CHAPTER 20

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THE RELATIONSHIP BETWEEN SYNTACTIC PRODUCTION AND COMPREHENSION

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20.1 INTRODUCTION

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LANGUAGE production and language comprehension are traditionally treated as separate areas within psycholinguistics, reflecting obvious differences between the processes involved in speaking on the one hand and listening or reading on the other hand. In speaking, we start with a prelinguistic thought that we want to convey to a listener, a "conceptual message" in the terminology of Levelt's (1989; Levelt et al., 1999) theory of language production. If that message is about some "giving" event, for example, it will include concepts such as the person who is the "giver" (e.g., *Peter*), the person who is the "receiver" (e.g., *Mary*), the thing that is given (e.g., *book*), and the action of giving itself. We will retrieve words ("lemmas") in our mental lexicon that correspond to these concepts. Retrieving the lemmas will make their grammatical properties available, such as word category (noun, verb, and so on), gender (e.g., masculine, feminine, neuter in a language with a three-way gender distinction) or the arguments a verb requires. Upon selection of a lemma we can retrieve its speech sounds and insert them into the syllables that constitute a phonological word. For articulation, the phonological words will be translated into phonetic representations and finally motor representations that steer our speech musculature.

For the production of sentences retrieving the words alone is insufficient, because we have to choose between different grammatical options to express the giving event. Among other options we could say *Peter gives a book to Mary* (active, prepositional object), *Peter gives Mary a book* (active, double object), or the corresponding passive sentences *A book is being given to Mary (by Peter)/ Mary is being given a book (by Peter)*. Although all these sentences express the giving event, they reflect different perspectives on this event and hence are not all felicitous under all circumstances. The conceptual message, therefore, must take into account the so-called information structure, in particular what is "old" information (i.e., known to the

addressee), what is new information and who or what is the topic of the message (*Do I want to make a statement about Peter, about Mary, or about the book?*). If, for example, the book is old information and the topic of our statement, we will choose the definite determiner *the* instead of the indefinite determiner *a* and a passive sentence structure in which *the book* is the subject. In Levelt's (1989) theory, the information structure contained in the conceptual message is used to build the grammatical structure of a sentence. This structure does not yet contain the words *Peter, Mary, book*, or *give*, but instead empty slots, for example a subject slot that is marked "noun, definite" and a slot for a verb with a passive argument structure. It is only after the words have been retrieved from the lexicon that they are inserted in the appropriate slots. Levelt took the notion of an empty syntactic structure that is then filled with content words over from earlier work by Garrett (1975; 1980; 1988), whose theory is based on the study of speech errors. He proposed an empty grammatical structure ("functional level representation") to account for certain speech error phenomena, for example the fact that word exchange errors (e.g., saying *Mary gives Peter a book* when *Peter gives Mary a book* was intended) tend to preserve the word category (i.e., nouns are exchanged with nouns). Assuming a process of inserting words into the slots of an empty but grammatically specified structure explains why exchange errors can happen (the word *Mary* is erroneously inserted in the wrong slot) and why they tend to preserve the word category (the slot is marked as a "noun" slot and *Mary* is lexically specified as a noun).

Whereas speakers thus encode a single syntactic structure based on a complex conceptual message, the situation is quite different for listeners and readers. They are faced with an incoming stream of words from which they have to derive a conceptual message. In many cases a short-cut going directly from the word meanings to the meaning of the sentence may be sufficient (Ferreira et al., 2002). For example, in the sentence *The cat chases a mouse* there is little doubt who does what to whom. However already in the sentences describing the "giving" event mentioned here, listeners have to perform a syntactic analysis ("parsing") to understand who is the giver and who is the receiver. Sentence comprehension theories agree that syntactic parsing is incremental (parsing begins with the first word and the syntactic structure grows word by word) and that parsing uses the lexically specified information of the incoming words. Theories differ with respect to the point in time at which different kinds of lexical information are used. Some assume that in a first step only syntactic information such as word category is taken into account (Bornkessel & Schlesewsky, 2006; Friederici, 2002; Frazier & Fodor, 1978). Others assume that non-syntactic lexical information, such as semantic information (e.g., animacy), general world knowledge, or even statistical knowledge about how often a particular verb occurs with a particular argument structure, immediately influences the build-up of the syntactic structure (Altmann & Steedman, 1988; MacDonald et al., 1994; Trueswell et al., 1994).

Crucially, due to the incrementality of parsing there is, most pronounced at the beginning of sentences, a great deal of uncertainty about the syntactic structure of the incoming sentence ("syntactic ambiguity"). For example, a sentence beginning with *Mary . . .* might evolve to an active sentence (*Mary gives a book to Peter*) or a passive sentence (*Mary is being given a book by Peter*). At points of ambiguity, parsers may wait for more information (i.e., the next words), compute several possible structures, or commit to one of several possible structures. The evidence provided by so-called "garden-path" sentences shows that at least to some degree parsers commit to one structure that may turn out to be wrong at a later point in the sentence (point of disambiguation). When encountering the morpho-syntactically ambiguous

word *floated* in the sentence *The boat floated down the river sank* (Sturt & Crocker, 1996), for example, the parser tends to prefer a past participle reading and build a corresponding structure with *floated* as the head of the verb phrase of a simple main clause. The alternative reading as a passive participle and head of the verb phrase in a reduced relative clause is only considered when *sank* is encountered and cannot be accommodated in the originally preferred syntactic structure.

In sum, listeners and readers incrementally build up a syntactic structure based on the syntactic (but at some point, influenced by non-syntactic) properties of the incoming words. Due to lexical ambiguities, intermediate tentative syntactic structures may have to be revised. In parallel, they build up a semantic structure based on word meanings (Kuperberg et al., 2007) which often may be sufficient to understand the sentence (Ferreira et al., 2002).

Hence quite different processes are involved in building up the syntactic structure of a sentence in language production and comprehension and some of their properties suggest that not only the processes but also their output representations are modality-specific. First of all, there is the fundamental difference that in comprehension a complete syntactic representation is not always necessary for understanding, whereas the "production system must get the details of form 'right' in every instance, whether those details are germaine to sentence meaning or not" (Garrett, 1980, p. 216). Note, furthermore, that because syntactic parsing in comprehension is driven by the incoming words, there is no place for an abstract or empty syntactic representation that is assumed for production in the models of Levelt (1989) and Garrett (1988). In consequence, the production model of Levelt (1989) assumes a separate comprehension pathway. It is this pathway that speakers use to monitor their own speech. Both their inner speech (a phonetic representation in Levelt, 1989, a phonological representation in Levelt et al., 1999) and their overt speech are fed into the comprehension system where they are processed up to the conceptual level just like external speech ("perceptual loop"). As the self-monitoring loop has no access to processing stages before phonological encoding, this architecture requires a comprehension-specific syntactic representation.

Although there are thus very good reasons to assume modality-specific syntactic representations, it is nonetheless conceivable that there is only one representation of the syntactic structure of a sentence, which, depending on whether we speak or listen (read), is the output of syntactic encoding or parsing processes. If that was the case, we would expect activation of a syntactic structure in one modality to have an immediate impact on the processing of that structure in the other modality. There is indeed experimental evidence for such cross-modal influences. Bock (1986) introduced a syntactic priming paradigm in which participants were asked to describe pictures. Bock showed that the syntactic structure (e.g., active or passive) that was chosen by the participants was influenced by the structure of their preceding utterance (which was manipulated by the experimenter). Crucially, in later studies, Bock and collaborators showed that listening to a preceding sentence with a particular structure also made this structure more likely to be used in a subsequent sentence production (e.g., Bock et al., 2007). Similar effects are also found as one kind of "alignment" in natural dialogue. Branigan et al., (2000) observed that interlocutors tend to use the same syntactic structures (see also Garrod, Tosi, & Pickering, this volume). Such cross-modal syntactic influences are easily accounted for under the assumption that syntactic representations are shared between production and comprehension. Going a step further, Pickering and Garrod (2007) propose that the two modalities do not only share the same representations but are also functionally

interleaved. Starting from the observation that listeners can and do predict grammatical properties of upcoming words (e.g., their grammatical gender; van Berkum et al., 2005), they suggest that during language comprehension simultaneous language production may act as a forward model predicting the upcoming input.

A recent experiment by Kempen et al. (2012) provided compelling evidence for production-based predictions influencing syntactic parsing in comprehension. Kempen et al. (2012) used a simultaneous reading and speaking paradigm to study how syntactic encoding and decoding interact during overlapping time intervals. In a "paraphrasing" task, they presented participants with sequential fragments of sentences including direct speech ending with a correct or incorrect reflexive pronoun (*The lottery winner said: "I have decided to buy a red car for myself/*himself"*). The participants were asked to change the sentences to indirect speech (*The lottery winner said that he had decided to buy a red car for himself*). In a "proofreading" task, they presented participants with indirect speech sentences ending with a correct or incorrect reflexive pronoun (*The lottery winner said that he had decided to buy a red car for *myself/himself*). The participants were asked to read out the sentences and to correct them when necessary, so that they produced the same responses as in the paraphrasing task (i.e., *The lottery winner said that he had decided to buy a red car for himself*). In both tasks, participants were also asked to judge the correctness of the input. Kempen et al. (2012) found that, not surprisingly, incorrect input resulted in prolonged voice onset times for the reflexive pronoun in the proofreading task. In the paraphrasing task, however, incorrect input facilitated the responses, presumably because the reflexive pronoun that was incorrect in direct speech was the correct pronoun in the paraphrasing indirect speech sentence. In addition, the participants' ability to judge the correctness of the input sentences was greatly reduced (i.e., they did not notice that the reflexive pronoun of the input was incorrect). These results suggest that the encoded syntax of the produced sentences overwrote the decoded syntactic representation of the input sentences and predicted the incorrect rather than the correct pronoun. Kempen et al. (2012) conclude that language production and comprehension cannot operate on different syntactic structures during overlapping time intervals and take this result as indicating that syntactic processing is shared by production and comprehension.

To sum up, considering the behavioral evidence there are very good arguments for as well as against shared syntactic representations for production and comprehension. In the remainder of this chapter, I will review the evidence from neurocognitive studies. To answer the question of whether syntactic parsing and encoding use the same neural resources I will first present the current evidence on the brain structures subserving sentence comprehension summarizing the results of a recent large-scale meta-analysis of language comprehension studies (Hagoort & Indefrey, 2014, henceforth known as H&I). For comparison, I will then conduct a meta-analysis of the much smaller number of studies investigating sentence production. To the extent that syntactic encoding and parsing rely on the same resources the observed brain networks should overlap. Finally, I will present the results of studies seeking to demonstrate direct interactions between syntactic parsing and encoding by testing for cross-modal functional magnetic resonance imaging (fMRI) syntactic adaptation effects. If the neural response to the production of a particular grammatical structure is affected by the preceding comprehension of the same structure (and vice versa), then it can be assumed that the neural populations representing that structure are shared between modalities.

20.2 Brain areas involved in sentence comprehension

In a recent meta-analysis of 151 hemodynamic studies on sentence processing, H&I investigated whether the neural activations related to syntactic aspects of sentence comprehension can be distinguished from neural activations related to semantic aspects of sentence comprehension. The activation foci and the spatial extent of 198 contrasts were coded in an anatomical reference system of 112 regions on the basis of the stereotaxic atlas of Talairach and Tournoux (1988) (for details, see Indefrey & Levelt 2000; 2004). For any particular region the reliability of its activation was assessed using the following estimate: The average number of activated regions reported per experiment divided by the number of regions (112) corresponds to the probability for any particular region to be reported in an experiment, if reports were randomly distributed over regions. Assuming this probability, the chance level for a region to be reported as activated in a certain number of experiments is given by a binomial distribution. The possibility that the agreement of reports about a certain region was coincidental was rejected if the chance level was below 5% (uncorrected for the number of regions). Regions with a chance level below 0.0004 survived a Bonferroni correction for 112 regions and were reported as 0.05 (corrected). This estimate considers that not all studies covered the whole brain owing to the heterogeneity of techniques and analysis procedures (for example, analyzing only regions of interest). The procedure also controls for the fact that the average number of activated regions per study differs between contrasts. In contrasts comparing sentences to low-level control conditions, the number of activated regions is typically higher than in contrasts comparing syntactically demanding to less demanding sentences; thus, the chances of coincidental agreements between studies are also higher.

About one-third of the studies compared sentences to non-sentential stimuli, ranging from word lists to cross-hair fixation or rest conditions (see Table 20.1 for a list of all contrasts and Table 20.2 for the studies reporting hemodynamic activations for the respective contrasts). The resulting brain activations could be expected to include whichever brain regions are involved in sentence-level syntactic and semantic processing. However, in these types of contrasts neural activation due to many other processes may also show up. About two-thirds of the studies compared syntactically or semantically demanding sentences to less demanding sentences. The latter studies controlled much more tightly for lower-level (e.g., lexical) differences between stimuli so that the resulting activations could be considered relatively specific to syntactic or semantic unification. Note, however, that these studies not only may have missed neural correlates of sentence-level processing that were shared between demanding and less demanding sentences, but also may have induced processes related to higher general cognitive demands, such as attention or error-related processes.

Frequent manipulations for increasing syntactic demands are the use of sentences containing syntactic violations or word-class ambiguities (e.g., *watch* as noun or verb) and the use of structurally more complex sentences, such as those containing object relative clauses (*The reporter who the senator attacked admitted the error*) compared to subject relative clauses (*The reporter who attacked the senator admitted the error*; Just et al., 1996). Manipulations for increasing semantic demands are semantic violations (e.g., *Dutch trains are sour . . .*; Hagoort et al., 2004) and lexical-semantic ambiguities (e.g.,

Table 20.1 Types of contrasts used in hemodynamic studies on sentence comprehension and production. For each type of contrast, the last four columns give the number of studies included in the meta-analysis and the distribution of presentation modalities (see Table 20.2 for the complete list of studies)

Contrast no.	Condition of interest	Control condition	No. Studies	Reading	Listening	Both
Sentence comprehension						
1	Sentence comprehension	Below sentence level	53	21	30	2
2	Sentence comprehension	Words	15	6	8	1
3	Sentence reading	Below sentence level	22	22	0	0
4	Sentence listening	Below sentence level	31	0	31	0
5	Passive sentence reading	Below sentence level	13	13	0	0
6	Passive sentence listening	Below sentence level	20	0	20	0
7	Syntax demanding	Syntax less demanding	57	39	15	3
8	Syntax demanding	Semantics demanding	6	3	3	0
9	Syntactic violation	No violation	18	13	3	2
10	Syntactic ambiguity	No ambiguity	4	3	1	0
11	Syntax complex	Syntax less complex	33	22	9	2
12	Complex relative clauses	Simpler relative clauses	20	14	5	1
13	Non-canonical word order	Canonical word order	7	4	2	1
14	Syntactic repetition	No repetition	5	2	2	1
15	Semantics demanding	Semantics less demanding	51	36	14	1
16	Semantics demanding	Syntax demanding	10	5	5	0
17	Semantic violation	No violation	19	12	6	1
18	Lexical constraint violation	No violation	14	8	6	0
19	World knowledge violation	No violation	7	4	2	1

(*continued*)

Table 20.1 Continued

Contrast no.	Condition of interest	Control condition	No. Studies	Reading	Listening	Both
20	Semantic ambiguity	No ambiguity	10	4	6	0
21	Semantics complex	Less complex	30	28	2	0
22	Metaphoric sentence	Literal sentence	17	17	0	0
23	Familiar metaphor	Literal sentence	7	7	0	0
24	Novel metaphor	Literal sentence	11	11	0	0
25	Additional semantic operations	No additional semantic operations	3	3	0	0
26	Speaker meaning	Literal sentence	11	9	2	0
27	Irony	Literal sentence	8	7	1	0
28	Indirect utterance	Literal sentence	3	2	1	0
Sentence production						
29	Sentence production	Word production	7			
30	More/complex syntactic production	Less/simpler syntactic production	7			
31	Syntactic repetition in production	No repetition	5			

Table 20.2 Studies included in the meta-analysis. The numbers in column 4 refer to the contrast numbers in column 1 of Table 20.1. For example, the study of Ahrens et al. (2007) contributed hemodynamic activation data for the contrasts 15 (semantics demanding–semantics less demanding), 21 (semantics complex–semantics less complex), 22 (metaphoric sentence–literal sentence), 23 (familiar metaphor–literal sentence), and 24 (novel metaphor–literal sentence)

Study	Year	Journal	Contrasts
Ahrens et al.	2007	*Brain Lang*	15, 21, 22, 23, 24
Argyropoulos et al.	2013	*NeuroImage*	30
Bahlmann et al.	2004	*Hum Brain Mapp*	1, 3, 5, 7, 11, 13
Bambini et al.	2011	*Brain Res Bull*	15, 21, 22
Bašnáková et al.	2014	*Cereb Cortex*	15, 21, 26, 28
Bavelier et al.	1997	*J Cogn Neurosci*	1, 3, 5
Bavelier et al.	1998	*Neuroreport*	1, 3
Bekinschtein et al.	2011	*J Neurosci*	15, 20
Ben-Shachar et al.	2003	*Psychol Sci*	7, 11
Ben-Shachar et al.	2004	*NeuroImage*	7(2×), 11(2×), 13
Bornkessel & Schlesewsky	2005	*NeuroImage*	7, 11, 13
Borofsky et al.	2010	*J Neuroling*	8, 16
Bottini et al.	1994	*Brain*	1, 2, 3, 15, 21, 22, 24
Braze et al.	2011	*Cortex*	7, 9, 15, 17, 19
Capek et al.	2004	*Cogn Brain Res*	1, 3
Caplan et al.	1998	*J Cogn Neurosci*	7, 11, 12
Caplan et al.	1999	*NeuroImage*	7, 11, 12
Caplan et al.	2000	*Hum Brain Mapp*	7, 11, 12
Cardillo et al.	2004	*J Cogn Neurosci*	15, 17, 18
Chee et al.	1999	*Neuron*	1, 3
Chen et al.	2006	*Cortex*	7, 11, 12
Chen et al.	2008	*Brain Lang*	15, 21, 22, 23
Chou et al.	2012	*Neuropsychologia*	7, 9
Christensen & Wallentin	2011	*NeuroImage*	7, 9, 11, 13
Collina et al.	2014	*PLoS ONE*	29
Constable et al.	2004	*NeuroImage*	1, 3, 4, 11, 12
Cooke et al.	2001	*Hum Brain Mapp*	7, 11, 12
Cooke et al.	2006	*Brain Lang*	7, 9
Dapretto & Bookheimer	1999	*Neuron*	7, 8, 16
Davis et al.	2007	*Proc Natl Acad Sci USA*	1, 4, 6
Den Ouden et al.	2008	*Brain Lang*	30

(*continued*)

Table 20.2 Continued

Study	Year	Journal	Contrasts
Desai et al.	2011	*J Cogn Neurosci*	15, 21, 22
Devauchelle et al.	2009	*J Cogn Neurosci*	14
Diaz et al.	2011	*Neuropsychologia*	15, 21, 22, 24
Diaz & Hogstrom	2011	*J Cogn Neurosci*	15, 21, 22, 24
Dien & O'Hare	2008	*Brain Research*	16
Embick et al.	2000	*Proc Natl Acad Sci USA*	7, 9
Eviatar & Just	2006	*Neuropsychologia*	21, 26, 27
Fiebach et al.	2004	*J Cogn Neurosci*	7, 10, 11
Fiebach et al.	2005	*Hum Brain Mapp*	7, 11
Friederici et al.	2000	*Brain Lang*	1, 4, 6
Friederici et al.	2003	*Cerebral cortex*	7, 9, 15, 16, 17, 18
Friederici et al.	2009	*Neuroreport*	7, 11
Gennari et al.	2007	*NeuroImage*	15, 20
Giraud et al.	2000	*Brain*	1, 4, 6
Golestani et al.	2006	*Neuropsychologia*	29
Grande et al.	2012	*NeuroImage*	30
Grewe et al.	2007	*NeuroImage*	7, 11, 13
Groen et al.	2010	*Cereb Cortex*	15, 17, 18, 19
Grossman et al.	2002	*NeuroImage*	7, 11, 12
Hagoort et al.	2004	*Science*	15, 17, 18, 19
Haller et al.	2005	*Neuropsychologia*	29
Hashimoto & Sakai	2002	*Neuron*	1, 2, 3
Hoen et al.	2006	*Cortex*	7, 9
Hoenig & Scheef	2005	*Hippocampus*	15, 20
Homae et al.	2002	*NeuroImage*	1, 4
Humphreys & Gennari	2014	*NeuroImage*	30
Humphries et al.	2001	*Neuroreport*	1, 4, 6
Humphries et al.	2005	*Hum Brain Mapp*	1, 2, 4, 6
Humphries et al.	2006	*J Cogn Neurosci*	1, 2, 4
Husband et al.	2011	*J Cogn Neurosci*	7, 9, 15, 16, 17, 21, 25
Indefrey et al. a	2001	*Proc Natl Acad Sci USA*	29, 30
Indefrey et al. b	2001	*NeuroImage*	1, 3
Indefrey et al.	2004	*Brain Lang*	1, 2, 4, 29, 30
Inui et al.	1998	*Neuroreport*	7, 11, 12
Jobard et al.	2007	*NeuroImage*	1, 2
Just et al.	1996	*Science*	7, 11, 12

Table 20.2 Continued

Study	Year	Journal	Contrasts
Kambara et al.	2013	*Language Sciences*	7, 9
Kang et al.	1999	*NeuroImage*	1, 3, 5
Kiehl et al.	2002	*NeuroImage*	15, 17, 18
Kinno et al.	2008	*Hum Brain Mapp*	7, 11, 13
Kircher et al.	2005	*British J Psychiatry*	30
Kircher et al.	2007	*NeuroImage*	15, 21, 22, 24
Kircher et al.	2009	*Neuropsychologia*	1, 4, 6
Koeda et al.	2006	*Biol Psychiatry*	1, 4, 6
Kuperberg et al.	2000	*J Cogn Neurosci*	1, 2, 4, 7, 9, 15, 17, 18, 19
Kuperberg et al.	2003	*J Cogn Neurosci*	7, 9
Kuperberg et al.	2006	*Neuromage*	15, 21, 25
Kuperberg et al.	2008	*Biol Psychiatry*	15, 17, 18
Kuperberg et al.	2008	*NeuroImage*	7, 9, 15, 17, 19
Love et al.	2006	*Cortex*	7, 11, 12
Maguire & Frith	2004	*NeuroImage*	1, 2, 4, 6
Mashal et al.	2009	*Brain Cogn*	15, 21, 22, 24
Mason & Just	2007	*Brain Res*	15, 20
Mazoyer et al.	1993	*J Cogn Neurosci*	1, 4, 6
Meltzer et al.	2010	*Cereb Cortex*	7, 11, 12
Menenti et al.	2011	*Psychol Sci*	14, 31
Menenti et al.	2012	*Brain Lang*	31
Meyer et al.	2000	*Cogn Brain Res*	7
Meyer et al.	2002	*Hum Brain Mapp*	1, 4
Meyer et al.	2003	*J Neurolinguistics*	1, 4
Michael et al.	2001	*Hum Brain Mapp*	7, 11 (2×), 12 (2×)
Moore–Parks et al.	2010	*Brain Lang*	15, 17, 18
Moro et al.	2001	*NeuroImage*	7, 9
Muller et al.	1997	*Neuroreport*	1, 4, 6
Naito et al.	2000	*Hear Res*	1, 4, 6
Nakai et al.	1999	*Neurosc Lett*	1, 4, 6
Nathaniel–James et al.	1997	*Neuropsychologia*	1, 3, 5
Neville et al.	1998	*Proc Natl Acad Sci USA*	1, 3, 5
Newman et al.	2001	*J Psycholinguist Res*	16
Newman et al.	2003	*Brain Res Cogn Brain Res*	7, 11, 12
Newman et al.	2010	*Brain Lang*	7, 11, 12
Ni et al.	2000	*J Cogn Neurosci*	1, 4, 15, 16, 17, 18

(*continued*)

Table 20.2 Continued

Study	Year	Journal	Contrasts
Nichelli et al.	1995	*Brain Lang*	7, 9
Nieuwland et al.	2012	*Hum Brain Mapp*	7, 9, 15, 16, 17, 18
Noguchi et al.	2002	*Hum Brain Mapp*	7, 8
Noppeney & Price	2004	*J Cogn Neurosci*	1, 3, 5, 14
Ozawa et al.	2000	*Neuroreport*	1, 4, 6
Pallier et al.	2011	*Proc Natl Acad Sci USA*	1 (2x), 2, 3 (2x), 5 (2x)
Peck et al.	2004	*NeuroImage*	29
Peelle et al.	2004	*Brain Lang*	7, 11, 12
Pylkkänen et al.	2014	*Cognition*	29
Raettig et al.	2010	*Cortex*	7, 9
Rapp et al.	2004	*Brain Res Cogn Brain Res*	1, 3, 15, 21, 22, 24
Rapp et al.	2010	*Brain Lang*	21, 26, 27
Rapp et al.	2011	*Brain Lang*	15, 21, 25
Robertson et al.	2000	*Psychol Sci*	1, 3
Rodd et al.	2005	*Cereb Cortex*	1(2×), 4(2×), 6, 15(2×), 20(2×)
Rodd et al.	2010	*Neuropsychologia*	1, 4, 7, 10, 15, 16, 20
Rodd et al.	2012	*Cereb Cortex*	15, 20
Röder et al.	2002	*NeuroImage*	7, 11, 13
Rogalsky & Hickok	2009	*Cereb Cortex*	1, 2, 4, 6
Ruschemeyer et al.	2006	*NeuroImage*	7, 8, 16
Salvi et al.	2002	*Hear Res*	1, 4, 6
Sanjuan	2010	*Eur Radiol*	1, 4
Schlosser et al.	1998	*Hum Brain Mapp*	1, 4, 6
Schmidt & Seger	2009	*Brain Cogn*	15, 21, 22
Schoot et al.	2014	*Frontiers Psychology*	31
Scott et al.	2000	*Brain*	1, 4, 6
Segaert et al.	2012	*Cereb Cortex*	14, 31
Segaert et al.	2013	*Brain Lang*	31
Shibata et al.	2007	*Brain Res*	15, 21, 22, 24
Shibata et al.	2010	*Brain Res.*	21, 26, 27
Shibata et al.	2011	*Neuropsychologia*	15, 21, 26, 28
Shibata et al.	2012	*Brain Lang*	15, 21, 22, 24
Snijders et al.	2009	*Cereb Cortex*	1–3, 5, 7, 10
Spotorno et al.	2012	*NeuroImage*	15, 21, 26, 27
Stowe et al.	1994	*J Psychol Res*	1, 3, 5, 7
Stowe et al.	1998	*Cereb Cortex*	11

Table 20.2 Continued

Study	Year	Journal	Contrasts
Stowe et al.	2004	*Brain Lang*	7, 10
Stringaris et al.	2006	*NeuroImage*	15, 21, 22, 23
Stringaris et al.	2007	*Brain Lang*	15, 17, 18, 21, 22, 23
Stromswold et al.	1996	*Brain Lang*	7, 11, 12
Suh et al.	2007	*Brain Res*	7, 11, 12
Suzuki & Sakai	2003	*Brain Res*	7, 8
Uchiyama et al.	2006	*Brain Res*	21, 26, 27
Uchiyama et al.	2008	*Neurosci Res*	1, 2, 4, 6, 7, 9
Uchiyama et al.	2012	*Cortex*	15, 21, 22, 23, 26, 27
van Ackeren et al.	2012	*J Cogn Neurosci*	15, 21, 26, 28
Vandenberghe et al.	2002	*J Cogn Neurosci*	1, 2, 3, 5, 15, 17, 18
Wakusawa et al.	2007	*NeuroImage*	21, 26, 27
Wang et al.	2006	*Soc Cogn Affect Neurosci*	21, 26, 27
Wang et al.	2008	*Neuropsychologia*	7, 8
Wartenburger et al.	2003	*J Neuroling*	7, 9
Waters et al.	2003	*NeuroImage*	7(2×), 11(2×), 12(2×)
Weber & Indefrey	2009	*NeuroImage*	1, 3, 5, 14
Wong et al.	1999	*Hear Res*	1, 2, 4, 6
Xu et al.	2005	*NeuroImage*	1, 2, 3, 5
Yang et al.	2009	*Brain Lang*	23, 24
Yang et al.	2010	*Neuropsychologia*	15, 21, 22, 23, 24
Ye & Zhou	2009	*NeuroImage*	15, 17, 19
Zempleni et al.	2007	*NeuroImage*	15, 20
Zhu et al.	2009	*NeuroImage*	15, 17, 19
Zhu et al.	2012	*NeuroImage*	15, 17, 18
Zhu et al.	2013	*NeuroImage*	15, 17, 18

bank) that did not affect the syntactic structure in comparing with the correct control sentences. Other instances of higher semantic demands were experimental manipulations that complicated the listener's ability to assign an overall meaning without inducing a syntactic difference. These instances included sentences with a metaphoric meaning (e.g., *A sailboat is a floating leaf*; Diaz & Hogstrom, 2011); sentences inducing semantic operations such as coercion (*The novelist began/wrote the book*; Husband et al. 2011), metonymy (*Africa is hungry/arid*; Rapp et al., 2011) and sentences making connections to the previous discourse context (*The boys were having an argument. They became more and more angry/They began hitting each other. The next day they had bruises*; Kuperberg et al.,

2006). These instances also included sentences requiring listeners to assess speakers' intentions (irony, indirect replies, or requests, e.g., *Did you like my presentation?/How hard is it to give a good presentation? It is hard to give a good presentation*; Bašnáková et al., 2014).

20.2.1 Sentences compared with control conditions below the sentence level

H&I found that, compared with control conditions below sentence level, the comprehension of sentences reliably activates the temporal lobes and the posterior inferior frontal gyrus (IFG) bilaterally, albeit with a clear left hemisphere dominance. There were some differences among the regions involved in processing written and spoken sentences. Some right hemisphere temporal regions were not reliably found in reading, and posterior frontal regions were less frequently found in listening. Interestingly, when the participants just listened or read for comprehension without performing any additional tasks, or when sentence processing was compared with the processing of word lists, the most dorsal part of the IFG (pars opercularis, Brodmann area, BA 44) was not found to be reliably activated (see Fig. 20.1A).

(A) Comprehension of sentences compared to words (15 studies)
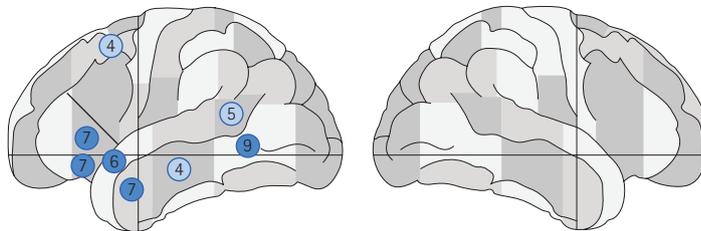
(B) Comprehension of syntactically complex compared to simpler sentences (33 studies)
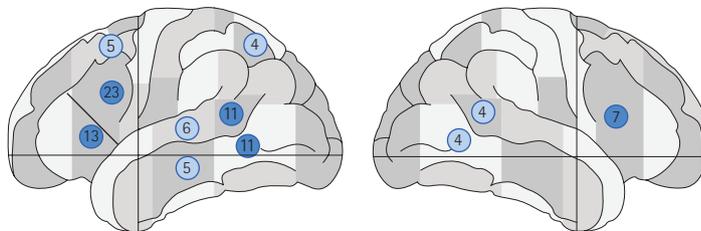
● Reliably activated $p < 0.05$, corr.   ○ Reliably activated $p < 0.05$, uncorr.

FIG. 20.1 Reliable neural activation increases for (A) sentence comprehension compared to word comprehension and (B) syntactically complex compared to simpler sentences.

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20.2.2 Sentences with higher demands on syntactic or semantic processing

In studies comparing syntactically or semantically more demanding sentences with simpler sentences confounding non-syntactic or non-semantic differences between conditions are typically much better controlled. A contribution of such differences to the resulting brain activations can hence be largely excluded. H&I found that higher syntactic processing demands most reliably activate the more dorsal parts of posterior left inferior frontal gyrus (LIFG) (BA 44/45), the right posterior IFG and the left posterior superior and middle temporal gyri (STG, MTG). In addition, the left precuneus, the left inferior parietal lobule, and the right posterior MTG all activated reliably. Higher semantic processing demands most reliably activate all parts of posterior LIFG (but BA 45/47 are reported twice as often as is BA 44), the right posterior IFG, and the left middle and posterior MTG. In addition, the data indicate a reliable activation of the medial prefrontal cortex that is not seen for higher syntactic processing demands and demonstrate activations of the left anterior insula, angular gyrus, and the posterior inferior temporal gyrus (ITG).

The results of 16 studies directly comparing sentences with high syntactic and high semantic processing demands confirmed that the medial prefrontal cortex is important for processing sentences with high semantic processing demands. Direct comparisons also demonstrated a syntactic/semantic gradient in LIFG: a reliably stronger activation of BA 44 is seen for syntactically, compared with semantically, demanding sentences; a reliably stronger activation of BA 45/47 is observed for semantically, compared with syntactically, demanding sentences.

H&I furthermore analyzed in which way different kinds of increased syntactic and semantic demands contributed to the overall result. Studies comparing sentences with syntactic violations (mostly agreement violations and phrase-structure/word-category violations) with correct sentences most reliably found BA 44/45 activation. Studies comparing sentences containing semantic violations with correct sentences most reliably found activation of all parts of the left posterior IFG, but activation of BA 45/47 was reported more often than was BA 44. Both semantic and syntactic violations generally activate the posterior temporal cortex less frequently than other kinds of demanding sentences do. Compared to unambiguous sentences, sentences containing local syntactic ambiguities (mostly word-class ambiguities, e.g., *He noticed that landing planes frightens some new pilots*) or semantic ambiguities (*The reporter commented that modern compounds react unpredictably*; examples from Rodd et al. 2010) activate the posterior IFG bilaterally and the left posterior MTG. For syntactic ambiguities, activation in the left posterior IFG was confined to BA 44. Semantic ambiguities activated the left posterior inferior medial temporal lobe.

Most studies manipulating syntactic complexity compared sentences containing complex relative clauses with simpler relative clauses. The main manipulation in the remaining studies was the use of non-canonical word order. Studies inducing semantic complexity typically used a condition in which understanding the meaning of the sentence required some additional effort compared with that required for syntactically identical control sentences. In most of the studies this goal was achieved by comparing sentences containing a metaphoric meaning with sentences containing a literal meaning. Another subset of

studies used ironic/sarcastic sentences or indirect replies/requests. Both syntactic and semantic complexity reliably induced stronger activation of the posterior IFG bilaterally and the left mid and posterior MTG (see Fig. 20.1B). Left posterior IFG activation again showed a gradient with activation of BA 44 for syntactic but not semantic complexity, and activation of BA 47 for semantic but not syntactic complexity. The posterior STG seemed to show additional activation only for syntactic complexity. Conversely, semantic complexity induced medial prefrontal activations that were not reliably seen for syntactic complexity manipulations.

Separate analyses of the two main kinds of syntactic complexity yielded results that were like the overall activation patterns induced by syntactic complexity; therefore, the mechanism that drives these activations seems to be shared by non-canonical word orders and relative clause complexity. Separate analyses of different kinds of semantic complexity, however, yielded differential activation patterns. Sentences with metaphoric meaning contributed most to the overall activation of BA 45/47 and left posterior MTG, replicating the findings of a recent voxel-based meta-analysis on metaphor processing (Bohrn et al., 2012). By contrast, sentences that required the listener to assess the speaker's intentions (irony, indirect requests/utterances) did not reliably activate BA 45 or the left posterior temporal lobe. These kinds of sentences most frequently activated the medial prefrontal cortex (also reliably reported for metaphoric sentences but in a relatively smaller number of studies) and the right temporoparietal cortex (mainly observed in studies using indirect utterances).

In sum, H&I's meta-analysis yielded several important results. The most robust result was a distinctive activation pattern in the posterior LIFG: syntactic demands activated more dorsal parts (BA 44/45) and semantic demands activated more ventral parts (BA 45/47) across all kinds of increased processing demands (violations, ambiguity, complexity). This pattern was corroborated by studies performing direct comparisons of high syntactic and semantic processing demands. In particular, BA 44 activation is clearly driven more strongly by syntactic than by semantic demands, suggesting that this region contains neuronal populations involved in syntactic operations as such or that the semantic consequences of syntactic demands (difficulty of thematic role assignment) are processed by neuronal populations that differ from those processing other kinds of semantic unification. This dorsal/ventral gradient observed in the left posterior IFG seems to be mirrored in the left posterior temporal lobe. Higher syntactic demands reliably activate STG and MTG, and higher semantic demands reliably activate MTG and ITG. These gradients in posterior frontal and temporal regions are remarkably consistent with a functional connectivity pattern found by Xiang et al. (2010), which links seed regions in BA 44, BA 45, and BA 45/47 to left posterior STG, MTG, and ITG, respectively. This finding clearly supports the idea that sentence-level unification relies on the coactivation of neuronal populations in a network of posterior frontal and temporal regions, with a similar functional gradient in both parts of the brain.

Another important observation is the degree to which posterior temporal lobe activation differs between violations and other kinds of higher processing demands. Syntactic violations do not seem to elicit posterior temporal lobe activations reliably, and reports about such activations are relatively infrequent for semantic violations. I will come back to the potential relevance of this observation after the discussion of the neural activations patterns observed for sentence production.

20.3 Brain areas involved in sentence production

Due to problems with motion artifacts in functional MRI there are far less studies on sentence production than there are on sentence comprehension. To avoid these problems the earliest studies either used the positron emission tomography (PET) technique (Indefrey et al., 2001; 2004) or covert sentence production (Golestani et al., 2006; Peck et al., 2004). Meanwhile, however, fMRI scanning and analysis techniques have been developed that allow for overt articulation in the scanner (see Willems & van Gerven, this volume) so that over the last years a sufficient number of studies on sentence production have been published to allow for a tentative meta-analytic assessment of the reliability of findings across studies. Using the same procedures as for the sentence comprehension studies here, I analyzed the activation foci reported in 17 studies with altogether 350 participants. Seven of these compared sentence or phrase production to word list production (Contrast 29 in Tables 20.1 and 20.2). Seven studies compared more/complex syntactic production to less/simpler syntactic production (Contrast 30 in Tables 20.1 and 20.2). Five studies used an fMRI syntactic adaptation paradigm (Contrast 31 in Tables 20.1 and 20.2) and will be discussed in section 4.

20.3.1 Sentence production compared with word production

Studies comparing sentence production to word production used two main paradigms. In one type of paradigm participants were presented with pictures or visual scenes and instructed to describe the visual stimuli in different conditions with sentences or word lists (Indefrey et al., 2001; Indefrey et al, 2004; Peck et al., 2004; Pylkkänen et al., 2014). In the other type of paradigm participants were visually presented with lists of words. They were instructed to generate sentences from these words or, in the baseline condition, to simply read them out (Collina et al., 2014; Golestani et al., 2006; Haller et al., 2005).

As can be seen in Figure 20.2A, there was a highly reliable agreement between studies with respect to stronger activation of the left posterior IFG (pars opercularis, BA 44) in the sentence production task compared to word production. Surrounding regions (left ventral precentral gyrus, posterior MFG, superior frontal gyrus (SFG) and IFG, pars triangularis, BA 45) as well as left inferior parietal and precuneus activation were found less often but are still reliable at an uncorrected threshold. Note, however, that sentence and word production were not always well matched with respect to the required degree of conceptual planning and the amount of material to be uttered. The latter point particularly raises serious concerns about the interpretation of the observed posterior IFG activations because this region is known to be recruited for single word production as well (Indefrey & Levelt, 2004; Indefrey, 2011a). For this reason, Indefrey et al. (2001; 2004) additionally manipulated the rate of visual scene presentation, such that the increase in syllables or words per minute between the faster rate and the slower rate corresponded to the difference between the sentence and the word list conditions, which was due to the additional grammatical morphemes and function words in the sentences. They found the higher word production rate to result in stronger activation of the bilateral auditory cortices and an adjacent part of left IFG but not in stronger activation of the
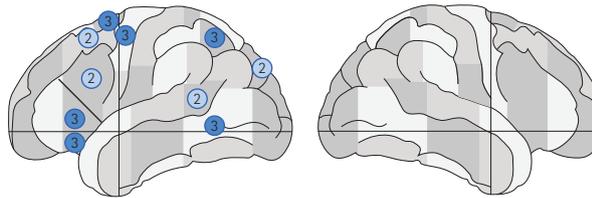
(A) Production of sentences compared to words (seven studies)
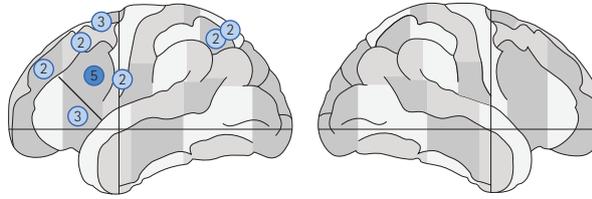
(B) Production of syntactically more complex compared to simpler sentences (seven studies)
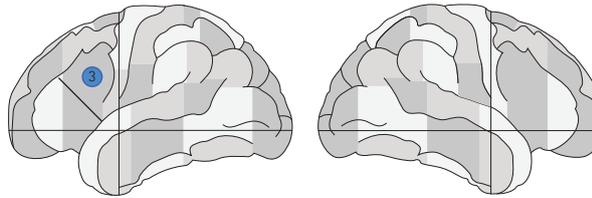
(C) fMRI syntactic adaptation in sentence production and comprehension (five studies)

● Reliably activated *p* <0.05, corr.   ○ Reliably activated *p* <0.05, uncorr.

FIG. 20.2 Reliable neural activation increases for (A) sentence production compared to word production and (B) production of syntactically more compared to less demanding sentences. (C) Reliable fMRI adaptation for the production and comprehension of sentences preceded by sentences with identical syntactic structures compared to sentences preceded by sentences with different syntactic structures.

region that was sensitive to the sentence/word list contrast suggesting that the hemodynamic response observed in BA 44 was indeed due to the increased demand on syntactic encoding rather than to changes in the number of syllables or words per minute.

3.2. Production of syntactically more versus less demanding sentences

In this group of studies, the degree of syntactic encoding was manipulated in different ways. Most studies compared grammatically more complex sentences to simpler ones (Den

Ouden et al., 2008; Humphreys and Gennari, 2014; Kircher et al., 2005). Indefrey et al. (2001; 2004) compared the production of sentences with the production of noun phrases. Argyropoulos et al. (2013) compared the generation of sentences with the repetition of sentences. Grande et al. (2012) used a very interesting and unusual paradigm: participants were asked to freely describe pictures while being scanned. The resulting speech samples were coded for (among other things) the syntactic completeness of sentences so that the hemodynamic activity of the brain during the production of syntactically complete and incomplete sentences could be compared post-hoc.

As can be seen in Figure 20.2B, there was only one region showing reliable agreement across studies. Three of the seven studies (Grande et al., 2012; Humphreys & Gennari, 2014; Indefrey et al., 2001) reported stronger activation of the left posterior IFG (BA 44) for the syntactically more demanding condition (see Fig. 20.2B). No other region was reported more than once.

20.3.3   Comparison of sentence comprehension and production activation patterns

The logic for presenting the evidence on reliable activation pattern for sentence comprehension and production was to test a prediction following from the assumption of shared processing resources for syntactic parsing and encoding: if that assumption is true, there should be some degree of overlap of the neural activation patterns. Figure 20.3 summarizes the most relevant findings from sentence comprehension and production studies. Unfortunately, at first sight our results do not seem to provide a clear answer, at least when looking at the activation patterns for the production and comprehension of simple sentences compared to words (Figs. 20.1A and 20.2A). In production the most reliably activated region is BA 44 and in comprehension just this region is not reliably observed (see also previous meta-analyses with the same finding; e.g., Indefrey, 2011b; Indefrey, 2012; Indefrey & Cutler, 2004). Instead, comprehension seems to recruit posterior temporal regions not found in production studies and more ventral parts of the left posterior IFG.

The picture looks different when comparing the outcome of studies that targeted syntactic processing more directly. Here the only reliably activated region in sentence production is BA 44 and just this region is also most frequently reported in comprehension studies (Figs. 20.1B and 20.2B). Again, however, highly reliable posterior temporal activations that are observed in comprehension are not observed in production. Note, that also in comprehension we found a dissociation between IFG and posterior temporal activations: syntactic violations activated the former but not the latter. This dissociation suggests a functional difference between the two regions that may also be relevant for the dissociation between production and comprehension. A tentative explanation accommodating all findings could be based on a distinction between Broca's area subserving sentence-level compositional processes, and the posterior temporal lobe subserving the retrieval of lexical syntactic and semantic information (Hagoort, 2005; Snijders et al., 2009). Syntactic violations only arise at a compositional processing stage and hence do not result in increased activation of posterior temporal cortex. Conversely, understanding simple spoken sentences does not necessarily require parsing their grammatical structure,
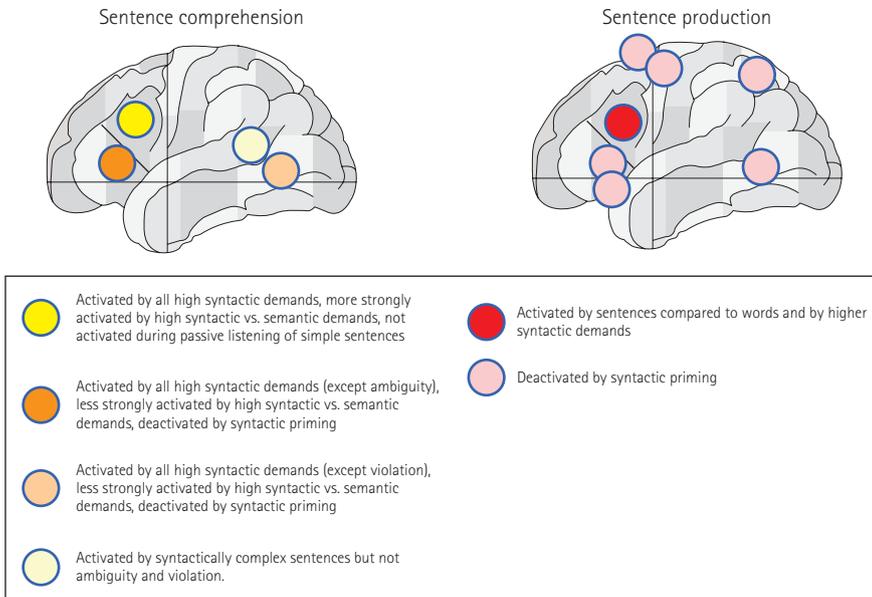
FIG. 20.3 Summary of the most reliable activation patterns for syntactic comprehension and sentence production.

because their meaning can be derived from the word meanings ("good-enough representations," Ferreira et al., 2002). Hence, the neural activation we observe may not reflect syntactic processing at all but rather word and sentence level semantic processing and, indeed, the activation pattern corresponds best to what H&I identified as the pattern for semantic processing. Sentence production of even the simplest sentences, by contrast, cannot do without syntax, because speakers need to express the syntactic relationships between words in the ways required by their language. On the other hand, compared to listeners, speakers have the advantage of not having to deal with lexical ambiguities. As they know which word of which syntactic category to retrieve from the lexicon there may not be much difference between the word retrieval effort for sentences and word lists and hence no observable posterior temporal activation for sentence processing. In this view, syntactic processing resources may well be shared between production and comprehension but the differential affordances of expressing a message and deriving it from acoustic input nonetheless result in differences in neural activation patterns.

As far as our considerations have been based on correspondences between activated regions for the production and comprehension of sentences, they remain speculative as long as it cannot be shown that activation of the same region really means activations of the same neuronal population. This type of evidence can in principle be provided by studies using the fMRI adaptation paradigm. We, therefore, now turn to the set of studies that used this paradigm to study the relationship between syntactic encoding and parsing.

20.4 WITHIN- AND BETWEEN-MODALITY SYNTACTIC REPETITION EFFECTS

The fMRI adaptation paradigm exploits the fact that the activation of a neuronal population decreases with repeated presentations of the stimuli that initially activated these neurons (Henson & Rugg, 2003). By manipulating which aspect of a stimulus is repeated, this technique allows to identify neuronal populations that are tuned to ("interested in") this particular aspect. In a series of studies, Menenti, Segaert, Schoot, Hagoort, and colleagues orthogonally manipulated semantic, syntactic, and word repetition during the production and comprehension of sentences. As shown in Figure 20.2C, reliable syntactic adaptation effects across studies were found in left posterior IFG, MFG, and SFG (supplementary motor area), as well as the left posterior temporal cortex and the inferior parietal cortex, replicating both earlier syntactic adaptation findings for comprehension (Weber & Indefrey, 2009) and the pattern of regions activated by syntactic processing in classic subtraction studies reported here. The surplus of this series of studies lies in the fact that the syntactic adaptation effects did not differ between speaking and listening (Menenti et al., 2011; Menenti et al., 2012, see also Tooley & Bock, 2014, for recent corresponding behavioral results), and, most importantly, were even found between modalities (Segaert et al., 2012; Segaert et al., 2013; Schoot et al., 2014). These results provide convincing evidence for shared neuronal populations engaged in syntactic processing in both sentence production and comprehension. Some caveats, however, should be mentioned. A close inspection of the results of Segaert et al. (2012) shown in Schoot et al. (2014) suggests that between-modality syntactic repetition suppression was mainly found from production to comprehension, much less from comprehension to production. It seems, therefore, possible that the participants' comprehension of their own utterances contributed to the priming effect. Furthermore, production priming effects were comparatively small in left posterior temporal cortex. This latter observation may help to reconcile the apparent contradiction between fMRI adaptation effects suggesting an involvement of left posterior MTG in syntactic processing in production and classic subtraction studies not reporting reliable activation of this region. As suggested here, there may be relatively little effort for the retrieval of lexical syntactic information in production. This is also reflected in the fMRI adaptation data. Nonetheless, this technique may be just sensitive enough to detect a small facilitation of the retrieval of lexical syntactic information, in particular, when the retrieval of a dispreferred argument structure such as the passive argument frame of a verb (Segaert et al., 2013) is primed.

20.5 CONCLUSIONS

The question investigated in this article was whether there is one syntactic system that is shared by language production and comprehension or whether there are two separate systems. The available evidence from hemodynamic studies suggests that the answer is: there is one system consisting of at least two functionally distinct cortical regions, the pars opercularis of the left posterior IFG (BA 44) and the left posterior temporal cortex. This

answer is mainly motivated by the compelling evidence from recent fMRI syntactic adaptation studies, showing cross-modal adaptation effects. There are differences in the activation patterns observed in classic subtraction fMRI studies between (a) sentence production and comprehension, (b) the comprehension of simple and syntactically complex sentences, and (c) syntactic violations and other types of syntactically demanding conditions. These differences can be accounted for by assuming a particular relevance of left posterior IFG for compositional syntactic processing and a particular relevance of the posterior temporal region for the retrieval of lexical syntactic information. Sentence production, the comprehension of simple and complex sentences, and the parsing of sentences containing grammatical violations tax these two functional components differently.

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