.4.3 Implications for production and comprehension models.

The current data is inline with psycholinguistic approaches that emphasise the differences between production and comprehension tasks (Bock & Levelt, 1994; Levelt, et al., 1999) (refer to Chapter 1, Psycholinguistic models). However, the results contradict certain claims from production models. For instance, the fact that semantic properties modulated activity in areas that are not associated with conceptual representations, such as various motor-related regions challenges the assumptions of encapsulated production models (Bock & Levelt, 1994; Levelt, et al., 1999) and is more in favour of an interactive production system in which conceptual levels interact with areas involved in word sequencing and planning.

The results also challenge certain assumptions from neurocognitive models regarding the role of motor-related areas in production. Certain models argue that these areas are not actively involved in the linguistic aspects of production and play only a peripheral role in the production system such as one of motor output (Hickok, 2012; Hickok, et al., 2011; Indefrey, 2011; Indefrey & Levelt, 2004). However, finding modulation of motor structure by a clearly semantic variable suggests that these regions play an active role in sentence-level processes, in particular syntactic planning and the positional sequencing of words in a sentence, otherwise referred to as the “functional” level of processing in sentence production models.

Finally, the findings have implications for certain comprehension models, such as the simulation approach. This approach has argued that language comprehension involves simulation of production planning, or covert imitation (D'Ausilio, et al., 2009; Liberman, et al., 1967), thus recruiting motor control systems (Pickering & Garrod, 2007). The current study shows clear asymmetries in the networks engaged by production and comprehension, and in particular, motoric regions were found to be involved in production but not in comprehension tasks. This challenges the assumptions of the simulation approach, and rather demonstrates a substantial degree of asymmetry in the neural mechanisms underlying production and comprehension processes.

5.4 Conclusions

To conclude, this chapter describes a series of studies that investigate the extent to which production and comprehension engage common or distinct mechanisms for similarity-based competition. The results show that despite parallel behavioural effects, the underlying mechanisms involved in resolving similarity-based competition differ across production and comprehension tasks, suggesting task-specific processes, although some general regulatory processes may be shared. These differences may be reflective of more general differences between production and comprehension tasks, where comprehension involves determining who-is-doing-what-to-whom based on information from incoming semantic and syntactic cues, whereas production involves syntactic planning and grammatical encoding processes.

Chapter 6

Discussion

The aim of this research was to investigate the relationship between sentence production and comprehension. Understanding the similarities and differences in generating and understanding language is critical to our understanding of language more generally, and this issue should form a key component of any language model. Despite the clear theoretical importance of this issue, it has been largely overlooked in the literature. This is for two principal reasons. Firstly, traditional psycholinguistic models tended to view production and comprehension as distinct processes, and as a consequence the two tasks have been studied and modelled separately. Secondly, sentence processing models in the neurocognitive literature are heavily biased towards comprehension. Therefore, the current work aimed to address the gap in research by investigating the extent to which sentence production and comprehension engage common or distinct mechanisms for competition resolution.

6.1 Summary of findings

As part of this thesis, a combination of behavioural and neuroimaging techniques were used to investigate the extent to which sentence production and comprehension displayed similar effects of competition in terms of behaviour or neural activation.

Chapters 2 – 4 investigated cue-based competition in which the influence of conflicting cues was compared across reading and sentence-completion tasks. Behavioural studies in Chapter 2 indicated that high-competition cases were more difficult to understand and produce than were low-competition cases, and that difficulty varied as a function of the number of alternative interpretations entertained during performance in both tasks. The common mechanisms suggested by this behavioural data were confirmed in Chapter 3, in which an fMRI study indicated that production and comprehension shared common competition mechanism within LIFG. However, this study also indicated that both tasks engage distinctive networks, with production eliciting a larger network beyond the fronto-temporal network typically found in comprehension. Further asymmetries across tasks were revealed in Chapter 4, in which behavioural results and neural networks were compared across adults and adolescents. The production deficit in adolescents was found to be more generalised and severe compared to comprehension, suggesting that production is a more difficult task and that the extent to which control mechanisms are engaged might vary across tasks. Chapter 4 also revealed qualitative and quantitative shifts in the neural networks involved in competition resolution throughout development, thereby providing a strong link between poor behavioural performance and the underdevelopment of pre-frontal inhibitory mechanisms in adolescents. These results therefore provide evidence for the critical role of pre-frontal cortex in competition mechanisms going beyond the correlational data provided in Chapter 3.

Chapter 5 investigated similarity-based competition, and used an improved experimental paradigm from that described in Chapters 3 and 4. The degree of noun-noun similarity predicted behavioural and neural responses in both production and comprehension. The results showed production elicits more activity than comprehension in a distributed network of areas that are associated with planning, retrieval and control processes. This confirms that production and comprehension engage task-specific processes. Interestingly, this study also revealed a common region of LIFG involved in both tasks, but also found differences within LIFG, suggesting the possibility of task-specific circuitry.

Together, the findings contribute to our understanding of the relationship between sentence production and comprehension in several ways. In particular they highlight what is potentially common or distinct between the two tasks, an issue to which we turn next.

6.2 What is the relationship between sentence production and comprehension?

6.2.1 Distinct Processes

The current research suggests that production and comprehension engage task-specific processes. In particular, they ignite largely distinct networks for competition resolution processes, with production especially showing an increased involvement of a wide network of areas that are involved in motor-planning (SMA, premotor cortex, and basal ganglia), retrieval and control (LIFG, hippocampus, parietal areas), and attentional processes (parietal areas) (Chapter 3 and 5). Furthermore, production and comprehension appear to engage distinct routes into LIFG, but they converge on a central zone (as discussed in Chapter 5). Finally, the tasks show developmental differences, with production developing at a slower rate and showing more severe deficits from the underdevelopment of inhibitory processing mechanisms (Chapter 4). These differences in the pattern of production and comprehension data likely reflect differences in the underlying processes engaged, as is discussed below.

6.2.1.1 Task differences.

As suggested by previous psycholinguistics studies, the present results suggest that production engages task-specific retrieval and planning processes that are absent in comprehension where the items and word-order are provided. This is evident as production engages areas associated with memory retrieval, for instance middle frontal gyrus, parietal structures, pMTG, and hippocampus, and motor-planning regions, including SMA, premotor cortex, and basal ganglia (Chapters 3 and 5). This activity is thought to reflect positional coding and sequencing processes that are specific to production.

The current results also clearly show that production and comprehension differ in terms of task-difficulty. Most obviously production and comprehension differ in terms of speed of processing; recognition in comprehension is achieved in milliseconds, however production retrieval and planning processes occur in the order of seconds (see Chapter 2). Differences in task-difficulty are also evident from the developmental data showing that production processes develop more slowly and are more severely affected by the underdevelopment of inhibitory control systems (see Chapter 4). Furthermore, the adult data also indicates differences in task-difficulty with greater frontal and parietal involvement in production compared with comprehension (Chapters 3 and 5) suggesting increased demands on control and attentional processes. Together these results suggest that production places greater executive demands on control processes.

This is because the processes required to accurately retrieve and sequence information, as in production, are more demanding than those involved in recognising and predicting information, as in comprehension.

6.2.1.2 Network differences and a convergence zone

The different processes involved in production and comprehension lead to differences in the functional networks engaged by the tasks. In particular production and comprehension differ in their involvement of the dorsal and ventral routes (Chapters 3 and 5). Evidence has shown that the dorsal and ventral routes have been shown to converge upon distinct LIFG regions with the dorsal route connecting motor and posterior temporal areas to dorsal regions of LIFG (pars opercularis), whilst the ventral route connects semantic areas in the temporal lobe to more ventral LIFG regions (pars opercularis and pars triangularis) (Catani, et al., 2005; Friederici, 2009; Petrides & Pandya, 2009; Saur, et al., 2008; Wilson, et al., 2011). The current results show that production more strongly engages the dorsal route, activating motor-planning structures and projecting to dorsal LIFG, an area involved in planning and sequencing processes (Bahlmann, et al., 2008; Bahlmann, et al., 2009; Tettamanti, et al., 2009), although it also activates those areas recruiting linguistic knowledge, such as the temporal lobe. In contrast, comprehension processes more strongly involve the ventral route that projects to more ventral regions of LIFG, which are known to be involved in semantic processing and the comprehension of sentences (Fiebach, et al., 2004; Obleser & Kotz, 2010; Rodd, et al., 2005; Rodd, Longe, et al., 2010; Tyler, et al., 2010). Indeed, the dorsal-ventral distinction within pars opercularis is supported by structural evidence showing different neuronal assemblies within dorsal and ventral pars opercularis (Amunts, et al., 2010; Amunts & Zilles, 2012), as well as models based on functional evidence (see review by Price, 2010).

Despite distinct dorsal and ventral projections into LIFG, the current data suggests that the two routes then converge within LIFG, as reflected by the common region of activation (refer to section below: Common Processes). In fact, the area that showed common production-comprehension activity aligns well across experiments. In particular, area of LIFG that showed production-comprehension overlap in Experiment 5 corresponds to the same region of LIFG that was used as an ROI in Experiment 2 (based on the Stroop-localiser), where a common pattern of activation was found across tasks (Appendix I shows the region of common activation across studies). Figure 6.1 shows a schematic representation of the dorsal and ventral streams and the convergence within LIFG. This shows how the dorsal and ventral routes project into distinct LIFG regions, yet the information converges in a central zone. This perspective is consistent with a wealth of data showing that information from widely distributed task-specific networks converge within LIFG where the diverse information is integrated (see reviews by Fuster, 2001; Miller & Cohen, 2001; Thompson-Schill, et al., 2005). For instance, single unit recordings in monkeys have shown that whereas dorsal and ventral visual pathways respond differentially to spatial and semantic information, neurons within lateral prefrontal cortex show modality invariant responses suggesting integrative properties (Rao, Rainer, & Miller, 1997).

Thus, these observations suggest that the networks involved in each task are largely determined by task demands, with different demands recruiting increasingly different networks that might include regions along either route, but both tasks nevertheless show recruitment of a convergence zone in pars opercularis that manages common linguistic processes (see below).

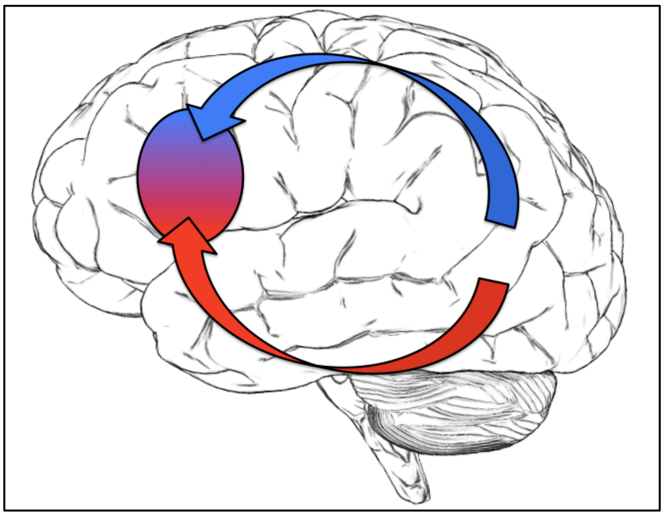


Figure 6.1 A schematic representation of the dorsal and ventral routes of processing. Information converges within the LIFG region.

1.1.1 Common processes

Despite the differences highlighted above, the current evidence suggests that there are also important commonalities between production and comprehension processes. In particular, the two tasks show a common effect of competition, both in terms of behavioural responses and in terms of shared fronto-temporal neural activation (Chapters 2, 3, and 5). As described below, this data suggests that production and comprehension share mechanisms that store the long-term linguistic associations between words and event-roles, and compute their higher order contingencies in sentence processing.

As mentioned earlier, production and comprehension are known to share linguistic knowledge, which includes how words are mapped into meaning and sentential structures, and how word sequences are mapped into larger event representations (Bock, et al., 2007; Chang, et al., 2006). These distributional properties arise from language experience, and affect both comprehension and production systems. In particular, comprehension is shaped by production experience; for instance, reading difficulty is predicted by the likelihood of a particular sequence being produced (Gennari & MacDonald, 2008, 2009), and in turn, production is also shaped by experience with comprehension. This is evident from studies that show syntactic priming from comprehension to production (Bock et al., 2007), and also from developmental studies showing that the structures that children produce are the ones that they have heard (Gennari & MacDonald, 2006; Kidd, Brandt, Lieven, & Tomasello, 2007).

Therefore, production and comprehension are sensitive to the same linguistic contingencies in language. In the current research this included the associations between animate/inanimate entities and their likely sentence roles. For instance, in Chapters 2-4 both production and comprehension were sensitive to cue-based competition that arose due to conflict between the syntactic structure of the sentence and the semantic roles associated with the animate and inanimate nouns (e.g. *The director that the movie…*). Also, in Chapter 5, production and comprehension were both sensitive to semantic competition from concepts that possess competing agent-patient associations. The finding of common behavioural results and activation patterns suggests that production and comprehension share mechanisms in the temporal lobe that store long-term linguistic associations, as well as frontal mechanisms that compute the higher order contingencies between linguistic cues. In particular, the results suggest that LIFG may be involved in mediating the contingencies between linguistic cues in production and comprehension tasks, such as the association between concepts, words, and structures. Indeed, this is consistent with the more general role of LIFG in mediating contingencies between cues and their associations in both linguistic and non-linguistic domains (Fuster, 2001; Koechlin & Jubault, 2006; Opitz & Friederici, 2003, 2004; Passingham, et al., 2000), and is involved in both producing and understanding grammatical cues in a sentence (Caplan, et al., 1996; Menenti, et al., 2011; Segaert, et al., 2011; Thothathiri, et al., 2010).

Therefore, the LIFG, and its interactive networks, manage linguistic contingencies, and thus, the anticipation or activation of information associated with words, concepts, and syntactic structures. These processes are common to production and comprehension tasks. However, despite commonalities in storing and managing abstract linguistic associations, production and comprehension differ in the manner by which linguistic information is used, as is evident by the recruitment of distinct networks.

6.3 Implications for existing language models

6.3.1 Psycholinguistic models

The current results have implications for existing psycholinguistic models. In particular, encapsulated production models (Bock, 1995; Levelt, et al., 1999) assume that information is not freely transferred between different processing levels. Therefore, according to these models the influence of semantic competition is restricted to the semantic processing level, and it cannot influence any other level of processing (e.g. syntactic, phonological, motor-planning). However, the current results challenge the assumptions of encapsulation. In particular, semantic competition was found to influence areas that are not typically associated with semantic processing, such as motor-planning structures (Chapters 2 and 5). These results thus argue against distinctive stages of lexical retrieval, planning and word sequencing and instead suggest parallel processing and interactivity across the network.

Therefore, the current data support interactive models of production (Dell, 1986). Some have claimed that production, like comprehension, can be modelled as a constraint-based process involving the interaction of multiple probabilistic sources of information (Haskell & MacDonald, 2003; Thornton & MacDonald, 2003; Vigliocco & Hartsuiker, 2002). Indeed, the data presented herein are compatible with a constraint-based model of production. For instance, the results from Chapter 2-4 show that the semantic associations of animate and inanimate nouns interact with the sentence structure to determine production difficulty. Also, Chapter 5 showed an interaction between the semantic associations of two animate entities and the positional sequencing of words in a sentence when both animate entities can plausibly play the subject role. Together these results suggest that production is the outcome of an interaction between the semantic associations of words and the syntactic functions they serve in a sentence. Therefore, the current data suggest that in both production and comprehension, multiple probabilistic constraints interact to influence processing, and that similar constraints apply to both tasks (see above section; Common Processes).

6.3.2 Neurocognitive models

The current results also have implications for neurocognitive models of language processing. The majority of neurocognitive models are biased heavily towards comprehension data. These assume that language engages a fronto-temporal network. The current data support this assumption as the fronto-temporal network was engaged by both tasks (Chapters 3 and 5). Within this network, the posterior temporal lobe is thought to store lexical knowledge, particularly that associated with verbs and their event structures (Bedny, Caramazza, et al., 2008; Dronkers, et al., 2004; Tyler & Marslen-Wilson, 2008), whereas the LIFG is thought to perform general regulatory functions, including memory maintenance, controlled retrieval and encoding, integration and selection/inhibition (Barde & Thompson-Schill, 2002; D'Esposito, et al., 1999; Fiebach, et al., 2006; Fuster, 2001; Miller & Cohen, 2001; Thompson-Schill, et al., 2005; A. D. Wagner, et al., 2001).

However, despite the common fronto-temporal pattern, the current data suggests increased demands on frontal processing in production compared to comprehension tasks (Chapters 4 and 5), and that production engages a far wider network of areas, including motor-planning and retrieval structures, and areas involved in directing attention. The role of these areas has been largely overlooked in language models due to the scarcity of production data. Therefore, further research is needed to incorporate these areas into neurocognitive models. The current data has implications regarding the roles of certain areas in production and comprehension processes.

6.3.2.1 The role of LIFG.

The notion that LIFG acts a mechanism to mediate linguistic contingencies is consistent with existing models. The mechanism used by LIFG to mediate these associations may be one that inhibits interference from related information in working memory, and selects the appropriate alternatives. This is consistent with the more general role of LIFG in inhibition/selection processes (Bedny, McGill, et al., 2008; Demb, et al., 1995; Gennari, et al., 2007; Gold & Buckner, 2002; Hoenig & Scheef, 2009; Rodd, et al., 2005; A. D. Wagner, et al., 2001). In the current research, the increased activation of LIFG for the high-competition cases presumably reflects the additional processing required to overrule strong semantic associations.

The current results also have implications for theories that assume task-general or task-specific LIFG processes. In particular, they show a common region of LIFG, pars opercularis, is sensitive to conflict in both production and comprehension tasks, as well as in the Stroop task localiser (Chapters 3 and 5). Therefore, the current results support the presence of a LIFG convergence zone that resolves conflicting responses across multiple tasks, as suggested by others in the literature (Duncan, 2010; Duncan & Owen, 2000; Gold, et al., 2005; January, et al., 2009; Novick, et al., 2009; Owen, et al., 2000; Rodd, Johnsrude, et al., 2010; Wright, et al., 2011; Ye & Zhou, 2009a, 2009b).

The current results also have implications for neurodevelopmental models of LIFG control processing. The data from Chapter 4 showed that the mechanisms that are involved in resolving competition within LIFG and the supporting networks do not develop until early adulthood. These findings provide support for the domain general theory that the underdevelopment of inhibitory control mechanisms in adolescents leads to poorer performance on wide range of tasks that involve selecting a response from competing alternatives (Bunge & Wright, 2007; Casey, et al., 2005; Durston, et al., 2006). The current results extend existing models to a linguistic domain and a more semantic level of processing, where the conflict derives from conflicting semantic and structural sentence cues. This data therefore adds to the existing literature showing that the prefrontal cortex plays a critical role in resolving competition between alternative responses across a wide range of tasks.

Therefore, the current results suggest that at least certain subsections of LIFG are involved in task-general conflict resolution processes. Yet, despite this, they also suggest some degree of task-specificity in LIFG responses. Therefore there may be a graded representation within LIFG, with different areas receiving task-specific input, which then converges upon a task-general convergence zone. This is consistent with theories that assign task-specific functions to different LIFG sub-regions that arise due to distinct cortico-cortical LIFG connections from the dorsal and ventral streams (Gough, et al., 2005; Xiang, et al., 2010). Therefore, the current results are compatible with a model where different LIFG regions receive task-specific inputs, with the information converging upon a central zone that is involved in task-general conflict resolution processes. However, further work is needed to determine the extent of task-general and task-specific LIFG responses, and to examine the structural and functional connectivity from dorsal and ventral pars-opercularis.

The effect of competition in each of the studies was localised within the pars opercularis of LIFG (BA44) rather than other LIFG subsections (pars triangularis or orbitalis). Suggestions have been made that pars opercularis might be specialised specifically for syntactic processes, whereas more anterior areas are involved in processing semantic level representations (Friederici, 2009; Hagoort, 2005; Indefrey, et al., 2001). The current results are not consistent with this interpretation. In Experiment 2, the competition was derived from conflicting semantic and syntactic information, however the manipulation in Experiment 5 was purely semantic. Other studies that have manipulated competition in sentences have also found pars opercularis activity, both for cases of semantic and syntactic difficulty (Fiebach, et al., 2004; Obleser & Kotz, 2010; Rodd, et al., 2011; Rodd, Longeb, et al., 2010; Tyler, et al., 2010). Therefore, whilst pars opercularis is clearly involved in sentence processing, it is not clear what factors determine its recruitment. However, what is clear from the current work is that the location of activation in each study is likely to be task-dependent. Further work is needed to determine the conditions under which pars opercularis is recruited.

The current LIFG data has been interpreted within a framework that assumes that LIFG acts as a tool for mediating the associations between cues by selecting/inhibiting information (Barde & Thompson-Schill, 2002; D'Esposito et al., 1999; Fiebach et al., 2006; Fuster, 2001; Miller & Cohen, 2001; Thompson-Schill, et al., 2005; Wagner et al., 2001). However, whilst the current data is certainly consistent with this role it is important to note that other theories of LIFG function in sentence processing have been proposed which could also explain the results. In particular, LIFG has been regarded as a "unification" mechanism which binds information into a coherent representation (Hagoort, 2005; Snijders et al., 2009). It is possible to incorporate the current findings within this model if one assumes that sentences that contain conflicting semantic/syntactic cues are more difficult to bind, and therefore the increased activation for high-competition conditions reflects the increased processing power needed to “unify” these sentences. The difference between the unification and the selection/inhibition model is that the unification model assumes that LIFG plays a necessary role in sentence level processing, whereas the selection/inhibition model suggests that LIFG is only necessary in difficult cases. Whilst the current data cannot distinguish between these perspectives several studies have shown that LIFG activity is absent for sentences which can be easily comprehended (Binder et al., 2000; Scott et al., 2000; Scott & Johnsrude, 2003) thus suggesting that LIFG activity may not always be essential for sentence processing.

6.3.2.2 The role of motor-related structures.

The current research also has implications regarding the role of motor-related structures in production and comprehension. Neurocognitive models of production (Hickok & Poeppel, 2000, 2004, 2007; Indefrey, 2011; Indefrey & Levelt, 2004) argue that the structures are involved in the planning and sequencing of motor output during production. The current finding of production-specific recruitment of motor-related areas is consistent with the results from other studies that have directly compared sentence production and comprehension (Menenti et al., 2011; Segaert et al., 2011). These results have typically been interpreted as reflecting articulatory processes, in line with the Hickok and Poeppel and Indefrey et al. models. However, whilst this is likely to be correct, results here suggest that these areas may also play a more active role in the linguistic aspects of production, and interact with frontal and semantic areas as part of a functional network. In particular, motor-related areas are modulated by conflicting semantic and syntactic cues (Chapter 3) and by conflicting semantic information (Chapter 5). Therefore, motor-planning areas are sensitive to linguistic properties of production. Indeed, others have implicated motor areas in sentence planning processes, such as selecting the appropriate sentence structure and the positional sequencing of words in a sentence (Acheson & MacDonald, 2009; Alario, et al., 2006; Ye, et al., 2011). This is in line with evidence of increasing activation of these areas for increasing syntactic complexity and linearization processes in production (Ye, et al., 2011), as well as the role of these areas in response selection and sequence learning in motor and non-motor tasks (Bahlmann, et al., 2009; Exner, et al., 2002; Forkstam, et al., 2006; Gerloff, et al., 1997; Hazeltine, et al., 1997; Simmonds, et al., 2008). Together, this data suggests an important role of motor-related areas in sentence production. Further work is needed to determine the precise role of different components of this motor network (e.g. SMA, premotor, basal ganglia).

Certain models have suggested that motor-related structure also play a critical role in comprehension processes. According to the simulation approach, anticipatory or predictive processes during comprehension involve simulations of production planning processes or covert imitation (D'Ausilio, et al., 2009; Liberman, et al., 1967), thus recruiting motor control systems (Pickering & Garrod, 2007). The current data provides no real support for this theory, as motor structures were found to be recruited in production alone. Studies that have found involvement of motor structures in comprehension have tended to involve tasks that require explicit phonemic judgements (D'Ausilio, et al., 2009; Pulvermuller, et al., 2006), and the results may therefore reflect the explicit nature of the task.

The indications herein are that motor structures do not play a necessary role in resolving semantic competition in sentence comprehension. Rather, the data presented would suggest that predictive processes in comprehension are handled by the fronto-temporal network.

6.3.2.3 The role of pMTG.

The role of pMTG in language processing is widely disputed. Certain models suggest that pMTG is involved in lexical-semantic retrieval (Friederici, 2002; Hagoort, 2005; Hickok & Poeppel, 2000, 2004, 2007; Indefrey & Levelt, 2004), whilst others suggest it is involved in pre-lexical semantic processes, for instance retrieving event-representations (Bedny, Caramazza, et al., 2008; Tranel, et al., 2003). Others still, have argued that the primary function of posterior temporal areas is in executive processes, such as semantic control (Jefferies & Lambon Ralph, 2006; Noppeney, et al., 2004). Overall, the results here suggest a similar engagement of pMTG across production and comprehension tasks. Specifically, pMTG showed similar modulation by competition in Chapters 3, a similar neurodevelopmental pattern in Chapter 4, and also a similar magnitude of activation in Chapter 5, when the tasks were directly compared. Little evidence was found that pMTG responds differently in production and comprehension tasks. Although Chapter 5 showed some evidence of differential pMTG involvement, this was limited to only one analysis using only a subset of the items. Whilst not conclusive, finding a pattern of common engagement of pMTG across tasks does not fully support models that assume pMTG is responsible for lexical retrieval or executive control, given that the demands on both processes are arguably greater in production compared to comprehension tasks. However, the results are more consistent with a pre-lexical role of pMTG, for instance in event-representation. This is plausible given that production and comprehension are known to engage a common semantic knowledge base. Nevertheless, this conclusion is tentative and further work is needed to more accurately determine the role of pMTG in language processing.

6.4 Future directions

The findings from this research suggest that production and comprehension differ in their engagement of the dorsal and ventral language pathways, and that these pathways project to distinct LIFG sub-regions yet converge upon a central zone. Future work is necessary to examine whether this model is accurate both in terms of anatomy and functional networks. This could be achieved by combining structural and functional connectivity techniques to examine the anatomical and effective connectivity between structures within the production and comprehension network. The results from these investigations will provide greater understanding with regard the neurocognitive basis of production and comprehension.

Investigations are also needed to further examine the nature of control processes, both within LIFG and in the wider cortex. For instance, it is unclear whether the LIFG conflict mechanisms found here respond selectively to linguistic conflict, or rather whether the same region is involved in domain-general conflict resolution processes. Evidence has shown that a region of pars opercularis responds selectively to conflict in the linguistic domain, thus arguing against domain-generality (Fedorenko, et al., 2011). Also, the current work found activation of the pars opercularis region of LIFG, whilst others have found that language more strongly recruits pars triangularis. It is clear that the activation of these structures is task dependent, however the factors that determine their recruitment have not been determined. Finally, the current results emphasise that LIFG does not operate in isolation to resolve conflict in language; rather it is part of a distributed functional network. The roles of areas beyond LIFG in control processing have often been over-looked. For example, the current results suggest that the SMA may be involved in task-specific control processes. It would be interesting to examine the extent to which SMA plays a necessary role in the positional coding of information in sentence production, using techniques such as TMS.

6.5 Conclusions

The results within this thesis suggest that production and comprehension share a common sensitivity to linguistic statistics, and engage common LIFG mechanisms for mediating the contingency between linguistic associations. Yet, they differ in how these associations are used. In particular, they differ in the networks that interact with LIFG, with production showing greater reliance on areas involved in planning and sequencing, and comprehension showing greater reliance on areas involved in selecting the appropriate sentence meaning. These network differences reflect underlying differences in production and comprehension tasks; production being more a task of retrieval and planning, whereas comprehension being more a task of determining the meaning of a message.

Appendices

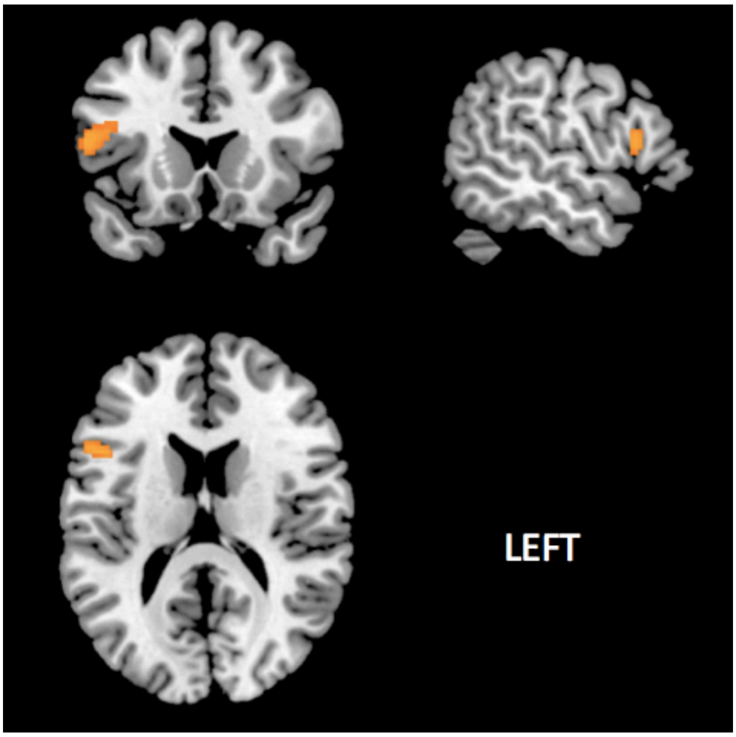
Appendix A The items used in the experiments in Chapters 2-4.

	Condition	Sentence	Comprehension question
1a	animate	The musician that the accident terrified was in the headlines	Did the accident terrify the musician?
1b	inanimate	The accident that the musician caused was in the headlines	Was the musician to blame for the accident?
2a	animate	The contestant that the prize delighted works in my office	Was the contestant unhappy with the prize?
2b	inanimate	The prize that the contestant misplaced was found in the office	Was the prize found in the park?
3a	animate	The soldier that the grenade injured was old	Was the soldier old?
3b	inanimate	The grenade that the soldier carried was old	Was it a new grenade?
4a	animate	The scientist that the book annoyed was renowned for his writings	Did the scientist like the book?
4b	inanimate	The book that the scientist reviewed was renowned for its arguments	Did the scientist review the book?
5a	animate	The director that the movie pleased had received a prize	Had the movie received a prize?
5b	inanimate	The movie that the director watched had received a prize	Did the director receive a prize?
6a	animate	The pupil that the school educated had performed well	Was the pupil successful?
6b	inanimate	The school that the pupil attended had performed well	Was it a good school?
7a	animate	The teacher that the play angered was interviewed on TV	Did the teacher dislike the play?
7b	inanimate	The play that the teacher watched was broadcast on TV	Was the play shown on television?
8a	animate	The employee that the incident bothered had misled the investigation	Did the employee help the investigation?
8b	inanimate	The incident that the employee reported had misled the investigation	Was the investigation helped by the employee's report?
9a	animate	The plumber that the wrench injured stayed in the bathroom	Did the plumber get hurt?
9b	inanimate	The wrench that the plumber dropped stayed in the bathroom	Is the wrench in the bathroom?
10a	animate	The banker that the loan worried was short of cash	Did the banker have a lot of money?
10b	inanimate	The loan that the banker refused was a lot of cash	Was the loan a large sum of money?
11a	animate	The lawyer that the trial confused was covered in the News	Did the lawyer understand the trial?
11b	inanimate	The trial that the lawyer reviewed was covered in the News	Did the lawyer review the trial?
12a	animate	The psychologist that the notes annoyed had gotten lost	Did the psychologist know his way around?
12b	inanimate	The notes that the psychologist printed had gotten lost	Did the psychologist get lost?
13a	animate	The child that the story scared was from a small village	Was the child frightened by the story?
13b	inanimate	The story that the child narrated was about a small village	Did the child tell the story?

14a	animate	The golfer that the game excited was ignored by the press	Did the golfer find the game boring?
14b	inanimate	The game that the golfer mastered was ignored by the press	Was the golfer good at the game?
15a	animate	The salesman that the product excited was mentioned in the newsletter	Did the salesman dislike the product?
15b	inanimate	The product that the salesman examined was mentioned in the newsletter	Did the salesman examine the product?
16a	animate	The fireman that the fire burned had caused trouble at the fire station	Did the fireman escape unscathed?
16b	inanimate	The fire that the fireman battled had caused serious damage to the house	Did the fire damage the house?
17a	animate	The fish that the lure attracted were close to the boat	Were the fish attracted to the lure?
17b	inanimate	The lure that the fish struck was close to the boat	Did the fish attack the lure?
18a	animate	The farmer that the tractor impressed had arrived at the store	Did the farmer dislike the tractor?
18b	inanimate	The tractor that the farmer purchased had arrived at the store	Did the farmer sell the tractor?
19a	animate	The gardener that the plants pleased lives near the shop	Did the gardener dislike the plants?
19b	inanimate	The plants that the gardener trimmed are near the shop	Are the plants far from the shop?
20a	animate	The pilot that the plane worried had worked at another company	Was the pilot concerned about the plane?
20b	inanimate	The plane that the pilot crashed had worked without maintenance	Was the plane well kept?
21a	animate	The executive that the wine relaxed was from France	Was the executive French?
21b	inanimate	The wine that the executive sipped was from France	Was the wine from France?
22a	animate	The actor that the play delighted had won an award	Did the actor win an award?
22b	inanimate	The play that the actor rehearsed had won an award	Did the actor practice the play?
23a	animate	The student that the instrument frustrated was worn out	Did the student enjoy playing the instrument?
23b	inanimate	The instrument that the student practiced was worn out	Was the instrument brand new?
24a	animate	The spy that the message alarmed was sent from Russia	Was the spy from the USA?
24b	inanimate	The message that the spy encoded was sent from Russia	Did the spy encode the message?
25a	animate	The journalist that the article bothered was part of a scandal	Was the article part of a scandal?
25b	inanimate	The article that the journalist composed was part of a scandal	Did the journalist write the article?
26a	animate	The minister that the meal satisfied was at a nice restaurant	Did the minister enjoy the meal?
26b	inanimate	The meal that the minister consumed was from a nice restaurant	Did the minister eat the meal?
27a	animate	The woman that the jewellery dazzled was very rich	Did the woman dislike the jewellery?
27b	inanimate	The jewellery that the woman coveted was very pricey	Was the jewellery cheap?
28a	animate	The dieter that the dessert tempted was really not very healthy	Was the dieter healthy?
28b	inanimate	The dessert that the dieter desired was really	Was the dessert

		not very healthy	unhealthy?
29a	animate	The pianist that the collision scared was on TV	Was the collision on TV?
29b	inanimate	The collision that the pianist caused was on TV	Was the pianist involved in the collision?
30a	animate	The contender that the award thrilled was anxious	Did the award excite the contender?
30b	inanimate	The award that the contender mislaid was precious	Did the contender lose the award?
31a	animate	The fighter that the missile injured came from America	Did the missile come from America?
31b	inanimate	The missile that the fighter employed came from America	Was the missile British?
32a	animate	The scholar that the article troubled was well-known	Was the article well known?
32b	inanimate	The article that the scholar scrutinised was well-known	Was the article well known?
33a	animate	The producer that the performance inspired was discussed in the news	Was the performance discussed in the news?
33b	inanimate	The performance that the producer directed was discussed in the news	Did the producer direct the performance?
34a	animate	The student that the college recruited achieved a good score	Did the student do badly?
34b	inanimate	The college that the student applied to achieved a good score	Did the college perform well?
35a	animate	The critic that the production pleased was in town for a day	Was the critic staying in town for a week?
35b	inanimate	The production that the critic attended was in town for a day	Did the critic miss the production?
36a	animate	The worker that the disturbance distressed was problematic	Was the worker upset by the disturbance?
36b	inanimate	The disturbance that the worker described was problematic	Was the disturbance a problem?
37a	animate	The judge that the case baffled was prominent	Was the judge little known?
37b	inanimate	The case that the judge oversaw was prominent	Was the case important?
38a	animate	The boy that the tale frightened did not like monsters	Was the boy scared by the story?
38b	inanimate	The tale that the boy listened to was about a monster	Did the boy listen to the story?
39a	animate	The mouse the cheese lured was in the kitchen	Was the mouse in the kitchen?
39b	inanimate	The cheese that the mouse discovered was in the kitchen	Was the cheese outside?
40a	animate	The businessman that the beer pleased was local	Was the businessman from far away?
40b	inanimate	The beer that businessman enjoyed was local	Was the beer imported?
41a	animate	The agent that the memo angered was on a special mission	Did the memo please the agent?
41b	inanimate	The memo that the agent composed was about a special mission	Did the agent write the memo?
42a	animate	The reporter that the story irritated covered the war	Did the story bother the reporter?
42b	inanimate	The story that the reporter drafted covered the war	Was the story about the war?

Appendix B   A whole-brain analysis of the contrast of high-competition vs. low competition items in the comprehension task in Experiment 2. The activation falls within LIFG, pars opercularis. Note that there was no significant activation in production at the whole-brain level.



Appendix C Comprehension networks for adult and adolescent groups for the contrast of Comprehension > baseline. The results from a whole-brain analysis (Cluster corrected, p < .05).

Brain area	*Z*	Voxel (MNI)		
		x	*y*	*z*
Adult Group				
Supramarginal Gyrus	5.74	-52	-44	2
Lateral Occipital Cortex	5.59	-40	-80	-22
Posterior Middle Temporal Gyrus	5.18	-66	-34	0
Inferior Frontal Gyrus, pars opercularis	4.90	-46	12	18
Precentral Gyrus	4.84	-44	-2	32
Anterior Middle Temporal Gyrus	4.46	-58	-4	-18
Inferior Frontal Gyrus, pars triangularis	4.05	-54	26	-4
Adolescent Group				
Lateral Occipital Cortex	5.95	-38	-76	-20
Precentral Gyrus	5.7	-48	4	46
Precentral Gyrus	5.59	-46	2	40
Lingual Gyrus	5.33	-10	-84	-2
Temporal Pole	5.33	-52	10	-20
Inferior Frontal Gyrus, pars opercularis	4.67	-50	14	22
Posterior Middle Temporal Gyrus	4.80	-62	-34	-4
Frontal Pole	3.8	-12	54	36
Supplementary Motor Cortex, Superior Frontal Gyrus	3.77	-6	6	56
Inferior Frontal Gyrus, pars triangularis	4.63	-52	34	-4
Superior Frontal Gyrus	3.58	-8	42	52
Superior Frontal Gyrus	3.33	-8	20	60
1.1.1.1 Adult > Adolescent				
Inferior Frontal Gyrus, pars opercularis	2.8	-60	16	16
1.1.1.2 Adolescent > Adult				
Temporal Pole	4.2	-50	4	-44
Superior Frontal Gyrus	3.4	-14	44	50

Appendix D Production networks for adult and adolescent groups for the contrast of Production > Control. The results from a whole-brain analysis (Cluster corrected, p < .05).

	Z	Voxel (MNI)		
Brain area		*x*	*y*	*z*
Adult Production > Control				
LIFG (BA44/BA45)	5.37	-58	20	10
LIFG (BA 47)	4.21	-54	34	-12
Precentral gyrus (BA 6)	2.65	-54	-4	48
Middle frontal gyrus (BA 6)	3.51	-46	6	52
Superior Frontal Gyrus (BA 9)	4.28	-10	56	38
Superior Frontal Gyrus (BA 6)	4.72	-12	16	60
pSTG (BA39)	3.47	-44	-62	16
MTG (BA 21)	4.46	-56	-30	-10
ATL (BA 21)	4.52	-50	12	-30
Inferior temporal gyrus (BA 20)	3.96	-42	-8	-42
Left Caudate	4.43	-16	12	12
Left ACC (BA 32)	4.49	-10	26	32
Thalamus	3.31	-2	-12	10
Adolescent Production > Control				
LSFG	4.7	-10.7	40.6	38.6
LIFG (pars triangularis, pars opercularis	4.58	-50.3	26	-2.32
Left Frontal Pole	4.30	-12	54	34
LSFG	3.90	-12	12	68
Left ACC	4.15	-8	34	24
Left Temporal Pole	2.54	-54	8	-24
Left Insular Cortex	2.52	-26	26	8
Adult > Adolescent	ns			
Adolescent > Adult	ns			

Appendix E Instructions for the similarity rating normings in Chapter 5.

Please note that this experiment targets native speakers of British or American English only. If you regard your English as another variant, please accept our apologies, and come back when we run another experiment.

In this experiment, we're interested in how people interpret pictures. We're going to show you some pictures, and ask you to judge how similar are the objects and people represented in the pictures.

First, you will see a picture depicting several characters and objects. Two things in the picture will be highlighted with a red square around them.

Your task will be to indicate in a scale from 1 to 7, how similar are the people and objects represented in the two squares. An answer of "7" indicates that the people or objects are highly similar and an answer of "1" indicates that the people or objects are not at all similar.

Similarity between two things can be evaluated according to several criteria. We would like you NOT to restrict your judgement to the visual similarity between the figures within the squares, for example, similarity of colour. When evaluating the similarity, think about the visual appearance AND any other characteristic property of the things or people to be compared, for example, the actions or events in which they take part and the particular way they do so.

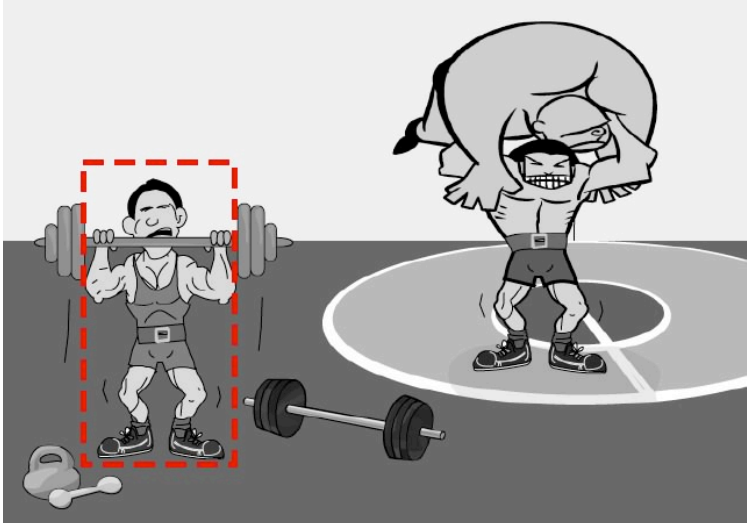
Appendix F Task instructions for Experiment 5b and 6 in Chapter 5

There will be two different language tasks:

a) Match the picture and sentence: In these trials you will be presented with a picture for 2 seconds. The picture will then be removed and then come back for 1 second. Then you will see a sentence that describes one character/object in the picture. On a few trials the sentence will not match anything in the picture. **Your task is to indicate when the sentence DOES NOT match the picture.** Note that this will be on very few of the trials but you will need to pay attention to the content of every trial in order to perform the task. Indicate your response by pressing **"1"** using your **left hand**.

b) Produce the sentence: These trials are similar to the others except for a few differences. In these cases you will have to **silently** produce the sentence that matches the picture rather than read the sentence. Like before, you will be presented with a picture for 2 seconds. The picture will then be removed and then come back for 1 second. When the picture is returned one of the characters or objects in the pictures will be highlighted by a red square. **Your task is to silently describe *Who/what is the highlighted character or object?*** You need to provide enough information such that the person/object can be uniquely identified. For instance, if there is a picture containing several of the same type of object you need to provide enough information so that a person could identify exactly which object you are referring to.

Here is an example of one of the pictures.



Who/what is the highlighted person or object?

s

You need to be a bit careful as to how you provide your answers. You need to use some feature of the picture to identify the relevant person/object, particularly if there is more than one character that can be described with the same word, e.g., "man" in the picture above. It is critical that you DO NOT use superficial features such as body positions, colours (like darker or lighter clothing) or left-right location that are specific to the picture. **Do not use** responses like *the man on the* *left of the picture* or *the small man* or *the man with the big muscles* or *the man with the full-body suit.*

Give your answers using the following:
- descriptive terms referring to the character (in this case, *a man*)
- the action that the character is performing or the action that's being performed on him (in this case, *lifting*)

So in this example, you should say ***The man that is lifting the weights*** .

You need to look at the picture carefully to see what action identifies the character being asked about. It is important to note that other participants won't see the same pictures you're seeing. Sometimes the darker or lighter colours will be changed, or the pictures will be left-right reversed, or the objects will be moved around. So there's no point in saying *the man on the right* or *the man next to the tree*, because these kinds of things might change. What will NOT change is what the character is doing (e.g. holding something, hitting something, pushing something, etc.) or what is being done TO that character (e.g. being pushed, being held, being hit, etc.).

So we would like you to answer the questions using short but informative identifying phrases in terms of who the characters are (man, woman, boy, girl, baby, boxer, etc.) and what ACTION they are performing, or is being performed onto them. It is not necessary to provide lots of details. Simply use the information that we have requested above.

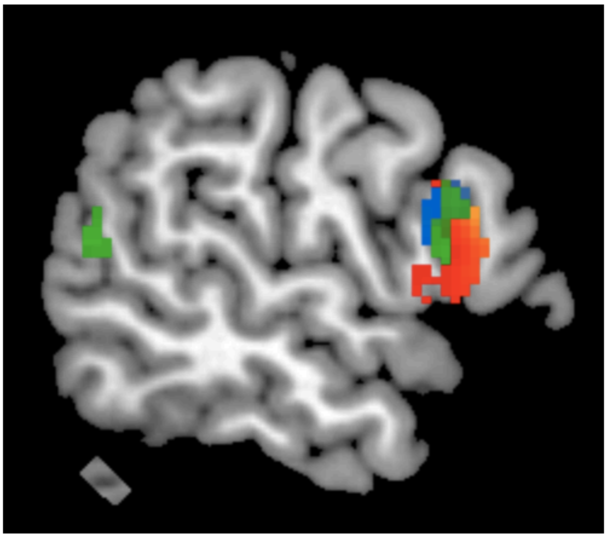
Appendix G The results from the whole-brain analysis directly contrasting all production and all comprehension items in Experiment 6 (cluster correct, p < .05).

			Voxel (MNI)		
Contrast	Brain Area	Z	*x*	*y*	*z*
Production > Comprehension	Left SMA	6.04	-2	-2	64
	Right Supramarginal Gyrus	5.37	58	-36	42
	Left Insular	5.32	-38	4	0
	Left Supramarginal Gyrus	4.72	-54	-44	46
	Left Inferior Temporal Gyrus	4.29	-56	-50	-22
	Left Cingulate Gyrus	4.18	-4	-20	38
	Right Precuneus	4.29	18	-64	52
	Left Frontal Pole	4.36	-8	58	12
	Right Precentral Gyrus	3.97	58	-4	36
	Left Superior Parietal Lobule	4.36	-12	-66	58
	Left Lateral Occipital Cortex	3.93	-36	-68	12
	Left Precentral Gyrus	3.29	-8	-32	64
	Right Frontal Pole	3.36	34	38	28
	Left Precentral Gyrus	5.03	-58	2	12
	Right Cerebellum	5.06	46	-56	-32
	Right Lateral Occipital Cortex	5.09	52	-66	-10
	Left Superior Frontal Gyrus	5.06	-14	6	60
	Left Inferior Frontal Gyrus, pars triangularis	2.71	-46	34	8
	Left Inferior Frontal Gyrus, pars opercularis	3.17	-52	14	2
	Left Cingulate Gyrus	4.39	-4	12	38
	Right Insular	4.96	36	8	2
	Right Putamen	4.64	20	10	2
	Left Putamen	4.39	-22	8	2
	Left Thalamus	3.06	-14	-14	2
	Left Middle Frontal Gyrus	4.79	-34	28	36
Comprehension > Production	Left Occipital Fusiform Gyrus	6.08	-28	-82	-18
	Left Lingual Gyrus	6.37	0	-82	-4
	Left Cerebellum	4.86	0	-62	-36
	Left Hippocampus	5.14	-22	-30	-6
	Right Hippocampus	4.7	22	-28	-6
	Left Temporal Occipital Fusiform Gyrus	2.85	-34	-52	-20
	Right Lingual Gyrus	5.84	12	-78	-12

Appendix H The results from a whole-brain analysis using similarity-rating score as a regressor in Experiment 6 (uncorrected, *p* < 001; cluster size > 100 voxels).

			Voxel (MNI)		
Contrast	Brain Area	Z	*x*	*y*	*z*
Production Similarity Correlation	Left putamen	3.03	-12	-8	-4
	SFG (SMA)	3.78	-4	12	58
	LIFG pars opercularis	2.94	-42	14	22
	Right cerebellum	4.2	42	-50	-26
	Right Middle Frontal Gyrus	2.8	28	0	50
	Left cerebellum	2.9	-42	-60	-24
	Left superior parietal lobule	2.63	-28	-54	38
Comprehension Similarity Correlation	Right cerebellum	3.94	4	-64	-20
	Right Hippocampus	3.16	26	-42	2
	Right lateral occipital cortex	3.2	58	-66	26
	LIFG (pars opercularis/triangularis)	2.87	-58	20	26
	Right temporal fusiform cortex	3.29	30	-12	-40

Appendix I **The location of production-comprehension overlap from the similarity-based competition analysis in Experiment 6 (production in blue and comprehension in red) corresponds to the site of the group-averaged Stroop localiser from Experiment 2 (green, cluster corrected, $p < .05$). The overlap occurs within central regions of pars opercularis.**



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