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The Working Memory of Argument–Verb Dependencies

Spatiotemporal Brain Dynamics during Sentence Processing

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Contents

PREFACE

Sentences are series of symbols arranged in a specific order. Some of these symbols are verbs, expressing actions—others of these symbols are arguments, expressing participants that join in the actions. This thesis investigates the spatiotemporal brain dynamics of two cognitive processes that enable the comprehension of the mutual dependencies between arguments and verbs. When an argument and its verb do not occur in succession, the argument must be remembered during the time interval between argument and verb. When the relative argument order differs from the order that the arguments combine in with their verb, reordering of the remembered arguments must take place.

Argument storage and reordering are working-memory processes: Storage is remembering, counteracting forgetting. Reordering is an executive process operating on stored items. Chapter 1 introduces this conceptualization from linguistic, psycholinguistic, and cognitive-neuropsychological viewpoints, as well as the open issues: Linguistics has a rich terminology for describing argument–verb dependencies, psycholinguistics has established the psychological reality of some of these terms, and cognitive neuropsychology can relate those terms that are psychologically real to the underlying cognitive processes and the subserving functional neuroanatomy.

The goal of this thesis is to understand the spatiotemporal brain dynamics that subserve argument storage and reordering during sentence processing. The goal is not to formulate a psycholinguistic theory of argument–verb-dependency processing, since multiple frameworks are already available. Because spatiotemporal brain dynamics can only be investigated exploiting high-resolution temporal and spatial brain-data-analysis methods, this thesis applied various data acquisition and analysis methods to a single experimental paradigm. Chapter 2 provides a critical overview of these methods, as well as the to-be-tested experimental paradigm.

The following experimental chapters are devoted to investigate the open issues in the spatiotemporal dynamics of argument storage and reordering: Chapter 3 asks about the behavioral relationship between argument storage and reordering. Chapter 4 asks about the functional neuroanatomy of argument storage and reordering. Chapter 5 asks about the consequences of selective damage to this functional neuroanatomy. Chapter 6 asks about the brain-electric substrate of argument storage. Chapter 7 asks about the spatiotemporal dynamics inside the functional-neuroanatomical brain network established in the previous chapters. Chapter 8 summarizes the experimental results, extracts their three *leitmotifs* and relates them to cognitive-neuropsychological research from outside the sentence-processing domain. Finally, Chapter 9 ends the thesis, proposing both a testable neurocognitive framework of argument–verb-dependency processing and a number of related research opportunities.

1

General Introduction

1.1 Argument–Verb Dependencies

In a sentence, arguments symbolize the who and whom, while a verb symbolizes an action jointly involving the who and whom (Bühler, 1934; Frege, 1879). Because arguments and verbs jointly constitute sentence meaning, they form mutual argument–verb dependencies, which are language's core device of symbolizing relations between entities. Hence, speakers' mental-lexical knowledge about stereotypical argument–verb combinations (argument–verb sets) reflects speakers' experience with stereotypical actions and stereotypically involved entities (Goldberg, 1992; Lapata, Keller, & Walde, 2001; Rumelhart, 1980; for an overview, see Tomasello & Merriman, 1995). This section provides an introduction to the linguistic properties of argument–verb dependencies.

A verb's mental-lexicon entry contains two sources of information about the type and number of arguments that need to co-occur with the verb to form a coherent sentence (Chomsky, 1965, 1981): The arguments' formal syntactic properties (e.g., nominative case) are specified by the subcategorization frame, whereas the arguments' functional thematic roles (e.g., the who performing an action) are specified by the θ-grid. The neuropsychological reality of subcategorization frames and θ-grids is suggested by clinical evidence on their selective disruptability (Bastiaanse, Edwards, Mass, & Rispens, 2003); in addition, the neurophysiological sensitivity to subcategorization frames and θ-grids is suggested by their neuroanatomical dissociability (Shetreet, Palti, Friedmann, & Hadar, 2007).

Psycholinguistic data support the significance of argument–verb dependencies for sentence processing: Fodor, Garrett, and Bever's (1968) early work suggests processing difficulty to increase with the number of possible argument–verb sets, with verbs that allow for multiple possible sets showing higher processing load than verbs whose mental-lexicon entry specifies only a single possible set. Later work showed that the combination of an argument and a transitive verb that belong to a joint argument–verb set pre-activates the syntactic characteristics of the second argument, and thus the verb's subcategorization frame (Clifton et al., 1984; for further discussion, see Trueswell & Kim, 1998). While Shapiro, Zurif, and Grimshaw (1989), Shapiro, Brookins, Gordon, and Nagel (1991), and McElree and Dosher (1993) suggested that argument pre-activation carries over to the θ-grid, McElree and Griffith's (1995) results suggest that subcategorization and θ-grid information are pre-activated serially: subcategorization violations are recognized quicker than θ-grid violations. Further studies extended these results (Garnsey, Pearlmutter, Myers, & Lotocky, 1997; Holmes, Stowe, & Cupples, 1989; Trueswell & Kim, 1998), also showing that argument–verb-set pre-activation is a two-way mechanism (cf. Friederici & Frisch, 2000): Verbs pre-activate their subcategorization frames and θ-grids, and to a lesser extent, arguments pre-activate their verbs (Kamide, Altmann, & Haywood, 2000; Kamide, Scheepers, & Altmann, 2003; Tsuzuki, Uchida, Yukihiro, Hisano, & Tsuzuki, 2004).

To infer sentence meaning, those phrases of a joint argument–verb set that constitute the who, the whom, and the action the who and whom are involved in must be linked to one another. Descriptive work has long assumed that argument–verb linking occurs in a serial order idiosyncratic to any particular language (Chomsky, 1955; Fodor, 1978)—for instance, subject–object–verb in German (Bader & Bayer, 2006; Haider, 1993). For English, which follows subject–verb–object order, Clifton et al. (1984) found evidence for this proposal: The authors observed that grammaticality judgment was slowed down when transitive verbs were not followed by their object, but by a prepositional phrase, suggesting that the missing argument at the post-verbal position had been predicted from the verb's subcategorization information in combination with the English subject–verb–object order (cf. Holmes, 1987; Shapiro, Gordon, Hack, & Killackey, 1993). Further work showed that the preference to interpret a post-verbal noun phrase as the verb's direct object is so strong as to erroneously hinder this noun phrase's interpretation as the subject of a subsequent sentence (Trueswell, Tanenhaus, & Kello, 1993).

Since a verb's subcategorization frame and θ-grid are activated on encounter, the number and type of required arguments becomes known with the verb; those arguments in the sentence whose syntactic features fit the verb's subcategorization frame can then be linked to the verb. There is evidence that this linking is triggered by an alignment of syntactic argument features (e.g., a suffix marking nominative case) with the verb's subcategorization frame and θ-grid: In an elegant study, Van Dyke and McElree (2006) manipulated the number of noun phrases whose syntactic features matched the verb subcategorization frame and θ-grid of a given verb, finding reading times at the verb to increase with the number of syntactically matching noun phrases (cf. Fedorenko, Gibson, & Rohde, 2006; Gordon, Hendrick, & Johnson, 2001).

Argument–verb linking may be straightforward when the arguments occur in the vicinity of their subcategorizing verb and in the serial order that arguments combine in with their subcategorizing verbs in that particular language. However, a direct argument–verb linking is not possible when arguments occur at sentential positions remote from their subcategorizing verb (e.g., an argument is in front of a sentence, whereas its verb is at the sentence ending), or when the relative order of arguments differs from the serial order that arguments combine in with their subcategorizing verbs (e.g., the object is in front of the subject). In the resulting argument–verb dependency, argument–verb linking can only occur indirectly by storing the remote argument across the resulting argument–verb distance and re-activating the remote argument at its verb. Section 1.2 will next discuss the underlying cognitive mechanisms that enable these processes, while Section 1.3 will then relate these mechanisms more specifically to the sentence-processing domain.

1.2 Working Memory

Working memory is the workbench of cognition, storing information while required for manipulation by the brain's executive processing systems (Baddeley, Eysenck, & Anderson, 2009; Rumelhart, Lindsay, & Norman, 1972; Shah & Miyake, 1999). Across sensory and cognitive domains, at least a visual- and a verbal-working-memory system are commonly differentiated, of which the latter is crucial to the cognitive processes investigated in the current thesis: It is clear that verbal working memory is involved in language processing (Baddeley & Hitch, 1974; Wingfield & Butterworth, 1984).

Current models largely agree that working memory is an active system involving executive components (Oberauer, Süß, Wilhelm, & Wittman, 2003; cf. Miyake & Shah, 1999). In particular, the contents of verbal working memory can constantly be refreshed by articulatory rehearsal, which effectively lengthens the possible retention interval (Baddeley, 2012). There is imaging evidence on the neuroanatomical dissociation of working-memory-storage and -rehearsal sub-systems (Awh, Smith, & Jonides, 1995; Paulesu, Frith, & Frackowiak, 1993; for discussion, see Chapter 4); furthermore, work on the elderly suggests that their reduced working-memory retention duration results from decreased brain activity in those prefrontal regions that underlie rehearsal (Johnson, Mitchell, Raye, & Greene, 2004; Johnson, Reeder, Raye, & Mitchell, 2002). In addition to rehearsal, Baddeley's (2012) model of working memory proposes executive sub-systems concerned with information manipulation. While there is some consensus that working memory does involve such systems (Miyake & Shah, 1999), there is little consensus as to which processes this entails (Baddeley, 1996).

Its active nature distinguishes working memory from other systems of short-period information retention: Echoic memory (Neisser, 1967) and short-term memory (Brown, 1958; Peterson & Peterson, 1959) have also been proposed as subservants of temporary information storage. While some authors treat these systems as synonymous with working memory, the content of echoic and short-term memory degenerates more rapidly than that retained in working memory. This rapid decay of the content stored by echoic memory and short-term memory has been proposed to result from their proximity to sensory input systems and their according lack of an information-refreshing sub-system (Baddeley & Larsen, 2007; Jones, Hughes, & Macken, 2007).

Information refreshing by rehearsal reduces the degeneration susceptibility of working memory, but its retention duration is still limited by decay and interference (Miller, 1956): Early work on forgetting suggests that decay induced by increased retention duration is an inherent property of working memory (Anderson, Reder, & Lebiere, 1996; Peterson & Peterson, 1959). The neural reality of decay is suggested by single-cell recordings in monkeys, which show neurons involved in retention to reduce their firing rates along the retention interval (Fuster, 1999). In addition to decay, similarity-based interference of synchronously stored items limits retention duration: Conrad and Hull (1964) find that acoustic similarity of to-be-remembered letters decreases memory span (cf. Lewandowsky, Geiger, & Oberauer, 2008; Oberauer & Lange, 2008; Potter, 1976; Shulman, 1970). It is, however, debated whether decay or interference is a stronger limiter of retention duration, ever since McGeoch (1932) argued that the task performed during retention limits retention duration over and above decay (cf. Altmann & Schunn, 2002; Campoy, 2012; Conrad, 1967; Keppel & Underwood, 1962; Lewandowsky, Oberauer, & Brown, 2009). Given this open discussion, the experiments of the current thesis controlled for interference as far as possible to isolate decay as a controlled experimental factor (see Section 2.3).

The susceptibility to degenerative factors might distinguish working memory from long-term memory[1]; however, Anders Ericsson and Kintsch (1995) proposed a direct link between working memory and long-term memory by conceptualizing working memory as an attentional mechanism that selectively activates long-term-memory content (Parkin, 2001; Unsworth & Engle, 2007; for discussion, see Cowan, 2008). The major argument for this conceptualization is the finding that individuals' working-memory performance can be predicted by their fields of expertise (Ericsson & Chase, 1982). For instance, professional chess players have been found to access long-term memories when verbally reporting on unfamiliar chess positions they were experimentally prompted to solve (de Groot, 1978), a finding which has been replicated for other fields of expertise (for review, see Anders Ericsson & Kintsch, 1995). To still account for the fact that working-memory processes may recur to novel information, Anders Ericsson and Kintsch (1995) propose a differentiation between short-term working memory and long-term working memory, of which the former designates the temporary storage of novel information, whereas the latter designates the temporary attentional selection of long-term-memory content. This conceptualization is particularly interesting given a possible neuroanatomical overlap between brain regions involved in working memory, attention, long-term memory, and the mental lexicon (cf. Chapter 8; see also Cabeza, Ciaramelli, & Moscovitch, 2012a).

A final issue to be addressed before turning to the specific role of working memory in argument–verb-dependency processing is the question of the fractionation of verbal working memory into phonological, semantic, and syntactic sub-parts. Martin, Shelton, and Yaffee (1994) suggested that a holistic view of verbal working memory may not capture the diversity of language processing: Martin et al. (1994) provide clinical evidence that phonological and semantic aspects of verbal working memory can be selectively impaired, backed up by functional-magnetic-resonance-imaging (fMRI) evidence from healthy populations (Shivde & Thompson-Schill, 2004). Martin and Romani's (1994) data additionally illustrate the possibility of a selectively impaired ability to store syntactic information. While these results principally demonstrate a fractionation of verbal working memory, disagreement prevails: Caplan

[1] Long-term memory may not be interference-proof during retrieval, and especially not during verbal retrieval (Cowan, 2008).

and Waters (1999) differentiate phonological and syntactic working memory, Fiebach, Friederici, Smith, and Swinney (2007), Martin and He (2004), and Shivde and Anderson (2011) focus on the semantic aspects, and Caspari, Parkinson, LaPointe, and Katz (1998) and Fedorenko, Gibson, and Rohde (2007) propose an additional working-memory system shared by any symbolic process, both during language processing and outside of the language-processing domain. Whether or not these fractionation proposals are of relevance to argument–verb-dependency processing will be discussed in the following section, which focuses on the role of verbal working memory in the processing of argument–verb dependencies.

1.3 Argument–Verb Dependencies and Working Memory

An important assumption of the current thesis is that working memory is the cognitive basis for argument–verb-dependency processing. The difficulty of argument–verb-dependency processing is determined by two cognitive processes: First, when an argument occurs at a sentential position remote from its subcategorizing verb, temporary storage of the argument in working memory becomes necessary, until the argument is retrieved for argument–verb linking at its subcategorizing verb. In this case, a so-called gap remains where the subcategorizing verb necessitates its now-remote argument; the argument itself has now become a so-called filler (Fodor, 1978; Frazier, Clifton, & Randall, 1983; Kluender & Kutas, 1993)[2]. Second, when multiple arguments of a joint argument–verb set occur in a relative order other than the serial order idiosyncratic to any particular language, working memory needs to recruit an executive mechanism of argument reordering (Carpenter & Just, 1989; Just & Carpenter, 1992; Kintsch & Van Dijk, 1978).

The psychological reality of argument storage was established by Wanner and Maratsos (1979), who found that concurrent memory load decreases performance during argument–verb-dependency processing (Gordon et al., 2001; Gordon, Hendrick, Johnson, & Lee, 2006; Gordon, Hendrick, & Levine, 2002; Van Dyke, 2007; cf. Frazier et al., 1983). Strong evidence for the neuropsychological reality of argument storage was later provided by Kluender and Kutas' (1993) seminal event-related-brain-potential (ERP) study: Their paradigm investigated sentences containing a pronoun-argument–verb dependency, and found a sustained negative effect spanning the argument–verb distance for these sentences when

[2] The theoretical precursor of Fodor's (1978) filler–gap dichotomy is Chomsky's (1955) antecedent–trace dichotomy; for a concise introduction, see Radford (1997).

compared to a baseline condition. Later studies corroborated these results (Phillips, Kazanina, & Abada, 2005; Ueno & Kluender, 2003), and extended the findings to interrogative-pronoun and full-noun-phrase arguments in German (Felser, Clahsen, & Münte, 2003; Fiebach, Schlesewsky, & Friederici, 2001, 2002; Matzke, Mai, Nager, Rüsseler, & Münte, 2002)[3]. It is, however, problematic that these prior studies did not separate argument storage and reordering: Object-first and subject-first sentences at long argument–verb distance were compared only, but never short and long argument–verb distances directly—in spite of evidence for argument storage being common to any argument order. I will come back to this critique when discussing the present experimental design (see Section 2.3).

In addition to argument storage, filler–gap dependencies also necessitate argument retrieval at their subcategorizing verbs (Lewis, 1996; Lewis & Vasishth, 2005). While Corbett and Chang's (1983) initial off-line results suggested that pronouns trigger retrieval of their antecedent nouns, Tanenhaus, Carlson, and Seidenberg (1985) on-line data suggested that an argument gap leads to argument retrieval: Tanenhaus et al. (1985) presented words that rhymed with a remote filler at its gap, finding that these words were primed. Nicol and Swinney (1989) report that Swinney, Ford, Frauenfelder, and Bresnan (1988) adapted Tanenhaus et al.'s (1985) cross-modal priming technique, finding that also words that are semantically related to a remote filler are primed at the remote filler's gap. Similar experiments by Bever and McElree (1988) and Love and Swinney (1996) concluded that argument retrieval does not only occur for pronoun reference and interrogative phrases, but for proper-noun phrases as well (for review, see Nicol, Fodor, & Swinney, 1994; Nicol & Swinney, 1989)[4].

So, we can reasonably deduce that argument–verb-dependency processing involves storage and retrieval. However, reports are equivocal as to whether these recur to phonological, semantic, or syntactic representations: The cross-modal priming studies discussed above mention fillers to elicit rhyme priming (Tanenhaus et al., 1985), prosodic priming (Nicholas Nagel, Shapiro, & Nawy, 1994), and semantic priming (Bever & McElree, 1988; Nicol & Swinney, 1989; Swinney et al., 1988) at subcategorizing verbs

[3] These effects are similar to sustained negative ERPs observed for verbal-working-memory-storage tasks outside of the sentence-processing domain (Johnson, 1995; Ruchkin et al., 1992). This points to a degree of domain-generality of the verbal-working-memory system involved in argument–verb-dependency processing—although Ruchkin et al.'s (1999) data suggest that words elicit increased sustained negative ERP effects relative to non-words.

[4] For brevity's sake, this section confines to the simplistic notion of argument retrieval at subcategorizing verbs. There is, however, evidence that arguments can be retrieved before the actual encounter of their subcategorizing verb; for discussion, see Section 6.4, Section 7.4.2, and Chapter 8.

(cf. Clahsen & Featherston, 1999; Featherston, 2001). Furthermore, self-paced-reading (SPR) studies suggest that syntactically interfering noun phrases increase both argument storage and retrieval efforts (Van Dyke & McElree, 2006). The data thus suggest that arguments are stored in a rich verbal code.

As any working-memory content, arguments decay over time (cf. Section 1.2). This led to the proposal that argument–verb distance be a major determinant of sentence-processing difficulty (Frazier, 1987; Frazier et al., 1983; Yngwe, 1960): The longer the argument–verb distance, the longer the argument-storage interval prior to retrieval, and the more the argument will degenerate. For the same reason, long argument–verb distances may exacerbate argument retrieval at the subcategorizing verb. Cross-linguistic experiments found that dependency length indeed increases argument–verb-linking efforts (Babyonyshev & Gibson, 1999; Cowper, 1976; Gibson, 2000; Grodner & Gibson, 2005)—rendering dependency length a reliable tool to query argument storage and retrieval during argument–verb-dependency processing[5].

So far, this section considered the interrelation between decay and argument–verb distance. However, when an argument–verb set's arguments do not occur in their idiosyncratic relative order, the re-establishment of their preferred relative order is an additional challenge to working memory (cf. Section 1.1)—necessitating the postulation of an executive mechanism of argument reordering in addition to argument storage. In support of this postulate, Osterhout and Swinney's (1993) cross-modal-priming study found that only the appropriate subject from a transitive object-first argument order primes semantically related words at the empty subject gap of a subsequent empty-subject sentence (cf. Nicol & Swinney, 1989). This implies that fillers are retrieved only at their appropriate gap. An overwhelming body of cross-linguistic behavioral evidence shows object-first as compared to subject-first argument orders to increase processing load (Hyönä & Hujanen, 1997; MacWhinney & Pléh, 1988; Mazuka, Itoh, & Kondo, 2002; Miyamoto & Takahashi, 2002), most profoundly at subcategorizing verbs (Frauenfelder, Segui, & Mehler, 1980; Grodner & Gibson, 2005). In a nutshell, a mismatch between occurrence order and gap order necessitates argument reordering.

[5] As an interesting linguistic aside, some authors have proposed that working-memory decay may be the evolutionary reason for the cross-linguistic tendency of languages to keep dependents—such as arguments—close to their heads—such as verbs (cf. Temperley, 2007).

Previous neuroimaging data on the proposed distinction between argument storage and reordering are not unequivocal. While studies on argument reordering from languages other than English agree on an involvement of inferior frontal brain regions (Ben-Shachar, Palti, & Grodzinsky, 2004; Friederici, Fiebach, Schlesewsky, Bornkessel, & von Cramon, 2006; Kim et al., 2009), Rogalsky and Hickok (2010) insist on a reductionist perspective equating reordering- and storage-related brain activations as both reflecting rehearsal. The picture is similarly complex for argument storage: While some studies suggest that inferior frontal cortex be involved in argument storage distinctly from argument reordering (Fiebach, Schlesewsky, Lohmann, von Cramon, & Friederici, 2005; Makuuchi, Bahlmann, Anwander, & Friederici, 2009; Santi & Grodzinsky, 2007), these studies contrasted different kinds of syntactic dependencies. They also disagree with work from the sentence-processing domain that found inferior parietal regions involved in argument storage (Novais-Santos et al., 2007). While Novais-Santos et al.'s (2007) result converges on work from outside the sentence-processing domain (for review, see Owen, McMillan, Laird, & Bullmore, 2005; Smith & Jonides, 1998; Wager, Keller, Lacey, & Jonides, 2005), their experimental paradigm confounded dependency length and phrasal size of the stored argument, leaving its result ambiguous. Clearly, the imaging literature is in need of better-controlled work.

This chapter has laid out the linguistic and psycholinguistic foundations of the argument–verb dichotomy, the underlying cognitive processing mechanisms, and their specific manifestations during filler–gap-dependency processing. When it comes to the neural reality of dependency-length-induced storage and retrieval load and order-mismatch-induced reordering, there are bodies of evidence available. Since these are under debate, they will be introduced in Section 1.4, alongside the open issues in the research on the spatiotemporal dynamics of argument–verb-dependency processing in the human brain.

1.4 Open Issues

The previous sections reported on attempts to segregate argument storage and retrieval (depending on working-memory decay) from argument reordering (depending on a mismatch between argument occurrence order and gap order). Throughout the thesis, this will guide the following hypothetical scenario: Argument–verb-dependency processing involves the storage of arguments across the argument–verb distance; at their subcategorizing verb, these arguments are retrieved, and in case of a relative argument order that deviates from the idiosyncratic order, argument reordering re-establishes this order.

While these hypotheses have firm bases, some authors do not assume active executive mechanisms, treating argument–verb-dependency processing as fully emerging from decay, interference, and syntactic-feature matching (Lewis, Vasishth, & Van Dyke, 2006), or simply rehearsal (Rogalsky & Hickok, 2010). These positions may result from the fact that English rarely allows for argument-order variations, and possible cases such as relative clauses or embedded questions confound argument–verb distance and argument order. While there is evidence for deriving the processing difficulty associated with increasing argument–verb-dependency length from increased decay-exposure of the filler (Frazier, 1987; Gibson, 2000), there is also clear evidence that argument-order variations decrease response accuracy—even if argument–verb-dependency length is controlled for (Obleser, Meyer, & Friederici, 2011). Because it is unclear whether argument storage and retrieval on the one side and argument reordering on the other side exhibit an independent or interactive relationship, Chapter 3 reports on a behavioral SPR and rating experiment that fully crossed the two factors.

While behavioral results can complement psycholinguistic theory, they do not suffice to conclude on the neural interdependence of argument storage on one side and argument reordering on the other: Behavioral interactions between experimental variables may result from brain-functional interactions, but they may also derive from brain-structural properties that selectively constrain the output of principally independent brain functions: If reordering and storage were performed by independent regions, their anatomical connection could selectively facilitate the processing of sentences that tax both reordering and storage. Because previous neuroimaging data do not speak to this possibility, Chapter 4 reports on an fMRI study on the paradigm used in Chapter 3, supplemented by an analysis of the involved regions' connectivity and anatomical substrates. To elucidate on the related question of the functional-neuroanatomical isomorphism between the storage–reordering and the storage–rehearsal dichotomies, Chapter 4 also investigated whether activations of the argument–verb-dependency network correlate with working-memory abilities.

Because fMRI evidence can in principle only work out the necessary, but not the sufficient brain parts involved in a cognitive process (for discussion, see Caplan, 2009), it needs backup by clinical data from patients with selective damage to—preferentially—one of those brain parts. This in mind, Chapter 5 presents a case study on a patient whose selective neuroanatomical damage gives reason to assume a selective deficit in those processes characterized in Chapter 3 and localized in Chapter 4.

The manifold previous research on the brain-electric equivalents of the working-memory processes involved in argument–verb-dependency processing does not speak to the differentiation between argument-storage and -retrieval processes and argument-reordering mechanisms. Furthermore, all previous electroencephalography (EEG) studies used ERPs, which present a valuable, yet somewhat remote characterization of brain-electric activity (as discussed in Section 2.2.1 and Section 2.2.2). Thus, Chapter 6 focuses on argument storage independently of argument order, approaching the paradigm from the previous experiments with a combination of time-frequency analysis (TFR) and source localization.

Chapter 7 asks how argument retrieval and reordering progress during argument–verb linking at subcategorizing verbs. It combines data from Chapter 4 and Chapter 6 into two methods of joint data analysis to exploit both spatial and temporal specificity. While there is a firm EEG literature on argument storage and diverse behavioral indications on argument retrieval at subcategorizing verbs, the spatiotemporal dynamics of these processes inside the underlying neuroanatomy are far from understood. When argument retrieval, as suggested by previous results, is common to subjects and objects, what is its functional relation to argument reordering? What is the spatiotemporal dimension of the neuroanatomical network established in Chapter 4 and Chapter 5?

In sum, the following chapters will approach the following questions: What is the behavioral relationship between argument storage and reordering (Chapter 3)? What is the functional neuroanatomy of argument storage and reordering, and what its connectivity? Are there individual differences in the functional neuroanatomy? How does the functional neuroanatomy subserving argument storage and reordering relate to the functional neuroanatomy underlying storage and rehearsal in working memory (Chapter 4)? Does a selective disruption of the involved regions' connectivity support the neuroanatomical dissociation of argument storage and reordering (Chapter 5)? What is the brain-electric counterpart of argument storage, regardless of the argument order (Chapter 6)? What are the spatiotemporal dynamics inside the functional-neuroanatomical brain network once argument storage has successfully been performed, and arguments need retrieval and reordering for final argument–verb linking (Chapter 7)? Since these questions have been approached with a number of acquisition and analysis techniques whose understanding is viable to understanding the experimental findings, Chapter 2 will provide the reader with a critical overview of these methods, followed by an exhaustive description of the experimental paradigm used in all experiments of the current thesis.

2

General Methodology

The goal of the current thesis is to understand the spatiotemporal brain dynamics that subserve argument storage and reordering. To this aim, spatially (i.e., magnetic resonance imaging (MRI); Section 2.1) and temporally (i.e., EEG; Section 2.2) fine-grained data acquisition and analysis methods were used, each of which has virtues and downsides. To exploit the former while circumnavigating the latter, detailed knowledge about the technical details of these analyses is important. Thus, this chapter will not so much focus on the basic principles of signal generation, but discuss data analysis *per se*[6].

2.1 Magnetic Resonance Imaging

2.1.1 Functional Magnetic Resonance Imaging

Assessing *in-vivo* the functional brain network underlying particular cognitive processes is made possible by fMRI, which can track neuronal activity on the whole-brain level by virtue of being sensitive to indirect measures of blood oxygenation. The physiological basis of this method is that neuronal activity during a cognitive task is followed by increased blood flow towards those neurons active in the task, since the neuronal metabolism consumes, *inter alia*, oxygen (Huettel et al., 2004). Blood contains hemoglobin, which binds oxygen and unloads it at consuming neurons. Thus, a brain region active in a cognitive task contains an increased amount of deoxygenated blood after activity. The magnetic moment of deoxygenated hemoglobin locally raises the energy level of the proton spins in surrounding

[6] For an introduction to the basic physical mechanisms behind MRI, I refer the reader to the exhaustive description by Huettel, Song, and McCarthy (2004); for an introduction to the electrophysiological basis of EEG signal generation, overviews can be found in the collection by Niedermeyer and Lopes da Silva (1993).

hydrogen molecules (Pauling, 1935). This shortens the time for the re-establishment of the original energy level of these spins (i.e., T2*), which leads to a delayed larger post-excitation MR spin echo in brain regions that engaged in a cognitive process during MR excitation (Huettel et al., 2004; Thulborn, Waterton, Matthews, & Radda, 1982), called the blood-oxygen-level-dependent (BOLD) signal. The correlation between neural activity and the BOLD signal was verified by Logothetis et al. (2001), who showed that BOLD correlates with local field potentials during intracranial recordings in monkeys. Computationally, fMRI quantifies the BOLD response during an experimentally administered cognitive task inside the cells of a three-dimensional spatial image grid of variable spacing. Depending on the acquisition duration, an fMRI experiment will acquire a large number of such images.

To reliably quantify the BOLD response, spatial correction of the acquired image volumes is necessary: Humans inside an MR scanner exhibit undesired movement, further amplified by physiological factors such as respiration and heartbeat. In effect, the values in an given sub-volume—or voxel—along the experimental time line do not correspond to a single brain voxel. To re-establish spatial correspondence, all images of the time line are re-aligned to the first image acquired (Friston, Frith, Frackowiak, & Turner, 1995). In addition to this spatial correction, temporal preprocessing steps are needed: Since whole-brain fMRI involves a temporally-staged slice-by-slice acquisition of two-dimensional voxel grids, there is a temporal offset between image slices (Sladky et al., 2011). Slice-timing correction compensates for this by first estimating an individual voxel's activation time course and then shifting its phase (Henson, Burgess, & Frith, 1999). Further preprocessing involves correcting for magnetic-field inhomogeneities (Jezzard & Balaban, 1995) and filtering of slow global signal changes (Della-Maggiore, Chau, Peres-Neto, & McIntosh, 2002). Typically, preprocessing ends with normalization of the individual data to a standard brain template, as well as spatial smoothing.

Statistical analysis of fMRI data requires accounting for an underlying property of the BOLD signal: BOLD is a sluggish measure of brain activity, since oxygenated blood reaches a consuming region only with a temporal delay (roughly 5 s; cf. Buxton, Wong, & Frank, 1998)[7]. As a result, BOLD magnitude depends on factors such as epoch length and stimulus length, which is compensated for by convolving the raw data with an *a-priori* hemodynamic-response function (HRF) that mimics

[7] This delay differs inter-individually and inter-regionally; see Schacter, Buckner, Koutstaal, Dale, and Rosen (1997) and Aguirre, Zarahn, and D'Esposito (1998) for discussion.

the prototypical BOLD time course (Glover, 1999). After convolution, an average BOLD signal is calculated for the experimental condition of interest and statistically compared to either a global baseline or another experimental condition. The resulting contrasts are then submitted to across-participants general-linear-model (GLM) statistics.

When using fMRI, it is important to keep in mind its methodological limitation: Due to the sluggishness of the BOLD response, fMRI data acquired with whole-brain coverage and at reasonable spatial resolution do not have a high temporal resolution. Thus, meaningful temporal conclusions (i.e., in the order of seconds) can only be drawn for stimuli of sufficient length—such as sentences (Friederici, Fiebach, et al., 2006) or extended delay periods (Ravizza, Hazeltine, Ruiz, & Zhu, 2011). Alternatively, a temporal dimension can be added to the data by recording data from the same paradigm used during fMRI data acquisition with a temporally-fine-grained acquisition modality (e.g., EEG), preferably in parallel to exclude any test–retest effects. An example for a combined analyses is given in Chapter 7 of the current thesis, in which EEG data were used to deduce the activation time course of a BOLD effect, and the activation magnitude of a BOLD effect was used to constrain an EEG topography.

2.1.2 Voxel-Based Morphometry

To perform *in-vivo* structural whole-brain analyses, voxel-based morphometry (VBM) allows for across-participant voxel-wise analyses of local microstructural brain-tissue properties (Wright et al., 1995). Its main challenge is to establish inter-individual voxel-wise spatial correspondence. While the inter-individual variability of anatomical features such as gyrification or thickness of the gray-matter layer is the main problem in alignment (Mechelli, Price, Friston, & Ashburner, 2005), it forms the basis of statistical analysis (cf. Ashburner & Friston, 2001): Paradoxically, efficient spatial alignment needs to enforce the global leveling-out of variability while locally keeping it.

To achieve spatial alignment, each voxel's gray value is first automatically assigned a probability value of belonging to one of multiple *a-priori*-defined tissue classes (Ashburner & Friston, 2005). For a typical anatomical brain scan, the original representation of light gray shades (fatty tissue, e.g. white matter) and dark gray shades (watery tissue, e.g. gray matter) is mapped onto p-values (exemplary tissue-probability-map-(TPM)-segmented gray-matter images are shown in panel A of Figure 2.1). While previous algorithms refined segmentation by applying this procedure recursively (Good et al., 2001), the current diffeomorphic-anatomical-registration-using-exponentiated-lie-algebra (DARTEL) approach involves an interactive progression of segmentation and registration (Ashburner, 2007). After segmentation (typically into white and gray matter, cerebrospinal fluid, and bones[8]), inter-individual alignment of the segments of interest (see Section 4.2.6.4) takes place. The approach used in the current thesis recursively warps the segmented individual tissue volumes of a given class onto their mean (Ashburner, 2007) to generate individual deformation fields and a constantly-self-refining template (an exemplary template, based on 24 participants from the current thesis, is shown in panel B of Figure 2.1)[9].

Finally, a process termed modulation is applied to the segmented and co-registered tissue volumes. Modulation compensates for the fact that non-linear registration compresses or inflates individual voxels to individual degrees: If, for instance, a given brain region is spatially extended in one participant but spatially confined in another participant, warping them to their common mean compresses the region in one participant while inflating it in another. To reduce this confound, each voxel's initial p-value is multiplied by its relative volume prior and after warping (Good et al., 2001), effectively darkening compressed voxels and lightening up inflated ones. The modulated volumes are then smoothed and optionally warped to a standard space (see panel C in Figure 2.1 and Section 4.2.6.4).

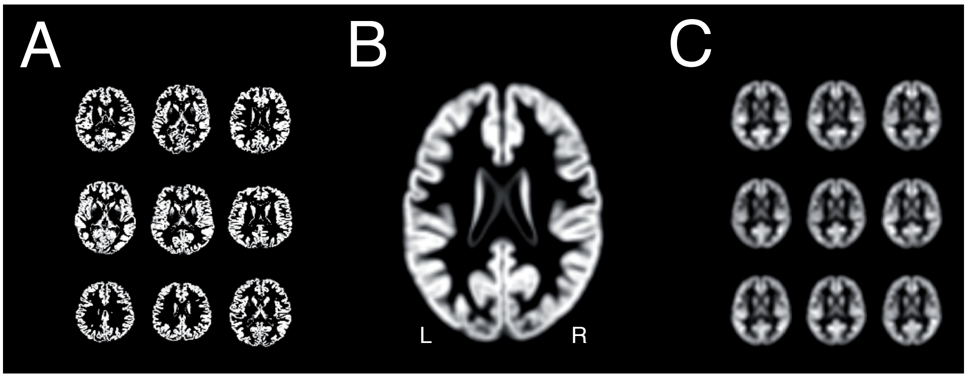

Figure 2.1: Segmentation, template-generation, and co-registration steps in the VBM pipeline: (A) individual gray-matter segments of 9 exemplary participants from the current investigation; (B) average group template after six rounds of iterative averaging; (C) final co-registered, smoothed, and Montreal-Neurological-Institute-(MNI)-normalized gray-matter segments of the same participants.

[8] Further tissue classes can be introduced, such as a lesion class for automated lesion mapping (Seghier, Ramlackhansingh, Crinion, Leff, & Price, 2008).

[9] Because of its superior quality (Klein et al., 2009; Takao, Abe, & Ohtomo, 2010; Yassa et al., 2010), DARTEL is used in functional imaging as well (cf. Wilson et al., 2010).

An important procedure that should be applied prior to statistical assessment relates to the non-uniform smoothness of segmented and co-registered structural brain images: Regions that exhibit a large spatial inter-participant correspondence before co-registration will keep a comparably low degree of spatial smoothness after co-registration as compared to regions with low spatial inter-participant correspondence—*et vice versa*. As a result, the occurrence probability of significant statistical tests increases in smooth regions, invalidating cluster-size statistics. To overcome this pitfall, Worsley, Andermann, Koulis, MacDonald, and Evans (1999) and Hayasaka, Phan, Liberzon, Worsley, and Nichols (2004) introduced a so-called non-stationarity correction, correcting observed clusters for the across-sample spatial smoothness of the underlying region.

While VBM is sophisticated, it is also limited: For once, computationally economical non-linear warping of a brain-tissue volume needs to constrain its spatial resolution (typically to 1.5-mm isotropic voxels). Furthermore, local inter-individual gyrification differences may result in registration errors (Bookstein, 2001). It should also be noted that the tissue-probability values assessed statistically do not exhibit an unambiguous neuroanatomical correlate, but rather reflect a mixture of neuron size, arborization of dendrites or axons, gray-matter thickness, and increased gyrification (Mechelli et al., 2005). While these concerns limit the neuroanatomical precision and meaningfulness of VBM results (Ridgway et al., 2008), they do certainly not imply arbitrariness of VBM-based microstructural structure-to-function mapping on a neuropsychologically adequate level—especially so if structural measures are interpreted in concert with their functional correlates (see Section 4.2.6.4).

2.1.3 Diffusion-Weighted Imaging and Diffusion-Tensor Imaging

While functional neuroimaging can investigate the building blocks of the functional neuroanatomy of language processing and VBM analyses are capable of assessing the micro-structural properties of the underlying brain tissue, the concerted interplay of these neuroanatomical substrates is only possible given structural connections between the concerned regions—which can be assessed using diffusion-weighted imaging (DWI). This technique tracks the local diffusion of water molecules, that is, proton-movement-related properties of brain tissue (Le Bihan et al., 1986; Mori, Wakana, Nagae-Poetscher, & Van Zijl, 2006).

The physical basis of DWI is the phenomenon that brain-tissue macrostructure constrains the natural, random, three-dimensional diffusion of water molecules (Brown, 1827): In an unconstrained medium, water molecules move freely and randomly due to internal thermodynamic excitation (Einstein, 1905), leading to so-called isotropic diffusion. However, external forces from surrounding particles—such as the myelin sheath of neuronal axons, *inter alia*—constrain this free random motion, effectively increasing diffusion directionality along white-matter fibers and decreasing diffusion directionality perpendicular to white-matter fibers, leading to so-called anisotropic diffusion (Mori et al., 2006).

To detect anisotropic diffusion, DWI applies symmetric spin-echo MR gradients along multiple spatial directions (at least six for a three-dimensional brain voxel). The MR signal is maximally attenuated (i.e., the MR echo is minimized) for the gradient applied in the main diffusion direction of the water molecules in a given voxel (Basser, Mattiello, & Le Bihan, 1994; Basser & Pierpaoli, 1996; Reese, Heid, Weisskoff, & Wedeen, 2003). The spin echo from all acquired diffusion directions in a given voxel forms a matrix, allowing for the voxel-wise reconstruction of the diffusion tensors to enable both the calculation of characteristic diffusion parameters and whole-brain structural-connectivity analyses.

The diffusion parameter most frequently analyzed in white-matter studies is the fractional anisotropy (FA), which parametrizes the shape of the diffusion tensor by dividing the variance of the spin-echo matrix eigenvalues by the overall magnitude of the tensor matrix. Basser and Pierpaoli (1996) showed that the FA effectively approaches zero in isotropic media (e.g., a sphere such as a drop of cerebrospinal fluid) and one in anisotropic media (e.g., a tube such as an axon)[10]. According to Basser et al. (1994), this computation ensures a more reliable estimation of the main diffusion direction: A diffusion-weighted imaging protocol that can be applied in an ethical scan time—and thus the matrix of spin echoes—does not provide an exhaustive picture of diffusion directionality. The inclusion of all acquired gradient directions in the computation of FA compensates for this problem.

Based on the voxel-wise calculation of diffusivity, tractography can be performed, which allows for the *in-vivo* assessment of short- and long-range connectivity in the brain (cf. Figure 2.2, panel C). To this end, algorithms for tracking the contiguity of the diffusion tensor across adjacent voxels have been

[10] Further information about the underlying white matter can be derived by calculating the axial (first eigenvalue of the diffusion tensor; i.e., axonal direction, cf. Galantucci et al., 2011; see also panel B in Figure 2.2), radial (mean of the two eigenvalues; i.e., axonal diameter, cf. Phillips et al., 2010), and mean diffusivities (mean of three first eigenvalues; i.e., average per-voxel diffusion irrespective of directionality, cf. Papoutsi, Stamatakis, Griffiths, Marslen-Wilson, & Tyler, 2011).

devised. The approach used in the current thesis assesses this contiguity by considering the deflection angle between diffusion tensors from adjacent voxels (Lazar et al., 2003)—if a smooth deflection of the incoming vector by the target eigenvector is given, a connection will be established; if a deflection angle is too steep, tracking will stop at the voxel. This procedure leads to a realistically-smooth curvature of the reconstructed fiber tracts, avoiding erroneously-steep tracking-continuation angles. When applied to all brain voxels, a tractogram (as shown in panel C of Figure 2.2) results, based on which selective deterministic (i.e., voxel-to-voxel, see Chapter 4) or explorative probabilistic (i.e., all tracts departing from a given voxel, see Chapter 5) fiber tracking can be performed.

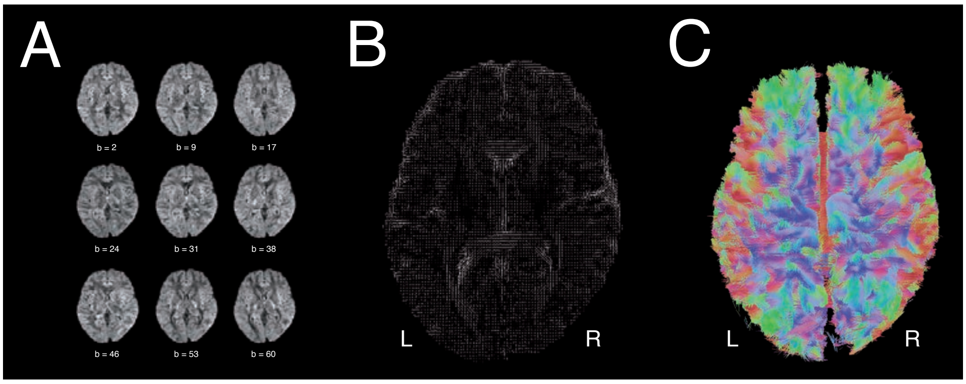

Figure 2.2: Overview of DWI analysis steps: (A) axial slices through diffusion-weighted data for 9 exemplary diffusion directions in a single participant; (B) reconstructed diffusion-tensor orientations for a single axial slice of the same participant; (C) exemplary three-dimensional result of the whole-brain fiber-tracking procedure.

When tract selection is constrained by functional-imaging or source-localization results, statistical analyses on the diffusion parameters are a powerful technique for establishing white-matter structure-to-function correlations—especially when combined with sophisticated non-linear white-matter-alignment algorithms (see Chapter 4). However, since fiber tracking necessitates high-level reconstruction techniques based on the calculated diffusion parameters, it involves the propagation of DWI-inherent degrees of freedom: At a typical resolution of DWI data, the FA of a given voxel does not necessarily provide the main diffusion direction of a single white-matter fiber tract. Rather, the voxel may contain fibers that are crossing, merging or fanning out, leading to an ambiguous FA value, potentially introducing streamlines of arbitrary angles into any diffusion-tensor-imaging

(DTI) reconstruction (Lazar et al., 2003). While an increase of the spatial resolution of DWI-data acquisition would circumvent this problem, it would also boost acquisition time above the duration practical and ethical for a human participant. As a compromise, parallel enhancement of acquisition resolution and speed (e.g., Jian & Vemuri, 2007) in combination with more sophisticated reconstruction methods that can extract multiple diffusion tensors from a single voxel (e.g. Descoteaux, Deriche, Knösche, & Anwander, 2009) seems a promising future direction. Having considered the acquisition and analysis methods for functional and structural MRI, the following section will provide a critical discussion of the EEG data analysis methods employed in the current thesis.

2.2 Electroencephalography

As noted in Section 2.1.1, MRI exhibits a high spatial resolution, but lacks temporal resolution. When questions about the timing of a cognitive process are in the focus of research, EEG is a classical tool: Depending on the recording hardware, EEG can reflect electrophysiological activity on the millisecond level and below (Rugg & Coles, 1995). The EEG records ongoing scalp-level voltage fluctuations that neurophysiologically originate from ion flow through dendritic membranes of post-synaptic neurons (mostly cortical pyramidal cells; cf. Allison, Wood, & McCarthy, 1986 and Speckmann & Elger, 1993).

When a sufficient number of neurons is oriented in parallel, a synchronous discharge of their assembly will yield an electric current between their apical dendrites (negative polarity) and cell bodies (positive polarity), leading to a measurable voltage change perpendicular to the cortical sheath (Regan, 1989). Electrodes positioned at the scalp can record such voltage changes against a remote reference electrode, which is positioned at a site relatively unaffected by the ongoing electrophysiological activity. The raw signal from the scalp electrodes is amplified on-line (typically at 60–100 dB; Kamp, Pfurtscheller, Edlinger, & Silva, 1993) to increase its magnitude over the noise exhibited by the analog recording equipment and to meet the dynamic range and recording resolution of the digital recording equipment.

2.2.1 Event-Related Brain Potentials

Since electrophysiological brain activity is the substrate of any cognitive process, external stimulation modulates the EEG. While the modulatory effect from a single stimulation (i.e., ± 1–$20\ \mu V$) is only a small fraction of the ongoing brain activity (as large as $\pm 100\ \mu V$), repeated stimulation with members of a pre-defined stimulus class and subsequent averaging across those epochs of the EEG that follow stimulation can unhinge the event-related part—the ERP—from the background EEG. When the ERPs to a set of stimulus classes are compared statistically, their difference and variance can guide inferences on the magnitude of the involvement of a neurophysiological process in the processing of these stimuli; this neurophysiological process is then presumed to underlie the cognitive process linked to the difference in stimulus classes (Kutas & Van Petten, 1994; Kutas, Van Petten, & Kluender, 2005).

To obtain a reliable ERP, preprocessing of the raw EEG is necessary. The raw EEG contains artifacts (i.e., voltage differences induced by electric currents stemming from internal muscular activity or external gear; for an overview, see Blume, Kaibara, & Young, 1995), which outsize the ERP in magnitude and thus may drive spurious ERP effects if not removed from the EEG. Various automatic techniques are available for artifact identification and removal, such as filtering (e.g., for steady-wave artifacts such as the mains frequency and its harmonics; cf. Edgar, Stewart, & Miller, 2005), amplitude-based identification (e.g., for muscular activity; cf. Oostenveld, Fries, Maris, & Schoffelen, 2011) or independent-component analysis (ICA; Bell & Sejnowski, 1995; Delorme, Sejnowski, & Makeig, 2007).

While ERPs are a relatively low-cost and easy-to-use method to study the neurophysiological apparatus, ERP analysis makes strong assumptions, some of which have been criticized. First, the assumption of latency invariance (which legitimizes across-trial averaging) may only hold for ERP components that link to physical stimulus properties—but not for those which reflect higher-level cognitive processing, for which jitter of single-trial ERPs increases (cf. Donchin & Heffley, 1978). Different circumventions have been devised, such as an artificial establishment of across-trial temporal correspondence (Woody, 1967); more recently, ICA techniques have been used to avoid averaging altogether and enable the analysis of single-trial ERPs (Jung et al., 2001; Turi et al., 2012). As a second questionable assumption, the classical, two-dimensional characterization of ERPs by latency and amplitude potentially neglects the multi-dimensionality of the neurophysiological bases of the EEG. Traditional ERP analysis assumes ongoing oscillatory activity—which constitutes a major part of the raw EEG—as random, normally distributed noise, whereas the ERP is assumed to be independent and invariantly time-locked to the stimulus. Since it is known that oscillations are functionally meaningful (cf. Berger, 1929; see also Section 2.2.2), these simplifications potentially underestimate stimulus-linked, but latency-jittered oscillatory influences on the ERP, such as band-specific amplitude increases or phase resetting (Başar, 1998;

Buzsáki, 2006). It is unclear whether oscillatory factors underlie the ERP altogether (for review, see Klimesch, Sauseng, Hanslmayr, Gruber, & Freunberger, 2007) or constitute an independent marker of electrophysiological brain activity (Fell et al., 2004; Fuentemilla, Marco-Pallarés, & Grau, 2006; Mäkinen, Tiitinen, & May, 2005). In either case, their potential condition-specific effect is not accounted for in the ERP and may be a lurking variable in statistical analysis.

2.2.2 Time–Frequency Analysis

While ERPs are a valuable tool for analyzing stimulus-dependent electrophysiological brain activity, they are restricted to capturing time-locked parameters of the EEG; also, their statistical analysis is vulnerable to condition-specific oscillatory effects (Makeig, Debener, Onton, & Delorme, 2004). Time–frequency analysis quantifies these oscillatory contributions to the EEG; on the scale that is accessible to scalp-level EEG, neural oscillations reflect the continuous periodic fluctuation of the membrane potentials of large groups (> 1000; cf. Nunez & Srinivasan, 1981) of cortical or subcortical neurons that are synchronized by synaptic interaction (for review, see Bremer, 1958 and Wang, 2010)[11].

Neural oscillations have been early found to be cognitively meaningful (cf. Berger, 1929), playing a major role in local neuronal processing and long-distance communication between neuronal ensembles. Potentially, local processing involves high-frequency oscillations, whereas long-distance communication involves lower frequency bands (Lisman & Idiart, 1995; Sarnthein, Petsche, Rappelsberger, Shaw, & von Stein, 1998): Groups of neurons may locally increase the amplitude of their fluctuations or lock their phase with external stimuli, other groups of neurons may lock their fluctuations with distant neuronal groups to enable joint processing.

The basic assumption underlying TFR is that oscillatory activity can be exhaustively expressed by a set of sinusoids (Buzsáki, 2006), defined by their amplitude and phase for a given frequency window. Decomposition of the EEG signal into such a set of amplitude–phase duplets (see panel (B) in Figure 2.3) for a given frequency window is classically performed by the Fourier transform (Fourier, 1822). While the output of this method is restricted to either the time or the frequency domain (since it assumes an infinite stationary signal), the later introduced Gabor transform—also known as short-time

[11] The full oscillatory spectrum is commonly divided into δ (0.5–4 Hz), θ (4–8 Hz), α (8–12 Hz), β (12–30 Hz), and γ (> 30 Hz) bands. The arbitrariness of this nomenclature has historical reasons.

Fourier transform (Allen, 1977)—enables decomposition for pre-defined time windows (which assumes stationarity only for each consecutive time window). While the Gabor transform limits the size of the analysis time window[12], the more recently introduced wavelet transform (Grossmann & Morlet, 1984; Lachaux, Rodriguez, Martinerie, & Varela, 1999; see also Chapter 6) circumvents this restriction by convolving the EEG across time–frequency windows with short sinusoidal periods of rising and falling amplitude (Samar, Bopardikar, Rao, & Swartz, 1999; see panel (A) in Figure 2.3)[13].

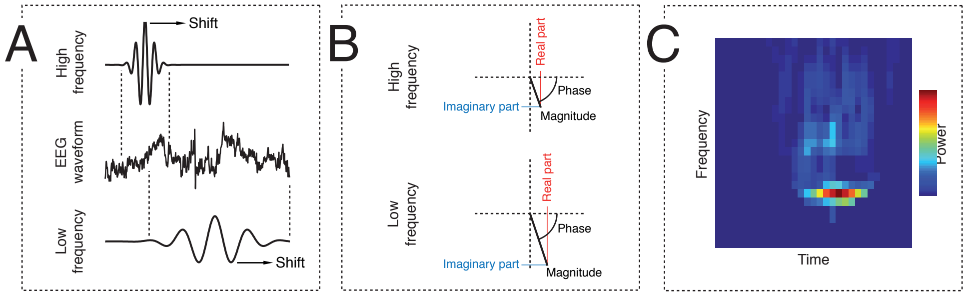

Figure 2.3: Overview of TFR steps in a wavelet analysis; (A) wavelet convolution of the preprocessed EEG and derivation of transformation coefficients for each time window (small-scale wavelet for high frequencies at the top, large-scale wavelet for low frequencies at the bottom); (B) calculation of phase and magnitude of the frequency components based on the transformation coefficients; (C) resulting time–frequency representation of the original signal, color shading indicating power inside a time–frequency bin (cf. Samar et al., 1999 and Roach & Mathalon, 2008).

After transformation of the EEG signal, the desired amplitude and phase parameters for a given frequency and time window correspond to the real and imaginary parts of the complex output of the short-time Fourier or wavelet transform (Roach & Mathalon, 2008); the squared Euclidean distance between the real and imaginary parts corresponds to the power inside a time–frequency window of the EEG spectrum (see panel (B) in Figure 2.3). Any of these parameters for a given experimental condition can then be compared to their counterpart in a baseline interval or another experimental condition to quantify stimulation-dependent changes.

[12] This is due to Heisenberg's (1927) uncertainty principle, which states that two parameters of a given observation cannot be measured simultaneously (cf. Quiroga, 1998); in other words: The Gabor transform *per definitionem* cannot exactly determine both amplitude and phase for small time windows.

[13] The scalability of these wavelets links their time and frequency domains and implies that time windows decrease with the analysis frequency. While this permits an asymptotically short analysis time window for high frequencies and an asymptotically long analysis time window for low frequencies, it also limits the frequency resolution (for discussion, see Başar, Demiralp, Schürmann, Başar-Eroglu, & Ademoglu, 1999 and Samar et al., 1999).

2.2.3 Source Localization

To infer the neuroanatomical sources of the results of ERP or TFR, source localization seeks to find those spatially-localized currents inside a model brain volume that best explain a measured scalp-level ERP or time–frequency topography (Ramírez, Wipf, & Baillet, 2010). The electrophysiological basis for source localization is that active neuronal compounds can be well expressed by directional currents in space (de Munck, Van Dijk, & Spekreijse, 1988; cf. Section 2.2.1), whose magnitude fluctuations over time drive the EEG topography.

The first step to source localization is to model how hypothetical dipole activity at pre-chosen sites inside a model brain volume propagates towards the scalp-level EEG electrodes, which is called the forward model or lead-field matrix (for review, see Grech et al., 2008). It contains micro-level information about the local current density of individual neurons as well as macro-level information about the propagation of electric fields inside the brain and the different head tissues. While early analyses had used single (Frank, 1952) or multiple concentric (Berg & Scherg, 1994) spheres to model the head's macro structure, more recent boundary-element models (BEMs) use a finer-grained three-dimensional representation of the brain, skull, and scalp surfaces (Besl & McKay, 1992; He et al., 1987; cf. Section 6.2.4 and Section 7.2.5). Following the classification of Grech et al. (2008), parametric (a.k.a. dipole models) and non-parametric (a.k.a. distributed-source models) forward models exist: Parametric models distribute a small number of dipoles across the model brain volume, whose locations and orientations are subject to solution. Non-parametric models distribute a large number of dipoles at known locations across the model brain volume, whose orientations are subject to solution.

In a second step, the forward model is inverted: While the lead-field matrix derives a hypothetical scalp topography based on hypothetical neural generators, inversion enters a measured ERP or time–frequency topography into the forward model to solve it for the neural generators. Both classes assess the ability of the dipole arrangement (location, orientation, amplitude) to generate the to-be-localized data by quantifying the divergence between generated and measured data.

Nevertheless, a drawback of source localization is that it suffers from a spatial version of the inverse problem (Ambarzumian, 1929; Helmholtz, 1881): In principle, a scalp-level EEG topography at a given time point can result from an infinite number and infinite arrangements of cortical generators (for review, see Grech et al., 2008). While this problem is mathematically ill-posed when only the EEG topography is provided for solution, it can be alleviated by incorporating prior knowledge (Ramírez et al., 2010): The model brain volume used in the forward computations can be further constrained by incorporating individual structural-MRI data. Second, individual EEG electrode positions can be determined during recording and linked exactly to the model brain volume. Thirdly, *a-priori* knowledge from prior or parallel fMRI studies can be used to constrain dipole positions (cf. Section 7.2.5).

After having critically reviewed the MRI and EEG acquisition and analysis techniques used in the current thesis, the following section will introduce the experimental paradigm used in all of the current experiments. Because this thesis interfaces linguistic syntax, experimental psycholinguistics of sentence processing, and the cognitive neuropsychology of working memory, this will concern the linguistic, psycholinguistic, and psychological considerations involved in the design of the current paradigm.

2.3 Experimental Paradigm

To address the research questions of the current thesis (cf. Chapter 1), German sentences were constructed that allow for the orthogonal manipulation of one factor each solely affecting argument-reordering and argument-storage and -retrieval demands. The 2 × 2 factorial design accordingly crossed the factors argument reordering (subject-first versus object-first argument order) and argument storage and retrieval (short versus long argument–verb distance), as shown in Figure 2.4.

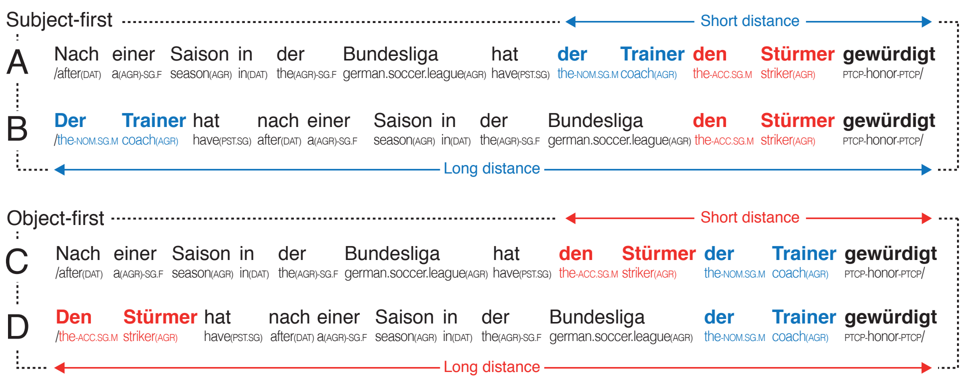

Figure 2.4: Overview of experimental materials; upper panel shows subject-first orders in the short (A) and long (B) distance variants, lower panel shows object-first orders in the short (C) and long (D) distance variants; interlinear glosses are provided below each example; subjects are marked in bold blue, objects are marked in bold red, main verbs are marked in bold black; arrows illustrate the argument–verb distance; (A) to (D) translate *After a season in the German soccer league, the coach honored the striker*.

In the first condition (A), subject and object are adjacent to the main verb—the argument order is subject-first, and the argument–verb distance is short. In the second condition (B), the argument order is still subject-first, while the subject is at the sentence beginning now. This increases storage demands by lengthening the retention interval for the critical information of the subject noun phrase. The third (C) and fourth (D) conditions involve the same two distance variants, but in object-first argument order: The object is in front of the subject. The manipulations maximized the contrast along an argument-reordering and an argument-storage-and-retrieval dimension, operationalizing argument reordering as an executive operation on the arguments stored in working memory (cf. Wingfield & Butterworth, 1984). The argument-reordering factor manipulated the relative argument order, while not interfering with the argument-storage-and-retrieval factor.

2.3.1 Linguistic Considerations

To maximize the short–long contrast (see Section 2.3.3), past-perfect tense was used in the experimental materials. In German, this tense necessitates the participle at the sentence-final position, enabling the resolution of the sentences' argument–verb dependencies only at the end of the sentence: Because the sentence-final participle is the main verb in German past-perfect tense, its lexical entry specifies the number and type of arguments and θ-roles (Binder, Duffy, & Rayner, 2001; Comrie, 1993).

German past-perfect tense also necessitates an auxiliary verb in sentence-second position, which provides information on the gender and number of the subject argument across conditions (Klein, 2000), thus enabling partial establishment of the subject–verb dependency across experimental conditions. However, the auxiliary marks neither the number nor the relative order of arguments—that is, the verb's subcategorization frame and θ-grid is not provided.

To further prevent an unbalanced premature determination of the verb's subcategorization frame and the relative argument order, the object in the subject-first sentences and the subject in the object-first sentences were positioned at the identical, verb-adjacent position across experimental conditions. Hence, across conditions, both a subject and an object would await integration in working memory at the verb-adjacent position. At all sentential positions prior to the verb, both subject-first and object-first sentences did not reveal the total number of arguments (e.g., the sentences theoretically still allowed for additional arguments of a ditransitive verb to occur).

2.3.2 Psycholinguistic Considerations

In addition to controlling for formal linguistic features (see Section 2.3.1), the design of the current paradigm aimed at controlling for a number of previously-reported processing phenomena which, if unaccounted for, could—possibly condition-specifically—confound the experimental manipulations.

First, the absolute position of the main verb in our stimuli is kept constant across conditions to counter an effect that has been termed sentence-final speed-up (Demberg & Keller, 2008; Ferreira & Henderson, 1993). Sentence-final speed-up describes the phenomenon that processing is cumulatively facilitated towards the end of sentences (Bastiaansen & Hagoort, 2006), potentially as an effect of the cumulative decrease in the number of possible sentence continuations (Kutas, Lindamood, & Hillyard, 1984; Kutas & Van Petten, 1994; Levy, 2008). Since this decreased processing difficulty has differential effects at different sentential positions, a variation of the main verb's position across experimental conditions can drive spurious effects, which would have been a particular problem when processing effects at the main verb are the object of study (e.g., the analyses described in Chapter 7).

To counter the contrary processing phenomenon of sentence-final wrap-up (Friederici & Frisch, 2000; Friedman, Simson, Ritter, & Rapin, 1975; Osterhout & Holcomb, 1993), we added an identical conjunct clause to all sentences of each four-sentence set (e.g., "und die Entwicklung bestätigt.", translating to *and stated the development.* for the examples in Figure 2.4). Sentence-final wrap-up means that processing difficulty increases in sentence-final regions, potentially due to working-memory saturation (King & Just, 1991) or argument–verb integration. Since the working-memory resources are limited (see Section 2.3.3), storing additional material gets increasingly difficult at the sentence ending (cf. Meyer, 2009). In sum, the conjunct clause separated the main verb (i.e., the critical integration point in a verb-final sentence) from the region in which wrap-up effects become visible.

As an additional global control measure to counteract the processing influence of individual lexical frequencies on the dependent variables (Allen, Badecker, & Osterhout, 2003; Van Petten, 1993; Van Petten, Kutas, Kluender, Mitchiner, & McIsaac, 1991), the words at the corresponding sentential positions across the 48 four-condition stimulus sets were selected according to a lemma-frequency and syllable-count matching using the CELEX database (Baayen, Gulikers, & Piepenbrock, 1995). Specifically, each verb's subject and object were balanced in syllable count and lemma frequency to avoid systematic confounding of the argument-reordering manipulation: If objects were of consistently higher lexical frequency than subjects across the stimulus set, any effects of increased argument-reordering demands might cancel out due to facilitated lexical access. In a similar vein, semantic coherence of each individual subject–object–verb set was ensured by a sentential-neighborhood analysis using the Projekt-Deutscher-Wortschatz database (Biemann, Bordag, Quasthoff, & Wolff, 2004): cross-linguistic behavioral work has shown that arguments and verbs semantically pre-activate remaining members of their argument–verb set (i.e., arguments and verbs) that they frequently co-occur with (Boland, 1993; Boland, Tanenhaus, Garnsey, & Carlson, 1995; Kamide et al., 2000, 2003; Marslen-Wilson, 1973; Pappert, Schließer, & Pechmann, 2008; Trueswell & Kim, 1998; Tsuzuki et al., 2004); if uncontrolled for, unbalanced typicality of the two arguments might have resulted in asymmetrical pre-activation effects.

2.3.3 Psychological Considerations

To experimentally query working-memory storage and retrieval, the current experiments manipulated argument–verb distance, that is, the length of an argument–verb dependency, which is a classical approach ever since it was recognized that long-distance dependencies impede comprehension (Behaghel, 1923; Cowper, 1976; Frazier, 1987; Gibson, 2000; Yngwe, 1960).

From the working-memory perspective of the current thesis, decay of the stored argument is the reason for the increasing processing difficulty associated with long argument–verb dependencies (cf. Baddeley, 2012; Miyake & Shah, 1999; Peterson & Peterson, 1959). With respect to our short–long dimension, this entails that either the subject or the object argument in a verb-final sentence will decay relatively more in a long as compared to a short argument–verb dependency. To maximize the contrast between the short and long conditions, the arguments in the two short conditions were kept immediately adjacent to the sentence-final main verb, minimizing the storage interval and according retrieval demands. In contrast, the two long conditions maximized the argument–verb distance by putting either the subject or the object argument immediately at the sentence beginning. Thus, the storage interval in the short conditions crosses a single phrase (i.e., the object in the short subject-first sentence and the subject in the short object-first sentence), whereas the storage interval in the long conditions crosses four phrases. The use of the past-perfect tense (see Section 2.3.1) ensured that storage demands be identical for the two short and the two long conditions, respectively.

2.3.4 General Hypotheses

The general hypotheses for the current experimental paradigm are the following: The manipulation of argument order (subject- versus object-first sentences) is assumed to increase reordering demands. This should increase behavioral (e.g., reaction time) and functional-neuroanatomical (e.g., BOLD) measures of processing difficulty for object- as compared to subject-first sentences. The experimental manipulation of argument–verb distance (short versus long argument–verb-dependency sentences) is assumed to increase both storage and retrieval demands and lead to according increases in the dependent measures when long argument–verb-dependency sentences are compared to short argument–verb-dependency sentences. For more detailed hypotheses with respect to the specific data acquisition and analysis methods, the reader is referred to the introductions of the following experimental chapters.

3

Behavioral Study

3.1 Introduction

In order to understand a sentence it is crucial to determine who is doing what to whom. This necessarily requires to link the doing—the verb—to the who, what, and whom—the arguments, e.g. subject and objects. To succeed, sentence processing has to both store arguments in working memory until the verb is reached (Aoshima, Phillips, & Weinberg, 2004; Clahsen & Featherston, 1999; Nakano, Felser, & Clahsen, 2002; Nicol et al., 1994; Nicol & Swinney, 1989) and reorder the arguments in case of object-first orders to re-establish the language's idiosyncratic argument order. While argument storage and reordering are intimately intertwined, we do not know exactly how.

There are proposals that inherent properties of working memory such as decay are sufficient to explain both argument storage and argument reordering (Nakatani & Gibson, 2008; Peterson & Peterson, 1959; Shulman, 1970; Vasishth & Lewis, 2006). These theories are based on behavioral paradigms that tap working memory by manipulating the argument–verb distance, thereby lengthening the argument-storage interval. Some of these paradigms have yielded increasing processing difficulty with increasing argument–verb distance (in English: Frazier, 1987; Gibson, 2000; Grodner & Gibson, 2005), whereas others found decreasing processing difficulty (in English: Jaeger, Fedorenko, & Gibson, 2005; in German: Konieczny, 2000; Konieczny & Döring, 2003; in Hindi: Vasishth, 2003). This contrast is usually explained by differences in speakers' working-memory experience and language-specific working-memory demands. These interpretations are interesting, but the behavioral findings have not been substantiated by recurrence to concrete neurocognitive substrates.

Experimental results from languages that allow for argument-order variations question these approaches: In German (Friederici, Fiebach, et al., 2006), Chinese (Hsiao & Gibson, 2003), Finnish (Hyönä & Hujanen, 1997), Hungarian (MacWhinney & Pléh, 1988), Korean (Mazuka et al., 2002), and Japanese (Miyamoto & Takahashi, 2002), object-first sentences were found to increase processing load, even when controlling for argument–verb distance. Furthermore, there is evidence that retrieval of arguments from working memory is insensitive to argument order (Nicol, 1993; Osterhout & Swinney, 1993). Working-memory-inherence approaches also disregard the strong evidence for the neural reality of argument reordering during sentence processing: Cross-linguistic neuroimaging work from German (Friederici, Fiebach, et al., 2006; Grewe et al., 2005), Hebrew (Ben-Shachar et al., 2004), and Japanese (Kim et al., 2009; Kinno, Kawamura, Shioda, & Sakai, 2008) has found that activation of the left inferior frontal gyrus (IFG) increases with argument-reordering demands. Although these languages use morphological markings to distinguish arguments, these markings may produce ambiguous structures, which can only be processed on the basis of argument-order information.

To elucidate on the conceptual dialectics of argument storage and reordering during sentence processing, we crossed an argument-order manipulation with an argument–verb distance manipulation in a behavioral study. To specifically pinpoint the locus of the assumed processing-difficulty sources, a classical SPR (i.e., on-line) experiment in combination with a rating (i.e., off-line) study was performed. The hypothesis is that both increasing argument-storage demands (as induced by increasing argument–verb distance) and increasing argument-reordering demands (as induced by changing subject-first to object-first order) linearly increase processing difficulty, independently of the respective second factor.

3.2 Methods

3.2.1 Participants

Forty participants took part (mean age 23.4 years, standard deviation (SD) 2.8 years; 20 females; all native speakers of German). All of them were right-handed as assessed by an abridged version of the Edinburgh Inventory (Oldfield, 1971), reported no neurological deficits, and had normal or corrected-to-normal vision. They never participated in another study using these stimuli or experimental paradigm and were naïve to the purpose of the study. They were paid €3.50 for participation of half an hour.

3.2.2 Materials

The full 192-stimuli set (see Section 2.3) was divided into four lists, and each subset was interleaved and pseudo-randomized with 72 fillers from previous experiments using MATLAB® (The MathWorks, Inc., Natick, MA, USA) scripts, giving a total of 120 stimuli per list and participant.

3.2.3 Procedure

Participants were seated in a dimly lit room 70 cm in front of a Sony Trinitron® Multiscan E200 cathode-ray tube (CRT) video graphics array (VGA) monitor with a refresh rate of 75 Hz (Sony Corporation, Tokyo, Japan), on which the sentences were presented in a proportional, sans-serif font (size 20 px, black letters, white background) using Presentation® (Neurobehavioral Systems, Inc, Albany, CA, USA). After a fixation cross for 1150 ms, sentences were presented phrase by phrase; participants were instructed to press the space bar of a computer keyboard to view each successive phrase once they had understood the previous one. Reading time at each phrasal position was the dependent measure. After another fixation cross of 1150 ms, a well-formedness-rating task on a 1–6 scale ($1 =$ very good; $6 =$ very bad) was presented, which participants were instructed to solve as intuitively as possible. Half of the fillers additionally introduced a yes–no comprehension question to maintain participants' attention.

3.3 Data Analysis

Data analysis was performed using SPSS® (SPSS Inc., Chicago, IL, USA). To check whether participants had attended to the stimuli, mean percentages of correct responses to the comprehension questions were compared to the overall mean. None of the participants' mean RTs were further than 3.29 SDs away from the mean, so none was excluded from statistical analysis. A participant-wise regression analysis was run to determine multivariate outliers ($n = 196$) from a Chi-Square statistic on each response's Mahalanobis distance (Tabachnick, Fidell, & Osterlind, 2001). To keep the normal distribution spread as wide as possible, only outliers with $p < 0.0005$ were excluded. The remaining responses were logarithmized to correct for the typically F-shaped RT distribution and fulfill the requirements of the Mixed-Model analysis (Baayen, 2008). Finally, Mixed-Model analyses were run on the RTs, including a participant regressor as random factor. On the ratings, a multivariate Analysis of Variance (ANOVA) was performed.

3.4 Results

On the ratings, a main effect of argument order was found ($F(1,39) = 78.3$, $p < 0.001$), as well as an interaction between argument order and argument–verb distance ($F(1,39) = 11.9$, $p < 0.002$)—see Figure 3.1. Clearly the well-formedness of object-first argument orders were rated worse than the well-formedness of subject-first argument orders; still, object-first argument orders at long argument–verb distance were rated significantly better than at short argument–verb distance, as were subject-first argument orders at short argument–verb distance as opposed to long argument–verb distance.

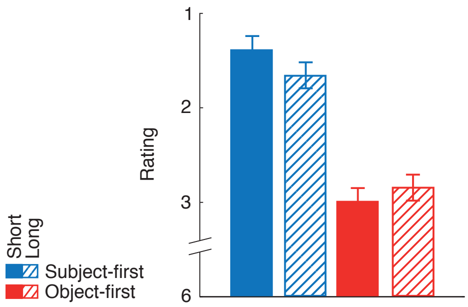

Figure 3.1: Average ratings (n=40); note that the y-axis is inverted (i.e., 1 = very good, 6 = very bad); error bars represent standard error of the mean (SEM); blue bars mark subject-first sentences, red bars mark object-first sentences, solid color marks short argument–verb-dependency sentences, striped color marks long argument–verb-dependency sentences.

The overall Mixed-Model analysis on the RTs revealed main effects of argument order and sentential position ($F(1,17064) = 54.3$, $p < 0.001$ and $F(1,17064) = 194.5$, $p < 0.001$), as well as interactions between argument order and argument–verb distance ($F(1,17064) = 13.0$, $p < 0.001$), argument order and position ($F(1,17064) = 2.0$, $p < 0.05$), argument–verb distance and argument order ($F(1,17064) = 148.1$, $p < 0.001$), all mirrored in a three-way interaction between argument order, argument–verb distance and position ($F(1,17064) = 7.4$, $p < 0.001$). The position-wise results of the Mixed-Model analysis are provided in Table 3.1 and Figure 3.2, showing a clear main effect of argument order at the short argument–verb distance at positions 4 to 8, while such an effect was only present at positions 3 and 4 for the long argument–verb distance.

Table 3.1: Significant position-wise RT effects.

Position	Argument order		Argument–verb distance		Interaction	
	F	P	F	P	F	P
1			32.72	< 0.001		
2			854.84	< 0.001	11.51	< 0.005
3			586.38	< 0.001	70.04	< 0.005
4	6.06	< 0.05	95.20	< 0.001	28.27	< 0.005
5	12.89	< 0.001	10.96	< 0.005	21.70	< 0.005
6	11.73	< 0.005			3.98	< 0.05
7	25.80	< 0.001	4.56	< 0.05		
8	10.92	< 0.005				
9						

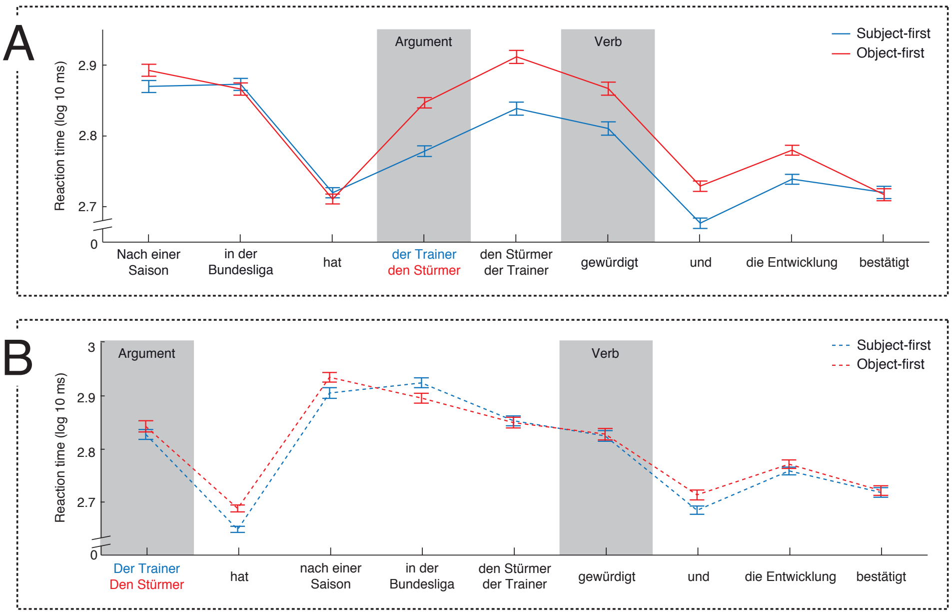

Figure 3.2: Position-wise reading times (log 10 ms; $n = 40$); (A) shows the short argument–verb-distance conditions (subject-first in blue and object-first in red), (B) shows the analogue for the long argument–verb-distance conditions; error bars represent SEM; the positions of the first argument and the verb are marked in gray.

3.5 Discussion

Our combination of an on-line and off-line study set out to give evidence to the conceptual and neurocognitive bisection of argument storage and argument reordering. To test whether these processes are functionally distinct, we combined an argument–verb-distance manipulation (short versus long argument–verb distances) with an argument-order manipulation (subject-first versus object-first sentences). As opposed to the original hypothesis of an independent linear influence of the two factors on behavioral performance, the results of the current study showed an interaction of argument–verb distance and argument order, both in the SPR and rating study: Increasing argument–verb distance seems to increase processing difficulty only for subject-first argument orders; for object-first argument orders, a long argument–verb distance seems to facilitate processing. We will now discuss possible explanations for this unexpected finding.

The current data fit results from English, Finnish, and Japanese that show objects in object-first argument orders to facilitate verb processing (Hyönä & Hujanen, 1997; Kamide & Mitchell, 1999; Nakatani & Gibson, 2008, 2010; Yamashita, 1997). As an example study from Japanese, Yamashita (1997) found that object-first argument orders—which collaterally increase the argument–verb distance in Japanese—do not increase processing load at sentence-final main verbs. As to English data, Nakatani and Gibson (2010) find that long-distance dependencies facilitate processing only for object-first sentences. Together, these results speak against proposals that long-distance dependencies in general facilitate processing over their short-distance counterparts: While Jaeger et al. (2005) found a processing facilitation of increasing argument–verb distance, their design did not disentangle argument order and argument–verb distance, which also holds true for work on German (Konieczny, 2000; Konieczny & Döring, 2003).

A possible explanation for these previous as well as the current order-dependent distance effects is that while argument order and argument–verb distance interact on a behavioral level, they may be processed by separate brain regions. If, for example, one brain region were responsible for the processing of argument order and a second brain region were responsible for argument storage, a direct neuroanatomical link between these two regions might selectively facilitate the processing of sentences that tax both argument storage and argument-reordering processes. This proposal would predict a behavioral interaction—in the absence of interactive effects on the neural level. Furthermore, this proposal would predict a neuroanatomical link between those brain regions that are active for argument reordering and those brain regions that are active for argument storage. Such a picture would also accommodate existing sentence-processing theories that postulate working-memory-inherent factors as sole processing determinants (Gibson, 2000; Gibson & Thomas, 1999; Lewis & Vasishth, 2005; Nakatani & Gibson, 2008): Working memory may be necessary for argument storage, but not sufficient for argument reordering.

A second possibility is that argument order and argument–verb distance interact both on the behavioral and neural level, as predicted by anticipation-driven or co-occurrence-frequency-based sentence-processing theories (Konieczny, 2000; Konieczny & Döring, 2003; Levy, 2008). Under such accounts, the occurrence of an object early in a sentence either opens a time window for semantic-anticipation mechanisms (Konieczny & Döring, 2003) or reduces the number of possible sentence continuations (Levy, 2008). Crucially, such a mechanism would be stronger for objects than subjects (cf. Bader & Bayer, 2006; Bader & Lasser, 1994; Friederici, Wang, Herrmann, Maess, & Oertel, 2000; Schlesewsky & Bornkessel, 2004): While virtually any verb subcategorizes a subject, not any verb subcategorizes an object (cf. Du Bois, 1987). Hence, the anticipation of a verb based on argument information might be easier in object-first sentences. In line with this interpretation, a body of cross-linguistic behavioral work has shown that arguments semantically pre-activate verbs they frequently co-occur with (Boland, 1993; Boland et al., 1995; Kamide et al., 2000, 2003; Marslen-Wilson, 1973; Pappert et al., 2008; Trueswell & Kim, 1998; Tsuzuki et al., 2004). On the neural level, this approach would suggest an interaction of argument storage and argument reordering, most possibly involving brain regions that are known to be sensitive to associative mechanisms in the mental lexicon.

Given these two interpretations for the behavioral results, the current experiment needed to be repeated using a sophisticated method that can uncover the neural factors that underlie behavioral patterns. Chapter 4 describes this experiment which used fMRI to tackle the neural substrates of the interactive behavioral effect.

4

MAGNETIC-RESONANCE-IMAGING STUDY

4.1 Introduction

As outlined in Chapter 1 and Section 2.3, arguments must be linked to their subcategorizing verb to determine who is doing what to whom from a sentence. This involves argument storage and reordering. Both storage and reordering are conceptually independent of the subvocal-rehearsal component of verbal working memory, evidence for which has been introduced in Section 1.2 and will be expanded in the following sections. Rehearsal refreshes stored information, constantly across the conditions of the current paradigm; reordering is an executive mechanism, operating on the representations stored and rehearsed by verbal working memory. While there are firm behavioral and ERP indications on the neuropsychological reality of both storage and reordering during argument–verb-dependency processing (Clahsen & Featherston, 1999; Felser et al., 2003; Fiebach et al., 2001; Kluender & Kutas, 1993; Nakano et al., 2002; Nicol et al., 1994; Nicol & Swinney, 1989; Phillips et al., 2005; Ueno & Kluender, 2003), their respective neural substrates are still a matter of intensive discussion (for review, see Rogalsky, Matchin, & Hickok, 2008). Furthermore, argument storage and reordering were found to interact behaviorally, questioning their neural independence. This in mind, an fMRI experiment was performed (Section 4.2.6.2 and Section 4.3.2). To also link the functional results to the underlying neuroanatomy more directly, additional diffusion-magnetic-resonance-imaging (dMRI; Section 4.2.6.5 and Section 4.3.4) and VBM (Section 4.2.6.4 and Section 4.3.3) analyses were performed[14].

[14] Modified versions of the fMRI and dMRI sections of this chapter have been published previously (Meyer, Obleser, Anwander, & Friederici, 2012).

With respect to storage, an imaging study from the sentence-processing domain reports activity of left inferior parietal cortex to increase with the retention interval for disambiguating information in ambiguous sentences, that is, storage demands (Novais-Santos et al., 2007). In addition, meta-analyses and imaging studies from outside the sentence-processing domain suggest left posterior brain regions as candidates for a storage substrate (Owen et al., 2005; Smith & Jonides, 1998; Wager et al., 2005). Paulesu et al.'s (1993) seminal study required monolingual English-speaking participants to read, store, and rehearse either English or Korean letters, of which only the English letters were hypothesized to activate a phonological code and subsequent storage. This study found the left supramarginal gyrus (SMG) to be active during the storage of English letters, a finding which was replicated by later studies (Awh et al., 1996, 1995; D'Esposito, Postle, Ballard, & Lease, 1999; Jonides et al., 1998; Petrides, Alivisatos, Meyer, & Evans, 1993). However, these studies contrast with other imaging work investigating aspects of working memory during sentence processing that reports Brodmann area (BA) 45, sometimes extending to the inferior frontal sulcus, in the left prefrontal cortex to play a role, using paradigms comparing different syntactic dependencies (Fiebach et al., 2005; Makuuchi et al., 2009; Santi & Grodzinsky, 2007, 2010).

With respect to reordering during sentence processing, cross-linguistic imaging research has found Broca's area in the inferior frontal cortex to activate in languages as diverse as Hebrew, German, and Japanese (Ben-Shachar, Hendler, Kahn, Ben-Bashat, & Grodzinsky, 2003; Bornkessel, Zysset, Friederici, von Cramon, & Schlesewsky, 2005; Friederici, Fiebach, et al., 2006; Kim et al., 2002). While these studies controlled for storage demands, they did not explicitly separate reordering and storage. One study directly contrasted word order and distance between the verb and its arguments, hinting at a certain independence of reordering and storage within the inferior frontal cortex, but restricted to specific types of syntactic dependencies (Fiebach et al., 2005). Another study neuroanatomically separated the processing of syntactic hierarchies in Broca's area from working memory in the left inferior frontal sulcus—but this study did not specifically vary reordering demands (Makuuchi et al., 2009).

Some authors have claimed that the role of Broca's area in sentence processing does not lie in reordering, but rather in subvocal rehearsal of information stored in working memory (Rogalsky & Hickok, 2010; Rogalsky et al., 2008). Although Broca's area was active during subvocal rehearsal in Paulesu et al.'s (1993) and subsequent studies from outside the sentence-processing domain (Awh et al., 1996, 1995; Petrides et al., 1993), no previous imaging results have disentangled reordering and rehearsal during sentence processing. Although Rogalsky et al. (2008) report a decline in sentence-processing performance under conditions of articulatory rehearsal, they found a control condition (finger tapping during a sentence-processing task) to also selectively decrease sentence-processing performance, merely suggesting that the presence of a secondary task can affect sentence processing behaviorally. Furthermore, the claim that activation in Broca's area during sentence processing stems from subvocal rehearsal is questioned by clinical evidence that reordering during sentence processing can be impaired independently from active subvocal rehearsal (Caplan & Waters, 1999; Waters & Caplan, 1996). Additionally, there is imaging evidence that subvocal rehearsal during sentence processing does not further increase brain activation in Broca's area (Caplan, Alpert, Waters, & Olivieri, 2000). In sum, while both rehearsal of syntactic information and reordering of arguments may rely on Broca's area, a conceptual and neuroanatomical identity between reordering and rehearsal is doubtful.

Based on the assumption that the minimal neural representation of subject, object, and verb involves at least a storage component which stores arguments across the argument–verb distance and a reordering component which reorders these arguments to avoid a who–whom confusion (cf. Chapter 1), the following was predicted: Argument reordering is supported by Broca's area, and the storage of relevant features of an argument over the argument–verb distance is supported by temporo-parietal (TP) regions. This hypothesis is tested in the present study, which fully crossed reordering (i.e., argument order) and storage (i.e., argument–verb distance) in an fMRI investigation. Importantly, if working memory supports sentence processing by storage rather than subvocal rehearsal, TP-region rather than prefrontal brain activation should be obtained for increased argument–verb distance. Moreover, if TP regions subserve storage and Broca's area subserves reordering, these regions should exhibit a direct fiber connection, and the local microstructural properties of the fiber bundle—as quantified by dMRI—should be related to the fMRI activations. To evaluate this, an analysis of dMRI data using deterministic tractography was conducted and followed by a voxel-based statistic on the characteristic diffusion parameters. Finally, I reasoned that interindividual variance of the functional activations (see Section 4.3.2) could be partially predictable from the local microstructural properties of the gray matter underlying these brain activations. This is especially relevant in the light of previous discussions on the lateralization of prefrontal brain regions involved in sentence processing (for review, see Bookheimer, 2002). To elucidate on the structure-to-function relation with respect to sentence processing, I performed a correlation analysis between the functional brain activations gathered from the fMRI data and microstructural properties of the underlying gray matter as gathered from an additional VBM analysis. For methodological reasons (see Section 4.2.6.4), this analysis was confined to the functional effects of the reordering factor.

4.2 Methods

4.2.1 Participants

Twenty-four university students (mean age 27.1 years, SD 3.2 years, 12 females, native German speakers) took part in the experiment. They were matched for their reading span being in the range between 3 and 5 (mean 3.89, SD 0.77) according to an abridged version of the reading-span test (Daneman & Carpenter, 1980). Participants were right-handed as assessed by an abridged version of the Edinburgh Inventory (Oldfield, 1971), had no reported neurological or hearing deficits, and normal or corrected-to-normal vision. Participants were paid €14 for participating. Written informed consent was obtained. All procedures received ethical approval by the local ethics committee (University of Leipzig).

4.2.2 Working-Memory Test

Participants' verbal-working-memory abilities for sequences of items were tested in the two digit-span sub-tests from the German version of the Wechsler test (Jacobs, 1887; Tewes, 1994); mean forward digit span was 9.54 (SD 1.69), mean backward digit span was 8.33 (SD = 2.10).

4.2.3 Materials

All sentences of the stimulus set described in Section 2.3 were recorded in a soundproof chamber by a trained female German speaker with a Sennheiser® MKH 40 condenser microphone and a Roland® CD-2 digital sound recorder. The recordings were cut and normalized in Praat (Boersma & Weenink, 2001) according to the root-mean-square amplitude of all files. To avoid onset and offset artifacts, a cosine fade-in and -out sequence of 5 ms was attached. For each participant, an individual pseudo-randomized list of 216 stimuli was generated using MATLAB® (The MathWorks, Inc., Natick, MA, USA). A list of 144 stimulus sentences (36 per condition), 36 filler sentences and 36 null events was drawn in a counterbalanced way from the entire stimulus pool. To maintain participants' attention, 24 trials introduced a who-did-what-to-whom yes–no comprehension question to be answered within a limited time (e.g., *Hat der Trainer den Stürmer geehrt? / Did the coach honor the center forward?*). Comprehension questions appeared in 16.7 % of trials in each of the four conditions at unpredictable positions in the stimulus set. The proportion of yes–correct and no–incorrect questions was balanced.

4.2.4 Procedure

Stimuli were presented using Presentation® (Neurobehavioural Systems, Inc., Albany, CA, USA). Auditory stimuli were presented using air-conduction headphones (Resonance Technology, Inc., Northridge, CA, USA). Visual stimuli were presented on a Sanyo PLC-XP50L liquid-crystal display (LCD) extended graphics array (XGA) mirror-projection system with a refresh rate of 100 Hz (Sanyo Electric Co., Ltd., Moriguchi, Japan), mounted onto the headcoil. A sans-serif font in black letters against a gray background (size 20 px) was used. A trial started with a fixation cross that stayed on screen for the whole trial. After a random jitter of either 0, 500, 1000 or 1500 ms, an auditory stimulus started (mean length 4.9 s, SD 0.36 s). To keep the number of acquired volumes constant across trials, a trial always lasted for 8 s, interpolating a silent period and an on-screen fixation cross between stimulus and trial end. In the case of a comprehension question, such a sequence was followed by a fixation cross of a random jitter and a visual comprehension question (16.7 % of all trials). The question remained on screen for 1500 ms and had to be answered by the participant as quickly as possible during this time period. Subsequent visual feedback was given for 1000 ms by a green happy or red sad emoticon. Again, in order to keep the duration of the comprehension probes constant, silence and an on-screen fixation cross were interpolated, such that each comprehension probe would last 4 s. Participants were instructed to carefully listen to the sentences and to answer the comprehension questions via button press with either their left or right hand, one hand corresponding to yes and the other to no. Button assignment was counterbalanced across participants. Since participants were not aware of whether a task trial would follow the auditory stimulus, all trials were included in the analysis.

4.2.5 Magnetic-Resonance-Imaging Data Acquisition

Functional-, structural-, and diffusion-MR images were acquired with a 3-T Siemens TIM TRIO scanner (Siemens Healthcare, Erlangen, Germany) at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig, Germany. Functional data were acquired with a 12-channel headcoil and a T2*-weighted gradient-echo echo planar imaging (EPI) sequence (data matrix 64 × 64, repetition time (TR) = 2.0 s, continuous scanning, echo time (TE) = 30 ms, flip angle = 90°, bandwidth 116 kHz, field of view (FOV) = 19.2 cm, in-plane resolution 3 × 3 mm^3, slice thickness 3 mm, interslice gap 1 mm, 30 horizontal slices parallel to the intercommissural (AC-PC) line, whole-brain coverage, 912 volumes), with a functional scan time of 30 min. Diffusion-weighted data were acquired in a separate session with the same scanner, equipped with a 32-channel phased-array head array coil. Images were acquired with a twice-refocused spin-echo EPI sequence (Reese et al., 2003; TE = 100 ms, TR = 12 s, 128 × 128 image matrix, FOV = 220 × 220 mm^2, 88 axial slices (no gap), resolution 1.72 × 1.72 × 1.7 mm^3). Additionally, fat saturation was employed together with 6/8 partial Fourier imaging and generalized auto-calibrating partially-parallel acquisitions (GRAPPA; acceleration factor = 2; Griswold et al., 2002). Diffusion-weighting was isotropically distributed along 60 diffusion-encoding gradient directions with a b-value of 1000 s/mm^2. Seven images with no diffusion-weighting (b0) were acquired initially and interleaved after each block of 10 diffusion-weighted images as anatomical reference for offline motion correction. The dMRI sequence lasted about 16 minutes. Anatomical T1-weighted 3D magnetization-prepared rapid gradient echo (MP-RAGE) images (Mugler III & Brookeman, 1990, inversion time (TI) = 650 ms, TR = 1300 ms, alpha = 10°, FOV = 256 × 240 mm^2, 2 acquisitions, 1 mm isotropic resolution) were previously acquired with a non-slice-selective inversion pulse followed by a single excitation of each slice.

4.2.6 Data Analysis

4.2.6.1 Behavioral Data

For the behavioral data, d'-scores and reaction times were calculated. D'-scores are a more adequate representation of participants' performance than mean-percentage-correct scores in that they eliminate participants' response bias (i.e., the individual tendency to either press the yes–correct or no–incorrect button; Macmillan & Creelman, 2005). A one-sample t-test on the difference between the d'-scores and chance-level performance (50 % correct responses) was performed. A 2 × 2 ANOVA was run on the response data to determine condition-specific effects. From the individual scores on the forward- and backward-digit-span subtests, a composite score—the Mahalanobis distance—was calculated, based on a zero-centered sample with covariance corresponding to the participant sample (Tabachnick et al., 2001).

4.2.6.2 Functional-Magnetic-Resonance-Imaging Data

Functional data analysis was performed using the SPM8 software package (Wellcome Imaging Department, University College, London, UK). Before undergoing statistical analysis, the functional data were co-registered using the corresponding high-resolution 3-D structural images. They were resampled to $3 \times 3 \times 3$ mm^3 voxel size. Further preprocessing was performed by realigning the functional time series to the first image, correcting them for slice timing and field inhomogeneities. Next, normalization to the standard MR template (gray-matter segmentation-based procedure) and smoothing using an isotropic 8-mm kernel were applied. For statistical analysis, a participant-wise GLM was estimated using the canonical HRF from the SPM8 software package, starting at sentence onset and spanning the individual stimulus length (mean 4.89 s, SD 0.36 s), and treating fillers, silent trials, and comprehension questions as regressors of no interest. In addition, I included the performance measures for each condition (see Section 4.3.1) as a regressor of no interest in order to factor out performance-related variance from the analysis. A high pass filter of 1/100 s was used to attenuate slow global signal changes. Contrast estimates for the four experimental conditions (compared against the global mean) were passed into a second-level within-subjects ANOVA, in which main effects and interactions were assessed. For thresholding of the statistical parametrical maps, an AFNI-implemented Monte-Carlo simulation (NIMH Scientific and Statistical Computing Core, Bethesda, MD, USA) ensured that a cluster extent of at least 51 voxels and an uncorrected voxel-wise p-value of 0.005 would protect against whole-volume type I error at $\alpha = 0.05$. For anatomical assessment of functional activations, cytoarchitectonic maps provided with the SPM anatomy toolbox (Eickhoff et al., 2005) as well as probability maps for the planum temporale (Westbury, Zatorre, & Evans, 1999) were used.

4.2.6.3 Correlation Analysis

Using the Marsbar toolbox (Brett, Anton, Valabregue, & Poline, 2002), the linear predictor values for each participant and design cell for the resulting regions of interest (ROIs)—as defined by the group-peak activation-clusters—were transformed into percentages of signal change. From these, difference values for the two main manipulation effects (i.e., the ordering and storage effect) were computed and Pearson's linear correlations between the individual activations and Mahalanobis-transformed composite digit-span scores (see Section 4.2.2) were run.

4.2.6.4 Voxel-Based Morphometry

The anatomical scans of the 23 participants who remained in the statistical analysis (see Section 4.3.1) underwent VBM analysis as implemented in SPM8. First, each participant's gray-matter voxels were segmented from the previously acquired T1 images using a rigid-body procedure (Ashburner & Friston, 2005). The segmented gray-matter volumes underwent DARTEL as described by Ashburner (2007): First, a group-specific template was generated by iteratively matching the individual participants' gray-matter images to a group-mean template. Second, each participant's individual gray-matter volume was warped onto this template image. The resulting images were modulated for normalization bias (i.e., differential non-linear warping magnitude per voxel; see Ashburner, 2009; Richardson et al., 2011), smoothed with an isotropic 8-mm kernel, and resampled to 1.5-mm isotropic voxels.

The available cytoarchitectonically-defined brain atlases do not yet contain reliable ROI definitions for the TP region; thus, our VBM analysis was confined only to the first half of our fMRI results (see Section 4.3.2). Using the probability maps provided with the SPM anatomy toolbox (Eickhoff et al., 2005), ROI volumes for the left and right BA 44 and 45 were generated (see Section 4.3.2). These volumes were used to extract the gray-matter probability values for the left and right BA 44 and 45 from participants' MNI-normalized gray-matter volumes. The same ROI volumes were used for the extraction of the functional data using the methodology described in Section 4.2.6.3.

To check for a direct correlation between the underlying neuroanatomy of the anatomically defined left and right IFG (i.e., BA 44 plus 45 for each hemisphere) and the functional activation during the experiment (see Section 4.3.2), I calculated asymmetry values for the underlying gray matter as well as the functional activations by subtracting the corresponding values for the left and right hemisphere. From these values, the minimum for each hemisphere was subtracted, and the resulting values were divided by the new maximum to arrive at difference values between minus one and one. Positive values of these scores indicate a rightward asymmetry of the functional activation or gray-matter probability values, respectively, whereas negative values indicate a leftward asymmetry.

Between the structural and functional lateralization indices, a partial Pearson's linear correlation analysis was run, factoring out participants' total intracranial volume (i.e., the summed volume of each individual's gray and white matter and cerebrospinal fluid) to avoid gross gray-matter-volumetric differences to obscure the statistical result.

4.2.6.5 Diffusion-Tensor Imaging and Fractional Anisotropy

For 22 of the 23 participants who remained in the analysis (see Section 4.3.1), dMRI data were available and were analyzed using LIPSIA (Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany), FSL (FMRIB, University of Oxford, United Kingdom) and SPM8 (Wellcome Imaging Department, University College, London, UK) on a Linux workstation. T1-weighted structural scans were skull-stripped and co-registered to Talairach space (Talairach & Tournoux, 1988). Motion correction for the diffusion-weighted images was performed based on the 7 reference images distributed over the entire sequence using rigid-body transformations (Jenkinson, Bannister, Brady, & Smith, 2002) implemented in FSL. Motion correction parameters were interpolated for all 67 volumes and combined with a global registration to the T1 anatomy. The transformations were applied for all volumes resulting in a 1-mm isotropic voxel resolution. The gradient direction for each volume was corrected using the rotation parameters. Finally, for each voxel, a diffusion-tensor model (Basser et al., 1994) was fitted, and the FA was computed (Basser & Pierpaoli, 1996).

To robustly analyze an across-participants correlation between the FA and the signal change inside the functional-activation clusters, the FA values within the skeleton of the fiber bundle connecting the activated areas were analyzed. Following the approach of tract-based spatial statistics (TBSS; Smith et al., 2006) implemented in FSL, all FA images were normalized into a standard brain space, and a group-average FA image was computed. A mean FA skeleton was created from this image, which represents the centers of all tracts common to the group. The local maxima of the individual aligned FA data representing the individual centers of the tracts were then projected onto this skeleton.

Anatomical connectivity between the functionally activated areas was investigated by tractography from the diffusion tensor maps to estimate the location of the corresponding fiber bundle within the individual brain volume (Anwander, Tittgemeyer, von Cramon, Friederici, & Knösche, 2007). Here, deterministic tractography using the entire diffusion tensor to deflect the estimated fiber trajectory was used (Lazar et al., 2003) as implemented in MedINRIA (Asclepios, INRIA, Sophia Antipolis, France) according to Fillard, Pennec, Arsigny, and Ayache (2007). The same preprocessing chain as for the computation of the FA maps described above was used, except for the fact that the diffusion tensors were computed with an isotropic resolution of 1.7 mm. Fiber trajectories were started in all voxels with an FA > 0.2 resulting in a complete set of trajectories within the whole brain.

To use the functional-activation clusters (see Section 4.3.2) as symmetric seed and target regions in deterministic fiber tracking, the group-average statistical maps were back-projected into each participant's native image space, and all fiber trajectories connecting the two regions in each individual participant were selected as white-matter connections. The resulting individual tract volume was mapped onto the voxel space of the individual anatomical scan. These tractograms were projected onto the group-average FA data set using the transformation matrices obtained in the TBSS analysis. Voxels inside these normalized tracts were included in an individual logical map, and these maps were summed across participants to obtain a group-level probability map. The probability map was thresholded at $p < 0.5$ (i.e., at least 50 % of participants had a tract at this voxel) to leave only the core volume intact (Reich, Ozturk, Calabresi, & Mori, 2010). This provided an across-participants search volume connecting the functional-activation clusters and only representing white-matter voxels present across participants.

This volume was used to mask a voxel-wise multiple-regression analysis in SPM8 on the aligned individual data as resulting from the TBSS procedure. Individual percent signal changes from the two functional clusters (see Section 4.3.2) were used as regressors, correcting for total intracranial volume, age, and gender. The volume for the statistical analysis encompassed only voxels inside the final tract volume (1561 voxels), and an AFNI-implemented Monte Carlo simulation (NIMH Scientific and Statistical Computing Core, Bethesda, MD, USA) ensured that a cluster of at least 7 voxels at a voxel-wise p-value of 0.05 protected against type I errors at $\alpha = 0.005$. All stereotaxic coordinates are reported in MNI space.

4.3 Results

4.3.1 Behavioral Results

Mean d'-score across conditions was 0.66 (SD 0.94) with a mean response bias of $c = -0.22$ (SD 0.59), and mean reaction time was 997 ms (SD 155 ms). One participant was excluded from all further analyses because his average response time of 450 ms was outside of the 95-% confidence interval (CI) for the group. Although the d′-scores indicate serious task challenges for the listeners, a one-sample t-test on these scores showed that participants' performance was significantly better than chance (i.e., a d′ of zero; $t(22) = 3.49$, $p < 0.005$). Furthermore, the 2 × 2 ANOVA on neither the condition-specific scores (Figure 4.1 A) nor RTs (Figure 4.1 B) yielded any main effects or interactions ($p > 0.2$). This indicates that the current design was free of processing-difficulty confounds.

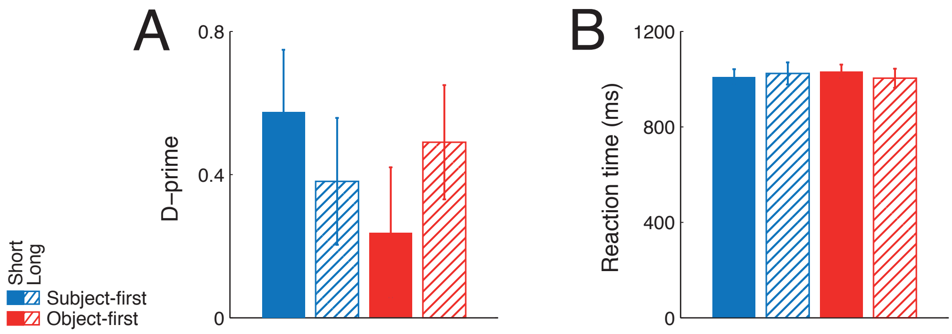

Figure 4.1: (A) d′-scores and (B) reaction times for all four conditions; error bars mark SEM.

4.3.2 Functional-Magnetic-Resonance-Imaging Results

For the main effects of both reordering and storage, focal and exclusive supra-threshold activations in the left hemisphere were obtained. As shown in the panels (A) and (B) of Figure 4.2 (shown in red), a test for a main effect of reordering elicited activation in the left pars opercularis of the IFG, peaking at x = –54, y = 10, z = 18. According to cytoarchitectonic maps (Eickhoff et al., 2005), 64.8 % of the obtained activation mapped onto BA 44, while 19.5 % mapped onto BA 45. Panels (B) and (C) of Figure 4.2 (shown in blue) illustrate the activation for the main effect of storage, which peaked at x = –42, y = –40, z = 10. This activation peak maps onto lateral superior parts of the left planum temporale (PT) with an across-participant probability of 26–45 %, (Westbury et al., 1999). Since this activation cluster included regions both in the temporal and inferior parietal region, it is referred to as TP activation. The interaction between the two factors did not produce significant activations; specifically, there was no evidence for prefrontal activation by the storage manipulation. The full set of activations is shown in Table 4.1.

Table 4.1: Overview of significant clusters in the functional contrasts surviving the 51-voxel threshold at $p < 0.005$ to achieve whole-volume type-I-error control at $p < 0.05$.

Site	MNI coordinate			Cluster size (mm^3)	Z-score
	X	Y	Z		
Object-first > subject-first					
Left BA 44 / pars opercularis*	–54	14	13	1602	3.76
Long > short					
Left planum temporale**	–42	–40	10		3.66
Left supramarginal gyrus***	–45	–28	22	1485	3.27
Left superior temporal gyrus***	–57	–25	1		2.89

*According to Eickhoff et al. (2005), **according to Westbury et al. (1999), ***according to Talairach and Tournoux (1988).

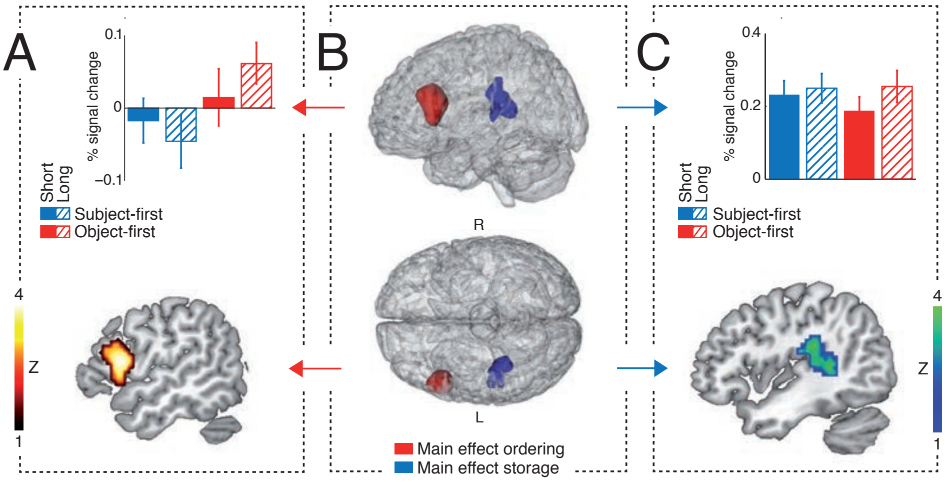

Figure 4.2: Brain activations and signal change (bar plots including SEM) for (A) the reordering effect (red clusters) and (C) the storage effect (blue clusters). Activations are thresholded at $p < 0.005$ at a minimum cluster size of 51 suprathreshold voxels to achieve type-I-error control at $p < 0.05$. For the reordering factor, 64.8 % of the activation is in the left BA 44 (peak at $x = -54$, $y = 14$, $z = 13$; $z = 3.76$); for the storage factor, the activation is found in the medial left TP region (peak at $x = -42$, $y = -40$, $z = 10$; $z = 3.66$).

Notably, a Pearson's linear correlation analysis found that the difference in signal change in the left TP ROI (as defined by the functional effect in the TP region) was negatively correlated with the combined digit-span scores ($r = -0.45$, $p < 0.05$). Participants with higher digit span show relatively less signal change in the contrast reflecting the storage effect (Figure 4.3 A). There was no substantial correlation between activity in the IFG in the storage contrast and the combined digit-span scores ($r = -0.22$, $p > 0.3$; see Figure 4.3 B). In sum, individual combined digit spans were able to explain $r^2 \approx 20$ % of the storage effect variance in the TP region, but only $r^2 \approx 4$ % of the analogue effect in the IFG.

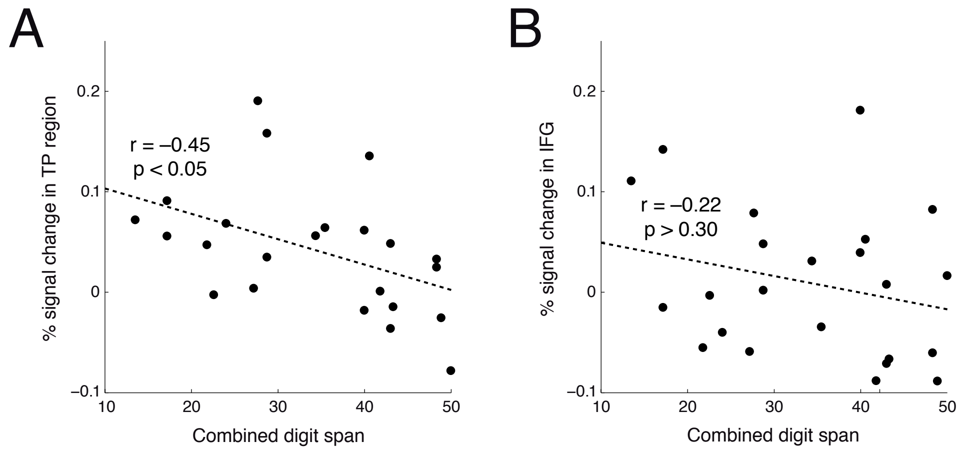

Figure 4.3: (A) Negative correlation of storage effect in the TP region with combined digit span ($r = -0.45$, $p < 0.05$); (B) analogue correlation between activation levels in BA 44 and combined digit span ($r = -0.22$, $p > 0.3$).

4.3.3 Voxel-Based-Morphometry Results

While most participants in the experimental sample ($n = 16$) showed left-hemispheric asymmetry (i.e., asymmetry scores > 0; see Figure 4.4) for the functional activation of the argument-reordering effect—and the main effect of argument reordering became significant only in the left IFG on the whole-brain level, see Section 4.3.2—, some participants ($n = 7$) showed a right-hemispheric asymmetry (i.e., asymmetry scores < 0; see Figure 4.4). For the structural data, asymmetry was balanced across the group (leftward $n = 12$, rightward $n = 11$).

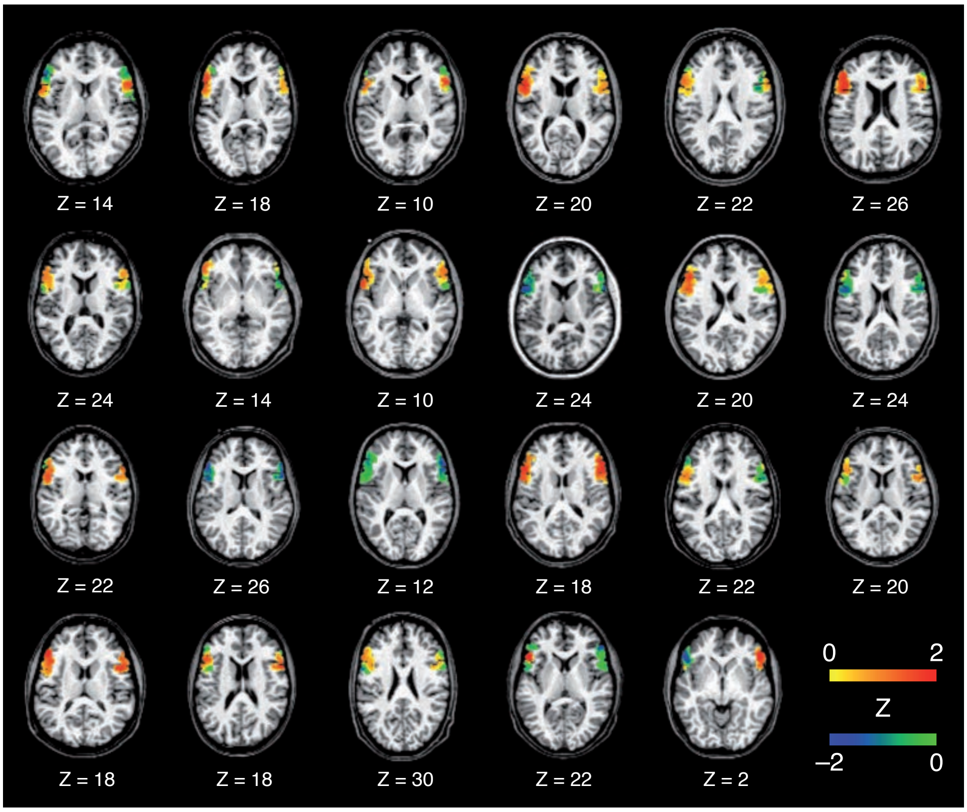

Figure 4.4: Individual brain activations (slices displayed in neurological convention) during the contrast object-first > subject-first for the 23 participants in the current analysis, masked for left and right BA 44 and 45.

A positive relationship between functional activation and gray-matter probability holds for the left and right hemispheric IFG ROI ($r^2 = 0.15$ and $r^2 = 0.13$, respectively; both $p > 0.05$). While the effect sizes were too low for the individual hemispheric regressions to reach significance (Cohen's $f^2 = 0.18$ and Cohen's $f^2 = 0.15$, respectively), the partial Pearson's linear correlation analysis between the lateralization values for the functional and structural data across the bilateral IFG ROI volumes yielded a significant correlation (partial $r = 0.66$, $p < 0.001$). Figure 4.5 shows the significant correlation between the functional and structural lateralization indices inside the left and right IFG ROI volumes (i.e., left versus right combined BA 44 and 45).

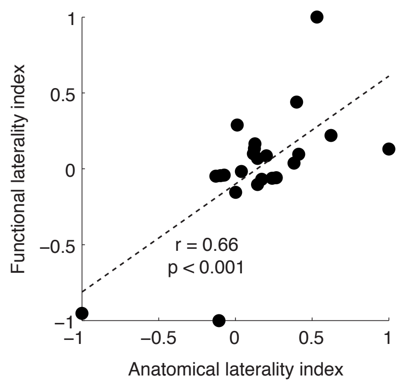

Figure 4.5: Correlation between functional and structural lateralization indices; negative values indicate rightward lateralization, positive values indicate leftward lateralization.

4.3.4 Diffusion-Tensor-Imaging and Fractional-Anisotropy Results

The correlation analysis on the FA values inside the thresholded probability map identified parts of the arcuate fasciculus (AF)/superior longitudinal fasciculus (SLF), connecting the posterior temporal cortex and the IFG, as differentially correlating with the experimental factors: A comparison between the storage and reordering correlations yielded supra-threshold clusters in the middle and posterior AF/SLF. The reverse comparison yielded a small supra-threshold cluster in the frontal AF/SLF, adjacent to the IFG. As can be seen in Figure 4.6, the posterior part of the correlation is adjacent to the functional cluster in the left TP region that was obtained for the main effect of storage and terminates below the middle superior temporal gyrus (STG). Table 4.2 provides an overview of the significant clusters.

Table 4.2: Significant clusters in the reordering > storage and storage > reordering contrasts on the FA values of the AF/SLF (thresholded at 7 voxels and $p < 0.05$, type-I-error-controlled at $p < 0.005$).

Site	MNI coordinate			Cluster size (mm^3)	Z-score
	X	Y	Z		
Reordering > storage					
AF/SLF	−38	−2	26	9	2.13
Storage > reordering					
AF/SLF	−34	−39	21	175	3.56
	−38	−16	28	80	3.33

*Labels according to Mori et al. (2006).

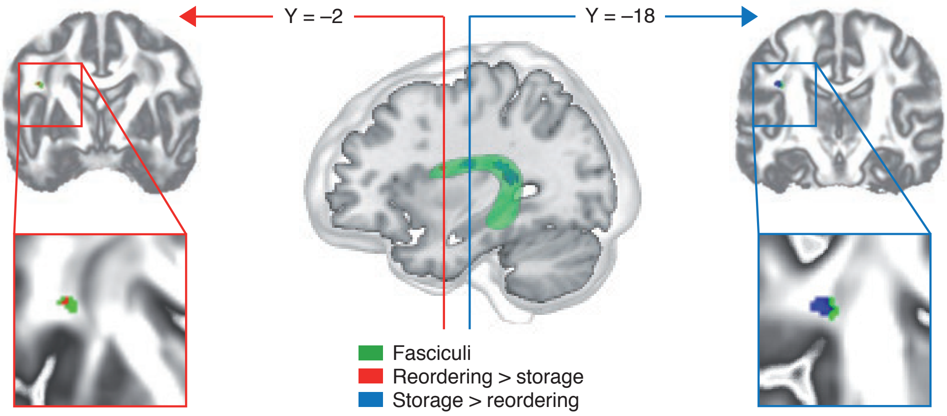

Figure 4.6: Correlation of FA values with signal change of the storage effect in the left TP region as compared to the reordering effect in the IFG (blue) as well as the reordering effect as compared to the storage effect (red). The regression analysis resulting from the averaging of the individual fiber tracts was carried out in a volume of 1561 voxels of the AF/SLF (green). Clusters were thresholded at $p < 0.05$ and a minimum cluster size of 7 suprathreshold voxels to control for family-wise error at $p < 0.005$.

4.4 Discussion

The current MRI study set out to separate the neural correlates of reordering and storage during sentence processing in the light of previous evidence on the neuropsychological reality of these two concepts. I also sought to elucidate on the ongoing discussion of the role of the structural and functional lateralization of Broca's area concerning these processes. In the following, I will first briefly discuss the behavioral results, before I turn in detail to the functional and structural MRI findings.

4.4.1 Behavioral Results

Although d'-scores were significantly above chance, for 7 participants, they were relatively low. I assume that the infrequent occurrence of task trials (16.7 % of trials) and the short time window in which participants had to respond (1500 ms) are responsible for this comparably poor performance. In addition to the fact that the inclusion of d'-scores as a regressor of no interest in the fMRI analysis accounted for performance-related variance in the data, it is noteworthy that an exploratory exclusion of these participants from the fMRI analysis affected the statistical results only quantitatively, that is, the overall pattern of activations was not changed—despite the low statistical power resulting from the small remaining group size, both effects were robust, with the IFG effect of 179 voxels ($z = 3.34$, peak at $x = -57$, $y = 17$, $z = 4$), and the TP-region effect encompassing multiple TP sub-peaks of 52 voxels altogether ($z = 2.71$, main peaks at $x = -60$, $y = -25$, $z = 46$ and $x = -45$, $y = -28$, $z = 22$).

This is in line with results by Caplan, Chen, and Waters (2008) and Newman, Lee, and Ratliff (2009), who observed that parts of the left IFG activate more for increased reordering demands, regardless of the experimental task performed or task performance. Furthermore, this is in line with the finding that none of the functional effects in the current study showed a correlation with d'-scores. Thus, I am confident that the experimental task did keep participants' attention directed towards the sentences, while leaving the functional results unbiased.

4.4.2 Functional-Magnetic-Resonance-Imaging Results

The findings from the functional experiment are straightforward: I found a clear activation for the reordering factor in the left IFG (object-first sentences leading to stronger activation than subject-first sentences) and an as-clear but remote activation for the storage factor (long argument–verb distances leading to stronger activation than short argument–verb distances) in the left TP region. There was no significant interaction between the reordering and storage factor, even though visual inspection of the signal change in the IFG and TP region may suggest differently (see Figure 4.2, A and C). Moreover, a correlation of memory scores with the storage-related activation of the TP region, but not the IFG, was observed (see Figure 4.3).

These findings suggest that the processing of complex sentences relies both on the storage of arguments in working memory, supported by left TP regions, and the reordering of arguments, supported by Broca's area. The correlation between activity in left TP regions and individual memory capacity further implies that the present "storage" manipulation did indeed tap storage. This highlights the role of the left TP region as a neural substrate of memory storage (e.g., Buchsbaum & D'Esposito, 2008; Jacquemot & Scott, 2006), and more importantly, it emphasizes that the TP region serves this function also in the processing of complex sentences.

The view that Broca's area supports sentence processing by its role in subvocal rehearsal is not supported by the current data: In the conception of Baddeley (2012; 2009), working memory necessarily involves both storage and rehearsal, the latter providing a constant refreshing of the content stored by the former. Paulesu et al.'s (1993) and subsequent working-memory studies (Awh et al., 1996, 1995; Petrides et al., 1993) have conceptualized the neural interplay of storage and rehearsal as a fronto-temporal network involving the IFG (implied in rehearsal) and TP regions (implied in storage). In the current study, the IFG did neither exhibit sensitivity to argument–verb distance (the working-memory factor in the current paradigm), nor did its activation correlate with behavioral measures of working-memory ability, unlike TP-region activation. To put it differently: While during verbal working memory the IFG may underlie subvocal rehearsal in the phonological loop, it is doubtful that IFG sensitivity to an argument-order manipulation in the present study reflects subvocal rehearsal. I will now discuss these findings in more detail.

4.4.2.1 The Left Inferior Frontal Gyrus Activates for Reordering

The increased activity in BA 44 elicited by increased reordering demands (i.e., object-first compared to subject-first sentences) in the present study is in line with previous cross-linguistic functional-neuroimaging research from languages as diverse as German (Friederici, Fiebach, et al., 2006; Obleser et al., 2011; Röder, Stock, Neville, Bien, & Rösler, 2002), Japanese (Kim et al., 2009; Kinno et al., 2008), and Hebrew (Ben-Shachar et al., 2003). In all of these studies, increased activation for object- as compared to subject-first sentences was elicited in the left IFG, but not in the left TP region.

First, in German, three studies directly contrasting object- and subject-first sentences reported the inferior pars opercularis (BA 44) to be increasingly active as a function of increased reordering demands. Friederici, Fiebach, et al.'s (2006) study which visually presented sentences, keeping the argument–verb distance constant across conditions, excluded a possible explanation in terms of storage demands. Obleser et al. (2011) used acoustic versions of the same stimuli, again finding activation in BA 44. Both results are in line with Röder et al.'s (2002) finding that object-first argument orders in acoustically presented sentences elicit activation in the left IFG. Second, similar evidence from Japanese strengthens this interpretation. Both Kinno et al. (2008) and Kim et al. (2009) contrasted Japanese object- and subject-first sentences in visual fMRI studies. The fact that Japanese allows for a constant argument–verb distance across both object- and subject-first sentences allowed their experimental paradigms to avoid differences in storage demands across experimental conditions. Both studies found very close areas in the left IFG to increase in activation for object- as compared to subject-first sentences. Third, evidence from a Hebrew study (Ben-Shachar et al., 2003) expands the cross-linguistic picture. Again, Hebrew is a language that allows the fixing of storage while manipulating reordering demands. Ben-Shachar et al.'s (2003) study used auditory presentation of object- or subject-first sentences, the contrast yielding activation peaks in the left IFG in both a whole-brain and a ROI analysis.

The fact that the current results converge on this body of work strengthens the position that BA 44 as part of Broca's area is engaged in the reordering of arguments; it furthermore suggests that this function is independent of a particular language and input modality, linking to English-language studies contrasting the processing of object- and subject-first sentences across input modalities (Constable et al., 2004) and sentences of varying processing difficulty across input modalities (Braze et al., 2011). An overview of these converging results is given in Figure 4.7.

In spite of this convergence, English-language data have resulted in the claim that the contribution of Broca's area to sentence processing is that of subvocal rehearsal as part of the working-memory network (Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Rogalsky & Hickok, 2010). Unfortunately, the data on which this view is based are not unequivocal, since the relevant studies on reordering and storage in English contrasted subject- and object-relative clauses. While such English clauses certainly scrutinize some aspect of working memory (by varying the number of phrases between an argument and the verb), they also collaterally introduce a reordering manipulation: While the former (short versus long argument–verb distance) would tax brain regions that subserve storage, the latter (object- versus subject-first sentences) would rather tax brain regions that are concerned with the reordering of arguments. Thus, the English results are partially ambiguous in that they might be ascribed to either storage or reordering.

Additionally, clinical evidence demonstrates that the ability to process sentences with increased reordering demands can be independently impaired from subvocal-rehearsal abilities (Caplan & Waters, 1999; Waters & Caplan, 1996), and imaging data suggest that subvocal rehearsal during sentence processing does not further increase brain activation in Broca's area (Caplan et al., 2000). Further patient data (Martin, 1987; Martin, Blossom-Stach, Yaffee, & Wetzel, 1995; Martin & Romani, 1994) are in line with these results in that they show that selectively impaired rehearsal abilities do not result in sentence-comprehension deficits. The results of the current correlation analyses are in line with these reports: If subvocal rehearsal was the driving force behind Broca's area's activity in the current study, one would have expected activation in BA 44 to correlate with participants' combined digit-span scores—instead, only brain activity in the TP region was correlated with combined digit-span scores.

In contrast to the above evidence that rehearsal and reordering are conceptually and neurally distinct, Rogalsky et al. (2008) report a decline in sentence-processing performance under conditions of articulatory rehearsal. This result, however, was not fully conclusive, in that a control condition (finger tapping during a sentence-processing task) also led to a selective decline in sentence-processing performance, suggesting that the presence of a secondary task can affect sentence processing behaviorally.

Figure 4.7 puts these data into a broader perspective, listing neuroimaging findings from studies inside and outside the sentence-processing domain. It becomes obvious that there is a relative proximity, but no full neuroanatomical overlap between those prefrontal brain regions that support reordering and those regions that support articulatory rehearsal. Thus, there may be a differentiation within the prefrontal cortex with respect to reordering and the rehearsal component of working memory which, in turn, is clearly separated from the storage component located in more posterior regions.

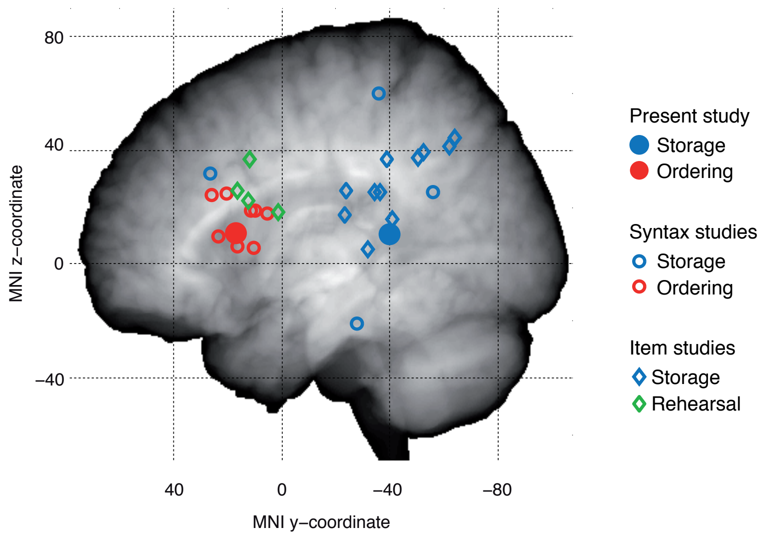

Figure 4.7: Overview of results from cited studies on verbal working memory in sentence-processing and non-sentence-processing paradigms. Circles mark sentence-processing studies, diamonds mark non-sentence-processing studies. It is visible that storage (blue) is more likely to activate TP regions, whereas prefrontal regions dissociate between reordering (red circles) and rehearsal (green diamonds).

4.4.2.2 The Left Temporo-Parietal Region Activates for Storage

This brings us to the second main finding, a cluster in the left TP region that showed both increased activation with increasing storage demands and a correlation with digit span. A number of studies suggest that the left TP region (mainly the PT, but often extending into or peaking in the SMG) is critically involved in storage processes as diverse as storing an ambiguous sentence structure, storing arguments at increasing argument–verb distances, and storing non-sentential items in the phonological loop, making left TP regions a strong candidate for the neural substrate of storage, both in sentence processing and item-based tasks (see Figure 4.7 for an overview of the studies discussed here).

Amongst this work are studies that searched for the neural correlates of the phonological loop (for review, see Baddeley, 2012), i.e., outside of sentence processing proper. Paulesu et al. (1993) suggested the left SMG as the main region subserving storage. Other imaging studies also consider left posterior regions to subserve storage; as mapped in Figure 4.7. However, the exact locations of the activation peaks in these studies encompassed various regions, including left STG (Kim et al., 2002), SMG (Awh et al., 1996; Clark et al., 2000; Paulesu et al., 1993), and left inferior and posterior parietal cortices (Awh et al., 1995; Becker et al., 1996; Bushara et al., 1999; Clark et al., 2000; Gruber & von Cramon, 2001, 2003; Jonides et al., 1998; Owen et al., 2005).

For sentence processing, Grossman et al. (2002) found that seniors who show difficulties in processing sentences with increased storage demands activated left parietal cortex relatively less as compared to younger participants. Accordingly, the authors suggest reduced storage resources in seniors amongst the sources of their sentence-processing difficulties. The location of the reported regions (see Figure 4.7) is in line with our finding that left TP activation correlates with digit span. The fact that this correlation is negative fits this interpretation: In the current study, participants with relatively better storage abilities (as tested by digit span) showed relatively less activation in the left TP region, suggesting more efficient storage in these participants.

Additional evidence for a general storage component in left posterior cortex comes from clinical studies on patients with damage to the left STG, SMG, or TP region. The observation that damage to the STG causes impaired storage abilities has been made by Leff et al. (2009), who found gray-matter integrity in the STG in stroke patients to correlate with digit span. Recently, these findings have been augmented by studies on conduction aphasia (Buchsbaum et al., 2011; Fridriksson et al., 2010) demonstrating a relation between speech-repetition problems, phonological-working-memory deficits, and gray-matter damage to the left SMG and TP region. While such results can be ambiguous in that conduction aphasics usually suffer from both gray- and white-matter lesions, direct causal evidence is provided by a repetitive-transcranial-magnetic-stimulation (rTMS) study (Romero, Walsh, & Papagno, 2006) showing that rTMS applied to the SMG causes a decrease in digit span.

These somewhat heterogenous localization patterns in the posterior regions across studies may result from distinct working-memory sub-processes tapped by the various paradigms employed, since in addition to rehearsal and storage as discussed above, retrieval is assumed to be a separate component of working memory. Evidence for a segregation of storage and retrieval comes from a recent working-memory fMRI study by Ravizza et al. (2011). In a series of ROI analyses, these researchers found storage of verbal material to correlate with brain activity in the left posterior STG, whereas retrieval of verbal material activated the left TP junction. Functional heterogeneity in this area related to differential working-memory processes has been previously suggested by Henson et al. (1999) and Buchsbaum, Hickok, and Humphries (2001), who report distinct sub-peaks during a working-memory task in the posterior STG and inferior parietal cortex. Although the current results can not decide on the neural underpinnings of separable storage and retrieval sub-processes, the activation observed in the left TP region involved two sub-peaks (see Table 4.1), one clearly in the PT, one in the SMG. Hence, the current experimental manipulation of argument–verb distance may have taxed both storage and retrieval, due to the longer retention interval and accordingly higher re-activation demands induced by memory decay (cf. Baddeley et al., 2009).

A final and important issue that needs to be addressed is the apparent contrast between the present data and some previous studies on working-memory demands during sentence processing. In English, direct comparisons of either pronoun binding and argument–verb dependencies (Santi & Grodzinsky, 2007) or argument–verb dependencies and embedded sentences (Santi & Grodzinsky, 2010) yielded brain activation in BA 45. Similarly, a German study found activity related to subject-argument–verb distance in the inferior frontal sulcus, dorsal to and extending into BA 45 (Makuuchi et al., 2009), whereby the argument–verb distance manipulation introduced a difference in the number of argument–verb dependencies. Finally, a second German study by Fiebach et al. (2005) found BA-45 activation for pronoun–verb distance, contrasting object-first sentences with an object pronoun (and a subject noun) to subject-first sentences with a subject pronoun (and an object noun). The asymmetric comparison of different syntactic dependencies across conditions in the above studies may have reflected the engagement of a syntactic-working-memory system, proposed to be distinct from the working memory used in other verbal tasks, and found to activate BA 45 (Caplan et al., 2000; Lewis et al., 2006; Van Dyke, 2007; Van Dyke & McElree, 2006). In contrast to the above studies, the current paradigm kept the type of syntactic dependency constant across conditions and required the storage of a given noun phrase across a variable distance, which is corroborated by the possibility that the experimental task in the current study was solvable using phonological strategies, which is also true for the digit-span task used in the correlation analysis. Thus, the contrast between TP and inferior frontal brain activations may reflect the difference between phonological and syntactic working memory, respectively. Yet, this suggestion only counts as a future research hypothesis.

4.4.3 Individual Differences: Asymmetry of the Inferior Frontal Gyrus

The current VBM analysis found a correlation between the asymmetry of the underlying cortical microstructure of the left and right IFG and the asymmetry of the functional activation of these regions by a classical argument-order manipulation in a sentence-processing paradigm; in other words: Structural asymmetry of the IFG in part predicts functional asymmetry of the IFG. The relationship between cortical microstructure and functional activation inside the IFG complements the discussions on the asymmetry of the IFG response during sentence processing (Bookheimer, 2002).

On the population level, a leftward asymmetry of the IFG response to increased argument-reordering demands is strongly suggested by the cross-linguistic picture discussed above. However, evidence for the general ability of the right IFG to support high-level language tasks comes from studies on cortical reorganization after stroke (Cao, Vikingstad, George, Johnson, & Welch, 1999; Rosen et al., 2000; Weiduschat et al., 2011; Winhuisen et al., 2005, 2007) as well as patients suffering from Parkinson's disease (Grossman et al., 2003). Cao et al. (1999), Rosen et al. (2000), Winhuisen et al. (2005), Winhuisen et al. (2007) converge in reporting brain reorganization of patients suffering from prefrontal brain lesions after stroke to involve increased activity in the right homologue of the left IFG during language processing. Grossman et al.'s (2003) data support these findings in that they report senior patients with Parkinson's disease and accordingly-reduced sentence-processing abilities to exhibit reduced brain activation in the right IFG compared to age-matched controls. A compensatory role of the right IFG is also in line with Tyler et al.'s (2010) report of increased right IFG activity in seniors who show relative atrophy of the left IFG. It is, however, important to point out that this functional reorganization is not sufficient for a full recovery of sentence-processing abilities in either patients (Rosen et al., 2000; Tyler et al., 2011; Winhuisen et al., 2005), or seniors (Tyler et al., 2010)—stressing the leftward functional asymmetry of the IFG on the population level.

The current data leave open the possibility that such a compensatory role of the right IFG can also account for differential results in the imaging literature on healthy participant groups—in line with the proposal of Just et al. (1996), who assigns the right IFG a supportive role for the language-dominant left IFG (Just et al., 1996). It is interesting to note that while most fMRI studies on argument-reordering report left-only IFG activations on the group level (Friederici, Fiebach, et al., 2006; Kinno et al., 2008; Obleser et al., 2011), a body of previous studies has consistently reported brain activation for increased argument-reordering demands not only in the left IFG, but also its right-hemispheric homologue (Ben-Shachar et al., 2003, 2004; Bornkessel-Schlesewsky, Schlesewsky, & von Cramon, 2009; Just et al., 1996; Wilson et al., 2010).

The reason for the divergence of these results—some studies observing right IFG activity, some not—may lie in across-studies lateralization differences between participant groups: While Obleser et al. (2011) and the current study did match their participants for high handedness indices (i.e., laterality quotient (LQ) > 80 in both studies; Oldfield, 1971), it is possible that Ben-Shachar et al. (2003, 2004), Bornkessel-Schlesewsky et al. (2009), and Just et al. (1996) applied less-strict lateralization-matching criteria to their experimental participants—also not controlling for familial handedness: Participants' familial history of handedness may bias their reliance on syntactic processing strategies during sentence processing, with familial right-handers relying more on syntax as compared to familial left-handers (Townsend, Carrithers, & Bever, 2001). Handedness and familial handedness may have increased the fraction of participants with less-strong leftward language lateralization in the respective samples (cf. Knecht et al., 2000). While this may sound *ad hoc* at first glance, the motif goes well with morphometry results by Foundas, Eure, Luevano, and Weinberger (1998), who state that structural asymmetry of both pars opercularis and triangularis of the IFG is dependent on participants' handedness, with left-handed participants showing reduced left-sided lateralization when compared to right-handed participants.

In turn, the structural–functional correlation in the current results entails that the functional involvement of the right IFG may directly depend on the asymmetry of the underlying gray matter in the left and right IFG—which may be tilted towards the right hemisphere in left-handers. Although LQ scores were available for 21 of our participants, these were not normally distributed due to the selection criteria of the current study (see Section 4.2.1). Thus, we median-split our participant sample for LQ and functional and structural lateralization indices to run Fisher's Exact Tests on the observed cell counts from the handedness–functional and handedness–structural pairings, which turned out highly significant in both cases ($p < 0.001$). This supports our interpretation that handedness is a key predictor of the structural lateralization of Broca's area as well as the functional lateralization of this brain structure during sentence processing. Figure 4.8 illustrates these relationships.

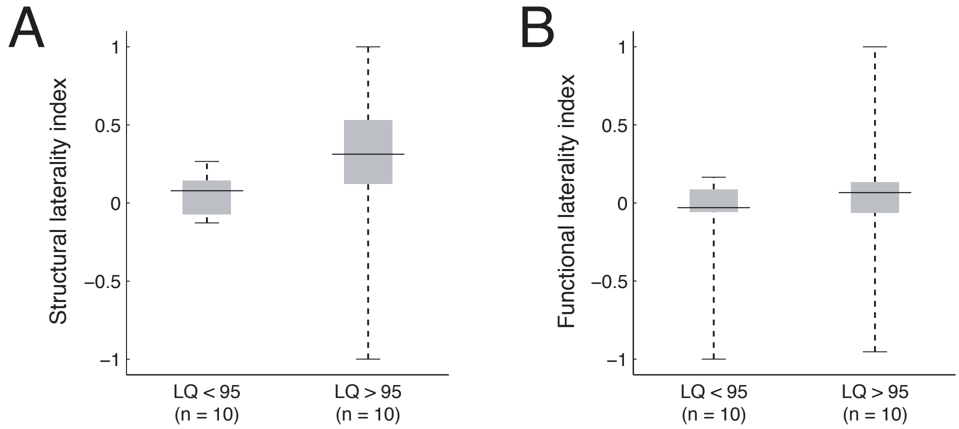

Figure 4.8: Boxplots of structural (A) and functional (B) lateralization, arranged by median-split participant groups (median LQ = 95, range 80–100). Whiskers mark range; negative values indicate rightward lateralization, whereas positive values indicate leftward lateralization. While the effect is clearly stronger for the structural data, Fisher's Exact Test found that significantly more strongly-right-handed participants (i.e., LQ > 95) show increased structural lateralization and left-lateralized functional engagement of Broca's area during sentence processing ($p < 0.001$).

As a cross-species aside on the relationship between handedness and leftward asymmetry of the IFG, it is interesting to mention that a leftward asymmetry of BA 44 in great apes (bonobos, chimpanzees, and gorillas) has been found predictive of communicative gesturing behavior using the right hand (Cantalupo & Hopkins, 2001; Hopkins, Russell, & Cantalupo, 2007; Schenker et al., 2010; Taglialatela, Cantalupo, & Hopkins, 2006). Combined with the fact that BA 44 and 45 exhibit cytoarchitectonic similarities between humans and other primates, such as macaques (for reviews, see Aboitiz, García, Bosman, & Brunetti, 2006 and Petrides, Tomaiuolo, Yeterian, & Pandya, 2012), this lends some credibility to the suggestion that human right-handedness has its evolutionary origin in the combination of gesturing and vocalizing in pre-linguistic communication (Aboitiz & García, 2009; Corballis, 2003; Corballis, Badzakova-Trajkov, & Häberling, 2011).

In sum, while the left IFG in humans certainly remains the dominant region for the processing of argument-reordering tasks on the population level (cf. Amunts et al., 1999; Amunts & Zilles, 2012), a fraction of the general population may additionally involve the right IFG in this process—or even show right-dominant IFG activity, as is evident from the individual data shown in Figure 4.5. The current finding brings up the future research question whether left-handedness is advantageous in recovering from left frontal stroke lesions or language deficits observed in Parkinson's disease.

4.4.4 Diffusion-Tensor-Imaging and Fractional-Anisotropy Results

Deterministic fiber tracking between the observed functional effects suggested a dorsal connection, including the AF/SLF. As to the correlation analysis of the FA values in the AF/SLF with the functional effects, a series of clusters was obtained. Clusters of FA along the superior and posterior parts of the AF/SLF correlated with increased storage demands as compared to increased reordering demands, and a single cluster in the more anterior part correlated with increasing reordering as compared to storage demands. The involvement of the AF/SLF, but not the inferior longitudinal fasciculus, suggests that the present effects are related to the dorsal pathway, linking the auditory cortex to the IFG via TP regions (Catani, Jones, & ffytche, 2005; Parker et al., 2005; Weiller, Musso, Rijntjes, & Saur, 2009). Generally, both the effects of reordering as compared to storage and storage as compared to reordering along the left AF/SLF are in accordance with the view that this tract is involved in sentence processing (Friederici, 2009b). This is in line with probabilistic-fiber-tracking results, which were based on functionally defined seeding points in the IFG (pars opercularis/BA 44; Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006) and are similar to the current data with regard to this. Specifically, it seems anatomically plausible that the neural basis of sentence processing involves a reordering process as subserved by the IFG that queries a storage component in TP regions through the AF/SLF.

The literature on an involvement of different fiber tracts in working memory from healthy populations is sparse, although initial DTI work is available (Charlton, Barrick, Lawes, Markus, & Morris, 2010). Charlton et al. (2010) used a composite working-memory score collating different working-memory measures to explore the white-matter network underlying working memory. Their results show a distributed array of MD and FA clusters in both hemispheres, including a tract that connects BA 40 to inferior frontal areas. But since none of the measures employed by Charlton et al. (2010) only tapped storage, their results do not easily map directly onto the current sentence-processing data. Thus, to my knowledge, the current study is the first to specify the role of the AF/SLF in sentence processing to lie in argument storage in working memory over a certain argument–verb distance and manipulating the argument order by syntactic working memory, such that the who and the whom of the sentence are not confused. While the present data—in combination with Charlton et al.'s (2010) results—may suggest a common role of the AF/SLF in storage both in- and outside of the sentence-processing domain, Section 8.4 will discuss whether such a unitary view can meet recent fiber-tracking evidence.

The common role of the AF/SLF may best be described as mediating a storage component in TP regions to a rehearsal component located in the dorsal prefrontal region for tasks outside of sentence processing and to a reordering system located in Broca's area for sentence processing proper. This interpretation fits both the finding of a correlation with storage involved in sentence processing (as measured by brain activation during increasing argument–verb distances) and outside of sentence processing (as measured by digit span). Also, the relatively weaker and less extensive correlations with argument order in the anterior portion of the AF/SLF as opposed to rather extensive effects of argument–verb distance suggest that the functional role of this tract is less specific to reordering itself than it is general to the storage of processing-relevant information.

In addition to work on healthy participants, there is evidence on the role of the left AF/SLF in sentence processing from patients with primary progressive aphasia (Wilson et al., 2011) and patients with conduction aphasia, who also show reduced working-memory capacities (Buchsbaum et al., 2011; Caramazza, Basili, Koller, & Berndt, 1981). Investigating patients with primary progressive aphasia, Wilson et al. (2011) found that damage to the AF/SLF causes severe sentence-processing difficulties in primary progressive aphasics, which was not the case for patients with damage to the ventrally located extreme capsule fiber system and uncinate fasciculus. The studies on conduction aphasia are of different degrees of neuroanatomical specificity. Friedmann and Gvion (2003) report that conduction aphasics show both reduced digit span and particular problems in argument retrieval at long argument–verb distances. Since the authors are not precise about lesion site and extent, this study does not allow to draw strong neuroanatomical conclusions. Yamada et al. (2007), however, report a case in which selective damage to the posterior part of the AF/SLF resulted in conduction aphasia, sparing the gray matter in the left TP region. Finally, Fridriksson et al. (2010) found that impaired speech repetition in conduction aphasics co-occurs with both damage to the white matter underlying the left SMG and reduced gray-matter integrity in the left SMG and TP junction, converging on data by Quigg and Fountain (1999) and Baldo, Klostermann, and Dronkers (2008). The current data agree with both the gray-matter and white-matter proposal. Together, this is solid ground for the proposal that the integrity of the left AF/SLF is crucial to the storage component of working memory and its linkage to Broca's area during the processing of argument–verb dependencies.

Turning to methodology, it is worth to briefly discuss the current white-matter analysis—in particular, because the fiber-tracking results were not used as a dependent variable in the correlation analysis, but merely as the search volume for the regression of functional data across FA maps. An alternative approach would have been to compare the reconstructed individual tracts themselves, e.g. the number of streamlines. However, Wakana et al. (2007) and Heiervang, Behrens, Mackay, Robson, and Johansen-Berg (2006) have pointed out that there is no proportional relation between individual FA values and the number of streamlines extracted by fiber tracking, and even less so at small sample sizes. Fiber tracking is sensitive to anatomical variability along the to-be-reconstructed tract, such as overall tract length, crossing fibers or tract diameter, *inter alia*. Thus, while fiber tracking is a valuable tool for anatomical description, FA values are a functionally more relevant and statistically more reliable measure of local microstructural properties (Reich et al., 2010).

Another issue with the applied FA analysis might be that the functional effects were used both as seeding points in the fiber-tracking analysis and as regressors in the correlation analysis between FA values and differences in functional activation. In principle, Kriegeskorte, Simmons, Bellgowan, and Baker (2009) point out that such an analysis could yield invalid results due to an overlap between dependent and independent variables. However, even though the functional-activation clusters were used as gray-matter seeding points, the DTI procedure reconstructed only white-matter tracts. In addition, these tracts were masked with the TBSS skeleton, which also only contains areas of high FA across participants, that is, white matter. Since the selection data at this point were not the functional data themselves, but a reconstructed tract volume, I consider the dependent measure (i.e.,voxel-wise FA of the fiber tracts connecting the IFG and TP region) to be different from the independent measure (i.e., the individual difference in functional-activation strength).

4.5 Conclusion

Our results show that, in sentence processing, the storage of arguments over increased argument–verb distance and the ordering of arguments rely on distinct neural subsystems. The direct comparison of these factors within one stimulus set shows that Broca's area (IFG) is mainly concerned with ordering, and less so with storage. Storage of a single argument in working memory across a given argument–verb distance activates the left TP region; a region classically assumed to subserve working-memory storage. The data, moreover, provide direct evidence for the role of the left AF/SLF in interfacing working-memory storage and ordering. The results suggest that a minimal cognitive architecture of sentence processing can be rooted in the interplay of concrete cognitive concepts, such as reordering and storage.

5

Patient Study

5.1 Introduction

The initial fMRI and dMRI experiment performed in the course of this thesis (see Chapter 4) yielded three key findings: First, the results strengthened the previous cross-linguistic evidence on an involvement of the left IFG in the processing of argument-reordering tasks during sentence processing. Second, the results showed that increasing verbal-working-memory load during sentence processing—as induced by an increased argument–verb distance—drives brain activity in the TP region. This suggests that the classical role of this brain region in verbal-working-memory storage carries over to sentence processing as well. Third, the results provided direct evidence for a functional role of the AF/SLF white matter structure in mediating working-memory storage and argument reordering.

While the fMRI and dMRI analyses so far point to a functional involvement of the AF/SLF, they do not allow for a generalization as to whether this functional involvement is causal, that is, whether the AF/SLF is a structure necessary for the mediation of working-memory storage and argument reordering. While clinical work by Charlton et al. (2010) and Yamada et al. (2007) shows a general role for the AF/SLF in verbal-working-memory storage outside the sentence-processing domain, clinical work from the sentence-processing domain lacks the anatomical specificity to tease apart causal influences of the TP-region gray matter and the white matter of the underlying AF/SLF: Neuroanatomically diffuse patient groups, such as primary progressive aphasics (Wilson et al., 2011) or conduction aphasics (Baldo et al., 2008; Buchsbaum et al., 2011; Fridriksson et al., 2010; Friedmann & Gvion, 2003), do not yield clear conclusions in this respect.

While there are electro-stimulation studies targeting the dorsal language-relevant fiber tracts (De Witt Hamer, Moritz-Gasser, Gatignol, & Duffau, 2011; Duffau, 2008; Duffau et al., 2002; Duffau, Gatignol, Denvil, Lopes, & Capelle, 2003), their results are not straightforwardly mapped onto the conceptual dialectics of storage and reordering: Duffau et al. (2002) and De Witt Hamer et al. (2011) report that electrical stimulation of the posterior-most limb of the dorsally running middle longitudinal fasciculus during surgery elicits anomia, while Duffau et al. (2003) find that a glioma involving the left parietal operculum in the TP region causes overt speech-repetition deficits as well as reduced digit span. Neither the overt speech task (Duffau et al., 2003), the naming tasks (De Witt Hamer et al., 2011; Duffau et al., 2002) nor the target area of stimulation (De Witt Hamer et al., 2011) directly correspond to the involvement of the AF/SLF in the conceptual dialectics of argument storage and reordering during sentence comprehension.

To instantiate a direct link between the proposed role of the AF/SLF in mediating argument storage and reordering during sentence processing, the current paradigm was used in a modified version in a case study on a patient who suffers from a focal, rupture-like lesion in the left TP region, reaching from the gray matter into the deep white matter underlying the region. Visual inspection of the patient's anatomical brain images suggested that the lesion might have caused focal damage to the AF/SLF, providing a test case for the hypothesis that the AF/SLF is specifically involved in mediating storage and reordering. If this were so, two hypotheses were possible with respect to our paradigm: First, it is possible that focal damage to the AF/SLF results in a general working-memory deficit as well as problems on sentences with long argument–verb dependencies, regardless of the relative argument order. A second possible hypothesis is that focal damage to the AF/SLF results in more specific problems in comprehending sentences that increase both argument-reordering and argument-storage demands (i.e., object-first sentences with long argument–verb dependencies), because the role of the AF/SLF is proposed to lie in the mediation of reordering and storage rather than one of the processes in particular. These hypotheses were tested in the current patient study, using the full 2 × 2 paradigm as well as a variety of working-memory tests.

5.2 Methods

5.2.1 Participants

A single female patient was tested (age 46 years). The patient was diagnosed with a cleft-like lesion following an intra-cerebral bleeding, spanning the gray matter of the left STG towards the SMG as well as the underlying white matter (see anatomical data, Figure 5.1). Time post-onset was 7.5 years. Behaviorally, the patient showed a productive deficit with phonological disruptions as well as a minor comprehension deficit involving morphosyntactic problems (Cunitz, 2011). In addition to the patient, an age-, gender- and education-matched control group of seven participants (mean age 47 years, SD 1.92) took part in the study. All participants were right-handed as determined by an abridged version of the Edinburgh inventory (Oldfield, 1971) and had German as their first language. Control participants reported no neurological or hearing deficits. Per hour of participation, the patient received €8, plus a travel reimbursement. Control participants were paid €7 per hour of participation.

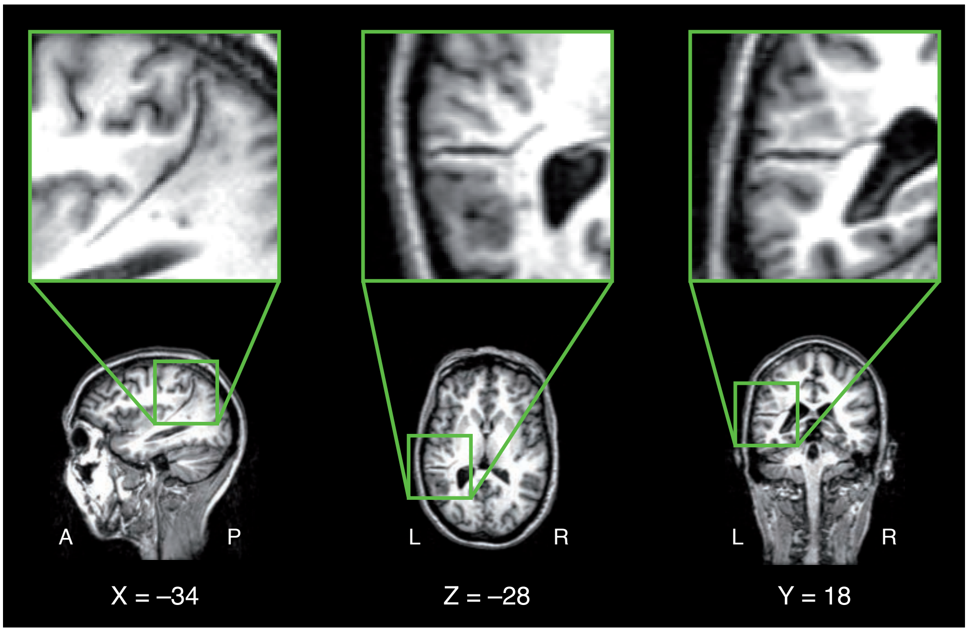

Figure 5.1: Recent anatomical scan of patient's brain in sagittal, axial, and coronal view; the enlargements show the lesion in the left TP region.

5.2.2 Working-Memory Test Battery

The patient and control participants underwent a battery of working-memory tests that focused on the ability to store, rehearse, and reorder phonological content. The involved tests were the forward- and backward-digit-span test (Jacobs, 1887) from the German version of the Wechsler test (Tewes, 1994), the Vorländer syllable-span and paronomasia test (Vorländer, 1986) and the Mottier pseudo-word-repetition test (Welte, 1981). The Vorländer syllable-span and paronomasia test (Vorländer, 1986) involves word repetition of multi-syllable words in three stages of increasing difficulty (words with two syllables, words with more than two syllables and one-syllable paronomasias). The three levels of the Mottier pseudo-word test (Welte, 1981) involve the repetition of pseudo-words of increasing syllable counts.

5.2.3 Materials

To use the sentences of the current stimulus set described in Section 2.3 as stimuli in a patient study, modifications to the stimuli were necessary to avoid overburdening the patient's language processing abilities. First, the conjunct clause—which had been attached to the original stimulus sentences to control for the possible effect of a sentence-final processing slowdown (Friedman et al., 1975; for details, see Section 2.3)—was removed from the stimuli. This also necessitated new recordings of the stimulus set, which were now carried out at a reduced syllable frequency as compared to the original stimuli. The same trained female German speaker as in the previous fMRI study (see Chapter 4) recorded the stimuli, and the same audio-preprocessing pipeline described in Section 4.2.3 was used. Again, 192 stimuli were recorded, of which a pseudo-randomized list of 96 items (24 for each of the four conditions) was generated for each participant using MATLAB® (The MathWorks, Inc., Natick, MA, USA) scripts. To increase the number of behavioral data points, each of these sentences introduced a who-did-what-to-whom yes–no comprehension question to be answered within a limited time. The proportion of yes–correct and no–incorrect questions was balanced.

5.2.4 Procedure

Stimuli were presented using Presentation® (Neurobehavioural Systems, Inc., Albany, CA, USA). Auditory stimuli were presented using a pair of ELAC Cool II stereo speakers (ELAC Electroacustic GmbH, Kiel, Germany). Visual stimuli were presented on a Sony Trinitron® Multiscan G400 CRT

VGA monitor with a refresh rate of 75 Hz (Sony Corporation, Tokyo, Japan), 70 cm in front of the participants. A sans-serif font in black letters against a gray background (size 20 px) was used.

A trial started with a fixation cross that stayed on screen for the whole trial. After a random jitter between 500 and 1000 ms, an auditory stimulus started (mean length 4.15 s, SD 0.30 s). After the auditory stimulus, the yes–no comprehension question would appear and stay on screen until a response would occur. After comprehension questions, visual feedback was given for 2000 ms by a happy green or sad red emoticon. Participants were instructed to carefully listen to the sentences and to answer the comprehension questions via button press with either their left or right hand, with one hand corresponding to yes and the other to no. Response button assignment was counterbalanced across participants.

5.2.5 Magnetic-Resonance-Imaging Data Acquisition

Structural and diffusion magnetic resonance images of the patient were acquired with a 3 Tesla Siemens TIM TRIO scanner (Siemens Healthcare, Erlangen, Germany) at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig, Germany.

Anatomical T1-weighted 3D MP-RAGE images (Mugler III & Brookeman, 1990, TI = 650 ms, TR = 1300 ms, alpha = 10°, FOV = 256 × 240 mm^2, 2 acquisitions, 1 mm isotropic resolution) were acquired with a non-slice-selective inversion pulse followed by a single excitation of each slice, and were available for preprocessing of the dMRI data.

Diffusion-weighted data were acquired with the same scanner, equipped with a 32-channel phased-array head array coil. Images were acquired with a twice-refocused spin-echo EPI sequence (Reese et al., 2003; TE = 100 ms, TR = 12 s, 128 × 128 image matrix, FOV = 220 × 220 mm^2, 88 axial slices (no gap), resolution 1.72 × 1.72 × 1.7 mm^3). Additionally, fat saturation was employed together with 6/8 partial Fourier imaging and GRAPPA (acceleration factor = 2; Griswold et al., 2002). Diffusion-weighting was isotropically distributed along 60 diffusion-encoding gradient directions with a b-value of 1000 s/mm^2. Seven images with no diffusion-weighting (b0) were acquired initially and interleaved after each block of 10 diffusion-weighted images as anatomical reference for offline motion correction. The dMRI sequence lasted about 16 minutes.

5.2.6 Data Analysis

5.2.6.1 Working-Memory Test Battery

The raw working-memory measures were split for the patient and control group, and 95-% CIs based on the control-group mean were generated using a bootstrapping approach (5000 random draws from the control population assuming a normal distribution). Memory scores of the patient were considered to differ from the control group when they fell outside of these CIs.

5.2.6.2 Behavioral Data

For the behavioral data, d′-scores and RTs were calculated for the patient and control participants. The RTs were logarithmized to correct for the typically F-shaped distribution of raw RTs. From the across-control-group d′-prime scores and logarithmized RTs, 95-% CIs were bootstrapped (based on 5000 random draws from the control population). D′-scores and RTs of the patient were considered to differ from the control group when they fell outside of these CIs.

5.2.6.3 Diffusion-Tensor Imaging

Diffusion-MRI data were analyzed using the pipeline described in Section 4.2.6.5: T1-weighted structural scans were used for skull stripping and the brain images were co-registered into Talairach space (Talairach & Tournoux, 1988). Motion correction was performed based on the 7 reference images without diffusion-weighting distributed over the entire sequence using rigid-body transformations (Jenkinson et al., 2002) implemented in FSL. The parameters were interpolated and combined with a global registration to the T1 anatomy, computed with the same method. The application of these transformations resulted in an isotropic voxel resolution of 1 mm. The gradient direction for each volume was corrected using the rotation parameters. For each voxel, a diffusion tensor model (Basser et al., 1994) was fitted and the FA was computed (Basser & Pierpaoli, 1996).

Based on prior data (Meyer, Obleser, Anwander, & Friederici, 2012; see Chapter 4), I selected two ROIs for probabilistic fiber tracking: Since the AF/SLF runs dorsally between BA 44 and the TP region (Catani et al., 2005; Friederici, 2009b, 2011; Weiller et al., 2009), a 5-mm sphere at the center of the anatomically defined BA 44 as provided with the SPM anatomy toolbox (Eickhoff et al., 2005) was generated as starting point for tracking using the Marsbar toolbox (Brett et al., 2002). As a control seed region, the same procedure was used to generate a control ROI at the center of BA 45. Both ROI volumes were back-projected into the patient's native image space, and all fiber trajectories passing through these respective ROI volumes were selected as white-matter projections by tractography from the diffusion-tensor maps (Anwander et al., 2007). Here I used probabilistic tractography (Lazar et al., 2003) as implemented in MedINRIA (Asclepios, INRIA, Sophia Antipolis, France; cf. Fillard et al., 2007). I used the same preprocessing chain as for the computation of the FA maps mentioned above, except for the fact that the diffusion tensors were computed with an isotropic resolution of 1.7 mm. Fiber trajectories were started in all voxels with an FA > 0.2 resulting in a complete set of trajectories within the whole brain.

5.3 Results

5.3.1 Working-Memory Results

On all working-memory measures, the patient was below the control-group mean, and outside of the bootstrapped CIs for six of the eight tests (all Mottier pseudo-word sub-tests, Welte, 1981; forward digit span, Tewes, 1994; two of three Vorländer syllable-span and paronomasia sub-tests, Vorländer, 1986). Scores of the patient with respect to the group average and the bounds of the bootstrapped 95-% CIs are given in Table 5.1, Figure 5.2 gives a graphical summary.

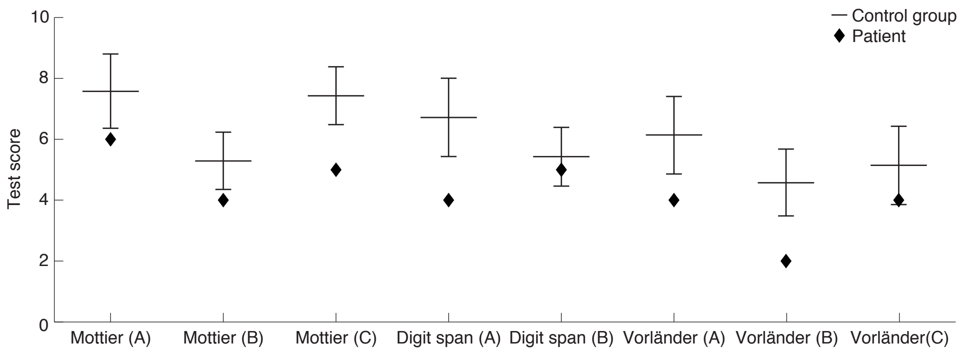

Figure 5.2: Working-memory-test-battery results; lines and error bars mark mean and bootstrapped 95-% confidence intervals for the control group; diamonds mark the raw scores of the patient.

Table 5.1: Working-memory test results; for the control group, mean and SD are given, for the patient, individual values are provided; lower and upper 95-%-CI limits are shown in the two rightmost columns.

Test	Control group		Patient	95-% CI	
	Mean	SD		Lower	Upper
Mottier					
Syllables	7.57	1.81	6	6.36	8.8
Pseudo-words (easy)	5.29	1.38	4	4.35	6.23
Pseudo-words (hard)	7.43	1.40	5	6.48	8.38
Digit span					
Forward	6.71	1.89	4	5.43	8
Backward	5.43	1.40	5	4.46	6.39
Vorländer					
Short words	6.14	1.87	4	4.86	7.41
Long words	4.57	1.62	2	3.48	5.68
Paronomasias	5.14	1.87	4	3.85	6.43

5.3.2 Sentence-Processing Results

Sentence-processing performance showed a selective picture: while the patient showed above-group RTs for all conditions, a selectively decreased performance (i.e., below-group d′-scores) was observed only for the long object-first conditions. For the remaining three conditions (short and long subject-first and short object-first sentences) the patient remained inside the control-group 95-% CI.

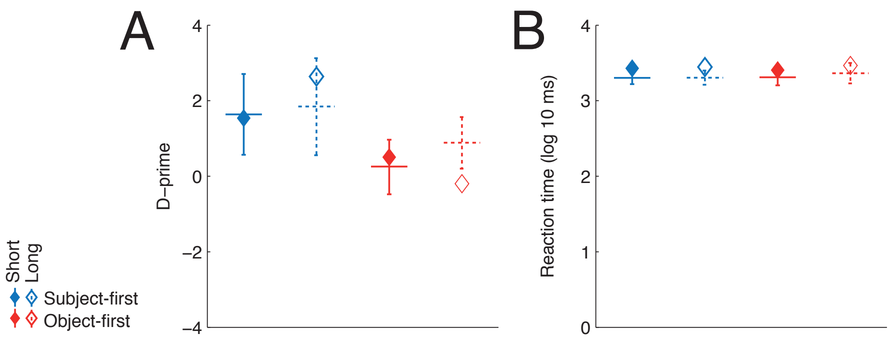

Figure 5.3: Sentence-processing results; (A) d′-scores, (B) RTs (log 10 ms); lines mark control-group mean and 95-% CI, diamonds mark the patient's values; blue color marks subject-first, red color marks object-first argument orders, solid lines mark short, dashed lines mark long argument–verb distances.

Table 5.2: Sentence-processing results; for the control group, mean and SD are given, for the patient, raw values are provided; lower and upper 95-%-CI limits are shown in the two rightmost columns.

Condition	Dependent	Control group		Patient	95-% CI	
		Mean	SD		Lower	Upper
Subject-first						
Short	d′	1.64	1.58	1.54	0.56	2.71
	RT	3.30	0.12	3.43	3.22	3.39
Long	d′	1.85	1.89	2.64	0.56	3.13
	RT	3.30	0.14	3.45	3.21	3.40
Object-first						
Short	d′	0.26	1.04	0.51	-0.47	0.98
	RT	3.31	0.15	3.41	3.20	3.42
Long	d′	0.89	0.99	-0.20	0.19	1.57
	RT	3.36	0.20	3.47	3.23	3.50

5.3.3 Diffusion-Tensor-Imaging Results

Probabilistic fiber tracking from the BA 44 and BA 45 ROIs showed a series of inter- and intra-hemispheric streamlines for the control ROI BA 45, including a ventral connection to the TP region. Seeding in BA 44, on the other hand, did not yield extensive streamlines—in particular, the patient showed no dorsal fiber tract from BA 44 to the TP region (see Figure 5.4).

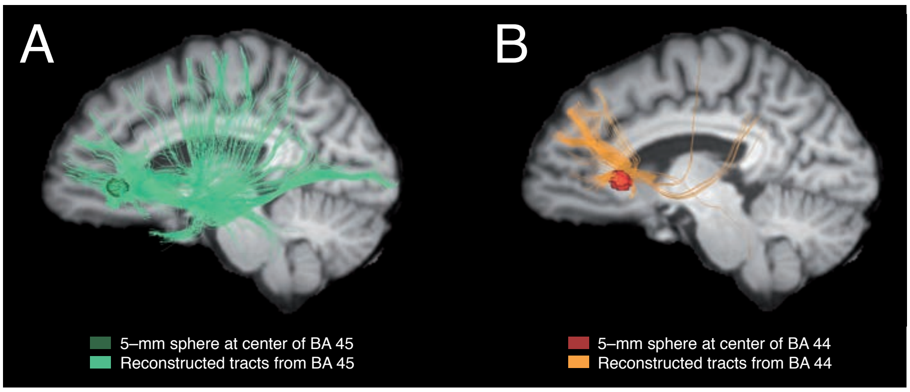

Figure 5.4: Results of DTI procedure; (A) from a 5-mm sphere at the center of BA 45 ROI; (B) from a 5-mm sphere at the center of BA 44. While a ventral connection to the TP region from BA 45 is evident in (A), no dorsal connection to the TP region from BA 44 is present in (B).

5.4 Discussion

Behaviorally, the patient showed impairments across most of the administered working-memory tests; also, generally increased RTs in the sentence-processing task were observed, with no condition-specific effects—pointing to a general processing slow-down in the patient. Response accuracy showed largely spared sentence-processing performance in case of easy (that is, subject-first sentences that involve no reordering) and working-memory non-intensive sentences (that is, short argument–verb dependencies that do not involve high verbal-working-memory storage demands). The patient did, however, show below-control group performance on long argument–verb dependencies in object-first sentences. Anatomically, DTI found that the patient apparently does not exhibit a dorsal fronto-temporal fiber tract from BA 44 to the TP region. The control tracking procedure from BA 45 showed a ventral fronto-temporal fiber tract from BA 45 to the TP region, suggesting that the absence of the dorsal BA-44–TP-region tract in the patient does not result from a global white-matter-integrity decrease in this patient. Together, this suggests that this patient's cleft-like lesion in the TP region (see Figure 5.1) is the cause of an interrupted AF/SLF in the patient, resulting in a selective deficit in the processing of sentences that tax both argument-reordering and argument-storage abilities. I will now discuss these findings in detail.

Only indirect evidence is available for a role of the AF/SLF in mediating argument storage and reordering, but no direct causal evidence. Duffau et al. (2002) report that electrical stimulation of the posterior-most limb of the AF/SLF during surgery elicits anomia. Since a case study by Duffau et al. (2003) finds that a glioma involving the left parietal operculum in the TP region causes overt speech-repetition deficits as well as reduced digit span, it is well possible that the anomia of the patients in Duffau et al.'s (2002) study may result from an underlying damage to the working-memory system. This interpretation is rather speculative, because neither the overt speech task (Duffau et al., 2003) nor the naming tasks (Duffau et al., 2002) are easily mapped onto the presumed involvement of the AF/SLF in the conceptual dialectics of argument storage and reordering during sentence comprehension. In addition, while the evidence delivered by electrical brain stimulation may be taken as causal, all patients in these studies suffered from extensive gray-matter lesions, mostly encompassing the TP region, leaving this work with the caveat of the possible attribution of the observed working-memory problems to either gray-matter damage or white-matter stimulation (cf. Section 4.4.4). Similarly indirect and potentially ambiguous evidence is delivered by the classical work on conduction aphasia already discussed in Section 4.4.4 (cf. Buchsbaum et al., 2011; Caramazza et al., 1981; Friedmann & Gvion, 2003): Fridriksson et al. (2010) and Baldo et al. (2008) converge on reporting impaired speech repetition in conduction aphasics co-occurring with both damage to the white matter underlying the left SMG and reduced gray-matter integrity in the TP region.

In spite of this indirect evidence, we suggest that the current clinical data constitute direct causal evidence for a role of the AF/SLF not only in verbal working memory, but, more specifically, in anatomically linking—and functionally mediating—a storage component in TP regions to a reordering system located in Broca's area during sentence processing. Yamada et al.'s (2007) case study may come close to deliver causal evidence for a direct role of the AF/SLF in working memory—their patient suffered from a focal lesion to the AF/SLF, presenting with a sustained language-repetition deficit. However, this result cannot easily be mapped onto the storage–reordering dichotomy. In the light of the above fMRI results from a healthy population (Chapter 4), it is noteworthy that the patient in the current study did only show a sustained sentence-comprehension deficit in the long object-first sentences, with spared comprehension of all other sentence types: If the above proposal is correct that argument reordering during sentence processing is subserved by the IFG, while argument storage is subserved by TP regions, a selective disconnection of the two regions should result in a selective comprehension deficit on sentences that involve both reordering and increased storage demands—which is exactly what the current patient data seem to suggest. It is left open for future work whether our full 2×2 paradigm might be able to verify the preliminary conclusion in that it could potentially show a selective deficit in frontal-lesion patients on object-first sentences (à la Grodzinsky, 2000, 2001; Grodzinsky, Piñango, Zurif, & Drai, 1999; Zurif & Piñango, 1999, but cf. Bastiaanse & van Zonneveld, 2006; Berndt & Caramazza, 1999), a selective deficit in posterior-lesion patients on long argument–verb-distance sentences (Friedmann & Gvion, 2003; Leff et al., 2009; Romero et al., 2006), and a selective deficit in AF/SLF-patients on long-distance object-first sentences.

As a final side note, it is interesting that while a general verbal-working-memory deficit on span tasks was observed in the patient (i.e., decreased performance on six of eight administered tests), the sentence-processing deficit was of a more selective nature rather than general to any sentence involving a long argument–verb dependency. I propose that this apparent conflict can be explained by the dissociation of reordering and rehearsal processes in the left inferior frontal cortex: As discussed above (Chapter 4), some authors (Just et al., 1996; Rogalsky & Hickok, 2010; Rogalsky et al., 2008) have equated reordering processes during sentence processing and subvocal rehearsal in the phonological loop (Baddeley, 2012; Baddeley et al., 2009). We have suggested above that this position neglects the evidence for a functional dissociation of the left inferior frontal cortex into dorsal (rehearsal) and more ventral (reordering) functions (cf. Figure 4.7). Given that our patient showed a general deficit for storage–rehearsal-type tasks, but a more selective deficit for a storage–reordering-type task, the current data point to a general involvement of the AF/SLF in storage and rehearsal outside of sentence processing and a specific involvement in storage and reordering for sentence processing proper. To put it differently: If reordering would boil down to rehearsal, a patient with focal damage to the AF/SLF should exhibit a deficit with any object-first sentence—contrary to what the current data show.

5.5 Conclusion

The current patient study set out to elucidate on the functional role of the AF/SLF with respect to the working-memory system in general as well as the storage–reordering dichotomy in sentence processing, in the light of previous indirect evidence from healthy and patient groups as well as potentially unequivocal electrical-stimulation studies. The current findings corroborate the conclusions from the above fMRI study on healthy participants. The AF/SLF seems to serve differential roles with respect to verbal-working-memory processes, depending on whether in- or outside of the sentence-processing domain: Inside the sentence-processing domain, a focal lesion to the AF/SLF can result in a selective deficit in processing sentences that involve both an object-first argument order and a long argument–verb dependency, pointing to its role in mediating reordering processes as subserved by the IFG and storage processes as subserved by the TP region. Outside of the sentence-processing domain, damage to the AF/SLF leads to a deficit on phonological-loop-type tasks, pointing to a functional segregation of reordering and rehearsal in spite of their possible common link to TP regions through the AF/SLF.

6

Electroencephalography Study

6.1 Introduction

Traditionally, it had been assumed that the human alpha rhythm (7–13 Hz; Berger, 1929) represents an idling cortical state (Pfurtscheller, Stancák, & Neuper, 1996), based mainly on the observation that alpha oscillations increase as a preface to sleep, during eye closure, or motor relaxation (for review, see Klimesch, Sauseng, & Hanslmayr, 2007)[15]. More recently, it has been proposed that the idea of alpha oscillations as an idling rhythm of the cortex may not reflect the full picture, in particular in the auditory domain (for review, see Weisz, Hartmann, Müller, Lorenz, & Obleser, 2011). Following Lehtelä, Salmelin, and Hari's (1997) report of a 10-Hz rhythm in primary auditory cortex which is sensitive to changes in auditory input, a number of recent articles have pointed out the significance of alpha oscillations for verbal working memory. For example, a magnetoencephalography (MEG) study by Jensen, Gelfand, Kounios, and Lisman (2002) used a modified version of Sternberg's (1966) letter-based working-memory paradigm, finding increased alpha power over posterior electrodes with increased verbal-working-memory load. Along these lines, Leiberg, Lutzenberger, and Kaiser (2006) reported increased alpha activity under conditions of increased verbal-working-memory-storage demands. Finally, Van Dijk, Nieuwenhuis, and Jensen (2010) reported increased alpha amplitude during storage of task-relevant pitch information. In sum, there is convincing evidence that enhanced alpha oscillations are a robust neural correlate of verbal working memory.

[15] The experiment reported in this chapter has been published in a modified version (Meyer, Obleser, & Friederici, 2012).

Given this role of alpha oscillations in item or pitch retention, we hypothesized that also higher-level cognitive processes in the auditory domain that exhibit increased verbal-working-memory demands—such as sentence processing—will increase alpha activity as well. Verbal working memory is commonly agreed upon to play an important role in sentence processing (Just & Carpenter, 1992; Rogalsky & Hickok, 2010; Waters & Caplan, 1996; Wingfield & Butterworth, 1984). Baddeley and Hitch's (1974) initial work found that concurrent memory load decreases reading-comprehension performance, inducing that reading comprehension is subserved by a capacity-constrained verbal working memory. More specific work showed that working-memory capacity determines the ability to store and retrieve the arguments (both subject and object) until they can be syntactically linked to the main verb of the sentence and the sentence meaning can be inferred (King & Just, 1991)—which is of particular relevance in languages with sentence constructions requiring the verb to be in sentence-final position such as German and Japanese.

While there is support for an involvement of verbal-working-memory resources during argument–verb dependency processing (i.e., domain-specific functions), this support is difficult to map onto the literature on alpha oscillations during verbal-working-memory storage outside of the sentence-processing domain. Previous ERP studies on verbal working memory from the sentence-processing domain rather focused on argument-reordering processes during sentence processing, mostly triggered by research questions derived from theoretical linguistics. Such studies isolated sustained negative ERP effects for object-first as compared to subject-first sentences (Felser et al., 2003; Fiebach et al., 2001, 2002; Kluender & Kutas, 1993; Phillips et al., 2005; Ueno & Kluender, 2003). However, more general work on working memory, in particular on visual working memory, suggests that the retention of order information may be distinct from mere (that is, order-indifferent) storage: Hsieh, Ekstrom, and Ranganath (2011) had their participants focus on either the presence or absence of an item or the order of items in a delayed-response paradigm, obtaining enhanced posterior alpha for storage only, independent of the order of items. Given that behavioral work suggests that argument retrieval in the vicinity of verbs is a mechanism common to both subject- and object-first sentences (Nicol & Swinney, 1989), we hypothesize common oscillatory dynamics of argument storage, independent of the relative order of arguments—as opposed to distinct sustained ERP indices which are sensitive to the relative order of arguments.

This experiment was performed to investigate verbal-working-memory-storage processes independent of a particular sentence structure, that is, ignoring the reordering factor from our original paradigm: These are required for the processing of any argument–verb dependency, regardless of the argument order. If alpha oscillations during sentence processing are independent from the processing of order information, such a result may help in disentangling verbal-working-memory and reordering processes during sentence processing.

While ERP findings from the sentence-processing domain are hard to link to the underlying neuroanatomy, a number of functional-imaging studies provide information about the neural underpinning of verbal working memory during sentence processing. As an example, Novais-Santos et al. (2007) reported left inferior parietal cortex to increase its activation with the retention interval for disambiguating information in ambiguous sentences, that is, verbal-working-memory load. In addition, Grossman et al. (2002) found an age-related decrease of brain activation related to increased argument–verb distance in the left parietal cortex, alongside sentence-processing difficulties in seniors. The notion of left parietal cortex as potential neural substrate of verbal working memory during sentence processing is in line with meta-analyses, imaging studies and clinical work from outside the sentence-processing domain (Awh et al., 1996, 1995; D'Esposito et al., 1999; Jonides et al., 1998; Leff et al., 2009; Owen et al., 2005; Petrides et al., 1993; Smith & Jonides, 1999; Wager & Smith, 2003). However, other studies focusing on verbal working memory during sentence processing reported BA 45 in the left prefrontal cortex to play a role, using paradigms comparing different syntactic dependencies (Fiebach et al., 2005; Makuuchi et al., 2009; Santi & Grodzinsky, 2007, 2010). Hence, the imaging results for verbal working memory during sentence processing and their relation to the ERP literature are unequivocal, and a temporally more fine-grained method may complement the discussion.

Due to the potential role of cortical alpha oscillations in higher-level cognitive tasks such as sentence processing, we investigated cortical oscillations during the processing of sentences that involve greater working-memory load without additionally increasing reordering demands. We hypothesized that any argument—regardless of whether it is a subject or an object—is stored in verbal working memory until the verb position at which retrieval of the argument becomes necessary for sentence interpretation. Consequently, we reasoned that oscillatory activity in the alpha band should increase with verbal-working-memory demands (Leiberg et al., 2006; Van Dijk et al., 2010) regardless of argument order. Testing this assumption will help to bridge the gap between the emerging literature on alpha oscillations in verbal working memory and the supposed role of verbal working memory during argument–verb-dependency processing. In a similar vein, we will link changes in oscillatory power during storage-intensive sentence processing to a classical working-memory measure from the sentence-processing domain, that is, reading span (Daneman & Carpenter, 1980). Finally, we investigate the neural generators of the observed responses using source localization to provide a tentative link to neuroimaging studies of sentence processing and verbal working memory.

6.2 Methods

6.2.1 Participants

Thirty-six participants took part in the study (mean age 26.4 years, SD 3 years; 18 males, all native speakers of German). All of them were right-handed as assessed by an abridged German version of the Edinburgh Inventory (Oldfield, 1971). They were matched for reading span (mean reading span 3.6, SD 0.8) according to an abridged version of the reading-span test (Daneman & Carpenter, 1980). None of the participants reported neurological or hearing deficits, and all had normal or corrected-to-normal vision. Participants were naïve as to the purpose of the study. They were paid €17.50 for participating.

6.2.2 Materials

Auditory recordings of all stimuli from the stimulus set described in Section 2.3 were available for the current EEG experiment (Section 4.2.3). For each participant, an individual pseudo-randomized list of all 192 stimuli was generated using MATLAB® (The MathWorks, Inc., Natick, MA, USA) scripts. As a task to maintain participants' attention and to get a behavioral performance measure, a yes–no comprehension question followed in 25 % of trials (e.g., *Hat der Trainer den Stürmer geehrt? / Did the coach honor the center forward?*); the proportion of yes–correct and no–incorrect questions was balanced.

6.2.3 Procedure

Participants were seated in a dimly-lit, magnetically-shielded, and sound-proof room. Stimuli were presented using the Presentation® software package (Neurobehavioral Systems, Inc., Albany, CA, USA). Auditory stimuli were presented using a pair of Infinity® Reference I MkII stereo speakers (Harman

International Industries, Inc., Stamford, CT, USA), approximately 100 cm to the left and right front of the participants. In a quarter of trials, comprehension questions were presented visually, using a proportional, sans-serif font (size 20 px), black characters on a light-gray background—a Sony Trinitron® Multiscan G220 CRT VGA monitor with a refresh rate of 75 Hz (Sony Corporation, Tokyo, Japan) was used, approximately 70 cm in front of the participants. A trial started with a green fixation cross of a random length between 2000 and 3500 ms. After this, the fixation cross turned red, and an auditory stimulus was presented—participants were instructed to blink only when the fixation cross showed up green, ensuring a low amount of blink artifacts in the data.

A sequence was either followed by the next trial or—in one fourth of the stimuli—by the yes–no comprehension question. Participants had to answer these questions by pressing one of the two buttons of a two-button response box. Response-button assignment was counterbalanced across participants. Prior to comprehension questions, a green fixation cross of a random length was presented to avoid task-preparation effects during the processing of the acoustic input. Comprehension questions were present on the screen until a button press occurred; this ensured participants were comfortable and avoided task artifacts (Hagoort, Brown, & Groothusen, 1993). Following a comprehension question, visual feedback was given for 800 ms in the form of a happy green or sad red emoticon. An experimental run, consisting of 192 trials, lasted for approximately 35 minutes. Including preparation, the experiment lasted approximately 1.5 hours. The EEG was recorded with a pair of Brainvision BrainAmp direct-current (DC) amplifiers (Brain Products GmbH, Munich, Germany) from 64 tin scalp electrodes, attached to an elastic cap (Electro-Cap International, Inc., Eaton, OH, USA). The electrodes were placed at the standard positions based on the extended international 10–20 system. Each of the electrodes was referenced to the left mastoid, and the setup grounded to the sternum. The vertical electrooculogram (EOG) was recorded from electrodes located above and below the left eye. The horizontal EOG was recorded from electrodes positioned at the outer canthus of each eye. The impedances of the electrodes were kept below 3 kΩ. The EEG and EOG were recorded continuously with a band-pass filter from DC to 250 Hz with a sampling rate of 500 Hz. Electrode positions were tracked using a Polhemus FASTRAK® electromagnetic motion tracker (Polhemus, Colchester, VT, USA). In five participants, tracking failed and mean positions of all other participants were used.

6.2.4 Data Analysis

All analyses were carried out using the Fieldtrip toolbox for EEG/MEG analysis (Oostenveld et al., 2011). An epoch of 3.5 s length was defined for analysis because we were interested in sentential oscillatory effects prior to the main verb, whose mean onset latency was 2933 ms (SD 276 ms). To resolve slow electrode drifts, the data were high-pass filtered at 0.03 Hz with a Hamming-windowed sixth-order two-pass finite-impulse-response (FIR) filter (Edgar et al., 2005). The experimental trials, including a 1-s pre-stimulus baseline, were then extracted from the data. For artifact rejection, EEG epochs were off-line re-referenced to linked-mastoid electrodes, and automatic EOG- and muscle-artifact rejection was performed on a trial-by-channel basis. Cutoffs for the EOG- and muscle-artifact rejection were set at $z = 3$ and $z = 7$ and performed inside frequency bands of 1–14 Hz and 110–140 Hz, respectively. The rejection procedure followed a distribution-based artifact-identification approach (as implemented in Fieldtrip), that is, z-scores for rejection result from the amplitude distribution across trials and channels; this resulted in a rejection rate of 34.40 % of trials, with no significant differences in rejection rates between conditions as verified by an ANOVA. After preprocessing, TFR was carried out using Morlet wavelets (Lachaux et al., 1999) in 50 frequency windows of 2 Hz each between 2 Hz and 100 Hz and in adjacent time windows of 50 ms length each. A fixed time–frequency resolution m of seven cycles was chosen. For statistical analyses, a massed cluster permutation test (Maris & Oostenveld, 2007) was carried out on the resulting (baseline-corrected) power-change estimates inside the time–frequency subspace from 5 Hz to 20 Hz. As outlined above, we tested our main hypothesis (higher oscillatory power during sentences with long argument–verb distances) in this massed-permutation-test framework using a paired t-test on data that were collapsed across the two levels of the factor deemed irrelevant to this analysis (i.e., argument order). To ensure that collapsing across the levels of the original argument-order factor would yield a statistically-reliable result, we also ran the identical analysis for this factor. A Monte-Carlo simulation with 1000 repetitions was used to identify significant clusters in time–frequency space, while controlling for false positives. We set the algorithm to first identify time–frequency bins that showed a significant effect at $p < 0.025$ and then searched for time–frequency–electrode clusters that behaved similarly, considering a minimum of three neighboring (i.e., inter-electrode distance < 6.5 cm) electrodes as a cluster.

6.2.5 Source Localization

Source localization of the significant alpha-band time–frequency cluster (see Section 6.3.2) first involved warping participants' individual electrode positions to the cortical mesh of a standard BEM as derived from a standard structural-MR image using a rigid-body transform (Besl & McKay, 1992). For each point along a 1-cm-spaced grid in this volume conductor, a forward model was estimated.

The source localization followed the workflow proposed by various previous studies using an adaptive beamformer in the frequency domain (the "dynamic imaging of coherent sources" beamformer, Gross et al., 2001; for applications, see e.g. Haegens, Osipova, Oostenveld, & Jensen, 2010; Jensen & Mazaheri, 2010; Medendorp et al., 2007; Obleser & Weisz, 2011): To attain a good spatial filter for all conditions, an additional frequency analysis on the data segments of interest (see Section 6.3.2) and their respective baselines was carried out, centered at 10 Hz (± 2 Hz spectral smoothing) and 2500 ms (± 250 ms relative to sentence onset, see Section 6.3.2; plus respective estimates from the –500–0 ms baseline intervals), using a multitaper approach (Mitra & Pesaran, 1999). From this, the cross-spectral density matrix was gathered for subsequent localization. In this way, a spatial filter for each grid point in the volume conductor was generated. Participant- and condition-specific source-activity estimates were derived by applying this spatial filter to the condition-specific sensor data. The resulting source-activity volumes were corrected for activity during the baseline period, collapsed across short and long conditions (see Section 6.1), and passed into a paired t-test. This procedure resulted in a source-level t statistic of alpha-power change for each voxel in the volume grid, which could then be mapped back onto a standard structural-MR image. Resulting peak coordinates in MNI space were converted into the space of Talairach and Tournoux' (1988) atlas using a non-linear transformation (Lacadie, Fulbright, Rajeevan, Constable, & Papademetris, 2008) for anatomical labeling.

6.2.6 Correlation Analysis

Because the behavioral performance as determined by d'-scores was positively correlated with reading-span-test scores (see Section 6.3.1), we also sought to further elucidate on the relation between participants' verbal-working-memory abilities and alpha power. To this end, we first computed individual differences between the individual averaged source-activity volumes for the long and short conditions (see Section 6.3.2). We masked these volumes for all voxels that had shown a significant difference in source activity between the two conditions of at least $t(35) > 2.5$ at the group level. All voxels inside these volumes underwent a linear regression analysis between the increase in source activity for the long as compared to the short argument–verb conditions and individual reading-span scores (see Section 6.3.2).

6.3 Results

6.3.1 Behavioral Results

We calculated d′-scores in order to avoiding participants' response bias (i.e., the individual tendency to respond either yes–correct or no–incorrect) from obscuring the behavioral result. Mean d′-scores for the yes–no sentence-comprehension task were 3.80 (SD 0.97) for the short and 3.96 (SD 1.00) for the long argument–verb dependencies. Mean percentage correct scores for the short and long conditions were 89.01 % (SD 7.89 %) and 92.06 % (SD 9.18 %), respectively. For comparison to d′-scores, we cleaned these mean percentage-correct scores for the mean response bias of $c = -0.24$ (short condition) and $c = -0.13$ (long condition) according to the procedure suggested by Macmillan and Creelman (2005). Bias-free percentage-correct estimates of 81.82 (short condition) and 82.56 (long condition) resulted. A dependent-samples t-test on the d′-scores found no significant difference between the two conditions. Also, mean d′-scores were positively correlated with reading-span-test scores across participants ($r = 0.38$, $p < 0.05$).

6.3.2 Time–Frequency Results

The statistical comparison between the time–frequency patterns of the short and long argument–verb distances yielded a single, sustained difference ($p < 0.025$), lasting from 2.25 s to 3.20 s in the 7–13 Hz (alpha-band) range. It was most pronounced at 10 Hz, ranging from 2.25 to 2.75 s. From 2.75 s onwards (i.e., adjacent to the sentence-final verb, which began at 2.9 s on average) this cluster broadened in frequency and ranged up to the 20-Hz limit (beta band) of our analysis window. For the second factor in the original design (argument order), no effect was obtained. Figure 6.1 summarizes the results: While baseline-corrected spectral power in the 4–20 Hz range is shown in the upper panel, the experimental manipulation elicits a significant increase of alpha activity for long as compared to short argument–verb dependencies (lower panel; shown are t-values from the statistical comparison).

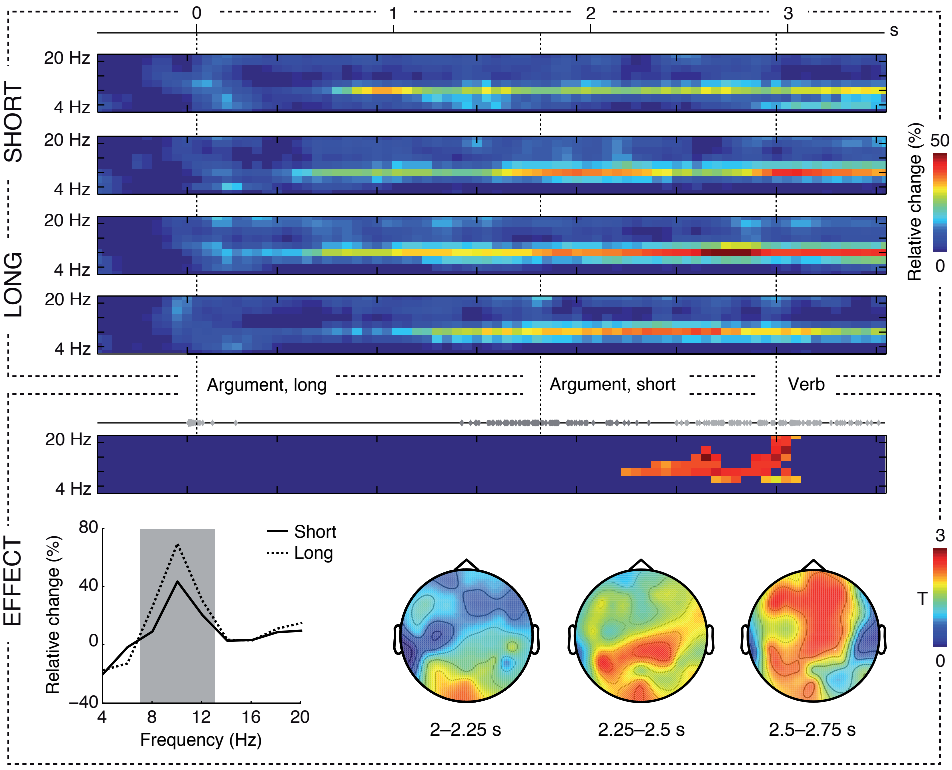

Figure 6.1: Time–frequency results in relation to the latency of the arguments and the sentence-final verb; upper panel shows grand-average sustained alpha activity (10 Hz) for the four conditions subject-first short, object-first short, subject-first long, and object-first long; lower panel displays the t-values from the paired-samples t-test on the long and short conditions, averaged across significant sensors. The alpha cluster starts about 0.75 s prior to and ends with the main-verb onset. The bottom left panel shows the average frequency spectrum, the bottom right panel shows the topography in the 10-Hz band in steps of 0.5 s, starting at 2 s (thresholded at $p < 0.025$, cluster-size corrected).

6.3.3 Source Localization of Alpha Activity: Results

Source localization on the cluster segment of interest from 2.25 to 2.75 s which showed a sustained effect at 10 Hz yielded maxima in bilateral occipital cortices (left: $x = -31$, $y = -88$, $z = 22$; right: $x = 7$, $y = -94$, $z = -20$; all coordinates in MNI-space) as well as in left parietal cortex ($x = -60$, $y = -14$, $z = 44$). The peaks correspond to the left superior occipital gyrus, right lingual gyrus, and the transition between the left SMG and left precentral gyrus, respectively. Statistical maps of these results are given in Figure 6.2.

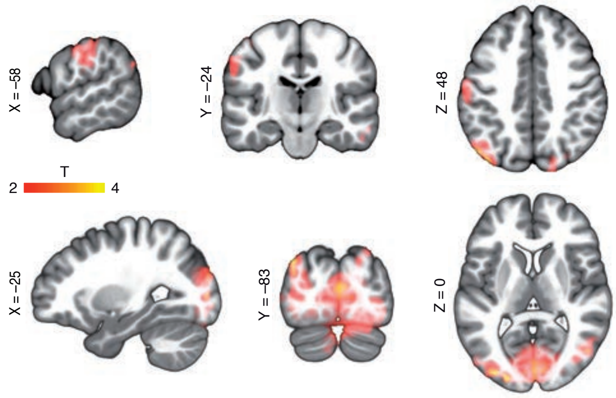

Figure 6.2: Statistical maps of the source-space comparison between alpha activity during the short and long conditions; upper row shows sagittal, coronal, and axial slices at local source maxima in the left parietal cortex; lower row shows slices for the local source maxima in the bilateral occipital cortices. (thresholded at $t(35) = 2$, approximating the uncorrected threshold from the statistical analysis).

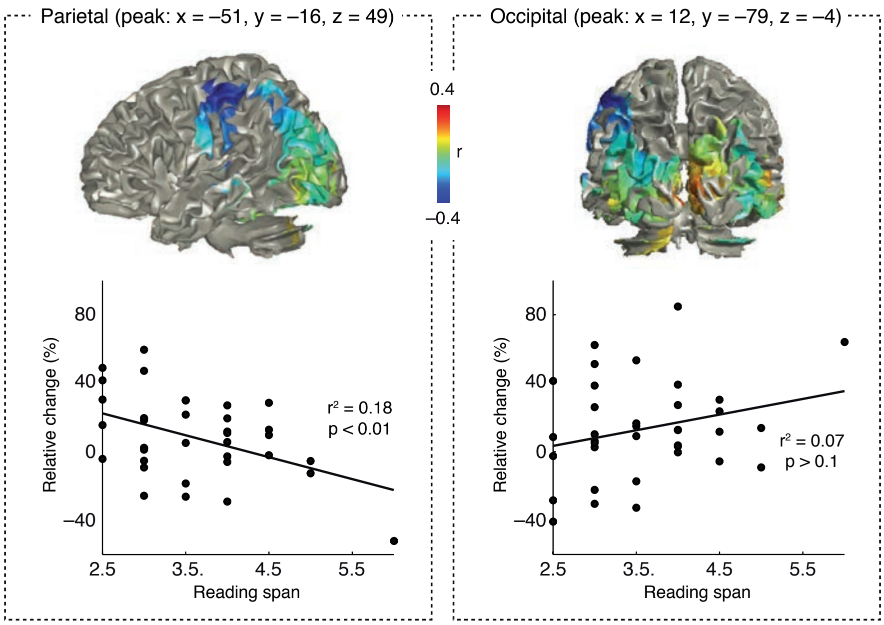

Figure 6.3: Whole-brain coefficient maps of the correlation between alpha-power change and reading span; left panels illustrate the distribution of the correlation across the left hemisphere, the scatterplot showing the negative correlation at the parietal peak; right panels show the correlation across bilateral occipital cortices, the scatterplot showing the non-significant correlation at the occipital peak.

6.3.4 Results of the Correlation Analysis

As can be seen in the right panel of Figure 6.3, a voxel-wise correlation analysis of individuals' source-level alpha-power change and reading span yielded a strong negative peak in the left parietal cortex (peak at x = –51, y = –16, z = 49; r = –0.42, $p < 0.01$), while no significant correlation was obtained in the occipital area (peak at x = 12, y = –79, z = –4; r = 0.26, $p > 0.1$).

6.4 Discussion

This study set out to elucidate the potential role of alpha oscillations during the processing of sentences that place high storage demands on verbal working memory, whereby verbal-working-memory storage was scrutinized by systematically varying the distance of an argument–verb dependency.

The results of this study show that long argument–verb distances in sentence processing elicit stronger sustained oscillations at 10 Hz (alpha band) during the storage phase than short argument–verb distances. This difference starts about 2 s after argument presentation with a maximum prior to memory retrieval at the main verb in sentence-final position. This effect turns into a transient beta-band effect (13–20 Hz) immediately at the main verb. As the time–frequency spectra in the upper panel of Figure 6.1 illustrate, the processing of all sentence types used in our paradigm elicits an alpha enhancement that builds up throughout the sentence. The lower panel of Figure 6.1 illustrates that this increase in alpha activity is significantly stronger for long as compared to short argument–verb dependencies.

The sources of this alpha-power increase were localized to bilateral occipital and left parietal cortices. Only in parietal cortex did source activity correlate significantly and negatively with reading span, a classical behavioral measure of verbal-working-memory ability from the sentence-processing domain. Because reading span was also predictive of participants' behavioral performance on the experimental task, we specifically suggest that left parietal cortex may be an important neural substrate for verbal working memory during sentence processing. We interpret these results as evidence that the role of alpha oscillations previously shown in verbal-working-memory tasks from outside the sentence-processing domain also applies to sentence processing. We will now discuss our time–frequency findings from a functional, psycholinguistic, and neuroanatomical perspective.

The functional significance of alpha oscillations for verbal working memory revealed in the present study is in line with data from various earlier working-memory studies conducted on pitch

(Van Dijk et al., 2010), letter (Krause, Heikki Lang, Laine, Kuusisto, & Pörn, 1996), syllable (Leiberg et al., 2006; Luo, Husain, Horwitz, & Poeppel, 2005), and digit retention (Schack, Klimesch, & Sauseng, 2005) in the auditory, non-sentential domain. In particular, the present result from a sentence-comprehension task converges on a seminal study on letter retention by Jensen et al. (2002), who report alpha power over posterior EEG sensors to increase with higher demands in the letter-retention task. Jensen et al.'s (2002) effect was most pronounced during the late storage phase, immediately prior to memory retrieval. In particular, this detail matches our data, since the observed alpha cluster in our data occurred in temporal proximity to the verb, where working-memory retrieval is most likely to take place, and was less pronounced during the early storage phase. Along these lines, Maltseva, Geissler, and Başar (2000) observed increased alpha phase locking prior to omitted stimuli when participants were given a series of identical auditory stimuli. Crucially, this increased alpha phase locking was observed prior to the anticipated retrieval of a stimulus, that is, during trials where no actual retrieval took place. Given this finding, we suggest that the increased alpha power in our results for the long argument–verb dependency reflects increased inhibition demands for the argument immediately prior to argument retrieval at the sentence-final verb. Since an increased likelihood for the sentence-final verb to occur entails a potential for argument retrieval, increased alpha activity in temporal proximity to the verb may index the inhibition of a premature argument release.

This view converges surprisingly well on a classical psycholinguistic theory of argument–verb dependency processing, the active-filler hypothesis (Clifton & Frazier, 1988), according to which a stored argument will be released from verbal working memory as soon as the verb which the argument will be linked to is likely to occur. In the light of our data, this view nicely goes together with a major theoretical approach of oscillatory brain activity that puts forward the idea of alpha oscillations as a domain-general mechanism for the functional inhibition of neural activity (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007). For the domain of working-memory processes, Klimesch, Sauseng, and Hanslmayr (2007) propose that alpha activity increases with inhibition demands to avoid premature information release. Under this view, our finding of a negative correlation between parietal alpha activity and reading span might index that participants with higher reading spans need to tax their functional-inhibition system less to achieve good sentence-comprehension performance, reflected in relatively less alpha power in high-span as compared to low-span participants in spite of an overall group-level alpha-power increase. This interpretation is supported by the fact that behavioral performance in our study was positively correlated with reading-span scores, in line with Klimesch, Sauseng, and Hanslmayr (2007), who find alpha power during task performance to be negatively correlated with cognitive abilities.

From a psycholinguistic point of view, the characterization of alpha power as an index of functional inhibition is in line with our finding that the present alpha-cluster offset closely matches the verb onset, rising into the beta band at this point (see Figure 6.1). Evidence for the view that arguments are retrieved in the vicinity of verbs comes from a number of behavioral cross-modal-priming studies (McElree, 2000; McElree, Foraker, & Dyer, 2003; Nicol et al., 1994; Nicol & Swinney, 1989; Tanenhaus et al., 1985). These studies showed that arguments which are encountered early in a sentence prime lexically or phonologically related target words at immediately pre- or post-verbal positions, pointing to argument reactivation in verbal working memory. Importantly, such behavioral priming effects were present independently of whether a subject or an object was reactivated.

The psycholinguistic evidence that arguments are retrieved in the vicinity of verbs may also explain why we also obtained more transient significant beta-band oscillations immediately at the sentence-final main verb, in addition to the prior alpha effect. This is in line with a recent report on the significance of beta oscillations for processes related to structural aspects of sentence processing (Bastiaansen, Magyari, & Hagoort, 2010). Enhanced oscillatory power in the beta band was found during the processing of syntactically-correct sentences as compared to word lists and violated sentence structures: Beta oscillations were visible in the violation condition until the violation could be detected, and increased during the ongoing sentence in the correct-sentence condition. The authors suggested that this effect is linked to the integration of incoming information into the ongoing syntactic representation. The beta effect in the current study is in line with this proposal in that it occurs at a point where a link between the incoming verb and the stored argument is established, that is, during argument retrieval from verbal working memory (McElree, 2000; McElree et al., 2003; Nicol et al., 1994; Nicol & Swinney, 1989; Tanenhaus et al., 1985). Evidence for this interpretation is further provided by data from Weiss et al. (2005), who report increasing beta coherence between anterior and posterior sensors at a sentence position where a subject argument needed to be linked to a sentence-final verb. Although not discussed in depth by Weiss et al. (2005), their data also show sustained increased alpha coherence towards the end of the argument-retention interval, prior to the beta-coherence increase, similar to our own effect.

Finally, a recent non-sentential study by Hsieh et al. (2011) gives reason to assume that the alpha oscillations observed in the present study reflect a different underlying mechanism than that reflected in the sustained negativity observed in previous ERP studies from the sentence-processing domain. While Hsieh et al. (2011) show that alpha oscillations during verbal-working-memory storage are independent of the order of memory items, the electrophysiological literature on argument–verb-dependency processing revealed a sensitivity of the sustained negative ERP effect to the relative order of subject and object (Clahsen & Featherston, 1999; Felser et al., 2003; Fiebach et al., 2001; Kluender & Kutas, 1993; Nakano et al., 2002; Phillips et al., 2005; Ueno & Kluender, 2003). In contrast, and in line with Hsieh et al.'s (2011) findings, our sentence-processing study did not show an oscillatory effect of argument order. Such an effect could have been expected since sustained negative ERP effects are sensitive to argument order. In sum, the evidence so far suggests that alpha-power changes can serve as an independent index of verbal-working-memory load during sentence comprehension.

Turning now to our source-localization results, the role of occipital and left parietal alpha sources for verbal-working-memory storage is partly corroborated by previous findings. We obtained both bilateral occipital and left parietal sources, but only found left parietal source activity during argument storage and prior to argument release to correlate with a behavioral measure of verbal-working-memory performance: that is, reading span. These findings can be linked to the imaging literature from both sentence processing and outside the sentence-processing domain, which also implies TP brain regions as a neural substrate for verbal-working-memory storage (Awh et al., 1996, 1995; D'Esposito et al., 1999; Grossman et al., 2002; Jonides et al., 1998; Leff et al., 2009; Meyer, Obleser, Anwander, & Friederici, 2012; Novais-Santos et al., 2007; Owen et al., 2005; Petrides et al., 1993; Smith & Jonides, 1999; Wager & Smith, 2003). For sentence processing, Grossman et al. (2002) found that brain activity in parietal cortex, related to increased argument–verb distance requiring increased verbal-working-memory-storage resources, is decreased in seniors who show reduced sentence-processing performance. Additional support comes from a study on the processing of temporarily-ambiguous sentences (Novais-Santos et al., 2007) that reported increased left parietal activity with increased length of ambiguous sentence segments: that is, increased verbal-working-memory-storage demands.

In contrast to these studies, other imaging work suggests that BA 45 in the inferior frontal gyrus, sometimes extending into the inferior frontal sulcus, subserves working memory during sentence processing (Fiebach et al., 2005; Makuuchi et al., 2009; Santi & Grodzinsky, 2007, 2010). However, these studies compared different kinds of syntactic dependencies across conditions. Particular syntactic dependencies in these studies may have engaged a syntactic-working-memory system, which has been suggested to be distinct from working memory used in other verbal tasks (Lewis et al., 2006; Van Dyke, 2007) and reported to activate BA 45 (Caplan et al., 2000). In contrast to the above studies, our paradigm kept the type of syntactic dependency constant across conditions. Furthermore, our experimental task was solveable using phonological strategies, which is also true for the reading-span task used in our correlation analysis. In sum, we suggest that the above contrast between TP and inferior frontal brain activations reflects the difference between phonological and syntactic working memory. An alternative hypothesis is that the frontal–posterior neural dichotomy rather mirrors a difference between domain-specific syntactic and domain-general attention-driven aspects of working-memory processing: Buchsbaum and D'Esposito (2008) point out the possibility that brain activations in the middle and superior parietal lobe (regions above BA 40) may imply attentional mechanisms of working memory rather than storage *per se* (for discussion, see Chapter 8). With respect to sentence processing, either suggestion must count as a hypothesis for future research.

With respect to parietal involvement in working memory during sentence processing, the connection between the current results, previous EEG findings and the fMRI literature also needs discussion: While Michels et al. (2010) reported a positive correlation between left parietal BOLD signal and left parietal alpha increase during a verbal-working-memory task in a combined fMRI and EEG study, Meltzer, Negishi, Mayes, and Constable (2007), report a negative correlation between bilateral parietal alpha and BOLD signal during a similar task. While our data cannot settle this argument, our localization agrees with the above studies in that it suggests a crucial role of left parietal cortex in verbal working memory. This supports the proposal of a functional relevance of this region in verbal-working-memory-related alpha oscillations during sentence processing.

While the data suggest a functional relevance of parietal alpha in higher-level cognitive processing, this is less straightforward for the occipital alpha sources. As occipital activity was not significantly correlated with reading-span-test scores, we suggest that occipital alpha activity does not reflect similar processes as the parietal alpha. This activity may rather reflect the inhibition of sensory bottom-up processes, potentially preventing incoming information from saturating the limited-capacity verbal-working-memory system (Jensen & Mazaheri, 2010; Just & Carpenter, 1992; King & Just, 1991; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). In the context of sentence processing, such a mechanism might serve to avoid new information from interfering with arguments already stored in verbal working memory (Lewis, 1996; Van Dyke, 2007; Van Dyke & McElree, 2006). While such a double role for alpha oscillations in the present study is speculative, a functional role of occipital cortices in verbal working memory is also unlikely given the fMRI data discussed above.

6.5 Conclusion

Our results show that in sentence processing, the storage of an argument (i.e., subject or object) over longer distances modulates and enhances alpha oscillations (10 Hz) in left parietal cortex. These oscillations are predictive of sentence-processing performance as measured by a standardized sentence-processing-specific verbal-working-memory test. Our results also support previous research that links argument–verb-dependency establishment to beta oscillations. The time course and brain topography of the alpha effect suggests that alpha oscillations play a role in functionally inhibiting the premature release of verbal information that will subsequently be integrated. This is the first evidence that verbal-working-memory storage during sentence processing relies on oscillatory processes similar to those observed for domain-general working memory outside of sentence processing. Thus, oscillatory dynamics in the alpha range are a candidate neural surrogate that links listeners' sentence-processing abilities to more domain-general neural and cognitive resources.

7

Combined Analyses

7.1 Introduction

In psycholinguistic research, argument–verb dependencies have been one of the most fruitful fields in studying the cognitive architecture of language processing. Following initial discoveries that concurrent working-memory load decreases reading-comprehension performance (Baddeley & Hitch, 1974), it was established early on that working memory plays an important role in sentence processing (Just & Carpenter, 1992; Wingfield & Butterworth, 1984). Specifically, King and Just (1991) indicated that an individual's working-memory capacity in part determines the ability to store subject and object until they can be retrieved and syntactically linked to the main verb of a sentence. This entails that the main role of working memory during sentence processing is in argument storage and retrieval[16].

Event-related-brain-potential studies studies provided further evidence for the role of working memory as argument storage during argument–verb-dependency processing by isolating sustained negative ERP effects for object-first as compared to subject-first sentences (Felser et al., 2003; Fiebach et al., 2001, 2002; Kluender & Kutas, 1993; Phillips et al., 2005; Ueno & Kluender, 2003). Most of these studies involved a direct comparison of object-first and subject-first sentences, not considering the influence of argument–verb distance on working-memory load independently of argument order. In a recent study (Meyer, Obleser, & Friederici, 2012; see Chapter 4), we directly compared short and long argument–verb dependencies irrespective of the relative order of subject and object. Oscillatory brain activity in the alpha range increased during working-memory storage of arguments across an in-

[16] The analyses of the current chapter have been submitted for publication (Meyer, Obleser, Kiebel, & Friederici, in revision).

creasing argument–verb distance; this effect was common to both subject-first and object-first sentences. This suggests that working-memory storage is employed independently of the syntactic status of the arguments.

In the present study, we assume that working-memory-storage demand increases for both subjects and objects with dependency length. If so, this increase in dependency length should also increase working-memory-retrieval demands for both subjects and objects at their subcategorizing verb (i.e., the verb that delivers the information about the number and kind of arguments), simply due to progressive working-memory decay (Lewis et al., 2006). Evidence that arguments occurring early in a sentence are retrieved from working memory in the vicinity of their subcategorizing verb comes from cross-modal-priming studies, where priming effects have been found to start at the subcategorizing verb and continue subsequently (McElree et al., 2003; Tanenhaus et al., 1985; Van Dyke, 2007). In addition, it was found that argument retrieval occurs for both subjects and objects during the processing of passive sentences, irrespective of the relative argument order (Nicol, 1993; Osterhout & Swinney, 1993). Thus, retrieval, as storage, may be indifferent to the relative order of subject and object.

The other important sentential process under consideration here, argument reordering, has been shown to differentially increase processing load during argument–verb-dependency resolution at subcategorizing verbs (Grodner & Gibson, 2005; Rösler, Pechmann, Streb, Röder, & Hennighausen, 1998). Both theoretical and empirical work suggests that this increased processing load may reflect the recovery of the original subject-first argument order from the incoming argument order as stored in working memory (Chomsky, 1981; Friederici, Fiebach, et al., 2006). From a working-memory perspective, argument reordering is thought to be distinct from retrieval operations, and may be conceptualized as an executive operation on the contents of working memory (Baddeley, 2012; Wingfield & Butterworth, 1984).

Which brain areas form the neuroanatomical basis of argument retrieval and argument reordering? In a recent fMRI study, we orthogonally manipulated argument-storage and argument-reordering demands (Meyer, Obleser, Anwander, & Friederici, 2012; see Chapter 4). We found significant activity in the left TP region for long as compared to short argument–verb distances, while the left IFG was significantly active for object-first as compared to subject-first argument orders. These results are in line with imaging research on the neural correlates of working memory during sentence processing (Grossman et al., 2002; Novais-Santos et al., 2007). Since a role of the left TP region in both working-memory storage and retrieval has been suggested previously (Buchsbaum et al., 2011; Henson et al., 1999), these results are also compatible with the proposal that increased argument-storage demands entail increased argument-retrieval demands. Furthermore, the IFG responsivity to increasing argument-reordering demands is in line with crosslinguistic data on argument-order processing (Ben-Shachar et al., 2003; Friederici, Fiebach, et al., 2006; Kinno et al., 2008).

In sum, a possible conceptual scenario for the working-memory sub-processes of argument retrieval and reordering is the following: Argument–verb dependency processing might involve the initial storage of incoming arguments in working memory across the argument–verb distance; at their subcategorizing verb, these arguments are retrieved; finally, an argument-reordering step is required to re-establish the original, that is, intended argument order (e.g. in case of object-first sentences). A sketch of this sequence of processes is provided in Figure 7.1.

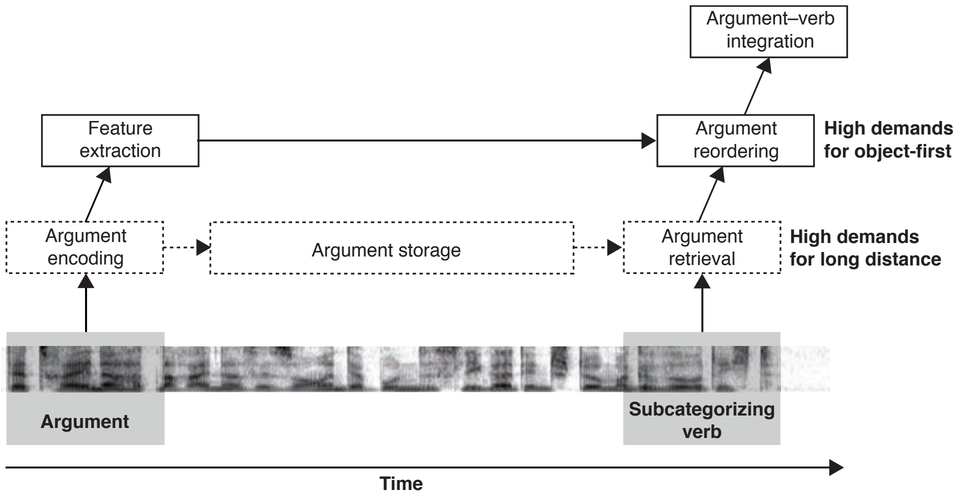

Figure 7.1: Conceptual sketch of possible working-memory sub-components involved in argument–verb-dependency processing: In brief, arguments are extracted from the speech stream on encounter, encoded, and stored in working memory. At their subcategorizing verb, arguments are retrieved and reordered into their original order based on their syntactic features; retrieval demands are higher for long argument–verb distances due to memory decay, whereas reordering demands are higher for object-first sentences.

In spite of the neurolinguistic evidence for an involvement of the left TP region in working-memory storage and retrieval and the cross-linguistic evidence for a role of the left IFG in argument reordering, it is unclear how these processes of argument retrieval and reordering map onto the spatiotemporal neuronal dynamics of this underlying neuroanatomical network.

The current study focused on these dynamics, using a previously implemented paradigm that orthogonally manipulated argument storage and argument reordering in German sentences. To perform the current combined fMRI–EEG analyses, previously acquired fMRI (Meyer, Obleser, Anwander, & Friederici, 2012) and EEG (Meyer, Obleser, & Friederici, 2012) data were re-analyzed from a sub-sample of 14 participants who had participated in both of these studies. Our combined analysis can principally map temporal EEG dynamics to spatially-precisely-defined regions derived from the fMRI results.

As outlined above, we expected that memory retrieval at subcategorizing verbs is harder for long as compared to short argument–verb distances due to increased memory decay (Baddeley, 2012; Gibson, 2000). Since memory retrieval has been related to the P300 range (cf. Ergen, Yildirim, Uslu, Gurvit, & Demiralp, 2012; see Section 7.4), we hypothesized that this difference results in early, increased brain activity in the working-memory-retrieval-related TP region in response to the subcategorizing verb, leading to an increased response in the TP-region EEG source time course for long as compared to short argument–verb dependencies. At the EEG sensor level, an increased correlation of the ERP over posterior sensors with the fMRI effect in the TP region is expected temporally proximate to the source response. Equivalently, we hypothesized that increased argument-reordering demands (object-first as compared to subject-first argument orders) subsequently increase brain responses in the left IFG during the processing of subcategorizing verbs. Accordingly, this should be reflected by a response in the IFG dipole time course (greater for object-first than for subject-first argument orders) as well as an increased correlation of the ERP over frontal sensors with the fMRI effect in the IFG region. Previous research has found argument-reordering demands to drive ERP effects in the P600 range (cf. Friederici, Steinhauer, & Pfeifer, 2002; see Section 7.4); therefore, we expected both the source- and sensor-level effects of argument reordering to occur in a similar time range. To test these hypotheses, we used two complementary analysis techniques: Firstly, we reconstructed the time course of the TP and IFG ROIs from ERP data to test the hypothesis about the temporal sequence of activation due to reordering and retrieval. Secondly, we correlated, across participants, task-specific fMRI activations of these two regions with the ERPs at the sensor level.

7.2 Methods

7.2.1 Participants

Data of fourteen participants (mean age 26.7 years, SD 3.5 years, 6 females, all native speakers of German) were analyzed. These data were taken from two larger studies of 24 participants (fMRI study) and 36 participants (EEG study), from which we chose those participants who had taken part in both experiments (in counterbalanced order; minimum time between sessions was 53 days, maximum 160 days). Participants had been matched for their reading span being in the range between 2.5 and 4.5 (sub-sample mean 3.8, SD 0.7) according to an abridged version of the reading-span test (Daneman & Carpenter, 1980). All participants were right-handed as assessed by an abridged version of the Edinburgh Inventory (Oldfield, 1971), reported no neurological or hearing deficits, and had normal or corrected-to-normal vision. Participants were paid €14 for participation in the fMRI study and an additional €17.50 for participation in the EEG study. Written informed consent was obtained from all participants. All procedures received ethical approval by the local ethics committee (University of Leipzig).

7.2.2 Materials

As described in Section 4.2.3 and Section 6.2.2, auditory recordings of all stimuli from the stimulus set described in Section 2.3 were used in the experiments. For the fMRI study, 192 additional filler sentences described in Section 4.2.3 were used. For the EEG study, we had chosen to not use filler sentences to keep the recording sessions as short as possible: Long-lasting EEG recording sessions tend to decrease participants' attention and increase the amount of recording artifacts towards the end of the experimental run. As a second step to counter participants' attention drop, we increased the percentage of task trials to 25 % (i.e., 48 sentences per participant).

For the fMRI study, each participant received an individual list of 216 stimuli; for the EEG study, each participant received the total stimulus set of 192 stimuli. As a task to maintain participants' attention in both the fMRI and the EEG study, 16.7 % (fMRI) and 25 % of trials (EEG) introduced a who-did-what-to-whom yes–no comprehension question. The proportion of yes–correct and no–incorrect questions was balanced. For further details on stimulus preparation, please refer to the respective sections above.

7.2.3 Procedure

I here repeat parts of Section 4.2.4 and Section 6.2.3, so the reader can grasp how details of the acquisition modality necessitated subtle changes to the respective procedures. The order of participation in the fMRI and EEG was counterbalanced across participants. For the fMRI study, the auditory stimuli were presented using air-conduction headphones (Resonance Technology, Inc., Northridge, CA, USA). Visual stimuli were presented on a Sanyo PLC-XP50L LCD XGA mirror-projection system with a refresh rate of 100 Hz (Sanyo Electric Co., Ltd., Moriguchi, Japan), mounted onto the headcoil. In the EEG study, auditory stimuli were presented using a pair of Infinity® Reference I MkII stereo speakers (Harman International Industries, Inc., Stamford, CT, USA). Visual stimuli were presented using a Sony Trinitron® Multiscan G220 CRT VGA monitor with a refresh rate of 75 Hz (Sony Corporation, Tokyo, Japan). Across recording modalities, visual stimuli appeared in a sans-serif font in black letters against a gray background (font size 20 px).

In the fMRI study, a trial started with a fixation cross that stayed on screen for the whole trial. After a random jitter of 0, 500, 1000 or 1500 ms, an auditory stimulus started (mean length 4.9 s, SD 0.36 s). To keep the number of acquired volumes (and thus the signal-to-noise ratio) constant across conditions, we interpolated a silent period and an on-screen fixation cross between stimulus and trial ending to arrive at a constant trial duration of 8 s. Such a sequence was either followed by the next trial or by a visual comprehension question. The question remained on screen for 1500 ms, and participants were instructed to answer the question as quickly as possible during this time period. Visual feedback was given for 1000 ms by a green happy or red sad emoticon. To also keep the duration of the comprehension probes constant, silence and an on-screen fixation cross were interpolated, such that each comprehension probe would last 4 s. Participants were instructed to answer the comprehension questions via button press with either their left or right hand, with one hand corresponding to yes and the other to no. Response button assignment was counterbalanced across participants. In the EEG study, a trial started with a green fixation cross of a random length between 2000 and 3500 ms. After this, the fixation cross turned red, and an auditory stimulus was presented. This extended prologue was used to avoid oculomotor artifacts, which else would threaten to decrease the signal-to-noise ratio. Additionally, participants were instructed to blink only when the fixation cross showed up green. Either the next trial followed, or a yes–no comprehension question. Participants had to answer these questions by using either their left or right hand to press one of the two buttons of a two-button response box, whereby response-button assignment was counterbalanced across participants. Prior to comprehension questions, a green fixation cross of a random length was presented to avoid task-preparation effects. To ensure participants' comfort and avoid task artifacts (Hagoort et al., 1993), comprehension questions stayed on screen until a button press occurred. Like in the fMRI procedure, visual feedback was given after comprehension questions for 800 ms in the form of a happy green or sad red emoticon. An experimental run, consisting of 192 trials, lasted for approximately 35 minutes. Including preparation and electromagnetic position tracking (see below), the experiment lasted approximately 1.5 hours.

7.2.4 Data Acquisition

Details of structural- and functional-MRI acquisition protocols can be found in Section 4.2.5; the details for the EEG data acquisition can be found in Section 6.2.3. The participant sub-sample of the current analyses did not contain individuals for whom electromagnetic electrode-position determination failed.

7.2.5 Data Analysis

For assessment of behavioral performance in both the fMRI and EEG study, d'-scores were available from the original experiments (see Section 4.2.6.1 and Section 6.3.1). For both the fMRI and EEG study, a one-sample t-test on the difference between the mean d'-scores and chance-level performance ($d' = 0$, i.e., 50 % correct responses) was performed. A 2 (fMRI versus EEG) × 2 (subject-first versus object-first) × 2 (short versus long) ANOVA was run on the response data.

Preprocessing and analysis of the fMRI data is described in Section 4.2.6.2. The resulting statistical maps were thresholded at $p < 0.005$. Details of the EEG data analysis are described in Section 6.2.4. For the participant sub-sample used in the present analyses, the overall trial-rejection rate was 16.3 %.

7.2.6 Combined Analyses in Sensor and Source Space

For the combined fMRI–EEG analysis in sensor space, fMRI-informed topographical correlation analyses were performed. To use the fMRI results as a regressor for the EEG data, we first calculated the individual signal change inside the functionally defined fMRI ROIs (see Section 7.3.2) for each of the four experimental levels (subject-first and object-first as well as short and long). To reduce the amount of data, we down-sampled the ERPs and their respective baseline periods to 100 Hz. We then calculated four mean ERPs for each participant, corresponding to the four design levels extracted from the fMRI data, resulting in an individual average ERP for the subject-first (short and long), object-first (short and long), short (subject-first and object-first) and long (subject-first and object-first) conditions. The fourteen individual ERPs for each of these four levels underwent across-participants electrode- and sample-wise Pearson's linear regression analyses with the fMRI-based regressors (see above), resulting in a time series of 120 (200 ms baseline period plus 1 s ERP) topographical coefficient maps for the correlation between the fMRI signal change and the ERPs for the four respective levels. To retrieve the final statistical maps for the two main effects of our design, we z-transformed these maps for the four levels and computed a difference map for the main effect of reordering (object-first minus subject-first) and retrieval (long minus short). The resulting difference values were divided by the difference between the standard errors, and converted to p-values, which underwent false-discovery-rate (FDR) correction across samples and electrodes (Benjamini & Hochberg, 1995) to control for the inflated type-I-error risk. For the combined fMRI–EEG analysis in source space, ERP-informed dipole-time-course analyses were performed in SPM8, using spatially precise fMRI priors (Daunizeau, Laufs, & Friston, 2010). First, the individual high-resolution anatomical scans were normalized to MNI space using both Fieldtrip and SPM8. After unified segmentation, individual BEMs (Besl & McKay, 1992) were generated, to which the individually determined electrode positions were co-registered. A lead-field matrix for each point in this volume conductor was generated using the Fieldtrip toolbox for EEG/MEG analysis (Oostenveld et al., 2011). For the source-time-course analysis, a variational-Bayesian equivalent-current dipole (VB-ECD) procedure (Kiebel, Daunizeau, Phillips, & Friston, 2008) was applied. We used subject-specific fMRI-based location priors for the IFG and TP region (see Section 7.3.2) to derive source time courses. Location priors were derived by determining the MNI coordinate of the individual statistical peak voxel inside the respective group-level ROI (see Section 7.3.2) where we used a first-level t-contrast for the respective main effect, masked for the respective ROI (i.e., object-first greater subject-first for the IFG ROI, long greater short for the TP-region ROI, see Section 7.3.2). The dipoles at these prior positions were allowed to relocate freely inside a radius of 0.5 cm and to change their orientation and moment, following the analysis strategy used by Friederici et al. (2000). The VB-ECD algorithm was set to perform iterations of minimizing the negative free energy F to fit the dipole locations and orientations to the actual sensor data across trials and conditions. The dipole locations and orientations were determined at convergence, and the individual EEG sensor data were projected onto these dipoles through the individual lead-field matrix—resulting in final time courses of dipole moments Q_x, Q_y, and Q_z in all three spatial directions. For each ROI, the first eigenvariate from a principal component analysis on these three dipole moments was used to arrive at a single time course for each trial. Finally, time courses for each ROI and participant were averaged and t-tests were performed on specific time windows (see Section 7.3.2).

7.3 Results

7.3.1 Behavioral Results

For the fMRI data, mean d′-score was 0.6 (SD 1.0), which was significantly different from chance ($t(13) = 2.17$, $p < 0.05$). For the EEG data, mean d′-score was 2.8 (SD 0.5), which was significantly different from chance as well ($t(13) = 21.05$, $p < 0.001$). The ANOVA on the condition-specific scores for the fMRI and EEG experiment showed a main effect of experiment (fMRI versus EEG; $F(2,13) = 116.60$, $p < 0.001$), with no other main effects or interactions present.

7.3.2 Combined Analyses

As functionally defined spatial priors for the combined fMRI–EEG analyses, two main activation foci were determined from the fMRI data, applying stimulus functions using the duration of the whole sentences (see above), shown in Figure 7.2.

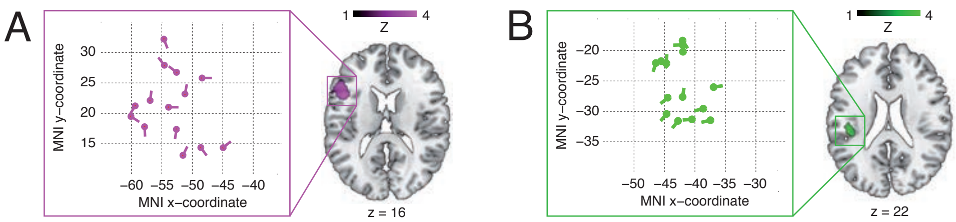

Figure 7.2: Brain activations for the main effects of argument order (magenta cluster in panel A) and argument–verb distance (green cluster in panel B). Activations are thresholded at $p < 0.005$ at a minimum cluster size of 20 supra-threshold voxels. The respective coordinate systems (left) illustrate the distribution of the individual dipole locations and orientations inside the IFG (A) and TP region (B) group-activation clusters in the axial plane after relocation.

A test for the main effect of reordering (object-first sentences leading to more activation than subject-first sentences) yielded a peak in the left IFG (group-level peak at x = –45, y = 14, z = 16; peak z-score 3.21; cluster size 127 voxels), shown in panel A of Figure 7.2. The activation focus for the main effect of retrieval (long argument–verb distances leading to stronger activation than short argument–verb distances due to increasing memory decay and accordingly increasing retrieval demands) was obtained in the left TP region, more specifically the Rolandic operculum (group-level peak at x = –42, y = –25, z = 22; peak z-score 3.38; cluster size 23 voxels), shown in panel B of Figure 7.2. Because no significant interactions were found on the whole-brain level, we restricted our combined analyses to the main effects of reordering (object-first versus subject-first) and retrieval (long versus short). Table 7.1 summarizes the activations (minimal cluster size 20 voxels).

Table 7.1: List of significant clusters in the fMRI contrasts, thresholded at $p < 0.005$ and a minimum cluster extent of 20 voxels*.

Site	MNI coordinate			Cluster size (mm^3)	Z-score
	X	Y	Z		
Object-first > subject-first					
	–45	14	16		3.21
IFG / BA 44*	–60	20	13	1143	3.14
	–51	20	22		3.13
IFG / BA 45*	–42	5	52	243	3.01
Long > short					
Rolandic operculum*	–42	–25	22	207	3.38
	–18	–34	49		2.92
Postcentral gyrus / area 3a*	–30	–31	–52	198	2.61
	–27	–40	46		2.60

*According to Eickhoff et al. (2005).

The fMRI-informed topographical correlation analysis in EEG sensor space at the subcategorizing verb yielded a significant late left frontal correlation for the reordering factor (i.e., a significant difference in correlations between the object-first and subject-first sentences with the signal change in the IFG ROI). This correlation difference was present at electrode AF7 (0–250 ms), electrodes FC5, F7, AF7, FP1, FP2 and F8 (251–500 ms), electrodes FC5, F5, F7, C3, FC3, F3, AF3, AF7 and CP3 (501–750 ms), and electrode F7 (751–1000 ms). In the average time course over these sensors the significant difference lasts from 300 ms to 740 ms (Figure 7.3 A; $p < 0.05$, FDR-corrected). The analog analysis for the retrieval factor (i.e., the difference in correlations between the long and short argument–verb dependencies with the signal change in the TP region ROI) yielded a significant early left posterior correlation at electrodes CP5, TP7, TP9, PO7 and O1 (0– 250 ms), and electrodes PO7 and O1 (251–500 ms), lasting from 10 ms to 470 ms in the average over these sensors (Figure 7.3 B; $p < 0.05$; FDR-corrected).

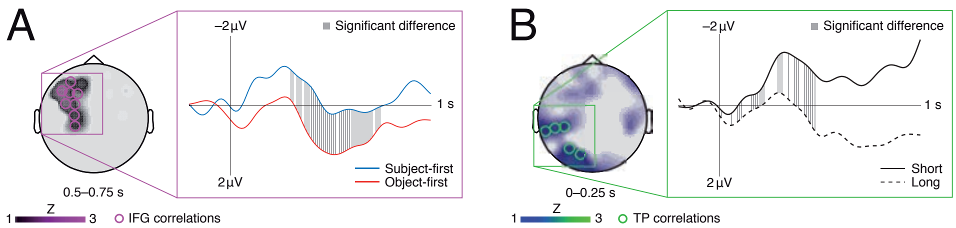

Figure 7.3: Results of the fMRI-informed topographical correlation analysis for the IFG (A) and TP region (B), respectively. Circles mark EEG sensors at which significant fMRI–EEG correlation differences were obtained, whereby the topography represents the average correlation across the named time window. Waveforms show the average ERPs across these EEG sensors. Gray lines mark significant sample-wise correlation differences ($p < 0.05$, FDR-corrected).

The dipole-time-course analysis in MRI source space for the main-verb epoch involved minor fMRI-prior relocations by the VB-ECD algorithm (< 1 mm), resulting in an average relocated IFG dipole position of $x = -53$, $y = 21$, $z = 20$ and an average relocated TP-region dipole position of $x = -42$, $y = -26$, $z = 20$ (individual dipole locations after relocation are shown in Figure 7.2). Statistical analyses of the dipole time courses (object-first and subject-first across the individual IFG dipole positions, long and short across the individual TP-region dipole positions) in two time windows defined by our prior hypotheses (300–500 ms for the IFG dipole time course, 200–300 ms for the TP-region time course) showed significantly increased dipole activity in the IFG for the object-first as compared to the subject-first argument orders from 300 to 500 ms. While our hypothesis-based time window for the TP-region time course did not yield a significant difference between the short and long conditions, visual inspection (see Figure 7.4 B) informed us about a second, earlier time window showing a difference (75 samples from 35 to 180 ms, see discussion). Although selected *post-hoc* and as such not a statistically significant result, for this time window we found $t(13) = 2.57$, $p < 0.05$ for the long as compared to the short argument–verb distances (Figure 7.4 B).

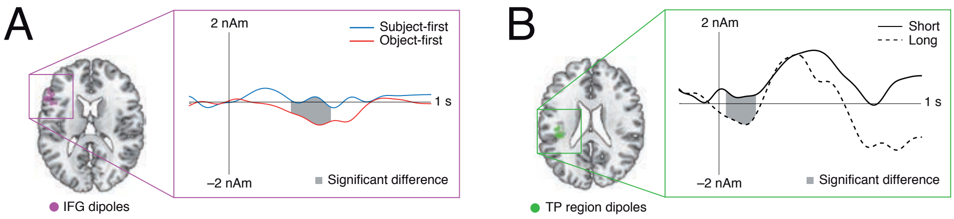

Figure 7.4: Results of the ERP-informed dipole-time-course analysis in MRI source space for the IFG (A) and TP-region (B) dipoles. Dots in the brain renderings mark the final dipole positions; the respective waveforms illustrate the reconstructed grand-average dipole time courses across IFG (A) and TP-region (B) dipoles; gray areas mark significant source-activation differences ($p < 0.05$, uncorrected). The TP region shows an early difference between the short and long argument–verb distances, surfacing as an early left posterior positivity. The IFG shows a late difference between the subject-first and object-first argument orders, surfacing as a late left frontal positivity.

7.4 Discussion

7.4.1 Behavioral Data

The statistical analysis on the behavioral data from our fourteen participants suggests that while behavioral performance in both the fMRI and the EEG study was significantly above chance, performance in the fMRI study was significantly worse than it was in the EEG study. As a second finding, there were no condition-specific effects in either the fMRI or the EEG study. While the second speaks in favor of a balanced design and no processing-difficulty confounds, the first means that the participants were able to process and comprehend all four conditions of our experimental paradigm. Given the overall better performance in the EEG study, the difference in performance between the fMRI and the EEG study may be explained by the different task procedures: The response window in the fMRI study was strongly time-constrained, whereas in the EEG study it was not. Given participants' ability to process our stimuli in the EEG study, we are confident that the task in the fMRI study served to keep participants' attention directed towards the sentences, rendering the results valid.

7.4.2 Combined Analyses

The current fMRI analyses are in line with the results from the full 24-participant sample (Meyer, Obleser, Anwander, & Friederici, 2012; see Chapter 4): The left IFG is sensitive to the relative order of arguments in transitive German sentences, while the left TP region is sensitive to argument–verb-dependency length. More importantly, the combined fMRI–EEG analyses at the subcategorizing verb—the main focus of the current study—suggest that IFG source activity occurs relatively late, whereas TP-region activity was only *post-hoc* found to occur earlier than predicted by our prior hypotheses (Figure 7.3). Topographical correlation analyses showed that IFG activity surfaces in a left frontal late positivity, while TP-region activity surfaces in an early left posterior positivity (Figure 7.4). Both correlation and source-space results speak in favor of a plausible role of the IFG and TP-region dipoles in the generation of the observed ERP response: Based on previous reports (Friederici, Fiebach, et al., 2006; Novais-Santos et al., 2007), we suggest that the reconstructed source time courses of the IFG and TP region, in response to the subcategorizing verb, reflect the activation time course of the neuroanatomical substrates of early argument retrieval (TP region) and late argument reordering (IFG) at subcategorizing verbs. Furthermore, we suggest that the sensor-level fMRI–EEG correlations mirror this functional course of retrieval and reordering. Before we turn to the combined fMRI–EEG findings, we will first briefly discuss the fMRI results.

Increased activation in the left IFG for object-first as compared to subject-first argument orders has been reported in previous imaging work from Hebrew, German, and Japanese (Ben-Shachar et al., 2003; Friederici, Fiebach, et al., 2006; Kinno et al., 2008; Obleser & Weisz, 2011), independent of working-memory demands (Caplan & Waters, 1999; Waters & Caplan, 1996). Increased activation in the TP region, on the other hand, suggests a role in retrieval of the argument at the main verb, which is plausible given previous reports of a role of the left SMG and inferior parietal regions during verbal-working-memory retrieval outside of sentence processing (Buchsbaum et al., 2001; Henson et al., 1999; Ravizza, Delgado, Chein, Becker, & Fiez, 2004; Ravizza et al., 2011). Furthermore, the posterior STG has been found active for verbal-working-memory storage during the processing of ambiguous sentences with long retention intervals for the disambiguating information (Novais-Santos et al., 2007). In addition, reduced verbal-working-memory-related parietal brain activity has been suggested as a source of sentence-processing difficulties in seniors (Grossman et al., 2002). For a more comprehensive discussion, we refer the reader to our previous study (Meyer, Obleser, Anwander, & Friederici, 2012). In the following, we will focus on the combined fMRI–EEG findings.

The increased TP-region activity for increasing argument–verb distances, surfacing as an early left temporo-parietal positivity in the current topographical correlation analysis, matches our hypothesis that long argument–verb distances result in increased argument-retrieval demands at the subcategorizing verb. Furthermore, we suggest that the combined fMRI–EEG result provides a possible link between the evidence on TP-region involvement in verbal working memory discussed above and previous reports of early positive ERP responses during verbal-working-memory retrieval (Donchin & Coles, 1988; Grossberg, 1984): The present results show at the sensor-level an early positive correlation with the fMRI TP-region activity. While there has been a previous proposal along these lines (Birbaumer, Elbert, Canavan, & Rockstroh, 1990), there remained a lack of fMRI–EEG studies that merit a direct connection.

In line with this proposal, a previous study reports a P300 during tone retrieval from working memory, whereby the latency of this effect was positively correlated with digit-span-test scores (Polich, Howard, & Starr, 1983). Ergen et al. (2012) found matching results for letter retrieval. Review studies stress these convergences (Friedman & Johnson, 2000; Polich, 2007; Rugg & Curran, 2007). Studies from the sentence-processing domain also observed positivities in the P300 range during verbal-working-memory retrieval: Friedman et al. (1975) performed a study in which the meaning of early words in a sentence could only be resolved at later words—requiring sentence-final working-memory retrieval, giving rise to a bilateral P300 response. Later work observed a parietally distributed positive response around 345 ms (P345) during ambiguity resolution at subcategorizing verbs (Friederici, Steinhauer, Mecklinger, & Meyer, 1998; Mecklinger, Schriefers, Steinhauer, & Friederici, 1995). Crucially, this response was larger in amplitude when the status of an ambiguous argument had to be revised from subject to object (Mecklinger et al., 1995). Also, its occurrence was tied to participants' reading span (Friederici et al., 1998). Hence, it is possible that the P345 indexes argument retrieval from verbal working memory for later modification, which is in line with Phillips et al.'s (2005) report of a positivity occurring as early as 300 ms during the resolution of an argument–verb dependency at a main verb. The positivity in the present findings has an even shorter latency. Congruent with this, previous results suggest that argument–verb-dependency resolution in verb-final languages may be initiated already prior to the main verb and continue throughout the verb (Aoshima et al., 2004; Friederici & Mecklinger, 1996; Phillips et al., 2005). This is also compatible with Fiebach et al.'s (2001) findings of a pre-verbal positivity during the resolution of argument–verb dependencies in German sentences, and may explain why the TP-region dipole time course effect occurred earlier than predicted.

An alternative explanation of the early topographical correlation effect is that it does rather not reflect a P300, but a negative ERP component peaking around 400 ms (N400), classically obtained for increased semantic-integration demands during sentence processing (Van Petten, 1993). A reduced N400 amplitude for the long as compared to the short argument–verb dependencies (Van Petten & Luka, 2012) is predicted under an anticipation-based parsing account (Konieczny & Döring, 2003; Levy, 2008): Here, an increased argument–verb distance should decrease processing load at the subcategorizing verb due to cumulative lexical pre-activation and subsequently-facilitated lexical access (Hagoort, Hald, Bastiaansen, & Petersson, 2004; Van Petten, 1993). This is compatible with both the ERP and the source time course in the TP region. For three reasons, however, we consider this interpretation less likely: First, the cortical generators of the N400 are rarely found in the left TP region, but rather involve middle temporal cortices (Johnson & Hamm, 2000; Maess, Herrmann, Hahne, Nakamura, & Friederici, 2006; Silva-Pereyra et al., 2003; Simos, Basile, & Papanicolaou, 1997) or a left-lateralized network of middle and inferior temporal cortices (Halgren et al., 2002; for review, see Lau, Phillips, & Poeppel, 2008). Second, the classical scalp distribution of the N400 during sentence processing involves bilateral parieto-occipital sensors, with a slight tilt towards the right hemisphere (Kutas & Van Petten, 1994; Lau et al., 2008). The ERP component at which we observed a stronger fMRI–EEG correlation for the long as compared to the short argument–verb distances had, however, a clearly left-lateralized posterior distribution. Third, the differential fMRI–EEG correlation for long as compared to short argument–verb dependencies occurred too early to index a lexical-semantic response.

In sum, it is most plausible that the short latency of the observed response is related to the pre-verbal initiation of argument retrieval (Fiebach et al., 2001; Phillips et al., 2005), triggered by a pre-head-attachment mechanism as described in the active-filler hypothesis (Clifton & Frazier, 1988). It is, however, impossible that a semantic N400 response to the subcategorizing verb occurs prior to the verb itself. Nevertheless, a partial overlap between a working-memory-retrieval-related P300 and an increased lexical-activation-related N400 for the short as compared to the long argument–verb dependencies is possible for a later time window—in line with an antagonism of lexically induced processing facilitation and working-memory-induced processing difficulty.

This leads us to the later brain activity in the left IFG that was sensitive to reordering demands. Considering that the topographical correlations showed a late-left-frontal-positivity correlate of IFG activity, we suggest that our combined fMRI–EEG analysis provides evidence for a close relationship between reordering-related IFG activity and reordering-related late positive ERP components occurring around 600 ms (P600). While the late effect in the dipole time course of the IFG is in line with this proposal, it is very unlikely that the IFG is the single generator of the P600: Service, Helenius, Maury, and Salmelin (2007) have shown that P600 generators may span from bilateral middle temporal to left inferior frontal generators across participants.

Inferior-frontal-gyrus activity can nevertheless account at least partly for the sensor-level time courses observed in the present data, and its involvement is directly implied by the source-level time courses. While responses in the P600 range were first observed in response to syntactic violations (Friederici, Pfeifer, & Hahne, 1993; Hagoort et al., 1993; Osterhout & Holcomb, 1992; Osterhout & Swinney, 1993), later work found that a P600 response at subcategorizing verbs does also occur in ambiguous sentences. These do not contain violations, but instead require the revision of an initial interpretation (Friederici et al., 1998). More recently, Kaan, Harris, Gibson, and Holcomb (2000) proposed to interpret the P600 as a general index of syntactic-processing difficulty, with sentential complexity giving rise to an anterior scalp distribution and revision processes giving rise to a posterior scalp distribution (Kaan & Swaab, 2003).

While we suggested above that early posterior positivities rather reflect retrieval from working memory, our proposal that late anterior P600 effects may more specifically index argument reordering is compatible with Kaan and Swaab's (2003) suggestion. Furthermore, the reordering proposal is in line with previous German data by Rösler et al. (1998), who report a P600 response for object-first as compared to subject-first argument orders, starting before and continuing during the occurrence of the verb. Converging on these data, Friederici et al. (2002) report a fronto-centrally distributed P600 for object-first as compared to subject-first sentences at subcategorizing verbs.

The interpretation of the current results in terms of a dissociation of late reordering-related fronto-central P600 components and the early retrieval-related posterior positive ERP responses is in line with the results of Vos, Gunther, Schriefers, and Friederici (2001). In their ERP study, they compared object-first and subject-first argument orders at the subcategorizing verb. The researchers find an increased late frontal positivity for object-first as compared to subject-first argument orders only for low-span participants; for high-span participants, the authors find an early posterior positivity instead. This dissociation fits our results in that it may reflect low-span participants' relative reliance on reordering processes (as indexed by the P600), whereas high-span participants may rely relatively stronger on their working-memory capacity (as indexed by the early positivity).

7.5 Conclusion

Based on combined fMRI–EEG results as well as evidence from the fMRI and EEG literature, we propose that working-memory retrieval of arguments and argument reordering are core neurocognitive functions of argument–verb-dependency resolution in sentence processing. During argument retrieval at the subcategorizing verb, the left TP region supports initial argument retrieval, while later argument reordering is subserved by left IFG. The data and preliminary framework presented here generate testable hypotheses for both behavioral and neuroimaging studies; they demonstrate that joint fMRI–EEG analyses provide the explanatory power to reconcile models from cognitive neuropsychology and psycholinguistics with our increasing knowledge on human functional neuroanatomy.

8

General Discussion

This thesis was concerned with the spatiotemporal brain dynamics of the following conceptualization: The working memory of argument–verb-dependency processing involves argument storage across the argument–verb distance; at their subcategorizing verb, arguments are retrieved, and in case of a relative argument order that deviates from the idiosyncratic order, argument reordering takes place. To address the according research questions, the 2 × 2 factorial design crossed the factors argument reordering (subject-first versus object-first argument order) and argument storage and retrieval (short versus long argument–verb distance). Across results, three *leitmotifs* were identified, which will be discussed after summarizing the experimental findings in Section 8.1. Section 8.2 will discuss whether the IFG is involved in reordering, rehearsal, or both; Section 8.3 will investigate the question whether the TP region is involved in storage, retrieval, or both. Section 8.4 will focus on the role of the AF/SLF across healthy and clinical populations.

8.1 Summary of Experimental Findings

Chapter 3 asked about the behavioral relationship between argument storage and reordering. Contrary to our hypotheses, the results show an interaction of the two factors, both using an on-line SPR and an off-line rating methodology: Increasing argument–verb distance exacerbates processing only for subject-first argument orders; for object-first argument orders, long argument–verb distance facilitates processing. Two possible interpretations were discussed. First, argument reordering and storage may interact behaviorally, but operate independently on a neural level: If distinct brain regions were responsible for each argument reordering and argument storage, a link between these regions could selectively facilitate the processing of sentences that necessitate both argument reordering and argument storage. Second, the two processes may also interact on the neural level, driven by a common underlying mechanism: Anticipation of a verb based on argument information might be easier in object-first sentences, since virtually any verb subcategorizes a subject, but not necessarily an object. The two competing interpretations necessitated a combined fMRI–dMRI study.

Chapter 4 asked about the functional neuroanatomy of argument storage and reordering, testing the current paradigm in a combined fMRI–dMRI study. The fMRI results show an activation for argument reordering in the left IFG, an activation for argument storage in the left TP region, and no interaction. Activation of the TP region, but not of the IFG, correlated with working-memory span measures. The dMRI results found the AF/SLF to connect the IFG and TP region, and correlation analyses stressed the functional significance of the AF/SLF. The additional VBM analysis found that the functional asymmetry of the reordering-related IFG activation across the left and right hemispheres is correlated with the underlying structural asymmetry, which is predicted by participants' handedness. In sum, these findings suggest that argument storage and reordering are independent on the neural level, but that the involved regions are linked by long-range white-matter bundles—giving rise to the behavioral pattern observed in Chapter 3. The absence of a functional interaction stresses that storage occurs independently of argument order, and that reordering occurs independently of argument–verb distance. The correlation between span measures and TP-region activation suggests that an isomorphism between the reordering–storage and rehearsal–storage dichotomies is restricted to storage, entailing a dissociation between reordering and rehearsal in the left inferior prefrontal cortex. The functional–structural–behavioral connection in the VBM results points to a general leftward structural asymmetry of the IFG and its functional leftward asymmetry during sentence processing; it also implies that left-handers may involve the right IFG in this process.

Chapter 5 asked whether selective damage to the AF/SLF results in a selective processing deficit in sentences that demand both argument reordering and argument storage. A patient for whom DTI revealed a disconnected AF/SLF was tested on our paradigm and a working-memory test battery. The patient showed reduced performance across working-memory tests and a selective deficit on sentences that jointly tax argument reordering and storage. The results reconcile the behavioral interaction in Chapter 3 with the functional main effects and their structural connection in Chapter 4: Argument reordering (IFG) and storage (TP region) operate independently on the neural level, but their anatomical connection facilitates the processing of object-first argument orders at long argument–verb distances only. The combination of a general working-memory deficit and a selective sentence-processing deficit implies the AF/SLF in a dual reordering–rehearsal role, entailing the functional segregation of the two.

Chapter 6 investigated the neuroelectric substrate of argument storage, regardless of argument order, since previous EEG research on working memory during argument–verb-dependency processing does not speak to the reordering–storage dichotomy. Short and long argument–verb conditions were contrasted in a TFR analysis. Long distances elicited stronger sustained alpha oscillations during the storage phase as well as a beta-band effect immediately at the main verb. The alpha-power increase was localized to bilateral occipital and left parietal cortices, whereby the latter source activity correlated with reading span. Reading span was also predictive of participants' behavioral performance. The results suggest that left parietal alpha oscillations be an important neural substrate of argument storage in working memory during argument–verb-dependency processing, potentially relating to the TP-region BOLD effect from Chapter 4. The alpha oscillations may serve a functional-inhibition mechanism of a premature filler release prior to an appropriate gap position, while the beta effect at the main verb may index argument retrieval for argument–verb linking.

Chapter 7 asked about the spatiotemporal dynamics of argument retrieval and argument reordering at subcategorizing verbs inside the functional-neuroanatomical brain network established in Chapter 4 and Chapter 5—as opposed to argument storage as investigated in Chapter 6. These fMRI–EEG analyses combined a sub-sample of data from Chapter 4 and Chapter 6 into two methods of joint analysis, focusing on the sentence-final main verb. Dipole time courses for the IFG and the TP region projected from sensor-level ERP data show increased early TP-region activity for increased argument-retrieval demands, followed by later IFG activity for increased argument-reordering demands. Topographical correlation analyses substantiate these findings, showing an early left posterior positivity for increased argument-retrieval demands, followed by a late left frontal positivity for increased argument-reordering demands. The results suggest that the reconstructed source time courses and correlated ERP effects in response to the subcategorizing verb reflect the spatiotemporal dynamics of early argument retrieval—involving the TP region—and late argument reordering—involving the IFG.

8.2 The Inferior Frontal Gyrus: Reordering, Rehearsal, or Both?

The first *leitmotif* of this thesis' experimental results is the distinction between reordering and rehearsal: Reordering is an executive operation on working-memory content, whereas rehearsal denotes the refreshing of working-memory content to counteract degenerative factors such as decay and interference. While there is evidence for a role of the IFG in both reordering and rehearsal, a confrontation remains between authors who maintain the conceptual and neuroanatomical distinction between reordering and rehearsal and those who propose their identity: On the one side, cross-linguistic fMRI research has found brain activity in BA 44 to increase with argument-reordering demands (Ben-Shachar et al., 2003; Friederici, Fiebach, et al., 2006; Kim et al., 2009). On the other side, rehearsal of working-memory content was found to increase brain activity in BA 44 and supplementary motor regions superior and posterior to BA 44, such as BA 6 (Awh et al., 1996; Paulesu et al., 1993; Petrides et al., 1993).

These similarities led some authors to propose the identity of reordering and rehearsal. First, Just et al.'s (1996) contrasting of English subject- and object-relative clauses yielded BA-44 activity, which Rogalsky and Hickok (2010) reviewed as reflecting rehearsal, due to the fact that English object-first sentences increase the argument–verb distance over their subject-first counterparts. Second, Rogalsky et al. (2008) report a performance decline in argument-reordering-intensive sentence processing during concurrent rehearsal, with a partial activation overlap of reordering and rehearsal in BA 44. However, both lines of argument are ambiguous: First, Just et al.'s (1996) English object-first sentences confounded argument–verb distance with argument order. Second, Rogalsky et al. (2008) report interference between a finger-tapping control task and sentence-processing performance in addition to reordering–rehearsal interference; this suggests that a secondary task *per se* decreases performance. In addition, other studies have demonstrated that reordering can be impaired independently of rehearsal (Caplan & Waters, 1999), and that concurrent rehearsal does not further increase reordering-related BA-44 activation (Caplan et al., 2000). Finally, there is clear evidence for a role of BA 44 in reordering from outside the sentence-processing domain: Gerton et al.'s (2004) PET study investigated the functional neuroanatomy of the forward- and backward-digit-span sub-tests—both of which need rehearsal, but only backward digit span needs reordering. While brain activity in the inferior parietal lobule and the superior medial vicinity of Broca's area was common to forward and backward digit span and reminiscent of the storage–rehearsal network, reordering-intensive backward digit span additionally activated BA 44.

This thesis adds three arguments against the identity of reordering and rehearsal. First, the correlation analysis on the fMRI data (see Chapter 4) yielded a correlation between digit-span scores and argument–verb-distance-related TP-region activation, but no such correlation was found for the argument-reordering-related BA-44 activation. The latter would have been expected if reordering and rehearsal were identical. As a second argument, the patient with an AF/SLF disconnection (see Chapter 5) showed a general working-memory deficit, but a specific processing deficit only on sentences that jointly demand reordering and storage. These results suggest that both the reordering–storage and the rehearsal–storage dichotomy recur to the AF/SLF to enable connective processing by left inferior frontal and TP regions. Still, a general working-memory deficit in combination with a selective sentence-processing deficit is only predicted by a conceptual distinction between reordering and rehearsal, as well as their neuroanatomical separation in the IFG; on the contrary, Rogalsky and Hickok's (2010) proposal would predict decreased performance on any long-argument–verb-distance sentence, regardless of argument order. As a third piece of evidence, consider the EEG-source-localization and -source-space-correlation data (see Chapter 6): First, the sources of the argument–verb-distance-related alpha-power increase were localized to bilateral occipital and left parietal cortices, with no significant BA-44 involvement. Second, only left parietal sources were correlated with reading-span scores. Rogalsky and Hickok (2010) predict the opposite of both findings.

The results of the current thesis join the cross-linguistic sentence-processing studies, the rehearsal–reordering non-interference data as well as the digit-span imaging data in underlining the conceptual and neuroanatomical distinction between reordering and rehearsal. The scope of the reordering concept with respect to BA 44 is, however, unclear—but the available data allow for speculation: Since the reordering of arguments (Meyer, Obleser, Anwander, & Friederici, 2012) and the reordering of a series of arbitrary digits (Gerton et al., 2004) both activate the dorsal BA 44, this region may play a general role in the reordering of verbal-working-memory content. Behavioral pilot data in favor of this proposal are available. In an experiment crossing the two long conditions (subject-first and object-first) from the current paradigm with the forward- and backward-digit-span task, participants heard a series of digits that was either to be rehearsed or—additionally—reordered during the subsequent auditory presentation of a sentence. The concurrent processing of object-first sentences was expected to selectively influence backward digit span. Preliminary results are shown in Figure 8.1.

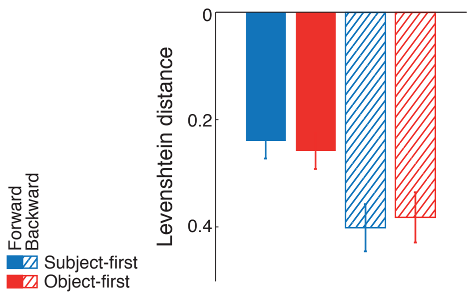

Figure 8.1: Results of the pilot study (n = 30); bars mark Levenshtein distance (smaller values indicate better performance, i.e., small difference between original and repeated digit series); error bars represent SEM; blue bars mark subject-first sentences, red bars mark object-first sentences; solid lines mark forward-digit-span (rehearsal-only) conditions, dashed lines mark backward-digit-span (rehearsal-plus-reordering) conditions; a significant interaction was obtained ($p < 0.05$).

As expected, performance was worse for backward digit span. Paradoxically, while rehearsal during forward digit span left the classical processing exacerbation of object-first argument orders untouched, digit reordering during backward digit span facilitated concurrent argument reordering. The facilitation may be captured by the general notions of task or structural priming (Scheepers et al., 2011; Waszak & Hommel, 2007) or the specific notion of syntactic priming[17] (for review, see Branigan, 2007; Pickering & Ferreira, 2008): In the sentence-processing domain, Bock (1986) reports that sentence structures from a prior comprehension task constrain subsequently-produced sentence structures. More recently, Scheepers et al. (2011) found across-domains structural priming, showing that mathematical formulae of adequate *gestalt* constrain participants' sentence continuations. Priming may have reduced BA-44 activity, causing the concurrent backward-digit-span task to facilitate the processing of object-first sentences: First, Makuuchi, Bahlmann, and Friederici (2012) show that structural processing in BA 44 may be common to language, working-memory, and mathematical processes; second, Wagner, Koutstaal, Maril, Schacter, and Buckner (2000) find across-tasks repetition priming to reduce BA-44 activity.

To finalize these speculations, the current VBM data (see Chapter 4) hint at an overarching role of Broca's area in reordering: The structural asymmetry of Broca's area predicts its functional asymmetry during argument reordering, with both functional and structural asymmetry predicted by handedness.

[17] Kaan, Wijnen, and Swaab (2004) use the related notion of syntactic recycling to denote the partial re-use of previously-processed phrases in ellipsis resolution.

This is suggestive considering reports in the great-apes literature that tie Broca's area's structural and functional asymmetry to handedness during communicative gesturing (Cantalupo & Hopkins, 2001; Hopkins et al., 2007; Schenker et al., 2010; Taglialatela et al., 2006). Imaging data in humans find Broca's area involved in deaf signers' gesture comprehension (MacSweeney, Brammer, Waters, & Goswami, 2009; Petitto et al., 2000), potentially reflecting internal reordering of gestural actions: In a recent study, Clerget, Badets, Duqué, and Olivier (2011) found that theta-burst transcranial magnetic stimulation (TMS) over BA 44 decreased performance during action sequencing. A conclusion would be premature, but it is possible that the dorsal BA 44 plays an overarching role in reordering during communication (cf. Kemmerer, 2012; Nishitani, Schurmann, Amunts, & Hari, 2005; Pastra & Aloimonos, 2012).

8.3 The Temporo-Parietal Region: Storage, Retrieval, or Both?

The TP region is the second *leitmotif* across the current experimental results. The fMRI (Chapter 4), EEG (Chapter 6), and combined analyses (Chapter 7) strongly suggest that the TP region is involved in working-memory storage and retrieval, both during sentence processing and outside the sentence-processing domain. While the fMRI and EEG alpha effects may reflect argument storage, the EEG beta effect, the early TP-region dipole activity as well as the related P300 in the combined fMRI–EEG analyses may index argument retrieval. These findings need clarification: First, the spatial commonalities between the BOLD and alpha effect might entail a positive BOLD–alpha relationship. Second, the BOLD and alpha effect suggest the TP region as a storage substrate, whereas the beta effect and the combined analyses suggest that TP-region activity reflects retrieval. Third, some previous findings suggest BA 45 rather than the TP region to subserve argument storage, which the current data argue against. Fourth, the imaging literature has implied the TP region in various cognitive functions other than working-memory storage and retrieval. These points will be addressed next.

One possibility for a joint interpretation of the BOLD and alpha effect is that both reflect TP-region activity in inhibiting a premature argument release. This relies on two assumptions: The BOLD and alpha sources must be at the same location, and their activity must be positively coupled. The first is possible given the method: Source localization is spatially less precise than fMRI, and reduced correspondence between the individual electrode positions and the canonical BEM may have further decreased its precision in our analyses. The second assumption of a positive BOLD–alpha coupling is less clear: During rest, Laufs et al. (2006) report negative coupling in both a parietal–occipital and parietal–frontal network, while Gonçalves et al. (2006) report that some participants show negative coupling across the brain, but some show positive coupling in frontal, left parietal and occipital regions. During verbal-working-memory tasks, the picture is unequivocal as well: Michels et al. (2010) report positive parietal coupling, Scheeringa et al. (2009) find no coupling in the working-memory network, and Meltzer et al. (2007) report negative bilateral parietal coupling.

According to a second interpretation, BOLD and alpha may reflect two distinct left parietal processes during working-memory storage. Such a dualism appeared in the respective discussions of the behavioral (see Chapter 3) and the combined-fMRI–EEG results (see Chapter 7): While long argument–verb dependencies expose the argument to increased storage and retrieval demands (cf. Gibson, 2000), they have also been argued to facilitate verb processing due to the cumulatively reduced number of possible sentence continuations (cf. Levy, 2008). For the storage phase, these approaches cannot be disentangled, since BOLD and alpha both occurred during this interval. But for retrieval, the two approaches may be captured by the combined analyses: While the sensor-space counterpart of the TP-region dipole effect was interpreted as an argument-retrieval-related P300, a partial overlap with a lexical-activation-related N400 was considered. Argument retrieval at the sentence-final main verb may trigger a P300 (Ergen et al., 2012; Friedman et al., 1975), but stronger expectations for the main verb towards sentence ending may trigger an N400 reduction (Van Petten, 1993; Van Petten & Luka, 2012); the two may be closely related, yet neuroanatomically different.

Of these two interpretations, it is more plausible that BOLD and alpha reflect the same mechanism: First, both BOLD and alpha were negatively correlated with working-memory span, stressing that both are related to working memory proper rather than lexical facilitation. Second, both the BOLD and alpha effect were sustained, making it illogical to link either to the transient effects in the combined analyses. Lexical facilitation can be further ruled out by the design of the experimental stimuli used across the current thesis: All four-sentence sets were balanced for aspects of lexical facilitation by keeping the main-verb position constant across conditions, precisely to achieve identical lexical facilitation and identical N400 reduction across conditions; for the same reason, the argument–verb sets of all stimulus items were controlled for argument–verb co-occurrence (see Chapter 2). In sum, BOLD and alpha may both reflect verbal-working-memory storage through a cortical-inhibition mechanism that enables a pinpoint argument release, the spatial differences being due to methodological factors.

Does the TP region, in addition to argument storage, also serve argument retrieval? While both BOLD (Chapter 4) and alpha (Chapter 6) may index storage, both beta (Chapter 6) and P300 (Chapter 7) may index retrieval—in spite of all relying on the TP region. Four arguments support this. First, the ambiguity of storage and retrieval is built into the current paradigm: If decay is the underlying reason for the processing exacerbation induced by long as compared to short argument–verb distances (cf. Gibson, 2000; Yngwe, 1960), distance increases both storage and retrieval demands. Second, the sluggish BOLD response and the temporal precision of the TFR analyses (see Chapter 2) imply that neither BOLD nor sustained alpha can reflect transient retrieval effects; hence, distinct neural substrates must be assumed. Third, the link between P300, TP region and verbal-working-memory retrieval is in line with previous findings (Ergen et al., 2012; Phillips et al., 2005), and may carry over to the beta burst: Given their synchronicity at the main verb, the fifty-milliseconds beta burst can simply be the P300's mirror image in the TFR domain. While the beta burst was not source-localized, the beta band has been implied in argument–verb linking, which presupposes retrieval (Bastiaansen et al., 2010; Wang et al., 2012). Fourth and last, reconsider the fMRI result: TP-region BOLD exhibited both peak-location and magnitude variance. Since the fMRI data were averaged across whole sentences, the differential SNR may have resulted in a strong—sustained—storage effect and a weak—transient—retrieval effect, each at distinct coordinates. In line with this, within-experiment distinct storage and rehearsal peaks in the TP region have been reported previously (Henson et al., 1999; Ravizza et al., 2011).

Next, I need to clarify the contrast between the current findings and previous work that suggests BA 45 in the IFG, sometimes extending into the inferior frontal sulcus, to subserve working memory during sentence processing, rather than the TP region. These reports must be taken with caution, since they compared different syntactic dependencies across conditions: Fiebach et al. (2005) contrasted pronoun–verb and noun–verb dependencies, while Santi and Grodzinsky (2007) contrasted pronoun–noun and noun–verb dependencies. Makuuchi et al. (2009) confounded argument–verb distance with the number of argument–verb dependencies, and did not control for additional pronoun–noun dependencies across conditions. Santi and Grodzinsky (2010) contrasted embedded sentences to sentences containing a single argument–verb dependency. Potential reconciliation is offered by Makuuchi, Grodzinsky, Amunts, Santi, and Friederici's (2012) recent study: Across dependencies, increased argument–verb distance activated the inferior frontal sulcus, the pars opercularis of BA 44, and the intraparietal sulcus. While the paradigm was well-designed in using noun–verb dependencies only, it did confound argument–verb distance with argument order. Hence, it is possible that the BA-44 and the inferior-frontal-sulcus activations in Makuuchi, Grodzinsky, et al.'s (2012) study do not stem from argument–verb distance *per se*. This may instead be true of their intraparietal-sulcus activation, which is close to the current TP-region peak. Given this interpretation as well as the current results, it seems plausible that argument storage relies more strongly on TP rather than inferior-frontal regions—in line with a vast body of research from outside the sentence-processing domain (see Chapter 4; for review, see Buchsbaum & D'Esposito, 2008; Jacquemot & Scott, 2006; Müller & Knight, 2006; Owen et al., 2005; Smith & Jonides, 1998; Wager et al., 2005).

The final issue to speculate on is how the working-memory role of the TP region relates to other cognitive processes. Based, for instance, on findings that the processing of items that are similar to items already stored in working memory is facilitated (for review, see Cabeza et al., 2012a; Gazzaley & Nobre, 2011), the diverse cognitive functions of the ventral parietal cortex—such as memory retrieval, personal-memory, and language processing—have been proposed to share a process of selective attention (for discussion, see Cabeza, Ciaramelli, & Moscovitch, 2012b; Nelson, McDermott, & Petersen, 2012). How would such a general process relate to the specific notion of verbal-working-memory storage and retrieval of arguments during sentence processing? A conceivable relationship recurs to Anders Ericsson and Kintsch's (1995) conceptualization of long-term working memory, according to which working memory is an attentional mechanism that selectively activates long-term memory content (see Chapter 1; for discussion, see Cowan, 2008). Since nouns—such as the arguments in the current experiments—are stored in the mental lexicon, they are represented in long-term memory. If working memory involves the selective-attentional activation of long-term-memory content, and the ventral parietal cortex is involved in selective attention across cognitive domains, the TP-region activation in our study may ultimately result from selective-attentional activation of arguments' long-term-memory representations. Imaging work indeed implies the SMG in the information-structural attentional focusing of arguments during sentence processing (Lœvenbruck, Baciu, Segebarth, & Abry, 2005) as well as the TP-region in the mental lexicon (for review, see Binder, Desai, Graves, & Conant, 2009).

8.4 The Dorsal Tract: Syntax, Working Memory, or Both?

As its third *leitmotif*, this thesis shelled out the role of the AF/SLF in working memory in- and outside of sentence processing. While the neural independence of argument reordering and storage (Chapter 4) contradicted their behavioral interaction (Chapter 3), the DTI analyses on a healthy sample (Chapter 4) and a patient (Chapter 5) reconciled the results: As structural link between BA 44 and the TP region, the AF/SLF is the functional mediator of reordering and storage, driving their behavioral interaction in spite of functional-neuroanatomical independence. Furthermore, the DTI (Chapter 4) and patient data (Chapter 5) suggest that the AF/SLF plays a dual role of linking storage in the TP region to reordering in BA 44 for sentence processing and to rehearsal in the dorsal IFG for tasks outside of sentence processing. This section will discuss three related questions: First, how can damage to the AF/SLF cause a selective sentence-processing deficit? Second, how can the AF/SLF selectively subserve sentence processing, but generally subserve working-memory? Third, is there an alternative to the dual-role hypothesis on the role of the AF/SLF in the brain circuitry of both sentence processing and working memory?

First, disruption of the AF/SLF caused the patient's selective sentence-processing deficit, which may result from the AF/SLF being the functional mediator between reordering and storage by linking BA 44 and the TP region (Chapter 5). If the tract played a reordering-only or storage-only role, the patient would be impaired on either all object-first or all long-distance sentences, respectively. This is corroborated by a comparison of the results of the patient study and the behavioral study (see Figure 8.2): Contrary to the patient, long-distance object-first sentences benefit over their short-distance counterparts in participants with an intact AF/SLF[18]. While the control-group pattern on object-first sentences in the patient study resembled the pattern in the behavioral study, the patient's performance on the long object-first sentences dropped below her own and the control group's performance on the short object-first sentences. In the patient study, the reduced difference between the short- and long-distance subject-first sentences both in the control group and the patient can be explained by the overall reduced working-memory load: The conjunct clause used in all current studies had been removed from the sentences to decrease processing difficulty for the elderly participants.

[18] Albeit not significant and constrained by the limited time window, the same pattern of results was obtained for the behavioral results in the fMRI study (see Chapter 4).

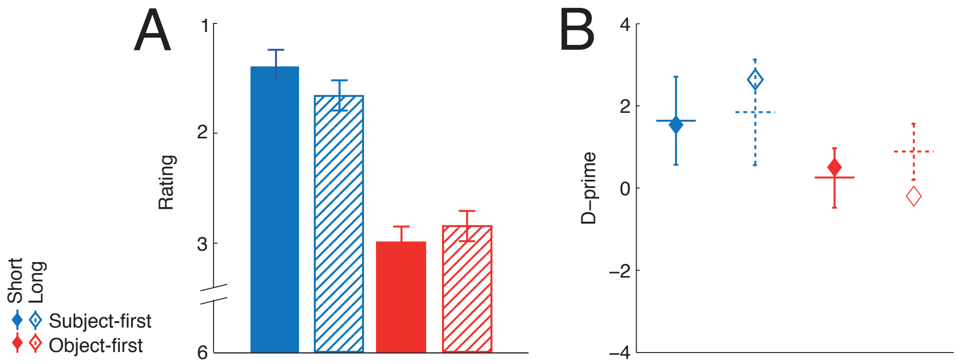

Figure 8.2: Contrast between behavioral results; (A) results of the behavioral rating study; an interaction between reordering and storage is present: Long-distance subject-first sentences exacerbate processing over their short-distance counterparts, object-first sentences generally exacerbate processing over subject-first sentences, and long-distance object-first sentences facilitate processing over their short-distance counterparts; (B) results from the patient yes–no comprehension study; the patient was selectively impaired in processing long-distance object-first sentences.

This leads to the second variation on the AF/SLF theme, the proposal that the tract subserves both the storage–reordering and the storage–rehearsal circuitry. While some authors stress the former (Caramazza et al., 1981; Friederici, 2011) and others the latter (Baldo et al., 2008; Yamada et al., 2007), the current patient data (Chapter 5) have reconciling implications. The patient was impaired across working-memory-span measures, but not across working-memory-intensive long argument–verb dependencies. Friedmann and Gvion's (2003) conduction-aphasia study and Wilson et al.'s (2011) primary-progressive-aphasia study find damage to the AF/SLF to impair sentence processing. Both studies used English subject- and object-relative sentences—which jointly tax reordering and storage, resembling the current findings. Friedmann and Gvion (2003) also report their subjects to exhibit general working-memory deficits—in line with classical findings of an impaired storage–rehearsal circuitry (for review, see Bernal & Ardila, 2009; Buchsbaum et al., 2011), which can result from AF/SLF-only damage (Yamada et al., 2007; but see Geldmacher, Quigg, & Elias, 2007). While Wilson et al. (2011) do not report working-memory deficits in primary progressive aphasics with AF/SLF damage, their sample overrepresented non-fluent- and underrepresented logopenic-variant patients, exaggerating sentence-processing deficits and understating working-memory deficits: As opposed to non-fluent patients, logopenic patients suffer from TP-regional degeneration and according working-memory deficits (Galantucci et al., 2011; Leyton et al., 2011; but see Rogalski et al., 2011).

In addition to the clinical data, the FA correlation analyses on the AF/SLF in healthy participants (Chapter 4) lend plausibility to the dual-role hypothesis: While both reordering and storage were found to correlate with the FA at differential sites along the tract, storage correlations were stronger and more extensive. Since the BOLD effect of storage in the TP region was found to correlate with digit span, the BOLD–FA correlations may reflect storage common to working memory in- and outside of the sentence-processing domain. Critically, the current findings from a healthy sample transcend the structure-to-behavior mapping of previous studies and suggest a direct structure-to-function-to-behavior mapping in healthy participants: While there is a body of fiber-tracking evidence on the presence of the AF/SLF in humans, these studies infer the tract's sentence-processing role from the functional involvement of its termination points in BA 44 and/or the TP region (Catani et al., 2005; Friederici, Bahlmann, et al., 2006; Glasser & Rilling, 2008; Parker et al., 2005; Saur et al., 2010; Weiller et al., 2009). Without assessment of the underlying diffusion characteristics, this does only allow for an indirect conclusion (cf. Friederici, 2009a; Heiervang et al., 2006; Wakana et al., 2007). To my knowledge, there are few exceptions that used an FA regression method to assign functional roles in sentence processing and working memory to the AF/SLF in healthy adults: While not easily mapped onto the reordering–storage dichotomy, the relevance of the AF/SLF in sentence processing is in line with Flöel, De Vries, Scholz, Breitenstein, and Johansen-Berg (2009) and Antonenko, Meinzer, Lindenberg, Witte, and Flöel (2012), who find the FA of dorsal fiber tracts starting in the IFG to predict artificial-grammar-learning success. A second role of the AF/SLF in mediating rehearsal and storage is suggested by Charlton et al. (2010), who find mean diffusivity and FA of a tract that connects BA 40 to inferior frontal areas to correlate with working-memory-span measures.

Still, this section's final paragraph provides an alternative to the proposed dual-role hypothesis of the AF/SLF: Sub-divisions may distinctly subserve sentence processing and working memory (for review, see Gierhan, in revision). In the current DTI study (Chapter 4), fiber tracking from the extensive IFG and TP-region seeding points may have erroneously lumped together AF and SLF, and the patient's extensive lesion (Chapter 5) may have affected both AF and SLF. Dorsal and ventral sub-divisions of the dorsal tract were first described in the rhesus monkey, where projections from superior and medial parietal cortex to the dorsal area 6 were separated from projections from inferior parietal cortex to the ventral areas 6 and 46[19] (Petrides & Pandya, 1984). More recent work separated AF and SLF in humans too, but their respective frontal and posterior termination points are still unclear: On the one hand, Frey et al. (2008) interpret their human DTI results from the monkey perspective, proposing that BA 6 and BA 44's pars opercularis are the AF's and SLF's respective frontal termination points, connecting to the inferior parietal lobe and the posterior STG, respectively. While less precise on the frontal termination points, Catani et al. (2005) suggest that the AF connects inferior frontal regions directly to the posterior STG and SMG, while the SLF runs from the inferior frontal lobe indirectly through the inferior frontal lobe into posterior STG and SMG.

As discussed by Catani et al. (2005), the distinction of AF and SLF may explain the distinction of conduction aphasia and transcortical motor aphasia: Deep TP-region lesions may result in AF damage, conduction aphasia and predominant working-memory deficits; but superficial TP-region lesions may instead result in SLF damage, transcortical motor aphasia and predominant higher-level language deficits (McCarthy & Warrington, 1984). While the former is in line with the classical view of conduction aphasia (Wernicke, 1874; for discussion, see Buchsbaum et al., 2011), the latter is in line with Dogil, Haider, Schaner-Wolles, and Husmann's (1995) report on a case of transcortical sensory aphasia who showed impaired repetition, but spared syntactic comprehension. Furthermore, Galantucci et al.'s (2011) study found non-fluent (i.e., sentence-processing impaired) primary progressive aphasics to suffer from SLF degeneration, but logopenic (i.e., working-memory impaired) primary progressive aphasics to show degeneration of the posterior segment of the indirect AF.

Given the proposal that rehearsal activates the dorsal IFG (Awh et al., 1996; Paulesu et al., 1993; Petrides et al., 1993) and reordering activates the ventral IFG (Ben-Shachar et al., 2003; Friederici, Fiebach, et al., 2006; Kim et al., 2009; Meyer, Obleser, Anwander, & Friederici, 2012), the data allow for the following speculation: The AF underlies verbal working memory, and the SLF underlies sentence processing proper. Due to methodological limitations, the current data cannot definitely decide in favor of this proposal[20].

[19] Rhesus-monkey area 46 lies anterior to and below area 6; recent cytoarchitectonic analyses suggest area 46 as a potential homologue of the human BA 44 (cf. Frey, Campbell, Pike, & Petrides, 2008; for review, see Petrides et al., 2012; Thiebaut de Schotten, Dell'Acqua, Valabregue, & Catani, 2012).

[20] The interested reader is referred to the related proposal that the white matter of the language network emerged from a memory connectome during evolution (Aboitiz, Aboitiz, & García, 2010; Aboitiz & García, 2009; Aboitiz et al., 2006).

9

Towards a Testable Framework

Before proposing a testable neurocognitive framework of argument–verb-dependency processing, I will recapitulate its underlying psycholinguistic and cognitive conceptualizations. In a sentence, arguments symbolize the who and whom, while a verb symbolizes an action jointly involving the two. To infer sentence meaning, arguments and their verb must be linked. Argument–verb linking takes place in the vicinity of subcategorizing verbs, in an order idiosyncratic to any particular language. The number and type of required arguments become known with the verb, and speaker's linguistic knowledge determines their desired idiosyncratic order. Thus, argument-order deviance and argument–verb non-adjacency each increase cognitive efforts: Due to increasing working-memory decay, non-adjacency of arguments and their subcategorizer increases argument-storage demands across the argument–verb distance; likewise, retrieval demands increase. Second, the deviance between the encountered argument order and the language-specific idiosyncratic order requires an executive mechanism of argument reordering to match the stored and desired argument orders.

To inform the framework, the following conclusions were drawn from this thesis' three *leitmotifs*: The TP region is a core functional-neuroanatomical substrate of working-memory storage of arguments: Increased BOLD responses to sentences that tax storage established the TP region's role, and EEG source localization showed this region to increase alpha oscillations during storage in response to the same sentences, clarifying its spatiotemporal dynamics. Since both BOLD and alpha effect were correlated with working-memory span measures, both appear to be genuine working-memory effects, potentially reflecting storage common to sentence processing and the verbal domain outside of sentence processing. On encounter of the stored argument's subcategorizing verb, combined fMRI–EEG analyses suggest that the TP region underlies argument retrieval, visible both in a scalp-level P300 and early positive TP-region dipole activity, potentially echoed in a beta burst in the EEG-TFR analyses. Following retrieval, IFG-dipole activity and a scalp-level P600 were linked to argument reordering. Because an IFG BOLD response had been observed previously, this clarified the spatiotemporal dynamics of the IFG's crucial role in argument reordering. The AF/SLF mediates the functional-neuroanatomical task-share between the independently-operating IFG and the TP region. More generally speaking, the IFG's reordering process exhibits top-down executive control, dynamically querying argument representations stored and retrieved by the TP region. Figure 9.1 links the linguistic description, cognitive processes, and functional neuroanatomy of argument–verb dependencies.

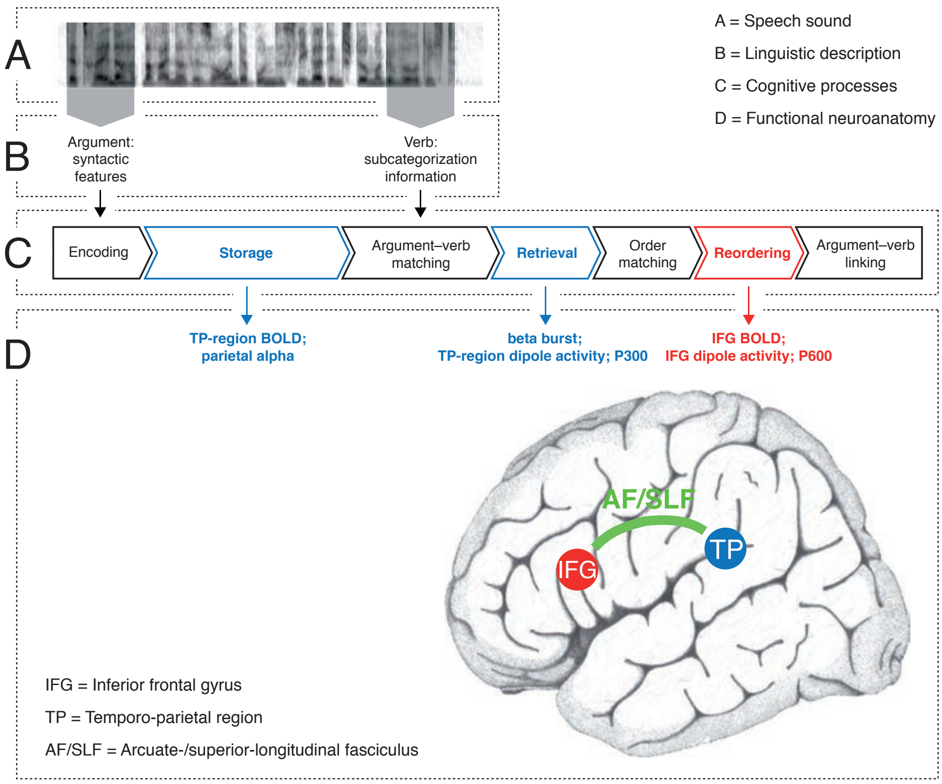

Figure 9.1: Functional neuroanatomy of storage, retrieval, and reordering; (A) spectrogram of an example long-distance object-first sentence; (B) linguistic description of the relevant information; (C) serial representation of cognitive processes involved in storage, retrieval, and reordering; (D) relation of these cognitive processes to the subserving spatiotemporal brain dynamics.

From a cognitive-neuropsychologist point of view, this framework has four critical advantages: First, the framework closely relates the linguistic, cognitive, and functional-neuroanatomical levels, relating concrete aspects of the linguistic description of speech to concrete aspects of brain structure. Second, the framework matches conceptual and empirical granularity: While state-of-the-art neuroscientific analysis methods exhibit increasing temporal and spatial resolution, the granularity of most psycholinguistic sentence-processing theories is beyond this resolution. Third, the framework is terminologically open: The current results suggest that some of the atomic cognitive processes involved in sentence processing share characteristics of working-memory processes; thus, neuroscientists from outside the sentence-processing domain can directly relate to the framework. Fourth, the fact that some of the brain phenomena measured in the current thesis appear across a multitude of cognitive processes suggests that it is possible to re-inform the psycholinguist's conceptual inventory: If a brain region or function is involved in a variety of tasks from various domains, these tasks may share an atomic cognitive process. Eventually, this approach may help in replacing abstract, descriptive linguistic notions with concrete, empirically sound cognitive concepts. The proposed framework generates hypotheses for future research, which I will address next.

9.1 Reordering: Beyond Sentence Processing

While it has independently been suggested that BA 44 be involved in argument reordering, action sequencing, and gesture comprehension in the deaf, none of the possible pairings have been systematically compared within participants. Hence, there is no positive evidence that BA 44 plays an overarching reordering role. Inspired by Gerton et al.'s (2004) and Makuuchi, Bahlmann, and Friederici's (2012) results, initial behavioral evidence was presented for structural priming from the processing of object-first argument orders to the processing of the backward-digit-span task (see Section 8.2). The experimental paradigm used may be suitable for an fMRI study: Judging from the behavioral results as well as the imaging literature that found across-tasks repetition priming to reduce BA-44 activity (Wagner et al., 2000), structural priming should yield decreasing BA-44 activation for the interaction contrast between argument and digit reordering. Such an effect would speak in favor of a general role in reordering across verbal-working-memory tasks and would form the basis for within-participants studies crossing gesture and action reordering with argument reordering.

9.2 The Inferior Parietal Cortex: Beyond Working Memory

Second, it was speculated that the working-memory role of the TP region may mirror an attention-related mechanism (Section 8.3): Argument storage, information-structural argument focusing, and the attentional activation of arguments' long-term-memory representations may open a window into how general attentional mechanisms underlie specific sentence-processing mechanisms. From a linguist's viewpoint, this falls into the realm of information structure (for an overview, see Krifka, 2008). From a cognitive neuropsychologist's viewpoint, it could link the sentence-processing, working-memory, and attention domains. A suitable fMRI paradigm would manipulate argument–verb distance as working-memory factor, while an attention factor would aim at directing attention towards a stored argument. To this end, previous studies have selectively cued stored items for later reuse in a delayed-response task (e.g., Lepsien, Thornton, & Nobre, 2011). For the spatial and object domains, fMRI studies have found shifts of selective attention amongst stored items to modulate parietal brain activation during working-memory storage (for review, see Gazzaley & Nobre, 2011). A possibly abridging to the sentence-processing domain is sketched in Figure 9.2.

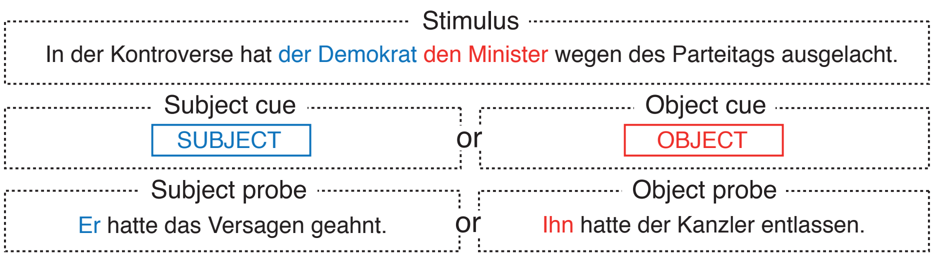

Figure 9.2: Paradigm proposal for modulating working-memory-related TP-region activation by attention; upper panel shows a stimulus sentence with the subject in blue and the object in red; middle panel shows subject and object cues to selectively direct attention amongst the two stored arguments; lower panel shows probe sentence, on which a delayed-response task is to be carried out.

In the proposed paradigm, both subject and object of a transitive verb must be stored in working memory, but only either subject or object is cued for the processing of the delayed-response task. The hypothesis for such an experiment would thus be that participants respond faster when the cue and the sentence-initial pronoun in the probe sentence match. The match is expected to modulate argument-storage-related TP-region BOLD during the delay interval.

9.3 Disentangling Reordering and Rehearsal

The dissociation of the reordering–storage and rehearsal–storage dichotomies (see Section 8.2) footed on the previous imaging literature, as well as negative experimental evidence: reordering-related BA-44 activation was not correlated with working-memory span, working-memory-related alpha generators did not include prefrontal sources, and the patient did not show a generalized deficit across long argument–verb dependencies. To provide positive evidence on a left-lateral-prefrontal dissociation into BA 44 subserving reordering and BA 6 subserving rehearsal, an experimental paradigm would have to fully cross the two. Storage-only, rehearsal-only, and rehearsal-plus-reordering conditions would be included, adapting a classical paradigm for the sentence-processing domain: Paulesu et al. (1993) disentangled storage and rehearsal by having on-screen letters being followed by a probe letter that either occurred amongst (storage condition) or rhymed with one of (rehearsal condition) the previously-presented digits. An orthogonal reordering dimension would be introduced by using short-distance subject- and object-first sentences (see Figure 9.3).

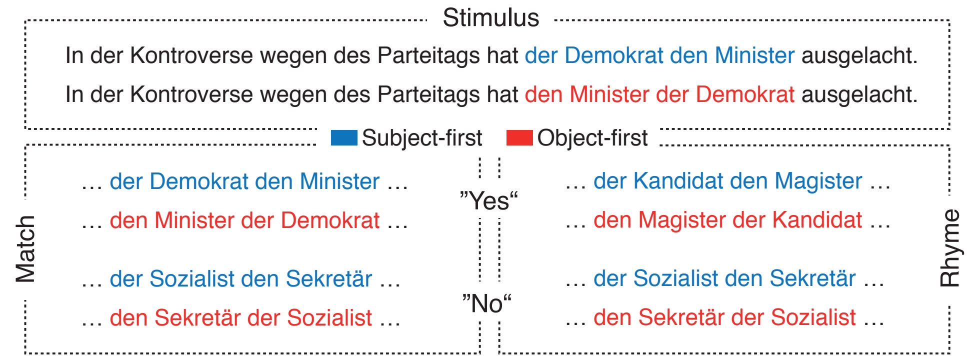

Figure 9.3: Paradigm proposal for dissociating reordering and rehearsal; upper panel shows subject-first (in blue) and object-first (in red) stimulus sentences; bottom left panel shows probe items for the match condition, bottom right panel shows probe items for the rhyme condition.

During the task interval, object-first sentences would conjointly tax reordering and activate BA 44, but rhyming tasks would conjointly tax rehearsal and activate BA 6; the matching task serves as a high-level baseline. The hypothesized prefrontal dissociation would be an excellent basis for disentangling the functional roles of the proposed sub-components of the dorsal fiber tract, with reordering relying on the SLF, but rehearsal relying on the AF.

9.4 Brain Oscillations and Fronto-Temporal Connectivity

One result of the current thesis is that the working memory of argument–verb dependencies involves gray-matter structures in the IFG and TP region, their white-matter connection through the AF/SLF, as well as alpha oscillations. Sarnthein et al. (1998; cf. Buzsáki, 2006) have underlined that remote brain regions' joint processing necessitates the oscillatory coupling of either their phases or amplitudes, either within or across frequency bands (cf. de Lange, Jensen, Bauer, & Toni, 2008). Thus, one must hypothesize that argument–verb-dependency processing involves oscillatory coupling of the IFG and TP region, and that the AF/SLF white matter is functionally determined to mediate coupling.

The underlying rationale of the current paradigm shows that argument reordering and storage are an excellent test for such hypotheses; a similar setup may suffice to show that executive processes (reordering) and representational processes (storage) of sentence processing interact by coupling their fronto-parietal network. Source-space analyses of MEG data from the IFG and TP region, combined with high-resolution fiber tracking, may be suited to tackle such an experiment: The accurate estimation of oscillatory coupling in source space (for recent demonstrations, see de Lange et al., 2008; Keil, Müller, Ihssen, & Weisz, 2012) and the advanced fiber-tracking methods now becoming available (Descoteaux et al., 2009) may be able to link the IFG–TP-region-coupling parameters to white-matter microstructural parameters to close the gap between indirect structural (i.e., DTI) and functional (i.e., BOLD) measures.

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Abbreviations

AC-PC	intercommissural line
AF	arcuate fasciculus
ANOVA	analysis of variance
BA	Brodmann area
BEM	boundary-element model
BOLD	blood-oxygen-level-dependent
CI	confidence interval
CRT	cathode-ray tube
DARTEL	diffeomorphic anatomical registration using exponentiated lie algebra
DC	direct current
dMRI	diffusion magnetic resonance imaging
DTI	diffusion-tensor imaging
EEG	electroencephalography
EOG	electrooculogram
EPI	echo planar imaging
ERP	event-related brain potential
FA	fractional anisotropy
FDR	false-discovery rate
FIR	finite impulse response
fMRI	functional magnetic resonance imaging
FOV	field of view

GLM	general linear model
GRAPPA	generalized auto-calibrating partially-parallel acquisition
HRF	hemodynamic response function
ICA	independent-component analysis
IFG	inferior frontal gyrus
LCD	liquid crystal display
LQ	laterality quotient
MEG	magnetoencephalography
MNI	Montreal Neurological Institute
MP-RAGE	magnetization-prepared rapid gradient echo
MR	magnetic resonance
MRI	magnetic resonance imaging
PT	planum temporale
ROI	region of interest
RT	reaction time
rTMS	repetitive transcranial magnetic stimulation
SD	standard deviation
SEM	standard error of the mean
SLF	superior longitudinal fasciculus
SMG	supramarginal gyrus
SNR	signal-to-noise ratio
SPR	self-paced reading
STG	superior temporal gyrus
TBSS	tract-based spatial statistics
TE	echo time
TFR	time–frequency analysis
TI	inversion time
TMS	transcranial magnetic stimulation
TP	temporo-parietal

TPM	tissue probability map
TR	repetition time
VB-ECD	variational-Bayesian equivalent-current dipole
VBM	voxel-based morphometry
VGA	video graphics array
XGA	extended graphics array

A

Stimuli from Behavioral, fMRI and EEG Studies*

1. `SF-SD` Während der Sitzung in der Hauptstadt hat der Minister den Sprecher getroffen und das Ergebnis berichtet.
   `SF-LD` Der Minister hat während der Sitzung in der Hauptstadt den Sprecher getroffen und das Ergebnis berichtet.
   `OF-SD` Während der Sitzung in der Hauptstadt hat den Sprecher der Minister getroffen und das Ergebnis berichtet.
   `OF-LD` Den Sprecher hat während der Sitzung in der Hauptstadt der Minister getroffen und das Ergebnis berichtet.
2. `SF-SD` Nach einer Saison in der Bundesliga hat der Trainer den Stürmer gewürdigt und die Entwicklung bestätigt.
   `SF-LD` Der Trainer hat nach einer Saison in der Bundesliga den Stürmer gewürdigt und die Entwicklung bestätigt.
   `OF-SD` Nach einer Saison in der Bundesliga hat den Stürmer der Trainer gewürdigt und die Entwicklung bestätigt.
   `OF-LD` Den Stürmer hat nach einer Saison in der Bundesliga der Trainer gewürdigt und die Entwicklung bestätigt.
3. `SF-SD` In der Verhandlung mit der Gewerkschaft hat der Arbeitgeber den Mitarbeiter angehört und den Arbeitskampf vermieden.
   `SF-LD` Der Arbeitgeber hat in der Verhandlung mit der Gewerkschaft den Mitarbeiter angehört und den Arbeitskampf vermieden.
   `OF-SD` In der Verhandlung mit der Gewerkschaft hat den Mitarbeiter der Arbeitgeber angehört und den Arbeitskampf vermieden.
   `OF-LD` Den Mitarbeiter hat in der Verhandlung mit der Gewerkschaft der Arbeitgeber angehört und den Arbeitskampf vermieden.
4. `SF-SD` Vor der Veranstaltung für die Elternschaft hat der Lehrer den Hausmeister überzeugt und das Klassenzimmer vorbereitet.
   `SF-LD` Der Lehrer hat vor der Veranstaltung für die Elternschaft den Hausmeister überzeugt und das Klassenzimmer vorbereitet.
   `OF-SD` Vor der Veranstaltung für die Elternschaft hat den Hausmeister der Lehrer überzeugt und das Klassenzimmer vorbereitet.
   `OF-LD` Den Hausmeister hat vor der Veranstaltung für die Elternschaft der Lehrer überzeugt und das Klassenzimmer vorbereitet.
5. `SF-SD` Wegen der Leistung in der Berufsschule hat der Meister den Lehrling entlassen und die Entscheidung bedauert.
   `SF-LD` Der Meister hat wegen der Leistung in der Berufsschule den Lehrling entlassen und die Entscheidung bedauert.
   `OF-SD` Wegen der Leistung in der Berufsschule hat den Lehrling der Meister entlassen und die Entscheidung bedauert.
   `OF-LD` Den Lehrling hat wegen der Leistung in der Berufsschule der Meister entlassen und die Entscheidung bedauert.
6. `SF-SD` Vor der Lage an dem Fachbereich hat der Professor den Doktor unterstützt und das Projekt fortgeführt.
   `SF-LD` Der Professor hat vor der Lage an dem Fachbereich den Doktor unterstützt und das Projekt fortgeführt.
   `OF-SD` Vor der Lage an dem Fachbereich hat den Doktor der Professor unterstützt und das Projekt fortgeführt.
   `OF-LD` Den Doktor hat vor der Lage an dem Fachbereich der Professor unterstützt und das Projekt fortgeführt.
7. `SF-SD` Nach dem Trainingslager mit dem Fußballverein hat der Spieler den Torwart verabschiedet und die Ehefrau begrüßt.
   `SF-LD` Der Spieler hat nach dem Trainingslager mit dem Fußballverein den Torwart verabschiedet und die Ehefrau begrüßt.
   `OF-SD` Nach dem Trainingslager mit dem Fußballverein hat den Torwart der Spieler verabschiedet und die Ehefrau begrüßt.
   `OF-LD` Den Torwart hat nach dem Trainingslager mit dem Fußballverein der Spieler verabschiedet und die Ehefrau begrüßt.

* Subject-first (SF), object-first (OF), short distance (SD), long distance (LD).

8. `SF-SD` Während des Prozesses an dem Gericht hat der Richter den Zeugen vernommen und den Zusammenhang aufgeklärt.
   `SF-LD` Der Richter hat während des Prozesses an dem Gericht den Zeugen vernommen und den Zusammenhang aufgeklärt.
   `OF-SD` Während des Prozesses an dem Gericht hat den Zeugen der Richter vernommen und den Zusammenhang aufgeklärt.
   `OF-LD` Den Zeugen hat während des Prozesses an dem Gericht der Richter vernommen und den Zusammenhang aufgeklärt.

9. `SF-SD` Nach dem Unfall auf der Landstraße hat der Notarzt den Verletzten behandelt und die Diagnose gestellt.
   `SF-LD` Der Notarzt hat nach dem Unfall auf der Landstraße den Verletzten behandelt und die Diagnose gestellt.
   `OF-SD` Nach dem Unfall auf der Landstraße hat den Verletzten der Notarzt behandelt und die Diagnose gestellt.
   `OF-LD` Den Verletzten hat nach dem Unfall auf der Landstraße der Notarzt behandelt und die Diagnose gestellt.

10. `SF-SD` An dem Jahrestag für die Belegschaft hat der Firmenchef den Arbeiter befördert und die Anstrengung gelobt.
    `SF-LD` Der Firmenchef hat an dem Jahrestag für die Belegschaft den Arbeiter befördert und die Anstrengung gelobt.
    `OF-SD` An dem Jahrestag für die Belegschaft hat den Arbeiter der Firmenchef befördert und die Anstrengung gelobt.
    `OF-LD` Den Arbeiter hat an dem Jahrestag für die Belegschaft der Firmenchef befördert und die Anstrengung gelobt.

11. `SF-SD` Während des Wettbewerbs in der Sporthalle hat der Athlet den Funktionär attackiert und den Leistungssport erschüttert.
    `SF-LD` Der Athlet hat während des Wettbewerbs in der Sporthalle den Funktionär attackiert und den Leistungssport erschüttert.
    `OF-SD` Während des Wettbewerbs in der Sporthalle hat den Funktionär der Athlet attackiert und den Leistungssport erschüttert.
    `OF-LD` Den Funktionär hat während des Wettbewerbs in der Sporthalle der Athlet attackiert und den Leistungssport erschüttert.

12. `SF-SD` In der Kontroverse wegen des Parteitags hat der Demokrat den Delegierten ausgelacht und die Parteiführung gestärkt.
    `SF-LD` Der Demokrat hat in der Kontroverse wegen des Parteitags den Delegierten ausgelacht und die Parteiführung gestärkt.
    `OF-SD` In der Kontroverse wegen des Parteitags hat den Delegierten der Demokrat ausgelacht und die Parteiführung gestärkt.
    `OF-LD` Den Delegierten hat in der Kontroverse wegen des Parteitags der Demokrat ausgelacht und die Parteiführung gestärkt.

13. `SF-SD` Vor der Kundgebung gegen den Straßenbau hat der Investor den Bauleiter informiert und die Befürchtungen geschildert.
    `SF-LD` Der Investor hat vor der Kundgebung gegen den Straßenbau den Bauleiter informiert und die Befürchtungen geschildert.
    `OF-SD` Vor der Kundgebung gegen den Straßenbau hat den Bauleiter der Investor informiert und die Befürchtungen geschildert.
    `OF-LD` Den Bauleiter hat vor der Kundgebung gegen den Straßenbau der Investor informiert und die Befürchtungen geschildert.

14. `SF-SD` Nach dem Essen in der Kantine hat den Chefkoch der Gourmet kritisiert und die Speisekarte bemängelt.
    `SF-LD` Der Gourmet hat nach dem Essen in der Kantine den Chefkoch kritisiert und die Speisekarte bemängelt.
    `OF-SD` Nach dem Essen in der Kantine hat der Gourmet den Chefkoch kritisiert und die Speisekarte bemängelt.
    `OF-LD` Den Chefkoch hat nach dem Essen in der Kantine der Gourmet kritisiert und die Speisekarte bemängelt.

15. `SF-SD` Bei dem Kampf an der Grenze hat der General den Offizier geopfert und die Armeeführung empört.
    `SF-LD` Der General hat bei dem Kampf an der Grenze den Offizier geopfert und die Armeeführung empört.
    `OF-SD` Bei dem Kampf an der Grenze hat den Offizier der General geopfert und die Armeeführung empört.
    `OF-LD` Den Offizier hat bei dem Kampf an der Grenze der General geopfert und die Armeeführung empört.

16. `SF-SD` Während der Diskussion zwischen den Künstlern hat der Bildhauer den Maler geachtet und die Auffassung geteilt.
    `SF-LD` Der Bildhauer hat während der Diskussion zwischen den Künstlern den Maler geachtet und die Auffassung geteilt.
    `OF-SD` Während der Diskussion zwischen den Künstlern hat den Maler der Bildhauer geachtet und die Auffassung geteilt.
    `OF-LD` Den Maler hat während der Diskussion zwischen den Künstlern der Bildhauer geachtet und die Auffassung geteilt.

17. `SF-SD` Vor dem Interview mit der Zeitung hat der Präsident den Journalist empfangen und die Reform dargestellt.
    `SF-LD` Der Präsident hat vor dem Interview mit der Zeitung den Journalist empfangen und die Reform dargestellt.
    `OF-SD` Vor dem Interview mit der Zeitung hat den Journalist der Präsident empfangen und die Reform dargestellt.
    `OF-LD` Den Journalist hat vor dem Interview mit der Zeitung der Präsident empfangen und die Reform dargestellt.

18. `SF-SD` Vor dem Vortrag an der Universität hat der Wissenschaftler den Experten aufgesucht und die Methode verteidigt.
    `SF-LD` Der Wissenschaftler hat vor dem Vortrag an der Universität den Experten aufgesucht und die Methode verteidigt.
    `OF-SD` Vor dem Vortrag an der Universität hat den Experten der Wissenschaftler aufgesucht und die Methode verteidigt.
    `OF-LD` Den Experten hat vor dem Vortrag an der Universität der Wissenschaftler aufgesucht und die Methode verteidigt.

19. SF-SD Nach dem Skandal auf dem Bauernhof hat der Naturschützer den Landwirt beleidigt und die Schließung gefordert.
SF-LD Der Naturschützer hat nach dem Skandal auf dem Bauernhof den Landwirt beleidigt und die Schließung gefordert.
OF-SD Nach dem Skandal auf dem Bauernhof hat den Landwirt der Naturschützer beleidigt und die Schließung gefordert.
OF-LD Den Landwirt hat nach dem Skandal auf dem Bauernhof der Naturschützer beleidigt und die Schließung gefordert.

20. SF-SD Wegen des Zustands in der Abteilung hat der Kollege den Personalrat benachrichtigt und die Wahrheit eröffnet.
SF-LD Der Kollege hat wegen des Zustands in der Abteilung den Personalrat benachrichtigt und die Wahrheit eröffnet.
OF-SD Wegen des Zustands in der Abteilung hat den Personalrat der Kollege benachrichtigt und die Wahrheit eröffnet.
OF-LD Den Personalrat hat wegen des Zustands in der Abteilung der Kollege benachrichtigt und die Wahrheit eröffnet.

21. SF-SD Nach der Halbzeit in dem Länderspiel hat der Schiedsrichter den Reporter abgewiesen und die Stellungnahme verweigert.
SF-LD Der Schiedsrichter hat nach der Halbzeit in dem Länderspiel den Reporter abgewiesen und die Stellungnahme verweigert.
OF-SD Nach der Halbzeit in dem Länderspiel hat den Reporter der Schiedsrichter abgewiesen und die Stellungnahme verweigert.
OF-LD Den Reporter hat nach der Halbzeit in dem Länderspiel der Schiedsrichter abgewiesen und die Stellungnahme verweigert.

22. SF-SD Bei dem Anschlag auf die Botschaft hat der Terrorist den Diplomat ermordet und das Gebäude gesprengt.
SF-LD Der Terrorist hat bei dem Anschlag auf die Botschaft den Diplomat ermordet und das Gebäude gesprengt.
OF-SD Bei dem Anschlag auf die Botschaft hat den Diplomat der Terrorist ermordet und das Gebäude gesprengt.
OF-LD Den Diplomat hat bei dem Anschlag auf die Botschaft der Terrorist ermordet und das Gebäude gesprengt.

23. SF-SD Vor dem Ausflug an die Küste hat der Reiseleiter den Busfahrer begrüßt und das Fahrzeug überprüft.
SF-LD Der Reiseleiter hat vor dem Ausflug an die Küste den Busfahrer begrüßt und das Fahrzeug überprüft.
OF-SD Vor dem Ausflug an die Küste hat den Busfahrer der Reiseleiter begrüßt und das Fahrzeug überprüft.
OF-LD Den Busfahrer hat vor dem Ausflug an die Küste der Reiseleiter begrüßt und das Fahrzeug überprüft.

24. SF-SD In der Vorstellung mit dem Orchester hat der Dirigent den Pianist irritiert und das Konzert unterbrochen.
SF-LD Der Dirigent hat in der Vorstellung mit dem Orchester den Pianist irritiert und das Konzert unterbrochen.
OF-SD In der Vorstellung mit dem Orchester hat den Pianist der Dirigent irritiert und das Konzert unterbrochen.
OF-LD Den Pianist hat in der Vorstellung mit dem Orchester der Dirigent irritiert und das Konzert unterbrochen.

25. SF-SD Während der Besprechung in der Firma hat der Geschäftsführer den Leiter berufen und den Erfolg gesichert.
SF-LD Der Geschäftsführer hat während der Besprechung in der Firma den Leiter berufen und den Erfolg gesichert.
OF-SD Während der Besprechung in der Firma hat den Leiter der Geschäftsführer berufen und den Erfolg gesichert.
OF-LD Den Leiter hat während der Besprechung in der Firma der Geschäftsführer berufen und den Erfolg gesichert.

26. SF-SD Nach der Krise wegen des Wahlversprechens hat der Redakteur den Kanzler verurteilt und den Neuanfang verlangt.
SF-LD Der Redakteur hat nach der Krise wegen des Wahlversprechens den Kanzler verurteilt und den Neuanfang verlangt.
OF-SD Nach der Krise wegen des Wahlversprechens hat den Kanzler der Redakteur verurteilt und den Neuanfang verlangt.
OF-LD Den Kanzler hat nach der Krise wegen des Wahlversprechens der Redakteur verurteilt und den Neuanfang verlangt.

27. SF-SD In der Debatte um die Finanzierung hat der Befürworter den Gegner überzeugt und die Niederlage vermieden.
SF-LD Der Befürworter hat in der Debatte um die Finanzierung den Gegner überzeugt und die Niederlage vermieden.
OF-SD In der Debatte um die Finanzierung hat den Gegner der Befürworter überzeugt und die Niederlage vermieden.
OF-LD Den Gegner hat in der Debatte um die Finanzierung der Befürworter überzeugt und die Niederlage vermieden.

28. SF-SD Vor der Ausstellung in der Galerie hat der Kunde den Maler angerufen und die Preise erfragt.
SF-LD Der Kunde hat vor der Ausstellung in der Galerie den Maler angerufen und die Preise erfragt.
OF-SD Vor der Ausstellung in der Galerie hat den Maler der Kunde angerufen und die Preise erfragt.
OF-LD Den Maler hat vor der Ausstellung in der Galerie der Kunde angerufen und die Preise erfragt.

29. SF-SD Bei dem Treffen über die Ausbildung hat der Bewerber den Direktor beeindruckt und die Stelle bekommen.
SF-LD Der Bewerber hat bei dem Treffen über die Ausbildung den Direktor beeindruckt und die Stelle bekommen.
OF-SD Bei dem Treffen über die Ausbildung hat den Direktor der Bewerber beeindruckt und die Stelle bekommen.
OF-LD Den Direktor hat bei dem Treffen über die Ausbildung der Bewerber beeindruckt und die Stelle bekommen.

30. SF-SD Vor der Lesung in der Buchhandlung hat der Verleger den Schriftsteller vorgestellt und den Roman präsentiert.
SF-LD Der Verleger hat vor der Lesung in der Buchhandlung den Schriftsteller vorgestellt und den Roman präsentiert.
OF-SD Vor der Lesung in der Buchhandlung hat den Schriftsteller der Verleger vorgestellt und den Roman präsentiert.
OF-LD Den Schriftsteller hat vor der Lesung in der Buchhandlung der Verleger vorgestellt und den Roman präsentiert.

31. SF-SD Wegen der Erfahrung in der Klinik hat der Pfleger den Patienten gemieden und die Station verlassen.
SF-LD Der Pfleger hat wegen der Erfahrung in der Klinik den Patienten gemieden und die Station verlassen.
OF-SD Wegen der Erfahrung in der Klinik hat den Patienten der Pfleger gemieden und die Station verlassen.
OF-LD Den Patienten hat wegen der Erfahrung in der Klinik der Pfleger gemieden und die Station verlassen.

32. SF-SD Während der Tagung an der Hochschule hat der Forscher den Besucher begeistert und das Fachpublikum enttäuscht.
SF-LD Der Forscher hat während der Tagung an der Hochschule den Besucher begeistert und das Fachpublikum enttäuscht.
OF-SD Während der Tagung an der Hochschule hat den Besucher der Forscher begeistert und das Fachpublikum enttäuscht.
OF-LD Den Besucher hat während der Tagung an der Hochschule der Forscher begeistert und das Fachpublikum enttäuscht.

33. SF-SD Nach der Begegnung in dem Studio hat der Regisseur den Schauspieler engagiert und das Drehbuch geändert.
SF-LD Der Regisseur hat nach der Begegnung in dem Studio den Schauspieler engagiert und das Drehbuch geändert.
OF-SD Nach der Begegnung in dem Studio hat den Schauspieler der Regisseur engagiert und das Drehbuch geändert.
OF-LD Den Schauspieler hat nach der Begegnung in dem Studio der Regisseur engagiert und das Drehbuch geändert.

34. SF-SD Bei dem Jubiläum in dem Finanzamt hat der Vorgänger den Nachfolger eingeführt und die Aufgaben erklärt.
SF-LD Der Vorgänger hat bei dem Jubiläum in dem Finanzamt den Nachfolger eingeführt und die Aufgaben erklärt.
OF-SD Bei dem Jubiläum in dem Finanzamt hat den Nachfolger der Vorgänger eingeführt und die Aufgaben erklärt.
OF-LD Den Nachfolger hat bei dem Jubiläum in dem Finanzamt der Vorgänger eingeführt und die Aufgaben erklärt.

35. SF-SD Bei dem Sommerfest in der Siedlung hat der Nachbar den Bürgermeister erwartet und den Empfang vorbereitet.
SF-LD Der Nachbar hat bei dem Sommerfest in der Siedlung den Bürgermeister erwartet und den Empfang vorbereitet.
OF-SD Bei dem Sommerfest in der Siedlung hat den Bürgermeister der Nachbar erwartet und den Empfang vorbereitet.
OF-LD Den Bürgermeister hat bei dem Sommerfest in der Siedlung der Nachbar erwartet und den Empfang vorbereitet.

36. SF-SD Nach der Ansprache an das Publikum hat der Leser den Autor bewundert und die Geschichte verschlungen.
SF-LD Der Leser hat nach der Ansprache an das Publikum den Autor bewundert und die Geschichte verschlungen.
OF-SD Nach der Ansprache an das Publikum hat den Autor der Leser bewundert und die Geschichte verschlungen.
OF-LD Den Autor hat nach der Ansprache an das Publikum der Leser bewundert und die Geschichte verschlungen.

37. SF-SD Vor dem Antrag gegen das Parlament hat der Politiker den Konkurrenten gefürchtet und die Wiederwahl bezweifelt.
SF-LD Der Politiker hat vor dem Antrag gegen das Parlament den Konkurrenten gefürchtet und die Wiederwahl bezweifelt.
OF-SD Vor dem Antrag gegen das Parlament hat den Konkurrenten der Politiker gefürchtet und die Wiederwahl bezweifelt.
OF-LD Den Konkurrenten hat vor dem Antrag gegen das Parlament der Politiker gefürchtet und die Wiederwahl bezweifelt.

38. SF-SD Vor der Übereinkunft mit den Eltern hat der Jugendliche den Erzieher ignoriert und das Jugendamt beunruhigt.
SF-LD Der Jugendliche hat vor der Übereinkunft mit den Eltern den Erzieher ignoriert und das Jugendamt beunruhigt.
OF-SD Vor der Übereinkunft mit den Eltern hat den Erzieher der Jugendliche ignoriert und das Jugendamt beunruhigt.
OF-LD Den Erzieher hat vor der Übereinkunft mit den Eltern der Jugendliche ignoriert und das Jugendamt beunruhigt.

39. SF-SD Während der Planung für die Initiative hat der Veranstalter den Teilnehmer beruhigt und die Aufregung verringert.
SF-LD Der Veranstalter hat während der Planung für die Initiative den Teilnehmer beruhigt und die Aufregung verringert.
OF-SD Während der Planung für die Initiative hat den Teilnehmer der Veranstalter beruhigt und die Aufregung verringert.
OF-LD Den Teilnehmer hat während der Planung für die Initiative der Veranstalter beruhigt und die Aufregung verringert.

40. SF-SD Wegen der Probleme bei der Produktion hat der Unternehmer den Lieferanten gewechselt und die Qualität verbessert.
SF-LD Der Unternehmer hat wegen der Probleme bei der Produktion den Lieferanten gewechselt und die Qualität verbessert.
OF-SD Wegen der Probleme bei der Produktion hat den Lieferanten der Unternehmer gewechselt und die Qualität verbessert.
OF-LD Den Lieferanten hat wegen der Probleme bei der Produktion der Unternehmer gewechselt und die Qualität verbessert.

41. `SF-SD` Nach der Ermittlung in dem Milieu hat der Polizist den Verbrecher beschuldigt und den Verdacht erhärtet.
`SF-LD` Der Polizist hat nach der Ermittlung in dem Milieu den Verbrecher beschuldigt und den Verdacht erhärtet.
`OF-SD` Nach der Ermittlung in dem Milieu hat den Verbrecher der Polizist beschuldigt und den Verdacht erhärtet.
`OF-LD` Den Verbrecher hat nach der Ermittlung in dem Milieu der Polizist beschuldigt und den Verdacht erhärtet.

42. `SF-SD` Mit der Mitteilung wegen des Zeugnisses hat der Schulleiter den Abiturient erschrocken und die Einschätzung unterstrichen.
`SF-LD` Der Schulleiter hat mit der Mitteilung wegen des Zeugnisses den Abiturient erschrocken und die Einschätzung unterstrichen.
`OF-SD` Mit der Mitteilung wegen des Zeugnisses hat den Abiturient der Schulleiter erschrocken und die Einschätzung unterstrichen.
`OF-LD` Den Abiturient hat mit der Mitteilung wegen des Zeugnisses der Schulleiter erschrocken und die Einschätzung unterstrichen.

43. `SF-SD` Mit der Premiere in dem Theater hat der Dichter den Kritiker überrascht und die Ansprüche erfüllt.
`SF-LD` Der Dichter hat mit der Premiere in dem Theater den Kritiker überrascht und die Ansprüche erfüllt.
`OF-SD` Mit der Premiere in dem Theater hat den Kritiker der Dichter überrascht und die Ansprüche erfüllt.
`OF-LD` Den Kritiker hat mit der Premiere in dem Theater der Dichter überrascht und die Ansprüche erfüllt.

44. `SF-SD` Wegen der Bilanz an der Börse hat der Beamte den Sekretär verhaftet und die Festnahme verteidigt.
`SF-LD` Der Beamte hat wegen der Bilanz an der Börse den Sekretär verhaftet und die Festnahme verteidigt.
`OF-SD` Wegen der Bilanz an der Börse hat den Sekretär der Beamte verhaftet und die Festnahme verteidigt.
`OF-LD` Den Sekretär hat wegen der Bilanz an der Börse der Beamte verhaftet und die Festnahme verteidigt.

45. `SF-SD` Nach dem Urteil in dem Verfahren hat der Anwalt den Angeklagten aufgegeben und den Widerstand beendet.
`SF-LD` Der Anwalt hat nach dem Urteil in dem Verfahren den Angeklagten aufgegeben und den Widerstand beendet.
`OF-SD` Nach dem Urteil in dem Verfahren hat den Angeklagten der Anwalt aufgegeben und den Widerstand beendet.
`OF-LD` Den Angeklagten hat nach dem Urteil in dem Verfahren der Anwalt aufgegeben und den Widerstand beendet.

46. `SF-SD` Vor der Entlassung aus dem Gefängnis hat der Psychologe den Häftling untersucht und die Einstellung überprüft.
`SF-LD` Der Psychologe hat vor der Entlassung aus dem Gefängnis den Häftling untersucht und die Einstellung überprüft.
`OF-SD` Vor der Entlassung aus dem Gefängnis hat den Häftling der Psychologe untersucht und die Einstellung überprüft.
`OF-LD` Den Häftling hat vor der Entlassung aus dem Gefängnis der Psychologe untersucht und die Einstellung überprüft.

47. `SF-SD` Wegen des Verlusts bei den Geschäften hat der Kaufmann den Bankier kontaktiert und den Kredit aufgenommen.
`SF-LD` Der Kaufmann hat wegen des Verlusts bei den Geschäften den Bankier kontaktiert und den Kredit aufgenommen.
`OF-SD` Wegen des Verlusts bei den Geschäften hat den Bankier der Kaufmann kontaktiert und den Kredit aufgenommen.
`OF-LD` Den Bankier hat wegen des Verlusts bei den Geschäften der Kaufmann kontaktiert und den Kredit aufgenommen.

48. `SF-SD` Nach der Aussprache mit der Familie hat der Bruder den Vater angelächelt und den Kompromiss akzeptiert.
`SF-LD` Der Bruder hat nach der Aussprache mit der Familie den Vater angelächelt und den Kompromiss akzeptiert.
`OF-SD` Nach der Aussprache mit der Familie hat den Vater der Bruder angelächelt und den Kompromiss akzeptiert.
`OF-LD` Den Vater hat nach der Aussprache mit der Familie der Bruder angelächelt und den Kompromiss akzeptiert.

B

Stimuli from Patient Study[†]

1. `SF-SD` Während der Sitzung in der Hauptstadt hat der Minister den Sprecher getroffen.
   `SF-LD` Der Minister hat während der Sitzung in der Hauptstadt den Sprecher getroffen.
   `OF-SD` Während der Sitzung in der Hauptstadt hat den Sprecher der Minister getroffen.
   `OF-LD` Den Sprecher hat während der Sitzung in der Hauptstadt der Minister getroffen.
2. `SF-SD` Nach einer Saison in der Bundesliga hat der Trainer den Stürmer gewürdigt.
   `SF-LD` Der Trainer hat nach einer Saison in der Bundesliga den Stürmer gewürdigt.
   `OF-SD` Nach einer Saison in der Bundesliga hat den Stürmer der Trainer gewürdigt.
   `OF-LD` Den Stürmer hat nach einer Saison in der Bundesliga der Trainer gewürdigt.
3. `SF-SD` In der Verhandlung mit der Gewerkschaft hat der Arbeitgeber den Mitarbeiter angehört.
   `SF-LD` Der Arbeitgeber hat in der Verhandlung mit der Gewerkschaft den Mitarbeiter angehört.
   `OF-SD` In der Verhandlung mit der Gewerkschaft hat den Mitarbeiter der Arbeitgeber angehört.
   `OF-LD` Den Mitarbeiter hat in der Verhandlung mit der Gewerkschaft der Arbeitgeber angehört.
4. `SF-SD` Vor der Veranstaltung für die Elternschaft hat der Lehrer den Hausmeister überzeugt.
   `SF-LD` Der Lehrer hat vor der Veranstaltung für die Elternschaft den Hausmeister überzeugt.
   `OF-SD` Vor der Veranstaltung für die Elternschaft hat den Hausmeister der Lehrer überzeugt.
   `OF-LD` Den Hausmeister hat vor der Veranstaltung für die Elternschaft der Lehrer überzeugt.
5. `SF-SD` Wegen der Leistung in der Berufsschule hat der Meister den Lehrling entlassen.
   `SF-LD` Der Meister hat wegen der Leistung in der Berufsschule den Lehrling entlassen.
   `OF-SD` Wegen der Leistung in der Berufsschule hat den Lehrling der Meister entlassen.
   `OF-LD` Den Lehrling hat wegen der Leistung in der Berufsschule der Meister entlassen.
6. `SF-SD` Vor der Lage an dem Fachbereich hat der Professor den Doktor unterstützt.
   `SF-LD` Der Professor hat vor der Lage an dem Fachbereich den Doktor unterstützt.
   `OF-SD` Vor der Lage an dem Fachbereich hat den Doktor der Professor unterstützt.
   `OF-LD` Den Doktor hat vor der Lage an dem Fachbereich der Professor unterstützt.
7. `SF-SD` Nach dem Trainingslager mit dem Fußballverein hat der Spieler den Torwart verabschiedet.
   `SF-LD` Der Spieler hat nach dem Trainingslager mit dem Fußballverein den Torwart verabschiedet.
   `OF-SD` Nach dem Trainingslager mit dem Fußballverein hat den Torwart der Spieler verabschiedet.
   `OF-LD` Den Torwart hat nach dem Trainingslager mit dem Fußballverein der Spieler verabschiedet.

[†] Subject-first (SF), object-first (OF), short distance (SD), long distance (LD).

8. `SF-SD` Während des Prozesses an dem Gericht hat der Richter den Zeugen vernommen.
   `SF-LD` Der Richter hat während des Prozesses an dem Gericht den Zeugen vernommen.
   `OF-SD` Während des Prozesses an dem Gericht hat den Zeugen der Richter vernommen.
   `OF-LD` Den Zeugen hat während des Prozesses an dem Gericht der Richter vernommen.
9. `SF-SD` Nach dem Unfall auf der Landstraße hat der Notarzt den Verletzten behandelt.
   `SF-LD` Der Notarzt hat nach dem Unfall auf der Landstraße den Verletzten behandelt.
   `OF-SD` Nach dem Unfall auf der Landstraße hat den Verletzten der Notarzt behandelt.
   `OF-LD` Den Verletzten hat nach dem Unfall auf der Landstraße der Notarzt behandelt.
10. `SF-SD` An dem Jahrestag für die Belegschaft hat der Firmenchef den Arbeiter befördert.
    `SF-LD` Der Firmenchef hat an dem Jahrestag für die Belegschaft den Arbeiter befördert.
    `OF-SD` An dem Jahrestag für die Belegschaft hat den Arbeiter der Firmenchef befördert.
    `OF-LD` Den Arbeiter hat an dem Jahrestag für die Belegschaft der Firmenchef befördert.
11. `SF-SD` Während des Wettbewerbs in der Sporthalle hat der Athlet den Funktionär attackiert.
    `SF-LD` Der Athlet hat während des Wettbewerbs in der Sporthalle den Funktionär attackiert.
    `OF-SD` Während des Wettbewerbs in der Sporthalle hat den Funktionär der Athlet attackiert.
    `OF-LD` Den Funktionär hat während des Wettbewerbs in der Sporthalle der Athlet attackiert.
12. `SF-SD` In der Kontroverse wegen des Parteitags hat der Demokrat den Delegierten ausgelacht.
    `SF-LD` Der Demokrat hat in der Kontroverse wegen des Parteitags den Delegierten ausgelacht.
    `OF-SD` In der Kontroverse wegen des Parteitags hat den Delegierten der Demokrat ausgelacht.
    `OF-LD` Den Delegierten hat in der Kontroverse wegen des Parteitags der Demokrat ausgelacht.
13. `SF-SD` Vor der Kundgebung gegen den Straßenbau hat der Investor den Bauleiter informiert.
    `SF-LD` Der Investor hat vor der Kundgebung gegen den Straßenbau den Bauleiter informiert.
    `OF-SD` Vor der Kundgebung gegen den Straßenbau hat den Bauleiter der Investor informiert.
    `OF-LD` Den Bauleiter hat vor der Kundgebung gegen den Straßenbau der Investor informiert.
14. `SF-SD` Nach dem Essen in der Kantine hat den Chefkoch der Gourmet kritisiert.
    `SF-LD` Der Gourmet hat nach dem Essen in der Kantine den Chefkoch kritisiert.
    `OF-SD` Nach dem Essen in der Kantine hat der Gourmet den Chefkoch kritisiert.
    `OF-LD` Den Chefkoch hat nach dem Essen in der Kantine der Gourmet kritisiert.
15. `SF-SD` Bei dem Kampf an der Grenze hat der General den Offizier geopfert.
    `SF-LD` Der General hat bei dem Kampf an der Grenze den Offizier geopfert.
    `OF-SD` Bei dem Kampf an der Grenze hat den Offizier der General geopfert.
    `OF-LD` Den Offizier hat bei dem Kampf an der Grenze der General geopfert.
16. `SF-SD` Während der Diskussion zwischen den Künstlern hat der Bildhauer den Maler geachtet.
    `SF-LD` Der Bildhauer hat während der Diskussion zwischen den Künstlern den Maler geachtet.
    `OF-SD` Während der Diskussion zwischen den Künstlern hat den Maler der Bildhauer geachtet.
    `OF-LD` Den Maler hat während der Diskussion zwischen den Künstlern der Bildhauer geachtet.
17. `SF-SD` Vor dem Interview mit der Zeitung hat der Präsident den Journalist empfangen.
    `SF-LD` Der Präsident hat vor dem Interview mit der Zeitung den Journalist empfangen.
    `OF-SD` Vor dem Interview mit der Zeitung hat den Journalist der Präsident empfangen.
    `OF-LD` Den Journalist hat vor dem Interview mit der Zeitung der Präsident empfangen.
18. `SF-SD` Vor dem Vortrag an der Universität hat der Wissenschaftler den Experten aufgesucht.
    `SF-LD` Der Wissenschaftler hat vor dem Vortrag an der Universität den Experten aufgesucht.
    `OF-SD` Vor dem Vortrag an der Universität hat den Experten der Wissenschaftler aufgesucht.
    `OF-LD` Den Experten hat vor dem Vortrag an der Universität der Wissenschaftler aufgesucht.

19. SF-SD Nach dem Skandal auf dem Bauernhof hat der Naturschützer den Landwirt beleidigt.
SF-LD Der Naturschützer hat nach dem Skandal auf dem Bauernhof den Landwirt beleidigt.
OF-SD Nach dem Skandal auf dem Bauernhof hat den Landwirt der Naturschützer beleidigt.
OF-LD Den Landwirt hat nach dem Skandal auf dem Bauernhof der Naturschützer beleidigt.

20. SF-SD Wegen des Zustands in der Abteilung hat der Kollege den Personalrat benachrichtigt.
SF-LD Der Kollege hat wegen des Zustands in der Abteilung den Personalrat benachrichtigt.
OF-SD Wegen des Zustands in der Abteilung hat den Personalrat der Kollege benachrichtigt.
OF-LD Den Personalrat hat wegen des Zustands in der Abteilung der Kollege benachrichtigt.

21. SF-SD Nach der Halbzeit in dem Länderspiel hat der Schiedsrichter den Reporter abgewiesen.
SF-LD Der Schiedsrichter hat nach der Halbzeit in dem Länderspiel den Reporter abgewiesen.
OF-SD Nach der Halbzeit in dem Länderspiel hat den Reporter der Schiedsrichter abgewiesen.
OF-LD Den Reporter hat nach der Halbzeit in dem Länderspiel der Schiedsrichter abgewiesen.

22. SF-SD Bei dem Anschlag auf die Botschaft hat der Terrorist den Diplomat ermordet.
SF-LD Der Terrorist hat bei dem Anschlag auf die Botschaft den Diplomat ermordet.
OF-SD Bei dem Anschlag auf die Botschaft hat den Diplomat der Terrorist ermordet.
OF-LD Den Diplomat hat bei dem Anschlag auf die Botschaft der Terrorist ermordet.

23. SF-SD Vor dem Ausflug an die Küste hat der Reiseleiter den Busfahrer begrüßt.
SF-LD Der Reiseleiter hat vor dem Ausflug an die Küste den Busfahrer begrüßt.
OF-SD Vor dem Ausflug an die Küste hat den Busfahrer der Reiseleiter begrüßt.
OF-LD Den Busfahrer hat vor dem Ausflug an die Küste der Reiseleiter begrüßt.

24. SF-SD In der Vorstellung mit dem Orchester hat der Dirigent den Pianist irritiert.
SF-LD Der Dirigent hat in der Vorstellung mit dem Orchester den Pianist irritiert.
OF-SD In der Vorstellung mit dem Orchester hat den Pianist der Dirigent irritiert.
OF-LD Den Pianist hat in der Vorstellung mit dem Orchester der Dirigent irritiert.

25. SF-SD Während der Besprechung in der Firma hat der Geschäftsführer den Leiter berufen.
SF-LD Der Geschäftsführer hat während der Besprechung in der Firma den Leiter berufen.
OF-SD Während der Besprechung in der Firma hat den Leiter der Geschäftsführer berufen.
OF-LD Den Leiter hat während der Besprechung in der Firma der Geschäftsführer berufen.

26. SF-SD Nach der Krise wegen des Wahlversprechens hat der Redakteur den Kanzler verurteilt.
SF-LD Der Redakteur hat nach der Krise wegen des Wahlversprechens den Kanzler verurteilt.
OF-SD Nach der Krise wegen des Wahlversprechens hat den Kanzler der Redakteur verurteilt.
OF-LD Den Kanzler hat nach der Krise wegen des Wahlversprechens der Redakteur verurteilt.

27. SF-SD In der Debatte um die Finanzierung hat der Befürworter den Gegner überzeugt.
SF-LD Der Befürworter hat in der Debatte um die Finanzierung den Gegner überzeugt.
OF-SD In der Debatte um die Finanzierung hat den Gegner der Befürworter überzeugt.
OF-LD Den Gegner hat in der Debatte um die Finanzierung der Befürworter überzeugt.

28. SF-SD Vor der Ausstellung in der Galerie hat der Kunde den Maler angerufen.
SF-LD Der Kunde hat vor der Ausstellung in der Galerie den Maler angerufen.
OF-SD Vor der Ausstellung in der Galerie hat den Maler der Kunde angerufen.
OF-LD Den Maler hat vor der Ausstellung in der Galerie der Kunde angerufen.

29. SF-SD Bei dem Treffen über die Ausbildung hat der Bewerber den Direktor beeindruckt.
SF-LD Der Bewerber hat bei dem Treffen über die Ausbildung den Direktor beeindruckt.
OF-SD Bei dem Treffen über die Ausbildung hat den Direktor der Bewerber beeindruckt.
OF-LD Den Direktor hat bei dem Treffen über die Ausbildung der Bewerber beeindruckt.

30. SF-SD Vor der Lesung in der Buchhandlung hat der Verleger den Schriftsteller vorgestellt.
SF-LD Der Verleger hat vor der Lesung in der Buchhandlung den Schriftsteller vorgestellt.
OF-SD Vor der Lesung in der Buchhandlung hat den Schriftsteller der Verleger vorgestellt.
OF-LD Den Schriftsteller hat vor der Lesung in der Buchhandlung der Verleger vorgestellt.

31. SF-SD Wegen der Erfahrung in der Klinik hat der Pfleger den Patienten gemieden.
SF-LD Der Pfleger hat wegen der Erfahrung in der Klinik den Patienten gemieden.
OF-SD Wegen der Erfahrung in der Klinik hat den Patienten der Pfleger gemieden.
OF-LD Den Patienten hat wegen der Erfahrung in der Klinik der Pfleger gemieden.

32. SF-SD Während der Tagung an der Hochschule hat der Forscher den Besucher begeistert.
SF-LD Der Forscher hat während der Tagung an der Hochschule den Besucher begeistert.
OF-SD Während der Tagung an der Hochschule hat den Besucher der Forscher begeistert.
OF-LD Den Besucher hat während der Tagung an der Hochschule der Forscher begeistert.

33. SF-SD Nach der Begegnung in dem Studio hat der Regisseur den Schauspieler engagiert.
SF-LD Der Regisseur hat nach der Begegnung in dem Studio den Schauspieler engagiert.
OF-SD Nach der Begegnung in dem Studio hat den Schauspieler der Regisseur engagiert.
OF-LD Den Schauspieler hat nach der Begegnung in dem Studio der Regisseur engagiert.

34. SF-SD Bei dem Jubiläum in dem Finanzamt hat der Vorgänger den Nachfolger eingeführt.
SF-LD Der Vorgänger hat bei dem Jubiläum in dem Finanzamt den Nachfolger eingeführt.
OF-SD Bei dem Jubiläum in dem Finanzamt hat den Nachfolger der Vorgänger eingeführt.
OF-LD Den Nachfolger hat bei dem Jubiläum in dem Finanzamt der Vorgänger eingeführt.

35. SF-SD Bei dem Sommerfest in der Siedlung hat der Nachbar den Bürgermeister erwartet.
SF-LD Der Nachbar hat bei dem Sommerfest in der Siedlung den Bürgermeister erwartet.
OF-SD Bei dem Sommerfest in der Siedlung hat den Bürgermeister der Nachbar erwartet.
OF-LD Den Bürgermeister hat bei dem Sommerfest in der Siedlung der Nachbar erwartet.

36. SF-SD Nach der Ansprache an das Publikum hat der Leser den Autor bewundert.
SF-LD Der Leser hat nach der Ansprache an das Publikum den Autor bewundert.
OF-SD Nach der Ansprache an das Publikum hat den Autor der Leser bewundert.
OF-LD Den Autor hat nach der Ansprache an das Publikum der Leser bewundert.

37. SF-SD Vor dem Antrag gegen das Parlament hat der Politiker den Konkurrenten gefürchtet.
SF-LD Der Politiker hat vor dem Antrag gegen das Parlament den Konkurrenten gefürchtet.
OF-SD Vor dem Antrag gegen das Parlament hat den Konkurrenten der Politiker gefürchtet.
OF-LD Den Konkurrenten hat vor dem Antrag gegen das Parlament der Politiker gefürchtet.

38. SF-SD Vor der Übereinkunft mit den Eltern hat der Jugendliche den Erzieher ignoriert.
SF-LD Der Jugendliche hat vor der Übereinkunft mit den Eltern den Erzieher ignoriert.
OF-SD Vor der Übereinkunft mit den Eltern hat den Erzieher der Jugendliche ignoriert.
OF-LD Den Erzieher hat vor der Übereinkunft mit den Eltern der Jugendliche ignoriert.

39. SF-SD Während der Planung für die Initiative hat der Veranstalter den Teilnehmer beruhigt.
SF-LD Der Veranstalter hat während der Planung für die Initiative den Teilnehmer beruhigt.
OF-SD Während der Planung für die Initiative hat den Teilnehmer der Veranstalter beruhigt.
OF-LD Den Teilnehmer hat während der Planung für die Initiative der Veranstalter beruhigt.

40. SF-SD Wegen der Probleme bei der Produktion hat der Unternehmer den Lieferanten gewechselt.
SF-LD Der Unternehmer hat wegen der Probleme bei der Produktion den Lieferanten gewechselt.
OF-SD Wegen der Probleme bei der Produktion hat den Lieferanten der Unternehmer gewechselt.
OF-LD Den Lieferanten hat wegen der Probleme bei der Produktion der Unternehmer gewechselt.

41. SF-SD Nach der Ermittlung in dem Milieu hat der Polizist den Verbrecher beschuldigt.
SF-LD Der Polizist hat nach der Ermittlung in dem Milieu den Verbrecher beschuldigt.
OF-SD Nach der Ermittlung in dem Milieu hat den Verbrecher der Polizist beschuldigt.
OF-LD Den Verbrecher hat nach der Ermittlung in dem Milieu der Polizist beschuldigt.

42. SF-SD Mit der Mitteilung wegen des Zeugnisses hat der Schulleiter den Abiturient erschrocken.
SF-LD Der Schulleiter hat mit der Mitteilung wegen des Zeugnisses den Abiturient erschrocken.
OF-SD Mit der Mitteilung wegen des Zeugnisses hat den Abiturient der Schulleiter erschrocken.
OF-LD Den Abiturient hat mit der Mitteilung wegen des Zeugnisses der Schulleiter erschrocken.

43. SF-SD Mit der Premiere in dem Theater hat der Dichter den Kritiker überrascht.
SF-LD Der Dichter hat mit der Premiere in dem Theater den Kritiker überrascht.
OF-SD Mit der Premiere in dem Theater hat den Kritiker der Dichter überrascht.
OF-LD Den Kritiker hat mit der Premiere in dem Theater der Dichter überrascht.

44. SF-SD Wegen der Bilanz an der Börse hat der Beamte den Sekretär verhaftet.
SF-LD Der Beamte hat wegen der Bilanz an der Börse den Sekretär verhaftet.
OF-SD Wegen der Bilanz an der Börse hat den Sekretär der Beamte verhaftet.
OF-LD Den Sekretär hat wegen der Bilanz an der Börse der Beamte verhaftet.

45. SF-SD Nach dem Urteil in dem Verfahren hat der Anwalt den Angeklagten aufgegeben.
SF-LD Der Anwalt hat nach dem Urteil in dem Verfahren den Angeklagten aufgegeben.
OF-SD Nach dem Urteil in dem Verfahren hat den Angeklagten der Anwalt aufgegeben.
OF-LD Den Angeklagten hat nach dem Urteil in dem Verfahren der Anwalt aufgegeben.

46. SF-SD Vor der Entlassung aus dem Gefängnis hat der Psychologe den Häftling untersucht.
SF-LD Der Psychologe hat vor der Entlassung aus dem Gefängnis den Häftling untersucht.
OF-SD Vor der Entlassung aus dem Gefängnis hat den Häftling der Psychologe untersucht.
OF-LD Den Häftling hat vor der Entlassung aus dem Gefängnis der Psychologe untersucht.

47. SF-SD Wegen des Verlusts bei den Geschäften hat der Kaufmann den Bankier kontaktiert.
SF-LD Der Kaufmann hat wegen des Verlusts bei den Geschäften den Bankier kontaktiert.
OF-SD Wegen des Verlusts bei den Geschäften hat den Bankier der Kaufmann kontaktiert.
OF-LD Den Bankier hat wegen des Verlusts bei den Geschäften der Kaufmann kontaktiert.

48. SF-SD Nach der Aussprache mit der Familie hat der Bruder den Vater angelächelt.
SF-LD Der Bruder hat nach der Aussprache mit der Familie den Vater angelächelt.
OF-SD Nach der Aussprache mit der Familie hat den Vater der Bruder angelächelt.
OF-LD Den Vater hat nach der Aussprache mit der Familie der Bruder angelächelt.

C

Fillers from Behavioral Study

1. A Der kranke Vorsitzende hat nach der Konferenz endlich den Job gekündigt und in ein Restaurant investiert.
   B Nach der Konferenz hat der kranke Vorsitzende endlich den Job gekündigt und in ein Restaurant investiert.
   C Der kranke Vorsitzende der seine Arbeit hasste hat nach der Konferenz mit den gierigen Aktionären endlich den Job gekündigt und in ein Restaurant investiert.
   D Nach der Konferenz mit den gierigen Aktionären hat der kranke Vorsitzende der seine Arbeit hasste endlich den Job gekündigt und in ein Restaurant investiert.
2. A Der fröhliche Schaffner hat an dem Bahnhof täglich die Regionalbahn bestiegen und auf seine Uhr geschaut.
   B An dem Bahnhof hat der fröhliche Schaffner täglich die Regionalbahn bestiegen und auf seine Uhr geschaut.
   C Der fröhliche Schaffner der seinen Beruf liebte hat auf dem Bahnhof in der kleinen Stadt täglich die Regionalbahn bestiegen und auf seine Uhr geschaut.
   D Auf dem Bahnhof in der kleinen Stadt hat der fröhliche Schaffner der seinen Beruf liebte täglich die Regionalbahn bestiegen und auf seine Uhr geschaut.
3. A Die fleißige Maus hat in einer Scheune heimlich am Saatgut geknabbert und von den Würsten genascht.
   B In einer Scheune hat die fleißige Maus heimlich am Saatgut geknabbert und von den Würsten genascht.
   C Die fleißige Maus die gerne Abenteuer erlebte hat in einer Scheune hinter der verlassenen Mühle heimlich am Saatgut geknabbert und von den Würsten genascht.
   D In einer Scheune hinter der verlassenen Mühle hat die fleißige Maus die gerne Abenteuer erlebte heimlich am Saatgut geknabbert und von den Würsten genascht.
4. A Die genervten Schüler sind nach dem Unterricht sofort zum Strandbad gefahren und in den See gesprungen.
   B Nach dem Unterricht sind die genervten Schüler sofort zum Strandbad gefahren und in den See gesprungen.
   C Die genervten Schüler die große Langeweile hatten sind nach dem Unterricht bei dem strengen Lehrer sofort zum Strandbad gefahren und in den See gesprungen.
   D Nach dem Unterricht bei dem strengen Lehrer sind die genervten Schüler die große Langeweile hatten sofort zum Strandbad gefahren und in den See gesprungen.
5. A Der kluge Bauer hat am letzten Freitag bereits die Kartoffeln geerntet und auf dem Wochenmarkt verkauft.
   B Am letzten Freitag hat der kluge Bauer bereits die Kartoffeln geerntet und auf dem Wochenmarkt verkauft.
   C Der kluge Bauer der aus Sachsen stammte hat am letzten Freitag nach dem großen Sturm bereits die Kartoffeln geerntet und auf dem Wochenmarkt verkauft.
   D Am letzten Freitag nach dem großen Sturm hat der kluge Bauer der aus Sachsen stammte bereits die Kartoffeln geerntet und auf dem Wochenmarkt verkauft.
6. A Das junge Ehepaar hat in der Nacht erneut über Umzugspläne gestritten und um einen Kompromiss gekämpft.
   B In der Nacht hat das junge Ehepaar erneut über Umzugspläne gestritten und um einen Kompromiss gekämpft.
   C Das junge Ehepaar das immer Streit hatte hat in der Nacht vor der ersehnten Reise erneut über Umzugspläne gestritten und um einen Kompromiss gekämpft.
   D In der Nacht vor der ersehnten Reise hat das junge Ehepaar das immer Streit hatte erneut über Umzugspläne gestritten und um einen Kompromiss gekämpft.

7. A Ein riesiges Schiff ist an der Ostküste plötzlich auf Grund gelaufen und in einem Unwetter gekentert.
   B An der Ostküste ist ein riesiges Schiff plötzlich auf Grund gelaufen und in einem Unwetter gekentert.
   C Ein riesiges Schiff das aus Russland kam ist an der Ostküste in einer nebligen Nacht plötzlich auf Grund gelaufen und in einem Unwetter gekentert.
   D An der Ostküste in einer nebligen Nacht ist ein riesiges Schiff das aus Russland kam plötzlich auf Grund gelaufen und in einem Unwetter gekentert.

8. A Der faule Student hat in einem Seminar wieder ein Referat gehalten und gegen die Formalien verstoßen.
   B In einem Seminar hat der faule Student wieder ein Referat gehalten und gegen die Formalien verstoßen.
   C Der faule Student der die Uni vernachlässigte hat in einem Seminar vor den ersehnten Ferien wieder ein Referat gehalten und gegen die Formalien verstoßen.
   D In einem Seminar vor den ersehnten Ferien hat der faule Student der die Uni vernachlässigte wieder ein Referat gehalten und gegen die Formalien verstoßen.

9. A Der beliebte Kanzler hat vor dem Parlament immer die Abgeordneten begrüßt und auf den Tagesplan hingewiesen.
   B Vor dem Parlament hat der beliebte Kanzler immer die Abgeordneten begrüßt und auf den Tagesplan hingewiesen.
   C Der beliebte Kanzler der sein Amt schätzte hat vor dem Parlament in der deutschen Hauptstadt immer die Abgeordneten begrüßt und auf den Tagesplan hingewiesen.
   D Vor dem Parlament in der deutschen Hauptstadt hat der beliebte Kanzler der sein Amt schätzte immer die Abgeordneten begrüßt und auf den Tagesplan hingewiesen.

10. A Ein wilder Braunbär hat in den Bergen gestern ein Schaf angegriffen und in den Abgrund getrieben.
   B In den Bergen hat ein wilder Braunbär gestern ein Schaf angegriffen und in den Abgrund getrieben.
   C Ein wilder Braunbär der aus Österreich kam hat in den Bergen nahe einer abgelegenen Weide gestern ein Schaf angegriffen und in den Abgrund getrieben.
   D In den Bergen nahe einer abgelegenen Weide hat ein wilder Braunbär der aus Österreich kam gestern ein Schaf angegriffen und in den Abgrund getrieben.

11. A Der geniale Professor ist nach der Arbeit unerwartet vom Balkon gestürzt und in der Arztpraxis aufgewacht.
   B Nach der Arbeit ist der geniale Professor unerwartet vom Balkon gestürzt und in der Arztpraxis aufgewacht.
   C Der geniale Professor der die Forschung mochte ist nach der Arbeit in seinem neuen Labor unerwartet vom Balkon gestürzt und in der Arztpraxis aufgewacht.
   D Nach der Arbeit in seinem neuen Labor ist der geniale Professor der die Forschung mochte unerwartet vom Balkon gestürzt und in der Arztpraxis aufgewacht.

12. A Der mürrische Winzer hat nach der Weinlese stets den Gottesdienst besucht und für die Kirche gespendet.
   B Nach der Weinlese hat der mürrische Winzer stets den Gottesdienst besucht und für die Kirche gespendet.
   C Der mürrische Winzer der lange Witwer war hat nach der Weinlese in den herbstlichen Hügeln stets den Gottesdienst besucht und für die Kirche gespendet.
   D Nach der Weinlese in den herbstlichen Hügeln hat der mürrische Winzer der lange Witwer war stets den Gottesdienst besucht und für die Kirche gespendet.

13. A Der übermüdete Flugkapitän ist nach seiner Landung gleich ins Hotel gefahren und in sein Bett gestiegen.
   B Nach seiner Landung ist der übermüdete Flugkapitän gleich ins Hotel gefahren und in sein Bett gestiegen.
   C Der übermüdete Flugkapitän dem die Augen zufielen ist nach seiner Landung auf dem fernen Flughafen gleich ins Hotel gefahren und in sein Bett gestiegen.
   D Nach seiner Landung auf dem fernen Flughafen ist der übermüdete Flugkapitän dem die Augen zufielen gleich ins Hotel gefahren und in sein Bett gestiegen.

14. A Der erfolgreiche Stürmer hat in jedem Spiel mindestens ein Tor geschossen und für den Sieg gesorgt.
   B In jedem Spiel hat der erfolgreiche Stürmer mindestens ein Tor geschossen und für den Sieg gesorgt.
   C Der erfolgreiche Stürmer der ein Volksheld war hat in jedem Spiel in seinem heimatlichen Stadion mindestens ein Tor geschossen und für den Sieg gesorgt.
   D In jedem Spiel in seinem heimatlichen Stadion hat der erfolgreiche Stürmer der ein Volksheld war mindestens ein Tor geschossen und für den Sieg gesorgt.

15. A Die besten Gärtner haben trotz aller Vorsorge schon mit Maulwürfen gerungen und mit ihren Tricks gehadert.
    B Trotz aller Vorsorge haben die besten Gärtner schon mit Maulwürfen gerungen und mit ihren Tricks gehadert.
    C Die besten Gärtner die jedem Schädling trotzen haben trotz aller Vorsorge gegen die dreisten Nager schon mit Maulwürfen gerungen und mit ihren Tricks gehadert.
    D Trotz aller Vorsorge gegen die dreisten Nager haben die besten Gärtner die jedem Schädling trotzen schon mit Maulwürfen gerungen und mit ihren Tricks gehadert.
16. A Die meisten Tänzer haben nach ihrem Ausscheiden weiter am Theater gearbeitet und auf der Bühne geholfen.
    B Nach ihrem Ausscheiden haben die meisten Tänzer weiter am Theater gearbeitet und auf der Bühne geholfen.
    C Die meisten Tänzer die ihre Karriere beendeten haben nach ihrem Ausscheiden aus der aktiven Laufbahn weiter am Theater gearbeitet und auf der Bühne geholfen.
    D Nach ihrem Ausscheiden aus der aktiven Laufbahn haben die meisten Tänzer die ihre Karriere beendeten weiter am Theater gearbeitet und auf der Bühne geholfen.
17. A Ein guter Polizist hat bei der Streife besonders kleine Details beachtet und in seinen Bericht geschrieben.
    B Bei der Streife hat ein guter Polizist besondern kleine Details beachtet und in seinen Bericht geschrieben.
    C Ein guter Polizist der die Verbrecher kennt hat bei der Streife dank seiner langen Erfahrung besonders kleine Details beachtet und in seinen Bericht geschrieben.
    D Bei der Streife dank seiner langen Erfahrung hat ein guter Polizist der die Verbrecher kennt besonders kleine Details beachtet und in seinen Bericht geschrieben.
18. A Ein starkes Gewitter hat bei einer Wanderung vorgestern fünf Bergsteiger überrumpelt und zu einem Umweg gezwungen.
    B Bei einer Wanderung hat ein starkes Gewitter vorgestern fünf Bergsteiger überrumpelt und zu einem Umweg gezwungen.
    C Ein starkes Gewitter das am Nachmittag aufzog hat bei einer Wanderung auf einer neuen Route vorgestern fünf Bergsteiger überrascht und zu einem Umweg gezwungen.
    D Bei einer Wanderung auf einer neuen Route hat ein starkes Gewitter das am Nachmittag aufzog vorgestern fünf Bergsteiger überrascht und zu einem Umweg gezwungen.
19. A Ein gefährliches Virus hat in dem Internat zuletzt zehn Schüler infiziert und vom normalen Betrieb ausgeschlossen.
    B In dem Internat hat ein gefährliches Virus zuletzt zehn Schüler infiziert und vom normalen Betrieb ausgeschlossen.
    C Ein gefährliches Virus das kein Arzt kannte hat in dem Internat in der entlegenen Gegend zuletzt zehn Schüler infiziert und vom normalen Betrieb ausgeschlossen.
    D An dem Internat in der entlegenen Gegend hat ein gefährliches Virus das kein Arzt kannte zuletzt zehn Schüler infiziert und vom normalen Betrieb ausgeschlossen.
20. A Eine düstere Wolke hat während des Festes drohend den Himmel verdunkelt und über dem Rathaus angehalten.
    B Während des Festes hat eine düstere Wolke drohend den Himmel verdunkelt und über dem Rathaus angehalten.
    C Eine düstere Wolke die die Stimmung drückte hat während des Festes für die siegreichen Fußballer drohend den Himmel verdunkelt und über dem Rathaus angehalten.
    D Während des Festes für die siegreichen Fußballer hat eine düstere Wolke die die Stimmung drückte drohend den Himmel verdunkelt und über dem Rathaus angehalten.
21. A Eine dreiste Dränglerin hat auf der Autobahn abends einen Audi abgedrängt und gegen die Leitplanke gedrückt.
    B Auf der Autobahn hat eine dreiste Dränglerin abends einen Audi abgedrängt und gegen die Leitplanke gedrückt.
    C Eine dreiste Dränglerin die einen Porsche fuhr hat auf der Autobahn an einer engen Stelle abends einen Audi abgedrängt und gegen die Leitplanke gedrückt.
    D Auf der Autobahn an einer engen Stelle hat eine dreiste Dränglerin die einen Porsche fuhr abends einen Audi abgedrängt und gegen die Leitplanke gedrückt.
22. A Ein gefährlicher Hai hat auf dem Meer offenbar einen Fischer überrascht und von seinem Boot gerissen.
    B Auf dem Meer hat ein gefährlicher Hai offenbar einen Fischer überrascht und von seinem Boot gerissen.
    C Ein gefährlicher Hai der im Atlantik lebt hat auf dem Meer in den frühen Morgenstunden offenbar einen Fischer überrascht und von seinem Boot gerissen.
    D Auf dem Meer in den frühen Morgenstunden hat ein gefährlicher Hai der im Atlantik lebt offenbar einen Fischer überrascht und von seinem Boot gerissen.

23. A Eine glückliche Mutter hat in der Klinik erstmals einen Jungen geboren und unter vielen Tränen umarmt.
    B In der Klinik hat eine glückliche Mutter erstmals einen Jungen geboren und unter vielen Tränen umarmt.
    C Eine glückliche Mutter die aus Hamburg kam hat in der Klinik auf der neuen Säuglingsstation erstmals einen Jungen geboren und unter vielen Tränen umarmt.
    D In der Klinik auf der neuen Säuglingsstation hat eine glückliche Mutter die aus Hamburg kam erstmals einen Jungen geboren und unter vielen Tränen umarmt.
24. A Ein arbeitsloser Schlosser hat in der Tombola zufällig eine Million gewonnen und in der Spielhalle verzockt.
    B In der Tombola hat ein arbeitsloser Schlosser zufällig eine Million gewonnen und in der Spielhalle verzockt.
    C Ein arbeitsloser Schlosser der immer Pech hatte hat in der Tombola auf der jährlichen Kirmes zufällig eine Million gewonnen und in der Spielhalle verzockt.
    D In der Tombola auf der jährlichen Kirmes hat ein arbeitsloser Schlosser der immer Pech hatte zufällig eine Million gewonnen und in der Spielhalle verzockt.

D

FILLERS FROM BEHAVIORAL AND MRI STUDIES

1. A Gestern hat der Vater dem Sohn den Schnuller gegeben und den Kopf gestreichelt.
   B Gestern hat dem Sohn der Vater den Schnuller gegeben und den Kopf gestreichelt.
   C Gestern hat dem Sohn den Schnuller der Vater gegeben und den Kopf gestreichelt.
   D Gestern hat der Vater gegeben dem Sohn den Schnuller und den Kopf gestreichelt.
2. A Heute hat der Opa dem Enkel den Lolli gekauft und das Eis geschenkt.
   B Heute hat dem Enkel der Opa den Lolli gekauft und das Eis geschenkt.
   C Heute hat dem Enkel den Lolli der Opa gekauft und das Eis geschenkt.
   D Heute hat der Opa gekauft dem Enkel den Lolli und das Eis geschenkt.
3. A Dort hat der Dieb dem Anwalt den Wagen zerkratzt und die Rache genossen.
   B Dort hat dem Anwalt der Dieb den Wagen zerkratzt und die Rache genossen.
   C Dort hat dem Anwalt den Wagen der Dieb zerkratzt und die Rache genossen.
   D Dort hat der Dieb zerkratzt dem Anwalt den Wagen und die Rache genossen.
4. A Gestern hat der Leser dem Bibliothekar den Artikel zurückgegeben und die Gebühren bezahlt.
   B Gestern hat dem Bibliothekar der Leser den Artikel zurückgegeben und die Gebühren bezahlt.
   C Gestern hat dem Bibliothekar den Artikel der Leser zurückgegeben und die Gebühren bezahlt.
   D Gestern hat der Leser zurückgegeben dem Bibliothekar den Artikel und die Gebühren bezahlt.
5. A Dann hat der Aufseher dem Besuch den Ausgang gezeigt und die Tür geöffnet.
   B Dann hat dem Besuch der Aufseher den Ausgang gezeigt und die Tür geöffnet.
   C Dann hat dem Besuch den Ausgang der Aufseher gezeigt und die Tür geöffnet.
   D Dann hat der Aufseher gezeigt dem Besuch den Ausgang und die Tür geöffnet.
6. A Heute hat der Mechaniker dem Rennfahrer den Motor repariert und die Reifen gewechselt.
   B Heute hat dem Rennfahrer der Mechaniker den Motor repariert und die Reifen gewechselt.
   C Heute hat dem Rennfahrer den Motor der Mechaniker repariert und die Reifen gewechselt.
   D Heute hat der Mechaniker repariert dem Rennfahrer den Motor und die Reifen gewechselt.
7. A Vielleicht hat der Chef dem Klempner den Vertrag verlängert und den Lohn erhöht.
   B Vielleicht hat dem Klempner der Chef den Vertrag verlängert und den Lohn erhöht.
   C Vielleicht hat dem Klempner den Vertrag der Chef verlängert und den Lohn erhöht.
   D Vielleicht hat der Chef verlängert dem Klempner den Vertrag und den Lohn erhöht.

8. A Offensichtlich hat der Arzt dem Bergsteiger den Arm verbunden und die Beine geschient.
   B Offensichtlich hat dem Bergsteiger der Arzt den Arm verbunden und die Beine geschient.
   C Offensichtlich hat dem Bergsteiger den Arm der Arzt verbunden und die Beine geschient.
   D Offensichtlich hat der Arzt verbunden dem Bergsteiger den Arm und die Beine geschient.
9. A Schliesslich hat der Bruder dem Bräutigam den Ring überreicht und die Hand geschüttelt.
   B Schliesslich hat dem Bräutigam der Bruder den Ring überreicht und die Hand geschüttelt.
   C Schliesslich hat dem Bräutigam den Ring der Bruder überreicht und die Hand geschüttelt.
   D Schliesslich hat der Bruder überreicht dem Bräutigam den Ring und die Hand geschüttelt.
10. A Überraschenderweise hat der Sekretär dem Fahrer den Umschlag anvertraut und das Beste gehofft.
    B Überraschenderweise hat dem Fahrer der Sekretär den Umschlag anvertraut und das Beste gehofft.
    C Überraschenderweise hat dem Fahrer den Umschlag der Sekretär anvertraut und das Beste gehofft.
    D Überraschenderweise hat der Sekretär anvertraut dem Fahrer den Umschlag und das Beste gehofft.
11. A Gestern hat der Portier dem Manager den Koffer getragen und das Trinkgeld angenommen.
    B Gestern hat dem Manager der Portier den Koffer getragen und das Trinkgeld angenommen.
    C Gestern hat dem Manager den Koffer der Portier getragen und das Trinkgeld angenommen.
    D Gestern hat der Portier getragen dem Manager den Koffer und das Trinkgeld angenommen.
12. A Dann hat der Friseur dem Metzger den Bart rasiert und die Haare geschnitten.
    B Dann hat dem Metzger der Friseur den Bart rasiert und die Haare geschnitten.
    C Dann hat dem Metzger den Bart der Friseur rasiert und die Haare geschnitten.
    D Dann hat der Friseur rasiert dem Metzger den Bart und die Haare geschnitten.
13. A Schliesslich hat der Designer dem Teddy den Hut aufgesetzt und die Schaufenster dekoriert.
    B Schliesslich hat dem Teddy der Designer den Hut aufgesetzt und die Schaufenster dekoriert.
    C Schliesslich hat dem Teddy den Hut der Designer aufgesetzt und die Schaufenster dekoriert.
    D Schliesslich hat der Designer aufgesetzt dem Teddy den Hut und die Schaufenster dekoriert.
14. A Dort hat der Hausmeister dem Mieter den Schlüssel überreicht und die Verträge erklärt.
    B Dort hat dem Mieter der Hausmeister den Schlüssel überreicht und die Verträge erklärt.
    C Dort hat dem Mieter den Schlüssel der Hausmeister überreicht und die Verträge erklärt.
    D Dort hat der Hausmeister überreicht dem Mieter den Schlüssel und die Verträge erklärt.
15. A Überraschenderweise hat der Zauberer dem Zuschauer den Trick verraten und den Vorgang wiederholt.
    B Überraschenderweise hat dem Zuschauer der Zauberer den Trick verraten und den Vorgang wiederholt.
    C Überraschenderweise hat dem Zuschauer den Trick der Zauberer verraten und den Vorgang wiederholt.
    D Überraschenderweise hat der Zauberer verraten dem Zuschauer den Trick und den Vorgang wiederholt.
16. A Offensichtlich hat der Kellner dem Gast den Braten serviert und die Getränke geholt.
    B Offensichtlich hat dem Gast der Kellner den Braten serviert und die Getränke geholt.
    C Offensichtlich hat dem Gast den Braten der Kellner serviert und die Getränke geholt.
    D Offensichtlich hat der Kellner serviert dem Gast den Braten und die Getränke geholt.
17. A Schliesslich hat der Ober dem Urlauber den Saft eingeschenkt und die Flaschen hingestellt.
    B Schliesslich hat dem Urlauber der Ober den Saft eingeschenkt und die Flaschen hingestellt.
    C Schliesslich hat dem Urlauber den Saft der Ober eingeschenkt und die Flaschen hingestellt.
    D Schliesslich hat der Ober eingeschenkt dem Urlauber den Saft und die Flaschen hingestellt.
18. A Dann hat der Chirurg dem Chefarzt den Befund vorgelesen und die Operationen vorgeschlagen.
    B Dann hat dem Chefarzt der Chirurg den Befund vorgelesen und die Operationen vorgeschlagen.
    C Dann hat dem Chefarzt den Befund der Chirurg vorgelesen und die Operationen vorgeschlagen.
    D Dann hat der Chirurg vorgelesen dem Chefarzt den Befund und die Operationen vorgeschlagen.

19. A Gestern hat der Sportler dem Richter den Unfall geschildert und die Angeklagten erkannt.
    B Gestern hat dem Richter der Sportler den Unfall geschildert und die Angeklagten erkannt.
    C Gestern hat dem Richter den Unfall der Sportler geschildert und die Angeklagten erkannt.
    D Gestern hat der Sportler geschildert dem Richter den Unfall und die Angeklagten erkannt.

20. A Vielleicht hat der Gärtner dem Freund den Rasenmäher ausgeliehen und die Blumen gebracht.
    B Vielleicht hat dem Freund der Gärtner den Rasenmäher ausgeliehen und die Blumen gebracht.
    C Vielleicht hat dem Freund den Rasenmäher der Gärtner ausgeliehen und die Blumen gebracht.
    D Vielleicht hat der Gärtner ausgeliehen dem Freund den Rasenmäher und die Blumen gebracht.

21. A Morgen wird der Bauleiter dem Maurer den Plan vorlegen und das Werk beginnen.
    B Morgen wird dem Maurer der Bauleiter den Plan vorlegen und das Werk beginnen.
    C Morgen wird dem Maurer den Plan der Bauleiter vorlegen und das Werk beginnen.
    D Morgen wird der Bauleiter vorlegen dem Maurer den Plan und das Werk beginnen.

22. A Heute wird der Detektiv dem Komissar den Fundort beschreiben und den Fall abschliessen.
    B Heute wird dem Komissar der Detektiv den Fundort beschreiben und den Fall abschliessen.
    C Heute wird dem Komissar den Fundort der Detektiv beschreiben und den Fall abschliessen.
    D Heute wird der Detektiv beschreiben dem Komissar den Fundort und den Fall abschliessen.

23. A Schliesslich wird der Schüler dem Lehrer den Aufsatz vorlesen und die Note erfahren.
    B Schliesslich wird dem Lehrer der Schüler den Aufsatz vorlesen und die Note erfahren.
    C Schliesslich wird dem Lehrer den Aufsatz der Schüler vorlesen und die Note erfahren.
    D Schliesslich wird der Schüler vorlesen dem Lehrer den Aufsatz und die Note erfahren.

24. A Morgen wird der Vertreter dem Rentner den Staubsauger verkaufen und die Raten festlegen.
    B Morgen wird dem Rentner der Vertreter den Staubsauger verkaufen und die Raten festlegen.
    C Morgen wird dem Rentner den Staubsauger der Vertreter verkaufen und die Raten festlegen.
    D Morgen wird der Vertreter verkaufen dem Rentner den Staubsauger und die Raten festlegen.

25. A Vielleicht wird der Einbrecher dem Wirt den Fernseher stehlen und die Möbel zerstören.
    B Vielleicht wird dem Wirt der Einbrecher den Fernseher stehlen und die Möbel zerstören.
    C Vielleicht wird dem Wirt den Fernseher der Einbrecher stehlen und die Möbel zerstören.
    D Vielleicht wird der Einbrecher stehlen dem Wirt den Fernseher und die Möbel zerstören.

26. A Dann wird der Lehrling dem Schreiner den Hammer reichen und die Nägel nehmen.
    B Dann wird dem Schreiner der Lehrling den Hammer reichen und die Nägel nehmen.
    C Dann wird dem Schreiner den Hammer der Lehrling reichen und die Nägel nehmen.
    D Dann wird der Lehrling reichen dem Schreiner den Hammer und die Nägel nehmen.

27. A Überraschenderweise wird der Millionär dem Diener den Besitz vererben und die Kinder vergessen.
    B Überraschenderweise wird dem Diener der Millionär den Besitz vererben und die Kinder vergessen.
    C Überraschenderweise wird dem Diener den Besitz der Millionär vererben und die Kinder vergessen.
    D Überraschenderweise wird der Millionär vererben dem Diener der Besitz und die Kinder vergessen.

28. A Morgen wird der Künstler dem Bürgermeister den Entwurf präsentieren und die Kritik anhören.
    B Morgen wird dem Bürgermeister der Künstler den Entwurf präsentieren und die Kritik anhören.
    C Morgen wird dem Bürgermeister den Entwurf der Künstler präsentieren und die Kritik anhören.
    D Morgen wird der Künstler präsentieren dem Bürgermeister den Entwurf und die Kritik anhören.

29. A Vielleicht wird der Kanzler dem Minister den Fehltritt verzeihen und die Probleme lösen.
    B Vielleicht wird dem Minister der Kanzler den Fehltritt verzeihen und die Probleme lösen.
    C Vielleicht wird dem Minister den Fehltritt der Kanzler verzeihen und die Probleme lösen.
    D Vielleicht wird der Kanzler verzeihen dem Minister den Fehltritt und die Probleme lösen.

30. A Dort wird der Leibwächter dem Erpresser den Revolver wegnehmen und die Polizei rufen.
  B Dort wird dem Erpresser der Leibwächter den Revolver wegnehmen und die Polizei rufen.
  C Dort wird dem Erpresser den Revolver der Leibwächter wegnehmen und die Polizei rufen.
  D Dort wird der Leibwächter wegnehmen dem Erpresser den Revolver und die Polizei rufen.

31. A Heute wird der Schauspieler dem Chauffeur den Vertrag kündigen und die Köche entlassen.
  B Heute wird dem Chauffeur der Schauspieler den Vertrag kündigen und die Köche entlassen.
  C Heute wird dem Chauffeur den Vertrag der Schauspieler kündigen und die Köche entlassen.
  D Heute wird der Schauspieler kündigen dem Chauffeur den Vertrag und die Köche entlassen.

32. A Morgen wird der Tenor dem Zuhörer den Platz reservieren und die Lieder singen.
  B Morgen wird dem Zuhörer der Tenor den Platz reservieren und die Lieder singen.
  C Morgen wird demZ uhörer den Platz der Tenor reservieren und die Lieder singen.
  D Morgen wird der Tenor reservieren dem Zuhörer den Platz und die Lieder singen.

33. A Überraschenderweise wird der Regisseur dem Darsteller den Film widmen und die Auszeichnungen überlassen.
  B Überraschenderweise wird dem Darsteller der Regisseur den Film widmen und die Auszeichnungen überlassen.
  C Überraschenderweise wird dem Darsteller den Film der Regisseur widmen und die Auszeichnungen überlassen.
  D Überraschenderweise wird der Regisseur widmen dem Darsteller den Film und die Auszeichnungen überlassen.

34. A Jetzt wird der Mörder dem Wanderer den Fuss abhacken und die Beweise vernichten.
  B Jetzt wird dem Wanderer der Mörder den Fuss abhacken und die Beweise vernichten.
  C Jetzt wird dem Wanderer den Fuss der Mörder abhacken und die Beweise vernichten.
  D Jetzt wird der Mörder abhacken dem Wanderer den Fuss und die Beweise vernichten.

35. A Jetzt wird der Gastgeber dem Pfarrer den Mantel umlegen und den Hut reichen.
  B Jetzt wird dem Pfarrer der Gastgeber den Mantel umlegen und den Hut reichen.
  C Jetzt wird dem Pfarrer den Mantel der Gastgeber umlegen und den Hut reichen.
  D Jetzt wird der Gastgeber umlegen dem Pfarrer den Mantel und den Hut reichen.

36. A Offensichtlich wird der Senator dem Richter den Betrug gestehen und die Ämter aufgeben.
  B Offensichtlich wird dem Richter der Senator den Betrug gestehen und die Ämter aufgeben.
  C Offensichtlich wird dem Richter den Betrug der Senator gestehen und die Ämter aufgeben.
  D Offensichtlich wird der Senator gestehen dem Richter den Betrug und die Ämter aufgeben.

37. A Offensichtlich wird der Schriftsteller dem Kritiker den Inhalt schildern und die Verbesserungen nennen.
  B Offensichtlich wird dem Kritiker der Schriftsteller den Inhalt schildern und die Verbesserungen nennen.
  C Offensichtlich wird dem Kritiker den Inhalt der Schriftsteller schildern und die Verbesserungen nennen.
  D Offensichtlich wird der Schriftsteller schildern dem Kritiker den Inhalt und die Verbesserungen nennen.

38. A Dort wird der Torwart dem Stürmer den Ball zuspielen und das Lob erhalten.
  B Dort wird dem Stürmer der Torwart den Ball zuspielen und das Lob erhalten.
  C Dort wird dem Stürmer den Ball der Torwart zuspielen und das Lob erhalten.
  D Dort wird der Torwart zuspielen dem Stürmer den Ball und das Lob erhalten.

39. A Jetzt wird der Steuerberater dem Gutachter den Fall vorlegen und die Entscheidungen abwarten.
  B Jetzt wird dem Gutachter der Steuerberater den Fall vorlegen und die Entscheidungen abwarten.
  C Jetzt wird dem Gutachter den Fall der Steuerberater vorlegen und die Entscheidungen abwarten.
  D Jetzt wird der Steuerberater vorlegen dem Gutachter den Fall und die Entscheidungen abwarten.

40. A Jetzt wird der Ehemann dem Schwager den Wein einschenken und das Gespräch anfangen.
  B Jetzt wird dem Schwager der Ehemann den Wein einschenken und das Gespräch anfangen.
  C Jetzt wird dem Schwager den Wein der Ehemann einschenken und das Gespräch anfangen.
  D Jetzt wird der Ehemann einschenken dem Schwager den Wein und das Gespräch anfangen.

41. A Dennoch wird der Offizier dem Admiral den Kapitän opfern und das Schiff retten.
    B Dennoch wird dem Admiral der Offizier den Kapitän opfern und das Schiff retten.
    C Dennoch wird dem Admiral den Kapitän der Offizier opfern und das Schiff retten.
    D Dennoch wird der Offizier opfern dem Admiral den Kapitän und das Schiff retten.

42. A Vielleicht wird der Arbeiter dem Bankier den Lehrling ausreden und den Lohn sparen.
    B Vielleicht wird dem Bankier der Arbeiter den Lehrling ausreden und den Lohn sparen.
    C Vielleicht wird dem Bankier den Lehrling der Arbeiter ausreden und den Lohn sparen.
    D Vielleicht wird der Arbeiter ausreden dem Bankier den Lehrling und den Lohn sparen.

43. A Anscheinend wird der Kommissar dem Priester den Flüchtling anvertrauen und die Familien schützen.
    B Anscheinend wird dem Priester der Kommissar den Flüchtling anvertrauen und die Familien schützen.
    C Anscheinend wird dem Priester den Flüchtling der Kommissar anvertrauen und die Familien schützen.
    D Anscheinend wird der Kommissar anvertrauen dem Priester den Flüchtling und die Familien schützen.

44. A Danach wird der Fluggast dem Stadtrat den Begleiter vorstellen und die Maschine verlassen.
    B Danach wird dem Stadtrat der Fluggast den Begleiter vorstellen und die Maschine verlassen.
    C Danach wird dem Stadtrat den Begleiter der Fluggast vorstellen und die Maschine verlassen.
    D Danach wird der Fluggast vorstellen dem Stadtrat den Begleiter und die Maschine verlassen.

45. A Offensichtlich wird dem Redakteur der Berater den Schreiber unterschieben und den Betrug begehen.
    B Offensichtlich wird dem Redakteur den Schreiber der Berater unterschieben und den Betrug begehen.
    C Offensichtlich wird der Berater dem Redakteur den Schreiber unterschieben und den Betrug begehen.
    D Offensichtlich wird der Berater unterschieben dem Redakteur den Schreiber und den Betrug begehen.

46. A Gestern hat der Zahnarzt dem Onkel den Zahn gezogen und die Schmerzen beendet.
    B Gestern hat dem Onkel der Zahnarzt den Zahn gezogen und die Schmerzen beendet.
    C Gestern hat dem Onkel den Zahn der Zahnarzt gezogen und die Schmerzen beendet.
    D Gestern hat der Zahnarzt gezogen dem Onkel den Zahn und die Schmerzen beendet.

47. A Ausserdem hat der Witwer dem Wahrsager den Schmuck geschenkt und das Geld bezahlt.
    B Ausserdem hat dem Wahrsager der Witwer den Schmuck geschenkt und das Geld bezahlt.
    C Ausserdem hat dem Wahrsager den Schmuck der Witwer geschenkt und das Geld bezahlt.
    D Ausserdem hat der Witwer geschenkt dem Wahrsager den Schmuck und das Geld bezahlt.

48. A Danach hat der Betreuer dem Rollstuhlfahrer den Schuh angezogen und den Weg erklärt.
    B Danach hat dem Rollstuhlfahrer der Betreuer den Schuh angezogen und den Weg erklärt.
    C Danach hat dem Rollstuhlfahrer den Schuh der Betreuer angezogen und den Weg erklärt.
    D Danach hat der Betreuer angezogen dem Rollstuhlfahrer den Schuh und den Weg erklärt.

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